

Iteroparity and its contribution to life-history variation in Atlantic salmon

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Abstract

Evolution of iteroparity is shaped by the trade-off between current and future reproduction. We studied variation in iteroparity among 205 050 individual Atlantic salmon caught in 179 rivers spanning 14° of latitude. The proportion of repeat spawners (iteroparous individuals) averaged 3.8% and ranged from 0% to 26% across rivers. Females were more often repeat spawners than males and had lower cost of reproduction in terms of lost body mass between spawning events. Proportion of repeat spawners for a given sea age at maturity, and the ratio of alternate to consecutive repeat spawners, increased with increasing population mean sea age at maturity. By combining smolt age, sea age at maturity, and age at additional spawning events, we identified 141 unique life-history types, and repeat spawners contributed 75% of that variation. Our results show that repeat spawners are important for life-history variation and suggest that the association between mean sea age and the frequency of repeat spawning is adaptive rather than a pleiotropic side effect arising from selection on sea age.

Key words: age at maturity, life-history evolution, local adaptation, repeat spawning, trade-off

Introduction

Allocation of limited resources results in trade-offs shaping life-history evolution. One essential trade-off is the partition of energy between current and future reproduction (Stearns 1992). This trade-off plays out differently among species, populations, and individuals, and has resulted in different breeding strategies to maximize fitness. Semelparity is a strategy characterized by one reproductive event followed by death, whereas iteroparity is characterized by two or more reproductive events (Cole 1954; Murphy 1968). To be favored by natural selection, a semelparous genotype must have greater fecundity compared with an iteroparous genotype at the first reproductive event (Young 1981). According to optimality theory, highly variable or low juvenile survival will favor iteroparity, whereas low adult survival will favor semelparity (Schaffer 1974). Orzack and Tuljapurkar (1989) argued that this is a simplified view and that the magnitude of environmental variation and correlation structures among vital rates are critical in determining the direction of evolution of the breeding strategy.

Atlantic salmon *Salmo salar* is an iteroparous species, but individuals show great variation in life history, including the number of reproductive events. There is large variation in time spent in rivers and at sea before first reproduction both within and among populations, but most individuals stay 1–4 years in freshwater (smolt age) and one to three winters at

sea (sea age) (Huitfeldt-Kaas 1946; Hutchings and Jones 1998; Klemetsen et al. 2003). Some individuals survive for a second spawning, and a few survive to spawn more than two times. Repeat spawners migrate to sea between each spawning event to regain energy to develop new gonads. The recondition period is usually 1 or 2 years (i.e., fish return as consecutive or alternate spawners). The proportion of repeat spawners within the total salmon run is usually lower than 10% but can be as high as 40% (Fleming 1996; Bordeleau et al. 2020).

Repeat spawners are important for Atlantic salmon population dynamics. For example, in four Canadian rivers, a repeat-spawning female contributed on average 1.4–1.6 times more eggs than a maiden female due to larger body size (Bordeleau et al. 2020). Even at relatively low proportions, the occurrence of repeat spawners can act as a stabilizing factor at times of low abundance of maiden spawners (Bordeleau et al. 2020). This was exemplified in 2014 in the River Etne, Norway, when there were few maiden spawners, and repeat-spawning females constituted 43% of the female spawning biomass (Harvey et al. 2022). In addition, repeat spawners increase the number of cohorts spawning simultaneously, which has been suggested to help maintain genetic diversity within populations (Erkinaro et al. 2019). Despite several studies on iteroparity in Atlantic salmon (e.g., Shaffer and Elson 1975; Jonsson et al. 1991a; Erkinaro et al. 2019;

Bordeleau et al. 2020), the drivers of variation in iteroparity among populations are not well understood.

Local adaptation and population differentiation in salmonids are favored by a high degree of homing (philopatry) by individuals to their natal river for spawning (Hendry et al. 2004). The number of years spent feeding at sea before first reproduction (sea age at maturity) is an important fitness-related trait known to vary genetically among populations of Atlantic salmon (Schaffer 2004; Barson et al. 2015). Individual body mass roughly doubles for each extra year spent feeding at sea (Bolstad et al. 2017), giving individuals staying at sea and delaying maturation higher fecundity and competitiveness but lower survival probability than individuals maturing and homing back to spawn (Fleming 1998). Hence, both sea age at maturity and recondition period represent the evolutionary trade-off between current and future reproduction. Because evolution of iteroparity is fundamentally related to the same trade-off, we expect populations that have evolved differences in mean sea age at maturity to also differ in degree of iteroparity. Populations dominated by early-maturing salmon are selected for current reproduction at the expense of future reproduction and are, therefore, expected to have lower degree of iteroparity as well as shorter recondition period compared with populations dominated by late-maturing salmon.

The genetic basis of local adaptation in sea age and size at maturity involves a large effect gene in the *vgll3* genomic region (Barson et al. 2015). The same genomic region is associated with probability of repeat spawning, where the genotype associated with early maturation and small body size has higher probability of repeat spawning than the genotype associated with late maturation, after controlling for sea age at maturity (Aykanat et al. 2019). Interestingly, changes in allele frequency of *vgll3* predict a negative relationship between population mean sea age at maturity (hereafter population mean sea age) and degree of iteroparity, which is opposite of the above prediction based on the trade-off between current and future reproduction.

Female Atlantic salmon are on average older and larger at reproduction than males (Fleming 1998). This sexual dimorphism is probably caused by a positive correlation between fecundity and body size in females, whereas male reproductive success mainly depends on access to females. Although large males have a competitive advantage, smaller males can adopt alternative tactics to fighting such as sneaking (Fleming 1996). Hence, the trade-off between current and future reproduction is toward future reproduction in females compared with males. This fits well with the higher proportion of females compared with males among repeat spawners (Bordeleau et al. 2020).

Here, we used a fish-scale collection to study variation in life history and iteroparity across 179 Atlantic salmon populations from Norwegian rivers spanning 14° of latitude (58°–71°N). First, we quantified the importance of repeat spawning in life-history variation. Second, we tested whether within-river life-history variation depended on sex, geographic region, and latitude. Third, we assessed whether probability of repeat spawning and probability of alternate versus consecutive spawning depended on sex, sea age at maturity,

geographic region, latitude, population mean sea age, and population mean smolt age. Finally, we evaluated the trade-off between current and future reproduction in terms of difference in body mass between repeat spawners and maiden fish with equal number of years since migrating to the sea for the first time.

Methods

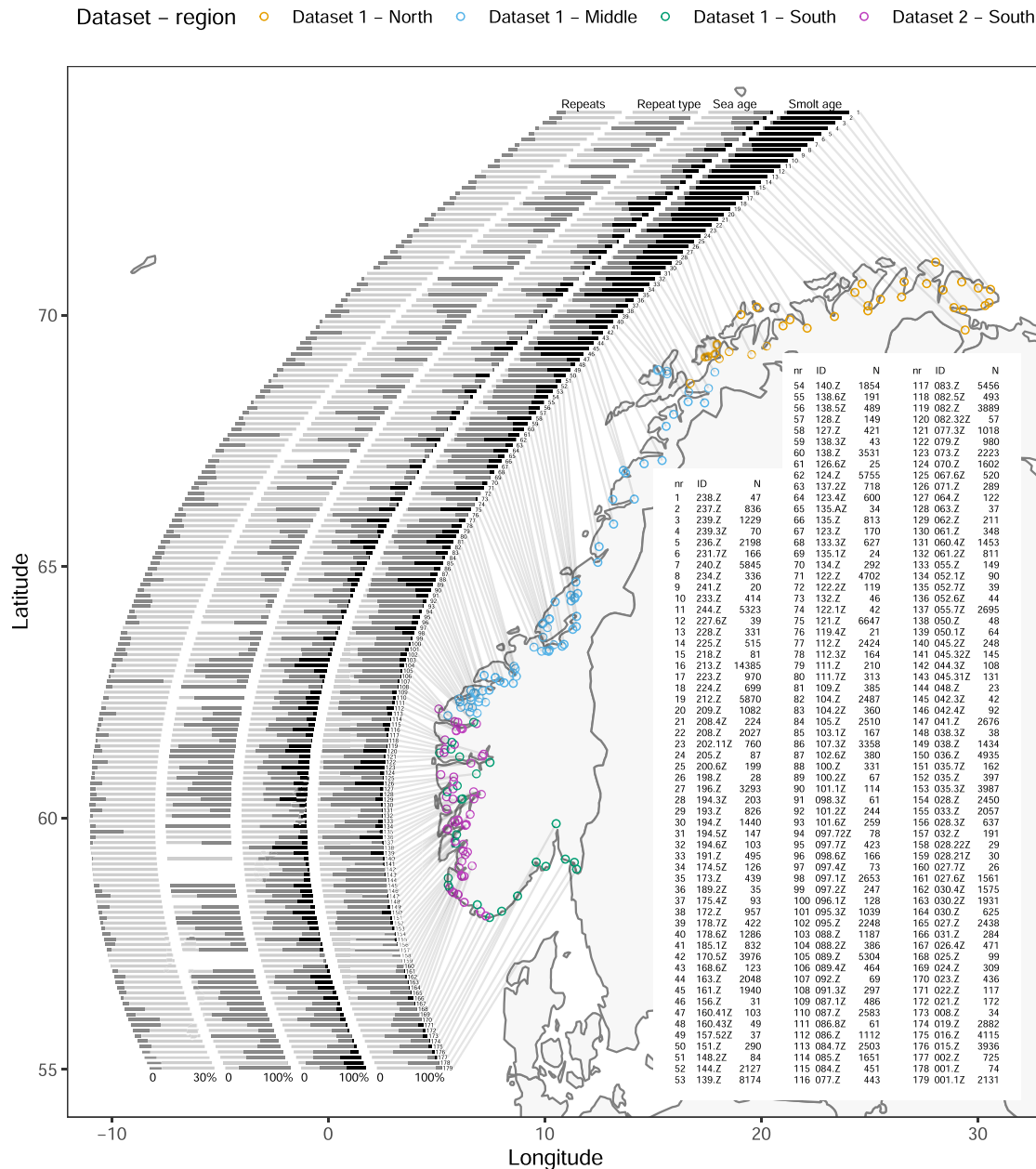
Data

We used two independent datasets with records of sea age and spawning history obtained from fish-scale collections. The scales were sampled from adult Atlantic salmon caught in rivers prior to spawning from 1989 to 2017. The largest dataset, Dataset 1 (159 367 salmon, of which 141 099 were sexed), covered all regions of Norway, whereas Dataset 2 (45 683 salmon, of which 39 516 were sexed) covered only the South region (Fig. 1). See also Figs. 2 and 3 for a detailed overview of the data and sample sizes. Dataset 1 was analyzed by scale readers at the Norwegian Institute for Nature Research (NINA) and Dataset 2 by scale readers at Rådgivende Biologer. Of the 179 rivers sampled, 122 rivers were only in Dataset 1, 31 rivers were only in Dataset 2, whereas 26 rivers were in both datasets. The 26 rivers included in both datasets typically had low sampling effort from one of the institutes and almost no temporal overlap (i.e., most often different sampling years in the two datasets). Due to institutional discrepancies in the interpretation of scale patterns (see the “Scale reading” section), the two datasets were analyzed separately.

The rivers were assigned to geographic regions following the regional division used by the International Council for the Exploration of the Sea (ICES 2021), but with South-West and South-East combined into one region (South), and the distinction between Middle and North adjusted to reflect the genetic differentiation between the Eastern Atlantic and the Barents–White Sea phylogenetic groups (Verspoor et al. 2005; Wennevik et al. 2019). The reasoning behind the sorting of rivers into geographic regions was that Atlantic salmon populations within a region share the ocean environment to a larger extent than between regions. This is supported by the high synchrony in marine growth between the South-West and South-East region, some synchrony between these two regions and the Middle region, and little synchrony between the North region and the three other regions (Vollset et al. 2022).

Most of the fish in our data were collected by rod fishing (91% rod and 9% fixed gear in Dataset 1, 100% rod in Dataset 2). The anglers provided information on body length and mass, sex, catch date, and geographic location. The angling catch is thought to be representative of the spawning population, because the angling season lasts during most of the salmon run and exploitation rates are high in Norway (40%–60%) (Bolstad et al. 2021). Population means based on rod versus fixed gear were correlated ($r = 0.48$ for mean sea age and $r = 0.69$ for mean mass; only means with $n \geq 20$ were included). However, catchability may vary according to life history, sex, and spawning history (Halttunen et al. 2013;

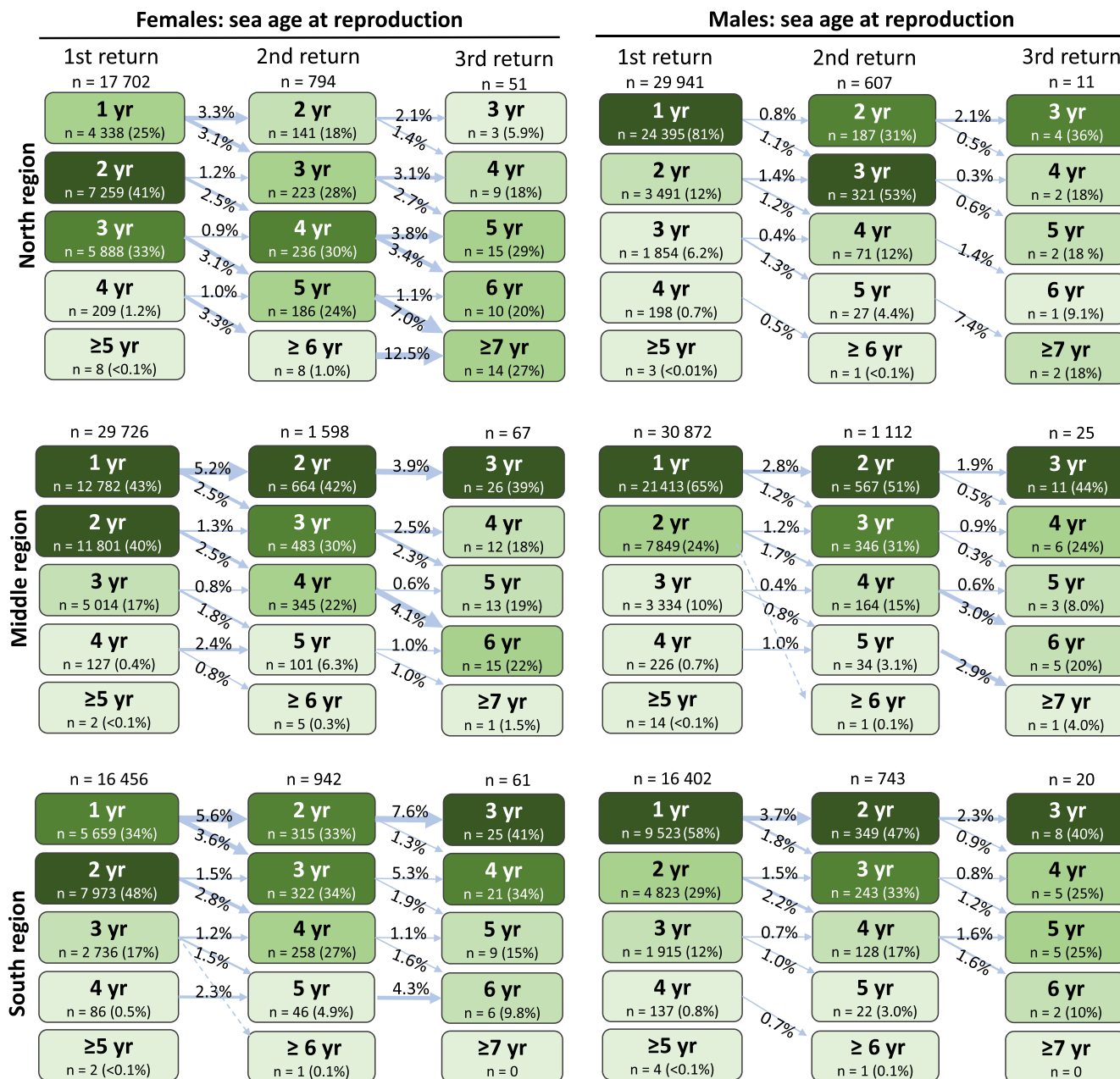
Fig. 1. Life-history variation and geographic location of the 179 Atlantic salmon populations in Norway that were included in this study. The bars from left to right indicate the percentage of repeat spawners (dark gray); distribution of type of repeat spawners: consecutive (light gray) and alternate (dark gray); distribution of maiden sea ages: 1SW (light gray), 2SW (dark gray), and 3–7SW (black); distribution of smolt ages: 1–2 years (light gray), 3 years (dark gray), and 4–8 years (black). Note that the first bar, percentage repeat spawners, only covers the range 0%–30%. The inset shows the river ID (Norwegian watercourse outlets issued by The Norwegian Water Resource and Energy Directorate) and sample size. Of total 205 050 individuals, 171 841 had information on smolt age. The map was generated using the R-package maps (Becker et al. 2021). The base map is from www.natureearthdata.com (WGS84 projection, coordinate system in degrees).



Harvey et al. 2022). Also, visually assessing the sex can be difficult, especially early in the angling season. Based on genetic assessment of sex, the most common error made by anglers is mistaking small females for males (Robertsen et al. 2021). The error rate of genetic females assigned as phenotypic males by anglers was 10%–20% (Robertsen et al. 2021). Therefore, the

data have biases and might not provide exact information on proportions of repeat spawners in the different rivers, but given the assumption that differences in catchability among life-history types do not vary substantially across rivers, clear patterns within datasets should reflect true biological differences.

Fig. 2. Variation in age at reproduction at first, second, and third return to rivers for spawning in Dataset 1. Each box represents a sea age at spawning, with number of salmon in absolute count and in % of the total number given above each column of boxes. The arrows represent transition probabilities, that is, the % salmon in the former sea age category that are also in the latter. Some transitions were left out for readability (typically the transitions where fish spent >2 years between spawning events), and all these had low probability ($\ll 1\%$). Sea age is here defined as number of winters since smolt out-migration.



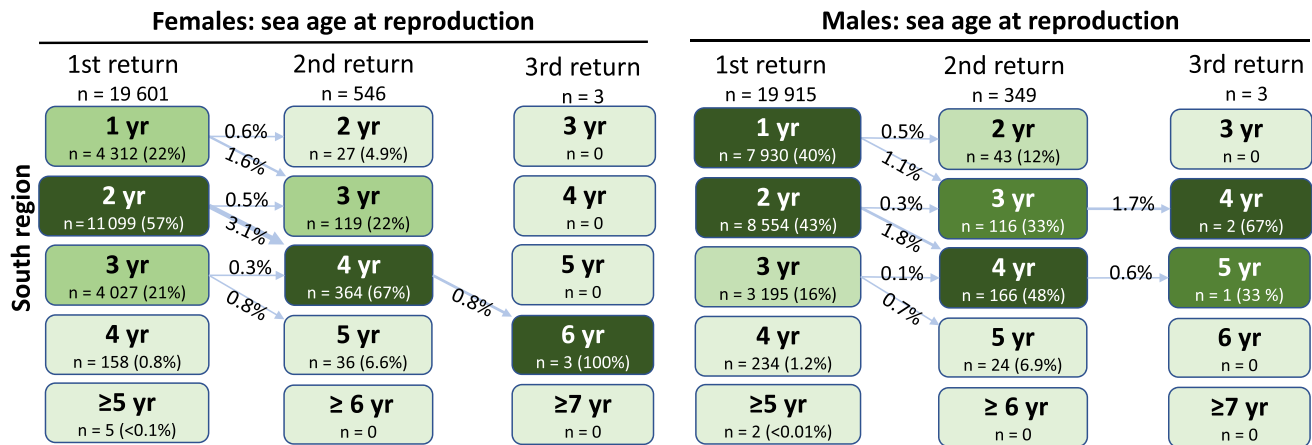
Scale reading

As fish grow, circuli are formed in the scale as dark concentric lines. When growth is slow, the circuli become narrowly spaced (winter band), and when growth is rapid, the circuli become more widely spaced (summer band) (ICES 1984, 2011). When adult fish spend time in freshwater, material is resorbed from the scale, causing erosion on the edge and sometimes on the surface of the scale. This pattern of erosion is called “spawning mark” and is used to identify events of previous spawning (ICES 1984). Identification of spawning

marks in the scales is a method used in several previous studies to identify repeat spawners (Niemelä et al. 2000; Aykanat et al. 2019; Erkinaro et al. 2019; Bordeleau et al. 2020). We acknowledge that males (in extremely rare occasions also females) can mature in freshwater and spawn as parr before later migrating to the sea, and in that sense are iteroparous, but these life-history types are not considered in this paper as we have no information about previous spawning in freshwater from the scale reading data. Scale reading is an acquired skill and based on experience in recognizing patterns, and

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Fig. 3. Variation in age at reproduction at first, second, and third return to rivers for spawning in Dataset 2. Each box represents a sea age at spawning with number of salmon in absolute count and in % of the total number given above each column of boxes. The arrows represent transition probabilities, that is, the % salmon in the former sea age category that are also in the latter. Some transitions were left out for readability (typically the transitions where fish spent >2 years between spawning events), and all these had low probability (<<1%). Sea age is here defined as number of winters since smolt out-migration.



there are features of the scales that may complicate the interpretation. Repeat spawners and their sea age may be complicated to identify, because spawning marks may be weak, and spawning may completely erode winter bands (ICES 1984).

The scale readers at both NINA and Rådgivende Biologer have many years of experience. However, scale readers at Rådgivende Biologer were more conservative than scale readers at NINA when evaluating number of spawning events. In Dataset 1 (NINA), 4.3% were identified as repeat spawners, compared with 2.2% in Dataset 2 (Rådgivende Biologer). In the 26 rivers represented in both datasets, the corresponding numbers were 5.1% and 2.4%. The number of years between spawning events was determined by counting the number of winter bands after the spawning mark, or between several spawning marks in the case of multiple spawning events. The scale readers at Rådgivende Biologer added 1 year to the number of years between spawning events when they suspected that a winter band had been eroded, taking the size of the fish into consideration. This contributed to a difference in the frequency of consecutive versus alternate repeat spawners between the two datasets. Some discrepancies between datasets may also be explained by the different geographical coverage.

Maiden spawners refer to fish that return to spawn for the first time, and maiden sea age, or sea age at maturity, refers to the number of winters the fish have spent at sea before their first reproduction. Fish that returned for their first reproduction after only one winter at sea are called one-sea-winter (1SW) fish, and fish that returned for their first reproduction after two or more winters at sea are called multi-sea-winter (MSW) fish. Sea age of repeat spawners refers to number of winters since smolt out-migration, because repeat spawners may overwinter in freshwater. Salmon from separate rivers are referred to as separate populations. Mean sea age of each population was calculated based on the sea age at maturity. Smolt age refers to the age when the fish left freshwater and

migrated to sea. Proportion of repeat spawners (Fig. 1) was calculated based on all returning females/males including 1SW fish. In addition, proportion of repeat spawners within the MSW fish component of the returning fish was analyzed (see below).

Consecutive spawners were defined as fish returning to spawn the following year after the first spawning event. Alternate spawners were defined as fish returning to spawn 2 years after their first spawning (or in odd cases 3 or more years after). Salmon may return to the sea shortly after spawning in the autumn, or they may remain in the river and return to the sea during the winter or next spring or early summer (Halttunen et al. 2013). Hence, consecutive spawners may have reconditioned at sea for up to nearly 1 year, or for only a few months, between each spawning. Alternate spawners may have reconditioned at sea from 1 to almost 2 years or more between each spawning. Age of repeat spawners was indicated by maiden sea age followed by the sea age at the second return. For 1SW fish, this means 1→2 for consecutive spawning and 1→3 for alternate spawning, and for 2SW fish, 2→3 for consecutive spawning and 2→4 for alternate spawning. Three consecutive spawning runs would be denoted as 1→2→3.

Statistics

Life-history types

We estimated the difference in number of life-history types among regions and sexes using simple least squares regression. Natural log number of sex-specific life-history types within each river was the response variable. Region within dataset (North, Middle and South in Dataset 1, and South in Dataset 2), sex, latitude, and natural log sample size were explanatory variables. The effect of the latter two variables was estimated separately for the two datasets, and we also included the interaction between sex and region within

dataset. Sample size (natural log transformed) was included because the number of observed life-history types was highly dependent on number of observed fish within each river. Latitude was centered on the region mean and sample size was centered on $\ln(424)$, where 424 is the average sample size within rivers and sex.

Repeat spawners

For probability of repeat spawning, we used a logistic mixed effect model with number repeat spawners as “successes” and number of maiden spawners as “failures” within each combination of river, capture year, maiden sea age, sex, and smolt age, hereafter called observation group. As fixed effects, we included region, sex, maiden sea age, smolt age, population mean sea age, population mean smolt age, and latitude, where the latter three variables were centered on their respective region means. Because the model includes sea age at both the individual level and the population level (population mean sea age), the estimated effect of population mean sea age is the effect controlling for individual sea age. The total effect of population mean sea age is the sum of the two effects, which is equivalent to the effect of population mean sea age in a model not including (controlling for) individual sea age. This type of multilevel analysis is often referred to as contextual analysis (see, e.g., [Heisler and Damuth 1987](#)). The random effect structure of the model was hierarchical with five levels nested within each other. The nesting structure from the highest to lowest level was as follows: river (population), capture year, maiden sea age, sex, and finally observation group. Observation group was included to account for overdispersion. Note that the among-river variance was estimated at zero, and therefore the random effect of river was not included in the final model fit. Hence, the highest level of the random effect structure was capture year within river. The residuals of the model were assumed to be binomially distributed. To avoid overparameterization, we did not include any interaction terms in this already complicated model. The model had nine fixed effect parameters to be estimated. Including pairwise interactions (and ignoring higher orders) would add an additional 27 fixed effect parameters to the model. Because no interactions were included, the model estimated the general, or main, effect of each variable across all data (after controlling for the other variables), but did not test, for example, whether the effect of population mean sea age differed among sexes, maiden sea ages, or regions. The model was fitted separately to Dataset 1 and Dataset 2, but without the fixed effect of region for the analysis of Dataset 2. The sample sizes were 5296 repeat spawners and 122 683 maiden spawners in Dataset 1 and 484 repeat spawners and 22 634 maiden spawners in Dataset 2. These were the individual fish for which we had complete records of sex, smolt age, and maiden sea age.

To estimate population differences in the composition of the MSW component of the population with regard to repeat spawners, we fitted a modified version of the above model for probability of repeat spawning. While the above model aimed at estimating the probability of repeat spawning for fish with

different previous life history, this model aimed at estimating the fraction of repeat spawners within sea ages at capture. Hence, the observation group was defined by all combinations of river, capture year, sea age at capture, and sex. The fixed effect structure was the same as the above model except that it did not include smolt age and maiden sea age, but instead included sea age at capture. The random effect structure was hierarchical with four levels nested within each other, from highest to lowest level: river, year, sea age at capture, and observation group. The model was fitted separately for Dataset 1 and Dataset 2. The sample sizes were 5796 repeat spawners and 62 164 maiden spawners for Dataset 1 and 895 and 26 619 maiden spawners for Dataset 2. These were the MSW fish for which we had complete records of sex and sea age at capture.

Alternate versus consecutive spawners

We modelled the probability of alternate versus consecutive spawning using the same model structure as for the model on probability of repeat spawning. Only repeat spawners were included in this model, with number of alternate spawners as “successes” and number of consecutive spawners as “failures”. For Dataset 1, there was no overdispersion and therefore the random effect of observation group was excluded. Contrary to the model on probability of repeat spawning, the random effect of river was retained. The sample size was 2711 consecutive and 2585 alternate spawners.

For Dataset 2, there were only 96 consecutive and 388 alternate spawners with complete records of sex, maiden sea age, and smolt age. To attain model convergence, we removed the effect of smolt age in the model. This increased the sample size to 164 consecutive and 731 alternate spawners (with complete records of sex and maiden sea age). The observation group in the model for Dataset 2 was defined by all combinations of river, capture year, maiden sea age, and sex. As fixed effects explanatory variables, we included sex, maiden sea age, population mean sea age, and latitude, where the latter three variables were centered on their means. The levels of the hierarchical random effect structure were river, year, maiden sea age, and observation group, but the among-population and among-observation group variance were estimated at zero. We therefore excluded these two levels in the random effects structure in the final model fit.

Cost of reproduction in terms of reduced body mass

The cost of reproduction includes both lost growth opportunities and postspawning mortality. As we only had data on fish that survived, we only analyzed cost of reproduction in terms of reduced body mass of repeat spawners (i.e., lost growth opportunities due to spawning). We estimated the difference in body mass at return between repeat and maiden spawners with the same number of years since smolt out-migration. We used a mixed model with identity link and normally distributed errors having natural log of mass (kg) at capture as response variable. In the model, we estimated the

following parameters: an intercept and a slope for each sex and sea age (at capture) combination for the maiden spawning type, and the difference in intercept and slope between the maiden spawning type and the consecutive or alternate spawning type for each sex and sea age combination. The slope was the effect of population mean sea age, which was centered on its region mean (as in the previous analyses). Random effects were river and sampling year nested within river. The model was fitted separately for Dataset 1 and Dataset 2. Only fish with sea ages 2SW, 3SW, or 4SW at capture were included, and the sample size was 58 183 fish for Dataset 1 and 27 164 fish for Dataset 2. All analyses were done with R (R Core Team 2020) using the lme4 package (Bates et al. 2015) for fitting models and the ggplot2 package (Wickham 2016) for creating figures.

Results

Variation in life histories

The Atlantic salmon showed great life-history variation among both individuals (Figs. 2 and 3) and populations (Fig. 1). Based on the combination of smolt age, maiden sea age, and sea age(s) at repeat spawning, there were 141 unique life-history types identified across all individuals. Most individuals had smolt age 2–5 years, sea age 1–3 years, and were not repeat spawners (Fig. 4). The most extreme life-history type was a single 12-year-old female (108 cm, 15.3 kg) caught in 2011 in the Alta River when she was returning for her fourth spawning after a total of 8 years since smolt out-migration.

Repeat-spawning individuals contributed to 106 (75%) of the 141 observed life-history types despite only 4% of the fish being repeat spawners. Females had 129 life-history types, of which 75% included repeat spawning. Males had 102 life-history types, of which 71% included repeat spawning (ignoring precocious maturation). The most common repeat-spawning types included fish that returned for their first spawning at sea age of 1SW or 2SW (maiden sea age) and then returned as alternate or consecutive spawners, constituting 89% of the repeat spawners across both datasets (Figs. 2 and 3). The remaining repeat-spawning life-history types constituted fish with higher maiden sea age and (or) longer time between spawning events. Repeat spawning substantially increased the number of unique life-history types, but even the most common repeat-spawning life-history types were rare (Fig. 4).

The observed number of life-history types varied greatly among rivers (Fig. 5; range: 1–51), but was highly dependent on number of sampled individuals within each river (Table 1). After controlling for sample size, the rivers of the North region stood out by having high life-history diversity in females (Fig. 5). Females in these rivers had 32% (i.e., 0.28 on the natural log scale) more life-history types than both males of the same region and females of the South region (the intercept) (Table 1). Dataset 2 had 18% fewer life-history types than the South region in Dataset 1 (Table 1). The effect of latitude in Dataset 2 was large but highly uncertain and not statistically significant in the sense that the magnitude of the estimate was smaller than two times its standard error (SE) (Table 1).

Estimated differences not mentioned above were small and not statistically significant (Table 1).

Repeat spawners

Probability of repeat spawning was highly dependent on region, sex, maiden sea age, population mean sea age, population mean smolt age, and latitude (Table 2; Fig. 6). The estimates of this analysis are in units of log odds, where the odds is a measure of the likelihood of a particular outcome. Hence, the exponent of the estimated differences in log odds gives the proportional change in this likelihood. Based on Dataset 1, fish from the South region had 1.4 times higher odds of becoming a repeat spawner compared with fish from the North region; females had 2.1 times higher odds compared with males; and fish maturing after one winter at sea had 1.9-times higher odds compared with fish maturing after two winters at sea. An increase of 1 year in population mean sea age increased the odds of becoming a repeat spawner by a factor of 1.6, while a decrease in 1 year of population mean smolt age increased the odds by a factor of 1.3. Within region, a change in latitude by 10° northward increased the odds of repeat spawning by a factor of 2.1. All these differences were statistically significant in the sense that the magnitude of each estimate exceeded two times its SE (Table 2). In addition, there was a weak but statistically significant effect of individual smolt age (Table 2); a fish smolting at age two had 1.06 times higher odds compared with a fish smolting at age three. Odds are nonlinearly related to probability. Therefore, to ease interpretation, the estimated effects of sex, sea age, and population mean sea age on probability of repeat spawning are shown in Fig. 6. Note that the estimated effect of population mean sea age is within maiden sea age (i.e., controlling for sea age composition). The total effect of population mean sea age was negative (-0.16 ± 0.01 log odds/yr), meaning that the occurrence of repeat spawners among all fish is lower in populations with high mean sea age compared with populations with low mean sea age.

The analysis of Dataset 2 was largely in agreement with that of Dataset 1 (Table 2), but the estimated effects of population mean sea age and population mean smolt age were much stronger. In contrast to the analysis of Dataset 1, there was a strong negative effect of latitude (Table 2) and a positive total effect of population mean sea age (1.75 ± 0.23 log odds/yr).

An alternative way of studying variation in proportion of repeat spawners among populations is in relation to the MSW component of the returning adults. This analysis is about the composition of the MSW fish in a population rather than variation in probability of repeat spawning among fish with different life history as in the above analysis. For the MSW component of returning adults in Dataset 1, there were proportionally fewer repeat spawners in the North region and proportionally more in the Middle region compared with the South region (Table 3). The proportion of repeat spawners was much higher among 3SW fish compared with 2SW fish (i.e., a positive effect of sea age at capture) and males had more repeat spawners than females (Table 3). The proportion of repeat spawners within sea age at capture was negatively

Fig. 4. Proportion of fish within different life-history types within region and datasets. Numbers on the x-axis (life history) represent smolt age; maiden sea age → sea age at repeat spawning. Only the 20 most common life-history types are shown.

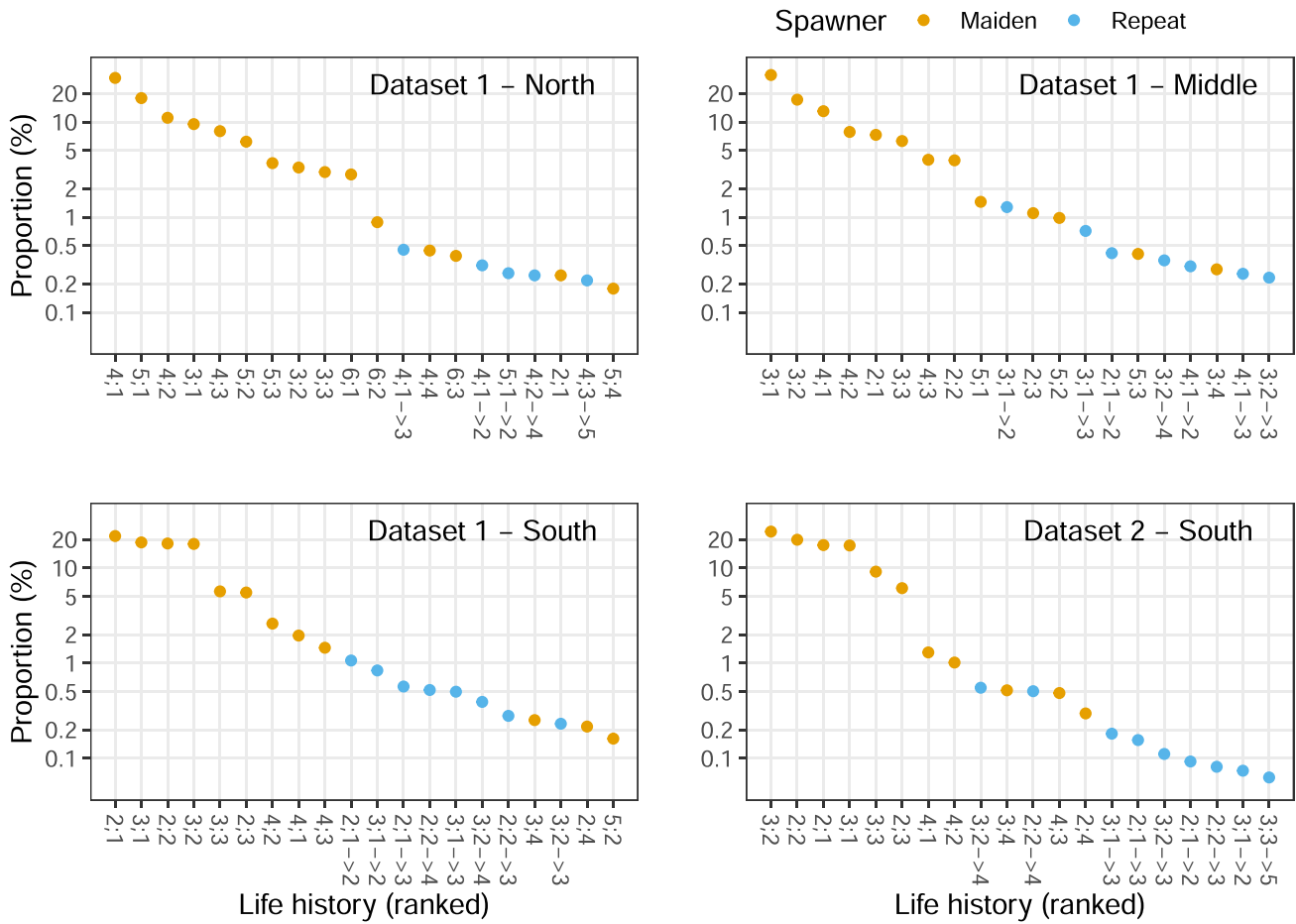


Fig. 5. Number of life-history types within each river (open circles). Vertical lines show estimated average number of life-history types for each region given a sample size of 424 fish (the average sample size) with 95% confidence interval indicated by the shaded area. See Table 1 for parameter estimates of the fitted model.

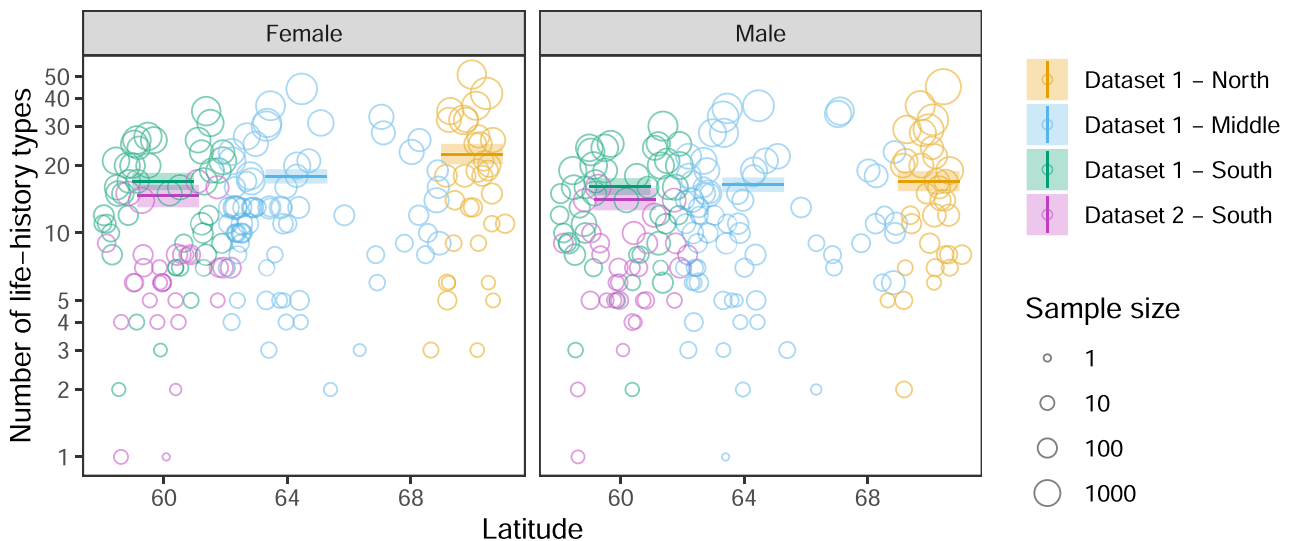


Table 1. Parameter estimates (\pm SE) for the linear model with natural log number of sex-specific life-history types in each river as a response variable.

Parameter	Estimate*
Intercept (F in D1—South)	2.84 \pm 0.05
Difference to F in D1—Middle	0.05 \pm 0.06
Difference to F in D1—North	0.28 \pm 0.07
Difference to F in D2—South	-0.20 \pm 0.10
Sex difference [†] in D1—South	-0.05 \pm 0.06
Sex difference [†] in D1—Middle	-0.09 \pm 0.05
Sex difference [†] in D1—North	-0.28 \pm 0.07
Sex difference [†] in D2—South	-0.03 \pm 0.08
Latitude D1	0.11 \pm 0.11
Latitude D2	0.52 \pm 0.37
Sample size D1	0.37 \pm 0.01
Sample size D2	0.35 \pm 0.03

Note: Fixed factors were regions within datasets (D1 and D2), sex (F = female), and sample size.

*All estimates are in units of $\ln(\text{number of life histories})/\ln(\text{number of individuals})$, and latitude, which is the change in $\ln(\text{number of life histories})$ for a 10° change northward.

[†]Difference from females to males within each region and dataset.

associated with increasing population mean smolt age and population mean sea age (Table 3). The total effect of population mean sea age (i.e., not controlling for individual sea age) was also negative and estimated at -1.34 ± 0.05 log odds/yr. There was no effect of latitude (Table 3).

The analysis of Dataset 2 was largely in agreement with that of Dataset 1 (Table 3). However, males did not differ much from females in proportion of repeat spawners among MSW fish, and there was a negative effect of latitude (Table 3).

Alternate versus consecutive spawners

According to our analysis of Dataset 1, the choice of reconditioning an extra year at sea between spawning events (alternate spawners) compared with returning 1 year after the previous spawning (consecutive spawners) depended on maiden sea age and sex (Table 4; Fig. 7). Females had 1.47 times higher odds than males of becoming an alternate spawner, and a fish with maiden sea age 2SW had 1.70 times higher odds than a fish with maiden sea age 1SW. In addition, repeat spawners shifted from being dominantly consecutive spawners in populations with low mean sea age to being dominantly alternate spawners in populations with high mean sea age (Table 4; Fig. 7). There was an increase in proportion alternate spawners with latitude within regions (Table 4). The Middle region had lower proportion alternate spawners than the South, while the difference between the South and North was estimated to be positive, but with an SE exceeding the magnitude of the estimate (Table 4). The results of Dataset 2 are in agreement with those of Dataset 1, but uncertainties are larger due to the lower sample size (Table 4).

Cost of reproduction in terms of reduced body mass

When fish return to spawn, they spend energy on reproduction, while fish staying at sea continue to invest in somatic growth. At low to intermediate population mean sea age, all repeat spawner categories had substantially reduced mass compared with maiden spawners with the same sea age at capture, but female alternate spawners maturing as 2SW and returning to spawn again as 4SW fish (the 2→4 category) stood out by having much higher relative mass than the other categories (Fig. 8). Male repeat spawners maturing as 2SW had lower relative mass than females in the same categories (male–female difference was -0.14 ± 0.03 and -0.27 ± 0.04 \ln kg for the 2→3 and 2→4 categories, respectively). Such a sex difference in relative mass was not observed for the 1SW maiden fish (male–female difference was 0.00 ± 0.02 and -0.02 ± 0.02 \ln kg for the 1→2 and 1→3 categories, respectively). The substantial reduction in relative body mass of repeat spawners was confirmed in the analysis of Dataset 2 (Table S1).

There were strong positive associations between population mean sea age and relative body mass for most repeat spawner categories (Fig. 8). The exceptions were for consecutive spawners maturing as 1SW (the 1→2 category), which had a negative association in females and no relationship in males (Fig. 8). The positive association in the 2→4 females was uncertain and not statistically significant. In Dataset 2, associations between population mean sea age and relative mass were highly uncertain (Table S1).

Discussion

We studied variation in iteroparity and its contribution to life-history complexity across 179 Atlantic salmon populations from rivers spanning 14° latitude. The proportion of repeat spawners varied between 0% and 26% among populations and was, on average, higher in the south than in the north of Norway. A total of 141 unique anadromous life-history types were identified. The repeat spawning individuals contributed to 75% of the variation in life-history types, which is very similar to the 76% of variation represented by repeat spawning individuals in the large Tana watercourse (Erkinaro et al. 2019). However, the overall proportion of repeat spawning individuals in our data was small, and most life-history types were rare. Among populations, both probability of repeat spawning and probability of alternate versus consecutive spawning were positively associated with population mean sea age. In addition, we observed a negative, and less pronounced, association between population mean smolt age and probability of repeat spawning.

Association between pairs of traits across populations, such as degree of repeat spawning and sea age, can arise through coinherence (e.g., pleiotropy) or “selective covariance”, where natural selection shapes the among-population trait covariance (Armbruster and Schwaegerle 1996). Aykanat et al. (2019) found coinherence between repeat spawning and sea age at maturity mediated by the genetic variation in

Table 2. Parameter estimates (\pm SE) for the logistic models with probability of repeat spawning as the response variable.

Parameter	Dataset 1	Dataset 2*	Units
Intercept (Females in South)	-1.95 ± 0.12	-4.23 ± 0.46	Log odds
Difference to Middle	-0.14 ± 0.08	-	Log odds
Difference to North	-0.35 ± 0.10	-	Log odds
Difference to Males	-0.75 ± 0.04	-0.61 ± 0.15	Log odds
Maiden sea age	-0.62 ± 0.04	-0.34 ± 0.13	Log odds/yr
Smolt age	-0.06 ± 0.03	-0.09 ± 0.13	Log odds/yr
Population mean sea age [†]	0.46 ± 0.12	2.10 ± 0.49	Log odds/yr
Population mean smolt age [†]	-0.28 ± 0.11	-1.16 ± 0.45	Log odds/yr
Latitude [†]	0.76 ± 0.24	-2.75 ± 0.73	Log odds/10°

*Dataset 2 does not include regions Middle and North.

[†]The variable was centered on its region means.

Fig. 6. Estimated relationships between population mean sea age and probability of repeat spawning for different sea ages at maturity in Dataset 1. The elevation of the relationships reflects the South region at the mean smolt age and latitude. Model parameters are given in Table 2.

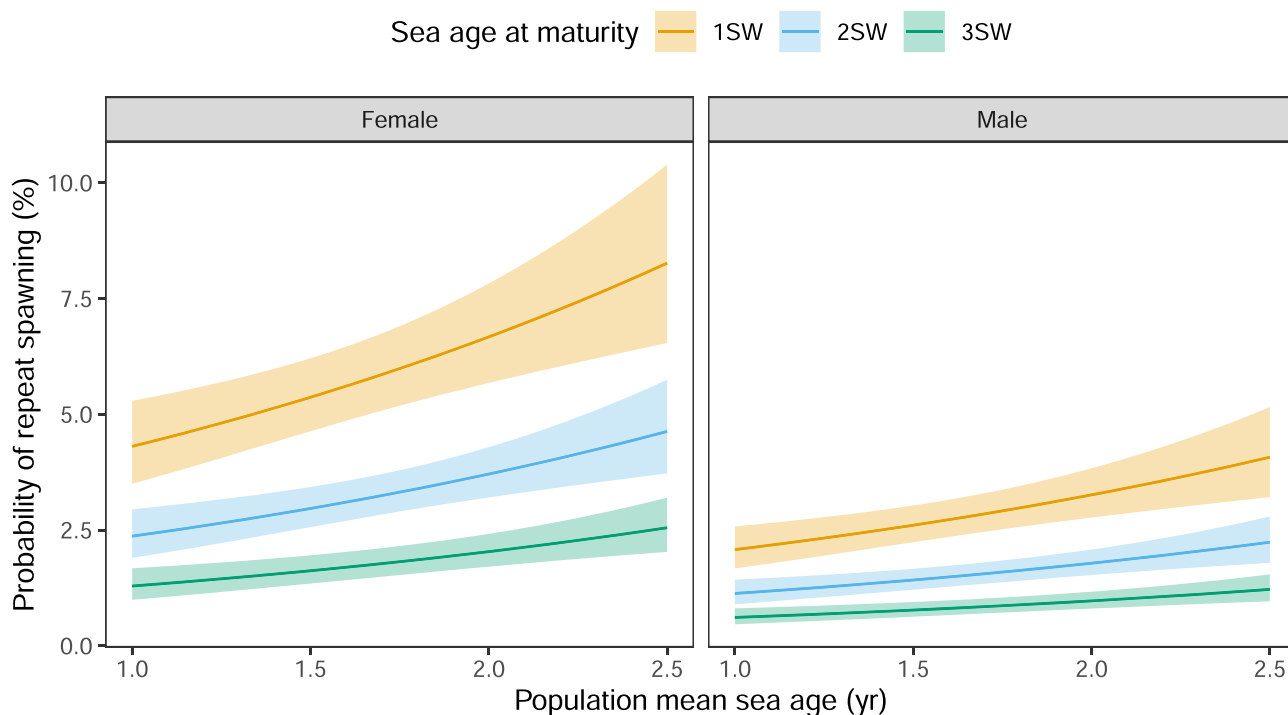


Table 3. Parameter estimates (\pm SE) for the logistic models with proportion of repeat spawners among MSW fish as the response variable.

Parameter	Dataset 1	Dataset 2*	Units
Intercept (females in South)	-8.87 ± 0.18	-15.08 ± 0.44	Log odds
Difference to Middle	0.31 ± 0.16	-	Log odds
Difference to North	-0.67 ± 0.18	-	Log odds
Difference to males	0.39 ± 0.05	-0.17 ± 0.12	Log odds
Sea age at capture	2.45 ± 0.05	3.85 ± 0.12	Log odds/yr
Population mean sea age [†]	-3.79 ± 0.24	-1.69 ± 0.65	Log odds/yr
Population mean smolt age [†]	-0.47 ± 0.20	-1.70 ± 0.61	Log odds/yr
Latitude [†]	0.14 ± 0.45	-4.39 ± 1.02	Log odds/10°

*Dataset 2 does not include regions Middle and North.

[†]The variable is centered on its region means.

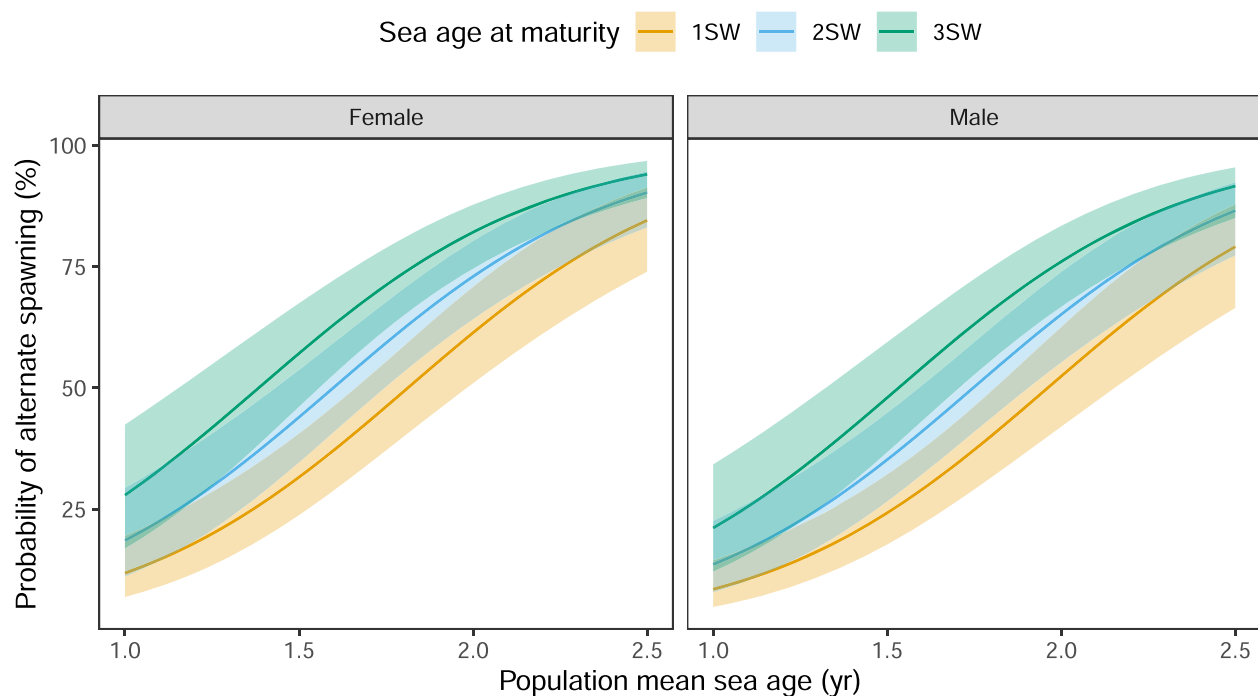
Table 4. Parameter estimates (\pm SE) for the logistic models with the probability of alternate rather than consecutive spawning as the response variable.

Parameter	Dataset 1	Dataset 2*	Units
Intercept (females in South)	-0.97 ± 0.27	2.00 ± 0.54	Log odds
Difference to Middle	-0.49 ± 0.22	–	Log odds
Difference to North	0.25 ± 0.27	–	Log odds
Difference to males	-0.37 ± 0.08	-0.35 ± 0.24	Log odds
Maiden sea age	0.53 ± 0.07	0.13 ± 0.26	Log odds/yr
Smolt age	0.04 ± 0.06	–	Log odds/yr
Population mean sea age [†]	2.47 ± 0.34	2.70 ± 0.73	Log odds/yr
Population mean smolt age [†]	0.00 ± 0.30	–	Log odds/yr
Latitude [†]	1.57 ± 0.65	1.10 ± 1.21	Log odds/10°

*Dataset 2 does not include regions Middle and North, and we excluded the effect of smolt age and population mean smolt age to increase sample size and facilitate model convergence.

[†]The variable is centered on its region means.

Fig. 7. Estimated relationships between population mean sea age and probability of alternate rather than consecutive spawning for different sea ages at maturity in Dataset 1. The elevation of the relationships reflects the South region at the mean smolt age and latitude. Model parameters are given in Table 4.

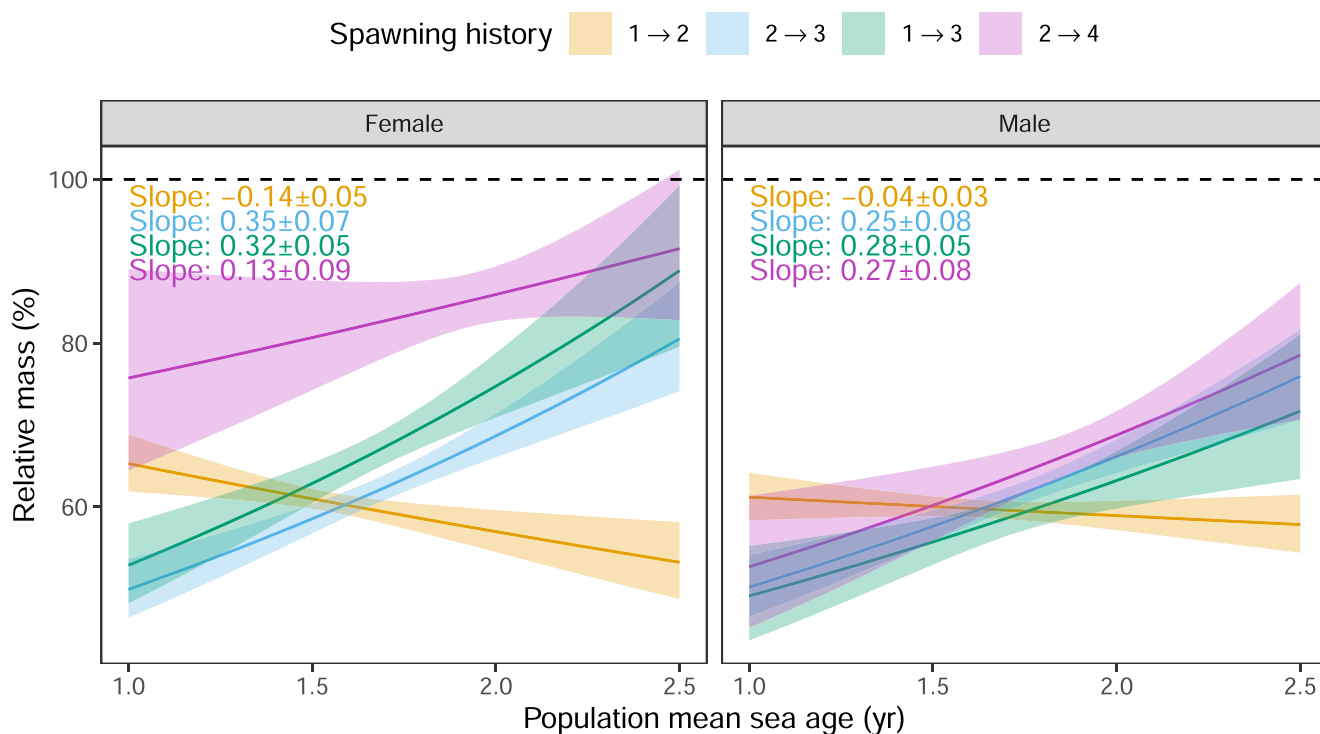


the *vgll3* genomic region, where individuals genetically predisposed to mature early had a higher probability of repeat spawning. In contrast, we found that the probability of repeat spawning increased with increasing population mean sea age. Therefore, the among-population differentiation in iteroparity cannot be caused by coinheritance with sea age. Instead, our results suggest that natural selection acting on genetic variation at additional genomic regions is important for shaping population differentiation in iteroparity. However, the *vgll3* genomic region may still be an important determinant of degree of iteroparity within populations, as shown by Aykanat et al. (2019), and supported by our findings of a higher probability of repeat spawning for fish that returned for their first reproduction after 1 year at sea (1SW maiden

fish) than fish with delayed reproduction (MSW maiden fish) (see also Jonsson et al. 1991a; Erkinaro et al. 2019).

The increasing degree of iteroparity with population mean sea age would be in accordance with optimality theory if populations with high mean sea age have lower, or more stochastic, juvenile survival compared with populations with low mean sea age (Schaffer 1974; Orzack and Tuljapurkar 1989). However, we currently lack empirical data on the relationship between mean sea age and juvenile survival to test this hypothesis. Among salmonids, iteroparous species have smaller egg size than semelparous species, suggesting that the iteroparous species invest less in offspring survival than the semelparous (Crespi and Teo 2002). In Atlantic salmon, egg size is correlated with body size (Thorpe et al. 1984) and

Fig. 8. Biomass at return of repeat spawners relative to maiden spawners of the same sea age at capture for different sexes and spawning histories in Dataset 1. Spawning histories are “maiden sea age” → “sea age at second reproduction”. The printed slopes (b) are on the natural log scale. Relative mass (%) was calculated as $100 \times \exp(a + bx)$, where \exp is the exponential function, a is the intercept, and b is the slope of the relationship on log scale. All parameter estimates of the model are in Table S1.



populations with high mean sea age have larger body size at sea age (Bolstad et al. 2017). Taken together with our results, this implies that degree of iteroparity is positively related to egg size among Atlantic salmon populations, the opposite pattern than Crespi and Teo (2002) observed across salmonid species. In addition, given the assumption that high smolt age is associated with lower juvenile survival due to increased risk of dying with time, the observed negative effect of population mean smolt age on probability of repeat spawning is the opposite of the prediction of optimality theory.

An alternative adaptive explanation for increased degree of iteroparity with increasing population mean sea age is selection arising from the trade-off between current and future reproduction. This hypothesis implies that the trade-off plays out differently among populations and affects not only the maiden sea age but also proportion of repeat spawners within sea age groups and the recondition period of the repeat spawners. Under this hypothesis, saving energy at first spawning to improve the chance of returning as a larger repeat spawner at the expense of current reproduction is more beneficial in populations with high mean sea age compared with populations with low mean sea age. This is particularly true for the large alternate repeat spawners, which are the dominating type of repeat spawners in populations with high mean sea age. In concordance with this hypothesis, we observed that the reduced mass of alternate spawners compared

with maiden spawners of the same sea age at capture was more pronounced in populations with low mean sea age than populations with high mean sea age. This suggests that alternate spawners in populations with high mean sea age save more energy at first reproduction than alternate spawners in populations with low mean sea age.

There may be additional explanations for variation among populations in repeat spawning patterns. Increased adult survival selects for increased degree of iteroparity (Charnov and Schaffer 1973). Hence, variation in adult overwintering conditions (e.g., presence of lakes or large pools suitable for overwintering) may contribute to the large among-population variation in proportion of repeat spawning (Fig. 1). If river overwintering conditions are correlated with population mean sea age or smolt age, this may be part of the explanation for the reported relationship between these two variables and degree of iteroparity. Variable energy expenditure during spawning migration in different rivers is also a possible factor contributing to different levels of iteroparity among populations (Jonsson et al. 1997). Variation in water flow may influence juvenile survival and hence affect the evolution of iteroparity. Variation in water flow has been suggested to underlie evolution of other bet-hedging spawning strategies such as increased number of redds to minimize risk of stranding (Barlaup et al. 1994). In addition, realized number of repeat spawners for a given probability is stochastic, and there is also among-year variation in probability of

repeat spawning, generating variation in observed number of repeat spawners.

Anadromous females and males that matured at a young age and a small size (1SW fish) were more likely to become repeat spawners than larger, late-maturing fish (MSW fish). This is expected, as smaller fish invest relatively less energy at spawning than larger fish, and the chance to survive to spawn a second time increases with decreasing energy investment at first spawning (Jonsson et al. 1991a, 1997; Christie et al. 2018; Bordeleau et al. 2019).

Despite their older mean sea age at maturity, females were more likely to become repeat spawners than males (ignoring precocious maturation). The higher postspawning survival of females (see also Jonsson et al. 1990; Jonsson and Jonsson 2003) may arise from a sex difference in the trade-off between current and future reproduction. Our observation that for repeat spawners with maiden sea age of 2SW, males had more reduced mass than females suggests a higher investment in current reproduction by males. However, we did not observe such a sex difference for repeat spawners with maiden sea age of 1SW. Jonsson et al. (1991b) found that 1SW males and 1SW females invested the same amount of energy at spawning, but their study was based on few fish from one river, and they compared the energy content of spawners and spent fish within a 3-month period only (November to January). The reproductive cost may not only be related to the total amount of energy invested. Female energy expenditure is mainly related to the development of eggs, whereas male energy expenditure is mainly somatic, related to activities like aggressive interactions on the spawning ground (Jonsson and Jonsson 2003). Injuries resulting from aggressive interactions among males on the spawning ground likely contribute to the lower postspawning survival of males compared with females (Jonsson et al. 1991b; Jonsson and Jonsson 2003). The ability to recondition after spawning may also be compromised to a larger extent in males than females due to the different energy expenditures (gonadal versus somatic).

The alternate strategy of reconditioning 2 or more years at sea before next spawning instead of 1 year was more common in late-maturing large fish than in early-maturing small fish. This is in line with previous research (Schaffer and Elson 1975; Jonsson et al. 1991a; Klemetsen et al. 2003). In addition, we observed that the proportion of alternate spawners increased with increasing population mean sea age. This correlation between mean sea age and recondition period suggests either a tight coinheritance between sea age and recondition period, or a strong selective covariance where natural selection has shaped the among-population correlation (Armbruster and Schwaegerle 1996). However, because the effect of population mean sea age was much stronger than the effect of sea age among individuals (within populations), the evidence is in favor of selective covariance.

The smaller proportion of repeat spawners in the north compared with the south of Norway can be related to variable environmental conditions. Freshwater conditions are believed to be the main driver of population differentiation and life-history variation across populations of Atlantic salmon

(Taylor 1991; Fleming 1996; Garcia de Leaniz et al. 2007). Both geology and climate (temperature and precipitation) have been found to be associated with potentially adaptive and neutral genetic divergence in Atlantic salmon on a regional scale (Bourret et al. 2013a). Growth opportunity, given by temperature and photoperiod, is negatively related to age at seaward migration as smolts (Metcalf and Thorpe 1990). Both the difficulty of upstream migration (Schaffer and Elson 1975) and river discharge (Jonsson et al. 1991a) are positively associated with mean sea age at maturity. In addition to differences in freshwater environment, salmon populations in the north have been suggested to use different feeding areas in the ocean compared with populations in the south of Norway (Rikardsen et al. 2021; Vollset et al. 2022). As oceanic conditions also vary, there is room for adaptation to occur; however, adaptation to the marine environment would likely happen at a larger spatial scale and with less selective pressure compared with freshwater environments (Fraser et al. 2011). There is also a different colonization history and genetic composition of the populations in the north compared with the rest of Norway (Verspoor et al. 2005; Bourret et al. 2013b). This might have contributed to the variation in iteroparity across regions, but increased knowledge of the genetic basis of repeat spawning is needed to further understand the potential effects of colonization history on iteroparity.

Scale readings provide ample opportunities for studying growth and life history of salmon. However, previous spawning is difficult to interpret because spawning marks are caused by erosion in freshwater, which may erode winter bands and make them more or less visible (ICES 1984). A study using occurrence of gill maggot (*Salmincola salmoneus*) as an independent indicator of repeat spawning showed that 96% of the fish with gill maggots (92 of 96 fish) were also identified as repeat spawners by the scale readers (Kusterle et al. 2013), confirming that scale reading is an appropriate method to identify previous spawning. In addition, the average proportion of repeat spawning estimated at 4.3% (Dataset 1) was very similar to the average of 4.6% reported almost a century ago by Huitfeldt-Kaas (1946). Despite experienced scale-reading personnel assembling both our datasets, there were discrepancies in proportion of repeat spawners and degree of consecutive spawning between the datasets. These discrepancies highlight the complicated matter of scale reading. International calibration exercises have been carried out to increase the quality of scale reading (e.g., ICES 1984, 2013), and methods to increase objectivity are also under development (ICES 2011). However, having two independent datasets is a strength of our study, because it reveals that conclusions are robust to methodological differences. The connection between iteroparity and population mean sea age, which may suggest local adaptation of repeat-spawning life history, was robust and confirmed in both datasets. Also, the difference in reproductive strategies between females and males was observed in both datasets.

In addition to methodological issues related to scale reading, there might be biases in catchability of repeat spawners compared with maiden fish that can cause an underestimation of proportion of repeat spawners (Halttunen 2011;

Harvey et al. 2022). This should only affect the estimated proportion of repeat spawners, but not its relationship to population mean sea age or smolt age, given the assumption that catchability differences do not vary among rivers. Systematic bias in sexing of fish, with small females sometimes being mistaken as males (Robertson et al. 2021), likely caused an overestimation of probability of repeat spawning in females compared with males. When we excluded fish where sexing is most unreliable (1SW maiden sea age), the effect of sex was still large in the analysis of probability of repeat spawning (Supplementary Table S2). The error in sexing the fish should not affect other results (i.e., other than the effect of sex), as we did not include any interaction between sex and other parameters in the models. Among the repeat spawners, for which sexing is thought to be more reliable, there were many more females than males (3334 female and 2462 male repeat spawners in Dataset 1 and 546 female and 349 male repeat spawners in Dataset 2), strongly suggesting that the females have a higher probability of repeat spawning than males. In contrast, males had a higher proportion of repeat spawners than females when analyzing the MSW component only. This can be explained by the lower number of maiden MSW males than maiden MSW females.

Using a large-scale analysis, this study aimed at providing new insights into the evolution and population divergence of repeat spawning. Improved understanding of drivers and influencing factors on repeat-spawning life history may benefit fisheries management and is important for Atlantic salmon conservation that aims to preserve genetic and life-history diversity as well as population integrity, demographics, and viability.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare that there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2022-0126>.

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