

Influences of migration phenology on survival are size-dependent in juvenile Atlantic salmon (*Salmo salar*)

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Abstract: Long-distance migratory species can reduce mortality risks by synchronizing the migration event and create confusion by swamping predators with high densities. To reduce confusion, predators are known to primarily select aberrant prey. We hypothesized that at the start of their sea sojourn, particularly small and large Atlantic salmon (*Salmo salar* L., 1758) would spread the risk by also migrating at other times of the year. Based on data from the Norwegian river Imsa between 1976 and 2015, we found that juveniles, 14–19 cm in total length, started their sea sojourn during a short period between late April and early June. However, more than 20% of fish 13 cm or shorter migrated downstream between October and March, whereas 55% of fish 20 cm or longer migrated downstream between July and September. The regular-sized, spring-migrating juveniles had 2–3 times higher survival at sea than similar-sized conspecifics migrating to sea at other times of the year. The survival at sea for smaller juveniles was not improved by migration in spring relative to winter, and the survival of the largest juveniles was similar in spring and summer. Thus, the migration phenology appears adapted to survival in a high-risk environment by changing the timing according to their sizes.

Key words: anadromous fish, Atlantic salmon, migration ecology, migration timing, mortality, predator avoidance, *Salmo salar*, smolts.

Résumé : Les espèces qui migrent sur de longues distances peuvent réduire leurs risques de mortalité en synchronisant leur migration, créant ainsi la confusion chez les prédateurs en les approchant en grande densité. Il est établi que, pour réduire cette confusion, les prédateurs sélectionnent en premier lieu des proies aberrantes. Nous avons postulé que, au début de leur séjour en mer, les saumons atlantiques (*Salmo salar* L., 1758) petits ou grands, en particulier, répartissent le risque en migrant aussi à d'autres moments de l'année. Des données provenant de la rivière Imsa, en Norvège, pour la période de 1976 à 2015, ont permis de constater que les juvéniles de 14 à 19 cm de longueur totale initiaient leur séjour en mer durant une courte période entre la fin d'avril et le début de juin. Toutefois, plus de 20 % des poissons de 13 cm ou moins migraient vers l'aval entre octobre et mars, alors que 55 % des poissons de 20 cm ou plus migraient de juillet à septembre. Les juvéniles à migration printanière de taille normale présentaient un taux de survie en mer de deux à trois fois plus élevé que leurs conspécifiques de taille semblable migrant vers la mer à d'autres périodes de l'année. La migration printanière n'améliorait pas la survie en mer des juvéniles plus petits par rapport à la migration hivernale, et la survie des juvéniles plus grands était semblable au printemps et en hiver. Ainsi, la phénologie de la migration semble s'adapter à la survie dans un milieu à haut risque par la modification du moment de la migration en fonction de la taille. [Traduit par la Rédaction]

Mots-clés : poisson anadrome, saumon atlantique, écologie de la migration, moment de la migration, mortalité, évitement des prédateurs, *Salmo salar*, saumoneaux.

Introduction

Extensive migrations, undertaken by many animals, can give them access to better feeding areas (Baker 1978), and thereby improve growth and fitness (Werner and Gilliam 1984; Charnov et al. 2013; Sloat et al. 2014). However, there are costs associated with migrations, such as increased risk of predators and pathogens, and metabolic expenses (Alerstam et al. 2003; Melnychuk et al. 2007; Milner-Gulland et al. 2011). To minimize costs, migratory organisms exhibit behavioural adaptations. One such risk-reduction mechanism is to vary the timing of migration, and by that reduce exposure to or foraging efficiency of their predators (Hedenström 2008).

Atlantic salmon (*Salmo salar* L., 1758) is a long-distance migratory species. It spawns in rivers where the young grow up. At a total length of 10 cm or more, the offspring migrate to sea for feeding.

In the river Imsa, the majority of the out-migrating juveniles are 14–19 cm long and are 1–3 (2) years of age (Jonsson and Jonsson 2014). Most juvenile migrants (smolts) leave the river in spring, between April and June. Atlantic salmon in this river feed for 1–2 years in the North Atlantic Ocean, and during that time, the individual mass of the fish increases from between 10 and 100 g to between 1 and 10 kg (Jonsson et al. 2016). However, the Atlantic Ocean is a high-risk habitat, and typically, less than 10% of the out-migrating juveniles in each cohort return to spawn in the home river, while approximately 6% of the recaptures in fresh water are found in other rivers. Predation, especially during early migration, is high (Larsson 1985; Sogard 1997; Beamish et al. 2004). For instance, predation by Atlantic cod (*Gadus morhua* L., 1758) on juvenile Atlantic salmon was estimated to be about 20% of the out-migrating smolts during their first week at sea (Hvidsten and Lund 1988). Adaptations that help juvenile Atlantic salmon to

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avoid predation can be profitable for some groups of the young fish, but may not be cost effective for others. For instance, small Atlantic salmon smolts are assumed to be more vulnerable to predators than larger ones (Jonsson et al. 1994; Saloniemi et al. 2004), and Ibbotson et al. (2011) reported that small smolts migrated more at night than large smolts, when they moved from the river to feed in the ocean. As Atlantic salmon are visual feeders (Jonsson and Jonsson 2011), increased survival may in this case be balanced against reduced feeding opportunities for the small juveniles during the outmigration.

Salmonid smolts can migrate to sea during any month of the year (Cunjak et al. 1989; Jonsson and Jonsson 2009, 2014; Pinder et al. 2007; Winter et al. 2016), but the majority typically emigrate from fresh water in small schools during a short period in spring (Jonsson and Ruud-Hansen 1985; McCormick et al. 1998; Otero et al. 2014). Schooling is predator-avoidance behaviour (Pitcher and Parrish 1993; Riley et al. 2014), and synchronization of the migration decreases foraging opportunities for predators (McCormick et al. 1998; Ibbotson et al. 2006; Furey et al. 2016). Predators easily become confused when attacking more than one prey and the confusion effect is strongest when they attack many phenotypically similar individuals (Rodgers et al. 2011). Small smolts may be particularly vulnerable to predators (Dill 1983), but also other aberrant individuals are positively selected by predators (Magurran 1990; Landeau and Terborgh 1986; Rutz 2012). Thus, deviant individuals may not benefit from migrating with many similar-looking conspecifics. We tested if particularly small and large individuals migrated to sea at different times of the year than most regular-sized smolts, and investigated whether they increased their survival to adulthood by doing so. Atypical individuals should be least protected in the schools of out-migrating fish, and may benefit from migrating at another time of the year when few predators may be present, waiting for the juvenile salmon (Wood 1985, 1987; McCormick et al. 1998; Furey et al. 2015).

We hypothesized that the migration timing of young Atlantic salmon of different sizes is positively associated with the survival at sea of the respective size groups. We tested this by comparing the size distribution of seaward migrating fish with their empirical survival until returning from the ocean, 1 or 2 years later. Furthermore, we tested the “big is better” hypothesis that survival at sea increased with the size of the smolts at out-migration (Sogard 1997). We used first-time migrants only, emigrating from the river between 1976 and 2013 and returning to the home river from 1977 to 2015.

Materials and methods

The 1 km long river Imsa, located in southwestern Norway (58°50'N, 05°58'E), drains into the Høgsfjord estuary (32‰ salt). The river supports a small population of anadromous Atlantic salmon. The mean annual number of smolts is approximately 1000 individuals, but varies between 1 (14%), 2 (78%), or ≥3 (8%) years, and most fish (on average, 82% of the returning adults) attain maturity after 1 year in the ocean (grilse) (Jonsson et al. 1998). The fish spawn in the river and the young use the river as a nursery before smolting and migration into the ocean. For more details on the population structure and dynamics of Atlantic salmon in the river Imsa, see Jonsson et al. (1998) and Jonsson and Jonsson (2017).

The fish were sampled in traps situated 150 m above the river estuary. A Wolf trap (Wolf 1951; apertures 10 mm, inclination 1:10) caught all descending fish longer than approximately 10 cm, while a box trap caught all ascending fish in the river. The traps (cf. Fig. 6.5 in Jonsson and Jonsson 2011) were emptied twice a day, at 0800 and 1500, during the study period (1976–2015), except for 1994, when the traps were closed because of an experiment that was performed in the river (Fleming et al. 2000).

Total length of the salmon was measured (0.1 cm), and the downstream-moving first-time migrants were tagged with individually numbered Carlin tags (Carlin 1955) after being anaesthetized with chlorbutanol. In total, 36 833 smolts were tagged when descending to the outlet of the river.

Recapture rate was used as an index of survival (Jonsson et al. 1998) and was estimated as number of adults recaptured divided by the number of seaward-migrating young. Our survival estimates were not adjusted for any possible mortality effect of tagging. However, experimental evidence suggests that the tagging, on average, may double the expected mortality at sea and is probably the highest for small smolts (Hansen 1988). Isaksson and Bergman (1978) estimated that the mortality at sea of 9.5–14.5 cm Carlin-tagged smolts was 3 times higher than for micro-tagged smolts of corresponding length. For longer smolts, the marine mortality was 1.5 times higher for Carlin-tagged than micro-tagged smolts. Thus, Carlin tags increase the mortality even for relatively large smolts.

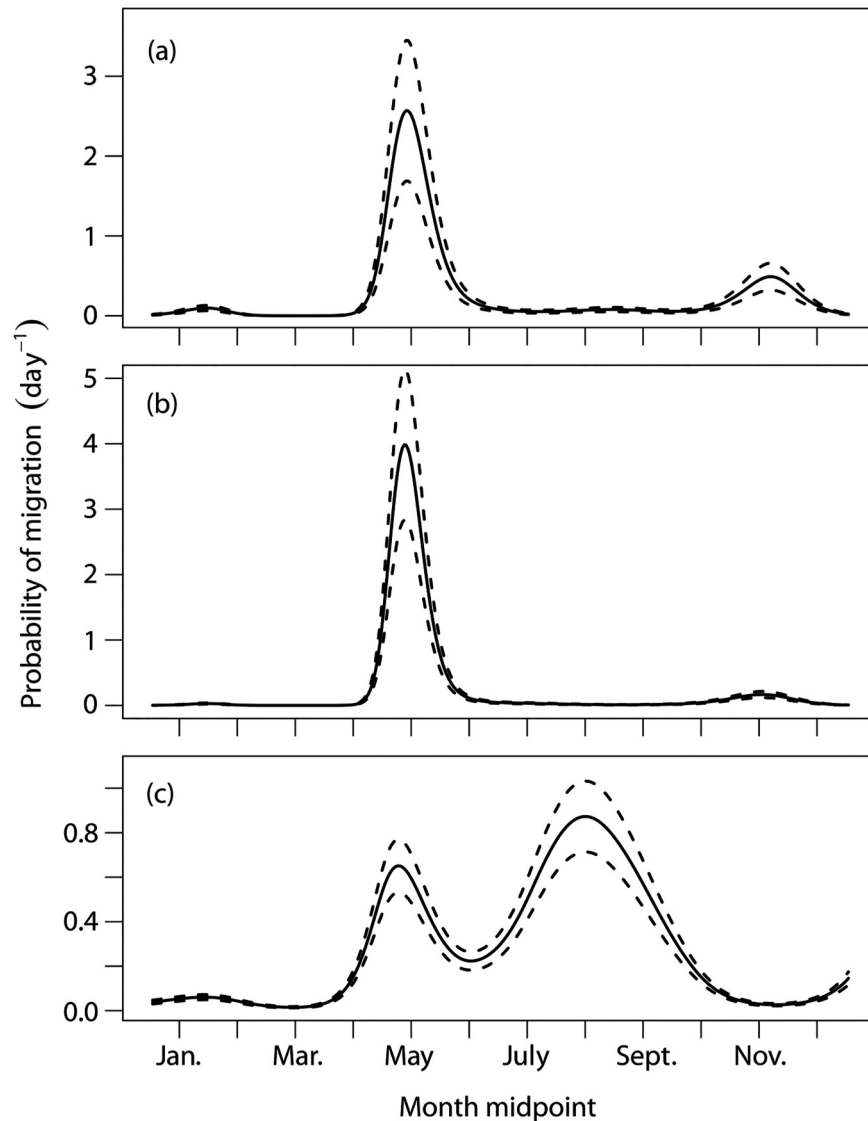
We do not know whether mortality caused by the tagging varied during the year, but it may be higher for fish tagged during summer than during the rest of the year (Strand et al. 2002). All fish were handled carefully and no fish was released before any visual effects of the anesthesia had disappeared. It was not known if fish that moved downstream passed the trap outside the smolt migration period were smolted or not. They were therefore denoted as juveniles and first-time migrants. Some of the smolts were previously mature male parr and were described in other studies (Bohlin et al. 1986; Hansen et al. 1989; review in Jonsson and Jonsson 2011).

There have been changes in marine salmon fisheries during the study period. The main changes were the closure of the long-line fishery north of the Faroe Islands (1991) and the cessation of the drift-net fishery (1989) in the Norwegian Sea (Jensen et al. 1999; Jacobsen et al. 2012). However, none of these alterations has probably influenced the present results much. Even though marine fisheries have been closed, we have seen no increase in the river catches, and the drift-net fishers reported few tagged fish only. One reason why the salmon from the river Imsa have been little affected is that the population largely consists of one-sea-winter salmon, too small in size to be targeted in these fisheries.

The relationship between the numbers of downstream-migrating juvenile Atlantic salmon and mean number of downstream migration per day was estimated for the following length groups: ≤13.9, 14.0–19.9, and ≥20.0 cm. A possible trend in downstream migration and survival in the ocean was evaluated by dividing the sample in the following size classes: <14, 14.0–15.9, 16.0–17.9 cm, 18.0–19.9, and ≥20 cm. Then, we estimated the percentage of emigrating juveniles in each length group and the proportion of adults that returned to the river Imsa for spawning from each group. Ninety-five percent confidence intervals were estimated using bootstrap methods.

The relationship between the numbers of downstream-migrating juvenile Atlantic salmon and the mean number of downstream migration per day was fitted by generalized adaptive models, i.e., quadratically penalized GLM using likelihood-type estimation. The response was taken to be Poisson, because the experiment was assumed to be an approximate Poisson process. This is an approximation because it is not clear that each trail in the analysis is independent. In particular, there was a small effect of year. We report the mean as a function of time of year, along with 95% confidence intervals of the mean. The optimal degree of smoothness was determined using cross validation (UBRE algorithm; Zuur et al. 2009). Since UBRE was employed, little further model selection (or validation) was done, but we report deviance explained and adjusted R^2 for reference. In analyzing the migration and the recapture of the adults, given their smolt length and time of migration, we computed the mean recapture rate as described in the previous paragraph. Ninety-five percent confidence intervals of

Fig. 1. Mean daily migration of juvenile Atlantic salmon (*Salmo salar*) downstream to the outlet of the Norwegian river Imsa between 1976 and 2013. (a) Juveniles shorter than 14.0 cm ($N = 2116$, $R^2_{\text{adjusted}} = 0.786$, deviance explained = 81.4%), (b) between 14.0 and 19.9 cm ($N = 32716$, $R^2_{\text{adjusted}} = 0.835$, deviance explained = 93.3%), and (c) longer or equal to 20.0 cm ($N = 2001$, $R^2_{\text{adjusted}} = 0.587$, deviance explained = 66.5%). Broken lines give the 95% confidence limits.



the mean recapture were computed by unparameterized bootstrapping on a sufficiently large bootstrap sample (10^7 bootstrap samples from roughly 10^4 observations) for each length group and migratory time interval.

Results

The chief smolt migration period was from late April to early June, when 86.1% ($N = 31\,702$) of all juveniles passed downstream of the river Imsa, compared with 13.9% ($N = 5\,131$) during the rest of the year. A second peak in migration from July through September was dominated by juveniles ≥ 20.0 cm in total length. Finally, a peak between October and March was made up largely of fish shorter than 14.0 cm and accounted for more than 20% of that size class (Figs. 1a–1c). The 95% confidence intervals are narrow and difficult to distinguish from the lines reporting the means, except for the largest size group (Fig. 1c).

The temporal out-migration pattern differed among the length groups tested (Fig. 2a). The difference was smallest between those emigrating from July through September and from October through March. Among fish 14.0–19.9 cm in total length, between 84% and

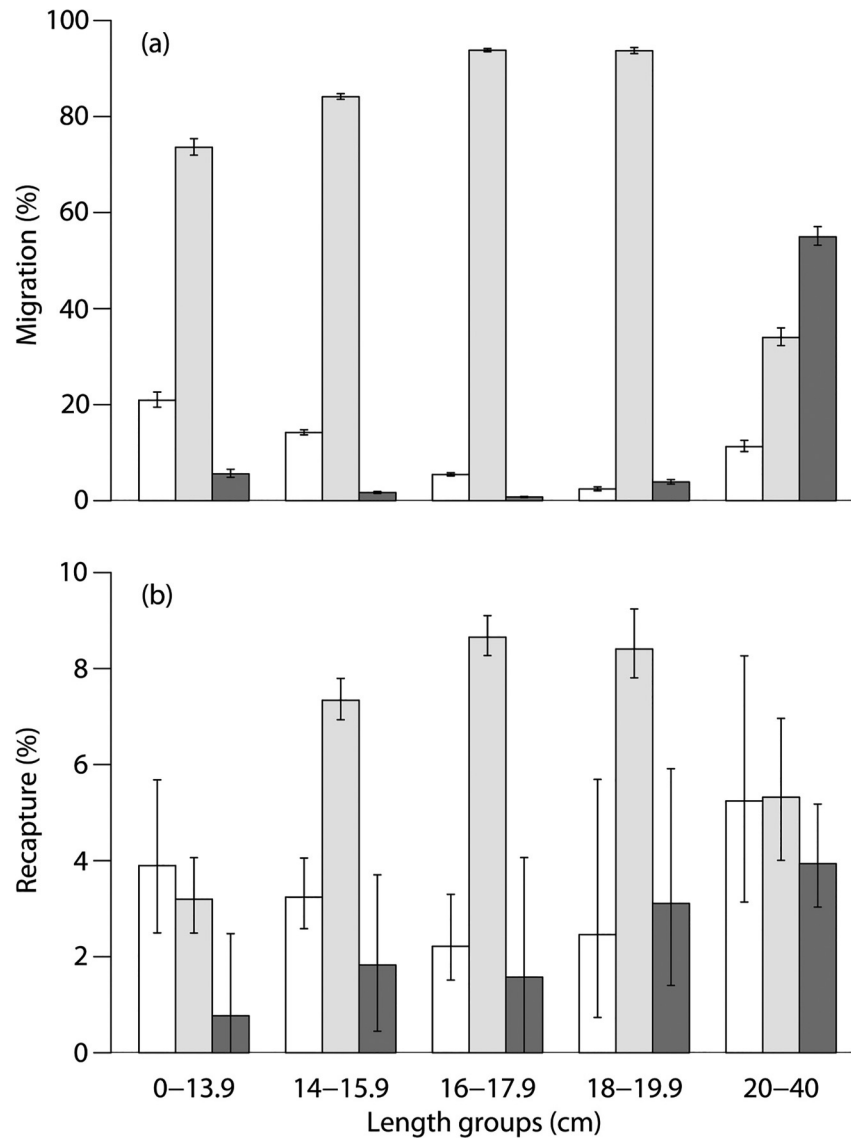
94% emigrated during April through June (Fig. 2a). Among fish shorter than 14.0 cm, just over 20% migrated downstream between October and March and approximately 5% migrated during July–September. Juveniles longer than 20 cm migrated downstream during all periods of the year.

Survival at sea and return to the river Imsa varied between those migrating during April–June and those migrating during the rest of the year for all groups from 14 to 19.9 cm (Fig. 2b). The sea survival of the smallest fish emigrating between July and September was poorer than for those emigrating from the river during the rest of the year. The sea survival of the largest emigrating fish was similar for all periods tested. For fish emigrating between April and June, the survival was between 3.2% and 8.6% for the length groups, compared with between 2.2% and 4.2% during the rest of the year. The survival advantage for the smallest and largest fish emigrating in spring was lower than for those between 14.0 and 19.9 cm.

Discussion

The present results, based on a long-term data set from a Norwegian salmon river, did not support the “big is better” hypothesis

Fig. 2. (a) Percent seaward-migrating juvenile Atlantic salmon (*Salmo salar*) in the Norwegian river Imsa between October and March (white bars), between April and June (light grey bars), and between July and September (dark grey bars), from 1976 to 2013. (b) Recapture at return to the river (percent out-migrating fish as an index of survival) of adult Atlantic salmon from 1977 to 2015. Ninety-five percent bootstrap confidence intervals of the means are included.



that return to the river was highest for fish that were largest at out-migration. Instead, return to the river was best for medium-sized juveniles, i.e., with total body length between 14 and 19.9 cm at the time when they reached the trap near the river mouth. Longer juveniles migrated to a large extent during summer from July through September, and their return to the river as adults was similar, independent of time of out-migration. The tagging may have reduced the survival of fish migrating in summer, because of the higher temperature (cf. Jonsson et al. 2016). However, this cannot explain the lower survival of large smolts compared with regular-sized smolts in spring, when the water temperature was low.

There was support for the second hypothesis that there were associations between time of seaward migration and survival at sea. For medium-sized migrants, which largely migrated in spring, survival was much higher than for similar-sized fish migrating downstream at other times of the year. This is in line with the predator-swamping hypothesis (Krebs and Davis 1984). Smaller and larger spring-migrating fish survived less well, and the asyn-

chronous migration timing of different-sized fish may be an adaptation to decrease predation risk. Atlantic salmon are known to leave fresh water in small schools (Hansen and Jonsson 1985; Riley et al. 2014); thus, decrease the probability of being killed by a predator, as reported for sockeye salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) (Furey et al. 2016). A strategy of predator swamping in spring may be less viable, especially for the largest migrants.

There are observations of early migration of large smolts from other systems (Nordeng 1977; Juttila and Jokikokko 2008). However, the present study is the first to show that large juvenile Atlantic salmon can migrate to sea in summer, after the end of the regular smolt migration period. Furthermore, more than 20% of the smallest smolt group migrated downstream to the river estuary between October and March. The sea survival and return to the river of this group was low. This may mean that they do not have the same predator-buffering benefit because they stand out compared with the norm, but may be also influenced by

poorer survival at sea because of the tagging (Isaksson and Bergman 1978).

Juvenile anadromous salmonids can move downstream towards the sea in the autumn, as also reported from other rivers in Europe (Pinder et al. 2007; Taal et al. 2014; Winter et al. 2016) and North America (Cunjak et al. 1989; Bennett et al. 2011). In coho salmon (*Oncorhynchus kisutch* (Walbaum, 1792)), Bennett et al. (2011) reported that autumn migrants were shorter than those emigrating to sea in spring. In brown trout (*Salmo trutta* L., 1758), on the other hand, the relationship appears reversed because the juvenile autumn migrants were larger than the corresponding spring migrants (Holmes et al. 2014), and older and larger individuals migrated earlier in the spring than smaller and younger conspecifics (Jonsson 1985; Jonsson and Jonsson 2009). Similarly, in Arctic grayling (*Thymallus arcticus* (Pallas, 1776)), a freshwater fish using seasonally available habitats within annual migratory circuits, larger and fatter fish migrated earlier in summer than smaller and leaner conspecifics. Heim et al. (2016) interpreted this in the context of size and energetic state-specific risks of overwinter starvation and mortality, which may influence individuals at greater risk to extend summer foraging in a risky, yet prey rich, habitat.

We did not investigate how the timing of the out-migration relates to the physiology of the fish, assumed to be important for their survival in seawater (Whalen et al. 1999). However, Atlantic salmon entering the downstream trap in the river Imsa between July and September appeared to migrate directly to sea, as indicated by the increased spacing between the growth rings (sclerites) of their scales (cf. Jonsson and Jonsson 2014). This may be possible because osmotic problems for salmonids in seawater decrease with both increasing water temperature and body size of the fish (Hoar 1988; McCormick 2013). But the majority of those migrating downstream to the outlet between October and March may have spent the winter in the estuary and migrated into the ocean during the subsequent spring, as we have found no indication of increased growth before this time of the year (Jonsson and Jonsson 2014). Atlantic salmon migrating to sea in winter appear unable to learn the migratory route and find their way back to the home river, as found in experimental releases of Atlantic salmon at sea outside the river Imsa (Hansen and Jonsson 1989). Atlantic salmon emigrating to the river estuary in late autumn may be poorly adapted to regulate ions in full seawater, as reported by Riley et al. (2008). Thus, there is reason to believe that fish migrating downstream between October and March remained in the river estuary until the subsequent spring, when they start the sea sojourn, as reflected by their scales (Jonsson and Jonsson 2014). If so, then the survival estimates of these fish are reduced by mortality occurring before they migrate into the ocean.

Smolting in salmon is a circannual event, and at the broadest scale, timing of the seaward migration is controlled by a heritable, endogenous, circannual rhythm synchronized by photoperiod. At a finer scale, the water temperature influences the onset of migration-activity temperature (McCormick 2013; Otero et al. 2014). However, despite the adaptive importance of timing the migration relative to the risk of predation, the mechanisms of this clock are little studied. Possibly, age of the fish may contribute to the timing of the migration if the circannual rhythm differs from 12 months. The smallest migrants are chiefly 1 year old, whereas the largest are 3 years old and a few possibly 4 years old (Jonsson et al. 2016). Jonsson et al. (1990) hypothesized such an effect of age on the timing of circannual events, but this is still little investigated in relation to smolting and seaward migration of salmon. Circannual cycles deviating from 12 months are best known from mammals and birds (Wikelski et al. 2008).

We know of no other study showing such a relationship between survival, body size, and timing of the feeding migration as found in the present salmon population. However, in sockeye salmon, Freshwater et al. (2016) suggested that delaying migration may be adaptive for small individuals if it allows them to increase

in size prior to moving offshore. Although this appears probable, growth in summer appeared of little importance for migration in the present study. Small fish migrated downstream in late autumn and winter, prior to the seaward migration in spring. It may be that they were seeking proper wintering habitats in the estuary prior to the sea migration. In birds, it is known that the size of the fat stores can influence when species, such as Garden Warblers (*Sylvia borin* (Boddaert, 1783)), leave stopover sites because the fat stores will be important for when they reach the breeding area (Goymann et al. 2010). Thus, the physiological status may affect migratory timing in many species, but traits influencing when to leave the habitat may vary according to which characters are important for survival and migratory success.

In all, the present findings support the view that time of seaward migration of different-sized salmon is adaptive and associated with the probability of surviving at sea and returning to the home river. Predation may be the main mortality factor influencing the variation. Small and large juveniles exhibited the poorest sea survival during spring and they were also most inclined to move to sea at other times of the year. This may be associated with their deviating size, making them susceptible to predation in the ocean when migrating in schools together with regular-sized smolts.

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