

Size-structured demographic models on marine phase of Atlantic salmon

Micro-project 2025 : Introduction

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1 Context

1.1 Environnemental context

Aquatic ecosystems are increasingly impacted by anthropogenic pressures, such as overexploitation, habitat degradation, and climate change. These disturbances significantly affect ecosystem functioning and the sustainability of natural resources (Worm et al. 2006; IPBES 2019).

Diadromous fish, such as the Atlantic salmon (*Salmo salar*), are especially vulnerable due to their reliance on both marine and continental ecosystems. Classified as ‘Near Threatened’ by the IUCN, salmons have faced threats in recent decades linked to alterations in the ecosystems (updated from ‘Least Concern’

to ‘Near Threatened’ in 2023). Salmon populations have experienced substantial declines in abundances during the last decades (Chaput 2012; ICES 2024) Figure 1. This decline is accompanied by shifts in life-history traits (LHT), such as early maturation (Jonsson, Jonsson, and Albretsen 2016; Olmos et al. 2019) and reduced adult size (Todd et al. 2012; Bal et al. 2017; Vollset et al. 2022) Figure 2, leading to lower fecundity (Hanson et al. 2020) and a loss of intra-population diversity, which weakens the ‘portfolio effect’ (Schindler et al. 2010; Carlson and Satterthwaite 2011). These changes ultimately compromise population resilience, making them more sensitive to environmental pressures and exploitation.

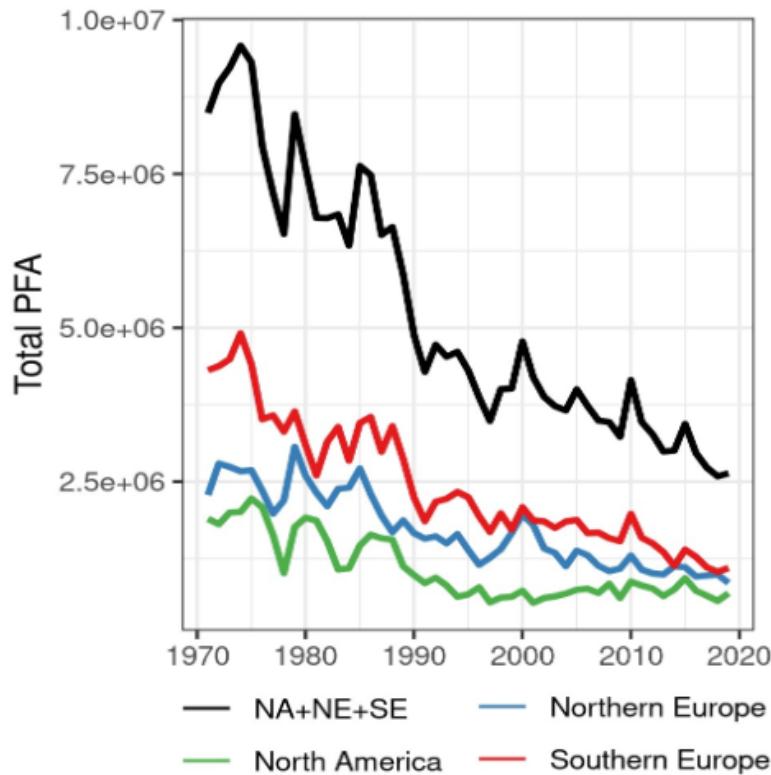


Figure 1: Southern Northeast salmon stock abundance of non-maturing individuals after 1 year at sea (Pre-Fishery Abundance) estimated from 1971 to 2019 (source: (ICES 2024)).

In this context, gaining a deeper understanding of the mechanisms that drive salmon populations’ responses to global change is crucial. This knowledge will improve our ability to assess their current state and inform the development of effective management strategies.

1.2 Main hypothesis

The rapid changes observed in the structure (LHT) and abundance of salmon populations suggest a response to changes in the marine ecosystem Figure 3. These changes are thought to be due in particular to a reduction in the quantity and quality of trophic resources available during this phase, leading to a reduction in the growth of salmon at sea (Vollset et al. 2022; ICES 2024) Figure 2.

Available data indicates that growth plays a crucial role in the main demographic transitions throughout the salmon life cycle. In fact :

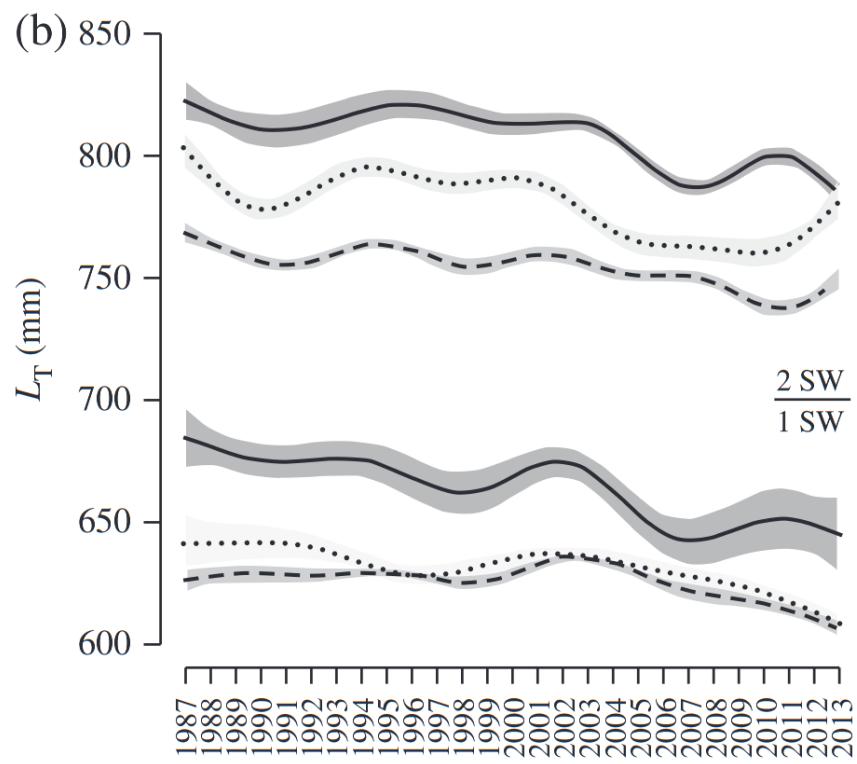


Figure 2: Change in total length (L_T) in one sea-winter (1SW) and two sea-winters (2SW) *Salmo salar* from Normandy (..), Brittany (- - -) and Aquitaine (—) 1997–2013. The shaded bands represent 95% c.i. (source: (Bal et al. 2017)).

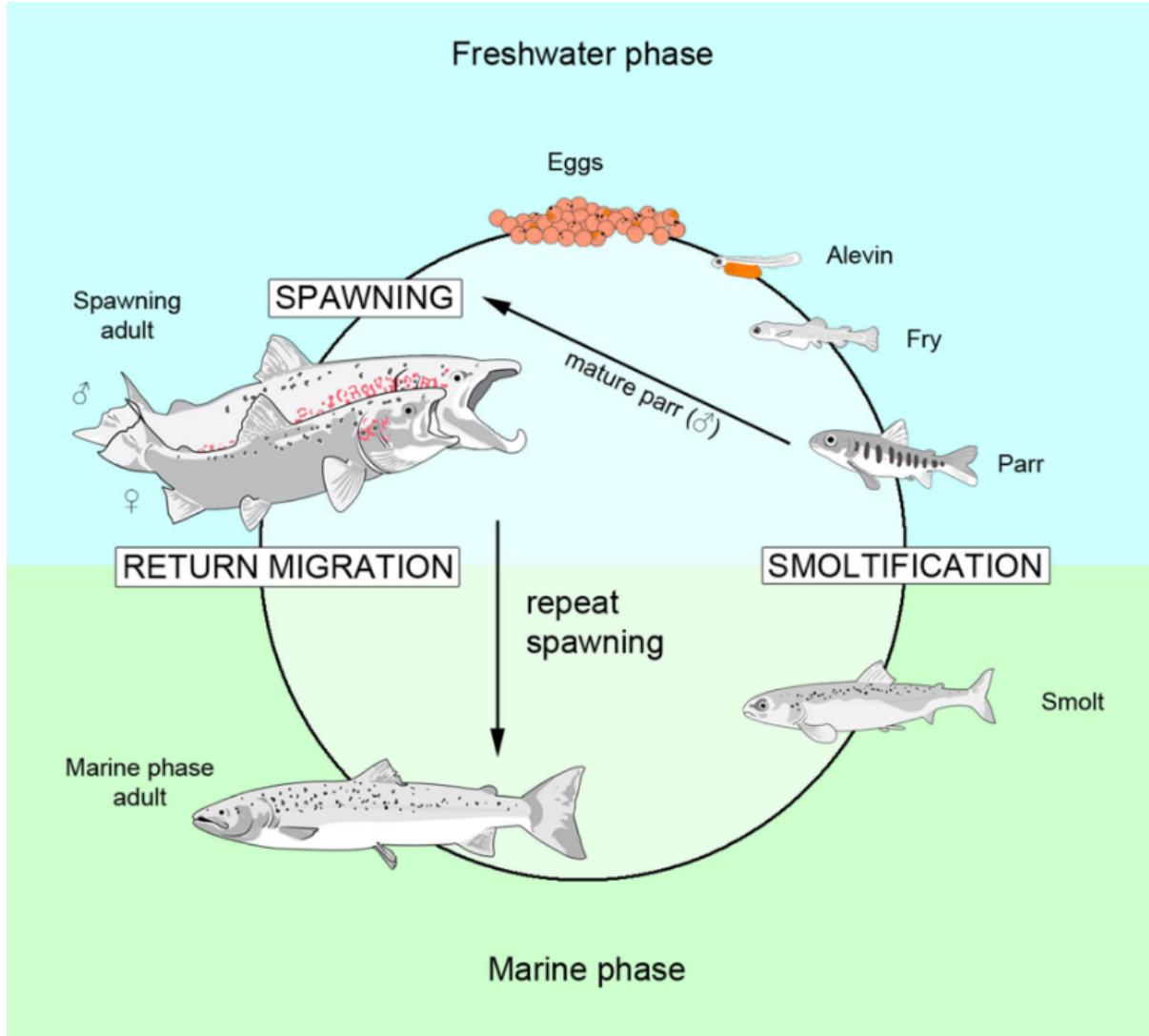


Figure 3: Atlantic salmon life cycle (source: (Mobley et al. 2021))

- Growth is a key integrative trait of global change (including climate change) that reflects an individual's ability to acquire resources from its environment, assimilate them, and allocate them to various functions.
- Growth is also a LHT influenced by trade-offs with other major LHTs (specific to each sex), such as individual mortality (Friedland et al. 2009) or size and age at maturation (Mobley et al. 2021), among others.

Specifically, the size of individuals during the smolt migration to the sea increases the probability of survival and successful return (*i.e* “bigger is better”: (Gregory et al. 2019; Simmons et al. 2021)). Additionally, the decision to sexually mature, which determines the return for reproduction, is partly influenced by reaching a size threshold at the end of the first summer at sea, with larger individuals having a greater likelihood of triggering maturation (Mobley et al. 2021; Tréhin 2022). This threshold is typically higher for females, who, on average, have a lower probability of maturing after just one winter at sea compared to males of similar size.

Given the importance of growth in demographic processes, any change in growth due to environmental variations will have significant impacts on population structure and, ultimately, population dynamics.

1.3 Modelisation context

However, current population models used for fish stock assessments struggle to explicitly account for the variability of phenotypic traits (*i.e* size) between individuals and/or over time (Rivot et al. 2004; Olmos et al. 2019; Tréhin 2022). By neglecting variations in size, these models generate biased estimates of population dynamics, limiting the relevance and accuracy of their projections. In contrast, individual-based models have investigated the influence of growth on the life histories of Atlantic salmon, but their complexity makes them challenging to apply for quantitative assessments based on field data (Piou and Prévost 2013; Phang et al. 2016).

To address this issue, the development of population models structured by life-stages and size is essential for improving our understanding of observed variations and enhancing our ability to predict population responses under multiple pressures. The Integral Projection Models (IPMs) approach is proposed as a promising alternative (Coulson 2012; Stubberud et al. 2019). Positioned between individual-based models and age-structured models in terms of complexity, IPMs offer a more effective framework for incorporating the impacts of growth on population dynamics (Plard et al. 2019).

1.4 Micro-project framework

This micro-project is part of a broader framework of a PhD research aiming to analyze the influence of individual growth variations on the population dynamics of Atlantic salmon. The goal is to improve the tools used to assess their status and propose more robust management measures adapted to environmental pressures. **The first step of this project involves characterizing key demographic transitions (survival and maturation) during the marine phase of Atlantic salmon in relation to individual size.**

A major challenge lies in drawing conclusions about the hidden processes that occur during the marine phase. **To address this challenge, indirect information on individual growth during these hidden stages is obtained through the analysis of archival tissues (see Section 3.2).**

A structured model has been developed to accommodate the complex life cycle of Atlantic salmon (see Section 3.3). It was built within an integrated hierarchical statistical modeling framework (Schaub and Abadi 2011; Zipkin, Inouye, and Beissinger 2019) in order to combine diverse sources of observations to infer hidden demographic processes.

2 Objectives

The current modeling has limitations, while it accounts for annual data and sex proportions, it does not incorporate these factors into the formalization of size-dependent survival and maturation transitions. **The first objective is to improve the modeling of survival and maturation processes by integrating annual variations and sex differences, based on existing literature.**

The current model uses indirect size information from scales, assuming an isometric relationship between scale size and body size. However, this assumption appears inconsistent with findings in the literature. **The second objective is to introduce back-calculation models (three different) for estimating salmon body size from scale size, chosen based on literature, and assess the variability introduced by their applications.**

Due to the current reliance on scale size modeling, no direct links with population state indicators used in management could be established. **The final objective is to leverage the three models with back-calculation and develop a direct connection to egg deposition (a proxy for fecundity and population renewal), which will provide valuable insights for management decisions.**

3 Resources

3.1 Study site

This work is based on long-term monitoring data (24 years of smolt cohorts from 1996 to 2019) of natural salmon populations collected by the *Observatoire de Recherche en Environnement petits Fleuves Côtiers* (ORE DiaPFC) and the *Centre National pour l'Interprétation des Captures de Salmonidés* (CNICS). These data are centralized in information systems managed by INRAE.

Specifically, the data pertain to the Scorff salmon population, a river in the Morbihan region of Brittany. The Scorff drains a 483 km² basin over a 77 km course, joining the Blavet at a common estuary near Lorient Figure 4. A migration monitoring station has been operational since 1994 at the *Moulin des Princes* (MdP) site in Pont-Scorff Figure 5. This station enables the trapping of smolts during downstream migration and adults during upstream migration. Each captured salmon is measured, weighed, and has scales sampled before being released. The collected scales are archived in the ichthyological collection COLISA (Marchand et al., n.d.), managed by INRAE and OFB.

3.2 Data

3.2.1 Abundance estimations

The counting data collected at the MdP station Figure 5 are imperfect, as some salmon can bypass the trap, particularly during periods of heavy rainfall. To address this, mark-recapture experiments are conducted to estimate:

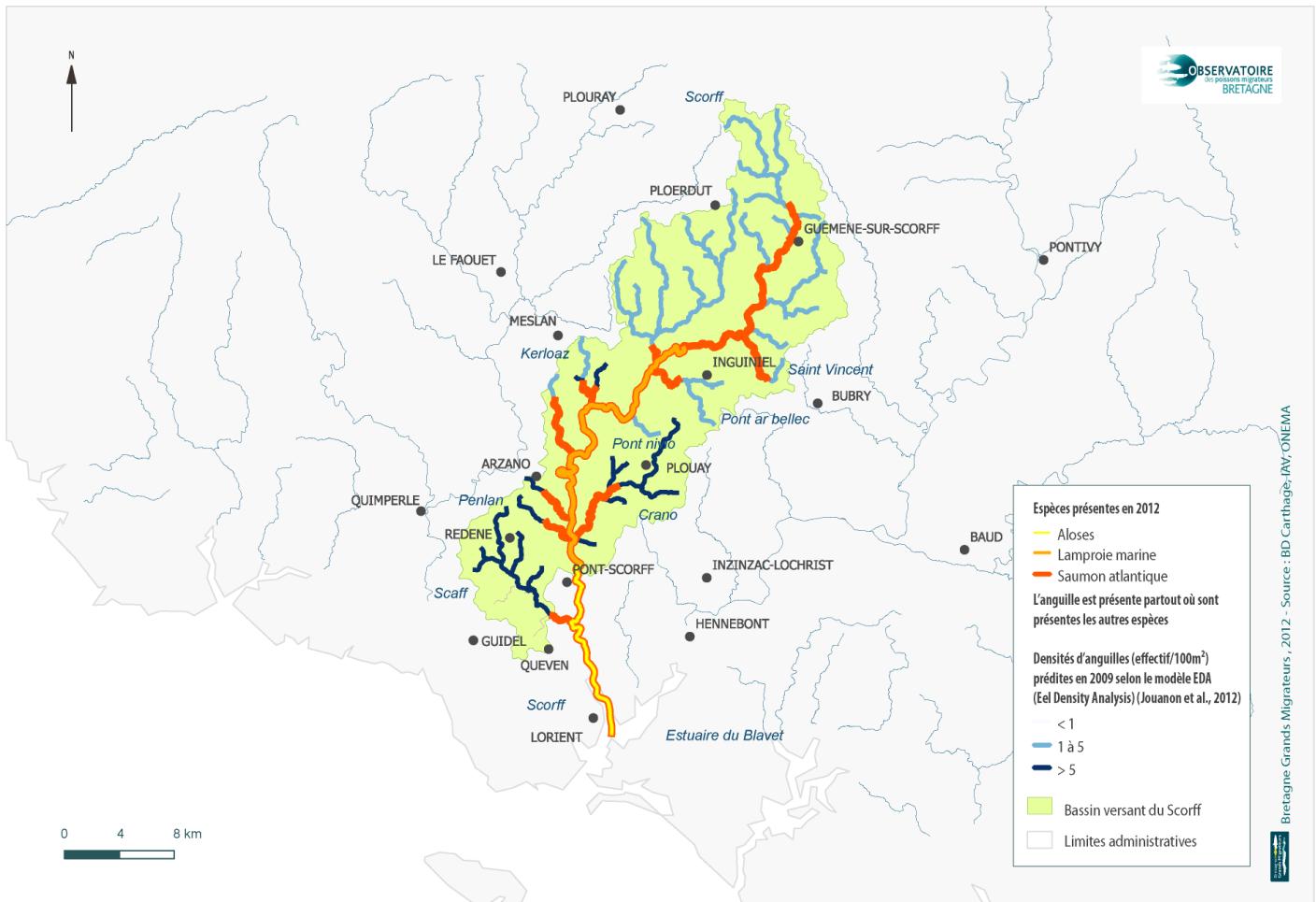


Figure 4: Distribution of amphihaline migrants in the Scorff catchment in 2012 (Sources & Production : @Bretagne Grands Migrateurs)

- **Trap efficiency** based on flow conditions,
- **The abundance of migrating smolts** (across all age classes),
- **The abundance of adult returns**, categorized into two age classes: 1SW (one-sea-winter) and 2SW (two-sea-winter).

These estimates, derived from 24 years of data, are produced using Bayesian hierarchical models that account for imperfect detection (Mathieu et al. 2019).



Figure 5: Moulin des Princes station on the Scorff river (Photo: @Eliot Boulaire)

3.2.2 Molecular sexing

Sexual dimorphism in salmon at the time of trapping (both at the smolt and adult stages) is not pronounced enough to allow reliable sex identification.

To address this, a sample of 30 scales from 30 different individuals per smolt cohort year and life-stage was selected to determine sex using DNA extracted from scale tissues (*i.e.*, molecular sexing: (Besnard et al., n.d.)). However, reliable sex identification was only possible for a subset of the sample, as DNA extracted from older scales was often too degraded. Additionally, since sexing was not performed after 2018, limited information is available for the most recent cohorts.

3.2.3 Scale size

The model uses individual data from scale readings to indirectly estimate the size structure of the population Figure 6. Scales are calcified structures that grow alongside the individual and allow the reconstruction of individual life histories. Moreover, they are easy to collect, and have minimal impact on the fish's life (compare to otoliths).

A sample of 30 scales from 30 different individuals per smolt cohort year and life-stage was selected to determine the growth ring sizes at various life-stages Figure 6. We used adult scales (1SW and 2SW) to assess the size structure of various latent life-stages (*i.e* post-smolts : see Section 3.3) with the main hypothesis that return adults are a sub-sample of each latent life-stages Figure 8.

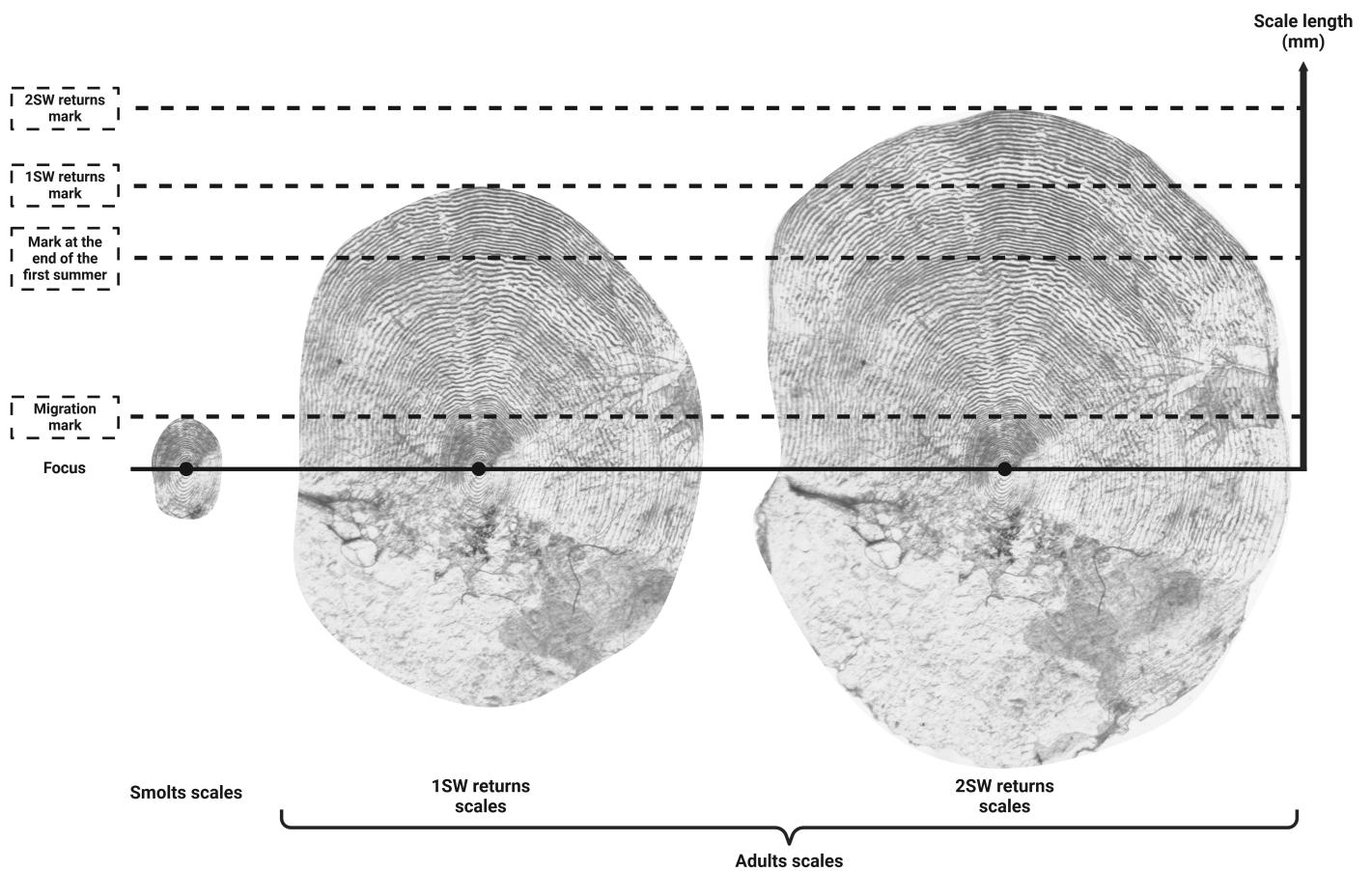


Figure 6: Schematic representation of the identification of length marks on scales of smolts, 1SW returns and 2SW returns adults. Discovery V8 stereomicroscope (Zeiss) and Infinity 3 optical camera (Lumenera). (Source: (Tréhin 2022) - Photo: @Ludivine Lamireau - Production: @Eliot Boulaire).

The scales are collected from a “standard zone” Figure 7 on the fish’s body, where scales first develop during the fry stage. The scale size from this area is the most strongly correlated with the salmon’s body size (Baglinière et al. 1985; Shearer 1992).

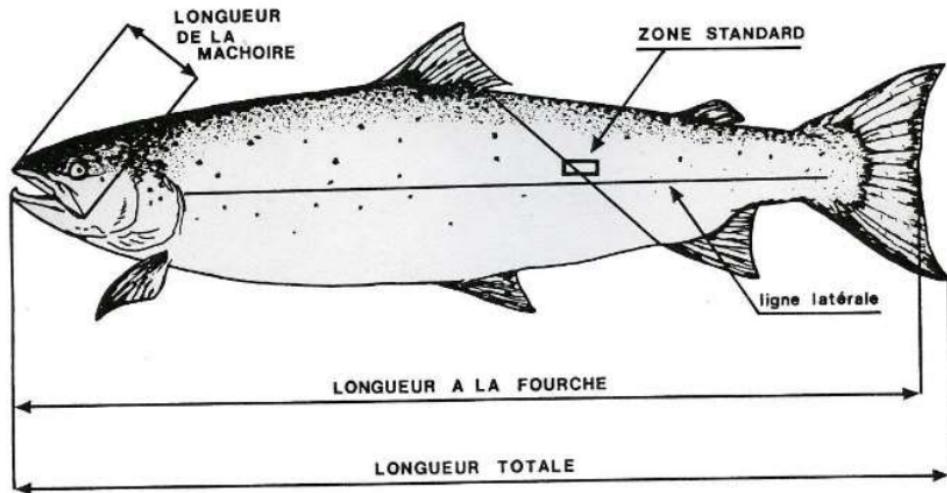


Figure 7: Lateral diagram of an Atlantic salmon and the standard scale collection area according to the international recommendations of the ICES report (Source: (ICES 2024) - Production: (Gueguen and Prouzet 1994)).

3.3 Model

A model structured by stage, age, sex, and size, with a focus on the marine phase, has been developed to track the population dynamics of Atlantic salmon from smolt migration downstream to the return of adults Figure 8.

- During downstream migration in april, smolts (N_3) experience low survival rates, particularly during the migration itself and the first month at sea. This survival appears to be size-dependent, forming a latent stage of post-smolts (N_4) in november.
- At the end of the first summer (november), post-smolts (N_4) face a maturation decision. This decision, also seemingly influenced by individual size, determines the age of adult returns (1SW or 2SW). This transition forms the maturing post-smolts (N_5) and the non-maturing ones (N_8).
- Then these post-smolts (N_5 & N_8) will face another survival rate during the second summer at sea (considered fixed) and depending on the time spending at sea. Maturing post-smolts will spend a lower time at sea (returning during of the smolt migration year +1), leading to 1SW adult returns (). Non-maturing post-smolts will spend a longer time (returning during of the smolt migration year +2), leading to 2SW adult returns.

It's important to note that the model currently does not explicitly incorporate growth processes, which is why we have disruptance in size structure (symbolizing by breaks) in the model. Instead, the model links abundance and sex ratios across transitions, without directly modeling growth dynamics. For more information's you can see the model R code with deeper explanations and glossary of variables names (see linked model in HTML format).

The integrated hierarchical framework synthesizes data on abundance, sex ratio, and size structure from both observable and latent stages to infer marine survival rate and maturity rates. Direct information on

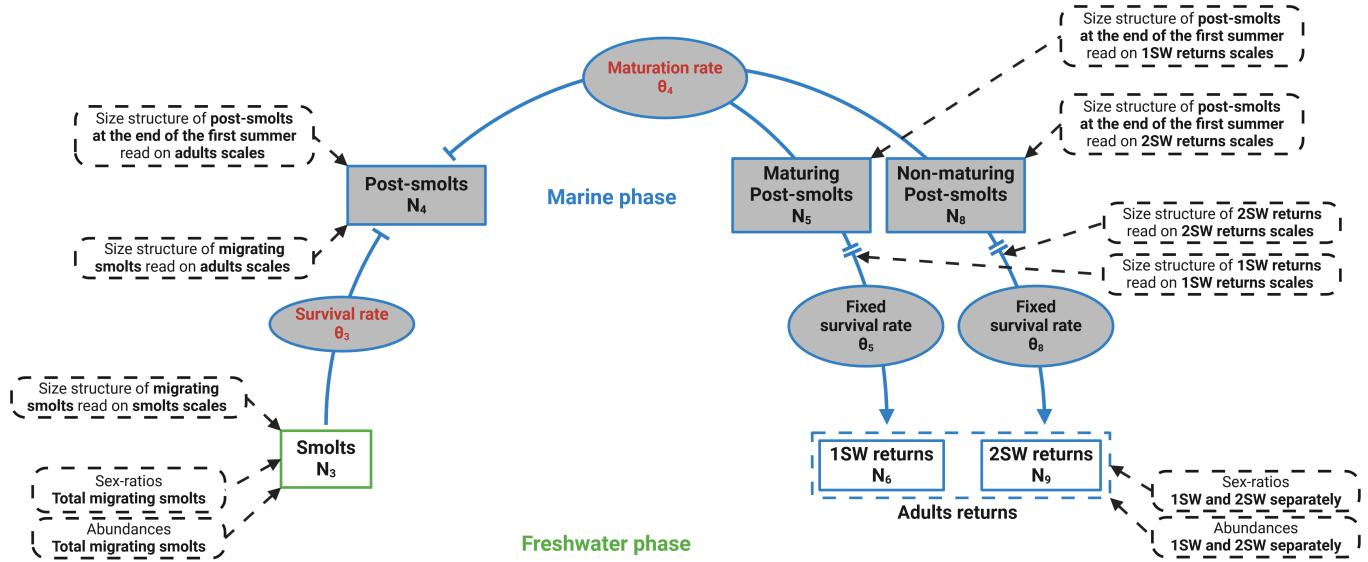


Figure 8: Schematic representation of the salmon stage-, age-, sex-, size-based life cycle model (boxes= life-stages, ovals= demographic transitions ; grey fill=latent variables, white fill= observed variables ; red color=estimated transitions, black color=fixed transitions ; blue outlines=marine phase, green outlines=freshwater phase). (Production: @Eliot Boulaire).

abundance, sex ratio, and size structure is available only for observable stages, while latent stages rely on indirect information about size structure.

Given the multiple life-history strategies in the marine environment (e.g., 1SW and 2SW returns), the model's temporal framework is normalized to the years of smolt cohorts at downstream migration, spanning cohorts from 1996 to 2019.

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