

Influence of gear switching on recapture of Atlantic salmon (*Salmo salar*) in catch-and-release fisheries

Robert J. Lennox^{1,2}, Ola H. Diserud², Steven J. Cooke¹, Eva B. Thorstad², Frederick G. Whoriskey³, Øyvind Solem², Torgeir B. Havn², Ingebrigt Uglem²

¹Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada

²Norwegian Institute for Nature Research, PO Box 5685, Sluppen, N-7485, Trondheim, Norway

³Ocean Tracking Network, c/o Dalhousie University, Halifax, NS B3H 4J1, Canada

Accepted for publication February 28, 2015

Abstract – Anglers that release Atlantic salmon (*Salmo salar*) in recreational fisheries do so with the intention that the fish will survive and contribute to succeeding generations. In some instances, salmon that are released may be recaptured, but mechanisms associated with recapture are unclear. To test whether gear avoidance influences recapture rates, we analysed data from tagging programmes in major Norwegian Atlantic salmon fishing rivers to determine how frequently salmon were recaptured by different gear than that by which they were initially captured (i.e. gear switch). Among 339 salmon captured, externally tagged and released in 2012 and 2013, 46 (14%) were recaptured; 70% of these recaptured salmon exhibited gear switch. To test whether this gear switch percentage could be expected in the absence of gear avoidance, a simulation was conducted, which accounted for variation in catch probability among rivers and across time with different gear types based on comprehensive catch data. Each simulation step provided a simulated rate of gear switch under the null hypothesis of no gear avoidance. A distribution was generated, which described the probability that we would observe 70% gear switch. The simulated results indicated that this rate of gear switch was highly unlikely ($P = 0.003$) if recapture gear is assumed to be independent of initial capture gear, suggesting that salmon avoided familiar gear types. Changes to behaviour after release, including learned hook avoidance, may explain our observation of gear avoidance by recaptured salmon.

Key words: fisheries management; recreational fisheries; fish behaviour

Introduction

Recreational angling is an important activity and may represent a considerable component of many regional economies (Arlinghaus & Cooke 2009; Cowx et al. 2010). Fishing can exert substantial pressure on fish stocks, and persistent effort from anglers may result in a large proportion of fish from a stock or population being captured (e.g. Gudjonsson et al. 1996). Individual differences in catchability occur within fish populations, meaning that certain individuals have traits that predispose them to being captured by anglers (Cox & Walters 2002). In some instances, behavioural or physiological traits that increase catch-

ability have a genetic basis (Consuegra et al. 2005; Philipp et al. 2009; Klefoth et al. 2013). It follows that individuals that are predisposed to capture by recreational fishers may be captured and released multiple times (Tsuboi & Morita 2004), potentially reducing the positive effects conferred by catch and release to some extent (Bartholomew & Bohnsack 2005). However, prior investigations into fish recapture by anglers have indicated that some species or individuals become difficult to recapture over time (Beukema & de Vos 1974; Askey et al. 2006; Kuparinen et al. 2010).

Recreational Atlantic salmon (*Salmo salar*) angling is an economically and culturally important activity

Correspondence: R. J. Lennox, Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada. E-mail: robert.lennox@carleton.ca

throughout coastal regions along the North Atlantic coast (Verspoor et al. 2008; Aas et al. 2011). Depending on local regulations, anglers are permitted to fish for salmon using a variety of terminal tackle, which may include artificial flies, lures or live bait. However, to compensate for declining stock sizes in many rivers (Parrish et al. 1998), salmon fisheries are increasingly using catch and release as a management strategy. In rivers that permit harvest, some anglers may nonetheless practice voluntary catch and release as a result of conservation ethic (Stensland et al. 2013; Gargan et al. 2015).

Efforts to understand factors that influence mortality of salmon in catch-and-release fisheries have been initiated to evaluate the benefits of the strategy for conservation and management. Studies have demonstrated that most salmon survive catch and release but that many go on to be recaptured, with rates reported in the literature varying between 4% and 11% (Webb 1998; Gowans et al. 1999; Whoriskey et al. 2000; Thorstad et al. 2003; Richard et al. 2013). Gear avoidance or selectivity has been demonstrated to affect catch rates in recreational fisheries (e.g. Beukema 1970; Beukema & Vos 1974), and it is possible that recapture rates in some salmon fisheries are affected by gear avoidance. If that were the case, it would be expected that salmon would be unlikely to be recaptured by the same fishing gear multiple times, a phenomenon termed gear switching. For instance, salmon caught by flies would be more likely to be recaptured by lures or worms rather than flies, or vice versa. In this study, we analysed recapture trends of tagged salmon in Norwegian recreational fisheries by testing whether the gear that a salmon was captured by a second time was independent of the gear that it was captured initially.

Methods

During the angling seasons (1 June–15 September in most rivers) of 2012 and 2013, adult Atlantic salmon returning to Norwegian rivers Gaula, Lakselva, Orkla and Otra from the ocean were captured by recreational anglers and externally tagged with either radio transmitters or t-bar anchor tags. Radio-tagged salmon were typically landed in knotless landing nets and transferred to a water-filled PVC tube (to ensure adequate gill ventilation) for tagging (Lennox et al. 2015). External radio-tagging methods followed those of Økland et al. (2001), in which rectangular radio transmitters (dimensions = 21 × 52 × 11 mm; model F2120 from Advanced Telemetry Systems, Isanti, MN, USA) were attached by steel wire through the musculature beneath the dorsal fin. For all other tagged fish, anchor tags (Floy Manufacturing, Washington, DC, USA) were inserted into the

dorsal musculature in pairs (to limit the effects of tag loss) with a cartridge-fed applicator (Dell 1968). Participating anglers were instructed on how to properly apply anchor tags to salmon including appropriate placement points for the tags, and best practices for salmon handling, such as the need to limit air exposure in order to maximise postrelease survival. Details about the capture location and time, size and sex of the fish, release methods and capture gear were recorded as available. If a tagged fish was later recaptured during the same fishing season, the individual was identified from its tag number. A relatively high reward (500 NOK) was offered to anglers in order to increase the probability of reporting recaptured salmon (Pollock et al. 2001). To ensure ease of reporting, a cellular phone and email address were printed on tags. The phone number and email address were dedicated exclusively to monitoring for reports of recaptures. Anglers that reported recaptured fish provided details about the date, time and location of capture, as well as the gear that they had used to capture the fish. All handling and tagging were conducted according to the Norwegian regulations for treatment and welfare of animals and approved by the Norwegian Animal Research Authority.

Data analysis

To test for gear avoidance using recapture data, it was necessary to compare the observed frequency of gear switch to the expected frequency of gear switch given no gear avoidance. If gear catch probabilities (i.e. probability that a fish would be captured by a fly, lure or worm) were equal across space (rivers) and time (month of a given year) in this study, the expected probability of gear switch would be 2/3 (because three different gear types were used). However, the probability that salmon would be captured by a given gear type varies in different rivers and over time because of different effort expended by anglers with each gear type (i.e. most anglers use flies) and due to changing river conditions (i.e. clarity, temperature and flow) during the season that may affect the efficiency of each gear type.

To account for the large variation in gear catch probability, we constructed a simulation in which each tagged and recaptured salmon, according to the null hypothesis of no gear avoidance, was assigned gear catch probabilities based on the river, year and month in which it was recaptured. Gear catch probability was estimated by the proportion of the total angling catch landed by each gear type in the space (i.e. river) and time (i.e. month) of interest, which were calculated from publically available catch logs from each river. For example, two tagged salmon were recaptured in River Gaula in August 2012. In

this river in August 2012, 68% of salmon were captured by flies, 17% by lures and 15% by worms; for the simulation, these values were assigned as gear catch probabilities for each of the two recaptured salmon.

Once gear catch probabilities were assigned to each recaptured salmon, the simulation was conducted. In each simulation step, every recaptured salmon was multinomially assigned a gear type using the respective gear catch probabilities. At the end of the simulation step, the percentage of fish for which simulated recapture gear type differed from tagging capture gear type (i.e. a gear switch had occurred) was calculated. To obtain the distribution of gear-switching frequency under the null hypothesis of no gear avoidance, the simulation was repeated 10,000 times. By comparing the observed percentage of gear switches to this simulated null distribution, it was possible to calculate the *P*-value of the hypothesis test, the *P*-value being the probability of observing an equal or greater number of gear switches than we did.

To test whether initial capture gear affected distance or time between capture and recapture, an analysis of variance (ANOVA) was conducted. To determine whether gear switching was associated with time to be recaptured or distance travelled between the capture and recapture site, two-tailed Student's *t*-tests were conducted comparing mean time elapsed and mean distance travelled between gear-switching salmon and non gear-switching salmon. Descriptive statistics of time and distance between capture and recapture are presented as mean \pm 1 SD. Statistics and figures were generated using the open-source statistical computing software R (R Core Team 2014).

Results

In 2012 and 2013, external tags were affixed to 339 Atlantic salmon (Table 1). Among the tagged salmon, most were initially caught on flies (67%), fol-

lowed by worms (18%) and lures (15%). Later in the season, 46 (14%) of the tagged salmon were recaptured and reported by anglers (Table 1). Among these 46 salmon recaptured in Gaula, Lakselva, Otra and Orkla, 32 (70%) exhibited gear switch (Fig. 1). The simulated null distribution of the percentage of gear switches for the 46 recaptured salmon (Fig. 2) has a mean percentage of gear switches of 52% (24 of 46). Given that we observed 70% of salmon exhibiting gear switch, gear switch occurred significantly more frequently than could be expected if salmon did not have any gear preference ($P = 0.003$; Fig. 2).

There were no differences among initial capture gear types in terms of time or distance elapsed between capture and recapture (time: $F_{2,43} = 0.62$, $P = 0.54$; distance: $F_{2,42} = 0.46$, $P = 0.63$). On average, salmon were recaptured 22 ± 17 days after initial capture (range = 0–78 days). There was no difference in distance from location of initial release to recapture ($t = 0.36$, d.f. = 23.50 $P = 0.72$) nor in the amount of elapsed time from initial release to recapture ($t = 1.19$, d.f. = 34.33, $P = 0.24$) between gear-switching salmon and those that did not switch gear. On average, salmon were recaptured 10 ± 16 km upriver of the initial release location (range = –10–50 km); however, 11 of the 46 salmon were recaptured below the initial release site, and 18 were recaptured within one km upriver or downriver of the initial release site. One salmon was recaptured in a different river than the release river and was excluded from the distance comparison.

Discussion

The recapture rates of caught-and-released salmon observed in this study are among the highest reported for Atlantic salmon in recreational fisheries (Webb 1998; Gowans et al. 1999; Whoriskey et al. 2000; Thorstad et al. 2003; Richard et al. 2013). It is apparent from our simulation of gear switch that recapture events were driven at least in part by salmon that were naïve to gear types that they had not previously

Table 1. Total salmon catches in the Norwegian study rivers in 2012 and 2013. Salmon catches were downloaded from the publically available catch databases. Salmon tagging data encompasses radio and anchor tags. For the total salmon catch, percentages of fish captured on different gears are given. The percentage of captured fish released in these two years in these rivers is also given. Recapture rates are calculated from the number of tags returned by anglers from salmon tagged during the same angling season.

River	Catch Data					Tagging Data	
	Total Catch	Fly %	Lure %	Worm%	Released %	Total tagged	Recaptured %
Gaula	7422	50	21	29	30	99	25
Lakselva	3520	93	6	1	36	77	8
Orkla	5423	56	19	25	50	67	10
Otra	3270	41	38	21	13	96	8
Total	19,635	58	21	22	38	339	14

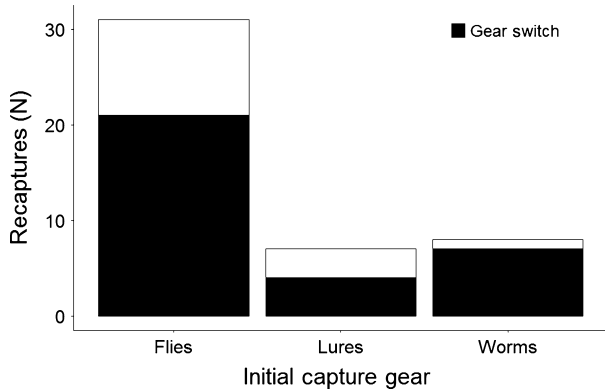


Fig. 1. Number of recaptured salmon ($N_{\text{total}} = 46$) initially captured by flies, lures and worms. The shaded area indicates the number of salmon that were recaptured by a different gear than they were first captured by (i.e. exhibited gear switch).

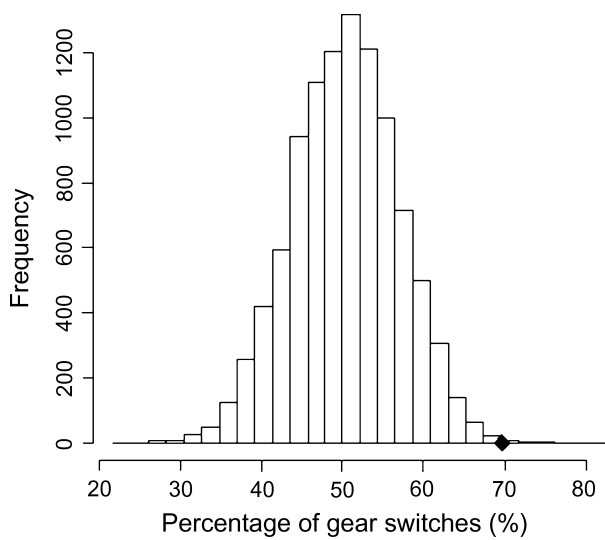


Fig. 2. Simulated probability distribution of the percentage of salmon that would exhibit gear switch in the absence of gear avoidance. The distribution represents the outcomes of 10,000 simulations, which multinomially assigned a recapture gear to 46 salmon based on gear catch probability. Among 46 salmon recaptured in Rivers Gaula, Lakselva, Orkla and Otra in 2012 and 2013, 32 (70%) exhibited gear switch, represented by the black diamond.

been captured by. We therefore demonstrated that salmon appear to avoid recapture by the same gear as they had previously been captured by.

Factors that affect the catchability of fish are typically attributed either to intraspecific variation in physiological or behavioural traits (i.e. ‘heterogeneity’; Marten 1970) or to changes to behaviour after release that affect the availability of fish in the river to be caught (i.e. ‘contagion’; Marten 1970). Learning could be considered contagion when salmon avoid familiar gear. Learned avoidance by released salmon may explain the observation that salmon were unlikely to be captured by the same gear type multi-

ple times in this study. Fish are capable of learning or changing patterns in behaviour as a result of past experiences (Dill 1983). Moreover, it is increasingly evident that learning is important to behavioural development of fish (Brown et al. 2011) and that learning to recognise future dangerous situations is adaptive (Lima & Dill 1990). Salmonids are capable of leaning, and it likely plays an important role in migratory behaviour (Dodson 1988). Raat (1985) identified declining catch per unit effort of common carp (*Cyprinus carpio*) in association with hooking and found that the avoidance behaviour was lost after a 1-year absence of fishing effort. Salmonids have also been demonstrated capable of discriminating against angling gear, and Askey et al. (2006) suggested that declining catch rates of rainbow trout (*Oncorhynchus mykiss*) after several days of angling resulted from released fish learning hook avoidance.

In our study, gear avoidance by salmon is consistent with observations from other studies that describe learned hook avoidance; however, an alternative explanation for the observed rate of gear switch is that salmon are not necessarily consciously discriminating among gear types, but implicitly doing so by changing their migratory behaviour or habitat selection. Huntingford & Wright (1989) described changes to habitat selection by stickleback (*Gasterosteus aculeatus*) in response to high predator burden. Behavioural changes often result from catch and release of salmon, particularly departure from normal migratory patterns immediately after release (i.e. fallback; Mäkinen et al. 2000; Thorstad et al. 2007). Cox & Walters (2002) described such changes in behaviour or habitat selection resulting from catch-and-release angling as changes to spatial vulnerability. Similarly, recaptured salmon may have switched gear because they were located in different areas of the river after catch and release than before, for example, by moving to deeper water. If released salmon seek out different areas of the river in which to recover, gears that have better access to such areas would have disproportionate success. For instance, if released salmon are more likely to be found in deeper habitat, they would become more likely to be recaptured by worms or spoons, which have better access to deep water than flies.

Gear-switching salmon were not necessarily recaptured longer after initial capture than non gear-switching salmon. The suggestion that salmon learn implies that they must eventually also forget (e.g. Raat 1985), in which circumstance it may be expected that gear-switching salmon would be recaptured soon after catch and release and non gear-switching salmon would be captured significantly longer after catch and release. Correspondingly, Thorley et al. (2007) found that salmon captured early in the angling season are most likely to be

recaptured, implying some role of forgetting supporting recapture in salmon fisheries. However, we did not identify a relationship between gear switching and time elapsed between capture and recapture. In Thorley et al. (2007), early run fish captured in February were most likely to be recaptured, whereas the angling season in Norway does not begin until June. The shorter period of time during which salmon could be captured may explain the differences in temporal recapture trends.

Salmon were often recaptured at or near the initial capture site, even after a long period of time elapsing between initial capture and recapture. This may occur because the salmon were captured the first time at spawning grounds and were therefore not likely to continue migrating. Alternatively, catch and release may reduce the capacity or motivation for salmon to continue migrating after catch and release. Several salmon were recaptured below the initial capture location. Fallback, downriver movement made by salmon after catch and release (Mäkinen et al. 2000; Thorstad et al. 2003) is often attributed to stress or exhaustion from angling. Mäkinen et al. (2000) suggested that the magnitude of fallback may be related to the degree of stress experienced based on a comparison between gill net and rod-caught salmon. However, the fitness consequences of fallback are not well understood, particularly in terms of whether salmon that fall back are less likely to reach their ultimate spawning destination, reproduce successfully or survive over the winter.

Various factors influence the propensity of different gear types to capture fish. Gear types may select for fish with different behavioural types and may result in different magnitude of hooking injury and mortality (e.g. Gargan et al. 2015), which could affect recapture rates with different gear types. Salmon may not necessarily categorise different gears the way that we did in this study (i.e. as flies, lures or worms). Colour, size, shape or depth fished may be proximate factors that are avoided and could be further investigated in a future study. Interestingly, olfactory cues may be an important factor that salmon learn to avoid after capture, particularly that of earthworms, which trigger the sense of smell, whereas flies or lures do not. Garrett (2002) stated that fish may not be able to discriminate well against live baits, and Beukema (1970) found that northern pike (*Esox lucius*) had difficulty learning to avoid worms relative to avoiding lures. We did not identify such a trend, perhaps because salmon have less difficulty learning to avoid worms given that they are not actively feeding during migration (Kadri et al. 1995; but see Johansen (2001), who found that Atlantic salmon may feed opportunistically on invertebrates during the migration).

Salmon recapture in this study was associated with gear switching, suggesting that recapture would be

most frequent in fisheries that permit the use of multiple gear types. However, gear usage is different depending on the river or region. Depending on local conventions, many different gears are used for catching salmon, for instance, in Ireland; Gargan et al. (2015) reported that anglers target migrating salmon using live prawns, which are not used in Norway. In some fisheries, management strategies may limit the use of live baits, control the use of weighted lines or flies or otherwise restrict fishing gear in an effort to reduce the efficiency with which anglers capture fish. Based on our findings, it could be expected that in fisheries where anglers are restricted from using many different types of gear there would be fewer instances of recapture relative to mixed-gear fisheries where gear switch may increase recapture rates. However, we could not identify any empirical support for this, particularly because most rivers are open to multiple gear types. The exception is Richard et al. (2013), which identified 5% recapture of tagged salmon in the Escoumins River, Canada, where angling is restricted to fly fishing. Although this is a relatively low rate of recapture, Thorstad et al. (2003) calculated a similarly low rate of recapture (4%) in River Alta, Norway, which is a mixed-gear fishery. More data would be necessary for accurately determining the effect of gear restrictions on salmon recapture.

Conclusions

Capturing migrating salmon is an economically and culturally important activity that is also relatively mysterious: neither scientists nor anglers truly understand why salmon that do not feed while migrating are catchable. Many salmon may be captured during the upriver migration (Gudjonsson et al. 1996), and individuals that are released may be captured multiple times. In this study, we have demonstrated that released salmon that are recaptured exhibited gear avoidance and were more frequently recaptured by different gear than they were first captured by. Improved understanding about mechanisms that underlie spatial and behavioural vulnerability of fish to angling provides some insight into salmon behaviour during the migration and has the potential to inform fisheries managers about factors that influence catches in recreational fisheries (Arlinghaus et al. 2013).

Acknowledgements

This study was funded by the Norwegian Research Council (Pr. no. 216416). RJL and SJC are supported by the Natural Sciences and Engineering Research Council of Canada (NSERC). SJC is additionally supported by Canada

Research Chairs Program and Carleton University. FGW is supported by Dalhousie's Ocean Tracking Network. Kim Whoriskey provided helpful direction for an early draft of the manuscript. We thank Egil Liberg, Ragnhild Brennslett, Torstein Rognes, Rune Kroghdal, John Olav Oldren, Harald Endresen, Jostein Mosby, Helge Anonsen, Steven Philip, Egil Odderstøl, Inge Odderstøl and Mark Taylor, as well as the many river owners and anglers that agreed to collaborate with us by contributing salmon for tagging, applying tags to salmon and reporting recaptured salmon. We also thank two anonymous reviewers for their comments on the manuscript.

References

- Aas, Ø., Policansky, D., Einum, S. & Skurdal, J. 2011. Salmon ecological research and conservation. In: Aas, Ø., Einum, S., Klemetsen, A. & Skudal, J., eds. Atlantic salmon ecology. Oxford: Wiley-Blackwell, pp. 445–456.
- Arlinghaus, R. & Cooke, S.J. 2009. Recreational fisheries: socioeconomic importance, conservation issues and management challenges. In: Dickson, B., Hutton, J. & Adams, W.A., eds. Recreational hunting, conservation and Rural Livelihoods: Science and Practice. Oxford: Blackwell Publishing, pp. 39–58.
- Arlinghaus, R., Cooke, S.J. & Potts, W. 2013. Towards resilient recreational fisheries on a global scale through improved understanding of fish and fisher behaviour. *Fisheries Management and Ecology* 20: 91–98.
- Askey, P.J., Richards, S.A., Post, J.R. & Parkinson, E.A. 2006. Linking angling catch rates and fish learning under catch-and-release regulations. *North American Journal of Fisheries Management* 26: 1020–1029.
- Bartholomew, A. & Bohnsack, J.A. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries* 15: 129–154.
- Beukema, J.J. 1970. Acquired hook-avoidance in the pike *Esox lucius* L. fished with artificial and natural baits. *Journal of Fish Biology* 2: 155–160.
- Beukema, J.J. & de Vos, G.J. 1974. Experimental tests of a basic assumption of the capture-recapture method in pond populations of carp *Cyprinus carpio* L. *Journal of Fish Biology* 6: 317–329.
- Brown, C., Laland, K.N. & Krause, J. 2011. Fish cognition and behaviour. Oxford: Wiley-Blackwell Scientific, 472 pp.
- Consuegra, S., Leániz, D., García, C., Serdio, A. & Verspoor, E. 2005. Selective exploitation of early running fish may induce genetic and phenotypic changes in Atlantic salmon. *Journal of Fish Biology* 67: 129–145.
- Cowx, I.G., Arlinghaus, R. & Cooke, S.J. 2010. Harmonizing recreational fisheries and conservation objectives for aquatic biodiversity in inland waters. *Journal of Fish Biology* 76: 2194–2215.
- Cox, S.P. & Walters, C. 2002. Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. *North American Journal of Fisheries Management* 22: 21–34.
- Dell, M.B. 1968. A new fish tag and rapid, cartridge-fed applicator. *Transactions of the American Fisheries Society* 97: 57–59.
- Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 40: 398–408.
- Dodson, J.J. 1988. The nature and role of learning in the orientation and migratory behavior of fishes. *Environmental Biology of Fishes* 23: 161–182.
- Gargan, P.G., Stafford, T., Økland, F. & Thorstad, E.B. 2015. Survival of wild Atlantic salmon (*Salmo salar*) after catch and release angling in three Irish rivers. *Fisheries Research* 161: 252–260.
- Garrett, G. 2002. Behavioral modification of angling vulnerability in largemouth bass through selective breeding. *American Fisheries Society Symposium* 31: 387–392.
- Gowans, A.R.D., Armstrong, J.D. & Priede, I.G. 1999. Movements of adult Atlantic salmon in relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology* 54: 713–726.
- Gudjonsson, S., Antonsson, T. & Tomasson, T. 1996. Exploitation ratio of salmon in relation to salmon run in three Icelandic rivers. ICES CM. (M: 8).
- Huntingford, F.A. & Wright, P.J. 1989. How sticklebacks learn to avoid dangerous feeding patches. *Behavioural Processes* 19: 181–189.
- Johansen, M. 2001. Evidence of freshwater feeding by adult salmon in the Tana River, northern Norway. *Journal of Fish Biology* 59: 1405–1407.
- Kadri, S., Metcalfe, N.B., Huntingford, F.A. & Thorpe, J.E. 1995. What controls the onset of anorexia in maturing adult female Atlantic salmon? *Functional Ecology* 9: 790–797.
- Klefoth, T., Pieterek, T. & Arlinghaus, R. 2013. Impacts of domestication on angling vulnerability of common carp, *Cyprinus carpio*: the role of learning, foraging behaviour and food preferences. *Fisheries Management and Ecology* 20: 174–186.
- Kuparinen, A., Klefoth, T. & Arlinghaus, R. 2010. Abiotic and fishing-related correlates of angling catch rates in pike (*Esox lucius*). *Fisheries Research* 105: 111–117.
- Lennox, R.J., Uglem, I., Solem, O., Thorstad, E.B., Havn, T., Naesje, T., Whoriskey, F.G. & Cooke, S.J. 2015. Does catch-and-release angling alter the behaviour and fate of adult Atlantic salmon during upriver migration? *Transactions of the American Fisheries Society* 144: 400–409.
- Lima, S.L. & Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619–640.
- Mäkinen, T.S., Niemelä, E., Moen, K. & Lindström, R. 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.
- Marten, G.G. 1970. A regression method for mark-recapture estimation of population size with unequal catchability. *Ecology* 51: 291–295.
- Økland, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R.S. & Thorstad, E.B. 2001. Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. *Journal of Fish Biology* 59: 862–874.
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. & Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences* 55: 281–287.
- Philipp, D.P., Cooke, S.J., Claussen, J.E., Koppelman, J.B., Suski, C.D. & Burkett, D.P. 2009. Selection for vulnerability

- to angling in largemouth bass. *Transactions of the American Fisheries Society* 138: 189–199.
- Pollock, K.H., Hoenig, J.M., Hearn, W.S. & Calingaert, B. 2001. Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* 21: 521–532.
- R Core Team. 2014. R. A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Raat, A.J.P. 1985. Analysis of angling vulnerability of common carp, *Cyprinus carp* L., in catch-and-release angling in ponds. *Aquaculture Research* 16: 171–187.
- Richard, A., Dionne, M., Wang, J. & Bernatchez, L. 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.
- Stensland, S., Aas, Ø. & Mehmetoglu, M. 2013. The Influence of norms and consequences on voluntary catch and release angling behavior. *Human Dimensions of Wildlife* 18: 373–385.
- Thorley, J.L., Youngson, A.F. & Laughton, R. 2007. Seasonal variation in rod recapture rates indicates differential exploitation of Atlantic salmon, *Salmo salar*, stock components. *Fisheries Management and Ecology* 14: 191–198.
- Thorstad, E.B., Næsje, T.F., Fiske, P. & Finstad, B. 2003. Effects of hook and release on Atlantic salmon in the River Alta, northern Norway. *Fisheries Research* 60: 293–307.
- Thorstad, E.B., Næsje, T.F. & Leinan, I. 2007. Long-term effects of catch-and-release angling on ascending Atlantic salmon during different stages of spawning migration. *Fisheries Research* 3: 316–320.
- Tsuboi, J.I. & Morita, K. 2004. Selectivity effects on wild white-spotted charr (*Salvelinus leucomaenis*) during a catch and release fishery. *Fisheries Research* 69: 229–238.
- Verspoor, E., Stradmeyer, L. & Nielsen, J.L. 2008. *The Atlantic Salmon: genetics, conservation, and management*. Oxford: Blackwell Publishing.
- Webb, J.H. 1998. Catch and release: the survival and behaviour 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., Prusov, S. & Crabbe, S. 2000. Evaluation of the effects of catch-and-release angling on the Atlantic salmon (*Salmo salar*) of the Ponoj River, Kola Peninsula, Russian Federation. *Ecology of Freshwater Fish* 9: 118–125.