Optimal size at seaward migration in an anadromous salmonid

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ABSTRACT: In this study, the probabilistic reaction norm was calculated for length at different ages of smolting before seaward migration of Atlantic salmon *Salmo salar* spawning in the Norwegian River Imsa. The reaction norm was compared with the optimal length at smolting estimated as the product of survival and female fecundity on the return, given their length at smolting. Logistic regression analysis on pre-migratory and migratory fish was used to estimate the probabilistic reaction norm. Length at 50% probability of smolting varied between 11.5 cm and 13.4 cm for age groups 1 to 3 yr with a minimum at Age-2. The estimated optimal length at smolting exhibited a maximum at 13.5 cm. Fecundity of adult females was not significantly affected by their length at smolting, making survival the chief variable influencing the optimal smolt size. The results lend support to the hypotheses that body length at 50% probability of seaward migration was similar for all smolt-age-groups independent of growth, and that mean length at each age of the young fish in fresh water reflected the probability of seaward migration. The slight difference between estimated optimal length at smolting and size at 50% probability of smolting may be chiefly caused by size dependent mortality at sea because of the tagging and larger pre-migratory mortality of young than older juveniles in the river. Thus, size appears crucially important for when to migrate.

KEY WORDS: Migration ecology · Anadromy · Probabilistic reaction norm · Reproductive rate · Logistic regression · Smolt length · Atlantic salmon · *Salmo salar*

INTRODUCTION

Migration is a key life history event and occurs in all major animal taxonomic groups (Dingle & Drake 2007). In changing and diverse environments, a single habitat may not offer the best conditions for survival of the young and feeding opportunities for the juveniles. By migrating, the individuals can use different habitats, food sources and breeding grounds and/or avoid adverse conditions, including predation. By doing this, they are assumed to maximize their net reproductive rate, defined as the product of expected survival and potential number of progeny they produce (Werner & Gilliam 1984, Charnov et al. 2013). Thus, the migration strategy is inextricably linked to the variability of the species, and the decision about when to migrate is one of the drivers for early life history success (Sloat et al. 2014).

Large-scale field studies can provide valuable insight into forces that drive trait evolution. For instance, by use of the size distribution at each age of pre-migratory and migratory individuals, one can calculate the probability of migration. Furthermore, one can estimate the survival of each length group and number of eggs produced by the same groups, and use this to estimate their reproductive rate as a proxy for fitness. Heino et al. (2002a) introduced logistic regression as a tool to estimate the probabilistic maturation reaction norm and tested the method on data of Atlantic cod *Gadus morhua*; corre-

sponding estimates have also been made for several other fish species (e.g. Morita et al. 2009, Olsen et al. 2014, Hunter et al. 2015). Although such probabilistic maturation reaction norms may not disentangle variation caused by phenotypic plasticity from genetic change (Kraak 2007), they are very useful. They overcome systematic biases, remove effects of varying mortality rates and average juvenile somatic growth rates, are defined at the level of individuals and serve as indispensable ingredients in process-based dynamical models of a population's age and size structure (Dieckmann & Heino 2007). Probabilistic reaction norms also have wider use and have been fitted for size at migration (Piou & Prévost 2012, Castellani et al. 2015). Thus, probability functions can describe length at migration, where each fish length is associated with a certain probability of migration. However, no one appears to have compared this reaction norm with a fitness estimate (cf. Jonsson & Hindar 1982).

Here, we use Atlantic salmon *Salmo salar* as an example of how size at migration can be estimated based on long-term monitoring data. The young, called smolts, typically emigrate to sea when they are between 12 and 20 cm in body length, and grow to adult size before they return to spawn (Hansen et al. 1993). They benefit from increased energy intake and growth during the oceanic excursion (Jonsson & Jonsson 2003). However, mortality in the ocean is high (Chaput 2012), and the risk of predation, which is assumed to be the main mortality factor, is influenced by body size, especially during early migration (Salminen 1997, Jonsson & Jonsson 2014). The fish leave the river in small schools and various trade-offs may determine size at migration. Predation may be high if the fish are small (Magurran 1990). On the other hand, the fish risk mortality in rivers and lose growth opportunities by staying longer in fresh water. For instance, growth at sea increases with decreasing size at outmigration (Jonsson & Jonsson 2007). Thus, it is important that the size at migration is well adapted so that the product of survival and growth is maximized when integrated over the entire life span (e.g. Jonsson et al. 1984, Charnov et al. 2013).

Salmonid smolts typically migrate to sea in spring (Jonsson & Jonsson 2014), and the decision about smolting is made in the previous autumn or winter (Thorpe 1987, Vainikka et al. 2012). The length and age at the decision can thus be estimated from the annuli marked in the fish's scales that are formed during winter (Jonsson 1976). In the present study, we used the back-calculated lengths at early ages of returning adults to the Norwegian River Imsa to esti-

mate the probabilistic reaction norm of how size varied with age at seaward migration of young Atlantic salmon. Body length at 50% probability of seaward migration was used as an index of the threshold size for seaward migration. We denote optimal length at smolting associated with the highest product of total survival and fecundity at adulthood. We hypothesized that (1) the probability of seaward migration is size-dependent and age-independent; and (2) for females, the reproductive rate is highest at 50% probability of seaward migration.

MATERIALS AND METHODS

The 1 km long River Imsa, south-western Norway (58° 50′ N, 5° 58′ E), drains into the Høgsfjord estuary (salinity 32), near Stavanger. The Atlantic salmon population produces approximately 1000 smolts annually, ranging from 325 to 3208 individuals during the study period. Smolt age varied between 1 and 4 yr (Jonsson et al. 1998b). For details on the population structure and dynamics see Jonsson et al. (1991, 1998a).

Atlantic salmon were sampled in traps situated 150 m above the river estuary. A Wolf trap (Wolf 1951; apertures 10 mm, inclination 1:10) catches all descending fish larger than ca. 10 cm, and a box trap catches all ascending Atlantic salmon in the river. The traps (illustrations in Jonsson & Jonsson 2011) were emptied twice a day, at 08:00 and 15:00 h, during the study period (1976–2014) except for 1994, when the river was closed because an experiment was performed in the river (Fleming et al. 2000). Total length (0.1 cm) and mass (g) of the fish were measured, and all smolts 12 cm and longer were anaesthetized with chlorobutanol and individually tagged with numbered Carlin tags (Carlin 1955) before they left the river. Adults were monitored on the return. They were sexed based on external characters, and scales were taken from a subsample (n = 671) of the fish for aging and back-calculation of growth.

In total, 33 638 smolts were tagged while descending the river in 1976–2011 and 1268 adults were caught on the return in 1977–2014 (Jonsson & Jonsson 2014). Age and length of the fish during the winter when they smolted, was estimated by scale analysis and back calculation, assuming a proportional relationship between scale and body growth as described by Bagenal (1978). Fecundity (F_L) at return to the River Imsa was estimated from the length (L, cm) of the females at maturity:

$$F_L = 0.052 \ (\pm 0.005) \cdot L^{2.67 \ (\pm 0.024)} \tag{1}$$

($r^2 = 0.95$, df = 2605, p < 0.001; cf. Jonsson et al. 1996)

We did not investigate the annual mortality of the pre-smolts in the river. Thus, this was set according to Symons (1979) as found for Canadian Atlantic salmon, at 60 % mortality during the first winter, 50 % mortality from Age-1 to Age-2 and 40 % annual mortality for older smolts. Survival from eggs to smolts in the River Imsa was estimated at 0.45 % (Jonsson & Jonsson 2016), which is similar to the total pre-smolt survival found in Canadian Atlantic salmon, ranging from 0.16 % to 0.52 % (Cunjak & Therrien 1998). Total survival (in freshwater and ocean) of each fish was calculated by applying the product-rule of probability theory (Devore & Berk 2012): Suppose the event A_j denotes survival in year j, then the probability to survive to year n is given by:

$$\begin{aligned} P(A_1 \cap A_2 \cap \cdots \cap A_n) = \\ P(A_1)P(A_2|A_1)\cdots P(A_n|A_1 \cap A_2 \cap \cdots \cap A_{n-1}) \end{aligned} \tag{2}$$

Fish longer than 20 cm at smolting are few and not included in the calculations. If included, we would have violated the assumption of homoscedasticity, or the variance for the whole interval would have increased substantially. Atlantic salmon are iteroparous, but repeat breeders are few (<2 %) and their effects on the estimates minimal.

For estimation of sea survival given their smolt length, we grouped the smolts in 0.25 cm groups, starting at lengths 11.0–11.25 cm, 11.25–11.50 cm, etc. Recapture rate (l) of the tagged fish was used as an index of survival at sea and estimated as number of adults recaptured divided by the number of seaward-migrating young of the same cohort (Jonsson & Jonsson 2014). The product-rule was used to estimate the probability of surviving in both river and at sea for each 2.5 mm group of smolts (l_L), and we used unparameterized bootstrapping to estimate lengths and number of fish that died in the river before smolting at Age-1, Age-2 and Age-3 (Heino et al. 2002b).

The reaction norm for size at smolting was estimated by 3 logistic regressions, using the bootstrap data along with the observed smolt data. We analyzed the relationship between the length at smolting (L) and the probability of migrating to sea at each age by the logistic model:

$$P(X = 1 \mid L) = \frac{\exp(\beta_0 + \beta_1 L)}{1 + \exp(\beta_0 + \beta_1 L)} \tag{3}$$

The curves were fitted using maximum likelihood estimation (Devore & Berk 2012), and we give 1, 25, 50, 75 and 99 % probability of smolting at ages 1, 2,

and 3 yr. Differences between the lengths at 50 % probability of smolting of the various age groups were evaluated by creating a 95 % bootstrap percentile confidence interval for each smolt age group.

To estimate the optimal length at migration we used the log-transformed linear regression of fecundity relative to length at smolting. Then, we fitted a fifth-degree polynomial to estimate mean survival rate given smolt length. A 95 % prediction interval was estimated for new observations of the random variable, assuming that the observations were independent, and normally distributed with constant variance. The reproductive rate (R) relative to length at smolting was estimated as $R = l_L \times F_L$, where l_L denotes total survival and F_L the fecundity of adult females, given their length at smolting (Mangel 1996). We did not separate survival by sea-age at return, because all individuals were tagged and all those that returned to the River Imsa were recaptured in the trap at the river mouth whether they stayed 1 or 2 yr at sea. Thus, survival at sea could be estimated for each 2.5 mm smolt length group independent of their sea-age at return.

RESULTS

Atlantic salmon of the River Imsa migrated to sea from Age-1 to Age-4, with the majority being Age-2 fish (Table 1). Mean smolt age (± SD) was 2.06 ± 0.32 yr, and mean length at seaward migration was 16.3 ± 1.5 cm. There was no significant difference in length at seaward migration between sexes (t = 0.87, df = 1238, p > 0.05), and there was no significant relationship between back-calculated length at the end of the first growth season and length at smolting (r^2 = 0.007, p > 0.05)

Younger salmon exhibited accelerated growth in the last year before smolting relative to those that smolted older (Table 1). For instance, back-calculated mean length of Age-1 smolts were 5 cm longer at the

Table 1. Back-calculated lengths (±SD, cm) of Atlantic salmon *Salmo salar* at the end of first (L-1), second (L-2), third (L-3) and fourth (L-4) growth season

Smolt age (yr)	n	L-1	L-2	L-3	L-4
1	11	11.8 ± 2.5			
2	613	6.8 ± 1.6	16.3 ± 2.4		
3	42	5.5 ± 1.4	11.7 ± 2.5	18.8 ± 3.7	
4	5	4.7 ± 1.5	9.8 ± 2.0	15.4 ± 2.7	20.7 ± 3.2

end of the first growth season than the length of the non-migrants at that age, that smolted at Age-2 (t = 6.6, df = 622, p < 0.001). Similarly, Age-2 smolts were significantly longer at the end of the second growth season than the non-migrants that smolted at Age-3 (t = 12.5, df = 653, p < 0.001), and Age-3 smolts were longer than Age-4 smolts at the end of their third year (t = 2.55, df = 45, p < 0.01). Moreover, mean smolt length increased with age: Age-4 smolts at 1 yr prior to smolting were already longer than the mean Age-1 smolt length. Back-calculated length in winter prior to smolting was on average 2 cm shorter than the observed length of the smolts when they left the river. This difference is due to growth in spring, following formation of the winter zone (annulus), but prior to

Fig. 1. Probability of smolting of Atlantic salmon *Salmo salar* given their length at (a) Age-1, test of regression coefficient = 0, p < 0.001, (b) Age-2, test of the regression coefficient = 0, p < 0.001, (c) Age-3 yr, test of the regression coefficient = 0, p < 0.02. The curves were fitted by logistic regression, circles along the left axes give length of pre-migratory fish, and circles along the right axes give length of migrating smolts. (d) Salmon probabilistic migration reaction norm, showing the reaction norm midpoint ($L_{50\%}$, solid line) and envelope ($L_{25\%}$–$L_{75\%}$, gray polygon), and $L_{1\%}$ and $L_{99\%}$ (dotted lines). Crosses: proportion of fish that smolted at the respective ages (relative to the probability lines); circles: estimated mean length of the salmon in the river at these ages

the fish leaving fresh water, and possibly underestimation caused by the scale-reading method.

The probability of seaward migration increased with size within each smolt-age-group (Fig. 1a–c). The fit was best for the 2 youngest age-groups. At Age-3, most of the remaining fish migrated. The reaction norm for 50% probability of migration to sea ($L_{50\%}$) was relatively flat, but with a minimum at Age-2, as $L_{50\%}$ was significantly higher at Age-1 than Age-2, but did not change significantly from Age-2 to Age-3 (Fig. 1d). Lengths at 50% probability of seaward migration were 13.0 cm, 11.5 cm and 13.4 cm at Age-1, Age-2 and Age-3, respectively. If not corrected for the effect of pre-smolt mortality in the river, the estimates would have been approximately 1 cm shorter than these lengths. The width of the migration envelope ($L_{25\%}$ to $L_{75\%}$) increased noticeably from Age-2 to Age-3. Within smolt age groups, fish that were shorter than $L_{50\%}$ most probably stayed in the river 1 yr longer, whereas longer fish most probably left, but there is no exact minimum length at migration. The probability of migrating at Age-1 was ca. 1%, and the corresponding estimated mean length of all the fish the first winter at Age-1 was 6.8 cm (Fig. 1d). At Age-2, the probability of migrating was 93% and estimated mean length was 15.9 cm, and at Age-3, 89% of the remaining fish migrated, and their mean length was 18.5 cm. Thus, there was close relationship between mean smolt length and the probability of seaward migration (error less than 5%).

Estimated female fecundity of the returning fish did not change significantly with increasing length at seaward migration (Fig. 2a). The variation in fecundity was large, showing that fecundity was not an important variable influencing variation in fitness among smolt-length groups. Total survival, on the other hand, varied depending on length at smolting with a maximum at 13.6 cm (Fig 2b). Thus, the estimated reproductive rates as measure of the optimal smolt length of the fish in the various smolt-length groups mimicked the survival curve with a maximum at 13.5 cm (Fig. 2c). If not corrected for the effects of pre-smolt mortality in fresh water, the maximum was estimated at 15.1 cm.

DISCUSSION

In the present time series data, there are significant correlations between year of outmigration and smolt length at Age-2, and year of outmigration and survival (r^2 = 0.4) (e.g. Jonsson & Jonsson 2004). We checked for possible effects of this on the probability
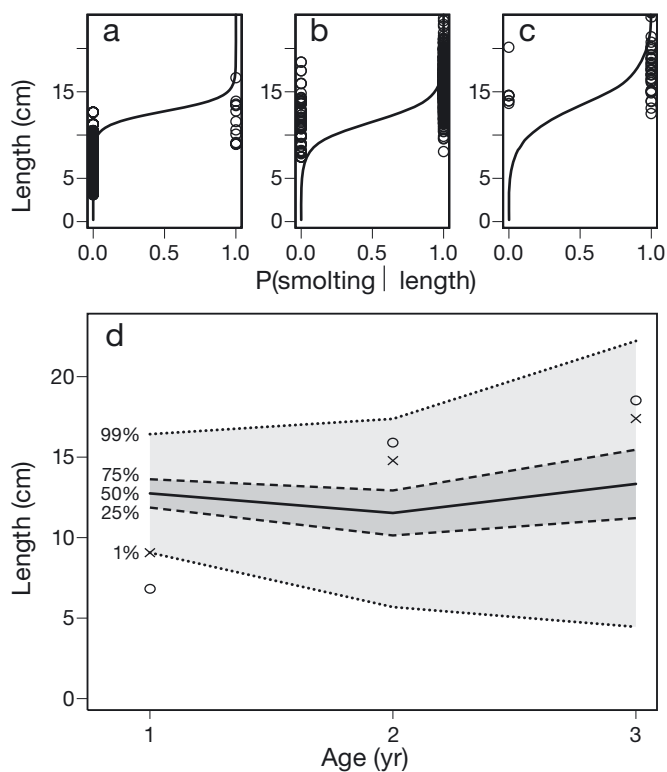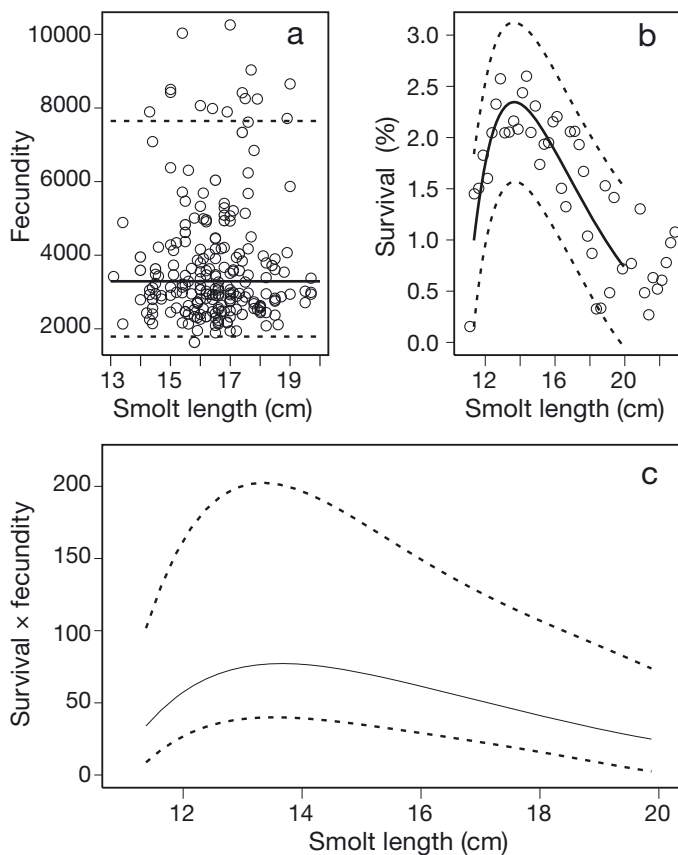
Fig. 2. (a) Predicted fecundity (eggs per fish) of returning adult female Atlantic salmon *Salmo salar* relative to their lengths at smolting estimated from their scales ($r^2 = 0.00$). Dashed lines give the 95% prediction interval for future fecundity values. (b) Survival (l_L) from the first autumn onwards was estimated for fish smolting at back-calculated length intervals (11.0–11.25, 11.25–11.5 cm, etc.) fitted by least squares regression. Dashed lines give 95% prediction interval. (c) Estimated reproductive rate (R, calculated as survival × fecundity) of adult females given their length at smolting (solid line) with 95% prediction interval (dashed lines)

of smolting and the reproductive rate, by recomputing the statistical analyses after linearly compensating for the dependencies. The recalculation showed that the reaction norm midpoint and envelope (Fig. 1) remained almost completely unchanged. The same was true for survival, fecundity and reproductive rate (Fig. 2). In all, less than 5% errors were induced by the time-correlations. Because of this, we give all the statistical results in terms of the raw data.

$L_{50\%}$ (~11.5–13.4 cm) was similar to (within the 95% confidence limits of Age-3 smolts) the length maximizing the reproductive rate (~13.5 cm), estimated as the product of survival at sea and fecundity at return to the river (hypothesis 2). In addition, the curve illustrating expected reproductive rate was

rather flat between 13 and 14 cm. Possibly, the slightly longer length maximizing the reproductive rate may be related to the mortality estimates of the pre-smolts and tagging mortality at sea. With a relatively higher survival of older than younger pre-smolts than used here (Symons 1979), the $L_{50\%}$ would have been longer and closer to the length maximizing the reproductive rate. On the other hand, the smolt length maximizing the reproductive rate of untagged fish may have been shorter than indicated by our estimates based on tagged fish, because tagging mortality increases with decreasing smolt size. 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 highest for small smolts (Hansen 1988). Isaksson & Bergman (1978) estimated marine mortality of Carlin-tagged smolts. They found that the mortality at sea of 9.5–14.5 cm long 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, but less so than for smaller smolts. It is uncertain how large the extra mortality cost for smaller body size may be, but if we adjust the estimate with extra mortality as found by Isaksson & Bergman (1978), the length of smolts giving maximum reproductive rate changed to 12.8 cm, which is within the variation at 50% probability of seaward migration. Thus, both our assumption about pre-smolt mortality in the river following Symons (1979) and higher tagging mortality of small smolts (Isaksson & Bergman 1978) may have contributed to our finding of the optimal smolt length at seaward migration being slightly longer than the reaction norm for 50% probability of smolting.

Survival at sea decreased for fish >13.5 cm at smolting. This may come as a surprise (cf. Sogard 1997, Saloniemi et al. 2004, Osterback et al. 2014); however, Koenings & Burkett (1987) reported that the survival of sockeye salmon *Oncorhynchus nerka* increased up to a certain smolt length (12 cm), and then decreased, which parallels the present findings for Atlantic salmon. Smolts migrate to sea in small schools, and predators may more easily spot fish larger in size than the majority (Rogers et al. 2015). Thus, larger body size may not give smolt better protection against predators, as assumed for larval fish (Miller et al. 1988, Meekan et al. 2006).

$L_{50\%}$ was little influenced by fish age. Still, the estimated smolt size increased with age at smolting

(Table 1). This may look like a paradox, and one could easily believe that age at smolting is growth-dependent as assumed by Økland et al. (1993). However, the observed result is theoretically expected (cf. Heino et al. 2002a, their Fig. 4), and parallels the finding by Morita et al. (2005) who showed that that the average size at maturity increases with age although the threshold size for maturity decreased with age in chum salmon *Oncorhynchus keta*. Based on the present data, length and not growth-rate appeared to be the major determinant for age at smolting, as expected if survival at sea is highly dependent on size and not age of the fish. This result lends support to our first hypothesis. Increasing smolt size with age is chiefly a consequence of the fact that older fish were larger the year prior to smolting; hence, relatively more fish surpassed $L_{50\%}$ in the subsequent year.

There is a close relationship between estimated mean length of the fish in an age group and the observed proportion of fish that migrate at this length. The present estimates of $L_{50\%}$ is ca. 2 cm longer than that suggested by Elson (1957) to be the minimum length at smolting for Atlantic salmon. More recent estimates of $L_{50\%}$ vary between 8.9 cm in the River Scorff, France (Piou & Prévost 2012), and 11.3 cm in the River Stryn, Norway (Hedger et al. 2013). There may be population-specific differences in smolt length among populations because of varying survival and growth (Jonsson et al. 1991), reflected by the genetics of the fish (Piché et al. 2008). Within populations, on the other hand, variation in size at migration may be chiefly due to phenotypic plasticity associated with variation in growth rate (Refstie et al. 1977, Metcalfe & Thorpe 1990).

Individual fecundity did not change significantly with smolt size. This may indicate that the same fish may not do equally well in fresh and salt water. For instance, Einum et al. (2002) reported a strong negative correlation between pre- and post-smolt growth, a difference that also holds for the River Imsa salmon (Jonsson & Jonsson 2007). The variation in individual fecundity also increases because age-at-return varies, which may decouple the relationship between smolt and adult sizes. We do not expect influences of variation in egg size on the optimal smolt size, because fecundity and egg size are highly correlated (Jonsson et al. 1996).

Survival was the chief factor responsible for variation in the expected reproductive rate of the fish moving to sea at different lengths. At sea, early natural mortality is high and may be chiefly related to predation (Craig et al. 2006, Mäntyniemi et al. 2012). There may be also a physiologically based mortality associated with migration from fresh to salt water (Hoar 1988, Webster & Dill 2006, Jonsson et al. 2016). Furthermore, Beamish & Mahnken (2001) hypothesized that coho salmon *Oncorhynchus kisuch* year-class strength is influenced by winter mortality during the first year in the ocean. They suggested that juvenile salmon that fail to reach a critical size by the end of their first marine summer do not survive the following winter. This may also hold for Atlantic salmon. So far, however, there is no knowledge about a minimum threshold size for winter survival in this species (Friedland et al. 2009).

In all, our empirical assessment shows that the probabilistic reaction norm approach performed well for size at seaward migration: mean length of pre-smolt fish relative to the reaction norm reflected the probability of migration. Furthermore, the probability of 50% migration appeared largely independent of fish age. The most important factor influencing the estimated reproductive rate of the fish was size-dependent survival at sea, which was highest for medium-sized smolts. In addition, the reaction norm of 50% probability of seaward migration appeared to be shorter than the length that maximized survival. The exact optimal size at migration is, however, difficult to estimate because of size-dependent tagging mortality and no information on how the pre-migratory mortality varied with age and size of the fish in the River Imsa.

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