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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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Running title: Diel migration pattern of smolts

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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 species’ 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 & Garnás 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
cover, water turbidity and latitude. Furthermore, Ibbotson et al. (2011) reported that small
more than large smolts migrate at night when they move from the river to the ocean for
feeding. As most smolt predators are visual predators, the timing of smolt migrations may be
linked to light intensity as small smolts may be more susceptible to predation than larger ones
(Jutila & Jokikokko 2007).

Less is known about smolt migration in sea trout (Salmo trutta) than Atlantic salmon.
However, since sea trout smolts tend to be larger than sympatric salmon smolts (Jonsson &
Jonsson 2011), their diel downstream migration pattern may be less influenced by predation
risk. For instance, the survival of sea trout smolts in the river Imsa, Norway, increased with
the concurrent abundance of Atlantic salmon smolts, possibly because Atlantic salmon were
more profitable prey (Jonsson & Jonsson 2009). Thus a comparative study of the diel smolt
migration of both Atlantic salmon and sea trout in the same river may shed light on the role of
predation risk as a forcing mechanism in salmonid diel migration patterns.

Here, we compared the time of the smolt run during seven years using data from a rotary
screw trap located at the mouth of river Storelva, a medium sized system in southern Norway.
There are northern pike (Esox lucius) in the lower part of the river in addition to
homeothermic predators such as mink (Neovison vison) and red-breasted merganser (Mergus
serrator). In addition, we examined the individual diel patterns of Atlantic salmon and sea
troul smolts during migration from late April to early June 2010 by using PIT (passive
integrated transponder) tagged smolts passing two swim-through PIT-antennas at the mouth
of the river. We hypothesised that the smolts would chiefly migrate at night during early
migration and that this tendency would be most pronounced in Atlantic salmon when the
water temperature was low. We expected increased daytime migration at temperatures above 12-13°C. We also explore effects of light intensities on migration pattern in wild salmonid smolts.

Materials and Methods

Study area

The river Storelva flows through the Aust-Agder county, Norway (58° 40’ N, 8°59’ E, Fig 1). Atlantic salmon and sea trout use the lowermost 20 km of the river as spawning and nursery habitats. The catchment area is 409 km², with an annual average water discharge of 12 m³s⁻¹ measured at the outlet of Lake Lundevatn. The watercourse is, since 2008, regulated for hydroelectric power production. Fosstveit power-plant is a run-of-the-river plant (no influence on river discharge) located 6 km above the river mouth. The descending smolts may pass the power-plant using a surface bypass notch located on the dam 0,5m from the tunnel inlet (using 4% of the turbine discharge). Downstream migrating salmonid smolts pass through Lake Lundevatn (surface area: 0.38km², max depth 19m) in the lower reach of the river before entering Songevannet estuary. In the lower reaches of the river, introduced northern pike prey on the salmonid smolts. Other predators are red-breasted merganser (Mergus serrator), great cormorant (Phalacrocorax carbo) and mink (Neovison vison). The tidal amplitude in Songevannet, at the outlet of the river Storelva, rarely exceeds 30 cm.
**Sampling**

During the study, all smolts of both species were captured by rotary screw fish traps. A rotary screw trap (RST) is a sampling gear that takes advantage of flowing water to gently capture and retain downstream migrating fish (Chaput & Jones 2004). During 2006-2012, migrating smolts were monitored by catches in a rotary screw trap located at the river mouth (Fig. 1).

The traps were monitored two times a day, in the morning and in the afternoon, occasionally once a day. Captured fish were identified to species, measured, scanned for tags, then released, and the catch information used to document inter-year differences in run timing for both Atlantic salmon and sea trout. Two additional rotary screw traps were installed at upstream locations (6 and 1.5 km above the river mouth, Fig 1) in 2010 to capture smolts that were subsequently marked with Passive Integrated Transponder (PIT) tags to provide detailed descriptions of fish movement. A total of 10711 Atlantic salmon smolts and 1773 sea trout smolts were captured in the three traps in 2010. All fish were measured (TL, mm) and 1879 Atlantic salmon and 651 sea trout from the uppermost trap with lengths > 120 mm were marked with PIT tags between 30 April and 21 May 2010.

The fish were anesthetized with benzocaine (30 mg/l) and tagged internally with passive integrated transponder (PIT) tags (23mm, half duplex, Oregon RFID), with a unique eight-digit code. The tags were inserted through a small incision made ventrally between the posterior tip of the pectoral fin and the anterior point of the pelvic girdle. Based on previous findings, the incision closed and healed without suturing within a few days. The fish were allowed to recover for one day before being released back into the river downstream of the uppermost screw trap.
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.

PIT-antenna detection probability ($p_{\text{PIT}}$) and catchability of RST ($p_{\text{RST}}$) 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 $0.75 \pm 0.03$ (SE) (fitted as an intercept model, i.e., $p_{\text{PIT}(.)}$ 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
fitted a CJS-model where PIT-to-RST survival was fixed at 1. Assuming all individuals to survive along this 150 m river stretch is probably very close to the truth, but will bias the RST catchability estimates low if there is substantial deviations from this assumption. Using this approach, we estimated the mean RST catchability to be 0.23±0.05. In addition to this approach, we estimated daily RST catchabilities using information about daily (day of year, DoY) PIT-antenna passages ($n_{\text{PIT,DoY}}$) of tagged individuals and subsequent RST recaptures of the same individuals ($n_{\text{RST,DoY}}$) within the same day ($p_{\text{RST,DoY}} = n_{\text{RST,DoY}} / n_{\text{PIT,DoY}}$) - again assuming all to survive. This last exercise was carried out both in 2008 and 2009, and yielded catchability estimates between 0.19 and 0.21 (Kroglund et al. 2011). Hence, the mean RST catchability seems to be around 0.2.

Day and night were defined according to sunset and sunrise. Time is given as local clock time (24h) and the solar noon was at 13:25h at the study site (PIT antenna location) during the study period. The crepuscular periods were defined as half an hour before sunrise (dusk) and half an hour after sunset (dawn). Smolts experienced variable light intensities due to daily variations in solar radiation, cloud cover and water turbidity. Ambient light intensities (Lux) and temperatures were registered every minute at the outlet of Lake Lundevann at one meter depth (HOBO Pendant®). Daily river temperatures (2006-2012) were measured at Fosstveit (id: 18.13.0 HYDRA database NVE), and river discharge was registered at the outlet of Lake Lundevann (id: 18.4.0, HYDRA database NVE). Sea surface temperature (SST) on the Skagerrak coast was obtained from the Lindesnes weather station (57°98´N; 7°05´E, available at http://www.eklima.no).
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.

Ordinary linear multinomials (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: \( \ln(\frac{\text{ToD}_i}{\text{ToD}_1}) = \alpha + \beta_1 x_1 + \ldots + \beta_n x_n \), where \( \text{ToD}_1 \) represents night counts and \( \text{ToD}_i \) represent counts during \( \text{ToD}_i \). \( \alpha \) and \( \beta \) constitute intercept and slope parameters under estimation, respectively, and the \( x \)s 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
migration pattern. Model selection was undertaken by means of the corrected Akaike’s Information Criterion, AICc (Burnham & Anderson 1998).

To explore whether early migration smolts differed from late migration smolts in diel migration patterns and responses towards light intensity (LUX), we split the data into three different time periods (05.05-17.05; 18-05-24.05; 25.05-07.06). In order to assess the light level at river descent, we estimated the selection ratio (Manly et al. 2002) using the wi-function in library adehabitat of R (Calenge 2006; R Core Team, 2015). This was performed on a periodic basis where measurements of LUX-level were used as “resource” availability data and smolt detection by the PIT antenna were used to access individual-specific selected LUX values.

Results

Inter-annual descent trajectories

Time of downstream smolt migration varied among years (2006-2012), and the date of 50\% cumulative smolt descent correlated significantly with the date when the river temperature exceeded 8°C for both Atlantic salmon ($R^2=0.91, P<0.001, df=5, Y_{50\%} = 1.1034* X_t+1.179$) and sea trout ($R^2=0.64, P<0.032, df=5, Y_{50\%} = 0.7472* X_t+44.184$). There was, however, a marginally significant positive correlation between the date when the sea surface temperature (SST) exceeded 8°C and date of 50 \% cumulative Atlantic salmon smolt descent ($R^2=0.53, P=0.06, df= 1$), and a positive, but not significant, correlation between date when the sea
surface temperature (SST) exceeded 8°C and the date of 50% cumulative sea trout smolt
descent ($R^2=0.46$, $P=0.10$, df=1). Number of degree-days from 1 January to the date of 50%
descent ranged from 249 to 521 between 2006 and 2012 and there were no significant
correlation to the date of 50% cumulative smolt descent.

The date of 25% cumulative Atlantic salmon smolt descent, measured by catches in the river
exit RST, was on average 2.4 days (SD ±5.8 days) after the 25% cumulative sea trout smolt
descent. Sea trout smolts generally started their migration ahead of Atlantic salmon, and their
migration period lasted longer. However, in 2007 and 2010, the Atlantic salmon smolts
started downstream migration earlier than the sea trout smolts. This pattern is further
supported by the fact that the cumulative 75% descent probability of Atlantic salmon was on
average 6.3 (± 4.6) days prior to the 75% sea trout descent date over the 2006-2012 period.

The 2010 descent

PIT-antenna detections showed that the Atlantic salmon and sea trout smolt migration began
in late April and ended in early June (Fig 2). The migration patterns of Atlantic salmon were
different from those of sea trout when using both PIT-antenna data and rotary screw trap
(RST) data (Two-sample Kolmogorov-Smirnov test, $D_{RST}=0.707$, $D_{PIT}=0.658$, both
$P<0.0001$). The PIT antenna detected tagged fish (date, hour, minute, second) while the smolt
RST (date) caught both tagged and untagged fish. The RST caught more smolts during the
initial stage of the migrating period than the PIT-antenna and the migration curves for the
RST and PIT-detection were statistically different for both Atlantic salmon (Two-sample
Kolmogorov-Smirnov test, $D=0.585$, $P<0.0001$) and sea trout ($D=0.488$, $P<0.0001$). The
catchability of the RST decreased from ca. 30% to ca. 10% during the smolt run based on
detection of tagged smolts in the upstream PIT-antenna. Day/night recapture ratios indicated
that the daytime migrating fish were underrepresented in the RST catches in the last part of
the migration period relative to the early catch.

-Figure 2.-

Smolts of both species migrated at all hours of the day. Early in the migration period, Atlantic
salmon smolts migrated mainly during night, but the numbers and proportion of night-
migrating smolts per hour decreased with time (Table 1). At the end of the migration period,
there was a predominance of day-time migration. In Atlantic salmon, there was a significant
difference in the diurnal migration pattern among the three migration periods ($\chi^2 = 62.80$, df = 6, $P < 0.0001$; Table 1). From 5 to 17 May, 59.8 % of the Atlantic salmon smolts migrated
during night, while between 25 May and 7 June, 13.2 % migrated at night. Sea trout smolts
exhibited a less clear diel pattern ($\chi^2 = 8.95$, df = 6, $P = 0.177$), but also for this species, there
was a predominance of daytime migration towards the end of the migration period. Number
of Atlantic salmon smolts per hour were high in the crepuscular periods, although this
relationship was not evident for sea trout smolts.

-Table 1.-

Water temperatures steadily increased, but not linearly, during the migration period. We
explored whether water temperature had different effects on the diel migration pattern
between the two species by fitting a set of LMNM candidate models. Amongst the candidate
models, an additive model (i.e., Species+temperature$^2$) received the highest AICc support
attaining 3.08 lower AICc values than the second-ranked interaction model. This additive model predicts Atlantic salmon smolts to migrate during daytime at lower probabilities than sea trout smolts at any water temperature as the species-effect \( \ln(\text{daytime/night}) \)-ratio intercept was negative (-0.543±0.228 (SE), Tab 2, Fig 3). Furthermore, the \( \ln(\text{daytime/night}) \)-ratio vs water temperature slope was positive (1.163±0.397). This implies that the tendency to migrate during daytime increases with increasing temperature, but the negative temperature\(^2\) coefficient (-0.035±0.014) slightly levels off this tendency. Migration during dusk and dawn was predicted to occur at low probabilities.

In Atlantic salmon, the hour-wise descent proportions differed significantly among the three migration periods (Chi square test: \( \chi^2=180.6, \text{df}=46, P<0.0001 \)). During the early migration period, most Atlantic salmon smolts descended from midnight to 03:00 (Fig 4). Later, descending fish exhibited a reduced night maximum and a new migration maximum period in the morning. During the latest migration period, many smolts descended during daytime until 20:00. A similar temporal change in hour-wise descent probability pattern was observed in sea trout, but the number of observations per hour was too low to allow for statistical testing.

Both Atlantic salmon and sea trout smolts exhibited a differentiated temporal pattern for light-intensity selectivity during the migration period (Fig. 5). In both species, early-descending smolt migrated at night and avoided high light intensities. During the mid-migration period,
Atlantic salmon smolts remained night-time migratory, whereas sea trout were less night-time migratory. Both species avoided the most light-intensive conditions (i.e., >2000 LUX), but some individuals of both species migrated under fairly high light conditions (1000-2000 LUX) during this period. During the last part of the migration period, both species migrated more during daytime with a preference for times when light-levels ranged from 1000-1500 LUX. Hence, both species exhibited increasing preferences towards migrating under higher light intensities as the migration period progressed, but sea trout smolts became light-prone earlier than Atlantic salmon smolts.

In both species, the average size of migrants increased as the season advanced. Among six candidate linear models fitted to quantify temporal trends in smolt size ($LT$, mm), the most AICc supported model included highly significant additive effects ($P<0.0001$) between day of year ($DoY$) and species ($SP$): $LT = 68.4+0.49DoY + 32.7SP_{brown trout}$. During the course of the 30-day smolt run period the mean smolt size increased by 1.5 cm in both species. When analysing time-of-day ($ToD$) effects on individual lengths in migrating smolts by species a difference in temporal trends appeared. In sea trout, there was a highly significant interaction effect ($P_{DoY*ToD}=0.004$) between $DoY$ and $ToD$, indicating that individuals migrating at night to be larger than daytime migrants in the early part of the run, whereas later in the season day and night migrants were of similar sizes. In Atlantic salmon, there was no evidence of a $ToD*DoY$ effect, but one-way anova revealed that night-migrating individuals were $0.34\pm 0.13(\text{SE})$ cm smaller ($P=0.009$) than daytime-migrating individuals throughout the migration period.

-Figure 5.-
Discussion

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
speed of the smolts (Aarestrup et al. 2002), properties pertinent to predator avoidance and
may thus fine-tune the downstream migration (diurnal and day-to-day decisions on when to
migrate).

The catch/detection trajectories were different between the PIT antenna and the rotary screw
trap at the river mouth during the 2010 smolt run. The difference was most pronounced during
later stages of the run period, when the rotary screw trap caught fewer smolts than were
detected by the PIT-antenna. Thus, the catchability/detectability appeared to differ between
the two sampling methods. The catchability in the rotary-screw trap appeared more sensitive
to changes in the smolt behaviour during the run period than the PIT antenna. Furthermore,
the smolts became more daytime active over the run period probably leading to increased trap
avoidance towards the end of the migratory period, owing to better visual conditions. This
behaviour-induced change in trap catchability over the course of the smolt run may also have
relevance to other studies. For instance, in the river Orkla, Hesthagen & Garnås (1986) found
low daytime smolt catches during later parts of the smolt run. There is no similar bias in
detecting PIT-tagged smolts, and this is a preferable method when studying dial patterns of
downstream migrating smolts.

Gradually more Atlantic salmon smolts migrated during the day as temperature increased, and
at a river temperature above 12-13°C, more smolts descended at day than during the night.
This concurs with Ibbotson et al. (2006) who observed nocturnal migration at temperatures
below ca. 12°C. When daily mean temperatures exceeded 12°C in the river Frome, there was
no difference between diurnal and nocturnal migration rate and no migration took place at
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
swimming speed of the smolt. At temperatures beyond 11 °C, the smolt would need some additional protection such as migrating under dark conditions, to reduce attacks from the now equally well performing predator. This prediction fits poorly with our results as we found night-time migration to occur largely during cold-water conditions. The Öhlund et al. (2015) experiment was not conducted using smolt as prey, but the size group used was similar as typical Storelva smolts (ca 15 cm) and northern pike predators were comparable to Storelva northern pike (49-71 cm). We therefore suggest the deviations from the experimental predictions to be due to either more feeding-motivated northern pike in the Storelva system or due to smolt thermal swimming speed responses to be different from non-smolt brown trout. Webb (1978) showed that, in rainbow trout (*Oncorhynchus mykiss*), speed and acceleration are affected by temperatures at 5–15 °C, but appeared temperature independent at higher temperatures (15–20 °C). Maximum swimming speed may be constrained by lack of oxygen at such high temperatures. In addition, thermal effects on predator-prey relationships, even when both are ectothermic, entails more than just swimming performance kinetics. Temperature influences escape response latencies with potential effect on responsiveness and vulnerability (Domenici & Blake 1997).

Furthermore, smolts may profit from migrating in warm water. They are themselves visual predators, and as the temperature increases, their needs for food increase especially because the energy density of sea trout smolts is low (Jonsson & Jonsson 1998). In Atlantic salmon, the somatic energy density, because of higher lipid content, is higher than in sea trout smolts, probably associated with their longer marine migration route and therefore higher energy needs (Jonsson & Jonsson 2003). Sea trout feed in estuaries and coastal areas typically close to their home river (Jonsson & Jonsson 2014a) whereas Atlantic salmon feed at high seas in the North Atlantic Ocean (Hansen et al. 1993).
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.
The size of the fish may also influence their dial migration pattern. Ibbotson et al. (2011) found that nocturnally migrating smolts were smaller than diurnally migrating smolts. They suggested that nocturnal migration is an adaptation helping small smolts to avoid predation by visual piscivores. A similar size difference was found for both species in the present study, but in sea trout this applied to the early migration period only. Small smolts are more vulnerable to predation than larger ones (Jonsson & Jonsson 2014b), and a higher degree of nocturnal migration may be a way for small fish to reduce their size disadvantage. Similarly, the smaller sizes of Atlantic salmon smolts compared to sea trout may make it more beneficial for the salmon to migration at low light intensity. Furthermore, mean length of the downstream migrating smolts increased by 0.5 mm per day during the study period. This may reflect individual growth during spring. An alternative would be that small individuals migrate early when light conditions are darker and predation risk lower. However, we feel that this latter contention is less probable. It contrasts earlier observations that large individuals start to migrate earlier than smaller ones (Jonsson & Ruud-Hansen 1985; Jonsson et al. 1990; Bohlin et al. 1996) and that large fish are better able to survive at low temperature in cold sea water (Hoar 1976).

In conclusion, the present study showed that the probability for daytime migration increased with river temperature for both Atlantic salmon and sea trout, but that this tendency is stronger in salmon than sea trout. The reason may be the larger body size of sea trout making them less vulnerable to predation.
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Legend to figures

Figure 1. The lowermost 7 km of River Storelva with Lake Lundevatn and outlet to the brackish Songevannet with locations for rotary screw traps and PIT antennas.

Figure 2. Cumulative percentage of down-stream migrating smolts of Atlantic salmon and sea trout at the mouth of River Storelva based on detection of pit-tagged smolts in the PIT antenna (solid line; Nsalmon= 512, Ntrout = 153) and untagged and tagged smolts caught in the rotary-screw-trap located at the River mouth (dashed line; Nsalmon= 933, Ntrout = 310) including daily number of released tagged smolt (grey columns) from Fosstveit.

Figure 3. Predicted probabilities for migrating at different ToD (Time of Day) as function of water temperature and species. Model predictions were retrieved from the multinomial model reported in Table 2.

Figure 4. Number of migrating smolts per hour for Atlantic salmon (upper) and sea trout (lower) passing the antenna at the River mouth of Storelva 2010 divided into the three migration periods. Arrows illustrate sunrise and sunset.

Figure 5. Light-intensity selection ratios (error bars = 95% CI) of migrating smolts of Atlantic salmon (circles) and sea trout (triangles) at different light intensities (LUX) during three smolt migration periods in Storeleva, 2010.
References


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