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Diel migration pattern of Atlantic salmon (*Salmo salar)* and sea trout (*Salmo trutta)* smolts: An assessment of environmental cues

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Abstract- The timing of smolt migration is a key phenological trait with profound implications for individual survival during both river descent and the subsequent sea-sojourn of anadromous fish. We studied relationships between the time of smolt migration, water temperature and light intensity for Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta).* During 2006-2012, migrating smolts descending the Southern Norway river Storelva were caught in a rotary screw trap located at the river mouth. The date of 50 % cumulative smolt descent correlated significantly with the date when the river temperature exceeded 8˚C for both Atlantic salmon and sea trout smolts. In 2010, smolts of both species were Passive Integrated Transponder (PIT) - tagged and the diel timing of their migration was precisely documented. The degree of night migration decreased in both species as the river temperature rose, and at temperatures above 12-13˚C, more smolts migrated during day than during night. A multinomial model was fitted for estimating temperature and species effects on probabilities of migration during night, daytime, dusk and dawn. Atlantic salmon smolts preferred migrating under lower light intensities than sea trout smolts during early, but not late spring when both species migrated during bright daylight. In accordance with the early-season tendency to migrate at night, Atlantic salmon smolts migrated more during darker hours of the day than sea trout. In both species, smaller smolts migrated under dark conditions than during light conditions. Most of the findings on thermal, light and temporal effects on the observed smolt migration pattern can be explained as adaptations to predation avoidance.

Introduction

Diel activity patterns of salmonids vary with season. The variation appears chiefly driven by water temperature and light intensity, and needs for food and avoidance of predators (Jonsson & Jonsson 2011; Watz et al. 2015). In anadromous salmonids, increasing temperature and day length (i.e., photoperiod) during spring stimulates the smolting process. Smolting involves morphological, behavioural and physiological adaptations for sea life, and initiates seaward migration (McCormick et al. 1998). The ultimate driver behind this ontogenetic habitat shift, where the young leave a relatively low-predation, but food-restricted, freshwater habitat to use a food- and predator-rich marine habitat, is the improved growth opportunities at sea (Gross et al. 1988; Harden Jones 1968). The improved growth opportunities are accompanied by enhanced energy costs associated with smolting and increased swimming activity, and increased risk of predation (Mather 1998). The smolting process is similar in principle in different salmonid species, but species may differ in degree of hyperosmotic capacity obtained (Urke et al. 2009; 2013b), corresponding to the salinity of their marine feeding habitats (e.g., Urke et al. 2013b). Since most smolt predators are visual predators, the diel timing of the migration may affect the survival probability.

The time of sea entry affects smolt survival (Antonsson et al. 2010). Ocean conditions are typically more stable and predictable than river conditions, and Atlantic salmon (*Salmo salar)* smolts appear to enter coastal waters when the sea surface temperature is 8 °C or warmer (Hvidsten et al. 1998; Whalen et al. 1999). As water temperature decreases towards the north in the northern hemisphere, smolts tend to migrate later in spring, but across the spesies` range including in the north, smolts have been exhibiting earlier migration over time in association with global climate change (Otero et al. 2014). Water temperature and change in

river flow has been found to be a key environmental trigger (Jonsson & Ruud-Hansen 1985; Otero et al. 2014; Jensen et al. 2012). Zydlewski et al. (2005) stated that the amount of heat from the beginning of January is a more relevant predictor. As spring temperature varies among rivers at the same latitudes, there may be population-specific differences in the timing of migration. This may explain the variability in conclusions from studies investigating environmental cues initiating smolt migrations. Furthermore, the optimal time for the smolt migration (migratory window) may be relatively short (Hansen & Jonsson 1989; McCormick et al. 1998), and the consequence of delaying migration an extra day may be greater for late than early migrating fish.

Some authors have maintained that smolt migrations are predominantly nocturnal (Antonsson & Gudjonsson 2002; Greenstreet 1992; Hesthagen & Garnås 1986; Moore et al. 1998; Urke et al. 2013). Others report that a high proportion of the smolts migrate during daylight (Fängstam et al. 1993; Moore et al. 1995; Ibbotson et al. 2006). These contrasting observations may be associated with different temperatures prior to, and during migration. For instance, in the river Frome, England, Ibbotson et al. (2006) found that most Atlantic salmon smolts migrated downstream during night at the beginning of the annual run. Once temperature increased during spring, a gradually larger proportion of the fish moved downstream during daytime, and as the temperature exceeded 12˚C, equal numbers descended during day and night. This change in diurnal behaviour pattern may be related to the ability of ectotherms, such as smolts, to more easily escape endothermic predators, such as piscivorous sea birds and mammals, in warm than in colder water. Fish swimming and manoeuvring performance increase with increasing water temperature (Heggenes et al. 1993; Valdimarsson & Metcalfe 1998). However, variation in diel smolt migration patterns among rivers may also be mediated by differences in light intensity. The latter varies with solar radiation, cloud

93 cover, water turbidity and latitude. Furthermore, Ibbotson et al. (2011) reported that small

94 more than large smolts migrate at night when they move from the river to the ocean for

95 feeding. As most smolt predators are visual predators, the timing of smolt migrations may be

96 linked to light intensity as small smolts may be more susceptible to predation than larger ones

97 (Jutila & Jokikokko 2007).

98

99 Less is known about smolt migration in sea trout (*Salmo trutta)* than Atlantic salmon.

100 However, since sea trout smolts tend to be larger than sympatric salmon smolts (Jonsson &

101 Jonsson 2011), their diel downstream migration pattern may be less influenced by predation

102 risk. For instance, the survival of sea trout smolts in the river Imsa, Norway, increased with

103 the concurrent abundance of Atlantic salmon smolts, possibly because Atlantic salmon were

104 more profitable prey (Jonsson & Jonsson 2009). Thus a comparative study of the diel smolt

105 migration of both Atlantic salmon and sea trout in the same river may shed light on the role of

106 predation risk as a forcing mechanism in salmonid diel migration patterns.

107

108 Here, we compared the time of the smolt run during seven years using data from a rotary

109 screw trap located at the mouth of river Storelva, a medium sized system in southern Norway.

110 There are northern pike (*Esox lucius)* in the lower part of the river in addition to

111 homeothermic predators such as mink (*Neovison vison*) and red-breasted merganser (*Mergus*

112 *serrator*). In addition, we examined the individual diel patterns of Atlantic salmon and sea

113 trout smolts during migration from late April to early June 2010 by using PIT (passive

114 integrated transponder) tagged smolts passing two swim-through PIT-antennas at the mouth

115 of the river. We hypothesised that the smolts would chiefly migrate at night during early

116 migration and that this tendency would be most pronounced in Atlantic salmon when the

117 water temperature was low. We expected increased daytime migration at temperatures above

118 12-13˚C. We also explore effects of light intensities on migration pattern in wild salmonid

119 smolts.

120

121

122 **Materials and Methods**

123

124 **Study area**

125

126 The river Storelva flows through the Aust-Agder county, Norway (58˚ 40' N, 8˚59' E, Fig 1).

127 Atlantic salmon and sea trout use the lowermost 20 km of the river as spawning and nursery

128 habitats. The catchment area is 409 km^2, with an annual average water discharge of 12 m^{3}s^{-1}

129 measured at the outlet of Lake Lundevatn. The watercourse is, since 2008, regulated for

130 hydroelectric power production. Fosstveit power-plant is a run-of-the-river plant (no influence

131 on river discharge) located 6 km above the river mouth. The descending smolts may pass the

132 power-plant using a surface bypass notch located on the dam 0,5m from the tunnel inlet

133 (using 4% of the turbine discharge). Downstream migrating salmonid smolts pass through

134 Lake Lundevatn (surface area: 0.38km^2, max depth 19m) in the lower reach of the river before

135 entering Songevannet estuary. In the lower reaches of the river, introduced northern pike prey

136 on the salmonid smolts. Other predators are red-breasted merganser (*Mergus serrator*), great

137 cormorant (*Phalacrocorax carbo*) and mink (*Neovison vison*). The tidal amplitude in

138 Songevannet, at the outlet of the river Storelva, rarely exceeds 30 cm.

139 *-Figure.1-*

140

142 **Sampling**

143 During the study, all smolts of both species were captured by rotary screw fish traps. A rotary

144 screw trap (RST) is a sampling gear that takes advantage of flowing water to gently capture

145 and retain downstream migrating fish (Chaput & Jones 2004). During 2006-2012, migrating

146 smolts were monitored by catches in a rotary screw trap located at the river mouth (Fig. 1).

147 The traps were monitored two times a day, in the morning and in the afternoon, occasionally

148 once a day. Captured fish were identified to species, measured, scanned for tags, then

149 released, and the catch information used to document inter-year differences in run timing for

150 both Atlantic salmon and sea trout. Two additional rotary screw traps were installed at

151 upstream locations (6 and 1.5 km above the river mouth, Fig 1) in 2010 to capture smolts that

152 were subsequently marked with Passive Integrated Transponder (PIT) tags to provide detailed

153 descriptions of fish movement. A total of 10711 Atlantic salmon smolts and 1773 sea trout

154 smolts were captured in the three traps in 2010. All fish were measured (TL, mm) and 1879

155 Atlantic salmon and 651 sea trout from the uppermost trap with lengths > 120 mm were

156 marked with PIT tags between 30 April and 21 May 2010.

157

158 The fish were anesthetized with benzocaine (30 mg/l) and tagged internally with passive

159 integrated transponder (PIT) tags (23mm, half duplex, Oregon RFID), with a unique eight-

160 digit code. The tags were inserted through a small incision made ventrally between the

161 posterior tip of the pectoral fin and the anterior point of the pelvic girdle. Based on previous

162 findings, the incision closed and healed without suturing within a few days. The fish were

163 allowed to recover for one day before being released back into the river downstream of the

164 uppermost screw trap.

165

Fish movements were detected using PIT-antennas and hand held PIT-readers for recaptures

in the RST. The lower antenna station consisted of two swim-through antennas. The loops ran

from the southern riverbank to the northern river bank attached to the river bed and back

again placed at the water surface. The river was 9 m wide and 0.9 m deep. The two swim-

through antennas were set 2.5 m apart and wired to two remote tuner boards, one for each

antenna. The two tuner boards were connected to an antenna reader box (TIRIS RI-CTL

MB2A; Oregon RFid, USA) and supplied with an 110Ah 12V battery, creating a magnetic

field in the antenna loop, covering the total water column. When a tagged fish passed through

the antenna loop the tag was energized, and the antenna number, date, time, and tag number

were recorded by the reader box (Zydlewski et al. 2006). Using this method the smolts were

detected without any handling or facing unnatural obstacles like dams, traps or canals. The

majority of the smolts passed through the two antennas at the river mouth in seconds to

minutes. Some smolts stayed at the antenna area for several minutes, which led to multiple

detections of the same fish. In such cases the first detection was used in the analyses.

180

PIT-antenna detection probability (p_{PIT}) and catchability of RST (p_{RST}) were estimated from

mark-recapture analysis in program MARK (White & Burnham 1999), by fitting sequential

Cormack-Jolly-Seber model (Lebreton et al. 1998) to the individual recapture histories (see

Urke et al. (2013b) for a similar application). The mean PIT-antenna detection probability was

estimated to be 0.75±0.03 (SE) (fitted as an intercept model, i.e., $p_{PIT}(.)$ in MARK notion).

Since there are no within-year subsequent catch or detection opportunities beyond the RST,

RST catchability and PIT-to-RST mortality cannot be separated. In order to overcome this

constraint, which is well known to all mark-recapture analyses (Lebreton et al. 1998), we

189   fitted a CJS-model where PIT-to-RST survival was fixed at 1. Assuming all individuals to

190   survive along this 150 m river stretch is probably very close to the truth, but will bias the RST

191   catchability estimates low if there is substantial deviations from this assumption. Using this

192   approach, we estimated the mean RST catchability to be 0.23 ± 0.05. In addition to this

193   approach, we estimated daily RST catchabilities using information about daily (day of year,

194   DoY) PIT-antenna passages ($n_{PIT,DoY}$) of tagged individuals and subsequent RST recaptures of

195   the same individuals ($n_{RST,DoY}$) within the same day ($p_{RST,DoY}= n_{RST,DoY}/n_{PIT,DoY}$) - again

196   assuming all to survive. This last exercise was carried out both in 2008 and 2009, and yielded

197   catchability estimates between 0.19 and 0.21 (Kroglund et al. 2011). Hence, the mean RST

198   catchability seems to be around 0.2.

199

200   Day and night were defined according to sunset and sunrise. Time is given as local clock time

201   (24h) and the solar noon was at 13:25h at the study site (PIT antenna location) during the

202   study period. The crepuscular periods were defined as half an hour before sunrise (dusk) and half an

203   hour after sunset (dawn). Smolts experienced variable light intensities due to daily variations in

204   solar radiation, cloud cover and water turbidity. Ambient light intensities (Lux) and

205   temperatures were registered every minute at the outlet of Lake Lundevann at one meter depth

206   (HOBO Pendant®). Daily river temperatures (2006-2012) were measured at Fosstveit (id:

207   18.13.0 HYDRA database NVE), and river discharge was registered at the outlet of Lake

208   Lundevann (id: 18.4.0, HYDRA database NVE). Sea surface temperature (SST) on the

209   Skagerrak coast was obtained from the Lindesnes weather station (57°98`N; 7°05`E, available

210   at http://www.eklima.no).

211

212

Quantitative analyses

Quantitative analyses were undertaken using the statistical software R (R Core Team, 2015).

Using inter-annual data from 2006-2012, we used least squares linear regression models for

exploring effects of river water temperatures, degree-days (measured from 1 January) and sea

surface temperature on the timing of smolt descent quantiles. Interspecies differences in

temporal descent trajectories were tested using a bootstrapping routine applied to the

Kolmogorov-Smirnov test (Sekhon 2011; Sokal & Rohlf 1981). This routine allows for

distribution ties (Abadie 2002). The tests were run using the ks.boot-function in the Matching

library of R (Sekhon 2011). When testing for differences in diel smolt-descent patterns

between Atlantic salmon and sea trout, chi-square tests were employed.

223

Ordinary linear multinomial models (LMNM) were used to quantify effects of water

discharge and temperature on diel descent patterns (Venables & Ripley 2002). The response

comprised probabilities for migrating at certain Time of Day (ToD: daytime, dawn, dusk or

night) as function of water temperature and/or water discharge. Technically, this was done by

fitting the following general model: $\ln(\mathrm{ToD}_i/\mathrm{ToD}_1)=\alpha_i+\beta_{1,i}x_{1,i}+\ldots+\beta_{n,i}x_{n,i},$ where ToD_1

represents night counts and $\mathrm{ToD}_i/$ represent counts during ToD_i. α and β constitute intercept

and slope parameters under estimation, respectively, and the xs are continuous predictor

variables. Continuous variables (e.g., water temperature) were fitted both as linear predictors

and as polynomials at degrees 2 and 3 – to explore eventual non-linear effects on the diel

migration pattern. The LMNM was fitted using the multinom procedure included in the nnet

library in R (Venables & Ripley 2002). Since there was little variation in river discharge

during the 2010 migration period, we only explored the effect from water temperature on diel

236   migration pattern. Model selection was undertaken by means of the corrected Akaike's

237   Information Criterion, AICc (Burnham & Anderson 1998).

238

239   To explore whether early migration smolts differed from late migration smolts in diel

240   migration patterns and responses towards light intensity (LUX), we split the data into three

241   different time periods (05.05-17.05; 18-05-24.05; 25.05-07.06). In order to assess the light

242   level at river descent, we estimated the selection ratio (Manly et al. 2002) using the wi-

243   function in library adehabitat of R (Calenge 2006; R Core Team, 2015). This was performed

244   on a periodic basis where measurements of LUX-level were used as "resource" availability

245   data and smolt detection by the PIT antenna were used to access individual-specific selected

246   LUX values.

247

248

249   **Results**

250

251   **Inter-annual descent trajectories**

252

253   Time of downstream smolt migration varied among years (2006-2012), and the date of 50 %

254   cumulative smolt descent correlated significantly with the date when the river temperature

255   exceeded 8˚C for both Atlantic salmon (R^2=0.91, P<0.001, df=5, $Y_{50\%}$ = 1.1034* X_t+1.179)

256   and sea trout (R^2=0.64, P<0.032, df=5, $Y_{50\%}$ = 0.7472* X_t+44.184). There was, however, a

257   marginally significant positive correlation between the date when the sea surface temperature

258   (SST) exceeded 8˚C and date of 50 % cumulative Atlantic salmon smolt descent (R^2=0.53,

259   P=0.06, df= 1), and a positive, but not significant, correlation between date when the sea

260　surface temperature (SST) exceeded 8˚C and the date of 50 % cumulative sea trout smolt

261　descent (R^2=0.46, P=0.10, df= 1). Number of degree-days from 1 January to the date of 50%

262　descent ranged from 249 to 521 between 2006 and 2012 and there were no significant

263　correlation to the date of 50 % cumulative smolt descent.

264

265　The date of 25% cumulative Atlantic salmon smolt descent, measured by catches in the river

266　exit RST, was on average 2.4 days (SD ±5.8 days) after the 25% cumulative sea trout smolt

267　descent. Sea trout smolts generally started their migration ahead of Atlantic salmon, and their

268　migration period lasted longer. However, in 2007 and 2010, the Atlantic salmon smolts

269　started downstream migration earlier than the sea trout smolts. This pattern is further

270　supported by the fact that the cumulative 75% descent probability of Atlantic salmon was on

271　average 6.3 (± 4.6) days prior to the 75% sea trout descent date over the 2006-2012 period.

272

273　**The 2010 descent**

274

275　PIT-antenna detections showed that the Atlantic salmon and sea trout smolt migration began

276　in late April and ended in early June (Fig 2). The migration patterns of Atlantic salmon were

277　different from those of sea trout when using both PIT-antenna data and rotary screw trap

278　(RST) data (Two-sample Kolmogorov-Smirnov test, D_{RST}=0.707, D_{PIT}=0.658, both

279　P<0.0001). The PIT antenna detected tagged fish (date, hour, minute, second) while the smolt

280　RST (date) caught both tagged and untagged fish. The RST caught more smolts during the

281　initial stage of the migrating period than the PIT-antenna and the migration curves for the

282　RST and PIT-detection were statistically different for both Atlantic salmon (Two-sample

283　Kolmogorov-Smirnov test, D=0.585, P<0.0001) and sea trout (D=0.488 , P<0.0001). The

284   catchability of the RST decreased from ca. 30% to ca. 10% during the smolt run based on

285   detection of tagged smolts in the upstream PIT-antenna. Day/night recapture ratios indicated

286   that the daytime migrating fish were underrepresented in the RST catches in the last part of

287   the migration period relative to the early catch.

288   *-Figure 2.-*

289

290   Smolts of both species migrated at all hours of the day. Early in the migration period, Atlantic

291   salmon smolts migrated mainly during night, but the numbers and proportion of night-

292   migrating smolts per hour decreased with time (Table 1). At the end of the migration period,

293   there was a predominance of day-time migration. In Atlantic salmon, there was a significant

294   difference in the diurnal migration pattern among the three migration periods (χ^2= 62.80, df =

295   6, $P <$ 0.0001; Table 1). From 5 to 17 May, 59.8 % of the Atlantic salmon smolts migrated

296   during night, while between 25 May and 7 June, 13.2 % migrated at night. Sea trout smolts

297   exhibited a less clear diel pattern (χ^2= 8.95, df = 6, $P =$ 0.177), but also for this species, there

298   was a predominance of daytime migration towards the end of the migration period. Number

299   of Atlantic salmon smolts per hour were high in the crepuscular periods, although this

300   relationship was not evident for sea trout smolts.

301   *-Table 1.-*

302

303   Water temperatures steadily increased, but not linearly, during the migration period. We

304   explored whether water temperature had different effects on the diel migration pattern

305   between the two species by fitting a set of LMNM candidate models. Amongst the candidate

306   models, an additive model (i.e., Species+temperature^2) received the highest AICc support

13

307   attaining 3.08 lower AICc values than the second-ranked interaction model. This additive

308   model predicts Atlantic salmon smolts to migrate during daytime at lower probabilities than

309   sea trout smolts at any water temperature as the species-effect ln(daytime/night)-ratio

310   intercept was negative (-0.543±0.228 (SE), Tab 2, Fig 3). Furthermore, the

311   ln(daytime/night)-ratio *vs* water temperature slope was positive (1.163±0.397). This implies

312   that the tendency to migrate during daytime increases with increasing temperature, but the

313   negative temperature^2 coefficient (-0.035±0.014) slightly levels off this tendency. Migration

314   during dusk and dawn was predicted to occur at low probabilities.

315   *-Table 2.-*

316   *-Figure 3.-*

317

318   In Atlantic salmon, the hour-wise descent proportions differed significantly among the three

319   migration periods (Chi square test: χ^2=180.6, df=46, *P*<0.0001). During the early migration

320   period, most Atlantic salmon smolts descended from midnight to 03:00 (Fig 4). Later,

321   descending fish exhibited a reduced night maximum and a new migration maximum period in

322   the morning. During the latest migration period, many smolts descended during daytime until

323   20:00. A similar temporal change in hour-wise descent probability pattern was observed in

324   sea trout, but the number of observations per hour was too low to allow for statistical testing.

325   *-Figure 4.-*

326

327   Both Atlantic salmon and sea trout smolts exhibited a differentiated temporal pattern for light-

328   intensity selectivity during the migration period (Fig. 5). In both species, early-descending

329   smolt migrated at night and avoided high light intensities. During the mid-migration period,

330   Atlantic salmon smolts remained night-time migratory, whereas sea trout were less night-time

331   migratory. Both species avoided the most light-intensive conditions (i.e., >2000 LUX), but

332   some individuals of both species migrated under fairly high light conditions (1000-2000

333   LUX) during this period. During the last part of the migration period, both species migrated

334   more during daytime with a preference for times when light-levels ranged from 1000-1500

335   LUX. Hence, both species exhibited increasing preferences towards migrating under higher

336   light intensities as the migration period progressed, but sea trout smolts became light-prone

337   earlier than Atlantic salmon smolts.

338   *-Figure 5.-*

339

340   In both species, the average size of migrants increased as the season advanced. Among six

341   candidate linear models fitted to quantify temporal trends in smolt size (*LT*, mm), the most

342   AICc supported model included highly significant additive effects (*P*<0.0001) between day of

343   year (*DoY*) and species (*SP*): $LT = 68.4 + 0.49 DoY + 32.7 SP_{\text{brown trout}}$. During the course of the

344   30-day smolt run period the mean smolt size increased by 1.5 cm in both species. When

345   analysing time-of-day (*ToD*) effects on individual lengths in migrating smolts by species a

346   difference in temporal trends appeared. In sea trout, there was a highly significant interaction

347   effect ($P_{DoY*ToD}$=0.004) between *DoY* and *ToD*, indicating that individuals migrating at night

348   to be larger than daytime migrants in the early part of the run, whereas later in the season day

349   and night migrants were of similar sizes. In Atlantic salmon, there was no evidence of a

350   *ToD*DoY* effect, but one-way anova revealed that night-migrating individuals were 0.34±

351   0.13(SE) cm smaller (*P*=0.009) than daytime-migrating individuals throughout the migration

352   period.

353

354

Discussion

356

Downstream migration of Atlantic salmon and sea trout smolts in the river Storelva appeared

more related to river temperature than sea surface temperature. The river flow was low and

declining through the migration period, and no floods were registered during the smolt run.

As a consequence, this potentially important environmental variable (e.g., Hesthagen &

Garnås 1986; Jensen et al. 2012) could not be adequately included in our analyses. Water

temperature has previously been found to be a key environmental trigger for salmonid smolt

runs (Jonsson & Ruud-Hansen 1985; Otero et al. 2014). Zydlewski et al. (2005) stated that the

amount of heat from the beginning of January, is a more relevant predictor for the initiation

and termination of the downstream movement, than a temperature threshold experienced by

the fish. After 649-700 degree-days (measured from 1 January), all smolts initiated

downstream movements, and there were no difference between groups that had experienced

differences in temperature. However, in our study there was large individual variation in

degree-days from 1 January to the smolt descent between years, as earlier found for Atlantic

salmon of the river Imsa, Norway (Jonsson & Jonsson 2014b). Probably, year-to-year

variation in the smolt-run timing is influenced by more factors than the amount of heat

experienced by the fish during winter and spring prior to migration. In particular, the actual

water temperature when migration starts seems to play an important role (Jonsson & Ruud-

Hansen 1985; Jonsson & Jonsson 2014b). In the present study, a large proportion of the fish

started to migrate a few days after the river temperature exceeded 8 °C as found elsewhere

(Hvidsten et al. 1998; Whalen et al. 1999). The preceding river temperatures may play a

pivotal role during the physiological smolting process, i.e., the smolts' readiness for

migration, whereas the actual river temperature influences manoeuvrability and swimming

379   speed of the smolts (Aarestrup et al. 2002), properties pertinent to predator avoidance and

380   may thus fine-tune the downstream migration (diurnal and day-to-day decisions on when to

381   migrate).

382

383   The catch/detection trajectories were different between the PIT antenna and the rotary screw

384   trap at the river mouth during the 2010 smolt run. The difference was most pronounced during

385   later stages of the run period, when the rotary screw trap caught fewer smolts than were

386   detected by the PIT-antenna. Thus, the catchability/detectability appeared to differ between

387   the two sampling methods. The catchability in the rotary-screw trap appeared more sensitive

388   to changes in the smolt behaviour during the run period than the PIT antenna. Furthermore,

389   the smolts became more daytime active over the run period probably leading to increased trap

390   avoidance towards the end of the migratory period, owing to better visual conditions. This

391   behaviour-induced change in trap catchability over the course of the smolt run may also have

392   relevance to other studies. For instance, in the river Orkla, Hesthagen & Garnås (1986) found

393   low daytime smolt catches during later parts of the smolt run. There is no similar bias in

394   detecting PIT-tagged smolts, and this is a preferable method when studying dial patterns of

395   downstream migrating smolts.

396

397   Gradually more Atlantic salmon smolts migrated during the day as temperature increased, and

398   at a river temperature above 12-13˚C, more smolts descended at day than during the night.

399   This concurs with Ibbotson et al. (2006) who observed nocturnal migration at temperatures

400   below ca. 12˚C. When daily mean temperatures exceeded 12˚C in the river Frome, there was

401   no difference between diurnal and nocturnal migration rate and no migration took place at

402   temperatures above 14 °C. Fourteen degrees, however, may not be the maximum for

migration of smolts. In the present study, the water temperature rose more or less steadily during the migration period and peaked at 18˚C with 12 days with daily mean temperatures above 14˚C. During this later stage with high water temperatures, most of the smolts migrated during daytime, and this may be a general pattern for Atlantic salmon smolts.

Nocturnal migration is probably a predator avoidance behaviour (Moore et al. 1995). The change to diurnal migration in warmer water may be because the ectothermic smolts are better at escaping endothermic predators, such as sea birds and mammals, as their metabolic rates increase (Domenici &Blake 1997; Valdimarsson &Metcalfe 1998). The extent of bird and mammal predation on the river Storelva smolts is unknown, but predation from Northern pike has been estimated at almost 30% for the entire smolt population (Kristensen et al. 2010). A recent experimental study by Öhlund et al. (2015) showed that swimming speed in brown trout and northern pike have non-parallel thermal responses when put together in the same tank. They found escape swimming speed of brown trout to be higher than northern pike attack speed at temperatures below 11 °C, and swimming speeds to be similar above this threshold temperature. In addition, attack rate from northern pike dropped to almost zero below 11 °C. Interestingly, the escape swimming speed of the northern pike (chased by man) showed a parallel thermal response as the brown trout, indicating the threshold response for the attack speed not to be due to physiological constraints. The authors suggest the threshold to have arisen from either neurological constraints at lower temperatures related to the far more complex process of catching and handling prey compared to the escape behaviour or simply due to reduced attack motivation (e.g., due to hunger or predation risk). Applying the findings in the Öhlund et al. (2015) study on the Storelva smolt vs northern pike system predicts the smolt to predominantly migrate prior to water temperatures reaching 11°C, and time of day should not be critical at these low temperatures due to the superior escape

428 swimming speed of the smolt. At temperatures beyond 11 °C, the smolt would need some

429 additional protection such as migrating under dark conditions, to reduce attacks from the now

430 equally well performing predator. This prediction fits poorly with our results as we found

431 night-time migration to occur largely during cold-water conditions. The Öhlund et al. (2015)

432 experiment was not conducted using smolt as prey, but the size group used was similar as

433 typical Storelva smolts (ca 15 cm) and northern pike predators were comparable to Storelva

434 northern pike (49-71 cm). We therefore suggest the deviations from the experimental

435 predictions to be due to either more feeding-motivated northern pike in the Storelva system or

436 due to smolt thermal swimming speed responses to be different from non-smolt brown trout.

437 Webb (1978) showed that, in rainbow trout (*Oncorhynchus mykiss*), speed and acceleration

438 are affected by temperatures at 5–15 °C, but appeared temperature independent at higher

439 temperatures (15–20 °C). Maximum swimming speed may be constrained by lack of oxygen

440 at such high temperatures. In addition, thermal effects on predator-prey relationships, even

441 when both are ectothermic, entails more than just swimming performance kinetics.

442 Temperature influences escape response latencies with potential effect on responsiveness and

443 vulnerability (Domenici & Blake 1997).

444

445 Furthermore, smolts may profit from migrating in warm water. They are themselves visual

446 predators, and as the temperature increases, their needs for food increase especially because

447 the energy density of sea trout smolts is low (Jonsson &Jonsson 1998). In Atlantic salmon,

448 the somatic energy density, because of higher lipid content, is higher than in sea trout smolts,

449 probably associated with their longer marine migration route and therefore higher energy

450 needs (Jonsson &Jonsson 2003). Sea trout feed in estuaries and coastal areas typically close to

451 their home river (Jonsson &Jonsson 2014a) whereas Atlantic salmon feed at high seas in the

452 North Atlantic Ocean (Hansen et al. 1993).

453

Sea trout, in contrast to Atlantic salmon, did not exhibit a switch from nocturnal to diurnal

migration at 12-13 ˚C, although the probability of daytime migration increased with river

temperature. Furthermore, their tendency throughout the season to migrate during the day was

higher than in Atlantic salmon smolts. These temperature-related diel response patterns are

very much in line with findings in Aldvén et al (2015). They found sea trout smolts typically

to have a higher probability of daytime migration than Atlantic salmon smolts, and for both

species daytime migration tendency increased with increasing temperature, and particularly so

at temperatures above 10 °C. Sea trout activity may be less constrained by cold water and/or

their need for food at high temperature may be stronger because of their lower energy density.

Sea trout may be approximately 2°C more cold-adapted than Atlantic salmon as inferred from

their thermal performance curves (Jonsson &Jonsson 2011), but still they migrated at

approximately the same river temperature. Possibly, the temperature at sea influences the time

of river descent because of selection over time, and similar marine conditions at the start of

the migration may be optimal for survival and growth for the two species. In addition, the

time of the sea trout migration may be adapted to that of the Atlantic salmon. Atlantic salmon

smolts are smaller and possibly easier prey for the predators present. Concurrent migration

time reduces the predation risk for sea trout (Jonsson & Jonsson 2009). In addition

Montegomery et al. (1983) documented synchrony in downstream migration in five

taxonomically and ecologically diverse fish species including Atlantic salmon. They

hypothesised that this may be inter- and intra-specific social interactions resulting from

migratory restlessness or migratory movements of one species, which may be selectively

advantageous if it reduces predation or otherwise increases survival during the migration.

476

477 The size of the fish may also influence their dial migration pattern. Ibbotson et al. (2011)

478 found that nocturnally migrating smolts were smaller than diurnally migrating smolts. They

479 suggested that nocturnal migration is an adaptation helping small smolts to avoid predation by

480 visual piscivores. A similar size difference was found for both species in the present study,

481 but in sea trout this applied to the early migration period only. Small smolts are more

482 vulnerable to predation than larger ones (Jonsson &Jonsson 2014b), and a higher degree of

483 nocturnal migration may be a way for small fish to reduce their size disadvantage. Similarly,

484 the smaller sizes of Atlantic salmon smolts compared to sea trout may make it more beneficial

485 for the salmon to migration at low light intensity. Furthermore, mean length of the

486 downstream migrating smolts increased by 0.5 mm per day during the study period. This may

487 reflect individual growth during spring. An alternative would be that small individuals

488 migrate early when light conditions are darker and predation risk lower. However, we feel

489 that this latter contention is less probable. It contrasts earlier observations that large

490 individuals start to migrate earlier than smaller ones (Jonsson & Ruud-Hansen 1985; Jonsson

491 et al. 1990; Bohlin et al. 1996) and that large fish are better able to survive at low temperature

492 in cold sea water (Hoar 1976).

493

494

495 In conclusion, the present study showed that the probability for daytime migration increased

496 with river temperature for both Atlantic salmon and sea trout, but that this tendency is

497 stronger in salmon than sea trout. The reason may be the larger body size of sea trout making

498 them less vulnerable to predation.

499

500

Acknowledgements

Legend to figures

511

512 **Figure 1.** The lowermost 7 km of River Storelva with Lake Lundevatn and outlet to the

513   brackish Songevannet with locations for rotary screw traps and PIT antennas.

514

515 **Figure 2.** Cumulative percentage of down-stream migrating smolts of Atlantic salmon and sea

516   trout at the mouth of River Storelva based on detection of pit-tagged smolts in the

517   PIT antenna (solid line; Nsalmon= 512, Ntrout = 153) and untagged and tagged

518   smolts caught in the rotary-screw-trap located at the River mouth (dashed line;

519   Nsalmon= 933, Ntrout = 310) including daily number of released tagged smolt

520   (grey columns) from Fosstveit.

521

522 **Figure 3.** Predicted probabilities for migrating at different ToD (Time of Day) as function of

523   water temperature and species. Model predictions were retrieved from the

524   multinomial model reported in Table 2.

525

526 **Figure 4.** Number of migrating smolts per hour for Atlantic salmon (upper) and sea trout

527   (lower) passing the antenna at the River mouth of Storelva 2010 divided into the

528   three migration periods. Arrows illustrate sunrise and sunset.

529 **Figure5.** Light-intensity selection ratios (error bars = 95% CI) of migrating smolts of Atlantic

530   salmon (circles) and sea trout (triangles) at different light intensities (LUX) during

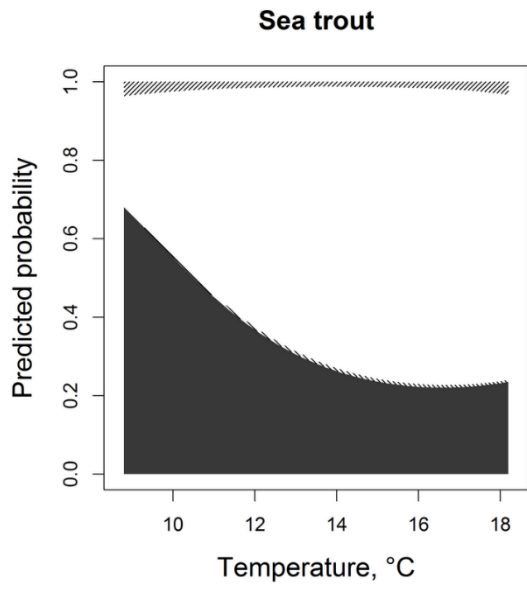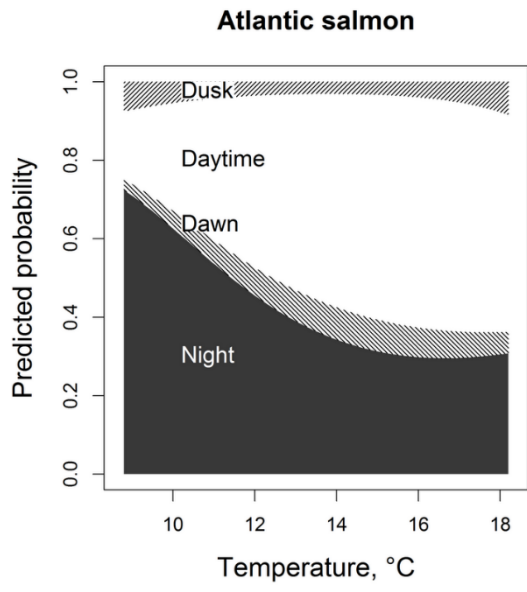531   three smolt migration periods in Storeleva, 2010.

532

Atlantic salmon

Sea trout

534

535

Light intensity (LUX)
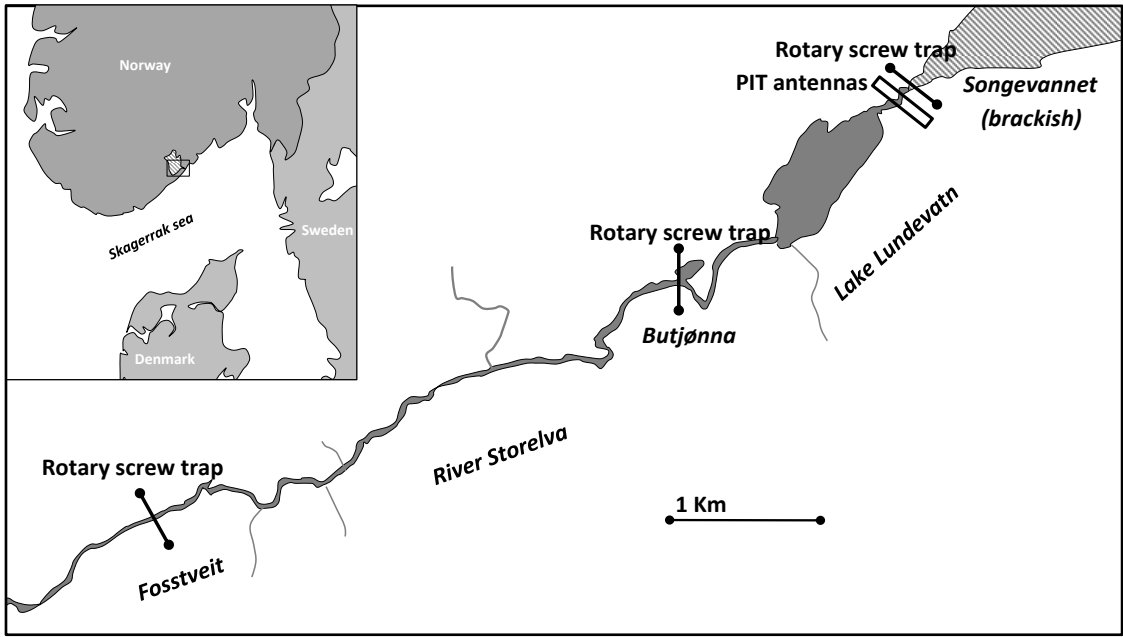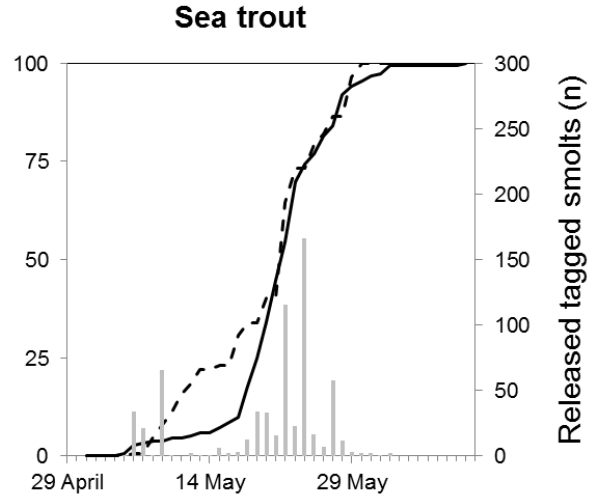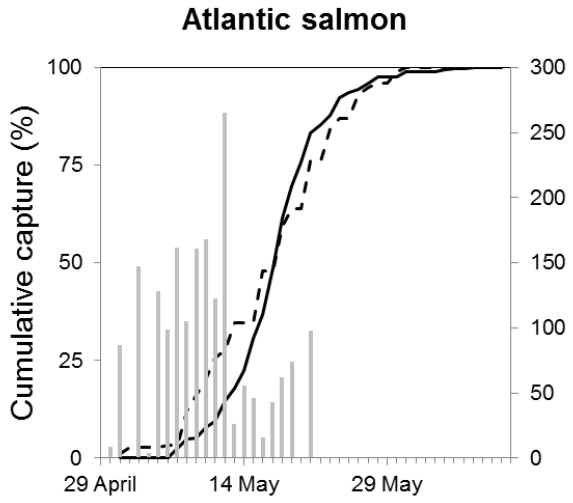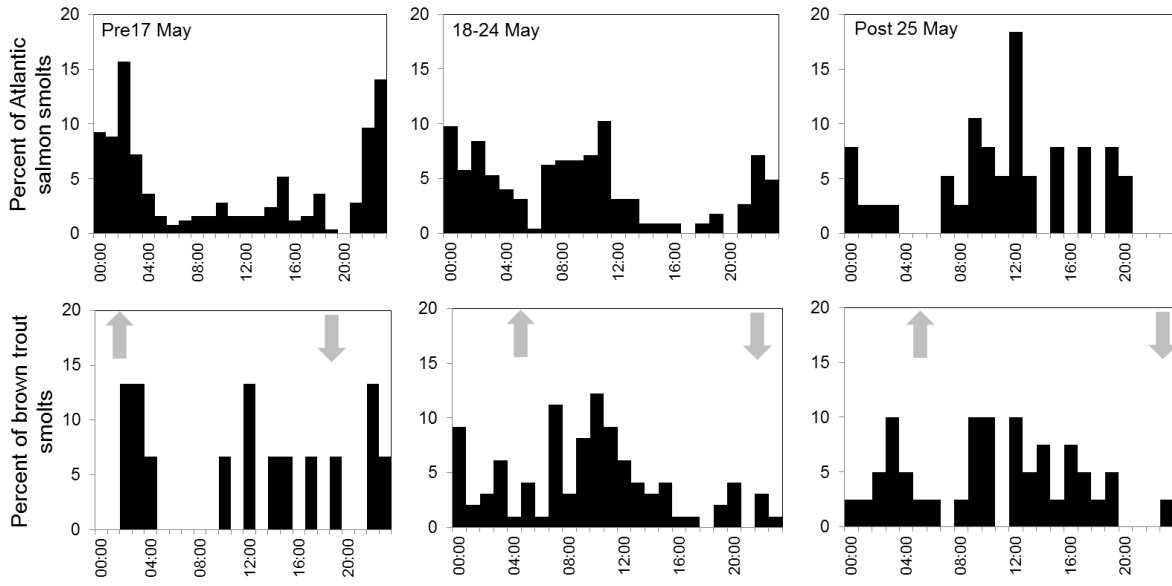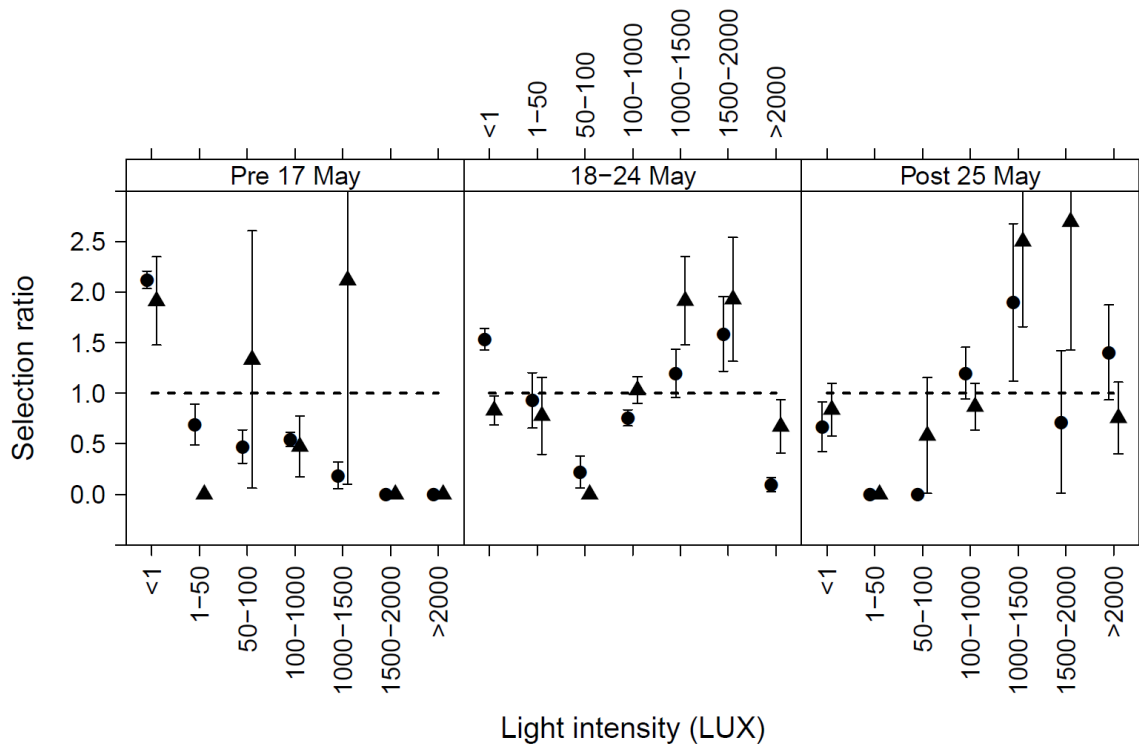
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