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

Donald Keefe[a*], Mark Young[a], Travis E. Van Leeuwen[b], Blair Adams[a]

[a]Department of Fisheries, Forestry and Agriculture, 192 Wheeler's Road, Corner Brook, Newfoundland, Canada, A2H 7S1

[b]Fisheries and Oceans Canada, 80 East White Hills Rd., St. John's, Newfoundland, Canada, A1C 5X1

November 22, 2021

(Submitted for publication in the Journal of Fisheries Management and Ecology)

Abstract

In recent decades, hook and release has become the dominant form of angling for Atlantic salmon in North America. However, hook and release fishing remains controversial in some regions. This opposition is driven by differences in resource use goals (e.g. consumption vs. recreation), ethical perspectives, and skepticism of post hook and release survival rates in the published literature. Skepticism of the supporting hook and release science among some anglers is linked to low sample sizes and potential confounding effects of release techniques, gear types, environmental conditions, and geographic variation. Most hook and release studies also cover a relatively short temporal window, and the long-term effects of hook and release are often not evaluated. To evaluate the scientific basis for hook and release as a management tool, a comprehensive three-year study was conducted with the largest sample size of any Atlantic salmon hook and release study. The four main objectives were, 1) compare long-term survival (300 days) between angled Atlantic salmon, that were radio tagged and released (n = 119) to a control group that were trapped at a salmon counting fence site, radio tagged and released (n = 164), 2) provide fishery specific survival rates for hooked and released Atlantic salmon during the study and across water temperatures, 3) determine if mortalities associated with hook and release occur before or after the spawning period and 4) compare the number of angled and control fish that overwintered and migrated downstream through a counting fence to sea (i.e. kelt survival). Overall, there was no significant difference in long-term survival between the angled group and the control group. Mean survival probability of angled salmon relative to the control group was between 0.94 and 0.98 over the course of the study (1 - 300 days). At cool to moderate water temperatures (10 to 18 °C) mean survival of angled salmon was predicted to be 0.98 (1 day post release), 0.97 (10 days post release) and 0.96 (30 days post release). Although the number of salmon hooked and released above 21 °C was low (n = 12) there was a slight reduction in catchability at warm water temperatures (21 to 25 °C) and mean survival probability above 21 °C was 0.69 (1 day post release), 0.62 (10 days post release) and 0.43 (30 days post release). Lastly, there was no difference in the number of fish that survived to the spawning period. However, the mean percentage of fish that overwintered and migrated downstream through a counting fence to sea (i.e. kelt survival) was 10 % for those that were hooked and released and 16 % for the control group. Results of this study suggest that mortality of hooked and released Atlantic salmon can be delayed but remains low at cool to moderate water temperatures.

Keywords: angling, catch and release, post-release survival, Salmo salar

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 (Soto et al. 2018; Lehnert et al. 2019; Thorstad et al. 2021; Dadswell et al. 2021). Newfoundland and Labrador (NL), Canada is home to more than 75 % of the wild Atlantic salmon in North America (ICES 2019) however, declines have occurred despite a commercial fishing closure since the early 1990s (Dempson et al. 2004) and substantial reductions in retention limits for the recreational fishery. Management measures in the NL recreational fishery to conserve Atlantic salmon, include the mandatory release of all large salmon (≥ 63 cm in fork length (1984); Randall 1990; O'Connell et al. 1992), gradual changes and reductions in daily retention (from 2 fish per day (1984) to 2 fish per season (2021) and hook and release limits (from no limit (1985) to 3 per day (2018); O'Connell et al. 1992; DFO 2019), closures of rivers or restricted angling times (e.g. morning fishing only (2019)) during warm water temperatures (varied between environmental thresholds of > 22°C (1988), >18 °C (2018) and >20 °C (2019)) and gear restrictions (e.g. fly-fishing only, mandatory use of non-weighted artificial flies, single barbless hook only (1999)).

While retention harvests still occur 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 hook and release (3 fish per day) fishing opportunities appears to be contributing to the increased hook and release angling in NL. This growing disparity in angling opportunity has been contentious and a point of public debate among retention and hook and release anglers. Among resource managers, hook and release is often used as a tool (Brownscombe et al. 2017), even when stocks are low (Tufts et al. 1991; Booth et al. 1995; Wilkie et al. 1996; Lennox et al. 2017), as it permits for a recreational fishery and associated cultural and economic benefits (tackle shops, lodge owners, license fees, guiding fees) to continue. Resource managers generally assume high survival and fitness of fish following release. Nevertheless, many anglers have ethical reservations and remain unconvinced that survival is high post release. These concerns are driven by differences in resource use goals (e.g. consumption vs. recreation), ethical perspectives, and skepticism of results from previous hook 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), likely driven by low sample sizes of previous studies, and potential confounding effects of release techniques, gear types, environmental conditions, and geographic variation. In a recent study by Van Leeuwen et al. (2020), the mean sample size from the 18 published studies on the survival of anadromous Atlantic salmon following hook and release was 40 and most hook and release studies covered a variable temporal window from 12 hrs (Brobbel et al. 1996) to 4 months (Thorstad et al 2003; Gargan et al. 2015). Although most studies suggest high survival of Atlantic salmon following hook and release (Lennox et al. 2017; Van Leeuwen et al. 2020), most studies also have debated weaknesses often raised by some anglers in NL. This inconsistency undermines the broad acceptance of hook and release in NL. Specifically, there are concerns related to the science hook and release is based because experimental procedures used to assess the effectiveness of hook and release (surgically inserted heart rate, acoustic or radio tags) may themselves have synergistic effects under certain environmental conditions (Wilkie et al. 1996; Anderson et al. 1998; Van Leeuwen et al. 2020). Furthermore, the ability to evaluate the effectiveness of hook and release management programs is difficult because previous studies often differ in gear types (lures vs. artificial flies, treble vs. single hooks, barbed vs. barbless hooks), techniques (simulated capture vs. actual capture, internal tags vs. external tags vs. holding fish in cages), geographic and physical location (laboratory or field), water conditions, duration over which hook and release survival is evaluated, suffer from low sample sizes at high water temperatures (only 4 studies with a mean = 16 for hooked and released fish >18°C) or lack a control group (7 / 18 published studies) needed to disentangle natural or procedural mortality from hook and release induced mortality (see Van Leeuwen et al. 2020 for breakdown). There is consensus among the angling community (both hook and release and retention anglers) and resource managers that survival following hook and release is dependent on angler practices (e.g. gear type, bait type), experience (e.g. handling, air exposure; Cooke and Wilde 2007; Lennox et al. 2017), and water temperature at time of capture (Wilkie et al. 1996; Havn et al. 2015; Lennox et al. 2017; Van Leeuwen et al. 2020, 2021). Although there is a broad belief among anglers that catch rates decline as water temperature increases. The literature on the subject is sparse, 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), there remains a clear gap in the understanding of the effects of hook and release angling on Atlantic salmon survival, especially over the long-term. Only a study of the size and rigor as presented here can address these gaps. Further, many of these variables that affect hook and release survival are often unique to a specific fishery. Thus, regional or jurisdiction specific hook 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 on-board anglers to fishery management strategies can undermine the fishery management process and substantially impede progress towards conservation objectives (Cote et al. 2021).

This study uses the largest hook and release Atlantic salmon radio telemetry deployment to date (n = 283) to achieve four objectives, 1) compare long-term survival (300 days) between Atlantic salmon that were angled, radio tagged and released (n = 119) to a control group of

Atlantic salmon that were trapped at a salmon counting fence site, radio tagged and released (n = 164), 2) provide fishery specific survival rates for hooked and released Atlantic salmon during the study and across water temperatures, 3) determine if mortalities associated with hook and release occur before or after the spawning period and 4) compare the number of angled and control fish that overwintered and migrated downstream through a counting fence to sea (i.e. kelt survival).

Methods

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 km^2. The headwaters contain 83 water bodies with the largest being Western Brook Pond (Figure 1).

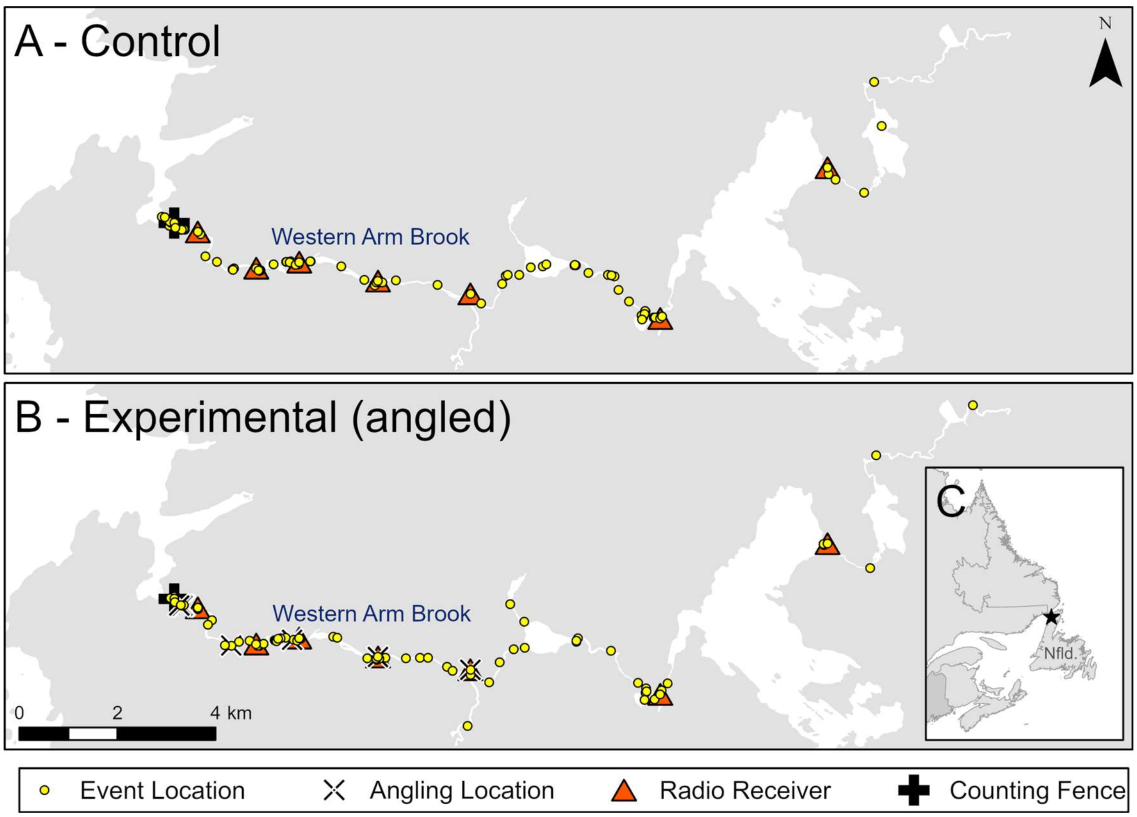

Figure 1. Event locations (i.e. last known location) of Atlantic salmon (yellow circles) that were counted and/or trapped at a salmon counting fence facility, radio-tagged and released (Control; panel A) and Atlantic salmon that were angled, radio-tagged and released (Experimental (angled); panel B), in addition to angling locations (crosshairs), radio receiver locations (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).

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

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 at either the counting fence or upstream of the counting fence, for those fish caught by study participants angling on the river. All research activities were completed under the guidelines of the Canadian Council on Animal Care and DFO permit numbers NL-4780-18, NL-5306-19 and NL-5934-20 for years 1 to 3 of the study. Counting fence fish (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 received internal radio tags and 87 received 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 received internal radio tags while 62 received external radio tags. Anglers were instructed to use typical angling behavior when landing fish. In all cases fish were 'played' until they could be dipped by an observer near shore. Detailed records were kept for every trapping and angling event including; water and air temperatures, 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 x 69mm; 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 x 15 mm, 1.5 g in air, 5 s burst rate with 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 a 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 that received a surgically implanted radio transmitter were also dorsally tagged with a 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 anesthetic. Fish were kept in the anesthetic for approximately 4 min (Figure 2F) prior to surgery then transferred to a holding trough designed with a battery powered shower that kept the gills and body of the fish constantly irrigated. All surgical equipment was sanitized with 95 % ethanol solution. Fork length, scales and a genetic sample was taken from each fish prior to surgery. An incision 2 to 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. A surgical grooved director was used to meet a 16 gauge 3.81 cm needle which penetrated the body cavity into the opened coeleomic cavity. The antenna was then looped into the grooved director and fed outside of the body cavity by withdrawing the needle with the antenna partially inserted into its tip. This process positioned the radio tag parallel with the body wall and the antenna extending on the exterior toward the tail of the fish. 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 was presumed normal (see Figure 2F for breakdown of procedure and recovery durations).

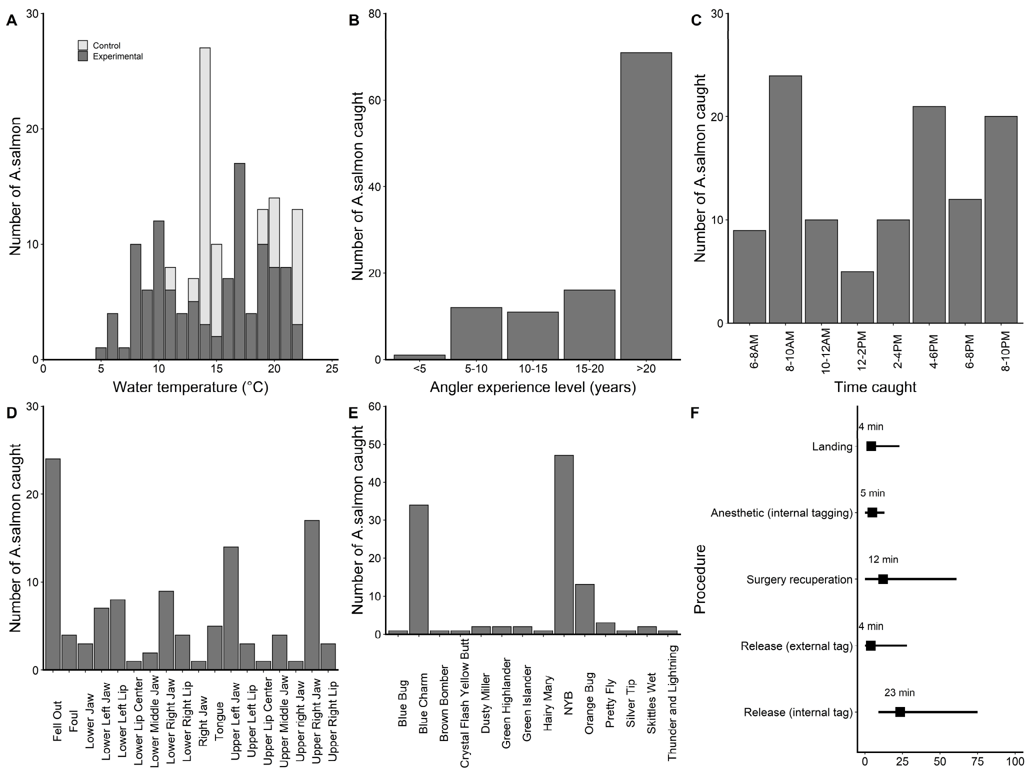

Figure 2. The number of Atlantic salmon that were either trapped at a salmon counting fence facility, radio tagged and released (control; light grey) or were angled, radio-tagged and released (experimental; dark grey) in relation to (A) water temperature, (B) angler experience, (C) time, (D) hooking location, (E) fly pattern at Western Arm Brook, Newfoundland and

Labrador, Canada. (F) is the minimum, mean and maximum durations of the various procedures used in the study. Release refers to the total time from hooking to release.

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 was 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 minutes (see Figure 2F for breakdown of procedure and recovery durations). In year one of our study externally tagged fish were handled with cotton gloves during the procedure. In years two and three, 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 3A & B).

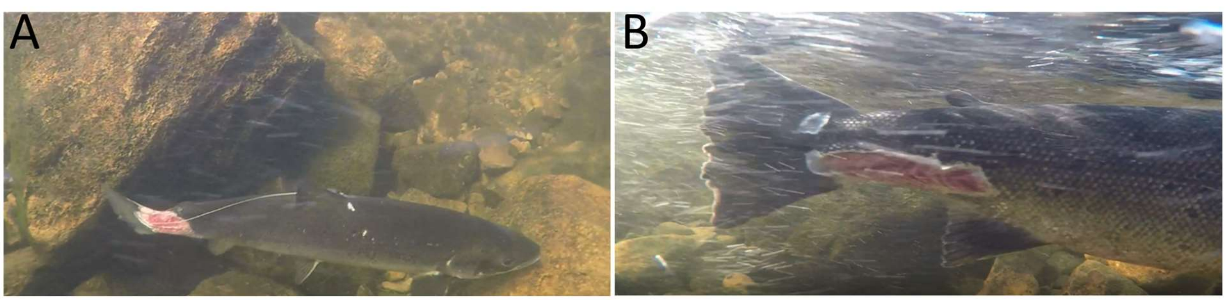

Figure 3. (A & B) Atlantic salmon that were part of the control treatment group from year 1 that received external radio tags and handled using cotton gloves at Western Arm Brook, Newfoundland and Labrador, Canada. Note: marks and sores presumed to be from the cotton gloves visible around the caudal peduncle

Seven remote radio telemetry fixed stations monitored the movements of tagged Atlantic salmon (Station 1 upstream from the counting fence to Station 7; Figure 1). Stations 1 through 6 were operational as of June 2018 with Station 7 added June 2019. 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. A waterproof sealed enclosure housed each receiver, batteries, and hardware on an elevated wooden construction platform. Yagi antennae pointed south to the opposite river bank (distance ranging from 50 to 100 m) at each location and was set at angles of less than 30 degrees, varying as per each sites unique tracking requirements. Additional to fixed station receiver data, telemetry data was collected by walking upstream and downstream from Station 1 using an SRX800-MD2 receiver and a folding 3-element Yagi antenna. Walking telemetry was also used, sporadically throughout the study, to identify and locate tags in the upper reaches of the watershed. Further, telemetry monitoring flights were conducted using a helicopter equipped with an SRX800-MD2 receiver, fixed 4-element Yagi antenna, gps antenna, and handheld tablet. Each telemetry signal received using helicopter monitoring flights automatically recorded latitude and longitude using the gps antennae attachment. All receiver data was downloaded using the tablet and SRX software. SRX receivers and software, Yagi antennae, gps antennae, and accompanying hardware were manufactured and supplied by Lotek Wireless Inc.

All salmon tagged at the counting fence or angled downstream from Station 1 were monitored using walking telemetry daily or until all fish had moved past Station 1. Telemetry data was recorded continuously at Station 1 through Station 6 and at Station 7 from June 2018 and June 2019, respectively, to June 2021. There were 49 monitoring flights performed over three years of the study. The flights were not uniformly scheduled and performed as weather, helicopter availability, and budget allowed. Data for each fish was sorted by tag number and an individual summary file for each fish created. Signals were then sorted for each telemetry record and those created by background noise, collision noise and erroneous records eliminated. This allowed determination of an initial and final detection date, position and time for each fish.

Environmental variables and angling specifics

In year one, 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 year two and three, aquameasure sensors (resolution ± 0.01°C) measured dissolved oxygen and water temperature every 5 and 10 minutes 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 (± 0.1°C) at the site of capture. In total, 1100 hours of angling (Figure 4A) was conducted by fly fishers (n = 14; experience range < 5 years to > 20 years; Figure 2B), using barbless, single hook artificial flies (Figure 2E) and who were instructed to practice typical hook and release behavior. All tagging and angling occurred during daylight hours (Figure 2C). Mean water temperature at time of capture for angled fish ± standard deviation (SD) was 14.4°C ± 4.8°C (min = 5.0°C, max = 22°C; Figure 2A), whereas mean water temperature at time of capture for control fish ± SD was 16.8°C ± 2.2°C (min = 11.0°C, max = 22.0°C; Figure 2A). Therefore, overall mean water temperature at time of capture ± SD was 15.8°C ± 3.8 °C (min.= 5.0°C, max. = 22.0°C). Mean size of fish for the study ± SD was 54.4 cm ± 3.2 cm (min = 45.0 cm, max = 74.0 cm).

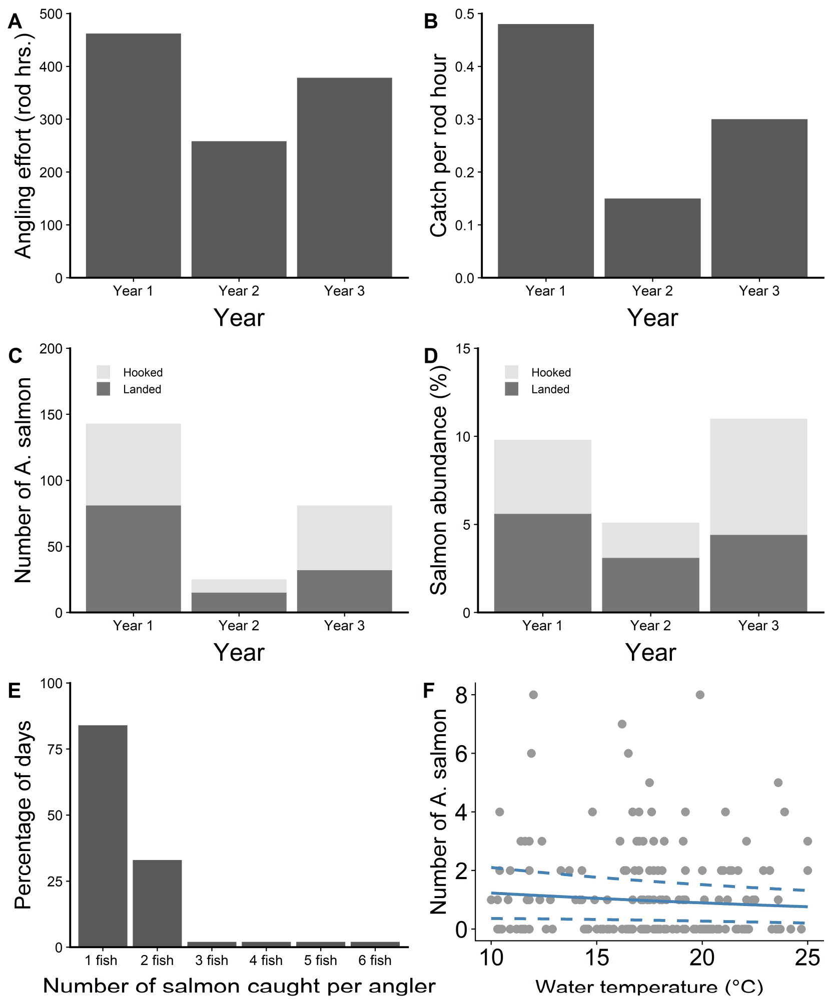

Figure 4. The amount of (A) angling effort, (B) Atlantic salmon catch per rod hour, (C) number of Atlantic salmon hooked and landed, (D) the percentage of Atlantic salmon hooked and landed in relation to total Atlantic salmon abundance, (E) the percentage of angling days that resulted in an angler landing 1 to 6 (maximum for the study) Atlantic salmon and (F) The relationship between the number of Atlantic salmon hooked and water temperature after correcting for angling effort, Atlantic salmon abundance and year, for years 1 – 3 of the hook and release study on Western Arm Brook, Newfoundland and Labrador, Canada.

Determination of 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 (Figures 1 & 5). Censoring occurred due to tag failure, maximum operational battery life exceeded, tag shedding, or other unknown causes and is common in long-term telemetry studies (Pollock et al. 1989). Data from these tagged fish up to the last known date confirmed alive was used in our survival analysis (Figures 1 & 5). The following three criteria were used to determine mortality: (1) we assumed fish repeatedly found in the same location had died (where possible, tags were located using walking telemetry and verified); (2) telemetry signals that did not change power signal on numerous approaches or deemed out of water due to signal strength; and (3) plotted signal strengths from fixed telemetry receiver stations that showed continuous repeated signal strength over prolonged periods (i.e. flat line). Further, when the 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 found 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 were used. 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 were coincidentally caught and tagged very early in the season at the start of the study. Dataset 2 excluded an additional 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 3A & B). It became apparent during year one that handling fish with cotton gloves may increase risk during the tagging procedure. Therefore, dataset 1 consisted of 152 control fish (70 received internal radio tags and 82 received external radio tags) and 111 angled fish (52 received internal radio tags and 59 received external radio tags) whereas dataset 2 consisted of 96 control fish (70 received internal radio tags and 26 received external radio tags) and 111 angled fish (52 received internal radio tags and 59 received external radio tags).

Determining 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 hook and release. The CPH model calculates the hazard ratio in relation to the instantaneous rate of an event occurrence (death of the fish) for each explanatory variable. Therefore, hazard ratio represents the difference in likelihood of mortality event occurrence between two groups. A Kaplan-Meier (KM) analysis using the R packages “survival” (Therneau 2015) and “survminer” (Kassambara 2021) and days to event (dead, censored, alive) was also used to determine survival rate estimates over the course of the study (1 to 300 days post-release, mean water temperature a time of capture ± SD of 15.8°C ± 3.8 °C) for angled and control fish from dataset 1 and dataset 2. Thus, the relative survival of hooked and released fish to the control, for a given time period since tagging and 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 (Tables 1 & 2; Figure 5) we assume the difference between the two to be 0 and assume the survival probability relative to the control is 1 (i.e. no difference). Days to event (i.e. mortality or censored) for individual fish was determined by calculating the number of days elapsed between the day of release and the day of last known fate using the criteria discussed above. Kaplan-Meier 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 (Pollock et al. 1989; Heupel and Simpfendorfer 2011; Hubbard et al. 2021).

Determining 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 generalized 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. Year was included as a random intercept because the number of fish hooked occurred across three years. Water temperature and daily number of salmon counted were best fit as linear terms. Angling effort was modelled with a spline fit (with $k = 3$).

A generalized 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 the angled and control Atlantic salmon at 1, 10 and 30 days post-release. Data included individuals of known fate (ie. dead or alive) based on the criteria above. Therefore, censored individuals (ie: individuals of unknown fate) were excluded from these analyses if they became censored prior to the time interval being assessed. This left 110 (52 internal radio tags, 58 external radio tags), 108 (52 internal radio tags, 56 external radio tags) and 103 (52 internal radio tags and 51 external radio tags) individuals for the hooked and release group at 1, 10 and 30 days post-release, and 152 (dataset 1; 70 internal radio tags and 82 external radio tags) / 96 (dataset 2; 69 internal radio tags and 27 external radio tags), 146 (dataset 1; 69 internal radio tags and 77 external radio tags) / 91 (dataset 2; 67 internal radio tags and 24 external radio tags), and 131 (67 internal radio tags and 64 external radio tags) / 80 (dataset 2; 64 internal radio tags and 16 external radio tags) individuals for the control group at 1, 10 and 30 days post-release. Therefore, the revised survival probability of hooked and released fish 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). In the event that the probability of survival for the angled fish was higher than that of the control for a given water temperature we assume the difference between the two to be 0 and assume the survival probability is equal to that determined for the hooked and released fish. This generally occurred at temperatures > 20°C as a result of increased error in the model as a result of low sample sizes or data gaps for the control group at these water temperatures (Figure 2A).

Determination of survival to spawning and kelt survival

Atlantic salmon in the recreational fishery are typically targeted during their upstream spawning migration in the spring and summer, and fish entering the rivers in a given year are likely to spawn in the fall of that year (Klemetsen et al. 2003). Some evidence of skip spawning or small non-reproductive salmon entering rivers (post-smolt) does exist in NL (Klemetsen et al. 2003; Rideout and Tomkiewicz 2011). However, this has not been reported previously for Western Arm Brook (Klemetsen et al. 2003; Rideout and Tomkiewicz 2011) and for the length of Atlantic salmon that bracketed those in our study. Spawning in Western Arm Brook generally occurs between mid-to-late October and mid-to-late November. Therefore, fish of known fate that survived greater than or equal to November 30th of the year they entered the river were presumed to be eligible to spawn. Kelt survival was determined by calculating the proportion of all tagged fish that migrated downstream through the counting fence.

Results

Hook and release considerations

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 (Figure 2C). Mean catch per rod hour for the study was 0.31 (min = 0.15, max = 0.48; Figure 4B) and on average 51% of salmon hooked were landed (Figure 4C). This represented on average 8.6% of the population being hooked and 4.4% of the population landed (Figure 4D). On average, fish took 4 min to land (min = < 1 min., max = 23 min.; Figure 2F) 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; Figure 2D; Muoneke & Childress 1994) and 8% sometimes considered critical (i.e.: foul hooked, tongue; Figure 2D; Muoneke & Childress 1994). The process of hooking, netting, de-hooking (if necessary), revival and release for an externally tagged salmon on average was 4.4 min. (min = < 1 min., max = 28 min; Figure 2F). Most anglers (84%) landed 1 fish per day (min = 1, max = 6; Figure 4E) despite no restriction.

Overall and relative survival for the study (i.e. mean water temperature ± SD *of* 15.8°C ± 3.8 °C*)*

Overall, there was no significant difference in long-term survival between Atlantic salmon that were hooked and released and the control group of Atlantic salmon that were trapped at the salmon counting fence site for dataset 1 (CPH, z = 0.22, p=0.83; Table 1; Figure 5A) or dataset 2 (CPH, z = 1.92, p=0.054; Table 2; Figure 5D). Additionally, there was no significant difference in survival between fish tagged with an internal or external radio tags (data set 1, CPH, z = -0.63, p=0.53, Table 1, Figure 5B; data set 2, CPH, z = 1.04, p=0.30; Table 2, Figure 5E) or among years of the study (data set 1, CPH, z = -1.44, p=0.15, Table 1, Figure 5C; data set 2, CPH, z = -0.21, p=0.83, Table 2, Figure 5F). Overall, KM estimates of survival between angled fish and control fish over the duration of the study (at day 300 post-release) differed at most by

9 % for dataset 1 (Table 1; Figure 5A) and 19 % for dataset 2 (Table 2; Figure 5D). Overall mean relative survival probability following hook and release, when compared to the control fish (1 to 300 days post-release) was 0.97 when using dataset 1 and 0.94 when using dataset 2 (Table 3).

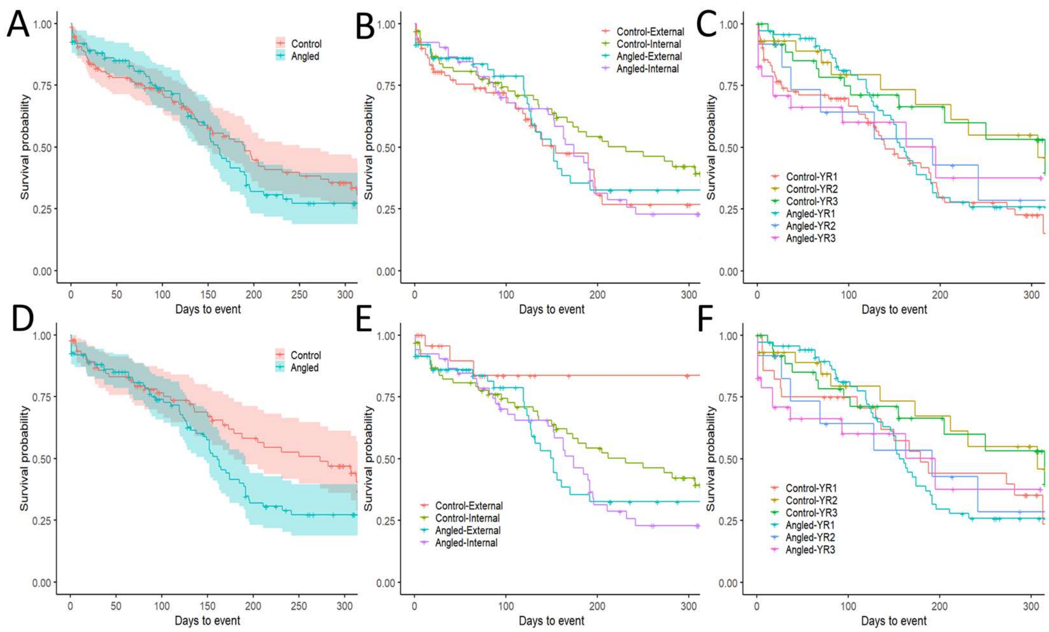

Figure 5. (A & D) Kaplan-Meier survival curves (mean ± 95% CI) for Atlantic salmon that were angled, radio-tagged and released (Angled) and for a control group of Atlantic salmon that were trapped at a salmon counting fence facility, radio-tagged and released (Control) at Western Arm Brook, Newfoundland and Labrador, Canada, (B & E) split by tag type and (C & F) split by year. Days to event for individual fish was 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. Panels A - C used data that excluded 22 fish that were either roughly handled during procedures (11 control fish and 2 angled fish), were recaptured during the study (6 controls and 1 angled fish) or of a different life stage not typically targeted in the recreational fishery (2 kelt). Panels D - F used data that excluded an additional 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. See Table 1 for survival estimates for Panels A - C and Table 2 for survival estimates for Panels D - F.

Table 1. Kaplan-Meier survival estimates (mean ± 95% CI) for Atlantic salmon that were caught, 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 2018 through 2020. Handling problem fish and recaptures removed refers to the exclusion of 22 fish that experienced procedural tagging and handling problems (11 control fish and 2 angled fish), were recaptured during the study (6 controls and 1 angled fish) or of a different life stage not typically targeted in the recreational fishery (2 kelt).Tables are presented as overall estimates for the study, split by tag type and by year. Day refers to days to event, the duration individuals were tracked, whereas N.risk and N.event refer to the sample size at a given duration of the study and the number of events that occurred up to that particular day duration of the study. Days to event for individual fish was determined by calculating the number of days elapsed between the day of release and the day of last known fate. Mean water temperature at time of capture (control fish and angled fish combined) for the study ± SD was 15.8°C ± 3.8 °C (min.= 5.0°C, max. = 22°C).

Handling problems and recaptures removed

				Survival probability		
Figure 5A	**Day**	**N.risk**	**N.event**	**Lower 95% CI**	**Mean**	**Upper 95% CI**
Overall						
Angled	1	111	8	0.88	0.93	0.98
Control	1	152	2	0.97	0.99	1.00
Angled	10	99	1	0.87	0.92	0.97
Control	10	129	12	0.86	0.91	0.95
Angled	30	90	4	0.82	0.88	0.94
Control	30	105	12	0.76	0.82	0.89
Angled	50	82	3	0.79	0.85	0.92
Control	50	98	5	0.72	0.78	0.85
Angled	150	43	23	0.48	0.57	0.69
Control	150	55	21	0.49	0.58	0.68
Angled	300	11	22	0.19	0.27	0.40
Control	300	20	18	0.27	0.36	0.47

				Survival probability		
Figure 5B	**Day**	**N.risk**	**N.event**	**Lower 95% CI**	**Mean**	**Upper 95% CI**
Split by tag type						
Angled/external tag	1	59	5	0.85	0.92	0.99
Control/external tag	1	82	0	1.00	1.00	1.00
Angled/internal tag	1	52	3	0.88	0.94	1.00
Control/internal tag	1	70	2	0.93	0.97	1.00
Angled/external tag	10	51	0	0.85	0.92	0.99
Control/external tag	10	67	8	0.84	0.90	0.97
Angled/internal tag	10	48	1	0.85	0.92	1.00
Control/internaltag	10	62	4	0.85	0.91	0.98
Angled/external tag	30	43	3	0.78	0.86	0.96
Control/external tag	30	50	7	0.72	0.81	0.90
Angled/internal tag	30	47	1	0.83	0.90	0.99
Control/internaltag	30	55	5	0.76	0.84	0.93
Angled/external tag	50	40	0	0.78	0.86	0.96
Control/external tag	50	45	3	0.66	0.76	0.86
Angled/internal tag	50	42	3	0.75	0.85	0.95
Control/internaltag	50	53	2	0.72	0.81	0.91
Angled/external tag	150	17	13	0.37	0.50	0.69
Control/external tag	150	18	11	0.38	0.51	0.67
Angled/internal tag	150	26	10	0.51	0.63	0.78
Control/internaltag	150	37	10	0.53	0.64	0.77
Angled/external tag	300	5	6	0.20	0.33	0.52
Control/external tag	300	3	7	0.15	0.27	0.47
Angled/internal tag	300	6	16	0.13	0.23	0.41
Control/internal tag	300	17	11	0.31	0.42	0.58

				Survival probability		
Figure 5C	**Day**	**N.risk**	**N.event**	**Lower 95% CI**	**Mean**	**Upper 95% CI**
Split by year						
Angled/YR1	1	70	2	0.93	0.97	1.00
Control/YR1	1	85	0	1.00	1.00	1.00
Angled/YR2	1	12	1	0.77	0.92	1.00
Control/YR2	1	29	2	0.84	0.93	1.00
Angled/YR3	1	29	5	0.70	0.83	0.98
Control/YR3	1	38	0	1.00	1.00	1.00
Angled/YR1	10	68	0	0.93	0.97	1.00
Control/YR1	10	68	12	0.78	0.86	0.94
Angled/YR2	10	11	0	0.77	0.92	1.00
Control/YR2	10	25	0	0.84	0.93	1.00
Angled/YR3	10	20	1	0.65	0.79	0.96
Control/YR3	10	36	0	1.00	1.00	1.00
Angled/YR1	30	65	1	0.91	0.96	1.00
Control/YR1	30	54	9	0.65	0.74	0.84
Angled/YR2	30	9	1	0.63	0.83	1.00
Control/YR2	30	23	0	0.84	0.93	1.00
Angled/YR3	30	16	2	0.56	0.71	0.90
Control/YR3	30	28	3	0.83	0.92	1.00
Angled/YR1	50	62	1	0.89	0.94	1.00
Control/YR1	50	51	2	0.62	0.71	0.82
Angled/YR2	50	8	1	0.52	0.73	1.00
Control/YR2	50	21	1	0.78	0.89	1.00
Angled/YR3	50	12	1	0.50	0.66	0.87
Control/YR3	50	26	2	0.74	0.85	0.98
Angled/YR1	150	32	20	0.48	0.59	0.73
Control/YR1	150	27	14	0.37	0.47	0.61
Angled/YR2	150	5	2	0.30	0.54	0.94
Control/YR2	150	12	3	0.57	0.73	0.95
Angled/YR3	150	6	1	0.43	0.60	0.84
Control/YR3	150	16	4	0.57	0.71	0.89
Angled/YR1	300	8	18	0.16	0.26	0.41
Control/YR1	300	6	12	0.14	0.23	0.38
Angled/YR2	300	1	2	0.10	0.29	0.84
Control/YR2	300	6	3	0.36	0.55	0.84
Angled/YR3	300	2	2	0.18	0.38	0.80
Control/YR3	300	8	3	0.35	0.53	0.80

Table 2. Kaplan-Meier survival estimates (mean ± 95% CI) for Atlantic salmon that were caught, 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 2018 through 2020. Handling problem fish, recaptures and YR 1 external/controls removed refers to the exclusion of 63 fish that experienced procedural tagging and handling problems (11 control fish and 2 angled fish), were recaptured during the study (6 controls and 1 angled fish), of a different life stage not typically targeted in the recreational fishery (2 kelt) or made up the entire control treatment group from year 1 that received external tags (41 fish), due to these individuals being the only group handled with cotton gloves. Tables are presented as overall estimates for the study, split by tag type and by year. Day refers to days to event, the duration individuals were tracked, whereas N.risk and N.event refer to the sample size at a given duration of the study and the number of events that occurred up to that particular day duration of the study. Days to event for individual fish was determined by calculating the number of days elapsed between the day of release and the day of last known fate. Mean water temperature at time of capture (control fish and angled fish combined) for the study ± SD was 15.8°C ± 3.8 °C (min.= 5.0°C, max. = 22°C).

Handling problems, recaptures and YR1 external/controls removed

				Survival probability		
Figure 5D	**Day**	**N.risk**	**N.event**	**Lower 95% CI**	**Mean**	**Upper 95% CI**
Overall						
Angled	1	111	8	0.88	0.93	0.98
Control	1	96	2	0.95	0.98	1.00
Angled	10	99	1	0.87	0.92	0.97
Control	10	85	4	0.89	0.94	0.99
Angled	30	90	4	0.82	0.88	0.94
Control	30	72	6	0.80	0.87	0.94
Angled	50	82	3	0.79	0.85	0.92
Control	50	68	3	0.76	0.83	0.91
Angled	150	43	23	0.48	0.58	0.69
Control	150	42	11	0.57	0.67	0.79
Angled	300	11	22	0.19	0.28	0.40
Control	300	19	11	0.36	0.47	0.61

				Survival probability		
Figure 5E	**Day**	**N.risk**	**N.event**	**Lower 95% CI**	**Mean**	**Upper 95% CI**
Split by tag type						
Angled/external tag	1	59	5	0.85	0.92	0.99
Control/external tag	1	26	0	1.00	1.00	1.00
Angled/internal tag	1	52	3	0.88	0.94	1.00
Control/internaltag	1	52	3	0.93	0.97	1.00
Angled/external tag	10	51	0	0.85	0.92	0.99
Control/external tag	10	23	0	1.00	1.00	1.00
Angled/internal tag	10	48	1	0.85	0.92	1.00
Control/internaltag	10	62	4	0.85	0.91	0.98
Angled/external tag	30	43	3	0.78	0.86	0.96
Control/external tag	30	17	1	0.88	0.96	1.00
Angled/internal tag	30	47	1	0.83	0.90	0.99
Control/internaltag	30	55	5	0.76	0.84	0.93
Angled/external tag	50	40	0	0.78	0.86	0.96
Control/external tag	50	15	1	0.77	0.90	1.00
Angled/internal tag	50	42	3	0.75	0.85	0.95
Control/internal tag	50	53	2	0.72	0.81	0.91
Angled/external tag	150	17	13	0.37	0.50	0.69
Control/external tag	150	5	1	0.68	0.84	1.00
Angled/internal tag	150	26	10	0.51	0.63	0.79
Control/internaltag	150	37	10	0.53	0.64	0.77
Angled/external tag	300	5	6	0.20	0.33	0.52
Control/external tag	300	2	0	0.68	0.84	1.00
Angled/internal tag	300	6	16	0.13	0.23	0.41
Control/internal tag	300	17	11	0.31	0.42	0.58

				Survival probability		
Figure 5F	**Day**	**N.risk**	**N.event**	**Lower 95% CI**	**Mean**	**Upper 95% CI**
Split by year						
Angled/YR1	1	70	2	0.93	0.97	1.00
Control/YR1	1	29	0	1.00	1.00	1.00
Angled/YR2	1	12	1	0.77	0.92	1.00
Control/YR2	1	29	2	0.84	0.93	1.00
Angled/YR3	1	29	5	0.70	0.83	0.98
Control/YR3	1	38	0	1.00	1.00	1.00
Angled/YR1	10	68	0	0.93	0.97	1.00
Control/YR1	10	24	4	0.74	0.86	1.00
Angled/YR2	10	11	0	0.77	0.92	1.00
Control/YR2	10	25	0	0.84	0.93	1.00
Angled/YR3	10	20	1	0.65	0.79	0.96
Control/YR3	10	36	0	1.00	1.00	1.00
Angled/YR1	30	65	1	0.91	0.96	1.00
Control/YR1	30	21	3	0.61	0.75	0.93
Angled/YR2	30	9	1	0.63	0.83	1.00
Control/YR2	30	23	0	0.84	0.93	1.00
Angled/YR3	30	16	2	0.56	0.71	0.90
Control/YR3	30	28	3	0.83	0.92	1.00
Angled/YR1	50	62	1	0.89	0.94	1.00
Control/YR1	50	21	0	0.61	0.75	0.93
Angled/YR2	50	8	1	0.51	0.73	1.00
Control/YR2	50	21	1	0.78	0.89	1.00
Angled/YR3	50	12	1	0.50	0.66	0.87
Control/YR3	50	26	2	0.74	0.85	0.98
Angled/YR1	150	32	20	0.48	0.59	0.73
Control/YR1	150	14	4	0.41	0.57	0.81
Angled/YR2	150	5	2	0.30	0.54	0.94
Control/YR2	150	12	3	0.57	0.73	0.95
Angled/YR3	150	6	1	0.43	0.60	0.84
Control/YR3	150	16	4	0.57	0.71	0.89
Angled/YR1	300	8	18	0.16	0.26	0.41
Control/YR1	300	5	5	0.20	0.35	0.61
Angled/YR2	300	1	2	0.10	0.29	0.84
Control/YR2	300	6	3	0.36	0.55	0.84
Angled/YR3	300	2	2	0.18	0.38	0.80
Control/YR3	300	8	3	0.35	0.53	0.80

Table 3. Kaplan-Meier survival estimates (mean ± 95% CI) for Atlantic salmon that were caught, radio-tagged and released (Angled) relative to 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. N.risk refers to the sample size at a given duration of the study. Days to event for individual fish was determined by calculating the number of days elapsed between the day of release and the day of last known fate. Dataset 1 used data that excluded 22 fish that were either roughly handled during procedures (11 control fish and 2 angled fish), were recaptured during the study (6 controls and 1 angled fish) or of a different life stage not typically targeted in the recreational fishery (2 kelt). Dataset 2 used data that excluded and additional 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. Mean water temperature at time of capture (control fish and angled fish combined) for the study ± SD was 15.8°C ± 3.8 °C (min.= 5.0°C, max. = 22°C).

Survival probability relative to control group							
		Dataset 1			Dataset 2		
Day	N.risk	Lower 95% CI	Mean	Upper 95% CI	Lower 95% CI	Mean	Upper 95% CI
1	111	0.91	0.94	0.98	0.93	0.95	0.98
10	99	1.00	1.00	1.00	0.98	0.98	0.98
30	90	1.00	1.00	1.00	1.00	1.00	1.00
50	82	1.00	1.00	1.00	1.00	1.00	1.00
150	43	0.99	0.99	1.00	0.91	0.91	0.90
300	11	0.92	0.91	0.93	0.83	0.81	0.79
Overall		**0.97**	**0.97**	**0.99**	**0.94**	**0.94**	**0.94**

Catchability and probability of survival for a given water temperature

There was a significant negative effect of water temperature on 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; Figure 4F) and a significant effect of water temperature at time of capture on the survival of Atlantic salmon following hook and release (1 day post release: GLM, $z_{109,108}$ = -2.39, p = 0.02, Figure 6A; 10 days post-release: GLM, $z_{107,106}$ = -2.48, p = 0.01, Figure 6B; 30 days post release: GLM, $z_{102,101}$ = -3.06, p = 0.002, Figure 6C). Revised mean hook and release survival probability predicted by our binomial model suggest that at water temperatures between 10 and 18 °C mean survival was 0.98 (1 day post release), 0.97 (10 days post release) and 0.96 (30 days post release; Table 4; Figure 6A - C). At temperatures of 18 °C, mean survival probability was 0.93 (1 day post release), 0.93 (10 days post release) and 0.81 (30 days post release; Table 4; Figure 6 A - C). At 20 °C mean survival probability was 0.86 (1 day post release), 0.80 (10 days post release) and 0.68 (30 days post release; Table 4; Figure 6 A - C). Lastly, at water temperatures between 21 and 25 °C mean survival probability was 0.69 (1 day post release), 0.62 (10 days post release) and 0.43 (30 days post release; Table 4; Figure 6 A - C).

Table 4. Survival probability (mean ± 95% CI) of a hooked and released Atlantic salmon at given water temperature, 1 (n = 110), 10 (n = 108) and 30 (n = 103) days post-release at Western Arm Brook, Newfoundland and Labrador, Canada. Survival probabilities were derived from a generalized 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. Mean of the angled fish (Mean) and Mean of the Control (Mean C1) used Dataset 1 that excluded 22 fish that were either roughly handled during procedures (11 control fish and 2 angled fish), were recaptured during the study (6 controls and 1 angled fish) or of a different life stage not typically targeted in the recreational fishery (2 kelt). Mean of the control (Mean C2) used Dataset 2 that excluded and additional 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. Revised survival probabilities relative to the control using Datatset 1 (Rev. S1) and Dataset 2 (Rev. S2) are presented in bold. Data included individuals of known fate (ie. dead or alive) only. See Figure 6 for survival curves. Note: water temperatures for the study ranged from 5 to 22 °C, therefore, predictions above and approaching 22°C (highlighted in grey) are bounded by a wide error margin and should be interpreted as such.

	Survival probability (1 day post release; Figure 6A)							Survival probability (10 days post release; Figure 6B)							Survival probability (30 days post release; Figure 6C)						
Water temp. (°C)	L 95% CI	Mean	U 95% CI	Mean C1	Mean C2	**Rev. S1**	**Rev. S2**	L 95% CI	Mean	U 95% CI	Mean C1	Mean C2	**Rev. S1**	**Rev. S2**	L 95% CI	Mean	U 95% CI	Mean C1	Mean C2	**Rev. S1**	**Rev. S2**
10	0.91	0.99	1.00	0.98	0.99	**1.00**	**1.00**	0.91	0.99	1.00	0.99	1.00	**1.00**	**0.99**	0.91	0.99	1.00	0.99	1.00	**1.00**	**0.99**
11	0.91	0.99	1.00	0.98	0.99	**1.00**	**1.00**	0.91	0.98	1.00	0.99	1.00	**0.99**	**0.98**	0.89	0.98	1.00	0.99	1.00	**0.99**	**0.98**
12	0.90	0.98	1.00	0.98	0.99	**1.00**	**0.99**	0.90	0.98	1.00	0.98	0.99	**1.00**	**0.99**	0.88	0.97	0.99	0.98	0.99	**0.99**	**0.98**
13	0.89	0.98	1.00	0.98	0.99	**1.00**	**0.99**	0.89	0.97	0.99	0.97	0.99	**1.00**	**0.98**	0.86	0.96	0.99	0.97	0.99	**0.99**	**0.97**
14	0.88	0.97	0.99	0.98	0.99	**0.99**	**0.98**	0.88	0.96	0.99	0.96	0.98	**1.00**	**0.98**	0.84	0.94	0.98	0.95	0.98	**0.99**	**0.96**
15	0.87	0.96	0.99	0.98	0.98	**0.98**	**0.98**	0.87	0.95	0.98	0.94	0.98	**0.95**	**0.97**	0.82	0.92	0.97	0.93	0.96	**0.98**	**0.96**
16	0.86	0.95	0.98	0.98	0.98	**0.97**	**0.97**	0.86	0.93	0.97	0.92	0.96	**0.93**	**0.97**	0.79	0.89	0.95	0.89	0.92	**1.00**	**0.97**
17	0.84	0.93	0.97	0.98	0.98	**0.95**	**0.95**	0.84	0.91	0.96	0.89	0.94	**0.91**	**0.97**	0.75	0.86	0.92	0.84	0.87	**0.86**	**0.99**
18	0.81	0.90	0.95	0.98	0.97	**0.92**	**0.93**	0.81	0.88	0.94	0.85	0.91	**0.88**	**0.97**	0.69	0.81	0.89	0.76	0.78	**0.81**	**0.81**
19	0.75	0.87	0.93	0.98	0.96	**0.89**	**0.91**	0.75	0.85	0.92	0.80	0.87	**0.85**	**0.98**	0.61	0.75	0.85	0.67	0.65	**0.75**	**0.75**
20	0.67	0.83	0.92	0.98	0.96	**0.85**	**0.87**	0.67	0.80	0.90	0.74	0.80	**0.80**	**0.80**	0.50	0.68	0.82	0.56	0.50	**0.68**	**0.68**
21	0.56	0.77	0.90	0.98	0.95	**0.79**	**0.82**	0.56	0.75	0.89	0.66	0.72	**0.75**	**0.75**	0.38	0.60	0.78	0.45	0.34	**0.60**	**0.60**
22	0.44	0.71	0.89	0.98	0.93	**0.73**	**0.78**	0.44	0.69	0.87	0.58	0.62	**0.69**	**0.69**	0.27	0.51	0.75	0.34	0.22	**0.51**	**0.51**
23	0.31	0.64	0.88	0.98	0.92	**0.66**	**0.72**	0.31	0.62	0.86	0.49	0.51	**0.62**	**0.62**	0.18	0.43	0.72	0.24	0.13	**0.43**	**0.43**
24	0.21	0.57	0.87	0.97	0.90	**0.60**	**0.67**	0.21	0.55	0.85	0.40	0.39	**0.55**	**0.55**	0.11	0.35	0.69	0.17	0.07	**0.35**	**0.35**
25	0.13	0.49	0.86	0.97	0.88	**0.52**	**0.61**	0.13	0.47	0.83	0.32	0.29	**0.47**	**0.47**	0.07	0.27	0.65	0.11	0.05	**0.27**	**0.27**

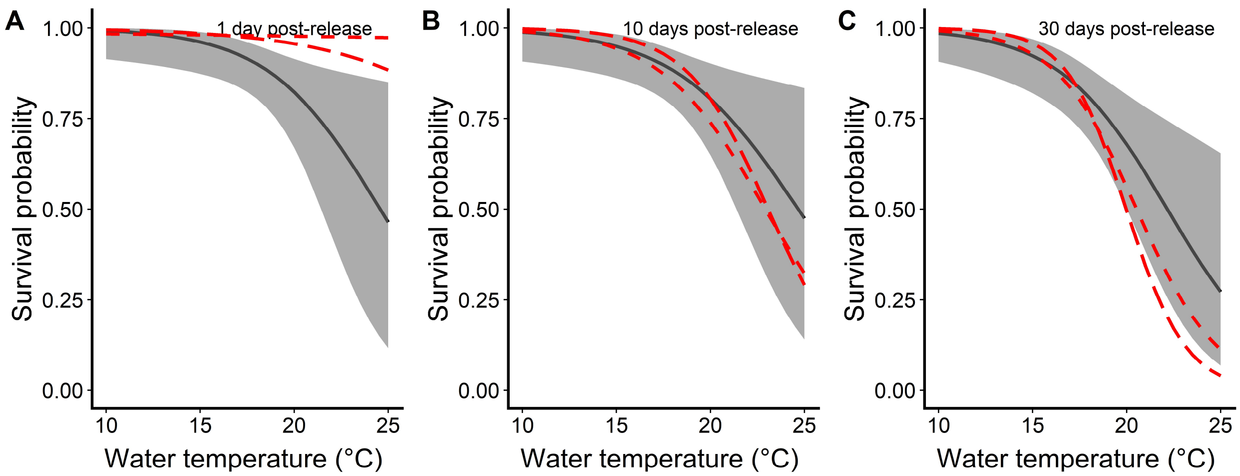

Figure 6. The relationship between survival probability (mean ± 95% CI) of an Atlantic salmon and water temperature, 1 day post-release (A), 10 days post-release (B) and 30 days post-release (C) from Western Arm Brook, Newfoundland and Labrador, Canada. Survival probabilities were derived from a generalized linear model with a binomial distribution (live or dead for an individual fish) and water temperature as a factor for both the angled fish (black line, shaded grey) and the control fish (red dashed lines). The short red dashed line represents survival probabilities from Dataset 1 that excluded 22 fish that were either roughly handled during procedures (11 control fish and 2 angled fish), were recaptured during the study (6 controls and 1 angled fish) or of a different life stage not typically targeted in the recreational fishery (2 kelt). The long red dashed line used Dataset 2 that excluded an additional 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. Data included individuals of known fate (ie. confirmed dead or alive) only. See Table 4 for survival estimates. Note: water temperatures for the study ranged from 5 to 22 °C, therefore, predictions above and approaching 22°C are bounded by a wide error margin and should be interpreted as such.

Fish survival to spawning time and kelt survival

Although the number of censored individuals was higher for the control fish than the angled fish, 59 % of the control fish and 70 % of the hooked and released fish, of known fate, were confirmed to have survived greater than or equal to November 30th of the year they entered the river for dataset 1 (Figure 7A). For dataset 2, 67 % of the control fish and 70 % of the hooked and released fish, of known fate, were confirmed to have survived greater than or equal to November 30th of the year they entered the river (Figure 7B). In addition, thirty-one Atlantic salmon (dataset 1) and twenty-eight 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 hooked and released fish)]. Interestingly, one salmon from the control group that was internally tagged on July 11, 2020, during its upstream spawning migration through the counting fence, was re-captured by commercial fishers in western Greenland (66.793612 °N, 53.480960 °W) on September 5, 2021, after it had presumably spawned and migrated past the counting fence as a kelt in early spring.

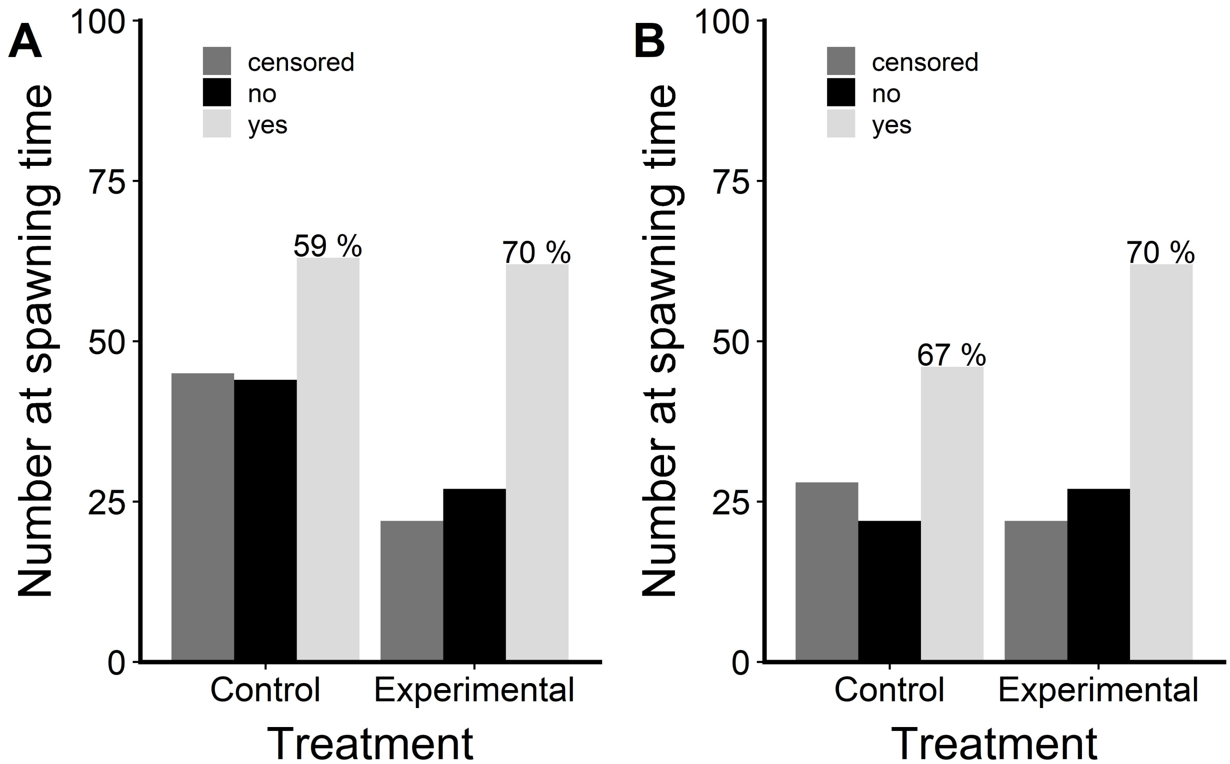

Figure 7. The number of Atlantic salmon that were either angled, radio-tagged and released (experimental) or trapped at a salmon counting fence facility, radio-tagged and released (Control) and survived (light grey) or died (black) before (no) or after (yes) the spawning period of the year they entered Western Arm Brook, Newfoundland and Labrador, Canada. Percentages refer to the percent of Atlantic salmon, of known fate (i.e. censored individuals removed), that survived beyond spawning. Censored individuals (dark grey) are those that survived up to a particular point in time but then lost from the study due to tag failure, max operational battery life exceeded, tag shedding, or other unknown causes. Panel A used data that excluded 22 fish that were either roughly handled during procedures (11 control fish and 2 angled fish), were recaptured during the study (6 controls and 1 angled fish) or of a different life stage not typically targeted in the recreational fishery (2 kelt). Panel B used data that excluded and additional 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.

Discussion

This study, the largest and most comprehensive of its kind, clearly demonstrates that the added mortality on Atlantic salmon caused by hook and release is low. In this study there was a 96 % probability an angled salmon would still be alive 30 days post release. This result is particularly impressive given the potential added stressors of applying the radio tags. The type of angling and conditions at Western Arm Brook; fly-fishing only, with barbless single hook, carried out with grilse salmon (1 sea winter - mean size of fish ± SD was 54.4 cm ± 3.2 cm) and at a range of water temperature of 11 to 22°C, are consistent with typical angling conditions in NL. Thus, the results are applicable to the vast majority of angled Atlantic salmon in NL, and likely indicative for much of the species range. These results provide clarity and are in agreement with several previous experiments that suggest high survival following hook and release at cool to moderate water temperatures (< 18°C) and when best practices (see Figure 8 for conceptual diagram of angling stages and best practices, including gear choice and considerations) are followed (Tufts et al. 1991; Booth et al. 1995; Wilkie et al. 1996; Dempson et al. 2002; Lennox et al. 2017; Van Leeuwen et al. 2020).

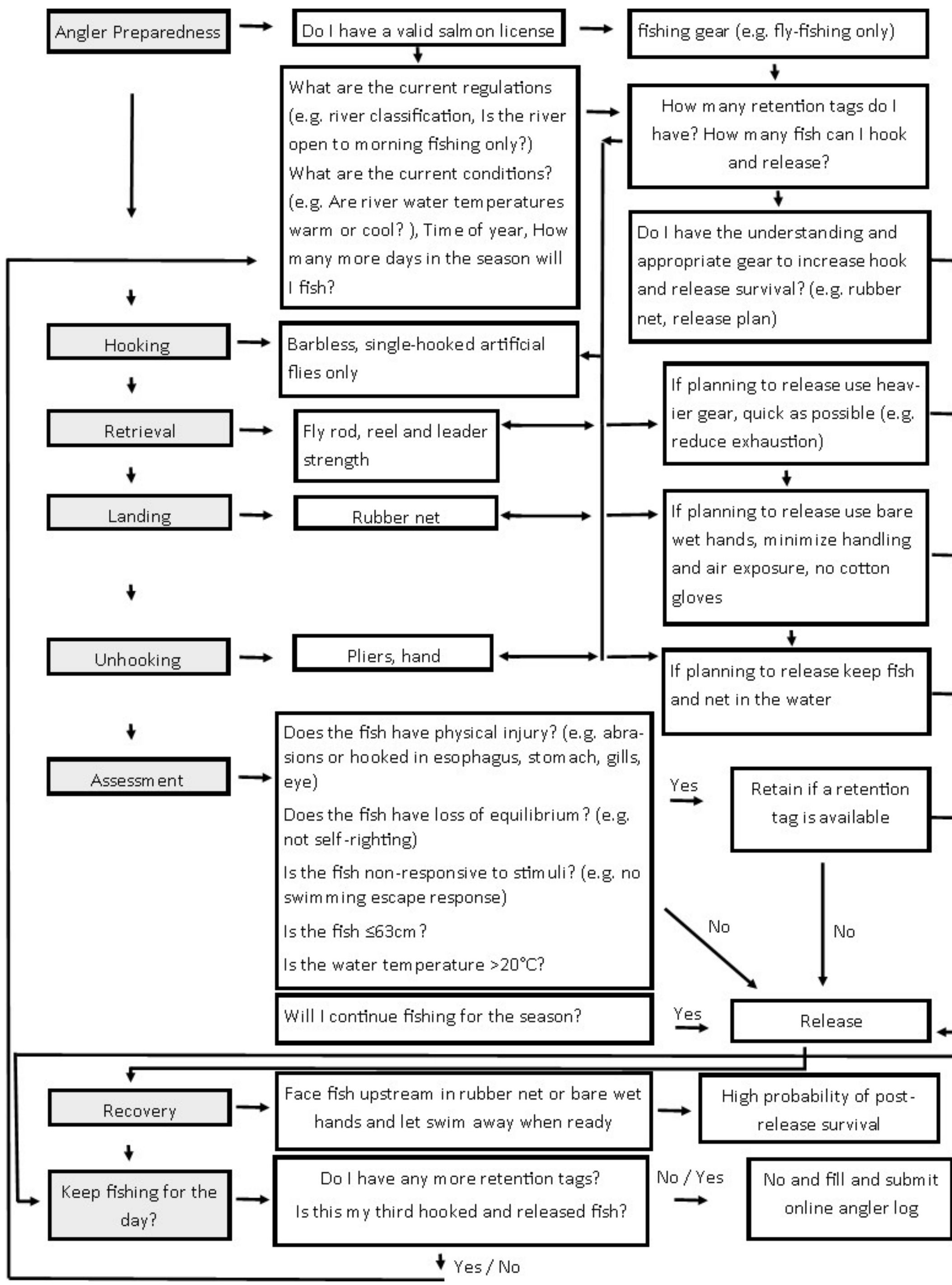

Figure 8. (Left column; grey boxes) Conceptual diagram of potential stages of a recreational angling event from angler preparedness to deciding if to keep angling or not (left boxes; from Brownscombe et al. 2016) and (middle and right column) angler best practices, including gear choice and considerations, at each potential stage of a Atlantic salmon recreational angling event.

Van Leeuwen et al. (2020), modeled hook 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 of 0.97 using dataset 1 and 0.94 using dataset 2. 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 hook 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 hook and release, three were conducted in NL rivers (Van Leeuwen et al. 2020). Dempson et al (2002) held angled and control fish (trapped at the counting fence facility) in large cages in Conne River for up to 40 days and found an overall survival probability of 0.92 at water temperatures ranging from 9.5 to 22.1 °C but 0.88 among angled salmon in water temperatures ≥17.9 °C. Anderson et al. (1998), used staged angling events on Atlantic salmon implanted with heart rate tags on Noel Paul's Brook and found a survival probability of 1.00 at 16.5 ± 1 °C and 0.20 at 20 ± 2 °C. Lastly, Lennox et al. (2019), used an exhaustive chase protocol on Atlantic salmon that were trapped at a counting fence facility, equipped with an accelerometer and radio tag and released in Campbellton River, and found survival probability to be between 0.86 and 0.91 at water temperatures ranging from 17.6 to 20.2 °C. However, salmon in these studies were held in somewhat controlled conditions (i.e. tanks, cages) and/or angling was only simulated. This led to concerns from anglers that the results were not representative of the actual hook and release events experienced by salmon on NL rivers. However the results of this study, which addressed these methodological concerns, are mostly congruent with Dempson et al (2002), Anderson et al. (1998), and Lennox et al. (2019). This reduces the uncertainty around the survival estimates of those studies and reinforces their value for developing a modeling framework for hook and release.

The results of this study and those that have evaluated shorter-term post-release survival, suggest post release survival is high in the first few days (i.e. there are not a lot of fish dying from injuries in the first 1-10 days post release; Tables 1 and 2, Figure 5). However, there is a paucity of studies that have examined post-release survival to the spawning period and beyond (although see Thorstad et al. 2007; Gargan et al. 2015; Havn et al. 2015; Lennox et al. 2015, for studies evaluating post-release survival to spawning). Our study showed that survival rates of both the angled and control fish dipped in early winter, and in both data sets survival rates of angled and control fish diverged at around 150 days, with control fish exhibiting higher survival. These differences indicate the need to examine survival for longer periods post-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 four minutes, a potential divergence in survival over 150 days post-release is surprising. If hook and release injuries were a driver of mortality for these salmon, a reasonable expectation would be divergent survival in the short-term (e.g. 1-30 days) with survival synchronizing over time as injured fish die and the remaining individuals fully recover. However, it is also possible that the divergence in survival rate after 150 days is spurious and driven by declining sample sizes at the longer periods post-release. From 50 to 150 days post release, the sample size of angled fish declines from 82 to 45 and at 300 days only 12 angled salmon, and 20 control salmon, remained (Table 3). The overwinter survival rates measured in this study are typical for Atlantic salmon in NL (Rideout and Tomkiewicz 2011; DFO 2019).

A determining factor in survival for hooked and released fish, including salmon, is temperature (Lennox et al. 2017; Van Leeuwen et al 2020) (Figure 6). A possible mitigating factor for predicted hook and release mortality at higher temperatures is declining catchability.

While catchability of Atlantic salmon did decline at warm water temperatures, it is clear that many salmon can still be caught in the 18 to 23°C range (Figure 2). Therefore, the importance of water temperature in ensuring the survivability of released Atlantic salmon should not be underestimated (Havn et al. 2015; Lennox et al. 2017; Van Leeuwen et al. 2020, 2021). At water temperatures between 10 and 18 °C mean survival probability across datasets in our study was 0.97 (1 to 30 days post release). At 18 °C it was 0.89 (1 to 30 days post release). At 20 °C mean survival probability was 0.78 (1 to 30 days post and release), and between 21 and 25 °C it was 0.58 (1 to 30 days post release). This decrease in hook and release survival at warmer water temperatures occurs because the synergistic effects of warm water temperature and lower dissolved oxygen, with exhaustive exercise during the capture process, can impede the fish's aerobic and anaerobic recovery (Wilkie et al., 1996; Arlinghaus et al., 2007; Breau, 2013). The results of this study suggest that hook and release as a resource management tool begins to increase in risk at 18 °C, and the mortality risk above 20 °C is likely unacceptable to many fisheries managers and anglers alike.

While radio telemetry is used widely to study aquatic species and shown to not alter survival (Jepson et al. 2015; Hubbard et al. 2021), it is important to recognize that 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. However, to ensure that survival was not adversely impacted using internally implanted radio transmitter tags (anesthetic and surgery) we also employed a less invasive external radio transmitter tagging procedure for comparison. There was no statistical differences in survival between the two techniques for both the control and angled groups, and the internal tags provided much longer battery life (~2 years, compared to ~6 months for external tags) and provided stronger signal strengths during walking telemetry and helicopter monitoring flights. Hubbard et al. (2021) compared survival, growth, and body condition of lake trout (*Salvelinus namaycush*) among surgically implanted transmitter tagged fish and untagged individuals over a 12-year period. The findings of Hubbard et al. (2021) supported the assumption that fish species tagged internally show no adverse effects as compared to untagged fish in the wild. Therefore, there appears to be no reason that future hook and release studies, provided similar methods are employed, should not use internal tagging procedures to collect similar long-term data. Additionally, no special care was taken to utilize ‘perfect’ hook and release procedures, instead anglers (with a range of experience) released fish as they had being doing for years on personal fishing outings (Figure 2). The realism of angling events combined with the short procedure times, especially for externally tagged fish (4.4 min. from hooking to release, including tagging), should provide confidence that the results here 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 the majority of anglers practice reasonable hook and release techniques population level mortality rates will be low.

Although the study was not designed to test specific handling procedures, we did observe the development of sores on body areas in contact with cotton gloves during fish handling (i.e. caudal peduncle; Figure 3A & B) 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 hook and release, increases 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 develop days to weeks later as a result of infection. While tracking individual salmon for this study we were able to observe the development of these sores. Ideally the fish should not be touched by the angler’s hands during a release.

Physical injury by hooking can be significant (Muoneke and Childress 1994). For example, the number of critical hooking events (eyes, esophagus, gills and tongue) for resident

Atlantic salmon (Ouananiche) in Moosehead Lake, USA were reported to be nine times higher when anglers used bait compared to anglers who used flies (Warner and Johnson 1978). Consistent with these findings 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, jaw) and 8 % sometimes considered critical (ie: foul hooked, tongue) (Muoneke & Childress 1994). When a salmon is badly injured by the hook, the injury is often immediately apparent to the angler. While overall survival for hooked and released salmon is high, the prognosis for individuals with obvious injuries is much worse. During the course of the study we were able to anecdotally predict the fate of clearly injured salmon. Although these critical injuries were rare during our study, given the low probability for survival when there is a obvious injury we would recommend that anglers consider retention if possible (see Figure 8 for a responsible angler breakdown).

In addition to evaluating long-term survival (1 to 300 days post-release) of Atlantic salmon following hook and release, we also evaluated whether there were differences in mortalities prior too or just after the assumed spawning period. Further, we also compared differences in survivorship among salmon that overwintered in fresh water and then migrated downstream past the counting fence to sea (i.e. kelt survival). Because approximately 96 % of returning adult salmon in Western Arm Brook are 1 sea winter maiden spawners, the number of individuals that survived beyond spawning time is arguably of greater importance [(from a management and stock perspective (egg deposition)] than the 300 day time duration or kelt survival because; 1) very few salmon will survive overwintering and leave the river as kelt naturally ([(13 % (data set 1), 19 % (dataset 2) of the control fish and 10 % (dataset 1), 9 % (dataset 2) of the hooked and released fish)] and 2) an even smaller percentage (if any from this study) will return from sea to spawn a second time (Rideout and Tomkiewicz 2011). Thus, it is encouraging that 70 % (dataset 1 and 2) of the hooked and released fish with known fates survived beyond the spawning period compared to the 59 % and 67 % (dataset 1 and 2, respectively) of control fish with known fates confirmed to have survived beyond the spawning period. This finding suggests hook and release angling is not preventing fish from surviving to spawn but highlight further gaps in knowledge about the long-term effects of hook and release fishing. Future research will evaluate the location of the tracked salmon relative to known spawning habitat during the spawning period.

Research on sub-lethal effects of hook and release on fine-scale migratory behaviour or reproductive success is limited. For example, by genetically sampling every returning adult Atlantic salmon on the Escomins River, Quebec, Canada and assigning parentage to the offspring, Richard et al. (2014) found an interactive negative effect of water temperature and air exposure time on the reproductive success of hooked and released salmon. Additionally, Papatheodoulou et al. (2021) found that Atlantic salmon collected near the end of their spawning migration and exposed to their most disturbed treatments of simulated hook and release (exercise and 120s air exposure) had higher growth 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. However, in another laboratory based study, which also used simulated hook and release, Booth et al. (1995) found no difference in egg survival between salmon that were angled and non-angled. Whatever the case, further studies investigating potential effects of hook and release on offspring survival are warranted.

Resource managers are tasked with determining what level of hook and release mortality is tolerable in a fishery relative to the social and economic benefits derived from hook and release angling. Based on the results of this study, when water temperatures are cool to moderate and fish are handled properly survival following hook and release is high. However, not all released fish survive and variation in survival will occur due to differences in biological and physical conditions, such as geography, timing and duration of snow melt, hydrology, period and duration of high river temperatures, run timing, angler experience, discharge, density of fish and availability of cold-water refuges and pools (e.g. Frechette et al. 2018). Therefore, it is incumbent on resource managers to consider these environmental conditions, as well as, the level of angler effort, catch rates, combined mortality of retention and hook and release angling, and the conservation status of the salmon population, when determining when and where hook and release angling is appropriate. Additionally, when considering the risk of hook and release to a salmon population, a resource manager must also consider the likely effect of the predicted mortality (effort x catch per unit effort x mortality rate = salmon removed from the population by hook and release) on overall salmon abundance. While often difficult to determine, this study provides an illustrative example. In this study most anglers (84 %) only landed 1 fish per day and overall only a relatively small percentage of the total population was landed (~4 %) in a given season. The low percentage of the total population landed was presumably due to low angling effort (~1100 hrs 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 those used in our study (15.8°C ± 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) we would estimate 1 to 4 mortalities would be attributed to hook and release in our study population. An overall mortality of 0.4 % of the population due to hook and release would likely be acceptable on any river that also had sufficient salmon for retention angling. However, it is important to note that the example of Western Arm Brook is based on low angling effort relative to the population size. On popular rivers the proportion of the population hooked by anglers is likely much higher. While undoubtedly a crude approximation, this example highlights the relatively low population level impact of hook and release at low to moderate levels of angler effort. This is consistent with values by Van Leeuwen et al. (2020) who estimated 0.3 to 2.6 % of salmon, relative to the population, died as a result of hook and release for various rivers across the island of Newfoundland in 2016. While the actual numbers of fish lost in the fishery is unknown, it is also important to note that unprecedented warm water temperatures (>20°C) early in the season (middle of June to end of July in NL), when most angling activity and retuning salmon are in their highest numbers, will likely determine if there are any meaningful population level impacts of hook and release on NL salmon populations (Van Leeuwen 2020).

This study conclusively demonstrates that hook and release can be an effective method of providing angling opportunities while minimizing impacts on Atlantic salmon abundance. There is no evidence that hook and release as it is typically practiced in NL would cause high mortality in Atlantic salmon populations. However, poor hook and release practices and allowing hook and release at high water temperatures are substantial risk factors. However, these risk factors can be mitigated through education and regulation (i.e. angler training, and prohibition on hook and release at high water temperatures). This study does not address the ethics debate associated with the practice of hook and release. However, resource managers must also consider values of anglers and the ethics of allowing a stress event on an animal for sport purposes. It is particularly important to consider the ethics of anglers as it relates to hook and release because any management regime, be it retention or hook and release, that ignores the ethical expectations of anglers, has the potential to disrupt angler engagement, regulatory compliance, and local stewardship of the resource (Cote et al. 2021).

Although the results of this study are definitive and well supported by the 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 time capture ± SD for the control group (16.8°C ± 2.2°C) was slightly higher than that for the angled fish (14.4°C ± 4.8°C), in addition to sample sizes were low at warmer water temperatures. Secondly, we assume that censoring is random and not linked to a higher probability of mortality after censoring of a fish has occurred.

The results of this study conducted in Western Arm Brook NL, Canada, suggest that 1) hook and release survival is high for Atlantic salmon under the typical conditions of the recreational fishery in NL, and 2) mortalities following hook and release can be minimized by not practicing hook and release when water temperatures are high (whether mandated closures are in place or not), and through the adoption of best practices (keep fish in the water, use of a knotless rubber net or sling, and minimizing physical contact with the salmon).

Acknowledgements

We would like to thank Chris Baldwin, Chris Callahan, Dave Chambers, Dion Rideout, Grant Dicks, Dale O'leary, Alvin Bromley, John Neville, Mark Breon, Nathan Spence, Shane Hann, Tina Leonard, Jamie Kennedy and Wayne Barney for help with angling of salmon for the study. Special thanks to pilots Derm Cain, Max Gaudin, and Justin Graveline and the staff of Canadian Helicopters for their invaluable support. A thank you to Clarisse Uwamahoro for early data collation. We are indebted to Kirk Pilgrm and the counting fence staff at Western Arm Brook for assistance. Thanks to Martha Robertson and Nick Kelly with suggestions for the field design. In addition, we would like to thank Christina Pretty for creating the map for Figure 1 and Kristin Loughlin, Julie Turner, Robert Perry, and Craig Purchase for their valuable insight and contribution to an early version of the manuscript. Funding for the study was provided by the Province of NL with in-kind support from Fisheries and Oceans Canada.

References

Anderson, W.G., Booth, R., Beddow, T.A., McKinley, R.S., Finstad, B., Økland, F., and Scruton, D. 1998. Remote monitoring of heart rate as a measure of recovery in angled Atlantic Salmon, Salmo salar (L.). Hydrobiol. 371: 233-240.

Arlinghaus, R., Cooke, S.J., Lyman, J., Policansky, D., Shwab, A., Suski, C., Sutton, S.G., and Thorstad, E.B. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Rev. Fish Sci. Aquac.15: 75-167.

Booth, R.K., Kieffer, J.D., Davidson, K., Bielak, A.T., and Tuft, B.L. 1995. Effects of late season catch and release angling on anaerobic metabolism, acid-base status, survival and gamete viability in wild Atlantic Salmon (Salmo salar). Can. J. Fish Aquat. Sci. 52: 283-290.

Breau, C. 2013. Knowledge of fish physiology used to set water temperature thresholds for in season closures of Atlantic Salmon (Salmo salar) recreational fisheries. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/163.

Brobbel, M.A., Wilkie, M.P., Davidson, K., Kieffer, J.D., Bielak, A.T., and Tufts, B.L. 1996. Physiological effects of catch and release angling in Atlantic Salmon (Salmo salar) at different stages of freshwater migration. Can. J. Fish. Aquat. Sci. 53: 2036-2043.

Brownscombe, J.W., Danylchuk, A.J., Chapman, J.M., Gutowsky, L.F.G., and Cooke, S.J. 2017. Best practices for catch-and-release recreational fisheries – angling tools and tactics. Fish. Res. 186: 693-705

Cooke, S.J., and Wilde, G.R. 2007. The fate of fish released by recreational anglers, Chapter 7, pp. 181-234. In: By-catch Reduction in the World's Fisheries. Kennelly, S.J. (ed.). Springer.

Cote, D., Van Leeuwen, T.E., Bath, A.J., Gonzales, E.K., and Cote, A.L. 2021. Social–ecological management results in sustained recovery of an imperiled salmon population. Res. Ecol. () 1-12.

Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K., and Lilly, J. 2021. The decline and Impending collapse of the Atlantic salmon (Salmo salar) Population in the North Atlantic Ocean: A review of possible causes. Rev. Fish. Sci. Aquac. () 1-44.

Dempson, J.B., O'Connell, M.F., and Schwarz, C.J. 2004. Spatial and temporal trends in abundance of Atlantic Salmon, Salmo salar, in Newfoundland with emphasis on impacts of the 1992 closure of the commercial fishery. Fish. Manag. Ecol. 11: 387-402.

Dempson, J.B., Furey, G., and Bloom, M. 2002. Effects of catch and release angling on Atlantic Salmon, Salmo salar L., of the Conne River, Newfoundland. Fish. Manag. Ecol. 9: 139-147.

DFO. 2019. 2018 Atlantic Salmon In-Season Review for the Newfoundland and Labrador Region. DFO Can. Sci. Advis. Sec. Sci. Resp. 2019/004.

Frechette, D.M., Dugdale, S.J., Dodson, J.J., and Bergeron, N.E. 2018. Understanding summertime thermal refuge use by adult Atlantic Salmon using remote sensing, river temperature monitoring, and acoustic telemetry. Can. J. Fish. Aquat. Sci. 75: 1999-2010.

Gargan, P.G., Stafford, T., Okland, F., and Thorstad. E.B. 2015. Survival of wild Atlantic Salmon (Salmo salar) after catch and release angling in three Irish rivers. Fish. Res.161: 252-260.

Havn, T.B., Uglem, I., Solem, Ø., Cooke, S.J., Whoriskey, F.G., and Thorstad, E.B. 2015. The effect of catch-and-release angling at high water temperatures on behaviour and survival of Atlantic Salmon (Salmo salar) during spawning migration. J. Fish Biol. 87: 342-359.

Hubbard, J.A.G., Hickie, B.E., Bowman, J., Hrenchuk, L.E., Blanchfield, P.J., and Rennie, M.D. 2021. No long-term effect of intracoelomic acoustic transmitter implantation on survival, growth, and body condition of a long-lived stenotherm in the wild. Can. J. Fish Aquat. Sci. 78: 173-183.

Heupel, M.R., and Simpfendorfer, C.A. 2011. Estuarine nursery areas provide a low-mortality environment for young bull sharks Carcharhinus leucas. Mar. Ecol. Prog. Ser. 433: 237-244.

ICES. 2019. Working Group on North Atlantic Salmon (WGNA). ICES Scientific Reports 1:16, 368 pp. doi.org/10.17895/ices.pub.4978.

Jepsen, N., Thorstad, E.B., Havn, T., and Lucas, M.C. 2015. The use of external electronic tags on fish: an evaluation of tag retention and tagging effects. Anim. Biotelemetry 3: 1-24.

Kassambara, A. 2021. Survminer: Drawing survival curves using ggplot2. Available from https://cran.r-project.org/package=survminer.

Klemetsen, A., Amundsen, P-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., and Mortensen, E. 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. Freshw. Fish. 12: 1-59.

Lehnert, S.J., Kess, T., Bentzen, P., Kent, M.P., Lien, S., Gilbey, J., Clément, M., Jeffery, N.W., Waples, R.S., and Bradbury, I.R. 2019. Genomic signatures and correlates of widespread population declines in salmon. Nat. Commun. 10: 2996.

Lennox, R.J., Uglem, I., Cooke, S.J., Nasje, T.F., Whoriskey, F.G., Havn, T.B., Ulvan, E.U., Solem, Ø., and Thorstad, E.B. 2015. Does catch-and-release angling alter the behaviour and fate of adult Atlantic salmon during upriver migration? Trans. Am. Fish. Soc. 144: 400-409.

Lennox, R.J., Cooke, S.J., Davis, C.R., Gargan, P., Hawkins, L.A., Havn, T.B., Johansen, M.R., Kennedy, R.J., Richard, A., Svenning, M., Uglem, I., Webb, J., Whoriskey, G.G., and Thorstad, E.B. 2017. Pan-Holarctic assessment of post-release mortality of angled Atlantic Salmon Salmo salar. Biol. Cons. 209: 150-158.

Lennox, R.J., Chapman, J.M., Twardek, W.M., Broell, F., Bøe, K., Whoriskey, F.G., Fleming, I.A., Robertson, M., and Cooke, S.J. 2019. Biologging in combination with biotelemetry reveals behavior of Atlantic salmon following exposure to capture and handling stressors. Can. J. Fish Aquat. Sci. 76: 2176-2183.

Miller, H.W., and Johnson, D.H. 1978. Interpreting the results of nesting studies. J. Wildl. Manage. 62:306-313.

Mullins, C.C., Caines, D., and Lowe, S.L. 2001. Status of the Atlantic salmon stocks of Lomond River, Torrent River and Western Arm Brook, Newfoundland, 2000. DFO Can. Sci. Advis. Sec. Sci. Resp. 2001/039.

Muoneke, M.I., and Childress, M.W. 1994. Hooking mortality: A review for recreational fisheries. Rev. Fish. Sci. Aquac. 2:123-156.

O'Connell, M.F., Dempson, J.B., and Reddin, D.G. 1992. Evaluation of the impacts of major management changes in the Atlantic Salmon (Salmo salar L.) fisheries of Newfoundland and Labrador, Canada, 1984-1988. ICES J. Mar. Sci. 49: 69-87.

Papatheodoulou, M., Závorka, L., Koeck, B., Metcalfe, N.B., and Killen, S.S. (2021). Simulated pre-spawning catch & release of wild Atlantic salmon (*Salmo salar*) results in faster fungal spread and opposing effects on female and male proxies of fecundity. Can. J. Fish. Aquat. Sci. (accepted manuscript).

Pollock, K.H., Winterstein, S.R., Bunck, C.M., and Curtis, P.D. 1989. Survival analysis in telemetry studies: The staggered entry design. J. Wildl. Manage. 53: 7-15.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Randall, R.G. 1990. Effect of the 1984-1988 management plan on harvest and spawning levels of Atlantic Salmon in the Restigouche and Miramichi rivers, New Brunswick. Can. Atlan. Fish. Sci. Advis. Com. Res. Doc. 90/45.

Richard, A., Bernatchez, L., Valiquette, E., and Dionne, M. 2014. Telemetry reveals how catch and release affects prespawning migration in Atlantic Salmon (Salmo salar). Can. J. Fish. Aquat. Sci. 71: 1730-1739.

Rideout, R.M., and Tomkiewicz, J. 2011. Skipped spawning in fishes: More common than you might think. Mar. Coast. Fish. 3: 176-189.

Robertson, H.A., and Westbrooke, I.M. 2005. A practical guide to the management and analysis of survivorship data from radio-tracking studies. Department of conservation technical series 31. Department of Conservation, Wellington, NZ.

Soto, D.X., Trueman, C.N., Samways, K.M., Dadswell, M.J., and Cunjak, R.A. 2018. Ocean warming cannot explain synchronous declines in North American Atlantic Salmon populations. Mar. Ecol. Prog. Ser. 601: 203-213.

Therneau, T.M. 2015. A package for survival analysis in R. Available from https://cran.r-project.org/package=survival.

Thorstad, E.B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L.E., Hatfield, E.M.C., Horsburgh, G., Hansen, H., Maoiléidigh, N.Ó., Sheehan, T., and Sutton, S.G. 2021. Atlantic salmon in a rapidly changing environment-Facing the challenges of reduced marine survival and climate change. Aquat. Conserv.: Mar. Freshw. Ecosyst. (): 1-12.

Thorstad, E.B., Næsje, T.F., Fiske, P., and Finstad, B. 2003. Effects of hook and release on Atlantic Salmon in the River Alta, northern Norway. Fish. Res. 60: 293-307.

Thorstad, E.B., Nasje, T.F., and Leinan, I. 2007. Long-term effects of catch-and-release angling on Atlantic salmon during different stages of return migration. Fish. Res. **85**: 330-334.

Tufts, B.L., Tang, Y., and Boutilier, R.G. 1991. Exhaustive exercise in wild Atlantic Salmon: acid base regulation and blood transport. Can. J. Fish. Aquat. Sci. 48: 868-874.

Van Leeuwen, T. E., Dempson, J. B., Burke, C. M., Kelly, N. I., Robertson, M. J., Lennox, R. J., Havn, T. B., Svenning, M.-A., Hinks, R., Guzzo, M. M., Thorstad, E. B., Purchase, C. F., and Bates, A. E. 2020. Mortality of Atlantic salmon after catch and release angling: Assessment of a recreational Atlantic salmon fishery in a changing climate. Can. J. Fish. Aquat. Sci. 77: 1518-1528.

Van Leeuwen, T.E., Brian Dempson, J.B., Cote, D., Kelly, N.I., and Bates, A.E. 2021. Catchability of Atlantic salmon at high water temperatures: Implications for river closure temperature thresholds to catch and release angling. Fish. Manag. Ecol., 28: 147-157.

Warner, K., and Johnson, P.R. 1978. Mortality of landlocked Atlantic Salmon hooked on flies and worms in a river nursery area. Trans. Am. Fish. Soc. 107: 772-775.

Wilkie, M.P., Davidson, K., Brobbel, M.A., Kieffer, J.D., Booth, R.K., Bielak, A.T., and Tufts, B.L. 1996. Physiology and survival of wild Atlantic Salmon following angling in warm summer months. Trans. Amer. Fish. Soc. 125: 572-580.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. 73: 3-36.