

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

3

4 Running Head: Salmon avoid familiar gear types in recreational fisheries

5

6 Robert J. Lennox^{1,2, §}, Ola H. Diserud², Steven J. Cooke¹, Eva B. Thorstad², Frederick G.

7 Whoriskey³, Øyvind Solem², Torgeir B. Havn, and Ingebrigt Uglem²

8

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

11 ²Norwegian Institute for Nature Research, P. O. Box 5685, Sluppen, N-7485 Trondheim,
12 Norway

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

14

15 [§]Corresponding Author- Email: robert.lennox@carleton.ca; telephone: 1-613-408-3474

16

Lennox, Robert J.; Diserud, Ola Håvard; Cooke, Steven J.; Thorstad, Eva Bonsak; Whoriskey, Frederick G.; Solem, Øyvind; Havn, Torgeir Børresen; Uglem, Ingebrigt.

17 Influence of gear switching on recapture of Atlantic salmon (*Salmo salar*) in catch-and- release fisheries. *Ecology of Freshwater Fish* 2016 ;Volum 25.(3) s. 422-428 DOI: 10.1111/eff.12223

18 Abstract

19 Anglers that release Atlantic salmon (*Salmo salar*) in recreational fisheries do so with the
20 intention that the fish will survive and contribute to succeeding generations. In some instances,
21 salmon that are released may be recaptured, but mechanisms associated with recapture are
22 unclear. To test whether gear avoidance influences recapture rates, we analyzed data from
23 tagging programs in major Norwegian Atlantic salmon fishing rivers to determine how
24 frequently salmon were recaptured by different gear than which they were initially captured (i.e.
25 gear switch). Among 339 salmon captured, externally tagged, and released in 2012 and 2013, 46
26 (14%) were recaptured; 70% of these recaptured salmon exhibited gear switch. To test whether
27 this gear switch percentage could be expected in the absence of gear avoidance, a simulation was
28 conducted, which accounted for variation in catch probability among rivers and across time with
29 different gear types based on comprehensive catch data. Each simulation step provided a
30 simulated rate of gear switch under the null hypothesis of no gear avoidance. A distribution was
31 generated, which described the probability that we would observe 70% gear switch. The
32 simulated results indicated that this rate of gear switch was highly unlikely ($P = 0.003$) if
33 recapture gear is assumed to be independent of initial capture gear, suggesting that salmon
34 avoided familiar gear types. Changes to behaviour after release, including learned hook
35 avoidance, may explain our observation of gear avoidance by recaptured salmon.

36 Keywords: fisheries management, recreational fisheries, fish behaviour

37 1. Introduction

38

39 Recreational angling is an important activity and may represent a considerable
40 component of many regional economies (Arlinghaus and Cooke 2009; Cowx et al. 2010).
41 Fishing can exert substantial pressure on fish stocks and persistent effort from anglers may result
42 in a large proportion of fish from a stock or population being captured (e.g. Gudjonsson et al.
43 1996). Individual differences in catchability occur within fish populations, meaning that certain
44 individuals have traits that predispose them to being captured by anglers (Cox and Walters
45 2002). In some instances, behavioural or physiological traits that increase catchability have a
46 genetic basis (Consuegra et al. 2005; Klefoth et al. 2013; Philipp et al. 2009). It follows that
47 individuals that are predisposed to capture by recreational fishers may be captured and released
48 multiple times (Tsuboi and Morita 2004), potentially reducing the positive effects conferred by
49 catch-and-release to some extent (Bartholomew and Bohnsack 2005). However, prior
50 investigations into fish recapture by anglers have indicated that some species or individuals
51 become difficult to recapture over time (Askey et al. 2006; Beukema and de Vos 1974;
52 Kuparinen et al. 2010).

53 Recreational Atlantic salmon (*Salmo salar*) angling is an economically and culturally
54 important activity throughout coastal regions along the North Atlantic coast (Aas et al. 2011;
55 Verspoor et al. 2008). Depending on local regulations, anglers are permitted to fish for salmon
56 using a variety of terminal tackle, which may include artificial flies, lures, or live bait. However,
57 to compensate for declining stock sizes in many rivers (Parrish et al. 1998), salmon fisheries are
58 increasingly using catch-and-release as a management strategy. In rivers that permit harvest,

59 some anglers may nonetheless practice voluntary catch-and-release as a result of conservation
60 ethic (Gargan et al. 2015; Stensland et al. 2013).

61 Efforts to understand factors that influence mortality of salmon in catch-and-release
62 fisheries have been initiated to evaluate the benefits of the strategy for conservation and
63 management. Studies have demonstrated that most salmon survive catch-and-release but that
64 many go on to be recaptured, with rates reported in the literature varying between 4% and 11%
65 (Gowans et al. 1999; Richard et al. 2013; Thorstad et al. 2003; Webb 1998; Whoriskey et al.
66 2000). Gear avoidance or selectivity has been demonstrated to affect catch rates in recreational
67 fisheries (e.g. Beukema, 1970; Beukema and de Vos 1974), and it is possible that recapture rates
68 in some salmon fisheries are affected by gear avoidance. If that were the case, it would be
69 expected that salmon would be unlikely to be recaptured by the same fishing gear multiple times,
70 a phenomenon termed gear switching. For instance, salmon caught by flies would be more likely
71 to be recaptured by lures or worms rather than flies, or vice versa. In this study, we analyzed
72 recapture trends of tagged salmon in Norwegian recreational fisheries by testing whether the gear
73 that a salmon was captured by a second time was independent of the gear that it was captured by
74 initially.

75

76 2. Methods

77

78 During the angling seasons (June 1 – September 15 in most rivers) of 2012 and 2013,
79 adult Atlantic salmon returning to Norwegian rivers Gaula, Lakselva, Orkla, and Otra from the
80 ocean were captured by recreational anglers and externally tagged with either radio transmitters
81 or t-bar anchor tags. Radio tagged salmon were typically landed in knotless landing nets and

82 transferred to a water-filled PVC tube (to ensure adequate gill ventilation) for tagging (Lennox et
83 al. In Press). External radio tagging methods followed those of Økland et al. (2001), in which
84 rectangular radio transmitters (dimensions = 21 × 52 × 11 mm, model F2120 from Advanced
85 Telemetry Systems, Minnesota, USA) were attached by steel wire through the dorsal
86 musculature beneath the dorsal fin. For all other tagged fish, anchor tags (Floy Manufacturing,
87 Washington, USA) were inserted into the dorsal musculature in pairs (to limit the effects of tag
88 loss) with a cartridge-fed applicator (Dell 1968). Participating anglers were instructed on how to
89 properly apply anchor tags to salmon including appropriate placement points for the tags, and
90 best practices for salmon handling, such as the need to limit air exposure in order to maximize
91 post-release survival. Details about the capture location and time, size and sex of the fish, release
92 methods, and capture gear were recorded as available. If a fish that had been tagged was later
93 recaptured during the same fishing season, the individual was identified from its tag number. A
94 relatively high reward (500 NOK) was offered to anglers in order to increase the probability of
95 reporting recaptured salmon (Pollock et al. 2001). To ensure ease of reporting, a cellular phone
96 and email address were printed on tags. The phone number and email address were dedicated
97 exclusively to monitoring for reports of recaptures. Anglers that reported recaptured fish
98 provided details about the date, time, and location of capture, as well as the gear that they had
99 used to capture the fish. All handling and tagging was conducted according to the Norwegian
100 regulations for treatment and welfare of animals and approved by the Norwegian Animal
101 Research Authority.

102

103 2.1 Data Analysis

104

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

114 To account for the large variation in gear catch probability, we constructed a simulation
115 in which each tagged and recaptured salmon, according to the null hypothesis of no gear
116 avoidance, was assigned gear catch probabilities based on the river, year, and month in which it
117 was recaptured. Gear catch probability was estimated by the proportion of the total angling catch
118 landed by each gear type in the space (i.e. river) and time (i.e. month) of interest, which were
119 calculated from publically available catch logs from each river. For example, two tagged salmon
120 were recaptured in River Gaula in August 2012. In this river in August 2012, 68% of salmon
121 were captured by flies, 17% by lures, and 15% by worms; for the simulation these values were
122 assigned as gear catch probabilities for each of the two recaptured salmon.

123 Once gear catch probabilities were assigned to each recaptured salmon, the simulation
124 was conducted. In each simulation step, every recaptured salmon was multinomially assigned a
125 gear type using the respective gear catch probabilities. At the end of the simulation step, the
126 percentage of fish for which simulated recapture gear type differed from tagging capture gear
127 type (i.e. a gear switch had occurred) was calculated. To obtain the distribution of gear switching

128 frequency under the null hypothesis of no gear avoidance, the simulation was repeated 10,000
129 times. By comparing the observed percentage of gear switches to this simulated null distribution,
130 it was possible to calculate the *P*-value of the hypothesis test; the *P*-value being the probability
131 of observing an equal or greater number of gear switches than we did.

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

140

141 3. Results

142

143 In 2012 and 2013, external tags were affixed to 339 Atlantic salmon (Table 1). Among
144 the tagged salmon, most were initially caught on flies (67%), followed by worms (18%), and
145 lures (15%). Later in the season, 46 (14%) of the tagged salmon were recaptured and reported by
146 anglers (Table 1). Among these 46 salmon recaptured in Gaula, Lakselva, Otra, and Orkla, 32
147 (70%) exhibited gear switch (Figure 1). The simulated null distribution of the percentage of gear
148 switches for the 46 recaptured salmon (Figure 2) has a mean percentage of gear switches of 52%
149 (24 of 46). Given that we observed 70% of salmon exhibiting gear switch, gear switch occurred
150 significantly more frequently than could be expected if salmon did not have any gear preference
151 ($P = 0.003$; Figure 2).

152 There were no differences among initial capture gear types in terms of distance or time
153 elapsed between capture and recapture (distance: $F_{2,42} = 0.46$, $P = 0.63$; time: $F_{2,43} = 0.62$, $P =$
154 0.54). On average, salmon were recaptured 22 ± 17 days after initial capture (range = 0 – 78
155 days). There was no difference in distance from location of initial release to recapture ($t = 0.36$,
156 $df = 23.50$ $P = 0.72$) nor in the amount of elapsed time from initial release to recapture ($t = 1.19$,
157 $df = 34.33$, $P = 0.24$) between gear switching salmon and those that did not switch gear. On
158 average, salmon were recaptured 10 ± 16 km upriver of the initial release location (range = -10 –
159 50 km), however, 11 of the 46 salmon were recaptured below the initial release site and 18 were
160 recaptured within one km upriver or downriver of the initial release site. One salmon was
161 recaptured in a different river than the release river and was excluded from the distance
162 comparison.

163

164 4. Discussion

165

166 The recapture rates of caught-and-released salmon observed in this study are among the
167 highest reported for Atlantic salmon recreational fisheries (Gowans et al. 1999; Richard et al.
168 2013; Thorstad et al. 2003; Webb 1998; Whoriskey et al. 2000). It is apparent from our
169 simulation of gear switch that recapture events were driven at least in part by salmon that were
170 naïve to gear types that they had not previously been captured by. We therefore demonstrated
171 that salmon appear to avoid recapture by the same gear as they had previously been captured by.

172 Factors that affect the catchability of fish are typically attributed to either intraspecific
173 variation in physiological or behavioural traits (i.e. “heterogeneity”; Marten 1970) or to changes
174 to behaviour after release that affect the availability of fish in the river to be caught (i.e.

175 “contagion”; Marten 1970). Learning could be considered contagion when salmon avoid familiar
176 gear. Learned avoidance by released salmon may explain the observation that salmon were
177 unlikely to be captured by the same gear type multiple times in this study. Fish are capable of
178 learning, or changing patterns in behaviour as a result of past experiences (Dill et al. 1983).
179 Moreover, it is increasingly evident that learning is important to behavioural development of fish
180 (Brown et al. 2011) and that learning to recognize future dangerous situations is adaptive (Lima
181 and Dill 1990). Salmonids are capable of leaning, and it likely plays an important role in
182 migratory behaviour (Dodson 1988). Raat (1985) identified declining catch per unit effort of
183 common carp (*Cyprinus carpio*) in association with hooking, and found that the avoidance
184 behaviour was lost after a one year absence of fishing effort. Salmonids have also been
185 demonstrated capable of discriminating against angling gear, and Askey et al. (2006) suggested
186 that declining catch rates of rainbow trout (*Oncorhynchus mykiss*) after several days of angling
187 resulted from released fish learning hook avoidance.

188 In our study, gear avoidance by salmon is consistent with observations from other studies
189 that describe learned hook avoidance, however, an alternative explanation for the observed rate
190 of gear switch is that salmon are not necessarily consciously discriminating among gear types,
191 but implicitly doing so by changing their migratory behaviour or habitat selection. Huntingford
192 and Wright (1989) described changes to habitat selection by stickleback (*Gasterosteus*
193 *aculeatus*) in response to high predator burden. Behavioural changes often result from catch-and-
194 release of salmon, particularly departure from normal migratory patterns immediately after
195 release (i.e. fallback; Mäkinen et al. 2000; Thorstad et al. 2007). Cox and Walters (2002)
196 described such changes in behaviour or habitat selection resulting from catch-and-release angling
197 as changes to spatial vulnerability. Similarly, recaptured salmon may have switched gear because

198 they were located in different areas of the river after catch-and-release than before, for instance
199 by moving to deeper water. If released salmon seek out different areas of the river in which to
200 recover, gears that have better access to such areas would have disproportionate success. For
201 instance, if released salmon are more likely to be found in deeper habitat, they would be more
202 likely to be recaptured by worms or spoons, which have better access to deep water than flies.

203 Gear switching salmon were not necessarily recaptured longer after initial capture than
204 non-gear switching salmon. The suggestion that salmon learn implies that they must eventually
205 also forget (e.g. Raat 1985), in which circumstance it may be expected that gear switching
206 salmon would be recaptured soon after catch-and-release and non-gear-switching salmon would
207 be captured significantly longer after catch-and-release. Correspondingly, Thorley et al. (2007)
208 found that salmon captured early in the angling season are most likely to be recaptured, implying
209 some role of forgetting supporting recapture in salmon fisheries. However, we did not identify a
210 relationship between gear switching and time elapsed between capture and recapture. In Thorley
211 et al. (2007), early run fish captured in February were most likely to be recaptured, whereas the
212 angling season in Norway does not begin until June. The shorter period of time during which
213 salmon could be captured may explain the differences in temporal recapture trends.

214 Salmon were often recaptured at or near the initial capture site, even after a long period
215 of time elapsing between initial capture and recapture. This may occur because the salmon were
216 captured the first time at spawning grounds and were therefore not likely to continue migrating.
217 Alternatively, catch-and-release may reduce the capacity or motivation for salmon to continue
218 migrating after catch-and-release. Several salmon were recaptured below the initial capture
219 location. Fallback, downriver movement made by salmon after catch-and-release (Mäkinen et al.
220 2000; Thorstad et al. 2003) is often attributed to stress or exhaustion from angling. Mäkinen et

221 al. (2000) suggested that the magnitude of fallback may be related to the degree of stress
222 experienced based on a comparison between gill net and rod caught salmon. However, the fitness
223 consequences of fallback are not well understood, particularly in terms of whether salmon that
224 fall back are less likely to reach their ultimate spawning destination, reproduce successfully, or
225 survive over the winter.

226 Various factors influence the propensity of various gear types to capture fish. Gear types
227 may select for fish with different behavioural types and may result in different magnitude of
228 hooking injury and mortality (e.g. Gargan et al. 2015), which could affect recapture rates with
229 different gear types. Salmon may not necessarily categorize different gears the way that we did
230 in this study (i.e. as flies, lures, or worms), and colour, size, shape, or depth fished may all be
231 proximate factors that are avoided and could be further investigated in a future study.

232 Interestingly, olfactory cues may be an important factor that salmon learn to avoid after capture,
233 particularly that of earthworms, which trigger the sense of smell whereas flies or lures do not.

234 Garrett (2002) stated that fish may not be able to discriminate well against live baits and
235 Beukema (1970) found that northern pike (*Esox lucius*) had difficulty learning to avoid worms
236 relative to avoiding lures. However, we did not identify such a trend and salmon may have less
237 difficulty learning to avoid worms given that they are not actively feeding during migration and
238 therefore not necessarily attracted to food the same way that a pike would be (Kadri et al. 1995;
239 but see Johansen [2001], who found that Atlantic salmon may feed opportunistically on
240 invertebrates during the migration).

241 Salmon recapture in this study was associated with gear switching, suggesting that
242 recapture would be most frequent in fisheries that permit the use of multiple gear types.
243 However, gear usage is different depending on the river or region. Depending on local

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

258

259 5. Conclusions

260

261 Capturing migrating salmon is an economically and culturally important activity that is
262 also relatively mysterious: neither scientists nor anglers truly understand why salmon that do not
263 feed while migrating are catchable. Many salmon may be captured during the upriver migration
264 (Gudjonsson et al. 1996), and individuals that are released may be captured multiple times. In
265 this study, we have demonstrated that released salmon that are recaptured exhibited gear
266 avoidance and were more frequently recaptured by different gear than they were first captured

267 by. Improved understanding about mechanisms that underlie spatial and behavioural
268 vulnerability of fish to angling provides some insight into salmon behaviour during the migration
269 and has the potential to inform fisheries managers about factors that influence catches in
270 recreational fisheries (Arlinghaus et al. 2013).

271

272 Acknowledgements

273

274 This study was funded by the Norwegian Research Council (Pr. no. 216416). RJL and SJC are
275 supported by the Natural Sciences and Engineering Research Council of Canada (NSERC). SJC
276 is additionally supported by Canada Research Chairs Program and Carleton University. FGW is
277 supported by Dalhousie's Ocean Tracking Network. Kim Whoriskey provided helpful direction
278 for an early draft of the manuscript. We thank Egil Liberg, Ragnhild Brennslett, Torstein
279 Rognes, Rune Kroghdal, John Olav Oldren, Harald Endresen, Jostein Mosby, Helge Anonsen,
280 Steven Philip, Egil Odderstøl, Inge Odderstøl, and Mark Taylor, as well as the many river
281 owners and anglers that agreed to collaborate with us by contributing salmon for tagging,
282 applying tags to salmon, and reporting recaptured salmon. We also thank two anonymous
283 reviewers for their comments on the manuscript.

284

285

286 References

287

288 Aas, Ø., Policansky, D., Einum, S., & Skurdal, J. 2011. Salmon ecological research and
289 conservation. In: Aas, Ø., Einum, S., Klemetsen, A. & Skudal, J., eds. Atlantic Salmon
290 Ecology. Oxford: Wiley-Blackwell, pp. 445-456.

291 Arlinghaus, R., & Cooke, S.J. 2009. Recreational fisheries: socioeconomic importance,
292 conservation issues and management challenges. In: Dickson, B., Hutton, J., & Adams,
293 W. A., eds. Recreational hunting, conservation and Rural Livelihoods: Science and
294 Practice. Oxford: Blackwell Publishing, pp. 39–58.

295 Arlinghaus, R., Cooke, S.J. & Potts, W. 2013. Towards resilient recreational fisheries on a global
296 scale through improved understanding of fish and fisher behaviour. Fisheries
297 Management and Ecology 20: 91-98.

298 Askey, P.J., Richards, S.A., Post, J.R. & Parkinson, E.A. 2006. Linking angling catch rates and
299 fish learning under catch-and-release regulations. North American Journal of Fisheries
300 Management 26: 1020-1029.

301 Bartholomew A., & Bohnsack J.A. 2005. A review of catch-and-release angling mortality with
302 implications for no-take reserves. Reviews in Fish Biology and Fisheries 15: 129-154.

303 Beukema, J.J. & Vos, G.J. 1974. Experimental tests of a basic assumption of the capture-
304 recapture method in pond populations of carp *Cyprinus carpio* L. Journal of Fish
305 Biology 6: 317-329.

306 Beukema, J.J. 1970. Acquired hook-avoidance in the pike *Esox lucius* L. fished with artificial
307 and natural baits. Journal of Fish Biology 2: 155-160.

308 Brown, C., Laland, K.N., & Krause, J. 2011. Fish Cognition and Behaviour. Oxford: Wiley-
309 Blackwell Scientific. 472 pp.

310 Consuegra, S., Leániz, D., García, C., Serdio, A., & Verspoor, E. 2005. Selective exploitation of
311 early running fish may induce genetic and phenotypic changes in Atlantic
312 salmon. *Journal of Fish Biology* 67: 129-145.

313 Cowx, I.G., Arlinghaus, R., & Cooke, S.J. 2010. Harmonizing recreational fisheries and
314 conservation objectives for aquatic biodiversity in inland waters. *Journal of Fish Biology*
315 76: 2194-2215.

316 Cox, S.P. & Walters, C. 2002. Modeling exploitation in recreational fisheries and implications
317 for effort management on British Columbia rainbow trout lakes. *North American Journal*
318 *of Fisheries Management* 22: 21-34.

319 Dell, M.B. 1968. A new fish tag and rapid, cartridge-fed applicator. *Transactions of the*
320 *American Fisheries Society* 97: 57-59.

321 Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of*
322 *Fisheries and Aquatic Sciences* 40: 398-408.

323 Dodson, J.J. 1988. The nature and role of learning in the orientation and migratory behavior of
324 fishes. *Environmental Biology of Fishes* 23: 161-182.

325 Gargan, P.G., Stafford, T., Økland, F. & Thorstad, E.B. 2015. Survival of wild Atlantic salmon
326 (*Salmo salar*) after catch and release angling in three Irish rivers. *Fisheries Research* 161:
327 252-260.

328 Garrett G. 2002. Behavioral modification of angling vulnerability in largemouth bass through
329 selective breeding. *American Fisheries Society Symposium* 31: 387–392.

330 Gowans, A.R.D., Armstrong, J.D. & Priede, I.G. 1999. Movements of adult Atlantic salmon in
331 relation to a hydroelectric dam and fish ladder. *Journal of Fish Biology* 54: 713-726.

332 Gudjonsson, S., Antonsson, T. & Tomasson, T. 1996: Exploitation ratio of salmon in relation to
333 salmon run in three Icelandic rivers. ICES CM. (M: 8).

334 Huntingford, F.A. & Wright, P.J. 1989. How sticklebacks learn to avoid dangerous feeding
335 patches. *Behavioural Processes* 19: 181-189.

336 Johansen, M. 2001. Evidence of freshwater feeding by adult salmon in the Tana River, northern
337 Norway. *Journal of Fish Biology* 59: 1405-1407.

338 Kadri, S., Metcalfe, N. B., Huntingford, F. A., & Thorpe, J. E. 1995. What controls the onset of
339 anorexia in maturing adult female Atlantic salmon? *Functional Ecology* 9: 790-797.

340 Klefoth, T., Pieterek, T., & Arlinghaus, R. 2013. Impacts of domestication on angling
341 vulnerability of common carp, *Cyprinus carpio*: the role of learning, foraging behaviour
342 and food preferences. *Fisheries Management and Ecology* 20: 174-186.

343 Kuparinen, A., Klefoth, T., & Arlinghaus, R. 2010. Abiotic and fishing-related correlates of
344 angling catch rates in pike (*Esox lucius*). *Fisheries Research* 105: 111-117.

345 Lennox, R.J., Uglem, I., Solem, O., Thorstad, E.B., Havn, T., Naesje, T., Whoriskey, F.G.,
346 Cooke, S.J. In Press. Is catch-and-release angling affecting the freshwater migration of
347 adult Atlantic Salmon *Salmo salar*? *Transactions of the American Fisheries Society* 00:
348 00-00.

349 Lima, S.L. & Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review
350 and prospectus. *Canadian Journal of Zoology* 68: 619-640.

351 Mäkinen, T.S., Niemelä, E., Moen, K. & Lindström, R. 2000. Behaviour of gill-net and rod-
352 captured Atlantic salmon (*Salmo salar* L.) during upstream migration and following radio
353 tagging. Fisheries Research 45: 117-127.

354 Marten, G.G. 1970. A regression method for mark-recapture estimation of population size with
355 unequal catchability. Ecology 51: 291-295.

356 Økland, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R.S. & Thorstad, E.B.
357 2001. Return migration of Atlantic salmon in the River Tana: phases of migratory
358 behaviour. Journal of Fish Biology 59: 862-874.

359 Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D., & Reeves, G.H. 1998. Why aren't
360 there more Atlantic salmon (*Salmo salar*)? Canadian Journal of Fisheries and Aquatic
361 Sciences 55: 281-287.

362 Philipp, D.P., Cooke, S.J., Claussen, J.E., Koppelman, J.B., Suski, C.D. & Burkett, D.P. 2009.
363 Selection for vulnerability to angling in largemouth bass. Transactions of the American
364 Fisheries Society 138: 189-199.

365 Pollock, K.H., Hoenig, J.M., Hearn, W.S. & Calingaert, B. 2001. Tag reporting rate estimation:
366 1. An evaluation of the high-reward tagging method. North American Journal of Fisheries
367 Management 21: 521-532.

368 R Core Team. 2014. R. A language and environment for statistical computing. R Foundation for
369 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL [http://www.R-](http://www.R-project.org)
370 [project.org](http://www.R-project.org).

371 Raat, A. J. P. 1985. Analysis of angling vulnerability of common carp, *Cyprinus carp* L., in
372 catch-and-release angling in ponds. Aquaculture Research 16: 171-187.

373 Richard, A., Dionne, M., Wang, J., & Bernatchez, L. 2013. Does catch and release affect the
374 mating system and individual reproductive success of wild Atlantic salmon (*Salmo salar*
375 L.)? *Molecular Ecology* 22: 187-200.

376 Stensland, S., Aas, Ø. & Mehmetoglu, M. 2013. The Influence of norms and consequences on
377 voluntary catch and release angling behavior. *Human Dimensions of Wildlife* 18: 373-
378 385.

379 Thorley, J. L., Youngson, A. F., & Laughton, R. 2007. Seasonal variation in rod recapture rates
380 indicates differential exploitation of Atlantic salmon, *Salmo salar*, stock
381 components. *Fisheries Management and Ecology* 14: 191-198.

382 Thorstad, E.B., Næsje, T.F. & Leinan, I. 2007. Long-term effects of catch-and-release angling on
383 ascending Atlantic salmon during different stages of spawning migration. *Fisheries*
384 *Research* 3: 316-320.

385 Thorstad, E.B., Næsje, T.F., Fiske, P. & Finstad, B. 2003. Effects of hook and release on Atlantic
386 salmon in the River Alta, northern Norway. *Fisheries Research* 60: 293-307.

387 Tsuboi, J. I., & Morita, K. 2004. Selectivity effects on wild white-spotted charr (*Salvelinus*
388 *leucomaenis*) during a catch and release fishery. *Fisheries Research* 69: 229-238.

389 Verspoor, E., Stradmeyer, L. & Nielsen, J.L. 2008. *The Atlantic Salmon: Genetics,*
390 *Conservation, and Management.* Blackwell Publishing, Oxford.

391 Webb, J.H. 1998. Catch and release: the survival and behaviour of Atlantic salmon angled and
392 returned to the Aberdeenshire Dee, in spring and early summer. *Scottish Fisheries*
393 *Research Report* 62: 1-15.

394 Whoriskey, F.G., Prusov, S. & Crabbe, S. 2000. Evaluation of the effects of catch-and-release
395 angling on the Atlantic salmon (*Salmo salar*) of the Ponoï River, Kola Peninsula, Russian
396 Federation. Ecology of Freshwater Fish 9: 118-125.

397

398

399

400

401

402 Table Captions

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

409

410 Tables

411 Table 1.

River	2012/2013 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	19635	58%	21%	22%	38%	339	14%

412

413

414

415 Figure Captions

416 Figure 1. Number of recaptured salmon ($N_{\text{total}} = 46$) initially captured by flies, lures, and worms.

417 The shaded area indicates the number of salmon that were recaptured by a different gear than
418 they were first captured by (i.e. exhibited gear switch).

419

420 Figure 2. Simulated probability distribution of the percentage of salmon that would exhibit gear

421 switch in the absence of gear avoidance. The distribution represents the outcomes of 10,000

422 simulations, which multinomially assigned a recapture gear to 46 salmon based on gear catch

423 probability. Among 46 salmon recaptured in Rivers Gaula, Lakselva, Orkla, and Otra in 2012

424 and 2013, 32 (70%) exhibited gear switch, represented by the black diamond.

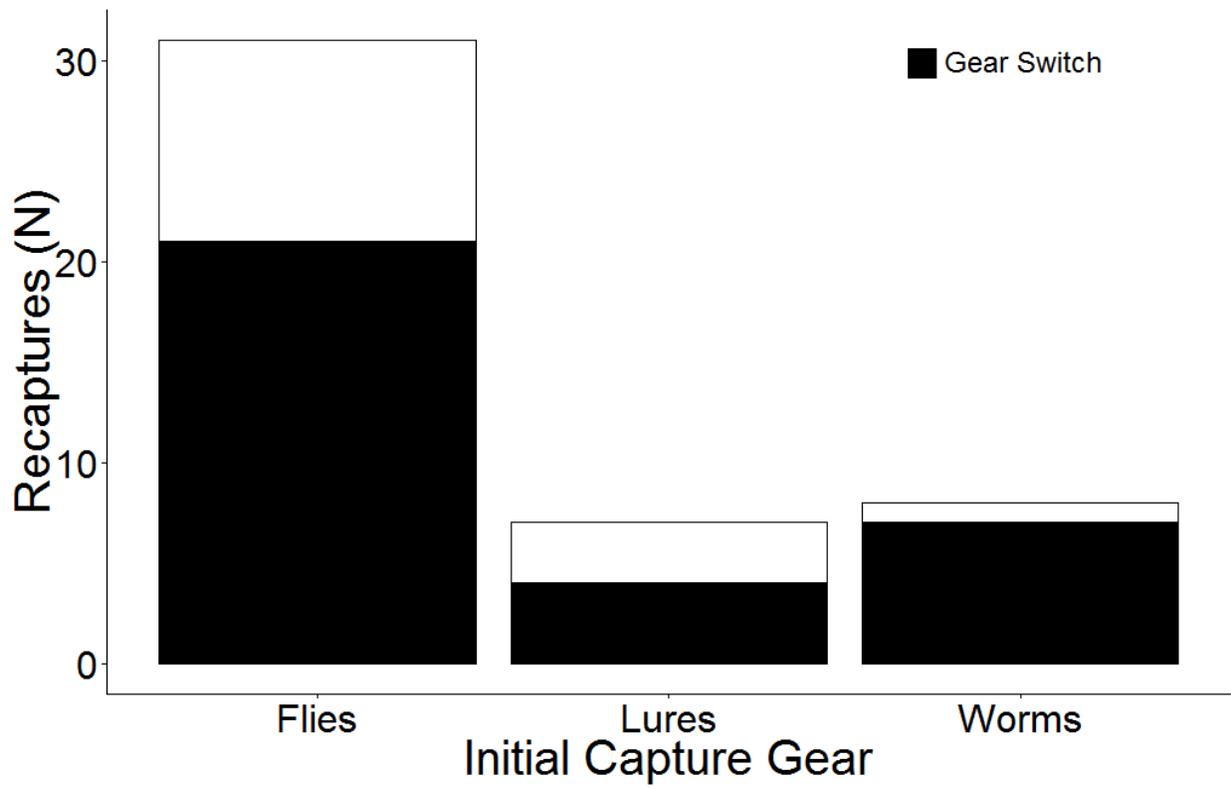
425

426

427

428

429



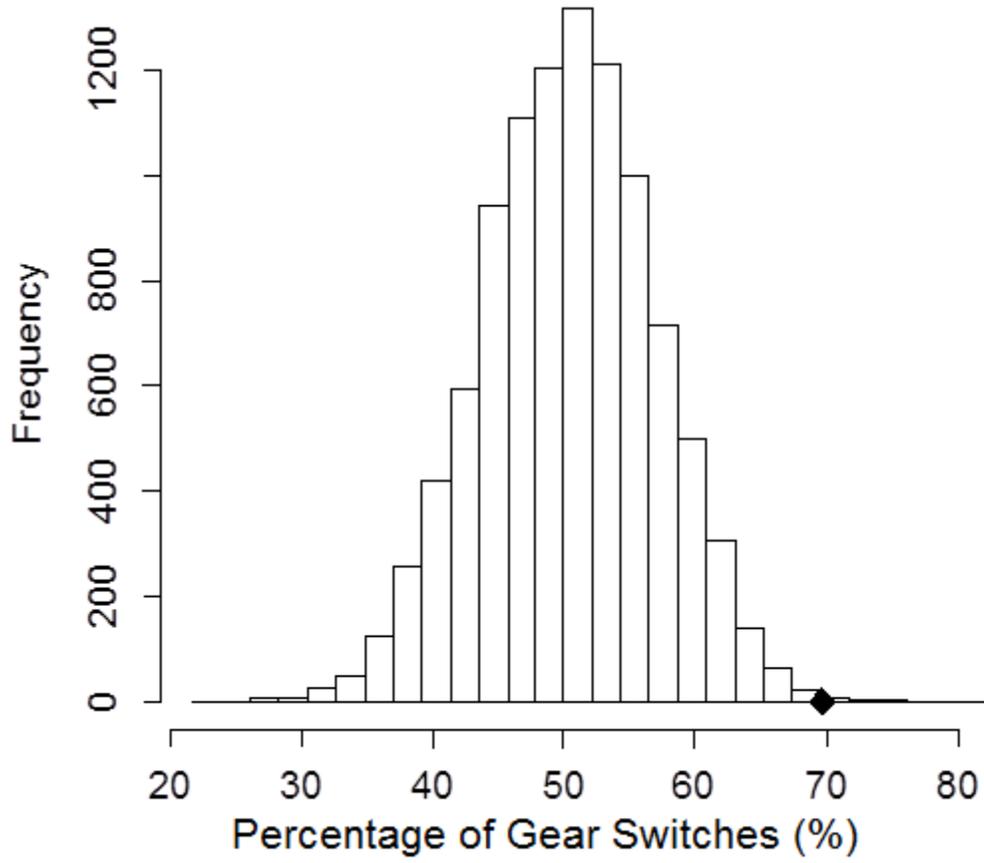
430

431 Figure 1.

432

433

434



435

436 Figure 2.

437

438

439

440

441

442