Is catch-and-release angling affecting the freshwater migration of adult Atlantic Salmon *Salmo salar*?

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<A> Abstract

To reproduce, Atlantic Salmon *Salmo salar* return to freshwater rivers and migrate upriver to spawning areas. This migration is the basis for recreational sport 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. Catch-and-release Atlantic Salmon were compared to a similarly radio tagged control group of 33 individuals caught at sea in bag nets before river entry. While none of the control fish died during the study period, there were three mortalities of the caught and released Atlantic Salmon (11%; P = 0.03). 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 catch-and-release Atlantic Salmon spent similar time resting below and in passing a large natural barrier to migration, an 80 m gorge. The catch-and-release Atlantic Salmon were distributed in similar locations throughout the river during the spawning season compared to control Atlantic Salmon, but those caught and released later in the season appeared to migrate shorter total distances than control Atlantic Salmon (P < 0.01). 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%; P = 0.73). 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 is therefore a tenable strategy for balancing the costs and benefits associated with the recreational fishery.

<A> Introduction

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 post-release. 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 post-release 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 that had 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, to a control group composed of Atlantic Salmon captured in bag nets at sea and that subsequently entered the river. Radio telemetry allowed 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 tool in recreational Atlantic Salmon fisheries.

<B> 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; see Figure 1). The total catchment area measures 3652 km^2. Average annual water discharge is relatively high in most seasons (93 m/s^3; 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, pers. comm.). Salmon enter the river during the spring, summer, and autumn and spawn during a period of approximately 23 days 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 (average catch = 6442, range = 4111-10468; Statistics Norway). 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 (Olaussen 2007) that intercepts some individuals from the River Gaula in nets prior to river entry.

Sample collection.— Wild Atlantic Salmon for the control group (N = 226, mean total length = 87 ± 12 cm, length range: 62 – 121 cm) were captured in bag nets prior to river entry at the outer part of the Trondheimsfjord, 48 kilometres 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 (see the description of the tagging protocol, below). 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 total length = 90 ± 10 cm, length 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 were harvested and not reported. To increase the likelihood that fish captured by anglers would be reported, a relatively high reward (500 NOK) 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 total length = 91 ± 10 cm, length 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 (e.g., Økland et al. 2001; Thorstad et al. 2003, 2007) and has been demonstrated not to effect swimming performance (Thorstad et al. 2000), however, 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 behaviour of Atlantic Salmon, which could be compared to that of caught-and-released Atlantic Salmon. Control Atlantic Salmon also provided an estimate of mortality experienced as a result of natural causes or 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 27 Atlantic Salmon eligible under river owner rules to be released back into the river (based on physical condition and likelihood of survival; http://www.gaula.no/sider/tekst.asp?side=92&valgtmenypunkt =84) were captured by recreational anglers and tagged by trained biologists (i.e., five of the present authors; Havn, Lennox, Solem, Thorstad, and Uglem). The average fork length of these fish was 87 cm (range = 67 – 108 cm). 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 PVC half pipe. In the half pipe, the fish's eyes were covered with a damp towel and its total length was measured to the nearest cm. Fish were externally tagged with rectangular (21 × 52 × 11 mm; mass in air = 15 grams) coded radio tags (model F2120 from Advanced Telemetry Systems [ATS], Minnesota, USA) in the frequency range 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 anaesthetic was administered because anaesthetic products can alter behaviour or survival of fish, 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 anaesthetised 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, with the last tracking time below the gorge considered to be the time at which an experimental animal initiated a successful attempt to ascend the 80 m gauntlet, and its first detection at the upstream station on gorge the point when transit was successfully completed. Water temperature and discharge velocity at the time of gorge passage were determined by a temperature logger (HOBO Pendant Temperature/Light Data Logger, Onset, Massachusetts, USA) at the Haga Bridge approximately 7 km upriver from the Gaulfossen and from the Norwegian Water Resources and Energy Directorate flow meter (available online at 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, Missouri, USA) operating concurrently to position the fish, with the substitution of an ATS 4-element Yagi antenna for more 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. GPS points were later transferred into ArcGIS software, with subsequent analysis determining the distance the fish had covered within the river from the head of the tide to the identified location, and 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 *a priori* establish 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 this 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. 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, given that 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).

Data analysis.— Likelihood ratio G-tests were used to compare survival between catch-and-release and control Atlantic Salmon. Generalized Linear Models (GLM) with a logit link function were 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 group using a non-parametric 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 GLM with a Gaussian link function 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 test), 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 Atlantic Salmon in each tributary but there were too few samples in each tributary to make statistical comparisons. Because many Atlantic 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 in order 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, and used a two-way Student’s t-test. A likelihood ratio G-test was used to compare the percentages of catch-and-release and control Atlantic Salmon that were captured by recreational anglers after tagging. When applicable, lowest AIC values were used for model selection and all statistics and figures were generated using the open source software package R (R Core Team 2008). Means are presented as ± standard deviation and in instances when data are skewed median is presented instead.

<A> Results

Timing of river entry and patterns of river ascent of experimental fish.— Twenty six control Atlantic Salmon entered Gaula in June, six in July, and one 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 minimum only 35 km from the head of the tide and up to 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 at an average water temperature of 13 °C (range: 8-18 °C) and were played for 15 ± 16 min (range: 5-75 minutes; Figure 2). Most of the Atlantic Salmon (N = 22) were captured on artificial flies, but five were captured using worms. 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 as it was no longer detected in the river after July 31; without evidence to the contrary, we categorized this individual as a survivor of catch-and-release. Atlantic Salmon from the catch-and-release group completed migration between 45 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 to the non-angled control group was significant (likelihood ratio test: G = 5.09, df= 1, P = 0.03), indicating that catch-and-release mortality was significantly different from natural mortality.

In the full 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 (ΔAIC = 4) included only angling duration, which was also not significant (z = -0.71, P = 0.48).

In-river movements.— Both control and catch-and-release Atlantic Salmon spent similar time resting in the pool below Gaulfossen (z = 0351, P = 0.61). Eventually, all catch-and-release Atlantic Salmon tagged in stretches below the gorge ascended (N = 8) as did 28 of the control Atlantic Salmon (three control fish were recaptured prior to passage and two completed migration in prior sections of the river). Catch-and-release Atlantic Salmon transited the gorge between June 7 and July 15 (median = June 18) whereas control Atlantic Salmon passed between June 12 and October 6 (median = June 22). 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. It took control and catch-and-release. There was no significant difference in the time taken to ascend the Gaulfossen between control and catch-and-release Atlantic Salmon. All Atlantic Salmon ascended the gorge at water flows between 23 and 245 m^3/s (Figure 3) and the median velocity at the time of passage was at 111 m^3/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).

Seven of the 27 caught-and-released Atlantic Salmon (26%) moved more than 100 m downriver (i.e., exhibited fallback) from their release site after release. Most of these individuals recovered upriver migratory behaviour, however, three were never tracked above their release site and two of these individuals were 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 Atlantic Salmon were tagged in the middle of the river (about 64 kilometres upstream from the fjord), and when we compared the final spawning position of Atlantic Salmon that migrated at least to that point (under the assumption that Atlantic Salmon completing migration in prior sections were not from comparable subpopulations; Heggberget et al. 1988), control (71-110 km, average position = 92 ± 13 km, N = 13) Atlantic Salmon migrated significantly farther than catch-and-release (68-102 km, average position = 79 ± 10 km; t = 2.94 P < 0.01; Figure 5).

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

<A> Discussion

This study provides a comparison of the migratory behaviour 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 behaviour 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 90-97%. Given the small number of mortalities (N = 3) in this study from catch-and-release, it was unlikely that the GLM 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 fifteen minutes post capture 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 16-19 ° C survived catch-and-release 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 stressors associated with angling, including accumulation of lactate and metabolic protons, which are byproducts of anaerobic glycolysis in the white muscle (Dobson and Hochachka 1987; Milligan and Wood 1986; Wood 1991). Lactate is costly and time consuming to clear from muscle tissues (Wood 1991; Jobling 1994) and metabolic protons contribute to intracellular acidosis, a factor often associated with post-release mortality of fish (Wood et al. 1983). Even without a quantitative relationship between these variables and mortality in the results presented here, the importance of angler care, which has been suggested elsewhere as an important factor (e.g., Dempson et al. 2002), in maximizing survival of released Atlantic Salmon, was nonetheless evident.

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 land-locked Atlantic Salmon relative to flies, which led to more serious tissue damage and bleeding than the shallow hooking that typically occurs from fly fishing. However, the Atlantic Salmon in Warner and Johnson (1978) were relatively small compared to those captured in Gaula. Although bait fishing did not result in mortalities for Atlantic Salmon in our experimental group, two of three Atlantic Salmon we initially considered but rejected for radio tagging due to due to poor condition had been captured by angling with worms. A more definitive comparison of the risks of mortality to fish 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 Atlantic 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; Richards et al. 2013). However, catch-and-release did not result in increased resting periods below the gorge, more days spent in the section of the river below the gorge, or slower ascent relative to control Atlantic Salmon. In fact, one catch-and-release Atlantic 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 stress such as being angled (Kieffer 2000), which is why it was relatively unexpected that Atlantic Salmon ascended the gorge so soon after catch-and-release. Because some of the fish were tagged in the pool immediately below the gorge, the first record that we have of them in the river is at that point, meaning that the number of days between tagging and ascension would likely be less than for control Atlantic Salmon that were recorded upon entry above the head of the tide. However, it is nonetheless interesting that they recovered migration 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 in order for Atlantic Salmon to once again use anaerobic muscular pathways for ascending the high water velocities at the gorge.

Some catch-and-released Atlantic Salmon in this study after their release first moved downstream from their release site, a behaviour 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 behaviour 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 rod caught (i.e., catch-and-release) Atlantic Salmon and related 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 whether it represents varying degrees of stress or exhaustion, whether it is a voluntary behavior, or whether it 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.

It was expected that control and catch-and-release Atlantic Salmon 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, pers. comm.). It was not expected, 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 Atlantic Salmon and the control Atlantic Salmon would have had to have existed (i.e., catchability increases when individuals reach spawning sites). One indication that the catch-and-release individuals were staging on spawning areas and not likely to continue migrating would have been observations of secondary sexual characteristics (i.e., brown colouration, 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 Atlantic Salmon we worked with were still bright and only one had developed significant secondary sexual characteristics. The conclusion that catch-and-release Atlantic Salmon migrated shorter distances than control Atlantic 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), and if catch-and-release obstructs them from accomplishing their migratory objective then there may be sub-lethal 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 non-natal areas and means that reduced migratory distance is not likely to be an important issue so 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 as 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 this 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 that this had negative fitness consequences because all fish were observed in spawning areas at spawning time. Importantly, well-treated catch-and-released Atlantic Salmon had high survival, recovered upriver movement and exhibited rapid passage of a large natural barrier, and remained behaviourally vulnerable to recapture in recreational fisheries. Evaluating the factors that affected mortality of the three Atlantic Salmon categorized as dead from catch-and-release in this study highlighted the obligation of anglers to practice responsible angling. Validation of an index such as reflex action mortality predictors (RAMP), which has been developed for assessing post-capture 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.

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Figure Titles

Figure 1. Map of Norway and the Trondheimsfjord near Trondheim, Norway. River Gaula extends approximately 110 kilometres from the Trondheimsfjord to the town of Haltdalen where the migratory stretch ends. Three major tributaries, the Rivers Sokna, Bua, and Fora, add approximately 90 kilometres of stream length to the distribution used by Atlantic Salmon. Catch-and-release Atlantic Salmon were captured at Kvål, Gaulfossen, and near the confluence of the Rivers Fora and Gaula. Control Atlantic Salmon were collected in the Trondheimsfjord near Agdenes, the location of which is indicated on the map.

Figure 2. Comparison of catch-and-release survival for Atlantic Salmon based on the water temperature at capture and the fight duration. Grey indicates Atlantic Salmon that survived catch-and-release whereas black indicates Atlantic Salmon that did not survive. Size of circles represents relative body size of Atlantic Salmon.

Figure 3. Profile of water velocity at the Gaulfossen gorge between June 1 and October 10. Values were measured every 15 minutes by an automated Norwegian Water Resources and Energy Directorate flow meter. Water velocity was generally higher in the early season because of input from glacial meltwater. Included in the figure are the passage times of tagged Atlantic Salmon, interpolated from a stationary logging station below the gorge. Atlantic Salmon that did not pass the gorge are not pictured. One individual that passed the gorge but was not logged by the stationary logging station (catch-and-release group) is also not pictured. Control individuals are coloured grey, whereas catch-and-release are coloured black.

Figure 4. Influence of water velocity and temperature on the time to ascend of the Gaulfossen gorge, a natural barrier to Atlantic Salmon migration. Water temperature and velocity fluctuated throughout the season, and most tagged Atlantic Salmon ascended early in the season when flows were highest. Time to ascend in the figure is log transformed, as it was in the model used to describe the relationship between ascension time, water velocity, and water temperature. Control individuals are coloured grey whereas catch-and-release are coloured black.

Figure 5. Spawning distribution of Atlantic Salmon that ascended River Gaula at least 64 kilometers. 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 spawning locations of catch-and-release to control Atlantic Salmon.

Figures

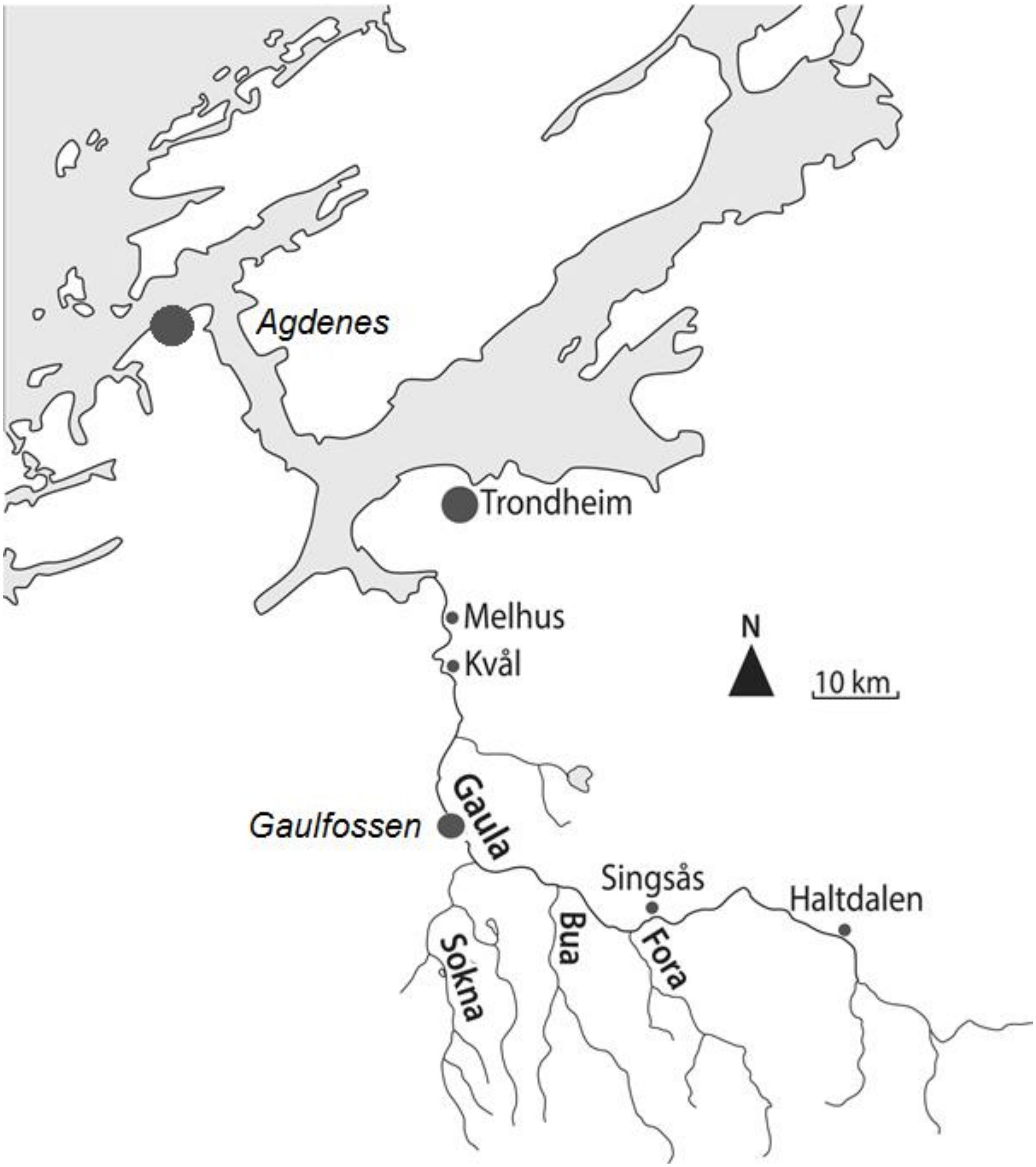

Figure 1.

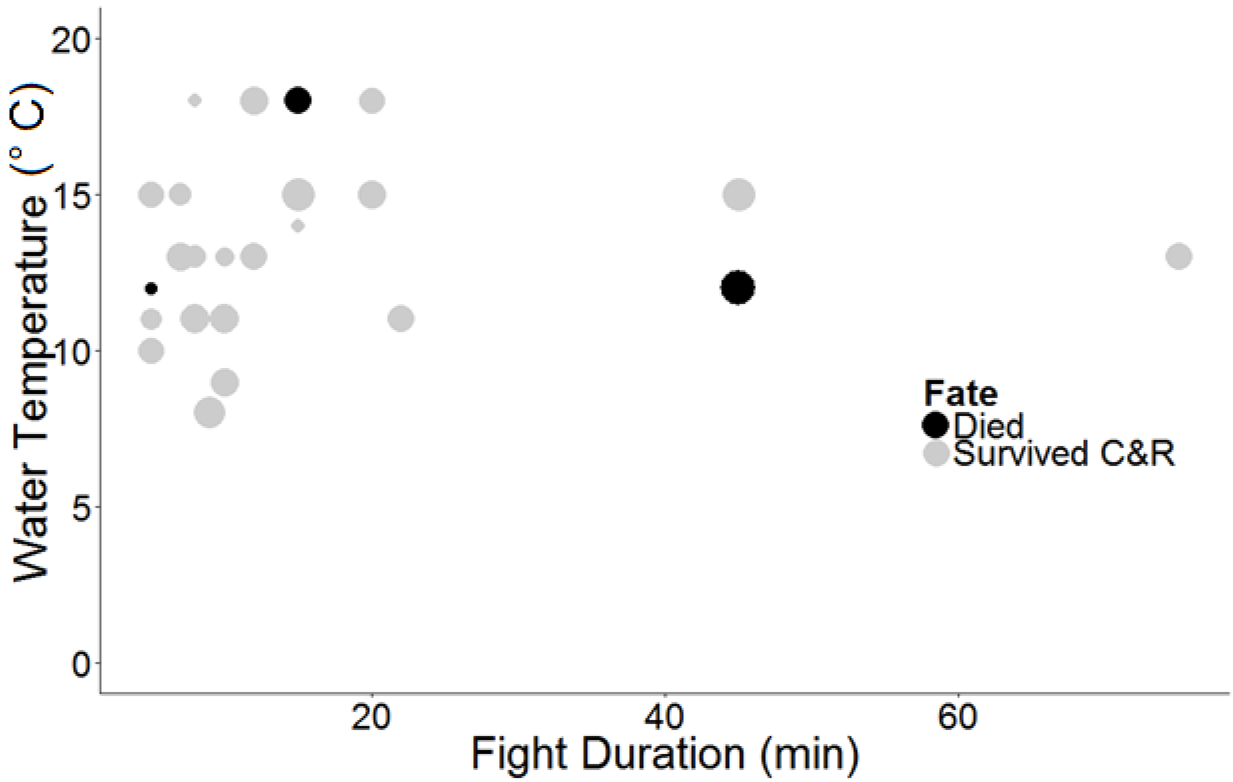
Water Temperature (° C)
20
15
10
5
0
20
40
60
Fight Duration (min)
Fate
Died
Survived C&R

Figure 2.

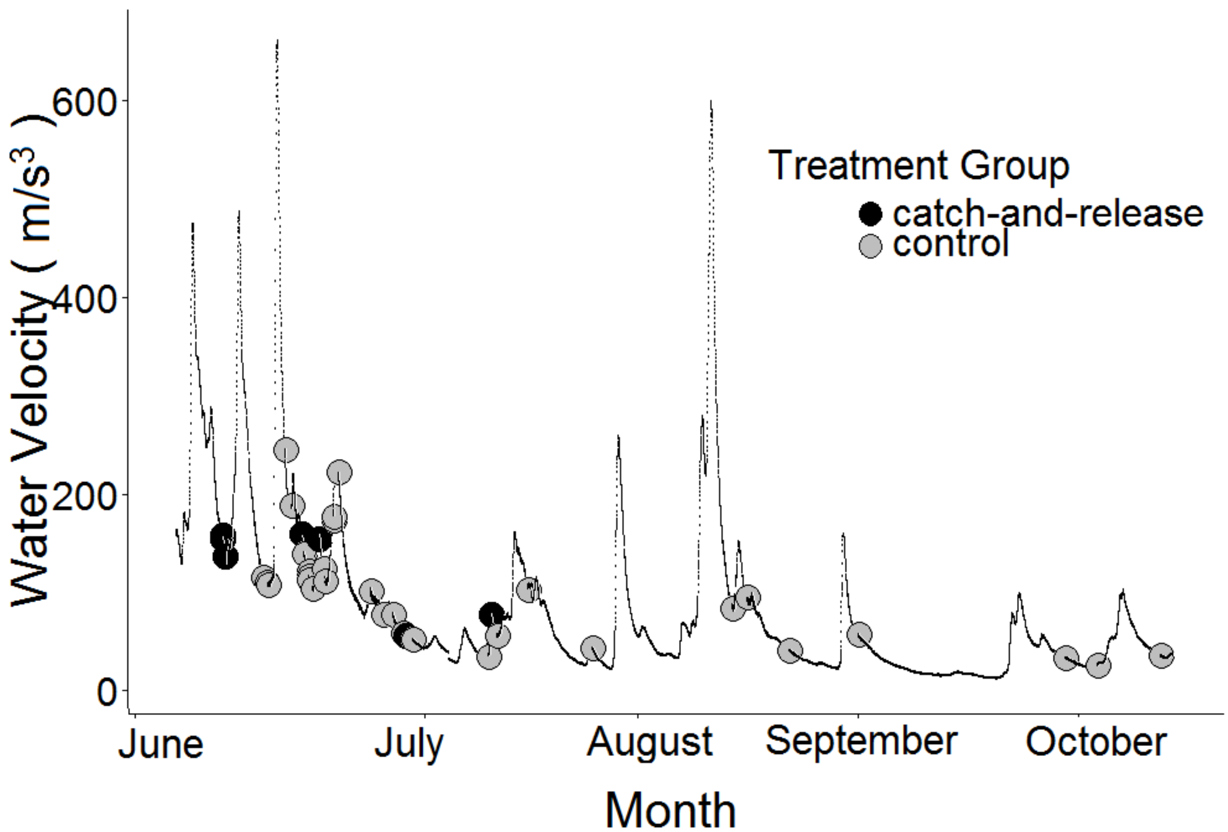
Treatment Group
catch-and-release
control
Water Velocity (m/s^3)
600
400
200
0
June
July
August
September
October
Month

Figure 3.

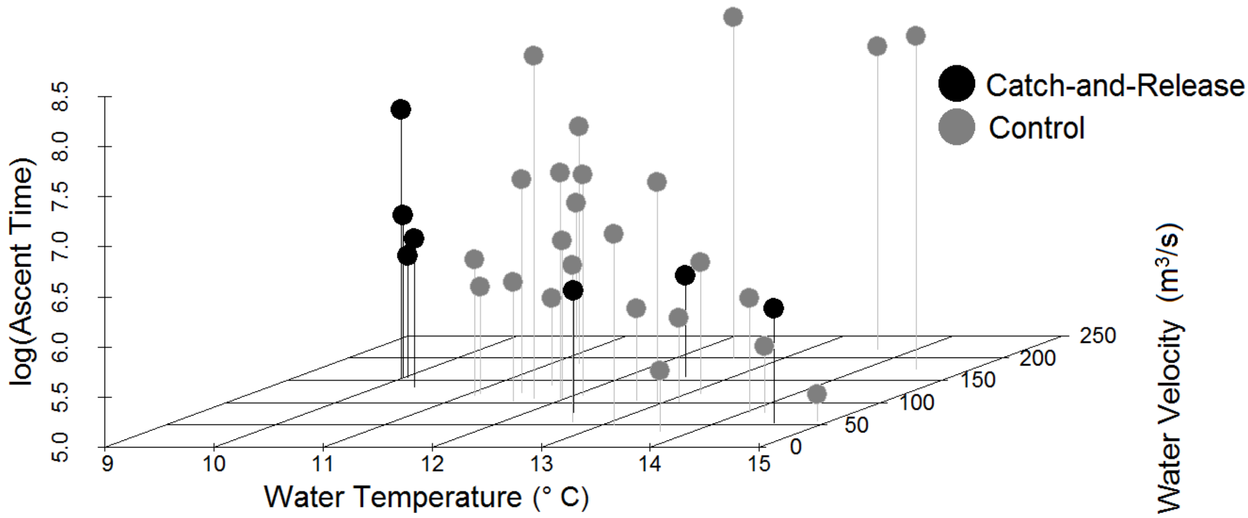
log(Ascent Time)
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9
10
11
12
13
14
15
Water Temperature (° C)
0
50
100
150
200
250
Water Velocity (m3/s)
Catch-and-Release
Control

Figure 4.

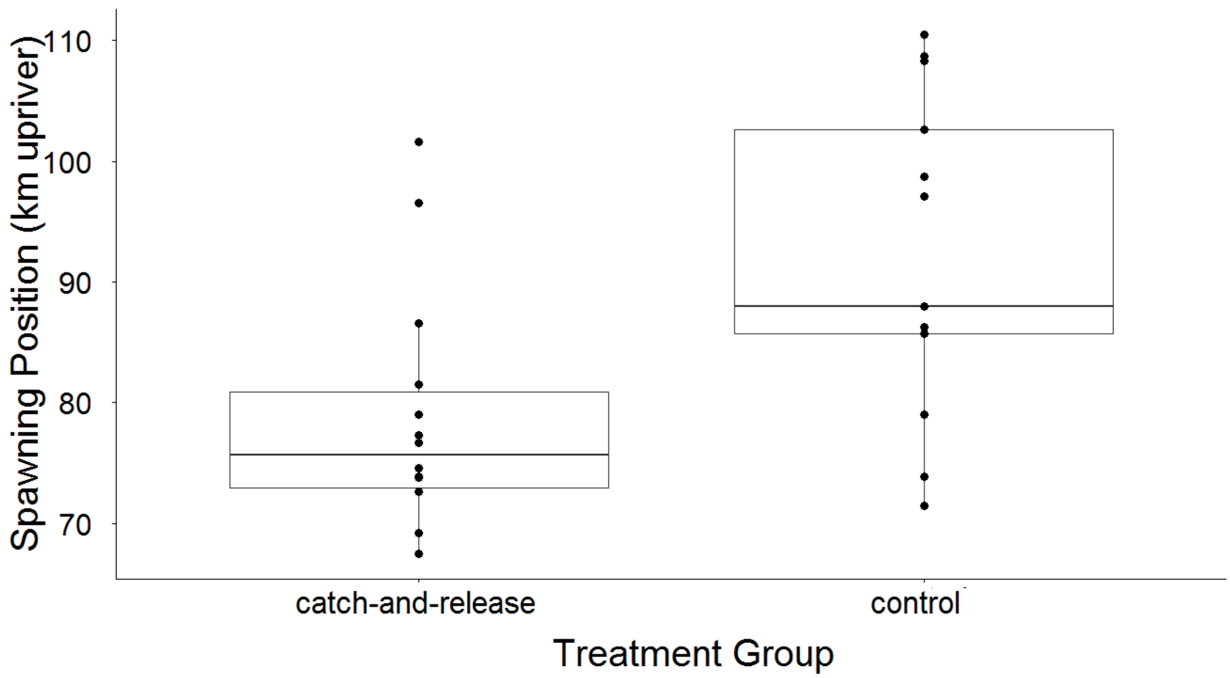
Spawning Position (km upriver)
110
100
90
80
70
catch-and-release
control
Treatment Group

Figure 5.