# *The role of freshwater and marine productivity in defining the overall outcome for an Atlantic salmon population*

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## Introduction

Understanding the demographic and ecological processes shaping the response of populations to multiple stressors is a prerequisite for scientific assessment of populations and their sound science-based management. This approach is particularly critical in the context of rapidly changing ecosystems under climate change (Cooke *et al.* 2023), but it is highly challenging to implement in the case of migratory species like Atlantic salmon (*Salmo salar*). Indeed, the anadromous life cycle of Atlantic salmon makes the species particularly vulnerable to multiple stressors acting at different times throughout their life cycles and across a wide range of ecosystems (fresh water, estuarine and marine) and spatial scales (Bull et al. 2022). They also highlight a large diversity of life-history strategies (Erkinaro *et al.* 2018), which further complicates the understanding of interactions between individuals, populations and their environment.

The freshwater and the marine ecosystems are two distinct environments separated in space and in the timing of their use throughout the life cycle. Nevertheless, influences of environmental conditions accumulate throughout the life history of individuals, and carry-over effects can have long-lasting consequences across life stages. The life of salmon in the marine environment thus partly dependents on its earlier life in fresh water. Similarly, the life of salmon returning to fresh water carry over the influence of its life at sea. However, the most visible changes may not always be the most impactful in terms of population dynamics and resilience.

Overall, understanding the processes that shape population productivity and resilience calls for an integrative approach to consider the cumulative influence of environmental conditions throughout the whole life cycle. Such an approach would consider both short term effects of stressors on specific life stages together with their propagation to future life stages through carry-over-effects. In the longer term this also calls for a comprehensive understanding of evolutionary processes that shape the evolution of life histories and the potential adaptation of salmon to climate change.

## Carry over effect of the environmental conditions experienced in fresh water on the marine life

Survival and growth of juveniles in fresh water is the first bottleneck of Atlantic salmon population dynamics and productivity, with both direct and carry-over effects on the marine phase. The early development of salmon in fresh water ends at the time of the migration of smolts to the sea. From an initial number of eggs spawned, density independent and density dependent processes, most of them being controlled by environmental conditions in the river,

such as food resources, temperature and flow, influence the survival and growth of salmon parrs. Thus, growth conditions and survival in fresh water controls the number of smolts released at sea and hence the expected number of individuals to return to spawn after the marine sojourn.

In the southern edge of the freshwater distribution area, growth conditions during the first year can be high hence offering the opportunity for male parr to mature precociously (Baglinière & Maisse 1985; Thorpe 2007). Proportion of precocious male parr may even increase in the future under climate change, in response to increasing temperature in fresh water, and reduced survival at sea (Caswell *et al.* 1984; Thorpe 2007). As a direct consequence, a non-negligible part of male individuals may complete their life cycle without migration to the sea. Although early maturation does not prevent later migration, it does result in higher mortality for parr (Buoro *et al.* 2010). Precocious maturation therefore has direct short-term consequences on population dynamics and productivity by substantially biasing the sex ratio, reducing the number of migrating smolts and hence the number of returning adults. Underlying genetic mechanisms and potential long term evolutionary consequence of precocious parr development are poorly known and deserve future research (Lepais *et al.* 2017).

Freshwater growth and genetic determinism partly drives the age at smoltification (Debes *et al.* 2020), and thus the smolts body size. The mean age of smolts in Europe follows a latitudinal gradient, ranging from 1.0 in southern France (Prouzet 1990) to 4.1 in northern Finland (Englund *et al.* 1999), as temperature and day length positively correlate with the productivity of the freshwater ecosystem and the length of the growing season (Metcalfe & Thorpe 1990). Comparatively, there is little difference in the mean body size of smolts between populations, suggesting that strong selection forces may be controlling this life history trait. Within populations, fast growing individuals are likely to smoltify at a young age (Buoro *et al.* 2010; Debes *et al.* 2020), while slow growers delay smoltification decision to take advantage of another year of growth and migrate to the sea with a larger body size (Russell *et al.* 2012). This heterogeneity in the size of smolts has significant implication for salmon life at sea, through survival and maturation. There is evidence that larger smolts are more likely to survive at sea than smaller ones (Russell *et al.* 2012; Gregory *et al.* 2018, 2019), as a larger size may confer better swimming performance for predator avoidance, lower vulnerability to gape-size limited predator, and a more rapid shift to high energetic piscivorous diet. In addition, there is evidence of a correlation between freshwater and marine growth, although the direction of the reported effect differs between studies (Nicieza & Braña 1993; Salminen 1997; Jonsson & Jonsson 2007). Any change in the marine growth may potentially impact the survival, the age at maturation and thus the age composition of the returning adults.

Another factor controlling survival of smolts at sea, which is likely to be climate dependent, is the phenology of smolts migration. The migration phenology of smolts is globally driven by the photoperiod, but the local freshwater conditions dictate annual population-specific run timing (Otero *et al.* 2014). Spring flood events and temperature changes for instance contribute to the onset of seaward migration (McCormick *et al.* 1998; Simmons *et al.* 2021). The run timing dictates the specific condition of the environment faced by smolts upon sea entry, such as the availability of prey, thermal conditions and current-induced transport. It is a site-specific evolutionary adaptation to maximise the chance of entering the sea during the window of optimal conditions for growth and survival (Thorstad *et al.* 2012). As climate change has profound and varied effects on the phenology of species through the modification of the ontogeny and environmental clues triggering migration e.g. thermal and hydrological regimes (Todd *et al.* 2012; Otero *et al.* 2014), there is a risk of increasing mismatch between the smolt migration phenology and the optimal windows in coastal and marine ecosystems.

Overall, the smolt body size and their timing of migration will have an impact on survival and growth at sea (Jonsson *et al.* 2017). But all smolts are not equal in their ability to survive, grow and mature in the marine environment, and this heterogeneity is partly driven by the conditions encountered by parrs during their life in fresh water. Thus, freshwater productivity should not only be assessed by the number of smolts, but also by their *quality*, or phenotype, and their underlying genotype.

**Carry over effect of the environmental conditions experienced at sea on the life back in fresh water**

The marine life of anadromous salmon ends with the return migration of maturing individuals to the fresh water, up to several months before the reproduction. The environments encountered during marine migration contribute to natural and fishery induced mortality and growth and maturation, that ultimately shape the abundance of returning individuals, as well as their phenotype (e.g. age, size, sex) and the underlying genotype (Debes *et al.* 2020; Mobley *et al.* 2021). From a population dynamics perspective, the main bottleneck is probably the number and the quality of egg produced, rather than the number of spawners itself. The number of eggs spawned is determined by the number of returning adults, survival in fresh water until spawning, and sex-specific fecundity. All these processes result from the interaction between individual characteristics derived from the migration in the marine environment, the timing of the transition from the sea to fresh water, and the conditions experienced in the freshwater environment until reproduction.

The maturation decision takes place at sea and has profound repercussions on the reproductive trajectories of individuals, on the migration routes and their vulnerability to fisheries and on the dynamics of the population. The timing of the maturation decision results from an interplay between the genotype and growth-related environmental conditions. Maturation decision controls the duration of the marine sojourn, and thus the size of returning fish, which positively correlates to fecundity and reproductive success. The advantage of a larger size in late maturing individuals in terms of per capita fecundity is counterbalanced by a higher mortality with longer time spend at sea and generally higher fishing mortality due to the selectivity of fisheries for larger fish. Maturation is also a sex-specific decision that is partly controlled by some major effect genes with sex-specific dominance (Barson *et al.* 2015). As a result of those genotypic interactions, the threshold of physiological condition that trigger maturation decision is higher in females than in males (Tréhin *et al.* 2021). This mechanism explains the high proportion of females in multi-sea winter salmon observed in most populations. All these elements support the idea that any change in the growth condition at sea affects the sex-ratio and the fecundity of salmon returning to the river, i.e. potential egg deposition. Furthermore, poor diet at sea by females might limit the energy content of the eggs, hence their quality, with potential consequences on the progeny (Maamela *et al.* 2023).

The timing of the return migration and entry in fresh water is another life history trait that may influence the sensitivity of salmon to environmental pressure and hence salmon productivity. It illustrates another carry-over effect, where the legacy of salmon life at sea persists beyond freshwater entry. The spawning migration phenology is strongly correlated to the age at maturation, with one sea winter (1SW) salmon generally returning later, i.e. in the summer, than multi-sea winter (MSW) salmon. This difference is particularly large in southern Europe where the long-lasting spring-summer season allows MSW to run as early as February or March and peak in April-May, while 1SW peak run is in July. For a given sea-age class, we also observe high variability in the timing of return migration between individuals and between years. Temporal trends are likely to be associated with climate change in the ocean (Valiente *et al.* 2011; Dempson *et al.* 2017), and trophic conditions in particular, as individuals in low

body condition may delay their return migration (Todd *et al.* 2012; Bal *et al.* 2017). As a first approach the phenology of salmon return migration does not seem to constrain the success of the reproduction as it occurs months in advance of the spawning activity, especially in southern Europe where reproduction generally takes place as late as mid-December. However, the time of river entry may be critical in determining the survival of pre-spawning salmon, by controlling the duration and the timing of the freshwater sojourn, and thus the exposure of salmon to environmental stressors like temperature or diseases, and in-river fisheries. Salmon entering fresh water in summer may suffer from high temperatures in the estuary and lower reaches, sometimes exceeding thermal tolerance, when early migrants have already reached cooler habitat far upstream (Baisez *et al.* 2011). Thermal stress is amplified in small river systems where thermal refuges may be absent.

**Towards an integrative approach of the salmon population dynamics, using life-cycle models**

Climate change affects daily salmon life, both in fresh water and in the marine environment. Because these interacting effects differ in intensity, direction, duration and in their consequence on population dynamics, studying a single effect in isolation may result in inaccurate and misleading conclusions.

As a rough figure, let's say that survival from egg to smolt is about 3‰, survival at sea is about 10%, while survival from return in fresh water to spawning is often ignored but may likely sit somewhere above 50%. Therefore, in a simplified representation of the life cycle with multiplicative effect of transition rates from eggs to eggs, increasing any of the transition rates by the same factor would ultimately have the same effect on the productivity from eggs to eggs. However, the different rates of transition that shape population dynamics throughout the life cycle are clearly not independent, as any change that affect one life stage can have multiple repercussions on the subsequent life stages. It is thus extremely difficult to anticipate the response of a population to a given change and identify leverages that would have a positive impact on its dynamics and resilience (Piou & Prévost 2013). To grasp this extremely complex picture of interacting effects and long-term consequences throughout the salmon life cycle, life-cycle models offer a relevant tool for integrating available knowledge throughout the salmon life cycle (Bull *et al.* 2022).

Life cycle models, whether they are individual (e.g. Piou & Prévost 2012) – or population-based (e.g. Rivot *et al.* 2004; Massiot-Granier *et al.* 2014), propose a unified framework that can be applied across different scales of time and space (e.g. index river, stock unit, oceanic basin). Age and stage-based life cycle models are useful tools to explore the influence of environmental changes on eco-evolutionary process that shape population dynamics and productivity. They are key tools to represent how the articulation of transition rates and their dependence throughout the life cycle control population dynamics and productivity. Retrospective models may have the potential to assess what transition contributed the most to past change in population growth rate, given a selected set of hypotheses.

Life-cycle models have the great advantage to provide a more realistic representation of the composition of the population, i.e. the diversity in individual characteristics that are of demographic relevance (e.g. sex, age, growth, genotype). This is critical as population dynamics and resilience is not only a matter of salmon abundance, as a given number of adults can produce a different number of eggs. For instance, marine return rate is not merely quantified as the ratio between the number of smolts and the number of returning adults. It is considered as the result of post-smolt survival, 1SW maturation, dispersal and balance between immigration and emigration, later survival, including fisheries. Thus, such models can allow to better assess the potential demographic mechanisms driving observed changes in salmon

abundance and productivity. As an illustration, the life-cycle model developed by Olmos *et al.* (2019) pointed at a decline in post-smolt survival concomitant to the increase in 1SW maturation in most North Atlantic salmon stock units. Life-cycle models also can integrate new knowledge gained from the recent development of molecular sexing, providing further support for sex-specific maturation decision, but also similar post-smolt survival in females and males (Tréhin 2022).

By adding external forcing of climate change within the model, it is possible to investigate stage-specific response to climate change and compare the relative contribution of different drivers to the population dynamics. Using an individual-based life-cycle model, Piou and Prévost (2013) simulated the response of a salmon population from southern Europe to different scenarios of climate change in fresh water and in the ocean. Within the context of the scenarios tested, they found that climate-induced change in the freshwater environment (water temperature and flow) during the juvenile stage alone would not lead to extinction of the population, while reduced oceanic growth appeared as a more significant threat for population persistence. In contrast, the large-scale multi-population model developed by Olmos *et al.* (2020) is not very specific about salmon life in fresh water. However, the explicit representation of successive oceanic domains used by salmon at sea pointed at temporal variations of sea surface temperature on feeding grounds common to multiple populations as a main driver of large-scale change in marine survival (Olmos *et al.* 2020).

Finally, many of the observed changes in salmon are affecting traits that have a heritable component, e.g. growth, migration timing, age at maturation. This is a reminder that the phenotype of an individual results from the interaction between its genotype and the environment. For example, following the theory of proximate mechanisms, smoltification and maturation decision is conceived as a comparison of the current status of the salmon (e.g. energy content) with a genetically determined threshold, which triggers a change of state (Thorpe *et al.* 1998). More and more studies shed light on the mechanisms and genetic architecture behind these life history decisions (e.g. sex-dependent dominance at a single locus for the age at maturation, following Barson *et al.* (2015)). An explicit representation of these evolutionary processes in the framework and time frame of population dynamics models is therefore necessary to better understand the phenotypic and demographic changes observed in the past and to evaluate the capacity to respond to climate change. If the environment changes, the set of life history traits that may maximise an individual's fitness (i.e. contribution to next generation) may change, as well as the selective pressure acting on those traits. Eco-evo models extend life-cycle population models and allow to estimate the selectivity of different forcing factors, and to investigate the evolution of traits and population resilience or adaptability for different scenarios (Lamarins *et al.* 2022).

A key challenge in investigating eco-evolutionary processes that shape population dynamics and productivity of salmon populations comes from the difficulty to observe individuals in the wild across the large range their spatial distribution. Embedding mechanistic life cycle modelling approaches within a statistical framework to derive inferences in the process remains a huge challenge. Building upon available knowledge of the biology and the ecology of Atlantic salmon, modern statistical tools relying on hidden state variables to embed complex eco-evo demographic and population models within statistical modelling can accommodate a variety of data, such as catch statistics and scientific surveys (Rivot *et al.* 2004; Peyrard & Gimenez 2022). They are powerful tools for both stock assessment and exploration of the consequences of possible scenarios combining climate change, exploitation regulation and mitigation measures (Piou *et al.* 2015).

**Toward predictive ecology to forecast effects of climate change in fresh water and at sea on North Atlantic salmon populations**

Atlantic salmon is one of the most studied vertebrate organisms worldwide. Currently available knowledge already fuels models of an increasing complexity. Life cycle models, whether individual or population-based, can be statistical, allowing inferences to be drawn from data on the processes that govern the eco-evolutionary dynamics of populations and the factors that condition them (e.g. effects of temperature on survival, growth on maturation). They are typically hindcast oriented but can be used to make short-term projections. Life cycle models can also be simulation-oriented by relying on data-estimated processes and parameters. They can aim at forecasting population futures (over several generations) in response to different scenarios of change in the environment and in management practices. These two approaches are thus complementary, despite having different goals.

Noteworthy, these models are still in their infancy relative to those used for climate predictions. Their ability to predict the fate of Atlantic salmon in the future remains an unachieved goal and this is not necessarily their main strength or interest. Indeed, predicting the physical characteristics of future climate and their consequences on the functioning of the ecosystems salmon live in remains highly uncertain as illustrated by the range of scenarios assessed by the Intergovernmental Panel on Climate Change (IPCC). Instead, life cycle models can be primarily useful for exploring and contrasting the potential consequences of scenarios on the future state of salmon populations and guiding managers in the choice of management measures favouring resilience and robustness to uncertainties. This approach is illustrated by Piou *et al.* (2015), which showed that current fishing practice is likely to worsen the effects of climate change in the marine environment. In this study, only scenarios of reduced fishing mortality on multi-sea winter would ensure population resilience towards a degradation of marine growth conditions. In response to the difficulty in assessing which is the most important transition in the life cycle, modellers and managers should better identify on which transition we can reasonably expect to act.

Uncertainties also arise from the complexity of the response of salmon to climatic conditions, and from their interaction with the response of other organisms, including anthropogenic activities. The difficulty in predicting the response of salmon to future changes is exacerbated by the fact that salmon are facing a set of environmental conditions that have never been encountered before, i.e. for which no historical observations are available. There is a clear need to increase the overall eco-physiological knowledge base, especially tolerance thresholds for major environmental stressors and how such stressors affect performance within, and beyond, their tolerated range (McKenzie *et al.* 2016). In addition, our understanding of the eco-evolutionary processes and mechanisms that govern population functioning (e.g., the influence of environmental effects vs. genetic changes) remains limited, restricting our ability to anticipate population response. Methodological developments are still needed to better integrate different types of available data and knowledge (Bull *et al.* 2022). This requires mobilizing data that embraces all life stages in both freshwater and marine phase, across a large range of scales and ecosystems (Diack *et al.* 2022). This would allow for changes in spatial scales within the model structure - from population (Rivot *et al.* 2004; Piou & Prévost 2012) to metapopulation (Lamarins *et al.* 2022) to regional stock unit (Massiot-Granier *et al.* 2014), and to the Atlantic basin as a whole (Olmos *et al.* 2020), and to develop indicators relevant for both ecological, evolutionary and management perspective.

In this context, both scientists and managers need to develop an honest and critical appraisal of model outputs, in order to not over-state their usage and realism in forecasting salmon's future. Still, life-cycle models are great tools to run projections under alternative scenarios of

climate change. They also provide a platform to foster cooperation between scientists and stakeholders and to guide management action (Bull *et al.* 2022).

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