RECEIVED
By Nova Scotia Aquaculture Review Board at 4:22 pm, Apr 26, 2021

NOVA SCOTIA AQUACULTURE REVIEW BOARD

Application by Kelly Cove Salmon Ltd. for a boundary amendment to marine finfish licence and lease AQ#1039 in the Annapolis Basin, Digby County

---

Affidavit of Jonathan W. Carr
affirmed on April 23, 2021

INDEX

Tab	Description
	Affidavit of Jonathan W. Carr affirmed April 23, 2021
A.	Exhibit A - Report for the Aquaculture Review Board
	Appendices to the Report
1.	ASC 2019
2.	Bouwmeester et al 2021
3.	Bradbury et al 2020a
4.	Bradbury et al 2020b
5.	DFO 2013a
6.	Ford and Myers 2008
7.	Glover et al 2017
8.	ICES 2016
9.	Karlsson et al 2016
10.	Kibenge 2019
11.	NASCO 2006
12.	NASCO 2010
13.	Olaussen 2018
14.	Shephard and Gargan 2017
15.	Sylvester et al 2019
16.	Wacker et al 2021
17.	Wringe et al 2018
B.	EXHIBIT B – CV of Jonathan W. Carr
C.	EXHIBIT C - CV of Stephen G. Sutton

NOVA SCOTIA AQUACULTURE REVIEW BOARD

Application by Kelly Cove Salmon Ltd. for a boundary amendment to marine finfish licence and lease AQ#1039 in the Annapolis Basin, Digby County

---

Affidavit of Jonathan W. Carr

I, Jonathan Weldon Carr, of the Town of St. Andrews, in the Province of New Brunswick, affirm as follows:

1. I have been asked to review and provide an expert opinion regarding impacts on wild Atlantic salmon that may result from the approval of the application by Kelly Cove Salmon Ltd. for a boundary amendment to marine finfish licence and lease AQ#1039 in the Annapolis Basin, Digby County (the "**Application**") on behalf of the intervenor, Gregory Heming.

2. Together with Dr. Stephen Sutton, I have co-authored a report detailing our analysis and conclusions regarding impacts of the Application on wild Atlantic salmon (the "**Report**"), attached hereto as **Exhibit "A"**.

3. My qualifications as a subject matter expert on wild Atlantic salmon are set out in my Curriculum Vitae attached hereto as **Exhibit "B"**.

4. I am the Vice President of Research and Environment at the Atlantic Salmon Federation, where I have been employed for approximately 25 years.

5. Based upon my education and experience, my area of expertise is the protection, conservation and recovery of wild Atlantic salmon.

6. My co-author, Dr. Stephen Sutton's qualifications as a subject matter expert on wild Atlantic salmon are set out in his Curriculum Vitae attached hereto as **Exhibit "C"**, which he provided to me and I do verily believe is true and accurate.

7. Dr. Stephen Sutton, is the Coordinator of Community Outreach and Engagement at Atlantic Salmon Federation, which position he has held since 2015.

8. The Report attached to this affidavit as Exhibit "A" represents my professional opinion with respect to possible impacts on wild Atlantic salmon resulting from the Application.

9. I affirm this affidavit in support of the Report and in support of Mr. Gregory Heming's intervention before the Aquaculture Review Board and for no other or improper purpose.

Affirmed before me on this
23rd day of April, 2021
at St. Andrews, New Brunswick

A Commissioner of Oaths in and for the
Province of New Brunswick
Being a Solicitor
David R Ames Q.C.

Jonathan W. Carr

This is **Exhibit "A"** mentioned and referred to in the affidavit of **Jonathan W. Carr** affirmed before me on this 23rd day of April, A.D. 2021

a Commissioner for taking affidavits

being a Solicitor

David R. Ames Q.C.

Report for the Aquaculture Review Board

Respecting an application by Kelly Cove Salmon Ltd. for a boundary amendment to marine finfish licence and lease AQ#1039 in the Annapolis Basin, Digby County

Jonathan Carr, M. Sc.

Stephen Sutton, Ph. D.

Table of Contents

Page

Scope of the Report 3

Summary of Findings 3

1. A substantial body of peer-reviewed scientific literature demonstrates the impacts of open net pen salmon aquaculture on wild salmon. 4
2. Aquaculture has been implicated in the decline of salmon in the Bay of Fundy and Southern Uplands of Nova Scotia. 4
3. Neither the applicant nor DFO have provided sufficient information to allay concerns about the impacts on wild salmon. 5
4. The existing regulatory framework is not sufficient to protect wild Atlantic salmon from the impacts of aquaculture. 6
5. There are several actions the applicant should take to avoid, mitigate, and monitor the impacts of the farm on wild Atlantic salmon. 7

Summary 8

Appendix 1 – Overview of the Impacts of Salmon Farms on Wild Salmon Populations 9

Farmed salmon escape and interbreed with wild populations

Sea lice proliferate in salmon farms and are transmitted to wild fish.

Salmon farms and escaped fish have negative ecological interactions with wild salmon

Diseases and pathogens proliferate in salmon farms and are transmitted to wild fish.

Salmon farms alter the local environment thereby changing the selective pressures to which locally-adapted wild populations are subject.

Appendix 2 – References **Tab**

ASC. 2019. ASC Salmon Standard Version 1.3. Aquaculture Stewardship Council. 1

Bouwmeester, MM, Goedknegt, MA, Poulin, R, Thieltges, DW. 2021. Collateral diseases: Aquaculture impacts on wildlife infections. *J Appl Ecol*. 2021; 58: 453– 464. 2

Bradbury IR, Duffy S, Lehnert SJ, Jóhannsson R, et al. 2020a. Model-based evaluation of the genetic impacts of farm-escaped Atlantic salmon on wild populations. Aquacult Environ Interact 12:45-59. 3

4 Bradbury IR, Burgetz I, Coulson MW, Verspoor E, et al. 2020b. Beyond hybridization: the genetic impacts of nonreproductive ecological interactions of salmon aquaculture on wild populations. Aquacult Environ Interact 12:429-445.

5 DFO. 2013a. Recovery Potential Assessment for Southern Upland Atlantic Salmon. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2013/009.

6 Ford J.S., Myers R.A. 2008. A global assessment of salmon aquaculture impacts on wild salmonids. PLoS Biol 6(2)

7 Glover, KA, Solberg, MF, McGinnity, P, et al. 2017. Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. Fish Fish.; 18: 890– 927.

8 ICES. 2016. Report of the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF), 1–3 March 2016, Charlottenlund, Denmark. ICES CM 2016/ACOM:42. 44 pp.

9 Karlsson, S., Diserud, O.H., Fiske, P., and Hindar, K. 2016. Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES Journal of Marine Science*, 73(10), 2488– 2498.

10 Kibenge, F.S.B. 2019. Emerging viruses in aquaculture. Current Opinions in Virology 34: 97-103.

11 NASCO. 2006. Resolution by the Parties to the Convention for the Conservation of Salmon in the North Atlantic Ocean to Minimise Impacts from Aquaculture, Introductions and Transfers, and Transgenics on the Wild Salmon Stocks. North Atlantic Salmon Conservation Organization, CNL(06)48. https://nasco.int/wp-content/uploads/2020/02/williamsburg.pdf

12 NASCO. 2010. Guidance on Best Management Practices to address impacts of sea lice and escaped farmed salmon on wild salmon stocks. North Atlantic Salmon Conservation Organization, SLG(09)5. https://nasco.int/wp-content/uploads/2020/02/BMP-Guidance.pdf

13 Olaussen, J.O. 2018. Environmental problems and regulation in the aquaculture industry. Insights from Norway, Marine Policy, 98: 158-163.

14 Shephard S, Gargan P. 2017. Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. Aquaculture Environment Interactions 9:181-192.

15 Sylvester, E.V.A, B.F. Wringe, S.J. Duffy, L.C. Hamilton, I.A. Fleming, M.Castellani, P.Bentzen, I.R. Bradbury. 2019. Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild population. Evolutionary Applications 12(4): 705-717.

16 Wacker, S, Aronsen, T, Karlsson, S, et al. 2021. Selection against individuals from genetic introgression of escaped farmed salmon in a natural population of Atlantic salmon. Evol Appl.

17 Wringe, B.F., Jeffery, N.W., Stanley, R.R.E. et al. 2018. Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. Commun Biol 1, 108.

Scope of the Report

We have been asked by intervenor Gregory Heming to review and provide an expert opinion regarding impacts on wild Atlantic salmon resulting from the application by Kelly Cove Salmon Ltd. for a boundary amendment to marine finfish licence and lease AQ#1039 in the Annapolis Basin, Digby County. We have reviewed the Application Package, Report on Outcomes of Consultation, and Report on Performance Review for the application. We note that the applicant is requesting a boundary change to reflect the location at which the farm has been operating for the past 18 years.

In this document, we limit our opinion to the following questions:

1. What impacts, if any, has the farm had on wild Atlantic salmon?;
2. Will the continued operation of the farm impede wild Atlantic salmon recovery efforts?; and
3. Are there steps the applicant could take to avoid or mitigate impacts on wild salmon in the event that the application is approved?

As such, we focus primarily on the information provided in Section 7 of the Application (The Sustainability of Wild Salmon), the section of the Report on Consultation containing the DFO Letter of Advice and CSAS Science Report 2020/015, and the Report on Performance Review.

Summary of Findings

Based on our review of these materials we offer the following opinions:

1. There is insufficient information provided to conclusively determine whether the existing farm has had or is currently having a negative impact on wild Atlantic salmon. Based on available information, it is reasonable to conclude the farm has likely had a negative impact on wild Atlantic salmon, the magnitude of which remains unknown.

2. The applicant's conclusion that aquaculture site Rattling Beach #1039 will have no foreseeable impact on wild Atlantic salmon restoration efforts in the Annapolis Basin and Digby area is not supported by the information provided by the applicant, DFO, or the scientific literature. The ongoing operation of the farm will likely impede wild salmon restoration efforts in the local area.

3. If the application is approved, there are several actions the applicant can take to avoid, mitigate, and monitor the impacts on wild salmon. These include: the use of sterile fish, monitoring of local rivers for escapes and genetic introgression, monitoring of wild salmon for increased sea lice and disease loads, and triggers for responses to sea lice and disease outbreaks that are specifically designed to protect wild salmon.

We arrived at these conclusions based upon the following:

1. **A substantial body of peer-reviewed scientific literature demonstrates the impacts of open net pen salmon aquaculture on wild salmon.**

The applicant, DFO, and the NS Government have all recognized the threats to wild Atlantic salmon posed by salmon aquaculture. In Appendix 1 we provide a brief review of the relevant literature which demonstrates at least five pathways through which aquaculture impacts wild salmon: 1) Farmed salmon escape and interbreed with wild salmon; 2) Sea lice proliferate in salmon farms and are transmitted to wild fish; 3) Salmon farms and escaped fish have negative ecological interactions with wild salmon; 4) Diseases and pathogens proliferate in salmon farms and are transmitted to wild fish; and 5) Salmon farms alter the local environment thereby changing the selective pressures to which locally-adapted wild populations are subject. As noted in Appendix 1, numerous studies have directly linked these impacts to declines in the abundance of wild salmon. The literature also indicates that the presence and magnitude of these impacts can vary from location to location depending on a range of environmental variables, farm characteristics, and farming practices. While the literature can not be used to draw firm conclusions about the impacts of specific sites such as AQ#1039, it does strongly suggest that impacts on wild salmon are to be expected when domesticated salmon are farmed in open net pens in proximity to wild populations. Given the large and increasing volume of science demonstrating the impacts of salmon aquaculture on wild salmon, it would be unreasonable to conclude that AQ#1039 is having no impact on local wild salmon populations in the absence of empirical evidence to support such a conclusion.

2. **Aquaculture has been implicated in the decline of salmon in the Bay of Fundy and Southern Uplands of Nova Scotia.**

As noted by the applicant, wild salmon in the Bay of Fundy and Southern Uplands region of Nova Scotia have declined significantly and have been assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The Inner Bay of Fundy populations have been listed as such under the Species at Risk Act (SARA) while listing decisions are pending for the Outer Bay of Fundy and Southern Uplands populations. The primary underlying cause of these declines is a decrease in marine survival due to changed ocean conditions which has affected wild Atlantic salmon across their range (Thorstad et al. 2021). It is notable, however, that on Canada's east coast, observed declines in areas where salmon aquaculture is present are an order of magnitude greater than observed declines in areas where aquaculture is absent, suggesting that wild salmon populations already made vulnerable by low marine survival are unable to cope with the additional stressors imposed by the impacts of aquaculture. In all areas of eastern Canada where aquaculture and wild salmon co-occur, wild salmon populations have been assessed by COSEWIC as Endangered or Threatened (including South Newfoundland and Eastern Cape Breton). Sufficient research has not been conducted to estimate the magnitude of the impact of aquaculture on wild salmon throughout eastern Canada. However, Fisheries and Oceans Canada recognizes open net pen salmon aquaculture as a threat to wild salmon in all areas where it occurs, including the Inner and Outer Bay of Fundy and Southern Uplands of Nova Scotia (DFO 2008, p.34; DFO 2013a, p.40 (Tab 5); DFO 2013b, p.20; DFO 2014a, p.17; DFO 2014b, p.25).

3. Neither the applicant nor DFO have provided sufficient information to allay concerns about the impacts on wild salmon.

The applicant and DFO recognize the presence of wild salmon within the zone of influence and the potential for the farm to impact them. The applicant provides a general overview of the status of wild salmon in the Maritimes region and identifies local populations, but no information about local rivers (e.g., size, habitat available to salmon, salmon production and abundance, etc.) has been provided. Compilation of existing data on local rivers and their salmon populations is an important and necessary first step in assessing the potential impacts of the farm on wild populations. Relevant information can be obtained through various DFO reviews and stock assessment documents (e.g., DFO 2019; DFO 2009).

The applicant has used very limited information in discussing the potential impacts to wild salmon populations. As discussed in Appendix 1, there is a substantial body of peer-reviewed scientific evidence demonstrating at least five pathways of impact that need to be considered. The discussion in Section 7.2.1 of the Application references none of that literature and is therefore inadequate to inform the reader about potential impacts or to demonstrate that the applicant adequately understands the potential for the farm to impact wild salmon. The discussion about potential impacts does not provide an adequate basis for developing avoidance, mitigation, or monitoring strategies.

As noted in the Report on Performance Review, the farm has been operating in its current boundaries for the past 18 years in contravention of the regulations. No information has been provided to indicate whether impacts on wild salmon were considered when the boundary change was made. Likewise, no information has been provided to enable an assessment as to whether operation of the farm over the past 18 years has impacted wild salmon or recovery efforts. Information required to make such an assessment would include: numbers of escapes annually, sea lice counts in the farm and on wild fish, records of disease outbreaks, surveys of local rivers for escapes, and testing of wild populations for genetic introgression. It is not clear whether such information is available or will be collected going forward. As we note in point #1 above, it would be unreasonable to conclude that there have been no impacts or that restoration programs will not be compromised in the absence of such information.

The applicant acknowledges two ongoing salmon restoration efforts on local rivers and concludes that the farm will have no foreseeable impacts on those efforts. The basis for that conclusion is unclear as the applicant has provided no supporting information or argument. Based on the information provided, it does not appear as though the applicant has a solid understanding of these restoration programs or how they could be affected by the farm. There is no evidence to indicate that the applicant has sought information or advice from the groups operating those projects to understand potential impacts and mitigation measures.

DFO notes that salmon from the Inner and Outer Bay of Fundy have the potential to migrate in the vicinity of the proposed expansion site and that the area in the vicinity of the Annapolis Basin is considered to be used as a feeding ground in support of wild salmon growth, maturation, and post-spawning conditioning (DFO 2019, p.23). DFO appears to dismiss any impacts on wild salmon "because no critical habitat was identified in the predicted exposure zone, the Annapolis Basin, and the proposed lease boundaries" (DFO Letter of Advice, p7). This statement is misleading. There has been no critical habitat for salmon identified because DFO has not conducted the necessary research to identify critical salmon habitat in the Bay of Fundy or the Annapolis Basin despite being required to do so under the Species at Risk Act listing for the Inner Bay of Fundy population. Given that wild salmon are known to use the local marine environment for migration and feeding, it is possible that critical habitat does exist within the exposure zone. The fact that critical habitat in the area has not been adequately studied and identified can not be used to support a conclusion that there have not been or will not be impacts on wild salmon.

The applicant has noted that "several mitigation measures can be employed to reduce the potential impacts of aquaculture on wild salmon populations." However, the applicant has provided no information about what those measures will be. The only reference to mitigation measures is referring to a Farm Management Plan which has not been provided. If these mitigation measures are developed based on advice provided by DFO in 1999, as proposed by the applicant, this advice predates most of the science that has been conducted on wild salmon-aquaculture interactions (as outlined in Appendix 1) and therefore does not incorporate up-to-date information and best practices. Mitigation efforts and any new or revised Farm Management Plan should be based on more recent best-practice guidelines (e.g., the "Guidance on Best Management Practices to address impacts of sea lice and escaped farmed salmon on wild salmon stocks" developed by NASCO and the International Salmon Farmers Association in 2010 (NASCO 2010, Tab 12) or the standards developed by the Aquaculture Stewardship Council (ASC 2019, Tab 1)) (see point 5 below).

4. The existing regulatory framework is not sufficient to protect wild Atlantic salmon from the impacts of aquaculture.

As demonstrated by our review of the relevant literature (Appendix 1), significant impacts of salmon aquaculture on wild salmon have been documented throughout the North Atlantic, including eastern Canada. It is important to note that in all jurisdictions where impacts have been demonstrated, the aquaculture industry is heavily regulated. In some jurisdictions, regulations provide equal or better protection to wild salmon than those in place in Nova Scotia (Anon. 2016). For example, Norway boasts one of the most stringent sea lice management programs which sets aquaculture production limits based on monitored levels of sea lice from salmon farms on wild salmon. Yet, the impacts of sea lice on wild salmon remains a major concern in Norway (Olaussen 2018, Tab 13). In the Bay of Fundy, despite the existence of farm management plans, codes of containment, and escape reporting requirements, farm escapees continue to be detected annually at the monitoring facility on the Magaguadavic River. Likewise, despite strict federal and provincial regulation on the importation of foreign genetic strains of salmon, genes from European salmon have recently been detected in the Inner Bay of Fundy live gene bank program. This genetic material is believed to have come from illegal importation of European salmon by the aquaculture industry (DFO 2018; O'Reilly et al. 2018). While the applicant will be required to comply with all applicable provincial and federal regulations, this should not be taken as evidence that the farm will have no impact on wild salmon or salmon restoration efforts.

5. **There are several actions the applicant should take to avoid, mitigate, and monitor the impacts of the farm on wild Atlantic salmon.**

The North Atlantic Salmon Conservation Organization (NASCO) is an intergovernmental organization established by international convention in 1984 with Canada as a founding member. NASCO's objective is to conserve, restore, enhance and rationally manage Atlantic salmon though international co-operation, taking account of best available scientific information. NASCO and its Parties (including Canada) recognize the impacts of aquaculture on wild salmon and the need to take effective action to avoid and mitigate these impacts (NASCO 2020b). In 2010 NASCO, in collaboration with the International Salmon Farmers Association (ISFA), agreed to goals for protecting wild salmon from aquaculture and developed a series of best management practices to guide government and industry efforts to address impacts of aquaculture on wild stocks. The agreed goals are:

a. 100% of farms to have effective sea lice management such that there is no increase in sea lice loads or lice-induced mortality of wild salmonids attributable to the farms; and
b. 100% farmed fish to be retained in all production facilities.

NASCO's Williamsburg Resolution (NASCO 2006, Tab 11) and Guidance on Best Management Practices (NASCO 2010, Tab 12) documents outline a range of actions that should be taken to protect wild salmon e.g., the use of sterile fish, mandatory reporting of all escapes, monitoring of local rivers for escapes and genetic introgression, monitoring of wild salmon for increased sea lice loads, and triggers for responses to sea lice and disease outbreaks that are specifically designed to protect wild salmon. NASCO has recently reviewed Canada's efforts to implement the Best Management Practices and meet the agreed goals. Their review concluded that Canada is unable to demonstrate any progress towards meeting these goals and that Canada has proposed no acceptable management actions to address the issues of escapes and sea lice for the 2020-2024 period (NASCO 2020a).

Likewise, the Aquaculture Stewardship Council's Salmon Standard outlines a management framework to address the key negative environmental and social impacts associated with the salmon aquaculture industry, including the health and genetic integrity of wild salmon populations e.g., maximum sea lice loads within farms during sensitive periods for wild fish, monitoring of sea lice levels on wild salmon, capping the number of escapes permitted, evidence of data and the farm's understanding of that data, around salmonid migration routes, migration timing and stock productivity in major waterways within 50 kilometres of the farm (ASC 2019, p.24, Tab 1).

In order to adequately protect wild salmon from the impacts of AQ#1039, if the boundary amendment application is approved the applicant should be required to implement the NASCO/ISFA Best Management Practices and ASC standards necessary to meet the goals for sea lice and escapes as outlined above and agreed by Canada.

Summary

There are several scientifically validated reasons to believe the Rattling Beach salmon aquaculture site (AQ#1039) is likely negatively affecting wild salmon and their recovery efforts. The information provided by the applicant and DFO is not sufficient to demonstrate otherwise. Application of all relevant federal and provincial regulations will not likely mitigate these impacts in the absence of additional conditions designed specifically to protect wild salmon. To ensure the sustainability of wild salmon, if the expansion is approved the applicant should be required to take additional steps such as the use of sterile fish, monitoring of local rivers for escapes and genetic introgression, monitoring of wild salmon for increased sea lice and disease loads, and triggers for responses to sea lice and disease outbreaks that are specifically designed to protect wild salmon, as outlined in detailed in the NASCO/ISFA Best Management Practices and ASC standards.

Appendix 1

Overview of the Impacts of Salmon Farms on Wild Salmon Populations

Growing domesticated salmon in sea cages in areas where there are wild Atlantic salmon invariably has negative impacts on local wild populations. These negative impacts have been well established by scientific studies (ICES 2016; Hutchinson 2006; Ford and Myers 2008; DFO 2013a). Salmon farms have been shown to impact wild Atlantic salmon populations in several ways which are briefly summarized here:

- **Farmed salmon escape and interbreed with wild populations**. Farmed Atlantic salmon have been selectively bred to improve commercially important traits (i.e. growth, feed utilization, filet quality) which results in them being poorly adapted to the natural environment (Solberg et al. 2013; Wacker et al. 2021, Tab 16). When farmed salmon escape and interbreed with wild salmon, the resulting offspring are genetically inferior to wild salmon and are therefore less fit for life in the wild (Flemming et al. 2000; McGinnity et al. 2003; Bourrett et al. 2011; DFO 2013b).

  Escaped farmed salmon have been observed in rivers in all regions where salmon farming occurs (Thorstad et al. 2008). Some estimates suggest the annual number of escapes from salmon farms in the North Atlantic may outnumber the total population of adult wild Atlantic salmon (Glover et al. 2017, Tab 7). Large-scale studies in Norway (Glover et al. 2013; Karlsson et al. 2016, Tab 9) and Canada (Wringe et al. 2018, Tab 17; Bradbury et al. 2020a, Tab 3) have demonstrated the significant extent to which interbreeding can occur when salmon farming overlaps with wild populations.

  The viability and recovery of wild Atlantic salmon populations is threatened by the introduction of genetic material (i.e., genetic introgression) from farmed fish (Glover et al. 2020; Wacker et al. 2021, Tab 16). Long-term population level consequences of introgression include erosion of genetic diversity, reduced productivity, decreased resilience, and declining abundance (Hindar et al. 2006; Glover et al. 2017, Tab 7; Skaala et al. 2012, 2019; Sylvester et al. 2019, Tab 15). Several studies have demonstrated a decrease in the total productivity of wild salmon following introgression of farmed salmon genes (Fleming et al. 2000; McGinnity et al. 1997; McGinnity et al. 2003; Wacker et al. 2021, Tab 16).

- **Sea lice proliferate in salmon farms and are transmitted to wild fish.** Sea lice are a naturally occurring parasite on wild Atlantic salmon. When farmed salmon are stocked into open net pens they pick up sea lice from the environment which leads to frequent infestations and outbreaks within the farm. This increases the abundance of sea lice in the local area which has been demonstrated to increase the abundance of lice on wild salmon (Frazer 2009) and to increase mortality (especially of smolts) in wild populations (Krkosek et al., 2007; Thorstad et al. 2015; ICES 2016, Tab 8).

  Numerous studies have demonstrated a link between salmon aquaculture and sea lice infestations on wild salmonids (Helland et al. 2012, 2015; Middlemas et al., 2010, 2013; Serra-Llinares et al. 2014). Elevated levels of sea lice on wild salmonids have been found up to 30km from salmon farms (Thorstad et al. 2015). Smolt mortality attributable to salmon lice has been demonstrated to result in a significant reduction in adult returns (Shepherd and Gargan 2017, Tab 14) and to influence the achievement of conservation requirements for affected stocks (Gargan et al. 2012, Krkošek et al. 2013; Shepherd and Gargan 2017, Tab 14). Sea lice infestation also imposes sub-lethal physiological impacts, including reduced swimming speed (Wagner et al., 2003), osmoregulatory failure (Grimnes and Jakobsen, 1996;) and slower post-smolt growth (Skilbrei and Wennevik, 2006; Skilbrei et al., 2013).

- **Salmon farms and escaped fish have negative ecological interactions with wild salmon.** These interactions include interfering with mating and competition for food and space (Naylor et al. 2005) and escapees spreading parasites and diseases to wild fish (Naylor et al. 2005; Krkosek et al., 2006; Krkosek et al., 2007). These interactions can lead to changes in productivity of native salmon populations through processes affecting growth and survival (Lacroix and Flemming, 1998; Hindar and Flemming, 2007).
- **Diseases and pathogens proliferate in salmon farms and are transmitted to wild fish.** The Atlantic salmon farming industry has the capacity to play a central role in transportation and transmission of pathogens to wild salmon (Garseth et al. 2013). Transmission of pathogens and diseases from aquaculture to wild fish can occur through populations that are infected at the hatchery source, through infected escapees, and through wild fish migrating or moving within plumes of an infected pen or disease outbreak (Madhun et al. 2015; Naylor et al. 2005; Johnsen and Jensen 1994). There is a continual emergence of viruses in net-pen salmon aquaculture (Kibenge 2019, Tab 10) prompting increasing concern about the impacts of these diseases on wild Atlantic salmon populations and other marine wildlife (Bouwmeester et al. 2021, Tab 2).
- **Salmon farms alter the local environment thereby changing the selective pressures to which locally-adapted wild populations are subject.** Changes in selective pressures can lead to decreased survival, reductions in population size, increased genetic drift, and a lowering of long-term adaptive capacity in wild populations (Ferguson et al. 2007; Verspoor et al. 2015; DFO 2013b). Bradbury et al. (2020b, Tab 4) identified several examples of altered selective landscapes and genetic changes in wild salmon resulting from ecological processes associated with salmon farming, predominately through pathogen or parasite transmission leading to reductions in wild population abundance.

Collectively, these impacts have been correlated with significant declines in wild salmon populations. A global study by scientists at Dalhousie University found a reduction in survival or abundance of wild populations (of both salmon and sea trout) of more than 50% per generation on average, associated with salmon farming (Ford and Myers 2008, Tab 6). Such declines have significant social and economic impacts as recreational, commercial, and First Nations fisheries are reduced or eliminated (Wiber 2012; Naylor et al. 2005). Naylor et al. (2005) conclude that risks to wild populations, ecosystems, and society are highest where salmon are farmed in their native range, when large numbers of salmon are farmed near small natural populations, and when exotic pathogens are introduced with farmed fish.

Appendix 2

References

Selected sources materials appended at Tabs hereto

Anon. 2016. An International Regulatory Review to Support Consistent and Improved Management of the Impacts of Sea Cage Salmon Aquaculture. Gardner Pinfold Consulting, Sackville, NB. https://www.asf.ca/assets/files/02-13ReportASFAquaReview.pdf

ASC. 2019. ASC Salmon Standard Version 1.3. Aquaculture Stewardship Council. https://www.asc-aqua.org/wp-content/uploads/2019/12/ASC-Salmon-Standard_v1.3_Final.pdf **(Tab 1)**

Bouwmeester, MM, Goedknegt, MA, Poulin, R, Thieltges, DW. 2021. Collateral diseases: Aquaculture impacts on wildlife infections. *J Appl Ecol*. 2021; 58: 453– 464. **(Tab 2)**

Bourret V, O'Reilly PT, Carr JW, Berg PR, Bernatchez L. 2011. Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (Salmo salar) population following introgression by farmed escapees. Heredity, 106, 500–510.

Bradbury IR, Duffy S, Lehnert SJ, Jóhannsson R, et al. 2020a. Model-based evaluation of the genetic impacts of farm-escaped Atlantic salmon on wild populations. Aquacult Environ Interact 12:45-59. **(Tab 3)**

Bradbury IR, Burgetz I, Coulson MW, Verspoor E, et al. 2020b. Beyond hybridization: the genetic impacts of nonreproductive ecological interactions of salmon aquaculture on wild populations. Aquacult Environ Interact 12:429-445. **(Tab 4)**

DFO. 2008. Recovery Potential Assessment for Inner Bay of Fundy Atlantic Salmon. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2008/050.

DFO. 2009. Status of Atlantic Salmon in Salmon Fishing Areas (SFAs) 19-21 and 23. DFO Can. Sci. Advis. Sec. Sci. Resp. 2009/007

DFO. 2013a. Recovery Potential Assessment for Southern Upland Atlantic Salmon. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2013/009. **(Tab 5)**

DFO. 2013b. Recovery Potential Assessment for the South Newfoundland Atlantic Salmon (Salmo salar) Designatable Unit. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2012/007.

DFO. 2014a. Recovery Potential Assessment for Outer Bay of Fundy Atlantic Salmon. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2014/021.

DFO. 2014b. Recovery Potential Assessment for Eastern Cape Breton Atlantic Salmon. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2013/072.

DFO. 2018. Review of the Science Associated with the Inner Bay of Fundy Atlantic SalmonLive Gene Bank and Supplementation Programs. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2018/041.

DFO. 2020. DFO Maritimes Region Review of Proposed Marine Finfish Aquaculture Boundary Amendment, Rattling Beach, Digby County, Nova Scotia. DFO Can. Sci. Advis. Sec. Sci. Resp. 2020/015.

Ferguson A., et al., editors. 2007. The Atlantic Salmon: Genetics, Conservation and Management. Blackwell, Oxford.

Fleming, IA, Hindar, K, Mjolnerod, IB, Jonsson, B, Balstad, T, and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. Proceedings of the Royal Society of London Series B-Biological Sciences, 267: 1517-1523.

Ford J.S., Myers R.A. 2008. A global assessment of salmon aquaculture impacts on wild salmonids. PLoS Biol 6(2) **(Tab 6)**

Frazer L. 2009. Sea-cage aquaculture, sea lice, and declines of wild fish. Conservation Biology, 23: 599–607.

Gargan, P.G., Forde, G., Hazon, N.F., Russell, D.J., and Todd, C.D. 2012. Evidence for sea lice-induced marine mortality of Atlantic salmon (Salmo salar) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. Canadian Journal of Fish and Aquatic Sciences, 69: 343-353.

Garseth ÅH, Ekrem T, Biering E. 2013. Phylogenetic Evidence of Long Distance Dispersal and Transmission of Piscine Reovirus (PRV) between Farmed and Wild Atlantic Salmon. PLoS ONE 8(12)

Glover, K.A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M., and Skaala, Ø. 2013. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genetics, 14:4.

Glover, KA, Solberg, MF, McGinnity, P, et al. 2017. Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. *Fish Fish*.; 18: 890–927. **(Tab 7)**

Glover, K.A., Wennevik, V., Hindar, K., Skaala, Ø., Fiske, P., Solberg, M. F., Diserud, O. H., Svåsand, T., Karlsson, S., Andersen, L. B., & Grefsrud, E. S. 2020. The future looks like the past: Introgression of domesticated Atlantic salmon escapees in a risk assessment framework. *Fish and Fisheries*, 21(6), 1077– 1091

Grimnes A., Jakobsen P.J. 1996. The physiological effects of salmon lice infection on post-smolt of Atlantic salmon. Journal of Fish Biology, 48: 1179–1194.

Helland, I.P., Finstad, B., Uglem, I., Diserud, O.H., Foldvik, A., Hanssen, F., Bjørn, P.A., et al. 2012. What determines salmon lice infections on wild salmonids? Statistical calculations of data from the national salmon lice surveillance program 2004–2010 (in Norwegian). NINA Report, 891. 51 pp.

Helland, I.P., Uglem, I., Jansen, P.A., Diserud, O, H., Bjørn, P.A., and Finstad, B. 2015. Statistical and ecological challenges of monitoring parasitic sea lice infestations in wild salmonid fish stocks. Aquaculture Environment Interactions, 7: 267-280.

Hindar K, Fleming IA. 2007. Behavioral and genetic interactions between escaped farm salmon and wild Atlantic salmon. In: Bert TM, ed. Ecological and genetic implications of aquaculture activities. Berlin: Springer, pp. 115–122.

Hindar, K., Fleming, I., McGinnity, P., Diserud, O. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results, *ICES Journal of Marine Science*, Volume 63(7): 1234–1247

Hutchinson P. 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. Proceedings of an ICES/NASCO Symposium held in Bergen, Norway, 18–21 October 2005. ICES J Mar Sci 63:(7).

ICES. 2016. Report of the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF), 1–3 March 2016, Charlottenlund, Denmark. ICES CM 2016/ACOM:42. 44 pp. **(Tab 8)**

Johnsen B.O. and Jensen A.J. 1994. The spread of furunculosis among salmonids in Norweigan rivers. J Fish Biol 45: 47–55

Karlsson, S., Diserud, O.H., Fiske, P., and Hindar, K. 2016. Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES Journal of Marine Science*, 73(10), 2488–2498 **(Tab 9)**

Kibenge, F.S.B. 2019. Emerging viruses in aquaculture. Current Opinions in Virology 34: 97-103. **(Tab 10)**

Krkosek, M., J. Ford, A. Morton, S. Lele, R.A. Myers, and M. Lewis. 2007. Declining wild salmon populations in relation to parasites from farm salmon. Science 318, 1772-1775.

Krkosek, M., et al. 2006. Epizootics of wild fish induced by farm fish. Proceedings of the National Academy of Sciences of the USA. 103, 15506-15510.

Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B., and Todd, C.D. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B: Biological Sciences 280: 20122359.

Lacroix, G. and I.A. Flemming. 1998. Ecological and Behavioural Interactions Between Farmed and Wild Atlantic Salmon: Consequences for Wild Salmon. Canadian Stock Assessment Secretariat Research Document 98/162.

Madhun, A.S., et al. 2015. Potential disease interaction reinforced: Double-virus-infected escaped farmed Atlantic salmon, *Salmo salar* L., recaptured in a nearby river. *Journal of Fish Diseases*, 38, 209–219.

McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., et al. 1997. Genetic impact of escaped farmed Atlantic salmon (Salmo salar L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES Journal of Marine Science, 54: 998-1008.

McGinnity P, et al. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, Salmo salar, as a result of interactions with escaped farm salmon. Proc R Soc Lond B Biol Sci 270: 2443–2450

Middlemas, S.J., Raffell, J.A., Hay, D.W., Hatton-Ellis, M. and Armstrong, J.D. 2010. Temporal and spatial patterns of sea lice levels on sea trout in western Scotland in relation to fish farm production cycles. Biology Letters 6, 548–551.

Middlemas, S.J., Fryer, R.J., Tulett, D. & Armstrong, J.D. 2013. Relationship between sea lice levels on sea trout and fish farm activity in western Scotland. Fisheries Management and Ecology, 20: 68–74.

NASCO. 2006. Resolution by the Parties to the Convention for the Conservation of Salmon in the North Atlantic Ocean to Minimise Impacts from Aquaculture, Introductions and Transfers, and Transgenics on the Wild Salmon Stocks. North Atlantic Salmon Conservation Organization, CNL(06)48. https://nasco.int/wp-content/uploads/2020/02/williamsburg.pdf **(Tab 11)**

NASCO. 2010. Guidance on Best Management Practices to address impacts of sea lice and escaped farmed salmon on wild salmon stocks. North Atlantic Salmon Conservation Organization, SLG(09)5. https://nasco.int/wp-content/uploads/2020/02/BMP-Guidance.pdf **(Tab 12)**

NASCO. 2020a. November 2020 Evaluation of the Revised Implementation Plan under the Third Reporting Cycle (2019 –2024) from the Review Group to Canada. North Atlantic Salmon Conservation Organization, P(20)09_Canada.
https://nasco.int/wp-content/uploads/2021/01/IP2009_Canada_Full-Feedback-to-Parties-Nov-2020.pdf

NASCO. 2020b. Aquaculture and related activities. https://nasco.int/conservation/aquaculture-and-related-activities/. Accessed April 21, 2021.

Naylor R. et al. 2005. Fugitive salmon: assessing risks of escaped fish from aquaculture. BioScience 55:427-437.

Olaussen, J.O. 2018. Environmental problems and regulation in the aquaculture industry. Insights from Norway, Marine Policy, 98: 158-163. **(Tab 13)**

O'Reilly, P.T, Harvie, C.J., and McWilliams-Hughes, S.M. 2018. Genetic Change in Inner Bay of Fundy Atlantic Salmon Across Three Generations of Captive Breeding and Rearing. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/044.

Serra-Llinares, R.M., Bjørn, P.A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M. & Asplin, L. 2014. Salmon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. Aquaculture Environment Interactions, 5, 1-16.

Shephard S, Gargan P. 2017. Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. Aquaculture Environment Interactions 9:181-192. **(Tab 14)**

Skaala, Ø., Glover, K.A., Barlaup, B.T., Svåsand, T., Besnier, F., Hansen M.M., Borgstrøm R. 2012. Performance of farmed, hybrids, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. Canadian Journal of Fisheries and Aquatic Science, 69: 1994–2006.

Skaala, Ø., et al. 2019. An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. *Evolutionary Applications*, 12, 1– 16.

Skilbrei O.T., Wennevik V. 2006. Survival and growth of sea-ranched Atlantic salmon, *Salmo salar* L., treated against sea lice before release. ICES Journal of Marine Science, 63: 1317–1325.

Skilbrei O.T., Finstad B., Urdal K., Bakke G., Kroglund F., Strand R. 2013. Impact of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 1997-2009. Journal of Fish Diseases, 36: 249–260.

Solberg MF, Skaala Ø, Nilsen F, Glover KA. 2013. Does Domestication Cause Changes in Growth Reaction Norms? A Study of Farmed, Wild and Hybrid Atlantic Salmon Families Exposed to Environmental Stress. PLoS ONE 8(1): e54469.

Sylvester, E.V.A, B.F. Wringe, S.J. Duffy, L.C. Hamilton, I.A. Fleming, M.Castellani, P.Bentzen, I.R. Bradbury. 2019. Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild population. Evolutionary Applications 12(4): 705-717. **(Tab 15)**

Thorstad, E.B., et al. 2008. Incidence and impacts of escaped farmed Atlantic salmon Salmo salar in nature. NINA Special Report 36. 110 pp. https://www.nina.no/archive/nina/PppBasePdf/temahefte/036.pdf

Thorstad, E.B. et al. 2015. Effects of salmon lice Lepeophtheirus salmonis on wild sea trout Salmo trutta — a literature review. Aquaculture Environment Interactions 7: 91–113.

Thorstad, E.B. et al. 2021 (in press). Atlantic salmon in a rapidly changing environment - facing the challenges of reduced marine survival and climate change. Aquatic Conservation: Marine and Freshwater Ecosystems

Verspoor, E., et al. 2015. The potential direct and indirect genetic consequences for native Newfoundland Atlantic Salmon from interbreeding with European-origin farm escapes. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/030.

Wacker, S, Aronsen, T, Karlsson, S, et al. 2021. Selection against individuals from genetic introgression of escaped farmed salmon in a natural population of Atlantic salmon. *Evol Appl*. **(Tab 16)**

Wagner G. N., McKinley R. S., Bjørn P. A., Finstad B. 2003. Physiological impact of sea lice on swimming performance of Atlantic salmon. Journal of Fish Biology, 62: 1000–1009.

Wiber et al. 2012. Impact of Aquaculture on Commercial Fisheries: Fishermen's Local Ecological Knowledge. Human Ecology Volume 40, Issue 1, pp 29-40

Wringe, B.F., Jeffery, N.W., Stanley, R.R.E. *et al.* 2018. Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. *Commun Biol* **1,** 108. **(Tab 17)**

ASC Salmon Standard

Version 1.3

Contact information:

Postal address:

Aquaculture Stewardship Council
P.O. Box 19107
3501 DC Utrecht
The Netherlands

Office address:

Aquaculture Stewardship Council
Arthur van Schendelstraat 650
3511 MJ Utrecht, the Netherlands
+31 30 239 31 10

www.asc-aqua.org

Trade register number 34389683

Table of Contents

VERSION CONTROL, AVAILABLE LANGUAGE(S) AND COPYRIGHT NOTICE 6

ABOUT THE AQUACULTURE STEWARDSHIP COUNCIL (ASC) 8

THE ASC DOCUMENT AND CERTIFICATION SYSTEM 9

STRUCTURE OF ASC STANDARDS 10

SCOPE AND UNIT OF CERTIFICATION 12

PRINCIPLE 1: COMPLY WITH ALL APPLICABLE NATIONAL LAWS AND LOCAL REGULATIONS 13

- Criterion 1.1 Compliance with all applicable local and national legal requirements and regulations......13

PRINCIPLE 2: CONSERVE NATURAL HABITAT, LOCAL BIODIVERSITY AND ECOSYSTEM FUNCTION 14

- Criterion 2.1 Benthic biodiversity and benthic effects......14
- Criterion 2.2 Water quality in and near the site of operation......16
- Criterion 2.3 Nutrient release from production 19
- Criterion 2.4 Interaction with critical or sensitive habitats and species 19
- Criterion 2.5 Interaction with wildlife, including predators 21

PRINCIPLE 3: PROTECT THE HEALTH AND GENETIC INTEGRITY OF WILD POPULATIONS ...24

- Criterion 3.1 Introduced or amplified parasites and pathogens 24
- Criterion 3.2 Introduction of non-native species......27
- Criterion 3.3 Introduction of transgenic species......28
- Criterion 3.4 Escapes......29

PRINCIPLE 4: USE RESOURCES IN AN ENVIRONMENTALLY EFFICIENT AND RESPONSIBLE MANNER 31

- Criterion 4.1 Traceability of raw materials in feed 31
- Criterion 4.2 Use of wild fish for feed 31
- Criterion 4.3 Source of marine raw materials......33
- Criterion 4.4 Source of non-marine raw materials in feed......35
- Criterion 4.5 Non-biological waste from production 37
- Criterion 4.6 Energy consumption and greenhouse gas emissions on farms 38
- Criterion 4.7 Non-therapeutic chemical inputs 39

PRINCIPLE 5: MANAGE DISEASE AND PARASITES IN AN ENVIRONMENTALLY RESPONSIBLE MANNER 41

Criterion 5.1 Survival and health of farmed fish 41
Criterion 5.2 Therapeutic treatments 43
Criterion 5.3 Resistance of parasites, viruses and bacteria to medicinal treatments 47
Criterion 5.4 Biosecurity management 48

PRINCIPLE 6: DEVELOP AND OPERATE FARMS IN A SOCIALLY RESPONSIBLE MANNER 49

Criterion 6.1 Freedom of association and collective bargaining 49
Criterion 6.2 Child labour 50
Criterion 6.3 Forced, bonded or compulsory labour....................51
Criterion 6.4 Discrimination....................52
Criterion 6.5 Work environment health and safety 53
Criterion 6.6 Wages....................54
Criterion 6.7 Contracts (labour) including subcontracting 55
Criterion 6.8 Conflict resolution....................55
Criterion 6.9 Disciplinary practices 56
Criterion 6.10 Working hours and overtime....................56
Criterion 6.11 Education and training 57
Criterion 6.12 Corporate policies for social responsibility....................58

PRINCIPLE 7: BE A GOOD NEIGHBOUR AND CONSCIENTIOUS CITIZEN 59

Criterion 7.1 Community engagement....................59
Criterion 7.2 Respect for indigenous and aboriginal cultures and traditional territories 60
Criterion 7.3 Access to resources....................61

SECTION 8: REQUIREMENTS FOR SUPPLIERS OF SMOLT....................62

Requirements related to Principle 1 62
Requirements related to Principle 2 62
Requirements related to Principle 3 63
Requirements related to Principle 4 64
Requirements related to Principle 5 64
Requirements related to Principle 6 66
Requirements related to Principle 7 66
Additional requirements for open (net-pen) production of smolt 67
Additional requirements for semi-closed and closed production of smolts 68

Appendix I: Methodologies Related to Principle 2 and Benthic Testing 70

Appendix I-1. Sampling methodology for calculation of faunal index, macrofaunal taxa, sulphide and redox, and copper 70
Appendix I-2. Calculation methodology for the percentage of fines in feed 72
Appendix I-3. Biodiversity-focused impact assessment 73
Appendix I-4. Methodology for sampling dissolved oxygen 74
Appendix I-5. Methodology for sampling nitrogen and phosphorous 74
Appendix II: Area-Based Management (ABM) Scheme 76
Appendix II-1. Attributes and required components of the ABM 76
Appendix II-2. Setting and revising ABM lice loads and on-farm lice levels 77
Appendix III: Methodologies and Thresholds Related to Monitoring Wild Salmonids 79
Appendix III-1. Methodologies for monitoring wild salmonids 79
Appendix IV: Feed Resource Calculations and Methodologies 80
Appendix IV-1. Forage Fish Dependency Ratio calculation 80
Appendix IV-2. Calculation of EPA and DHA in feed 81
Appendix IV-3. Explanation of FishSource scoring 82
Appendix V: Energy Records and Assessment 84
Appendix V-1. Energy use assessment and GHG accounting for farms 84
Appendix V-2. GHG accounting for feed 85
Appendix VI: Transparency of Farm-Level Performance Data 87
Appendix VII: Parasiticide Treatment Methodology 92
Appendix VIII: Methodologies Related to Water Quality and Smolt Systems 95
Appendix VIII-1. Calculation of Total Phosphorous discharged per ton of smolt produced 95
Appendix VIII-2: Water quality sampling methodology and data sharing for land-based systems 96
Appendix VIII-3: Sampling methodology for benthic macro-invertebrate surveys 96
Appendix VIII-4: Sludge BMPs for closed and semi-closed smolt systems 99
Appendix VIII-5: Assimilative capacity assessment for cage (net-pen) smolt systems 99
Appendix VIII-6: Receiving water monitoring for open (net-pen) smolt systems 101
Appendix VIII-7: Trophic status classification and determining baseline trophic status 102

VERSION CONTROL, AVAILABLE LANGUAGE(S) AND COPYRIGHT NOTICE

The Aquaculture Stewardship Council (ASC) is the owner of this document.

For comments or questions regarding the content of this document, please contact the Standards and Science Team of ASC via standards@asc-aqua.org.

Version control

Document version history:

Version:	Release date:	Effective date:	Remarks/changes:
V1.3	July 11th, 2019	December 26th, 2019	Based on the PTI & Smolt review/revision cycle, the following indicators have been updated/modified: • Criteria 5.2 ('PTI review'): Rationale amended; 5.2.5 & 5.2.6 (reference to PTI removed, WNMT & parasiticide requirements added); 5.2.7 (new indicator, WNMT-related), 5.2.8 (new indicator: Integrated Pest Management /IPM), 5.2.9 (new indicator: IMP measures transparency), 5.2.10 (new indicator: monitoring of parasiticide residue levels outside AZE), 5.2.11 (indicator # changed: was 5.2.7 in v1.2); 5.2.12 (indicator # changed: 5.2.8 in v1.2); 5.2.13 (indicator # changed: 5.2.9 in v1.2); 5.2.14 (indicator # changed: 5.2.10 in v1.2); 5.2.15 (indicator # changed: 5.2.11 in v1.2). 5.3.3 (new indicator: Specific rotation medicinal treatment product) • Section 8 ('Smolt review'): "Additional requirements for open (net-pen) production of smolt': 8.24(requirement changed), former (in v1.2) indicators [8.24,8.26-8.31] deleted and replaced by 8.24. New Rationale for 8.24. Indicators 8.25, 8.26, 8.27 & 8.28 correspond to 'old' (i.e. in v1.2) indicators 8.32, 8.33, 8.34 & 8.35 (requirements unchanged). • Appendix VI (content changed for items #30, 31, 32), item 33 v1.2 removed, items 33,34,35,36 correspond to 'old'(i.e in v1.2) items 34,35,36,37. • Appendix VII (content changed: 'Parasiticide Treatment Methodology', instead of PTI). • Other updates include layout & UK English-consistent spell-check.
v1.2	March 7th, 2019	March 15th, 2019	Update of the standard to meet ASC style requirements (e.g. inclusion of structure of the standards, formatting and wording). Align the scope, 'about the ASC' and 'overview of the ASC

			system'. The content of the actual Standard, as defined by criteria/indicators/requirements under Principles [1-7], remains unchanged.
v1.1	April 26th, 2017	October 31st, 2017	Based on the first review/revision cycle: • following has been <u>updated</u> (in v1.1): 2.2.4 (requirement changed); 3.1.5 (updated footnote 43); 3.2.2 (updated footnote 50; requirement change); 4.2.1 (requirement changed); 4.2.2 (requirement changed); 4.3.1 (requirement changed); 4.3.2 (requirement updated); 4.3.4 (indicator expanded); 4.4.2 (requirement updated); 4.6.3 (requirement updated); 5.1.1 (indicator expanded); 5.2.6 (requirement updated); 5.4.4 (updated footnote 119); 6.11.1 (indicator expanded); 8.4 (requirement updated). • following is <u>added</u> (in v1.1): 2.2.6, 4.3.5, footnote 162. • following is <u>removed</u> (from v1.0): 2.5.2.
v1.0	June, 2012	July, 2012	Original version developed and approved by the Salmon Aquaculture Dialogue Steering Committee under the original title "Salmon Aquaculture Dialogue" and handed over to the Aquaculture Stewardship Council.

It is the responsibility of the user of the document to use the latest version as published on the ASC-website.

Available language(s)

The Salmon Standard document is available in the following language(s):

Versions:	**Available languages**
v1.3 v1.2 v1.1 v1.0	English (official language)
v1.0	Japanese

In case of any inconsistencies and/or discrepancies between available translation(s) and the English version, the online English version (pdf-format) will prevail.

Copyright notice

ABOUT THE AQUACULTURE STEWARDSHIP COUNCIL (ASC)

The Aquaculture Stewardship Council (ASC) is an independent, not-for-profit organisation that operates a voluntary, independent third-party certification and labelling programme based on a scientifically robust set of standards.

The ASC standards define criteria designed to help transform the aquaculture[1] sector[2] towards environmental sustainability and social responsibility, as per the ASC Mission.

ASC Vision

A world where aquaculture plays a major role in supplying food and social benefits for mankind whilst minimising negative impacts on the environment.

ASC Mission

To transform aquaculture towards environmental sustainability and social responsibility using efficient market mechanisms that create value across the chain.

ASC Theory of Change

A Theory of Change (ToC) is an articulation, description and mapping out of the building blocks required to achieve the organisation's vision**.**

ASC has defined a ToC which explains how the ASC certification and labelling programme promotes and rewards responsible fish farming practices through incentivising the choices people make when buying seafood.

ASC's Theory of Change can be found on the ASC website.

---

[1] **Aquaculture**: Aquaculture is the farming of aquatic organisms, including fish, molluscs, crustaceans and aquatic plants. Farming implies some form of intervention in the rearing process to enhance production, such as regular stocking, feeding, protection from predators, etc. Farming also implies individual or corporate ownership of the stock being cultivated (FAO).

[2] **Aquaculture sector**: Represents a group of industries (e.g. feed, farming, processing, etc.) and their markets that share common attributes (i.e. aquaculture products).

THE ASC DOCUMENT AND CERTIFICATION SYSTEM

ASC is a full member of the ISEAL Alliance and implements a voluntary, independent third-party certification system[3] consisting of three independent actors:

I.	Scheme Owner	i.e. Aquaculture Stewardship Council
II.	Accreditation Body	i.e. Assurance Services International (ASI)
III.	Conformity Assessment Body (CAB)	i.e. Accredited CAB's

Scheme Owner

ASC, as scheme owner:

- sets and maintains standards according to the ASC Standard Setting Protocol which is in compliance with the "ISEAL Code of Good Practice - Setting Social and Environmental Standards". The ASC standards are normative documents;

- sets and maintains Implementation Guidance which provides guidance to the Unit of certification (UoC) on how to interpret and best implement the indicators within the Standard;

- sets and maintains the Auditor Guidance which gives guidance to the auditor how to best assess a UoC against the indicators within the Standard;

- sets and maintains the Certification and Accreditation Requirements (CAR) which adheres at a minimum to the "ISEAL Code of Good Practice - Assuring compliance with Social and Environmental Standards". The CAR describes the accreditation requirements, assessment requirements and certification requirements. The CAR is a normative document.

These above listed documents are publicly available on the ASC-website.

Accreditation Body

Accreditation is the assurance process of assessing the Conformity Assessment Body (CAB) against accreditation requirements and is carried out by an Accreditation Body (AB). The appointed AB of ASC is Assurance Services International (ASI, "Accreditation Services International" prior to January 2019) which uses the CAR as normative document for the accreditation process.

Assessment findings of ASI-accreditation audits and an overview of current accredited CABs is publicly available via the ASI-website (http://www.accreditation-services.com).

---

[3] **Third-party Certification System**: Conformity assessment activity that is performed by a person or body that is independent of the person or organisation that provides the object, and of the user interests in that object (ISO 17000).

Conformity Assessment Body

The UoC contracts the CAB which employs auditor(s) that conduct a conformity assessment (hereafter 'audit') of the UoC against the relevant standard. The management requirements for CABs as well as auditor competency requirements are described in the CAR and assured through ASI accreditation.

ASC Audit and Certification Process

The UoC is audited at Indicator-level.

An ASC audit follows strict process requirements. These requirements are detailed in the CAR. Only ASI-accredited CABs are allowed to audit and certify a UoC against ASC standards. As scheme owner, ASC itself is not - and cannot be - involved in the actual audit and/or certification decision of a UoC. Granted certificates are the property of the CAB. ASC does not manage certificate validity.

Audit findings of all ASC audits, including granted certificates, are made publicly available on the ASC-website. These include the audit findings that result in a negative certification decision.

Note: in addition to the Standard's, there are certification requirements that apply to UoCs seeking certification; these requirements are detailed in the CAR.

ASC Logo use

ASC-certified entities shall only sell their product carrying the ASC Logo if a Logo Licence Agreement (LLA) has been signed. On behalf of the ASC, the Marine Stewardship Council (MSC) Licensing Team will issue logo license agreements and approve logo use on products. For more information see: ASC Logo.

Unauthorised logo display is prohibited and will be treated as a trademark infringement.

STRUCTURE OF ASC STANDARDS

A Standard is “*a document that provides, for common and repeated use, rules, guidelines or characteristics for products or related processes and production methods, with which compliance is not mandatory*”.

ASC Standards are as follows designed:

- ASC Standards consist of multiple Principles – a Principle is a set of thematically related Criteria which contribute to the broader outcome defined in the Principle title;
- Each Principle consists of multiple Criteria – each Criterion defines an outcome that contributes to achieving the outcome of the Principle;
- Each Criterion consists of one or several Indicators – each Indicator defines an auditable state that contributes to achieving the Criterion outcome.

Both Principles and Criteria include Rationale statements providing a set of reasons (backed by reference notes if needed) as to why the Principle or Criterion is needed.

SCOPE AND UNIT OF CERTIFICATION

Linked to the ASC Vision, the Scope of the ASC Salmon Standard (hereafter “the Standard”) addresses the key negative environmental and social impacts associated with the salmon aquaculture industry. An ASC-certified salmon farm contributes to the ASC Vision by reducing, mitigating or eliminating these negative impacts.

The Scope of the Standard is translated into seven Principles that apply to every UoC:

- Principle 1 – Comply with all applicable national laws and local regulations
- Principle 2 – Conserve natural habitat, local biodiversity and ecosystem function
- Principle 3 – Protect the health and genetic integrity of wild populations
- Principle 4 – Use resources in an environmentally efficient and responsible manner
- Principle 5 – Manage disease and parasites in an environmentally responsible manner
- Principle 6 – Develop and operate farms in a socially responsible manner
- Principle 7 – Be a good neighbour and conscientious citizen
- Section 8 – Requirements for suppliers of smolt

The Criteria within the Principles apply to every UoC.

Unit of Certification (UoC)

The applicable UoC is determined by the CAB/ auditor and adheres to the Standard’s Criteria UoC-requirements as outlined in the CAR.

Biological and geographic scope to which the Standard applies

The ASC Salmon Standard v1.3 is applicable to salmonid (i.e. salmon and trout) species belonging to the genus *Salmo* and *Oncorhynchus,* farmed in all marine locations [with the current exclusion/exception of smolt produced or held in net pens and/or [in future/soon] Smolt having to be certified under the FW Trout Standard] and types of aquaculture production systems.

How to read this document?

In the following pages, tables with indicators and their corresponding requirements are included. Within each criterion, requirements tables are followed by a rationale section that provides a brief overview of why the issues are important and how the proposed requirements address them.

Definitions are provided in footnotes.

The ASC Salmon Standard will be supplemented by an auditor guidance document detailing the methodologies used to determine if the ASC Salmon Standard is being met, as well as guidance for producers to achieve compliance to the ASC Salmon Standard.

Metric Performance Levels

Several Indicators in the Standard require a Metric Performance Level (MPL). The applicable MPL is directly listed after the Indicator (“Requirement” section).

PRINCIPLE 1: COMPLY WITH ALL APPLICABLE NATIONAL LAWS AND LOCAL REGULATIONS

Principle 1 is intended to ensure that all farms aiming to be certified against the ASC Salmon Standard standards meet their legal obligations as a baseline requirement. Adhering to the law will ensure that producers meet the basic environmental and social requirements and the minimal structures, such as legitimate land tenure rights, on which the effectiveness of the requirements will stand.

Criterion 1.1 Compliance with all applicable local and national legal requirements and regulations

INDICATOR	REQUIREMENT
1.1.1 Presence of documents demonstrating compliance with local and national regulations and requirements on land and water use	Yes
1.1.2 Presence of documents demonstrating compliance with all tax laws	Yes
1.1.3 Presence of documents demonstrating compliance with all relevant national and local labour laws and regulations	Yes
1.1.4 Presence of documents demonstrating compliance with regulations and permits concerning water quality impacts	Yes

Rationale - Salmon aquaculture operations must, as a baseline, adhere to the national and local laws of the regions where production is taking place. Farm operations that, intentionally or unintentionally, break the law violate a fundamental benchmark of performance for certified farms. It is important that aquaculture operations demonstrate a pattern of legal and responsible behaviour, including the implementation of corrective actions for any legal violations.

PRINCIPLE 2: CONSERVE NATURAL HABITAT, LOCAL BIODIVERSITY AND ECOSYSTEM FUNCTION

Principle 2 is intended to address potential impacts from salmon farms on natural habitat, local biodiversity and ecosystem function. Specifically, the key impact areas of benthic impacts, siting, effects of chemical inputs and effects of nutrient loading are addressed within this principle.

Criterion 2.1 Benthic biodiversity and benthic effects[4]

INDICATOR	REQUIREMENT
2.1.1 Redox potential or[5] sulphide levels in sediment outside of the Allowable Zone of Effect (AZE),[6] following the sampling methodology outlined in Appendix I-1	Redox potential > 0 mV, or, Sulphide ≤ 1,500 μMol /L
2.1.2 Faunal index score indicating good[7] to high ecological quality in sediment outside the AZE, following the sampling methodology outlined in Appendix I-1	AZTI Marine Biotic Index (AMBI[8]) score ≤ 3.3, or, Shannon-Wiener Index score > 3, or, Benthic Quality Index (BQI) score ≥ 15, or, Infaunal Trophic Index (ITI) score ≥ 25
2.1.3 Number of macrofaunal taxa in the sediment within the AZE, following the sampling methodology outlined in Appendix I-1	≥ 2 highly abundant[9] taxa that are not pollution indicator species

---

[4] Closed production systems that can demonstrate that they collect and responsibly dispose of > 75% of solid nutrients from the production system are exempt from standards under Criterion 2.1. See Appendix VI for requirements on transparency for 2.1.1, 2.1.2 and 2.1.3.

[5] Farm sites can choose whether to use redox or sulphide. Farms do not have to demonstrate that they meet both.

[6] **Allowable Zone of Effect** (AZE) is defined under this standard as 30 metres. For farm sites where a site-specific AZE has been defined using a robust and credible modelling system such as the SEPA AUTODEPOMOD and verified through monitoring, the site-specific AZE shall be used.

[7] "***Good***" Ecological Quality Classification: The level of diversity and abundance of invertebrate taxa is slightly outside the range associated with the type-specific conditions. Most of the sensitive taxa of the type-specific communities are present.

[8] http://ambi.azti.es/ambi/.

[9] **Highly abundant**: Greater than 100 organisms per square metre (or equally high to reference site(s) if natural abundance is lower than this level).

2.1.4 Definition of a site-specific AZE based on a robust and credible[10] modelling system[11]	Yes

Rationale - This suite of indicators provides multiple layers of security related to benthic impacts, using a chemical proxy for health combined with biodiversity measurements both below and a distance from the cages. Technical experts suggest the chemical proxy of redox potential and sulphide levels, which are good chemical indicators for benthic health. Given that both methods are valid, audited farms can choose their preference for one or the other. Requirements have been set for both. Through the consultation of technical experts and review of Hargrave et al.[12] (2008), a level of µMol /L sulphide levels and equivalent redox potential of > 0 mV was set to ensure acceptable and transitory benthic conditions. As a precautionary approach, these requirements are applicable regardless of the depth of the site.

When considering benthic effects, experts recommended measuring effects below the cages and away from the cages, within and outside the AZE. Though an AZE is difficult to identify as a constant, experts discuss this in terms of 25 metres to 125 metres depending on a range of factors, including currents. In an effort to take a precautionary approach to permissible zone of benthic impact, the ASC Salmon Standard defines the AZE as a distance of 30 metres from cages. For sites where a site-specific AZE has been determined using a valid modelling and video surveillance system, farms will use the site-specific AZE and sampling stations based on actual depositional patterns. Within three years of the publication of the ASC Salmon Standard, all certified farms must have undertaken the appropriate analysis to determine the site-specific AZE and depositional patterns. This will help ensure that sampling is taking place in areas most appropriate to protect benthic health around farms.

Potential negative impacts on benthic biodiversity are addressed in the ASC Salmon Standard through the incorporation of an analysis using a benthic faunal index and minimum score at multiple monitoring stations outside the AZE, including a reference site (see Appendix I-1). Farms can use their choice of these four faunal indices to further establish the environmental quality of the soft-bottom benthos. The indices are calculated using the same dataset. Equivalencies for these indices were set using Hargraves et al. (2008) and Zettler et al. (2007)[13] and through consultation with experts. The scores were set to relate to an environmental quality status of good or better according to the definitions of the EU Water Framework Directive.[14] Within the AZE, a demonstration that two or more benthic

---

[10] **Robust and credible**: The SEPA AUTODEPOMOD modelling system is considered to be an example of a credible and robust system. The model must include a multi-parameter approach. Monitoring must be used to ground-truth the AZE proposed through the model.

[11] The CAB shall confirm that the AZE is correct and then to default to the social principles (P6 and P7) to ensure the farm is responding to stakeholder comments with the intention that the AZE is not arbitrary and meets stakeholder expectations.

[12] Hargrave, B.T., Holmer, M. and Newcombe, C.P. 2008. Towards a classification of organic enrichment in marine sediments based on biogeochemical indicators. Marine Pollution Bulletin 56, 810–824. https://www.researchgate.net/publication/5509807_Towards_a_classification_of_organic_enrichment_in_marine_sediments_based_on_biogeochemical_indicators

[13] Zettler, M.L., Schiedek, D. and Bobertz, B. 2007. Benthic biodiversity indices versus salinity gradient in the southern Baltic Sea. Marine Pollution Bulletin 55, 258–270. https://www.io-warnemuende.de/tl_files/bio/ag-benthische-organismen/pdf/zettler_et_al-2007-mpb.pdf

[14] Additional references for index equivalencies:

macrofaunal species, such as sessile macrophytes and worms, are present in high abundance is required to ensure that impacts fall within an acceptable level.

Criterion 2.2 Water quality in and near the site of operation [15]

INDICATOR	REQUIREMENT
2.2.1 Weekly average percent saturation[16] of dissolved oxygen (DO)[17] on farm, calculated following methodology in Appendix I-4	≥ 70%[18]
2.2.2 Maximum percentage of weekly samples from 2.2.1 that fall under 2 mg/L DO	5%
2.2.3 For jurisdictions that have national or regional coastal water quality targets[19], demonstration through third-party analysis that the farm is in an	Yes[22]

- Borja, A., Franco, J. and Perez, V. 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Mar. Poll. Bull. 40, 1100–1114. http://www.ecasa.org.uk/Documents/AMBI-MarineBioticIndex.pdf
- Muxika, I., Borja, A. and Bonne, W. 2005. The suitability of the marine biotic index (AMBI) to new impact sources along European coasts. Ecological Indicators 5, 19–31. http://agris.fao.org/agris-search/search.do?recordID=AV20120155174
- Muniz, P. et al. 2005. Testing the applicability of a Marine Biotic Index (AMBI) to assessing the ecological quality of soft-bottom benthic communities in the South America Atlantic region. Marine Pollution Bulletin 50, 624–637. http://www.basqueresearch.com/uploads/fitxategiak/2769_1AMBI.pdf

[15] See Appendix VI for transparency requirements for 2.2.1, 2.2.2, 2.2.3 and 2.2.5.

[16] **Percent saturation**: Percent saturation is the amount of oxygen dissolved in the water sample compared to the maximum amount that could be present at the same temperature and salinity.

[17] Averaged weekly from two daily measurements (proposed at 6 am and 3 pm).

[18] An exception to this standard shall be made for farms that can demonstrate consistency with a reference site in the same water body.

[19] Related to nutrients (e.g. N, P, chlorophyll A).

[22] Closed production systems that can demonstrate the collection and responsible disposal of > 75% of solid nutrients as well as > 50% of dissolved nutrients (through biofiltration, settling and/or other technologies) are exempt from standards 2.2.3 and 2.2.4.

	area recently[20] classified as having "good" or "very good" water quality[21]	
2.2.4	For jurisdictions without national or regional coastal water quality targets, evidence of monitoring of nitrogen and phosphorous[23] levels on farm and at a reference site, following methodology in Appendix I-5	Consistency with reference site
2.2.5	Demonstration of calculation of biochemical oxygen demand (BOD[24]) of the farm on a production cycle basis	Yes
2.2.6	Appropriate controls are in place that maintains good culture and hygienic conditions on the farm which extends to all chemicals, including veterinary drugs, thereby ensuring that adverse impacts on environmental quality are minimised.	Yes

Rationale - Water quality is essential for the health of farmed salmon and wild species surrounding a farm. One component of water quality, dissolved oxygen (DO), is particularly critical for the survival and good performance of farmed salmon. As a result, most farms regularly measure DO. DO levels (in mg/l) naturally fluctuate in the environment. This is due to a range of factors, including temperature, time of day and upwelling of oxygen-poor waters from deep in the ocean. Low DO levels can also be a sign of excessive nutrient loading. DO provides a useful overall proxy for a water body's ability to support healthy biodiversity and supplements the benthic indicators that will also pick up excessive nutrient loading.

Salmon ideally need a level of dissolved oxygen over 5 mg/L to avoid any possible stress, although they are able to live under lower oxygen concentrations, particularly if only for short periods. Under routine production, the average minimum percent saturation of DO in the water column should be above

---

[20] Within the two years prior to the audit.

[21] Classifications of "***good***" and "***very good***" are used in the EU Water Framework Directive. Equivalent classification from other water quality monitoring systems in other jurisdictions are acceptable, it is acceptable to use a benchmark level of water quality from farm monitoring data as defined in Appendix I-5.

[23] Farms shall monitor total N, NH_4, NO_3, total P and Ortho-P in the water column. Results shall be submitted to the ASC database. Methods such as a Hach kit are acceptable.

[24] **BOD** calculated as: ((total N in feed – total N in fish)*4.57) + ((total C in feed – total C in fish)*2.67). A farm may deduct N or C that is captured, filtered or absorbed through approaches such as IMTA or through direct collection of nutrient wasted. In this equation, "fish" refers to harvested fish. Reference for calculation methodology: Boyd C. 2009. Estimating mechanical aeration requirement in shrimp ponds from the oxygen demand of feed. In: Proceedings of the World Aquaculture Society Meeting; Sept 25-29, 2009; VeraCruz, Mexico. And: Global Aquaculture Performance Index BOD calculation methodology available at http://web.uvic.ca/~gapi/explore-gapi/bod.html.

70 per cent. Measuring DO as a percent saturation takes into account salinity and temperature at the farm site. Additionally, compliance with the requirement will limit the number of low DO readings in the water column below 2 mg/L to less than 5 per cent incidence rate, which will allow for periodic physical phenomena, such as upwelling. The requirement also addresses natural fluctuations in DO levels and percent saturation through allowing comparison to a reference site as a means to meet requirement 2.2.1. This will ensure that if the percent saturation is lower than ideal, it is the result of natural conditions in the water body and not due to nutrient release from the salmon farm.

The requirements also require that farms demonstrate they are located in areas of “good” or “very good” water quality, in jurisdictions such as the European Union that have coastal targets. Not all salmon-producing regions have such targets, however. In these situations, farms must collect data on nutrient levels near the farm and at a reference site and make that data available under Appendix VI. No threshold is placed on this requirement whilst the key factor, as with oxygen in Indicator 2.2.1, is that the requirement should address natural fluctuations in N and P levels through allowing comparison to a reference site as a means to meet requirement 2.2.3.

Lastly, the requirements require farms to calculate the BOD associated with their production cycle in order to better understand the input of nutrients from the farm to the water body. There is no performance threshold associated with this requirement, and the data from this requirement will provide data to better understand nutrient loads, ranges of performance, the degree to which different systems reduce BOD, and the relationship between calculated BOD and the other water quality indicators in the ASC Salmon Standard.

The SAD technical working group on nutrient loading identified the potential link between nutrients around salmon farms and harmful algal blooms as one that had yet to be established but around which there remained some uncertainty and for which there was an intuitive concern around the effect of the cumulative anthropogenic nutrient load into coastal waters. The group noted a shortage of field studies to validate hypotheses from lab-based work. The data collected under this criterion can be used to help better understand potential linkages around salmon farming, ambient nutrient levels and environmental phenomena such as harmful algal blooms. Farm operators may also find this data useful in management decisions, and it can be useful in ensuring that nutrient inputs from salmon farms and other sources fall within the carrying capacity of the water body. Data collected with regard to BOD and nutrient levels shall be reviewed, and the setting of a threshold related to nutrient loads should be seriously considered when the ASC Salmon Standard is updated. The ASC intend to develop a metric for indicator 2.2.6 good culture and hygienic conditions. Until which time the standard will include this best management practice type measure.

Criterion 2.3 Nutrient release from production

INDICATOR	REQUIREMENT
2.3.1 Percentage of fines[25] in the feed at point of entry to the farm[26] (calculated following methodology in Appendix I-2)	< 1% by weight of the feed

Rationale - The release of nutrients into the environment from salmon farms was identified by SAD participants as a key impact of production. The impact is addressed throughout the requirements with a range of water quality and benthic performance metrics. Requirement 2.3.1 complements these other requirements by addressing the direct release of uneaten feed in the form of fines into the environment. By setting a maximum percentage of fines in the feed, it addresses the efficient and proper transport, storage and physical delivery of feed pellets to the farm site. Poor performance in any of the above phases of feed handling will result in a higher percentage of fines (fine particles of feed) and potentially increased environmental impacts, due to an increase in suspended organic particles and nutrients released into the environment.

Criterion 2.4 Interaction with critical or sensitive habitats and species

INDICATOR	REQUIREMENT
2.4.1 Evidence of an assessment of the farm's potential impacts on biodiversity and nearby ecosystems that contains at a minimum the components outlined in Appendix I-3	Yes

---

[25] **Fines**: Dust and fragments in the feed. Particles that separate from feed with a diameter of 5 mm or less when sieved through a 1 mm sieve, or particles that separate from feed with a diameter greater than 5 mm when sieved through a 2.36 mm sieve. To be measured at farm gate (e.g. from feed bags after they are delivered to farm).

[26] To be measured every quarter or every three months. Samples that are measured shall be chosen randomly. Feed may be sampled immediately prior to delivery to farm for sites with no feed storage where it is not possible to sample on farm. Closed production systems that can demonstrate the collection and responsible disposal of > 75% of solid nutrients and > 50% of dissolved nutrients (through biofiltration, settling and/or other technologies) are exempt.

2.4.2 Allowance for the farm to be sited in a protected area[27] or High Conservation Value Areas[28] (HCVAs)	None[29]

Rationale - The intent of the requirements under criterion 2.4 is to minimise the effects of a salmon farm on critical or sensitive habitats and species. The habitats and species to consider include marine-protected areas or national parks, established migratory routes for marine mammals, threatened or endangered species, the habitat needed for endangered and threatened species to recover, eelgrass beds and HCVAs, where these have been defined. These requirements are consistent with the Global Reporting Index indicators EN12, EN14 and EN15, which relate to the identification and description of significant impacts of activities on biodiversity, protected habitats and threatened species, and the communication of strategies to manage these impacts and restore sensitive habitats (as defined by the assessment carried out for indicator 2.4.1).[30]

The requirements under Criteria 2.4 ensure that a farm is aware of any nearby critical, sensitive or protected areas, understands the impacts it might have on those areas, and has a functioning plan in place to address those potential impacts. They also ensure that extra care is taken in areas that are recognised for ecological importance either through designation as a protected area or through designation as being an area of high conservation value, by not allowing production in these areas to be eligible for certification, with some exceptions made if extra conditions are met to ensure that the farms are compatible with the conservation goals of the areas.

---

[27] **Protected area**: "A clearly defined geographical space, recognised, dedicated and managed through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values." Source: Dudley, N. (Editor) (2008), Guidelines for Applying Protected Area Management Categories, Gland, Switzerland: IUCN. x + 86pp. http://cmsdata.iucn.org/downloads/guidelines_for_applying_protected_area_management_categories.pdf

[28] **High Conservation Value Areas** (HCVA): Natural habitats where conservation values are considered to be of outstanding significance or critical importance. HCVA are designated through a multi-stakeholder approach that provides a systematic basis for identifying critical conservation values—both social and environmental—and for planning ecosystem management in order to ensure that these high conservation values are maintained or enhanced (http://www.hcvnetwork.org/).

[29] The following exceptions shall be made for Standard 2.4.2:

- For protected areas classified by the International Union for the Conservation of Nature (IUCN) as Category V or VI (these are areas preserved primarily for their landscapes or for sustainable resource management).
- For HCVAs if the farm can demonstrate that its environmental impacts are compatible with the conservation objectives of the HCVA designation. The burden of proof would be placed on the farm to demonstrate that it is not negatively impacting the core reason an area has been identified as a HCVA.
- For farms located in a protected area if it was designated as such after the farm was already in operation and provided the farm can demonstrate that its environmental impacts are compatible with the conservation objectives of the protected area and it is in compliance with any relevant conditions or regulations placed on the farm as a result of the formation/designation of the protected area. The burden of proof would be placed on the farm to demonstrate that it is not negatively impacting the core reason an area has been protected.

[30] Verification at the aquaculture facility shall include whether restoration is necessary, to what degree (evidence could include maps, aerial photos, satellite images, government certification etc.) and whether that the active restoration is suitable (i.e., will it be successful and restore a suitable area of sensitive habitat).

Criterion 2.5 Interaction with wildlife, including predators[31]

INDICATOR	REQUIREMENT
2.5.1 Number of days in the production cycle when acoustic deterrent devices (ADDs) or acoustic harassment devices (AHDs) were used	0
2.5.2 Number of mortalities[32] of endangered or red-listed[33] marine mammals or birds on the farm	0
2.5.3 Evidence that the following steps were taken prior to lethal action[34] against a predator: 1. All other avenues were pursued prior to using lethal action 2. Approval was given from a senior manager above the farm manager 3. Explicit permission was granted to take lethal action against the specific animal from the relevant regulatory authority	Yes[35]
2.5.4 Evidence that information about any lethal incidents on the farm has been made easily publicly available[36]	Yes
2.5.5 Maximum number of lethal incidents[37] on the farm over the prior two years	< 9 lethal incidents,[38] with no more than two of the incidents being marine mammals

---

[31] See Appendix VI for transparency requirements for 2.5.2, 2.5.5 and 2.5.6.

[32] **Mortalities**: Includes animals intentionally killed through lethal action as well as accidental deaths through entanglement or other means.

[33] Species listed as endangered or critically endangered by the IUCN or on a national endangered species list.

[34] **Lethal action**: Action taken to deliberately kill an animal, including marine mammals and birds.

[35] Exception to these conditions may be made for a rare situation where human safety is endangered. Should this be required, post-incident approval from a senior manager should be made and relevant authorities must be informed.

[36] Posting results on a public website is an example of “easily publicly available.” Shall be made available within 30 days of the incident and see Appendix VI for transparency requirements.

[37] **Lethal incident**: Includes all lethal actions as well as entanglements or other accidental mortalities of non-salmonids.

[38] Standard 2.5.6 applicable to incidents related to non-endangered and non-red-listed species. This standard complements, and does not contradict, 2.5.3.

2.5.6 In the event of a lethal incident, evidence that an assessment of the risk of lethal incident(s) has been undertaken and demonstration of concrete steps taken by the farm to reduce the risk of future incidences	Yes

Rationale - The suite of requirements related to mortalities and lethal incidents of predators or other wildlife is intended to ensure that certified farms have minimal impact on populations of wildlife, placing limits on both accidental and intentional mortalities of these species. The requirements ensure that endangered species have not died as a result of interaction with the farm and require transparency of farms on any lethal incidents and wildlife mortalities for non-threatened species. Good management practices with regards to when to take action and how to reduce risk of future incidents are also required.

A large variety of acoustic deterrent (and harassment) devices is used in salmon aquaculture. Based on available research[39] it appears that the effectiveness of these devices in reducing farmed salmon predation by marine mammals can vary widely including by location, marine mammal species, period of use, etc. Available research suggests that noise and high-pitched sounds resulting from currently available acoustic devices can cause pain to dolphins, porpoises and whales. As intended, acoustic devices can cause marine mammals including seals, porpoises and whales to avoid areas that may be important for feeding, breeding and travel/migration. While the devices may be initially effective in deterring marine mammals in certain scenarios, research studies suggest that they lose their effectiveness over several years. Additionally, evidence suggests that alternative measures such as promptly removing dead fish, reducing stocking densities, net tensioning and use of seal blinds are important in reducing depredation on salmon farms.

Given the impacts associated with ADDs/AHDs and the availability of other, potentially less impactful and more effective deterrence practices, the requirements ensures that farms do not use ADDs/AHDs. An exception to this requirement for new technologies may be granted by the Technical Advisory Group

---

[39] References for the section of the rationale related to ADDs/AHDs:

- Northridge, S.P., Gordon, J.G., Booth, C., Calderan, S., Cargill, A., Coram, A., Gillespie, D., Lonergan, M. and Webb, A. 2010. Assessment of the impacts and utility of acoustic deterrent devices. Final Report to the Scottish Aquaculture Research Forum, Project Code SARF044. 34pp. http://www.sarf.org.uk/cms-assets/documents/28820-18834.sarf044---final-report.pdf
- Morton, A. B., and Symonds, H. K. 2002. Displacement of *Orcinus orca* (L.) by high amplitude sound in British Columbia, Canada. ICES Journal of Marine Science, 59: 71–80. https://oup.silverchair-cdn.com/oup/backfile/Content_public/Journal/icesjms/59/1/10.1006_jmsc.2001.1136/3/59-1-71.pdf?Expires=1499859194&Signature=URpngb2fKVR8B2kFgMguget42wf4uSn3nDVMqD6C-nymcyQlow3frZfVe4l9aLUpkGsJ5H0M4y3h2S6WVJJKOBa0~gFl5fuVjJ2lQhobfCbLu3JkiexGslvDncRW498rq6-06oV8Qsk2Y-Up3QBNujCKBN-07SWDpXdX3GvFsJTvxeEecDNojXRgLrYV7z6~iWsFHiVW4CiFO4arHhveN8tpu0yhYte~-byBwFih0BNCPpwQnRblOCuwclq6cVlsifQSDbMNSdkYUT72t3KJyocHMvMhvfPYBbAwvoZFYC3Bpvf~3pD4U0NjlkI9YnHQoY6zwShaORjbkq0CfRvc6w__&Key-Pair-Id=APKAIUCZBIA4LVPAVW3Q
- Scottish Association for Marine Science and Napier University (SAMS)2002. Review and synthesis of the environmental impacts of aquaculture. Scottish Executive Research Unit. www.scotland.gov.uk/cru/kd01/green/reia-00.asp.
- Milewski, I. 2001. Impacts of salmon aquaculture on the coastal environment: a review. https://www.iatp.org/sites/default/files/Impacts_of_Salmon_Aquaculture_on_the_Coastal_E.pdf
- Young, S. 2001. Potential adverse effects of aquaculture on marine mammals: in Tlusty, M.F., Bengston, D.A., Halvorson, H.O., Oktay, S.D., Pearce, J.B., Rheault, Jr., R.B. (eds.). Marine Aquaculture and the Environment: A Meeting for Stakeholders in the Northeast. Cape Cod Press, Falmouth, Massachusetts.

of the ASC if there is clear scientific evidence that future ADD/AHD technology presents significantly reduced risk to marine mammals and cetaceans.

PRINCIPLE 3: PROTECT THE HEALTH AND GENETIC INTEGRITY OF WILD POPULATIONS

The primary aim of Principle 3, in combination with Principle 5, is to ensure that salmon farms do not harm the health of wild fish populations. This principle addresses impacts associated with disease and parasites, escapes and siting.

Criterion 3.1 Introduced or amplified parasites and pathogens[40, 41]

INDICATOR	REQUIREMENT
3.1.1 Participation in an Area-Based Management (ABM) scheme for managing disease and resistance to treatments that includes coordination of stocking, fallowing, therapeutic treatments and information sharing. Detailed requirements are in Appendix II-1.	Yes
3.1.2 A demonstrated commitment[42] to collaborate with NGOs, academics and governments on areas of mutually agreed research to measure possible impacts on wild stocks	Yes
3.1.3 Establishment and annual review of a maximum sea lice load for the entire ABM and for the individual farm as outlined in Appendix II-2	Yes

---

[40] Farm sites for which there is no release of water that may contain pathogens into the natural (freshwater or marine) environment are exempt from the standards under Criterion 3.1.

[41] See Appendix VI for transparency requirements for 3.1.1, 3.1.3, 3.1.4, 3.1.6 and 3.1.7.

[42] **Commitment**: At a minimum, a farm and/or its operating company must demonstrate this commitment through providing farm-level data to researchers, granting researchers access to sites, or other similar non-financial support for research activities.

3.1.4 Frequent[43] on-farm testing for sea lice, with test results made easily publicly available[44] within seven days of testing	Yes
3.1.5 In areas with wild salmonids,[45] evidence of data[46] and the farm's understanding of that data, around salmonid migration routes, migration timing and stock productivity in major waterways within 50 kilometres of the farm	Yes
3.1.6 In areas of wild salmonids, monitoring of sea lice levels on wild out-migrating salmon juveniles or on coastal sea trout or Arctic char, with results made publicly available. See requirements in Appendix III-1	Yes
3.1.7 In areas of wild salmonids, maximum on-farm lice levels during sensitive periods for wild fish.[47] See detailed requirements in Appendix II, subsection 2	0.1 mature female lice per farmed fish

Rationale - Salmon farms interact with wild fish populations that live or migrate near the open net pens. A particular concern is the interaction with wild salmon and sea trout with regard to pathogens and parasites. There is significant debate in the scientific literature about the extent of the interaction and impact. The Disease Report[48] commissioned by the SAD concluded that there is "shared benefit to farm

---

[43] Testing must be weekly during and immediately prior to sensitive periods for wild salmonids, such as outmigration of wild juvenile salmon. Testing must be at least monthly during the rest of the year, unless water temperature is so cold that it would jeopardise farmed fish health to test for lice (below 4 degrees C). Within closed production systems, alternative methods for monitoring sea lice, such as video monitoring, may be used.

[44] Posting results on a public website is an example of "easily publicly available."

[45] For purposes of these standards, "**areas with wild salmonids**" are defined as areas within 75 kilometres of a wild salmonid migration route or habitat. This definition is expected to encompass all, or nearly all, of salmon-growing areas in the northern hemisphere.

[46] Farms do not need to conduct research on migration routes, timing and the health of wild stocks under this standard if general information is already available. Farms must demonstrate an understanding of this information at the general level for salmonid populations in their region, as such information is needed to make management decisions related to minimizing potential impact on those stocks. Such "evidence" would consist of, for example, peer review studies; publicly available government monitoring and reporting.

[47] Sensitive periods for migrating salmonids is during juvenile outmigration and approximately one month before.

[48] This report and other reports on State of Information of key impacts commissioned by the Salmon Aquaculture Dialogue are available at http://www.worldwildlife.org/pages/creating-standards-for-responsibly-farmed-salmon

productivity and to minimising impacts on wild fish by continually seeking to reduce disease on salmon farms."

Sea lice have emerged as a pressing challenge for the salmon industry and its potential impacts on wild populations. The SAD's Sea Lice Technical Report concluded that the "weight of evidence is that sea lice of farm origin can present, in some locations and for some host species populations, a significant threat." The report called for a "concerted precautionary approach" in managing the issue.

Requirements under Criterion 3.1, in combination with requirements under Criterion 5.4, seek to address these concerns by establishing best practice in managing potential disease and parasite risks to wild populations. The requirements recognise that the cumulative impacts from a group of farms in an area can become harmful even when an individual farm is operating its own production in a responsible way. Farms located in areas of wild salmonids, defined as farms situated within 75 km of a migration route or sea trout habitat, have additional requirements because of the transmission of disease between farms and wild salmonids.

Area-based management (ABM) is a requirement. Some salmon-growing jurisdictions have begun to require ABM or are considering it because neighbouring farms can achieve significantly improved results when coordinating management of diseases and biosecurity measures. Conversely, a lack of coordination can lead to negative outcomes, such as resistance to treatments. Farms that don't have ABM schemes already established in their jurisdiction will need to show leadership in working with neighbouring farms to establish such a scheme, even if the regulatory structure doesn't require it.

The commitment to research required under 3.1.2 intends to ensure that farms are working with researchers and regulators to address the many gaps in understanding around a farm's interaction with wild populations. A demonstrated commitment means that the farm is participating in joint research efforts. Although funding of research is encouraged, transparency around site-level data and/or access to sites is seen as an extremely valuable contribution to scientific research and is, therefore, the requirement.

The requirements address the challenge of sea lice in several ways. Firstly, farms seeking certification must be able to demonstrate that the ABM scheme has set a maximum lice load for the entire area that reflects regulatory requirements. In areas of wild salmonids, the ABM must also show how this maximum load reflects the results of monitoring of wild populations (more below on monitoring).

The requirements also call for an enhanced level of transparency around sea lice monitoring data. Secondly, farms must conduct frequent testing of on-farm lice levels and make those results publicly available. This transparency reflects the goal of building credibility among the interested public around the actual experience of sea lice levels on the farm and in the wild.

Farms located in areas of wild salmonids must participate in monitoring of lice levels on wild out-migrating juvenile salmon or other important salmonids in the area, such as coastal sea trout or arctic char. The requirements assume this monitoring will be conducted in collaboration with researchers and/or regulatory bodies. Area-based management schemes must demonstrate how the scheme has incorporated the results of wild monitoring into maximum lice loads permitted across the area. These requirements require farms to show leadership in managing the interaction with wild populations. This leadership will mean that some farms seeking certification will need to take on roles and responsibilities that they previously didn't view to be inside the scope of responsibility for an individual farm. Enhanced leadership is an essential part of showing best practice in this high-priority issue of farm interaction with wild populations.

Under 3.1.7, the requirements also require farms located in areas of wild salmonids to demonstrate precautionary low lice levels near zero during sensitive periods for wild fish, such as during juvenile out-migration and immediately prior.

The monitoring and disease management presuppose that farmers are aware of salmon migration routes, the timing of out migration and basic information around stock status. This information, along with sea lice monitoring results, should be compiled by ASC in an effort to consolidate data and promote future research.

If national or local regulations prohibit the handling of wild salmonids then it should be clear that wild populations are being monitored and protected in another way. Cooperation from the farm is necessary so it must be able to provide the data, but the farm is not expected to catch the salmon themselves. The farm could, for example, provide existing evidence to the CAB on how control agents are impacting wild populations.

Criterion 3.2 Introduction of non-native species

INDICATOR	REQUIREMENT
3.2.1 If a non-native species is being produced, demonstration that the species was widely commercially produced in the area by the date of publication of the ASC Salmon Standard	Yes[49]
3.2.2 If a non-native species is being produced, evidence of scientific research[50] completed within the past five years that investigates the risk of establishment of the species within the farm's jurisdiction and these results submitted to ASC for review[51]	Yes [52]

---

[49] Exceptions shall be made for production systems that use 100 percent sterile fish or systems that demonstrate separation from the wild by effective physical barriers that are in place and well-maintained to ensure no escapes of reared specimens or biological material that might survive and subsequently reproduce.

[50] The research must at a minimum include multi-year monitoring for non-native farmed species, use credible methodologies and analysis, and undergo peer review.

[51] If the review demonstrates there is increased risk, the ASC will consider prohibiting the certification of farming of non-native salmon in that jurisdiction under this standard. In the event that the risk tools demonstrate "high" risks, the SAD expects that the ASC will prohibit the certification of farming of non-native salmon in that jurisdiction. The ASC intends to bring this evidence into future revision of the standard and those results taken forward into the revision process.

[52] Farms are exempt from this standard if they are in a jurisdiction where the non-native species became established prior to farming activities in the area and the following three conditions are met: eradication would be impossible or have detrimental environmental effects; the introduction took place prior to 1993 (when the Convention on Biological Diversity (CBD) was ratified); the species is fully self-sustaining.

3.2.3 Use of non-native species for sea lice control or on-farm management purposes	None

Rationale - Accidental or intentional introductions of non-native species are significant global environmental problems.[53] Aquaculture is considered one of the major pathways for introducing non-native aquatic plants and animals that may become harmful invasive species. The ASC believes these standards are in line with FAO guidelines that permit the culture of non-native species only when they pose an acceptable level of risk to biodiversity. This requirement does not permit introductions of non-native salmonids, unless farming of the species already occurs in the area, or a completely closed production system is used, or all cultured fish are sterile.

Research to date, reviewed by the SAD Technical Working Group on Escapes, has not shown that the production of farmed salmon has led to the establishment of viable populations in the wild of non-native species. Given this research and existing analyses of the risks associated with the farming of salmonids as either a native or non-native species, this requirement permits the certification of farming of non-native species in locations where production already exists.

Nonetheless, the requirement also requires that farms producing non-native salmon demonstrate new research every five years that investigates the risks of establishment in that jurisdiction. The requirement is intended to create an incentive for continuing research.

The use of alternatives to chemical treatments for farm management, such as the use of cleaner fish for sea lice control, is permitted and encouraged under the ASC Salmon Standard. However, any wrasse, cleaner fish or other species used for management during production must be native species in order to prevent introduction of new species to an area.

Criterion 3.3 Introduction of transgenic species

INDICATOR	REQUIREMENT
3.3 Use of transgenic[54] salmon by the farm	None

---

[53] Leung, K.M.Y. and Dudgeon, D. 2008. Ecological risk assessment and management of exotic organisms associated with aquaculture activities. In M.G. Bondad-Reantaso, J.R. Arthur and R.P. Subasinghe (eds.) Understanding and applying risk analysis in aquaculture. FAO Fisheries and Aquaculture Technical Paper. No. 519. Rome, FAO. pp. 67–100. http://www.fao.org/3/a-i0490e/i0490e01e.pdf

[54] **Transgenic**: An organism, with the exception of human beings, in which the genetic material has been altered in a way that does not occur naturally by mating and/or natural recombination. Source EFSA.

Rationale - Transgenic fish are not permitted under this requirement because of concerns about their unknown impact on wild populations. The culture of genetically enhanced[55] salmon is acceptable under the ASC Salmon Standard. This allows for further progress in feed conversion, which should increase the efficient use of local resources. Also allowed under the Standard is the cultivation of triploid or all female fish, as long as those fish are not transgenic.

Criterion 3.4 Escapes[56]

INDICATOR	REQUIREMENT
3.4.1 Maximum number of escapees[57] in the most recent production cycle	300[58]
3.4.2 Accuracy[59] of the counting technology or counting method used for calculating stocking and harvest numbers	≥ 98%
3.4.3 Estimated unexplained loss[60] of farmed salmon is made publicly available	Yes
3.4.4 Evidence of escape prevention planning and related employee training, including: net strength testing; appropriate net mesh size; net traceability; system robustness; predator management; record keeping and reporting of risk events (e.g. holes, infrastructure issues, handling errors, reporting and follow up of escape	Yes

---

[55] **Genetic enhancement:** The process of genetic improvement via selective breeding that can result in better growth performance and domestication but does not involve the insertion of any foreign genes into the genome of the animal.

[56] See Appendix VI for transparency requirements for 3.4.1, 3.4.2 and 3.4.3.

[57] Farms shall report all escapes; the total aggregate number of escapees per production cycle must be less than 300 fish. Data on date of escape episode(s), number of fish escaped and cause of escape episode shall be reported as outlined in Appendix VI.

[58] A rare exception to this standard may be made for an escape event that is clearly documented as being outside the farm's control. Only one such exceptional episode is allowed in a 10-year period for the purposes of this standard. The 10-year period starts at the beginning of the production cycle for which the farm is applying for certification. The farmer must demonstrate that there was no reasonable way to predict the events that caused the episode. See auditing guidance for additional details.

[59] Accuracy shall be determined by the spec sheet for counting machines and through common estimates of error for any hand-counts.

[60] Calculated at the end of the production cycle as: Unexplained loss = Stocking count – harvest count – mortalities – other known escapes. Where possible, use of the pre-smolt vaccination count as the stocking count is preferred.

events); and worker training on escape prevention and counting technologies	

Rationale - Escaped farmed salmon have the potential to disrupt ecosystems and alter the overall pool of genetic diversity through competition with wild fish and interbreeding with local wild stocks of the same population. It has been shown that interbreeding of farmed with wild salmon of the same species can result in reduced lifetime success, lowered individual fitness and decreases in production over at least two generations.[61] The most effective way to address these risks is to reduce the number of escapes of farmed salmon to zero or near zero.

Escapes can occur in large events that are immediately noticeable at a farm, smaller events that are still noticeable, and through slower, lower levels of losses of fish that might go unnoticed. These requirements place a cap on the total amount of escapees. The cap effectively prevents a farm that has had a significant escape event from being certified, except under extremely unusual circumstances in which the farm can demonstrate there was no reasonable way to predict the cause.

The requirements require transparency about unexplained loss of salmon to help the farm and the public understand trends related to the cumulative numbers of losses of fish that go unnoticed during production. The accuracy of these numbers is limited by the margin of error of fish counting machines and other counting techniques. The requirements seek to encourage farmers to use counting devices that are as accurate as possible, requiring a minimum 98 per cent accuracy of the counting method.

A number of other requirements throughout the document complement the requirements on escapes from grow-out sites in terms of minimising impact on wild salmon populations. The ASC Salmon Standard includes requirements related to escapes from smolt production facilities, and a move away from production of smolts in open systems to closed and semi-closed systems with lower risk of escapees. Requirements related to escapees from smolt systems are particularly important in minimising the potential for interbreeding, as some studies show comparatively high reproductive success rates in escaped precocious male parr.[62] The ASC Salmon Standard also includes requirements related to siting in protected or high conservation value areas, including areas that are designated as such in order to protect threatened wild salmonid populations.

---

[61] Thorstad, E.B., Fleming, I.A., McGinnity, P., Soto, D., Wennevik, V. and Whoriskey, F. 2008. Incidence and impacts of escaped farmed Atlantic salmon *Salmo salar* in nature. NINA Special Report 36. 110 pp. http://www.fao.org/3/a-aj272e.pdf

[62] Garant, D., Fleming I.A., Einum, S. and Bernatchez, L. Alternate male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. Ecology Letters 2003;6: 541-549.

PRINCIPLE 4: USE RESOURCES IN AN ENVIRONMENTALLY EFFICIENT AND RESPONSIBLE MANNER

Principle 4 is intended to address negative impacts that stem from resource use, including feed and non-therapeutic chemical inputs.

Criterion 4.1 Traceability of raw materials in feed

INDICATOR	REQUIREMENT
4.1.1 Evidence of traceability, demonstrated by the feed producer, of feed ingredients that make up more than 1% of the feed.[63]	Yes

Rationale - Raw material traceability is fundamental to many of the ASC Salmon Standard and, therefore, is required under this requirement. This requirement will make raw material sourcing more transparent. It must be demonstrated at the feed manufacturer or feed producer level. For some feed ingredients, this will be evidence of traceability with regard to country of origin, while for other feed ingredients that relate specifically to other requirements, this may be a finer level of detail, such as traceability back to the fishery as outlined in the following criteria 4.2 and 4.3.

Criterion 4.2 Use of wild fish for feed[64]

INDICATOR	REQUIREMENT
4.2.1 Fishmeal Forage Fish Dependency Ratio (FFDRm) for grow-out (calculated using formulas in Appendix IV- 1)	< 1.2

---

[63] Traceability shall be at a level of detail that permits the feed producer to demonstrate compliance with the standards in this document (i.e., marine raw ingredients must be traced back to the fishery, soy to the region grown, etc.). Feed manufacturers will need to supply the farm with third-party documentation of the ingredients covered under this standard.

[64] See Appendix VI for transparency requirements for 4.2.1 and 4.2.2.

4.2.2 Fish Oil Forage Fish Dependency Ratio (FFDRo) for grow-out (calculated using formulas in Appendix IV- 1), or, Maximum amount of EPA and DHA from direct marine sources[65] (calculated according to Appendix IV-2)	FFDRo < 2.52, or, (EPA + DHA) < 30 g/kg feed

Rationale - The salmon aquaculture industry has significantly reduced the inclusion rates of fishmeal and fish oil from forage fish in salmon feeds during the past two decades. The Forage Fish Dependency Ratios (FFDR) contained in these requirements aim to support the trend toward lower inclusion rates and increasingly efficient use of marine resources, which are expected to continue. Fishmeal and fish oil are both finite resources that are shared across a range of users with increasing demands, from direct human consumption to aquaculture to pig and poultry production. The ASC Salmon Standard intends to promote the efficient use of these resources, producing increasing amounts of farmed salmon from a given input of fishmeal and oil.

The ratios, one for fishmeal and another for fish oil, calculate the dependency on forage fisheries through an assessment of the quantity of live fish from small pelagic fisheries required to produce the amount of fishmeal or fish oil needed to produce a unit of farmed salmon. The ASC Salmon Standard offers the calculation of levels of EPA and DHA from wild fish in feeds as an alternate method of measuring dependency on forage fisheries. The requirement encourages producers who want to produce salmon with high levels of omega-3 fatty acids to do so by sourcing the EPA and DHA from sources other than fish oil derived from direct industrial fisheries. The ratios complement the requirements described in criterion 4.3, which will move farms toward using feed with marine ingredients from fisheries certified as responsibly managed. Producers will be able to improve their FFDR by using a greater percentage of fishmeal and fish oil from trimmings and offal, using other sources of meal and oil (e.g. vegetables) and improving their feeding efficiency.

---

[65] Calculation excludes DHA and EPA derived from fisheries by-products and trimmings. Trimmings are defined as by-products when fish are processed for human consumption or if whole fish is rejected for use of human consumption because the quality at the time of landing does not meet official regulations with regard to fish suitable for human consumption.

Fishmeal and fish oil that are produced from trimmings can be excluded from the calculation as long as the origin of the trimmings is not any species that are classified as critically endangered, endangered or vulnerable in the IUCN Red List of Threatened Species (http://www.iucnredlist.org).

Criterion 4.3 Source of marine raw materials

Note: In November 2016 ASC published an Interim Solution for ASC Marine Feed Ingredients, which will replace indicators 4.3.1, 4.3.2 of this Standard. This solution applies to all ASC's Standards, which have indicators for marine raw material origin, including this ASC Salmon Standard . This interim solution will apply until the ASC Feed Standard will be available or until further official and public notice by ASC.

INDICATOR		REQUIREMENT
4.3.1	Timeframe for all fishmeal and fish oil used in feed to come from fisheries[66] certified under a scheme that is an ISEAL member[67] and has guidelines that specifically promote responsible environmental management of small pelagic fisheries	**see note above**
4.3.2	Prior to achieving 4.3.1, the FishSource score[65, 68] for the fishery(ies) from which all marine raw material in feed is derived	**see note above**
4.3.3	Prior to achieving 4.3.1, demonstration of third-party verified chain of custody and traceability for the batches of fishmeal and fish oil which are in compliance with 4.3.2.	Yes
4.3.4	Feed containing fishmeal and/or fish oil originating from: by-products[69] or trimmings from IUU[70] catch	None[72]

---

[66] This standard and standard 4.3.2 apply to fishmeal and oil from forage fisheries, pelagic fisheries, or fisheries where the catch is directly reduced (including krill) and not to by-products or trimmings used in feed.

[67] Meets ISEAL guidelines as demonstrated through full membership in the ISEAL Alliance, or equivalent as determined by the Technical Advisory Group of the ASC.

[68] Or equivalent score using the same methodology. See Appendix IV-3 for explanation of FishSource scoring.

[69] **Trimmings** are defined as by-products when fish are processed for human consumption or if whole fish is rejected for use of human consumption because the quality at the time of landing does not meet official regulations with regard to fish suitable for human consumption.

[70] **IUU**: Illegal, Unregulated and Unreported.

[72] For species listed as "vulnerable" by IUCN, an exception is made if a regional population of the species has been assessed to be *not* vulnerable in a National Red List process that is managed explicitly in the same science-based way as IUCN. In

or from fish species that are categorized as vulnerable, endangered or critically endangered, according to the IUCN Red List of Threatened Species,[71] whole fish and fish meal from the same species and family as the species being farmed.	
4.3.5 Presence and evidence of a responsible sourcing policy for the feed manufacturer for marine ingredients that includes a commitment to continuous improvement of source fisheries.[73]	Yes

Rationale - Wild fish harvested from the ocean and reduced into fishmeal and fish oil are an important component of salmon feeds. Many wild small pelagic fish resources are fished at capacity or overfished.[74] Demand for these resources is increasing as the aquaculture industry expands and as forage fish are increasingly consumed by humans or by other industries including other animal production. There is concern that higher demand could lead to the overfishing—and collapse—of small forage fish stocks. Wild small pelagic fish play a critical role in the ecosystem and the marine food chain. Some conservation groups and scientists are concerned that even fisheries that are not classified as overfished from a population perspective are, or could be, overfished from an ecological perspective.

These indicators strive to ensure that marine-based feed ingredients come from sustainable sources in the short- and long-term. The requirements aim to align industry incentives to support processes that will lead to improved fisheries management and ultimately the certification of forage fisheries as an independent measure of the ecological health of those fisheries.

In the medium term, the requirements will require marine ingredients in feed to be certified by a widely recognised authority. This recognised authority must be a member of the ISEAL Alliance, which promotes transparent, multi-stakeholder processes. The authority must also have a methodology that specifically addresses the ecological role of low trophic-level species. As of the date of publication of this ASC Salmon Standard, the Marine Stewardship Council (MSC) is the only fishery scheme that is a full member of ISEAL, and MSC is in the process of developing specific requirements for small pelagic fisheries. Additional schemes may emerge in the future that meet these requirements. This requirement begins to be applicable five years after the publication of the ASC Salmon Standard because there is a current lack of such certified sources of fishmeal and fish oil and the transformation of the industry will

---

cases where a National Red List doesn't exist or isn't managed in accordance with IUCN guidelines, an exception is allowed when an assessment is conducted using IUCN's methodology and demonstrates that the population is not vulnerable.

[71] The International Union for the Conservation of Nature reference can be found at http://www.iucnredlist.org/.

[73] The policy should be written and include an assessment of source fishery status and identification of improvement needs and work plan to deliver improvements. The policy must include a commitment and timeline to source aquaculture and fishery products from responsible/best practice sources, such as those certified a standard benchmarked at minimum consistent with relevant FAO's eco-labelling guidelines or by identified independent risk assessment.

[74] FAO, The State of World Fisheries and Aquaculture (SOFIA), 2010.

take some time. The ASC Salmon Standard encourages fisheries to begin immediately to make any needed management changes or regulatory reforms needed to achieve certification.

In the short term, the requirements restrict fisheries currently known to have the poorest status from being used for fishmeal and fish oil and places traceability requirements on the fishmeal and fish oil used in the feed. Requirement 4.3.2 requires the fishmeal and fish oil from forage fisheries to originate from fisheries meeting a minimum score using the FishSource scoring methodology, which is outlined in Appendix IV-3.

Rigorous traceability requirements are built into requirement 4.3.3. The traceability scheme must also incorporate baseline measures related to sustainability that serve as an additional measure to ensure that fish from unsustainable fisheries are not used in feed. The International Fishmeal and Fish Oil Organization's Global Standard for Responsible Supply[75] or a future equivalent that might emerge can be used to meet this requirement.

Last, requirement 4.3.4 prevents the use of by-products and trimmings that come from species categorized as vulnerable or worse on the IUCN Red List of Threatened Species. Using by-products from fisheries for human consumption in salmon feeds is a valuable use of products that may otherwise be wasted. However, a minimum level of sustainability of these fisheries is still required under the ASC Salmon Standard. For species classified globally as vulnerable by IUCN, the requirement offers the opportunity for feed suppliers to demonstrate through a scientific process that a regional population of a species is not actually vulnerable.

Criterion 4.4 Source of non-marine raw materials in feed

INDICATOR	REQUIREMENT
4.4.1 Presence and evidence of a responsible sourcing policy for the feed manufacturer for feed ingredients that comply with recognised crop moratoriums[76] and local laws[77]	Yes
4.4.2 Percentage of soya or soya-derived ingredients in the feed that are certified by the Roundtable for Responsible Soy (RTRS) or equivalent[78]	100%

---

[75] http://www.iffo.net/iffo-rs

[76] **Moratorium**: A period of time in which there is a suspension of a specific activity until future events warrant a removal of the suspension or issues regarding the activity have been resolved. In this context, moratoriums may refer to suspension of the growth of defined agricultural crops in defined geographical regions.

[77] Specifically, the policy shall include that vegetable ingredients, or products derived from vegetable ingredients, must not come from areas of the Amazon Biome that were deforested after July 24, 2006, as geographically defined by the Brazilian Soy Moratorium. Should the Brazilian Soy Moratorium be lifted, this specific requirement shall be reconsidered.

[78] Any alternate certification scheme would have to be approved as equivalent by the Technical Advisory Group of the ASC.

4.4.3 Evidence of disclosure to the buyer[79] of the salmon of inclusion of transgenic[80] plant raw material, or raw materials derived from transgenic plants, in the feed	Yes, for each individual raw material containing > 1% transgenic content[81]

Rationale - The ASC Salmon Standard aims to promote responsible sourcing of all feed ingredients. Thus, the ASC Salmon Standard requires producers to provide evidence that they are sourcing feed products from feed manufacturers that have a sustainable sourcing policy for feed ingredients.

Feed ingredients sourced from areas where significant ecological damage has occurred was of concern to the ASC. Therefore, the requirement requires producers to source feed from feed producers who comply with any relevant, recognised crop moratoriums that, at the time of the writing of these requirements, includes only the Brazilian Soy Moratorium,[82]. Such moratoriums are temporary measures intended to protect defined geographic regions. Looking to the future, the ASC Salmon Standard incorporates a requirement for feed manufacturers to use soy certified by the RTRS, which the ASC Salmon Standard recognises as the most environmentally meaningful soy certification process today. Because the scheme is recently starting up, the requirements build in a five-year window for this requirement.

Transgenic plants are commonly used in aquaculture and animal feeds throughout the world. Some consumers and retailers want to be able to identify food products, including farmed salmon, that are genetically modified or that have been fed genetically modified ingredients. The ASC Salmon Standard ensure transparency (above one per cent) around any transgenic material used in the feed in order to support informed choices by retailers and consumers. The ASC Salmon Standard require that the producer disclose to the first-order buyer of their salmon the use of any genetically modified ingredients in feed, and publicly disclose whether transgenic ingredients are used under Appendix VI.

---

[79] The company or entity to which the farm or the producing company is directly selling its product. This standard requires disclosure by the feed company to the farm and by the farm to the buyer of their salmon.

[80] **Transgenic**: An organism, with the exception of human beings, in which the genetic material has been altered in a way that does not occur naturally by mating and/or natural recombination. Source EFSA.

[81] See Appendix VI for transparency requirement for 4.4.3.

[82] See http://www.abiove.org.br/site/index.php?page=soy-moratorium&area=MTEtMy0x for additional information on the soy moratorium.

Criterion 4.5 Non-biological waste from production

INDICATOR	REQUIREMENT
4.5.1 Presence and evidence of a functioning policy for proper and responsible[83] treatment of non-biological waste from production (e.g. disposal and recycling)	Yes
4.5.2 Evidence that non-biological waste (including net pens) from grow-out site is either disposed of properly or recycled	Yes

Rationale - The purpose of these indicators is to ensure that all non-biological waste produced by a farm is recycled, reused or disposed of properly and does not affect neighbouring communities. Proper handling and treatment of wastes may vary across farms depending on the remoteness of the farm site and the disposal and recycling options available in the region.

---

[83] Proper and responsible disposal will vary based on facilities available in the region and remoteness of farm sites. Disposal of non-biological waste shall be done in a manner consistent with best practice in the area. Dumping of non-biological waste into the ocean does not represent "proper and responsible" disposal.

Initial Auditing Guidance

The ASC Salmon Standard recognises that some farms are located in extremely remote locations with no viable recycling systems nearby and where waste disposal presents challenges. Auditing guidelines will need to clarify what “proper” disposal means and be flexible enough to recognise that what is “proper” on one site is different from what is “proper” on another site. Regardless of the remoteness of a farm, these requirements would, for example, prohibit the dumping of non-biological waste (e.g. feedbags or nets) into the ocean.

Criterion 4.6 Energy consumption and greenhouse gas emissions on farms[84]

INDICATOR	REQUIREMENT
4.6.1 Presence of an energy use assessment verifying the energy consumption on the farm and representing the whole life cycle at sea, as outlined in Appendix V-1	Yes, measured in kilojoule/t fish produced/production cycle
4.6.2 Records of greenhouse gas (GHG[85]) emissions[86] on farm and evidence of an annual GHG assessment, as outlined in Appendix V-1	Yes
4.6.3 Documentation of GHG emissions of the feed[87] used during the previous production cycle, as outlined in Appendix V, subsection 2	Yes

Rationale - Climate change represents perhaps the biggest environmental challenge facing current and future generations. Because of this, energy consumption used in food production has become a source of major public concern. The ASC Salmon Standard recognises the importance of efficient and sustainable energy use. Therefore, these indicators will require that energy consumption in the production of fish should be monitored on a continual basis and that growers should develop means to improve efficiency and reduce consumption of energy sources, particularly those that are limited or carbon-based. The data collected in this process will help the ASC Salmon Standard set a meaningful

---

[84] See Appendix VI for transparency requirements for 4.6.1, 4.6.2 and 4.6.3.

[85] For the purposes of this standard, **GHGs** are defined as the six gases listed in the Kyoto Protocol: carbon dioxide (CO_2); methane (CH_4); nitrous oxide (N_2O); hydrofluorocarbons (HFCs); perfluorocarbons (PFCs); and sulphur hexafluoride (SF_6).

[86] GHG emissions must be recorded using recognised methods, standards and records as outlined in Appendix V.

[87] GHG emissions from feed can be given based on the average raw material composition used to produce the salmon (by weight) and not as documentation linked to each single product used during the production cycle. Feed manufacturer is responsible for calculating GHG emissions per unit feed. Farm site then shall use that information to calculate GHG emissions for the volume of feed they used in the prior production cycle.

numerical requirement for energy use in the future. Energy assessments are a new area for producers. Requiring that farms do these assessments will likely raise awareness of the issues related to energy and build support for adding a requirement in the future related to the maximum energy of GHG emissions allowed.

Criterion 4.7 Non-therapeutic chemical inputs[88,89]

INDICATOR	REQUIREMENT
4.7.1 For farms that use copper-treated nets[90], evidence that nets are not cleaned[91] or treated in situ in the marine environment	Yes
4.7.2 For any farm that cleans nets at on-land sites, evidence that net-cleaning sites have effluent treatment[92]	Yes
4.7.3 For farms that use copper nets or copper-treated nets, evidence of testing for copper level in the sediment outside of the AZE, following methodology in Appendix I-1	Yes
4.7.4 Evidence that copper levels[93] are < 34 mg Cu/kg dry sediment weight, or, in instances where the Cu in the sediment exceeds 34 mg Cu/kg dry sediment weight, demonstration that the Cu concentration falls within the range of background concentrations as	Yes

---

[88] Closed production systems that do not use nets and do not use antifoulants shall be considered exempt from standards under Criterion 4.7.

[89] See Appendix VI for transparency requirements for 4.7.1, 4.7.3 and 4.7.4.

[90] Under the SAD, "**copper-treated net**" is defined as a net that has been treated with any copper-containing substance (such as a copper-based antifoulant) during the previous 18 months, or has not undergone thorough cleaning at a land-based facility since the last treatment. Farms that use nets that have, at some point prior in their lifespan, been treated with copper may still consider nets as untreated so long as sufficient time and cleaning has elapsed as in this definition. This will allow farms to move away from use of copper without immediately having to purchase all new nets.

[91] Light cleaning of nets is allowed. Intent of the standard is that, for example, the high-pressure underwater washers could not be used on copper treated nets under this standard because of the risk of copper flaking off during this type of heavy or more thorough cleaning.

[92] Treatment must have appropriate technologies in place to capture copper if the farm uses copper-treated nets.

[93] According to testing required under 4.7.3. The standards related to testing of copper are only applicable to farms that use copper-based nets or copper-treated nets.

	measured at three reference sites in the water body	
4.7.5	Evidence that the type of biocides used in net antifouling are approved according to legislation in the European Union, or the United States, or Australia	Yes

Rationale - Copper (Cu) is an abundant trace element found in a variety of rocks and minerals. It is an essential micronutrient and is also necessary for a wide range of metabolic processes in animals and plants. At elevated levels, however, Cu becomes toxic. Collectively, the set of requirements related to copper encourage any sites that can do so to not use copper. Simultaneously, they recognise that in some situations phasing out copper usage may not yet be possible if, for example, alternate antifoulants or cleaning methods don't leave nets at a given site clean enough for the use of wrasse to manage sea lice to be feasible. In situations where copper is used, the requirements ensure precautionary healthy levels of copper in the benthos.

In order to minimise release of Cu from salmon farms into the environment, the requirement includes better management practices of not cleaning copper treated nets in the aquatic environment and requires that land-based cleaning facilities have the appropriate effluent treatment.

Additionally, a maximum level of Cu concentration in the sediment outside of the AZE is built into the requirement to ensure that any benthic effect that may occur from the use of copper on the net pens is minimal. The variability in environmental factors makes it very difficult to identify a generic threshold of copper in the environment that can be used to define the environmental risk. However, experts suggest that the threshold of 34mg/kg sediment adequately protects the benthos. The level of 34 mg is also consistent with the level at which Scottish regulation requires some action to ensure benthic health, and with levels recognised by other jurisdictions as the level at which there may be possible environmental effect. Under the ASC Salmon Standard, if Cu levels in the sediment just outside the AZE are higher than the threshold, as may be the case in areas with naturally high levels of Cu, the farm must demonstrate that the level just outside of the AZE is consistent with reference sites and the background levels in the area.

The ASC Salmon Standard is aware that other biocides are commercially applied to netting material. It is difficult to address all biocides used or to be used in the future. To address the high variability of biocides used, the ASC Salmon Standard elected to limit use to those chemicals approved for legal use by the European Union, the United States or Australia. The ASC Salmon Standard encourages the development and review of alternative antifoulants that are protective of the marine environment. The European Union, the United States and Australia were selected as a representation of jurisdictions that were viewed to be undertaking rigorous analyses of biocides.

PRINCIPLE 5: MANAGE DISEASE AND PARASITES IN AN ENVIRONMENTALLY RESPONSIBLE MANNER

Principle 5 aims to address negative impacts of salmon farming associated with disease, parasites and therapeutic chemical inputs. The ASC Salmon Standard recognises the role of proper fish handling and minimised levels of fish stress as an important element in good husbandry and in reducing levels of disease on farms, mortalities and therapeutic treatments. In addition to addressing environmental risks, compliance with requirements under Principle 5 helps ensure farmed fish health and welfare.

Criterion 5.1 Survival and health of farmed fish[94]

INDICATOR	REQUIREMENT
5.1.1. Evidence of a fish health management plan for the identification and monitoring of fish diseases, parasites and environmental conditions relevant for good fish health, including implementing corrective action when required	Yes
5.1.2 Site visits by a designated veterinarian[95] at least four times a year, and by a fish health manager[96] at least once a month	Yes
5.1.3 Percentage of dead fish removed and disposed of in a responsible manner	100%[97]
5.1.4 Percentage of mortalities that are recorded, classified and receive a post-mortem analysis	100%[98]

---

[94] See Appendix VI for transparency requirements for 5.1.4, 5.1.5 and 5.1.6.

[95] A **designated veterinarian** is the professional responsible for health management on the farm who has the legal authority to diagnose disease and prescribe medication. In some countries such as Norway, a fish health biologist or other professional has equivalent professional qualifications and is equivalent to a veterinarian for purposes of these standards. This definition applies to all references to a veterinarian throughout the standards document.

[96] A **fish health manager** is someone with professional expertise in managing fish health, who may work for a farming company or for a veterinarian, but who does not necessarily have the authority to prescribe medicine.

[97] The SAD recognises that not all mortality events will result in dead fish present for collection and removal. However, such situations are considered the exception rather than the norm.

[98] If on-site diagnosis is inconclusive, this standard requires off-site laboratory diagnosis. A qualified professional must conduct all diagnosis. One hundred percent of mortality events shall receive a post-mortem analysis, not necessarily every fish. A statistically relevant number of fish from the mortality event shall be analysed.

5.1.5 Maximum viral disease-related mortality[99] on farm during the most recent production cycle	≤ 10%
5.1.6 Maximum unexplained mortality rate from each of the previous two production cycles, for farms with total mortality > 6%	≤ 40% of total mortalities
5.1.7 A farm-specific mortalities reduction programme that includes defined annual targets for reductions in mortalities and reductions in unexplained mortalities	Yes

Rationale - Farmed salmon are susceptible to numerous diseases that have the potential to be amplified and transferred, thereby posing a risk to the health of fish and other marine organisms in adjacent ecosystems. One of the best ways to mitigate the risk of disease transfer to wild stocks is to reduce or eliminate the disease from happening initially.

These requirements seek to ensure proactive health management on the farm through a detailed health management plan and frequent visits by the designated veterinarian and other fish health professionals. The requirements under Criterion 5.1 are complemented by requirements related to the health of smolts, as outlined under Section 8 of this document. Requirements related to smolt seek to ensure that farmed salmon have all relevant vaccinations and enter the water as healthy as possible.

Healthy farms also must keep detailed records of all mortalities and cause of death. The post-mortem analysis required in this requirement is essential to provide an early warning against emerging diseases. Repeated high mortality rates, or a high rate of unexplained mortalities, may indicate poor management or poor siting. The mortality requirements in 5.1.5 and 5.1.6 are not intended as a goal, but rather a minimum required. The requirement focuses on mortalities from viral disease and unknown causes, as those categories were highlighted by experts as presenting a greater potential risk to wild fish populations and neighbouring farms. The requirement requires that mortalities from viral disease be kept at or below 10 per cent. Only farms with mortality rates greater than six per cent per production cycle must also then meet the requirement related to percentage of unexplained mortalities. The farm must be able to demonstrate that it is working seriously to reduce its mortalities, including tracking diseases and carrying out a farm-specific plan to reduce diseases and mortalities. The information collected on mortalities will be useful for future revisions of the requirements.

---

[99] Viral disease-related mortality count shall include unspecified and unexplained mortality as it could be related to viral disease.

Criterion 5.2 Therapeutic treatments[100]

INDICATOR	REQUIREMENT
5.2.1 On-farm documentation that includes, at a minimum, detailed information on all chemicals[101] and therapeutants used during the most recent production cycle, the amounts used (including grams per ton of fish produced), the dates used, which group of fish were treated and against which diseases, proof of proper dosing, and all disease and pathogens detected on the site	Yes
5.2.2 Allowance for use of therapeutic treatments that include antibiotics or chemicals that are banned[102] in any of the primary salmon producing or importing countries[103]	None
5.2.3 Percentage of medication events that are prescribed by a veterinarian	100%
5.2.4 Compliance with all withholding periods after treatments	Yes
5.2.5 The farm shall publicly report (via Appendix VI) the: 1. Weighted Number of Medicinal Treatments (see Appendix VII) for each production cycle 2. The parasiticide load for each agent over the production cycle 3. The benthic parasiticide residue levels	Yes

---

[100] See Appendix VI for transparency requirements for 5.2.1, 5.2.5, 5.2.6 and 5.2.10.

[101] Chemicals used for the treatment of fish.

[102] "**Banned**" means proactively prohibited by a government entity because of concerns around the substance. A substance banned in any of the primary salmon-producing or importing countries, as defined here, cannot be used in any salmon farm certified under the SAD, regardless of country of production or destination of the product. The SAD recommends that ASC maintain a list of a banned therapeutants.

[103] For purposes of this standard, those countries are Norway, the UK, Canada, Chile, the United States, Japan and France.

5.2.6 The Weighted Number of Medicinal Treatments shall be at or below the country Entry Level (see Appendix VII)	Yes
5.2.7 The farm shall reduce the Weighted Number of Medicinal Treatments, after achieving indicator 5.2.6, with 25% per 2 years until the WNMT is at or below the Global Level (see Appendix VII).	Yes
5.2.8 The farm shall implement Integrated Pest Management (IPM) according to the guidance in Appendix VII.	Yes
5.2.9 The farm shall public present (e.g. via company website) the IPM-measures that the company applies which need to be approved by a authorised veterinarian.	Yes
5.2.10 The farm shall monitor parasiticide residue levels annually in the benthic sediment directly outside the AZE.	Yes
5.2.11 Allowance for prophylactic use of antimicrobial treatments[104]	None
5.2.12 Allowance for use of antibiotics listed as critically important for human medicine by the World Health Organization (WHO[105])	None[106]
5.2.13 Number of treatments[107] of antibiotics over the most recent production cycle	≤ 3
5.2.14 If more than one antibiotic treatment is used in the most recent production cycle, demonstration that	Yes[109]

---

[104] The designated veterinarian must certify that a pathogen or disease is present before prescribing medication.

[105] The fifth edition of the WHO list of "Critically important antimicrobials for human medicine" was released in 2017 and is available at: http://apps.who.int/iris/bitstream/10665/255027/1/9789241512220-eng.pdf?ua=1 .

[106] If the antibiotic treatment is applied to only a portion of the pens on a farm site, fish from pens that did not receive treatment are still eligible for certification.

[107] A **treatment** is a single course medication given to address a specific disease issue and that may last a number of days.

[109] Reduction in load required, regardless of whether production increases on the site. Farms that consolidate production across multiple sites within an ABM can calculate reduction based on the combined antibiotic load of the consolidated sites.

the antibiotic load[108] is at least 15% less that of the average of the two previous production cycles	
5.2.15 Presence of documents demonstrating that the farm has provided buyers[110] of its salmon a list of all therapeutants used in production	Yes

Rationale - When disease outbreaks occur on salmon farms, farmers often opt to treat using chemical therapeutants as a means of protecting on-farm fish and the health of wild populations near the farm. With any chemical introduction into a wild environment, there is a need to ensure that non-target organisms are not being negatively impacted by the use of that chemical. Accurate and detailed documentation of all treatments is the first step to ensure proper dosing and safe use of therapeutants. The data collected from this requirement will also help the ASC set more measurable requirements in the future.

To minimise the risk of treatments posing a risk to the environment, farms shall not use treatments that have been banned by any of the regulatory bodies in the world's largest salmon-producing or importing countries. The chemical must have been proactively prohibited or banned, versus being not approved. Part of a farm's responsibility to operate within the law involves taking appropriate measures to ensure that its product complies with import laws of the countries where the salmon is eventually sold. Requirement 5.2.15 above ensures that buyers and importers have the information they need to verify that the product complies with import regulations.

Prophylactic use of antimicrobial treatments, and treatments that aren't prescribed by a licensed professional, are unacceptable under the requirement because they open the door to overuse and abuse of therapeutants.

Stakeholders within the SAD shared a common interest and common goal of reducing the use of parasiticides and reducing the risk of needed chemical treatments to the environment. The ultimate goal would be that farms could meet the ASC Salmon Standard without using therapeutants or without the risk of those therapeutants negatively impacting the environment. Simultaneously, the SAD focused on protecting wild stocks of salmonids and thus sets low thresholds (requirement 3.1.7) for allowable lice on farmed fish in areas with wild salmonids. Taking into account current technology and knowledge, and balancing between the objectives of minimising impact on wild stocks and at the same time addressing threats to the environment related to unrestricted use of therapeutants, the SAD allowed restricted use of parasiticides to treat sea lice under the requirement.

The purpose of the requirement of 5.2.5 is to place a limit on the number of treatments using parasiticides, while taking into account regional differences in ecosystems and epidemiology, including differences in lice species, wild host reservoirs and susceptibility to lice attack, together with differences in mandatory regulatory requirements in the different countries. The standard seeks to use a progressive indicator which encourages reductions in medicinal product use and the associated risks of resistance from overuse whilst incentivising an increasing shift to non-medicinal means of control through expansion of integrated pest management (IPM) strategies. To promote this, the entry to the

---

[108] **Antibiotic load** = the sum of the total amount of active ingredient of antibiotics used (kg).

[110] **Buyer**: The company or entity to which the farm or the producing company is directly selling its product.

process is relatively inclusive in order to promote the progressive changes sought. For this purpose, after the first audit, the farm should show improvement in management against a progress ladder based on the principles of IPM against a time bound plan (Appendix VII) and a shift towards low to zero medicinal product usage (Indicator 5.2.7).

Indicator 5.2.5 addresses the number of medicinal treatments used on certified farms. The total amount of active ingredient used for medicinal treatments will be provided by the parasiticide load. In addition, some more direct assessment of the fate of the various agents in the environment, is to be encouraged (Indicator 5.2.10) by requiring some monitoring of the concentration of the various agents in the sediment outside the Allowable Zone of Effects (AZE) either by using tools such as direct assay or models that have been scientifically validated (e.g. by peer review and documented testing) and which are approved by national regulatory bodies

In order to monitor effective progress in reduction of medicinal treatments, Indicator 5.2.7 requires that at the end of the second certification cycle following the introduction of the new requirements, that is after 6 years, and of every subsequent cycle, the WMNT can be audited over the preceding 6 years for an overall downward trend indicative of a reduction in medicinal treatment frequency. By this means there should be at least 4 or 5 data points upon which to base judgment. Reductions can be demonstrated at the individual farm or Area Based Management (ABM) level.

These requirements are consistent with industry efforts to reduce both frequency and amount of parasiticide used, as well as with initiatives to develop treatment methods that do not release parasiticides into the environment. To encourage thinking about cumulative use across a broader area, tracking of total use of parasiticides is required under the ABM.

With regards to the use of antibiotics, there is a global effort led by the WHO to ensure that antibiotics important for human medicine are used in a way that doesn’t jeopardise their effectiveness in treating human diseases. These requirements seek to be in line with that effort. The requirements set a cap on a maximum allowable number of treatments of antibiotics on certified farms that is intended to set a reasonable limit on what may be needed on a well-managed farm and excludes any farms that fail to follow industry guidelines for prudent use of antibiotics. Through 5.2.14, the ASC Salmon Standard addresses environmental risk from cumulative load of antibiotics entering the environment from certified farms. The requirement requires a reduction, of the actual load of antibiotics released from farms that use more than one treatment of antibiotics. This is in line with industry goals to reduce total antibiotic use and with trends in industry to use precise pen-by-pen treatments when appropriate.

Additionally, the SAD’s technical working group on chemical inputs recommended that antibiotics important for human health only be used with extreme reluctance. These requirements are also intended to further raise awareness within the aquatic veterinary community on the use of medically important antimicrobial drugs in food-animal production, and the public health risks associated with antibiotic resistance. This issue is addressed in requirement 5.2.12 and through a coordination requirement within the ABM related to the use of antibiotics classified by the WHO as “highly important” for human health.

Criterion 5.3 Resistance of parasites, viruses and bacteria to medicinal treatments

INDICATOR	REQUIREMENT
5.3.1 Bio-assay analysis to determine resistance when two applications of a treatment have not produced the expected effect	Yes
5.3.2 When bio-assay tests determine resistance is forming, use of an alternative, permitted treatment, or an immediate harvest of all fish on the site	Yes
5.3.3 Specific rotation, providing that the farm has >1 effective medicinal treatment product available, every third treatment must belong to a different family of drugs.	Yes

Rationale - One of the more serious risks of overusing medicinal treatments is the development of parasite drug resistance, which lowers the overall effectiveness of treatments. In some salmon-growing regions, resistance to a number of drugs has become a growing problem, increasing the challenge for salmon farmers to control sea lice on farmed and wild fish.

Efforts to prevent and monitor resistance are made most effectively through an area-based approach. Timely, accurate sea lice counts on the farm can detect when sea lice treatment is no longer effective. Bioassays are important to confirm if resistance is developing and a limit has been set on the number of repeat treatments of the same family of drugs that can be applied. A single treatment is considered to have taken place when the majority of a site (more than half of all cages) is treated. No more than two such treatments should use the same family of drugs; that is, at least every third treatment should be with a drug of a different class.

Criterion 5.4 Biosecurity management[111]

INDICATOR	REQUIREMENT
5.4.1 Evidence that all salmon on the site are a single year class[112]	100%[113]
5.4.2 Evidence that if the farm suspects an unidentifiable transmissible agent, or if the farm experiences unexplained increased mortality,[114] the farm has: 1. Reported the issue to the ABM and to the appropriate regulatory authority 2. Increased monitoring and surveillance[115] on the farm and within the ABM 3. Promptly[116] made findings publicly available	Yes
5.4.3 Evidence of compliance[117] with the OIE *Aquatic Animal Health Code*[118]	Yes
5.4.4 If an OIE-notifiable disease[119] is confirmed on the farm, evidence that:	Yes

---

[111] See Appendix VI for transparency requirements for 5.4.2 and 5.4.4.

[112] Gaps of up to six months between inputs of smolts derived from the same stripping are acceptable as long as there remains a period of time when the site is fully fallow after harvest.

[113] Exception is allowed for: 1) farm sites that have closed, contained production units where there is complete separation of water between units and no sharing of filtration systems or other systems that could spread disease, or, 2) farm sites that have ≥95% water recirculation, a pre-entry disease screening protocol, dedicated quarantine capability and biosecurity measures for waste to ensure there is no discharge of live biological material to the natural environment (e.g. UV or other effective treatment of effluent) .

[114] **Increased mortality**: A statistically significant increase over background rate on a monthly basis.

[115] Primary aim of monitoring and surveillance is to investigate whether a new or adapted disease is present in the area.

[116] Within one month.

[117] Compliance is defined as farm practices consistent with the intentions of the Code, to be further outlined in auditing guidance. For purposes of this standard, this includes an aggressive response to detection of an exotic OIE-notifiable disease on the farm, which includes depopulating the infected site and implementation of quarantine zones in accordance with guidelines from OIE for the specific pathogen. Quarantine zones will likely incorporate mandatory depopulation of sites close to the infected site and affect some, though not necessarily all, of the ABM. Exotic signifies not previously found in the area or had been fully eradicated (area declared free of the pathogen).

[118] OIE 2017. Aquatic Animal Health Code. http://www.oie.int/en/international-standard-setting/aquatic-code/access-online/

[119] **OIE-notifiable diseases** relevant to salmon aquaculture were: Epizootic haematopoietic necrosis, Infectious haematopoietic necrosis (IHN), Infectious salmon anemia (ISA), Viral hemorrhagic septicemia (VHS) and Gyrodactylosis

1. the farm at a minimum, immediately culled the pen(s) in which the disease was detected 2. the farm immediately notified the other farms in the ABM[120] 3. the farm and the ABM enhanced monitoring and conducted rigorous testing for the disease 4. the farm promptly[121] made findings publicly available	

Rationale - Biosecurity measures reduce the risk of disease transmission to the wild and between farms. These requirements aim to ensure that farms don't harm the health of wild populations by amplifying or spreading disease. It is recognised that disease flow is bidirectional between farmed and wild fish, and these requirements aim to minimise effect of disease transmission and retransmission. The ASC recognises that broad-level response to disease, in particular aggressive response to OIE-notifiable disease, must be led by regulators in the jurisdiction. This is important both because of legal implications of actions and because a mandatory response required by government has greatest potential to be effective.

PRINCIPLE 6: DEVELOP AND OPERATE FARMS IN A SOCIALLY RESPONSIBLE MANNER

Principle 6 aims to address potential negative social impacts related to farm development and operation, including labour concerns.

Criterion 6.1 Freedom of association and collective bargaining[122]

INDICATOR	REQUIREMENT
6.1.1 Evidence that workers have access to trade unions (if they exist) and union representative(s)	Yes

---

(Gyrodactylus salaris). The actions required are applicable to exotic OIE notifiable diseases. Actions taken need to comply with national regulations.

[120] This is in addition to any notifications to regulatory bodies required under law and the OIE Aquatic Animal Health Code.

[121] Within one month.

[122] **Bargain collectively**: A voluntary negotiation between employers and organizations of workers in order to establish the terms and conditions of employment by means of collective (written) agreements.

chosen by themselves without managerial interference	
6.1.2 Evidence that workers are free to form organizations, including unions, to advocate for and protect their rights	Yes
6.1.3 Evidence that workers are free and able to bargain collectively for their rights	Yes

Rationale - Having the freedom to associate and bargain collectively is a critical right of workers because it enables them to engage in collective bargaining over issues such as wages and other working conditions. Freedom of Association and the effective recognition of the right to collective bargaining is one of the core principles of the International Labor Organization's (ILO) "Declaration on Fundamental Principles and Rights at Work." The declaration was adopted in 1998 by the 86th International Labor Conference and has since been ratified by the overwhelming majority of ILO's 183 member nation-states.

Criterion 6.2 Child labour

INDICATOR	REQUIREMENT
6.2.1 Number of incidences of child[123] labour[124]	None

---

[123] **Child**: Any person under 15 years of age. A higher age would apply if the minimum age law of an area stipulates a higher age for work or mandatory schooling. Minimum age may be 14 if the country allows it under the developing country exceptions in ILO convention 138.

[124] **Child Labour**: Any work by a child younger than the age specified in the definition of a child.

6.2.2 Percentage of young workers[125] that are protected[126]	100%

Rationale - The effective abolition of child labour is one of the core principles of the ILO "Declaration on Fundamental Principles and Rights at Work." Adherence to the child labour codes and definitions included in this section indicates compliance with what the ILO and international conventions generally recognise as the key areas for the protection of child and young workers. Children are particularly vulnerable to economic exploitation, due to their inherent age-related limitations in physical development, knowledge and experience. Children and youth need adequate time for education, development and play. Therefore, they should not have to work or be exposed to working hours and conditions that are hazardous[127,128] to their physical or mental well-being. To this end, the requirements related to what constitutes child labour will protect the interests of children and young workers at salmon farms certified to these requirements.

Criterion 6.3 Forced, bonded or compulsory labour

INDICATOR	REQUIREMENT
6.3.1 Number of incidences of forced,[129] bonded[130] or	None

---

[125] **Young Worker**: Any worker between the age of a child, as defined above, and under the age of 18.

[126] **Protected**: Workers between 15 and 18 years of age will not be exposed to hazardous health and safety conditions; working hours shall not interfere with their education and the combined daily transportation time and school time, and work time shall not exceed 10 hours.

[127] **Hazard**: The inherent potential to cause injury or damage to a person's health (e.g. unequipped to handle heavy machinery safely, and unprotected exposure to harmful chemicals).

[128] **Hazardous work**: Work that, by its nature or the circumstances in which it is carried out, is likely to harm the health, safety or morals of workers (e.g. heavy lifting disproportionate to a person's body size, operating heavy machinery, exposure to toxic chemicals).

[129] **Forced (Compulsory) labour**: All work or service that is extracted from any person under the menace of any penalty for which a person has not offered himself/herself voluntarily or for which such work or service is demanded as a repayment of debt. "Penalty" can imply monetary sanctions, physical punishment, or the loss of rights and privileges or restriction of movement (e.g. withholding of identity documents).

[130] **Bonded labour**: When a person is forced by the employer or creditor to work to repay a financial debt to the crediting agency.

compulsory labour	

Rationale - Forced labour - such as slavery, debt bondage and human trafficking - is a serious concern in many industries and regions of the world. The elimination of all forms of forced or compulsory labour is one of the core principles of the ILO “Declaration on Fundamental Principles and Rights at Work.” Ensuring that contracts are clearly articulated and understood by workers is critical to determining that labour is not forced. The inability of a worker to freely leave the workplace and/or an employer withholding original identity documents of workers are indicators that employment may not be at-will. Adherence to these policies shall indicate that an aquaculture operation is not using forced, bonded or compulsory labour forces.

Criterion 6.4 Discrimination[131]

INDICATOR		REQUIREMENT
6.4.1	Evidence of comprehensive[132] and proactive anti-discrimination policies, procedures and practices	Yes
6.4.2	Number of incidences of discrimination	None

Rationale - The elimination of discrimination in respect of employment and occupation is one of the core principles of the ILO “Declaration on Fundamental Principles and Rights at Work.” Unequal treatment of workers based on certain characteristics (such as sex or race), is a violation of a workers’ human rights. Additionally, widespread discrimination in the working environment can negatively affect overall poverty and economic development rates. Discrimination occurs in many work environments and takes many forms. A common form is discrimination against women workers.

In order to ensure that discrimination does not occur at salmon farms certified to this requirement, employers must demonstrate their commitment to equality with an official anti-discrimination policy, a policy of equal pay for equal work, and clearly outlined procedures to raise, file and respond to a discrimination complaint in an effective manner. Evidence, including worker testimony, of adherence to

---

[131] **Discrimination**: Any distinction, exclusion or preference that has the effect of nullifying or impairing equality of opportunity or treatment. Not every distinction, exclusion or preference constitutes discrimination. For instance, a merit- or performance-based pay increase or bonus is not by itself discriminatory. Positive discrimination in favour of people from certain underrepresented groups may be legal in some countries.

[132] Employers shall have **written anti-discrimination policies** stating that the company does not engage in or support discrimination in hiring, remuneration, access to training, promotion, termination or retirement based on race, caste, national origin, religion, disability, gender, sexual orientation, union membership, political affiliation, age or any other condition that may give rise to discrimination.

these policies and procedures will indicate minimisation of discrimination. “Positive” discrimination (i.e., special treatment to protect the rights and health of particular groups of workers, or to provide opportunities for groups which have historically been disadvantaged) is allowed, and often required by laws related to such issues as maternity and affirmative action.

Criterion 6.5 Work environment health and safety

INDICATOR		REQUIREMENT
6.5.1	Percentage of workers trained in health and safety practices, procedures[133] and policies on a yearly basis	100%
6.5.2	Evidence that workers use Personal Protective Equipment (PPE) effectively	Yes
6.5.3	Presence of a health and safety risk assessment and evidence of preventive actions taken	Yes
6.5.4	Evidence that all health- and safety-related accidents and violations are recorded and corrective actions are taken when necessary	Yes
6.5.5	Evidence of employer responsibility and/or proof of insurance (accident or injury) for 100% of worker costs in a job-related accident or injury when not covered under national law	Yes
6.5.6	Evidence that all diving operations are conducted by divers who are certified	Yes

Rationale - A safe and healthy working environment is essential for protecting workers from harm. It is critical for a responsible aquaculture operation to minimise these risks. One of the key risks to workers is hazards resulting from accidents and injuries. Consistent, effective and regular worker training in health and safety practices is an important preventative measure. When an accident, injury or violation occurs, the company must record it and take corrective action to identify the root causes of the incident, remediate, and take steps to prevent future occurrences of similar incidents. This addresses violations and the long-term health and safety risks. Finally, while many national laws require that employers assume responsibility for job-related accidents and injuries, not all countries require this and not all workers (in some cases migrant and other workers) will be covered under such laws. When not covered

---

[133] **Health and safety training** shall include emergency response procedures and practices.

under national law, employers must prove they are insured to cover 100 per cent of worker costs when a job-related accident or injury occurs.

Criterion 6.6 Wages

INDICATOR		REQUIREMENT
6.6.1	The percentage of workers whose basic wage[134] (before overtime and bonuses) is below the minimum wage[135]	0 (None)
6.6.2	Evidence that the employer is working toward the payment of basic needs wage[136]	Yes
6.6.3	Evidence of transparency in wage-setting and rendering[137]	Yes

Rationale - Wages and the process for setting wages are important components of the ILO core principles. For this reason, it is important to highlight under these requirements the importance of workers' basic wages meeting the legal minimum wage and being rendered to workers in a convenient manner. Unfortunately, minimum wage in many countries does not always cover the basic needs of workers. Unfairly and insufficiently compensated workers can be subject to a life of sustained poverty. Therefore, it is important for socially responsible employers to pay or be working toward paying a basic needs wage. The calculation of a basic needs wage can be complex, and it is important for employers to consult with workers, their representatives and other credible sources when assessing what a basic needs wage would be.

Certified salmon farms shall also demonstrate their commitment to fair and equitable wages by having and sharing a clear and transparent mechanism for wage-setting and a labour conflict resolution policy[138] that tracks wage-related complaints and responses. Having these policies outlined in a clear and transparent manner will empower the workers to negotiate effectively for fair and equitable wages that shall, at a minimum, satisfy basic needs.

---

[134] **Basic wage**: The wages paid for a standard working week (no more than 48 hours).

[135] If there is no legal minimum wage in a country, basic wages must meet the industry-standard minimum wage.

[136] **Basic needs wage**: A wage that covers the basic needs of an individual or family, including housing, food and transport. This concept differs from a minimum wage, which is set by law and may or may not cover the basic needs of workers.

[137] Payments shall be rendered to workers in a convenient manner.

[138] See Criterion 6.8.

Criterion 6.7 Contracts (labour) including subcontracting

INDICATOR		REQUIREMENT
6.7.1	Percentage of workers who have contracts[139]	100%
6.7.2	Evidence of a policy to ensure social compliance of its suppliers and contractors	Yes

Rationale - Fair contracting is important to ensure transparency between the employer and employee and fairness in the employment relation. Short-term and temporary contracts are acceptable but cannot be used to avoid paying benefits or to deny other rights. The company shall also have policies and mechanisms to ensure that workers contracted from other companies for specific services (e.g. divers, cleaning or maintenance) and the companies providing them with primary inputs or supplies have socially responsible practices and policies.

Criterion 6.8 Conflict resolution

INDICATOR		REQUIREMENT
6.8.1	Evidence of worker access to effective, fair and confidential grievance procedures	Yes
6.8.2	Percentage of grievances handled that are addressed[140] within a 90-day timeframe	100%

Rationale - Companies must have a clear labour conflict resolution policy in place for the presentation, treatment and resolution of worker grievances in a confidential manner. Workers shall be familiar with the policy and its effective use. Such a policy is necessary to track conflicts and complaints raised, and responses to conflicts and complaints.

---

[139] **Labor-only contracting relationships** or **false apprenticeship** schemes are not acceptable. This includes revolving/consecutive labor contracts to deny benefit accrual or equitable remuneration. False Apprenticeship Scheme: The practice of hiring workers under apprenticeship terms without stipulating terms of the apprenticeship or wages under contract. It is a "false" apprenticeship if its purpose is to underpay people, avoid legal obligations or employ underage workers. Labor-only contracting arrangement: The practice of hiring workers without establishing a formal employment relationship for the purpose of avoiding payment of regular wages or the provision of legally required benefits, such as health and safety protections.

[140] **Addressed**: Acknowledged and received, moving through the company's process for grievances, corrective action taken when necessary.

Criterion 6.9 Disciplinary practices

INDICATOR	REQUIREMENT
6.9.1 Incidences of excessive or abusive disciplinary actions	None
6.9.2 Evidence of a functioning disciplinary action policy whose aim is to improve the worker[141]	Yes

Rationale - The rationale for discipline in the workplace is to correct improper actions and maintain effective levels of worker conduct and performance. However, abusive disciplinary actions can violate workers' human rights. The focus of disciplinary practices shall always be on the improvement of the worker. Fines or basic wage deductions shall not be acceptable as methods for disciplining workforce. A certified salmon farm shall never employ threatening, humiliating or punishing disciplinary practices that negatively impact a worker's physical and mental[142] health or dignity.

Criterion 6.10 Working hours and overtime

INDICATOR	REQUIREMENT
6.10.1 Incidences, violations or abuse of working hours[143] and overtime laws	None
6.10.2 Overtime is limited, voluntary,[144] paid at a premium rate and restricted to exceptional circumstances	Yes

---

[141] If disciplinary action is required, progressive verbal and written warnings shall be engaged. The aim shall always be to improve the worker; dismissal shall be the last resort. Policies for bonuses, incentives, access to training and promotions are clearly stated and understood, and not used arbitrarily. Fines or basic wage deductions shall not be acceptable disciplinary practices.

[142] **Mental Abuse**: Characterised by the intentional use of power, including verbal abuse, isolation, sexual or racial harassment, intimidation or threat of physical force.

[143] In cases where local legislation on working hours and overtime exceed internationally accepted recommendations (48 regular hours, 12 hours overtime), the international standards will apply.

[144] Compulsory overtime is permitted if previously agreed to under a collective bargaining agreement.

Rationale - Abuse of overtime working hours is a widespread issue in many industries and regions. Workers subject to extensive overtime can suffer consequences in their work-life balance and are subject to higher fatigue-related accident rates. In accordance with better practices, workers in certified salmon farms are permitted to work—within defined guidelines—beyond normal work week hours but must be compensated at premium rates.[145] Requirements for time off, working hours and compensation rates as described should reduce the impacts of overtime.

Criterion 6.11 Education and training

INDICATOR		REQUIREMENT
6.11.1	Evidence that the company regularly performs training of staff in fish husbandry, general farm and fish escape management and health and safety procedures	Yes

Rationale - Education and training can be beneficial to companies and enable workers to improve their incomes. Such human capital development should be encouraged where it is in the interest of the company. Incentives, such as subsidies for tuition or textbooks and time off prior to exams, should be offered. The offer of training may be contingent on workers committing to stay with the company for a pre-arranged time. This should be made clear to participants before they start the training.

Workers employed in husbandry activities require specific and adequate training and are aware of their responsibilities in aquatic animal health management practices.

---

[145] **Premium rate**: A rate of pay higher than the regular work week rate. Must comply with national laws/regulations and/or industry standards.

6.12 Corporate policies for social responsibility

INDICATOR	REQUIREMENT
6.12.1 Demonstration of company-level[146] policies in line with the requirements under 6.1 to 6.11 above	Yes

Rationale - Companies must be able to demonstrate that not only are the specific farm sites applying for certification able to meet this robust set of social and labour requirements, but that they also have company-wide policies related to these key issue areas that are in line with the ASC Salmon Standard requirements. Such policies must relate to all of the company's salmon operations in the region, whether they be smolt production facilities, grow-out facilities or processing plants.

---

[146] Applies to the headquarters of the company in a region or country where the site applying for certification is located. The policy shall relate to all of the company's operations in the region or country, including grow-out, smolt production and processing facilities.

PRINCIPLE 7: BE A GOOD NEIGHBOUR AND CONSCIENTIOUS CITIZEN

Principle 7 aims to address any broader off-site potential social impacts associated with salmon production, including interactions with local communities.

Criterion 7.1 Community engagement

INDICATOR	REQUIREMENT
7.1.1 Evidence of regular and meaningful[147] consultation and engagement with community representatives and organizations	Yes
7.1.2 Presence and evidence of an effective[148] policy and mechanism for the presentation, treatment and resolution of complaints by community stakeholders and organizations	Yes
7.1.3 Evidence that the farm has posted visible notice[149] at the farm during times of therapeutic treatments and has, as part of consultation with communities under 7.1.1, communicated about potential health risks from treatments	Yes

Rationale - A salmon farm must respond to human concerns that arise in communities located near the farm and to concerns related to the farm's overall operations. In particular, appropriate consultation must be undertaken within local communities so that risks, impacts and potential conflicts are properly identified, avoided, minimised and/or mitigated through open and transparent negotiations. Communities shall have the opportunity to be part of the assessment process (e.g. by including them in the discussion of any social investments and contributions by companies to neighbouring communities).

Channels of communication with community stakeholders are important. Regular consultation with community representatives and a transparent procedure for handling complaints are key components of this communication. Negative impacts may not always be avoidable. However, the process for addressing them must be open, fair and transparent and demonstrate due diligence. A company shall

---

[147] **Regular and meaningful**: Meetings shall be held at least bi-annually with elected representatives of affected communities. The agenda for the meetings should in part be set by the community representatives. Participatory Social Impact Assessment methods may be one option to consider here.

[148] **Effective**: In order to demonstrate that the mechanism is effective, evidence of resolutions of complaints can be given.

[149] Signage shall be visible to mariners and, for example, to fishermen passing by the farm.

share with neighbouring communities' information about any potential human health risks that may be associated with the use of therapeutic treatments and communicate about typical treatment patterns. They shall also post notices around the farm during times of treatment.

Criterion 7.2 Respect for indigenous and aboriginal cultures and traditional territories

INDICATOR		REQUIREMENT
7.2.1	Evidence that indigenous groups were consulted as required by relevant local and/or national laws and regulations	Yes
7.2.2	Evidence that the farm has undertaken proactive consultation with indigenous communities	Yes[150]
7.2.3	Evidence of a protocol agreement, or an active process[151] to establish a protocol agreement, with indigenous communities	Yes

Rationale - Interactions with and evidence of due diligence to prevent and mitigate negative impacts on communities is important globally, and takes on an additional dimension in regions where indigenous or aboriginal people or traditional territories are involved. In some jurisdictions, aboriginal groups have legal rights related to their territories. These shall be respected, as in Principle 1. It is also expected that operations seeking to meet the ASC Salmon Standard have directly consulted with bodies functioning as territorial governments and have come to agreement with indigenous governments, or are working towards an agreement, for farms that are operating in indigenous territories. The requirements are designed to be consistent with the United Nations Declaration on the Rights of Indigenous Peoples.

---

[150] All standards related to indigenous rights only apply where relevant, based on proximity of indigenous territories.

[151] To demonstrate an **active process**, a farm must show ongoing efforts to communicate with indigenous communities, an understanding of key community concerns and responsiveness to key community concerns through adaptive farm management and other actions.

Criterion 7.3 Access to resources

INDICATOR		REQUIREMENT
7.3.1	Changes undertaken restricting access to vital community resources[152] without community approval	None
7.3.2	Evidence of assessments of company's impact on access to resources	Yes

Rationale - Companies should make a maximum effort to not affect the surrounding community's access to vital resources as a result of its presence and activities. Some change in access is expected. What is to be prevented is an unacceptable degree of change.

---

[152] Vital community resources can include freshwater, land or other natural resources that communities rely on for their livelihood. If a farm site were to block, for example, a community's sole access point to a needed freshwater resource, this would be unacceptable under the ASC Salmon Standard.

INDICATORS AND REQUIREMENTS FOR SMOLT PRODUCTION

This section of the document contains the full suite of principles, criteria, indicators and requirements for responsible salmon farming at freshwater smolt sites.

SECTION 8: REQUIREMENTS FOR SUPPLIERS OF SMOLT

A farm seeking certification must have documentation from all of its smolt suppliers to demonstrate compliance with the following requirements.[153] *The requirements are, in general, a subset of the requirements in Principles 1 through 7, focusing on the impacts that are most relevant for smolt facilities. In addition, specific requirements are applied to open systems (net pens), and to closed and semi-closed systems (recirculation and flow-through).*

Requirements related to Principle 1

INDICATOR	REQUIREMENT
8.1 Compliance with local and national regulations on water use and discharge, specifically providing permits related to water quality	Yes
8.2 Compliance with labour laws and regulations	Yes

Rationale - Please see the relevant Rationale in Principle 1. The requirements do not require the smolt producer to provide confidential business documents such as tax documentation.

Requirements related to Principle 2

INDICATOR	REQUIREMENT
8.3 Evidence of an assessment of the farm's potential impacts on biodiversity and nearby ecosystems that contains the same components as the assessment for grow-out facilities under 2.4.1	Yes

---

[153] The SAD SC proposed this approach to addressing environmental and social performance during the smolt phase of production. In the medium term, the SC anticipates a system to audit smolt production facilities on site. In the meantime, farms will need to work with their smolt suppliers to generate the necessary documentation to demonstrate compliance with the standards. The documentation will be reviewed as part of the audit at the grow-out facility.

8.4 Maximum total amount of phosphorus released into the environment per metric tonne (t) of fish produced over a 12-month period (see Appendix VIII-1)	4 kg /t of fish produced over a 12-month period

Rationale - Please see the relevant Rationale in Principle 2. See also the relevant Rationale related to Additional Requirements for both open net-pen smolt production and closed and semi-closed smolt production.

Requirements related to Principle 3

INDICATOR	REQUIREMENT
8.5 If a non-native species is being produced, the species shall have been widely commercially produced in the area prior to the publication[154] of the ASC Salmon Standard	Yes[155]
8.6 Maximum number of escapees[156] in the most recent production cycle	300[157] fish
8.7 Accuracy[158] of the counting technology or counting method used for calculating the number of fish	≥98%

Rationale - Please see the relevant Rationale in Principle 3.

---

[154] **Publication**: Refers to the date when the final standards and accompanying guidelines are completed and made publicly available. This definition of publication applies throughout this document.

[155] Exceptions shall be made for production systems that use 100 percent sterile fish or systems that demonstrate separation from the wild by effective physical barriers that are in place and well-maintained to ensure no escapes of reared specimens or biological material that might survive and subsequently reproduce.

[156] Farms shall report all escapes; the total aggregated number of escapees per production cycle must be less than 300 fish.

[157] A rare exception to this standard may be made for an escape event that is clearly documented as being outside of the farm's control. Only one such exceptional episode is allowed in a 10-year period for the purposes of this standard. The 10-year period starts at the beginning of the production cycle for which the farm is applying for certification. The farmer must demonstrate that there was no reasonable way to predict the events that caused the episode. Extreme weather (e.g. 100-year storms) or accidents caused by farms located near high-traffic waterways are not intended to be covered under this exception.

[158] **Accuracy** shall be determined by the spec sheet for counting machines and through common estimates of error for any hand counts.

Requirements related to Principle 4

INDICATOR	REQUIREMENT
8.8 Evidence of a functioning policy for proper and responsible treatment of non-biological waste from production (e.g. disposal and recycling)	Yes
8.9 Presence of an energy-use assessment verifying the energy consumption at the smolt production facility (see Appendix V subsection 1 for guidance and required components of the records and assessment)	Yes, measured in kilojoule / t fish produced /production cycle
8.10 Records of greenhouse gas (GHG[159]) emissions[160] at the smolt production facility and evidence of an annual GHG assessment (See Appendix V, subsection 1)	Yes

Rationale - Please see the relevant Rationale in Principle 4.

Requirements related to Principle 5

INDICATOR	REQUIREMENT
8.11 Evidence of a fish health management plan, approved by the designated veterinarian, for the identification and monitoring of fish diseases and parasites	Yes
8.12 Percentage of fish that are vaccinated for selected diseases that are known to present a significant	100%

---

[159] For the purposes of this standard, **GHGs** are defined as the six gases listed in the Kyoto Protocol: carbon dioxide (CO_2); methane (CH_4); nitrous oxide (N_2O); hydrofluorocarbons (HFCs); perfluorocarbons (PFCs); and sulphur hexafluoride (SF_6).

[160] GHG emissions must be recorded using recognised methods, standards and records as outlined in Appendix V.

risk in the region and for which an effective vaccine exists[161]	
8.13 Percentage of smolt groups[162] tested for select diseases of regional concern prior to entering the grow-out phase on farm[163]	100%
8.14 Detailed information, provided by the designated veterinarian, of all chemicals and therapeutants used during the smolt production cycle, the amounts used (including grams per ton of fish produced), the dates used, which group of fish were treated and against which diseases, proof of proper dosing and all disease and pathogens detected on the site	Yes
8.15 Allowance for use of therapeutic treatments that include antibiotics or chemicals that are banned[164] in any of the primary salmon producing or importing countries[165]	None
8.16 Number of treatments of antibiotics over the most recent production cycle	≤ 3

---

[161] The farm’s designated veterinarian is responsible for undertaking and providing written documentation of the analysis of the diseases that pose a risk in the region and the vaccines that are effective. The veterinarian shall determine which vaccinations to use and demonstrate to the auditor that this decision is consistent with the analysis.

[162] A **smolt group** is any population that shares disease risk, including environment, husbandry and host factors that might contribute to sharing disease agents for each group. Only diseases that are proven, or suspected, as occurring in seawater (and for which seawater fish-to-fish transmission is a concern) but originating in freshwater should be on the list of diseases tested. The designated veterinarian to the smolt farm is required to evaluate, based on scientific criteria and publicly available information, which diseases should be tested for. This analysis shall include an evaluation of whether clinical disease or a pathogen carrier state in fresh water is deemed to have a negative impact on the grow-out phase, thereby disqualifying a smolt group from being transferred. A written analysis must be available to the certifier on demand.

[163] Suitable measures must be in place to ensure that hatchery-raised seed are free from relevant/important pathogens before stocking for grow-out. This includes addressing on farm disease and parasite transfer (such as the ability to quarantine diseased stocks, separating equipment) as well as between the facility and natural fauna (such as disinfection of effluents for diseased stocks, fallowing). The approach should be relevant to the species, production system, scale of production, and legal requirements. Appropriate procedures or systems should include specific requirements or actions defined by the aquaculture facility through a suitable risk assessment or other evidence such as local or national regulations. Appropriate management measures in these cases could include treatment trigger levels of parasite numbers on the farm-facility or siting requirements that require that the aquaculture facility is located at suitable distances from wild populations. The CAB should verify that the management measures are suitable and employed.

[164] “**Banned**” means proactively prohibited by a government entity because of concerns around the substance.

[165] For purposes of this standard, those countries are Norway, the UK, Canada, Chile, the United States, Japan and France.

8.17 Allowance for use of antibiotics listed as critically important for human medicine by the WHO[166]	None[167]
8.18 Evidence of compliance[168] with the OIE *Aquatic Animal Health Code*[169]	Yes

Rationale - Please see the relevant Rationale in Principle 5.

Requirements related to Principle 6

INDICATOR	REQUIREMENT
8.19 Evidence of company-level policies and procedures in line with the labour standards under 6.1 to 6.11	Yes

Rationale - Please see the relevant Rationale in Principle 6.

Requirements related to Principle 7

INDICATOR	REQUIREMENT
8.20 Evidence of regular consultation and engagement with community representatives and organizations	Yes
8.21 Evidence of a policy for the presentation, treatment and resolution of complaints by community stakeholders and organizations	Yes

---

[166] The fifth edition of the WHO list of "Critically important antimicrobials for human medicine" was released in 2017 and is available at: http://apps.who.int/iris/bitstream/10665/255027/1/9789241512220-eng.pdf?ua=1 .

[167] If the antibiotic treatment is applied to only a portion of the pens on a farm site, fish from pens that did not receive treatment are still eligible for certification.

[168] **Compliance** is defined as farm practices consistent with the intentions of the Code, to be further outlined in auditing guidance. For purposes of this standard, this includes an aggressive response to detection of an exotic OIE-notifiable disease on the farm, which includes depopulating the infected site and implementation of quarantine zones in accordance with guidelines from OIE for the specific pathogen. Exotic signifies not previously found in the area or had been fully eradicated (area declared free of the pathogen).

[169] OIE 2017. Aquatic Animal Health Code. http://www.oie.int/en/international-standard-setting/aquatic-code/access-online/

8.22 Where relevant, evidence that indigenous groups were consulted as required by relevant local and/or national laws and regulations	Yes
8.23 Where relevant, evidence that the farm has undertaken proactive consultation with indigenous communities	Yes

Rationale - Please see the relevant Rationale in Principle 7.

Additional requirements for open (net-pen) production of smolt

In addition to the requirements above, if the smolt is produced in an open system, evidence shall be provided that the following is met:

INDICATOR	REQUIREMENT
8.24 Allowance for stocking smolts produced in cage-culture	Permitted only if supplying farms are 1) operated in a region where indigenous salmonids are present of the same species being cultivated and 2) the farm is certified to the ASC Freshwater trout Standard

Rationale - Due to the broader range of impacts associated with cage-culture smolt production in non-native regions, the ASC Salmon Standard prohibits the use of smolts produced in cage-culture in regions without indigenous salmonid species.

Using smolts produced from cage-culture is only allowed if they are produced in regions where indigenous salmonids are present of the same species being cultivated, and, if the farm is certified to the ASC Freshwater Trout Standard.

Additional requirements for semi-closed and closed production of smolts

Additionally, if the smolt is produced in a closed or semi-closed system (flow through or recirculation) that discharges into freshwater, evidence shall be provided that the following are met:[170]

INDICATOR		REQUIREMENT
8.25	Water quality monitoring matrix completed and submitted to ASC (see Appendix VIII-2)	Yes[171]
8.26	Minimum oxygen saturation in the outflow (methodology in Appendix VIII-2)	60%[172,173]
8.27	Macro-invertebrate surveys downstream from the farm's effluent discharge demonstrate benthic health that is similar or better than surveys upstream from the discharge (methodology in Appendix VIII-3)	Yes
8.28	Evidence of implementation of biosolids (sludge) Best Management Practices (BMPs) (Appendix VIII-4)	Yes

Rationale - Effluent from semi-closed and closed smolt facilities can have an environmental effect on rivers, streams and other bodies of water that receive the discharge. Phosphorus is the key limiting nutrient in most temperate and cool freshwater systems. It is a stable nutrient in that it does not volatilize like nitrogen compounds. It is also added to feeds in proportions that can allow estimations of other waste constituents (organic matter and nitrogen). Thus, phosphorus is an ideal variable to set load limits for freshwater aquaculture. The SAD developed the phosphorus load requirement (8.4) based on a unit of production, making it an indicator of how well a farm is minimising nutrient discharges per ton of fish produced. From an environmental standpoint, farms should aim for as low an annual load of phosphorus per ton of fish as possible. Farms can lower their phosphorus load on the environment by using a better feeding strategy (ratio and feed distribution), improving feed conversion efficiency through the improvement of the environmental conditions in the farm, utilizing feed that is more digestible and has lower phosphorus content, and by employing cleaning technologies such as settling ponds and filters. Smolt production facilities are encouraged to develop methodologies to reduce their phosphorus

---

[170] Production systems that don't discharge into fresh water are exempt from these standards.

[171] See Appendix VI for transparency requirements for 8.25.

[172] A single oxygen reading below 60 per cent would require daily continuous monitoring with an electronic probe and recorder for at least a week demonstrating a minimum 60 per cent saturation at all times.

[173] See Appendix VI for transparency requirements for 8.26.

burdens over time, while ensuring farmed fish are getting the appropriate nutrients to protect the health of the smolt.

In an attempt to limit the oxygen burden on natural water bodies from the release of nutrients, these requirements include a minimum saturation level of dissolved oxygen at discharge. Benthic biodiversity is often a measure of aquatic ecosystem health. These requirements use faunal surveys as a reference for a farm's actual impact on the environment. By comparing surveys downstream and upstream from the farm's effluent discharge, the requirement aims to isolate the impact of the production facility and ensure that no significant impact is occurring.

Biosolids are a mixture of organic waste and sediment produced or accumulated through the farming activity. Biosolids discharged into natural water bodies are of concern because solids can restrict light penetration in water bodies, accumulate downstream, cover plants and habitat, and cause general shallowing of water bodies. Additionally, the organic component of biosolids will exert an oxygen demand as the organic matter decays. The simplest and best way to minimise these impacts is to remove sediments from the water column and allow organic matter to decay prior to discharge. Functionally, this infers the use of settling basins or ponds to let solids settle out of the water column, and for bacterial decomposition and oxygen depletion to occur at the same time prior to disposal of biosolids. To provide assurance of appropriate disposal of biosolids, these requirements include a small number of BMPs. These requirements do not require a specific effluent monitoring regime beyond the dissolved oxygen requirement and benthic analyses. However, the requirements do require farms to submit to the ASC the results of the effluent monitoring they conduct as part of their regulatory requirements. In particular, the requirement requires data on any sampling of phosphorus, nitrogen, total suspended solids (TSS) and biological oxygen demand (BOD). This data will help to distinguish the performance of farms certified by this requirement over time and assist in revisions to the requirement.

Appendix I: Methodologies Related to Principle 2 and Benthic Testing

Subsections

1. Sampling methodology for calculation of faunal index, macrofaunal taxa, sulphide and redox, and copper
2. Calculation methodology for the percent fines in feed
3. Biodiversity-focused impact assessment
4. Methodology for sampling dissolved oxygen
5. Methodology for sampling nitrogen and phosphorous

Appendix I-1. Sampling methodology for calculation of faunal index, macrofaunal taxa, sulphide and redox, and copper[174]

Grab sampling for the faunal index, macrofaunal taxa measurements, and sulphide and redox should be conducted at nine stations in duplicate during peak cage biomass for the production cycle.

1. Two stations should be from the cage edge, one at each end of the long axis of the farm.
2. Three should be from within the Allowable Zone of Effect (AZE), 25 metres from the edge of the array of cages at slack tide measured with a marked line and recorded using GPS. Of these three, one should be upstream and one downstream with respect to the direction of the residual current, and the other should be to one side of the farm in a direction orthogonal to the residual current.
3. Three should be 25 metres outside the AZE, or 55 metres from the edge of the array of cages measured with a marked line and recorded using GPS. Of these, one should be upstream and one downstream with respect to the direction of the residual current, and the other should be to one side of the farm in a direction orthogonal to the residual current.
4. One from a reference site 500-1000 metres from the farm (edge of the array of cages), in similar water depth and substratum type (where this exists), and recorded using GPS.
5. For farm sites using a site-specific AZE, sampling locations shall be determined based on that AZE, at distances consistent from the boundary of the AZE as for other farms (e.g. five metres inside of AZE and 25 metres outside of the AZE, recorded using GPS, and in multiple directions as determined appropriate through the modelling.
6. Values for requirements in Criterion 2.1 must be calculated using the results of samples from the edge of the AZE and the reference point. The CAB shall confirm that the AZE is correct and then to default to the social principles (P6 and P7) to ensure the farm is responding to stakeholder comments with the intention that the AZE is not arbitrary and meets stakeholder expectations.

---

[174] When biomass is estimated at ≥75% until harvest the audit can take place according to this guidance.

For farms using copper-based nets or copper-treated nets, copper sampling shall be conducted at the same locations outside the AZE as the other benthic sampling, at three stations outside the AZE, in duplicate. The reference site used shall also be the same, and two additional reference sites are needed. Timing shall also be the same, sampling at peak cage biomass during the production cycle.

Although the site visit should coincide with harvest period, it may be undertaken before end of harvest (at >75% peak biomass) and estimates of indicators requiring data from peak biomass / end of cycle provided in the draft report. The CAB shall review actual figures before the certification decision is made and include these figures in the final report.

Methodology for auditing indicators relating to peak biomass and end of cycle:

1) CABs shall carry out site visit audit at >75% peak biomass.

2) At the time of the audit the farm shall provide the CAB with estimates of values at that date for indicators that rely on information only available with the farm reaches peak biomass / end of cycle. The Farm shall provide the CAB with values of samples taken at peak biomass and end of cycle when they become available.

3) CAB shall raise a non-conformity for indicators where estimated values are used instead of actual values and note the estimated value in the draft audit report. It shall be explained in the draft audit report where figures are estimated and explain that these are to be updated in the final audit report.

4) CAB shall review the actual values and supporting evidence when they come back at peak biomass / end of cycle in order to make a certification decision.

5) CAB shall not make a certification decision and issue final report until actual values are provided for all indicators except biotic indicators 2.1.2 and 2.1.3.

6) In the case that biotic values are not available at the time of drafting the final report the CAB shall carry out a risk assessment to evaluate whether the biotic values are likely to meet the ASC standard. If the CAB finds evidence that the results of the biotic analyses are likely to meet the ASC standard then certification can be granted.

7) The CAB shall review biotic findings at the surveillance audit and raise non-conformities as appropriate when results have been found not meet the ASC standard.

Appendix I-2. Calculation methodology for the percentage of fines in feed

Introduction

This method determines the fines (dust and small fragments) in finished fish feed product, which has a diameter of 3 mm or more.

The amount of dust and fragments shall be determined when the feed is delivered to the farming site.[175]

Procedure

The test can be performed either by use of a sieving machine or by a manual test.

The sample of feed shall be put through a sieve with a maximum sieve opening of:

1. 1 mm when the particle diameter is equal to 5 mm or less
2. 2.36 mm when the particle diameter is more than 5 mm

Manual test

1. Put the accumulation box and the sieves on top of each other, with the accumulation box on the lowest part, then the smallest sieve and the biggest on top
2. Place the sieves on the balance and tare it
3. Weigh at least 300 g of the feed on the upper sieve, note the weight (**m0**)
4. Put on the lid
5. Sieve the feed smoothly and carefully for about 30 seconds
6. Remove the lid and weigh what is left in the accumulation box
7. Use a brush to remove all the particles from the sieves
8. The feed particles that have passed through all sieves are called dust (**md**)
9. If the feed is fatty, or if dust is unevenly distributed, two replicates must be taken

Sifting machine

1. Put the accumulation box and the sieves on top of each other, with the accumulation box at the bottom and the biggest sieve on top
2. Place the sieves on the balance and tare it
3. Weigh at least 300 g of feed on the upper sieve, note the weight (**m0**)
4. Place the sieves on the sifting machine and then close the cover properly
5. Press the "START" button by holding it for 2-3 seconds, and then run the machine twice (2 x 1 min)

---

[175] Feed can be sampled prior to delivery to farm site for sites where there is no feed storage.

6. Remove the sieves and weigh what is left in the accumulation box
7. The feed particles that have passed through all sieves are called dust (md)

Calculations

1. Weight of feed before sieving = **m0**
2. Weight of feed that has passed through all sieves = **md**

Dust % = (md / m0) x 100

Feed Sampling Protocol

Sampling of feed lots—delivered as material in bulk, big bags or small bags—shall, at a minimum, be sampled as follows:

1. Cut a minimum of six increment samples from the lot, evenly distributed throughout the lot
2. Each increment sample should have a mass of approximately 500 grams
3. Make a pooled sample from all the increment samples and be sure to use all sampled material (i.e., around 6 kg)
4. Reduce the pooled sample to one analysis sample (for testing), each of approximately 500 grams

Appendix I-3. Biodiversity-focused impact assessment

Requirement 2.4.1 requires the farm to demonstrate that a biodiversity-focused environmental impact assessment has been undertaken for the farm.

The assessment shall include habitats and species that could reasonably be impacted by the farm. For example, cold-water corals near the farm could be impacted by nutrients, or whale populations in the region could be impacted by acoustic deterrent devices.

The assessment shall incorporate:

1. Identification of proximity to critical, sensitive or protected habitats and species:
    a. This includes key wild species within the marine environment around the farm
    b. Particular attention to be paid to species listed on International Union for the Conservation of Nature (IUCN) or national threatened/endangered lists and on any areas that have been identified as HCVAs, areas important for conservation/biodiversity or the equivalent
    c. Sensitive species may include non-threatened species of high economic value in the area that may be affected by the salmon farm (e.g. lobsters)
2. Identification and description of the potential impacts the farm might have on biodiversity, with a focus on those habitats or species
3. Description of strategies and current and future program(s) underway on the farm to eliminate or minimise any identified impacts the farm may have, and for the monitoring of outcomes of said programs and strategies
4. Where damage of sensitive habitats has been caused by the farm (as defined in the impact assessment) previously and where restoration is possible and effective; restoration efforts will

or have resulted in a meaningful amount of restored habitat; either through direct on-farm restoration or by an off-farm offsetting approach. Grandfathering of historical losses is allowed.

Appendix I-4. Methodology for sampling dissolved oxygen

Requirements 2.2.1 and 2.2.2 require the sampling of dissolved oxygen on the farm site and the calculation of the percent saturation for those samples.

- DO, salinity and temperature shall be measured twice daily (proposed at 6 am and 3 pm, but with recognition that this will vary depending on region and operational practices). Percent saturation shall be calculated for each sample from the data and a weekly average percent saturation shall result.
    - A minimal amount of missed samples due to extreme weather conditions will be considered acceptable.
    - Sampling once daily shall also be considered acceptable, though not preferred.
- DO shall be measured at a depth of five metres at a location where the conditions of the water will be similar to those the fish experience. For example, measurements can be taken at the edge of the net-pen array, in the downstream direction of the current, or off a feed shed or housing structure on the site. Measurements shall be taken at the same location, recorded with GPS, at the same time to allow for comparison between days.
- Weekly averages shall be calculated and remain at or above 70 per cent saturation.
- Should a farm not meet the minimum 70 per cent weekly average saturation requirement, the farm must demonstrate the consistency of percent saturation with a reference site. The reference site shall be at least 500 metres from the edge of the net pen array, in a location that is understood to follow similar patterns in upwelling to the farm site and is not influenced by nutrient inputs from anthropogenic causes including aquaculture, agricultural runoff or nutrient releases from coastal communities.

Appendix I-5. Methodology for sampling nitrogen and phosphorous

Under requirement 2.2.4, some farms are required to monitor nitrogen and phosphorous levels on the farm and at reference sites. Farms shall monitor total N, NH4, NO3, total P and Ortho-P in the water column. Monitoring of nitrogen and phosphorous shall follow the following methodology or an equivalent:

- This sampling regime should be carried out monthly for the first year to create the baseline against which long term changes can be assessed.
- The N and P sampling shall then be conducted four times a year (quarterly), once during each of the seasons, with three replicate samples at the edge of the AZE and three at the reference site 500m downstream on each occasion.
- Samples should be taken using a VanDorn or Kemmerer type water sampler. 500 ml samples should be placed in clear plastic bottles, placed on ice and in a cooler, and analysed within 48 hours. Ideally, analyses shall be done by a private (third-party) laboratory following standard methods. However, Hach field kits can be used. Clear and detailed records or the sampling

frequency and analytical results must be kept. For best practice, the samples from Hach kits should be sent periodically (e.g. once a quarter and at minimum once a year) to an independent laboratory for analysis to ensure consistency of results and ensure/establish quality control.

Appendix II: Area-Based Management (ABM) Scheme

Subsections

1. Attributes and Required Components of the ABM
2. Setting and Revising ABM Lice Loads and On-farm Lice Levels

Appendix II-1. Attributes and required components of the ABM

Participation in an area-based scheme[176] for managing disease and parasites and resistance to treatments is required under the ASC Salmon Standard. This appendix outlines the main components of the area-based management scheme that the ASC Salmon Standard requires under Criteria 3.1 and 5.4.

The purpose of the area-based management scheme is to improve health and biosecurity management on the farm, with the ultimate goal of minimising potential negative impacts on wild populations.

II-1. A Definition of “area”

If area-based management is already a regulatory requirement of the farm’s jurisdiction, then farms will use this definition of “area” for the purposes of these requirements. In jurisdictions where ABM is not a regulatory requirement, the area covered under the ABM must reflect a logical geographic scope such as a fjord or a collection of fjords that are ecologically connected. The boundaries of an area should be defined, taking into account the zone in which key cumulative impacts on wild populations may occur, water movement and other relevant aspects of ecosystem structure and function.

II-1. B Requirements related to participation in the scheme

Within the defined area, at least 80 per cent of farmed production (by weight) must participate in the area-based management scheme, even if not all farms are seeking certification under this requirement. Without the vast majority of farms participation, the scheme will likely be ineffective. All farms owned by the company applying for certification in the area must participate in the ABM, though not all must be applying for certification.

II-1. C ABM components and guidance

In order to be considered as applicable under the ASC Salmon Standard, the ABM scheme used by a farm must ensure that there is:

1. Clear documentation of the farms/companies included in the ABM, contact people (including contact information) and mechanisms for communication
2. Development and documentation of shared disease management goals and objectives for the ABM. Goals shall include components related to understanding and minimising risk of on-farm disease to wild fish. Objectives shall be updated regularly based on new information, including concerns raised to the farms in the ABM from communities and wild fish interests are part of company engagement with stakeholders as outlined under 7.1.1.

---

[176] For more information on the principles of place-based or area-based management, see Young et al., 2007. Solving the Crisis in Ocean Governance: Place-Based Management of Marine Ecosystems. Environment: Volume 49, Number 4, pages 20–32.

3. Information and data-sharing among farms of any data needed to ensure coordination, including plans for stocking and fallowing; on-farm disease and parasite monitoring results including sea lice numbers; suspicion of an unidentifiable transmissible agent, information on therapeutic treatments; and data on resistance including information related to treatments not being as effective as expected.

The ABM scheme must include coordination among farms as relates to:

1. <u>Application and rotation of treatments:</u>
    a. Farmers must be able to demonstrate a coordinated treatment plan and evidence that the schedule and rotation of treatments are being implemented.
    b. Consideration of the cumulative use, and potential risks[177] of this use, of antibiotics classified as "highly important" by the WHO[178] is a required component of coordination and information-sharing about treatments.
    c. Where applicable, treatments and/or strategic harvesting of salmon is coordinated prior to outmigration of wild salmonids to ensure minimal on-farm lice levels at this sensitive time period for those species (as has been determined under 3.1.5).
    d. Tracking of cumulative use of parasiticides (by chemical, annually and by production cycle) within the ABM.
2. <u>Stocking:</u> Records must demonstrate that all stocked fish within the ABM are of the same year class and that stocking dates were coordinated with other farms.
3. <u>Fallowing:</u> Coordination of fallowing between each production cycle to help break disease cycles, with a clear period of time when there are no farmed salmon in the area in the water.
4. <u>Monitoring schemes</u>:
    a. On-farm disease and pathogen monitoring and information sharing among farms
    b. On-farm resistance monitoring and information sharing among farms
    c. For farms located in areas where there are wild salmonids, monitoring of wild salmonid populations that is relevant for the area must occur as specified under 3.1.6, either under the auspices of the ABM or under some other auspices
5. <u>Setting and revising a maximum ABM lice load</u>:
    a. The entire ABM scheme will set a maximum lice load, expressed as total mature female lice on all farms in the area. In areas of wild salmonids, the ABM scheme must demonstrate how the scheme incorporates the results of wild monitoring into revisions of this total lice load over time (see Section 2 below for additional details on this feedback loop).

Appendix II-2. Setting and revising ABM lice loads and on-farm lice levels

---

[177] Assessment of risk shall take into account the cumulative use of these antibiotics from salmon production within the area in order to assess the potential risk to human health from the development of resistance in the environment. Prescribing antibiotics highly important for human health shall be considered as a last resort.

[178] The fifth edition of the WHO list of "Critically important antimicrobials for human medicine" was released in 2017 and is available at: http://apps.who.int/iris/bitstream/10665/255027/1/9789241512220-eng.pdf?ua=1 .

Requirement 3.1.3 requires that the ABM scheme set a maximum lice load. A core purpose of this requirement is to be able to see the potential cumulative infection pressure from on-farm lice, expressed as the number of mature female lice on all farms in the scheme. This “total load” figure is a better reflection of the potential risks to wild populations than on-farm lice levels, measured as lice per farmed fish.

An ABM scheme shall initially set this total load figure based on the regulatory obligations of the jurisdiction in which it operates and the results of any wild monitoring done to date. In practice, this would mean that farms in most ABM schemes would take the on-farm lice levels they are required to achieve by regulators, and multiply them times the number of farmed fish in the area. This would be a starting place.

For farms located in areas of wild salmonids, the ABM scheme shall demonstrate how the scheme is using the results of wild monitoring to review and potentially revise the maximum lice load for the area each year and/or production cycle. Adjustments to the area’s lice load would lead to corresponding limits on lice levels on individual farms. This feedback loop must be transparent and document how the ABM scheme is being protective of wild fish through the interpretation of wild monitoring data. Given the time lag in collecting and analysing data from wild monitoring, it is expected that the ABM scheme will look at data from previous periods, particularly sensitive periods such as outmigration of wild salmon juveniles.

Requirement 3.1.7 requires farms seeking certification to maintain on-farm lice levels at 0.1 mature female lice (leps) during and immediately prior to sensitive periods, particularly outmigration of wild juvenile salmon. The results of wild monitoring must inform this level over time, with a similar type of feedback loop as described for the ABM total lice level. If wild monitoring reveals that 0.1 mature female lice are not being protective of wild populations, the farm must set a lower level in subsequent sensitive periods. Conversely, data from wild monitoring that consistently demonstrates healthy wild populations would allow a farm to make the case for a level higher than 0.1. This case would need to be made for the ABM as a whole to the Technical Advisory Group of the ASC.

Appendix III: Methodologies and Thresholds Related to Monitoring Wild Salmonids

Appendix III-1. Methodologies for monitoring wild salmonids

The ASC Salmon Standard requires all farms located in areas of wild salmonids to participate in monitoring of sea lice on wild salmonids. The purpose of this monitoring is to assist in clarifying the link between the health of wild and farmed fish through objective information. These requirements do not demand a specific methodology for this monitoring. Nonetheless, the monitoring must comply with the following requirements:

- The methodology, the results and the analysis are made publicly available and demonstrate scientific rigor in the sampling size, location and method.
- Monitoring must be geographically relevant to the area where the farm/ABM is located, so it provides meaningful information for ABM management practices.
- The process must involve third parties beyond the farm, such as independent scientists. Government programs, in which the company may be contributing little or nothing are acceptable, given the programme is geographically relevant.
- Numbers of lice per wild fish, and prevalence of lice are both meaningful metrics that could be considered in the research.
- Species should be chosen based on importance to area (i.e., sea trout vs. salmon vs. arctic char).

Appendix IV: Feed Resource Calculations and Methodologies

Subsections

1. Forage Fish Dependency Ratio calculation
2. Calculation of EPA and DHA in feed
3. Explanation of FishSource scoring

Appendix IV-1. Forage Fish Dependency Ratio calculation

Feed Fish Dependency Ratio (FFDR) is the quantity of wild fish used per quantity of cultured fish produced. It is expected that the CABs raise major NCRs when FFDRs do not meet ASC requirements. This measure can be calculated based on fishmeal (FM) and/or fish oil (FO). In the case of salmon currently, in most cases the FFDR for fish oil will be higher than that for fishmeal. The dependency on wild forage fish resources shall be calculated for both FM and FO using the formulas noted below. This formula calculates the dependency of a single site on wild forage fish resources, independent of any other farm.

$$FFDR_m = \frac{(\text{\% fishmeal in feed from forage fisheries}) \times (\text{eFCR})}{24}$$

$$FFDR_o = \frac{(\text{\% Fish oil in feed from forage fisheries}) \times (\text{eFCR})}{\text{5.0 or 7.0, depending on source of fish}}$$

Where:

1. Economic Feed Conversion Ratio (eFCR) is the quantity of feed used to produce the quantity of fish harvested (net production is the live weight).

$$\text{eFCR} = \frac{\text{Feed, kg or mt}}{\text{Net aquacultural production, kg or mt (wet weight)}}$$

i.

2. The percentage of fishmeal and fish oil excludes fishmeal and fish oil derived from fisheries' by-products.[179] Only fishmeal and fish oil that is derived directly from a pelagic fishery (e.g. anchoveta) or fisheries where the catch is directly reduced (such as krill or blue whiting) is to be included in the calculation of FFDR. Fishmeal and fish oil derived from fisheries' by-products (e.g. trimmings and offal) should not be included because the FFDR is intended to be a calculation of direct dependency on wild fisheries.

---

[179] Trimmings are defined as by-products when fish are processed for human consumption or if whole fish is rejected for use of human consumption because the quality at the time of landing do not meet official regulations with regard to fish suitable for human consumption. Restrictions on what trimmings are allowed for use under the standard are under 4.3.4.

3. The amount of fishmeal in the diet is calculated back to live fish weight by using a yield of 24%.[180] This is an assumed average yield.
4. The amount of fish oil in the diet is calculated back to live fish weight by using an average yield in accordance with this procedure:
    a. Group a - Fish oil originating from Peru and Chile and Gulf of Mexico, five per cent yield of fish oil
    b. Group b - Fish oil originating from the North Atlantic (Denmark, Norway, Iceland and the UK) seven per cent yield of fish oil
    c. If fish oil is used from other areas than mentioned above, they should be classified as belonging to group a if documentation shows a yield less than six per cent, and into group b if documentation shows a yield more than six per cent.
5. FFDR is calculated for the grow-out period in the sea as long as the smolt phase does not go past 200 grams per smolt. If the smolt phase goes past 200g then FFDR is calculated based on all feed used from 200 grams and onwards. If needed, the grow-out site shall collect this data from the smolt supplier.

Appendix IV-2. Calculation of EPA and DHA in feed

In order to demonstrate compliance with the requirement related to the maximum amount EPA and DHA from direct forage fisheries in the feed, the calculations shall be done according to the following formula:

$$\begin{aligned}&\text{Grams of EPA and DHA in feed}\\&=\frac{((\text{grams of fish oil per kg feed})\times(\%\text{ of EPA and DHA in fish oil}))}{100}\text{Grams of EPA and DHA in feed}\\&=\frac{((\text{grams of fish oil per kg feed})\times(\%\text{ of EPA and DHA in fish oil}))}{100}\end{aligned}$$

Where:

1. If the fish oil content varies in different feeds used during the production cycle, a weighted average can be used. The grams of fish oil relate to fish oil originating from forage fisheries for industrial purposes.
2. The content of EPA and DHA of the fish oil shall be calculated using the average figures:
    a. group a - Fish oil originating from Peru and Chile and Gulf of Mexico, 30 per cent EPA and DHA in fish oil

---

[180] Reference for FM and FO yields: Péron, G., et al. 2010. Where do fishmeal and fish oil products come from? An analysis of the conversion ratios in the global fishmeal industry. Marine Policy, doi:10.1016/j.marpol.2010.01.027.

b. group b - Fish oil originating from the North Atlantic (Denmark, Norway, Iceland and UK) 20 per cent EPA and DHA in fish oil

c. If fish oil is used from other areas than mentioned above, they should be classified as belonging to group a if analyses of EPA and DHA is above 25 per cent, and into group b if analyses of EPA and DHA is below 25 per cent.

Analyses of EPA and DHA are the percentage of fatty acids in the oil that are EPA and DHA. In the calculation above, we make the simplification that 100 per cent of the oil consists of fatty acids. EPA and DHA originating from fish oil originating from by-products and trimmings are not included in the calculation above. The feed producer can justify and demonstrate the amount of fish oil coming from trimmings and by-products by using a percentage of fish oil originating from trimmings based on information from purchases in an annual year, either using information related to the current year when the feed is produced or the previous year.

Appendix IV-3. Explanation of FishSource scoring

FishSource scores provide a rough guide to how a fishery stacks up against existing definitions and measures of sustainability. The FishSource scores currently only cover five criteria of sustainability, whereas a full assessment—such as that by the Marine Stewardship Council (MSC)—will typically cover more than 60. As such, the FishSource scores are not a firm guide to how a fishery will perform overall. Nonetheless, the FishSource scores do capture the main outcome-based measures of sustainability.

FishSource scores are based on common measures of sustainability, as used by the International Council for the Exploration of the Seas, the National Marine Fisheries Service and the MSC, among others (e.g. current fishing mortality relative to the fishing mortality target reference point, or current adult fish biomass relative to its maximum sustainable yield (B_{msy})).

Components of the FishSource score

Issue	Measure	Underlying Ratio
Is the management strategy precautionary?	Determine whether harvest rates are reduced at low stock levels	$F_{advised}/F_{target\ reference\ point}$ or $F_{actual}/F_{target\ reference\ point}$
Do managers follow scientific advice?	Determine whether the catch limits set by managers are in line with the advice in the stock assessment	Set TAC / Advised TAC
Do fishers comply?	Determine whether the actual catches are in line with the catch limits set by managers	Actual Catch / Set TAC
Is the fish stock healthy?	Determine if current biomass is at long-term target levels	SSB/B_{40} (or equivalent)
Will the fish stock be healthy in future?	Determine if current fishing mortality is at the long-term target level	$F/F_{target\ reference\ point}$

If existing measures of sustainability consider a fishery to be relatively well-managed, then it will typically score eight or more out of 10 on FishSource. If the fishery is judged to be doing okay, but requires improvement, then it will typically score between six and eight on FishSource. A fishery falling short of minimum requirements of existing measures of sustainability is scored six or below, with the score declining as the condition of the fishery deteriorates.

The key relation between the MSC scoring system and FishSource scores is “80 <-> 8”. For example, a FishSource score of eight or above would mean an unconditioned passing for that particular aspect on the MSC system. Sustainable Fisheries Partnership devised scores in a way that, departing from eight, a score of six relates to a score of 60, and below six, an MSC “below 60”, “no-pass” condition. Please note, however, that the MSC criteria have been interpreted through time with a substantial degree of variability among fisheries.

More information on FishSource is available at www.fishsource.com, and an overview of the FishSource indices is available at http://www.fishsource.org/indices_overview.pdf.

About scoring and availability of product meeting a minimum score

A typical full assessment of a fishery through the MSC will include significantly more areas/criteria assessed than through FishSource, typically including more than 60 sustainability criteria. A fishery is deemed sustainable by the MSC if it scores 60 or more in every performance indicator, and an average of 80 or more at the principle level. The MSC requires certified fisheries to take corrective actions to improve any areas of the fishery that scored between 60 and 80, with the intention of achieving a score of 80 or above in every area of the fishery.

As of May 2011, FishSource released updated information on the ratings of the 25 principal forage fisheries around the Atlantic and South America in their “Reduction Fisheries League Table 2011.” Ten of the 25 fisheries met a minimum FishSource score of six in all categories with a minimum score of eight in the biomass category. These ten fisheries had a total combined 2009 catch of 9157 thousand t, accounting for just over 66 per cent of the total catch of those 25 forage fisheries.

The ratings of fisheries under the FishSource methodology will change over time based on the performance of those fisheries. Farms undergoing certification and feed companies should be attuned to updates of the “Reduction Fisheries League Table” and use the latest version publicly available. Auditing guidelines will be developed around the timing of purchasing of fishmeal and fish oil and the updates of the ratings to ensure reasonable interpretation of the requirement and timing of shifts in purchasing if a fishery’s performance declines to a point where it fails to meet the minimum score needed under the requirement.

Appendix V: Energy Records and Assessment

Subsections

1. Energy use assessment and greenhouse gas (GHG) accounting for farms
2. GHG accounting for feed

Appendix V-1. Energy use assessment and GHG accounting for farms

The ASC encourages companies to integrate energy use assessments and GHG accounting into their policies and procedures across the board in the company. However, this requirement only requires that operational energy use and GHG assessments have been done for the farm sites that are applying for certification.

Assessments shall follow either the GHG Protocol Corporate Standard or ISO 14064-1 (references below). These are the commonly accepted international requirements, and they are largely consistent with one another. Both are also high level enough not to be prescriptive and they allow companies some flexibility in determining the best approach for calculating emissions for their operations.

If a company wants to go beyond the requirement of the ASC Salmon Standard and conduct this assessment for their entire company, then the full protocols are applicable. If the assessment is being done only on sites that are being certified, the farms shall follow the GHG Protocol Corporate Standard and/or ISO 14064-1 requirements pertaining to:

- Accounting principles of relevance, completeness, transparency, consistency and accuracy
- Setting operational boundaries
- Tracking emissions over time
- Reporting GHG emissions

Regarding the operational boundaries, farm sites shall include in the assessment:

- Scope 1 emissions, which are emissions that come directly from a source that is either owned or controlled by the farm/facility.
  - For example, if the farm has a diesel generator, this will generate Scope 1 emissions. So will a farm-owned/-operated truck.
- Scope 2 emissions, which are emissions resulting from the generation of purchased electricity, heating, or cooling.

Quantification of emissions is done by multiplying activity data (e.g. quantity of fuel or kwh consumed) by an emission factor (e.g. CO2/kwh). For non-CO2 gases, you then need to multiply by a Global Warming Potential (GWP) to convert non-CO2 gases into the CO2-equivalent. Neither the GHG Protocol nor the ISO require specific approaches to quantifying emissions, so the ASC Salmon Standard provides the following additional information on the quantification of emissions:

- Farms shall clearly document the emission factors they use and the source of the emission factors. Recommended sources include the Intergovernmental Panel on Climate Change (IPCC) or factors provided by national government agencies such as the United States Environmental Protection Agency (USEPA). Companies shall survey available emission factors and select the one that is most accurate for their situation, and transparently report their selection.

- Farms shall clearly document the GWPs that they use and the source of those GWPs. Recommended sources include the IPCC 2nd Assessment Report, on which the Kyoto Protocol and related policies are based, or more recent Assessment Reports.

References:

- GHG Protocol Corporate Standard Website: http://www.ghgprotocol.org/standards/corporate-standard
- ISO 14064-1 available for download (with fee) at http://www.iso.org/iso/catalogue_detail?csnumber=38381
- Some information on ISO 14064-1 is at http://www.iso.org/iso/pressrelease.htm?refid=Ref994
- IPCC 2nd Assessment Report: http://www.ipcc.ch/pdf/climate-changes-1995/ipcc-2nd-assessment/2nd-assessment-en.pdf
- All IPCC Assessment Reports: http://www.ipcc.ch/publications_and_data/publications_and_data_reports.shtml#1

Appendix V-2. GHG accounting for feed

The requirement requires the calculation of the GHG emissions for the feed used during the prior production cycle at the grow-out site undergoing certification. This calculation requires farms to multiply the GHG emissions per unit of feed, provided to them by the feed manufacturer, by the amount of feed used on the farm during the production cycle.

The feed manufacturer is responsible for calculating GHG emissions per unit feed. GHG emissions from feed can be calculated based on the average raw material composition used to produce the salmon (by weight) and not as documentation linked to each single product used during the production cycle.

The scope of the study to determine GHG emissions should include the growing, harvesting, processing and transportation of raw materials (vegetable and marine raw materials) to the feed mill and processing at feed mill. Vitamins and trace elements can be excluded from the analysis. The method of allocation of GHG emissions linked to by-products must be specified.

The study to determine GHG emissions can follow one of the following methodological approaches:

1. A cradle-to-gate assessment, taking into account upstream inputs and the feed manufacturing process, according to the GHG Product Standard
2. A Life Cycle Analysis following the ISO 14040 and 14044 requirements for life cycle assessments

Should the feed manufacturer choose to do a cradle-to-gate assessment:

1. It shall incorporate the first three phases from the methodology, covering materials acquisition and processing, production, and product distribution and storage (everything upstream and the feed manufacturing process itself).

Should the manufacturer follow the ISO 14040 and 14044 requirements for Life Cycle Assessment:

1. Feed manufacturers may follow either an ISO-compliant life cycle assessment methodology or the GHG Protocol product standard.

Regardless of which methodology is chosen, feed manufacturers shall include in the assessment:

- Scope 1 emissions, which are emissions that come directly from a source that is either owned or controlled by the farm/facility.
- Scope 2 emissions, which are emissions resulting from the generation of purchased electricity, heating or cooling.
- Scope 3 emissions, which are emissions resulting from upstream inputs and other indirect emissions, such as the extraction and production of purchased materials, following the Scope 3 standard.

Quantification of emissions is done by multiplying activity data (e.g. quantity of fuel or kwh consumed) by an emission factor (e.g. CO2/kwh). For non-CO2 gases, you then need to multiply by a Global Warming Potential (GWP) to convert non-CO2 gases into CO2-equivalent. The ASC Salmon Standard provides the following additional information on the quantification of emissions:

- Farms shall clearly document the emission factors they use and the source of the emission factors. Recommended sources include the IPCC or factors provided by national government agencies, such as the USEPA. Companies shall survey available emission factors and select the one that is most accurate for their situation, and transparently report their selection.
- Farms shall clearly document the GWPs that they use and the source of those GWPs. Recommended sources include the IPCC 2nd Assessment Report, on which the Kyoto Protocol and related policies are based, or more recent Assessment Reports.

References:

- GHG Product Standard: http://www.ghgprotocol.org/product-standard
- ISO 14044 available for download (with fee) at: http://www.iso.org/iso/iso_catalogue/catalogue_tc/catalogue_detail.htm?csnumber=38498
- Some information on ISO 14064-1 is at: http://www.iso.org/iso/pressrelease.htm?refid=Ref994
- IPCC 2nd Assessment Report: http://www.ipcc.ch/pdf/climate-changes-1995/ipcc-2nd-assessment/2nd-assessment-en.pdf
- All IPCC Assessment Reports: http://www.ipcc.ch/publications_and_data/publications_and_data_reports.shtml#1

Appendix VI: Transparency of Farm-Level Performance Data

The farm must provide evidence that it has submitted to ASC in the requested format the following information about its environmental and social performance.

Information pertaining to biomass and or stocking from which production volumes, timing and financial information can be extracted or inferred should be considered confidential in order to not put certified companies at a competitive disadvantage. Information related to production volumes or harvest timing may be made public with a time delay (e.g. if released post-harvest and sale).

Item	Option	Relevant Requirement	Measurement	Units	Measurement Frequency	Calculations and Sampling Methodologies, Additional Notes
1			Species in production	species		
2	a	2.1.1	Redox potential	mV	production cycle	Appendix I-1
	b		Sulfide levels	µMol/L	production cycle	Appendix I-1
3	a	2.1.2	AZTI Marine Biotic Index (AMBI)	AMBI score	production cycle	Appendix I-1
	b		Shannon-Wiener Index	S-WI score	production cycle	Appendix I-1
	c		Benthic Quality Index (BQI)	BQI score	production cycle	Appendix I-1
	d		Infaunal Trophic Index (ITI)	ITI score	production cycle	Appendix I-1
4		2.1.3	# of microfaunal taxa	#	production cycle	Appendix I-1
5		2.2.1	Average % DO saturation	%	weekly	Appendix I-4
6		2.2.2	Max % samples under 1.85 mg/L DO	%	weekly	Appendix I-4
7		2.2.4	Nitrogen monitoring	mg N/L	quarterly	Appendix I-5
8		2.2.4	Phosphorous monitoring	mg P/L	quarterly	Appendix I-5
9		2.2.5	Calculated BOD		production cycle	Footnote in 2.2.5
10		2.5.2	# days ADDs/AHDs	#	ongoing[181],	

---

[181] Ongoing: Logged as needed or as occurs. Data shall be logged such that it can be analysed on both an annual and a production cycle basis. This definition of “ongoing” applies throughout Appendix VI.

Item	Option	Relevant Requirement	Measurement	Units	Measurement Frequency	Calculations and Sampling Methodologies, Additional Notes
11		2.5.5 and 2.5.6	Lethal incidents of marine mammals and birds	#, species and cause per episode	ongoing	To be made publicly available (e.g. on web) by farming company shortly after incident
12		3.1.1	Fallowing period	dates		
13		3.1.3	Maximum sea lice load set for the ABM	number	annual	Appendix II and III
14		3.1.4 and 3.1.7	Weekly, on-farm sea lice levels		weekly	To be made directly publicly available by farming company within a week
15		3.1.6	In areas of wild salmonids, monitoring of sea lice on out-migrating salmon juveniles or costal sea trout			Appendix III, to be made publicly available within eight weeks of completion of monitoring
16		3.4.1-3.4.2	Escapes data	# episodes	production cycle	
				date of episode	ongoing	
				cause of episode	ongoing	
				# escapees per episode	ongoing	
				# total escapees	production cycle	
17		3.4.2	Counting technology accuracy	%	production cycle	Footnote 58
		3.4.3	Estimated unexplained loss	#	production cycle	Footnote 59
18		4.2.1	FFDR fishmeal (during grow-out)	FFDRm	production cycle	Appendix IV

Item	Option	Relevant Requirement	Measurement	Units	Measurement Frequency	Calculations and Sampling Methodologies, Additional Notes
19	a	4.2.2	FFDR fish oil (during grow-out)	FFDRo	production cycle	Appendix IV
	b		Max amount EPA and DHA	g/kg feed	production cycle	Appendix IV
20		4.4.3	Transgenic feed ingredients	Y/N	production cycle	
21		4.6.1	Energy use	kJ/t fish	production cycle	Appendix V-1
22		4.6.2	GHG emissions on farm		annual	Appendix V-1
23		4.6.3	GHG emissions of feed		production cycle (not immediately applicable)	Appendix V-2
24		4.7.1	Copper-based antifoulants	Y/N	production cycle	
25		4.7.3 and 4.7.4	Results of copper sampling (outside AZE and at reference sites), if required	mg Cu/kg sediment	production cycle	Appendix I-1
26		5.1.5	Total mortality of farmed fish	%	ongoing	
27		5.1.4	Cause of mortalities (post-mortem analysis)	# mortalities per cause or disease	ongoing	
28		5.1.6	Maximum unexplained mortalities	% of total mortality	production cycle	
29		5.2.1	Amount of each chemical/therapeutant used for each (antibiotics, parasiticides, etc.)	product name	ongoing	Also 5.2.9
				active component name	ongoing	
				reason for use	ongoing	
				date	ongoing	
				kg	ongoing	
				t fish treated	ongoing	
				dosage	ongoing	

Item	Option	Relevant Requirement	Measurement	Units	Measurement Frequency	Calculations and Sampling Methodologies, Additional Notes
				# of treatments	ongoing	
				WHO classification (antibiotics only)	ongoing	
30		5.2.7	Reduction in WNMT	%	per 2 year after first audit after effective date	
			Amount of each parasiticide used	product name	ongoing	
				Active component name	ongoing	
				date	ongoing	
				kg	ongoing	
				t fish treated	ongoing	
				dosage	ongoing	
				Application method	ongoing	
				# of treatments	ongoing	
31		5.2.6	Weighted Number of Medicinal Treatments (WNMT)	No.	WNMT	Appendix VII
32		5.2.10	Results of environmental monitoring of benthic parasiticide levels	Name of active ingredient and/or residue found		Public disclosure of results within 30 days of findings
33		5.4.2	Unidentifiable transmissible agent	Date(s) concern raised; disease detected from monitoring (if applicable)	ongoing	Public disclosure of results of surveillance within 30 days of findings
34		5.4.4	OIE-notifiable disease detected on farm	Disease(s), exotic or endemic, and detection date(s)	ongoing	Public disclosure of detection and results of surveillance

Item	Option	Relevant Requirement	Measurement	Units	Measurement Frequency	Calculations and Sampling Methodologies, Additional Notes
						within 30 days of findings
35		Section 8	Type of smolt production system	Open, semi or closed	production cycle	
36		8.25 and 8.26	Monitoring results from water quality analyses	See Appendix VIII-2		

Appendix VII: Parasiticide Treatment Methodology

Continuous reduction of applying medicinal parasiticide treatments

The ASC Salmon Standard requires farms to continuously reduce the number of medicinal treatments applied in treating sealice, a persistent marine ectoparasite. The ultimate vision is to no longer having to treat sealice with medicinal treatments. However, at the same time it is also recognised that this scenario is not yet achievable for the far majority of the industry at this moment in time.

In order to incentivise the development and implementation of non-medicinal measures (e.g. biological and mechanical control), the relevant indicators under Criteria 5.2 require farms to meet an Entry Level (EL) that expresses the Weighted Number of Medicinal Treatments (WNMT), after which a fixed rate of reduction needs to be achieved until the WNMT meets the defined Global Level (GL).

Parallel to the improvement process as described above, the Standard requires that farms apply Integrated Pest Management (IPM) in order to mitigate in an effective manner.

This Appendix gives more detail on the various concepts referenced above, as well as providing metric levels that relate to the EL, GL and rate of reduction.

Weighted Number of Medicinal Treatments (WNMT)[182]

The Weighted Number of Medicinal Treatment frequency is the total number medicinal parasiticide treatments applied over the production cycle, within the UoC. Partial treatments should be counted as a proportion of the cages treated.

Some examples are given on how to count the WNMT, e.g.

- treating an entire farm (all cages) once, counts as WNMT = 1;
- treating 1 cage, out of 10, once, will count as WNMT = 0.1;
- treating 1 cage, out of 10, twice (i.e. two unique treatments), will count as WNMT = 0.2;
- treating 5 cages, out of 20, once, will count as WNMT = 0.25.

Additional considerations:

1. Hydrogen peroxide (H_2O_2) must be considered as medicinal parasiticide treatment and thus be included in the WNMT-count;
2. If a *single* bath-treatment is prescribed to be applied as “coupled-treatment” (i.e. one treatment at t_1 and a follow-up treatment at t_2), then each treatment (t_1 and t_2) must be included in the WNMT-count.

Some more examples are given on how to count the WNMT, e.g.

- treating 1 cage, out of 10, once with hydrogen peroxide (H_2O_2), will count as WNMT = 0.1;

---

[182] Medicinal parasiticide includes hydrogen peroxide.

- treating 1 cage, out of 10, once with hydrogen peroxide (H_2O_2) as a coupled-treatment, will count as WNMT = 0.2;

Defining Entry Level (EL) and Global Level (GL)

A detailed statistical study was conducted and reviewed by a Technical Working Group in order to understand the regional characteristics of the number of sealice treatments applied per production cycle within the various production regions. The study, including the used data (in Excel) is publicly available on the ASC-website.

In summary, the study used 4 datasets, resulting in N = 896 data points. The data sets covered the following production regions: West Canada (BC), Chile, Faroe Islands, Ireland, Norway and Scotland. Subsequently, the study established distribution curves of the number of medicinal treatments applied per region and one global curve on the basis of N = 896.

On the basis of the 50th percentile for each of the regional curves, regional WNMT-numbers are set that form an Entry Level for farms in that region. Farms must be below, or at, EL for compliance. The results are presented in the table below:

Region	Entry Level (WNMT)	Global Level (WNMT)
Canada (BC)	1	3*
Chile	9	
Faeroes	6	
Ireland	3	
Norway	5	
Scotland	9	

Table: Regional Entry Level and Global Level (both in WNMT)

* GL is set at 3 WNMT, unless twice a "coupled-treatment" is applied (counted as 2*2 = 4 WNMT), then GL = 4 WNMT applies. In case of this exception, additional medicinal treatments applied will result in exceedance of GL=4

In addition to the defined regional Entry Levels, a Global Level (GL) was determined as well. It is required that farms progress from EL to GL according to a fixed timeframe. The GL is based on the 20-25th percentile of the used overall dataset. This resulted into GL = 3 WNMT. However, some bath-treatments are given as "coupled-treatment" (as per above), which with a GL = 3, could result into having a part of the treatment falling beyond GL = 3. In order to reflect the realities of applying these coupled-treatments, an exception is defined in case two times a coupled-treatment is applied. For this specific situation, GL = 4 WNMT applies. Situations that do not meet this exception, shall apply GL = 3 WNMT.

Reducing from EL to GL

It is required for farms to reduce from ≤EL to GL by means of a fixed rate of reduction. This rate is determined at 25% WNMT per 2-year.

Integrated Pest Management (IPM)

Integrated Pest Management (IPM) has long been recognised as being critical to effective and robust sea lice management. IPM is based upon the implementation of a number of proven techniques and approaches developed for pest management in terrestrial agriculture systems, often with the central aim of slowing the development of drug resistance in pest species.

The strategy of IPM generally involves coordinated application and integrated use of all available management practices, with surveillance, communication and cooperation between operators within a defined area. IPM seeks in particular to reduce reliance upon medicinal treatments, thus reducing scope for development of drug resistance and is therefore a process that ASC intends to promote.

The ASC Salmon Standard already contains several aspects of IPM through its current Criteria and Indicators, namely:

- Adherence to relevant thresholds/limits on sea lice levels and required action (Ind. 3.1.4)
- Regular counting and reported of sea lice levels (Ind. 3.1.7)
- Maintenance of treatment records (Appendix VI)
- Single year-class stocking (Ind. 5.4.1)
- Fallowing between cycles (Ind. 3.1.1)
- Health management / veterinary health plan (Ind. 5.1.1)
- Cleaning of nets to increase water flow
- Routine removal of moribund fish (Ind. 5.1.3)
- Monitoring of fish state (*e.g*. behaviour – 5.1.1)
- Monitoring and control of other fish diseases (Ind. 5.1.1)
- Strategic use of medicines *i.e.* the appropriate medicine used for the targeted stage/s of lice (Ind. 5.1.1)
- Medicine rotation, where possible (Crit. 5.3)
- Medicine resistance surveillance (site or area) (Crit. 5.3)
- Monitoring of treatment efficacy (Crit. 5.3)
- Area coordinated planning and management (Ind. 3.1.3)

In addition to the list above, the use of non-medicinal, mechanical and biological controls should be applied in order to reduce sea lice load and risk for resistance built-up. Some examples are given here: https://globalsalmoninitiative.org/en/what-is-the-gsi-working-on/biosecurity/non-medicinal-approaches-to-sea-lice-management/.

As applying these measures depends on various factors – including state of technological development, unintended health side-effects on fish, site-specific situations like strong currents – the standard requires farms to prepare a strategic plan that outlines which non-medicinal measures are (to be) applied at the farms. The plan must be made public and signed-off by an authorized veterinarian. It is required that the plan is reviewed and updated on a production cycle basis to reflect the effectiveness of applied methods and determine next approaches.

Appendix VIII: Methodologies Related to Water Quality and Smolt Systems

Appendix VIII-1. Calculation of Total Phosphorous discharged per tonne of smolt produced

Requirement 8.4 looks at how much phosphorus is discharged from the farm per unit of smolt produced. The requirement is set at 5 kg/t for the first three years from date of publication of the ASC Salmon Standard, dropping to 4 kg/t thereafter. Smolt facilities would calculate their discharge using a “mass balance” approach that calculates the discharge from the phosphorus in the feed and the phosphorus in the fish biomass. Farms would be able to subtract P that is physically removed in sludge (documented sludge removal with P levels tested).

To calculate P released to the environment, one must calculate the P used to produce one unit of fish and subtract the P taken up by the fish and P removed in sludge. The basic formula per time period, to be calculated for a maximum period of 12 months, is:

P released to the water body per unit of smolt produced = (P in – P out)/biomass produced

Where:

> ***P in = Total P in feed***
>
> ***P out= (Total P in biomass produced) + (Total P in sludge removed)***

Where the following definitions of the parameters apply in the basic formula:

1. *Total P in feed*
    a. ∑(Total amount of feed type (product) multiplied by content of phosphorus) $_{1.......X}$), where 1…….X represents the number of different feed types (products) used.
        i. The phosphorus content per feed type can be determined either by chemical analyses of the feed type, or based on declaration by the feed producer of phosphorus content in the feed type in jurisdictions where national legislation order phosphorus content of feed to be declared.
2. *Biomass produced*
    a. Biomass of fish produced over the specific time period is calculated as: (biomass harvested + biomass of mortalities + remaining standing biomass) – biomass at start of time period.
3. *P content in biomass produced*
    a. P content in biomass produced = (biomass produced)*(% of P in fish)
        i. For purposes of calculating this requirement, the following phosphorus percentages will be used for harvested fish or mortalities:
            1. Less than 1 kg: 0.43%
            2. More than 1 kg: 0.4%
4. *Total P in removed sludge*
    a. P content in sludge removed = (sludge removed) * (% of P in sludge)
        i. Phosphorus in sludge removed per unit shall be determined based on analytical values that are representative of the batch of sludge removed from the farm.
        ii. The smolt farm must demonstrate the sludge was physically removed from the farm site and that the sludge was deposed of according to the principles in requirement 8.35.

Appendix VIII-2: Water quality sampling methodology and data sharing for land-based systems

Land-based farms (flow-through and recirculation systems) must measure dissolved oxygen in the effluent. They also must submit to ASC the results from the effluent monitoring they conduct to comply with their local regulatory requirements. In particular, the requirement requires data on any sampling of phosphorus, nitrogen, TSS and BOD. This data will help to distinguish the performance of farms certified by this requirement over time, and assist in revisions to the ASC Salmon Standard.

Oxygen saturation must be measured at least monthly in the early morning and late afternoon. A single oxygen reading below 60 per cent would require daily continuous monitoring with an electronic probe and recorder for at least a week demonstrating a minimum 60 per cent saturation at all times.

Farms shall use the following table to submit the results of effluent monitoring to ASC. Please list each analysis separately over the previous 12-month period.

Date	**Analysis** (*TP, TN, BOD, TSS, etc.*)	**Location** (*Effluent, Inlet, etc.*)	**Method** (*Single grab, 24-hour bulk, etc.*)	**Sampling by Third Party?** (*Yes/No*)	**Analysis by Third Party?** (*Yes/No*)	**Result** (*including units*)

Appendix VIII-3: Sampling methodology for benthic macro-invertebrate surveys

Land-based smolt production systems must conduct sampling of the benthic macro-invertebrate habitats in the receiving body of water downstream and upstream of the effluent discharge point. The requirement requires that the downstream benthic status be similar or better than the upstream benthic status. To demonstrate this, the survey must demonstrate that the downstream location has the same or better benthic health classification as the upstream location.

Below are required components of the sampling methodology and classification scheme that a farm shall use. It is expected that a farm will use the faunal sampling regime in its own jurisdiction, as long as the regime includes the following minimum requirements.

This appendix also includes additional suggested ideas on conducting the surveys. The suggestions are intended as a guide only. The entity conducting the faunal survey should use its own discretion based on local knowledge, national fauna index systems, and expertise as to what specific sub-element or parameter will provide the best representation to document the status of the benthic macro invertebrates and the impact that the fish farm may have on this environment in the receiving water body.

Minimum requirements for faunal surveys:

Classification System

- The benthic health classification system must have at least five categories of benthic status.

Focus of the survey

- The survey must detect the composition, abundance diversity and presence of benthic invertebrate fauna in the receiving water body (upstream and downstream from farm outlet). The survey must focus on key sensitive indicator species for the region.

When and how often

- The samples must be collected once every year upstream and downstream from the farm outlet. In case the downstream survey drops a category according to the faunal index, two consecutive faunal surveys must be conducted during the following 12 months, using the same faunal index system, that demonstrate compliance with the requirement.
- After three years of demonstrating consistent results, a farm may reduce sampling to once every two years.

Where to sample

- The samples must be taken from both midstream and near the bank and must also include marginal areas with slacker water flow.
- All efforts must be made to isolate the impact of the farm, for example by seeking similar conditions, such as type of bottom, water flow and/or substrate types present along the bank, in the upstream and downstream locations.
- The location of sampling sites downstream from the farm must reflect a scientific assessment of the most likely area of potential impact from the farm, with consideration to the mixing of water and the minimum and maximum distance from the farm outlet.

Number of samples

- The survey must collect samples in at least three transects (10 metres apart), with at least four samples in each transect across the river. This must be conducted both upstream and downstream from the farm outlet.

Analysis of the samples and how to samples

- All collected samples must be analysed by an accredited laboratory and the sampling methodology must be approved by the laboratory conducting the analysis.

Further recommendations to sampling:

When and how

When collecting macro-invertebrates, consideration should be given to the seasonality of the presence of the macro-invertebrate species, namely insects in their larval stage of the life cycle. It is generally recommended that samples are conducted during summer and/or winter. In geographical regions like Scandinavia, spring and autumn are recommended as the best times for sampling.

Sampling gear

The sampling should be undertaken using standard equipment such as surber sampler, handnet and grab. More detailed sampling guidelines can also be found in ISO standards ISO 8265, 7828 and 9391.

References:

- Common Implementation Strategy for the Water Framework Directive (2000/60/EC) *Guidance document no. 7.* Monitoring under the Water Framework Directive.
- Biological assessment of running waters in Denmark: introduction to the Danish Stream Fauna Index (DSFI) Skriver et al.; 2000.
- The performance of a new biological water quality score system based on macro-invertebrates over a wide range of unpolluted running-water sites. Amitage, P.D. et al., 1982.
- Common Implementation Strategy for the Water Framework Directive (2000/60/EC) *Guidance document no. 13.* Overall approach to the classification of ecological status and ecological potential.
- UN/ECE Task Force on Monitoring & Assessment under the Convention on the Protection and Use of Transboundary Watercourses and International Lakes (Helsinki, 1992) Volume 3:Biological Assessment Methods for Watercourses.

Appendix VIII-4: Sludge BMPs for closed and semi-closed smolt systems

Methods to mitigate the impacts from fish metabolic wastes on water can range from the employment of simple settling ponds to the use of advanced technology filters and biological process. Dealing responsibly with the waste (sludge, liquid slurry, biosolids) from these processes is a critical element to responsible smolt facility management. The ASC acknowledges that BMPs related to other principles such as correct feed composition and texture as well as good feed management practices—such as not storing feed for too long—can also influence the effectiveness of biosolids capture, however this section deals with practices for cleaning, storage and disposal that will minimise the potential impacts of sludge/biosolids being released into the environment.

All closed and semi-closed smolt systems shall employ/undertake the following in relation to sludge/biosolids:

1. A process flow drawing that tracks/maps the water and waste flow of a farm including treatment of waste, transfer of wastes, waste storage and final waste utilisation options. Flow diagram should demonstrate the farm is dealing with biosolids responsibly.
2. Farm shall have a management plan for sludge/biosolids that details cleaning and maintenance procedures of the water treatment system. The plan must also identify and address the farm's specific risks such as—but not limited to—loss of power, fire and drought. The management can be evaluated in relation to maintenance records.
3. Farm must keep detailed records/log of sludge/bio-solid cleaning and maintenance including how sludge is discarded after being dug out of settlement ponds/basins.
4. Biosolids accumulated in settling ponds/basins shall not be discharged into natural water bodies.

Appendix VIII-5: Assimilative capacity assessment for cage (net-pen) smolt systems

Under 8.26, all open smolt farms in lake or reservoir settings must demonstrate that an assimilative capacity assessment has been conducted to determine if there is sufficient capacity from a water quality perspective to allow for the level of additional loading to the system.

Many suitable models exist that can help determine assimilative capacity, such as Dillon and Rigler (1975), Kirchener and Dillon (1975), Reckhow (1977), and Dillon and Molot (1996). The requirement does not favour one existing model over another but it is important to outline key elements of a credible assimilative capacity study.

At a minimum, the study must do the following:

- Undertake assessment as to allocation of capacity for the whole water body
- Undertake assessment as to land use, slope, sewage, other discharges, stream input
- Account for retention in lake and mixing
- Predict total phosphorus concentration
- Classify trophic status
- Undertake impact assessment of fish farm

The study must pay particular attention to the nature and morphology of the lake basin where the farm will be established. The study must analyse at a minimum:

1. Mixing of the surface and bottom waters
2. Whether bottom waters are isolated within the water body
3. The naturally occurring oxygen levels in the surface and bottom waters
4. Whether the water forms part of an enclosed basin, or an area with isolated bottom waters

Appendix VIII-6: Receiving water monitoring for open (net-pen) smolt systems

Sampling Regime for Receiving Water Quality Monitoring

Location of sampling stations: Stations will be established at the limit of the cage farm management zone on each side of the farm, roughly 50 metres from the edge of the cages and at reference stations located approximately 1-2 kilometres (km). All sampling locations will be identified with GPS coordinates on a schematic outline of the farm operations and on available satellite imagery.

Sampling methods: All water samples testing for total phosphorus shall be taken from a representative composite sample through the water column to a depth of the bottom of the cages. Samples will be submitted to an accredited laboratory for analysis of TP to a method detection limit of $\leq$ 0.002 mg/L. Dissolved oxygen measurements will be taken at 50 centimetres from the bottom sediment.

Frequency: At least once every three months during periods without ice, including at peak biomass.

**NOTE: Some flexibility on the exact location and method of sampling is allowed to avoid farms needing to duplicate similar sampling for their local regulatory regime.

	Boundary Stations (Note: if the farm is attached to land via a walkway, only three stations would be used)				**Reference Stations**	
	North	South	East	West	Upcurrent	Downcurrent
TP (mg/L)	X	X	X	X	X	X
DO profile (mg/L)	X	X	X	X	X	X

Appendix VIII-7: Trophic status classification and determining baseline trophic status

Requirement 8.30 requires a farm to determine a baseline trophic status for the water body and demonstrate through monitoring that the status is maintained. The ASC Salmon Standard use a modified version of the trophic status system developed by the Organization for Economic Cooperation Development (OECD) (Vollenweider and Kerekes, 1982). Trophic status is determined by the concentration of total phosphorus.

Trophic Status	Range of Total Phosphorus Concentration (≤ 20 µg/l)
Ultra-oligotrophic	< 4
Oligotrophic	4-10
Mesotrophic	10-20
Meso-eutrophic	20-35
Eutrophic	35-100
Hyper-eutrophic	> 100

(Note: these ranges are identical to ones described in an Environment Canada report titled “Canadian Guidance Framework for the Management of Phosphorus in Freshwater Systems, Science-based Solutions Report 1-8, February 2004”)

Determining Baseline

Basic approach: Use the concentration in the most pristine area of the water body as possible, i.e., far from point sources of nutrients such as stream inflows, wastewater runoff, the farm or other fish farms. If the regulatory body has determined a historical baseline for the water body, that baseline shall be used.

Received: 15 April 2020 | Accepted: 18 September 2020

DOI: 10.1111/1365-2664.13775

REVIEW

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Collateral diseases: Aquaculture impacts on wildlife infections

Mark M. Bouwmeester[1] | M. Anouk Goedknegt[2] | Robert Poulin[3] |
David W. Thieltges[1]

[1]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, The Netherlands

[2]UMR 5805 EPOC, Station Marine d'Arcachon, CNRS, Université de Bordeaux, Arcachon, France

[3]Department of Zoology, University of Otago, Dunedin, New Zealand

Correspondence
David W. Thieltges
Email: David.Thieltges@nioz.nl

Handling Editor: Nathalie Pettorelli

Abstract

1. Aquaculture is a promising source of fish and other aquatic organisms to ensure human food security but it comes at the price of diverse environmental impacts. Among others, these include diseases which often thrive under the conditions in aquaculture settings and can cause high economic losses. These diseases may also affect wildlife, however, the impacts of aquaculture on disease dynamics in wild species in surrounding ecosystems are poorly understood.
2. In this Review, we provide a conceptual framework for studying the effects of aquaculture on wildlife diseases, and illustrate the different mechanisms identified with examples from the literature. In addition, we highlight further research needs and provide recommendations for management and policy.
3. We identified five potential means by which farmed populations may alter wildlife disease dynamics: (a) farmed species may co-introduce parasites to the new environment, which infect wild conspecifics without infecting other species (intraspecific parasite spillover); (b) these co-introduced parasites from farmed species may infect other wild host species potentially leading to emerging diseases (interspecific parasite spillover); (c) parasites from other wild host species may infect farmed species, amplifying parasite numbers and increasing parasite infections when spilling back to wild hosts (interspecific parasite spillback); (d) farmed species may acquire parasites from wild conspecifics, increasing parasite population size and subsequently raising infection loads in the wild host population (intraspecific parasite spillback); and (e) farmed species may be neither hosts nor parasites, but affect the transmission of parasites between wild host species (transmission interference). Although these mechanisms can alter wildlife disease dynamics, we found large knowledge gaps regarding collateral disease impacts and strong biases in terms of production countries, aquaculture practices and host taxa.
4. *Synthesis and applications*. The strong potential for aquaculture to affect the dynamics of diseases in wildlife populations calls for the consideration of collateral disease impacts in risk assessments and biosecurity protocols regarding aquaculture. In particular, comprehensive parasite inventories of both farmed and wild hosts as well as disease monitoring in wildlife surrounding farms will be necessary to increase our knowledge on aquaculture impacts on wildlife disease and to develop adequate prevention and mitigation measures.

KEYWORDS

aquaculture, biosecurity, disease ecology, environmental impact, risk assessment, wildlife diseases

1 | INTRODUCTION

The per capita consumption of fish and other aquatic animals such as crustaceans and molluscs has considerably increased over the previous decades, reaching a record-high of 20.3 kg per capita per year in 2016 (FAO, 2018). Meeting the global demand for fish and other aquatic food products and ensuring human food security are therefore becoming increasingly challenging (Béné et al., 2015; Jennings et al., 2016). While capture fisheries are unable to keep up with the demand for aquatic food products, aquaculture, i.e. the farming of aquatic organisms, has been responsible for the ever increasing supply for human consumption, with 53 percent of global aquatic food production coming from aquaculture in 2016 (FAO, 2018; Figure 1). Aquaculture is practiced inland, in coastal and in marine environments in a variety of aquaculture systems, ranging from ponds and cages to highly sophisticated water reuse systems (Boyd & McNevin, 2005; Lucas et al., 2019). Like the variety of culture systems, the range of different species produced in these facilities varies extensively. While the bulk of species produced in aquaculture is comprised of fish, many species of other taxa are also farmed, such as crustaceans and molluscs, and their production is increasing as well (Metian et al., 2020).

Although promising from the point of human food security, the rapid growth of aquaculture has also raised concerns about its ecological impacts; ensuring the environmental sustainability of future growth constitutes one of the main challenges for aquaculture (Barrett et al., 2019; Beveridge et al., 1994; Campbell et al., 2019; Costello et al., 2019; Diana, 2009; Hall et al., 2011; Subasinghe et al., 2019; Subasinghe et al., 2009). Among the ecological impacts of aquaculture activities are the widespread use of wild fish as feed for aquaculture stocks (Naylor et al., 2000, 2009; Tacon & Metian, 2009, 2015), the genetic pollution of wild stocks (Cross et al., 2008; Glover et al., 2012; Jørstad et al., 2008; McGinnity et al., 1997), water quality issues such as local eutrophication (Pitta et al., 2009; Price et al., 2015) as well as the introduction of non-native species through escapees from farms or the co-introduction of other species with the translocation of aquaculture stocks (Diana, 2009; Naylor et al., 2001; Peeler et al., 2011; Savini et al., 2010).

Another ecological impact that affects aquaculture itself is related to diseases. The specific nature of aquaculture practices makes farmed aquatic organisms particularly prone to disease outbreaks: (a) the translocation and introduction of aquaculture stocks can lead to the co-introduction of pathogens and parasites (Peeler et al., 2011), (b) the often low genetic diversity of aquaculture stocks can increase the susceptibility of hosts and increase the virulence of pathogens (Kennedy et al., 2016) and (c) stocking densities in aquaculture settings are often much higher than would be found in natural environments which provides excellent conditions for pathogens and parasites to thrive (Krkošek, 2010; Salama & Murray, 2011). Accordingly, disease outbreaks frequently occur in aquaculture settings (Lafferty et al., 2015; Leung & Bates, 2013; Sweet & Bateman, 2015) and there are numerous examples of diseases ravaging farmed salmon (e.g. salmon lice *Lepeophtheirus salmonis* and *Caligus elongatus* (Revie et al., 2002), infectious salmon anaemia (Mullins et al., 1998) and infectious haematopoietic necrosis (Saksida, 2006)), shrimp (e.g. white spot syndrome (Chou et al., 1995) and acute hepatopancreatic necrosis disease (Soto-Rodriguez et al., 2015)) and other cultured organisms (Lafferty et al., 2015). The economic losses associated with such disease outbreaks in aquaculture, including the costs of disease control measures, are enormous. For example, sea lice infections of salmon in Norway generate economic costs equivalent to 9% of farm revenues and have led to damages estimated at >US$ 400 million in 2011 alone (Abolofia et al., 2017). On a global scale, economic losses in aquaculture due to diseases are estimated to amount to at least several billion US$ per year (World Bank, 2014). Due to these considerable economic risks, disease outbreaks represent one of the main obstacles for the sustainable growth of aquaculture (Stentiford et al., 2012; Subasinghe et al., 2019) and the problem has been termed the 'global aquaculture disease crisis' (Stentiford et al., 2017).

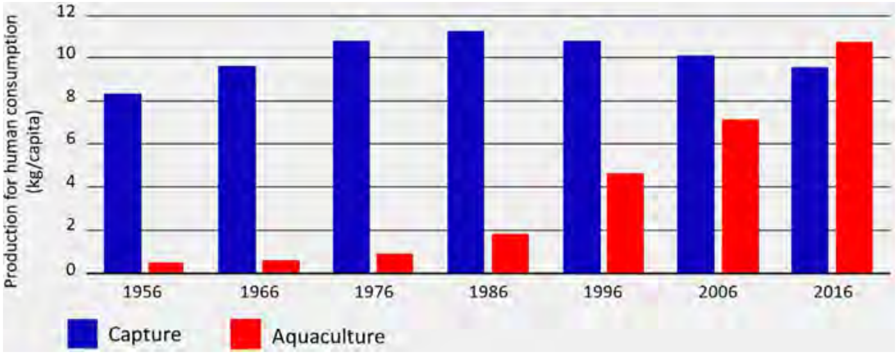


FIGURE 1 Origin of aquatic food production for human consumption over the past five decades, showing the increasing share of aquatic food products originating from aquaculture and capture of wild fish (for commercial, industrial, recreational and subsistence purposes). Data retrieved from FAO (2018)

Given the tremendous economic risks associated with disease outbreaks in farms, it comes as no surprise that diseases in aquaculture have been extensively studied, in particular with respect to the identification and treatment of responsible agents and the prevention of disease outbreaks based on risk assessments and biosecurity protocols (Hine et al., 2012; Subasinghe et al., 2019). However, diseases in aquaculture settings are not necessarily confined to farms themselves but can affect and interact with wild hosts in the vicinity of farms as well, with aquaculture held responsible for several reported cases of wildlife diseases (Diana, 2009; Lafferty et al., 2015). For example, salmon lice originating from farmed salmon in North America have been shown to infect wild juvenile pink salmon *Oncorhynchus gorbuscha* when passing salmon farms during their migration, leading to strong population declines and local risk of extinction of the wild host species (Krkošek et al., 2007). However, studies into the effects of aquaculture on wildlife disease ecology have been few, and the diversity and magnitude of impacts of aquaculture activities on disease dynamics in wild hosts in surrounding ecosystems are generally poorly understood.

This review examines the possible effects of aquaculture on wildlife disease dynamics and provides a conceptual framework for studying the effects of aquaculture on parasite–host interactions, borrowing from mechanisms and conceptual frameworks developed for biological invasions (e.g. Dunn & Hatcher, 2015; Goedknegt et al., 2016; Kelly et al., 2009; Young et al., 2016). As discussed above, aquaculture introduces host or parasite species to environments where they had been absent before. Therefore, many of the mechanisms of parasite and disease exchange between farmed and wild hosts may be similar to interactions between introduced and native hosts and parasites. In the following, we first review the most common methods used in aquaculture to pinpoint possible means of parasite exchange between farmed organisms and wildlife. We then identify the various ways in which these exchanges can affect parasite–host interactions, and illustrate the different mechanisms with examples from the literature. Finally, we highlight further research needs and recommendations for management and policy.

2 | THE MANY FORMS OF AQUACULTURE

Aquaculture is practised in many different ways. Species are cultured in freshwater, brackish and marine environments, with the majority of production coming from inland freshwater facilities (FAO, 2018). According to FAO (2018), based on known and documented practices, there are 598 different species of organisms used in aquaculture, and these include 369 fishes, 109 molluscs, 64 crustaceans, nine other invertebrates, seven amphibians and 40 algae (FAO, 2018). A variety of distinct methods are used for cultivating such a wide range of species. In the following, we describe some of the most commonly used methods, and identify the possible routes of parasite exchange with the environment surrounding the facilities.

2.1 | Ponds

Ponds are the most commonly used system for fish and crustacean aquaculture, with an estimated 11×10^6 ha of global aquaculture pond surface area (Verdegem & Bosma, 2009). Ponds can be constructed in several ways. Watershed ponds are created by building a dam to confine runoff, either from overland flow of rainfall or from an existing stream (Boyd & McNevin, 2005). Ponds may also be excavated or constructed by building an earthen embankment, a so called embankment pond, which is the main type of system used in shrimp farming (Boyd & Clay, 1998; Boyd & McNevin, 2005; Figure 2a). These types of ponds usually require a water supply from an external source such as a stream, well or irrigation system (Boyd & McNevin, 2005). This external water supply offers a potential vector by which parasites from the wild are able to enter the pond system. Additionally, ponds are usually equipped with drainage structures to discharge excess water or to drain them entirely, which is common practice during harvest (Boyd & McNevin, 2005; Verdegem & Bosma, 2009). When inadequate action is taken to disinfect this effluent, drainage of culture ponds has the potential to release parasites of cultured species in the environment, thus offering a mechanism for parasite exchange from farmed to wild organisms (Kurath & Winton, 2011).

2.2 | Cages and net pens

Another frequently used aquaculture system is the use of enclosures situated in natural bodies of water, usually cages or net pens (Figure 2b). These enclosures can be as small as 1 m^3 or as large as 1,000 m^3 and are stocked with fish densities ranging from <20 to over 200 kg/m^3 (Schmittou, 1993). Atlantic salmon *Salmo salar*, the most common marine aquaculture species, are usually grown out in enclosures at sea, but the method can also be applied to other species such as marine shrimps (FAO, 2018; Paquotte et al., 1998). Because cages and net pens are placed directly in the natural environment and allow for free water exchange with the surrounding environment, the chance of parasite exchange between wild and farmed fish stocks is particularly high for these types of systems (Johansen et al., 2011). Furthermore, the likelihood of fish escaping from net pens is high, and escapes are known to occur on a regular basis (Diana, 2009; Johansen et al., 2011). In addition, cages and net pens attract aggregations of wild fish seeking food or shelter, further increasing the risk of parasite exchange between farmed and wild fish and between neighbouring farms (Dempster et al., 2009; Johansen et al., 2011).

2.3 | Flow through raceways

A system often used for farming rainbow trout is a raceway supplied with water originating from a natural water source such as a

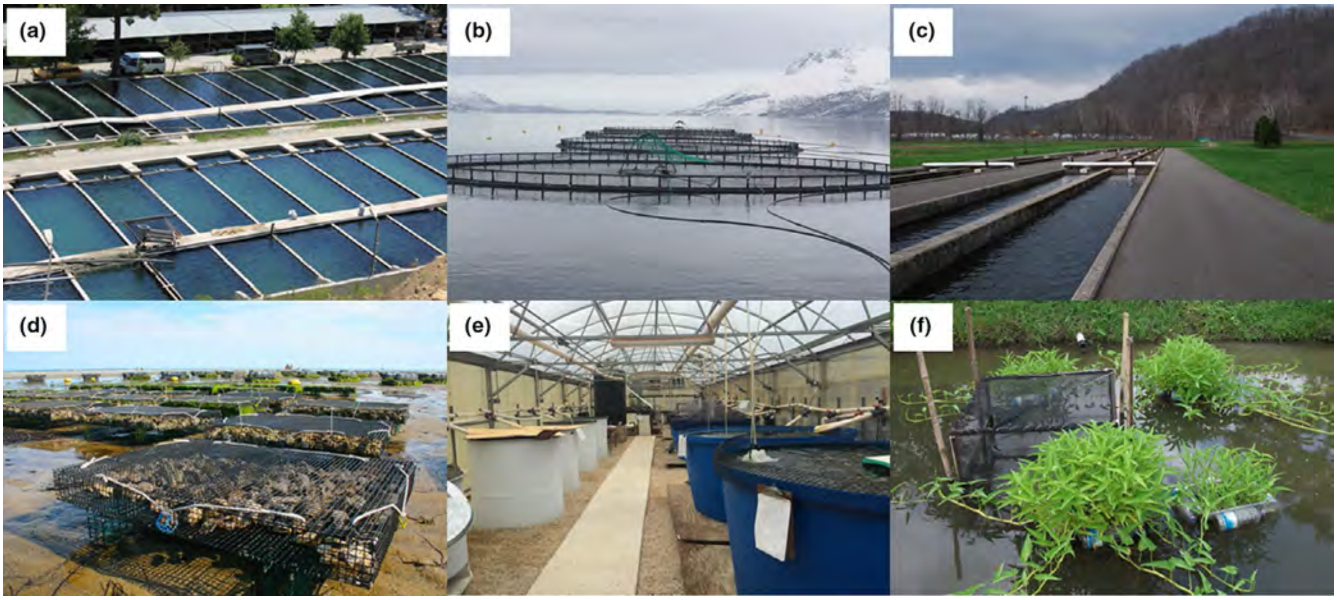


FIGURE 2 Examples of the various methods used for aquaculture: (a) fish farming in ponds, (b) marine cage aquaculture facility, (c) freshwater flow-through raceway system, (d) off-bottom oyster cages, (e) indoor recirculating aquaculture system (RAS), and (f) small scale integrated multi-trophic aquaculture (IMTA) system in a freshwater pond. Photo credits: (a) Vera Kratochvil, Wikimedia Commons, Public Domain, (b) Thomas Bjørkan, Wikimedia Commons, CC BY-SA 3.0, (c) Brian M. Powell, Wikimedia Commons, CC BY-SA 3.0, (d) Pixabay, Public Domain, (e) Narek Avetisyan, Wikimedia Commons, CC BY-SA 4.0, (f) Saifullahrony, Wikimedia Commons, CC BY-SA 3.0 [Colour figure can be viewed at wileyonlinelibrary.com]

spring, stream or lake (Boyd & McNevin, 2005). They are usually made of concrete and positioned in series, in which the water from the upper units flows into the units below (Figure 2c). Water exchange occurs via gravity flow at a rate of approximately two or three times the volume of a culture unit per hour and from the lowermost unit it is discharged into a natural body of water (Boyd & McNevin, 2005). These raceways generally harbour higher stock densities than ponds, ranging from 80 to 160 kg/m^3 for rainbow trout (Soderberg, 1994). High stocking densities along with the release of effluent into natural waterbodies provide risks of parasite exchange with wild populations, and could be cause for concern.

2.4 | Mollusc and seaweed culture

Bivalve molluscs and seaweeds are generally produced in coastal waters, although there are a few species which are cultured in ponds. Bivalves and seaweed are either grown out on the bottom (on-bottom culture), or by so called off-bottom culture in which spat or seaweed propagules are fixed to longlines, rafts or racks for grow-out (Boyd & McNevin, 2005; Figure 2d). The latter method is deemed more efficient as it eliminates the limiting effects of benthic predators and impaired sediment quality while permitting three-dimensional use of the water column (Boyd & McNevin, 2005). Because culture occurs directly in natural coastal waters, parasites can be exchanged between farmed and wild populations, seemingly without any restriction.

2.5 | Recirculating aquaculture systems

Recirculating aquaculture systems (RAS) are closed culture systems in which waste water is treated and subsequently re-used to allow for a more efficient use of water and a greater fish production per volume of water (Figure 2e). Waste water from culture units usually passes into a sedimentation basin, where coarse solid waste is removed. Subsequently the water is purified naturally or through technologically more complex purification systems (Boyd & McNevin, 2005). As a result, waste water volume released into the environment is greatly reduced (Boyd & McNevin, 2005; Edwards, 2015), lowering the chances of parasites from culture organisms being released into the wild.

2.6 | Integrated multi-trophic aquaculture

In some cases, extractive species such as bivalve molluscs or seaweeds are used as a means of removing excess nutrients and other waste, both in closed RAS and open systems such as cages or net pens (Figure 2f). These extractive species are then harvested as well. This use of multiple species of different trophic levels in a single culture system is known as integrated multi-trophic aquaculture (IMTA). Although this relatively new approach has been the subject of ongoing research and many of these are positive about its potential, there is some debate regarding the efficiency of bivalves in capturing organic wastes from fish cultures, especially in open systems (Edwards, 2015). In IMTA systems, extractive species have the potential to change parasite–host interactions, as they have been shown to be capable of reducing free-living parasite stages in the water, so called transmission interference (Burge, Closek, et al., 2016; Molloy et al., 2011). However, the addition of more species to a farm could also lead to the introduction of additional parasites along with these extractive species, with the potential to infect native hosts. In addition, there is a possibility for amplification of already pre-existing parasite populations (Burge, Closek, et al., 2016; Kelly et al., 2009).

3 | AQUACULTURE IMPACTS ON WILDLIFE DISEASES

Considering the aforementioned possibilities of parasite exchange between aquaculture farms and surrounding wildlife, and the numerous examples of cultured species escaping and becoming invasive, aquaculture has the potential to alter parasite–host interactions and diseases in wildlife inhabiting the environment surrounding farms. In the following, we identify the different mechanisms by which aquaculture affects wildlife parasite–host interactions and diseases and provide examples of their occurrence from the literature. By doing so, we provide a conceptual framework for studying the effects of aquaculture on wildlife diseases (Figure 3). The mechanisms presented are not mutually exclusive, it is possible that several or even all of the different mechanisms occur in a specific aquaculture setting. For our review, we extensively searched the literature for studies on aquaculture disease impacts on wildlife using Web of Science and Google Scholar, as well as by scanning existing reviews and books on aquatic diseases and aquaculture. Although we did not conduct a formal meta-analysis, we believe that we have found the majority of existing studies and we thus consider our overview of examples to be reasonably representative.

3.1 | Interspecific parasite spillover

Whenever a species is taken from its environment and transported to a new one, there is a possibility of transporting parasites along with them. In invasion ecology, the process of introducing a parasite along with its host is known as parasite co-introduction (Goedknegt et al., 2016; Lymbery et al., 2014). This principle can be applied to aquaculture as well. When a parasite is co-introduced with a host species to an environment which is inhabited by other naive potential host species, there is a possibility of the parasite switching hosts. The switch from the original host to naive wild host species is known in invasion ecology as parasite spillover (Kelly et al., 2009). When aquaculture species are farmed in systems that allow for water exchange with the environment, interspecific spillover events to wild species are known to occur (Peeler et al., 2011). A similar phenomenon can be observed in domestic animals when parasites spill over from domestic animals to wildlife populations living in proximity (Daszak et al., 2000). There are numerous examples of diseases from aquaculture farms affecting

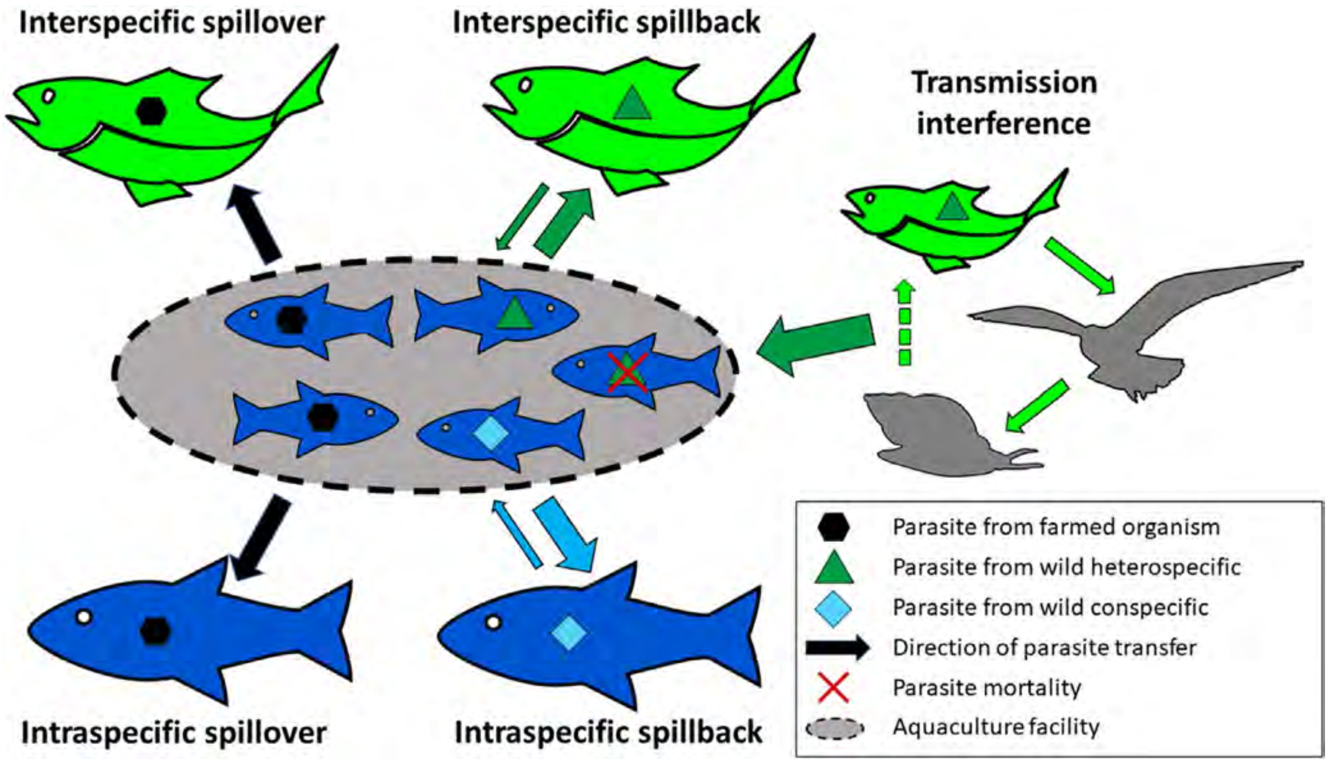


FIGURE 3 Conceptual framework showing the five different mechanisms through which aquaculture activities can affect diseases in wildlife in the environment surrounding aquaculture facilities. See main text for further details and examples of each of these mechanisms [Colour figure can be viewed at wileyonlinelibrary.com]

wild populations. Out of 35 interspecific spillover events of invasive parasites to native species in marine ecosystems listed in a review by Goedknegt et al. (2016), aquaculture was named as the most likely vector for 20, and five more were caused by stocking for fisheries. One example of such an interspecific spillover event involves the parasitic copepod *Mytilicola orientalis*, co-introduced to Europe with the Pacific oyster *Crassostrea gigas* imported for aquaculture. This parasite has been found in wild populations of several native bivalve species such as blue mussels *Mytilus edulis*, common cockles *Cerastoderma edule* and Baltic tellins *Macoma balthica*, indicating an interspecific spillover effect (Goedknegt et al., 2017). Another example involves infectious hypodermal and haematopoietic necrosis virus (IHHNV) in penaeid shrimps in the Gulf of California. This disease probably did not occur in wild shrimp populations in this region prior to 1987, but has become established in wild populations of Pacific blue shrimp *Penaeus stylirostris* and possibly other native shrimp species, following importation of *Penaeus vannamei* postlarvae to local shrimp farms (Pantoja et al., 1999).

Although many of the aforementioned interspecific spillover events of aquaculture parasites are the result of escaping culture species or close contact between farmed and wild populations in open farm systems, direct contact between species might not always be necessary for parasite spillover to occur. The parasitic swimbladder nematode *Anguillicoloides crassus* which affects eels (*Anguilla* spp.) was co-introduced in Europe with Japanese eel *Anguilla japonica* in the 1980s and spilled over to native European eel *Anguilla anguilla*, spreading rapidly across the continent (Kennedy & Fitch, 1990; Kirk, 2003; Koops & Hartmann, 1989). The spread of *A. crassus* was mainly due to the transport of live eels, which may have escaped (Kennedy & Fitch, 1990; Koops & Hartmann, 1989). However, infective stages of this parasite are capable of surviving and remaining infective for up to 2 weeks in the water column and introductions in Britain occurred mainly along the routes of lorries transporting eels, which exchange water several times during transport (Kennedy & Fitch, 1990). Therefore it is possible that at certain locations *A. crassus* interspecific spillover into European eels occurred via infective stages that were flushed out with waste water (infecting freshwater copepod intermediate hosts), rather than direct contact between eels (Kennedy & Fitch, 1990; Kirk, 2003; Peeler et al., 2011). Furthermore, *Anguilla japonica* has also been responsible for the interspecific spillover of two monogeneans *Pseudodactylogyrus anguillae* and *P. bini* to European eel *Anguilla anguilla* and American eel *Anguilla rostrata* in Europe and the US, respectively (Hayward et al., 2001; Morozińska-Gogol, 2009).

Diseases that occur in a novel species after an interspecific spillover event are known as emerging diseases, and can have devastating consequences (Daszak et al., 2000). Due to the fact that naive hosts do not have a co-evolutionary history with the novel parasite, they can be particularly vulnerable, leading to negative effects on the new host species, communities and even entire ecosystems (Goedknegt et al., 2016). This can be especially dangerous if the parasite does not cause high mortality rates in its original host, but does so in the novel host, while the original host remains present as a reservoir of the disease. For instance, the crayfish plague, a fungal disease caused by *Aphanomyces astaci*, spilled over from American signal crayfish *Pacifastacus leniusculus* to European crayfish *Astacus astacus*. While *P. leniusculus* rarely succumbs to the disease, it causes extremely high mortality rates in *A. astacus*, threatening the latter species with extinction (Alderman, 1996; Peeler et al., 2011).

3.2 | Intraspecific parasite spillover

Many cultured species are not bred in captivity, but larvae or juveniles are caught from the wild and transported to aquaculture facilities for grow-out (Boyd & McNevin, 2005). If these juveniles are infected, parasites are co-introduced to the farm environment, potentially leading to disease outbreaks within the farmed stock. In invasions, co-introduced parasites do not always lead to infections in wild native hosts by switching hosts, but affect only the invader (Goedknegt et al., 2016). In the same way, outbreaks of co-introduced parasites in aquaculture species do not have to lead to interspecific spillover in other wild species. However, a co-introduced parasite is likely to spread to neighbouring wild populations of the same species, as it does not need to cross the species barrier. For example, ostreid herpesvirus OsHV-1 μVar has recently been co-introduced to European oyster aquaculture with imports of Pacific oysters *C. gigas* from East-Asia, causing up to 90% mortality in farmed oyster, but has so far only affected this species in Europe (Goedknegt et al., 2016; Mineur et al., 2015). However, this virus has been found in wild (invasive) populations of *C. gigas* in the Dutch Wadden Sea (Gittenberger et al., 2016), although mortalities in wild populations are unknown. Similarly, intraspecific spillover was the source of bonamiasis outbreaks in European flat oysters *Ostrea edule*, caused by the parasitic protozoan *Bonamia ostreae*. The parasite is invasive and reached Europe via oyster transports from Europe to North America and back to France, bringing the parasite with them and spilling over to wild oyster populations (Chew, 1990; Engelsma et al., 2014). Intraspecific parasite spillover has also been observed in fish aquaculture. The monogenean parasite *Gyrodactylus salaris* which infects Atlantic salmon *S. salar* has been introduced to Norwegian waters with translocated salmon from hatcheries in the Baltic Sea, where salmon populations are tolerant or resistant to infections. In contrast, Norwegian salmon populations proved to be highly susceptible to the parasite and high mortalities in wild salmon populations have occurred (Bakke et al., 2007; Johansen et al., 2011; Johnsen & Jensen, 1992). This example shows that intraspecific spillover events can have important ecological implications as they can have an intense regulatory effect on the population dynamics of affected wild populations, which in turn may alter competitive interactions between affected hosts and other wild species (Goedknegt et al., 2016).

3.3 | Interspecific parasite spillback

In addition to wild species acquiring parasites from cultured species, parasites from wild species in the proximity of aquaculture farms may also spillover into cultured species, a phenomenon similar to the 'reverse spill-over' of parasites from wild populations to susceptible domesticated animals (Daszak et al., 2000). When aquaculture species are competent hosts for wild parasites, they could amplify parasite populations, which can subsequently spill back into wild hosts, increasing the number of parasite infections in wild host species (Goedknegt et al., 2016; Kelly et al., 2009; Leung & Bates, 2013). This is because the high stocking densities used in aquaculture can increase local host densities and thus boost parasite propagule production, which in turn can increase the risk for wild hosts to become infected. For example, the shell boring polychaete *Polydora ciliata* which infects the shells of wild molluscs in European seas has been acquired by the Pacific oyster *C. gigas* which is cultured in oyster farms and has also spread outside farms. In the wild, the parasite is more prevalent in Pacific oysters than in blue mussels *M. edulis* (Goedknegt et al., 2019), potentially leading to an interspecific spillback effect for wild mussels (Goedknegt et al., 2019). Another example comes from Atlantic salmon *S. salar* which is cultured along the Chilean Pacific coast and has become infected with copepods *Caligus rogercresseyi* and nematodes *Hysterothylacium aduncum* originating from a wide range of wild host species (Sepúlveda et al., 2004). Due to the high infection levels, it is likely that these parasites spill back to wild hosts, leading to increased infection levels in wild host populations. Likewise, American brine shrimp *Artemia franciscana* have been commercially imported from North America to the southern Iberian Peninsula where they escaped aquaculture farms and entered habitats with wild native *Artemia* populations (Green et al., 2005). Here, the invasive brine shrimp became infected with a variety of native cestodes that cause high infection prevalences in wild brine shrimp (*A. parthenogenetica* and *A. salina*; Georgiev et al., 2007). These examples indicate that interspecific parasite spillback can have large consequences for wild species and that the effects may not only originate from the aquaculture farms themselves but also from populations that escaped from these facilities.

3.4 | Intraspecific parasite spillback

Aquaculture species are not always newly introduced to an area, wild species are also commonly farmed locally. This leads to unnaturally high local densities of wild species within, for example, cages or net pens, while wild conspecifics live at much lower densities in the surrounding waters. This is for instance the case in the farming of salmon species, where the species farmed also naturally occur in the wild. Many disease outbreaks in salmon farms may have been acquired through exchanges with wild salmon populations, although it is often not clear whether disease originated from farmed or wild stocks. However, when a parasite is transferred from wild to farmed salmon stock it could be amplified during an outbreak in the farm, due to the high stocking densities, and subsequently spill back high numbers of infective stages to the wild population, similar to the interspecific spillback previously described, except without the need for a shift in host species. Such intraspecific spillback events are known for salmon lice *L. salmonis* and sea lice *Caligus* spp., which are naturally occurring parasites of salmonids. They can be exchanged between wild salmonids, such as the pink salmon *Oncorhynchus gorbuscha*, and farmed conspecifics along the Pacific coast of North America. Juvenile pink salmon in close proximity to salmon farms have been shown to have high rates of lice infestation, higher than those in areas without salmon aquaculture, leading to high juvenile mortality (Krkošek et al., 2007). Similar effects occur in salmon lice in farmed Atlantic salmon *S. salar* in Europe where these parasites are naturally present in wild Atlantic salmon populations. They are known to cause massive outbreaks in salmon farms and there is evidence that they subsequently cause elevated infection levels in wild salmon populations (Costello, 2009; Thorstad & Finstad, 2018; Torrissen et al., 2013). Likewise, intraspecific spillover may also affect the oyster *Ostrea chilensis*, native to New Zealand, which is cultured in Foveaux Strait between the South Island and Stewart Island in New Zealand, where wild populations also exist. Cultured oysters have experienced epizootics of the parasite *Bonamia exitiosa*, which have been catastrophic for the industry and will most likely have affected wild populations as well (Cranfield et al., 2005). Although the evidence for intraspecific spillover events is limited, spillback effects from farmed to wild conspecifics are very likely as there is no threshold for host switching that needs to be overcome, and this may be a highly underestimated effect of aquaculture on parasite–host dynamics in wildlife. Like interspecific parasite spillback between different species, intraspecific parasite spillback has the potential to induce high mortalities in wild populations, and in doing so, negatively affect wild ecosystem functioning.

3.5 | Transmission interference

One subtle effect of cultivated species on wild parasite–host interactions does not involve acting as a host or a parasite. Instead they might disturb wild parasite transmission from one host to the next, so called transmission interference (Burge, Closek, et al., 2016; Goedknegt et al., 2016; Thieltges et al., 2009). In general, many farmed and wild species that do not act as a host for a particular parasite can be so called dead-end hosts, predate on infective stages or interfere in other ways (see review by Thieltges et al., 2008). An aquaculture species which has been shown to interfere with the transmission of wild parasites is the Pacific oyster *C. gigas*, which can remove the free-living infective larval stages of wild trematode parasites affecting blue mussels *M. edulis* by filter feeding, without being infected itself (Goedknegt et al., 2015; Thieltges et al., 2009; Welsh et al., 2014). Pacific oysters are also extensively cultured in open systems in coastal waters. It is possible that oysters in farm cultures filter infective larval stages of parasites in the same way their escaped counterparts have been shown to do. This could lead to lower infection levels in wild blue mussels in close vicinity of the farm. The extent to which filter feeding organisms can remove infective stages of parasites depends on a number of factors such as the prey size range of the filter-feeder, the transmission mode and host specificity of a particular parasite (Burge, Closek, et al., 2016). Whether such transmission interference by aquaculture farms truly occurs remains unknown, as it is yet to be studied. If it is the case, it could lead to substantial increases in the wild host population, especially if a heavy parasite burden is lifted due to the interference. This way, transmission interference has the potential to change the local communities surrounding the aquaculture facility and affect both the farm and wild ecosystem. In a similar way, certain aquaculture practises themselves, such as parasite control treatments or effluents dispersing from farms into ecosystems, may affect parasite transmission in wild hosts. However, such indirect effects of parasite control treatments on wildlife diseases are beyond this review.

4 | COLLATERAL DISEASE RISK, RESEARCH NEEDS AND RECOMMENDATIONS FOR MANAGEMENT AND POLICY

The chances of the above mechanisms occurring in a specific aquaculture facility and causing collateral disease risk for wildlife depend on the interactions between farmed and wild populations. In closed systems, where effluent water is kept to a minimum, parasite exchange between farm and wild populations is unlikely to play a major role. In pond systems, interactions are more likely, as pond water is often released in the environment during harvest or heavy rainfall. Aquaculture systems that are partially or entirely open such as raceways, cages, net pens and coastal mollusc cultures pose the highest risk for parasite exchange between farmed and wild populations, through any of the five mechanisms in our conceptual framework. These systems allow for free flow of water potentially containing infective stages and have a high risk of escapes that may establish wild populations.

Although the various aquaculture practices probably have different impacts on the collateral disease risk for wildlife, there is very limited research on this issue to date. A recent global meta-analysis of the wider impacts of aquaculture activities on the environment included only 22 studies regarding potential disease transmission between farmed and wild populations, most of which were about sea lice (Barrett et al., 2019). Only 11 of those studies actually investigated changes in infection levels in wild fish associated with farms, all of which found higher infection levels in the presence of active fish farms (Barrett et al., 2019). There are most likely more diseases in wildlife that can be affected by aquaculture practices but the extent of these collateral disease effects remains elusive, mainly due to the lack of baseline information on background prevalence of parasites and diseases in wildlife (Lafferty et al., 2015). An important step will thus be to identify the parasite communities in wildlife surrounding aquaculture facilities prior to stocking. In addition to parasite screenings of aquaculture stocks to be introduced, such comprehensive inventories could (a) indicate potential candidates for spillover and spillback scenarios for which further experimental work on transmission and host specificity could evaluate the risk of disease exchange, and (b) establish baselines to monitor ensuing changes in disease prevalence in the course of aquaculture activities. Unfortunately, parasites and diseases are generally difficult to detect in natural ecosystems but emerging technologies such as environmental DNA (eDNA) are promising tools in addition to traditional methods of parasite detection, such as histology (Bass et al., 2015; Burge, Friedman, et al., 2016; Gomesa et al., 2017). Given the likelihood of farm–wildlife disease exchanges and the potentially dramatic effects of collateral diseases on wildlife, we propose to implement wide-scale parasite and disease screenings of wildlife surrounding proposed farm sites prior to aquaculture activities in risk assessments and biosecurity protocols. Biosecurity measures are already generally in place for aquaculture activities (Arthur et al., 2009; Hine et al., 2012; Subasinghe & Bondad-Reantaso, 2006; Subasinghe et al., 2019) but they currently mainly focus on the health of stocks and specific parasites relevant for the farmed species. Adding a stronger wildlife perspective to aquaculture biosecurity and identifying the potential for farm–wildlife disease exchange prior to stocking activities would strongly help to reduce the risk for parasite spillover and spillback scenarios and associated collateral disease impacts.

The establishment of reliable baseline information on background prevalence of parasites and diseases in wildlife in the vicinity of farms would also allow to monitor changes in wildlife diseases once aquaculture activities have started. If implemented in biosecurity protocols, wildlife disease monitoring would make the early detection of collateral disease impacts possible and thus help to initiate containment and eradication or mitigation measures to reduce further impact. Disease monitoring should include both farmed and wild hosts so that the exchange between farmed stocks and surrounding wildlife can be quantified. Any disease monitoring should ideally be further supplemented by monitoring of the population dynamics of wildlife potentially at risk of collateral disease impacts so that any effects on host populations can be detected. This in turn may then initiate further experimental research into the underlying mechanisms.

A general implementation of collateral disease impacts in aquaculture biosecurity protocols would also help to redress the current knowledge gaps in regard to the pervasiveness and magnitude of collateral disease impacts and the biases in existing information in regard to producing nations and culture systems. This bias also exists for aquaculture impacts in general. The global meta-analysis by Barrett et al. (2019) noted that research effort on interactions between wildlife and aquaculture is not equally distributed among producing countries and significantly correlated with a country's developmental index and the size of its aquaculture industry. However, several major producing countries did not follow this trend. China, by far the largest aquaculture producer in the world, was not represented in the relevant English-language studies found in the analysis, as were other major Asian producers. This is in line with our experience, as we did not find a single English-language study on diseases in wildlife related to aquaculture activities from China. According to the analysis of Barrett et al. (2019), research effort into the general environmental effects of aquaculture was also biased regarding production systems, with sea cages being overrepresented and freshwater systems being clearly underrepresented. The high representation of sea cages is not surprising, however, considering the open nature of those systems, allowing for interactions between farm and wildlife populations. The same pattern is also true for disease related studies as we could only trace very few studies regarding inland freshwater aquaculture. Finally, our current knowledge on the collateral disease effect of aquaculture activities is also biased with respect to the host taxa covered by existing studies. Most studies to date have focused on fish (mainly on salmon species) and to a lesser extent on crustaceans and molluscs as sources of farm-wildlife disease transfers. Hence, studies are needed that widen the taxonomic scope of aquaculture impacts on wildlife diseases.

5 | CONCLUSIONS

This review demonstrates that aquaculture activities can have an array of effects on wildlife diseases in the surrounding environment. The conceptual framework developed here provides a basis for further studies on the impacts of aquaculture on wildlife disease ecology and we propose to integrate collateral disease impacts in risk assessments and biosecurity protocols regarding aquaculture.

The risk of disease transfers related to aquaculture activities echoes similar risks in other food production environments such as agriculture and livestock management. There is a wealth of information on disease exchanges between natural ecosystems and crops or livestock (Blitzer et al., 2012; Daszak et al., 2000; Power & Mitchell, 2004). For example, many natural populations of animals serve as reservoirs for livestock diseases, such as badgers for tuberculosis in cattle in the UK (Donnelly et al., 2003) and bison that may transmit brucellosis to livestock in the US (Dobson & Meagher, 1996), creating conditions for spill back into wild host populations. Similarly, plant pathogens might transfer to cultivated crops and spill back when their wild hosts spread into cultivated areas, such as the transfer of crown rust and stem rust from wild to cultivated oats in Australia (Burdon et al., 1983; Oates et al., 1983). Examples of parasite spillover from cultivated to natural systems have also been documented (reviewed by Blitzer et al., 2012). For instance, foot-and-mouth-disease in domestic cattle in Mongolia caused an outbreak in wild gazelles (Nyamsuren et al., 2006). Parasite spillover from agriculture settings can also cause problems for nature conservation when co-introduced parasites infect vulnerable and rare species (Blitzer et al., 2012), e.g. when parasites spillover from commercial pollinators to infect wild bees (Lipa & Triggiani, 1988; Otterstatter & Thomson, 2007). These examples from terrestrial ecosystems demonstrate that more research on similar interactions between aquaculture activities and aquatic wildlife is warranted. Given that the impact of aquaculture is expected to rapidly intensify with the expanding global aquaculture production, increased research efforts into the risks of collateral diseases are urgently needed.

ACKNOWLEDGEMENTS

We would like to thank Nadine Bleile for her insightful feedback on the manuscript and her suggestions to help clarify the figures.

AUTHORS' CONTRIBUTIONS

All authors designed the study and contributed to the writing led by M.M.B.; all authors revised the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

For this review article no new data have been used.

ORCID

Mark M. Bouwmeester https://orcid.org/0000-0002-2574-4837
M. Anouk Goedknegt https://orcid.org/0000-0002-8637-0779
Robert Poulin https://orcid.org/0000-0003-1390-1206
David W. Thieltges https://orcid.org/0000-0003-0602-0101

REFERENCES

Abolofia, J., Wilen, J. E., & Asche, F. (2017). The cost of lice: Quantifying the impacts of parasitic sea lice on farmed salmon. *Marine Resource Economics*, *32*, 329–349. https://doi.org/10.1086/691981

Alderman, D. J. (1996). Geographical spread of bacterial and fungal diseases of crustaceans. *Revue Scientific et Technique, Office International Des Epizooties (OIE)*, *15*, 603–632. https://doi.org/10.20506/rst.15.2.943

Arthur, J. R., Bonda-Reantaso, M. G., Campbell, M. L., Hewit, C. L., Philips, M. J., & Subasinghe, R. P. (2009). *Understanding and applying risk analysis in aquaculture: A manual for decision-makers*. FAO Fisheries and Aquaculture Technical Paper 519/1. FAO.

Bakke, T. A., Cable, J., & Harris, P. D. (2007). The biology of Gyrodactylid monogeneans: The 'Russian-doll killers'. *Advances in Parasitology*, *64*, 161–376.

Barrett, L. T., Swearer, S. E., & Dempster, T. (2019). Impacts of marine and freshwater aquaculture on wildlife: A global meta-analysis. *Reviews in Aquaculture*, *11*, 1022–1044. https://doi.org/10.1111/raq.12277

Bass, D. W., Stentiford, G. D., Littlewood, D. T. J., & Hartikainen, H. (2015). Diverse applications of environmental DNA methods in parasitology. *Trends in Parasitology*, *31*, 499–513. https://doi.org/10.1016/j.pt.2015.06.013

Béné, C., Barange, M., Subasinghe, R., Pinstrup-Andersen, P., Merino, G., Hemre, G.-I., & Williams, M. (2015). Feeding 9 billion by 2050 – Putting fish back on the menu. *Food Security*, *7*, 261–274. https://doi.org/10.1007/s12571-015-0427-z

Beveridge, M. C. M., Ross, L. G., & Kelly, L. A. (1994). Aquaculture and biodiversity. *Ambio*, *23*, 497–502.

Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A.-M., Rande, T. A., & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems and Environment*, *146*, 34–43. https://doi.org/10.1016/j.agee.2011.09.005

Boyd, C. E., & Clay, J. W. (1998). Shrimp aquaculture and the environment. *Scientific American*, *278*, 58–65. https://doi.org/10.1038/scientificamerican0698-58

Boyd, C. E., & McNevin, A. A. (2005). *Aquaculture, resource use, and the environment*. John Blackwell & Sons.

Burdon, J. J., Oates, J. D., & Marshall, D. R. (1983). Interactions between *Avena* and *Puccinia* species. 1. The wild hosts: *Avena barata* Pott ex Link, *Avena fatua* L., *Avena ludoviciana* Durieu. *Journal of Applied Ecology*, *20*, 571–584.

Burge, C. A., Closek, C. J., Friedman, C. S., Groner, M. L., Jenkins, C. M., Shore-Maggio, A., & Welsh, J. E. (2016). The use of filter-feeders to manage disease in a changing world. *Integrative and Comparative Biology*, *56*, 573–587. https://doi.org/10.1093/icb/icw048

Burge, C. A., Friedman, C. S., Getchell, R., House, M., Lafferty, K. D., Mydlarz, L. D., Prager, K. C., Sutherland, K. P., Renault, T., Kiryu, I., & Vega-Thurber, R. (2016). Complementary approaches to diagnosing marine diseases: A union of the modern and the classic. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150207. https://doi.org/10.1098/rstb.2015.0207

Campbell, I., Macleod, A., Sahlmann, C., Neves, L., Funderud, J., Øverland, M., Hughes, A. D., & Stanley, M. (2019). The environmental risks associated with the development of seaweed farming in Europe – Prioritizing key knowledge gaps. *Fronties in Marine Science*, *107*. https://doi.org/10.3389/fmars.2019.00107

Chew, K. K. (1990). Global bivalve shellfish introductions. *Journal of the World Aquaculture Society*, *21*, 9–22.

Chou, H.-Y., Huang, C.-Y., Wang, C.-H., Chiang, H.-C., & Lo, C.-F. (1995). Pathogenicity of a baculovirus infection causing white spot syndrome in cultured penaeid shrimp in Taiwan. *Diseases of Aquatic Organisms*, *23*, 165–173. https://doi.org/10.3354/dao023165

Costello, C., Cao, S., Gelcich, S., Cisneros-Mata, M. A., Free, C. M., Froehlich, H. E., Golden, C. D., Ishimura, G., Maier, J., Macadam-Somer, I., & Thilsted, S. H. (2019). *The future of food from the sea*. World Resources Institute. Retrieved from www.oceanpanel.org/future-food-sea

Costello, M. J. (2009). How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3385–3394. https://doi.org/10.1098/rspb.2009.0771

Cranfield, H. J., Dunn, A., Doonan, I. J., & Michael, K. P. (2005). *Bonamia exitiosa* epizootic in *Ostrea chilensis* from Foveaux Strait, southern New Zealand between 1986 and 1992. *ICES Journal of Marine Science*, *62*, 3–13. https://doi.org/10.1016/j.icesjms.2004.06.021

Cross, T. F., Burnell, G., Coughlan, J., Culloty, S., Dillane, E., McGinnity, P., & Rogan, E. (2008). Detrimental genetic effects of interactions between reared strains and wild populations of marine and anadromous fish and invertebrate species. In M. Holmer, K. Black, C. M. Duarte, N. Marbà, & I. Karakassis (Eds.), *Aquaculture in the ecosystem* (pp. 117–154). Springer.

Daszak, P., Cunningham, A. A., & Hyatt, A. D. (2000). Emerging infectious diseases of wildlife – Threats to biodiversity and human health. *Science*, *287*, 443–449. https://doi.org/10.1126/science.287.5452.443

Dempster, T., Uglem, I., Sanchez-Jerez, P., Fernandez-Jover, D., Bayle-Sempere, J., Nilsen, R., & Bjørn, P. A. (2009). Coastal salmon farms attract large and persistent aggregations of wild fish: An ecosystem effect. *Marine Ecology Progress Series*, *385*, 1–14. https://doi.org/10.3354/meps08050

Diana, J. S. (2009). Aquaculture production and biodiversity conservation. *BioScience*, *59*, 27–38. https://doi.org/10.1525/bio.2009.59.1.7

Dobson, A., & Meagher, M. (1996). The population dynamics of brucellosis in the Yellowstone National Park. *Ecology*, *77*, 1026–1036. https://doi.org/10.2307/2265573

Donnelly, C. A., Woodroffe, R., Cox, D. R., Bourne, J., Gettinby, G., Le Fevre, A. M., McInerney, J. P., & Morrison, W. I. (2003). Impact of localized badger culling on tuberculosis incidence in British cattle. *Nature*, *426*, 834–837. https://doi.org/10.1038/nature02192

Dunn, A. M., & Hatcher, M. J. (2015). Parasites and biological invasions: Parallels, interactions, and control. *Trends in Parasitology*, *35*, 189–199. https://doi.org/10.1016/j.pt.2014.12.003

Edwards, P. (2015). Aquaculture environment interactions: Past, present and likely future trends. *Aquaculture*, *447*, 2–14. https://doi.org/10.1016/j.aquaculture.2015.02.001

Engelsma, M. Y., Culloty, S. C., Lynch, S. A., Arzul, I., & Carnegie, R. B. (2014). *Bonamia* parasites: A rapidly changing perspective on a genus of important mollusc pathogens. *Diseases of Aquatic Organisms*, *110*, 5–23. https://doi.org/10.3354/dao02741

FAO. (2018). *The State of World Fisheries and Aquaculture 2018 – Meeting the sustainable development goals*. FAO.

Georgiev, B. B., Sánchez, M. I., Vasileva, G. P., Nikolov, P. N., & Green, A. J. (2007). Cestode parasitism in invasive and native brine shrimps (*Artemia* spp.) as a possible factor promoting the rapid invasion of *A. franciscana* in the Mediterranean region. *Parasitology Research*, *101*, 1647–1655. https://doi.org/10.1007/s00436-007-0708-3

Gittenberger, A., Voorbergen-Laarman, M. A., & Engelsma, M. Y. (2016). Ostreid herpesvirus OsHV-1 µVar in Pacific oysters *Crassostrea gigas* (Thunberg 1793) of the Wadden Sea, a UNESCO world heritage site. *Journal of Fish Diseases*, *39*, 105–109.

Glover, K. A., Quintela, M., Wennevik, V., Besnier, F., Sørvik, A. G. E., & Skaala, Ø. (2012). Three decades of farmed escapees in the wild: A spatio-temporal analysis of Atlantic salmon population genetic structure throughout Norway. *PLoS ONE*, *7*, e43129. https://doi.org/10.1371/journal.pone.0043129

Goedknegt, M. A., Feis, M. E., Wegner, K. M., Luttikhuizen, P. C., Buschbaum, C., Camphuysen, K. C. J., Van der Meer, J., & Thieltges, D. W. (2016). Parasites and marine invasions: Ecological and evolutionary perspectives. *Journal of Sea Research*, *113*, 11–27.

Goedknegt, M. A., Nauta, R., Markovic, M., Buschbaum, C., Folmer, E. O., Luttikhuizen, P. C., van der Meer, J., Waser, A. M., Wegner, K. M., & Thieltges, D. W. (2019). How invasive oysters can affect parasite infection patterns in native mussels on a large spatial scale. *Oecologia*, *190*, 99–113. https://doi.org/10.1007/s00442-019-04408-x

Goedknegt, M. A., Schuster, A.-K., Buschbaum, C., Gergs, R., Jung, A. S., Luttikhuizen, P. C., van der Meer, J., Troost, K., Wegner, K. M., & Thieltges, D. W. (2017). Spillover but no spillback of two invasive parasitic copepods from invasive Pacific oysters (*Crassostrea gigas*) to native bivalve hosts. *Biological Invasions*, *19*, 365–379. https://doi.org/10.1007/s10530-016-1285-0

Goedknegt, M. A., Welsh, J. E., Drent, J., & Thieltges, D. W. (2015). Climate change and parasite transmission: How temperature can decrease parasite infectivity via increased predation on infective stages. *Ecosphere*, *6*, 96. https://doi.org/10.1890/ES15-00016.1

Gomesa, G. B., Hutson, K. S., Domingos, J. A., Chung, C., Hayward, S., Miller, T. L., & Jerrya, D. R. (2017). Use of environmental DNA (eDNA) and water quality data to predict protozoan parasites outbreaks in fish farms. *Aquaculture*, *479*, 467–473. https://doi.org/10.1016/j.aquaculture.2017.06.021

Green, A. J., Sánchez, M. I., Amat, F., Figuerola, J., Hontoria, F., Ruiz, O., & Hortas, F. (2005). Dispersal of invasive and native brine shrimps *Artemia* (Anostraca) via waterbirds. *Limnology and Oceanography*, *50*, 737–742. https://doi.org/10.4319/lo.2005.50.2.0737

Hall, S. J., Delaporte, A., Phillips, M. J., Beveridge, M., & O'Keefe, M. (2011). *Blue frontiers: Managing the environmental costs of aquaculture*. The WorldFish Center.

Hayward, C. J., Iwashita, M., Crane, J. S., & Ogawa, K. (2001). First report of the invasive eel pest *Pseudodactylogyrus bini* in North America and in wild American eels. *Diseases Aquatic Organisms*, *44*, 53–60. https://doi.org/10.3354/dao044053

Hine, M., Adams, S., Arthur, J. R., Bartley, D., Bondad-Reantaso, M. G., Chávez, C. J. H., Dalsgaard, A., Flegel, T., Gudding, R., & Wardle, R. (2012). Improving biosecurity: A necessity for aquaculture sustainability. In R. P. Subasinghe, J. R. Arthur, D. M. Bartley, S. S. De Silva, M.

Halwart, N. Hishamunda, C. V. Mohan, & P. Sorgeloos (Eds.), *Farming the waters for people and food. Proceedings of the Global Conference on Aquaculture 2010, Phuket, Thailand* (pp. 437–449). FAO and NACA.

Jennings, S., Stentiford, G. D., Leocadio, A. M., Jeffery, K. R., Metcalfe, J. D., Katsiadaki, I., Auchterlonie, N. A., Mangi, S. C., Pinnegar, J. K., Ellis, T., Peeler, E. J., Luisetti, T., Baker-Austin, C., Brown, M., Catchpole, T. L., Clyne, F. J., Dye, S. R., Edmonds, N. J., Hyder, K., … Verner-Jeffreys, D. W. (2016). Aquatic food security: Insights into challenges and solutions from an analysis of interactions between fisheries, aquaculture, food safety, human health, fish and human welfare, economy and environment. *Fish and Fisheries*, *17*, 893–938. https://doi.org/10.1111/faf.12152

Johansen, L.-H., Jensen, I., Mikkelsen, H., Bjørn, P.-A., Jansen, P. A., & Bergh, Ø. (2011). Disease interaction and pathogens exchange between wild and farmed fish populations with special reference to Norway. *Aquaculture*, *315*, 167–186. https://doi.org/10.1016/j.aquaculture.2011.02.014

Johnsen, B. O., & Jensen, A. J. (1991). The *Gyrodactylus* story in Norway. *Aquaculture*, *98*, 289–302. https://doi.org/10.1016/0044-8486(91)90393-L

Jørstad, K. E., van der Meeren, T., Paulsen, O. I., Thomsen, T., Thorsen, A., & Svåsand, T. (2008). 'Escapes' of eggs from farmed cod spawning in net pens: Recruitment to wild stocks. *Reviews in Fisheries Science*, *16*, 285–295. https://doi.org/10.1080/10641260701678017

Kelly, D. W., Paterson, R. A., Townsend, C. R., Poulin, R., & Tompkins, D. M. (2009). Parasite spillback: A neglected concept in invasion ecology? *Ecology*, *90*, 2047–2056. https://doi.org/10.1890/08-1085.1

Kennedy, C. R., & Fitch, D. J. (1990). Colonization, larval survival and epidemiology of the nematode *Anguillicola crassus*, parasitic in the eel, *Anguilla anguilla*, in Britain. *Journal of Fish Biology*, *36*, 117–131. https://doi.org/10.1111/j.1095-8649.1990.tb05588.x

Kennedy, D. A., Kurath, G., Brito, I. L., Purcell, M. C., Read, A. F., Winton, J. R., & Wargo, A. R. (2016). Potential drivers of virulence evolution in aquaculture. *Evolutionary Applications*, *9*, 344–354.

Kirk, R. S. (2003). The impact of *Anguillicola crassus* on European eels. *Fisheries Management and Ecology*, *10*, 385–394.

Koops, H., & Hartmann, F. (1989). *Angulillicola*-infestations in Germany and in German eel imports. *Journal of Applied Ichthyology*, *1*, 41–45.

Krkošek, M. (2010). Host density thresholds and disease control for fisheries and aquaculture. *Aquaculture Environment Interactions*, *1*, 21–31.

Krkošek, M., Ford, J. S., Morton, A., Lele, S., Myers, R. A., & Lewis, M. A. (2007). Declining wild salmon populations in relation to parasites from farm salmon. *Science*, *318*, 1772–1775.

Kurath, G., & Winton, J. (2011). Complex dynamics at the interface between wild and domestic viruses of finfish. *Current Opinion in Virology*, *1*, 73–80.

Lafferty, K. D., Harvell, C. D., Conrad, J. M., Friedman, C. S., Kent, M. L., Kuris, A. M., Powell, E. N., & Rondeau, D., & Saksida, S. M. (2015). Infectious diseases affect marine fisheries and aquaculture economics. *Annual Review of Marine Science*, *7*, 471–496.

Leung, T. L. F., & Bates, A. E. (2013). More rapid and severe disease outbreaks for aquaculture at the tropics: Implications for food security. *Journal of Applied Ecology*, *50*, 215–222.

Lipa, J. J., & Triggiani, O. (1988). *Crithidia bombi* sp. n. a flagellated parasite of a bumble bee *Bombus terrestris* L. (Hymenoptera, Apidae). *Acta Protozoologica*, *27*, 287–290.

Lucas, J. S., Southgate, P. C., & Tucker, C. S. (Eds.). (2019). *Aquaculture: Farming aquatic animals and plants*. John Wiley & Sons Ltd.

Lymbery, A. J., Morine, M., Gholipour Kanani, H., Beatty, S. J., & Morgan, D. L. (2014). Co-invaders: The effects of alien parasites on native hosts. *International Journal for Parasitology: Parasites and Wildlife*, *3*, 171–177.

McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., & Cross, T., & Ferguson, A. (1997). Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: Use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES Journal of Marine Science*, *54*, 998–1008.

Metian, M., Troell, M., Christensen, V., Steenbeek, J., & Pouil, S. (2020). Mapping diversity of species in global aquaculture. *Reviews in Aquaculture*, *12*, 1090–1100.

Mineur, F., Provan, J., & Arnott, G. (2015). Phylogeographical analyses of shellfish viruses: Inferring a geographical origin for ostreid herpesviruses OsHV-1 (Malacoherpesviridae). *Marine Biology*, *162*, 181–192. https://doi.org/10.1007/s00227-014-2566-8

Molloy, S. D., Pietrak, M. R., Bouchard, D. A., & Bricknell, I. (2011). Ingestion of *Lepeophtheirus salmonis* by the blue mussel *Mytilus edulis*. *Aquaculture*, *311*, 61–64. https://doi.org/10.1016/j.aquaculture.2010.11.038

Morozińska-Gogol, J. (2009). Alien species of fish parasites in the coastal lakes and lagoons of the southern Baltic. *Oceanologia*, *51*, 105–115. https://doi.org/10.5697/oc.51-1.105

Mullins, J. E., Groman, D., & Wadowska, D. (1998). Infectious salmon anaemia in salt water Atlantic salmon (*Salmo salar* L.) in New Brunswick, Canada. *Bulletin of the European Association of Fish Pathologists*, *18*, 110–114.

Naylor, R. L., Goldburg, R. J., Primavera, J. H., Kautsky, N., Beveridge, M. C. M., Clay, J., Folke, C., Lubchenco, J., Mooney, H., & Troell, M. (2000). Effect of aquaculture on world fish supplies. *Nature*, *405*, 1017–1024. https://doi.org/10.1038/35016500

Naylor, R. L., Hardy, R. W., Bureau, D. P., Chiu, A., Elliott, M., Farrell, A. P., Forster, I., Gatlin, D. M., Goldburg, R. J., Hua, K., & Nichols, P. D. (2009). Feeding aquaculture in an era of finite resources. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 15103–15110. https://doi.org/10.1073/pnas.0905235106

Naylor, R. L., Williams, S. L., & Strong, D. R. (2001). Aquaculture – A gateway for exotic species. *Science*, *294*, 1655–1656.

Nyamsuren, D., Joly, D. O., Enkhtuvshin, S., Odonkhuu, D., Olson, K. A., Draisma, M., & Karesh, W. B. (2006). Exposure of Mongolian gazelles (*Procapra gutturosa*) to foot and mouth disease virus. *Journal of Wildlife Diseases*, *42*, 154–158. https://doi.org/10.7589/0090-3558-42.1.154

Oates, J. D., Burdon, J. J., & Brouwer, J. B. (1983). Interactions between *Avena* and *Puccinia* species. 2. The pathogens: *Puccinia coronata* Cda. and *P. graminis* f. sp. *avenae* Eriks. and Henn. *Journal of Applied Ecology*, *20*, 585–596.

Otterstatter, M. C., & Thomson, J. D. (2007). Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies. *Oecologia*, *154*, 411–421. https://doi.org/10.1007/s00442-007-0834-8

Pantoja, C. R., Lightner, D. V., & Holtschmit, K. H. (1999). Prevalence and geographic distribution of infectious hypodermal and hematopoietic necrosis virus (IHHNV) in wild blue shrimp *Penaeus stylirostris* from the Gulf of California, Mexico. *Journal of Aquatic Animal Health*, *11*, 23–34.

Paquotte, P., Chim, L., Martin, J.-L.-M., Lemos, E., Stern, M., & Tosta, G. (1998). Intensive culture of shrimp *Penaeus vannamei* in floating cages: Zootechnical, economic and environmental aspects. *Aquaculture*, *164*, 151–166. https://doi.org/10.1016/S0044-8486(98)00183-5

Peeler, E. J., Oidtmann, B. C., Midtlyng, P. J., Miossec, L., & Gozlan, R. E. (2011). Non-native aquatic animals introductions have driven disease emergence in Europe. *Biological Invasions*, *13*, 1291–1303. https://doi.org/10.1007/s10530-010-9890-9

Pitta, P., Tsapakis, M., Apostolaki, E., Tsagaraki, T., Holmer, M., & Karakassis, I. (2009). 'Ghost nutrients' from fish farms are transferred up the food web by phytoplankton grazers. *Marine Ecology Progress Series*, *374*, 1–6. https://doi.org/10.3354/meps07763

Power, A. G., & Mitchell, C. E. (2004). Pathogen spillover in disease epidemics. *The American Naturalist*, *164*, 79–89. https://doi.org/10.1086/424610

Price, C., Black, K. D., Hargrave, B. T., & Morris, J. A. (2015). Marine cage culture and the environment: Effects on water quality and primary production. *Aquaculture Environment Interactions*, *6*, 151–174. https://doi.org/10.3354/aei00122

Revie, C. W., Gettinby, G., Treasurer, J. W., Grant, A. N., & Reid, S. W. J. (2002). Sea lice infestations on farmed Atlantic salmon in Scotland and the use of ectoparasitic treatments. *Veterinary Record*, *151*, 753–757.

Saksida, S. M. (2006). Infectious haematopoietic necrosis epidemic (2001 to 2003) in farmed Atlantic salmon *Salmo salar* in British Columbia. *Diseases of Aquatic Organisms*, *72*, 213–223. https://doi.org/10.3354/dao072213

Salama, N. K. G., & Murray, A. G. (2011). Farm size as a factor in hydrodynamic transmission of pathogens in aquaculture fish production. *Aquaculture Environment Interactions*, *2*, 61–74. https://doi.org/10.3354/aei00030

Savini, B. D., Occhipinti-Ambrogi, A., Marchini, A., Tricarico, E., Gherardi, F., Olenin, S., & Gollasch, S. (2010). The top 27 animal alien species introduced into Europe for aquaculture and related activities. *Journal of Applied Ichthyology*, *26*, 1–7. https://doi.org/10.1111/j.1439-0426.2010.01503.x

Schmittou, H. R. (1993). *High density fish culture in low volume cages*. American Soybean Association.

Sepúlveda, F., Marín, S., & Carvajal, J. (2004). Metazoan parasites in wild fish and farmed salmon from aquaculture sites in southern Chile. *Aquaculture*, *235*, 9–100. https://doi.org/10.1016/j.aquaculture.2003.09.015

Soderberg, R. W. (1994). *Flowing water fish culture*. CRC Press.

Soto-Rodriguez, S. A., Gomez-Gil, B., Lozano-Olvera, R., Betancourt-Lozano, M., & Morales-Covarrubias, M. S. (2015). Field and experimental evidence of *Vibrio parahaemolyticus* as the causative agent of acute hepatopancreatic necrosis disease of cultured shrimp (*Litopenaeus vannamei*) in northwestern Mexico. *Applied and Environmental Microbiology*, *81*, 1689–1699. https://doi.org/10.1128/AEM.03610-14

Stentiford, G. D., Neil, D. M., Peeler, E. J., Shields, J. D., Small, H. J., Flegel, T. W., Vlak, J. M., Jones, B., Morado, F., Moss, S., Lotz, J., Bartholomay, L., Behringer, D. C., Hauton, C., & Lightner, D. V. (2012). Disease will limit future food supply from the global crustacean fishery and aquaculture sectors. *Journal of Invertebrate Pathology*, *110*, 141–157. https://doi.org/10.1016/j.jip.2012.03.013

Stentiford, G. D., Sritunyalucksana, K., Flegel, T. W., Williams, B. A. P., Withyachumnarnkul, B., Itsathitphaisarn, O., & Bass, D. (2017). New paradigms to help solve the global aquaculture disease crisis. *PLoS Pathogenes*, *13*, e1006160. https://doi.org/10.1371/journal.ppat.1006160

Subasinghe, R. P., & Bondad-Reantaso, M. G. (2006). Biosecurity in aquaculture: International agreements and instruments, their compliance, prospects and challenges for developing countries. In A. D. Scarfe, C.-S. Lee, & P. O'Bryen (Eds.), *Aquaculture biosecurity: Prevention, control and eradication of aquatic animal disease* (pp. 9–16). Blackwell Publishing.

Subasinghe, R. P., Delamare-Deboutteville, J., Mohan, C. V., & Phillips, M. J., (2019). Vulnerabilities in aquatic animal production. *Revue Scientifique et Technique (International Office of Epizootics)*, *38*, 423–436. https://doi.org/10.20506/rst.38.2.2996

Subasinghe, R., Soto, D., & Jia, J. (2009). Global aquaculture and its role in sustainable development. *Reviews in Aquaculture*, *1*, 2–9. https://doi.org/10.1111/j.1753-5131.2008.01002.x

Sweet, M. J., & Bateman, K. S. (2015). Diseases in marine invertebrates associated with mariculture and commercial fisheries. *Journal of Sea Research*, *104*, 16–32. https://doi.org/10.1016/j.seares.2015.06.016

Tacon, A. G. J., & Metian, M. (2009). Fishing for aquaculture: Non-food use of small pelagic forage fish – A global perspective. *Reviews in Fisheries Science*, *17*, 305–317. https://doi.org/10.1080/10641260802677074

Tacon, A. G. J., & Metian, M. (2015). Feed matters: Satisfying the feed demand of aquaculture. *Reviews in Fisheries Science & Aquaculture*, *23*, 1–10. https://doi.org/10.1080/23308249.2014.987209

Thieltges, D. W., Jensen, K. T., & Poulin, R. (2008). The role of biotic factors in the transmission of free-living endohelminth stages. *Parasitology*, *135*, 407–426. https://doi.org/10.1017/S0031182007000248

Thieltges, D. W., Reise, K., Prinz, K., & Jensen, K. T. (2009). Invaders interfere with native parasite – Host interactions. *Biological Invasions*, *11*, 1421–1429. https://doi.org/10.1007/s10530-008-9350-y

Thorstad, E. B., & Finstad, B. (2018). Impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout. *NINA Report*, *1449*, 1–22.

Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O. T., Nilsen, F., Horsberg, T. E., & Jackson, D. (2013). Salmon lice – Impact on wild salmonids and salmon aquaculture. *Journal of Fish Diseases*, *36*, 171–194. https://doi.org/10.1111/jfd.12061

Verdegem, M. C. J., & Bosma, R. H. (2009). Water withdrawal for brackish and inland aquaculture, and options to produce more fish in ponds with present water use. *Water Policy*, *11*, 52–68. https://doi.org/10.2166/wp.2009.003

Welsh, J. E., van der Meer, J., Brussaard, C. P. D., & Thieltges, D. W. (2014). Inventory of organisms interfering with transmission of a marine trematode. *Journal of the Marine Biological Association of the United Kingdom*, *94*, 697–702. https://doi.org/10.1017/S0025315414000034

World Bank. (2014). *Reducing disease risks in aquaculture*. World Bank Report 88257-GLB.

Young, H. S., Parker, I. M., Gilbert, G. S., Guerra, A. N., & Nunn, C. L. (2016). Introduced species, disease ecology, and biodiversity–disease relationships. *Trends in Ecology & Evolution*, *32*, 41–54. https://doi.org/10.1016/j.tree.2016.09.008

How to cite this article: Bouwmeester MM, Goedknegt MA, Poulin R, Thieltges DW. Collateral diseases: Aquaculture impacts on wildlife infections. *J Appl Ecol*. 2021;58:453–464. https://doi.org/10.1111/1365-2664.13775

Vol. 12: 45–59, 2020
https://doi.org/10.3354/aei00346

AQUACULTURE ENVIRONMENT INTERACTIONS
Aquacult Environ Interact

Published February 13

Model-based evaluation of the genetic impacts of farm-escaped Atlantic salmon on wild populations

Ian R. Bradbury[1,*], Steve Duffy[1], Sarah J. Lehnert[1], Ragnar Jóhannsson[2], Jon Hlodver Fridriksson[2], Marco Castellani[3], Ingrid Burgetz[4], Emma Sylvester[1], Amber Messmer[1], Kara Layton[1], Nicholas Kelly[1], J. Brian Dempson[1], Ian A. Fleming[5]

[1]Science Branch, Fisheries and Oceans Canada, 80 East White Hills Rd., St. John's, NL A1C 5X1, Canada
[2]Marine and Freshwater Research Institute, Skulagata 4, 101 Reykjavik, Iceland
[3]Department of Mechanical Engineering, University of Birmingham, Birmingham B15 2TT, UK
[4]Fisheries and Oceans Canada, 200 Kent Street Ottawa, ON K1A 0E6, Canada
[5]Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada

ABSTRACT: Genetic interactions (i.e. hybridization) between wild and escaped Atlantic salmon *Salmo salar* from aquaculture operations have been widely documented, yet the ability to incorporate predictions of risk into aquaculture siting advice has been limited. Here we demonstrate a model-based approach to assessing these potential genetic interactions using a salmon aquaculture expansion scenario in southern Newfoundland as an example. We use an eco-genetic individual-based Atlantic salmon model (IBSEM) parameterized for southern Newfoundland populations, with regional environmental data and field-based estimates of survival, to explore how the proportion of escapees relative to the size of wild populations could potentially influence genetic and demographic changes in wild populations. Our simulations suggest that both demographic decline and genetic change are predicted when the percentage of escapees in a river relative to wild population size is equal to or exceeds 10% annually. The occurrence of escapees in southern Newfoundland rivers under a proposed expansion scenario was predicted using river and site locations and models of dispersal for early and late escapees. Model predictions of escapee dispersal suggest that under the proposed expansion scenario, the number of escapees is expected to increase by 49% and the highest escapee concentrations will shift westward, consistent with the location of proposed expansion (20 rivers total >10% escapees, max 24%). Our results identify susceptible rivers and potential impacts predicted under the proposed aquaculture expansion scenario and illustrate how model-based predictions of both escapee dispersal and genetic impacts can be used to inform both aquaculture management decisions and wild salmon conservation.

KEY WORDS: Hybridization · Atlantic salmon · Aquaculture · Management · Newfoundland

1. INTRODUCTION

Genetic interactions (i.e. hybridization) between wild and escaped Atlantic salmon *Salmo salar* from aquaculture operations have been documented across the natural range of the species where the 2 co-occur (Glover et al. 2017, Keyser et al. 2018). Escaped farmed Atlantic salmon regularly occur in both Europe and Atlantic Canada (Keyser et al. 2018, Diserud et al. 2019, Glover et al. 2019) and have been commonly found in rivers at distances of up to 200 km from the nearest aquaculture site, although distant occurrences at sea have also been reported (Hansen et al. 1993, 1997, Hansen & Jacobsen 2003, Jensen et al. 2013). As a consequence, hybridization between wild and domestic salmon can be both spatially extensive and represent a significant proportion of a population's annual production (Glover et al. 2013,

---

*Corresponding author: ibradbur@me.com

Publisher: Inter-Research · www.int-res.com

2017, Karlsson et al. 2016, Sylvester et al. 2018, Wringe et al. 2018). Both experimental and field studies have demonstrated decreased survival of hybrids in the wild (Fleming et al. 2000, McGinnity et al. 2003, Sylvester et al. 2019), and suggest that wild population decline and genetic change are the likely outcomes of hybridization and introgression (Hindar et al. 2006, Castellani et al. 2015, 2018, Sylvester et al. 2019). As a result, genetic interactions with escaped farmed salmon have been identified as a significant threat to the persistence and stability of wild Atlantic salmon populations (Forseth et al. 2017).

In Atlantic Canada, Atlantic salmon aquaculture escapees (Morris et al. 2008, Keyser et al. 2018) and hybridization with wild individuals have been observed throughout the region (O'Reilly et al. 2006, DFO 2018a, Sylvester et al. 2018, Wringe et al. 2018). In particular, recent studies have documented widespread hybridization between wild salmon and aquaculture escapees following a single escape event that occurred in 2013 in southern Newfoundland (Wringe et al. 2018). Model-based projections following this escape event using cohort-based estimates of survival suggest negative impacts on population productivity and genetic integrity (Sylvester et al. 2019). These results are consistent with evidence of genetic changes in wild Norwegian salmon populations, which show levels of introgression as high as 47% (Karlsson et al. 2016), reductions in productivity (Fleming et al. 2000, Skaala et al. 2019), and changes in key life history traits (Bolstad et al. 2017). In Atlantic Canada, Atlantic salmon aquaculture expansion has been proposed for several regions, including those with threatened or at-risk wild salmon populations. Salmon populations in the Bay of Fundy, eastern Nova Scotia, and southern Newfoundland have been classified as threatened or endangered by the Committee on The Status of Endangered Wildlife In Canada (COSEWIC 2010), with many populations at record lows of abundance (DFO 2018a, b, 2019). Accordingly, there is a pressing need to develop approaches to predict the genetic impacts of salmon net-pen aquaculture on wild populations for use in aquaculture management and spatial planning.

Model-based approaches to explore escape events from net-pens and their impacts on wild populations allow the opportunity to evaluate escape scenarios and management decisions and are currently under development for salmonids as well as other marine species (e.g. Baskett et al. 2013). For Atlantic salmon, several models of genetic and demographic interactions among wild and farm escapees have been developed and applied, including OMEGA (ICF International 2012), IBSEM (Castellani et al. 2015), and that of Hindar et al. (2006). Of these, IBSEM, an individual-based eco-genetic Atlantic salmon life history model, has been most extensively used. Applications include understanding how the proportion of escapees scales with demographic and genetic impacts in Norway (Castellani et al. 2015, 2018), how natural straying may mitigate these impacts (Castellani et al. 2018), and how varying the strength of selection against offspring of aquaculture escapees in the wild influences population outcomes (Sylvester et al. 2019). In addition to these modeling efforts, a recent study has modeled the escape, dispersal, and survival of escapees from release sites to wild rivers in Iceland (e.g. Johannsson et al. 2017).

The combination of model-based estimates of impact with empirical data provides an unprecedented opportunity to inform management and policy decisions related to genetic outcomes for populations affected by escaped farmed Atlantic salmon. Consequently, the goal of this study was to illustrate the potential for model-based approaches to (1) predict genetic and demographic change as a result of escapees under a proposed Atlantic salmon aquaculture expansion scenario and (2) to contribute to aquaculture siting and management decisions. Specifically, the population impacts (i.e. demographic and genetic) of farm escapees were examined using IBSEM, parameterized for southern Newfoundland populations (Castellani et al. 2015, 2018). To further illustrate potential applications to siting and risk assessment, we modeled the distribution of escapees in the wild prior to and following an aquaculture expansion scenario in southern Newfoundland using a spatial model of dispersal and survival recently implemented in Iceland (Johannsson et al. 2017). This study builds directly on modeling and empirical studies from across Canada and Europe (Castellani et al. 2015, 2018, Johannsson et al. 2017, Sylvester et al. 2019) and demonstrates how consideration of genetic impacts of escapees on wild salmon populations may be incorporated into management decisions.

2. METHODS

2.1. Individual-based modeling of direct genetic impacts

Detailed modeling methods using IBSEM are described in Castellani et al. (2015, 2018) and Sylvester et al. (2019). IBSEM models wild population changes in abundance, genotype, and individual size in response to the introduction of domesticated individuals. The model considers the duration of invasion, wild population size, number of invaders, environmental conditions, individual size, and genotypic and phenotypic differences between individuals of farm and wild origin. Growth and survival are simulated by stochastic processes that are influenced by genotype, fish size and age, water temperature, and population density at 3 life stages: embryo, juvenile, and adult. Simulated loci are unlinked with possible gamete recombination and random inheritance, and have a range of influences on phenotype and therefore performance in the environment. The sum of the genetic effects is linearly related to phenotype, such that genotypic values approaching 1 are associated with growth and survival rates typical of wild salmon, and values approaching 0 are associated with rates observed in farm escapees. Reproductive success of farm escapees is reduced relative to wild salmon, and the success of both is sex-specific, with female fertility dependent upon weight and male reproductive success dependent upon length, with the possibility of precocial sexual maturation as parr. A full list of parameters representative of Newfoundland salmon and environmental conditions in the region can be found in Sylvester et al. (2019).

Simulations utilized estimates of feral fry and parr survival calculated from genetic analysis of individual cohorts following an escape event in southern Newfoundland in 2013 (Wringe et al. 2018, Sylvester et al. 2019). These estimates of survival are lower than most previous estimates of relative survival of feral parr (McGinnity et al. 1997, Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2019), and increasing survival in freshwater has been shown to increase both genetic and demographic impacts (Sylvester et al. 2019). We simulated the population consequences of invasion over a 50 yr period in a wild population of 500 individuals with the proportion of invaders varying from 0 to 100% of that of the wild population annually. The model simulates the accumulation of changes (i.e. allele frequency) over this 50-yr period resulting from both the continual influx of escapees and any successfully returning hybrid or escapee progeny. All models were run for 100 yr prior to invasion to ensure model stability and for 100 yr after the 50-yr invasion period ceased. We compared the change in combined adult population abundance (both wild and escaped farmed fish) and the sum of the genetic effects across the adult set of genes included in the simulation to observe changes in the genetic fitness of the population. For each iteration, we calculated the adult population abundance or allele frequency at the end of the invasion period and compared this to the mean value (10 replicates) for the no invasion scenario at the same time point. We used the mean value for the zero-invasion scenario instead of the initial starting value for the respective scenarios because at this initial time point (start of invasion period), farmed individuals are introduced into the population and thus it does not represent a baseline value.

2.2. Propagule pressure

To explore the potential changes in genetic interactions between wild and domestic salmon associated with the proposed expansion scenario in Newfoundland, we calculated propagule pressure following Keyser et al. (2018) for both the existing and proposed production regimes. Propagule pressure was calculated for each river using maximum stocking allowable at an aquaculture site (number of individuals, see below), divided by the distance from the river to that site (km), and summed across all aquaculture sites. That is:

$$\text{Propagule pressure for a given river } (R) = \sum_{i,y=1}^{S} \frac{F_{i,y}}{\text{LCD}\left(S_{i,y} \text{ to } R\right)} \quad (1)$$

where $S_{i,y}$ represents an aquaculture site (i) in a given year (y), R represents a given river, $F_{i,y}$ is the number of fish at site S_i, and LCD represents the least-cost distance function. This metric has been shown to correlate with both the occurrence of escapees and genetic interactions between wild and farm escapees in Atlantic Canada (Keyser et al. 2018).

2.3. Dispersal modeling of escapees

To model the distribution of farm escapees and to allow scenario testing, we applied a simple dispersal model that incorporates the best information on local levels of production, rates of escape, survival, behavior, environment, and size of wild populations. Details on the dispersal model can be found in Johannsson et al. (2017), but a summary is included below. Three main categories of data were considered. First, the production data were considered and included locations, biomass, size, age, and average proportion of escapees per unit harvest. Second, geographic factors considered include distribution of rivers along the coast, and any directionality of local currents. Finally, the model included any existing life history data and behavioral differences between wild and farmed salmon. Two independent models were used, one for early escapees (i.e. smolts), and one for late escapees (i.e. adults) to allow for differences in behavior and survival among life stages. The model was implemented in R (R Development Core Team 2016) with a web-based interface.

For this analysis, we focused on 76 rivers known to have wild Atlantic salmon populations along the south coast of Newfoundland, spanning the region from Bear Cove Brook to Renews River (Fig. 1). This region has been demonstrated previously to encompass genetic impacts following escape events in the region (Keyser et al. 2018, Wringe et al. 2018). As information is generally lacking on the size of wild populations in the majority of these rivers (Porter et al. 1974, DFO 2013, 2018b), such estimates of population size were derived using an established relationship between river size and wild population size for Newfoundland following Wringe et al. (2018). River size was calculated as axial length to complete obstruction using data from Porter et al. (1974). However, as the relationship derived by Wringe et al. (2018) is based on habitat, the estimates may not reflect population declines experienced over recent decades (COSEWIC 2010, DFO 2018b) and therefore may overestimate the current population size and underestimate the proportion of escapees. In the event of any error in our initial parameters, the estimates of the proportion of escapees would be more conservative than would likely be the case in the field. Nonetheless, they represent the only available estimates of population size for most of these systems.

Reported stocking, harvest information, and licensed maximum stocking allowable from 2013 to 2017 were obtained for all existing aquaculture locations in southern Newfoundland from Aquaculture Management of Fisheries and Oceans (C. Hendry pers. comm.). For consistency among existing and proposed sites, we used the maximum licensed stocking numbers. Numbers of fish were converted to harvest biomass using an individual fish weight of 3 kg, reducing by 25% to account for fallow periods and the production/fallow cycle, and finally multiplying by 0.65, a ratio estimated from a comparison of stocking and harvest that excludes sites with catastrophic losses. The expected number of escapees per unit production is required to estimate escapees in the environment. In the absence of an extensive escapee monitoring program in southern Newfoundland, we rely on Norwegian statistics of annual production and escape events for the period 2009–2016 to estimate the expected number of escapees per ton of fish production (www.fiskeridir.no/English/Aquaculture/Statistics). However, these estimates of escapees have been shown to be an underestimate (Skilbrei et al. 2015, Glover et al. 2017); therefore, they were adjusted following Skilbrei et al. (2015) as per Johannsson et al. (2017). As a result, the estimate is ~0.8 fish per ton of production, but, given uncertainty in this value for Newfoundland, extensive sensitivity analyses were conducted to explore the effect of other values from 0.2 to 1.2.

The proportion of escapees that enter estuaries and could ascend rivers was estimated to be 17% based on Hamoutene et al. (2018), with correction for estuaries without receivers. This calculation assumes all escapees detected in estuaries will enter adjacent rivers, and although it is actually unknown what proportion of escapees in estuaries will enter rivers, es-

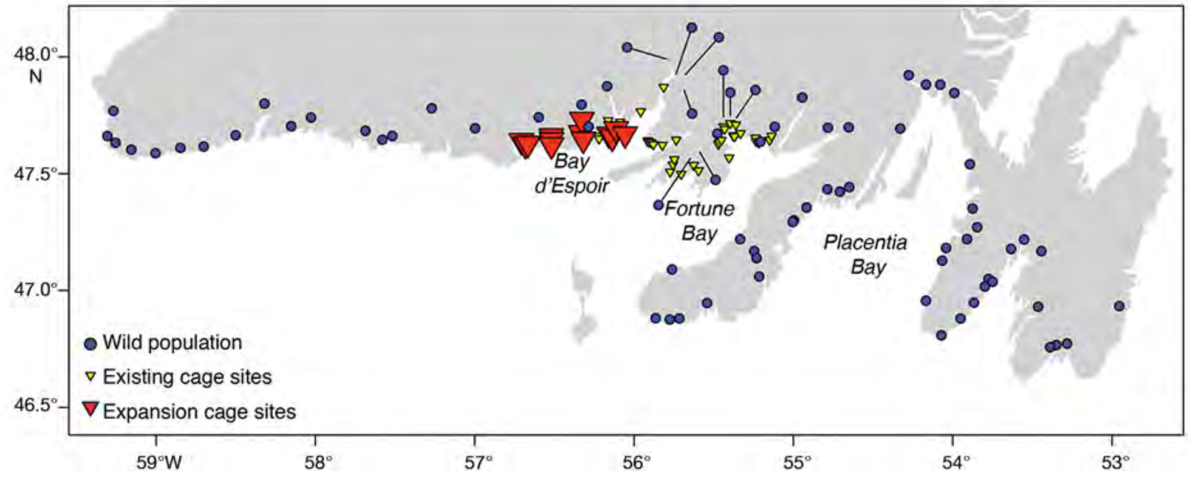


Fig. 1. Southern Newfoundland rivers known to contain wild Atlantic salmon, existing aquaculture sites, and proposed expansion sites

capees have been detected in rivers throughout the region (Hamoutene et al. 2018, Keyser et al. 2018), and 17 % represents the best information at present. The proportion of escapees that are reproductively mature during freshwater entry has been estimated for the Garnish system in southern Newfoundland (located on the east side of Fortune Bay) as 63 %, calculated using counting fence data for 2015–2017. This is, however, based only on individuals phenotypically identified as escapees (i.e. late escapees) at the counting fence, and, as early escapees could be undetected, this is likely an underestimate. Overall, based on the best available data, we estimate that the proportion of escapees that enter freshwater and mature is ~11 %. This is comparable to a value of 15 % currently in use in similar modeling exercises in Iceland (Johannsson et al. 2017).

Two models of dispersal were calculated, one for early escapees (i.e. smolts) and one for late escapees (i.e. adults), and we assumed an equal split between the 2 in absence of data on early escapees. The number of late escapees from a single site that arrive at rivers (E_G) was calculated using Eq. (2), where P is aquaculture production, S_G is the escapees per ton of production, and M is the likelihood that an escapee becomes sexually mature and enters freshwater. $\frac{R}{T}$ represents the time period (R) relative to the total time (T) in the cages that an individual could escape, survive, and sexually mature. We estimated this ratio at 0.66 as it is unlikely an escapee would survive beyond this time (i.e. 1 yr) in the wild (Hansen & Youngson 2010, Hamoutene et al. 2018).

$$E_G = PS_G \frac{R}{T} M \tag{2}$$

The total number of early escapees from a single site that make it to local rivers was calculated using Eq. (3), where S_s is the escapees per ton of production, L represents the proportion of smolts that survive at sea in the wild, and $\frac{L_f}{L_w}$ is the ratio of farmed to wild smolt survival.

$$E_s = PS_s\, L\left(\frac{L_f}{L_w}\right) \tag{3}$$

At present, the marine survival (smolt to adult) of Atlantic salmon in monitored rivers of Newfoundland varies from ~4 to 8 % (DFO 2018b); therefore, we set a value of 6 % for this exercise. The relative survival of farm to wild smolts was set at 0.37 following Hindar et al. (2006).

To simulate the dispersal of escapees from cage sites to rivers, we used a Weibull distribution shaped by 2 parameters, representing both the width and the shape or skewness of the distribution. To estimate the width of the distribution, or the distance escapees may disperse along the coast, we used a combination of experimental release data (Hamoutene et al. 2018), escapee recaptures (Keyser et al. 2018), and genetic estimates of hybridization for Newfoundland (Sylvester et al. 2018, Wringe et al. 2018). Similarly, Morris et al. (2008) reported escaped farmed salmon occurring in 56 of 62 Canadian rivers within 300 km of aquaculture operations. We set a maximum distance at 200 km, which is smaller than used elsewhere (i.e. Johannsson et al. 2017), but still larger than both tagging and genetic indications of escapee dispersal in southern Newfoundland. Modifying the shape or skewness of the distribution can allow projections to account for the influence of ocean currents, which can influence distribution patterns (Hansen & Youngson 2010). Ocean currents in the region are largely wind-driven and predominately from the northeast in winter and spring and southwest in summer and fall. Recent tagging work (Hamoutene et al. 2018) suggests no obvious east or west bias in movements along the coast. Therefore, we used a symmetrical distribution for the dispersal of both early and late escapees. See Johannsson et al. (2017) for further details regarding the spatial dispersal model.

Sensitivity analyses were conducted by varying several parameters separately and examining the resultant number and distribution of escapees in rivers under the proposed expansion scenario. First, the number of escapees per unit harvest was varied from 0.2 to 1.2 fish per ton. Second, we varied the proportion of early to late escapees from all early, equal proportions of both, and all late escapees. Finally, we varied the proportion of late escapees that mature and enter rivers from 0.06, and 0.11, and 0.16.

3. RESULTS

3.1. Individual-based modeling of direct genetic impacts

Individual-based model simulations allowed trends in population abundance and allele frequency to be examined in response to varying levels of invasion by escaped farmed salmon. The annual levels of invasion were varied from 0 to 100 % of the size of the wild population (500 individuals). All runs stabilized near a wild population size of 500 individuals pre-invasion and all levels of invasion ranging from 10 to

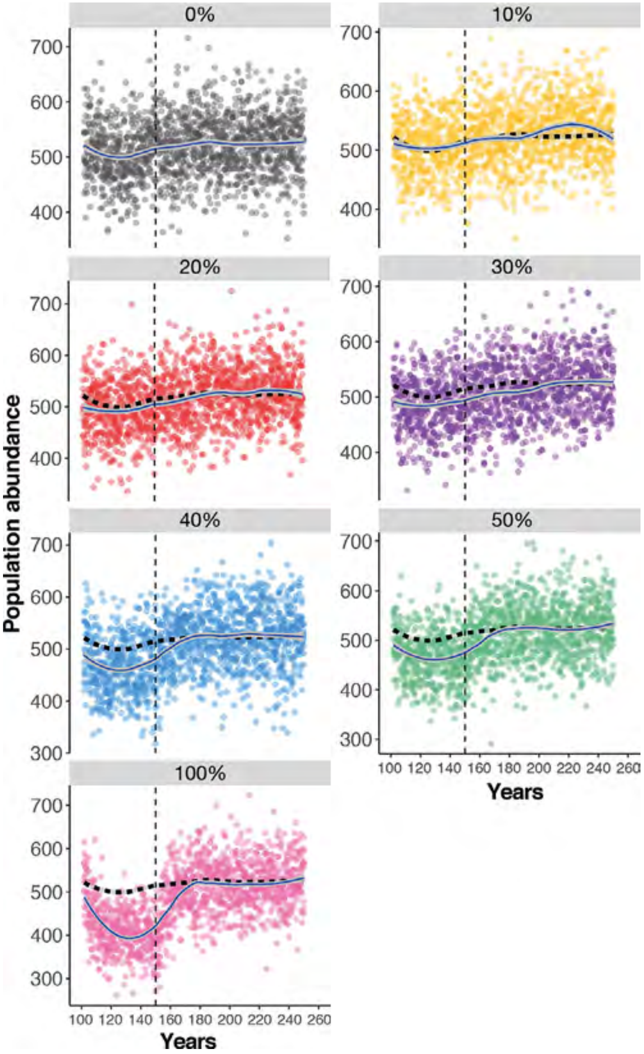


Fig. 2. Demographic changes over time during and following 50 yr of invasion by escaped farmed salmon in southern Newfoundland. All simulations were conducted using IBSEM; see Section 2 and Castellani et al. (2015, 2018), Sylvester et al. (2019) for details. Horizontal dashed line represents the smoothed line of the zero-invasion simulation with 90 % CI (grey shading); vertical dashed line represents the end of simulated invasion of escaped farmed salmon. Solid blue lines represent the smoothed line of 10 replicates shown by the points. Smoothed lines were generated using the geom_smooth function in the R package ggplot2 with the loess regression and a span of 0.5

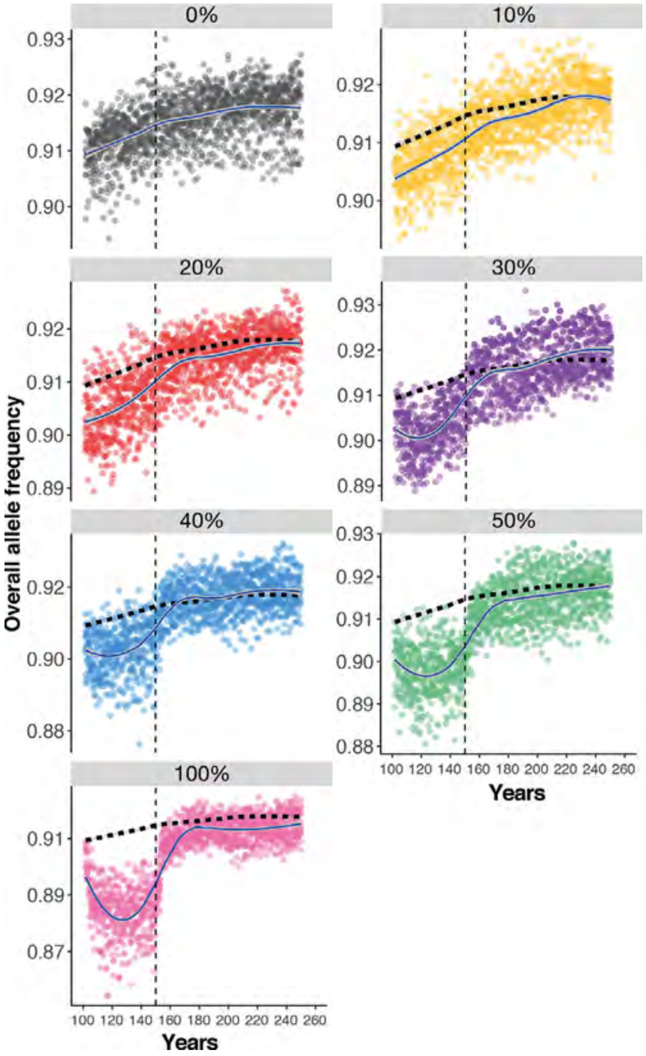


Fig. 3. Changes in overall allele frequency over time during and following 50 yr of invasion by escaped farmed salmon in southern Newfoundland. Wild populations characterized by an allele frequency of 1 and aquaculture populations an allele frequency of 0. See Fig. 2 for further details

100 % displayed evidence of demographic decline (Fig. 2) and genetic change (Fig. 3) in the wild population. Overall, the magnitude of demographic decline and genetic change increased with increasing proportions of farm escapees present when compared to the no invasion scenario (Fig. 4). The magnitude of demographic decline resulting from genetic changes ranged from ~0 % under no invasion to ~25 % decline under 100 % annual invasion (Figs. 2 & 4). The amount of genetic change predicted varied from <1 % to ~3 % (Figs. 3 & 4). The time to recover both population size and allele frequency once invasion ceased increased with level of invasion and varied from a few yr to 50+ yr (Figs. 3 & 4). Overall, the simulations suggest that both demographic decline and genetic change are predicted when the proportion of escapees relative to wild population size equals or exceeds 10 % annually (Fig. 4). As such, a threshold of 10 % escapees relative to the wild population of a given river was used as a threshold for subsequent simulations, see below. Levels of invasion between 1 and 9 % were also examined but were

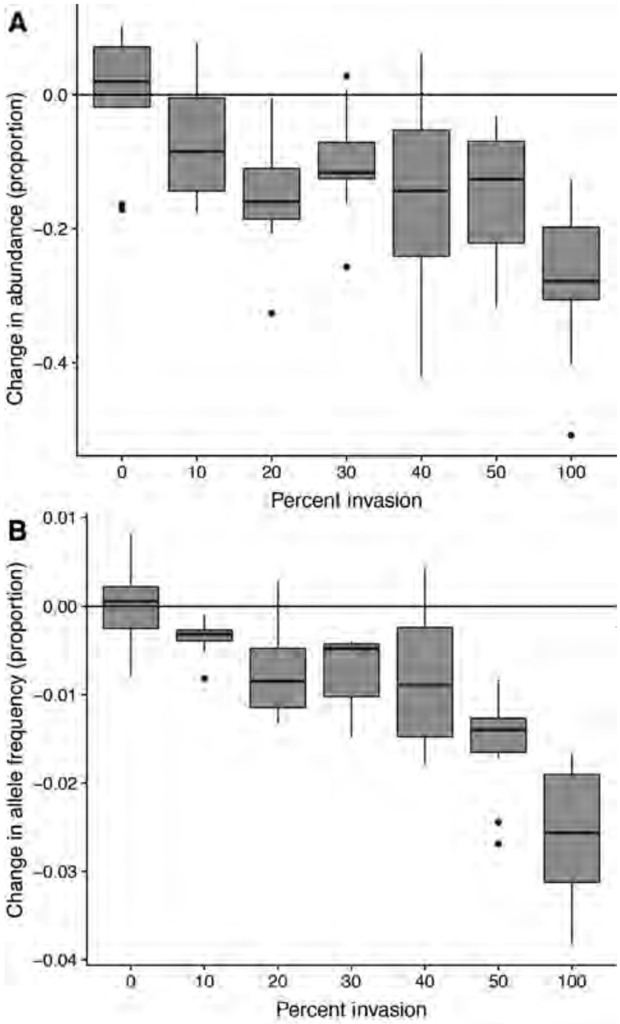


Fig. 4. (A) Magnitude of demographic decline and (B) genetic change observed after 50 yr of invasion by escaped farmed salmon into a wild population. Annual levels of invasion vary from 0 to 100% of the wild population. Changes were calculated by comparing each scenario (and iteration) against the mean of the zero-invasion scenario at the end of the invasion period. The box limits represent the third (75th percentile) and first (25th percentile) quartile, with whiskers showing the 1.5× interquartile range. The centre line within boxes represents the median and the points outside the boxes represent outliers. Each boxplot represents results based on 10 iterations for the scenario

highly variable, displayed no consistent trend, and largely did not differ from the zero-invasion scenario.

3.2. Propagule pressure

Our calculation of propagule pressure under the current magnitude and distribution of production (Fig. 1) indicates that the areas of highest expected propagule pressure are located at the head of Fortune Bay (Fig. 5). Under the proposed expansion scenario (Fig. 1), the areas of highest propagule pressure are predicted to expand to the west and include the Bay d'Espoir area (Fig. 5), where the propagule pressure is expected to at least double in 7 rivers.

3.3. Dispersal modeling of escapees

Under the existing level and distribution of production, the total number of escapees predicted to reach rivers in southern Newfoundland is estimated at 1278 individuals annually. Under this regime, 19 rivers are predicted to meet or exceed the 10% threshold, with a maximum value of 15.6% (Fig. 6). Escapees are predicted to occur in all but 11 rivers in Fortune Bay and westwards, with numbers ranging from 1 to 150 escapees per river. Rivers characterized by the largest percentage of escapees are concentrated in Fortune Bay, as well as a few Bay d'Espoir rivers (Fig. 6). Model predictions for the Garnish River suggested 13 escapees annually, which is comparable to the average of 6 escapees detected at the counting fence during the summer months annually.

Under the proposed expansion scenario, the total number of escapees predicted to reach rivers was estimated at 1915 individuals annually, which represented a 49% increase in the number of escapees predicted in rivers along the coast (Fig. 6). Twenty rivers were predicted to meet or exceed the 10% threshold, with 8 rivers exceeding 20% escapees and a maximum value of 24% (Fig. 6). Escapees were predicted to occur in all but 8 rivers in Fortune Bay and west, with numbers ranging from 1 to 275 escapees per river. Under the proposed expansion, the rivers characterized by the largest number of escapees shift to the head of Bay d'Espoir and to the west (Fig. 6).

We explored the sensitivity of the model predictions to changes in several key parameters. Research using simulated escape events in Norway suggests the actual number of escapees per ton is likely between 0.4 and 0.8 (Skilbrei et al. 2015). We thus varied the number of escapees per ton of harvest from 0.2 to 1.2. The total number of escapees doubled with each doubling of the number of escapees per harvest (Fig. 7A). We also examined how varying the proportion of late or early escapees per ton influenced model predictions (Fig. 7B). Interestingly, we observed a 2.75-fold increase in the percentage of escapees predicted to occur when only late escapees are considered versus early escapees, with estimates ranging from 2860

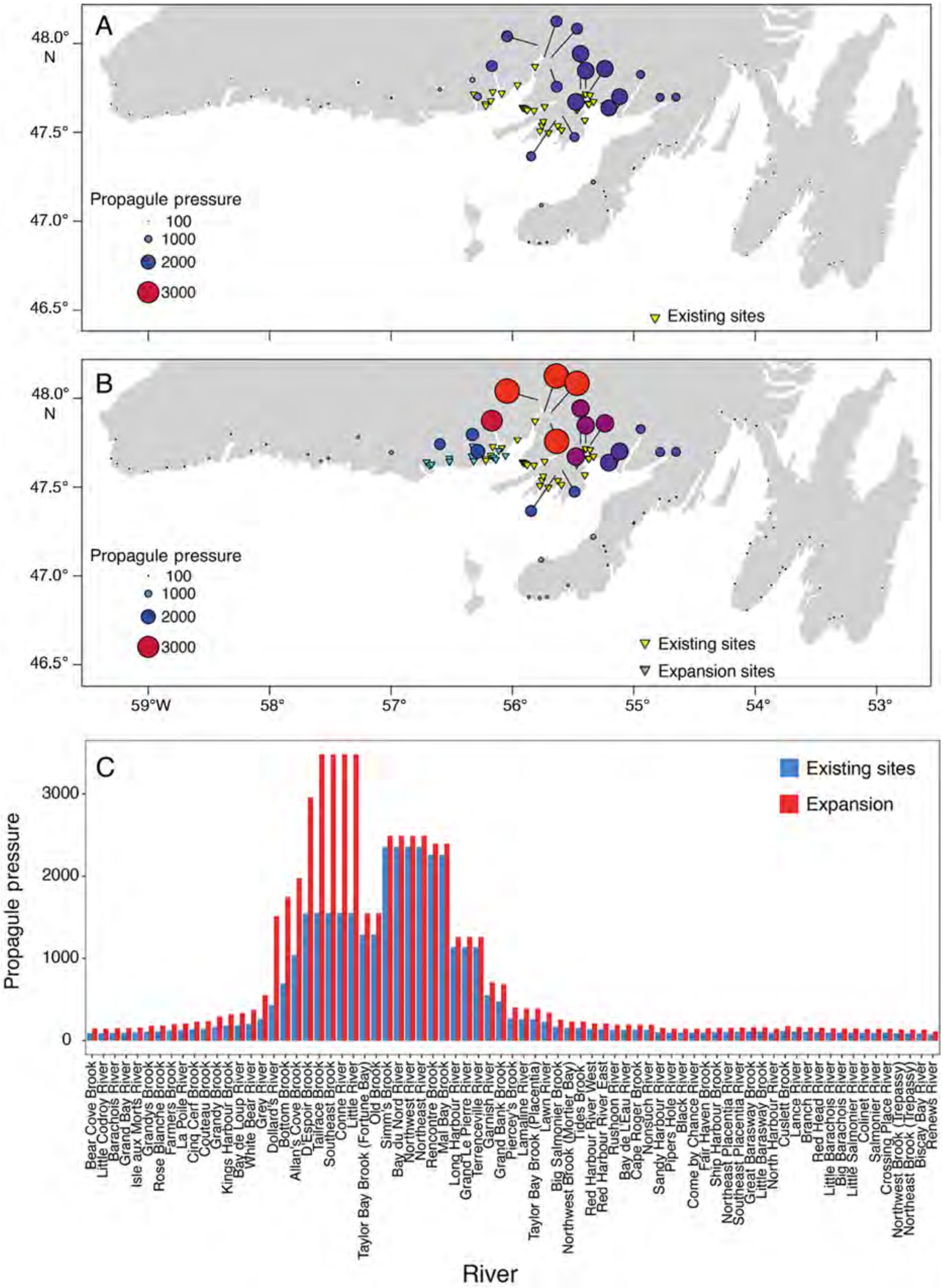


Fig. 5. Propagule pressure calculated following Keyser et al. (2018) for southern Newfoundland under (A,C) the existing production regime and (B,C) the proposed expansion scenario. See Section 2 for details. (C) Rivers are arranged west to east along the *x*-axis

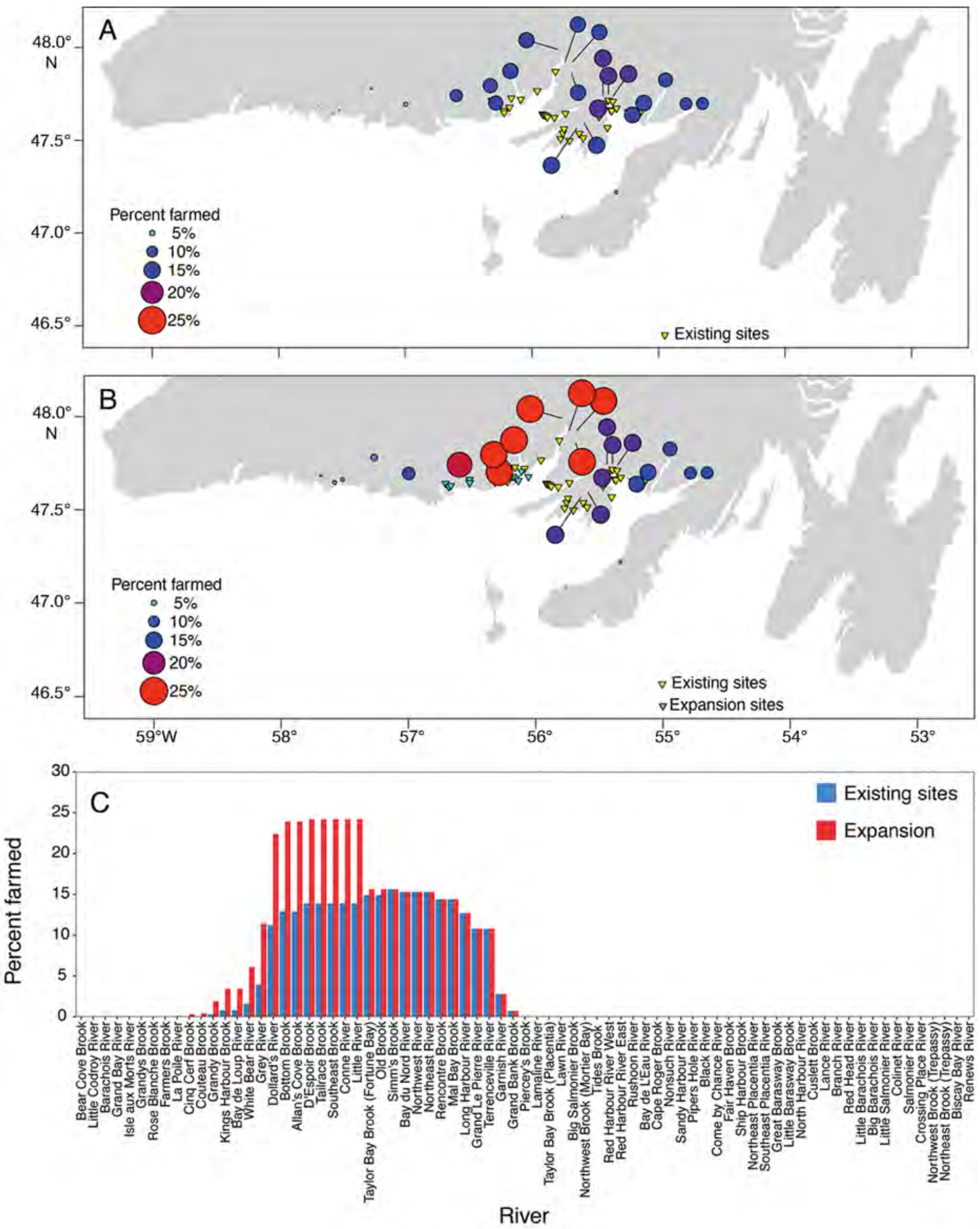


Fig. 6. Predicted spatial distribution and relative percentage of escaped farmed salmon to wild salmon for southern Newfoundland under (A,C) the existing production regime and (B,C) the proposed expansion scenario. See Section 2 for details

(late only) to 970 escapees (early only). For the late escapees only scenario, escapees were also distributed across more locations with higher percentages of escapees compared with only early escapees (Fig. 7B). Varying the proportion of late escapees resulted in numbers of escapees in rivers ranging from 1265 to 2565 (Fig. 7C). However even under the lowest probability examined (e.g. 0.06), 14 rivers were

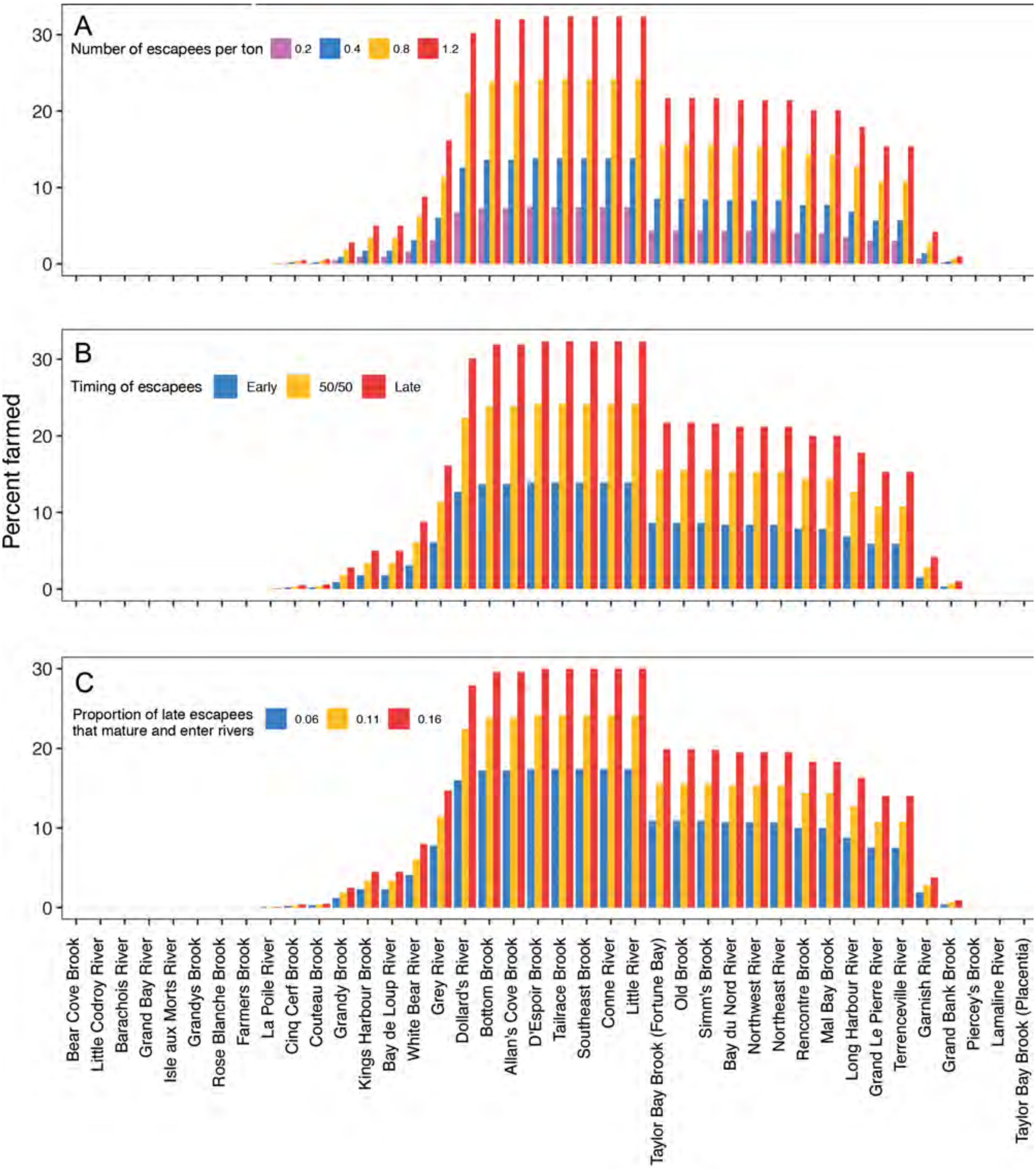


Fig. 7. Predicted relative percentage of escaped farmed salmon to wild salmon in rivers of southern Newfoundland under the proposed expansion scenario, varying (A) the number of escapees per unit harvest, (B) the proportion of early to late escapees, and (C) the proportion of late escapees that mature and enter rivers. See Section 2 for details regarding simulations. Rivers are arranged west to east along the *x*-axis

still predicted to exceed 10% escapees under the proposed expansion scenario (Fig. 7C).

Modifying the maximum dispersal distance did not significantly alter the number of escapees found in rivers overall; only the distribution of escapees across rivers (Fig. 8). At a maximum dispersal distance of 100 km, escapees were only predicted to occur in 21 rivers with a maximum percentage of 25.4% es-

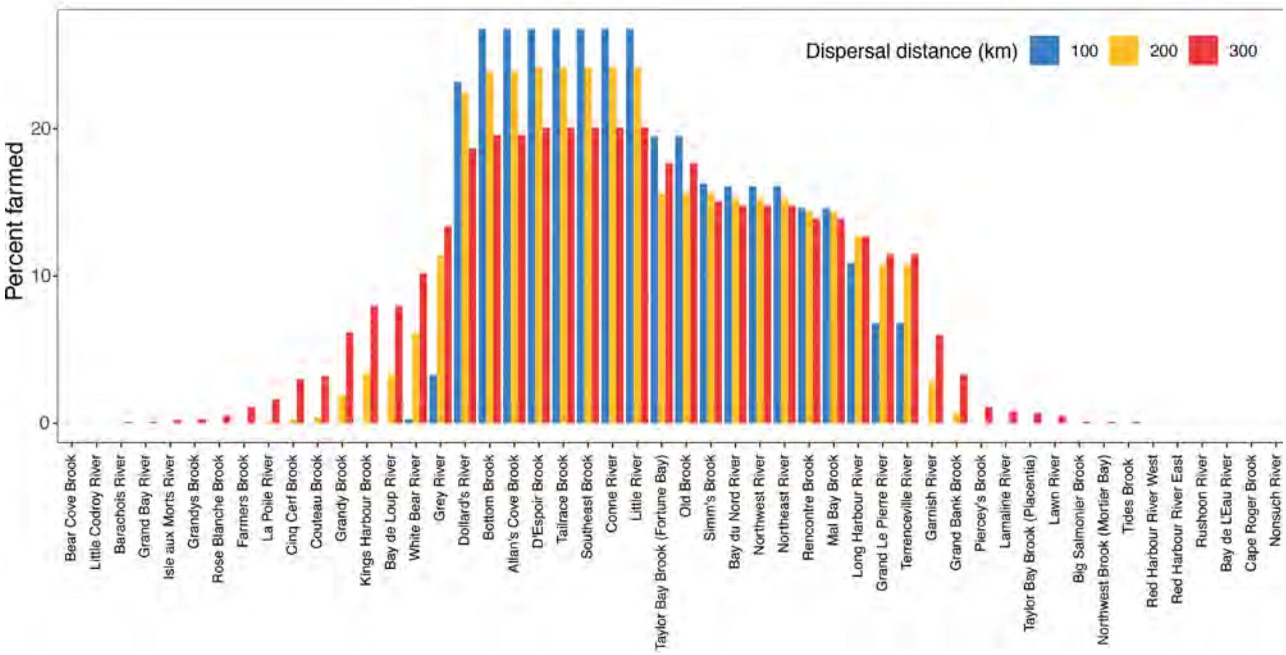


Fig. 8. Predicted relative percentage of escaped farmed salmon to wild salmon in rivers of southern Newfoundland under the proposed expansion scenario, varying the maximum dispersal distance for escapees. See Section 2 for details regarding simulations. Rivers are arranged west to east along the *x*-axis

capees. At a maximum dispersal distance of 200 km, escapees were predicted to occur in 29 rivers with a maximum percentage of 23.3 % escapees (Fig. 8). Finally, at a maximum dispersal distance of 300 km, escapees were predicted to occur in 37 rivers with a maximum percentage of 19.6 % escapees (Fig. 8).

4. DISCUSSION

Genetic interactions between wild and escaped Atlantic salmon have been documented both in Europe (Glover et al. 2017) and North America (Bourret et al. 2011, Sylvester et al. 2018, Wringe et al. 2018) and represent a significant threat to the persistence of wild salmon populations where they occur (Forseth et al. 2017). Nonetheless, the ability to incorporate predictions of risk into aquaculture siting advice and management decisions has been limited to date. Our goal was to demonstrate the utility of recently developed model-based approaches (e.g. Castellani et al. 2015, Johannsson et al. 2017) to predict potential genetic interactions resulting from escapees using a proposed site expansion scenario in southern Newfoundland as an example. Our individual-based simulations suggest that as the proportion of escapees within a population increases beyond 10 %, both population decline and genetic change are expected, and thus allow an assessment of the risk various levels of escapees pose to wild populations. Our analysis of propagule pressure and simulations of escapee dispersal into southern Newfoundland rivers (estimated population size ~22 000 individuals, COSEWIC 2010) suggest increased numbers of escapees (49 % or 1.5-fold increase) and westward shifts in the predicted distribution of escapees associated with the proposed expansion scenario. Our results directly build on previous modeling and empirical studies (Hindar et al. 2006, Glover et al. 2017, Castellani et al. 2018, Keyser et al. 2018, Sylvester et al. 2019) and directly illustrate how predictions of genetic impacts from aquaculture site expansion can be used to inform management decisions and salmon conservation.

4.1. Individual-based model predictions of impact

Population impacts of hybridization with escaped farmed salmon have been shown to vary (Glover et al. 2017, Sylvester et al. 2018) and, as such, predicting population responses to the presence of escaped farmed salmon remains a challenge. Our individual-based eco-genetic simulations suggest that demographic decline and genetic change are apparent once the percentage of escapees in rivers equals or exceeds 10 %, and that the observed impacts increase with the proportion of escapees. These predictions are consistent with empirical estimates of reduced aquaculture offspring survival (Fleming et al. 2000, McGinnity et al. 2003, Skaala et al. 2012, Sylvester et al. 2019) and reductions in wild population productivity resulting from hybridization with farm escapees (Fleming et al. 2000, Castellani et al. 2018, Sylvester et al. 2019). For example, Fleming et al. (2000) report a reduction of >30% in productivity of a wild population experiencing hybridization. The magnitude of the predicted demographic changes observed here varied with the proportion of escapees present in the river, but ranged from <10% to >50% decline and were generally less than 30% for most simulations over the modeled 50 yr period. The predicted genetic changes are consistent with both local evidence of hybridization and introgression in the region following escape events (Sylvester et al. 2018, Wringe et al. 2018) and recent studies suggesting significant changes to key life history traits due to introgression (Bolstad et al. 2017, Skaala et al. 2019). As these impacts scale with the proportion of escapees present, the ultimate impact to wild populations experiencing escapees may be significantly greater in small or depressed populations and existing empirical data support this hypothesis (Heino et al. 2015, Sylvester et al. 2018, Wringe et al. 2018).

A significant outcome of the individual-based modeling is the prediction that genetic and demographic impacts are likely when the proportion of escapees in a river equals or exceeds 10%. Estimates of the proportion of escapees occurring in rivers have been used as a management or conservation tool elsewhere and model predictions of population impacts of escapees can directly inform siting decisions and mitigation action. In Norway, extensive summer and autumn surveys for escapees are used to estimate an index of the proportion of escapees in rivers (Svenning et al. 2017, Diserud et al. 2019, Glover et al. 2019). Based on these surveys, the incidence of escapees in rivers is designated as clearly above or below 10% and used to prioritize rivers for mitigation action such as the active removal of escapees (Glover et al. 2019). Similarly, a recent risk assessment in Iceland opted for a 4% threshold for the proportion of escapees in rivers to provide a precautionary approach to siting as the industry develops (Johannsson et al. 2017). These values are consistent with both levels of straying in the wild (<10%, Stabell 1984, Thorstad et al. 2010) and our observations here that demographic and genetic change are likely when the percentage of escapees equals or exceeds 10%. This value of 10% escapees relative to wild salmon provides a useful metric against which to evaluate field detections of escapees and predictions of future impact.

Ultimately, although the best available regional data were used to parameterize the individual-based model, improved empirical estimates of several key parameters may improve these model predictions and any subsequent management advice. The population-specific life history and environmental data considered here were from the Conne River, which represents the best studied population/river in southern Newfoundland. Although these data are likely representative of the region, additional data from other populations would allow regional variation in demography, life history, and environmental features to be considered in model predictions. Similarly, potential key variables such as stage specific survival of aquaculture escapees and offspring have been shown to be both spatially and temporally variable (Skaala et al. 2019). Moreover, recent work suggests that population outcomes may be highly influenced by differences in the survival of escapees and hybrids (Sylvester et al. 2019) as well as rates of straying among wild populations (Castellani et al. 2018). As such, further refinement of empirical estimates of these interactions is needed to improve predictions of population outcomes. It is also worth noting that we did not vary the level of invasion annually during the invasion period, and although high annual rates of invasion (50–100%) may be unlikely for large populations, many of the populations under consideration here likely have small population sizes (<100 adults returning annually) for which these levels of invasion seem possible. Previous modeling studies have varied the levels of invasion annually and reported contrasting results, with either greater impacts from intermittent large escape events (Hindar et al. 2006) or from low level continual invasion (Baskett et al. 2013).

4.2. Predictions of escapee dispersal

Ultimately the magnitude and spatial extent of hybridization between wild salmon and domestic escapees will be dependent on the number of escapees, the scale of escapee dispersal in the wild, and the size of wild populations. Our use of a simplified dispersal kernel informed by all available data on escapee dispersal patterns suggests that under the existing distribution of production in the region, the head of Fortune Bay is likely to be characterized by the highest numbers of mature escapees entering rivers. Under the proposed expansion plan, the number of escapees is predicted to increase 1.5-fold (49%), and the area with the highest number of mature escapees entering rivers will shift to the head of Bay d'Espoir. This shift is entirely consistent with our estimates of propagule pressure, the proposed increases in production (~50%), and the shift in location of dominant production to the area west of Fortune Bay. Although field detections of aquaculture salmon indicate regional as well as season- and size-specific dispersal patterns (Morris et al. 2008, Keyser et al. 2018, Glover et al. 2019), our model results are consistent with the emerging consensus for escapees in Atlantic Canada, suggesting they are usually found in rivers at moderate to small distances (i.e. 10s to 100s km) from escape locations (Morris et al. 2008, Keyser et al. 2018). These observations are supported by experimental releases conducted by Hamoutene et al. (2018) in southern Newfoundland indicating maximum dispersal distances of 80 km, with most salmon remaining in the embayment of release. Moreover, genetic identification of hybrids following a single escape event in southern Newfoundland detected first generation hybrids at distances of up to 100 km from the escape event (Sylvester et al. 2018, 2019, Wringe et al. 2018). Similarly, Morris et al. (2008) reported escaped farmed salmon occurring in 56 of 62 maritime rivers within 300 km of aquaculture operations.

When considering the predicted proportions of escapees to wild individuals, it is important to note that there is uncertainty in both the estimates of predicted escapees and the estimates of wild population size. The estimates of escapees per unit production used here are based on Norwegian statistics, and there is uncertainty as to their applicability to Newfoundland. Also, the estimates of wild population size used here are the best currently available for many of the rivers considered and are based on habitat-abundance associations identified using a larger geographic area. However, as stated above, these estimates may not adequately reflect recent declines in population size that have occurred in southern Newfoundland (COSEWIC 2010, DFO 2013, 2018b). As such, our predictions of the proportions of escapees in wild populations may be underestimated in some instances, particularly in small populations. Improved estimates of wild population size and the presence of escapees for rivers in the region would improve the assessment of genetic and demographic risk. It is also noteworthy that our predicted number of escapees at the Conne River (located at the head of the Bay d'Espoir) under the current production regime significantly exceed detections there to date based on the summer monitoring period. Although escapees and hybrids have been detected in Conne River (Dempson et al. 2004, Wringe et al. 2018), the proportions have generally been low even following significant escape events. The mechanism for this discrepancy is unknown at this time, but it is possible that escapees are entering the environment undetected, possibly at times outside the limited monitoring period, are being diverted to the adjacent rivers based on flow patterns in the area, or are not surviving.

The dispersal kernels used in our simulations were parameterized to provide predictions consistent with detections of escapees at the Garnish River counting fence, which is the only monitoring facility regularly detecting escapees in the region. Simulating the observed number of escapees at the Garnish River required using a maximum dispersal distance of 200 km. However, this value exceeds existing empirical estimates for the region, and therefore the model may overestimate dispersal potential in some instances. By comparison, our sensitivity analysis indicated that reducing the maximum dispersal distance to 100 km reduced the spatial scale of impact but increased the number of escapees predicted to occur in the Bay d'Espoir area under the proposed expansion, with 7 rivers predicted to experience 25% escapees. Also, we assume the influence of ocean currents in the region on the shape of the dispersal kernel is negligible. This assumption is consistent with the dominance of wind-driven flow in the area and existing tagging data of escapees in the region (Hamoutene et al. 2018).

Examinations of the sensitivity of the spatial model results were used to explore the influence of varying several parameters, including the life stage of escapees, the survival and maturity probability of escapees, and the magnitude of escapees per unit harvest produced. In all 3 cases, the number of predicted escapees increased with increased values for these parameters. It is notable that in most scenarios tested, the rivers in the Bay d'Espoir area were predicted to be characterized by >10% escapees under the proposed expansion. Overall, our use of sensitivity analyses provides invaluable insight into the scope for uncertainty in our chosen parameters to influence predictions of impact and ultimately demonstrates that our conclusions are generally robust to changes in key parameters.

5. CONCLUSIONS

Genetic impacts of escaped farmed salmon on wild populations have been demonstrated in both Canada and Europe (Glover et al. 2017), and escapees have been identified as an ongoing threat to the persistence of wild salmon populations (Forseth et al. 2017). Our individual-based population simulations suggest that as the percentage of escapees within a population equals or exceeds 10%, both demographic decline and genetic change are expected, and the magnitude of these changes increases with increasing proportions of escapees present. Model predictions of escapee dispersal under the examined expansion scenario suggest increases and shifts in both the number and distribution of escapees in southern Newfoundland rivers, consistent with estimates of propagule pressure. In future, spatial predictions could be improved with data on escapees in the region, including the number and distribution of escapees in the wild, the proportion of early and late escapees that actually enter freshwater, and the temporal occurrence of escape events across the production cycle. Ultimately, the approaches applied here allow the identification of potential impacts predicted under aquaculture expansion and illustrate how model-based predictions of escapee dispersal and genetic impacts can be used to inform both aquaculture management decisions and wild salmon conservation.

Acknowledgements. The authors thank R. Gregory and T. Kess for comments on this manuscript. Funding was provided through the Fisheries and Oceans Program for Aquaculture Regulatory Research. This work has benefited greatly from a 3 year Canada-EU Galway Statement for the Transatlantic Ocean Research Alliance Working Group on modelling genetic interactions among wild and farm escaped Atlantic Salmon in the North Atlantic, involving participants from 7 countries. The models applied here were evaluated and discussed as part of this working group.

LITERATURE CITED

Baskett ML, Burgess SC, Waples RS (2013) Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. Evol Appl 6:1090–1108

Bolstad GH, Hindar K, Robertsen G, Jonsson B and others (2017) Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. Nat Ecol Evol 1:0124

Bourret V, O'Reilly PT, Carr JW, Berg PR, Bernatchez L (2011) Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. Heredity 106:500–510

Castellani M, Heino M, Gilbey J, Araki H, Svåsand T, Glover KA (2015) IBSEM: An individual-based Atlantic salmon population model. PLOS ONE 10:e0138444

Castellani M, Heino M, Gilbey J, Araki H, Svåsand T, Glover KA (2018) Modeling fitness changes in wild Atlantic salmon populations faced by spawning intrusion of domesticated escapees. Evol Appl 11:1010–1025

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2010) COSEWIC assessment and status report on the Atlantic salmon *Salmo salar* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa

Dempson JB, Furey G, Bloom M (2004) Status of Atlantic salmon, *Salmo salar*, in Conne River, SFA 11, Newfoundland, 2003. DFO Can Sci Adv Sec Res Doc 2004/057

DFO (2013) Recovery potential assessment for the south Newfoundland Atlantic salmon (*Salmo salar*) designatable unit. DFO Can Sci Advis Sec Sci Advis Rep 2012/007,

DFO (2018a) Review of the science associated with the inner Bay of Fundy Atlantic salmon live gene bank and supplementation programs. DFO Can Sci Advis Sec Sci Advis Rep 2018/041

DFO (2018b) Stock assessment of Newfoundland and Labrador Atlantic salmon — 2017. DFO Can Sci Advis Sec Sci Advis Rep 2018/38

DFO (2019) 2018 Atlantic salmon in-season review for the Newfoundland and Labrador region. DFO Can Sci Advis Sec Sci Rep 2019/004

Diserud OH, Fiske P, Sægrov H, Urdal K and others (2019) Escaped farmed Atlantic salmon in Norwegian rivers during 1989–2013. ICES J Mar Sci 76:1140–1150

Fleming IA, Hindar K, Mjølnerød IB, Jonsson B, Balstad T, Lamberg A (2000) Lifetime success and interactions of farm salmon invading a native population. Proc R Soc B 267:1517–1524

Forseth T, Barlaup BT, Finstad B, Fiske P and others (2017) The major threats to Atlantic salmon in Norway. ICES J Mar Sci 74:1496–1513

Glover KA, Pertoldi C, Besnier F, Wennevik V, Kent MP, Skaala Ø (2013) Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genet 14:74

Glover KA, Solberg MF, McGinnity P, Hindar K and others (2017) Half a century of genetic interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. Fish Fish 18:890–927

Glover KA, Urdal K, Næsje T, Skoglund H and others (2019) Domesticated escapees on the run: the second-generation monitoring programme reports the numbers and proportions of farmed Atlantic salmon in >200 Norwegian rivers annually. ICES J Mar Sci 76:1151–1161

Hamoutene D, Cote D, Marshall K, Donnet S and others (2018) Spatial and temporal distribution of farmed Atlantic salmon after experimental release from sea cage sites in Newfoundland (Canada). Aquaculture 492:147–156

Hansen LP, Jacobsen JA (2003) Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. ICES J Mar Sci 60:110–119

Hansen LP, Youngson AF (2010) Dispersal of large farmed Atlantic salmon, *Salmo salar*, from simulated escapes at fish farms in Norway and Scotland. Fish Manag Ecol 17: 28–32

Hansen LP, Jacobsen JA, Lund RA (1993) High numbers of farmed Atlantic salmon. *Salmo salar* L., observed in oceanic waters north of the Faroe Islands. Aquacult Res 24:777–781

Hansen LP, Reddin DG, Lund RA (1997) The incidence of reared Atlantic salmon (*Salmo salar* L.) of fish farm origin at West Greenland. ICES J Mar Sci 54:152–155

Heino M, Svåsand T, Wennevik V, Glover KA (2015) Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. Aquacult Environ Interact 6: 185–190

Hindar K, Fleming IA, McGinnity P, Diserud A (2006) Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. ICES J Mar Sci 63:1234–1247

IFC International (2012) Offshore mariculture escapes genetic/ecological assessment (OMEGA) model version 1.0 model overview and user guide. August. Seattle, WA. Prepared for NOAA Fisheries, Seattle, WA

Jensen AJ, Karlsson S, Fiske P, Hansen LP, Hindar K, Ostborg GM (2013) Escaped farmed Atlantic salmon grow, migrate and disperse throughout the Arctic Ocean like wild salmon. Aquacult Environ Interact 3:223–229

Jóhannsson R, Guðjónsson S, Steinarsson A, Friðriksson J (2017) Áhættumat vegna mögulegrar erfðablöndunar milli eldislaxa og náttúrulegra laxastofna á Íslandi. Marine and Freshwater Research Institute, Reykjavik

Karlsson S, Diserud OH, Fiske P, Hindar K (2016) Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. ICES J Mar Sci 73: 2488–2498

Keyser F, Wringe BF, Jeffery NW, Dempson JB, Duffy S, Bradbury IR (2018) Predicting the impacts of escaped farmed Atlantic salmon on wild salmon populations. Can J Fish Aquat Sci 75:506–512

McGinnity P, Stone C, Taggart JB, Cooke D and others (1997) Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES J Mar Sci 54:998–1008

McGinnity P, Prodöhl P, Ferguson A, Hynes RA and others (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proc R Soc B 270: 2443–2450

Morris MRJ, Fraser DJ, Heggelin AJ, Whoriskey FG, Carr JW, O'Neil SF, Hutchings JA (2008) Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. Can J Fish Aquat Sci 65: 2807–2826

O'Reilly PT, Carr JW, Whoriskey FG, Verspoor E (2006) Detection of European ancestry in escaped farmed Atlantic salmon, *Salmo salar* L., in the Magaguadavic River and Chamcook Stream, New Brunswick, Canada. ICES J Mar Sci 63:1256–1262

Porter TR, Riche LG, Traverse GR (1974) Catalogue of rivers in insular Newfoundland, Vol D. Data Record Series No. NEW/D-74-9. Resource Development Branch, Fisheries and Marine Service, Newfoundland Region, St. John's

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Skaala Ø, Glover KA, Barlaup BT, Svåsand T, Besnier F, Hansen MM, Borgstrøm R (2012) Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. Can J Fish Aquat Sci 69: 1994–2006

Skaala Ø, Besnier F, Borgstrøm R, Barlaup B and others (2019) An extensive common garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. Evol Appl 12:1001–1016

Skilbrei OT, Heino M, Svåsand T (2015) Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. ICES J Mar Sci 72:670–685

Stabell OB (1984) Homing and olfaction in salmonids: A critical review with special reference to the Atlantic salmon. Biol Rev Camb Philos Soc 59:333–388

Svenning MA, Lamberg A, Dempson B, Strand R, Hanssen ØK, Fauchald P (2017) Incidence and timing of wild and escaped farmed Atlantic salmon (*Salmo salar*) in Norwegian rivers inferred from video surveillance monitoring. Ecol Freshwat Fish 26:360–370

Sylvester EVA, Wringe BF, Duffy SJ, Hamilton LC, Fleming IA, Bradbury IR (2018) Migration effort and wild population size influence the prevalence of hybridization between escaped farmed and wild Atlantic salmon. Aquacult Environ Interact 10:401–411

Sylvester EVA, Wringe BF, Duffy SJ, Hamilton LC and others (2019) Estimating the relative fitness of escaped farmed salmon offspring in the wild and modeling the consequences of invasion for wild populations. Evol Appl 12:705–717

Thorstad EB, Whoriskey F, Rikardsen AH, Aarestrup K (2010) Aquatic nomads: the life and migrations of the Atlantic salmon. In: Aas, Ø, Einum, S, Klemetsen, A, Skurdal, J (eds) Atlantic salmon ecology. Wiley-Blackwell, Oxford, p 1–32

Wringe BF, Jeffery NW, Stanley RRE, Hamilton LC and others (2018) Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. Commun Biol 1:108

Editorial responsibility: Tim Dempster,
Melbourne, Victoria, Australia

Submitted: September 12, 2019; Accepted: November 29, 2019
Proofs received from author(s): February 5, 2020

Vol. 12: 429–445, 2020
https://doi.org/10.3354/aei00376

AQUACULTURE ENVIRONMENT INTERACTIONS
Aquacult Environ Interact

Published October 22

REVIEW

Beyond hybridization: the genetic impacts of non-reproductive ecological interactions of salmon aquaculture on wild populations

I. R. Bradbury[1,*], I. Burgetz[2], M. W. Coulson[2], E. Verspoor[3], J. Gilbey[4], S. J. Lehnert[1], T. Kess[1], T. F. Cross[5], A. Vasemägi[6,7], M. F. Solberg[8], I. A. Fleming[9], P. McGinnity[5]

[1]Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, 80 E White Hills Rd, St. John's, Newfoundland, A1C 5X1, Canada
[2]Fisheries and Oceans Canada, 200 Kent Street Ottawa, Ontario, K1A 0E6, Canada
[3]Rivers and Lochs Institute, University of the Highlands and Islands, Inverness, IV3 5SQ, UK
[4]Marine Scotland Science, Freshwater Fisheries Laboratory, Pitlochry, Scotland PH16 5LB, UK
[5]School of Biological, Earth and Environmental Sciences, University College, Cork, T12 YN60, Ireland
[6]Chair of Aquaculture, Institute of Veterinary Medicine and Animal Sciences, Estonian University of Life Sciences, 51014 Tartu, Estonia
[7]Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, 17893 Drottningholm, Sweden
[8]Population Genetics Research Group, Institute of Marine Research, 5817 Bergen, Norway
[9]Memorial University of Newfoundland, Department of Ocean Sciences, St. John's, Newfoundland, A1C 5S7, Canada

ABSTRACT: Cultured Atlantic salmon *Salmo salar* are of international socioeconomic value, and the process of domestication has resulted in significant behavioural, morphological, and allelic differences from wild populations. Substantial evidence indicates that direct genetic interactions or interbreeding between wild and escaped farmed Atlantic salmon occurs, genetically altering wild salmon and reducing population viability. However, genetic interactions may also occur through ecological mechanisms (e.g. disease, parasites, predation, competition), both in conjunction with and in the absence of interbreeding. Here we examine existing evidence for ecological and non-reproductive genetic interactions between domestic Atlantic salmon and wild populations and the potential use of genetic and genomic tools to resolve these impacts. Our review identified examples of genetic changes resulting from ecological processes, predominately through pathogen or parasite transmission. In addition, many examples were identified where aquaculture activities have either altered the selective landscape experienced by wild populations or resulted in reductions in population abundance, both of which are consistent with the widespread occurrence of indirect genetic changes. We further identify opportunities for genetic or genomic methods to quantify these impacts, though careful experimental design and pre-impact comparisons are often needed to accurately attribute genetic change to aquaculture activities. Our review indicates that ecological and non-reproductive genetic interactions are important, and further study is urgently needed to support an integrated understanding of aquaculture–ecosystem interactions, their implications for ecosystem stability, and the development of potential mitigation and management strategies.

KEY WORDS: Atlantic salmon · Aquaculture · Management · Genetic

1. INTRODUCTION

Atlantic salmon *Salmo salar* aquaculture is of international socioeconomic importance, and the process of domestication has resulted in significant phenotypic (i.e. physiological, Handeland et al. 2003; behavioural, Fleming et al. 1996; morphological, Fleming et al. 1994); and genetic (Cross & King 1983, Karlsson et al.

---

*Corresponding author: ibradbur@me.com

Publisher: Inter-Research · www.int-res.com

2011, Wringe et al. 2019) differences from wild populations. Escape events from Atlantic salmon net pen aquaculture are a regular occurrence (Keyser et al. 2018), and the number of escapees can equate to an appreciable fraction of, or exceed, wild Atlantic salmon census size (Morris et al. 2008, Skilbrei et al. 2015, Wringe et al. 2018). There is substantial evidence that direct genetic interactions, defined as interbreeding, occurs between wild Atlantic salmon and escaped domestic individuals (Karlsson et al. 2016, Glover et al. 2017, Wringe et al. 2018) and can genetically alter wild salmon and reduce population viability (McGinnity et al. 2003, Bourret et al. 2011, Glover et al. 2013, Bolstad et al. 2017, Bradbury et al. 2020). Both in Canada and Norway, recent evidence suggests hybridization may be extensive following escape events (Karlsson et al. 2016, Wringe et al. 2018) and accounts for a substantial proportion of production in smaller rivers (Sylvester et al. 2018b). Accordingly, escaped farmed salmon and direct genetic interactions have been identified as a major threat to the persistence and stability of wild Atlantic salmon across the North Atlantic (Forseth et al. 2017, Bradbury et al. 2020).

However, genetic impacts may also occur, either in concert with or in the absence of hybridization (Verspoor et al. 2015), due to ecological interactions such as competition, predation, and disease or parasite transfer. These non-reproductive genetic changes in wild populations can result from ecological changes that either alter the selective landscape experienced by native fish, and thus change allele frequencies of loci linked to fitness, and/or reduce population abundance, resulting in a loss of genetic diversity (Fig. 1). As these effects do not involve hybridization, they can arise whether domestic animals escape or remain in containment and impact wild populations of any native species. Although practices to limit reproductive genetic interactions with wild Atlantic salmon have been implemented in many areas through the use of sterilization (Verspoor et al. 2015), exotic species, and improved containment strategies (Diserud et al. 2019), these efforts do not prevent non-reproductive genetic effects. In other species such as brown trout *Salmo trutta* or Pacific salmon species (*Oncorhynchus* spp.) where hybridization with escapees is not common or possible, ecologically induced genetic interactions with Atlantic salmon aquaculture remain an ongoing concern (e.g. Coughlan et al. 2006, Ford & Myers 2008). Moreover, given recent trends in industry expansion (e.g. DFO 2016, 2018) and growing concerns regarding the amplification of pests and pathogens such as sea lice through net pen aquaculture (e.g. Vollset et al. 2016, Karbowski et al. 2019), the potential for both ecological and non-reproductive genetic interactions is likely to increase. Nonetheless, despite the potentially broad reaching and significant impacts of non-reproductive genetic interactions on wild Atlantic salmon and other species, the evidence for their presence and our ability to quantify their magnitude has been limited to date (Verspoor et al. 2015).

The goal of this review is to highlight evidence pertaining to the potential for ecological and associated non-reproductive genetic impacts of Atlantic salmon aquaculture on wild populations. Specifically, our

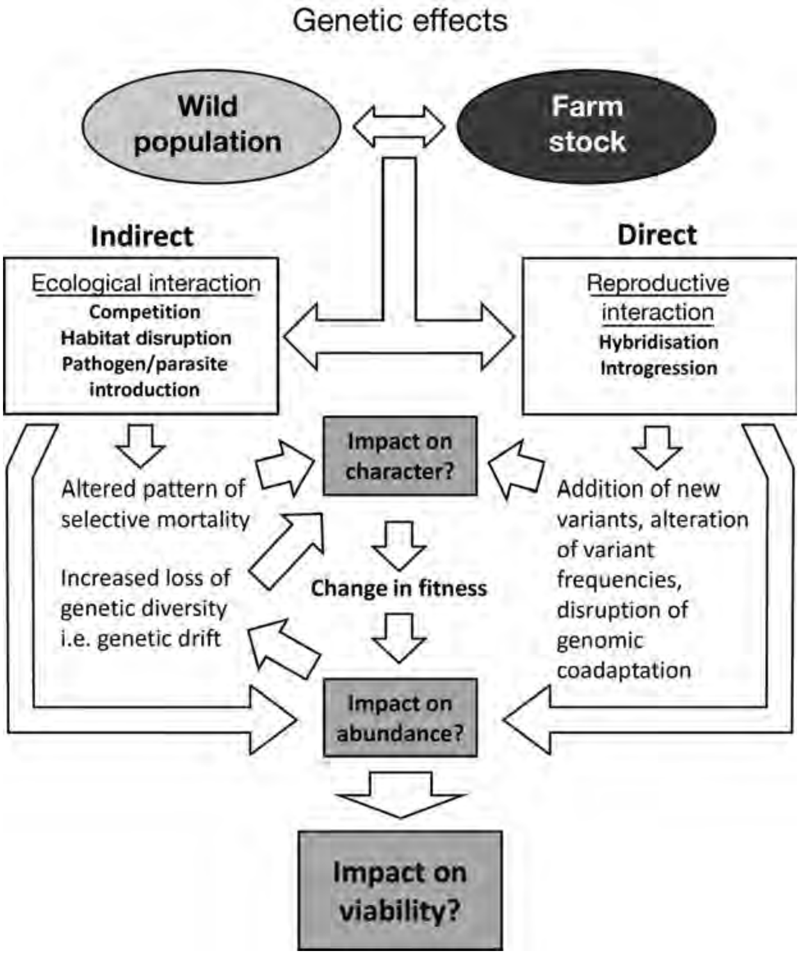


Fig. 1. Schematic of reproductive and non-reproductive genetic interactions between wild and domestic Atlantic salmon *Salmo salar*

objectives are to (1) review examples of genetic changes in wild populations resulting from ecological interactions, or likely more common, evidence for changes in population abundance or the environment experienced by wild populations; and (2) discuss the opportunity recent advances in population genomic approaches present for the assessment of these genetic impacts. Through our review, we highlight opportunities for the further study of non-reproductive genetic impacts of Atlantic salmon aquaculture on wild populations. We directly build on previous reviews and empirical studies focusing on hybridization and introgression (e.g. Karlsson et al. 2016, Glover et al. 2017, Bradbury et al. 2020) and on risk assessments considering both reproductive and non-reproductive effects (e.g. Verspoor et al. 2015). Ultimately, we suggest that ecological and subsequent non-reproductive genetic impacts are likely ubiquitous wherever salmon farming occurs, and that further research is urgently required to better understand the magnitude of these interactions and provide advice regarding impact management and mitigation.

2. EVIDENCE FOR ECOLOGICAL AND NON-REPRODUCTIVE GENETIC IMPACTS

Atlantic salmon net pen aquaculture represents a substantial change to the natural environment and thus the adaptive landscape experienced by wild individuals (Garcia de Leaniz et al. 2007). As such, it can alter the stability and future evolutionary trajectories of wild populations. Furthermore, it might be expected that adjustments to a new adaptive landscape will result in reductions in productivity through increased maladaptation predicted by theoretical demographic-evolutionary models (Bürger & Lynch 1995, Gomulkiewicz & Holt 1995, Kirkpatrick & Barton 1997). Existing studies address genetic changes in naïve populations through disease and parasite transmission, the potential for recovery of disease or parasite resistance through natural selection, observations on genetic changes in co-occurring congener species, and impacts of the farming of non-native species or subspecies. Examples of the latter are the farming of European origin salmon on both the east and west coasts of North America as well as in western South America or Australia. Below we review the literature related to non-reproductive genetic interactions associated with disease and parasite transfer, increased predation pressure, and finally, increased competition (see Table 1). In each case, we first highlight examples of genetic change resulting from these interactions and then set out evidence of demographic decline or the potential for selection consistent with significant genetic impacts. In practice, it can be difficult to distinguish the impacts of reproductive and non-reproductive genetic interactions in examples related to wild Atlantic salmon. As such, here we focus on instances where mechanisms have been identified which are clearly non-reproductive in nature.

2.1. Ecological and non-reproductive genetic changes through disease transmission

Ecological and genetic interactions via disease transmission may result in both alterations to the selective landscape potentially impacting immune associated genetic variation as well as reductions in overall genetic diversity due to demographic decline. To date, few studies have examined the presence of genetic changes due to disease transfer (Table 1A). However, de Eyto et al. (2007, 2011) present evidence of genetic impacts due to novel disease exposure associated with aquaculture activities. In these studies, the progeny of Atlantic salmon from a river without previous exposure to aquaculture were transferred to a river with a long history of associated farming and captive breeding that was expected to have acquired novel micro- and macro-parasitic communities. This experimental design enabled the exposure of animals to novel disease challenges associated with escapes or inadvertent or deliberate introductions. Comparison of observed and expected genotype frequencies at a marker locus for the MHC class II alpha gene and control neutral microsatellite loci of parr and migrant Atlantic salmon stages in the wild demonstrated that genetic change had occurred, and that selection was likely a result of disease-mediated natural selection, rather than any demographic event.

A substantial and growing body of research supports the hypothesis that wild salmon populations are adapted to local pathogen communities both in space and time (Dionne et al. 2007, Tonteri et al. 2010, Consuegra et al. 2011, Kjærner-Semb et al. 2016, Pritchard et al. 2018, Zueva et al. 2018). This suggests a genetic basis for differences in population immunity and that the introduction of new pathogens into susceptible populations could both impose novel selection pressures and reduce genetic diversity through demographic decline. The possibility that pathogen transfer from domestic to wild salmon could drive genetic change in wild populations is supported by

Table 1. Summary of studies presenting evidence for or consistent with the potential for ecological and non-reproductive genetic interactions among Atlantic salmon *Salmo salar* aquaculture and wild salmonid populations. N/A: not applicable

Interaction	Primary observation	Evidence (direct or supportive)	Selection / demographic	Species impacted	Reference
(A) Disease transfer					
Common garden experiment (naïve non-local wild population introduced into different river system as eggs)	Evidence of allele frequency change at major histocompatibility (MH) genes during first 6 months in introduced population; no change in local population)	Supportive	Selection	Atlantic salmon *S. salar*	de Eyto et al. (2007)
Common garden experiment (naïve non-local wild population introduced into different river as eggs)	Evidence of different allele frequency change at major histocompatibility (MH) genes in introduced population from 6 months to 18 months; no change in local population)	Supportive	Selection	Atlantic salmon *S. salar*	de Eyto et al. (2011)
Genetic survey of natural populations (not associated with aquaculture)	Evidence of clinal geographical response in major histocompatibility (MH) genes in response to water temperature variation)	Supportive	Selection	Atlantic salmon *S. salar*	Dionne et al. (2007)
Genetic survey of natural populations potentially sensitive and tolerant of *Gyrodactylus salaris*	Evidence of clinal geographical response in major histocompatibility (MH) & other immune relevant genes in response to water temperature variation)	Supportive (possible direct link to *G. salaris* parasite)	Selection	Atlantic salmon *S. salar*	Tonteri et al. (2010)
Genetic survey of natural populations in areas with and without aquaculture activity	Evidence of spatial allele variation at major histocompatibility (MH) genes	Supportive (possible direct link to viral pathogens)	Selection	Atlantic salmon *S. salar*	Consuegra et al. (2011)
Genetic survey of natural populations in region of significant aquaculture activity	Evidence of SNP variation associated with selective sweeps of immune response genes	Supportive (source of selective agent unknown)	Selection	Atlantic salmon *S. salar*	Kjærner-Semb et al. (2016)
Genetic survey of natural populations within single large river complex (not associated with aquaculture)	Evidence of SNP variation associated with major histocompatibility (MH) genes	Supportive	Selection	Atlantic salmon *S. salar*	Pritchard et al. (2018)
Disease screening of escaped farmed Atlantic salmon in a wild river	Virus infected escaped farmed salmon entering rivers near cage sites	Supportive	Both	Atlantic salmon *S. salar*	Madhun et al. (2015)
Disease screening of returning wild Atlantic salmon in Norway at 6 sites	Evidence for the infection of wild salmon from escaped farmed salmon at marine feeding areas	Supportive	Both	Atlantic salmon *S. salar*	Madhun et al. (2018)
Genetic screening of PRV in wild and farmed Atlantic salmon	Evidence for long distance transmission of PRV likely associated with aquaculture industry	Supportive	Both	Atlantic salmon *S. salar*	Garseth et al. (2013)

Table continued on next page

Table 1 (continued)

Interaction	Primary observation	Evidence (direct or supportive)	Selection / demgraphic	Species impacted	Reference
Review of studies documenting furunculosis prevalence in Norway from 1964–1992	Evidence for the transfer of furunculosis from fish farms to wild salmonids in Norway	Supportive	Demographic	Various salmonids	Johnsen & Jensen (1994)
Genetic screening of ISAV variants in wild and farmed salmon in Norway	Evidence for the horizontal transmission of ISAV variants seen in farmed salmon to wild populations	Supportive	Both	Atlantic salmon *S. salar*	Nylund et al. (2019)
(B) Parasite transfer					
Statistical modeling of the effect on return rates of sea lice levels (low/med/high) over a 26 year period for 1SW Erriff salmon	Wild salmon returns were strongly reduced (>50%) following years with high lice levels during smolt out-migration (farms located at the mouth of the estuary)	Supportive	Both	Atlantic salmon *S. salar*	Shephard & Gargan (2017)
Tag/recapture experiment of prophylactically treated smolts exposed to different farm-origin sea lice pressure	Recapture rate of untreated adult salmon following exposure to high sea lice density was 0.03% compared to treated salmon (1.86%)	Direct	Both	Atlantic salmon *S. salar*	Bøhn et al. (2020)
Association between sea lice counts on farmed Atlantic salmon and wild out-migrating chum salmon	Significant positive association between the sea lice abundance on farms and the likelihood that juvenile chum salmon would be infested. Increased abundance of lice on farms was not significantly associated with the levels of infestation observed on juvenile chum salmon	Supportive	Both	Chum salmon *Oncorhynchus keta*	Nekouei et al. (2018)
Experimental sea lice infection of wild brown trout post-smolts and examinations of marine migratory behavior	Experimental sea lice infection associated with increased mortality, and decreased migration distance, and marine residency	Supportive	Both	Sea trout *S. trutta*	Serra-Llinares et al. (2020)
Review paper: integrating laboratory and field observational studies of lice on out-migrating *S. salar* and *S. trutta*	Sea lice loads on out-migrating sea trout in areas with aquaculture commonly exceed threshold levels that are known to induce physiological compromise or mortality in laboratory experiments	Supportive	Both	Sea trout *S. trutta*	Thorstad & Finstad (2018)
Review paper: integrating laboratory and field observational studies of lice on out-migrating *S. salar* and *S. trutta*	Premature migratory return	Direct	Demographic	Sea trout *S. trutta*	Thorstad & Finstad (2018)

Table continued on next page

Table 1 (continued)

Interaction	Primary observation	Evidence (direct or supportive)	Selection / demographic	Species impacted	Reference
Review paper: integrating laboratory and field observational studies of lice on out-migrating *S. salar* and *S. trutta*	Summary of meta-analysis and tagged treated smolt survival to returning adults experiment	Supportive	Both	Atlantic salmon *S. salar*	Thorstad & Finstad (2018)
Sea lice abundance on out-migrating pink salmon and chum salmon differences pre- and post-exposure to Atlantic salmon farms	Quantitative estimate of transmission rates from farm to out-migrating pink and chum salmon, including subsequent transmission dynamics of lice within the wild population	Supportive	Demographic	Pink salmon *O. gorbuscha* and chum salmon *O. keta*	Krkošek et al. (2005)
Hierarchical model of stock-recruit dynamics of coho salmon with differential sea lice infestation	Coho salmon population productivity in an area of intensive salmon aquaculture was depressed approximately sevenfold during a period of salmon louse infestations compared to unexposed populations.	Supportive	Demographic	Coho salmon *O. kisutch*	Connors et al. (2010)
Modeling effect of sea lice infections on population abundance of pink salmon	Pink salmon populations exposed to salmon farms; mortality rate caused by sea lice was estimated to range from 16 to 97 %	Supportive	Demographic	Pink salmon *O. gorbuscha*	Krkošek et al. (2007)
Analysis of spawner-recruit data and sea lice abundance on farms	Sea lice counts on fish farms were negatively associated with adult returns of 2 species of Pacific salmon	Supportive	Demographic	Pink salmon *O. gorbuscha* and Coho salmon *O. kisutch*	Krkošek et al. (2011a)
Screening of pyrethroid resistance genotype in *Lepeophtheirus salmonis* over time	Widespread changes in the frequency of genotype associated with pyrethroid resistance in sea lice across the North Atlantic	Direct	Selection	Salmon louse *Lepeophtheirus salmonis*	Børretzen Fjørtoft et al. (2020)
G. salaris infection associated with wild salmon population decline	Wild stocks decreased in size by an average of 85 % and smolt numbers decreased by as much as 98 % following introduction of *G. salaris* into Norway	Supportive	Demographic	Atlantic salmon *S. salar*	Denholm et al. (2016)
Genomic basis of resistance to *G. salaris*	Identified 3 genomic regions associated with adaptation to parasite resistance in wild salmon	Supportive	N/A	Atlantic salmon *S. salar*	Zueva et al. (2014)
Genomic basis of resistance to *G. salaris*	Identified 57 candidate genes potentially under positive selection associated with *G. salaris* resistance and enriched for lymph node development, focal adhesion genes and anti-viral responses	Supportive	N/A	Atlantic salmon *S. salar*	Zueva et al. (2018)

Table continued on next page

several recent findings documenting the potential for exposure and supporting pathogen transfer as mechanisms for genetic impacts (Table 1A). First, Madhun et al. (2015) report the detection of virus infected escaped farmed salmon entering rivers near cage sites, suggesting clear evidence of exposure of freshwater rearing juvenile salmon populations to aquaculture associated pathogens. Second, Madhun et al. (2018) also document the presence of piscine orthoreovirus (PRV) in returning wild adult Atlantic salmon in Norway, and that the frequency of infection increased with body size and displayed no geographic signal, suggesting infection was occurring between escapees and wild salmon at marine feeding areas. Nylund et al. (2019) report that infectious salmon anemia virus (ISAV) variants in farmed salmon are increasing in prevalence in the wild consistent with horizontal transmission from farmed salmon to wild populations. Similarly, Garseth et al. (2013) examine pathogen transfer between wild and farmed salmon using analysis of protein coding sequences in PRV in Norway and suggest occurrence in the wild is due to long distance transmission likely associated with the aquaculture industry. Finally, several studies have documented the spread of furunculosis, a septicemic bacterial disease, from fish farms to wild salmonids in Norwegian rivers (Johnsen & Jensen 1994). Taken together, these findings indicate that ecologically induced genetic impacts on wild salmon populations associated with disease transmission from aquaculture populations are highly likely. However, both the magnitude of new selection pressures and demographic impacts are uncertain and likely case specific.

Diseases, introduced or increased in incidence by salmon aquaculture activities, could also have an impact on co-occurring wild species such as anadromous brown trout, as implied by the steep decline in anadromous trout numbers in many Irish, Scottish, and Nor-

Table 1 (continued)

Interaction	Primary observation	Evidence (direct or supportive)	Selection / demographic	Species impacted	Reference
Growth and survival of sea lice infected Arctic Charr	Infection intensity correlated positively with mortality and negatively with growth in experimental trials	Supportive	Both	Arctic charr *Salvelinus alpinus*	Fjelldal et al. (2019)
(C) Predation					
Increased predation on wild species	Increased avian predation on wild salmon and brown trout following the release of captive bred smolts	Supportive	Demographic / selective?	Brown trout *S. trutta*	Kennedy & Greer (1988)
Predation on released farmed escapes	High levels of predation on released farmed Atlantic salmon near cage sites	Supportive	Demographic / selective?	Atlantic salmon *S. salar*	Hamoutene et al. (2018)
(D) Competition					
Competition between wild and farmed juvenile Atlantic salmon in freshwater	30% reduction in wild population productivity in the presence of farmed fish	Supportive	Demographic	Atlantic salmon *S. salar*	Fleming et al. (2000)
Competition between wild and farmed juvenile Atlantic salmon in freshwater	Overlap in diet among types of crosses demonstrates competition	Supportive	Demographic	Atlantic salmon *S. salar*	Skaala et al. (2012)
Metabolic rate and survival of farmed Atlantic salmon offspring	Presence of wild-farmed hybrids reduced survival of wild individuals	Supportive	Demographic	Atlantic salmon *S. salar*	Robertsen et al. (2019)

wegian rivers since the late 1980s, which may be linked to sea lice infestations (see Section 2.2) associated with marine salmonid farming. A study by Coughlan et al. (2006) in some Irish rivers suggested that salmon farming and ocean ranching could indirectly affect, most likely mediated by disease, the genetics of cohabiting anadromous brown trout by reducing variability at major histocompatibility class I genes. A significant decline in allelic richness and gene diversity at the Satr-UBA marker locus, observed since aquaculture started, which may indicate a selective response, was not reflected by similar reductions at neutral loci. Subsequent recovery of variability at the Satr-UBA marker, seen among later samples, may reflect an increased contribution by resident brown trout to the remaining anadromous population. Similarly, Miller et al. (2011) link genomic profiles consistent with viral infection with increased likelihood of mortality prior to spawning in Fraser River sockeye salmon *Oncorhynchus nerka*. Morton et al. (2017) document piscine orthoreovirus (PRV) in 95% of farmed Atlantic salmon in British Columbia, Canada, and infection rates in wild Pacific salmon of 37–45% near salmon farms, and of 5% at sites distant to farms suggesting PRV transfer is occurring from salmon farms to wild salmon populations.

2.2. Ecological and non-reproductive genetic effects through parasites

Like disease transfer, the introduction of novel parasites could both impose new selection pressures and drive demographic decline. Although no examples of genetic change attributable to parasite transfer from salmon aquaculture were identified, substantial research has demonstrated the (1) transfer of parasites from aquaculture salmon to wild populations, (2) significant demographic impacts resulting, and (3) a genetic basis to resistance, all of which support the presence of genetic change occurring as a result. Examples to date have most notably been via infections of sea lice or the monogenetic trematode *Gyrodactylus salaris* (Table 1B). Declines in wild stocks attributed to sea lice outbreaks in farm-intensive areas have been documented in Ireland, Scotland and Norway. Thorstad & Finstad (2018) reviewed the literature related to sea lice impacts on wild stocks documenting 12–29% fewer returning adult spawners due to lice-induced mortality from fish farms. In one of the most extreme cases documented to date, Shephard & Gargan (2017) suggested that one-sea-winter (1SW) salmon returns on the River Erriff were more than 50% lower in years following high lice levels on nearby farms. This increased mortality was in addition to decreased returns due to poorer marine survival. Similarly, Bøhn et al. (2020) tagged and released Atlantic salmon smolts both with a prophylactic treatment against lice and without such treatment, and recaptured survivors returning to freshwater after spending 1–4 yr at sea. They report that the mortality of untreated smolts was as much as 50 times higher compared to treated smolts during sea lice outbreaks. It is worth noting that these estimates of lice-induced mortality among Atlantic salmon should be considered as minimum estimates for species such as anadromous brown trout, whose marine migrations are more coastal, thus increasing their exposure to net pen sites (Thorstad & Finstad 2018). Recent work by Serra-Llinares et al. (2020) reports increased mortality, reduced marine migrations, and reduced marine residency in brown trout experimentally infested with sea lice, consistent with significant demographic impacts of sea lice infection in brown trout. Similarly, for migratory Arctic char *Salvelinus alpinus* exposed to elevated sea lice burden due to fish farming activity (Bjørn et al. 2001), the negative impact on growth and survival may potentially lead to selection against anadromy (Fjelldal et al. 2019).

In addition to potential impacts on Atlantic salmonids, evidence also exists that the transfer of sea lice from farmed Atlantic salmon to Pacific salmon species occurs (e.g. Nekouei et al. 2018), again consistent with the potential non-reproductive genetic interactions. For example, out-migrating juvenile pink salmon *O. gorbuscha* and chum salmon *O. keta*, are estimated to experience 4 times greater sea lice infection pressure near Atlantic salmon farms compared to background infection levels (Krkošek et al. 2005), and in juvenile sockeye salmon *O. nerka*, infection rates were elevated after migration past these salmon farms (Krkošek et al. 2005, Price et al. 2011). For Coho salmon *O. kisutch*, ecological interactions with infected species, as well directly with Atlantic salmon farms, can result in higher infection levels (Connors et al. 2010). These lice infections in Pacific salmon species have also been associated with population declines. Krkošek et al. (2007) found that sea lice infestation from Atlantic salmon farms on out-migrating pink salmon smolts have led to declines in wild populations in the Broughton Archipelago, with forecasting models suggesting that local extinction was imminent. For these pink salmon populations exposed to salmon farms, mortality rate caused by sea lice was estimated to range from 16 to 97% (Krkošek et al. 2007), and population declines were also observed in Coho salmon populations (Connors et al. 2010). Krkošek et al. (2011a) demonstrated that sea lice abundance on fish farms in British Columbia, Canada, were negatively associated with nearby returns of both pink salmon and Coho salmon. Furthermore, changes in parasite management on salmon farms have been shown to help reduce infection rates on wild salmon (Peacock et al. 2013), supporting this linkage and suggesting mitigation might be possible.

Given evidence of significant sea lice associated demographic declines, it seems likely that sea lice-induced mortality could drive reductions in genetic diversity. However, a large body of research suggests resistance to sea lice may have a genetic basis and be heritable (Tsai et al. 2016, Correa et al. 2017, Robledo et al. 2019), making it highly likely that wild populations would change in response to new selection pressures. In support of this hypothesis, Børretzen Fjørtoft et al. (2020) documented large-scale genetic changes in sea lice in response to chemotherapeutant usage across the North Atlantic. They observed significant temporal changes in wild sea lice populations in the frequency of a genotype associated with pyrethroid resistance due to strong selection pressure associated with its usage in Atlantic salmon aquaculture. Similarly, Dionne et al. (2009) reported significant changes in myxozoan resistance associated MHC alleles in Atlantic salmon, most likely linked with an infection-related mortality event, further supporting the potential for parasite-associated genetic impacts in wild populations.

The first appearance of *G. salaris* in Norway has been linked to the introduction of Atlantic salmon from Baltic catchments, resulting in high levels of mortality among wild populations (Johnsen & Jensen 1991). Admittedly, the spread of *G. salaris* in the wild does not seem primarily linked to salmon aquaculture. Instead, the transfer of individuals associated with stocking activities seems to have played a dominant role in transmission. Nonetheless, it is included here, as it clearly illustrates the potential for the introduction of non-native individuals to transfer parasites to local populations, the potential for subsequent significant demographic impacts, and a genetic basis to parasite resistance. In *G. salaris* infections, very high rates of mortality in naïve wild populations strongly supports the potential for significant demographic decline, losses of genetic diversity, and parasite driven selection, as has been recently concluded (Karlsson et al. 2020). For example, following several independent introductions of *G. salaris* into Norway, exposed wild populations decreased in abundance by an average of 85%, and smolt numbers decreased by as much as 98% (Denholm et al. 2016). Several studies suggest a genetic basis to *G. salaris* resistance among wild salmon populations in Europe. Gilbey et al. (2006) identified 10 genomic regions associated with heterogeneity in both innate and acquired resistance using crosses of resistant Baltic and susceptible Atlantic populations. Zueva et al. (2014) compared Baltic and Atlantic Atlantic salmon populations characterized by different levels of resistance to *G. salaris* and identified 3 genomic regions potentially experiencing parasite-associated adaptation in the wild. More recently, Zueva et al. (2018) compared salmon populations from northern Europe classified as extremely susceptible or resistant to *G. salaris*. They identify 57 candidate genes potentially under resistance-associated selection and this set of loci was shown to be enriched for genes associated with both innate and acquired immunity. These findings suggest that ecological and non-reproductive genetic impacts on wild populations associated with parasite transmission, such as sea lice from aquaculture installations, are highly likely, both because of the potential for substantial mortality to occur through exposure and for it to be selective through a clear genetic basis to population differences in resistance.

2.3. Ecological and non-reproductive genetic effects through predation

Increased predation associated with salmon aquaculture activities could result in both declines in abundance and selective mortality. Although direct estimates are lacking, some evidence exists to support the possibility of such a link, most likely through predators being attracted to aquaculture activities (Table 1C). Aquaculture sites have been shown to attract wild fish, invertebrates, marine mammals, and birds, likely due to the addition of food, and the farmed salmon themselves (see review in Callier et al. 2018), and the end result may be increased predation on wild individuals in the vicinity. Although it is possible that escapees could distract predators and reduce predation on wild populations through predator swamping, there is no evidence to date to support this. In fact, Kennedy & Greer (1988) reported heavy predation on hatchery smolts and wild Atlantic salmon and brown trout from the river Bush in Northern Ireland by the great cormorant *Phalacrocorax carbo*. This suggested a link between the release of captive bred smolts (a proxy for farm escapes), the attraction of increased numbers of these predatory birds to the river, and increased predation on the river's wild Atlantic salmon and brown trout. Similarly, Hamoutene et al. (2018) conducted experimental releases and tracking of aquaculture Atlantic salmon near cage sites in southern Newfoundland, Canada. They found that most released fish were not detected beyond a few weeks of release, with temperature and movement data supporting predation as a cause. Increased predation of wild salmon smolts or adults near sea cages could therefore drive demographic decline or potentially act as a selective agent if predators cued on size, behaviour, or other traits. Moreover, rates of predation may be higher for individuals already experiencing infections, such as sea lice (see Section 2.2). Krkošek et al. (2011b) reported experimental evidence that predators selectively consuming infected prey which could simultaneously impose predation associated impacts and amplify disease or parasite associated selection and mortality.

2.4. Ecological and non-reproductive genetic effects through competitive interactions

Ecological and non-reproductive genetic effects have also been suggested via evidence for competitive interactions among farm and wild salmon. These competitive effects could be the result of ecological interactions among wild, farm escaped and hybrid offspring involving differences in behaviour among cross types such as in aggression, dominance, risk proneness, feeding/foraging activity. And as such, competition associated with these behavioral differences may influence survival and the selective environments experienced by wild fish. Given the clear overlap in habitat use-, and evidence for density dependence, these seem most likely to take place in freshwater during the juvenile stage (Table 1D). This has been illustrated by the work of Fleming et al. (2000), who released sexually mature farm and wild Atlantic salmon into the River Imsa in Norway. Despite the farm fish achieving less than one-third of the breeding success compared to wild fish, there was evidence of resource competition and competitive displacement, as the productivity of the wild fish was depressed by more than 30%. Fleming et al. (2000) concluded that invasions of farm fish have the potential for impacting wild population productivity both via changes to locally adaptive traits as well as reductions in genetic diversity. Skaala et al. (2012) documented similar effects in another natural system in Norway. These authors compared the performance of farm, wild, and hybrid Atlantic salmon and suggested that overlap in diets and competitions can impact wild productivity, which could reduce genetic variation in wild populations. Supporting this hypothesis, Robertsen et al. (2019) demonstrated that the presence of farmed–wild hybrids reduced the survival of wild half-sibs under semi-natural conditions. There is also clear evidence that escaped farmed salmon can compete for spawning habitats and may superimpose redds on top of those of wild Atlantic salmon (Webb et al. 1991, 1993a,b, Fleming et al. 1996). Such superimposition of redds could affect both spawning time and location of wild fish, as well as the growth and survival of wild offspring. Overall, it seems highly probable that increased competition can result in changes to the selective landscape experienced by wild individuals and in reductions in population size.

3. QUANTIFYING GENETIC EFFECTS OF NON-REPRODUCTIVE ECOLOGICAL INTERACTIONS

The studies reviewed above demonstrate strong potential for non-reproductive genetic interactions to occur in wild populations. However, quantifying these interactions between wild populations and domestic strains remains a major challenge, particularly when hybridization is occurring (i.e. direct genetic interactions). Dramatic increases in DNA sequencing capacity over the last decade present new opportunities for the use of genomic tools to quantify the impacts of net pen aquaculture on wild populations. Non-reproductive genetic interactions represent a special, more complex challenge, and the utility of genetic and genomic tools to resolve these genetic interactions will depend on the route and genomic scale of impact. That said, a large body of literature has been produced in recent years on the use of genetic/genomic tools to quantify both adaptive diversity and neutral diversity and effective population size or changes therein. As such, a clear opportunity exists to apply genetic and genomic methods to quantify these impacts.

3.1. Detecting changes in adaptive diversity

In the context of impacts due to changes in the selective landscape driven by ecological change, genomic change could be associated with a single gene, or many genes (i.e. polygenic). Genetic and genomic tools are increasingly being used to quantify the magnitude of natural selection in the wild (Vitti et al. 2013) and many approaches have been developed (Table 2A). One of the best approaches to quantify

Table 2. Summary of available genetic and genomic methods to evaluate non-reproductive genetic interactions

Method	Comparison	Statistics/tests	Reference
(A) Changes in adaptive diversity			
Time-series analysis	Changes in allele frequency	Empirical likelihood ratio test (ELR)	Feder et al. (2014)
	Changes in allele frequency	Frequency increment test (FIT)	Feder et al. (2014)
Temporal comparisons, pre- vs. post-impact	Changes in allele frequencies	Principal component analysis, outlier detection, genetic differentiation (F_{ST})	Bitter et al. (2019)
Temporal comparisons, pre- vs. post-impact	Changes in allele frequencies in response to size-selection gradients	% polymorphism, nucleotide diversity, & allele frequency shifts (controls vs. experimental samples)	Therkildsen et al. (2019)
Domestic ancestry estimation under different stocking intensities	Relationship between domestic ancestry and recombination rate at different genomic scales		Leitwein et al. (2019)
Outlier detection	Locus-specific comparison of posterior probabilities of models with and without selection	F_{ST} coefficient & and Bayes factor scores	Foll & Gaggiotti (2008)
Outlier detection	Tests of neutrality based on principal components analysis	Mahalanobis distance	Luu et al. (2017)
Impacted vs. non-impacted	Signatures of selection that covary with environmental stressor (e.g. pollution)	F_{ST}, population branch statistic, differences in nucleotide diversity along 20-kilobase sliding window	Oziolor et al. (2019)
Impacted vs. non-impacted	Signatures of selection associated with environmental stressor	F_{ST} outlier (FDIST2)	Dayan et al. (2019)
Genome-wide association studies	Polygenic associations with population decline involving genomic regions related to metabolism, developmental & physiological processes	Change in μ (signature of selective sweeps) between declining and non-declining population status of Atlantic salmon; Redundancy analysis (RDA) for detection of outliers, polygenic risk scores	Lehnert et al. (2019)
Soft selective sweeps	Identification of new alleles to intermediate frequency against a background of unusually long haplotypes of low nucleotide diversity	Integrated haplotype scores (iHS)	Voight et al. (2006)
Soft selective sweeps	Identification of selected alleles nearing or having achieved fixation in one population but that remains polymorphic in the wider group of populations.	Extended cross population haplotype homozygosity (XP-EHH)	Sabeti et al. (2007)
Soft selective sweeps	Detection of positive selection acting to increase haplotype homozygosity; combines distribution of fragment lengths between mutations and number of segregating sites between all pairs of chromosomes; ratio of haplotype homozygosity for derived & ancestral alleles.	Number of segregating sites by length (nSL); similar to iHS but (1) a genetic map is not required and (2) more robust to recombination and/or mutation rate variation	Ferrer-Admetlla et al. (2014)

Table continued on next page

Table 2 (continued)

Method	Comparison	Statistics/Tests	Reference
Machine learning	Correlates of habitat/environmental variables with observed genetic structure	Random Forest; PCA loadings; outlier detection	Sylvester et al. (2018a)
Machine learning	Detection of loci of small phenotypic effect on a key life-history variable (e.g. run timing) across multiple populations	Random forest; outlier detection; PCA	Brieuc et al. (2015)
(B) Changes in neutral diversity or effective population size			
Effective population size	Single-sample method based on linkage disequilibrium to estimate effective populations size	Contemporary N_e	Waples & Do (2010), Waples et al. (2016)
Effective population size	Single-sample method to estimate changes in contemporary N_e by comparing linkage disequilibrium estimates with recombination rates estimated from physical linkage or genomic position	Contemporary N_e estimates at various times in the past	Hollenbeck et al. (2016)
Effective population size	Application of Hollenbeck et al. (2016) for range-wide populations of Atlantic salmon and associations of genomic regions to decline status	Contemporary N_e estimates over time	Lehnert et al. (2019)

the presence of selection is either the comparison of representative pre- and post-impact genetic samples in the absence of hybridization or the examination of situations with the capacity to quantify and correct for signatures of recent or current hybridization (Leitwein et al. 2019). For time series analysis of changes in allele frequency associated with selection, differentiation measures such as the fixation index (F_{ST}) are commonly used, and several tests have been recently proposed using bi-allelic loci, including the empirical likelihood ratio test (ELRT) and the frequency increment test (FIT) (Feder et al. 2014). Recent temporal comparisons of natural selection in ecological, climate adaptation, and fishery-impact studies have revealed detectable increases in genomic differentiation over even short timeframes (e.g. 1 to 4 generations; Bitter et al. 2019, Leitwein et al. 2019, Therkildsen et al. 2019), indicating genomic tools show high power to detect changes in natural selection when recent pre-impact baselines are available. Where replicate temporal comparisons across sites can be made, this may allow uncovering parallel patterns and non-parallel signatures of adaptation. Knowledge of pre-impact genomic variation across replicates could quantify both the source and magnitude of non-reproductive genetic impacts; sites with similar starting genomic variation are more likely to show parallel responses, unless source or strength of selection differs.

In the absence of pre-impact samples, traditional tests for the presence of outliers (e.g. Foll & Gaggiotti 2008, Luu et al. 2017), trait associations, or selective sweeps (e.g. Nielsen 2005) may be applied using genome-wide polymorphism data, though the ability to attribute a given impact to these loci may be problematic. Similar to pre- and post-impact temporal comparisons, tests for genomic differentiation using metrics such as F_{ST} between sites with differing levels of exposure to stressors can be used to detect the magnitude and location of genomic change between these impacted and pristine sites (e.g. Dayan et al. 2019, Oziolor et al. 2019). Genome-wide association and genome–environment association methods also show promise in measuring aquaculture impacts, but have traditionally been used to estimate correlations between genomic variants and trait or environmental variation (Rellstab et al. 2015, Santure & Garant 2018). A recent genomic study by Lehnert et al. (2019) instead used decline status as the trait in genome-wide association and uncovered polygenic associations with population decline and variation in immune and developmental genes. This approach could be further refined in future studies by incorporating continuous measures of aquaculture exposure such as magnitude of escape, site proximity, or pathogen load.

Rapid evolutionary change is often associated with selection on standing genetic variation ('soft sweeps') rather than new mutations (Messer et al. 2016, Hermisson & Pennings 2017). Methods that utilize differences in frequency and diversity of haplotypes such as integrated haplotype score (iHS; Voight et al. 2006), extended cross population haplotype homozygosity (XP-EHH; Sabeti et al. 2007), and number of segregating sites by length (nSL; Ferrer-Admetlla et al. 2014) can identify signatures of soft selective sweeps. Identification of sweep signatures that are exclusive to aquaculture-impacted populations may provide an additional way of both validating genomic changes induced by non-reproductive genetic impacts and uncovering implicated target genes. Machine learning approaches have also shown promise in identifying subtle signatures of environment (Sylvester et al. 2018a), trait associations (Brieuc et al. 2015), and selective sweep signatures (Kern & Schrider 2018). These provide additional research areas for future studies into the genetic impacts of aquaculture exposure that may not be detected by traditional statistical approaches. Lastly, gene ontology (Rivals et al. 2007) and gene set (Daub et al. 2017) enrichment methods can be used to characterize functional impacts and parallel responses at biological levels above changes at individual genes (Jacobs et al. 2020) and can help clarify potential targets of selection from aquaculture interactions.

3.2. Detecting changes in neutral diversity or effective population size

Genomic approaches can also be applied in the context of resolving a loss of diversity due to demographic declines associated with non-reproductive genetic impacts and applied to quantify genome-wide trends in diversity over time or estimate trends in the effective population size (Table 2B; see Waples & Do 2010). Large genomic datasets offer new opportunities for enhanced estimates of effective population size (Waples et al. 2016) as well as retrospective estimates of changes in effective population size over time (e.g. Hollenbeck et al. 2016). For example, B. Watson (pers. comm.) evaluated the performance of estimates of effective population size (N_e) using large genomic datasets to assess and approximate population declines. This was used to establish a genomic baseline to detect non-reproductive genetic interactions in southern Newfoundland Atlantic salmon populations following the use of largely sterile Atlantic salmon in aquaculture. Their results suggest that large genomic datasets (≥1000 SNPs) were able to detect population declines significantly earlier, and with increased accuracy, than small genetic or genomic datasets (25 microsatellites or 100 SNPs). However, monitoring using effective size requires samples from multiple time points, which is not always possible. As an alternative, Hollenbeck et al. (2016) present a method that uses linkage information to bin loci by rates of recombination and reconstruct trends in N_e decades into the past. Lehnert et al. (2019) applied this method to Atlantic salmon across the North Atlantic and estimated that 60% of all populations have declined in recent decades. Finally, molecular approaches to mark-recapture abundance estimation (i.e. CKMR, Bravington et al. 2016) also offer the potential to quantify changes in population size over time and have been used in marine and freshwater fish species (Bravington et al. 2016, Waples et al. 2018, Ruzzante et al. 2019). Such approaches could be used to quantify population trends in effective size in the absence of assessment data and monitor for ecological and non-reproductive genetic interactions in future.

4. CONCLUSIONS

Ultimately, despite an abundance of relevant and informative research, the relative importance of hybridization and non-reproductive genetic interactions between domestic individuals and wild populations remains largely unresolved. Nonetheless, the literature suggests that ecological interactions arising from salmon aquaculture have the realistic potential to result in substantial genetic change in wild salmon populations, as well as other species. It is worth noting that, at present, there is a significant knowledge gap regarding the non-reproductive genetic impacts of increased predation or competition due to salmon aquaculture on wild populations. Fortunately, recent advances in genetic and genomic methods present a new scope for quantifying these impacts. However, careful experimental design and pre-impact comparisons will in most cases be needed to accurately attribute any genetic change to non-reproductive genetic interactions with salmon aquaculture activities.

Future research should explore the sensitivities and power of these approaches to detect changes in genetic diversity and character over time. Given that both reproductive and non-reproductive interactions co-occur within the native range of Atlantic salmon, there may be benefit to focus studies on instances where interbreeding is unlikely or impossible. This could involve the study of ecological and genetic impacts in other species such as Pacific salmon species or in Atlantic salmon in regions where sterility is employed as a containment or mitigation measure. Alternatively, genomic approaches could potentially be used to disentangle reproductive and non-reproductive interactions from indirect interactions based on the identification of hybrids, introgressed ancestry blocks, or signatures of selection.

Our review suggests that non-reproductive genetic interactions represent both a broad reaching and largely unresolved source of genetic impact on wild populations exposed to Atlantic salmon aquaculture activities. Thus, further study is urgently needed to support an integrated understanding of aquaculture–ecosystem interactions, their implications for ecosystem stability, and the identification of potential pathways of effect. This information will be essential to the development of potential mitigation and management strategies.

Acknowledgements. This review was conducted as part of the ICES Working Group on Genetic Applications to Fisheries and Aquaculture between 2018 and 2020. Funding was provided through the Fisheries and Oceans Program for Aquaculture Regulatory Research. This work also benefited greatly from a 3-year Canada-EU Galway Statement for the Transatlantic Ocean Research Alliance Working Group on modelling genetic interactions among wild and farm escaped Atlantic salmon in the North Atlantic. The authors thank Brian Dempson and several anonymous reviewers for comments on this manuscript.

LITERATURE CITED

Bitter MC, Kapsenberg L, Gattuso JP, Pfister CA (2019) Standing genetic variation fuels rapid adaptation to ocean acidification. Nat Commun 10:5821

Bjørn PA, Finstad B, Kristoffersen R (2001) Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. Aquacult Res 32: 947–962

Bøhn T, Gjelland KØ, Serra-Llinares RM, Finstad B and others (2020) Timing is everything: survival of Atlantic salmon *Salmo salar* postsmolts during events of high salmon lice densities. J Appl Ecol 57:1149–1160

Bolstad GH, Hindar K, Robertsen G, Jonsson B and others (2017) Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. Nat Ecol Evol 1:0124

Børretzen Fjørtoft H Nilsen F, Besnier F, Espedal PG and others (2020) Aquaculture-driven evolution: distribution of pyrethroid resistance in the salmon louse throughout the North Atlantic in the years 2000–2017. ICES J Mar Sci 77:1806–1815

Bourret V, O'Reilly PT, Carr JW, Berg PR, Bernatchez L (2011) Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. Heredity 106:500–510

Bradbury IR, Duffy S, Lehnert SJ, Jóhannsson R and others (2020) Model-based evaluation of the genetic impacts of farm-escaped Atlantic salmon on wild populations. Aquacult Environ Interact 12:45–59

Bravington MV, Grewe PM, Davies CR (2016) Absolute abundance of southern bluefin tuna estimated by close-kin mark-recapture. Nat Commun 7:13162

Brieuc MSO, Ono K, Drinan DP, Naish KA (2015) Integration of Random Forest with population-based outlier analyses provides insight on the genomic basis and evolution of run timing in Chinook salmon (*Oncorhynchus tshawytscha*). Mol Ecol 24:2729–2746

Bürger R, Lynch M (1995) Evolution and extinction in a changing environment: a quantitative genetic analysis. Evolution 49:151–163

Callier MD, Byron CJ, Bengtson DA, Cranford PJ and others (2018) Attraction and repulsion of mobile wild organisms to finfish and shellfish aquaculture: a review. Rev Aquacult 10:924–949

Connors BM, Krkošek M, Ford J, Dill LM (2010) Coho salmon productivity in relation to salmon lice from infected prey and salmon farms. J Appl Ecol 47:1372–1377

Consuegra S, de Eyto E, McGinnity P, Stet RJM, Jordan WC (2011) Contrasting responses to selection in class I and class IIα major histocompatibility-linked markers in salmon. Heredity 107:143

Correa K, Lhorente JP, Bassini L, López ME and others (2017) Genome wide association study for resistance to *Caligus rogercresseyi* in Atlantic salmon (*Salmo salar* L.) using a 50K SNP genotyping array. Aquaculture 472:61–65

Coughlan J, McGinnity P, O'Farrell B, Dillane E and others (2006) Temporal variation in an immune response gene (MHC I) in anadromous *Salmo trutta* in an Irish river before and during aquaculture activities. ICES J Mar Sci 63:1248–1255

Cross TF, King J (1983) Genetic effects of hatchery rearing in Atlantic salmon. Aquaculture 33:33–40

Daub JT, Moretti S, Davydov II, Excoffier L, Robinson-Rechavi M (2017) Detection of pathways affected by positive selection in primate lineages ancestral to humans. Mol Biol Evol 34:1391–1402

Dayan DI, Du X, Baris TZ, Wagner DN, Crawford DL, Oleksiak MF (2019) Population genomics of rapid evolution in natural populations: polygenic selection in response to power station thermal effluents. BMC Evol Biol 19:61

de Eyto E, McGinnity P, Consuegra S, Coughlan J and others (2007) Natural selection acts on Atlantic salmon major histocompatibility (MH) variability in the wild. Proc R Soc B 274:861–869

de Eyto E, McGinnity P, Huisman J, Coughlan J and others (2011) Varying disease-mediated selection at different life-history stages of Atlantic salmon in fresh water. Evol Appl 4:749–762

Denholm SJ, Hoyle AS, Shinn AP, Paladini G, Taylor NGH, Norman RA (2016) Predicting the potential for natural recovery of Atlantic salmon (*Salmo salar* L.) populations following the introduction of *Gyrodactylus salaris* Malmberg, 1957 (Monogenea). PLOS ONE 11:e0169168

DFO (2016) Proposed use of European-strain triploid Atlantic salmon in Marine cage aquaculture in Placentia Bay, NL. DFO Can Sci Advis Sec Sci Resp 2016/034. https://waves-vagues.dfo-mpo.gc.ca/Library/40621248.pdf

DFO (2018) Review of the environmental impact statement for the Placentia Bay Atlantic salmon aquaculture project. DFO Can Sci Advis Sec Sci Resp 2018. https://waves-vagues.dfo-mpo.gc.ca/Library/40738899.pdf

Dionne M, Miller KM, Dodson JJ, Caron F, Bernatchez L (2007) Clinal variation in MHC diversity with temperature: evidence for the role of host-pathogen interaction on local adaptation in Atlantic salmon. Evolution 61: 2154–2164

Dionne M, Miller KM, Dodson JJ, Bernatchez L (2009) MHC standing genetic variation and pathogen resistance in wild Atlantic salmon. Philos Trans R Soc B 364: 1555–1565

Diserud OH, Fiske P, Sægrov H, Urdal K and others (2019) Escaped farmed Atlantic salmon in Norwegian rivers during 1989–2013. ICES J Mar Sci 76:1140–1150

Feder AF, Kryazhimskiy S, Plotkin JB (2014) Identifying signatures of selection in genetic time series. Genetics 196: 509–522

Ferrer-Admetlla A, Liang M, Korneliussen T, Nielsen R (2014) On detecting incomplete soft or hard selective sweeps using haplotype structure. Mol Biol Evol 31:1275–1291

Fjelldal PG, Hansen TJ, Karlsen Ø, Wright DW (2019) Effects of laboratory salmon louse infection on Arctic char osmoregulation, growth and survival. Conserv Physiol 7:coz072

Fleming IA, Jonsson B, Gross MR (1994) Phenotypic divergence of sea-ranched, farmed, and wild salmon. Can J Fish Aquat Sci 51:2808–2824

Fleming IA, Jonsson B, Gross MR, Lamberg A (1996) An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). J Appl Ecol 33:893–905

Fleming IA, Hindar K, Mjølnerød IB, Jonsson B, Balstad T, Lamberg A (2000) Lifetime success and interactions of farm salmon invading a native population. Proc R Soc B 267:1517–1524

Foll M, Gaggiotti O (2008) A Genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. Genetics 180:977–993

Ford JS, Myers RA (2008) A global assessment of salmon aquaculture impacts on wild salmonids. PLOS Biol 6: e33

Forseth T, Barlaup BT, Finstad B, Fiske P and others (2017) The major threats to Atlantic salmon in Norway. ICES J Mar Sci 74:1496–1513

Garcia de Leaniz C, Fleming IA, Einum S, Verspoor E and others (2007) A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. Biol Rev Camb Philos Soc 82:173–211

Garseth ÅH, Ekrem T, Biering E (2013) Phylogenetic evidence of long distance dispersal and transmission of piscine reovirus (PRV) between farmed and wild Atlantic salmon. PLOS ONE 8:e82202

Gilbey J, Verspoor E, Mo TA, Sterud E and others (2006) Identification of genetic markers associated with *Gyrodactylus salaris* resistance in Atlantic salmon (*Salmo salar*). Dis Aquat Org 71:119–129

Glover KA, Pertoldi C, Besnier F, Wennevik V, Kent M, Skaala Ø (2013) Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genet 14:74

Glover KA, Solberg MF, McGinnity P, Hindar K and others (2017) Half a century of genetic interaction between farmed and wild Atlantic salmon: status of knowledge and unanswered questions. Fish Fish 18:890–927

Gomulkiewicz R, Holt RD (1995) When does evolution by natural selection prevent extinction? Evolution 49:201–207

Hamoutene D, Cote D, Marshall K, Donnet S and others (2018) Spatial and temporal distribution of farmed Atlantic salmon after experimental release from sea cage sites in Newfoundland (Canada). Aquaculture 492:147–156

Handeland SO, Björnsson BT, Arnesen AM, Stefansson SO (2003) Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*) of wild and farmed strains. Aquaculture 220:367–384

Hermisson J, Pennings PS (2017) Soft sweeps and beyond: understanding the patterns and probabilities of selection footprints under rapid adaptation. Methods Ecol Evol 8: 700–716

Hollenbeck CM, Portnoy DS, Gold JR (2016) A method for detecting recent changes in contemporary effective population size from linkage disequilibrium at linked and unlinked loci. Heredity 117:207

Jacobs A, Carruthers M, Yurchenko A, Gordeeva NV and others (2020) Parallelism in eco-morphology and gene expression despite variable evolutionary and genomic backgrounds in a Holarctic fish. PLOS Genet 16:e1008658

Johnsen BO, Jensen AJ (1991) The *Gyrodactylus* story in Norway. Aquaculture 98:289–302

Johnsen BO, Jensen AJ (1994) The spread of furunculosis in salmonids in Norwegian rivers. J Fish Biol 45:47–55

Karbowski CM, Finstad B, Karbowski N, Hedger RD (2019) Sea lice in Iceland: assessing the status and current implications for aquaculture and wild salmonids. Aquacult Environ Interact 11:149–160

Karlsson S, Moen T, Lien S, Glover KA, Hindar K (2011) Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. Mol Ecol Resour 11(Suppl 1):247–253

Karlsson S, Diserud OH, Fiske P, Hindar K (2016) Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. ICES J Mar Sci 73: 2488–2498

Karlsson S, Bolstad GH, Hansen H, Jansen PA, Moen T, Noble LR (2020) The potential for evolution of resistance to *Gyrodactylus salaris* in Norwegian Atlantic salmon. NINA Report 1812, Norwegian Institute for Nature Research, Trondheim

Kennedy GJA, Greer JE (1988) Predation by cormorants *Phalacrocorax carbo* (L.), on an Irish river. Aquacult Fish Manage 19:159–170

Kern AD, Schrider DR (2018) diploS/HIC: an updated approach to classifying selective sweeps. G3 (Bethesda) 8: 1959–1970

Keyser F, Wringe BF, Jeffery NW, Dempson JB, Duffy S, Bradbury IR (2018) Predicting the impacts of escaped farmed Atlantic salmon on wild salmon populations. Can J Fish Aquat Sci 75:506–512

Kirkpatrick M, Barton NH (1997) Evolution of species' range. Am Nat 150:1–23

Kjærner-Semb E, Ayllon F, Furmanek T, Wennevik V and others (2016) Atlantic salmon populations reveal adaptive divergence of immune related genes — a duplicated genome under selection. BMC Genomics 17:610

Krkošek M, Lewis MA, Volpe JP (2005) Transmission dynamics of parasitic sea lice from farm to wild salmon. Proc Biol Sci 272:689–696

Krkošek M, Ford JS, Morton A, Lele S, Myers RA, Lewis MA (2007) Declining wild salmon populations in relation to parasites from farm salmon. Science 318:1772–1775

Krkošek M, Connors BM, Morton A, Lewis MA, Dill LM, Hilborn R (2011a) Effects of parasites from salmon farms on productivity of wild salmon. Proc Natl Acad Sci USA 108:14700–14704

Krkošek M, Connors BM, Ford H, Peacock S and others (2011b) Fish farms, parasites, and predators: implications for salmon population dynamics. Ecol Appl 21:897–914

Lehnert SJ, Kess T, Bentzen P, Kent MP and others (2019) Genomic signatures and correlates of widespread population declines in salmon. Nat Commun 10:2996

Leitwein M, Cayuela H, Ferchaud AL, Normandeau É, Gagnaire PA, Bernatchez L (2019) The role of recombination on genome-wide patterns of local ancestry exemplified by supplemented brook charr populations. Mol Ecol 28: 4755–4769

Luu K, Bazin E, Blum MGB (2017) pcadapt: an R package to perform genome scans for selection based on principal component analysis. Mol Ecol Resour 17:67–77

Madhun AS, Karlsbakk E, Isachsen CH, Omdal LM and others (2015) Potential disease interaction reinforced: double-virus-infected escaped farmed Atlantic salmon, *Salmo salar* L., recaptured in a nearby river. J Fish Dis 38:209–219

Madhun AS, Isachsen CH, Omdal LM, Einen ACB and others (2018) Prevalence of piscine orthoreovirus and salmonid alphavirus in sea-caught returning adult Atlantic salmon (*Salmo salar* L.) in northern Norway. J Fish Dis 41:797–803

McGinnity P, Prodöhl P, Ferguson A, Hynes R and others (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proc R Soc B 270: 2443–2450

Messer PW, Ellner SP, Hairston NG Jr (2016) Can population genetics adapt to rapid evolution? Trends Genet 32: 408–418

Miller KM, Li S, Kaukinen KH, Ginther N and others (2011) Genomic signatures predict migration and spawning failure in wild Canadian salmon. Science 331:214–217

Morris MRJ, Fraser DJ, Heggelin AJ, Whoriskey FG, Carr JW, O'Neil SF, Hutchings JA (2008) Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. Can J Fish Aquat Sci 65:2807–2826

Morton A, Routledge R, Hrushowy S, Kibenge M, Kibenge F (2017) The effect of exposure to farmed salmon on piscine orthoreovirus infection and fitness in wild Pacific salmon in British Columbia, Canada. PLOS ONE 12:e0188793

Nekouei O, Vanderstichel R, Thakur K, Arriagada G and others (2018) Association between sea lice (*Lepeophtheirus salmonis*) infestation on Atlantic salmon farms and wild Pacific salmon in Muchalat Inlet, Canada. Sci Rep 8:4023

Nielsen R (2005) Molecular signatures of natural selection. Annu Rev Genet 39:197–218

Nylund A, Brattespe J, Plarre H, Kambestad M, Karlsen M (2019) Wild and farmed salmon (*Salmo salar*) as reservoirs for infectious salmon anaemia virus, and the importance of horizontal- and vertical transmission. PLOS ONE 14:e0215478

Oziolor EM, Reid NM, Yair S, Lee KM and others (2019) Adaptive introgression enables evolutionary rescue from extreme environmental pollution. Science 364:455–457

Peacock SJ, Krkošek M, Proboszcz S, Orr C, Lewis MA (2013) Cessation of a salmon decline with control of parasites. Ecol Appl 23:606–620

Price MH, Proboszcz SL, Routledge RD, Gottesfeld AS, Orr C, Reynolds JD (2011) Sea louse infection of juvenile sockeye salmon in relation to marine salmon farms on Canada's west coast. PLOS ONE 6:e16851

Pritchard VL, Mäkinen H, Vähä JP, Erkinaro J, Orell P, Primmer CR (2018) Genomic signatures of fine-scale local selection in Atlantic salmon suggest involvement of sexual maturation, energy homeostasis and immune defence-related genes. Mol Ecol 27:2560–2575

Rellstab C, Gugerli F, Eckert AJ, Hancock AM, Holderegger R (2015) A practical guide to environmental association analysis in landscape genomics. Mol Ecol 24:4348–4370

Rivals I, Personnaz L, Taing L, Potier MC (2007) Enrichment or depletion of a GO category within a class of genes: which test? Bioinformatics 23:401–407

Robertsen G, Reid D, Einum S, Aronsen T and others (2019) Can variation in standard metabolic rate explain context-dependent performance of farmed Atlantic salmon offspring? Ecol Evol 9:212–222

Robledo D, Gutiérrez AP, Barría A, Lhorente JP, Houston RD, Yáñez JM (2019) Discovery and functional annotation of quantitative trait loci affecting resistance to sea lice in Atlantic salmon. Front Genet 10:56

Ruzzante DE, McCracken GR, Førland B, MacMillan J and others (2019) Validation of close-kin mark–recapture (CKMR) methods for estimating population abundance. Methods Ecol Evol 10:1445–1453

Sabeti PC, Varilly P, Fry B, Lohmueller J and others (2007) Genome-wide detection and characterization of positive selection in human populations. Nature 449:913–918

Santure AW, Garant D (2018) Wild GWAS — association mapping in natural populations. Mol Ecol Resour 18: 729–738

Serra-Llinares RM, Bøhn T, Karlsen Ø, Nilsen R and others (2020) Impacts of salmon lice on mortality, marine migration distance and premature return in sea trout. Mar Ecol Prog Ser 635:151–168

Shephard S, Gargan P (2017) Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population. Aquacult Environ Interact 9:181–192

Skaala Ø, Glover KA, Barlaup BT, Svåsand T, Besnier F, Hansen MM, Borgstrøm R (2012) Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. Can J Fish Aquat Sci 69: 1994–2006

Skilbrei OT, Heino M, Svåsand T (2015) Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. ICES J Mar Sci 72:670–685

Sylvester EVA, Beiko RG, Bentzen P, Paterson I and others (2018a) Environmental extremes drive population structure at the northern range limit of Atlantic salmon in North America. Mol Ecol 27:4026–4040

Sylvester EVA, Wringe BF, Duffy SJ, Hamilton LC, Fleming IA, Bradbury IR (2018b) Migration effort and wild population size influence the prevalence of hybridization between escaped farmed and wild Atlantic salmon. Aquacult Environ Interact 10:401–411

Therkildsen NO, Wilder AP, Conover DO, Munch SB, Baumann H, Palumbi SR (2019) Contrasting genomic shifts underlie parallel phenotypic evolution in response to fishing. Science 365:487–490

Thorstad EB, Finstad B (2018) Impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout. NINA Report 1449, Norwegian Institute for Nature Research, Trondheim

Tonteri A, Vasemägi A, Lumme J, Primmer CR (2010) Beyond MHC: signals of elevated selection pressure in Atlantic salmon (*Salmo salar*) immune-relevant loci. Mol Ecol 19: 1273–1282

Tsai HY, Hamilton A, Tinch AE, Guy DR and others (2016) Genomic prediction of host resistance to sea lice in farmed Atlantic salmon populations. Genet Sel Evol 48:47

Verspoor E, McGinnity P, Bradbury I, Glebe B (2015) The potential direct and indirect genetic consequences for native Newfoundland Atlantic salmon from interbreeding with European-origin farm escapes. DFO Can Sci Advis Sec Res Document 2015/030:viii + 36. https://waves-vagues.dfo-mpo.gc.ca/Library/359696.pdf

Vitti JJ, Grossman SR, Sabeti PC (2013) Detecting natural selection in genomic data. Annu Rev Genet 47:97–120

Voight BF, Kudaravalli S, Wen X, Pritchard JK (2006) A map of recent positive selection in the human genome. PLOS Biol 4:e72

Vollset KW, Krontveit RI, Jansen PA, Finstad B and others (2016) Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish Fish 17:714–730

Waples RS, Do C (2010) Linkage disequilibrium estimates of contemporary N_e using highly variable genetic markers: a largely untapped resource for applied conservation and evolution. Evol Appl 3:244–262

Waples RK, Larson WA, Waples RS (2016) Estimating contemporary effective population size in non-model species using linkage disequilibrium across thousands of loci. Heredity 117:233–240

Waples RS, Grewe PM, Bravington MW, Hillary R, Feutry P (2018) Robust estimates of a high N_e/N ratio in a top marine predator, southern bluefin tuna. Sci Adv 4:eaar7759

Webb JH, Hay DW, Cunningham PD, Youngson AF (1991) The spawning behaviour of escaped farmed and wild adult Atlantic salmon (*Salmo salar* L.) in a northern Scottish river. Aquaculture 98:97–110

Webb JH, McLaren IS, Donaghy MJ, Youngson AF (1993a) Spawning of farmed Atlantic salmon in the second year after their escape. Aquacult Fish Manage 24:557–561

Webb JH, Youngson AF, Thompson CE, Hay DW, Donaghy MJ, McLaren IS (1993b) Spawning of escaped farmed Atlantic salmon, *Salmo salar* L., in western and northern Scottish rivers: egg deposition by females. Aquacult Fish Manage 24:663–670

Wringe BF, Jeffery NW, Stanley RRE, Hamilton LC and others (2018) Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. Commun Biol 1:108

Wringe BF, Anderson EC, Jeffery NW, Stanley RRE, Bradbury IR (2019) Development and evaluation of SNP panels for the detection of hybridization between wild and escaped Atlantic salmon (*Salmo salar*) in the West Atlantic. Can J Fish Aquat Sci 76:695–704

Zueva KJ, Lumme J, Veselov AE, Kent MP, Lien S, Primmer CR (2014) Footprints of directional selection in wild Atlantic salmon populations: evidence for parasite-driven evolution? PLOS ONE 9:e91672

Zueva KJ, Lumme J, Veselov AE, Kent MP, Primmer CR (2018) Genomic signatures of parasite-driven natural selection in north European Atlantic salmon (*Salmo salar*). Mar Genomics 39:26–38

Editorial responsibility: Kevin Glover,
Bergen, Norway

Submitted: June 8, 2020; Accepted: August 31, 2020
Proofs received from author(s): October 12, 2020

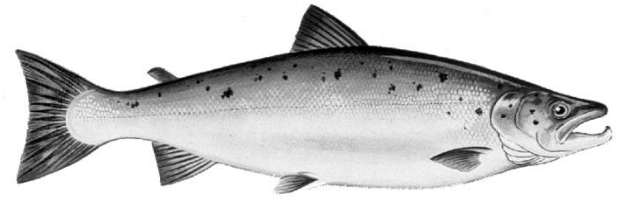
Fisheries and Oceans Canada
Science

Pêches et Océans Canada
Sciences

Maritimes Region

Canadian Science Advisory Secretariat
Science Advisory Report 2013/009

RECOVERY POTENTIAL ASSESSMENT FOR SOUTHERN UPLAND ATLANTIC SALMON



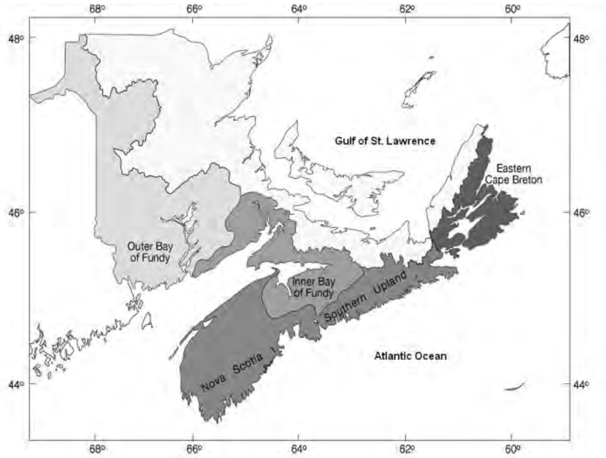


Figure 1. Map showing the location of the Southern Upland relative to the three other designatable units for Atlantic salmon in the Maritimes Region.

Context

The Nova Scotia Southern Upland (SU) population of Atlantic salmon was evaluated as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in November 2010. This population assemblage (designatable unit) occupies rivers on the mainland of Nova Scotia, including all rivers south of the Canso Causeway on both the Eastern Shore and South Shore of Nova Scotia draining into the Atlantic Ocean (Figure 1), as well as the Bay of Fundy rivers southwest of Cape Split. The unique phylogenetic history of SU Atlantic salmon, the minimal historical gene flow between the SU and surrounding regions, the low rates of straying from other regions, and the evidence for local adaption to environmental conditions in the SU region support the view that SU salmon differ from salmon in other areas.

A Recovery Potential Assessment (RPA) process has been developed by Fisheries and Oceans Canada (DFO) Science to provide the information and scientific advice required to meet the various requirements of the Species at Risk Act (SARA). The scientific information provided in the RPA serves as advice to the Minister regarding the listing of the species under SARA and is used when analyzing the socio-economic impacts of listing, as well as during subsequent consultations, where applicable. It is also used to evaluate activities that could contravene the SARA should the species be listed, as well as in the development of a recovery strategy. This assessment considers the scientific data available to assess the recovery potential of SU Atlantic Salmon.

This Science Advisory Report is from the May 22-25, 2012, Recovery Potential Assessment for Southern Upland Atlantic salmon. Additional publications from this meeting will be posted on the *Fisheries and Oceans Canada (DFO) Science Advisory Schedule* as they become available.

March 2013

SUMMARY

- Available indices show that abundance of Atlantic salmon is very low in the Southern Upland designatable unit and has declined from levels observed in the 1980s and 1990s.
- Annual adult abundance in four rivers declined 88% to 99% from observed abundance in the 1980s, a similar trend is observed in the recreational catch.
- Region-wide comparisons of juvenile density data from more than 50 rivers indicate significant ongoing declines between 2000 and 2008/2009 and provide evidence for river-specific extirpations.
- Population modeling for two of the larger populations remaining in the Southern Upland designatable unit (LaHave and St. Mary's) indicates a high probability of extirpation (87% and 73% within 50 years for these two populations respectively) in the absence of human intervention or a change in survival rates for some other reason.
- Population viability analyses indicate that the loss of past resiliency to environmental variability and extreme environmental events is contributing to the high risk of extinction.
- Juvenile Atlantic salmon were found in 22 of 54 river systems surveyed in 2008/2009. Given the reductions in freshwater habitat that have already occurred and the current low population size with ongoing declines, all 22 rivers include important habitat for Southern Upland Atlantic salmon. Restoration of these populations is expected to achieve the distribution component of the recovery target. If additional rivers are found to contain salmon, the consideration of these rivers as important habitat would have to be re-evaluated.
- The estuaries associated with these 22 rivers are considered to be important habitat for Atlantic salmon as successful migration through this area is required to complete their life cycle.
- While there is likely to be important marine habitat for Southern Upland Atlantic salmon, given broad temporal and spatial variation, it is difficult to link important life-history functions with specific marine features and their attributes.
- Proposed recovery targets for Atlantic salmon populations in the Southern Upland designatable unit have both abundance and distribution components. Abundance targets for Southern Upland Atlantic salmon are proposed as the river-specific conservation egg requirements. The distribution target should encompass the range of genetic and phenotypic variability among populations, and environmental variability among rivers, and would include rivers distributed throughout the designatable unit to allow for gene flow between the rivers/populations. There is the expectation that including a wider variety of populations in the distribution target will enhance persistence as well as facilitate recovery in the longer term.
- Interim recovery targets for Southern Upland Atlantic salmon can be used to evaluate progress towards recovery. First, halt the decline in abundance and distribution in rivers with documented Atlantic salmon populations. Next, reduce the extinction risk in rivers with documented Atlantic salmon populations by increasing the abundance in these rivers. Then, as necessary, expand the presence and abundance of Atlantic salmon into other rivers currently without salmon to fill in gaps in distribution within the Southern Upland designatable unit and facilitate metapopulation dynamics.
- Recovery targets will need to be revisited as information about the dynamics of the recovering population becomes available. Progress towards recovery targets can be evaluated using survival and extinction risks metrics.
- Two dwelling places were evaluated for their potential consideration as a residence for Atlantic salmon. Of these, redds most closely match the definition of a residence because they are constructed, whereas home stones are not.
- Threats to persistence and recovery in freshwater environments identified with a high level of overall concern include (importance not implied by order): acidification, altered hydrology,

invasive fish species, habitat fragmentation due to dams and culverts, and illegal fishing and poaching.

- Threats in estuarine and marine environments identified with a high level of overall concern are (importance not implied by order): salmonid aquaculture and marine ecosystem changes.
- From analyses of land use in the Southern Upland region, previous and on-going human activities are extensive in the majority of drainage basins and have likely altered hydrological processes in Southern Upland watersheds. Watershed-scale factors have the potential to override factors controlling salmon abundance at smaller spatial scales (i.e., within the stream reach).
- River acidification has significantly contributed to reduced abundance or extirpation of populations from many rivers in the region during the last century. Although most systems are not acidifying further, few are recovering and most are expected to remain affected by acidification for more than 60 years.
- Acidification and barriers to fish passage are thought to have reduced the amount of freshwater habitat by approximately 40%, an estimate that may be conservative. However, given the low abundance of salmon at present, habitat quantity is not thought to be currently limiting for populations in rivers where barriers and acidification are not issues. Whether freshwater habitat becomes limiting in the future depends on the dynamics of recovered populations.
- Population modeling for the LaHave River (above Morgan Falls) and the St. Mary's River (West Branch) salmon populations indicated that smolt-to-adult return rates, a proxy for at-sea survival, have decreased by a factor of roughly three between the 1980s and 2000s. Return rates for Southern Upland salmon are currently about ten times higher than they are for inner Bay of Fundy salmon populations.
- In contrast with inner Bay of Fundy salmon populations, for which at-sea survival is so low that recovery actions in fresh water are expected to have little effect on overall viability, recovery actions focused on improving freshwater productivity are expected to reduce extinction risk for Southern Upland salmon.
- Remediation actions to address land use issues will not produce immediate population increases for Southern Upland salmon. However, large-scale changes are the most likely to bring about substantial population increase in Southern Upland salmon because they should have a greater impact on total abundance in the watershed rather than on localized density, and they would address issues at the watershed scale. Coordination of activities at small scales may produce more immediate effects but of shorter duration than addressing landscape-scale threats.
- Population viability analyses indicate that relatively small increases in either freshwater productivity or at-sea survival are expected to decrease extinction probabilities. For example, for the LaHave River (above Morgan Falls) population, increasing freshwater productivity by 20% decreases probability of extinction within 50 years from 87% to 21%, while a freshwater productivity increase of 50% decreases the probability of extinction within 50 years to near zero. Larger changes in at-sea survival are required to restore populations to levels above their conservation requirements.
- Sensitivity analysis examining the effect of starting population size on population viability highlights the risks associated with delaying recovery actions; recovery is expected to become more difficult if abundance continues to decline, as is predicted for these populations.
- Atlantic salmon is one of the most-studied fish species in the world. Readers are referred to the supporting research documents, which form part of the advisory package for this designatable unit, for more information than is contained in this summary document.

BACKGROUND

Rationale for Assessment

When the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed aquatic species as Threatened or Endangered, Fisheries and Oceans Canada (DFO), as the responsible jurisdiction under the *Species at Risk Act* (SARA), is required to undertake a number of actions. Many of these actions require scientific information on the current status of the species, population or designable unit (DU), threats to its survival and recovery, habitat needs, and the feasibility of its recovery. Formulation of this scientific advice has typically been developed through a Recovery Potential Assessment (RPA) that is conducted as soon as possible after the COSEWIC assessment. This timing allows for the consideration of peer-reviewed scientific analyses into SARA processes including listing decisions and recovery planning.

Southern Upland (SU) Atlantic salmon (*Salmo salar*) was assessed as Endangered by COSEWIC in November 2010 (COSEWIC 2011). DFO Science was asked to undertake an RPA for the Nova Scotia Southern Upland DU based on DFO's protocol for conducting RPAs (DFO 2007). Information on 22 Terms of Reference was reviewed at this meeting.

Southern Upland DU

The Southern Upland DU of Atlantic salmon consists of the salmon populations that occupy rivers in a region of Nova Scotia extending from the northeastern mainland near Canso, into the Bay of Fundy at Cape Split (COSEWIC 2011). This region includes rivers on both the Eastern Shore and South Shore of Nova Scotia draining into the Atlantic Ocean (Figure 1), as well as Bay of Fundy rivers south of Cape Split. Historically, it has been divided into three Salmon Fishing Areas (SFAs): SFA 20 (Eastern Shore), SFA 21 (Southwest Nova Scotia), and part of SFA 22 (Bay of Fundy Rivers inland of the Annapolis River).

Based on genetic evidence, regional geography and differences in life history characteristics SU Atlantic salmon is considered to be biologically unique (Gibson et al. 2011) and its extirpation would constitute an irreplaceable loss of Atlantic salmon biodiversity. Additional information on the genetic analysis of SU Atlantic salmon is provided in O'Reilly et al. (2012).

The exact number of rivers inhabited by SU Atlantic salmon is not known, but salmon likely used most accessible habitat in this area at least intermittently in the past. There are 585 watersheds (streams of various sizes draining directly into the ocean) in the region; 72 are considered to have historically contained Atlantic salmon populations (Figure 2).

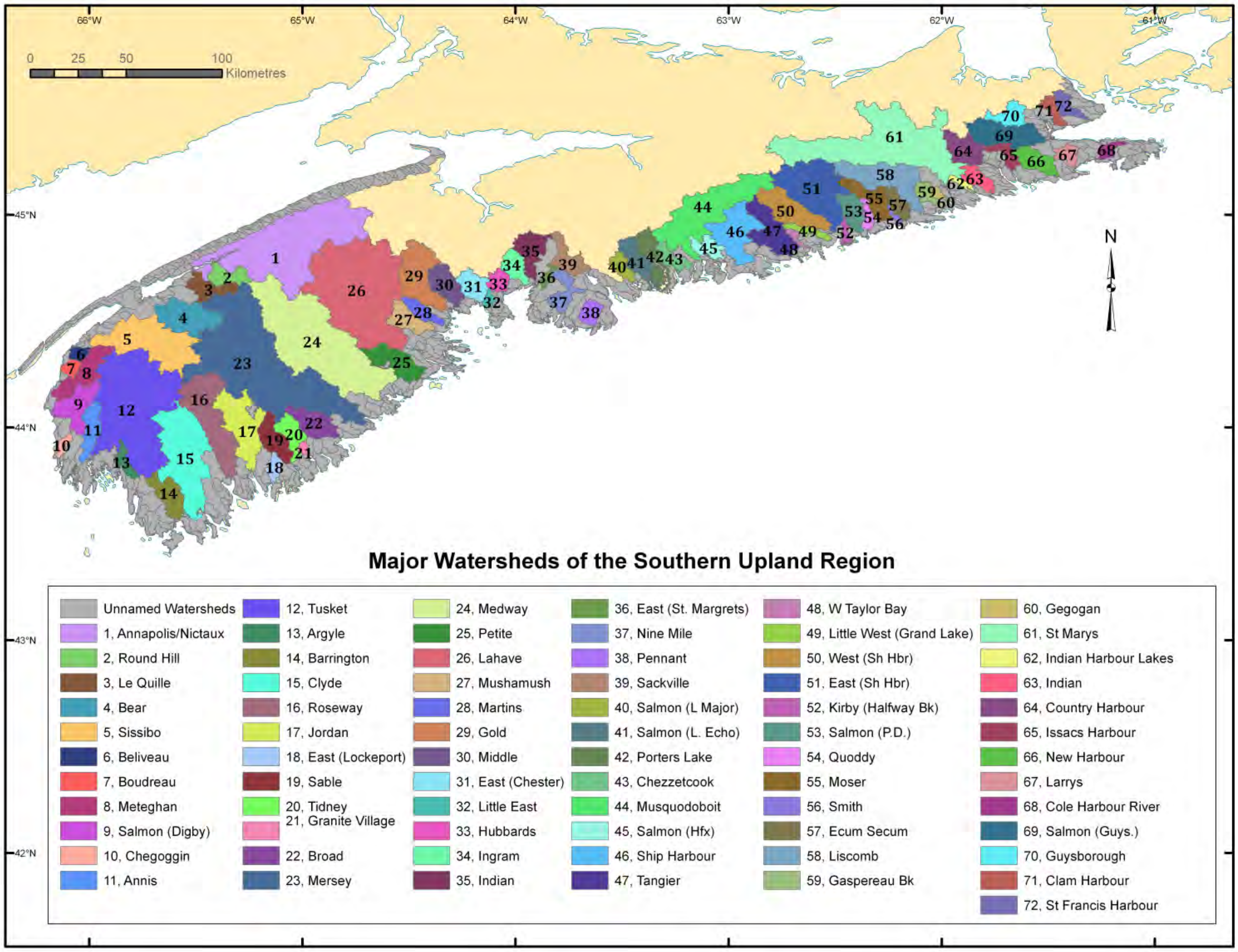


Figure 2. Map of the watersheds contained in the Southern Upland region, labelled by number and colour, where the boundaries were determined from the Secondary Watersheds layer for ArcGIS developed by the Nova Scotia Department of the Environment. Watersheds that are not labelled by number, but are still contained within the Southern Upland region are shown in grey.

Information on the life cycle of SU Atlantic salmon is contained in Gibson and Bowlby (2013). Within the SU populations, salmon mature after either one or two winters at sea (called “one sea-winter salmon” or 1SW, “two sea-winter salmon” or 2SW, respectively), although historically a small proportion also matured after three winters at sea (called “three sea-winter salmon” or 3SW). The proportion of salmon maturing after a given number of winters at sea is highly variable among populations and 3SW salmon are now very rare or absent from most populations in the Southern Upland.

Atlantic salmon is one of the most-studied fish species in the world. Readers are referred to the supporting research documents, which form part of the advisory package for this DU, for more information than is contained in this summary document.

ASSESSMENT

Status and Trends

Data available for evaluating the abundance and trends of SU Atlantic salmon include assessments of adult salmon returning to the St. Mary's River (West Branch), LaHave River (above Morgan Falls), and East River (Sheet Harbour) populations, estimates of smolts abundance for these populations, and estimates of the abundance of juvenile salmon (fry and parr) in many rivers. In the past, abundance has been assessed for the Liscomb River population as well. A detailed discussion of the abundance and trends of SU Atlantic salmon is contained in Bowlby et al. (2013a).

Adult Abundance

Available indices show that abundance of Atlantic salmon is very low in the SU DU and has declined from levels observed in the 1980s and 1990s. Annual adult abundance in four rivers declined by 88% to 99% from observed abundance in the 1980s (Figure 3); a similar trend is observed in the recreational catch time series.

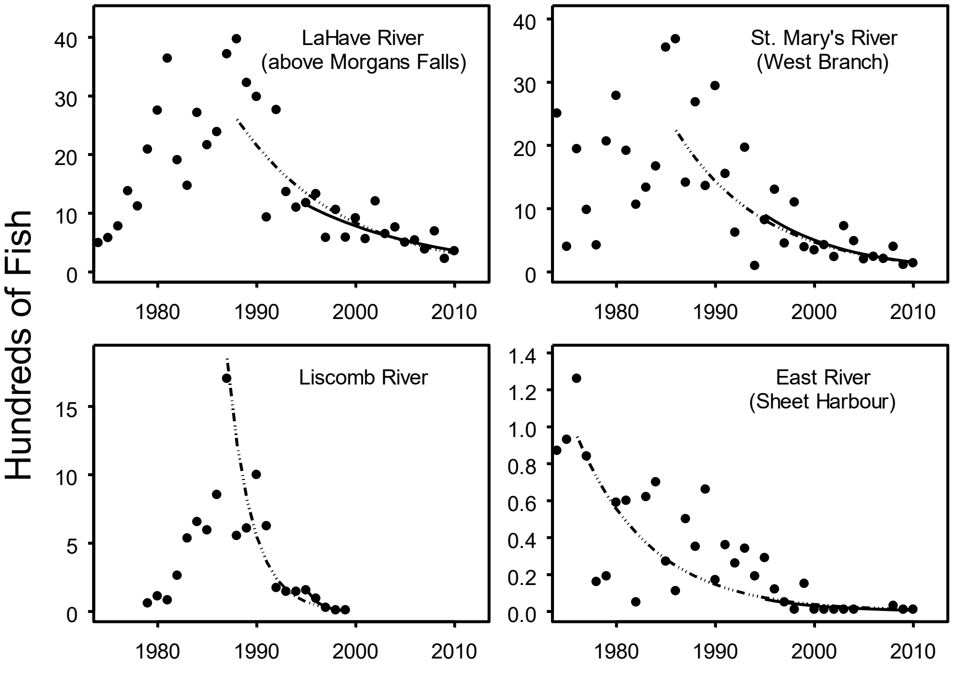


Figure 3. Atlantic salmon adult abundance time series based on adult count data (points) for four rivers in the Southern Upland from 1974 to 2010. The lines show the trends estimated by log-linear regression over the previous 3 generations (solid lines) and from the year of maximum abundance (dashed lines).

Juvenile Abundance and Distribution

Region-wide comparisons of juvenile density data (obtained by electrofishing) from more than 50 rivers indicate significant ongoing declines between 2000 and 2008/2009 and provide evidence for river-specific extirpations. In 2008/2009, juvenile Atlantic salmon were found in 22 of 54 surveyed rivers within the DU, but were not found in 4 rivers where they had been found in 2000 (Figure 4). Despite fishing effort in the two surveys being similar, only one quarter as many salmon juveniles were captured in the 2008/09 survey as in 2000 (1,019 versus 3,733).

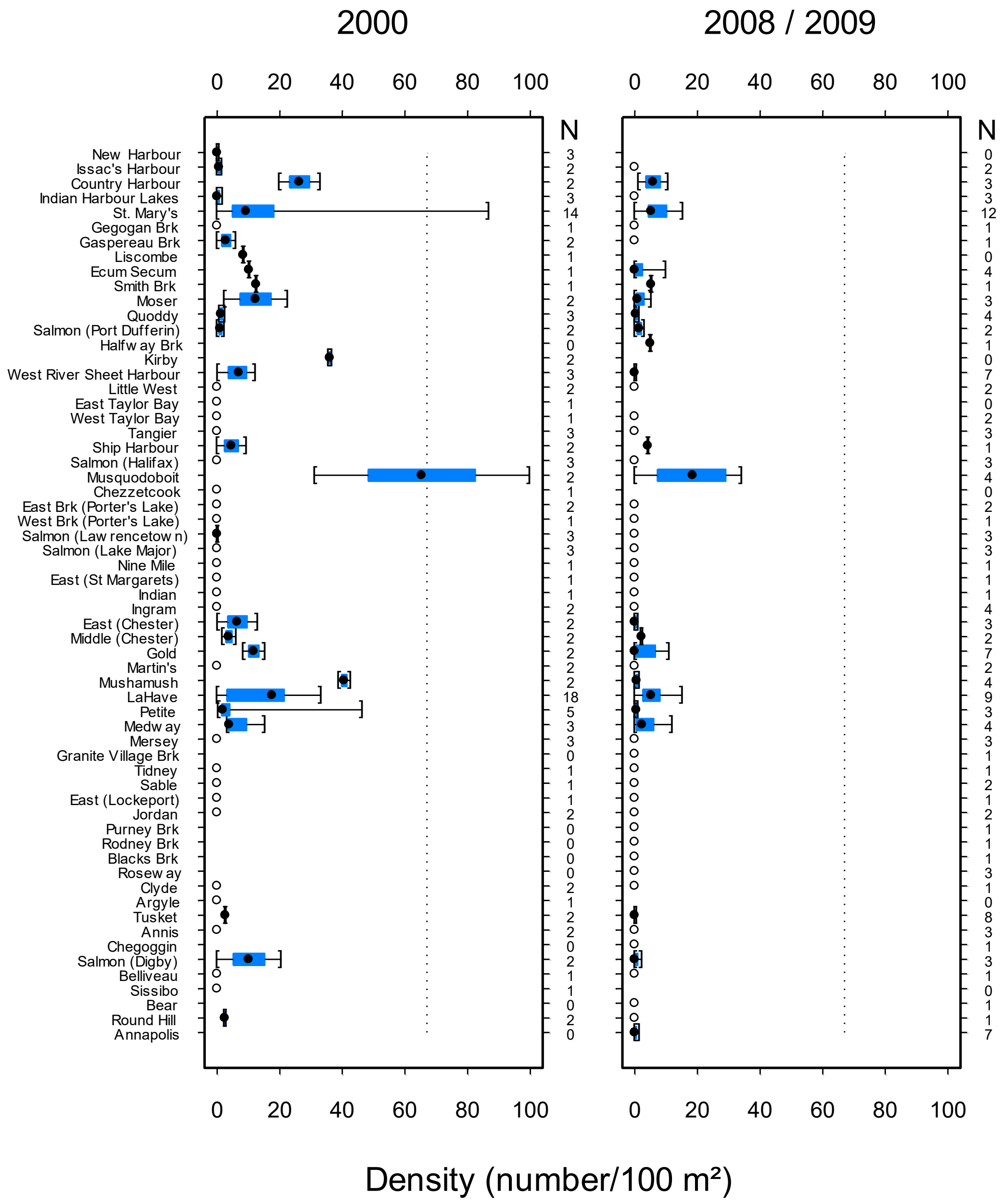


Figure 4. Boxplots of Atlantic salmon juvenile densities (age 0, age 1, and age 2+ combined) in rivers sampled by electrofishing during the survey in 2000 (left panel) and in 2008/2009 (right panel). The number of sites sampled in each river is given on the right-hand axis in both panels, and sites in which no salmon were captured are represented by open circles. The vertical dotted line shows Elson's norm for total juvenile abundance in both panels. Box plots are interpreted as follows: the black symbols are the medians, the rectangle shows the interquartile range and the whiskers the minimum and maximum values. Reprinted from Gibson et al. (2011).

Where present in 2008/2009, the observed densities of juvenile salmon ranged from 0.3 to 33.8 fish per 100 m^2 (Figure 4). Observed densities of fry (age 0) ranged from 0.3 to 28.0 fish per 100 m^2 and of parr (age 1 and age 2+) ranged from 0.2 to 16.1 fish per 100 m^2, with the highest values being recorded on the Musquodoboit River. In general, the mean density of either age class was lower than Elson's norm (30 age 0 fish per 100 m^2 and 24 age 1 and older fish per 100 m^2), values that have been used as a reference for juvenile production in fresh water.

Range and Distribution

The evaluation of range and present distribution of SU Atlantic salmon in fresh water is based on juvenile salmon surveys (Figure 4), although salmon may be present in some rivers not included in the survey. The full extent of the marine range of SU Atlantic salmon is not known, but tagging studies indicate that SU Atlantic salmon can be found along the entire coast of Nova Scotia, from the inner Bay of Fundy to the tip of Cape Breton, throughout most, if not all, of the year. Additionally, they may be found along the coast of northern New Brunswick, Newfoundland, northern Quebec, and the tip of Labrador, migrating northward until a proportion reach the Labrador Sea, Irminger Sea, or along the coast of West Greenland. For the high-seas fisheries in Labrador and West Greenland, few of the tag recaptures were assigned a latitude and longitude when recovered; therefore, it is not possible to determine how far off-shore Atlantic salmon may frequent in these areas. Assuming that these data represent general distribution patterns in the marine environment, there appears to be limited use of the Gulf of St. Lawrence (including the coastal areas around the Magdalen Islands, northern New Brunswick, or Quebec near Anticosti Island) by SU Atlantic salmon. Further details of the analysis of the tagging data are provided in Bowlby et al. (2013b).

Population Dynamics

A life history-based population dynamics model was used to evaluate population viability. The population dynamics model consists of two parts: a freshwater production model that provides estimates of the expected smolt production as a function of egg deposition, and an egg-per-smolt (EPS) model that provides estimates of the rate at which smolts produce eggs throughout their lives. These components are combined via an equilibrium analysis that provides estimates of the abundance at which the population would stabilize if the input parameters remained unchanged. This combined model is then used to evaluate how equilibrium population size has changed through time, as well as how the population would be expected to change in response to changes in carrying capacity, survival, or life stage transition probabilities. Parameter estimates from the model are used in the population viability analysis (PVA) for the recovery scenarios. Analyses are presented for the two larger rivers for which there are sufficient monitoring data: the LaHave River (above Morgan Falls), and the St. Mary’s River (West Branch).

Life-History Parameter Estimates

Life-history parameter estimates were derived using a statistical, life history-based population dynamics model. Methods and results of this analysis are described in detail in Gibson and Bowlby (2013). Some key parameters are described below, including indications of where these have changed over time.

Freshwater Productivity

Analyses for LaHave River (above Morgan Falls) indicate that for the 1974 to 1985 time period, the maximum number of smolts produced per egg was 0.017 and that this value decreased to 0.013 in the 1985 to 2010 time period. Similarly, the carrying capacity for smolt production decreased from 147,700 to 119,690 (5.7 to 4.6 smolts per 100 m^2) between the two periods. For the St. Mary’s River (West Branch), the carrying capacity of age-1 parr was estimated to be 11.76 parr per 100 m^2 and is considered to be low relative to other populations. The estimated number of smolts produced per egg is 0.034 and the carrying capacity for smolt is estimated to be 104,120 smolts (4.7 smolts per 100 m^2) (average values for the time period 1974 to 2010).

Details about these analyses, as well as age- and stage-specific survival rates for these populations, are provided in Gibson and Bowlby (2013).

Survival of Emigrating Smolts and Kelts in Rivers and Estuaries

The survival of emigrating SU smolts and kelts in rivers and estuaries is reasonably well studied, and provides an indication of how much survival could be changed by recovery actions that were focused on this life history event.

The survival of emigrating smolts in the LaHave, St. Mary's and Gold rivers was studied during 2010, and in West River (Sheet Harbour), during 2008, 2009 and 2010. Observed survival from release to the head of tide (the freshwater zone) ranged from 71.9% to 100%, and survival to the open ocean ranged from 39.4% to 73.5% (Table 1).

There are two studies of kelt survival in SU estuaries. In the St. Mary's River, 24 acoustically tagged kelts were detected leaving the river in the spring and all these fish survived to leave the estuary. In a study of the survival and behaviour of migrating kelts in freshwater, estuarine, and coastal habitat using LaHave River salmon, 27 of 30 acoustically tagged fish were detected leaving coastal habitat, indicating that survival was at least 90% while migrating through those environments. Further details on these studies are provided in Gibson and Bowlby (2013).

Table 1. Cumulative survival (%) and standardized survival (% per km of habitat zone length) of smolts upon exit from four habitat-zones (FW – freshwater; IE – inner estuary; OE – outer estuary; Bay / Overall). Smolts detected dead less than 1 km from release were excluded from estimates of observed survival. Reprinted from Halfyard et al. (2012).

	Observed Cumulative Survival Upon Exit			
River-Year	**FW**	**IE**	**OE**	**BAY / Overall**
LaHave	76.5% 98.9% $\cdot km^{-1}$	76.5% 100.0% $\cdot km^{-1}$	73.5% 99.7% $\cdot km^{-1}$	73.5% 100.00% $\cdot km^{-1}$
Gold	100.0% 100.0% $\cdot km^{-1}$	88.2% 92.4% $\cdot km^{-1}$	79.4% 97.8% $\cdot km^{-1}$	61.8% 97.6% $\cdot km^{-1}$
St. Mary's	79.4% 99.3% $\cdot km^{-1}$	76.5% 98.7% $\cdot km^{-1}$	73.5% 98.7% $\cdot km^{-1}$	67.6% 98.3% $\cdot km^{-1}$
West 2008	78.9% 97.0% $\cdot km^{-1}$	52.6% 83.8% $\cdot km^{-1}$	47.4% 96.5% $\cdot km^{-1}$	47.4% 100.0% $\cdot km^{-1}$
West 2009	96.0% 99.5% $\cdot km^{-1}$	76.0% 90.5% $\cdot km^{-1}$	72.0% 98.3% $\cdot km^{-1}$	68.0% 98.8% $\cdot km^{-1}$
West 2010	71.9% 95.5% $\cdot km^{-1}$	54.5% 91.0% $\cdot km^{-1}$	51.5% 98.0% $\cdot km^{-1}$	39.4% 95.0% $\cdot km^{-1}$

At-Sea Survival of Smolts and Kelts

One of the main threats to SU Atlantic salmon is thought to be the change in smolt-to-adult return rates, although estimates of the return rates for wild smolts are not available prior to the mid-1990s because smolt abundance was not being monitored before then. To resolve this issue, a model was set up to estimate past return rates using time series of estimated egg depositions, age-specific abundances of fry and parr, and the more recent age-specific smolt abundance time series.

The observed and estimated return rates of 1SW and 2SW salmon to the river mouth for the LaHave River (above Morgan Falls) population increased in the mid-1980s coincident with the closure of the commercial fisheries on Nova Scotia's coast (Figure 5). Return rates generally declined from 1985 to 1995 and have fluctuated without a clear trend since. In the 1980s, return rates varied between 2.87% and 17.60% for 1SW salmon and between 0.31% and 1.21% for 2SW salmon for the LaHave River (above Morgan Falls) population (Table 2); whereas, in the 2000s, return rates varied between 2.25% and 4.14% for 1SW salmon and between 0.31% and 1.21% for 2SW salmon. Similarly, for the St. Mary's River (West Branch) population, return rates in the 1980s varied between 1.17% and 5.52% for 1SW salmon and between 0.54% and 2.11% for 2SW salmon. In the 2000s, return rates varied between 0.18% and 2.11% and between 0.00% and 0.30% for 1SW and 2SW salmon respectively (Table 2). Return rates for Southern Upland salmon are currently about ten times higher than they are for inner Bay of Fundy salmon populations.

Population modeling for the LaHave River (above Morgan Falls) and the St. Mary's River (West Branch) salmon populations indicated that smolt-to-adult return rates, a proxy for at-sea survival, have decreased by a factor of roughly three between the 1980s and 2000s.

Table 2. A summary of the average return rates (percent) of one sea-winter and two sea-winter wild Atlantic salmon for the 1980 to 1989 and 2000 to 2009 time periods for the populations in the LaHave River (above Morgan Falls) and in the West Branch of the St. Mary's River.

	LaHave River (above Morgan Falls)		St. Mary's River (West Branch)	
	1980-1989	2000-2009	1980-1989	2000-2009
Return rates to river mouth (%)				
1SW mean	7.28	2.25	3.33	1.18
1SW minimum	2.87	1.19	1.17	0.54
1SW maximum	17.60	4.14	5.52	2.11
2SW mean	0.74	0.33	0.74	0.09
2SW minimum	0.31	0.10	0.18	0.00
2SW maximum	1.21	0.52	1.54	0.30

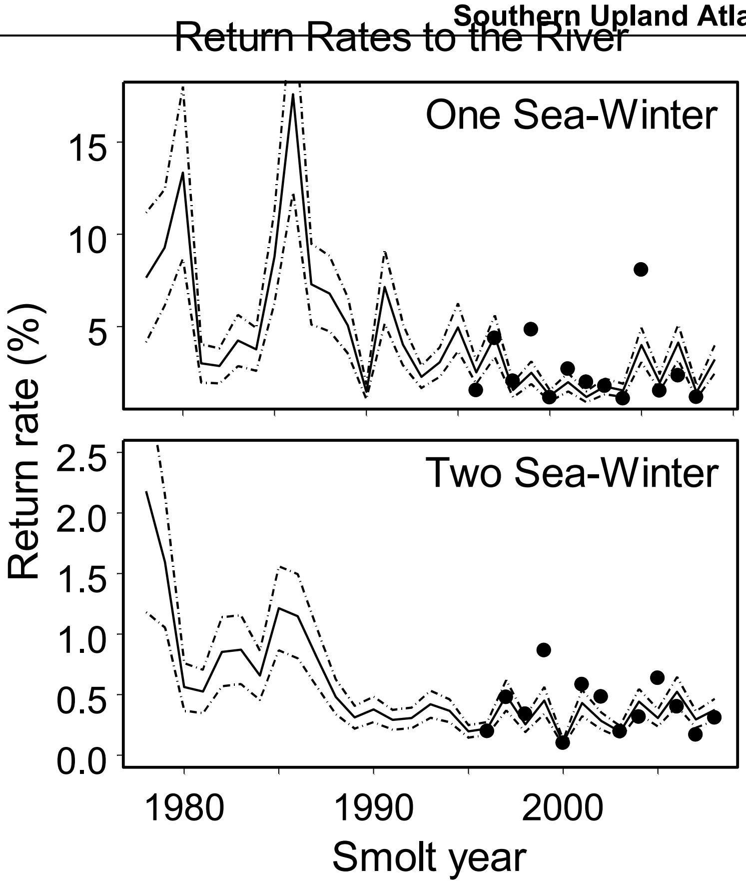


Figure 5. Observed (points) and estimated (lines) return rates for one sea-winter and two sea-winter wild Atlantic salmon for the LaHave River (above Morgan Falls) population, as estimated with the life history model. The broken lines show 95% confidence intervals based on normal approximations. Return rates are to the mouth of the river.

In addition to the changes in survival of smolts, the survival of adult salmon has also decreased since the 1980s. Details of research based on LaHave River salmon are summarized in Gibson and Bowlby (2013). The resulting estimates of mortality in the first year between spawning events increased throughout the time series, whereas mortality in the second year between spawning events increased but tended to oscillate (Figure 6). Decadal comparisons of parameter estimates indicate that mortality in the first year has continued to trend upward, indicating increasing mortality in freshwater or marine near-shore regions (near-field), whereas average second-year mortality values increased from the 1980s to the 1990s, consistent with a regime shift in the oceanic (far-field) environments. The probability of consecutive spawning varied during the time without any obvious trend in period. Fluctuations in the second-year mortality parameter matched fluctuations in the winter North Atlantic Oscillation Index (Figure 6), although this relationship was less apparent after 2000, possibly indicating a change in the regulatory mechanism in the later time period.

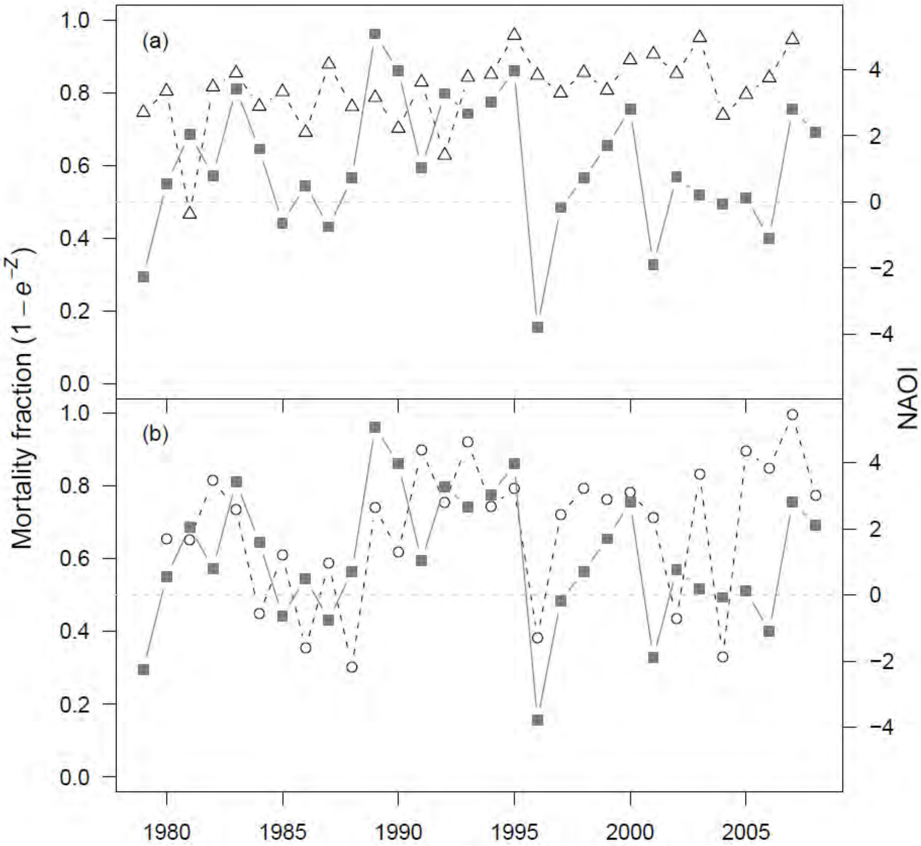


Figure 6. Annual mortality rate of LaHave River salmon as the proportion of potential mature Atlantic salmon that die in a given first year plotted alongside the winter North Atlantic Oscillation Index (NAOI) (■), an environmental variable thought to influence the marine ecology of Atlantic salmon. The NAOI is compared to mortality in the first year (Δ), which occurs mainly in freshwater (a) and mortality in the second year (○), which occurs mainly in the marine environment (b). A horizontal dashed line is provided for reference and represents an NOAI of 0 or an annually mortality rate of 50%. Reprinted from Hubley and Gibson (2011).

Population Dynamics: Past and Present

Due to the decreases in survival described above, the number of eggs expected to be produced by a smolt through its life (EPS) has also decreased. For the LaHave population, EPS values ranged between 87 and 489 eggs/smolt in the 1980s and between 29 and 111 eggs/smolt in the 2000s, a statistically significant decrease. Similar changes were estimated for the St. Mary's population, although the EPS values were generally lower.

The estimates of freshwater productivity (the rate at which eggs produce smolts) and the EPS estimates (the rate at which smolts produce eggs) were combined via an equilibrium analysis to provide estimates of the abundance at which the population will stabilize if the input parameters remain unchanged. This combined model is then used to evaluate how equilibrium population size has changed through time, as well as how the population would be expected to change in response to changes in carrying capacity, survival, or life stage transition probabilities.

The equilibrium population size for the LaHave River population varied substantially in the 1980s because of changes in the return rates and the repeat spawning component (Figure 7). However, even at the minimum values observed during that time period, the equilibrium population was greater than one. During the 2000s, the mean equilibrium for the LaHave population was zero (Table 3), indicating that the population will extirpate in the absence of human intervention or another factor that causes a change in the life history parameter values. The equilibrium population size for the St. Mary's population is slightly greater than zero (Table 4), but is low enough that the population is expected to be at high risk of extirpation due to the effects of random environmental variability.

Maximum lifetime reproductive rates for the LaHave and St. Mary's populations (Table 4) have decreased from averages of 3.59 and 4.44 in the 1980s, respectively, to averages of 0.84 and 1.02 during the 2000s. These values mean that during the 2000s, at low abundance and in the absence of density dependence (which further lowers reproductive rates), a salmon in the LaHave River produces on average a total of 0.84 replacement salmon throughout its life. Because this value is less than one (which would indicate that each spawner could replace themselves), the population is not considered viable. In the St. Mary's River, a salmon produces on average a maximum of 1.02 replacement salmon throughout its life, indicating that the population has almost no capacity to rebuild if environmental events such as floods or droughts lower survival at some point in time. Note that the minimum rate indicates that there are years of low survival, which is why this population is at risk from environmental stochasticity.

Additional information about the population dynamics of SU salmon is provided in Gibson and Bowlby (2013).

Table 3. A summary of the equilibrium population sizes and maximum lifetime reproductive rates for wild Atlantic salmon for the 1980 to 1989 and 2000 to 2009 time periods for the populations in the LaHave River (above Morgan Falls) and in the West Branch of the St. Mary's River. The values are the maximum likelihood estimates from the life history models. Two sets of values are provided: those derived using return rates to the river mouth, and those derived based on survival to the time of the assessments during the fall. The difference in the values is an indicator of the effect of the recreational fishery on the population dynamics in each time period.

	LaHave River (above Morgan Falls)		St. Mary's River (West Branch)	
	1980-1989	2000-2009	1980-1989	2000-2009
Values using return rates to river mouth				
Equilibrium egg deposition				
mean	23,188,000	0	10,651,000	71,262
minimum	3,898,900	0	1,179,800	0
maximum	63,289,000	4,378,700	21,864,000	3,428,700
Equilibrium smolt abundance				
mean	106,590	0	80,646	2,339
minimum	44,841	0	28,703	0
maximum	129,410	39,342	91,189	54,680
Max. lifetime reproductive rate				
mean	3.59	0.84	4.44	1.02
minimum	1.44	0.39	1.38	0.39
maximum	8.08	1.49	8.05	2.11

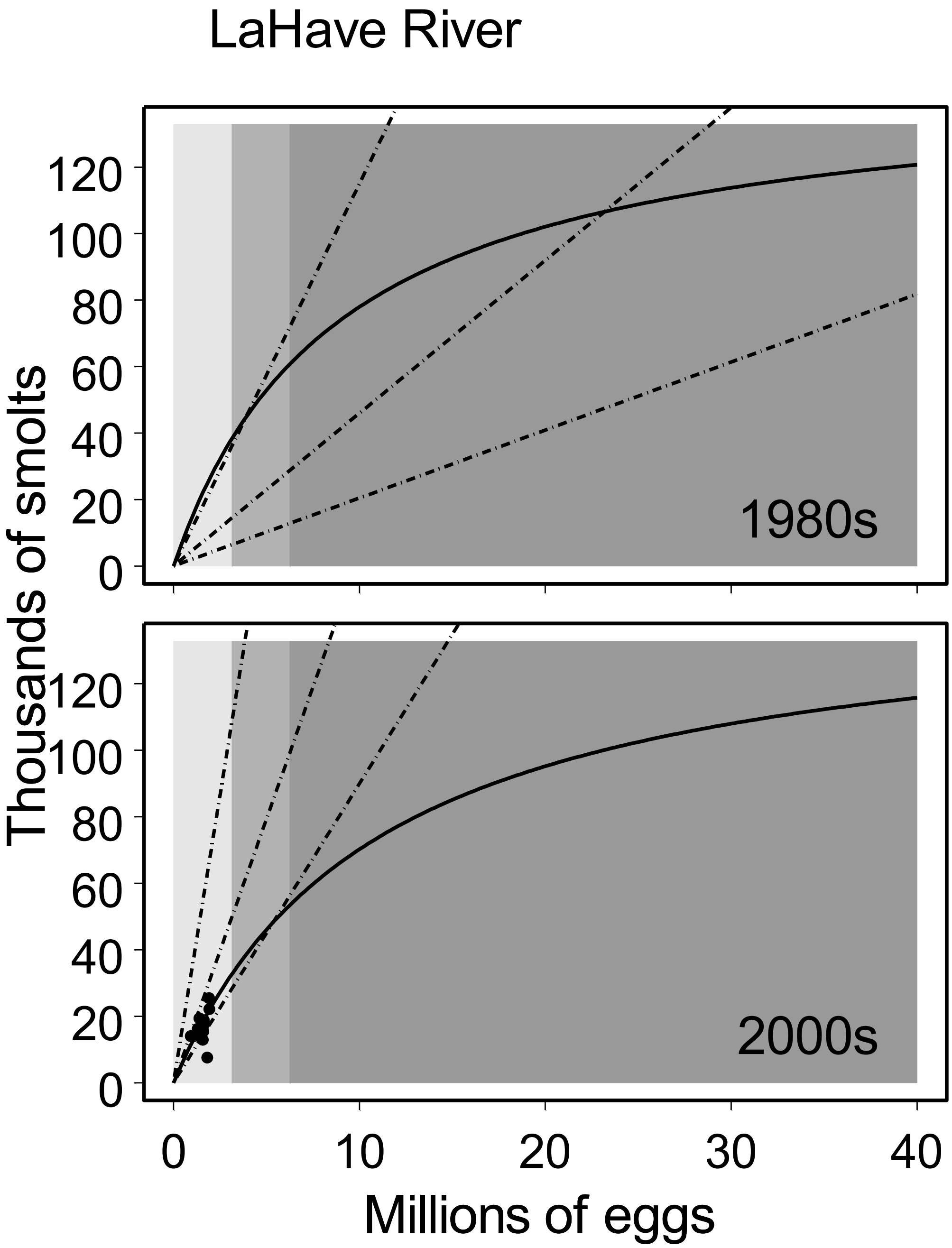


Figure 7. Equilibrium analysis of the dynamics of the Atlantic salmon population in the LaHave River, above Morgan Falls. The points are the observed egg depositions and smolt production for the 2000 to 2008 (lower panel) egg deposition years. The curved, solid line represents freshwater production. The straight, dashed lines represent marine production as calculated at the minimum observed return rates, the mean observed return rates, and the maximum observed return rates for 1SW and 2SW adults during the two time periods. Dark shading indicates egg depositions above the conservation egg requirement, medium shading is between 50% and 100% the egg requirement, and the light shading is below 50% of the requirement.

Population Viability under Present Conditions

Population viability analyses were carried out for both the LaHave River (above Morgan Falls) and the St. Mary's River (West Branch) salmon populations, using both the 1980s ("past") and 2000s ("present") dynamics. Populations are modeled as closed populations, meaning that they are not affected by either immigration or emigration. For each scenario analyzed with the PVA, 2000 population trajectories were simulated and the extinction and recovery probabilities were calculated as the proportion of populations that go extinct by a specified time. For both the past and present scenarios, the population was projected forward from a starting abundance equal to the estimated adult population size in 2010. The numbers of eggs, parr, smolt and adults, as well as their age, sex and previous spawning structure, at the start of each simulation were calculated from the adult abundance using the life-history parameter values specific to the simulation. Populations were assumed to be extinct if the simulated abundance of females dropped below 15 females for two consecutive years. When evaluating recovery probabilities, the conservation requirement was used as the recovery target.

Abundances for each life stage were projected forward for 100 years even though there is considerable uncertainty about what the dynamics of these populations will be at that time. The reason for using these projections is to evaluate longer term viability for each scenario (i.e. does it go to zero or not) and not to estimate abundance at some future time. These projections are used to determine whether the populations are viable for each combination of life history parameters, random variability and extreme events included in the scenario. In the results that follow, emphasis is placed on the LaHave River (above Morgan Falls) population.

Population modeling for two of the larger populations remaining in the Southern Upland DU (LaHave and St Mary's) indicates a high probability of extirpation (87% and 73% within 50 years for these two populations respectively) in the absence of human intervention or a change in survival rates for some other reason.

Abundance trajectories for the LaHave River (above Morgan Falls) salmon population (Figure 8) indicate that, given the present (2000s) population dynamics, this population will extirpate and has zero probability of reaching its recovery target (Figure 9; Table 4). The probability of extinction increases rapidly after about 15 years, with 31% of the simulated populations being extinct within 30 years and >95% going extinct within 60 years (Table 4). None of the 2000 simulated population trajectories met the recovery target within 100 years. This result is consistent with the maximum lifetime reproductive rate estimate of less than one (indicating that the population should continually decline under current dynamics) and the equilibrium population size of zero.

The results for the St. Mary's River (West Branch) salmon population (details in Gibson and Bowlby 2013) are similar. Even though the St. Mary's River (West Branch) salmon population has a maximum lifetime reproductive rate estimate of just over one, this population is also expected to extirpate due to the effects of natural variability in survival. Extinction probabilities also increased rapidly, with 30% of the simulated populations extirpating within 30 years, and 86% of the simulated populations becoming extirpated within 60 years. None of the 2000 simulated populations met the recovery target at any point within 100 years indicating a recovery probability of near zero based on the present dynamics.

Table 4. Probabilities of extinction and of recovery within 1 to 10 decades for the LaHave River (above Morgan Falls) Atlantic salmon population. Two scenarios are shown, one based on the 1980s dynamics (past dynamics) and one based on the 2000s dynamics (present dynamics). The same random numbers are used for each scenario to ensure they are comparable. Probabilities are calculated as the proportion of 2000 Monte Carlo simulations of population trajectories that either became extinct or met the recovery target.

	Probability of Extinction		Probability of Recovery	
Dynamics:	Present	Past	Present	Past
Year				
10	0.00	0.00	0.00	0.34
20	0.05	0.00	0.00	0.97
30	0.31	0.00	0.00	1.00
40	0.66	0.00	0.00	1.00
50	0.87	0.00	0.00	1.00
60	0.96	0.00	0.00	1.00
70	0.99	0.00	0.00	1.00
80	1.00	0.00	0.00	1.00
90	1.00	0.00	0.00	1.00
100	1.00	0.00	0.00	1.00

Population Viability under Past Conditions

In contrast, abundance trajectories using the past (1980s) dynamics (Figure 8) indicate rapid population growth. None of the simulated population trajectories extirpate within 100 years (Figure 9; Table 4) and all simulations reach the recovery target within 30 years.

As was the case with the LaHave River (above Morgan Falls) population, abundance trajectories using the past (1980s) dynamics for St. Mary's River (West Branch) indicate rapid population growth. None of the simulated population trajectories extirpate within 100 years and 97% of the simulated populations reach the recovery target within 30 years. Not all populations remain above the recovery target all of the time because of the low carrying capacity for age-1 parr estimated for this population.

Effects of Extreme Environmental Events

The population viability analyses indicate that the loss of past resiliency to environmental variability and extreme environmental events is contributing to the high risk of extinction. Extreme environmental events that markedly reduce the abundance of juvenile Atlantic salmon do occasionally occur. One such event potentially occurred in the fall of 2010 with very high water levels occurring shortly after the spawning season. Extremely high water events can lead to disturbance or destruction of redds or overwintering habitat for juveniles resulting in higher mortality. The effects of environmental variability and extreme events were investigated using the St. Mary's River (West Branch) population model. The St. Mary's example was chosen rather than the LaHave because it has an equilibrium population size greater than zero, and, therefore, would not become extinct in the absence of environmental variability. However, when random variability is added to the projections (using the same life history parameter values as in the base model), the median time to extinction becomes just under 70 years with 10% of the populations becoming extinct within 40 years. When extreme events are added, 10% of the populations are extinct in 22 years, and half of the populations are extinct within 40 years. Changing the frequency and magnitude of the extreme events changes the extinction probabilities as expected. However, when the same random variability and extreme event scenarios are modeled using the 1980s dynamics, none of the 10,000 simulated population trajectories become extinct and most met the recovery target. This highlights the resiliency that these salmon populations had in the past to environmental variability. Restoring this resiliency, resulting from distributing reproductive effort over multiple years coupled with higher survival, will be an important component of recovering SU Atlantic salmon.

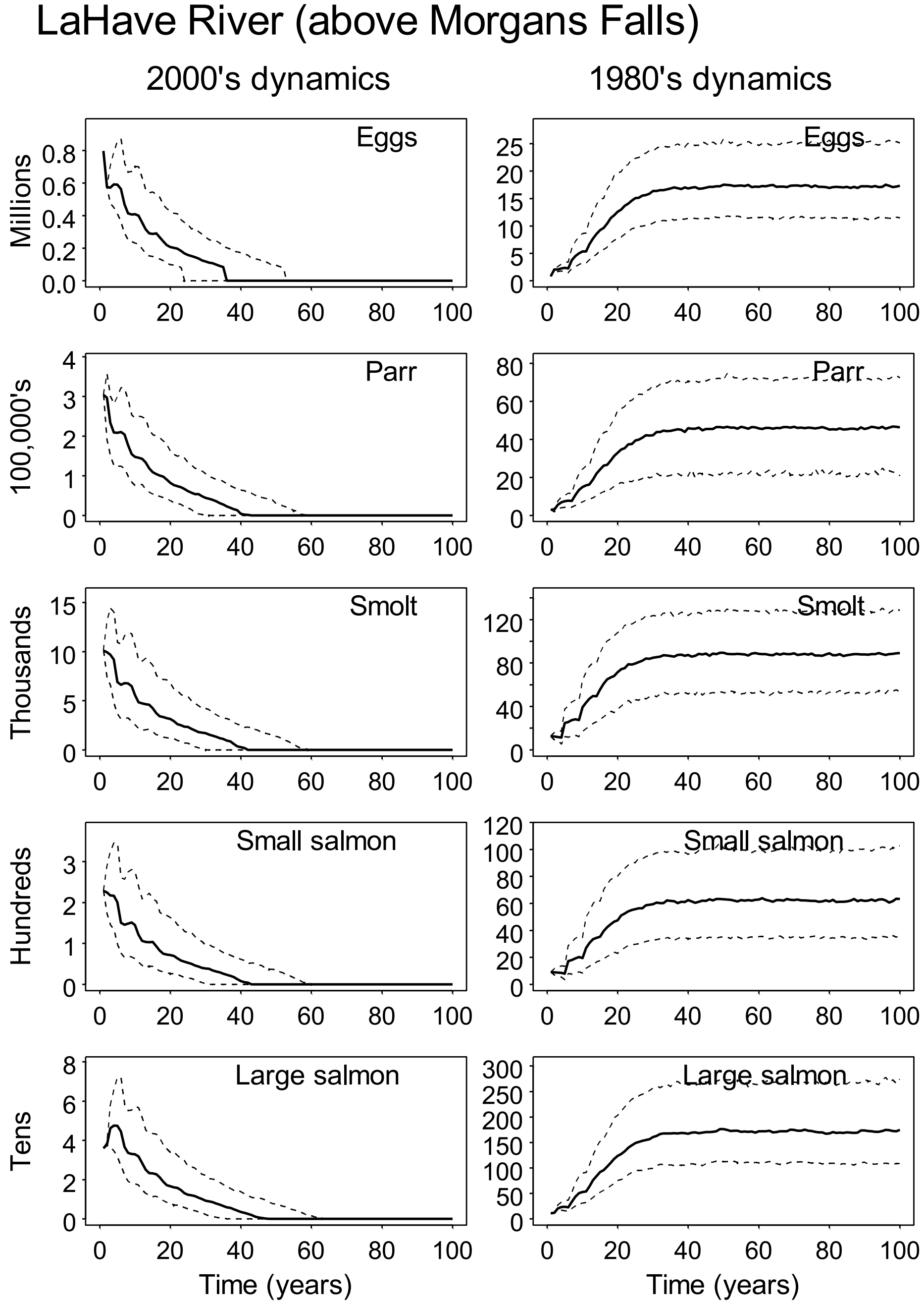


Figure 8. Simulated median abundance (solid line) with the 10th and 90th percentiles (dashed lines) for each of five life history stages from Monte Carlo simulations of the LaHave River (above Morgan Falls) Atlantic salmon population viability model. Two scenarios are shown, one based on the 1980s dynamics (right panels) and one based on the 2000s dynamics (left panels). The graphs summarize 2000 simulations for each scenario.

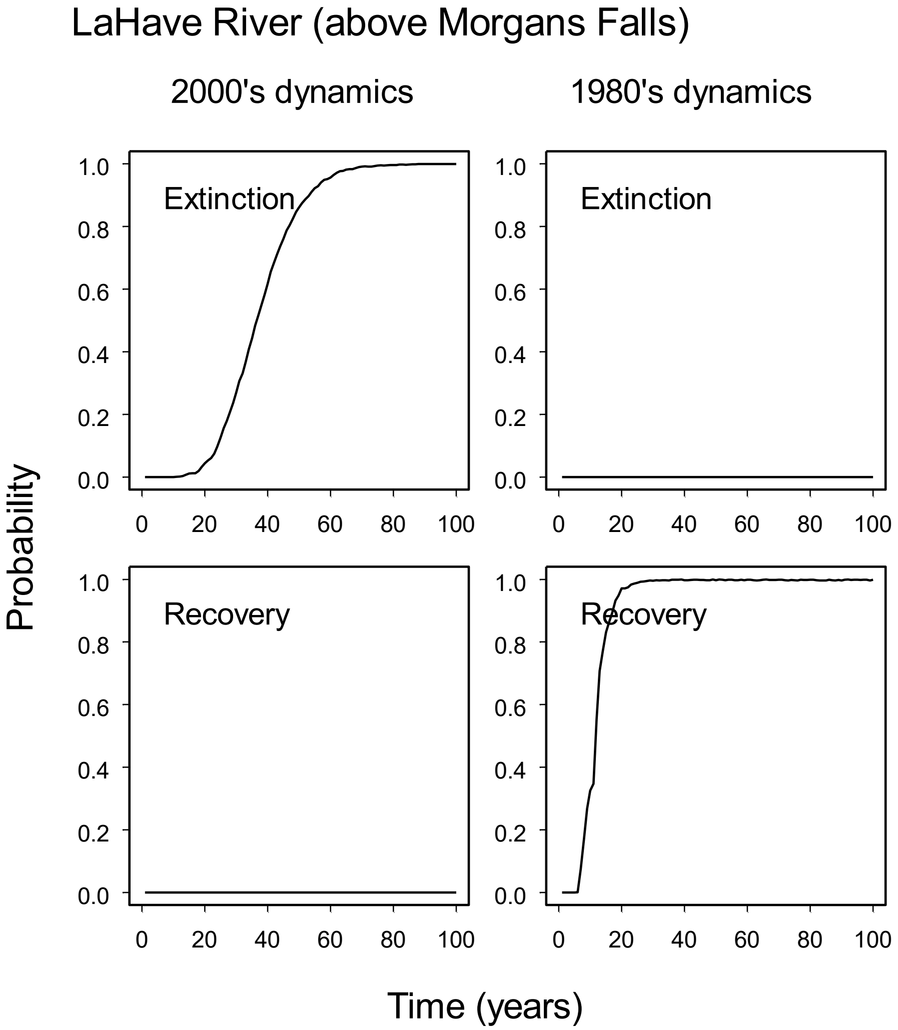


Figure 9. The probability of extinction and the probability of recovery as a function of time for the LaHave River (above Morgan Falls) Atlantic salmon population. Two scenarios are shown, one based on the 1980s dynamics (right panels) and one based on the 2000s dynamics (left panels). Probabilities are calculated as the proportion of 2000 Monte Carlo simulations of population trajectories that either went extinct or met the recovery target.

Habitat Considerations

Functional Descriptions of Habitat Properties

Detailed descriptions of aquatic habitat that SU Atlantic salmon need for successful completion of all life-history stages can be found in Bowlby et al. (2013b).

Freshwater Environment

Adult Atlantic salmon return to rivers in the SU as early as April and as late as November, but the largest proportion of the population enters the rivers in May to August, and fish can spend up to 6 to 7 months in fresh water prior to spawning. The upstream migration appears to generally consist of a migration phase with steady progress upriver interspersed with stationary resting periods, and a long residence period called the holding phase. Habitat properties required for successful migration into rivers include: appropriate river discharge (e.g. it has been suggested that upstream migration will initiate at a river discharge rate of >0.09 m^3/s per meter of river width), pools of sufficient depth and proximity in which to hold (spending weeks to months in a single pool), and unimpeded access throughout the length of the river.

Atlantic salmon in the SU spawn in October and November, with eggs incubating in redds through the winter and hatching in April. Successful incubation and hatching depends on: river discharge, water depth (e.g. generally between 0.15 to 0.76 m for redd construction) and velocity (e.g. 0.3-0.5 m/s preferred at spawning sites), substrate composition (e.g. coarse gravel and cobble with a median grain size between 15 and 30 mm forms the majority of the substrate of redds, with fine sediments found at low concentrations), water temperature (e.g. stable cold temperatures for egg development), and water quality (e.g. uncontaminated water with a pH >5.0 for development of embryos and alevins).

Juvenile SU Atlantic salmon remain in fresh water for one to four years after emergence, with most migrating to the sea two years after emergence. Habitat properties that are important for the successful rearing of juveniles (fry and parr) include: water depth (e.g. age 0 fry tend to occupy water 15-25 cm deep) and velocity (e.g. fry tend to be found in riffles with surface velocities >40 cm/s, parr are found in a wider range of velocities with an optimum between 20-40 cm/s; juvenile Atlantic salmon are rarely found at water velocities <5 cm/s or >100 cm/s, and, in the winter juveniles seek out lower velocity water, presumably to minimize energy expenditure); substrate composition (e.g. preferred substrate for age 0 salmon is in the range 16-256 mm diameter (gravel to cobble) and 64-512 mm diameter (cobble to boulder) for age 1 and older parr); the presence of cover; water temperature (typically between 15ºC and 25ºC); and water quality (uncontaminated water of pH > 5.4).

Salmon smolts do not have the same freshwater habitat requirements as parr, but rather require the environmental conditions necessary to trigger the changes associated with smoltification as well as to successfully emigrate to salt water. Environmental characteristics influencing the process of smoltification are: photoperiod, water temperature, and river discharge. The main characteristics influencing successful emigration from the river are: unimpeded access throughout the length of the river, and sufficient water discharge.

Relatively little is known about freshwater habitat use by post-spawning adult salmon (kelts) in the SU. Kelts have been shown to over-winter in deep water habitats and descend the river in the spring, although some kelts may exit the river relatively soon after spawning. Whether some SU kelts over-winter in estuaries is unknown. The proportion of the population that remains in the river during winter likely depends on the availability of pools, lakes, and stillwaters in the watershed. In a 2010 and 2011 acoustic tagging study in the St. Mary's River, all 24 of the tagged salmon left the river in spring after spawning; no kelts emigrated immediately after spawning or during the winter. The earliest observed salmon leaving the river was on March 16th, but most salmon exited the river between April 22nd and May 11th. This suggests that the proportion of adults remaining in SU rivers after spawning to overwinter in fresh water is high, particularly in rivers with suitable overwintering habitat.

Estuarine Environment

Once smolts leave fresh water, they swim actively, moving continuously through the estuary without a long period of acclimation to salt water. Migration patterns are not necessarily directly toward the open ocean, and residency times in the estuary are varied. This cyclical movement pattern has been exhibited by SU smolts. Residency patterns only suggest where and when smolts occupy estuaries, not the physical habitat characteristics that may be required. Given that smolts are thought to swim near the surface within the fastest flowing section of the water column, and use an ebb tide pattern of migration, habitat choice is unlikely to be based on physical habitat characteristics (e.g. substrate type). It is more likely that the oceanographic conditions in estuaries and coastal areas influence movement and habitat choice in estuaries.

Adult Atlantic salmon return to rivers in the SU throughout the spring, summer, and fall months. Similar to smolt use of estuaries, a variety of estuarine residency times for adults have been observed, from moving through estuaries in a matter of days to spending 3.5 months holding in an estuary before moving into the river. Estuaries appear to be mainly staging areas, and movements within them are frequently slow (<0.2 body lengths per second), following the sinusoidal pattern of the tidal currents. While holding in the estuary, adults seem to favour deep water of intermediate salinities ranging from 5 to 20 parts per thousand.

The limited information on residency times or habitat use by kelts in estuaries suggests that estuaries are used predominantly as staging areas and migratory corridors in the spring. In spring, kelts pass relatively quickly through estuaries on their way to open ocean. The one study on acoustically tagged kelts in the LaHave River found that kelts tagged in fresh water in April exited the estuary within five weeks of release. There was no typical migration pattern; one kelt exhibited non-stop migration seaward and others interspersed periods of continuous movement, residence, and backtracking.

Marine Environment

Habitat use in the marine environment for immature Atlantic salmon (individuals that have undergone smoltification, migrated to the ocean, but have not yet returned to fresh water for the first time to spawn, also known as post-smolts) has been mainly hypothesized based on physiological requirements and/or tolerances of Atlantic salmon in the marine environment. At sea, salmon tend to be found in relatively cool (4°C to 10°C) water, avoiding cold water (<2°C), and modifying their migratory route in space and time in response to ocean temperature conditions. For example, in years where coastal water temperatures are warmer, salmon arrive at home rivers earlier. Tagging studies suggest that immature salmon are pelagic, spending the majority of their time in the top few meters of the water column, following the dominant surface currents and remaining in the warmest thermocline. Although movement patterns and distribution have been correlated with water temperature and other abiotic factors, the availability of prey and potential for growth are assumed to determine actual distribution at sea. As such, marine distribution patterns would be expected to vary in space and time as well as among years, based primarily on the distribution of suitable prey items.

Recent studies in the Northeast Atlantic demonstrate that immature salmon begin to feed extensively on marine fish larvae and to a lesser extent on high-energy crustaceans, experiencing a rapid increase in growth in the near-shore environment. Atlantic salmon are opportunistic feeders, leading to geographical differences in the type and amount of prey consumed. There is some indication that Atlantic salmon in the Northwest Atlantic have a larger proportion of insects and crustaceans in their diet than those in the Northeast Atlantic, but gadoids, herring and sand lance are also important prey items.

Growth patterns of scale circuli from two populations in the SU region combined with tag returns from commercial fishing suggest that these populations experience similar oceanographic conditions and use similar temporal and spatial routes during marine migration. A coastal or near-shore migration route along the North American continent is generally accepted (as described in the Spatial Extent of Habitat section). The location of primary feeding and staging grounds for immature salmon destined to return after one winter at sea to rivers in the SU is less well known. It may include all near-shore areas along the North American coast with suitable surface temperatures, extending northward to the Labrador Sea, but is more likely to correspond to areas of high prey density within that broad range.

After spawning, the majority of adults exit rivers in the spring of the following year for a period of reconditioning before spawning again. The length of time adults spend in the ocean between spawning events likely determines marine habitat use and distribution patterns. Consecutive spawners return in the same year as their kelt migration and have a relatively short ocean residence period (< 6 months), while alternate spawners return the following year and can spend up to a year and a half in the marine environment. Tagging studies demonstrate that alternate spawners travel as far north as West Greenland, likely following a similar migration route as immature salmon along the coastal or near-shore habitats of North America. The marine habitat use of consecutive spawning adults is less well known, but it is very unlikely that individuals would be able to reach the Labrador Sea or West Greenland in the time between spawning events. One acoustically tagged kelt from the LaHave River reconditioned over a period of 79 days before re-ascending the river, but spent this time outside the estuary. As with immature salmon, marine distribution and habitat use of adults is thought to be determined primarily by the distribution and abundance of suitable prey. Fish are the majority of the diet of adult salmon, and the species consumed include capelin, sand eels, herring, lanternfishes and barracudina. Amphipods, euphausids (krill) and other invertebrates are also consumed, and there is some indication that the proportion of invertebrates consumed increases in more southerly feeding areas.

Spatial Extent of Habitat

Freshwater Environment

Wild Atlantic salmon exhibit nearly precise homing to natal rivers, which results in significant population structuring at the river scale. There is no information which suggests that salmon do not use all available rivers in the SU at least intermittently, and assessment data demonstrates that there is no apparent minimum watershed size for occupancy. As described in the Background section, the number of watersheds that are known to have contained salmon populations is 72 (Figure 2). However, 513 additional watersheds in the SU have been identified by the Nova Scotia Department of the Environment (NS DoE), of which 256 are larger than Smith Brook (the smallest watershed known to have contained salmon). These other watersheds have a total drainage area of 6,586 km^2 (excluding coastal islands), and each has the potential to support Atlantic salmon.

Combining information from all watersheds known to have contained salmon (Figure 2), there is an estimated 20,981 km^2 of drainage area, which contains 783,142 habitat units (100 m^2) of rearing area for Atlantic salmon. The 10 largest systems contain slightly more than half of this productive area (436,572 habitat units), and only 4 watersheds have an estimated rearing area that is less than 1,000 habitat units.

Estuarine Environment

The use of particular habitat types within estuaries by smolts, adults and kelts is relatively unknown for SU Atlantic salmon, but estuarine habitat availability is not thought to be limiting.

Marine Environment

Marine distribution patterns for SU Atlantic salmon were assessed based on recovery locations of tagged smolts and adults reported by commercial and recreational fisheries.

In total, there were 5,158 recaptures of individuals tagged in the SU region (1,899 from SFA 20 and 3,259 from SFA 21). Recapture rates from groups of tagged fish were extremely low, generally less than 5% (mean = 3.9%, median = 0.8%, range: 0.02% - 73%). All of the higher recapture rates were associated with releases upstream of continuously monitored facilities, like Morgan Falls fishway on the LaHave River. There were very few release events of exclusively wild-origin fish (either adult or smolt) or of adults (either hatchery or wild. Therefore, the data presented are based entirely on recaptures of hatchery-origin or mixed-origin (wild plus hatchery in the same release group) smolts. Due to the relative scarcity of recapture information, marine distribution patterns of SU Atlantic salmon are presented as a group, although there are likely differences among populations in marine habitat use. Three time periods were evaluated: distribution in the year of release, distribution in the year following release, and distribution two years following release.

First Year Following Release (Figure 10): The majority of tagged smolts were released in fresh water in April and May. By late May and throughout June, smolts had begun leaving fresh water and moving along the coast of Nova Scotia, both in a southern and northern direction (Figure 10). By July, individuals had spread out along the entire coast of Nova Scotia, from the inner Bay of Fundy to the tip of Cape Breton, while a smaller proportion had moved substantially farther northward, to Eastern Newfoundland, Northern Quebec and the tip of Labrador (Figure 10). A similar pattern exists during August. From September until the following March, there were very few tag recaptures; these indicated that a proportion of SU salmon remained along the coast of NS during the winter months. Interestingly, there were no recaptures of immature SU Atlantic salmon off the coasts of Newfoundland, Quebec, and Labrador after September. This may suggest that immature Atlantic salmon from the SU do not over-winter this far north in their first winter at sea, or that they arrive after the close of the various fishing seasons (i.e. after November). Additionally, immature salmon were not captured in the West Greenland fishery in the first year following release (based on a total of 430 recapture events), which may indicate that they do not travel this far north in their first year or are too small to be captured by the fishing gear.

Second Year Following Release (Figure 11): In the second year, there would be salmon that return to natal rivers to spawn after 1SW as well as salmon that remain at sea for the second year (and will return as 2SW or older). The earliest recaptures in the spring were still off the coast of Nova Scotia (Figure 11), suggesting that a proportion of the individuals remained relatively localized for their entire first year at sea. Beginning in May, the largest number of recaptures was along the northern coast of NL and spread to more southerly locations in June, concentrated off the coast of Nova Scotia (Figure 10). Recaptures in the high-seas fishery off West Greenland took place from July to November (Figure 10), and the relative scarcity of recaptures in July, October and November may reflect reduced fishing effort rather than movement into or out of this area. The catch from the West Greenland fishery is thought to consist almost entirely of individuals destined to return to natal rivers as 2SW spawners, so these tag returns represent the 2SW component of populations. It is possible that the recaptures off the northern coast of Newfoundland and Labrador during the spring, summer and fall months (Figure 11) also consist of a proportion of 2SW individuals, as well as those returning to their natal rivers to spawn. It is likely that most of the recaptures of salmon off the coast of Nova Scotia in the summer months represent 1SW individuals (Figure 11). It is similarly likely that the distribution of 1SW and 2SW fish partially overlap during the summer months.

Third Year Following Release (Figure 12): In the third year, there would be salmon returning to the marine environment after spawning as 1SW salmon and salmon returning to natal rivers to spawn as 2SW adults. Based on results of kelt tagging in the LaHave River, it is likely that some portion of the marine recaptures off the coast of Nova Scotia in April and early May (Figure 12) are salmon that over-wintered in fresh water and returned to recondition in the marine environment. The other portion of the recaptures was likely first-time spawners. There were recaptures off the coast of Newfoundland from May to November (Figure 12), potentially representing two groups: salmon moving from West Greenland and the Labrador Sea on their way to natal rivers (2SW spawners) and salmon moving northward to recondition after previously spawning.

Assuming that these data represent general distribution patterns in the marine environment, there seems to be very limited use of the Gulf of St. Lawrence (including the coastal areas around the Magdalen Islands, northern New Brunswick, or Quebec near Anticosti Island) by SU Atlantic salmon. However, they do move along both coasts of Newfoundland, and they have been recaptured at locations south of where they were released. Contrary to predictions of progressive northward movement for immature individuals to over-wintering areas in the Labrador Sea or West Greenland, these tagging data suggest that SU Atlantic salmon are widely distributed in coastal marine habitats throughout their first year, particularly during the summer months.

Although it is not possible to explicitly describe the movement patterns of the various life stages of SU Atlantic salmon from these data, the inferences above highlight a crucial point when designating critical habitat in the marine environment. Although different life stages may transiently occupy similar habitats, their overall direction of movement could be in opposite directions, potentially leading to a relatively ubiquitous distribution from Nova Scotia to the Labrador Sea and West Greenland throughout most of the year. Given the variability in run-timing, both within and among populations, similar variability is likely to exist in movement of SU Atlantic salmon along the near-shore environments of the Northeast Atlantic, meaning that marine distribution (and therefore habitat use) cannot be clearly delineated on a seasonal basis.

Freshwater Spatial Constraints: Influence of Barriers and Water Chemistry on Habitat Accessibility

Assessing the impact of physical barriers on the amount of habitat in a watershed is difficult because structures can be entirely or seasonally impassable for various life stages depending on stream flow. An ArcGIS layer detailing available information on barriers in SU watersheds was compiled jointly by the NS DoE and the DFO Habitat Management (HM). This layer contains the characteristics of known barriers, including fish passage capabilities (e.g. classified as passable to fish or not). These data represent the best regional information, but data were collected over multiple years. The most recent updates to specific records span the years from 2007 to 2010 (a total of 37 out of 586 records do not list a date). Any recent changes would not have been captured in the database.

By intersecting the stream network from the National Hydrographic Service with the barrier locations, it was possible to calculate the percentage of the flow network (stream length) affected by barriers in each of the SU watersheds. There is an essentially linear relationship between the length of the flow network and the drainage area in watersheds in the SU (data not shown), so these percentages were multiplied by the amount of rearing area in a watershed to approximate the impact of barriers on habitat availability. The accessible rearing area was estimated at 57.0 million m² (73.2% of total rearing area) and the inaccessible area was estimated to be 21.0 million m² (26.8% of total rearing area).

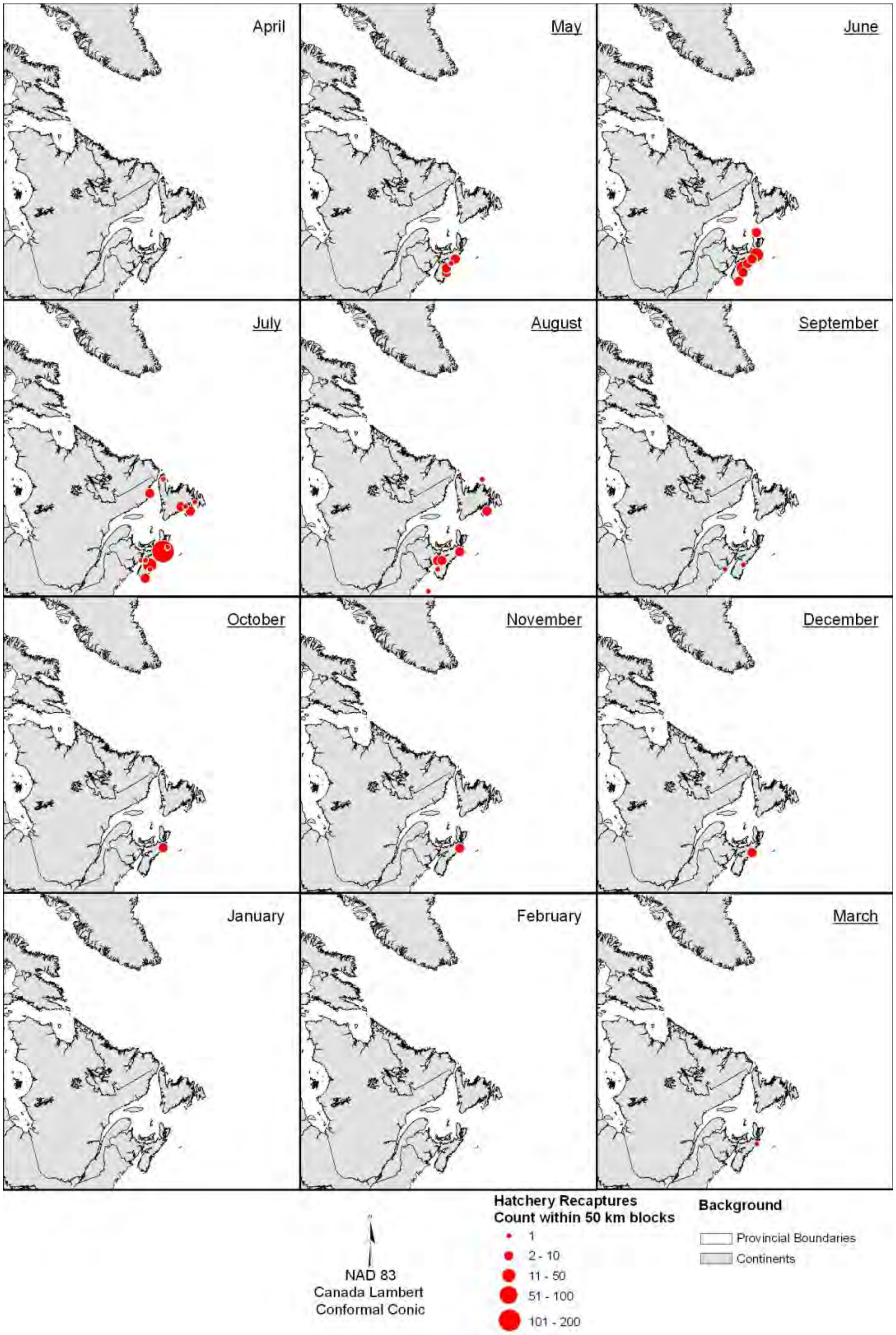


Figure 10. Recapture locations in the marine environment of individually tagged, hatchery-origin smolts in the first year following release, where the size of the point on the map is proportional to the number of recaptures within a 50 km^2 grid.

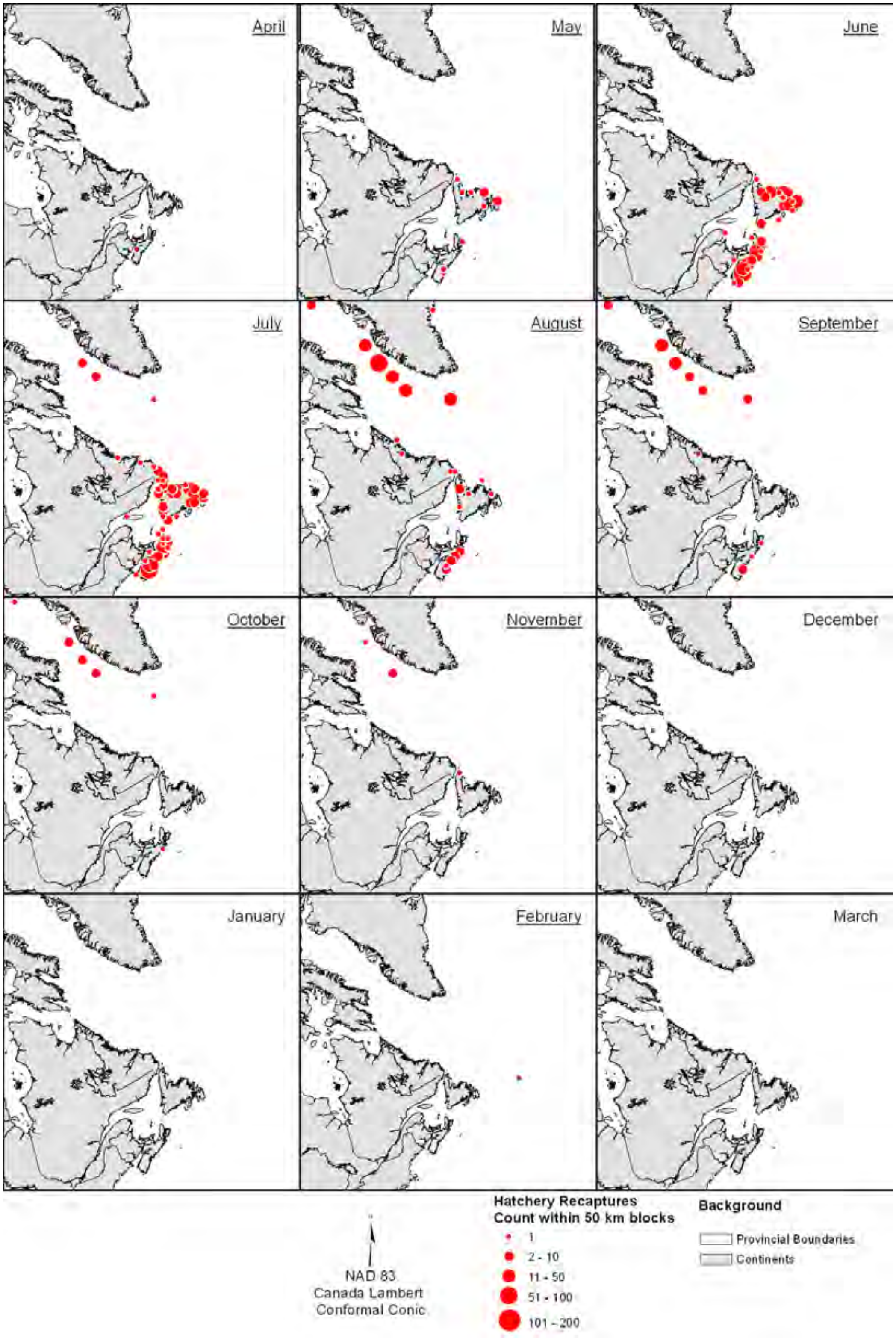


Figure 11. Recapture locations in the marine environment of individually tagged, hatchery-origin smolts in the second year following release, where the size of the point on the map is proportional to the number of recaptures within a 50 km^2 grid.

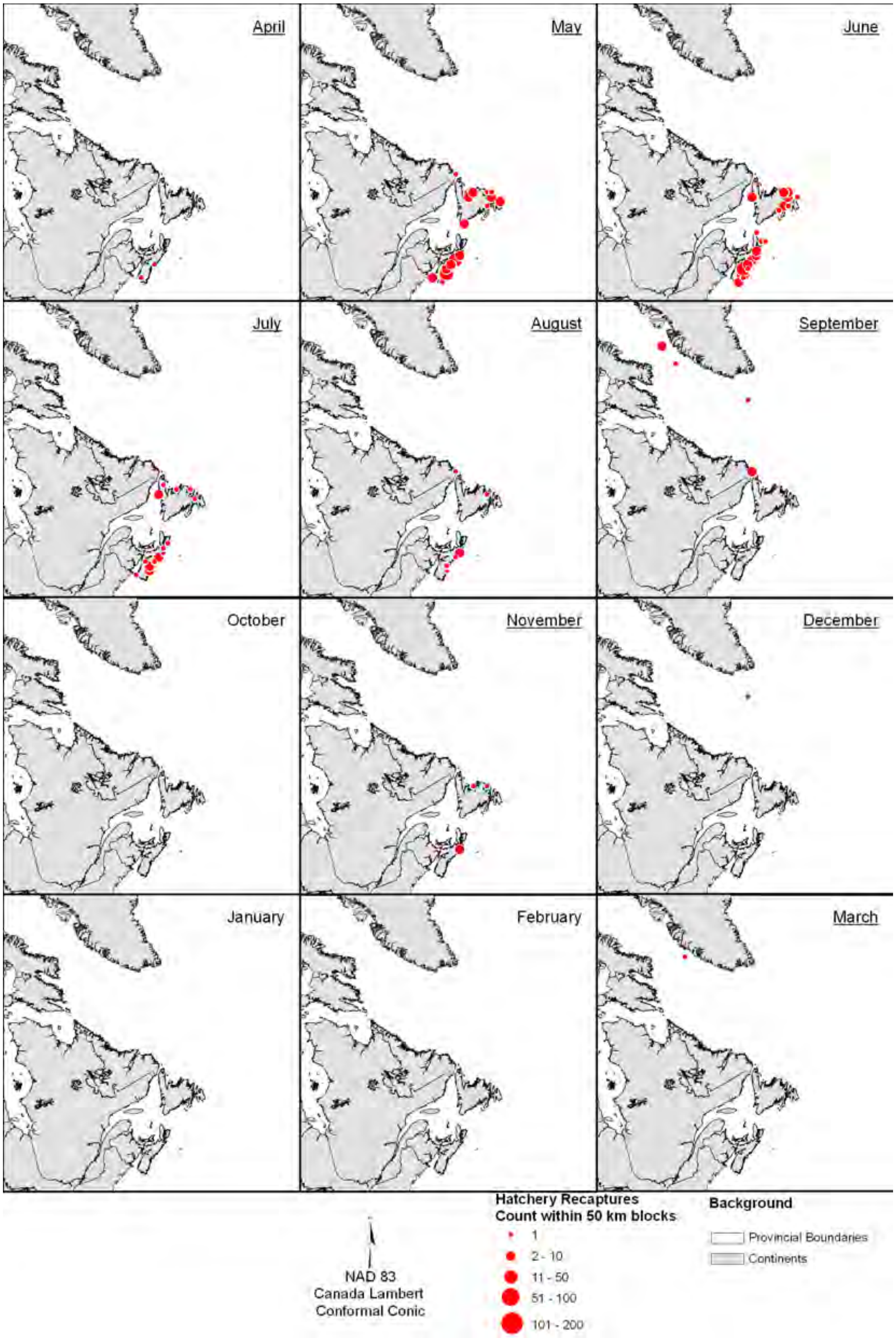


Figure 12. Recapture locations in the marine environment of individually tagged, hatchery-origin smolts in the third year following release, where the size of the point on the map is proportional to the number of recaptures within a 50 km^2 grid.

Acidification (low pH) is a major factor limiting the production of Atlantic salmon in many SU rivers. It can partially or completely eliminate suitable habitat within a watershed. Highly acidified water is not a barrier *per se* because adults can still enter the river and spawn;

however, the habitat is unsuitable because their progeny die. Thirteen rivers are considered to be unsuitable for spawning and juvenile rearing based on their acidity level (mean annual pH < 4.7), conclusion supported by the juvenile density estimates from the electrofishing surveys (0/100m^2). These 13 rivers contain a total of 100,198 habitat units (100 m^2) [or 10 million m^2] that is considered unsuitable for Atlantic salmon production.

None of the 5 watersheds that are identified as impassable due to barriers at head-of-tide are among the 13 watersheds that unsuitable for Atlantic salmon due to acidification. Thus, 18 watersheds have very little or no rearing area available for Atlantic salmon. Of the remaining 54 rivers, 25 contain total barriers that block from 0.1% to 94.5% of the watershed. There are 29 rivers that do not contain a known total barrier, and these tend to be either smaller systems or watersheds along the Eastern Shore of Nova Scotia. Of the 783,142 habitat units (100 m^2) available in rivers in the SU region, only 476,746 (61%) remain accessible to Atlantic salmon populations (Figure 13).

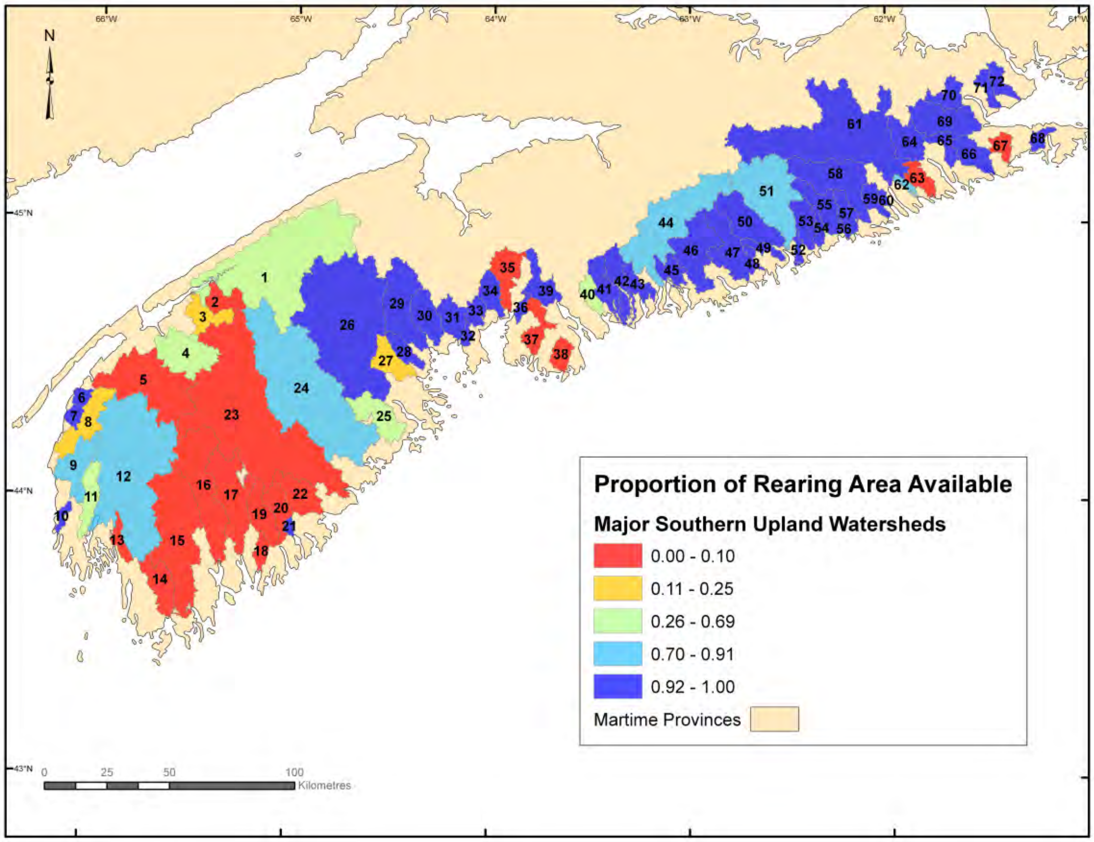


Figure 13. Proportion of rearing area available to Atlantic salmon for watersheds in the Southern Upland based on accessible habitat area (i.e. area below impassable dams) as well as pH category (where mean annual pH < 4.7 is considered unusable). Watershed numbers correspond to the legend in Figure 2.

Thus, together, acidification and barriers to fish passage are thought to have reduced the amount of freshwater habitat by approximately 40%. Thirteen individual watersheds are thought to contain essentially no useable habitat (based on acidification) and a range of 0.1% to 95% of habitat (based on stream length) is lost in other watersheds. These estimated reductions in habitat quantity are likely conservative. However, given the low abundance of salmon at present, habitat quantity is not thought to be currently limiting in rivers unaffected by barriers and acidification. .

Supply of Suitable Habitat

Current juvenile densities estimated for rivers in the SU are very low (Figure 4), particularly when compared to historical estimates of juvenile salmon production that have been used as a reference levels in the past (29 age 0 fish/100 m^2 and 38 age 1 and older fish/100 m^2: known as Elson's norm) . In other regions, where Atlantic salmon populations are thought to be meeting or close to conservation requirements, juvenile density estimates for all age classes regularly exceed Elson's norm. Although rivers in the SU may have lower productive potential than those in other areas because of their underlying geology, the amount of rearing habitat for juveniles in a given watershed (i.e. habitat of suitable gradient) is unlikely to be limiting population size for unobstructed systems and non-acid impacted systems at present. Low juvenile abundance is more likely the result of low adult abundance (in part due to low at-sea survival) and effects of human activity in these watersheds. As described above, physical barriers and water quality have likely reduced the quantity of freshwater habitat available to spawning adults by at least 40%, which would be expected to reduce adult abundance by the same amount if other life history parameters remained unchanged. In these rivers, supply of suitable habitat likely would not meet the demand.

The production of juvenile Atlantic salmon in freshwater habitats is governed by density dependent growth, survival, and habitat use. However, potential for growth is inversely related to density and, as populations become larger (with no change in the quality and quantity of available habitat), the potential rate of population growth declines. At high abundance, populations exhibit relatively constant juvenile production over a very large range of egg deposition values. In the context of habitat limitation for SU Atlantic salmon at very high abundance, this demonstrates that the productive capacity of freshwater habitats (i.e. habitat quality and quantity) will ultimately limit population size.

Regardless of the present value for carrying capacity in a specific river, the marine survival rates experienced by populations would affect whether freshwater habitat is limiting population growth at a given level of abundance. The equilibrium analysis presented earlier shows that the mean marine survival rates observed on the St. Mary's and LaHave rivers were sufficient to enable population growth in excess of the conservation requirement during the 1980s. However, under current dynamics, these populations would not be predicted to reach the conservation requirement even at the maximum observed marine survival rates during the 2000s. Ultimately, whether freshwater habitat becomes limiting in the future depends on the dynamics of recovered populations. If survival in the marine environment were to meet or exceed levels of the 1980s, freshwater habitat is not expected to become limiting until the population had reached abundance levels in excess of the conservation requirement. Conversely, if marine survival remains at current levels or undergoes a modest increase, it is predicted that increases in freshwater productivity would be necessary to reduce extinction risk or promote population increase for SU Atlantic salmon populations. The question of whether available habitat will become limiting as populations increase depends on the productive capacity of freshwater habitats as well as the mortality rates experienced by Atlantic salmon in the marine environment.

Trade-offs Associated with Habitat Allocation Options

Allocation of freshwater habitat (i.e. for consideration as critical habitat for SU salmon) can occur on at least two scales: at the watershed scale and within a watershed. At a watershed scale, freshwater habitat should be allocated to minimize extinction risk for SU Atlantic salmon populations by ensuring that the remaining genetic diversity of SU Atlantic salmon is protected, and by facilitating the re-establishment of wild self-sustaining populations in other rivers.

Specifically, watersheds that are currently known to contain Atlantic salmon and those that have a high probability of containing useable freshwater habitat are considered priorities.

Juvenile Atlantic salmon were found in 22 of the 72 (54 surveyed) river systems in 2008/2009, with knowledge of others. Given the reductions in habitat that have already occurred and the current low population size with ongoing declines, all 22 rivers include important habitat for SU Atlantic salmon. Restoration of these populations is expected to achieve the distribution component of the recovery target described below. If additional rivers are found to contain salmon, the consideration of these rivers as important habitat would have to be evaluated.

Barriers and pH are two factors that have a large effect on freshwater habitat availability and quality, respectively, and depending on the extent of each, can be difficult or costly to remediate. Therefore, rivers or parts of rivers that remain accessible to Atlantic salmon (due to the absence of total barriers) or rivers that remain mildly or un-impacted by acidification (mean annual pH that is greater than 5.0; category 3 and 4 rivers) should also be considered very important in terms of habitat allocation for SU Atlantic salmon (Figure 14). Even if the specific river does not contain Atlantic salmon at present, these areas likely contain useable freshwater habitat that could support populations in the future. Including some rivers with varying levels of pH should also help to protect the remaining genetic diversity among populations in the SU, given that there are wild populations remaining with greater tolerance to low pH (e.g. salmon in the Tusket River have a higher tolerance of low pH than other populations in Nova Scotia).

At smaller spatial scales, habitat allocation decisions can be made to ensure that habitat availability for a single life stage does not become limiting. Atlantic salmon have a complex life cycle with different habitat requirements for each life stage. Habitat for all life stages, as well as habitat connectivity, needs to be considered when identifying priority habitats for allocation, to avoid having one habitat type limiting population growth.

In addition, the estuaries associated with these rivers are considered to be important habitat for Atlantic salmon, with successful migration through this area essential to the completion of their life history.

While there is likely important marine habitat for SU Atlantic salmon, given broad temporal and spatial variation, it is difficult to link important life-history functions with specific marine features and their attributes. Further research into marine distribution patterns is unlikely to reveal distinct areas that should be considered for marine habitat allocation. Habitat allocation decisions could potentially be made at a broad scale, and the evaluation of activities likely to impact this habitat could be based on the extent to which they reduce the capacity of the larger area to provide salmon habitat.

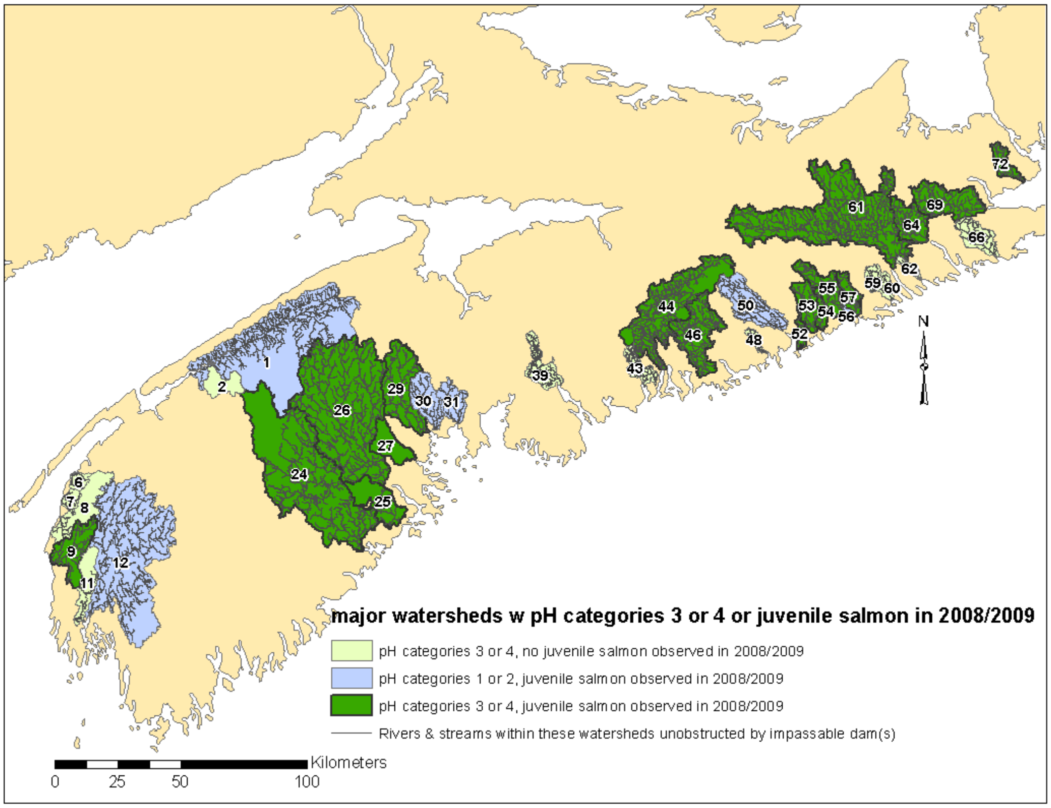


Figure 14. Location of freshwater habitats that exhibit one (or more) of three characteristics: have a pH greater than 5.0 (rivers in pH categories 3 or 4; see also Figure 16), have a high proportion of the watershed not impacted by barriers to fish passage, and/or contained Atlantic salmon in the most recent (2008/09) electrofishing survey. Watershed numbers correspond to the legend in Figure 2.

Recovery Targets

Long-term goals for the recovery of Atlantic salmon in the SU region include increasing the size and total number of populations, as well as their distribution. However, determining how many populations are needed to attain this long-term goal or how large they must be to ensure recovery of SU Atlantic salmon is not possible from a quantitative perspective because the dynamics of recovered populations of SU Atlantic salmon are not known. Previous research on abundance targets as well as theoretical research on how species distribution relates to persistence or recovery can be used as a basis for decision-making.

Proposed recovery targets for Atlantic salmon populations in the Southern Upland DU have both abundance and distribution components.

Abundance targets for Southern Upland Atlantic salmon are proposed as the river-specific conservation egg requirements, which are based on the estimated amount of juvenile rearing area and an egg deposition rate of 2.4 eggs/m^2. Attaining the conservation requirement is consistent with attaining long-term population persistence, maintaining the ecological function of the watersheds in which salmon formerly resided, and increasing the potential for human benefits if populations were recovered in as many rivers as possible. Overall population size is positively related to population persistence for a range of fish species, which suggests that increasing population size for salmon in the SU region is important for recovery. However, population size alone is not an indicator of population viability, and precisely how large populations need to be depends on their dynamics during population rebuilding.

The distribution target should encompass the range of genetic and phenotypic variability among populations, environmental variability among rivers, and include rivers distributed throughout the DU to allow for gene flow between the rivers/populations. There is the expectation that including a wider variety of populations in the distribution target will enhance persistence as well as facilitate recovery in the longer term. The following criteria can be used to help prioritize among river systems when setting distribution targets: current population size, complexity (in population life history, local adaptation and genetic distinctiveness), connectivity with surrounding populations (metapopulation structure), and the number and location of source populations.

There is population and genetic structuring within the SU region, which means all populations of Atlantic salmon cannot be considered equivalent. Furthermore, each population has the potential to contribute genetically and/or demographically to the long term persistence of SU Atlantic salmon (and possibly the species itself) so it is intrinsically important. Preserving the maximum amount of genetic variation will maximize the evolutionary potential of SU Atlantic salmon, ensuring that the DU as a whole will have the ability to respond or adapt to environmental change and a chance of re-colonizing rivers that have been extirpated. Preserving both populations with high genetic variation and populations with high genetic divergence will be important for recovery. If populations were prioritized for recovery based on within-river genetic variation, the Medway, St. Mary's (East Branch) and Salmon River (Guysborough) would all be important populations (see O'Reilly et al 2012). If populations were prioritized based on genetic divergence, the Moser and Musquodoboit rivers would become important (see O'Reilly et al. 2012).

Local adaptation among populations is thought to result primarily from environmental heterogeneity (i.e. habitat variation), and to be maintained by the homing behavior of Atlantic salmon. A cluster analysis identified 3 main groupings of rivers and 6 subgroupings (Figure 15) that could be representative of environmental heterogeneity within the region (see Bowlby et al. 2013b for details). At a minimum, all three groups should be represented in the distribution target for SU Atlantic salmon but choosing populations representative of the six smaller groupings would further increase the diversity in the target populations. It is generally accepted that larger rivers (populations) are better source populations for emigration and colonization than are smaller rivers. Further, having as many populations included in the distribution target as is practically feasible is expected to increase the long-term persistence of the DU. Having more than one population from each group is expected to help protect against catastrophic loss.

Interim recovery targets for SU Atlantic salmon can be used to evaluate progress towards recovery. Progress towards recovery targets, particularly with respect to halting the decline, can be evaluated using survival and extinction risks metrics. Proposed interim targets are:

- First, halt the decline in abundance and distribution in rivers with documented Atlantic salmon populations.
- Next, reduce the extinction risk in the rivers with documented Atlantic salmon populations by alleviating threats in these rivers.
- Then, as necessary, expand the presence and abundance of Atlantic salmon into other rivers currently without salmon to fill in gaps in distribution within the SU DU and facilitate metapopulation dynamics.

Recovery targets will need to be revisited as information about the dynamics of the recovering population becomes available.

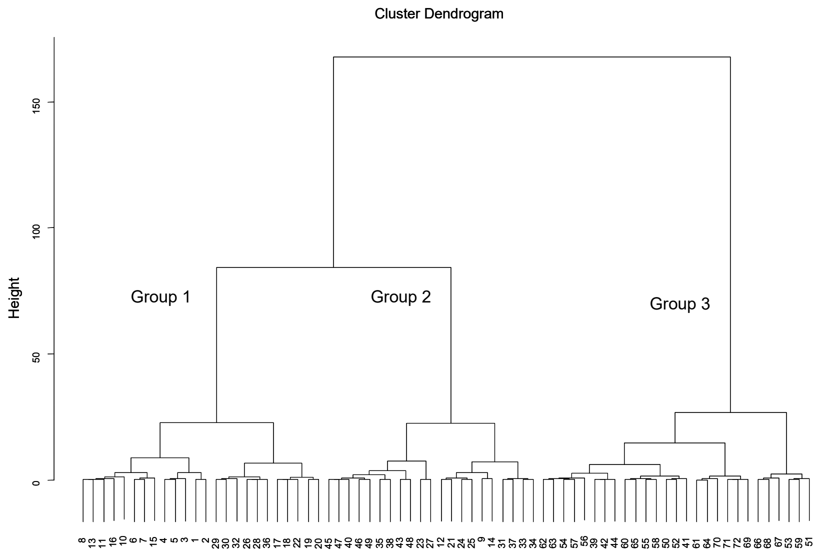


Figure 15. Dendrogram representing the degree of dissimilarity among watersheds (refer to Figure 2 for the names corresponding to each river number) as identified by the hierarchical cluster analysis. More similar watersheds are more closely joined.

Residence Requirements

Under *SARA*, a residence is defined as a dwelling-place that is occupied or habitually occupied by one or more individuals during all or part of their life cycles, including breeding, rearing, staging, wintering, feeding or hibernating (*SARA* section 2.1). DFO's Draft Operational Guidelines for the Identification of Residence and Preparation of a Residence Statement for an Aquatic Species at Risk (DFO, unpublished report) uses the following four conditions to determine when the concept of a residence applies to an aquatic species: (1) there is a discrete dwelling-place that has structural form and function similar to a den or nest, (2) an individual of the species has made an investment in the creation, modification or protection of the dwelling-place, (3) the dwelling-place has the functional capacity to support the successful performance of an essential life-cycle process such as spawning, breeding, nursing and rearing, and (4) the dwelling place is occupied by one or more individuals at one or more parts of its life cycle.

Two dwelling places (used by three life stages) were evaluated for their potential consideration as a residence for Atlantic salmon. These were redds (used by eggs and alevins) and home stones (used by juvenile salmon in fresh water). Each of these is habitually occupied during part of the salmon's life cycle, individuals invest energy in its creation or defense, and it provides specific functions to enable the successful completion of the Atlantic salmon's life-cycle. Of these, redds most closely match the definition of a residence because they are constructed, whereas home stones are not.

Eggs and alevins reside in redds from late October/early November until spring (mid-May or early June) when fry emerge and begin feeding. Redds are essential to protect eggs and alevins from disturbance (e.g. ice scour, bedload transport, physical impact by debris), currents, changing water levels and predators. Redds provide hydraulic eddies that capture expressed eggs and, after being covered with gravel by the adult salmon, provide interstitial space for water flow and oxygen for the incubation of the eggs and development of alevins prior to emergence. As such, they minimize movement of the eggs, prevent eggs from being displaced into unfavorable habitats, and can provide protection from some predators. Redds are typically 2.3 and 5.7 m^2 in size, and consist of a raised mound of gravel or dome under which most of the eggs are located and an upstream depression or 'pot'. Burial depths are about 10 to 15 cm^2.

Redds are typically constructed in water depths of 17 to 76 cm and velocities between 26 to 90 cm/s^2.

Juvenile Atlantic salmon are territorial, remaining relatively stationary near a home stone that they actively defend from other juveniles. Occupancy (prior residency) is a key determinant for successful defense. Home stones provide eddies that shelter parr from instream currents and cover for predator avoidance, as well as influence the availability of invertebrate drift for feeding (depending on the location of the stone relative to water flow). Therefore, the choice of a territory or home stone directly impacts the potential for individual growth and successful rearing in the freshwater environment. The ability to obtain and defend a territory has been linked to growth, age-of-smoltification, and hence age-at-maturity, a key life history parameter. Although juvenile salmon may change home stones intermittently, movement is thought to be limited. For example, one study found that 61.8% of young-of-the-year salmon moved less than 1 meter during July and August. Typical home stones range from <10 cm to > 40 cm in diameter, and there is some indication that the size of stone selected increases from summer to autumn, i.e. preferred sizes increase as juveniles grow. Home stones are occupied soon after emergence from the gravel in the spring and used until juveniles return to the substrate in late autumn.

Threats

Threats are defined as any activities or processes that have, are, or may cause harm, death or behavioural changes to populations, and/or impairment of habitat to the extent that population-level effects occur. This definition includes natural and anthropogenic sources for threats. Current SU salmon populations have little ability to increase in size, so it is expected that threats that act intermittently would have longer-lasting effects on populations than when productivity was higher. Additionally, human activities that reduce Atlantic salmon populations often represent an assemblage of threats to fish and fish habitat. Thus, it is difficult to discuss a specific threat in isolation given the cumulative and correlated nature of the majority of threats.

Detailed information on each major potential threat to SU Atlantic salmon individuals and their habitat is contained in Bowlby et al. (2013b), with a summary provided here in Appendix A. The overall level of concern ascribed to a specific threat takes into account the severity of impacts on populations, how often they occur, as well as how widespread the threat is in the SU DU.

In general, there is a lot of information on how threats affect Atlantic salmon in terms of changes to growth, survival or behaviour of a given life stage (predominantly juveniles). However, comparatively little research links threats in SU watersheds with changes in adult abundance of specific Atlantic salmon populations. From analyses of land use in the SU region (Bowlby et al. 2013b), previous and on-going human activities are extensive in the majority of drainage basins and have likely altered hydrological processes in SU watersheds. Landscape factors controlling hydrology operate at hierarchically nested spatial scales (regional, catchment, reach, instream habitat), which means they often override factors controlling salmon abundance at small spatial scales.

Threats with a high level of concern are discussed below. Threats to persistence and recovery in freshwater environments identified with a high level of overall concern include (importance not implied by order): acidification, altered hydrology, invasive fish species, habitat fragmentation due to dams and culverts, and illegal fishing and poaching. Threats in estuarine and marine environments identified with a high level of overall concern are (importance not implied by order): salmonid aquaculture and marine ecosystem changes.

Acidification

Watersheds in the SU region have been heavily impacted by acidification, which has predominantly originated from atmospheric deposition (i.e. acid rain) due to industrial sources in North America. The underlying geology of the SU is such that rivers have little buffering capacity and have mildly to substantially decreased in pH. River acidification has significantly contributed to reduced abundance or extirpation of populations from many rivers in the region during the last century. In addition to ongoing effects of acidification, contemporary declines in non-acidified rivers indicate that other factors are also influencing populations. Although most systems are not acidifying further, few are recovering and most are expected to remain affected by acidification for more than 60 years. Rivers in the southwestern portion of the SU tend to be more highly acidified than those in the northeastern portion.

Low pH reduces the survival of juvenile Atlantic salmon through direct mortality or increased susceptibility to predation or disease, as well as reduced ability to compete for food or space and interference with the smoltification process. Fry (age 0) are thought to be the most severely affected life stage, with cumulative mortality curves predicting 50% mortality at a pH of 5.3. Mean annual pH values of <4.7 are considered insufficient for the continued maintenance of Atlantic salmon populations. Korman et al. (1994) developed toxicity functions by life stage based on studies available in the literature and used these to estimate egg-to-smolt mortality rates associated with pH for specific periods. Mortality estimates by life stage from these functions for surface pH values of 4.5 to 5.5 are provided in Table 5. These rates are in addition to natural mortality and mortality from other causes.

Table 5. Mortality rates (%) and toxic accumulation (TD - proportion dying weekly) of juvenile Atlantic salmon as a function of surface pH as derived from the toxicity functions in Korman et al. (1994). Values outside the interval 0-100% were assigned the limit value. Rates and pH values are specific to the time period. Mortality rates are in addition to natural mortality and mortality from other causes. Adapted from Korman et al. (1994).

Life Stage	Time Period	Rate	Average Surface pH 4.50	4.75	5.0	5.25	5.50
Egg	Nov. – Apr.	Mortality	57.1%	37.3%	17.6%	0%	0%
Alevin	May	Mortality	36.3%	16.6%	7.6%	3.5%	1.6%
Fry	June	Mortality	100%	100%	56.7%	31.7%	17.7%
Parr	All year	TD	0.19	0.017	0.0016	0.0001	0.0000
Wild smolt	May	TD	0.19	0.017	0.0016	0.0001	0.0000
Hatchery Smolt	May 15-25	TD	0.19	0.017	0.0016	0.0001	0.0000

Sixty rivers in the SU have been classified based on mean annual pH (Figure 16). Salmon populations in extremely acidified systems (pH <4.7) are thought to be extirpated (13 rivers), reduced by 90% in moderately impacted systems (pH = 4.7-5.0; 20 rivers), reduced by about 10% in slightly impacted systems (pH = 5.1-5.4; 14 rivers), and apparently unaffected when pH >5.4 (13 rivers) based on research in the 1980s. However, juvenile densities calculated in the 2008/09 electrofishing survey suggest that reductions in productivity could be even higher (95% and 58% respectively for moderately and slightly impacted systems). This means 316,726 to 334,322 habitat units (out of a total of 351,918) from moderately impacted rivers, and 19,431 to 112,701 habitat units (out of a total of 194,312) from mildly impacted rivers would be unsuitable for juvenile production.

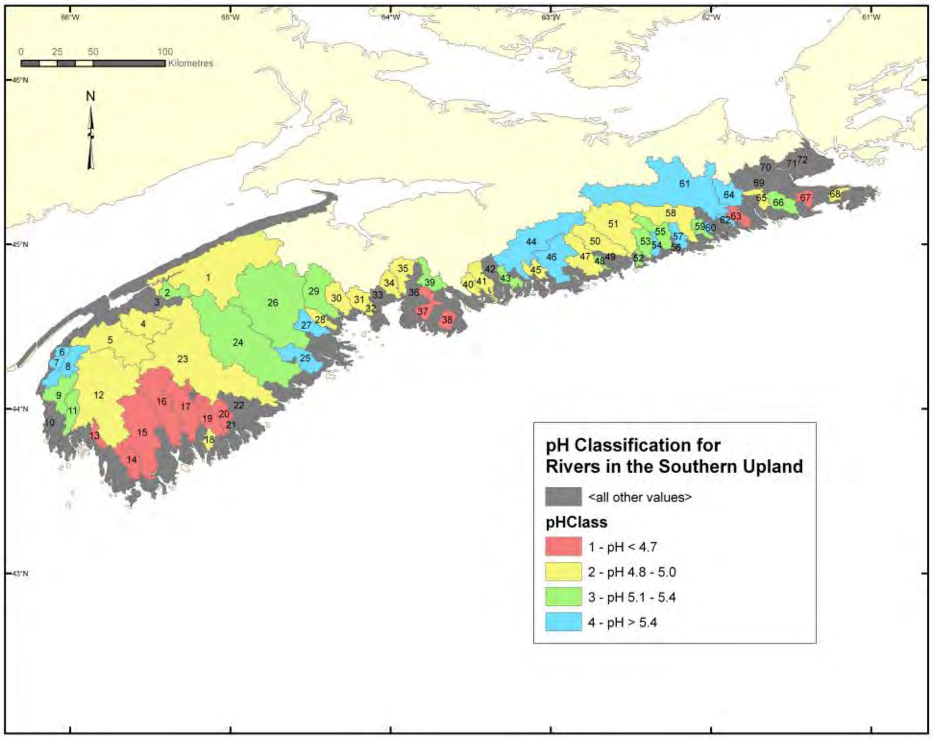


Figure 16. Classification of mean annual pH for rivers in the Southern Upland region; data are from Amiro (2006). Watershed numbers correspond to the legend in Figure 2.

Altered Hydrology

The hydrological regime of a riverine system may be altered by a large variety of human activities. These include direct withdrawal of water for industrial, agricultural or municipal purposes, intensive land use affecting overland and groundwater flow, water diversions for power generation, and an operating schedule of water release at power generating stations not consistent with the natural flow regime. These activities can have significant effects on salmon spawning and rearing habitat, especially when stream base flows are substantially reduced.

River discharge in systems of the SU DU is highly variable among years. However, natural variability may be exacerbated by intensive land use (e.g. forestry, agriculture, urbanization), which can accelerate the rate of runoff from land and entrance into stream channels. This can make a river more prone to flooding and increase the frequency and duration of both large freshets and droughts. Extreme low flows can increase the incidence of temperature extremes, reduce seasonal habitat availability in a watershed and influence food supply. The survival of eggs, alevins and juveniles has been directly linked to stream discharge, with better survival in years with higher flows during the summer and winter months. Extremely high flows can cause large scale erosion and significant changes in channel and bed morphology. All of these processes influence the quality and quantity of habitat available in fresh water. Under extremely high flows, juvenile salmon tend to seek refuge in the substrate, but can experience increased mortality from physical displacement, turbulence, abrasion, and transportation of the substrate.

Altered hydrological regimes directly affect water temperature thereby affecting the behaviour, growth, and survival of all freshwater life stages of Atlantic salmon, and can limit the amount of useable habitat in a watershed. Extreme high temperatures can lead to direct mortality of juveniles if they cannot move to cold water refugia, or can reduce survival indirectly through impacts on growth, predator avoidance responses, or individual susceptibility to disease and parasites. Extreme low temperatures during winter can result in direct mortality by freezing redds or physical disturbances from ice scour, in addition to reducing developmental rates of eggs and alevins. In addition to extreme hydrological events, loss of riparian cover, excessive groundwater extraction as well as water management at reservoirs and hydroelectric generating stations can contribute to extreme temperature events.

Additionally, returning adult spawners have been found to initiate spawning migrations as water levels rise, as well as to require sufficient water for distribution throughout the river system and to hold in pools. Spring high water is potentially a trigger for smolt migration, and survival of smolts has been shown to be higher under years of high discharge than low in some systems.

Invasive Species (Fish)

Chain pickerel and smallmouth bass have substantially increased in abundance and distribution since first being introduced into the SU region. Chain pickerel are currently found in 69 documented locations in the SU, while smallmouth bass are more widely distributed in 174 documented locations (see Bowlby et al. 2013b). Both are recognized as being significant piscivores. Chain pickerel are thought to influence Atlantic salmon populations directly through predation rather than through competition. Preliminary studies in the SU region suggest that pickerel presence in a lake substantially reduces the abundance and species richness of the native fish community. Introduced smallmouth bass influence fish communities through competition as well as predation, and their presence has been linked to community shifts and extirpations of native fishes. Atlantic salmon juveniles have been found to shift habitat use in areas where smallmouth bass are also found, although these results were dependent on water temperature and discharge conditions.

Habitat Fragmentation Due to Dams, Culverts and Other Permanent Structures

Permanent structures are often placed in or along rivers for three main purposes: water impoundment (reservoirs for hydro, municipal drinking water, or other industrial uses), bank stabilization (to prevent movement of the stream channel), or water diversion (for industrial and recreational uses or flood prevention). There are 233 dams or barrier structures identified by the NS DoE and DFO HM in watersheds in the SU region (Figure 17), 44 of which are thought to be passable to fish populations.

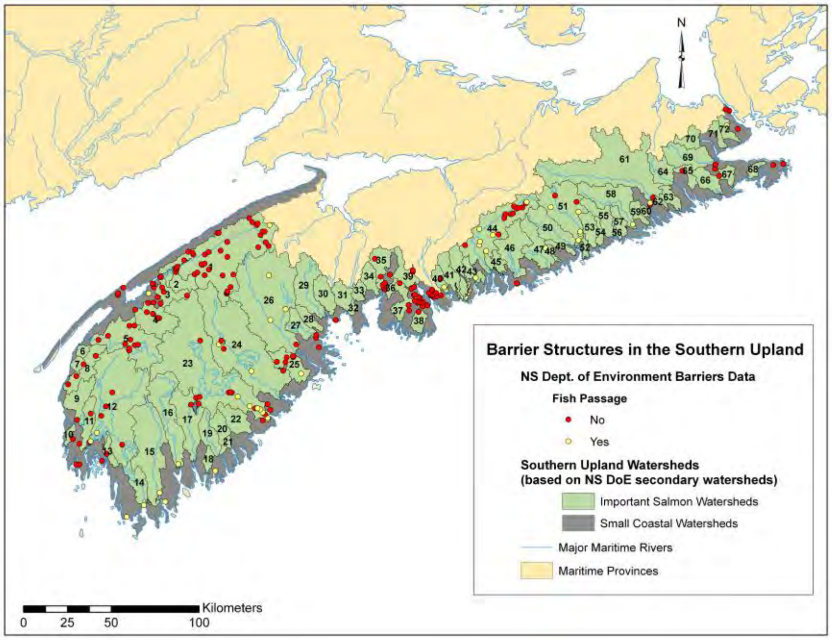


Figure 17. All barrier structures in the Southern Upland region listed on the barriers layer from the Nova Scotia Department of the Environment and DFO Habitat Management (Maritimes). Those without fish passage are shown in red, while those with at least partial passage are shown in blue. Watershed numbers correspond to the legend in Figure 2.

Due to poor design, improper installation or inadequate maintenance, culverts contribute to habitat fragmentation in watersheds by becoming seasonal or complete barriers to fish movement. Recent surveys of culverts in Nova Scotia suggest that barriers to fish passage are prevalent, with 37% assessed as full barriers and 18% assessed as partial barriers in the Annapolis watershed, and 61% assessed as full barriers from a random sample of 50 culverts in Colchester, Cumberland, Halifax and Hants Counties. Out of 62 culverts assessed on the St. Mary's River, 40 did not meet criteria for water depth, 35 exceeded velocity criteria, and 24 had an outfall drop potentially preventing passage. Similar results have been obtained for watersheds containing Atlantic salmon in Newfoundland and the continental U.S. as well watersheds containing Pacific salmon and other trout species in Alaska and British Columbia. Activities such as timber harvesting, urbanization, infrastructure (like new highways) or other land development tend to increase the number of culvert installations in a watershed. Using road crossings as a proxy for culverts (Figure 18), SU watersheds in more populated areas as well as those impacted the most heavily by forestry or agriculture had the highest road densities and thus the greatest potential for impact from culverts.

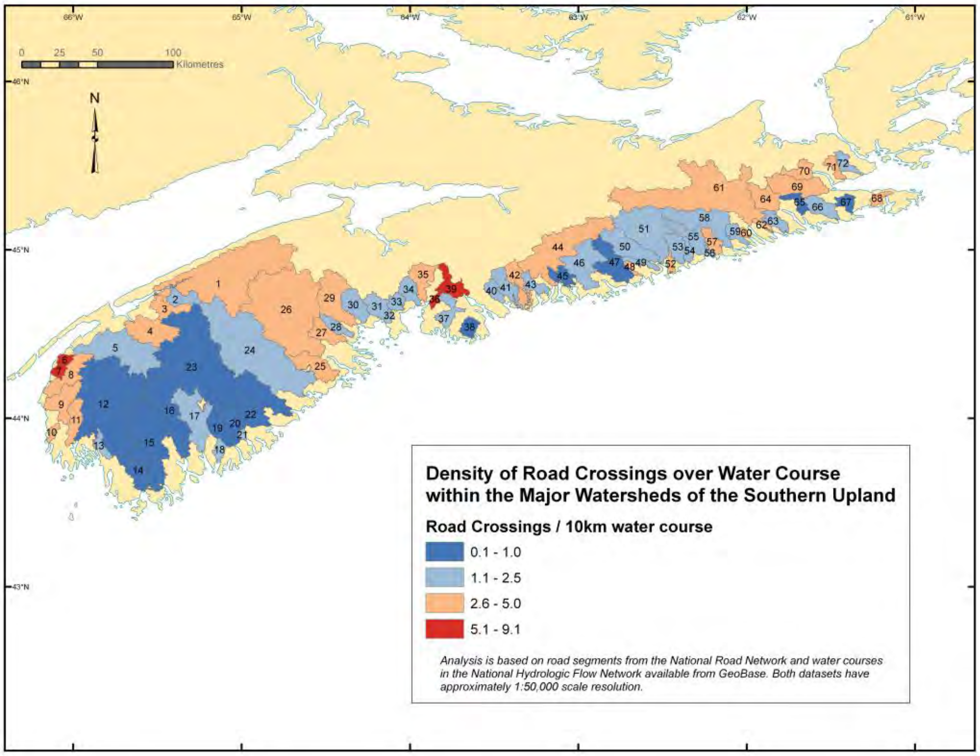


Figure 18. The density of road crossings within watersheds of the Southern Upland region. Watershed numbers correspond to the legend in Figure 2.

Illegal Fishing and Poaching

There have been many anecdotal reports of illegal fishing (e.g. targeting salmon while fishing with a general license) and harvests (i.e. poaching) of Atlantic salmon in the SU region, either using recreational fishing gear, gillnets, or other capture methods. The magnitude of this threat to specific populations is not possible to quantify; however, poaching would be expected to have the greatest impact when population sizes are small (as they are at present) because a larger proportion of the population would be affected. Additionally, the population dynamics modeling presented here indicates that populations have very little capacity to recover from any illegal removals (i.e. are not able to quickly increase in size).

Population Level Effects of Recreational Fishing

While recreational fishing is currently identified as a low threat (Appendix A) to SU Atlantic salmon, the population level effects of recreational fishing are described here.

Recreational fishing seasons, regulations and practices in the SU have changed through time from fisheries that were primarily retention fisheries for both large and small salmon, to virtually all hook-and-release fisheries, to closures throughout the SU Region in 2010.

Hook and release recreational fisheries provide an intermediate management strategy between a full retention fishery and fishery closure for populations that are below target levels. The effects are conditional on the life history and dynamics, such as freshwater productivity, survival at-sea and repeat spawning frequency. Catch and release fisheries would be expected to result in populations sizes that are higher than those in a full retention fishery, but lower than those expected to result from fishery closure. A similar relationship is expected for the lifetime reproductive rates. As such, they have the potential to slow recovery rates relative to fishery closures, although population growth is expected to be more rapid with a catch and release fishery than a full retention fishery.

Highly variable rates of fish mortality associated with a fish being hooked and subsequently released have been reported in the literature. Water temperature is cited as an important factor; angling at low temperatures (i.e. below 17-18°C) generally results in lower mortalities than catch-and-release angling that occurs at higher water temperatures. In addition to temperature, fish mortality associated with catch-and-release angling is also believed to be affected by an angler's level of experience; fish mortality is believed to be lower for more experienced anglers than for less experienced anglers. Although there are several studies that show low direct mortality associated with catch-and release recreational fisheries if conducted at low water temperatures (i.e. below 17-18 C), there is little information available about other effects of catch and release salmon fishing (e.g. potential effects on migration, reproduction, habitat impacts, transfer of pathogens).

The LaHave River (above Morgan Falls) salmon population is the only SU population with sufficient data to evaluate the effects of recreational fisheries on population dynamics. In the 1980s when retention fisheries were in effect, the recreational fisheries reduced survival to spawning escapement by up to 31% for 1SW salmon, with lesser effects on 2SW in part due to the timing of the increase in recreational fishing effort and the shift to hook-and-release fisheries for large salmon. This led to a reduction in the annual equilibrium population size of up to 48% and reductions in maximum lifetime reproductive rates of up to 23%. With the switch to hook-and release fisheries, the impact of the fishery on the dynamics of the population is much less (nearly negligible), although this conclusion is conditional on the assumed 4% hook-and-release mortality rate and on the assumptions that both the non-lethal effects of hook-at-release and habitat impacts are minor. These effects would be greater if the fishing season extends into periods with warmer water temperatures. Additionally, these values should be interpreted in the context of the past impacts of the fisheries on these populations. In the future, any impacts to populations from the recreational fishery would depend on fishing intensity and management regulations with respect to timing of the fishery, as well as the associated mortality rate.

Aquaculture

Commercial aquaculture of Atlantic salmon in the marine environment of Nova Scotia typically occurs in net pens anchored in coastal estuaries or sheltered near-shore sites. Effects on wild Atlantic salmon populations from aquaculture would occur either by interaction in the immediate vicinity of the net-pens or by interactions between escaped aquaculture salmon and wild salmon. Aquaculture escapes, migration of wild salmon to or past aquaculture sites, and a combination of escapes and migration can potentially result in predator attraction, disease and pathogen exchanges, competition and genetic effects.

Rivers in close proximity to existing aquaculture lease sites include many of those that contain the larger remaining populations of Atlantic salmon in the SU region. Individuals from populations such as the Annapolis/Nictaux have the potential to pass or interact with all salmonid aquaculture sites in the SU region as they move through coastal areas, while this would be less likely for more northern populations (e.g. those near Canso).

Interbreeding between wild populations and aquaculture escapes causes reduced fitness in the hybrids as they are less adapted to local conditions and, thus, exhibit lower survival rates and less resilience to environmental change. The larger the genetic difference between wild and farmed populations, the greater these effects will be. The use of broodstock from other areas leads to greater genetic differences. Such changes can be permanent when genes from farmed fish become fixed in the wild genome (introgression). Despite poor reproductive success, the large number of escaped salmon in some areas of Canada has resulted in reports of significant numbers reproducing. For example, 20% of redds in the Magaguadavic River, New Brunswick were thought to belong to females of aquaculture origin in the 1992/1993 spawning period. Research in Europe has demonstrated that the number of farmed salmon entering rivers is proportional to the number of farms, and that escapes will enter multiple rivers in the vicinity of aquaculture sites. Aquaculture escapes in North American rivers have been reported in 54 of 62 (87%) rivers investigated within a 300 km radius of the aquaculture industry since 1984. Aquaculture escapes made up an average of 9.2% (range: 0% to 100%) of the adult population in these rivers. The prevalence of escapes suggests that farmed salmon pose a significant risk to the persistence of wild populations, and a recent meta-analysis has demonstrated that reduced survival and abundance of several salmonid species (including Atlantic salmon) are correlated with increases in aquaculture.

More direct sources of mortality to wild Atlantic salmon populations from aquaculture sites have been hypothesized to come from competition for resources, predator attraction to net-pens, as well as disease transfer from captive to wild fish. However, the available evidence suggests that growth and survival of immature Atlantic salmon in the marine environment are not limited by food, and predator attraction to net-pens has not been directly linked to increased mortality in wild populations. Similarly, there are no proven cases in Canada where disease or sea-lice outbreaks in wild populations can be directly linked to aquaculture sites, although research in epidemiology demonstrates that exposure and the frequency of exposure are important contributing factors to the spread of disease.

Aquaculture impacts would be expected to decline with distance from a specific site as well as with the recipient population size. For a given number of farmed salmon entering a river, the population-level impacts of interbreeding are expected to decrease with increases in size of the wild population, suggesting that one potentially important mitigation measure for this threat is to increase abundance of wild salmon by addressing other threats.

Marine Ecosystem Changes

The abundance and distribution of prey species and predators is thought to be an important factor affecting marine growth and survival of Atlantic salmon populations. Recent evidence of a whole ecosystem regime shift in the Eastern Scotian Shelf (ESS) demonstrates that significant change to the ecological communities experienced by wild Atlantic salmon populations at sea is likely, particularly if individuals use areas farther from the coast. The ESS ecosystem has shifted from dominance by large-bodied demersal fish, to small pelagic and demersal fish, and macroinvertebrates; a change that is also thought to be occurring in surrounding regions (i.e. Western Scotian Shelf (WSS)), albeit at a slower pace. One aspect of this shift is that strong trophic interactions between the remaining top predators, as well as fundamentally altered energy flow and nutrient cycling, appear to be maintaining the new ecological state. It has been hypothesized that changes in the abundance and distribution of small pelagic fishes affects food availability and thus marine survival of Atlantic salmon, and that increased grey seal (*Halichoerus grypus*) populations (as seen on the ESS) may lead to significantly higher predation pressure. However, empirical evidence of either impact has not been found for SU Atlantic salmon.

Large-scale changes to atmospheric and oceanographic conditions have been observed throughout the marine range of Atlantic salmon. For example, the WSS experienced a cold period during the 1960s, was warmer than average until 1998, and then significantly cooled after cold water intrusion from the Labrador Sea. The ESS cooled from about 1983 to the early 1990s and bottom temperatures have remained colder than average since. Sea-ice cover in the Gulf of St. Lawrence and off Newfoundland and Labrador in winter 2009/2010 was the lowest on record for both regions since the beginning of monitoring in 1968/1969. This lack of ice was in part due to warmer temperatures, but also to early season storms breaking up and suppressing new ice growth. The NAO has been shifting from mostly negative to mostly positive values from the 1970s to the early 2000s. Winter NAO is strongly negatively correlated with sea-surface temperature and thus could influence Atlantic salmon overwintering behaviour and mortality rates at sea. Most research that has found a correlation between Atlantic salmon catches, sea-age at maturity, or smolt-to-adult survival and recruitment with winter NAO values has been from European populations, although there are weakly correlated examples in North America. However, as discussed previously, partitioning mortality of adult salmon between spawning events into that experienced predominantly in freshwater, estuarine and near-shore environments (first year) and that experienced in more distant marine environments (second year) demonstrated a strong correlation between NAO and survival in the second year for alternate-spawning Atlantic salmon from the LaHave River.

Highest marine mortality rates are hypothesized to occur soon after immature salmon reach the open ocean while they are still in the near-shore environment. One hypothesis is that faster growth and lower mortality of immature Atlantic salmon is associated with entry into the ocean at a time when larval fish prey are abundant and at a consumable size. Thus, the environmental factors controlling primary marine production (which would determine prey availability and size) may have a large impact on early marine survival and growth.

Mitigation and Alternatives

Restoring marine or freshwater habitat quality requires the ability to quantify the impact of a given threat on a given population, something that is much more likely in fresh water than in the marine environment. Threats in fresh water are also more localized and can be addressed with remediation actions in the short term. It is likely that increasing habitat quality and quantity in fresh water will prevent further extirpations and promote self-sustaining populations at low size. Some threats (like acidification) have well-known remediation actions (liming) that can lead to population growth. In other cases, recovery actions addressing multiple threats simultaneously might be required to increase abundance. It has been suggested that watershed restoration for salmon species should focus first on reconnecting isolated fish habitats (i.e. remediating barriers) before moving on to restoring hydrologic, geologic and riparian processes at a watershed scale, and lastly to focusing on in-stream habitat enhancement. When choosing rivers for restoration, an attempt should be made to capture the range of variation among systems in the SU and to prioritize the larger remaining populations for recovery.

Remediation actions to address land use issues will not produce immediate population increases for SU Atlantic salmon. For example, it would take many years before riparian vegetation would grow to a size that would significantly reduce sediment inputs, which would be expected to increase habitat quality and reduce juvenile mortality in the river. Such large-scale changes are the most likely to bring about substantial population increase in Atlantic salmon because they should have a greater impact on total abundance in the watershed rather than on localized density, and they would address issues at the watershed scale.

Remediation of landscape-level threats to watersheds (e.g. forestry, agriculture, urbanization, roads) requires working at a much larger scale than the stream reach, and typically includes actions that are distant from the actual streambed (e.g. replanting riparian vegetation, revisiting regulations on pesticide use, community outreach on invasive species). Coordination of activities at small-scales may produce more immediate effects.

Sensitivity analysis on the effect of starting population size on population viability highlights the risks associated with delaying recovery actions; recovery is expected to become more difficult if abundance continues to decline, as is expected for these populations with the continued passage of time. Recovery actions should be initiated as soon as possible.

Mitigation and alternatives for freshwater, marine and estuarine threats were not addressed in detail at this meeting.

Assessment of Recovery Potential

The PVA described in the Population Dynamics section was also used to evaluate how the probability of extinction and probability of meeting the recovery target would be expected to vary with increased freshwater productivity and increased at-sea survival. Twenty-four scenarios were evaluated for both the St. Mary's River (West Branch) and LaHave River (above Morgan Falls) salmon populations. At-sea survival values considered in the analyses used the 1980s and 2000s dynamics as upper and lower estimates respectively, with the two intermediate scenarios evenly spaced between these (i.e. at one-third and two-thirds the difference between past and present values).

Increased freshwater production was modeled by increasing smolt production by factors of 1.0 (no increase), 1.2 (20% increase), 1.5 (50% increase) and 2.0 (double or 100% increase). This is the same as changing the parr mortality parameter by equivalent amounts. For example, the annual mortality of parr older than age-1 was estimated to be 0.72 for the LaHave River (above Morgan Falls) population. This is a survival of 28% annually. The increased freshwater productivity scenario of 1.5 equates to a survival of 42% annually.

Each combination of increased freshwater productivity and at-sea survival was modeled for a total of 16 scenarios (Table 6). In addition, eight other scenarios are presented to investigate the effects of extreme events. In these, freshwater productivity was increased by a factor of 1.5 and simulations were carried out for all four at-sea survival values. For each scenario, the probabilities of extinction and recovery were evaluated using 2000 simulated population trajectories.

Abundance trajectories, extinction probabilities and recovery probabilities for each scenario are provided in Figures 19, 20 and 21 and Table 6 for the LaHave River (above Morgan Falls) population. The results of these analyses clearly indicate how close SU Atlantic salmon are to the threshold between becoming extinct and being viable. Panel "A" in each figure shows the results using the current dynamics; as previously described, both populations will extirpate in the absence of human intervention or a change in vital rates for some other reason. Panel "B" shows the effect of increasing freshwater productivity by 20%. This improvement is not large, but it does markedly reduce extinction risk, even if marine mortality rates remain unchanged (Figure 20). For the LaHave River (above Morgan Falls) population, the probability of extinction within 30 years drops from 31% to 3% with this increase in survival. Increases of 50% (Panel C) drop the extinction probability to 0% for more than 50 years for both populations. Although small, numerically-viable populations are produced, none of the simulated population trajectories reached the recovery targets (Figures 19, 21). Small increases in marine survival (Panels G to J) have a similar effect. None of the simulated populations extirpated in the third increase scenarios and a small proportion reached their recovery targets for both populations. The proportion reaching the recovery target increases as freshwater productivity increases (Figure 21; compare Panels G to J). Recovery probabilities exceed 50% in 50 years for all scenarios that include a two-thirds increase in at-sea survival (Panels M to X) and extinction probabilities are zero. Within limits, these conclusions are robust to how the frequency of extreme events is modeled (Panels E, K, Q, W, F, L, R, X). When the frequency of the extreme events is reduced, the probability of recovery increases and extinction probability is reduced (e.g. compare Panels H and K). Results for the St. Mary's River (West Branch) salmon population are similar.

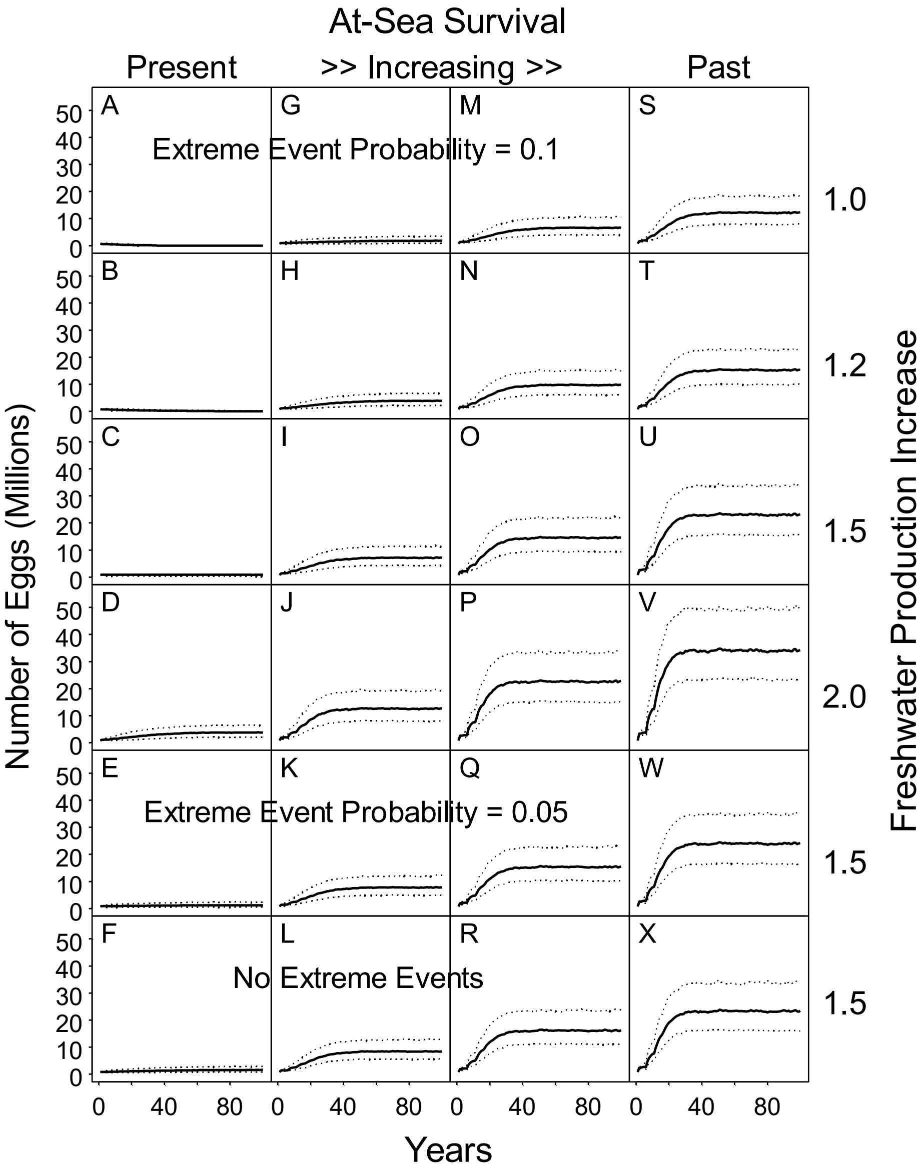


Figure 19. The effects of increasing at-sea survival and freshwater productivity on the simulated abundance of eggs for the LaHave River (above Morgan Falls) Atlantic salmon population. The graphs summarize 2000 simulations for each scenario. The median abundance (solid line), and the 10th and 90th percentiles (dashed lines) are shown. Panels on the right and the left are based on the 1980s and 2000s at-sea survival respectively, and the middle panels show scenarios using survivals increased by 1/3 and 2/3's of the difference in these values. The return rates of 1SW and 2SW salmon and survival between repeat spawning events are increased. The 2000's freshwater production is used in all scenarios. The top four rows show the effect of increasing freshwater productivity by factors of 1 (no change), 1.2 (20% increase), 1.5 (50% increase) and 2.0 (100% increase). The bottom two rows show the effect of changing the frequency of event events to an average of 1 every 20 years (5th row) and to no extreme events (bottom row).

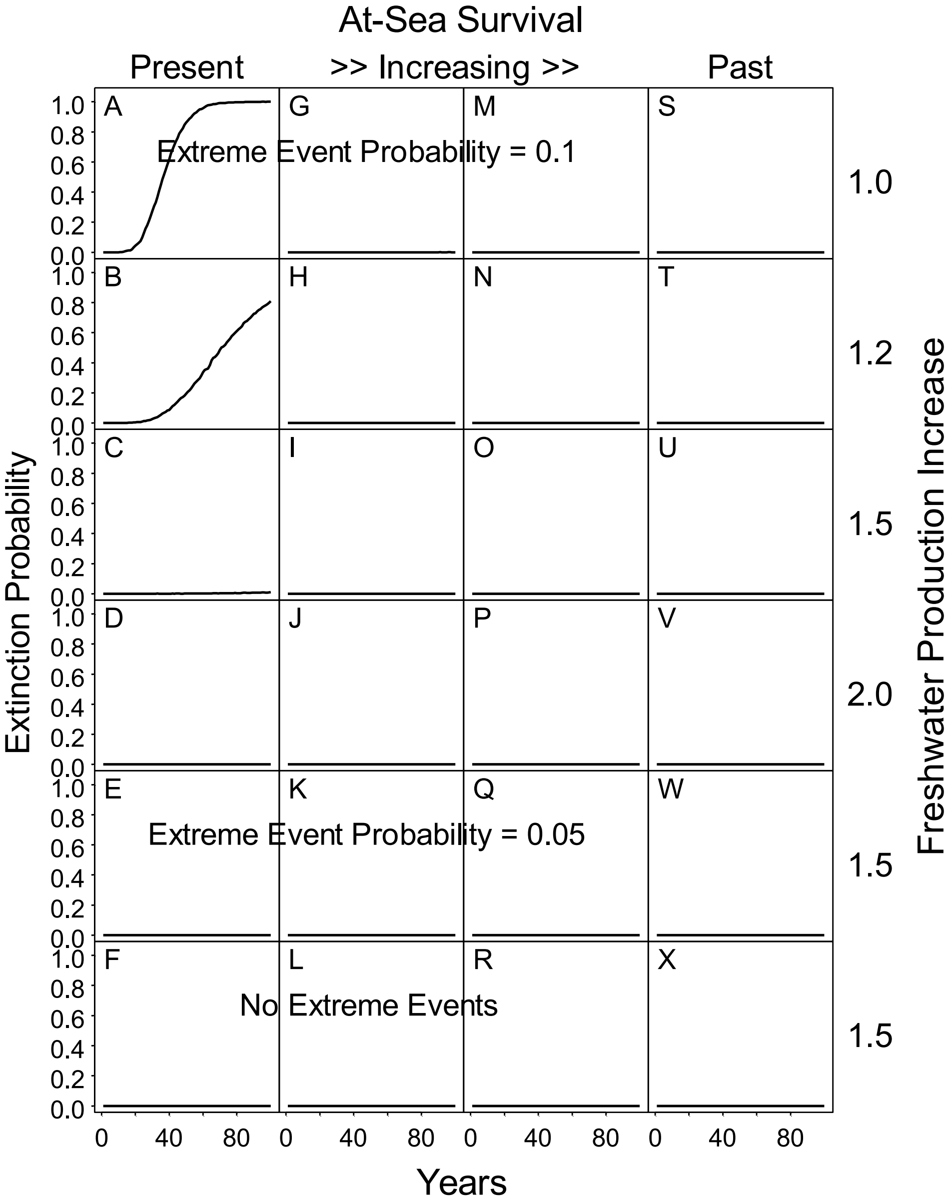


Figure 20. The effects of increasing at-sea survival and freshwater productivity on the probability of extinction for the LaHave River (above Morgan Falls) Atlantic salmon population. Panels are described in the caption for Figure 19.

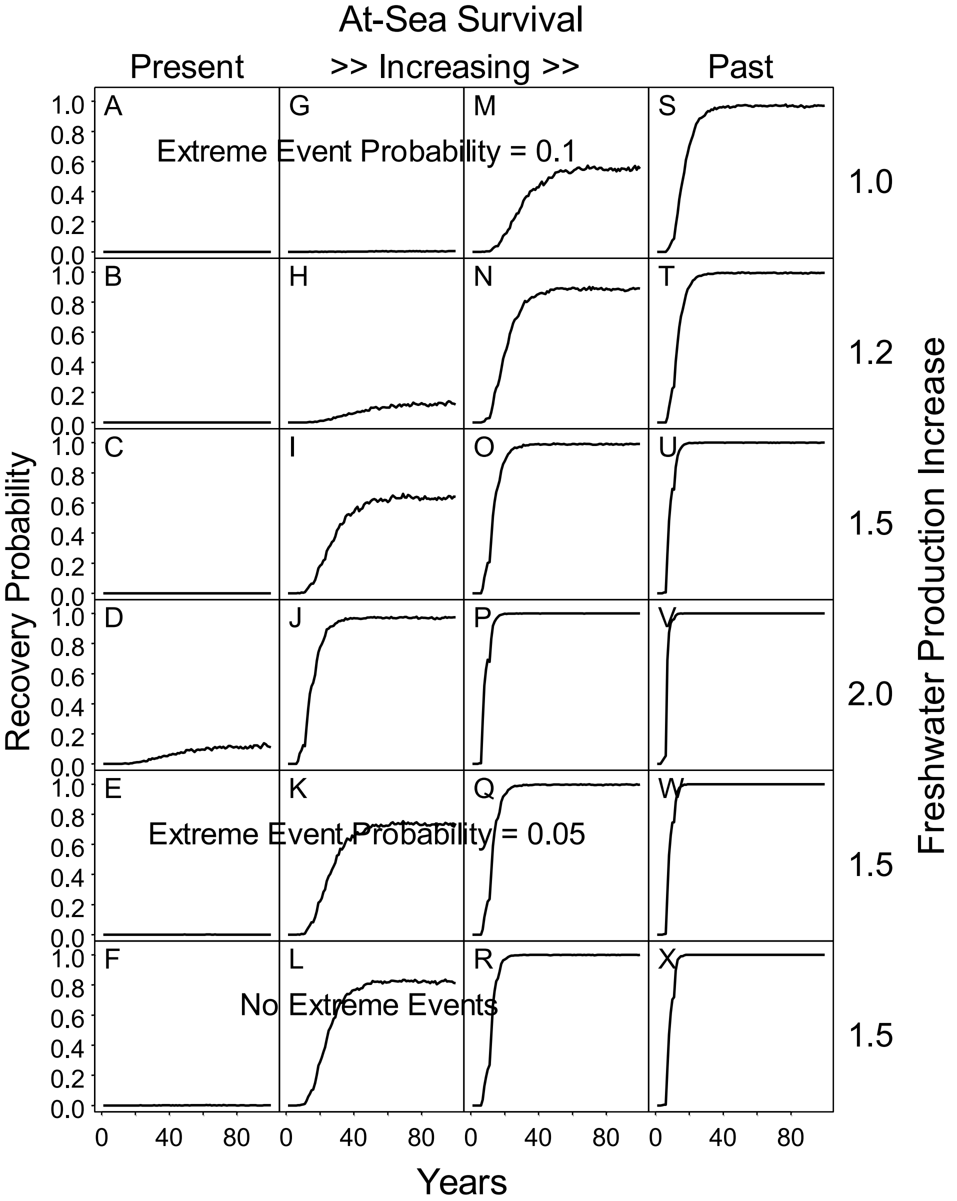


Figure 21. The effects of increasing at-sea survival and freshwater productivity on the probability of meeting the recovery target for the LaHave River (above Morgan Falls) Atlantic salmon population. Panels are described in the caption for Figure 19.

Table 6. Proportions of 2000 simulated population trajectories that either go extinct or meet the recovery target within 10, 20, 30 and 50 year time horizons based on recovery scenarios for the LaHave River (above Morgan Falls) Atlantic salmon population. The marine scenarios reflect changes from the present levels (2000s) of at-sea survival to those in the past (1980s). The freshwater scenarios reflect increases in freshwater productivity from the present level (1) to 2 times the present level. The lettering for the runs corresponds to those in Figures 19-21. Extreme event scenarios are the average frequency of extreme events and the reduction in egg to fry survival corresponding to the event.

				Proportion Extinct				Proportion Recovered			
Run	Marine Scenario	Freshwater Scenario	Extreme Event Scenario	10 yr	20 yr	30 yr	50 yr	10 yr	20 yr	30 yr	50 yr
a	present	1	10 yr; 0.2	0.00	0.05	0.31	0.87	0.00	0.00	0.00	0.00
b	present	1.2	10 yr; 0.2	0.00	0.01	0.03	0.21	0.00	0.00	0.00	0.00
c	present	1.5	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
d	present	2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.01	0.03	0.09
e	present	1.5	20 yr; 0.1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
f	present	1.5	none	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
g	intermediate 1/3	1	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
h	intermediate 1/3	1.2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.01	0.04	0.10
i	intermediate 1/3	1.5	10 yr; 0.2	0.00	0.00	0.00	0.00	0.01	0.19	0.43	0.62
j	intermediate 1/3	2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.12	0.80	0.95	0.97
k	intermediate 1/3	1.5	20 yr; 0.1	0.00	0.00	0.00	0.00	0.01	0.24	0.53	0.73
l	intermediate 1/3	1.5	none	0.00	0.00	0.00	0.00	0.01	0.32	0.66	0.83
m	intermediate 2/3	1	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.12	0.34	0.53
n	intermediate 2/3	1.2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.03	0.49	0.78	0.89
o	intermediate 2/3	1.5	10 yr; 0.2	0.00	0.00	0.00	0.00	0.21	0.90	0.99	0.99
p	intermediate 2/3	2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.68	1.00	1.00	1.00
q	intermediate 2/3	1.5	20 yr; 0.1	0.00	0.00	0.00	0.00	0.24	0.94	1.00	1.00
r	intermediate 2/3	1.5	none	0.00	0.00	0.00	0.00	0.27	0.98	1.00	1.00
s	past	1	10 yr; 0.2	0.00	0.00	0.00	0.00	0.09	0.74	0.94	0.97
t	past	1.2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.24	0.92	0.99	1.00
u	past	1.5	10 yr; 0.2	0.00	0.00	0.00	0.00	0.69	1.00	1.00	1.00
v	past	2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.96	1.00	1.00	1.00
w	past	1.5	20 yr; 0.1	0.00	0.00	0.00	0.00	0.75	1.00	1.00	1.00
x	past	1.5	none	0.00	0.00	0.00	0.00	0.72	1.00	1.00	1.00

In conclusion, population viability analyses indicate that relatively small increases in either freshwater productivity or at-sea survival are expected to decrease extinction probabilities. For example, for the LaHave River (above Morgan Falls) population increasing freshwater productivity by 20% decreases the probability of extinction within 50 years from 87% to 21%, while a freshwater productivity increase of 50% decreases the probability of extinction within 50 years to near zero. These must be accompanied by increases in at-sea survival in order to restore populations to levels above their conservation requirements.

In contrast with inner Bay of Fundy salmon populations, for which at-sea survival is so low that recovery actions in fresh water are expected to have little effect on overall viability, recovery actions focused on improving freshwater productivity are expected to reduce extinction risk for SU salmon.

These must be accompanied by larger (value) changes in at-sea survival in order to restore populations to levels above their conservation requirements, although at present the contributing factors limiting marine survival are not known.

Sensitivity to Starting Population Size

The effect of delaying recovery activities was examined by running the PVA (base model) for the LaHave River (above Morgan Falls) population starting at 100%, 50%, 25% and 10% of the 2010 abundance estimates (300 small salmon and 53 large salmon). Using the present dynamics, further reductions in population size have the effect of shortening time to extinction. A reduction in starting population size of 50% reduced the time to which 50% of the simulated populations are extinct by about 10 years, whereas a reduction in size of 75% reduced the time to which 50% of the simulated populations are extinct to about 15 years. Similarly using the 1980s dynamics, time to recovery was similarly increased. The effects of further reductions in population size prior to the initiation of recovery are most evident in scenarios where populations are on the edge of recovery. For example, with an increase in freshwater production of 1.2 times, the probability of extinction within 25 years is 1% when the starting population size equals the 2010 abundance. This value increases to 10%, 45% and 97% for reductions in the starting population size of 50%, 25% and 10% of the 2010 abundance. The effect is not so great for an increase in at-sea survival of one third because the increase in overall survival (i.e. survival from egg to adult) is greater than for an increase in freshwater production. Additional details of this analysis are provided in Gibson and Bowlby (2013).

Sources of Uncertainty

Detecting the presence of juveniles at very low abundance levels can be difficult; therefore, rivers in which salmon were not observed do not necessarily represent complete extirpation.

As described in Gibson and Bowlby (2013) the electrofishing catchability coefficient used in the freshwater production model was for the St. Mary’s River (West Branch) population could not be estimated and a value based on LaHave River (above Morgan Falls) production model was assumed. Had a different value been assumed, it is expected that the age- and stage-specific survival rates would change but the overall freshwater productivity curve would remain the same.

The dynamics of future, recovered SU salmon populations is unknown, and as a result, the sizes of those populations are unknown. Therefore, there is uncertainty about whether the proposed recovery targets for abundance are sufficient to ensure long-term population viability, but they are not considered to be unrealistically high given past abundance.

The importance of migration among rivers for ensuring numerical stability and genetic integrity within the DU is unknown; therefore, the number of populations that need to be included in the distribution component of the recovery target is also unknown.

The landscape cluster analysis used as a basis for developing distribution recovery targets is dependent on the data inputs and using additional or different environmental variables, as well as more or fewer feature classes within a variable, would affect the particular watersheds contained in the predicted number of clusters. Therefore, the watershed groupings should not be considered fixed in the sense that no other groupings are possible. However, the cluster analysis is a meaningful way of grouping landscape level patterns and demonstrates that all watersheds in the SU region cannot be considered equivalent in terms of protecting the biological diversity of Atlantic salmon populations. Diversity could also be characterized using the Eco-Districts present within the SU or using a lower level in the dendrogram presented in the Recovery Target section (e.g. the six clusters in the next tier).

PVA is a powerful and widely used technique in conservation biology to explore current conditions, assess risks and simulate how future management actions could affect a population in decline. They are known not to provide accurate estimates of the true probability of extinction or recovery, but they are useful for the relative evaluation of management actions.

The PVA models were set up with the assumption that the populations were at equilibrium abundances and age structure for the given scenario being modeled. This leads to starting abundances that can be higher than those recently observed. Short-term extinction risk would be higher if recent abundances were used for the starting values.

The PVAs were developed using a quasi-extinction threshold of 15 female salmon. Population viability analyses are known to be sensitive to the assumed threshold. This value is very low relative to the past abundances of salmon in these rivers. If depensatory dynamics exist, populations may not be able to recover from low abundances, even ones that are higher than this threshold. When scenarios were run using the 2000s dynamics, times to extinction decreased when the threshold was increased. However, this threshold has nearly no effect on time to recovery when the 1980s dynamics are used.

The PVA models were constructed such that the freshwater dynamics were independent of the marine dynamics. Marine survival rates may be improved by changes in the freshwater environment or in the freshwater population dynamics. For example, improved pH conditions may result in better marine survival of smolts as short-term exposure of smolts to low pH has been inferred to reduce early marine survival. Increased smolt production resulting in larger schools of smolts may improve early marine survival rates through prey-swamping effects when migrating through predator fields. As such, improved productivity in freshwater may directly affet marine return rates, the benefits of which will be reduced probabilities of extinction and improved probabilities of recovery. These dynamics are poorly understood in Atlantic salmon populations.

Marine distribution patterns for SU Atlantic salmon were assessed from historical tagging programs of smolts and adults combined with reported recaptures by commercial and recreational fisheries. Release data span the years from 1966 to 1998 and only include information from fish that were individually tagged (generally with numbered carlin or floy tags) and subsequently recaptured (i.e. releases with zero recaptures are not considered). Tags recovered in fisheries (or by people associated with the fishing industry such as fish plant workers) were returned voluntarily for a monetary reward. When interpreting these data, it is important to remember that sampling effort in the marine environment was non-random over space and time (i.e. the distribution of tag returns depends on the distribution of fishing effort as well as the distribution of the fish). In the Maritime Provinces and much of Newfoundland, commercial trap nets for salmon were often at fixed locations accessible from shore. For the high-seas fisheries in Labrador and West Greenland, few of the tag recaptures were assigned a latitude and longitude when recovered; therefore, recaptures were ascribed to the mid-point of each West Greenland fishing district or to locations or communities along the coast of Labrador. Therefore, it is not possible to determine how far off shore Atlantic salmon may frequent from these data and it is similarly difficult to correlate recapture locations with environmental or oceanographic variables. Furthermore, the scarcity of tag recaptures during specific months (e.g. December to March) is largely due to the lack of sampling effort and may not reflect actual distribution patterns.

Watershed characteristics and human activities within watersheds were derived using geo-spatial data, some of which is becoming outdated. While the data used are the most current, specific information may require validation.

Although home stones potentially meet the criteria to be a residence, practically there is no way to identify whether a stone in a river is being used as a home stone.

SOURCES OF INFORMATION

This Science Advisory Report is from the May 22-25, 2012, Recovery Potential Assessment for Southern Upland Atlantic salmon. Additional publications from this meeting will be posted on the *Fisheries and Oceans Canada (DFO) Science Advisory Schedule* as they become available.

Amiro. 2006. A synthesis of fresh water habitat requirements and status for Atlantic salmon (Salmo salar) in Canada. DFO CSAS Res. Doc. 2006/017

Bowlby,H.D., A.J.F. Gibson, and A. Levy. 2013a. Recovery Potential Assessment for Southern Upland Atlantic Salmon: Status, Past and Present Abundance, Life History and Trends. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/005 (*In press*).

Bowlby,H.D., T. Horsman, S.C. Mitchell, and A.J.F. Gibson. 2013b. Recovery Potential Assessment for Southern Upland Atlantic Salmon: Habitat Requirements and Availability, Threats to Populations, and Feasibility of Habitat Restoration. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/006 (*In press*).

COSEWIC. 2011. COSEWIC Assessment and Status Report on the Atlantic Salmon *Salmo salar* (Nunavik Population, Labrador Population, Northeast Newfoundland Population, South Newfoundland Population, Northwest Newfoundland Population, Quebec Eastern North Shore Population, Quebec Western North Shore Population, Anticosti Island Population, Inner St. Lawrence Population, Lake Ontario Population, Gaspé-Southern Gulf of St. Lawrence Population, Eastern Cape Breton Population, Nova Scotia Southern Upland Population, Inner Bay of Fundy Population, Outer Bay of Fundy Population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

DFO. 2007. Revised Protocol for Conducting Recovery Potential Assessments. DFO. Can. Sci. Advis. Sec. Advis. Rep. 2007/039.

DFO and MRNF. 2009. Conservation Status Report, Atlantic Salmon in Atlantic Canada and Quebec: PART II – Anthropogenic Considerations. Can. Manus. Rep. Fish. Aquat. Sci.. 2870.

Gibson, A.J.F., and H.D Bowlby. 2013. Recovery Potential Assessment for Southern Upland Atlantic Salmon: Population Dynamics and Viability. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/142 (*In press*).

Gibson, A.J.F., H.D. Bowlby, D. Hardie, and P. O'Reilly. 2011. Populations on the Brink: Atlantic Salmon (*Salmo salar*) in the Southern Upland Region of Nova Scotia, Canada. North Amer. J. Fish. Manag. 31:733–741.

Halfyard, E.A., D.E. Ruzzante, M.J.W. Stokesbury, A.J.F. Gibson, and F.G. Whoriskey. 2012. Estuarine Migratory Behaviour and Survival of Atlantic Salmon Smolts from the Southern Upland, Nova Scotia, Canada. J. Fish Biol. 81: 1626-1645.

Hubley, P.B., and A.J.F. Gibson. 2011. A Model for Estimating Mortality of Atlantic Salmon, *Salmo salar*, Between Spawning Events. Can. J. Fish. Aquat. Sci. 68:1635-1650.

Korman, J., D.R. Marmorek, G.L Lacroix, P.G. Amiro, J.A. Ritter, W.D. Watt, R.E. Cutting, and D.C.E. Robinson. 1994. Development and Evaluation of a Biological Model to Assess Regional-Scale Effects of acidification on Atlantic Salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 51:662-680.

O'Reilly, P., S. Rafferty, and J. Gibson. 2012. Within- and Among-Population Genetic Variation in the Southern Upland Designatable Unit of Maritime Atlantic Salmon (*Salmo salar* L.) DFO Can. Sci. Advis. Sec. Res. Doc. 2012/077.

APPENDIX A

Threats tables for the freshwater, estuarine and marine environments, summarizing human activities or sources of environmental change that either negatively impact Atlantic salmon populations (i.e. cause reduced abundance) or cause reduced quality and/or quantity of habitat in the SU region.

Definition of Table Headings and Column Values

Threat Category: The general activity or process (natural and anthropogenic) that has caused, is causing, or may cause harm, death, or behavioural changes to a species at risk; or the destruction, degradation, and/or impairment of its habitat to the extent that population-level effects occur.

Specific Threat: The specific activity or process causing stress to Atlantic salmon populations in the Southern Upland DU, where stress is defined as changes to ecological, demographic, or behavioural attributes of populations leading to reduced viability.

Level of Concern: Signifies the level of concern for species persistence if a threat remains unmitigated; where a High level of concern reflects threats that are likely to lead to substantial declines in abundance or loss of populations in the absence of mitigation, a Medium level of concern reflects threats that are likely to limit populations to low abundance and thus increase extinction risk, while a Low level of concern reflects threats that might lead to slightly increased mortality but are expected to have a relatively small impact on overall population viability. This criterion is based on the evaluation of all other information in the table with an emphasis on the extent of the threat in the DU and the number of populations likely to be affected at each level of Severity (see definition below).

Location or Extent: The description of the spatial extent of the threat in the SU was largely based on the criteria developed for the Conservation Status Report Part II (DFO and MRNF 2009), where Low corresponds to < 5% of populations affected, Medium is 5-30%, High is 30-70% and Very High is > 70%. Where possible, the actual proportion of SU Atlantic salmon populations affected by a specific threat is given in brackets.

Occurrence and Frequency: Occurrence: Description of the time frame that the threat has affected (H - historical), is (C - current) or may be (A - anticipatory) affecting Atlantic salmon populations in the Southern Upland DU. Historical – a threat that is known or is thought to have impacted salmon populations in the past where the activity is not ongoing; Current – a threat that is known or thought to be impacting populations where the activity is ongoing (this includes situations in which the threat is no longer occurring but the population-level impacts of the historical threat are still impacting the populations); Anticipatory – a threat that is not presently impacting salmon populations but may have impacts in the future (this includes situations where a current threat may increase in scope). Frequency: Description of the temporal extent of the threat over the course of a year (seasonal, recurrent, continuous).

Severity: Describes the degree of impact a given threat may have or is having on individual Atlantic salmon populations subjected to the threat given the nature and possible magnitude of population-level change. See Table A1 for definitions/examples of how severity has been evaluated.

Table A1. Definitions/examples of how severity has been evaluated.

Category	Definition/Examples
Negligible	• Habitat alteration within acceptable guidelines that does not lead to a reduction in habitat quality or quantity. • No change in population productivity.
Low	• Minor or easily recoverable changes to fish habitat (e.g. seasonal or changes <1 year). • Little change in population productivity (< 5% decline in spawner abundance)
Medium	• Moderate impact to fish habitat with medium term for habitat recovery (3-5 years). • Moderate loss of population productivity (5-30% decline in spawner abundance)
High	• Substantial damage to fish habitat such that the habitat will not recover for more than 5 years. • Substantial loss of population productivity (> 30% decline in spawner abundance)
Extreme	• Permanent and spatially significant loss of fish habitat • Severe population decline with the potential for extirpation.

Causal Certainty: Two-part definition. Part 1: Reflects the strength of the evidence linking the threat (i.e. the particular activity) to the stresses (e.g. changes in mortality rates) affecting populations of Atlantic salmon in general. As such, evidence can come from studies on any Atlantic salmon population. Part 2: Reflects the strength of the evidence linking the threat to changes in productivity for populations in the Southern Upland DU specifically. See Table A2 for definitions/examples of how causal certainty has been evaluated. Note: Does not apply to threats that are anticipatory.

Table A2. Definitions/examples of how causal certainty has been evaluated.

Causal certainty	Description
Negligible	Hypothesized.
Very Low	< 5%: Unsubstantiated but plausible link between the threat and stresses to salmon populations.
Low	5% - 24%: Plausible link with limited evidence that the threat has stressed salmon populations.
Medium	25% - 75%: There is scientific evidence linking the threat to stresses to salmon populations.
High	76% - 95%: Substantial scientific evidence of a causal link where the impact to populations is understood qualitatively.
Very High	> 95%: Very strong scientific evidence that stresses will occur and the magnitude of the impact to populations can be quantified.

Table A3. Threats to Atlantic salmon populations in the freshwater environment of the SU DU.

Threat Category	**Specific Threat**	**Level of Concern**	**Location or Extent**	**Occurrence and Frequency**	**Severity**	**Causal Certainty**	
		for the DU as a whole	of the threat in the DU	of the threat in the DU	of population level impacts	evidence linking the threat to stresses in general	evidence for changes to viability of SU salmon populations
Freshwater Environment							
Water quality and quantity	Acidification	**High**	Very High (78% of assessed populations affected)	H, C and A Continuous and recurrent	Extreme	Very High	Very High
	Extreme temperature events	**Medium**	High to Very High (anecdotal information suggests the majority of rivers are affected)	H, C and A Seasonal	High	High	Medium
	Altered hydrology	**High**	High to Very High	H, C and A Seasonal	High	High	Medium
	Water extraction	**Low**	Low	H, C and A Recurrent	Negligible to High (dependent upon timing and magnitude of extraction/alteration)	High	Low
	Chemical contaminants	**Low**	Unknown (anecdotal information suggests the majority of populations affected)	H, C and A Seasonal	Negligible to High (dependent upon concentration (dose) and time of exposure (duration)	High	Low
	Silt and sediment	**Medium**	Very High (100%)	H and C Continuous	Negligible to High (dependent upon concentration (dose) and time of exposure (duration)	High	Low
Changes to biological communities	Invasive species (fish)	**High**	Medium (22% of assessed populations)	H, C and A Continuous	High	High	Medium

Threat Category	**Specific Threat**	**Level of Concern**	**Location or Extent**	**Occurrence and Frequency**	**Severity**	**Causal Certainty**	
		for the DU as a whole	of the threat in the DU	of the threat in the DU	of population level impacts	evidence linking the threat to stresses in general	evidence for changes to viability of SU salmon populations
Freshwater Environment							
	Invasive species (other)	**Low**	Low	A Continuous	Low to High	Medium	Very Low
	Stocking for fisheries enhancement using traditional methods	**Medium**	Very High	H and C Continuous	Medium to Extreme (dependent upon number of fish stocked and length of period of stocking)	High (rate of fitness recovery after stocking ends is unknown)	Low
	Stocking (current)	**Low**	Low (several Fish Friends projects; educational programs)	C and A Continuous	Low to High (dependent upon number of juveniles stocked and size of recipient population)	High	Low
	Other salmonid stocking (rainbow, brown, & brook trout)	**Low**	Medium	H, C and A Continuous	Low to High (dependent upon number stocked and type of recipient waterbody (lake vs. river))	Medium	Low
	Salmonid aquaculture (commercial)	**Low**	Low	H, C and A Continuous	Medium	High	Low
	Avian predators	**Medium**	High	C and A Seasonal	High	Medium	Medium
	Genetic effects of small population size	**Medium**	Medium (mostly focused in southwest area of DU)	H, C and A Continuous	Negligible to High (dependent upon length of time at small population size, stocking history, and site specific conditions)	High	None (Not evaluated)
	Allee (small population size) effects	**Medium** (abundance specific)	Very High (abundance is low in all rivers)	H, C and A Continuous	Low to High (dependent on population-specific abundance)	Medium	Low

Threat Category	**Specific Threat**	**Level of Concern**	**Location or Extent**	**Occurrence and Frequency**	**Severity**	**Causal Certainty**	
		for the DU as a whole	of the threat in the DU	of the threat in the DU	of population level impacts	evidence linking the threat to stresses in general	evidence for changes to viability of SU salmon populations
Freshwater Environment							
	Scientific activities	**Low**	Low (Two Index Rivers and occasional surveys/sampling of other rivers)	H, C, A Seasonal	Low	Low	Low
Physical obstructions	Habitat fragmentation due to dams, culverts and other permanent structures	**High**	Medium to Very High	H, C and A Continuous	Low to Extreme (Dependent upon design of structure and location within watershed)	Very High	Very High
	Reservoirs	**Medium**	Medium	H, C and A Continuous	Low to High (Dependent upon size of individual reservoirs and number in series on a system)	High	Medium
Habitat alteration	Infrastructure (roads)	**Medium**	Very High (all rivers)	H, C and A Continuous	Low to High (dependent upon road density within watershed or sub-watershed)	Medium	Low
	Pulp and paper mills	**Low**	Low (only two known pulp mills in DU)	H and C Continuous	Medium to High (Dependent upon process used and effluent discharge quality)	High	Low
	Hydro power generation	**Medium**	Medium	H, C and A Continuous	Medium to Extreme (dependent upon facility design and operating schedule)	High	Medium

Threat Category	Specific Threat	Level of Concern	Location or Extent	Occurrence and Frequency	Severity	Causal Certainty	
		for the DU as a whole	of the threat in the DU	of the threat in the DU	of population level impacts	evidence linking the threat to stresses in general	evidence for changes to viability of SU salmon populations
Freshwater Environment							
	Urbanization	**Medium**	Medium	H, C and A Continuous	Low to High (dependent upon density of urbanization and infrastructure development)	High	Medium
	Agriculture	**Medium**	High	H, C and A Seasonal	Low to High (dependent upon extent within watershed and practices used)	Medium	Low
	Forestry	**Medium**	High	H, C and A Continuous	Low to High (dependent upon extent within watershed and practices used)	Medium	Low
	Mining	**Medium**	Unknown	H, C and A Continuous	Low to High (dependent upon type of mine, processes used, and susceptibility to Acid Rock Draiange)	Medium	Low
Directed salmon fishing (current)	Aboriginal FSC fishery	**Low**	Low	H, C and A Seasonal	Negligible	Very High	High
	Recreational fishery (angling)	**Low**	Low	H and A Seasonal	Negligible	Very High	High
	Illegal fishing and poaching	**High**	Unknown (but potentially high)	H, C and A Seasonal	Low to High (dependent on number of salmon removed and size of impacted population)	High	High
By-catch in other fisheries	Aboriginal or commercial fisheries	**Low**	Low	H, C and A Seasonal	Low	High	High

Threat Category	**Specific Threat**	**Level of Concern**	**Location or Extent**	**Occurrence and Frequency**	**Severity**	**Causal Certainty**	
		for the DU as a whole	of the threat in the DU	of the threat in the DU	of population level impacts	evidence linking the threat to stresses in general	evidence for changes to viability of SU salmon populations
Freshwater Environment							
	Recreational fisheries	**Low**	High	H, C and A Seasonal	Low	High	High
	Recreational fishery: illegal targeting of Atlantic salmon while fishing under a general license	**Medium**	High	H, C and A Seasonal	Low to High (dependent upon angling pressure)	High	High

Table A4. Threats to Atlantic salmon populations in the marine or estuarine environments of the SU DU.

Threat	**Specific Threat**	**Level of Concern**	**Location or Extent**	**Occurrence and Frequency**	**Severity**	**Causal Certainty**	
		for the DU as a whole	of the threat in the DU	of the threat in the DU	of population level impacts	evidence linking the threat to stresses in general	evidence for changes to viability of SU salmon populations
Marine or Estuarine Environment							
Changes to biological communities	Invasive species	**Low**	Very High (all populations)	C and A Continuous	Low	Low	Low
	Salmonid aquaculture	**High**	Very High	H, C and A Continuous	Medium to High (dependent upon location of aquaculture facilites and operating practices)	High	Low
	Other species aquaculture	**Low**	Very High (all populations)	H, C and A Seasonal	Negligible to Medium (dependent upon species under culture, location of fsaacility, and operating practices)	Low	Low
	Diseases and parasites	**Medium**	Very High (all populations)	H, C and A Continuous	Low to High (dependent upon irruptive behavior of disease/parasites resulting in outbreaks)	Low	Low
Changes in oceanographic conditions	Marine ecosystem change (including shifts in oceano-graphic conditions and changes in predator/prey abundance)	**High**	Very High (all populations)	H, C and A Continuous	Low to Extreme (dependent upon magnitude of change and sensitivity of salmon to change)	Medium	Low

Threat	**Specific Threat**	**Level of Concern**	**Location or Extent**	**Occurrence and Frequency**	**Severity**	**Causal Certainty**	
		for the DU as a whole	of the threat in the DU	of the threat in the DU	of population level impacts	evidence linking the threat to stresses in general	evidence for changes to viability of SU salmon populations
Marine or Estuarine Environment							
Physical or abiotic change	Shipping, transport, noise, seismic activity	**Low**	Very High (all populations)	H, C and A Seasonal	Uncertain; likely Negligible to Low (dependent upon proximity of salmon to source of noise/activity)	Low	Low
	Contaminants and spills (land- or water-based)	**Low**	Very High (all populations)	H, C, A Episodic	Low to Extreme (dependent upon identity and magnitude of contamination, and efficacy of cleanup)	Low	Low
	Tidal power	**Low**	Low	C and A Seasonal	Medium to High (dependent upon facility design and operating schedule)	High	Medium
Directed salmon fisheries	Subsistence fisheries (Aboriginal and Labrador residents)	**Low**	Low	H and A Seasonal	Negligible	High	High
	International fisheries (Greenland; St. Pierre-Miquelon)	**Medium**	Very High (MSW component of all populations)	H, C and A Seasonal	Negligible to High	High	Medium
By-catch in other fisheries	Commercial fisheries	**Low**	Very High (all populations)	H, C and A Seasonal	Low	High	High
Fisheries on prey species of salmon	Commercial fisheries	**Low**	Very High (all populations)	H, C and A Seasonal	Low to High (dependent upon reduction of prey species and availability of other forage species)	Low	Low

THIS REPORT IS AVAILABLE FROM THE:

Centre for Science Advice (CSA)
Maritimes Region
Fisheries and Oceans Canada
PO Box 1006, Station B203
Dartmouth, Nova Scotia
Canada B2Y 4A2

Telephone: 902-426-7070
Fax: 902-426-5435
E-Mail: XMARMRAP@mar.dfo-mpo.gc.ca
Internet address: www.dfo-mpo.gc.ca/csas-sccs/

ISSN 1919-5087

Correct Citation for this Publication:

DFO. 2013. Recovery Potential Assessment for Southern Upland Atlantic Salmon. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2013/009.

Aussi disponible en français :

MPO. 2013. Évaluation du potentiel de rétablissement du saumon atlantique des hautes terres du Sud. Secr. can. de consult. sci. du MPO, Avis sci. 2013/009.

A Global Assessment of Salmon Aquaculture Impacts on Wild Salmonids

Jennifer S. Ford*, **Ransom A. Myers**†

Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada

Since the late 1980s, wild salmon catch and abundance have declined dramatically in the North Atlantic and in much of the northeastern Pacific south of Alaska. In these areas, there has been a concomitant increase in the production of farmed salmon. Previous studies have shown negative impacts on wild salmonids, but these results have been difficult to translate into predictions of change in wild population survival and abundance. We compared marine survival of salmonids in areas with salmon farming to adjacent areas without farms in Scotland, Ireland, Atlantic Canada, and Pacific Canada to estimate changes in marine survival concurrent with the growth of salmon aquaculture. Through a meta-analysis of existing data, we show a reduction in survival or abundance of Atlantic salmon; sea trout; and pink, chum, and coho salmon in association with increased production of farmed salmon. In many cases, these reductions in survival or abundance are greater than 50%. Meta-analytic estimates of the mean effect are significant and negative, suggesting that salmon farming has reduced survival of wild salmon and trout in many populations and countries.

Citation: Ford JS, Myers RA (2008) A global assessment of salmon aquaculture impacts on wild salmonids. PLoS Biol 6(2): e33. doi:10.1371/journal.pbio.0060033

Introduction

Since the late 1970s, salmon aquaculture has grown into a global industry, producing over 1 million tonnes of salmon per year [1]. The majority of this biomass is held in open net pens in coastal areas through which wild salmon migrate on their way to and from the ocean. A number of studies have predicted or evaluated the impacts of salmon farming on wild salmon through a single mechanism, in a given area. It is clear that some salmonids are infected and killed by sea lice originating from salmon farms [2–5], that other diseases have been spread to wild populations from salmonid farming activities [6,7], and there is evidence that salmon parr are at lower density in areas of Scotland where there is salmon aquaculture [8]. In addition, farmed salmon escape in all areas where salmon aquaculture is practiced, and although their breeding success may be low on average, competition for mates and hybridization with wild salmon are likely to reduce survival of wild populations [9,10].

It is well established that wild salmonids can be negatively affected by salmon farming [11], however, the importance of these interactions at the population level has rarely been determined [2]. To determine population level impacts, we examined temporal trends in the abundance and survival of wild salmonids (Figure 1 and Figure S1). Our study contrasted trends in wild populations exposed to potential aquaculture impacts with those of populations not exposed. Populations in which juvenile salmonids pass by salmon farms during their migration were considered to be exposed to impacts of salmon farming. Exposed populations were carefully paired with control populations in the same region whose migrations did not lead past farms, but which otherwise experienced similar climate and anthropogenic disturbances. Use of such paired comparisons allowed us to control for confounding factors such as climate to detect population level impacts. Using the Ricker stock recruit model [12], we performed 11 comparisons, involving many stocks from both sides of the Atlantic and from British Columbia in the Pacific (Table 1, Data section of Materials and Methods).

Results

All estimates of the effect of aquaculture on survival or returns were negative. Both random effects estimates of the mean effect were negative and highly significant (Figure 2), indicating a very large reduction in survival and returns in populations exposed to aquaculture. Under the dynamics of Equation 1 (see Materials and Methods), percent change in survival or returns is represented by $(1-\exp(\hat{\gamma}_{\ k}) * P^{1/2} * 100)$ where γ is the coefficient of aquaculture production (P) for region k. For example, the estimated change in survival per tonne of salmon farming (γ_k) for Bay d'Espoir in Newfoundland was estimated to be 0.026 (Figure 2). In 2003, the farmed salmon harvest from this area was 1,450 tonnes (t), so the estimated decrease in survival is $(1-\exp(-0.026 * 1450^{1/2})) * 100 = 63\%$ (95% CI: 44%–80%), relative to what it would be in the absence of farms. Survival and total returns of many stocks were found to be reduced by more than 50% (Figure 2), for each generation. If all exposed populations were passing by farms with a total annual harvest of 15,000 t, the mean estimated total reduction in survival would be 73% (95% CI: 29%–90%) (Figure 2). Many regions now have farmed salmon production in excess of 20,000 t/y.

Generally, Atlantic salmon populations were depressed more than Pacific salmon populations, particularly Atlantic

Academic Editor: Callum Roberts, University of York, United Kingdom

Received October 17, 2006; **Accepted** January 3, 2008; **Published** February 12, 2008

Abbreviations: AIC, Akaike information criteria; BC, British Columbia; DFO, Fisheries and Oceans Canada; SA, statistical area

* To whom correspondence should be addressed. E-mail: jenford@ecologyaction.ca

† Deceased

Author Summary

The impact of salmon farming on wild salmon and trout is a hotly debated issue in all countries where salmon farms and wild salmon coexist. Studies have clearly shown that escaped farm salmon breed with wild populations to the detriment of the wild stocks, and that diseases and parasites are passed from farm to wild salmon. An understanding of the importance of these impacts at the population level, however, has been lacking. In this study, we used existing data on salmon populations to compare survival of salmon and trout that swim past salmon farms early in their life cycle with the survival of nearby populations that are not exposed to salmon farms. We have detected a significant decline in survival of populations that are exposed to salmon farms, correlated with the increase in farmed salmon production in five regions. Combining the regional estimates statistically, we find a reduction in survival or abundance of wild populations of more than 50% per generation on average, associated with salmon farming. Many of the salmon populations we investigated are at dramatically reduced abundance, and reducing threats to them is necessary for their survival. Reducing impacts of salmon farming on wild salmon should be a high priority.

salmon in Atlantic Canada. Irish sea trout were also estimated to have been very strongly reduced by impacts of salmon farming, whereas estimated impacts on Atlantic salmon in Scotland depended on the data used. In British Columbia (Pacific Canada), only pink salmon showed significant declines correlated with salmon aquaculture.

Results are reported for a model including autocorrelated errors and with λ set at 0.5, rather than 1 or 2, because this minimized the Akaike information criteria (AIC) for most regions [13]. The parameter λ allows for the impacts of salmon farming to change nonlinearly with the aquaculture production. A λ of 0.5 indicates that relatively small amounts of aquaculture will depress wild populations, but the effect does not increase proportionally to aquaculture production. See Tables S1 and S2 for results of alternative models.

For the New Brunswick comparison, the outer Bay of Fundy rivers are located much closer to salmon farms than the other exposed rivers. If only these outer Bay of Fundy rivers are considered exposed to salmon farming, and other Bay of Fundy rivers (inner Bay of Fundy and Saint John River) are included among the controls, the overall estimates (i.e., meta-analytic means) are still significant and negative in both versions of the analysis.

Discussion

We have estimated a significant increase in mortality of wild salmonids exposed to salmon farming across many regions. However, estimates for individual regions are dependent on assumptions detailed in the Materials and

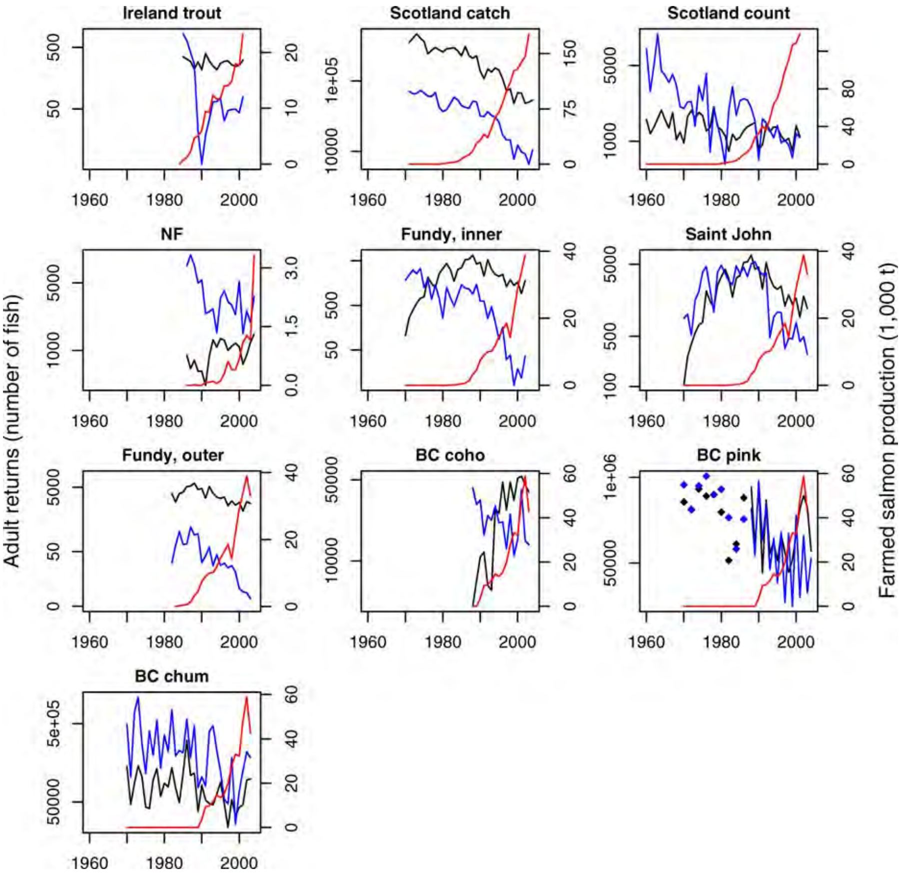


Figure 1. Adult Returns of Wild Salmonids in Control (Black) and Exposed (Blue) Stocks, with Aquaculture Production (Red)

For plotting only, the returns to controls and exposed stocks have been separately summarized by a multiplicative model ($\log(Returns_{i,y}) = a_i + d_y + e_{i,y}$; variables are the same as in Equation 1). The mean returns across stocks for each year are shown. Note that left-hand axes are on a log scale. Only even year values are available for pink salmon prior to 1989. Irish salmon are not included because only marine survivals (not returns) are available.

doi:10.1371/journal.pbio.0060033.g001

Table 1. Summary of Populations Included

ID	Species	Country	Exposed		Control		Type[a]	Reference
			Region	n[b]	Region	n[b]		
1	Sea trout	Ireland/UK	Ireland (Western Region)[c]	16	Wales	32	C	[26,16,17]
2	Atlantic salmon	Scotland	West Coast[c]	1	East Coast	1	C	[e]
3		Scotland	West Coast[c]	2	East Coast	10	T	[29]
4		Ireland	Western Region[d]	4	Rest of Ireland	9	T,S	[28]
5		Canada	Bay d'Espoir[d]	1	Rest of Newfoundland	4	T	[31]
		Canada	Bay d'Espoir[c]	1	Rest of Newfoundland	21	T,S	[31]
6		Canada	Fundy, Inner	2	Gulf of St Lawrence, Atlantic Coast	4	T,S	[28,35,36,39]
7		Canada	St John River	2	Gulf of St Lawrence, Atlantic Coast	4	T,S	[28,37,39,40]
8		Canada	Fundy, Outer	2	Gulf of St Lawrence, Atlantic Coast	4	T,S	[28,37,39,40]
9	Coho salmon	Canada	Johnstone Strait	2	BC Central Coast	4	S	[f]
10	Pink salmon	Canada	Johnstone Strait	2	BC Central Coast	4	S	[f]
11	Chum salmon	Canada	Johnstone Strait	2	BC Central Coast	4	S	49

[a] Type C refers to catches, T refers to scientific traps, and S refers to other scientific surveys.

[b] n is the number of populations; i.e., rivers, or SAs in BC.

[c] Used in returns analysis only.

[d] Used in survival analysis only.

[e] J. MacLean, FRS Scotland, unpublished data.

[f] NuSEDS database, DFO Pacific, unpublished data.

doi:10.1371/journal.pbio.0060033.t001

Methods section, and the estimates often have large confidence intervals. Given that the data analysed are affected by considerable noise—including changes in fishing and environmental factors—the important result of this study is that we are nonetheless able to detect a large, statistically significant effect correlated with trends in farmed salmon production. The significant increase in mortality related to salmon farming that we have estimated in almost all cases is in addition to mortality that is also acting on the control populations. In most cases, control populations were also experiencing decreases in marine (and sometimes freshwater) survival, for reasons that are only partially understood. At the same time, fishing mortality has been reduced or eliminated in many areas, which may have partially masked high mortalities associated with aquaculture.

A key assumption in this study is that exposed and control areas do not differ in a systematic way across regions. We have identified three possible ways that exposed and control sites could differ systematically: first, salmon farms could be established only in areas where wild stocks have already collapsed; second, salmon farms could be established in areas where habitat is more disturbed by human activities; or, third, climate factors could differ between the exposed areas and the controls in a systematic way.

Declines in control and exposed salmonid populations preceded the growth of the salmon aquaculture industry in some regions, but inspection of the data used do not indicate that salmon populations in the majority of our regions had declined dramatically in the exposed areas only, before the start of salmon farming (averaged returns data are shown in Figure 1). In regions such as Scotland, where declines precede the start of salmon farming, the strong aquaculture effect estimated reflects a faster decline in exposed populations concurrent with the growth of salmon farming.

Areas that we consider exposed do not seem to be more developed than control areas in general. In the Atlantic, most areas have been highly altered by human activities for hundreds of years, but there is no obvious difference between the control and exposed groups in this regard. In British Columbia, all areas considered are very remote, and the main type of anthropogenic disturbance in rivers would be forestry. Comprehensive forestry records at the watershed scale are not easily available, but logging in British Columbia's Central Coast is extensive, both historically and recently [14]. It should be noted that the comparisons in British Columbia include large numbers of rivers (> 80 rivers in each case), so differences in anthropogenic effects would have to hold over many watersheds to explain the effects we estimate.

Finally, it is also very unlikely that our results are due to a climate driven trend in which more southerly populations show stronger declines than populations to the north. Although our exposed populations are to the south of control populations in three of five regions, differences in latitude are small. In New Brunswick, the control populations are to the north of the exposed populations, but by less than 200 km, and the headwaters of some of the exposed populations are adjacent to those of the controls. In Newfoundland, the difference in latitude between exposed and control populations is similarly small. In British Columbia, the control populations are also to the north, but by less than 300 km. Also, Mueter et al. [15] found that pink and coho salmon from all of the British Columbia populations we have examined respond similarly to large-scale climate trends. Thus, the pattern we found in this study does not seem attributable to a systemic difference between the control and exposed areas.

We estimated higher impacts on populations in the Atlantic than those in British Columbia, possibly because Atlantic salmon populations are conspecific with farmed salmon, and therefore susceptible to genetic effects from

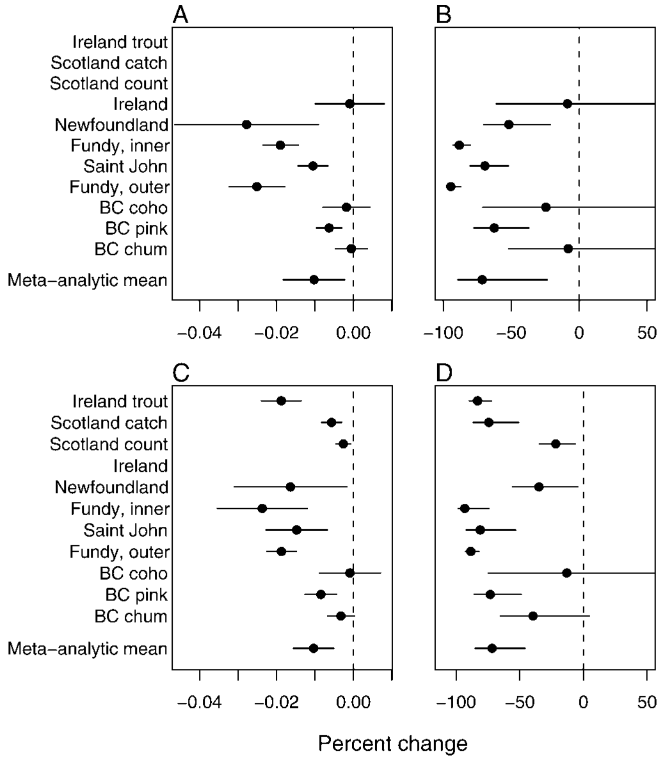


Figure 2. Estimated Effects of Salmon Farming

All estimates are for Atlantic salmon unless otherwise noted.

(A) Estimated percent change in survival of wild salmonids associated with salmon farming, per generation per tonne of farmed salmon production.

(B) Estimated percent change in survival of wild salmonids associated with salmon farming, per generation, at the mean tonnage of farmed salmon harvested in each region, during the study period. The meta-analytic mean has been scaled to show mean reduction in survival when harvest of farmed salmon in the region is 15,000 t.

(C and D) As for (A) and (B), but representing the change in returns to each stock (rather than survival). The bars represent 95% confidence intervals.

doi:10.1371/journal.pbio.0060033.g002

interbreeding with escaped farm salmon, in addition to disease or other impacts. Estimated impacts in British Columbia may also be lower because we aggregated over large numbers of populations for pink, chum, and coho salmon, because estimates of fishing mortality were only available at a very coarse scale. The individual populations may vary in their exposure to salmon farms.

The large apparent impact of Atlantic salmon farming on Irish sea trout, in contrast, can not be explained by interbreeding. In the mid-western region of Ireland (the exposed region), the total rod catch decreased from almost 19,000 sea trout in 1985 to 461 in 1990 [16]. In the few rivers where data were available, catch declines could not be explained by reduced effort [16]. Welsh sea trout catches (the controls) have remained relatively constant during the same time period, whereas fishing effort has decreased considerably [17]. Sea trout (anadromous brown trout) might be expected to experience higher mortalities, because they spend lengthy periods in coastal areas near salmon farms, relative to Atlantic salmon, thus being exposed to disease or parasites for a longer time [18].

The time period over which we are estimating impacts of aquaculture includes the establishment of the industry in each region. Improvements in management as industries mature may explain our finding that impacts of salmon farming on wild salmon do not increase linearly with the tonnage of farmed salmon. Better management should decrease the impact of salmon farming on a per tonne basis, although such improvements may not be able to keep pace with the growth of the salmon farming industry. The estimated reduction in survival of wild salmonids is large, and would be expected to increase if aquaculture production increases.

Materials and Methods

We modeled survival and, in a separate analysis, total returns to each stock, using a general linear mixed effects model for each region. To model survival, we used a Ricker model extended to include the production of farmed salmon in the area through which exposed juvenile salmon migrated, with random effects for each stock and year [19].

Let $S_{i,y}$ be an index of the number of fish that smolted, i.e., migrated to sea in the spring, in year y from stock i, let $R_{i,y}$ be the estimated number of those fish that would subsequently return to spawn in the absence of fishing, and let $P_{i,y}$ be the aquaculture production that those smolts were exposed to (in tonnes). The dynamics are assumed to be given by

$$\log\left(\frac{R_{i,y}}{S_{i,y}}\right) = \beta_0 + a_i + d_y + \beta_i S_{i,y} + \gamma(P_{i,y})^{\lambda} + e_{i,y} \qquad (1)$$

where β_0 is the fixed intercept for the average stock and year with no aquaculture production, a_i is the random deviation of the i^{th} stock intercept from β_0, d_y is the random deviation of the y^{th} year, β_i is the fixed slope of mortality (the density dependence parameter) that will vary with each stock i, and γ is the coefficient of aquaculture mortality that is assumed to scale with a possibly nonlinear function of aquaculture production, $(P_{i,y})^{\lambda}$. The random error, $e_{i,y}$, is assumed to be first order autocorrelated. We assume the a_i's and d_y's come from normal distributions with zero mean. The autocorrelation and the random year effect are included to account for established temporal and spatial correlations (respectively) in environmental effects [20].

The effects of aquaculture are summarized by the coefficient γ for each region. The regional coefficients were combined using meta-analysis to obtain an overall estimate of the change in wild salmonid survival related to aquaculture. Because the best functional form for the aquaculture term in the model $(P_{i,y})^{\lambda}$ was not known, we investigated a linear increase in impacts with aquaculture, a square relationship, and a square root relationship. We selected models by AIC, and we tested our results under alternative formulations.

To test the robustness of the conclusions, and because only returns data were available for some regions, we repeated the analysis with number of returning adults as the response variable. This analysis used Equation 1 but dropped the $S_{i,y}$ and β_i terms. The response variables for this analysis included rod catches, rod plus marine catches, counts of salmon returning to rivers, and estimates of returns to rivers in the absence of fishing (see Data sources and treatment, below).

Outer Bay of Fundy salmon in New Brunswick, Canada, have been reduced to zero in one river and to a handful in another river. For this region only, we assumed negative binomial errors.

For the meta-analysis, we added a subscript, k, to identify each region, to γ, which summarizes the effect of aquaculture for each region. For a fixed assumption about λ, the γ_k's are in the same units and can be directly compared. We modeled the effects of aquaculture as a mixed effects model,

$$\hat{\gamma}_k \sim N(\alpha_0, \sigma^2 + s_k^2) \qquad (2)$$

here $\hat{\gamma}_k$ is the estimated value of γ_k, α_0 is the intercept, σ^2 is the among-region variance, and s_k^2 is the variance of the kth estimate (which is taken from the analysis in Equation 1, and is held fixed). A fixed effects meta-analysis is obtained by constraining σ to be zero. We used maximum likelihood estimation and selected models by AIC.

For robustness, we considered five classes of models: different regions used as controls, different mixed model assumptions, different error assumptions, different functional forms for the aquaculture effect, and different autocorrelational structures, as well as performing a Bayesian meta-analysis. Overall, the results were very similar for all models. (See Tables S1 and S2 for results of alternative models and Text S1 for details of the Bayesian analysis.)

Data sources and treatment. We analysed data for five species of wild salmonid in five regions: Ireland and Wales, Scotland, Newfoundland (Canada), New Brunswick (Canada), and British Columbia (Canada). There are three further regions with both wild salmonids and salmon aquaculture for which we could not carry out analyses: Norway, the west coast of Vancouver Island (Canada), and Maine (United States). We were unable to carry out analyses for Norway for three reasons. First, salmon farming in Norway is so widespread [21] that it was difficult to establish controls. Second, the adult population in many rivers has been found to contain over 50% aquaculture escapees [22], making trends in returns to rivers difficult to interpret. Third, there are confounding effects from acidification and disease [23, 24]. For the west coast of Vancouver Island, it was not possible to obtain aquaculture production data by region over time, and Maine was not included because of a lack of nearby wild populations to serve as controls.

Most populations that we considered to be exposed breed in rivers that discharge into bays or channels containing at least one salmon farm. Others breed in rivers flowing into bays without salmon farms very close to areas containing many farms. Salmon from control rivers are very unlikely to pass by salmon farms early in their life cycle, due to the direction of their migration. However, some controls may be relative, in the sense that salmon may pass by farms from a considerable distance, later during their migrations. This would tend to be conservative with respect to our study, since we would then have to detect local effects that are additional to any impacts from distant farms. Data from scientific surveys, e.g., counting fences, were used if possible; for Scottish salmon and Irish and Welsh sea trout, only catch data were available, so results are given for only the impacts on returns (not survival).

Ireland sea trout. We compared rod catches of sea trout in Ireland's Western Region to rod plus in-river fixed engine catches in Wales, from 1985 to 2001 (there are no fixed engine fisheries directed at sea trout in Ireland). Salmon farming is concentrated in the Western Region (Connemara area) of Ireland, but does occur in other parts of the country [25]. Based on farm locations [25], it was estimated that all rivers considered exposed are located less than 50 km from a salmon farm, but most will enter the ocean less than 30 km from a salmon farm. There is no salmon farming in Wales. There were 16 rivers in Western Ireland considered exposed: Athry, Bhinch (Lower), Bhinch (Middle), Bhinch (Upper), Burrishoole, Costello, Crumlin, Delphi, Erriff, Gowla, Inagh, Inverbeg, Invermore, Kylemore, Newport, and Screebe [16]. The following 32 Welsh rivers served as controls: Aeron, Afan, Arto, Cleddau, Clwyd, Conwy, Dee, Dwyfawr, Dwyryd, Dyfi, Dysynni, Glaslyn, Gwendreath, Gwyrfai, Llyfni, Lougher, Mawddach, Neath, Nevern, Ogmore, Ogwen, Rheidol, Rhymney, Seiont, Taf, Taff, Tawe, Teifi, Tywi, Usk, Wye, and Ystwyth [26,27]. Trout caught and released are included in catch data from both countries. Only catch estimates were available for most of these rivers. Recruitment could not be derived, because anadromous brown trout interbreed with freshwater resident trout, about which very few data are available, so this stock was only included in the returns modeling (not survival). Farmed salmon production for all of Ireland was used in modeling [28], because the majority of farms are in the region where the exposed populations breed. This will tend to have a conservative effect, resulting in a lower estimate of the impact of aquaculture, per tonne of salmon farming.

Scotland catch data. We compared marine plus rod catches of Atlantic salmon from the east coast of Scotland to catches from the west coast of Scotland for the years 1971 to 2004. Salmon farms appear to be located in the majority of bays on the west coast of Scotland in well over 300 sites (http://www.marlab.ac.uk/Uploads/Documents/fishprodv9.pdf), so all salmon from rivers on this coast were considered exposed. There is no salmon farming on the east coast, so salmon from east coast rivers were controls. For each coast, a single time series of total catch was used in modeling. Marine catch records were from the International Council for the Exploration of the Sea (ICES) Working Group on North Atlantic Salmon [28] and rod catch records were from Fisheries Research Services of Scotland (J. MacLean, personal communication). Rod catches included salmon caught and released. These data were only used in modeling returns. Farmed salmon production for all of Scotland was used in modeling [28], because regional production data were not available.

Scotland count data. We also used counts of Atlantic salmon of all ages returning to rivers from 1960–2001 in Scotland from Thorley et al (2005) [29]. The fish counters are maintained by Fisheries Research Services or by Scottish and Southern Energy plc. There were two exposed populations. One is from the Awe Barrage, which empties into a bay with numerous salmon farms. The other is from the Morar River, which is less than 20 km from the nearest salmon farm, in an area of the coast with many farms [8]. Salmon from the control rivers (on the east coast) do not pass by salmon farms in Scotland because of the direction of their migration routes [30], unless they approach the Norwegian coast. There were ten control populations from the following rivers: Aigas, Beanna, Torr Achilty, Dundreggan, Invergarry, Logie, Westwater, Cluni, Erich, and Pitlo. Farmed salmon production for all of Scotland was used in modeling [28] because regional production data were not available.

Ireland Atlantic salmon. Estimates of marine survival to one sea winter for hatchery (and two wild) Atlantic salmon populations from Ireland and Northern Ireland (1980–2004) were collected and reported by the ICES Working Group on North Atlantic Salmon [28]. Because only survival estimates are provided, these data were only used in the survival analysis. Salmon from hatcheries on the Screebe, Burrishoole, Delphi, and Bunowen Rivers were considered exposed. Populations from hatcheries on the Shannon, Erne, Lee, Bush, and Corrib Rivers, plus wild populations from the Bush and Corrib Rivers were used as controls.

Production data were not available on a regional basis, so national values [28] were apportioned to bays into which exposed rivers empty by assuming that 30% of national production is in the Kilkieren Bay, 10% is in Clew Bay, 5% is in each of Killary Harbour and Ballinakill Bay. These proportions are based on maps of salmon farm locations from the Irish Marine Institute [25], and they approximately match stock numbers collected by the Central Fisheries Board in the years for which stock numbers are available (P. Gargan, personal communication). Years in which each bay was fallowed were obtained from the Central Fisheries Board (P. Gargan, personal communication), and in these years, the fallowed bays are assigned a production of zero. All exposed rivers empty into bays with salmon farms [25], while control rivers are at least 55 km away from the nearest farm.

Newfoundland, Canada. Two data sets from Newfoundland were examined—marine survival estimates of wild Atlantic salmon from four rivers from 1987 to 2004 were used in the survival analysis, and grilse returns to 21 rivers from 1986 to 2004 were used in the returns modeling [31]. Salmon farming in Newfoundland is confined to Bay d'Espoir on the south coast [32] (http://www.fishaq.gov.nl.ca/aquaculture/pdf/aqua_sites.pdf). Only the Conne River (in Bay d'Espoir) was considered exposed; the Little River (also in Bay d'Espoir) was excluded because it has been regularly stocked [31]. The Exploits and Rocky Rivers were also removed from the analysis because of stocking [33]. This left three control rivers for the survival analysis: the Campbellton River, the Northeast Brook (Trepassey), and Western Arm Brook. For the returns analysis, there were 18 control rivers: Campbellton, Crabbes, Fischells, Flat Bay Brook, Highlands, Humber, Lomond, Middle Brook, Middle Barachois, Northeast Brook (Trepassey), Northeast (Placentia), Northwest, Pinchgut Brook, Robinsons, Salmon, Terra Nova (upper and lower), Torrent, and Western Arm Brook. Salmon from control rivers are very unlikely to pass salmon farms because of the direction of their migrations [34]. Farmed salmon production data are from Fisheries and Oceans Canada (DFO) Statistical Services [32].

New Brunswick and Nova Scotia, Canada. We compared Atlantic salmon returns to six rivers in the Bay of Fundy (New Brunswick and Nova Scotia, Canada) to returns to four rivers from other areas of New Brunswick and Nova Scotia. We grouped the six exposed rivers into three groups and estimated the impact of aquaculture on each group separately, because salmon from these three groups have different degrees of exposure to salmon farming. The three groups of exposed rivers are the inner Bay of Fundy group (Stewiacke and Big Salmon Rivers), the Saint John River group (Saint John and Nashwaak Rivers), and the outer Bay of Fundy group (St. Croix and Magaguadavic Rivers). Salmon farming in New Brunswick is highly concentrated in the Quoddy region of the outer Bay of Fundy (http://www.gnb.ca/0177/10/Fundy.pdf), although some farms are also found along the Nova Scotia coast of the Bay of Fundy. Salmon from control rivers enter into the Atlantic directly (LaHave River) or into the Gulf of St. Lawrence (Restigouche River, Miramichi River, Catamaran Brook) and do not pass by farms during their migrations. The same controls are used for all comparisons in New Brunswick and Nova Scotia. The estimates of returns to the rivers are published by DFO [28,35–40]. Outer Bay of Fundy salmon must pass through an area containing many salmon farms early during their migrations [41]. Although Saint John River salmon enter the ocean in an area without salmon farms, they are known to pass through the region containing many farms early during their migrations [41]. Salmon from inner Bay of Fundy rivers are considered exposed to salmon farming despite being up to 260 km away because of historical information indicating that juvenile salmon from these populations are found during the summer and fall in the area where salmon farms are currently located [42]. However, the evidence that this region is important habitat for inner Bay of Fundy and Saint John River populations is mixed [43]. For this reason, we ran an alternative model with only outer Bay of Fundy populations considered exposed, and all other New Brunswick and Nova Scotia rivers as controls.

For all New Brunswick rivers, an estimate of egg deposition was used as an index of spawners, to account for a significant increase in the age of spawners in many rivers over the study period. The number of grilse (salmon maturing after one winter at sea) and large spawners (repeat spawners or salmon maturing after two or three winters at sea) in each year was multiplied by a river-specific estimate of fecundity for a salmon of that size. Then, the index of spawners in a given year was derived by adding up all the eggs that could produce smolts in a year y, using river-specific ages at smolting from the literature. Returning hatchery-origin spawners are also added to the "spawners" but not to "returns." "Recruits" is the number of grilse that return to each river in year $y+1$, so that $\frac{R_{i,y}}{S_{i,y}}$ (in Equation 1) is the number of grilse returning per egg that would have smolted in year y. Estimates of returns to rivers from traps and other surveys were used in the returns analysis. No corrections were made to account for marine fisheries, but marine exploitation has been quite limited since the late 1980s, when salmon farming became a substantial industry [44]. Farmed salmon production data are from DFO Statistical Services [32].

British Columbia, Canada, coho salmon. For coho salmon in British Columbia (BC), spawner estimates are based on DFO's escapement database (NuSEDS), which includes estimates of spawning salmon of all species for hundreds of rivers and streams on the BC coast since 1950 (P. VanWill, DFO Pacific, unpublished data). We considered rivers on the east side of the Queen Charlotte and Johnstone Straits to be exposed (all rivers from Wakeman Sound to Bute Inlet, DFO Statistical Areas [SAs] 12 and 13). All rivers on the BC Central Coast from Finlayson Channel to Smith Inlet (SAs 7, 8, 9, and 10) were included as controls. In the regions considered exposed in BC, all salmon must pass by farms to get into the open ocean, although in some cases, the farms are at the end of long channels down which the salmon migrate (as far as 90 km in the most extreme case). Control populations to the north do not pass by farms, because of the direction of their migration routes [45].

Coverage in the NuSEDS database varies considerably in time and space, as does the quality of the estimates. We changed all indicators of unknown values (including "none observed" and "adults present") to a common missing value indicator. To reduce effects of inconsistent monitoring procedures, only data since 1970 were included in the analysis. All rivers known to be regularly stocked with hatchery salmon or to contain constructed spawning channels were also removed from exposed and control areas, leaving 49 exposed and 70 control rivers. Estimates were combined for each SA, the smallest areas for which catch rates are estimated. This was done by modeling returns to each SA and year, using a generalized linear model with negative binomial errors. The predicted returns for each SA were then used as spawner estimates ($S_{i,y}$ in Equation 1). To derive recruitment estimates, we followed Simpson et al. (2004) [46], applying exploitation rate estimates from Toboggan Creek (J. Sawada, DFO Pacific, personal communication) to the controls, and the average of the exploitation rates for Quinsam Hatchery, Big Qualicum Hatchery, and the Black Creek wild indicator population to the exposed stocks. After 1998, only the estimates from Black Creek were used for exposed stocks. Recruitment estimates for coho were based on the assumption that coho follow a fixed 3-y life cycle.

For pink, chum, and coho salmon, aquaculture production estimates include all salmon species farmed in SAs 12 and 13 (the Queen Charlotte and Johnstone Straits) from 1990 to 2003 (H. Russell, BC Ministry of Agriculture, Food, and Fisheries, unpublished data). In years when two or fewer companies were raising salmon in either area, estimates were not available. BC salmon farm locations are made available at http://www.al.gov.bc.ca/fisheries/licences/MFF__Sites__Current.htm.

British Columbia, Canada, pink salmon. Estimates of pink salmon spawner abundance were derived in the same manner as described above for coho salmon. "Returns" are spawners plus catch for a given year, assuming a fixed two year life cycle. The same regions were considered exposed, but because enumeration varies by species, there were only 36 exposed rivers from SAs 12 and 13 (from Wakeman Sound to Bute Inlet) included. Wood et al. (1999) [47] consider the pink salmon catches in SAs 8, 9, and 10 to consist mainly of salmon returning to those areas (respectively), so catch data from DFO [48] were used in each of these SAs. Area 7 was excluded from the survival analysis because catches for SA 7 are difficult to estimate due to the adjacent regions being much larger [47], leaving 47 control rivers from Burke Channel to Smith Inlet.

For Queen Charlotte and Johnstone Straits (the exposed areas), DFO does not estimate catches at the level of individual SA. To obtain approximate returns to each exposed SA, we found the proportion of total escapement to the Straits that was in our dataset (i.e., regularly enumerated rivers on the east side of the Straits without a major hatchery or constructed spawning channel) and assumed the same proportion of the total catch would be returning to those rivers (i.e., assumed equal catchability across stocks). For odd years, we used estimates from the Pacific Salmon Commission (B. White, unpublished data) of the catch of pink salmon in Johnstone and Georgia Straits that were not returning to the Fraser River. In even years, there is no pink salmon run on the Fraser River, so total returns to the Straits could be used.

British Columbia, Canada, chum salmon. For chum salmon, we used estimates of returns (i.e., before exploitation) and spawners to large coastal areas [49]. Chum from the east side of Queen Charlotte and Johnstone Straits, from Wakeman Sound to Bute Inlet (SAs 12 and 13) were considered exposed to salmon farming, while chum from the Central Coast from Bute Channel to Seymour Inlet (SAs 8–11) were considered controls. Estimates were available as a single time series for the exposed area, and a time series for each SA for the controls. An index of recruits per spawner was generated by lining up returns with spawners according to age distributions given in Ryall et al. (1999) [50], to 1998, and then the average values from 1988–1998 for the subsequent years, to 2003.

Supporting Information

Figure S1. Survivals of Salmonids in Control (Black) and Exposed (Blue) Stocks, along with Aquaculture Production (Red)

The returns have been summarized by a multiplicative model ($\log\left(\frac{R_{i,y}}{S_{i,y}}\right) = a_i + d_y + e_{i,y}$); the mean survival across stocks for each year is plotted. Survivals for exposed Saint John River stocks have been multiplied by 10 for clarity (dashed line). Survival is estimated across different portions of the life cycle in different regions; from smolt to adult for Irish salmon and Newfoundland, from egg to adult for Bay of Fundy and Saint John River stocks, and from adult to adult in BC stocks.

Found at doi:10.1371/journal.pbio.0060033.sg001 (15 KB PDF).

Table S1. Results of Alternative Models for the Survival Analysis

Effect size estimates (y's) and their standard errors have been multiplied by 10^3, 10^4, or 10^8 (as labeled), to make numbers easier to read.

Found at doi:10.1371/journal.pbio.0060033.st001 (22 KB PDF).

Table S2. Results of Alternative Models for the Returns Analysis

Effect size estimates (y's) and their standard errors have been multiplied by 10^3, 10^4, or 10^8 (as labeled), to make numbers easier to read.

Found at doi:10.1371/journal.pbio.0060033.st002 (23 KB PDF).

Text S1. Alternative Model Formulations, Including the Bayesian Analysis

Found at doi:10.1371/journal.pbio.0060033.sd001 (58 KB PDF).

Acknowledgments

We thank W. Blanchard, J. Gibson, C. Herbinger, J. Hutchings, J. MacPherson, K. Mengersen, and R. Routledge for statistical assistance and comments and P. Amiro, G. Chaput, B. Dempson, D. Dobson, L. Godbout, J. Irvine, R. Jones, A. Morton, J. Sawada, P. VanWill, B. White, and C. Wood (Canada); E. Fahy, G. Forde, P. Gargan, C. Minto, and N. Ó Maoiléidigh (Ireland); J. MacLean (Scotland); P. Fiske, J. H. L'abée-Lund, and K. B. Rian (Norway), and J. Erkinaro (Finland) for assistance in obtaining and understanding data.

Author contributions. JSF and RAM conceived of and designed the project jointly. All writing and analyses were done by JSF, with

guidance from RAM, with the exception of the SAS code for performing the meta-analysis and the Bayesian section of the Text S1, which were written by RAM.

Funding. This work was supported by the Lenfest Ocean Program, the Census of Marine Life, and the Natural Sciences and Engineering Research Council of Canada.

Competing interests. The authors have declared that no competing interests exist.

References

1. ICES (2006) Report of the Working Group on North Atlantic Salmon (WGNAS),13 April 2006,ICES Headquarters. ICES CM 2006/ACFM: 23.
2. Krkošek M, Ford JS, Morton A, Lele S, Myers RA, et al. (2007) Declining wild salmon populations in relation to parasites from farm salmon. Science 318: 1772–1775.
3. Morton A, Routledge R, Peet C, Ladwig A (2003) Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada. Can J Fish Aquat Sci 61: 147–157.
4. Bjørn PA, Finstad B (2002) Salmon lice, *Lepeophtheirus salmonis* (Krøyer), infestation in sympatric populations of Arctic char, *Salvelinus alpinus* (L.), and sea trout, *Salmo trutta* (L.), in areas near and distant from salmon farms. ICES J Mar Sci 59: 131–139.
5. Gargan PG, Tully O, Poole WR (2003) Relationship between sea lice infestation, sea lice production and sea trout survival in Ireland, 1992–2001. In: Mills D, editor, Salmon at the edge, Oxford: Blackwell Science. pp. 119–135.
6. Johnsen BO, Jensen AJ (1994) The spread of furunculosis among salmonids in Norweigan rivers. J Fish Biol 45: 47–55.
7. ICES (2001) Report of the Working Group on North Atlantic Salmon (WGNAS). ICES Headquarters Copenhagen,3–13 April 2002.
8. Butler JRA, Watt J (2003) Assessing and managing the impacts of marine salmon farms on wild Atlantic salmon in western Scotland: identifying priority rivers for conservation. In: Mills D, editor, Salmon at the edge, Oxford: Blackwell Science. pp. 93–118.
9. McGinnity P, Prodöhl P, Ferguson A, Hynes R, Ó Maoiléidigh N, et al. (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proc R Soc Lond B Biol Sci 270: 2443–2450.
10. Weir LK, Hutchings JA, Fleming IA, Einum S (2004) Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, *Salmo salar*. J Anim Ecol 73: 1069–1079.
11. Hutchinson P, editor (2006) Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. Proceedings of an ICES/NASCO Symposium held in Bergen, Norway, 18–21 October 2005. ICES J Mar Sci 63:(7)
12. Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191. Ottawa: Department of the Environment, Fisheries and Marine Service.
13. Akaike H (1974) A new look at statistical model identification. IEEE Transactions on Automatic Control AU 19: 716–722.
14. Harvey B, MacDuffee M (2002) Ghost runs: the future of wild salmon on the north and central coasts of British Columbia. Victoria (British Columbia): Raincoast Conservation Society.
15. Mueter FJ, Peterman RM, Pyper BJ (2002) Opposite effects of ocean temperature on survival rates on 120 stocks of Pacific Salmon (*Oncorhynchus* spp.) in northern and southern areas. Can J Fish Aquat Sci 59: 456–482.
16. Sea Trout Review Group (2002) Report of the Sea Trout Review Group 2002, Ireland. 32 p.
17. Cefas and Environment Agency (2006) Salmon stocks and fisheries in England and Wales, 2006: Preliminary assessment prepared for ICES, April 2007.
18. Klemetsen A, Amundsen PA, Dempson JB, Jonsson B, Jonsson N, et al. (2003) Atlantic salmon *Salmo salar* (L.), brown trout *Salmo trutta* (L.) and arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecol Freshwater Fish 12: 1–59.
19. Myers RA, Bowen KG, Barrowman NJ (1999) Maximum reproductive rate of fish at low population sizes. Can J Fish Aquat Sci 56: 2404–2419.
20. Myers RA, Mertz G, Bridson J (1997) Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Can J Fish Aquat Sci 54: 1400–1407.
21. Directorate for Nature Management (2004) The Atlantic wild salmon is threatened. Available at: http://english.dirnat.no/archive/images/01/12/salmo042.pdf. Accessed 9 January 2008.
22. Fiske P, Lund RA, Østborg GM, Fløystad L (2001) Escapees of reared salmon in coastal and riverine fisheries in the period 1989–2000. NINA Oppdragsmelding 704: 1–26.
23. Hesthagen T, Hansen LP (1991) Estimates of the annual loss of Atlantic salmon, *Salmo salar*, in Norway due to acidification. Aquac Fish Manage 22: 85–91.
24. Heggberget TG, Johnsen BO, Hindar K, Jonsson B, Hansen LP, et al. (1993) Interactions between wild and cultured Atlantic salmon: a review of the Norweigan experience. Fish Res 18: 123–146.
25. O'Donohoe P, Kennedy S, Copley L, Kane F, Naughton O, et al. (2003) National survey of sea lice *Lepeophtheirus salmonis Krøyer* and *Caligus elongates Nordmann* on fish farms in Ireland - 2002. Marine Institute Fishery Leaflet 183, 2003.
26. Russell IC, Ives MJ, Potter ECE, Buckley AA, Duckett L (1995) Salmon and migratory trout statistics for England and Wales 1951–1990. Fish Res Data Report No 38, 252 p.
27. Environment Agency (2005) Salmonid and freshwater fisheries statistics for England and Wales, 2004.
28. ICES (2005) Report of the Working Group on North Atlantic Salmon (WGNAS), 5–14 April 2005,Nuuk, Greenland. ICES CM 2005/ACFM:17.
29. Thorley JL, Eatherley DMR, Stephen AB, Simpson I, MacLean JC, et al. (2005) Congruence between automatic fish counter data and rod catches of Atlantic salmon *Salmo salar* in Scottish rivers. ICES J Mar Sci 62: 809–817.
30. Holst JC, Shelton R, Holm M, Hansen LP (2000) Distribution and possible migration routes of post-smolt Atlantic salmon in the Northeast Atlantic. In: Mills D, editor, The ocean life of Atlantic salmon: environmental and biological factors influencing survival, Oxford: Blackwell Science. pp. 65–73.
31. O'Connell MF, Dempson JB, Reddin DG, Bourgeois CE, Porter TR, et al. (2005) Status of Atlantic salmon (*Salmo salar* L.) stocks of insular Newfoundland (SFAs 3–14A), 2004. DFO CSAS Res Doc 2005/064.
32. DFO Statistical Services (2006) Aquaculture production statistics for Canada. Available at: http://www.dfo-mpo.gc.ca/communic/statistics/aqua/index_e.htm. Accessed 14 January 2008.
33. Mullins CC, Bourgeois CE, Porter TR (2003) Opening up new habitat: Atlantic salmon (*Salmo salar* L.) enhancement in Newfoundland. In: Mills D, editor, Salmon at the edge. Oxford: Blackwell Science. pp. 200–221.
34. Reddin DG (1985) Ocean life of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic. In: Mills D, Piggins D, editors, Atlantic salmon: planning for the future. Portland (Oregon): Timber Press. pp. 483–507.
35. Gibson AJF, Jones RA, Amiro PG, Flanagan JJ (2003) Abundance of Atlantic salmon (*Salmo salar*) in the Big Salmon River, NB, from 1951 to 2002. DFO CSAS Res Doc 2003/119.
36. Gibson AJF, Amiro PG (2003) Abundance of Atlantic salmon (*Salmo salar*) in the Stewiacke River, NS, from 1965 to 2002. DFO CSAS Res Doc 2003/108.
37. Jones RA, Anderson L, Goff T (2004) Assessments of Atlantic salmon stocks in southwest New Brunswick, an update to 2003. DFO CSAS Res Doc 200/019.
38. Chaput G, Prévost E (1999) Annual and decadal change in Atlantic salmon (*Salmo salar*) abundance in eastern Canada. DFO CSAS Res Doc 1999/30.
39. DFO (2003) Atlantic salmon Maritime Provinces overview for 2002. DFO Science SSR 2003/026.
40. Chaput G, Moore D, Hayward J, Sheasgreen J, Dubee B (2001) Stock status of Atlantic salmon (*Salmo salar*) in the Miramichi River, 2000. DFO CSAS Res Doc 2001/008.
41. Lacriox GL, McCurdy P, Knox D (2004) Migration of Atlantic salmon in relation to habitat use in a coastal system. Trans Am Fish Soc 133: 1455–1471.
42. Jessop BM (1976) Distribution and timing of tag recoveries from native and non-native Atlantic salmon (*Salmo salar*) released into the Big Salmon River, New Brunswick. J Fish Res Board Can 33: 829–833.
43. Lacriox GL, Knox D (2005) Distribution of Atlantic salmon (*Salmo salar*) post-smolts of different origins in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth, and survival. Can J Fish Aquat Sci 56162: 1363–1376.
44. Chase S (2003) Closing the North American mixed-stock commercial fishery for wild Atlantic salmon. In: Mills D, editor, Salmon at the edge. Oxford: Blackwell Science. pp. 84–92.
45. Groot C, Margolis L (1991) Pacific salmon life histories. Vancouver (British Columbia): UBC Press.
46. Simpson K, Chamberlain M, Fagan J, Tanasichuk RW, Dobson D (2004) Forecast for southern British Columbia coho salmon in 2004. DFO CSAS Res Doc 2004/135.
47. Wood C, Rutherford D, Jantz L (1999) Trends in abundance and 1999 stock size forecasts for major sockeye, chum and pink salmon stocks in Northern British Columbia. DFO CSAS Res Doc 1999/126.
48. DFO (2006) Salmon catch statistics. Available at: http://www.pac.dfo-mpo.gc.ca/sci/sa/Commercial/default_e.htm. Accessed 9 January 2008.
49. Godbout L, Irvine JR, Bailey D, Will PV, McConnell C (2004) Stock status of wild chum salmon (*Oncorhynchus keta Walbaum*) returning to British Columbia's Central Coast and Johnstone and Georgia Straits (excluding the Fraser River). DFO CSAS Res Doc 2004/007.
50. Ryall P, Murray C, Palermo V, Bailey D, Chen D (1999) Status of clockwork chum salmon stock and review of the clockwork management strategy. DFO CSAS Res Doc 1999/169.

Received: 24 June 2016 | Accepted: 25 January 2017

DOI: 10.1111/faf.12214

ORIGINAL ARTICLE

WILEY FISH and FISHERIES

Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions

Kevin A Glover[1,2] | Monica F Solberg[1] | Phil McGinnity[3,4] | Kjetil Hindar[5] | Eric Verspoor[6] | Mark W Coulson[6] | Michael M Hansen[1,7] | Hitoshi Araki[8] | Øystein Skaala[1] | Terje Svåsand[1]

[1]Institute of Marine Research, Nordnes, Bergen, Norway

[2]Institute of Biology, University of Bergen, Bergen, Norway

[3]School of Biological, Earth & Environmental Sciences, University College Cork, Cork, Ireland

[4]Marine Institute, Furnace, Newport, Co. Mayo, Ireland

[5]Norwegian Institute for Nature Research (NINA), Trondheim, Norway

[6]Rivers and Lochs Institute, University of the Highlands and Islands, Inverness College, Inverness, UK

[7]Department of Bioscience, Aarhus University, Aarhus C, Denmark

[8]Research Faculty of Agriculture, Hokkaido University, Sapporo, Japan

Correspondence
Kevin A Glover, Institute of Marine Research, Nordnes, Bergen, Norway.
Email: kevin.glover@imr.no

Funding information
Research Council of Norway (RCN), Grant/Award Number: 200510 and 216105; Norwegian Ministry for Trade and Fisheries (NFD); JSPS KAKENHI, Grant/Award Number: JP26292102; Danish Council for Independent Research; Natural Sciences, Grant/Award Number: 1323-00158A; Beaufort Marine Research Award; Irish Government

Abstract

Atlantic salmon (*Salmo salar*) is one of the best researched fishes, and its aquaculture plays a global role in the blue revolution. However, since the 1970s, tens of millions of farmed salmon have escaped into the wild. We review current knowledge of genetic interactions and identify the unanswered questions. Native salmon populations are typically genetically distinct from each other and potentially locally adapted. Farmed salmon represent a limited number of wild source populations that have been exposed to ≥12 generations of domestication. Consequently, farmed and wild salmon differ in many traits including molecular-genetic polymorphisms, growth, morphology, life history, behaviour, physiology and gene transcription. Field experiments have demonstrated that the offspring of farmed salmon display lower lifetime fitness in the wild than wild salmon and that following introgression, there is a reduced production of genetically wild salmon and, potentially, of total salmon production. It is a formidable task to estimate introgression of farmed salmon in wild populations where they are not exotic. New methods have revealed introgression in half of ~150 Norwegian populations, with point estimates as high as 47%, and an unweighted average of 6.4% across 109 populations. Outside Norway, introgression remains unquantified, and in all regions, biological changes and the mechanisms driving population-specific impacts remain poorly documented. Nevertheless, existing knowledge shows that the long-term consequences of introgression is expected to lead to changes in life-history traits, reduced population productivity and decreased resilience to future challenges. Only a major reduction in the number of escapees and/or sterility of farmed salmon can eliminate further impacts.

KEYWORDS
aquaculture, evolution, fish farming, fitness, genetic, hybrid

1 | INTRODUCTION

Natural resources are increasingly exposed to anthropogenic pressures that compromise or threaten their persistence. The Millennium Ecosystem Assessment (Anon 2005) identified five major threats to native plants and animals: habitat change, climate change, invasive species, over-exploitation and pollution. Not included on this list, but an increasing problem, is the interaction between wild populations and their domesticated conspecifics (Hindar, Ryman, & Utter, 1991; Hutchings & Fraser, 2008; Laikre, Schwartz, Waples, Ryman, & Ge, 2010; Randi, 2008). While not fitting exactly into one of the Millennium Assessment categories, it is related to the type of challenges posed by invasive species and problems that stem from over-exploiting wild populations. Furthermore, many of these stressors can interact with each other to exacerbate the negative impact of a single cause, for example the combined impact of the release of captive-bred fish and climate change on recipient wild populations (McGinnity et al., 2009).

As exploitation of wild living resources becomes increasingly unsustainable (Hutchings, 2000; Myers & Worm, 2003), domestication and captive production of the same species intuitively represents an obvious alternative (Teletchea & Fontaine, 2014). However, when selective breeding programmes are undertaken, and releases or escapes occur into the wild, there is potential for direct negative genetic impacts on wild populations from gene flow. This problem has been acknowledged for a long time in a variety of organisms (Ellstrand, Prentice, & Hancock, 1999; Randi, 2008), but has been found to be particularly serious in fishes, where harvesting wild populations is replaced by large-scale aquaculture production, as in salmonids. Salmonids represent a continuum of both the quantity and technological concerns associated with their production (Lorenzen, Beveridge, & Mangel, 2012).

At one end of the scale, wild populations may be deliberately supplemented by stocking hatchery-reared offspring of local or exogenous origin that have only been briefly exposed to the cultured environment; this procedure is particularly applied in North America, where hatcheries located on individual rivers are used for propagating offspring of returning spawners (Kostow, 2009). At the other end of the scale, wild populations may be accidently exposed to escapees from farming operations where the fish are non-local, and have been subject to all aspects of domestication, including directional selection for economically important traits. As selection programmes increasingly cause genetic divergence between captive and wild populations for biologically important traits, then the potential for negative genetic consequences of interbreeding between wild and farmed fish also increases until their fitness in the wild becomes severely compromised (Baskett, Burgess, & Waples, 2013; Huisman & Tufto, 2012). In Atlantic salmon (*Salmo salar*, Salmonidae) (hereon referred to as salmon), these issues have been so pervasive that it has emerged as a major model for studying genetic interactions between farmed and wild organisms.

The commercial production of salmon for human consumption first started in the late 1960s in Norway when smolts were placed into sea cages by the company Mowi A/S in Bergen in 1969 and by the Grøntvedt brothers on Hitra in 1970 (Gjedrem, 2010; Gjedrem, Gjoen, & Gjerde, 1991). Since the pioneering days in the early 1970s, rapid and almost continual growth has meant that this industry has now achieved status as one of the world's most economically important industries within the fisheries and aquaculture sectors (Bostock et al., 2010). In 2014, global production of salmon exceeded 2.3 million tons with Norway (1.26 million tons), Chile (0.62 million tons) and the UK (0.165 million tons) representing the primary producers (FAO 2016) (Figure 1). In total, 10 countries produced more than 10,000 tons in 2014.

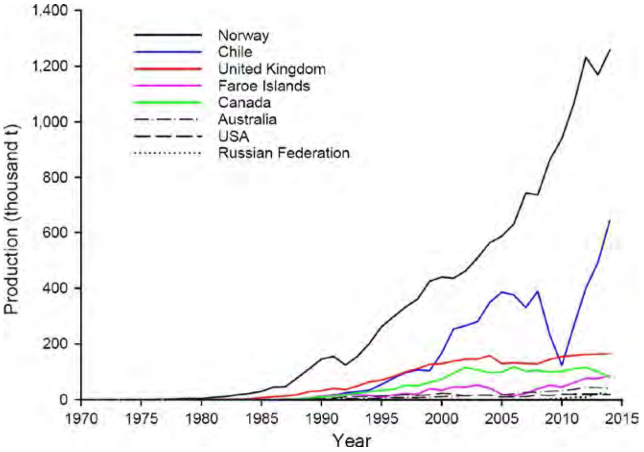


FIGURE 1 Aquaculture production of Atlantic salmon based on the eight largest global producers in 2015

Globally, the production of farmed salmon was rated as number eight by amount for aquaculture fish species, and was by far, the most valuable cultured fish species in 2014 (14.6 billion USD (FAO 2016)). Today, more than 99% of all salmon consumption arises from aquaculture production, and the reported wild catch is as low as 1/1000 of the reported aquaculture production (FAO 2016). As a form of food production, aquaculture is being increasingly considered as one solution to the world's growing demand for protein (FAO 2016), although not all share this optimism (Bovenkerk & Meijboom, 2012; Merino et al., 2012). Nevertheless, commercial aquaculture, including salmon farming, continues to expand globally.

The phenomenal expansion of the salmon aquaculture industry has not occurred without meeting a diverse array of sustainability-related challenges along the way. Farmed escapees may result in both ecological (Jonsson & Jonsson, 2006; Thorstad et al., 2008) and genetic interactions with wild populations (Ferguson et al., 2007; Hindar et al., 1991). In addition, impacts may extend beyond problems with direct biological impacts, including socio-economic (Liu, Olaussen, & Skonhoft, 2011) and general ethical issues (Olesen, Myhr, & Rosendal, 2011), use of marine resources such as fish oil and fish meal for production of high protein feeds (Naylor et al., 2000; Torrissen et al., 2011), general effects on local ecosystems (Buschmann et al., 2006), benthic community impacts (Kutti, Ervik, & Hoisaeter, 2008), use of chemical agents such as antibiotics and antiparasitical agents (Burridge, Weis, Cabello, Pizarro, & Bostick, 2008) and transfer of parasites to native populations (Krkosek, Lewis, & Volpe, 2005; Torrissen et al., 2013).

Many of these factors, individually or collectively, have potentially important consequences for the persistence of wild salmonid populations. In a meta-analysis of available data, a reduction in marine survival of a range of salmonid species in regions of intense salmon farming activity was observed throughout the Pacific and Atlantic basins (Ford & Myers, 2008). Although the range of challenges linked with salmon aquaculture are diverse, an annual risk assessment of Norwegian salmon aquaculture identified inadvertent accumulation of sea lice from fish farms and genetic interactions with farmed escapees as the two primary challenges to the sustainable development of the salmon aquaculture industry in Norway (Taranger et al., 2015).

Salmon farming typically involves hatching eggs and rearing juveniles in land-based incubators and tanks during the freshwater stage of the life cycle, then transferring smolts to sea cages in sheltered coastal areas where they are reared until market size and thereafter slaughtered. The production cycle takes 2.5–3 years. While significant advances in robustness of production systems have taken place, technical and operational failures nevertheless occur and are the primary reason for incidences of escapes (reviewed by Jensen, Dempster, Thorstad, Uglem, & Fredheim, 2010). Each year, hundreds of thousands of farmed salmon escape into the wild. Some of these escapees find their way onto the spawning grounds of native populations (Carr & Whoriskey, 2006; Fiske, Lund, & Hansen, 2006; Walker, Beveridge, Crozier, Maoileidigh, & Milner, 2006) and partake in spawning (Carr, Anderson, Whoriskey, & Dilworth, 1997; Lura & Saegrov, 1991; Webb et al., 1993), with the possibility of gene flow from farmed to wild populations.

The fact that large numbers of farmed escapees have been observed on the spawning grounds of some native populations has generated widespread concerns regarding the consequences this may have for the short-term fitness and long-term evolutionary capacity of recipient populations. Several earlier review and synthesis articles have broadly addressed this topic (Ferguson et al., 2007; Heggberget, Johnsen et al., 1993; Hindar et al., 1991; Naylor et al., 2005; Thorstad et al., 2008). Scientific reviews have also been conducted on overlapping topics such as the potential for salmon populations to display adaptations to their natal rivers in a process known as local adaptation (Fraser, Weir, Bernatchez, Hansen, & Taylor, 2011; Garcia de Leaniz et al., 2007; Taylor, 1991), and the potential responses of populations to fisheries and farming induced evolution (Hutchings & Fraser, 2008). In addition, the fitness of hatchery fish produced for deliberate introduction into the wild via supportive breeding has been reviewed (Araki & Schmid, 2010; Araki, Berejikian, Ford, & Blouin, 2008).

There are key differences in the potential for genetic interaction and likely consequences for wild populations, between when the latter are supplemented by deliberate supportive breeding programmes using native broodstock collected from the wild, or when exposed to accidental releases into the wild of non-local, domesticated farmed escapees. The last decade has seen both a rise in concern regarding the direct genetic impacts of farmed escapees and a large number of new studies bearing on this issue, and there is an urgent need to review current understanding. This is amplified by the development of aquaculture production of other species, which also involves potential genetic interactions with wild conspecifics (Glover, Dahle, & Jorstad, 2011; Somarakis, Pavlidis, Saapoglou, Tsigenopoulos, & Dempster, 2013; Varne et al., 2015).

The salmon is viewed as the model system for understanding direct genetic interactions between domesticated and wild fish stocks (Bekkevold, Hansen, & Nielsen, 2006). Given the many years since salmon farming was initiated, it is pertinent to ask several questions regarding the introgression of farmed salmon into native populations. In particular, what do we know, what we do not know, and what should we know? Here, we provide a comprehensive review of the literature dedicated to this topic and discuss the extent and patterns of introgression, in addition to the short- and long-term evolutionary consequences in recipient populations. We concentrate on direct (i.e. interbreeding) as opposed to indirect genetic effects. Finally, we highlight what the major breakthroughs have been in this field of research in the past decade, and what unanswered questions remain.

2 | ECOLOGY PRECEDING INTROGRESSION

2.1 | How many escapees are there in the wild?

So long as facilities are not fully contained, the escape of farmed fish into the wild is inevitable (Bentsen & Thodesen, 2005; Jensen et al., 2010). While the number of escapees has declined over time as a proportion of the number of salmon in farms, it has remained high as production has expanded (Figures 1 and 2). Salmon production is typically based on the following stages: eggs and fry (~3–4 months); juveniles (~6–12 months); post-smolt/adults (~18–24 months) (Wall, 2011). Each of these stages represents different risks of escape that can be expected to vary from farm to farm and region to region.

Most egg and early-juvenile production is conducted in land-based hatcheries. While escapes at this stage have been typically few, the technological shift towards recirculating systems means that only a very low number of salmon escape into the wild at this stage. Thereafter, several approaches have and continue to be used for juvenile and smolt production. Often, fry are reared to the smolt stage in tanks using flow through systems. Escapes of juveniles from such systems may occur. More recently, there has been an increase in the use of tank recirculating systems, which practically eliminates juvenile escapes into the wild. Alternatively, once large enough, juveniles are transferred to open freshwater pens similar to those used to rear post-smolts in salt water but with finer mesh sizes. This approach, rarely used in Norway and Canada, was used extensively in Chile but is now being phased out in support of disease control (Alvial et al., 2012). In contrast, in Scotland, 42 freshwater pen rearing sites underpin the annual production of smolts to the order of half of all fish produced (~20 million) (Franklin, Verspoor, & Slaski, 2012). These cages, like the ones used for on-growing of post-smolts to adults in the sea, offer the greatest opportunities for escape as there is only a net barrier between the fish and the wild.

Escapes of salmon have been documented during the freshwater stage as juveniles, both from hatcheries (Carr & Whoriskey, 2006; Clifford, McGinnity, & Ferguson, 1998a; Stokesbury & Lacroix, 1997) and from freshwater cages (Coulson, 2013; Franklin et al., 2012; Verspoor, Knox, & Marshall, 2016). These escapees may compete directly with wild juveniles for resources (Jonsson & Jonsson, 2006; Thorstad et al., 2008). A portion of the juvenile males that survive can mature precociously and may potentially spawn with wild fish. Juvenile escapees of both sexes that survive may also migrate to sea and return as adults (Lacroix & Stokesbury, 2004) and attempt to spawn with wild fish as mature adults. Detection of returning freshwater escapes, at least on the basis of superficial morphological characteristics (Lund & Hansen, 1991), is expected to be difficult as they are unlikely to have some of the more obvious diagnostic features of older farmed fish, such as eroded fins or clumped body shape. Escapes of post-smolts and adults from marine cages occur extensively (Crozier, 1993; Glover, 2010) and typically dominate escapees in the wild (although this is region dependent). However, escapees from marine cages first need to migrate back to freshwater before they can potentially spawn and interbreed with native populations.

Official statistics for the reported numbers of escapees are publicly available in some of the regions where salmon farming is practiced, for example Norway and Scotland (Figure 2). These statistics are based on reports by the farmers themselves and, for several reasons discussed below, are likely to underestimate, significantly in some circumstances, the actual number of fish escaping from farms. In support of this claim, DNA methods to identify escapees back to the farm of origin have been successfully implemented in multiple cases of unreported escapes in Norway (Glover, 2010; Glover, Skilbrei, & Skaala, 2008). Similarly, in Scotland, freshwater escapes identified through vaccination marks were not part of a reported escape event (Franklin et al., 2012). Additionally, there is a lack of correlation between the incidence of farmed escapees in Norwegian rivers and the reported numbers of escapees, while in contrast, there is a correlation between the standing stock of fish in farms and incidence of farmed salmon escapees in Norwegian rivers (Fiske et al., 2006). Finally, a recent meta-analysis of catch statistics and tagging studies has estimated that the real numbers of escapees in Norway were 2–4 times higher than the numbers reported by the farmers alone in the period 2005–2011 (Skilbrei, Heino, & Svåsand, 2015). In other countries, the level of underestimation in escape statistics is unknown.

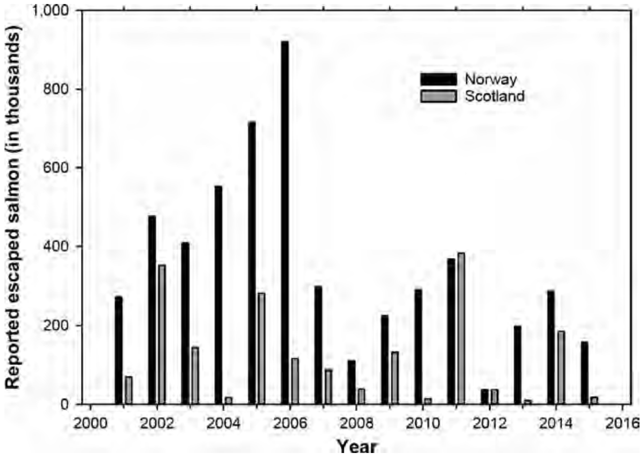


FIGURE 2 Reported numbers of farmed escaped Atlantic salmon in Scotland www.aquaculture.scotland.gov.uk and Norway www.fiskeridir.no in the period 2001 to 2015. Triploid salmon constituted ~54 000 of the 157 000 reported escaped salmon in Norway in 2015, although such statistics are not available for other years. A recent analysis estimated that the correct number of farmed salmon escaping from Norwegian farms in the period 2005–2011 was 2–4 times higher than the official statistics (Skilbrei, Heino et al., 2015)

An analysis of available data from Norway indicates that less than 20% of escape incidents account for more than 90% of the number of reported escapees (Jensen et al., 2010). Despite the fact that large escape events account for a large number of escapees, drip leakage (i.e. multiple small-scale losses usually associated with routine daily activities on farms) may be more important than indicated by the official escapes statistics, considering the under-reporting of farmed salmon escaping as smolts (Skilbrei, Heino et al., 2015).

Each year, hundreds of thousands of escapees are reported from salmon farms across its production range (Figure 2). Given that these statistics are underestimates, it can be reasonably assumed that millions of farmed salmon escape into the wild yearly. In Norway, which produces approximately 50% of all farmed salmon globally, the estimated number of salmon escaping annually from commercial fish farms has probably been in the millions in the period 2005–2011 (Skilbrei, Heino et al., 2015). Put into perspective, the estimated number of wild adult salmon returning to the Norwegian coastline to spawn (i.e. pre-fishery abundance) each year in the period 1983–2014 declined from ~1 million in the mid-1980s to ~0.5 million during the last few years (Anon 2015b). Therefore, in Norway, the only area where data allow such an assessment, the number of salmon escaping from farms is probably in excess of the number wild adult salmon returning to rivers in most years.

The potential for farmed salmon to display genetic interaction with wild salmon will depend on their behaviour after escape. The movements of farmed salmon escapees have been extensively studied in the marine environment (Hansen, 2006; Jensen et al., 2013; Skilbrei & Wennevik, 2006; Skilbrei, Holst, Asplin, & Holm, 2009; Skilbrei, Holst, Asplin, & Mortensen, 2010; Solem et al., 2013; Whoriskey, Brooking, Doucette, Tinker, & Carr, 2006; Zhang et al., 2013) as well as in freshwater (Butler, Cunningham, & Starr, 2005; Carr, Lacroix, Anderson, & Dilworth, 1997; Heggberget, Okland, & Ugedal, 1993; Moe et al., 2016; Okland, Heggberget, & Jonsson, 1995; Thorstad, Heggberget, & Okland, 1998; Webb, Hay, Cunningham, & Youngson, 1991). Available evidence suggests that most escapees from marine cages disappear in the sea and do not return to freshwater (Hansen, 2006; Skilbrei, 2010; Whoriskey et al., 2006). Observation of the empty stomachs in farmed escapees captured in coastal areas (Abrantes, Lyle, Nichols, & Semmens, 2011; Hislop & Webb, 1992), in combination with the lack of change in fatty acid profile in escapees over time (Olsen & Skilbrei, 2010), suggests that escapees from marine cages often struggle to adapt to feeding on natural food items once they are in the sea. In some regions, seal predation is also suspected to cause mortality of the escapees (Whoriskey et al., 2006). While the evidence indicates that survival to sexual maturity of feral escapes is very low, and only a small proportion of escapees manage to survive and enter rivers, the number is often numerically high due simply to the high number of escapees. The actual numbers, however, can be expected to be dependent on both the stage of the life cycle and the time of the year at which they escape (reviewed by Skilbrei, Heino et al., 2015).

An overview of the methods used to identify farmed escapees is given in Thorstad et al. (2008). In short, escapees are typically identified based on external morphological divergence from wild salmon (e.g. body condition and fin erosion). In Norway, identification of farmed escapees is generally validated by reading scales (Fiske et al., 2006; Lund & Hansen, 1991) and in some cases intra-abdominal adhesions caused by vaccination marks (Lund, Midtlyng, & Hansen, 1997). The relative frequency of adult farmed salmon entering rivers that have escaped into the sea early as opposed to later in the life cycle is variable. Reading fish scales provides an opportunity to identify the stage at which the salmon escaped from a farm (Thorstad et al., 2008). Also, recent developments in fatty acid profiling now make it possible to identify early (those salmon having been in the wild for some time, a year or more before entry to freshwater) as opposed to late (those having recently escaped, and certainly the same year in which they entered the river) escapees accurately (Skilbrei, Normann, Meier, & Olsen, 2015). This method is based on the fact that farmed salmon are fed a diet including a high concentration of terrestrial lipids that are high in medium chain polyunsaturated fatty acids (PUFAs) such as 18:2n-6 (Olsen, Taranger, Svasand, & Skilbrei, 2013) and that its concentration decreases with time after escape (Skilbrei, Normann et al., 2015). Studies using this and other approaches have shown that one half or more of escapees entering freshwater have escaped from farms in the same year that they entered freshwater (Madhun et al., 2015; Quintela et al., 2016; Skilbrei, Normann et al., 2015).

Farmed escapees have been documented in rivers in most regions where there is commercial aquaculture; Norway (Fiske et al., 2006; Fiske, Lund, Østborg, & Fløystad, 2001; Gausen & Moen, 1991; Lund, Okland, & Hansen, 1991; Okland et al., 1995), the Finnish region of the River Teno (Tana in Norwegian) that flows out in Norway (Erkinaro et al., 2010), the UK including Northern Ireland (Butler et al., 2005; Crozier, 1998; Milner & Evans, 2003; Walker et al., 2006; Webb et al., 1991), Ireland (Clifford, McGinnity, & Ferguson, 1998b), Atlantic North America (Carr, Anderson et al., 1997; Lacroix & Stokesbury, 2004; Morris et al., 2008; O'Reilly, Carr, Whoriskey, & Verspoor, 2006; Stokesbury & Lacroix, 1997; Stokesbury, Lacroix, Price, Knox, & Dadswell, 2001; Utter & Epifanio, 2002), Pacific North America (Fisher, Volpe, & Fisher, 2014; Volpe, Taylor, Rimmer, & Glickman, 2000), Chile (Sepulveda, Arismendi, Soto, Jara, & Farias, 2013) and Australia (Abrantes et al., 2011). In addition, escapees have been reported in oceanic feeding areas (Hansen & Jacobsen, 2003; Hansen, Reddin, & Lund, 1997; Jensen et al., 2013), as well as in rivers far away from major farming regions (Gudjonsson, 1991; Piccolo & Orlikowska, 2012). Therefore, escapees display considerable potential for long-distance dispersal/migration. That said, in Norway, the incidence of farmed escaped salmon in rivers is correlated with the volume of farming within that region (Fiske et al., 2006), and, in Scotland, lower numbers of escapees occur in rivers on the east coast, where there are no marine salmon farms, than on the west coast where farming occurs (Green et al., 2012; Youngson, Webb, MacLean, & Whyte, 1997). Specifically for juvenile escapes, there is a close link between their presence in rivers and nearby hatcheries (Carr & Whoriskey, 2006; Clifford et al., 1998a) or freshwater cages (Verspoor et al., 2016).

A Norwegian study based on reading fish scales from summer angling surveys, as well as dedicated autumn angling surveys, in the period 1989–2004 reported weighted mean annual per cent of farmed salmon in a cross section of rivers between approximately 0%–6% and 2%–30% for the two survey types, respectively (unweighted averages were 2%–12% summer, 9%–32% autumn) (Fiske et al., 2006). A new monitoring programme for escapees was established in Norway in 2014, and based on data from several survey methods (summer angling, autumn angling, autumn snorkelling), 30 of the 140 rivers surveyed in 2014, and 17 of 165 rivers surveyed in 2015 displayed an observed frequency of >10% escapees (Anon 2015a, 2016). This gave unweighted averages for summer angling surveys of 5.4% and 3.4% and dedicated autumn angling surveys of 11.2% and 9.1%, in 2014 and 2015, respectively. These numbers are similar to those reported for straying rates of wild and hatchery-produced salmon (Stabell, 1984).

In regions outside Norway, such as the UK and Ireland, catch statistics have also revealed significant numbers of farmed escapees in the rivers (Walker et al., 2006), but in many cases, less than the numbers typically observed in Norway. For example, an analysis of all available data for rivers in Scotland in the period 1991–2004 (or as sampling data allowed), illustrated that the per cent of farmed salmon were typically less than 1% for many rivers and years, although exceptions as high as 10% were observed. Whether these differences to the frequencies observed in Norway are meaningful, however, is uncertain, as methods used for the enumeration of farmed fish in Scottish rivers is often based on morphology without validation using scale analysis. In Northern Ireland, large numbers of escapees have been observed in single rivers in years following single large-scale escape events (Crozier, 1993), and this is also the case in other countries where single events have resulted in large number of escapees in some rivers in some years. In many rivers in Atlantic North America, the numbers of juvenile escapees have been periodically very high, and in some rivers in some years (many years in some cases), farmed escaped juveniles have even outnumbered wild juveniles (Carr & Whoriskey, 2006; Stokesbury & Lacroix, 1997; Stokesbury et al., 2001). There have been significant numbers of adult escapees found in the same rivers (Carr, Anderson et al., 1997).

2.2 | Do farmed escapees spawn in the wild?

While frequency varies in time and space, not all farmed salmon that escape from sea cages and thereafter enter rivers are sexually mature (Carr, Lacroix et al., 1997; Lacroix, Galloway, Knox, & MacLatchy, 1997; Madhun et al., 2015). Escapees may also ascend rivers outside the normal migratory times for wild salmon and even outside the spawning period. Indeed, triploid escapees, which are sterile, may enter freshwater albeit at a considerably reduced frequency compared to diploid escapees (Glover et al., 2015, 2016). In addition, not all male juveniles escaping to freshwater will become sexually mature as parr, especially because the tendency for parr maturation in farmed strains is lower than in wild populations (Debes & Hutchings, 2014; Einum & Fleming, 1997; Morris, Fraser, Eddington, & Hutchings, 2011; Yates, Debes, Fraser, & Hutchings, 2015). Therefore, not all escapees found in rivers will reproduce and hybridize with native fish.

Data from early surveys conducted in Norway revealed unweighted annual average maturation of escapes captured in rivers as 91.9% (range 77%–100% over the 12 years) and 86.8% (range 64%–100%) for males and females, respectively (Fiske et al., 2001). Also, in a recent study conducted in the River Namsen, middle Norway, most of the escapees entering the river were mature or maturing (Moe et al., 2016). In contrast, all of 29 small (0.4 kg) escapees captured in the River Steinsdalselva in western Norway in 2012 were immature (Madhun et al., 2015), and observations of large numbers of immature adults have been reported in rivers in Canada (Carr, Lacroix et al., 1997; Lacroix et al., 1997). Additionally, maturation status may differ between escapees captured in the very low reaches of rivers and river mouths, and further up in the system where spawning grounds typically occur. Despite the clear implications for patterns of introgression, maturation status, location of capture in the river and the life stage of escape are often poorly documented in monitoring programmes (Anon 2016).

Spawning of adult escapees has been reported in rivers in Scotland (Butler et al., 2005; Webb et al., 1991, 1993), Norway (Lura & Saegrov, 1991; Lura, Barlaup, & Saegrov, 1993; Saegrov, Hindar, Kalas, & Lura, 1997) Canada (Carr, Anderson et al., 1997) and outside the species' native range on the Pacific coast of North America (Volpe et al., 2000). These reports are based on visual observations and/or the analysis of diagnostic pigmentation in eggs that is derived from the commercial diet of the farmed fish, which not only permits validation of successful spawning but, also its quantification. In the River Vosso in western Norway for example, an estimated 81% of the redds dug in the autumn of 1995 were by farmed escaped females (Saegrov et al., 1997). In a study conducted across 16 rivers in the west and north of Scotland in 1991, farmed females were documented to spawn in 14 rivers with a mean of 5.1% of juveniles originating from farmed females (Webb et al., 1993). In the Magaguadavic River in Canada, from a total of 20 redds sampled in 1993, a minimum of 20% of the eggs deposited were from farmed females (Carr, Anderson et al., 1997).

On average, the relative spawning success of adult farmed salmon escapees is significantly lower than for wild salmon (Fleming et al., 2000; Fleming, Jonsson, Gross, & Lamberg, 1996; Weir, Hutchings, Fleming, & Einum, 2004). Based on studies conducted in seminatural spawning arenas, estimates of the spawning success of farmed escapees, in comparison with wild salmon, are ~1%–3% for males and ~30% for females, respectively (Fleming et al., 1996), although their relative success may vary and be case specific (Fleming et al., 1996, 2000; Weir et al., 2004). For example, adult farmed males attained a high of 24% success in the spawning arenas in Ims (Fleming et al., 2000). Comparative spawning studies between wild and farmed salmon have also been conducted in the wild, supporting the conclusion that farmed escapees are inferior competitors (Fleming et al., 2000). Studies have also shown that the relative spawning success of adult farmed escapees probably varies considerably with the life stage at which the fish escaped (Fleming, Lamberg, & Jonsson, 1997; Weir et al., 2004). It is likely that recently escaped adults that have compromised fin quality, body shape and swimming performance, are unlikely to compete as well as farmed salmon that have escaped in freshwater as juveniles or smolts, or post-smolts early in the marine rearing phase that have had the opportunity to develop a more wild-type body shape and behaviours during their longer exposure to natural conditions.

There are two highly significant implications from the results of the spawning studies. First, they imply that if there are 10% adult farmed escapees on the spawning grounds, their genetic contribution is likely to be significantly lower than 10% (although this will vary in time and space). Second, large and consistent differences in success between the sexes strongly indicate that the clear majority of the genetic contribution is likely to be from farmed females spawning with wild males, thus producing hybrids.

While farmed escapees may successfully spawn in the same areas of rivers as wild fish (Butler et al., 2005), studies have shown that adult farmed escapees do not necessarily use the same regions of a river during the spawning season as wild fish (Moe et al., 2016; Okland et al., 1995; Thorstad et al., 1998). Furthermore, in the absence of significant migration barriers such as large waterfalls, farmed escapees have a tendency to migrate to the upper reaches of rivers (Moe et al., 2016; Thorstad et al., 1998). In addition to area use differences, the timing of farmed salmon spawning may not be synchronized with the native population (Fleming et al., 2000; Moe et al., 2016; Saegrov et al., 1997; Webb et al., 1991). Variations in "time and space," in addition to the documented competitive inferiority of farmed escapees under spawning, may contribute to a partial or total miss-match of spawning relative to wild salmon under certain conditions and thereafter influence patterns of introgression and offspring survival.

The spawning success of escaped male farmed parr in the wild has not been investigated. However, wild male parr contribute significantly to breeding in native populations (Herbinger, O'Reilly, & Verspoor, 2006; Johnstone, O'Connell, Palstra, & Ruzzante, 2013; Taggart, McLaren, Hay, Webb, & Youngson, 2001), and in experimental studies, farmed male parr have been documented to successfully compete for and spawn with wild salmon (Garant, Fleming, Einum, & Bernatchez, 2003; Weir, Hutchings, Fleming, & Einum, 2005). Therefore, it is likely that they contribute to introgression, especially in rivers where large numbers of escaped juveniles occur (Carr & Whoriskey, 2006; Stokesbury & Lacroix, 1997; Stokesbury et al., 2001). Indeed, although not unequivocally demonstrated, an early study of introgression conducted in Ireland based on escapes of farmed parr into the river suggested that mature parr probably contributed to spawning (Clifford et al., 1998a).

Parr spawning is potentially of critical importance and may "fast track" introgression of farmed salmon in natural populations as the escapees do not have to survive until adulthood to spawn. The potential effect of this on introgression within wild populations has been highlighted based on modelling studies (Hindar, Fleming, McGinnity, & Diserud, 2006). However, the actual impact and relative spawning success for male parr of farmed, hybrid and wild origin is uncertain. One study observed a several fold higher spawning success of farmed male parr (Garant et al., 2003), while a similar study found smaller differences and a higher success of hybrid than either wild or farmed parr (Weir et al., 2005).

Sperm quality can influence the reproductive success of farmed escapees in the wild. Experimental studies have shown that there are significant differences in sperm morphology (Gage et al., 2004; Gage, Stockley, & Parker, 1998) and fertilization success among individual males (Gage et al., 2004). However, when farmed and wild salmon have been reared under identical conditions (Yeates, Einum, Fleming, Holt, & Gage, 2014), or taken directly from farms and from the wild (Camarillo-Sepulveda et al., 2016), no systematic differences in sperm and egg quality or *in vitro* fertilization success have been observed between farmed and wild salmon. This leads to the conclusion that if individual farmed escaped adults manage to partake in spawning in the wild, despite their general competitive inferiority, they will have similar fertilization success to wild adults.

Egg size is positively correlated with female size (Kazakov, 1981; Thorpe, Miles, & Keay, 1984), and when body size is adjusted for, farmed escapees display smaller eggs than wild salmon (Fleming et al., 2000; Lush et al., 2014; Srivastava & Brown, 1991). However, if the escapees entering the river are larger than the wild fish, as is sometimes the case, egg sizes of farmed offspring can be comparable to those of wild salmon (Solberg, Dyrhovden, Matre, & Glover, 2016; Solberg, Fjelldal, Nilsen, & Glover, 2014). In addition, the number of eggs per farmed female will be comparable to or greater than for wild fish. Egg size is important in early offspring survival in the wild, with larger eggs leading to larger offspring and higher survival (Einum & Fleming, 2000; Skaala et al., 2012).

3 | GENETICS

3.1 | What level of farmed salmon introgression has occurred in native populations?

Genetic changes in native populations because of farmed escaped salmon successfully spawning have been documented in several scientific studies stretching back to the early 1990s. The first documentation was obtained from the Glenarm River in Northern Ireland when a fish cage broke in the local bay in 1990 leading to a large intrusion of adult escapes (Crozier, 1993). By genotyping several allozymes, introgression of the farmed escaped salmon was documented. This was straightforward to demonstrate because the farmed salmon were of Norwegian origin and thus displayed fully diagnostic alleles at some of the loci compared to the wild Northern Irish population. Seven years later, the farm-diagnostic alleles were still present in juveniles sampled in the river, demonstrating the persistence of the non-native farmed fish in the population (Crozier, 2000). The author also observed a new non-native allele in the population that was not detected in the initial study, suggesting further introgression had occurred.

Two studies were conducted in NW Ireland in the 1990s. One of these used a combination of a semidiagnostic allele at a minisatellite locus, and a diagnostic haplotype in mitochondrial DNA (mtDNA), to identify introgression of farmed salmon in the local river that supported a hatchery facility for commercial farming of Norwegian salmon (Clifford et al., 1998a). These authors concluded that juveniles had escaped from the farm into the upper part of the river, smoltified, migrated to the sea and thereafter homed back to the site of escape to successfully interbreed with the wild population. Moreover, breeding of farmed males in the lower part of the river was also indicated, but this could have been due to mature farmed male parr that had moved downstream from the farm and successfully spawned together with the native population.

The next Irish study was conducted by the same research group and using the same genetic markers in two rivers in NW Ireland (Clifford et al., 1998b). Here, the authors were able to document the successful introgression of adult farmed salmon in two native populations studied in the period 1993–1995, as a result of larger individually reported escape events. Importantly, in both studies conducted by this group, the independent occurrence of the semi-diagnostic or diagnostic alleles in the juveniles captured in the river demonstrated that not only had the farmed fish successfully spawned, but they had hybridized with the local populations. Thus, already by the mid-1990s, cases of the successful genetic hybridization and introgression of juvenile and adult farmed escaped salmon in native populations had been documented, at least in Ireland and Northern Ireland where farmed salmon of non-native origin were reared.

The first genetic study to address introgression of farmed salmon in wild populations outside Ireland was conducted in Norway approximately a decade later (Skaala, Wennevik, & Glover, 2006). There are important differences between the studies in Ireland (including Northern Ireland) and Norway. The first is that the Norwegian study was conducted one to two decades after farmed escaped salmon had been observed in high frequencies on the spawning grounds of some of the rivers investigated (Fiske et al., 2006; Gausen & Moen, 1991; Saegrov et al., 1997). This posed two challenges. It meant that the study investigated long-term and cumulative introgression of farmed salmon rather than a well-defined or a single escape episode. Also, it meant that historical fish scale samples, collected from angling, were required to recreate the genetic structure of the populations prior to or in the early stages of farming to assess genetic changes. The authors genotyped temporal samples for seven populations using microsatellite markers, an approach that had been previously (Nielsen, Hansen, & Loeschcke, 1997) and subsequently (Nielsen & Hansen, 2008) demonstrated as an effective way to investigate temporal genetic stability in populations in the face of anthropogenic challenges.

The second key difference between the early Irish and first Norwegian studies was the genetic power of the molecular markers used. The early Irish studies exploited fixed or almost fixed allele differences between the Norwegian farmed salmon being reared in the region and the local wild population(s). However, Norwegian farmed salmon originate from a diverse range of Norwegian wild populations (Gjedrem, 2010; Gjedrem, Gjoen et al., 1991) such that the allele frequencies of Norwegian farmed strains overlap with wild Norwegian populations for several classes of genetic markers (Karlsson, Moen, Lien, Glover, & Hindar, 2011; Skaala, Hoyheim, Glover, & Dahle, 2004; Skaala, Taggart, & Gunnes, 2005). This presents significant statistical challenges to identify and quantify introgression in wild Norwegian populations, especially when gene flow over time arises from multiple farmed strains (Besnier, Glover, & Skaala, 2011).

Despite these analytical challenges, the first Norwegian study detected temporal genetic changes in some of the populations investigated (Skaala et al., 2006). These authors suggested that introgression of farmed escaped salmon was the primary cause of the changes. This was based on the high frequencies of escapees on the spawning ground of these rivers, and increased allelic diversity in some of the populations. At the same time, a loss in genetic diversity among wild populations between the historical and contemporary samples was observed.

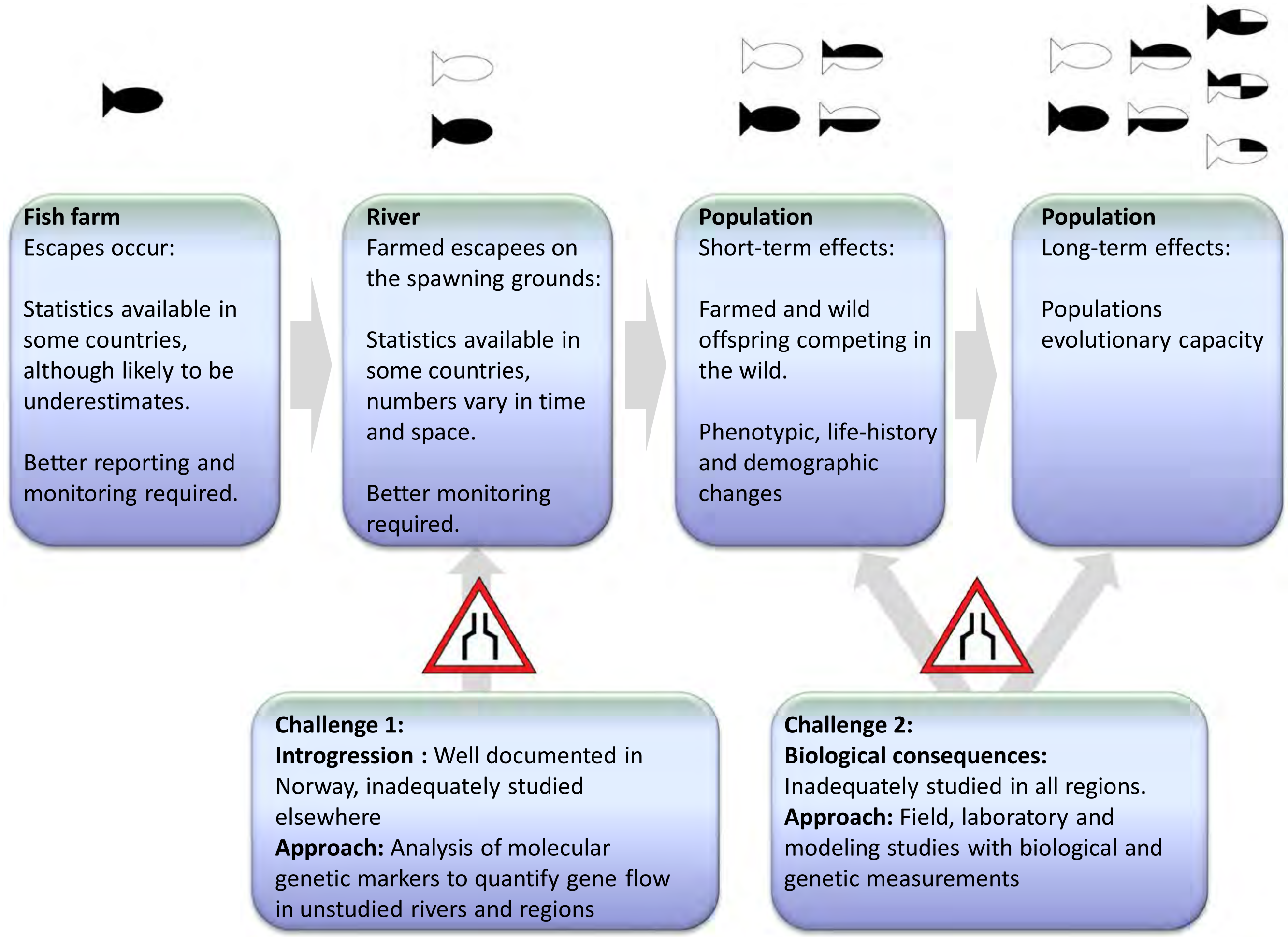
The study of Skaala and colleagues (2006) was later expanded upon. Using 22 microsatellite markers, a spatio-temporal analysis of genetic structure across 21 populations covering the entire Norwegian coastline was examined using archived samples from as far back as the 1970s (Glover et al., 2012). Temporal genetic changes were observed in some wild populations, while not in others. The study also considered the among-population patterns of introgression, and why it occurred in some rivers, but not in others with apparently similar frequencies of farmed escapees over the same period. The authors suggested that the density of the native population was probably a major factor modifying the level of introgression, via spawning (Fleming et al., 1996) and thereafter, juvenile competition (Fleming et al., 2000; McGinnity et al., 1997, 2003; Skaala et al., 2012). This mechanism has also been observed in other species where deliberate releases of hatchery fish and the level of admixture in the recipient population were suggested to be linked with density and thus resilience of the native population (Hansen & Mensberg, 2009).

The second Norwegian study (Glover et al., 2012) of farmed salmon introgression also demonstrated a decrease in among-population genetic structure over time. This was especially noticeable among populations which displayed the strongest temporal changes. Notably, all the temporally unstable populations gained new alleles with time. The potential loss of genetic diversity among wild populations following introgression of farmed salmon escapees had been earlier hypothesized (Mork, 1991) as farmed salmon have a limited genetic background (Gjedrem, 2010; Gjedrem, Gjoen et al., 1991). Finally, through simulations using the observed effective population sizes, the authors excluded genetic drift as a major contributory factor of the observed temporal genetic changes in those populations and, thus, concluded that introgression of farmed escapees was the primary driver of the observed temporal genetic changes.

Using a 7K single nucleotide polymorphism (SNP) chip, a panel of SNP markers have been identified that permit the differentiation of farmed Norwegian salmon and wild Norwegian salmon, irrespective of the origin of the domesticated strain or the wild population (Karlsson et al., 2011). These markers circumvent the statistical challenge where gene flow from multiple farmed strains tends to cancel each other out (Besnier et al., 2011). Using these collectively informative SNP markers, a reference panel of Norwegian farmed salmon, historical and contemporary samples from 20 wild salmon populations distributed throughout Norway, and approximate Bayesian computation-based estimates, the first estimation of cumulative gene flow from farmed salmon to wild salmon was produced (Glover et al., 2013). These authors estimated that over the period of the study (three to four decades), introgression of farmed salmon ranged from 0% to 47% per population, with a median of 9.1%. This represented an important quantum-step in knowledge, as it provided the first empirical evidence for Challenge 1 (Figure 3), which is a key step in quantifying and understanding the potential genetic effect of farmed escapees on wild populations. Glover et al. (2013) demonstrated that the observed frequency of escapees in rivers was a significant but not the only driving force explaining interpopulation introgression levels. The results obtained supported earlier suggestions that the density of the native population played a major role in influencing introgression success of farmed salmon (Glover et al., 2012). This conclusion was further supported in a subsequent modelling study that related introgression rates and observed incidence of escapees in the rivers studied (Heino, Svåsand, Wennevik, & Glover, 2015).

The most recent and extensive investigation of introgression was conducted in 147 Norwegian salmon rivers, representing three-quarters of wild salmon spawners in Norway (Karlsson, Diserud, Fiske, & Hindar, 2016). Their approach used the panel of SNPs developed for identification of farmed and wild salmon (Karlsson et al., 2011) and a recently developed statistical approach to estimate the proportion of the wild genome *P(wild)* remaining (Karlsson, Diserud, Moen, & Hindar, 2014). This statistical approach has the advantage that it can be used to compute individual fish admixtures, in addition to the fact that it does not require a historical baseline, which was a requirement of the methodology implemented in Glover et al. (2013). Karlsson et al. (2016) found statistically significant introgression in half of the wild populations studied and levels of introgression above 10% in 27 of 109 rivers represented by modern adult samples. Overall, they reported a mean and median introgression rate of 6.4 and 2.3%, respectively, in 109 populations with a contemporary adult sample of 20 fish or more. These authors also reported a correlation between incidence of escapees in the rivers and introgression levels, supporting earlier observations across 20 Norwegian populations (Glover et al., 2013).

Studies of introgression in other regions are more limited. The analysis of microsatellites in a recent study of a small coastal stream in western Scotland (Verspoor et al., 2016) found no detectable evidence for introgression despite being in the centre of a marine production area and the catchment being used for freshwater cage rearing of farm smolts. However, the power of the analysis to be informative was constrained by the historical data and sample sizes. In contrast, an earlier study documented European ancestry among farmed escaped salmon in the Chamcook Stream and the Magaguadavic River, New Brunswick, Atlantic Canada, despite the fact that farming salmon of European ancestry has never been permitted in this region (O'Reilly et al., 2006). Some evidence has also been reported of genetic variation in the Penobscot River that is typically only found in salmon of European ancestry (Lage & Kornfield, 2006). The only published study investigating genetic changes in native populations in this region was conducted on the Magaguadavic River where juvenile and adult escapees had been observed among the wild spawners over a period of approximately 20 years (Carr & Whoriskey, 2006; Carr, Anderson et al., 1997). The combined analysis of microsatellites and SNPs revealed temporal genetic changes in the population in the period



Fish farm
Escapes occur:

Statistics available in some countries, although likely to be underestimates.

Better reporting and monitoring required.

River
Farmed escapees on the spawning grounds:

Statistics available in some countries, numbers vary in time and space.

Better monitoring required.

Population
Short-term effects:

Farmed and wild offspring competing in the wild.

Phenotypic, life-history and demographic changes

Population
Long-term effects:

Populations evolutionary capacity

Challenge 1:
Introgression : Well documented in Norway, inadequately studied elsewhere
Approach: Analysis of molecular genetic markers to quantify gene flow in unstudied rivers and regions

Challenge 2:
Biological consequences:
Inadequately studied in all regions.
Approach: Field, laboratory and modeling studies with biological and genetic measurements

FIGURE 3 The two major challenges limiting current documentation of genetic impact of farmed escaped Atlantic salmon on wild populations. It is important to note that challenge 1 has recently been addressed in ~150 Norwegian rivers (Glover et al., 2013; Karlsson et al., 2016), but challenge 2 remains more or less completely unaddressed

1980 to 2002 and simultaneously demonstrated that the wild population had become more similar to samples of farmed fish in the region with time (Bourret, O'Reilly, Carr, Berg, & Bernatchez, 2011). These authors also observed an increase in linkage disequilibrium (LD) with time, but no drop in allelic diversity was observed, even though the population displayed a near total collapse in adult spawners during this period. This last observation parallels the observations, for example, in the River Vosso in Norway which displayed a population collapse but retained significant allelic diversity due to farmed salmon introgression (Glover et al., 2012).

3.2 | Is the Atlantic salmon domesticated?

Farmed salmon is regarded as one of the most domesticated fish species farmed for food (Teletchea & Fontaine, 2014) and was the first to be subject to a systematic family-based selective breeding programme (Gjedrem, 2010). The world's first commercial salmon breeding programme was initiated in Norway in the period 1971–1974 when gametes from mature adult salmon from one Swedish and 40 Norwegian rivers were collected and transferred to the Sundalsøra research facilities of the Agricultural University of Norway (Gjedrem, 2010; Gjedrem, Gjoen et al., 1991). These fish formed four genetically distinct substrains (Gjoen & Bentsen, 1997; Skaala et al., 2004) each with a four-year generation time, that were subject to a combination of within- and among-family selection for commercially important traits. These four initial substrains form the basis of the genetic material now produced by Aqua-Gen and have arguably the best documented genetic backgrounds that are publicly available (Gjedrem, 2000, 2010; Gjedrem, Gjoen et al., 1991). Other local strains of farmed salmon, based on either single or multiple local river stocks, were also established in Norway in the early days of the aquaculture industry. These include the Mowi and Rauma strains owned by Marine Harvest and SalMar, respectively. They also include other strains, for example Jakta and Bolaks, which have been merged into what now forms the basis of the breeding company SalmoBreed. The three primary Norwegian strains (Aqua-Gen, SalmoBreed and Mowi–Marine Harvest) dominate global production of salmon, although their frequency of use varies greatly from country to country. For example in Atlantic Canada, only the St. John River domesticated strain (Friars, Bailey, & Oflynn, 1995; Quinton, McMillan, & Glebe, 2005; Wolters, Barrows, Burr, & Hardy,

2009) is permitted for use in commercial aquaculture, while in Scotland, some local-based strains, for example Landcatch, are also being used in addition to Norwegian strains (Powell, White, Guy, & Brotherstone, 2008; Tsai, Hamilton, Guy et al., 2015). Other strains under selection are also in existence in other countries, such as Tasmania, Australia (Taylor, Kube, Muller, & Elliott, 2009; Taylor, Wynne, Kube, & Elliott, 2007) and Chile (Lhorente, Gallardo, Villanueva, Carabano, & Neira, 2014; Yanez et al., 2014).

The first breeding programme, that ultimately ended up as forming the basis of the commercial strain now commonly known as Aqua-Gen, concentrated on improving growth rates and body size from 1972 onwards (Gjedrem, 2000, 2010; Gjedrem, Gjoen et al., 1991). Thereafter, this programme included other traits of commercial importance, such as age of sexual maturation from 1980, furunculosis susceptibility from 1989, fat content and fillet colour in 1990 and susceptibility to infectious salmon anaemia from 1992 (Gjedrem, 2000, 2010). Inclusion of these traits in the breeding programme occurred in parallel to a suite of genetic studies that demonstrated significant heritability estimates for relevant traits: body weight (Gjerde & Gjedrem, 1984; Gunnes & Gjedrem, 1978); susceptibility to mortality associated with vibriosis infection (Gjedrem & Aulstad, 1974); and smoltification rates (Refstie, Steine, & Gjedrem, 1977).

Subsequent studies of heritability in these and other strains of farmed salmon have supported early findings, and estimates of heritability for additional traits such as survival during early life (Rye, Lillevik, & Gjerde, 1990), sea age of sexual maturation (Gjerde, Simianer, & Refstie, 1994), susceptibility to furunculosis (Gjedrem, Salte, & Gjoen, 1991), susceptibility to sea lice (Glover, Aasmundstad, Nilsen, Storset, & Skaala, 2005; Kolstad, Heuch, Gjerde, Gjedrem, & Salte, 2005; Mustafa & MacKinnon, 1999; Yanez et al., 2014) and susceptibility to amoebic gill disease (Taylor et al., 2007, 2009) have been reported. Many of these traits have been included in breeding programmes, although this varies between programmes and regions. Today, the oldest breeding programmes have advanced to 12+ generations, and in 2005, Aqua-Gen changed from the traditional four-year generation time to a three-year generation time to increase the rate of genetic gain. In addition, some of the strains have been separated into distinct lines, while others compressed from multiple into single strains. The genetic gains from these breeding programmes have been remarkable and are addressed in the following chapter.

Recent developments in genomic tools and their application in animal breeding have opened new opportunities to understand the underlying genetic basis of commercially important traits and how to exploit them in breeding programmes. For example, QTLs (quantitative trait loci) have been identified and validated for a variety of traits including growth (Baranski, Moen, & Vage, 2010; Tsai, Hamilton, Guy et al., 2015; Tsai, Hamilton, Tinch et al., 2015), susceptibility to pancreatic disease (Gonen et al., 2015), susceptibility to infectious pancreatic necrosis (Houston et al., 2010; Moen, Baranski, Sonesson, & Kjoglum, 2009) and survival in the wild (Besnier et al., 2015). Furthermore, genomewide association studies identified single genes that influence important phenotypes, such as the *vgll3* locus acting on age of maturation in adult salmon (Ayllon et al., 2015; Barson et al., 2015). This gene could represent an effective target of selection to inhibit early maturation during the marine phase of the rearing cycle, which is especially problematic in males when not hindered through effective light treatment (Taranger et al., 2010). As a result of the above developments, and helped by the development of advanced genomic resources for the salmon (Houston et al., 2014; Lien et al., 2016; Tsai et al., 2016), QTL and genome-based selection is now being utilized in several of the commercial breeding programmes. It is likely that within the coming years, genome-based selection will become standard within salmon breeding. This is likely to increase the number of traits that can be selected for and the rate of genetic gain. In turn, these developments will lead to further genetic divergence from wild salmon.

3.3 | What genetic differences exist between wild and farmed salmon?

There are four primary reasons why farmed salmon are genetically different to wild salmon: 1. directional selection for commercially important traits within breeding programmes (which changes both target traits and any others which may be subject to hitch-hiking/coselection); 2. domestication selection (inadvertent genetic changes associated with general adaptation to the human-controlled environment and its associated reduction in natural selection pressure, as well as trait shifts due to trade-offs); 3. random genetic changes during domestication (initially founder effects and thereafter genetic drift across generations); 4. ancestry differences as farmed salmon may be of non-local or mixed-origin (Ferguson et al., 2007).

Currently, the only direct method of examining quantitative-genetic differences among wild, farmed and hybrid salmon is to carry out common-garden experiments, where fish are reared in a communal environment. As environmental variability is minimal or eliminated, any differences between the genetic groups, with the exception of maternal and potential epigenetic effects, will reflect genetic differences (although, depending on the experimental environmental conditions, cryptic genetic variation may not be detectable (Ghalambor, McKay, Carroll, & Reznick, 2007)). Multiple experimental approaches to elucidate and quantify the genetic differences between farmed and wild salmon have been implemented. Broadly, these approaches can be grouped into the following categories: analysis of molecular-genetic polymorphisms (Table 1), analysis of gene-transcription profiles (Table 2), comparative studies of genetic-based phenotypic response(s) under controlled hatchery or net pen conditions (Tables 3–8) and seminatural conditions (Table 9) and finally experimental comparisons in the natural environment (section below).

There are several key elements which provide significant challenges to conduct comparative experiments to quantify the genetic differences between farmed and wild salmon. First, many of the farmed strains now in existence were founded using brood fish collected from multiple wild populations or were subsequently mixed with other farmed strains at some stage of strain development. Thus, due to the fact that genetic differences in a wide range of traits are also observed among wild populations (Garcia de Leaniz et al., 2007; Taylor, 1991), it may be difficult to disentangle the relative influence

TABLE 1 Studies of molecular marker variation within and among farmed and wild salmon strains

Marker	Primary observation	Reference
20 enzymes	Comparison: 11 hatchery groups vs. 7 wild rivers. Heterozygosity: F < W Magnitude of difference = 26%	(Verspoor, 1988)
6 enzymes	Comparison: 5 Scottish and/or Norwegian farmed strains vs. 9 wild Irish populations. Heterozygosity & number of alleles: F < W (80%, comparisons including fixation of some loci)	(Cross & Challanain, 1991)
6 enzymes	Comparison: 9 Scottish and 7 Norwegian farmed strains vs. 18 Scottish wild populations. Heterozygosity F ≈ W. All farmed strains differed from their wild source populations and were on the same order as between wild populations	(Youngson, Martin, Jordan, & Verspoor, 1991)
12 enzymes, 3 single locus markers, 1 minisat	Comparison: 1 farmed strain and 2 wild populations. Genetic variation: F < W for multiple marker systems	(Mjolnerod et al., 1997)
Minisatellites	Comparison: Norwegian Mowi vs. Irish wild. Heterozygosity and number of alleles: F < W. Magnitude of difference = 53% and 56%, respectively	(Clifford et al., 1998b; Clifford, 1996)
15 microsatellites	Comparison: 3 farmed strains vs. 4 wild populations (Irish and Norwegian). Allelic diversity: F < W. Heterozygosity: F ≈ W	(Norris et al., 1999)
12 microsatellites	Comparison: 5 major farmed strains vs. 4 wild Norwegian populations. Allelic richness: F < W. Magnitude of difference = 58%. Genetic distances among farmed strains 2–8 × higher than between wild populations	(Skaala et al., 2004)
8 enzymes	Comparison: 5 major farmed strains vs. 4 wild Norwegian populations. Heterozygosity, # alleles, & polymorphic loci: F < W. Magnitude of differences = 12%–17%	(Skaala et al., 2005)
16 microsatellites, 26 SNPs	Comparison: 2 farmed strains vs. 5 wild populations (Norway & Scotland). An AquaGen strain expressed the highest degree of heterozygosity for both microsatellites and SNPs, while the highest allelic diversity was found in two wild populations	(Rengmark, Slettan, Skaala, Lie, & Lingaas, 2006)
12 microsatellites, 19 SNPs in mtDNA	Comparison: 4 Norwegian farmed strains vs. 4 Norwegian wild populations. Microsatellites—allelic richness & heterozygosity: F < W. MtDNA variability: F > W	(Karlsson et al., 2010)
112 SNPs, 8 microsatellites	Comparison: Farmed and wild-caught salmon from Magaguadavic River, Canada. A SNP marker differed between the two groups and was closely associated with parr marks	(Bourret et al., 2011)
7000 SNPs	Comparison: 13 Norwegian wild and 12 Norwegian farmed strains. 60 collectively diagnostic SNPs identified all farmed, wild and *in silico* F1 hybrids	(Karlsson et al., 2011)
261 SNPs, 70 microsatellites	Comparison: Three independent domesticated/captive strains and their wild progenitors. Genetic diversity: D ≈ W, and in one comparison D > W	(Vasemagi et al., 2012)
5650 SNPs, resulting in 2797 to 4733 polymorphic markers pr. Strain	Comparison: Same as Vasemagi et al., 2012;. Heterozygosity: Mixed evidence (D < W, W < D, D ≈ W). Few genomic regions under selection and not consistently identified in all comparisons	(Makinen et al., 2015)
7000 SNPs	Comparison: Cermaq strain vs. four Norwegian populations. 44 loci under selection, linked to molecular functions associated with domestication-related traits	(Gutierrez et al., 2016)

Note: Comparisons in genetic diversity when a sample(s) from a random fish cage as opposed to the main strain(s) itself has been used to compare to a wild population has not been included in the above table. This is because a cage on a commercial farm typically contains fish resulting from a low or relatively low number of families and does therefore not accurately represent the genetic diversity nor allele frequencies of the actual farmed strain itself. The reader is referred to the following publications for data related to variation in allele profiles between cages on and among fish farms (Glover et al., 2008; Glover, Hansen, & Skaala, 2009; Glover, Skaala, Sovik, & Helle, 2011; Zhang et al., 2013). F, farm, W, wild, D, domesticated (combination of farmed and hatchery-reared fish).

TABLE 2 Common-garden comparisons of gene-transcription profiles in farmed and wild salmon under controlled hatchery conditions

Tissue	Life stage/tissue	Primary observation	Matched	Reference
Whole fry	Yolk-sac resorption	1.4%–1.7% of genes investigated: F ≠ W. Magnitude of difference: 18%–25%	Age, stage	(Roberge et al., 2006)
Whole fry	Yolk-sac resorption	6% of genes investigated: BC ≠ W Magnitude of difference: 76%	Age, stage	(Roberge et al., 2008)
Liver	Fry	32–39 transcripts: F ≠ W 23–26 transcripts: BC ≠ W 11–53 transcripts: F ≠ BC	Age	(Normandeau et al., 2009)
Gill	Mature males	2.3% (67 genes) of genes investigated: F ≠ H ≠ W Genes related to energy metabolism and immunity altered	Age, stage	(Debes et al., 2012)
Whole fry	Yolk-sac fry	mRNA translation-related pathways: F > W Nervous and immune system related pathways: F < W	Age, stage	(Bicskei et al., 2014)
Whole fry	Feeding fry	Digestive and endocrine activities, carbohydrate, energy, amino acid and lipid metabolism pathways: F > W Environmental information processing and immune system pathway: F < W	Age, stage	(Bicskei et al., 2014)
Eggs	Eyed-eggs	ECM receptor interactions pathways: F < W Genetic information processing and metabolism pathways: F > W Additive, maternal dominance and overdominance inheritance	Age, stage	(Bicskei et al., 2016)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

of domestication (in its broad sense) from origin-based (i.e. ancestry) population-specific differences.

One way to circumvent this challenge is to use a farmed strain that is known to be based on a single or low number of wild populations, either from the onset of domestication (Debes & Hutchings, 2014; Solberg et al., 2014), or by altered strain contributions through the first generations of domestication (Einum & Fleming, 1997). An alternative is to include multiple farmed strains and/or wild populations to identify evidence of parallel evolution. While the former has been done in several studies (Debes & Hutchings, 2014; Einum & Fleming, 1997; Fleming, Agustsson, Finstad, Johnsson, & Bjornsson, 2002; Solberg et al., 2014; Thodesen, Grisdale-Helland, Helland, & Gjerde, 1999), the latter is more resource demanding, although it has been carried out for several common-garden studies (Fraser, Cook, Eddington, Bentzen, & Hutchings, 2008; Glover, Hamre, Skaala, & Nilsen, 2004; Harvey, Glover, Taylor, Creer, & Carvalho, 2016; Normandeau, Hutchings, Fraser, & Bernatchez, 2009; Solberg et al., 2016) and for studies of polymorphic genetic markers (Karlsson, Moen, & Hindar, 2010; Norris, Bradley, & Cunningham, 1999; Skaala et al., 2004). In addition, a few studies have combined both approaches by comparing multiple farmed and/or wild strains, while also including the major wild founding population (Harvey, Glover et al., 2016; Neregard et al., 2008; Solberg et al., 2016).

A second key challenge in attempting to identify genetic differences between farmed and wild salmon is when the traits under study are correlated with fish size, growth rate or developmental timing. This represents a challenge because the offspring of farmed salmon display higher growth rates than wild salmon, will therefore outgrow the wild fish during an experiment, be larger than the wild fish upon initiation of certain types of experiments or may reach certain life stages at an earlier age. This may result in challenges to disentangle cause and effect on the target trait. To make comparisons, one can select the smallest farmed fish and largest wild fish to create overlapping size distributions but at the cost of random sampling (Fleming & Einum, 1997; Fleming et al., 2002; Morris et al., 2011). One can also undertake a time-staggered experiment so that all groups are of the same size or developmental stage without having to sort the fish subsequently (Thodesen et al., 1999; Zhang et al., 2016) (even though this may in turn cause developmental and/or environmental-related differences due to varying age at size, or age at stage). One can also compensate or account for variations in body size in the data analyses (Debes & Hutchings, 2014; Glover et al., 2004), manipulate growth of the farmed or wild salmon by changing temperature and or feed rations or use a combination of approaches such as investigating both size-matched individuals and age-matched individuals to reduce potential bias (as has been made in the case of a rainbow trout (*Oncorhynchus mykiss*, Salmonidae) domestication study) (White, Sakhrani, Danzmann, & Devlin, 2013). Alternatively, experiments can be conducted on the very early life-history stages (Bicskei, Bron, Glover, & Taggart, 2014; Debes, Fraser, McBride, & Hutchings, 2013; Fraser, Minto, Calvert, Eddington, & Hutchings, 2010; Solberg et al., 2014) before intrinsic growth differences lead to differences in size. However, while the latter represents the most "unbiased approach," it obviously limits measurements to early life-history stages.

Another significant challenge in disentangling the genetic differences between wild and farmed salmon is that among-family variation within strains is typically large (Harvey, Glover et al., 2016; Reed et al., 2015; Skaala et al., 2012; Solberg et al., 2016; Solberg, Glover, Nilsen, & Skaala, 2013; Solberg, Zhang, Nilsen, & Glover, 2013). Overlooking

TABLE 3 Common-garden comparisons of growth-related traits of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
Growth/body weight	Freshwater, 0+	F > W	Size, Age	(Einum & Fleming, 1997)
	Freshwater, 0+	F ≥ W, intraspecific ≠ interspecific competition	Size, Age	(Fleming & Einum, 1997)
	Freshwater, 1+	F > W	Age	(Fleming & Einum, 1997)
	Salt water, smolt 1+ and 2+	F > W	Stage	(Thodesen et al., 1999)
	Freshwater, 1+ and 2+ Salt water, 2+	Freshwater: F = W Salt water: F > W	Size (1+), Age	(Fleming et al., 2002)
	Salt water, smolt 1+	F = W (1 month after seawater transfer) F > W (>1 month after seawater transfer)	Size, Age	(Handeland, Bjornsson, Arnesen, & Stefansson, 2003)
	Freshwater, adult 3+	F > W	Age	(Dunmall & Schreer, 2003)
	Freshwater and salt water, 1+ and 2+	F > H > W	Age	(Glover & Skaala, 2006)
	Freshwater, 1+	F > H > W	Age	(Glover, Bergh et al., 2006)
	Freshwater, 1+	F > H > W	Age	(Glover, Skar et al., 2006)
	Fresh and salt water, 0+, 1+ and 2+	F > H > W	Age	(Glover, Ottera et al., 2009)
	Freshwater, 1+	F > W	Size, Age	(Wolters et al., 2009)
	Freshwater, 1+	BC ≥ W	Age	(Darwish & Hutchings, 2009)
	Freshwater, 2+	F > H (F1,F2,BC) > W	Age	(Fraser, Houde et al., 2010)
	Freshwater, 1+	F > H (F1,F2,BC) > W	Size, Age	(Morris et al., 2011)
	Freshwater, 0+	F > W	Age	(Solberg, Glover et al., 2013)
	Freshwater, 0+ and 1+	F > W, intraspecific = interspecific competition	Age	(Solberg, Zhang et al., 2013)
	Fresh and brackish water, 2+ and 3+	F > F2 > F1 > BC > W	Age	(Debes et al., 2014)
	Freshwater, 0+	F ≥ H ≥ W	Age	(Solberg et al., 2016)
	Freshwater, 0+	F ≥ H ≥ W	Age	(Harvey, Glover et al., 2016)
	Freshwater, 0+	F ≥ H ≥ W	Age	(Harvey, Juleff et al., 2016)
	Freshwater, 0+	F ≥ H ≥ W	Age	(Harvey, Solberg et al., 2016)
Endocrine growth regulation	Freshwater, 1+ and 2+ Salt water, 2+	Pituitary and plasma GH[a]: F > W Plasma IGF-1[b]: F = W	Size (1+), Age	(Fleming et al., 2002)
	Salt water, smolt 1+	Plasma GH levels: F = W	Size, Age	(Handeland et al., 2003)
	Freshwater, 0+ (liver)	GH treatment: Growth response: F < W Plasma GH and IGF-1: F = W IGF-1 and GHR[c] mRNA levels: F = W	Size, Age	(Neregard et al., 2008)
	Freshwater, 0+ (head kidney)	IGF-1 mRNA levels: F > W	Age	(Solberg, Kvamme, Nilsen, & Glover, 2012)
Feed intake and utilization	Salt water, smolt 1 + and 2+	Relative feed intake: F > W Feed efficiency ratio (FER): F > W	Stage	(Thodesen et al., 1999)
	Salt water, smolt 1+	Relative feed intake: F = W Feed efficiency ratio (FER): F > W	Size, Age	(Handeland et al., 2003)
	Freshwater, 1+	Relative feed intake: F > W Feed conversion ratio (FER): F = W	Age	(Wolters et al., 2009)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.
[a]Growth hormone, [b]insulin-like growth factor, [c]Growth hormone receptor.

family variation may lead to erroneous conclusions regarding the degree of genetic differentiation between farmed and wild salmon. Large-scale experiments using thousands of experimental animals, where both the within-strain family variation and the interstrain differences are investigated, represent the most robust analysis (Solberg et al., 2014; Solberg, Glover et al., 2013; Solberg, Zhang et al., 2013).

TABLE 4 Common-garden comparisons of life stage development of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
Embryonic development	Egg + yolk-sac fry	Days to 50% hatch: BC< or >W Length at hatch: BC = W	Age	(Darwish & Hutchings, 2009)
	Egg	Degree days to hatch: F > H (F1,F2,BC) > W	Age	(Fraser, Minto et al., 2010)
	Yolk-sac fry	Length at hatch: F ≥ H (F1,F2,BC) ≥ W Length at first feeding: F ≥ H (F1,F2,BC) ≥ W Yolk-sac conversion efficiency: F ≤ H (F1,F2,BC) ≤ W	Age	(Fraser, Houde et al., 2010)
	Egg + yolk-sac fry	Degree days to hatch: F = H (F1,F2,F3,BC) = W Yolk-sac conversion efficiency: F = H (F1,F2,F3,BC) = W Length at first feeding: F > H (F1,F2,F3,BC) > W	Age	(Debes et al., 2013)
	Egg + yolk-sac fry	Degree days to hatch: F > H > W Length at yolk-sac absorption: F = H = W	Age	(Solberg et al., 2014)
Parr maturation	Freshwater, 0+	Maturation rate: F < W	Age	(Fleming & Einum, 1997)
	Freshwater, 1+	Maturation rate: F < F1 < F2 < W < BC	Size, Age	(Morris et al., 2011)
	Freshwater, 0+	Maturation rate: F1 < BC < W	Age	(Yates et al., 2015)
Smolting	Freshwater, 1+	Smolting rate: F > W	Age	(Fleming & Einum, 1997)
	Freshwater, 1+	Smolting rate: F > H > W	Age	(Glover, Ottera et al., 2009)
	Freshwater, 2+	Smolting rate: F > H (F1,F2,BC) > W	Age	(Fraser, Houde et al., 2010)
Adult maturation	Salt water, 1SW	Maturation: F < H < W (only ♂ in F, only ♀ in W)	Age	(Glover, Ottera et al., 2009)
	Fresh and salt water, post-smolt	Maturation rate: F < W (♀ < ♂ in F, ♀ = ♂ in W). ♂: F > H (F1,F2,BC), ♀: F < H (F1,F2,BC)	Age, Stage	(Debes et al., 2014)
Reproduction	Freshwater, gametes	Sperm form, function, N and competitiveness: F = W Egg and sperm fertility: F = W Egg–sperm compatibility: F = W	Age	(Yeates et al., 2014)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

TABLE 5 Common-garden comparisons of behavioural traits of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
Aggression	Freshwater, 0+	F > W	Size, Age	(Einum & Fleming, 1997)
	Freshwater, 0+	F > W	Size, Age	(Fleming & Einum, 1997)
	Freshwater, 0+	F ≥ W, F1 > W, BC ≥ W	Size	(Houde et al., 2010a)
Dominance	Freshwater, 0+	F > W	Size, Age	(Einum & Fleming, 1997)
	Freshwater, 0+	F ≤ W	Size, Age	(Fleming & Einum, 1997)
	Freshwater, 0+	When given no prior residency: F > W When F given prior residency: F > W When W given prior residency: F < W	Age	(Metcalfe et al., 2003)
Antipredator behaviour	Freshwater, 0+	Refuge time: F < W	Size, Age	(Einum & Fleming, 1997)
	Freshwater, 0+	Response time: F = W Refuge time: F < W	Size, Age	(Fleming & Einum, 1997)
	Freshwater, 1+ and 2+	Flight and heart response: F < W (1+), F = W (2+)	Size, Age	(Johnsson, Hojesjo, & Fleming, 2001)
	Freshwater, 0+	Refuge time after simulated attack: F < H < W F1, F2, BC < W	Age	(Houde et al., 2010b)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

TABLE 6 Common-garden comparisons of plasticity (reaction norms) in farmed and wild salmon under controlled hatchery conditions

Variable	Life stage/tissue	Primary observation	Matched	Reference
Temperature	Freshwater, 0+	Effect on growth: F = W	Size, Age	(Fleming & Einum, 1997)
	Salt water, smolt	Mortality after exposure to cold temperatures: F = H = W	Age	(Hamoutene, Costa, Burt, Lush, & Caines, 2015)
	Freshwater, 0+	Cold temperature effect on early survival F = W Cold temperature effect on early growth F ≠ W	Age	(Solberg et al., 2016)
	Freshwater, 0+	Effect on growth F ≠ W	Age	(Harvey, Glover et al., 2016)
	Freshwater, 0+	Effect on survival to hatch and length at hatch: BC = W Effect on time to 50% hatch: BC ≠ W Effect on post-feeding growth: BC = W	Age	(Darwish & Hutchings, 2009)
	Freshwater, 0+	Effect on growth: F1 ≈ BC ≈ W Effect on parr maturation: F1 = BC = W	Age	(Yates et al., 2015)
Acid tolerance	Freshwater, 0+ (alevins + parr)	Effect on mortality: F or F1 H ≥ W, F2 H ≤ W	Age	(Fraser et al., 2008)
Salinity	Salt water, smolt 1+	Mortality following seawater transfer: F > W	Size, Age	(Handeland et al., 2003)
	Fresh and salt water, post-smolt	Effects on growth rate: F ≠ H (F1,F2,BC) ≠ W	Age, Stage	(Debes et al., 2014)
	Salt water, smolt	Mortality following seawater transfer: F = H = W	Age	(Hamoutene et al., 2015)
Sediments	Salt water, 1 SW	Transcriptional plasticity: F = H = W	Age	(Debes et al., 2012)
	Fresh and salt water, post-smolt	Effect on growth reduction: F = H (F1 = F2 = BC) = W	Age, Stage	(Debes et al., 2014)
Environmental stress	Freshwater, 0+	Stress induced growth reduction: F < W	Age	(Solberg, Glover et al., 2013)
Nutrition levels	Freshwater, 1+	Compensatory growth after food limitations: F = H (F1,F2,BC) = W	Size	(Morris et al., 2011)
	Freshwater, 0+	Growth reduction at restricted rations: F > W	Age	(Solberg, Zhang et al., 2013)
	Freshwater, 0+	Effect of varying feed availability on growth: F = H = W	Age	(Harvey, Solberg et al., 2016)
Density	Freshwater, 0+	Effect on growth: F = H = W	Age	(Harvey, Juleff et al., 2016)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

However, such experiments are resource demanding, and where extensive physiological, observational or other measurements are involved, such extensive sampling is rarely feasible.

Not all experiments comparing farmed and wild salmon have effectively dealt with the above-mentioned challenges, and as such, results should be interpreted critically. Nevertheless, a growing body of literature addressing this topic is now published, unveiling a comprehensive list of genetic-based differences between farmed and wild salmon (Tables 2–9). Some of the most important and extensive differences between these groups are discussed below.

3.3.1 | Studies of molecular-genetic markers

Analysis of assumed selectively neutral, or close to selectively neutral, molecular-genetic markers in farmed strains and wild populations simultaneously can provide information about the levels of genetic diversity within (including potential inbreeding) and among the strains and populations. Where farmed strains are based on a single wild population (which is less often), it can also quantify genetic divergence that may have occurred due to neutral processes such as founder effects and genetic drift. Most studies investigating allelic variation in farmed strains and wild populations have clearly demonstrated reduced genetic diversity (measured primarily as a reduction in the number of alleles but also as a reduction in heterozygosity in some studies) in farmed strains either in relation to their wild donor populations, or in relation to other wild populations chosen for the comparison (Table 1). This is consistent with the finite number of breeding adults used in each strain, and the inevitable consequences this has on the rate of inbreeding.

Highly polymorphic markers with large numbers of alleles, such as microsatellites, are highly sensitive to changes in genetic variation. This is because they often display many alleles that are typically

TABLE 7 Common-garden comparisons of morphology and physiology of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
External morphology	Freshwater, 0+	F ≠ W in 13 of 28 traits. F more robust, deeper, bodies and smaller rayed fins than W	Age	(Fleming & Einum, 1997)
Various commercial traits	Salt water, adult (full commercial cycle)	Fat content: F = W Skin coloration: F = W Flesh texture: F = W Blood and muscle pH: F = W Astaxanthin content: F > H > W	Age	(Glover, Ottera et al., 2009)
	Freshwater, 1+	Fat content: F > W	Age	(Wolters et al., 2009)
	Freshwater, 0+ (liver)	Liver lipid content: F ≠ W Muscle lipid content: F = W	Size, Age	(Neregard et al., 2008)
Swimming and cardiac performance	Freshwater, adult 3+	Swimming performance: F = W Cardiac output, heart rate and stroke volume: F = W	Age	(Dunmall & Schreer, 2003)
	Freshwater, 0+	Swimming performance: F > W Respiratory training response: F < W	Size	(Zhang et al., 2016)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

TABLE 8 Common-garden comparisons of disease susceptibility of farmed and wild salmon under controlled hatchery conditions

Trait	Life stage/tissue	Primary observation	Matched	Reference
Salmon lice (*Lepeophtheirus salmonis*, Crustacea)	Salt water, 4 months post-transfer	Infection levels: F ≥ W	Age	(Glover et al., 2004)
	Salt water, 1–8 months post-transfer	Infection levels: F > H = W	Age	(Glover & Skaala, 2006)
Furunculosis	Freshwater, 1+	Mortality: F = H = W (after controlling for body size)	Age	(Glover, Bergh et al., 2006)
ISAV	Freshwater, 1+	Timing of mortality and overall mortality: F = H = W	Age	(Glover, Skar et al., 2006)
Vibriosis	Freshwater, 1+	Mortality: F ≤ W	Age	(Lawlor et al., 2009)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

present in very low frequencies in the population, which are rapidly lost within just a few generations due to founder effects or genetic drift. Due to founder effects, finite population size and more or less complete genetic isolation (except where strains have been mixed), reductions of up to 50% in allelic variation in highly polymorphic markers such as microsatellites have been reported in farmed strains as a consequence of genetic drift (Norris et al., 1999; Skaala et al., 2004). However, studies based on bi-allelic markers or markers with few alleles have not observed such strong reductions in genetic variation (Makinen, Vasemagi, McGinnity, Cross, & Primmer, 2015; Skaala et al., 2005; Vasemagi et al., 2012). In fact, Vasemagi et al. (2012), observed non-significant differences in the levels of diversity between wild and domesticated strains, and one comparison showed higher diversity in the domesticated strain compared to its wild progenitor. The disproportionate loss of alleles in highly polymorphic as opposed to bi-allelic makers such as SNPs is expected and has been well documented in other organisms taken into culture, and even under strong inbreeding regimes (Hamre, Glover, & Nilsen, 2009; Skern-Mauritzen et al., 2013).

The effect of marker type on levels of genetic diversity within and among farmed strains and wild populations is further evidenced in studies of mtDNA. Analysis of mtDNA haplotypes in four Norwegian farmed strains and four Norwegian wild populations has revealed greater numbers of haplotypes in the farmed strains, even when the same strains simultaneously displayed reduced diversity in highly polymorphic markers (Karlsson et al., 2010). This result is counterintuitive given that the effective population size for mtDNA is normally lower than for nuclear loci, reflecting haploid and maternal inheritance of mtDNA. However, there are two possible explanations. First, farmed strains were founded using multiple geographically diverse wild populations (Gjedrem, Gjoen et al., 1991) and consequently were established with a larger number of mtDNA haplotypes than would be found in any typical wild population. Second, the breeding schemes often employed in aquaculture involve using more females than males

TABLE 9 Common-garden comparisons of farmed and wild salmon under seminatural conditions

Trait	Study area	Life stage	Feed	Primary observations	Reference
Reproduction	Circular stream channels	Parr	Natural	Spawning success: F > H = W Fertilization success: F=H ≥ W	(Garant et al., 2003)
		Parr	Natural	Aggression: F = H = W. Onset of spawning: F = W < H (late spawning in H) Fertilization success: H > W > F	(Weir et al., 2005)
Growth, survival and maturation	Circular stream channels	Parr	Natural	Growth rate: F < W (size matched prior to experiment). Predation-related growth depression: F < W (n.s. trend). Natural mortality/recovery rate: F = W	(Fleming & Einum, 1997)
		Parr	Pellets (restricted)	Growth: F > H > W (less differences than under hatchery conditions). Mortality: F = H < W	(Solberg, Zhang et al., 2013)
		Parr	Pellets (restricted)	Susceptibility to an artificial predator: F = H = W	(Solberg et al., 2015)
		Parr	Natural	Mortality and dispersal: F = W	(Sundt-Hansen et al., 2015)
		Parr	Pellets	Growth rate: F > H > W Density effect on growth: F = H = W	(Harvey, Juleff et al., 2016)
	Oblong stream channels	Parr	Natural	Mortality: F < W, high density = low density. Body mass: F > W, high density < low density	(Sundt-Hansen et al., 2015)
	Tanks with gravel	Parr	Live feed + pellets	Growth: F > W Size selective predation susceptibility: F < W Predation-related stress tolerance: F > W Parr maturation: F < W	(Debes & Hutchings, 2014)

F, farm; H, hybrid; W, wild. F1, first-generation hybrid; F2, second-generation hybrid; BC, backcross.

as broodstock. In turn, this provides a higher effective population size for maternally inherited mtDNA that would be expected at more equal sex ratios.

Large-scale genomewide SNP panels have been used to investigate genetic differences within and among farmed and wild salmon strains and populations. SNP panels, in addition to partial or whole-genome resequencing approaches, offer at least two main advantages over other marker types in characterizing genetic differences between farmed strains and wild populations. Firstly, the number of genetic markers available for routine screening, ranging from 100s to 100 000s of markers, increases the likelihood of finding a diagnostic subset that distinguishes routinely between farmed strains and wild populations. Karlsson et al. (2011) screened 12 farmed strains and 13 wild populations for a 7K SNP chip and identified a set of 60 SNPs that were collectively diagnostic in distinguishing between wild Norwegian populations and Norwegian farmed strains. They concluded that these SNPs potentially reflect signatures of selection based on (i) common shifts in allele frequencies in the farmed strains away from those of the wild populations and (ii) overall higher levels of genetic differentiation among different farmed strains than among the different wild populations, consistent with information on the origin of the farmed stains.

The second advantage of high-density genomewide SNP panels and sequencing approaches is the ability to identify genomic regions under selection and associated with the domestication process, by finding SNPs that map to traits, or are linked to loci influencing traits that are the targets of selection in aquaculture. Two studies have conducted genome scans for signatures of selection on the same samples among three independent domesticated/captive salmon strains and their wild progenitors using 331 (SNPs and microsatellites) markers and a 15K SNP chip (~4K polymorphic SNPs after filtering and quality control), respectively (Makinen et al., 2015; Vasemagi et al., 2012). These studies identified few genomic regions/outliers under selection, and the regions identified were not always the same in the different comparisons.

These authors, as well as an earlier study (Karlsson & Moen, 2010), demonstrated that the power to detect selection at a single locus depends primarily on the number of generations since domestication, the strength of selection and the number of populations under investigation. It should also be noted that in these two studies (Makinen et al., 2015; Vasemagi et al., 2012), both farmed and hatchery strains were used. The hatchery strains were based on captive-bred populations, which were not subject to artificial selection and were deliberately released into the wild as smolts for supplementation and experimental purposes and therefore the type and strength of selection these fish were subjected to will differ considerably from that which farm strains are exposed to. This may go some way to explaining the observations reported (Makinen et al., 2015; Vasemagi et al., 2012). Alternatively, and importantly, many traits subject to selection are complex, that is, with several different loci underlying the traits and with epistatic effects. This may leave weak footprints on each of the loci involved, even though the phenotypic effects are strong (McKay & Latta, 2002; Pritchard & Di Rienzo, 2010). Genome scans therefore have limitations in identifying genomic footprints of the selection that has occurred in aquaculture, but use of novel statistical methods has provided promising results (Brieuc, Ono, Drinan, & Naish, 2015).

A recent study comparing the Cermaq strain (which is a strain reared in British Columbia, Canada, estimated to have undergone 12 generations of selection) with four wild Norwegian populations using the 7k SNP chip identified 44 loci under selection (Gutierrez, Yanez, & Davidson, 2016). Many of these loci were associated with molecular functions that could be related to selection for economically important traits such as growth, as well as traits that would be likely connected with the process of domestication, such as the response to pathogens and environmental stressors. With an increasing number of SNPs available for screening, higher density maps are expected to lead to a higher probability of identifying genomic regions under selection (Davey et al., 2011) and should be investigated on a wide range of farmed strains which should vary in their origin and length of time they have been domesticated.

3.3.2 | Studies of gene transcription

A handful of studies have investigated gene-transcription profiles of farmed and wild salmon reared under controlled conditions. These have revealed a large number of different expression profiles during very early developmental stages (Bicskei et al., 2014; Bicskei, Taggart, Glover, & Bron, 2016; Roberge, Einum, Guderley, & Bernatchez, 2006; Roberge, Normandeau, Einum, Guderley, & Bernatchez, 2008), as well as later juvenile and post-smoltification stages (Debes, Normandeau, Fraser, Bernatchez, & Hutchings, 2012; Normandeau et al., 2009) (Table 2).

A recent study conducted on hatchery-raised steelhead trout demonstrated that just a single generation of domestication can cause changes in gene-transcription profiles (Christie, Marine, Fox, French, & Blouin, 2016). However, gene transcription is strongly influenced by environmental variation (e.g. Evans, Hori, Rise, & Fleming, 2015), which makes extracting general trends in transcription patterns between farmed and wild fish, among the various studies conducted (which includes life stage and environmental variation), a challenge. This is further complicated by the fact that gene-by-environment effects play a significant role in the transcriptomic responses of farmed salmon (Evans et al., 2015) and that transcription profiles for genes that are differentially expressed between the farmed and wild salmon do not always display additive genetic variation, and thus, hybrids often display non-intermediate profiles (Bicskei et al., 2016; Normandeau et al., 2009; Roberge et al., 2008). These complexities make our prediction of the consequences of different gene expression in farmed salmon and their offspring in the wild difficult.

Despite the highlighted challenges, studies of gene transcription in salmon have revealed some trends and identified processes that may be linked with domestication-mediated evolutionary changes. Processes such as environmental information processing and signalling pathways in addition to immune-related genes have been reported to be more highly expressed in wild relative to farmed salmon (Bicskei et al., 2014, 2016). In contrast, processes linked to, for example, protein synthesis and metabolism have been demonstrated to be upregulated in farmed compared to wild salmon (Bicskei et al., 2014; Roberge et al., 2006). The latter is also supported from evidence in other salmonid species exposed to domestication regimes (Devlin, Sakhrani, Tymchuk, Rise, & Goh, 2009; White et al., 2013). While the degree to which the changes in these processes reflect evolutionary responses in response to directional and domestication selection remains unquantified, indirect selection for a more docile animal that displays higher growth rates is consistent with some of the apparent transcription trade-offs revealed by these studies. Furthermore, gene-transcription studies in coho salmon (*Oncorhynchus kisutch*, Salmonidae) (Devlin et al., 2009) and rainbow trout (Devlin, Sakhrani, White, & Overturf, 2013) have revealed that domestication changes seem to stimulate similar molecular pathways as growth hormone (GH) treatment. This is also possibly the case in salmon, a suggestion indirectly supported by the fact that GH treatment gives a stronger growth response in wild as opposed to domesticated salmon, suggesting overlapping pathways already partially stimulated or utilized through domestication (Neregard et al., 2008).

Investigations among multiple salmon strains and backcross variants have led to the conclusion that many of the differences in gene-transcription patterns between farmed and wild salmon may be population specific (Normandeau et al., 2009). However, other studies have found evidence of parallel changes in different domesticated and wild strains (Roberge et al., 2006), which further supports the notion that many of the observed transcriptional differences between farmed and wild salmon are linked to domestication. The magnitude of differences in gene-transcription profiles between farmed and wild salmon has also been reported to increase with age of the fish. For example, in an experiment investigating transcription in yolk-sac fry and after first-feeding fry, a greater number of differences in transcription patterns were observed between the farmed and wild groups at the first-feeding stage (Bicskei et al., 2014). These changes between pre- and post-external feeding stages included differential upregulation of metabolic-linked processes in the farmed fry, which could be linked (causatively or otherwise) with their genetically determined higher growth rates.

3.3.3 | Comparative studies under hatchery or seminatural conditions

Here, we review papers comparing farmed and wild salmon that have been reared under identical conditions from hatching (with a few exceptions in time due to some of the above-mentioned limitations with comparative studies of fast-growing farmed versus wild salmon) (Table 3–9). Thus, the experiments can be regarded as “common garden” where the observed phenotypes of farmed and wild salmon are the result of the expression of their genotypes under those specific sets of conditions (de Villemereuil, Gaggiotti, Mouterde, & Till-Bottraud, 2016). Experiments where the salmon were raised in different environments (i.e. hatchery vs. wild or in different hatcheries) have not been included as any potential differences reflect both environmental and genetic differences. Using the common-garden approach, experimental studies under hatchery or net pen conditions have revealed genetic differences between farmed and wild salmon in traits ranging from growth (Table 3) to maturation and developmental timing (Table 4), behavioural traits (Table 5), plasticity (Table 6), morphology and physiology (Table 7) and disease tolerance (Table 8). A few comparative studies, focusing on traits such as survival and growth, parr maturation, and predation, have also been performed under seminatural conditions (Table 9). These studies have primarily involved juveniles, possibly due to logistical and experimental constraints; however, some studies have been conducted for the entire life cycle.

The trait displaying the largest and most consistent difference between wild and farmed salmon is growth (Table 3). Selection for increased growth rate has been the backbone of the domestication breeding programmes from the initiation of the industry (Gjedrem, 2000, 2010), and it is therefore expected that this is the trait displaying the greatest divergence. While growth rate and fish size have been measured in slightly different ways between studies, it is estimated that a ~10%–20% gain in growth rate has been obtained per generation from the early stages of domestication (up to the 5th generation) due to selection (O’Flynn, Bailey, & Friars, 1999; Thodesen et al., 1999).

The results of more recent studies, performed on farmed salmon of 7–10th generation vs. wild salmon, have reported continuously increasing ratios in body size between farmed fish and wild fish when reared under common-garden rearing conditions (Glover et al., 2009; Solberg, Glover et al., 2013; Solberg, Zhang et al., 2013), illustrating that a quantifiable genetic gain per generation is still being achieved (Figure 4). For example, size ratios of approximately 2–2.5:1 were observed for both juveniles and adults in a study conducted with approximately 7–8th generation of Norwegian farmed salmon (Glover, Ottera et al., 2009), while a more recent study using juveniles of the same farmed strain in the approximately 9–10th generation displayed a ratio of approximately 2.9:1 under standard hatchery conditions and 3.5:1 under hatchery conditions where growth was restricted through chronic stress (Solberg, Glover et al., 2013).

In Canadian salmon, growth ratios of approximately 3:1 have been documented between juvenile farmed salmon exposed to five generations of selection in respect of their wild founding population (Debes & Hutchings, 2014). Although growth ratios as high as 4.9:1 have been documented between farmed and wild salmon (Solberg, Zhang et al., 2013), it is worth pointing out that not all studies with domesticated salmon of ~10 generations have revealed such high size ratios under hatchery conditions (Harvey, Glover et al., 2016; Solberg et al., 2016) (Figure 4). The underlying causes of variations among studies remain unclear, although population-specific factors contribute.

Most of the growth studies have compared a single farmed strain with a wild population, and growth has always been higher in the farmed fish under hatchery conditions. Furthermore, when F1 hybrids have been studied, they have always displayed intermediate or close to intermediate growth rates (Glover, Bergh, Rudra, & Skaala, 2006; Glover, Ottera et al., 2009; Solberg, Glover et al.,

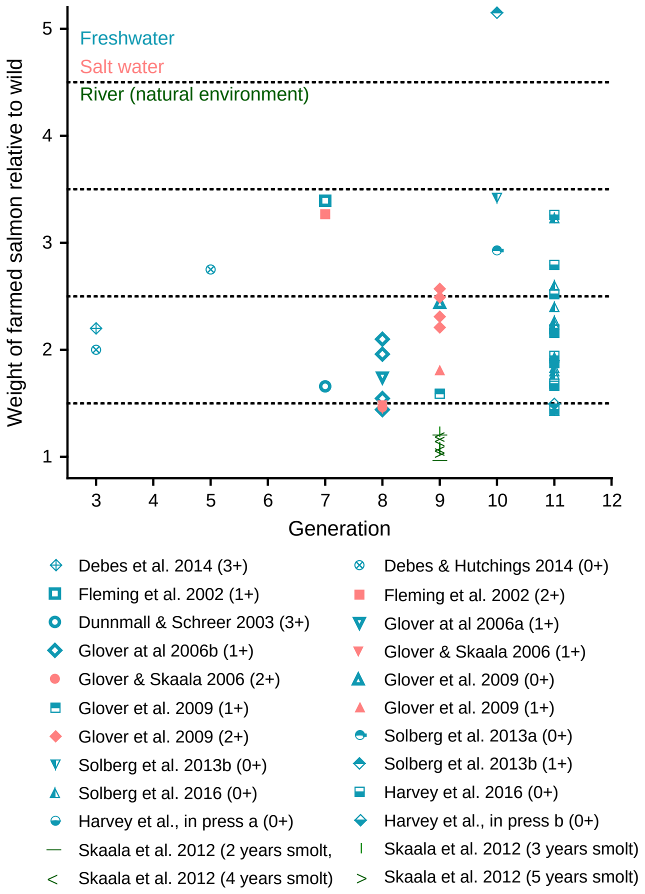


FIGURE 4 Growth of farmed relative to wild salmon. Open symbols (blue) illustrate studies performed in freshwater in tanks; closed symbols (coral) illustrate studies performed in salt water in tanks or sea cages; line-based (- | > <) symbols (green) illustrate studies performed in a river under natural conditions. The two studies performed on Canadian farmed salmon are illustrated with open symbols with a cross; all other studies are performed on Norwegian farmed salmon. Only common-garden studies documenting growth, in terms of body weight (i.e. not length), in non-sized matched salmon of similar age, sampled after their first summer are included. Not all studies report the exact number of generations of domestication; thus, ± one generation may occur. Growth differences under experimental treatments, that is differing temperature, salinity, feed levels, are not included here. Only studies performed under standard fish farming or natural conditions are included, one exception is Debes & Hutchings, 2014 that is performed under seminatural conditions

2013; Solberg, Zhang et al., 2013) which is consistent with the concept that the majority of the variation for this trait is under additive genetic control of many genes. However, non-additive variation for growth has been observed and may account for as much as 25%–50% of the expression of this trait, as has been documented in multigenerational hybrids and backcrossed variations between these forms (Debes, Fraser, Yates, & Hutchings, 2014). Thus, non-additive genetic factors, such as dominance, overdominance and epistasis, may make it hard to predict the outcome of introgression between farmed and wild salmon, especially as non-additive inheritance of other traits of importance for survival in the wild has also been documented (Einum & Fleming, 1997; Houde, Fraser, & Hutchings, 2010a).

Higher heritability estimates for growth have been documented in wild relative to farmed salmon (Solberg, Glover et al., 2013). As a larger portion of the phenotypic variation of this trait is thus attributable to genetic variation in the wild as compared to the farmed salmon, this finding indicates a slightly reduced genetic variation for growth in farmed salmon. Such a finding is consistent with the general predictions of domestication and furthermore supported by the detection of reduced variation for both mass and length in farmed, as compared to wild salmon (although not significantly different) (Morris et al., 2011).

After growth, behaviour represents one of the major areas where the genetic differences between wild and farmed salmon have been investigated. Behavioural studies can be broadly grouped into those investigating aggression and competition and those addressing predator avoidance. Both sets of traits are highly important in salmonids in the natural environment, enabling individuals to be able to compete for resources such as territories and food, while avoiding predation. Behavioural changes linked directly or indirectly with the process of domestication have been well studied in fish (Huntingford, 2004; Ruzzante, 1994). Examples of both increases and decreases in aggression have been documented, and it has been suggested that the direction of the behavioural response is likely to be specific to the conditions in which the domestication selection was imposed, and therefore, which behaviour (e.g. increased or decreased aggression) favours access to and use of resources under the context-specific conditions (Ruzzante, 1994). Thus, it is perhaps not surprising that, when one looks specifically at comparative studies in farmed and wild salmon, examples of farmed salmon showing increased (Einum & Fleming, 1997; Houde et al., 2010a), similar (Fleming & Einum, 1997; Houde et al., 2010a) and decreased (Fleming & Einum, 1997) aggression and dominance abilities as compared to wild fish have been observed. Hybrids have been shown to display both intermediate competitive levels and to dominate both their farmed and wild counterparts (Einum & Fleming, 1997; Houde et al., 2010a). However, prior residency (Metcalfe, Valdimarsson, & Morgan, 2003), and possibly fish size (Symons, 1968), remains as important factors influencing such behavioural trials and given the large growth differences between the groups this makes such experiments challenging and potentially difficult to interpret, also when size-matched individuals have been used.

Predation–avoidance behaviour experiments have revealed genetic differences between farmed and wild salmon. Although experiment designs have varied, the few studies published have demonstrated that farmed fish display more naive behaviour towards artificial predators such as shorter times to re-emergence following exposure to an artificial predator (Einum & Fleming, 1997; Fleming & Einum, 1997; Houde, Fraser, & Hutchings, 2010b). This behaviour has most likely arisen due to the relaxation of natural selection in the hatchery environment, combined with a positive selection for growth and thus tolerance to the hatchery conditions where predators do not reflect a selective force. Indeed, such a trade-off between growth and survival rates has been documented in other salmonids (Biro, Abrahams, Post, & Parkinson, 2004, 2006).

Further evidence of reduced predator awareness comes from studies which demonstrate that offspring of wild salmon displayed a drop in growth in the presence of a predator (with low or no predation), while in contrast, domesticated salmon show a smaller decline in growth (Fleming & Einum, 1997) or no decline at all (Debes & Hutchings, 2014). Given the fact that the offspring of farmed salmon display a lower survival than that of wild salmon in the wild (see section below) and that predation is a known component of mortality of salmonids in freshwater (Feltham & MacLean, 1996; Henderson & Letcher, 2003; Vik, Borgstrom, & Skaala, 2001), it is likely that behavioural traits have changed as a result of domestication and therefore contribute to the lower fitness of the progeny of farmed fish in the wild. Nevertheless, the direct connection between increased risk taking behaviour- and predation-related mortality rates in farmed as compared to wild salmon is yet to be demonstrated (Skaala, Glover, Barlaup, & Borgstrom, 2014; Solberg, Zhang, & Glover, 2015).

3.3.4 | Studies conducted in the natural environment

Common-garden experiments undertaken in the wild are a relatively recent development and only made possible with the development of DNA profiling for accurate parentage assignment (Ferguson et al., 1995). Previously, salmon had to be reared separately before they were large enough to tag physically. By taking experiments into the wild, experimental populations can be exposed to the vicissitudes of complex ecosystems, which are impossible to replicate in the laboratory. These involve both the river and the sea, and the transition between them.

Depending on the life-history stage investigated, studies conducted in the wild also display a huge range in spatial scale, from tens of metres to thousands of kilometres. A range of environmental factors vary continuously in the wild, for example temperature, light, water velocity, pH and salinity. In turn, these factors pose local biological challenges in respect of food availability, exposure to pathogens, parasites and predators, and interspecific competition for resources. Typically for wild salmon, more than 90% of the eggs introduced into the river will be dead by the end of the first summer, roughly only 1 or 2% of eggs will make it to the smolt stage and usually no more than 10% and often less of the smolts that go to sea will make it back from the ocean to spawn. Assuming that the traits contributing to fitness are heritable and there is sufficient variance in survival among families within different groups, such high rates of attrition provide the opportunity for intense levels of natural selection. Any mismatch between the fish and the environment will be readily exposed, revealing adaptive differences between native and non-native populations. Thus far, only three published studies have addressed survival and development of farmed, hybrid and wild salmon in the natural environment. This is not surprising given the fact that they are exceptionally demanding on research facilities, in addition to experimental and financial logistics.

The first common-garden study in the wild was conducted in Ireland and involved planting eggs of Norwegian farmed (Mowi strain), F1 hybrid and wild (local) parentage into a section of the Burrishoole River (McGinnity et al., 1997, 2003; Reed et al., 2015). The progeny of the experimental parental fish was sampled in the river at different life-history stages using a combination of electrofishing, together with downstream (juvenile seaward migration) and upstream (adults returning to spawn) traps, and was identified to family and experimental group using DNA profiling. As insufficient adult returns would have been obtained from smolts produced naturally in the river, the marine phase of the life cycle was examined by ranching, that is smolts from the same families that were introduced into the experimental river were reared in a hatchery and released to the sea to complete their life cycle and captured and sampled on their return. These fish were followed through two generations using the surviving adults returning from the sea to propagate the second generation. The authors concluded that the lifetime survival of farmed fish was just 2% of wild fish and that the relative fitness increased along a gradient towards the offspring of a F1 hybrid survivor spawning together with a wild salmon (=wild backcross) which displayed a lifetime survival of 89% compared to the offspring of two wild salmon, indicating additive genetic variation for survival (McGinnity et al., 2003). This was a fundamental observation.

The study dispelled the previously held idea that farm-wild hybrids might display enhanced performance due to heterosis (hybrid vigour). Secondly, it showed that there was likely to be a penalty in respect of fitness following hybridization and introgression of farmed escapees into recipient wild populations. This is extremely important as in many cases where escaped farmed salmon enter a river, production of F1 hybrids rather than pure farmed offspring is the outcome (in part due to the differences in spawning success between female and male farmed escapees). Thus, part of the potential wild juvenile recruitment is converted to hybrids in the first generation, and to backcrosses in the second, and subsequent generations (Figure 3). The lower lifetime reproductive success of hybrids will, therefore, reduce the average fitness of the wild population. It also suggested the possibility of a predictive capability, which would have general applicability with respect to establishing the likely biological consequences for affected populations where escaped salmon may have spawned in the wild. Additive genetic effects were also apparent for most of the phenotypic traits measured in the Burrishoole experiment related to growth and performance with mid-range values found for juvenile size at age, including 0+ and 1+ parr; smolt size; propensity for precocious maturation; tendency for autumn smolt migration; sea age of maturity (McGinnity et al., 1997, 2003, 2007; Reed et al., 2015); these intermediate phenotypes being neither adapted to the river nor the farm. The authors thus further concluded that repeated invasions of farmed salmon in a wild population will cause the fitness of the recipient native population to seriously decline and potentially in extreme cases enter an "extinction-vortex" should the incidence of escapes in terms of numbers and frequency be sufficiently large and recurring.

The extension of the Burrishoole experiment into the second generation also facilitated a rare insight into the operation of outbreeding depression in the F2 generation (McGinnity et al., 2003). The highest egg mortality occurred in the F2 hybrid group and most probably reflected outbreeding depression as might be expected from a breakdown of co-adapted sets of alleles following recombination of parental chromosomes, that is principally the “intrinsic” interaction between genes (Edmands, 2007). Remarkably, the F2 hybrids performed extraordinarily well subsequently and were anomalously, very highly represented in the river as 0+ and 1+ parr relative to the other groups. In the case of certain F2 hybrid families, a plausible explanation could be that the blend of divergent wild and farmed parental genomes produced rare offspring recombinant genotypes that were fortuitously well adapted to the local conditions through heterosis (Reed et al., 2015).

The Burrishoole study also yielded some valuable ecological insights into the interaction of farmed and wild origin fish. While the farmed and hybrid offspring of farmed parents showed reduced survival compared to wild salmon, they grew faster as juveniles and appeared to displace slower growing and thus smaller wild parr. Where suitable habitat for these displaced parr is absent, this competition would result in reduced wild smolt production. The effects of this competitive displacement were more profound at higher stocking densities (eggs planted at a density of 5.8 m^{-2} in 1993 versus eggs planted at a density of 8.4 m^{-2} in 1994).

It was apparent from the relative survival of the progeny of farmed and wild fish in the Burrishoole experiment that the marine environment presented the greatest challenge to the non-native fish; an approximate twofold reduction in survival for farmed fish in the river, when planted as eggs, was more than ten times lower in the sea, when released as smolts. It would appear that the traits associated with the marine environment or the transition between local river environments and marine environments (or indeed carry-over effects from the freshwater environment that are important for life in the sea) are of substantially greater importance in respect of local adaptation than the more obviously local factors in the river environment. Such traits may include ocean entry timing, predator avoidance and the ability to orientate into favourable ocean currents for transportation to feeding grounds. Likewise, a successful return to the natal river and arrival to the spawning grounds will be contingent on homing orientation; time spent at sea, timing of return and timing of river entry.

The seeming discordance between the farmed phenotype and the marine environment regarding Irish conditions would prove a serious impediment to subsequent gene flow to the wild from this source and to the integrity of the wild population. Compared to the pure farmed progeny, the relative success of the various combinations of hybrids was much greater and would indicate these as a more likely conduit for the transfer of genetic material from farmed fish into the wild. These studies remain as the only two-generation comparison of farmed and wild salmon in the natural environment.

In Norway, a slightly different but complimentary experiment to the study conducted in Burrishoole was conducted in the River Imsa during the same time period (Fleming et al., 2000). Here, the authors released adult salmon of farmed (the Norwegian AquaGen strain) and wild (local) origin above a two-way fish trap in the River Imsa, once they had been biopsy sampled. Thus, this study incorporated an important additional behavioural component in respect of reproductive performance of farmed and wild salmon into the experimental design. Therefore, the fish were allowed to spawn naturally in the river and their offspring were sampled by electrofishing, in addition to downstream and upstream traps located in the river. This study reported a breeding success of farmed salmon at less than one-third the breeding success of wild salmon and a lifetime fitness of farmed salmon from one generation to the next (i.e. escaped adult fish in the river to adults returning from the sea) of 16% in comparison with wild salmon (Fleming et al., 2000).

The observed difference in survival between farmed and wild salmon was very similar in magnitude to the differences observed in Burrishoole in Ireland. It is also notable that the rank order of wild > hybrids > farmed (for survival) was also found to be the same. Important additional data from this study were the fact that population productivity, measured by the total number of smolts produced, and the numbers of smolts of wild parentage, dropped by c. 30% following the permitted spawning intrusion of farmed salmon. The observed reduction in total and wild smolt productivity was attributed to the fact that the offspring of the farmed and hybrid salmon competed with wild salmon for both territory and resources, and the dynamics of this may vary across life-history stages (Sundt-Hansen, Huisman, Skoglund, & Hindar, 2015). The study also indicated significantly higher juvenile and smolt size for fish with farmed parents compared to the fish of wild parents and a significantly lower age at smoltification (see Figure 2 in the paper).

As noted earlier, observations on the reproductive behaviour of farmed and wild salmon by Fleming et al. (2000) showed that adult farmed fish were competitively and reproductively inferior, achieving less than one-third the breeding success of the native fish. Moreover, this inferiority was sex-biased, being more pronounced in males than females, identifying it as an important route for gene flow involving native males mating with farmed females. This confirms the earlier behavioural studies conducted in seminatural spawning arenas (Fleming et al., 1996). The lower early survival of the juvenile farmed genotypes in the Imsa River experiment (Fleming et al., 2000) also appeared to constrain invasion by farmed escapes, but it did so to a lesser extent than breeding. As was reported in the study conducted in Burrishoole (McGinnity et al., 1997), results from the Imsa experiment detected indications of a competitive effect with displacement of the progeny of wild fish with offspring distributions differing despite native and farmed females having had similar spawning locations.

In contrast to the Burrishoole study, no differences in marine survival and age of maturity were found between the progeny of wild and farmed salmon in the Imsa experiment. This illustrates the contribution of life-history variation to fitness in given circumstances, as the parental fish differed markedly between both experiments in respect to their phenotype, size and age of maturity. At Imsa, the farmed salmon parents used in the experiment were 1sea winter (SW) and 2SW fish and were relatively well matched in size to the wild fish. In contrast, large 3SW and 4SW fish of Norwegian farmed origin were used in the initial 1993 and 1994 Irish experiments, while 2SW fish of the same provenance were used in the 1998 experiment, as compared to the small 1SW Burrishoole wild population.

The most recent published study to address the relative fitness of farmed and wild salmon in a natural environment was conducted in the River Guddal in Norway (Skaala et al., 2012). These authors used a similar design to the Irish study, planting nearly a quarter of a million eggs of farmed (a mixture of Norwegian farmed fish with unknown background, and Norwegian Mowi), hybrid and wild (non-local, Lærdal from the Norwegian gene bank) parentage into the river, and followed their growth and survival until smoltification. The study included planting out three cohorts in successive years with gradually increasing egg density and therefore the level of competition, and permitted for the first time, comparisons of family as well as group performance (farmed, hybrid and wild). It showed several important results.

Large differences in survival were observed among the 69 experimental families from egg-smolt, both within and among experimental groups. Interestingly, the highest surviving family was of farmed parentage in the first cohort, although wild, hybrid and farmed families were among the highest and lowest ranked families for survival. Farmed salmon smolts were also on average larger than the wild smolts in the Guddal study (7%, 25% and 6% larger in cohorts one, two and three, respectively). The authors also detected a significant positive effect of egg size on survival, a phenomenon noted in other studies of salmonid early life history in the wild (Einum & Fleming, 2000). In the Guddal study, farmed salmon eggs were larger than the wild salmon eggs (this will vary from case to case), and when this effect was controlled for in the statistical model applied, the offspring of farmed fish displayed a significantly higher mortality than the offspring of wild fish (relative farmed family survival = 0.8 and 0.62 of wild fish for cohort two and three, respectively). Thus, the relative survival of the farmed fish decreased with an increase in density and competition across the cohorts planted. When looking at half-siblings where egg size was identical, families sired with wild males displayed higher survival than families sired with farmed males in 15 of 17 pairwise comparisons. A subsequent analysis by Reed et al. (2015) on the Burrishoole data also showed substantial interfamily differences in survival and size at age in 0+ and 1+ parr. They found egg size had a significant positive effect on the fork length and mass of 0+ fry caught by electrofishing, whereas no egg size effect was found for 1+ parr sampled the following year. However, positive effects of egg size on survival of both 0+ and 1+ parr were also found. The Guddal study also revealed that farmed and wild salmon overlapped in diet in the river, an observation also reported from an earlier small-scale planting study (Einum & Fleming, 1997) and from the full-generation study in Imsa (Fleming et al., 2000).

Studies validating and examining the underlying details, mechanisms and genomics of the observed survival differences between offspring of farmed and wild salmon in natural habitats have also been published using data from the study in Burrishoole and Guddal (Besnier et al., 2015; Reed et al., 2015). These studies have revealed further details, including identification of QTLs for growth and importantly survival (Besnier et al., 2015), and provided estimates for heritability in the wild (Reed et al., 2015). In the case of salmonid fish, quantitative-genetic parameters, such as estimates of heritability, calculated under farm or hatchery conditions have limited relevance for wild populations given the environmental sensitivity of these parameters. This further justifies the need to undertake common-garden experiments under natural conditions.

To address the ecological mechanisms underlying the observed differences in survival between the offspring of farmed, hybrid and wild salmon in the wild, an additional experiment was conducted in the River Guddal (Skaala et al., 2014). Extensive electrofishing was conducted for wild brown trout (*Salmo trutta*, Salmonidae) in the proximity where the experimental eggs were planted out. Of the 760 trout non-lethally sampled, 4.2% of them had ingested a total of 46 salmon fry. These fry were thereafter genotyped to identify them to experimental family and farmed, hybrid or wild group. When predation of these groups was compared to the numbers of eggs released for each group, there was no significant difference in predation between the farmed, hybrid and wild offspring. A similar result has also been reported in seminatural arenas (Solberg et al., 2015). These observations stand in contrast to the results of predator awareness or avoidance studies where domesticated salmon have been demonstrated to display less caution than wild salmon (Einum & Fleming, 1997; Fleming & Einum, 1997; Houde et al., 2010b).

Despite the obvious differences in provenance, history of domestication in farmed strains and environmental context of the experiments reported in the studies above, there is a remarkable consistency in the outcomes of the experiments in Norway and Ireland and among cohorts compared in the same locations (Fleming et al., 2000; McGinnity et al., 1997, 2003; Skaala et al., 2012). Furthermore, the recurring evidence of additive genetic effects contributes to explain observed traits and rates of survival. While all experiments by their nature will be somewhat case or situation specific, not unexpectedly there are also some dissimilarities between experiments, particularly in the magnitude of the differences. However, the basic similarities in outcomes suggest that results have general transferability in considering biological consequences to actual escape events.

4 | DISCUSSION OF FITNESS IMPLICATIONS FOR WILD POPULATIONS

4.1 | Will there be changes in juvenile and adult abundance?

Density-dependent factors set the limit on a river's carrying capacity for juvenile and smolt production (Bacon et al., 2015; Jonsson, Jonsson, & Hansen, 1998). Offspring of farmed salmon compete with wild salmon for resources such as food and space (Einum & Fleming, 1997; Fleming et al., 2000; Skaala et al., 2012). Therefore, when farmed salmon manage to spawn in the wild, and their offspring (either from two farmed parents or from more likely a farmed and a wild parent) constitute a component of a given river′s juvenile population, the production of juveniles with a pure wild background (i.e. two wild parents) will be depressed through competition for these resources.

Theoretical studies suggest that populations that are well adapted to their local environments increase towards the carrying capacity, while those whose trait values lie far from the local optimum decline (Burger & Lynch, 1995; Garcia de Leaniz et al., 2007; Kirkpatrick &

Barton, 1997). In addition, a demographic penalty is expected when populations undergo the process of adapting to changing environments (Burger & Lynch, 1995; Kirkpatrick & Barton, 1997). This type of demographic penalty might be assumed to occur in native populations following spawning intrusion of mal-adapted farmed escapees. In this case, the population rather than the environment changes, although both plausibly could occur at the same time. Field studies of salmon agree with these theoretical predictions and indicate that the total production of smolts in a river (i.e. fish of all genetic backgrounds) may decrease following spawning intrusion of farmed salmon (Fleming et al., 2000; McGinnity et al., 1997). While the mechanisms underpinning the decrease are not completely understood, this may arise because farmed salmon offspring and hybrids can competitively displace wild salmon under certain environmental conditions (McGinnity et al., 1997; Sundt-Hansen et al., 2015), whereas their egg-to-smolt survival is lower than for wild offspring.

The effect on total productivity will also depend in part on whether selection against maladaptive farmed or introgressed salmon dominates before or after density-dependent selection has occurred and "thinned out" the total population (Baskett et al., 2013). If density-dependent selection occurs before selection against maladapted domesticated genotypes, there will be a drop in total numbers of smolts produced; however, if selection against maladapted genotypes occurs before or in concert with density-dependent selection, a drop in juvenile production is not necessarily expected. The competitive balance and impact on total smolt productivity may also be influenced by the level of farm-wild hybridization within a population (Houde et al., 2010a), and the density of the recipient population and level of juvenile competition (Skaala et al., 2012). Maternal factors, such as egg size variation, may also negatively impact total smolt production where farmed salmon eggs are larger than wild salmon eggs (Lush et al., 2014; Srivastava & Brown, 1991)), which may offer an initial maternal survival advantage (Skaala et al., 2012).

Introgression of farmed salmon may also decrease the number of fish returning to spawn in the wild beyond the potential reduction resulting from the reduced smolt migration alone. This is less well understood than freshwater effects. Studies of released smolts in the Burrishoole River in Ireland (McGinnity et al., 1997, 2003) found during the marine phase of the life cycle a lower survival of farmed and hybrid salmon offspring than those of wild salmon. No difference in marine mortality was observed between naturally produced smolts of farmed and wild salmon origin in the Imsa study, but later experiments based on smolt releases showed relative marine survival rates of farmed smolts to be 37% of wild smolts, with hybrid smolts not being significantly different to wild (Hindar et al., 2006). A decrease in marine survival would be expected to decrease adult returns in proportion to the extent that emigrating smolts are composed of farmed or mix farmed-wild individuals. This suggestion is supported by modelling (Baskett et al., 2013; Castellani et al., 2015). However, models have also indicated that changes (i.e. decrease) in the numbers of returning adults in admixed populations may be difficult to detect in non-experimental populations in the short-term. This is because the high natural variation in numbers of adult salmon returning to rivers due to variations in oceanic conditions (Friedland, Hansen, Dunkley, & MacLean, 2000; Jonsson, Jonsson, & Albretsen, 2016; Vollestad et al., 2009; Youngson, MacLean, & Fryer, 2002) may potentially mask short-term changes.

In general, the survival of salmon smolts on a trajectory of spending 3 years at sea as opposed to just one or two years is reduced (Chaput, 2012). It is therefore unknown to what degree the observed relative marine survival difference between farmed and wild salmon (McGinnity et al., 1997, 2003) is linked to inherent differences in survival between salmon that display 1–3 years in the sea, or to domestication-driven differences between farmed and wild salmon in general. In the Burrishoole River in Ireland, the native population was predominantly of 1 sea winter and the farmed strain multisea winter (which could have contributed to the observed difference). Despite the increased fecundity of the larger returning hybrid and multisea winter farmed salmon, this was not enough to prevent a drop in egg deposition due to their higher rates of marine mortality associated with their genetic heritage (McGinnity et al., 2003). This suggests that both the number of returning adults and the overall number of eggs deposited may decrease with the introgression of farmed salmon. However, the marine survival of farmed, hybrid and wild salmon is poorly studied compared to the freshwater stage of the life cycle.

4.2 | Will there be changes in phenotypic and life-history characters?

Farmed salmon are genetically different to wild populations. In whole-river experiments (Fleming et al., 2000; McGinnity et al., 1997, 2003; Skaala et al., 2012), heritable differences in freshwater growth and body shape, timing of smolt migration, age of smoltification, incidence of male parr maturation, sea age at maturity and growth in the marine environment have been observed between the offspring of farmed and wild salmon. Therefore, where farmed salmon have introgressed in natural populations, it is expected that recipient populations will display changes in phenotypic and life-history traits in the direction of the intruding farmed strains. Significantly, the phenotypes of the hybrid progeny of farmed and wild crosses have, in many of the experiments undertaken in the wild, been shown to be intermediate for the life-history traits listed above (McGinnity et al., 2003, 2007) and thus maladapted to both environments. Any changes in the direction of the farmed strain are likely to be associated with and contributing to a loss of fitness, given that phenotypic and life-history traits are strongly associated with fitness in the wild (Fraser et al., 2011; Garcia de Leaniz et al., 2007; Taylor, 1991).

The magnitude of genetic changes in phenotypic and life-history traits will scale with the level of introgression and most likely follow a dose–response relationship (Castellani et al., 2015). Changes caused by low or modest levels of genetic introgression may be difficult to detect, especially in the short term (Castellani et al., 2015), given that many phenotypic traits in salmon are highly plastic (Debes et al., 2014; Garcia de Leaniz et al., 2007), and yearly environmental variation, as well as environmental change through time, may also influence life-history traits. This has recently been observed for age of maturity in wild salmon in relation to changing sea temperatures (Jonsson et al., 2016), which may serve as a confounding effect on genetic changes in this trait due to introgression. Other mechanisms, for example high mortality during early life-history stages and lower survival of farmed salmon juveniles (Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2012), may also collectively contribute to masking population-level changes in phenotype and life history.

A good example to illustrate the potential challenge(s) to identifying and quantifying genetic changes in fitness-related traits in wild populations as a consequence of introgression of farmed escaped salmon is growth. It is both one of the most plastic traits in fish (Debes et al., 2014; Karjalainen et al., 2016) and the one that displays the greatest genetic difference between wild and farmed salmon (Table 3). Farmed salmon typically achieve body weights 2–3 times greater than wild salmon when reared in common-garden studies under hatchery conditions. However, when investigated in the wild, freshwater growth differences between the offspring of farmed and wild salmon are much smaller than in the hatchery, sometimes by one or more orders of magnitude less (Fleming et al., 2000; Reed et al., 2015; Skaala et al., 2012) (Table 3; Figure 4). Given the reaction norm variation of this trait seen across divergent environmental conditions (Table 5), under low or perhaps even modest levels of genetic introgression and hybridization, changes in wild growth rate and body size in a population will be difficult to detect. More sensitive experimental approaches, for example, examining the genetic background and growth rates of individuals within a population, will be needed to assess whether changes have occurred. Despite these challenges, changes in some traits may be detectable where farmed populations show a large deviation from an impacted wild population. This is the case, for example, where adults in wild stocks return predominantly after 1 sea winter as is the case on the West Coast of Ireland, Scotland and in Newfoundland, as compared to farmed stocks where most are multisea winter, although there can be considerable variation from river to river.

In an investigation of the River Ewe stock in Scotland, following a massive intrusion of both juvenile and adult escapes over several years (Butler et al., 2005), no population-level changes in fish size or age of maturation were observed, although a small decrease in age of smoltification was found consistent with a gain in freshwater growth rate. However, actual levels of introgression were not known in the study, and the observations could have been explained by density-dependent changes.

At present, studies considering phenotypic and life-history changes in native populations are effectively lacking (Challenge 2, Figure 3). Thus, there is an urgent need for detailed investigation of both the actual levels of interbreeding and introgression and the phenotypic and life-history changes that arise from admixture with farmed salmon (Figure 3).

4.3 | Will population genetic structure change?

The Atlantic salmon is characterized by widespread structuring into genetically distinct and differentiated populations (Bourret et al., 2013; King, Kalinowski, Schill, Spidle, & Lubinski, 2001; Ståhl, 1987; Verspoor et al., 2005). This is conditioned by the evolutionary relationships among populations (Dillane et al., 2008; Dionne, Caron, Dodson, & Bernatchez, 2008; Perrier, Guyomard, Bagliniere, & Evanno, 2011) and adaptive responses to historical and contemporary environmental differences (Garcia de Leaniz et al., 2007; Taylor, 1991). The largest genetic differences are observed between populations residing on different continents (Gilbey, Knox, O'Sullivan, & Verspoor, 2005; Taggart, Verspoor, Galvin, Moran, & Ferguson, 1995; Tonteri, Veselov, Zubchenko, Lumme, & Primmer, 2009), where chromosome-number differences are also observed (Brenna-Hansen et al., 2012; Lubieniecki et al., 2010). Within continents and smaller geographic regions, population genetic structuring is often, but not always, a function of isolation by distance (Dillane et al., 2007; Glover et al., 2012; Perrier et al., 2011), but is modified by various factors such as colonization history and landscape features (Dillane et al., 2008). Consequently, populations can display genetic differences between regional groups (Bourret et al., 2013), between rivers (Perrier et al., 2011; Tonteri et al., 2009; Wennevik, Skaala, Titov, Studyonov, & Naevdal, 2004) and between tributaries within river systems (Dillane et al., 2007, 2008; Dionne, Caron, Dodson, & Bernatchez, 2009; Vaha, Erkinaro, Niemela, & Primmer, 2007). These genetic differences may be in respect of gene frequencies and variants present at individual loci but may also involve differences in genomic organization as regards aspects such as chromosome structure and number which will affect linkage relationships (Brenna-Hansen et al., 2012) which may have non-additive fitness consequences that are difficult to predict (Cauwelier, Gilbey, Jones, Noble, & Verspoor, 2012).

Simulations have suggested that interpopulation genetic diversity will gradually erode with introgression of farmed escaped salmon (Mork, 1991). Studies of Norwegian populations exposed to farmed escapees have indeed observed a decrease in interpopulation genetic diversity over time (measured as a drop in pairwise or overall F_{ST}) (Glover et al., 2012; Skaala et al., 2006). At the same time, the admixed wild populations became more similar to a pool of Norwegian farmed salmon (Glover et al., 2013). Potential changes in population genetic structure have not been assessed outside Norway. While genetic changes studied so far may be of no functional significance, they may mark general patterns of genomic change, although to what extent this is the case remains an open question. To robustly address this issue, studies of changes in functional genetic variation known to have phenotypic or fitness implications are needed (Consuegra et al., 2005; Coughlan et al., 2006; Ryynanen & Primmer, 2004; Verspoor et al., 2005).

4.4 | Will the severity of impacts vary among wild populations?

Data from empirical studies (Glover et al., 2012, 2013; Karlsson et al., 2016), as well as from models (Castellani et al., 2015; Heino et al., 2015; Hindar et al., 2006), have demonstrated that the levels of introgression are correlated with the number of escapees. This is further modified by the abundance or density of the native population (Glover et al., 2012; Heino et al., 2015), which probably links to spawning and juvenile competition. Thus, wild populations that are already experiencing natural declines in adult abundance will be more vulnerable to introgression of farmed salmon due to the reduced level of competition faced by the escapees once on the spawning grounds. However, other factors will also condition the level of introgression, and how it varies among populations.

Important factors affecting gene flow and relating to the characteristics of the invading farmed escapees themselves include their body size, the stage at which they escaped and whether they mature as juveniles or adults. Just as important in modifying the competitive success of the farmed escapees will be the biological characteristics of the wild population being invaded. This reaches beyond the density of adults on the spawning ground, but also includes other characteristics such as the predominant sea age of wild returning spawners (i.e. one, two or three sea winters), the propensity for maturation in male parr, and the phylogenetic history of the population. River-specific non-biological factors are also likely to influence the degree of gene flow between farmed escapees and wild salmon. For example, it is likely that rivers with upstream migration challenges (rapids and waterfalls), or large lakes/rivers with smaller tributaries, may hinder the ascent of farmed salmon to higher spawning grounds in some rivers, limiting their scope for interbreeding with wild fish. These biotic and abiotic factors need to be identified to fully understand impacts and which populations are at lesser or greater risk of introgression.

Once gene flow from farmed escapees has occurred, phenotypic, life-history and demographic consequences for wild populations will scale with the level of gene flow. Modifying factors aside, in any given river, increased numbers of escapees will on average increase the probability for introgression and, thereafter, the probability of negative impacts (i.e. changes in life-history and demographics). The level of negative genetic impact may also scale with the degree of domestication and adaptive divergence from wild populations (Castellani et al., 2015). However, the relationship of domestication-driven and ancestry-related divergence with potential for decreases in adult abundance resulting from interbreeding of farmed escapees is not necessarily linear or clear-cut (Baskett et al., 2013). First, the impact on wild population fitness may be at its highest at intermediate genetic divergence between wild and farmed fish (Baskett & Waples, 2013; Huisman & Tufto, 2012), and not when farmed fish resemble wild fish or when they are vastly divergent from wild fish. Second, the effect may depend upon the timing of selection against maladapted farmed fish in relation to spawning (Baskett & Waples, 2013; Baskett et al., 2013). Strongly maladapted escapees may not survive to interbreed with wild populations and, therefore, have no direct genetic impact. However, if selection against farmed fish occurs after spawning, then the negative impact due to hybridization may be severe. Conversely, escapees that are not strongly domesticated, and therefore display a high fitness in the wild, may cause higher levels of introgression than maladapted salmon. However, in such cases, the fitness consequences for the recipient population will not necessarily be as significant, even though qualitative changes in the genetic make-up of the recipient population may occur.

The gradient of divergence between the wild and farmed populations will display differences both regionally and from case to case. For example, farmed salmon are likely to display greater genetic differences to wild salmon in Ireland because of both domestication and non-native origin of the Norwegian salmon that are predominantly farmed there. In contrast, in Norway, the farmed salmon, while displaying domestication-driven differences to the wild salmon, will have originated from the same phylogeographic lineage, except in the Barents sea rivers (Bourret et al., 2013). In Scotland, where both Norwegian and Scottish strains are farmed, the issue will be more complex. Uncertainty about whether greater or lesser divergence from wild populations is better makes it difficult to advise regulators on whether local or non-local farmed strains present a smaller or greater risk if escapes occur (Verspoor, McGinnity, Bradbury, & Glebe, 2015).

A given level of gene flow from farmed salmon is unlikely to elicit the same degree of consequence for all wild populations. Response variation will be controlled by a complicated set of biotic and abiotic population and river-specific factors. Some of the genetic differences between farmed and wild salmon are likely to be population-specific. This includes traits such as growth under different thermal regimes (Harvey, Glover et al., 2016), gene expression patterns (Normandeau et al., 2009), survival and life history in the wild (Fleming et al., 2000; McGinnity et al., 1997; Skaala et al., 2012), competitive balance (Houde et al., 2010a), acid tolerance (Fraser et al., 2008) and pathogen susceptibility (Glover & Skaala, 2006; Lawlor, Dacanay, Hutchings, Brown, & Sperker, 2009). In addition, the competitive balance between farmed and wild salmon may differ with environmental conditions (Fraser et al., 2008; Harvey, Glover et al., 2016; Solberg, Zhang et al., 2013). In addition, the response of F1 hybrids and different backcross types may not always manifest in an additive manner (Debes et al., 2013; Einum & Fleming, 1997; Houde et al., 2010b), and differs among populations (Einum & Fleming, 1997; Houde et al., 2010b). Finally, variation in differences in egg size among the invading farmed escapees and the specific wild population will also influence the competitive balance and potential consequences. Egg size is positively correlated with alevin size (Einum & Fleming, 2000; Solberg et al., 2014) and survival in the wild (Einum & Fleming, 2000; Skaala et al., 2012). In general, farmed escapees display smaller eggs than wild salmon (Lush et al., 2014; Srivastava & Brown, 1991) although egg sizes can vary substantially among populations in the wild and egg size variation may be adaptive (Riddell, Leggett, & Saunders, 1981). However, egg size is positively correlated with female size (Kazakov, 1981; Thorpe et al., 1984). Therefore, even if eggs are smaller for farmed salmon for a given fish size, farmed salmon may produce eggs equal in size to wild fish if the escapees entering the river are much larger than the wild fish (Solberg et al., 2014, 2016). Thus, the effect of phenotypic differences, such as egg size, between escapees, the native population and their subsequent hybrids and offspring will influence the competitive interactions in the wild. These are difficult to predict.

Recent quantitative-genetic simulations have suggested that drip-leakage events (i.e. continuous low level leakage of escapees) are more likely to cause genetic changes in fitness traits in natural populations than single large-scale escape events (Baskett et al., 2013). Their conclusion contrasted with that of Hindar et al. (2006), who suggested that there is likely to be a greater effect of large pulses of salmon aquaculture escapees on wild populations. This difference arises because of the focus by Baskett et al. (2013) on equilibrium outcomes as compared to Hindar et al.'s (2006) emphasis on short-term dynamics. Despite these differences, the nature of spawning intrusion may have important implications for the fitness of native populations. Closely linked with this aspect is the fact that the pattern of introgression and admixture will have potentially important consequences for the fitness of the native population and, importantly, the ability for natural selection to "purge" admixed individuals out of the population over time. For example, a single massive spawning intrusion in one population in 1 year could theoretically lead to complete hybridization of the population, effectively hindering natural selection to purge admixed individuals out and leaving pure wild individuals (this admittedly represents an extreme hypothetical scenario). In a contrasting scenario, long-term but small-scale intrusion may lead to fragments of the population being wild, hybrid, admixed (backcrossed to wild) and farmed, leaving other opportunities for natural selection to purge maladapted genotypes from the population. The admixture profile of individual salmon in rivers subject to introgression of farmed escapees has not been thoroughly examined thus far. However, there is great potential for this using recently developed statistical approaches to identify individual admixture from diverse domesticated lines (Karlsson et al., 2014). Clearly, differences in individual admixture profiles among populations will also contribute to population-specific impacts and recovery profiles.

4.5 | What are the expected long-term consequences?

The conservation of genetic variation within and among populations (as outlined in the Biodiversity Declaration) is important for the resilience of local salmon stocks to human or natural disturbances (Ryman, 1991; Schindler et al., 2010), and in the long term, reduced genetic variability will affect a species' ability to cope with a changing environment (Lande & Shannon, 1996; McGinnity et al., 2009; Satake & Araki, 2012). Therefore, one-way gene flow, as occurs through the successful spawning of farmed escapees, potentially represents a powerful evolutionary force. It erodes genetic variation among wild populations (Glover et al., 2012) and, in the long run, may also erode the genetic variation within populations under certain situations (Tufto & Hindar, 2003). Wild populations will also become more similar to the less variable farmed populations.

Although evolutionary theory permits us to outline general trajectories, it remains difficult to predict and demonstrate the evolutionary fate of individual wild populations receiving farmed immigrants. The severity and nature of the effect depends on a multitude of factors, including the magnitude of the differences between wild and farmed populations (both historical and adaptive differences), the mechanisms underlying genetic differences between wild and farmed salmon, the frequency of intrusions of farmed fish and the numbers of intruding farmed fish relative to wild spawning population sizes (Hutchings & Fraser, 2008). Furthermore, many wild salmon populations are already under evolutionary strain from a wide variety of anthropogenic challenges (Lenders et al., 2016; Parrish, Behnke, Gephard, McCormick, & Reeves, 1998), and such populations are more likely to be vulnerable to the potential negative effects of genetic introgression. Therefore, genetic introgression must be seen in the context of other challenges.

5 | CONCLUSIONS

5.1 | What have been the largest developments in knowledge in the past decade?

As has been evident throughout this review, much was already known in respect of the potential impact of farmed salmon spawning in the wild on recipient wild populations by the late 1990s and early 2000s. This has provided the regulatory authorities with enough knowledge of potential negative effects of escapees to take appropriate actions. However, at that stage, two major bottlenecks in our capacity to *quantify* the impacts of escapees were still to be satisfactorily resolved, that is, the ability to measure accurately the level of introgression that has occurred, particularly over multiple generations (Challenge 1 – Figure 3), and what the biological consequences are in respect of responses in life history and population abundance and resilience (Challenge 2 – Figure 3).

What critical new knowledge has come to light in the past decade of research? In addition to greater clarity and detail in all aspects linked with escapees and direct genetic interactions, it can be argued that three highly significant advances have been made. Firstly, there is globally unprecedented and unequivocal evidence of introgression of farmed salmon into ~150 native Norwegian populations (ranging from 0% to 47%) (Glover et al., 2013; Karlsson et al., 2016). While this has only been quantified in Norwegian rivers/populations, Norway is currently the world's largest farmed and wild salmon producing country and therefore represents the principal focus of the concern in respect of threats posed by farmed escaped salmon on their wild conspecifics. These studies have moved the debate from "has introgression occurred," to "what is the consequence of this introgression." There is no longer room for doubt regarding the reality of introgression.

The second significant advance in our knowledge is the volume and detail of work on our understanding of the genetic differences that distinguish farmed and wild salmon because of domestication. Approximately half of the studies addressing this have been conducted in the past decade. These do not only provide us with knowledge that furthers our understanding of the potential consequences of genetic interactions, they provide us with a better understanding relating to the underlying mechanisms. Furthermore, this knowledge is highly transferrable to other aquaculture systems where genetic interactions between cultured and wild organisms can occur (Araki & Schmid, 2010). These non-salmonid aquaculture systems can use the salmon as the "model system" to understand genetic interactions between farmed escapees and wild conspecifics (Bekkevold et al., 2006). Finally, but not least, the results of these studies have provided breeding companies with unique insights into the changes elicited by their selective regimes. In turn, this may help adjust future breeding plans and approaches.

The third major recent advance has been the development of genomic resources, especially the recently published salmon genome (Lien et al., 2016). While the potential of the entire salmon genome sequence has yet to make a major contribution (but see its immediate impact on our understanding of maturation (Ayllon et al., 2015; Barson et al., 2015)), other genomic developments such as high-density SNP chips and linkage maps together with transcriptomics tools have underpinned some of the recent advancements detailed above. For example, a SNP chip was instrumental in the discovery of genetic markers that permit identification of farmed and wild salmon irrespective of their population or strain of origin (Karlsson et al., 2011), which have thereafter been used to quantify introgression (i.e. the single biggest advance). These recently and continuously emerging genomic resources now provide us with opportunities that were previously impossible.

5.2 | What major questions remain unanswered?

There are two broad and vitally important questions that remain to be fully elucidated in the grand scheme of things: 1. the current lack of unequivocal documentation and quantification of the biological consequences (productivity and abundance, resilience, life-history profiles) of introgression in natural populations (challenge 2 – Figure 3) and 2. our knowledge of and the potential need to establish threshold tolerance limits, if they exist. These are discussed briefly below.

It is well documented that farmed and wild salmon differ in many phenotypic traits (Tables 1-9). Also, there is experimental evidence showing negative fitness effects of introgression by farmed fish into wild populations. However, there is still a lack of documentation of the biological changes in natural populations at present. This can be broken down into the following interrelated questions: a) To what extent have biological changes occurred in wild populations following direct genetic interactions with farmed escapees? b) Among the many traits at which farmed and wild salmon differ, which are the ones that contribute the most to fitness loss in introgressed populations? c) How and how fast can natural selection purge maladaptive variation from recipient wild populations if farmed escapes could be minimized or discontinued? d) What is the genetic architecture (genome, transcriptome, epigenome) of traits important for fitness in the wild? The sequencing of the genome and the rapidly emerging genomics tools described above provide valuable resources for addressing these challenges.

Mining farmed-wild diagnostic loci from genomic data (Karlsson et al., 2011) now provides us with vastly improved ability to compute admixture in individual fish and connect these estimates together with ecological and biological (i.e. phenotypic traits) measurements in the wild. This will help us unravel and quantify the population-level impacts. Furthermore, monitoring adaptive genetic change can be conducted by analysing time series of samples from wild populations using high-resolution genomic methods (e.g. dense SNP chips) (Hansen, Olivieri, Waller, Nielsen, & Ge, 2012). By analysing multiple temporal samples before, during and after events of escapes and introgression it would be possible to identify loci where alleles derived from farmed salmon are under strong negative selection in the wild and follow their fate from introgression to possible purging. This would permit us to start quantifying the strength of natural selection to purge and/or naturalize farmed salmon and their hybrids in natural populations where introgression has occurred. Thus, it is likely that within the near future, the process of addressing and answering one of the most significant questions, that is what biological changes have occurred because of introgression, should emerge.

Once biological changes have been documented and quantified, there will arguably be one more question, and perhaps the “ultimate” one remaining which concerns defining possible tolerance threshold limits. Do wild populations display the evolutionary plasticity (both genetic and environmental) to absorb for example 1%, 5% or 10% introgression of farmed escapees without changing their key parameters (life-history and demographic), and without losing future evolutionary potential to other challenges such as climate change and further anthropogenic forces? It is beyond the scope of this review to evaluate mitigation strategies, but, to our knowledge, Norway is the first and only country in the world to establish threshold limits of “sustainability” linked to the frequency of farmed escapees and genetic impact on the native population (Taranger et al., 2015). The established thresholds for the incidence of farmed escapees in a wild population were set for <4% (no to low), 4%–10% (low to moderate) and >10% (high) probability of genetic change in the wild population, respectively. These threshold categories were established using a “best guess” based on current knowledge. They remain, however, scientifically unvalidated. Approaches to answer this question have been to relate the allowable amount of gene flow between cultured and wild salmon to the observed level of genetic differentiation occurring between them (Ryman, Utter, & Hindar, 1995). For most levels of genetic differentiation observed among salmon populations, this would translate into low numbers of migrants between them. For subspecies of cutthroat trout (*Oncorhynchus clarki*, Salmonidae), some have argued that there is no other defensible limit on genetic introgression than a very small one (Allendorf et al., 2004).

5.3 | Summary and scientific recommendations

I. *Spawning success of farmed escapees, and how this varies in time and space, requires further quantification to predict introgression.* Experiments show that adult escapees have reduced spawning success compared to wild salmon that depends on the life stage at which they escape into the wild, mature, and attempt to spawn with wild fish, and the level of competition with wild fish on the spawning grounds. Furthermore, farmed females display a greater relative spawning success than farmed males, which will increase the relative frequency of hybrid as opposed to pure farmed offspring.

Farmed escapee sperm and egg quality appears equal to that of wild adults, but farmed females tend to produce eggs that are smaller than wild eggs when corrected for body weight. However, whether the offspring of farmed or hybrid salmon that have lived their entire lives in the wild will always have a lower reproductive fitness than wild salmon remains unclear.

II. *There is a need to use molecular-genetic markers to quantify introgression in populations, especially in knowledge poor regions.* Introgression of farmed salmon is documented in many Norwegian populations and varies greatly among studied rivers (0%–47%), but remains largely unquantified elsewhere. Using molecular markers to quantify introgression, and accurately compute individual admixture, depends upon markers being diagnostic for farmed fish. This is affected by factors such as the ancestry of the specific farmed strains and wild populations involved. A better understanding of the genomic basis of domestication would help to identify better markers. At the same time, better insights into how biotic (wild population characteristics) and abiotic (river temperature, length, gradient, number of upstream migration challenges) factors influence introgression would help us to identify populations most at risk.

III. *The genetic differences between farmed and wild salmon that affect fitness need to be better understood to predict the impact of introgression.* A wide number of differences in genetic-based phenotypic traits have been observed between farmed and wild salmon including those associated with selection for economic and domestication traits. As not all trait differences may influence fitness in the wild, there is a need to identify which traits have the most negative impact in any given wild population subject to introgression.

IV. *Further information is needed on the fitness of farmed, admixed and wild salmon in different rivers, either using planting experiments that combine genetic and ecological measurements, or by monitoring offspring following spawning intrusions, and on selective change.* Only two whole-generation studies have been conducted in the wild, producing estimated relative fitness of farmed salmon to be 2%–16% that of wild salmon. A further study has demonstrated that the offspring of farmed salmon may display relatively high, though still lower, survival in the freshwater stage. However, the relative survival of farmed salmon offspring in the wild is likely to vary from case to case.

V. *Biological consequences (life-history, phenotypic and demographic) of farmed salmon introgression have been inadequately studied in the wild.* An increase in within-population genetic variation and a simultaneous loss in genetic diversity among populations have been observed in Norwegian populations exposed to gene flow from farmed escapees. A combination of empirical data from laboratory and field experiments together with evolutionary theory and synthesis through models suggest that when exposed to gene flow from farmed escapees, genetic changes in wild populations will occur in the direction of the invading farmed strains in phenotypic and life-history traits. Furthermore, as the offspring of farmed salmon compete with wild salmon for resources in the river, introgression will also lead to a reduction in the production of wild (two wild parents) smolts, as well as a potential reduction in the total number of smolts and returning adults (all genetic backgrounds). Detecting population-level changes will be challenging in the short-term and under low-to-modest introgression scenarios because wild populations are plastic in their phenotypic and life-history responses. Together with environmental stochasticity, this will tend to mask early changes. Also, the force of natural selection to purge maladapted genotypes from native populations following introgression remains to be quantified. This makes it imperative to undertake *in situ* studies and to have a commitment to long-term, pedigree-based, longitudinal studies of natural populations.

VI. *Evaluation of direct genetic impact of farmed escapes on wild populations must be seen in the context of additional challenges.* The genetic impact of escapees on the genetic integrity and long-term evolutionary capacity of native populations will scale with the numbers of escapees entering the rivers, in addition to each population′s specific characteristics. This effect may interact negatively with other challenges faced by these populations such as climate change, disease and pathogen challenges, habitat loss, overfishing, acidification.

VII. *The long-term consequences of introgression on native populations can be expected to lead to changes in life-history traits, reduced population productivity and decreased resilience to future impacts such as climate change (i.e. less fish and more fragile stocks).* Conducting research on various aspects of the genetic interactions between farmed escapees and wild conspecifics is crucial to understand mechanisms, quantify impacts, determine resiliency and estimate the recuperative potential of wild populations. Such research will, however, not solve the problem. This requires additional research into impact avoidance or mitigation strategies that can hinder or stop further erosion of genetic integrity. Finally, it is important to make it unequivocally clear that only a substantial or complete reduction in the number of escapees in rivers, and/or creating a reproductive barrier through sterilization of farmed salmon, will represent a solution to the challenge.

ACKNOWLEDGEMENTS

Most the time of the senior author (KAG) related to the writing the first draft of the review was financed by the Research Council of Norway (RCN) INTERACT project grant number 200510, and the Norwegian Ministry for Trade and Fisheries (NFD). In addition to these primary funding sources, the RCN project QUANTESCAPE (grant no. 216105) financed written contributions from several Norway-based collaborators. The involvement of the contributors from outside Norway was financed by a diverse array of funding bodies whose support is gratefully acknowledged (JSPS KAKENHIJP26292102); the Danish Council for Independent Research, Natural Sciences (grant no. 1323-00158A to MMH), as are the helpful discussions with other colleagues and collaborators on various elements of the manuscript. PMcG was supported by the Beaufort Marine Research Award in Fish Population Genetics funded by the Irish Government under the Sea Change Programme. We would like to thank the three anonymous referees and the handling editor for constructive input.

REFERENCES

Abrantes, K. G., Lyle, J. M., Nichols, P. D., & Semmens, J. M. (2011). Do exotic salmonids feed on native fauna after escaping from aquaculture cages in Tasmania, Australia? *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 1539–1551.

Allendorf, F. W., Leary, R. F., Hitt, N. P., Knudsen, K. L., Lundquist, L. L., & Spruell, P. (2004). Intercrosses and the US Endangered Species Act: Should hybridized populations be included as Westslope cutthroat trout? *Conservation Biology*, *18*, 1203–1213.

Alvial, A., Kibenge, F., Forster, J., Burgos, J. M., Ibarra, R., & St-Hilaire, S. (2012) The Recovery of the Chilean Salmon Industry: The ISA Crisis and its Consequences and Lessons. In: The Global Aquaculture Alliance. 83 pp.

Anon. (2005) Ecosystems and Human Well-being: Synthesis. Washington DC. Retrieved from http://www.millenniumassessment.org/documents/document.356.aspx.pdf. Last accessed April 2016.

Anon. (2015a) Rømt oppdrettslaks i vassdrag. Rapport fra det nasjonale overvåkningsprogrammet 2014. Fisken og Havet, særnr. 2b-2015.

Anon. (2015b) Status for norske laksebestander i 2015. Rapport fra Vitenskapelig råd for Lakseforvaltning nr 8, 300s. (In Norwegian).

Anon. (2016) Rømt oppdrettslaks i vassdrag. Rapport fra det nasjonale overvåkningsprogrammet 2015. Fisken og Havet, særnr. 2b-2016.

Araki, H., Berejikian, B. A., Ford, M. J., & Blouin, M. S. (2008). Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, *1*, 342–355.

Araki, H., & Schmid, C. (2010). Is hatchery stocking a help or harm? Evidence, limitations and future directions in ecological and genetic surveys. *Aquaculture*, *308*, 2–11.

Ayllon, F., Kjaerner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M. F., Dahle, G., … Wargelius, A. (2015). The vgll3 locus controls age at maturity in wild and domesticated Atlantic Salmon (*Salmo salar* L.) males. *Plos Genetics*, *11*(11), e1005628.

Bacon, P. J., Malcolm, I. A., Fryer, R. J., Glover, R. S., Millar, C. P., & Youngson, A. F. (2015). Can conservation stocking enhance juvenile emigrant production in wild Atlantic Salmon? *Transactions of the American Fisheries Society*, *144*, 642–654.

Baranski, M., Moen, T., & Vage, D. I. (2010). Mapping of quantitative trait loci for flesh colour and growth traits in Atlantic salmon (*Salmo salar*). *Genetics Selection Evolution*, *42*, 17.

Barson, N. J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G. H., Fiske, P., … Primmer, C. R. (2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature*, *528*, 405–+.

Baskett, M. L., Burgess, S. C., & Waples, R. S. (2013). Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. *Evolutionary Applications*, *6*, 1090–1108.

Baskett, M. L., & Waples, R. S. (2013). Evaluating alternative strategies for minimizing unintended fitness consequences of cultured individuals on wild populations. *Conservation Biology*, *27*, 83–94.

Bekkevold, D., Hansen, M. M., & Nielsen, E. E. (2006). Genetic impact of gadoid culture on wild fish populations: Predictions, lessons from salmonids, and possibilities for minimizing adverse effects. *Ices Journal of Marine Science*, *63*, 198–208.

Bentsen, H. B., & Thodesen, J. (2005) Genetic interactions between farmed and wild fish, with examples from the Atlantic Salmon case in Norway. In: T. Gjedrem (Ed.), *Selection and breeding programs in aquaculture* (pp. 319–334). Netherlands: Springer.

Besnier, F., Glover, K. A., & Skaala, O. (2011). Investigating genetic change in wild populations: Modelling gene flow from farm escapees. *Aquaculture Environment Interactions*, *2*, 75–86.

Besnier, F., Glover, K. A., Lien, S., Kent, M., Hansen, M. M., Shen, X., & Skaala, O. (2015). Identification of quantitative genetic components of fitness variation in farmed, hybrid and native salmon in the wild. *Heredity*, *115*, 47–55.

Bicskei, B., Bron, J. E., Glover, K. A., & Taggart, J. B. (2014). A comparison of gene transcription profiles of domesticated and wild Atlantic salmon (*Salmo salar* L.) at early life stages, reared under controlled conditions. *Bmc Genomics*, *15*, 884.

Bicskei, B., Taggart, J. B., Glover, K. A., & Bron, J. E. (2016). Comparing the transcriptomes of embryos from domesticated and wild Atlantic salmon (*Salmo salar* L.) stocks and examining factors that influence heritability of gene expression. *Genetics Selection Evolution*, *48*, 1–16.

Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2004). Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society B-Biological Sciences*, *271*, 2233–2237.

Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2006). Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology*, *75*, 1165–1171.

Bostock, J., McAndrew, B., Richards, R., Jauncey, K., Telfer, T., Lorenzen, K., … Corner, R. (2010). Aquaculture: Global status and trends. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *365*, 2897–2912.

Bourret, V., O'Reilly, P. T., Carr, J. W., Berg, P. R., & Bernatchez, L. (2011). Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. *Heredity*, *106*, 500–510.

Bourret, V., Kent, M. P., Primmer, C. R., Vasemagi, A., Karlsson, S., Hindar, K., … Lien, S. (2013). SNP-array reveals genome-wide patterns of geographical and potential adaptive divergence across the natural range of Atlantic salmon (*Salmo salar*). *Molecular Ecology*, *22*, 532–551.

Bovenkerk, B., & Meijboom, F. L. B. (2012). The Moral Status of Fish. The importance and limitations of a fundamental discussion for practical ethical questions in fish farming. *Journal of Agricultural & Environmental Ethics*, *25*, 843–860.

Brenna-Hansen, S., Li, J. Y., Kent, M. P., Boulding, E. G., Dominik, S., Davidson, W. S., & Lien, S. (2012). Chromosomal differences between European and North American Atlantic salmon discovered by linkage mapping and supported by fluorescence in situ hybridization analysis. *Bmc Genomics*, *13*, 432.

Brieuc, M. S. O., Ono, K., Drinan, D. P., & Naish, K. A. (2015). Integration of Random Forest with population-based outlier analyses provides insight on the genomic basis and evolution of run timing in Chinook salmon (*Oncorhynchus tshawytscha*). *Molecular Ecology*, *24*, 2729–2746.

Burger, R., & Lynch, M. (1995). Evolution and extinction in a changing environment – a quantitative genetics analysis. *Evolution*, *49*, 151–163.

Burridge, L., Weis, J. S., Cabello, F., Pizarro, J., & Bostick, K. (2008). Chemical use in salmon aquaculture: A review of current practices and possible environmental effects. *Aquaculture*, *306*, 7–23.

Buschmann, A. H., Riquelme, V. A., Hernandez-Gonzalez, M. C., Varela, D., Jimenez, J. E., Henriquez, L. A., … Filun, L. (2006). A review of the impacts of salmonid farming on marine coastal ecosystems in the southeast Pacific. *Ices Journal of Marine Science*, *63*, 1338–1345.

Butler, J. R. A., Cunningham, P. D., & Starr, K. (2005). The prevalence of escaped farmed salmon, *Salmo salar* L., in the River Ewe, western Scotland, with notes on their ages, weights and spawning distribution. *Fisheries Management and Ecology*, *12*, 149–159.

Camarillo-Sepulveda, N., Hamoutene, D., Lush, L., Burt, K., Volkoff, H., & Fleming, I. A. (2016). Sperm traits in farmed and wild Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, *88*, 709–717.

Carr, J. W., Anderson, J. M., Whoriskey, F. G., & Dilworth, T. (1997). The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. *Ices Journal of Marine Science*, *54*, 1064–1073.

Carr, J. W., Lacroix, G. L., Anderson, J. M., & Dilworth, T. (1997). Movements of non-maturing cultured Atlantic salmon (*Salmo salar*) in a Canadian river. *Ices Journal of Marine Science*, *54*, 1082–1085.

Carr, J. W., & Whoriskey, F. G. (2006). The escape of juvenile farmed Atlantic salmon from hatcheries into freshwater streams in New Brunswick, Canada. *Ices Journal of Marine Science*, *63*, 1263–1268.

Castellani, M., Heino, M., Gilbey, J., Araki, H., Svasand, T., & Glover, K. A. (2015). IBSEM: An individual-based Atlantic Salmon population model. *PLoS One*, *10*(9), e0138444.

Cauwelier, E., Gilbey, J., Jones, C. S., Noble, L. R., & Verspoor, E. (2012). Asymmetrical viability in backcrosses between highly divergent populations of Atlantic salmon (*Salmo salar*): Implications for conservation. *Conservation Genetics*, *13*, 1665–1669.

Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *Ices Journal of Marine Science*, *69*, 1538–1548.

Christie, M. R., Marine, M. L., Fox, S. E., French, R. A., & Blouin, M. S. (2016). A single generation of domestication heritably alters the expression of hundreds of genes. *Nature Communications*, *7*, 10676.

Clifford, S. L. (1996) *The genetic impact on native Atlantic salmon populations resulting from the escape of farmed salmon*. PhD Thesis, Queen's University, Belfast.

Clifford, S. L., McGinnity, P., & Ferguson, A. (1998a). Genetic changes in an Atlantic salmon population resulting from escaped juvenile farm salmon. *Journal of Fish Biology*, *52*, 118–127.

Clifford, S. L., McGinnity, P., & Ferguson, A. (1998b). Genetic changes in Atlantic salmon (*Salmo salar*) populations of northwest Irish rivers resulting from escapes of adult farm salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 358–363.

Consuegra, S., Megens, H. J., Schaschl, H., Leon, K., Stet, R. J. M., & Jordan, W. C. (2005). Rapid evolution of the MH class I locus results in different allelic compositions in recently diverged populations of Atlantic salmon. *Molecular Biology and Evolution*, *22*, 1095–1106.

Coughlan, J., McGinnity, P., O'Farrell, B., Dillane, E., Diserud, O., de Eyto, E., … Cross, T. F. (2006). Temporal variation in an immune response gene (MHC I) in anadromous Salmo trutta in an Irish river before and during aquaculture activities. *Ices Journal of Marine Science*, *63*, 1248–1255.

Coulson, M. (2013) Report on genetic tool development for distinguishing farmed vs wild fish in Scotland. In: Rivers and fisheries Trusts of Scotland Report. Retrieved from http://www.rafts.org.uk/wp-content/uploads/2013/02/MIAP_Genetic_report_final.pdf. Last accessed April 2016.

Cross, T. F., & Challanain, D. N. (1991). Genetic characterization of Atlantic salmon (*Salmo salar*) lines farmed in Ireland. *Aquaculture*, *98*, 209–216.

Crozier, W. W. (1993). Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L) in a Northern Irish river. *Aquaculture*, *113*, 19–29.

Crozier, W. W. (1998). Incidence of escaped farmed salmon, *Salmo salar* L., in commercial salmon catches and freshwater in Northern Ireland. *Fisheries Management and Ecology*, *5*, 23–29.

Crozier, W. W. (2000). Escaped farmed salmon, *Salmo salar* L., in the Glenarm River, Northern Ireland: Genetic status of the wild population 7 years on. *Fisheries Management and Ecology*, *7*, 437–446.

Darwish, T. L., & Hutchings, J. A. (2009). Genetic variability in reaction norms between farmed and wild backcrosses of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 83–90.

Davey, J. W., Hohenlohe, P. A., Etter, P. D., Boone, J. Q., Catchen, J. M., & Blaxter, M. L. (2011). Genome-wide genetic marker discovery and genotyping using next-generation sequencing. *Nature Reviews Genetics*, *12*, 499–510.

de Villemereuil, P., Gaggiotti, O. E., Mouterde, M., & Till-Bottraud, I. (2016). Common garden experiments in the genomic era: New perspectives and opportunities. *Heredity*, *116*, 249–254.

Debes, P. V., Normandeau, E., Fraser, D. J., Bernatchez, L., & Hutchings, J. A. (2012). Differences in transcription levels among wild, domesticated, and hybrid Atlantic salmon (*Salmo salar*) from two environments. *Molecular Ecology*, *21*, 2574–2587.

Debes, P. V., Fraser, D. J., McBride, M. C., & Hutchings, J. A. (2013). Multigenerational hybridisation and its consequences for maternal effects in Atlantic salmon. *Heredity*, *111*, 238–247.

Debes, P. V., Fraser, D. J., Yates, M., & Hutchings, J. A. (2014). The between-population genetic architecture of growth, maturation, and plasticity in Atlantic salmon. *Genetics*, *196*, 1277–1291.

Debes, P. V., & Hutchings, J. A. (2014). Effects of domestication on parr maturity, growth, and vulnerability to predation in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 1371–1384.

Devlin, R. H., Sakhrani, D., Tymchuk, W. E., Rise, M. L., & Goh, B. (2009). Domestication and growth hormone transgenesis cause similar changes in gene expression in coho salmon (*Oncorhynchus kisutch*). *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 3047–3052.

Devlin, R. H., Sakhrani, D., White, S., & Overturf, K. (2013). Effects of domestication and growth hormone transgenesis on mRNA profiles in rainbow trout (*Oncorhynchus mykiss*). *Journal of Animal Science*, *91*, 5247–5258.

Dillane, E., Cross, M. C., McGinnity, P., Coughlan, J. P., Galvin, P. T., Wilkins, N. P., & Cross, T. F. (2007). Spatial and temporal patterns in microsatellite DNA variation of wild Atlantic salmon, *Salmo salar*, in Irish rivers. *Fisheries Management and Ecology*, *14*, 209–219.

Dillane, E., McGinnity, P., Coughlan, J. P., Cross, M. C., de Eyto, E., Kenchington, E., … Cross, T. F. (2008). Demographics and landscape features determine intrariver population structure in Atlantic salmon (*Salmo salar* L.): The case of the River Moy in Ireland. *Molecular Ecology*, *17*, 4786–4800.

Dionne, M., Caron, F., Dodson, J. J., & Bernatchez, L. (2008). Landscape genetics and hierarchical genetic structure in Atlantic salmon: The interaction of gene flow and local adaptation. *Molecular Ecology*, *17*, 2382–2396.

Dionne, M., Caron, F., Dodson, J. J., & Bernatchez, L. (2009). Comparative survey of within-river genetic structure in Atlantic salmon; relevance for management and conservation. *Conservation Genetics*, *10*, 869–879.

Dunmall, K. M., & Schreer, J. F. (2003). A comparison of the swimming and cardiac performance of farmed and wild Atlantic salmon *Salmo salar*, before and after gamete stripping. *Aquaculture*, *220*, 869–882.

Edmands, S. (2007). Between a rock and a hard place: Evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Molecular Ecology*, *16*, 463–475.

Einum, S., & Fleming, I. A. (1997). Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *Journal of Fish Biology*, *50*, 634–651.

Einum, S., & Fleming, I. A. (2000). Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution*, *54*, 628–639.

Ellstrand, N. C., Prentice, H. C., & Hancock, J. F. (1999). Gene flow and introgression from domesticated plants into their wild relatives. *Annual Review of Ecology and Systematics*, *30*, 539–563.

Erkinaro, J., Niemela, E., Vaha, J. P., Primmer, C. R., Brors, S., & Hassinen, E. (2010). Distribution and biological characteristics of escaped farmed salmon in a major subarctic wild salmon river: Implications for monitoring. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 130–142.

Evans, M. L., Hori, T. S., Rise, M. L., & Fleming, I. A. (2015). Transcriptomic responses of Atlantic Salmon (*Salmo salar*) to environmental enrichment during Juvenile rearing. *PLoS One*, *10*(3), e0118378.

FAO (2016) The state of worlds fisheries and aquaculture 2016. Food and Agriculture Organization of the United Nations, Rome. Last accessed April 2016.

Feltham, M. J., & MacLean, J. C. (1996). Carlin tag recoveries as an indicator of predation on salmon smelts by goosanders and red-breasted mergansers. *Journal of Fish Biology*, *48*, 270–282.

Ferguson, A., Taggart, J. B., Prodohl, P. A., McMeel, O., Thompson, C., Stone, C., … Hynes, R. A. (1995). The application of molecular markers to the study and conservation of fish populations, with special reference to Salmo. *Journal of Fish Biology*, *47*, 103–126.

Ferguson, A., Fleming, I. A., Hindar, K., Skaala, Ø., McGinnity, P., Cross, T., & Prodohl, P. (2007). Farm escapees. In: E. Verspoor, L. Stradmeyer

& J. L. Nielsen (Eds.), *The Atlantic salmon. Genetics, Conservation and Management* (pp. 357–398). Oxford, UK: Blackwell.

Fisher, A. C., Volpe, J. P., & Fisher, J. T. (2014). Occupancy dynamics of escaped farmed Atlantic salmon in Canadian Pacific coastal salmon streams: Implications for sustained invasions. *Biological Invasions*, *16*, 2137–2146.

Fiske, P., Lund, R. A., Østborg, G. M., & Fløystad, L. (2001). Rømt oppdrettslaks i sjø- og elvefisket i årene 1989-2000. *NINA oppdresgsmelding*, *704*, 1–26. (In Norwegian).

Fiske, P., Lund, R. A., & Hansen, L. P. (2006). Relationships between the frequency of farmed Atlantic salmon, *Salmo salar* L., in wild salmon populations and fish farming activity in Norway, 1989-2004. *Ices Journal of Marine Science*, *63*, 1182–1189.

Fleming, I. A., Jonsson, B., Gross, M. R., & Lamberg, A. (1996). An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *Journal of Applied Ecology*, *33*, 893–905.

Fleming, I. A., & Einum, S. (1997). Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. *Ices Journal of Marine Science*, *54*, 1051–1063.

Fleming, I. A., Lamberg, A., & Jonsson, B. (1997). Effects of early experience on the reproductive performance of Atlantic salmon. *Behavioral Ecology*, *8*, 470–480.

Fleming, I. A., Hindar, K., Mjolnerod, I. B., Jonsson, B., Balstad, T., & Lamberg, A. (2000). Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *267*, 1517–1523.

Fleming, I. A., Agustsson, T., Finstad, B., Johnsson, J. I., & Bjornsson, B. T. (2002). Effects of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *59*, 1323–1330.

Ford, J. S., & Myers, R. A. (2008). A global assessment of salmon aquaculture impacts on wild salmonids. *Plos Biology*, *6*, 411–417.

Franklin, P., Verspoor, E., & Slaski, R. (2012) Study into the impacts of open pen freshwater aquaculture production on wild fisheries. In: Report for Marine Scotland by Homarus Ltd., Beaulieu, Hampshire, UK. Final Report P/SFWP/286, 160 pp.

Fraser, D. J., Cook, A. M., Eddington, J. D., Bentzen, P., & Hutchings, J. A. (2008). Mixed evidence for reduced local adaptation in wild salmon resulting from interbreeding with escaped farmed salmon: Complexities in hybrid fitness. *Evolutionary Applications*, *1*, 501–512.

Fraser, D. J., Houde, A. L. S., Debes, P. V., O'Reilly, P., Eddington, J. D., & Hutchings, J. A. (2010). Consequences of farmed-wild hybridization across divergent wild populations and multiple traits in salmon. *Ecological Applications*, *20*, 935–953.

Fraser, D. J., Minto, C., Calvert, A. M., Eddington, J. D., & Hutchings, J. A. (2010). Potential for domesticated-wild interbreeding to induce maladaptive phenology across multiple populations of wild Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *67*, 1768–1775.

Fraser, D. J., Weir, L. K., Bernatchez, L., Hansen, M. M., & Taylor, E. B. (2011). Extent and scale of local adaptation in salmonid fishes: Review and meta-analysis. *Heredity*, *106*, 404–420.

Friars, G. W., Bailey, J. K., & Oflynn, F. M. (1995). Applications of selection for multiple traits in cage-reared Atlantic salmon (*Salmo salar*). *Aquaculture*, *137*, 213–217.

Friedland, K. D., Hansen, L. P., Dunkley, D. A., & MacLean, J. C. (2000). Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *Ices Journal of Marine Science*, *57*, 419–429.

Gage, M. J. G., Stockley, P., & Parker, G. A. (1998). Sperm morphometry in the Atlantic salmon. *Journal of Fish Biology*, *53*, 835–840.

Gage, M. J. G., Macfarlane, C. P., Yeates, S., Ward, R. G., Searle, J. B., & Parker, G. A. (2004). Spermatozoal traits and sperm competition in Atlantic salmon: Relative sperm velocity is the primary determinant of fertilization success. *Current Biology*, *14*, 44–47.

Garant, D., Fleming, I. A., Einum, S., & Bernatchez, L. (2003). Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecology Letters*, *6*, 541–549.

Garcia de Leaniz, C., Fleming, I. A., Einum, S., Verspoor, E., Jordan, W. C., Consuegra, S., … Quinn, T. P. (2007). A critical review of adaptive genetic variation in Atlantic salmon: Implications for conservation. *Biological Reviews*, *82*, 173–211.

Gausen, D., & Moen, V. (1991). Large-scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 426–428.

Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, *21*, 394–407.

Gilbey, J., Knox, D., O'Sullivan, M., & Verspoor, E. (2005). Novel DNA markers for rapid, accurate, and cost-effective discrimination of the continental origin of Atlantic salmon (*Salmo salar* L.). *Ices Journal of Marine Science*, *62*, 1609–1616.

Gjedrem, T., & Aulstad, D. (1974). Selection experiments with salmon 1. Differences in resistance to vibrio disease of salmon parr (*Salmo salar*). *Aquaculture*, *3*, 51–59.

Gjedrem, T., Gjoen, H. M., & Gjerde, B. (1991). Genetic-origin of Norwegian farmed Atlantic salmon. *Aquaculture*, *98*, 41–50.

Gjedrem, T., Salte, R., & Gjoen, H. M. (1991). Genetic-variation in susceptibility of Atlantic salmon to furunculosis. *Aquaculture*, *97*, 1–6.

Gjedrem, T. (2000). Genetic improvement of cold-water fish species. *Aquaculture Research*, *31*, 25–33.

Gjedrem, T. (2010). The first family-based breeding program in aquaculture. *Reviews in Aquaculture*, *2*, 2–15.

Gjerde, B., & Gjedrem, T. (1984). Estimates of phenotypic and genetic-parameters for carcass traits in Atlantic salmon and rainbow-trout. *Aquaculture*, *36*, 97–110.

Gjerde, B., Simianer, H., & Refstie, T. (1994). Estimates of genetic and phenotypic parameters for body-weight, growth-rate and sexual maturity in Atlantic salmon. *Livestock Production Science*, *38*, 133–143.

Gjoen, H. M., & Bentsen, H. B. (1997). Past, present, and future of genetic improvement in salmon aquaculture. *Ices Journal of Marine Science*, *54*, 1009–1014.

Glover, K. A., Hamre, L. A., Skaala, O., & Nilsen, F. (2004). A comparison of sea louse (*Lepeophtheirus salmonis*) infection levels in farmed and wild Atlantic salmon (*Salmo salar* L.) stocks. *Aquaculture*, *232*, 41–52.

Glover, K. A., Aasmundstad, T., Nilsen, F., Storset, A., & Skaala, O. (2005). Variation of Atlantic salmon families (*Salmo salar* L.) in susceptibility to the sea lice *Lepeophtheirus salmonis* and *Caligus elongatus*. *Aquaculture*, *245*, 19–30.

Glover, K. A., Bergh, O., Rudra, H., & Skaala, O. (2006). Juvenile growth and susceptibility to Aeromonas salmonicida subsp salmonicida in Atlantic salmon (*Salmo salar* L.) of farmed, hybrid and wild parentage. *Aquaculture*, *254*, 72–81.

Glover, K. A., & Skaala, O. (2006). Temporal stability of sea louse *Lepeophtheirus salmonis* Kroyer populations on Atlantic salmon *Salmo salar* L. of wild, farm and hybrid parentage. *Journal of Fish Biology*, *68*, 1795–1807.

Glover, K. A., Skar, C., Christie, K. E., Glette, J., Rudra, H., & Skaala, O. (2006). Size-dependent susceptibility to infectious salmon anemia virus (ISAV) in Atlantic salmon (*Salmo salar* L.) of farm, hybrid and wild parentage. *Aquaculture*, *254*, 82–91.

Glover, K. A., Skilbrei, O. T., & Skaala, O. (2008). Genetic assignment identifies farm of origin for Atlantic salmon *Salmo salar* escapees in a Norwegian fjord. *Ices Journal of Marine Science*, *65*, 912–920.

Glover, K. A., Hansen, M. M., & Skaala, O. (2009). Identifying the source of farmed escaped Atlantic salmon (*Salmo salar*): Bayesian clustering analysis increases accuracy of assignment. *Aquaculture*, *290*, 37–46.

Glover, K. A., Ottera, H., Olsen, R. E., Slinde, E., Taranger, G. L., & Skaala, O. (2009). A comparison of farmed, wild and hybrid Atlantic salmon (*Salmo salar* L.) reared under farming conditions. *Aquaculture*, *286*, 203–210.

Glover, K. A. (2010). Forensic identification of fish farm escapees: The Norwegian experience. *Aquaculture Environment Interactions*, *1*, 1–10.

Glover, K. A., Dahle, G., & Jorstad, K. E. (2011). Genetic identification of farmed and wild Atlantic cod, *Gadus morhua*, in coastal Norway. *Ices Journal of Marine Science*, *68*, 901–910.

Glover, K. A., Skaala, O., Sovik, A. G. E., & Helle, T. A. (2011). Genetic differentiation among Atlantic salmon reared in sea-cages reveals a non-random distribution of genetic material from a breeding programme to commercial production. *Aquaculture Research*, *42*, 1323–1331.

Glover, K. A., Quintela, M., Wennevik, V., Besnier, F., Sørvik, A. G. E., & Skaala, O. (2012). Three decades of farmed escapees in the wild: A spatio-temporal analysis of population genetic structure throughout Norway. *PLoS One*, *7*(8), e43129.

Glover, K. A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M., & Skaala, Ø. (2013). Atlantic salmon populations invaded by farmed escapees: Quantifying genetic introgression with a Bayesian approach and SNPs. *Bmc Genetics*, *14*, 4.

Glover, K. A., Madhun, A. S., Dahle, G., Sorvik, A. G. E., Wennevik, V., Skaala, O., … Fjelldal, P. G. (2015). The frequency of spontaneous triploidy in farmed Atlantic salmon produced in Norway during the period 2007-2014. *Bmc Genetics*, *16*, 37.

Glover, K. A., Bos, J. B., Urdal, K., Madhun, A. S., Sørvik, A. G. E., Unneland, L., … Wennevik, W. (2016). Genetic screening of farmed Atlantic salmon escapees demonstrates that triploid fish display reduced migration to freshwater. *Biological Invasions*, *18*, 1287–1294.

Gonen, S., Baranski, M., Thorland, I., Norris, A., Grove, H., Arnesen, P., … Houston, R. D. (2015). Mapping and validation of a major QTL affecting resistance to pancreas disease (salmonid alphavirus) in Atlantic salmon (*Salmo salar*). *Heredity*, *115*, 405–414.

Green, D. M., Penman, D. J., Migaud, H., Bron, J. E., Taggart, J. B., & McAndrew, B. J. (2012). The impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on catch statistics in Scotland. *PLoS One*, *7*(9), e43560.

Gudjonsson, S. (1991). Occurrence of reared salmon in natural salmon rivers in Iceland. *Aquaculture*, *98*, 133–142.

Gunnes, K., & Gjedrem, T. (1978). Selection experiments with salmon. 4. Growth of Atlantic salmon during 2 years in sea. *Aquaculture*, *15*, 19–33.

Gutierrez, A. P., Yanez, J. M., & Davidson, W. S. (2016). Evidence of recent signatures of selection during domestication in an Atlantic salmon population. *Marine genomics*, *26*, 41–50.

Hamoutene, D., Costa, I., Burt, K., Lush, L., & Caines, J. (2015). Survival of farmed, wild and first generation hybrid Atlantic salmon (*Salmo salar* Linnaeus, 1758) to low temperatures following seawater transfer. *Journal of Applied Ichthyology*, *31*, 333–336.

Hamre, L. A., Glover, K. A., & Nilsen, F. (2009). Establishment and characterisation of salmon louse (*Lepeophtheirus salmonis* (Krøyer 1837)) laboratory strains. *Parasitology International*, *58*, 451–460.

Handeland, S. O., Bjornsson, B. T., Arnesen, A. M., & Stefansson, S. O. (2003). Seawater adaptation and growth of post-smolt Atlantic salmon (*Salmo salar*) of wild and farmed strains. *Aquaculture*, *220*, 367–384.

Hansen, L. P., Reddin, D. G., & Lund, R. A. (1997). The incidence of reared Atlantic salmon (*Salmo salar* L) of fish farm origin at West Greenland. *Ices Journal of Marine Science*, *54*, 152–155.

Hansen, L. P., & Jacobsen, J. A. (2003). Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. *Ices Journal of Marine Science*, *60*, 110–119.

Hansen, L. P. (2006). Migration and survival of farmed Atlantic salmon (*Salmo salar* L.) released from two Norwegian fish farms. *Ices Journal of Marine Science*, *63*, 1211–1217.

Hansen, M. M., & Mensberg, K. L. D. (2009). Admixture analysis of stocked brown trout populations using mapped microsatellite DNA markers: Indigenous trout persist in introgressed populations. *Biology Letters*, *5*, 656–659.

Hansen, M. M., Olivieri, I., Waller, D. M., Nielsen, E. E., & The Genetic Monitoring Working Group (2012). Monitoring adaptive genetic responses to environmental change. *Molecular Ecology*, *21*, 1311–1329.

Harvey, A., Glover, K. A., Taylor, M. I., Creer, S., & Carvalho, G. R. (2016). A common garden design reveals population-specific variability in potential impacts of hybridization between populations of farmed and wild Atlantic salmon, *Salmo salar* L. *Evolutionary Applications*, *9*, 435–449.

Harvey, A., Juleff, G., Carvalho, G. R., Taylor, M. I., Solberg, M. F., Creer, S., … Glover, K. A. (2016). Does density influence relative growth performance of farmed, wild, and F1 hybrid Atlantic salmon in semi-natural and hatchery common garden conditions? *Royal Society Open Science*, *3*, 160152.

Harvey, A., Solberg, M. F., Glover, K. A., Taylor, M. I., Creer, S., & Carvalho, G. R. (2016). Plasticity in response to feed availability – does feeding regime influence the relative growth performance of domesticated, wild and hybrid Atlantic salmon *Salmo salar* parr? *Journal of Fish Biology*, *89*, 1754–1768.

Heggberget, T. G., Johnsen, B. O., Hindar, K., Jonsson, B., Hansen, L. P., Hvidsten, N. A., & Jensen, A. J. (1993). Interactions between wild and cultured Atlantic salmon – a review of the Norwegian experience. *Fisheries Research*, *18*, 123–146.

Heggberget, T. G., Okland, F., & Ugedal, O. (1993). Distribution and migratory behavior of adult wild and farmed Atlantic salmon (*Salmo salar*) during return migration. *Aquaculture*, *118*, 73–83.

Heino, M., Svåsand, T., Wennevik, V., & Glover, K. A. (2015). Genetic introgression of farmed salmon in native populations: Quantifying the relative influence of population size and frequency of escapees. *Aquaculture Environment Interactions*, *6*, 185–190.

Henderson, J. N., & Letcher, B. H. (2003). Predation on stocked Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*, 32–42.

Herbinger, C. M., O'Reilly, P. T., & Verspoor, E. (2006). Unravelling first-generation pedigrees in wild endangered salmon populations using molecular genetic markers. *Molecular Ecology*, *15*, 2261–2275.

Hindar, K., Ryman, N., & Utter, F. (1991). Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*, 945–957.

Hindar, K., Fleming, I. A., McGinnity, P., & Diserud, A. (2006). Genetic and ecological effects of salmon farming on wild salmon: Modelling from experimental results. *Ices Journal of Marine Science*, *63*, 1234–1247.

Hislop, J. R. G., & Webb, J. H. (1992). Escaped farmed Atlantic salmon, *Salmo salar* L., feeding in Scottish coastal waters. *Aquaculture and Fisheries Management*, *23*, 721–723.

Houde, A. L. S., Fraser, D. J., & Hutchings, J. A. (2010a). Fitness-related consequences of competitive interactions between farmed and wild Atlantic salmon at different proportional representations of wild-farmed hybrids. *Ices Journal of Marine Science*, *67*, 657–667.

Houde, A. L. S., Fraser, D. J., & Hutchings, J. A. (2010b). Reduced anti-predator responses in multi-generational hybrids of farmed and wild Atlantic salmon (*Salmo salar* L.). *Conservation Genetics*, *11*, 785–794.

Houston, R. D., Haley, C. S., Hamilton, A., Guy, D. R., Mota-Velasco, J. C., Gheyas, A. A., … Bishop, S. C. (2010). The susceptibility of Atlantic salmon fry to freshwater infectious pancreatic necrosis is largely explained by a major QTL. *Heredity*, *105*, 318–327.

Houston, R. D., Taggart, J. B., Cezard, T., Bekaert, M., Lowe, N. R., Downing, A., … Hamilton, A. (2014). Development and validation of a high density SNP genotyping array for Atlantic salmon (*Salmo salar*). *Bmc Genomics*, *15*, 90.

Huisman, J., & Tufto, J. (2012). Comparison of non-gaussian quantitative genetic models for migration and stabilizing selection. *Evolution*, *66*, 3444–3461.

Huntingford, F. A. (2004). Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *Journal of Fish Biology*, *65*, 122–142.

Hutchings, J. A. (2000). Collapse and recovery of marine fishes. *Nature*, *406*, 882–885.

Hutchings, J. A., & Fraser, D. J. (2008). The nature of fisheries- and farming-induced evolution. *Molecular Ecology*, *17*, 294–313.

Jensen, O., Dempster, T., Thorstad, E. B., Uglem, I., & Fredheim, A. (2010). Escapes of fishes from Norwegian sea-cage aquaculture: Causes, consequences and prevention. *Aquaculture Environment Interactions*, *1*, 71–83.

Jensen, A. J., Karlsson, S., Fiske, P., Hansen, L. P., Hindar, K., & Ostborg, G. M. (2013). Escaped farmed Atlantic salmon grow, migrate and disperse throughout the Arctic Ocean like wild salmon. *Aquaculture Environment Interactions*, *3*, 223–229.

Johnsson, J. I., Hojesjo, J., & Fleming, I. A. (2001). Behavioural and heart rate responses to predation risk in wild and domesticated Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 788–794.

Johnstone, D. L., O'Connell, M. F., Palstra, F. P., & Ruzzante, D. E. (2013). Mature male parr contribution to the effective size of an anadromous Atlantic salmon (*Salmo salar*) population over 30 years. *Molecular Ecology*, *22*, 2394–2407.

Jonsson, N., Jonsson, B., & Hansen, L. P. (1998). The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, *67*, 751–762.

Jonsson, B., & Jonsson, N. (2006). Cultured Atlantic salmon in nature: A review of their ecology and interaction with wild fish. *Ices Journal of Marine Science*, *63*, 1162–1181.

Jonsson, B., Jonsson, N., & Albretsen, J. (2016). Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic Ocean. *Journal of Fish Biology*, *88*, 618–637.

Karjalainen, J., Urpanen, O., Keskinen, T., Huuskonen, H., Sarvala, J., Valkeajarvi, P., & Marjomaki, T. J. (2016). Phenotypic plasticity in growth and fecundity induced by strong population fluctuations affects reproductive traits of female fish. *Ecology and Evolution*, *6*, 779–790.

Karlsson, S., & Moen, T. (2010). The power to detect artificial selection acting on single loci in recently domesticated species. *Bmc Research Notes*, *3*, 232.

Karlsson, S., Moen, T., & Hindar, K. (2010). Contrasting patterns of gene diversity between microsatellites and mitochondrial SNPs in farm and wild Atlantic salmon. *Conservation Genetics*, *11*, 571–582.

Karlsson, S., Moen, T., Lien, S., Glover, K. A., & Hindar, K. (2011). Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. *Molecular Ecology Resources*, *11*, 247–253.

Karlsson, S., Diserud, O. H., Moen, T., & Hindar, K. (2014). A standardized method for quantifying unidirectional genetic introgression. *Ecology and Evolution*, *4*, 3256–3263.

Karlsson, S., Diserud, O. H., Fiske, P., & Hindar, K. (2016). Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *Ices Journal of Marine Science*, *73*, 2488–2498.

Kazakov, R. V. (1981). The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. *Journal of Fish Biology*, *19*, 353–360.

King, T. L., Kalinowski, S. T., Schill, W. B., Spidle, A. P., & Lubinski, B. A. (2001). Population structure of Atlantic salmon (*Salmo salar* L.): A range-wide perspective from microsatellite DNA variation. *Molecular Ecology*, *10*, 807–821.

Kirkpatrick, M., & Barton, N. H. (1997). Evolution of a species' range. *American Naturalist*, *150*, 1–23.

Kolstad, K., Heuch, P. A., Gjerde, B., Gjedrem, T., & Salte, R. (2005). Genetic variation in resistance of Atlantic salmon (*Salmo salar*) to the salmon louse *Lepeophtheirus salmonis*. *Aquaculture*, *247*, 145–151.

Kostow, K. (2009). Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies. *Reviews in Fish Biology and Fisheries*, *19*, 9–31.

Krkosek, M., Lewis, M. A., & Volpe, J. P. (2005). Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proceedings of the Royal Society B-Biological Sciences*, *272*, 689–696.

Kutti, T., Ervik, A., & Hoisaeter, T. (2008). Effects of organic effluents from a salmon farm on a fjord system. III. Linking deposition rates of organic matter and benthic productivity. *Aquaculture*, *282*, 47–53.

Lacroix, G. L., Galloway, B. J., Knox, D., & MacLatchy, D. (1997). Absence of seasonal changes in reproductive function of cultured Atlantic salmon migrating into a Canadian river. *Ices Journal of Marine Science*, *54*, 1086–1091.

Lacroix, G. L., & Stokesbury, M. J. W. (2004). Adult return of farmed Atlantic salmon escaped as juveniles into freshwater. *Transactions of the American Fisheries Society*, *133*, 484–490.

Lage, C., & Kornfield, I. (2006). Reduced genetic diversity and effective population size in an endangered Atlantic salmon (*Salmo salar*) population from Maine, USA. *Conservation Genetics*, *7*, 91–104.

Laikre, L., Schwartz, M. K., Waples, R. S., Ryman, N., & Ge, M. W. G. (2010). Compromising genetic diversity in the wild: Unmonitored large-scale release of plants and animals. *Trends in Ecology & Evolution*, *25*, 520–529.

Lande, R., & Shannon, S. (1996). The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution*, *50*, 434–437.

Lawlor, J., Dacanay, A., Hutchings, J., Brown, L., & Sperker, S. (2009). Differences in pathogen resistance within and among cultured, conservation-dependent, and endangered populations of Atlantic salmon, *Salmo salar* L. *Environmental Biology of Fishes*, *84*, 69–78.

Lenders, H. J. R., Chamuleau, T. P. M., Hendriks, A. J., Lauwerier, R., Leuven, R., & Verberk, W. (2016). Historical rise of waterpower initiated the collapse of salmon stocks. *Scientific Reports*, *6*, 29269.

Lhorente, J. P., Gallardo, J. A., Villanueva, B., Carabano, M. J., & Neira, R. (2014). Disease resistance in Atlantic Salmon (*Salmo salar*): Coinfection of the intracellular bacterial pathogen *Piscirickettsia salmonis* and the Sea Louse *Caligus rogercresseyi*. *PLoS One*, *9*(4), e95397.

Lien, S., Koop, B. F., Sandve, S. R., Miller, J. R., Kent, M. P., Nome, T., … Davidson, W. S. (2016). The Atlantic salmon genome provides insights into rediploidization. *Nature*, *533*, 200–+.

Liu, Y. J., Olaussen, J. O., & Skonhoft, A. (2011). Wild and farmed salmon in Norway-A review. *Marine Policy*, *35*, 413–418.

Lorenzen, K., Beveridge, M. C. M., & Mangel, M. (2012). Cultured fish: Integrative biology and management of domestication and interactions with wild fish. *Biological Reviews*, *87*, 639–660.

Lubieniecki, K. P., Jones, S. L., Davidson, E. A., Park, J., Koop, B. F., Walker, S., & Davidson, W. S. (2010). Comparative genomic analysis of Atlantic salmon, *Salmo salar*, from Europe and North America. *Bmc Genetics*, *11*, 105.

Lund, R. A., & Hansen, L. P. (1991). Identification of wild and reared Atlantic salmon, *Salmo salar* L., using scale characters. *Aquaculture and Fisheries Management*, *22*, 499–508.

Lund, R. A., Okland, F., & Hansen, L. P. (1991). Farmed Atlantic salmon (*Salmo salar*) in fisheries and rivers in Norway. *Aquaculture*, *98*, 143–150.

Lund, R. A., Midtlyng, P. J., & Hansen, L. P. (1997). Post-vaccination intra-abdominal adhesions as a marker to identify Atlantic salmon, *Salmo salar* L., escaped from commercial fish farms. *Aquaculture*, *154*, 27–37.

Lura, H., & Saegrov, H. (1991). Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. *Aquaculture*, *98*, 151–159.

Lura, H., Barlaup, B. T., & Saegrov, H. (1993). Spawning behavior of a farmed escaped female Atlantic salmon (*Salmo salar*). *Journal of Fish Biology*, *42*, 311–313.

Lush, L., Burt, K., Hamoutene, D., Camarillo-Sepulveda, N., Perez-Casanova, J. C., Kenny, S., … Collier, C. (2014). Size and ATP content of unfertilized eggs from farmed and wild Atlantic Salmon in Newfoundland. *North American Journal of Aquaculture*, *76*, 138–142.

Madhun, A. S., Karlsbakk, E., Ischsen, C. H., Omdal, L. M., Sørvik, A. G. E., Skaala, Ø., … Glover, K. A. (2015). Potential disease interaction reinforced: Double-virus infected escaped farmed Atlantic salmon, *Salmo salar* L., recaptured in a nearby river. *Journal of Fish Diseases*, *38*, 209–219.

Makinen, H., Vasemagi, A., McGinnity, P., Cross, T. F., & Primmer, C. R. (2015). Population genomic analyses of early-phase Atlantic Salmon (*Salmo salar*) domestication/captive breeding. *Evolutionary Applications*, *8*, 93–107.

McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., … Ferguson, A. (1997). Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: Use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *Ices Journal of Marine Science*, *54*, 998–1008.

McGinnity, P., Prodohl, P., Ferguson, K., Hynes, R., O'Maoileidigh, N., Baker, N., … Cross, T. (2003). Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society of London Series B-Biological Sciences*, *270*, 2443–2450.

McGinnity, P., de Eyto, E., Cross, T. F., Coughlan, J., Whelan, K., & Ferguson, A. (2007). Population specific smolt development, migration and maturity schedules in Atlantic salmon in a natural river environment. *Aquaculture*, *273*, 257–268.

McGinnity, P., Jennings, E., DeEyto, E., Allott, N., Samuelsson, P., Rogan, G., … Cross, T. (2009). Impact of naturally spawning captive-bred Atlantic salmon on wild populations: Depressed recruitment and increased risk of climate-mediated extinction. *Proceedings of the Royal Society B-Biological Sciences*, *276*, 3601–3610.

McKay, J. K., & Latta, R. G. (2002). Adaptive population divergence: Markers, QTL and traits. *Trends in Ecology & Evolution*, *17*, 285–291.

Merino, G., Barange, M., Blanchard, J. L., Harle, J., Holmes, R., Allen, I., … Rodwell, L. D. (2012). Can marine fisheries and aquaculture meet fish demand from a growing human population in a changing climate? *Global Environmental Change-Human and Policy Dimensions*, *22*, 795–806.

Metcalfe, N. B., Valdimarsson, S. K., & Morgan, I. J. (2003). The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. *Journal of Applied Ecology*, *40*, 535–544.

Milner, N. J., & Evans, R. (2003). The incidence of escaped Irish farmed salmon in English and Welsh rivers. *Fisheries Management and Ecology*, *10*, 403–406.

Mjolnerod, I. B., Refseth, U. H., Karlsen, E., Balstad, T., Jakobsen, K. S., & Hindar, K. (1997). Genetic differences between two wild and one farmed population of Atlantic salmon (*Salmo salar*) revealed by three classes of genetic markers. *Hereditas*, *127*, 239–248.

Moe, K., Naesje, T. F., Haugen, T. O., Ulvan, E. M., Aronsen, T., Sandnes, T., & Thorstad, E. B. (2016). Area use and movement patterns of wild and escaped farmed Atlantic salmon before and during spawning in a large Norwegian river. *Aquaculture Environment Interactions*, *8*, 77–88.

Moen, T., Baranski, M., Sonesson, A. K., & Kjoglum, S. (2009). Confirmation and fine-mapping of a major QTL for resistance to infectious pancreatic necrosis in Atlantic salmon (*Salmo salar*): Population-level associations between markers and trait. *Bmc Genomics*, *10*, 368.

Mork, J. (1991). One-generation effects of farmed fish immigration on the genetic differentiation of wild Atlantic salmon in Norway. *Aquaculture*, *98*, 267–276.

Morris, M. R. J., Fraser, D. J., Heggelin, A. J., Whoriskey, F. G., Carr, J. W., O'Neil, S. F., & Hutchings, J. A. (2008). Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*, 2807–2826.

Morris, M. R. J., Fraser, D. J., Eddington, J., & Hutchings, J. A. (2011). Hybridization effects on phenotypic plasticity: Experimental compensatory growth in farmed-wild Atlantic salmon. *Evolutionary Applications*, *4*, 444–458.

Mustafa, A., & MacKinnon, B. M. (1999). Genetic variation in susceptibility of Atlantic salmon to the sea louse Caligus elongatus Nordmann, 1832. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, *77*, 1332–1335.

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, *423*, 280–283.

Naylor, R. L., Goldburg, R. J., Primavera, J. H., Kautsky, N., Beveridge, M. C. M., Clay, J., … Troell, M. (2000). Effect of aquaculture on world fish supplies. *Nature*, *405*, 1017–1024.

Naylor, R., Hindar, K., Fleming, I. A., Goldburg, R., Williams, S., Volpe, J., … Mangel, M. (2005). Fugitive salmon: Assessing the risks of escaped fish from net-pen aquaculture. *BioScience*, *55*, 427–437.

Neregard, L., Sundt-Hansen, L., Hindar, K., Einum, S., Johnsson, J. I., Devlin, R. H., … Bjornsson, B. T. (2008). Wild Atlantic salmon *Salmo salar* L. strains have greater growth potential than a domesticated strain selected for fast growth. *Journal of Fish Biology*, *73*, 79–95.

Nielsen, E. E., Hansen, M. M., & Loeschcke, V. (1997). Analysis of microsatellite DNA from old scale samples of Atlantic salmon *Salmo salar*: A comparison of genetic composition over 60 years. *Molecular Ecology*, *6*, 487–492.

Nielsen, E. E., & Hansen, M. M. (2008). Waking the dead: The value of population genetic analyses of historical samples. *Fish and Fisheries*, *9*, 450–461.

Normandeau, E., Hutchings, J. A., Fraser, D. J., & Bernatchez, L. (2009). Population-specific gene expression responses to hybridization between farm and wild Atlantic salmon. *Evolutionary Applications*, *2*, 489–503.

Norris, A. T., Bradley, D. G., & Cunningham, E. P. (1999). Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. *Aquaculture*, *180*, 247–264.

O'Flynn, F. M., Bailey, J. K., & Friars, G. W. (1999). Responses to two generations of index selection in Atlantic salmon (*Salmo salar*). *Aquaculture*, *173*, 143–147.

O'Reilly, P. T., Carr, J. W., Whoriskey, F. G., & Verspoor, E. (2006). Detection of European ancestry in escaped farmed Atlantic salmon, *Salmo salar* L., in the magaguadavic river and Chamcook Stream, New Brunswick. *Canada. Ices Journal of Marine Science*, *63*, 1256–1262.

Okland, F., Heggberget, T. G., & Jonsson, B. (1995). Migratory behavior of wild and farmed Atlantic salmon (*Salmo salar*) during spawning. *Journal of Fish Biology*, *46*, 1–7.

Olesen, I., Myhr, A. I., & Rosendal, G. K. (2011). Sustainable aquaculture: Are we getting there? Ethical perspectives on salmon farming. *Journal of Agricultural & Environmental Ethics*, *24*, 381–408.

Olsen, R. E., & Skilbrei, O. T. (2010). Feeding preference of recaptured Atlantic salmon *Salmo salar* following simulated escape from fish pens during autumn. *Aquaculture Environment Interactions*, *1*, 167–174.

Olsen, R. E., Taranger, G. L., Svasand, T., & Skilbrei, O. T. (2013). Improved method for triacylglycerol-derived fatty acid profiling by various non-lethal and lethal sampling techniques in Atlantic salmon. *Aquaculture Environment Interactions*, *4*, 251–261.

Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D., & Reeves, G. H. (1998). Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 281–287.

Perrier, C., Guyomard, R., Bagliniere, J. L., & Evanno, G. (2011). Determinants of hierarchical genetic structure in Atlantic salmon populations: Environmental factors vs. anthropogenic influences. *Molecular Ecology*, *20*, 4231–4245.

Piccolo, J. J., & Orlikowska, E. H. (2012). A biological risk assessment for an Atlantic salmon (*Salmo salar*) invasion in Alaskan waters. *Aquatic Invasions*, *7*, 259–270.

Powell, J., White, I., Guy, D., & Brotherstone, S. (2008). Genetic parameters of production traits in Atlantic salmon (*Salmo salar*). *Aquaculture*, *274*, 225–231.

Pritchard, J. K., & Di Rienzo, A. (2010). Adaptation – not by sweeps alone. *Nature Reviews Genetics*, *11*, 665–667.

Quintela, M., Wennevik, V., Sørvik, A. G. E., Skaala, Ø., Skilbrei, O. T., Urdal, K., … Glover, K. A. (2016). Siblingship tests connect two seemingly independent farmed Atlantic salmon escape events. *Aquaculture Environment Interactions*, *8*, 497–509.

Quinton, C. D., McMillan, I., & Glebe, B. D. (2005). Development of an Atlantic salmon (*Salmo salar*) genetic improvement program: Genetic parameters of harvest body weight and carcass quality traits estimated with animal models. *Aquaculture*, *247*, 211–217.

Randi, E. (2008). Detecting hybridization between wild species and their domesticated relatives. *Molecular Ecology*, *17*, 285–293.

Reed, T. E., Prodohl, P., Hynes, R., Cross, T., Ferguson, A., & McGinnity, P. (2015). Quantifying heritable variation in fitness-related traits of wild, farmed and hybrid Atlantic salmon families in a wild river environment. *Heredity*, *115*, 173–184.

Refstie, T., Steine, T. A., & Gjedrem, T. (1977). Selection experiments with salmon. 2. Proportion of Atlantic salmon smoltifying at 1-year of age. *Aquaculture*, *10*, 231–242.

Rengmark, A. H., Slettan, A., Skaala, O., Lie, O., & Lingaas, F. (2006). Genetic variability in wild and farmed Atlantic salmon (*Salmo salar*) strains estimated by SNP and microsatellites. *Aquaculture*, *253*, 229–237.

Riddell, B. E., Leggett, W. C., & Saunders, R. L. (1981). Evidence of adaptive polygenic variation between 2 populations of Atlantic salmon (*Salmo salar*) native to tributaries of the SW Miramichi river, NB. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*, 321–333.

Roberge, C., Einum, S., Guderley, H., & Bernatchez, L. (2006). Rapid parallel evolutionary changes of gene transcription profiles in farmed Atlantic salmon. *Molecular Ecology*, *15*, 9–20.

Roberge, C., Normandeau, E., Einum, S., Guderley, H., & Bernatchez, L. (2008). Genetic consequences of interbreeding between farmed and wild Atlantic salmon: Insights from the transcriptome. *Molecular Ecology*, *17*, 314–324.

Ruzzante, D. E. (1994). Domestication effects on aggressive and schooling behavior in fish. *Aquaculture*, *120*, 1–24.

Rye, M., Lillevik, K. M., & Gjerde, B. (1990). Survival in early life of Atlantic salmon and rainbow trout – estimates of heritabilities and genetic correlations. *Aquaculture*, *89*, 209–216.

Ryman, N. (1991). Conservation genetics in fishery management. *Journal of Fish Biology*, *39*, 211–224.

Ryman, N., Utter, F., & Hindar, K. (1995) Introgression, supportive breeding and genetic conservation. In: J. D. Balloux, M. Gilpin & T. J. Foose (Eds.), *Population management for survival & recovery* (pp. 341–365). New York: Columbia University Press.

Ryynanen, H. J., & Primmer, C. R. (2004). Distribution of genetic variation in the growth hormone 1 gene in Atlantic salmon (*Salmo salar*) populations from Europe and North America. *Molecular Ecology*, *13*, 3857–3869.

Saegrov, H., Hindar, K., Kalas, S., & Lura, H. (1997). Escaped farmed Atlantic salmon replace the original salmon stock in the River Vosso, western Norway. *Ices Journal of Marine Science*, *54*, 1166–1172.

Satake, A., & Araki, H. (2012). Stocking of captive-bred fish can cause long-term population decline and gene pool replacement: Predictions from a population dynamics model incorporating density-dependent mortality. *Theoretical Ecology*, *5*, 283–296.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*, 609–612.

Sepulveda, M., Arismendi, I., Soto, D., Jara, F., & Farias, F. (2013). Escaped farmed salmon and trout in Chile: Incidence, impacts, and the need for an ecosystem view. *Aquaculture Environment Interactions*, *4*, 273–283.

Skaala, O., Hoyheim, B., Glover, K., & Dahle, G. (2004). Microsatellite analysis in domesticated and wild Atlantic salmon (*Salmo salar* L.): Allelic diversity and identification of individuals. *Aquaculture*, *240*, 131–143.

Skaala, O., Taggart, J. B., & Gunnes, K. (2005). Genetic differences between five major domesticated strains of Atlantic salmon and wild salmon. *Journal of Fish Biology*, *67*, 118–128.

Skaala, O., Wennevik, V., & Glover, K. A. (2006). Evidence of temporal genetic change in wild Atlantic salmon, *Salmo salar* L., populations affected by farm escapees. *Ices Journal of Marine Science*, *63*, 1224–1233.

Skaala, Ø., Glover, K. A., Barlaup, B. T., Svåsand, T., Besnier, F., Hansen, M. M., & Borgstrøm, R. (2012). Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*, 1994–2006.

Skaala, O., Glover, K. A., Barlaup, B. T., & Borgstrom, R. (2014). Microsatellite DNA used for parentage identification of partly digested Atlantic salmon (*Salmo salar*) juveniles through non-destructive diet sampling in salmonids. *Marine Biology Research*, *10*, 323–328.

Skern-Mauritzen, R., Malde, K., Besnier, F., Nilsen, F., Jonassen, I., Reinhardt, R., … Glover, K. A. (2013). How does sequence variability affect de novo assembly quality? *Journal of Natural History*, *47*, 901–910.

Skilbrei, O. T., & Wennevik, V. (2006). The use of catch statistics to monitor the abundance of escaped farmed Atlantic salmon and rainbow trout in the sea. *Ices Journal of Marine Science*, *63*, 1190–1200.

Skilbrei, O. T., Holst, J. C., Asplin, L., & Holm, M. (2009). Vertical movements of "escaped" farmed Atlantic salmon (*Salmo salar* L.): A simulation study in a western Norwegian fjord. *Ices Journal of Marine Science*, *66*, 278–288.

Skilbrei, O. T. (2010). Adult recaptures of farmed Atlantic salmon post-smolts allowed to escape during summer. *Aquaculture Environment Interactions*, *1*, 147–153.

Skilbrei, O. T., Holst, J. C., Asplin, L., & Mortensen, S. (2010). Horizontal movements of simulated escaped farmed Atlantic salmon (*Salmo salar*) in a western Norwegian fjord. *Ices Journal of Marine Science*, *67*, 1206–1215.

Skilbrei, O. T., Heino, M., & Svåsand, T. (2015). Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages, from farms sites in Norway. *Ices Journal of Marine Science*, *72*, 670–685.

Skilbrei, O. T., Normann, E. S., Meier, S., & Olsen, R. E. (2015). Use of fatty acid profiles to monitor the escape history of farmed Atlantic salmon. *Aquaculture Environment Interactions*, *7*, 1–13.

Solberg, M. F., Kvamme, B. O., Nilsen, F., & Glover, K. A. (2012). Effects of environmental stress on mRNA expression levels of seven genes related to oxidative stress and growth in Atlantic salmon *Salmo salar* L. of farmed, hybrid and wild origin. *Bmc Research Notes*, *5*, 672.

Solberg, M. F., Glover, K. A., Nilsen, F., & Skaala, Ø. (2013). Does domestication cause changes in growth reaction norms? A study of farmed, wild and hybrid Atlantic salmon families exposed to environmental stress. *PLoS One*, *8*(1), e54469.

Solberg, M. F., Zhang, Z. W., Nilsen, F., & Glover, K. A. (2013). Growth reaction norms of domesticated, wild and hybrid Atlantic salmon families in response to differing social and physical environments. *Bmc Evolutionary Biology*, *13*, 234.

Solberg, M. F., Fjelldal, P. G., Nilsen, F., & Glover, K. A. (2014). Hatching time and alevin growth prior to the onset of exogenous feeding in farmed, wild and hybrid Norwegian Atlantic salmon. *PLoS One*, *9*(12), e113697.

Solberg, M. F., Zhang, Z., & Glover, K. A. (2015). Are farmed salmon more prone to risk than wild salmon? Susceptibility of juvenile farm, hybrid and wild Atlantic salmon *Salmo salar* L. to an artificial predator. *Applied Animal Behaviour Science*, *162*, 67–80.

Solberg, M. F., Dyrhovden, L., Matre, I. H., & Glover, K. A. (2016). Thermal plasticity in farmed, wild and hybrid Atlantic salmon during early development: Has domestication caused divergence in low temperature tolerance? *Bmc Evolutionary Biology*, *16*, 38.

Solem, O., Hedger, R. D., Urke, H. A., Kristensen, T., Okland, F., Ulvan, E. M., & Uglem, I. (2013). Movements and dispersal of farmed Atlantic salmon following a simulated-escape event. *Environmental Biology of Fishes*, *96*, 927–939.

Somarakis, S., Pavlidis, M., Saapoglou, C., Tsigenopoulos, C. S., & Dempster, T. (2013). Evidence for 'escape through spawning' in large gilthead sea bream *Sparus aurata* reared in commercial sea-cages. *Aquaculture Environment Interactions*, *3*, 135–152.

Srivastava, R. K., & Brown, J. A. (1991). The biochemical characteristics and hatching performance of cultured and wild Atlantic salmon (*Salmo salar*) eggs. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, *69*, 2436–2441.

Stabell, O. B. (1984). Homing and olfaction in salmonids – a critical review with special reference to the Atlantic salmon. *Biological Reviews of the Cambridge Philosophical Society*, *59*, 333–388.

Ståhl, G. (1987) Genetic population structure of Atlantic salmon. In: N. Ryman & F. Utter (Eds.), *Population genetics and fishery management* (pp. 121–140). Seattle: University of Washington press.

Stokesbury, M. J., & Lacroix, G. L. (1997). High incidence of hatchery origin Atlantic salmon in the smolt output of a Canadian River. *Ices Journal of Marine Science*, *54*, 1074–1081.

Stokesbury, M. J. W., Lacroix, G. L., Price, E. L., Knox, D., & Dadswell, M. J. (2001). Identification by scale analysis of farmed Atlantic salmon juveniles in southwestern New Brunswick Rivers. *Transactions of the American Fisheries Society*, *130*, 815–822.

Sundt-Hansen, L., Huisman, J., Skoglund, H., & Hindar, K. (2015). Farmed Atlantic salmon *Salmo salar* L. parr may reduce early survival of wild fish. *Journal of Fish Biology*, *86*, 1699–1712.

Symons, P. E. K. (1968). Increase in aggression and in strength of social hierarchy among juvenile Atlantic salmon deprived of food. *Journal of the Fisheries Research Board of Canada*, *25*, 2387–2401.

Taggart, J. B., Verspoor, E., Galvin, P. T., Moran, P., & Ferguson, A. (1995). A minisatellite DNA marker for discriminating between European and North American Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 2305–2311.

Taggart, J. B., McLaren, I. S., Hay, D. W., Webb, J. H., & Youngson, A. F. (2001). Spawning success in Atlantic salmon (*Salmo salar* L.): A long-term DNA profiling-based study conducted in a natural stream. *Molecular Ecology*, *10*, 1047–1060.

Taranger, G. L., Carrillo, M., Schulz, R. W., Fontaine, P., Zanuy, S., Felip, A., … Hausen, T. (2010). Control of puberty in farmed fish. *General and Comparative Endocrinology*, *165*, 483–515.

Taranger, G. L., Karlsen, O., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., … Svasand, T. (2015). Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *Ices Journal of Marine Science*, *72*, 997–1021.

Taylor, E. B. (1991). A review of local adaptation in salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, *98*, 185–207.

Taylor, R. S., Wynne, J. W., Kube, P. D., & Elliott, N. G. (2007). Genetic variation of resistance to amoebic gill disease in Atlantic salmon (*Salmo salar*) assessed in a challenge system. *Aquaculture*, *272*, S94–S99.

Taylor, R. S., Kube, P. D., Muller, W. J., & Elliott, N. G. (2009). Genetic variation of gross gill pathology and survival of Atlantic salmon (*Salmo salar* L.) during natural amoebic gill disease challenge. *Aquaculture*, *294*, 172–179.

Teletchea, F., & Fontaine, P. (2014). Levels of domestication in fish: Implications for the sustainable future of aquaculture. *Fish and Fisheries*, *15*, 181–195.

Thodesen, J., Grisdale-Helland, B., Helland, S. J., & Gjerde, B. (1999). Feed intake, growth and feed utilization of offspring from wild and selected Atlantic salmon (*Salmo salar*). *Aquaculture*, *180*, 237–246.

Thorpe, J. E., Miles, M. S., & Keay, D. S. (1984). Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. *Aquaculture*, *43*, 289–305.

Thorstad, E. B., Heggberget, T. G., & Okland, F. (1998). Migratory behaviour of adult wild and escaped farmed Atlantic salmon, *Salmo salar* L., before, during and after spawning in a Norwegian river. *Aquaculture Research*, *29*, 419–428.

Thorstad, E. B., Fleming, I. A., McGinnity, P., Soto, D., Wennevik, V., & Whoriskey, F. (2008) Incidence and impacts of escaped farmed Atlantic salmon *Salmo salar* in nature. NINA special report 36. 110 pp.

Tonteri, A., Veselov, A. J., Zubchenko, A. V., Lumme, J., & Primmer, C. R. (2009). Microsatellites reveal clear genetic boundaries among Atlantic salmon (*Salmo salar*) populations from the Barents and White seas, northwest Russia. *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 717–735.

Torrissen, O., Olsen, R. E., Toresen, R., Hemre, G. I., Tacon, A. G. J., Asche, F., Hardy, R. W., & Lall, S. (2011). Atlantic Salmon (*Salmo salar*): The "super-chicken" of the sea? *Reviews in Fisheries Science*, *19*, 257–278.

Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O. T., Nilsen, F., Horsberg, T. E., & Jackson, D. (2013). Salmon lice – impact on wild salmonids and salmon aquaculture. *Journal of Fish Diseases*, *36*, 171–194.

Tsai, H. Y., Hamilton, A., Guy, D. R., Tinch, A. E., Bishop, S. C., & Houston, R. D. (2015). The genetic architecture of growth and fillet traits in farmed Atlantic salmon (*Salmo salar*). *Bmc Genetics*, *16*, 51.

Tsai, H. Y., Hamilton, A., Tinch, A. E., Guy, D. R., Gharbi, K., Stear, M. J., … Houston, R. D. (2015). Genome wide association and genomic prediction for growth traits in juvenile farmed Atlantic salmon using a high density SNP array. *Bmc Genomics*, *16*, 969.

Tsai, H. Y., Robledo, D., Lowe, N. R., Bekaert, M., Taggart, J. B., Bron, J. E., & Houston, R. D. (2016). Construction and Annotation of a High Density SNP Linkage Map of the Atlantic Salmon (*Salmo salar*) Genome. *G3-Genes Genomes*. *Genetics*, *6*, 2173–2179.

Tufto, J., & Hindar, K. (2003). Effective size in management and conservation of subdivided populations. *Journal of Theoretical Biology*, *222*, 273–281.

Utter, F., & Epifanio, J. (2002). Marine aquaculture: Genetic potentialities and pitfalls. *Reviews in Fish Biology and Fisheries*, *12*, 59–77.

Vaha, J. P., Erkinaro, J., Niemela, E., & Primmer, C. R. (2007). Life-history and habitat features influence the within-river genetic structure of Atlantic salmon. *Molecular Ecology*, *16*, 2638–2654.

Varne, R., Kunz, K. L., Johansen, T., Westgaard, J. I., Uglem, I., & Mork, J. (2015). Farmed cod escapees and net-pen spawning left no clear genetic footprint in the local wild cod population. *Aquaculture Environment Interactions*, *7*, 253–266.

Vasemagi, A., Nilsson, J., McGinnity, P., Cross, T., O'Reilly, P., Glebe, B., … Primmer, C. R. (2012). Screen for footprints of selection during domestication/captive breeding of Atlantic salmon. *Comparative and functional genomics*, *2012*, 628204.

Verspoor, E. (1988). Reduced genetic variability in 1st generation hatchery populations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *45*, 1686–1690.

Verspoor, E., Beardmore, J. A., Consuegra, S., De Leaniz, C. G., Hindar, K., Jordan, W. C., … Cross, T. F. (2005). Population structure in the Atlantic salmon: Insights from 40 years of research into genetic protein variation. *Journal of Fish Biology*, *67*, 3–54.

Verspoor, E., McGinnity, P., Bradbury, I., & Glebe, B. D. (2015). The potential direct and indirect genetic consequences for native Newfoundland Atlantic Salmon from interbreeding with European-origin farm escapes. *DFO Canadian Science Advisory Secretariat* 2015/030., viii +36 p.

Verspoor, E., Knox, D., & Marshall, S. (2016). Assessment of interbreeding and introgression of farm genes into a small Scottish Atlantic salmon Salmo salar stock: Ad hoc samples–ad hoc results? *Journal of Fish Biology*, *89*, 2680–2696.

Vik, J. O., Borgstrom, R., & Skaala, O. (2001). Cannibalism governing mortality of juvenile brown trout, *Salmo trutta*, in a regulated stream. *Regulated Rivers-Research & Management*, *17*, 583–594.

Vollestad, L. A., Hirst, D., L'Abee-Lund, J. H., Armstrong, J. D., MacLean, J. C., Youngson, A. F., & Stenseth, N. C. (2009). Divergent trends in anadromous salmonid populations in Norwegian and Scottish rivers. *Proceedings of the Royal Society B-Biological Sciences*, *276*, 1021–1027.

Volpe, J. P., Taylor, E. B., Rimmer, D. W., & Glickman, B. W. (2000). Evidence of natural reproduction of aquaculture-escaped Atlantic salmon in a coastal British Columbia river. *Conservation Biology*, *14*, 899–903.

Walker, A. M., Beveridge, M. C. M., Crozier, W., Maoileidigh, O. N., & Milner, N. (2006). Monitoring the incidence of escaped farmed Atlantic salmon, *Salmo salar* L., in rivers and fisheries of the United Kingdom and Ireland: Current progress and recommendations for future programmes. *Ices Journal of Marine Science*, *63*, 1201–1210.

Wall, T. (2011) Farmed fish. In: J. Webster (Ed.), *Husbandry and welfare of farm animals: UFAW farm handbook* (p. 614). Wiley-Blackwell.

Webb, J. H., Hay, D. W., Cunningham, P. D., & Youngson, A. F. (1991). The spawning behavior of escaped farmed and wild adult Atlantic salmon (*Salmo salar* L) in a Northern Scottish river. *Aquaculture*, *98*, 97–110.

Webb, J. H., Youngson, A. F., Thompson, C. E., Hay, D. W., Donaghy, M. J., & McLaren, I. S. (1993). Spawning of escaped farmed Atlantic salmon, *Salmo salar* L., in western and northern Scottish rivers; egg deposition by females. *Aquaculture and Fisheries Management*, *24*, 557–561.

Weir, L. K., Hutchings, J. A., Fleming, I. A., & Einum, S. (2004). Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, *Salmo salar*. *Journal of Animal Ecology*, *73*, 1069–1079.

Weir, L. K., Hutchings, J. A., Fleming, I. A., & Einum, S. (2005). Spawning behaviour and success of mature male Atlantic salmon (*Salmo salar*) parr of farmed and wild origin. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*, 1153–1160.

Wennevik, V., Skaala, O., Titov, S. F., Studyonov, I., & Naevdal, G. (2004). Microsatellite variation in populations of Atlantic salmon from North Europe. *Environmental Biology of Fishes*, *69*, 143–152.

White, S. L., Sakhrani, D., Danzmann, R. G., & Devlin, R. H. (2013). Influence of developmental stage and genotype on liver mRNA levels among wild, domesticated, and hybrid rainbow trout (*Oncorhynchus mykiss*). *Bmc Genomics*, *14*, 673.

Whoriskey, F. G., Brooking, P., Doucette, G., Tinker, S., & Carr, J. W. (2006). Movements and survival of sonically tagged farmed Atlantic salmon released in Cobscook Bay, Maine, USA. *Ices Journal of Marine Science*, *63*, 1218–1223.

Wolters, W. R., Barrows, F. T., Burr, G. S., & Hardy, R. W. (2009). Growth parameters of wild and selected strains of Atlantic salmon, *Salmo salar*, on two experimental diets. *Aquaculture*, *297*, 136–140.

Yanez, J. M., Lhorente, J. P., Bassini, L. N., Oyarzun, M., Neira, R., & Newman, S. (2014). Genetic co-variation between resistance against both *Caligus rogercresseyi* and *Piscirickettsia salmonis*, and body weight in Atlantic salmon (*Salmo salar*). *Aquaculture*, *433*, 295–298.

Yates, M. C., Debes, P. V., Fraser, D. J., & Hutchings, J. A. (2015). The influence of hybridization with domesticated conspecifics on alternative reproductive phenotypes in male Atlantic salmon in multiple temperature regimes. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1138–1145.

Yeates, S. E., Einum, S., Fleming, I. A., Holt, W. V., & Gage, M. J. G. (2014). Assessing risks of invasion through gamete performance: Farm Atlantic salmon sperm and eggs show equivalence in function, fertility, compatibility and competitiveness to wild Atlantic salmon. *Evolutionary Applications*, *7*, 493–505.

Youngson, A. F., Martin, S. A. M., Jordan, W. C., & Verspoor, E. (1991). Genetic protein variation in Atlantic salmon in Scotland – comparisons of wild and farmed fish. *Aquaculture*, *98*, 231–242.

Youngson, A. F., Webb, J. H., MacLean, J. C., & Whyte, B. M. (1997). Frequency of occurrence of reared Atlantic salmon in Scottish salmon fisheries. *Ices Journal of Marine Science*, *54*, 1216–1220.

Youngson, A. F., MacLean, J. C., & Fryer, R. J. (2002). Rod catch trends for early-running MSW salmon in Scottish rivers (1952-1997): Divergence among stock components. *Ices Journal of Marine Science*, *59*, 836–849.

Zhang, Z., Glover, K. A., Wennevik, V., Svåsand, T., Sørvik, A. G. E., Fiske, P., … Skaala, O. (2013). Genetic analysis of Atlantic salmon captured in a netting station reveals multiple escapement events from commercial fish farms. *Fisheries Management and Ecology*, *20*, 42–51.

Zhang, Y. F., Timmerhaus, G., Anttila, K., Mauduit, F., Jorgensen, S. M., Kristensen, T., … Farrell, A. P. (2016). Domestication compromises athleticism and respiratory plasticity in response to aerobic exercise training in Atlantic salmon (*Salmo salar*). *Aquaculture*, *463*, 79–88.

How to cite this article: Glover KA, Solberg MF, McGinnity P, et al. Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. *Fish Fish*. 2017;18:890–927. https://doi.org/10.1111/faf.12214

ICES WKCULEF REPORT 2016

ICES ADVISORY COMMITTEE

ICES CM 2016/ACOM:42

Report of the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF)

1–3 March 2016

Charlottenlund, Denmark

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

H. C. Andersens Boulevard 44–46
DK-1553 Copenhagen V
Denmark
Telephone (+45) 33 38 67 00
Telefax (+45) 33 93 42 15
www.ices.dk
info@ices.dk

Recommended format for purposes of citation:

ICES. 2016. Report of the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF), 1–3 March 2016, Charlottenlund, Denmark. ICES CM 2016/ACOM:42. 44 pp.

Contents

Executive summary **1**

1 Introduction **4**

- 1.1 Workshop rationale and objectives 4
- 1.2 Participants 5
- 1.3 Background 6

2 The effects of sea lice on Atlantic salmon **10**

- 2.1 Introduction 10
- 2.2 Physiological effects 10
- 2.3 Evidence from monitoring programmes 11
- 2.4 Population effects 12
- 2.5 Summary 13
- 2.6 Knowledge gaps and research priorities 14

3 Escapees, genetic interactions and effects on wild Atlantic salmon **15**

- 3.1 Numbers of escapees and observations in rivers 15
- 3.2 Identification of escapees 16
- 3.3 Intraspecific hybridisation and introgression 16
- 3.4 Domestication and divergence from wild salmon 17
- 3.5 Fitness studies 18
- 3.6 Short-term consequences of introgression for wild salmon populations (i.e. a few salmon generations) 19
- 3.7 Long-term consequences of introgression for wild salmon populations (i.e. more than a few generations) 20
- 3.8 Summary 21
- 3.9 Knowledge gaps and research priorities 22

Annex 1: Working documents submitted to the Workshop on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic, 1–3 March, 2016 .... **23**

Annex 2: References cited **24**

Annex 3: Participants list **34**

Annex 4: Technical minutes from the Review Group on Possible effects of salmonid aquaculture **37**

Executive summary

Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic [WKCULEF], Copenhagen, Denmark, 1–3 March 2016.

Chairs: Ian Russell (UK) and Ole Torrissen (Norway).

Number of meeting participants: 25 representing six countries: Norway (ten), Ireland (four), UK (Scotland) (four), Canada (three), UK (England & Wales) (two) and USA (one). Additional participants also attended from the ICES Secretariat.

WKCULEF met to consider a question posed to ICES by the North Atlantic Salmon Conservation Organisation (NASCO): *Advise on possible effects of salmonid aquaculture on wild Atlantic salmon populations focusing on the effects of sea lice, genetic interactions and the impact on wild salmon production*.

This question was originally included among a suite of questions developed by NASCO, and due to be addressed by the annual meeting of the Working Group on North Atlantic Salmon (WGNAS). However, given that the question was pertinent to other Expert Groups at ICES, particularly the Working Group on Aquaculture (WGAQUA), the Working Group on Pathology and Diseases of Marine Organisms (WGPDMO) and the Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM), it was recommended that the question would be best addressed by means of a Workshop, independent of the Working Groups. WKCULEF enabled experts in aquaculture effects, wild Atlantic salmon, disease transmission and genetic interaction to share and discuss relevant information and recent findings, in order to meet the objectives and timeline of the request.

The terms of reference were addressed though a comprehensive review of the recent peer-reviewed literature. This was facilitated by a range of presentations from participants, by reviewing working documents prepared ahead of the meeting as well as the development of documents and text for the report during the meeting. The report is structured in two main sections, one focusing on the effects of sea lice and the other on genetic interactions. The third issue specified in the question from NASCO, namely the impact of salmon farming on wild salmon production, has been relatively poorly researched and most information derives from attempts to evaluate population level effects related to sea lice infestation and genetic introgression. This information has therefore been reported in the sea lice and genetics sections of the report, respectively.

WKCULEF briefly discussed microbial diseases in aquaculture and the potential impact on wild salmon. However, it was not possible to review this issue in detail and it has not been included in this report.

The key findings of the Workshop were:

Sea lice

- The sea louse (*Lepeophtheirus salmonis*) has widespread geographic distribution, is an important parasite of salmonids and has been a serious problem for the Atlantic salmon farming industry since the 1970s. Sea lice have a greater economic impact on the industry than any other parasite and control of lice levels on farms is of key importance.

- Salmon farming has been shown to increase the abundance of lice in the marine environment and the risk of infection among wild salmonid populations. However, there is considerable uncertainty, and spatial and temporal variability, about the extent of the zones of elevated risk.
- It has been shown in laboratory studies that 0.04–0.15 lice per gramme fish weight can increase stress levels. Laboratory studies have also demonstrated that infections of 0.75 lice per gramme fish weight, or approximately eleven sea lice per fish, can kill a recently emigrated wild salmon smolt of about 15 g if all the sea lice develop into pre-adult and adult stages.
- A number of studies in Norway and Ireland have estimated the relative marine survival of smolts treated to provide lice resistance and control groups. All studies have reported an overall improved return rate for treated salmon, but all showed significant spatial and temporal variability in the magnitude of the treatment effect.
- The survival of Atlantic salmon during their marine phase has fallen in recent decades. This downturn in survival is evident over a broad geographical area and is associated with large-scale oceanographic changes. Viewed against current marine mortality rates commonly at or above 95%, the 'additional' mortality attributable to sea lice has been estimated at around 1%.
- In some studies, the impact of sea lice has also been estimated as losses of returning adult salmon to rivers. These estimates indicate marked variability, with losses in individual experiments ranging from 0.6% to 39%. These results suggest that sea lice induced mortality has an impact on Atlantic salmon returns, which may influence the achievement of conservation requirements for affected stocks.
- Much of the heterogeneity among trials comparing the survival to adulthood of juvenile salmon administered sea lice medicines and control groups could be explained by the release location, time period and baseline (i.e. marine) survival. In a recent meta-analysis of Norwegian data, baseline survival was reported to be the most important predictor variable. When this was low, the effect of treatment was high. In contrast, when baseline survival was high, the effect of treatment was undetectable. However, it is unclear whether baseline survival is affected by sea lice exposure.

Genetic effects

- Each year, large numbers of domesticated salmon escape from commercial fish farms. While many of these are reported, the true number of escapees is likely to be significantly higher. Escapees are observed in rivers in all regions where farming occurs, although the numbers of escapees vary both spatially and temporally. It has been noted that in some rivers in some years, the numbers of escapees have approached 50% or more of the spawning population.
- The spawning success of escaped farmed salmon is much lower than wild salmon. Despite this, genetic studies have demonstrated that farmed salmon have displayed widespread introgression in a large number of Norwegian populations where this has been investigated. Introgression has also been shown in other countries, but the full extent of introgression remains to be investigated.

- Farmed salmon are domesticated and display significant genetic differences to wild salmon in a wide range of fitness-related traits. Whole-river experimental studies have demonstrated that the offspring of farmed and cultured salmon in general, display lower fitness than their wild counterparts in the wild.
- Juvenile escapees and the offspring of farmed salmon compete with wild salmon for territory and food. Therefore, their presence in the natural habitat will reduce the total production of wild fish. Studies have also shown this can result in a decreased overall productivity of the population.
- Where farmed salmon have successfully interbred with natural populations, it is likely that recipient populations will display changes in life-history traits. These changes are likely to be maladaptive for the wild population.
- The long-term consequences of introgression across river stocks can be expected to lead to reduced productivity and decreased resilience to future impacts such as climate change (i.e. less fish and more fragile stocks).
- The evidence from studies in the wild, and the extensive literature relating to salmonids in general, demonstrates that the offspring of farmed salmon display reduced fitness in the wild. However, the results of these studies suggest that the relative success of farmed salmon and, likewise, the relative potential negative effect on a native population, is likely to vary in time and space. Wild populations that are already under evolutionary strain from other challenges such as disease pressure, sea lice infection, over exploitation, habitat destruction and poor water quality are more likely to be sensitive to the potential negative effects of genetic introgression and loss of fitness. Therefore, such effects have to be seen in the context of other challenges.
- While recognising that there were still uncertainties, WKCULEF considered that the evidence relating to the impacts of escapees / genetic introgression provided a clear indication of impacts on wild salmon populations. A substantial reduction of escaped farmed salmon in the wild, or sterilization of farmed salmon, would be required in order to minimize effects on native populations.

In reviewing the latest evidence pertaining to sea lice and genetic interactions, WKCULEF considered where there were gaps in current knowledge and identified areas for further investigation.

1 Introduction

1.1 Workshop rationale and objectives

At its 2015 Statutory Meeting, ICES resolved (C. Res. 2015/2/ACOM10) that the Working Group on North Atlantic Salmon [WGNAS] (chaired by: Jonathan White, Ireland) would meet at ICES, Copenhagen, 30 March–8 April 2016 to consider various questions posed to ICES by the North Atlantic Salmon Conservation Organisation (NASCO). However, one of these questions, relating to the possible effects of salmonid aquaculture on wild Atlantic salmon, has a particularly broad remit and cuts across the work of a number of ICES Groups. In subsequent discussions between the ICES Secretariat and WGNAS participants, it was agreed that responding to this question required the input of experts from a range of disciplines and different Expert Groups within ICES. Given the timing of the annual meetings of these different Expert Groups and the requirement for the advice to be drafted, reviewed and made available by early May 2016, it was decided that an independent workshop needed to be convened to address this question.

ICES subsequently resolved (C. Res. 2015/2/ACOM:42) that the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF), chaired by Ole Torrissen (Norway) and Ian Russell (UK), will meet at ICES, Copenhagen 01–03 March 2016.

WKCULEF was publicised on the ICES website and members of the following relevant ICES Expert Groups were encouraged to send appropriate representation: the Working Group on Aquaculture (WGAQUA), the Working Group on North Atlantic Salmon (WGNAS), the Working Group on Pathology and Diseases of Marine Organisms (WGPDMO) and the Working Group on the Application of Genetics in Fisheries and Mariculture (WGAGFM). ICES Workshops are open to all interested parties and participants from academic and stakeholder organisations also registered to attend WKCULEF. The level of interest in the Workshop was such that numbers of participants exceeded the space originally set aside for the meeting at ICES. The workshop was therefore relocated to DTU-Aqua, located at Charlottenlund just to the north of Copenhagen.

The terms of reference for WKCULEF are to:

a) Identify the possible effects of salmonid aquaculture on wild Atlantic salmon populations, focusing on the effects of sea lice, genetic interactions and the impact on wild salmon production.

b) Based on the issues identified in (a):

  i) Update the findings of the 2005 ICES/NASCO symposium on the impacts of aquaculture.

  ii) Update the ICES advice provided to OSPAR in 2010 and 2014 (ICES, 2010; 2014).

  iii) Prepare the first draft of the advice to address the NASCO request.

WKCULEF will report by 11 March, 2016 for the attention of the ICES Advisory Committee.

WKCULEF were advised that NASCO plan to hold a Theme-based Special Session on the topic of developments in relation to minimizing the impacts of farmed salmon on wild salmon stocks at their annual meeting in June 2016, and the advice will provide a very useful input to that process. ICES are expected to provide the opening presentation at this event.

The terms of reference for WKCULEF focus on interactions between salmon farming and Atlantic salmon and supporting evidence utilised in this report primarily draws upon the scientific literature pertaining specifically to this species. Salmon farming activities can impact on other salmonid species, in particular sea trout and Arctic char, and there is an extensive literature related to these species. However, the majority of such work has not been incorporated into this report.

In addressing the terms of reference, WKCULEF felt that it was particularly difficult to disentangle the issue of the possible impact of salmon aquaculture on wild salmon production from the sea lice and genetic interaction questions. As a result, information pertaining to population level effects was integrated into both these sections and has not been included as a separate section of the report. WKCULEF sought to highlight where there were gaps in current knowledge and identified areas where further investigation was required.

WKCULEF briefly discussed microbial diseases in aquaculture and the potential impact on wild salmon. However, it was not possible to review this issue in detail and such information has not been included in the report.

In response to the Terms of Reference, the Workshop considered 14 Working Documents / presentations submitted by participants (Annex 1); other references cited in the Report are given in Annex 2. A full address list for the meeting participants is provided in Annex 3.

1.2 Participants

Member	**Country**
Jonathan Carr	Canada
Catherine Collins	UK (Scotland)
Anne Cooper	ICES Secretariat, Denmark
Mark Coulson	UK (Scotland)
Bengt Finstad	Norway
Kevin Glover	Norway
Paddy Gargan	Ireland
Kjetil Hindar	Norway
Dave Jackson	Ireland
Martin Jaffa	UK (England & Wales)
Simon Jones	Canada
Bjørn Olav Kvamme	Norway
Marie Lillehammer	Norway
John Martell	Canada

Philip McGinnity	Ireland
Olav Moberg	Norway
David Morris	UK (Scotland)
Kjell Emil Naas	Norway
Hans Petter Næs	Norway
Michael Pietrak (by Skype)	USA
Ian Russell (chair)	UK (England & Wales)
Terje Svåsand	Norway
Ole Torrissen (chair)	Norway
Eric Verspoor	UK (Scotland)
Jonathan White	Ireland

1.3 Background

The farming of Atlantic salmon has expanded rapidly since the early 1980s. Production of farmed salmon in the North Atlantic is now approximately 1.5 million tonnes (over 2 million tonnes worldwide) and vastly exceeds the nominal catch of wild Atlantic salmon (FishstatJ, FAO, 2013). In 2014, it was estimated that farmed Atlantic salmon production exceeded the nominal wild catch in the North Atlantic by over 1900 times (ICES, 2015).

Interactions between salmon farming and wild stocks have raised concerns, in particular related to disease, parasite, genetic and ecological interactions. Such issues have been subject to extensive research and dialogue as efforts have been made to balance the needs of industry with the requirement to safeguard wild stocks. The topic remains an area of continued intensive research interest. In seeking fresh advice from ICES on the possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic, NASCO have highlighted that this should update previous findings and advice, citing in particular the ICES/NASCO symposium on the impacts of aquaculture held in 2005 and previous ICES advice to OSPAR on aquaculture impacts. The following paragraphs provide a brief overview of these earlier information sources.

ICES/NASCO Symposium, 2005

The ICES/NASCO Symposium (*Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: Science and management, challenges and solutions*) was held in Bergen, Norway in October 2005. This, in turn, aimed to build on two earlier international symposia on the subject. In 1991, an initial symposium was convened by the Norwegian Directorate For Nature Management and NASCO in Loen, Norway (Hansen *et al.*, 1991), and this was followed by an ICES/NASCO symposium in Bath, UK in 1997 (Hutchinson, 1997). This latter symposium helped to inform development of a NASCO resolution aimed at minimising impacts from aquaculture, introductions and transfers, and transgenics on wild salmon stocks (Williamsburg Resolution; NASCO, 2006).

The objectives of the 2005 ICES/NASCO symposium were:

i) to summarise available knowledge of the interactions between aquaculture and wild salmon stocks and other diadromous fish species;

ii) to identify gaps in current understanding of these interactions and to develop recommendations for future research priorities;

iii) to review progress in managing interactions, the remaining challenges, and possible solutions; and

iv) to make recommendations for additional measures to ensure that aquaculture practices are sustainable and consistent with the Precautionary Approach.

A convener's report was prepared (Hansen and Windsor, 2006) with many of the papers included in a special edition of the ICES Journal of Marine Science (Hutchinson, 2006).

The issues covered by the symposium in relation to sea lice included:

- *Gaining a better understanding of the behaviour and ecology of sea lice*. Topics covered: the impact of temperature and salinity on development, behaviour and dispersal of lice; population structure and genetic diversity of sea lice; dispersal patterns / models; evaluation of changes in lice levels relative to the farm production cycle; and the refinement of pest management strategies, including assessing risks to wild populations and possible vaccine development.
- *Evaluation of interactions / impacts*. Topics covered: the effects of lice on the physiology and osmoregulation of fish; infection pressure relative to farm proximity, site and year; the possible development of 'threshold' levels and predictors of mortality to aid management. A particular gap was the lack of information on the effects of lice on wild populations, with the hope that 'new' studies would provide such assessments.
- *Sea lice management*. Topics covered: monitoring programmes; the heavy reliance on a few key medicines and treatments; development of resistance to treatments; alternative controls measures (e.g. wrasse); and the importance of effective integrated pest management strategies.

The issues covered by the symposium in relation to genetic and ecological interactions included:

- *Escapees*. Topics covered: improvements in reporting (both successes and failures) and in understanding the causes of escapes and in management responses; dispersal investigations and variable survival / behaviour with timing of release (and other factors); indications that levels of farmed salmon in cages were a better predictor of escapees rather than reported losses (suggesting possible failure to account for 'trickle' losses / concerns about the reliability of reporting); cage design developments; escape of juveniles from freshwater hatcheries and risks posed by hatchery releases and stocking.
- *Genetic developments and interactions*. Topics covered: genetic selection in farms and 'domestication' of strains; potential for the genetic tracing of the source of escapees; clear evidence of farmed fish contributing to spawning

in rivers and of changes in genetic composition of wild stocks over time (reduced population differentiation can occur quite quickly); impacts on wild stocks related to numbers of farm-origin spawners; application of models to predict cumulative effects over generations; and meta analysis suggesting reduced productivity of wild populations in proximity of farms.

In an overview, the conveners concluded that the symposium had provided significant advances in understanding in the management of both sea lice and escapees. However, significant challenges remained and risks were not fully understood. They welcomed the recognition from industry representatives that farming can have damaging impacts on wild stocks. This was seen as a clear prerequisite to cooperative action, but needed to to be continued and enhanced if solutions to remaining challenges were to be found. Ongoing data sharing, trust and cooperation between industry, regulators and wild fish interests was seen as essential to developing effective management control strategies.

The conveners noted that numbers of escapees remained large relative to wild stocks, with risk of irreversible damage to the stock structure and diversity of wild salmon and potential consequences for the fitness and productivity of stocks and their ability to adapt to environmental change. As a result, they proposed that interactions needed to be virtually eliminated, not just reduced, and that containment measues needed to be much improved, or production shifted to the use of sterile salmon.

Priorities for further work were seen as improving understanding in:

- The dispersal and spawning success of escapees;
- Impacts on wild populations;
- Genetic techniques for tracing the origin of escapees;
- The potential for using sterile fish / triploids;
- Sea lice treatments and other emerging disease challenges;
- Cage designs and the possible increased risk from storms related to climate change.

ICES advice to OSPAR

In recent years, ICES has been asked to provide advice to OSPAR on interactions between wild and farmed fish (ICES, 2010; 2014). These requests have extended to all finfish mariculture activities, although such activities are dominated by Atlantic salmon production.

In 2010, ICES was asked to provide advice on the current state of knowledge of the interaction of finfish mariculture on the condition of wild fish populations at a local and regional scale, including from parasites, escaped fish and the use of fish feed in mariculture. Advice was also requested on how the interactions will change as a result of an expansion of mariculture activities. ICES collated available information and completed a risk analysis of interactions between mariculture and wild fish populations. The summary of the advice generated noted that the degree of interactions may be 'moderate' between finfish mariculture and wild fish populations at the scale of a river local to a salmon farm, but are lower at a broader scale.

In 2014, the request from OSPAR identified a number of potential pressures arising from mariculture on which advice was required:

i) introduction of antibiotics and other pharmaceuticals;
ii) transfer of disease and parasite interactions;
iii) release of nutrients and organic matter;
iv) introgression of foreign genes, from both hatchery-reared fish and genetically modified fish and invertebrates, in wild populations;
v) effects on small cetaceans, such as the bottlenose dolphin, due to their interaction with aquaculture cages;
vi) non-indigenous species.

ICES provided a brief update on the knowledge in each of these areas, commented on potential management solutions to mitigate pressures and outlined monitoring needs. The advice summary was similar to that in 2010 in concluding that most interactions examined in the request are expected to be localized to the vicinity of the mariculture sites. However, the advice noted that although there is reasonable evidence that interactions occur, scientific support for the significance of identified interactions is generally weak. ICES advised that formal risk assessments prior to establishing new mariculture developments may help identify issues and prevent the development of negative interactions. ICES further advised that the inclusion of genetic risks in such assessments is critical and often over-looked.

2 The effects of sea lice on Atlantic salmon

2.1 Introduction

All fish are susceptible to parasitic infections. The sea louse (*Lepeophtheirus salmonis*), also commonly called the salmon louse, has widespread geographic distribution, is an important parasite of salmonids and has been a serious problem for the Atlantic salmon farming industry since the 1970s (Thorstad *et al.*, 2015). Sea lice have a greater economic impact on the industry than any other parasite (ICES, 2010) and control of lice levels on farms is of key importance. The high density of salmon in cages has provided a large number of potential hosts and promoted the transmission and population growth of the parasite (Torrissen *et al.*, 2013). As a result, salmon farming has been shown to increase the abundance of lice in the marine environment. However, knowledge of parasite infection rates and resulting effects in wild populations of fish is relatively poor.

Historically, naturally occurring lice levels on wild salmonids have typically been low - a few (0–10) adult lice per returning salmon and sea trout (Torrissen *et al.*, 2013; Serra-Llinares *et al.*, 2014). Elevated levels of sea lice on wild salmonids collected from coastal areas in the vicinity of salmon farms has been regarded as evidence that mariculture is a main source of the infections and studies have demonstrated a link between fish-farming activity and sea lice infestations on wild salmonids (Helland *et al.*, 2012; 2015; Middlemas *et al.*, 2010; 2013; Serra-Llinares *et al.*, 2014). Thus, the risk of infection among wild salmon populations can be elevated in areas that support salmon mariculture, although louse management activities can reduce the prevalence and intensity of infection on wild fish (Penston and Davies, 2009; Serra-Llinares *et al.*, 2014). There is considerable uncertainty about the extent of the zones of elevated risk of infection and this will be subject to both spatial and temporal variability, for example as a result of changes in local hydrological processes (Amundrud and Murray, 2009; Salama *et al.*, 2013; 2015; Jones *et al.*, 2015; Johnsen *et al.*, 2016).

The extent to which elevated infections of sea lice pose a risk to the health of wild salmon populations has been the subject of extensive research. However, there are many difficulties in quantifying effects at the population level, particularly for fish stocks that are characterised by highly variable survival linked to environmental variables, such as Atlantic salmon (Vollset *et al.*, 2015; Helland *et al.*, 2015). The following sections aim to summarise the current state of knowledge in relation to the impact of sea lice on Atlantic salmon.

2.2 Physiological effects

Several laboratory studies have presented the effect of sea lice on host physiology of Atlantic salmon, sea trout and Arctic charr smolts (reviewed in Finstad and Bjørn, 2011; Thorstad *et al.*, 2015). Major primary (nervous, hormonal), secondary (blood parameters) and tertiary (whole body response) physiological effects, including high levels of plasma cortisol and glucose, reduced osmoregulatory ability and reduced non-specific immunity in the host occur when the lice develop from the sessile chalimus 2 stage to the mobile first pre-adult stage. Sublethal tertiary effects, such as reduced growth, reduced reproduction; reduced swimming performance and impaired immune defence have also been reported (see Finstad and Bjørn, 2011 for references). In addition, differences in genetic susceptibility to sea lice are recognised among host stocks and species.

It has been shown in laboratory studies that 0.04–0.15 lice per gramme fish weight can increase stress levels, reduce swimming ability and create disturbances in water and salt balance in Atlantic salmon. In sea trout, around 50 mobile lice are likely to give direct mortality, and 13 mobile lice, or approximately 0.35 lice per gramme fish weight might cause physiological stress in sea trout (weight range of 19–70 g). Moreover, around 0.05–0.15 lice per gramme fish weight were found to affect growth, condition and reproductive output in sexually maturing Arctic charr (Tveiten *et al.*, 2010).

Laboratory studies have also indicated that infections of 0.75 lice per gramme fish weight, or approximately eleven sea lice per fish, can kill a recently emigrated wild salmon smolt of about 15 g if all the sea lice develop into pre-adult and adult stages (Finstad *et al.*, 2000). Studies of naturally infested wild salmon post-smolts indicate that only those with less than ten lice survived the infection. This is consistent with field studies on sea lice infections in salmon post-smolts in the Norwegian Sea where more than 3000 post-smolts have been examined for lice, but none observed carrying more than ten adult lice. Fish with up to ten mobile lice were observed to be in poor condition with a low haematocrit level and poor growth (Holst *et al.*, 2003). Further support for this threshold comes from an experimental study of naturally infected migrating salmon smolts collected during a monitoring cruise. Half of the fish were deloused as a control, and the health of the two fish groups were monitored in the laboratory. Only fish carrying eleven mobile lice or less survived (Holst *et al.*, 2003). The results have been further verified in the laboratory on wild-caught Atlantic salmon post-smolts infected with sea lice and showing the same level of tolerance for sea lice infections (Karlsen *et al.*, in prep.)

These results have been used in Norway to provide estimates of death rates according to lice densities on migrating salmon smolts as a management tool and have been adopted in the Norwegian risk assessment for fish farming (Taranger *et al.*, 2015). The categories are: 100% mortality in the group >0.3 lice per gramme fish weight, 50% mortality in the group 0.2–0.3 lice per gramme fish weight, 20% mortality in the group 0.1–0.2 lice per gramme fish weight and 0% mortality in the group <0.1 lice per gramme fish weight. Wagner *et al.* (2008) discuss the wider factors that should be taken into account when estimating sea louse threshold levels detrimental to a host.

2.3 Evidence from monitoring programmes

Monitoring programmes have been implemented in a number of countries to assess lice levels to inform management decisions. Given the difficulties of sampling outmigrating wild salmon smolts, sea trout are commonly sampled and in some cases may be used as a proxy for potential levels on salmon (Thorstad *et al.*, 2014).

In Norway, the lice infection on wild salmonid populations is estimated through a national monitoring programme (Serra-Llinares *et al.*, 2014; Taranger *et al.*, 2015). The aim of the sea lice monitoring programme is to evaluate the effectiveness and consequences of zone regulations in national salmon fjords (areas where salmon farming is prohibited), as well as the Norwegian strategy for an environmentally sustainable growth of aquaculture.

Monitoring is carried out during the salmon smolt migration and in summer to estimate lice levels on sea trout and Arctic charr. The fish are collected using traps, fishing nets and surface trawling (Holm *et al.*, 2000; Holst *et al.*, 2003; Heuch *et al.*, 2005; Bjørn *et al.*, 2007). Also, sentinel cages have been used to investigate infestation rates (Bjørn *et al.*, 2011).

The results indicate considerable variation between years and sampling locations in the risk of lice related mortality, based on the Norwegian risk assessment criteria for detrimental lice threshold levels (low: <10%, moderate 10–30% and high: >30%). The risk for sea trout (and also Arctic charr in the Northern regions) is higher compared with Atlantic salmon post-smolts and the results show moderate-to-high risk of lice related mortality on sea trout in most counties with high salmon farming activity.

The estimated risk of lice-related mortality for Atlantic salmon varies between years and sites, and was low at most sites in 2010 and 2013, but moderate and high at several sites in 2011, 2012 and 2014.

In Scotland, analysis of wild sea trout monitored over five successive farm cycles found that lice burdens above critical levels (based on laboratory studies of sea trout) were significantly higher in the second year of the production cycle (Middlemas *et al.*, 2010). In Norway, preliminary analysis of data from fallowing zones indicate that lice levels in farming areas are also correlated with farmed biomass. In years with high biomass lice epidemics are present in some zones, but such epidemics are not seen in years with low biomass (Serra-Llinares *et al.*, submitted).

2.4 Population effects

Population level impacts of sea lice infestation have been estimated in Atlantic salmon post-smolts from a series of long-term studies and analyses in Ireland and Norway involving the paired release of treated and control groups of smolts (Jackson *et al.*, 2011 a and b; Jackson *et al.*, 2013; Gargan *et al.*, 2012; Skilbrei *et al.*, 2013; Krkošek *et al.*, 2013; Vollset *et al.*, 2014; 2015). These studies assumed that the sea louse treatments were efficacious, and that released smolts were exposed to sea lice during the period of the outmigration in which the treatment was effective. Furthermore, the studies were not designed to discriminate between lice from farm and non-farm sources.

Survival estimates have been based on a statistical analysis of differential survival to adults among release groups (Gargan *et al.*, 2012; Jackson *et al.*, 2011 a, b; 2013) including odds ratios (Jackson *et al.*, 2013; Skilbrei *et al.*, 2013; Krkošek *et al.*, 2013; Torrissen *et al.*, 2013; Vollset *et al.*, 2015). An odds ratio is a measure of association between an exposure and an outcome and represents the odds that an outcome will occur given a particular exposure, compared to the odds of the outcome occurring in the absence of that exposure. Thus, in these studies, the odds ratio represented the probability of being recaptured in the treated group divided by the probability of being recaptured in the control group. All studies reported an overall improved return rate for treated vs. control salmon, but all showed significant spatial and temporal variability in the magnitude of the treatment effect.

Gargan *et al.* (2012) reported that the ratio of return rates of treated:control fish in individual trials ranged from 1:1 to 21.6:1, with a median ratio of 1.8:1. Similarly, odds ratios of 1.1:1 to 1.2:1 in favour of treated smolts were reported in Ireland and Norway, respectively (Torrissen *et al.*, 2013). Krkošek *et al.* (2013) reported that treatment had a significant positive effect with an overall odds ratio of 1.29:1 (95% CI: 1.18–1.42). A recent meta-analysis of Norwegian data (Vollset *et al.*, 2015) based on 118 release groups (3989 recaptured out of 657 624 released), reported an overall odds ratio of 1.18:1 (95% CI: 1.07–1.30) in favour of treated fish. Further analysis found that the age of returning salmon was on average higher and weight lower in untreated fish compared with treated fish (Vollset *et al.*, 2014; Skilbrei *et al.*, 2013).

The survival of Atlantic salmon during their marine phase has fallen in recent decades (Chaput, 2012; ICES, 2015). This downturn in survival is evident over a broad geographical area and is associated with large-scale oceanographic changes (Beaugrand and Reid, 2003; Friedland *et al*., 2000; 2005; 2009; 2014). For monitored stocks around the North Atlantic, current estimates of marine survival are at historically low levels with typically fewer than 5% of out-migrating smolts returning to their home rivers for the majority of wild stocks, with lower levels for hatchery-origin fish (ICES 2015). Viewed against marine mortality rates at or above 95%, the 'additional' mortality attributable to sea lice has been estimated at around 1% (Jackson *et al*., 2013).

In some studies, the impacts of sea lice have also been estimated as losses of returning adult fish to rivers. Such estimates indicate marked variability, ranging from 0.6% to 39% in individual trials (Gargan *et al*., 2012; Krkošek *et al*., 2013; Skilbrei *et al*., 2013). These results suggest that sea lice induced mortality has an impact on Atlantic salmon returns which may influence the achievement of conservation requirements for affected stocks (Gargan *et al*., 2012).

Vollset *et al.* (2015) concluded that much of the heterogeneity among trials could be explained by the release location, time period and baseline (i.e. marine) survival. Baseline survival was reported to be the most important predictor variable. When this was low (few recaptures from the control group), the effect of treatment was relatively high (odds ratio of 1.7:1). However, when baseline survival was high, the effect of treatment was undetectable (odds ratio of ~1:1). One explanation for this finding is that the detrimental effect of lice is exacerbated when the fish are subject to other stressors; the findings of other studies support this hypothesis (Finstad *et al*., 2007; Connors *et al*., 2012; Jackson *et al*., 2013; Godwin *et al*., 2015). Vollset *et al.* (2015) concluded that their study supported the hypothesis that sea lice contribute to the mortality of salmon. However, they cautioned that the effect was not consistently present, was strongly modulated by other risk factors and suggested that population-level effects of sea lice on wild salmon stocks cannot be estimated independently of the other factors that affect marine survival.

2.5 Summary

- The sea louse (*Lepeophtheirus salmonis*) has widespread geographic distribution, is an important parasite of salmonids and has been a serious problem for the Atlantic salmon farming industry since the 1970s. Sea lice have a greater economic impact on the industry than any other parasite and control of lice levels on farms is of key importance.
- Salmon farming has been shown to increase the abundance of lice in the marine environment and the risk of infection among wild salmonid populations. However, there is considerable uncertainty, and spatial and temporal variability, about the extent of the zones of elevated risk.
- It has been shown in laboratory studies that 0.04–0.15 lice per gramme fish weight can increase stress levels. Laboratory studies have also demonstrated that infections of 0.75 lice per gramme fish weight, or approximately eleven sea lice per fish, can kill a recently emigrated wild salmon smolt of about 15 g if all the sea lice develop into pre-adult and adult stages.
- A number of studies in Norway and Ireland have estimated the relative marine survival of smolts treated to provide lice resistance and control groups. All studies have reported an overall improved return rate for treated salmon, but all showed significant spatial and temporal variability in the magnitude of the treatment effect.

- The survival of Atlantic salmon during their marine phase has fallen in recent decades. This downturn in survival is evident over a broad geographical area and is associated with large-scale oceanographic changes. Viewed against current marine mortality rates commonly at or above 95%, the 'additional' mortality attributable to sea lice has been estimated at around 1%.
- In some studies, the impact of sea lice has also been estimated as losses of returning adult salmon to rivers. These estimates indicate marked variability, with losses in individual experiments ranging from 0.6% to 39%. These results suggest that sea lice induced mortality has an impact on Atlantic salmon returns, which may influence the achievement of conservation requirements for affected stocks.
- Much of the heterogeneity among trials comparing the survival to adulthood of juvenile salmon administered sea lice medicines and control groups could be explained by the release location, time period and baseline (i.e. marine) survival. In a recent meta-analysis of Norwegian data, baseline survival was reported to be the most important predictor variable. When this was low, the effect of treatment was high. In contrast, when baseline survival was high, the effect of treatment was undetectable. However, it is unclear whether baseline survival is affected by sea lice exposure.

2.6 Knowledge gaps and research priorities

- Factors influencing marine mortality of Atlantic salmon need to be identified and quantified.
- Efficacious salmon lice management procedures need to be further developed for farmed salmon.
- Transmission dynamics of salmon lice between farmed fish and wild salmonids in time and space need to be better understood.
- Long-term effects of sea lice impact on the stability of wild salmon stocks need to be assessed, relative to the number of returning adults, their condition and age.
- Improved methods are needed to assess the risk of sea lice impacts from salmon aquaculture on wild salmon, particularly during their early marine migration.
- The impact of salmon farming on wild salmon production has been relatively poorly researched, and it is timely to increase the knowledge within this area.

3 Escapees, genetic interactions and effects on wild Atlantic salmon

3.1 Numbers of escapees and observations in rivers

Although aquaculture technology and fish-farm safety has significantly increased over the past decade or more, each year, large numbers of Atlantic salmon still escape from aquaculture installations into the wild. While many of these are reported, for example see the statistics from the Norwegian Directorate of Fisheries for reported escapes from Norwegian farms (http://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemmingsstatistikk), in many circumstances, escapes go unnoticed. Therefore, the numbers of escapees are likely to be significantly higher than the reported numbers and, in Norway, the true numbers escaping from farms have been estimated to be 2–5 times higher than the official statistics (Skilbrei *et al.*, 2015). In other salmon producing countries, for example Scotland http://aquaculture.scotland.gov.uk/data/fish_escapes.aspx, eastern Canada and USA http://www.nasco.int/pdf/reports_annual/2015%20Commissions%20Report.pdf the numbers of farmed escapees are also reported. The degree of underreporting in these regions remains unquantified.

Farmed salmon may escape at both the freshwater (Clifford *et al.*, 1998a; Carr and Whoriskey, 2006; Uglem *et al.*, 2013) and marine stages of production (Clifford *et al.*, 1998b; Webb *et al.*, 1991; Carr *et al.*, 1997a). Most known escapes occur from sea cages (Jensen *et al.*, 2010). However, due to differences in rearing practices between countries and regions, the extent of freshwater escapes may differ. In some countries, such as Scotland, it is likely to be higher than, for example, in Norway. In Scotland, in the order of 20 million smolts are produced annually from freshwater pens (Franklin *et al.*, 2012). In Norway, most smolts are produced in land-based tanks from which escape is less likely.

Although the probability of surviving to adulthood and maturing vary between the different life-history stages at which the salmon escape, the great majority of salmon that escape from farms disappear never to be seen again (Skilbrei, 2010a; Skilbrei, 2010b; Hansen, 2006; Whoriskey *et al.*, 2006). Nevertheless, some of the escapees are in or enter into rivers where native salmon populations exist. While not all escapees in rivers are sexually mature (Carr *et al.*, 1997b; Madhun *et al.*, 2015) or indeed in the process of maturing, most are, and these may attempt to spawn with wild salmon (this includes both parr and adults). Farmed escaped salmon have been observed in rivers in all regions where Atlantic salmon farming occurs; Norway (Gausen and Moen, 1991; Fiske *et al.*, 2006), UK (Youngson *et al.*, 1997; Webb *et al.*, 1991; Green *et al.*, 2012), eastern Canada and USA (Morris *et al.*, 2008; Carr *et al.*, 1997a), and Chile (Sepulveda *et al.*, 2013). Furthermore, farmed salmon can migrate great distances post escape (Hansen and Jacobsen, 2003; Jensen *et al.*, 2013), and have been observed in rivers outside farming dense regions for example Iceland (Gudjonsson, 1991). Still, the incidence of farmed escaped salmon in rivers is likely to be correlated with the volume of farming within the region, as determined by a study conducted in Norway (Fiske *et al.*, 2006), and in Scotland (where there are differences between the east and west coasts) (Green *et al.*, 2012).

While the incidence of farmed escaped salmon has been investigated in a number of rivers in Norway in the period 1989 to 2013 (Fiske *et al.*, 2006), a new national monitoring programme for farmed escaped salmon was established in Norway in 2014, and based upon data from angling catches, dedicated autumn angling and diving surveys 30 out of the 140 rivers surveyed displayed a frequency of >10% escapees (http://www.imr.no/publikasjoner/andre_publikasjoner/romt_oppdrettslaks_i_vassdrag/nb-no). These surveys demonstrate that the number of escapees within rivers varies in time and space (Gausen and Moen, 1991; Fiske *et al.*, 2006).

Farmed salmon escapees may attempt to partake in spawning with wild salmon or among themselves. Several studies have reported observations of farmed salmon spawning with wild fish in rivers. This has for example been reported in rivers in Scotland (Webb *et al.*, 1991; Webb *et al.*, 1993; Butler *et al.*, 2005), Norway (Lura and Saegrov, 1991; Saegrov *et al.*, 1997) and Canada (Carr *et al.*, 1997a). However, experiments demonstrate that the spawning success of farmed salmon is significantly reduced (Fleming *et al.*, 1996; Fleming *et al.*, 2000; Weir *et al.*, 2004), perhaps just 1–3% and <30% of the success of wild males and females respectively (Fleming *et al.*, 1996). However, the relative spawning success is likely to also vary with the life-stage at which the fish escaped (Fleming *et al.*, 1997; Weir *et al.*, 2005). Therefore, if a river has for example 10% farmed escapees observed on the spawning grounds, the genetic contribution to the next generation is likely to be significantly lower than 10%.

3.2 Identification of escapees

Farmed salmon escapees are typically identified using external morphological characteristics and growth patterns on fish scales (Fiske *et al.*, 2006; Lund and Hansen, 1991). In Norway, genetic methods to identify farmed escaped salmon back to their farm(s) of origin has been developed and is routinely implemented in cases of unreported escapes (Glover *et al.*, 2008; Glover, 2010). As of 01.01.2016, the method has been used in ~20 cases of unreported escape and has resulted in initiation of legal investigations successfully resulting in fines for companies found in breach of regulations (Glover, 2010). Since 2003, all aquaculture salmon in Maine must be marked before placement into marine net pens so that in the event of an escape the fish can be traced to the farm of origin (NMFS, 2005). Maine's marking programme utilises a genetic pedigree based approach to identify fish. In other countries, no formal active identification programmes are in place. There are ongoing efforts to develop other genetic and non-genetic tagging methods to permit the routine identification of escapees back to their farms of origin.

3.3 Intraspecific hybridisation and introgression

There are still just a few published studies that have addressed genetic changes in wild populations following invasion of escaped farmed salmon. This may be due to the fact that such studies are often challenging. For example, they often require representative samples of the wild populations ideally before and after invasion, and access to representative farmed samples, as well as informative set of molecular genetic markers (Besnier *et al.*, 2011; Karlsson *et al.*, 2011).

The first studies of introgression were conducted in Ireland (Clifford *et al.*, 1998b; Clifford *et al.*, 1998a) and Northern Ireland (Crozier, 1993; Crozier, 2000) demonstrating introgression of farmed salmon in rivers as a response to escapes from local farms. These escapees originated from both cage escapes in salt water, as well as escapes from freshwater smolt rearing facilities located within rivers. Later on, a set of experiments looking at genetic changes in Norwegian populations was conducted. The first of these studies demonstrated temporal genetic changes in three out of seven populations located on the west and middle parts of Norway, and concluded that introgression of farmed salmon was the primary driver (Skaala *et al.*, 2006). Later, a spatio-temporal investigation of 21 populations across Norway revealed significant temporal genetic changes in several rivers caused by introgression of farmed salmon, and importantly, observed an overall reduction in interpopulation genetic diversity (Glover *et al.*, 2012). The latter observation is consistent with predictions of population homogenization as a result of farmed salmon interbreeding (Mork, 1991). Importantly, all rivers that displayed temporal genetic changes due to spawning of farmed escapees, displayed an increase in genetic variation revealed as total number of alleles observed in the population. This is consistent with introgression from fish of a non-local source. The final published study in Norway used recently developed diagnostic genetic markers for identification of farmed and wild salmon (Karlsson *et al.*, 2011) to estimate cumulative introgression of farmed salmon escapees in 20 wild populations (Glover *et al.*, 2013). In this study, cumulative introgression over 2–3 decades was estimated between 0–47% among rivers. Differences in introgression levels between populations was positively linked with the observed proportions of escapees in the rivers, but it was also suggested that the density of the wild population, and therefore level of competition on the spawning grounds and during juvenile stages, also influenced introgression (Glover *et al.*, 2013). A recent study conducted in the Magaguadavic River in eastern Canada demonstrated introgression of farmed escapees with the native population (Bourret *et al.*, 2011).

The most recent and by far the most extensive investigation of introgression of farmed salmon was recently published as a report in Norwegian by researchers from NINA and IMR (http://www.nina.no/english/News/News-article/ArticleId/3984). Here, a total of 125 Norwegian salmon populations were classified using a combination of the estimate of wild genome P(wild) (Karlsson *et al.*, 2014) and the introgression estimates from the study by Glover *et al.* (2013). These authors established four categories of introgression: green = no genetic changes observed; yellow = weak genetic changes indicated but less than 4% farmed salmon introgression; orange = moderate genetic changes documented 4–10% farmed salmon introgression; red = large genetic changes demonstrated >10% farmed salmon introgression. Based upon these analyses, 44, 41, nine and 31 of the populations studied fell into categories green–red respectively. This huge volume of data therefore provides a comprehensive status for many Norwegian populations but is lacking for all other regions.

3.4 Domestication and divergence from wild salmon

From the very start of the Atlantic salmon aquaculture industry in the early 1970s, breeding programmes to select salmon for higher performance in culture were initiated (Gjedrem *et al.*, 1991; Ferguson *et al.*, 2007; Gjoen and Bentsen, 1997). The largest and most significant of these programmes globally are those initiated in Norway which are based upon material originating from >40 Norwegian rivers (Gjedrem *et al.*, 1991). Other programmes in Norway were also established from wild salmon, and in other countries salmon breeding programmes have also been established. Farmed salmon originating from the three main breeding companies in Norway: Marine Harvest - Mowi strain, Aqua Gen AS, and SalmoBreed AS, dominate global production although this varies from country to country. For example, in eastern Canada only the St John River domesticated strain (Friars *et al.*, 1995) is permitted for use in commercial aquaculture, and in Scotland some locally based strains e.g. Landcatch (Powell *et al.*, 2008) are also being used.

Initially, salmon breeding programmes concentrated on increasing growth, but rapidly expanded to include other traits that are also of commercial importance, such as flesh characteristics, age at maturation and disease resistance (Gjedrem, 2000; Gjedrem, 2010). Today, breeding programmes have advanced to 12+ generations, and genome-assisted selection is being utilised in several of the breeding programmes. QTL selected sub-strains are now commercially available displaying characteristics such as reduced sensitivity to specific diseases (Moen *et al.*, 2009) and increased growth. It is likely that full utilisation of genomic selection will increase the diversity of traits that can be accurately targeted by selection for rapid gains in breeding. For example, the recently identified strong influence of the vgll3 locus on age in maturation in salmon (Ayllon *et al.*, 2015; Barson *et al.*, 2015) could represent an effective target to inhibit grilsing (i.e. early maturation) in aquaculture.

As a result of: (1) directional selection for commercially important traits, (2) inadvertent domestication selection (the widespread genetic changes associated with adaptation to the human-controlled environment and its associated reduction in natural selection pressure), (3) non-local origin, and (4) random genetic changes (drift), farmed salmon display a range of genetic differences to wild salmon (Ferguson *et al.*, 2007). Examples of these differences include growth rate under controlled conditions (Glover *et al.*, 2006; Glover *et al.*, 2009; Solberg *et al.*, 2013 a and b; Thodesen *et al.*, 1999), gene transcription patterns (Bicskei *et al.*, 2014; Roberge *et al.*, 2006; Roberge *et al.*, 2008), stress tolerance (Solberg *et al.*, 2013a), and behavioural traits including predator avoidance and dominance (Einum and Fleming, 1997). In addition, farmed salmon strains typically display lower levels of allelic variation when compared to wild salmon strains (Norris *et al.*, 1999; Skaala *et al.*, 2004), although not all classes of genetic marker reveal the same trends (Karlsson *et al.*, 2010). Looking at the level of genetic variation coding for phenotypic traits such as growth, some data are emerging suggesting a possibly reduced variation in farmed strains (Solberg *et al.*, 2013a; Reed *et al.*, 2015). The latter observation is expected given the fact that farmed fish have been selected for this trait since the early 1970s.

3.5 Fitness studies

Thus far, only three published studies have addressed survival of farmed, hybrid and wild salmon in the natural environment. Such studies are exceptionally demanding on logistics, and require experimental periods extending beyond what typical funding sources permit.

The first study was conducted in the River Burrishoole in Ireland, and involved planting eggs of farmed, hybrid and wild parentage into a natural river system (McGinnity *et al.*, 1997). These fish were identified using DNA profiling and followed through a two-generation experiment. The authors concluded that the lifetime fitness of farmed fish was just 2% of wild fish, and that the relative-fitness increased along a gradient towards the offspring of a F1 hybrid survivor spawning together with a wild salmon (= back cross) that displayed a lifetime survival of 89% compared to the offspring of a wild salmon (McGinnity *et al.*, 2003). The authors concluded that repeated invasions of farmed salmon in a wild population may cause the fitness of the native population to seriously decline, and potentially enter an “extinction-vortex” in extreme cases.

In Norway, a slightly different but complimentary experiment was conducted in the River Imsa (Fleming *et al.*, 2000). Here, the authors permitted migrating adult salmon of farmed and wild native origin entry to the River Imsa, once they had been sampled in the upstream trap. They thereafter spawned naturally and their offspring were monitored until adulthood. This study reported a lifetime fitness of farmed salmon (i.e. escaped adult to adult) of 16% compared with wild salmon (Fleming *et al*., 2000). Important additional data from this study was the fact that productivity of the wild salmon from the river decreased, following the permitted invasion of farmed salmon, both with respect to the total smolt production and when smolt production from native females was considered alone (Fleming *et al*., 2000). This is because the offspring of the farmed and hybrid salmon competed with wild salmon for both territory and resources, and the dynamics of this may vary across life-history stages (Sundt-Hansen *et al*., 2015).

The most recently published study to address the relative fitness of farmed and wild Atlantic salmon in a natural environment was conducted in the River Guddal in Norway (Skaala *et al*., 2012). Here, these authors used a similar design to the Irish study, releasing large numbers of farmed, hybrid and wild salmon eggs into the river and following their survival. The study included planting out eggs across three cohorts, and permitted for the first time, comparisons of family as well as group fitness (farmed hybrid and wild) in freshwater. The study did not use a local wild fish, but salmon from the Norwegian gene bank as a wild fish proxy. While these authors reported reduced genetic fitness of farmed salmon offspring compared to the non-local wild salmon, egg size was closely related to family survival in the river. Therefore, some farmed salmon families with large eggs displayed surprisingly high survival rates in freshwater (higher than some wild families), although when egg size was adjusted for, farmed salmon offspring displayed significantly lower survival in freshwater compared to the wild salmon. To illustrate this, in 15 of 17 pairwise comparisons of maternal half-sib groups, families sired with wild males performed better compared with families sired with farmed fish. The study also revealed that farmed and wild salmon overlapped in diet in the river, an observation also reported from an earlier small-scale planting study (Einum and Fleming, 1997) and from the full-generation study in the River Imsa (Fleming *et al*., 2000).

Studies cross-examining the underlying details, mechanisms, and genomics of the observed survival differences between farmed and wild salmon in natural habitats have also been published (Besnier *et al*., 2015; Reed *et al*., 2015), although the exact mechanisms still remain elusive. For example, attempts at quantifying predation in the wild (Skaala *et al*., 2014), and predation susceptibility in semi-natural contests (Solberg *et al*., 2015) have not revealed greater predation of farmed salmon offspring than wild salmon offspring, despite earlier studies suggesting reduced predation awareness caused by domestication (Einum and Fleming, 1997).

Collectively, the results of the whole-river studies outlined above are supported by the widespread literature demonstrating the reduced fitness of hatchery reared salmonids, as part of supplementation programmes, in the wild (Araki *et al*., 2007; Araki *et al*., 2009).

3.6 Short-term consequences of introgression for wild salmon populations (i.e. a few salmon generations)

In natural habitats such as rivers, territory and food resources are typically limited, and survival is often controlled by density-dependent factors, and habitats have carrying capacities (Jonsson *et al*., 1998; Bacon *et al*., 2015). Studies have demonstrated that the offspring of farmed salmon compete with wild salmon for resources such as food and space (Skaala *et al*., 2012; Fleming *et al*., 2000). Therefore, when farmed salmon manage to spawn, and their offspring constitute a component of a given river's juvenile population, the production of juveniles with a pure wild background will be depressed though competition for these resources. In addition, data from controlled studies have indicated that the total productivity of smolts in the river following introgression of farmed salmon can decrease (Fleming *et al.*, 2000; McGinnity *et al.*, 1997).

As discussed in the section above, farmed salmon display a range of genetic differences to wild populations, which includes various life-history and behavioural traits. In controlled experiments with farmed and wild salmon (McGinnity *et al.*, 1997; McGinnity *et al.*, 2003; Fleming *et al.*, 2000; Fraser *et al.*, 2010 a; Skaala *et al.*, 2012) differences in freshwater growth and body shape, timing of hatching and smolt migration, age of smoltification, incidence of male parr maturation, sea age-at-maturity and growth in the marine environment have been observed, with some variation across farmed–wild comparisons (Fraser *et al.*, 2010 b). Therefore, where farmed salmon have introgressed in natural populations, it is likely that recipient populations will display changes in life-history traits in the direction of the farmed strains. Given that life-history traits are likely to be associated with fitness in the wild and local adaptation (Garcia de Leaniz *et al.*, 2007; Taylor, 1991; Fraser *et al.*, 2011; Barson *et al.*, 2015), these changes in life-history characteristics are likely to be associated with a loss of fitness (which will also contribute to an overall reduction in productivity). These changes will be difficult to detect against the background of natural variability in stock abundance and require long-term studies to quantify accurately, and at the present, there is a lack of empirical data demonstrating such changes in effected wild populations.

The short-term consequences for wild populations will scale with the magnitude and frequency of interbreeding events. For example, in rivers where density of wild spawners is low, spawning success of escapees will increase compared with locations where density of wild spawners is high. Similarly, low density of wild juveniles with relaxed competition, will give farm offspring better survival opportunities than they will have in locations with high density of wild juveniles. Thus, when populations are under stress and density of individuals goes down, impact from escapees is expected to increase, which is in agreement with studies on observed introgression rates in salmon (Glover *et al.*, 2012; Heino *et al.*, 2015; Glover *et al.*, 2013), but also supported for example by studies on brown trout supplemented by non-local hatchery fish (Hansen and Mensberg, 2009).

Atlantic salmon river stocks are characterized by widespread structuring into genetically distinct and differentiated populations (Ståhl, 1987; Verspoor *et al.*, 2005). This is conditioned by the evolutionary relationships among populations (Dionne *et al.*, 2008; Perrier *et al.*, 2011; Dillane *et al.*, 2008) and adaptive responses to historical and contemporary to environmental differences (Garcia de Leaniz *et al.*, 2007; Taylor, 1991). A spatio-temporal genetic study of 21 populations in Norway revealed an overall reduction in interpopulation diversity caused by interbreeding of farmed escaped salmon (Glover *et al.*, 2012). It is likely that further introgression of farmed salmon will continue to erode this diversity.

3.7 Long-term consequences of introgression for wild salmon populations (i.e. more than a few generations)

The conservation of genetic variation within and among populations (as outlined in the UN Convention on Biological Diversity, 1992) is important for the resilience of local stocks to human or natural disturbances (Ryman, 1991; Schindler *et al.*, 2010), and in the long term, reduced genetic variability will affect the species' ability to cope with a changing environment (McGinnity *et al.*, 2009; Lande and Shannon, 1996). Therefore, one way gene flow, as occurs through the successful spawning of farmed escapees potentially represents a powerful evolutionary force. It erodes genetic variation among wild populations (Glover *et al.*, 2012), and in the long run, may also erode the genetic variation within populations under certain situations (Tufto and Hindar, 2003) as the recipient wild populations become more similar to the less variable farmed populations.

Although evolutionary theory permits us to outline general trajectories, it remains difficult to predict and demonstrate the evolutionary fate of specific wild populations receiving farmed immigrants. The severity and nature of the effect depends on a number of factors, including the magnitude of the differences between wild and farmed populations (both historical and adaptive differences), the mechanisms underlying genetic differences between wild and farmed salmon, the frequency of intrusions of farmed fish, and the numbers of intruding farmed fish relative to wild spawning population sizes (Hutchings and Fraser, 2008). Furthermore, wild populations that are already under evolutionary strain from other challenges such as disease pressure, sea lice infection, overharvest, habitat destruction and poor water quality, etc. are more likely to be sensitive to the potential negative effects of genetic introgression and loss of fitness. Therefore, genetic introgression has to be seen in the context of other challenges also.

Taken collectively, existing understanding makes it clear that the long-term consequences of introgression across river stocks can be expected to lead to reduced productivity and decreased resilience to future impacts such as climate change (i.e. less fish and more fragile stocks). Therefore, a substantial reduction or even total elimination of escaped farmed salmon in the wild is essential in order to minimize or avoid negative effects on native populations.

3.8 Summary

- Each year, large numbers of domesticated salmon escape from commercial fish farms. While many of these are reported, the true number of escapees is likely to be significantly higher. Escapees are observed in rivers in all regions where farming occurs, although the numbers of escapees vary both spatially and temporally. It has been noted that in some rivers in some years, the numbers of escapees have approached 50% or more of the spawning population.
- The spawning success of escaped farmed salmon is much lower than wild salmon. Despite this, genetic studies have demonstrated that farmed salmon have displayed widespread introgression in a large number of Norwegian populations where this has been investigated. Introgression has also been shown in other countries, but the full extent of introgression remains to be investigated.
- Farmed salmon are domesticated and display significant genetic differences to wild salmon in a wide range of fitness related traits. Whole-river experimental studies have demonstrated that the offspring of farmed and cultured salmon in general, display lower fitness than their wild counterparts in the wild.
- Juvenile escapees and the offspring of farmed salmon compete with wild salmon for territory and food. Therefore, their presence in the natural habi-

tat will reduce the total production of wild fish. Studies have also shown this can result in a decreased overall productivity of the population.

- Where farmed salmon have successfully interbred with natural populations, it is likely that recipient populations will display changes in life-history traits. These changes are likely to be maladaptive for the wild population.
- The long-term consequences of introgression across river stocks can be expected to lead to reduced productivity and decreased resilience to future impacts such as climate change (i.e. less fish and more fragile stocks).
- The evidence from studies in the wild, and the extensive literature relating to salmonids in general, demonstrates that the offspring of farmed salmon display reduced fitness in the wild. However, the results of these studies suggest that the relative success of farmed salmon and, likewise, the relative potential negative effect on a native population, is likely to vary in time and space. Wild populations that are already under evolutionary strain from other challenges such as disease pressure, sea lice infection, over exploitation, habitat destruction and poor water quality are more likely to be sensitive to the potential negative effects of genetic introgression and loss of fitness. Therefore, such effects have to be seen in the context of other challenges.
- While recognising that there were still uncertainties, WKCULEF considered that the evidence relating to the impacts of escapees / genetic introgression provided a clear indication of impacts on wild salmon populations. A substantial reduction of escaped farmed salmon in the wild, or sterilization of farmed salmon, would be required in order to minimize effects on native populations.

3.9 Knowledge gaps and research priorities

- To increase the level of monitoring and dedicated studies looking into the numbers of escapees and their genetic introgression in native populations, especially in knowledge poor regions. This will also include further characterisation of aquaculture strains and development of monitoring tools across countries through international collaboration.
- To increase understanding of the environmental and biological factors that influence levels of farmed salmon introgression and their ecological consequences including productivity.
- To understand the genomic architecture of domestication and the underlying genetic differences between farmed and wild salmon in both the hatchery and natural environments, and how this affects fitness.
- To identify and quantify adaptive genetic changes in wild populations that have been subject to introgression of farmed escaped salmon. This includes quantification of natural selection and fitness.

Annex 1: Working documents submitted to the Workshop on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic, 1–3 March, 2016

WP NO.	AUTHORS	TITLE
1	Glover, K.A., Skaala, Ø., Solberg, M., Skilbrei, O.T., Svåsand, T. and Wennevik, V.	Salmon escapees and status of knowledge.
2	Jackson, D.	Sea Lice - introduction, background and current state of knowledge.
3	Lillehammer, M.	Stochastic simulations of introgression of farmed salmon into wild populations.
4	Finstad, B. and Gargan, P.	Effects of sea lice on Atlantic salmon - from individual- to population effects.
5	Jaffa, M.	Sea lice in context.
6	Hindar, K.	Genetic introgression from farmed to wild salmon.
7	Coulson, M.	Fish-farm escapes to stay or go? Imlications for the River Polla.
8	Karlsbakk, E.	Microbial diseases in aqauculture and impact on wild salmonids.
9	McGinnity, P.	Effects of farm escapees on salmon production.
10	Svasand, T.	Risk asessment - environmental impacts of Norwegan fish farming.
11	Verspoor, E.	Assessment of interbreeding and introgression of farm genes in a small Scottish Atlantic salmon (*Salmo salar*) stock: *ad hoc* samples - *ad hoc* results?
12	Gargan, P.	Sea lice - perspectives on studies in Ireland.
13	Svasand, T.	Sea lice monitoring and modelling in Norway.
14	Kvamme, B.O.	National sea lice monitoring programme.

Annex 2: References cited

Amundrud, T.L. and Murray, A.G. 2009. Modelling sea lice dispersion under varying environmental forcing in a Scottish sea loch. Journal of Fish Diseases, 32: 27–44.

Araki, H., Cooper, B., and Blouin, M. S. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science, 318: 100–103.

Araki, H., Cooper, B., and Blouin, M. S. 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. Biology Letters, 5: 621–624.

Ayllon, F., Kjaerner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M. F., Dahle, G., Taranger, G. L., *et al*. 2015. The vgll3 Locus Controls Age at Maturity in Wild and Domesticated Atlantic Salmon (*Salmo salar* L.) Males. Plos Genetics, 11.

Bacon, P. J., Malcolm, I. A., Fryer, R. J., Glover, R. S., Millar, C. P., and Youngson, A. F. 2015. Can Conservation Stocking Enhance Juvenile Emigrant Production in Wild Atlantic Salmon? Transactions of the American Fisheries Society, 144: 642–654.

Barson, N. J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G. H., Fiske, P., Jacq, C., *et al*. 2015. Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. Nature, 528: 405–408.

Besnier, F., Glover, K. A., and Skaala, Ø. 2011. Investigating genetic change in wild populations: modelling gene flow from farm escapees. Aquaculture Environment Interactions, 2: 75–86.

Besnier, F., Glover, K. A., Lien, S., Kent, M., Hansen, M. M., Shen, X., and Skaala, Ø. 2015. Identification of quantitative genetic components of fitness variation in farmed, hybrid and native salmon in the wild. Heredity, 115: 47–55.

Beaugrand, G. and Reid, F.C. 2003. Long term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology 9: 801–817.

Bicskei, B., Bron, J. E., Glover, K. A., and Taggart, J. B. 2014. A comparison of gene transcription profiles of domesticated and wild Atlantic salmon (*Salmo salar* L.) at early life stages, reared under controlled conditions. BMC Genomics, 15:884.

Bjørn, P.A., Finstad, B., Kristoffersen, R., Mckinley, R.S. and Rikardsen, A.H. 2007. Differences in risks and consequences of salmon louse, *Lepeophtheirus salmonis* (Krøyer), infestation on sympatric populations of Atlantic salmon, brown trout, and Arctic charr within northern fjords. ICES Journal of Marine Science, 64, 386–393.

Bjørn, P.A., Sivertsgård, R., Finstad, B., Nilsen, R., Serra-Llinares, R.M. and Kristoffersen, R. 2011. Area protection may reduce salmon louse infection risk to wild salmonids. Aquaculture Environment Interactions, 1: 233–244.

Bourret, V., Bernatchez, L., O'Reilly, P. T., Carr, J. W., and Berg, P. R. 2011. Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. *Heredity*, *106*, 3, 500–510.

Butler, J. R. A., Cunningham, P. D. and Starr, K. 2005. The prevalence of escaped farmed salmon, *Salmo salar* L., in the River Ewe, western Scotland, with notes on their ages, weights and spawning distribution. Fisheries Management and Ecology, 12: 149–159.

Carr, J.W., Anderson, J.M., Whoriskey, F.G. and Dilworth, T. 1997a. The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. ICES Journal of Marine Science, 54: 1064–1073.

Carr, J.W., Lacroix, G.L., Anderson, J.M. and Dilworth, T. 1997b. Movements of non-maturing cultured Atlantic salmon (*Salmo salar*) in a Canadian river. ICES Journal of Marine Science, 54: 1082–1085.

Carr, J.W., and Whoriskey, F.G. 2006. The escape of juvenile farmed Atlantic salmon from hatcheries into freshwater streams in New Brunswick, Canada. ICES Journal of Marine Science, 63: 1263–1268.

Chaput, G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. ICES Journal of Marine Science, 69: 1538–1548.

Clifford, S.L., McGinnity, P. and Ferguson, A. 1998a. Genetic changes in an Atlantic salmon population resulting from escaped juvenile farm salmon. Journal of Fish Biology, 52: 118–127.

Clifford, S.L., McGinnity, P. and Ferguson, A. 1998b. Genetic changes in Atlantic salmon (*Salmo salar*) populations of northwest Irish rivers resulting from escapes of adult farm salmon. Canadian Journal of Fisheries and Aquatic Sciences, 55: 358–363.

Connors, B.M., Braun, D.C., Peterman, R.M. *et al.* 2012. Migration links ocean-scale competition and local ocean conditions with exposure to farmed salmon to shape wild salmon dynamics. Conservation Letters 5, 304–312.

Crozier, W. W. 1993. Evidence of genetic interaction between escaped farmed salmon and wild Atlantic salmon (*Salmo salar* L) in a Northern Irish river. Aquaculture, 113: 19–29.

Crozier, W. W. 2000. Escaped farmed salmon, *Salmo salar* L., in the Glenarm River, Northern Ireland: genetic status of the wild population 7 years on. Fisheries Management and Ecology, 7: 437–446.

Dillane, E., McGinnity, P., Coughlan, J. P., Cross, M. C., de Eyto, E., Kenchington, E., Prodohl, P., *et al*. 2008. Demographics and landscape features determine intra-river population structure in Atlantic salmon (*Salmo salar* L.): the case of the River Moy in Ireland. Molecular Ecology, 17: 4786–4800.

Dionne, M., Caron, F., Dodson, J. J., and Bernatchez, L. 2008. Landscape genetics and hierarchical genetic structure in Atlantic salmon: the interaction of gene flow and local adaptation. Molecular Ecology, 17: 2382–2396.

Einum, S., and Fleming, I. A. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology, 50: 634–651.

FAO. 2013. FishStat J, www.fao.org

Ferguson, A., Fleming, I. A., Hindar, K., Skaala, Ø., McGinnity, P., Cross, T., and Prodohl, P. 2007. Farm escapees. In The Atlantic salmon. Genetics, Conservation and Management, pp. 357–398. Ed. by E. Verspoor, L. Stradmeyer, and J. L. Nielsen. Blackwell, Oxford, UK.

Finstad, B., Bjørn, PA., Grimnes, A., and Hvidsten, N.A. 2000. Laboratory and field investigations of salmon lice [(*Lepeophtheirus salmonis* (Krøyer)] infestation on Atlantic salmon (*Salmo salar* L.) post-smolts. Aquaculture Research, 31: 795–803.

Finstad B., Kroglund F., Strand R., Stefansson S.O., Bjørn P.A., Rosseland B.O., Nilsen T.O. and Salbu B. 2007. Salmon lice or suboptimal water quality - reasons for reduced postsmolt survival? Aquaculture 273, 374–383.

Finstad, B. and Bjørn, P.A. 2011. Present status and implications of salmon lice on wild salmonids in Norwegian coastal zones. In: Salmon Lice: An Integrated Approach to Understanding Parasite Abundance and Distribution. (Jones, S. and Beamish, R. Eds.). Wiley-Blackwell, Oxford, UK, 281–305.

Fiske, P., Lund, R.A., and Hansen, L.P. 2006. Relationships between the frequency of farmed Atlantic salmon, *Salmo salar* L., in wild salmon populations and fish farming activity in Norway, 1989–2004. ICES Journal of Marine Science, 63: 1182–1189.

Fleming, I.A., Jonsson, B., Gross, M.R., and Lamberg, A. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). Journal of Applied Ecology, 33: 893–905.

Fleming, I.A., Lamberg, A., and Jonsson, B. 1997. Effects of early experience on the reproductive performance of Atlantic salmon. Behavioural Ecology, 8: 470–480.

Fleming, I.A., Hindar, K., Mjolnerod, I.B., Jonsson, B., Balstad, T. and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. Proceedings of the Royal Society of London Series B-Biological Sciences, 267: 1517–1523.

Franklin, P., Verspoor, E. and Slaski, R. 2012. Study into the impacts of open pen freshwater aquaculture production on wild fisheries. Report for Marine Scotland by Homarus Ltd., Beaulieu, Hampshire, UK. Final Report P/SFWP/286, 160 pp.

Fraser D.J., Minto, C., Calvert, A.M., Eddington, J.D. and Hutchings, J.A. 2010 a. Potential for domesticated-wild interbreeding to induce maladaptive phenology across multiple populations of wild Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences, 67, 1768–1775.

Fraser, D.J., Houde, A.L.S., Debes, P.V., O'Reilly, P., Eddington, J.D. and Hutchings, J.A. 2010b. Consequences of farmed-wild hybridization across divergent populations and multiple traits in salmon. Ecological Applications, 20, 935–953.

Fraser, D.J., Weir, L.K., Bernatchez, L., Hansen, M.M. and Taylor, E.B. 2011. Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. Heredity, 106: 404–420.

Friars, G. W., Bailey, J. K., and Oflynn, F. M. 1995. Applications of selection for multiple traits in cage-reared Atlantic salmon (*Salmo salar*). Aquaculture, 137: 213–217.

Friedland, K., Hansen, D.L.P., Dunkley, D.A. and MacLean, J.C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. ICES Journal of Marine Science 57: 419–429.

Friedland, K.D., Chaput, G. and Maclean, J.C. 2005. The emerging role of climate in post-smolt growth of Atlantic salmon. ICES Journal of Marine Science 62: 1338–1349.

Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Ó Maoiléidigh, N. and McCarthy, J.L. 2009. The recruitment of Atlantic salmon in Europe. ICES Journal of Marine Science 66: 289–304.

Friedland, K.D., Shank, B.V., Todd, C.D., McGinnity, P. and Nye, J.A. 2014. Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal oscillation. Journal of Marine Systems 133, 77–87.

Garcia de Leaniz, C., Fleming, I. A., Einum, S., Verspoor, E., Jordan, W. C., Consuegra, S., Aubin-Horth, N., *et al.* 2007. A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. Biological Reviews, 82: 173–211.

Gargan, P. G., Forde, G., Hazon, N., F., R. D. J. and Todd, C. D. 2012. Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. Canadian Journal of Fish and Aquatic Sciences, 69: 343–353.

Gausen, D., and Moen, V. 1991. Large-scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. Canadian Journal of Fisheries and Aquatic Sciences, 48: 426–428.

Gjedrem, T., Gjoen, H. M., and Gjerde, B. 1991. Genetic-Origin of Norwegian Farmed Atlantic Salmon. Aquaculture, 98: 41–50.

Gjedrem, T. 2000. Genetic improvement of cold-water fish species. Aquaculture Research, 31: 25–33.

Gjedrem, T. 2010. The first family-based breeding program in aquaculture. Reviews in Aquaculture, 2: 2–15.

Gjoen, H. M., and Bentsen, H. B. 1997. Past, present, and future of genetic improvement in salmon aquaculture. ICES Journal of Marine Science, 54: 1009–1014.

Glover, K.A., Bergh, O., Rudra, H., and Skaala, Ø. 2006. Juvenile growth and susceptibility to *Aeromonas salmonicida* subsp *salmonicida* in Atlantic salmon (*Salmo salar* L.) of farmed, hybrid and wild parentage. Aquaculture, 254: 72–81.

Glover, K.A., Skilbrei, O.T., and Skaala, Ø. 2008. Genetic assignment identifies farm of origin for Atlantic salmon *Salmo salar* escapees in a Norwegian fjord. ICES Journal of Marine Science, 65: 912–920.

Glover, K.A., Ottera, H., Olsen, R.E., Slinde, E., Taranger, G.L., and Skaala, Ø. 2009. A comparison of farmed, wild and hybrid Atlantic salmon (*Salmo salar* L.) reared under farming conditions. Aquaculture, 286: 203–210.

Glover, K.A. 2010. Forensic identification of fish farm escapees: The Norwegian experience. Aquaculture Environment Interactions, 1: 1–10.

Glover, K.A., Quintela, M., Wennevik, V., Besnier, F., Sørvik, A.G.E., and Skaala, Ø. 2012. Three decades of farmed escapees in the wild: A spatio-temporal analysis of population genetic structure throughout Norway. Plos One, 7(8) e43129.

Glover, K.A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M., and Skaala, Ø. 2013. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genetics, 14:4.

Godwin, S.C., Dill, L.M., Reynolds, J.D. and Krkošek, M. 2015. Sea lice, sockeye salmon, and foraging competition: lousy fish are lousy competitors. Canadian Journal of Fisheries and Aquatic Sciences 72, 8.

Green, D. M., Penman, D. J., Migaud, H., Bron, J. E., Taggart, J. B., and McAndrew, B. J. 2012. The Impact of Escaped Farmed Atlantic Salmon (*Salmo salar* L.) on Catch Statistics in Scotland. Plos One, 7.

Gudjonsson, S. 1991. Occurrence of reared salmon in natural salmon rivers in Iceland. Aquaculture, 98: 133–142.

Hansen, L.P., Håstein, T., Naevdal, G., Saunders, R.L., and Thorpe, J.E. (Eds). 1991. Interactions between cultured and wild Atlantic salmon. Proceedings of a symposium hosted by the Directorate for Nature Management and Norwegian Institute for Nature Research, held in the Hotel Alexandria, Loen, Norway, 23–26 April 1990. Aquaculture, 98: 1–324.

Hansen, L. P., and Jacobsen, J. A. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. ICES Journal of Marine Science, 60: 110–119.

Hansen, L.P. 2006. Migration and survival of farmed Atlantic salmon (*Salmo salar* L.) released from two Norwegian fish farms. ICES Journal of Marine Science, 63: 1211–1217.

Hansen, L.P. and Windsor, M. 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. NINA Special Report 34. 74 pp. Trondheim, October, 2006.

Hansen, M.M., and Mensberg, K.L.D. 2009. Admixture analysis of stocked brown trout populations using mapped microsatellite DNA markers: indigenous trout persist in introgressed populations. Biology Letters, 5: 656–659.

Heino, M., Svåsand, T., Wennevik, V., and Glover, K. A. 2015. Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. Aquaculture Environment Interactions, 6: 185–190.

Helland, I.P., Finstad, B., Uglem, I., Diserud, O.H., Foldvik, A., Hanssen, F., Bjørn, P.A., *et al*. 2012. What determines salmon lice infections on wild salmonids? Statistical calculations of data from the national salmon lice surveillance program 2004–2010 (in Norwegian). NINA Report, 891. 51 pp.

Helland, I.P., Uglem, I., Jansen, P.A., Diserud, O, H., Bjørn, P.A. and Finstad, B. 2015. Statistical and ecological challenges of monitoring parasitic sea lice infestations in wild salmonid fish stocks. Aquaculture Environment Interactions, 7: 267–280.

Heuch, P.A., Bjorn, P.A., Finstad, B., Holst, J.C., Asplin, L. and Nilsen, F. 2005. A review of the Norwegian 'National Action Plan against Salmon Lice on Salmonids': The effect on wild salmonids. Aquaculture, 246, 79–92.

Holm, M., Holst J. C. and Hansen L. P. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. ICES Journal of Marine Science, 57, 955–964.

Holst, J.C., Jakobsen, P.J., Nilsen, F., Holm, M., Asplin, L. and Aure, J. 2003. Mortality of seaward-migrating post-smolts of Atlantic salmon due to Salmon lice infection in Norwegian salmon stocks. In: Salmon at the Edge. (Mills, D. Ed). Wiley-Blackwell, Oxford, UK. Pp. 136–137.

Hutchings, J. A., and Fraser, D. J. 2008. The nature of fisheries- and farming-induced evolution. Molecular Ecology, 17: 294–313.

Hutchinson, P. (Ed). 1997. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. ICES Journal of Marine Science, 54: 963–1225.

Hutchinson, P. (Ed). 2006. Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions. ICES Journal of Marine Science, 63: 1159–1371.

ICES. 2010. Effect of mariculture on populations of wild fish. ICES Advice 2010, Book 1, 195–208.

ICES. 2014. OSPAR request on interactions between wild and captive fish stocks. ICES Advice 2014, Book 1, 1–6.

ICES. 2015. Report of the Working Group on North Atlantic Salmon (WGNAS), 17–26 March 2014, Moncton, Canada. ICES CM 2015/ACOM:09. 330 pp.

Jackson, D., Cotter, D., O'Maoileidigh, N., O'Donohoe, P., White, J., Kane, F., Kelly, S., McDermott, T., McEvoy, S., Drumm, A. and Cullen, A. 2011a. Impact of early infestation with the salmon louse *Lepeophtheirus salmonis* on the subsequent survival of outwardly migrating Atlantic salmon smolts from a number of rivers on Ireland's south and west coast. Aquaculture 319, 37–40.

Jackson, D., Cotter, D., O'Maoileidigh, N., O'Donohoe, P., White, J., Kane, F., Kelly, S., McDermott, T., McEvoy, S., Drumm, A., Cullen, A. and Rogan, G. 2011b. An evaluation of the impact of early infestation with the salmon louse *Lepeophtheirus salmonis* on the subsequent survival of outwardly migrating Atlantic salmon, *Salmo salar* L., smolts. Aquaculture 320, 159–163.

Jackson, D., Cotter, D., Newell, J., McEvoy, S., O'Donohoe, P., Kane, F., McDermott, T., Kelly, S. and Drumm, A. 2013. Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar* L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. Journal of Fish Diseases 36 (3), 273–281.

Jensen, Ø., Dempster, T., Thorstad, E.B., Uglem, I. and Fredheim, A. 2010. Escapes of fishes from Norwegian Sea cage aquaculture: causes, consequences and prevention. Aquaculture Environment Interactions, 1, 71–83.

Jensen, A.J., Karlsson, S., Fiske, P., Hansen, L.P., Hindar, K. and Østborg, G. 2013. Escaped farmed Atlantic salmon in the Arctic Ocean. Aquaculture Environment Interactions, 3, 223–229. Jensen *et al*., 2010.

Johnsen, I.A., Asplin, L.C., Sandvik, A.D. and Serra-Llinares, R.M. 2016. Salmon lice dispersion in a northern Norwegian fjord system and the impact of vertical movements. Aquaculture Environment Interactions, 8, 99–116.

Jones, S.R.M., Bruno, D., Madsen, L., and Peeler, E.J. 2015. Disease management mitigates risk of pathogen transmission from maricultured salmonids. Aquaculture Environment Interactions, 6, 119–134.

Jonsson, N., Jonsson, B., and Hansen, L. P. 1998. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. Journal of Animal Ecology, 67: 751–762.

Karlsen, Ø. *et al.* In preparation. The effect of salmon lice infections on wild caught Atlantic salmon (*Salmo salar*) - a laboratory study.

Karlsson, S., Moen, T., and Hindar, K. 2010. Contrasting patterns of gene diversity between microsatellites and mitochondrial SNPs in farm and wild Atlantic salmon. Conservation Genetics, 11: 571–582.

Karlsson, S., Moen, T., Lien, S., Glover, K.A., and Hindar, K. 2011. Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. Molecular Ecology Resources, 11: 247–253.

Karlsson, S., Diserud, O.H., Moen, T. and Hindar, K. 2014. A standardized method for quantifying unidirectional genetic introgression. Ecology and Evolution, 4: 3256–3263.

Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B., and Todd, C.D. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B: Biological Sciences 280: 20122359. (a) http://dx.doi.org/10.1098/rspb.2012.2359.

Lande, R., and Shannon, S. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution, 50: 434–437.

Lund, R. A., and Hansen, L. P. 1991. Identification of wild and reared Atlantic salmon, *Salmo salar* L., using scale characters. Aquaculture and Fisheries Management, 22: 499–508.

Lura, H., and Saegrov, H. 1991. Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. Aquaculture, 98: 151–159.

Madhun, A.S., Karlsbakk, E., Ischsen, C.H., Omdal, L.M., Sørvik, A.G.E., Skaala, Ø., Barlaup, B.T., *et al.* 2015. Potential disease interaction reinforced: double-virus infected escaped farmed Atlantic salmon, *Salmo salar* L., recaptured in a nearby river. Journal of Fish Diseases, 38: 209–219.

McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., *et al.* 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES Journal of Marine Science, 54: 998–1008.

McGinnity, P., Prodohl, P., Ferguson, K., Hynes, R., O'Maoileidigh, N., Baker, N., Cotter, D., *et al*. 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proceedings of the Royal Society of London Series B-Biological Sciences, 270: 2443–2450.

McGinnity, P., Jennings, E., DeEyto, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K., *et al*. 2009. Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. Proceedings of the Royal Society B-Biological Sciences, 276: 3601–3610.

Middlemas, S.J., Raffell, J.A., Hay, D.W., Hatton-Ellis, M. and Armstrong, J.D. 2010. Temporal and spatial patterns of sea lice levels on sea trout in western Scotland in relation to fish farm production cycles. Biology Letters 6, 548–551.

Middlemas, S.J., Fryer, R.J., Tulett, D. and Armstrong, J.D. 2013. Relationship between sea lice levels on sea trout and fish farm activity in western Scotland. Fisheries Management and Ecology, 20: 68–74.

Moen, T., Baranski, M., Sonesson, A.K. and Kjøglum, S. 2009. Confirmation and fine-mapping of a major QTL for resistance to infectious pancreatic necrosis in Atlantic salmon (*Salmo salar*): population-level associations between markers and trait. BMC Genomics, 10 (368).

Mork, J. 1991. One-generation effects of farmed fish immigration on the genetic differentiation of wild Atlantic salmon in Norway. Aquaculture, 98: 267–276.

Morris, M. R. J., Fraser, D. J., Heggelin, A. J., Whoriskey, F. G., Carr, J. W., O'Neil, S. F., and Hutchings, J. A. 2008. Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. Canadian Journal of Fisheries and Aquatic Sciences, 65: 2807–2826.

NASCO. 2006. Resolution by the Parties to the Convention for the Conservation of Salmon in the North Atlantic Ocean to Minimize Impacts from Aquaculture, Introductions and Transfers, and Transgenics on the Wild Salmon Stocks, the Williamsburg Resolution (Adopted at the Twentieth Annual Meeting of NASCO in June 2003 and amended at the Twenty-First Annual Meeting of NASCO in June 2004, and at the Twenty-Third Annual Meeting of NASCO in June 2006). North Atlantic Salmon Conservation Organization (NASCO), Edinburgh, Scotland, UK. Council document CNL(06)48. 44 pp.

National Marine Fisheries Service and US Fish and Wildlife Service. 2005. Final Recovery Plan for the Gulf of Maine Distinct Population Segment of Atlantic Salmon (*Salmo salar*). National Marine Fisheries Service, Silver Spring, Maryland. 325 pp.

Norris, A. T., Bradley, D. G., and Cunningham, E. P. 1999. Microsatellite genetic variation between and within farmed and wild Atlantic salmon (*Salmo salar*) populations. Aquaculture, 180: 247–264.

Penston, M.J. and Davies, I.M. 2009. An assessment of salmon farms and wild salmonids as sources of *Lepeophtheirus salmonis* (Krøyer) copepodids in the water column in Loch Torridon, Scotland. Journal of Fish Diseases, 32: 75–88.

Perrier, C., Guyomard, R., Bagliniere, J. L., and Evanno, G. 2011. Determinants of hierarchical genetic structure in Atlantic salmon populations: environmental factors vs. anthropogenic influences. Molecular Ecology, 20: 4231–4245.

Powell, J., White, I., Guy, D., and Brotherstone, S. 2008. Genetic parameters of production traits in Atlantic salmon (*Salmo salar*). Aquaculture, 274: 225–231.

Reed, T. E., Prodohl, P., Hynes, R., Cross, T., Ferguson, A. and McGinnity, P. 2015. Quantifying heritable variation in fitness-related traits of wild, farmed and hybrid Atlantic salmon families in a wild river environment. Heredity, 115: 173–184.

Roberge, C., Einum, S., Guderley, H., and Bernatchez, L. 2006. Rapid parallel evolutionary changes of gene transcription profiles in farmed Atlantic salmon. Molecular Ecology, 15: 9–20.

Roberge, C., Normandeau, E., Einum, S., Guderley, H. and Bernatchez, L. 2008. Genetic consequences of interbreeding between farmed and wild Atlantic salmon: insights from the transcriptome. Molecular Ecology, 17: 314–324.

Ryman, N. 1991. Conservation genetics considerations in fishery management. Journal of Fish Biology, 39: 211–224.

Saegrov, H., Hindar, K., Kalas, S., and Lura, H. 1997. Escaped farmed Atlantic salmon replace the original salmon stock in the River Vosso, western Norway. ICES Journal of Marine Science, 54: 1166–1172.

Salama, N.K.G., Collins, C.M., Fraser, J.G., Dunn, J., Pert, C.C., Murray, A.G. and Rabe, B. 2013. Development and assessment of a biophysical dispersal model for sea lice. Journal of Fish Diseases, 36, 323–337.

Salama, N.K.G., Murray, A.G. and Rabe, B. 2015. Simulated environmental transport distances of *Lepeophtheirus salmonis* in Loch Linnhe, Scotland, for informing aquaculture area management structures. Journal of Fish Diseases, doi:10.1111/jfd.12375.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., and Webster, M. S. 2010. Population diversity and the portfolio effect in an exploited species. Nature, 465: 609–612.

Sepulveda, M., Arismendi, I., Soto, D., Jara, F., and Farias, F. 2013. Escaped farmed salmon and trout in Chile: incidence, impacts, and the need for an ecosystem view. Aquaculture Environment Interactions, 4: 273–283.

Serra-Llinares, R.M., Bjørn, P.A., Finstad, B., Nilsen, R., Harbitz, A., Berg, M. and Asplin, L. 2014. Salmon lice infection on wild salmonids in marine protected areas: an evaluation of the Norwegian 'National Salmon Fjords'. Aquaculture Environment Interactions, 5, 1–16.

Serra-Llinares, R.M., Bjørn, P.A., Sandvik, A.D., Lindstrom, N.M., Johnsen, I.A., Halttunen, E., Nilsen, R., Finstad, B., Skardhamar, J. and Asplin, L. Submitted. The effectiveness of synchronized fallowing for the control of salmon lice infestations on wild salmonids. Aquaculture Environment Interactions.

Skaala, Ø., Hoyheim, B., Glover, K., and Dahle, G. 2004. Microsatellite analysis in domesticated and wild Atlantic salmon (*Salmo salar* L.): allelic diversity and identification of individuals. Aquaculture, 240: 131–143.

Skaala, Ø., Wennevik, V., and Glover, K.A. 2006. Evidence of temporal genetic change in wild Atlantic salmon, *Salmo salar* L., populations affected by farm escapees. ICES Journal of Marine Science, 63: 1224–1233.

Skaala, Ø., Glover, K.A., Barlaup, B.T., Svåsand, T., Besnier, F., Hansen, Michael, M., and Borgstrøm, R. 2012. Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. Canadian Journal of Fisheries and Aquatic Sciences, 69: 1994–2006.

Skaala, Ø., Glover, K.A., Barlaup, B.T. and Borgstrøm, R. 2014. Microsatellite DNA used for parentage identification of partly digested Atlantic salmon (*Salmo salar*) juveniles through non-destructive diet sampling in salmonids. Marine Biology Research, 10: 323–328.

Skilbrei, O. T. 2010a. Adult recaptures of farmed Atlantic salmon post-smolts allowed to escape during summer. Aquaculture Environment Interactions, 1: 147–153.

Skilbrei, O.T. 2010b. Reduced migratory performance of farmed Atlantic salmon post-smolts from a simulated escape during autumn. Aquaculture Environment Interactions, 1: 117–125.

Skilbrei, O.T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F. and Strand, R. 2013. Impact of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 1997–2009. Journal of Fish Diseases 36: 249–260. doi:10.1111/jfd.12052.

Skilbrei, O.T., Heino, M. and Svåsand, T. 2015. Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages, from farms sites in Norway. ICES Journal of Marine Science, 72: 670–685.

Solberg, M.F., Glover, K.A., Nilsen, F. and Skaala, Ø. 2013a. Does Domestication Cause Changes in Growth Reaction Norms? A Study of Farmed, Wild and Hybrid Atlantic Salmon Families Exposed to Environmental Stress. Plos One, 8 (1) e54469.

Solberg, M.F., Zhang, Z.W., Nilsen, F. and Glover, K.A. 2013b. Growth reaction norms of domesticated, wild and hybrid Atlantic salmon families in response to differing social and physical environments. BMC Evolutionary Biology, 13 (234).

Solberg, M.F., Zhang, Z. and Glover, K.A. 2015. Are farmed salmon more prone to risk than wild salmon? Susceptibility of juvenile farm, hybrid and wild Atlantic salmon *Salmo salar* L. to an artificial predator. Applied Animal Behaviour Science, 162: 67–80.

Ståhl, G. 1987. Genetic population structure of Atlantic salmon. In Population genetics and fishery management, pp. 121–140. Ed. by N. Ryman, and F. Utter. University of Washington press, Seattle.

Sundt-Hansen, L., Huisman, J., Skoglund, H., and Hindar, K. 2015. Farmed Atlantic salmon *Salmo salar* L. parr may reduce early survival of wild fish. Journal of Fish Biology, 86: 1699–1712.

Taranger, G.L., Karlsen, Ø., Bannister, R.J., Glover, K.A., Husa, V., Karlsbakk, E., Kvamme, B.O., Boxaspen, K.K., Bjørn, P.A., Finstad, B., Madhun, A.S., Craig Morton, H. and Svåsand, T. 2015. Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. ICES Journal of Marine Science, 72(3): 997–1021.

Taylor, E.B. 1991. A review of local adaptation in salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture, 98: 185–207.

Thodesen, J., Grisdale-Helland, B., Helland, S. J., and Gjerde, B. 1999. Feed intake, growth and feed utilization of offspring from wild and selected Atlantic salmon (*Salmo salar*). Aquaculture, 180: 237–246.

Thorstad, E.B., Todd, C.D., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kålås, S., Uglem, I., Berg, M. and Finstad, B. 2014. Effects of salmon lice on sea trout - a literature review. NINA Report 1044: 1–162.

Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kålås, S., Berg, M. and Finstad, B. 2015. Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta*-a literature review. Aquaculture Environment Interactions, 7: 91–117.

Torrissen, O., Jones, S., Asche, F., Guttormsen, A., Skilbrei, O.T., Nilsen, F., Horsberg, T.E. and Jackson, D. 2013. Salmon lice - impact on wild salmonids and salmon aquaculture. Journal of Fish Diseases, 36: 171–194.

Tufto, J. and Hindar, K. 2003. Effective size in management and conservation of subdivided populations. Journal of Theoretical Biology, 222: 273–281.

Tveiten, H., Bjørn, P. A., Johnsen, H. K., Finstad, B. and McKinley, R. S. 2010. Effects of the sea louse *Lepeophtheirus salmonis* on temporal changes in cortisol, sex steroids, growth and reproductive investment in Arctic charr *Salvelinus alpinus*. Journal of Fish Biology, 76: 2318–2341.

Uglem, I., Økland, F., and Rikardsen, A. H. 2013. Early marine survival and movements of escaped Atlantic salmon *Salmo salar* L. juveniles from a land-based smolt farm during autumn. Aquaculture Research, 44: 1824–1834.

Verspoor, E., Beardmore, J.A., Consuegra, S., De Leaniz, C.G., Hindar, K., Jordan, W.C., Koljonen, M.L., *et al*. 2005. Population structure in the Atlantic salmon: insights from 40 years of research into genetic protein variation. Journal of Fish Biology, 67: 3–54.

Vollset, K.W., Barlaup, B.T., Skoglund, H., Normann, E.S., Skilbrei, O.T. 2014. Salmon lice increase the age of returning Atlantic salmon. Biology Letters, 10: 20130896. http://dx.doi.org/10.1098/rsbl.2013.0896.

Vollset, K.W., Krontveit, R. I., Jansen, P., Finstad, B., Barlaup, B.T., Skilbrei, O.T., Krkošek, M., Romunstad, P., Aunsmo, A., Jensen, A.J. and Dahoo, I. 2015. Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish and Fisheries; doi:10.1111/faf.12141.

Wagner, G.N., Fast, M.D. and Johnson, S.C. 2008. Physiology and immunology of *Lepeophtheirus salmonis* infections of salmonids. Trends in Parasitology, 24(4): 176–183.

Webb, J.H., Hay, D.W., Cunningham, P.D., and Youngson, A.F. 1991. The spawning behaviour of escaped farmed and wild adult Atlantic salmon (*Salmo salar* L) in a Northern Scottish river. Aquaculture, 98: 97–110.

Webb, J.H., Youngson, A.F., Thompson, C.E., Hay, D.W., Donaghy, M.J., and I.S., M. 1993. Spawning of escaped farmed Atlantic salmon, *Salmo salar* L., in western and northern Scottish rivers; egg deposition by females. Aquaculture and Fisheries Management, 24: 557–561.

Weir, L.K., Hutchings, J.A., Fleming, I.A., and Einum, S. 2004. Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, *Salmo salar*. Journal of Animal Ecology, 73: 1069–1079.

Weir, L.K., Hutchings, J.A., Fleming, I.A. and Einum, S. 2005. Spawning behaviour and success of mature male Atlantic salmon (*Salmo salar*) parr of farmed and wild origin. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1153–1160.

Whoriskey, F.G., Brooking, P., Doucette, G., Tinker, S., and Carr, J.W. 2006. Movements and survival of sonically tagged farmed Atlantic salmon released in Cobscook Bay, Maine, USA. ICES Journal of Marine Science, 63: 1218–1223.

Youngson, A. F., Webb, J. H., MacLean, J. C., and Whyte, B. M. 1997. Frequency of occurrence of reared Atlantic salmon in Scottish salmon fisheries. ICES Journal of Marine Science, 54: 1216–1220.

Annex 3: Participants list

NAME	ADDRESS	PHONE/FAX	E-MAIL
Jonathan Carr	Atlantic Salmon Federation PO Box 5200 St Andrews NB E5B 3S8 Canada	Office: +1 506 529-1385 Cell: +1 506 754-5079 Fax: +1 506 529-4985	jcarr@asf.ca
Catherine Collins	Marine Scotland Science Marine Laboratory 375 Victoria Road Aberdeen AB11 9DB Scotland, UK	Office: +44 1224 425521 fax: +44 1224 295511	Catherine.Collins@scotland.gsi.gov.uk
Anne Cooper	ICES Secretariat H.C. Andersens Blvd. 44–46 1553 Copenhagen V Denmark	Office:	anne.cooper@ices.dk
Mark Coulson	Rivers and Lochs Institute University of the Highlands and Islands 1 Inverness Campus Inverness IV2 5NA Scotland, UK	Office: +44 1463 273576	mark.coulson.ic@uhi.ac.uk
Bengt Finstad	Norwegian Institute for Nature Research PO Box 5685 Sluppen 7485 Trondheim Norway	Office:	Bengt.Finstad@nina.no
Kevin Glover	Institute of Marine Research PO Box 1870 Nordnes 5817 Bergen Norway	Office: +47 480 40 035	kevin.glover@imr.no
Patrick Gargan	Inland Fisheries Ireland 3044 Lake Drive Citywest Business Campus Dublin 24 Ireland	Office: +353 884 2616 Fax: +353 1 836 0060	paddy.gargan@fisheriesireland.ie
Sigurdur Gudjonsson	Institute of Freshwater Fisheries Vagnhöfda 7 Reykjavik 110 Iceland	Office:	sigurdur.gudjonsson@veidimal.is

NAME	ADDRESS	PHONE/FAX	E-MAIL
Kjetil Hindar	Norwegian Institute for Nature Research PO Box 5685 Sluppen Høgskoleringen 9 7485 Trondheim Norway	+47 934 66 746 cell +47 934 66 746 fax +47 73 80 14 01	Kjetil.Hindar@nina.no
Dave Jackson	Marine Institute Rinville Oranmore Co Galway Ireland		dave.jackson@marine.ie
Martin Jaffa	Callander McDowell Manchester M45 0FN UK	+44 7944 996 552	mrj@callandermcdowell.co.uk
Simon Jones	Pacific Biological Station 3190 Hammond Bay Road Nanaimo BC V9T 6N7 Canada	+1 250 729 8351 fax +1 250 756 7053	simon.jones@dfo-mpo.gc.ca
Bjørn Olav Kvamme	Institute of Marine Research PO Box 1870 Nordnes 5817 Bergen Norway	+47 416 12 076	Bjornok@IMR.no
Marie Lillehammer	NOFIMA Muninbakken 9–13 Breivika 9291 TRomsø Norway	+47 64 97 04 05	marie.lillehammer@nofima.no
John Martell	Fisheries and Oceans Canada 200 Kent Street Ottawa ON K1A 0E6 Canada		john.martell@dfo-mpo.gc.ca
Philip McGinnity	University College Cork Cork Ireland	+353 (0)21 490 4554 fax +353 (0)21 490 4664	p.mcginnity@ucc.ie
Olav Moberg	Directorate of Fisheries PO Box 185 Sentrup 5804 Bergen Norway		Olav.Moberg@fiskeridir.no
David Morris	Freshwater Laboratory Faskally Pitlochry PH16 5LB United Kingdom	Tel +44 1224 294411 S/B +44 1224 294400 Fax +44 1796 473523	david.morris@gov.scot d.morris@marlab.ac.uk

NAME	ADDRESS	PHONE/FAX	E-MAIL
Kjell Emil Naas	The Research Council of Norway Division for Marine Biological Resources and Environmental Research PO Box 564 1327 Lysaker Norway	Tlf +47 22 03 74 15 Tlf mob + 47 90 16 57 01	ken@forskningsradet.no
Hans Petter Næs	Norwegian Seafood Research Fund Universitetsgatan 10 PO Box 429 0164 Oslo Norway	+47 23 89 64 08 mobile: +47 95236684	hans.petter.naes@fhf.no
Mike Pietrak by SfB	National Cold Water Marine Aquaculture Center Agriculture Research Service 25 Salmon Farm Road Franklin ME 04634 US	+1 207 422-2723 Cell 01 207 812-0605	Michael.pietrak@ars.usda.gov
Ian Russell chair	Cefas Pakefield Road Lowestoft Suffolk NR33 0HT UK	+44 1502 524330 fax +44 1502 513865	ian.russell@cefas.co.uk
Terje Svåsand	Institute of Marine Research PO Box 1870 Nordnes 5817 Bergen Norway	+47 5523691 fax +47 55236379	terje.svaasand@imr.no
Ole Torrissen chair	Institute of Marine Research PO Box 1870 Nordnes 5817 Bergen Norway		ole.torrissen@imr.no
Eric Verspoor	Rivers and Lochs Institute University of the Highlands and Islands 1 Inverness Campus Inverness IV2 5NA Scotland, UK	+44 1463 273226 cell: +44 07827955591	eric.verspoor.ic@uhi.ac.uk
Jonathan White	Marine Institute Oranmore Co Galway Ireland	+353 (0)91 387361	Jonathan.White@Marine.ie

Annex 4: Technical minutes from the Review Group on Possible effects of salmonid aquaculture

- RGAQUA
- Deadline: 21 April 2016
- Participants: Martin Krkošek, Robin Waples and Einar E. Nielsen (Chair)
- Expert Group: WKCULEF

Review of: Report of the Workshop to address the NASCO request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF).

The review group would like to compliment the workshop participants for a very clear, well-structured, insightful and comprehensive report. In our view only very few points have been missed and we agree with the vast majority of the conclusions presented. We still have a few suggestions for amendment in relation to issues that may be unclear, could be treated in more detail or are missing altogether in the draft report. We hope that our comments/suggestions can help to improve the report and look forward to work with you in relation to completing the final draft advice.

Similar to the report, we have split our comments and suggestions into two sections, relating to sea-lice and genetic interactions respectively. Our main comments are outlined below. However for both sections we think that the link between the main text and the sections on "Knowledge gaps and research priorities" is relatively weak. It is difficult to find a direct justification for the outlined research priorities. We suggest numbering the priorities, and subsequently provide direct appropriate reference to each of them in the main text.

There is a general bias in the published literature and available data with respect to effects on wild salmon populations from salmonid aquaculture (both sea lice and genetics) in countries and areas that have intensive salmon farming industries. This is a consequence of the importance of the parasite to management of farmed salmon and the expected magnitude of interactions. However, it also presents a challenge to understand the scale of sea lice and genetic effects on wild salmon in salmon farming areas relative to areas without salmon farms. Likewise, it is mentioned (page 19)… " the great majority of salmon that escape from farms disappear never to be seen again". That could well be true, especially given how hard it is to track escapees. But just because they are never seen again, does not mean they have no effects on wild populations in regions which are not subject to intense monitoring and/or reported in the scientific literature. Thus, a general recommendation to also investigate effects in geographic regions without intensive aquaculture could be warranted.

Sea lice

The review presents two different interpretations of % mortality caused by sea lice that are reported in the literature, but that give different representations of the effect of sea lice on salmon populations (Jackson *et al.*, 2013; Krkošek *et al.*, 2013). The interpretations seem incompatible, which can be confusing, and more effort is needed to clarify how the interpretations are related and how they differ. In one view (Jackson *et al.*, 2013), the emphasis is placed on the absolute difference in marine mortality between fish treated with parasiticides and those that are not. The example given in the review is a difference of one percent, where mortality in treated groups is 95% compared to 96% in untreated groups. The additional one percent mortality between groups is attributed to sea lice, which is interpreted as a small number compared to the 95% mortality from the treatment groups. The other interpretation of this same example is in terms of the percent loss of recruitment or abundance of adult salmon due to exposure to sea lice. In this interpretation, the same example corresponds to a 20% loss in adult salmon abundance due to sea lice; for every five fish that return as adults in the treated groups (95% mortality), there are four fish that return as adults in the untreated group (96% mortality). In other words, one in five fish are lost to sea lice effects. These differences in interpretation of the same data differ by 20x and reflect the nuances of interpreting survival data. It is therefore important to clarify for non-expert readers how to interpret the results. It is true that natural marine mortality of salmon is high and multiple factors are involved, but it is also true that a small incremental increase in marine mortality due to sea lice (or any other factor) can result in losses of salmon abundance that are relevant for fisheries and conservation management.

The review has an emphasis on the physiological responses to sea lice infection as well as experimental data on lethal infection loads. However, there could be more discussion and explanation of the environmental/biological stressors and ecological processes that mediate the relationship between lice and marine survival of Atlantic salmon. While laboratory estimates of lethal loads and physiological responses are attractive to predict impacts on wild populations, this is likely an over-simplified view because natural ecological processes such as predation and competition are likely to remove infected fish before the lice kill the fish directly. In this view, sublethal effects seen in the lab may increase or decrease mortality in the field (e.g. Pacific salmon) (Peacock *et al.*, 2014), and so laboratory results need to be connected with behavioural changes in the fish that alter predator–prey interactions between the smolts and their predators as well as the smolts and their prey (e.g. migration behaviour) (Birkeland and Jakobsen, 1997). Also, early marine growth is important for smolts to escape predation and also access a more diverse prey field and so it is therefore particularly relevant under resource-limited or parasitized conditions. Finally, there are also abiotic stressors such as pollutants that may affect the effects of sea lice on salmon smolts. These potentially interactive effects of multiple factors are likely to be important for explaining the result from meta-analysis that the effect of sea lice on salmon survival depends on the baseline survival of untreated fish (Vollset *et al.*, 2015). However, in that work, the baseline survival used is that from untreated groups, which is itself likely to be affected by louse abundance, introducing a circularity that leaves the interactive effects between lice and other factors on salmon survival poorly characterized.

There is little mention of recent difficulties in controlling sea lice on salmon farms in some areas. The difficulties are because lice have evolved resistance to the common chemical treatments. This presents a challenge to controlling lice on farms, and therefore is relevant to the wild salmon that migrate through those areas. Alternative methods and technologies are needed to provide more effective and sustainable control of sea lice on salmon farms. Work in this area includes alternative medicines, biocontrol using wrasse, and hydrogen peroxide bath treatments in specialized vessels that service farms.

The literature reviewed mixes results from Pacific salmon together with results from Atlantic salmon (as also done in this review). It is unclear to what extent the mechanisms of lice effects on wild salmon are the same between these two areas. There are key differences between Pacific and Atlantic situations, including differences in the genome of the lice themselves as well as the ecological context of the salmon. In the

Pacific, salmonids are more diverse in their life-history traits, species composition, and abundance. Also, the salmon farming industry is smaller. Thus, the extent to which the results from the Pacific on sea lice effects on wild salmon are transferable to the Atlantic situation should be at least briefly discussed.

Genetic effects

There is little reference to previous attempts to model the persistence of wild salmon populations interbreeding with farmed conspecifics. Early modelling work by Hutchings (1991) predicted that the extinction risk of native genomes is largest when interbreeding occurs and when farmed fish occur frequently and at high densities. The risk is largest in small wild populations, which is related to both demographic and genetic effects. Hindar *et al.* (2006) refined this work by using life-stage specific fitness and narrowing the modelling to realistic scenarios based on experimental data. They found that under high intrusion scenarios the recovery of the wild population is not likely under all circumstances even when interbreeding has been ceased for many decades. Baskett *et al.* (2013) used a model with coupled demographic and genetic dynamics to evaluate how genetic consequences of aquaculture escapes depend on how divergent the captive and wild populations are. They found negative genetic consequences increased with divergence of the captive population, unless strong selection removes escapes before they reproduce. Recent modelling work by Castellani *et al.* (2015) has focused on using individual based eco-genetic models, which are parameterized taking processes such as growth, mortality and maturation as well environmental and genotypic variation into account. This should allow improved power for predicting the outcome of genetic and ecological interactions between wild and farmed salmon.

“3.9 Knowledge gaps.” A key issue that was not discussed involves the timing and pace of escapes. For example, given a fixed number N of escapes over a fixed time period T, is it worse for the wild population if they come in one big pulse, or gradually in small amounts of "leakage"? Hindar *et al.* (2006) concluded that large pulses of escapes are more damaging, while Baskett *et al.* (2013) reached the opposite conclusion; that constant, small-scale leakage created greater fitness losses to the wild population. The different conclusions can be largely explained by different time frames of reference: Hindar *et al.* focused on short-term effects, while Baskett *et al.* evaluated mean effects over long periods of time. However, this topic merits more detailed study. Also, Baskett *et al.* did not explicitly consider overlapping generations. So, more work is needed in order to evaluate results as a function of escapes across generations in species with age structure like Atlantic salmon. This is important to resolve; as it is convenient to ignore low-level leakage because it is very difficult to eliminate or even monitor, but some results at least suggest it can have extremely important effects on wild populations.

Regarding variable estimates of relative spawning success of escapes: Apart from natural variability and sampling error, a logical explanation for the wide range of estimates is that the lower estimates apply to escapes from aquaculture stocks that are the most strongly domesticated. If so, then those interbreeding events likely have more serious per capita consequences than interbreeding events involving less domesticated stocks. This would mean that simply focusing on the rate of interbreeding will not necessarily provide a full picture of the genetic consequences of escapes. For discussion see Basket and Waples (2013).

Regarding the text on page 23 that mentions reduced fitness of hatchery fish used in salmon supplementation, the review paper of Christie *et al*. (2014) on this topic could be cited.

References

Baskett, M. L. and Waples, R. S. 2013. Minimizing unintended fitness consequences of cultured individuals on wild populations: keep them similar or make them different? Conservation Biology 27:83–94.

Baskett, M. L., Burgess, S. C. and Waples, R. S. 2013. Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. Evolutionary Applications **6**:1090–1108.

Birkeland, K. and Jakobsen P. J. 1997. Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. Environmental Biology of Fishes **49**:129–137.

Castellani, M., Heino, M., Gilbey, J., Araki, H., Svåsand, T. and Glover, K. A. 2015. IBSEM: An Individual-Based Atlantic Salmon Population Model. PLoS ONE 10: e0138444.

Christie, M. R., Ford, M. J. and Blouin, M. 2014. On the reproductive success of early-generation hatchery fish in the wild. Evolutionary Applications **7**:883–896.

Hutchings, J. A. 1991. The threat of extinction to native populations experiencing spawning intrusions by cultured Atlantic salmon. Aquaculture **98**: 119–132.

Jackson, D., Cotter, D., Newell, McEvoy, J. S., O'Donohoe, P., Kane, F. McDermott, T. Kelly, S and Drumm, A. 2013. Impact of *Lepeophtheirus salmonis* infestations on migrating Atlantic salmon, *Salmo salar* L., smolts at eight locations in Ireland with an analysis of lice-induced marine mortality. Journal of Fish Diseases **36**:273–281.

Krkošek, M., Revie, C., Gargan, P., Skilbrei, O. T., Finstad, B. and Todd, C. D. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B **280**: 2012.2359.

Hindar, K., Fleming, I. A., McGinnity, P., and Diserud, O. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. ICES Journal of Marine Science, **63**: 1234–1247.

Peacock, S., B. Connors, M. Krkošek, J. Irvine, and M. A. Lewis. 2014. Can reduced predation offset negative effects of sea louse parasites on chum salmon? Proceedings of the Royal Society B **281**:2013.2913.

Vollset, K., R. Krontveit, P. Jansen, B. Finstad, B. Barlaup, O. Skilbrei, M. Krkošek, A. Romunstad, A. Aunsmo, A. Jansen, and I. Doohoo. 2015. Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish and Fisheries **7**:91–113.

ICES Journal of
Marine Science

ICES CIEM International Council for the Exploration of the Sea
Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science (2016), 73(10), 2488–2498. doi:10.1093/icesjms/fsw121

Editor's Choice

Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations

Sten Karlsson*,‡, Ola H. Diserud‡, Peder Fiske, and Kjetil Hindar

Norwegian Institute for Nature Research (NINA), Sluppen, No 7485, P.O. Box 5685, Trondheim, Norway

**Corresponding author*: tel: +47 91124058; fax: +4773851401; e-mail: sten.karlsson@nina.no
‡Shared first authorship.

Karlsson, S., Diserud, O. H., Fiske, P., and Hindar, K. Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. – ICES Journal of Marine Science, 73: 2488–2498.

Received 7 March 2016; revised 8 June 2016; accepted 15 June 2016; advance access publication 22 July 2016.

Farmed Atlantic salmon (*Salmo salar*) escape from net pens and enter rivers to spawn, potentially resulting in genetic introgression and reduced fitness of wild salmon. Here, we quantify genetic introgression of farmed to wild salmon, using molecular genetic markers, in populations from 147 salmon rivers, representing three-quarters of the total wild salmon spawning population in Norway. For 109 rivers with adult modern samples and sample sizes of 20 or more, the average level of farmed genetic introgression was 6.4% (median = 2.3%), with a range between 0.0% and 42.2%. Fifty-one of these rivers showed significant farmed genetic introgression when compared with historical reference samples. We observed a highly significant correlation between estimated farmed introgression and average proportion of escaped farmed salmon. We quantify levels of introgression as unweighted averages or weighted by population sizes, to compare geographical regions and to compare levels of introgression in rivers and fjords designated as locations deserving a high level of protection. We found a generally lower level of introgression in National Salmon Rivers and National Salmon Fjords subjected to formal protection by parliament. We conclude that farmed to wild genetic introgression is high in a large proportion of Norwegian salmon rivers, with the highest levels found in the most intensive areas of salmon farming. The extensive genetic introgression documented here poses a serious challenge to the management of farmed and wild Atlantic salmon in Norway and, in all likelihood, in other regions where farmed-salmon escape events occur with regularity

Keywords: atlantic salmon, aquaculture, farmed salmon, genetic introgression, genetics, SNPs.

Introduction

Farmed Atlantic salmon differ genetically from wild salmon because of a variety of causes. Breeding programs of farmed Atlantic salmon were established in Norway in the early 1970s based on salmon collected from several populations in Central and Western Norway (Gjedrem *et al.*, 1991; Gjøen and Bentsen, 1997). The breeding program has successfully changed the genetics of farmed Atlantic salmon to improve commercially important traits, such as growth, utilization of feed, and filet quality (Thodesen *et al.*, 1999; Gjedrem and Baranski, 2009; Solberg *et al.*, 2013). These genetic improvements have undoubtedly contributed to the rapid expansion of the Atlantic salmon farming industry in Norway, with a production close to 1.3 million tons in 2015.

Farmed Atlantic salmon also differ genetically from wild salmon because of selection to captivity, and loss of genetic variation from a limited number of wild founders and subsequent genetic drift (Hutchings and Fraser, 2008). Because of the reduced fitness (Fleming *et al.*, 2000; McGinnity *et al.*, 2003; Skaala *et al.*, 2012; Reed *et al.*, 2015) and lower genetic variation in farmed salmon (Mjølnerød *et al.*, 1997; Skaala *et al.*, 2004, 2005; Karlsson *et al.*, 2010) compared with their wild conspecifics, there is a concern that genetic introgression of escaped farmed salmon to wild salmon might reduce the viability of wild Atlantic salmon. Reported numbers of escaped farmed salmon in Norway have ranged from 39 000 to 920 000 since 1993, with an average of 380 000 (Norwegian Directorate of Fisheries, http://www.fiskeridir.no/English). Inventories since 1989 have shown high proportions of escaped farmed salmon in many Norwegian rivers, with large variations between years (Fiske *et al.*, 2006) and rivers (Gausen and Moen, 1991; Diserud *et al.*, 2013). A similar situation has been documented in eastern North America with a large number of escaped farmed entering salmon rivers, in many rivers outnumbering the wild spawning population and with extensive variation between rivers and years (Morris *et al.*, 2008).

Genetic introgression of escaped farmed salmon to wild salmon populations has been modelled (Hindar *et al.*, 2006) based on relative fitness estimates (Fleming *et al.*, 2000; McGinnity *et al.*, 2003) and observed proportions of escaped farmed salmon (Fiske *et al.*, 2006). The spawning success of escaped farmed salmon (Fleming *et al.*, 1996, 1997) and survival of their offspring (Fraser *et al.*, 2008, 2010; Skaala *et al.*, 2012; Sundt-Hansen *et al.*, 2015) depend on a variety of factors in wild populations, farmed escapes and the environment in which they meet, and make it difficult to accurately predict farmed to wild genetic introgression. The development of improved models with important and more precise parameters requires quantification of the farmed to wild genetic introgression (Heino *et al.*, 2015).

Several molecular genetic markers for quantifying genetic introgression of farmed escaped salmon in wild salmon populations have been identified (Karlsson *et al.*, 2011). These markers were used to quantify genetic introgression in 20 Norwegian salmon populations, based on observed temporal genetic changes and Approximate Bayesian Computation (ABC) of the farmed-to-wild gene flow that is consistent with these changes (Glover *et al.*, 2013). The ABC method is restricted, as it relies on the existence of historical samples from each population to be analysed. From the generic genetic differences observed at the genetic markers identified by Karlsson *et al.* (2011), an alternative standardized method was developed by Karlsson *et al.* (2014). This method does not rely on historical samples from all populations, but uses the directional genetic change from farm-to-wild introgression, and not genetic changes stemming from genetic drift and/or gene flow between wild populations. In short, the method uses historical samples from many wild populations and samples from the Norwegian breeding kernels for farmed salmon, and estimates for each individual of interest the proportion of membership to these two groups, using STRUCTURE (Pritchard *et al.*, 2000).

The objective of the present study was to obtain an extensive coverage of farmed to wild Atlantic salmon genetic introgression using the new molecular genetic and analytical methods. We analysed 21 562 Atlantic salmon hatched in the wild in 147 Norwegian rivers, including 16 407 adults and 5155 juveniles. Here, we first present a comprehensive geographical coverage of status with respect to farmed to wild introgression. Second, we compare estimates of introgression in samples based on juveniles with samples based on returning adults from the same population. Third, we assess the relationship between long-term proportions of escaped farmed salmon and genetic introgression. Finally, we assess to what extent a major conservation policy decision in Norway, designating 52 rivers as National Salmon Rivers and 29 fjords as National Salmon Fjords where important salmon populations receive extra protection (e.g. Vøllestad *et al.*, 2014), has an effect on the levels of introgression.

Material and methods

To quantify genetic introgression resulting from spawning of escaped farmed salmon in the wild, we analysed only fish hatched in the wild. We excluded fish classified as escaped farmed salmon, or with uncertain classification, based on their growth patterns in the scales (Lund and Hansen, 1991; Fiske *et al.*, 2005). Samples of juvenile, pre-smolt salmon can safely be regarded as hatched in the wild, because the escape of juvenile farmed salmon from land-based facilities to rivers in this study is unlikely.

We extracted total genomic DNA from scales of adult salmon and from fin-clips of juvenile salmon using DNEASY tissue kit (QIAGEN). Initially, we used the Sequenom SNP-genotyping platform for genotyping of 5897 individuals at 99 SNP loci, with PCR amplifications in 4 multiplexes. Primer extension reactions followed recommendations from Sequenom (www.sequenom.com) and fragments were separated and identified using Sequenom Mass ARRAY^{TM} analyzer (Autoflex mass spectrometer). We conducted genotyping in real time depending on the presence or absence of a mass peak in expected mass range for each locus (Tang *et al.*, 1999) using the MassARRAY^{TM} RT 3.4 software. We obtained reliable genotypes from 59 SNPs described as being collectively diagnostic in differentiating between wild and farm salmon (Karlsson *et al.*, 2011; Jensen *et al.*, 2013). For the remaining 15 293 individuals, we used the EP1^{TM} 96.96 Dynamic array IFCs genotyping platform (Fluidigm, San Francisco, CA). Reliable genotypes were obtained for 48 of the same SNPs genotyped by the Sequenom platform (Karlsson *et al.*, 2011). The SNP genotypes from the Sequenom and the Fluidigm SNP genotypes were merged for the 48 common SNP loci (Supplementary Table S1).

As a reference for farmed salmon, we used genotypes from 503 individuals from the three leading breeding companies (Marine Harvest, Salmobreed and AquaGen) from the year classes 2004–2009 (MH), 2004–2007 (SB) and 1998–2001, 2008 (AG). Each yearclass represented one of four different breeding kernels from each breeding company. In 2005, AquaGen pooled the four breeding kernels into one big kernel, represented by the 2008 sample. To investigate historical genetic signatures of farmed salmon, we used 129 samples from 1982 to 1988 from the four AquaGen breeding kernels. As references for non-admixed wild salmon, we used historical samples of 2187 wild individuals from 39 populations, geographically distributed in rivers from southern to northern Norway. In agreement with previous studies (Bourret *et al.*, 2013; Jensen *et al.*, 2014), the Norwegian populations clustered into an Atlantic and a Barents–White Sea phylogenetic group, with the latter including populations from Finnmark County and the former including populations south of Finnmark (Figure 1). All founder populations for the farm strains are from the Atlantic Sea phylogenetic group, as judged from the genetic contributions from source populations in the third generation of the breeding program (Gjøen and Bentsen, 1997). Although the Atlantic and the Barents–White Sea phylogenetic groups are well separated, some populations in Troms County represent a transition between them. We analysed samples from 147 Norwegian rivers, including 5155 juvenile individuals and 16 407 adult individuals. From 109 of these populations, we had adult modern samples with sample sizes of >20. For the remaining 38 populations we had only juveniles, historical samples, sample sizes <20 (for detailed information, see Supplementary Table S2). Scale samples of adult salmon were obtained from sport fishing, and from catches of broodfish for stocking or during autumn monitoring, while juvenile samples were obtained by electrofishing.

Statistical analyses

We applied the method by Karlsson *et al.* (2014) to estimate the level of farmed to wild genetic introgression. This method uses the STRUCTURE program (Pritchard *et al.*, 2000) in a manner that avoids bias from the level of heterogeneity and different sample sizes as described by Kalinowski (2011) and standardizes the estimates of admixture when introgression occurs from several farmed populations. We generated an idealized wild and farmed population in Hardy–Weinberg proportions from a pool of reference individuals of wild and farmed salmon using the HybridLab program (Nielsen *et al.*, 2006). For the farmed salmon, we used all modern samples from the three breeding companies. For the wild salmon, we generated one population for the Atlantic phylogenetic group and one for the Barents–White Sea group. Samples used for creating these wild centre points are indicated in Supplementary Table S2, column "REF Year". These ideal populations ($n = 100$) represented centre points for the three groups to which the probability of belonging was estimated (Figure 1). In an analysis of molecular variance (AMOVA), including the farmed reference samples and the historical wild reference samples from the Barents–White-Sea group, 18.01% of the variance was ascribed to variations between these groups ($p < 0.001$), and 4.08% to variance among populations within the groups ($p < 0.001$). In a comparison between farmed populations and the historical wild reference population from the Atlantic group, 7.19% of the variance was ascribed to variations between these groups ($p < 0.001$) and 3.48% to variance among populations within groups ($p < 0.001$). Single individuals were analysed with the farmed centre point and the two wild centre points representing the correct phylogenetic group for that individual, using an admixed model, 50 000 repetitions as burn in and 100 000 repetitions after burn in as implemented in STRUCTURE (Pritchard *et al.*, 2000). For each fish, the probability of belonging to the wild centre point, hereafter *P(Wild)*, was recorded.

For statistical analyses of farmed introgression, we generated probability distributions of belonging to the wild centre point for historical wild salmon (all samples in column "REF Year" in Supplementary Table S2) and for modern farmed salmon. Four populations (rivers Skibotnelva [river ID 205.Z], Signaldalselva [204.Z], Målselv [196.Z], and Skipsfjordelva [202.11Z]) represented genetic transitions between the Atlantic and the Barents–White Sea phylogenetic groups and could not be analysed using the Atlantic or the Barents–White Sea centre points. Instead, they were analysed by generating *in silico* populations from historical samples for each of these populations, except for Signaldalselva for which we did not have historical samples. Samples from the nearby River Skibotnelva were used as the analytical centre point for the Signaldalselva population.

From the distribution of individual probabilities of belonging to the wild centre point *P*(*Wild*) for a given sample (population and year), we estimated genetic introgression from escaped farmed salmon into this year's wild Atlantic salmon populations (Karlsson *et al.*, 2014). *P*(*Wild*) was logit-transformed before the statistical inference (Warton and Hui, 2011). For each contemporary sample with a historical reference from the same river, we tested whether this population was introgressed with a two-sample test for comparing means, assuming random sampling and equal variances for contemporary and reference samples. Further, we assumed that all wild populations had the same variance, estimated as the weighted average of the historical wild reference sample variances. Although the distributions for logit-transformed *P*(*Wild*) for wild reference samples are relatively symmetric (see example in Figure 2), they depart too much from normality to perform standard tests for homogeneity of variances. By resampling squared deviations from all wild references, we found that 8.6% (3 of 35) of the wild population variances were significantly different from the pooled variance with a 5% significance level and were close to what we expected under the homogeneity assumption. Several of the wild reference populations have significantly different averages, so when testing whether a population without historical reference is introgressed we needed to consider this variance in wild population average values within a phylogenetic group. For populations without a historical reference from the same river, the contemporary average was therefore

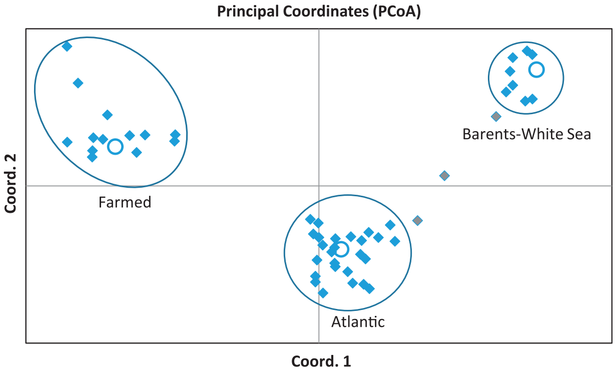


Figure 1. PCoA plot of pairwise F_{ST} estimates between historical samples from 39 Atlantic salmon populations and 13 farmed strain populations (diamonds), clustered into one farmed group (Farmed), one wild Atlantic salmon group from Finnmark (Barents–White Sea), and one wild Atlantic salmon group form South of Finnmark (Atlantic). Grey diamonds are populations (River Skibotnelva, River Målselva, and River Skipsfjordelva) outside the clusters and genetic introgression is analysed by using the local historical samples. Open circles are *in silico* generated populations from a pool of the historical samples within each cluster.

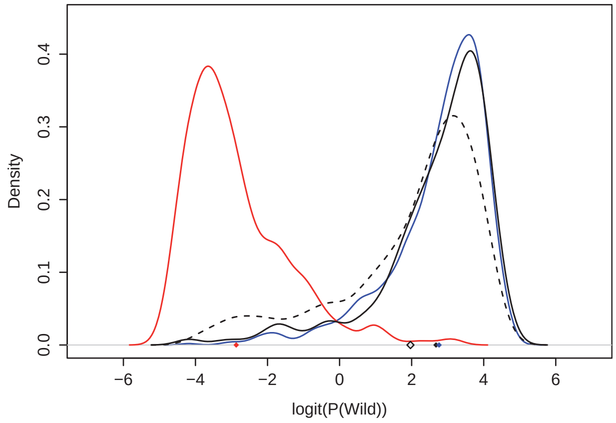


Figure 2. Distribution of logit-transformed probabilities of being of wild origin *P*(*Wild*), for farmed reference (red line; mean value indicated by the red diamond), wild references for the whole Atlantic phylogenetic group (blue line and diamond), wild reference for River Eira (black line and diamond) and contemporary sample for River Eira (dashed black line and open black diamond; $n = 786$ for years 2012, 2013, 2014, 2015 pooled).

compared with the overall wild average for this phylogenetic group with this additional variance component included in the sampling distribution. For both tests, the null hypothesis states no genetic introgression; that is, mean $P(Wild)$ from the contemporary population equals the mean $P(Wild)$ from the historical reference population. The alternative hypothesis states that the contemporary mean $P(Wild)$ is smaller than the historical mean.

The distributions for individual $P(Wild)$ values for the samples are illustrated for the River Eira (104.Z) in Figure 2. Notable is the distinctiveness of the distribution for the farm references (red line). The distribution for the contemporary sample (pooled sample for the years 2012–2015; dashed black line) has a mean value significantly smaller than both the historical distribution for the River Eira population (solid black line) and the distribution for the whole Atlantic phylogenetic group (solid blue line).

For many samples, the observed change in mean value may not be significant, even if the populations show signs of genetic introgression. As in Figure 2, the contemporary distribution can indicate that a proportion of the population is introgressed by having a heavy left tail while the majority of the population is still mostly wild-like. Genetic introgression into a subpopulation can be tested by, e.g. inspecting the lower 5-percentile of the distributions. Expected tail properties will be sensitive to distribution assumptions, so we opted for a randomization test approach. If the 5-percentile of a contemporary sample of a given size is much lower than expected from a sample of the same size from the historical distribution, it indicates that this sample has a too large proportion of individuals that genetically are admixed with farmed salmon. This effect was evaluated by simulating $n = 10\,000$ samples of the same size as the contemporary sample from the historical reference for the whole phylogenetic group, and registering the 5-percentiles of each simulated sample. The proportion of simulated 5-percentiles that was lower than the 5-percentile of the historical reference is the p value of the test.

Juveniles of farmed and admixed origin show lower survival to adulthood than juveniles of pure wild origin (Fleming *et al.*, 2000; McGinnity *et al.*, 2003). We expected therefore to find a higher level of introgression in juveniles than in adults in the same cohorts. To explore this in our data, we compared juvenile samples with adult samples from the same river, using a quasi-cohort comparison. Specifically, we compared farmed introgression between juvenile and adult samples in 26 rivers, where sampling of juveniles occurred 3–5 years earlier than sampling of adults. Even though this is not a formal cohort analysis, at least some of the same year classes are likely represented in both the juvenile and adult samples.

Regional averages of introgression were constructed as unweighted averages and as averages weighted by spawning population size in each river studied (Forseth *et al.*, 2013). We defined regions as counties from the northernmost, Finnmark County, to the southernmost in western Norway, Rogaland County, whereas the counties from southernmost Norway to the south-eastern border with Sweden, were treated as one region (Fiske *et al.*, 2006) denoted Southeast.

A major conservation policy for wild Atlantic salmon in Norway, National Salmon Rivers and National Salmon Fjords, was established by the Norwegian Parliament in 2003 (completed 2007) to increase the level of protection of Atlantic salmon, including protection from fish farming. By the final decision in 2007, 52 rivers were designated as National Salmon Rivers (of which we studied 48, cf. Vøllestad *et al.*, 2014) and 29 coastal areas were designated National Salmon Fjords (all are represented by our samples). We calculated unweighted and weighted averages for these groups of rivers in the same manner as for counties.

To study associations between group levels of introgression and average proportions of escaped farmed salmon, we used the method developed by Fiske *et al.* (2006) and Diserud *et al.* (2010) to calculate an "annual incidence" of escaped farmed salmon, by averaging proportions of escaped farmed salmon in anglers' catches in summer and in organized surveys in autumn and by calculating a weighted average by river catches. At the individual river level, Diserud *et al.* (2012, 2013) developed a long-term "average annual incidence" for the years 1989–2012 for all rivers that were represented by four or more years in the time series.

Results

Based on adult modern samples from 109 salmon rivers with a sample size of 20 or more, we observed significant genetic introgression from escaped farmed salmon in 51 wild salmon populations (47%) and an estimated level of introgression >10% in 27 populations, between 4% and 10% in 19 populations and < 4% in 63 populations (Supplementary Table S2 and Figure 3). When all samples were considered, significant genetic introgression was observed in 77 of 147 rivers (Supplementary Table S2).

Comparisons in 26 rivers of juvenile samples with adult samples taken 3–5 years later, presumably representing the same cohorts, showed an average reduction of 2.5 percentage points between estimates of introgression in juvenile and adult life stages. Variation between rivers was high ranging from a 13% increase to a 17% reduction in farmed introgression from juvenile to adult samples.

Geographical distribution of farmed to wild genetic introgression

In the following, the presentation of level of introgression is based on pooled adult samples from recent sampling years in 109 rivers with a sample size of at least 20 individuals. National Salmon Rivers with special protection against anthropogenic impacts, including salmon farming, had on average lower levels of farmed genetic introgression (unweighted average, 4.5%) than salmon rivers without protection (unweighted average, 7.8%). The protecting effect of National Salmon Fjords appeared to be smaller as salmon rivers in and outside these fjords had similar (average, 6.4%) levels of farmed genetic introgression (Table 1). When considering population size (weighted averages), rivers within the National Salmon Fjords had however a lower level of introgression (1.8%) than other rivers (3.5%).

Genetic introgression has occurred in all regions of Norway, and the highest genetic introgression is found in the most intensive salmon farming regions (Figure 3). Unweighted averages of genetic introgression were largest in Troms County (14.5%) and Hordaland County (13.9%) and smallest in Nord-Trøndelag County (0%) and Rogaland County (1.8%) (Table 2). However, four regional averages were based on <10 rivers, Troms and Nord-Trøndelag being two of them. We also found significant introgression in samples excluded because of sample sizes <20, including adult samples (Byaelva [128.Z] and Salvassdraget [140.Z]) from Nord-Trøndelag (Supplementary Table S2). Hence, no region in Norway is without farmed introgression.

Table 1. Farmed genetic introgression for Norwegian Atlantic salmon rivers with and without the protection status of being National Salmon Rivers, and for salmon rivers in and not in fjords with the a protection status of being National Salmon Fjords.

Group	*N* Ind	*N* pop	Farm introgression—unweighted average/median	Farm introgression—weighted average/median
National rivers	4347	47	0.045/0.016	0.016/0.000
Not national rivers	4741	62	0.078/0.028	0.048/0.014
National fjords	5337	59	0.064/0.018	0.018/0.000
Not national fjords	3751	50	0.064/0.026	0.035/0.025

Farm introgression values are given as averages and medians, both unweighted and weighted with estimated population size.

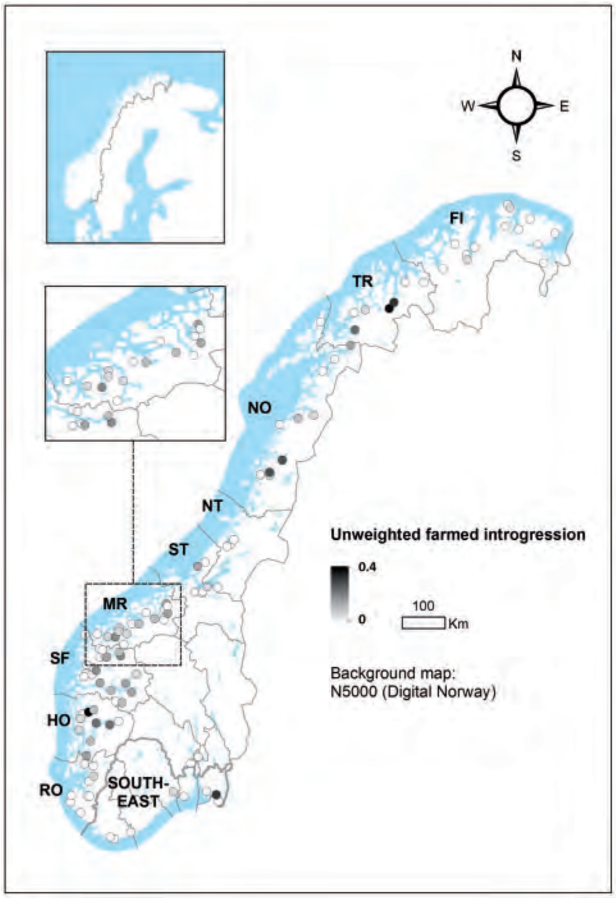


Figure 3. Map of Norway showing estimated farmed genetic introgression in 109 Norwegian salmon rivers from contemporary adult samples. Codes used for counties: FI = Finnmark, TR = Troms, NO = Nordland, NT = Nord-Trøndelag, ST = Sør-Trøndelag, MR = Møre og Romsdal, SF = Sogn og Fjordane, HO = Hordaland, RO = Rogaland, and SOUTHEAST is the southeasternmost counties pooled into one region.

Weighted averages by wild population size in the sampled rivers within each county were largely determined by status of the largest rivers and illustrate the geographical distribution of farmed introgression relative to the number of genes of farmed origin (proportion of farmed genomes). Hordaland County had the largest proportion of genomes with farmed origin (11.1%), and Nord-Trøndelag County the smallest (0%). In the two phylogenetic groups of Norway, we found more introgression in the Atlantic group (unweighted average = 6.9%, weighted average = 2.6%) than in the Barents–White Sea group (unweighted average = 2.6%, weighted average = 1.0%). Nationally, unweighted and weighted estimated proportions of farmed genomes were 6.4%, and 2.1%, respectively (Table 2).

Genetic introgression relative to farmed escapees

We observed a highly significant relationship between accumulated genetic introgression and average annual proportion of escaped farmed salmon, explaining 24% of the variance in introgression between rivers (Figure 4). The relationship was stronger at the region level, with proportion of escaped farmed salmon explaining 56% of the variance when weighted by population size (open diamonds in Figure 4). For populations in the Atlantic Sea phylogenetic group, the relationship was highly significant (red solid diamonds and dashed red line in Figure 4; $p < 0.01$, $R^2 = 0.19$, gradient = 0.3), while for populations in the Barents–White Sea phylogenetic group the relationship was weak and not significant (blue solid diamonds and dashed line, Figure 4; $p > 0.05$, $R^2 = 0.05$, gradient = 0.05).

Temporal trends

We had samples from different periods (decades) in 27 populations, allowing us to examine temporal trends in the level of genetic introgression. Twelve of the populations showed an increase in genetic introgression, seven a decrease and six showing no introgression over time. In three populations for which we had more than two samples in time, there were increases followed by decreases in genetic introgression. Populations with downward trends had initial levels of genetic introgression between 1.8% and 6.1%, and in a more recent sample levels of introgression were between 0.0% and 3.8% (median = 0.2%). River Kinso (050.1Z) showed a decrease from a high of 24.7% in the 2000s to 12.7% in the 2010s. However, the trend in River Kinso is uncertain because there was only one sampling year representing the 2010s period and only 15 fish were analysed. A sample of juveniles from 2011 showed 29.4% introgression. A majority of the populations with an upward trend in genetic introgression had initial levels of genetic introgression between 0.0% and 7.5%, but showed large increases in genetic introgression with temporal differences in genetic introgression ranging from 1.5% to 23.7% (median = 11.2%).

Detecting early genetic introgression

We tested to what extent our set of SNP markers and the standardized method for detecting introgression (Karlsson *et al.*, 2014) worked for characterizing earlier generations of farmed salmon than those used for selecting SNPs differentiating between farmed (breeding kernel year classes 1998–2009) and historical wild salmon (Karlsson *et al.*, 2011). A comparison of distributions of *P*(*Wild*) between historical (1982–1988) and contemporary

Table 2. Farmed genetic introgression in Norwegian geographical regions.

Region	*N* Ind	*N* pop	Farm introgression, unweighted	Farm introgression, weighted
Southeast	899	11	0.038/0.000	0.015/0.000
Rogaland	1070	9	0.018/0.008	0.007/0.000
Hordaland	922	10	0.139/0.108	0.114/0.108
Sogn og Fjordane	1992	21	0.068/0.042	0.064/0.000
Møre og Romsdal	1946	16	0.062/0.044	0.039/0.014
Sør-Trøndelag	365	6	0.047/0.020	0.013/0.012
Nord-Trøndelag	162	4	0.000/0.000	0.000/0.000
Nordland	556	12	0.079/0.028	0.077/0.078
Troms	324	7	0.145/0.083	0.067/0.083
Finnmark	852	13	0.026/0.021	0.010/0.000
National	9088	109	0.064/0.023	0.021/0.000

Regions are set as counties (Figure 3), except for region Southeast which includes the south and the southeastern counties (Østfold, Akershus, Buskerud, Vestfold, Telemark, Aust-Agder and Vest-Agder). Regional farm introgression values are given as averages and medians, both unweighted and weighted with estimated population size.

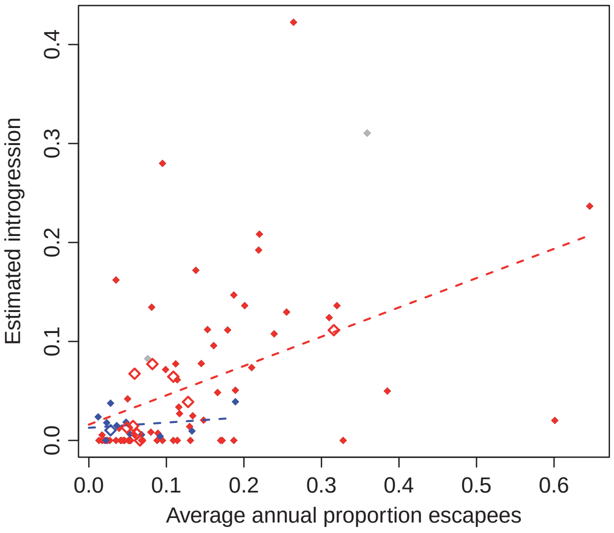


Figure 4. Relationship between mean annual proportions of escaped farmed salmon between 1989 and 2012 and estimated proportion of farmed genetic introgression from molecular genetic markers for 77 salmon populations (solid diamonds and dashed lines), and averaged for populations within geographical regions (open diamonds). Observations from the Atlantic Sea phylogenetic group are shown in red, from the Barents-White Sea phylogenetic group shown in blue, and two populations from the transition area are shown in grey.

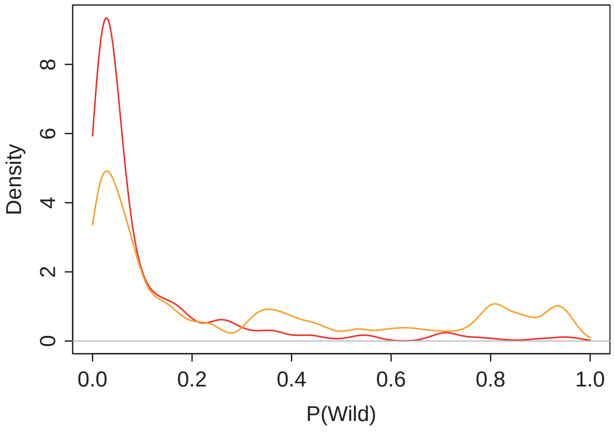


Figure 5. Distribution of STRUCTURE-generated probabilities of being of wild origin *P*(*wild*) for modern (red line) and historical (orange line) samples from the AquaGen farmed strains.

AquaGen samples indicated that the historical farmed populations appeared to be more wild than modern samples of farmed salmon (Figure 5).

Discussion

We quantified genetic introgression of farmed Atlantic salmon into 21 562 wild salmon from 147 populations. Levels of introgression >10% can now be found in any part of Norway in juveniles, as well as in adult salmon that have completed a life cycle in the wild. As expected, the level of introgression in wild populations is significantly associated with the average proportion of escaped farmed salmon in the river over the last 25 years.

Our method allows quantification of introgression from the individual level to populations, regions and the national level, and in rivers with and without a historical baseline. We found the highest levels of introgression in the counties of Norway where escaped farmed salmon have been present in highest proportions.

In Hordaland County, western Norway, one of the two cradles of fish farming, several populations show high levels of introgression, with the rivers Opo (048.Z), Granvin (052.1Z; juveniles) and Dale (061.Z) showing recent levels of introgression >40% and three other rivers [Vosso (062.Z), Kinso (050.1Z), and Etne (041.Z)] showing introgression >10%. Affected rivers are found both along the coast and within the major (Hardangerfjord) and minor fjords in the county. Highly affected rivers in this county were also found in a study of 20 Norwegian rivers by Glover *et al.* (2013).

Other rivers with high levels of introgression are found in Troms County in northern Norway, Sogn og Fjordane County and Møre og Romsdal County in western Norway. Rivers with low levels of introgression are most common in south-eastern Norway, Rogaland County in the southwest and Finnmark County in the northeast. The river holding Norway's largest Atlantic salmon population, River Tana (234.Z) on the border with Finland, has a low level of introgression (0 in our Supplementary Table S2). The spawning population (or rather, populations, see Vähä *et al.*, 2008) of the Tana is so large

(> 40 000 fish), compared the other salmon rivers (average = 1900, range: 100–18 000), that it strongly affects regional weighted averages in Finnmark, the Barents–White Sea phylogenetic group and even the national average.

Current levels of introgression are likely underestimated

The farmed references in the present study are representative for introgression that occurred between the 1990s and present. They cover a large part of this period (year classes hatched 1998–2009) and may be representative of more years, as a previous study showed no significant change in allele frequencies at microsatellites in two breeding kernels sampled one generation (Karlsson *et al.*, 2010).

Intrusion of farmed Atlantic salmon on the spawning grounds of wild salmon was detected on a large scale from 1986 onwards (Gausen and Moen, 1991). Introgression during this early time period is, however, likely underestimated, because we found a weaker genetic contrast between historical wild salmon and farmed salmon samples from the 1982–1988 than in the farmed salmon samples from 1998 to 2009 used as farmed references. Our statistical method has been tested against simulated data sets and has been shown to give precise estimates of introgression at the population level (Karlsson *et al.*, 2014). Precaution is therefore warranted in our evaluation of the status of populations with no or only weak levels of farmed introgression detected in the present study.

Introgression varies by farmed intrusion and phylogeographic origin

Geographical variation in levels of introgression may have several explanations, the most immediate being that the proportion of escaped farmed salmon in spawning populations also varies. On both local (river) and regional (county) levels, we found a significant, positive correlation between average annual proportions of escaped farmed salmon 1989–2012 (Diserud *et al.*, 2013) and introgression in recent samples.

The most impacted rivers, with respect to long-term average proportions of escaped farmed salmon, are found in the counties of Hordaland (Opo [048.Z], Kinso [050.1Z], Eio [050.Z] and Frugardselva [044.3Z]) being highest among those studied genetically, all with average proportions 1989–2012 of escaped farmed salmon >50% according to Diserud *et al.*, 2013) and Troms (River Salangselva [191.Z] with 65%, Diserud *et al.*, 2013).

Our samples of wild Atlantic salmon are represented by two phylogenetic groups, the Atlantic group and the Barents–White Sea group (Bourret *et al.*, 2013). Even though wild populations from both phylogenetic groups were represented among the source populations (Gjedrem *et al.*, 1991), only the Atlantic group was represented in the third generation of farmed salmon in the breeding programme (cf. Gjøen and Bentsen, 1997). Interestingly, we found a significant association between proportions of escaped farmed salmon and introgression for the Atlantic group and not for the Barents–White Sea group, and a steeper gradient in the Atlantic group (Figure 4). This might reflect differences in genomic architecture between the two phylogenetic groups and a higher barrier to introgression in the Barents–White Sea group. The barrier is not absolute, as we found significant introgression in several of the Barents–White Sea populations, even in numerically strong populations like River Alta (212.Z) and Vestre Jakobselv (240.Z). The number of samples from the Barents–White Sea group is however limited, and a conclusion about barriers to introgression in relation to phylogenetic origin must await further study.

Additional explanations of variation in introgression

A large proportion of the variance in the level of introgression could not be explained by proportions of escaped farmed salmon (Figure 4). This is not unexpected, as one of the main conclusions from a review of genetic effects following releases was the wide variety of outcomes, ranging from no detectable effect to complete introgression or displacement of the native population (Hindar *et al.*, 1991). Experimental studies of farmed and wild salmon, however, point to some general findings about causes of variation.

It has been shown experimentally that farmed salmon escaping early from captivity have higher reproductive success in competition with wild salmon than later escaping farmed salmon, i.e. comparing hatchery-released smolts with farmed adults (Fleming *et al.*, 1996, 1997). So far, this has not been accounted for in analyses of how escaped farmed salmon leads to introgression, but will be possible in the future as scale reading advances to include the likely size at which farmed salmon escape.

The density of wild Atlantic salmon on the spawning ground may also be important. The breeding behavior of Atlantic salmon involves female-to-female competition for access to high-quality spawning sites to excavate the nests, and male-to-male competition for access to females (Fleming and Einum, 2011). Lura (1995) suggested that the spawning success of escaped farmed females was density dependent because the contributions of eyed eggs, relative to their proportion among the spawners, were lower in rivers and years with high densities of spawners. Likely explanations may be that farmed females are outcompeted from the most favourable nest sites at high densities (Lura, 1995), and there may be a larger proportion of unspawned eggs in farmed than in wild salmon at high densities (Jonsson *et al.*, 1990; Fleming *et al.*, 1996, 2000). For males, Fleming *et al.* (1997) showed density-dependent spawning success in an experimental study of hatchery-reared vs. wild River Imsa males. In contrast, late-escaping farmed males showed poor reproductive success regardless of density in the same spawning arenas (Fleming *et al.*, 1996). We do not yet know whether there are differences in reproductive success among the various selected strains of farmed salmon, but we know that farmed fish vary in their genetic relationships with wild salmon (Karlsson *et al.*, 2011, 2010, 2014).

Lower average introgression is found in National Salmon Rivers and to a lesser extent in rivers within a National Salmon Fjord. This indicates that national salmon fjords and rivers provide increased protection from farmed introgression. One common factor among these populations is that emphasis was put on the numerically strongest populations when rivers were chosen for designation as National Salmon Rivers. Population size in itself may be a protective measure from introgression (Heino *et al.*, 2015), which is also supported by the difference between unweighted and weighted averages found here (Table 2). Another type of protection is the increased distance between aquaculture operations and wild salmon rivers, which makes it less likely for a salmon river in a National Salmon Fjords to receive escaped farmed salmon, than outside of such a fjord, other things being equal (Fiske *et al.*, 2013).

However, we do not see low introgression levels in all salmon populations with this protective regime. For example, River Daleelva (061.Z), River Vosso (062.Z), River Vikja (070.Z), River Årøyelva (077.Z), River Jølstra (084.Z), River Olden (088.1Z), River Røssåga (155.Z) and River Beiarelva (161.Z) are National Salmon Rivers or are situated in a National Salmon Fjord and have > 10% farmed genetic introgression. One explanation for the variation in the protecting effect of National salmon rivers and fjords might be the size of the protected region, exemplified by the large Trondheimsfjord. The entire Trondheimsfjord is a National Salmon Fjord in a highly intensive farming region, where a high level of introgression was found in a coastal population (River Teksdalselva [134.Z]), but consistently lower levels were found in rivers inside the major Trondheimsfjord. In the Hardangerfjord system, on the other hand, only a small part (<5% of the fjord area) is designated as a National Salmon Fjord, Etnefjorden. Most rivers in the Hardangerfjord show high levels of introgression, as does River Etne (041.Z). Another explanation for high levels of introgression in salmon populations within National Salmon Fjords is that some of these rivers have occasionally had low levels of wild spawners, because of the parasite *Gyrodactylus salaris* (Vikja, Røssåga, Beiarelva; Johnsen and Jensen, 1991), or of other anthropogenic factors. A likely mechanism is easier access to spawning opportunities when wild population size is low (Sægrov *et al.*, 1997).

An explanation for the variable effect of National Salmon Rivers and Fjords not yet highlighted is the possibility that an introgressed population may impact neighbouring populations through straying of wild offspring of cultured fish (Felsenstein, 1997). An important question in this regard is a potentially weaker homing of offspring from escaped farmed salmon compared with the locally adapted wild salmon, because of different genetic (Jonsson *et al.*, 2003) or epigenetic origins (Christie *et al.*, 2016). In experiments with wild and farmed Atlantic salmon, hatchery-produced smolts of farmed origin showed a higher straying rate than hatchery-produced Imsa salmon released into the Imsa (Jonsson *et al.*, 2003).

Differential survival of introgressed individuals

Levels of introgression were similar between juvenile and adult salmon samples in our study. Experimental studies generally show a lower lifetime survival of farmed offspring than wild offspring, with hybrid groups being intermediate (McGinnity *et al.*, 1997, 2003; Fleming *et al.*, 2000; Skaala *et al.*, 2012). It is therefore expected that within the same cohort, a general reduction in mean *P*(*Wild*) should be observed across life stages from alevin, to parr, to smolt, to returning adults. In our material, we could not make a formal cohort analysis, but some populations could be compared between juvenile and adult samples that likely showed some year-class overlap. The average reduction was estimated at 2.5 percentage points, with a large variation between populations, including some where the level of introgression was higher among adults than among juveniles. Observational studies that control for year class (cohort) are needed before the effect of viability selection on introgression can be quantified more precisely.

What do the levels of introgression found in this study mean?

This question may be discussed at several different levels: genetics, fitness and viability, ecology and life-history, management, and conservation. With respect to genetics, three concerns are important: loss of genetic variation within populations, loss of genetic variation between populations and loss of fitness (Waples *et al.*, 2012). Farmed Atlantic salmon have in general lower genetic variation than wild Atlantic salmon (Mjølnerød *et al.*, 1997; Skaala *et al.*, 2004, 2005; Karlsson *et al.*, 2010), and the long-term prediction from escapes is that lower genetic diversity will eventually lead to a drop in diversity in recipient wild populations (Tufto and Hindar, 2003), even though in the short-term, genetic variation may increase from interbreeding with farmed salmon. Loss of genetic variation between populations as a result of introgression from farmed Atlantic salmon has been demonstrated both theoretically (Mork, 1991) and empirically (Skaala *et al.*, 2006; Glover *et al.*, 2012, 2013). Loss of fitness has been demonstrated in controlled rivers in Ireland (McGinnity *et al.*, 1997, 2003) and Norway (Fleming *et al.*, 2000; Skaala *et al.*, 2012) and in large-scale experiments in Canada (Fraser *et al.*, 2010). The loss of viability is also indicated by these same studies, as well as in meta-analysis of the population dynamics of salmon populations near or far from aquaculture operations (Ford and Myers, 2008; Vøllestad *et al.*, 2009). For the latter studies, however, several mechanisms in addition to introgression may be at work, such as increased mortality caused by parasites associated with fish farming activities (e.g. Krkosek *et al.*, 2013).

Ecological change in introgressed individuals was evident from experiments in controlled, natural rivers showing changes in growth rate, condition factor (length–weight relationship) and age at smoltification and maturation (Fleming *et al.*, 2000; McGinnity *et al.*, 2003). This was also true in a large-scale observational study that tested whether *P*(*Wild*) had an impact on ecological key traits (Geir Bolstad, NINA *et al.* in prep.). This change in ecological traits also likely has a negative effect on fitness (Tufto, 2001; Huisman and Tufto, 2012; Baskett *et al.*, 2013).

Implications for management and conservation

In a management and conservation context, a pertinent question is how much introgression can be allowed (Ryman *et al.*, 1995). While there is no simple answer to this question, it is clear that near-zero limits need to be set in order not to compromise the genetic integrity of wild populations. Ryman *et al.* (1995) suggested that a defensible strategy, based on population genetic considerations, could be to allow gene flow at a rate that matched equilibrium levels of gene flow between semi-isolated populations, as quantified by Wright's fixation index, F_{ST}. This would allow only a small number of reproductively capable escaped farmed salmon spawning in wild populations every generation.

In considerations of the Endangered Species Act listing of populations of westslope cutthroat trout (*Oncorhynchus clarki lewisi*) in danger of hybridization with rainbow trout (*O. mykiss*) and Yellowstone cutthroat trout (*O. c. bouvieri*), Allendorf *et al.* (2004) suggested that listing only non-hybridized populations was the only alternative that could be defended from the perspective of possessing local adaptations important for long-term persistence of this sub-species. An alternative criterion, allowing 10% introgression from the other taxa, was discarded because it could lead to hybridized populations acting as a source for further introgression. These considerations deal with sub-species and species differences, and may be too conservative for our Atlantic salmon study that deals with farmed and wild population differentiation and introgression. The developmental and evolutionary forces acting on farmed Atlantic salmon are so unlike those in the wild that two distinct biologies are being created within the Atlantic salmon species (Gross, 1998; see also Roberge *et al.*, 2006; Christie *et al.*, 2016). Gross (1998) even suggested that farmed and wild Atlantic Salmon be recognized as different "species", and that farmed salmon be treated as "exotic" when they escaped to the wild, as a measure to prevent further impact from aquaculture. The calculation of *P*(*Wild*) at the level of individuals has an immediate use in practical management and conservation. In many rivers, hydropower companies have to compensate for the reduction in natural productivity of a river by releasing hatchery-produced fish. In other rivers, releases of offspring from local brood stock is practiced on a voluntary basis. Regardless of purpose, a genetic test compulsory for all brood stock being used was introduced in 2014 by the Norwegian Environment Agency to limit the likelihood of spreading farmed salmon genotypes through stock enhancement. In autumn 2014, the calculation of individual *P*(*Wild*) led to 14% of potential broodstock in Norway being discarded for genetic reasons, and in 2015, 18% of potential brood stock was discarded (Karlsson *et al.*, 2015, 2016). In the highly impacted Hardangerfjord rivers (average introgression 13.2%), calculations of *P*(*Wild*) during autumn 2015 showed that only 83 of 141 fish (escaped farmed salmon excluded) qualified as wild-origin brood stock to create a live gene bank for the most impacted populations.

The probability distribution of *P*(*Wild*) may help characterize the stage reached in an accumulation of farmed introgression. In some populations, the probability distribution for being wild shows distinct modes with fish at several stages of introgression, including "pure wild", "hybrid" and "farmed" (Tufto, 2000). At later stages of introgression, with a wide range of admixed groups in the population, we expect a smoother distribution of individual *P*(*Wild*) values without distinct modes. At this time, the proportion of individiuals with pure wild origin is low, and management has to be cautious to preserve all ecotypes (e.g. late-spawning fish; upper river spawners) in the remaining historically wild populations (Hansen *et al.*, 2006).

To protect the genetic integrity of wild Atlantic salmon populations, only low levels of introgression from escaped farmed salmon can be allowed into wild populations. We found significant introgression in half of the populations studied, and levels of introgression >10% in nearly one-quarter of the populations. The rivers we studied represent three-quarters of the entire Norwegian wild salmon spawning population. Further introgression is likely, unless substantial reduction of escaped farmed salmon in the wild, or sterilization of farmed salmon, can be achieved.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

We are grateful to Torveig Balstad, Line Eriksen, Merethe Spets for conducting the genotyping at NINA, Sigbjørn Lien, Matthew Peter Kent, Arne Roseth, and Kristil Sundsasen for conducting the genotyping at CIGENE, Thomas Moen at AquaGen for providing script for creating input files and running structure in batch mode, Rådgivande Biologer, the Veterinary Institute, UNI Research Miljø, Kunnskapssenter for Laks og Vannmiljø, LUKE Finland, Marine Harvest, Salmobreed, AquaGen, and a number of colleagues for providing samples. This study was financed by the Research Council of Norway (QuantEscape, project 216105), the Norwegian Environment Agency, and by Norwegian hydropower companies and county fishery offices.

Funding

The analysis was also partially funded by the NINA Strategic Institute Initiative "Interactions between aquaculture and wild salmonids".

References

Allendorf, F. W., Leary, R. F., Hitt, N. P., Knudsen, K. L., Lundquist, L. L., and Spruell, P. 2004. Intercrosses and the U.S. Endangered Species Act: should hybridized populations be included as westslope cutthroat trout? Conservation Biology, 18: 1203–1213.

Baskett, M. L., Burgess, S. C., and Waples, R. S. 2013. Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. Evolutionary Applications, 6: 1090–1108.

Bourret, V., Kent, M. P., Primmer, C. R., Vasemägi, A., Karlsson, S., Hindar, K., McGinnity, P., *et al.* 2013. SNP-array reveals genome-wide patterns of geographical and potential adaptive divergence across the natural range of Atlantic salmon (*Salmo salar*). Molecular Ecology, 22: 532–551.

Christie, M. R., Marine, M. L., Fox, S. E., French, R. A., and Blouin, M. S. 2016. A single generation of domestication heritably alters the expression of hundreds of genes. Nature Communications, 7: 10676.

Diserud, O. H., Fiske, P., and Hindar, K. 2010. Regional impact of escaped farm salmon on wildsalmon populations in Norway. NINA Report, 622: 1–40. (In Norwegian, English summary)

Diserud, O. H., Fiske, P., and Hindar, K. 2012. Forslag til kategorisering av laksebestander som er påvirket av rømt oppdrettslaks. NINA Rapport, 782: 1–32. (In Norwegian)

Diserud, O. H., Fiske, P., and Hindar, K. 2013. Forslag til kategorisering av laksebestander som er påvirket av rømt oppdrettslaks – oppdatering for perioden 1989–2012. NINA Rapport, 976: 1–22. (In Norwegian)

Felsenstein, J. 1997. Population differentiation and evolutionary processes, *In* Genetic Effects of Straying of Non-Native Hatchery Fish into Natural Populations: Proceedings of the Workshop. Ed. by W. S. Grant. U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-NWFSC-30, 130 pp.

Fiske, P., Diserud, O. H., Robertsen, G., Foldvik, A., Skilbrei, O., Heino, M., Helland, I. P., *et al.* 2013. Midtveisvurdering av nasjonale laksevassdrag og nasjonale laksefjorder. Rømt oppdrettslaks og bestandsstatus. NINA Minirapport, 470: 24. (In Norwegian)

Fiske, P., Lund, R. A., and Hansen, L. P. 2005. Identifying fish farm escapees. *In* Stock Identification Methods; Applications in Fishery Science. Ed. by S. X. Cadrin, K. D. Friedland, and J. R. Waldman. Elsevier Academic Press, Amsterdam. 659–680 pp.

Fiske, P., Lund, R. A., and Hansen, L. P. 2006. Relationships between the frequency of farmed Atlantic salmon, *Salmo salar* L, in wild salmon populations and fish farming activity in Norway, 1989–2004. ICES Journal of Marine Science, 63: 1182–1189.

Fleming, I. A., and Einum, S. 2011. Reproductive ecology: a tale of two sexes. *In* Atlantic Salmon Ecology. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Wiley-Blackwell, Chichester. 33–65 pp.

Fleming, I. A., Hindar, K., Mjølnerød, I. B., Jonsson, B., Balstad, T., and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. Proceedings of the Royal Society of London B, 267: 1517–1523.

Fleming, I. A., Jonsson, B., Gross, M. R., and Lamberg, A. 1996. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). Journal of Applied Ecology, 33: 893–905.

Fleming, I. A., Lamberg, A., and Jonsson, B. 1997. Effects of early experience on reproductive performance of Atlantic salmon. Behavioural Ecology, 8: 470–480.

Ford, J.S., and Myers, R. A. 2008. A global assessment of salmon aquaculture impacts on wild salmonids. Plos Biology, 6: 411–417.

Forseth, T., Fiske, P., Barlaup, B., Gjøsæter, H., Hindar, K., and Diserud, O. H. 2013. Reference point based management of Norwegian Atlantic salmon populations. Environmental Conservation, 40: 356–366.

Fraser, D. J., Cook, A. M., Eddington, J. D., Bentzen, P., and Hutchings, J. A. 2008. Mixed evidence for reduced local adaptation in wild salmon resulting from interbreeding with escaped farmed salmon: complexities in hybrid fitness. Evolutionary Applications, 1: 501–512.

Fraser, D. J., Minto, C., Calvert, A. M., Eddington, J. D., and Hutchings, J. A. 2010. Potential for domesticated-wild interbreeding to induce maladaptive phenology across multiple populations of wild Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences, 67: 1768–1775.

Gausen, D., and Moen, V. 1991. Large scale escapes of farmed Atlantic salmon (*Salmo salar*) into Norwegian rivers threaten natural populations. Canadian Journal of Fisheries and Aquatic Sciences, 48: 426–428.

Gjedrem, T., and Baranski, M. 2009. Selective Breeding in Aquaculture: An Introduction. Springer, London.

Gjedrem, T., Gjøen, H. M., and Gjerde, B. 1991. Genetic origin of Norwegian farmed salmon. Aquaculture, 98: 41–50.

Gjøen, H. M., and Bentsen, H. B. 1997. Past, present, and future of genetic improvement in salmon aquaculture. ICES Journal of Marine Science, 54: 1009–1014.

Glover, K. A., Quintela, M., Wennevik, V., Besnier, F., Sørvik, A.G.E., and Skaala, Ø. 2012. Three decades of farmed escapees in the wild: a spatio-temporal analysis of population genetic structure throughout Norway. PLoS One, 7: e43129.

Glover, K. A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M., and Skaala, Ø. 2013. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genetics, 14: 74.

Grant, W. S. (ed.). 1997. Genetic Effects of Straying of Non-Native Hatchery Fish into Natural Populations: Proceedings of the Workshop. U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-NWFSC-30, 130 pp.

Gross, M. R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Canadian Journal of Fisheries and Aquatic Sciences, 55(Suppl. 1): 131–144.

Hansen, M. M., Bekkevold, D., Jensen, L. F., Mensberg, K. -L. D., and Nielsen, E. E. 2006. Genetic restoration of stcoked brown trout *Salmo trutta* population using microsatellite DNA analysis of historical and contemporary samples. Journal of Applied Ecology, 43: 669–679.

Heino, M., Svåsand, T., Wennevik, V., and Glover, K. A. 2015. Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. Aquaculture Environment Interactions, 6: 185–190.

Hindar, K., Ryman, N., and Utter, F. 1991. Genetic effects of aquaculture on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences, 48: 945–957.

Hindar, K., Fleming, I. A., McGinnity, P., and Diserud, O. 2006. Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results. ICES Journal of Marine Science, 63: 1234–1247.

Huisman, J., and Tufto, J. 2012. Comparison of non-Gaussian quantitative genetic models for migration and stabilizing selection. Evolution, 66: 3444–3461.

Hutchings, J. A., and Fraser, D. J. 2008. The nature of fisheries- and farming-induced evolution. Molecular Ecology, 17: 294–313.

Jensen, A. J., Karlsson, S., Fiske, P., Hansen, L. P., Hindar, K., and Østborg, G. 2013. Escaped farmed Atlantic salmon in the Arctic Ocean. Aquaculture Environment Interactions, 3: 223–229.

Jensen, A. J., Karlsson, S., Fiske, P., Hansen, L. P., Østborg, G., and Hindar, K. 2014. Origin and life history of Atlantic salmon *Salmo salar* near the northernmost oceanic limit. Canadian Journal of Fisheries and Aquatic Sciences, 71: 1740–1746.

Johnsen, B. O., and Jensen, A. J. 1991. The Gyrodactylus story in Norway. Aquaculture, 98: 289–302.

Jonsson, B., Jonsson, N., and Hansen, L. P. 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon? Behavioral Ecology and Sociobiology, 26: 225–230.

Jonsson, B., Jonsson, N., and Hansen, L. P. 2003. Straying in Atlantic salmon. Journal of Fish Biology, 62: 641–657.

Kalinowski, S. T. 2011. The computer program STRUCTURE does not reliably identify the main genetic clusters within species: simulation and implications for human population structure. Heredity, 106: 625–632.

Karlsson, S., Diserud, O. H., Moen, T., and Hindar, K. 2014. A standardized method for quantifying unidirectional genetic introgression. Ecology and Evolution, 4: 3256–3263.

Karlsson, S., Florø-Larsen, B., Balstad, T., and Eriksen, L. 2015. Stamlakskontroll 2014. NINA Rapport, 1143: 13. (In Norwegian)

Karlsson, S., Florø-Larsen, B., Balstad, T., Eriksen, L., and Spets, M. H. 2015. Stamlakskontroll 2015. NINA Rapport, 1266: 14. (In Norwegian)

Karlsson, S., Moen, T., Lien, S., Glover, K. A., and Hindar, K. 2011. Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. Molecular Ecology Resources, 11(Suppl. 1): 247–253.

Karlsson, S., Thomas, M., and Hindar, K. 2010. Contrasting patterns of gene diversity between microsatellites and mitochondrial SNPs in farm and wild Atlantic salmon. Conservation Genetics, 11: 571–582.

Krkosek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B., and Todd, C.D. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B, 280: 20122359.

Lund, R. A., and Hansen, L. P. 1991. Identification of wild and reared Atlantic salmon, *Salmo salar* L., using scale characters. Aquaculture and Fisheries Management, 22: 499–508.

Lura, H. 1995. Domesticated female Atlantic salmon in the wild: spawning success and contribution to local populations. Dr. Scient. Thesis, University of Bergen.

McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Maoiléidigh, N. Ó., Rogan, G, Taggart, J., *et al.* 2003. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interaction with escaped farm salmon. Proceedings of the Royal Society London B, 270: 2443–2520.

McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C., *et al.* 1997. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. ICES Journal of Marine Science, 54: 998–1008.

Mjølnerød, I. B., Refseth, U. H., Karlsen, E., Balstad, T., Jakobsen, K. S., and Hindar, K. 1997. Genetic differences between two wild and one farmed population of Atlantic salmon (*Salmo salar*) revealed by three classes of genetic markers. Hereditas, 127: 239–248.

Mork, J. 1991. One generation effects of farmed fish immigration on the genetic differentiation of wild Atlantic salmon in Norway. Aquaculture, 98: 267–276.

Morris, M. R. J., Fraser, D. J., Heggelin, A. J., Whoriskey, F. G., Carr, J. W., O'Niel, S. F., and Hutchings, J. A. 2008. Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. Canadian Journal of Fisheries and Aquatic Sciences, 65: 2807–2826.

Nielsen, E. E., Bach, L. A., and Kotlicki, P. 2006. HYBRIDLAB (version 1.9): a program for generating simulated hybrids from population samples. Molecular Ecology Notes, 6: 971–973.

Pritchard, J. K., Stephens, M., and Donnelly, P. 2000. Inference of population structure using multilocus genotype data. Genetics, 155: 945–959.

Reed, T. E., Prodöhl, P., Hynes, R., Cross, T., Ferguson, A., and McGinnity, P. 2015. Quantifying heritable variation in fitness-related traits of wild, farmed and hybrid Atlantic salmon families in a wild river environment. Heredity, 115: 173–184.

Roberge, C., Einum, S., Guderley, H., and Bernatchez, L. 2006. Rapid parallel evolutionary changes of gene transcription profiles in farmed Atlantic salmon. Molecular Ecology, 15: 9–20.

Ryman, N., Utter, F., and Hindar, K. 1995. Introgression, supportive breeding, and genetic conservation. *In* Population Management for Survival and Recovery: Analytical Methods and Strategies in Small Population Conservation. Ed. by J. D. Ballou, M. Gilpin, and T. J. Foose. Columbia University Press, New York. 341–365 pp.

Sægrov, H., Hindar, K., Kålås, S., and Lura, H. 1997. Escaped farmed Atlantic salmon replaces the original salmon stock in the River Vosso. ICES Journal of Marine Science, 54: 1166–1172.

Skaala, Ø., Glover, K. A., Barlaup, B. T., Svåsand, T., Besnier, F., Hansen, M. M., and Borgstrøm, R. 2012. Performance of farmed, hybrids, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. Canadian Journal of Fisheries and Aquatic Science, 69: 1994–2006.

Skaala, Ø., Høyheim, B., Glover, K., and Dahle, G. 2004. Microsatellite analysis in domesticated and wild Atlantic salmon (*Salmo salar* L.) allelic diversity and identification of individuals. Aquaculture, 240: 131–143.

Skaala, Ø., Taggart, J. B., and Gunnes, K. 2005. Genetic differences between five major domesticated strains of Atlantic salmon and wild salmon. Journal of Fish Biology, 67: 118–128.

Skaala, Ø., Wennevik, V., and Glover, K. A. 2006. Evidence of temporal genetic change in wild Atlantic salmon (*Salmo salar* L.) populations affected by farmed escapees. ICES Journal of Marine Science, 63: 1224–1233.

Solberg, M. F., Skaala, Ø., Nilsen, F., and Glover, K. A. 2013. Does domestication cause changes in growth reaction norms? A study of farmed, wild and hybrid Atlantic salmon families exposed to environmental stress. PLoS One, 8: e54469.

Sundt-Hansen, L., Huisman, J., Skoglund, H., and Hindar, K. 2015. Farmed Atlantic salmon *Salmo salar* L. parr may reduce early survival of wild fish. Journal of Fish Biology, 86: 1699–1712.

Tang, K., Fu, D. J., Julien, D., Braun, A., Cantor, C. R., and Kösner, H. 1999. Chip-based genotyping by mass spectrometry. Proceedings of the National Academy of Sciences of the United States of America, 96: 10016–10020.

Thodesen, J., Grisdale-Helland, B., Helland, S. J., and Gjerde, B. 1999. Feed intake, growth and feed utilization of offspring from wild and selected Atlantic salmon (*Salmo salar*). Aquaculture, 180: 237–246.

Tufto, J. 2000. Quantitative genetic models for the balance between migration and stabilizing selection. Genetical Research, 76: 285–293.

Tufto, J. 2001. Effects of releasing maladapted individuals: A demographic-evolutionary model. American Naturalist, 158: 331–340.

Tufto, J., and Hindar, K. 2003. Effective size in management and conservation of subdivided populations. Journal of Theoretical Biology, 222: 273–281.

Vähä, J. P., Erkonaro, J., Niemelä, E., and Primmer, C. R. 2008. Temporally stable genetic structure and low migration in an Atlantic salmon population complex: implications for conservation and management. Evolutionary Applications, 1: 137–154.

Vøllestad, L. A., Hirst, D., L'Abée-Lund, J. H., *et al.* 2009. Divergent trends in anadromous salmonid populations in Norwegian and Scottish rivers. Proceedings of the Royal Society B, 276: 1021–1027.

Vøllestad, L. A., Skurdal, J., and L'Abée-Lund, J. H. 2014. Evaluation of a new management scheme for Norwegian Atlantic salmon *Salmo salar*. Fisheries Management and Ecology, 21: 133–139.

Waples, R. S., Hindar, K., and Hard, J. J. 2012. Genetic risks associated with marine aquaculture. U.S. Dept. of Commerce, NOAA Tech. Memo., NMFS-NWFSC-119, 149 p.

Warton, D. I., and Hui, F. K. C. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology, 92: 3–10.

Handling editor: W. Stewart Grant

Available online at www.sciencedirect.com
ScienceDirect
ELSEVIER
Current Opinion in Virology

Emerging viruses in aquaculture

Frederick SB Kibenge

Aquaculture remains the world's fastest-growing sector producing food of animal origin. Unlike in terrestrial animal agriculture, in aquaculture both farmed and wild aquatic animals in the same water column experience the same virus challenges. Additionally, the burgeoning international aquaculture expansion and expanding global trade in live aquatic animals and their products have been accompanied by long distance geographical redistribution of aquatic animal species and their viruses. The outcome is a continuous emergence of viral diseases in aquaculture, which may be driven by virus factors, animal host factors, environmental factors, and/or anthropogenic factors. Examples of emerging viruses in aquaculture include viral haemorrhagic septicaemia virus, infectious haematopoietic necrosis virus, infectious salmon anaemia virus, piscine orthoreovirus, Tilapia lake virus, Covert mortality nodavirus, Shrimp hemocyte iridescent virus, and Abalone herpesvirus.

Address
Department of Pathology and Microbiology, Atlantic Veterinary College, University of Prince Edward Island, 550 University Ave., Charlottetown, P E I C1A 4P3, Canada

Corresponding author: Kibenge, Frederick SB (kibenge@upei.ca)

Current Opinion in Virology 2019, **34**:97–103

This review comes from a themed issue on **Emerging viruses: inter-species transmission**

Edited by **Adolfo García-Sastre** and **Juergen A Richt**

For a complete overview see the Issue and the Editorial

Available online 1st February 2019

https://doi.org/10.1016/j.coviro.2018.12.008

Introduction

Aquaculture, the intensive water rearing of fish, mollusks, and crustaceans, remains the world's fastest-growing sector producing food of animal origin. As in the case of terrestrial animal agriculture, bringing together large numbers of animals than occur naturally involves substantial animal stress which facilitates virus multiplication and clinical disease. However, aquaculture presents unique challenges in contrast to all other intensive animal production systems, in that the aquatic farmed and wild animals occur in the same water column, and the aquatic environmental parameters cannot be very closely controlled as for captive livestock agriculture (for example as in the poultry and swine industries). Viruses, carried by wild aquatic animals where they are often not sufficient to sustain the natural transmission cycle density, are readily facilitated by the high density of hosts in aquaculture, which with the associated chronic stress provide opportunities for the emergence of viral diseases [1••]. Additionally, the burgeoning international aquaculture expansion and expanding global trade in live aquatic animals and their products have been accompanied by rapid long-distance geographical redistribution of aquatic animal species and their viruses with emergence in the same or different aquatic animal species. The outcome of these events is a continuous emergence of viral diseases in aquaculture, which may be driven by virus factors, animal host factors, environmental factors, and/or anthropogenic factors [1••]. For example, the wide use of 'cleaner fish' in marine farmed salmonids as a biological control for sea lice *Lepeophtheirus salmonis* in Europe and Canada is now considered a new route of emergence of viruses (such as viral haemorrhagic septicaemia virus (VHSV) and Cyclopterus lumpus virus) in fish aquaculture [2]. This practice is not only akin to mixing of species in fish farms, but has routinely involved use of wild-caught cleaner fish directly in the salmon farms or as broodstock for hatchery-raised cleaner fish [2]. Moreover, progressive farming practices now enable discovery of emerging viruses through surveillance and laboratory diagnosis. Indeed, several new viruses infecting aquatic organisms have been discovered through Next-generation sequencing (NGS) methods [3].

Several emerging, and re-emerging viruses in aquaculture will be highlighted in this overview. Many are listed by the World Organization for Animal Health (OIE), which means that countries free of these viruses can refuse imports of live aquatic animals and their products from areas that have not been declared virus-free, regardless of existing free trade agreements [4].

Carrier status in global movement of live aquatic animals and their products

The potential for dissemination of aquatic viruses because of aquaculture and movements of live cultured aquatic animals or their eggs is extremely high where persistent viral infections occur in the absence of clinical disease (i.e. 'healthy carrier' aquatic animals/subclinical infections in aquatic animals). Although life-long infections are known to occur among herpesvirus infections and retrovirus infections, there are several other virus groups where infection is not cleared by the host and the virus persists in a carrier state including species susceptible to infection without displaying clinical signs, age-related resistance to virus infection (e.g. adult fish), and infection with virus strains of low pathogenicity. There could also be situations of persistent infections where the virus level falls below detectable levels but not completely cleared from the host. All such infected animals are considered 'healthy' and may pass regulatory inspections for movement and/or export. This would be expected not only for new emerging viruses like piscine orthoreovirus (PRV) and tilapia lake virus (TiLV), which have been in existence but unknown until they were discovered [1••], and diagnostic tools developed not only for their detection, but also for re-emerging viruses such as VHSV, infectious haematopoetic necrosis virus (IHNV), infectious pancreatic necrosis virus (IPNV), and infectious salmon anaemia virus (ISAV) that cause persistent viral infections associated with lower virus levels in affected fish that may be difficult to detect through routine surveillance programs [5]. Most recently, 8000 juvenile Atlantic salmon at a commercial hatchery in Washington State-USA had to be destroyed because they tested positive for a strain of PRV found in Iceland. The virus is considered to have originated from fish eggs imported from Iceland. The source company for the eggs reported that they have an optional service of screening against PRV customers may choose as an extra risk measure to avoid vertical transmission (Owen E, 2018. https://salmonbusiness.com/egg-supplier-responds-to-washington-prv-salmon-cull/). In both examples above of new emerging viruses and re-emerging viruses where broodstock would have been persistently infected, the viruses would be disseminated via broodstock, fry or smolt movements, or egg transport into disease free farms, zones or countries. Where apparently 'healthy' aquatic animals are delivered to processing plants, the viruses would be disseminated via global trade in aquaculture products. In areas where these viruses are enzootic, clinical disease may manifest with the introduction of virus in imported aquatic material as for example with IPNV in Ireland where all reported clinical outbreaks were associated with imported IPNV isolates. In case of IHNV, in European countries where the main mode of virus transfer is by trade in infected fish, IHNV may remain undetected once introduced on a farm site [5].

The situation is even more concerning where international regulatory methods of control (e.g. for OIE listed diseases) dictate depopulation of affected farms upon virus detection in a few animals with few or none with clinical disease. In such situations, the affected animals may be allowed for human consumption and through international trade serve to introduce virus to new geographical areas. For example, White spot syndrome virus (WSSV), a highly infectious virus with a very wide crustacean host range has spread to all prawn-producing countries in the world with global movement of live shrimp. Until 2016, the Australian prawn industry was considered free of WSSV. Australia's biosecurity arrangements were breached by WSSV from Asia resulting in an outbreak in commercial *Penaeus monodon* prawn farms in Queensland in November–December 2016. The most likely route of infection appears to be via imported infected retail prawns used for human consumption and as bait by fishers (Loynes K. 2017.https://www.aph.gov.au/About_Parliament/Parliamentary_Departments/Parliamentary_Library/pubs/rp/rp1718/Chronology/WhiteSpotDiseaseAustralia). It is generally accepted that freezing seafood results in reduced infectivity of associated aquatic viruses.

Selected emerging viruses in fish aquaculture

Viral haemorrhagic septicaemia (VHS) virus (VHSV)

VHSV belongs to the species *Oncorhynchus 2 novirhabdovirus*, genus *Novirhabdovirus* within the family *Rhabdoviridae* [6]. Genotyping in accordance with VHSV G-gene and N-gene reveals four major genotypes (I–IV) that correspond with the broad geographical origins and host specificity of isolates. VHS is a notifiable disease to the OIE [7]. VHSV has been isolated from more than 82 marine and freshwater fish species, with at least 44 of these species shown to be susceptible [7] although its economic importance is primarily to the rainbow trout and turbot aquaculture in Europe and Japanese flounder (*Paralichthys olivaceus*) in Japan and olive flounder (*Paralichthys olivaceus*) in Korea.

VHSV is assumed to be endemic among a wide range of marine and anadromous fish species in the northern hemisphere [7], occasionally emerging in aquaculture as shown by transmission events reported for rainbow trout reared in marine and brackish waters in Finland, Norway, and Sweden, and the recent detections of VHSV III in wrasse species (*Labridae*) used as cleaner fish in Atlantic salmon farms in Scotland and VHSV IVd in wild lumpfish (*Cyclopterus lumpus*) brought to a land-based farm in Iceland, to serve as broodfish [8••].

Infectious haematopoietic necrosis virus (IHNV)

IHNV belongs to the species *Oncorhynchus 1 novirhabdovirus*, genus *Novirhabdovirus* within the family *Rhabdoviridae* [6]. In contrast to VHSV in the same genus, IHNV has a relatively narrow host range restricted to salmonids, fish families *Oncorhynchus* and *Salmo*. Genotyping according to the glycoprotein gene reveals five major genogroups. Three of the genotypes, on the basis of a 303-nucleotide variable region ('mid-G'), are designated as U (upper), M (middle), and L (lower), respectively, to correlate with the geographic areas in the Pacific Northwest of North America; the fourth and fifth genogroups based on the full-length glycoprotein gene, are 'E' and 'JRt' or 'J', consisting of European and Japanese rainbow trout isolates, respectively. IHNV is endemic to western North America where it was first described in Sockeye salmon (*Oncorhynchus nerka*) fry hatcheries in the early 1950s, and is considered to have spread to Europe and Japan via shipments of IHNV-contaminated rainbow trout eggs or fry. IHNV appears to travel through Europe without significant restrictions, termed viral 'tourism' as a consequence of frequent fish trade between private farms [9••]. IHN is a notifiable disease to the OIE [10]. Phylogenetic analysis of recent IHNV isolates in China indicate existence of a recently introduced virus via transfer of eggs or fish from North America where endemic virus continues to circulate undetected [11].

Infectious salmon anaemia virus (ISAV)

ISAV belongs to the species *Salmon isavirus*, genus *Isavirus* within the family *Orthomyxoviridae*. Genotyping based on the haemagglutinin-esterase (HE) gene reveals two basic genotypes, North American and European. ISAV strain designation is mostly based on sequence deletions/insertions in a 35-amino acid highly polymorphic region (HPR) of the HE protein [12]. Viruses without any deletion/insertion in HPR are designated ISAV-HPR0 to indicate 'full-length HPR' and are resistant to growth in cell culture, nonpathogenic, replicate only in epithelial cells of Atlantic salmon gills, and cause transient infection [12]. All ISAV isolated in fish cell lines to date from clinical disease have deletions in HPR relative to HPR0 and are referred to as ISAV-HPR-deleted (ISAV-HPRΔ). Virulent ISAV-HPRΔ targets endothelial cells resulting in systemic haemorrhagic disease. ISA is one of the most important salmonid viruses and is notifiable to the OIE [13]. Since 2012, ISAV outbreaks have been reported mostly in Norway, Canada and Chile. ISAV-HPRΔ was detected by RT-PCR but could not be isolated in cell culture, at a Chinese entry-exit port in 1 of 79 batches of eviscerated fresh salmon imported from Norway in 2015; the shipment was disposed of without entering Chinese aquaculture [14]. China currently has one of the world's biggest fully submerged net cage farming Atlantic salmon in the Yellow Sea (Owen E, 2018. https://salmonbusiness.com/chinas-gets-ready-to-harvest-first-batch-of-farmed-salmon-from-huge-deep-sea-fully-submersible-fish-cage/). The level of risk of introducing ISAV into a disease free country via importation of frozen whole salmon or fillets may be lower than with non-frozen salmon products as ISAV is sensitive to freezing and thawing [15].

Another fish orthomyxovirus, rainbow trout orthomyxovirus (RbtOV) isolated from juvenile rainbow and spawning steelhead trout (both *Oncorhynchus mykiss*) has been suggested to belong to a new genus, proposed name *Mykissvirus*, in the family *Orthomyxoviridae* [16]. RbtOV appears to have a relatively low prevalence in trout populations, grows in cell culture but is nonpathogenic in fish [16].

Tilapia lake virus (TiLV)

TiLV is a new orthomyxovirus of fish. It has a genome of 10 segments of linear negative sense single stranded RNA. It belongs to the species *Tilapia tilapinevirus*, genus *Tilapinevirus* within the family *Orthomyxoviridae*. Since its discovery as the etiological cause of massive losses of tilapia in Israel and Ecuador in 2009 [17••], TiLV has emerged as a significant cause of fish disease with mortality rates of 10–90% in farmed tilapia and the wild population in 12 countries across 3 continents (Asia, Africa, South America) [18]. TiLV represents an important risk for the fast-growing worldwide tilapia production sector. Tilapia is the world's second-most-farmed fish after carp [19]. It is possible that international trade may have been circulating TiLV worldwide through movement of live fish for aquaculture in the absence of knowledge of the existence of an associated risk [19,20]. It was recently shown that TiLV is inactivated in tilapia fillets stored at −20°C for 90–120 days [21] demonstrating that frozen seafood (e.g. whole fish or fillets) imports may be associated with lower risk of virus dissemination than non-frozen products. TiLV has not yet been detected in North America tilapia stocks [22].

Salmonid alphavirus (SAV)

SAV belongs to the genus *Alphavirus* within the family *Togaviridae*. SAV is the cause of pancreas disease (PD) and sleeping disease (SD), viral diseases of serious concern for salmon aquaculture in Northern Europe [23,24]. Genomic, antigenic, and histopathological studies have shown that SPDV and SDV isolates are closely related strains of the same virus now referred to as SAV. Six different subtypes of SAV (SAV1-6) have been identified using phylogenetic analysis with partial glycoprotein E2 and nonstructural protein-3 (nsP3)-gene sequence data, providing evidence that some subtypes are dominant in certain geographical regions [25], and each subtype likely represents a single and separate introduction to aquaculture from a wild reservoir in or around the North Sea. SAV has been isolated from wild common dab *Limanda limanda* and plaice *Pleuronectes platessa* in Scotland and Ireland. The disease, which was first recorded in 1976 in Scotland, has continued as a significant threat to sustainable salmon production in Scotland, Ireland, Norway, France, Spain, Germany, Switzerland, and most recently Poland. SAV infections are on the OIE list of notifiable aquatic animal diseases [25]. To date there has been no confirmed reports of SAV in North America [26].

Piscine orthoreovirus (PRV)

PRV belongs to the family *Reoviridae*, subfamily *Spinareovirinae*. The PRV genome comprises of 10 segments of double-stranded RNA and all of them have been sequenced [27,28]. PRV is considered to be ubiquitous in farmed Atlantic salmon. It is an emerging virus of salmon aquaculture that is associated with an ever-increasing list of clinical syndromes including heart and skeletal muscle inflammation (HSMI) in farmed Atlantic salmon in Norway, Chile and BC-Canada [27,29–31]. The PRV genomic segment S1 sequence differentiates PRV isolates into two genotypes, I and II [28,29], and each of them into two major subgenotypes designated Ia and Ib, and IIa and IIb (Kibenge *et al.*, unpublished). Figure 1 shows the PRV genotypes and subtypes, and their geographical locations and associated clinical conditions.

Selected emerging viruses in crustacean aquaculture

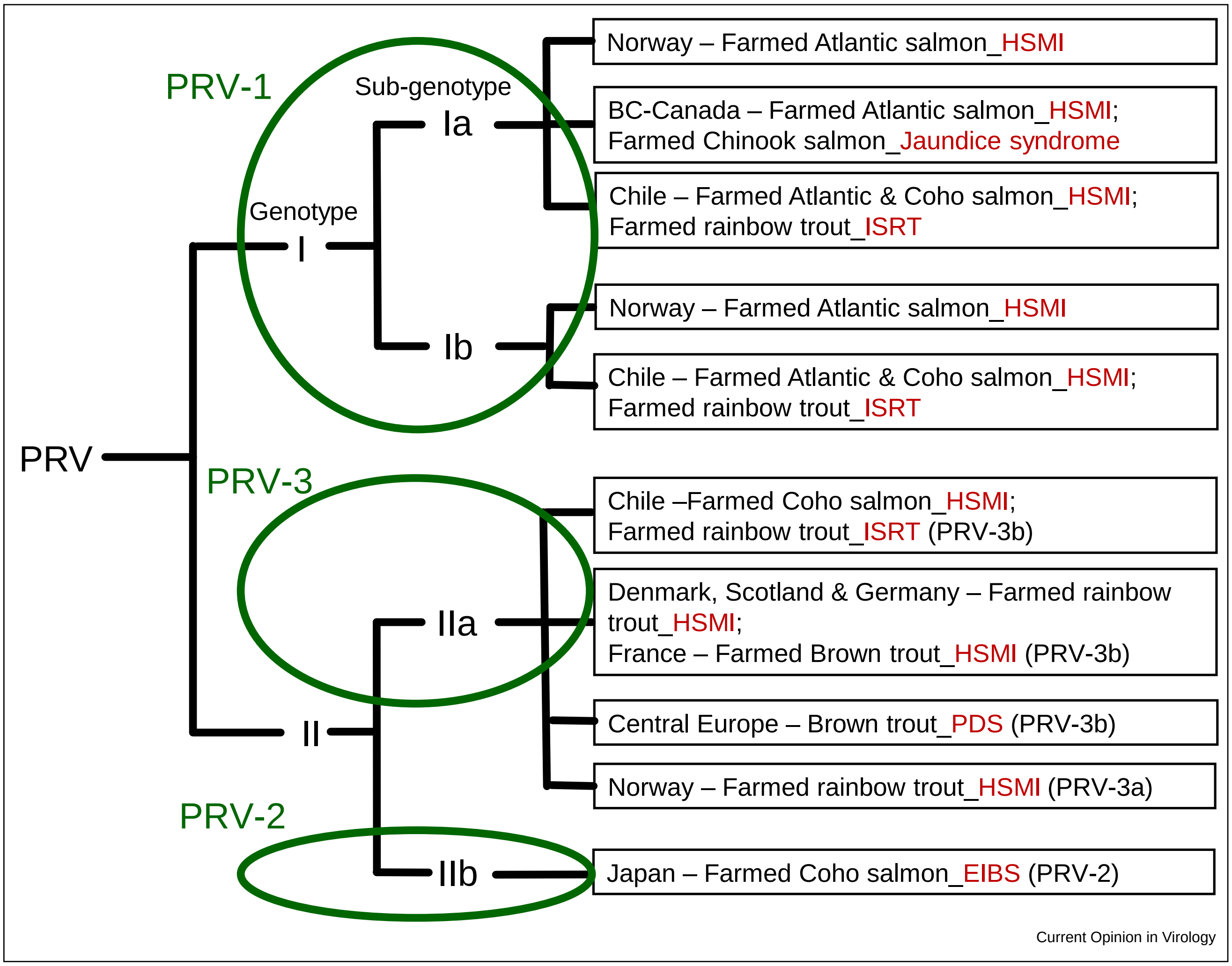
Shrimp hemocyte iridescent virus (SHIV)

A new virus of the family *Iridoviridae* isolated in China, results in a high mortality rate in white leg shrimp (*Litopenaeus vannamei*) [32]. The virus is proposed to be a member of the new genus *Xiairidovirus* [33] in family *Iridoviridae*. SHIV was detected in *L. vannamei*, *Fenneropenaeus chinensis*, and *Macrobrachium rosenbergii* in samples collected during 2014–2016 from 5 provinces in China [32].

Covert mortality nodavirus (CMNV)

CMNV is a new virus of the family *Nodaviridae*, genus *Alphanodavirus*. It is the cause of viral covert mortality disease of shrimp [34] which has caused serious loss in China since its emergence in 2002–2003. Shrimp infected with CMNV are commonly found in deep water on the

Figure 1



Piscine orthoreovirus (PRV) genotypes, subtypes, geographical location and associated fish diseases. Phylogenetic analysis of genome segment S1 groups PRV into two genotypes (I and II) and four subgenotypes (Ia, Ib, IIa and IIb) [28,29, Kibenge *et al.*, unpublished]. Following order of discovery, Genotype I is also referred as PRV-1, subgenotype IIb as PRV-2 [29], and subgenotype IIa as PRV-3 [Kibenge *et al.*, unpublished]. All the PRV-3 isolates can be further subdivided into PRV-3a from rainbow trout from Norway [41,42], and PRV-3b from the rest of Europe [42–44] and Chile [45,46].

HSMI = Heart and skeletal muscle inflammation in farmed Atlantic salmon [29–31]. In other fish species (coho salmon, rainbow trout, brown trout), the disease is referred to as 'HSMI-like' disease [29,41,42,44].

Jaundice and anemia (Jaundice syndrome) in farmed Chinook salmon in BC-Canada [47,48].

ISRT = Idiopathic syndrome of rainbow trout in fared rainbow trout in Chile [45].

EIBS = Erythrocyte inclusion body syndrome in farmed juvenile coho salmon in Japan [29].

bottom of the shrimp pond rather than swimming on the surface or in shallow water like shrimp infected with White spot syndrome virus (WSSV) [35]. The disease causes economic losses in hatcheries and farms due to high mortality rates of up to 80% commonly found within 60–80 days post-stocking. CMNV should not be confused with other nodavirus infections such as infectious myonecrosis virus (IMNV), *Macrobrachium rosenbergii* nodavirus (MrNV) and *Penaeus vannamei* nodavirus (PvNV) [35]. These viruses do not cause hepatopancreatic atrophy and necrosis, unlike CMNV.

CMNV has a wide host range among cultured shrimp species, with a high prevalence and wide distribution in Southeast Asia, and Latin American countries [34]. CMNV was found in eleven species of invertebrates collected from shrimp ponds of cultured shrimp species affected with VCMD, which may be vectors and reservoirs of CMNV [36]. CMNV has also naturally crossed the species barrier (i.e. jumped species) and infected several species of fish such as *Mugilogobius abei*, a common marine fish in shrimp farming ponds and coastal water in China, another marine fish *Chaeturichthys hexanema* found in the Yellow sea [37], and farmed Japanese flounder (*Paralichthys olivaceus*) [38••].

Selected emerging viruses in molluscan aquaculture

Abalone herpesvirus (AbHV)

AbHV is the cause of abalone viral ganglioneuritis (AVG) in farmed and wild abalone primarily in Australia and Chinese Taipei [39] and is listed by the OIE [40]. The virus is a member of the family *Malacoherpesviridae* [39] which includes Ostreid Herpesvirus-1 and is tentatively placed in a new genus *Haliotivirus*. The disease first occurred in Australia in 2005 [40].

Future perspectives

Aquaculture is important now and will continue in the future as a principal source of animal protein for human consumption, as will the global trade in live aquatic animals and their products. Aquatic animal viral diseases are inherent in aquaculture, and they continue to negatively impact aquaculture significantly. Considering that seafood is the most traded commodity globally, it, therefore, virtually impossible to have 'aquatic virus-leakproof' international borders. The implementation of strict biosecurity measures on aquaculture farms on land, in lakes and the sea, and in processing plants or other natural source for aquaculture helps to limit but does not eliminate the risk of dissemination of aquatic viruses. Biosecurity management will remain an on-going effort for the foreseeable future. The best options for keeping abreast of the continuous emergence of viral diseases in aquaculture are ideally at the farm level where better knowledge about the viral diseases and their improved diagnosis, inspection and surveillance programs translate into higher profits for the farmer and, therefore, motivation for a sustainable industry.

Acknowledgement

The continued funding of FSBK's laboratory by the Natural Sciences and Engineering Research Council of Canada (NSERC) has made this review possible.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Kibenge FSB: **Determinants of emergence of viral diseases in aquaculture**. In *Aquaculture Virology.* Edited by Kibenge FSB, Godoy MG. Elsevier Inc., Academic Press; 2016:95-116.
••
This book chapter is a 'must read' about emerging viruses in aquaculture. It presents a detailed context for understanding the drivers responsible for the emergence of viral diseases in aquaculture and fisheries. The most recent definition of an 'emerging infectious disease' is used to group emerging aquatic animal viruses into eight categories: (1) a virus introduced in a new host and new geographic area; (2) a virus infecting the same host but introduced in a new geographic area; (3) enzootic virus with increased pathogenicity in same host (manifesting as increased incidence or more severe disease); (4) enzootic virus with increased host range; (5) enzootic virus with expanded geographic range; (6) increased awareness; (7) improved diagnosis and surveillance; and (8) newly discovered viral cause of existing disease. An emerging aquatic animal viral disease may fit in several of these categories depending on the sequence of events involved and geographical area concerned. The drivers (attributes or causal factors) of emerging viruses can be categorized into virus drivers, animal host drivers, environment drivers and anthropogenic drivers. The interplay of these drivers manifests into new or previously unrecognized viral diseases or re-emerging viral diseases in aquaculture and fisheries. A separate distinct category is introduced for those viral diseases whose incidence is decreasing as a result of anthropogenic means or through natural means, as this is the ultimate goal of disease control and prevention.

2. Murray AG: **A modelling framework for assessing the risk of emerging diseases associated with the use of cleaner fish to control parasitic sea lice on salmon farms**. *Transbound Emerg Dis* 2016, **63**:e270-e277.

3. Munang'andu HM, Mugimba KK, Byarugaba DK, Mutoloki S, Evensen Ø: **Current advances on virus discovery and diagnostic role of viral metagenomics in aquatic organisms**. *Front Microbiol* 2017, **8**:406.

4. World Organization for Animal Health (OIE): *Aquatic Animal Health Code*. edn 21. 2018 . Available at: *http://www.rr-africa.oie.int/docspdf/en/Codes/en_csaa.pdf*.

5. Dixon P, Paley R, Alegria-Moran R, Oidtmann B: **Epidemiological characteristics of infectious hematopoietic necrosis virus (IHNV)**. *Vet Res* 2016, **47**:63.

6. Afonso CL, Amarasinghe GK, Bányai K, Báo Y, Basler CF, Bavari S, Bejerman N, Blasdell KR, Briand F-X, Briese T *et al.*: **Taxonomy of the order Mononegavirales: update 2016**. *Arch Virol* 2016, **161**:2351-2360.

7. World Organization for Animal Health (OIE): *Manual of Diagnostic Tests for Aquatic Animals; Viral Haemorrhagic Septicaemia*. 2018 . Chapter 2.3.10. Available at: *http://www.oie.int/fileadmin/Home/eng/Health_standards/aahm/current/chapitre_vhs.pdf*.

8. Guðmundsdóttir S, Vendramin N, Cuenca A, Sigurðardóttir H, Kristmundsson A, Iburg TM, Olesen NJ: **Outbreak of viral haemorrhagic septicaemia (VHS) in lumpfish (*Cyclopterus lumpus*) in Iceland caused by VHS virus genotype IV**. *J Fish Dis* 2019, **42**:47-62 http://dx.doi.org/10.1111/jfd.12910.
••
The authors provided a detailed account of characterization of new VHSV isolates originating from wild lumpfish on the south coast of Iceland. These VHSV isolates clearly constitute a new subtype (IVd) never reported before, although the authors remain very cautious in interpretation of their findings.

9. Cieslak M, Wahli T, Diserens N, Haenen OLM, Schuétze H:
•• **Phylogeny of the infectious hematopoietic necrosis virus in European aquaculture**. *PLoS One* 2017, **12**:e0184490.

The authors confirm what has been known for a long time that IHNV is transmitted throughout Europe through active trout trade.

10. World Organization for Animal Health (OIE): *Manual of Diagnostic Tests for Aquatic Animals; Infectious Haematopoietic Necrosis*. 2018 . Chapter 2.3.4. Available at: *http://www.oie.int/fileadmin/Home/eng/Health_standards/aahm/current/chapitre_ihn.pdf*.

11. Jia P, Breyta RB, Li Q, Qian X, Wu B, Zheng W, Wen Z, Liu Y, Kurath G, Hua Q *et al.*: **Insight into infectious hematopoietic necrosis virus (IHNV) in Chinese rainbow trout aquaculture from virus isolated from 7 provinces in 2010–2014**. *Aquaculture* 2018, **496**:239-246.

12. Kibenge FSB, Kibenge MJT: **Orthomyxoviruses of fish**. In *Aquaculture Virology*. Edited by Kibenge FSB, Godoy MG. Elsevier Inc, Academic Press; 2016:299-326.

13. World Organization for Animal Health (OIE): *Manual of Diagnostic Tests for Aquatic Animals; Infectious Salmon Anaemia*. 2018 . Chapter 2.3.5. Available at: *http://www.oie.int/fileadmin/Home/eng/Health_standards/aahm/current/chapitre_isav.pdf*.

14. Xiao L, Lin H, Yang M, Chen S, An W, Wu X, Liu H, Li D, Yan Y, Hu J *et al.*: **The first instance of HPR-deleted ISAV detection in eviscerated, fresh salmon at a Chinese entry-exit port**. *Aquaculture* 2018, **485**:220-224.

15. Ramírez R, Marshall SH: **Identification and isolation of infective filamentous particles in infectious salmon anemia virus (ISAV)**. *Microb Pathog* 2018, **117**:219-224.

16. Batts WN, LaPatra SE, Katona R, Leis E, Ng TFF, Brieuc MSO, Breyta RB, Purcell MK, Conway CM, Waltzek TB *et al.*: **Molecular characterization of a novel orthomyxovirus from rainbow and steelhead trout (*Oncorhynchus mykiss*)**. *Virus Res* 2017, **230**:38-49.

17. Bacharach E, Mishra N, Briese T, Zody MC, Kembou Tsofack JE,
•• Zamostiano R, Berkowitz A, Ng J, Nitido A, Corvelo A *et al.*: **Characterization of a novel Orthomyxo-like virus causing mass die-offs of tilapia**. *MBio* 2016, **7** e00431-00416.

The authors were the first to characterize a novel orthomyxovirus with 10 genome segments as the cause of a new viral disease of tilapia. Using next-generation sequence methodology, the authors found only one of the genomic segments (segment 1) to have weak sequence similarity with Gammainfluenzavirus; all the other nine genome segments were identified based on conserved terminal sequences characteristic of orthomyxoviruses.

18. Jansen MD, Dong HT, Mohan CV: **Tilapia lake virus: a threat to the global tilapia industry?** *Rev Aquacult* 2018:1-15 http://dx.doi.org/10.1111/raq.12254.

19. Food and Agriculture Organization of the United Nations (FAO): *FAO Fisheries and Aquaculture Circular No. 1135/5 2017*. 2017 . Available at: *http://www.fao.org/3/a-i6875e.pdf*.

20. Dong HT, Ataguba P, Khunrae T, Rattanarojpong T, Serapin S: **Evidence of TiLV infection in tilapia hatcheries from 2012 to 2017 reveals probable global spread of the disease**. *Aquaculture* 2017, **479**:579-583.

21. Thammatorn W, Rawiwan P, Surachetpong W: **Minimal risk of tilapia lake virus transmission via frozen tilapia fillets**. *J Fish Dis* 2019, **42**:3-9 http://dx.doi.org/10.1111/jfd.12924.

22. Al-Hussinee L, Subramaniam K, Ahasan MS, Keleher B, Waltzek TB: **Complete genome sequence of a tilapia lake virus isolate obtained from Nile tilapia (*Oreochromis niloticus*)**. *Genome Announc* 2018, **6** e00580-18.

23. Hjortaas MJ, Bang Jensen B, Taksdal T, Olsen AB, Lillehaug A, Trettenes E, Sindre H: **Genetic characterization of salmonid alphavirus in Norway**. *J Fish Dis* 2016, **39**:249-257.

24. Deperansińska I, Schulz P, Simicki AK: **Salmonid alphavirus (SAV)**. *J Vet Res* 2018, **62**:1-6.

25. World Organization for Animal Health (OIE). Manual of diagnostic tests for aquatic animals; Salmonid alphavirus, Chapter 2.3.6. Available at: http://www.oie.int/fileadmin/Home/eng/Health_standards/aahm/current/chapitre_salmonid_alphavirus.pdf.

26. Purcell MK, Powers RL, Evered J, Kerwin J, Meyers TR, Stewart B, Winton JR: **Molecular testing of adult Pacific salmon and trout (*Oncorhynchus* spp.) for several RNA viruses demonstrates widespread distribution of piscine orthoreovirus (PRV) in Alaska and Washington**. *J Fish Dis* 2018, **41**:347-355.

27. Kibenge FSB, Godoy MG: **Reoviruses of aquatic organisms**. In *Aquaculture Virology*. Edited by Kibenge FSB, Godoy MM. Elsevier Inc, Academic Press; 2016:205-236.

28. Takano T, Nawata A, Sakai T, Matsuyama T, Ito T, Kurita J, Terashima S, Yasuike M, Nakamura Y, Fujiwara A *et al.*: **Full-genome sequencing and confirmation of the causative agent of erythrocytic inclusion body syndrome in coho salmon identifies a new type of piscine orthoreovirus**. *PLoS One* 2016, **11**:e0165424.

29. Godoy MG, Kibenge MJT, Wang Y, Suarez R, Leiva C, Vallejos F, Kibenge FSB: **First description of clinical presentation of piscine orthoreovirus (PRV) infections in salmonid aquaculture in Chile and identification of a second genotype (Genotype II) of PRV**. *Virol J* 2016, **13**:98.

30. Alarcon M, Dahle M, Taksdal T: **Heart and skeletal muscle inflammation**. In *The Health Situation in Norwegian Aquaculture 2015*. Edited by Hjeltnes H, Walde C, Bang Jensen B, Haukaas A. Veterinærinstituttet Rapportserie; 2016:28-29. (in Norwegian).

31. Di Cicco E, Ferguson HW, Schulze AD, Kaukinen KH, Li S, Vanderstichel R, Wessel Ø, Rimstad E, Gardner IA, Hammell KL *et al.*: **Heart and skeletal muscle inflammation (HSMI) disease diagnosed on a British Columbia salmon farm through a longitudinal farm study**. *PLoS One* 2017, **12**:e0171471.

32. Qiu L, Chen MM, Wan XY, Li C, Zhang QL, Wang RY, Cheng DY, Dong X, Yang B, Wang XH *et al.*: **Characterization of a new member of Iridoviridae, Shrimp hemocyte iridescent virus (SHIV), found in white leg shrimp (*Litopenaeus vannamei*)**. *Sci Rep* 2017, **7**:11834.

33. Qiu L, Chen MM, Wang R-Y, Wan XY, Li C, Zhang QL, Dong X, Yang B, Xiang JH, Huang J: **Complete genome sequence of shrimp hemocyte iridescent virus (SHIV) isolated from white leg shrimp, *Litopenaeus vannamei***. *Arch Virol* 2018, **163**:781-785.

34. Zhang Q, Xu T, Wan X, Liu S, Wang X, Li X, Dong X, Yang B, Huang J: **Prevalence and distribution of covert mortality nodavirus (CMNV) in cultured crustacean**. *Virus Res* 2017, **233**:113-119.

35. Pooljun C, Direkbusarakom S, Chotipuntu P, Hirono I, Wuthisuthimethaveea S: **Development of a TaqMan real-time RT-PCR assay for detection of covert mortality nodavirus (CMNV) in penaeid shrimp**. *Aquaculture* 2016, **464**:445-450.

36. Liu S, Wang X, Xu TT, Li X, Du L, Zhang Q: **Vectors and reservoir hosts of covert mortality nodavirus (CMNV) in shrimp ponds**. *J Invertebr Pathol* 2018, **154**:29-36.

37. Zhang QL, Liu S, Li J, Xu TT, Wang XH, Fu GM, Li XP, Sang SW, Bian XD, Hao JW: **Evidence for cross-species transmission of covert mortality nodavirus to new host of Mugilogobius abei**. *Front Microbiol* 2018, **9**:1447.

38. Wang C, Liu S, Li X, Hao J, Tang KFJ, Zhang Q: **Infection of covert**
•• **mortality nodavirus in Japanese flounder reveals host jump in the emerging alphanodavirus**. *J Gen Virol* 2018 http://dx.doi.org/10.1099/jgv.0.001177. [Epub ahead of print].

The authors report a unique occurrence of newly discovered virus in shrimp (belonging to a virus group,*Alphanodavirus*, known to infect only insects) having jumped from shrimp to a new host species (fish). It is not clear how long the virus had existed in shrimp before successfully infecting fish.

39. Renault T: **Malacoherpesviruses of mollusks**. In *Aquaculture Virology*. Edited by Kibenge FSB, Godoy MG. Elsevier Inc, Academic Press; 2016:513-524.

40. World Organization for Animal Health (OIE): *Manual of Diagnostic Tests for Aquatic Animals; Abalone Herpesvirus*. 2018 . Chapter 2.4.1. Available at: In: *http://www.oie.int/fileadmin/Home/eng/*

Health_standards/aahm/current/chapitre_abalone_herpesvirus.pdf.

41. Hauge H, Vendramin N, Taksdal T, Olsen AB, Wessel Ø, Mikkelsen SS, Alencar ALF, Olesen NJ, Dahle MK: **Infection experiments with novel Piscine orthoreovirus from rainbow trout (*Oncorhynchus mykiss*) in salmonids**. *PLoS One* 2017, **12**: e0180293.
42. Dhamotharan K, Vendramin N, Markussen T, Wessel Ø, Cuenca A, Nyman IB, Olsen AB, Tengs T, Dahle MK, Rimstad E: **Molecular and antigenic characterization of Piscine orthoreovirus (PRV) from Rainbow Trout (*Oncorhynchus mykiss*)**. *Viruses* 2018, **10**:170.
43. Kuehn R, Stoeckle BC, Young M, Popp L, Taeubert J-E, Pfaffl MW, Geist J: **Identification of a piscine reovirus-related pathogen in proliferative darkening syndrome (PDS) infected brown trout (*Salmo trutta* fario) using a next generation technology detection pipeline**. *PLoS One* 2018, **13**:e0206164.
44. Adamek M, Hellmann J, Flamm A, Teitge F, Vendramin N, Fey D, Riße K, Blakey F, Rimstad E, Steinhagen D: **Detection of piscine orthoreoviruses (PRV-1 and PRV-3) in Atlantic salmon and rainbow trout farmed in German**. *Transbound Emerg Dis* 2019, **66**:14-21 http://dx.doi.org/10.1111/tbed.13018.
45. Cartagena J, Tambley C, Sandino AM, Spencer E, Tello: **Detection of piscine orthoreovirus in farmed rainbow trout from Chile**. *Aquaculture* 2018, **493**:79-84.
46. Bohle H, Bustos P, Leiva L, Grothusen H, Navas E, Sandoval A, Bustamante F, Montecinos K, Gaete A, Mancilla M: **First complete genome sequence of piscine orthoreovirus variant 3 infecting coho salmon (*Oncorhynchus kisutch*) farmed in southern Chile**. *Genome Announc* 2018, **6** e00484-18.
47. Miller KM, Günther OP, Li S, Kaukinen KH, Ming TJ: **Molecular indices of viral disease development in wild migrating salmon**. *Conserv Physiol* 2017, **5** cox036.
48. Di Cicco E, Ferguson HW, Kaukinen KH, Schulze AD, Li S, Tabata A, Günther OP, Mordecai G, Suttle CA, Miller KM: **The same strain of Piscine orthoreovirus (PRV-1) is involved with the development of different, but related, diseases in Atlantic and Pacific Salmon in British Columbia**. *FACETS* 2018, **3**:599-641.

Council

CNL(06)48

Resolution by the Parties to the Convention for the Conservation of Salmon in the North Atlantic Ocean to Minimise Impacts from Aquaculture, Introductions and Transfers, and Transgenics on the Wild Salmon Stocks

The Williamsburg Resolution

(Adopted at the Twentieth Annual Meeting of NASCO in June 2003
and amended at the Twenty-First Annual Meeting of NASCO in June 2004
and at the Twenty-Third Annual Meeting of NASCO in June 2006)

CNL(06)48

Resolution by the Parties to the Convention for the Conservation of Salmon in the North Atlantic Ocean To Minimise Impacts from Aquaculture, Introductions and Transfers, and Transgenics on the Wild Salmon Stocks

The Williamsburg Resolution

(Adopted at the Twentieth Annual Meeting of NASCO in June 2003 and amended at the Twenty-First Annual Meeting of NASCO in June 2004 and at the Twenty-Third Annual Meeting of NASCO in June 2006)

The Parties,

NOTING the provisions of the Convention for the Conservation of Salmon in the North Atlantic Ocean of 2 March 1982 (the "Convention"), which seeks to promote the conservation, restoration, enhancement and rational management of salmon stocks;

WELCOMING the achievements in salmon conservation by the Parties to the Convention, within the framework of the Convention, and the role of the North Atlantic Salmon Conservation Organization (the "Organization") therein;

NOTING that NASCO and its Contracting Parties have agreed to apply the Precautionary Approach to the conservation of salmon and acknowledging the need for measures taken in accordance with this Resolution to be consistent with the Precautionary Approach;

AWARE of the need for cooperation between the Parties in order to maintain and to restore the wild salmon stocks, and promote sustainable conservation and management of such stocks;

RECOGNISING the benefits, including the socio-economic benefits, which have resulted from the development of salmon aquaculture;

CONSCIOUS of the threats to the wild stocks of salmon from different human activities, including possible adverse effects from aquaculture, introductions and transfers and transgenics;

RECOGNISING that in order to protect wild salmon stocks from adverse impacts that can or might be caused by aquaculture, introductions and transfers, and transgenics, there is a need to take into account local conditions in determining appropriate management measures;

DESIRING to minimise the possible adverse impacts of aquaculture, introductions and transfers and transgenics on the wild stocks and noting the earlier initiatives taken by the Organization in this respect;

RESOLVE as follows:

ARTICLE 1

Cooperation between the Parties

The Parties shall cooperate in order to minimise adverse effects to the wild salmon stocks from aquaculture, introductions and transfers and transgenics.

ARTICLE 2

Definitions

For the purposes of this Resolution definitions are as given in Annex 1.

ARTICLE 3

Burden of Proof

Each Party, in accordance with the Precautionary Approach, should require the proponent of an activity covered by this Resolution to provide all information necessary to demonstrate that the proposed activity will not have a significant adverse impact on wild salmon stocks or lead to irreversible change.

ARTICLE 4

Risk Assessment

Risk assessment is integral to the implementation of the Precautionary Approach and serves to promote transparency in the decision-making process. Risk assessment should include identification of options and consideration of mitigation measures. The Parties should develop and apply appropriate risk assessment methodologies in considering the measures to be taken in accordance with this Resolution.

ARTICLE 5

Measures to Minimise Impacts of Aquaculture and Introductions and Transfers

Each Party shall take measures, in accordance with Annexes 2, 3 and 4 to this Resolution, to:

- minimise escapes of farmed salmon to a level that is as close as practicable to zero through the development and implementation of action plans as envisaged under the Guidelines on Containment of Farm Salmon (CNL(01)53);
- minimise impacts of ranched salmon by utilizing local stocks and developing and applying appropriate release and harvest strategies;
- minimise the adverse genetic and other biological interactions from salmon enhancement activities, including introductions and transfers;
- minimise the risk of disease and parasite transmission between all aquaculture activities, introductions and transfers, and wild salmon stocks.

Movements into a Commission area of reproductively viable Atlantic salmon or their gametes that have originated from outside that Commission area should not be permitted.

ARTICLE 6

Non-Indigenous Fish

No non-indigenous fish should be introduced into a river containing Atlantic salmon without a thorough evaluation of the potential adverse impacts on the Atlantic salmon population(s) which indicates that there is no unacceptable risk of adverse ecological interactions.

Introductions into any Commission area of reproductively viable non-indigenous anadromous salmonids or their gametes should not be permitted.

ARTICLE 7

Transgenic Salmonids

The Parties should apply the Guidelines for Action on Transgenic Salmon, CNL(97)48 (Annex 5), to protect against potential impacts from transgenic salmonids on wild salmon stocks. In view of the current lack of scientific knowledge on the impact of transgenic salmonids on wild salmon stocks, the use of transgenic salmonids should be considered a high-risk activity. There should be a strong presumption against any such use.

ARTICLE 8

River Classification and Zoning

For the purposes of developing management measures concerning aquaculture and introductions and transfers, Parties should, as appropriate, develop and apply river classification and zoning systems. Details of such systems should be established in accordance with the guidance in Annex 6.

ARTICLE 9

Mitigation and Corrective Measures

Where significant adverse impacts on wild salmon stocks are identified, the Parties should initiate corrective measures without delay and these should be designed to achieve their purpose promptly.

Mitigation measures can include activities to safeguard against potential future impacts (e.g. contingency planning, gene banks).

ARTICLE 10

Implementation

In order to have confidence that the wild stocks are protected from irreversible genetic change, from significant ecological impacts and from significant impacts of diseases and parasites, full implementation of the measures in this Resolution and its Annexes is essential. Local conditions may warrant consideration of stronger measures. All measures should be regarded as adaptable to improved salmon aquaculture technologies and methodologies (e.g. use of sterile fish, lice vaccines, etc.)

Where detailed agreements are developed by a regional Commission of NASCO in support of this Resolution, they will be appended. Appendix 1 indicates the current situation within the North American Commission. Appendix 2 contains a Memorandum of Understanding between Canada and the USA intended to reconcile the differences between the methods used to authorise introductions and transfers in the two countries. Any further guidelines to assist in implementing this Resolution will be annexed.

Each Party shall report annually to the Organization on the measures adopted and actions taken under Articles 5, 6, 7 and 9.

ARTICLE 11

Research and Development

Each Party should encourage research and data collection in support of this Resolution (as detailed in Annex 7) and should take steps to improve the effectiveness of the measures contained in this Resolution.

Each Party shall report annually to the Organization on the research and development carried out.

ARTICLE 12

Dissemination of Information

Educational materials should be developed and distributed to increase awareness of the risks that introductions and transfers of aquatic species may pose to wild salmon stocks and the need for the measures that control these activities.

Annex 1

Definitions relating to Salmon Aquaculture, Introductions and Transfers and Transgenics

Term	**Definition**
Containment	Physical containment: Prevention of escapes of farmed salmon into the freshwater and marine environments. Containment of diseases and parasites: Implementation of measures to prevent the transfer (spread) of diseases and parasites between aquaculture facilities and wild fish.
Epidemiological zones	Zones defined by lack or presence of specific pathogens.
Introduction	The intentional or accidental release of a species into an environment outside its native or natural range.
Mitigation stocking	Stocking conducted as a voluntary action or statutory requirement to mitigate lost production due to an activity that cannot be removed.
Non-indigenous	Not originating or occurring naturally in a particular environment; introduced outside its native or natural range.
Population	A group of organisms of a species occupying a specific geographical area.
Rehabilitation	The rebuilding of a diminished population of a finfish species, using a remnant-reproducing nucleus, toward the level that its environment is now capable of supporting.
Restoration	The re-establishment of a finfish species in waters occupied in historical times.
Risk assessment	The process of identifying and describing the risks of activities having an impact on fisheries resources, habitat or aquaculture before such activities take place; the process of identifying a hazard and estimating the risk presented by the hazard, in either qualitative or quantitative terms.
River classification	Designation of a river or watershed according to the degree of human impact.
Salmon aquaculture*	The culture or husbandry of Atlantic salmon, including salmon farming, salmon ranching and salmon enhancement activities.
Salmon enhancement	The augmentation of wild stocks in individual river systems by the release of Atlantic salmon at different stages in their life-cycles.
Salmon farming	Production system which involves the rearing of Atlantic salmon in captivity for the duration of their life-cycle until harvested.
Salmon ranching*	The release of reared Atlantic salmon smolts with the intention of harvesting all that return.
Salmonid*	All species and hybrids of the family Salmonidae.

Stock* (Management unit)	A management unit comprising one or more salmon populations.
Stock (local)	A stock from a river or tributary in close proximity to the river to be stocked. This may refer to rivers with a common bay of entry or closely related catchment areas.
Stocking	The deliberate release of Atlantic salmon into the wild at any stage of their life-cycle for enhancement, mitigation, restoration, rehabilitation or ranching purposes.
Transfer*	The deliberate or accidental transport of Atlantic salmon within their native or natural range.
Transgenic	An organism that has been modified by genetic engineering to contain DNA from an external source.
Wild salmon	Fish that have spent their entire life-cycle in the wild and originate from parents which were also spawned and continuously lived in the wild.
Zone	Geographic area reflective of the degree of degradation or manipulation of wild Atlantic salmon populations.

* for the purposes of the NAC Protocols, a different definition is used, see NAC(94)14

Annex 2

General Measures to Minimise Impacts

This Annex is designed to provide guidance to NASCO's Parties on minimising impacts of salmon aquaculture and introductions and transfers on wild salmon stocks. The guidelines will be regularly reviewed and updated as appropriate in the light of new scientific information and changing technologies and methodologies.

1. Siting and Operation of Aquaculture Activities

1.1 Salmon aquaculture facilities should only be located where hydrographical, epidemiological, biological and ecological standards can be met. Factors which may be taken into consideration include: availability of water supply and receiving waters for discharge; water quality and exchange; water depth; site protection; separation distances between aquaculture facilities; and distance from salmon rivers. Further guidance on containment is provided in Annex 3.

1.2 Consideration should be given to the establishment of "wild salmon protection areas" where salmon aquaculture is restricted or prohibited. Such protection areas may minimise genetic, disease, parasite and environmental impacts.

1.3 The designation of "aquaculture regions", where all the steps in the production process are carried out and which are separated from similar regions by areas without aquaculture, could also be considered. Such regions could provide a framework for management of the aquaculture industry and could assist in controlling the spread of fish diseases and parasites.

1.4 The separation distance between aquaculture facilities at marine sites should be based on a general assessment of local conditions. Wherever possible, different generations of salmon should be reared in separate locations. As local conditions permit, a fallowing regime should be practised as a means of minimising outbreaks of disease and parasites. Aquaculture production should be adapted to the holding capacity of an individual site and should not exceed density levels based on science and good husbandry practices.

1.5 Dead and dying fish should be removed immediately from aquaculture production facilities, taking into account worker safety, and weather and sea state conditions. Mortalities should be disposed of, along with waste materials, in an approved manner. Procedures should be established to address the effective removal and disposal of infectious material. Contingency plans should be established for the disposal of mortalities from emergency situations.

1.6 Depending on local regulations and protocols, tagging or marking or inventory tracking systems will be used in order to facilitate the identification of farmed salmon in the wild and their separation from wild fish, to determine the source of escapes and to assess the interactions of escaped farmed salmon with the wild stocks. These systems could be coupled with river monitoring and recapture systems that allow holding and close examination of returning fish in the rivers.

2. Diseases and Parasites

2.1 All steps in the aquaculture production process from hatchery to processing plant, including transportation of live fish materials, should be conducted in accordance with appropriate fish health protection practices. This includes attention to the application of appropriate husbandry techniques to minimise the risk of disease in the reared stock. These might include vaccination, use of optimal stocking densities, careful handling, frequent inspection of fish, proper diet and feeding regimes, avoidance of unnecessary disturbance of the fish, detailed health inspections, disinfection of transportation equipment and the use of foot baths at production facilities.

Specified diseases and parasites

2.2 Mapping of the presence of serious diseases and parasites should be used to establish epidemiological zones (either with or without specific pathogens). Management measures within these zones should include monitoring to confirm the disease status of a zone and eradication. These zones should be established for at least the following diseases: Viral Haemorrhagic Septicaemia (VHS), Infectious Haematopoietic Necrosis (IHN), Infectious Salmon Anaemia (ISA) and the parasite *Gyrodactylus salaris*.

2.3 Movements of live salmonids and their eggs from a zone where any of the specified diseases is present to a zone free of these diseases should not be permitted. However, movements of salmonid eggs may be permitted where there is minimal risk of transmission of the specified diseases or parasite.

2.4 A list of the prevailing infectious diseases and parasites, and the methods in practice for their control, should be maintained by the appropriate authorities.

Unknown diseases and parasites

2.5 Procedures should be established for the early identification and detection of, and rapid response to, an outbreak of any new disease or parasitic infection likely to affect Atlantic salmon. These procedures should include the establishment of official surveillance services responsible for the monitoring of the health of both wild and farmed fish. The procedures should also demand the rapid introduction of restrictions on the movement of salmonids in the case of an outbreak of a disease or parasitic infection until the status of the disease or parasitic infection is known.

2.6 Even with such procedures, it may not be possible to respond in time to prevent the spread of such a disease or parasitic infection. It is recommended that the Contracting Parties, when establishing or reviewing rules on transfers of fish, consider additional protective measures such as:

- **the establishment of zones:** the intention of such zones, between which the movement of live salmonid fish and their gametes should be restricted and which might be defined using geographical, climatic or biological criteria, is to limit the spread of parasites and diseases to wild stocks;

- **the movement of salmonids:** for disease prevention purposes, the trade in eggs is safer than the trade in live fish. It must, however, be recognised that some serious diseases, such as IPN, BKD and IHN, may be transferred with eggs and ovarian fluid;

- **diseases of wild fish:** there is a need to strengthen and amend disease controls to minimise disease transfer between aquaculture activities and wild fish.

Health inspections of donor facilities

2.7 Movements of live salmonids and their eggs from hatcheries to areas containing Atlantic salmon stocks, or to facilities where there is a risk of transmission of infection to such areas, should only take place from facilities where regular inspections have not detected significant diseases and parasites.

Use of medicines and disinfectants

2.8 Medicines and disinfectants to control diseases and parasites must be used with care and in accordance with the manufacturer's instructions and any Codes of Practice, and in compliance with regulatory authorities.

3. Gene Banks

3.1 Various activities may result in serious adverse impacts on salmon stocks and strains such that the potential exists that a portion of the salmon genome is lost. In order to protect against this possibility, Parties should consider the establishment of gene banks for stocks that are in danger of extirpation. This could provide a source of genetic material for future restoration programmes.

Annex 3

Guidelines on Containment of Farm Salmon, CNL(01)53

Section 1: Introduction

1.1 The North Atlantic salmon farming industry and the North Atlantic Salmon Conservation Organization (NASCO) have established a Liaison Group. This Liaison Group recognised the importance of conserving and enhancing wild salmon stocks and of supporting a sustainable salmon farming industry and is seeking to establish mutually beneficial working arrangements in order to make recommendations on wild salmon conservation and sustainable farming practices. To this end the Liaison Group has developed guidelines on containment to apply throughout the NASCO Convention area.

1.2 Both Parties recognise that a number of guidelines and measures, outlined below, should apply to all salmon aquaculture activities. The Liaison Group should be updated annually on progress on the development of parallel measures in relation to these activities.

Section 2: Objectives

2.1 These guidelines are intended to result in the prevention of escapes of farmed salmon in the freshwater and marine environments.

Section 3: Site Selection

3.1 Sites shall be selected having regard to the capability of the equipment to withstand the weather and other environmental conditions likely to be experienced at that site;

3.2 In the interest of avoiding collision damage, equipment shall comply with the relevant national and international regulations regarding navigation and marking;

3.3 Careful consideration shall be given to the siting of land-based facilities, so as to minimise the risk of escapes from these facilities.

Section 4: Equipment and Structures

4.1 Nets, cages and mooring systems shall be designed, constructed and deployed to prevent escapes, having proper regard to the prevailing conditions at the site. Mooring systems should have a significant in-built safety margin;

4.2 Nets and cages should be marked with an identification number; adequate records of each net and cage in use should be maintained in order to assess its fitness for purpose;

4.3 Nets shall be: compatible with the cages with which they will be used; secured to the cage collar so that the collar alone bears the strain; and adequately UV-protected. Net weights shall be installed in such a way as to prevent damage to the nets;

4.4 Tank systems shall be designed to contain fish effectively and to minimise the chances of fish escaping. Where the outflow from tanks passes into a settling pond, the outflow from the settling pond should incorporate a screen of suitable size and construction to minimise the chances of fish escaping;

4.5 Effective predator deterrence methods shall be implemented as appropriate; these should be up-graded as improved, site-appropriate and cost-effective systems of proven efficacy become available; records of predator attacks that may have caused escapes should be maintained for audit;

4.6 Salmon farming systems should be upgraded as improved, site-appropriate and cost-effective systems of proven efficacy become available.

Section 5: Management System Operations

5.1 Farm management procedures shall ensure supervision by appropriately trained, qualified or experienced personnel. There is a need for constant vigilance during operations that could result in escapes;

5.2 Procedures shall be adopted to ensure that escapes are prevented during movement and handling of stocks (e.g. during stocking, counting, grading, transport, transfers, treatment and harvesting of fish), and during net changes and cleaning;

5.3 Regular preventative maintenance, inspection and repair procedures shall be adopted in order to prevent escapes;

5.4 Stress testing of all nets in use shall be conducted on a regular basis and testing protocols, minimum breaking strengths and thresholds for net replacement should be specified in action plans. Records of the results of the tests shall be retained throughout the period the net is in use;

5.5 When it is necessary to tow cages, great care shall be taken to avoid damage to the nets;

5.6 Storm preparation procedures shall be developed to minimise the risk of damage from storms detailing the actions to be taken to ensure that the site is made ready; after each storm all nets, cages and mooring systems shall be inspected for damage;

5.7 Vessels shall be operated so as to minimise the risk of accidental damage to the equipment;

5.8 Where practicable, security systems should be installed so as to deter acts of vandalism and malicious damage.

Section 6: Verification

6.1 Management systems should include as a minimum all details of introductions, grading, transfers, treatments, handling or any other incident or occurrence that may have led to an escape. These details shall be recorded and retained for audit. Detailed records should allow estimates of escapes to be made. It is recognised that not all discrepancies will be the result of escapes;

6.2 When an event occurs which leads to an escape defined as significant under the action plan, the operator shall advise the appropriate authorities immediately;

6.3 A site-specific contingency plan shall be developed for use when an event occurs which may have led to an escape defined as significant under the action plan. The contingency plan shall include details of the method of recapture to be used and the area and timeframe over which a recapture programme would apply. Efforts shall be made to recapture farmed salmon immediately provided that this is practicable and does not adversely affect wild Atlantic salmon populations;

6.4 Action plans should require appropriate authorities to take all reasonable efforts to issue permits for facilitating the contingency plans developed for each farm.

Section 7: Development of Action Plans

7.1 Each jurisdiction should draw up a national action plan, or regional plans, at the earliest opportunity, based on these guidelines. The action plan is the process through which internationally agreed guidelines on containment would be implemented at national or regional level through existing or new voluntary codes of practice, regulations, or a combination of both;

7.2 Each action plan should:

7.2.1 create a systematic basis for minimising escapes so as to achieve a level of escapes that is as close to zero as is practicable;

7.2.2 include a mechanism for reporting information on the level and causes of escapes;

7.2.3 include a mechanism for reporting and monitoring in order to assess compliance and to verify the plan’s efficacy;

7.2.4 identify areas for research and development.

7.3 The action plan should be based on co-operation between industry and the relevant authorities and should include the allocation of responsibilities under the plan(s) and a timetable for implementation.

Section 8: Reporting to the Liaison Group

8.1 Each jurisdiction should advise the Liaison Group annually on progress in implementing its action plan(s).

Section 9: Revision

9.1 These guidelines shall be subject to revision, with the agreement of the Liaison Group, to take account of new scientific, technical and other relevant information.

Annex 4

Guidelines for Stocking Atlantic Salmon

I. Introduction

The term “stocking” is defined as “the deliberate release of Atlantic salmon into the wild at any stage of their life-cycle for enhancement, mitigation, restoration, rehabilitation or ranching purposes,” as defined in Annex 1 of this Resolution.

Stocking is widely carried out by many government and private entities for the reasons listed above. While these programmes are sometimes successful, it is now known that stocking can also have negative impacts on wild salmon populations and other species and that poor hatchery practices may negatively impact the characteristics of the wild salmon population that we wish to conserve. Potential consequences include: depression of the survival and abundance of indigenous populations and straying of stocked fish into nearby rivers. There is thus a need to consider fully the risks as well as the benefits arising from stocking.

Codes of Practice for stocking are widely available as are very detailed stocking manuals. These codes and manuals are designed to address issues of local or national relevance.

The present document is designed to provide guidance to NASCO’s Parties on applying the Precautionary Approach to the authorisation and conduct of any stocking of Atlantic salmon into the wild. The guidelines will be regularly reviewed and updated as appropriate in the light of new scientific information.

II. Rationale for Stocking

There are many possible causes for decline of Atlantic salmon populations and stocking may not be an appropriate solution. Where a river is at or close to carrying capacity there may be little or no benefit from stocking. In addition, stocking is carried out for ranching purposes.

NASCO’s Guidelines on the Use of Stock Rebuilding Programmes, CNL(04)55, provide guidance on compliance assessment, evaluation of the problem, development of a management plan and monitoring and evaluation of progress. In addition, to assist its Parties in applying the Precautionary Approach, NASCO has developed a Decision Structure for Management of North Atlantic Salmon Fisheries, CNL31.332, and a Plan of Action for the Protection and Restoration of Atlantic Salmon Habitat, CNL(01)51. It is recommended that these documents be consulted in determining if stocking is an appropriate management response to a perceived problem.

In accordance with the Precautionary Approach appropriate risk assessment methodology should be developed and applied by the Parties to proposals for stocking. Proponents must provide all information necessary to demonstrate that a proposed stocking activity will not have a significant adverse impact on wild salmon populations or have an unacceptable impact on the ecosystem.

III. Guidelines for Conducting Stocking

A. Definition of river classes

For the purposes of these guidelines, three types of river are defined on the basis of the extent to which salmon and their habitats have been affected by human activities: Class I, Class II and Class III.

Rivers are classified as Class I when they are pristine. Class I rivers have no significant human-induced habitat alterations, and neither any history of introductions or transfers of fish into the watersheds nor any fish-rearing operations in the watersheds, and no aquaculture has been conducted in marine cage culture within a specified distance of the river.

Rivers are classified as Class II if one or more of the following conditions occur: the habitat has been altered; non-indigenous wild or hatchery-reared Atlantic salmon populations have been released; or aquaculture has been conducted in marine cage culture within a specified distance of the river. Non-indigenous species may be present in land-based facilities. Introduced species such as rainbow trout would be treated as indigenous if a population has been established for 10 or more years. Many rivers around the North Atlantic will belong to this class.

Rivers are classified as Class III if habitats have been altered or if fish communities are destabilised, such as the loss of component populations, or non-indigenous species are present.

B. Guidelines applicable to all rivers

1. Atlantic salmon of European origin, including Icelandic origin, should not be released in the North American Commission area and Atlantic salmon of North American origin should not be released in the North-East Atlantic Commission area.

2. Prior to any transfer of eggs, juveniles or broodstock, health inspections of the donor facility will be undertaken. No fish will be transferred from the facility to other facilities or released into waters within the NASCO Convention area if emergency diseases, as defined by national, state, or provincial authorities, are detected at the donor facility.

3. Fish with restricted diseases, as defined by national, state, or provincial authorities, may be transferred between facilities or released into waters within the NASCO Convention area, provided that this does not result in changing the disease status of the receiving facility or waters. These transfers must also comply with national, state or provincial regulations.

4. Where hatchery rearing programmes are used in support of stocking programmes specialist advice should be sought in order to minimise genetic impacts in resultant generations. Hatchery rearing programmes should comply with the following measures:

    (a) Wherever possible, use eggs or progeny of wild fish;

(b) Ensure that wild fish removal will not significantly adversely impact on donor population(s);

(c) Derive broodstock from all phenotype age groups and components of a donor population[1];

(d) Careful consideration must be given to the size of the effective breeding population and its management. Geneticists have generally recommended that a minimum of a random group of 50 pairs be used for each cohort. However, that advice may not always be appropriate. For rehabilitation projects, where wild populations may be severely limited (i.e. remnant populations and live gene bank situations), it is essential that specialist advice be sought in order to minimise genetic impacts in resultant generations;

(e) Ideally, for genetic reasons, each male should be mated separately with a female so that the contribution of all males is equal (i.e. do not mix milt of males prior to fertilization, which can promote sperm competition);

(f) Where a river, or tributary, has completely lost its salmon population(s), several populations might be used for stocking to provide wide genetic variability for natural selection. However, genetic advice should be sought;

(g) Where there are suitable areas of unoccupied habitat, stocking with eggs or fry is recommended as stocked populations will benefit from natural selection during the juvenile phase.

5. Stocking and management programmes should take account of the fact that most Atlantic salmon in rivers are structured into a number of populations.

C. Guidelines applicable to Class I rivers

1. *General*

(a) No Atlantic salmon reared in a fish culture facility are to be released into a Class I river, another river which has its estuary within an appropriate, specified distance of a Class I river, or a marine site that is within an appropriate, specified distance of a Class I river;

(b) In general, no non-indigenous[2] Atlantic salmon are to be released into a Class I river.

2. *Rehabilitation*

(a) Generally, rehabilitation is not necessary in Class I rivers. However, where human-induced or natural events impact on a Class I river the preferred methods are to improve degraded habitat and to ensure escapement of sufficient spawners through fisheries management.

---

[1] The term 'population' here is used to denote a genetic population, i.e. populations are groups of animals within which mating is more or less random and among which interbreeding is more or less constrained.

[2] Not belonging to the local genetic population.

3. *Restoration (or establishment) of Atlantic salmon in a river or part of a watershed where there are no salmon*

(a) Expert advice should be sought to identify the best option, based on the genetic and ecological characteristics of the donor population or the habitat characteristics of the donor stream;

(b) Consideration should be given to the impacts on the existing fish community and fisheries.

4. *Ranching*

(a) Atlantic salmon ranching should only take place at release sites located greater than an appropriate, specified distance from the estuary of a Class I river and if it is demonstrated that the activity will not significantly affect wild Atlantic salmon populations.

D. Guidelines applicable to Class II rivers

1. *General*

(a) Atlantic salmon, with the exception noted in III-B-1 of these guidelines, may be considered for stocking, if fish health and genetic protocols are followed and risk assessments show, on the basis of careful ecological impact evaluation, that negative impacts on local populations of Atlantic salmon will be minimal. Use of non-indigenous fish should only be used as a last resort.

2. *Rehabilitation*

(a) The preferred methods are to improve degraded habitat and to ensure escapement of sufficient spawners through fisheries management;

(b) If further measures are required, residual population(s) of wild fish should be used. If the residual populations are too small, thorough genetic and ecological assessments should be carried out to identify the best option for rehabilitation purposes.

3. *Restoration (or establishment) of Atlantic salmon in a river or part of a watershed where there are no salmon*

(a) For restoration, use a population(s) from a tributary within the same watershed or from a nearby river(s) that has similar genetic and ecological characteristics to the original population(s);

(b) For establishment, use a population(s) from a tributary within the same watershed or from a nearby river(s) that has similar habitat characteristics;

(c) Consideration should be given to the impacts on the existing fish community and fisheries.

4. ***Ranching***

(a) Atlantic salmon ranching should only take place at release sites located greater than an appropriate, specified distance from the estuary of a Class II river and if it is demonstrated that the activity will not significantly affect wild Atlantic salmon populations.

E. Guidelines applicable to Class III rivers

1. ***General***

(a) Atlantic salmon, with the exception noted in item III-B-1 of these Guidelines, may be considered for stocking, if fish health and genetic protocols are followed and risk assessments show, on the basis of careful ecological impact evaluation, that negative impacts on local populations of Atlantic salmon will be minimal.

2. ***Rehabilitation***

(a) The preferred methods are to improve degraded habitat and to ensure escapement of sufficient spawners through fisheries management;

(b) Rehabilitation may be achieved by stocking cultured fish.

3. ***Establishment or restoration of Atlantic salmon in a river or part of a watershed where there are no salmon***

(a) For restoration, use a population(s) from a tributary within the same watershed or from a nearby river(s) that has similar genetic and ecological characteristics to the original population(s);

(b) For establishment, use a population(s) from a tributary within the same watershed or from a nearby river(s) that has similar habitat characteristics;

(c) Consideration should be given to the impacts on the existing fish community and fisheries.

4. ***Ranching***

(a) Ranching of Atlantic salmon should only be permitted if it is demonstrated that the activity will not significantly affect wild Atlantic salmon populations.

IV. Guidelines for Authorising Stocking

A. Introduction

Both proponents and agencies responsible for managing Atlantic salmon must ensure that the risk of adverse effects on wild Atlantic salmon populations from stocking is minimised.

B. Responsibility of proponent of stocking

1. Proponents must submit an application for stocking of Atlantic salmon to the permit-issuing agency (see Box 1).

2. The application should provide a full justification for stocking and sufficient documentary evidence to allow for an evaluation of the impacts of the proposed stocking activities on the wild Atlantic salmon and its habitats.

3. The lead-time required for notice and justification of stocking will be determined by the permit-issuing agency.

4. Proponents must report all stockings that are conducted.

C. Responsibility of those with the authority to issue permits

1. Enact laws to protect wild populations of Atlantic salmon and prevent the release of Atlantic salmon that will significantly affect the productivity of existing wild Atlantic salmon populations.

2. Draw the Guidelines to the attention of all proponents of stocking at the application stage.

3. Establish, maintain, and operate a permit system and inventory for all stockings of Atlantic salmon.

4. Enact regulations to control the stocking of Atlantic salmon.

5. Establish a formal scientific evaluation process to review all applications (private and government agencies) for the stocking of Atlantic salmon and recommend conditional acceptance or rejection of the proposed stocking(s) based on the potential impact on the ecosystem.

6. Establish an evaluation process to determine the effectiveness of stocking activities and their impacts on wild Atlantic salmon populations.

7. Within a class of rivers, each agency may be more restrictive in setting salmon stocking requirements.

8. Submit to NASCO, as requested, information of a scope to be determined by the Council in relation to the application of these Guidelines.

Box 1. Guidance for proponents in the preparation of stocking proposals

The following information should be provided to the permit-issuing agency with all applications to stock Atlantic salmon so as to enable the risk of adverse effects from the proposed activities on wild Atlantic salmon populations to be evaluated.

(1) Name the population and/or strain and, where available, its genetic characteristics, and include:

  (a) Time and quantity of stocking;

  (b) A list of anticipated future stockings;

  (c) A list of previous stockings.

(2) Area, place, river or hatchery from which the fish will be obtained.

(3) Proposed place of release and any interim rearing sites.

(4) Disease status of donor hatchery, river or other location from which fish are obtained.

(5) Disease status of recipient facility or stream (where available).

(6) Objectives of the stocking and the rationale for not using a local population (if such use is not proposed).

(7) Details of the available biological characteristics of the donor population. This would include such characteristics as run timing, time of spawning, age-at-maturity, size-at-age, etc. and potential for competition with local populations of Atlantic salmon in the recipient waters or nearby waters.

(8) Information on similar stockings.

(9) Proposed procedure for transportation from donor to recipient site.

(10) Measures to be taken to prevent transmission of disease agents and to reduce the risk of escape of fish.

(11) Species composition at proposed site of introduction and adjacent rivers.

(12) Climatic regime and water chemistry, including pH of waters at the site of proposed introduction and of adjacent rivers.

(13) Potential of stocked fish to disperse to nearby streams.

(14) A bibliography of pertinent literature.

(15) A plan for monitoring, in order to assess how successful stocking has been.

Annex 5

NASCO Guidelines for Action on Transgenic Salmonids, CNL(04)41

THE PARTIES to NASCO are aware of the development of transgenic salmonids. While there may be benefits from the introduction of such salmonids if, for example, they could not interbreed with wild stocks the Council recognises that there are also risks which may lead to irreversible genetic changes and ecological interactions.

The Council considers that there is an urgent need to take steps to ensure the protection of the wild stocks and has therefore agreed to cooperate to develop means such that transgenic salmonids cannot impact upon wild salmon stocks. The following specific steps are agreed.

The Parties will:

a) advise the NASCO Council of any proposal to permit the rearing of transgenic salmonids and provide details of the proposed method of containment and other measures to safeguard the wild salmon stocks;

b) take all possible actions to ensure that the use of transgenic salmonids, in any part of the NASCO Convention Area, is confined to secure, self-contained, land-based facilities;

c) inform their salmon producers of the potentially serious risks to wild stocks of this development and consult with the salmon farming industry on this matter through the Liaison Group established between NASCO and the international salmon farming industry;*

d) take steps, as appropriate, to improve knowledge on the potential impacts of transgenic salmonids on the wild salmon stocks and their habitat;

e) examine the trade implications associated with transgenic salmonids in accordance with World Trade Organization Agreements and other instruments of international law.

Furthermore, those Parties to NASCO that are also Parties to the Cartagena Protocol on Biosafety to the Convention on Biological Diversity should take into account the provisions of that Protocol.

*Note: At its Seventeenth General Meeting in Galway, Ireland, in September 1996, the International Salmon Farmers' Association (ISFA) adopted its Policy on Transgenic Salmon, which states that "In accordance with sound environmental practices, the ISFA firmly rejects transgenic salmon production".

Annex 6

River Classification and Zoning

For the purpose of developing management measures concerning aquaculture, introductions and transfers, Contracting Parties should classify their Atlantic salmon rivers. Where appropriate, consideration should be given to grouping neighbouring or biologically (or otherwise) similar river systems into complementary management zones. River classification and zonation systems are useful to identify specific rivers and/or areas that need special protection. For example, rivers and/or areas that have been subject to significant enhancement efforts may need to be differentiated from rivers and/or areas that have not. This could allow managers to easily identify the rivers and/or areas where future enhancement efforts may or may not be appropriate.

The NAC Protocols and the NASCO Salmon Rivers Database provide examples of river classification systems. Contracting Parties should consider these examples in developing classification systems that are appropriate to their needs. Parties are further encouraged to work co-operatively in developing such systems (e.g. NEAC Parties could develop a classification system that complements the Water Framework Directive).

In conducting a risk assessment for a proposed aquaculture, or introductions and transfers, activity, the classification of the river(s) and/or zone(s) should be taken into account and class/zone-specific factors should be considered. Furthermore, in developing measures appropriate to each class of river or management zone, it is recognised that local conditions are a very significant factor and should also be considered.

Annex 7

Research and Development and Data Collection

Research and data collection should be carried out, as appropriate, in support of this Resolution. Recognising that research requirements are continually developing, a list of current research areas is identified in this Annex. Where appropriate, successful research results should be taken forward to pilot testing

Areas for research and pilot testing include:

Sterile fish

Methodology and techniques for sterilization are now well developed; research should now focus on developing strains of sterile fish which could perform at a level similar to current strains of fish used in farm production. Trials should be encouraged to evaluate the performance of strains of sterile fish under production conditions.

Tagging and marking

Tagging and marking is being used on a small scale in order to facilitate the identification of farmed salmon in the wild and their separation from wild fish, to determine the source of escapes and to assess the interactions of escaped farmed salmon with the wild stocks. Full evaluation of those trials should be conducted in order to assess effectiveness, the feasibility of large-scale marking, and associated costs. Consideration should also be given to food safety, product quality and animal welfare.

Evaluation of production methods

There should be an ongoing evaluation of current and new production methods and technology (e.g. improved containment techniques, development of suitable strains of sterile fish, development of sea lice vaccines, etc.).

Aquaculture broodstock

Research is recommended on broodstock selection methodology to minimise impacts on wild salmon stocks.

Genetics

Great advances have been made in genetic research in the past decade. These methods should be applied in investigating, in greater detail, interactions between wild salmon and salmon of aquaculture origin, including the extent of hybridization, composition of stocks, and identification of disease strains and appropriate treatment.

Diseases and parasites

The transmission of diseases and parasites between salmon reared in aquaculture and the wild stocks is an area of considerable concern. Research on vectors for transmission, and methods to prevent and control disease and parasite outbreaks in wild salmon and in aquaculture, should be encouraged.

Interactions

Information should be collected and analyzed on the extent of intermingling in rivers and at sea between wild salmon and salmon of aquaculture origin.

Risk assessment frameworks

There has been considerable activity in the development of risk assessment frameworks. There remains a need to identify the appropriate factors to be included in a risk assessment in order to evaluate the potential impacts of aquaculture, introductions and transfers, and transgenics on wild salmon stocks.

Biological impacts

Further work is recommended on biological interactions between wild salmon and salmon of aquaculture origin including competition and behavioural interactions that may affect the viability and success of the wild populations.

Escape prevention

Research into escape detection technologies and improved containment systems should be encouraged.

Appendix 1

North American Commission Protocols for the Introduction and Transfer of Salmonids Summary of Protocols by Zone, NAC(94)14

Note:

This document contains only summary Protocols and should be read in conjunction with document NAC(92)24.

1 ZONING OF RIVER SYSTEMS

The NAC has adopted the concept of Zoning for application of these protocols to the NAC Area. Three zones have been designated based on the degree of degradation or manipulation of the wild Atlantic salmon populations (Figure 1). The NAC recognizes that Atlantic salmon populations have been variously affected by human activities. These activities include over-harvesting, selective fishing, habitat degradation, mixing of stocks, introduction of non-indigenous fish species, and spreading fish diseases. Atlantic salmon stocks in northern areas (Zone I) have generally been least affected, and those stocks in the southern area (Zone III) have been most affected, by humans.

In order to allow operational flexibility within a Zone, river systems have been classified as Class I, II, or III rivers. Generally, rivers will have the same classification as the Zone in which they occur. For example, in Zone II, river systems will be mainly categorized as Class II. However, a river system may be assigned a higher classification than the Zone in which it is located (e.g. Class I river in Zone II) to allow additional protection for valuable Atlantic salmon stocks. In extenuating circumstances and if a river is sufficiently isolated from other rivers, it is acceptable to have a river with a lower classification than the Zone in which it is located (e.g. Class III rivers within Zone II or Class II rivers in Zone I).

All rivers are generally classified at the same level as the Zone designation. Member countries wishing to change the location of Zone boundaries or to have rivers of a lower classification within a Zone should submit their recommendations, with scientific justifications, to NAC.

2 DESCRIPTION OF ZONES

Zone I: Geographic Area: Northern Quebec, Labrador, Anticosti Island and the major salmon-producing rivers in Newfoundland north of Cape Ray and west of Cape Saint John; namely: all rivers from Cape Ray to Cape Anguille and in Bay of Islands, Lomond River, Portland Creek, River of Ponds, Torrent River, Castors River, St. Genevieve River, Western Arm Brook, Salmon River (Hare Bay), Northeast River (Canada Bay), and Main River (Sop's Arm).

Rivers are classified primarily as Class I. They are pristine rivers with no significant man-made habitat alterations, no history of transfers of fish into the watersheds, and no fish-rearing operations in the watersheds.

Zone II: Geographic Area: Quebec rivers flowing into Gulf of St. Lawrence south of Pte. des Monts, Gaspé region of Quebec, Magdalen Islands, Prince Edward Island, New Brunswick, Nova Scotia, Newfoundland (except rivers designated as Class I rivers, referenced above in description of Zone I) and State of Maine east of Rockland.

Rivers are classified primarily as Class II watersheds in which one or more of the following conditions occur: the habitat has been altered; non-indigenous wild or hatchery-reared Atlantic salmon stocks have been released; or aquaculture has been conducted in marine cage culture. Non-indigenous species may be present in land-based facilities. Introduced species such as rainbow trout would be treated as indigenous if a population has been established for ten or more years.

Zone III: Geographic Area: Lake Ontario, southern Quebec draining to St. Lawrence River, State of Maine west of Rockland, New Hampshire, New York, Connecticut, Massachusetts, New Jersey, Rhode Island, and Vermont.

Rivers are classified primarily as Class III watersheds in which habitats have been altered, or where fish communities are destabilized, or exotic species are present.

3 PROTOCOLS

3.1 Protocols applicable to all three Zones

(1) Reproductively viable strains of Atlantic salmon of European origin, including Icelandic origin, are not to be released or used in Aquaculture in the North American Commission Area. This ban on importation or use of European-origin Atlantic salmon will remain in place until scientific information confirms that the risk of adverse genetic effects on wild Atlantic salmon stocks is minimal.

(2) No live salmonid fishes, fertilized eggs, gametes, or fish products are to be imported from IHN enzootic areas, unless sources have an acceptable history of disease testing demonstrating the absence of IHN (e.g. Great Lakes Fish Health Disease Committee protocol requirements). IHN infected areas currently include State of Washington, Oregon, Idaho, California, Alaska, British Columbia, Japan, and parts of Taiwan and France.

(3) Prior to any transfer of eggs, juveniles or brood stock a minimum of three health inspections of the donor facility will be undertaken during the two-year period immediately preceding the transfer; and

- No fish will be transferred from the facility to other facilities or released in waters within the NAC Area if emergency diseases are detected at a rearing facility (see Annex III, Part II of NAC(92)24);

- Fish with restricted diseases may be transferred or released in the NAC Area provided that this does not result in changing the disease status of the receiving facility or waters. These transfers must also comply with national, state or provincial regulations (see Annex III, Part II of NAC(92)24).

(4) Prior to any movement of non-native fishes into a river system or rearing site inhabited by Atlantic salmon the agency with jurisdiction shall review and evaluate fully the potential for interspecific competition which would adversely impact on the productivity of wild Atlantic salmon populations. Such evaluations should be undertaken, to the extent possible, with information on the river in which the introduction is to occur and from similar situations.

(5) Hatchery rearing programmes to support the introduction, re-establishment, rehabilitation and enhancement of Atlantic salmon should try to comply with the following measures:

(a) Use only F1 progeny from wild stocks;

(b) Derive broodstock from all phenotype age-groups and the entire run of a donor population;

(c) Avoid selection of the "best" fish during the hatchery rearing period; and

(d) During spawning, make only single paired matings from a broodstock population of no less than 100 parents. Should the number of one sex be fewer than 50, the number of spawners of the other sex should be increased to achieve a minimum effective population size (N_e) of 100.

$$N_e = \frac{4N♂N♀}{N♂+N♀}$$

3.2 Protocols applicable to Zone I

Zone I consists of Class I watersheds where every effort must be made to maintain the existing genetic integrity of Atlantic salmon stocks. The following summary protocols apply.

3.2.1 General within Zone I

No Atlantic salmon reared in a fish culture facility are to be released into a Class I river, another river which has its estuary less than 30 km from a Class I river, or a marine site less than 30 km from a Class I river (distances would be measured in a straight line(s) headland to headland).

No non-indigenous fish species, other than Arctic charr and brook trout, or non-indigenous Atlantic salmon stock is to be introduced into a Class I watershed.

3.2.2 Rehabilitation

Fisheries management techniques will be used to ensure sufficient spawners such that spawning escapement exceeds a minimum target level to maintain an effective breeding population.

Habitat that becomes degraded will be restored to the greatest extent possible.

3.2.3 Establishment or re-establishment of Atlantic salmon in a river or part of a watershed where there are no salmon

Use transfers of adults or juvenile salmon from the residual population in other parts of the watershed.

A nearby salmon stock which has similar phenotypic characteristics to the lost stock could be transferred if there is no residual stock in the recipient watershed and provided an effective breeding population is maintained in the donor watershed (See Section 3.1 (5)).

If the biological characteristics of the original stock are not known or there was no previous stock in the recipient watershed, then transfer broodstock or early life stages from a nearby river having similar habitat characteristics.

3.2.4 Aquaculture

(i) Rearing in marine or freshwater cages, or land-based facilities:

- Reproductively viable Arctic charr and brook trout may be reared in marine and freshwater cages and in land-based facilities;

- Rearing of other salmonids or non-indigenous fishes is not permitted in the marine environment within 30 km of a Class I river, in a Class I river, or in a watershed with its estuary less than 30 km from the estuary of a Class I river. (30 km is measured in a straight line(s) headland to headland);

- Rearing of reproductively viable indigenous species and reproductively sterile non-indigenous species is permitted in land-based facilities;

- Reproductively sterile salmonids may be reared in the marine environment, and/or in a watershed with its estuary greater than 30 km from a Class I river, provided that the risk of adverse effects on wild salmon stocks is minimal;

- Natural or man-made ponds which have adequate screening of the outlet and inlet streams, such that the risk of fish escaping is low, can also be treated as land-based facilities.

(ii) Commercial ranching:

- No commercial ranching of salmonids is permitted within 30 km of the estuary of a Class I river (measured in a straight line(s) headland to headland);

- At locations greater than 30 km from the estuary of a Class I river, reproductively sterile Atlantic salmon, reproductively viable brook trout or Arctic charr, and reproductively sterile non-indigenous species may be ranched provided that the risk of adverse effects on wild Atlantic salmon stocks are minimal.

3.3 Protocols applicable to Zone II

3.3.1 General within Zone II

Reproductively viable non-indigenous species, other than Arctic charr and brook trout, and reproductively viable Atlantic salmon stocks, non-indigenous to the NAC area, are not to be introduced into watersheds or into the marine environment of Zone II.

Restoration, enhancement and aquaculture activities are permitted in the freshwater and marine environments.

3.3.2 Rehabilitation

The preferred methods are to improve degraded habitat and ensure escapement of sufficient spawners through fisheries management.

If further measures are required, use residual stocks for rehabilitation and enhancement. If the residual stock is too small, select a donor stock having similar life-history and biochemical characteristics from a tributary or nearby river.

Stocking of hatchery-reared smolts is preferred, to reduce competition with juveniles of the natural stocks.

3.3.3 Establishment or re-establishment of Atlantic salmon in a river or part of a watershed where there are no salmon

To establish an Atlantic salmon stock, use a stock from a nearby river having similar stream habitat characteristics.

If re-establishing a stock, use a stock from a nearby river which has similar biological characteristics to the original stock.

It is preferable to stock rivers with broodstock or early life-history stages (eggs and fry); this would allow selection and imprinting by juveniles to occur.

If eggs are spawned artificially, use single pair matings and optimize the effective number of parents (See Section 3.1(5)).

3.3.4 Aquaculture

(i) Rearing in marine or freshwater cages, and land-based facilities:

- It is important to apply methods which minimize escapes;

- Reproductively viable Arctic charr and brook trout may be reared in marine and freshwater cages and in land-based facilities;

- Develop domesticated salmon broodstock using local stocks; or, if local stocks are limited, use nearby stocks;

- Reproductively viable non-indigenous species may only be introduced into land-based facilities where risk of escapement is minimal;

- Non-indigenous salmonid stocks may be introduced into the wild or used in cage rearing operations if the fish are reproductively sterile and the risk of adverse ecological interactions is minimal.

(ii) Commercial ranching:

- Commercial Atlantic salmon ranching will only be permitted at release sites located greater than 20 km from the estuary of a Class II river (measured in a straight line(s) headland to headland) and it is demonstrated that the activity will not negatively affect wild Atlantic salmon stocks;

- Non-indigenous species or distant national Atlantic salmon stocks may be used if the fish are reproductively sterile and the risk of adverse ecological interactions is minimal.

3.4 Protocols applicable to Zone III

3.4.1 General within Zone III

Indigenous and non-indigenous salmonid and non-salmonid [except reproductively viable Atlantic salmon stocks non-indigenous to the NAC Area] fishes may be considered for introduction or transfer if fish health and genetic protocols are followed and negative impacts on Atlantic salmon can be shown to be minimal using careful ecological impact evaluation.

3.4.2 Rehabilitation

Habitat quality should be upgraded wherever possible.

Rebuilding stocks can be achieved by controlling exploitation and by stocking cultured fish.

3.4.3 Establishment or re-establishment of Atlantic salmon in a river or part of a watershed where there are no salmon

Transfer source stocks from nearest rivers having similar habitat characteristics.

Stock with juvenile stages (eggs, fry and/or parr). If eggs are spawned artificially, use single pair matings and optimize the effective number of parents (Section 3.1(5)).

3.4.4 Aquaculture

(i) Rearing in marine or freshwater cages, or land-based facilities:

- Use of local stocks is preferred but non-indigenous stocks may be cultured;
- Marine cage culture can be widely practised; but preferred locations are at least 20 km from watersheds managed for salmon production (measurements are by straight lines from headland to headland);
- Culture of non-indigenous species in land-based facilities on Class III watersheds is permitted in adequately controlled facilities where risk of escapement is minimal.

(ii) Commercial ranching:

- Commercial ranching of salmonids is permitted if it is demonstrated that the activity will not negatively affect Atlantic salmon rehabilitation or enhancement programmes or the development of wild Atlantic salmon stocks.

4 GUIDELINES FOR APPROVAL OF INTRODUCTIONS AND TRANSFERS

Both proponents and agencies responsible for managing salmonids have a responsibility for ensuring that risk of adverse effects on Atlantic salmon stocks from introductions and transfers of salmonids and other fishes is low. Reasonable laws to protect wild stocks should be enacted by each agency, as necessary. Resource management agencies will determine protection for habitats with Atlantic salmon potential.

4.1 Responsibility of proponent

The proponent must submit an application for introduction or transfer of fishes to the permit-issuing agency. This request must provide a full justification for the introduction or transfer such that a complete evaluation will be possible prior to issuance of a permit. The list of information to be included in the justification for introductions and transfers is in Section 4.4 below. The lead time required for notice and justification of introductions and transfers will be determined by the permit-issuing agency. Proponents should be aware of the protocols established for introductions and transfers.

4.2 Responsibility of government agencies having the authority to issue permits

These agencies shall be those entities having the responsibility for fishery management within the receiving area. The responsibilities of the agencies shall include:

(1) Establish, maintain, and operate a permit system and inventory for all introductions and transfers of fishes;

(2) Enact regulations required to control the introductions and transfers of fishes as per established protocols;

(3) Establish a formal scientific evaluation process to review all applications (private and government agencies) for the introduction and transfer of all species and recommend conditional acceptance or rejection of the proposed

introductions and transfers based on the potential impact on the productivity of Atlantic salmon;

(4) Within the Zones each agency may be more restrictive in classifying individual watersheds. Rarely, a less restrictive classification may be applied to an individual watershed if its estuary is at least 30 km in Zone I, or 20 km in Zone II (measured in straight lines headland to headland) from a watershed with a higher classification;

(5) Annually, submit to the NAC Scientific Working Group the results of the permit submission/review process, and a list of introductions and/or international transfers proposed for their jurisdiction;

(6) Prevent the release of fishes which will adversely affect the productivity of wild Atlantic salmon stocks.

4.3 Responsibilities of the NAC Scientific Working Group on Salmonid Introductions and Transfers

(1) Maintain an inventory of all introductions of salmonids, transfers of salmonids from IHN-infected areas, and importation of salmonids across national boundaries into the Commission Area.

(2) Review and evaluate all introductions and transfers referenced in Section 4.3(1) above in relation to the NAC protocols and report the results to the North American Commission.

4.4 Preparation of proposals

The following information is required, by the permit-issuing agency, with applications involving introductions and transfers of salmonids, except for restocking into source river. This information will be used to evaluate the risk of adverse effects on Atlantic salmon stocks.

(1) Name the species, strain and quantity to be introduced or transferred, and include:

   (a) Time of introduction or transfer;

   (b) List anticipated future introductions or transfers;

   (c) List previous introductions and/or transfers.

(2) Area, place, river or hatchery from which the fish will be obtained.

(3) Proposed place of release and any interim rearing sites.

(4) Disease status of donor hatchery, river or other location from which fish are obtained.

(5) Disease status of recipient facility or stream (where available).

(6) Objectives of the introduction or transfer and the rationale for not using local stock or species.

(7) For non-indigenous species, provide the available information on the proposed species' life-history, preferred habitat, potential parasites and disease agents, and potential for competition with Atlantic salmon in the recipient waters or nearby waters.

(8) Information on similar transfers or introductions.

(9) Proposed procedure for transportation from donor to recipient site.

(10) List measures to be taken to prevent transmission of disease agents and to reduce the risk of escape of fish.

(11) Species composition at proposed site of introduction and adjacent rivers.

(12) Climatic regime and water chemistry, including pH of waters at the site of proposed introduction and of adjacent rivers.

(13) For indigenous species determine the life-history and biological characteristics of donor stock. This would include such characteristics as run timing, time of spawning, age-at-maturity, size-at-age etc.

(14) Potential of introduced or transferred fish to disperse to nearby streams.

(15) A bibliography of pertinent literature should be appended to the proposal.

4.5 Evaluation of proposals

The evaluation of proposals will be the responsibility of the permitting agency and will focus on the risk to Atlantic salmon production and potential production associated with the proposed introductions and/or transfers. The evaluation will be based on the classification of the recipient watershed. All requests for introductions or transfers must provide sufficient detail (Section 4.4 above) such that the potential risk of adverse effects to Atlantic salmon stocks can be evaluated.

The evaluation of potential adverse effects on fish health will consider the disease history of the donor and recipient facility and/or watershed with specific reference to the potential for transferring emergency diseases. The risk of detrimental genetic effects of introducing a non-indigenous stock into a river will be evaluated taking into consideration the phenotypic and life-history characteristics of the donor stock, the biochemical information (mitochondrial/nuclear DNA and enzyme frequencies, if available), and geographic distance between donor and recipient locations. The evaluation of the risk of ecological effects on Atlantic salmon populations is more involved. Introduction of non-indigenous Atlantic salmon stocks and/or non-indigenous species will be evaluated by considering the life-history and habitat requirements of the transferred fish.

The introduction of non-indigenous species poses a significant risk to the productivity of the Atlantic salmon stocks. Evaluation will be by comparison of the habitat requirement and behaviour of both the proposed introduced species and the indigenous Atlantic salmon stock at all life stages. The habitat requirements and areas of possible interactions with Atlantic salmon have been described for 13 fish species (see Part IV, Ecological Subgroup report). These can be used to provide a cursory evaluation of the life-history stage at which interactions would occur. However, more detailed information on stocks and habitats in both donor and recipient locations would be required in the form of an envirogram (example is provided in Part IV). Where insufficient data are available, research will be required prior to permitting the introduction or transfer.

An outline example of the type of information which is available in the species summaries (Part IV) is presented below for rainbow trout:

(1) Conditions under which interactions may occur:

- spawning rainbow trout may overcut Atlantic salmon redds and displace developing eggs;
- competitive interaction of juveniles: (i) exploitative competition for food; and (ii) interference competition;
- rainbow trout juveniles are more aggressive than juvenile Atlantic salmon, and may displace salmon from pools; and
- large rainbow trout are piscivorous and could prey on all stages of young salmon including emigrating smolts.

(2) Low interaction:

- in streams which Atlantic salmon do not utilize;
- in streams in which salmon are well established; and
- aquaculture using sterile fish or land-based facility.

(3) Conditions under which no interaction would occur. It would be permissible to use reproductively viable rainbow trout:

- in habitats with pH less than 5.5;
- if rainbow trout are already present in recipient stream; and
- in disturbed ecosystems where Atlantic salmon are absent and sport fishing would be improved.

5 GLOSSARY

Applicant: See proponent.

Aquaculture: The culture or husbandry of aquatic fauna other than in research, in hobby aquaria, or in governmental enhancement activities.

Commercial ranching: The release of a fish species from a culture facility to range freely in the ocean for harvest and for profit.

Competition: Demand by two or more organisms or kinds of organism at the same time for some environmental resource in excess of the available supply.

Containment: Characteristic of a facility which has an approved design which minimizes operator error to cause escape of fish, or unauthorized persons to release contained fish.

Diversity: All of the variations in an individual population or species.

Enhancement: The enlargement or increase in number of individuals in a population by providing access to more or improved habitats or by using fish culture facility production capability.

Exotic: See introduced species.

Fish: A live finfish.

Fish culture facility: Any fish culture station, hatchery, rearing pond, net pen, or container holding, rearing, or releasing salmonids.

Gamete: Mature germ cell (sperm or egg) possessing a haploid chromosome set and capable of formation of a new individual by fusion with another gamete.

Genetics: A branch of biology that deals with the heredity and variation of organisms and with the mechanisms by which these are effected.

Indigenous: Existing and having originated naturally in a particular region or environment.

Introduced species: Any finfish species intentionally or accidentally transported or released by Man into an environment outside its native or natural range.

Introduction: The intentional or accidental release of a species into an environment outside its native or natural range.

Isolation: Means restricted movement of fish and fish pathogens within a facility by means of physical barriers, on-site sanitary procedures and separate water supply and drain systems and cultural equipment.

Mariculture: Aquaculture in sea water.

Native: See indigenous.

N_e: Effective population size $= \dfrac{4N♂N♀}{N♂+N♀}$

Niche: A site or habitat supplying the sum of the physical and biotic life-controlling factors necessary for the successful existence of a finfish in a given habitat.

Non-indigenous: Not originating or occurring naturally in a particular environment; introduced outside its native or natural range.

Population: A group of organisms of a species occupying a specific geographic area.

Predator: An individual that preys upon and eats live fish, usually of another species.

Proponent: A private or public group which requests permission to introduce or transfer any finfish within or between countries and lobbies for the proposal.

Quarantine: The holding or rearing of fish under conditions which prevent the escape or movement of fish and fish disease agents. (For a detailed description of a quarantine facility see Annex IX of Part II).

Rehabilitation: The rebuilding of a diminished population of a finfish species, using a remnant reproducing nucleus, toward the level that its environment is now capable of supporting.

Restoration: The re-establishment of a finfish species in waters occupied in historical times.

Salmonid: All species and hybrids of the Family Salmonidae covered by the AFS checklist special publication No. 12, “A list of Common and Scientific Names of Fishes from the United States and Canada (1980)”.

Species: A group of interbreeding natural populations that are reproductively isolated from other groups.

Stock: Population of organisms sharing a common gene pool which is sufficiently discrete to warrant consideration as a self-perpetuating system which can be managed.

Strain: A group of individuals with a common ancestry that exhibits genetic, physiological, or morphological differences from other groups as a result of husbandry practices.

Transfer: The deliberate or accidental movement of a species between waters within its native or natural geographic range, usually with the result that a viable population results in the new locations.

Transferred species: Any finfish intentionally or accidentally transported and released within its native or natural geographic range.

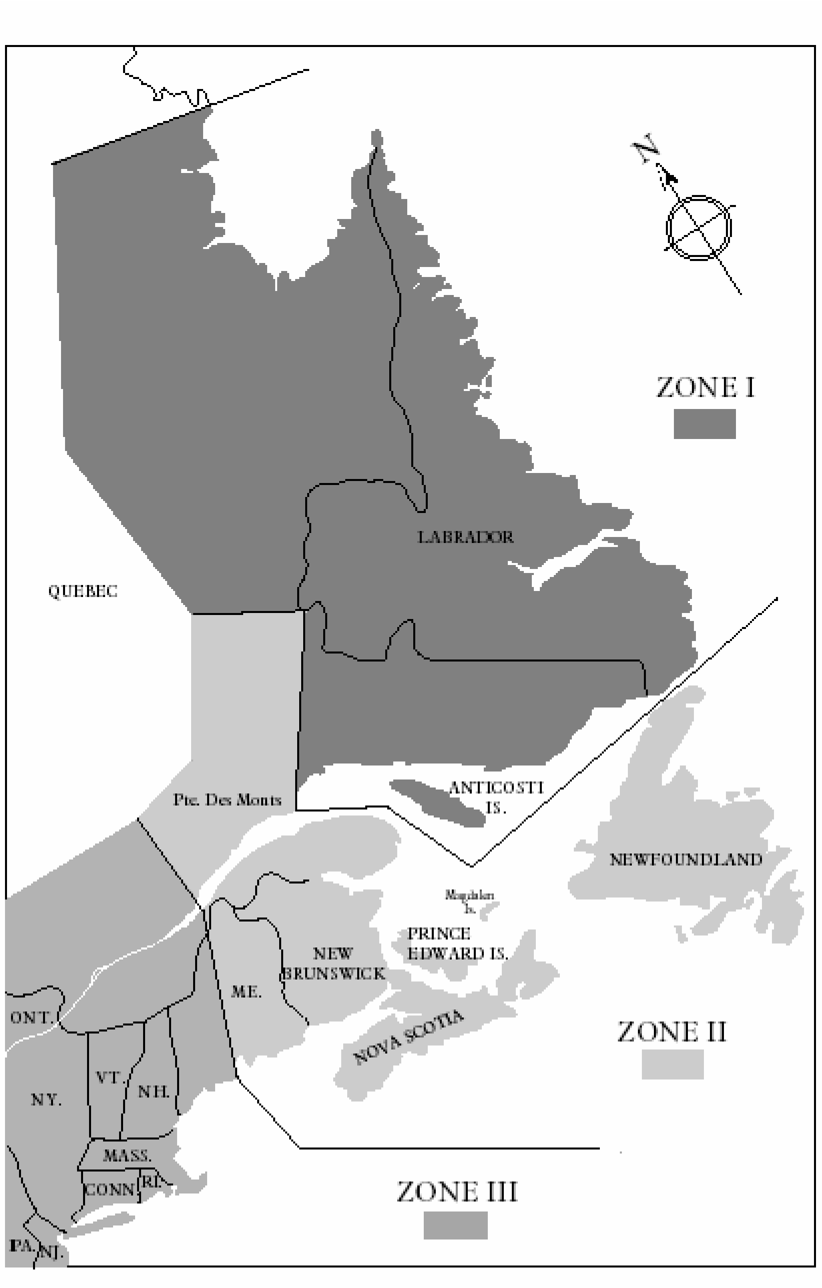


Figure 1.

Map of eastern Canada and northeastern USA showing the three zones designated for implementation of the Protocols. Certain rivers on the west coast of Newfoundland are designated as Zone I, even though Newfoundland is shown as being in Zone II.

Appendix 2

NAC(05)7

Memorandum of Understanding between Canada and USA

Preamble

The North American Commission (NAC) of NASCO recognizes the potential effects that introductions and transfers of aquatic species can have on fish health, genetics, and their ecology. In 2003, NASCO adopted the Williamsburg Resolution which referenced the NAC Protocols as contained in NAC(92)24 and ancillary document NAC(94)14. In Canada, the National Code on Introductions and Transfers of Aquatic Organisms was adopted in 2001. It is acknowledged that Canada and the United States utilize different methods within their countries for authorization of introductions and transfers. This Memorandum of Understanding is meant to reconcile the differences between the methods used but recognizes the common goal is the conservation and protection of wild Atlantic salmon.

Memorandum of Understanding

Canada and the United States have agreed to record the following in connection with the introductions and transfers of salmonids in the North American (NAC) area:

A. Authorizations of Introductions and Transfers

In Canada, the National Code on Introductions and Transfers of Aquatic Organisms is the mechanism for approval of introductions and transfers which is authorized by permits. In the United States, state and federal permits are the mechanisms for authorizing introductions and transfers.

B. Requirement to Report

The Parties agree to report to the NAC annually on any decision made under their respective jurisdiction that has an impact on the other jurisdiction. In particular, any decisions made that are not consistent with the NAC Protocols will be identified.

C. Requirement to Consult

The Parties agree to consult with each other if either jurisdiction receives a proposal for an introduction or transfer that may have an impact on the other, including any proposal that would be inconsistent with the NAC Protocols.

D. Need for Review

The Parties agree to convene the NAC Scientific Working Group, from time to time, to review the provisions of the Williamsburg Resolution with respect to developments that may have an application on introductions and transfers in the NAC area and provide recommendations to the Parties for their consideration and action, if required.

SLG(09)5

Guidance on Best Management Practices to address impacts of sea lice and escaped farmed salmon on wild salmon stocks
(Adopted in June 2009 and Revised in June 2010)

1. Since 1990, NASCO has co-convened three major international symposia to ensure that it had the best available information on interactions between wild and farmed salmon to guide its decisions. In 1994, in response to the information presented at these symposia, NASCO adopted the 'Oslo Resolution' designed to minimise impacts of aquaculture on the wild salmon stocks. The Oslo Resolution had been developed in consultation with the salmon farming industry and, in order to strengthen this relationship, a Liaison Group was established in 2000. The objective of the Liaison Group is to establish mutually beneficial working arrangements in order to make recommendations on wild salmon conservation and sustainable salmon farming practices, to maximise potential benefits and to minimise potential risks to both. Through the Liaison Group Guidelines on Containment of Farm Salmon were developed and reports on progress with developing and implementing containment action plans are made to the Liaison Group. These guidelines, together with Guidelines on Stocking and elements to ensure consistency with the Precautionary Approach, were incorporated into a new Resolution, the Williamsburg Resolution, CNL(06)48, adopted in 2003 and amended in 2004 and 2006.

2. The most recent NASCO/ICES symposium held in Bergen in 2005 highlighted that while much progress had been made in addressing impacts of aquaculture and in better understanding the nature of these impacts, sea lice and escaped salmon were identified as continuing challenges both for the industry and the wild stocks and on which further progress was urgently needed. NASCO, therefore, decided that it would establish a Task Force comprising representatives of the Parties, the salmon farming industry and NASCO's accredited NGOs with the aim of: identifying a series of best practice guidelines and standards to address the impacts of aquaculture on wild salmon stocks; to identify knowledge gaps and research requirements to address them; and to consider if, and how, impact targets can be identified. In accordance with its Terms of Reference, the Task Force collated existing Codes of Practice as contained in document ATF(09)7 and developed this guidance on best management practices, framed around the elements of the Williamsburg Resolution, designed to achieve international goals to address the impacts of sea lice and escaped salmon on wild Atlantic salmon. The guidance provides a range of measures from which those most appropriate to the local conditions should be put into place to safeguard the wild salmon stocks.

3. This guidance is intended to supplement the Williamsburg resolution and to assist the Parties and jurisdictions: in managing salmon aquaculture, in cooperation with their industries; in developing future NASCO Implementation Plans; and in preparing their 2010 and subsequent Focus Area Reports on aquaculture and related activities. It is anticipated that the triennial reviews of the FARs will provide a mechanism for assessing progress towards achievement of the international goals. It is the intention that NASCO and its jurisdictions explore, in collaboration with industry, opportunities for cooperative scientific research in support of the goals.

	Sea lice	Containment
International Goals	**100% of farms to have effective sea lice management such that there is no increase in sea lice loads or lice-induced mortality of wild salmonids attributable to the farms.**	**100% farmed fish to be retained in all production facilities**
	Use Williamsburg Resolution as basic guidance, supplemented as below	
Best Management Practices (BMPs)	Area management, risk-based, integrated pest management (IPM) programmes that meet jurisdictional targets for lice loads at the most vulnerable life-history stage of wild salmonids.	Codes of Containment including operating protocols
	Single year-class stocking	Technical standards for equipment
	Fallowing	Verification of compliance
	Risk-based site selection	Risk-based site selection
	Trigger levels appropriate to effective sea lice control	Mandatory reporting of escape events and investigation of causes of loss
	Strategic timing, methods and levels of treatment to achieve the international goal and avoid lice resistance to treatment	Adaptive management in response to monitoring results to meet the goal
	A comprehensive and regulated fish health programme that includes routine sampling, monitoring and disease control	
	Lice control management programmes appropriate to the number of fish in the management area	
	Adaptive management in response to monitoring results to meet the goal	
Reporting & Tracking	Monitoring programme appropriate for the number of farmed salmon in the management area and sampling protocols effective in characterising the lice loads in the farms and wild salmonid populations.	Number of incidents of escape events and standardised descriptions of the factors giving rise to escape events
	Lice loads on wild salmonids compared to areas with no salmon farms	Number and life-stage of escaped salmon (overall number; % of farmed production)
	Lice-induced mortality of wild salmonids (e.g. as monitored using sentinel fish, fish-lift trawling, using batches of treated smolts)	Number of escaped salmon in both rivers and fisheries (overall number; % of farmed production) and relationship to reported incidents
	Monitoring to check the efficacy of lice treatments	

	Sea lice	Containment
Factors Facilitating Implementation	Development of a monitoring programme appropriate for the number of farmed salmon in the management area and sampling protocols effective in characterising the lice loads in the farms	Monitoring of rivers for escaped salmon
	Access to a broad suite of therapeutants, immunostimulants and management tools	Site appropriate technology
	Collation and assessment of site selection and relocation criteria	Advanced permitting to facilitate recapture and exchange of information on effectiveness of recapture efforts
	Regulatory regimes which facilitate availability of alternative sites, as necessary, to support achievement of the goal	Technology development (e.g. cage design, counting methods for farmed salmon, methods to track origin of escaped salmon and their progeny)
	Training at all levels in support of the goal and to increase awareness of the environmental consequences of sea lice	Training at all levels in support of the goal and to increase awareness of the environmental consequences of escaped salmon
	Monitoring of lice levels: in areas with and without farms; before, during and after a farm production cycle; and in plankton samples	Assessments of the relative risks to the wild stocks from escaped salmon from freshwater compared to marine facilities and from large but infrequent escape events compared to small but frequent escape events.

Marine Policy xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Marine Policy

journal homepage: www.elsevier.com/locate/marpol

Environmental problems and regulation in the aquaculture industry. Insights from Norway

Jon Olaf Olaussen

NTNU Business School, Norwegian University of Science and Technology, Norway

ARTICLE INFO

JEL codes:
Q13
Q18
Q25

Keywords:
Salmon farming
Environmental problems
Regulation
Sea lice
Escapement

ABSTRACT

Since the beginnings of the aquaculture industry in Norway, the salmon farming industry has grown from a pioneering niche to a massive industrial adventure. Since 1992, Norwegian salmon production has increased to ten times its 1992 level. By 2015, the Norwegian production constituted 53% of the world's production of Atlantic salmon. Therefore, it could be said that salmon farming is the most important industry in rural Norway today, with a yearly landing value of about 6.1 billion EUR. As the production has grown, along with the income, numerous environmental issues have arisen. The present paper gives an overview of these environmental problems and discusses potential solutions, as well as the need for a better and more holistic regulation of the industry. The experience from Norwegian salmon farming with respect to environmental issues and regulation may give important insights to both other salmon producing countries as well as producers of other fish species.

1. Introduction

Norway has been a world leader in farmed salmon since the production technique was pioneered in the late 1960s. Since then, Norwegian salmon production has risen steadily from 600 t in 1974 to about 1,300,000 t today (Asche and Bjørndal [9], [46]). Since the start of aquaculture production in Norway, the salmon farming industry has grown from a niche market to a massive industrial adventure. Salmon farming is, arguably, one of the most important industries in rural Norway today, with a yearly landing value of about NOK 60 billion (6.5 billion EUR). Production methods have been improved and obstacles solved at a rapid speed. From the time when the first farmers decided to put net cages in the fjords to today's massive production facilities, the need for management and regulation of the industry has changed dramatically.

As with any industrial production, there are costs and benefits associated with farmed salmon production. About 6000 jobs are created in the industry, and the contribution to GDP of Norway is in the range from 0,5-1% yearly [46]. Salmon production has ten doubled since 1992, and doubled since 2005. In 2015, Norwegian salmon production constituted 53% of the world's production of Atlantic salmon, while the Chilean production was 25% of the world market. As production has grown, along with the profits gained, the environmental impact has also increased in turn.

The salmon production industry not only affects the wild salmon populations, but also the sea trout populations, the coastal fisheries (especially shrimps and coastal cod), and the sea floor, due to environmental, noise, and visual pollution. The problem that has received the most attention is that of maintaining wild salmon stock, which spawns in the salmon streams of Norway. Currently, Norway has more than 400 watercourses with Atlantic salmon populations and holds about 25% of the world's healthy populations [25]. Consequently, Norwegian authorities have taken a particular responsibility to protect the species and its populations. According to the scientific board of salmon management, the two most severe challenges for this species is the escapement from fish farms and the high sea lice densities [17,4].

The escapement from fish farms has always been a challenge, causing both direct economic losses to the sea farmers, as well as cross-spawning and hybrid (farmed and wild) salmon populations. Sea lice are parasites that attach to the skin of the salmon. Under natural conditions, this parasite is not a major problem for the wild salmon, but due to the enormous number of hosts in the fjords year round (the farmed salmon), the number of sea lice in the fjords has proliferated. First and foremost, this is a problem for the wild smolt (young salmon) when they leave their river and migrate offshore to grow. On this migration route, they have to pass the fish farms and high lice density areas in the fjords. It has been found that if more than 10 lice attach to the skin of the young fish, they may die [22]. In addition, it turns out it may be an even bigger problem for the sea trout populations due to their longer sea journey (sometimes they stay in the fjord all year).

Pollution from aquaculture production takes many forms. One of the problems is that the high density of fish in small cages produces a lot of

---

E-mail address: jon.o.olaussen@ntnu.no.

https://doi.org/10.1016/j.marpol.2018.08.005
Received 30 January 2018; Received in revised form 25 July 2018; Accepted 2 August 2018

Please cite this article as: Olaussen, J.O., Marine Policy (2018), https://doi.org/10.1016/j.marpol.2018.08.005

excrement and undigested feed. A carpet of sludge may cover the bottom floor, both beneath and around the aquaculture facilities. Another pollution problem is associated with sea lice. In order to keep sea lice numbers low in the farms, the industry has used several kinds of chemical treatments over the years. While the treatments target the sea lice in the farm, it may also be a problem for shrimps and other crustaceans in the surroundings of the farms. Unfortunately, sea lice can develop resistance to the chemicals, while wild crustaceans likely remain vulnerable.

2. Regulation

In the late 60 s, farmers started experimenting with feeding salmon in sea cages. The activity was supported by the government as a means of adding to the income among small-scale farmers. Regulation was poor at this time as the activity was not considered especially important. In fact, in these early years of aquaculture production, escapements from fish farms were common, and the farmers received insurance money in association with such accidents. In 1973, the first law on concessions in salmon aquaculture was issued, and permission was needed to start sea farms [1]. In 1985, the first aquaculture law was issued. Unfortunately, this law failed to require concessions for hatchery production of smolt, and this resulted in an overinvestment in this sector. This overproduction resulted in a four-year period, where the salmon prices went down to half the previous level. In 1991, while as the industry faced allegations of dumping in the US market, the concession law was changed to allow one owner to have several concessions. This changed the structure in the sector dramatically, and small-scale farmers were replaced by fewer and bigger companies. In 2005, a new aquaculture law was issued. This time, the focus shifted towards sustainable production and growth in the sector [37]. As of 2013, among the regulations a salmon farm must follow is the total number of salmon allowed per cage, which is restricted to 200,000 salmon. In addition, they have to remain under the total allowed biomass per concession, which is 780 t (945 t in the northernmost counties Troms and Finnmark). Moreover, to control the sea lice problem, they have to count the number of lice per salmon on a regular basis and take action if the number of adult female sea lice per fish is above 0,2 on average in week 16–22 (the migration period for wild smolts) [5]. The limit is less than 0.5 in remaining season [5]. This rule is now under change as the new traffic light system, issued in October 2017, puts aside this requirement, instead focusing on the presumed effect on the wild salmon mortality (see below).

3. Challenges with salmon production

3.1. Escapement

Since the very beginning of the salmon farming industry, salmon have unintentionally escaped from net pens that are damaged by storms, seals, and otters, or by daily wear and tear. The number of accidental escapes decreased in the mid-1990s because of safety investments in the sea ranches. Nevertheless, approximately 200,000 salmon still escape yearly from fish farms in Norway (Fig. 1), which equals approximately half of the average total wild adult returns [4]. The yearly escapement numbers are uncertain, but according to the official statistics, farmed salmon escapes constitutes around half of the total yearly in-run of wild Atlantic salmon to Norwegian rivers. In addition, a recent meta-analysis of catch statistics and tagging studies has estimated that the actual numbers of escapees in Norway were 2–4 times higher than the numbers reported by the farmers during the period spanning 2005 to 2011 [45].

In Norway, the wild Atlantic salmon stock is traditionally harvested in two different fisheries during its spawning run. First, the commercial and subsistence marine fishery catches a share of the marine returns in fishnets in the fjords and inlets. The remaining stock then enters the rivers and is exploited by a recreational fishery. According to the catch reports from 2013–2017, about 43% of the total catch is caught in the marine fishery, while the rest is caught in the rivers [47,48]. When the fishing season in the river closes, the remaining fish spawns.

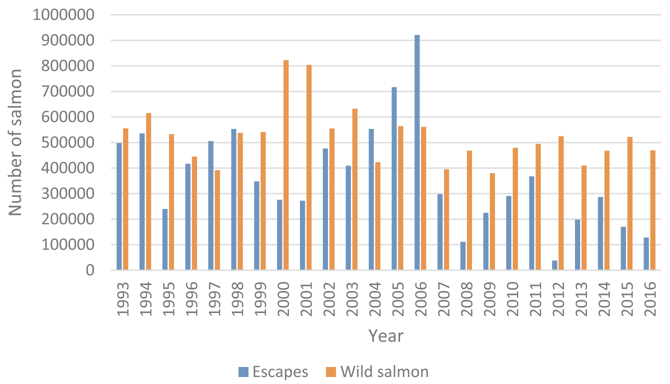


Fig. 1. Yearly escape of salmon from fish farms and inflow of wild salmon to Norwegian rivers. Source: Fiskeridirektoratet [16] and Anon [4].

The farmed escapees interact with the native species in various ways. Ecologically, they may interact through competition, predation, hybridization, colonization, and spreading diseases and parasites [17]. Escaped farmed salmon may hence have a number of effects on the natural growth and economic value of wild salmon. The most important effects are the spread of diseases and the mixing of genes through interbreeding (introgession), which affect the reproduction rate [15,19,34]. Farmed salmon digs in the natives' spawning gravel, and their offspring are more aggressive and risk prone. Once farmed escapees survive and strive in the environment where native individuals reside, they become a part of the ecosystem and directly and indirectly interact with native individuals. For instance, farmed salmon can escape to the rivers, where they compete with native salmon. This competition over the natural habitat and food sources, as well as mates, may result in changes in the structure and productivity of the native stock [14]. In the case of escaped farmed salmon, it is reported that successful inbreeding between escaped farmed and native salmon reduces the fitness and productivity [34], dilutes the genetic gene pools [14,35,43], and threatens the survival of the native salmon offspring [24]. Karlsson et al. [29] found statistically significant introgression in half of the wild populations studied and levels of introgression above 10% in 27 of 109 rivers represented by adult samples.

In addition, escaped farmed salmon can increase the sea lice density [20]. Also, escaped farmed salmon may spread diseases and parasites, thus leading to the augmented mortality of native salmon [11,18,30]. If the number of escapees is low, the effects may be negligible, but the effects become severe as the number of escapees gets larger. In particular, some vulnerable native stocks may potentially go extinct with repeated invasion.

However, escaped farmed salmon may also be regarded as having positive effects. Farmed salmon can potentially increase the salmon stock available for both marine and recreational catches, *ceteris paribus*, and thus improve the profitability of these fisheries [40]. As reported in Fig. 1, escaped farmed salmon constitute a substantial part of the stock. This is not to say that invasion is no problem for the society as a whole, but it may reveal economic forces inducing a lack of incentives for different agents to control the invasion. In a sense, the large number of escaped farmed fish, which may constitute as much as 50% of the yearly catch of salmon in the sea fishing sector, may also hide the problem of a decreasing wild stock. Hence, escaped farmed species may generate economic impacts through markets. If invasive fish have a similar economic value as native wild fish, escaped farmed fish may increase the total stock level for harvesting.

Escaped farmed salmon (both Pacific and Atlantic salmon) is of great concern in a number of countries with fish farming industry, for example, United Kingdom, Scotland, Ireland, Iceland, Chile, USA, and Canada. In addition, the increasing farming of other fish species, such as cod, halibut, clams, and crabs, highlights the importance of addressing this issue. The bioeconomics of the interrelation between aquaculture and fisheries is studied by Anderson [7], Ye and Beddington [50], Hannesson [21], Olaussen et al. [40], Liu et al. [32], and Liu et al. [31] while market interactions have been studied by Anderson [7], Anderson and Wilen [8], and Asche et al. [10]. Olaussen and Liu [39] have studied the economic effects in terms of anglers reduced willingness to pay when the river catch consists of a large share of escaped farmed salmon.

3.2. *Sea lice*

The collective term “sea lice” normally refers to a number of copepod crustaceans of the family *Caligidae* (Revie et al. [42]). Sea lice are external parasites that live on the skin of marine and anadromous species. The most common and extensively studied species is the *Lepeophtheirus salmonis,* which is a parasite specific to the salmonid species. This parasite is a problem in both the Atlantic and Pacific Oceans, while the Chilean farming industry experiences challenges with *Caligus teres* and *Caligus rogercresseyi* (Revie et al. [42]). The lice are mainly a problem for the salmon post-smolts on their seaward migration journey, as they have to pass the farm areas before they reach their offshore winter habitat. A recent study ranks the high sea lice densities, together with escaped farmed salmon from aquaculture, as the two most significant and expanding threats to the wild salmon populations in Norway [17]. Salmon aquaculture increases the sea lice density in the fjords and along the coast because they amplify the number of hosts for the lice by a magnitude of 100 [23]. Smolt infected by less than 10 sea lice are affected but typically survive whereas smolt with more than 10 lice have high mortality ([23,49]; Holst et al. [27]). In some cases, close examinations of the infected fish have revealed up to 100 sea lice per fish, which cause certain death (Revie et al. [42]). It is not possible to give an accurate estimate regarding how much the smolt survival is reduced due to sea lice-induced mortality on a national scale. The effect varies between fjords, and from river to river. Recent results suggest an extensive exchange of lice between farmed and wild hosts, indicating that in farming-dense regions in Norway, aquaculture represents a major driver of salmon louse population structure [14]. Furthermore, the annual loss of wild salmon to Norwegian rivers due to salmon lice was estimated at 50,000 adult salmon for the years 2010–2014. This corresponds to an annual loss of about 10% on a national level [4]. As indicated, other salmon stocks, such as Pacific salmon, are also threatened by sea lice infections, and Krkošek et al. [30] found a lice-induced mortality for pink salmon commonly exceeding 80%. Increased sea lice densities may be considered a type of biological pollution, and thus, a unidirectional externality running from the farmed salmon sector to the wild salmon sector.

3.2.1. *Treatment*

In order to cope with the increasing sea lice problems, chemical and mechanical treatments have been tried, as can be seen in Fig. 2. The problem with chemicals is that the sea lice seems to be very adaptable. It can take a few years for evidence of resistance to appear following a new treatment with a new chemical. One solution has been to switch between different treatment methods, but the problem of resistance seems to be hard to overcome, and multi-resistance has emerged. In recent years, freshwater treatment has also become part of the toolbox, and the fear may be that the sea lice develops more tolerance for freshwater as well. If this happens, the problem in the rivers for the wild salmon population may be serious, because today they are, in some sense, protected by the fact that the sea lice cannot handle freshwater. Another problem that has recently been highlighted by coastal shrimp fishermen and others, is that the chemical treatments may also affect coastal shrimp and other crustaceans populations, as well as fish. As Samuelsen et al. [44] states, “During medication, most wild fauna contained teflubenzuron residues, and polychaetes and saith had highest concentrations. Eight months later, only polychaetes and some crustaceans contained drug residues. What dosages that induce mortality in various crustaceans following short or long-term exposure is not known, but the results indicate that the concentrations in defined individuals of king crab, shrimp, squat lobster, and Norway lobster were high enough shortly after medication to induce mortality if moulting was imminent”. Fortunately, it can also be argued that as the sea lice becomes resistant to a new chemical treatment, it will make no sense to continue using it, and this may in turn reduce the threat to crustaceans in general.

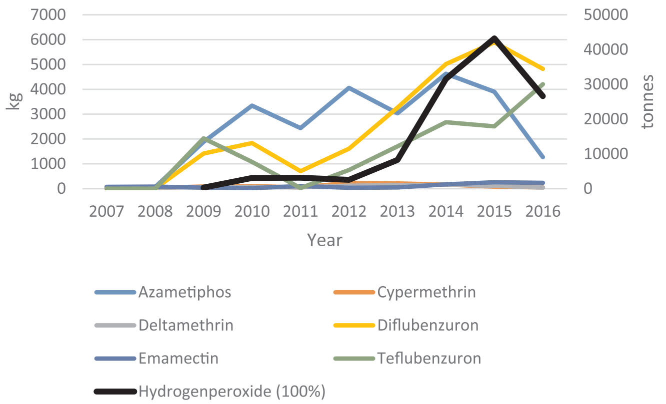


Fig. 2. Yearly use of sea lice treatment chemicals. Hydrogen peroxide (Black line) measured in tons (right axes). Source: Folkehelseinstituttet [16].

The treatment of the sea lice problems also involves costs to the industry. Abolofia et al. [2] estimated that the cost of sea lice treatment constituted production costs ranging from 0.12 to 0.67 US$/kg, or in the range of 2.27 to 13.10% of yearly revenues. In addition, the increase in “other production costs”, where sea lice treatment constitutes 80% of the costs, is the main driver of increased production costs, increasing from an average of 0.36 US$ per kg on average in 2008 to 0.78 US$ per kg in 2015 [13].

On the positive side, the use of antibiotics in the aquaculture industry in Norway is very low (see Fig. 3). In 1987, the use of antibiotics was 887 mg per kg fish produced, while it was down to 0.20 mg in 2015 [6]. In Chile, on the other hand, the use was still 660 mg per kg produced fish [28].

3.3. *Fish welfare*

The question of fish welfare is closely related to the topics of sea lice

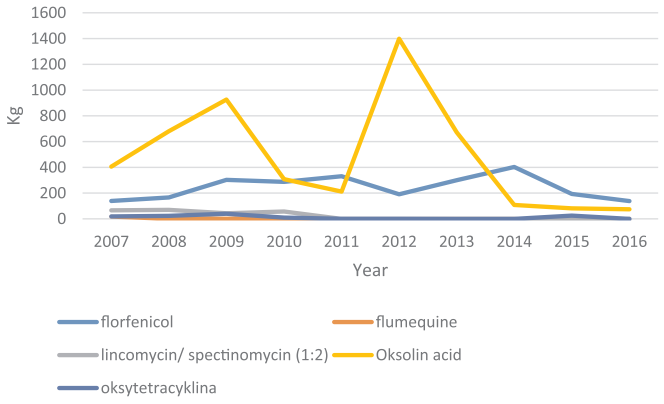


Fig. 3. Yearly use of drugs for the treatment of fish. Source: Folkehelseinstituttet [16].

treatment and fighting off diseases. In 2016, 19% of the salmon died in the sea-cage stage [26], corresponding to 53 million fish. In a study focusing on the cause of death in the sea cage stage, poor smolt quality and infections were pointed out as being the two most significant causes, while the other three categories were mechanical injury, environmental causes, and miscellaneous [12]. Sea lice infections lead to death, either through infections in the skin from wounds, or due to chemical and/or mechanical treatment [26]. In addition, the high densities of hosts leads to challenges with respect to other diseases, such as Pancreas disease (PD) and infectious salmon anemia (ISA) [12].

Another aspect of fish welfare is associated with one of the sea lice fighting strategies. By using cleaning fish, that is, fish species that feed on sea lice, the aquaculture industry has tried to reduce the treatment with chemicals. The cleaning fish species are labrid fish (mostly ballan wrasse, *Labrus bergylta*, and goldsinny wrasse, *Ctenolabrus rupestris*), and lumpfish *Cyclopterus lumpus* [41]. It turns out the mortality rate of these species is very high at an average of 33% after only 6 months in the sea. For the lumpfish, the mortality rate was 48% after 6 months [36]. This indicates that the ethics of the use of cleaner fish is an issue, with very little debate thus far. This is quite surprising, given that fish welfare in aquaculture is explicitly regulated by law, which stipulates that the operation must be satisfactory with respect to health and welfare [33].

3.4. Pollution

As with all industrial production, the aquaculture industry brings a level of pollution along with it. We have already mentioned sea lice treatment chemicals. In addition, the aquaculture industry constitutes a major part of the release of nutrition to Norwegian fjords. This is mainly due to releases from feed and fish faeces. Due to the present high level of production, the release of nutrition from the sector is at the same level as the sewage from about 10 million people, or about twice the Norwegian population. Interestingly, while there is a focus on release from land-based industry, this issue has been more or less ignored in the fjords. The result is seen in Fig. 4 and 5, where the release of phosphorus from the aquaculture industry is about 45 times higher than the total from the rest of the Norwegian industry, and about 9 times as high as the natural drainage. In addition, the release of nitrogen from aquaculture production is about 24 times the release from the remaining industry and is almost as high as the natural drainage (0.7 times natural drainage).

4. New regulation, traffic light system

Sea lice infection on salmon farms has been regulated since 1997 to reduce the harmful effects of lice on farmed and wild fish [23]. Regulations set thresholds for the maximum mean number of sea lice per fish and a compulsory reporting system for all mobile stages of infective lice. From 2000 to 2013, the legal lice infection thresholds were set to 0.5 adult female lice per fish, or 3 lice per fish of other mobile stages (i.e., adult males or pre-adult mobiles) during the period spanning Jan 1–Aug 31, and 1 adult female or 5 other mobiles per fish across the period between Sep 1–Dec 31. From 2013, the limits for taking action have been 0,2 lice per salmon on average in week 16–22 (the wild smolt migration period), and less than 0.5 lice per salmon in remaining season [5]. This threshold is enforced by the Norwegian Food Safety Authority (NFSA). If thresholds are exceeded, it is mandatory for the farmer to treat or slaughter their fish within two weeks. The NFSA requires farmers to regularly count sea lice in their pens and report the highest mean count during a month.[1] Before August 2009, farmers were mandated to report the highest mean counts of sea lice from a 20-fish sample from a single net pen. After this date, farmers were required to report the means from samples of 10 fish from 50% of all active pens. In addition, all pens are to be counted for every two rounds of sampling in order to improve control [2].

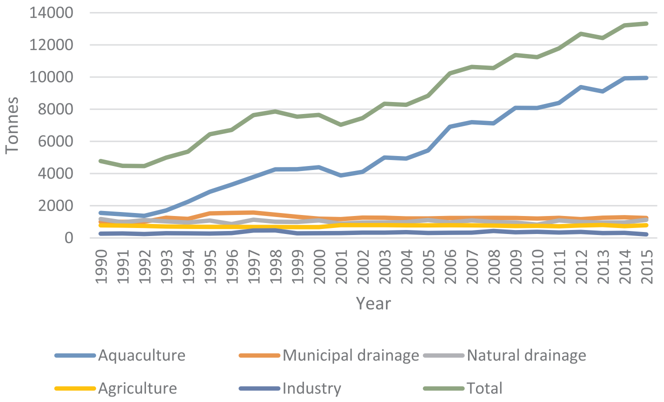


Fig. 4. Phosphor disposal to fjords by source. Source: Norwegian Environment Agency [38].

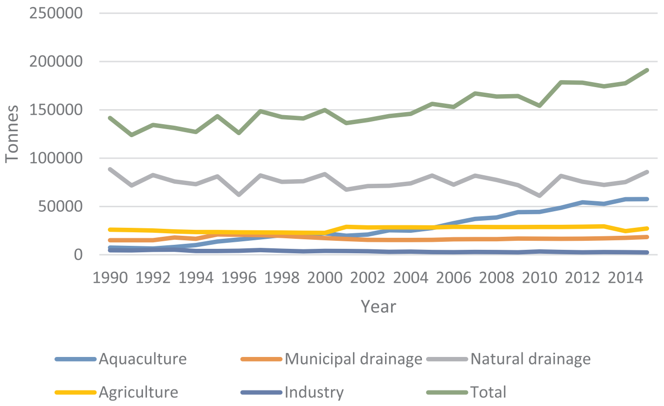


Fig. 5. Nitrogen disposal to fjords by source. Source: Norwegian Environment Agency [38].

The government of Norway has decided to introduce a new system for growth in the aquaculture sector, labelling it as a traffic light system. The idea is that the key to growth is the sea lice pressure. This means that the sea lice effect on wild salmon mortality will be the indicator with respect to production growth. In areas where sea lice cause wild salmon smolt mortality less than 10%, a green light for increasing production by 6% will be given. A yellow light will be given in the case where sea lice induced mortality is between 10 and 30%. A yellow light means that the growth is on hold, i.e., constant production. If an area gets a red light, the sea lice induced mortality is higher than 30%, and production should be reduced. However, this reduction will not take place before the next evaluation period.

There are several problems with this system. First, basing potential growth on only one indicator is a rather strange idea (see Fig. 6). As mentioned above, and as the figure indicates, there are several other factors, and one of them, escapement from fish farms, is considered equally important for the protection of the wild salmon stock. One reason why escapement is not yet included may be the poor correlation between the size of the farming industry in an area and the occurrence of farmed fish in the rivers. This is because escaped farmed salmon migrate over long distances and do not necessary return to spawn in rivers near where they escaped. This asymmetry between escapement location and damage location may point in the direction of adding escapement as an indicator on the national, not regional level.

In addition, as mentioned above, measures to fight sea lice may introduce new challenges, such as the effect of chemicals on shrimps, other crustaceans, and local fish populations (see Fig. 6). Second, in the

---

[1] If the sea temperature is above 4 °C, the counts must be performed on a weekly basis, otherwise every 14th day [3].

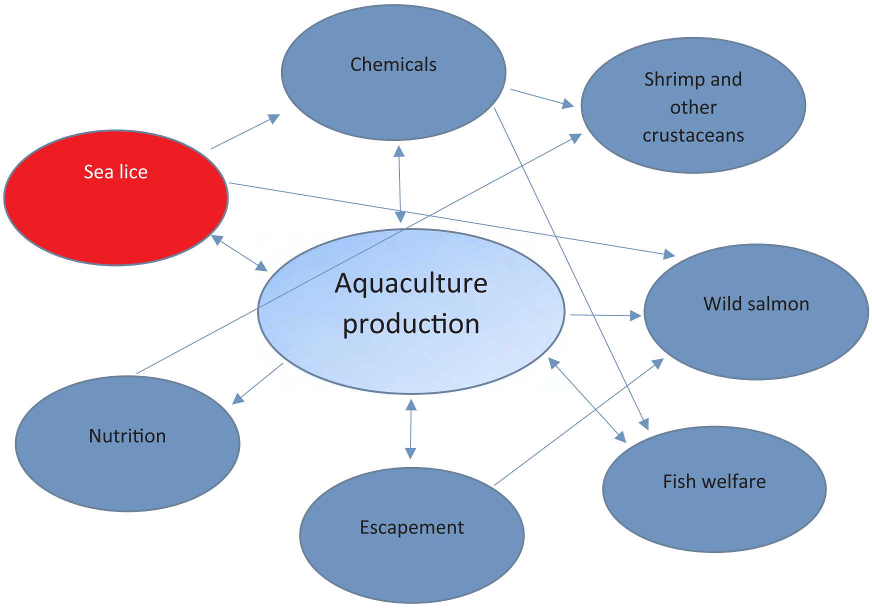


Fig. 6. A schematic overview of the interdependencies and externalities in aquaculture production.

former regime, there is a rule associated with the number of sea lice per fish, that is, an objective criteria. The new criteria is more open for discussion, as someone will have to estimate how different sea lice densities affect the mortality of wild salmon, which is a challenging task. To be fair, there is a large group of scientists within a well-organized system that do the assessment of infestation and mortality risk and make these recommendations, but probability considerations are always open for debate. Third, as the focus is only on one challenge, the incentives to invest in technologies that mitigate other problems, such as escapement, will probably be less, as the focus will shift towards sea lice treatment.

Fourth, there is a fish welfare perspective that is completely neglected. The aquaculture sector is a sector where 19% of the fish (2016) die in the nets before they reach the market size (Hjeltnes et al. [26]).

Overall, and to sum up, there seems to be many reasons why one should reconsider the narrow indicator system introduced through the traffic light system. When the system and problem is complex, and negative externalities multidimensional, regulating without a holistic perspective may be directly damaging. On the other hand, sea lice is no doubt a severe challenge, and it may be argued that the system, at least in part can give an incentive to develop new and less damaging ways of production, since growth may be limited in areas with high infection pressure. Also, it should be mentioned that Norwegian authorities in parallel has introduced systems for “green concession” and “technology developing concessions”. While some of these concessions are issued mainly to initiatives addressing the sea lice problem, there are also other that aim for more holistic solutions, such as land-based and closed containment production systems.

5. Discussion and concluding remarks

The main problem with the previous and current regulation in light of environmental concerns seems to be that there are too weak incentives to shift towards new and less damaging ways of production. One of the most promising solutions would be the development of closed containment production systems for salmon aquaculture, that is, a transmission from the open net cages to more closed containment facilities. Small-scale aquaculture production is already available, and projects of a commercial scale have also been conducted in Canada and Denmark. Investing in such technologies will be costly in the short run for the aquaculture sector, but may turn out beneficial in the long run; in any case, this technology has the potential to solve many of the challenges between the wild and farmed salmon. Since closed containment systems separate farmed fish from wild fish and the environment, it will alleviate or eliminate most of the problems caused by open cage farming, such as escapees, spread of diseases, and sea lice. As a result, the impact of farming on the wild salmon would be considerably reduced.

The underlying institutional challenge in the regulation of the aquaculture sector is that aquaculture is managed by the Ministry of Trade, Industry, and Fisheries in Norway, while the wild salmon is under the management of another department, the Ministry of Climate and Environment [32]. This problem was highlighted already in the first year of the traffic light system, as the Ministry of Trade, Industry and Fisheries acknowledged the advice for yellow light from the scientific committee in one of the counties, that is a hold signal. However, he executed his right to let other matters count, and as a result the county were given a green light and the possibility to grow with 6%. It may seem unfortunate that the Ministry of Climate and Environment is not part of this decision process, as this could spell weak support from the government regarding wild salmon interests.

The present paper has highlighted environmental concerns in the Norwegian salmon aquaculture production. The problems are transferable to other aquaculture producing countries as well as producers of other fish species, and many of these challenges are shared with Chilean and North American producers. Hopefully, the apparent problems due to rapid growth experienced in the Norwegian region may prevent and help other potential international producers to manage their aquaculture production in a sustainable way, whether in salmon farming or other production.

References

[1] B. Aarseth, S.-E. Jakobsen, Political regulation and radical institutional change: the case of aquaculture in Norway, Marine Policy 33 (2009) 280–287.

[2] J. Abolofia, F. Asche, J.E. Wilen, The cost of lice: quantifying the impacts of Parasitic Sea lice on farmed salmon, Marine Resource Economics 32 (3) (2017) 329–348.

[3] Anon, Bransjeveileder lakselus, lusedata.no, 2013. ⟨http://lusedata.no/for-naeringen/veileder-for-telling-av-lakselus/⟩.

[4] Anon, Status for norske laksebestander i 2017. Rapport fra Vitenskapelig råd for lakseforvaltning no 10, 2017, p. 152.

[5] Anon, Forskrift om bekjempelse av lakselus i akvakulturanlegg. Lovdata, 2017. ⟨https://lovdata.no/dokument/SF/forskrift/2012-12-05-1140⟩.

[6] Anon, 2016. Usage of antimicrobial agents and occurrence of antimicrobial

resistance in Norway. NORM-VET (2016). Tromsø/Oslo.

[7] J.L. Anderson, Market interactions between aquaculture and the common-property commercial fishery, Mar. Resour. Econ. 2 (1) (1985) 1–24.

[8] J.L. Anderson, J.E. Wilen, Implications of private salmon aquaculture on prices, production, and management of salmon resources, Am. J. Agric. Econ. 68 (1986) 866–879.

[9] F. Asche, T. Bjørndal, The Economics of Salmon Aquaculture, Second edition, Wiley-Blackwell, 2011.

[10] F. Asche, A.G. Guttormsen, T. Sebulonsen, E.H. Sissener, Competition between farmed and wild salmon: the Japanese salmon market, Agric. Econ. 33 (2005) 333–340.

[11] P.A. Bjorn, B. Finstad, Salmon lice, Lepeophtheirus salmonis (Kroyer), infestation in sympatric populations of arctic char, Salvelinus alpinus (L.), and sea trout, Salmo trutta (L.), in areas near and distant from salmon farms, ICES J. Mar. Sci. 59 (2002) 131–139.

[12] H. Bleie, A. Skrudland, Tap av laksefisk i sjø. Rapport fra Matilsynet, 2014.

[13] Fiskeridirektoratet, Rømmingsstatistikk, 2017. ⟨www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemmingsstatistikk⟩.

[14] H.B. Fjørtoft, F. Besnier, A. Stene, F. Nilsen, P.A. Bjørn, A. Tveten, B. Finstad, V. Aspehaug, K.A. Glover, The Phe362Tyr mutation conveying resistance to organophosphates occurs at high frequencies in salmon lice collected from wild salmon and trout, Sci. Rep. (2017) (Available online 10.27.2017).

[15] I.A. Fleming, K. Hindar, I.B. Mjølnerud, B. Johnsson, T. Balstad, A. Lamberg, Lifetime success and interactions of farm salmon invading a native population, Proc. R. Soc. Lond. B 267 (2000) 1517–1523.

[16] Folkehelseinstituttet, Statistikk. Legemidler i fiskeoppdrett 2016, 2017. ⟨www.fhi.no/hn/legemiddelbruk/fisk/2016-salg-av-lakselusmidler-er-synkende/⟩.

[17] T. Forseth, B.T. Barlaup, B. Finstad, P. Fiske, H. Gjøsæter, M. Falkegård, K. Hindar, T.A. Mo, A.H. Rikardsen, E.B. Thorstad, A. Vøllestad, V. Wennevik, The major threats to Atlantic salmon in Norway, ICES J. Mar. Sci. 74 (2017) 1496–1513.

[18] P.G. Gargan, O. Tully, W.R. Poole, The relationship between sea lice infestation, sea lice production and sea trout survival in Ireland, 1992–2001, in: D. Mills (Ed.), Salmon on the Edge, Blackwell Science Ltd, Oxford, UK, 2002, pp. 119–135.

[19] K.A. Glover, M.F. Solberg, P. McGinnity, K. Hindar, E. Verspoor, M.W. Coulson, M.M. Hansen, Ø. Skaala, T. Svåsand, Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions, Fish Fish. (2017) 1–38.

[20] A. Grimnes, K. Birkeland, P.J. Jakobsen, B. Finstad, Lakselus-Nasjonal og Internasjonal Kunnskapsstatus, NINA fagrapport, 1996, p. 18.

[21] R. Hannesson, Aquaculture and fisheries, Mar. Pol. 27 (2003) 169–178.

[22] P.A. Heuch, C.W. Revie, G. Gettinby, A comparison of epidemiological patterns of salmon lice, Lepeophtheirus salmonis, infections on farmed Atlantic salmon, Salmo salar L., in Norway and Scotland, J. Fish Dis. 26 (2003) 539–551.

[23] P.A. Heuch, P.A. Bjørn, B. Finstad, J.C. Holst, L. Asplin, F. Nilsen, A review of the Norwegian' national action plan against salmon lice on salmonids, Aquaculture 246 (2005) 79–92.

[24] K. Hindar, I.A. Fleming, P. McGinnity, O. Diserud, Genetic and ecological effects of salmon farming on wild salmon: modelling from experimental results, ICES J. Mar. Sci. 63 (2006) 1234–1247.

[25] K. Hindar, J.A. Hutchings, O.H. Diserud, P. Fiske, Stock, recruitment and exploitation, in: Ø. Aas, S. Einum, A. Klemetsen, J. Skurdal (Eds.), Atlantic Salmon Ecology, Wiley-Blackwell, Oxford, UK, 2011, pp. 299–332.

[26] B. Hjeltnes, G. Bornø, M.D. Jansen, A. Haukaas, C. Walde, The Health Situation in Norwegian Aquaculture 2016, Norwegian Veterinary Institute, Oslo, 2017.

[27] J.C. Holst, P. Jakobsen, F. Nilsen, M. Holm, L. Asplin, J. Aure, Mortality of seaward-migrating post-smolts of Atlantic salmon due to salmon lice infectionin Norwegian salmon populations, in: D. Mills (Ed.), Salmon at the Edge, Wiley-Blackwell, Oxford, 2003, pp. 136–137.

[28] P.M. Jensen, Høyeste antibiotikabruk i Chile på 9 år. Kyst.no, 2017. ⟨https://kyst.no/nyheter/hoyeste-antibiotikabruk-i-chile-pa-9-ar/⟩.

[29] S. Karlsson, O.H. Diserud, P. Fiske, K. Hindar, Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations, ICES J. Mar. Sci. 73 (2016) 2488–2498.

[30] M. Krkošek, M.A. Lewis, A. Morton, L.N. Frazer, J.P. Volpe, Epizootics of native fish induced by farm fish, Proc. Natl. Acad. Sci. USA 103 (42) (2006) 15506–15510.

[31] Y. Liu, O.H. Diserud, K. Hindar, A. Skonhoft, An ecological-economic model on the effects of interactions between escaped farmed and wild salmon, Fish Fish. 14 (2) (2012) 158–173.

[32] Y. Liu, J.O. Olaussen, A. Skonhoft, Wild and farmed salmon in Norway. A review, Mar. Policy 35 (2011) 413–418.

[33] Lovdata, Forskrift om drift av akvakulturanlegg (akvakulturforskriften), §5, 2008. ⟨https://lovdata.no/dokument/SF/forskrift/2008-06-17-822⟩.

[34] P. McGinnity, P. Prodöhl, A. Ferguson, R. Hynes, N.O. Maoile´idigh, N. Baker, D. Cotter, B. O'Hea, D. Cooke, G. Rogan, J. Taggart, T. Cross, Fitness reduction and potential extinction of wild populations of atlantic salmon, salmo salar, as a result of interactions with escaped farmed salmon, Proc. R. Soc. Lond. B 270 (2003) 2443–2450.

[35] P. McGinnity, P. Prodöhl, N.O. Maoile´idigh, R. Hynes, D. Cotter, N. Baker, B. O'Hea, A. Ferguson, Differential lifetime success and performance of native and non-native Atlantic salmon examined under communal natural conditions, J. Fish Biol. 65 (1) (2004) 173–187.

[36] A. Nilsen, H. Viljugrein, M.V. Røsæg, D. Colquhoun, Rensefiskehelse- kartlegging av dødelighet og dødelighetsårsaker. Veterinærinstituttets rapportserie 12-2014. Oslo: Veterinærinstituttet, 2014.

[37] Norges Sjømatråd, Laksefakta, 2016. ⟨https://laksefakta.no/⟩.

[38] Norwegian Environment Agency, Eutrophication, 2017. ⟨http://www.environment.no/topics/marine-and-coastal-waters/eutrophication/⟩.

[39] J.O. Olaussen, Y. Liu, On the willingness-to-pay for recreational fishing -escaped farmed versus wild Atlantic salmon, Aquac. Econ. Manag. 15 (4) (2011) 245–261.

[40] J.O. Olaussen, A. Skonhoft, On the economics of biological invasion: an application to recreational fishing, Nat. Resour. Model. 21 (4) (2008) 625–653 2008.

[41] A. Powell, J.W. Treasurer, C.L. Pooley, A.J. Keay, R. LIoyd, A.K. Imsland, C.G. de Lean, Use of lumpfish for sea-lice control in salmon farming: challenges and opportunities, Rev. Aquac. (2017), https://doi.org/10.1111/raq.12194.

[42] C. Revie, l. Dill, B. Finstad, C. Todd, Sea lice working group report, in: NINA Special Report 39, 2009, http://www.nina.no/archive/nina/PppBasePdf/temahefte/039.pdf.

[43] C. Roberge, E. Normandeau, S. Einum, H. Guderley, L. Bernatchez, Genetic consequences of interbreeding between farmed and native Atlantic Salmon: Insights from the transcriptome, Mol. Ecol. 17 (1) (2008) 314–324.

[44] O.B. Samuelsen, B.T. Lunestad, R. Hannisdal, R. Bannister, S. Olsen, T. Tjensvoll, E. Farestveit, A. Ervik, Distribution and persistence of the anti sea-lice drug teflubenzuron in wild fauna and sediments around a salmon farm, following a standard treatment, Sci. Tot. Environ. 508 (2015) 115–121.

[45] O.T. Skilbrei, M. Heino, T. Svåsand, Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages, from farms sites in Norway, ICES J. Mar. Sci. 72 (2015) 670–685.

[46] Statistics Norway, Aquaculture, 2017. ⟨https://www.ssb.no/jord-skog-jakt-og-fiskeri/statistikker/fiskeoppdrett⟩.

[47] Statistics Norway, Elvefiske etter laks, sjøaure og sjørøye, 2018. ⟨https://www.ssb.no/jord-skog-jakt-og-fiskeri/statistikker/fiske-og-fangst⟩.

[48] Statistics Norway, Sjøfiske. Fangst etter fiskeslag og vektklasse, 2018. ⟨https://www.ssb.no/jord-skog-jakt-og-fiskeri/statistikker/fiske-og-fangst⟩.

[49] E.B. Thorstad, B. Finstad, Impacts of salmon lice emanating from salmon farms on wild Atlantic salmon and sea trout, NIN Rep. 1449 (2018) 1–22.

[50] Y. Ye, J.R. Beddington, Bioeconomic interactions between the capture fishery and aquaculture, Mar. Resour. Econ. 11 (2) (1996) 105–123.

Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population

Article *in* Aquaculture Environment Interactions · May 2017

DOI: 10.3354/aei00223

2 authors:

Samuel Shephard
Inland Fisheries Ireland
72 PUBLICATIONS **891** CITATIONS

Paddy Gargan
Inland Fisheries Ireland
57 PUBLICATIONS **994** CITATIONS

Vol. 9: 181–192, 2017
https://doi.org/10.3354/aei00223

AQUACULTURE ENVIRONMENT INTERACTIONS
Aquacult Environ Interact

Published May 5

Quantifying the contribution of sea lice from aquaculture to declining annual returns in a wild Atlantic salmon population

Samuel Shephard*, Patrick Gargan

Inland Fisheries Ireland, 3044 Lake Drive, CityWest Business Campus, Dublin 24, D24 Y265, Ireland

---

ABSTRACT: Atlantic salmon *Salmo salar* has shown declines in abundance associated with reduced survival during marine life stages. Key impacts on survival may include a changing ocean environment and salmon louse *Lepeophtheirus salmonis* infestation from aquaculture. A 26 yr record from the Erriff River (Western Ireland) was used to evaluate the contribution of sea lice from salmon aquaculture to declining returns of wild 1 sea-winter (1SW) salmon. Statistical models suggested that returns were >50% lower in years following high lice levels on nearby salmon farms during the smolt out-migration. The long-term impact of salmon lice was explored by applying predicted annual loss rates as a multiplier to observed 1SW salmon returns. This produced a 'lice-corrected' return time series, i.e. an estimate of how returns might have looked in the absence of a serious aquaculture lice impact. The corrected time series was adjusted to account for some reduction in recruitment due to lost spawners. Comparing observed and lice-corrected time series suggested that salmon lice have strongly reduced annual returns of 1SW Erriff salmon, but that the salmon lice impact does not explain a declining trend in this population.

KEY WORDS: *Lepeophtheirus salmonis* · *Salmo salar* · Salmon smolts · Salmon farming · Ricker stock recruitment

---

INTRODUCTION

Atlantic salmon *Salmo salar* is an iconic anadromous fish species that has shown marked declines in abundance in recent decades (Limburg & Waldman 2009). Decreased survival rate in the marine environment, rather than in natal rivers, seems to explain the current poor state of many salmon populations (ICES 2016). Marine survival can be partitioned into coastal (transitional and inshore waters) and oceanic (offshore and open ocean) components. The coastal component operates during the first migration of juvenile salmon (smolts) out of their natal river. Events during such early life stages can have an impact on subsequent marine survival of salmon (Holsman et al. 2012). The oceanic component refers to fish in summer nursery areas offshore and in winter feeding areas. In addition to natural mortality, each component of marine survival is influenced by anthropogenic pressures.

Coastal pressures frequently interact (Parrish et al. 1998) and include local pollution (Larsson et al. 1996, McCormick et al. 1998, Johnson et al. 2007) and increased rates of sea lice *Lepeophtheirus salmonis* infestation associated with salmon aquaculture (e.g. Krkošek et al. 2007, Costello 2009). Sea cage aquaculture causes sea lice on sympatric wild fish to increase (Frazer 2009). Marine survival of wild pink salmon has been related negatively to lice density on farmed salmon (Marty et al. 2010, Krkošek et al. 2011) and to observed lice infestation on out-migrating juvenile wild fish (Peacock et al. 2013). The negative impact of sea lice on salmonid survival appears to be exacerbated by warmer environmental conditions (Bateman et al. 2016, Shephard et al. 2016). In the ocean, salmon respond to large-scale climate

---

*Corresponding author: sam.shephard@fisheriesireland.ie

Publisher: Inter-Research · www.int-res.com

forcing (ICES 2016) by the North Atlantic Oscillation (NAO) and the Atlantic Multi-decadal Oscillation (AMO) that drive sea surface temperature (SST) and thus salmon thermal habitat (Friedland et al. 1993, 2003, Jonsson & Jonsson 2004, Mills et al. 2013) and associated prey dynamics (Beaugrand & Reid 2012, Defriez et al. 2016). Recent studies suggest that ocean warming has had a negative impact on oceanic growth and survival (McCarthy et al. 2008, Todd et al. 2008, Friedland et al. 2009) and genetic diversity (Horreo et al. 2011) of Atlantic salmon.

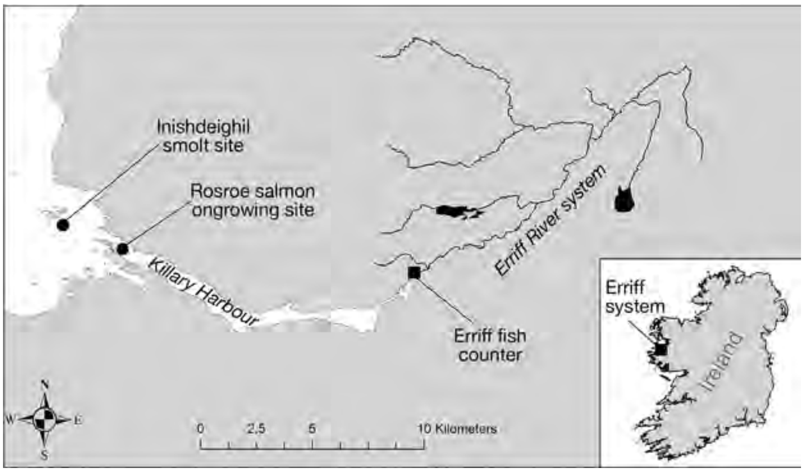


Fig. 1. Erriff River system and Killary Harbour, Ireland, showing the location of the salmon aquaculture sites and the fish counter

Strong environmental impacts on marine life stages of salmon have made it difficult to use observational data to separate the effects of sea lice from other effects on survival, and so much relevant work applies field trials using cultivated salmon smolts treated with anti-parasitic agents (Gargan et al. 2012, Krkošek et al. 2012). Some trials indicate that baseline survival of smolts has an important influence on the success of lice treatment, with poorer environmental conditions increasing vulnerability to sea lice impacts. Hence, population-level effects of sea lice on wild salmon cannot be estimated independently of the other factors that affect marine survival (Vollset et al. 2016). The contribution of sea lice to overall marine survival of wild Atlantic salmon remains an important knowledge gap, particularly in the context of changing oceanographic conditions and the long-term decline of many populations. Parsing out coastal sea lice effects might contribute to understanding of changing high-seas marine survival, and possibly guide management of lice on salmon farms to reduce impacts on wild populations (Peacock et al. 2013).

The Erriff River system in the west of Ireland is designated as a Special Area of Conservation for Atlantic salmon under the European Union Habitats Directive (92/43/EEC). This system has supported salmon angling since the late 19th century, with annual returns of fish to the river being recorded for several decades. Salmon aquaculture commenced in the Erriff estuary (Killary Harbour) in the mid-1980s, and licensed annual production increased from 450 t in 1986 to 2200 t by 2006. Levels of sea lice infestation on the Killary salmon farm have been recorded since 1991. The position of this salmon farm at the entrance to a narrow fjord (Fig. 1) makes the Erriff system an excellent 'natural experiment' on the possible effects of sea lice from aquaculture on marine survival of a wild Atlantic salmon population. We used a 26 yr record from the Erriff to investigate relationships between sea lice (salmon lice *Lepeophtheirus salmonis*; hereafter simply sea lice) infestation on the Killary salmon farm and annual returns of wild 1 sea-winter (1SW) Erriff salmon, while accounting for unexplained inter-annual variability in marine survival of this population.

MATERIALS AND METHODS

Study system

The Erriff River has a catchment area of 166 km^2 and discharges into Killary Harbour, a 15 km long fjord in the west of Ireland (Fig. 1). Data series used in the current study comprised:

(1) Annual wild Atlantic salmon *Salmo salar* returns: (a) count of 1SW Erriff fish returning to the river, and (b) estimated return (accounting for annual commercial fishing mortality at sea, F; see below) of Erriff salmon to the Irish coast (1987–2016).

(2) Annual aquaculture lice count estimate: average number of mobile (pre-adult and adult) sea lice (*Lepeophtheirus salmonis*) fish^{-1} on the Killary salmon farm (Fig. 2) in April (www.marine.ie/Home/site-area/areas-activity/aquaculture/sea-lice), multiplied by an estimate of the total number of fish on the farm (taken as 0 in 1986 prior to farming and recorded for 1991–2016. For years when the smolt on-growing site (Fig. 1) was active, estimated total lice from this site were added to the total for the salmon farm. The current analysis related the number of returning 1SW

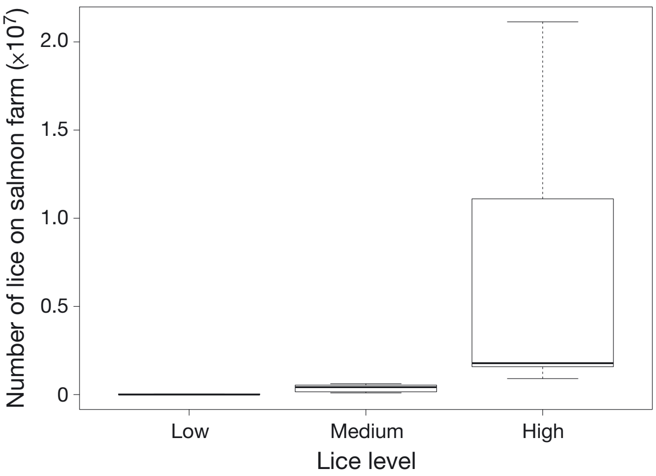


Fig. 2. Numbers of sea lice in each level of the categorical lice variable $Lcat2_i$. Summary statistics are the median of the data, the lower and upper quartiles (25% and 75%) and the minimum and maximum values. There are 8 data points (years) for the Low lice level, and 9 data points in each of Medium and High lice levels

salmon to the number of sea lice on aquaculture sites in the previous year, i.e. when those 1SW fish outmigrated as smolts. Aquaculture lice counts for April were used as an index of lice infestation pressure on wild migrating salmon smolts because records from 2002–2016 (N = 15 684 smolts, Inland Fisheries Ireland unpublished data) indicated that 88% of the wild salmon smolt run in the Erriff catchment occurs between 1 April and 10 May.

Estimation of annual wild salmon returns

Two salmon return series were used. Salmon entering the Erriff are recorded by a fish counter approximately 200 m upstream of the river mouth. The annual count of 1SW salmon S returning to the Erriff River in year i (S_{iRiver}) was calculated as the sum of 1SW salmon rod caught (killed) below the fish counter and the number recorded by the counter. S_{iRiver} represents exact known counts of fish entering the river, but does not account for variable levels of F prior to return. Estimated return to the Irish coast (S_{iCoast}) was estimated by using F time series to expand S_{iRiver}. Commercial drift and draft net fisheries for wild salmon both operated off the Irish coast during the early study period, viz. 1987–2006, but fishing was restricted to inshore draft netting from 2007–2016. F was calculated slightly differently for these 2 time periods:

(1) Combined (drift and draft net) mean annual exploitation rate F for 1SW salmon has been calculated for 2 west of Ireland salmon stocks: Corrib and Burrishoole (Ó Maoiléidigh et al. 2015). These averaged F estimates (Fig. 3) were used to raise S_{iRiver} to an estimate of S_{iCoast} for 1987–2006, where $S_{iCoast} = S_{iRiver} / (1 - F)$. These estimated S_{iCoast} values suggest that Erriff fish contributed about 1.3% to the total annual catch of salmon in the Irish drift net fishery. This value is somewhat uncertain, as F was derived from a subsample of the overall commercial catch (Ó Maoiléidigh et al. 2015). However, it is similar to independent estimates of the contribution of Erriff salmon to the drift net catch based on assigning captured fish to their natal river using a genetic signature. Genetic assignment suggested that the total drift net catch comprised 1.7% Erriff fish in 2005 and 2.5% Erriff fish in 2006 (Anon 2008).

(2) Total annual catch in the Killary draft net fishery S_{id} is recorded and can be allocated to 3 local rivers including the Erriff. These 3 rivers have salmon conservation limits (CLs) of 1383 (Erriff), 136 (Culfin) and 165 (Delphi), where CL is defined as the spawning stock level that produces long term average maximum sustainable yield as derived from the adult to adult stock and recruitment relationship, and is quantitatively derived for each river by the Irish Standing Scientific Committee for Salmon. The Erriff CL represents 82% of the summed CL for the 3 rivers in Killary; F for 2007–2016 was thus calculated as $0.82 \times S_{id} / (0.82 \times S_{id}) + S_{iRiver}$, and $S_{iCoast} = S_{iRiver} / (1 - F)$ as above.

Statistical analysis: estimating the lice effect on salmon returns

By observation i, the data consisted of (S_i, Y, L_i), where S_i is the number of Erriff salmon returning (to either the river or the coast) in sampling year $Y_{i\ 1,\ldots,30}$ (1987–2016) and L_i is the estimated total number of sea lice on the Killary salmon farm (on-growing and smolt sites) in the previous year Y_{i-1} (no data for 1987–1990). Sea lice number was also interpreted as a categorical variable with 3 intensity levels (Low, Medium, High) in order to facilitate interpretation of lice impacts across (continuous) Y_i. Two approaches to categorizing L_i were tested: (1) $Lcat_i$ according to 0–25th, 25th–75th and 75th–100th percentiles of L_i, and (2) $Lcat2_i$ using natural divisions in L_i, which had groups of data points at 3 distinct levels (Fig. 2).

We developed statistical models to quantify possible effects of sea lice on each of S_{iRiver} and S_{iCoast} (1987 and 1992–2016), while accounting for an observed declining trend in salmon returns, and also for other

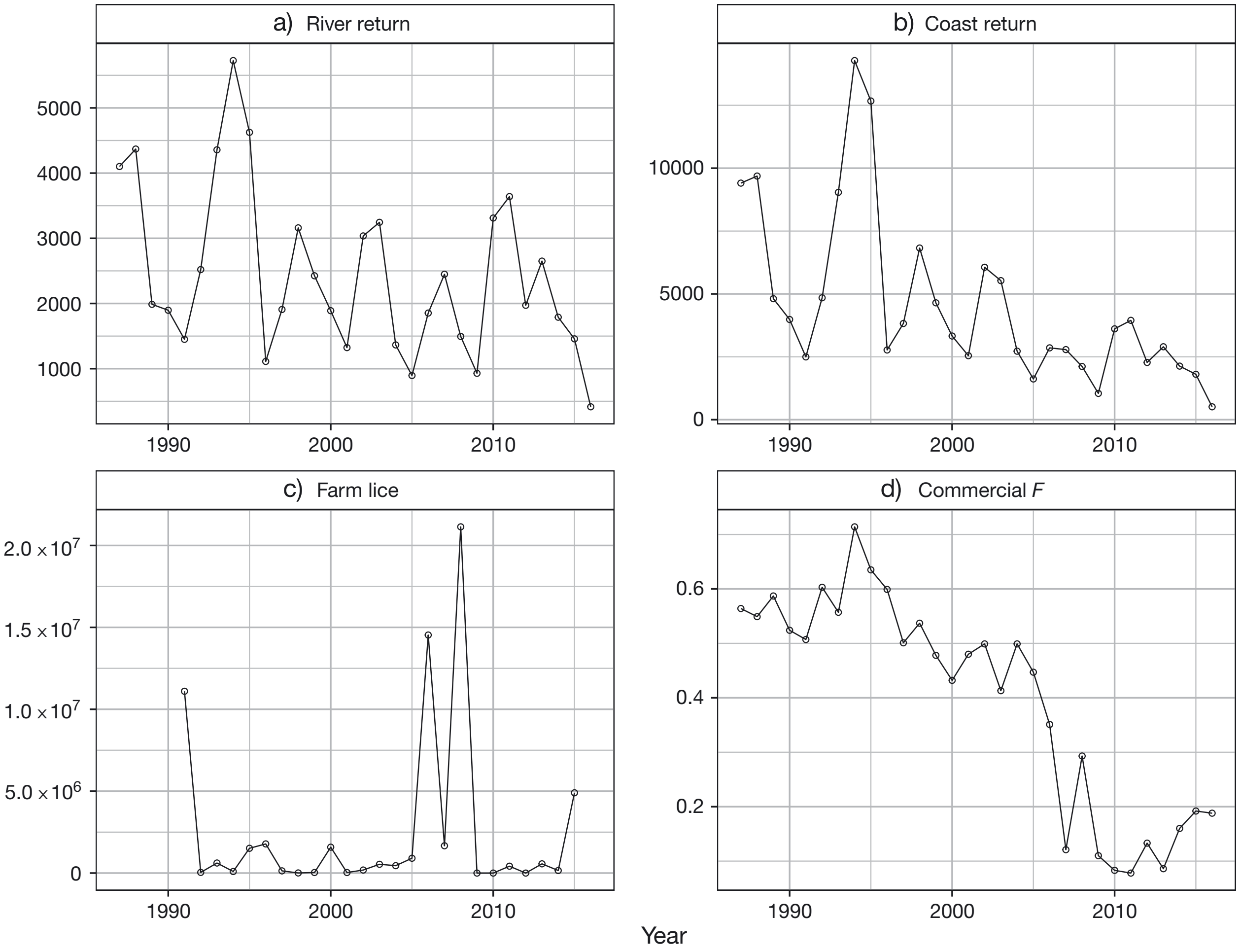


Fig. 3. Time series of returns of 1 sea-winter (1SW) Erriff River Atlantic salmon (a) to the river (S_{iRiver}) and (b) to the Irish coast (S_{iCoast}); (c) estimated number of sea lice in the Killary salmon farm; and (d) estimated commercial fishing mortality (F) for Erriff salmon

unexplained annually varying environmental drivers of marine mortality. The negative trend in Erriff salmon returns was incorporated by using standardised (subtracting the mean and dividing by the standard deviation) Y_i as a continuous fixed variable. Unexplained annual effects on salmon returns were incorporated by specifying year as a categorical variable $Ycat_i$, and including this variable as a random effect α_i on the intercept. $Ycat_i$ thus captures inter-annual effects on returns that cannot be accounted for by the lice and Y_i covariates (see Elston et al. 2001) and which are expected to largely comprise environmental variability. As an observation level random effect (OLRE), $Ycat_i$ also acts as a simple and robust means to account for overdispersion in count data (Harrison 2014). The 5 variables specified above (S_i, Y_i, L_i, $Lcat_i$, $Lcat2_i$) were used to specify a comprehensive set of 7 candidate models, all including $Ycat_i$ as a random effect α_i (Table 1).

The same modelling process was applied to each of S_{iRiver} and S_{iCoast} separately. In each case, the model set (Table 1) was fit using a Poisson GLMM (lme4 package in R, Bates et al. 2015). The full model had the form:

Table 1. Set of 7 candidate models of the number of 1 sea-winter (1SW) Erriff River Atlantic salmon returning to the river and to the Irish coast (1987 and 1992–2016). Model parameters are defined in 'Materials and methods'

No.	Model
1	$\log(\mu_i) = Y_i + \alpha_i$
2	$\log(\mu_i) = \ln(L_i) + \alpha_i$
3	$\log(\mu_i) = \ln(L_i) + Y_i + \alpha_i$
4	$\log(\mu_i) = Lcat1_i + \alpha_i$
5	$\log(\mu_i) = Lcat1_i + Y_i + \alpha_i$
6	$\log(\mu_i) = Lcat2_i + \alpha_i$
7	$\log(\mu_i) = Lcat2_i + Y_i + \alpha_i$

$$S_i \sim \text{Poisson}(\mu_i) \quad (1)$$

$$E(S_i) = \text{var}(S_i) = \mu_i \quad (2)$$

$$\log(\mu_i) = L_i + Y_i + \alpha_i \quad (3)$$

$$\alpha_i \sim N(0, \sigma^2_{Ycat}) \quad (4)$$

Akaike's Information Criterion (AIC) was used to compare model fits, where any models within 2 AIC units of the best-fitting model would be considered to have similar fit to the data. Various diagnostics were used to explore model fit and statistical assumptions: (1) plots of standardised (Pearson) residuals were checked for homogeneity, (2) linearity in the relationships between salmon return and tested (continuous) covariates was evaluated by plotting Pearson residuals against each covariate in the model and fitting a GAM to visualize any non-linear patterns, and (3) temporal autocorrelation in model residuals was evaluated using the acf function in R.

Selected (lowest AIC) final models for both S_{iRiver} and S_{iCoast} included sea lice characterised as $Lcat2_i$. The effect on return of 1SW Erriff salmon of sea lice level ($Lcat2_i$: Low, Medium, High) in each of these selected models was visualized using the R package 'Effects', where other variables were held at average values (Fox 2003). The random effect of year $Ycat_i$ was plotted with 95% confidence intervals. Salmon returns at each lice level were also predicted (predict function in R) and plotted for each level of $Ycat_i$ (26 levels, i.e. years), considering 3 periods of the time series Y_i (Early, Mid, Recent) to show how the predicted (within year) lice effect on salmon returns compared to the (across year) random year effect (assumed to express annually-varying environmental effects on returns).

Predicting long-term salmon returns without sea lice

The models above predicted that the average return of 1SW Erriff salmon to the river is reduced by 18.6% following a year of Medium lice levels and 52.2% following a year of High lice levels; returns to the coast were predicted to be reduced by 2.3 and 49.6%, respectively. We used these lice impact levels and a fitted stock-recruitment relationship to estimate how annual salmon returns might have looked over the last 25 yr in the absence of a serious impact of sea lice from aquaculture:

(1) Observed annual salmon returns (each of S_{iRiver} and S_{iCoast}) were first 'lice-corrected' (multiplied up) according to the annual loss rates predicted from modelling; loss rates were expressed as the percentage difference between predicted salmon returns at each of Medium and High lice levels and the predicted return at Low lice levels in an average year. For example, the observed return to the river in 1992 was 2520 salmon, but because the lice level was 'High' during the smolt run in 1991, it is predicted that this run represents a 52.2% reduction compared to the run that would have happened in Low lice conditions (given average environmental conditions as expressed by $Ycat_i$). The lice-corrected return Se_i was thus calculated as $Se_{1992} = 2520 / (100 - 52.2) \times 100 = 5272$ salmon.

(2) To realistically estimate the cumulative impact of sea lice on long-term returns of Erriff salmon, it was then necessary to account for likely diminished recruitment associated with loss of potential spawners (hereafter 'missing spawners') that never returned to the river/coast because they suffered lice-related mortality as smolts. 85% of Erriff salmon migrate as 2 yr smolts, resulting in a 4 yr generation time (White et al. 2016). Adult-to-adult Ricker stock recruitment (*SR*) relationships were produced for each of river and coast returns (see Fig. 6), where S is the observed return S_i and R is the lice-corrected return 4 yr later, Se_{i+4}. These *SR* curves were used to estimate peak (asymptotic) recruitment Rp, and the peak stock Sp at Rp, for each of S_{iRiver} and S_{iCoast}. The number of 'missing spawners' Sm_i in each year was then estimated as $Sm_i = Se_i - S_i$, with Se_i being capped at Sp on the assumption that once Sp is exceeded, there is no further positive effect on subsequent recruitment.

(3) A lice-corrected adult-to-adult return rate, RR, was then estimated for each year Y_i in each of S_{iRiver} and S_{iCoast}, assuming that each S_i comprised 85% 4 yr and 15% 5 yr fish (White et al. 2016), such that RR_i is the weighted mean of (Se_i / S_{i-4}) and (Se_i / S_{i-5}) with weightings being 85 and 15, respectively. These RR_i are an estimate of the number of returning fish expected (given Low lice levels) from each parent fish. 85% of missing fish Sm_i were then allowed to contribute recruits Sr_i to the return 4 yr later according to the estimated return rate RR_i, where this contribution $Sr_{i+4} = (0.85 \times Sm_i) \times RR_{i+4}$. The remaining 15% of missing fish contributed to recruitment 5 yr later as $Sr_{i+5} = (0.15 \times Sm_i) \times RR_{i+5}$. To restrict un-quantified uncertainty in this process, missing fish were only considered to contribute recruits to a single generation.

(4) Finally, a total expanded return $Stot_i$, including the annual lice-correction and the associated (1 generation) effect on recruitment, was calculated as $Stot_i = Se_i + Sr_i$. Time series of S_i and $Stot_i$ were plotted together for visual comparison, with the first 4 yr of $Stot_i$ obviously not including any Sr_i as there were no lice data for their respective parent generations.

RESULTS

Estimating the lice effect

Model 7 (see Table 1) was the best fitting model for both S_{iRiver} (ΔAIC = 3.8) and S_{iCoast} (ΔAIC = 4.0). The model including only year as a continuous variable (Model 1, Table 1), had ΔAIC > 8.0 compared to Model 7 fitted to S_{iRiver}, and ΔAIC > 11.0 compared to Model 7 fitted to S_{iCoast}, indicating that $Lcat2_i$ strongly improved model fit. Diagnostic plots did not show important heterogeneity or non-linearity in residuals, and there was no significant temporal autocorrelation. There were significant negative effects of the continuous year variable Y_i on each of S_{iRiver} and S_{iCoast}, i.e. long-term declines in 1SW salmon returns (Table 2). There were also significant negative effects of High sea lice levels $Lcat2_i$ during the smolt outmigration on each of S_{iRiver} and S_{iCoast} in the following year (Table 2). Predicted returns were reduced at Medium and strongly reduced at High lice levels. For an average random year $Ycat_i$ and continuous year Y_i: the predicted S_{iRiver} (1394 fish) at High lice levels was 52.2% less than the predicted return (2919 fish) at Low lice levels (Fig. 4a); predicted S_{iCoast} (2226 fish) at High lice levels was 49.6% less than the predicted return (4419 fish) at Low lice levels (Fig. 4b).

The OLRE $Ycat_i$ captures any important patterns in the response variable that cannot be modelled by other terms in the model (Zuur et al. 2015). Strong variation in salmon returns across levels of $Ycat_i$ indicated considerable inter-annual variation in salmon returns to the river and coast (Fig. 5), probably reflecting environmental effects. However, the predicted 52.2% reduction in S_{iRiver} following 'High' lice levels is greater than the average year-to-year ($Ycat_i$ to $Ycat_{i+1}$) change in predicted returns (mean = 44.6%, range = 0.6% to 262.7%) for the Early value of Y_i, suggesting that the lice impact is meaningful in the context of background environmental forcing. This comparison showed similar results for S_{iCoast}.

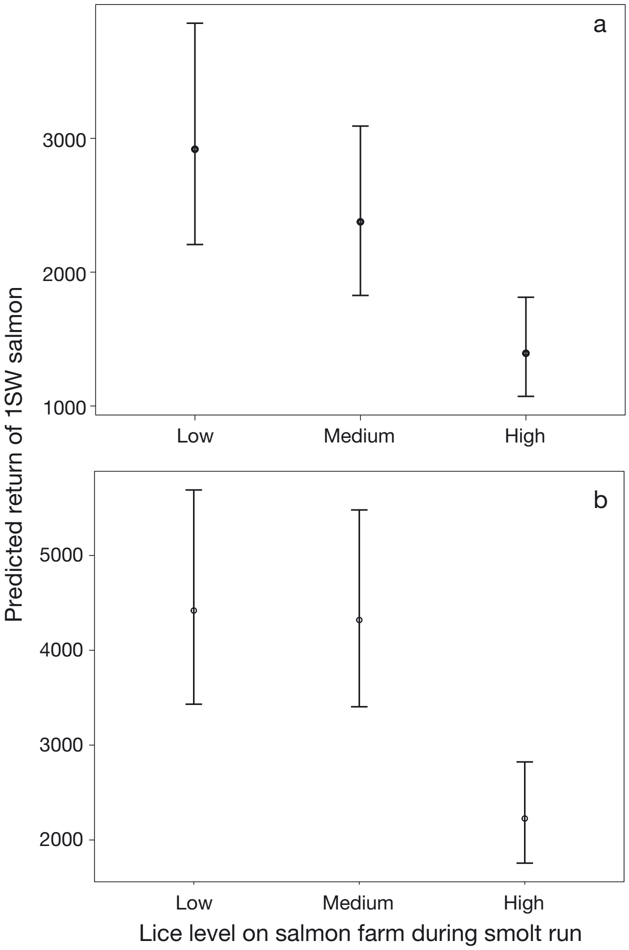


Fig. 4. Predicted return of 1 sea-winter (1SW) Erriff River Atlantic salmon to (a) the river (S_{iRiver}) and (b) the Irish coast (S_{iCoast}) at 3 levels of sea lice density at the Killary salmon farm during the smolt run. Error bars are 95% confidence intervals

Table 2. Results from selected models (Model 7, see Table 1) of annual returns of 1 sea-winter (1SW) Erriff River Atlantic salmon returning to the river (S_{iRiver}) and to the Irish coast (S_{iCoast})

River returns	Estimate	SE	*z*-value	p
(Intercept)	7.979	0.143	55.917	<0.001
Year	−0.277	0.081	−3.412	<0.001
Lice level Medium	−0.206	0.197	−1.045	0.296
Lice level High	−0.739	0.196	−3.772	<0.001
Coast returns				
(Intercept)	8.394	0.129	65.064	<0.001
Year	−0.551	0.073	−7.512	<0.001
Lice level Medium	−0.023	0.178	−0.128	0.898
Lice level High	−0.686	0.177	−3.871	<0.001

Predicting the contribution of sea lice impacts to long-term returns of Erriff salmon

Adult-to-adult Ricker *SR* curves, assuming a 4 yr generation time, showed a (visually) reasonable fit for both river and coast returns, suggesting that estimates of *Rp* and *Sp* were acceptable (Fig. 6). Comparing observed salmon returns S_i with lice-corrected returns $Stot_i$ for S_{iRiver} and S_{iCoast} (Fig. 7) showed that while the sea lice effect can strongly reduce annual returns S_i, 'correcting' for this effect

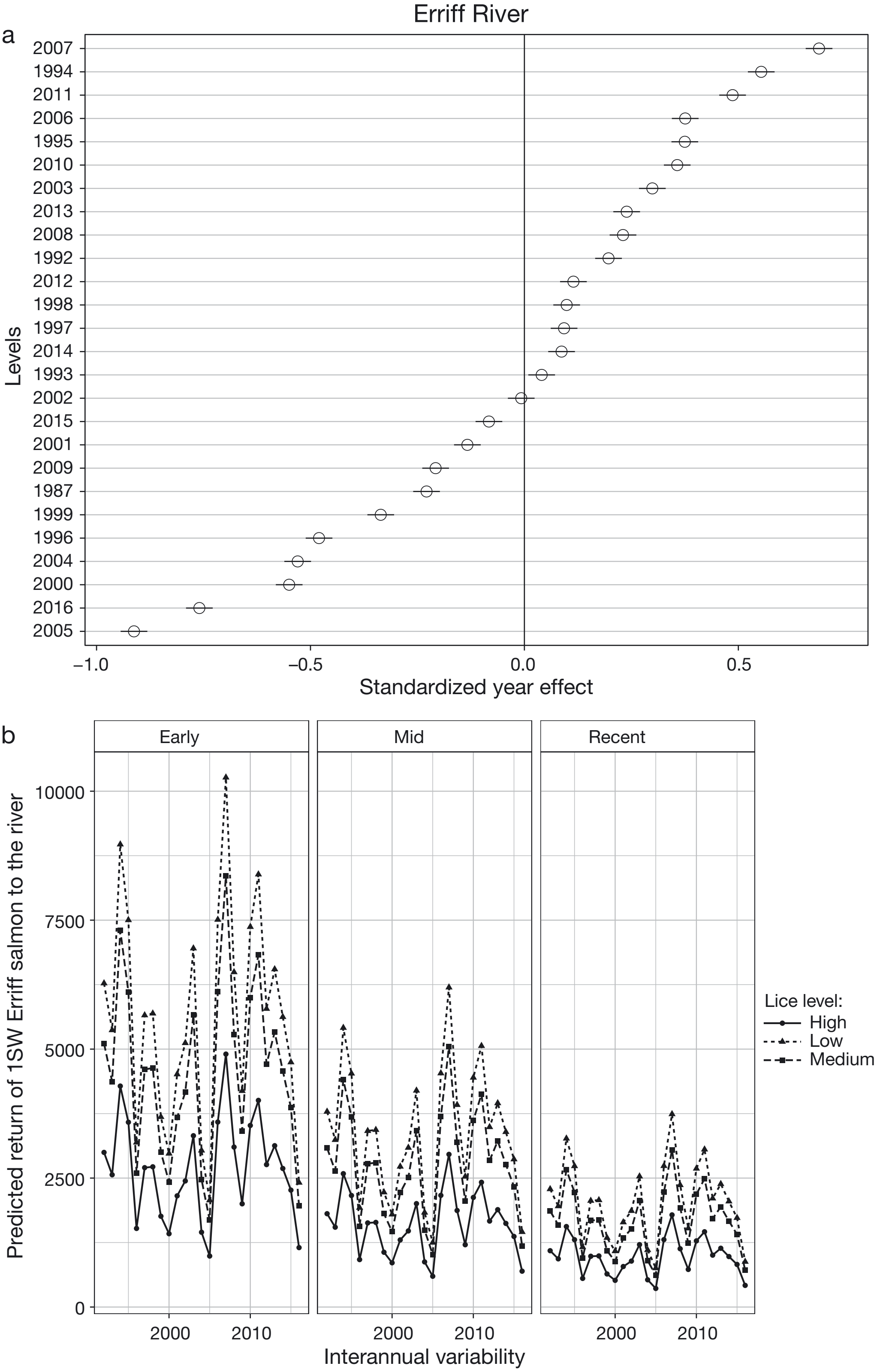


Fig. 5. (a,c) Random effects (with 95 % CI) on the intercept of year ($Ycat_i$) from the selected model (Model 7, Table 1) of returns of 1 sea-winter (1SW) Erriff River Atlantic salmon to (a) the river (S_{iRiver}) and (c) the Irish coast (S_{iCoast}). (b,d) Random year effect (assumed to express unexplained inter-annual variability) on predicted returns of these salmon to (b) the river and (d) the Irish coast in 3 different periods of the return time series (Early, Mid, Recent) and at 3 levels of estimated salmon lice infestation ($Lcat2_i$) on the Killary salmon farm

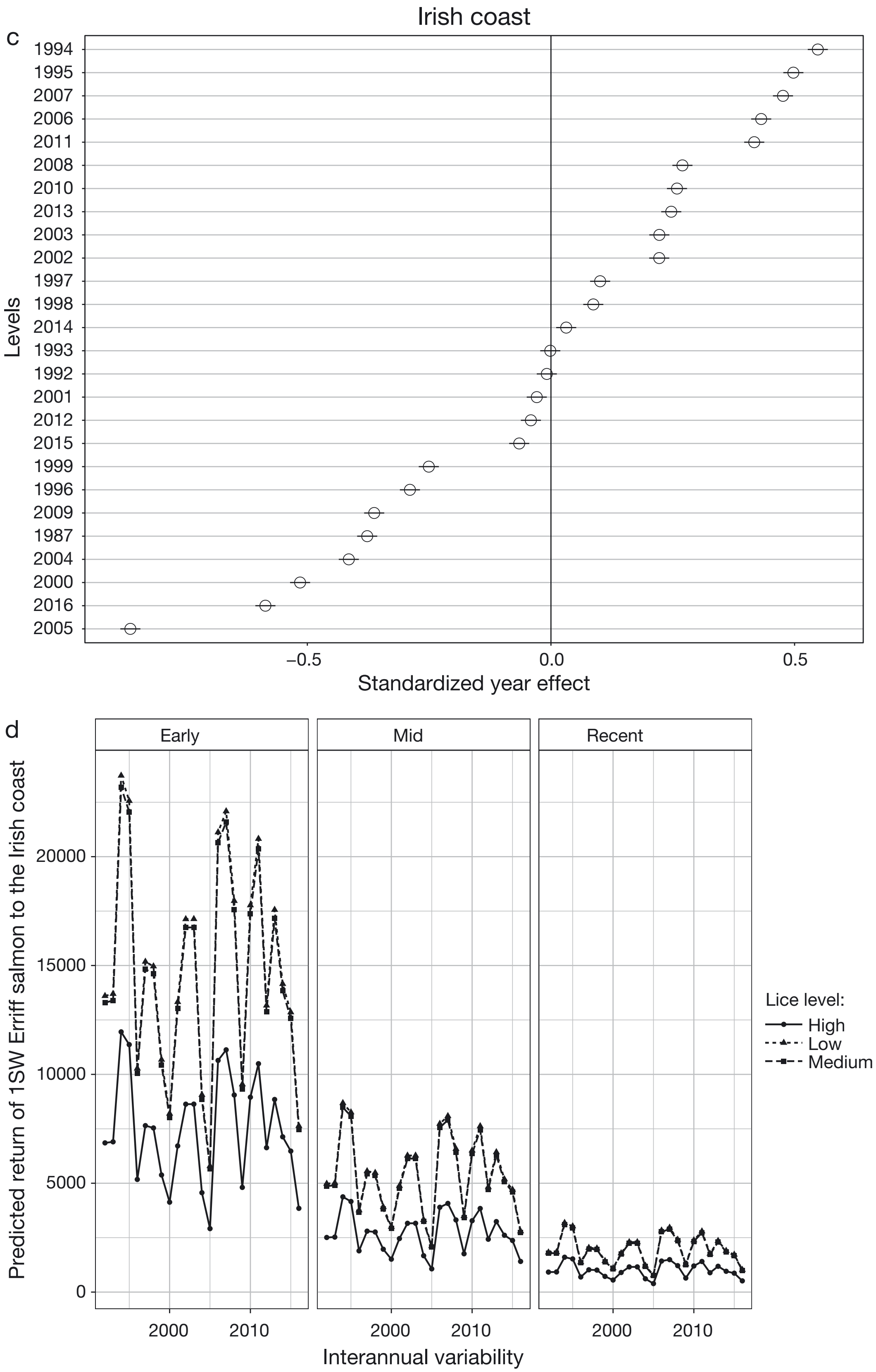


Fig. 5 (continued)

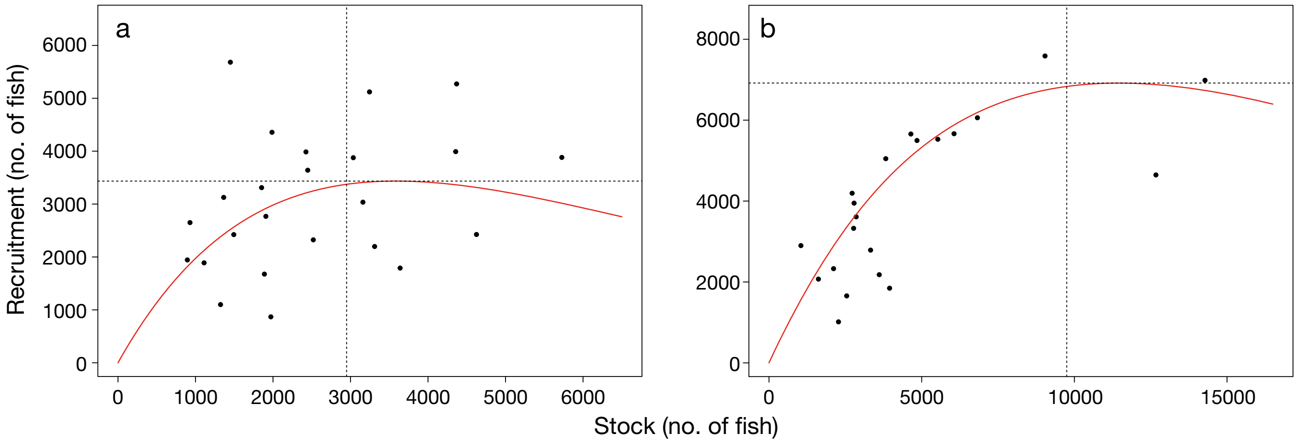


Fig. 6. Ricker stock recruitment curves fit to adult-to-adult stock-recruitment data for 1 sea-winter (1SW) Erriff River Atlantic salmon returns to (a) the river (S_{iRiver}) and (b) the Irish coast (S_{iCoast}). Stock values are observed returns; recruitment values are 'corrected' according to the annual lice effect estimated from statistical models. A 4 yr generation time (adult return to adult return) is assumed. The horizontal dashed lines are peak recruitment (*Rp*) and the vertical lines are peak stock (*Sp*)

does not remove the declining trend. The marked decline in the last 3 yr of both time series reflects relatively low estimated salmon return rates RR_i for these years (Table 3).

DISCUSSION

We analysed a 30 yr time series of returns of 1SW Erriff salmon, with 26 yr of corresponding estimated lice counts from the Killary salmon farm. Wild salmon returns were strongly reduced (>50%) following years when there had been high lice levels on the salmon farm during the smolt out-migration. This result accounts for the effect of unexplained among-year variation in returns, which probably reflects how marine survival varies naturally independent of lice-induced mortality (Vollset et al. 2016). 'Correcting' for the estimated lice effect predicted that Erriff salmon returns might now be twice as large without observed anthropogenic sea lice impacts, but would probably show a similar long-term decline.

Infectious disease is a contributing factor in 8% of cases where a species is listed by the IUCN as Critically Endangered (Smith et al. 2006). Peacock et al. (2013) estimated that the percentage mortality of pink salmon in the Broughton Archipelago of British Columbia, Canada, due to sea lice infestations ranged from 3.8% for returns in 2010 to 90.1% for returns in 2002; Bateman et al. (2016) estimated that lice-induced mortality in the same region was 9 to 39% in 2015. Our results demonstrate that sea lice infestation from coastal salmon aquaculture is likely to be an important contributor to observed decline in

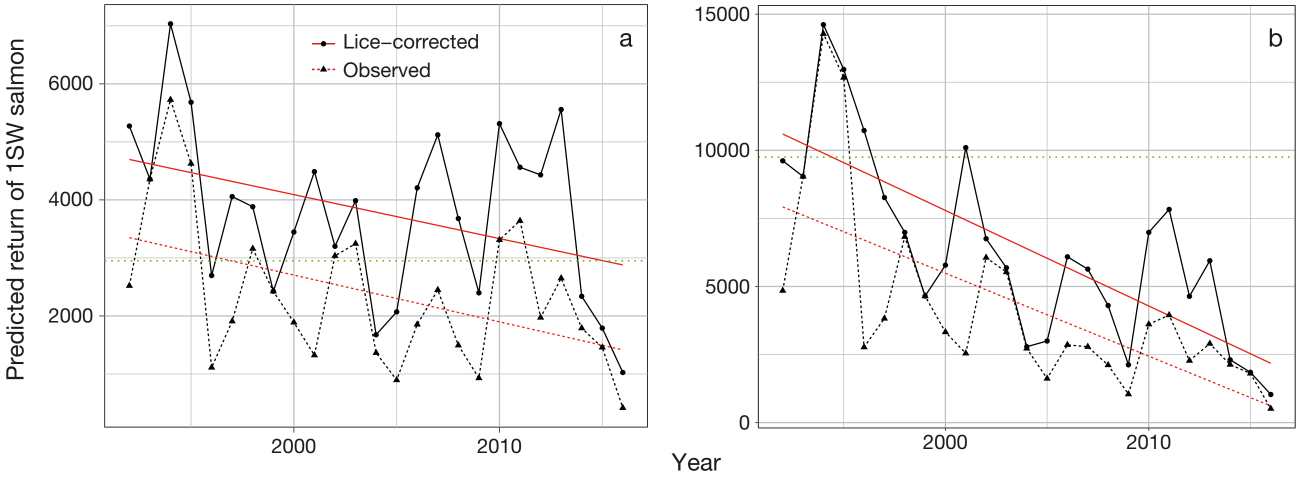


Fig. 7. Observed (S_i) and 'lice-corrected' (Se_i) returns of 1 sea-winter (1SW) Erriff River Atlantic salmon to (a) the river and (b) the Irish coast. The green line is peak recruitment (*Rp*) estimated from the Ricker curve (see Fig. 6)

Table 3. Estimated annual adult-to-adult return rates (RR_i) for 1 sea-winter (1SW) Erriff River Atlantic salmon to the river or the Irish coast

Year	River RR_i	Coast RR_i
1992	1.21	0.99
1993	2.01	1.74
1994	3.68	3.58
1995	3.78	4.91
1996	1.02	1.29
1997	1.02	0.95
1998	0.71	0.53
1999	0.51	0.36
2000	1.51	1.06
2001	1.61	1.40
2002	1.05	0.99
2003	1.58	1.16
2004	0.86	0.80
2005	0.79	0.63
2006	1.53	1.13
2007	1.60	0.99
2008	2.09	1.42
2009	2.06	1.20
2010	2.08	1.41
2011	1.56	1.41
2012	1.53	1.06
2013	2.69	2.57
2014	0.92	0.82
2015	0.50	0.48
2016	0.41	0.42

returns of wild Atlantic salmon to the Erriff River system. This finding upholds a substantial literature on the impacts of sea lice on salmonids, and successive experiments using anti-parasite lice treatments. A meta-analysis of differential survival between control and parasiticide-treatment groups of cultured Atlantic salmon showed that returns of treated fish were 39% greater (Krkošek et al. 2012). Our results for the Erriff predict that the return of 1SW salmon migrating in a high lice year may be reduced by more than 50% compared to the return from wild smolts that were not exposed to high levels of sea lice from salmon aquaculture during early out-migration.

Sea lice present during the spring smolt outmigration through Killary Harbour could have salmon farm and/or wild salmon sources. Gargan et al. (2012) found that the number of wild salmonids was very low during this period, and that sea lice abundance on local farmed salmon was 3 to 4 orders of magnitude greater than the estimate for wild salmonids. A study on the production of sea lice larvae from farmed and wild salmon and its relation to the infestation of wild sea trout found that farmed salmon contributed 95% of the total production of *L. salmonis* nauplii in the mid-west Irish coast region (Tully & Whelan 1993). These observations suggest that sea lice infestation pressure on wild Erriff smolts originates overwhelmingly from aquaculture.

Lice-induced mortality may have 2 components. Short-term mortality probably occurs when attached lice reach the pre-adult and adult life stages, causing severe osmoregulatory problems indicated by highly elevated plasma chloride levels and increased plasma osmolality (Bjørn & Finstad 1997, Dawson et al. 1998, Wells et al. 2006). A longer-term reduction in survival may be associated with impacts that impair on-going fitness during migration. The impact of sea lice seems to vary with baseline survival of salmon; a meta-analysis of studies using anti-parasite treatments on salmon smolts found that in groups with low recapture in the control group (low baseline survival), the effect of treatment was high, while in groups with high recapture in the control group (high baseline survival), there was no effect of treatment (Vollset et al. 2016). This result implies that the detrimental effect of lice is exacerbated in situations when the salmon smolts also have to cope with increased pressure from other causes of mortality, e.g. unfavourable environmental conditions. A post hoc plot of standardised salmon returns to the Erriff S_{iRiver} shows that observed returns approximately track the random year effect $Ycat_i$ (expressing environmental variability). However, the 4 lowest returns on record occurred when a high lice year coincided with poor baseline survival, while the only 2 occasions when a high lice year produced a greater than average run (1992 and 2007) were during high baseline survival (Fig. 8).

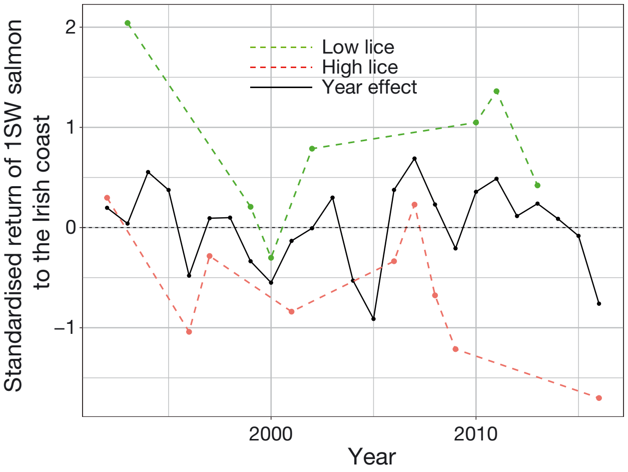


Fig. 8. Observed Erriff River Atlantic salmon returns to the river (S_{iRiver}), standardised to 0 for years estimated to have 'High' and 'Low' levels of sea lice (years of Medium lice level are excluded for clarity). Year effect is the random effect of year ($Ycat_i$), assumed to express environmental effects on salmon returns

Our results show very low return rates of Erriff salmon in the most recent years, corresponding to apparent declines in marine survival of Atlantic salmon (ICES 2016). Oceanic life stages of salmon are susceptible to climate forcing by the NAO and the AMO that drive SST and thus thermal habitat (Friedland et al. 1993, 2003, Jonsson & Jonsson 2004, Mills et al. 2013) and associated prey dynamics (Beaugrand & Reid 2012, Defriez et al. 2016). Recent studies suggest that warming SST has had a negative impact on oceanic growth and survival (McCarthy et al. 2008, Todd et al. 2008, Friedland et al. 2009) of Atlantic salmon, possibly mediated through productivity and trophic interactions (Beaugrand & Reid 2003, Mills et al. 2013). Hence, aquaculture sea lice impacts on wild Atlantic salmon are imposed upon possibly declining baseline survival.

The negative effect of sea lice from aquaculture may be unusually strong for the Erriff wild salmon population because the Killary salmon farm is located in the mouth of a long and narrow fjord. It is also the case that the 26 yr time series of salmon runs and lice counts, while valuable, still refer to only a single system. A preliminary analysis using these records attempted to identify specific environmental components of marine mortality in addition to sea lice. There were insufficient data for this exercise and so the simpler and more robust random year approach presented here was followed. Despite this limitation, it seems reasonable to expect important lice impacts in other systems where salmon farm(s) with high spring lice levels occur in bays and estuaries with rivers having wild salmon populations. A study of chemically treated and untreated salmon smolt releases in 3 west of Ireland bays (including Killary) found that lice-induced mortality of adult salmon can be significant, and that an increase in mortality of salmon smolts can be expected where farm lice levels are not maintained at sufficiently low levels in spring (Gargan et al. 2012). This observation is consistent with research on pink salmon (e.g. Bateman et al. 2016). A potential 50 % lice-induced reduction in annual return of wild Atlantic salmon is likely to have serious general implications for long-term viability of populations in aquaculture areas. Natal homing in salmon results in a high level of genetic structuring, and smaller salmon rivers typically have a relatively low effective population size (Nikolic et al. 2009). As such populations decline, they are likely to become vulnerable to inbreeding and related demographic problems (e.g. Lande et al. 2003) that can erode future evolutionary potential of salmon populations (McGinnity et al. 2003) and lead to an extinction vortex (Fagan & Holmes 2006). Many Atlantic salmon populations are already under pressure from (possibly climate-mediated) reductions in marine survival. The addition of significant lice-related mortality during the coastal stage of smolt out-migration could be critical.

Acknowledgements. The Inland Fisheries Ireland staff at the Erriff are gratefully acknowledged for operation of fish counter facilities and provision of rod catch data.

LITERATURE CITED

Anon (2008) National Atlantic Salmon Genetic Stock Identification Project ST-05-002. Final Report January 2008. Prepared by University College Cork, the Central & Regional Fisheries Boards and the Irish Marine Institute. Funded under the Irish National Development Plan. www.fisheriesireland.ie/fisheries-research-1/1409-national-salmon-genetic-stock-identification-project-report-2008/file

Bateman AW, Peacock SJ, Connors B, Polk Z, Berg D, Krkošek M, Morton A (2016) Recent failure to control sea louse outbreaks on salmon in the Broughton Archipelago, British Columbia. Can J Fish Aquat Sci 73:1164–1172

Bates D, Maechler M, Bolker B, Walker S (2015) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-9. https://CRAN.R-project.org/package=lme4

Beaugrand G, Reid PC (2003) Long term changes in phytoplankton, zooplankton and salmon related to climate. Glob Change Biol 9:801–817

Beaugrand G, Reid PC (2012) Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. ICES J Mar Sci 69:1549–1562

Bjørn PA, Finstad B (1997) The physiological effects of salmon lice infection on sea trout post smolts. Nord J Freshw Res 73:60–72

Costello MJ (2009) How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. Proc R Soc Lond B Biol Sci 276:3385–3394

Dawson LHJ, Pike AW, Houlihan DF, McVicar AH (1998) Effects of salmon lice *Lepeophtheirus salmonis* on sea trout *Salmo trutta* at different times after seawater transfer. Dis Aquat Org 33:179–186

Defriez EJ, Sheppard LW, Reid PC, Reuman DC (2016) Climate change-related regime shifts have altered spatial synchrony of plankton dynamics in the North Sea. Glob Change Biol 22:2069–2080

Elston DA, Moss R, Boulinier T, Arrowsmith C, Lambin X (2001) Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. Parasitology 122: 563–569

Fagan WF, Holmes EE (2006) Quantifying the extinction vortex. Ecol Lett 9:51–60

Fox F (2003) Effect displays in R for generalised linear models. J Stat Softw 8:1–27

Frazer L (2009) Sea-cage aquaculture, sea lice, and declines of wild fish. Conserv Biol 23:599–607

Friedland KD, Reddin DG, Kocik JF (1993) Marine survival of North American and European Atlantic salmon: effects of growth and environment. ICES J Mar Sci 50: 481–492

Friedland KD, Reddin DG, Castonguay M (2003) Ocean thermal conditions in the post-smolt nursery of North American Atlantic salmon. ICES J Mar Sci 60:343–355

Friedland KD, MacLean JC, Hansen LP, Peyronnet AJ and others (2009) The recruitment of Atlantic salmon in Europe. ICES J Mar Sci 66:289–304

Gargan PG, Forde G, Hazon N, Russell DJF, Todd CD (2012) Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. Can J Fish Aquat Sci 69:343–353

Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616

Holsman KK, Scheuerell MD, Buhle E, Emmett R (2012) Interacting effects of translocation, artificial propagation, and environmental conditions on the marine survival of Chinook salmon from the Columbia River, Washington, USA. Conserv Biol 26:912–922

Horreo JL, Machado-Schiaffino G, Ayllon F, Griffiths AM, Bright D, Stevens JR, Garcia-Vazquez E (2011) Impact of climate change and human-mediated introgression on southern European Atlantic salmon populations. Glob Change Biol 17:1778–1787

ICES (International Council for the Exploration of the Sea) (2016) ICES advice on fishing opportunities, catch, and effort: North Atlantic Salmon Stocks. Report of the ICES Advisory Committee to the NASCO. ICES Advice 2016, Book 10. ICES, Copenhagen

Johnson LL, Ylitalo GM, Arkoosh MR, Kagley AN and others (2007) Contaminant exposure in outmigrant juvenile salmon from Pacific Northwest estuaries of the United States. Environ Monit Assess 124:167–194

Jonsson B, Jonsson N (2004) Factors affecting marine production of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 61:2369–2383

Krkošek M, Ford JS, Morton A, Lele S, Myers RA, Lewis MA (2007) Declining wild salmon populations in relation to parasites from farm salmon. Science 318:1772–1775

Krkošek M, Connors BM, Morton A, Lewis MA, Dill LM, Hilborn R (2011) Effects of parasites from salmon farms on productivity of wild salmon. Proc Natl Acad Sci USA 108:14700–14704

Krkošek M, Revie CW, Gargan PG, Skilbrei OT, Finstad B, Todd CD (2012) Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proc R Soc Lond B Biol Sci 280:2012–2359

Lande R, Engen S, Saether BE (2003) Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford

Larsson P, Backe C, Bremle G, Eklöv A, Okla L (1996) Persistent pollutants in a salmon population (*Salmo salar*) of the southern Baltic Sea. Can J Fish Aquat Sci 53:62–69

Limburg KE, Waldman JR (2009) Dramatic declines in North Atlantic diadromous fishes. Bioscience 59:955–965

Marty GD, Saksida SM, Quinn TJ (2010) Relationship of farm salmon, sea lice, and wild salmon populations. Proc Natl Acad Sci USA 107:22599–22604

McCarthy JL, Friedland KD, Hansen LP (2008) Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen River, Norway. J Fish Biol 72:1572–1588

McCormick SD, Hansen LP, Quinn TP, Saunders RL (1998) Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 55:77–92

McGinnity P, Prodöhl P, Ferguson A, Hynes R and others (2003) Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. Proc R Soc Lond B Biol Sci 270:2443–2450

Mills KE, Pershing AJ, Sheehan TF, Mountain D (2013) Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. Glob Change Biol 19:3046–3061

Nikolic N, Butler JR, Bagliniere JL, Laughton R, McMyn IA, Chevalet C (2009) An examination of genetic diversity and effective population size in Atlantic salmon populations. Genet Res (Camb) 91:395–412

Ó Maoiléidigh N, White J, Dillane M, Bond N and others (2015) National report for Ireland - the 2014 salmon season. Working Paper 27. ICES Working Group on North Atlantic Salmon, 17th March–26th March 2015, Moncton, Canada. ICES, Copenhagen

Parrish DL, Behnke RJ, Gephard SR, McCormick SD, Reeves GH (1998) Why aren't there more Atlantic salmon (*Salmo salar*)? Can J Fish Aquat Sci 55:281–287

Peacock SJ, Krkošek M, Proboszcz S, Orr C, Lewis MA (2013) Cessation of a salmon decline with control of parasites. Ecol Appl 23:606–620

Shephard S, MacIntyre C, Gargan P (2016) Aquaculture and environmental drivers of salmon lice infestation and body condition in sea trout. Aquacult Environ Interact 8: 597–610

Smith KF, Sax DF, Lafferty KD (2006) Evidence for the role of infectious disease in species extinction and endangerment. Conserv Biol 20:1349–1357

Todd CD, Hughes SL, Marshall C, MacLean JC, Lonergan ME, Biuw E (2008) Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. Glob Change Biol 14:958–970

Tully O, Whelan KF (1993) Production of nauplii of *Lepeophtheirus salmonis* (Krøyer) (Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (*Salmo trutta* L.) off the west coast of Ireland in 1991. Fish Res 17:187–200

Vollset KW, Krontveit RI, Jansen P, Finstad B and others (2016) Impacts of parasites on marine survival of Atlantic salmon: a meta-analysis. Fish Fish 17:714–730

Wells A, Grierson CE, MacKenzie M, Russon IJ and others (2006) Physiological effects of simultaneous, abrupt seawater entry and sea lice (*Lepeophtheirus salmonis*) infestation of wild, sea-run brown trout (*Salmo trutta*) smolts. Can J Fish Aquat Sci 63:2809–2821

White J, Ó Maoiléidigh N, Gargan P, de Eyto E and others (2016) Incorporating natural variability in biological reference points and population dynamics into management of Atlantic salmon (*Salmo salar L.*) stocks returning to home waters. ICES J Mar Sci 73:1513–1524

Zuur AF, Hilbe JM, Ieno EN (2015) A beginner's guide to GLM and GLMM with R. A frequentist and Bayesian perspective for ecologists. Highland Statistics, Newburgh

Editorial responsibility: Bengt Finstad,
Trondheim, Norway

Submitted: November 2, 2016; Accepted: March 27, 2017
Proofs received from author(s): April 18, 2017

Received: 14 September 2018 | Revised: 9 November 2018 | Accepted: 14 November 2018
DOI: 10.1111/eva.12746

ORIGINAL ARTICLE

WILEY Evolutionary Applications Open Access

Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations

Emma V. A. Sylvester[1] | Brendan F. Wringe[2] | Steven J. Duffy[1] | Lorraine C. Hamilton[3] | Ian A. Fleming[4] | Marco Castellani[5] | Paul Bentzen[6] | Ian R. Bradbury[1]

[1]Science Branch, Fisheries and Oceans Canada, St. John's, Newfoundland and Labrador, Canada

[2]Science Branch, Department of Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada

[3]Aquatic Biotechnology Laboratory, Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada

[4]Memorial University of Newfoundland, Department of Ocean Sciences, St. John's, Newfoundland and Labrador, Canada

[5]Department of Mechanical Engineering, University of Birmingham, Birmingham, UK

[6]Marine Gene Probe Laboratory, Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada

Correspondence
Emma V.A. Sylvester, Science Branch, Department of Fisheries and Oceans Canada, St. John's, NL, Canada.
Email: e.sylvester@dal.ca

Funding information
Fisheries and Oceans Canada; Genomics Research and Development Initiative of Canada; Natural Sciences and Engineering Research Council of Canada; Atlantic Salmon Federation

Abstract

Throughout their native range, wild Atlantic salmon populations are threatened by hybridization and introgression with escapees from net-pen salmon aquaculture. Although domestic–wild hybrid offspring have shown reduced fitness in laboratory and field experiments, consequential impacts on population abundance and genetic integrity remain difficult to predict in the field, in part because the strength of selection against domestic offspring is often unknown and context-dependent. Here, we follow a single large escape event of farmed Atlantic salmon in southern Newfoundland and monitor changes in the in-river proportions of hybrids and feral individuals over time using genetically based hybrid identification. Over a three-year period following the escape, the overall proportion of wild parr increased consistently (total wild proportion of 71.6%, 75.1% and 87.5% each year, respectively), with subsequent declines in feral (genetically pure farmed individuals originating from escaped, farmed adults) and hybrid parr. We quantify the strength of selection against parr of aquaculture ancestry and explore the genetic and demographic consequences for populations in the region. Within-cohort changes in the relative proportions of feral and F1 parr suggest reduced relative survival compared to wild individuals over the first (0.15 and 0.81 for feral and F1, respectively) and second years of life (0.26, 0.83). These relative survivorship estimates were used to inform an individual-based salmon eco-genetic model to project changes in adult abundance and overall allele frequency across three invasion scenarios ranging from short-term to long-term invasion and three relative survival scenarios. Modelling results indicate that total population abundance and time to recovery were greatly affected by relative survivorship and predict significant declines in wild population abundance under continued large escape events and calculated survivorship. Overall, this work demonstrates the importance of estimating the strength of selection against domestic offspring in the wild to predict the long-term impact of farmed salmon escape events on wild populations.

KEYWORDS
aquaculture impacts, fish farming, introgression, population eco-genetic modelling, relative fitness, *Salmo salar*

1 | INTRODUCTION

The threat of invasion from domesticated Atlantic salmon (*Salmo salar*) into wild populations is of growing concern to management and conservation efforts (Clifford, McGinnity, & Ferguson, 1998a, 1998b; Forseth et al., 2017; Glover et al., 2012; Gross, 1998; Le Cam, Perrier, Besnard, Bernatchez, & Evanno, 2015). Farmed escapees often outnumber wild populations annually, and hybridization and genetic introgression between farmed and wild salmon have been detected throughout their native range (Bourret, O'Reilly, Carr, Berg, & Bernatchez, 2011; Glover et al., 2017). Mating of farmed and wild salmon may result in reduced genetic integrity of the wild population (Fleming et al., 2000; McGinnity et al.., 2003; Skaala et al., 2012; Solberg, Dyrhovden, Matre, & Glover, 2016) and, under pressure from continual invasion, a loss of overall population fitness (Baskett, Burgess, & Waples, 2013; McGinnity et al., 2003). The degree of genetic impact on wild populations due to invasion is often population-specific (Baskett et al., 2013; Karlsson, Diserud, Fiske, & Hindar, 2016) and may be highly dependent on the selective pressures acting on invading individuals and their progeny (Thurman & Barrett, 2016).

Current methods of estimating these selective pressures or relative fitness of aquaculture offspring (i.e., hybrid and feral) under wild conditions are often family-specific (Skaala et al., 2012) and rely on laborious experimental approaches (McGinnity et al., 2003, 1997; Miller, Close, & Kapuscinski, 2004). Field experiments suggest that the relative fitness of hybrid and feral individuals may follow a pattern of additive genetic inheritance (Einum & Fleming, 1997; Fleming et al., 2000; McGinnity et al., 2003), although maternal environmental effects are potentially also influential in early life stages (Houde, Black, Wilson, Pitcher, & Neff, 2015). Due to the complexity of interactions and effects on individual fitness, estimating the strength of selection at the population or regional scale remains difficult. Namely, hybridization success and selection pressures can widely vary across even small spatial scales (Sylvester et al., 2018), and controlled experiments (Skaala et al., 2012) may not reflect the conditions of wild populations and landscapes (Fleming et al., 2000). Also, the impacts of invasion by farmed individuals have been shown to vary depending on the demography of the native population (Heino, Svåsand, Wennevik, & Glover, 2015; Wringe, Jeffery, et al., 2018) and the degree of relatedness between farmed salmon and the wild populations they invade (Baskett et al., 2013). Similarly, wild individuals straying from nearby rivers may buffer the impact of domesticated invasion in populations (Castellani et al., 2018). Given this inherent complexity, enhanced understanding of the relative fitness of domestic offspring at the population level in a range of natural environments is required to better predict and mitigate impacts of escaped farmed salmon on wild populations.

Here, we capitalize on a large escape event that occurred in 2013 in southern Newfoundland to explore how these changes may be monitored and applied to understand long-term consequences for wild populations. This single event resulted in the escape of 20,000 adult farmed salmon into a region supporting an approximately equal number of wild salmon. Previous work has documented widespread hybridization between wild and farmed escaped salmon following this escape event (Wringe, Jeffery, et al., 2018). By observing temporal changes in hybrid class composition after an influx of invaders into a system, the strength of selection against aquaculture-derived individuals may be directly estimated for a real-world system of invasion. As such, we aim to (a) monitor the changes in the proportion of wild, hybrid and feral parr over time, (b) use these data to estimate survivorship as a proxy of the strength of selection against feral and hybrid offspring, and (c) using these realistic estimates of selection, model the consequences for these populations over various invasion scenarios, exploring the sensitivity to the strength of selection. We build directly on previous work which developed genetic and analytical tools to identify hybrids (Anderson & Thompson, 2002; Wringe, Stanley, Jeffery, Anderson, & Bradbury, 2017a, 2017b; Wringe, Stanley, et al., 2018) and documented interbreeding between escaped farmed and wild salmon following this escape event (Wringe, Jeffery, et al., 2018). We expand on these studies and others (Clifford, McGinnity, & Ferguson, 1998a, 1998b; Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2012) by estimating the strength of selection against domestic and hybrid offspring in the wild, and explore the importance of obtaining accurate estimates of relative survival for predicting long-term consequences of invasion.

2 | MATERIALS AND METHODS

2.1 | Sampling and genotyping

A total of 4,619 parr were collected by electrofishing across 19 rivers in southern Newfoundland, Canada (Figure 1), in the summers of 2014, 2015 and 2016. As emergence of alevins in southern Newfoundland generally occurs in early June, summer sampling allows for collection of newly emerged individuals, that is, individuals from the previous spawning season or young-of-year (YoY), as well as parr remaining in streams from earlier spawning seasons, generally up to 2–4 years in Newfoundland (Porter, 1975). Individuals were assigned to an age class based on length (YoY: 0–70 mm, 1+: 71–110 mm, 2+: >110 mm) and stored in 95% ethanol for later DNA extraction and analysis. In addition to these samples, 301 wild individuals (previously identified as pure wild with high certainty) and

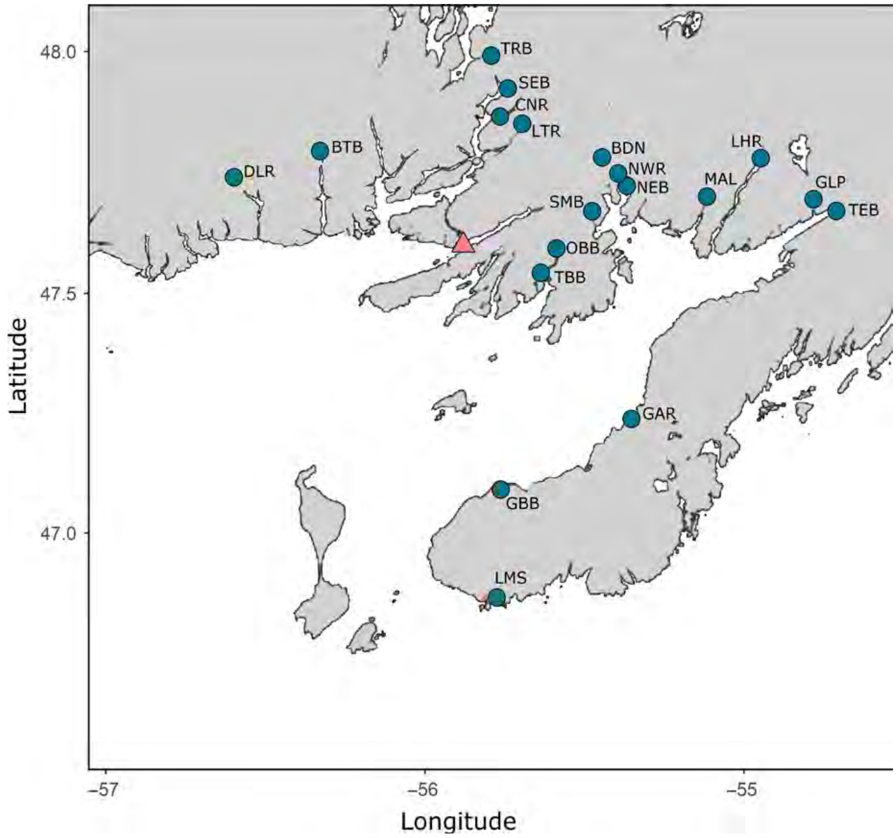


FIGURE 1 Sites in southern Newfoundland sampled in 2014–2016. Sample sizes per site and year can be found in Table 1. The location of the 2013 escape event is indicated by the pink triangle

156 farmed reference individuals were analysed as baseline samples. Farmed references were provided from three cage sites within Newfoundland and are likely representative of escapees sampled throughout the region as salmon cages in Atlantic Canada are presently stocked only with individuals from a single, non-local Saint John River population.

DNA was extracted using QIAamp 96 DNA QIAcube HT Kit (Qiagen, Toronto, Ontario, Canada) on a QIACube HT (Qiagen) following the manufacturer's protocol. Tissue samples were disrupted using a Tissue-Lyser II (Qiagen) mixing 2×10 s at $20\ s^{-1}$. DNA was eluted twice in 100 μl Buffer AE (Qiagen) preheated to 70°C. DNA extracts were quantified using QuantiT PicoGreen dsDNA Assay Kit (Thermo Fisher Scientific, Waltham, MA USA) and read on a FLUOStar OPTIMA fluorescence plate reader (BMG Labtech, Ortenberg, Germany). Individuals were genotyped using SNP Type assays (Fluidigm) following the manufacturer's protocols, targeting 95 SNPs previously established for the classification of farmed and wild salmon in Newfoundland (Wringe, Stanley, et al., 2018). At the applied posterior probability threshold (see below), this panel has been shown to assign individuals to a genetic class with over 90% accuracy, based on simulations in “hybriddetective” (Wringe, Stanley, Jeffery, Anderson, & Bradbury, 2017a; Wringe, Stanley, et al., 2018), with high congruency to genetic class assignment conducted using STRUCTURE (Pritchard, Stephens, & Donnelly, 2000; Sylvester et al., 2018). Each plate extraction included 10 redundant samples to detect processing errors. A total of 220, 190 and 214 samples from 2014, 2015 and 2016, respectively, were genotyped a second time to estimate the genotyping discordance rate which was used as a proxy for the genotyping error rate for each year (Pompanon, Bonin, Bellemain, & Taberlet, 2005).

2.2 | Statistical analyses

All analyses were run and figures created using R v. 3.4.1, and data manipulation and conversion conducted using “genepopedit” (Stanley, Jeffery, Wringe, DiBacco, & Bradbury, 2017). Wild and farmed baseline individuals were simulated and centred (see Karlsson, Diserud, Moen, and Hindar (2014)) from the actual baseline samples using the R package “hybriddetective” (Wringe et al., 2017a) to reduce the erroneous interpretation of naturally occurring inter-river genetic variation as evidence of introgression. Samples were classified into one of six genetic classes: pure wild, feral, first-generation hybrids (F1), second-generation hybrids (F2), backcross wild (BCW) or backcross feral/farmed (BCF) using NewHybrids (Anderson & Thompson, 2002). This approach implements a Bayesian Markov chain Monte Carlo approach for assignment, producing a posterior probability per class for each individual based on the provided baselines. NewHybrids was run using the R package “parallelnewhybrid” (Wringe, Stanley, Jeffery, Anderson, & Bradbury, 2017b) with a burn-in of 50,000 and 100,000 sweeps. All samples were pooled together by year, with samples from each river run independently to reduce bias, such that naturally occurring genetic differentiation between rivers was not misinterpreted as signals of introgression. We then filtered

TABLE 1 Sample size per sampling year and age class for each river, after filtering at a minimum posterior probability threshold in NewHybrids. Relative survivorship was estimated from a single cohort spanning all three years (2014 young-of-year (YoY), 2015 1+ and 2016 2+; see Methods)

	2014	2015		2016		
River	YoY	YoY	1+	YoY	1+	2+
BDN	0	49	60	45	51	16
BTB	16	3	17	29	1	22
CNR	364	19	0	77	26	3
DLR	18	20	20	54	15	10
GAR	193	52	50	96	109	21
GBB	39	15	25	3	75	26
GLP	102	9	51	4	34	2
LHR	124	41	84	44	72	3
LTR	120	0	0	68	23	6
LMS	40	89	11	59	56	7
MAL	10	28	49	0	26	13
NEB	103	0	15	46	46	0
NWR	41	0	10	76	4	4
OBB	14	0	0	34	39	17
SEB	14	0	11	0	2	52
SMB	62	20	49	76	5	6
TBB	111	0	0	1	20	1
TEB	71	3	0	25	24	1
TRB	37	2	33	35	25	13
Total	1,479	350	485	772	653	223

TABLE 2 Estimated relative fitness (and standard error of estimates across rivers) for the first two years of development (young-of-year (YoY) to 1+, 1+ to 2+) based on changes in population composition of genetic class

	Wild	F1	Feral
YoY to 1+	1 (0.09)	0.81 (0.26)	0.15 (0.11)
1 + to 2+	1 (0.10)	0.83 (0.42)	0.26 (0.24)

individuals at a minimum posterior probability of assignment to a single class of 0.8 (Wringe, Jeffery, et al., 2018), resulting in 3,962 assigned individuals (see Table 2 for a breakdown of final sample size by age class). Per-river class proportions were calculated for all parr, young-of-year (YoY) parr only and parr within a single cohort. Overall proportions were estimated after weighing by the axial length of each river (the distance along a straight line along the longest axis of the river; Porter, Riche, & Traverse, 1974) to reduce bias in sampled population size (Wringe, Jeffery, et al., 2018).

The relative fitness of wild, feral and first-generation (F1) hybrids was estimated using a single cohort of individuals (2014 YoY, 2015 1+, 2016 2+) for each age/time step (YoY to 1+, 1+ to 2+). Relative fitness estimates of second-generation hybrids (F2 and backcross) were not calculated due to restrictions in sample sizes. Traditional methods of estimating the relative fitness (or relative survival as a proxy of relative fitness; Hendry, 2017; Rice, 2004) of individuals of a known genotype (i.e., AA, Aa and aa) were applied to individuals of known genetic class (i.e., pure wild, F1 and pure feral; Thurman & Barrett, 2016). We calculated the proportional change in the population composition of a genetic class (P_{t+1}/P_t, where P is the class proportion at year t) within each river, then averaged across rivers and divided by the maximum proportional change (i.e., the average proportional change of the wild class) to obtain the relative, overall survivorship of each class across the region. Sites with fewer than 10 individuals per age class were removed from the calculation. Additionally, if the formula for the proportional change of a given genetic class at time t resulted in a denominator of 0, these rivers were removed for that time point calculation for that genetic class. This estimate of relative survivorship was interpreted as the relative fitness (w) of each genetic class.

2.3 | Individual-based modelling approach

We used an individual-based salmon eco-genetic model (IBSEM) developed by Castellani et al. (2015) to explore the possible long-term effects of various invasion scenarios and relative survival associated with the farmed genotype in southern Newfoundland. IBSEM models the outcome of Atlantic salmon populations in response to invasion of domesticated individuals. Duration of invasion and recovery, wild population size and number of invaders, environmental conditions, individual size and genotypic and phenotypic differences between individuals of farm and wild origin are considered to model population changes in abundance, genotype and individual size. Growth and survival are simulated by stochastic procedures that are influenced by genotype, fish size and age, temperature and population density at three life stages: embryo, juvenile and adult. The effects of the genetic make-up in the life history of the individuals are modelled through three independent sets of loci, one set for each life stage. The distribution of genetic effects across the 21 loci is modelled via an exponentially declining function, where the last locus has no effect and is used as a neutral marker. Through the influence of genotype, the differential between growth and survival of wild and feral individuals can be set and the consequences observed over time. Simulated loci are unlinked with possible gamete recombination and random inheritance (and are therefore influenced by drift), and a range of influences on phenotype and therefore suitability to the environment. The sum of the genetic effects is linearly related to phenotype, such that genotypic values approaching 1 are associated with growth and survival rates typical of wild salmon, and values approaching zero are associated with rates observed in farm escapees. Reproductive success of both wild and domestic individuals is sex-specific, with female fertility dependent upon weight, and male reproductive success dependent upon length, with the possibility of precocial sexual maturation. Farm escapees are given a reduced spawning success than fish of any genetic make-up that are born in the wild. We tested three temporal scenarios of invasion to

TABLE 3 Scenarios tested in an individual-based salmon eco-genetic modelling (IBSEM) approach (Castellani et al., 2015). All other parameters were consistent across scenarios and can be found in the Supporting Information. Each of the three values for number of invaders was modelled using each pair of relative survival parameters (low, calculated and high), resulting in nine models for each temporal scenario (see Figures 3 and 4)

Temporal scenario	Invasion time (years)	Number of invaders annually	Relative survival (parr0/parr1)
Scenario 1: Short-term	10	0, 500, 1,000	0.075/0.13, 0.15/0.26, 0.3/0.52
Scenario 2: Intermediate	50	0, 100, 200	0.075/0.13, 0.15/0.26, 0.3/0.52
Scenario 3: Long-term	100	0, 50, 100	0.075/0.13, 0.15/0.26, 0.3/0.52

investigate the impacts of consistent, annual invasion as a (a) short-term, large escape event over 10 years of invasion relative to an (b) intermediate invasion rate (over 50 years) and (c) long-term, trickle escapes (over 100 years; Table 3). For each temporal scenario, three levels of the magnitude of invasion were tested (no invasion, intermediate invasion and high invasion). Invasion levels were set such that the total number of invaders was equal across scenarios (i.e., 0, 500 and 1,000 invaders annually for 10 years; 0, 100 and 200 invaders annually for 50 years; and 0, 50 and 100 invaders annually for 100 years). Each temporal scenario and magnitude of invasion was tested at three levels of relative feral parr survival: our estimated value, low survival (half our estimate) or high survival (double our estimate). Our estimates of hybrid relative survival were not incorporated as IBSEM infers this based on additive genetic inheritance. It should be noted that the high survival scenario, while high relative to that estimated for southern Newfoundland populations, is still lower than most previous estimates of relative survival of feral parr (McGinnity et al., 2003, 1997). We compared the change in adult population abundance (both wild and escaped farmed fish) and sum of the genetic effects across the adult set of genes included in the simulation to observe changes in the genetic fitness of the population. All models were run for 100 years prior to invasion to ensure model stability and for 100 years after the invasion period ceased to assess time to recovery. All other parameters remained consistent across models. A full list of parameters, set to be representative of Newfoundland salmon and environmental conditions in the region

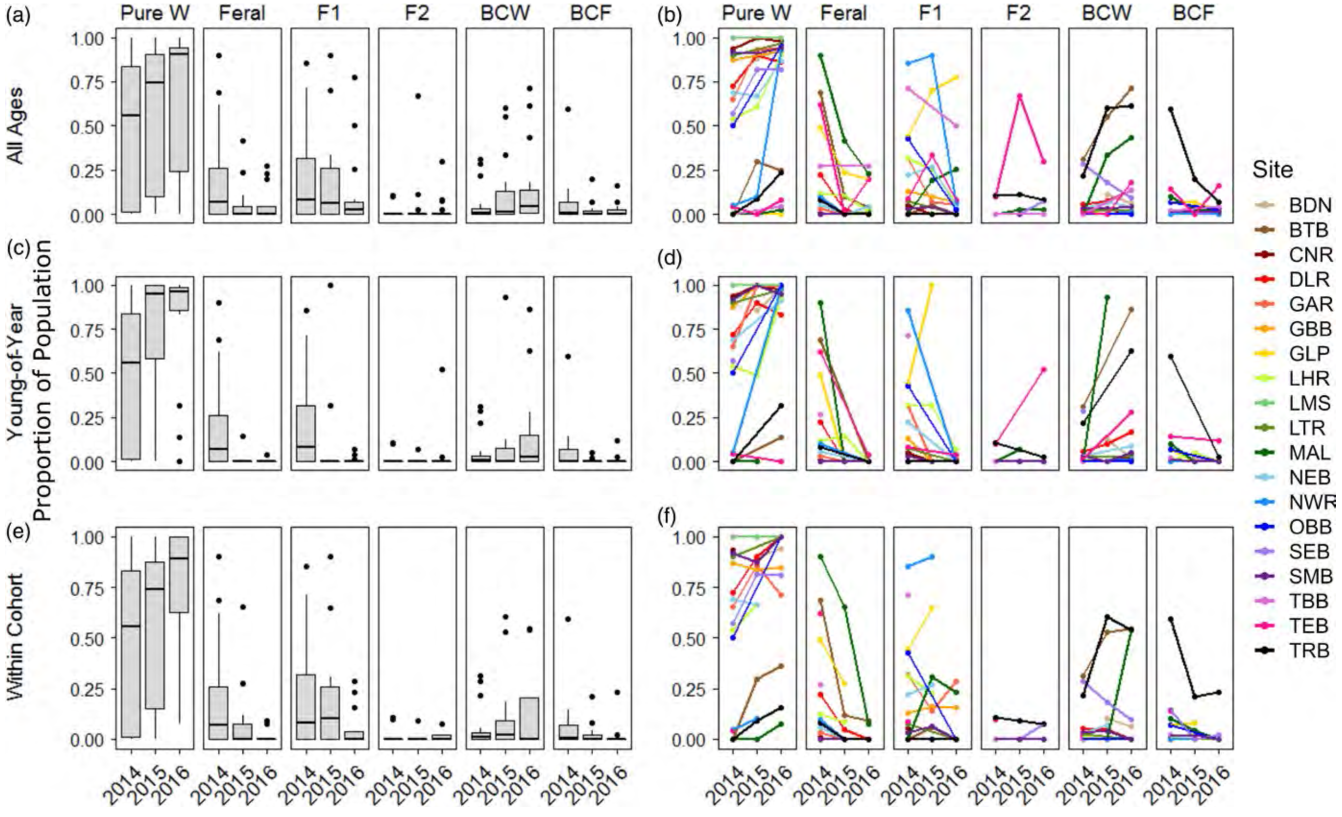


FIGURE 2 Per cent population composition by genetic class (pure feral, pure wild, F1, F2, backcross wild (BCW) and backcross feral (BCF)) across three sampled years including (row 1) individuals of all ages, (row 2) young-of-year (YoY) only and (row 3) within cohort (2014 YoY, 2015 1+, 2016 2+). Each panel comprises a single genetic class, including (a, c, e) boxplots of overall trends and (b, d, f) individual river proportion indicated by colour. Sites with fewer than 5 assigned samples were removed to avoid bias in river composition. Temporal fluctuations in within-cohort population composition were used to estimate relative survival as a proxy of relative fitness for pure wild, feral and F1 genetic classes (see Methods)

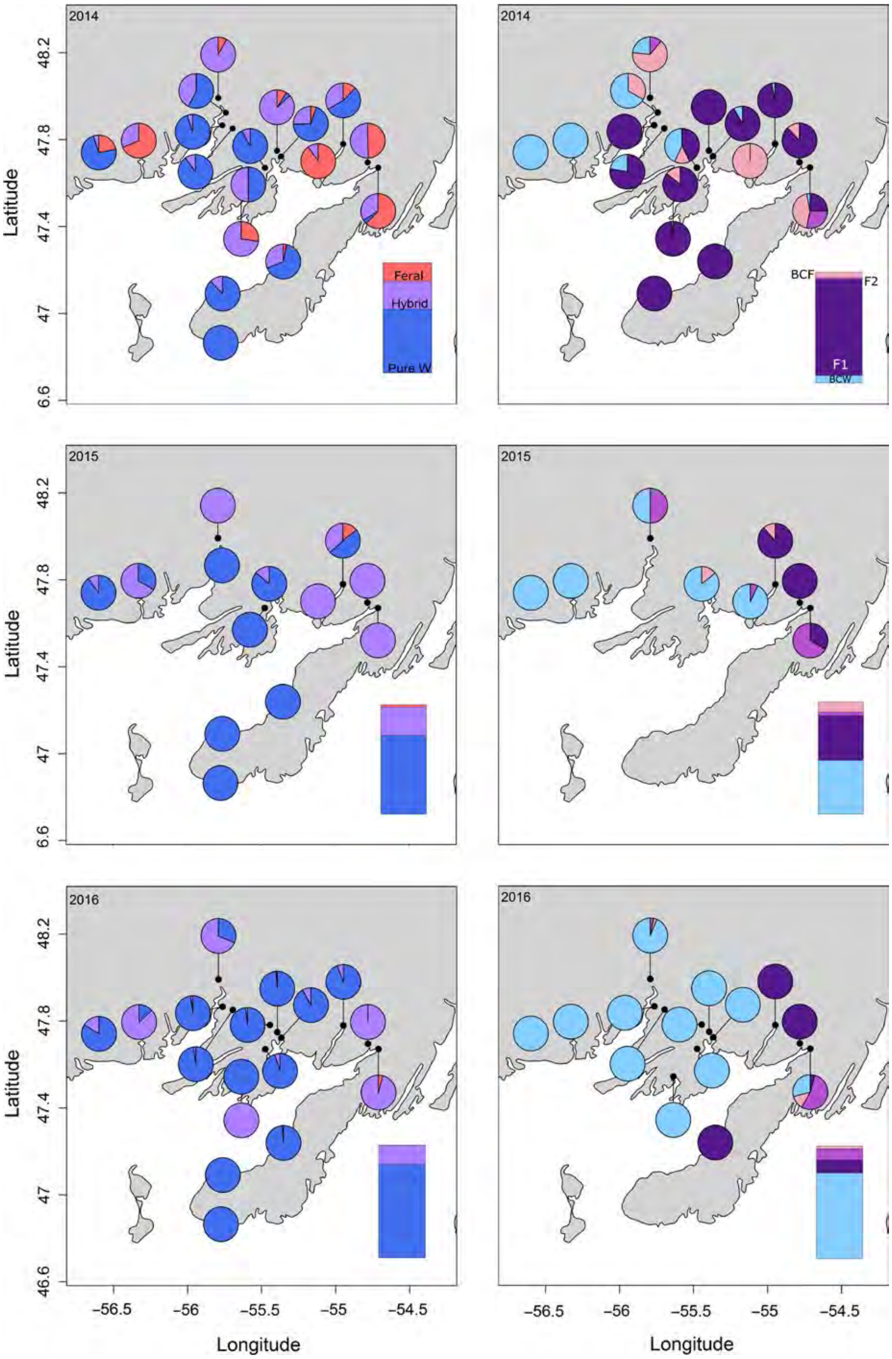


FIGURE 3 Genetic class (pure wild, pure feral, F1, F2, backcross wild (BCW) and backcross feral (BCF)) proportion for each sampled river as determined using NewHybrids for young-of-year (YoY) samples across all sampled years. Panels in column one convey proportions of wild, feral and hybrid parr (all hybrid classes combined) while panels in column two convey proportions of hybrid classes (F1, F2, backcross wild (BCW), backcross feral (BCF)) for each river with hybrid individuals detected in that year (row), as indicated in purple in column one. Bars in each panel represent overall proportions after standardizing by river size (axial length). Corresponding figures for other age classes can be found in Supporting Information Figure S1

(Veinott et al., 2018; correspondence with Dr. Brian Dempson) or set as default, can be found in the Supporting Information. Two parameters reflective of overall wild survival were selected by trial-and-error to achieve a consistent (stable) population size under a zero invasion scenario with all other parameters set as described in Supporting Information Table S1.

3 | RESULTS

A total of 4,619 parr were genotyped using the SNP panel. The genotype error rate was estimated to be 0.17%, 0.01% and 0.13% for 2014, 2015 and 2016, respectively. Of all samples, 86% of individuals were classified by NewHybrids above the posterior probability threshold of 0.8. Across age classes, pure wild parr were the most prevalent class, followed by hybrids and feral parr (Figure 2a,b), with few exceptions in particular rivers. After scaling by river size (axial length), wild population proportion increased overall (increasing by a factor of 1.05 and 1.16 in the first and second year, respectively), with a corresponding decline in feral (by a factor of 0.62, 0.33) and hybrid parr (by a factor of 0.93, 0.57; Figure 2). First-generation hybrids (F1) were the most common hybrid class in 2014, with a steady decline in most rivers (Figures 2 and 3) in subsequent years (by a factor of 0.68 and 0.25 in the first and second year, respectively).

Population proportion of backcross wild (BCW) parr increased during the first year (by a factor of 4.8), driven mostly by dramatic increases in BCW proportion in three rivers, MAL, BTB and TRB. BCW proportion remained generally constant (population proportion decreased by a factor of 0.91) in the second year of life. These trends were consistent within young-of-year (YoY) parr (Figures 2c,d and 3) and within a single cohort (Figure 2e,f). Increasing class proportions within a cohort suggest a higher relative fitness compared with those classes that are observed to decrease with time. We applied this reasoning to estimate relative survival as a proxy of fitness and strength of selection against classes that are seen to decrease over time, relative to wild types within a single cohort. As such, the relative fitness of the wild class was 1 for all estimates. Relative fitness was higher for F1 than for feral salmon and was slightly lower for both classes in the first year of development than the second year (Table 2). Variance (reported as standard error) in the relative survival of F1 parr was considerably higher than that of feral or wild individuals (Table 2). Although low within-river sample sizes at single time points limited our ability to estimate river-specific relative survival of genetic classes, we report these estimates in Supporting

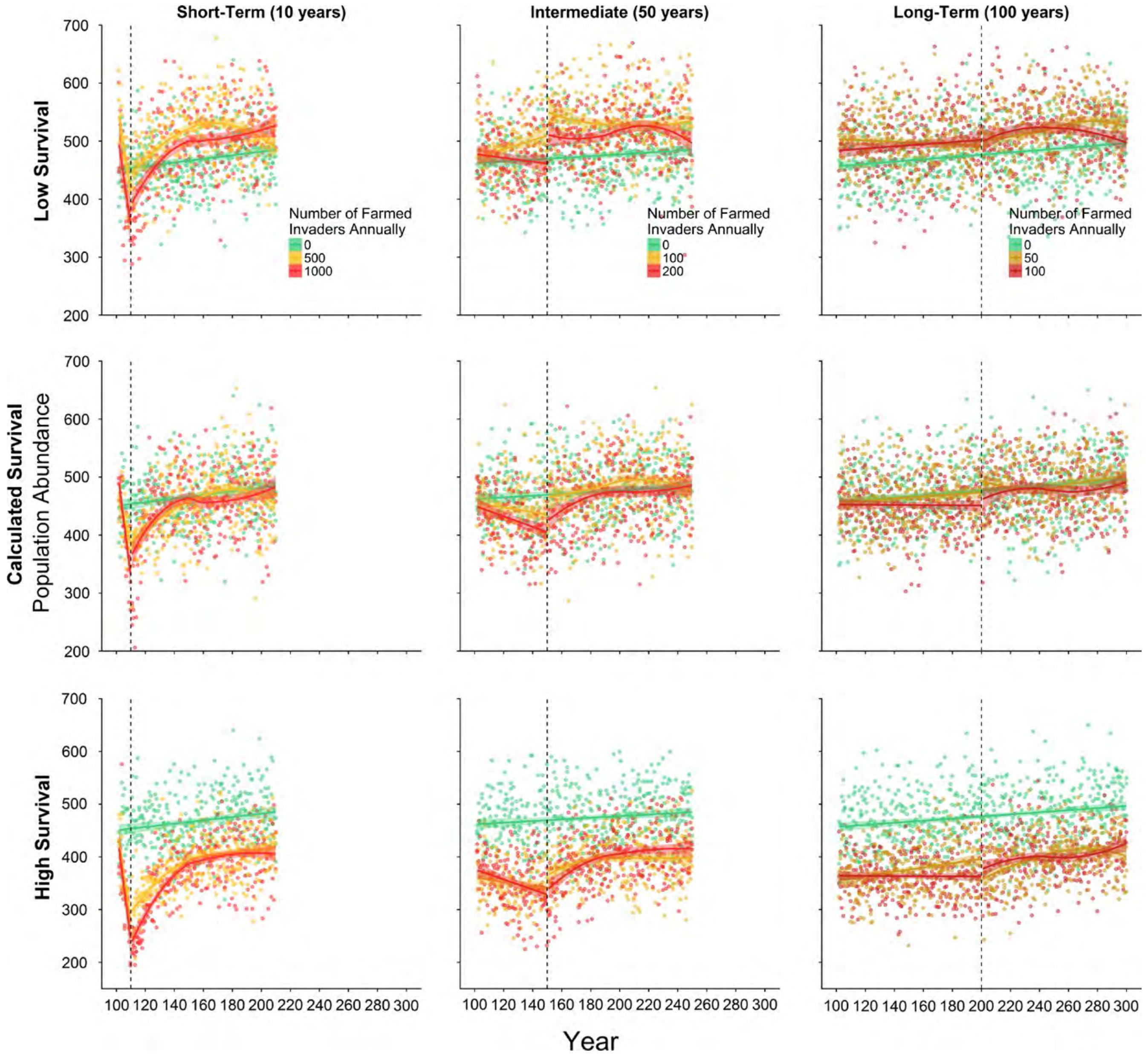


FIGURE 4 Adult population abundance as estimated using IBSEM (Castellani et al., 2015) for all tested scenarios (see Table 3). Three invasion scenarios (columns: short-term, intermediate and long-term) were each modelled at three levels of relative survival for feral parr (rows: half calculated relative survival, calculated relative survival for the study region (as shown in Table 2) and double calculated relative survival). Each of these nine scenarios was tested with three levels of invasion (number of farmed invaders) as indicated by colour. Invasion started after 100 years of settling; the time at which invasion ceased (duration of invasion) is indicated by a vertical dashed line. Loess curves are used for visualization of trends in the data

Information Table S2 to demonstrate variance in estimated relative survival across rivers.

Our estimates of average relative survival of individuals with feral genotypes (see Table 2) were incorporated into the individual-based modelling approach (IBSEM). We examined three temporal scenarios (Table 3), and three relative survival scenarios: our calculated relative survival, half and twice that value. These scenarios revealed differences in population response and recovery, affirming the importance of estimating relative survival in predicting population response to invasion. Severity of the population crash and time to recovery increased with increasing relative survival of feral parr and decreasing duration or increasing intensity of invasion (Figure 4). In calculated relative survival models, full recovery was observed after 30–40 years post-invasion in the short-term invasion scenario, less than 20 years in the intermediate scenario and immediately after invasion ceased in the low invasion scenario. High relative survival of farmed invaders and the short-term temporal scenario resulted in the greatest decrease in overall population abundance, to as few as 200 individuals after 10 years of invasion, from a stable population of approximately 475 under a zero invasion scenario (Figure 4).

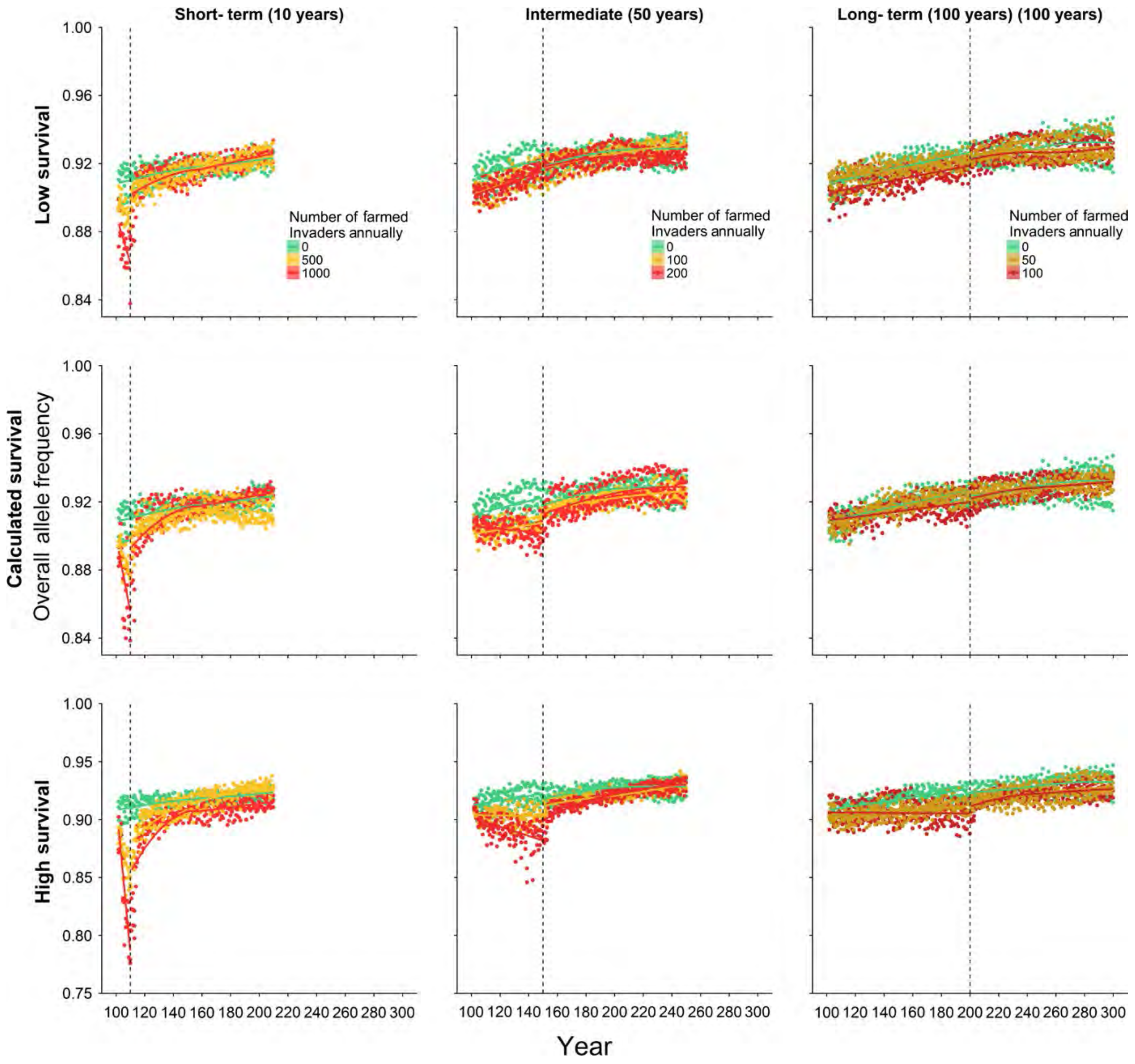


FIGURE 5 Average allele frequency across 21 simulated genotypes as estimated using IBSEM (Castellani et al., 2015) for all tested scenarios (see Table 3). Three invasion scenarios (columns: short-term, intermediate and long-term) modelled at three levels of relative survival for feral parr (rows: half calculated relative survival, calculated relative survival for the study region (as shown in Table 2) and double calculated relative survival). Each of these nine scenarios was tested with three levels of invasion (number of farmed invaders) as indicated by colour. Invasion started after 100 years of settling; the time at which invasion ceased (duration of invasion) is indicated by a vertical dashed line. Loess curves are used for visualization of trends in the data

Additionally, high relative survival tests did not fully recover after 100 years in any of the invasion scenarios. Overall, modelled allele frequencies shifted towards the farmed genotype in all temporal and survivorship scenarios following similar patterns as population abundance. That is, the severity of the change in allele frequency increased with increasing relative survival of feral parr and increasing intensity (decreasing duration) of invasion (Figure 5). Time to recover to allele frequencies comparable with the zero invasion models were similar and rapid across all scenarios, with the longest recovery time observed at approximately 50 years after ceasing invasion in short-term invasion models at high relative survival.

4 | DISCUSSION

With the continued growth of Atlantic salmon aquaculture, understanding and predicting the impacts of escape events of farmed Atlantic salmon are central to the persistence of wild populations across the species range (Forseth et al., 2017; Glover et al., 2017). The survival and fitness of farmed escapee Atlantic salmon relative to the wild populations they invade has the potential to ultimately determine the genetic impacts of invasion on wild populations, yet population- or region-specific relative survival of individuals of aquaculture ancestry in the wild is rarely estimated. Here, we build on previous work investigating the extent of hybridization following a large escape event in southern Newfoundland (Wringe, Jeffery, et al., 2018) and calculate relative survival and associated strength of selection against feral and hybrid parr using temporal changes in population composition. We demonstrate decreased survival of offspring of aquaculture escapees relative to pure wild individuals and explore how relative survival and rates of invasion may impact wild populations using an individual-based modelling approach (Castellani et al., 2015). This method of estimating survival and consequential long-term genetic impacts of farmed invasion provides a novel field-based approach that has previously generally been limited to controlled experiments that do not account for population or regional variation. By modelling various invasion and survival scenarios, we highlight the importance of considering region-specific relative survival when predicting population trajectories under various rates of invasion with the potential to inform approaches to population conservation and fisheries management.

We examined temporal changes in the proportion of hybrids within young-of-year (YoY) samples and within a single cohort to illuminate the factors influencing the presence and survival of farmed escaped offspring in the wild. Temporal changes in hybrid proportions within a cohort reflected continued declines in hybrids and feral parr with an increase in wild-type individuals over time as noted elsewhere (DFO, 2018; McGinnity et al., 2003, 1997; Skaala et al., 2012). Changes in the relative proportions of hybrid types also followed a similar pattern with a relative decrease in F1s and an increase in backcross wild individuals. This change in population composition over time suggests reduced relative fitness of feral and hybrid offspring compared to pure wild. Interestingly, our estimates of relative survival are considerably lower than some previous estimates for feral parr (ranging from 0.61 to 1.53, relative to pure wild survival of 1; Hindar, Fleming, McGinnity, & Diserud, 2006) but comparable to that of previous studies for F1 parr (Fleming et al., 2000; McGinnity et al., 2003, 1997; Skaala et al., 2012). Relative survival of feral individuals in the wild is likely related to the degree of genetic differentiation between wild and farmed strains. Our low estimates of feral survival may thus reflect high domestication selection or drift in domestic salmon (Glover et al., 2017; Gross, 1998) or pre-existing genetic differences between wild Newfoundland populations and the Saint John River lineage currently stocked in the region (Bradbury et al., 2015; Moore et al., 2014). Consequential genetic divergence may result in reduced suitability to conditions in southern Newfoundland (Vandersteen, Biro, Harris, & Devlin, 2011). Our observations of an increase in the proportion of wild backcrossed individuals (BCW) in some populations suggest comparable survival to pure wild individuals, consistent with previous findings of higher performance in backcross classes (Fraser, Cook, Eddington, Bentzen, & Hutchings, 2008; McGinnity et al., 2003, 1997).

In 2014, the year immediately following a large escape event, levels of hybridization were consistent with reported impacts elsewhere (Glover et al., 2017; Karlsson et al., 2016), with all but one of 18 rivers showing evidence of hybrid or feral parr presence. In subsequent years, the overall proportion of hybrids and of F1 hybrids decreased, suggesting that mating between farmed escapees and wild salmon was highest immediately following the escape, likely due to the large influx of farmed individuals. This decrease is consistent with reduced contributions from this escape event over time. The presence of second-generation hybrids throughout our sampling years indicates that hybrid individuals and therefore farmed invaders unrelated to the escape event are present in these rivers, indicative of continued low-level trickle invasion (Wringe, Stanley, et al., 2018). While general temporal trends are consistent across rivers, there is a large degree of spatial variation in genetic class proportion at a given time point, as previously reported by Sylvester et al. (2018), with consequential variation in relative survival estimates. Due to low within-river sample size at individual time points, we focus on average relative survival of parr in the sampled region. However, the approach for estimating relative survival applied here can be easily applied for river-scale estimates of relative survival when sample sizes are adequate.

The precocious maturation of hybrid or feral male parr may influence levels of hybridization and introgression and thus alter allele frequency (Gjerde, Simianer, & Refstie, 1994) and lower productivity. This phenomenon may increase the relative fitness of feral parr as evidence suggests that reproductive success of farmed precocious males may be higher than that of wild individuals (Garant, Fleming Ian, Einum, & Bernatchez, 2003). Genetic introgression may be exacerbated by feral precocial males contributing to the population as allele frequency shifts towards the farmed genotype to a greater extent in early life stages (Castellani et al., 2015). Although aquaculture breeding practices often select against early maturation, early maturation is also largely environmentally determined (Good

& Davidson, 2016; Jonsson, Jonsson, & Finstad Anders, 2012), and high rates of sexual precocity have been reported in wild southern Newfoundland populations (Dalley, Andrews, & Green, 1983; Myers, 1984). However, common garden experiments have revealed male parr maturation to be lower in farmed progeny than in wild parr (McGinnity et al., 2007), with F1 hybrids demonstrating an intermediate likelihood of precocial maturation. Estimates of rates of hybrid precocial maturation and fitness in the region would enhance the ability to predict rates of introgression between and wild and farmed salmon.

Our modelling results suggest that consequences of invasion of farmed salmon could vary dramatically with the magnitude and temporal scope of escape events. Repeated large pulses of invasion were more detrimental to wild population productivity than continued low-level escape events. Interestingly, previous modelling efforts have disagreed on the relative impact of low-level chronic or large pulse escape events. Hindar et al. (2006) and Hindar and Diserud (2007) suggest greater impacts following large pulses of escapees contrasting the results of Baskett et al. (2013) who suggest that low-level leakage may be more detrimental to wild populations due to a gradual shift towards the farmed genotype. This variation in results has been suggested to be due to the time period considered and equilibrium status of model simulations (Baskett et al., 2013). However, the temporal scenarios modelled here made very little difference to long-term population trajectories compared to the impact of the parr survivorship parameters. Under the most extreme scenarios (i.e., high relative survival), wild population abundance did not fully recover regardless of the temporal scenario even after 100 years of recovery, although overall genetic effects were not substantially different after 100 years of recovery, suggesting that recovery in population abundance is limited despite shifts in allele frequency towards the wild type after invasion has ceased. Decreasing population abundance with increasing relative survival of feral parr is likely due to an overall reduction in population productivity as a consequence of higher feral and hybrid presence and thus contribution to the gene pool, compared to models with lower relative survival of feral parr. In the models with our calculated relative survival rates for southern Newfoundland, population abundance and allele frequency recovered shortly after invasion ceased. In reality, however, southern Newfoundland wild populations continue to decline (COSEWIC, 2011; DFO, 2013). This suggests that farmed invasion may be ongoing or that other factors such as at-sea survival, habitat degradation or fishing pressures may be at play (Bourret et al., 2011; Vähä, Erkinaro, Niemelä, & Primmer, 2007), exacerbating large-scale population declines.

Although IBSEM is a comprehensive Atlantic salmon individual-based model, there are additional factors such as the introduction of disease, fishing pressure and river flow that may influence population response to invasion (Castellani et al., 2015). IBSEM implements a constant or random number or proportion of farmed invaders, and constant relative survival and reproduction. Consequently, more realistic escape scenarios such as constant low-level invasion combined with a large, single-year event or multiple invasions at infrequent intervals are not currently considered, possibly limiting our understanding of population response to domestic invasion. Relative survival in IBSEM is generally reflective of marine survival, as this is known to strongly influence overall survival rates (Jonsson, Jonsson, & Hansen, 2003; McGinnity et al., 2003). However, although we have attempted to parameterize to reflect conditions in southern Newfoundland, a paucity of available region-specific data (such as relative marine survival) may reduce the accuracy of these models. With ongoing investigations within the region, estimates of marine return may be informed by subsequent sampling, allowing for future modifications and improvements to these simulations. Despite the current limitations, simulations such as those conducted here allow an unprecedented opportunity to explore long-term population responses to invasion of farmed escaped salmon and can directly inform decisions regarding management practices and the conservation of wild populations.

Extending our survival estimates with the inclusion of numerous cohorts would provide additional support for our estimates; however, sample sizes of 2015 YoY individuals were insufficient to include this cohort in our analysis. Also, limiting the analysis to only the highly supported hybrid assignments by filtering individuals by posterior probability in NewHybrids may bias our results for some hybrid classes as individuals that do not reach this threshold are more likely to be second-generation hybrids, backcrosses or further introgressed individuals (Sylvester et al., 2018). However, as this bias is consistent across years, we expect temporal fluctuations in hybrid classes to be robust and with little to no effect on our parameter estimates as we did not estimate relative survival of second-generation hybrid classes.

Existing efforts to estimate relative fitness and, accordingly, strength of selection against feral or hybrid parr in wild Atlantic salmon populations invaded by farmed escapees are often labour-intensive, requiring experimental manipulation in the laboratory or in rivers, and do not consider how variation in landscape and susceptibility of a wild population to introgression may differentially impact survival of individuals of aquaculture ancestry. We present a novel approach utilizing genetic data following a large escape event to classify individuals to a genetic class (pure wild, pure feral, F1, F2, BCW, BCF) and infer relative fitness based on within-cohort changes to class composition, applied to a region of southern Newfoundland. These approaches may be easily applied at any scale with sufficient sampling. We further apply our estimates to demonstrate that survival of feral parr, relative to their wild counterparts, affects long-term levels of introgression, particularly under stochastic invasion conditions. Wild population abundance was greatly affected by the relative survival of feral parr without full recovery in all invasion scenarios (short-term, intermediate and long-term) at high relative survival of feral parr. These results indicate the importance of obtaining accurate estimates of region- or population-specific relative fitness to predict population response to farmed invasion. Incorporating this knowledge may allow a deeper understanding of possible impacts on wild populations and may inform management and conservation decisions accordingly.

ACKNOWLEDGEMENTS

The authors thank the staff of the Newfoundland DFO Salmonids section for juvenile tissue sampling; F. Keyser, Dr A. Hendry and T. Thurman for assistance and advice in analysis; Dr E. Anderson for helpful discussion and comments on an early version of the manuscript; and Dr B. Dempson for data informing parameters for southern Newfoundland population modelling. Acquisition of aquaculture salmon baseline samples was facilitated by G. Perry, C. Hendry, DFO Aquaculture section Newfoundland Region, and by industry partners Cooke Aquaculture and Northern Harvest Sea Farms. We also thank the staff of the Aquatic Biotechnology Laboratory of the Bedford Institute of Oceanography for their work in the SNP genotyping. This study was funded through the Program for Aquaculture Regulatory Research of Fisheries and Oceans Canada, the Genomics Research and Development Initiative of Canada, as well as the Natural Sciences and Engineering Research Council of Canada, and support from the Atlantic Salmon Federation.

CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

Data for this study are available at the Dryad Digital Repository: Genotype data of 2014 and 2015 samples can be found at https://doi.org/10.5061/dryad.3k888n7. Genotype data of 2016 samples and field ages assigned to all individuals can be found at https://doi.org/10.5061/dryad.2kc5rh0.

ORCID

Emma V. A. Sylvester https://orcid.org/0000-0002-6030-4327

Ian R. Bradbury https://orcid.org/0000-0002-8152-4943

REFERENCES

Anderson, E. C., & Thompson, E. A. (2002). A model-based method for identifying species hybrids using multilocus genetic data. *Genetics*, *160*, 1217–1229.

Baskett, M. L., Burgess, S. C., & Waples, R. S. (2013). Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. *Evolutionary Applications*, *6*(7), 1090–1108. https://doi.org/10.1111/eva.12089

Bourret, V., O'Reilly, P. T., Carr, J. W., Berg, P. R., & Bernatchez, L. (2011). Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. *Heredity*, *106*(3), 500–510. https://doi.org/10.1038/hdy.2010.165

Bradbury, I. R., Hamilton, L. C., Rafferty, S., Meerburg, D., Poole, R., Dempson, J. B., … Bernatchez, L. (2015). Genetic evidence of local exploitation of Atlantic salmon in a coastal subsistence fishery in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(1), 83–95. https://doi.org/10.1139/cjfas-2014-0058

Castellani, M., Heino, M., Gilbey, J., Araki, H., Svåsand, T., & Glover, K. A. (2015). IBSEM: An individual-based Atlantic salmon population model. *PLoS ONE*, *10*(9), e0138444. https://doi.org/10.1371/journal.pone.0138444

Castellani, M., Heino, M., Gilbey, J., Araki, H., Svåsand, T., & Glover Kevin, A. (2018). Modeling fitness changes in wild Atlantic salmon populations faced by spawning intrusion of domesticated escapees. *Evolutionary Applications*, *11*(6), 1010–1025. https://doi.org/10.1111/eva.12615

Clifford, S. L., McGinnity, P., & Ferguson, A. (1998a). Genetic changes in Atlantic salmon, *Salmo salar* populations of NW Irish rivers resulting from escapes of adult farm salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 358–363.

Clifford, S. L., McGinnity, P., & Ferguson, A. (1998b). Genetic changes in an Atlantic salmon population resulting from escaped juvenile farm salmon. *Journal of Fish Biology*, *52*, 118–127.

COSEWIC (2011). *COSEWIC assessment and status report on the Atlantic salmon* Salmo salar *in Canada*. Ottawa, Canada: Committee on the Status of Endangered Wildlife in Canada. Retrieved from www.sararegistry.gc.ca/status/status_e.cfm

Dalley, E. L., Andrews, C. W., & Green, J. M. (1983). Precocious male Atlantic salmon Parr (*Salmo salar*) in Insular Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*(5), 647–652. https://doi.org/10.1139/f83-086

DFO (2013). *Recovery potential assessment for the South Newfoundland Atlantic salmon* (Salmo salar) *designatable unit*. Retrieved from DFO Canadian Science Advisory Secretariat Science Advisory Report.

DFO (2018). Proceedings of the Regional Science Peer Review of the Inner Bay of Fundy Atlantic Salmon Science Associated with the Live Gene Bank; June 13–16, 2017. Dartmouth, NS: DFO Canadian Science Advisory Secretariat, Proceedings Series 2018/008.

Einum, S., & Fleming, I. A. (1997). Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *Journal of Fish Biology*, *50*(3), 634–651. https://doi.org/10.1111/j.1095-8649.1997.tb01955.x

Fleming, I. A., Hindar, K., Mjølnerød, I. B., Jonsson, B., Balstad, T., & Lamberg, A. (2000). Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*, 1452–1517.

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., … Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, *74*(6), 1496–1513. https://doi.org/10.1093/icesjms/fsx020

Fraser, D., Cook, A., Eddington, J., Bentzen, P., & Hutchings, J. (2008). Mixed evidence for reduced local adaptation in wild salmon resulting from interbreeding with escaped farmed salmon: Complexities in hybrid fitness. *Evolutionary Applications*, *1*(3), 501–512. https://doi.org/10.1111/j.1752-4571.2008.00037.x

Garant, D., Fleming Ian, A., Einum, S., & Bernatchez, L. (2003). Alternative male life-history tactics as potential vehicles for speeding introgression of farm salmon traits into wild populations. *Ecology Letters*, *6*(6), 541–549. https://doi.org/10.1046/j.1461-0248.2003.00462.x

Gjerde, B., Simianer, H., & Refstie, T. (1994). Estimates of genetic and phenotypic parameters for body weight, growth rate and sexual maturity in Atlantic salmon. *Livestock Production Science*, *38*(2), 133–143. https://doi.org/10.1016/0301-6226(94)90057-4

Glover, K. A., Quintela, M., Wennevik, V., Besnier, F., Sørvik, A. G. E., & Skaala, Ø. (2012). Three decades of farmed escapees in the wild: A spatio-temporal analysis of Atlantic salmon population genetic structure throughout Norway. *PLoS ONE*, *7*(8), e43129. https://doi.org/10.1371/journal.pone.0043129

Glover, K. A., Solberg, M. F., McGinnity, P., Hindar, K., Verspoor, E., Coulson, M. W., … Svåsand, T. (2017). Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. *Fish and Fisheries*, *18*(5), 890–927. https://doi.org/10.1111/faf.12214

Good, C., & Davidson, J. (2016). A review of factors influencing maturation of Atlantic salmon, *Salmo salar*, with focus on water recirculation aquaculture system environments. *Journal of the World Aquaculture Society*, *47*(5), 605–632. https://doi.org/10.1111/jwas.12342

Gross, M. R. (1998). One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 131–144. https://doi.org/10.1139/d98-024

Heino, M., Svåsand, T., Wennevik, V., & Glover, K. (2015). Genetic introgression of farmed salmon in native populations: Quantifying the relative influence of population size and frequency of escapees. *Aquaculture Environment Interactions*, *6*, 185–190. https://doi.org/10.3354/aei00126

Hendry, A. P. (2017). *Eco-evolutionary dynamics*. Princeton, NJ: Princeton University Press.

Hindar, K., & Diserud, O. (2007). *Vulnerability analysis of wild salmon populations towards escaped farm salmon*. NINA Report, 244, 45 pp.

Hindar, K., Fleming, I. A., McGinnity, P., & Diserud, O. (2006). Genetic and ecological effects of salmon farming on wild salmon: Modelling from experimental results. *ICES Journal of Marine Science*, *63*(7), 1234–1247. https://doi.org/10.1016/j.icesjms.2006.04.025

Houde, A. L. S., Black, C. A., Wilson, C. C., Pitcher, T. E., & Neff, B. D. (2015). Genetic and maternal effects on juvenile survival and fitness-related traits in three populations of Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(5), 751–758. https://doi.org/10.1139/cjfas-2014-0472

Jonsson, B., Jonsson, N., & Finstad Anders, G. (2012). Effects of temperature and food quality on age and size at maturity in ectotherms: An experimental test with Atlantic salmon. *Journal of Animal Ecology*, *82*(1), 201–210. https://doi.org/10.1111/j.1365-2656.2012.02022.x

Jonsson, N., Jonsson, B., & Hansen, L. P. (2003). The marine survival and growth of wild and hatchery-reared Atlantic salmon. *Journal of Applied Ecology*, *40*(5), 900–911. https://doi.org/10.1046/j.1365-2664.2003.00851.x

Karlsson, S., Diserud, O. H., Fiske, P., & Hindar, K. (2016). Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES Journal of Marine Science*, *73*(10), 2488–2498. https://doi.org/10.1093/icesjms/fsw121

Karlsson, S., Diserud, O. H., Moen, T., & Hindar, K. (2014). A standardized method for quantifying unidirectional genetic introgression. *Ecology and Evolution*, *4*(16), 3256–3263. https://doi.org/10.1002/ece3.1169

Le Cam, S., Perrier, C., Besnard, A.-L., Bernatchez, L., & Evanno, G. (2015). Genetic and phenotypic changes in an Atlantic salmon population supplemented with non-local individuals: A longitudinal study over 21 years. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), 20142765. https://doi.org/10.1098/rspb.2014.2765

McGinnity, P., de Eyto, E., Cross, T. F., Coughlan, J., Whelan, K., & Ferguson, A. (2007). Population specific smolt development, migration and maturity schedules in Atlantic salmon in a natural river environment. *Aquaculture*, *273*, 257–268. https://doi.org/10.1016/j.aquaculture.2007.10.008

McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., ó Maoiléidigh, N., Baker, N., & Rogan, G. (2003). Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*, 2443–2450. https://doi.org/10.1098/rspb.2003.2520

McGinnity, P., Stone, C., Taggart, J., Cooke, D., Cotter, D., Hynes, R., … Ferguson, A. (1997). Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: Use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES Journal of Marine Science*, *54*, 998–1008. https://doi.org/10.1016/S1054-3139(97)80004-5

Miller, L. M., Close, T., & Kapuscinski, A. R. (2004). Lower fitness of hatchery and hybrid rainbow trout compared to naturalized populations in Lake Superior tributaries. *Molecular Ecology*, *13*(11), 3379–3388. https://doi.org/10.1111/j.1365-294X.2004.02347.x

Moore, J. S., Bourret, V., Dionne, M., Bradbury, I., O'Reilly, P., Kent, M., … Bernatchez, L. (2014). Conservation genomics of anadromous Atlantic salmon across its North American range: Outlier loci identify the same patterns of population structure as neutral loci. *Molecular Ecology*, *23*(23), 5680–5697. https://doi.org/10.1111/mec.12972

Myers, R. A. (1984). Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *41*(9), 1349–1353. https://doi.org/10.1139/f84-165

Pompanon, F., Bonin, A., Bellemain, E., & Taberlet, P. (2005). Genotyping errors: Causes, consequences and solutions. *Nature Reviews Genetics*, *6*(11), 847–859. https://doi.org/10.1038/nrg1707

Porter, T. R. (1975). *Biology of Atlantic salmon in Newfound and Labrador*. Information Report Series No New/N-75-2, Resource Development Branch Newfoundland Region: Fisheries and Marine Science, Department of the Environment. St. John's, NL.

Porter, T., Riche, L., & Traverse, G. (1974). *Catalogue of Rivers in Insular Newfoundland, Volume B*. Resource Development Branch Newfoundland Region: Fisheries and Marine Science, Department of the Environment. St. John's, NL.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945–959.

Rice, S. H. (2004). *Evolutionary Theory: Mathematical and conceptual foundations*. Sunderland, MA: Sinauer Associates, Inc. Publishers.

Skaala, Ø., Glover, K. A., Barlaup, B. T., Svåsand, T., Besnier, F., Hansen, M. M., & Borgstrøm, R. (2012). Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(12), 1994–2006. https://doi.org/10.1139/f2012-118

Solberg, M. F., Dyrhovden, L., Matre, I. H., & Glover, K. A. (2016). Thermal plasticity in farmed, wild and hybrid Atlantic salmon during early development: Has domestication caused divergence in low temperature tolerance? *BMC Evolutionary Biology*, *16*(1), 38. https://doi.org/10.1186/s12862-016-0607-2

Stanley, R. R., Jeffery, N. W., Wringe, B. F., DiBacco, C., & Bradbury, I. R. (2017). genepopedit: A simple and flexible tool for manipulating multilocus molecular data in R. *Molecular Ecology Resources*, *17*(1), 12–18.

Sylvester, E. V. A., Wringe, B. F., Duffy, S. J., Hamilton, L. C., Fleming, I. A., & Bradbury, I. R. (2018). Migration effort and wild population size influence the prevalence of hybridization between escaped-farmed and wild Atlantic salmon. *Aquaculture Environment Interactions*, *10*, 401–411. https://doi.org/10.3354/aei00277

Thurman, T. J., & Barrett, R. D. H. (2016). The genetic consequences of selection in natural populations. *Molecular Ecology*, *25*(7), 1429–1448. https://doi.org/10.1111/mec.13559

Vähä, J. P., Erkinaro, J., Niemelä, E., & Primmer, C. R. (2007). Life-history and habitat features influence the within-river genetic structure of Atlantic salmon. *Molecular Ecology*, *16*(13), 2638–2654. https://doi.org/10.1111/j.1365-294X.2007.03329.x

Vandersteen, W., Biro, P., Harris, L., & Devlin, R. (2011). Introgression of domesticated alleles into a wild trout genotype and the impact on seasonal survival in natural lakes. *Evolutionary Applications*, *5*(1), 76–88. https://doi.org/10.1111/j.1752-4571.2011.00210.x

Veinott, G. I., Robertson, M. J., Bradbury, I., Dempson, J. B., Grant, C., Kelly, N., …Poole, R. (2018). Status of Atlantic Salmon (*Salmo salar* L.) stocks within the Newfoundland and Labrador Region (Salmon Fishing Areas 1-14B), 2016. DFO Canadian Science Advisory Secretariat Report, Research Document 2018/008, 38pp.

Wringe, B., Jeffery, N., Stanley, R., Hamilton, L., Anderson, E., Fleming, I., … Bradbury, I. (2018). Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. *Communications Biology*, *1*, 108. https://doi.org/10.1038/s42003-018-0112-9

Wringe, B., Stanley, R., Jeffery, N., Anderson, E., & Bradbury, I. (2017a). hybriddetective: A workflow and package to facilitate the detection of hybridization using genomic data in r. *Molecular Ecology Resources*, *17*(6), e275–e284. https://doi.org/10.1111/1755-0998.12704

Wringe, B., Stanley, R., Jeffery, N., Anderson, E., & Bradbury, I. (2017b). parallelnewhybrid: An R package for the parallelization of hybrid detection using newhybrids. *Molecular Ecology Resources*, *17*, 91–95. https://doi.org/10.1111/1755-0998.12597

Wringe, B., Stanley, R., Jeffery, N., Hamilton, L., Anderson, E., & Bradbury, I. (2018). Development and evaluation of SNP panels for the detection of hybridization between wild and escaped Atlantic salmon (*Salmo salar*) in the West Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*. https://doi.org/10.1139/cjfas-2017-0394

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Sylvester EVA, Wringe BF, Duffy SJ, et al. Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations. *Evol Appl*. 2019;12:705–717. https://doi.org/10.1111/eva.12746

Received: 30 June 2020 | Revised: 14 January 2021 | Accepted: 26 February 2021

DOI: 10.1111/eva.13213

Evolutionary Applications Open Access WILEY

ORIGINAL ARTICLE

Selection against individuals from genetic introgression of escaped farmed salmon in a natural population of Atlantic salmon

Sebastian Wacker | **Tonje Aronsen** | **Sten Karlsson** | **Ola Ugedal** | **Ola H. Diserud** | **Eva M. Ulvan** | **Kjetil Hindar** | **Tor F. Næsje**

Norwegian Institute for Nature Research, Trondheim, Norway

Correspondence
Sebastian Wacker, Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgarden, NO 7485 Trondheim, Norway.
Email: sebastian.wacker@nina.no

Funding information
Grieg Seafood Finnmark AS; NRS Farming AS Region Finnmark; Cermaq Norway AS Region Finnmark; Norwegian Directorate for Nature Management; Statkraft AS; Norwegian Institute for Nature Research; Norwegian Directorate of Fisheries; Alta Salmon Fishery Partnership (ALI)

Abstract

The viability of wild Atlantic salmon populations is threatened by genetic introgression from escaped farmed salmon. Farmed Atlantic salmon are genetically improved for important commercial traits and a life in captivity but are poorly adapted to the natural environment. The rate of gene flow from escaped farmed to wild salmon depends on their spawning success and on offspring survival at various life stages. We here investigate relative survival of introgressed juvenile Atlantic salmon (parr) in a river in northern Norway. The studied population has experienced genetic introgression from farmed salmon for about four generations (20 years). We followed two cohorts of parr from the year of hatching (0+) to the age of 2 years (2+). Farmed genetic introgression was quantified at the individual level and on a continuous scale using diagnostic SNPs. Population-level genetic introgression decreased from 0+ to 2+ by 64% (2011 cohort) and 37% (2013 cohort). This change was driven by a 70% (2011 cohort) and 49% (2013 cohort) lower survival from age 0+ to 2+ in introgressed parr compared to parr of wild origin. Our observations show that there is natural selection against genetic introgression with a potential cost of lower productivity.

KEYWORDS

aquaculture, Atlantic salmon, farmed salmon, genetic introgression, *Salmo salar*, survival

1 | INTRODUCTION

Domesticated animals that escape from captivity or are released intentionally may hybridize with wild conspecifics, leading to unidirectional gene flow into wild populations. Examples of genetic introgression from domesticated animals into wild populations include mammals (Anderson et al., 2019; Kidd et al., 2009), birds (Brisbin & Peterson, 2007; Wu et al., 2020), fish (Letourneau et al., 2018) and insects (Seabra et al., 2019). Genetic introgression from domesticated animals alters the gene pool of wild populations and may constrain their viability and evolutionary potential (Glover et al., 2017; Naylor et al., 2005). Farmed domesticated animals are adapted to a captive environment and selected for characteristics that are of commercial importance. The same characteristics may reduce survival and reproductive success in the natural environment (Araki et al., 2007; Bertolotti et al., 2020). Domesticated animals may also originate from a limited set of founder populations and from a geographical range that does not reflect the genetic diversity of the species (Hindar et al., 1991). Reduced genetic diversity and non-native origin are also commonly found in captive-bred animals that are intentionally released into the environment for the purpose of stocking wild populations (Kitada, 2018; Letourneau et al., 2018). Due to domestication selection and the origin of founder populations, genetic introgression from escaped farmed animals and intentionally released domesticated animals is expected to reduce genetic diversity and to interfere with local adaption of wild populations.

The fast-growing aquaculture industry commonly involves farming of fish species outside their natural distribution and farming of highly domesticated fish species (Bostock et al., 2010; Naylor et al., 2001). Escaped farmed fish threaten native species through the introduction of invasive species and through hybridization between domesticated individuals and wild conspecifics (Araki & Schmid, 2010). Among the best-documented examples of genetic introgression from farmed domesticated fish into wild populations is Atlantic salmon (*Salmo salar*) (Forseth et al., 2017; Glover et al., 2017; Karlsson et al., 2016; Wringe et al., 2018). Farmed Atlantic salmon in Norway originate from several wild founder populations from western Norway and have been selected for traits that are favourable in aquaculture since the 1970s (Gjedrem & Baranski, 2009; Gjedrem et al., 1991). They hold lower genetic variation compared to wild Atlantic salmon and differ in fundamental life-history traits such as growth and maturation (Bolstad et al., 2017; Glover et al., 2017). Farmed Atlantic salmon kept in aquaculture outnumber their wild conspecifics 1000-fold and escape events occur frequently (Fiske et al., 2006; Glover et al., 2019, 2020).

Escaped farmed Atlantic salmon may enter rivers and hybridize with wild Atlantic salmon, leading to unidirectional gene flow and genetic introgression (Glover et al., 2013; Karlsson et al., 2016). Hybrid and farmed offspring are able to survive to maturity in the wild and to return to freshwater for spawning (Fleming et al., 2000; McGinnity et al., 2003). Genetic introgression from escapees is thereby carried over to future generations and manifested in wild populations (Glover et al., 2013; Karlsson et al., 2016). Such farmed genetic introgression has been found in many geographic regions where wild Atlantic salmon co-occur with Atlantic salmon farming, including Canada, Ireland and Norway (Glover et al., 2017). There was large spatial and temporal variation in the incidence of escaped farmed salmon in rivers across Norway over a 25-year period (1989–2013), with average incidences ranging from ca. 8%–29% across geographical regions and with high incidences during the early 1990s and the early 2000s (Diserud et al., 2019). Hybridization of escaped farmed salmon with wild Atlantic salmon has resulted in an average level of farmed genetic introgression of 6.4% (range 0%–42%) in 109 rivers across Norway (Karlsson et al., 2016). These estimates are from adult salmon sampled after having spent their entire life in the wild. At the juvenile stages, the level of introgression is expected to be higher, but few comparisons exist (Karlsson et al., 2016).

Hybrids of farmed and wild Atlantic salmon are poorly adapted to the natural environment (Bolstad et al., 2017) and show lower survival and reproductive success than wild conspecifics (Fleming et al., 2000; McGinnity et al., 2003). Hybridization may thereby substantially reduce population-level fitness of wild Atlantic salmon populations. At the same time, reduced survival and reproductive success of hybrids may limit genetic introgression into wild populations (Glover et al., 2017; Hindar et al., 2006), as found for stocking of brook charr (*Salvelinus fontinalis*) (Letourneau et al., 2018) and for hybridization between native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and invasive rainbow trout (*O. mykiss*) (Kovach et al., 2016). Knowledge of survival and reproductive success of farmed hybrids is therefore important for the prediction of both population-level fitness and genetic introgression in wild Atlantic salmon.

The early survival of hybrid Atlantic salmon from eggs to smolt in the wild has previously been studied in field experiments. Farmed and wild Atlantic salmon were allowed to interact and spawn freely in experimental rivers (Fleming et al., 2000), or eggs from crossings were planted into experimental rivers (McGinnity et al., 2003; Skaala et al., 2019). Juveniles sampled at later stages were genetically assigned to farmed and wild parents. Studies that quantified total survival in freshwater from eggs to out-migrating smolt uniformly reported a reduced survival of farmed and hybrid individuals (Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2012, 2019). Field experiments that quantified survival from age 0+ to out-migrating smolt found variable survival of farmed and hybrid parr in Ireland (McGinnity et al., 1997, 2003), but little variation between groups in Norway (Fleming et al., 2000). A recent study used diagnostic SNPs to estimate the abundance of farmed and hybrid Atlantic salmon parr in a range of rivers in Canada, after a single large aquaculture escape (Sylvester et al., 2019; Wringe et al., 2018). From age 0+ to 2+, there was a reduction in the relative abundance of farmed parr and hybrids (Sylvester et al., 2019; Wringe et al., 2018). In summary, field studies uniformly reported decreased survival of hybrid and farmed offspring during the entire freshwater stage (eggs to smolt), while the evidence was mixed for parr survival (Fleming et al., 2000; McGinnity et al., 2003; Sylvester et al., 2019).

Earlier field studies on the survival of farmed and hybrid individuals in freshwater have focussed on first-generation offspring of farmed Atlantic salmon and their crossing with wild fish. Genetic introgression from escaped farmed salmon over many generations is expected to result in offspring of various hybrid classes. Field studies in Ireland found reduced parr survival (0+ to out-migrating smolt) for farmed and first-generation hybrids, while second-generation hybrids and second-generation backcrosses between hybrids and farmed or wild fishes had reduced survival at the egg stage but not as parr (McGinnity et al., 2003). Earlier studies also focussed on high proportions of farmed and hybrid offspring (ca. 25%–75%) and on scenarios of single large-scale introgression events (Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2019; Wringe et al., 2018). The relative survival of hybrid parr may depend on whether they primarily compete with hybrid parr or with wild parr. Farmed parr show higher levels of aggression than wild parr (Einum & Fleming, 1997), and under constant density, the presence of farmed parr, but not the presence of wild parr, has been found to reduce the survival of wild parr (Robertsen et al., 2019; Sundt-Hansen et al., 2015). Knowledge of the survival of hybrid parr under moderate levels of genetic introgression is also important because the negative effects of genetic introgression on wild populations may be more severe under low-level introgression over prolonged time than under rare large-scale introgression events (Baskett et al., 2013). The relative survival of farmed and hybrid Atlantic salmon parr has not been studied in rivers that have experienced genetic introgression over prolonged time and under moderate levels of genetic introgression.

Here, we study changes in genetic introgression over time in two cohorts (years of hatching) of Atlantic salmon parr in the River Alta in northern Norway. The Atlantic salmon in River Alta is part of the Barents–White Sea phylogenetic group, while all founder populations of the farmed strains are part of the Eastern Atlantic phylogenetic group (Bourret et al., 2013; Karlsson et al., 2016). Large genetic divergence between native River Alta Atlantic salmon and farmed escapees may increase maladaptation and thereby mortality of introgressed individuals (Baskett et al., 2013; Bolstad et al., 2017; Huisman & Tufto, 2012). Escaped farmed salmon have been recorded in River Alta since the late 1980s (Ugedal et al., 2016). The relative abundances of escaped farmed salmon in catches of adult spawners in the autumn ranged from 0% to 22% between 1991 and 2018 (Ugedal et al., 2016) (Table S1). The overall level of genetic introgression in parr of the studied cohorts was moderate. To study relative survival of introgressed and wild salmon in a natural population, we quantified genetic introgression in parr at the ages of 0+, 1+ and 2+ within two cohorts. We hypothesized that the level of genetic introgression would decrease as the cohort grew older. This study aims at understanding the ability of natural selection to reduce the level of genetic introgression of escaped farmed salmon. The results add new knowledge about the consequences of escaped farmed salmon in wild populations.

2 | METHODS

2.1 | River Alta

River Alta is an Atlantic salmon river in northern Norway (70°N 23°E) with an average discharge of 98.9 m^3/s and an average catch of salmon of 16 tonnes per year (Ugedal et al., 2016). The River Alta has been utilized for hydroelectric generation purposes since 1987 and the outlet of the water tunnel from the power plant is located at the upper end of the salmon producing section, which is limited to the lower 50 km of the 160 km long main stem (Ugedal et al., 2008).

The population level of farmed genetic introgression, measured in adult fish and with the same methods as used in this study (described under Statistical analysis), in River Alta varied between 0% and 5.4% from 2012 to 2016 (Karlsson et al., 2016). This study was conducted in the uppermost section of River Alta, called Sautso (Figure 1), which in many years had a higher proportion of escaped farmed Atlantic salmon than the lower parts of the river (Table S1). Tagging studies have shown that escaped farmed salmon have a higher propensity than wild salmon to migrate to the upper parts of River Alta (Heggberget et al., 1996).

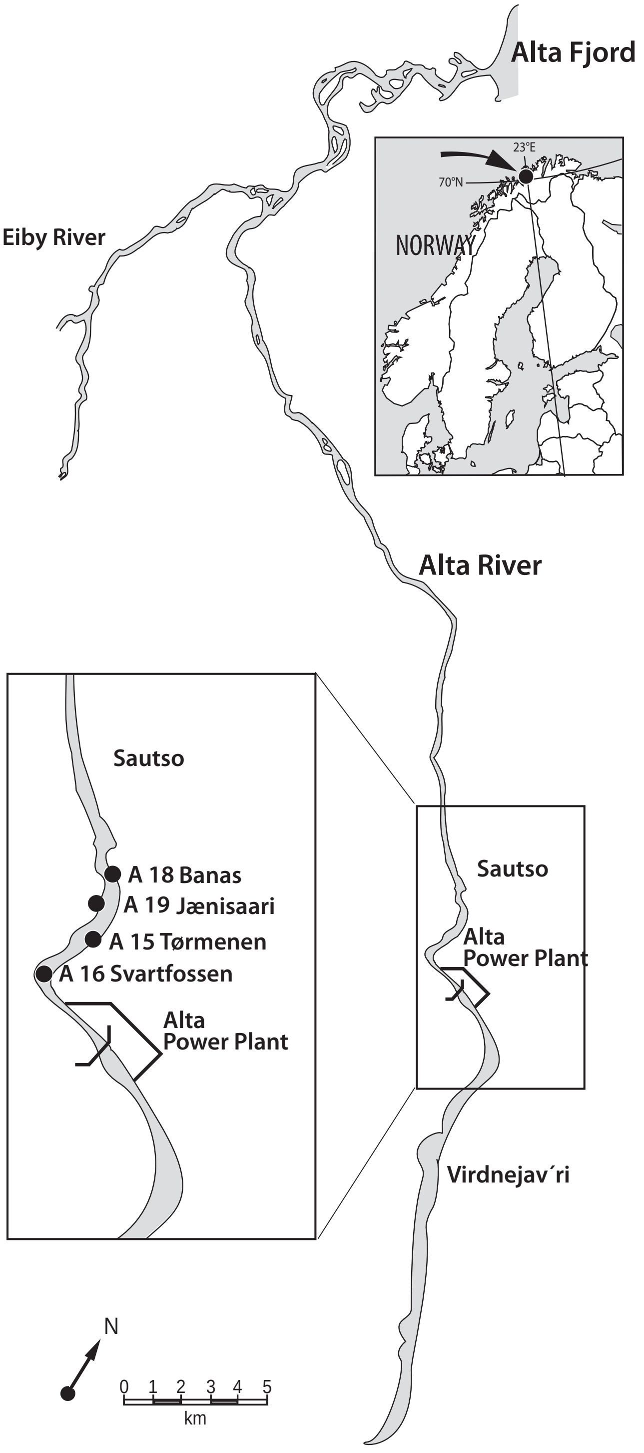


FIGURE 1 River Alta with the anadromous part of the river from the Alta Fjord to the hydropower station (Alta Power Plant). The study was conducted in the uppermost part of the river (Sautso), and samples were collected at four sampling locations (A16, A15, A19 and A18)

2.2 | Sampling of fish

In order to study changes in the level of farmed genetic introgression within cohorts of juvenile Atlantic salmon, fish were sampled at the year of hatching (0+), 1 year after hatching (1+) and 2 years after hatching (2+). Samples were accordingly collected in 2012, 2013 and 2014 for breeding year 2011 and in 2014, 2015 and 2016 for breeding year 2013. Juveniles were collected by electrofishing at four sampling locations (Figure 1) and stored in ethanol (breeding year 2011: 0+, 1+, 2+; breeding year 2013: 0+) or frozen (breeding year 2013: 1+ and 2+). Juveniles were thereafter measured for fork length to the nearest mm, and measurements were back-calculated to live fork length using previously established relationships (Thorstad et al., 2007). Age of juveniles was determined from readings of scales and otoliths. Sampling took place between August and October, with, in most instances, two sampling days per age class and cohort (Table 1). The habitat at sampling location A19 is not suitable for 2+ parr and only a single and no fish of that age were caught at sampling location A19 for the breeding years 2011 and 2013, respectively (Table 1). We present results for the cohorts from the breeding years 2011 and 2013. For a third cohort (breeding year 2014), juveniles were collected at the ages of 0+ and 1+ and analysed for farmed genetic introgression. The level of genetic introgression in the 2014 cohort was marginal and not statistically significant at the age of 0+ (0.5%) and 1+ (1.5%). The data were therefore not suited to test for a change in the level of genetic introgression with increasing age.

2.3 | Genetic analysis

DNA was extracted from juvenile fish stored in ethanol using the DNEASY tissue kit (Qiagen) and genotyped at 81 nuclear and 15 mitochondrial SNPs using a EP1™ 96.96 Dynamic array IFCs platform (Fluidigm). Forty-eight of the nuclear SNPs have been identified by Karlsson et al. (2011) as showing large genetic differences between Norwegian farmed and wild salmon regardless of farmed strain and wild population, and these were used for estimating wild and farmed ancestry of individual fish (Karlsson et al., 2014, 2016).

2.4 | Estimating genetic introgression

We estimated genetic introgression with the method described by Karlsson et al. (2014). The method uses the programme STRUCTURE (Pritchard et al., 2000) to estimate the likelihood of an individual to belong to a wild salmon reference sample versus a farmed salmon reference sample. We hereafter refer to this likelihood as *P*(*Wild*) (Karlsson et al., 2014). The wild reference sample is given by historical samples collected before the onset of commercial Atlantic salmon farming. River Alta belongs to the Barents–White Sea phylogenetic group (Bourret et al., 2013) and historical samples from a range of populations belonging to this phylogenetic group were used as wild reference (Karlsson et al., 2014, 2016). Samples from the Norwegian breeding kernels for farmed salmon were used as farmed salmon reference (Karlsson et al., 2014, 2016).

Genetic introgression on the population level (proportion of the genome being of farmed origin) was estimated from individual *P*(*Wild*) estimates. Individual *P*(*wild*) estimates range from zero to one, so wild reference samples will always have an average *P*(*wild*) estimate less than one, while the farmed salmon reference sample has an average *P*(*wild*) estimate larger than zero (Karlsson et al., 2014). When estimating genetic introgression on population level, the scale must therefore be calibrated by the respective average observed *P*(*Wild*) in the wild and farmed reference samples (Karlsson et al., 2014). Historical samples from River Alta collected in 1981 and 1982 (Karlsson et al., 2016) were used as wild reference sample for calibrating the scale of population-level genetic introgression. This procedure ensured unbiased estimation of genetic introgression for River Alta.

The power of quantifying introgression on individual and population level with the above methods has been explored in simulations (Karlsson et al., 2014). On population level, introgression was estimated with high precision; that is, the estimate was close to the simulated proportion of the genome being of farmed origin. On the individual level, introgression is estimated with larger uncertainty and *P*(*wild*) estimates for first-generation hybrids may cover the whole range from 0 to 1 (Karlsson et al., 2014).

2.5 | Statistical analysis

We tested whether population-level genetic introgression was significantly larger than 0 within each cohort and age class. This was done by testing if the observed mean *P*(*Wild*) was smaller than the mean *P*(*Wild*) of the historical sample from the River Alta (Karlsson

TABLE 1 Numbers of juvenile Atlantic salmon from two cohorts (breeding years 2011 and 2013) collected at four sampling locations in River Alta (A15, A16, A18, A19)

	2011			2013		
	0+	1+	2+	0+	1+	2+
A15	23 (0 + 23)	26 (25 + 1)	26 (11 + 15)	24 (24 + 0)	24	46 (18 + 28)
A16	26 (19 + 7)	25 (17 + 8)	24 (12 + 12)	25 (0 + 25)	29	24 (9 + 15)
A18	24 (0 + 24)	26 (26 + 0)	24 (2 + 22)	22 (22 + 0)	24	30 (14 + 16)
A19	22 (8 + 14)	23 (12 + 11)	1 (1 + 0)	22 (22 + 0)	18	0
Total	95 (27 + 68)	100 (80 + 20)	75 (26 + 49)	93 (68 + 25)	95	100 (41 + 59)

Note: Juveniles were sampled at the year of hatching (0+) and at the age of one and two years (1+ and 2+). When sampling of a given cohort and age class took place at two different occasions, numbers of fish sampled at the first and second sampling date, respectively, are given in brackets.

et al., 2016) with a two-sample t test. *P*(*Wild*) estimates (proportion data varying from zero to one) were logit-transformed before testing to achieve that transformed proportions are approximately normally distributed (Karlsson et al., 2014). Tests assumed equal variance of samples (Karlsson et al., 2014, 2016).

A linear model was used to test for a temporal change of genetic introgression within cohorts, that is an effect of age on *P*(*Wild*). The model was fitted with *P*(*Wild*) as response variable and with age (continuous variable) and cohort (factor) as explanatory variables. In graphical exploration, there was no indication for a difference in slopes among the two cohorts and the model was fitted without an interaction between age and cohort. Sampling of juveniles of a given cohort and in a given year was carried out at two dates (Table 1), with 25–70 days in between. Changes in genetic introgression within cohorts may occur over time between years and between sampling dates within years, and age was therefore entered into the model as a continuous variable. Age was included in the model as the number of days counted from August 14 (the earliest date 0+ juveniles were sampled) in the year 0+ samples of the respective cohort were collected. On this scale, the age of 0+ samples was 0–77 days, the age of 1+ samples was 365–395 days, and the age of 2+ samples was 730–800 days. *P*(*Wild*) is a likelihood estimate measured on a scale from zero to one and was logit-transformed prior to analysis and residuals inspected for deviation from normal distribution.

We also tested for a temporal change in the proportion of introgressed individuals within cohorts, classifying individuals as introgressed or wild depending on their *P*(*wild*). In contrast to the above-described analysis of changes in *P*(*wild*), results from this analysis can be more directly related to earlier studies on the relative survival of introgressed parr, which reported abundances and relative survival of wild and hybrid parr (Fleming et al., 2000; McGinnity et al., 2003; Wringe et al., 2018). We used a generalized linear model with a binomial distribution to test for an effect of age on the likelihood of juveniles to be of wild origin. The response variable in the model was the classification of each juvenile as wild (entered as value one) or introgressed (entered as value zero) and explanatory variables were age (continuous variable) and cohort (factor). In graphical exploration, there was no indication for a difference in slopes among the two cohorts and the model was fitted without an interaction between age and cohort. There was indication for overdispersion of the residuals and the model was therefore fitted with a quasibinomial error distribution.

We classified juveniles as introgressed that had a *P*(*Wild*) below a given threshold. The threshold was based on the *P*(*Wild*) distribution of historical samples of Atlantic salmon from the Barents–White Sea phylogenetic group in Finnmark county, Norway ($N = 1000$). Those historical samples were collected before the onset of commercial Atlantic salmon farming and did therefore not include introgressed individuals. Using a threshold from the lower end of the *P*(*wild*) distribution of those historical samples ensured that juveniles from River Alta that were classified as introgressed were unlikely to be of pure wild origin. We analysed the data using three alternative lower percentiles of the historical distribution: the 5 percentile (*P*(*Wild*) = 0.8315), the 3 percentile (*P*(*Wild*) = 0.7420) and the 1 percentile (*P*(*Wild*) = 0.5528). Because of moderate levels of genetic introgression in the studied cohorts, a large proportion of juveniles were classified as wild. The number of truly wild juveniles expected to be wrongly classified as introgressed (1%–5% depending on the threshold) was therefore relatively high compared to the number of truly introgressed juveniles and highest when using the 5 percentile threshold. When the 1 percentile was used, few juveniles were classified as introgressed, increasing uncertainty in the statistical estimation of the proportion of introgressed individuals. We therefore present results based on the 3 percentile in the main text. Results for all three considered percentiles are presented in Table S2.

Classification of juveniles into wild and introgressed was also used to calculate survival of introgressed juveniles relative to survival of wild juveniles. Relative survival of introgressed juveniles was calculated for the two cohorts separately and for the entire time period (0+ to 2+ age), as well as for the time periods from 0+ to 1+ and from 1+ to 2+ separately. Relative survival of hybrid juveniles was calculated by dividing the ratio of introgressed to wild individuals in the first sample (e.g. 0+ age) by the ratio of introgressed to wild individuals in the second sample (e.g. 2+ age).

The fact that a substantial proportion of juveniles classified as introgressed was likely truly wild renders our analysis of a temporal change in introgression within cohorts conservative, because potential differences in survival between wild and introgressed juveniles are partly masked. This effect is expected to be stronger under a higher *P*(*Wild*) threshold.

Parr mortality may be related to body size which again can be related to genetic introgression (Fleming et al., 2000; Reed et al., 2015; Solberg et al., 2013). The effect of genetic introgression on growth is a potential route for reduced survival in hybrid parr, and we therefore tested for an effect of *P*(*Wild*) on fork length. The effect was tested with separate linear models for each age class (0+, 1+, 2+). Models were fitted with fork length (continuous variable) and cohort (factor) as explanatory variables. There was no indication for a difference in slopes among the two cohorts and the model was fitted without an interaction between fork length and cohort.

3 | RESULTS

We detected moderate farmed genetic introgression in juvenile Atlantic salmon from River Alta. Estimated population-level genetic introgression ranged from 0.02 to 0.10 within a cohort and age class (Figure 2) and between 3% and 16% of the sampled parr were classified as hybrids (*P*(*Wild*) < 0.7420; Figure 3). Population-level genetic introgression was significantly higher than 0 for all age classes in the 2013 cohort (all $p < 0.001$) and for the 0+ and 1+ age classes in the 2011 cohort (both $p < 0.05$) (Figure 2).

Estimated population-level genetic introgression decreased with the age of parr within cohorts. In the 2011 cohort, genetic introgression (the estimated proportion of the genome being of farmed origin) changed from 0.050 at 0+ age to 0.018 at 2+ age (64% reduction).

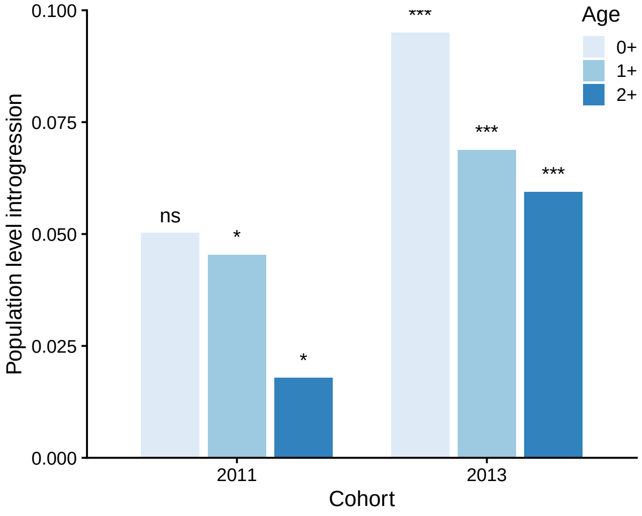


FIGURE 2 Estimated population-level farmed introgression (proportion of the genome being of farmed origin) in juvenile Atlantic salmon from River Alta of two cohorts (2011 and 2013) at the age of 0+ to 2+. Symbols above bars indicate whether introgression was statistically significantly higher than 0 (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns $p > 0.05$)

In the 2013 cohort, genetic introgression changed from 0.095 at 0+ age to 0.059 at 2+ age (37% decrease) (Figure 2). We tested for a temporal change in individual *P*(*Wild*) (the probability of belonging to the wild reference sample) within cohorts and there was a statistically nonsignificant trend for an increase with parr age (slope ±SE: 0.000459 ± 0.000260 logit *P*(*wild*)*day^{-1}; $F = 3.1$, $p = 0.078$; Figure 4a). Overall the level of genetic introgression was higher in the 2013 than in the 2011 cohort, with a lower *P*(*Wild*) (intercept: $F = 11.1$, $p < 0.001$; Figure 4a).

The proportion of juveniles that were classified as wild (*P*(*Wild*) ≥ 0.7420) increased with the age of parr (slope: $\chi^2 = 4.8$, $p = 0.029$; Figure 4b; Table S2). An overall lower proportion of juveniles was classified as wild in the 2011 cohort than in the 2013 cohort (intercept: $\chi^2 = 5.2$, $p = 0.023$; Figure 4b). The estimated temporal increase in the proportion of individuals classified as wild was stronger when a lower *P*(*wild*) threshold was used and weaker when a higher *P*(*wild*) threshold was used (Table S2).

The survival of introgressed juveniles from 0+ to 2+, relative to the survival rate of wild parr, was estimated at 0.30 (0+ to 1+: 0.82; 1+ to 2+: 0.36) and 0.51 (0+ to 1+: 0.55; 1+ to 2+: 0.93) in the 2011 and 2013 cohorts, respectively. The proportion of juveniles

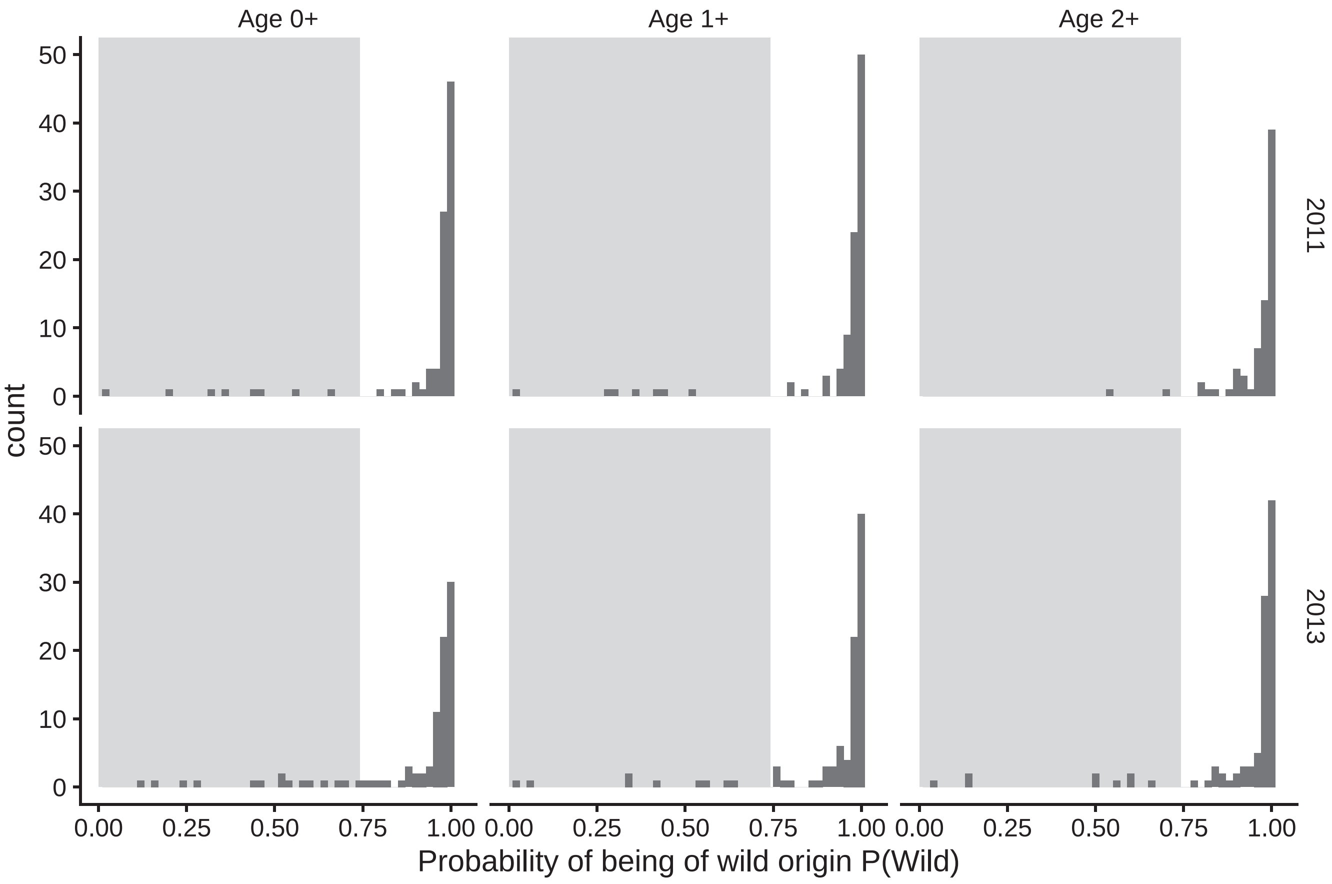


FIGURE 3 Distribution of individual *P*(*Wild*) estimates (probability of belonging to a wild reference sample) in juvenile Atlantic salmon from River Alta of two cohorts (2011 and 2013) sampled at the age of 0+, 1+ and 2+. Shaded areas indicate the range within which individuals were classified as farmed or hybrid offspring based on a *P*(*wild*) threshold of 0.7420

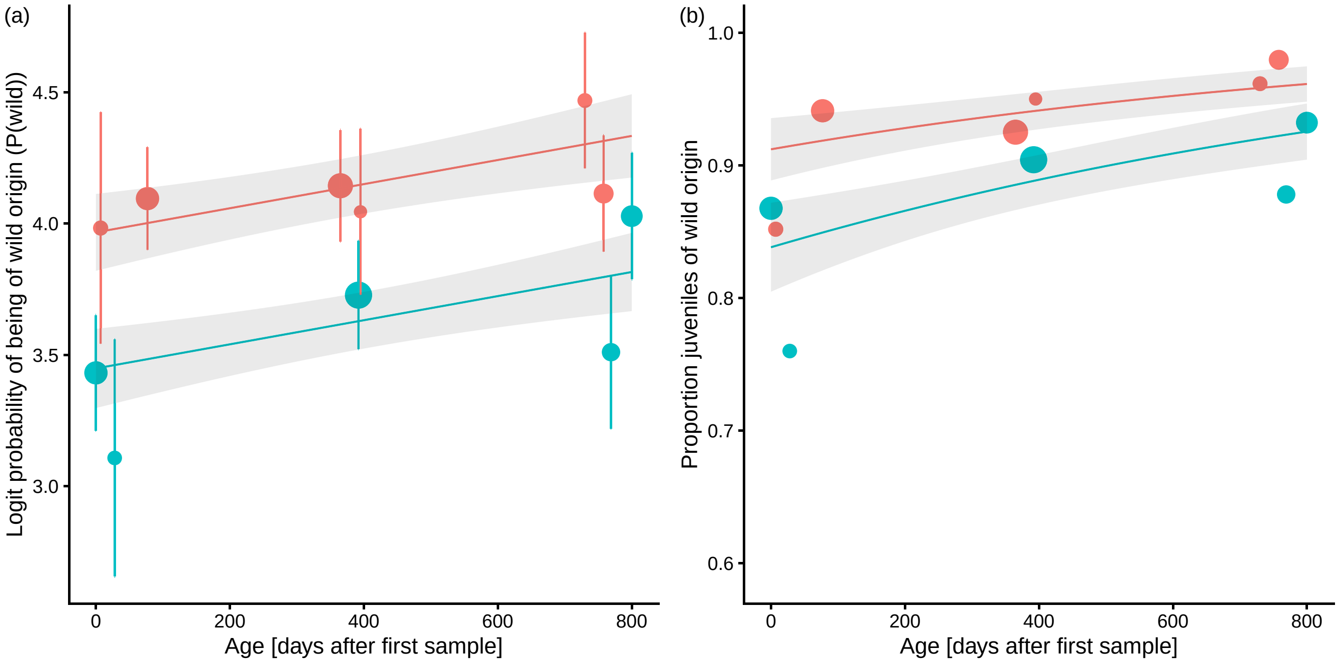


FIGURE 4 Effect of age on genetic introgression in two cohorts (red =2011, green =2013) of juvenile Atlantic salmon from River Alta. Age is given as the number of days after first sampling in the year of hatching for each cohort: 0+ (0–77 days), 1+ (365–395 days) and 2+ (730–800 days). Genetic introgression is given as (a) logit-transformed probability of being of wild origin *P*(*Wild*) and (b) the classification of individuals as being of wild origin or as introgressed, based on their *P*(*Wild*). Points indicate means per sampling date and the size of points indicates sample size (*N* between 20 and 94 individuals). For (a) *P*(*Wild*), bars indicate one standard error. Lines indicate effects estimated in (a) a linear model and (b) a generalized linear model, with shaded areas indicating one standard error

that were classified as introgressed varied widely among sampling localities, but decreased with age in most sampling localities within breeding years (Figure S1).

Parr length was significantly negatively associated with *P*(*Wild*); that is, introgressed parr were larger than wild parr, at the age of 1+ ($F = 5.0$, $p = 0.027$; Figure 5b), and there was a statistically nonsignificant trend for such a relationship at the age of 2+ ($F = 3.6$, $p = 0.06$; Figure 5c), but not at the age of 0+ ($F = 6.7$, $p = 0.55$; Figure 5a). At the age of 1+, there was an estimated decrease of 7.2% in fork length between the fish of lowest *P*(*Wild*) (2011 cohort: 78.3 mm) and the individual of highest *P*(*Wild*) (2011 cohort: 72.7 mm). In the model of length at 1+ age, cohort and logit *P*(*Wild*) together explained approximately 8% of the variation in fork length.

4 | DISCUSSION

Farmed genetic introgression decreased over the first 2 years after hatching in two cohorts of Atlantic salmon. The results show that introgressed parr had a lower survival than wild parr in River Alta. Survival of introgressed parr in the wild has previously been studied in Canada after a major escape event (Wringe et al., 2018) and in field experiments in Norway and Ireland (Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2012, 2019). In line with our results, introgressed parr had a lower survival than wild parr in Canada (Sylvester et al., 2019; Wringe et al., 2018). Temporal changes in the relative abundance of introgressed parr differed widely in strength and direction among the thirteen rivers studied, but on average the relative abundance of farmed and hybrid parr was halved from the age of 0+ to 2+ (Sylvester et al., 2019). Reduced survival of farmed parr and first-generation hybrids was also found in Ireland (0+ to out-migrating smolt), after eggs from crossings of farmed and wild Atlantic salmon were planted into an experimental river (McGinnity et al., 1997, 2003; Reed et al., 2015). Fleming et al. (2000) released wild and farmed adult Atlantic salmon into an experimental river in Norway and quantified breeding success and offspring survival. Breeding success and early survival were lower for farmed than for wild fish, but there was no evidence for reduced survival of introgressed offspring in the parr stage (0+ in autumn to out-migrating smolt). Our results add to previous evidence of reduced survival of farmed and hybrid parr from Canada and Ireland.

We found reduced relative survival of introgressed parr in a river with moderate levels of genetic introgression. In the studied cohorts, population-level genetic introgression was only 5%–10% at the age of 0+, with 9%–16% of parr detected as introgressed. Despite moderate levels of genetic introgression, there was a substantial decrease in introgression from 0+ to 2+ (37%–64%) and the relative survival of introgressed parr was 0.30–0.51 across the same time period. There was considerable uncertainty in estimating those changes, as expected when analysing low rates of introgression and low proportions of introgressed parr. With a sample size of approximately 300 individuals per cohort, we detected significant introgression in both cohorts and a significant reduction in introgression with age, but the statistical significance was around the 0.05 acceptance

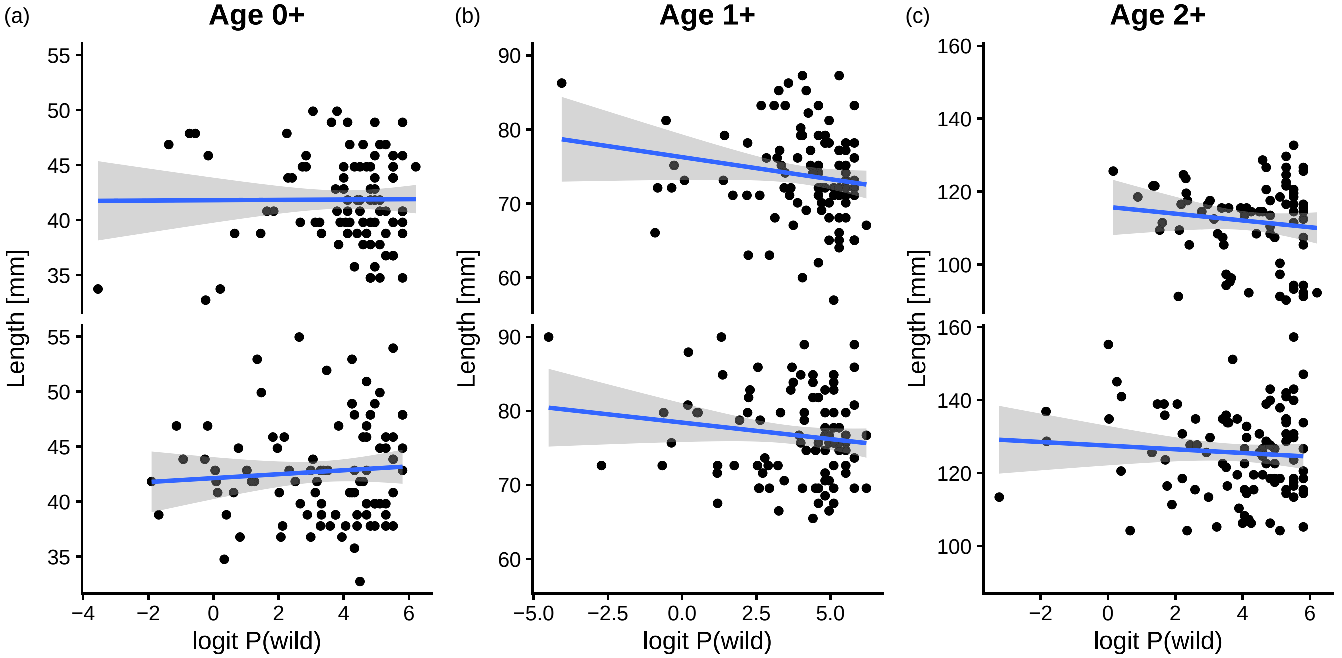


FIGURE 5 Relationship between genetic introgression (logit *P*(*Wild*)) and fork length [mm] in two cohorts (2011 upper panel and 2013 lower panel) of Atlantic salmon parr sampled in River Alta at the age of 0+ (a), 1+ (b) and 2+ (c). Blue lines indicate relationships estimated by linear regression, and grey shades indicate 95% confidence intervals. Note that scales on both axes differ among panels

threshold in several tests. Despite those uncertainties, our study shows that introgressed Atlantic salmon parr show reduced survival under moderate levels of introgression. Reduced survival of introgressed parr under moderate levels of introgression is a finding that complements earlier studies that quantified the survival of hybrid parr under higher relative abundances in field experiments (Fleming et al., 2000: >25%; McGinnity et al., 2003: 75%) and in Canadian rivers (median relative abundance 50%; Wringe et al., 2018). Our results also show that the survival of hybrid parr is reduced in rivers experiencing moderate levels of genetic introgression over prolonged time periods. This result is important for predicting the effect of genetic introgression on the viability of wild populations, which is expected to be stronger under constant low-level genetic introgression than under rare events of strong genetic introgression (Baskett et al., 2013). Together with previous studies, our results show reduced survival of introgressed parr across a range of levels of genetic introgression.

Our study considered introgression resulting after about 20 years of varying abundances of escaped farmed salmon (Table S1) (Diserud et al., 2019). Introgressed parr were therefore expected to belong to various hybrid classes, resulting from backcrosses between farmed, wild, and hybrid parents over several generations. Previous experimental studies followed survival of first-generation (Fleming et al., 2000; McGinnity et al., 1997) or first- and second-generation hybrids (McGinnity et al., 2003). This was also primarily the case in the observational study in Canada, where a large-scale escape event affected previously little introgressed rivers (Sylvester et al., 2019; Wringe et al., 2018). This may affect results because the effects of genetic introgression on survival and fitness vary among the different backcross types, and variation does not necessarily follow an additive manner (Debes et al., 2013; McGinnity et al., 2003; Wringe et al., 2018). McGinnity et al. (2003) found reduced survival for farmed parr and first-generation hybrids, but not for second-generation hybrids or backcrosses, which experienced increased relative mortality only at the egg stage. Our study did not detail survival rates for specific hybrid and backcross types. Instead, our results show that the total level of genetic introgression within cohorts decreased in parr over 2 years in a population that had experienced interbreeding with escaped farmed salmon over several generations.

Variation in the relative survival of introgressed parr may ultimately have a strong effect on the rate of gene flow into wild populations. In models based on experimental studies from Norway and Ireland, 0+ to smolt was the life stage at which differences in survival rates among experiments affected genetic introgression the most (Hindar et al., 2006). The relative survival of introgressed parr in our study was at the lower end of the range considered in those models, implying a reduction in population-level introgression under a given abundance of farmed escapees (Hindar et al., 2006). Relative survival of introgressed parr was also found to largely affect the rate of gene flow in models based on observations made after a large-scale escape of farmed salmon in Canada (Sylvester et al., 2019). Variation in the effects of introgression on survival has also been observed at other life stages, including early development and from smolt to returning adults (McGinnity et al., 2003; Robertsen et al., 2019; Sundt-Hansen et al., 2015). In consequence, the relative contribution of those effects to the relative fitness of introgressed Atlantic salmon varied. Together, those effects are likely to contribute to the elusive factors explaining the relationship between abundances of escaped farmed Atlantic salmon and resulting genetic introgression across Norwegian rivers (Karlsson et al., 2016).

The negative impact of genetic introgression may not only depend on the rate of gene flow but also on genetic divergence between farmed and wild strains (Baskett et al., 2013; Castellani et al., 2015; Glover et al., 2017; Huisman & Tufto, 2012). Larger genetic divergence is expected to result in larger genetic impact on locally adapted wild populations. At the same time, larger genetic divergence may increase mortality of introgressed Atlantic salmon and thereby slow down the rate of gene flow. The negative impact may therefore be more severe under moderate genetic divergence (Baskett et al., 2013; Huisman & Tufto, 2012). Genetic divergence is largest when farmed strains originate from other phylogenetic groups than the local wild populations belong to. This is the case for Irish populations, but also for wild populations in northern Norway, which are part of the Barents–White Sea phylogenetic group, while all founder populations of the farmed strains are part of the Eastern Atlantic phylogenetic group (Bourret et al., 2013; Karlsson et al., 2016). Genetic introgression has therefore a potentially large genetic impact in River Alta and other populations of the Barents-White Sea phylogenetic group. Bolstad et al. (2017) found a significant effect of genetic introgression on sea-age and size at maturity and that this effect was different, and for some comparisons larger, in the Barents–White Sea phylogenetic group compared to the effects in the Eastern Atlantic phylogenetic group. The high relative mortality of introgressed parr found in this study is in line with the expectation that high genetic divergence leads to more pronounced maladaptation and mortality of introgressed individuals.

Possible mechanisms for the effect of introgression on survival are related to the faster growth rate of introgressed Atlantic salmon parr. Differences in growth rate between farmed and wild parr are substantial under farming conditions (Glover et al., 2009, 2018), but reduced under semi-natural (Einum & Fleming, 1997; Sundt-Hansen et al., 2015) and natural conditions (Fleming et al., 2000; Reed et al., 2015; Solberg et al., 2013). We found a moderate increase in body length (ca. 8%) with the level of introgression at age 1+ and 2+, but introgression explained only a small part of size variation. Increased growth rates under natural conditions may be an overproportional investment into growth at the cost of fat reserves, which may in turn increase winter mortality (Finstad et al., 2004). Overproportional investment into growth may be particularly costly in terms of survival in northern regions, where local populations show adaptations to long winters (Finstad et al., 2010; Finstad & Forseth, 2006) and due to the negative energy balance fat reserves may be important for their survival throughout the winter (Næsje et al., 2006). Farmed Atlantic salmon parr may be maladapted to such northern conditions as a result of selection for commercially important traits and because of their origin from western Norwegian populations (Gjedrem & Baranski, 2009).

An alternative mechanism for the effect of introgression on survival is predation, as farmed parr have been shown to be more risk-prone than wild parr (Einum & Fleming, 1997). Recently, an experimental study found that predation of brown trout (*S. trutta*) on Atlantic salmon juveniles could explain the markedly lower survival of farmed and hybrid offspring, whereas the same experimental groups had similar survival in the absence of trout (Solberg et al., 2020).

Temporal changes in genetic introgression may not only have been affected by the relative survival of introgressed parr but also by movement of parr between the studied upper part of River Alta and lower parts of the river. Larger introgressed parr may be superior in ecological competition with wild parr and have been found to displace wild parr under semi-natural conditions (Sundt-Hansen et al., 2015) and in natural rivers (McGinnity et al., 2003). Displacement of wild parr by introgressed parr cannot be excluded in our study, but would render our analysis conservative, given that survival of displaced wild parr would result in a stronger decrease in population-level introgression within cohorts.

ACKNOWLEDGEMENTS

The authors thank Laila Saksgård, Sigrid Skoglund and the employees of Alta Salmon Fishery Partnership (Alta Laksefiskeri I/S) for the sampling of fish and the preparation of samples, Line Birkeland Eriksen, Merethe Hagen Spets and Hege Brandsegg for conducting the genotyping at NINA and Kari Sivertsen for the map of the sampling localities. Special thanks to Tor Erland Nilsen (Alta Laksefiskeri I/S) for input during the early phase of the project. This study was funded through the Norwegian Environment Agency, Norwegian Directorate of Fisheries, Grieg Seafood Finnmark AS, Cermaq Norway AS Region Finnmark, NRS Farming AS Region Finnmark, Statkraft AS and Norwegian Institute for Nature Research.

CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.9kd51c5gm.

ORCID

Sebastian Wacker https://orcid.org/0000-0002-3035-8615

REFERENCES

Anderson, D., Toma, R., Negishi, Y., Okuda, K., Ishiniwa, H., Hinton, T. G., Nanba, K., Tamate, H. B., & Kaneko, S. (2019). Mating of escaped domestic pigs with wild boar and possibility of their offspring migration after the Fukushima Daiichi Nuclear Power Plant accident. *Scientific Reports*, *9*, 1–6. https://doi.org/10.1038/s41598-019-47982-z

Araki, H., Cooper, B., & Blouin, M. S. (2007). Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. *Science*, *318*(5847), 100–103. https://doi.org/10.1126/science.1145621

Araki, H., & Schmid, C. (2010). Is hatchery stocking a help or harm? Evidence, limitations and future directions in ecological and genetic surveys. *Aquaculture*, *308*, S2–S11. https://doi.org/10.1016/j.aquaculture.2010.05.036

Baskett, M. L., Burgess, S. C., & Waples, R. S. (2013). Assessing strategies to minimize unintended fitness consequences of aquaculture on wild populations. *Evolutionary Applications*, *6*(7), 1090–1108. https://doi.org/10.1111/eva.12089

Bertolotti, A. C., Layer, R. M., Gundappa, M. K., Gallagher, M. D., Pehlivanoglu, E., Nome, T., Robledo, D., Kent, M. P., Røsæg, L. L., Holen, M. M., Mulugeta, T. D., Ashton, T. J., Hindar, K., Sægrov, H., Florø-Larsen, B., Erkinaro, J., Primmer, C. R., Bernatchez, L., Martin, S. A. M., … Macqueen, D. J. (2020). The structural variation landscape in 492 Atlantic salmon genomes. *Nature Communications*, *11*(1), 5176. https://doi.org/10.1038/s41467-020-18972-x

Bolstad, G. H., Hindar, K., Robertsen, G., Jonsson, B., Sægrov, H., Diserud, O. H., Fiske, P., Jensen, A. J., Urdal, K., Næsje, T. F., Barlaup, B. T., Florø-Larsen, B., Lo, H., Niemelä, E., & Karlsson, S. (2017). Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. *Nature Ecology and Evolution*, *1*(5), 124. https://doi.org/10.1038/s41559-017-0124.

Bostock, J., McAndrew, B., Richards, R., Jauncey, K., Telfer, T., Lorenzen, K., Little, D., Ross, L., Handisyde, N., Gatward, I., & Corner, R. (2010). Aquaculture: Global status and trends. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *365*(1554), 2897–2912. https://doi.org/10.1098/rstb.2010.0170

Bourret, V., Kent, M. P., Primmer, C. R., Vasemagi, A., Karlsson, S., Hindar, K., McGinnity, P., Verspoor, E., Bernatchez, L., & Lien, S. (2013). SNP-array reveals genome-wide patterns of geographical and potential adaptive divergence across the natural range of Atlantic salmon (*Salmo salar*). *Molecular Ecology*, *22*(3), 532–551. https://doi.org/10.1111/mec.12003

Brisbin, I. L., & Peterson, A. T. (2007). Playing chicken with red junglefowl: Identifying phenotypic markers of genetic purity in *Gallus gallus*. *Animal Conservation*, *10*(4), 429–435. https://doi.org/10.1111/j.1469-1795.2007.00112.x

Castellani, M., Heino, M., Gilbey, J., Araki, H., Svasand, T., & Glover, K. A. (2015). IBSEM: An individual-based Atlantic salmon population model. *PLoS One*, *10*(9), https://doi.org/10.1371/journal.pone.0138444

Debes, P. V., Fraser, D. J., McBride, M. C., & Hutchings, J. A. (2013). Multigenerational hybridisation and its consequences for maternal effects in Atlantic salmon. *Heredity*, *111*(3), 238–247. https://doi.org/10.1038/hdy.2013.43

Diserud, O. H., Fiske, P., Sægrov, H., Urdal, K., Aronsen, T., Lo, H., Barlaup, B. T., Niemelä, E., Orell, P., Erkinaro, J., Lund, R. A., Økland, F., Østborg, G. M., Hansen, L. P., & Hindar, K. (2019). Escaped farmed Atlantic salmon in Norwegian rivers during 1989–2013. *ICES Journal of Marine Science*, *76*(4), 1140–1150. https://doi.org/10.1093/icesjms/fsy202

Einum, S., & Fleming, I. A. (1997). Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. *Journal of Fish Biology*, *50*(3), 634–651. https://doi.org/10.1111/j.1095-8649.1997.tb01955.x

Finstad, A. G., Berg, O. K., Forseth, T., Ugedal, O., & Naesje, T. F. (2010). Adaptive winter survival strategies: Defended energy levels in juvenile Atlantic salmon along a latitudinal gradient. *Proceedings of the Royal Society B-Biological Sciences*, *277*(1684), 1113–1120. https://doi.org/10.1098/rspb.2009.1874

Finstad, A. G., & Forseth, T. (2006). Adaptation to ice-cover conditions in Atlantic salmon, *Salmo Salar* L. *Evolutionary Ecology Research*, *8*(7), 1249–1262.

Finstad, A. G., Ugedal, O., Forseth, T., & Naesje, T. F. (2004). Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(12), 2358–2368. https://doi.org/10.1139/F04-213

Fiske, P., Lund, R. A., & Hansen, L. P. (2006). Relationships between the frequency of farmed Atlantic salmon, *Salmo salar* L., in wild salmon populations and fish farming activity in Norway, 1989-2004. *ICES Journal of Marine Science*, *63*(7), 1182–1189. https://doi.org/10.1016/j.icesjms.2006.04.006

Fleming, I. A., Hindar, K., Mjolnerod, I. B., Jonsson, B., Balstad, T., & Lamberg, A. (2000). Lifetime success and interactions of farm salmon invading a native population. *Proceedings of the Royal Society B-Biological Sciences*, *267*(1452), 1517–1523. https://doi.org/10.1098/rspb.2000.1173.

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T. A., Rikardsen, A. H., Thorstad, E. B., Vøllestad, L. A., & Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science*, *74*(6), 1496–1513. https://doi.org/10.1093/icesjms/fsx020

Gjedrem, T., & Baranski, M. (2009). *Selective breeding in aquaculture: An introduction*. Springer.

Gjedrem, T., Gjoen, H. M., & Gjerde, B. (1991). Genetic-origin of Norwegian farmed Atlantic salmon. *Aquaculture*, *98*(1–3), 41–50. https://doi.org/10.1016/0044-8486(91)90369-I

Glover, K. A., Ottera, H., Olsen, R. E., Slinde, E., Taranger, G. L., & Skaala, O. (2009). A comparison of farmed, wild and hybrid Atlantic salmon (*Salmo salar* L.) reared under farming conditions. *Aquaculture*, *286*(3–4), 203–210. https://doi.org/10.1016/j.aquaculture.2008.09.023

Glover, K. A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M., & Skaala, O. (2013). Atlantic salmon populations invaded by farmed escapees: Quantifying genetic introgression with a Bayesian approach and SNPs. *BMC Genetics*, *14*, 74. https://doi.org/10.1186/1471-2156-14-74.

Glover, K. A., Solberg, M. F., Besnier, F., & Skaala, O. (2018). Cryptic introgression: Evidence that selection and plasticity mask the full phenotypic potential of domesticated Atlantic salmon in the wild. *Scientific Reports*, *8*, 1–10. https://doi.org/10.1038/s41598-018-32467-2

Glover, K. A., Solberg, M. F., McGinnity, P., Hindar, K., Verspoor, E., Coulson, M. W., Hansen, M. M., Araki, H., Skaala, Ø., & Svåsand, T. (2017). Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. *Fish and Fisheries*, *18*(5), 890–927. https://doi.org/10.1111/faf.12214

Glover, K. A., Urdal, K., Næsje, T., Skoglund, H., Bakke, G., Otterå, H., Fiske, P., Heino, M., Aronsen, T., Sægrov, H., Diserud, O., Barlaup, B. T., Hindar, K., Bakke, G., Solberg, I., Lo, H., Solberg, M. F., Karlsson, S., Skaala, Ø., … Wennevik, V. (2019). Domesticated escapees on the run: The second-generation monitoring programme reports the numbers and proportions of farmed Atlantic salmon in >200 Norwegian rivers annually. *ICES Journal of Marine Science*, *76*(4), 1151–1161. https://doi.org/10.1093/icesjms/fsy207

Glover, K. A., Wennevik, V., Hindar, K., Skaala, Ø., Fiske, P., Solberg, M. F., Diserud, O. H., Svåsand, T., Karlsson, S., Andersen, L. B., & Grefsrud, E. S. (2020). The future looks like the past: Introgression of domesticated Atlantic salmon escapees in a risk assessment framework. *Fish and Fisheries*, *21*(6), 1077–1091. https://doi.org/10.1111/faf.12478

Heggberget, T. G., Økland, F., & Ugedal, O. (1996). Prespawning migratory behaviour of wild and farmed Atlantic salmon, *Salmo Salar* L, in a North Norwegian River. *Aquaculture Research*, *27*(5), 313–322. https://doi.org/10.1111/j.1365-2109.1996.tb01258.x

Hindar, K., Fleming, I. A., McGinnity, P., & Diserud, O. H. (2006). Genetic and ecological effects of salmon farming on wild salmon: Modelling from experimental results. *ICES Journal of Marine Science*, *63*(7), 1234–1247. https://doi.org/10.1016/j.icesjms.2006.04.025

Hindar, K., Ryman, N., & Utter, F. (1991). Genetic-effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(5), 945–957. https://doi.org/10.1139/f91-111

Huisman, J., & Tufto, J. (2012). Comparison of non-Gaussian quantitative genetic models for migration and stabilizing selection. *Evolution*, *66*(11), 3444–3461. https://doi.org/10.1111/j.1558-5646.2012.01707.x

Karlsson, S., Diserud, O. H., Fiske, P., & Hindar, K. (2016). Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES Journal of Marine Science*, *73*(10), 2488–2498. https://doi.org/10.1093/icesjms/fsw121

Karlsson, S., Diserud, O. H., Moen, T., & Hindar, K. (2014). A standardized method for quantifying unidirectional genetic introgression. *Ecology and Evolution*, *4*(16), 3256–3263. https://doi.org/10.1002/ece3.1169

Karlsson, S., Moen, T., Lien, S., Glover, K. A., & Hindar, K. (2011). Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. *Molecular Ecology Resources*, *11*, 247–253. https://doi.org/10.1111/j.1755-0998.2010.02959.x

Kidd, A. G., Bowman, J., Lesbarreres, D., & Schulte-Hostedde, A. I. (2009). Hybridization between escaped domestic and wild American mink (*Neovison vison*). *Molecular Ecology*, *18*(6), 1175–1186. https://doi.org/10.1111/j.1365-294X.2009.04100.x

Kitada, S. (2018). Economic, ecological and genetic impacts of marine stock enhancement and sea ranching: A systematic review. *Fish and Fisheries*, *19*(3), 511–532. https://doi.org/10.1111/faf.12271

Kovach, R. P., Hand, B. K., Hohenlohe, P. A., Cosart, T. F., Boyer, M. C., Neville, H. H., & Luikart, G. (2016). Vive la resistance: Genome-wide selection against introduced alleles in invasive hybrid zones. *Proceedings of the Royal Society B-Biological Sciences*, *283*(1843), 20161380. https://doi.org/10.1098/rspb.2016.1380

Letourneau, J., Ferchaud, A. L., Le Luyer, J., Laporte, M., Garant, D., & Bernatchez, L. (2018). Predicting the genetic impact of stocking in Brook Charr (*Salvelinus fontinalis*) by combining RAD sequencing and modeling of explanatory variables. *Evolutionary Applications*, *11*(5), 577–592. https://doi.org/10.1111/eva.12566

McGinnity, P., Prodohl, P., Ferguson, K., Hynes, R., O'Maoileidigh, N., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., Taggart, J., & Cross, T. (2003). Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proceedings of the Royal Society B-Biological Sciences*, *270*(1532), 2443–2450. https://doi.org/10.1098/rspb.2003.2520

McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., & Ferguson, A. (1997). Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: Use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES Journal of Marine Science*, *54*(6), 998–1008. https://doi.org/10.1016/S1054-3139(97)80004-5

Næsje, T. F., Thorstad, E. B., Forseth, T., Aursand, M., Saksgard, R., & Finstad, A. G. (2006). Lipid class content as an indicator of critical periods for survival in juvenile Atlantic salmon (*Salmo salar*). *Ecology of Freshwater Fish*, *15*(4), 572–577. https://doi.org/10.1111/j.1600-0633.2006.00173.x

Naylor, R., Hindar, K., Fleming, I. A., Goldburg, R., Williams, S., Volpe, J., & Mangel, M. (2005). Fugitive salmon: Assessing the risks of escaped fish from net-pen aquaculture. *BioScience*, *55*(5), 427–437. https://doi.org/10.1641/0006-3568(2005)055[0427:FSATRO]2.0.CO;2%JBioScience

Naylor, R. L., Williams, S. L., & Strong, D. R. (2001). Aquaculture - A gateway for exotic species. *Science*, *294*(5547), 1655–1656. https://doi.org/10.1126/science.1064875

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945–959

Reed, T. E., Prodohl, P., Hynes, R., Cross, T., Ferguson, A., & McGinnity, P. (2015). Quantifying heritable variation in fitness-related traits of wild, farmed and hybrid Atlantic salmon families in a wild river environment. *Heredity*, *115*(2), 173–184. https://doi.org/10.1038/hdy.2015.29

Robertsen, G., Reid, D., Einum, S., Aronsen, T., Fleming, I. A., Sundt-Hansen, L. E., Karlsson, S., Kvingedal, E., Ugedal, O., & Hindar, K. (2019). Can variation in standard metabolic rate explain context-dependent performance of farmed Atlantic salmon offspring? *Ecology and Evolution*, *9*(1), 212–222. https://doi.org/10.1002/ece3.4716

Seabra, S. G., Silva, S. E., Nunes, V. L., Sousa, V. C., Martins, J., Marabuto, E., Rodrigues, A. S. B., Pina-Martins, F., Laurentino, T. G., Rebelo, M. T., Figueiredo, E., & Paulo, O. S. (2019). Genomic signatures of introgression between commercial and native bumblebees, *Bombus terrestris*, in western Iberian Peninsula-Implications for conservation and trade regulation. *Evolutionary Applications*, *12*(4), 679–691. https://doi.org/10.1111/eva.12732

Skaala, Ø., Besnier, F., Borgstrøm, R., Barlaup, B. T., Sørvik, A. G., Normann, E., Østebø, B. I., Hansen, M. M., & Glover, K. A. (2019). An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. *Evolutionary Applications*, *12*(5), 1001–1016. https://doi.org/10.1111/eva.12777

Skaala, O., Glover, K. A., Barlaup, B. T., Svasand, T., Besnier, F., Hansen, M. M., & Borgstrom, R. (2012). Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(12), 1994–2006. https://doi.org/10.1139/f2012-118

Solberg, M. F., Robertsen, G., Sundt-Hansen, L. E., Hindar, K., & Glover, K. A. (2020). Domestication leads to increased predation susceptibility. *Scientific Reports*, *10*(1), 1929. https://doi.org/10.1038/s41598-020-58661-9

Solberg, M. F., Zhang, Z. W., Nilsen, F., & Glover, K. A. (2013). Growth reaction norms of domesticated, wild and hybrid Atlantic salmon families in response to differing social and physical environments. *BMC Evolutionary Biology*, *13*, 234. https://doi.org/10.1186/1471-2148-13-234

Sundt-Hansen, L., Huisman, J., Skoglund, H., & Hindar, K. (2015). Farmed Atlantic salmon *Salmo salar* L. parr may reduce early survival of wild fish. *Journal of Fish Biology*, *86*(6), 1699–1712. https://doi.org/10.1111/jfb.12677

Sylvester, E. V. A., Wringe, B. F., Duffy, S. J., Hamilton, L. C., Fleming, I. A., Castellani, M., Bentzen, P., & Bradbury, I. R. (2019). Estimating the relative fitness of escaped farmed salmon offspring in the wild and modelling the consequences of invasion for wild populations. *Evolutionary Applications*, *12*(4), 705–717. https://doi.org/10.1111/eva.12746

Thorstad, E. B., Finstad, A. G., Jensen, A. J., Museth, J., Naeje, T. F., & Saksgard, L. M. (2007). To what extent does ethanol and freezing preservation cause shrinkage of juvenile Atlantic salmon and European minnow? *Fisheries Management and Ecology*, *14*(4), 295–298. https://doi.org/10.1111/j.1365-2400.2007.00553.x

Ugedal, O., Næsje, T. F., Saksgård, L. M., & Thorstad, E. B. (2016). *Fiskebiologiske undersøkelser i Altaelva. Samlerapport for 2011- 2015. (NINA report 1265).*

Ugedal, O., Næsje, T. F., Thorstad, E. B., Forseth, T., Saksgård, L. M., & Heggberget, T. G. (2008). Atlantic salmon (*Salmo salar*) in the regulated River Alta: Changes in juvenile and adult abundance. *Hydrobiologia*, *609*, 9–23.

Wringe, B. F., Jeffery, N. W., Stanley, R. R. E., Hamilton, L. C., Anderson, E. C., Fleming, I. A., Grant, C., Dempson, J. B., Veinott, G., Duffy, S. J., & Bradbury, I. R. (2018). Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. *Communications Biology*, *1*, 1–9. https://doi.org/10.1038/s42003-018-0112-9

Wu, M. Y., Low, G. W., Forcina, G., van Grouw, H., Lee, B. P. Y. H., Oh, R. R. Y., & Rheindt, F. E. (2020). Historic and modern genomes unveil a domestic introgression gradient in a wild red junglefowl population. *Evolutionary Applications*, *13*(9), 2300–2315. https://doi.org/10.1111/eva.13023

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Wacker S, Aronsen T, Karlsson S, et al. Selection against individuals from genetic introgression of escaped farmed salmon in a natural population of Atlantic salmon. *Evol Appl*. 2021;00:1–11. https://doi.org/10.1111/eva.13213

COMMUNICATIONS BIOLOGY

ARTICLE

DOI: 10.1038/s42003-018-0112-9 OPEN

Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic

Brendan F. Wringe[1,2], Nicholas W. Jeffery[1,3], Ryan R.E. Stanley[4], Lorraine C. Hamilton[5], Eric C. Anderson[6], Ian A. Fleming[2], Carole Grant[1], J. Brian Dempson[1], Geoff Veinott[1], Steven J. Duffy[1] & Ian R. Bradbury[1,2,3]

Domestication is rife with episodes of interbreeding between cultured and wild populations, potentially challenging adaptive variation in the wild. In Atlantic salmon, *Salmo salar*, the number of domesticated individuals far exceeds wild individuals, and escape events occur regularly, yet evidence of the magnitude and geographic scale of interbreeding resulting from individual escape events is lacking. We screened juvenile Atlantic salmon using 95 single nucleotide polymorphisms following a single, large aquaculture escape in the Northwest Atlantic and report the landscape-scale detection of hybrid and feral salmon (27.1%, 17/18 rivers). Hybrids were reproductively viable, and observed at higher frequency in smaller wild populations. Repeated annual sampling of this cohort revealed decreases in the presence of hybrid and feral offspring over time. These results link previous observations of escaped salmon in rivers with reports of population genetic change, and demonstrate the potential negative consequences of escapes from net-pen aquaculture on wild populations.

---

[1] Science Branch, Fisheries and Oceans Canada, 80 East White Hills Road, St. John's, Newfoundland A1C 5X1, Canada. [2] Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada. [3] Faculty of Computer Science, Dalhousie University, Halifax, NS B3H 4R2, Canada. [4] Science Branch, Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, NS B2Y 4A2, Canada. [5] Aquatic Biotechnology Laboratory, Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, NS B2Y 4A2, Canada. [6] Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Santa Cruz, CA 95060, USA. Correspondence and requests for materials should be addressed to I.R.B. (email: ian.bradbury@dfo-mpo.gc.ca)

The process of domestication results in genetically-based phenotypic divergence from wild populations, through both intentional and unintentional selection[1–3]. Modern genomic data in both plant[4–6] and animal systems[3,7,8] have revealed that recurrent hybridization and gene flow between cultured and wild populations can occur, not only during the early stages of domestication[9], but throughout the entire period of culture[10]. Repeated episodes of hybridization between cultured and wild populations can be detrimental for wild populations, resulting in the introduction of non-native alleles[6], erosion of adaptive diversity in the wild[4,11], and ultimately a loss-of-wild population viability[12,13]. The management and conservation of wild populations, confronted with domesticated conspecifics, requires the accurate quantification of potential genetic and ecological impacts to inform risk assessment and mitigation strategies.

The Atlantic salmon, *Salmo salar*, is of considerable socio-economic value both in culture and in the wild. Domestication of Atlantic salmon was initiated in 1969 in Norway[14], and separately in 1979 in Eastern Canada[15]. Despite this short period, the process of domestication has resulted in genetic differences between cultured and wild Atlantic salmon[16–18] which are likely maladaptive, and lead to lower relative survival of cultured salmon in the wild[19]. Domesticated Atlantic salmon exhibit lower relative fitness and spawning success compared to wild Atlantic salmon[13,19–21], and interbreeding can impart lasting, heritable, population-level reductions in fitness to wild populations[12]. Escapes from Atlantic salmon net-pen aquaculture are a regular occurrence[22], and the number of escapees can equate to an appreciable fraction of, or exceed, wild census size[23,24]. As such, genetic changes in wild populations consistent with introgression from domesticated salmon have been detected in nearly all regions where salmon aquaculture and wild populations co-occur, including: Norway[25,26], Ireland[27,28], Northern Ireland[29,30], and Canada[31]. Furthermore, methodological and theoretical improvements[32,33] have allowed the degree of hybridization within a single river[29,30] or the cumulative impact of introgression at large spatial scales (i.e., >100 populations in Norway[34,35]), to be resolved. Nonetheless, the unequivocal quantification of the magnitude and geographic scale of domestic-wild hybridization associated with single-escape events across a broad landscape of wild salmon populations has remained elusive.

Here we quantify the presence and magnitude of hybridization between wild and escaped domestic individuals following an escape of ~20,000 sexually mature, domestic Atlantic salmon from a single aquaculture net-pen in southern Newfoundland, Canada. This event occured on September 18, 2013, just prior to the natural spawning period for salmon in this region (Fig. 1a). The southern Newfoundland region is analytically favorable for the detection of hybrids; because the domestic broodstock currently in use originates from a single-non-local source (Saint John River, New Brunswick, Canada), the magnitude of industry production in the region has been limited until recently, and finally estimates of the abundance of wild salmon throughout southern Newfoundland (~20,000 individuals) are approximately equal to the magnitude of the escape[22,36]. Juvenile salmon were collected from the region and screened using 95 single nucleotide polymorphisms (SNPs) to identify hybrids, hybrid classes, and feral individuals present following this escape event. Next, we evaluated factors influencing the distribution of hybrids, and the magnitude of hybridization. Finally, using repeated temporal sampling, we examined and compared relative changes in the abundance of various hybrid classes over time. We report widespread evidence of hybridization (27.1% and hybrids detected in 17/18 rivers) following this escape event. Hybrids were observed in higher frequency in smaller rivers, and repeated annual sampling revealed decreases in the presence of hybrid and feral offspring over time. These results demonstrate the potential genetic consequences of a single-escape event from net-pen aquaculture on wild Atlantic salmon populations.

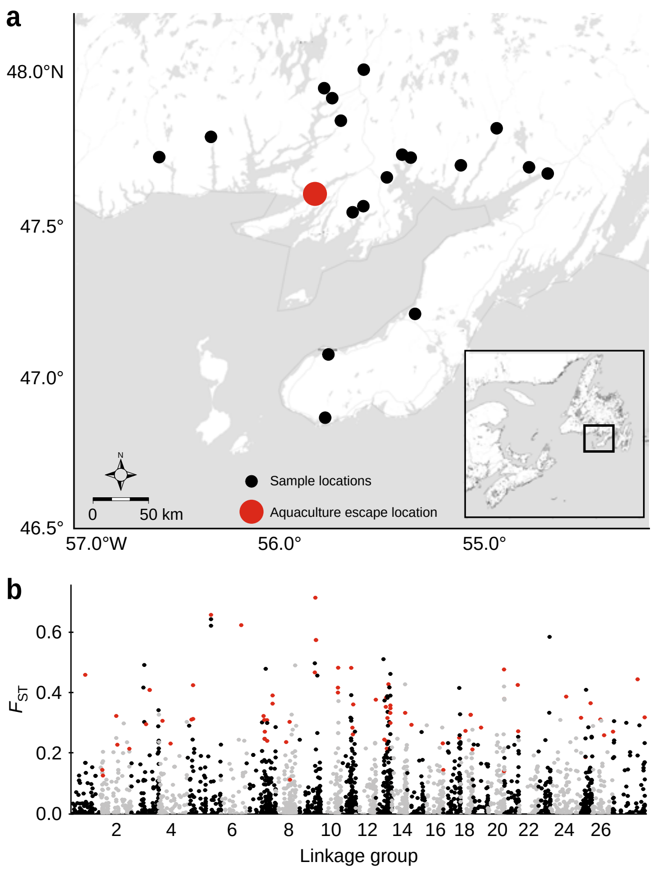


Fig. 1 Geographic distribution of sampling relative to aquaculture escape event and genome-wide comparison of wild and domestic salmon. **a** Map of southern Newfoundland, location relative to eastern Canada shown in inset. Black dots represent rivers surveyed; the red dot denotes the location of the 2013 aquaculture escape event. **b** Manhattan plot illustrating the genome-wide genetic differentiation (F_{ST}) between the wild and aquaculture baseline samples (Supplementary Table 7) used in the validation of the SNP panel accuracy. The red circles indicate the loci included in the 95 SNP collectively diagnostic panel. Linkage positions are from Brenna-Hansen et al.[64]

Results

Hybrid identification and genomic-based screening. In 2014, we collected 1704 young-of-the-year (YoY; i.e., fertilized the fall of the year of the escape, and hatched in the spring of the year of sampling) salmon from 18 rivers in the area adjacent to the escape event (Fig. 1; Table 1). Samples were again collected in 2015 ($n = 836$ of YoY and the 2014 cohort as 1+ juveniles; Table 1). All samples were screened using 95 genome-wide SNPs that were selected to maximize hybrid identification power and accuracy (Fig. 2; see Methods for further details as well as Supplementary Figures 1-3).

Our panel of 95 highly informative genome-wide SNPs identified 27.1% of the sampled YoY in 2014 as being of aquaculture ancestry based on a posterior probability assignment >0.80 (i.e., any of feral, F_1, F_2, and backcrosses, Fig. 3a). Hybrids were detected in 17 of the 18 rivers sampled (Fig. 3a, b), and feral

Table 1 Sample sizes of the juvenile Atlantic salmon screened for hybridization and introgression, the river from which they were collected, and the location of the river mouths

River name	Abbreviation	2104 YoY	2015 1+	2015 YoY	Lat (°N)	Long (°W)
Bottom Brook	BTB	32	33	0	47.765	56.322
Conne River	CNR	370	0	20	47.866	55.765
Dollard's Brook	DLR	25	24	22	47.708	56.555
Northwest Brook	FBN	41	0	0	47.720	55.393
Garnish River	GAR	199	50	56	47.239	55.353
Grand Bank Brook	GBB	42	26	15	47.104	55.754
Grand LaPierre	GLP	118	76	14	47.674	54.781
Long Harbour River	LHR	137	94	49	47.780	54.948
Salmonier Brook	LMS	40	22	89	46.865	55.775
Little River	LTR	130	0	0	47.809	55.743
Mal Bay Brook	MAL	17	70	36	47.669	55.131
Northeast Brook	NEB	115	19	0	47.723	55.367
Old Bay Brook	OBB	18	0	0	47.563	55.593
Southeast Brook	SEB	31	19	0	47.920	55.750
Simm's Brook	SMB	69	53	30	47.641	55.458
Taylor Bay Brook	TBB	120	0	0	47.543	55.637
Terrenceville Brook	TEB	120	0	0	47.671	54.711
Tailrace Brook	TRB	80	50	0	47.940	55.772

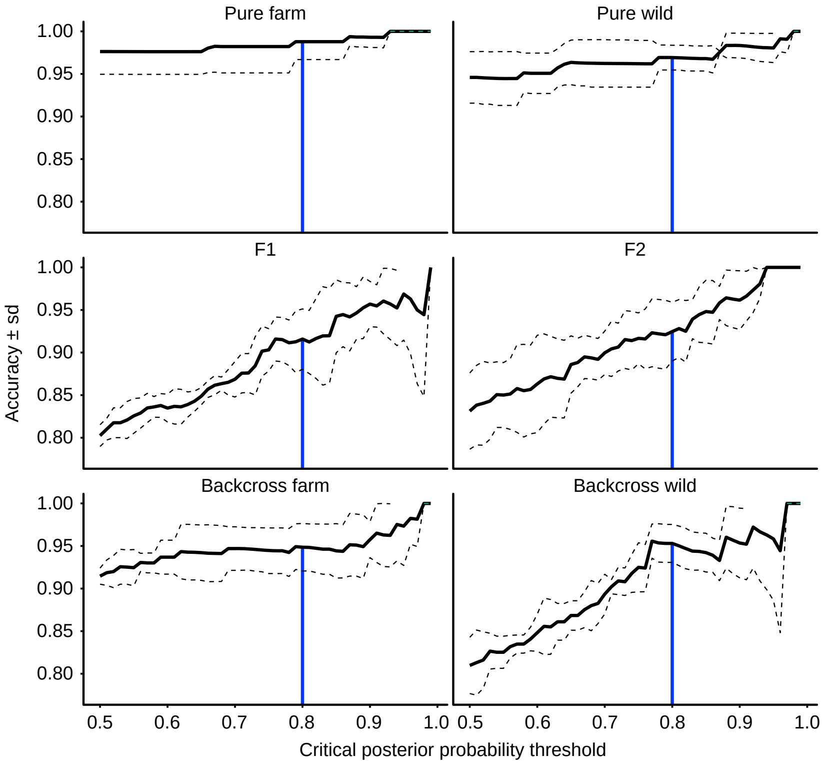


Fig. 2 Accuracy of detection of each of the genotype frequency classes across a range of critical posterior probability thresholds for the 95 SNP panel used in this study. The black line represents the mean of three replicate analyses of each of three independently simulated datasets and the dotted lines are the standard deviation. The vertical blue line is meant to highlight the critical posterior probability of assignment threshold (>0.8) used in this study

(i.e., offspring of two domestic salmon) offspring were detected in 13 rivers (Fig. 3a), revealing that the impacts of this escape event were substantial and region-wide. F_1 hybrids were the most common hybrid class detected in 2014, but F_2 and backcross individuals were also present (Fig. 3b). Observations of post-F_1 hybrids (i.e., F_2 and backcrosses) in 2014 YoY reveals that escape events had occurred prior to 2013, and that genetic introgression was occurring in some rivers. Observations of feral offspring indicative of successful reproduction among escapees has not been previously reported to our knowledge within the natural range of Atlantic salmon[18]. However, the potential for the establishment of feral populations remains unclear. Sibship

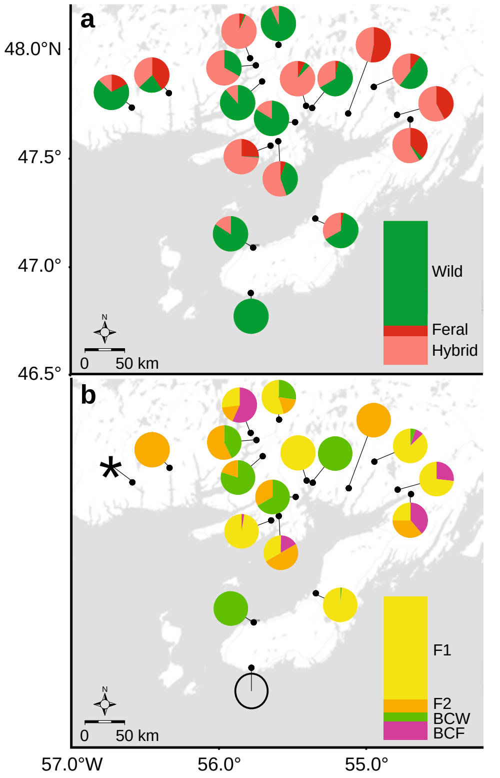


Fig. 3 Distribution and extent of hybridization following a large escape event of domestic Atlantic salmon. **a** Geographic distribution of wild, feral, or hybrid young-of-the-year Atlantic salmon across sample locations in 2014. **b** River-specific proportions of hybrid young-of-the-year salmon partitioned by hybrid genotype class (i.e., F_1, F_2, backcross wild (BCW), and backcross farm (BCF)). The open circle indicates a sample in which no hybrids were found, the asterisk signifies a location where accurate assignment to hybrid class was not possible. Bar graphs represent the overall proportions of each class in the entire sampling range, taking into account the varying sizes of the sampled populations (i.e., weighting by the axial distance, the distance along a straight line along the longest axis of the river), and colors therein are used as the legend

reconstruction revealed multiple unique parents for the hybrid and feral individuals in each river, suggesting that the over representation of a few families did not skew the river-specific estimation of hybrid proportion (Supplementary Tables 1-3).

Factors influencing hybridization. Levels of hybridization detected in 2014 were significantly associated with wild population size (Fig. 4; Supplementary Table 4). This was evident in significant associations between levels of hybridization and two proxies for salmon population size: river axial distance (i.e., the length of a straight line along a river's path), and average annual angling harvest (2010–2014), which correlate with salmon population size in this region (see Methods and Supplementary Figure 4). The proportion of hybrid YoY was negatively related to axial distance (Fig. 4b) and average annual angling (Fig. 4c); whereas, the opposite was true of the proportion of wild YoY (both $p < 0.001$, Supplementary Table 4). However, there was no statistical relationship between the proportion of feral YoY and either axial distance or average annual angling harvest (both $p > 0.10$; Supplementary Table 4). There was no evidence that distance between the location of the large escape event and river mouths influenced the proportion of wild, feral, or hybrid offspring detected in the year following the escape event (all $p > 0.28$; Supplementary Table 5).

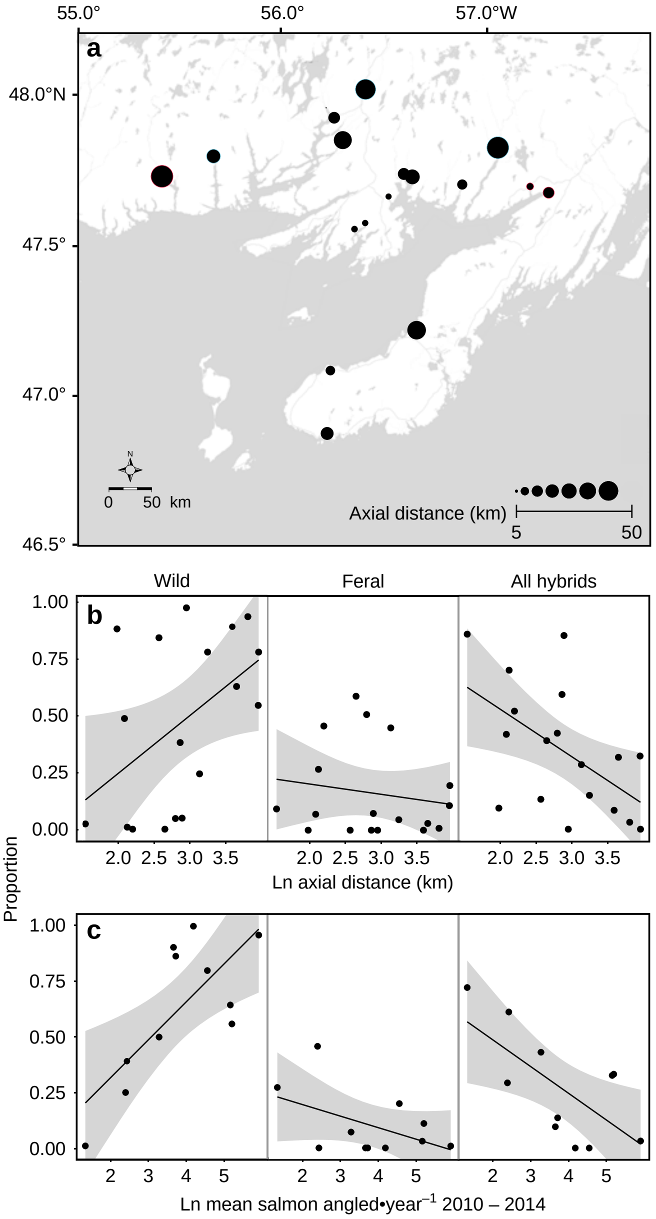


Fig. 4 Association between wild population size and levels of hybridization. **a** River axial distance (i.e., the distance along a straight line along the longest axis of the river). **b** Relationship between river axial distance and the proportions of wild, feral, and all hybrid (i.e., sum of proportions of F_1, F_2, BC wild, and BC farm) young-of-the-year Atlantic salmon sampled in 2014. **c** Relationship between mean number of salmon angled (2010–2014) and the proportions of wild, feral, and hybrid young-of-the-year Atlantic salmon sampled in 2014. The gray shading is the 95% CI of the prediction of the linear models. See Supplementary Table 4 for model parameter estimates

Temporal variation. To explore changes in the relative proportion of hybrids within the 2014 cohort over time, YoY and 1+juvenile salmon were sampled and analyzed in 2015 from across the region. In comparison to the YoY sampled in 2014, these 2015 YoY samples revealed an almost complete absence of feral

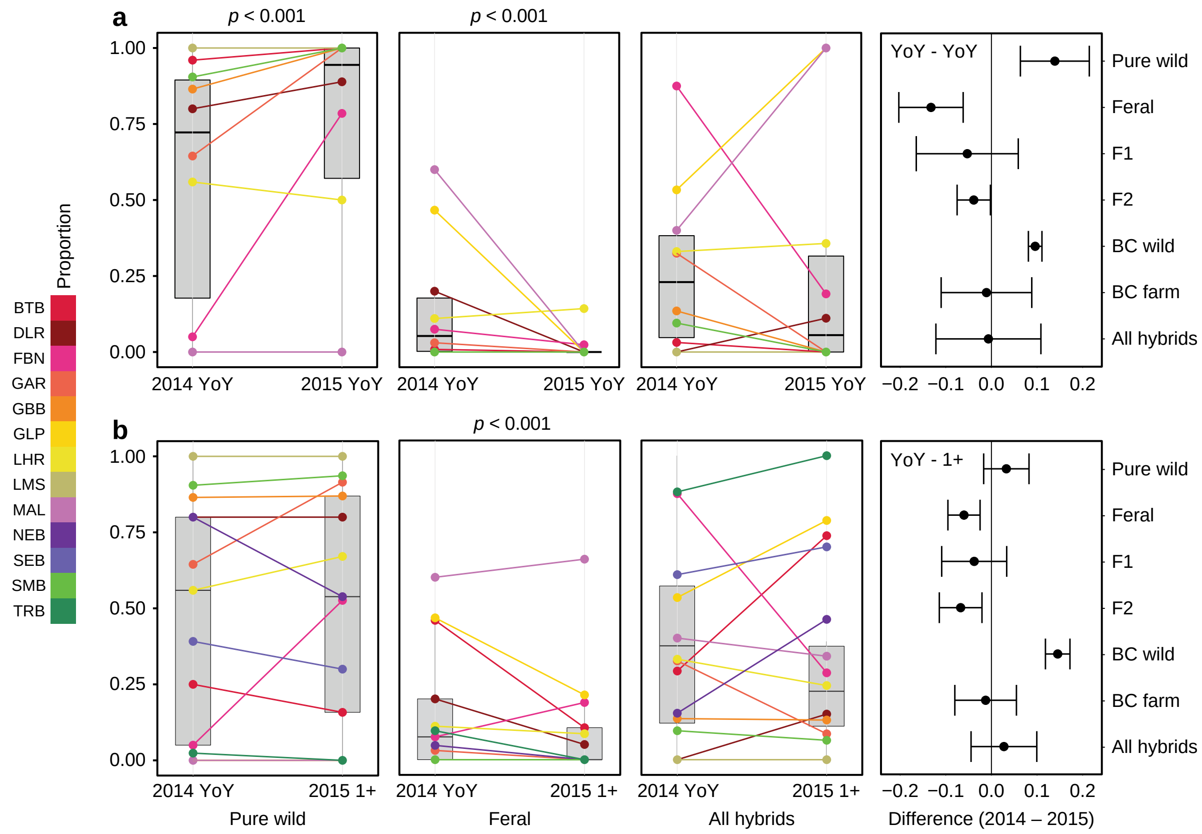


Fig. 5 Temporal variation (2014–2015) in levels of hybridization. **a** River specific and overall trends in the proportion of wild, feral, and hybrid young-of-the-year Atlantic salmon between 2014 and 2015. Gray shaded boxplots illustrate the overall proportions across all rivers, midline represents the medians, the upper and lower bounds the interquartile ranges, and the whiskers extend to 1.5 times the interquartile range. Black dots represent the mean difference (±SE) between 2014 and 2015 in the proportion of each pure and hybrid class present. All hybrids is the sum of proportions of F_1, F_2, BC wild, and BC farm. **b** River specific and overall trends in the proportion of wild, feral, and hybrid young-of-the-year and one year old (1+) Atlantic salmon sampled in 2014 and 2015, respectively. Gray shaded boxplots illustrate the overall proportions across all rivers. The midline represents the medians, the upper and lower bounds the interquartile ranges, and the whiskers extend to 1.5 times the interquartile range. Black dots represent the mean difference (±SE) across rivers between 2014 and 2015 in the proportion of each pure and hybrid class present of young-of-the-year and 1-year-old individuals. All hybrids is the sum of proportions of F_1, F_2, BC wild, and BC farm. See Fig. 1 and Table 1 for location information, and sample sizes

individuals and declines in the prevalence of most hybrid classes. This is likely reflective of overall lower numbers of escapees in 2014, a year in which no escape events were reported (Fig. 5a). The decline in feral individuals was significant ($p < 0.001$), as was the consequent increase in the proportion wild ($p < 0.001$). However, whereas most hybrid classes were found to decrease, the change in the overall proportion of hybrids was offset by the increase in backcross wild individuals resulting in no significant difference between years ($p = 0.56$; Fig. 5a).

Potential offspring from the 2013 escape event (1+individuals in 2015), showed that the proportion classified as feral declined significantly after a single year of selection in the wild ($p < 0.001$; Fig. 5b). There was no significant difference in the proportion of wild individuals ($p = 0.06$) and while there were decreases in most hybrid groups, the increase in backcross wild individuals muted any consistent statistical trend between years and among rivers and hybrid classes ($p = 0.20$; Fig. 5b). This decrease in the prevalence of offspring with part or full domestic ancestry is consistent with the reductions in relative hybrid survivorship observed in experimental studies[13,21,37] and expected selection against these individuals in the wild. Nonetheless, the continued presence of F_2 and backcross individuals, as well as the observed increases in prevalence of wild backcross individuals indicates introgression is occurring.

Discussion

We report unambiguous landscape-scale evidence of interbreeding between wild and escapee Atlantic salmon resulting from a single-escape event, and of particular note, the first documented instance of which we are aware of feral offspring within the native range of Atlantic salmon[18]. The combination of a highly informative panel of genome-wide SNPs with a large escape event of non-local domestic individuals into largely pristine wild populations allowed unprecedented resolution of the magnitude and geographic scale of hybridization following a single-escape event. Hybrid and feral offspring were widespread geographically, occurring at distances of up to100 km from the escape event, and accounted for ~27% of juvenile salmon surveyed. Moreover, the detection of F_2 and backcross individuals, presumably resultant from previous escape events, strongly supports the continued survival and reproductive viability of some hybrids, as well as the potential for significant demographic and genetic change as reported elsewhere[18].

Our results demonstrate a clear association between the size of wild populations and the degree of hybridization (Fig. 4) suggesting that smaller salmon populations are at greater risk of hybridization and introgression with escaped domestic individuals as noted in Norway[34,38]. This relationship is consistent with the dilution of domestic individuals in larger wild populations, as well the consequences of increased competition between wild and domestic individuals both on the spawning grounds and at juvenile stages[26,34]. Although, we lack actual estimates of wild population census size for many of the rivers included, the two correlates used here (river axial distance and annual angling harvest) are highly associated with population size on monitored rivers within the region (Supplementary Figure 5) and likely reflective of spatial trends in population census size.

Our results provide evidence consistent with declines in the proportion of offspring with domestic ancestry (e.g., hybrid, and feral) over time following the escape event. Comparison of the hybrid class composition of 1-year-old individuals sampled in 2015 relative to young-of-the-year sampled in 2014, revealed decreases in most hybrid classes, with only wild and wild backcrosses increasing in prevalence (Fig. 5b). Reduced wild-domestic hybrid survivorship for Atlantic salmon has previously been reported in experimental studies[13,21,37], but, we believe this is the first documentation following a single-escape event in the wild (Fig. 5b). The observed loss of feral and hybrid individuals over time is consistent with expected selection against these individuals in the wild. Interestingly, hybrid class composition of young-of-the-year sampled in 2015 revealed an almost complete absence of feral individuals and declines in the prevalence of most hybrid classes. This is consistent with an absence of reported escape events in 2015 and a reduced influence of the 2013 escape event. Despite evidence of declines in the proportion of domestic offspring or hybrids over time, the continued presence of F_2s and backcrosses is clear evidence of introgression and that significant genetic change is occurring in these wild populations[39].

The identification and quantification of introgression and hybridization between domestic and wild Atlantic salmon is a critical first step toward understanding, predicting, and managing the genetic impacts of net-pen salmon aquaculture on wild populations. Our clear resolution of hybridization and introgression between escapee and wild Atlantic salmon in the Northwest Atlantic is the first to our knowledge, and is consistent with observations of genetic perturbation from aquaculture escapees[31] both in the Canadian Maritimes and in Europe[14,34,35]. Our results link previous observations of escapes of domesticated Atlantic salmon with reports of population-level genetic changes[31,35] and regional declines of Atlantic salmon populations[36]. Moreover, these results further demonstrate the potential consequences of escapes from net-pen aquaculture on wild Atlantic salmon populations.

Methods

Development of collectively diagnostic SNP panel. The collection of wild samples used for the development of our single nucleotide polymorphism (SNP) panel has been previously detailed in Bradbury et al.[40]. Briefly, juvenile Atlantic salmon ($n = 260$, 0+ to 3+ years of age), were collected via electrofishing during the summers of 2008–2010 (sample sizes are found in Supplementary Table 6; genetic differentiation between populations are described in Supplementary Table 7). All wild collections were conducted under the auspices of Fisheries and Oceans collection permits. Aquaculture samples ($n = 156$) were obtained from two cage sites located within the region shown in Fig. 1. No effort was made to screen for or remove potential sibs from these baseline groups[41]. These baseline individuals were first screened using a 5568 SNP-locus panel developed by the Centre for Integrative Genomics (CIGENE, Norway[42,43]) as per Bradbury et al.[44]. Locus calls were visually confirmed and loci were retained if call rates were >0.85 and with overall minor allele frequencies >0.01 or a minor allele frequency >0.05 in either population[44]. The loci retained after quality control filtering were ranked by Weir and Cockerham's[45] F_{ST} between the two pooled reference groups (wild and domestic salmon), and the 95 most informative loci for which suitable assays could be developed were incorporated into the custom Fluidigm EPI array (see below). Linkage disequilibrium was not considered explicitly, however, the final panel provided genome-wide coverage (Fig. 1).

For each candidate locus, sequences from identified targets were downloaded from GenBank (SNP database, www.ncbi.nlm.nih.gov) and submitted to D3 Assay Design application (www.d3.fluidigm.com) for SNP Type assay design (Fluidigm, San Francisco, CA, USA). Assays were tested on samples with known genotype and the selection criteria for inclusion in the final panel included: correct genotypes for known samples and positive controls (see below); genotypes being reproducible across multiple chip runs; the ranking of the target SNP in the prioritized list; and assays not requiring the STA (Specific Target Amplification) step. Positive controls consisted of normalized solutions of synthesized double stranded DNA (gBlocks (Integrated DNA Technologies, Coralville, IA, USA))[46]. SNP genotyping was performed using SNP type assays (Fluidigm) per the manufacturer's protocols, without the STA (Specific Target Amplification) step, using 96.96 genotyping Integrated Fluidic Circuits (IFC) and read on an EP1 (Fluidigm) and analyzed using SNP Genotyping Analysis software (Fluidigm). Each 96-well plate extraction included 10 samples that were repeated on the plate (redundants) to detect processing errors (row or plate reversal) and ensure consistent clustering interpretation. The setup for each IFC also included positive controls (see above for details). To calculate the genotype error rate, 11.3% of the samples were reanalyzed from the original tissue where tissue samples were permitted. Based on Pompanon et al.[47], the genotype error rate was calculated to be 0.01%.

Hybrids. We used the R[48] package hybriddetective[49] to simulate pure wild, farmed, and hybrid populations to evaluate the power of this panel to identify hybrids and hybrid classes. Using hybriddetective we simulated multigenerational (viz. pure wild, pure farm, F_1, F_2, and backcrosses to wild and farm) hybrid datasets based on the genotypes of our wild and farmed baselines at the 95 SNPs in our panel. A random subset of 90% of the individuals from the wild and farmed baselines was first taken. A centered wild baseline was created by randomly sampling two alleles per locus from those of the randomly sampled subset without replacement. The same was done to create a centered farmed baseline. Centering was done following Karlsson et al.[33] and has the effect of removing linkage and deviances from Hardy-Weinberg equilibrium that may have been present in a pooled sample of populations. Next, using the centered baselines, individuals in generation $t+1$ were created by randomly sampling without replacement one allele per locus from each of the parental populations (i.e., wild baseline subsample and farmed baseline subsample) at time t[49]. Three independently simulated datasets were each in turn analyzed three times in parallel using NewHybrids[32] and the R package parallelnewhybrid[50], with a burn-in of 50,000 followed by 100,000 sweeps. NEWHYBRIDS calculates the posterior probability that an individual belongs to each of, in our case, six hybrid classes[32]. The results of the analyses of these simulated datasets were used to determine the efficiency and accuracy[51] of our 95 SNP panel.

To evaluate the efficacy of our panel, two metrics were considered: the panel's accuracy and its efficiency. For both these measures, we use the definitions provided by Vähä and Primmer[51]. First, accuracy is the proportion of all individuals that were assigned to a hybrid class that truly belong in that hybrid class (i.e., number of individuals correctly assigned to a hybrid class divided by the total number of individuals assigned to that class), and is calculated independently for each hybrid class. Efficiency, is also calculated independently for each hybrid class, and measures the proportion of individuals that are known a priori to belong to a hybrid class that were assigned to that class (i.e., number of individuals correctly assigned to a hybrid class divided by total number of individuals known a priori to belong to a class). The accuracies and efficiencies calculated from the analyses of these simulated datasets across a range of posterior probability of assignment thresholds are shown in Fig. 2 and Supplementary Figures 1-3. From Fig. 2 (and also Supplementary Figure 3) it can be seen that the proportion of simulated individuals correctly assigned as either pure wild or feral are the highest across all posterior probability of assignment thresholds, while F_1, F_2, and backcross wild were comparatively lower. However, at all posterior probabilities of assignment shown, the accuracy for all hybrid classes was >80%, suggesting the potential impact of miss-assignments is low. Similarly, efficiencies (Supplementary Figures 1 and 2) were above 90% for posterior probability of assignments thresholds between 0.5 and 0.8 (used in this analysis), suggesting the majority of individuals were assigned. Taken together, the high accuracy indicates that of those individuals assigned to a given class the majority were assigned correctly (i.e., little false assignment bias), while the high efficiency suggests that most individuals were assigned. A posterior probability of assignment threshold of 0.8 for individual classification was chosen based on the simulations and calculation of efficiency and accuracy (Fig. 2, Supplementary Figures 1-3). Individuals which did not meet the 0.8 posterior probability threshold for any hybrid class were considered only for the assignment as wild, farmed, or hybrid, and excluded from analyses focusing on specific hybrid classes. Convergence of the MCMC chains in NewHybrids was also confirmed using *hybriddetective*[49].

We evaluated both assignment to each of the six genotype frequency classes (Fig. 2 and Supplementary Figure 1), and pooled hybrid class identification (Supplementary Figures 2 and 3) separately, and accepted individual assignments to a class if their posterior probability of assignment to that class met, or exceeded a threshold of 0.8. We chose the threshold of 0.8, which is more conservative than what is typically used (e.g., 0.5[51,52]), because, we wanted to maximize the accuracy of assignments (Fig. 2 and Supplementary Figures 3).

Sample collection and analysis. On 18 September 2013, 20,000 sexually mature Atlantic salmon weighing between 4.5 and 7 kg (10–15 lbs) escaped from an open cage culture facility in southern Newfoundland, Canada. A number of these escapees were subsequently detected and captured in nearby rivers by technicians working for Fisheries and Oceans Canada (DFO). Gross morphological examination, in addition to necropsies conducted by DFO employees, showed that the recovered salmon were sexually mature, and in spawning condition. In 2014, the year following the large escape event, young-of-the-year (YoY) salmon were collected by electrofishing stream and river habitats in the 18 rivers shown in Fig. 1. Sampling included both rivers with historical records of established salmon populations (Conne River, Little River, Garnish River) and smaller streams lacking prior information on the presence or status of Atlantic salmon populations. With the exception of a few monitored rivers, information on the status of the wild populations in these rivers is largely lacking[36]; what information does exist suggests recent declines in abundance.

Individuals were approximately age-binned based on an expected size–size age distribution from 200 K aged Newfoundland parr with a 97.5% accuracy in YoY identification. All YoYs captured were euthanized and stored whole in 95% ethanol for later DNA extraction. Sample sizes by year for each river are listed in Table 1. Sampling was repeated in 2015 using the same methodology, with the exception that both YoY and 1+individuals were retained. The 1+individuals collected in 2015 belong to the same cohort of fish that were spawned following the escape event in 2013, and collected as YoY in 2014. Conversely, the YoY collected in the 2015 sampling were spawned in 2014, a year in which no escape events were reported in Newfoundland, and are thus expected to be reflective of the background rates of hybridization and introgression.

DNA was isolated from tissue samples using QIAamp 96 DNA QIAcube HT Kit (Qiagen, Toronto, ON, Canada) on a QIACube HT (Qiagen) per the manufacturer's protocol with some modifications. Tissue samples were manually disrupted using a Tissue Lyser II (Qiagen) mixing 2×10 s at $20\ s^{-1}$. DNA was eluted twice in 100 µL buffer AE (Qiagen) pre-heated to 70 °C. DNA extracts were quantified using Quant-iT PicoGreen dsDNA Assay Kit (Thermo Fisher Scientific, Waltham, MA, USA) and read on a FLUOStar OPTIMA fluorescence plate reader (BMG Labtech, Ortenberg, Germany). All individuals were screened using the custom Fluidigm SNP panel and NEWHYBRIDS was used to quantify the proportion of individuals from different genotype frequency classes present in a river sample[32]. Samples from each river, and each year, were run independently. Prior information on allele frequencies of baseline farm and wild salmon were also provided to NEWHYBRIDS during analyses by including simulated pure farm and pure wild individuals (i.e., the same individuals used in the testing of the accuracy and efficiency of the panel described above). The known class (i.e., pure wild and pure farm) were indicated to NEWHBYRIDS, as well as the fact that they were not to be included as part of the mixture[53]. Like in the determination of the efficacy of our panel described above, NEWHBYRIDS was run with a burn-in of 50,000 followed by 100,000 sweeps, which was found to be sufficient to ensure convergence during the panel testing. Proportions assigned to the various hybrid classes are shown in Supplementary Tables 8-10.

COLONY[54] was used to simultaneously infer the parentage and sibships of the YoY sampled in 2014, and the YoY and 1+individuals sampled in 2015. Each river, sampling year, and year class was analyzed separately in COLONY and parents were assigned an ancestry (wild, farm, or F_1) based on the hybrid class in question (i.e., if an individual was feral, both parents must be farmed, if an individual was an F1, one parent must be farmed and the other wild, if an individual is an F2, both parents must themselves have been F1s, etc.). For each river, sampling year, and year class, locus-specific allelic dropout rates were estimated using the "missing" function in PLINK[55,56], and these were provided to COLONY. Allele frequencies were estimated by COLONY from the data provided. In running COLONY, because all samples were wild caught, no information about numbers of candidate males or females provided. Both sexes were assumed to be polygynous, and "long" runs with "VeryHigh" precision were used. Because, we were not attempting to assign parentage, merely estimate the number of families present in each sample, and show that the proportions of hybrid classes detected was not the result of over representation of one, or a few families, the full-sib grouping for each individual with the highest probability was accepted. It should also be noted that because no parental genotypes were provided to COLONY, it was unable to meaningfully assign sexes to parents. Therefore, the total number of parents are presented.

Statistical analyses. All statistical analyses were conducted in R version 3.4[48]. The proportion of wild, feral, and hybrid at each location was explored for associations with wild population size; in this case two proxies were used (axial river distance and average annual harvest). For the Newfoundland region, wild population size[57] is associated with river axial distance[58] (the distance along a straight line along the longest axis of the river; linear model, $R^2 = 0.6944$, $F_{1,8} = 18.18$, $p < 0.01$; Supplementary Figure 4) and as such, axial distance was used as a proxy for population size. We also used average annual harvest (2010–2014) as a proxy of population size; because, the two were related (linear model, $F_{1,8} = 40.47$, $R^2 = 0.835$, $p < 0.001$). Harvest statistics are collected annually by Fisheries and Oceans Canada[59], and counts of population size and estimates of annual harvest were available for 10 rivers (Supplementary Table 11).

Exponential models for effect of distance from the escape event were used because straying of farmed salmon generally follows a negative exponential distribution[60]. The relationship between the proportion feral, wild, and hybrids detected in each river and the distance between the river mouths and the site of the escape were tested and fit using the R function *nls*. No significant relationships were found for distance from the escape event (all $p > 0.28$; Supplementary Table 5), so this factor was not considered further. The impact of the relative size of the native salmon populations in respective rivers on proportions was tested using linear models with the R function *lm*. The proportion wild, the proportion feral, and the proportion hybrid were tested separately as a function of axial distance, and then average annual angling harvest between 2010 and 2014.

We tested for differences in proportion of wild, feral, or hybrid individuals between years within the same cohort (i.e., the YoY collected in 2014 and the 1+collected in 2015), and between years with and without reported large escape events (i.e., YoY collected in 2014 and YoY collected in 2015) using binomial mixed-effects models with river as the random effect using the R function *glmer*[61]. The proportions of wild, feral, and hybrid were tested with separate models, and *p*-values were adjusted using the false discovery rate[62].

Data availability. Genotype, river characteristic, salmon and angling count data for this study are available in the Dryad Digital repository[63] at: https://doi.org/10.5061/dryad.3k888n7

Received: 6 December 2017 Accepted: 16 July 2018

References

1. Meyer, R. S. & Purugganan, M. D. Evolution of crop species: genetics of domestication and diversification. *Nat. Rev. Genet.* **14**, 840–852 (2013).
2. Sweeney, M. T. et al. Global dissemination of a single mutation conferring white pericarp in rice. *PLoS Genet.* **3**, e133 (2007).
3. Frantz, L. A. F. et al. Evidence of long-term gene flow and selection during domestication from analyses of Eurasian wild and domestic pig genomes. *Nat. Genet.* **47**, 1141–1148 (2015).
4. Feurtey, A., Cornille, A., Shykoff, J. A., Snirc, A. & Giraud, T. Crop-to-wild gene flow and its fitness consequences for a wild fruit tree: towards a comprehensive conservation strategy of the wild apple in Europe. *Evol. Appl.* **10**, 180–188 (2017).
5. Hufford, M. B. et al. Comparative population genomics of maize domestication and improvement. *Nat. Genet.* **44**, 808–811 (2012).
6. Oka, H. I. & Chang, W. T. Hybrid swarms between wild and cultivated rice species, *Oryza perennis* and *O. Sativa*. *Evolution* **15**, 418–430 (1961).
7. Eriksson, J. et al. Identification of the *yellow skin* gene reveals a hybrid origin of the domestic chicken. *PLoS Genet.* **4**, e1000010 (2008).
8. Kadwell, M. et al. Genetic analysis reveals the wild ancestors of the llama and the alpaca. *Proc. R. Soc. B Biol. Sci.* **268**, 2575–2584 (2001).
9. Brown, T. A., Jones, M. K., Powell, W. & Allaby, R. G. The complex origins of domesticated crops in the Fertile Crescent. *Trends Ecol. Evol.* **24**, 103–109 (2009).
10. Dempewolf, H., Hodgins, K. A., Rummell, S. E., Ellstrand, N. C. & Rieseberg, L. H. Reproductive isolation during domestication. *Plant Cell* **24**, 2710–2717 (2012).
11. Cornille, A., Giraud, T., Smulders, M. J. M., Roldan-Ruiz, I. & Gladieux, P. The domestication and evolutionary ecology of apples. *Trends Genet.* **30**, 57–65 (2014).
12. McGinnity, P. et al. Fitness reduction and potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* **270**, 2443–2450 (2003).
13. Fleming, I. A. et al. Lifetime success and interactions of farm salmon invading a native population. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* **267**, 1517–1523 (2000).
14. Ferguson, A. et al. in *The Atlantic Salmon Genetics, Conservation and Management* (eds E. Verspoor, L. Stradmeyer, & J. L. Nielsen) pp. 357–398 (Blackwell Publishing Ltd, Oxford, 2007).
15. Carr, J. W., Anderson, J. M., Whoriskey, F. G. & Dilworth, T. The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. *ICES J. Mar. Sci.* **54**, 1064–1073 (1997).
16. Cross, T. F. & King, J. Genetic effects of hatchery rearing in Atlantic salmon. *Aquaculture* **33**, 33–40 (1983).
17. Karlsson, S., Moen, T., Lien, S., Glover, K. A. & Hindar, K. Generic genetic differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip. *Mol. Ecol. Res.* **11**(Suppl 1), 247–253 (2011).
18. Glover, K. A. et al. Half a century of genetic interaction between farmed and wild Atlantic salmon: Status of knowledge and unanswered questions. *Fish. Fish.* **18**, 890–927 (2017).
19. Fleming, I. A. & Einum, S. Experimental tests of genetic divergence of farmed from wild Atlantic salmon due to domestication. *ICES J. Mar. Sci.* **54**, 1051–1063 (1997).

20. Fleming, I. A., Jonsson, B., Gross, M. R. & Lamberg, A. An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *J. Appl. Ecol.* **33**, 893–905 (1996).
21. McGinnity, P. et al. Genetic impact of escaped farmed Atlantic salmon (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES J. Mar. Sci.* **54**, 998–1008 (1997).
22. Keyser, F. et al. Predicting the impacts of escaped farmed Atlantic salmon on wild salmon populations. *Can. J. Fish. Aquat. Sci.* **75**, 506–512 (2018).
23. Morris, M. R. J. et al. Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. *Can. J. Fish. Aquat. Sci.* **65**, 2807–2826 (2008).
24. Skilbrei, O. T., Heino, M. & Svåsand, T. Using simulated escape events to assess the annual numbers and destinies of escaped farmed Atlantic salmon of different life stages from farm sites in Norway. *ICES J. Mar. Sci.* **72**, 670–685 (2015).
25. Skaala, O., Wennevik, V. & Glover, K. A. Evidence of temporal genetic change in wild Atlantic salmon, *Salmo salar* L., populations affected by farm escapees. *ICES J. Mar. Sci.* **63**, 1224–1233 (2006).
26. Glover, K. A. et al. Three decades of farmed escapees in the wild: a spatio-temporal analysis of Atlantic salmon population genetic structure throughout Norway. *PLoS ONE* **7**, e43129 (2012).
27. Clifford, S. L., McGinnity, P. & Ferguson, A. Genetic changes in Atlantic salmon (*Salmo salar*) populations of northwest Irish rivers resulting from escapes of adult farm salmon. *Can. J. Fish. Aquat. Sci.* **55**, 358–363 (1998).
28. Clifford, S. L., McGinnity, P. & Ferguson, A. Genetic changes in an Atlantic salmon population resulting from escaped juvenile farm salmon. *J. Fish. Biol.* **52**, 118–127 (1998).
29. Crozier, W. W. Evidence of genetic interaction between escaped farmed Salmon and Wild Atlantic Salmon (*Salmo salar* L) in a Northern Irish River. *Aquaculture* **113**, 19–29 (1993).
30. Crozier, W. W. Escaped farmed salmon, *Salmo salar* L., in the Glenarm River, Northern Ireland: genetic status of the wild population 7 years on. *Fish. Manag. Ecol.* **7**, 437–446 (2000).
31. Bourret, V., O'Reilly, P. T., Carr, J. W., Berg, P. R. & Bernatchez, L. Temporal change in genetic integrity suggests loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following introgression by farmed escapees. *Heredity* **106**, 500–510 (2011).
32. Anderson, E. C. & Thompson, E. A. A model-based method for identifying species hybrids using multilocus genetic data. *Genetics* **160**, 1217–1229 (2002).
33. Karlsson, S., Diserud, O. H., Moen, T. & Hindar, K. A standardized method for quantifying unidirectional genetic introgression. *Ecol. Evol.* **4**, 3256–3263 (2014).
34. Glover, K. A. et al. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. *BMC Genet.* **14**, 74–93 (2013).
35. Karlsson, S., Diserud, O. H., Fiske, P. & Hindar, K. Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations. *ICES J. Mar. Sci.* **73**, 2488–2498 (2016).
36. COSEWIC. COSEWIC assessment and status report on the Atlantic Salmon *Salmo salar* (Nunavik population, Labrador population, Northeast Newfoundland population, South Newfoundland population, Southwest Newfoundland population, Northwest Newfoundland population, Quebec Eastern North Shore population, Quebec Western North Shore population, Anticosti Island population, Inner St. Lawrence population,Lake Ontario population, Gaspé-Southern Gulf of St. Lawrence population, Eastern Cape Breton population, Nova Scotia Southern Upland population, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. xlvii+136 (Ottawa, 2010).
37. Skaala, O. et al. Performance of farmed, hybrid, and wild Atlantic salmon (*Salmo salar*) families in a natural river environment. *Can. J. Fish. Aquat. Sci.* **69**, 1994–2006 (2012).
38. Heino, M., Svåsand, T., Wennevik, V. & Glover, K. A. Genetic introgression of farmed salmon in native populations: quantifying the relative influence of population size and frequency of escapees. *Aquacult. Environ. Inter.* **6**, 185–190 (2015).
39. Bolstad, G. H. et al. Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. *Nat. Ecol. Evol.* **1**, 0124 (2017).
40. Bradbury, I. R. et al. Landscape structure and climatic variation determine Atlantic salmon genetic connectivity in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* **71**, 246–258 (2014).
41. Waples, R. S. & Anderson, E. C. Purging putative siblings from population genetic data sets: a cautionary view. *Mol. Ecol.* **26**, 1211–1224 (2017).
42. Bourret, V. et al. SNP-array reveals genome-wide patterns of geographical and potential adaptive divergence across the natural range of Atlantic salmon (*Salmo salar*). *Mol. Ecol.* **22**, 532–551 (2013).
43. Bourret, V., Dionne, M., Kent, M. P., Lien, S. & Bernatchez, L. Landscape genomics in Atlantic salmon (*Salmo salar*): searching for gene-environment interactions driving local adaptation. *Evolution* **67**, 3469–3487 (2013).
44. Bradbury, I. R. et al. Transatlantic secondary contact in Atlantic Salmon, comparing microsatellites, a single nucleotide polymorphism array and restriction-site associated DNA sequencing for the resolution of complex spatial structure. *Mol. Ecol.* **24**, 5130–5144 (2015).
45. Weir, B. S. & Cockerham, C. C. Estimating F-statistics for the analysis of population-structure. *Evolution* **38**, 1358–1370 (1984).
46. Richards-Hrdlicka, K. L. A genomic approach to finding and understanding how the amphibian chytrid fungus is genetically structured in Northeastern America, PhD thesis, Yale University, New Haven, Connecticut (2014).
47. Pompanon, F., Bonin, A., Bellemain, E. & Taberlet, P. Genotyping errors: causes, consequences and solutions. *Nat. Rev. Genet.* **6**, 847–859 (2005).
48. R Development Core Team. *R: A language and environment for statistical computing.* (R Foundation for Statistical Computing, 2016).
49. Wringe, B. F., Stanley, R. R. E., Jeffery, N. W., Anderson, E. C. & Bradbury, I. R. hybriddetective: a workflow and package to facilitate the detection of hybridization using genomic data in r. *Mol. Ecol. Resour.* **17**, e275–e284 (2017).
50. Wringe, B. F., Stanley, R. R., Jeffery, N. W., Anderson, E. C. & Bradbury, I. R. parallelnewhybrid: an R package for the parallelization of hybrid detection using newhybrids. *Mol. Ecol. Resour.* **17**, 91–95 (2017).
51. Vähä, J. P. & Primmer, C. R. Efficiency of model-based Bayesian methods for detecting hybrid individuals under different hybridization scenarios and with different numbers of loci. *Mol. Ecol.* **15**, 63–72 (2006).
52. Pritchard, V. L. et al. Single nucleotide polymorphisms to discriminate different classes of hybrid between wild Atlantic salmon and aquaculture escapees. *Evol. Appl.* **9**, 1017–1031 (2016).
53. Anderson, E. C. User's guide to the program NewHybrids Version 1.1 beta. (2003).
54. Jones, O. R. & Wang, J. L. COLONY: a program for parentage and sibship inference from multilocus genotype data. *Mol. Ecol. Res.* **10**, 551–555 (2010).
55. Purcell, S. PLINK 1.07 v. 1.07 (2007), http://zzz.bwh.harvard.edu/plink/contact.shtml#cite.
56. Purcell, S. et al. PLINK: a tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* **81**, 559–575 (2007).
57. DFO. Atlantic Salmon (*Salmo salar*) Stock Status Update in Newfoundland and Labrador for 2014. *DFO Can. Sci. Advis. Sec. Sci.* Resp. 2015/023. (2015). http://publications.gc.ca/collections/collection_2015/mpo-dfo/Fs70-7-2015-023-eng.pdf
58. Porter, T. R., Riche, L. G. & Traverse, G. R. Catalogue of Rivers in Insular Newfoundland. Volume B. 287 (Environment Canada, Fisheries and Marine Service, Resource Development Branch, Newfoundland Region, 1974).
59. DFO. Stock Assessment of Newfoundland and Labrador Atlantic Salmon – 2016. *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* 2017/035. (2017).
60. Jonsson, B., Jonsson, N. & Hansen, L. P. Atlantic salmon straying from the River Imsa. *J. Fish. Biol.* **62**, 641–657 (2003).
61. Bates, D., Machler, M., Bolker, B. M. & Walker, S. C. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
62. Benjamini, Y. & Hochberg, Y. Controlling the False Discovery Rate - a practical and powerful approach to multiple testing. *J. Roy. Stat. Soc. Ser. B.* **57**, 289–300 (1995).
63. Wringe, B. et al. Data from: extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. Dryad Digital Repository. https://doi.org/10.5061/dryad.3k888n7
64. Brenna-Hansen, S. et al. Chromosomal differences between European and North American Atlantic salmon discovered by linkage mapping and supported by fluorescence in situ hybridization analysis. *BMC Genom.* **13**, 432 (2012).

Acknowledgements

The authors wish to thank Laura K. Weir, Paul Bentzen, and Sarah J. Lehnert for helpful and insightful comments on previous versions of this manuscript. Staff of DFO Salmonids section Newfoundland Region were responsible for the collection of juvenile tissue samples. Acquisition of aquaculture salmon baseline samples was facilitated by G. Perry, C. Hendry, DFO Aquaculture section Newfoundland Region, and by industry partners Cooke Aquaculture and Northern Harvest Sea Farms. We also thank the staff of the Aquatic Biotechnology Laboratory of the Bedford Institute of Oceanography for their work in the SNP genotyping. This study was funded through the Program for Aquaculture Regulatory Research of Fisheries and Oceans Canada, the Genomics Research and Development Initiative of Canada, as well as the National Sciences and Engineering Research Council of Canada, and support from the Atlantic Salmon Federation.

Author contributions

B.F.W., I.R.B., C.G., and I.A.F. conceived of and designed the study. Statistical and genomic analyses were conducted by B.F.W., E.C.A., and L.C.H. Figures were produced by B.F.W., N.W.J., R.R.E.S., and I.R.B. All authors wrote and approved the final draft of the manuscript.

Additional information

Supplementary information accompanies this paper at https://doi.org/10.1038/s42003-018-0112-9.

Competing interests: The authors declare no competing interests.

This is **Exhibit** "B" mentioned
and referred to in the affidavit of
Jonathan W. Carr affirmed before
me on this 23rd day of April, A.D.
2021

a Commissioner for taking affidavits
being a Solicitor
David R. Ames Q.C.

CURRICULUM VITAE

JONATHAN WELDON CARR

(April 2021)

PERSONAL

Address:	Atlantic Salmon Federation P.O. Box 5200, St. Andrews, NB, Canada E5B 3S8
Telephone:	506-754-5079
Email:	jcarr@asf.ca
Birthplace:	Oromocto, NB, Canada
Citizenship:	Canada

EDUCATION

1995. Master of Science (Biology), University of New Brunswick.
Thesis: Interactions between wild and aquaculture Atlantic salmon.

1992. Bachelor of Science, University of New Brunswick, Fredericton.

PROFESSIONAL WORK EXPERIENCE

Experience:

2016 - Present	Vice President, Research & Environment, Atlantic Salmon Federation. Chamcook, NB, Canada.
2014 - 2016	Executive Director, Research & Environment, Atlantic Salmon Federation. Chamcook, NB, Canada.
2010 - 2013	Director, Research & Environment, Atlantic Salmon Federation. Chamcook, NB, Canada.
1996 - 2010	Research Biologist, Atlantic Salmon Federation. Chamcook, NB, Canada.
1994 - 1996	Project Manager, Magaguadavic Watershed Management Association. St. George, NB, Canada.
1993 - 1995	Teaching Assistant, University of New Brunswick, Fredericton, New Brunswick.
1992 - 1993	Fishery Biologist, Atlantic Salmon Federation. Chamcook, NB, Canada.

1990-1991 Pest Management Surveyor, Department of Natural Resources & Energy, Timber Management Branch, Fredericton, NB.

PUBLICATIONS

Peer Review Articles

Carr, J.W., Anderson J.M., Whoriskey, F.G. & Dilworth T. 1997. The occurrence and spawning of cultured Atlantic salmon (*Salmo salar*) in a Canadian river. – ICES Journal of Marine Science, 54: 1064-1073.

Carr, J.W., Hammond, G.E., Ambali, A.J.D & Anderson, J.M. 1997. The Magaguadavic River as an index river for interactions between wild and aquaculture Atlantic salmon. – AAC Special Publication No. 2, 74-76.

Carr, J.W., Lacroix, G.L., Anderson, J.M. & Dilworth T. 1997. Movements of non-maturing cultured Atlantic salmon (*Salmo salar*) in a Canadian river. – ICES Journal of Marine Science, 54: 1082-1085.

Carr, J.W. 1999. Atlantic Salmon (*Salmo salar* L.) smolt migration patterns in the dam-impacted St. John River system. –Habitat Restoration and Enhancement, 217-227.

Whoriskey, F. G. & Carr, J.W. 2001. Returns of transplanted adult, escaped, cultured Atlantic salmon to the Magaguadavic River, New Brunswick. –ICES Journal of Marine Science, 58:504-509.

Carr, J.W. & Whoriskey, F.G. 2004. Sea lice infestation rates on wild and escaped Atlantic salmon (*Salmo salar* L.) entering the Magaguadavic River, New Brunswick. Aquaculture Research 35: 723-729.

Carr, J.W., Whoriskey, F.G. & O'Reilly, P 2004. Efficacy of releasing captive reared broodstock into an imperilled wild Atlantic salmon population as a recovery strategy. Journal of Fish Biology 65(Supplement A): 38-54.

Carr, J.W., Whoriskey, F.G. & Courtemanche, D. 2004. Landlocked Atlantic salmon: movements to sea by a putative freshwater life history form. Aquatic telemetry: advances and applications, 141-150.

Whoriskey, F.G. Brooking, P., Doucette, G., Tinker, S., & Carr. J.W. 2005. Movements and survival of sonically tagged farmed Atlantic salmon released in Cobscook Bay, Maine, USA. ICES Journal of Marine Science, 63: 1218-1223.

Carr, J.W. & Whoriskey, F.G. 2006. The escape of juvenile farmed Atlantic salmon from hatcheries into freshwater streams in New Brunswick, Canada. ICES Journal of Marine Science, 63: 1263-1268.

O'Reilly, P.T., Carr, J.W., Whoriskey, F.G. & Verspoor, E. 2006. Detection of European ancestry in escaped farmed Atlantic salmon, *Salmo salar* L., in the Magaguadavic River and Chamcook Stream, New Brunswick, Canada. ICES Journal of Marine Science, 63: 1256- 1262.

Whoriskey, F.G., Brooking, P., Doucette, G., Tinker, S. & Carr, J.W. 2006. Movements and survival of sonically tagged farmed Atlantic salmon released in Cobscook Bay, Maine, USA. ICES Journal of Marine Science, 63: 1218-1223.

Carr, J.W. & Whoriskey, F.G. 2008. Migration of silver American eels past a hydroelectric dam and through a coastal zone. Fish. Manag. Ecol. 15: 393-400.

Morris, M.R.J., Fraser, D.J., Heggelin, A.J., Whoriskey, F.G., Carr, J.W., O'Neil, S.F. & Hutchings, J.A. 2008. Prevalence and recurrence of escaped farmed Atlantic salmon (*Salmo salar*) in eastern North American rivers. Can. J. Fish. Aquat. Sci. 65: 2807-2826.

Bradford, R.G., Carr, J.W., Page, F.H. & Whoriskey, F. 2009. Migration of Silver American Eels Through a Macrotidal Estuary and Bay. Amer. Fish. Soc. Symp. 69: 18pp.

Carr, J.W. & Whoriskey, F.G. 2009. Atlantic Salmon (Salmo salar) and Smallmouth Bass (Micropterus dolomieu) Interactions in the Magaguadavic River, New Brunswick. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/074. Iv + 10pp.

Bourett, V, O'Reilly, P.T, Carr, J.W, Berg, P.R & Bertatchez, L. 2011. Temporal change in genetic integrity suggest loss of local adaptation in a wild Atlantic salmon (*Salmo salar*) population following genetic introgression by farmed escapees. Heredity 106:500-510.

Cote, D. Fleming, I.A., Carr, J.W. and McCarthy, J.H. In Press. Ecological Impact Assessment of the Use of European Origin Atlantic Salmon in Newfoundland Aquaculture Facilities. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/073. v +28 p.

Strom,J., Thorstad, E.B., Chafe, G., Sorbye, S.H. Rigthon, D., Rikardsen, A.H. and Carr, J. 2017 Ocean migration of pop-up satellite archival tagged Atlantic salmon from the Miramichi River in Canada. – ICES Journal of Marine Science, doi:10.193/icesjms/fsw220.

Daniels, J., Chaput, G., Carr, J. Can J. 2018. Estimating consumption rate of Atlantic salmon smolts (*Salmo salar) by striped bass (Morone saxatilis)* in the Miramichi River estuary using acoustic telemetry. Fish.Aquat.Sci 75:1811-1822.

Chaput, G., Carr, J., Daniels, J., Tinker, S., Jonsen, I., Whoriskey, F. 2018. Atlantic Salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence northwest Atlantic. ICES Journal of Marine Science, doi:10.193/icesjms/fsy156.

Brunsdon, E., Daniels, J., Hanke, A., and Carr, J. 2019. Tag retention and survival of Atlantic salmon (*Salmo salar*) smolts surgically implanted with dummy acoustic transmitters during the transition from fresh to salt water. – ICES Journal of Marine Science, doi:10.193/icesjms/fsz139, 10 pp.

Daniels, J., Sutton, S., Webber, D., and Carr, J. 2019. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (Salmo salar) as suggested by a novel acoustic tag. Anim Biotelemetry 7/16 (2019) doi:10.1186/s40317-019-0178-2, 11 pp.

Strom, J., Campana, S., Righton, D., Carr, J., Aarestrup, K., Stokesbury, M., Gargan, P., Javierr and Thorstad, E. 2019. Ocean Predation and Mortality of Adult Atlantic Salmon. Scientific Reports 9. No.1 (December 2019): 7890. https://doi.org/10.1038/s41598-019-44041-5.

Roloson, S.D., Landsman, S., Tana, R., Hicks., Carr, J, Whoriskey, F., and VanDen Heuvel, M.R. 2020 "Otolith Microchemistry and Acoustic Telemetry Revel Anadromy in Non-Native Rainbow Trout (*Oncorhynchus Mykiss*) in Prince Edward Island, Canada. Canadian Journal of Fisheries and aquatic Sciences 77, no.7 (July 2020): 1117-30. https://doi.org/10.1139/cjfas-20190229.

Teffer, Amy K., Carr, J., Tabata, A., Schulze, A., Bradbury, I., Deschamps, D., Gillis, C.A., Brunsdon, E.B., Mordecai, G., and Miller, K.M. 2020. A Molecular Assessment of Infectious Agents Carried by Atlantic Salmon at Sea and in Three Eastern Canadian Rivers, Including Aquaculture Escapees and North American and European Origin Wild Stocks. FACETS 5, no. 1 (January 1, 2020): 234-63. https://doi.org/10.1139/facets-2019-0048.

Carr, J., Kocik, J., and Edwards, P. 2020. Report of the Telemetry and Atlantic Salon Workshop: Next Steps from Estuary to the North Atlantic Ocean. Canadian Manuscript Report of Fisheries and Aquatic Sciences 3208.vi + 25p. http://publications.gc.ca/collections/collection_2020/mpo-dfo/Fs97-4-3208-eng.pdf.

Technical Reports

Carr, J. 1997. Downstream movements of presmolt in the Tobique River: 1996 tracking summary, Atlantic Salmon Federation: 74pp.

Carr, J.W. 1998. Initial Results: 1997 Downstream Movement of Presmolt in St. John River Drainage. Atlantic Salmon Federation: 4pp.

Carr, J.W. & Whoriskey, F.G. 1998. Atlantic salmon (*Salmo salar*) in the Magaguadavic River New Brunswick 1992-1997. Atlantic Salmon Federation: 45pp.

Whoriskey, F.G., Carr, J.W., Lacroix, G.L. & Stokesbury, M. 1998. A review and update of aquaculture impact studies carried out on the Magaguadavic River, Southern Bay of

Fundy, New Brunswick. Presented at a Dept. of Fisheries & Oceans Workshop On Interactions of Wild & Farmed Atlantic Salmon Moncton, NB, 1998: 49pp.

Whoriskey, F. G. & Carr, J.W. 1999. Homing of escaped aquaculture Atlantic salmon to the Magaguadavic River, New Brunswick. Atlantic Salmon Federation, 12pp.

Carr, J.W. & Whoriskey, F.G. 2000. A review of aquaculture impact studies carried out on Southwestern New Brunswick outer Bay of Fundy Rivers, with emphasis on the Magaguadavic River. Atlantic Salmon Federation, 57pp.

Carr, J.W. 2000. Summary of Downstream Migration of Juvenile Salmon in the Tobique River System, 1999- Atlantic Salmon Federation, 4pp.

Carr, J.W. 2001. A review of downstream movements of juvenile Atlantic salmon (*Salmo salar)* in the dam-impacted Saint John River drainage. Atlantic Salmon Federation, 85pp.

Carr, J.W. 2001. Downstream Migration of Juvenile Salmon in the Tobique River System 2000 Summary Report. Atlantic Salmon Federation, 5pp.

Whoriskey, F. G. & Carr, J.W. 2001. Interactions of escaped farmed salmon, and wild salmon, in the Bay of Fundy region. Atlantic Salmon Federation, 11pp.

Carr, J.W. & Whoriskey, F.G. 2002. Assessment of Atlantic salmon in Southwestern New Brunswick outer Bay of Fundy Rivers, with emphasis on the Magaguadavic River, 1992-2001 project report. Atlantic Salmon Federation, 46pp.

Carr, J.W. 2002. Western Fundy Atlantic Salmon Recovery Program, Progress Report October 2002. Atlantic Salmon Federation, 2pp.

Whoriskey, F. G., O'Reilly, P., & Carr, J.W. 2002. Reversal of the recent decreasing trend of escaped farmed Atlantic salmon entering the Magaguadavic River, New Brunswick, Canada, and genetic evidence for the presence of escaped juvenile and adult farmed salmon of European ancestry. Atlantic Salmon Federation and Department of Fisheries and Oceans, 11pp.

Carr, J.W. & Whoriskey, F.G. 2003. 'Rearing Magaguadavic Broodstock at Huntsman Marine Science Center' Final Report. Atlantic Salmon Federation, 5pp.

Carr, J.W. & Whoriskey, F.G. 2003. Western Fundy Atlantic Salmon Recovery Program Final Report. Atlantic Salmon Federation, 34pp.

Carr, J.W. & Whoriskey, F.G. 2003. Magaguadavic River Monitoring and Recovery Program. Atlantic Salmon Federation, 24pp.

Carr, J.W. & Whoriskey, F.G. 2004. Restoration of Western Fundy Atlantic Salmon- Project Report. Atlantic Salmon Federation, 46pp.

Carr J.W. 2004. Feasibility of using landlocked salmon in anadromous salmon recovery program. Atlantic Salmon Federation, 34pp.

Carr, J.W. & Whoriskey, F.G. 2005. Fish Passage Effects Monitoring Program for St. George Hydroelectric Redevelopment. Atlantic Salmon Federation, 25pp.

Carr, J.W. 2005. Restoration of Western Fundy Atlantic Salmon- Final Report. Atlantic Salmon Federation, 34pp.

Carr, J.W. 2006. Status of rainbow trout in New Brunswick watercourses. Atlantic Salmon Federation, 47pp.

Carr, J.W. 2006. Multi Species Recovery Program with emphasis on Atlantic salmon- Final Report. Atlantic Salmon Federation, 34pp.

Carr, J.W. 2008. Magaguadavic River Anadromous Fish Restoration and Monitoring Program. Atlantic Salmon Federation, ETF and NBWTF Final Report. 36pp

Carr, J.W. 2009. Outer Bay of Fundy Atlantic Salmon and Alewife Recovery Program. Project No. F308-037. Submitted to the New Brunswick Wildlife Trust. 26pp.

Carr, J.W. 2010. At Sea Interactions of Atlantic Salmon Kelt and Smolt from Bay of Fundy Region. Project No. F309-026. Submitted to the New Brunswick Wildlife Trust. 19pp.

Carr, J.W. 2011. Salmon Smolt Tracking and Assessment. Submitted to the Atlantic Salmon Conservation Foundation. 9pp.

Carr, J.W. 2010. 2009 Summary Report on Monitoring Times, Locations, and Fish Handling in Outer Bay of Fundy Rivers. License 322376. Submitted to Department of Fisheries and Oceans. 6pp.

Carr, J.W. 2010. Magaguadavic River Exotic Fish Species Inventory and Public Awareness. Project No. F309-050. Submitted to the New Brunswick Wildlife Trust. 2pp.

Carr, J.W. 2011. 2010 Summary Report on Monitoring Times, Locations, and Fish Handling in Outer Bay of Fundy Rivers. License 322376. Submitted to Department of Fisheries and Oceans. 5pp.

Carr, J.W. 2011. Magaguadavic River Recovery Program. No. F300-031. Submitted to the New Brunswick Wildlife Trust. 6pp.

Carr, J.W. 2012. Salmon Smolt Tracking and Assessment. Submitted to the Atlantic Salmon Conservation Foundation. 12pp.

Carr, J.W. 2013. ASF Tracking Research – 2013. Submitted to the Atlantic Salmon

Conservation Foundation. 10pp.

Summerfelt, Steven, Waldrop, T., Good, C., Davidson, J., Backover, P., Vinci, B., Carr, J. 2013 Freshwater Growout Trial of St. John River Atlantic Salmon in a Commercial Scale Land-Based Closed Containment System. Freshwater Institute, January 2013. https://www.conservationfund.org/images/projects/files/FI-ASF_Final-Report_March-20131.pdf.

Carr, J., Trial, J., Sheehan, T., Gibson, J., Giffin, G., Meerburg, D. 2015. Summary of Proceedings of the Symposium: What Works? A Workshop on the Wild Atlantic Salmon Recovery Programs. Atlantic Salmon Federation, St. Andrews, New Brunswick, Canada, 24 pp.

Sheehan, T., Carr, J. Chafe, G., Renkawitz, M.,Robertson, M., Lyberth, B., and Bradbury, I. 2019. Update on Pop-off satellite tagging Atlantic salmon at Greenland. ICES-2019/30.

Popular Articles

Carr, J. 2013. Making it work - ASF co-hosts an international symposium summit on land-based fish farming. Atlantic Salmon Journal, Winter 2013, Vol. 62, No. 4, 2pp.

Carr, J. 2017. A Two-way Street. Atlantic Salmon Journal, Spring 2017, Vol 66, No. 1.

Carr, J. 2018. Breaking the Ice. Atlantic Salmon Journal, Spring 2018, Vol 67, No. 1.

Carr, J. 2016. Using Telemetry as a Tool to Help Unravel the Mystery of Salmon Lost at Sea. SPAWNER 2018.

Carr, J. 2018. Friends in Far Places. Atlantic Salmon Journal, Winter 2018, Vol 67, No 4.

PROFESSIONAL MEMBERSHIPS

American Fisheries Society

Aquaculture North America

Canadian Aquaculture Association

Fisheries Society of the British Isles

IntraFish Magazine

PROFESSIONAL APPOINTMENTS AND SERVICES

Consultant and training, Workshop for age determination and discrimination between wild and farmed Atlantic salmon. St. Andrews, NB. July 2002.

Co-developed and implemented Effects Monitoring Program (fish passage studies) at Magaguadavic River hydroelectric dam, 2004-2010.

Consultant and Training, Workshop for age determination and discrimination between wild and farmed Atlantic salmon. St. Andrews, NB. February 2007.

Board Member, Eastern Charlotte Waterways. 2010-2020.

Member, Huntsmen Marine Science Center Committee, 2010 -

Member of Restigouche River Watershed Science Committee, 2010 –

External Reviewer of COSEWIC Assessment and Status report on the Atlantic Salmon. 2010

Honorary Research Associate in School of Graduate Studies, University of New Brunswick, 2011-

Organizer, Didymo (invasive species) workshop in Plaster Rock, NB in 2011.

Member of ICES Working Group on Age Determination of Salmon (WKADS), 2011.

Consultant and Training, Workshop for age determination and discrimination between wild and farmed Atlantic salmon. St. Andrews, NB. July 2011.

External; Reviewer of DFO CSAS Sea lice monitoring and non-chemical treatment methods Process. 25-27 September 2012.

Co-Organizer, Salmon Land-Based Closed Containment Workshop. St. Andrews, NB. October 2012.

Co- Organizer, Salmon Farming in Land-Based Closed Containment Systems. Halifax, NS. October 2012.

External Reviewer of CSAS Science National Review Process: Potential effects surrounding the importation of European origin cultured Atlantic salmon to Atlantic salmon populations and habitats in Newfoundland. March 2013.

Co-Organizer, Aquaculture Innovation Workshop. Shepherdstown, WV. September 2013.

CO-Organiser, Symposium: What works? A workshop on wild Atlantic salmon recovery programs. September 2013.

Consultant and Training, Workshop for age determination and discrimination between wild and farmed Atlantic salmon. St. Johns, NL. October 2013.

Member, Aquaculture Association of Nova Scotia Codes of Containment Committee. 2014-2016

Co-Organizer, Salmon Containment Workshop. St. Andrews, NB. April 2014.

Chaired special session on Life History, Molecular Ecology and Evolution of Salmonids at the 2nd International Conference on Integrative Salmonid Biology, Vancouver BC, June 2014.

Consultant and Training, Workshop for age determination and discrimination between wild and farmed Atlantic salmon. Conner River, NL. July 2013.

Co-Organizer, Aquaculture Innovation Workshop. Vancouver, BC. October 2014.

Co-Organizer, Aquaculture Innovation Workshop. Shepherdstown, WV. October 2015.

Co-Organizer, Aquaculture Innovation Workshop. Roanoke, WV. August 2016.

Member of Atlantic Salmon Research Joint Venture Science Committee, 2016 -

Member of ICES Advisory Committee to address the North Atlantic Salmon Conservation Organization (NASCO) request for advice on possible effects of salmonid aquaculture on wild Atlantic salmon populations in the North Atlantic (WKCULEF), 2016.

Member, Nova Scotia Aquaculture Salmon Traceability Committee, 2016 -

Co-Chair of New Brunswick Aquaculture Containment, 2016 – 2018

Co-Organizer, Aquaculture Innovation Workshop. Vancouver, BC. November 2017.

External Reviewer of CSAS Science National Peer-Review Process: Environmental and Indirect Human Health Risk Assessment for the Manufacture and Production of Sterile AquAdvantage Salmon at a Land-Based and Contained Facility near Rollo Bay, PEI. December 2018

External Reviewer of CSAS document "Mortality of Atlantic salmon after catch and release angling: assessment of a recreational Atlantic salmon fishery in a changing climate. 2019.

Expert technical review of DFO's draft Framework for Aquaculture Risk Management. 7 February 2019

Member, Steering Committee, Environmental Studies Research Fund: Atlantic salmon in the Eastern Canadian offshore regions – assessing timing, duration, and effects of environmental variability and climate change. 2020-

External Reviewer of Pre- COSEWIC Assessment for Atlantic Salmon in Newfoundland and Labrador, Maritimes, Gulf and Quebec Regions. 2020/2021.

MAJOR RESEARCH GRANTS

As Principal Investigator

2017-2018 Atlantic Salmon Post-Smolt Trawl and Troll Survey in the Strait of Belle Isle and Current Status of Knowledge, Data, and Research Efforts on Atlantic Salmon at Greenland. Atlantic Salmon Research Joint Venture. $171,200.

2018-2019 Mapping Spatial and Temporal Distribution of Atlantic Salmon Mixed Stocks in the North Atlantic. Atlantic Salmon Research Joint Venture. $166,980.

2019-2020 Mapping Spatial and Temporal Distribution of Atlantic Salmon Mixed Stocks in the North Atlantic. Atlantic Salmon Research Joint Venture. $146,280.

As Co-Investigator

2015-2015 Establishment of a water temperature monitoring network for Atlantic salmon: phase1., Natural Sciences and Engineering Research Council of Canada, $24,000.

2014-2017 Evolutionary and ecological impact of the escape of farmed salmon": policy and mitigation strategies. Natural Sciences and Engineering Research Council of Canada, $602,000.

2020-2025 Assessing the timing, duration, and effects of environmental variability and climate change for Atlantic salmon in the Eastern Canadian offshore regions. Environmental Studies Research Fund, $11,840,000.

STUDENTS SUPERVISED

2013 - 2020: External supervising committee for graduate student, UPEI.

Sept 2013 - Jan 2014: Supervised graduate student from Agro Campus, Rennes, France.

Sept 2012 - Jan 2013: Supervised graduate student from Agro Campus, Rennes, France.

May 2011- Sept 2011: Supervised graduate student from Netherlands.

Feb 2009 - May 2009: Supervised undergraduate student from University of Zeeland, Netherlands.

PRESENTATIONS AND SEMINARS

1998

Invasions of escaped cultured salmon and exotic smallmouth bass into wild salmon riffle habitats. 1998.

2001

A Review of Downstream Movements of Juvenile Atlantic Salmon in the Dam-Impacted Saint John River Drainage. Presented at the Canadian River Heritage Conference. June 2001.

2002

Scale Reading. Used for Discrimination Between Wild and Aquaculture Salmon. July 2002.

Genetic evidence of European loci in Atlantic salmon from a North American river. Presented at the AIC meeting. September 2002.

2003

Sea lice infestation rates on wild and escaped farmed Atlantic salmon entering the Magaguadavic River, New Brunswick. Presented at the 6ht International Sea Lice Conference. 2003

Magaguadavic River Smolt Monitoring Program. February 2003.

Seaward migration of landlocked Atlantic salmon: Implications for anadromous salmon recovery program. Presented to the American Fisheries Society. Quebec, City, QC. August 2003.

2004

Atlantic Salmon: What do you want to know? Presented to the NB Womans Institute. May 2004.

Efficacy of releasing captive reared broodstock into an imperiled wild salmon population as a recovery strategy. Presented at the Fisheries Society of the British Isles Annual International Conference. 22 July 2004.

Efficacy of releasing captive reared broodstock into an imperiled wild salmon population as a recover strategy. Presented at the 6th Bay of Fundy Workshop as part of the Bay of Fundy Ecosystem Partnership. September 2004.

Efficacy of releasing captive reared broodstock into an imperiled wild salmon population as a recovery strategy. Presented to the Atlantic International Chapter American Fisheries Society 30th Annual Meeting. Fairlee, Vermont. September 2004.

Efficacy of releasing reared broodstock into an imperiled wild salmon population as a recovery strategy. Presented at the Bay of Fundy Ecosystem Partnership 6th Bay of Fundy Workshop. September 2004.

2005

Magaguadavic River Salmon Restoration: The Dam Challenge. Presented at the Atlantic International Fisheries Society 31st Annual Meeting. Rangeley, ME, USA. 26 September 2005.

The escape of juvenile salmon from hatcheries into freshwater streams in New Brunswick, Canada. Presented at the ICES/NASCO Symposium. Bergen, Norway. 18 – 21 October 2005.

2006

Fisheries Management Applications: Magaguadavic River Studies. Presented at the College of Atlantic, Bar Harbour, ME, USA. 12 May 2006.

Effects Monitoring Program for St. George Hydroelectric Redevelopment. Progress Report. Presented to JDI. 7 April 2006.

2007

Scale Reading. Workshop. February 2007.

Magaguadavic River Atlantic Salmon Restoration Program. Presented to St. Stephen Middle School. 18 April 2007.

Migration of American Eels, *Anguilla rostrata*, past a Hydroelectric Dam and Through a Coastal Zone. Presented at the 7th International Fish Telemetry Conference. Silkeborg, Denmark. 21- 24 June 2007.

Using Acoustic Telemetry to Track the Movements of Adult Alewives, *Alosa pseudoharengus*, in a Freshwater and Coastal Zone. Presented at the 33rd Annual Meeting of the Atlantic International Chapter of the American Fisheries Society. French Village, NB. 23 – 25 September 2007.

Magaguadavic River Atlantic Salmon Restoration Program. Presented at the NBSGA Technical Session. 14 December 2007.

2008

Downstream Fish Passage by Hydroelectric Dams. Presented at the Renewable Energy Projects & Their Interactions with Wildlife Atlantic Society of Fish & Wildlife Biologists. Mount Allison University, Sackville, NB. 16 April 2008.

The Early Days. Vemco Days. September 2008.

Migration of American Eels, *Anguilla rostrata*, past a Hydroelectric Dam and Through a Coastal Zone. Meeting with JDI. 8 September 2008.

Migration of American Eels, *Anguilla rostrata*, past a Hydroelectric Dam and Through a Coastal Zone. Presented at an AIC Meeting. Digby, NS. 21- 23 September 2008.

2009

Sonic Tracking of Atlantic salmon smolts to sea: correlates of survival and lesson on the migration pathway. Maine. 10 January 2009.

Atlantic Salmon and Smallmouth Bass Interaction in the Magaguadavic River, New Brunswick. Presented at the Gulf Region Science Advisory Process. Moncton, NB. 28 January 2009.

Using acoustic telemetry to track the movements of river herring (*Alosa pseudoharengus*) in a freshwater and coastal zone. Presented at the 8th International Fish Telemetry Conference. Umea, Sweden. 14 – 18 September 2009.

Dam Delays. JDI Meeting. 27 October 2009.

2010

Magaguadavic River Atlantic Salmon Restoration Program. Presented at Inner Bay of Fundy & Atlantic Salmon Forum and Workshop. 27 October 2010.

ASF Research and Environment Department Report. ASF Fall Board Meetings. New York City, NY. November 2010.

2011

Atlantic Salmon Federation: Strategic Initiatives. Presented to Aquaculture. April 2011.

Sonic Tracking of Atlantic Salmon: lessons on the migration pathways, mortality points, and social dynamics. Presented in Restigouche. 2 April 2011.

ASF Research and Environment Department Report. Spring ASF Board Meetings. April 2011.

Outstanding research challenges for ASF. Fall Board Meetings. New York City, NY. November 2011.

Sonic Tracking of Atlantic salmon smolts and kelts to sea. ASF Fall Board Meetings. New York City, NY. 9 November 2011.

Sonic Tracking of Atlantic Salmon and Kelts to Sea. Presented in Quebec City, QC. 16 November 2011.

Sonic Tracking of Atlantic Salmon and Kelts to Sea. Presented at Fish Friends Summit in Doaktown, NB. 1 December 2011.

2012

Sonic tracking of Atlantic salmon: lessons on the migration pathways, mortality points, and social dynamics. Presented at the Nova Scotia Agricultural College, Truro, NS. 18 January 2012.

Sonic tracking of Atlantic salmon: lessons on the migration pathways, mortality points, and social dynamics. Restigouche Science Meeting, Campbellton, NB. 25 January 2012.

Sonic telemetry of Atlantic salmon smolts and kelts to sea: lessons on the migration pathways and mortality points. University of New Brunswick, Fredericton, NB. 27 January 2012.

Serpentine Atlantic Salmon Run in the St John River: Does it still exist? Miramichi Salmon Association Symposium, Boston, MA. 4 February 2012.

Sonic telemetry of Atlantic salmon smolts and kelts to sea: lessons on the migration pathways and mortality points. University of New Brunswick, Saint John, NB. 28 February 2012.

Salmon at Sea: Scientific advances and their implications for management. Nova Scotia Salmon Association Annual General Meeting, Halifax, NS. 3 March 2012.

Sonic telemetry of Atlantic salmon smolts and kelts to sea: lessons on the migration pathways and mortality points. Luncheon Speaker at Ocean Reef, Florida. 29 March 2012.

Update on Atlantic Salmon Growout Trial in Freshwater Closed- Containment System. Inner Bay of Fundy Recovery Team, Amherst, NS. 17 April 2012

Atlantic Salmon Federation Research & Environment Report. ASF Board Meetings, Toronto, ON. 25 April 2012.

Update on Atlantic Salmon Growout Trial in Freshwater Closed- Containment System, ASF Board Meetings, Toronto, ON. 25 April 2012.

Sonic telemetry of Atlantic salmon smolts and kelts to sea: lessons on the migration pathways and mortality points. Somerset Hills Country Club
Bernardsville, NJ. 15 May 2012.

Penobscot River Project : Not just a salmon project – leveraging resources. Somerset Hills Country Club, Bernardsville, NJ. 15 May 2012.

Update on Atlantic Salmon Grow out Trial in Freshwater Closed- Containment System. Aquaculture Canada 2012 Conference: New Frontiers – Bridging Technology and Economic Growth. Charlottetown, Prince Edward Island. 27-30 June 2012.

Sonic telemetry of Atlantic salmon smolts and kelts to sea: lessons on the migration pathways and mortality points. Luncheon speaker at Wilfred Carter Conservation Center, St. Andrews, NB. 1 August 2012.

Atlantic Salmon Federation Research & Environment Report. ASF Board Meetings, New York, NY. 14 November 2012.

Salmon Aquaculture: A Roadmap to Sustainability. Seminar presented to University of New Brunswick undergraduate students. Atlantic Salmon Federation, Chamcook, NB. 27 November 2012.

Summerfelt, S., Waldrop T., Good C., Davidson J., Backover P., Vinci B., Carr J. 2013. Freshwater Growout Trial of St John River Strain Atlantic Salmon in a Commercial-Scale, Land-based, Closed-Containment System. The Conservation Fund's Freshwater Institute. 17 pp.

2013

Escape Management From an NGO Perspective. Prevention and Management of Fish Escapes from Sea Cage Aquaculture in Atlantic Canada workshop. Halifax, NS. 23 January 2013.

Sonic Tracking of Atlantic Salmon. Restigouche River Science Meeting. Campbellton NB, 24 January 2013.

Freshwater Aquatic Invasives in New Brunswick. 2nd Annual New Brunswick Lakes Conference. Mactaquac Resort and Conference Center, Mactaquac, NB. 26 January 2013.

Salmon Aquaculture: A Roadmap to Sustainability. Miramichi Salmon Association Boston Symposium, Burlington, MA. 2 February 2013.

Salmon Aquaculture: A Roadmap to Sustainability. LaHave Salmon Association Annual General Meeting, Bridgewater, NS. 7 April 2013.

Farmed Salmon Escapee Management: An NGO Perspective. Inner Bay of Fundy Recovery Team Meeting. Amherst, NS. 17 April 2013.

Atlantic Salmon Federation Research & Environment Report. ASF Board Meetings, Montreal, QC, 1 May 2013.

Sonic telemetry of Atlantic salmon smolt and kelt to sea: lessons on the migration pathways and mortality points. Seminar given to Société Cascapédia, St. Jules Quebec. 23 May 2013.

Sonic telemetry of Atlantic salmon smolt and kelt to sea: lessons on the migration pathways and mortality points. Salmon Guides Night, Matapedia, QC. 23 May 2013.

Salmon Aquaculture: A Roadmap to Sustainability. Hammond River Angling Association Meeting, Hampton, NB. 10 June 2013.

Restoration of Alewives in Maine and New Brunswick Rivers. International St. Croix River Watershed Board Public Meeting, St. Stephen, NB. 17 June 2013.

One step forward two steps back: Obstacles to salmon recovery in the Magaguadavic River. What works? A Workshop on Wild Atlantic Salmon Recovery Programs, St Andrews, NB. 18 September 2013.

Scale Reading Used for Discriminating Between Wild and Aquaculture Salmon Workshop on Atlantic Salmon Scale Reading. Northwest Atlantic Fisheries Centre Fisheries and Oceans Canada St. Johns, NL. 22 October 2013.

Escape Management From an NGO Perspective. Workshop on Atlantic Salmon Scale Reading. Northwest Atlantic Fisheries Centre Fisheries and Oceans Canada St. Johns, NL. 22 October 2013.

Salmon Aquaculture: A Roadmap to Sustainability. Miawpukek First Nation 7th Annual General Staff Meeting Se't A'newey School Conne River, NL. 7 November 2013.

Atlantic Salmon Federation Research & Environment Report. ASF Board Meetings, New York, NY. 13 November 2013.

What Works: A Workshop on Wild Atlantic Salmon Recovery Programs. IBIS/AST Salmon Stocking Conference, Glasgow City, UK. 27 November 2013.

Salmon Aquaculture: A Roadmap to Sustainability Aquaculture Review Panel Target Meeting, Halifax, NS. 3 December 2013.

2014

Lessons on the migration pathways and mortality points of salmon at sea. Atlantic Salmon Ecosystems Forum, University of Maine, Orono, ME 8 January 2014

What Works: A Workshop on Wild Atlantic Salmon Recovery Programs
Atlantic Salmon Ecosystems Forum, University of Maine, Orono, ME 9 January 2014

Smolt and Kelt Tracking Update. Miramichi Salmon Association Board of Directors Meeting, Boston, MA. 31 January 2014.

Atlantic Salmon Smolt and Kelt Tracking Update. Restigouche River Watershed Management Committee Science Committee Meeting, Campbellton NB 4 February 2014.

Lessons on the migration pathways and mortality points of salmon at sea, VEMCO Workshop, St. Andrews, NB 26 March 2014.

Atlantic Salmon Federation Research & Environment Report. ASF Board Meetings, St. Andrews, NB. 21 May 2014.

Scale Reading Used for Discriminating Between Wild and Aquaculture Salmon Workshop on Atlantic Salmon Scale Reading. Miawpukek First Nation, Conne River, NL. 26 May 2014.

Escape Management From an NGO Perspective. Workshop on Atlantic Salmon Scale Reading. Miawpukek First Nation, Conne River, NL. 26 May 2014.

Salmon Aquaculture: A Roadmap to Sustainability. Kedgwick Salmon Lodge. 21 June 2014.

Sonic telemetry of Atlantic salmon smolt and kelt to sea: lessons on the migration pathways and mortality points. Kedgwick Salmon Lodge. 21 June 2014.

Lessons on the Migration Pathways of Atlantic Salmon Smolt and Kelt at Sea. 144th Annual Meeting American Fisheries Society, Quebec City. 21 August 2014.

Bayesian hierarchical modeling of 11 years of inter-stage survival rates of wild Atlantic salmon smolts and post-smolts from three rivers of eastern Canada. ICES Annual Science Conference. A Coruna, Spain. 15 September 2014.

Lessons on the Migration Pathways of Atlantic Salmon Smolt and Kelt at Sea. Ecology of Estuarine Fishes Course, Anderson House, St Andrews, NB. 23 September 2014.

The Atlantic Salmon Federation: The Wild Atlantic Salmon and Our Conservation Role. UNB Fredericton Marine Ecology Course, St. Andrews, NB. 25 September 2014.

SoBI Summary for Derek Simon Nunatukavut Consultation. Sonically Tagged Smolts & Kelts. 29 September 2014.

Lesson on the Migration Pathways of Atlantic Salmon Smolt and Kelt at Sea. Nunatukavut Meeting. 1 October 2014.

Aquaculture Issues Escapees & Code of Containment. ASF Research and Environment Meeting. University Club, 1-54th Street West, New York, NY. 12 November 2014.

Closed Containment Projects. ASF Board Research and Environment Meeting. University Club, 1-54th Street West, New York, NY. 12 November 2014.

ASF Research & Environment Report on Low Marine Survival ASF Board Research and Environment Meeting. University Club, 1-54th Street West, New York, NY. 12 November 2014.

What happened to salmon in 2014? ASF Board Meeting University Club, 1-54th Street West, New York, NY. 13 November 2014.

ASF Research & Environment Report. Aquaculture Issues. University Club, 1-54th Street West, New York, NY. 15 November 2014.

Regulations of Aquaculture: Current Challenges and Future Prospects for Industry in Canada. Senate Committee Briefing, Moncton NB. 20 November 2014.

Lessons on the Migration Pathways of Atlantic Salmon Smolt and Kelt at Sea. Salmon Summit: Stewardship and Sustainable Management of Atlantic Salmon in the Gespe'gewa'gi, Listuguj, Quebec. 25 November 2014.

2015

What Works: A Workshop on Wild Atlantic Salmon Recovery Programs. Miramichi

Salmon Association Symposium. Boston Marriott, Burlington, MA. 31 January 2015.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Migration at Sea. Deborah Pratt Dawson Conservation Symposium. 14 March 2015.

Summary of NASCO's International Atlantic Salmon Research Board's Telemetry Workshop. Shangri-La Hotel, Toronto, Ontario. 29 April 2015.

ASF Research & Environment Report. Low Marine Survival. ASF Board Meetings. Toronto, Ontario. 29 April 2015.

ASF Research & Environment Report. Aquaculture Issues. Shangri-La Hotel Toronto, Ontario. 29 April 2015.

North American Wild Atlantic Salmon Recovery Strategy. Atlantic Salmon Federation Board Meeting. Shangri-La Hotel. Toronto, Ontario. 30 April 2015.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Migrations at Sea. The Mount Royal Club. Montreal Dinner. Montreal, Quebec. 6 May 2015.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Migrations at Sea. The Country Club. Chestnut Hill, MA. Boston Dinner. 13 May 2015.

Aquaculture Issues Escapees & Code of Containment. Governor General's Leadership Conference. ASF's Wild Salmon Center, Chamcook, NB. 25 May 2015.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Migration at Sea. Cascapédia Société. Cascapédia St. Jules, Quebec. 4 June 2015.

Bayesian modeling of Atlantic salmon smolt inter-stage survival from Canadian rivers. 3rd International Conference on Fish Telemetry. Halifax, Nova Scotia. 13 – 17 July 2015.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Migrations at Sea. CAST Presentation. UNB. 9 September 2015.

The Wild Atlantic Salmon and Our Conservation Role. UNB Fredericton Marine Ecology Course. St. Andrews. 5 October 2015.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Migrations at Sea. Canadian Museum of History (Montreal Dinner). Gatineau, QC. 7 October 2015.

Low Marine Survival. ASF Board Meetings. University Club. 1-54th Street West, New York, NY. 11 November 2015.

Research & Environment Proposed Budget 2015 – 2016. ASF Board Meetings. University Club. 1-54th Street West, New York, NY. 11 November 2015.

Aquaculture Issues. Closed Containment Update. ASF Research & Environment Meeting. ASF Board Meetings. New York, NY. 11 November 2015.

Aquaculture Issues. Escapees & Code of Containment. ASF Board Meeting. University Club. 1-54th Street West, New York, NY. 11 November 2015.

North American Wild Atlantic Salmon Recovery Strategy. Listiguj Salmon Summit. Listiguj, Quebec. 19 November 2015.

Smolt & Kelt Tracking Program. Listiguj Salmon Summit. Listiguj, Quebec. 19 November 2015.

2016

Wild Atlantic Salmon Recovery Planning: What Works? Atlantic Salmon Ecosystems Forum. Orono, Maine. 6 January 2016.

Sonic telemetry of Atlantic Salmon Smolts and Kelt to Sea: Lesson on the Migration Pathway and Mortality. River Dee Tracking Workshop. Banchory Lodge Hotel, Aberdeenshire, Scotland. 12 February 2016.

Salmon Aquaculture in Newfoundland: A Roadmap to Sustainability. CAN: & ASF Meeting with Hon. Steve Crocker, NL Minister of Fisheries & Aquaculture. St. John's, NL. 23 February 2016.

Aquaculture Issues. ASF Research & Environment Meeting. Montreal Board Meetings. 27 April 2016.

Collaboration for Atlantic Salmon Tomorrow (CAST). ASF Board Meeting. Montreal, Quebec. 27 April 2016.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Mortalities at Sea. ASF 24th Annual Fredericton Dinner. Fredericton, NB. 12 May 2016.

North Atlantic Salmon Marine Tracking Studies. National Fish and Wildlife Foundation. Washington, DC. 25 May 2016.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Mortalities at Sea. New Derreen Camp, Cascapedia, Quebec. 24 June 2016.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Mortalities at Sea. Joint Venture Meeting. 30 June 2016.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Mortalities at Sea. ASF Staff Forum. Chamcook, NB. 17 August 2016.

Presentation to the Standing Committee on Fisheries and Oceans. Subject: Wild Salmon in Eastern Canada. Kinsmen Centre, Miramichi, NB. 29 September 2016.

Low Marine Survival. ASF Fall Board Meetings. University Club. 1-54th Street West, New York, NY. 9 November 2016.

2017

Using telemetry to Unravel the Mystery of Atlantic Salmon Mortalities at Sea. Annual Montreal Dinner. Club Saint James. 26 April 2017

Aquaculture Issues. Research & Environment Meeting. ASF Spring Board Meeting Saint Andrews, NB. 17 May 2017.

Tracking Salmon: Unravelling the Mystery of Where our Fish are Dying at Sea. Atlantic Salmon Trust 50th Anniversary Gala Celebrations. Science Symposium. Syon House, United Kingdom. 25 May 2017.

Tracking Salmon: Unravelling the Mystery of When and Where our Fish are Dying at Sea. Scotland's Salmon Festival Science Conference. Inverness College. 30 August 2017.

Tracking Salmon: Unravelling the Mystery of When and Where our Fish are Dying at Sea. 14th Annual Toronto Benefactor Dinner. Toronto Club. 12 October 2017.

Research and Environment Committee meeting. ASF Fall Board Meeting. University Club. 1-54th Street West, New York, NY. 8 November 2017.

Low Marine Survival. Atlantic Salmon Telemetry Planning Meeting: Expanding the tracking network into the North Atlantic. Halifax NS. 5 December 2017

2018

Tracking Salmon: Unravelling the Mystery of Where our Fish are Dying at Sea. Atlantic Salmon Conservation Fund Webinar. 21 February 2018.

Using Telemetry to Explore Atlantic Salmon Marine Mortality. Fisheries and Oceans Atlantic Salmon Assessment Meeting. St. Johns NL. 28 February 2018.

Science Update: The State of the Stocks. Managing the Challenges. New Approaches and New Technologies. North Atlantic Salmon Fund – The Orri Fund Salmon Summit. Reykjavik, Iceland. 21 & 22 March 2018.

Using Telemetry to Explore Atlantic Salmon Marine Mortality. ICES, 7 April 2018.

Research and Environment Committee Meeting. ASF Spring Board Meetings. King Edward Hotel. 37 King St., Toronto, ON. 2 May 2018.

Low Marine Survival. Research and Environment Committee Meeting. ASF Spring Board Meetings. King Edward Hotel. 37 King St., Toronto, ON. 2 May 2018.

Status of Tracking Salmon in the Ocean: Overview of Acoustic Tracking. ROAM

Workshop. Woods Hole, MA. 7 June 2018.

Research and Environment Update. Staff Forum, Saint Andrews, NB. 9 August 2018.

ASF Research Update. New Derreen, Cascapédia, QC. 14 August 2018.

Atlantic Salmon Federation Research and Environment Committee Meeting. University Club, 1-54th St West, New York, NY. 7 November 2018.

2019

Using Telemetry to Unravel the Mystery of Atlantic Salmon Migrations at Sea. Mont Joli, QC. 28 January 2019.

Atlantic Salmon Federation Research Update. Restigouche River Watershed Management Committee Science Advisory Meeting. Campbellton, NB. 30 January 2019.

Tracking the Marine Migrations of Atlantic Salmon. Fisheries and Oceans Assessment of Atlantic Salmon in Newfoundland and Labrador. St. Johns, NL. 5 March 2019.

Using Telemetry to Map the Spatial and Temporal Distribution of Atlantic Salmon in the Ocean. Atlantic Salmon Ecosystem Forum. Quebec City, QC. 13 March 2019.

Using Telemetry to Map the Spatial and Temporal Distribution of Atlantic Salmon in the Ocean. ASF Director Dinner. St. James Club, Montreal, QC. 23 April 2019.

Low Marine Survival. Research and Environment Committee Meeting. Le Windsor Ballroom, 1170 Peel St, Montreal, QC. 24 April 2019.

West Greenland Atlantic Salmon Telemetry Program. 23rd Annual Boston Dinner, Boston MA. 8 May 2019.

Using Telemetry to Map the Spatial and Temporal Distribution of Atlantic Salmon in the Ocean. ICES Working Group: WKSalmon. Copenhagen, Denmark. 24 June 2019.

Using Telemetry to Map the Spatial and Temporal Distribution of Atlantic Salmon in the Ocean. Atlantic Salmon Conservation Schools Network. ASF Conservation Center. Chamcook, NB. 31 July 2019.

Using Telemetry to Map the Spatial and Temporal Distribution of Atlantic Salmon in the Ocean. World Salmon Forum. Fairmont Olympic Hotel. Seattle, WA. 22 August 2019.

Using Telemetry to Map the Spatial and Temporal Distribution of Atlantic Salmon in the Ocean. Greenland Fisheries License Control Authority. NUUK, Greenland. 16 September 2019.

RAFOS Ocean Acoustic Monitoring (ROAM) Tag. SAMARCH International Salmonid Coastal and Marine Telemetry Workshop. Southhampton, UK. 5 November 2019.

Using Telemetry to Map the Spatial and Temporal Distribution of Atlantic Salmon in the Ocean. SAMARCH International Salmonid Coastal and Marine Telemetry Workshop. Southhampton, UK. 5 November 2019.

Low Marine Survival. ASF Research and Environment Committee Meeting. University Club, 1-54th St West, New York, NY. 13 November 2019.

2020

A molecular assessment of infectious agents carried by Atlantic salmon at sea and in three eastern Canadian rivers, including aquaculture escapees and North American and European origin wild stocks. Atlantic Salmon Ecosystems Forum. Orono, Maine. 14 January 2020.

Mapping Mixed Stocks in the North Atlantic. Atlantic Salmon Research Joint Venture Meeting. Moncton, NB. 12 February 2020.

Telemetry and the Atlantic Salmon Workshop: Next Steps from Estuary to the North Atlantic Ocean. Atlantic Salmon Research Joint Venture Meeting. Moncton, NB. 12 February 2020.

Atlantic Salmon Federation Research and Environment Update. ASF Board Information Session. Virtual Meeting. 14 May 2020.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Mortalities at Sea. Salmon – Great Leap for a Future. The Explorers Club Public Lecture Series, New York, NY. Virtual. 24 August 2020.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Mortalities at Sea. Salmon – Great Leap for a Future. The Explorers Club Public Lecture Series, New York, NY. Virtual. 24 August 2020.

Using Telemetry to Unravel the Mystery of Atlantic Salmon Mortalities at Sea. Salmon – Great Leap for a Future. Chicago Fund Raising 'Virtual' Dinner. 7 October 2020.

Atlantic Salmon Federation Research and Environment Update. ASF Board Meeting. Virtual. 11 November 2020.

2021

Atlantic Salmon Federation Research and Environment Committee Meeting. 25 March 2021.

This is **Exhibit** "C" mentioned and referred to in the affidavit of **Jonathan W. Carr** affirmed before me on this 23rd day of April, A.D. 2021

a Commissioner for taking affidavits
Being a Solicitor
David R. Ames Q.C.

CURRICULUM VITAE

STEPHEN GORDON SUTTON

(April 2021)

PERSONAL

Address:
Atlantic Salmon Federation
15 Rankine Mill Road
Chamcook, NB Canada
E5B 3A9

Telephone: (506) 529 1020
Email: ssutton@asf.ca

Place of Birth: St. John's, Newfoundland, Canada
Citizenship: Canadian, Australian

EDUCATION

Degrees and Qualifications

Ph.D.	2001	Texas A&M University College Station, TX	Wildlife and Fisheries Science
M.Sc.	1997	Memorial University St. John's, NL	Biology
B.Sc. (Hons.)	1994	Memorial University St. John's, NL	Biology (Ecology)
Grad. Cert. Educ.	2013	James Cook University Townsville, QLD	Tertiary Teaching

Theses

Ph.D.	Understanding Catch-and-Release Behaviour of Recreational Anglers.
M.Sc.	The Mystery Fish of Bonavista North: A Multidisciplinary Approach to Research and Management of a Unique Recreational Salmonid Fishery in Newfoundland.
B.Sc. (Hons.)	Spatial and Temporal Variability in the Fat Content and Condition of Juvenile Atlantic Salmon, *Salmo salar*, in a Newfoundland River System.

PROFESSIONAL WORK EXPERIENCE

August 2015 – Present
Director of Community Engagement
Atlantic Salmon Federation
Chamcook, New Brunswick, Canada

September 2002 – December 2014
Research Fellow/Principal Research Fellow/Associate Professor
School of Earth and Environmental Sciences
James Cook University, Townsville, Queensland, Australia

September 2001 – September 2002
Biologist, Department of Fisheries and Oceans Canada
St. John's, Newfoundland, Canada

September 1997 – May 2001
Graduate Research Assistant, Department of Wildlife and Fisheries Sciences
Texas A&M University, College Station, Texas, USA

PUBLICATIONS

Edited Volumes

Beard, T.D., R. Arlinghaus, and **S.G. Sutton**, Editors. 2011. The Angler in the Environment: Social, Economic, Biological, and Ethical Dimensions. American Fisheries Society, Bethesda, Maryland.

S.G. Sutton, A. Danylchuk, K. Freire. 2016. Proceedings of the 7th World Recreational Fisheries Conference. Fisheries Management and Ecology 23 (3/4), 177-333

Journal Articles

Thorstad, E., D. Bliss, C. Breau, K. Damon-Randall, L. Sundt-Hansen, E. Hatfield, G. Horsburgh. H. Hansen, N. Ó'Maoiléidigh, T. Sheehan, **S.G. Sutton**. 2021. Atlantic salmon in a rapidly changing environment - facing the challenges of reduced marine survival and climate change. Aquatic Conservation: Marine and Freshwater Ecosystems.

Bower, S.D., Ø. Aas, R. Arlinghaus, T. D. Beard, I. G. Cowx, A. J. Danylchuk, K. M. F. Freire, W. M. Potts, **S.G. Sutton**, S. J. Cooke. 2020. Knowledge Gaps and Management Priorities for Recreational Fisheries in the Developing World, Reviews in Fisheries Science & Aquaculture, 28:4, 518-535

J Daniels, **SG Sutton**, D Webber, J Carr. 2019. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (Salmo salar) as suggested by a novel acoustic tag. Animal Biotelemetry 7 (1), 16

SD den Haring, **SG Sutton.** 2019. Comparing intended, self-reported, and observed behavior of snorkelers in the Mombasa Marine Park and Reserve, Kenya. Tourism in Marine Environments 14 (1-2), 1-17.

Oh, C., **S.G. Sutton.** 2017. Comparing the Developmental Process of Consumptive

Orientation Across Different Population Groups, Leisure Sciences, 41 (3), 167-185

Wynveen, C.J., **S.G. Sutton.** 2017. Engaging Great Barrier Reef Stakeholders: Mediation Analyses of Barriers Among the Antecedents of Pro-Environmental Behavior. Human Dimensions of Wildlife, 22 (2), 126-141.

Bergseth, B.J., D.H. Williamson, G.R. Russ, **S.G. Sutton**, J.E. Cinner. 2017. A social–ecological approach to assessing and managing poaching by recreational fishers. Frontiers in Ecology and the Environment, 15 (2), 67-73.

van Riper, C.J., G.T. Kyle, B.C. Sherrouse, K.J. Bagstad, **S.G. Sutton**. 2017. Toward an integrated understanding of perceived biodiversity values and environmental conditions in a national park. Ecological Indicators 72, 278-287.

Gratani, M., **S.G. Sutton**, J.R.A. Butler, E.L. Bohensky, S. Foale. 2016. Indigenous environmental values as human values. Cogent Social Sciences 2 (1), 1185811.

van Riper, C.J., **S.G. Sutton**, G.T. Kyle, W. Stewart, R.C. Tobin. 2016. Bridging Managers' Place Meanings and Environmental Governance of the Great Barrier Reef Marine Park. *Society & Natural Resources*, 29(11): 1342-1358.

Arlinghaus, R., Cooke, S.J., **Sutton, S.G.**, Danylchuk, A.J., Potts, W., Freire, K., Alós, J., Silva, E.T., Cowx, I.G., Anrooy, R. 2016 Recommendations for the future of recreational fisheries to prepare the social-ecological system to cope with change. *Fisheries Management and Ecology,* 23, 177–186

Heard M, **Sutton S.G.**, Rogers P, Huveneers C. 2016. Actions speak louder than words: Tournament angling as an avenue to promote best practice for pelagic shark fishing. *Marine Policy*, 64:168–73.

Li, O., Gray, S. A. and **Sutton, S.G.** 2016. Mapping recreational fishers' informal learning of scientific information using a fuzzy cognitive mapping approach to mental modelling. *Fisheries Management and Ecology*, 23: 315–329

Wynveen, C.J. and **S.G. Sutton**. 2015. Engaging the public in climate change-related pro-environmental behaviors to protect coral reefs: The role of public trust in the management agency. *Marine Policy,* 53, 131-140.

Sutton, S.G., and E. Gyuris. 2015. Optimizing the Environmental Attitudes Inventory: establishing a baseline of change in students' attitudes. *International Journal of Sustainability in Higher Education,* 16 (1), 16-33.

Wynveen, C.J., B.J. Wynveen, and **S.G. Sutton**. 2015. Applying the value-belief-norm theory to marine contexts: Implications for encouraging pro-environmental behavior. *Coastal Management,* 43 (1), 84-103.

Sutton, S.G., and C. Oh. 2015. How do recreationists make activity substitutions? A case of recreational fishing. *Leisure Sciences,* 37 (4), 332-353.

Kamrowski, R.L., **S.G. Sutton**, R.C. Tobin, and M. Hamann. 2015. Balancing artificial light at night with turtle conservation? Coastal community engagement with light-glow reduction. *Environmental Conservation*, 42 (02), 171-181.

D. Gledhill, A.J. Hobday, D. J. Welch, **S.G. Sutton**, M. J. Lansdell, M. Koopman, A.Jeloudev, A. Smith and P. R. Last. 2015. Collaborative approaches to determining ecological change in eastern Australia: coastal fish and recreational spearfishing club data. *Marine and Freshwater Research*, 66 (3), 195-201.

Smith, A.M. and **S.G. Sutton**. 2014. Motivating wildlife conservation actions among zoo visitors: A case for anthropomorphism in zoos. *World Association of Zoos and Aquariums Magazine*, 15: 45-48.

Wynveen, C.J, G.T. Kyle, and **S.G. Sutton**. 2014. Environmental worldview, place attachment, and awareness of environmental impacts in a marine environment. *Environment and Behaviour*, 46(8): 993-1017.

Kamrowski, R.L., **S.G. Sutton**, R.C. Tobin, and M. Hamann. 2014. Potential applicability of persuasive communication to light-glow reduction efforts: A case study of marine turtle conservation. *Environmental Management* 54(3): 583-595.

Gratani, M., E. Bohensky, J. Butler, **S.G. Sutton**, and S. Foale. 2014. Experts' perspectives on the integration of indigenous knowledge and science in Wet Tropics natural resource management. *Australian Geographer*, 45(2): 167-184.

Farr, M.N., Stoeckl, and **S.G. Sutton**. 2014. Recreational fishing and boating: Are the determinants the same? *Marine Policy*, 47: 126-137.

Crossley, R., C. M. Collins, **S.G. Sutton**, and C. Huveneers. 2014. Public perception and understanding of shark attack mitigation measures in Australia. *Human Dimensions of Wildlife, 19:*154–165 .

Arias, A., and **S.G. Sutton**. 2013. Understanding recreational fishers' compliance with no-take zones in the Great Barrier Reef Marine Park. *Ecology and Society*, 18(4):18.

Yoon, J.I., G. Kyle, **S.G. Sutton**, C. van Riper, and R.C Tobin. 2013. Testing the effects of constraints on climate change-friendly behavior among groups of Australian residents. *Coastal Management*, 41: 457-469.

Oh, C.O., **S.G. Sutton**, and M. G. Sorice. 2013. Assessing the role of recreation specialization in fishing site substitution. *Leisure Sciences*, 35:256-272.

De Freitas, D.M, **S.G. Sutton**, J.M. Moloney, E.J.I. Lédée, and R.C. Tobin. 2013. Spatial substitution strategies of recreational fishers in response to zoning changes in the Great Barrier Reef Marine Park. *Marine Policy*, 40:145-153.

Hunt, L., **S.G. Sutton**, and R. Arlinghaus. 2013. Illustrating the critical role of human dimensions research for understanding and managing recreational fisheries within a social-ecological system framework. Fisheries Management and Ecology, 20:111-124.

Busilacchi, S, G.R. Russ, A.J. Williams, **S.G. Sutton,** and G.A. Begg. 2013. The role of subsistence fishing in the hybrid economy of an Indigenous community. *Marine Policy*, 37:183-191

Busilacchi, S, G.R. Russ, A.J. Williams, G.A. Begg, and **S.G. Sutton.** 2013. Quantifying changes in the subsistence coral reef fishery of indigenous communities in Torres Strait, Australia. *Fisheries Research*, 137:50-58.

van Riper, C.J., G.T. Kyle, **S.G. Sutton**, J.I. Yoon, and R.C. Tobin. 2013. Australian residents' attitudes toward pro-environmental behavior and climate change impacts on the Great Barrier Reef. *Journal of Environmental Planning and Management*, 56:494-511.

Sutton, S.G., and R.C. Tobin. 2012. Social resilience and commercial fishers' responses to management changes in the Great Barrier Reef Marine Park. *Ecology and Society* 17(3): 6.

van Riper, C.J., G.T. Kyle, **S.G. Sutton**, M. Barnes, and B.C. Sherrouse. 2012. Mapping outdoor recreationists' perceived social values for ecosystem services at Hinchinbrook Island National Park, Australia. *Applied Geography* 35: 164-173.

Wynveen, C.J., G.T. Kyle, and **S.G. Sutton**. 2012. Natural area visitors' place meaning and place attachment ascribed to a marine setting. *Journal of Environmental Psychology* 32:287-296.

Setiawan, A., J.E. Cinner, **S.G. Sutton**, and A. Mukminin. 2012. The perceived impact of customary marine resource management on household and community welfare in northern Sumatra, Indonesia. *Coastal Management*, 40:239-249

Lédée, E.J.I, **S.G. Sutton,** R.C. Tobin, and D.M. De Freitas. 2012. Responses and adaptation strategies of commercial and charter fishers to zoning changes in the Great Barrier Reef Marine Park. *Marine Policy* 36:226-234.

Sutton, S.G., and R.C. Tobin. 2011. Constraints on community engagement with Great Barrier Reef climate change reduction and mitigation. *Global Environmental Change* 21: 894-905.

Tobin, R. C., and **S.G. Sutton**. 2011. Perceived benefits and costs of recreational-only fishing areas to the recreational and commercial estuarine fishery within north Queensland. Pages 125-140 *in* T. D. Beard, Jr., R. Arlinghaus, and S. G. Sutton, editors. The Angler in the Environment. American Fisheries Society, Bethesda, Maryland.

Cardona-Pons, F., B. Morales-Nin, and **S.G. Sutton**. 2010. Scientists and recreational fishers: Communication manners and its efficiency. *Fisheries Research*, 106:575-578.

McCook, L.J, T. Ayling, M. Cappo, J.H. Choat, R.D. Evans, D.M. De Freitas, M. Heupel, T.P. Hughes, G.P. Jones, B. Mapstone, H. Marsh, M. Mills, F. Molloy, C.R. Pitcher, R.L.

Pressey, G.R. Russ, **S.G. Sutton**, H. Sweatman, R. Tobin, D.R. Wachenfeld, D.H. Williamson. 2010. Adaptive management and monitoring of the Great Barrier Reef reserve network: A globally significant case study in marine conservation. *Proceedings of the National Academy of Sciences* 107(43):18278-18285..

Wynveen, C., G. Kyle, and **S.G. Sutton**. 2010. Place meanings ascribed to marine settings: the case of the Great Barrier Reef Marine Park. *Leisure Sciences* 32(3):270-287 .

Li., O, and **S.G. Sutton**. 2010. Communicating scientific information to recreational fishers. *Human Dimensions of Wildlife,* 15(2):106 -118.

Lynch. AM, **S.G. Sutton**, and C.S. Simpfendorfer. 2010. Implications of recreational fishing for elasmobranch conservation in the Great Barrier Reef Marine Park. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20:312-318.

Sutton, S.G. and R. Tobin. 2009. Recreational fishers' attitudes towards the 2004 rezoning of the Great Barrier Reef Marine Park. *Environmental Conservation* 36 (3): 245-252.

Sutton, S.G., K. Dew, and J. Higgs. 2009.. Why do people drop out of recreational fishing? A study from Queensland, Australia. *Fisheries,* 34(9): 443-452.

Bartlett, C.Y., C. Manua, J. Cinner, **S. Sutton**, R. Jimmy, R. South, J. Nilsson, J. Rania. 2009. Comparison of outcomes of permanently closed and periodically harvested coral reef reserves. *Conservation Biology* 23(6):1475-1484.

Smith, A.M., and **S.G. Sutton.** 2008. The role of a flagship species in the formation of ecological intentions. *Human Dimensions of Wildlife* 13:1-14.

Sutton, S.G. 2007. Constraints on recreational fishing participation in Queensland, Australia. *Fisheries* 32(2):73-83.

Marshall, N.A., D.M. Fenton, P.M. Marshall, and **S.G Sutton.** 2007. How resource dependency can influence social resilience within a primary resource industry. *Rural Sociology* 72(3): 359-390.

Cinner, J.E., **S.G. Sutton**, and T.G. Bond. 2007. Apparent thresholds of commercialization, population, and modernization that erode customary management of marine resources. *Conservation Biology 21:*1603-1611.

Sutton, S.G., and S.L. Bushnell. 2007. Socio-economic aspects of artificial reefs: considerations for the Great Barrier Reef Marine Park. *Ocean and Coastal Management* 50: 829-846.

Arlinghaus, R., S.J. Cooke, J. Lyman, D. Policansky, A. Schwab, C. Suski, **S.G. Sutton**, and E.B. Thorstad. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science* 15: 75-167.

Sutton, S.G. 2006. Understanding recreational fishers' participation in public consultation programs. *Human Dimensions of Wildlife* 11:329-341.

Sutton, S.G. 2005. Factors influencing satisfaction of boaters in Australia's Great Barrier Reef Marine Park. *Tourism in Marine Environments* 2:13-22.

Sutton, S.G., and R.B. Ditton. 2005. The substitutability of one type of fishing for another. *North American Journal of Fisheries Management* 25:536-546..

Shields, J.D., D.M Taylor, **S.G. Sutton**, P.G. O'Keefe, D.W. Ings, and A.L. Pardy. 2005. Epidemiology of Bitter Crab Disease (*Hematodinium* Sp.) in snow crabs *Chionoecetes opilio* from Newfoundland, Canada. *Diseases of Aquatic Organisms* 64: 253-264.

Ditton, R.B., and **S.G. Sutton.** 2004. Substitutability in recreational fishing. *Human Dimensions of Wildlife* 9: 87-102.

Sutton, S.G. 2003. Personal and situational determinants of catch-and-release behavior of freshwater anglers. *Human Dimensions of Wildlife* 8: 109-126.

Sutton, S.G., J.R. Stoll, and R.B. Ditton. 2001. Understanding anglers' willingness to pay increased fishing license fees. *Human Dimensions of Wildlife* 6:115-130.

Sutton, S.G., and R.B. Ditton. 2001. Understanding catch-and-release behavior among U.S. Atlantic bluefin tuna anglers. *Human Dimensions of Wildlife* 6: 49-66.

Sutton, S.G., T.P. Bult, and R.L. Haedrich. 2000. Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. *Transactions of the American Fisheries Society* 129:527-538.

Book Chapters

Schratwieser, J. **S.G. Sutton**, and R. Arlinghaus. 2011. Introduction. Pages 1-9 *in* T. D. Beard, Jr., R. Arlinghaus, and S. G. Sutton, editors. The Angler in the Environment: Social, Economic, Biological, and Ethical Dimensions. American Fisheries Society, Bethesda, Maryland.

Wightman, R., **S.G. Sutton**, B. Matthews, K. Gillis, J. Coleman, and J. Samuelsen. 2008. Recruiting new anglers: driving forces, constraints and examples of success. Pages 303-323 *in* O. Aas, editor. Global Challenges in Recreational Fisheries. Blackwell Publishing, Oxford.

Gentner, B., and **S.G. Sutton,**. 2008. Substitutability in recreational fishing. Pages 150-169 *in* O. Aas, editor. Global Challenges in Recreational Fisheries. Blackwell Publishing, Oxford.

Sutton, S.G. 2000. Local knowledge and community watershed management of recreational fisheries resources in Newfoundland. In: Neis, B. and L. Felt (eds.) *Finding our Sea Legs: Linking Fishery People and Their Knowledge With Science and Management.* ISER Press, St. John's.

Conference Proceedings

van Riper, C.J., Kyle, G.T., **S.G. Sutton,** Tobin, R., & Stronza, A. 2012. Place meanings among resource and recreation managers of the Great Barrier Reef Marine Park, Australia. In S. Weber (Ed.), *Rethinking Protected Areas in a Changing World Proceedings of the 2011 George Wright Society Conference on Parks, Protected Areas, and Cultural Sites* (pp. 344-349). Hancock, MI: The George Wright Society.

van Riper, C.J., Kyle, G.T., Yoon, J.I., and **S.G. Sutton**. 2010. Australian community members' attitudes toward climate change impacts at the Great Barrier Reef. In C. E. Watts & C. L. Fisher (Eds.), Proceedings of the 2010 Northeastern Recreation Research Symposium. General Technical Report. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station.

Smith, W.E., Kyle, G., & **S.G. Sutton.** 2010. Angler segmentation using perceptions of experiential quality in the Great Barrier Reef Marine Park. In C. E. Watts & C. L. Fisher (Eds.), Proceedings of the 2010 Northeastern Recreation Research Symposium. General Technical Report. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station.

Yoon, J.I., Kyle, G.T., van Riper, C.J., and **S.G. Sutton.** 2010. Climate change and environmentally responsible behavior on the Great Barrier Reef, Australia. In C. E. Watts & C. L. Fisher (Eds.), Proceedings of the 2010 Northeastern Recreation Research Symposium. General Technical Report. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station.

Wynveen, C.J., Kyle, G.T., and **S.G. Sutton.** 2011. Recreational visitors' place meaning and place attachment in a marine setting. Northeast Recreation Research Symposium. Bolton Landing, NY. Proceedings of the 2010 Northeastern Recreation Research Symposium. USDA-FS-Northeastern Research Station.

Wynveen, C. J., Kyle, G. T., and **S.G. Sutton.** 2009. Place meanings ascribed to marine recreation areas: The case of Australia's Great Barrier Reef. Proceedings of the 2009 Northeastern Recreation Research Symposium. USDA-FS-Northeastern Research Station, GTR-NRS-P-66.

Sutton, S.G., and R.B. Ditton. 2002. Understanding catch-and-release behavior among U.S. Atlantic bluefin tuna anglers. Pages 205-207 *In* Lucy, J. and Strudholme, L. (editors). Catch and Release in Marine Recreational Fisheries. American Fisheries Society Symposium 30.

Stoll, J.R., J.W. Milon, R.B. Ditton, **S.G. Sutton**, and S.M. Holland. 2002. The economic impact of charter and party boat operations in the Gulf of Mexico. *Proceedings of the 53rd Annual Meeting of the Gulf and Caribbean Fisheries Institute.*

Ditton, R.B., **S.G. Sutton**, J.R. Stoll, S.M. Holland, and J.W. Milon. 2001. A longitudinal perspective on the social and economic characteristics of the U.S. Gulf of Mexico charter and party boat industry. *Proceedings of the 52nd Annual Meeting of the Gulf and Caribbean Fisheries Institute*: 372-384.

Technical Reports

D. Gledhill, D. J. Welch, A. Hobday, S.G. Sutton, A. Jeloudev, M. Koopman, M. Lansdell, A. Smith, P. Last. 2013. Identification of climate-driven species shifts and adaptation options for recreational fishers: learning lessons from a data-rich case. FRDC-DCCEE 1010/524

Creighton, C., W. Sawynok, **S.G Sutton**, D. D'Silva, I. Stagles, C. Pam, R. Saunders, D. Welch, D. Grixti, and D. Spooner. 2013. Climate Change and Recreational Fishing: Implications of Climate Change for Recreational Fishers and the Recreational Fishing Industry. Fisheries Research and Development Corporation project report #2011/037.

Van Riper, C.J., G.T. Kyle, **S.G. Sutton**, and R.C. Tobin. 2011. Final Technical Report of Managers' Place Meanings and Environmental Governance. Human Dimensions of Natural Resources Laboratory, Texas A&M University, College Station, Texas.

Sutton, S.G., and R. Tobin. 2010. Socio-economic indicators for users of the Great Barrier Reef World Heritage Area. Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns, Australia.

Sutton, S.G, E. J. Lédée, R.C. Tobin, D. M. De Freitas. 2010. Impacts of the 2004 Rezoning of the Great Barrier Reef Marine Park on Commercial Line, Trawl and Charter Fishers. Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns, Australia.

Tobin, RC, **Sutton, SG** and Penny, AL. 2010. Towards Evaluating the Socio-economic Impacts of Changes to Queensland's Inshore Fishery Management. Fishing and Fisheries Research Centre Technical Report No. 9., James Cook University, Townsville.

Tobin, A, Schlaff, A, Tobin, R, Penny, A, Ayling, T, Ayling, A, Krause, B, Welch, D, **Sutton, S.G,** Sawynok, B, Marshall, N, Marshall, P and Maynard, J (2010). Adapting to Change: Minimising Uncertainty about the Effects of Rapidly-Changing Environmental Conditions on the Queensland Coral Reef Fin Fish Fishery, Fishing and Fisheries Research Centre Technical Report No. 11, James Cook University, Townsville, Australia.

Tobin, RC, **Sutton, SG,** Penny, A, Williams, L, Maroske, J and Nilsson, J. 2010. Baseline Socio-Economic Data for Queensland East-Coast Inshore and Rocky Reef Fishery Stakeholders. Part A: Commercial Fishers, Technical Report No. 5. FRDC Project No. 2007/048, Fishing and Fisheries Research Centre, Townsville, Australia.

Morgan C, **Sutton SG** and Tobin R. 2010. What drives fishers to comply with regulations, and how do you measure it? A literature review. Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns.

Tobin, RC, Beggs, K, **Sutton, SG**, Penny, A, Maroske, J and Williams, L. 2010. Baseline Socio-Economic Data for Queensland East Coast Inshore and Rocky Reef Fishery Stakeholders Part B: Charter Fishers, Technical Report No. 6. FRDC Project No.

2007/048, Fishing and Fisheries Research Centre, Townsville, Australia.

Tobin, RC, Beggs, K, **Sutton, SG** and Penny, A. 2010. Baseline Socio-Economic Data for Queensland East-Coast Inshore and Rocky Reef Fishery Stakeholders. Part C: Recreational Fishers, Technical Report No. 7. FRDC Project No. 2007/048, Fishing and Fisheries Research Centre, Townsville, Australia.

Tobin, RC, Beggs, K, **Sutton, SG** and Penny, A. 2010. Baseline Socio-Economic Data for Queensland East-Coast Inshore and Rocky Reef Fishery Stakeholders. Part D: Seafood Consumers, Technical Report No. 8. FRDC Project No. 2007/048, Fishing and Fisheries Research Centre, Townsville, Australia.

Nilsson, J.A., **S.G. Sutton**, and R.C Tobin. 2009. A survey of climate change and the Great Barrier Reef. Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns, Australia.

Lynch, A.M, **S.G. Sutton**, and R.C Tobin. 2009. A review of community perceptions of climate change: Implications for the Great Barrier Reef. Report to the Great Barrier Reef Marine Park Authority, Townsville, Australia.

Tobin R.C., Simpfendorfer C.A., **Sutton S.G.**, Goldman B., Muldoon G., Williams A.J., Ledee E. 2009. A review of the spawning closures in the Coral Reef Fin Fish Fishery. A Report to Queensland's Primary Industries and Fisheries, Queensland, Australia.

Sutton, S.G. 2008. Recreational fishers' perceptions about the costs and benefits of the 2004 Great Barrier Reef Marine Park Zoning Plan. Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns (44pp.)

Little, L.R., G.A. Begg, B. Goldman, N. Ellis, B.D. Mapstone, A.E. Punt, A. Jones, **S.G. Sutton**, and A. Williams. 2008. Modelling multi-species targeting of fishing effort in the Queensland Coral Reef Fin Fish Fishery. Fishing and Fisheries Research Centre Technical Report No. 2. James Cook University, Townsville.

Sutton, S.G. 2006. An assessment of the social characteristics of Queensland's recreational fishers. Report prepared for the CRC Reef Research Centre, Townsville.

Shields, J.D., D.M. Taylor, **S.G. Sutton**, P.G. O'Keefe, D.W. Ings, and A.L. Pardy. 2004. Aspects of the epidemiology of bitter crab disease (hematodinium sp.) in snow crabs, *Chionocetes opilio* from Newfoundland, Canada. Canadian Science Advisory Secretariat Resarch Document 2004/077.

Sutton, S.G., and R.B. Ditton. 2001. Understanding an urban fishery: Braunig Lake and Calaveras Lake, San Antonio, Texas. Report prepared for Texas Parks and Wildlife Department. Texas A&M University, College Station.

Ditton, R.B., D.K. Anderson, B.L. Bohnsack, and **S.G. Sutton**. 2000. The 1999 Texas International Fishing Tournament: participants' characteristics, participation in fishing, attitudes, expenditures, and economic impacts. Human Dimensions of Fisheries Laboratory

Technical Report to Texas International Fishing Tournament, Inc. Texas A&M University, College Station, Texas.

Ditton, R.B., D.K. Anderson, J.F. Thigpen III, B.L. Bohnsack and **S.G. Sutton**. 2000. The 1999 Pirate's Cove Big Game Tournaments: participants' characteristics, participation in fishing, attitudes, expenditures, and economic impacts. Human Dimensions of Fisheries Laboratory Technical Report. Texas A&M University: College Station, TX.

Sutton, S.G., R.B. Ditton, J.R. Stoll, and J.W. Milon. 1999. A cross-sectional study and longitudinal perspective on the social and economic characteristics of the charter and party boat fishing industry of Alabama, Mississippi, Louisiana, and Texas. Human Dimensions of Fisheries Laboratory Technical Report to the National Marine Fisheries Service. Texas A&M University, College Station, Texas.

Ditton, R.B., and **S.G. Sutton.** 1998. A social and economic study of Fort Hood anglers. Human Dimensions of Fisheries Laboratory Technical Report to the U.S. Fish and Wildlife Service. Texas A&M University, College Station, Texas.

Sutton, S.G. and R.S. Pritchett. 1995. Assessment of the 1995 winter fishery on Paddy's Pond and Cochrane Pond using a roving creel survey. Report submitted to the Department of Fisheries, Food and Agriculture, Government of Newfoundland and Labrador.

CONFERENCE PRESENTATIONS

Sutton, S.G., D. Gledhill, A.J. Hobday, D. J. Welch, M. J. Lansdell, M. Koopman, A.Jeloudev, A. Smith and P. R. Last. 2014. A collaborative approach to using historical spearfishing competition records to identify climate-induced environmental changes. 7th World Recreational Fishing Conference, Campinas, Brazil, September 1-4, 2014.

Sutton, S.G. 2013. Engaging the recreational fishing community in conservation of Australia's marine resources. 26th International Congress on Conservation Biology, Baltimore Maryland.

Sutton, S.G., and R.C. Tobin. 2012. Understanding commercial fishers' compliance with go-slow zones in the Great Sandy Marine Park. Pathways to Success 2012: Integrating Human Dimensions into Management of Fisheries and Wildlife. Breckenridge, Colorado.

Sutton, S.G. and L. Hunt. 2011. Human dimensions of recreational fisheries: Challenges, opportunities, and emerging research needs. Keynote Address, 6th World Recreational Fishing Conference. Berlin, Germany, August 1-4, 2011.

Sutton, S.G. 2010. Human Dimensions of Recreational Fisheries Research in Australia: Opportunities and Constraints. Pathways to Success 2010: Integrating Human Dimensions into Management of Fisheries and Wildlife, Estes Park, Colorado.

Sutton, S.G., R. Tobin, C. Simpfendorfer, B. Goldman, G. Muldoon, A. Williams. 2010. Reviewing Spawning Closures for Queensland's Coral Reef Finfish Fishery: A Multi-disciplinary Approach. 16th International Symposium on Society and Resource Management, Corpus Christi, Texas.

Sutton, S.G., J. Nilsson, and R. Tobin. 2009. Constraints on community engagement in Great Barrier Reef climate change action strategies. Paper presented at the 15th International Symposium on Society and Resource Management. Vienna, Austria.

Sutton, S.G., J. Nilsson, and R. Tobin. 2009. Constraints on community engagement in Great Barrier Reef climate change action strategies. Paper presented at the 23rd Annual Meeting of the Society for Conservation Biology. Beijing, China.

Sutton, S.G., J. Nilsson, and R. Tobin. 2009. Constraints on community engagement in Great Barrier Reef climate change action strategies. Paper presented at the Paper presented at the 3rd Annual Marine and Tropical Research Facility Conference, Townsville, Australia.

Sutton, S.G. and R. Tobin 2008. Recreational fishers perceptions of the costs and benefits of rezoning Australia's Great Barrier Reef Marine Park. Paper presented at the 5th World Recreational Fisheries Conference, Dania Beach, Florida, USA.

Sutton, S.G. and R. Tobin. 2008. Recreational fishers perceptions of the costs and benefits of rezoning Australia's Great Barrier Reef Marine Park. Paper presented at the 11th International Coral Reef Symposium, Fort Lauderdale, Florida, USA.

Sutton, S.G. and R. Tobin. 2008. Recreational fishers perceptions of the costs and benefits of rezoning Australia's Great Barrier Reef Marine Park. Paper presented at the 14th International Symposium on Society and Resource Management. Burlington, Vermont, USA.

Sutton, S.G. and R. Tobin. 2008. Recreational fishers perceptions of the costs and benefits of rezoning Australia's Great Barrier Reef Marine Park. Paper presented at the 2008 Australian Society for Fish Biology Conference, Sydney, Australia.

Sutton, S.G. 2008. Recreational fishers perceptions of the costs and benefits of the 2004Great Barrier Reef Marine Park Zoning Plan. Paper presented at the 2nd Annual Marine and Tropical Research Facility Conference, Cairns, Australia.

Sutton, S.G., and W. Sawynok. 2007. CapReef: Engaging the community in Great Barrier Reef science. Poster presented at the 13th International Symposium on Society and Resource Management. June 17-21, Park City, Utah, USA.

Sutton, S.G. 2006. Towards effective engagement of recreational fishers in the marine protected area planning and management process. Paper presented at the Recfishing Research National Seminar on Marine Protected Areas. November 3-4, Brisbane, Australia.

Sutton, S.G., 2006. Understanding the effects of marine protected areas on recreational fishers. Paper presented at the Recfishing Research National Seminar on Marine Protected Areas. November 3-4, Brisbane, Australia.

Sutton, S.G. 2006. Why do people drop out of recreational fishing? A study from Queensland, Australia. Paper presented at the 12th International Symposium on Society and

Resource Management. June 3-8, Vancouver, Canada.

Sutton, S.G., R. Pears, S. Bushnell, D. Williams. 2005. Does scientific evidence support popular beliefs about artificial reefs in the Great Barrier Reef Marine Park? Paper presented at the Rainforest Meets Reef Conference. November 22-34, Townsville, Australia.

Sutton, S.G. 2005. Understanding Recreational Fishers' Participation in Public Consultation Programs in Queensland, Australia. Paper presented at the 11th International Symposium on Society and Resource Management. June 16-19 2005, Ostersund, Sweden.

Sutton, S.G. 2005. Understanding Constraints on Recreational Fishing Activity in Queensland, Australia. Paper presented at the 4th World Recreational Fisheries Conference. June 12-16, Trondheim, Norway.

Mapleston, A., D. Welch, G. Begg, I. Brown, A. Butcher, I. Halliday, J. Kirkwood, M. McLennan, W. Sumpton, B. Sawynok, **S. Sutton.** 2005. Increasing the survival of released line caught fish: Australian tropical and sub-tropical species. Paper presented at the 4th World Recreational Fisheries Conference. June 12-16, Trondheim, Norway.

Sutton, S.G. 2004. Factors influencing satisfaction of anglers fishing in Australia's Great Barrier Reef Marine Park. Paper presented at the 10th International Symposium on Society and Resource Management, June 2004, Keystone, Colorado.

Sutton, S.G., B. Goldman, G. Begg, and B. Mapstone. 2004. Using social science to inform models of the Great Barrier Reef Line Fishery. Paper presented at the 10th International Symposium on Society and Resource Management, June 2004, Keystone, Colorado.

Sutton, S.G., and K.M. Hunt. 2000. Measuring the importance anglers place on catch-related aspects of the angling experience. Paper presented at the 130th Annual Meeting of the American Fisheries Society, August 2000, St. Louis, Missouri.

Sutton, S.G., J.R. Stoll, and R.B. Ditton. 2000. Contingent valuation methodology predicts consequences of fishing license fee increases. Poster presented at the 8th International Symposium on Society and Resource Management, June 2000, Bellingham, Washington.

Sutton, S.G., and R.B. Ditton. 1999. Understanding catch-and-release behavior among U.S. Atlantic bluefin tuna anglers. Paper presented at the National Symposium on Catch and Release Angling in Marine Fisheries, December 5-8 1999, Virginia Beach, Virginia.

Sutton, S.G., R.B. Ditton, J.R. Stoll, and J.W. Milon. 1999. Economic importance of the charter and party boat fishing industry to Texas, Louisiana, Mississippi and Alabama. Paper presented at the International Workshop on Evaluating the Benefits of Recreational Fishing, June 1-3 1999, Vancouver, British Columbia.

Sutton, S.G., and R.B. Ditton. 1998. Comparison of three methods of estimating the effects of non-response bias on angler surveys. Paper presented at the 128th Annual Meeting of the American Fisheries Society, August 1998, Hartford, Connecticut.

Sutton, S.G., and R.B. Ditton. 1998. Understanding tagging behavior among Atlantic bluefin tuna anglers. Paper presented at the 128th Annual Meeting of the American Fisheries Society, August 1998, Hartford, Connecticut.

Sutton, S.G. 1998. The Southwest Pond Trout: Local knowledge and recreational fisheries management in Newfoundland. Paper presented at the International Workshop on Local Knowledge and Fisheries Management, May 1998, St. John's, Newfoundland.

Sutton, S.G., R.L. Radtke and R.L. Haedrich. 1997. Use of otolith microchemistry to describe life history variation in a unique population on Atlantic salmon (*Salmo salar*) in Newfoundland, Canada. Paper presented at the 127th Annual Meeting of the American Fisheries Society, August 1997, Monterrey, California.

Sutton, S.G, and R.L. Haedrich. 1995. Atlantic salmon parr lose fat in the fall. Poster presented at the 75th Annual Meeting of the American Society of Ichthyologists and Herpetologists, June 1995, Edmonton, Alberta.

MAJOR RESEARCH GRANTS

As Principal Investigator

2012-2013	Predicting the impacts of climate change on the recreational fishing industry in northern Australia. Fisheries Research and Development Corporation, $30,000
2010-2011	Recreational fishing of sharks in the Great Barrier Reef Marine Park: Species composition and catch-and-release stress. Marine and Tropical Sciences Research Facility, $22,840.
2010-2010	Evaluating science communication in Great Barrier Reef fisheries. $22,466.
2008-2009	Understanding community perceptions of the impacts of climate change on the Great Barrier Reef. Marine and Tropical Sciences Research Facility, $50,000
2006-2010	Incorporating stakeholders and their values in management of the Great Barrier Reef Marine Park. Marine and Tropical Sciences Research Facility, $612,000
2005-2007	Measuring the impacts of Great Barrier Reef Marine Park rezoning on recreational fishers. CRC Reef Research Centre, $179,000
2003-2005	Understanding the social characteristics of recreational fishers in Queensland, Australia. CRC Reef Research Centre, $86,000

As Co-Investigator

2013-2015	Adapt or fail: Risk management and business resilience in Queensland commercial fisheries. Fisheries Research and Development Corporation, $350,000 (PI: Renae Tobin, JCU)
2011-2013	Handling practices that reduce mortalities of sharks in commercial fisheries. Caring for our Country, $ 299,930 (PI: Barry Bruce, CSIRO)
2011-2013	Identification of climate-driven species shifts and adaptation options for recreational fishers: learning general lessons from a data rich case. National

	Adaptation Research Program, $150,000. (PI: Daniel Gledhill, CSIRO)
2010-2010	Investigating the motivations of commercial and recreational fishers to comply with Great Barrier Reef Marine Park zoning. Marine and Tropical Sciences Research Facility, $67,500 (PI: Renae Tobin, JCU).
2009-2011	Whose fish is it anyway? Investigation of co-management and self-governance solutions to local issues in Queensland's inshore fisheries. Fisheries Research and Development Corporation. $300,000, (PI: Daryl McPhee, Bond University)
2007-2010	Towards evaluating the socio-economic impacts of changes to Queensland's inshore fishery management. Fisheries Research and Development Corporation, $220,552. (PI: Renae Tobin, James Cook University)
2009-2010	Adapting to Change - Exploring the response of the GBR Coral Reef Fin Fish Fishery to a major environmental event (Cyclone Hamish) Marine and Tropical Sciences Research Facility, $23,000. (PI: Renae Tobin, James Cook University)
2007-2008	Review of Spawning Closures in the Coral Reef Fin Fish Management Plan. Queensland Department of Primary Industries and Fisheries, $93,620. (PI: Ashley Williams, James Cook University)

STUDENTS SUPERVISED TO COMPLETION

Doctor of Philosophy

Owen Li (JCU, 2016) – Employing informal learning theory and network analysis to improve the way we communicate scientific information to fisheries stakeholders. (Principal Supervisor).

Monica Gratani (JCU, 2015) – Promoting the inclusion of indigenous knowledge in natural resource management: a case study from the wet tropics of Queensland, Australia. (Principal Supervisor).

Sander den Haring (JCU, 2015) - Effective interpretation for recreational marine resource use in the Mombasa Marine Park and Reserve, Kenya. (Principal Supervisor).

Leanne Currey (JCU, 2015) - Movement of an exploited coral reef teleost across spatial and temporal scales. (Associate Supervisor).

Ruth Kamrowski (JCU, 2014) - Coastal light pollution in Australia: Insights and implications for marine turtle conservation. (Co-Supervisor).

Marina Farr (JCU, 2014) - Economic values assigned to boating and fishing trips in the Great Barrier Reef Marine Park. (Co-Supervisor).

Carena van Riper (Texas A&M, 2014) - Understanding and mapping values for ecosystem services among visitors to protected areas. (External Associate Supervisor).

Kathryn Larsen (JCU, 2013) - A social-ecological systems analysis of the potential for Indigenous Protected Areas on Cape York Peninsula, Australia. (Co-Supervisor/Principal

Supervisor).

Alyson Lankester (JCU, 2013) - The influence of identity and learning on engagement in sustainability behaviour among extensive graziers in north Queensland, Australia. (Co-Supervisor).

Jillian Grayson (JCU, 2012) - Characteristics of traditional dugong and green turtle fisheries in Torres Strait: Opportunities for management. (Associate Supervisor).

William Smith (Texas A&M, 2012) - Using specialization theory to understand diversity among Texas recreational fishing guides. (External Co-Supervisor).

Sarah Busilacchi (JCU, 2011) – The subsistence reef fish fishery in the Torres Strait: monitoring protocols and assessment. (Co-Supervisor/Principal Supervisor).

Chris Bartlett (JCU, 2010) – Emergence, evolution, and outcomes of marine protected areas in Vanuatu: Implications for social-ecological governance. (Co-Supervisor).

Debora DeFreitas (JCU, 2010) - The role of public participation, spatial information and GIS in natural resource management of the dry tropical coast, northern Australia. (Co-Supervisor).

Chris Wynveen (Texas A&M, 2009) – Place meaning and attitudes towards impacts on marine environments in the Great Barrier Reef. (External Associate Supervisor).

Renae Tobin (JCU, 2006) - The effectiveness of recreational only fishing areas in north Queensland estuaries for reducing conflict and improving recreational catches. (Co-Supervisor/Principal Supervisor).

Joshua Cinner (JCU, 2006) - How socioeconomic factors influence traditional coral reef management in Papua New Guinea. (Co-Supervisor/Principal Supervisor).

Nadine Marshall (JCU, 2006) – A conceptual and operational understanding of social resilience in a primary resource industry – insights for optimizing social and environmental outcomes in the management of Queensland's commercial fishing industry. (Co-Supervisor/Principal Supervisor).

Master of Science

Roxanne Crossley (Imperial College, 2013) - Public perception and understanding of shark attack mitigation measures in Australia.

Natasha Szczecinski (JCU, 2012) - Catch susceptibility and life history of barred javelin in north eastern Australia.

Fernanda De Faria (JCU, 2012) - Catch composition and post-release stress of recreationally caught sharks in the Great Barrier Reef.

Master of Applied Science

Eline Kjoerven (JCU, 2014) - How anthropomorphism can influence perception of similarity to self, and its potential as a conservation tool.

Brian Gilmore (JCU, 2014) – Recreational fishers' attitudes towards a recreational fishing license in Queensland, Australia.

Lan Nguyen Hong (JCU, 2014) – Assessing the vulnerability of Vietnam's coastal aquaculture sector to climate change.

Andres Ramirez-Yaksic (JCU, 2014) - Recreational and commercial fishers in the Great

Barrier Reef, what they value, perceive and their climate change beliefs.

Jensi Sartin (JCU, 2013) - Evaluating fishers' perception towards MPAs development and its impacts: case study in Bali, Indonesia.

Shwetha Dona (JCU, 2014) - Influence of risk perceptions on public participation in Environmental Impact Assessment

Imron Rosyidi (JCU, 2011) - An alternative mechanism to tuna fishing quota allocations among parties of the commission for the conservation of southern bluefin tuna case study: Southern bluefin tuna fishery in Indonesia .

Adityo Setiawan (JCU, 2010) - The perceived impact of the Panglima Laot system on community welfare in Nangroe Aceh Darussalam (NAD), Indonesia.

Charlotte Morgan (JCU, 2010) – Analysis of fisheries compliance data for the Great Barrier Reef Marine Park.

Adrian Arias (JCU, 2009) – Using random response theory to measure compliance of recreational fishers to zoning in the Great Barrier Reef Marine Park.

Chai-Yen Cheong (JCU, 2008) - Recreational fishers' motivations for participating in the CapReef community-based monitoring program in Queensland, Australia.

Roger Beeden (JCU, 2006) - A content analysis of attitudes to recreational fishing in Queensland, Australia.

Rima Jabado (JCU, 2006) – Attitudes and knowledge of Great Barrier Reef area residents towards sharks.

Kiri Peat (JCU, 2005) - Demographic and social influences on recreational fishers' social value orientations in Queensland, Australia.

Nicola Doss (JCU, 2005) - Influence of Socio-Economic Factors on Perceptions and Awareness of Marine Ecosystems and Management: A Case Study of Kepulauan Karimun Jawa Marine National Park, Indonesia.

Amy Smith (JCU, 2004) – The role of a flagship species in the formation of ecological intentions.

Honours

Ana Wegner (JCU 2011) – Recreational fishers' participation in public consultation programs.

Owen Li (JCU 2008) – Communicating scientific information to recreational fishers.

Ann-Maree Lynch (JCU 2007) – Implications of recreational fishing for elasmobranch conservation in the Great Barrier Reef Marine Park.

Alana White (JCU 2005) – Boaters' perceptions of speed guidelines introduced for dugong conservation: Use of the theory of reasoned action as a guiding tool to understand non-Compliance

Kara Dew (JCU 2004) - Land-based fishing activities and the importance of fishing to Traditional Owners of Girringun Country, North Queensland.

CURRENT STUDENTS

Brock Bergseth (PhD) – Confronting non-compliance in marine reserves. (Co-Supervisor).

James Higgs (PhD) – Response of the recreational small boat fleet to changes in marine park zoning arrangements. (Principal Supervisor).

Amy Smith (PhD) - Using flagship species to motivate conservation behaviour of zoo visitors. (Principal Supervisor).

TEACHING EXPERIENCE

James Cook University

2010-2014	Foundations of Natural Resource Management. One of four lecturers responsible for designing and delivering the course to undergraduate and graduate students across two campuses. Served as course coordinator (Townsville Campus) in 2011.
2012-2014	Human Dimensions of Environment, Nature, and Conservation. Course designer, coordinator, and principal lecturer.
2012-2014	Managing Tropical Fisheries. One of two lecturers responsible for designing, coordinating, and delivering the course.

Texas A&M University

2001	Principals of Fisheries Management. Designed and taught the laboratory and field component.

Memorial University

1994-1997	Laboratory tutor for multiple undergraduate courses in the Department of Biology, including Ichthyology, Vertebrate Biology, and Quantitative Methods in Biology.

PROFESSIONAL SERVICE

Journal editorial board membership

Transactions of the American Fisheries Society
Associate Editor 2008-2015

Human Dimensions of Wildlife: An International Journal
Editorial Board 2010-present
Associate Editor 2015-Present

Conference organizing committee membership

5th World Recreational Fisheries Conference
Organizing committee member 2007-2008 and Proceedings co-editor (AFS Books)

6th World Recreational Fisheries Conference
Organizing committee member 2008-2011

7th World Recreational Fisheries Conference
International advisory board member 2011-present

Research committee membership

Capricorn Community Based Fisheries Monitoring Program (CapReef)

Steering committee member 2005-present

Fisheries Research and Development Corporation Recfishing Research Committee
Steering committee member 2005-2013

Fisheries Research and Development Corporation Social Sciences Coordination Program
Technical reference committee member 2009-2011

Other professional service

Moderator, Human Dimensions of Recreational Fisheries Listserv
1999-2001; 2008-present