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

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Complete List of Authors:	Jonsson, B.; NINA Oslo, Jonsson, Marius; Universitetet i Oslo, Department of Physics Jonsson, N.; NINA Oslo
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18 **Abstract:** Influences of migration phenology on survival is size dependent in juvenile
19 Atlantic salmon (*Salmo salar*).

20 Jonsson, Bror, Jonsson, Marius, and Jonsson, Nina

21 Long-distance migratory species can reduce mortality risks by synchronizing the migration
22 event and create confusion by swamping predators with high densities. To reduce confusion,
23 predators are known to primarily select aberrant prey. We hypothesized that at the start of
24 their sea-sojourn, particularly small and large Atlantic salmon (*Salmo salar* L., 1758) would
25 spread the risk by also migrating at other times of the year. Based on data from the Norwegian
26 River Imsa 1976-2015, we found that juveniles, 14-19 cm in total length, started their sea-
27 sojourn during a short period between late April and early June. However, more than 20% of
28 the fish 13 cm or shorter migrating downstream October and March, whereas 55% of fish 20
29 cm or longer between July and September. The regular-sized, spring-migrating juveniles had
30 2-3 times higher survival at sea than similar-sized conspecifics migrating to sea at other times
31 of the year. The survival at sea for smaller juveniles was not improved by migration in spring
32 relative to winter, and the survival of the largest juveniles was similar in spring and summer.
33 Thus, the migration phenology appears adapted to survival in a high-risk environment by
34 changing the timing according to their sizes.

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

38 Introduction

39 Extensive migrations, undertaken by many animals, can give them access to better
40 feeding areas (Baker 1978), and thereby improve growth and fitness (Werner and Gilliam
41 1984; Charnov et al. 2013; Sloat et al. 2014). However, there are costs associated with
42 migrations, such as increased risk of predators and pathogens, and metabolic expenses
43 (Alerstam et al. 2003; Melnychuk et al. 2007; Milner-Gulland et al. 2011). To minimize costs,
44 migratory organisms exhibit behavioural adaptations. One such risk-reduction mechanism is
45 to vary the timing of migration, and by that reduce exposure to or foraging efficiency of their
46 predators (Hedenström 2008).

47 Atlantic salmon (*Salmo salar* L., 1758) is a long-distance migratory species. It spawns
48 in rivers where the young grow up. At a total length of 10 cm or more, the offspring migrate
49 to sea for feeding. In the River Imsa, the majority of the outmigrating juveniles are 14-19 cm
50 long, and 1-3 (2) years of age (Jonsson and Jonsson 2014). Most of the juvenile migrants
51 (smolts) leave the river in spring, between April and June. Atlantic salmon in this river feed
52 for 1 to 2 years in the North Atlantic Ocean, and during that time, the individual mass of the
53 fish increases from between 10 and 100 g to between 1 and 10 kg (Jonsson et al. 2016).
54 However, the Atlantic Ocean is a high-risk habitat, and typically, less than 10% of the
55 outmigrating juveniles in each cohort return to spawn in the home river, while approx. 6% of
56 the recaptures in fresh water are found in other rivers. Predation, especially during early
57 migration, is high (Larsson 1985; Sogard 1997; Beamish et al. 2004). For instance, predation
58 by Atlantic cod (*Gadus morhua* L., 1758) on juvenile Atlantic salmon was estimated to be
59 about 20% of the outmigrating smolts during their first week at sea (Hvidsten and Lund
60 1988). Adaptations that help Atlantic salmon juveniles to avoid predation can be profitable for
61 some groups of the young fish, but may not be cost-effective for others. For instance, small
62 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 (Rogers 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, one or two years later. Furthermore, we tested the ‘big is better’ hypothesis that survival at sea increased with the size of the smolts at outmigration (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.

Methods

The 1-km long River Imsa, located in south-western Norway (58°50’N, 5°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 ca. 1000 individuals, but varies between 1 (14%), 2 (78%) or ≥ 3 (8%) years, and most of the fish (on average 82% of the returning adults) attain maturity after one year in the ocean (grilse) (Jonsson et al. 1998). The fish spawn in the river and the young use the river as 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 (2016).

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 ca. 10 cm, and a box trap catches all ascending fish in the river. The traps (c.f. Fig. 6.5 in Jonsson and Jonsson 2011) were emptied twice a day, at 08:00 and 15:00 hours, 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 chlorobutanol. In total 36833 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 probably 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 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 juveniles and first-time migrants. Some of the smolts were previously mature male parr and 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 long-line fishery north of the Faroe Islands (1991) and the cessation of the driftnet 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 River Imsa salmon 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 cm, 14.0-19.9 cm 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 cm, 14.0-15.9 cm, 16.0-17.9 cm, 18.0-19.9 cm and ≥ 20 cm. Then, we estimated percent of emigrating juveniles in each length group and 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 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, since the experiment 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 give the mean as a function of time of year, along with 95% confidence intervals for 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 give deviance explained and adjusted R-squared for reference. In analysing the migration and the recapture of the adults, given their smolt length and time of migration, we computed mean recapture rate as described in the previous paragraph. Ninety-five percent confidence intervals of 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 the River Imsa, compared with 13.9 % ($N = 5\,131$) during 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 (Fig. 1a-c). The 95% confidence intervals are narrow and difficult to distinguish from the lines giving the means, except for the largest size-group (Fig. 1c).

The temporal outmigration 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% came during July-September. Juveniles longer than 20 cm migrated downstream all periods of the year.

Survival at sea and return to the River Imsa varied between those migrating during April – June and 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 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 that return to the river was highest for fish that were largest at outmigration. 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 outmigration. 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 than 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 asynchronous migration timing of different sized fish may be an adaptation decreasing predation risk. Atlantic salmon are known to leave freshwater in small schools (Hansen and Jonsson 1985; Riley et al. 2014), and by that, decrease the likelihood of being killed by a predator, as reported for sockeye salmon (*Oncorhynchus nerka* Walbaum, 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; Jutila and Jokikokko 2007). However, the present study is the first showing that large Atlantic salmon juveniles 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 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; Bennet et al. 2011). In coho salmon (*Oncorhynchus kisutch* Walbaum, 1792), Bennet 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 as 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 outmigration relates to the physiology of the fish, assumed to be important for their survival in sea water (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 Jonson 2014). This may be possible because osmotic problems for salmonids in sea water decrease with both increasing water temperature and body size of the fish (Hoar 1988; McCormick 2013). But most 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 ionoregulate 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, 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, endogeneous, 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 is 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 one year old whereas the largest are three years and a few possibly four years of age (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. In sockeye salmon however, 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 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 return 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 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 the regular sized smolts.

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Legend to figures

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 ($N = 2116$, $R^2_{\text{adj}} = 0.786$, deviance explained = 81.4%), (b) between 14.0 cm and 19.9 cm ($N = 32716$, $R^2_{\text{adj}} = 0.835$, deviance explained = 93.3%), and (c) longer or equal to 20.0 cm ($N = 2001$, $R^2_{\text{adj}} = 0.587$, deviance explained = 66.5%). Broken line gives 95% confidence limits.

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

Fig. 1. Probability of migrating given in percent per day for 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 ($N = 2116$, $R^2_{\text{adj}} = 0.417$), (b) between 14.0 cm and 19.9 cm ($N = 32716$, $R^2_{\text{adj}} = 0.523$), and (c) longer or equal to 20.0 cm ($N = 2001$, $R^2_{\text{adj}} = 0.463$). Broken line gives 95% confidence limits for the mean.

215x287mm (300 x 300 DPI)

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

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