Pan-Holarctic assessment of post-release mortality of angled Atlantic salmon Salmo salar

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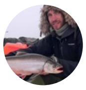

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ABSTRACT

Recreational Atlantic salmon *Salmo salar* fisheries are culturally and economically important, but confronted with global population declines, catch-and-release has frequently replaced harvest in these fisheries. Many studies have evaluated the effects of catch-and-release angling on Atlantic salmon; however, studies typically focused on a single system and had small sample sizes. Using data from Atlantic salmon catch-and-release studies conducted in 12 rivers throughout the pan-Holarctic range of wild Atlantic salmon, we modeled delayed mortality data using logistic regression. The model was based on 512 salmon (75 ± 15 cm TL) captured and released with electronic tags (i.e. radio or acoustic transmitters), which permitted the determination of fish fate after release (delayed mortality). The percentage of salmon categorized as survivors after release was high (93%). Salmon with longer body length tended to be played for longer durations ($R^2 = 0.60$) but there was no significant effect of fish length or playing time on mortality. Water temperature at capture emerged as a significant predictor of delayed mortality of salmon. Individuals captured by flies had significantly higher survival (96%) compared to lure (86%) and natural bait (85%) caught salmon. Data from throughout the range of Atlantic salmon confirm that fish captured by anglers adhering to best practices have high probability of surviving catch-and-release angling.

1. Introduction

Fisheries can have substantial and diverse impacts on ecosystems and on the environment (Chuenpagdee et al., 2003; Dayton et al., 1995; Large et al., 2015). For some fish that escape fisheries (Chopin and Arimoto, 1995) or are released (Arlinghaus et al., 2007), interactions with fishing gear can cause physical damage, physiological stress and/or cognitive impairment that contribute to decreased fitness (Raby et al., 2014; Wilson et al., 2014). Encounters can be also be lethal. Some fish die upon capture but more may experience delayed mortality after release arising from physical injuries, or prolonged physiological responses (Arlinghaus et al., 2007; Bartholomew and Bohnsack, 2005; Muoneke and Childress, 1994). For these reasons, increased adoption of catch-and-release in recreational fisheries has been confronted by concerns arising from doubts that the practice provides the anticipated population conservation benefits (Barnhart, 1989; Spitler, 1998). Therefore, substantial efforts have been made to document the effects of recreational angling on individual fish as well as fish populations to determine the sustainability of recreational catch-and-release fisheries and to manage their risk against the conservation, economic, and cultural benefits (Arlinghaus et al., 2007; Cooke and Suski, 2005; Muoneke and Childress, 1994).

The Atlantic salmon has a pan-Holarctic distribution and has been targeted by fisheries for millennia (Hindar et al., 2007, 2010; Turrero et al., 2014), with recreational fisheries increasing in popularity during the 1800s and spreading from the British Isles to other nations by the end of that century (Verspoor et al., 2008). Conservation concerns resulted in catch-and-release being advocated as early as the mid-1800s (Nettle, 1857). During the 20th century, declining salmon stocks

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resulted in the closure of many commercial fisheries (Dempson et al., 2004) as well as implementation of catch-and-release as a regulatory strategy for recreational Atlantic salmon fisheries (Barnhart, 1989), which was believed to maximize the socioeconomic value society derived from each salmon while concurrently minimizing fishery impacts on populations (Policansky, 2002). However, Atlantic salmon catch-and-release has received specific criticism from stakeholders (e.g. Wydoski, 1976; Barnhart, 1989) arising from concerns that released fish may frequently show delayed mortality post-release as a consequence of the capture event.

A number of investigators have examined the effects of recreational angling on individual Atlantic salmon behaviour, wounding, or survival. These include studies of captive fish on the impacts of various hook types (Warner and Johnson, 1978; Warner, 1979), the short and long-term physiological effects of angling (Tufts et al., 1991; Wilkie et al., 1996, 1997), and short-term survival in cages or pens (Booth et al., 1995; Dempson et al., 2002). Most recently, there has been an interest in documenting the fate of fish after release (i.e. delayed mortality) by integrating electronic tagging fish and then releasing them back to the wild (Donaldson et al., 2008). Electronic tagging and tracking have permitted intensive remote monitoring of behaviour and survival of released wild salmon (Dee River Trust, 2010; Gargan et al., 2015; Havn et al., 2015; Lennox et al., 2015, 2016; Richard et al., 2013; Thorstad et al., 2003; Webb, 1998). Most of these studies have reported that survival of salmon after release can be relatively high (>90%). However, individual studies have suffered from an inability to collect and tag sufficient numbers of salmon in order to meet a key study objective: identify factors that can be used to explain mortality of salmon released by anglers and potentially predict the outcome of salmon catch-and-release events.

By compiling the data available from a variety of published and unpublished studies on Atlantic salmon released from recreational angling gear, we overcame the small sample size problem to explain causes of delayed mortality in sport fisheries throughout the Atlantic salmon's geographic range. Data sharing is an important part of contemporary science and integral to broad analyses (Kowalczyk and Shankar, 2011; Parr and Cummings, 2005; Tenopir et al., 2011). We focused on data from telemetry studies in which the post-release fate of free-swimming fish could be quantified over the long-term from detection data. The data used were collated from studies conducted throughout the distribution of wild Atlantic salmon, generally with the common goal of calculating the post-release delayed mortality of adult salmon prior to spawning in order to identify the factors contributing to mortality.

2. Methods

2.1. Data collection

Data from telemetry studies in which wild Atlantic salmon were tagged after being captured on recreational angling gear were shared among the authors. Data were collected from rivers throughout the range of Atlantic salmon (Fig. 1; graphics created with the maptools package in R [Bivand and Lewin-Koh, 2015] and ggplot2 [Wickham, 2009]). All available metadata about salmon that were tagged, including fish size, the year and location of the study, and the date and water temperature when the fish were captured, were collated (Table 1).

Most data were collected from studies in which a biologist worked alongside recreational anglers fishing from riverbanks, with biologists tagging the salmon prior to release. In the Escoumins River, fish released by anglers were marked by adipose fin punch, verified by genetic analysis, and were then recaptured in an upstream fish ladder and tagged then (see Richard et al., 2014). Although the anglers had a range of experience, they were generally described as being experienced in salmon fishing and handling. Both radio and acoustic tags were used to monitor the movement and survival of salmon after release. In studies on Norwegian salmon, individuals that were assessed as having life-threatening wounds were not tagged, therefore the information necessary for modelling was not available. Fish were anaesthetized with clove oil in the Escoumins River and in tricaine methanesulfonate in Rivers Dee and Bann. No anaesthetic was used for tagging in the other studies. For the analysis, fishing gear types were reduced to three categories: fly (e.g. dry fly, wet fly, tube fly, bead head nymph, fly suspended under a float indicator), natural bait (e.g. worms, shrimp), and lures (e.g. spoons, spinners, wobblers). Reported fork lengths of salmon were converted to total length by multiplying fork length by 1.046; fish weight in Webb (1998) was converted to length from a standard length-weight conversion chart developed for the River Dee (Hawkins, unpublished data). Hooking locations were classified in two categories: superficial (e.g. jaw/mouth/foul) and deep (e.g. gills, eyes, throat/esophagus, roof of mouth, tongue). When a multi-pronged hook was lodged in both a superficial and a deep location, the fish was considered to be deep hooked.

Because studies were conducted independently, not all datasets were fully complete and we encountered an analytical problem with missing data. Instead of deleting entries with missing data, we opted to impute missing values. Completing data sets with imputation is useful for preserving relationships between predictor and outcome

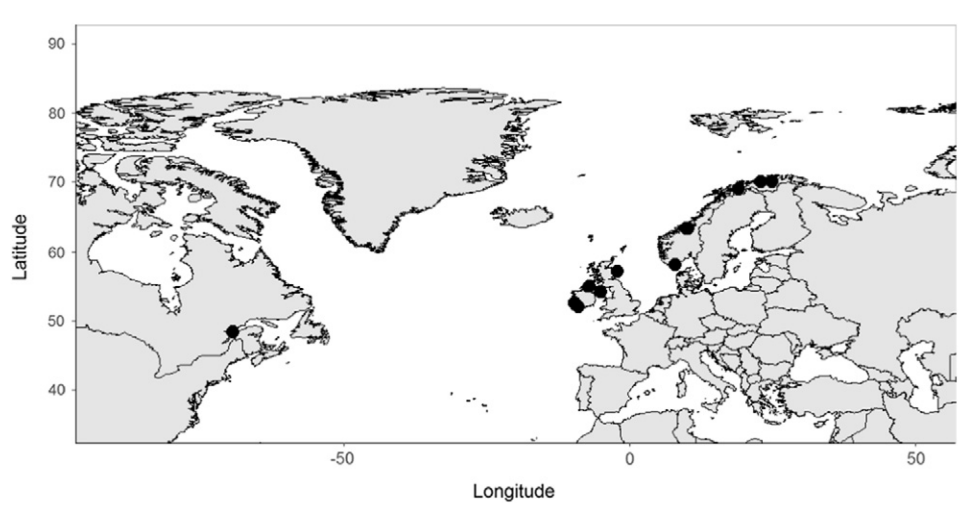

Fig. 1. Geographic distribution in North America and Europe of 12 Atlantic salmon rivers with catch-and-release data included in this study.

Table 1
Summary of data collected and shared for this project including the number of salmon tagged, average length (±1 SD), location and average water temperature (±1 SD) of fish capture. Studies that did not have the associated data are marked by NA (see Methods for details on how missing data were handled). See Fig. 1 for a map of the study sites.

Study	Mean tagging date	Year	River	Nation	Tag type	Total N	Mortalities	Mean length (cm)	Mean water temperature (°C)	Fate determination
Dee River Trust, 2010	8 October	2008	Dee	Scotland	Gastric Radio	20	0	76 ± 9	NA	Cessation of movement and observation of carcass
Dee River Trust, 2010	28 September	2009	Dee	Scotland	Gastric Radio	60	3	76 ± 10	NA	Cessation of movement and observation of carcass
Dee River Trust, 2010	1 October	2010	Dee	Scotland	Gastric Radio	60	0	73 ± 8	NA	Cessation of movement and observation of carcass
Gargan et al. (2015)	7 September	2006	Owenmore	Ireland	External Radio	21	0	59 ± 7	13 ± 1	No upstream movement of tagged fish.
Gargan et al. (2015)	17 September	2007	Owenmore	Ireland	External Radio	31	1	58 ± 6	13 ± 1	No upstream movement of tagged fish.
Gargan et al. (2015)	28 September	2006	Feale	Ireland	External Radio	15	1	60 ± 6	14 ± 1	No upstream movement of tagged fish.
Gargan et al. (2015)	26 August	2007	Mulkear	Ireland	External Radio	9	4	56 ± 6	11 ± 1	No upstream movement of tagged fish.
Havn et al. (2015)	25 July	2012	Otra	Norway	External Radio	52	9	68 ± 9	17 ± 1	Transmitter recorded in same location through study with no upstream movement.
Havn et al. (2015)	2 August	2013	Otra	Norway	External Radio	23	4	65 ± 10	20 ± 1	Transmitter recorded in same location through study with no upstream movement.
Johansen et al. (unpublished)	18 July	2013	Orkla	Norway	External Radio	6	0	76 ± 15	12 ± 1	Transmitter recorded in same location through study with no upstream movement.
Kennedy et al. (unpublished)	26 July	2013	Bann	Northern Ireland	Acoustic	11	5	58 ± 4	20 ± 2	Transmitter did not move through the receiver array and did not enter a spawning tributary
Lennox et al. (2015)	1 July	2013	Gaula	Norway	External Radio	27	3	89 ± 10	14 ± 3	Visual confirmation of survival during spawning. One fish that disappeared considered a survivor.
Lennox et al. (2016)	3 August	2014	Lakselva	Norway	External Radio	39	1	90 ± 16	14 ± 1	Visual confirmation of survival during spawning. One fish that disappeared considered a survivor.
Richard et al. (2014)	23 June	2011	Escoumins	Canada	Gastric Radio	20	0	77 ± 5	15 ± 1	Motion sensor in tag. One fish that regurgitated tag excluded.
Svenning et al. (unpublished)	9 July	2006	Målselva	Norway	Radio	31	0	83 ± 14	11 ± 1	Stationary transmitter
Thorstad et al. (2003)	1 August	1999	Alta	Norway	External Radio	14	0	81 ± 17	11 ± 1	Stationary transmitter
Thorstad et al. (2003)	25 July	2000	Alta	Norway	External Radio	16	1	84 ± 24	13 ± 1	Stationary transmitter
Thorstad et al. (2003)	22 July	2001	Alta	Norway	External Radio	14	0	91 ± 18	14 ± 1	Stationary transmitter
Thorstad et al. (2003)	5 July	2003	Alta	Norway	External Radio	18	1	96 ± 12	13 ± 1	Stationary transmitter
Webb (1998)	6 April	1996	Dee	Scotland	Gastric Radio	25	1	69 ± 8	NA	Tag stationary during flow events and during spawning period. Regurgitated tags

variables without biasing regression coefficients (Harrell, 2015b). The dataset was therefore completed using multiple imputation implemented by the *aregImpute* function in the R (R Core Team, 2016) package Hmisc (Harrell, 2014), which uses simple bootstrapping and predictive mean matching to replace missing values based on observations from the non-missing target variables (Harrell, 2014). The *aregImpute* function generates values by fitting a flexible additive model based on all non-missing observations available for that variable. The number of knots used for continuous variables by the *aregImpute* function was specified to be 0 and the number of imputations was set to 5 as recommended by the package documentation (Harrell, 2014). In an effort to provide additional information to the imputation algorithm to predict missing water temperature values, the latitude of the study river was included as well as an estimated mean air temperature at the closest weather station on the date of capture. Air temperatures were downloaded using the *getWeatherForDate* function in the weatherData package (Narasimhan, 2014). Data for 1996 were not available for Dee River so 1997 data were used.

Detections of tagged fish were used to establish the fate of Atlantic salmon that were released using both radio and acoustic telemetry receivers (Table 1). Given that the data were collected in various contexts with different study designs and limitations, there were some differences among studies in how the endpoint of mortality of the fish was determined (Table 1). Generally, observations that the tag had ceased movement without up- or down-river movement during or after spawning was interpreted as mortality. Fish that were recaptured by anglers were considered survivors.

2.2. Data analysis

To avoid biasing parameter estimates and in order to increase predictive power, a single set of candidate predictors was established for the full model, without reduction (Harrell, 2015b). Gear type, date of year (i.e. Julian day), hook location, play time, water temperature, and total length were considered as potentially relevant fixed effects as well as the interaction between water temperature and play time. Air exposure was not included because data for air exposure were not consistently reported as a continuous variable. Information on the extent of bleeding was also excluded because it was not collected in a consistent manner and there was likely to be significant observer bias among studies; instead, hook location was used as an index of injury. Sex was excluded because external sex determination can be difficult for immature adult salmon (Kadri et al., 1997) and incorrect assignment would add uncertainty to our model.

Survival was modeled by logistic regression. Each study was conducted independently in various rivers using slightly different tagging techniques and methods of determining survival, so the study (Table 1) was incorporated as a random intercept in the model in consideration of possible lack of independence. Mixed effects logistic regression was implemented by the *glmer* function in the R package lme4 (Bates et al., 2015). Continuous predictors were scaled because the original model failed to converge due to large eigenvalue ratios. Model fit was assessed with the *hoslem_gof* function in the sjstats package (Lüdecke, 2016). Factors with few levels that are used as random effects can result in small or null intercept values of random effects. Although comparison of models fitted with random effects is possible with linear models by using information criteria, it is trivial for generalized linear models. The variance estimate of the random effect was 0, indicating that the variation among studies was small (see Supplementary file 1 for details of mixed effects model). We therefore opted for a fixed effects logistic regression implemented by *lrm* in the rms package (Harrell, 2015a). Logistic regression fitted without random effects is more flexible for testing model fit and modelling predicted probabilities (calculated using the *Predict* function in rms with continuous variables set to the mean and categorical predictors set to the most frequent value). Index adjusted (Steyerberg et al., 2010) Brier's Score and Harrell's *c* (equivalent to area under the curve; Harrell et al., 1996) were used to evaluate predictive performance of the logistic regression model. Odds ratios are presented to highlight the importance of predictor variables on mortality by exponentiating regression coefficients. Model fit of the logistic regression was assessed with the native test in the rms package, which is the le Cessie - van Houwelingen - Copas - Hosmer unweighted sum of squares test for global goodness of fit (Hosmer et al., 1997) at $\alpha = 0.05$.

3. Results

We collated salmon telemetry data from 12 rivers between the 48th and 70th northern parallel latitudes in Canada, Ireland, Scotland, Northern Ireland, and Norway (Fig. 1). Survival data were available from 512 individuals (mean fork length 75 ± 15 cm TL; range: 44–122 cm TL). The studies generating the data were conducted between 1996 and 2014 and all fish were captured between March 2 and October 15 (median date of capture = August 9). Salmon were captured at water temperatures ranging from 7.5 to 22 °C (mean = 14 ± 3 °C; 176 missing values). On average, salmon were played for 9 ± 7 min (range: 2–70 min; 199 missing values). There was a positive correlation between salmon size and playing time ($R^2 = 0.60$). Most salmon were captured by artificial flies (N = 279) with others captured on natural bait (N = 11) or lures (N = 56; 166 missing values). Most (N = 288) salmon were hooked superficially in the jaw or mouthparts but some were deep hooked (N = 20). Others were foul hooked (N = 9) and there were 195 missing values. Among the 512 salmon caught and released in these studies, 478 were categorized as catch-and-release survivors (93%).

Table 2
Regression coefficients, p-values, and odds ratios for logistic regression model fit to Atlantic salmon survival data from 11 studies. Odds ratios indicate odds of survival and are for a one-unit (day for date, cm for total length, s for play time, °C for water temperature) increase of continuous predictors and for a change in odds between levels of categorical predictors. The reference level for hook location is deep hooked and for gear the reference level is bait. Odds ratios <1 are a decrease in odds.

	Estimate ± SE	z-value	P-value	Odds ratio
Intercept	4.53 ± 2.87	1.58	0.11	
Date	0.00 ± 0.01	0.42	0.68	1.00
Total length	0.01 ± 0.02	0.69	0.49	1.10
Play time	−0.21 ± 0.16	−1.27	0.20	0.81
Water temperature	−0.33 ± 0.11	−3.08	<0.01	0.72
Hook location (superficial)	0.33 ± 0.78	0.42	0.68	1.39
Gear (fly)	1.74 ± 0.82	2.12	0.03	5.71
Gear (lure)	0.56 ± 0.85	0.66	0.51	1.75
Water temperature × play time	0.01 ± 0.01	1.06	0.29	1.01

3.1. Regression modelling

Total length of fish (z = 0.69, P = 0.49; Table 2; Fig. 2) and playing time (z = −1.27, P = 0.20; Table 1; Fig. 3) exerted no significant effect on salmon survival. Delayed mortality, however, was significantly influenced by water temperature at the time of capture (z = −3.08, P < 0.01; Table 2). Odds of mortality increased by 1.38 for each °C unit increase in water temperature. Model-predicted probability of mortality for salmon captured at the mean temperature of 14 °C was 4%, and 16% at the max temperature of 22 °C (Fig. 4). Salmon captured by flies had higher survival (95%) than salmon captured by lures (85%) or bait (86%). Correspondingly, odds of survival increased by 5.55 for fly-caught fish relative to those captured by bait (z = 2.12, P = 0.03), and by 1.75 for lure-caught fish relative to bait-caught fish (z = 0.66, P = 0.51; Table 2; Fig. 5). Flies more frequently deep hooked fish (8%) compared to bait (0%) and lures (3%). Survival was high for fish hooked in deep (96%) and superficial (93%) anatomical locations and was not a significant predictor of mortality (z = 0.42, P = 0.72; Table 2; Fig. 6). The model fit the data (z = 1.05, P = 0.29) and had moderate predictive performance (Brier's Score = 0.06; Harrell's *c* = 0.73). Output of the mixed effects model was similar to the fixed effects model and is presented in Supplementary material.

4. Discussion

Recreational Atlantic salmon fisheries in spawning rivers can be highly exploitative and capture a large percentage of the total adult population during their upriver migration (Downton et al., 2001; Erkinaro et al., 1999; Gudjonsson et al., 1996). Therefore, mortality due to catch-and-release fishing could exert significant population-scale effects on this species, particularly given that Atlantic salmon fishing is selective for particular behavioural, physiological, and life history phenotypes (e.g., large fish, repeat spawners which tend to be females, the bolder fish; Consuegra et al., 2005; Hard et al., 2008; Pérez et al., 2005). Whereas most catch-and-release mortality studies have observed infrequent delayed mortality of released salmon ascending to spawning grounds, small sample sizes have mostly precluded an accurate assessment of risk factors contributing to delayed mortality. Our approach has reaffirmed that survival of released salmon is frequent in catch-and-release fisheries (93%), supporting the implementation of catch-and-release as a tool for managing these fisheries. However, we also identified significant risk factors that were important predictors of mortality. This knowledge can help guide management of recreational salmon fisheries.

The most salient finding from our analysis was that Atlantic salmon mortality increased when water temperature at capture increased. Water temperature had previously been recognized as a significant risk factor in catch-and-release salmon fisheries (Dempson et al., 2002; Havn et al., 2015; Wilkie et al., 1996, 1997). At high water temperatures, exhausted fish have impaired ability to replenish intramuscular glycogen and cannot restore intramuscular pH associated with high levels of lactate (Wood et al., 1983). Wilkie et al. (1996) found that angling at temperatures above 20 °C resulted in complete exhaustion of anaerobic muscular fuels. Havn et al. (2015) identified fallback and long delays before recovering upriver migration for salmon caught and released at high water temperature (data included in this study). In our analysis, water temperature was a significant predictor of delayed mortality. Some fisheries have adopted seasonal or threshold-based closures as management practices to reduce fishing effort during physiologically sensitive warm-water periods for Atlantic salmon (Dempson et al., 2001). It is always controversial to close rivers for extended periods during angling seasons because of the economic consequences (Bielak, 1996) but it is relevant to have data that can contribute to estimates of survival for fish captured during these periods.

Physical injury caused by hooking is the most important predictor of post-release fisheries mortality (Muoneke and Childress, 1994). Hooks

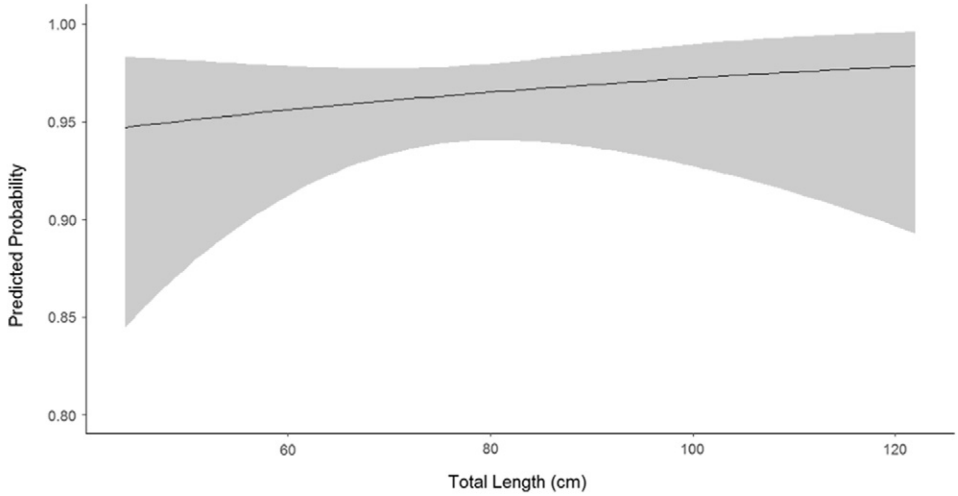

Fig. 2. Model predicted probability of survival for Atlantic salmon released from recreational fisheries as a function of total length. Predictions are based on a logistic regression model with continuous predictors adjusted to the mean value and categorical predictors adjusted to the most frequent value. Shaded area corresponds to the 95% confidence interval.

that penetrate vital organs or tissues can cause critical damage or result in exsanguination (Bartholomew and Bohnsack, 2005; Muoneke and Childress, 1994). In our data, there were no differences in odds of survival for deep hooked fish compared to those that were superficially hooked. However, we emphasize that by focusing on delayed mortality this might underestimate the impacts of deep hooking because those fish are not often released by anglers (see Methods). There was only one mortality among 20 released salmon that had been deep hooked, perhaps because fish were captured and handled by experienced anglers with the necessary tools to remove hooks without damage. Anglers that carefully remove the hooks may therefore release salmon that are deep hooked and expect them to survive. In other fisheries, cutting the line rather than attempting to remove the hook has been demonstrated to be effective for mitigating delayed mortality of deeply hooked fish (Fobert et al., 2009); however, similar research is lacking for Atlantic salmon and cutting the line was not included in our analysis.

The fishing gear used by anglers can influence the hooking damage and condition of fish captured by anglers. When allowed by local regulations, salmon anglers use a variety of methods when targeting salmon, which we simplified to flies, lures, and bait. Warner and Johnson (1978) demonstrated higher survival of fly-caught juvenile landlocked salmon (*Salmo salar*) relative to worm-caught (bait) salmon. This was suggested to be one of the most needed catch-and-release research priorities for Atlantic salmon by Hühn and Arlinghaus (2011). Fly-caught fish had significantly higher post-release survival than those captured by lures or bait. This is probably because flies tend to be fished with smaller hooks than lures or bait, and future research should focus more specifically on the effects of hook size to determine whether smaller hooks paired with lures would improve post-release survival. Higher post-release survival of fish captured by flies is not necessarily an indictment of fishing with other methods but can be a consideration when estimating the extent of post-release mortality of salmon expected in a given fishery.

Adult Atlantic salmon body size can vary greatly depending primarily on the number of years an individual fish has spent feeding at sea. Our analysis included data from various rivers that hold salmon with different life history traits, including rivers Alta and Lakselva where the fish tend to spend more time at sea than occurs for other populations and consequently have larger body size at maturity (Lennox et al., 2016; Thorstad et al., 2003). Larger fish tend to be more exhausted by angling due to longer playing and handling times (Meka and McCormick, 2005) and correspondingly have greater extents of physiological disturbance to muscular tissue (Ferguson et al., 1993; but see Booth et al., 1995) as well as greater impairment of their reproductive

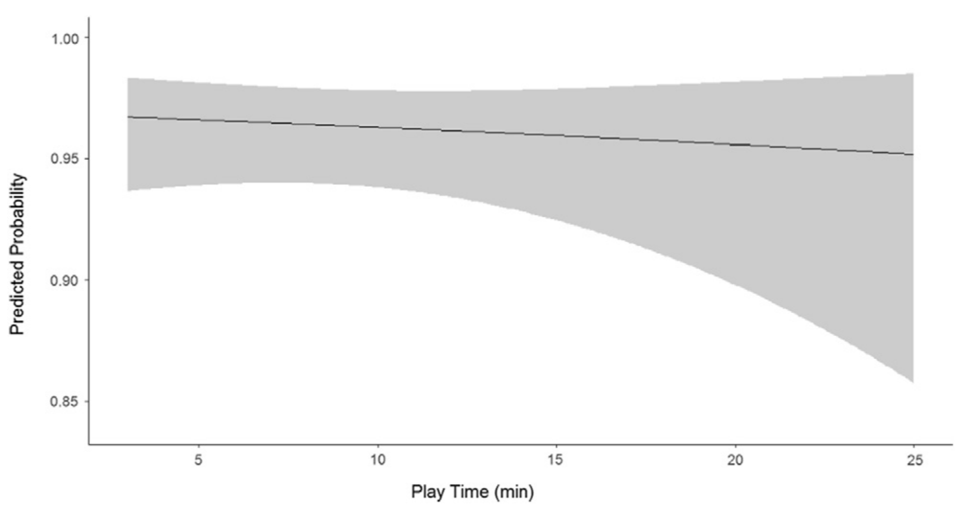

Fig. 3. Model predicted probability of survival for Atlantic salmon released from recreational fisheries as a function of the time played by anglers. Predictions are based on a logistic regression model with continuous predictors adjusted to the mean value and categorical predictors adjusted to the most frequent value. Shaded area corresponds to the 95% confidence interval.

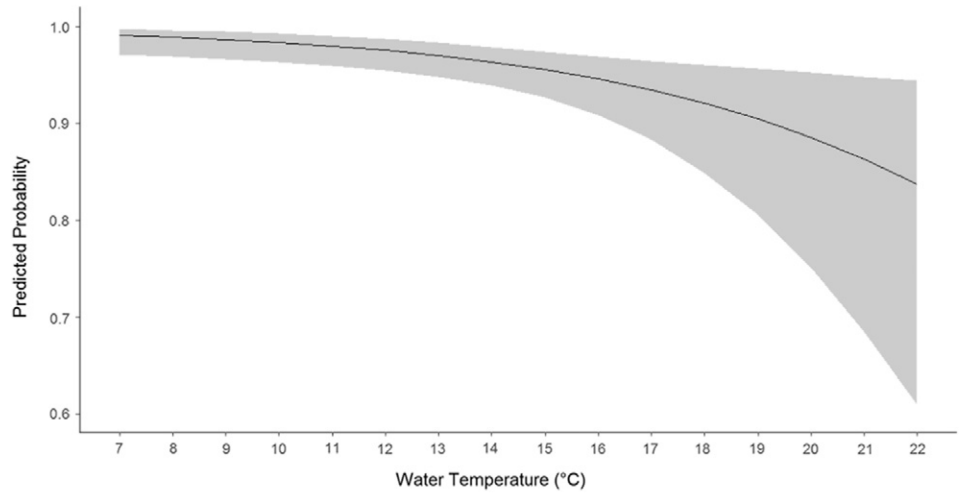

Fig. 4. Model predicted probability of survival for Atlantic salmon released from recreational fisheries as a function of water temperature at capture. Predictions are based on a logistic regression model with continuous predictors adjusted to the mean value and categorical predictors adjusted to the most frequent value. Shaded area corresponds to the 95% confidence interval.

success (Richard et al., 2013). We predicted an effect of body size on catch-and-release mortality, but found limited evidence that body size influenced post-release survival. Moreover, we did not find an effect of playing time. This suggests that playing times are not of serious concern to salmon mortality in recreational fisheries, but anglers and managers should be aware that extended playing times arising from using incorrect methods or inexperience with landing and handling fish may nonetheless be detrimental (Richard et al., 2013). The effect of playing time and handling probably increase when water temperatures rise (Gingerich et al., 2007). Although not a significant factor in our data, the interaction of factors (particularly between water temperature and others) is an area that requires further research for recreational fisheries in general.

The data were collected with various methods for tagging, tracking, and determining mortality. This can introduce variation that violates the assumption of independence in regression models, which is why we considered modelling the data using the mixed effects regression with study as a random intercept. However, the variance estimate of the random effects in the mixed effects model was 0, indicating nominal influence of the random component on the model. It could be that the variation among studies was captured by the fixed effects. Although there were methodological differences among studies, the studies varied mostly by the size distribution of the fish captured, gear used in the study rivers, and water temperature in the rivers, which were tested as fixed effects. Mixed effects modelling may differ more from logistic regression in instances where systematic variation in vulnerability to fishing-induced mortality existed among populations, such as differences in thermal sensitivity. Anttila et al. (2014) found only minor differences in thermal plasticity of Atlantic salmon between individuals from northern and southern populations, suggesting that the species probably does not have highly significant among-population differences that would affect delayed mortality.

The fate of fish released by anglers is difficult to quantify and telemetry offers an opportunity to study free-living fishes for this purpose (Donaldson et al., 2008). However, proper design of telemetry studies to evaluate post-release mortality is important and there was variation among studies in our review that imposed some statistical limitations. Studies did not use identical criteria for assigning fates to fish that were released, based on the implementation of different tag technology (i.e. radio or acoustic transmitters), tracking (i.e. fixed array or active tracking), or other approaches. Moreover, transmitter loss/malfunction can be difficult to separate from mortality. It is important to consider that transmitter loss has been shown to be higher for gastric radio tagging methods than external attachment or implantation (Smith and Campbell, 1998; Thorstad et al., 2013), which might bias the estimation of mortality; albeit given the small number of total mortalities it is

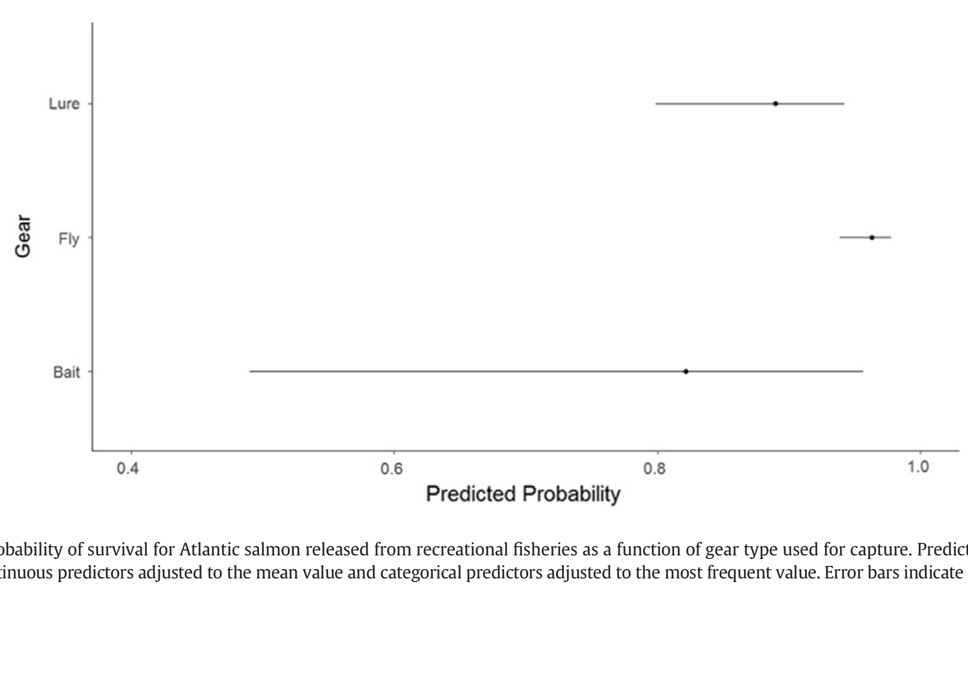

Fig. 5. Model predicted probability of survival for Atlantic salmon released from recreational fisheries as a function of gear type used for capture. Predictions are based on a logistic regression model with continuous predictors adjusted to the mean value and categorical predictors adjusted to the most frequent value. Error bars indicate the 95% confidence interval.

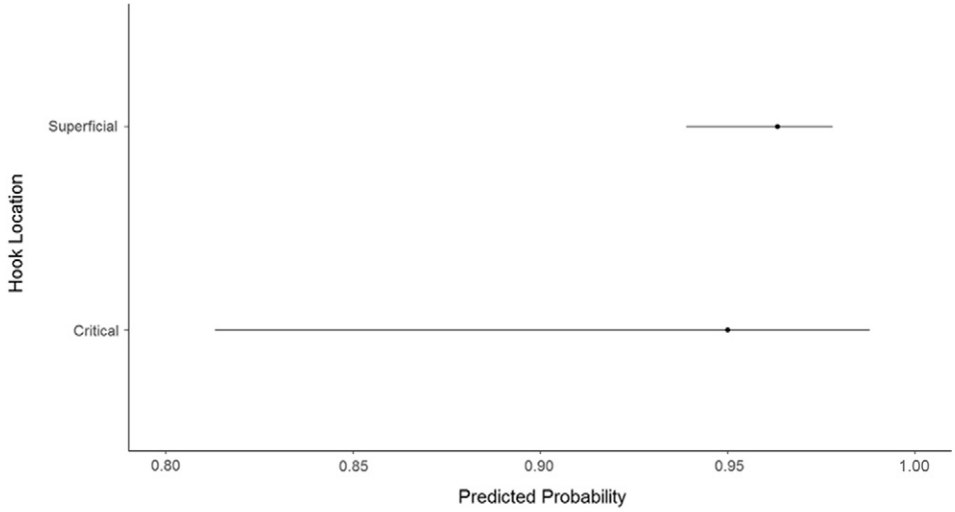

Fig. 6. Model predicted probability of survival for Atlantic salmon released from recreational fisheries as a function of hooking location. Predictions are based on a logistic regression model with continuous predictors adjusted to the mean value and categorical predictors adjusted to the most frequent value. Error bars indicate the 95% confidence interval.

unlikely to have introduced systematic error. Visual surveys may be necessary to accurately classify survival (Lennox et al., 2016) or activity sensors in the tags that can be used to infer mortality more accurately (e.g. Richard et al., 2014). In some cases, post-release predation can contribute to fisheries mortality (Raby et al., 2014); in this study, some mortalities registered in River Bann may have been due to seal (*Phoca vitulina*) predation. Given that risk factors (i.e. water temperature, injury) that govern vulnerability to post-release predation are not well understood (Raby et al., 2014), we opted to include these fish in the analysis under the rationale that post-release predation is a component of overall catch-and-release mortality. Nonetheless, we recognize how such challenges could influence interpretations of models. We also acknowledge that the delayed mortality rate we present in this study probably represents a maximum estimate given the methods used to quantify mortality were mostly inferential rather than direct.

Logistic regression is effective for generating predictions but has lower power than survival analysis for detecting important predictors (Murray, 2006). Survival analysis is properly suited to handling telemetry data because it allows for disappearance of some individuals (i.e. right censoring), delayed entry (i.e. left censoring), and has more power to detect significant predictors of survival (Murray, 2006; Harrell, 2015b). Survival analysis was not possible in our study based on the nature of the sampling designs, but small changes to the sampling design could enable future studies to implement such an analysis by relocating fish at fixed intervals. Data-driven approaches to managing fisheries can assist with management and facilitate emergency closures or other restrictions in order to meet conservation targets. In salmon fisheries, our model suggests that delayed mortality is sufficiently rare that it is difficult to systematically predict which individuals are likely to die after release. Nonetheless, the identification of significant factors is relevant for understanding how delayed mortality operates across the range of Atlantic salmon.

Although mortality is catastrophic for individual fitness, catch-and-release can also impart sublethal effects on fish that could significantly impair lifetime fitness that may be underrepresented when mortality is the only metric used to assess fishery sustainability. There is evidence for sublethal effects of catch-and-release on Atlantic salmon migration (Lennox et al., 2016) and reproductive success (Richard et al., 2013), albeit equivocal evidence of reduced reproductive output (Booth et al., 1995; Richard et al., 2013). Our study intended to analyze delayed mortality of Atlantic salmon and we have confirmed that it is a relatively rare occurrence that is difficult to predict. Future research must address questions related to the spawning activity and energetics of salmon released by anglers and determine whether post-spawning behaviour and survival are negatively affected.

5. Conclusions

Catch-and-release can be an effective conservation measure for recreational fisheries. Yet, some fish die after catch-and-release; understanding why this occurs can provide important insight for managing recreational fisheries. Although Atlantic salmon are considered to be a well-studied species in the context of catch-and-release fisheries (Cooke and Suski, 2005; Hühn and Arlinghaus, 2011), it was clear from the available literature that the relative importance of many potentially influential factors was not well understood as a result of small sample size from individual studies. Our collaborative approach therefore provides improved insight into the effects of angler practices, extrinsic conditions, and inter-individualistic differences that can be used to predict salmon mortality in fisheries. Our hope is that the predictor variables considered in this paper will facilitate a better understanding of delayed mortality of salmon and recognition that salmon handled using best practices are likely to survive to spawning, which will lead to a more sustainable approach to Atlantic salmon recreational fishing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.01.022.

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