

Optimal timing of return migration in Atlantic salmon

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Abstract

In many populations of Atlantic salmon, individuals return to rivers months or even a year prior to spawning. This premature arrival in fresh water by far exceeds the time needed for upstream migrations to spawning areas. Leaving the ocean early means forgoing substantial growth and incurring high metabolic costs of fasting in freshwater. Differences in timing of return migration has been shown to have a genetic basis, and different sea age classes return to rivers at different times. Previously suggested explanations regarding the cause for this behaviour have included both environmental factors and life history trade-offs, but these hypotheses have not been tested. Here, we combine data on marine growth and mortality of Atlantic salmon with the calculations of energetic expenditures of fasting in freshwater to explore how timing of river entry affects the probability of survival and energy recourses available for spawning. Our results show that to maximize the product of survival until spawning and energy available at spawning, multi sea winter fish in general must enter rivers earlier than one sea winter fish. And that for a large range of sea survival rates, the optimum river entry date for multi sea winter fish is as early as possible. This strongly suggests that the phenomena of premature arrival in Atlantic salmon is adaptive behaviour.

KEYWORDS

Atlantic salmon, energy, migration, premature migration, run timing, sea survival

1 | INTRODUCTION

Among the many unsolved problems in the life history of the Atlantic salmon one of the most interesting is concerned with the time at which the salmon enter the rivers for spawning.

(Belding & Kitson, 1934)

For Atlantic salmon, the main growth and feeding occurs during the marine phase of the lifecycle, and the size of the adults is strongly related to the length of time spent in the ocean before returning to rivers to spawn (Bacon et al., 2011). Throughout the geographic range of Atlantic salmon, some adults will leave the

feeding areas in the ocean and enter rivers many months or even a year before spawning (Berg, 1948; Lysenko, 1997; Power, 1981; Quinn et al., 2016; Studenov et al., 2008; Thorstad et al., 2011). After river entry, feeding opportunities are negligible, and the fish will need to rely on the energy reserves accumulated in the ocean for the duration of the river stay. Differences in the timing of return migration has been shown to have a genetic basis (Cauwelier et al., 2018; Stewart et al., 2002). Also, different sea age classes tend to return to rivers at different times, with the oldest and largest returning first (Borgstrøm et al., 2010; Gurney et al., 2015; Harvey et al., 2017; Power, 1981; Thorstad et al., 2011). For both sexes, size and/or energy reserves are important for the reproductive success, making premature arrivals puzzling. So, why do

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Atlantic salmon forego growth opportunities in the ocean, and incur the metabolic cost of fasting during a protracted freshwater stay?

Premature arrivals can be defined as an arrival in fresh water earlier than required for fish to reach the spawning area and reproduce (Quinn et al., 2016). Although some Atlantic salmon have long river migrations (e.g. Pechora 1809 km Studenov et al., 2008, Loire 940 km Prouzet, 1990 and Tornio 522 km Huusko et al., 2023), most salmon rivers have considerable shorter stretches accessible to salmon, for example, most Norwegian salmon rivers are shorter than 15 km (L'Abée-Lund et al., 2004). Estimated speed of upstream migration is between 1.6 and 31 km per day (Thorstad et al., 2008). With spawning occurring late in the year, this implies that the vast majority of observed early arrivals of Atlantic salmon in spring is premature. Quinn et al. (2016, Appendix A) suggest two not mutually exclusive hypothesis to explain premature migration (i) fish are forced to migrate earlier than otherwise optimal due to environmental conditions, or (ii) early migration is the result of fish balancing marine growth against survival probability.

Seasonal changes in environmental factors such as temperature and water discharge have been suggested to restrict freshwater migrations and potentially forcing migration to occur much earlier than needed to reach spawning grounds (Quinn et al., 2016). Water temperature and flow are in most rivers not independent and both high and low temperature extremes will often occur at low water discharges. Low discharge can prevent upstream migration of salmon both by making upstream movement difficult and by affecting motivation of fish (Erkinaro, Økland, Moen, Niemelä, & Rahiala, 1999; Jensen, 1999; Lilja & Romakkaniemi, 2003; Power, 1981). High water temperatures can be lethal to migrating adults (Baisez et al., 2011), and fish migrating during high temperatures will incur higher energetic costs (Lennox et al., 2018). Upstream migration prior to onset of high temperatures, allowing the fish to reach higher and cooler tributaries or other thermal refuges, has been suggested as a factor shaping early migration in populations in Main and Connecticut, U.S. (Power, 1981) and the River Allier, France (Baisez et al., 2011).

At low temperatures, swimming capacity of Atlantic salmon is reduced (Beach, 1984), potentially affecting their ability to ascend rivers. Several studies have shown that water temperature must be above certain levels for Atlantic salmon to be motivated to and/or have the swimming capacity necessary to pass obstacles such as waterfalls and fish ladders (Jensen, 1999). In northern populations, the Atlantic salmon enters and ascend rivers after ice breakup (Lilja & Romakkaniemi, 2003; Power, 1981), suggesting that low temperatures and ice cover are constraints on the upstream movement of adult salmon. In some rivers in Scotland, England, France, Germany and Denmark, Atlantic salmon ascend(ed) in most months of the year (Nordqvist, 1924; Shearer, 1990; Thorstad et al., 2011). These rivers appear to lack the environmental conditions (temperature and ice) that restrict migration in other rivers that have higher seasonal variation in temperature and/or discharge. In addition to environmental

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factors influencing upstream migration, availability of holding and resting habitats such as lakes and deep pools have been shown to affect the incidence of premature migration (Reed et al., 2017). Given that rivers differ in length and seasonal timing of the period(s) of time where environmental factors allow upstream migration of Atlantic salmon, this could potentially explain some of the variation in premature migration between populations. Such differences could, however, for most populations be viewed as just setting the limits for when migration can occur, and with a few potential exceptions mentioned above, does not explain why premature migration is so common.

The second hypothesis suggested in Quinn et al. (2016, Appendix A) is that Atlantic salmon are striking a balance between the costs of early river entry against the costs of remaining in the ocean. The two main costs of early river entry are the increased energetic expenditure due to fasting in fresh water and the lost growth that could have been achieved by remaining in the ocean.

The energetic cost of river entry will strongly depend on the length of the freshwater stay and the water temperature the fish experiences, and the amount of marine growth that is forgone is inversely related to river entry date. Both energetic costs of the freshwater stay and marine growth have allometric variation, meaning different size individuals may differ in the timing of optimal river entry. The main cost of remaining in the ocean is suggested to be higher mortality risk, and the hypothesis is completely dependent on the premise that the marine mortality is significantly higher than freshwater mortality.

Here, we test the hypothesis of premature migration being an optimal trade-off between growth and survival by combining data on marine growth of Atlantic salmon with estimated metabolic costs of freshwater stay and mortality rates. We do this by first exploring how different river entry times affect the total energy left at spawning for different sized/aged fish. We then use the product of energy available for spawning and probability of surviving until spawning as a proxy for relative fitness to assess optimal timing of river entry.

2 | METHODS

The optimal timing of river entry must maximize the product of probability of survival until spawning and the reproductive success (Figure 1). Here, we use total energy content of fish at spawning as a proxy for reproductive success. Total energy at spawning for different river entry dates was found by combining energy gained in the ocean until a given river entry date with subsequent energy loss during freshwater stay. Although not a perfect measure, total energy content of fish is directly related to how much reproductive effort fish can afford to invest in eggs and reproductive activities (females) or competition for access to mates (males). For females, body size is commonly the most important determinant of breeding success, while for males, the relationship is much weaker (Fleming & Einum, 2010). Probability of survival for different exit dates from salt water was included using a range of marine mortality rates from Strøm et al. (2019). The river entry date with the highest product of survival and total energy was considered optimal. A schematic overview of how we have calculated optimal river entry date is given in Figure 1.

2.1 | Marine somatic growth and total energy content

Analysis of marine growth was conducted based on scale samples from Atlantic salmon caught in bag nets at two locations in central

Norway (Figure 2) in the period 1997–2016. The 5972 scale samples included in this analysis were a subsample of a much larger collection of scale samples, and the criteria for being selected was that they had been aged and that length at different life stages/sea ages had been back calculated (using methods in ICES, 1984, 2011, 2013). In the analysis, growth in the year of capture, defined as growth from the last winter annulus was used. Fish that were classified by scale reading to be of hatchery or aquaculture origin were removed. Also, to avoid complications regarding classification of sea age, fish that had previously spawned were removed.

For each fish, date of capture and body length was registered (Figure 3a). The fish weight was recorded for a subset ($n=3502$). Fish caught in the Namsenfjord can be assumed to be dominated by fish returning to the River Namsen (Moe et al., 2016), while the fish caught at the entry of the Trondheimsfjord are likely of more mixed origin and will be dominated by fish returning to the rivers Gaula, Orkla and Stjørdalselva (Aronsen et al., 2016). Mark-recapture studies conducted with fish caught at the same bag net locations as used in this study, showed that in the Trondheimsfjord salmon on average enter rivers within 8–15 days after tagging (Aronsen et al., 2016) and in the Namsenfjord only 2 days after tagging (Næsje et al., 2013). It therefore is reasonable to assume that the fish included in this analysis were caught shortly before they would have entered freshwater.

The expected total energy content of an average fish of each sea age class was calculated for river entries ranging day of year

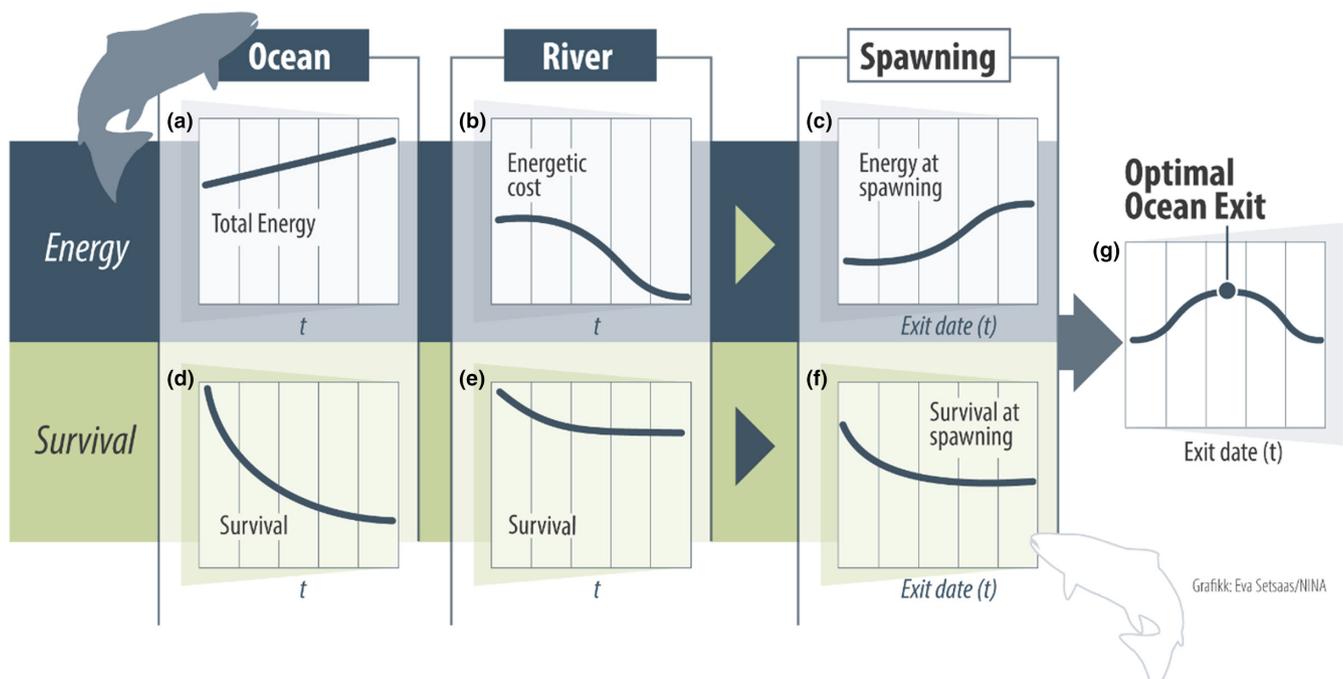


FIGURE 1 Schematic overview of how optimal river entry date was calculated. **Energy** (top grey panel): Total energy of the salmon at spawning (c) for a given river entry date, is the total accumulated energy in ocean until river entry date t (a), minus the metabolic cost of freshwater stay from day t to spawning (b). **Survival** (bottom green panel): For a given river entry date, the probability of survival to spawning (f) is the product of probability of marine survival until day of river entry (d) and the probability of survival in fresh water for the remaining number of days until spawning (e). **Optimal timing of river entry** (right white panel): Optimal river entry date (*) was defined at the date with the highest product of survival to spawning (f) and energy at spawning (c).

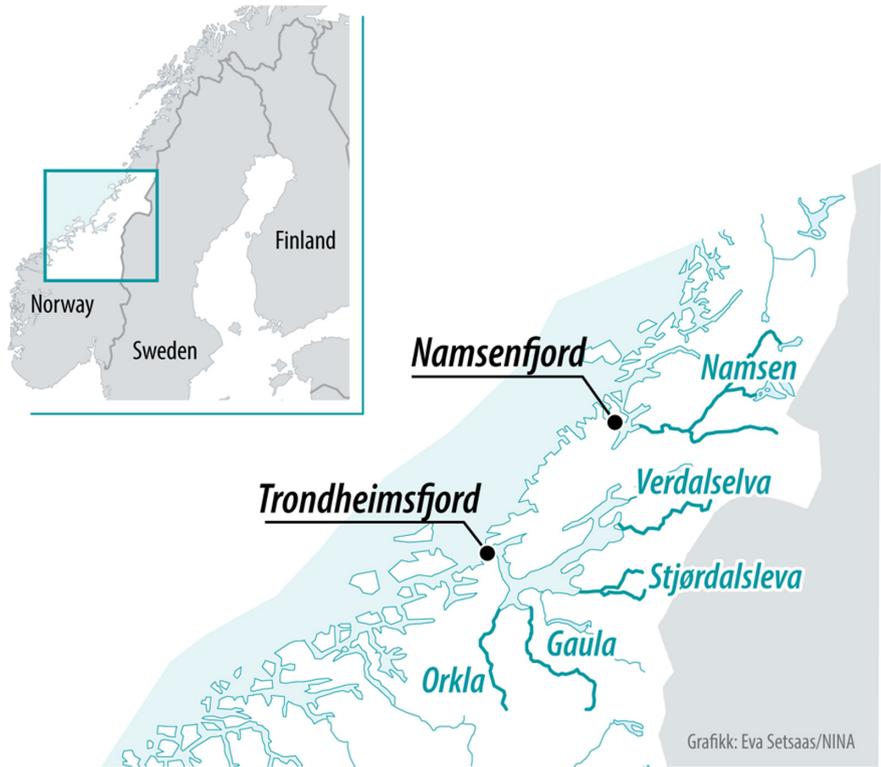


FIGURE 2 Map showing the two bagnet locations (black circles) where Atlantic salmon were caught, and the salmon rivers in the region (black lines).

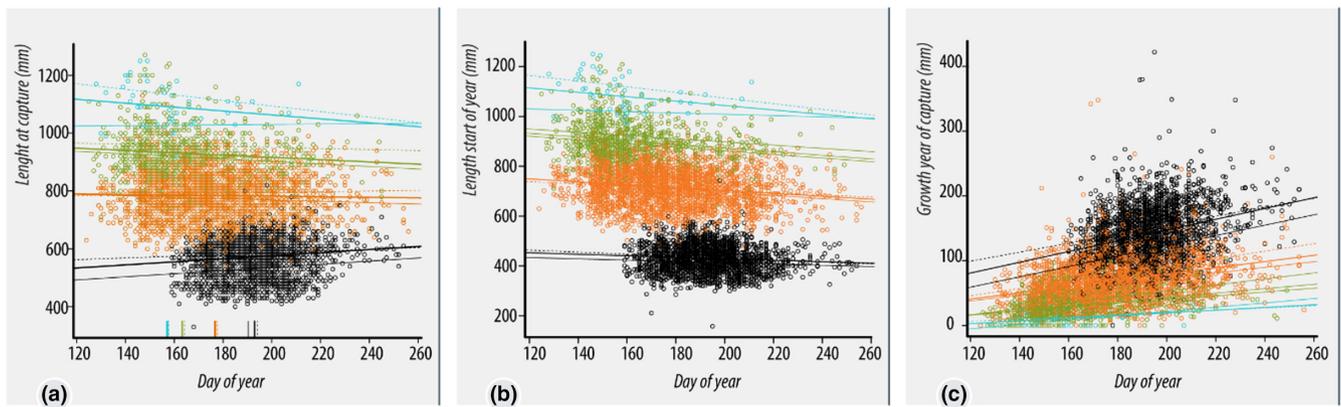


FIGURE 3 Atlantic salmon caught in bag nets in central Norway. Date of capture (x-axis) and (a) length of Atlantic salmon, (b) length at the last winter annulus, back calculated from scale samples and (c) growth from last winter annulus until date of capture. Colours of points indicate age in sea-winters (SW), black 1-SW, red 2-SW, green 3-SW and blue 4- and 5-SW. Bold lines show linear regressions of length (a), winter length (b) and growth (c) against capture date for all fish within a sea age group, and thin and dashed lines represent the same regressions but for female and males, respectively. In (a) vertical lines on the x-axis represent the mean capture date for the different sea ages and for females and males within the sea age groups.

120–300 (April 30th–October 27th). Day of year 300 is used as a cut off as this date is the middle of the spawning period in the river Gaular in the Trondheimsfjord (Heggberget, 2011), in our dataset no fish were caught prior to day of year 120. Calculation of the energy was done by first selecting the average winter length of each sea age class (Figure 3b) and then adding estimated growth per day of each sea age class based on linear regression (Figure 3c) for day of year 120–300. Length in cm (L) was then converted to total energy content in kJ (E) using the relationship,

$$\ln E = 0.044L + 6.99 \quad (1)$$

from Jonsson et al. (1997), and then converted to kcal using the conversion factor 0.239. Based on this, the expected total energy content of the average fish of each sea age at day of year 120–300 was calculated (Figure 4).

2.2 | Metabolic costs of freshwater stay before spawning

The resting metabolic rate of Atlantic salmon in freshwater will strongly depend on water temperature, and metabolic rate also

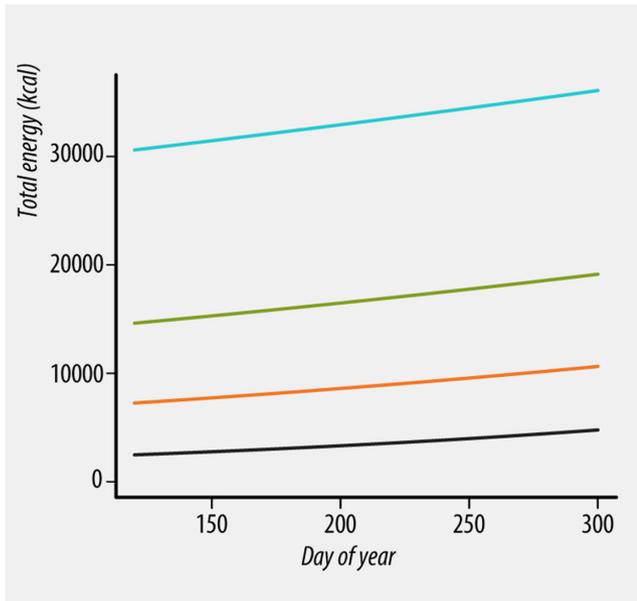


FIGURE 4 Estimated total energy content (kcal) of the average fish of sea age classes (y-axis); black 1-SW, red 2-SW, green 3-SW and blue 4- and 5-SW leaving the sea at different dates (x-axis).

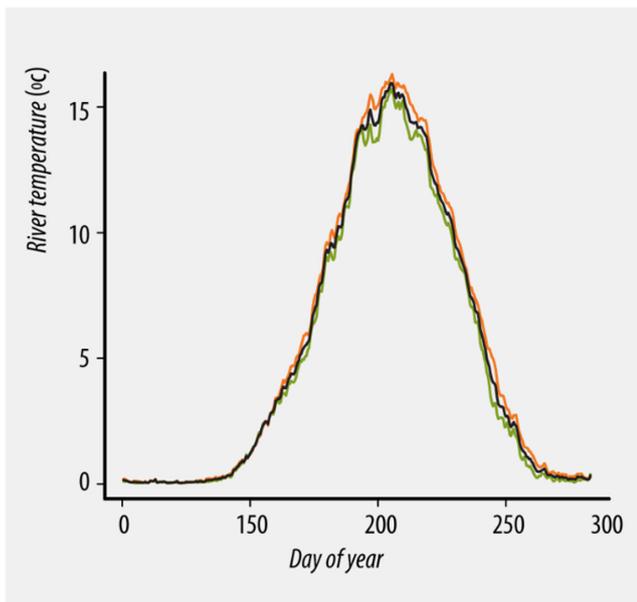


FIGURE 5 Daily average temperatures from the rivers Namsen (1986–2017, red) and Gaula (1984–2017, green) and the two combined (black).

depends on the size of fish. We used data on resting metabolic rate of Atlantic salmon from Lennox et al. (2018) in combination with water temperatures to calculate total energy expenditure during freshwater stay for river entry dates ranging day of year 120–300. River temperatures from the Namsen (1986–2017) and Gaula (1984–2017) rivers were obtained from The Norwegian Water Resources and Energy Directorate and combined to a daily average river temperature (Figure 5).

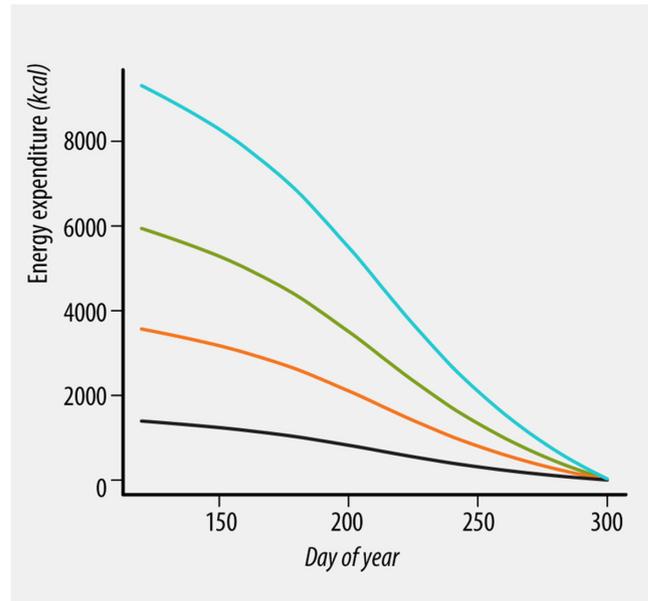


FIGURE 6 Cumulative energy expenditure (y-axis) for different day of river entry (x-axis) to day of year 300. Only energy expenditure in terms of resting metabolism is included and is calculated for the average size fish of sea ages 1 (black), 2 (red), 3 (green) and ≥ 4 (blue).

Daily energy consumption was calculated by using the daily average river temperature (T , °C) and data on resting metabolism of a 2.67 kg salmon (Lennox et al., 2018)

$$0.55e^{(0.705 T)} \text{ O}_2 \text{ kg}^{-1} \text{ min}^{-1} \quad (2)$$

This value was multiplied by 1440 to get $\text{O}_2 \text{ kg}^{-1} \text{ day}^{-1}$, and allometric scaling of this rate for the average size of different age classes was done using an equation from Steffensen et al. (1994).

$$MO2_{scaled} = MO2_{initial} \left(\frac{Mass_{initial}}{Mass_{scaled}} \right)^{1-a} \quad (3)$$

where $MO2_{initial}$ and $Mass_{initial}$ are the metabolic rate and weight of the salmon from Lennox et al. (2018) and, $MO2_{scaled}$ is the scaled metabolic rate of a fish of weight $Mass_{scaled}$ and a is the scaling parameter 0.80.

Average weight of the different age classes used for allometric scaling of metabolic rate was found by calculating the Fulton's condition-factor (K) (Nash et al., 2006; Ricker, 1975)

$$K = 100 \frac{W}{L^3} \quad (4)$$

where W is weight in g and L is length in cm, of the different sea age classes and using the expected length at day of year 120 to calculate an average weight of each age class. This weight was used for scaling of metabolic rate regardless of entry date and was not corrected for weight losses due to energy expenditure during river stay.

Cumulative energy expenditure of the average fish of each age class for entry dates ranging from 120 to 300 were calculated as the sum of daily expenditure from day of entry until day of year 300

(Figure 6). Energy expenditure related to upstream migration is not included in these calculations.

2.3 | Total energy at spawning

The energy status at spawning is a function of marine growth until the date of river entry and metabolic costs from that date until spawning. For each day of year between 120 and 300, the estimated total energy of the average fish of each sea age class (Figure 3) was found and cumulative energy expenditure from that date until day of year 300 (Figure 5) was subtracted. The resulting numbers show the differences in total energy at spawning that arise from different river entry dates (Figure 7).

$$T_i = E_{[120,i]} - M_{[i,300]}, \quad (5)$$

where T_i is total energy at spawning given river entry date i , $E_{[120,i]}$ is energy of fish at river entry date i and $M_{[i,300]}$ is the metabolic cost of fresh water stay from river entry date i to spawning (day of year 300).

2.4 | Optimal timing of river entry

To assess if the differences in observed river entry dates between sea age groups can reflect different optimal strategies, survival probability needs to be included. First, if there is no difference in daily marine and river mortality or if river mortality is higher than marine mortality, the optimal river entry time will be as late as possible for

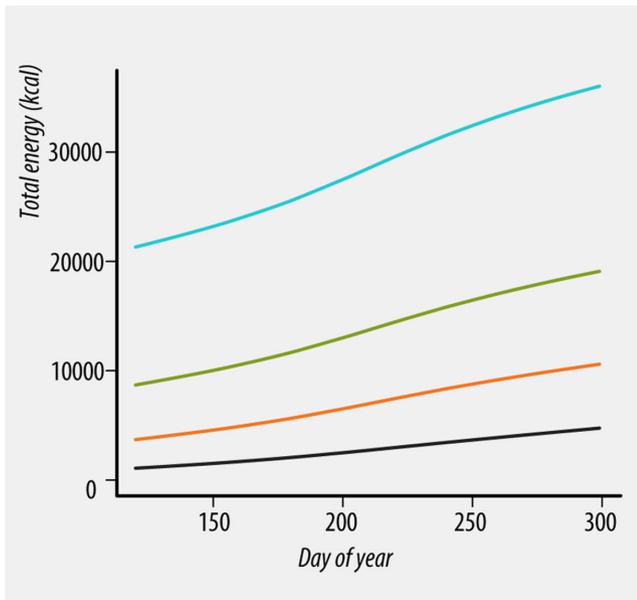


FIGURE 7 Total energy of fish (y-axis) at day of year 300 for river entry dates (x-axis) calculated for the average size fish of sea ages 1 (black), 2 (red), 3 (green) and ≥ 4 (blue). Total energy is the accumulated energy during marine growth from day of year 120 until river entry (Figure 4), minus the cumulative energy expenditure from river entry until day of year 300 (Figure 6).

all sea ages. This will combine the maximum growth with the least mortality. As very little is known about the spatial and temporal aspects of marine mortality, we explore how different assumptions regarding mortality affects predicted optimal river entry dates for the different sea age classes.

Optimization in terms of life history traits is most commonly thought of as strategies that maximize the product of survival and reproductive success (Roff, 1993). In our analysis, we use total body energy as a proxy for reproductive success. This is clearly not an accurate measure, but this metric should scale well with the amount of resources available to be invested in the current spawning or allocated towards post-spawning survival and hence future spawning. For Atlantic salmon, there is a clear trade-off between the amount of energy invested in the current spawning event and post spawning survival (Jonsson et al., 1997), and the allocation of energy towards reproductive expenditure or subsequent survival can be viewed as a separate optimization problem (Schaffer, 2004). Assessment was done by scaling the total energy left at spawning (day of year 300) for river entry dates in the period day of year 120–300 to values between 0 and 1, by dividing values by the maximum value for each sea age class (Figure 8).

Inclusion of survival in the model was done by assuming fish alive at day of year 120 and constructing survivorship curves for different river entry dates ranging day of year 120–300. Survivorship functions from Strøm et al. (2019) were used.

$$S = e^{-ZT}, \quad (6)$$

where S is the survival probability, Z is the instantaneous rate of mortality, and T is time given as the fraction of 1 year.

For each river entry date, total survival probability was calculated as the product of marine survival for the period up to river entry and freshwater survival probability from river entry to spawning (day of year 300).

$$S_i = e^{-Z_o((i-120)/365)} e^{-Z_f((300-i)/365)}, \quad (7)$$

where S_i is the survivorship curve for river entry date i , Z_o and Z_f are instantaneous marine and freshwater mortality rates (Figure 9). Freshwater survival was set equal to the highest reported marine survival rate in Strøm et al. (2019).

Survivorship curves were multiplied by the proxy for reproductive success (total energy at spawning, Figure 8), and the river entry date that gives the highest product of these is regarded as the optimum for a given combination of marine and freshwater survival (Figure 10). Optimum river entry date was calculated for marine survival probabilities spanning 0 to 1 for the period day of year 120–300 for all sea age classes (Figure 11).

3 | RESULTS

Average capture date of the different sea age classes decreased with increasing sea age (Figure 3a). For all sea age groups, females tended to arrive slightly earlier than males. Size at capture date increased

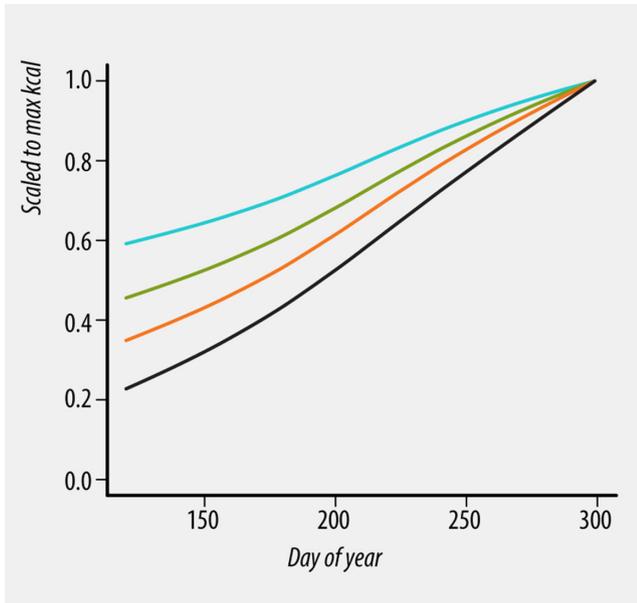


FIGURE 8 Scaled total energy of fish (y-axis) at day of year 300 for river entry dates (x-axis) calculated for the average size fish of sea ages 1 (black), 2 (red), 3 (green) and ≥ 4 (blue). Scaling was done by dividing total energy of fish (Figure 7) by the maximum value for each sea age class.

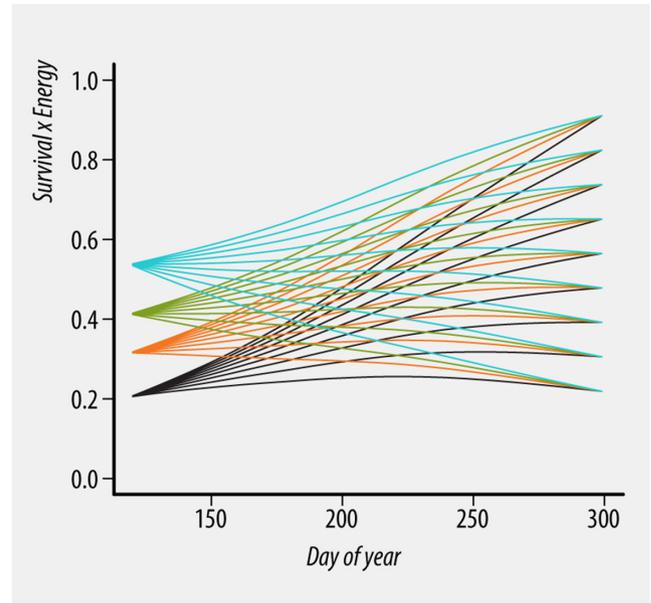


FIGURE 10 Lines illustrate the product of the scaled total energy at spawning (Figure 8) and the nine survivorship curves (Figure 9, y axis), for different river entry dates (x axis) for the average size fish of sea ages 1 (black), 2 (red), 3 (green) and ≥ 4 (blue).

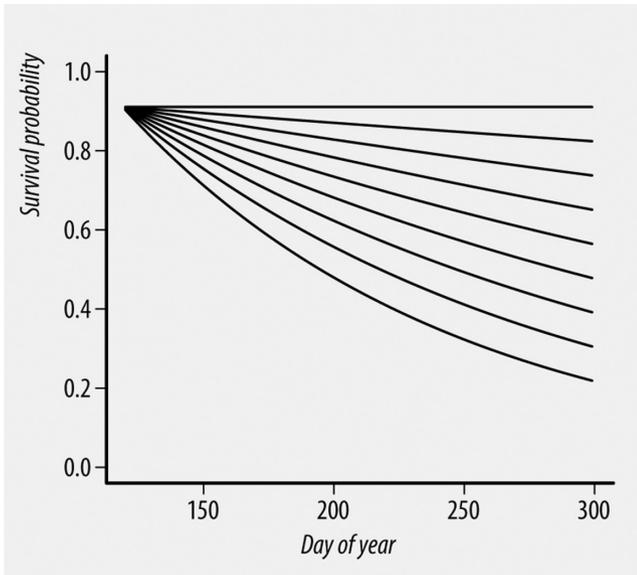


FIGURE 9 Illustration of survivorship curves (y-axis) for different river entry dates (x-axis), combining marine mortality until date of exit and freshwater mortality from exit until day of year 300. With nine marine survival rates (Equation 7) spanning the min. and max. values from Strøm et al. (2019) S (0.0046–0.827 year⁻¹) and freshwater survival set equal to the highest marine survival value.

markedly for 1-SW, was fairly stable for 2-SW and decreased for >3 -SW (Figure 3a). For all sea age groups, winter length, defined as size at the last winter annulus before capture, was negatively related to capture date (Figure 3b). The amount of growth fish had achieved

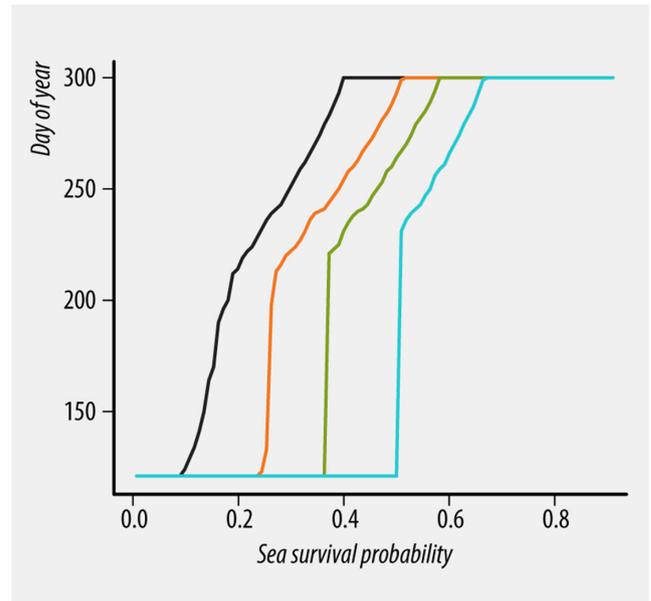


FIGURE 11 Optimal river entry date (y axis) restricted for day of year between 120 and 300 for marine survival probabilities spanning 0–1 (x axis) for the average size fish of sea ages 1 (black), 2 (red), 3 (green) and ≥ 4 (blue).

from last winter annulus to date of capture, increased with capture date for all sea ages (Figure 3c).

By combining the expected total energy of the average fish in the sea age groups at different river entry dates (Figure 4) with metabolic costs of being in freshwater from the date of river entry until spawning (Figure 6), the total energy of the fish at spawning

(day of year 300) for different river entry dates was estimated (Figure 7). The metabolic cost of the freshwater stay was strongly influenced by both the length of the period spent in freshwater and the temperature experienced (Figure 5). Scaling the energy of fish at spawning for the different river entry dates to the maximum achievable value of each sea age (Figure 8) showed clear differences between sea ages in how much they have to gain by remaining in the sea. For 1-SW river entry date, 120 would result in having only about 20% of the maximum achievable energy at spawning, while ≥ 4 -SW exiting at day 120 are expected to have about 60% of the maximum (Figure 8).

The maximum product of energy left at spawning scaled to the maximum achievable value (Figure 8) and the survivorship curves (Figure 9), give the optimum river entry date in terms of maximizing energy and survival to spawning (Figure 10). Optimal river entry dates were found for sea survival rates ranging 0–1 for the different sea age classes (Figure 11).

For all sea age classes, optimal river entry date was influenced by sea survival, with later optimal river entry date with increasing sea survival. However, the optimal river entry date for the different sea age classes differs substantially in the level of increase in survival that was needed to shift the optimum from being as early as possible to intermediate dates. For 1-SW, this occurs at roughly 0.1 while for ≥ 4 -SW, this occurs at roughly 0.5, and between these for 2-SW and 3-SW. The shift from the optimum being at intermediate dates to being to arrive as late as possible occurs at lower survival for 1-SW fish than for the older age classes. The range of sea survival rates that produce optimums at intermediate dates decrease with increasing sea age.

4 | DISCUSSION

By combining data on marine growth of Atlantic salmon with metabolic costs of freshwater stay, we estimated what different river entry dates result in in terms of energy available at spawning. Inclusion of marine survival curves from Strøm et al. (2019) on adult salmon show that optimal river entry date, defined as the river entry date that produces the highest product of reproductive success (energy available at spawning) and survival, will depend on both size (sea age) of the fish and mortality rates.

Here, we find that larger individuals have both relatively less to gain by staying longer in the ocean and lower metabolic costs in freshwater compared to smaller individuals. In general, this leads to earlier optimal river entry dates for larger individuals. By including marine survival rates, we show that optimum river entry date can span the range from leaving the ocean as early as possible in the season to as late as possible depending on marine survival rate (Figure 11).

For sea age classes ≥ 2 -SW, the relationship between marine survival and optimum river entry date changes abruptly when marine survival exceeds the level where the optimum is to arrive as early as possible. For example, for ≥ 4 -SW, the optimum shifts from arriving

as early as possible (day of year 120) to arriving at day 225 almost instantaneous around marine survival 0.5. This abrupt change does not occur for 1-SW. The mean observed river entry dates of the different sea ages in the fish caught in bag nets (Figure 2a) was day of year 193, 177, 163 and 157 for 1-SW, 2-SW, 3-SW and ≥ 4 -SW, respectively. For these observed river entry dates to represent the optimum would imply that marine survival rates for the 180 day period also vary between the sea age classes vary from ca. 0.16, 0.24, 0.36 and 0.50, respectively. These survival rates seem plausible, both in absolute levels and the increased survival for larger fish relative to smaller fish (Chaput et al., 2003; Pardo et al., 2021). But the small range over which optimums for older fish shift from arriving as early as possible to late in the season seem less likely to produce the observed intermediate river entry dates (Figure 3a).

Optimal river entry dates will also be influenced by the shape of the survivorship curves. The survivorship curves used here (Equation 7; Figure 9) assume constant mortality rates and produce convex relationships. Convex survivorship curves will tend to give optimums at extremes, and result in a narrow range of survival rates that give optimal river entry dates at intermediate dates. Concave survivorship curves could occur if there is a seasonal change in marine instantaneous mortality rate from low to high. If the survivorship curves were concave rather than convex, optimums would increasingly be found at intermediate dates. This can be shown by making survivorship curves using unique instantaneous mortality rates linearly increasing from the lowest (day of year 120) to the highest (day of year 300). For each arrival date, survival rates until spawning can be calculated as the product of instantaneous marine mortality from day of year 120 until river entry and the same freshwater mortality rate from arrival until spawning.

$$S_i = e^{-Zf\left(\frac{300-i}{365}\right)} \prod_{j=120}^i e^{-Z_o\left(\frac{j}{365}\right)} \quad (8)$$

where S_i is the survivorship curve for river entry date i , Zf is the instantaneous freshwater mortality rate and Z_o is the instantaneous marine mortality rate on day of year j .

The concave survivorship curves (Figure 12a) vastly increase the range of optimal arrival dates that occur at intermediate dates (Figure 12c). The reason for this is that the product of the concave survivorship curves and the scaled total energy at spawning (Figure 12b) produces more hump shaped relationships than the convex survivorship curves (Figure 9). The concave survivorship curves produce intermediate optimal river entry dates for all ages for marine survival rates below approx. 0.4, and for a given marine survival rate, the order of river entry, with the oldest sea ages arriving first and youngest last, is as expected. For the observed river entry dates (Figure 3a) to represent the optimum, this would imply that marine survival rates for the 180 day period also vary between the sea age classes vary from ca. 0.01, 0.01, 0.02 and 0.06 for 1-SW, 2-SW, 3-SW and ≥ 4 -SW, respectively, which seems unrealistically low.

Although none of these models can be used to pinpoint the observed river entry dates without making assumptions regarding

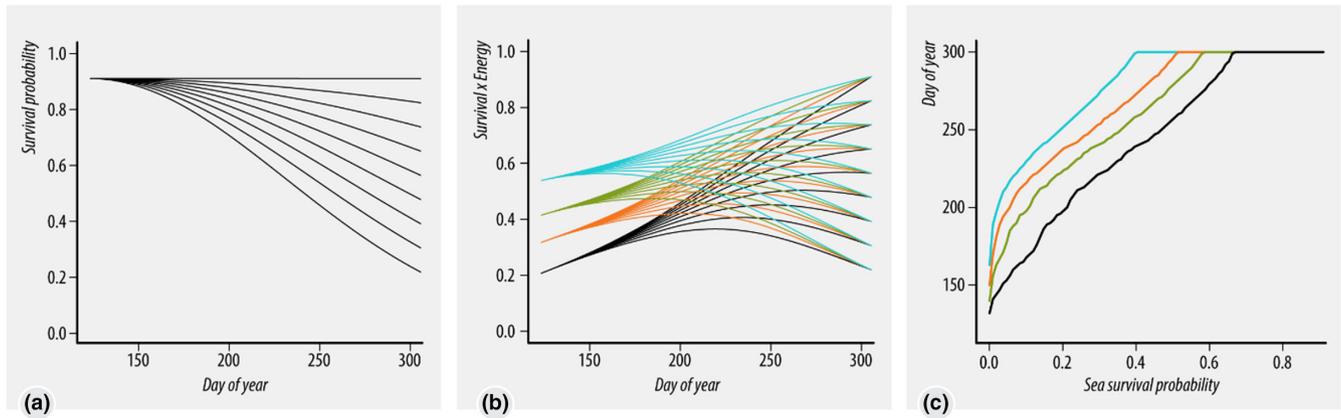


FIGURE 12 (a) Illustration of concave survivorship curves (y-axis) for different river entry dates (x-axis), combining marine mortality until date of arrival and freshwater mortality from exit until day of year 300. The nine survivorship curves were created using Equation 8, with freshwater survival set equal to the highest marine survival value from Strøm et al. (2019) and marine survival linearly decreasing with day of year so that survival for river entry at day 300 equals the survival at day 300 of the nine survivorship curves in Figure 9. (b) Lines showing the product of the scaled total energy at spawning (Figure 8) and the nine survivorship curves in (a) (y axis), for different river entry dates (x axis) for the average size fish of sea ages 1 (black), 2 (red), 3 (green) and ≥ 4 (blue). (c). Optimal river entry date (y axis) for different marine survival probabilities spanning 0–1 (x axis) for the average size fish of sea ages 1 (black), 2 (red), 3 (green) and ≥ 4 (blue).

marine mortality, the results show that both convex and concave shaped survivorship curves can create both extreme and intermediate optimums, as appears to be case in nature. Further, the results show that the relative differences in timing of river entry between sea age groups are consistent regardless of assumptions regarding sea survival.

Our analysis is based on assumptions regarding mortality that might not hold true, and also ignore potentially important factors shaping the energy budget and reproductive success. In relation to mortality, we assume that river mortality is equal to or lower than marine mortality. Exploitation rates in rivers can be substantial (see results and discussion in Erkinaro, Økland, Moen, & Niemelä, 1999). However, the probability of capture of individual fish decreases rapidly in the period after river entry (Harvey et al., 2017), and given a fishing season that covers the period salmon ascend, mortality from fishing can be viewed as a risk that is equal regardless of river entry date. This might have been the case for most rivers historically, today this will not be the case, meaning that placement and duration of fishing season in rivers has a clear potential to affect optimal timing of river entry (Harvey et al., 2017).

Using total body energy as a proxy for reproductive success, is as mentioned in the methods, not an accurate measure. For females, body size or number of eggs could be alternative proxies (Fleming, 1998) but using either of these measures would preclude subtraction of metabolic costs related to the length of freshwater stay. As an iteroparous species, Atlantic salmon can allocate available energy either towards the current reproductive event or preserve energy for post-spawning survival and subsequent spawning, and both probability of repeat spawning and reproductive expenditure are size dependent (Fleming & Eium, 2010; Jonsson et al., 1997). By using the product of survival and total body energy as a proxy for relative fitness, the optimum river entry date will also result in the highest product of survival and energy (available for

the current spawning or post-spawning survival) regardless of how this is allocated. However, the potential Atlantic salmon have for repeat spawning could involve strategies not considered here (e.g. bet-hedging) that potentially could result in different optimal river entry dates.

In our analysis, we have also omitted the energetic costs related to upstream migration. Estimates of expenditure will depend on both temperature and speed of migration, and in addition both migration distance and elevation have to be considered. In Gaula, migration distance and elevation will range between approximately 10 and 120 km and 4 and 530 m.a.s.l, and in Namsen, approximately between 20 and 95 km and 2 and 200 m.a.s.l respectively. These ranges in distance and altitude can cause substantial variation within rivers with regard to the amount of energy needed to reach spawning grounds. There can also be substantial cost of arriving too early or late for spawning both in terms of energy, survival and reproductive success, and both have a clear potential to change the shape of the relationship between river entry and survival and reproductive success.

Overall, the above results indicate that both premature return migration and the observed differences in timing of migration between sea age groups could represent behaviours maximizing relative fitness. Viewing timing of river entry as a behaviour that balances energetic cost against mortality, is also supported by the research on behaviour of post-spawned Atlantic salmon. Halttunen et al. (2013) showed that the probability of returning to the ocean in the autumn shortly after spawning was negatively related to energetic condition. Also, for individuals that spent the winter in the river, the timing of spring/summer return to the ocean was determined by energetic status. Indicating that given sufficient energetic resources, it is advantageous to prolong freshwater stay also after spawning. In lakes with landlocked forms of Atlantic salmon, predation on adult salmon can be assumed to be substantially lower than in the ocean.

This should, based on our models, result in optimum timing of river entry for larger/older fish to occur at later dates in these populations. This also appears to be the case for the landlocked salmon in Lake Vänern (Sweden), which ascend rivers from July to November (Nordqvist, 1924; Ros, 1981).

The wide geographic occurrence of large multi sea winter fish ascending rivers during the winter months (Nordqvist, 1924) together with our results make it reasonable to assume that this indeed is behaviour optimizing reproduction and survival. Extremely premature migrations as seen in the rivers of the Kola peninsula, White sea basin and Pechora (Russia) (Berg, 1948; Lysenko, 1997; Moore, 1997; Studenov et al., 2008), where large proportions of Atlantic salmon ascend the river a year ahead of spawning, has also been reported from some rivers in the north of Norway (Alta, Tana, Neiden) and northeast of Canada (Power, 1981), all rivers with physical conditions preventing winter ascent. The data presented here on Atlantic salmon from central Norway show that the individuals arriving in early May have little if any growth during the year of capture, and the energetic cost of entering the river in November and remaining until spawning the following year will not be much higher than for entering in May. This is due to the heavy influence of high water temperature during summer on metabolic expenditure. However, low water temperature during winter, low discharge and ice cover, are factors seen as restricting Atlantic salmon migration. In the Varzuga (Kola peninsula), water temperature starts to increase slightly later in the spring but is also slightly higher during summer (Jensen et al., 1998) compared to Gaula and Namsen, making it unlikely that there are large differences in metabolic costs of freshwater stay or period where conditions allow migration between these rivers. A potentially important difference between these rivers is the distance to the ocean feeding areas. Population from the north eastern Norway appear to feed in the ocean directly outside the rivers and also utilize the Barents Sea (Rikardsen et al., 2021). While tagged adult salmon from central Norway appear to move fast and direct to the North Atlantic Ocean between Iceland and Svalbard (Rikardsen et al., 2021). This difference could allow Atlantic salmon from north-eastern populations like Varzuga and Ponoï to remain in the ocean during the

entire maximum growth season and still have time to return to the river before conditions prevent river migration. Salmon from the more southern Norwegian populations, that have a substantially longer ocean migration, would need to forgo part of the growth season to make it back in time to spawn, arriving with lower energy content and also potentially paying a higher price in terms of returning to ocean feeding areas if arriving too late.

Based on these examples, it seems reasonable to consider the timing of river entry for Atlantic salmon as a product of mainly two factors (Figure 13), when conditions (temperature, discharge, ice) make it possible to enter and ascend rivers (Power, 1981) and when during this period, it is optimal in terms of balancing energetic and mortality risks associated with ocean and freshwater stay (Quinn et al., 2016). The hypothesis of river conditions causing premature migration (Quinn et al., 2016) might be important for some populations with extremely high summer temperatures in the lower reaches. For most Norwegian populations, where the earliest multi sea winter fish enter rivers in April–May, river conditions might be a factor preventing even more premature arrival. As in some Scottish populations with less restricted river migration, multi sea winter fish will commonly arrive January to March (Shearer, 1990; Sparholt et al., 2018).

The validity of the analysis and speculations above depend strongly on assumptions regarding marine mortality. Marine mortality varies among years, locations and life stages (Jonsson et al., 2003; Strøm et al., 2019; Thorstad et al., 2012) and is the part of Atlantic salmon ecology which is most difficult to collect data on. Detailed knowledge on both spatial and temporal variation in marine mortality is largely missing. Further, exploitation of Atlantic salmon has seen large changes both in rivers and ocean during the last centuries. While assuming that premature migration is an evolved adaptive behaviour, it is important to recognize that current observed exploitation rates and mortality in rivers and ocean may not represent the same conditions the behaviour evolved under (Adams et al., 2022).

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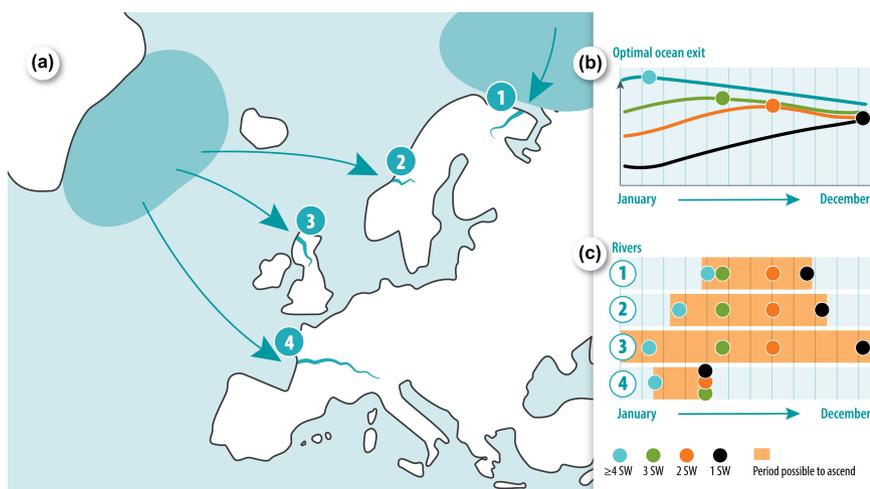


FIGURE 13 Conceptual relationship between optimal date of river entry and time period where entering and ascending rivers is possible for four different rivers (a). (b) Optimal river entry dates for different sea age classes (filled circles), is (c) restricted by period where entering and ascending rivers is possible (yellow shaded area).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and scripts used in this study are available from https://osf.io/y8nkh/?view_only=94d85e17ff4d4fca97f663e8e4a6336.

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