Atlantic salmon under climate change.

Understanding the influence of growth in demographics and population dynamics.

Context

Recent climate-induced environmental changes in the marine ecosystem (Hoegh-Guldberg and Bruno 2010), combined with other direct or indirect anthropic pressures like habitat degradation (Halpern et al. 2008) and over harvesting (Christensen et al., 2003; Worm et al., 2006) affect the productivity of many fish populations. Understanding the demographic and ecological mechanisms shaping the response of fish populations to multiple stressors is a prerequisite for scientific expertise on the status of population and for sound science based management (Soulé 1991; Butchart et al. 2010). There is already growing evidence of reduced recruitment in fish population, which is particularly visible in the North Atlantic (Britten et al. 2016). Other reported changes affect fish survival at older stages as well as their phenotypes, like maturation age, body length or body weight with consequences on the productivity and resilience of populations.

Still, stock assessment models are generally primarily designed to capture variation in abundance and rarely explicitly address the variability in phenotypic traits among individuals or over time in response to environmental changes (Pepin et al., 2022; Szuwalski et al., 2023). Failure to consider variability of key phenotypic traits, such as body size, sex-ratio or fecundity, and the processes that drive them, can lead to biased estimates of demographic rates and ultimately of population dynamics and productivity (Mangel et al., 2010). As a result, biological and management reference points derived from those models may be biased with regards to the current level of population productivity (Thorson et al., 2015; Miller et al., 2018; Szuwalski et al., 2023). This may also impede the use of stock assessment models to forecast future population dynamics and population productivity in the context of environmental changes. Developing stage-based population models that explicitly capture the effect of environmental changes on key life history traits can provide a better understanding of past changes, can improve our capacity to forecast population dynamics and productivity in a context of climate change, and can ultimately help informing the management and conservation of aquatic resources within an ecosystem-based management framework.

For many fish species, growth and the body length reached at some key stages in the life cycle is driving key demographic transitions like survival and maturation. Growth is the result of individual capacity to acquire and assimilate resources within a given environment, thus any change in the environment (temperature, trophic resources) is likely to influence individual growth (Woodward et al., 2021). Hence, understanding the drivers and mechanisms that control the variations of growth of individuals and how those changes affect life history traits and demographic parameters is therefore critical to assess the response of individuals and populations to environmental changes.

Quantifying the effects of multiple pressures on the life cycle is particularly challenging for anadromous fishes that share their life cycle between a freshwater breeding habitat and the marine environment where they need to acquire sufficient resources for a surge in body growth and maturation (Gross 2019; Thorstad et al. 2021). This is even more difficult as the as marine phase of anadromous fishes is difficult to observe. Distributed across the north Atlantic ocean and the Baltic sea, the abundance of many wild Atlantic salmon (*Salmo salar*) populations declined dramatically over the last decades (Limburg and Waldman, 2009; Chaput 2012; Olmos et al. 2019; ICES 2021). The decline in A. salmon abundance is most often attributed to a decline in smolt survival (Chaput 2012; ICES 2021). In addition, other marked changes observed in the demographic structure and phenotypes of adults returning to rivers after the marine sojourn may impact population dynamics and productivity (Mobley et al. 2021). Reduction in the size at age, which is particularly visible in South European populations (Todd et al. 2012; Jonsson et al. 2016; Bal et al. 2017) is expected to further exacerbate the impact of ongoing changes through a reduction in females fecundity (Hanson et al. 2020). In addition, changes in the sea-age composition of returning fish have been observed widely, as the proportion of early maturing fish increased from the 1970's to the early 2000's, and then reached a plateau or even declined over the last 20 years (Jonsson et al. 2016; Olmos et al. 2019). In addition, recent literature suggests a pan-population common decline in growth during the first summer at sea (Vollset et al., 2022; Tréhin et al., accepted), likely due to a bottom-up response to climate change in the marine environment, and correlated with a rise in temperature and a decline in abundance and energetic quality of available salmon preys (Olmos et al., 2020; Vollset et al., 2022).

Even if the underlying mechanisms of those changes are still unclear, the available knowledge strongly suggests that the first months of life at sea, from the time of smolt migration to the end of the first summer-autumn at sea, is a critical period for both survival (Friedland et al. 2009) and maturation (Mobley et al. 2021). Indeed, there is now growing evidence that the growth and body length of fish at certain audit point in the life cycle has a critical influence during this critical phase. In particular, body length of smolts at migration has been shown to modulate return rates, with bigger smolts having a higher probability of returning (the "bigger-is-better" hypothesis; Gregory et al., 2018; Gregory et al. 2019; Simmons et al. 2021). In addition, evidences now accumulate that the body length reached at the end of the first summer at sea partly determines the decision to mature after only one winter at sea or to delay maturation. Recent modeling work proposes probabilistic maturation reaction norm as a proximate mechanism: the maturation decision would depend on an individual body length threshold at the end of the first summer at sea, with small size increasing the probability to delay maturation decision (Tréhin et al. 2021). Available results also provide strong evidence for a difference between males and females in the maturation decision, with females having a lower probability to mature as 1SW than males of similar size (Mobley et al. 2020; Tréhin et al. 2021). Any changes in the sea-age composition of adults can dramatically affect the amount of eggs spawned in rivers. Indeed, the proportion of females, together with females' body length and weight dramatically increase with the duration of the marine sojourn. Nevertheless, a longer marine sojourn also means a higher risk of mortality before reproduction (Mobley et al. 2020). Hence, the observed decline in marine growth could result in dramatic changes in life history and phenotypic traits of returning fish and may in turn result in a widespread reduction in reproductive potential and marine survival, further precipitating the large-scale and long-term declines in salmon return rates observed throughout the North Atlantic basin (ICES, 2021a).

Yet, the complexity of salmon life history, and the difficulty in observing salmon at sea still fuels uncertainties on the mechanisms and the drivers of the changes in survival, maturation, and the resulting abundance and composition of returns. In particular, the way variations in growth during both the freshwater and the marine phase may shape demographic and population dynamics remain difficult to quantify. Improving our understanding of the drivers and mechanisms underlying those variations is therefore critical to better understand the response of populations to environmental changes, anticipate their capacity of adaptation to future changes and propose the most adapted management measures.

Working hypotheses and objectives

Population dynamic models of salmon life cycle developed so far (Olmos et al., 2019; Olmos et al., 2020; Tréhin, 2022) are not structured by length and hence cannot explicitly represent how demographic parameters depend on growth and/or length of fish. In particular, the dependence of post-smolt marine survival to the body length at smolt migration and the sex-specific dependence of the probability to mature as 1SW to the body length of fish at the end of the first summer at sea have not been tested empirically within a length structured life cycle model. The "bigger-is-better" hypothesis developed by Gregory et al. (2019) and Simmons et al. (2021) is based on results demonstrating that bigger smolt have a higher return rates, but their approaches do not consider the potential influence of the length-dependent maturation process on the return rate.

The objectives of this internship are to test the hypothesis that the variability in abundance, sea-age composition, sex-ratios and length structure in adult returns are shaped by the articulation of length-dependent survival and maturation demographic transitions. Expectations to be tested are:

- We expect the post-smolt survival to be highly variable among years;
- We expect large temporal variations in the maturation schedule, and differences between sex, with females having a lower maturation rate after 1 year at sea than males;

- We expect the distribution of body length at smolt migration and growth during the first summer at sea to be good predictors of the variation in the survival and the maturation rates.

The proposed approach is to develop a life cycle model structured by sex, age, stage and length that proposes an explicit representation of transitions occurring during the first and second year at sea, i.e. post-smolt survival, sex-specific maturation decision, and survival after the maturation decision in order to investigate the contribution of key demographic and ecological drivers to the variability in abundance, sea-age composition and sex-ratios in returns and the resulting egg deposition. Salmon are typically observed and sampled when they migrate to the sea at the smolt stage and when they return as adults, but no direct observations are available between those two stages. The model will be built within an Integrated Population Modelling (IPM) framework. IPM are appropriate tools to combine various sources of observations to draw inferences on hidden (non-directly observed) demographic processes (Parent and Rivot, 2012; Schaub and Abadi, 2011; Zipkin et al., 2019). The Bayesian framework (based on tools like Nimble or STAN) will be used for inferences.

The model will be developed based on an extensive data set from the survey of the A. salmon population of the Scorff river (Brittany, France; one of four index river for A. salmon in France (ICES 2021)) between 1996 and 2018. Data mainly consists in:

- estimates of abundance of migrating smolts and of adults that returns after the marine phase, including uncertainty (based on a model developed by (Buoro et al. 2019));
- data on the sex and age structure of smolts and adults (from scale reading and molecular sexing);
- length structure of the smolt and returning adults;
- proxies of individual growth trajectories based on scale reading of returning adults

<u>Main steps of the internship</u>

- Develop a demographic model structured by sex, age, stage, and length for the transition from smolt to adult return;
- Introduce size selective post-smolt survival and size selective maturation within this model;
- Develop a back-calculation model to infer fish length based on scale reading (based on the model developed by V. Sylve (Sylve, 2019);
- Combine the demographic model with multiple sources of observation within a Bayesian integrated Population Modelling framework to draw inferences and test the aforementioned ecological hypotheses;
- If time available, explore the capacity to estimate temporal variation of the survival after the maturation stage (considered constant in all models so far).

All those models will be developed with R and Nimble (or STAN for statistical inferences). The applicant will beneficiate from data sets already compiled. The models won't be developed from scratch as the applicant will beneficiate from pre-existing models and codes.

Collaborations

Le/la stagiaire bénéficiera d'un contexte de travail local dynamique : l'UMR DECOD est une des équipes de recherche leader sur le fonctionnement des populations de salmonidés migrateurs, et bénéficiant d'une grande expérience dans la modélisation démographique/dynamique de population.

Le stage s'inscrit dans une dynamique de recherche en développement au sein de l'UMR DECOD autour des modèles de populations structurés en taille. Le travail s'inscrira dans une collaboration avec d'autres équipes de l'UMR DECOD (notamment basées Ifremer Brest) développant des approches similaires sur des poissons petits pélagiques marins (anchois, sardines). Un stage de M2 sur ces modèles d'étude devrait être lancé en parallèle, et des échanges sont prévus entre les deux cas d'application.

Le stage s'inscrit aussi dans une collaboration de long terme avec l'UMR ECOBIOP et en particulier

Étienne Prévost et Mathieu Buoro (maîtrise des données du Scorff et des questions de démographie et de dynamique des populations). Il mobilise en outre les données de l'ORE DiaPFC et les liens de longue date avec l'unité U3E. Enfin il entre en résonnance avec les activités de recherche-développement du Pôle MIAME OFB/INRAE/institut Agro/UPPA.

Intérêt du stage en termes d'acquis pour la/le stagiaire

- Modélisation démographique et dynamique des populations
- Approche intégrée des cycles de vie dans les dimensions spatiales et temporelles
- Outils de modélisation génériques pour l'écologie statistique: Modèles Bayesiens Hiérarchiques, modélisation des cycles de vie, approche multi-échelles, covariation spatiale, analyse des incertitudes

Lieu du stage / Encadrement

Lieu du stage — UMR DECOD, Rennes

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Eric Edeline, UMR DECOD, INRAE, Brest

Maxime Olmos, Christophe Lebigre, UMR DECOD, Ifremer, Brest

Profil requis

Ce stage comporte une forte composante d'analyse quantitative (dynamique de population, modélisation, analyse des données, statistiques). Il s'adresse aussi bien à *i*) un étudiant de Master 2 « Recherche » orienté « modélisation et statistiques » intéressé par la modélisation pour l'écologie et la gestion des ressources renouvelables ; *ii*) un étudiant en 3ème année d'école d'ingénieur (type Agro) intéressé par la recherche pouvant justifier d'une compétence en analyse quantitative.

Compétences requises : Connaissances en écologie, dynamique des populations, bio-mathématiques, bio-statistiques. Une connaissance préalable de l'analyse statistique Bayesienne est préférable.

Période / Rémunération

Période : 6 mois entre Janvier et Août 2024

Indemnité : Indemnité de stage règlementaire (~ 550 euros / mois)

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