Environmental cues and downstream migration of anadromous brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts

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Several environmental cues have been suggested to govern the initiation of the downstream migration of smolts (e.g. light, temperature and discharge). Here we investigated the effect of these cues on the initiation of the downstream migration in anadromous brown trout and Atlantic salmon in a small river on the Swedish west coast during two consecutive years. The total smolt production was assessed using a smolt trap and by modelling data from standardized electrofishing. The results show that it is possible to estimate smolt numbers using electrofishing, but that the model had a tendency to overestimate the number of smolts from electrofishing as compared with that from captures with the smolt trap. Discharge had the greatest effect on downstream migration, but temperature was also important when there was no increase in discharge. These results reveal that discharge and temperature govern the initiation of downstream migration but their effect may depend on the amount of precipitation.

Introduction

All salmonids begin their life in fresh water, but later they may migrate to large lakes or the sea. Before this migration they develop tolerance to sea water and undergo morphological changes, i.e. smoltification (McCormick *et al*. 1987, Björnsson *et al*. 2011), whose timing is controlled by environmental cues, of which photoperiod is thought to be the most important (Björnsson *et al*. 2011).

Previous studies have indicated that the downstream migration of smolts begins at different times, depending on where they are located in the river (Hvidsten *et al*. 1995, Stewart *et al*. 2006). The migration is foremost nocturnal, but a shift to a diurnal migration pattern when the water temperature increases towards the end of the migration period has also been reported (Thorpe *et al*. 1994, Ibbotson *et al*. 2006). The increased temperature positively affects swimming performance (Virtanen and Forsman 1987, Forsman and Virtanen 1989), thereby lowering the risk of predation during daytime migration (Rikardsen *et al*. 2004, Hvidsten *et al*. 2009). Other studies have found that the time of sea entry coincides with a sea water temperature above 8 °C, a temperature "optimal" for sea

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entry as feeding conditions and salinity tolerance are improved above this temperature (Sigholt and Finstad 1990, Hvidsten *et al*. 1998). Obviously, the smolt cannot detect the temperature in the sea while still in the river and therefore other environmental cues, must be governing the timing of migration. Among these cues, temperature and discharge are the ones most commonly considered as being triggers for downstream migration, but lunar cycle and photoperiod have also been reported to regulate the initiation of smoltification (Grau *et al*. 1982, Jonsson and Ruud-Hansen 1985, Jonsson 1991, Hvidsten *et al*. 1995, Hembrel *et al*. 2001). The understanding of how different environmental cues trigger downstream migration is of great importance. Many streams and rivers have been disturbed by anthropogenic changes such as weirs and dams altering migratory routes (Poff *et al*. 1997), hence it is of utmost importance to study the effects of these cues on downstream migration in order to maintain sustainable fish stocks. Manmade dams have been observed to affect survival and speed during downstream migration (Jepsen *et al*. 1998, Olsson *et al*. 2001). Change in climate may also affect downstream migration as precipitation directly influences temperature and water flow in the stream, affecting swimming speed and turbidity. However, there is no conclusive understanding of how the different environmental cues initiate downstream migration.

In this study, we investigated the downstream migration of brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) smolts in the Himleån, a river on the west coast of Sweden, during two consecutive spring seasons (2011 and 2012), with the aim of investigating how different environmental factors affect the downstream migration. To our knowledge this has previously not been done in Sweden. Another aim was to investigate if electrofishing could produce reliable estimates of smolt numbers by comparing the electrofishing data with the actual number of smolts caught in a smolt trap. Estimating the smolt numbers in a river normally requires some kind of a smolt trap, but this is expensive due to high costs of the construction and maintenance of the trap. Therefore, smolt production has generally been estimated from the number of pre-smolts caught in autumn using electrofish-

ing (Bohlin 1981). Few peer-reviewed articles provide information on how to estimate salmonid smolt production from electrofishing data, although such production estimates are often reported to HELCOM (Helsinki Commission — Baltic marine environment protection commission, e.g. HELCOM 2011). Here, we compared the estimated smolt production obtained from the national model used within HELCOM with the estimates from the smolt trap.

Material and methods

The study was conducted in the Himleån, a river situated on the west coast of Sweden (57°N, 12°E). The river flows 38 km from its source (76.7 m a.s.l.) to an estuary before draining into the sea (Fig. 1). The water discharge averaged 2.25 m^3 s^{-1} (min 0.72 m^3 s^{-1}; max 7.13 m^3 s^{-1}) during the study period and the water temperature ranged from 2–4 °C in the beginning of the study period to 13–16 °C towards its end.

A smolt trap (*see* Fig. 1) was used to capture the fish. In 2011, the trap consisted of a wooden box (length × width × height: 174 × 152 × 110 cm) covered in a steel mesh (0.9 cm mesh size) placed approximately in the middle of the stream 2 km upstream of the estuary. Two steel racks were spread from the trap to each side of the river in order to lead the smolt into the trap box. In front of the box a 100 × 70 cm entrance hole was fixed through which the smolts could enter. Once a smolt had entered the box, it followed the current down into a side compartment (indicated with '2' in the box diagram in Fig. 1) where it became trapped. When the trap was emptied a door was placed in front of the entrance hole, to prevent smolts from escaping.

In 2012, a smolt trap was custom-built for the stream, using a similar design as that of the trap used in 2011 (Fig. 1). A large aluminium box (length × width × height length: 300 × 170 × 100 cm), covered in a steel mesh (0.9 cm mesh size) was placed close to the river bank.

During days with very high flows, the trap was out of order due to rapidly increasing water flow and flooding of the trap. Consequently the numbers of migrating smolts had to be estimated. The estimation was done graphically from a
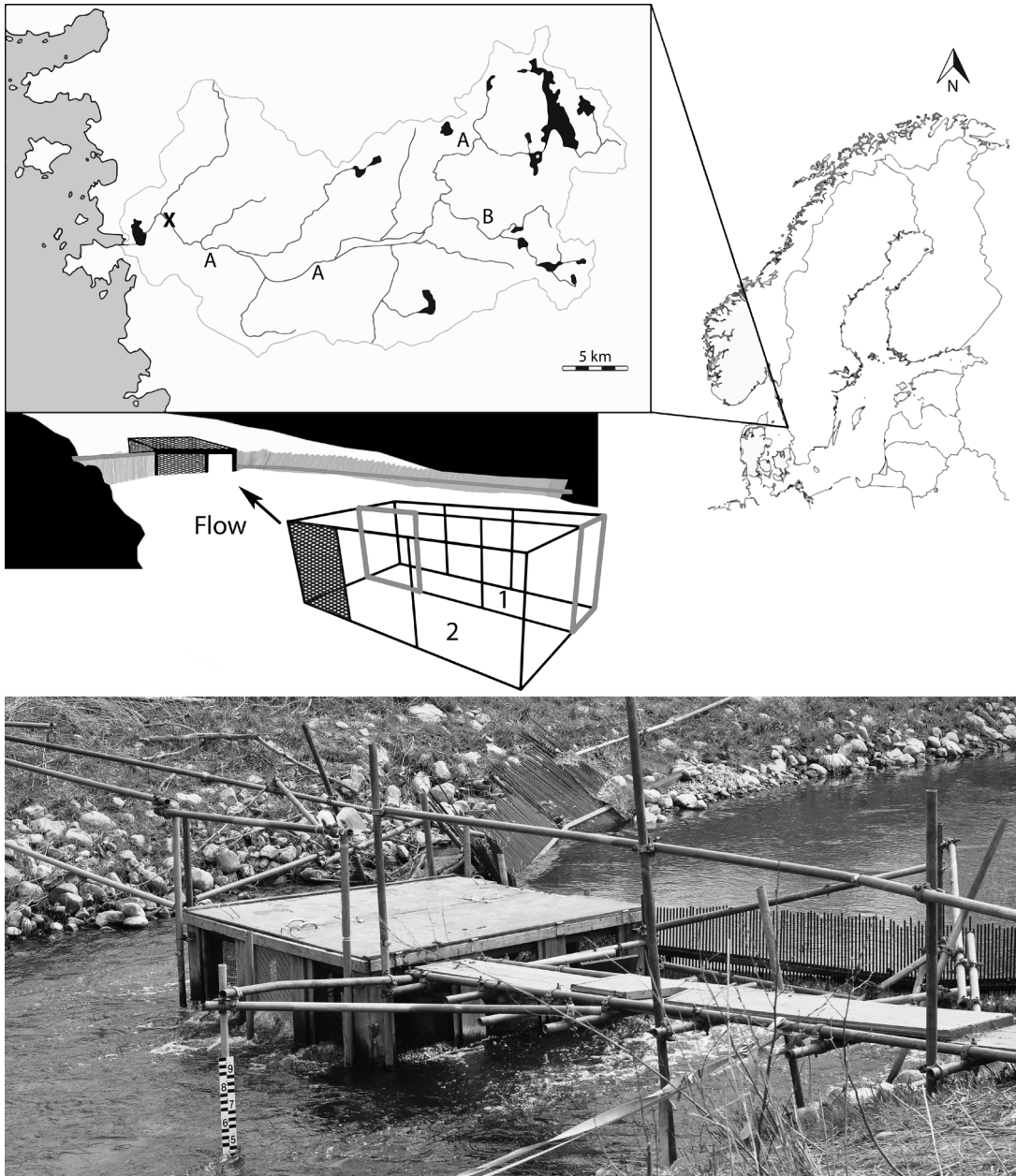
Fig. 1. Map showing the Himleån (A), its main tributary Stenån (B), the smolt-trap position (X). The diagram shows the trap in the river (see also the photograph below), and the trap box [gray lines indicate closable openings in the trap, (1) the entrance compartment and (2) the side compartment].

loess line over number of smolts and days, set to a degree of smoothing so that the line passed through as many points as possible. To assess the number of daytime and nighttime migrants, the trap was emptied twice a day (at 8:00 a.m. and 5:00 p.m.) Temperature and discharge were measured daily prior to emptying of the trap and the water was classified as turbid or clear. The photoperiod (light:dark) during the study period ranged from 12:12 hours in March to 18:6 hours in June. The trap was operated between 16 March and 20 May 2011, and between 16 March

and 15 June in 2012. All captured fish were classified to species (a total of 14 species) and then released downstream of the trap. In order to see how the degree of smoltification varied throughout the period, smolts were examined for smoltification status and classified as follows: fully smoltified (S1), two slightly visual parr marks (S2), and three clearly visual parr marks (S3).

The measured environmental factors (water temperature, discharge, photoperiod and lunar cycle) were tested for normality, collinearity, heterogeneity of variance and outliers using the protocol given in Zuur *et al*. (2010). For both years collinearity was detected among all the examined factors. Therefore, discharge and temperature were the only factors included in the models as these are considered the most important factors governing the initiation of downstream migration of smolts.

Due to the large variation in environmental conditions between the years, we decided to model each year independently.

The distribution of the response variables (number of smolts of trout and salmon) was negative binominal (zero inflation), and due to this generalized additive models (GAMs) where used to model the response variables against temperature and discharge. The *gam* function of the R package *mgcv* was used for calculation (R Development Core Team 2008, Wood 2011).

Models were fitted to determine the relationship between the number of smolts caught in the trap and water temperature and discharge. In 2012 the collinearity between temperature and discharge was avoided in the model by using the residuals obtained from a regression analysis between temperature and photoperiod

$$Y = \alpha + \beta + f(\delta) + f(\theta) + \varepsilon$$

where Y is the number of smolts, δ is the discharge (m³ s⁻¹), θ the residual temperature and ε the estimated error of the model. This was not applicable to data from 2011 as collinearity was still present even when these residuals were used. Therefore, two models were used; one with temperature: $Y = \alpha + \beta + f(\tau) + \varepsilon$ [where τ is the temperature (°C)], and one with discharge: $Y = \alpha + \beta + f(\delta) + \varepsilon$ [where θ is the discharge (m³ s⁻¹)], for each of the species, and these models were

then tested against each other using model selection criteria (AIC).

The effect of discharge during turbid and clear conditions was analysed using a Kruskal-Wallis test. The difference between numbers of smolts caught during turbid and clear conditions was analysed using a χ^2-test.

Smolt production estimates were calculated using electrofishing data on abundance, area of available stream habitat, the winter survival of 1+ trout parr and migration mortality. On the Swedish west coast, the majority of trout smolts are two years old (Dellefors and Faremo 1988, Metcalfe and Thorpe 1990). Of 2579 analysed salmon spawners during 1993–2012 the average smolt age was 2.3 years (Degerman *et al*. 2013). The smolt production in streams on the Swedish west coast has long been predicted as: 0.30 × abundance of 1+ trout parr (Bohlin *et al*. 1989). In an attempt to improve the previous smolt production model, migration mortality has been added and is often set to 0%–12% per km in running sections of a stream depending on habitat quality and flow characteristics (Nilsson *et al*. 2010). In this study, the cumulative migration mortalities (calculated as: $1 - e^{(-0.03d)}$, where d is the distance between electrofishing localities) were: 27% in the Himleån (10 km), 39% in the Stensån (16 km) tributary and 27% for other tributaries (10 km). The parr production habitats, i.e. suitable areas for parr with respect to substrate, depth and current velocity, were mapped by the Regional fisheries agency according to the method used for all salmonid streams on the Swedish west coast. The available parr production habitat was six hectares in the Himleån, one hectare in the tributary Stensån and one hectare in the smaller tributaries counted together. The 1+ salmon and trout parr densities were calculated as the average of all electrofishing occasions in 2007–2012. Electrofishing was carried out by wading using a bank-based generator and operated by a crew of two using a single, hand-held anode. The electrofishing apparatus used were of the national brand LUGAB, using non-pulsed DC of 600 V. Sampling was performed from August to mid-September, according to the national standards. The sampling effort, i.e. the number of successive removals, varied between one and three. Population densities of different
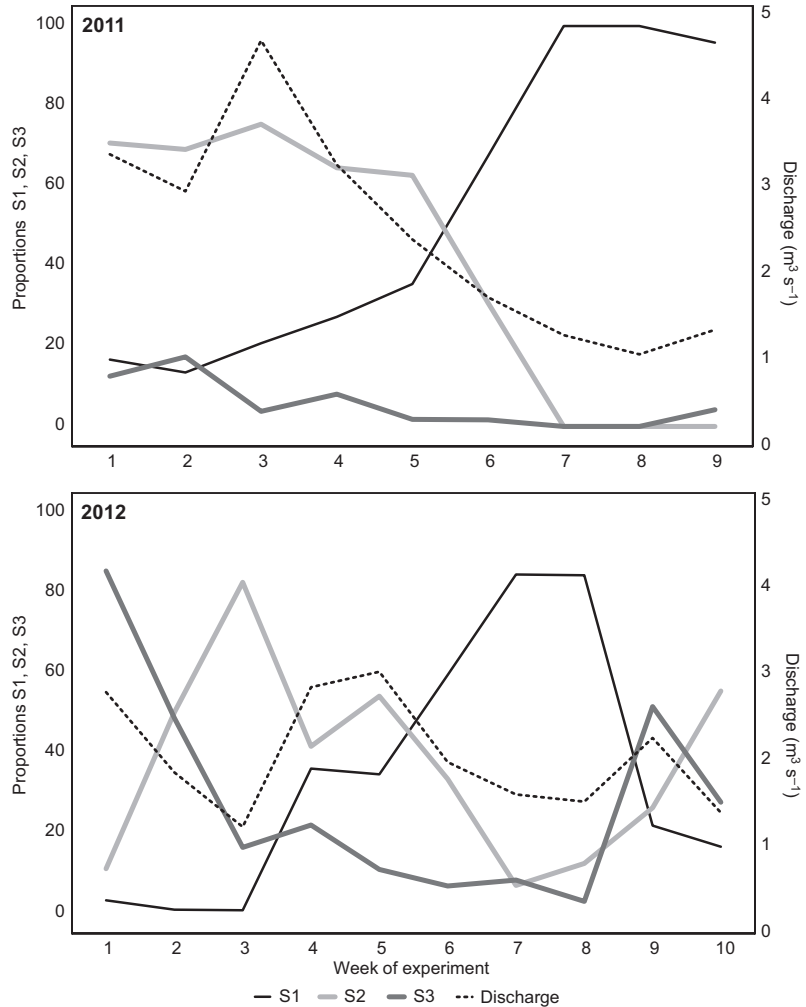
Fig. 2. Weekly proportions of migrating brown trout and Atlantic salmon smolts (S1: fully smolted, S2: slightly visible parr marks, S3: clearly visible parr marks) and discharge.

species were calculated according to Bohlin *et al*. (1989) when electrofishing was performed with successive removals. If only one removal was made (5.8% of occasions), densities were calculated from the average catch efficiency of the given species and age-class in the river.

Results

The downstream migration of brown trout and salmon began in mid-March and ended in the beginning of June. All salmonid fishes caught in the trap had already started to smolt or were already fully smolted and the degree of smoltification was similar between the two years.

In 2011, a clear pattern in smoltification (both salmon and trout) status was observed, i.e., a shift from a majority of fish classified as S3 and S2 in the beginning of the season, to a majority of S1 fish at end of the season (Fig. 2). In 2012, this pattern was not detectable towards the end of the season, due to an increase in discharge (Fig. 2). Due to a high discharge levels, the traps were out of order during three days in 2011 and during seven days in 2012. The numbers of brown trout and Atlantic salmon smolts passing the traps were therefore estimated at 3275 and 3696, respectively, in 2011; and 697 and 2995, respectively, in 2012. The numbers of captured smolts were 3165 trout and 691 salmon in 2011, and 2681 trout and 2200 salmon in 2012. In
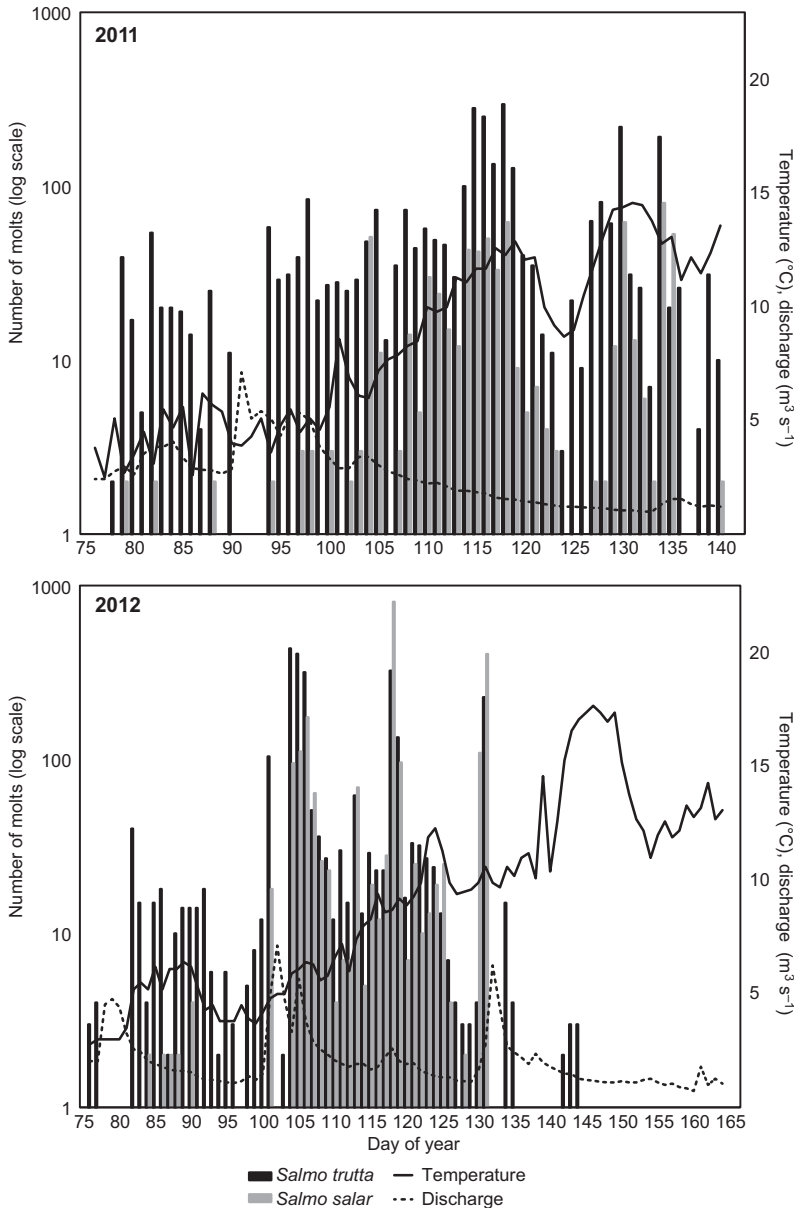
Fig. 3. Numbers of downstream migrating smolts of brown trout and Atlantic salmon, discharge and temperature, during the migration season.

2012, the peak of migration of both brown trout and salmon coincided with increases in discharge in the river (GAM: Trout: $p < 0.001$, estimated degrees of freedom EDF for model terms: discharge 8.92, residual temperature 2.67; deviance explained = 68.8%, $n = 89$; Salmon: $p < 0.001$, EDF: discharge 8.91, residual temperature 8.7; deviance explained = 70.4%, $n = 89$) (Fig. 3). However in 2011, the peak of migration coincided with increased temperature (GAM: Trout: $p < 0.001$, EDF: temperature 2.41; deviance

explained = 18.1%, $n = 65$. Salmon: $p = 0.001$, EDF: temperature 7.02, deviance explained = 40.9%, $n = 65$), and the two main peaks occurred slightly after the temperature increased above 10 °C (Fig. 3). The AIC indicated that the preferred model for 2011 was the one containing temperature (AIC 395.3 for temperature compared to 415.9 for discharge). Increased water discharge was measured approximately eight hours after rainfall. This increase in discharge also turned the water turbid (Kruskal-Wallis test:
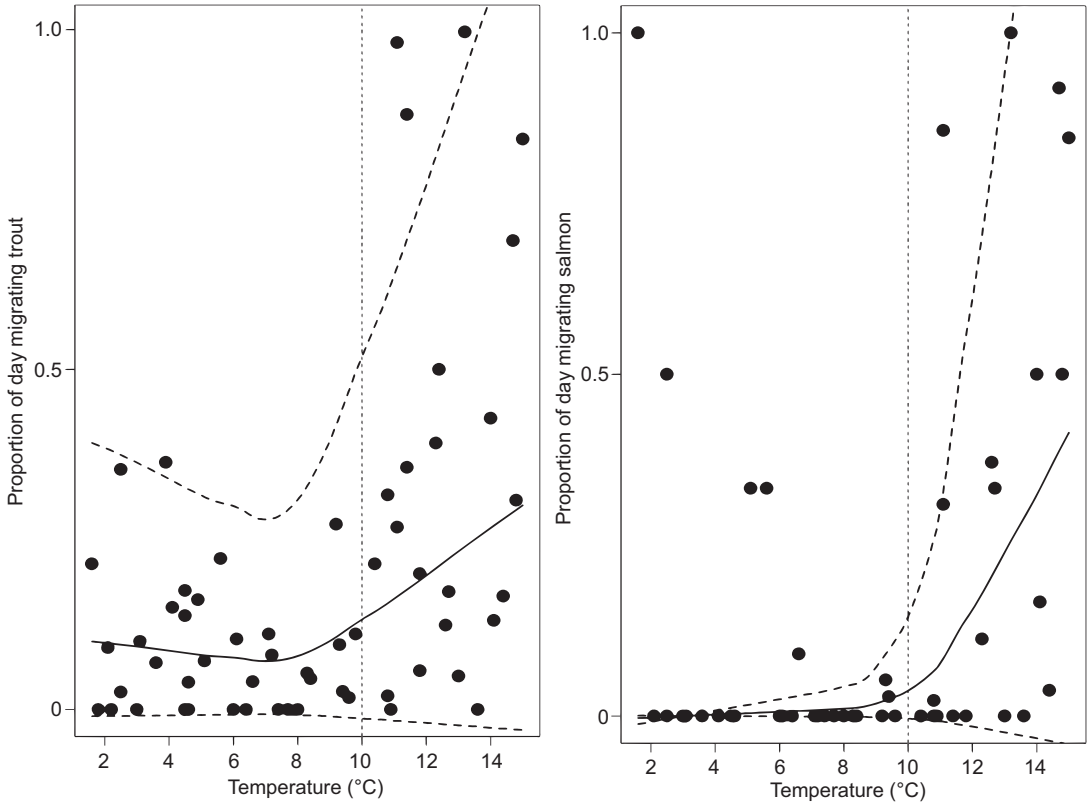
Fig. 4. Proportions of brown trout and Atlantic salmon smolts migrating during daytime plotted against temperature (2011) with a fitted loess line with standard error (dotted lines). Vertical dotted lines indicate water temperature of 10 °C.

$\chi^2 = 38.238$, $p < 0.001$, $n = 154$). The ratios between clear and turbid water over the period were 51:14 and 69:20, in 2011 and 2012, respectively. There were 21 days with precipitation in 2011 (total rainfall = 63.3 mm) and 32 in 2012 (total rainfall = 158.8 mm). The proportion of smolts migrating during turbid water conditions varied between the two years, with significantly more smolts migrating in turbid than clear water in 2012 (3664 *vs*. 1220; χ^2-test: 42.034, $p < 0.01$), whereas no such pattern was observed in 2011 (448 *vs*. 3567; χ^2-test: 0.605, $p = 0.44$). An increase in discharge also affected to some degree the water temperature in the river (linear regression: $r^2 = 0.376$ $p < 0.001$, $n = 154$).

In 2011, migrants were nocturnal early in the season but when the temperature rose above 10 °C the smolts became diurnal (Fig. 4). In 2012 this pattern was observed only in salmon, whereas trout showed no such pattern.

During both seasons, smolts were observed schooling in size-matched, mixed-species shoals, consisting of roach, salmon and trout. This observation was made upstream of the trap in clear-water conditions.

The average densities (mean ± SD) of 1+ trout and salmon parrs per 100 m² in the Himleån ($n = 29$ fishing occasions at 13 different sites) were 10.0 ± 8.8 and 15.3 ± 17.6, respectively. In the tributary Stenån ($n = 22$ occasions at 7 sites) the corresponding values were 10.2 ± 8.4 and 9.6 ± 13.7. In the smaller tributaries ($n = 17$ occasions at 6 sites) the average densities per 100 m² of the species were 120 ± 87 and 1.8 ± 5.0. If the expected survival from parr to smolt is 30% and taking into consideration different in-stream mortalities, we estimated that 4100 trout and 2200 salmon smolts reached the trap. These figures were 18% and 19% higher than the numbers of smolts trapped in 2011 and 2012.

Discussion

In this study, we found that both water discharge and temperature influenced the downstream migration of salmon and trout with a peak migration at temperatures and discharge above 5 °C and 1 m³ s⁻¹, respectively, which also is consistent with the findings by Hvidsten *et al.* (1995). However, previous studies have also found photoperiod to be an important factor for both species (McCormick *et al.* 1987, Björnsson *et al.* 2011), probably acting more as a key environmental trigger for smoltification (Björnsson *et al.* 2011). Lunar cycle has also been found to have an effect on the smolts, most likely as a trigger for smoltification by affecting the level of thyroxine (Grau *et al.* 1982).

As compared with photoperiod and lunar cycle, discharge and temperature are more likely to trigger migration if salmonids are physiologically and morphologically prepared (smoltified). Increased water turbidity during intensified water flow may provide smolts with greater protection from visual predators, e.g. cormorants and gulls (Gregory and Levings 1998). In our study, in 2012 smolts tended to migrate during periods of high discharge in highly turbid water. However, during 2011 due to low amount of precipitation resulting in low discharge and low water turbidity, smolts were forced to migrate in greater numbers in clear-water conditions. An increase in discharge also makes the downward migration less energetically costly (Jonsson 1991).

As a consequence of low precipitation in 2011, smolts remained in the river even when the temperature reached 10 °C. At this temperature a shift from a nocturnal to a diurnal migration pattern was observed by us and in other studies (Thorpe *et al.* 1994, Pirhonen *et al.* 1998, Ibbotson *et al.* 2006). This shift could be explained by an increased escape response as the water temperature increases (Rikardsen *et al.* 2004, Hvidsten *et al.* 2009).

Solomon (1978) and Jonsson (1991) found threshold temperatures that initiated migration, whereas others found merely a general effect of temperature on the timing of migration (White 1939, Fried *et al.* 1978, Jonsson and Ruud-Hansen 1985, Whalen *et al.* 1999). In this study, no threshold temperature for the initiation of migration was found but a general effect (a shift from nocturnal to diel migration at 10 °C) only was observed. This may support the notion that temperature affects the downstream migration in different ways in different locations probably due to local genetic adaptations (Antonsson and Gudjonsson 2002), or as response to spatial and temporal environmental variations (Jonsson and Ruud-Hansen 1985, Hembrel *et al.* 2001).

Smolts were also found to form schools (Hvidsten *et al.* 1995, Davidsen *et al.* 2005, Stewart *et al.* 2006). However only one study reported mixed shoals consisting of both trout and salmon (Jonsson and Jonsson 2009). To our knowledge, we were the first to observe smolts of salmon and trout schooling with other species such as roach. This mixing of species during downstream migration is likely to increase protection from predators, as predators usually attack the more easily caught prey (Vinyard 1980). But given that the roach is not a diadromous species these shoals will probably break up as the fishes reach the estuary (Chapman *et al.* 2011), and only the salmon and trout are likely to follow each other into the sea.

The smolt production data derived from the nationally used model based on electrofishing data gave 18%–19% higher estimates as compared with the results obtained from the smolt trap. The cause of this may be due to several factors: the selection of fishing sites, the fixed estimate of 30% parr becoming smolt, the fixed value for migration loss, or the result of an underestimation of the number of captured smolts in the trap. If habitats more suitable for trout parr are overrepresented, this will lead to an overestimation of parr densities in the river. This is probably the case here, because the selection of fishing sites was done in order to study salmonid recruitment, which lead to selection of sites that where high quality salmonid habitats. However, our results show that it may be possible to improve smolt production estimates, and investigate variations in smolt numbers over the years using electrofishing data. In order to do this a comprehensive habitat description and improvement of available models (Milner *et al.* 1998) would be required and sampling of all habitat classes will have to be performed. Also migration loss and the proportion of 1+ trout parr

becoming smolt needs to be further validated.

In conclusion, this study presents evidence that both temperature and discharge can trigger the downstream migration of salmonids, and that these factors probably work in combination. Depending on the level of precipitation the relative importance of discharge and temperature as a trigger may, as in this study, differ between years. The model for estimating smolt production worked although the production of smolts as compared with the catches from the trap was overestimated. This indicates uncertainties in the model which need to be considered in future studies. However, our results indicate that data obtained from electrofishing can be used as an estimate of smolt production, which could be a useful and cost efficient tool for stream management.

References

Antonsson T. & Gudjonsson S. 2002. Variability in timing and characteristics of Atlantic salmon smolt in Icelandic rivers. *Transactions of the American Fisheries Society* 131: 643–655.

Björnsson B.T., Stefansson S.O. & McCormick S.D. 2011. Environmental endocrinology of salmon smoltification. *General and Comparative Endocrinology* 170: 290–298.

Bohlin T. 1981. Methods of estimating total stock, smolt output and survival of salmonids using electrofishing. *Rep. Inst. Freshw. Res. Drottningholm* 59: 5–14.

Bohlin T., Hamrin S., Heggberget T.G., Rasmussen G. & Saltveit S.J. 1989. Electrofishing — theory and practice with special emphasis on salmonids. *Hydrobiologia* 173: 9–43.

Chapman B.B., Hulthen K., Blomqvist D.R., Hansson L.A., Nilsson J.A., Brodersen J., Nilsson P.A., Skov C. & Bronmark C. 2011. To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters* 14: 871–876.

Davidsen J., Svenning M.A., Orell P., Yoccoz N., Dempson J.B., Niemelä E., Klemetsen A., Lamberg A. & Erkinaro J. 2005. Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana. *Fisheries Research* 74: 210–222.

Degerman E., Persson J., Sers B. & Östergren J. 2013. *Fisheries, management and status of Atlantic salmon stocks in Sweden. 2012*. National report for 2012, Working Group on North Atlantic Salmon, Paper 2013/23.

Dellefors C. & Faremo U. 1988. Early sexual maturation in males of wild sea trout, *Salmo trutta* L., inhibits smoltification. *Journal of Fish Biology* 33: 741–749.

Forsman L. & Virtanen E. 1989. Responses of juvenile and sexually mature two-summer-old salmon (*Salmo salar* L.) to prolonged swimming. *Aquaculture* 82: 245–255.

Fried S.M., McCleave J.D. & LaBar G.W. 1978. Seaward migration of hatchery-reared Atlantic salmon, *Salmo salar*, smolts in the Penobscot River Estuary, Maine: riverine movements. *Journal of the Fisheries Research Board of Canada* 35: 76–87.

Grau E.G., Specker J.L., Nishioka R.S. & Bern H.A. 1982. Factors determining the occurrence of the surge in thyroid activity in salmon during smoltification. *Aquaculture* 28: 49–57.

Gregory R.S. & Levings C.D. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. *Transactions of the American Fisheries Society* 127: 275–285.

Hembrel B., Arnekleiv J.V. & L'Abée-Lund J.H. 2001. Effects of water discharge and temperature on the seaward migration of anadromous brown trout, *Salmo trutta*, smolts. *Ecology of Freshwater Fish* 10: 61–64.

Hvidsten N.A., Heggberget T.G. & Jensen A.J. 1998. Sea water temperatures at Atlantic salmon smolt enterance entrance. *Nordic Journal of Freshwater Research* 74: 79–86.

Hvidsten N.A., Jensen A.J., Vivas H., Bakke O. & Heggberget T.G. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. *Nordic Journal of Freshwater Research* 70: 38–48.

Hvidsten N.A., Jensen A.J., Rikardsen A.H., Finstad B., Aure J., Stefansson S., Fiske P. & Johnsen B.O. 2009. Influence of sea temperature and initial marine feeding on survival of Atlantic salmon *Salmo salar* post-smolts from the rivers Orkla and Hals, Norway. *Journal of Fish Biology* 74: 1532–1548.

Ibbotson A.T., Beaumont W.R.C., Pinder A., Welton S. & Ladle M. 2006. Diel migration patterns of Atlantic salmon smolts with particular reference to the absence of crepuscular migration. *Ecology of Freshwater Fish* 15: 544–551.

Jepsen N., Aarestrup K., Okland F. & Rasmussen G. 1998. Survival of radio-tagged Atlantic salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) smolts passing a reservoir during seaward migration. *Hydrobiologia* 372: 347–353.

Jonsson B. & Ruud-Hansen J. 1985. Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 593–595.

Jonsson B. & Jonsson N. 2009. Migratory timing, marine

survival and growth of anadromous brown trout Salmo trutta in the River Imsa, Norway. *Journal of Fish Biology* 74: 621–638.

Jonsson N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research* 66: 20–35.

McCormick S.D., Saunders R.L., Henderson E.B. & Harmon P.R. 1987. Photoperiod control of parr-smolt transformation in Atlantic salmon (*Salmo salar*) — changes in salinity tolerance, gill Na$^+$,K$^+$-atpase activity, and plasma thyroid-hormones. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 1462–1468.

Metcalfe N.B. & Thorpe J.E. 1990. Determinants of geographical variation in the age of seaward migrating salmon, *Salmo salar*. *Journal of Animal Ecology* 59: 135–145.

Milner N., Wyatt R. & Broad K. 1998. HABSCORE — applications and future developments of related habitat models. *Aquatic Conservation: Marine and Freshwater Ecosystems* 8: 633–644.

Nilsson N., Degerman E., Andersson H.C. & Halldén A. 2010. Uppdatering av modell för beräkning av örings-moltproduktion. *Fisk i Vattendrag och stora sjöar* 2010:07: 1644.

Olsson I.C., Greenberg L.A. & Eklov A.G. 2001. Effect of an artificial pond on migrating brown trout smolts. *North American Journal of Fisheries Management* 21: 498–506.

Pirhonen J., Forsman L., Soivio A. & Thorpe J. 1998. Movements of hatchery reared *Salmo trutta* during the smolting period, under experimental conditions. *Aquaculture* 168: 27–40.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. 1997. The natural flow regime. *Bioscience* 47: 769–784.

Rikardsen A.H., Thorpe J.E. & Dempson J.B. 2004. Modelling the life-history variation of Arctic charr. *Ecology of Freshwater Fish* 13: 305–311.

Sigholt T. & Finstad B. 1990. Effect of low-temperature on seawater tolerance in Atlantic salmon (*Salmo salar*) smolts. *Aquaculture* 84: 167–172.

Solomon D.J. 1978. Some observations on salmon smolt migration in a chalkstream. *Journal of Fish Biology* 12: 571–574.

Stewart D.C., Middlemas S.J. & Youngson A.F. 2006. Population structuring in Atlantic salmon (*Salmo salar*): evidence of genetic influence on the timing of smolt migration in sub-catchment stocks. *Ecology of Freshwater Fish* 15: 552–558.

R Development Core Team 2008. *R: a language and environment for statistical computing*. R Foundation Statistical Computing, Vienna, Austria.

Thorpe J.E., Metcalfe N.B. & Fraser N.H.C. 1994. Temperature dependence of switch between nocturnal and diurnal smolt migration in Atlantic salmon. In: MacKinlay D.D. (ed.), *High performance fish: Proceedings of an International Fish Physiology Symposium held at the University of British Columbia in Vancouver, Canada, July 16–21*, Fish Physiology Association, Vancouver, pp. 83–86.

Whalen K.G., Parrish D.L. & McCormick S.D. 1999. Migration timing of Atlantic salmon smolts relative to environmental and physiological factors. *Transactions of the American Fisheries Society* 128: 289–301.

White H.C. 1939. Factors influencing descent of Atlantic salmon smolts. *Journal of the Fisheries Research Board of Canada* 4b: 323–326.

Vinyard G.L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibhosus*) predation. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 2294–2299.

Virtanen E. & Forsman L. 1987. Physiological responses to continuous swimming in wild salmon (*Salmo salar* L.) parr and smolt. *Fish Physiology and Biochemistry* 4: 157–163.

Wood S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B* 73: 3–36.

Zuur A.F., Ieno E.N. & Elphick C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3–14.