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ABSTRACT

Small pelagic fish have shown a general decrease in size and body condition over the past two decades in several European regional seas. Although the underlying processes are still not well understood, recent studies point to a bottom-up control. In order to better understand how the
25 environment impacts the main individual life history traits, which themselves control the dynamic of the population, we developed a comparative approach between two species, European anchovy and sardine, and across three regions of the Northeast Atlantic and Mediterranean Sea: the English Channel in the north, to the Bay of Biscay and the Gulf of Lion in the south. We developed a bioenergetic modeling framework based on the Dynamic Energy Budget theory (DEB). Our DEB
30 models were forced using two different representations of the lower trophic levels, POLCOMS-ERSEM and SEAPODYM models. Our models were calibrated for the Bay of Biscay and then projected on to the other regions, over the early 2000s (period with bigger fish) and the early 2010s (period with smaller fish). The environment alone, temperature and zooplankton, explained a significant part of the observed regional differences in growth. However, the temporal trends
35 simulated by the lower trophic levels models, when transcribed through bioenergetics, could not explain the strong decrease in length and weight that occurred in the Bay of Biscay (-30% in weight for anchovy and -20% for sardine) and in the Gulf of Lion (-30% for anchovy and -50% for sardine). Through a scenario approach, we estimated that a decrease in zooplankton quality could be a significant driver of the observed decrease in size both in the Bay of Biscay and in the Gulf of
40 Lion (decrease in assimilable energy of 4 to 5% and 15 to 17% in the Bay of Biscay and the Gulf of

Lion, respectively). For such a decrease in size, a zooplankton biomass of the same quality should have been reduced by between 17 and 31 % in the Bay of Biscay over a 10- to 15-year period, while no biologically realistic estimations were obtained for the Gulf of Lion. The validity of these proposed changes in biomass and quality is discussed in context of alternative explanations.

45 **KEYWORDS**

Pelagic environment, Bioenergetics, Life history traits, Small pelagic fish, Zooplankton, English Channel, Bay of Biscay, Gulf of Lion

1. INTRODUCTION

50 As forage fish, small pelagic fish represent a key trophic level in marine ecosystems. Species such as anchovy and sardine feed on plankton and are a key intermediate for energy transfer towards higher trophic levels in marine food webs (Cury et al., 2000; Essington et al., 2015). These short-lived species are characterized by rapid growth, high fecundity and large variations in abundance. Although their population dynamics have been shown to heavily depend on environmental

55 conditions (Hjort, 1914; Cushing, 1990; Chambers and Trippel, 2012), the underlying processes remain challenging to establish. In a context of global change, understanding this relation between the population dynamics of small pelagic fish and their environment becomes even more crucial to achieve sustainable fishery management.

60 Climate change may act upon organisms in three main ways: a shift in species distribution (Poloczanska et al., 2013; Lenoir et al., 2020), *e.g.* through egg or larval transport (Takeshige et al., 2015), a change in their phenology (Walther et al., 2002; Durant et al., 2007) and a potential decrease in mean body size (Gardner et al., 2011; Audzijonyte et al., 2019). These phenomena are linked to changes in physiology to maintain suitable ranges of environmental conditions for survival

65 and reproduction, but also results from trade-offs in physiology and energetics. For some European fish populations, this decrease in mean body size is characterized by a shift in population age structure, with an increasing proportion of young individuals, but also to a global decrease in size-at-age (Daufresne et al., 2009). Over the past two decades, European anchovy (*Engraulis encrasicolus*) and European sardine (*Sardina pilchardus*) have shown a decrease in average size,

70 weight, growth and body condition in the North East Atlantic (Doray et al., 2018a; Veron et al., 2020; Boëns et al., 2021) and the Mediterranean Sea (Brosset et al., 2017; Albo-Puigserver et al., 2021) for each age class. This decrease in size-at-age is concomitant with a disappearance of older individuals (Saraux et al., 2019) and may have socio-economic impacts. In the Gulf of Lion for instance, the remaining sardine are too small and thin to be sold to the canning industry, leading to a

75 decline in landings (Saraux et al., 2019). Although the precise reasons remain unclear, a bottom-up control is so far the most likely cause to explain this decrease in size over the past twenty years. In

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the Gulf of Lion, recent studies dismissed a top-down effect (fishing and natural predation) and potential diseases and parasites (Van Beveren et al. 2016b; Saraux et al., 2019). Using statistical approaches, correlations were found between temperature, phytoplankton and zooplankton with

80 small pelagic fish weight and condition both in the Gulf of Lion and in the Bay of Biscay (Brosset et al., 2016a; Veron et al., 2020, Boëns et al., 2021). Furthermore, Queiros et al. (2019) demonstrated the prominent role of food size on sardine growth through experimental approaches, all these studies supporting a bottom-up effect in terms of food quantity or food quality.
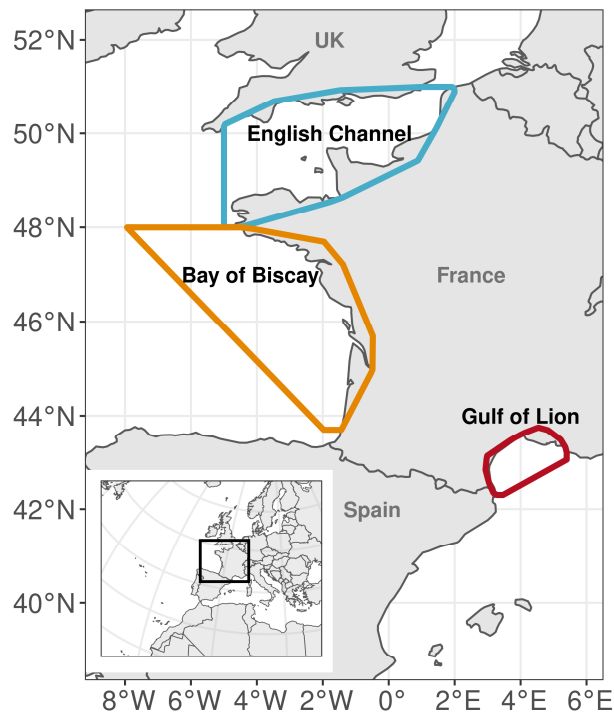
85 Figure 1 - Map of the three studied regions

Using both a comparative and a mechanistic approach, the present work aims to further investigate whether this bottom-up control underlies the observed decline in size-at-age i) of two different species, anchovy and sardine, ii) in two different regions, the Bay of Biscay (BoB) and the Gulf of

90 Lion (GoL, Fig. 1). We test here the assumption that phenotypic plasticity could explain most of the observed spatio-temporal variability of traits, rather than adaptation and genetic variability. Phenotypic plasticity being the potential of a single genotype to display contrasted phenotypes in different environmental conditions (Whitman and Agrawal, 2009). Previous studies (Huret et al. 2019, Bueno-Pardo et al. 2020) used the same modeling framework, developed by Gatti et al.

95 (2017), to compare anchovy and sardine bioenergetics in the Bay of Biscay, but on anchovy alone, either at a larger spatial scale (Huret et al. 2019) or including the effect of fishing at the population level (Bueno-Pardo et al. 2020). None compared anchovy and sardine in contrasted environments in order to reveal if these decreases in size in both species could result from the same mechanisms (*i.e.* here similar changes in their local environmental conditions).

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100   The English Channel (EC,Fig. 1) is included as a third region, with data for both anchovy and sardine. While the time-series in this region was too short to study temporal trends, short temporal overlap with data from the other regions allowed us to investigate the presence of latitudinal increase in mean size-at-age for the two species, with individuals being bigger towards higher latitudes. This latitudinal gradient in growth was already discussed in relation to temperature and

105   food across European waters, for both sardine and anchovy (Silva et al., 2008; Huret et al., 2019; Hattab et al., 2021). If indeed local environmental conditions were able to explain the spatial gradient in size between the three regions, our method could also reveal underlying mechanisms through time, *i.e.* whether the decrease in size can be explained by temporal trend in the environment. Indeed, the contrasting environmental conditions across space served as a baseline on

110   how much phenotypic plasticity, through our model, explains the observed variability in traits. As spatial gradients in fish traits can inform on observed or future temporal trends (Audzijonyte et al., 2020), here we used regional variability to explore the role of the environmental changes that could explain the observed trends in the traits of a given species. Studying two species with distinct traits and life history strategies within the same comparative framework should eventually make our

115   conclusions more robust.

As we aimed to disentangle the effect of temperature, food quantity and quality, we developed a mechanistic modeling approach. Our objective was to explicitly link average temperature and food conditions in each region to mean size-at-age for the two species using a common bioenergetic

120   framework based on Dynamic Energy Budget theory (DEB, Nisbet et al., 2000; Kooijman, 2010). Bioenergetic models simulate the energy flows within living systems. DEB theory describes the energy assimilation and its allocation to the main biological functions, namely growth, reproduction and maintenance throughout the life cycle of an organism. Energy fluxes therefore depend on the environment (food and temperature) and the state of the organism.

125   To force our bioenergetic model we used the outputs of two different ecosystem models, POLCOMS-ERSEM (Butenschön et al., 2016) and SEAPODYM (Lehodey et al., 2010), both providing synoptic information over space and time on temperature and zooplankton. They were, to our knowledge, the only models available over the geographical and temporal scales of interest. By using these two different sources of environmental information, we aimed to study the uncertainty

130   with respect to the zooplankton forcing and, as such, strengthen the robustness of our conclusion. Each environmental model relies on different hypotheses, data assimilation scheme and level of complexity to represent marine ecosystems. Their predictions might thus differ, especially for zooplankton that still represent a challenge in ecosystem modeling (Daewel et al., 2014; Everett et al., 2017).

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In this paper, we first provide updated information on the evolution of the size- and weight-at-age of anchovy and sardine in our three regions of interest over the last two decades. Then, we explored the spatio-temporal variability of the environment, as provided by two environmental models, to test their capacity to explain the observed variability in life history traits. Next, temperature and zooplankton were used as forcing variables in a DEB model to mechanistically simulate both regional and temporal differences in anchovy and sardine size. Finally, through a scenario-based approach, we estimated the change in the environment required to explain the observed decrease in fish size over time. These scenarios focus on a potential decrease in *quantity* and in *quality* of zooplankton. The results are discussed with respect to the quality of our forcing on one hand, and to the literature on the evolution of the food quality and quantity from *in-situ* observations, on the other hand.

2. MATERIALS AND METHODS

2.1. Studied populations and regions

Two of the studied regions are located in the North East Atlantic Ocean: the English Channel (48-51°N, 2.5-5.4°E) and the Bay of Biscay (43-48°N, 8-0.1°W). The Gulf of Lion is in the North West Mediterranean Sea (42.3-44°N, 2.5-5.4°E). Regions were studied separately as they corresponds to different fishery management units and probable different genetic populations (Huret et al., 2020; Caballero-Huertas et al., 2022). These regions also represent different environmental conditions for both anchovy and sardine and reveal a latitudinal gradient in terms of productivity and temperature, with more oligotrophic waters towards lower latitudes. The hydrography of the Gulf of Lion is strongly influenced by the Rhône river, while the Bay of Biscay is driven by the open ocean as well as by large rivers such as the Loire and the Gironde. Finally, the English Channel is a shallow and well-mixed water body connecting the Atlantic Ocean and the North Sea.

All regions represent fishing grounds for small pelagic fish, although exploitation levels are relatively low in the English Channel. In the Bay of Biscay, anchovy landings dropped in the early 2000s, leading to a moratorium from July 2005 to 2010 (Bueno-Pardo et al., 2020). Landings have since increased thanks to several years of good recruitments. In the Gulf of Lion, landings of both anchovy and sardine have declined since the 2000s because of a decrease in body size and condition (Saraux et al., 2019).

2.2. Model description

2.2.1. Model design

The model considers five state variables, expressed in kJ : (E) - the amount of energy in reserve, (V) - the volume of structural mass, (R) - the reproduction buffer, (G) - the gametes and (H) - the level of maturity. Assimilated food goes to reserve (E), which is directly linked to food availability.

Reserve does not need any maintenance and will fuel the other metabolic processes. The energy is then allocated either to structure (V), or to maturation (H) before the adult stage or reproduction (R) when reaching the adult stage. Unlike reserve, structure and maturation require maintenance costs.

The energy allocation within the organism is based on the kappa-rule. A fixed fraction κ is allocated to somatic maintenance and growth, whereas the remaining fraction $(1 - \kappa)$ is allocated to maturity maintenance and maturation (juvenile) or reproduction (adult) (Fig. 2, see Van der Meer, 2006; Kooijman, 2010; Jusup et al., 2011). In the DEB model used in this study, individuals become adults when they reach a particular maturity threshold (Table A.3, Hp). This threshold value is species-specific. The length at first maturity, *i.e.* the length at which the organism reaches the maturity level $H = H_p$ and has sufficient energy to spawn during the reproduction period will therefore depends on the environment history encountered by individuals, and thus will be region- and species-specific.

This model has been developed by Gatti et al. (2017) and has been used to explore variability of traits in anchovy (Huret et al., 2019) and anchovy dynamics in the Bay of Biscay (Bueno-Pardo et al., 2020). In this DEB model, energy can be reallocated from the reproduction buffer and/or gametes to somatic maintenance ($\dot{p}_{M2}$ and $\dot{p}_{M3}$) if the individual does not have enough energy for somatic maintenance, as proposed by Pethybridge et al. (2013).
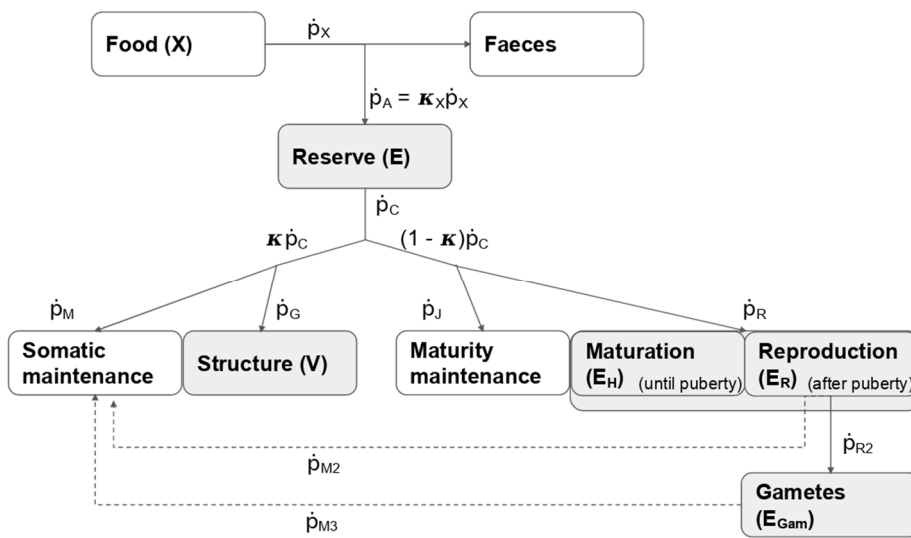
Figure 2 – Conceptual diagram of our DEB model. Definition of the parameters and their values can be found in Appendix A.

2.2.2. Feeding strategies

Anchovy and sardine both feed on diverse plankton organisms with a preference for copepods, although this can differ according to season (Plounevez and Champalbert, 1999, 2000; Costalago et al., 2014; Bachiller and Irigoien, 2015, Pablo et al., 2016a; Chen et al., 2021). In this study, the amount of available food in the environment (X, food density), is the gross quantity of zooplankton

(mgC.m^{-3}) which is provided as forcing variable. The scaled functional response (f $\in$ [0 ; 1]) is then computed and corresponds to the intake rate of the predator as a function of food density. It is constructed as a Holling type II function : $f = \dfrac{X}{X + X_K}$

where X_K is the half saturation rate coefficient.

2.2.3. Spawning strategies

The spawning season corresponds to the period when energy is allocated to gametes from the reproduction buffer ($\dot{p}_{R2}$) and their release in the environment. For anchovy, the spawning season is the same regardless of the region (Motos et al., 1996; Brosset et al., 2016b; Gatti et al., 2017; Huret et al., 2018). However, sardine spawns in spring and autumn in the English Channel (Stratoudakis et al., 2007, Coombs et al., 2010) and in the Bay of Biscay (Gatti et al., 2017) and in winter in the Gulf of Lion (Brosset et al., 2016b) (Table 1). The spawning peak is considered as the date of birth for both species in our model.

For the sake of parsimony, the reproduction period is not triggered by any environmental variable, such as temperature. This to limit the sources of variability without removing the effect of temperature which already impacts the dynamics of $\dot{p}_R$ and $\dot{p}_{R2}$.

Table 1 - Description of the spawning seasons used in this study. Light gray indicates the spawning months and dark gray indicates the spawning peak and date of birth in our model, anc : anchovy, sar : sardine

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Anc	English Channel					light	**dark**	light	light				
	Bay of Biscay					light	**dark**	light	light				
	Gulf of Lion					light	**dark**	light	light				
Sar	English Channel			light	light	light	**dark**			light	light	light	
	Bay of Biscay			light	**dark**	light	light				light	light	
	Gulf of Lion	**dark**	light	light							light	light	light

2.3. Biological and "environmental data"

2.3.1. Biological data

The results presented in this study focus on the adult stage, but data over the whole life cycle is needed for the calibration of the DEB model. Length and wet weight data for larvae and juveniles were collected between 1999 and 2013 in spring/summer and in autumn in the Bay of Biscay (Table 2). Details can be found in Gatti et al., (2017, see their Fig. 5).

Table 2 - Synthesis of fish observations collected during Ifremer scientific surveys, unless stated otherwise (Anc : anchovy, Sar : sardine)

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	Area	Source	Time series	Month coverage	Variables	Species
Larvae	Bay of Biscay	PLAGIA	1999	Jun-Jul	Length, weight	Anc
	Bay of Biscay	MICRODYN	2004	Jun	Length, weight	Anc
	Bay of Biscay	ECLAIR	2008	Jun-Aug	Length, weight	Anc
	Bay of Biscay	SENTINELLE	2010	Jul	Length, weight	Anc, Sar
	Bay of Biscay	PELGAS	2009;2011	May	Length, weight	Anc
	Bay of Biscay	PELGAS	2009-2013	May	Length, weight	Sar
Juveniles	Bay of Biscay	JUVESU	1999	Sep	Length, weight	Anc
	Bay of Biscay	JUVAGA	2003	Oct	Length, weight	Anc
	Bay of Biscay	Pro Juv[a]	2005	Sep	Length, weight	Anc
	Bay of Biscay	JUVENA	2014	Sep	Length, weight	Anc
Adults	English Channel	PELTIC[b]	2014-2019	Oct	Length, weight	Anc, Sar
	English Channel	CAMANOC	2014	Sep-Oct	Energy density	Anc, Sar
	English Channel	CGFS	2015	Oct	Energy density	Anc, Sar
	English Channel	Commercial landings	2015-2016	Mar;May;Jul:Nov	Energy density	Sar
	Bay of Biscay	PELGAS	2000-2019	May	Length, weight	Anc, Sar
	Bay of Biscay	PELGAS	2014-2015	May	Energy density	Anc, Sar
	Bay of Biscay	EVHOE	2014-2015	Oct	Energy density	Anc, Sar
	Bay of Biscay	Commercial landings	2014-2015	Fev:Nov	Energy density	Anc, Sar
	Gulf of Lion	PELMED	2002-2019	Jul	Length, weight	Anc, Sar

[a] Professional partnership
[b] CEFAS survey

The length and weight data for adult stage were obtained from the dedicated annual pelagic surveys in each of the three studied regions, PELTIC for the English Channel (Doray et al., 2021), PELGAS for the Bay of Biscay (Doray et al., 2000, 2018b) and PELMED (Bourdeix and Hattab, 1985) for the Gulf of Lion (Table 2). For each region, these data were standardized in order to avoid bias across time or space and were averaged by age and year. Fish acoustic densities were scrutinized based on spatial and spectral signatures of schools, and associated to nearest identification trawl haul catches, to derive small pelagic fish abundance estimates per 1 nautical mile long Elementary Distance Sampling Units (EDSUs). Abundances at length per EDSU were calculated by splitting abundance using length distributions from nearest trawl haul. Global mean weights and lengths at age were estimated by: i) calculating total abundance per length class over all ESDUs, ii) splitting total abundance per length class between ages using a global length-age relationship, iii) calculating total abundance per age by summing abundance at age over length class, iv) calculating mean weights at age by applying global length-weight relationships to abundances-at-age (Doray et al., 2021). This was performed using v1.3.9 EchoR package in R (Doray, 2013).

Energy density (kJ.g^{-1}), defined as the amount of energy per unit of mass, was used to calibrate the DEB model. It measures lipid and protein energy density as water and ash do not have any energetic potential. Lipids are the main driver of the seasonal variability in anchovy and sardine weight thus, they are also the main driver of the seasonal variability in energy density. Proteins are linked to body structure and define the baseline of energy density. This data was measured for adults and at different months to account for seasonality (Gatti et al., 2018). This was done following the methods of Dubreuil and Petitgas (2009) and Spitz and Jouma'a (2013). The whole fish was dried

and then ground up to obtain an homogenized powder. Subsamples were then placed in an adiabatic
bomb calorimeter to measure the energy released by combustion.

2.3.2. Forcing variables from POLCOMS-ERSEM and SEAPODYM

Environmental variables (temperature, °C and zooplankton, $mgC.m^{-3}$) were used as forcing variables for the DEB model. The only existing sources to get such variables, synoptic in time and space, is from ecosystem models. Two models were available over our three regions and the time period considered, each with different properties: the regional physical-biogeochemical model POLCOMS-ERSEM (Allen et al., 2001; Holt et al., 2004; Butenschön et al., 2016), and the SEAPODYM zooplankton and micronekton model (Lehodey et al., 2010, 2015; https://marine.copernicus.eu/).

These two models included physical and biogeochemical variables. On the one hand there was a coupling between the hydrodynamic model POLCOMS and the biogeochemical model ERSEM and on the other, temperature and currents from the NEMO hydrodynamic model act as forcing variables to the plankton variables of SEAPODYM (Conchon, 2016). The interaction between physical and biogeochemical variables is more developed in POLCOMS-ERSEM, but the main difference resides in the structure of the biogeochemical part. Zooplankton dynamics is particularly important in our study, as it is the main factor defining the growth and starvation period with low food income. This dynamic depends on the properties of each environmental model. ERSEM is one of the most established models regarding the lower trophic levels and simulates the cycles of carbon and other major nutrient elements within the low trophic levels of the marine ecosystem. This model is based on a set of variables, with three size based groups of phytoplankton plus diatoms and two groups of zooplankton (Butenschön et al., 2016). SEAPODYM is simpler and rather parsimonious as it simulates one group of zooplankton which relies directly on energy transfer from primary production, the latter being forced by satellite data in our studied areas (Conchon, 2016; Titaud et al., 2021). Zooplankton dynamics also rely on a temperature based relationship, defining both recruitment and turnover, which is tuned to fit zooplankton biomass observations (Conchon, 2016).

Our study uses a configuration in zero dimension (0D), where only time is variable and no migration or spatial patterns are considered. It aims to understand the average individual fish response to average environmental conditions in each of the three studied regions. No spatialization has been made within each region and the average value of temperature and zooplankton per cubic meter and per day, over the whole region, has been computed. SEAPODYM does not permit to extract data at a specific depth layer, thus only the epipelagic layer (0 to 1.5 times the euphotic

290   depth) was used. POLCOMS-ERSEM allows to be more specific about the extraction depth. To fit
       to the life cycle of anchovy and sardine, the forcing variables from POLCOMS-ERSEM were
       averaged vertically over 0-30m (eggs, larvae and juveniles) and 0-150m (adults) for temperature
       and 0-50m for zooplankton following Gatti et al. (2017) model configuration.

       In this study, the DEB model's inputs were daily climatologies. These were built for two different
295   periods, the beginning of the time series, representative of bigger fish (2000-2005) and the end of
       the time series, representative of smaller fish (2010-2015). As POLCOMS-ERSEM simulations
       were not available after 2015, the extent of the studied period was constrained to 2000-2015.
       Moreover, as 2014 was the first year with available data for PELTIC survey, we used the 2014-
       2018 fish data as an estimation of the second studied period (2010-2015), supposing length and
300   weight have not undergone profound changes in the English Channel in this short period. Same
       periods were used in the three different regions. This approach aimed at reducing the noise due to
       inter-annual variability and better representing the average patterns rather than modeling single
       cohorts.

305   The spatio-temporal variability of both environmental models has been investigated and compared.
       The regional variability analysis focused on the comparison of the seasonal patterns between
       regions, rather than within each region. Regarding the temporal variability, trends have been
       explored by fitting linear models over the past two decades.

310   **2.4. Calibration of the DEB model**
       For each species, DEB model parameters were calibrated on the Bay of Biscay and this model was
       subsequently forced by environmental variables from the different regions. The set of parameters
       has been established by Gatti et al. (2017), either based on literature or estimated by calibration.
       The calibration has been done for the Bay of Biscay, using the whole fish data set available then
315   (1999-2014), with environmental forcing coming from a hindcast of ECOMARS 3D (Huret et al.,
       2013) and averaged over 1980-2008. This set of parameters has proven to be robust when tested
       with different data sources (Huret et al., 2019).

       As this study uses different environmental variables to force the DEB model, especially regarding
320   the differences in absolute values of zooplankton (see 3.2.1.), the half saturation coefficient for food
       (X_K) had to be calibrated again for each species and each environmental model. This new
       calibration has been done on the first five years of the studied period (2000-2005), using both
       environmental models and averaged size- and weight-at-age data from those years. However, the
       dataset related to larvae and juveniles and the one related to energy density lacked sufficient years

10

325   during the 2000-2005 period. Thus all the available data regarding larvae or juvenile have been used in the Bay of Biscay, without being period specific.

The DEB model was then used with the same set of parameters and forced with the averaged environment corresponding to the end of the studied period (2010-2015). Using the same set of parameters over the two periods assumes that no genetic selection or changes occurred between

330   2000 and 2015. Only the effect of a potential change in the environment is explored.

However, this new estimation was not satisfactory when applied to the Gulf of Lion. The half saturation for food (X_K) and the assimilation efficiency ($\kappa_X \in [0 ; 1]$) had to be estimated specifically for this area, using only length and weight data from the Gulf of Lion. This relies on the

335   hypothesis that the zooplankton quality might differ in the Gulf of Lion, either with different communities and/or different energy values for a given taxa implying that small pelagic fish do not assimilate the same energy fraction for a similar ingested biomass.

We used the downhill simplex optimization method (amoeba subroutine in Fortran 90, Nelder and

340   Mead, 1965), which was appropriate to estimate a small set of parameters. This Simplex method aims at minimizing the following cost function :

$$F_{cost} = \sum_i^{stages} \sum_j^{variables} \frac{1}{n_{obs_{i,j}}} \sum_k^{n_{obs_{i,j}}} \left(\frac{x_{i,j,k} - y_{i,j}}{\sigma_{obs_{i,j}}} \right)^2$$

345   with $n_{obs_{i,j}}$ the number of observations for variable j at life stage i, x the observations, y the predictions and $\sigma_{obs_{i,j}}$ the observed standard deviation of variable j at life stage i. Four variables are considered : length, weight, energy density and the number of batches, at different life stages : larvae, juveniles and adults for which each age group is considered as one stage (according to data availability). Different parameters initial values have been tested in order to avoid the selection of

350   parameters corresponding to local minima of the cost function.

DEB model calibrations and simulations have been run on Fortan 90 software while all model's outputs have been analyzed and plotted using the R software (v4.2.1).

2.5. Environmental scenarios

355   In addition to the impact of environmental changes as provided by POLCOMS-ERSEM and SEAPODYM, we also evaluated the required environmental changes that could best explain the observed trends in fish growth over time, through two scenarios. The first one (SC1) was based on the hypothesis that the sole change was in food quantity. A coefficient ($c_X \in [0 ; 1]$) was added in the scaled functional response.

360

$$f = \frac{c_X * X}{c_X * X + X_K}$$

11

The second scenario (SC2) was based on a potential change in food quality through κ_X, the assimilation efficiency.

$$\dot{p}_A = \kappa_X * \dot{p}_X$$

365   with $\dot{p}_A$ the assimilation rate and $\dot{p}_X$ the ingestion rate (function of the scaled functionnal response, see Appendix A.1).

This can be linked to a decrease in energy in the zooplankton or a potential change in the zooplankton community composition for which small pelagic fish might have different assimilation capacities. For both scenarios, parameters were calibrated to best fit the data of the late period

370   (2010-2015) using the previously presented cost function.

The goodness of fit of our calibrations and simulations were assessed using Taylor Diagrams. These diagrams provide a statistical summary of the adequacy between observations and predictions using the correlation coefficient, the root mean square difference and the ratio of the standard deviations (Taylor, 2001). Only size- and weight-at-age data for adult stage were considered for Taylor

375   Diagrams, as the other observations were not comprehensive enough on both periods.

3. RESULTS

3.1. Spatio-temporal variability in length and weight from survey data
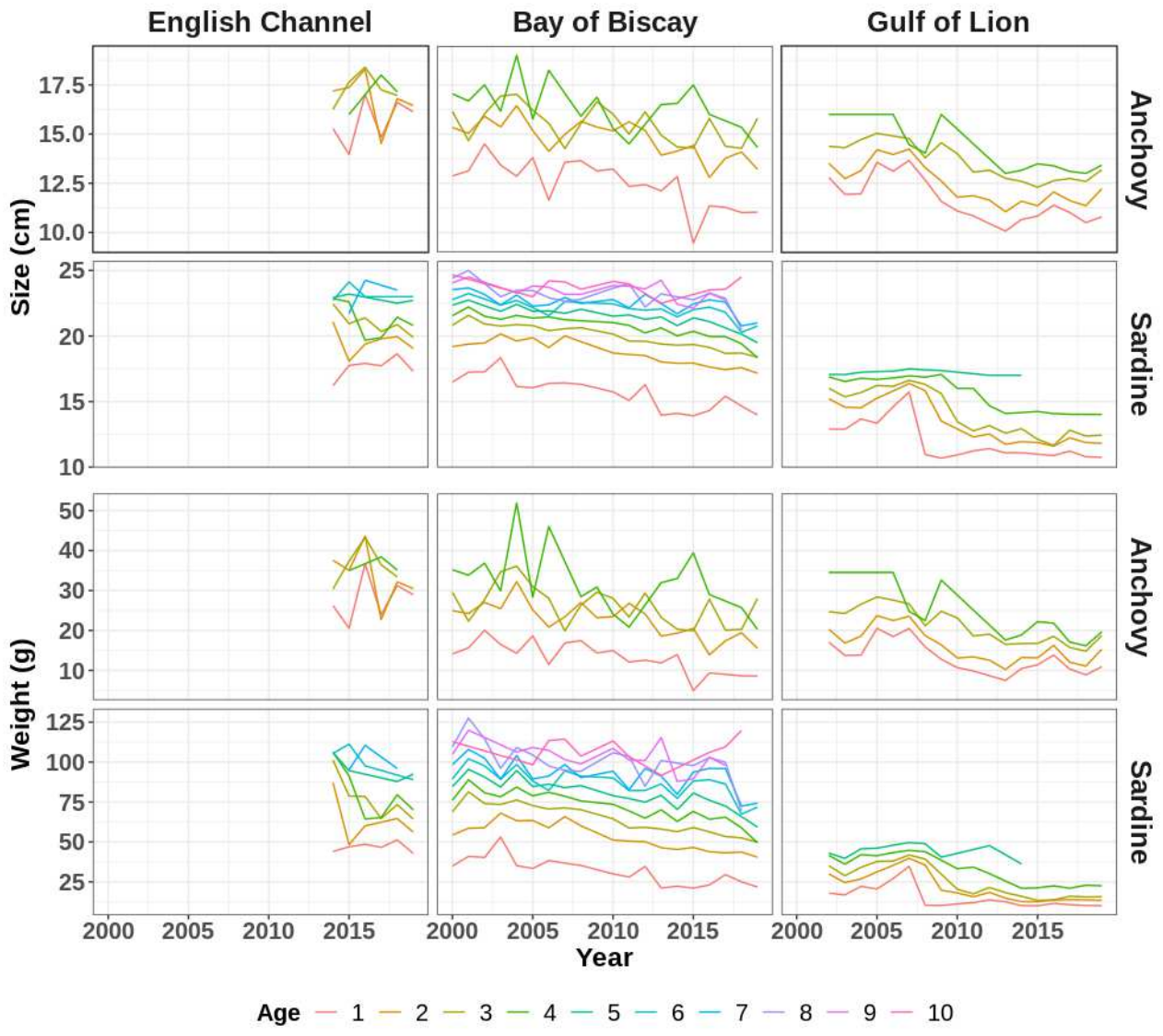
Figure 3 – Mean length and weight at age for anchovy and sardine in the English Channel, the Bay of Biscay and the Gulf of Lion. Pelagic survey data available over 2014-2019 in the English Channel (PELTIC survey), 2000-2019 in the Bay of Biscay (PELGAS survey) and 2002-2019 in the Gulf of Lion (PELMED survey)

Fish were generally bigger at higher latitudes (Fig. 3), with length and weight at age being almost systematically higher in the northern regions, no matter the year. Survey data showed an important decrease in size of both anchovy and sardine over the past two decades in the Bay of Biscay and in the Gulf of Lion (Fig. 3). It was not possible to determine if the same pattern occurred in the English Channel as the time series was too short (2014-2019). The decrease was relatively smooth between the early 2000s and the late 2010s, except for sardine in the Gulf of Lion (Fig. 3) where a sharp decline was observed from 2007 to 2011, especially for age 1. Between the beginning and the end of the time series and on average over all age groups, anchovy length has decreased by 10% (30% in weight), both in the Bay of Biscay and in the Gulf of Lion. Sardine has decreased by 9%

and 20% (20% and 50% in weight) in the Bay of Biscay and the Gulf of Lion, respectively. Over the studied period a disappearance of age five has been observed for sardines in the Gulf of Lion. Similarly, individuals older than age 7 have disappeared in the Bay of Biscay.

3.2. Environmental characteristics

3.2.1. Regional variability in the environment

A large regional variability was observed in both POLCOMS-ERSEM and SEAPODYM data (Fig. 4). Absolute temperature values and seasonal patterns were consistent between models. Differences observed, mostly during the warm and stratified season, were mainly due to the different depth layers selected for each forcing. SEAPODYM mean estimations were generally higher than POLCOMS-ERSEM, except in the EC during summer and in the GoL (February 2000-2005 - EC: + 0.24 °C, BoB : +0.16°C, GoL : - 0.47°C ; February 2010-2015 - EC : +0.42°C, BoB : +0.26°C, GoL : -0.23 °C ; August 2000-2005 - EC : -1.15°C, BoB : +0.64°C, GoL : -0.22°C ; August 2010-2015 – EC : -0.92°C, BoB : +0.71°C, GoL : -0.06°C). Differences were larger regarding the values and the seasonality patterns of zooplankton between the two environmental models (Fig. 4). The orders of magnitude for this variable were much higher in SEAPODYM ([20.8 - 238.6] $mgC.m^{-3}$) than in POLCOMS-ERSEM ([0.029 - 74.8] $mgC.m^{-3}$). This difference between the two environmental models was overcome in our study using a different half saturation coefficient X_K for each zooplankton dataset for the scaled functional response f, which links the zooplankton concentration to the assimilated energy (see section 2.2.2). However, the productivity peak in the Bay of Biscay occurred almost two months later for SEAPODYM during the 2000-2005 period, and both periods showed a sharper decrease in July-August in comparison to POLCOMS-ERSEM, for which the summer decrease was smoother. The most important seasonal differences were observed in the Gulf of Lion where the productivity peak was reached in spring (March-May) with SEAPODYM and in summer (June-August) with POLCOMS-ERSEM. The same offset was observed for the lowest values which occurred in early fall (August-October) with SEAPODYM and in winter (December-March) with POLCOMS-ERSEM, where the values remained extremely low for three months.
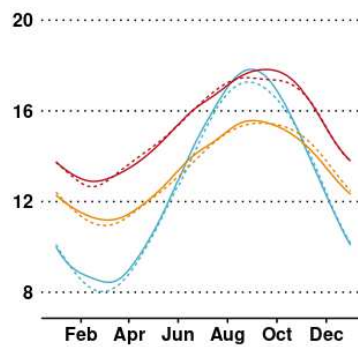
On average, zooplankton from SEAPODYM was 1.5 times higher across regions when moving towards higher latitudes (EC : 113.4, BoB : 69.6, GoL : 48.5 $mgC.m^{-3}$). This gradient was found in POLCOMS-ERSEM between the English Channel and the Bay of Biscay (EC : 40.3, BoB : 25.3 $mgC.m^{-3}$), but the difference was more notable between the Bay of Biscay and the Gulf of Lion with a factor of 3 (GoL : 8.1 $mgC.m^{-3}$).
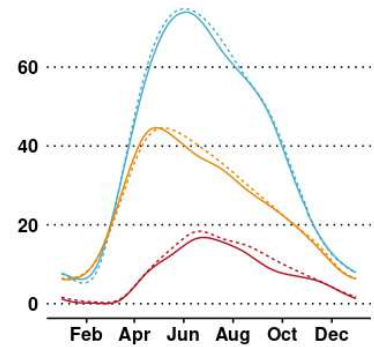
POLCOMS-ERSEM
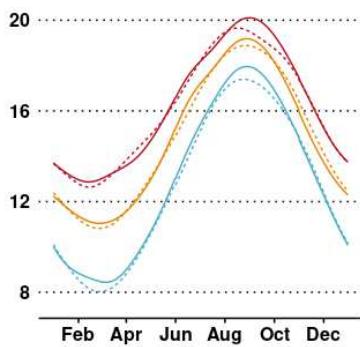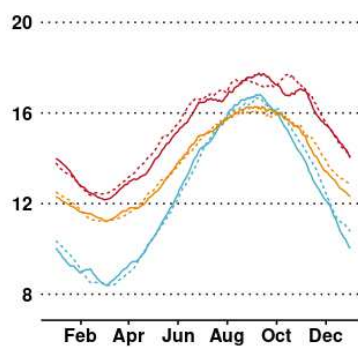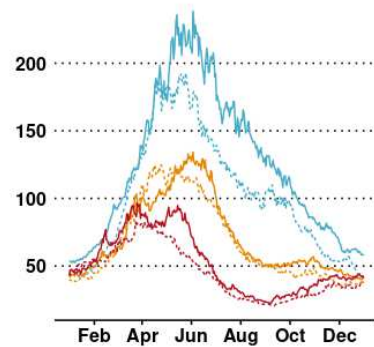
Temperature 0-30m | Temperature 0-150m | Zooplankton 0-50m

SEAPODYM

Temperature 1.5 EuphDepth | Zooplankton 1.5 EuphDepth

Period
— 2000-2005
··· 2010-2015

Area
— English Channel
— Bay of Biscay
— Gulf of Lion

Figure 4 – Daily climatologies of temperature (°C) and zooplankton (mgC.m^{-3}), averaged over 2000-2005 (solid line) and 2010-2015 (dotted line) for each environmental model (POLCOMS-ERSEM, top panel and SEAPODYM, bottom panel) per region (blue - English Channel, orange - Bay of Biscay, red - Gulf of Lion)

3.2.2. Temporal trends

POLCOMS-ERSEM did not reveal any significant trends in temperature, whereas SEAPODYM indicated an increase of 0.002 °C.year^{-1} in the Gulf of Lion over the studied period (Appendix B). Zooplankton showed opposite trends, with a small increase in POLCOMS-ERSEM (EC and BoB : + 0.006 mgC.m^{-3}.year^{-1}, GoL : + 0.007 mgC.m^{-3}.year^{-1}) and a decrease in SEAPODYM (EC : - 0.19 mgC.m^{-3}.year^{-1}, GoL : - 0.07 mgC.m^{-3}.year^{-1}).

3.3. Variability in modeled growth

After the estimation of the half saturation coefficient (X_K) for the Bay of Biscay (Table 3), DEB models for both species and both environmental forcing fitted well to the observed data (Fig. 5). Regarding the ability of the DEB model to reproduce the spatial gradient, no data were available in the English Channel for the early period 2000-2005, but the prediction had a satisfactory fit to the late period, 2010-2015, for anchovy (Fig. 5A, B). For sardine, the best fit was observed for the older age groups, whereas the prediction seemed to overestimate growth until age five (Fig. 5C, D).

15

In the Gulf of Lion, two parameters had to be adjusted to provide realistic predictions: the half saturation coefficient and the assimilation efficiency (X_K and κ_X). The agreement between observations and predictions was appropriate for the early period 2000-2005 (Fig. 5).

Table 3 – Summary of the DEB parameters estimates for calibration and both scenario, X_K : half saturation coefficient, c_X : food decreasing coefficient, κ_X : assimilation efficiency, BoB : Bay of Biscay, GoL : Gulf of Lion, SC1 : change in food quantity and SC2 : change in food quality (- means no difference with the calibration on 2000-2005).

	Parameter	Region	POLCOMS-ERSEM			SEAPODYM		
			2000-2005	2010-2015 (SC1)	2010-2015 (SC2)	2000-2005	2010-2015 (SC1)	2010-2015 (SC2)
Anchovy	X_K	BoB	6.27	-	-	18.8	-	-
		GoL	0.0036	-	-	5.12	-	-
	c_X	BoB	1	0.89	-	1	0.83	-
		GoL	1	0.012	-	1	0.57	-
	κ_X	BoB	0.8	-	0.76	0.8	-	0.76
		GoL	0.59	-	0.49	0.65	-	0.55
Sardine	X_K	BoB	3.46	-	-	9.99	-	-
		GoL	0.0189	-	0.0011	7.27	-	0.23
	c_X	BoB	1	0.69	-	1	0.77	-
		GoL	1	0.22	-	1	0.80	-
	κ_X	BoB	0.8	-	0.77	0.8	-	0.77
		GoL	0.52	-	0.39	0.59	-	0.45

Secondly, when applying the environmental forcing corresponding to the late period 2010-2015, without changing the DEB parameters, almost none of the simulations showed significant differences with those from 2000-2005. The regional environmental conditions were not sufficiently different to explain the decrease in size of small pelagic fish whatever the environmental model used as forcing. The only exception was the SEAPODYM forcing in the English Channel, which generated a decrease in size and weight for both species (Fig. 5B, D).

In the Gulf of Lion, the number of batches spawned during the life cycle was always higher with POLCOMS-ERSEM in comparison to SEAPODYM. This higher batch number can be related to the relatively flat seasonal pattern of the functional response obtained with the POLCOMS-ERSEM forcing (Fig. 5A, C), for which the food income was relatively low but without seasonal stress.
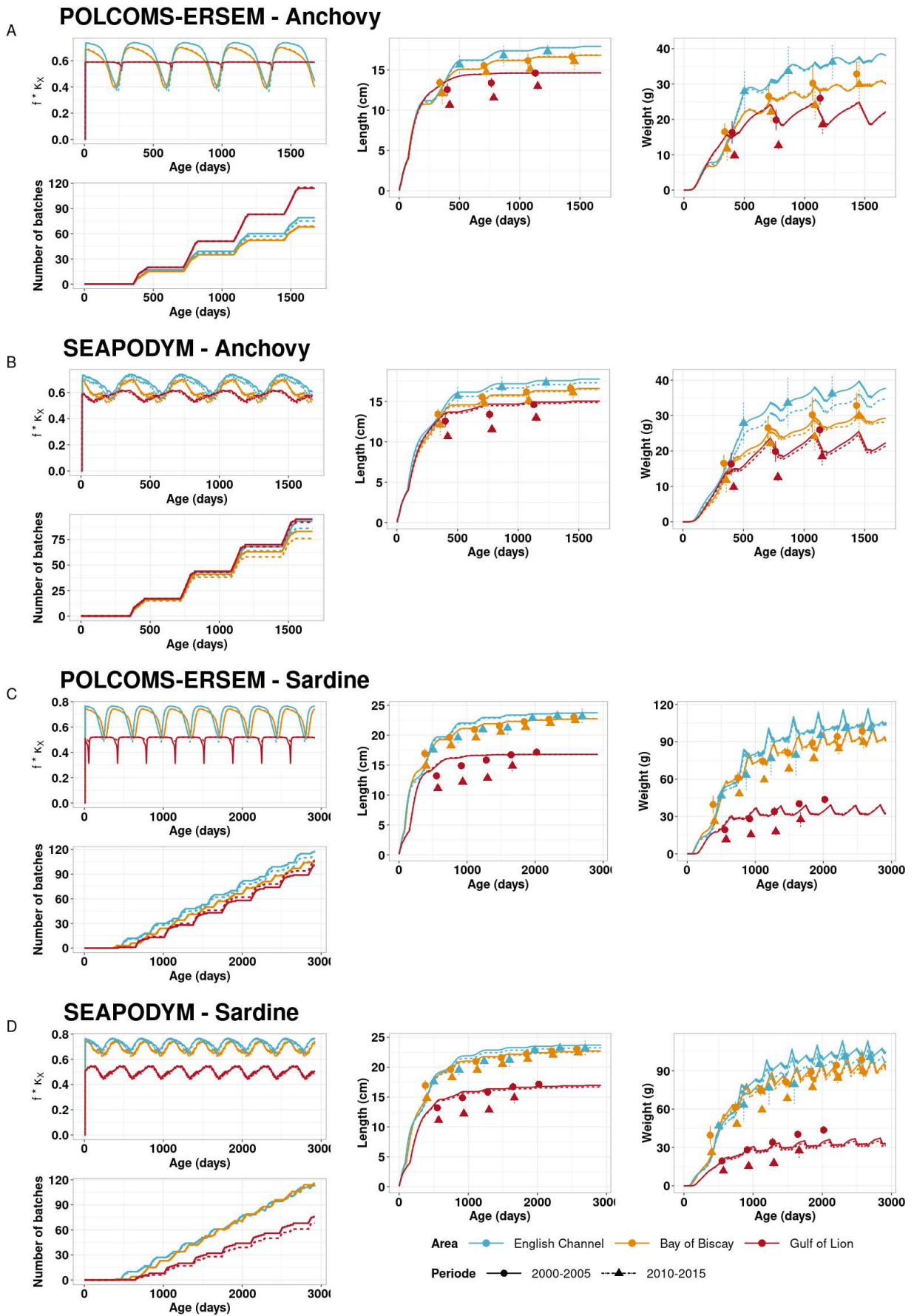
Figure 5 - Growth models for anchovy and sardine, each forced with POLCOMS-ERSEM or SEAPODYM, with regional climatologies averaged over 2000-2005 (solid line for predictions and

dots for observations) and 2010-2015 (dotted line for prediction and triangles for observation). Each
475 panel shows the functional response for food multiplied by the assimilation efficiency, the number
of batches spawned, length and weight as functions of age.

3.4. Scenarios of change in food availability

3.4.1. Change in zooplankton biomass

480 The first scenario (SC1) explored the effect of a potential decrease of total zooplankton
concentration. For this purpose, a constant decrease (c_X) was estimated over the climatology to fit
the observed fish traits. Seasonal variability was not considered. Our simulations assumed a
decrease of 17 to 30% (Table 3) of the total zooplankton biomass to explain the decrease in size in
the Bay of Biscay, with satisfactory fit for both species and both environmental models, except for
485 anchovy with POLCOMS-ERSEM forcing (Fig. 6) (POLCOMS-ERSEM, sardine : -31% |
SEAPODYM, anchovy : -17% and sardine : -23%).

When applied to the English Channel, this scenario caused a decrease in size and weight for
anchovy with SEAPODYM forcing, that was not expected given the observations made over the
late period. However, the decrease in biomass was not as sharp with POLCOMS-ERSEM (-11%,
490 Table 3) and it matched the observations (Fig. 6). The zooplankton biomass decrease scenario
reproduced the observed length and weight decrease of younger sardines (age 5 and below, Fig. 6).
Under this scenario, our DEB model predicted that sardine would have undergone a decrease in size
in the English Channel (POLCOMS-ERSEM : -3.5% in size, -12.4% in weight | SEAPODYM : -
4.4% in size, -14.8% in weight) .
495 In the Gulf of Lion, almost none of the simulations were satisfactory as the individuals were either
oversized or died at a very young stage. The best fit was obtained for anchovy with SEAPODYM
forcing; however, individuals could not invest energy in reproduction and died at age two (Fig. 6,
Appendix C.1B).

500 Regarding body condition, simulations showed a slight decrease for sardine while anchovy
displayed a greater decline in energy density, especially with SEAPODYM and for older ages
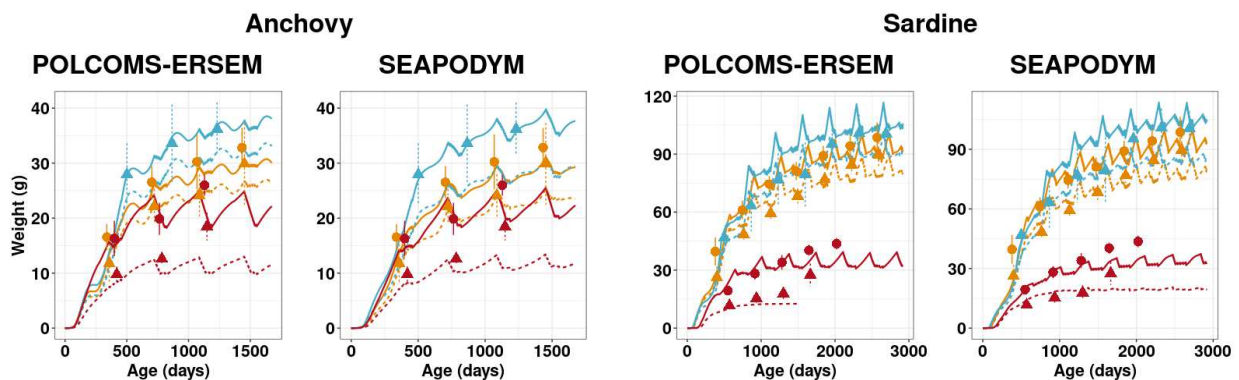(Appendix D.2).
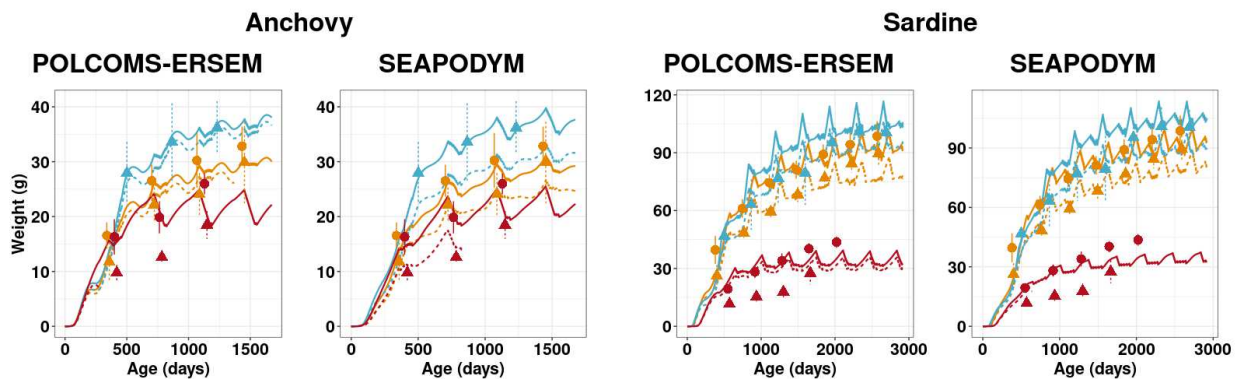
505   Figure 6 - Weight predictions for the 2010-2015 period (dotted line, dots for data) based on first scenario (SC1: optimized change in food biomass) based on either POLCOMS-ERSEM or SEAPODYM forcing. Simulations 2000-2005 (solid line, triangle for data), set for comparison, are the same as in Fig.5

510 **3.4.2. Change in zooplankton quality**

The second scenario (SC2) tested was based on a potential decrease of zooplankton quality which would imply a decline of assimilation efficiency, *i.e.* the assimilable energy fraction decreased for the same food concentration. The magnitude of the assimilation efficiency decrease was adjusted to reproduce the decrease in fish length and weight. Results were similar for both environmental

515   models in the Bay of Biscay, with a potential decrease of 5% for anchovy and 3.8% for sardine of the assimilation efficiency (Table 3). When applied to the English Channel, this decrease in quality reproduced the same pattern as in SC1, *i.e.* the DEB model predicted smaller anchovies than observed, whereas sardine length and weight fitted well until age four (Fig. 7). Under this scenario, our DEB model also predicted that sardine could have undergone a decrease in size in the English

520   Channel (POLCOMS-ERSEM : -4.2% in size, -13.9% in weight | SEAPODYM : -5.5% in size, -17.9% in weight) .

In the Gulf of Lion, anchovy needed an assimilation efficiency decrease of 16.9% with POLCOMS-ERSEM and 15.4% with SEAPODYM to fit to the observed data (Table 3). Regarding sardine, none of the environmental forcing allowed to reproduce observed fish size decrease and close their

525   life cycle, even when re-estimating multiple parameters (half saturation and assimilation efficiency). If length and weight were realistic, individuals displayed very low or no reproduction (Fig. 7, Appendix C.2C, D).

Simulations displayed a similar decreasing body condition as for the first scenario, even though

530   they were in a slightly better condition in SC2. There was an exception for the sardine of the Gulf of Lion which showed a much lower energy density with an almost disappearance of its seasonal cycle, mostly due to the absence or very low reproduction (Appendix D.3).

535 Figure 7 – Figure 7 - Weight predictions for the 2010-2015 period (dotted line, dots for data) based on second scenario (SC2: optimized change in food quality) based on either POLCOMS-ERSEM or SEAPODYM forcing. Simulations 2000-2005 (solid line, triangle for data), set for comparison, are the same as in Fig.5

540 **3.5. Goodness of fit among scenarios**

Figure 8 presents Taylor Diagrams that quantify the fit of our predictions to the observable data (value one on the x-axis corresponding to a correlation coefficient of 1 between the model and the data, a NRMSE of 0, and an identical standard deviation).

When considering anchovy in the Bay of Biscay as an example, both environmental models show
545 similar results for the calibration on the 2000-2005 period. However when applying the environment from the 2010-2015 period, predictions deteriorate, as shown by the increase of both standard deviation and NRMSE, because of an overestimation of size and weight. Simulations fit to the data improved when applying the scenarios, with a slight overestimation of size and weight with POLCOMS-ERSEM for SC1. Models parametrized for both species and three regions displayed a
550 good fit, with a pattern correlation coefficient up to 0.9 and root-mean-square below 0.5, except for the Gulf of Lion.
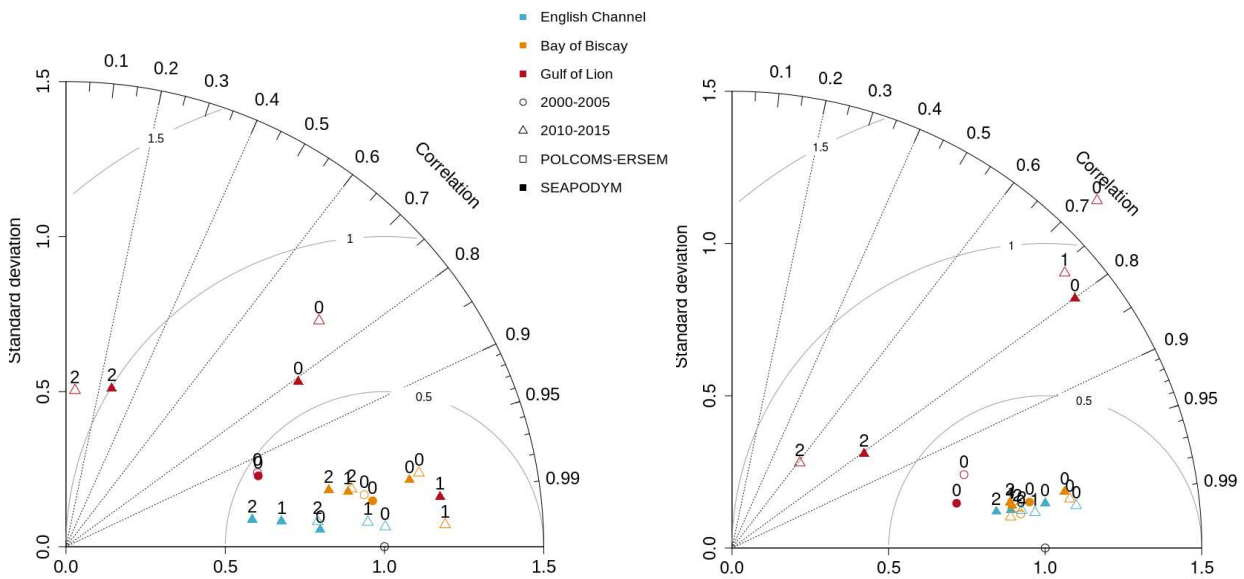
555 Figure 8 – Taylor diagrams displaying the ratio of the standard deviations (y- and x-axis), centered root mean squared (isolines) and correlation coefficients between observed and simulated lengths and weights for anchovy (left panel) and sardine (right panel). Numbers corresponding to simulations with parameters from the calibration or scenarios (0 – calibration, 1 – food quantity scenario, 2 – food quality scenario).

560

4. DISCUSSION

Using bioenergetic modeling forced by lower trophic models, we investigated the spatio-temporal variability of life history traits, mostly length and weight, among three populations of European anchovy and sardine, in relation to their local habitats. Recent data confirmed the decreasing trend in size of small pelagic fish observed in the Bay of Biscay and in the Gulf of Lion. In this study, emphasis was given to the bottom-up control hypothesis and our process-based approach allowed us to better understand the cause-and-effect relationship between the environment alone and observed growth patterns, as well as to disentangle the role of food from temperature. The underlying hypotheses rely on phenotypic plasticity, being defined as the potential of an organism to produce a range of observable characteristics according to different environmental conditions (DeWitt et al., 1998; Whitman and Agrawal, 2009), rather than adaptation or genetic variability across regions and/or throughout time.

Our results suggested that variability in growth across regions is largely due to differences in respective environments, with the effect of zooplankton dominating the effect of temperature. However, trends represented by lower trophic levels models did not seem strong enough to explain local temporal trends in traits. Our mechanistic modeling approach then allowed to run 'what-if' scenarios of temporal changes in the environment that would not been captured by the available forcing, such as change in food quality.

4.1. Spatial variability in traits

Over comparable periods, anchovy and sardine follow a positive latitudinal gradient in length and weight. This was found for the end of the time-series (2015-2020) across the three regions, and also between the Gulf of Lion and the Bay of Biscay throughout the whole time-series. This gradient was already highlighted for anchovy by Huret et al. (2019) between the Aegean Sea in the eastern Mediterranean Sea, the Bay of Biscay and the North Sea. Based on a literature review, Dimarchopoulou et Tsikliras (2022) showed a similar gradient for sardine between the Mediterranean Sea and the Atlantic Ocean. Gatti et al. (2018) presented data from 2014 that suggested that sardine and anchovy were bigger and in better condition in the English Channel than in the Bay of Biscay. Silva et al. (2008) also highlighted this spatial gradient from Morocco to northern France in the Atlantic, as well as a potential decline in length-at-age from the western to the eastern Mediterranean. Hattab et al. (2021) explored the correlation between temperature and body size across the Mediterranean Sea. But, no latitudinal gradient was found for anchovy and sardine. However, body size was negatively correlated to temperature (-3.01% and -3.43% per 1°C respectively). One of the hypotheses for this lack of latitudinal gradient was the presence of a negative west-east gradient in primary production. Although these results can be moderated on a smaller spatial scale in the western Mediterranean Sea, as an opposite gradient in size has been observed for sardine, with smaller individuals towards northern latitudes (Albo-Puigserver et al.,

2021). Bachiller et al. (2020) reported a potential trophic explanation with lower energetic contents towards higher latitudes. All these studies raised the environment as a potential key feature in explaining this spatial gradient, while also discussing other possible factors such as fishing or genetic adaptation.

The two low trophic levels models used, POLCOMS-ERSEM and SEAPODYM, showed strong spatial patterns between our three regions. Temperature outputs were comparable between models and on average, zooplankton concentrations were 1.5 times higher across regions towards northern latitudes. The only exception was between the Gulf of Lion and the Bay of Biscay with POLCOMS-ERSEM, where the gradient was stronger by a factor of 3.

Using bioenergetic modeling, plasticity explained the observed regional variability in size and weight. We obtained a high goodness of fit for the Bay of Biscay and the English Channel, especially for anchovy. Sardine simulations slightly overestimated growth for younger stages (under age five), but performed better for older stages. However, lower goodness of fit was obtained with the simulations in the Gulf of Lion, especially for sardine. This study was based on a plastic response hypothesis, thus all DEB parameters were kept constant among populations in order to remove the potential effects of genetic differences between the three populations. Although it is not yet well established if sardine display three genetically different populations (Caballero-Huertas et al., 2022), this is the case for anchovy (Huret et al., 2020). Thus, local adaptation is likely to have occurred and future studies could include some parameter variation among regions in order to account for genetic variability. Moreover, Brosset et al. (2016b) suggested that in the Gulf of Lion, individuals could prioritize reproduction to survival by starting reproduction earlier in the case of anchovy: in April (since 2008) instead of May (before 2006). These processes could also be integrated in order to further explore the specificities of the Gulf of Lion populations.

For the Gulf of Lion, two parameters linked to food ingestion and assimilation, the half saturation coefficient and the assimilation efficiency, had to be adjusted to reproduce the observed length and weight data for both species. The hypotheses underlying the re-estimation of those two parameters assume differences in the available food source and/or its assimilation, between the Bay of Biscay and the Gulf of Lion. This is realistic as we know that current zooplankton diversity in the Mediterranean results from a combination of species from several neighboring regions (Bianchi and Morri, 2000; Zenetos et al., 2010; Benedetti et al., 2018). Estimations of half saturation coefficient can appear very low when forced by POLCOMS-ERSEM, especially in the Gulf of Lion (0.0036 and 0.0189). This was necessary to balance the very low winter estimations of POLCOMS-ERSEM (min in 2000-2005 : 0.029 mgC.m^{-3}). However, we can not fully exclude the possibility that

differences regarding food assimilation could also be linked to local adaptations since studies have previously indicated genetic distinctions among those populations (Jemaa et al., 2015 (a), (b); Huret et al., 2020; Caballero-Huertas et al., 2022).

The seasonal pattern of zooplankton concentration differed between environmental models, especially in the Gulf of Lion where the minimum occurred during winter for POLCOMS-ERSEM and during summer for SEAPODYM. This discrepancy in the seasonal pattern of zooplankton was quite surprising. Ramirez-Romero et al. (2020) performed skill assessments of different coupled physical–biogeochemical models in the North-western Mediterranean, among them POLCOMS-ERSEM. They found that the representation of physical processes was appropriate, but they pointed out large differences in the biogeochemical variables. POLCOMS-ERSEM has proven to have non-realistic winter mixing in the Gulf of Lion, which implied issues with the timing and the magnitude of the phytoplankton bloom occurring in winter-spring in this region. Moreover, modeling of nutrient concentrations near river mouths, like the Rhône, are thought to be inaccurate in POLCOMS-ERSEM (Marsh et al., 2019). Those variables could affect seasonal pattern in zooplankton, especially given the relative small size of the region. Lastly, zooplankton dynamics were highly impacted by the modeling choices regarding feeding, growth and mortality terms. In NPZD models such as ERSEM, natural mortality of zooplankton is mainly represented by a closure term because of unknown or uncertain top-down formulations (Edwards and Yool, 2000; Travers et al., 2007). However, ERSEM distinguishes micro- from mesozooplankton, which SEAPODYM does not, despite important disparities in their individual and population dynamics, especially in the North Atlantic (Holt et al., 2014). These reasons could explain the discrepancy of zooplankton between the two environmental models and highlights the importance of finding the right level of complexity for such environmental models.

4.2. Temporal variability in traits

Over all age groups, we estimated that anchovy has lost 10% of its length (30% of its weight) over the past twenty years in both the Bay of Biscay and the Gulf of Lion. Sardine has lost 9% of its length (20% of its weight) in the Bay of Biscay and 20% (50% of its weight) in the Gulf of Lion. Those results confirm the on-going trends already observed in the Bay of Biscay (Doray et al., 2018a; Veron et al., 2020) and in the Gulf of Lion (Van Beveren et al., 2014) regarding the decrease in length and weight. As a consequence of this decrease, anchovy is now smaller in the Bay of Biscay than the one observed in the Gulf of Lion in the early 2000s (especially at age 1), which is not the case for sardine. Brosset et al. (2017) showed a similar decreasing trend over time in the Mediterranean Sea, with a global decrease in body condition and maximum size for most anchovy and sardine populations (Northern Spain, Gulf of Lion, Adriatic, Strait of Sicily). Only sardine in

the Alboran Sea (Eastern Spain) showed an increase in body condition over their last studied period (2011-2013). To our knowledge no study has shown temporal trends in size or body condition for anchovy or sardine in the English Channel. However, their abundance have increased towards the North and Baltic Seas since the mid-1990s, most likely because of favorable climatic conditions (Alheit et al., 2012; Petitgas et al., 2012).

Our two environmental models did not show the same temporal trends, with a slight increase of zooplankton biomass in POLCOMS-ERSEM and an increase of temperature combined with a decrease of zooplankton biomass in SEAPODYM. In the English Channel and the Gulf of Lion, POLCOMS-ERSEM predicted a slight increase of zooplankton, driven by an increase of phytoplankton. This contradicts previous observations in those regions, which showed a decline of Chlorophyll-a (Gohin et al., 2019; Feuilloley et al., 2020), questioning the reliability of the interannual variability of the zooplankton component simulated by POLCOMS-ERSEM. Ramirez-Romero et al. (2020) advised NPZD models should be used with caution in the Mediterranean Sea, as they might not be robust enough to reproduce the interannual variation of phytoplankton biomass, which affects the zooplankton biomass. The lack of significant trends or robustness in the environmental data, might be enhanced by the relative short (15 years) time series considered.

After having assessed the temporal trends in the environmental models and the capacity of our DEB model to successfully reproduce the regional variability observed in fish size and weight, we evaluated the impacts of modeled environment variability on small pelagic fish size over the past two decades. Despite differences in the temporal trends of the environmental models, they did not predict strong enough temporal trends to mechanistically explain the drastic size and weight loss observed for anchovy and sardine.

4.3. Are we missing temporal changes in our forcing variables ?

The impact of an increase in temperature on fish bioenergetics was explored through our first simulations (Fig. 5). According to the low change in temperature between the two studied periods, the model response on fish growth was negligible. The temperature trends and seasonal patterns were consistent among both environmental models as they use similar atmospheric and river forcing based on monthly climatologies (Holt and James, 2001; Lehodey et al., 2010, 2015; Titaud et al., 2021). Thus we were confident in their ability to reproduce realistic temporal trends in temperature. As mentioned above, there is much more uncertainty regarding the zooplankton predictions of such environmental models.

Moreover, a bottom-up control was the likely cause behind the temporal changes occurring in the Gulf of Lion (Saraux et al., 2019). The decline in body condition, observed since the mid-2000s (Van Beveren et al., 2014), was found to be related to food availability, specifically zooplankton concentrations (Brosset et al., 2015). This decline in body condition was also observed in the Bay of Biscay (Veron et al., 2020).

Therefore, we chose to focus on zooplankton rather than temperature to explain the decreasing trend in growth of the two small pelagic fish species. According to our different scenarios and assuming that zooplankton composition was similar between the English Channel and the Bay of Biscay, our study suggests that anchovy might not have undergone a significant decrease in size over the past twenty years in the English Channel. However, it might be the case for sardine, for which our scenario based simulations predicted an average decrease of 3.5% in size and 12.4% in weight since 2000. Growth curve simulations from the 2010-2015 period in the English Channel were similar to those observed in the Bay of Biscay ten years earlier.

4.4. Potential changes in food quantity

Based on our food quantity decrease scenario, we estimated that zooplankton biomass should have decreased by 17 to 31% in the Bay of Biscay to reproduce the decrease in size observed in small pelagic fish. In the Gulf of Lion, none of our model predictions were considered satisfactory, with individuals being too big (sardine) or dying before age two (anchovy and sardine). Those results might appear unrealistic as they would imply a fast decrease in zooplankton biomass within just fifteen years.

However, large shifts in zooplankton communities have been observed in the Northeast Atlantic shelf area over the last decades. Using Continuous Plankton Recorder (CPR) data, Schmidt et al. (2020) showed a 50% decrease of summer copepods abundance over the last 60 years (1958-2017) and Edwards et al. (2020) described a decline of 70% of total *Calanus* biomass in the North Sea between the 1960s and the 1990s. Those declines are higher than ours, although they occurred over multiple decades (60 and 30 years respectively), in comparison to our study, which only covered a 15 year period.

Over four regions from the Arctic waters to Norwegian Sea, Vollset et al. (2022) highlighted a sharp decline of 50% of spring zooplankton biomass between 2000 and 2010 which could have lead to a decrease in marine salmon growth over the same period. Focusing on one monitoring site on the west coast of Scotland, Wells et al. (2021) showed a decrease of 80% in annual coastal zooplankton abundance between 2011 and 2017. In the English Channel a strong decline of small copepods has been observed by Bedford et al. (2020).

Most studies have described a decrease in either copepod biomass or abundance during late spring or summer, rather than our estimation of a decrease of total zooplankton biomass over the whole

year. Strong biogeographical shifts in all copepod assemblages occurred in the North East Atlantic and European shelf seas since the mid 1980s. These shifts are associated with an range expansion of more than 10° towards northern latitudes by warm-water species, while the number of cold-water species decreased (Beaugrand et al., 2002; Beaugrand, 2003). Beaugrand (2003) advanced the hypothesis that an increase of sea surface temperature might have triggered a change in phytoplankton communities, which led to an increase in smaller phytoplankton species, like flagellates. The prominent role of abiotic factors, such as temperature, on the structure of copepods biodiversity has also been highlighted (Villarino et al., 2020). A change of environmental conditions towards warmer conditions would benefit to thermophilic and opportunistic species of copepods, whereas species representative of colder ecosystems are disadvantaged (Beaugrand et al., 2002; Valdés et al., 2007). Those shifts seem to have particularly impacted copepods rather than the wider zooplankton community which questions our estimates of high rates of zooplankton biomass decrease. However, as these studies point towards species shifts, the quality of the zooplankton could be affected. As this variable was not available in environmental models, the second scenario of our study explored this hypothesis.

4.5. Potential changes in food quality

In the food quality decrease scenario, the assimilable energy for small pelagics should have decreased by 3.8 to 5% in the Bay of Biscay and by 15.4 to 16.9% in the Gulf of Lion to reproduce observed changes in fish condition. While no time series of zooplankton quality data are available to evaluate those results, the decrease in small pelagic fish food quality can be studied through several observed proxies.

First, a general decrease in size has been documented for both marine phytoplankton (Sommer et al., 2017) and zooplankton (Daufresne et al., 2009; Horne et al., 2016; Pan et al., 2017) in a context of long term warming temperatures. Secondly, the nutritional quality of phytoplankton may have changed as a result of a change in functional groups (Schmidt et al., 2020; Lau et al., 2021). Schmidt et al. (2020) highlighted the increasing proportion of pico-phytoplankton and especially cyanobacteria across the Northeast Atlantic shelves. They are considered as poor primary producers in energy transfer through marine food web because of their lack of polyunsaturated fatty acids and sterols. Schmidt et al. (2020) suggested that this summer decrease in phytoplankton quality, combined with earlier spring blooms, might have an effect on the decrease of summer copepod abundance observed in the North East Atlantic.

Those findings support our results which suggested that the decrease in size and body condition of small pelagic fish might be linked to a decrease in quantity and/or quality of zooplankton. In the Gulf of Lion a shift in the diet of anchovy and sardine occurred around 2008 (Brosset et al., 2016a),

switching from a diet consisting of a high proportion of large copepods or cladocerans, to mostly small copepods. Moreover, there was at reduction in prey diversity observed in the diet of both

780   species (Brosset et al., 2016a), which could be linked to higher competition for food. Simultaneously, sprat biomass increased tenfold (Van Beveren et al., 2014) and isotopic niches of anchovy, sardine and sprat tended to overlap since 2010 (Brosset et al., 2016a), further suggesting an increase of trophic competition with a reduction of prey availability in the Gulf of Lion. Additionally, Bachiller et al. (2020) highlighted a latitudinal gradient in diet in the western

785   Mediterranean Sea, with smaller pelagic fish observed where the prey size was smaller, according to stomach contents.

Food size has been liked to consumption rate for particulate feeding fish, Lesser sandeel (*Ammodytes tobianus*) doubled its food consumption when feeding on larger copepods (van Deurs et al., 2014). Moreover, food size alone has proven to be a key factor for small pelagic fish size and

790   body condition (Queiros et al., 2019; Thoral et al., 2021). Queiros et al. (2019) suggested that, for identical global energy content, smaller preys might provide less energy to small pelagic fish because of the energy cost of switching from particulate- (larger preys) to filter- (smaller preys) feeding.

795   **5. Conclusion**

Our mechanistic modeling approach allowed to further test the bottom-up hypothesis, examining whether the observed decline in small pelagic fish size, is due to decrease in zooplankton *quantity* or *quality*. This study highlighted the ongoing challenges and barriers in the representation of zooplankton dynamics for ecosystem modeling, which remains crucial to simulate the upper trophic

800   levels dynamics. Our estimations were hard to verify, possibly due to the presence of other hidden phenomena which were not taken into account here, such as genetic adaptation, density-dependance or selective mortality. Some of these phenomena could also be linked to the observed disappearance of larger and older individuals in the Bay of Biscay and the Gulf of Lion, in addition to the overall decrease in length- and weight-at-age discussed in the present study. To include these mechanisms,

805   future studies will need to couple the individual to the population modeling scale, up to the ecosystem level. The drastic decrease in body size of small pelagic fish might be among the first examples of the upcoming threats to marine socio-ecosystems, particularly given their role in energy transfer towards higher trophic levels and their socio-economic values.

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6. APPENDICES
6.1. APPENDIX A

Table A.1 - State variables of the DEB model

Fluxes	Formula
Assimilation	$\dot{p}_A = \dot{p}_{Am} f L^2 cor_L$
Catabolic utilisation	$\dot{p}_C = \left(\frac{E}{L^3}\right)\frac{\dot{\nu}[EG]L^2 + \dot{p}_M}{[EG] + \kappa\frac{E}{L^3}}$
Somatic maintenance	$\dot{p}_M = [\dot{p}_M]L^3$
Growth	$\dot{p}_G = max(\kappa\dot{p}_C - \dot{p}_M, 0)$
Maturity maintenance	$\dot{p}_j = \dot{k}_j H$
Reproduction/development	$\dot{p}_R = (1 - \kappa)\dot{p}_C - \dot{p}_J$
Reproduction buffer mobilisation	$\dot{p}_{R2} = min(E_{batch}, R)$
Gamete allocation	$\dot{p}_{Gam} = max(0, K_R(\dot{p}_{R2} - \dot{p}_{M2}))$
Energy maintenance	$\dot{p}_{M2} = min(-\dot{p}_G, R)$
Atresia	$\dot{p}_{M3} = min(K_R G, -\dot{p}_{Gam} - \dot{p}_{M2})$

Table A.2 - Energy fluxes of the DEB model

State variables/buffers	Formula
Reserve	$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C$
Volumetric length	$\frac{dL}{dt} = \frac{\dot{p}_G}{3[EG]L^2}$
Maturity level	$\frac{dE_H}{dt} = \dot{p}_R$
Reproduction	$\frac{dE_R}{dt} = \dot{p}_R - \dot{p}_{R2} - \dot{p}_{M2}$
Gametes	$if\ E_{Gam} >= 2E_{batch}, \frac{dE_{Gam}}{dt} = \dot{p}_{Gam} - \dot{p}_{M3} - E_{batch}$
	$if\ E_{Gam} < 2E_{batch}, \frac{dE_{Gam}}{dt} = \dot{p}_{Gam} - \dot{p}_{M3}$

Table A.3 - Parameters of the DEB model ; * if optimized according to forcing variables (See Table
1115   3; adapted from Gatti et al., 2017)

| Parameters	Symbol	Units	Anchovy	Sardine
Primary DEB parameters				
Maximum assimilation rate	$\dot{p}_{Am}$	$J.cm^{-2}.d^{-1}$	884	987
Assimilation efficiency	κ_X	-	0.8	0.8
Volume specific cost for structure	$[EG]$	$J.cm^{-3}$	3725	2803
Volume specific maintenance cost	$[\dot{p}_M]$	$J.cm^{-3}.d^{-1}$	158	103
Energy conductance	$\dot{\nu}$	$cm.d^{-1}$	0.49	0.42
Fraction of energy allocated to growth	κ	-	0.71	0.53
Maturity maintenance rate coefficient	$\dot{k}_j = \frac{[\dot{p}_M]}{[EG]}$	d^{-1}		
Maturity threshold at birth	H_b	J	0.09	0.09
Maturity threshold at puberty	H_p	J	12026	49912
Half saturation coefficient for food	X_K	$mgC.m^{-3}$	*	*
Fraction of energy fixed into eggs	$K_R = \frac{\rho_G}{\rho_R}$	-		
Auxiliary and compound DEB parameters				
Reference temperature	T_{ref}	K	293	293
Arrhenius temperature	T_A	K	7722	12989
Shape coefficient (adult)	δ	-	0.2	0.2
Size at first feeding	l_b	mm	4.0	4.0
Size at metamorphosis	l_j	cm	4.0	4.0
Energy in reserve at first feeding	E_b	J	0.11	0.11
Energy of eggs	E_0	$J.eggs^{-1}$	0.66	1.11
Relative batch fecundity	R_{bf}	$eggs.g^{-1}$	478.9	400
Spawning frequency	$\dot{S}_f$	d^{-1}	0.25	0.084
Shape coefficient (early larva)	δ_b	-	0.08	0.07
Acceleration factor (larvae)	f_{acc}	-	0.13	0.18
Density of structure	d_V	$g.cm^{-3}$	0.11	0.11
Energy density of structure	ρ_V	$J.g^{-1}$	20098	20098
Energy density of reserve	ρ_E	$J.g^{-1}$	31332	31332
Energy density of reproduction reserve	ρ_R	$J.g^{-1}$	24937	24937
Energy density of gametes	ρ_G	$J.g^{-1}$	23880	23880
Maximum storage density	$[E_m] = \frac{\dot{p}_{Am}}{\dot{\nu}}$	$J.cm^{-3}$		

6.2. APPENDIX B
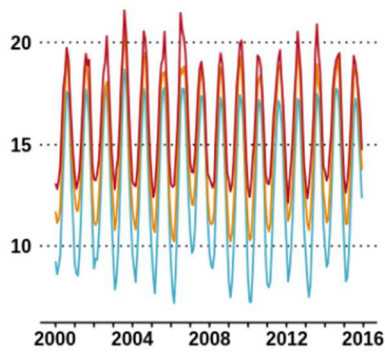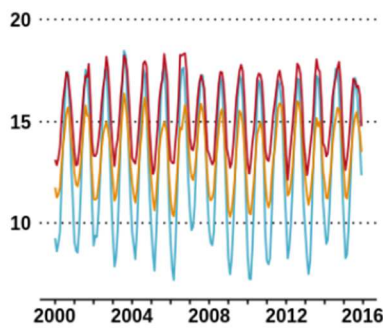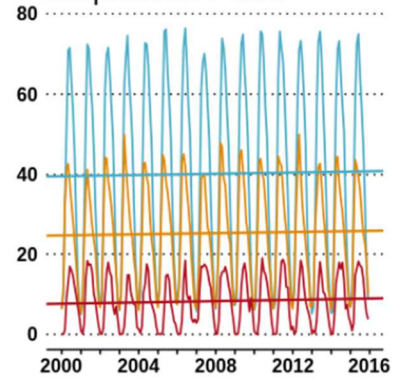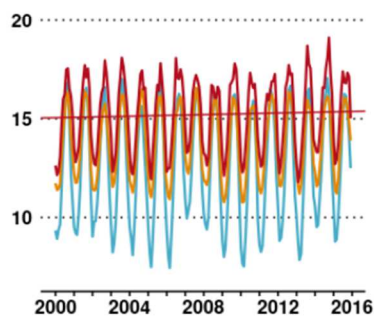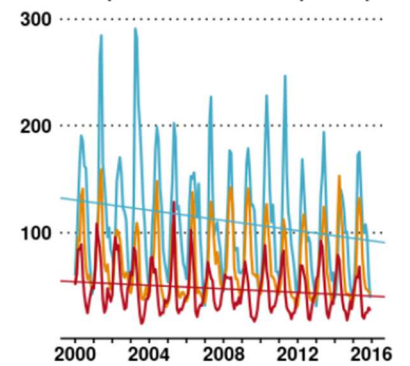
Figure B.1 – Time series of temperature (°C) and zooplankton (mgC.m^{-3}) for each environmental model (POLCOMS-ERSEM in the top panel and SEAPODYM in the bottom panel) per region (blue - English Channel, orange - Bay of Biscay, red - Gulf of Lion). Significant (pval < 0.05) linear trends were added to the plot.
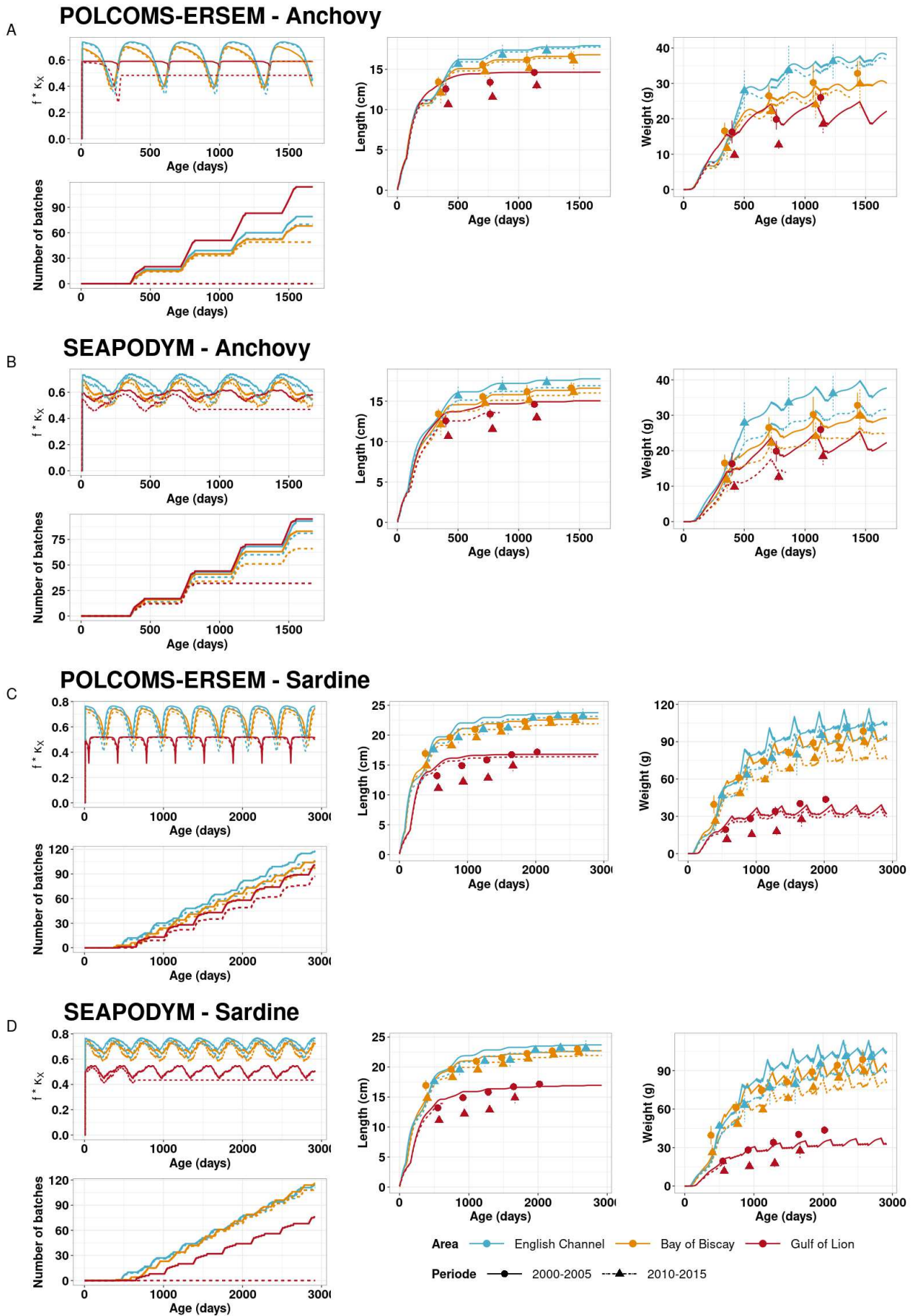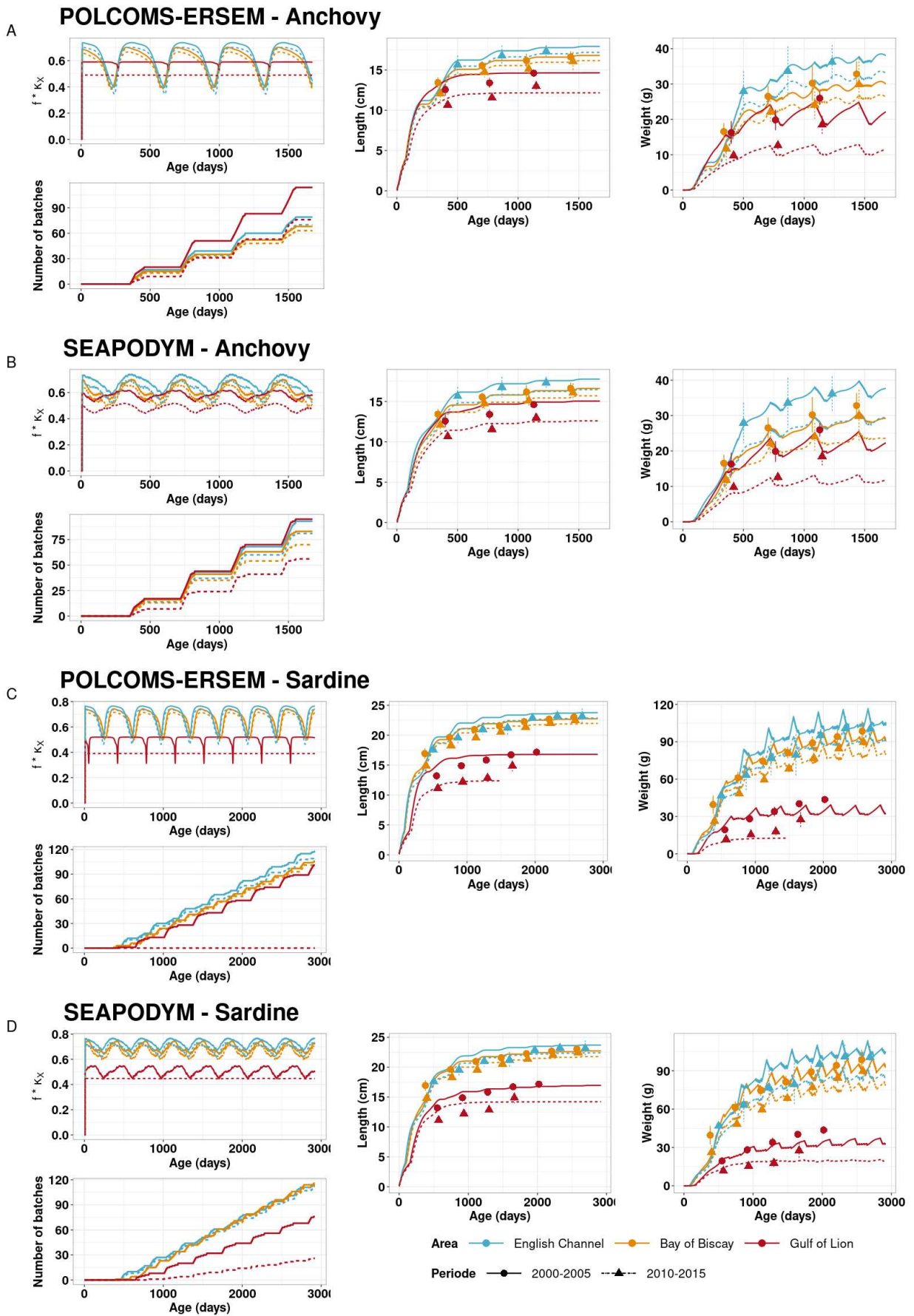
Figure C.1 - SC1 quantity loss - Growth model for anchovy and sardine, each forced with
POLCOMS-ERSEM or SEAPODYM, with regional climatologies averaged over 2000-2005 (solid

line for predictions and dots for observations) and 2010-2015 (dotted line for predictions and triangles for observations). Each panel shows the functional response for food multiplied by the assimilation efficiency, the number of batches spawned, length and weight as functions of age. The 2000-2005 prediction is the same as in Fig. 5, *i.e.* without any forcing scenario.

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POLCOMS-ERSEM - Anchovy

SEAPODYM - Anchovy

POLCOMS-ERSEM - Sardine

SEAPODYM - Sardine

Figure C.2 - SC2 quality loss - Growth model for anchovy and sardine, each forced with POLCOMS-ERSEM or SEAPODYM, with regional climatologies averaged over 2000-2005 (solid

1135   line for predictions and dots for observations) and 2010-2015 (dotted line for predictions and triangles for observations). Each panel shows the functional response for food multiplied by the assimilation efficiency, the number of batches spawned, length and weight as functions of age. The 2000-2005 prediction is the same as in Fig. 5, *i.e.* without any forcing scenario.
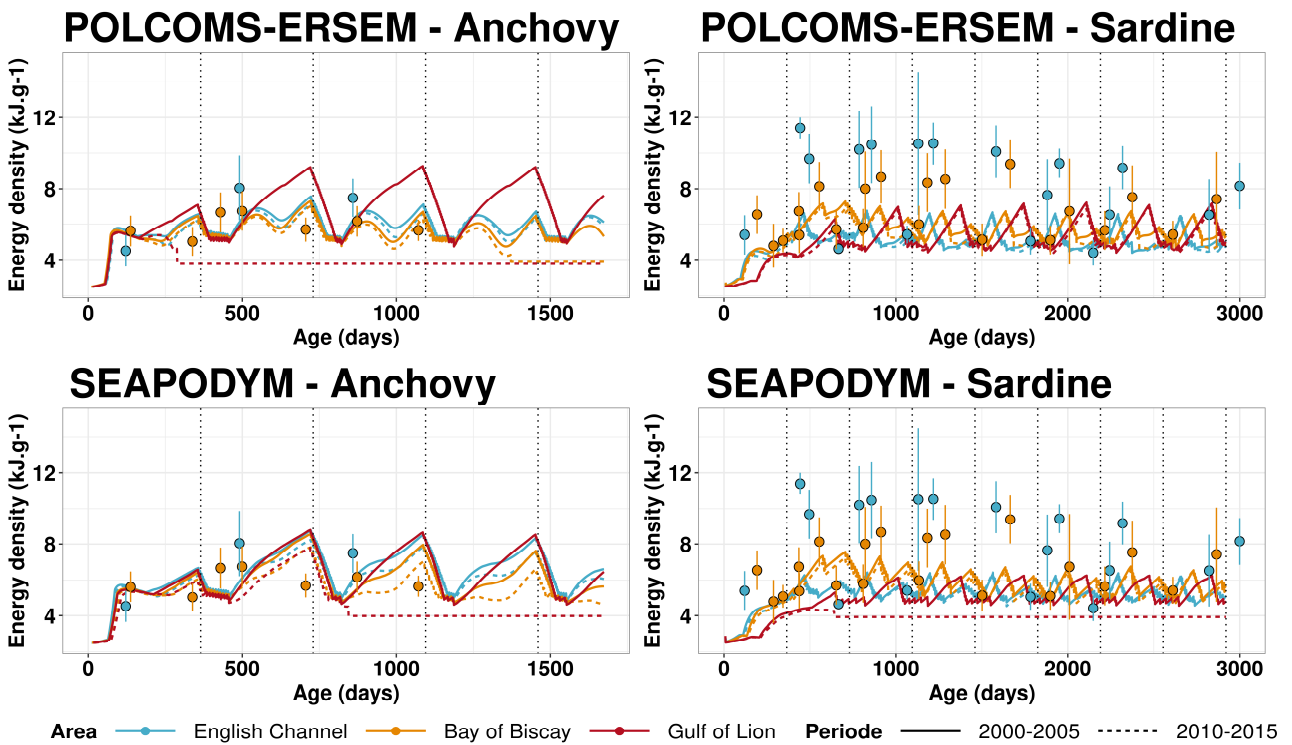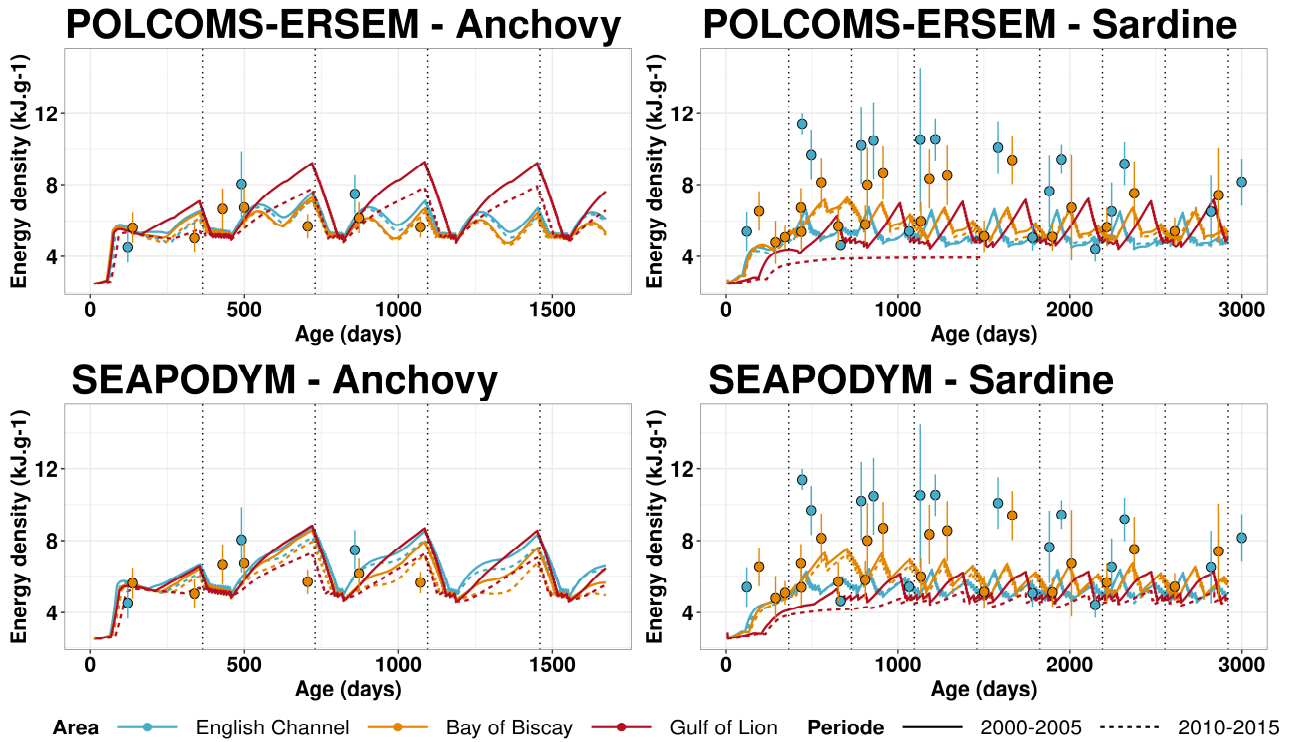
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6.4. APPENDIX D
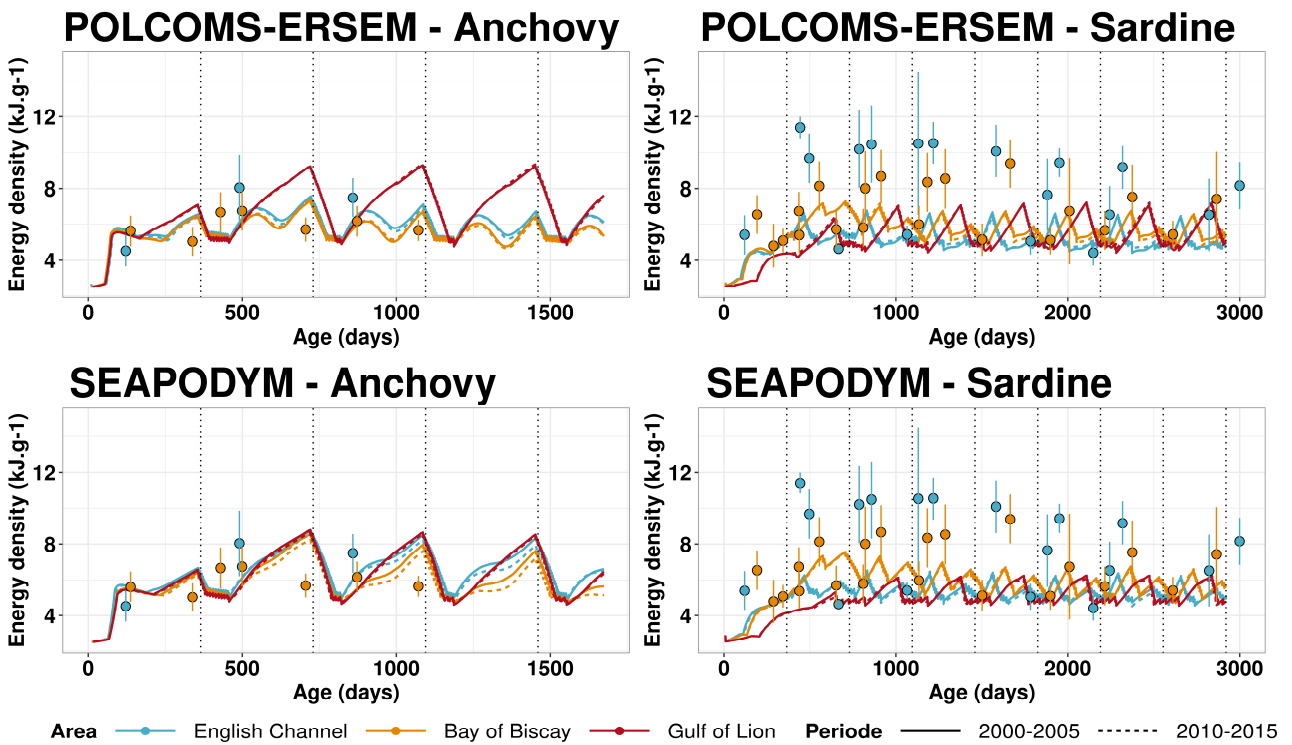
Figure D.1 - Energy density model for anchovy and sardine, each forced with POLCOMS-ERSEM or SEAPODYM, with regional climatologies averaged over 2000-2005 (solid line for predictions) and 2010-2015 (dotted line for predictions). Seasonal mean observations are represented by dots (data available for 2014-2015-2016).

Figure D.2 - SC1 quantity loss - Energy density model for anchovy and sardine, each forced with POLCOMS-ERSEM or SEAPODYM, with regional climatologies averaged over 2000-2005 (solid

line for predictions) and 2010-2015 (dotted line for predictions). The 2000-2005 prediction is the same as in Fig. D1, *i.e.* without any forcing scenario. Seasonal mean observations are represented by dots (data available for 2014-2015-2016).

Figure D.3 - SC2 quality loss - Energy density model for anchovy and sardine, each forced with POLCOMS-ERSEM or SEAPODYM, with regional climatologies averaged over 2000-2005 (solid line for predictions) and 2010-2015 (dotted line for predictions). The 2000-2005 prediction is the same as in Fig. D1, *i.e.* without any forcing scenario. Seasonal mean observations are represented by dots (data available for 2014-2015-2016).