Ecological Modelling 333 (2016) 43–50

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Use of simulation approaches to evaluate the consequences of catch-and-release angling on the migration behaviour of adult Atlantic salmon (*Salmo salar*)

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ARTICLE INFO

Article history:
Received 4 December 2015
Received in revised form 29 February 2016
Accepted 8 April 2016
Available online 4 May 2016

Keywords:
Telemetry
Recreational fisheries
Sublethal effects
Angling
Simulation

ABSTRACT

Given most Atlantic salmon (*Salmo salar*) released by anglers survive (proportion = 0.97 in this study), economically and culturally important recreational Atlantic salmon fisheries are increasingly incorporating catch-and-release. Sublethal alterations to behaviour with potential individual fitness costs are a possible consequence of catch-and-release but are difficult to measure empirically relative to uncaptured fish. To test for sublethal effects of angling on migratory movements, 39 salmon were captured by recreational anglers, externally tagged with radio transmitters, and released. Data from the annual visual drift count of spawning salmon were used to calculate the probability of spawning in each pool of the river and input into simulation models. Simulation models were used to test the hypothesis that catch-and-release did not affect the upriver movement of 30 salmon tracked to spawning grounds. Ten thousand simulation steps selected a spawning pool for each of the tagged salmon, permitting a calculation of the average expected movement by salmon for comparison to the average movement observed with telemetry. The average observed movement by the released salmon was significantly less than the average expected movement generated by all three null models, indicating a sublethal effect of catch-and-release on the migration of Atlantic salmon.

1. Introduction

Atlantic salmon (*Salmo salar*) migration in freshwater incorporates multiple phases of activity including active upriver movement, holding, and searching with upstream and downstream movements before staging near the eventual spawning destination weeks or months in advance of spawning (Økland et al., 2001; Finstad et al., 2005; Thorstad et al., 2011). Atlantic salmon are philopatric with most individuals able to locate their natal rivers (Fleming, 1996) and even specific tributaries within a system (Heggberget et al., 1988; Verspoor et al., 1991). The timing and speed of migration by Atlantic salmon through freshwater depends on a variety of factors, including sex (Lucas et al., 1993), size (Kristinsson et al., 2015), and experience (Niemelä et al., 2006). However, anthropogenic challenges including pollution (Thorstad et al., 2005), artificial barriers (Croze, 2008), and climate change (Baisez et al., 2011) alter migratory patterns exhibited by salmon. In addition, recreational fishery practices such as catch-and-release have the potential to influence the migratory behaviour of salmon in rivers.

Recreational fisheries are popular worldwide and can be important components of the economy for many communities (Arlinghaus and Cooke, 2008). The sustainability of recreational fisheries, however, depends on the ability of the targeted fish population to persist in spite of harvest and non-harvest mortality imposed by angling activities (Coggins et al., 2007; Cooke and Schramm, 2007). Traditionally, many recreational anglers harvested their catch; however, catch-and-release is now increasing in many fisheries. From a regulatory perspective, catch-and-release focuses on maintaining the socio-economic benefits of fisheries while sustaining fish populations that are being exploited. As a result, catch-and-release practices assume that fish released by anglers have high survival and experience limited sublethal consequences to their lifetime reproductive success (Arlinghaus et al., 2007; Wilson et al., 2014). Catch-and-release is increasingly

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http://dx.doi.org/10.1016/j.ecolmodel.2016.04.010
0304-3800/

practiced in recreational salmon fisheries but scientific evaluations of catch-and-release for salmon have focused on documenting mortality for caught-and-released fish (e.g. Thorstad et al., 2003; Gargan et al., 2015). Mortality studies alone probably underestimate the impacts of catch-and-release because they do not consider sublethal effects (Cooke et al., 2002). Sublethal effects occur as a consequence of aerobic debt (Kieffer, 2000; Lee et al., 2003), metabolic disturbance (Wood et al., 1983), physiological stress (Pankhurst, 2011), and exhaustion induced by angling. The resulting prolonged recovery can manifest in behaviour and may cause significant indirect and direct impairments to potential fitness (Cooke et al., 2002; Wilson et al., 2014). Sublethal effects of catch-and-release can be difficult to measure because equating a capture event to fitness is challenging. However, migrating salmonids provide a useful model for identifying sublethal effects of angling because the upriver migration towards spawning grounds might be a reflection of fitness (Dingle, 1980).

There is correlative evidence that angling alters migration patterns of Atlantic salmon. Two documented alterations to migratory patterns that have been observed for Atlantic salmon released by anglers are downriver movement from the release site (i.e. fallback; Mäkinen et al., 2000; Thorstad et al., 2003; Havn et al., 2015) and shortened migration distance (Tufts et al., 2000; Lennox et al., 2015a). However, the extent to which catch-and-release actually causes significant changes to an individual's migration is unclear. Determining whether migration is impacted by angling requires an estimation of where salmon would spawn if anglers did not capture them. It is difficult to know where salmon are destined to spawn in the river prior to the spawning period itself, necessitating the development of a novel tool incorporating an estimate of the spawning distribution of non-angled fish within the river as a proxy for the ultimate distribution of released fish at spawning time. This information provides a natural baseline against which hypotheses about the impacts of catch-and-release can be tested. We developed such a model and tested model-predicted movement against observed movement of tagged salmon with a null hypothesis of no effect of catch-and-release. Model predictions were generated from the distribution of salmon at spawning time based on the results of a passive drift count. These were compared to the upriver progress and spawning locations used by Atlantic salmon after catch-and-release as determined by radio telemetry.

2. Methods

2.1. Study area

River Lakselva drains into the Porsangerfjord in Porsanger, Finnmark, Norway. Lakselva is a large river with one major tributary (Vuolajohka) and two large lakes (Fig. 1). Atlantic salmon enter Lakselva during the spring and summer and spawn in Lakselva in September–October (E. Liberg, Personal Communication). About 45 km of the river is accessible to Atlantic salmon. The recreational fishery is co-managed by the Lakselva Landowner's Association, which limits access to most of the fishery via a licensing system. There are also stretches of river where angling is co-managed by landowners or local lodges. The annual salmon fishing season in Lakselva begins June 1 and continues through August 31. Average annual catch in Lakselva (2007–2015) is 1464 ± 229 (SD) Atlantic salmon (www.scanatura.no).

2.2. Tagging

Historical catch records indicated that few salmon enter this river in June; therefore, we focused our tagging efforts between July 13 and August 28, 2014. Salmon selected for tagging (*N* = 39) were those that were typical of caught-and-released fish, and not moribund (see Lennox et al., 2015a). After being landed by an angler, salmon were transferred to a water-filled tube where they were placed in a prone position. The individual was measured and a radio transmitter in the frequency range 142.114–142.213 (Advanced Telemetry Systems [ATS], Minnesota, USA) was attached externally below the dorsal fin. The tagging methods followed Lennox et al. (2015a), using sterile hypodermic needles and stainless steel wire to secure the radio tag through the dorsal musculature. Anglers that captured salmon handled them naturally and we did not attempt to interfere with their fish handling (e.g. by telling them to use a net, not to air expose the fish too long, etc.). However, we declined to tag two angled salmon; one salmon was critically injured (hooked in gills) and the other was too small to support the tag properly. In total, 39 Atlantic salmon (mean = 89 ± 16 cm TL, range: 62–121 cm) captured by anglers were radio tagged and released. Mean water temperature at capture was 14 ± 1 °C whereas temperature stress begins to become an important issue in Atlantic salmon angling at >20 °C (Dempson et al., 2002; Havn et al., 2015). All handling and tagging were conducted according to Norwegian regulations for treatment and welfare of animals.

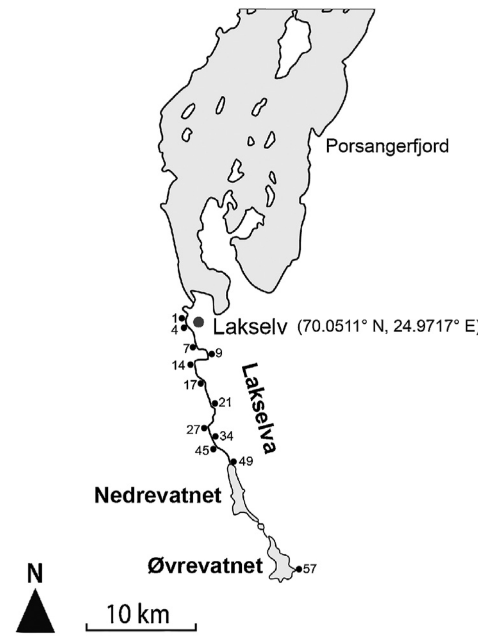

Fig. 1. River Lakselva watershed in Porsanger, Finnmark, Norway. The watershed incorporates two major lakes, Øvrevatnet and Nedrevatnet. Atlantic salmon return to the river from the ocean through the Porsangerfjord throughout the summer and migrate upriver to spawning grounds. For this study, salmon released by anglers were tagged at various points in the river, although mostly in the lower reaches. Some pool numbers are provided for reference. Note that the river flows south to north.

2.3. Tracking

To ensure adequate coverage of the watershed, four stationary data logging stations were established at key points in the river to monitor passage of salmon. Data logging receivers (Advanced Telemetry Systems [ATS], Minnesota, USA; R4500CD Coded Receiver–Datalogger) were established with paired antennas (Lotek, Newmarket, Canada; six element Yagi tuned to 142 MHz; one pointing upriver and one pointing downriver) to establish directionality of movement by salmon past the receiver. The stations were established above and below each of the lakes and also near the mouth of the tributary Vuolajohka (Fig. 1). Data were downloaded from receivers biweekly and the receivers remained active from June–October. In addition to the stationary logging stations, mobile tracking was conducted along the river using a vehicle mounted receiver and a magnetic whip antenna (Magnetic Roof-Mount Dipole, Laird Technologies, Missouri, USA). Salmon positions were determined on alternating days starting on July 14 and continuing through the end of the angling season on August 31, 2014. After the salmon fishing season, positioning occurred on September 2, September 15, September 24, and October 24. On September 24–25, a snorkel survey was conducted in conjunction with radio tracking to confirm survival of some salmon with nominal movement after release.

2.4. Drift count

Each year in Lakselva, the Landowner's Association conducts a visual count to estimate the total number of salmon in the river. The count is conducted by two experienced persons who drift passively downriver while snorkeling. For each section of the river (typically delineated by pools), the number of spawning salmon is estimated based on these visual observations. Although drift counts are considered underestimates of the total number of salmon, Orell and Erkinaro (2007) found that they provided accurate estimates of spawning biomass during the salmon spawning season. In 2014, the drift count in Lakselva was conducted on September 13–14, and spawning was observed to have commenced based on observations of salmon redds and some spent salmon (E. Liberg, Personal Communication). Staff was aware of and noted the presence of tagged salmon based on visual identification of the external radio tags. We collected drift count data from Lakselva for 2011, 2013, 2014, and 2015.

2.5. Data analysis

Each pool in the drift count was assigned a number, with the pool closest to the fjord being Pool 1 and the pool farthest upriver being number 57 (Fig. 1). Pools for which salmon could not be enumerated by divers due to poor visibility were assigned zero salmon for the purposes of analysis. Atlantic salmon generally spawn during the autumn (September–November) over a period generally extending up to one month (Heggberget, 1988). In Lakselva, spawning generally occurs in mid-late September through October (E. Liberg, Personal Communication) and had commenced in mid-September 2014 according to visual observations during the annual drift count. Although salmon move between spawning redds (Taggart et al., 2001), in general, they migrate quickly upriver and hold for long periods in close proximity to their ultimate spawning grounds (Økland et al., 2001; Finstad et al., 2005; Thorstad et al., 2011). Salmon attempt to spawn multiple times during the spawning season and move between redds to do so. Females complete spawning earlier than males and often move downriver after spawning. For our analysis, we used radio tracking data from September 24 to determine the spawning pool used by tagged salmon in Lakselva. Although some salmon may have moved into other pools to spawn, the positions on September 24 were considered representative of the pool salmon inhabited during spawning given that salmon were highly likely to have completed their migration by that time and that movements during this period were unlikely to be significant.

The release and spawning pools were compared to assess the movement of salmon released by anglers. The analyses could be conducted on 30 of the 39 tagged salmon because one died, one exited the river, and seven were recaptured and killed by anglers prior to spawning season. We used a Pearson correlation to quantify the relationship between the salmon's release and spawning pools. To test whether catch-and-release affected the movement of salmon within the river, a series of simulations was conducted to create a distribution of the most probable average movement of salmon from the release site under the null hypothesis of no effect of catch-and-release.

The simulation tests were implemented as follows: each pool was assigned a probability that a salmon would spawn there based on the proportion of salmon observed there during the 2014 drift count. These pool probabilities were calculated and applied to each of the 30 radio tagged salmon (Table 1). A single simulation step was implemented using the *sample* function in R (R Core Team, 2014), which selected a spawning pool for each salmon based on the assigned probabilities, permitting a calculation of expected movement by subtracting the number of the release pool from the number of the simulated spawning pool. For example, a fish captured and released in Pool 1 could be assigned Pool 10 as a spawning pool in a simulation step, equating to an expected movement of nine pools. Averaging the expected movement among the 30 salmon and repeating the simulation 10,000 times generated a probability distribution that described the average expected movement of salmon from the site of their release to spawn. The average expected movement was then compared to the average observed movement of the 30 radio tracked salmon. The p-value for the two-sided alternative hypothesis was calculated as $2\times$ the proportion of simulations smaller than the test statistic (i.e. the average observed salmon movement). We ran three simulations each using different assumptions (described below). All models tested the null hypothesis that catch-and-release had no effect on a salmon's upriver movement to spawning grounds.

Finally, we present data from the drift count in Lakselva for 2011, 2013, 2014, and 2015 to assess temporal stability in the distribution of spawning salmon within the river. We used violin plots as implemented by ggplot2 (Wickham, 2009), which show the density of spawners along the longitudinal axis of the river. To test for differences in the distribution of spawning positions across years we used a Kruskal–Wallis non-parametric analysis of variance.

2.5.1. Free distribution

In the first simulation, radio tagged salmon were assumed in the null model to distribute anywhere in the river to spawn, independently of where they were caught-and-released. The probability of choosing a given spawning pool was estimated as the proportion of the total number of spawners in the river observed in this particular pool during the drift count. This corresponds to assuming that salmon will freely distribute in a river and concentrate in some areas, presumably of high quality spawning substrate. Although salmon are positively rheotactic and migrate upriver to spawning sites, this simulation assumed that no matter where salmon were captured, they could in theory move up or down independent of the release location by maintaining equal spawning pool probabilities for all salmon.

2.5.2. Salmon only move upriver

In the second simulation, spawning pool probabilities were adjusted based on the release pool for each radio tagged salmon such that any pools downriver of the release pool had zero probability of salmon spawning there and upriver pool spawning probabilities were adjusted accordingly for each fish.

2.5.3. Most salmon move upriver

The third simulation was identical to the second, with the exception that it excluded salmon that spawned at or below the release site. This restricted the simulation to 15 salmon that spawned at least one pool upriver from the release location. Fifteen salmon that spawned at or below the release pool were excluded under the assumption that these fish were captured after completing their migration whereas the other 15 were captured during their upriver migration.

Table 1
Individual data on the radio tagged salmon in the Lakselva River, Norway. Thirty-nine salmon were captured between July 13 and August 28 2014, nine of which were recaptured later in the migration, one of which disappeared, and one of which died. Two of the recaptured salmon were re-released and remained in the river for spawning. The spawning pool was determined by radio tracking in the fall during the spawning season and the net movement is the number of pools. Net movement after catch-and-release was calculated by subtracting the spawning pool as determined on September 24 from the release pool.

Capture date	Total length (cm)	Fate	Release pool	Spawning pool	Net movement (number of pools)
July 13	73	Survived to spawn	7	18	11
July 14	97	Recaptured			
July 15	98	Recaptured			
July 16	91	Recaptured			
July 16	90	Survived to spawn	21	27	6
July 17	95	Survived to spawn	1	1	0
July 17	80	Recaptured			
July 19	95	Survived to spawn	17	27	10
July 19	62	Disappeared			
July 24	66	Survived to spawn	1	1	0
July 26	63	Survived to spawn	8	10	2
July 27	121	Survived to spawn	2	2	0
July 30	111	Survived to spawn	18	24	6
July 30	103	Recaptured	18	34	16
July 30	81	Survived to spawn	18	14	−4
July 31	102	Survived to spawn	2	1	−1
August 1	111	Survived to spawn	18	18	0
August 2	109	Survived to spawn	18	18	0
August 2	93	Survived to spawn	18	14	−4
August 2	112	Survived to spawn	18	14	−4
August 5	112	Survived to spawn	21	18	−3
August 9	67	Recaptured			
August 9	90	Died			
August 10	64	Survived to spawn	1	3	2
August 10	94	Survived to spawn	1	2	1
August 12	94	Survived to spawn	2	3	1
August 13	99	Survived to spawn	2	10	8
August 13	69	Survived to spawn	14	20	6
August 14	69	Survived to spawn	1	2	1
August 14	84	Recaptured	1	13	12
August 14	91	Survived to spawn	27	21	−6
August 15	76	Recaptured			
August 15	89	Survived to spawn	27	27	0
August 16	101	Survived to spawn	21	24	3
August 17	102	Recaptured			
August 17	112	Survived to spawn	2	2	0
August 20	83	Survived to spawn	21	27	6
August 24	77	Survived to spawn	21	21	0
August 28	66	Survived to spawn	1	2	1

3. Results

3.1. Catch-and-release

Only one of the 39 tagged salmon is known to have died. This occurred soon after catch-and-release, and its drifting carcass was observed by an angler downriver of the release site just hours later (E. Liberg, Personal Communication). Therefore, survival from catch-and-release was high (proportion = 0.97 of released fish). Total mortality ($N = 2$) from angling was 0.95 (total $N = 40$) after including one moribund salmon that was not released because of bleeding. One tagged salmon left from the river in August, which was a grilse (i.e. one-sea-winter salmon) that had exhibited erratic behaviour after release, first moving upriver within hours of release and eventually moving downriver two kilometres below the initial release site before exiting in August (last tracked August 24), several weeks prior to the spawning period. Given the movement trajectory of that salmon, it was determined that it had survived catch-and-release but we were unable to test whether its river exit was associated with catch-and-release or whether it left the river to spawn in another, adjacent river (see Havn et al., 2015 where salmon exited River Otra and were found spawning in adjacent tributaries). Nine salmon (0.23) were reported as having been recaptured by anglers later in the angling season, with seven of them being harvested and two re-released. One of the seven harvested salmon was recaptured twice before being killed. Two tagged salmon that were captured multiple times remained in the river through the spawning season. One of the recaptured salmon was angled as a kelt in the river the year after tagging on June 20, 2015.

3.2. Spawning distribution of catch-and-release salmon

There was a strong positive correlation between the catch-and-release location and the final spawning position, indicating that there was limited upriver movement ($R^2 = 0.74$ Fig. 2). During the spawning period, all of the salmon that were still present in the river

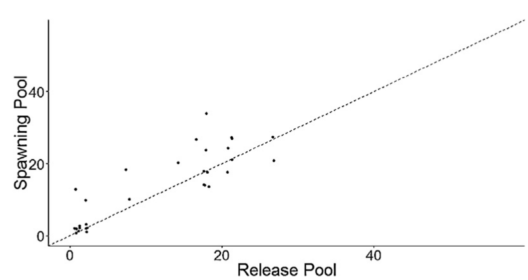

Fig. 2. Relationship between the release location and spawning position of 30 salmon released by anglers. Spawning pools were assigned based on locations where spawning counts occurred in September 2015. The dashed line indicates a 1:1 relationship between release pool and spawning pool (i.e. no upriver movement). Points are jittered to reduce overlap. $R^2 = 0.74$.

were located in regions of the river known to be spawning locations for salmon. In addition, 20 of the tagged salmon that remained in the river during spawning (0.71) were visually identified in spawning aggregations during the drift count. The Lakselva Landowners' Association counted 1341 salmon spawning in Lakselva during the drift count in 2014. The drift count was conducted in 72 pools in the river, which we consolidated into 57 pools for analysis based on the locations of pools in the river and counts from previous years. According to the drift count, the majority of salmon spawned below the lakes, with only ten salmon counted above Øvrevatnet. However, there were some areas in the river that were too turbid for the counting staff to conduct the count, making some areas of the river appear depauperate in the count. Most notably, sections of the river between Øvrevatnet and Nedrevatnet were not counted to poor visibility, nor was the tributary Vuolajohka. However, given that these regions were upstream of where all the tagged salmon spawned we suggest that this would not affect our results.

3.3. Simulation tests

3.3.1. Free distribution

When the simulation permitted salmon to distribute themselves anywhere within the river to spawn, salmon were predicted to move on average 9.43 pools upriver from the catch-and-release site (Fig. 3A). In other words, a theoretical 30 salmon released in the given pools (Table 1) would move on average 9.34 pools each toward spawning grounds if they were assumed to freely distribute themselves as the wild fish in the river did. This was mostly because the majority of radio tagged fish were captured in lower reaches of the river and would therefore be most likely to move upriver where the majority of the salmon were counted during the drift count. Based on fish positions from tracking data from September, the tagged salmon moved on average only 2.33 pools upriver from the release site, significantly less than expected based on the free distribution hypothesis ($p < 0.01$).

3.3.2. Salmon only move upriver

When salmon in this null model were restricted from backtracking to downriver spawning grounds, the simulation indicated that salmon would be expected to move on average 19.92 pools upriver from the release location. However, as noted above, the radio tracked fish displayed limited movement with average observed movement of 2.33 pools per individual, a highly significant difference from the model's prediction ($p < 0.01$; Fig. 3B).

3.3.3. Most salmon move upriver

When the second simulation was repeated excluding all salmon that exhibited any null or downriver net movements, we found that the simulation reduced the predicted movement per fish to only 18.56 pools upriver per individual. For the radio tracked sample, after removing the salmon that moved downriver, the observed movement was 6.07 pools per individual, a highly significant difference compared to the model's expected movement ($p < 0.01$; Fig. 3C).

3.4. Seasonal differences in drift count observations

Average spawning pools were calculated from historic drift counts and it was determined that the average spawning pools in Laksevla were pool number 30 in 2011 ($N = 849$; i.e. the total fish counted during this season), pool number 25 in 2013 ($N = 1254$), pool number 21 in 2014 ($N = 1337$), and pool number 26 in 2015 ($N = 832$; refer to Fig. 1). We observed some temporal inconsistency in the distribution of spawning salmon within Lakselva (Fig. 4). Indeed, there was a significant difference in the median position of spawners across years ($\chi^2 = 250.22$, df = 3, $p < 0.01$). However,

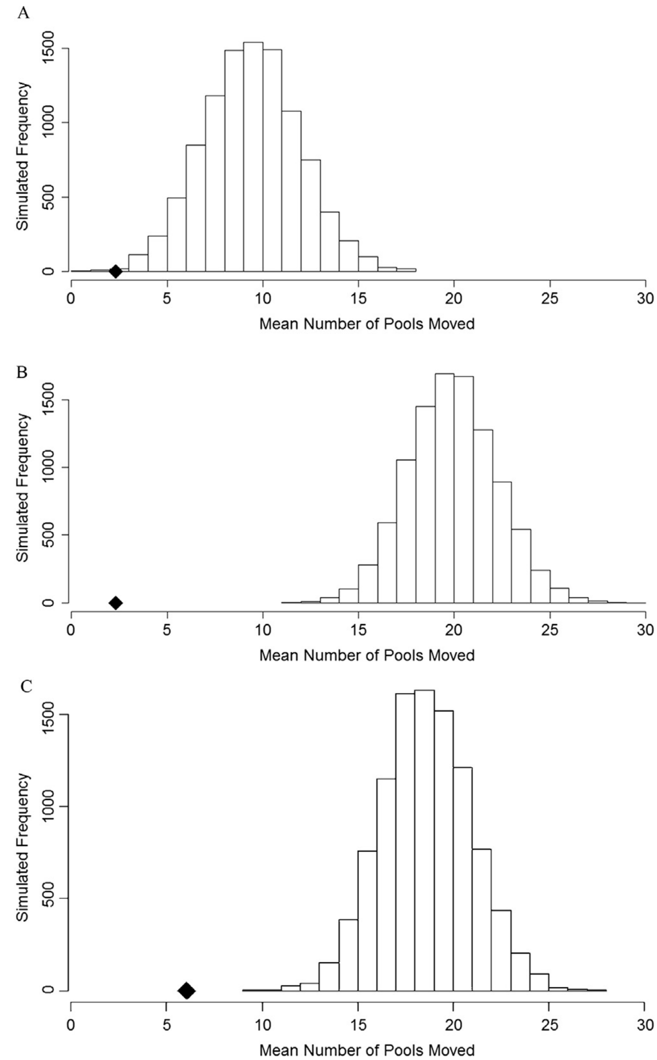

Fig. 3. Simulated test statistic distributions for the mean number of pools moved for Atlantic salmon under the null hypothesis of no effect of catch-and-release on post release movements and final choice of spawning pool. The black diamonds indicate the observed mean number of pools moved from the release location to the spawning location among the tagged salmon. Panel A gives the simulated distribution for the free distribution of salmon, B shows the distribution for the upriver movement only simulation, and C the distribution for the upriver movement simulation that excludes all salmon that spawned at or below the release site. Observed movement (black diamond) in Panels A and B are based on 30 salmon whereas panel C includes 15 salmon after removing individuals that spawned downriver of the release site (see Table 1 for list of salmon with negative movement that were excluded).

the majority of spawning salmon were consistently below Pool 49, which was the last pool prior to the first lake. Correspondingly, each year most salmon in the river spawned in pools in the middle of the anadromous stretch of the river (Fig. 4).

4. Discussion

Similar to other studies on the effects of catch-and-release angling on Atlantic salmon, we identified high survival of the fish released by anglers. One mortality among 39 salmon represents a high probability of survival for salmon given good angling practices. Interestingly, we calculated a high recapture rate of salmon in Lakselva. Lennox et al. (In Press) calculated a recapture frequency of about 0.18 from multiple Norwegian rivers (including Lakselva) in 2012–2013. In this study, 0.23 salmon that we tagged were recaptured in Lakselva including one individual that was recaptured twice (but counted in the proportion only once) and excluding one

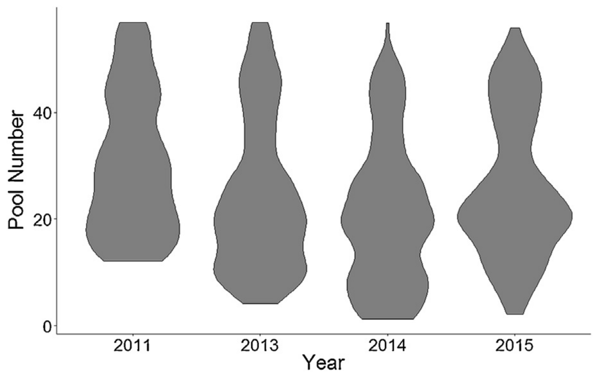

Fig. 4. Violin plots of annual drift counts in Lakselva. The width of violins indicate the spawning densities at corresponding pools of the river based on observations by drift counters. Note that across years there was some inconsistency in visibility, excluding some pools from the count; for example, the lower pools in the 2011 and 2015 counts. Only data from the 2014 count were used for the simulation models.

individual that was recaptured as a kelt (i.e. spent spawning salmon that overwintered in the river) the following summer. This frequent recapture is interesting because there have been no studies on the effects of multiple capture on salmon during their spawning migration. Some individuals tend to have higher vulnerability to angling than others do and would be captured more frequently than expected by chance (Cox and Walters, 2002; Tsuboi and Morita, 2004). However, Lennox et al. (2015a) found that salmon in a control group (captured prior to river entry by bag net) were not captured less frequently than salmon that had already been captured by anglers. That a relatively high proportion of salmon released by anglers was recaptured questions the effectiveness of catch-and-release in some fisheries where a high percentage of the population is captured by anglers (e.g. Gudjonsson et al., 1996; Downton et al., 2001). Frequent recapture of salmon suggests that further research is necessary to evaluate the physiological and behavioural effects of recapture for salmon during a potentially physiologically sensitive life stage. Indeed, encounters with recreational anglers are stressful for fish in the short-term. Burst exercise during angling increases the concentration of circulating stress hormones and results in osmoregulatory disruptions (Wood, 1991; Kieffer, 2000; Barton, 2002). After release, there is an energetic burden associated with repayment of oxygen debt (Scarabello et al., 1991) and restoration of intramuscular fuels (Kieffer, 2000).

Our simulation models demonstrated that the caught-and-released salmon in Lakselva had shorter migrations than expected from model inputs. Two other studies have identified reduced migratory distances traveled by salmon as a sublethal consequence of catch-and-release (Tufts et al., 2000; Lennox et al., 2015a). However, those studies used a reference group of radio tagged fish that had been captured using means other than angling (traps or nets), and these capture methods could also have stressed the fish, potentially confounding their utility as controls. The novel approach that we implemented in this study to use uncaptured fish from a passive count facilitated a more robust estimate of expected movement by released salmon.

We rejected our null hypothesis that angling did not affect the movement of Atlantic salmon; however, it is not clear what the impacts of movement reductions would have on individual fitness and salmon population dynamics. For Atlantic salmon released by anglers, reduced upriver migration resulting from catch-and-release has the potential to decrease fitness via density-dependent egg or fry mortality (Einum and Nislow, 2005). Salmon that do not fully distribute within a system and cluster in small territories will risk crowding spawning substrate and oversaturation with eggs, reducing recruitment within the river. The fitness impairments could be amplified by outbreeding effects if salmon that do not successfully reach their natal spawning destination spawn with salmon from other populations and lose adaptations evolved for successfully colonizing stream reaches or tributaries (Heggberget et al., 1986). However, this assumes significant genetic substructuring by Atlantic salmon within rivers; in fact, genetic substructuring is probably low in general (Garant et al., 2000) particularly within smaller rivers such as Lakselva that do not have major tributaries (Jordan et al., 1992; Vähä et al., 2011).

The causal mechanism behind the shortened migrations in this study is unclear, but shortened migrations likely arise from fish that experience stress or exhaustion precluding continued upriver progress. Prolonged stress or exhaustion could influence breeding success because breeding success is influenced by physiological condition on spawning grounds (de Gaudemar and Beall, 1998; Hendry and Beall, 2004). However, other studies of released salmon have found that parr densities increased in years following catch-and-release (Whoriskey et al., 2000; Thorstad et al., 2003), that late season catch-and-release does not affect gamete or fry quality (Davidson et al., 1994; Booth et al., 1995), and that wild salmon released by anglers are able to successfully reproduce (Richard et al., 2013). Ultimately, if reduced migration following catch-and-release corresponds to reduced activity overall, there could be fewer reproductive encounters by released salmon corresponding with decreased fitness. Even though salmon in Lakselva did not travel as far as was expected based on the simulation, every salmon (except one that exited the river prematurely and the one that died) was tracked at suitable spawning territory and many were visually observed in aggregations of spawning conspecifics during drift counting.

An alternative explanation for our findings is that the salmon captured by anglers never intended to continue migrating because they were in the holding phase of migration (Økland et al., 2001). This implies that salmon are more likely to be captured by anglers at the end of migration than during the upriver migration phase. Vulnerability to recreational angling is a complex function of the biotic and abiotic environment (Stoner, 2004), individual-level characteristics (Cooke et al., 2007), and the fisheries environment (i.e. gear types used; Lennox et al., In Press). However, changing vulnerability to angling at different stages of fish migration has not previously been explored, although behaviour does change at different stages of the migration, potentially influencing angling vulnerability. For example, dominant males become aggressive on spawning grounds (Hendry and Beall, 2004), a behavioural change that could influence vulnerability to angling. Therefore, behavioural vulnerability could increase when salmon arrive at spawning grounds and indeed many fish remain in holding pools near spawning grounds for long periods of time prior to spawning (Økland et al., 2001), meaning that salmon spend most of their time in freshwater at or near their spawning sites. This suggests that angling vulnerability—and capture probability—should be higher on spawning grounds than during the migration and that the "shortened migration" we observed was actually a function of this change in capture probability.

Combining a visual survey with the radio telemetry in this study proved important for estimating survival of salmon after catch-and-release. We had several salmon exhibit limited post-release movement, including some that would have been categorized as dead using established protocols for the interpretation of electronic tagging data based on their lack of movement, that were confirmed to be alive via visual observation. Indeed, telemetry studies can also underestimate the movement of animals (Ovidio et al., 2000), particularly without fine-scale positioning systems (Hanson et al., 2007). Although we are confident that our periodic tracking allowed us to accurately identify the movements of salmon at a coarse scale (i.e. among pools), it is possible for salmon to make forays up or downriver in short periods of time that could have been missed (i.e. searching behaviour; Økland et al., 2001). For example, one salmon tagged in Pool 2 was tracked once in Pool 5; however, it returned to Pool 2 before the next tracking and remained there until spawning. Such transient movements can only be detected by chance when tracking is periodic. Moreover, Taggart et al. (2001) noted that salmon might move up to 5 km between redds during the spawning season. Although we accept that our methods may not have captured all movements caught-and-released salmon made, the overall trend observed among salmon was striking because upriver movement was largely restricted throughout the remainder of the summer and into the spawning season.

Using simulation methods to test hypotheses about salmon movement was a novel approach for answering our research question. Salmon are dynamic animals and although well studied, their behaviour remains somewhat cryptic. Simulation provided an analytical tool for exploring different but equally rational hypotheses based on what is known about the migratory biology of salmon to develop models of expected movement by the released salmon. There are some additional parameters that could be used to expand on our simulation model, including date of river entry, size, and sex, which have been correlated with migration distance by some authors (e.g. Laughton and Smith, 1992; Økland et al., 2001). However, the connections between traits and migration distance of salmon are tenuous and probably limited to very larger rivers (Thorstad et al., 2008). The best evidence available indicated that the salmon we tagged and released in Lakselva were equally likely to travel upriver from the release site independent of river entry, size, sex, or capture date, which is why we did not incorporate these factors in our simulation.

Although we found that there was some inconsistency in the spawning distribution of salmon in Lakselva across years, it was interesting and important to our study to note that general trends were similar. Ultimately, the results of all three simulations were concordant allowing us to make inferences about the population that we studied. Annual visual spawning counts of fish similar to those that we used to generate spawning pool probabilities are available for many rivers making this method a valuable tool for work over and beyond stock assessment in the future.

5. Conclusion

Consistent with other studies, high survivorship of salmon released by anglers in Lakselva is promising for salmon conservation efforts and demonstrates the utility of catch-and-release for management of the salmon fishery. However, our model predicted longer migrations after catch-and-release than we observed, suggesting that the upriver migration could have been hindered by angling, which could be a relevant sublethal effect of catch-and-release. Future research into the behavioural vulnerability of salmon at different stages of migration is necessary to develop a mechanistic understanding of these observations. Moreover, studies that monitor the fitness-related endpoints of released salmon could provide important information about the effects of catch-and-release on reproduction including gamete development prior to spawning, intraspecific competition for mating opportunities, or fertilization success.

Acknowledgements

We thank Egil Liberg and the Lakselva River Owner's Association for their support of this study. RJL was funded by a Natural Sciences and Engineering Research Council (NSERC) graduate scholarship. Field research was financed by the Research Council of Norway, contract 216416/O10 and by the Norwegian Environmental Agency. Cooke was supported by the Canada Research Chairs Program and NSERC. Cooke and Whoriskey were supported by OTN Canada. We thank Colin Davis for assisting with simulation coding.

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