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Exploration des mécanismes de mortalité, de croissance et de recrutement chez les petits poissons pélagiques via la construction d'un modèle hiérarchique bayésien multi-espèces de cycle de vie

Par : Alice BORDES



Soutenu à Rennes le 15/09/2023

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**Unraveling mortality, growth and recruitment processes underlying
the population dynamics of a small pelagic system using a
hierarchical Bayesian two-species life-cycle model**

By : Alice BORDES



Defended in Rennes on September 15, 2023

In the presence of the jury composed of

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Acknowledgement (in french)

Ce rapport a beau présenter de nombreux résultats fort intéressants sur des populations de poissons, il omet de mentionner les humains incroyables que j'ai pu côtoyer au cours de mon stage.

J'adresse d'immenses et sincères remerciements à mes 5 encadrants de stage, Maxime Olmos, Martin Huret, Etienne Rivot, Mathieu Doray et Eric Edeline, qui n'ont cessé de nourrir les débats (au cours de longues réunions) écologiques et statistiques et m'ont épaulée avec bienveillance tout au long de mon stage.

Tu pourras toujours essayer l'inférence par maximum de vraisemblance ou bayésienne, mes remerciements à ton égard, Maxime Olmos, ne sont pas quantifiables. Merci pour ta bonne humeur (immuable), ta rigueur (de l'extrême), les petits secrets divulgués sur les state-space models et le bayésien, les opportunités que tu m'as offertes dans le monde de la recherche (la conférence internationale à Bilbao) et tout le temps et l'attention que tu m'as consacrés. On recommence le stage quand tu veux !

Merci à toi également Martin, pour m'avoir intégrée à la vie de l'unité, pour ta bienveillance, pour ta mine de connaissance sur les petits pélagiques et pour t'être toujours rendu disponible.

J'ai particulièrement apprécié la sympathie de toute l'équipe LBH (Laboratoire Halieutique de Biologie), chacun de vous ayant enduré (avec un peu d'amusement) mes tergiversations sur mon avenir et le choix d'une thèse, non de LA thèse. Finalement, je suivrai tes traces sur les tétras-lyres Christophe!

Je voudrais vous signifier à quel point mon stage a été passionnant. Apprendre à maîtriser de nouveaux outils de modélisation a été une gymnastique plaisante, et ma participation à la campagne PELGAS une expérience formidable et un souvenir inoubliable. Parcourir les 7 ponts du Thalassa (matériel photo sur le dos), trier les *Capros*, sentir le poisson, être maculée d'écailles, la jovialité de l'équipe pêche (alimentée par l'humour d'Hervé), contempler les oiseaux et les dauphins, sauver les *Mola mola*, les chamailleries avec Christophe qui s'étale sur son bureau en salle acoustique, ma colocataire de cabine Cécile, les déambulations dans les couloirs du navire et entre les ponts avec Raphaëlle et Aurel, les délicieux repas, les levers et couchers de soleil au large.... Je garderai en mémoire tous ces moments qui font de PELGAS une expérience incroyable.

Vivre à Brest une seconde fois a été un réel plaisir tant mes colocos, Baptiste, Raphaëlle et Perrine, étaient (et le seront toujours) formidables !

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Preface

The work in this report will be presented at the Annual Science Conference of the International Council for the Exploration of the Sea (ASC ICES) on September 2023 in Bilbao, Spain.

This report will be the subject of a paper and, for this purpose, it is “coarsly” written as a draft to be submitted as a scientific paper.

All the steps of the internship, further details on material and methods and exploratory results are presented in Supplementary Materials ([SUPPLEMENTARY MATERIAL 1 TO 8](#)).

1. Introduction

Understanding the response of populations to global changes is critical to support ecosystem-based management (Schaub and Abadi, 2011). But changes in environmental conditions can interact with the numerous processes that govern populations dynamics, making difficult to unravel the mechanisms underlying populations responses to global changes. Observed changes in population dynamics are the result of ecological processes occurring at different stages of the population life cycle. In particular variations in population abundances and mean body size are likely correlated due to the interconnection of two main processes, mortality and growth, through density- and size- dependent growth and mortality mechanisms (Stige et al., 2019). To better understand changes in population dynamics, it is then important to be able to jointly consider variations in abundances and size by accounting for interconnected changes in mortality and growth, and then identifying the intrinsic or extrinsic factors that likely impact these two main demographic processes.

On the one hand, intrinsic factors can be defined as factor of ecological dynamics within the studied system, such as demographic variability (abundance and body sizes for different ages and stages of the populations), intra and inter (when the system accounts for multiple species) specific interactions depicted by density or size dependent mechanisms. Among the intrinsic factors, intra-specific density or inter-specific density, may have critical effects on growth and mortality rates (Rose et al., 2001; Grossman and Simon, 2020; Matte et al., 2020). A positive effect of density on mortality is often interpreted as intra or interspecific competition caused either by limited resources in the environment or behavioral interactions (such as reduced food accessibility or cannibalism) (Larkin, 1956; Jones, 1991). A negative effect of density on growth can occur through spatial processes. Density-dependence increase spreading of the population, with occupation of sub-optimal habitats where food might be scarcer or of lesser quality (Post et al., 1999; Boëns et al., 2021). Intra-specific size, may also has a critical effect on mortality and growth. Survival chances may be lower for early stages, which are, by their small size, more vulnerable to predation (Arendt, 1997; Metcalfe and Monaghan, 2003). Intra-specific size, which is both a result of earlier growth (rate and duration), is potentially also an influent factor on future growth (Post and Evans, 1989). On the other hand, extrinsic factors are external to the biological component of the system but have an impact on it, such as extra-system species density and environmental variability (Ross et al., 2021). Among the extrinsic factors, the fishing pressure can generate age-truncation of exploited populations, driven by size-selective fishery removals (Hsieh et al., 2010). Size-selective fishing mortality may then induce a rapid evolution of life-history traits in few generations, such as a decline in age and size at maturity or in growth rate, especially for collapsed fish populations (Jørgensen et al., 2007; Swain et al., 2007). Environmental factors, such as temperature and trophic resources, also may affect growth and mortality rates. Effects of starvation can be due to both the scarcity of food and the decrease of food quality (Menu et al., 2023). Food shortage could locally occur when avoiding predation places fishes in sub-optimal habitats (Peer et al., 2006; Brosset et al., 2015). Wind, circulation and temperature could have an impact on the trophic web and thus on fish condition, which makes them more or less vulnerable to starvation or predation (Cargnelli and Gross, 1997; Hurst, 2007; Brosset et al., 2015; Vagner et al., 2019).

The mechanisms underpinning the impact of these intrinsic and extrinsic factors on population growth and natural mortality, and their consequences for population dynamics in terms of variations in abundance and size, remain poorly understood. In fisheries science, single-species population dynamics models are useful to represent the processes driving the population dynamics such as reproduction, growth, maturation, fishing, natural mortality and recruitment. They allows to reconstruct the variations in abundances and are common in stock assessment models (Hilborn and

Walters, 1992; Quinn and Deriso, 1999). Nevertheless, those models do not account for correlations between variation in mean size and abundance because they do not represent mechanisms between density-dependent and size-dependent processes, their relationship with environmental factors and their relative impact on mortality and growth. Moreover, few are the multispecies models that represent the interaction between species that shared common habitat, and/or a same trophic level during a specific life stage. This limits our understanding of multispecies competition for habitat and food and its relative impact on species specific mortality and growth.

Understanding mechanisms underlying variations in population dynamics within a changing ecosystem requires then to represent the ecological processes of mortality and growth driving fish productivity at different life stages. Indeed, different life stages might experience a variety of habitats, pressures and species interactions because their biotic and abiotic needs may change across life stages. It is also necessary to account for the inter and intraspecific variability in those mechanisms. Life cycle models that consider and incorporate the temporal heterogeneity of ecological mechanisms are useful for examining the effects of intrinsic and extrinsic factors that interact in a hierarchy of scales (Jørgensen et al., 2007; Rochette et al., 2013; Cunningham et al., 2018; Olmos et al., 2019; Olmos et al., 2020). Embedding life cycle models within a multispecies system might help to investigate inter and intra specific mechanisms underlying variations in growth and natural mortality at different stages of the life cycle. In this study we thus aim at quantifying the interacting effects of density-dependent, size-dependent processes and environmental factors on fish population dynamics sharing the same habitat. We investigated this question using small pelagic fish in the Bay of Biscay as a case study. In particular, we defined our studied system as consisting of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) populations in the Bay of Biscay.

Sardines and anchovies are clupeiforms sharing the same trophic niche and the same habitats (Bachiller and Irigoien, 2015; Doray et al., 2018a). Since 2001 in the Bay of Biscay, sardine and anchovy stocks have decreased in length and weight (Doray et al., 2018a; Véron et al., 2020). For both species, this decline is particularly marked at ages 1 and 2, the life stages that contribute the most to the biomass of the stock (Doray et al., 2018a). From 2003 to 2005, anchovy biomass in the Bay of Biscay dropped, leading to the fishery closure from 2005 to 2010. Since 2006, the total biomass increased again. This leads to a Good Environmental Status of the stock, according to the *International Council for the Exploration of the Sea (ICES)*'s definition (Doray et al., 2018a; Doray et al., 2018b; Biseau, 2021). Since 2001, despite a peak in 2003, sardine total biomass has dropped. Since 2021, the sardine stock of the Bay of Biscay is considered collapsed (Doray et al., 2018b; Biseau, 2021). A decline of size and growth over time at population level may result from a decline in growth rate over the years, from an increase of size selective mortality (fewer large individuals), or both. It is unlikely that fishing pressure alone, which can induce rapid evolution of life-history traits in few generations, explains this trend in small pelagic fish stocks of the Bay of Biscay (Jørgensen et al., 2007; Boëns et al., 2021). Since the population dynamics of small pelagic fish are very dependent on the environment, it is assumed that the effect of fishing takes a secondary role, but remains an important factor since it may amplify the changes (Essington et al., 2015). Henceforth, we may assume that other processes are involved to explain these changes in size and growth. Indeed, they are probably due to environmental changes in the Bay of Biscay, although the precise mechanisms remain difficult to elucidate. One strong hypothesis is a response of population that would involve bottom-up mechanisms due to a change in the quality and/or quantity of trophic resources occurring at different life stages (Menu et al., 2023). Additionally, small coastal pelagic fishes of similar size and body form often school together regardless of species (Bakun and Cury, 1999). Individuals of a less abundant species are likely to be entrained in schools that are dominated numerically by a more abundant species (Bakun and Cury, 1999). It is frequently noticed in some geographic areas an alternation of abundance trends between sardines and anchovies (Bakun and Cury, 1999; Chavez et al., 2003). These alternations might be the result of differences in migratory capacities and food requirements, adult sardines effectively filtering smaller

food particles than anchovies. To clarify the mechanisms at stake under the influences of the multiple intrinsic and extrinsic factors, a joint analysis of small pelagic populations throughout the Bay of Biscay is needed. In particular, this requires a population dynamic framework that can assess the interacting effects of intrinsic and extrinsic factors on growth and mortality at different stages of the life cycle and their consequences for small pelagic population dynamics.

In this master thesis we rely on and significantly extend the framework developed by Stige et al. (2019). *Stige et al., 2019* developed a statistical state-space modelling approach to identify the importance of abundance and body size for growth and natural mortality. First, *Andrieux et al., 2022* in her Master thesis, enhanced the framework developed by *Stige et al., 2019* by (i) embedding *Stige et al., 2019*'s model within a population dynamic model to separated out fishing and natural mortality, (ii) assessing the impact of environmental extrinsic factors on growth and mortality and (iii) applied this framework to anchovy (*Engraulis encrasicolus*) in the Bay of Biscay.

However, *Andrieux et al., 2022* 's study encountered some limits in the understanding of the mortality and growth processes underlying the population dynamics of anchovies. First, in *Andrieux et al (2022)*, first year abundances are defined using informative priors based on the average abundances over the time series for each age, which does not allow us to represent the dynamic link between the spawning stock and the recruits and thus limits our understanding of the population dynamics. Secondly, only the effect of total density of anchovies on mortality and growth is tested, while it is not demonstrated that all age classes share the same habitat. This suggested that classes, individually, could have different effects. Thirdly, the total abundance effect is included in the model as a covariate whereas the same data are used to infer the mortality and growth through model likelihood, meaning the same data is used twice i.e within a likelihood function and as a covariate. Finally, *Andrieux et al., 2022* 's model is monospecific and does not allow us to verify the hypothesis of the interaction of densities between small pelagic fishes of different life stages or species that can explain their abundances dynamics.

In this study, we conducted a two-species (sardines and anchovies) analysis of the mechanisms linking density-dependent and size-dependent processes (intrinsic factors) to natural mortality, growth and their potential relationship with environmental factors (extrinsic factors). We built a two-species life cycle model within a state space framework to represent the entire population dynamics of small pelagic fish, including fishing mortality, natural mortality, growth and stock recruitment processes. Within the life cycle model, we then modeled density-dependent and size-dependent intrinsic mechanisms affecting these processes and assessed the effect of extrinsic factors on them.

2. Materials and methods

2.1. Studied system: a two small pelagic species system in the Bay of Biscay

2.1.1. Survey data

Abundance and mean size data per age class of sardines and anchovies were collected during the annual spring acoustic surveys PELGAS (Doray et al., 2018a). PELGAS is an integrated ecosystem survey, which takes place every May since 2000, conducted by *Ifremer* on board RV “Thalassa”, over the French shelf of the Bay of Biscay (Doray et al., 2018b). Abundances (in fish numbers) are derived from acoustic densities. Additionally, we also used commercial catches per age class (in fish numbers) from the Working Class on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA) of the International Council for the Exploration of the Sea (ICES) (TABLE 1). Maturity annual rates at age were obtained by visual determination of gonadal maturity stages during the survey.

Table 1 : Summary of the data available for the small pelagic fishes (anchovies and sardines) of the Bay of Biscay

FISH DATA			SARDINES		ANCHOVIES	
			Years	Ages	Years	Ages
Fisheries	Annual catches within ages	2002 to 2020	age 1 to 6+	2000 to 2020	age 1 to 4	
PELGAS survey	Abundances within ages	2000 to 2019, 2021	age 1 to 8+	2000 to 2019, 2021	age 1 to 4+	
	Mean size and COV within ages	2000 to 2019, 2021	age 1 to 10	2000 to 2019, 2021	age 1 to 4	

*COV: Coefficient of variation

2.1.2. Environmental data

In this study, the living environment of sardines and anchovies is characterized by the water temperature of the euphotic layer (surface layer) and by the concentration of zooplankton in this layer (proxy of the food availability of fish). For the Bay of Biscay (ICES divisions 27.8a and 27.8b), these two data sets are generated by the numerical model SEAPODYM (Lehodey et al., 2010 ; <https://marine.copernicus.eu/>) that uses sea surface temperature and chlorophyll-a concentration (FIGURE 1). Additionally, we used monthly indexes of the *Atlantic Multidecadal Oscillation* (AMO) and *North Atlantic Oscillation* (NAO) global indicators and (<https://psl.noaa.gov/data/timeseries/AMO/> ; <https://www.ncei.noaa.gov/access/monitoring/nao/>). We also used the abundance data of sprat (*Sprattus sprattus*), another clupeid potentially sharing the same habitat and trophic niche, which is not part of the studied system (considered as extrinsic factor), but which constitutes an environmental data item since only total abundance was available from the PELGAS survey.

More details about the data and the mechanisms involving those environmental data can be found in section 2.2.3.

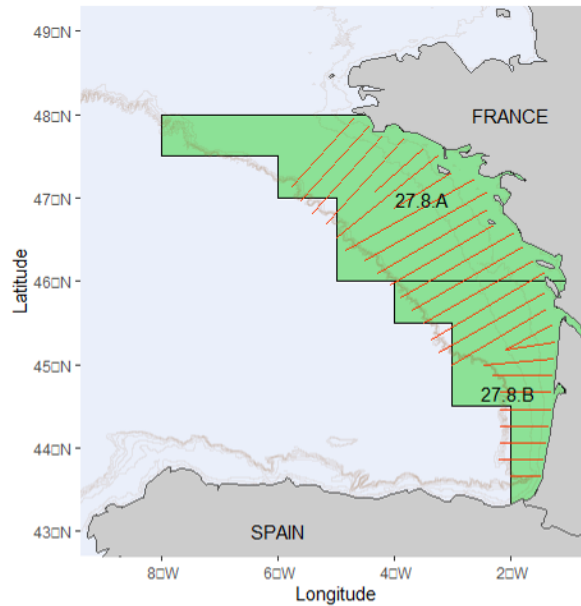


Figure 1 : PELGAS survey sampling scheme (red lines), and zooplankton and temperature zones (ICES divisions 27.8.a and 27.8.b zones from SeaPoDym model).

2.2. The modelling approach

2.2.1. Outlines

The model is formulated in a Bayesian hierarchical state-space framework (Parent & Rivot, 2012; Rivot, Prévost, Parent, & Baglinière, 2004) that incorporates stochasticity in population dynamics as well as observation errors. This integrated modelling frameworks includes four main components:

- i. A two-species integrated life cycle model to represent the entire population dynamics of small pelagic fish (anchovies and sardines), including fishing mortality, natural mortality, growth and stock recruitment processes (section 2.2.2).
- ii. The life cycle model is connected to the temporal dynamic of mean body size for each species, life-stage and year. This body size dynamic is controlled by pseudo-growth that we defined as a parameter representing both growth and mortality processes. Indeed, inter-annual variations in the mean body size of a given species for a specific life-stage and year at the population level may be the result of mortality and growth processes, as size is a discrete variable defined within a size interval, which includes individual variability. For example, in a discrete interval, the death of a smaller individual will have the same consequence as lower average population growth in this same size interval (section 2.2.2).
- iii. Within the life cycle model, we quantified the effects of inter- and intra-specific density-dependent intrinsic effects, size-dependent intrinsic effects, and extrinsic effects on three key demographic processes: natural mortality, pseudo-growth and recruitment processes (section 2.2.3).
- iv. We implemented the Stochastic Search Variable Selection (SSVS) method (George and McCulloch, 1993; Bret et al., 2017), within the life-cycle model to determine the most influential factors affecting natural mortality and growth. (section 2.2.4).

2.2.2. A two-species life-cycle model to track abundance dynamics and size dynamics

2.2.2.1. A life cycle model for abundance dynamics

The model is an age- and stage-based life cycle model (**FIGURE 3**), that tracks the abundances $N_{e,s,t}$ of small pelagic species (indexed by e , 1= sardines, 2=anchovy), for different stages (indexed s , $s=SS$ represent the spawning stock and, s = ages from 1 to 4+ for sardine and s = ages from 1 to 6+ for anchovy) across years (index t , from 2000 to 2021) (**Equation 1**).

For all stages except when $s=SS$, the life-stage-specific abundance over time and species is controlled by total mortality $Z_{e,s,t}$ (**Equation 2, FIGURE 2**), over species, life-stages and time.

$$N_{e,s+1,t+1} = N_{e,s,t} \times e^{-Z_{e,s,t}} \quad (1)$$

$$Z_{e,s,t} = M_{e,s,t} + F_{e,s,t} \quad (2)$$

$Z_{e,s,t}$ represent the sum of the fishing mortality $F_{e,s,t}$ and the natural mortality $M_{e,s,t}$ (**Equation 2, FIGURE 2**), for all stages except when $s=SS$

When $s=SS$, $Z_{e,SS,t}$ represents the stock recruitment process for each year t and each species e (**Equation 3**). This parameter accounts for all hidden processes occurring between the spawning stock abundance $N_{e,SS,t}$ for year t and species e , and first-year abundance $N_{1,e,t+1}$ for year $t+1$ and species e . Multiple demographic processes such as fecundity, egg and larvae mortality are approximated within this demographic transition parameter ($Z_{e,SS,t}$).

$$N_{e,1,t+1} = N_{e,SS,t} \times Z_{e,SS,t} \quad (3)$$

The spawning stock abundance $N_{e,SS,t}$ is the sum of abundances of all life-stages multiply by a maturity rate ($maturity_{e,s,t}$), for a given year t and a given species (**Equation 4**).

$$N_{e,SS,t} = \sum_{s=1}^{s \text{ life stages}} N_{e,s,t} \times maturity_{e,s,t} \quad (4)$$

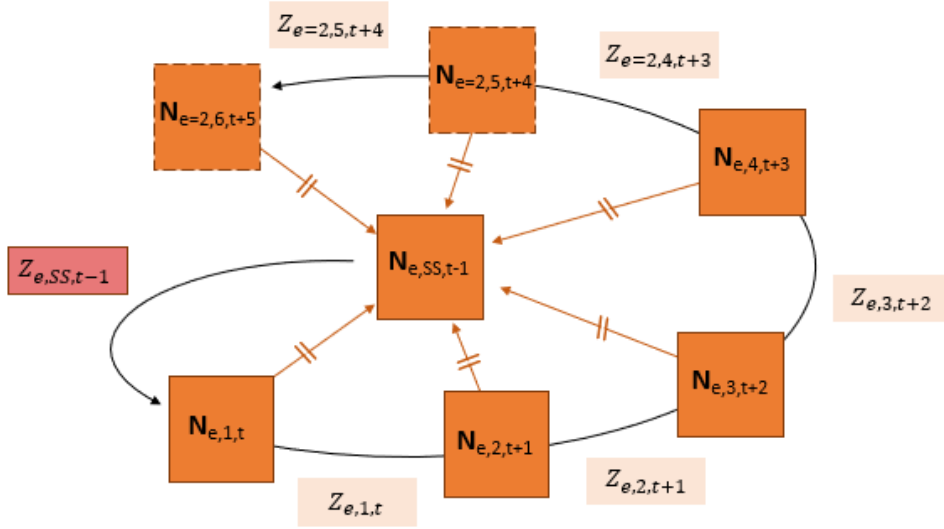


Figure 2: Structure of the age-based life cycle model for anchovy and sardine populations

Squares with dotted lines are specific stages only defined for sardines (for anchovy, year-classes 5 and 6, $N_{e=2,5,t}$ and $N_{e=2,6,t}$ do not exist). $N_{e,1,t}$ is the first year-class abundance calculated from $N_{e,SS,t-1}$. $N_{e,SS,t}$ is the spawning stock abundance, composed of the total abundance of mature fish of all the life-stages at year t . Double bars indicate where cut in the time indices has been introduced to make notations easier. $Z_{e,s,t}$ represent the total mortality (natural and by fishing) occurring between one year-class to the next. In the special case of $Z_{e,SS,t}$, it represents both a mortality rate (of eggs and larvae) and a fecundity rate. States variables are represented in squares. Reconstructed variables are represented with a colored background. Estimated total mortality rates from the model are represented with a light orange background and the stock recruitment process with a red background.

For both species, all life-stages except SS, and all years, Baranov's catch equation links fishing mortality and natural mortality through the catch variable $C_{e,s,t}$, assuming they occur together throughout the year (Equation 5).

$$C_{e,s,t} = \frac{F_{e,s,t}}{M_{e,s,t} + F_{e,s,t}} \times (1 - e^{-(M_{e,s,t} + F_{e,s,t})}) \times N_{e,s,t} \quad (5)$$

Each species is considered as a single stock within the Bay of Biscay (division 8 abd) (ICES WGHANSA 2022) and we assumed that migratory movements inside and outside the Bay of Biscay stocks are negligible.

2.2.2.2. Size dynamics

In addition to tracking the dynamics of abundance, the model also tracks the dynamics of size within life-stages, controlled by a pseudo growth rate which represents mean size transition occurring between two consecutive life-stages (FIGURE 3). Indeed, this pseudo-growth parameter does not only represent the average population growth of a given life-stage, but also a size-selective mortality within the life-stage. We define the mean size $L_{e,s+1,t+1}$ of the life-stage $s+1$ in year $t+1$, species e , as the product of the mean size $L_{e,s,t}$ of life-stage s at year t , species e , and the pseudo-growth rate $g_{e,s,t}$ of life-stage s except SS, year t and species e :

$$L_{e,s+1,t+1} = L_{e,s,t} \times g_{e,s,t} \quad (6)$$

2.2.3. Mechanisms linking density-dependent and size-dependent processes to natural mortality, growth and recruitment processes and their potential relationship with environmental factors

2.2.3.1. *Intrinsic and extrinsic variables and mechanisms*

Demographic- and size-dependent mechanisms inside the small pelagic system (**FIGURE 3**) are defined as intrinsic mechanisms, as opposed to extrinsic mechanisms which involved a dependence on external factors to the small pelagic system, such as environmental dependence.

To investigate the potential existence of such mechanisms, we tested the effect of intrinsic and extrinsic factors, on natural mortality, pseudo-growth and recruitment processes. The definition of the factors used in the model to detect density-, size- and environment-dependent processes are given below:

Intrinsic factors used to test the existence of density- and size-dependent processes

As we assumed all life stages of the small pelagic system potentially share same habitats, we tested the effect of each life-stage abundance of both species (sardine and anchovy) on each process.

- **Density-dependent mechanisms:** We expect to find positive density-dependent natural mortality mechanisms as a result of food competition or predation pressure in response to spatial aggregation or to the formation of schools (Furuichi et al., 2022 ; Ibaibarriaga et al., 2013). We assume this mechanism can be intra- or extra-specific, as sardines and anchovies potentially share the same habitats since their trophic niche overlaps, and may form mixed schools (Bakun and Cury, 1999; Bachiller and Irigoien, 2015; Doray et al., 2018a). We also assume pseudo-growth might be positively density-dependent in case of food competition limiting growth at key periods of the year. We expect recruitment to be more regulated by environment than by demographic factors, even though cannibalism or larval density could affect age-0 mortality (Canales et al., 2020).

For the size effects, we tested the effect of mean size on the process affecting the same life-stage because we assume fish size determines energetic demand, foraging capacity, resistance to starvation and vulnerability to predators.

- **Size-dependent mechanisms:** We assume a negative correlation between intra-specific size and natural mortality might exist, as survival chances may be lower for smaller fish, more vulnerable to predation (Arendt, 1997; Metcalfe and Monaghan, 2003). Also, intra-specific size, as a result of earlier growth (rate and duration), could impact future growth (Post and Evans, 1989).

Extrinsic factors used to test the existence of environment-dependent processes

- **Temperature (SUPPLEMENTARY MATERIAL 7):** We calculated standardized average sea surface temperature (SST) for a given period reflecting conditions encounter by fish over the year (November to February: possible starvation, March to May (sardine) or April to June (anchovy): spawning period, June to October (anchovy) or July to October (sardine): growth period) from SEAPODYM in ICES divisions 27.8a and 27.8b (Temp.apr_jun, Temp.mar_may, Temp.jun_oct, Temp.jul_oct, Temp.nov_dec, Temp.jun_oct_ante, Temp.jul_oct_ante, Temp.nov_dec_ante). Warmer temperatures are expected to induce increasing individual growth during the spawning period or the growth period, since increased temperatures may lead to faster growth

and thus reduce the time spent at the most critical period of life (Bailey and Houde, 1989; Pankhurst and Munday, 2011). Conversely, increased temperatures are expected to have a negative impact on natural mortality during winter, since warmer temperatures might increase the metabolism and so energetic demand in a period where food can be scarce (Hurst, 2007).

- **Zooplankton** (**SUPPLEMENTARY MATERIAL 7**): standardized average concentration of zooplankton for a given period reflecting conditions encountered by fish over the year (November to February: possible starvation, March to May (sardine) or April to June (anchovy): spawning period, June to October (anchovy) or July to October (sardine): growth period ; factors reflecting the conditions encountered by spawners are suffixed with “ante” and are only tested on recruitment) calculated from from SEAPODYM in ICES divisions 27.8a and 27.8b (Zoo.apr_jun, Zoo.mar_may, Zoo.jun_oct, Zoo.jul_oct, Zoo.nov_dec, Zoo.jun_oct_ante, Zoo.jul_oct_ante, Zoo.nov_dec_ante). Zooplankton biomass represents prey availability and is expected to be negatively correlated to natural mortality and recruitment (possible starvation if reduced food availability, especially for early-stages, or reduced egg production if spawners are in bad body condition). Zooplankton biomass is also expected to be negatively correlated to pseudo-growth (possible food competition) (Somarakis et al., 2004; Somarakis et al., 2019).
- **Sprat**: yearly total abundance standardized in the Bay of Biscay from PELGAS survey (nsprat)
- **Large scale indicators** (yearly average standardized per month and defined for May to May):
 - **Atlantic Multidecadal Oscillation (AMO)**: The AMO is described as the de-trended annual sea surface temperature anomaly over the North Atlantic Ocean, defined by the area covering 0° to 70°N and 75°W to -7.5°W. It is a low-frequency and basin-wide climate index reflecting sea surface temperature variability over the last century. The AMO signal alternate between cold and hot periods, with a period of 65-70 years. 1960-1990 was characterized as a cold period and since 1995, the North Atlantic Ocean is in a warm period, as characterized by positive values of AMO (Enfield et al., 2001). Since AMO is based on sea surface temperatures, it may be a relevant indicator for explaining climate-induced regime shifts in plankton and fish communities (Auber et al., 2015).
 - **North Atlantic Oscillation (NAO)**: NAO is a commonly used climate index that describes large scale atmospheric forcing over the North Atlantic (Wanner et al., 2001). This index is based on the difference of the normalized sea level pressures between high subtropical (Lisbon, Portugal) and low subpolar (Reykjavik, Iceland) areas (John and Reid, 2001). The NAO is related to several climatic components, including precipitations and the direction/intensity of wind (Auber et al., 2015). Positive values of NAO are associated with strong westerlies and vice versa (Wanner et al., 2001). The NAO index might be a relevant indicator for explaining changes in marine ecosystems. In Atlantic small pelagic fish, a high NAO index might lead to a lower recruitment due to the colder temperatures (because of strong winds) and offshore eggs and larvae drift (Drinkwater et al., 2003). Thus, we expected a negative correlation between NAO and recruitment. We assume NAO can have an effect on natural mortality and individual growth though the nature of zooplankton communities. However, it is difficult to predict the sign of the effect of NAO on natural mortality and pseudo-growth, as its effect on food (plankton) is assumed to be tightly dependent from local environment (Beaugrand et al., 2000).

2.2.3.3. *Quantifying the effects of intrinsic (inter and intraspecific) and extrinsic factors on mortality, pseudo growth and recruitment process*

To unravel the mechanisms linking density and size to natural mortality, pseudo growth and recruitment processes and their potential relationship with environmental factors, we quantified the inter and intra specific density-dependent and size-dependent intrinsic effects, as well as extrinsic effects, on each process, within the life cycle model. To do so, we modelled the natural mortality $M_{e,s,t}$ and the pseudo growth $g_{e,s,t}$ for each species e , life-stage s and year t , as a linear function in the logscale of intrinsic and extrinsic factors (**FIGURE 3**, Equation 7 and 8).

For $s \neq SS$:

$$\log(M_{e,s,t}) \sim \text{Normal} \left(\mu_{M_{e,s}} + \alpha_{e,s} \times N_{e,s,t} + \beta_{e,s} \times L_{e,s,t} + \sum_{k=1}^{k \text{ indexes}} \delta_{e,s,k} \times X_{e,s,k}, \sigma_{M_{e,s}}^2 \right) \quad (7)$$

$$\log(g_{e,s,t}) \sim \text{Normal} \left(\mu_{g_{e,s}} + \gamma_{e,s} \times N_{e,s,t} + \varepsilon_{e,s} \times L_{e,s,t} + \sum_{k=1}^{ncov} \xi_{e,s,k} \times X_{e,s,k}, \sigma_{g_{e,s}}^2 \right) \quad (8)$$

We modelled the recruitment $Z_{e,SS,t}$ for each species e and year t , as a linear function in the logscale of intrinsic and extrinsic factors (**FIGURE 3**, Equation 9).

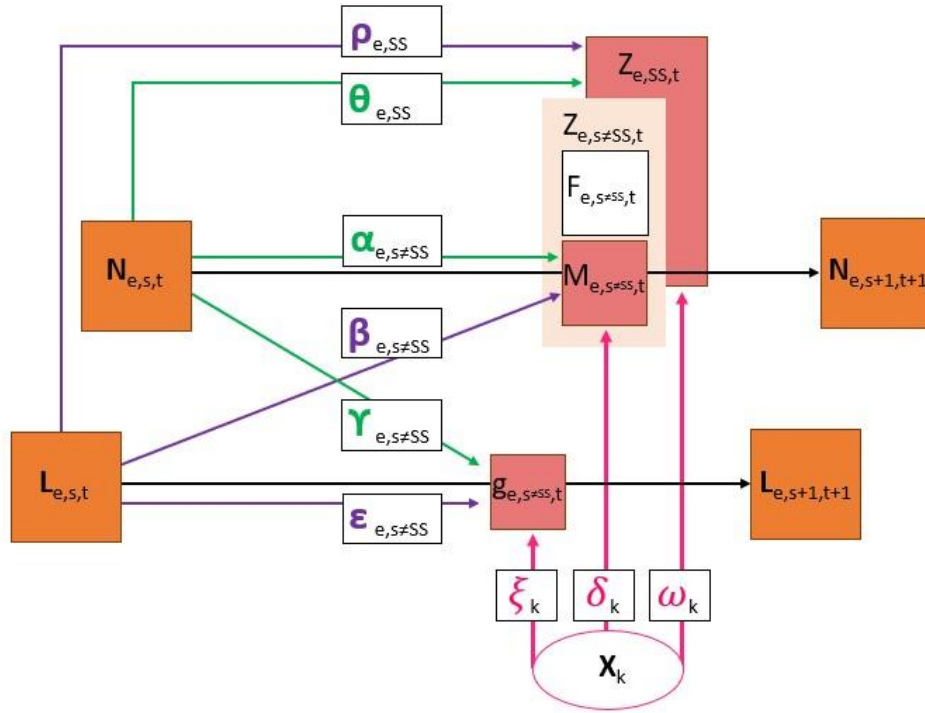
For $s = SS$:

$$\log(Z_{e,SS,t}) \sim \text{Normal} \left(\mu_{Z_{e,SS}} + \theta_{e,SS} \times N_{e,SS,t} + \rho_{e,SS} \times L_{e,SS,t} + \sum_{k=1}^{ncov} \omega_{e,SS,k} \times X_{e,SS,k}, \sigma_{Z_{e,SS}}^2 \right) \quad (9)$$

Equation 7,8 and 9 can be seen as extended Ricker models (Corani and Gatto, 2007) where $\alpha_{e,s \neq SS}$, $\gamma_{e,s \neq SS}$ and $\theta_{e,SS}$ represent the intra and/or interspecific density-dependent parameters affecting natural mortality, pseudo-growth and recruitment respectively. $\beta_{e,s \neq SS}$, $\varepsilon_{e,s \neq SS}$ and $\rho_{e,SS}$ represent the intraspecific size-dependent parameters affecting natural mortality, pseudo-growth and recruitment respectively. $\mu_{M_{e,s}}$ and $\mu_{g_{e,s}}$ are demographic (i.e density and size) and environmental independent parameters. $\mu_{Z_{e,SS}}$ is the environmental dependent parameter.

$\sigma_{M_{e,s \neq SS}}^2$, $\sigma_{g_{e,s \neq SS}}^2$ and $\sigma_{Z_{e,SS}}^2$ are the variances of natural mortality, pseudo-growth and recruitment processes respectively. $N_{e,s,t}$ and $L_{e,s,t}$ are the abundance and the mean size (total length), respectively, for species e , stage s and year t . In these equations, $\alpha_{e,s \neq SS}$, $\beta_{e,s \neq SS}$, $\gamma_{e,s \neq SS}$, $\varepsilon_{e,s \neq SS}$, $\theta_{e,SS}$ and $\rho_{e,SS}$ are the coefficients related to $N_{e,s,t}$ and $L_{e,s,t}$ latent variables.

For species e and stage s , $\alpha_{e,s \neq SS}$ and $\beta_{e,s \neq SS}$ coefficients respectively represent the density effect and the size effect on natural mortality; $\gamma_{e,s \neq SS}$ and $\varepsilon_{e,s \neq SS}$ coefficients respectively represent the density effect and the size effect on the pseudo-growth; and $\theta_{e,SS}$ and $\rho_{e,SS}$ coefficients respectively represent the density effect and the size effect on the recruitment. $\delta_{e,s \neq SS,k}$ and $\xi_{e,s \neq SS,k}$ are the coefficients related to each covariate $X_{e,s,k}$ defined for different extrinsic factors k .



$N_{e,s,t}$: Life-stage abundance

$L_{e,s,t}$: Mean size (total length)

$M_{e,s≠SS,t}$: Natural mortality

$g_{e,s≠SS,t}$: Pseudo-growth

$Z_{e,s,t} \begin{cases} F_{e,s,t} + M_{e,s,t} \text{ if } s \neq SS, s = 1 : 4^+ (e = 1, \text{anchovy}) \text{ or } s = 1 : 6^+ (e = 2, \text{sardine}), \text{total mortality rate} \\ Z_{e,SS,t} \text{ if } s = SS, \text{recruitment rate} \end{cases}$

$F_{e,s≠SS,t}$: Fishing mortality

$X_{e,s,k}$: Environmental factor

Intrinsic effects

$\alpha_{e,s≠SS}$: Inter and/or intraspecific natural mortality density-dependent effect

$\beta_{e,s≠SS}$: Intraspecific natural mortality size-dependent effect

$\gamma_{e,s≠SS}$: Inter and/or intraspecific pseudo-growth density-dependent effect

$\epsilon_{e,s≠SS}$: Intraspecific pseudo-growth size-dependent effect

$\theta_{e,SS}$: Inter and/or intraspecific recruitment density-dependent effect

$\rho_{e,SS}$: Intraspecific recruitment size-dependent effect

Extrinsic effects

δ_k : environmental-dependent effect on natural mortality

ξ_k : environmental-dependent effect on pseudo-growth

ω_k : environmental-dependent effect on pseudo-growth

Figure 3: Schematic outline of main mechanisms that link abundance and mean size of an age-class for each species (e.g. $e =$ anchovy or sardine) of the small pelagic fish system, at subsequent life-stages (e.g. $s = 1, 2, 3$ and 4^+ years of age for anchovy and $s = 1, 2, 3, 4, 5$ and 6^+ years of age for sardine) and time (e.g. $t =$ year 2000 to year 2023).

For $s=SS$ in $Z_{e,s,t}$, linking $N_{e,SS,t}$ to $N_{e,1,t+1}$, natural mortality and fishing mortality are not defined but are summarized in $Z_{e,SS,t}$. States variables are represented in squares and the observed covariable in oval. Reconstructed variables are represented with an orange background. Estimated parameters from the model are represented with a white background. Demographic processes (natural mortality, pseudo-growth and recruitment) affected by intrinsic and extrinsic factors are represented with a red background. Intrinsic factors and mechanisms are represented in green (density-dependent) or purple (size-dependent); extrinsic factors and mechanisms in pink.

2.2.4. Stochastic Search for Variable Selection (SSVS)

We quantified inter- and intra-specific density-dependent and intra-specific size-dependent intrinsic effects, and extrinsic effects, on mortality, pseudo-growth and recruitment processes using the Stochastic Search for Variable Selection.

2.2.4.1. SSVS: Global approach

Selection of the covariates of importance: Stochastic Search Variable Selection (SSVS)

The Stochastic Search Variable Selection (SSVS) method (George and McCulloch, 1993), has been used in several studies to identify environmental covariates related to fish ecology (Bret et al., 2017). This method was implemented inside the life-cycle model to determine the most influential covariates affecting natural mortality and growth. The effect of important covariates is taken into account in mortality and growth mechanisms, while the effect of other covariates is minimized (close to 0). The principle is to introduce coefficients as latent variables associated with each covariate to be tested in the process equation (natural mortality, pseudo-growth and recruitment) (Equation 10). Then, each introduced coefficient (δ_{X_k}) is itself defined using auxiliary variables I_{X_k} that indicate the presence ($I_{X_k} = 1$) or absence ($I_{X_k} = 0$) of the covariate X_k in the process equation (Equation 11). When $I_{X_k} = 0$, δ_{X_k} is given a very informative normal prior distribution centered on 0 (spike prior $\delta 0_{X_k}$), in order to neglect this effect. When $I_{X_k} = 1$, δ_{X_k} is given a less informative prior distribution (slab prior $\delta 1_{X_k}$), likely to be updated if this covariate has an influence. I_{X_k} is given an a priori equiprobable distribution. If the posterior frequency of inclusion I_{X_k} is $> 50\%$, the effect has an influence on the process (natural mortality, pseudo-growth or recruitment).

$$P_{e,s,t} \sim \text{LogN} \left(E_{\log} \mu_{p_{e,s}} + \sum_{k=1}^{k \text{ covariates}} \delta_{X_k} \times X_k, \sigma_{p_{e,s}}^2 \right) \quad (10)$$

$$P(\delta_{X_k} | I_{X_k}) = (1 - I_{X_k}) \times \delta 0_{X_k} + I_{X_k} \times \delta 1_{X_k} \quad (11)$$

With $E_{\log} \mu_{p_{e,s}}$ intercept of the process equation (mortality: $E_{\log} \mu_{M_{e,s}}$; pseudo-growth: $E_{\log} \mu_{g_{e,s}}$; or recruitment: $E_{\log} \mu_{e,z,ss}$), $\sigma_{p_{e,s}}^2$ standard variation of the process equation for life-stage s ; I_{X_k} inclusion indicator variable for the covariate X_k , $\delta 0_{X_k}$ and $\delta 1_{X_k}$ slope coefficients associated to each covariate X_k . k is a unique index to designate a given environmental factor, that differs according to the species or the life stage on which it is tested.

For further details on SSVS parameters, see [SUPPLEMENTARY MATERIAL 3](#) and [5](#).

2.2.4.2. Determination of intrinsic effects affecting ecological processes and model selection (model exploration using SSVS method)

In a first step, we used the integrated SSVS approach to identify intrinsic effects affecting natural mortality ($M_{e,s \neq SS,t}$), pseudo-growth ($g_{e,s \neq SS,t}$) and recruitment processes ($Z_{e,ss,t}$) for each year, stage and species.

In a preliminary analysis; standardized abundance and mean size variables were firstly included in the life-cycle SSVS model (M0) as covariates (M1). Then, important intrinsic covariates (I_{X_k} is $> 50\%$) selected from the SSVS method were included into the model as latent variables (M2). This aims to

avoid redundant inclusion of observation data, as observed data are already implemented through the likelihood equations (TABLE 2).

We compared the parsimony of models using the W-AIC criterion. The WAIC is appropriate to compare hierarchical models of any structure fitted to the same data sets (Gelman et al., 2013; Watanabe, 2013; Gelman et al., 2014; Hooten and Hobbs, 2015). It can be considered as a generalization of the Deviance Information Criterion (Gelman et al., 2013; Gelman et al., 2014; Vehtari et al., 2017) and has the advantage of being directly related to the posterior predictive ability of the model. Using the common convention for information criteria on the deviance scale, differences of W-AIC between models can be roughly interpreted according to the following rules of thumb: a difference of 1-2 units offers little to no support in favor of a particular model; a difference of between 4 and 7 units offers considerable support for the model with the lowest W-AIC; and a difference of >10 units offers full support for the model with the lowest W-AIC (Burnham and Anderson, 2002; Gelman et al., 2013; Gelman et al., 2014).

Table 2: Intermediate models (M0, M1, M2) and final model (M3) used during the exploration of the model to increase its complexity. Model complexity increases from M0 to M3.

Life cycle model	Intrinsic factors	Extrinsic factors	WAIC
M0	no	no	15610.3
M1	As covariate	no	15601.6
M2	As latent variable	no	15581.1
M3 : full model describe in eq (1) : (10)	As latent variable	As covariates	15601.5

2.2.4.3. Determination of extrinsic effects affecting ecological processes (SSVS method)

In a second step, we used the integrated SSVS approach to identify extrinsic effects (AMO, NAO, sprats abundance, zooplankton abundance and sea surface temperature as defined in section 2.2.3.1) affecting natural mortality, pseudo-growth and recruitment processes (M3) (TABLE 2). Further details the definition of extrinsic covariates is available in (SUPPLEMENTARY MATERIAL 7).

2.2.5. Observation model

The likelihood function for the state-space model is based on the combination of all observation equations for the survey (abundances and mean size) and fishery data (commercial catches) for each year, life-stage and species. We defined for likelihood log-normal equations for both species, all life-stages \neq SS and all years, given that abundances, mean size and catches can only be positive values. Details on likelihoods are available in SUPPLEMENTARY MATERIAL 4.

We handled the fish-poor older age classes summing the abundances of 4 to 5 (anchovy) or 6 to 10 (sardine) age classes to create the age plus classes 4+ for anchovy and 6+ for sardines. Concerning the mean size of age-plus classes, for anchovies, we kept the mean size of the age-4 class, since few age 4 were sampled and almost no age 5. For sardines, we obtained a 6+ mean size by retaining the weighted mean of age classes 6, 7 and 8+, since age 7 to 10 were scarce among samples.

2.2.6. Parameters and Bayesian inference

The model estimates the fishing mortality ($F_{e,s\neq SS,t}$) for all ages, years and species and the coefficients of the effects of intrinsic and extrinsic factors on natural mortality, pseudo growth and recruitment processes, for all stages, species and years, and the parameters of the SSVS: the inclusion

indicator variable (I_{X_k}) for the covariate X_k , and the slope coefficients associated to each covariate X_k ($\delta 0_{X_k}$ and $\delta 1_{X_k}$).

All details about the parameters (fixed, predefined and hierarchical structure with priors can be found in [\(SUPPLEMENTARY MATERIAL 5\)](#).

We used a Bayesian framework, meaning that the parameters are considered as random variables (versus fixed variables in the frequentist approach) with a probability distribution resulting from sampling using Markov chain Monte Carlo (MCMC) algorithms. The Bayesian MCMC approach uses, *a priori* knowledge on parameters, expressed as a prior distribution and combined with observation data through a likelihood function to determine the posterior distribution the parameters.

Bayesian posterior distributions were approximated using Monte Carlo Markov Chain (MCMC) methods in JAGS (<https://mcmc-jags.sourceforge.io/>; release 3.4.0) through the Rjags (<https://www.r-project.org/>) package (JAGS code is available on GitHub: https://github.com/AliceBordes/IPM_small_pelagic_fish/tree/main). The first 5000 iterations were used as a burn-in period. To reduce the autocorrelation in the MCMC sample used for final inferences, one out of 100 iterations post burn-in was kept and this sample of 300 000 iterations per chain was used to characterize the posterior distribution. Three independent MCMCs with dispersed initialization values were used.

2.2.7. Model checking

To check the validity of the model, for each variable, we looked at the convergence of the MCMC chains, the *a posteriori* distribution and the fit between prediction and observations for abundances, sizes and catches time series. Convergence was assessed using the Gelman–Rubin statistic (Brooks and Gelman, 1998) as implemented in the R Coda package (*gelman.diag()*) [SUPPLEMENTARY MATERIAL 8](#).

Model fit to each data source was assessed by verifying that the credibility envelope of the posterior predictive distribution of each variable contained the observation [SUPPLEMENTARY MATERIAL 8](#).

3. Results

3.1. Preliminary Results

3.1.1. Data exploration

We performed generalized linear models (GLM) and generalized additive models (GAM) on mean size and abundance of both species and for each age group from age-1, investigating the effect of year (student test at a threshold of 5% or 10%). We noticed a significant decline in size for both species and all age groups, except for age-10. Abundance analyses reveals a significant increase of early life-stages abundance for both species (age-1 sardines, age-1 and age-2 anchovies) and a significant decrease for old life-stages of sardines 6, 7 and 8+.

We used principal component analyses (PCA) to explore size and abundances correlations between age groups and species, and correlations with environment. We found no correlations between size and abundance variables with seasonal temperature and zooplankton biomass.

Details on exploratory analyses of data abundance and data size can be found in [SUPPLEMENTARY MATERIAL 2](#).

3.1.2. Model exploration

Model exploration using SSVS method enable to highlight important intrinsic effects on natural mortality and recruitment. There is no intrinsic effect on pseudo-growth. Then, intrinsic effects are modeled as latent variables in the final model (M3) and are interpreted in section [3.3.3.1](#).

Details on SSVS exploratory analyses for the selection of latent demographic variables can be found in [SUPPLEMENTARY MATERIALS 6](#).

W-AIC was used to test whether making the model more realistic in terms of demographics (intrinsic factors) and more representative of ecosystem interactions (extrinsic factors) would better explain the data. First, explicitly accounting for intrinsic factors (as latent variable, M2) is strongly supported by the data. Indeed, W-AIC differences between M2 and M0 (no intrinsic factors) or M2 and M1 (intrinsic factors as covariates) are >9 units (with M0 having the lowest W-AIC). Then, when comparing M2 and M3, even if M2 has the lowest WAIC, we choose to retain model M3 because only M3 can help us to understand the impact of extrinsic factors on demographic processes ([TABLE 2](#)).

3.2. Estimation of abundance and size dynamics of all life stages

The model reconstructs the time series of mean size and abundances for all years, all life-stages and both species (anchovy and sardine).

3.2.1. Abundance

Posterior estimates abundance of early life stages, age-1 anchovy, age-2 anchovy and age-1 sardine, increase over the second half (2011-2022) of the time series by a factor of 7.4, 3.9 and 2.5 respectively compared to the first period (2000-2011) ([FIGURE 4](#)). Posterior estimates of the spawning stock abundance follow the trend of early life-stages, since they account for most of the abundance. Age-1 anchovy abundance shows a pronounced peak in abundance in 2015. From 2000-2002 to 2021-2022, strong declines in abundance of 16%, 38%, 63% and 80% are observed for older life-stages in sardine populations, for age class 3, 4, 5 and 6+ respectively. Age-3 anchovy abundance and age-2 sardine abundance show a stable trend over the time series. Strong variations over the time series are noticed for the older life-stage (4+ for anchovy and 6+ for sardine).

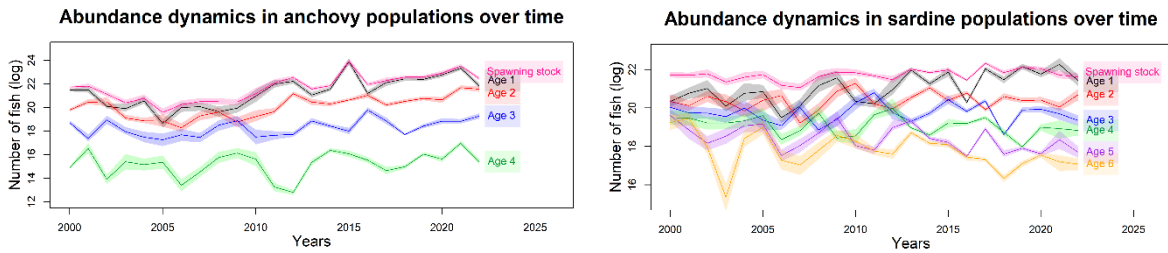


Figure 4 : Time series of estimated abundances at various life-stages for anchovy (left graph) and sardine (right graph) populations (solid line = median value of MCMC draws ; pastel zone around solid line = Bayesian confidence interval: 95% of the MCMC draws). The life-stages considered are defined by the labels.

3.2.2. Size

Both sardine and anchovy population show a strong decline in mean size, more marked in early stages (FIGURE 5). By calculating the average size of the estimated median over the first 5 years and the estimated median over the 5 last years, our results show an important decline in size at age for all species.

For anchovy, early stages (age 1 and 2) have lost 2.4 cm while older life stages (age 3 and 4) have lost 2 cm (in details: loss of 2.4, 2.4, 2.0 and 2.0 respectively for age classes 1, 2, 3 and 4+) (FIGURE 5).

For sardine, the size of early life stages (1 and 2) decreases by 2.8 cm, whereas size of older life stage decreases by 2.2 cm (in details: decrease by 2.8, 2.7, 2.2, 2.2, 2.2 and 2.3 respectively for age classes 1, 2, 3, 4, 5 and 6+). The biggest drop was in mean size of the spawning stock, which decline by 2.8 cm for anchovy and 3.8 cm for sardine (FIGURE 5).

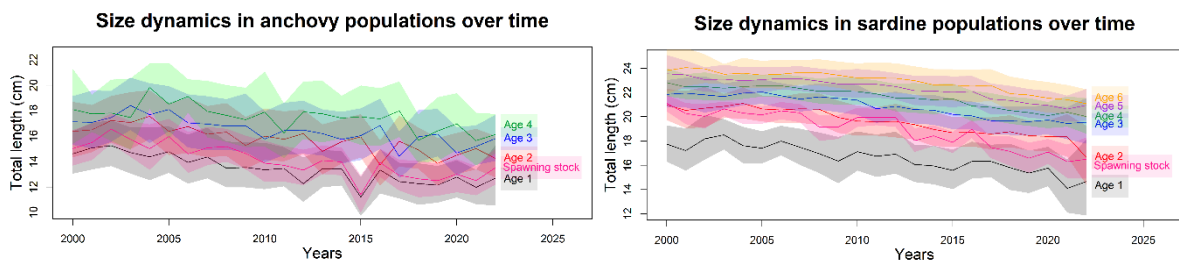


Figure 5 : Time series of estimated abundances at various life-stages for anchovy (left graph) and sardine (right graph) populations (solid line = median value of MCMC draws ; pastel zone around solid line = Bayesian confidence interval: 95% of the MCMC draws). The life-stages considered are defined by the labels.

3.3. Inferring interdependent natural mortality, growth and recruitment mechanisms

The model estimates the fishing mortality for all life-stages, years and species, the coefficients of the effects of intrinsic and extrinsic factors on natural mortality, pseudo-growth and recruitment processes, for all life-stages and species, allowing to reconstruct the times series of those three processes of interest.

3.3.1. Estimation of time varying fishing mortality

In average, fishing mortality (all life-stages taken together) is higher for anchovies (0.79, or 0.45 in the scale of the survival) than for sardines (0.22, or 0.80 in the scale of the survival) (FIGURE 6).

Age-1 anchovy fishing mortality (0.31) is around three time less than age-2 (0.92) and age-3 (1.13). Fishing mortality was null between 2007 and 2009, when the anchovy fishery was closed. Since 2017, fishing mortalities are globally decreasing.

Sardine fishing mortalities are homogenous between life-stages and stable over time. They are very low for all life-stages and varies between 0.05 and 0.59.

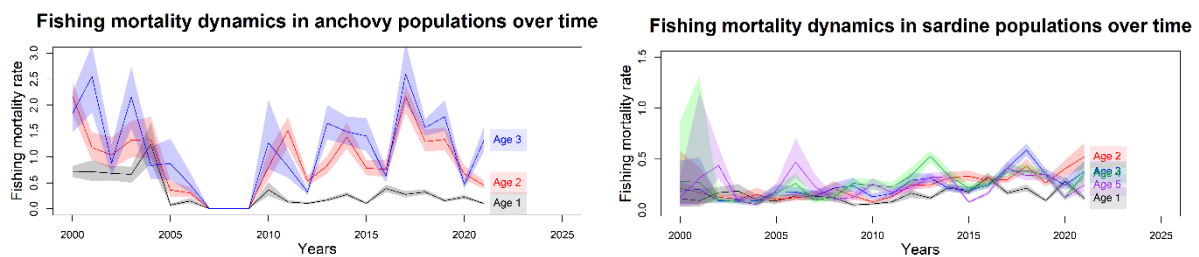


Figure 6: Time series of estimated fishing mortality rates at various life-stages for anchovy (left graph) and sardine (right graph) populations (solid line = median value of MCMC draws ; pastel zone around solid line = Bayesian confidence interval: 95% of the MCMC draws). The life-stages considered are defined by the labels.

3.3.2. Estimation of time varying natural mortality, pseudo-growth and recruitment processes

3.3.2.1. Natural mortality

For all life-stages of both species, the natural mortality is between 0 (for M5) and 2 (i.e between $\exp(-4)=0.02$ (2%) and $\exp(0)=1$ (100%) in the scale of the survival), except for age-3 anchovies which can reach up to 4.5 (0.01 in survival scale) (FIGURE 7). For all anchovy life-stages and for age-1 sardines, natural mortality rates increase around 2016.

Age-3 anchovy natural mortality rate is 1.85 (0.16 in survival scale) in average, which is 2.2 times higher than the average of age-1 and age-2 natural mortality, estimated at 0.84 (in details: 0.86, 0.81 for age classes 1 and 2 respectively) (FIGURE 7). Yearly variations in posterior estimates of age-3 anchovy natural mortality are higher (between 0.08 and 4.5) than for early life-stages, (between 0.26 and 2.7 (age 1) or between 0.04 and 2.0 (age 2)).

For sardines, mortality rates are generally homogenous across of all life-stages (FIGURE 7). In average, across all life-stages, the natural mortality rate is 0.46 (in details: 0.5, 0.4, 0.44, 0.46 and 0.49 for the mortality affecting age classes 1, 2, 3, 4 and 5 respectively). Older stages (age-4 and age-5) have higher annual variations (the mortality rate varies between 0.01 and 1.9 for age-4 or 0 and 2.4 for age-5) than age-1 and age-2 (the mortality rate varies between 0.04 and 1.7, between 0.1 and 1.2, and between 0.04 and 1.2 for age 1, 2 and 3 respectively).

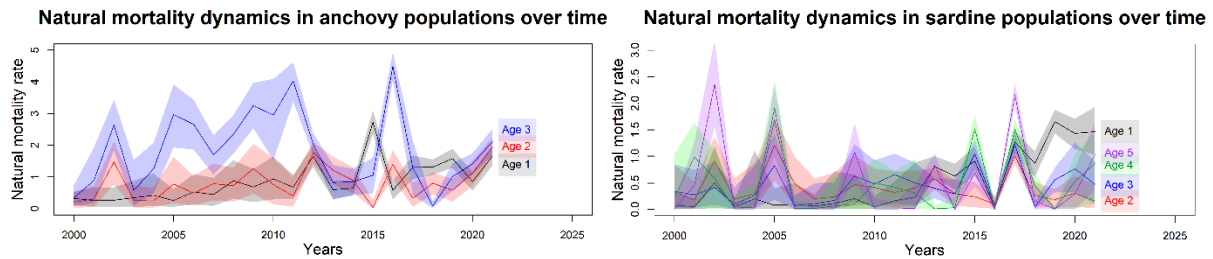


Figure 7 : Time series of estimated natural mortality rates at various life-stages for anchovy (left graph) and sardine (right graph) populations (solid line = median value of MCMC draws ; pastel zone around solid line = Bayesian confidence interval: 95% of the MCMC draws). The life-stages considered are defined by the labels.

3.3.2.2. Pseudo-growth

For both species and all life-stages, the estimated pseudo-growth is mostly constant over time (FIGURE 8). For both species, the pseudo-growth at age-1 is significantly higher than at other ages. For anchovy, average annual pseudo-growth estimated over the time series is 1.17 for the age-1, varying between 1.12 and 1.22, while it is lower for age-2 and age-3 (1.04 and 1.06 respectively), varying between 1.00 and 1.08 (age-2) or 1.00 and 1.11 (age-3) over the time series. For sardine, the average annual growth estimated over the time series is 1.17 for the first-year class, varying between 1.14 and 1.2, while it is lower and similar for other age classes (1.06, 1.03, 1.03 and 1.02 respectively), varying between 1.02 and 1.07 over the time series.

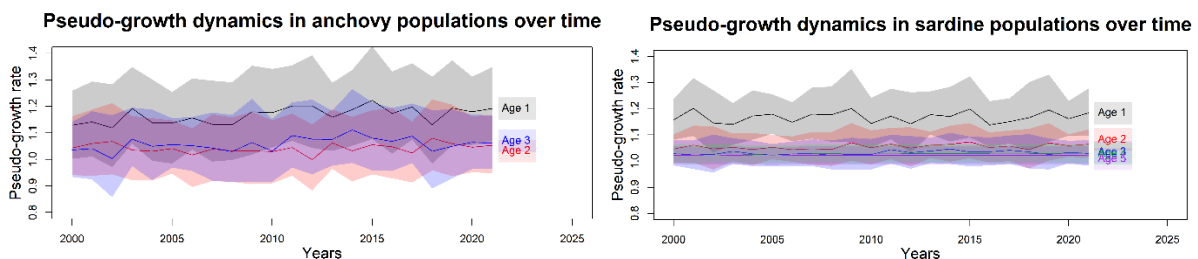


Figure 8 : Time series of estimated pseudo-growth rates at various life-stages for anchovy (left graph) and sardine (right graph) populations (solid line = median value of MCMC draws ; pastel zone around solid line = Bayesian confidence interval: 95% of the MCMC draws). The life-stages considered are defined by the labels.

3.3.2.3. Recruitment processes

The stock recruitment process shows large annual variations over the time series (FIGURE 9).

For anchovy, recruitment shows a temporally sporadic pattern, with very high recruitment in 2015 (value of 7.6). In other words, this particular year, the number of first year anchovy juveniles is 7.6 times more than the whole spawning stock abundance (FIGURE 9). For other years, recruitment varies between 0.07 and 2.3 for anchovy population. For sardines, recruitment process varies between 0.11 and 1.8, meaning that some years the stock ($N_{e=1,SS,t}$) is 10 time bigger that recruitment, while during other years the recruitment is twice the stock.

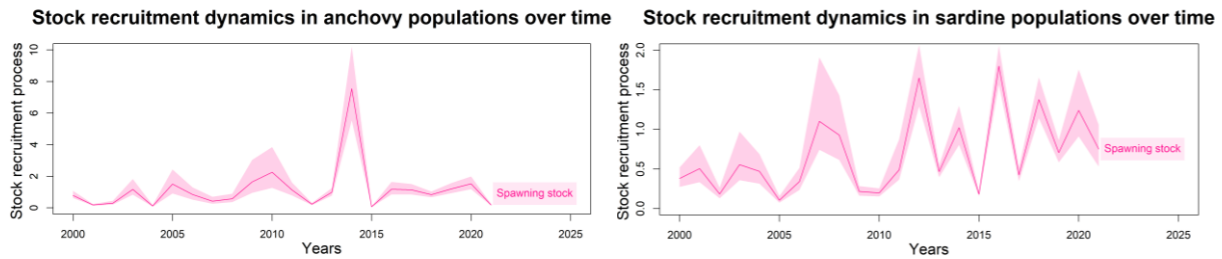


Figure 9 : Time series of estimated stock recruitment process at various life-stages for anchovy (left graph) and sardine (right graph) populations (solid line = median value of MCMC draws ; pastel zone around solid line = Bayesian confidence interval: 95% of the MCMC draws). The life-stage considered is defined by the label.

3.3.3. Effect of intrinsic and extrinsic factors

Overall, the model does not estimate any interspecific density-dependent effect (FIGURE 10). Concerning intraspecific effects, the model estimates several density-dependent effects on natural mortality for both species, and a size-dependent effect on natural mortality in anchovy population. The model does not estimate any environment-dependent effect on pseudo-growth, but only on natural mortality and recruitment. Finally, the model estimates an intraspecific density-dependent effect on recruitment in anchovy population.

For intrinsic factors we decided to only plot the posterior distribution of the significative coefficients of the SSVS performed on demographic covariates (See section 2.2.4.2, M2 ; SUPPLEMENTARY MATERIAL 6).

For extrinsic factors we plotted all effects of covariates on the three demographic processes of interest (natural mortality, pseudo-growth, and stock recruitment) (FIGURE 10, FIGURE 11, FIGURE 12).

3.3.3.1. Intrinsic factors

For anchovy, the model revealed a negative size-dependent effect ($\beta_{1,1} = -0.7$) on age-1 natural mortality. The model estimates a strong intraspecific density-dependence effect on age-1, age-2 mortalities and on the stock recruitment process (FIGURE 10, left graph), but the signs of those effects change, depending on age classes. In particular, age-1 abundance has a strong unexpected negative effect ($\alpha_{1,1} = -2.1$) on age-2 natural mortality, (FIGURE 10, left graph) but abundance of age-2 has a strong positive effect ($\alpha_{1,2} = 2.4$) on age-2 mortality. Finally, the stock recruitment relation is also density-dependent with the spawning stock biomass having a strong negative effect ($\theta_{1,SS} = -1.78$) on the stock recruitment process (resulting in a $Z_{e=1,SS,t} < 0$).

For sardine, natural mortality of age-1 and age-3 are density-dependent (FIGURE 10, right graph). In particular, age-1 abundance has a strong positive effect on both age-1 ($\alpha_{2,1} = 3.3$) and age-3 natural mortality ($\alpha_{2,1} = 1.4$). Also, old stages abundances have a strong effect on age-3 natural mortality ($\alpha_{2,3;6+} = 2.3$) whereas age-2 has a slight effect ($\alpha_{2,2} = 0.2$). There is no intrinsic effect on sardine recruitment.

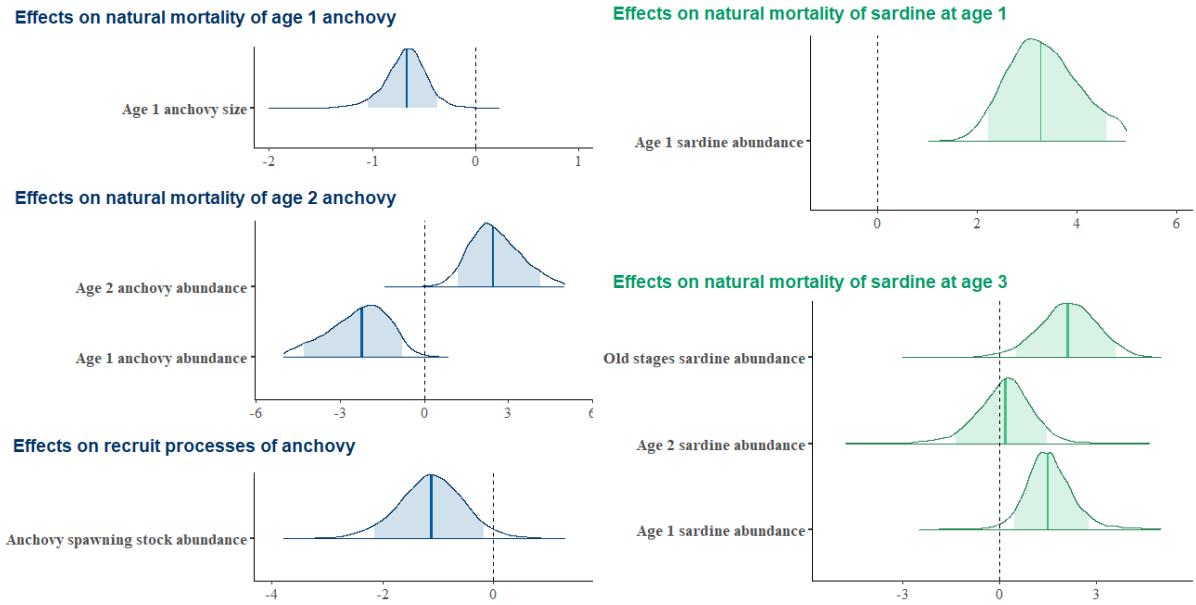


Figure 10 : Intrinsic effects impacting natural mortality, pseudo-growth and stock recruitment processes in anchovy (left graph) and sardine (right graph) populations.

All plotted intrinsic effects are the ones selected by the integrated SSVS method. Posterior distributions (median = solid line) of the coefficient linked to each latent variable affecting natural mortality. Posterior distributions are filled with colors representing 90% posterior Bayesian credibility intervals. All effects are significant at 10%, meaning the 90% posterior Bayesian credibility interval does not include 0 (dotted line), except age-2 density effect on age-3 sardine abundance which is significant at 75% (the 25% posterior Bayesian credibility interval does not include 0).

3.3.3.2. Extrinsic factors

The model estimates environment-dependent effects on age-3 natural mortality and recruitment for both species. The model also estimates an environment-dependent effect on natural mortality of age-1 anchovy. Finally, the model does not estimate any environment-dependent effect on pseudo-growth.

The signs and the absolute values of regression coefficients of extrinsic covariates strongly differ and depend on the species. First, the global indicator NAO (*North Atlantic Oscillation*) has a negative effect on the age-3 natural mortality for both species (median estimates are $\gamma_{NAO} = -1.2$ and $\gamma_{NAO} = -0.5$ for anchovy and sardine respectively) (FIGURE 11, FIGURE 12).

For anchovy, zooplankton during autumn has a negative significant (as defined in the SSVS method) effect ($\omega_{Zoo_{jul-oct}} = -0.6$) on stock recruitment processes (FIGURE 11). The global indicators AMO (*Atlantic Multidecadal Oscillation*) has a significant effect on age-3 natural mortality (FIGURE 11), but almost null ($\gamma_{AMO} = 0.1$). Also, AMO has a significant slight effect on age-1 anchovy mortality ($\gamma_{AMO} = 0.4$).

For sardines, temperature during spawning has a positive effect on sardine stock recruitment process ($\omega_{temp_{mar-may}} = 0.4$) (FIGURE 12).

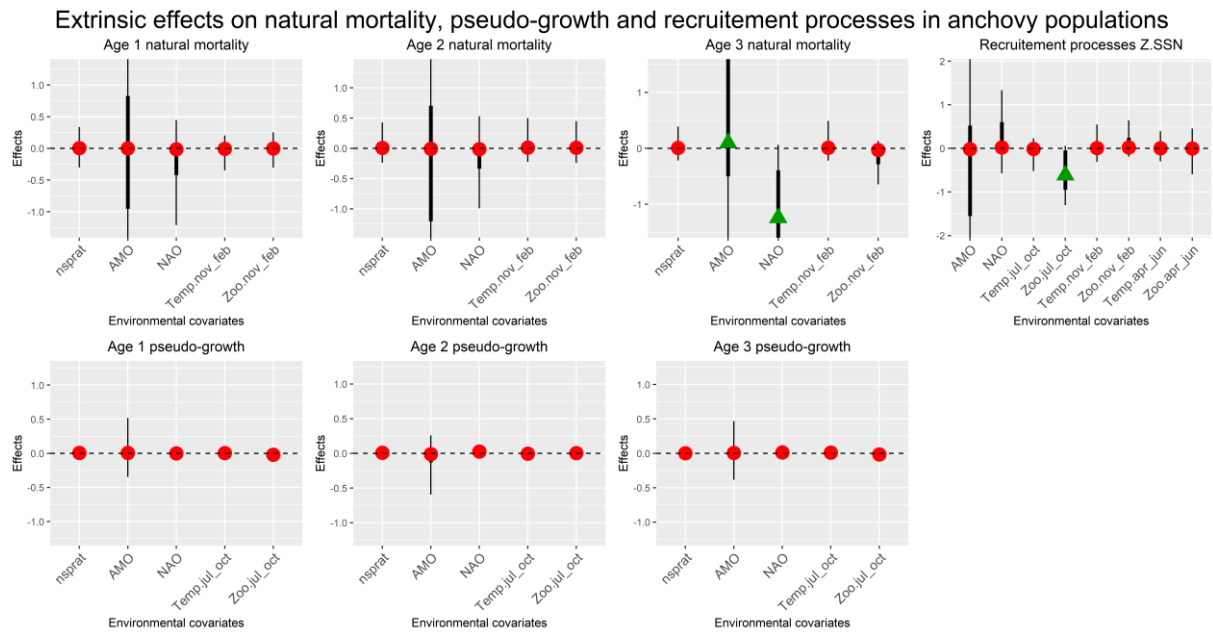


Figure 11 : Important extrinsic effects impacting natural mortality, growth and recruit processes in anchovy populations.

Important covariates selected from the Stochastic Search Variable Selection (SSVS) method. Median of the significant effects (posterior frequency of inclusion $I_x > 50\%$): green triangle. Median of the non-significant effects (posterior frequency of inclusion $I_x < 50\%$): red points. Thick confident interval: 90% of mcmc draws ; thin confident interval: 99% of mcmc draws.

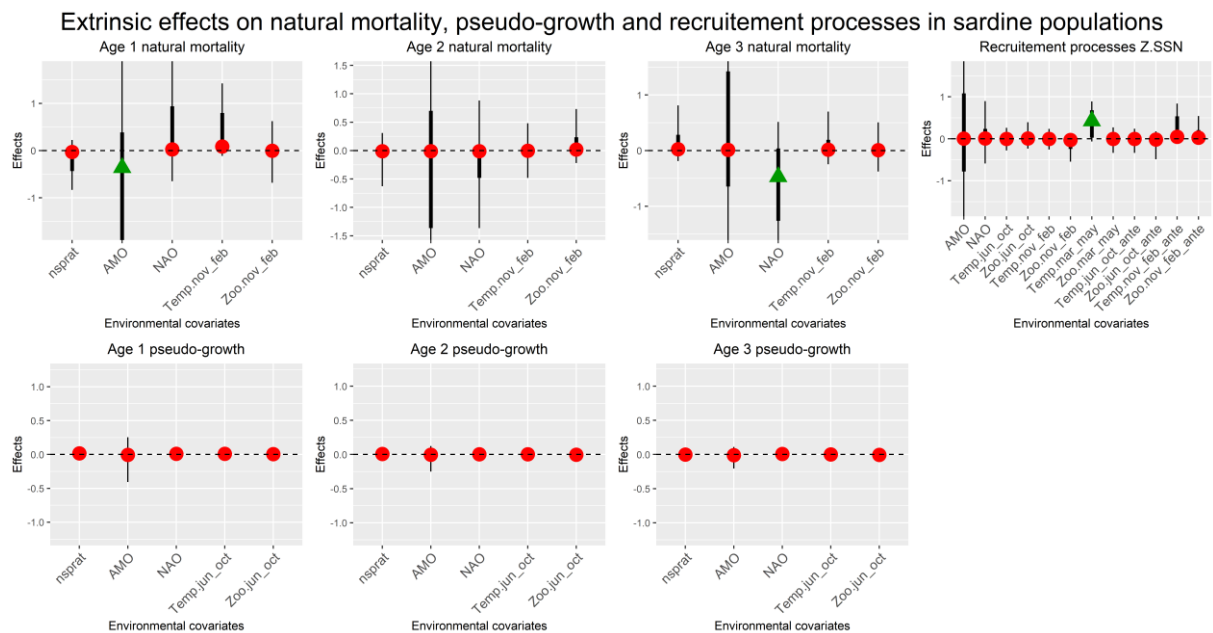


Figure 12 : Important extrinsic effects impacting natural mortality, growth and recruit processes in sardine populations.

Important covariates selected from the Stochastic Search Variable Selection (SSVS) method. Median of the significant effects (posterior frequency of inclusion $I_x > 50\%$): green triangle. Median of the non-significant effects (posterior frequency of inclusion $I_x < 50\%$): red points. Thick confident interval: 90% of mcmc draws ; thin confident interval: 99% of mcmc draws.

4. Discussion

In this study we developed an innovative approach to model the entire population dynamics of two small pelagic fish (sardine and anchovy), using a two-species Bayesian life cycle model. This new stage-based life cycle model provides a framework to unravel the interconnected mechanisms between three key demographic processes i.e, natural mortality, pseudo-growth and recruitment processes, underlying the population dynamics within the small pelagic system of the Bay of Biscay. Especially, by embedding a stochastic selection for variable search (SSVS) within a two species hierarchical life cycle model we have been able to identify intrinsic and extrinsic effects on those three interconnected processes. First, even if sardines and anchovies share the same habitat, our model did not reveal any dependence in the dynamic of those two species. Concerning intrinsic factors, for anchovy we demonstrated a strong intraspecific size-dependence natural mortality on age-2 and density dependence natural mortality on age-2 and on stock recruitment process whereas for sardines, density dependence natural mortality occurs on age-1 and age-3 natural mortality. Our study reveals some extrinsic factors have effects on anchovy and sardine dynamics. For anchovy, stock recruitment process is correlated with the abundance of zooplankton (in July-October) and large ecosystemic index (AMO and NAO) are correlated to age-3 natural mortality. For sardines, temperature (March-May) is correlated with stock recruitment processes, age-1 and age-3 are correlated with large ecosystemic indexes (AMO and NAO respectively).

Our results also highlight an increase in natural mortality in the recent years especially for the early ages for both sardines and anchovy. The findings support the hypothesis of a response of anchovy and sardines to large climate-induced changes in the Bay of Biscay involving density-dependent and bottom-up mechanisms. However, even if our results provide new information on the mechanisms that govern the dynamics of sardines and anchovies at population level, the explicit representation of these mechanisms remains very complex. For example, understanding and disentangling the mechanisms underlying density dependence is arduous with data defined at the population level, as highlighted by *Krebs, 1991* :“the density dependence paradigm is bankrupt because it is descriptive and a posterior” and because “no mechanisms are specified” (*Murray, 1994*). We argue that it is even more difficult because mechanisms at the individual level and populational level can interact and are difficult to disentangle. In view of the results we obtained, we propose in the following paragraph to provide and discuss hypothetical underlying mechanisms (at both the population and individual levels) regarding the estimated effect of intrinsic and extrinsic factors impacted the three key demographic processes we studied.

4.1. Abundance and size dynamics of all life stages resulting from natural mortality, growth and recruitment processes

Similarly to the study of *Doray et al., 2018a*, based on the same data, our model showed an increase abundance for early life-stages of anchovy (ages 1 and 2) and sardine (age 1). For these life-stages, natural mortality increases around 2016, while the fishing mortality is decreasing and low. This might be explained by a reduced catchability of early-life stages because of their smaller size (more than 2 cm less than at the beginning of 2000's), or by the fact that fishermen attempt to target older anchovies and sardines because of their larger size, meaning a better price on the market (*Boëns et al., 2021*). The decline in abundance for older life-stages of sardine population seems related to an increased natural mortality after 2015. The estimated pseudo-growth rates are quite stable over the time series, while mean length is decreasing for all life-stages of both species. If variations in the pseudo-growth rate are unable to explain variations in average length over time, it is probably because we are not representing real growth in the model. That is why we called it pseudo-growth, as it represents both the result of size-selective mortality within the age class and the result of the average individual growth of a given age class. This accounts for the insensitivity of the pseudo-growth to any

factor (intrinsic or extrinsic). It may be explained by a compensatory response to these two processes, individual and populational, on the age class average size. To be able to model real growth, resulting from individual growth, a life-stage a size-structured model should be developed instead of an age-structured model (Jacobsen et al., 2019).

One limit of our model, is that it does not allow us to distinguish all the processes included in the recruitment processes such as egg, larval and juvenile survival. So, we were not able to assess intrinsic and extrinsic effects affecting the dynamics of younger life-stages, which are known to be key stages of fish life cycle (Hjort, 1914; Houde, 1987). These dynamics are more difficult to model as they are characterized by huge abundance variations, large mortality rate due to their dependence to the habitat and environmental conditions, and growth can hardly be investigated *in vivo* during the May PELGAS survey, as it is highly dependent on spawning phenology (Bailey and Houde, 1989). Besides, representing the age class 0 would allow us to investigate two mechanisms documented for anchovy and sardine in literature: the effect of cannibalism on eggs and the effect of predation of adult sardines on anchovy eggs, or vice versa (Szeinfeld, 1991; Petitgas et al., 2010).

4.2. Effect of intrinsic and extrinsic factors

4.2.1. *Intrinsic factors*

The analysis of intrinsic factor reveals only one significant size-dependent effect, on age-1 natural mortality affecting first-year anchovies. This negative size-dependent effect might be interpreted as a higher vulnerability to predation and trophic stress, leading to higher natural mortality in small fish (Arendt, 1997; Metcalfe and Monaghan, 2003). Also, smaller fish might be more sensitive to starvation, as they have lower energy reserves than larger fish and use up those reserves more rapidly due to the allometry of metabolic rate (Hurst, 2007).

The investigation of intrinsic factors revealed intra-specific density-dependent effects on both species, but no inter-specific effect, minimizing the interaction between sardine and anchovy populations, suggesting they might use their environment differently. Anchovies are known to forage more offshore than sardines, on a larger diversity of preys (Chouvelon et al., 2014). A positive density-dependent effect on natural mortality suggests that a higher abundance of fish induced a higher mortality, as it is the case for age-2 anchovies, age-1 sardines and age-3 sardines. This effect could be the consequence of spatial aggregation of these life-stages, leading to a competition for local food resources and causing food limitation and potentially starvation, or the consequence of the formation of larger schools more accessible to predators (Furuichi et al., 2022 ; Ibaibarriaga et al., 2013). In sardine population, age-3 natural mortality is positively affected by the abundance of all life-stages, suggesting a spatial aggregation of all life-stage or the formation of mixed life-stages shoals (Ibaibarriaga et al., 2013). The negative density-dependent effect of age-1 anchovy on the natural mortality affecting age-2 anchovies is unexpected and more difficult to understand. One possible hypothesis lies in the fact that an increased fish density leads to the formation of larger shoals, with higher detection ability of predators (collective vigilance) and causing confusion among predators (Rieucou et al., 2015; Furuichi et al., 2022). As the first-year class represent the bigger abundance, they might have their importance in mixed age-1 and age-2 anchovy shoals.

The study of intrinsic factors revealed a Ricker-type stock-recruitment relationship to characterize recruitment, reflected in the negative density-dependent effect of the spawning stock on recruitment (Ricker, 1954). This kind of relationship suggests an auto-regulation of the fish group, often explained by cannibalism on eggs and larvae. This behavior have been reported in small pelagic fish as anchovies (Pájaro, 1998; Pájaro et al., 2007; Petitgas et al., 2010; Canales et al., 2020). Surprisingly, the investigation of intrinsic effects do not reveal this kind of relationship on sardine population, while cannibalism is also documented (Petitgas et al., 2010).

4.2.2. Extrinsic factors

For both species, environmental factors impact age-3 natural mortality and recruitment processes. First, the impact of environmental factors such as temperature, on recruitment processes, included egg and larvae survival, could be expected as this life-stages are generally characterized by high mortality rate and are more vulnerable than adults to environmental fluctuations (Pankhurst and Munday, 2011). In particular, eggs and larvae are usually very sensitive to temperatures. Warmer temperatures could have a positive impact on larval survival, since increased temperatures may lead to faster growth and thus reduce the time spent at the most critical period of life (Bailey and Houde, 1989; Pankhurst and Munday, 2011). This could explain the positive effect of temperatures during the spawning period in sardine population (March to May) on recruitment processes. Nevertheless, the negative effect of zooplankton at autumn on recruitment process in anchovy population is less obvious. Indeed, our results suggest that recruitment decreases, when abundance of zooplankton increases in autumn. This result is unexpected, as autumn is the season of juvenile growth, and more food available (zooplankton) should increase juvenile survival. This negative correlation between recruitment and zooplankton can be explained by two reasons. First, covariates are defined as an average of a large spatial area, i.e. the entire Bay of Biscay. So, a low overall quantity of food can conceal a high local abundance of food. Secondly, we are only studying the impact of food quantity on natural mortality, pseudo-growth and recruitment processes while food quality would be worth studying (Menu et al., 2023). Changes in plankton quality can result from changes in species diversity, leading to differences in fish lipid content, i.e. in energetic reserves, with consequences for the ability to cope with starvation (Brosset et al., 2015). Anchovies and sardines might not be impacted similarly by plankton quality, since anchovy shows more effective predation on larger preys (e.g. euphausiids and decapods) than sardine or sprat (Bachiller and Irigoien, 2015).

Regarding the global index, we showed the *Atlantic Multidecadal Oscillation* (AMO) has a negative effect on age-1 sardine natural mortality. The AMO is a low-frequency and basin-wide climate index reflecting Sea Surface Temperature (SST) variability over the last century (Enfield et al., 2001; Alheit et al., 2014). Our results suggest an unexpected negative effect of AMO on first-year anchovy natural mortality, suggesting that when global temperature trends in the Bay of Biscay increases, natural mortality decreases. However, the intensity of the effect of AMO on mortality is very low and it is then very difficult to provide any significant interpretation. For both species, there is a negative effect of *North Atlantic Oscillation* (NAO) on age-3 natural mortality. The interpretation of the sign of large indicators effects is very complex, in spite of that, existing effect of AMO and NAO might reflect plankton shifts triggered by sea surface temperatures or currents changes. Therefore, we might interpret these indicators as proxy of food quality, supporting the bottom-up regulation of sardine and anchovy abundance and size dynamics by food quality (Auber et al., 2015; Boëns et al., 2021; Menu et al., 2023).

Among all the extrinsic factors tested (temperature, zooplankton, sprat abundance or AMO and NAO global indicators), few of them appear to have an effect on natural mortality, pseudo-growth and recruitment processes. Our results suggest that for several life-stages, processes are quite environment-independent, especially for early life-stages (age-1 and age-2) of both species. This could be explained by 2 main reasons. First the absence of spatial dimension in our model might lead us to consider a uniformed repartition of small pelagic fish and of environmental parameters in the Bay of Biscay. Yet, spatial fish aggregation patterns are likely to differ seasonally and vary in specific and age groups composition. Indeed, in anchovy population, in spring, age 1 individuals are more likely to be found in shallow waters close to the coast, while older individuals seem to be found mainly on the shelf break (Ibaibarriaga et al., 2013). In a similar way, plankton distributions differ in biomass and in communities throughout the Bay of Biscay and over the seasons (Lampert et al., 2002). To enhance our approach, we could think about a spatially integrated population model taking into account the spatial distribution heterogeneity of small pelagic fish belonging to different life-stages, in the Bay of Biscay (Olmos et al., 2023).

Secondly, our model is an age-based life-cycle model. However, natural mortality, growth and recruitment are size-dependent processes. Using a size-based model, might help us to better represent the growth process and the interaction between growth and mortality than an age-based model, where it is not possible to disentangle mortality and growth within the pseudo growth processes. We argue that a size-based model will help to (i) better represent the specific variability associated to mortality, growth, and recruitment process, (ii) better represent the interconnection between those three processes and (iii) better estimate the specific effect of intrinsic and extrinsic factors on those parameters.

Finally, for purposes of parsimony and to avoid over-parametrization of the model, we choose not to estimate different coefficients according to the year. This does not take account the fact that all these ecological interactions and pressures (predation, cannibalism, trophic limitation...) might change over time, in the longer or shorter term, and so population dynamics (Jørgensen et al., 2007).

4.3. Perspectives

In further studies, we propose here some areas for improvement. First, migration phenomena, likely to occur in sardine population, are potential bias for the estimation of natural mortality. Considering a larger scale and using additional data, the inclusion of the Iberian and the Celtic Sea stocks of sardines to the model might provide an accurate estimation of the natural mortality. Additionally, a spatially integrated model might allow us to test local environmental effects. However, we may still be limited by the lack of knowledge about the seasonal aggregation pattern of small pelagic fishes. One hypothesis, which remains untested but which is often advanced, is a bottom-up regulation of sardine and anchovy abundance and size dynamics by food quality induced by shifts in plankton communities, leading to changes in energetic supplies. Then, the structuration of the model by sizes rather by ages would allow both to unravel the growth occurring at individual level and the size-selective mortality occurring at population level, and to accurate the estimation of recruitment. Another research avenue would be to better represent the processes between the stock and the recruitment. Based on *Takasuka et al., 2019, 2021*, we argue density-dependent processes should be disentangled between density-dependent effects on egg production and survival from egg to recruitment. This might help to demonstrate the existence of intraspecific and interspecific density dependence in egg production (as shown by *Takasuka et al., 2019* for sardine (*Sardinops melanostictus*) and anchovy (*Engraulis japonicus*). Furthermore, a finer temporal scale might allow us to take into account the seasonal variability of sardine recruitment, as sardine may have two periods of reproduction during the year. Combining state-space models and Individual Based Models (IBM) might better represent the processes occurring at different life-stages of the life cycle by accounting for fecundity, egg survival or larval drift survival for example (Rochette et al., 2013).

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Supplementary materials

S1: Supplementary material for “Building steps of the model tracking sardine and anchovy population dynamics, conjointly”

S2: Supplementary material for “Exploratory analysis of the demographic trends in sardine and anchovy populations and of the environmental factors in the Bay of Biscay”

S3: Supplementary material for “Sensitivity analyses on the priors of the Stochastic Search for Variable Selection (SSVS) method”

S4: Supplementary material for “the likelihood functions of the life-cycle model”

S5: Supplementary material for “model parameters”

S6: Supplementary material for “SSVS for intrinsic (demographic) factors”

S7: Supplementary material for “definition of extrinsic covariates”

S8: Supplementary material for “model checking”

S1: Supplementary material for “Building steps of the model tracking sardine and anchovy population dynamics, conjointly” (2023)

Alice Bordes

Final joint model
Technically and realistically improved model, representing identified (from the SSVS) intrinsic effects on the ecological processes as latent variables and integrated SSVS method, used on extrinsic covariables in the model

[SUPP.MAT.\(S7 ; S8\)](#)

Joint model to represent species interactions between sardine and anchovy populations

[SUPP.MAT.\(S4 ; S5\)](#)

Two independent models for anchovy and sardine populations

Life-cycle model looping abundance dynamics for both populations

Selection of the effects affecting the ecological processes of natural mortality, pseudo-growth and recruitment

- 1) Building sub-models to test the effects (one by one) on the outputs of natural mortality, pseudo-growth and recruitment from the life-cycle model
- 2) Developing a Stochastic Search for Variable Selection (SSVS) method / sensitivity analysis on SSVS priors [SUPP.MAT.\(S3\)](#)
- 3) Selection of the demographic (abundance and size) effects affecting ecological processes of natural mortality, growth and recruitment using the SSVS method included in the model [SUPP.MAT.\(S6\)](#)

Exploratory analyses: linear (GLM) and non-linear (GAM) models, multivariate analyses (PCA) performed on abundance and size
[SUPP.MAT.\(S2\)](#)

Andrieux's IPM model, based on Stige's work, tracking abundance and size dynamics in anchovy



S2: Supplementary material for “Exploratory analysis of the demographic trends in sardine and anchovy populations and of the environmental factors in the Bay of Biscay” (2023)

Alice Bordes

1. Methods

1.1. Data

See the related master thesis.

1.2. Abundance – size observed interactions between ages and species

In this work, we explore the demographic tendencies of abundance and size in sardine and anchovy populations of the Bay of Biscay since 2000. To do so, generalized linear models (GLM) and generalized additive models (GAM) were performed on the mean size and abundance for each age group, for both species, investigating the effect of year (student test at a threshold of 5%). GAM and GLM have been compared (graphically and based on the AIC criterion).

Then, we used principal component analyses (PCA) to explore size and abundances correlations between age groups and species.

2. Results

2.1. Size

Over the last 20 years, a decrease in mean size (total length) within all ages, for both sardine and anchovy of the Biscay Bay, is graphically noticed (**FIGURE 1**).

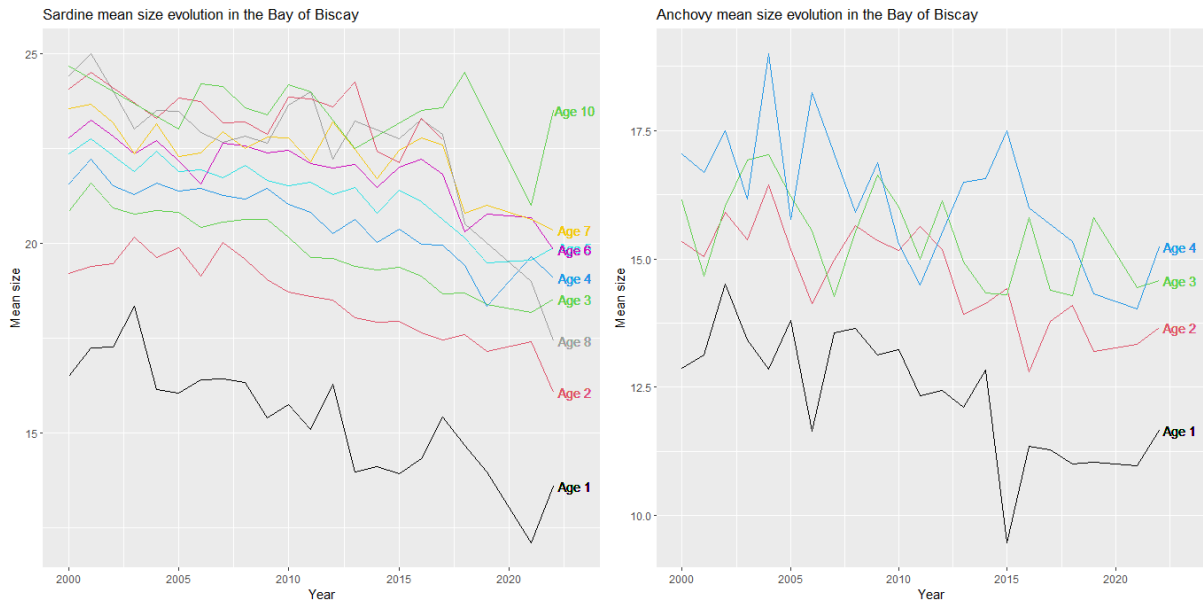


Figure 1 : Mean size evolution of sardines (right graph) and anchovies (left graph) for each age group in the Bay of Biscay

For both sardines and anchovies, the decrease of mean size is significant at 5%, for each age group, except for age 10 (which is a much smaller sample and so less reliable) (FIGURE 2, FIGURE 3).

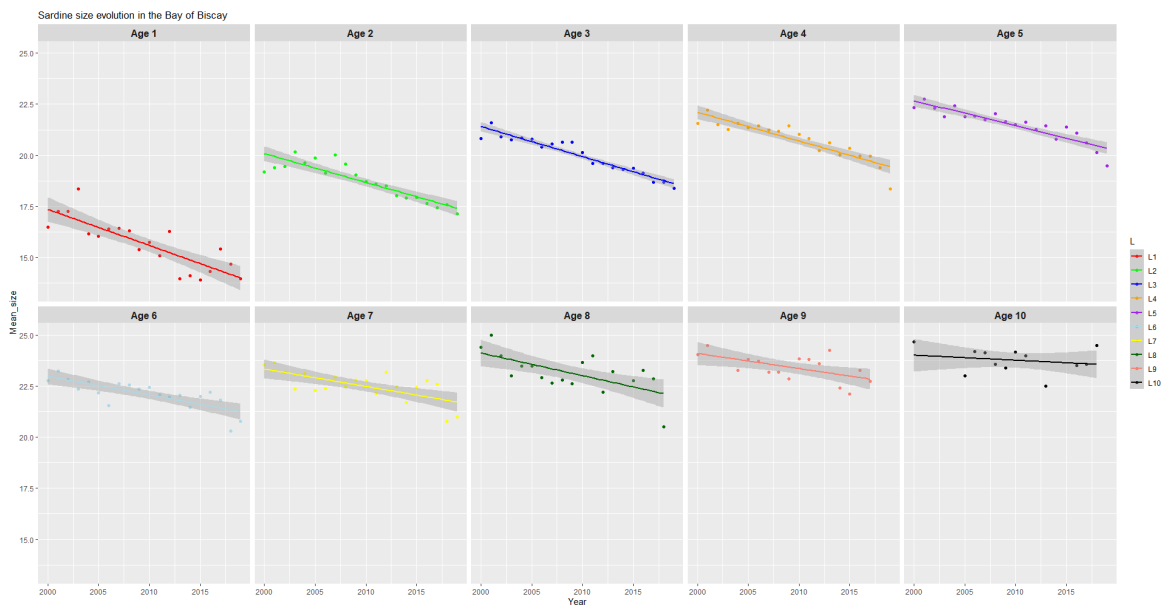


Figure 2 : Mean size evolution of sardines for each age group in the Bay of Biscay

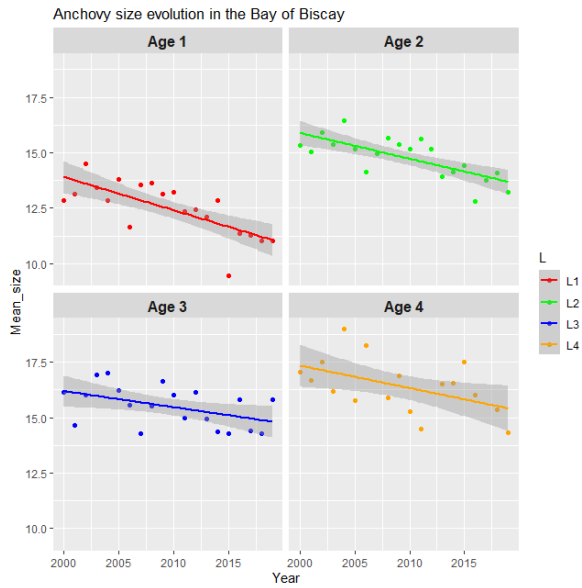


Figure 3 : Mean size evolution of anchovies at each age in the Bay of Biscay

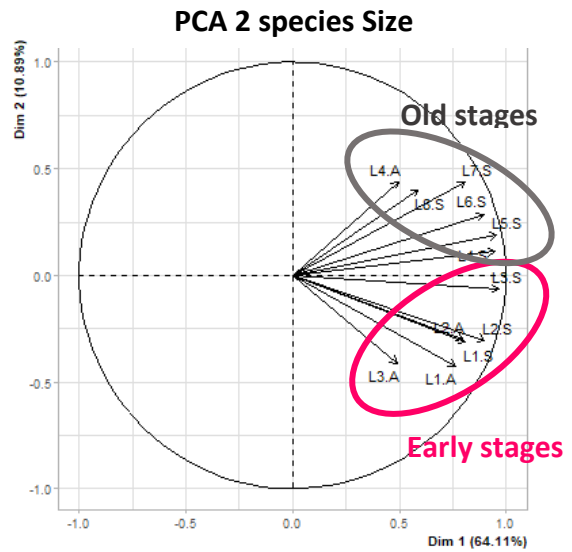


Figure 4 : Principal component analysis on size. Size correlations between age groups and between species (S=sardine, A=anchovy ; L=mean body length of the corresponding age group)

The PCA exploratory analysis of size correlations (all years confused) has shown strong correlations only between consecutive ages of a species (FIGURE 4).

The same PCA has been performed with Temperature and Zooplankton of the 4 seasons as supplementary variables. It does not show correlations with the active variables (S2 Annexes).

2.2. Abundance

There is a significant increase of abundance at 5 or 10% only for early stages : at age 1 for sardines and at age 1 (at 10%) and 2 for anchovies. Conversely, there is a significant decrease of abundance at 5 or 10% for old stages of sardines : at ages 6, 7 and 8+ (FIGURE 4, FIGURE 5).

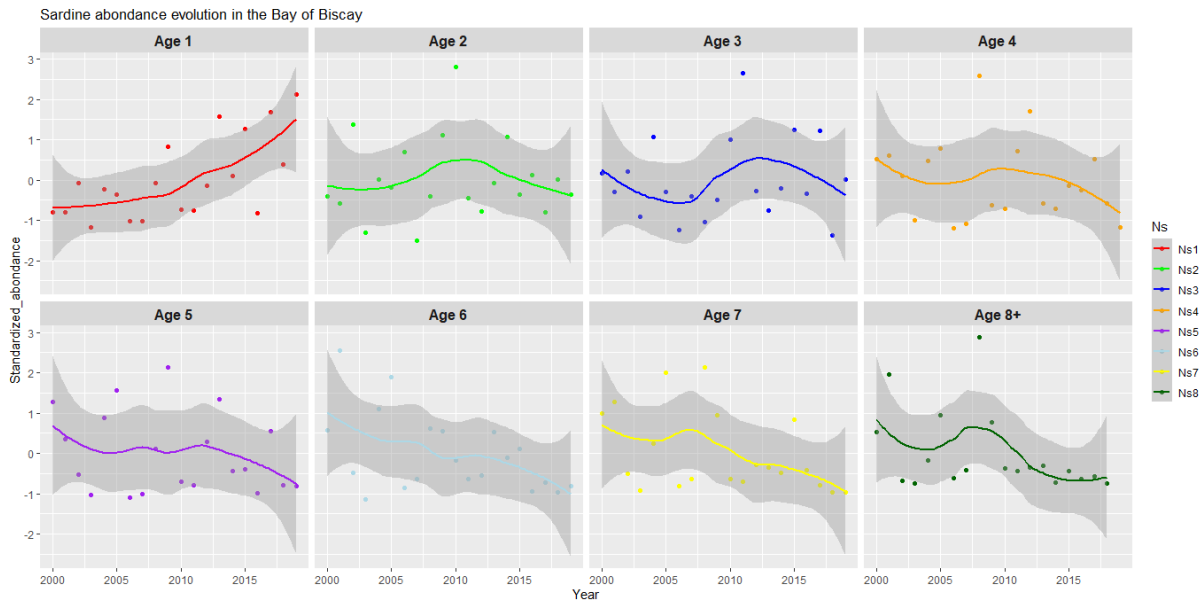


Figure 5 : Abundance evolution of sardines at each age in the Bay of Biscay

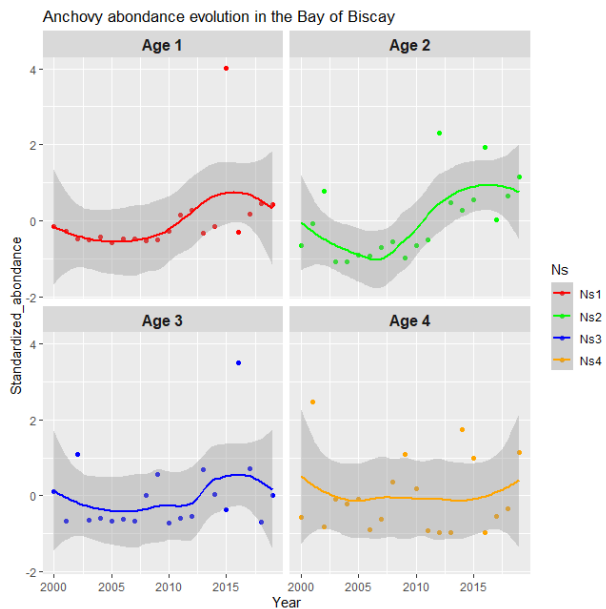


Figure 6 : Abundance evolution of sardines at each age in the Bay of Biscay

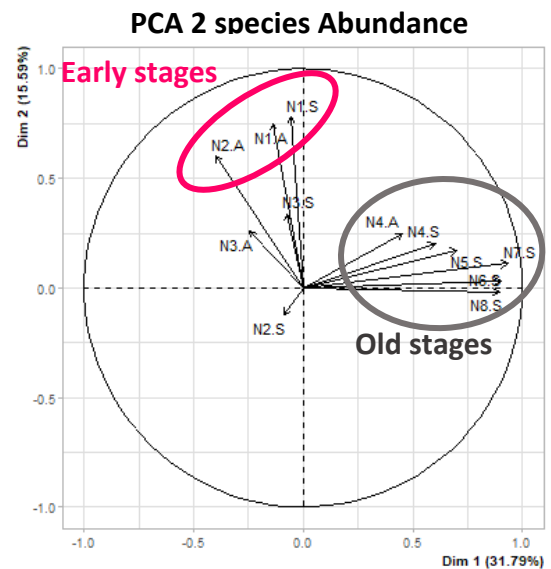


Figure 7 : Principal component analysis on abundance. Abundance correlations between ages and between species

The PCA of abundance correlations (all years confused) have shown strong correlations between the abundance of early stages of anchovies, ages 1 and 2, and with the abundance of sardines age 1. Oppositely, old stages seem correlated. Globally, consecutive ages are strongly correlated.

The same PCA has been performed with temperature and zooplankton of the 4 seasons as supplementary variables. It does not show correlations with the active variables (S2 Annexes).

2.3. Size – Abundance interactions

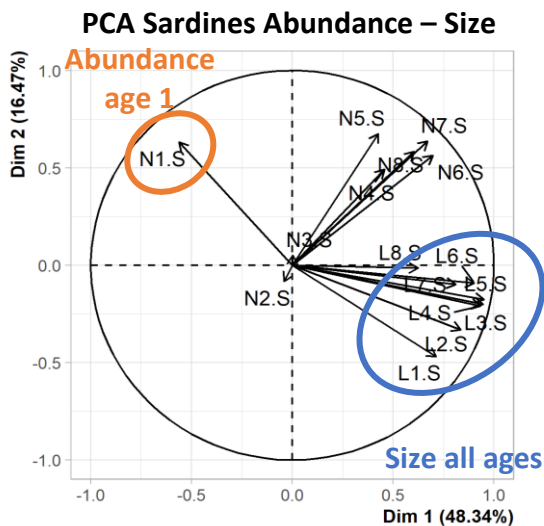


Figure 8 : Principal component analysis on abundance and size of sardines. Abundance correlations between ages

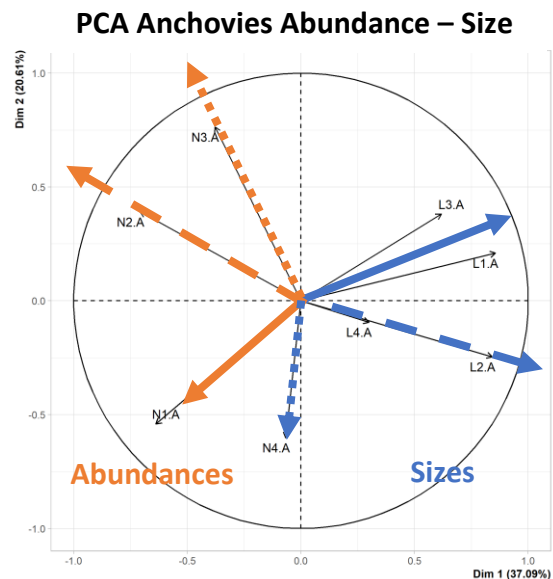


Figure 9 : Principal component analysis on abundance and size of anchovies. Abundance correlations between ages

The PCA of sardine abundance and mean size correlations turned out an anti-correlation between the abundance of the first-year class and the mean sizes of age groups 1 to 5.

The PCA of anchovy abundance and size correlations turned out an anti-correlation between abundance and size for early stages (age 1 and 2). Also, there is an anti-correlation between abundance of the age group 1 and size of the age group 3, as well as between abundances of age groups 3 and age 4.

The same PCA was performed with temperature and zooplankton of the 4 seasons as supplementary variables. It does not show correlations with the active variables (S2 Annexes).

3. Interpretation

Overall, early stages (1 and 2) and old stages appear to be segregated according to the size and the abundance, indicating these life-stages are differently impacted by ecological pressures.

3.1. Size

There is a decline of mean size at all life stages in the Bay of Biscay, since the 2000's. This could be due to a decrease in food quantity or food quality impacting individual growth. This also could be refer to selective size-mortality explained by predation or to a size-dependent vulnerability to environmental stress.

3.2. Abundance

Strong correlations between consecutive years may reflect a "cohort effect" (the fish of age a at time t , are the same fish as those of age $a+1$, at time $t+1$) expected insofar as the analyses were carried out over all years combined.

3.3. Size – Abundance interactions

The opposition between size and abundance in early stages could reflect a compensatory effect of the density on growth due to trophic competition. Indeed, a high abundance can induce a reduced prey availability per fish and lead to a limitation in growth. Conversely, larger fishes at early stages might increase the pressure on food and induce death by limited local food availability, so resulting in a decrease of abundance in early stages. This death could happen consecutively to starvation or caused by medium-term trophic competition. It seems less probable that the opposition between size and abundance in early stages reflects an effect of predation or cannibalisme, as age-2 fish can not be large enough to eat first-year fish.

All these hypotheses will be investigated in the related master's thesis and discussed in the light of the scientific literature.

S2 Annexes

Sardine_size	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
	-	-	-	-	-	-	-	-	-	-
glm_coef	0,1767 8667	0,1406 2967	0,1472 2121	0,1405 9688	0,1220 6105	0,0908 6685	0,0849 4529	0,1105 8467	0,0736 9471	0,0248 6221
glm_significativity_t_test	4,6302 E-06	9,807E -08	3,0685 E-11	3,518E -08	3,3892 E-08	7,5725 E-05	0,0008 8371	0,0035 6261	0,0185 8804	0,5098 7534
gam_coef										
gam_significativity_t_test	0	0	0	2,3555 E-06	0	0,0004 6726	0,0033 1973	0,0107 2282	0,0185 8973	0,0382 1987

Anchovy_size	L1	L2	L3	L4
	-	-	-	-
glm_coef	0,14922229	0,11605637	0,07251837	-0,1014811
glm_significativity_t_test	0,00027983	0,00023685	0,03800565	0,04130983
gam_coef				
gam_significativity_t_test	0,0005574	0,0005574	0,03800385	0,17334073

Sardine_size	AIC	deltaAIC	best
M1glm.s	46,8290047	37,8059814	M1gam.s
M1gam.s	9,02302322		
M2glm.s	26,4635403	17,440517	M2gam.s
M2gam.s	9,02302322		
M3glm.s	7,77239115	4,59496869	
M3gam.s	3,17742246		
M4glm.s	23,6806055	12,6122332	M4gam.s
M4gam.s	11,0683723		
M5glm.s	17,9259491	10,3682569	M5gam.s
M5gam.s	7,55769215		
M6glm.s	29,5863054	2,26154106	
M6gam.s	27,3247643		
M7glm.s	36,7937037	2,83320039	
M7gam.s	33,9605033		
M8glm.s	44,8676429	3,83121025	
M8gam.s	41,0364327		
M9glm.s	30,4715461	1,917E-10	
M9gam.s	30,4715461		
M10glm.s	27,3296901	39,7890752	M10gam.s
M10gam.s	- 12,4593851		

S2 Annexes

Anchovy_size	df	AIC	deltaAIC	best
M1glm.a	3	54,4313053	12,6771398	M1gam.a
M1gam.a	3,86001504	41,7541655		
M2glm.a	3	43,7089741	1,95480861	
M2gam.a	3,86001504	41,7541655		
M3glm.a	3	53,4436503	1,4296E-11	
M3gam.a	3	53,4436503		
M4glm.a	3	55,5800913		
M4gam.a	5,84107719	55,371347	0,20874436	

Sardine_abundance	N1	N2	N3	N4	N5	N6	N7	N8+
glm_coef	326451 933	3096248 ,57	8832468 ,51	1210631 4,2	9108874 ,23	1047080 7,4	5441578 ,72	7126308 ,84
glm_significativity	0,00188 259	0,94656 503	0,70305 963	0,41062 458	0,28640 337	0,02747 554	0,06674 206	0,09694 897
gam_coef								
gam_significativity	0,94656 653	0,94656 653	0,70305 935	0,41062 35	0,28640 241	0,02747 386	0,06674 063	0,09694 844

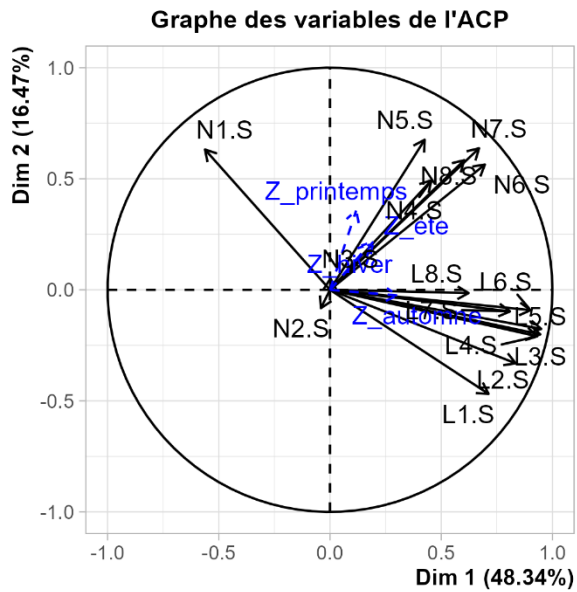
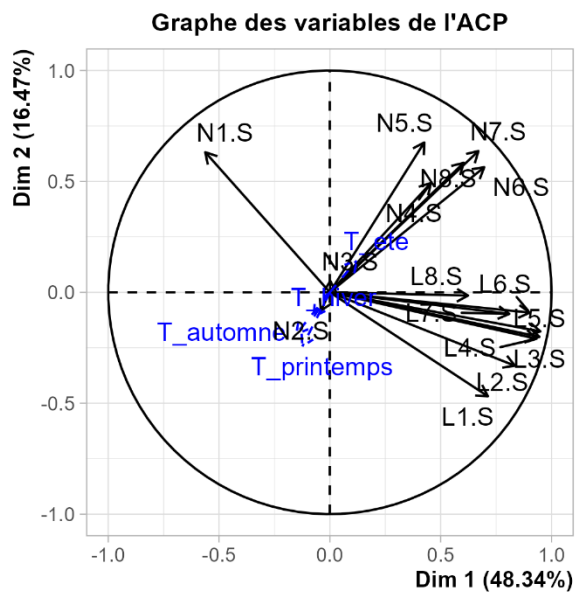
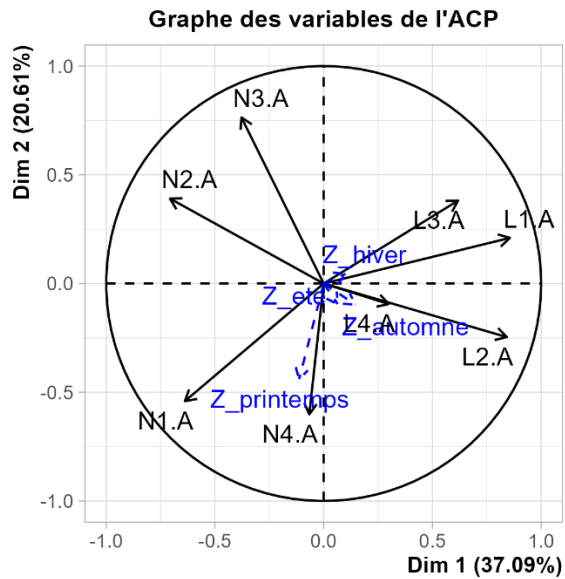
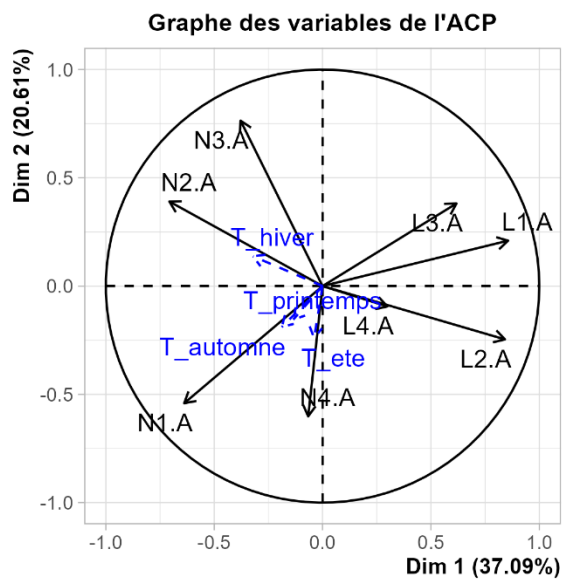
Anchovy_abundance	N1	N2	N3	N4
glm_coef	951886714	104782655	10428549,1	3394,11475
glm_significativity	0,06045986	0,00830703	0,24775293	0,99430576
gam_coef				
gam_significativity	0,02117209	0,02117209	0,24775175	0,99430707

Sardine_abundance	df	AIC	deltaAIC	best
M1glm.N.s	3	923,144022	27,1176902	M1gam.N.s
M1gam.N.s	3	896,026332		
M2glm.N.s	3	896,026332	1,4302E-10	
M2gam.N.s	3	896,026332		
M3glm.N.s	3	868,343865	3,8995E-11	
M3gam.N.s	3	868,343865		
M4glm.N.s	3	849,876156	7,9922E-11	
M4gam.N.s	3	849,876156		
M5glm.N.s	3	827,873525	1,6098E-10	
M5gam.N.s	3	827,873525		
M6glm.N.s	3	802,205779	2,45E-10	
M6gam.N.s	3	802,205779		
M7glm.N.s	3	784,28624	6,0254E-12	
M7gam.N.s	3	784,28624		
M8glm.N.s	3	756,574496	2,6398E-10	
M8gam.N.s	3	756,574496		

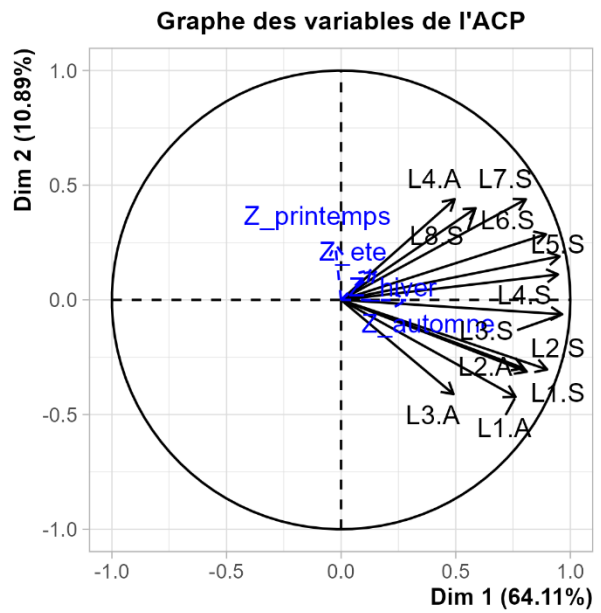
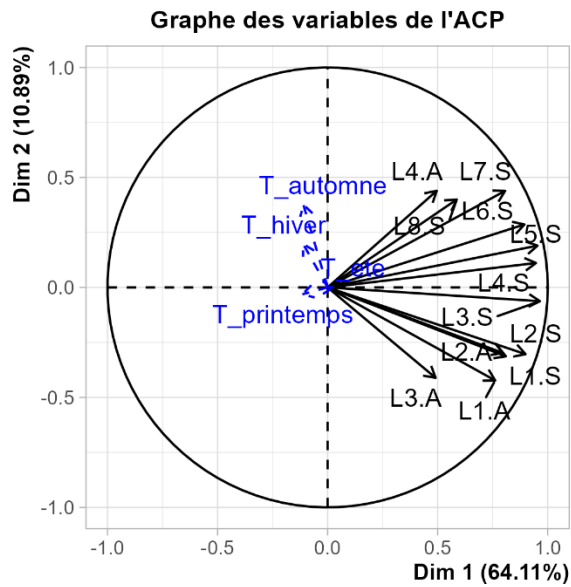
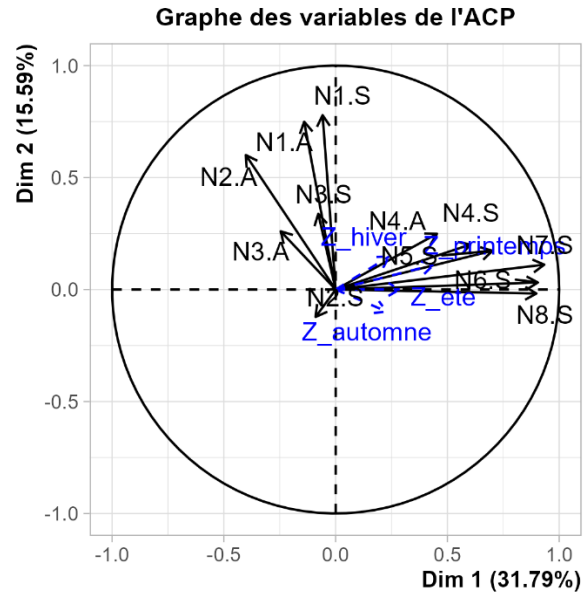
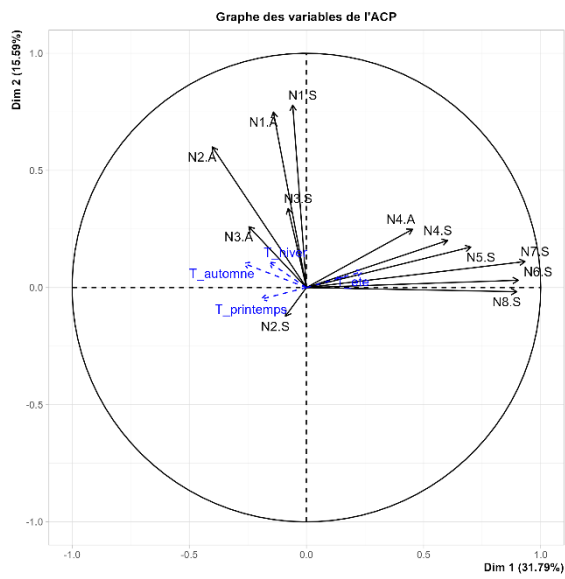
S2 Annexes

Anchovy_abundance	df	AIC	deltaAIC	best
M1glm.N.a	3	989,816491	105,802858	M1gam.N.a
M1gam.N.a	4,65047783	884,013633		
M2glm.N.a	3	885,877875	1,86424192	
M2gam.N.a	4,65047783	884,013633		
M3glm.N.a	3	829,936386	1,03E-10	
M3gam.N.a	3	829,936386		
M4glm.N.a	3	712,98276	1,47E-10	
M4gam.N.a	3	712,98276		

S2 Annexes



S2 Annexes



S3: Supplementary material for “Sensitivity analyses on the priors of the Stochastic Search for Variable Selection (SSVS) method” (2023)

Alice Bordes

Table 1 : Sensitivity analysis on σ parameter of the SSVS prior, at $c = 1000$

Anchovy	$\sigma_I = 10, 5 \text{ or } 1$	$\sigma_I = 0.1$	$\sigma_I = 0.05$	$\sigma_I = 0.01$	$\sigma_I = 0.005$
M1	• 0 SC	• 1 SC	• 1 SC	• 5 SC	• 7 SC
M2	• 0 SC	• 1 SC	• 2 SC	• 3 SC	• 8 SC
M3	• 0 SC	• 1 SC	• 2 SC	• 3 SC	• 3 SC

*SC : significative/important covariate as define in the master's thesis

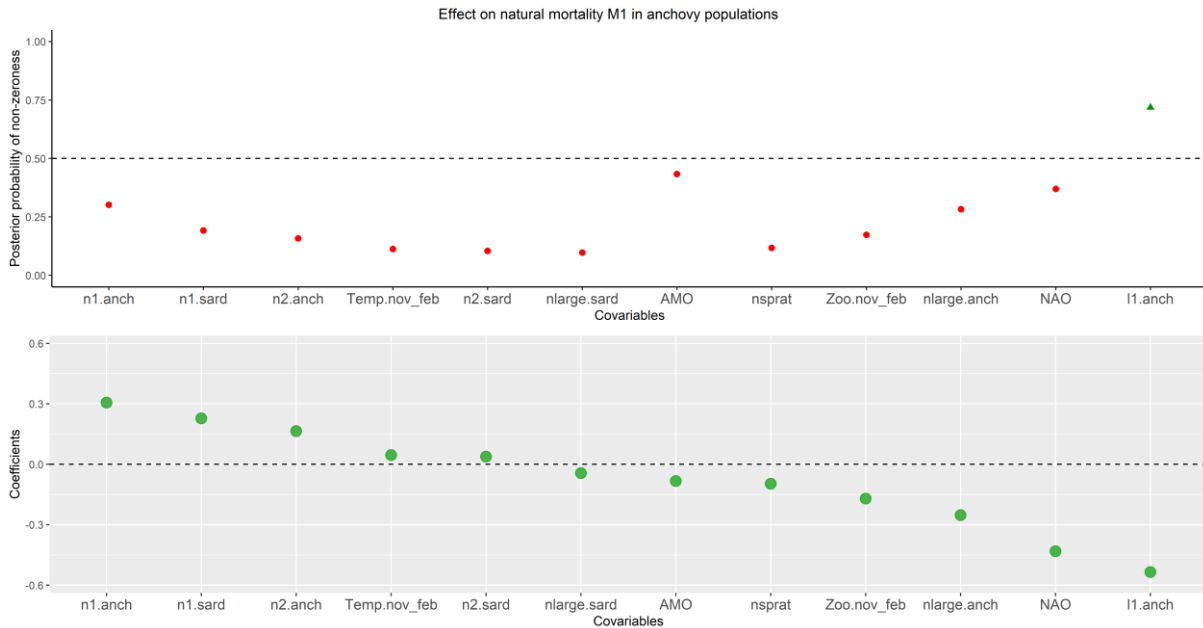
Table 2 : Sensitivity analysis on c parameter of the SSVS prior, at $\sigma = 0.05$

Anchovy	$c = 1000$	$c = 500$	$c = 100$
M1	• 1 SC	• 1 SC	• 3 SC
M2	• 2 SC	• 2 SC	• 3 SC
M3	• 2 SC	• 2 SC	• 5 SC

The sensitivity analysis conducted on the two parameters of the spike (σ_I) and slab (σ_I and c) priors reveals that the optimum parameter values for the variable selection are $\sigma_I = 0.05$ and $c = 1000$. These parameters are close to the ones used in *Bret et al., 2017* ($\sigma_I = 0.05$ and $c = 500$). For $\sigma_I = 0.05$ and $c = 1000$, the spike prior is centered on 0 and 90% of draws are include between -0.08 and 0.08, whereas the slab prior is centered on 0 and 90% of draws are include between -2.72 and 2.34 (ANNEX 4). We chose the optimum parameter values based on the number of significative covariates relative relation to the total number of covariates tested. We aim to set parameter in order to have a parsimonious number of covariates and contrasting posterior frequency of inclusion (I_{X_k}) between “turn on” ($I_{X_k} > 50\%$, , significative) and “turn off” ($I_{X_k} < 50\%$, , non-significative) covariates (TABLE 1, TABLE 2). The sensitivity analysis was performed for the natural mortality and the growth of anchovy population and some results relating to age 1 natural mortality are presented in (ANNEX 1, ANNEX 2, ANNEX 3).

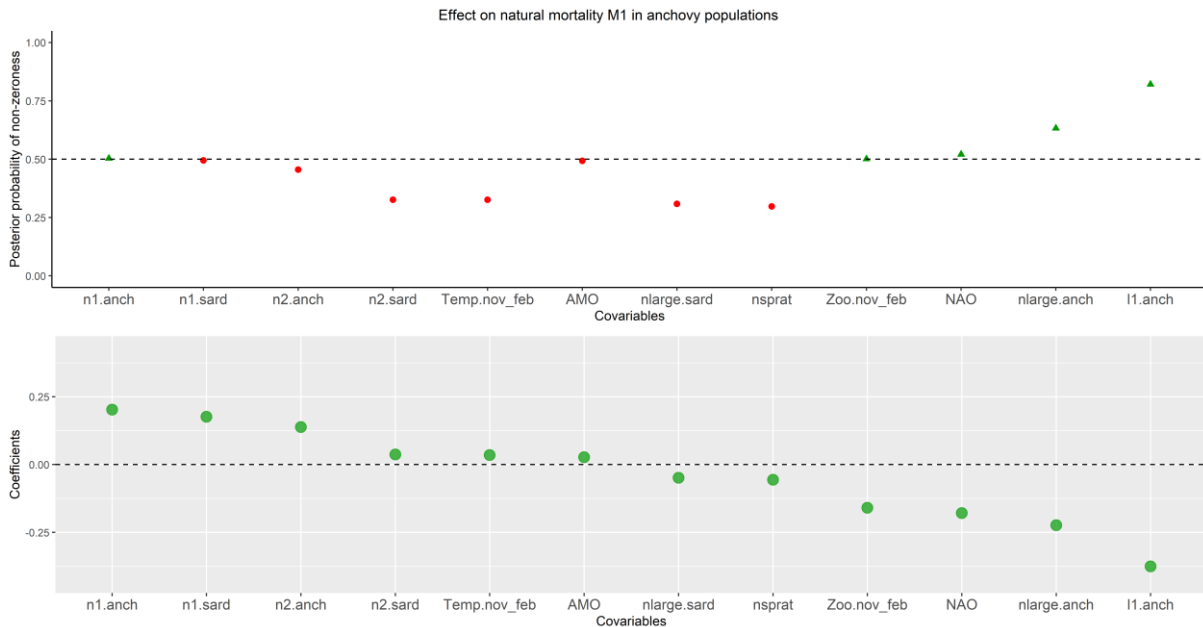
S3 Annexes

Annex 1 : SSVS conducted on age 1 natural mortality with prior parameters $\sigma = 0.05$ and $c = 1000$



On the top graph. Covariates “turn on” ($I_{X_k} > 0.5$; green triangle) and “turn off” ($I_{X_k} < 0.5$; red point). On the bottom graph. Value of the median of the coefficient posterior distributions (green points).

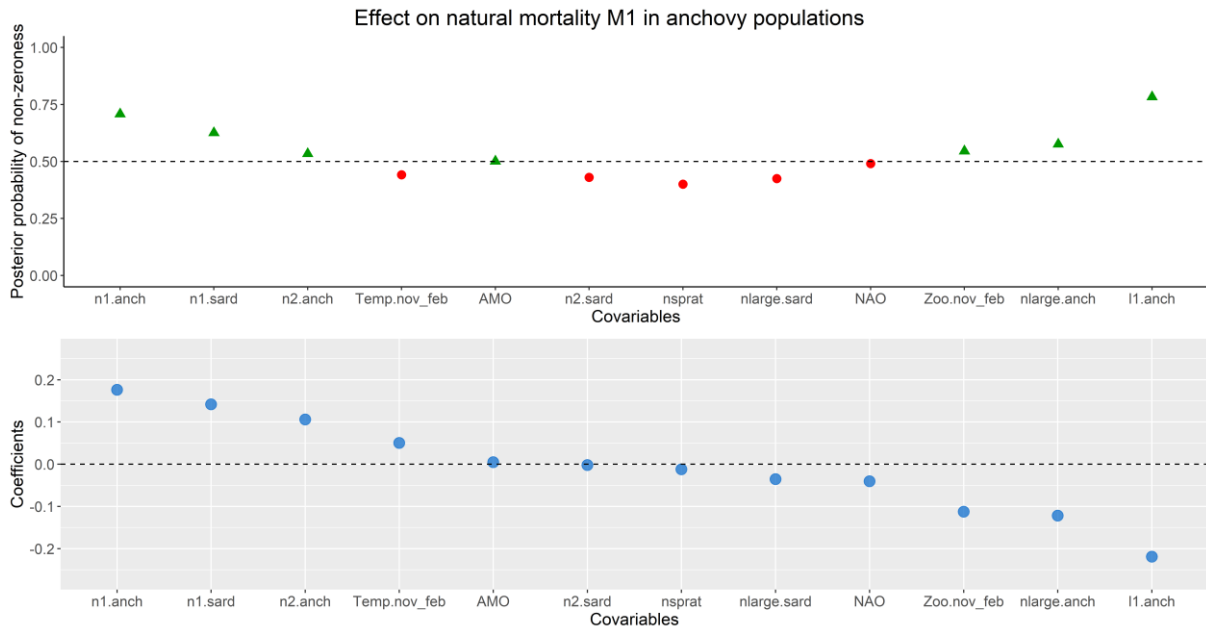
Annex 2 : SSVS conducted on age 1 natural mortality with prior parameters $\sigma = 0.01$ and $c = 1000$



On the top graph. Covariates “turn on” ($I_{X_k} > 0.5$; green triangle) and “turn off” ($I_{X_k} < 0.5$; red point). On the bottom graph. Value of the median of the coefficient posterior distributions (green points).

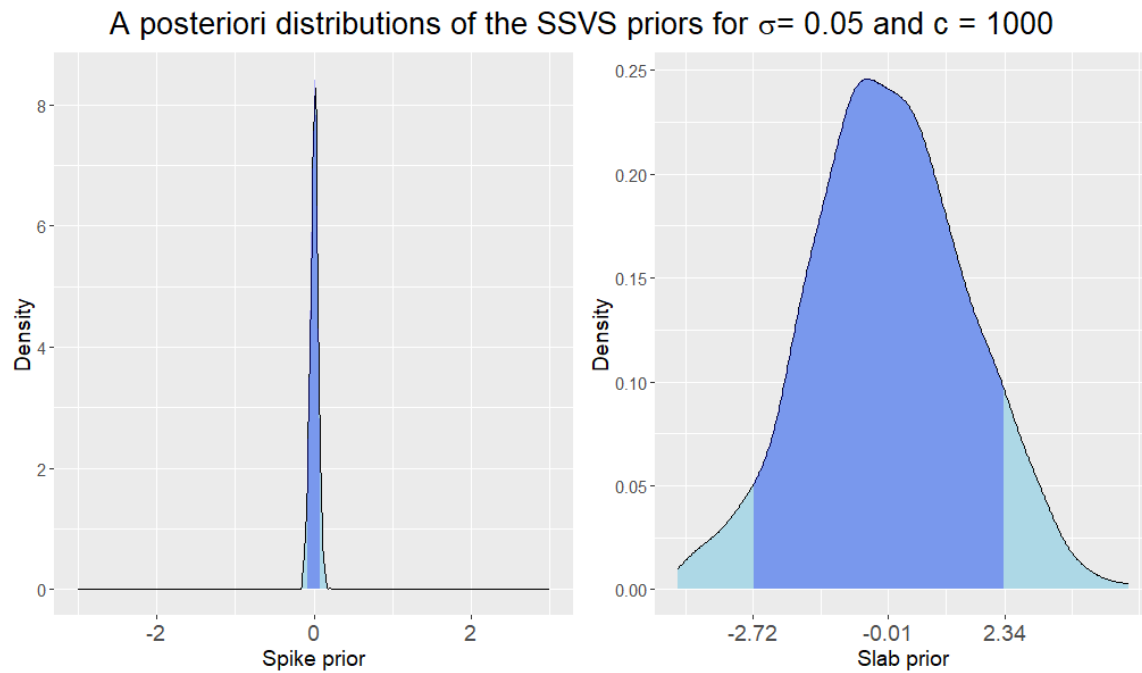
S3 Annexes

Annex 3 : SSVS conducted on age 1 natural mortality with prior parameters $\sigma = 0.005$ and $c = 1000$



On the top graph. Covariates “turn on” (I_{X_k} posterior frequency > 0.5 ; green triangle) and “turn off” (I_{X_k} posterior frequency < 0.5 ; red point). On the bottom graph. Value of the median of the coefficient posterior distributions (blue points).

Annex 4 : Set SSVS priors



The interval in dark blue represents 90% of the draws.

S4: Supplementary material for “the likelihood functions of the life-cycle model” (2023)

Alice Bordes

The likelihood term for catches is modelled as:

$$C. obs_{e,s,t} \sim \log N\left(\log(C_{e,s,t}) - \frac{\sigma_{C.obs_{e,s}}^2}{2}, \frac{1}{\sigma_{C.obs_{e,s}}^2}\right) \quad (1)$$

Where $C_{e,s,t}$ is the total catches from the state process, linking natural mortality and fishing mortality for all life-stages $s \neq SS$ and year t , through Baranov's equation ; with $C. obs_{e,s,t}$ observed commercial catches and $\sigma_{C.obs_{e,s}}^2$ observed standard error. Laurent's correction ($-\frac{\sigma_{C.obs_{e,s}}^2}{2}$) was applied to the models to obtain unbiased estimations from log-transformed data (Laurent, 1963).

The likelihood term for abundances is modelled as:

$$N. obs_{e,s,t} \sim \log N\left(\log(N_{e,s,t}) - \frac{\sigma_{N.obs_{e,s}}^2}{2}, \frac{1}{\sigma_{N.obs_{e,s}}^2}\right) \quad (2)$$

Where $N_{e,s,t}$ is the abundance of the species e , for all life-stages $s \neq SS$ and year t , from the state process ; with $N. obs_{e,s,t}$ observed abundances and $\sigma_{N.obs_{e,s}}^2$ observed standard error from PELGAS survey.

The likelihood term for sizes is modelled as:

$$L. obs_{e,s,t} \sim \log N\left(\log(L_{e,s,t}) - \frac{\sigma_{L.obs_{e,s}}^2}{2}, \frac{1}{\sigma_{L.obs_{e,s}}^2}\right) \quad (3)$$

Where $L_{e,s,t}$ is the mean length of the species e , for all life-stages $s \neq SS$ and year t , from the state process ; with $L. obs_{e,s,t}$ observed sizes and $\sigma_{L.obs_{e,s}}^2$ observed standard error from the PELGAS surveys.

S5: Supplementary material for “model parameters” (2023)

Alice Bordes

Table 1: Variables, definition, prior distributions, hyperparameters and related equations of all parameters used in the model.

	Variables	Definition	Prior distribution	Hyperparameters	Related equation
Initial years	$N_{e=1,s=1:4,t=1}$ $N_{e=2,s=1:6,t=1}$	Abundance for anchovy (e=1) and sardine (e=2) at life-stage s to initialize the dynamics (t=1)	$Unif\left(\text{mean}\left(\frac{N.obs_{e,s,t=1:5}}{2}\right) * Q_e ; \text{mean}(N.obs_{e,s,t=1:5}) * 2 * Q_e\right)$	$Q_{e=1} = 0.39$ $Q_{e=2} = 0.43$	Eq.1 Eq.5
	$L_{e=1,s=1,t=23}$ $L_{e=1,s=2:4,t=1}$ $L_{e=2,s=2:6,t=1}$	Mean length for anchovy (e=1) and sardine (e=2) at life-stage s to initialize the dynamics (t=23 or t=1)	$LogNormal\sim\left(\log\left(\frac{L.obs_{e,s=1,t=19:23}}{2}\right), \frac{1}{\sigma_{Le,s}^2}\right)$ $LogNormal\sim\left(\log\left(\frac{L.obs_{e,s=2:4,t=1:5}}{2}\right), \frac{1}{\sigma_{Le,s}^2}\right)$ $LogNormal\sim\left(\log\left(\frac{L.obs_{e,s=2:6,t=1:5}}{2}\right), \frac{1}{\sigma_{Le,s}^2}\right)$	$\sigma_{Le,s} = 1$	Eq.6
	$C_{e,s \neq SS,t}$	Commercial catches of the life-stage s at year t for the species e			Eq.5
Population dynamics model	$F_{e,s \neq SS,t}$	Fishing mortality of the life-stage s at year t for the species e	$logNormal\left(\log \mu_{Fe,s}, \frac{1}{\sigma_{Fe,s}^2}\right)$	$\log \mu_{Fe,s} \sim Normal(\log(\mu_{Fe,s}), 0.1)$ $\sigma_{Fe,s} \sim Uniform(0,10)$ $\mu_{Fe=1,s=1} = 0.2660$ $\mu_{Fe=1,s=2} = 0.6507$ $\mu_{Fe=1,s=3} = 0.5469$ $\mu_{Fe=2,s=1} = 0.112$ $\mu_{Fe=2,s=2:5} = 0.155$	Eq.2 Eq.5
				Source: Uriarte et al., 2016 and ICES WGMHSA Report 2021	

Processes	$M_{e,s \neq SS,t}$	Natural mortality of the life-stage s at year t for the species e	$\logNormal(E_log_mu_{Me,s}, \frac{1}{\sigma_{Me,s}^2})$	$\log_mu_{Me,s} \sim Normal(\log(\mu_{Me,s}), 0.1)$ Eq.7 $\sigma_{Me,s} \sim Uniform(0,5)$ $\mu_{Me=1,1} = 0.733$ $\mu_{Me=1,s=2:3} = 1.326$ $\mu_{Me=2,s=1} = 0.61$ $\mu_{Me=2,s=2} = 0.47$ $\mu_{Me=2,s=3} = 0.40$ $\mu_{Me=2,s=4} = 0.36$ $\mu_{Me=2,s=5} = 0.35$
	$g_{e,s \neq SS,t}$	Pseudo-growth of the life-stage s at year t for the species e	$\logNormal(E_log_mu_{ge,s}, \frac{1}{\sigma_{ge,s}^2})$	$\mu_{g_{e,s}} = \text{mean}\left(\frac{L.\text{obs}_{e,s+1,t=1:23}}{L.\text{obs}_{e,s,t=1:23}}\right)$ Eq.8 $\sigma_{g_{e,s}} \sim Uniform(0,10)$
	$Z_{e,SS,t}$	Stock-recruitment parameter linking the spawning stock (SS) stage to the first-year group at year t for the species e	$\logNormal(\log_mu_{Ze,SS}, \frac{1}{\sigma_{Ze,SS}^2})$	$\mu_{Ze=1,SS} = 1.223$ Eq.3 $\mu_{Ze=2,SS} = 0.796$ Eq.9 $\sigma_{Ze,SS} \sim Uniform(0,5)$
Intrinsic factors on natural mortality	$\alpha_{e,s \neq SS}$	Intra or inter-specific density-dependent coefficient on natural mortality	$\alpha_{e,s} \sim Uniform(-5,5)$	Eq.7
	$\beta_{e,s \neq SS}$	Intra-specific size-dependent coefficient on natural mortality	$\beta_{e,s} \sim Uniform(-5,5)$	Eq.7
Intrinsic factors on pseudo-growth	$\gamma_{e,s \neq SS}$	Intra or inter-specific density-dependent coefficient on pseudo-growth	$\gamma_{e,s} \sim Uniform(-5,5)$	Eq.8

Source: Uriarte et al., 2016 and ICES WGMHSA Report 2021

	$\varepsilon_{e,s} \neq SS$	Intra-specific size-dependent coefficient on pseudo-growth	$\varepsilon_{e,s} \sim Uniform(-5,5)$		Eq.8
Intrinsic factors on recruitment	$\theta_{e,SS}$	Intra or inter-specific density-dependent coefficient on recruitment	$\theta_{e,SS} \sim Uniform(-5,5)$		Eq.9
	$\rho_{e,SS}$	Intra-specific size-dependent coefficient on recruitment	$\rho_{e,SS} \sim Uniform(-5,5)$		Eq.9
SSVS	I_{X_k}	Inclusion indicator variable for covariate X_k affecting life-stages (1 for presence of 0 for absence)	$Bernoulli \sim (0.5)$		Eq.10
	$\delta 0_{X_k}$	slope coefficient associated to X_k covariate when ($I_{X_k}=0$)	$Normal(0, \frac{1}{\sigma_{I_{X_k}}^2})$ (spike prior)	$\sigma_{I_{X_k}} = 0.05$	Eq.11
	$\delta 1_{X_k}$	slope coefficient associated to X_k covariate when ($I_{X_k}=1$)	$Normal(0, \frac{1}{(\sigma_{I_{X_k}} \times c)^2})$ (slab prior)	$\sigma_{I_{X_k}} = 0.05$ $c = 1000$	Eq.11

Note: Q_e is the acoustic correction for the bias introduced in the conversion of acoustic density data (from the PELGAS survey) into fish abundance.

S6: Supplementary material for “SSVS for intrinsic (demographic) factors” (2023)
 Alice Bordes

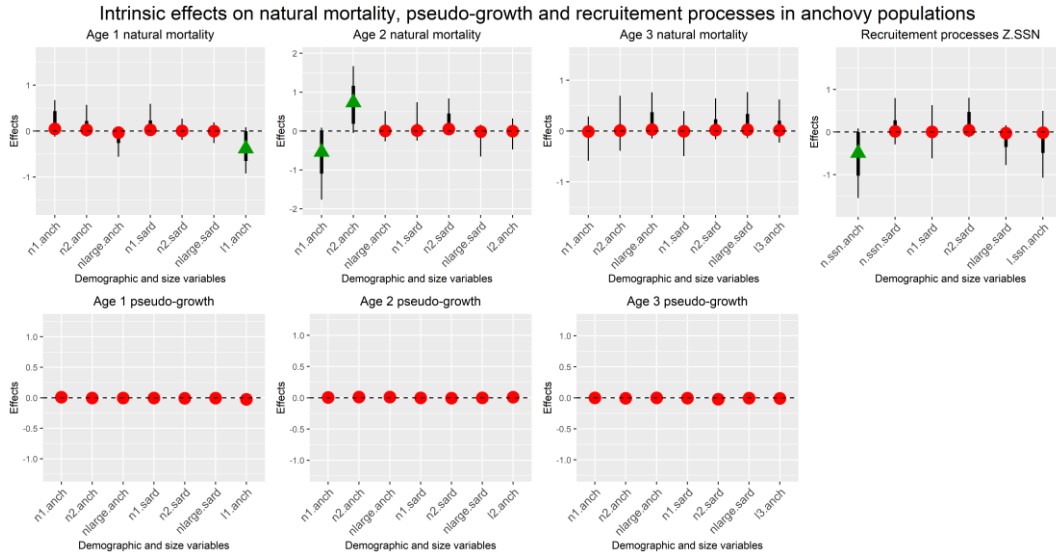


Figure 1 : Important intrinsic effects impacting natural mortality, growth and recruit processes in anchovy populations.

Important covariates selected from the Stochastic Search Variable Selection (SSVS) method. Median of the significant effects (posterior frequency of inclusion $I_X > 50\%$): green triangle. Median of the non-significant effects (posterior frequency of inclusion $I_X < 50\%$): red points. Thick confident interval: 90% of mcmc draws ; thin confident interval: 99% of mcmc draws.

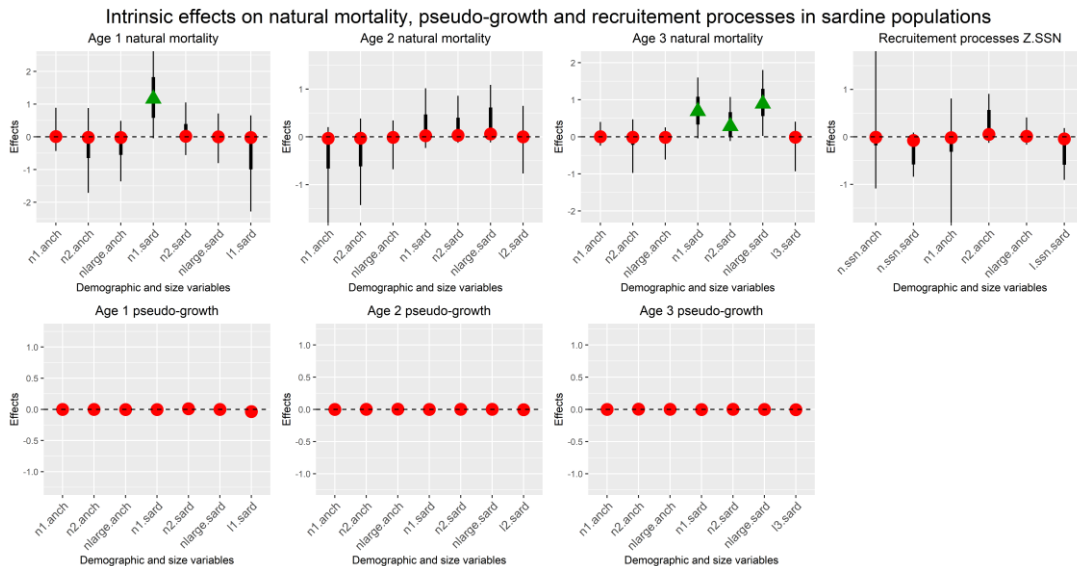


Figure 2 : Important intrinsic effects impacting natural mortality, growth and recruit processes in sardine populations.

Important covariates selected from the Stochastic Search Variable Selection (SSVS) method. Median of the significant effects (posterior frequency of inclusion $I_X > 50\%$): green triangle. Median of the non-significant effects (posterior frequency of inclusion $I_X < 50\%$): red points. Thick confident interval: 90% of mcmc draws ; thin confident interval: 99% of mcmc draws.

S7: Supplementary material for “definition of extrinsic covariates” (2023)

Alice Bordes

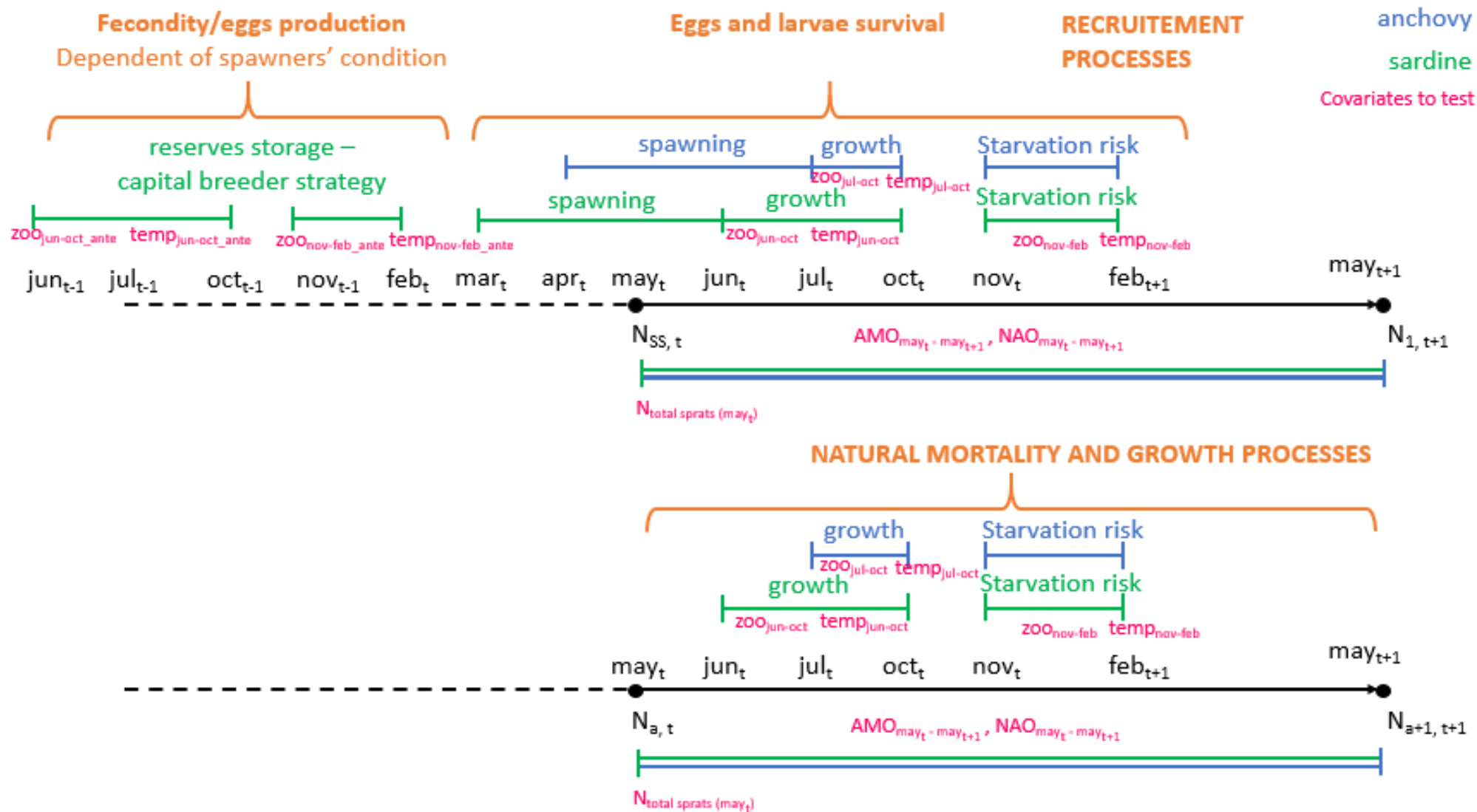


Figure 1 : Schematic timeline containing the extrinsic effects tested on natural mortality, pseudo-growth and recruitment of sardines and anchovies, all life-stages. Months are indexed by the year t .

S8: Supplementary material for “model checking” (2023)

Alice Bordes

1. Convergence checking

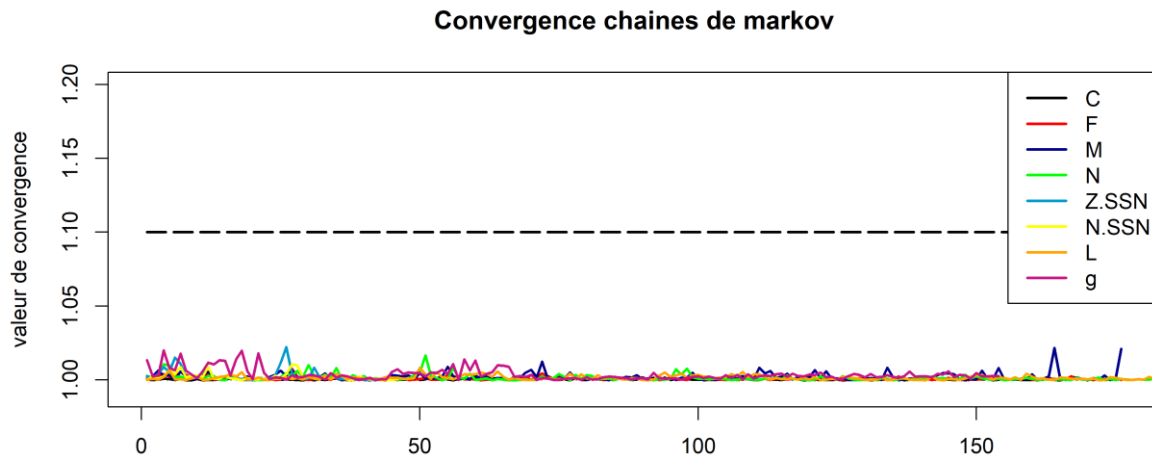


Figure 1 : Convergence diagnostic (R ratio of the Gelman-Rubin test; should be <1.05 , dotted line) for a selection of key variables and parameters (both species, all life-stages, all years).

2. Posterior distributions of the variables of the model

Available upon request.

3. Times series of each variable and fit between prediction and observations for abundances, sizes and catches time series

Available upon request.

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Date de naissance* : 04/08/1998

Nb pages : 25

Annexe(s) : 8

Année de soutenance : 2023

Organisme d'accueil : Ifremer Plouzané

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Titre français : Exploration des mécanismes de mortalité, de croissance et de recrutement chez les petits poissons pélagiques via la construction d'un modèle hiérarchique bayésien multi-espèces de cycle de vie

Titre anglais : Unraveling mortality, growth and recruitment processes underlying the population dynamics of a small pelagic system using a hierarchical Bayesian two-species life-cycle model

Résumé

Comprendre les processus écologiques qui régissent les dynamiques des populations de poissons s'avère essentiel pour établir une gestion écosystémique des ressources marines. Dans cette étude, nous avons cherché à comprendre les mécanismes qui relient la densité, la taille et l'environnement à la mortalité naturelle, à la pseudo-croissance et aux processus de recrutement chez des petits poissons pélagiques du golfe de Gascogne (Atlantique, France). Nous avons représenté les dynamiques de populations de deux espèces susceptibles d'interagir, l'anchois (*Engraulis encrasicolus*) et la sardine (*Sardina pilchardus*). Pour cela, nous avons construit un modèle de cycle de vie multi-espèces dans un cadre bayésien à espace d'état. Le modèle n'a pas permis de mettre en évidence d'interaction entre ces deux espèces, mais celui-ci a révélé plusieurs mécanismes intraspécifiques de densité-dépendance à différents stades de vie. Nous avons mis en évidence des effets densité-dépendants sur la mortalité naturelle des anchois d'âge 1 et 2, et des sardines d'âge 1 et 3. Le recrutement est densité-dépendant chez les sardines. La mortalité naturelle de l'anchois d'âge 1 est taille-dépendante. Il s'avère que certains facteurs environnementaux, tels que le zooplancton, la température, les indicateurs globaux (AMO et NAO), ont un impact sur la mortalité naturelle à l'âge 3 et le recrutement chez les deux espèces, ainsi qu'à l'âge 1 chez les anchois. Le modèle n'a révélé aucun effet sur la pseudo-croissance, celle-ci résultant à la fois de la croissance individuelle et de la mortalité taille-sélective, deux phénomènes susceptibles de se compenser. Nos résultats fournissent de nouvelles informations sur les mécanismes qui régissent la dynamique des populations des sardines et des anchois, que nous avons discutées en proposant des interprétations hypothétiques des mécanismes sous-jacents aux trois processus étudiés.

Abstract

Understanding ecological processes driving populations dynamics within fish ecosystems is critical to support ecosystem-based management. In this study, we aimed to unravel the mechanisms linking density, size and environment to natural mortality, pseudo growth and recruitment processes within a small pelagic fish system of the Bay of Biscay (French Atlantic coast). We modeled population dynamics of two species likely to interact, anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) and built a two-species life-cycle model in a state-space framework, using Bayesian inference. We found no evidence of interaction between these two species but intraspecific density dependence occurring at different life stages. We highlighted density-dependent effects on natural mortality of age-1 and age-2 for anchovies, and of age-1, age-3 and on recruitment for sardines. Also, age-1 anchovy natural mortality is size-dependent. We found environment factors such as, zooplankton, temperature, global indicators *Atlantic Multidecadal Oscillation* (AMO) and *North Atlantic Oscillation* (NAO), impacting age-3 natural mortality and recruitment in both species populations and age-1 natural mortality in anchovy population. We found no effect on pseudo-growth, as it results of both individual growth and size-selective mortality inside a life-stage, two phenomena that are likely to offset each other. Our results provide new information on the mechanisms that govern the dynamics of sardines and anchovies at population level, which we discussed by proposing hypothetical interpretations of the mechanisms underlying the three processes investigated.

Mots-clés : dynamique des populations, croissance, mortalité, densité-dépendance, taille-dépendance, modèle hiérarchique, bayésien, modèle de cycle de vie, modèle multi-espèces, modèle à espace d'état, sardine, anchois

Key Words: population dynamics, growth, mortality, density dependence, size dependence, hierarchical model, Bayesian, stage-based life cycle model, multispecies model, state-space model, sardine, anchovy