State-dependent migratory timing of post-spawned Atlantic salmon (*Salmo salar*)

Elina Halttunen[a], Jenny Lovisa Alexandra Jensen[a], Tor Fredrik Næsje[b], Jan Grimsrud Davidsen[a,c], Eva Bonsak Thorstad[a,b], Cedar Marget Chittenden[a], Sandra Hamel[a], Raul Primicerio[a], Audun Håvard Rikardsen[a]

[a] Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, University of Tromsø, NO-9037 Tromsø, Norway

[b] Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

[c] Museum of Natural History and Archaeology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

Corresponding author: Elina Halttunen. Tel.: +47 77 64 60 20; fax.: +47 77 62 08 53; e-mail address: elina.halttunen@uit.no

E-mail addresses of co-authors: jenny.jensen@uit.no, tor.naesje@nina.no, jan.davidsen@ntnu.no, eva.thorstad@nina.no, cedar.m.chittenden@uit.no, sandra.hamel@uit.no, raul.primicerio@uit.no, audun.rikardsen@uit.no

Abstract

Atlantic salmon (*Salmo salar*) often survive spawning and migrate back to the sea to feed, either shortly after spawning in autumn or in the following spring. We conducted a four-year observational field study using telemetry to evaluate the determinants of migration timing in Atlantic salmon post-spawners (kelts). We found that individuals with low energy reserves migrated early to the risky but productive marine habitat, whereas individuals with greater energy reserves stayed in the safe but less productive river habitat until staying became energetically more costly than migrating. For males, the likelihood of overwintering in the river instead of migrating in autumn increased 27-fold with each increase in body condition index, whereas almost all females overwintered in the river. Among spring migrants, body condition was the strongest determinant of migration timing, and females left the river about five days later than males. Our study suggests that migration timing in Atlantic salmon kelts is the outcome of adaptive state-dependent habitat use, related to individual and sexual differences in energy allocation during spawning.

Keywords: telemetry, life-history, reproduction, iteroparity, behaviour

Introduction

Anadromous salmonids reproduce in fresh water, but achieve the bulk of their growth at sea (Gross 1987). The marine part of the lifecycle is generally characterised by low survival and rapid growth, whereas the freshwater residency offers poorer growth (Jonsson and Jonsson 1993). This difference exists because both the predation pressure and production are higher in the marine than in the freshwater habitat (Gross 1987; Ward and Hvidsten 2010). As salmonids are ectotherms, they also grow faster with increasing temperature up to a growth optimum (Jobling 1994, Jobling et al. 2010). Therefore, salmonids grow especially well in the summer when both the temperature and the food availability are high at sea (Ingvaldsen and Loeng 2009; Rikardsen and Dempson 2010).

In contrast to most Pacific salmon species, Atlantic salmon (*Salmo salar* L.1758) often survive spawning in the river (Jonsson et al. 1990; 1991*a*), and perform repeated marine feeding migrations to build new reserves for re-occurring spawning events (Fleming 1996). The low temperatures experienced by the surviving post-spawning salmonids after spawning (late autumn/winter) restrict their activity and growth potential (see Knutsen et al. 2004) both in the river and at sea. Therefore, the winter season is not ideal for re-building depleted energy resources. This may explain the large individual variation in the timing of feeding migration observed in post-spawning Atlantic salmon (kelts); they either migrate shortly after spawning in the autumn, or during the following spring/summer (Jonsson et al. 1990; 1991*a*; Niemelä et al. 2000; Webb et al. 2007).

Here, we hypothesize that the variation in migration timing is the outcome of adaptive state-dependent habitat use, related to differences in energy allocation during spawning. In order to address this hypothesis, we analysed data from a four-year observational field study based on remote sensing of individual behaviour. We tagged a total of 352 Atlantic salmon, and

65   registered their post-spawning freshwater survival and migratory timing by means of acoustic

66   and radio telemetry. For Atlantic salmon, the likelihood of repeat spawning is negatively

67   related to energy depletion during the previous spawning event (Fleming 1996). The asset-

68   protection principle (Clark 1994) predicts that individuals with low energy reserves and a low

69   probability of future reproduction should accept risky, productive habitats, whereas

70   individuals with large reserves and a high probability of future reproduction should choose

71   safe but less productive habitats. Therefore, applying the asset-protection principle to the

72   migration of Atlantic salmon kelts, we predicted that kelts with low energy reserves would

73   migrate to the sea shortly after spawning, whereas kelts with larger reserves would stay in the

74   river until reaching an energetic threshold, determined by a trade-off between metabolic costs

75   and gains in fresh waters versus marine waters. We thus expected the migration timing to be

76   governed by individual factors related to state-dependency, specifically the individual's body

77   condition, size and sex. As large Atlantic salmon individuals tend to allocate relatively more

78   energy to spawning than small individuals (Jonsson et al. 1997), and as males have higher

79   energy expenditure than females (Jonsson et al. 1991*b*; Fleming et al. 1997; Niemelä et al.

80   2000), we expected that (*i*) individuals in poor body condition would leave the river early, (*ii*)

81   males would leave the river earlier than females, and (*iii*) large individuals would leave the

82   river earlier than small individuals.

83

Material and Methods

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Study area

85

86 The study was conducted in Alta River and Fjord in northern Norway (70°N, 23°E, Fig. 1)

87 during 2007-2010. Alta River has a catchment area of 7400 km^2 and a mean annual water

88 discharge of 75 m^3 s^{-1}. It supports a large Atlantic salmon population with annual in-river

89 catches between 6 and 32 t, with a mean mass of 5.2 kg for individual Atlantic salmon

90 (Ugedal et al. 2008). Most spawners spend one or three years in the sea, where one-sea-

91 winter fish (1SW) are mainly males (76%, mean 2.3 kg) and three-sea-winter fish (3SW) are

92 mainly females (77%, mean 10.0 kg) (Ugedal et al. 2008). Repeat spawning is more common

93 in females than in males, and the large majority of both female and male repeat spawners

94 spend one year at sea before returning to spawn again (Halttunen et al. 2011). The river

95 length accessible to Atlantic salmon is 46 km, and a hydropower plant was constructed above

96 this stretch in 1987. Winter freeze-up usually occurs in November, and spring ice break-up

97 normally occurs in early May. There are numerous suitable areas for kelts to overwinter

98 (deep pools, still waters), and a minimum discharge of 20-30 m^3 s^{-1} is maintained by the

99 hydropower plant during the winter. The peak spawning run of Atlantic salmon occurs from

100 mid-June through July, and spawning commences during the first half of October (Ugedal et

101 al. 2008).

102

Tagging

103

104 The post spawning survival and seaward-migration timing of Atlantic salmon kelts was

105 assessed by the use of radio and acoustic telemetry (Cooke et al. 2004). Both methods enable

106 monitoring movements of individual fish by using electronic tags that transmit individually

107 coded signals. Radio telemetry was used to assess the post-spawning survival and the overall

108 seaward-migration timing of kelts. The method was chosen because it enabled tracking of

109 fish through ice during the winter. Acoustic telemetry was used for a higher resolution study

110 of out-migration timing versus energy reserves in the spring. The method was chosen because

111 it enables tracking fish in saline water.

112

113 ***Radio tagging***

114 We tagged a total of 166 returning Atlantic salmon in the Alta Fjord and River between June

115 and September 2008-2009 (Table 1). Multi-sea-winter (MSW) fish (56 males, 2-5SW, mean

116 fork length 95 cm; 92 females, 2-6SW, mean fork length 94 cm) were captured in bag nets in

117 the Alta Fjord during their spawning migration towards the Alta River from June to August

118 2008-2009. Uninjured specimens were placed in a 400 L tank with oxygenated water in the

119 research vessel (time in tank 5-120 min), and thereafter externally tagged with radio

120 transmitters (Model F2120, Advanced Telemetry Systems (ATS), MN, flat with outline

121 dimensions 21×52×11 mm, mass in air 15 g, estimated battery lifetime 10 or 13 months).

122 Individuals could be identified by using unique combinations of frequencies and pulse-rates.

123 The fish were anaesthetised prior to tagging (2-phenoxy-ethanol, EC No. 204-589-7, SIGMA

124 Chemical Co., MO, 0.5 ml L^{-1}, mean time 2 min 40 sec), and thereafter placed in a water-

125 filled tube with the head and gills submerged. The radio transmitters were attached through

126 the musculature 3-4 cm below the dorsal fin by use of 0.8 mm stainless-steel wires, and

127 anchored to a 10×40 mm plastic back plate. The mean tagging time was 1 min 50 sec, and the

128 mean handling time was 5 min 20 sec. The tagged fish were left to recover in the oxygenated

129 tank under observation (mean time 2 min 50 sec), whereupon they were released back into

130 the fjord to resume their migration towards the river.

131 One-sea-winter Atlantic salmon often escape bag nets due to the large mesh sizes. Therefore,

132 the radio-tagged group was biased towards MSW males, and so the radio-tagged group was

6

133   more similar in size than the acoustically tagged group (see Table 1). To increase the number

134   of 1SW males in the study, eight additional individuals (mean fork length 57 cm) were

135   captured by rod and reel in the upper parts of the river between 6 and 30 September 2009,

136   and tagged using similar procedures as described above. An additional 10 MSW Atlantic

137   salmon (eight females, two males, mean fork length 92 cm,) were captured in the same area

138   and tagged during the same period (Table 1).

139

140   *Acoustic tagging*

141   We tagged a total of 202 kelts (57 males, 1-3SW, mean fork length 65 cm; 145 females, 2-

142   7SW, mean fork length 94 cm, Table 1) with acoustic tags (Vemco Inc., Canada, model V13-

143   1L, cylindrical with dimensions 13 mm×36 mm, mass in air 11 g, and Thelma AS, Norway,

144   model MP-13, 13 mm×31mm, mass in air 11 g, estimated battery life 13 or 37 months) in the

145   Alta River during April - May 2007-2009. The kelts were captured in the river by angling

146   with barbless treble hooks, anaesthetised and tagged internally according to Halttunen et al.

147   (2010). All kelts were also externally tagged with modified Carlin tags with contact and

148   reward information for the report of recaptures.

149

150   **Tracking**

151   *Radio tracking*

152   To detect radio-tagged fish descending the river, automatic stationary receivers storing

153   information on tag ID and time of registration (R4500S Scientific receiver, ATS, connected

154   to a four- or nine-element Yagi-antenna) were installed 1 and 8 km upstream from the river

155   outlet during both study years (Fig. 1). In addition, stationary receivers were operative 15 and

156   19 km upstream from mid-October 2009. The scan time on the receiver for each frequency

157   used on radio transmitters was 5 sec, giving a total scan time ranging from 2 min 30 sec to 4

158   min 10 sec to cover all frequencies used and to be able to register fish within the detection

159   area of the receiver (approximately 1 km).

160

161   The positions and possible predation events of the radio-tagged fish within the river were

162   determined by manual tracking using a portable receiver (R410 Scanning receiver, ATS,

163   connected to a three-element Yagi-antenna). The fish were positioned with an accuracy of

164   approximately ± 300 m, i.e. fish were localized to a specific pool in the river. Tracking was

165   performed approximately every second week from spawning (October) until the river froze

166   (~mid-November), on a monthly basis during winter, and every third week from ice break-up

167   (~mid-April) until the end of July. Due to unstable ice conditions during the winter 2008-

168   2009, tracking in December and January could not be performed because accessing these

169   remote areas in wintertime requires snowmobile transport on the river ice.

170

171   *Acoustic tracking*

172   To detect acoustically tagged fish descending the river, eleven acoustic receivers (model

173   VR2, Vemco Inc.) were deployed at 5 m depth, spaced 400 m apart, in an array across the

174   Alta Fjord 4 km from river mouth (Fig. 1) between April and October 2007-2009. In addition,

175   two receivers were deployed near the river mouth in the lower reaches of the river.

176   Information on the time of registration and the tag ID were stored in the acoustic receivers

177   whenever an individual passed within the detection range. The receivers were able to detect

178   fish at a range varying from 200-600 m, depending on environmental conditions. Hence, all

179   fish passing the receiver arrays were within the detection range.

180

Sampling

A total of 144 kelts (46 males and 68 females, mean fork length 82 cm, range 50-112 cm) were sacrificed during tagging in the river (2007-2009), and their stomach contents were analysed. The water temperature and discharge in the river were measured hourly at Kista hydrographical station 28 km upriver, and the sea temperature was measured at an average of 10 days interval at Ingøy hydrographical station (N 71°08' E 24°01') at one meter depth.

Data analysis

The minimum survival of Atlantic salmon kelts

Because we chose small tags to minimize potential tag effects on behaviour (Thorstad et al. 2000), some of the batteries were dead before the fish left the river. Due to the uncertain fates of fish with undetected exit, we based the survival rate estimate strictly on confirmed survived fish, i.e. fish with detected exit and recaptured fish, and therefore our survival estimate is a minimum estimate. We considered fish reported recaptured and released by anglers in the river during 1 June – 31 August to be alive with a high survival probability, despite being caught and released (Halttunen et al. 2010). Predation was assessed from tagged carcasses detected in the vicinity of the river.

Analyses of seaward-migration timing of Atlantic salmon kelts

Two separate models were used to test the determinants for the timing of seaward-migration; a logistic regression model to assess the probability of the radio-tagged fish migrating either during autumn (defined here as before end of January) or spring (defined her as after onset of April), and a linear regression model to explain *sea entry date* (in Julian days using 1 May as day 1) of the acoustically tagged fish in the spring. For both analyses, we were interested in

assessing the influence of *sex*, *length* (fork length in cm), *body condition index* and *their*

interactions. The *body condition index* consisted of the residuals of log [mass] regressed on

log [length], and was chosen in order to avoid co-linearity between the explanatory variables

length and body condition ($R = 0.34$). The *body condition index* was calculated from length

and mass measured at tagging, i.e. it represented the body condition in two distinct phases of

the spawning migration; before spawning for the radio tagged fish and after spawning and

overwintering for acoustically tagged fish. The variable *year* was included to account for

among-year variation in the environment, which can be considerable; for example, the timing

and intensity of the flood peak varied greatly among the study years (range 400-816 m^3s^{-1},

Fig. 2). The variable *tag site* was included as a covariate in the linear model explaining *sea*

entry date to control for distances between tagging sites and the sea.

For the logistic regression model predicting spring migration, only 2 females out of 63 left in

autumn (3%) compared with 9 out of 21 males (43%). Therefore, we only analysed the

probability of spring migration for males. Because we had very few males in this analysis, we

could not assess the influence of interactions. In addition, to prevent type II errors owing to

the low power of the test (4 estimates -*intercept*, *year*, *condition*, *length*- for 21 data points),

we performed stepwise removal of least significant variables. We performed a Pearson χ^2

statistic to assess the goodness-of-fit of the model, which showed no evidence of over-

dispersion ($P = 0.99$). We present odds ratio (with 95% confidence intervals), which is a

measure of effect size in logistic regression (Nakagawa and Cuthill 2007). For continuous

variables like *length* and *body condition index*, the odds ratio is the odds of migration

occurring in the spring with an increase of one unit, e.g. the ratio of the odds when length

equals 100 cm to the odds of it occurring when it equals 101 cm. An odds ratio of 1 indicates

that spring migration is equally probable with change of one unit. When the ratio moves

towards 0, spring migration is more likely to occur with a decrease of one unit, whereas when

230   it moves towards infinity, it is more likely to occur with an increase of one unit. To assess the

231   performance of the logistic model, we report the area under the receiver operating

232   characteristic curve (AUC), which measures the overall predictive accuracy of the model

233   independent of a specific threshold (Fielding and Bell 1997, R package "lrm"). AUC values

234   vary from 0.5 to 1, and represent the percentage of randomly drawn pairs (i.e. one of each

235   group) that the model classifies correctly. Generally, the predictive accuracy of a model is

236   classified as "worthless" with an AUC close to 0.5 and "excellent" with an AUC close to 1.0.

237   All variables in both models were centred to allow interpretation of main effects

238   independently of interactions (Schielzeth 2010). In addition, all continuous variables were

239   standardized in order to provide standardized parameter estimates that allow comparing the

240   magnitude of the effects, and hence, the importance of each variable (Schielzeth 2010).

241   Because the models included a categorical variable, we used two standard deviations to

242   standardize the continuous variables, therefore permitting comparison between categorical

243   and continuous variables (Gelman 2008; Schielzeth 2010). All statistical analyses were

244   conducted using the open source R language for statistical computing and graphics (R

245   Development Core Team 2009).

Results

The minimum survival of Atlantic salmon kelts

The minimum survival of Atlantic salmon kelts was 63% (98/156 individuals included in the analysis, both study years pooled). Out of these survivors, 13% (13/98) left the river in the autumn, and the remaining 87% (85/98) left in the spring. The majority of the autumn migrants (10 of 13, 77%) were MSW males. The minimum survival rate was higher for MSW females (74%) than for MSW males (43%; χ^2-test, $P < 0.001$), but there was no difference in survival between MSW females and 1SW males (62%; Fisher's exact test, $P = 0.70$).

Overall seaward-migration timing of Atlantic salmon kelts

Despite no difference in the body condition between the males and females (t test assuming equal variances: $t = 1.99$, $P = 0.29$, df $= 80$) upon entry, almost all females started their migration in spring (97%) whereas almost half of the males migrated in the autumn (43%). Even though salmons had a slight tendency to enter later with lower body condition (Pearson correlation coefficient: $r = -0.20$, $P = 0.08$, n $= 76$), the river entry date was not correlate with the exit date (Pearson correlation coefficient: $r = -0.05$, $P = 0.69$). Among males, the complete model (with low power because it is getting towards saturation with about 5 data points available for each estimate) showed a tendency for males in better condition to leave in the spring (Table 2). Model reduction, increasing the power of the analysis, confirmed the effect of condition on the probability of spring migration (odds ratio [CI] = 26.7 [2.2;1265.0], Wald $\chi^2 = 2.1$, $P = 0.036$). Males were 27 times more likely to migrate in the spring with each increase of one unit in body condition index (Fig. 3). In general, the probability of males migrating to sea in the spring was 50% if their body condition index was close to 0 or

269   positive, meaning fish of average or higher than average condition (Fig. 3). Overall, the

270   model had an excellent predictive power, as indicated by the high AUC value (Table 2).

271

272   **Migration timing among spring migrating Atlantic salmon kelts**

273   In total, 188 (93%) of all the acoustically-tagged spring migrants were detected on the

274   acoustic arrays in the fjord. Among sex, body condition, and fork length, body condition had

275   the strongest influence on migration timing of detected fish: fish in better body condition

276   migrated later, and this effect was stronger for females than for males (Table 3, Fig. 4a). Sex

277   was the second strongest predictor but its effect was three times smaller than that of body

278   condition (Table 3). On average, females migrated five days later than males (Table 3). Fish

279   length did not affect sea entry date in the spring, but its interaction with sex was a strong

280   predictor (Table 3, Fig. 4b); males entered the sea slightly later with increasing fork length,

281   whereas females' sea entry date did not vary with length. Sea entry date varied among years,

282   but variation among tag sites was negligible (Table 3). The median migration date during the

283   study period was 9 June (Fig. 2).

284

285   **River and sea temperatures, feeding and predation in the river**

286   The river winter temperatures (1 November – 30 April) in 2007-2010 ranged between 0.0-

287   3.0^{o}C (average of 0.4^{o}C), while the sea temperatures ranged between 4.1-7.8^{o}C (average of

288   5.6^{o}C). The river temperatures surpassed the sea temperatures each year in the middle of June

289   (Fig 2). None of the sampled kelts had stomach contents, and we observed no predation on

290   the tagged fish.

Discussion

Consistent with our expectations, fish in poorer condition left the river earlier than fish in
better condition, both when comparing between autumn and spring migrating males, and
among spring migrating females and males. This indicates that there may be an inherent
advantage to prolonging the freshwater residency instead of initiating the seaward-migration
as soon as possible. We suggest that the advantage may be related to the differences between
the river and marine habitat during winter, in relation to metabolic costs vs. gains, and
predation risk. The river is a low-cost, low-gain, and low-risk habitat for overwintering kelts.
Fish that overwinter in the river at temperatures close to 0 °C should have very low metabolic
costs (Jobling 1994). We found no evidence for metabolic gains through feeding (because
kelts had empty stomachs), and the kelts risk little or no predation in the river, as they are
virtually untouchable under the protective ice cover. The known predators of Atlantic salmon
in the River Alta are white-tailed sea eagles *Haliaeetus albicilla* and European otters *Lutra
lutra*, and as a rule, they feed on dead fish after spawning before the river freezes (E.
Halttunen, personal observations). The marine environment, on the other hand, is a
productive but more risky habitat for kelts. Despite lower marine production during winter,
there are prey (fish, amphipods, euphausiids) available in the sea throughout the year. In
addition, even though marine predation on adult Atlantic salmon is not considered an
important factor for mortality (reviewed by Mather 1998), large predators like seals and
whales are known to predate upon adult salmon (Ward and Hvidsten 2011, own unpublished
data). Therefore, we suggest that individuals that can energetically afford to do so, should
overwinter in the river and migrate to the sea when increased temperatures improve feeding
opportunities. This hypothesis is further supported by the fact that the median outmigration
date among the spring migrants coincided roughly with the equalising of temperatures in the
river and along the outer coast, therefore rendering the metabolic costs of staying in the river

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316 higher than that of migrating to the sea. As Atlantic salmon migrate between the river and

317 marine habitats, where they cover large distances (Klemetsen et al. 2003), optimizing each

318 leg of the migration to the lowest possible risk and the highest possible gain is likely

319 important for the overall survival and lifetime fitness.

320

321 Consistent with our expectations, males left the river earlier than females, both when

322 comparing autumn to spring migrants and spring migrants among each other. Atlantic salmon

323 males generally invest more of their somatic energy (36%) in spawning than females (25%,

324 Jonsson et al. 1991*b*) as a result of active and aggressive behaviour and investments in

325 secondary sexual traits (Fleming 1998). This somatic energy loss, when added to injuries

326 acquired during intense male-male competition during spawning, may lead to poor

327 physiological status and high post-spawning mortality among males (Jonsson et al. 1990;

328 Baglinière et al. 1991; Fleming 1998). However, Atlantic salmon males display two

329 alternative reproductive strategies. They return from their sea feeding migration either after

330 one winter as small individuals, or after multiple winters as large individuals. Small males

331 invest less of their total energy in spawning (40-50%) compared to large males (up to 70%),

332 and larger males fight more violently (Fleming 1996; Jonsson et al. 1997; Jonsson and

333 Jonsson 2003). Accordingly, the mortality among large males in this study was higher than

334 among females and small males, and almost all of the autumn migrants were large males.

335 Small males may minimize their involvement in the spawning event to conserve their energy,

336 therefore increasing their chances of surviving to spawn again (Seamons and Quinn 2010).

337 This seems to be the case in River Alta, where small males have a much higher repeat

338 spawning probability than large males (Halttunen 2011).

339

340 Almost all females (98%) overwintered in the river and started their ocean migration in the

341 spring, despite large variations in body condition when entering the river. This shows a clear

342 difference in the overall migration strategy between the sexes, and most likely, a difference in

343 energy allocation during spawning. Atlantic salmon females generally allocate most of their

344 energy reserves in egg production (~30%; Jonsson and Jonsson 2003) and little in aggression

345 and competition, therefore suffering lower post-spawning mortality (Jonsson et al 1990;

346 Baglinière et al. 1990, 1991; Fleming 1998). Consequently, females have a higher repeat-

347 spawning probability than males (Heggberget 1989; Jonsson et al. 1990; Niemelä et al. 2000).

348 Females in River Alta can spawn multiple times (Halttunen 2011). Therefore, according to

349 the asset protection principle (Clark 1994), females should choose safe but less productive

350 habitats like the river after spawning, and hence prioritise the next spawning occasion

351 because they have a high future reproductive probability. As the large majority of the repeat

352 spawning females and males spend a year in the sea before returning, i.e. spawn alternate

353 years (Halttunen 2011), the difference in the migration behaviour between sexes cannot result

354 from a difference in repeat spawning.

355

356 Based on the knowledge that larger fish tend to use more energy than small fish during

357 spawning (Jonsson et al. 1997), we expected large individuals to leave the river earlier than

358 small individuals, and this was certainly true for the overall migration pattern of males, where

359 almost all of the autumn migrants were large males. However, we observed the contrary

360 among the spring migrating males; larger males left the river at a later date than smaller

361 males (Fig 4b). For spring migrating females, length had no effect on migration timing (Fig

362 4b). There might be several factors accounting for large size not advancing the outmigration

363 date in the spring. Especially for females, large size is an asset worth protecting, as size

364 correlates positively with fecundity (Fleming 1996). Large fish also have a lower metabolic

365 rate in relation to body size than small fish (Jobling 1994), and might use relatively less

366 energy than small fish during overwintering. In addition, large fish might be more dependent

367 on good feeding conditions to meet the demands of growth compensation. Growth

368 compensation (Jobling 1994, 2010; Ali et al. 2003) is a phenomenon occurring in Atlantic

369 salmon after a period of starvation, induced by the loss of body mass and reduced lipid

370 reserves. It leads to high feeding rates, and a growth rate above that normally recorded in fish

371 that feed regularly. Growth compensation may have far-reaching consequences, as there are

372 trade-offs between growth and other fitness-related traits, such as physiological costs in the

373 form of reduced swimming performance, immune capacity and developmental stability

374 (Jobling 2010; Ali et al. 2003). Therefore, waiting for good growth conditions before starting

375 the feeding migration might be crucial for adult post-spawners, and especially for large ones.

376

377 Variation among years affected the overall (autumn/spring) migration timing of Atlantic

378 salmon kelts, likely due to annual changes in environmental factors. The river temperatures

379 Atlantic salmon experience prior to and during spawning will have an immediate effect on

380 their energy expenditure through metabolic costs (Jobling 1994). As we suggest that out-

381 migration is related to body condition, this could explain the differences between years in the

382 likelihood of migrating in the autumn. Environmental factors had also a significant effect on

383 the out-migration during spring. The migration timing of kelts varied in accordance to the

384 timing of the flood peak (earliest in 2009 and latest in 2008, Table 3, Fig. 2), and hence the

385 spring flood may be an important environmental cue for kelt migration initiation. This

386 concurs with the migratory timing of Atlantic salmon smolts, which synchronize their out-

387 migration with environmental cues in an attempt to match the most profitable growth

388 conditions at sea (Hvidsten et al. 2009; Rikardsen and Dempson 2010). However, despite the

389 clear effect of environmental cues, the out-migration of kelts spanned out over a period of 6-

390   12 weeks, whereas the smolts migrate over a more concentrated time period (Jensen et al.

391   2012). This might be because kelts are considerably larger than smolts, and therefore not

392   dependent on the safety of a crowd under migration. Also, kelts have larger mouths, and

393   therefore, a larger feeding repertoire than smolts, whereas smolts are dependent on certain

394   seasonal prey types (e.g. zooplankton; Hvidsten et al. 2009; Rikardsen and Dempson 2010).

395   Finally, even though kelts might also benefit from entering the sea in the most productive

396   season, they might be forced to leave the river earlier than would be optimal for feeding

397   opportunities at sea due to poor body condition.

398

399   On a more general note, the morphology and hydrography of rivers can play an important

400   role in the migration timing of post-spawning Atlantic salmon. The decision to overwinter in

401   the river is likely dependent on suitable overwintering areas and adequate water discharge

402   throughout the winter (as documented in *e.g.* brown trout *Salmo trutta* and Arctic charr

403   *Salvelinus alpinus*; Olsen et al. 2006; Jensen and Rikardsen 2012), as well as on a favourable

404   temperature regime and relative differences between river and sea temperatures. Therefore,

405   the individual condition and the future reproductive prospects of the fish work most likely in

406   concert with environmental factors in determining the overall migration timing of spent

407   Atlantic salmon. This study, however, demonstrates the importance of physical condition in

408   migration timing, and provides a theoretical framework for future salmonid migration studies.

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422

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Table 1. The number, average length, and average mass of tagged Atlantic salmon in Alta River and Fjord in 2007 – 2009, according to sex and tagging technique. Ranges (minimum-maximum) are given in parenthesis.

Year		2007			2008			2009	
		n	Fork length (cm)	Mass (kg)	n	Fork length (cm)	Mass (kg)	n	Fork length (cm)	Mass (kg)
Radio tagging; tagged before river entry	**Males**	-	-	-	25	98 (71-122)	11.9 (3.9-23.3)	41	83 (54-110)	10.1* (4.8-15.0)
	Females	-	-	-	54	96 (83-116)	11.2 (6.5-17.8)	46	94 (82-113)	10.0* (6.8-17.0)
Acoustic tagging; tagged before river exit	**Males**	27	62 (54-82)	1.6 (0.9-3.4)	0	-	-	30	67 (57-102)	2.7 (1.3-10.3)
	Females	33	93 (75-115)	6.1 (2.6-12.9)	73	93 (75-116)	6.0 (2.9-11.5)	39	97 (89-108)	7.1 (4.0-10.2)

Note: *mass average based on 28 and 38 individuals, respectively, as data was not available for all tagged individuals

Table 2. Probability (odds ratio with 95% confidence interval - CI) of migrating in the spring (after onset of April) rather than in the autumn (before end of January) in relation with length and body condition while controlling for year, for radio tagged Atlantic salmon (n = 84) in Alta River and Fjord (2007 – 2009).

Predictor	Odds ratio	95% CI	Wald χ^2	*P*	Model diagnostics*
Intercept	1.9	0.9 – 118.7	0.9	0.4	
Year	5.5	1.3 – 53.0	1.9	**0.06**	AUC = 0.93
Length	29.9	1.0 – 16596.7	1.5	0.13	$R^2 = 0.65$
Condition	265.2	4.32 – 576885.1	1.7	**0.08**	

Note: * The area under the receiver operating characteristic curve (AUC) and Naglekerke R^2 (Nagelkerke 1991) present the predictive and explanatory power of the model, respectively.

Table 3. Effects of sex, length and body condition, while controlling for year and tag site, on the migration timing (sea entry date) among spring migrants (n=186), for Atlantic salmon tagged with acoustic transmitters in Alta River (2007-2009).

Predictor	Level	Estimate	95% CI	df	*F*	*P*
Intercept		40.9	33.2 – 48.7			
Year	2008	5.5	-1.8 – 12.9	2	41.6	**<0.001**
	2009	-5.8	-12.6 – 0.9			
Tag site	2	-1.4	-9.6 – 6.9	5	0.9	0.5
	3	-1.5	-7.5 – 4.4			
	4	-1.1	-8.4 – 6.2			
	6	-2.2	-10.1 – 5.6			
	7	4.0	-3.0 – 11.0			
Sex	F	4.8	0.1 – 9.4	1	54.2	**<0.001**
Condition		12.6	8.0 – 17.3	1	50.6	**<0.001**
Length		4.6	-2.7 – 11.9	1	1.4	0.2
Sex * Condition	F	8.1	0.7 – 15.5	1	7.9	**0.005**
Sex * Length	F	-8.4	-15.7 – -1.2	1	4.6	**0.03**
Length * Condition		-6.2	-19.5 – 7.2	1	0.8	0.4

Note: F = female, Level = category level which is associated with the estimate. CI = confidence interval, df = degrees of freedom. Model R^2 = 0.55.
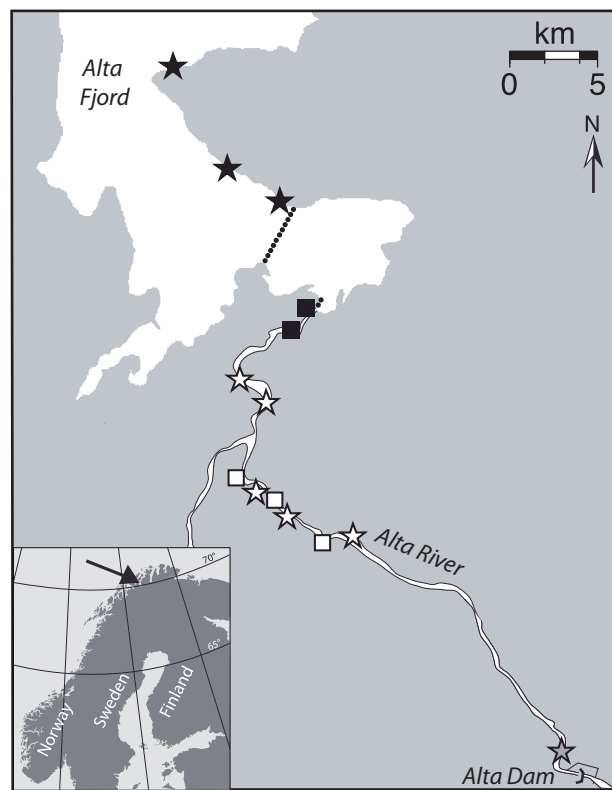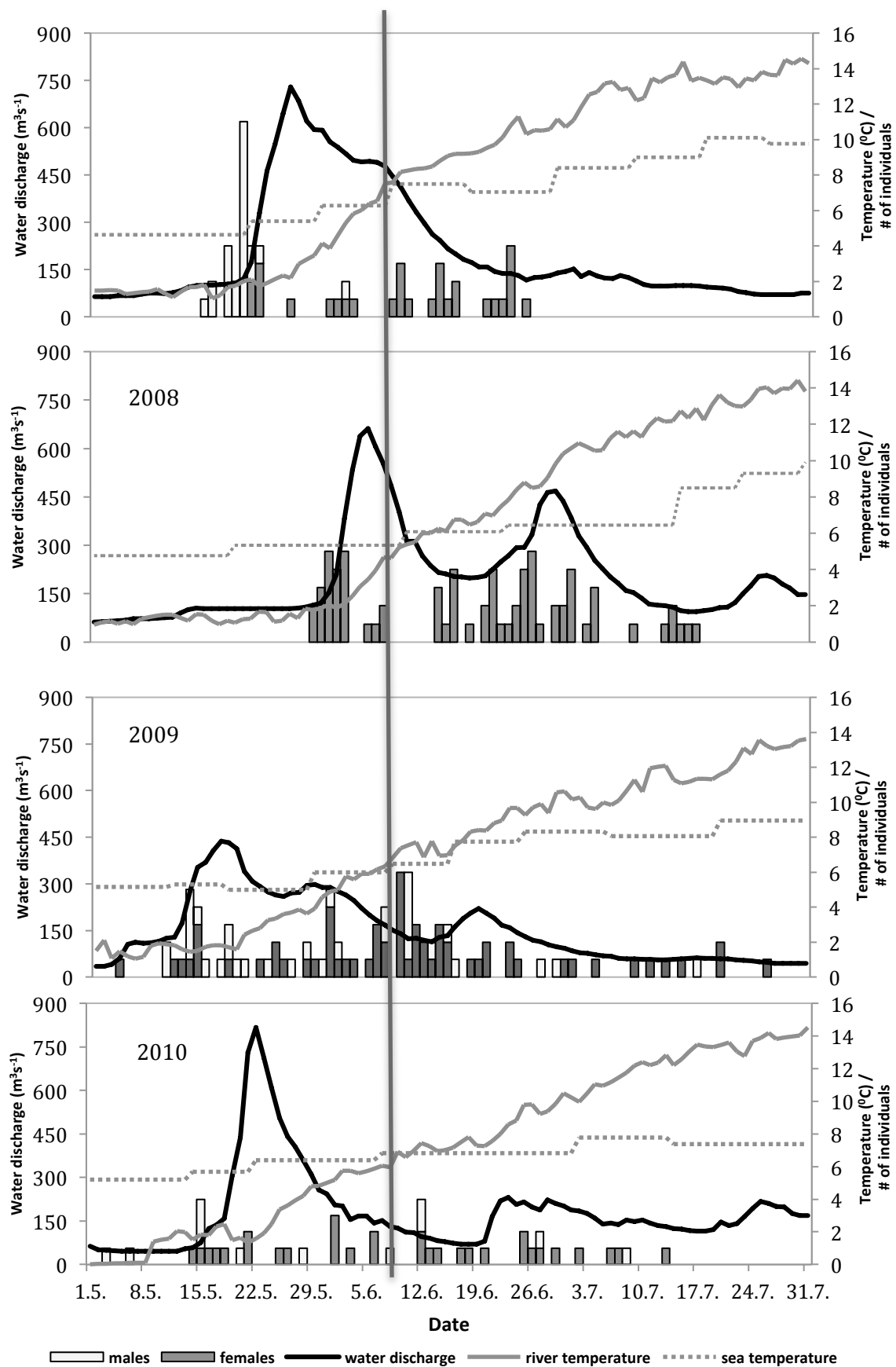
Figure captions

Fig. 1. Map of the lower part of the Alta River and Fjord showing the position of the acoustic receiver arrays (dotted line and single dots), the stationary radio loggers (black and white squares; the white squares depicts radio loggers in use only in 2008), and the tagging sites both in the river and the fjord (stars; the black stars mark the tagging sites for radio tagged Atlantic salmon, the white stars for acoustically tagged Atlantic salmon, and the grey star an additional tagging site for radio tagged Atlantic salmon in 2009).

Fig. 2. The marine migration start of acoustically tagged kelts in 2007-2009 in Alta River in relation to water discharge, river temperature, and sea temperature. The grey vertical line marks the median migration date across all years (9 June).

Fig. 3. The probability (± SE) for Atlantic salmon kelts in Alta River of migrating in autumn (0) or spring (1) in relation to body condition in 2009-2010. The thin dotted lines underline the body condition and length values where fish had a 50% probability of migrating in spring rather than in autumn. Vertical lines on the x-axis represent the distribution of the data, i.e. each line represents a tagged male.

Fig. 4. Sea entry date (in Julian days using 1 May as day 1) of Atlantic salmon kelts in Alta River in relation to body condition (a) and fork length (b). Lines represent model predictions (± SE), and dots the data.
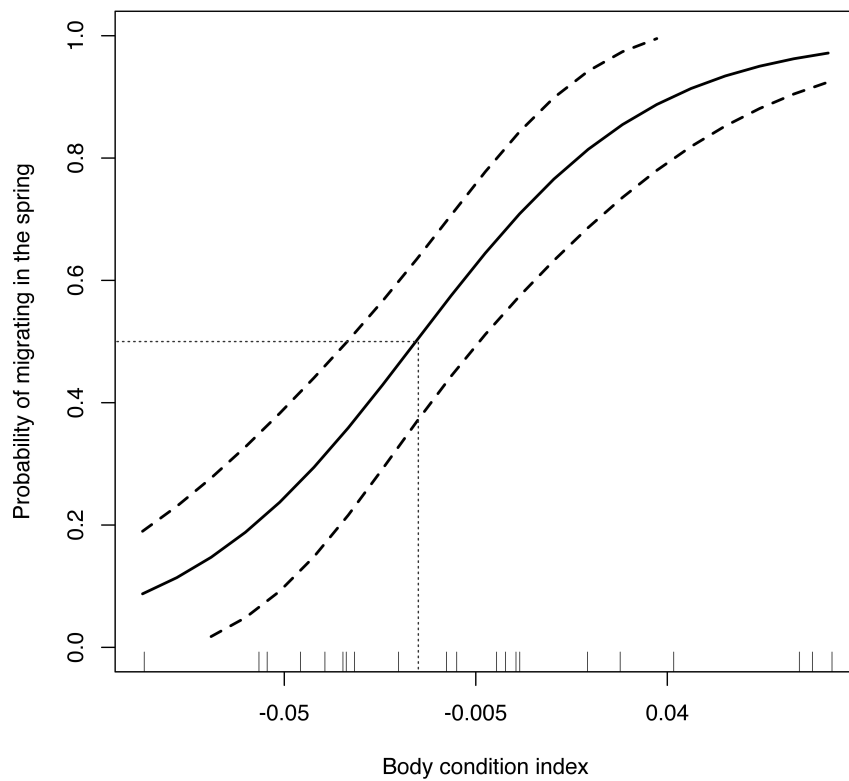
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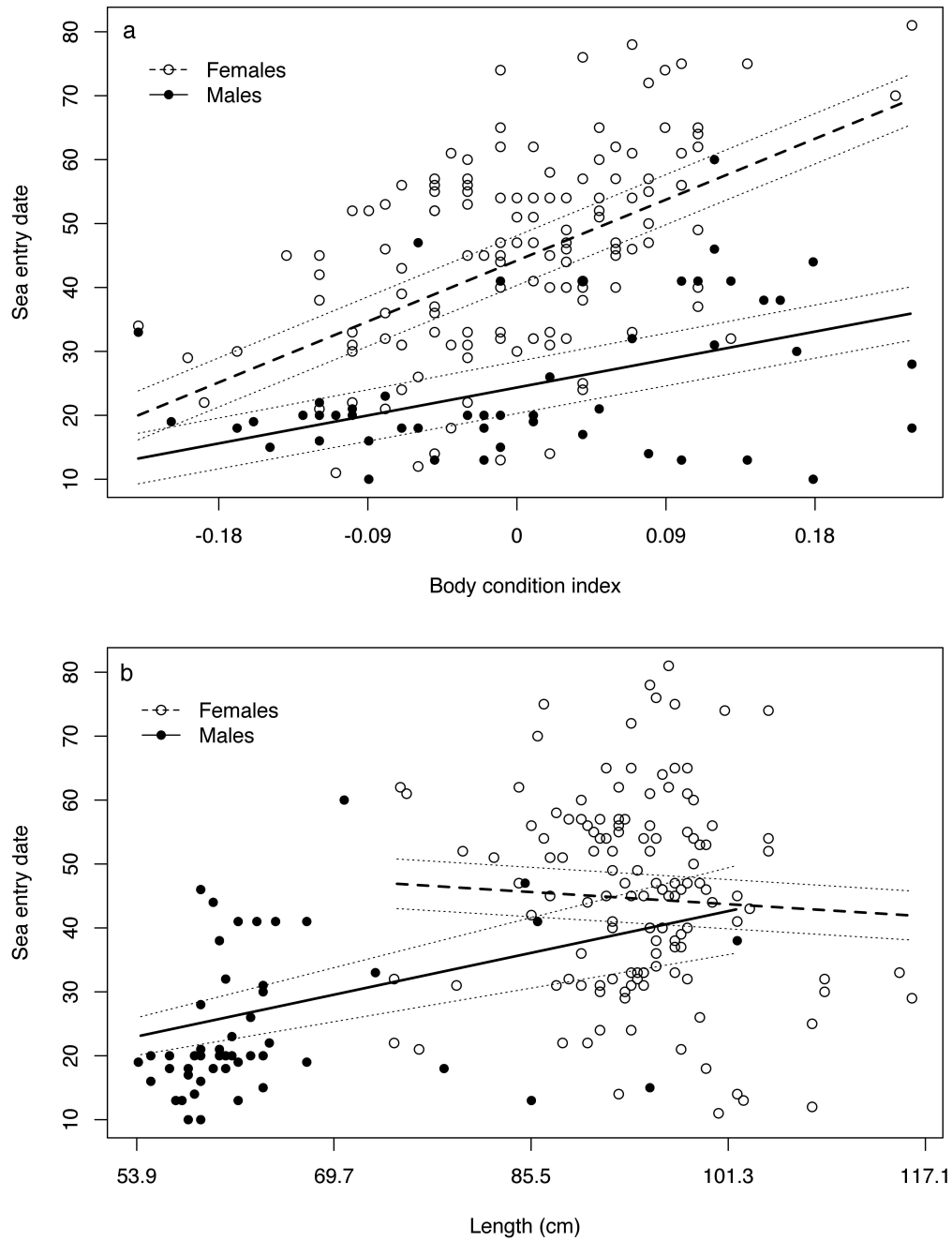
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