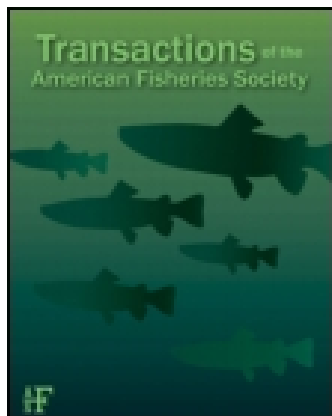


This article was downloaded by: [174.114.9.40]

On: 06 March 2015, At: 13:49

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



[Click for updates](#)

Transactions of the American Fisheries Society

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/utaf20>

Does Catch-and-Release Angling Alter the Behavior and Fate of Adult Atlantic Salmon During Upriver Migration?

Robert J. Lennox^{ab}, Ingebrigt Uglem^b, Steven J. Cooke^a, Tor F. Næsje^b, Frederick G. Whoriskey^c, Torgeir B. Havn^b, Eva M. Ulvan^b, Øyvind Solem^b & Eva B. Thorstad^b

^a Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada

^b Norwegian Institute for Nature Research, Post Office Box 5685, Sluppen, Trondheim N-7485, Norway

^c Ocean Tracking Network, c/o Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia B3H 4J1, Canada

Published online: 04 Mar 2015.

To cite this article: Robert J. Lennox, Ingebrigt Uglem, Steven J. Cooke, Tor F. Næsje, Frederick G. Whoriskey, Torgeir B. Havn, Eva M. Ulvan, Øyvind Solem & Eva B. Thorstad (2015) Does Catch-and-Release Angling Alter the Behavior and Fate of Adult Atlantic Salmon During Upriver Migration?, Transactions of the American Fisheries Society, 144:2, 400-409, DOI: [10.1080/00028487.2014.1001041](https://doi.org/10.1080/00028487.2014.1001041)

To link to this article: <http://dx.doi.org/10.1080/00028487.2014.1001041>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

ARTICLE

Does Catch-and-Release Angling Alter the Behavior and Fate of Adult Atlantic Salmon During Upriver Migration?

Robert J. Lennox*

Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada; and Norwegian Institute for Nature Research, Post Office Box 5685, Sluppen, Trondheim N-7485, Norway

Ingebrigt Uglem

Norwegian Institute for Nature Research, Post Office Box 5685, Sluppen, Trondheim N-7485, Norway

Steven J. Cooke

Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada

Tor F. Næsje

Norwegian Institute for Nature Research, Post Office Box 5685, Sluppen, Trondheim N-7485, Norway

Frederick G. Whoriskey

Ocean Tracking Network, c/o Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia B3H 4J1, Canada

Torgeir B. Havn, Eva M. Ulvan, Øyvind Solem, and Eva B. Thorstad

Norwegian Institute for Nature Research, Post Office Box 5685, Sluppen, Trondheim N-7485, Norway

Abstract

To reproduce, Atlantic Salmon *Salmo salar* return to freshwater rivers and migrate upriver to spawning areas. This migration is the basis for recreational fisheries, which for conservation reasons are increasingly characterized by catch-and-release angling. The effectiveness of catch and release for Atlantic Salmon conservation is contingent on the ability of individuals to recover from angling, resume migration, and reach spawning grounds at appropriate times. We monitored 27 caught and released Atlantic Salmon in River Gaula in 2013, a prominent and relatively pristine Norwegian river, by affixing external radio transmitters to them. Those fish were compared with a control group of 33 individuals caught and radio-tagged at sea in bag nets before river entry. Whereas none of the control fish died during the study period, there were three mortalities among the caught-and-released fish (11%; significant difference). All mortalities were qualitatively associated with poor angler care, emphasizing the responsibility of anglers in practicing effective catch and release of Atlantic Salmon. Both control and caught and released Atlantic Salmon spent similar time resting below and in transiting a large natural barrier to migration, an 80-m gorge. The angled and released Atlantic Salmon were distributed in similar locations throughout the river during the spawning season compared with control fish, but those caught and released later in the season appeared to migrate shorter total distances than control fish. Among the caught and released Atlantic Salmon, 17% were recaptured by anglers, which was similar to the rate of recapture of the control fish (21%). Ultimately, individual and population fitness was not likely to be significantly compromised as a result of catch and release because individuals were recorded in spawning areas at appropriate times. Catch and release can therefore be considered a tenable strategy for balancing the costs and benefits associated with the recreational fishery.

*Corresponding author: robert.lennox@carleton.ca

Received September 26, 2014; accepted December 16, 2014

Recreational angling for Atlantic Salmon *Salmo salar* spread from the British Isles to other countries with native Atlantic Salmon populations in the 19th century (Verspoor et al. 2008). Traditionally, Atlantic Salmon fisheries have been highly exploitative, and anglers have harvested a high percentage of the total migratory population from rivers (e.g., Downton et al. 2001). However, global declines of wild Atlantic Salmon (Parrish et al. 1998) have endangered many important fisheries (McKibben and Hay 2004) and necessitated active conservation of Atlantic Salmon populations. As such, there is a trend towards catch and release in Atlantic Salmon fisheries (ICES 2013). Although releasing Atlantic Salmon is seemingly a promising measure towards conservation objectives, catch and release can be a contentious issue (Spitler 1998), and its viability as a conservation tool in general depends on the ability of released individuals of all species to recover from catch and release with negligible fitness consequences (Cooke and Schramm 2007).

Because negative effects of catch and release may not kill a fish immediately (Muoneke and Childress 1994), true mortality may be underestimated if the fate of fish that are released is not monitored for an extended period postrelease (Coggin et al. 2007). Telemetry studies with appropriate control groups are important tools to extend monitoring periods and detect delayed mortality of caught and released fish in their natural environment (Pollock and Pine 2007; Donaldson et al. 2008). Most catch-and-release studies evaluating postrelease survival of Atlantic Salmon have demonstrated high survivorship (Webb 1998; Mäkinen et al. 2000; Tufts et al. 2000; Whoriskey et al. 2000; Thorstad et al. 2003; Thorstad et al. 2007; Jensen et al. 2010; Richard et al. 2013) and reproductive capacity (Davidson et al. 1994; Booth et al. 1995; Richard et al. 2013). However, among telemetry studies, few have incorporated a control group (i.e., fish that have not undergone catch and release) into their experimental design (but see Tufts et al. 2000; Jensen et al. 2010).

To better understand how catch-and-release angling affects the lifetime fitness of Atlantic Salmon, we used radio telemetry to compare the migration of Atlantic Salmon that had been caught and released in a riverine recreational fishery with a control group composed of Atlantic Salmon captured in bag nets at sea and that subsequently entered the river. Radio-telemetry enabled us to monitor the migration of Atlantic Salmon from both groups and determine whether survival, migratory activity, and catchability (recapture in the ongoing recreational fishery in the river) differed between the two groups. The comparisons between control and experimental Atlantic Salmon provided a proximate estimate of the individual fitness consequences from catch-and-release angling, helping to evaluate potential costs of implementing catch and release as a conservation strategy in recreational Atlantic Salmon fisheries.

METHODS

Study location.—Atlantic Salmon were studied in the River Gaula watercourse in central Norway near the city of Trondheim (Figure 1). From the head of the tide, 110 km of river is accessible to Atlantic Salmon in the main stem of the river, with an additional 90 km in major tributaries: Sokna, Bua, and Fora (Stensland 2012; Figure 1). The total catchment area measures 3,652 km². Average annual water discharge is relatively high in most seasons (93 m³/s; L'Abée-Lund and Aspås 1999) and the 80-m-long Gaulfossen Gorge near the town of Hovin (Figure 1) can have particularly high water flows in the spring due to meltwater, which creates a temporary migration barrier (Torstein Rognes, personal communication). Salmon enter the river during the spring, summer, and autumn and spawn during a period of approximately 23 d in mid-October (Heggberget 1988).

The River Gaula is one of the 30 Atlantic Salmon rivers draining into the Trondheimsfjord, and is considered one of the most prominent destinations for recreational anglers in Norway (Stensland 2012). Between 2002 and 2012, the River Gaula was the third most productive Atlantic Salmon fishery in Norway by total catch (mean = 6442, range = 4,111–10,468; Statistics Norway, <http://www.ssb.no>). Recreational Atlantic Salmon angling is restricted to the summer months normally beginning June 1 and closing August 31. During the spring and early summer, the Trondheimsfjord supports a commercial Atlantic Salmon fishery (Olausen 2007) that

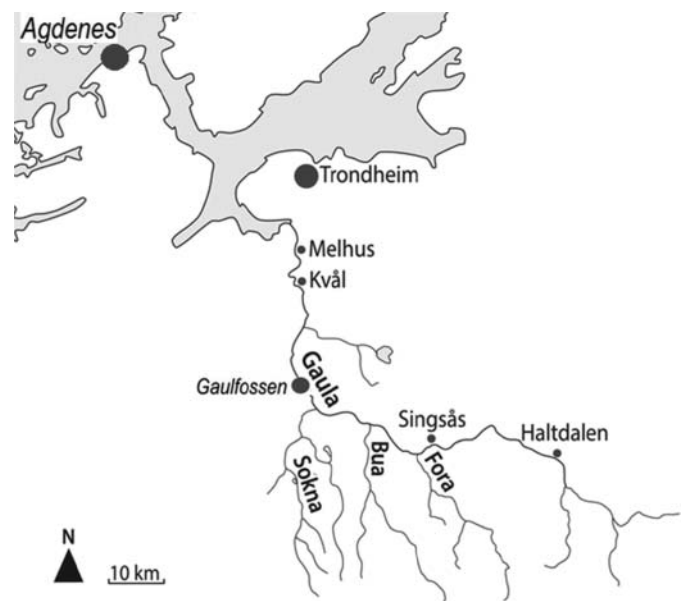


FIGURE 1. Map of Norway and the Trondheimsfjord near Trondheim. River Gaula extends approximately 110 km from the Trondheimsfjord to the town of Haldalen where the migratory stretch ends. Three major tributaries, the Rivers Sokna, Bua, and Fora, add approximately 90 km of stream length to the distribution used by Atlantic Salmon.

intercepts some individuals from the River Gaula in nets prior to river entry.

Sample collection.—For the control group, 226 wild Atlantic Salmon (mean = 87 cm TL, SD = 12 cm, range = 62–121 cm) were captured in bag nets prior to river entry at Agdenes, which is located along the outer part of the Trondheimsfjord, 48 km from the mouth of River Gaula (Figure 1). Bag nets are a weir-like capture method in which Atlantic Salmon are funnelled by leads into a holding chamber where they are confined, typically unharmed. Bag nets were set throughout the spring and summer, and Atlantic Salmon captured here and destined to enter River Gaula were tagged between May 15 and August 19, 2013. Only completely undamaged fish were tagged. Because the Atlantic Salmon tagged in the fjord could have originated from any of the rivers draining into the Trondheimsfjord, we anticipated that only a subset of these animals would enter River Gaula. This was confirmed, as among the 226 Atlantic Salmon tagged in the fjord, only 48 were recorded within River Gaula during the study (mean = 90 cm TL, SD = 10, range = 72–114 cm), entering between June 2 and October 25, 2013. However, nine of these did not migrate far into the river and may have strayed into River Gaula and subsequently left, or they were harvested and not reported. To increase the likelihood that fish captured by anglers would be reported, a relatively high reward (500 Nkr, roughly US\$85 at that time) was offered for tag reporting. In addition, four Atlantic Salmon that entered River Gaula were subsequently determined to be of farmed origin by scale analysis, and two that entered after the angling season was complete (date of entry: October 25) were excluded because peak spawning season was already complete.

Ultimately, the control group for this study was comprised of 33 wild Atlantic Salmon (mean = 91 cm TL, SD = 10, range = 72–114 cm) that entered Gaula between June 2 and August 16, 2013. It is possible that some Atlantic Salmon tagged in the fjord did not survive to enter River Gaula, either because of predation, harvest by commercial nets, migratory abandonment, or mortality associated with tagging effects. The radio-tagging method that was used is standard for Atlantic Salmon projects (e.g., Økland et al. 2001; Thorstad et al. 2003, 2007) and has been demonstrated not to affect swimming performance (Thorstad et al. 2000). Because radio signals do not transmit well in the marine environment it was not possible to identify tagging effects on the control group, and therefore, tag and handling related mortality in the control group could not be estimated. Control fish were instead used to identify normal migratory behavior of Atlantic Salmon, which could be compared with those caught and released. The control salmon also provided an estimate of mortality experienced from natural causes and harvest by recreational anglers for fish that had survived to enter the river. We are aware that due to their handling and tagging, the control fish may not be fully representative of the movements and fate of fish that had not had any prior human intervention.

Between June 1 and July 23, 2013, recreational anglers took 27 Atlantic Salmon (mean = 87 cm TL, SD = 10 cm, range = 67–108 cm) that were subsequently tagged and released by trained biologists (i.e., authors R.J.L., I.U., T.B.H., Ø.S., and E.B.T.); these fish were eligible under river owner rules to be released back into the river, based on their physical condition and likelihood of survival (<http://www.gaula.no/sider/tekst.asp?side=92&valgtmenypunkt=84>). Between June 1 and June 15, 2013, eight Atlantic Salmon were captured below the Gaulfossen (four in the pool below the Gaulfossen and four at Kvål; Figure 1), and one was captured in the river section above the Gaulfossen. Between June 29 and July 23, 2013, 18 Atlantic Salmon were captured above the Gaulfossen near the confluence of River Gaula with River Fora (Figure 1). Variables recorded at the time of capture included fight duration and water temperature. Capture gear, angler name, hooking location, bleeding, and any other damages were identified to provide information about stressors that could have influenced individual survival.

Tagging protocol.—Atlantic Salmon were individually transferred in a plastic cradle filled with water from the river to a water-filled polyvinyl chloride (PVC) half pipe. In the half pipe, the fish's eyes were covered with a damp towel and its total length was measured (cm). Fish were externally tagged with rectangular (21 × 52 × 11 mm, mass in air = 15 g) coded radio tags (model F2120 from Advanced Telemetry Systems [ATS], Isanti, Minnesota) in the frequency range of 142.014–142.262 MHz. All tags were attached by passing 0.8-mm steel wires through the tag and affixing it through the dorsal musculature below the dorsal fin using the methods of Økland et al. (2001) modified to include a plastic backplate with rounded corners on the side of the animal opposite the radio tag. In accordance with external radio-tagging methods used in other studies (Økland et al. 2001; Thorstad et al. 2003), no anesthetic was administered because anesthetic products can alter behavior and survival, thereby confounding interpretations about the effects of catch and release. Moreover, many of the Atlantic Salmon that we tagged were likely to be recaptured, harvested, and consumed by humans, and fish anaesthetized with approved analgesics cannot be consumed by humans without a detoxification period that was not practical for this study (Cooke et al. 2005).

Radio tracking.—Entry of the fish from the fjord into River Gaula and subsequent movements in the river were monitored by two stationary radio-receiver logging stations. Each station was set up in pairs separated by approximately 100 m with two yagi antennas per station (one oriented upriver and one oriented downriver) to establish directional movements. One pair was approximately 10 km upriver from the head of the tide in the town of Melhus, and a second pair was set up at the Gaulfossen gorge 35 km from the head of the tide (Figure 1). Stationary loggers on top of and below the Gaulfossen gorge were used to monitor the passage of fish through the Gaulfossen; the last tracking time below the gorge was considered to

be the time at which a tagged animal initiated a successful attempt to ascend the 80-m gauntlet, and its first detection at the upstream station on gorge was the point when transit was successfully completed. Water temperature at the time of gorge passage were determined by a temperature logger (HOBO Pendant Temperature/Light Data Logger, Onset, Massachusetts) at the Haga Bridge approximately 7 km upriver from the Gaulfossen and discharge velocity was recorded via a Norwegian Water Resources and Energy Directorate flowmeter (see, www2.nve.no/) below the Gaulfossen. In addition to the stationary receivers, tagged fish were manually tracked from a vehicle twice weekly (June 6–July 30) and once monthly thereafter until January 2014. Manual tracking was conducted using two vehicle-mounted receivers (ATS R4520CD Coded Receiver-Datalogger) and antennas (Magnetic Roof-Mount Dipole, Laird Technologies, Earth City, Missouri) operating concurrently to position the fish; an ATS 4-element Yagi antenna was substituted for fine-scale positioning. Active tracking was conducted from two major highways (Highway E6, Highway 30), which run adjacent to River Gaula and River Sokna. To cover fish that may have entered the tributaries Bua or Forda, routes Fv631 and Fv603 were followed. To ensure comprehensive coverage of the river, all accessible access roads and bridges were used. Whenever a fish was detected, its identity and GPS location within the river were determined. The GPS points were later transferred into ArcGIS software, subsequent analysis determining the distance the fish had covered within the river from the head of the tide to the identified location, as well as rates of movement, migration delays, patterns of upriver migration, and arrival on spawning areas during the study.

To make accurate conclusions about survivorship, it is necessary to establish a priori criteria to define dead fish (Hightower et al. 2001). These are typically based on a lack of movement of tags (Bendock and Alexandersdottir 1993; Bettoli and Osborne 1998). For our study, Atlantic Salmon were categorized as dead as a result of catch and release if they did not move from positions they had occupied soon after release and were not found in suitable holding areas over the winter. Because Atlantic Salmon make various upriver and downriver movements during the spawning season and typically move downriver after spawning (Lévesque et al. 1985; Bardonnet and Baglinière 2000), control fish were to be categorized as dead during upriver migration if they remained stationary for a period of time that extended through the spawning season and into the winter.

Data analysis.—Likelihood ratio *G*-tests were used to compare survival between catch-and-release and control Atlantic Salmon. A multiple logistic regression model was used to identify factors that contributed to mortality (coded as a binary variable) among catch-and-release Atlantic Salmon, including length, water temperature, fish total length, bleeding, gear (worm or fly), and playing time. Time spent in the pool below Gaulfossen prior to ascent was compared between the catch-

and-release and control groups using a nonparametric Mann–Whitney *U*-test. Number of days between the first record in the river and ascent of the Gaulfossen was also compared between the two groups with a Mann–Whitney *U*-test. A multiple linear regression was used to identify factors associated with ascent time at the Gaulfossen Gorge, including water velocity, water temperature, fish total length, and treatment group (i.e., catch and release or control). To satisfy normality of residuals (Shapiro–Wilk *W*), passage time of Gaulfossen was log-transformed. To compare final spawning positions of catch-and-release and control Atlantic Salmon within Gaula, a Mann–Whitney *U*-test was used. This analysis excluded individuals that entered tributaries because the distance and elevation that they traveled were not comparable to fish that migrated only within the main stem of Gaula; comparisons would have to have been made between catch-and-release and control salmon in each tributary, but there were too few samples in each tributary to make such comparisons. Because many salmon in the catch-and-release group were tagged 64 km upriver, we repeated the analysis without these fish that already had completed migration to the spawning grounds. This was done via a two-way Student's *t*-test to test whether there was a difference in final spawning position between control and catch-and-release fish that had migrated at least 64 km upriver after tagging. A likelihood ratio *G*-test was used to compare the percentages of catch-and-release and control salmon that were captured by recreational anglers after tagging. When applicable, lowest Akaike information criteria (AIC) values were used for model selection, and all statistics and figures were generated using the open source software package R (R Development Core Team 2008).

RESULTS

River Entry and Ascent Patterns

A total of 26 control Atlantic Salmon entered Gaula in June, 6 more in July, and 1 in August. Migration of the control Atlantic Salmon was typically characterized by a relatively rapid ascent of the river with a long holding period in proximity to where they were located during spawning. Many of the Atlantic Salmon had reached their spawning destinations by the month of August, and did not move from August through October. One individual from the control group disappeared from the river after July 31. Control Atlantic Salmon spawned at locations throughout the river at 21–110 km from the head of the tide. Control fish also spawned in the tributaries Sockna and Bua.

Atlantic Salmon in the catch-and-release group ($N = 27$) were caught and released between June 1 and July 23 when the average water temperature was 13°C (range, 8–18°C); they were played for an average of 15 min (SD = 16, range = 5–75 min; Figure 2). Most of the Atlantic Salmon ($N = 22$) were captured on artificial flies with barbed treble hooks, but

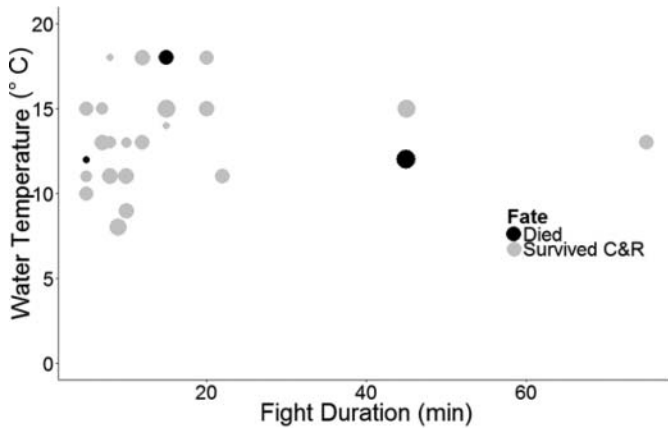


FIGURE 2. Comparison of catch-and-release (C&R) survival for Atlantic Salmon based on the water temperature at capture and the fight duration. Size of circles represents relative body size of Atlantic Salmon.

five were captured using worms on single barbed hooks. No Atlantic Salmon captured using worms died from catch and release. Three Atlantic Salmon suffered hook wounds that caused mild superficial bleeding. One individual had an undetermined fate, ceasing to be detected in the river after July 31; without evidence to the contrary, we categorized this individual as a survivor of catch and release. Salmon from the catch-and-release group completed migration between 52 and 102 km from the head of the tide and were tracked in all three major tributaries during the spawning season.

Survival

There was no evidence from the tracking data that any of the control fish died during migration after entering the river. However, three Atlantic Salmon (11%) were judged to have died from catch and release. The difference in survival to spawning for Atlantic Salmon that were caught and released compared with the nonangled control group was significant ($G = 5.09$, $df = 1$, $P = 0.03$), indicating that catch-and-release mortality was significantly different from natural mortality.

In the full logistic regression model used to predict factors that influenced mortality of catch-and-release fish, three variables were not significant: water temperature ($z = -0.24$, $P = 0.81$), playing time ($z = -0.79$, $P = 0.45$), and total length ($z = 0.27$, $P = 0.78$). The optimal model ($\Delta AIC = 4$) included only angling duration, which was also not significant ($z = -0.71$, $P = 0.48$).

In-River Movement

Both control and catch-and-release Atlantic Salmon spent similar time resting in the pool below Gaulfossen ($z = 0.351$, $P = 0.61$). Eventually, all 8 catch-and-release salmon tagged in stretches below the gorge ascended, as did 28 of the control salmon (3 were recaptured prior to passage and 2 completed

migration in lower sections of the river). However, one individual from each treatment group was not logged by the stationary logger, and they were therefore excluded from analyses. Catch-and-release salmon transited the gorge between June 7 and July 15 (median = June 18), whereas control salmon passed between June 12 and October 6 (median = June 22). Atlantic Salmon remained in the pool below the Gaulfossen for variable durations, some for minutes and others for months. Catch-and-release salmon typically ascended within days of being caught and released, whereas control fish tended to have more variable stays; however, there was no significant difference between catch-and-release and control salmon in terms of duration spent in the pool below the Gaulfossen ($z = 0.51$, $P = 0.61$). Water temperature fluctuated between 7°C (June 5) and 20°C (July 29) but ascents were only recorded when water temperatures were between 10°C and 15°C. There was no significant difference in the time taken to ascend the Gaulfossen between control and catch-and-release salmon given that treatment group was dropped from the model during model selection. All Atlantic Salmon ascended the gorge at water flows between 23 and 245 m³/s (Figure 3), and the median velocity at the time of passage was at 111 m³/s. Log-transformed time to ascend (Figure 4) was influenced by water temperature ($t = -2.35$, $P = 0.03$), water velocity ($t = -2.391$, $P = 0.03$), and interactively by both ($t = 2.80$, $P = 0.01$).

Of the 27 caught and released salmon, 7 (26%) moved more than 100 m downriver (i.e., exhibited fallback) from their release site after release. Most of these individuals recovered upriver migratory behavior, however, 3 were never tracked above their release site and 2 of these individuals were

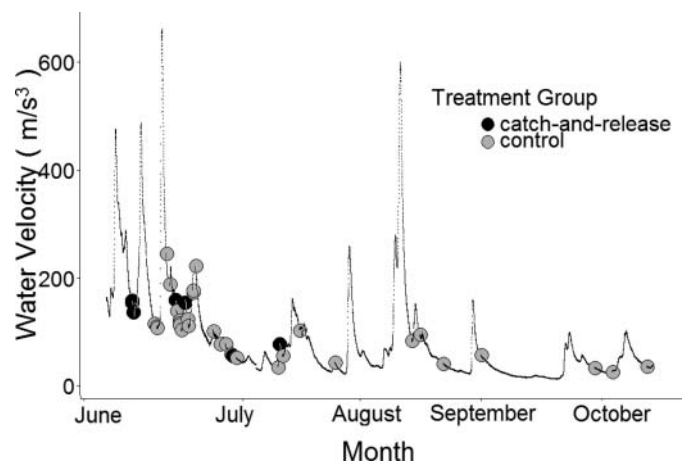


FIGURE 3. Profile of water velocity at the Gaulfossen Gorge between June 1 and October 10. Values were measured every 15 min by an automated Norwegian Water Resources and Energy Directorate flowmeter. Passage times of tagged Atlantic Salmon are interpolated from a stationary logging station below the gorge. Atlantic Salmon that did not pass the gorge and one catch-and-release individual that passed the gorge but was not logged by the stationary logging station are not included.

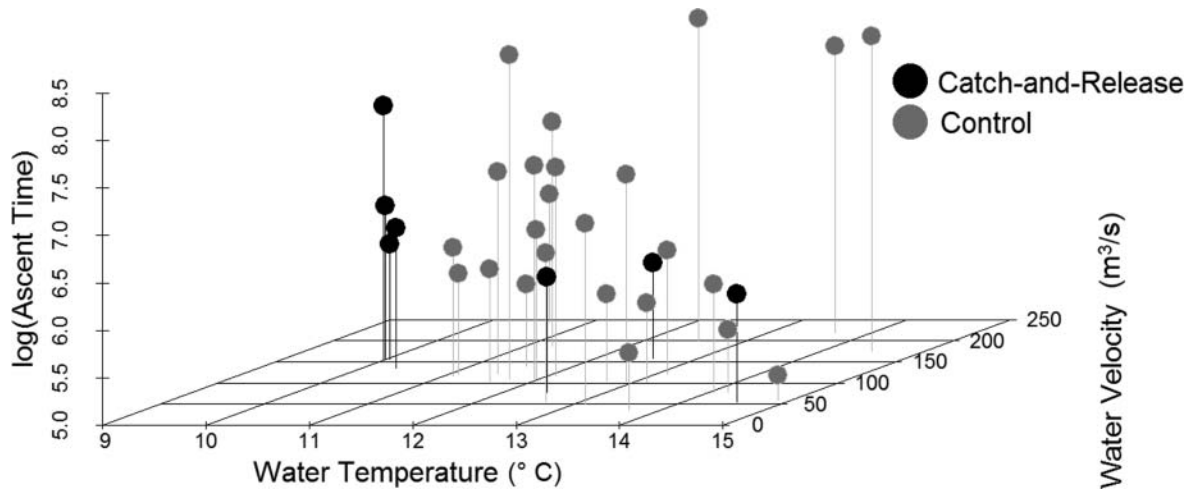


FIGURE 4. Influence of water velocity and temperature on Atlantic Salmon time to ascend of the Gaulfossen Gorge. Time to ascend was log-transformed because in the model it was used to describe the relationship between ascension time, water velocity, and water temperature.

categorized as dead. Downriver movements were also made by control group Atlantic Salmon, with 21 (63%) tracked at least 100 m downriver from a previous logged location.

Catch-and-release and control Atlantic Salmon both completed their migrations at similar locations in the river ($z = 0.19$, $P = 0.85$). However, many of our catch-and-release salmon were tagged in the middle of the river (about 64 km upstream from the fjord). When we compared the final spawning position of Atlantic Salmon that migrated at least to that point, control Atlantic Salmon migrated significantly farther (average = 92 km, SD = 13, range = 71–110 km, $N = 13$) than catch-and-release (average = 79 km, SD = 10, range = 68–102 km, $N = 14$; $t = 2.94$, $P < 0.01$; Figure 5)—i.e., assuming that Atlantic Salmon completing migration in prior sections were not from comparable subpopulations (Heggberget et al. 1988).

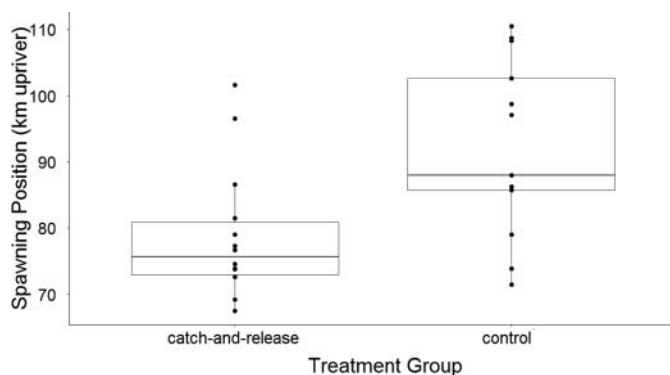


FIGURE 5. Spawning distribution of Atlantic Salmon that ascended at least 64 km up the River Gaula. Spawning locations were inferred from tracking data in mid-October, which is the peak spawning period of Atlantic Salmon in River Gaula. Individual points represent individual Atlantic Salmon positions and boxplots around the points are used to compare mean catch-and-release versus control salmon spawning locations.

Recreational Capture

Four individuals (17% of the 24 Atlantic Salmon that survived catch and release) were recaptured by anglers after release. Recaptures occurred upriver from the initial capture site at 8, 12, 13, and 44 d after initial capture. Among the 33 wild control group fish that entered and migrated up River Gaula, 7 (21%) were captured by recreational anglers. The frequency at which catch-and-release and control salmon were recaptured by anglers did not differ significantly ($G = 0.12$, $df = 1$, $P = 0.73$).

DISCUSSION

This study provides a comparison of the migratory behavior of catch-and-release Atlantic Salmon to a control group in a prominent and relatively pristine river. Control groups are important for making determinations about behavior of released fish (Wilde 2003; Pollock and Pine 2007); however, most Atlantic Salmon research to date has not included controls for logistical and other reasons. Our ability to provide a control group has permitted a rare comparative assessment of the potential impacts of catch and release on the movements and survival of Atlantic Salmon and has provided evidence that catch and release affected the freshwater migration of maturing Atlantic Salmon.

Survival of Atlantic Salmon during this study was high, and the observed catch-and-release mortality of 11% was similar to that observed in other telemetry studies (Webb 1998; Mäkinen et al. 2000; Whoriskey et al. 2000; Dempson et al. 2002; Thorstad et al. 2003; Thorstad et al. 2007), where survival estimates of caught and released fish typically range between 90 and 97%. Given the small number of catch-and-release mortalities ($N = 3$), it was unlikely that the multiple logistic regression model had the statistical power to identify any significant predictors of mortality. However, mortalities

could be qualitatively attributed to angling practices, for instance, one of the Atlantic Salmon that died was held for at least 15 min postcapture in shallow, low-velocity water that was relatively warm (18°C). High water temperature can result in significant migratory delay and even mortality for Atlantic Salmon (22–26°C; Baisez et al. 2011). Although warm water increases enzymatic activity that is important for clearing lactate from the muscle, it also causes significant physiological disturbance (Wilkie et al. 1996, 1997), and catch-and-release mortality in Atlantic Salmon tends to become more frequent as water temperature increases above 18°C (Dempson et al. 2002). However, a recent study from southern Norway found that most Atlantic Salmon caught and released at water temperatures between 16°C and 19°C survived and were present at spawning grounds in autumn (Havn 2014). Two mortalities recorded in Gaula were associated with prolonged playing time (Figure 2). Prolonged playing time increases the physiological alterations associated with angling, including accumulation of lactate and metabolic protons, which are byproducts of anaerobic glycolysis in the white muscle (Milligan and Wood 1986; Dobson and Hochachka 1987; Wood 1991). Lactate is costly and requires time to clear from muscle tissues (Wood 1991; Jobling 1994), and metabolic protons contribute to intracellular acidosis, a factor often associated with postrelease mortality of fish (Wood et al. 1983). Although we found no quantitative relationship between these variables and mortality, the importance of angler care in maximizing survival of released Atlantic Salmon was nonetheless evident and has been suggested elsewhere as an important mortality factor (e.g., Dempson et al. 2002).

Notably, none of the five fish captured by angling with worms were categorized as dead after release, even though it is generally thought that fishing with worms or other baits increases the likelihood that hooks will be ingested deeply, resulting in tissue and organ damage associated with angling mortality (Muoneke and Childress 1994; Bartholomew and Bohnsack 2005; Arlinghaus et al. 2007). Warner and Johnson (1978) found that fishing with bait increased deep-hooking incidents among landlocked Atlantic Salmon relative to flies, which led to more serious tissue damage and bleeding than the shallow-hooking, which typically occurs from fly fishing. However, the Atlantic Salmon in Warner and Johnson (1978) were relatively small compared with those captured in Gaula. Another difference is that anglers in Gaula fished flies with treble hooks, albeit Warner (1978) found that treble hooks did not increase mortality of landlocked Atlantic Salmon relative to single hooks. Although bait fishing did not result in mortalities for Atlantic Salmon in Gaula, two of three salmon we initially considered but rejected for radiotagging due to due to poor condition had been captured by angling with worms. A more definitive comparison of the risks of fish mortality from the use of worm, lure, and fly fishing for anadromous Atlantic Salmon will require a larger sample size than we obtained.

Catch-and-release salmon readily ascended the Gaulfossen gorge. Other studies have shown successful passage of barriers by Atlantic Salmon after catch and release, although studies have mostly focused on passage of artificial barriers rather than natural barriers (e.g., Gowans et al. 1999; Richard et al. 2013). Catch and release did not result in increased resting periods below the gorge or slower ascent relative to control salmon. In fact, one catch-and-release salmon passed within a day of release and most passed within a few days. Exercise associated with angling depletes ATP, phosphocreatine, and glycogen and results in accumulation of lactate anions as well as intracellular acidosis (Wood et al. 1983; Milligan and Wood 1986; Dobson and Hochachka 1987; Wood 1991) in the anaerobic white muscle. The anaerobic muscular pathway is important for swimming against high water flows (e.g., Burnett et al. 2014) but takes time to recover after exercise (i.e., being angled; Kieffer 2000), which is why it was relatively unexpected that salmon ascended the gorge so soon after catch and release. Because some were tagged in the pool immediately below the gorge, the first record that we have of them in the river is at that point; therefore, the number of days between tagging and ascension would likely be less for these fish than for control salmon that were recorded upon entry above the head of the tide. However, it is nonetheless interesting that they recovered to continue migrating relatively quickly, especially given that these individuals were typically captured at low water temperatures, temperatures at which Wilkie et al. (1997) demonstrated relatively slow clearance of lactate and resynthesis of glycogen, a process that would be necessary for Atlantic Salmon to once again use anaerobic muscular pathways for ascending the high water velocities at the gorge.

Some of the caught and released Atlantic Salmon first moved downstream from their release site, a behavior typically termed “fallback.” Fallbacks have been previously observed for Atlantic Salmon following catch and release (Mäkinen et al. 2000; Thorstad et al. 2003; Jensen et al. 2010; Havn 2014) and are presumed to be a maladaptive behavior manifesting energetic, psychological, or physiological stress associated with catch-and-release angling (Thorstad et al. 2003) or other stressful events (Mäkinen et al. 2000). However, it is not clear why some fish fall back and others do not (Frank et al. 2009), making interpretation of these observations somewhat difficult. Mäkinen et al. (2000) found that gill-netted Atlantic Salmon moved farther down than angled and released Atlantic Salmon and attributed the differences to the magnitude of stress experienced. Økland et al. (2001) described downriver movements during the normal search phase of migration when Atlantic Salmon are seeking natal territories or searching for suitable substrate upon which to spawn. However, explanations for fallback lack a mechanistic basis, and it remains uncertain whether it represents varying degrees of stress or exhaustion, a voluntary behavior, or is an adaptive response to seek cover or some other refuge is uncertain. Although two of the three individuals that died after catch

and release exhibited fallback, it is not clear whether they had died after moving downriver or whether the fallback was attributable to the drifting of a carcass.

We expected that control fish and those exposed to catch and release would complete migration and spawn throughout the river. Annual redd counts by the local landowners association have shown that suitable substrate exists throughout the river and annually identifies redds along the entire length of the river from the head of the tide to about 110 km upriver (T. Rognes, personal communication). We did not expect, however, that control fish would spawn in reaches significantly farther upriver. It may be suggested that the difference represented natural variances between the catch-and-release fish that completed migration near the release site and control fish that continued migrating past the 64-km mark. In order for that to be true, some catchability difference between the catch-and-release and the control salmon would have had to have existed (i.e., catchability increases when individuals reach spawning sites). Had the catch-and-release individuals been staging on spawning areas, and therefore unlikely to continue migrating, they would have displayed secondary sexual characteristics (i.e., brown coloration, jaw remodeling). Development of secondary sexual characteristics is not likely to occur until active upriver migration is complete because it is typically fueled by digesting protein, a process that would hinder migration (Hendry and Berg 1999). However, most of the salmon we worked with were still bright, and only one had developed significant secondary sexual characteristics. The conclusion that the catch-and-release salmon migrated shorter distances than control salmon is supported by Tufts et al. (2000), who also suggested that catch and release may reduce migration distance of Atlantic Salmon, based on tracking observations of angled Atlantic Salmon in the Upsalquitch River, New Brunswick.

If catch and release does affect migratory motivation or capacity and causes shortened migrations, reproductive output is not necessarily affected. In one study, reproductive contributions of catch-and-release Atlantic Salmon were confirmed by genotyping parents and offspring and assigning parr to parents that had experienced catch and release (Richard et al. 2013). In addition, Davidson et al. (1994) and Booth et al. (1995) found similar egg survival, hatching time, fry survival, and timing of fry swim-up between offspring of control and catch-and-release parents. In River Gaula there was no evidence that spawning near the release site was detrimental for Atlantic Salmon that completed migration at lower reaches relative to control individuals. At least some Atlantic Salmon are believed to return to spawn in close proximity to the precise areas in the river where they themselves hatched (Heggberget et al. 1988); if catch and release obstructs them from accomplishing their migratory objective, then there may be sublethal fitness consequences associated with shorter migrations that we could not have identified in this study. One study has identified constrained redd distribution as a consequence of human

impacts (i.e., implementation of weirs), which suggests that Atlantic Salmon will spawn in nonnatal areas and means that reduced migratory distance is not likely to be an important issue as long as suitable spawning substrate remains available (Tentelier and Piou 2011).

Catch and release is practiced by a minority of anglers in Norway (Aas and Kaltenborn 1995; ICES 2013), but interest in the practice is growing in order to meet national Atlantic Salmon conservation objectives. A high percentage of the total migratory population in many Atlantic Salmon rivers is caught in recreational fisheries (e.g., Gudjonsson et al. 1996), and catch and release as a management tool can therefore be essential for maintaining a heterogeneous spawning population and avoiding selective harvest of some stock components (e.g., female-biased angling; Pérez et al. 2005). In harvest-oriented fisheries, such as those in many rivers in Norway, being captured by an angler is often fatal for anadromous Atlantic Salmon, meaning that those individuals have no lifetime fitness (Dingle 1980). Relatively high survival of released Atlantic Salmon can therefore be important for sustaining high densities of spawning fish and is associated with higher parr densities at rearing grounds (Whoriskey et al. 2000; Thorstad et al. 2003; Richard et al. 2013). In addition, catch and release can increase the catchable population within a river because Atlantic Salmon can be caught multiple times (Richard et al. 2013). Indeed, released Atlantic Salmon were recaptured with similar frequency to that at which control Atlantic Salmon were captured, indicating that they did not learn to avoid angling, although only one of the four recaptures was taken on the same gear by which it was initially captured.

The high survivorship of Atlantic Salmon released in our study is similar to that observed in other studies. There was some evidence of shorter migrations by catch-and-release Atlantic Salmon but no indication of negative fitness consequences because all fish were observed in spawning areas at spawning time. Importantly, well-treated caught and released Atlantic Salmon had high survival, recovered upriver movement, exhibited rapid passage of a large natural barrier, and remained behaviorally vulnerable to recapture in recreational fisheries. Evaluating the factors that affected mortality of the three Atlantic Salmon we categorized as dead from catch and release highlighted the obligation of anglers to practice responsible angling. Validation of an index, such as reflex action mortality predictors (RAMP; developed for assessing postcapture condition of other salmonids; Raby et al. 2012; Gale et al. 2014), could provide an accessible tool for anglers that have welfare concerns about catch and release.

ACKNOWLEDGMENTS

This research was financed by the Research Council of Norway, contract 216416/O10. Additional support was provided by the Norwegian Institute for Nature Research, Carleton University, the Natural Sciences and Engineering Research

Council of Canada (NSERC), the Canada Research Chairs Program, the Norwegian Seafood Federation, the Norwegian Environment Agency, The Ministry of Trade, Industry, and Fisheries, and the County Governor of Sør-Trøndelag. R. J. Lennox was additionally supported by an NSERC graduate scholarship. The authors thank A. Jørrestol, A. Foldvik, M. Rognli, D. Karlsen, T. Rognes, and R. Krogdahl for assisting with data analysis and collection. Anglers that volunteered Atlantic Salmon for this study are thanked for facilitating the research. R. J. Lennox is especially grateful to Matt Hayes and the Winsnes Family as well as the Winsnes Fly Fishing Lodge in Singsås.

REFERENCES

- Aas, Ø., and B. P. Kaltenborn. 1995. Consumptive orientation of anglers in Engerdal, Norway. *Environmental Management* 19:751–761.
- Arlinghaus, R., S. J. Cooke, J. Lyman, D. Policansky, A. Schwab, C. Suski, S. G. Sutton, and E. B. Thorstad. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. *Reviews in Fisheries Science* 15:75–167.
- Baisez, A., J. M. Bach, C. Leon, T. Parouty, R. Terrade, M. Hoffmann, and P. Laffaille. 2011. Migration delays and mortality of adult Atlantic salmon *Salmo salar* en route to spawning grounds on the River Allier, France. *Endangered Species Research* 15:265–270.
- Baridonnet, A., and J. L. Baglinière. 2000. Freshwater habitat of Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:497–506.
- Bartholomew, A., and J. A. Bohnsack. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* 15:129–154.
- Bendock, T., and M. Alexandersdottir. 1993. Hooking mortality of Chinook Salmon released in the Kenai River, Alaska. *North American Journal of Fisheries Management* 13:540–549.
- Bettoli, P. W., and R. S. Osborne. 1998. Hooking mortality and behavior of Striped Bass following catch-and-release angling. *North American Journal of Fisheries Management* 3:609–615.
- Booth, R. K., J. D. Kieffer, B. L. Tufts, K. Davidson, and A. T. Bielak. 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*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:283–290.
- Burnett, N. J., S. G. Hinch, D. C. Braun, M. T. Casselman, C. T. Middleton, S. M. Wilson, and S. J. Cooke. 2014. Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult Sockeye Salmon. *Physiological and Biochemical Zoology* 87:587–598.
- Coggins, L. G., M. J. Catalano, M. S. Allen, W. E. Pine, and C. J. Walters. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. *Fish and Fisheries* 8:196–210.
- Cooke, S. J., G. T. Crossin, D. A. Patterson, K. K. English, S. G. Hinch, J. L. Young, R. F. Alexander, M. C. Healey, G. Van Der Kraak, and A. P. Farrell. 2005. Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of Sockeye Salmon: development and validation of a technique. *Journal of Fish Biology* 67:1342–1358.
- Cooke, S. J., and H. L. Schramm. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. *Fisheries Management and Ecology* 14:73–79.
- Davidson, K., J. Hayward, M. Hambrook, A. T. Bielak, and J. Sheasgreen. 1994. The effects of late-season angling on gamete viability and early fry survival in Atlantic Salmon. *Canadian Technical Report of Fisheries and Aquatic Sciences* 1982:1–12.
- Dempson, J. B., G. Furey, and M. Bloom. 2002. Effects of catch-and-release angling on Atlantic Salmon, *Salmo salar* L., of the Conne River, Newfoundland. *Fisheries Management and Ecology* 9:139–147.
- Dingle, H. 1980. Ecology an evolution of migration. Pages 1–101 in S. A. Gauthreaux, editor. *Animal migration, orientation, and navigation*. Academic Press, New York.
- Dobson, G. P., and P. W. Hochachka. 1987. Role of glycolysis in adenylate depletion and repletion during work and recovery in teleost white muscle. *Journal of Experimental Biology* 129:125–140.
- Donaldson, M. R., R. Arlinghaus, K. C. Hanson, and S. J. Cooke. 2008. Enhancing catch-and-release science with biotelemetry. *Fish and Fisheries* 9:79–105.
- Downton, P. R., D. G. Reddin, and R. W. Johnson. 2001. Status of Atlantic Salmon (*Salmo salar* L.) in Campbellton River, Notre Dame Bay (SFA 4), Newfoundland in 2000. *Canadian Science Advisory Secretariat Research Document* 2001/031.
- Frank, H. J., M. E. Mather, J. M. Smith, R. M. Muth, J. T. Finn, and S. D. McCormick. 2009. What is “fallback”? metrics needed to assess telemetry tag effects on anadromous fish behavior. *Hydrobiologia* 63:237–249.
- Gale, M. K., S. G. Hinch, S. J. Cooke, M. R. Donaldson, E. J. Eliason, K. M. Jeffries, E. G. Martins, and D. A. Patterson. 2014. Observable impairments predict mortality of captured and released Sockeye Salmon at various temperatures. *Conservation Physiology* [online serial] 2:cou029.
- Gowans, A. R. D., J. D. Armstrong, and I. G. Priede. 1999. Movements of adult Atlantic Salmon in relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology* 54:713–726.
- Gudjonsson, S., T. Antonsson, and T. Tomasson. 1996. Exploitation ratio of Atlantic Salmon in relation to Atlantic Salmon run in three Icelandic rivers. *International Council for the Exploration of the Sea, Statutory Meeting ANACAT (Anadromous and Catadromous Fish) Committee M:8*, Copenhagen.
- Havn, T. B. 2014. The effect of catch-and-release angling at high water temperatures on behavior and survival of Atlantic Salmon (*Salmo salar* L.). Master's thesis. Norwegian University of Science and Technology, Trondheim.
- Heggberget, T. G. 1988. Timing of spawning in Norwegian Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 45:845–849.
- Heggberget, T. G., L. P. Hansen, and T. F. Næsje. 1988. Within-river spawning migration of Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 45:1691–1698.
- Hendry, A. P., and O. K. Berg. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in Sockeye Salmon. *Canadian Journal of Zoology* 77:1663–1675.
- Hightower, J. E., J. R. Jackson, and K. H. Pollock. 2001. Using telemetry methods to estimate natural and fishing mortality of Striped Bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society* 130:557–567.
- ICES (International Council of the Exploration of the Sea). 2013. Report of the working group on North Atlantic salmon (WGNAS). *ICES, CM 2013/ACOM:09*, Copenhagen.
- Jensen, J. L., E. Halttunen, E. B. Thorstad, T. F. Næsje, and A. H. Rikardsen. 2010. Does catch-and-release angling alter the migratory behaviour of Atlantic Salmon? *Fisheries Research* 106:550–554.
- Jobling, M. 1994. *Fish bioenergetics*. Chapman and Hall, London.
- Kieffer, J. D. 2000. Limits to exhaustive exercise in fish. *Comparative Biochemistry and Physiology Part A* 126:161–179.
- L'Abée-Lund, J. H., and H. Aspås. 1999. Threshold values of river discharge and temperature for anglers' catch of Atlantic Salmon, *Salmo salar* L. *Fisheries Management and Ecology* 6:323–333.
- Lévesque, F., R. Le Jeune, and G. Shooner. 1985. Synthèse des connaissances sur le saumon Atlantique (*Salmo salar*) au stade post-fraie. [Synthesis of

- knowledge on the Atlantic Salmon (*Salmo salar*) at the post-spawning stage.] Rapport Manuscrit Canadien des Sciences Halieutiques et Aquatiques [Canadian Manuscript Report of Fisheries and Aquatic Sciences] 1827.
- Mäkinen, T. S., E. Niemelä, K. Moen, and R. Lindström. 2000. Behaviour of gill-net and rod-captured Atlantic Salmon (*Salmo salar* L.) during upstream migration and following radio tagging. *Fisheries Research* 45:117–127.
- McKibben, M. A., and D. W. Hay. 2004. Distributions of planktonic sea lice larvae *Lepeophtheirus salmonis* in the inter-tidal zone in Loch Torridon, western Scotland in relation to Atlantic Salmon farm production cycles. *Aquaculture Research* 35:742–750.
- Milligan, C. L., and C. M. Wood. 1986. Intracellular and extracellular acid-base status and H⁺ exchange with the environment after exhaustive exercise in the Rainbow Trout. *Journal of Experimental Biology* 123:93–121.
- Muoneke, M. I., and W. M. Childress. 1994. Hooking mortality: a review for recreational fisheries. *Reviews in Fisheries Science* 2:123–156.
- Økland, F., J. Erkinaro, K. Moen, E. Niemelä, P. Fiske, R. S., McKinley, and E. B. Thorstad. 2001. Return migration of Atlantic Salmon in the River Tana: phases of migratory behaviour. *Journal of Fish Biology* 59:862–874.
- Olaussen, J. O. 2007. Playing chicken with Atlantic Salmon. *Marine Resource Economics* 22:173–193.
- Parrish, D. L., R. J. Behnke, S. R. Gephard, S. D. McCormick, and G. H. Reeves. 1998. Why aren't there more Atlantic Salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences* 55:281–287.
- Pérez, J., J. I. Izquierdo, J. D. L. Hoz, and E. Garcia-Vazquez. 2005. Female biased angling harvests of Atlantic Salmon in Spain. *Fisheries Research* 74:127–133.
- Pollock, K. H., and W. E. Pine 2007. The design and analysis of field studies to estimate catch-and-release mortality. *Fisheries Management and Ecology* 14:123–130.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: <http://www.R-project.org>. (January 2015).
- Raby, G. D., M. R. Donaldson, S. G. Hinch, D. A. Patterson, A. G. Lotto, D. Robichaud, K. K. English, W. G. Willmore, A. P. Farrell, M. W. Davis, and S. J. Cooke. 2012. Validation of reflex indicators for measuring vitality and predicting the delayed mortality of wild Coho Salmon bycatch released from fishing gears. *Journal of Applied Ecology* 49:90–98.
- Richard, A., M. Dionne, J. Wang, and L. Bernatchez. 2013. Does catch-and-release affect the mating system and individual reproductive success of wild Atlantic Salmon (*Salmo salar* L.)? *Molecular Ecology* 22:187–200.
- Spitler, R. J. 1998. The animal rights movement and fisheries: they're heeereee! *Fisheries* 23(1):21–22.
- Stensland, S. 2012. Typology of landowners in Norwegian Atlantic Salmon angling: attitudes towards river owner organisations and management actions. *Fisheries Management and Ecology* 19:273–282.
- Tentelier, C., and C. Piou. 2011. Obstacles to migration constrain nest distribution of Atlantic Salmon. *Ecology of Freshwater Fish* 20:400–408.
- Thorstad, E. B., T. F. Næsje, P. Fiske, and B. Finstad. 2003. Effects of hook and release on Atlantic Salmon in the River Alta, northern Norway. *Fisheries Research* 60:293–307.
- Thorstad, E. B., T. F. Næsje, and I. Leinan. 2007. Long-term effects of catch-and-release angling on ascending Atlantic Salmon during different stages of spawning migration. *Fisheries Research* 85:316–320.
- Thorstad, E. B., F. Økland, and B. Finstad. 2000. Effects of telemetry transmitters on swimming performance of adult Atlantic Salmon. *Journal of Fish Biology* 57:531–535.
- Tufts, B. L., K. Davidson, and A. T. Bielak. 2000. Biological implications of “catch-and-release” angling of Atlantic Salmon. Pages 100–138 in F. G. Whoriskey Jr. and K. B. Whelan, editors. *Managing wild Atlantic Salmon—new challenges, new techniques*. Atlantic Salmon Federation, St. Andrews, New Brunswick.
- Verspoor, E., L. Stradmeyer, and J. L. Nielsen. 2008. *The Atlantic Salmon: genetics, conservation and management*. Wiley Blackwell, Oxford, UK.
- Warner, K. 1978. Hooking mortality of lake-dwelling landlocked Atlantic Salmon, *Salmo salar*. *Transactions of the American Fisheries Society* 107:518–522.
- Warner, K., and P. R. Johnson. 1978. Mortality of landlocked Atlantic Salmon (*Salmo salar*) hooked on flies and worms in a river nursery area. *Transactions of the American Fisheries Society* 107:772–775.
- Webb, J. H. 1998. Catch and release: the survival and behavior of Atlantic Salmon angled and returned to the Aberdeenshire Dee in spring and early summer. *Scottish Fisheries Research Report* 62:1–15.
- Whoriskey, F. G., S. Prusov, and S. Crabbe. 2000. Evaluation of the effects of catch-and-release angling on the Atlantic Salmon (*Salmo salar*) of the Ponoï River, Kola Peninsula, Russian Federation. *Ecology of Freshwater Fish* 9:118–125.
- Wilde, G. R. 2003. Estimation of catch and release fishing mortality and its sampling variance. Pages 83–85 in A. P. M. Coleman, editor. *Regional experiences for global solutions: proceedings of the 3rd world recreational fishing conference*. Department of Business, Industry and Resource Development, Fisheries Group, Fisheries Report 67, Darwin, Australia.
- Wilkie, M. P., M. A. Brobbel, K. G. Davidson, L. Forsyth, and B. L. Tufts. 1997. Influences of temperature upon the postexercise physiology of Atlantic Salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:503–511.
- Wilkie, M. P., K. Davidson, M. A. Brobbel, J. D. Kieffer, R. K. Booth, A. T. Bielak, and B. L. Tufts. 1996. Physiology and survival of wild Atlantic Salmon following angling in warm summer waters. *Transactions of the American Fisheries Society* 125:572–580.
- Wood, C. M. 1991. Acid-base and ion balance, metabolism, and their interactions, after exhaustive exercise in fish. *Journal of Experimental Biology* 160:285–308.
- Wood, C. M., J. D. Turner, and M. S. Graham. 1983. Why do fish die after severe exercise? *Journal of Fish Biology* 22:189–201.