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Long-term survival of Atlantic salmon following catch and release: Considerations for anglers, scientists and resource managers

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Abstract

To evaluate the scientific basis for catch and release as a management tool, a comprehensive 3-year study compared long-term survival of Atlantic salmon that were either angled, radio-tagged and released, or trapped, radio-tagged and released (control). Overall, the mean survival probability of angled salmon relative to the control group was between 0.94 and 0.98. At cool to moderate water temperatures (10–18°C) mean survival of angled salmon was between 0.96 and 0.98. Although the number of salmon caught and released above 21°C was low, catchability was slightly reduced at warm water temperatures (21–25°C) and the mean survival probability was between 0.43 and 0.69. Lastly, the number of fish that survived the spawning period did not differ between the angled group and the control group. However, the mean percentage of fish that overwintered and migrated downstream through a counting fence to sea was between 9% and 10% for those that were caught and released and between 13% and 19% for the control group. Results of this study suggest that mortality of caught and released Atlantic salmon can be delayed but remains low at cool to moderate water temperatures.

KEYWORDS

angling, hook and release, post-release survival, *Salmo salar*

1 | INTRODUCTION

Endemic to the northern portions of Eastern North America and Western Europe, Atlantic Salmon (*Salmo salar* L.) abundance has declined across the North Atlantic (Dadswell et al., 2021; Lehnert et al., 2019; Soto et al., 2018; Thorstad et al., 2021). Newfoundland and Labrador (NL), Canada are home to more than 75% of the wild Atlantic salmon in North America (ICES, 2019). However, abundance declines have occurred despite a commercial fishing closure since the early 1990s (Dempson et al., 2004) and substantial reductions in retention and catch-and-release limits for the recreational fishery (DFO, 2019; O'Connell et al., 1992). Management measures in

the NL recreational fishery to conserve Atlantic salmon include the mandatory release of all salmon ≥ 63 cm in fork length (O'Connell et al., 1992; Randall, 1990), closures of rivers or restricted angling times, and gear restrictions (e.g., fly-fishing only, mandatory use of non-weighted artificial flies and single barbless hook only).

While retention harvest still occurs in recreational Atlantic salmon fisheries in NL and elsewhere, the mandatory and voluntary release of caught salmon is common, and in many cases increasing (ICES, 2019). The disparity between retention (2 fish per year) versus catch-and-release (3 fish per day) fishing opportunities appears to be contributing to increased catch-and-release angling in NL. This growing disparity in angling opportunity has been a

contentious point of public debate among retention and catch-and-release anglers. Among resource managers, survival and fitness of fish following catch and release is generally assumed to be high and often used as a tool (Brownscombe et al., 2017) when stocks are low (Booth et al., 1995; Lennox et al., 2017; Tufts et al., 1991; Wilkie et al., 1996) to enable a recreational fishery and associated cultural and economic benefits (tackle shops, lodge owners, license fees and guiding fees). Nevertheless, many anglers have ethical reservations and remain unconvinced that survival is high after release. These concerns are driven by differences in resource use goals (e.g., consumption vs. recreation), and skepticism of results from previous catch-and-release research. Skepticism regarding the supporting science has been linked to high variability in survival estimates (survival probabilities in the primary literature range from 0.2 to 1.0; Van Leeuwen et al., 2020). In a recent study (Van Leeuwen et al., 2020), the mean sample size from 18 published studies on the survival of anadromous Atlantic salmon following catch and release was 40 (however, only 4 studies with a mean = 16 for caught and released fish >18°C) and most catch-and-release studies ranged from 12 h (Brobbel et al., 1996) to 4 months (Gargan et al., 2015; Thorstad et al., 2003). In addition, previous studies often differed in gear types (lures vs. artificial flies, treble vs. single hooks and barbed vs. barbless hooks), techniques (simulated capture vs. actual capture and internal tags vs. external tags vs. holding fish in cages), geographic and physical location (laboratory or field), water conditions, or lacked a control group (7/18 published studies) needed to disentangle natural or procedural mortality from catch-and-release-induced mortality (Van Leeuwen et al., 2020). Although most studies suggest high survival of Atlantic salmon following catch and release (Lennox et al., 2017; Van Leeuwen et al., 2020), inconsistencies among studies have undermined broad acceptance of catch and release in NL, and the ability to evaluate the effectiveness of catch-and-release management programs. However, the angling community (both catch-and-release and retention anglers) and resource managers agree that survival following catch and release depends on angler practices (e.g., gear type and bait type), experience (e.g., handling, air exposure; Cooke & Wilde, 2007; Lennox et al., 2017) and water temperature at the time of capture (Havn et al., 2015; Lennox et al., 2017; Van Leeuwen et al., 2020, 2021; Wilkie et al., 1996). Although anglers broadly believe that catch rates decline as water temperature increases, perhaps because fish move less, with one study suggesting that salmon are reluctant to take a fly or lure at warm water temperatures (Breau, 2013), and two studies suggesting that substantial numbers of salmon can still be caught at warm water temperatures (Mowbray & Locke 1999; Van Leeuwen et al., 2021).

Given the limitations of previous studies identified by Lennox et al. (2017) and Van Leeuwen et al. (2020), the long-term effects of catch-and-release angling on Atlantic salmon survival are poorly understood. Further, variables that affect catch-and-release survival are often unique to a specific fishery. Thus, regional or jurisdiction-specific catch-and-release studies are important to resource managers and anglers to ensure transparency

in the decision-making process, and compliance with regulations (e.g., social-ecological management; Cote et al., 2021). Failure to engage anglers in the development of fishery management strategies can undermine the fishery management process and substantially impede progress toward conservation objectives (Cote et al., 2021).

This study aims to use the largest catch-and-release Atlantic salmon radio-telemetry deployment to date ($n = 283$) to achieve four objectives: (1) determine if long-term survival (300 days) differed among Atlantic salmon that were angled, radio-tagged and released ($n = 119$) and a control group of Atlantic salmon that were trapped at a salmon counting fence, radio-tagged and released ($n = 164$); (2) determine if fishery-specific survival rates for caught and released Atlantic salmon differed among water temperatures; (3) determine if mortalities associated with catch and release occurred before or after the spawning period and (4) determine if the number of fish that overwintered and migrated downstream through a counting fence to sea (i.e., kelt survival) differed between catch-and-release and control groups.

2 | MATERIALS AND METHODS

2.1 | Study location and background

Western Arm Brook lies on the western side of the Great Northern Peninsula, in NL, Canada. The watershed has a total surface area of 2560 hectares and a drainage area of approximately 149 km². The headwaters contain 83 water bodies with the largest being Western Brook Pond (Figure 1).

A salmon counting fence (Figure 1) was established on Western Arm Brook in 1971 (Mullins et al., 2001) by Fisheries and Oceans Canada (DFO). The counting fence generally operated from May to September as a complete barrier to upstream fish passage. The fence contained a gated opening fitted with a video counter and trap so that biological samples could be collected. This trap was the only route for fish passage through the fence, thereby allowing for accurate counts and easy access to returning adult salmon for study. Returning adults were primarily 1 sea-winter (SW) maiden spawners (≤ 63 cm; 96%) with an average total return of 924 fish (min. = 234 in 1991 and max. = 1935 in 2008).

2.2 | Ethical statement, Fish collection, radio tagging (internal and external attachment) and tracking

All internal radio telemetry tagging was performed by two Government of Newfoundland and Labrador staff members, and all research activities and use of experimental animals complied with the Canadian Council on Animal Care guidelines and policies as approved by DFO permit numbers NL-4780-18, NL-5306-19 and NL-5934-20 for years 1–3 of the study. Counting fence fish

FIGURE 1 Event locations (i.e., last known location) of Atlantic salmon (yellow circles) that were trapped at a salmon counting fence facility, radio-tagged and released (Control; panel a) and Atlantic salmon that were angled, radio-tagged and released (Experimental (angled); panel b) to evaluate survival following catch and release, in addition to angling locations (crosshairs), radio receiver locations, used to track individual salmon (red triangles, from station 1 above the counting fence to station 7), and the counting fence location (cross) at Western Arm Brook, Newfoundland and Labrador, Canada (c)

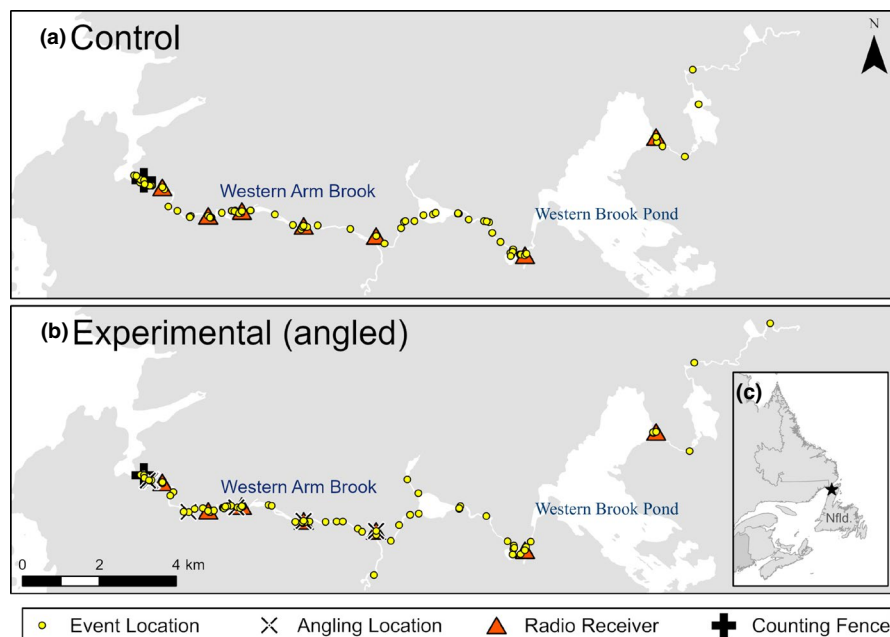
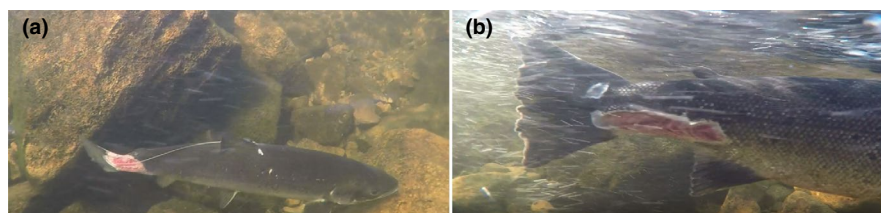


FIGURE 2 (a and b) Marks and sores were observed on Atlantic salmon that were handled with cotton gloves at Western Arm Brook, Newfoundland and Labrador, Canada



($n = 164$) were collected using a knotless rubber mesh dip net from the trap at the counting fence (Figure 1) in July and August of 2018, 2019 and 2020 and September of 2019. These fish were used as the control group and were not subjected to the additional stressors associated with capture and retrieval during angling. Of the 164 fish tagged at the counting fence (control group), 77 were implanted with internal radio tags and 87 were affixed with external radio tags. In addition, 119 Atlantic salmon (experimental group) received an additional stressor by being angled at various locations on the river (Figure 1) during July, August and September of 2018, 2019 and 2020 and October of 2018. Of the angled fish, 57 were implanted with internal radio tags while 62 were affixed with external radio tags. Anglers were instructed to use typical angling behavior when landing fish. In all cases, fish were “played” until they could be netted by an observer near shore. Detailed records were kept for every trapping and angling event, including water and air temperature, angler experience, time, location, hook location on the salmon, fly pattern, duration of play, injuries to the salmon and other anomalies during the hooking, trapping and releasing events.

Internally implanted radio transmitters were MCFT2-3LM tags (12×69 mm; 16 g in air, 5 s burst rate and an operational life of 819–1330 days), whereas externally attached radio transmitters were NTF-5-2 tags (8.2×15 mm, 1.5 g in air, 5 s burst rate with an operational life of approximately 299 days) operating at 151.890 Hz (Lotek Wireless Inc.). The NTF-5-3 tags were modified to allow external attachment by placing electrical shrink-wrap around the

NTF-5-3 tag and the streaming end of an FD-68BC anchor tag (Floy Tag and Manufacturing Incorporated) and gently applying heat with a heat gun until the NTF-5-3 tag was fixed to the streaming end of the FD-68BC anchor tag (Floy Tag and Manufacturing Incorporated). Modified tags were then attached externally in the musculature adjacent to the dorsal fin of the fish using a Mark II Long Pistol Grip Gun (Floy Tag and Manufacturing Inc.). The Floy-tag number and colour remained visible after application to each fish. Additionally, fish with a surgically implanted radio transmitter was also dorsally tagged with an FD-68BC anchor tag that showed an identifying colour and number for ease of external identification if recaptured.

All control and angled salmon tagged internally were transferred from their site of capture (counting fence or angling location) using a knotless rubber mesh dip net to a large cooler. The cooler contained a solution of 38 L water and 2 mL clove oil, used as an anesthetic. Fish were kept in the anesthetic for approximately 4 min prior to surgery and then transferred to a holding trough designed with a battery-powered shower to irrigate the gills and body. All surgical equipment was sanitised with 95% ethanol solution. Fork length, scales and a genetic sample were taken from each fish prior to surgery. An incision 2–3 cm and penetrating the coelomic cavity was made forward of the pelvic-fin girdle. The radio tag was implanted into the coelomic cavity with the antennae pointing upward and out of the incision. The incision was closed with two or three absorbable sutures (2-0 with C-16 cutting needle). After surgery, salmon were placed in a 189 L perforated plastic tote in

the riverbed and aerated with two battery-powered aquarium air pumps or were placed in a recuperation pool outlined with boulders in the river substrate. Fish were released from holding areas when activity appeared normal.

Externally tagged fish were either dip netted then transferred by hand to a holding trough within the counting fence trap area (control), or held in a rubber knotless dip net in shallow water at the edge of the riverbank (angled fish). Once confined, fork length and a genetic sample were taken and the modified external radio tag inserted. Fish were then transferred from the trough or dip net by hand and released within 1–3 min. In year 1, externally tagged fish were handled with cotton gloves during the procedure. In years 2 and 3, wetted bare hands were used to hold, move and transfer fish during the external tagging process due to observed marks and sores on areas that were commonly in contact with cotton gloves during fish handling (i.e., caudal peduncle; Figure 2a & b).

Seven remote radio telemetry fixed stations monitored movement of tagged Atlantic salmon (Station 1 upstream from the counting fence to Station 7; Figure 1). Each station was equipped with an SRX800-D receiver and a 4-element Yagi antenna. Stations were solar-powered using an 85-watt module panel and two 12-volt 100 Ahr solar cell batteries. Additional to fixed station receiver data, telemetry data were collected by walking upstream and downstream using an SRX800-MD2 receiver and a folding 3-element Yagi antenna. Further, 49 telemetry monitoring flights were conducted over 3 years of the study using a helicopter equipped with an SRX800-MD2 receiver, fixed 4-element Yagi antenna and gps antenna. Each telemetry signal received using helicopter monitoring flights automatically recorded latitude and longitude using the gps antennae attachment. All receiver data were downloaded using a tablet and SRX software. SRX receivers and software, Yagi antennae, gps antennae and accompanying hardware were manufactured and supplied by Lotek Wireless Inc.

All data were sorted by tag number and an individual summary file for each fish was created. Signals were then sorted for each telemetry record and those created by background noise, collision noise and erroneous records were eliminated. This allowed the determination of an initial and final detection date, position and time for each fish.

2.3 | Environmental variables and angling specifics

In year 1, the water temperature was recorded every hour using Minilog II-T temperature data loggers submerged to the bottom substrate at Stations 1, 3, 4 and 6, and at a falls pool on the lower river section. In years 2 and 3, aqua-measure sensors (resolution $\pm 0.01^\circ\text{C}$) measured water temperature every 5 and 10 min at Stations 1, 3, 5 and 7. Each year, the sensors were placed in May and removed in November prior to ice formation. During fly fishing events, air temperature and surface water temperatures were recorded using a hand-held digital thermometer ($\pm 0.1^\circ\text{C}$) at

the site of capture. Angling effort totaled 1100 h by fly fishers ($n = 14$; experience range <5 to >20 years) using barbless, single-hook artificial flies. All tagging and angling were during daylight hours. Mean water temperature at the time of capture for angled fish $\pm$ standard deviation (SD) was $14.4^\circ\text{C} \pm 4.8^\circ\text{C}$ (min = 5.0°C and max = 22°C), whereas mean water temperature at the time of capture for control fish $\pm$ SD was $16.8^\circ\text{C} \pm 2.2^\circ\text{C}$ (min = 11.0°C and max = 22.0°C). Therefore, the overall mean water temperature at the time of capture $\pm$ SD was $15.8^\circ\text{C} \pm 3.8^\circ\text{C}$ (min. = 5.0°C and max. = 22.0°C). Mean size of fish for the study $\pm$ SD was $54.4 \text{ cm} \pm 3.2 \text{ cm}$ (min = 45.0 cm and max = 74.0 cm) and all individuals were sea-run fish.

2.4 | Salmon fate and criteria for excluding individuals from analyses

Tagged Atlantic salmon known to survive up to a particular point in time, but then lost from the study, were recorded as censored individuals. Censoring was due to tag failure, exceedance of maximum operational battery life, or fish emigration from the system (e.g., overwintered and left the river as a kelt the following spring). Therefore, a censored individual was just as likely to be alive as dead across experimental treatments and is a common designation used in long-term telemetry studies (Pollock et al., 1989) when the fate of an individual becomes unknown. Data from censored fish up to the last known date confirmed alive were used for survival analysis. Consistent with previous studies, the following three criteria were used to determine mortality (Jepsen et al., 2000; Hightower et al., 2001; Heupel & Simpfendorfer 2002; Waters et al., 2005): (1) telemetry signals from a tag repeatedly found in the same location were assumed to be dead (where possible, tags were located using walking telemetry and verified ($n = 31$)); (2) telemetry signals that did not change power signal on numerous approaches or were out of the water due to signal strength and (3) plotted signal strengths from fixed telemetry receiver stations that showed continuously repeated signal strength over prolonged periods (i.e., flat line). Although we cannot rule out the possibility of an incorrectly identified mortality event due to a shed tag, the fact that 100% (8/8) of individuals recaptured during the study (mean days to recapture = 70 days, min = 5 days and max = 359 days) had intact tags, and no angled fish captured during the study had marks associated with previous downstream tagging procedures that occurred at the counting fence (i.e., for the tagging of control fish), suggests that tag retention was likely very high throughout the study and the probability of incorrectly identified mortalities, as a result of a shed tag, were likely low or non-existent. When the exact date of death was not known, we used the midpoint between when the animal was last known to be alive and the date on which the animal was either found dead or determined to be dead, if dates were 15 or fewer days apart. If the interval exceeded 15 days, we used the date after 40% of the time interval between the



last location and the discovery of death had elapsed (Miller & Johnson, 1978; Robertson & Westbrooke, 2005).

For analyses, two datasets differed on whether the control group included or excluded individuals handled with cotton gloves. Dataset 1 excluded 22 fish; 13 due to procedural tagging and handling problems (11 control fish and 2 angled fish), 7 were recaptured during the study (6 controls and 1 angled fish) and 2 were kelt, a different life stage not typically targeted in the recreational fishery but coincidentally caught and tagged early in the season at the start of the study. Dataset 2 included those same individuals as Dataset 1, but excluded 41 fish that made up the entire control treatment group from year 1 that received external tags due to these individuals being the only group handled with cotton gloves (Figure 2a & b). During year 1, handling fish with cotton gloves may have increased risk, because marks and sores were observed on some fish. However, whether all fish subjected to handling with cotton gloves developed the marks and sores could not be determined, so no formal analysis of the “cotton glove effect” was possible. What is clear is that not all the fish from this group died. Nevertheless, to acknowledge the potential for added mortality, analyses are presented with (dataset 1) and without (dataset 2) these individuals, the only group handled with cotton gloves.

2.5 | Overall probability of survival for the study

We used a Cox proportional hazards (CPH) analysis using the R package “survival” (Therneau, 2015) and “survminer” (Kassambara, 2021) on dataset 1 and dataset 2 to examine potential effects of

treatment (control vs. angled), year and tag type (internal vs. external) on the survival of Atlantic salmon following catch and release. The CPH model calculates the hazard ratio in relation to the instantaneous rate of an event (death of the fish) for each explanatory variable. Therefore, the hazard ratio represents the difference in the likelihood of a mortality event between two groups. A Kaplan–Meier (KM) analysis using the R packages “survival” (Therneau, 2015) and “survminer” (Kassambara, 2021) and days to the event (dead, censored and alive) was also used to determine survival rate estimates over the course of the study (1–300 days post-release, mean water temperature a time of capture $\pm$ SD of $15.8^{\circ}\text{C} \pm 3.8^{\circ}\text{C}$) for angled and control fish from dataset 1 and dataset 2. Thus, the relative survival of caught and released fish to the control, for a given period since tagging for each dataset, was calculated by first subtracting the probability of survival for the control fish (assumed estimate of natural mortality) from the probability of survival for the angled fish and then subtracting from 1 (i.e., 100% survival). In the event that the probability of survival for the angled fish was higher than that of the control fish for a point in time (Table S1; Figure 3), we assumed the difference between the two to be 0 and the survival probability relative to the control is 1 (i.e., no difference). Days to the event (i.e., mortality or censored) for individual fish was calculated as the number of days elapsed between the day of release and the day of last known fate using the criteria discussed above. KM analyses have been used previously for calculating survival rates and are particularly useful in telemetry studies, where fish of unknown fate (i.e., censored individuals) and staggered entry of animals are common (Heupel & Simpfendorfer, 2011; Hubbard et al., 2021; Pollock et al., 1989).

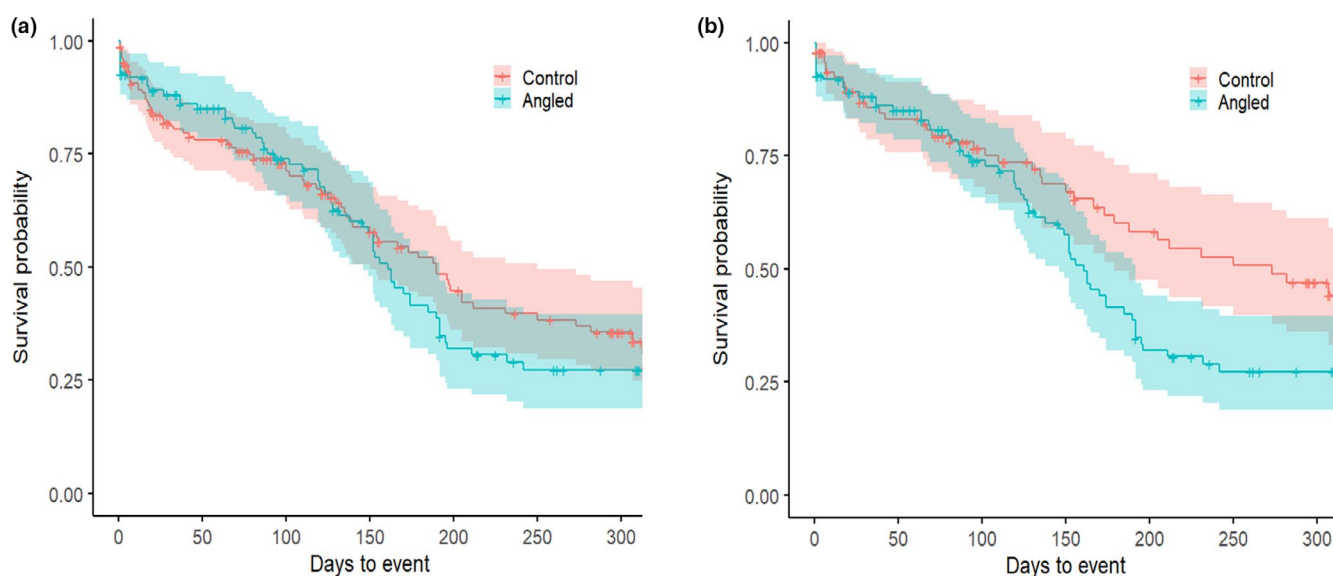


FIGURE 3 Kaplan–Meier survival curves (mean $\pm$ 95% CI) for Atlantic salmon that were angled, radio-tagged and released (Angled) and for a control group of Atlantic salmon that were trapped at a salmon counting fence facility, radio-tagged and released (Control) at Western Arm Brook, Newfoundland and Labrador, Canada, to evaluate survival following catch and release. Panels a and b refer to whether control fish from year 1 that were handled with cotton gloves were included (a) or excluded (b). Days to the event for individual fish were determined by calculating the number of days elapsed between the day of release and the day of last known fate. Vertical tick marks represent censored individuals (i.e., unknown fate). See Table S1 for survival estimates

2.6 | Catchability and probability of survival for a given water temperature

To determine the relationship between catchability of Atlantic salmon and water temperature, the total number of Atlantic salmon hooked per day was modelled using a generalised additive mixed-effects model in the package *mcgv* and the function “*gamm*” (Wood, 2011) in R (R Core Team, 2017) fitted with a Poisson distribution. Covariates included water temperature, angling effort (rod hours) and daily salmon counts. The year was included as a random intercept because the number of fish hooked occurred across 3 years. Water temperature and the daily number of salmon counted were the best fit as linear terms. Angling effort was modelled with a spline fit (with $k = 3$).

A generalised linear model in the statistical package R, with a binomial distribution (live or dead for an individual fish) and water temperature as a factor was used to determine survival probability for both angled and control Atlantic salmon at 1, 10 and 30 days post-release. Data included individuals of known fate (i.e., dead or alive) based on the criteria above. Therefore, censored individuals (i.e., individuals of unknown fate) were excluded from these analyses if they were censored prior to the period being assessed. Thirty days post-release was used as a cut-off for this analysis because estimates of survival for control and angled salmon appeared to converge at 10- and 30-days post-release.

Revised survival probability of caught and released fish relative to the control, for a given water temperature, was calculated by first subtracting the probability of survival for the control fish (assumed estimate of natural mortality) from the probability of survival for the angled fish and then subtracting from 1 (i.e., 100% survival). If the probability of survival for the angled fish was higher than that of the control for a given water temperature, we assumed the difference between the two to be 0 and survival probability was equal to that determined for caught-and-released fish. This generally occurred at temperatures $>20^{\circ}\text{C}$ because of increased error in the model as a result of low sample size or data gaps for the control group at these water temperatures.

2.7 | Survival to spawning and kelt survival

Atlantic salmon in the recreational fishery were typically targeted during their upstream spawning migration in spring and summer, and fish entering rivers in a given year were likely to spawn in the fall of that year (Klemetsen et al., 2003). Skip spawning and small non-reproductive salmon entering rivers (post-smolt) are evident in NL (Klemetsen et al., 2003; Rideout & Tomkiewicz, 2011). However, this has not been reported previously for Western Arm Brook (Klemetsen et al., 2003; Rideout & Tomkiewicz, 2011) and for the size of Atlantic salmon similar to those in our study. Spawning in Western Arm Brook generally occurred between mid-to-late October and mid-to-late November. Therefore, fish of known fate that survived on or after November 30th of the year they entered the river were assumed to be eligible to spawn. Kelt survival was calculated as the proportion of all tagged fish that migrated downstream through the counting fence.

3 | RESULTS

3.1 | Environmental variables and angling specifics

The number of angled salmon varied throughout the day, with most fish caught (44%) between 8 and 10 am and the least caught (4.5%) between 12 and 2 pm. Mean catch per rod hour was 0.31 (min = 0.15 and max = 0.48) and 51% of salmon hooked were landed. This represented on average 8.6% of the population being hooked and 4.4% of the population landed. On average, fish took 4 min to land (min = <1 min. and max = 23 min.) and upon capture, 22% of fish had hooks that did not require removal (i.e., the hook “fell out”), 92% of hooking locations were considered non-critical (e.g., lip, jaw; Muoneke & Childress, 1994) and 8% sometimes considered critical (i.e., foul hooked, tongue; Muoneke & Childress, 1994). The process of hooking, netting, de-hooking (if necessary), revival and release for an externally tagged salmon averaged 4.4 min. (min = <1 min. and max = 28 min). Most anglers (84%) landed 1 fish per day (min = 1 and max = 6) despite no restriction.

3.2 | Overall probability of survival for the study

Overall, long-term survival did not differ significantly between Atlantic salmon that were caught and released and the control group that was trapped at the salmon counting fence site, whether cotton glove handled fish were included (dataset 1; CPH, $z = 0.22$, $p = 0.83$; Table S1; Figure 3a) or excluded (dataset 2; CPH, $z = 1.92$, $p = 0.054$; Table S1; Figure 3b). Additionally, survival did not differ significantly between fish tagged with an internal or external radio tag (data set 1, CPH, $z = -0.63$, $p = 0.53$; data set 2, CPH, $z = 1.04$, $p = 0.30$) or among years of the study (data set 1, CPH, $z = -1.44$, $p = 0.15$; data set 2, CPH, $z = -0.21$, $p = 0.83$). Overall mean relative survival probability following catch and release, when compared to the control fish (1, 10, 30, 50, 150 and 300 days post-release) was 0.97 when cotton glove handled fish were included and 0.94 when cotton glove handled fish were excluded.

3.3 | Catchability and probability of survival for a given water temperature

Water temperature was negatively related to both the number of fish hooked, after statistically controlling for angling effort and daily count of salmon (GAMM, $t = -2.26$, $n = 200$, $p = 0.03$), and the survival of Atlantic salmon following catch and release (1 day post release: GLM, $z_{109,108} = -2.39$, $p = 0.02$, Figure 4a; 10 days post-release: GLM, $z_{107,106} = -2.48$, $p = 0.01$, Figure 4b; 30 days post release: GLM, $z_{102,101} = -3.06$, $p = 0.002$, Figure 4c). Revised mean catch-and-release survival probability differed slightly between datasets with the control group included (dataset 1) or excluded (dataset 2) but converged between 10- and 30-days post-release. At water temperatures between 10 and 18°C , mean

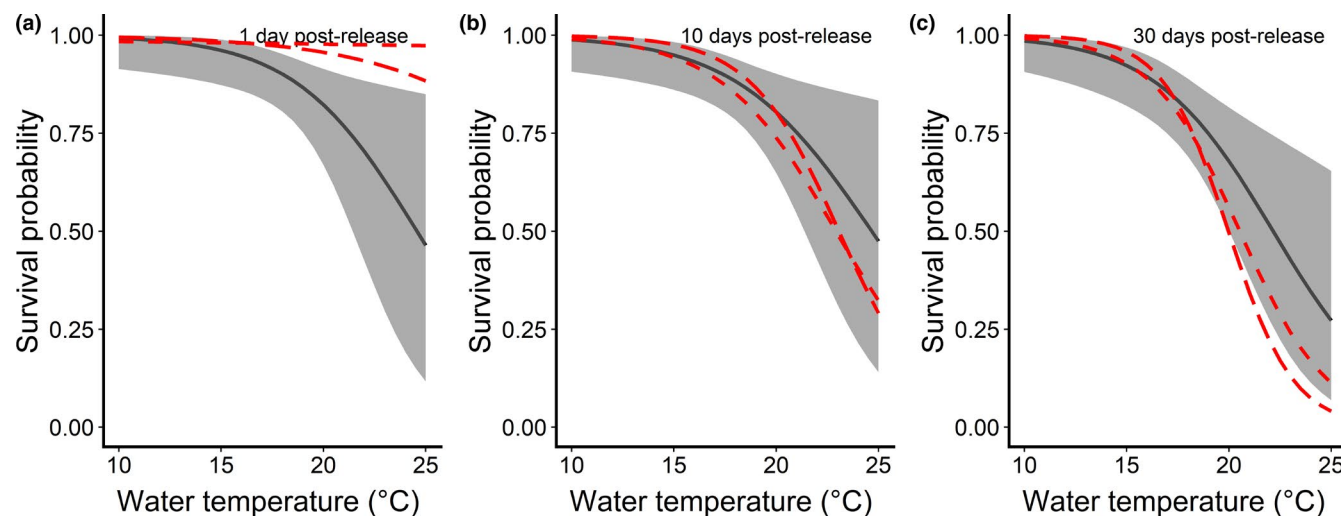


FIGURE 4 The relationship between survival probability of Atlantic salmon that were either caught, radio-tagged and released (Angled, black line; mean $\pm$ 95% CI, shaded grey) or trapped at a salmon counting fence facility, radio-tagged and released (Control; red dotted lines) at a given water temperature, 1 ($n = 110$), 10 ($n = 108$) and 30 ($n = 103$) days post-release. Survival probabilities were derived from a generalised linear model with a binomial distribution (live or dead for an individual fish) and water temperature as a factor for both the angled fish and the control fish. The short and long red dashed lines refer to whether control fish from year 1 that were handled with cotton gloves were included (short) or excluded (long). See Table S2 for survival estimates. Note: predictions above and approaching 22°C are bounded by a wide error margin and should be interpreted as such

survival was 0.98 for datasets 1 and 2 (1 day post release), 0.96 for dataset 1 and 0.98 for dataset 2 (10 days post release) and 0.96 for datasets 1 and 2 (30 days post release; Table S2; Figure 4a–c). At temperatures of 18°C, mean survival probability was 0.92 for dataset 1 and 0.93 for dataset 2 (1 day post release), 0.88 for dataset 1 and 0.97 for dataset 2 (10 days post release) and 0.81 for data sets 1 and 2 (30 days post release; Table S2; Figure 4a–c). At 20°C, mean survival probability was 0.85 for dataset 1 and 0.87 for dataset 2 (1 day post release), 0.80 for datasets 1 and 2 (10 days post release) and 0.68 for datasets 1 and 2 (30 days post release; Table S2; Figure 4a–c). Lastly, at water temperatures between 21 and 25°C, mean survival probability was 0.66 for dataset 1 and 0.72 for dataset 2 (1 day post release), 0.62 for datasets 1 and 2 (10 days post release) and 0.43 for datasets 1 and 2 (30 days post release; Table S2; Figure 4a–c).

3.4 | Survival to spawning and kelt survival

Although the number of censored individuals was higher for the control group than the angled group, 59% of the control fish and 70% of the caught and released fish, of known fate, survived to or past November 30th of the year they entered the river when the control group included the cotton glove handled fish (dataset 1). When the control group excluded the cotton glove-handled fish (dataset 2), 67% of the control fish and 70% of the caught and released fish, of known fate, survived greater to or past November 30th of the year they entered the river. In addition, 31 Atlantic salmon (dataset 1) and 28 Atlantic salmon (dataset 2), overwintered and migrated downstream to sea as kelt [(13% (data set 1), 19% (dataset 2) of the control

fish and 10% (dataset 1), 9% (dataset 2) of the caught-and-released fish]. Interestingly, one salmon (fork length = 50 cm) from the control group that was internally tagged on 11 July 2020, during its upstream spawning migration through the counting fence, was recaptured by commercial fishers in western Greenland (66.793612°N, 53.480960°W) on 5 September 2021, after it spawned and migrated past the counting fence as a kelt in early spring.

4 | DISCUSSION

After accounting for natural mortality and tagging effects, survival of caught and released salmon was 100% after 50 days and between 91% and 99% after 150 days, depending on whether the cotton glove-handled fish were included (Dataset 1) or excluded (Dataset 2). The type of angling and conditions at Western Arm Brook; fly-fishing only, with a barbless single hook, carried out with grilse salmon (1 sea winter – mean size of fish $\pm$ SD was 54.4 cm $\pm$ 3.2 cm) and at a range of water temperature of 11–22°C, are consistent with typical angling conditions in NL. Thus, our results are applicable to most angled Atlantic salmon in NL, and likely much of the species range. Our results agree with several previous experiments that suggest high survival following catch and release at cool to moderate water temperatures (<18°C) and when best practices are followed (Booth et al., 1995; Dempson et al., 2002; Lennox et al., 2017; Tufts et al., 1991; Van Leeuwen et al., 2020; Wilkie et al., 1996).

Van Leeuwen et al. (2020), modeled catch-and-release survival across previous studies, and for an equivalent water temperature and gear type used here, predicted survival to be between 0.91 and 0.96, very similar to the estimated mean relative survival from this

study. The congruence between this study and Van Leeuwen et al. (2020), suggests that a modelling framework based on the data from this study can be used by resource managers for predicting catch-and-release survival in recreational Atlantic salmon fisheries in NL and elsewhere assuming similar conditions and gear types are used.

Of the 18 published studies that used anadromous Atlantic salmon to evaluate aspects of catch and release, three were conducted in NL rivers (Van Leeuwen et al., 2020). For angled and control fish (trapped at the counting fence facility) held in large cages in Conne River for up to 40 days, the overall survival probability was 0.92 at water temperatures ranging from 9.5 to 22.1°C and 0.88 among angled salmon in water temperatures $\geq 17.9^\circ\text{C}$ (Dempson et al., 2002). For staged angling events on Atlantic salmon implanted with heart rate tags on Noel Paul's Brook, survival probability was 1.00 at $16.5 \pm 1^\circ\text{C}$ and 0.20 at $20 \pm 2^\circ\text{C}$ (Anderson et al., 1998). Lastly, for Atlantic salmon that were trapped at a counting fence facility, subjected to an exhaustive chase protocol, equipped with an accelerometer and radio tag and released in Campbellton River, survival probability was between 0.86 and 0.91 at water temperatures ranging from 17.6 to 20.2 °C (Lennox et al., 2019). However, salmon in these studies were held in somewhat controlled conditions (i.e., tanks and cages) or angling was only simulated, which led to angler concerns that results were not representative of actual catch-and-release events experienced by salmon on NL rivers. However, the results of this study, which addressed these methodological concerns, are mostly congruent with earlier studies by Dempson et al. (2002), Anderson et al. (1998), and Lennox et al. (2019). This reduces the uncertainty around survival estimates of those earlier studies and reinforces their value for developing a modeling framework for catch and release.

The results of this study and those that evaluated shorter-term post-release survival, suggest post-release survival is high in the first few days (i.e., few fish dying from injuries in the first 1–10 days after release). However, few studies have examined post-release survival to the spawning period and beyond (although see Gargan et al., 2015; Havn et al., 2015; Lennox et al., 2015; Thorstad et al., 2007, for studies evaluating post-release survival to spawning). Our study showed that survival rates of both angled and control fish declined in early winter, presumably due to spawning-related mortality. However, survival rates of angled and control fish appeared to diverge at around 150 days, with higher survival of control fish, independent of whether the control group included or excluded the cotton glove-handled fish. These differences indicate the need to examine survival for longer periods after release, although this divergence was not enough to drive a significant difference in overall survival between control and angled fish. Given that the mean duration of an angling event was just over 4 min, a potential divergence in survival over 150 days post-release is surprising. If catch-and-release injuries drove mortality of these salmon, a reasonable expectation would be divergent survival in the short-term (e.g., 1–30 days), with survival synchronising over time as injured fish die and remaining individuals recover. However, the divergence in survival rate after 150 days may be spurious and driven by declining sample sizes at

longer post-release periods, especially given that survival probabilities of control and angled fish appeared to converge at 10- and 30-days post-release, after accounting for water temperature. From 50- to 150-days post-release, the sample size of angled fish declined from 82 to 45 fish, and at 300 days only 11 angled salmon and 20 control salmon remained in dataset 1 and 19 remained in dataset 2.

A determining factor in survival for caught and released Atlantic salmon is the water temperature at the time of capture (Lennox et al., 2017; Van Leeuwen et al., 2020). However, a possible mitigating factor for population-level impacts of catch-and-release angling at higher temperatures is declining catchability (Van Leeuwen et al., 2021). While the catchability of Atlantic salmon did decline at warm water temperatures, many salmon can still be caught in the 18 to 23°C range. Therefore, although population-level impacts of catch-and-release angling at higher water temperatures may be somewhat mitigated by declining catchability, impacts can potentially increase as the water warms. The mean survival probability of angled fish in our study was 0.97 at 10–18°C, 0.89 at 18°C, 0.78 at 20°C and 0.58 at 21–25°C (1–30 days post-release). This decrease in catch-and-release survival at warmer water temperatures occurs because warm water temperature and lower dissolved oxygen, combined with exhaustive exercise during the capture process, can impede the fish's aerobic and anaerobic recovery (Arlinghaus et al., 2007; Breau, 2013; Wilkie et al., 1996). Therefore, given that mortality risk of catch and release increased at 18°C, and accelerated quickly above 20°C, management actions should increase as water temperatures warm, especially if post-release mortality is an issue in a fishery.

While radio telemetry is used widely to study aquatic species and shown to not alter survival (Hubbard et al., 2021; Jepson et al., 2015), control fish used in this study were subjected to the stress of tagging procedures (e.g., increased handling, anesthetic or confinement) that they would not normally experience. To ensure that survival was not reduced by internally implanted radio transmitter tags (anesthetic and surgery), a less-invasive external radio transmitter tagging procedure was used for comparison. Survival did not differ significantly between the two techniques for both control and angled groups, and the internal tags provided much longer battery life (~2 years, compared to ~6 months for external tags) and stronger signal strengths during walking telemetry and helicopter monitoring flights. Survival, growth, and body condition of lake trout (*Salvelinus namaycush*) did not differ between surgically implanted transmitter-tagged fish and untagged individuals over a 12-year period (Hubbard et al., 2021). Therefore, future catch-and-release studies that use similar methods should not hesitate to use internal tagging procedures to collect similar long-term data. Additionally, no special care was taken to utilise “perfect” catch-and-release procedures, instead anglers (with a range of experience) released fish as they had been doing for years on personal fishing outings. The realism of angling events combined with short procedure times, especially for externally tagged fish (4.4 min. from hooking to release, including tagging), should provide confidence that our results are representative of the recreational fishery in NL and elsewhere, where similar restrictions and environmental conditions occur. Ultimately, the level



of handling and air exposure actually taking place in the broader fishery is unknown, but if most anglers practice reasonable catch-and-release techniques under a similar management regime in NL of decreased fishing opportunities when water temperatures are above 20°C, population-level mortality rates will likely be low.

Although our study was not designed to test specific handling procedures, the development of sores on body areas in contact with cotton gloves during fish handling (i.e., caudal peduncle) was observed in year 1 that were not observed in years 2 and 3 of the study when fish were handled with wetted bare hands only during procedures. Handling salmon, especially while using cotton gloves, and perhaps all gloves during catch and release may increase the risk to the salmon due to the removal of skin mucus that acts as a physical and chemical barrier to pathogens. The removal of the skin mucus and resulting sores are not immediately apparent to anglers, but rather, develop days to weeks later as a result of infection. Ideally, the fish should not be touched by the angler's hands during release.

Physical injury by hooking can be significant in some fisheries (Muoneke & Childress, 1994; Warner & Johnson, 1978). However, consistent with previous studies (Muoneke & Childress, 1994; Warner & Johnson, 1978), the use of barbless single hook artificial flies in our study resulted in 22% of angled fish not requiring hook removal (i.e., the hook "fell out"), 92% of hooking locations considered non-critical (e.g., lip and jaw) and 8% sometimes considered critical (i.e., foul hooked, eyes, gills and tongue) (Muoneke & Childress, 1994). When a salmon was badly injured by the hook, the injury was often immediately apparent to the angler. Therefore, in situations when there is an obvious injury, we recommend that anglers consider retention if possible.

In addition to evaluating long-term survival (1–300 days post-release) of Atlantic salmon following catch and release, differences in mortalities prior to or shortly after the assumed spawning period were also evaluated. Further, differences in survival among salmon that overwintered in fresh water and then migrated downstream past the counting fence to sea (i.e., kelt survival) were also compared. Because 96% of returning adult salmon in Western Arm Brook are 1 sea winter maiden spawners, the number of individuals that survived to spawn time is arguable of greater importance to management and reproduction than the 300-day duration or kelt survival because (1) very few salmon survive overwintering and (2) an even smaller percentage will return from the sea to spawn a second time (Rideout & Tomkiewicz, 2011). Thus, we were encouraged to find that 70% of caught-and-released fish with known fates survived beyond the spawning period, compared to only 59%–67% of control fish (depending on whether cotton glove handled fish were included or excluded). This finding suggests catch-and-release angling did not prevent fish from surviving to spawn.

Even though our study found high survival of adult salmon to the spawning time following catch and release, we cannot rule out possible sub-lethal effects of catch and release on reproductive success. For example, based on the genetic sampling of returning adult Atlantic salmon on the Escomins River, Quebec, Canada, and assigned parentage of offspring, water temperature and air exposure time negatively

affected reproductive success of caught and released salmon (Richard et al., 2013). Additionally, Atlantic salmon collected near the end of their spawning migration and exposed to disturbed treatments of simulated catch and release (exercise and 120s air exposure) had higher infestation rates of the fungus *Saprolegnia* spp. over their body, and males had an increase in the maximum duration of sperm motility, whereas females spawned at the usual time but with fewer eggs (Papatheodoulou et al., 2021). However, in a laboratory study, which also used simulated catch and release, egg survival did not differ between salmon that were angled and non-angled (Booth et al., 1995). Whatever the case, further studies of the sub-lethal effects of catch and release on offspring survival are warranted.

Resource managers are tasked with determining the tolerable level of catch-and-release mortality for a fishery relative to desired social and economic benefits derived from catch-and-release angling. Based on our results, when water temperatures are cool to moderate, and fish are handled properly, survival following catch and release is high. However, resource managers must still consider environmental conditions and the level of angler effort, catch rates, combined mortality of retention and catch-and-release angling and the conservation status of the salmon population when determining when and where catch-and-release angling is appropriate. Additionally, when considering the risk of catch and release to a salmon population, a resource manager must also consider the likely effect of the predicted mortality (effort $\times$ catch per unit effort $\times$ mortality rate = salmon killed by catch and release) on overall salmon abundance. In this study, for example, most anglers (84%) only landed 1 fish per day, so only ~4% of the total population was landed in a season. The low percentage of the total population landed was presumably due to low angling effort (~1100 h total). Although Western Arm Brook is closed to recreational fishing, if anglers released fish at the provincial average (~52% release rate), at water temperatures and angling effort consistent with our study (15.8°C $\pm$ 3.8°C and ~1100 hrs.) and assuming a mean abundance of 924 salmon (mean salmon abundance of Western Arm Brook from 1971 to 2020), only 1–4 salmon mortalities would be attributed to catch and release. Therefore, an overall mortality rate of 0.4% is not likely to limit populations unless they are very small or significantly below their conservation limit. However, on popular rivers, the proportion of the population caught and released by anglers is likely much higher. While undoubtedly a crude approximation, our example highlights the relatively low population-level impact of catch and release at low to moderate levels of angler effort. This is consistent with estimates of 0.3%–2.6% of salmon populations that died from catch and release for rivers across Newfoundland in 2016 (Van Leeuwen et al., 2020). While the actual numbers of fish lost in the fishery are unknown, unprecedented warm water temperatures (>20°C) early in the season (middle of June to end of July in NL), when most angling activity and returning salmon are at their highest numbers, will likely determine population-level impacts of catch and release on NL salmon populations (Van Leeuwen, 2020).

Although the results of our study are well supported by existing literature, there are some caveats. Survival estimates in some cases were slightly higher for a point in time for angled fish than for the control group. One possibility for this occurring is because water temperature at the time of capture $\pm$ SD for the control group ($16.8^{\circ}\text{C} \pm 2.2^{\circ}\text{C}$) was slightly higher than for angled fish ($14.4^{\circ}\text{C} \pm 4.8^{\circ}\text{C}$), in addition to low sample sizes at warmer water temperatures. Secondly, although the fate of individual fish could be confidently determined during our study, "mortality events" could have been caused by shed tags, despite a 100% tag retention of recaptured fish. Lastly, although our results are presented with and without the cotton glove-handled fish for the control group to ensure transparency, the true extent of this effect was impossible to evaluate because all fish subjected to the cotton gloves may not have developed marks and sores. In addition, any such comparisons between the survival of fish handled with and without cotton gloves were also confounded by year (i.e., only control fish from the externally tagged group from year 1 were handled with cotton gloves).

Despite these potential caveats, our results demonstrated that catch and release can be an effective method of providing angling opportunities while minimising impacts on Atlantic salmon abundance. Therefore, we found no evidence that catch and release, as typically practiced in NL, would cause unacceptably high mortality in Atlantic salmon populations. However, poor catch-and-release practices and allowing catch and release at high water temperatures are substantial risk factors. Yet, both of these risk factors can be mitigated through angler training and prohibition of catch and release when water temperatures are high.

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CONFLICT OF INTEREST

The authors declare no conflict of interest for this article.

DATA AVAILABILITY STATEMENT

Data will be made available upon request.

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