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Influence des caractéristiques des modèles de Bas Niveaux Trophiques sur les dynamiques des poissons simulées par le modèle OSMOSE appliqué au Golfe de Gascogne

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22/08/2024

Lucia DOTTIN

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INTRODUCTION

Over the last three decades, regional and global marine ecosystem models have been widely developed, ranging from ocean geochemistry to higher trophic levels, in order to follow impacts of fishing effort (Y. Shin et Cury 2001). In this context, Models aim to provide as accurate as possible a representation of marine ecosystems, to better understand their evolution and illustrate energy fluxes between all trophic levels (Fulton, Smith, et Johnson 2003). However, the spatial scale considered is an important factor in performance, as is the choice of variable representations, both of which affect the quality of outputs (Payne et al. 2016). In the context of climate change, models aim to explore the future of marine ecosystems and their ecological dynamics. Projections of anthropogenic and climate impacts serve as a basis for assessing the sustainability of fisheries and ecosystems. Models can be ecosystemic, like Ecopath or Atlantis, which model all trophic levels, or coupled, like the OSMOSE model. Coupling models allows us to understand the spatio-temporal dynamics between lower and higher trophic levels and their evolution by modelling distinct ecosystem compartments. Ecosystem model studies often aim to explore the dynamics of the entire food web, but due to the high cost of model development, uncertainties in results are rarely assessed. Interactions between environmental factors, phytoplankton, and zooplankton dynamics are a significant source of uncertainty in models that can affect the production available for the rest of the marine food web (Rohr et al. 2023).

Zooplankton plays a key role in the marine food web, accounting for approximately 40% of the world's marine biomass (Heneghan et al. 2023). This biomass provides links between lower trophic levels (LTL), represented by plankton (both auto- and heterotrophic), and higher trophic levels (HTL), such as small pelagic fish (SPF). However, the processes that control the dynamics of plankton populations (both phytoplankton and zooplankton) remain partially unexplained or misunderstood (Zhao et al. 2008). In the Bay of Biscay, the influence of specific structures and mixing water phenomena on zooplankton community dynamics remains unknown (Albaina and Irigoien 2004). Furthermore, zooplankton is often oversimplified in ecosystem models, with only one or two functional groups considered. In biogeochemical models, zooplankton is often treated as the "closure term," represented by a simple equation (Daewel et al. 2014). Models do not explicitly consider interactions within zooplankton groups such as predation and cannibalism. Within such models, only 1% of the zooplankton production is considered to be transferred to higher trophic level (Mitra 2009) . All of this has major implications for the accuracy of climate change projections (Heneghan et al. 2023) and the real transfer values.

Zooplankton is regularly structured in size, which plays a primary role in ecosystems. Particularly, the diameter of particles is involved in most of ecological traits. Therefore, most marine organisms are opportunistic feeders and size partially determined predators diet (Stemmann et Boss 2012). Variability in zooplankton dynamics can affect HTL, especially variability in size, a crucial factor in energy flow (Vandromme et al. 2014).

Several studies recently demonstrated that zooplankton biomass dynamics have been changing in the Bay of Biscay for the past 15 years, which has affected small pelagic fish. The observed decline of small pelagic fish size in the Bay of Biscay is partly due to changes in environmental conditions (Menu et al. 2023). Grandremy (2023) observed changes in the composition of

zooplankton communities, probably resulting from the impact of climate change, particularly the rise in temperature. This study revealed that coastal areas host high zooplankton abundance and a prevalence of small individuals. Conversely, offshore areas exhibit low abundance but with large individuals (Grandremy 2023). Mesozooplankton is the major prey for small pelagic fish. It is mostly represented by copepods. Copepods also eat on diverse source of plankton, which make them to be important driver for the whole food web (Poulet, Laabir, et Chaudron 1996). There is also Chaetognaths, which are strictly carnivorous and feed on copepods. The gender calanoid is the main present in community. Because of the difficulty of sampling zooplankton, its study is relatively recent. It would appear that zooplankton is a community that is difficult to characterise because its reproduction and predation strategies are complex (Turner 2004).

The OSMOSE (Object-oriented Simulator of Marine ecOSystEms) model is currently in development in the Bay of Biscay and the aim is to evaluate the ecosystem 'interactions, from primary producer to top predators with both ecological and bioenergetics approach. In this context, this internship aims to explore the influence of low trophic levels models which could be coupled with OSMOSE to reproduce the past ecosystem and make projections according to diverse climate scenarios.

More precisely, the aim of this study is to investigate how the various biogeochemical models for the Bay of Biscay represent the spatio-temporal dynamics of zooplankton and to estimate the impact of LTL zooplankton characteristics on the structure of fish communities modelled using the HTL model OSMOSE, coupled with different LTL models.

To achieve these objectives, we will first explore various biogeochemical models that simulate the Bay of Biscay and their dynamic representation of the spatio-temporal dynamics of zooplankton in this region. Specifically, we will focus on the spatio-temporal dynamics of mesozooplankton, which is the primary prey for fish. The characteristics of the zooplankton community are modelled differently across the available LTL models. All LTL models used are based on size compartments representing functional groups, with varying degrees of precision. We will also examine the outputs under different climate scenarios for projection models.

The second part of this work involves running a version of the OSMOSE model (without bioenergetics) in the Bay of Biscay by varying parameters specific to the LTL models provided as input. We will also evaluate the ability of the zooplankton variables to match historical data. According to the available model data, the outputs will be observed in two separate time blocks: from 2006 to 2015 for historical mean values and from 2040 to 2049 for future projections.

MATERIAL AND METHODS

1. Study Area

The Bay of Biscay is a large gulf that extends between the northern coast of Spain and the western coast of France. The central part of the area is an abyssal plain that reaches a depth of 4,800 meters. This plain is separated from the continental shelf by a sharp shelf break. The continental shelf is very wide along the French coast, whereas it is quite narrow along the Spanish coast (figure 1). Hydrological conditions in this area are influenced by various abiotic processes such as big river runoffs (from Loire and Gironde for the principals), coastal upwelling, and seasonal currents (Lazure et al. 2009). These processes have a significant influence on the spatio-temporal dynamics of phytoplankton. During spring, a first plankton bloom can be observed, dominated by diatoms, and a late second bloom occurring from summer to autumn (Maguer et al. 2009). Mesozooplankton is dominated by copepods, which also show seasonal patterns. Large copepods are more dominant in spring than in summer (Benedetti et al. 2019).

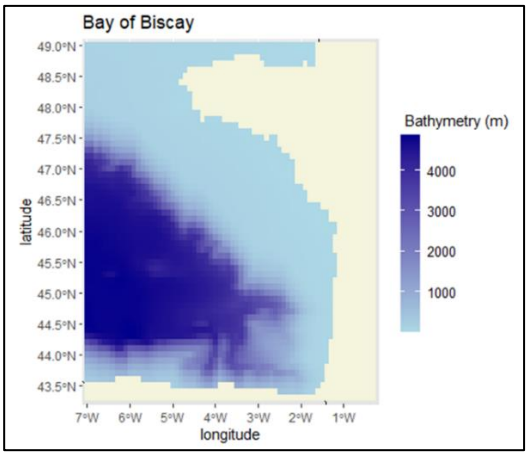


Figure 1: Bathymetry of the Bay of Biscay from the biogeochemical model POLCOMS ERSEM

For the rest of this study, the model outputs are analysed only for the Bay of Biscay, defined using the following coordinates: between 43° to 48° North latitude and between -8° to 0° East longitude.

2. The High Trophic Level model OSMOSE

OSMOSE is a spatial multispecies and individual-based model which simulates exploited fish species. The model is built on opportunistic predation based on size suitability and spatial co-occurrence between predator and its prey. Simulations run two dimensions migrations of schools, which are constituted from several individuals of the same species. It's an end-to-end model simulating the entire fish life cycle through the processes of growth, reproduction, migration and mortality from starvation, fishing and predation (Y. Shin et Cury 2001).

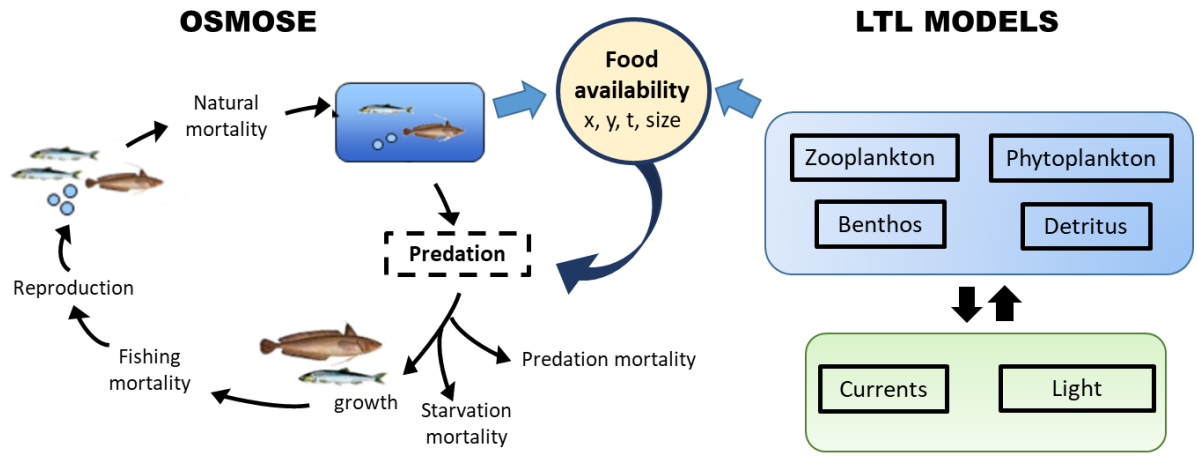


Figure 2: OSMOSE and LTL models coupling scheme (adapted from osmose-model.org). x, y are spatial dimensions, t is time

The coupling between OSMOSE and LTL models is effected with predation. In fact, the transfer of energy between models takes place through predation between the different trophic levels (Travers-Trolet, Shin, et Field 2014). In OSMOSE, each species have a specific size ratio and coefficients of prey accessibility to describe the predation mechanism. This coefficient of accessibility allow to represent the vertical dimension in this two dimension model. The model gives outputs twice a month, giving a good representation of the seasonal variations of different species. All these characteristics allowed permanent information exchanges with the LTL model input. This predation characteristic allows information exchange with the LTL model input.

The model version used here described 18 Bay of Biscay species (Table 1) and is non-calibrate. Phytoplankton, zooplankton biomasses and temperature, salinity, oxygen values are provided by LTL models. For first years, the models give eggs in the environment from each species. Then, the LTL model parameter afford preys biomass for fish. The horizontal resolution is the whole Bay of Biscay ([-8° – 0°] degrees East and [43° - 48°] degrees North).

Table 1: Bay of Biscay species modelled in OSMOSE

Species	Scientific name	Group
Sardine	*Sardina pilchardus*	Pelagic
Anchovy	*Engraulis encrasicolus*	Pelagic
Sprat	*Sprattus sprattus*	Pelagic
Blue whiting	*Micromesistius poutassou*	Demersal
Whiting	*Merlangius merlangus*	Demersal
Mackerel	*Scomber scombrus*	Pelagic
Horse mackerel	*Trachurus trachurus*	Pelagic
Boarfish	*Capros aper*	Demersal
Pouting	*Trisopterus luscus*	Demersal
Sole	*Solea solea*	Benthic
Sea bass	*Dicentrarchus labrax*	Demersal
Hake	*Merluccius merluccius*	Demersal
Anglerfish	*Lophius budegassa*	Benthic
Norway lobster	*Nephrops norvegicus*	Benthic
Cuttlefish	*Sepia officinalis*	Benthic
Squid	*Lolligo forbessi*	Demersal
Lesser spotted dogfish	*Scyliorhinus canicula*	Benthic
Albacore tuna	*Thunnus alalunga*	Pelagic

3. Low Trophic Level models

3.1 Models characteristics

Different biogeochemical models exist and based on their characteristics and forcing, they can simulate different zooplankton spatio-temporal dynamics. The following models come from different modelling teams and their runs were available for the Bay of Biscay:

- POLCOMS ERSEM (from Plymouth Marine Laboratory, United Kingdom, also available from CMEMS[1] and CDS[2])
- NEMO ERSEM (from Plymouth Marine Laboratory, United Kingdom, also available from CMEMS and CDS)
- NEMO PISCES (from Mercator Ocean International, IBI reanalysis, France, also available from CMEMS)
- NEMO MEDUSA (from National Oceanography Center, United Kingdom, made available by AZTI Centro de Investigacion Marina y Alimentaria, Spain)
- SEAPODYM (from Mercator Ocean International, France, also available from CDS)

All models used, except SEAPODYM, are coupled models consisting of two models: one about the physical ocean circulation and the other about biogeochemistry, providing primary and secondary productions.

For all models except NEMO MEDUSA, hindcast runs were available, which are simulations of the past whereas forecast runs were only available for POLCOMS ERSEM and NEMO MEDUSA. Forecast runs were provided under Representative Concentration Pathways (rcp) 4.5 which assumes that emissions will stabilize and decrease before 2100 and under rcp 8.5 scenario which assumes that emissions will increase until 2100. For POLCOMS ERSEM, NEMO ERSEM and NEMO PISCES, outputs were also available based on reanalyse runs. Reanalysis runs consist of modelling the environment while correcting it with available past data. The NEMO ERSEM version used here is reanalysis with in-situ Sea Surface Temperature (SST). For these three models, the reanalysed versions are used. SEAPODYM is used in hindcast.

3.1.1 POLCOMS and NEMO

POLCOMS (Proudman Oceanographic Laboratory Coastal Ocean Modelling System)(Holt et James 2001) and NEMO (Nucleus for European Modelling of the Ocean) (Madec 2008) are both physical ocean circulation models.

POLCOMS was originally developed for the Northeast Atlantic Ocean and it is able to represent deep ocean and continental shelf interactions thanks to specific equations of water movement in a various topography environment like the Bay of Biscay. It's a globally recognised and validated model that works well in the Bay of Biscay (O'Dea et al. 2012). It is built on a regular grid.

In contrast, the NEMO model was originally developed to model the open ocean. Since the model has been developed, it has been possible to model the coastline more precisely. NEMO is now a state-of-the-art modelling framework of the ocean and includes sea-ice dynamics (Edwards, Barciela, et Butenschön 2012). It is built on a curvilinear orthogonal grid.

[1] Copernicus Marine Environment Monitoring Service
[2] Copernicus Climate Data Store

Both models have also a third vertical dimension which is not regular for each model but can follows variations in bathymetry. This parameter enables good vertical resolution to be maintained, particularly on the coast.

3.1.2 ERSEM, PISCES, MEDUSA and coupling systems

ERSEM (European Regional Seas Ecosystem Model) is a coupled pelagic-benthic ecosystem model developed using couplers with hydrodynamic models. It's a regional model built for northwest European shelf and the Mediterranean Sea. It is also one of the most detailed marine biogeochemical models fully describing carbon and nutrients (nitrogen, phosphate, silica) dynamics (Artioli et al. 2012). POLCOMS is coupled with ERSEM using a bespoke coupler, whereas NEMO-ERSEM uses a standard coupler, the Framework for Aquatic Biogeochemical Model coupler.

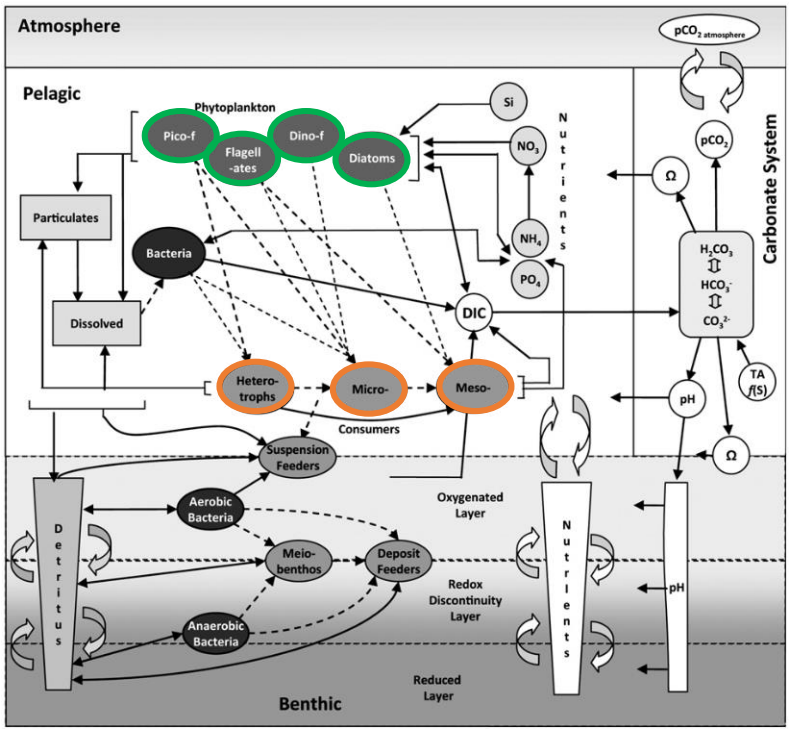


Figure 3 : ERSEM functional groups and interactions between physical and biological variables (from Artioli et al., 2012)

ERSEM describes three size-based categories of zooplankton: heterotrophic nanoflagellates, micro-zooplankton and meso-zooplankto The predatory capacity of zooplankton compartments varies according to their size, enabling them to prey on different types of prey (Butenschön et al. 2016). Zooplankton predates phytoplankton and benthos is connected by interaction between microzooplankton and suspension feeders' species. Additionally, three benthic communities and three bacteria groups are included in the model interactions, as illustrated in Figure 3. The currency used to track functional groups biomass is carbon concentration.

PISCES-v2 (Pelagic Interaction Scheme for Carbon and Ecosystem Studies v2) is also a biogeochemical model that describes biological productivity, carbon cycle and nutrients (phosphate, nitrate and ammonium, silicate and iron). In contrast to ERSEM, PISCES can be configured for both regional and global resolutions (Aumont et al. 2015). Furthermore, the model only considers two zooplankton size categories (meso- and microzooplankton) and two phytoplankton communities, namely diatoms and nano-phytoplankton. The benthos community and bacteria are not explicitly modelled (see Figure 4).

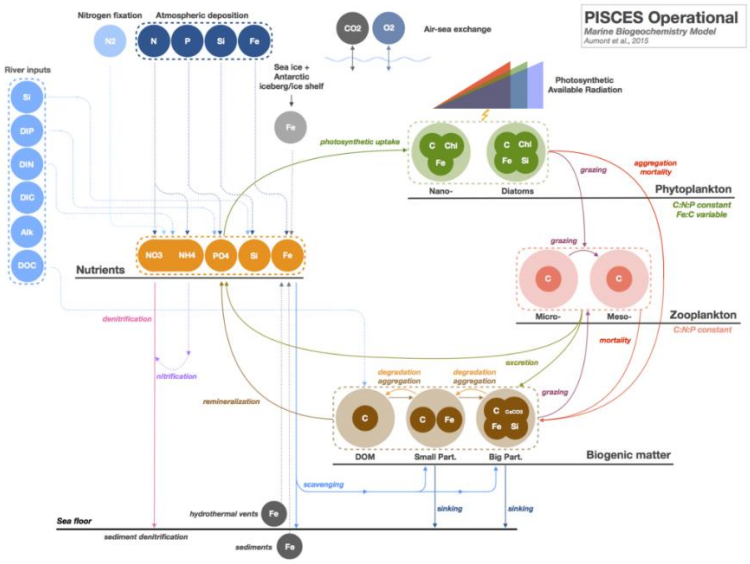


Figure 4 : Schematic diagram of NEMO PISCES (from(« Model Description – The PISCES Community », s. d.)

MEDUSA (Model of Ecosystem Dynamics nutrient Utilisation, Sequestration and Acidification) is consider as an "intermediate complexity" plankton ecosystem model (Yool, Popova, et Anderson 2013). Like the other models, nitrogen and carbon cycle are followed but as contrary, variables in NEMO MEDUSA are expressed according to nitrogen concentration and assumed fixed stoichiometric relationships. MEDUSA modelled 2 Zooplankton communities and 2 phytoplankton like PISCES between diatoms and non-diatoms (figure 5). Similarly, the benthic community is not explicitly modelled but is simply described as dissolved inorganic matter.

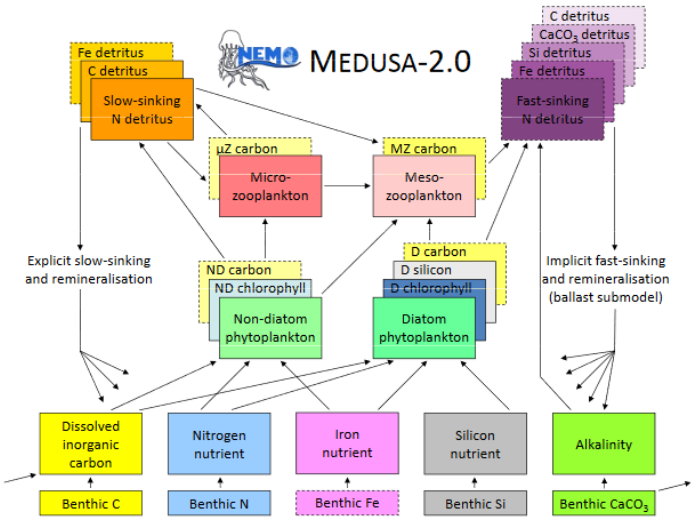


Figure 5 : Schematic diagram of MEDUSA – 2.0 interactions (Yool, Popova, et Anderson 2013)

3.1.3 SEAPODYM

The SEAPODYM (Spatial Ecosystem And Population Dynamics Model) Low and Mid-Trophic Levels 3.0 version model (Lehodey et al. 2010) can be global or regional. Currents control the transport of organisms, temperature drives the time of development and primary productivity is the biomass source, fuelling zooplankton and different micronekton functional groups. In the model, micronekton is defined as species making diel vertical migration between deep layers and the surface. It's modelled in 6 independent functional groups (2 – 20cm), expressed in wet weight and migrating between the different

layers. Zooplankton variable is expressed in gC/m² and is also only present in the first epipelagic layer (without migration) while micronekton migrates during day and night (European Union-Copernicus Marine Service 2021).This version provides hindcast daily simulations without data assimilation.

3.2 Plankton functional groups

All these models present diverse characteristics, like the number of phytoplankton and zooplankton functional groups, the type of available simulation scenarios, vertical, horizontal and spatio-temporal resolution. POLCOMS-ERSEM and NEMO-ERSEM both used mgC/m^3 as units for most of biological variables whereas NEMO PISCES used $mmolC/m^3$ and NEMO MEDUSA used $mmolN/m^3$ (Table 2).

Furthermore, those models describe zooplankton communities according to their size, which are basically classified as:

- Mesozooplankton ϵ [0,2 – 2mm]
- Microzooplankton ϵ [20 - 200 µm]
- Nanozooplankton < 20 µm

There is also 4 phytoplankton groups by size:

- Picophytoplankton < 2µm
- Nanophytoplankton ϵ [2 - 20µm]
- Microphytoplankton ϵ [2µm - 20 µm]
- Diatoms ϵ [20 µm – 200 µm]

*Table 2: Characteristics of available models runs outputs (*Z = zooplankton groups, P = phytoplankton groups)*

Models	Type of data	Period available	Horizontal resolution	Vertical resolution	Temporal resolution	Plankton groups*	Plankton unit
POLCOMS ERSEM	Projections rcp 4.5	2006 - 2099	1/10°	40	1/month	3Z x 4P	mgC/m^3
POLCOMS ERSEM	Projections rcp 8.5	2006 - 2099	1/10°	40	1/month	3Z x 4P	mgC/m^3
POLCOMS ERSEM	Reanalysis	2000 - 2015	1/10°	40	1/month	3Z x 4P	mgC/m^3
NEMO ERSEM	Reanalysis	2000 - 2023	1/9° x 1/15°	51	1/month	3Z x 4P	mgC/m^3
NEMO PISCES	Reanalysis	2000 - 2022	1/12° x 1/16°	75	1/month	2Z x 2P	$mmolC/m^3$
NEMO MEDUSA	Projections rcp 8.5	2000 - 2099	1/4° x 1/6°	75	6/month	2Z x 2P	$mmolN/m^3$
SEAPODYM	Hindcast	2000 - 2022	1/12°	3	1/day	1Z	gC/m^2

The different characteristics of the available LTL models runs make their comparative studies difficult, which is why a data homogenization step is necessary, also to fit OSMOSE resolutions.

4. Data transformation for homogenisation

Among all the variables available in each models, zooplankton, phytoplankton and benthos communities were retained, as well as environmental variables such as temperature and salinity.

Vertical and horizontal resolutions differ between LTL models. Regarding temporal scale, available LTL outputs vary between daily to monthly resolution (Table 2). For NEMO MEDUSA and SEAPODYM which provide several outputs per month, a monthly mean was calculated.

For PISCES and MEDUSA, carbon and nitrogen moles were converted into carbon biomass according to Equation 1 and Equation 2:

$$\mathbf{X\ mmol\ C\ x\ M_{Carbon} = Y\ mg\ C} \qquad \textit{(Equation 1)}$$

$$\mathbf{X\ mmol\ N\ x\ R_{C:N}\ x\ M_{Carbon} = Y\ mg\ C} \qquad \textit{(Equation 2)}$$

With X mmol of C or N provided by LTL, Y the resulting conversion of mmol in mgC, M_{Carbon} = 12.01 mg/mmol and $R_{C:N}$ = 4.5 the ratio for zooplankton (Walve 1999) and $R_{C:N}$ = 6.6 for phytoplankton which is the Redfield ratio (Redfield, Ketchum, et Richards 1963)

4.1 Data Vertical Integration

In order to compare homogeneous biomasses, whatever the original model, and because OSMOSE requires two dimension values for variables, the analyses will relate to a weighted density of biomass expressed in mg C/m².

All LTL models are designed in 3 dimensions (longitude, latitude and depth). Furthermore, LTL models have different vertical resolution (from 3 to 75 layers) with varying methods (Figure 6):

- POLCOMS ERSEM models comprise 40 vertical layers with each layer having a distinct height. The height of each layer is dependent on the bathymetry of the respective location. The NEMO ERSEM model is based on the same system but comprises 51 vertical layers.
- NEMO PISCES and NEMO MEDUSA have a higher vertical resolution than ERSEM, with 75 layers, which are of different heights but identical in all horizontal cells. Some layers may not contain a value, depending on depths.
- SEAPODYM is built with 3 vertical layers: epipelagic, upper and lower mesopelagic layers. They are defined according to the euphotic zone depth

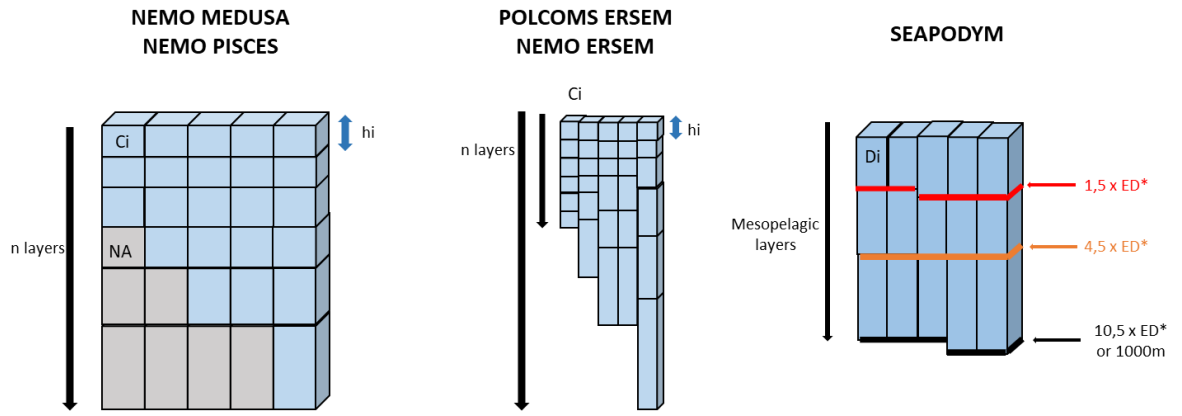


*Figure 6: Schematic representation of the vertical resolution according to the different LTL models used. Here with six vertical layers instead of n = 75, 51 or 40 depending on models. Blue cells represent cells with associated model value. *ED = Euphotic depth Zone, hi = height of the cell i, Ci concentration in the cell i*

To reduce the vertical dimensions by integration, we only take into account layers less than or equal to 200m deep. For the limit layer containing the 200m, the height h_i is equal to the difference between 200m and the top of the limit layer. In SEAPODYM, zooplankton biomass is already expressed in density. For biological variables, expressed in concentration, we calculate the weighted density for each vertical layers, based on its specific height cell (Equation 3):

$$\mathbf{D = \sum^{i} h_i\ x\ C_i} \qquad \textit{(Equation 3)}$$

with D the integrated density, $h_{i\ the}$ height of the vertical layer i and C_i the concentration in the cell.

For abiotic variables like temperature and salinity, we defined the Sea Surface Temperature and salinity (SST and SSS respectively) extracted from the first vertical layer, the Sea Bottom Temperature and salinity (SBT and SBS respectively) extracted from the last vertical layer and a mean temperature and salinity calculated by a weighted mean based on the height of each layer.

4.2 Spatial regridding

For horizontal resolution, we homogenise the different resolutions by regridding all model data onto a single grid with the same resolution for all models by interpolation. We chose the resolution of the OSMOSE model, which is 1/4° in longitude and 1/6° in latitude, to compare models. For all LTL models, the regridding consists in decreasing the precision scale. For this, the xesmf on Python library is used (Jiawei Zhuang et al. 2023), with a conservative interpolation method ("**`conservative_normed`**"): each origin cell that will be part of the final cell is taken into account according to its overlapping surface with the final cell (Equation 4, Figure 7).

$$\mathbf{V_{target} = (\sum^{i} \omega_i \, x \, V_{source}) / N} \qquad \textit{(Equation 4)}$$

With V_{target} the interpolated value of the target cell, ω_i the weight of source cell overlapping the target cell, V_{source} the value of the source cell i and N the normalized value (Equation 5).

$$\mathbf{N = \sum^{i} \omega_i} \qquad \textit{(Equation 5)}$$

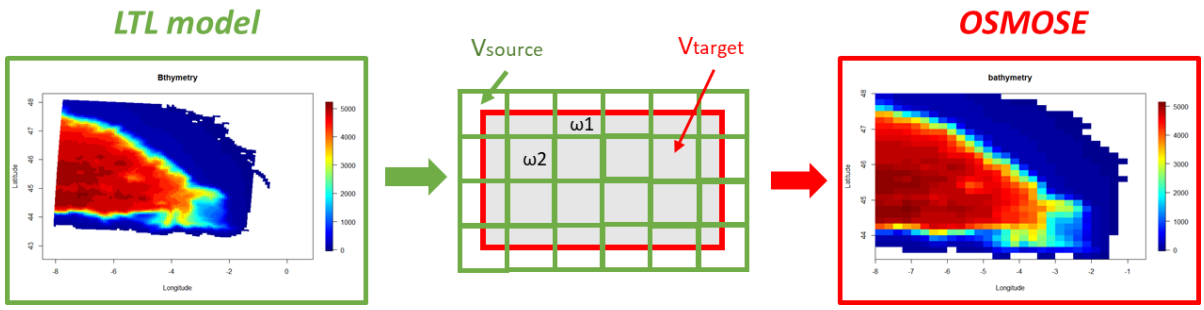


Figure 7: Scheme of the "conservative_normed" interpolation from LTL NEMO PISCES to OSMOSE horizontal resolution. Here ω2 = 1 because the entire source cell contributes to the target cell and ω1 = 0.5 because half of the source cell contributes to part of target cell.

We also applied the same OSMOSE "mask" to all LTL models, i.e., to differentiate land cells with NA values from sea cells, in order to have the same coastline between models.

5. LTL model comparisons

After regridding all models, in order to compare seasonal and spatial LTL dynamics with a focus on zooplankton in the gulf, only continental shelf was conserved. To select the French continental shelf, an isobath at 200m depth is defined to keep only values inside, others values are rescaled on 0 (Figure 8).

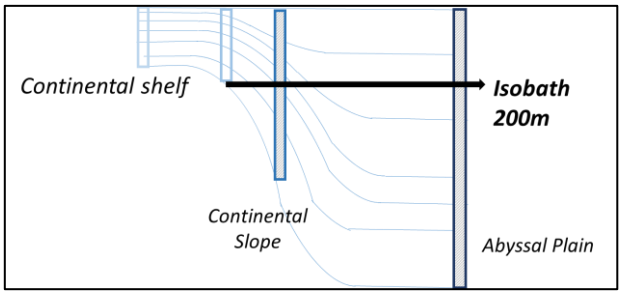


Figure 8: vertical representation of the Bay of Biscay

6. HTL forcing simulations

The effects of LTL models on HTL models can come from various sources, such as simulation dynamics, discretization of planktonic functional groups or the state of fish ecosystem.

In order to test these hypotheses, two series of runs are applied. The first series of runs will be considering a single zooplankton group and single phytoplankton functional group, and the second serie of runs will consider two zooplankton groups divided by size between mesozooplankton and microzooplankton and one phytoplankton group. The size range differs because the first forcing series considers all zooplankton including nanozooplankton modelled by POLCOMS ERSEM whereas this group is not considered in the second forcing series (Table 3).

LTL outputs are provided as monthly means to force OSMOSE over two time ranges, past (2006-2015) and future (2040-2049). In fact, to test the relative size evolution influence of zooplankton through projections, in parallel of the two series using past another runs will be tested with POLCOMS ERSEM and NEMO MEDUSA in rcp scenarios.

For all series, benthos species are keeping because there are not included in zooplankton functional groups. In order to only observe the effects of LTL models on OSMOSE, we focus on pelagic species and do not includes top predators in simulations. This includes the following species: Whiting, Hake, Sea Bass, Squid, Pouting, Albacore and Lesser spotted dogfish (referring to Table 1). Each model simulation is repeated four times to limit hazard bias.

Table 3 : Osmose runs characteristics:

Forcing serie	*Plankton Groups*	*Mean Years*	*Size range of zooplankton (mm)*	*Number of replicates*
1	1 Phytoplankton and 1 Zooplankton	2006 - 2015	[0.002 – 2]	4
1.1	1 Phytoplankton and 1 Zooplankton	2040 - 2049	[0.002 – 2]	4
2	1 Phyto and 2 Zoo (Meso and Micro)	2006 - 2015	[2 – 0.2] & [0.2 – 0.02]	4
2.1	1 Phyto and 2 Zoo (Meso and Micro)	2040 - 2049	[2 – 0.2] & [0.2 – 0.02]	4

SEAPODYM data do not include phytoplankton biomass (not explicitly modelled), thus preventing the comparison of the seasonal dynamics of primary producers for the different LTL models. The only variable that is close to the biomass is the net primary production (NPP). Consequently and to allow SEAPODYM to be used as forcing model in OSMOSE, a monthly ratio between zooplankton and phytoplankton from the other reanalysed models (POLCOMS and NEMO ERSEM and NEMO PISCES) is averaged to obtain a ratio allowing calculating of an average phytoplankton biomass for SEAPODYM, using zooplankton density. The means ratio of each models and the ratio for SEAPODYM are summarised in Table 2.

Table 2: Monthly mean ratio Zooplankton/Phytoplankton biomass according to reanalysis models between 2006 and 2015 and applied mean values for SEAPODYM

Model / Month	POLCOMS ERSEM	NEMO ERSEM	NEMO PISCES	SEAPODYM
Jan	0.263	0.152	0.832	0.416
Feb	0.267	0.100	0.844	0.404
Mar	0.345	0.083	0.937	0.455
Apr	0.423	0.105	0.951	0.493
May	0.619	0.242	0.931	0.598
Jun	0.682	0.421	0.904	0.669
Jul	0.667	0.495	0.849	0.670
Aug	0.637	0.546	0.812	0.665
Sep	0.601	0.567	0.807	0.658
Oct	0.555	0.613	0.847	0.671
Nov	0.428	0.440	0.922	0.597
Dec	0.315	0.222	0.915	0.484

For the second series of runs (two separated zooplankton groups), the same method is applied: the monthly average of the mesozooplankton ratio for the reanalysed models is calculated and applied to get a meso and micro zooplankton proportion for this model (see Appendice A for results).

For the aim of this study, we will focus on the influence of zooplankton dynamics in HTL models. This means we will not examine each species of the model individually but will concentrate only on pelagic species, as zooplankton constitute a major food source. We will have a look only on three pelagic fish: anchovy, sardine and mackerel. To avoid a potential bias of mortality due to top predators, the mortality rate for larval stages of high trophic predators is set to 30, whereas for other species, it is set to 1.

RESULTS

1. Variations of zooplankton's dynamics according to LTL models and scenarios

1.1 Zooplankton seasonality contrasts between the models

1.1.1 Temporal pattern

The seasonal fluctuations in zooplankton biomass are a consistent feature of all models. However, the amplitude of biomass variations differs importantly between the models. The occurrence of the zooplankton bloom is consistent across all models, occurring during the spring season with a maximum in May for POLCOMS ERSEM and SEAPODYM and in April for NEMO MEDUSA and NEMO PISCES. However, in NEMO ERSEM, the bloom occurs in summer. SEAPODYM demonstrates a higher biomass density across all months. The spring and winter months also exhibit the greatest discrepancy between models in terms of estimated biomass density, whereas in summer, these differences are less pronounce (Figure 9). The two POLCOMS ERSEM rcp scenarios exhibit similar variations in biomass between 2006 and 2015, as the rcp scenarios does not indicate any notable differences between these years.

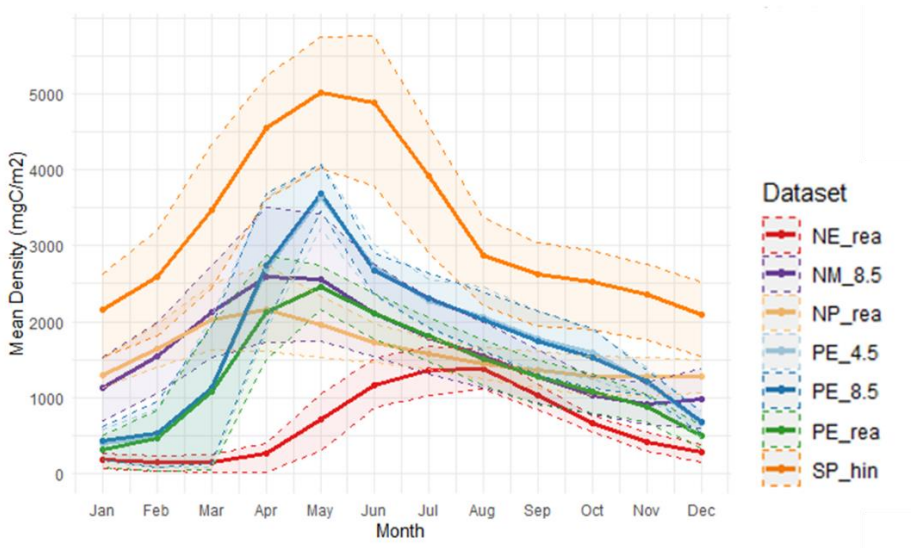


Figure 9: Mean Zooplankton biomass density between 2006 and 2015 with first and third quantiles according to models (NE_rea = NEMO ERSEM reanalysis, NP_rea = NEMO PISCES reanalysis, PE_rea = POLCOMS ERSEM reanalysis, PE_4.5 = POLCOMS ERSEM rcp 4.5, PE_8.5 = POLCOMS ERSEM rcp 8.5, SP_hin = SEAPODYM hindcast, NM_8.5 = NEMO MEDUSA rcp 8.5)

1.1.2 Spatial pattern

In order to facilitate spatial comparison between models which have sometimes important variations of biomasses, all biomasses have been normalised. The POLCOMS ERSEM reanalysis has a heterogeneous spatial distribution. In winter, most of the biomass is located at the coast, with a very marked cost/offshore gradient in spring (Figure 10). This gradient decreases sharply a few kilometres off to the coast and persists throughout the year, but to a lesser extent in autumn. The difference in distribution between north and south of the Gulf is not very marked. On the other hand, NEMO ERSEM shows a south strong biomass presence during the bloom period (July), which is the opposite of the NEMO PISCES pattern. NEMO PISCES demonstrates a pronounced north/south pattern during the bloom period, with a density three times higher in the northern BoB region than in the southern. Also, the coast/offshore gradients in NEMO PISCES and NEMO ERSEM are opposite to POLCOMS ERSEM with stronger biomasses at the limit of the plateau. Biomasses are more evenly distributed over the year in NEMO PISCES than in NEMO ERSEM and POLCOMS ERSEM reanalysis. In SEAPODYM, the coast/offshore gradient is present like in POLCOMS ERSEM, but apart from May when the density becomes very high near the mouths of the Loire and Gironde estuaries, the biomass is distributed throughout the year.

The rcp versions of POLCOMS ERSEM show similar pattern contrasting with POLCOMS ERSEM reanalysis only with a negative biomass gradient from the coast to the large. NEMO MEDUSA spatial pattern is close to the NEMO PISCES one with strong density in the north in spring, and lower density at the coast than at large (see Appendice B for these last three models).

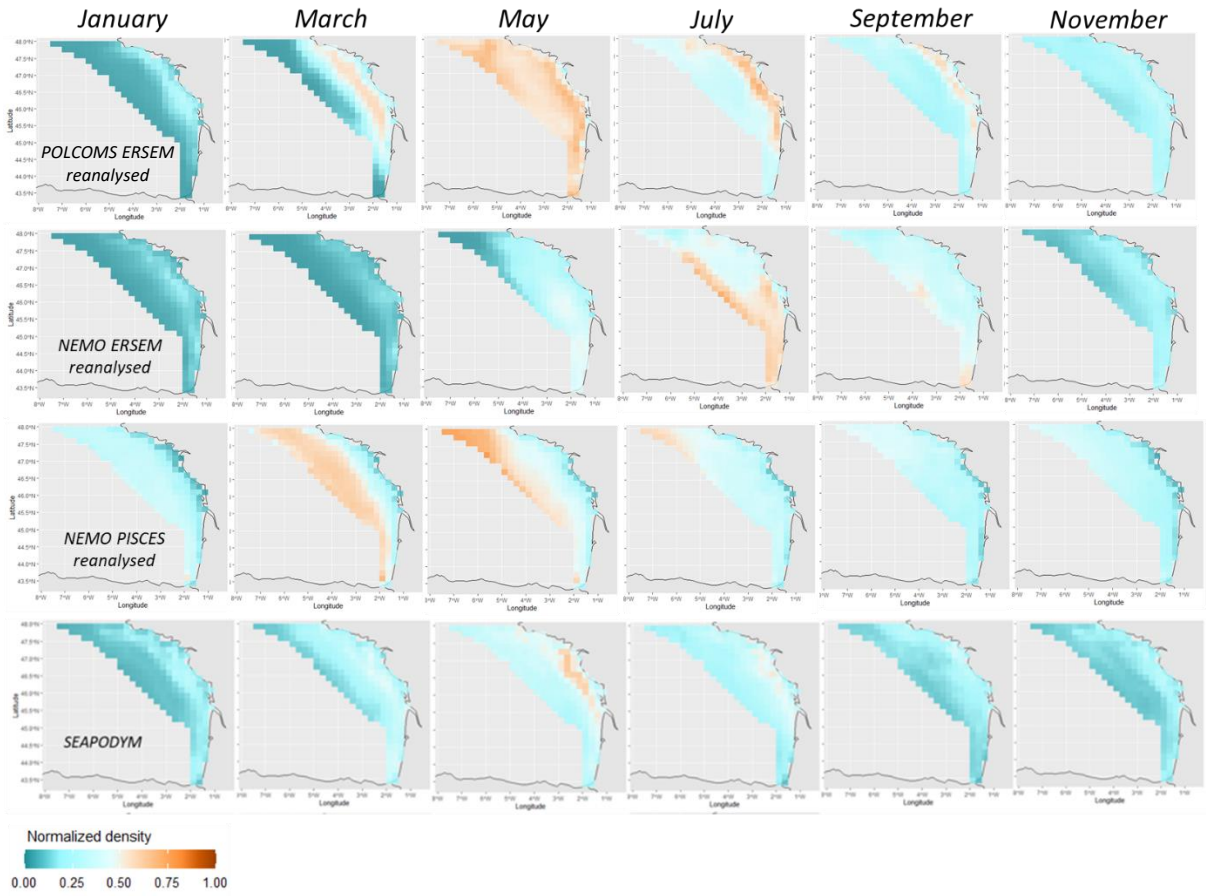


Figure 10: Annual spatial distribution normalized of Zooplankton mean biomass according to POLCOMS ERSEM, NEMO ERSEM and NEMO PISCES between 2006 and 2015 on the continental shelf.

Given that models divide zooplankton into several size compartments, it is interesting to see how the models represent the dynamics of mesozooplankton, which is the main prey of pelagic fish.

1.1.3 Mesozooplankton dynamics

The Mesozooplankton ratio (resulting of mesozooplankton biomass divided the global zooplankton biomasses) seasonality shows the same trend for almost all models except NEMO ERSEM whose seasonality of the ratio seems opposite to the other models with a ratio close 20% in May whereas it's between 45% and 70% for other models (Figure 11). SEAPODYM ratio is not represented because it was calculated on model means (refer to materials and method).

The temporal variations of the mesozooplankton fraction biomass is also depending on models and differences are more important during winter and spring than in summer. When mesozooplankton fraction represent more than 55% of total zooplankton biomass in January in NEMO ERSEM, it's only 25% part in POLCOMS ERSEM rcps and around 45% for NEMO PISCES and NEMO MEDUSA. We also see that NEMO ERSEM fraction of mesozooplankton is lower in spring and higher in winter. In addition, NEMO ERSEM and POLCOMS ERSEM reanalysis show a second biomass peak in summer, which is lower than the spring peak. NEMO PISCES illustrates a very stable ratio throughout the year, fluctuating between 40% and 55%. March is the month when the models show the closest ratios (20% maximum difference).

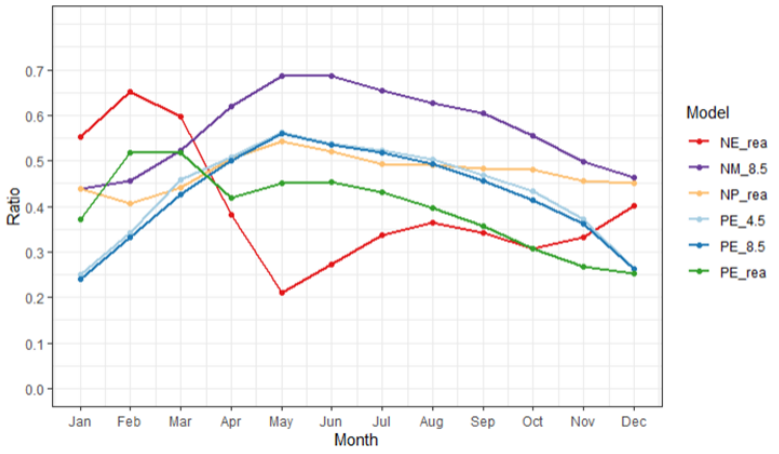


Figure 11: Monthly mean fraction of Mesozooplankton biomass in the total zooplankton biomass between 2006 and 2015

To the spatial pattern side, mesozooplankton pattern is quite resembling to the global pattern in spring because mesozooplankton is part of the biomass bloom, but in winter, dynamics changes to leave the majority biomass for smaller zooplankton (figure 12). POLCOMS ERSEM reanalysis describes a marked mesozooplankton distribution gradient to the north and along the edge of the plateau. The coast/offshore gradient is still present with a majority of mesozooplankton at the coast. The POLCOMS ERSEM rcps have a fairly similar distribution of mesozooplankton, but less marked than with the reanalysed version. The ratio does not exceed 60% but stay longer a majority while reanalysis rises to 80% but declines more rapidly from May onwards (see projections in Appendice C). NEMO ERSEM follows this dynamic more broadly in the Gulf with a predominance of distribution to the north and offshore. This distribution reverses after spring, with mesozooplankton becoming the majority near the coast and the minority offshore. Furthermore, at the edge of the plateau in March, the proportion of mesozooplankton in the community is almost total. NEMO PISCES shows a predominance of mesozooplankton at the coast whatever the time of year. NEMO MEDUSA, on the other hand, does not show any heterogeneity in the distribution of the meso, which is mainly distributed over the entire

continental shelf. The differences between the coast and the offshore and between north and south are not very marked.

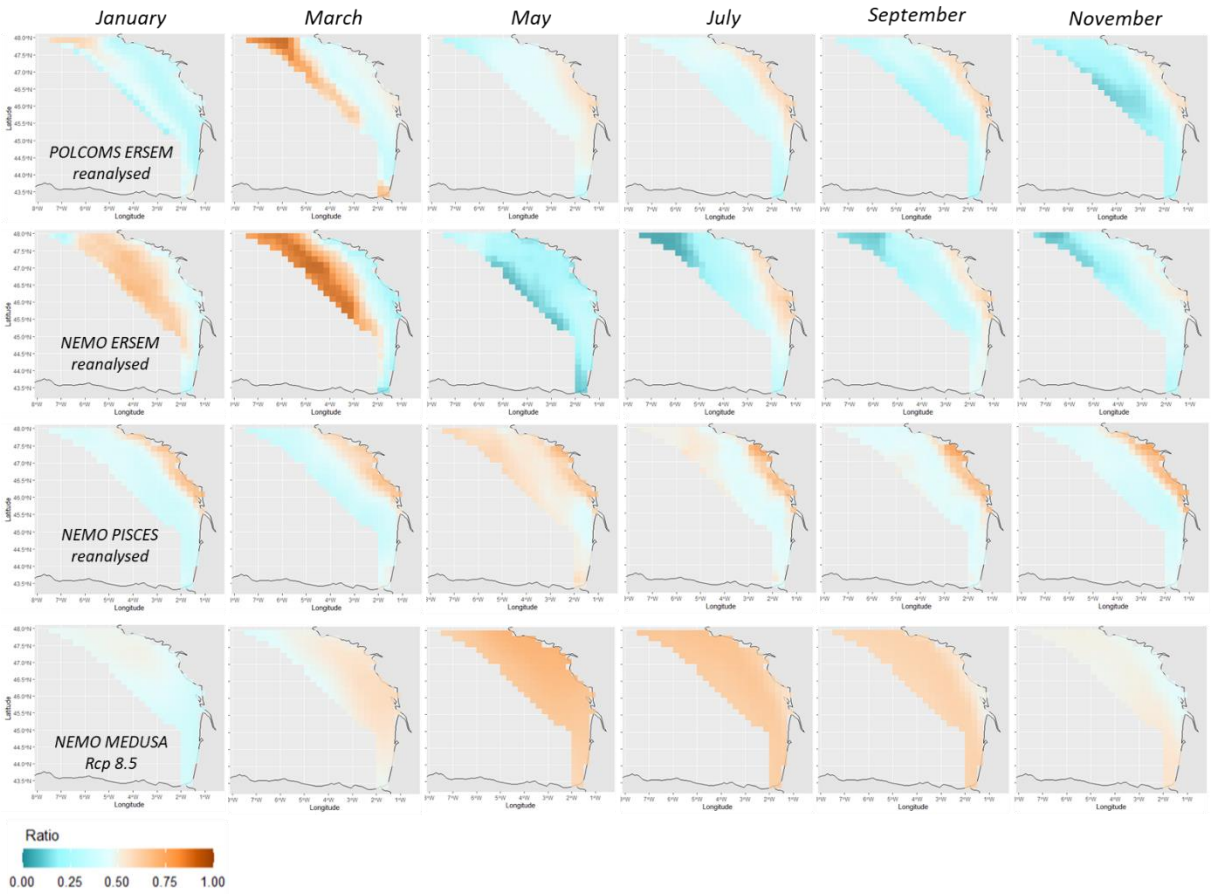


Figure 12: Spatial distribution of the mean relative proportion of Mesozooplankton biomass between 2006 and 2015 according to reanalysis models

The available rcp model outputs can also be used to study the spatio-temporal dynamics in projections to see evolutions of the zooplankton community. A mean state is calculated between 2040 and 2049 for the three models projections : POLCOMS ERSEM rcp 4.5 and 8.5 and NEMO MEDUSA rcp 8.5.

1.2 Changes in zooplankton biomass in projections based on different scenarios

1.2.1 Temporal evolutions through projections

Model projections show few differences in global annual trend, with the spring bloom of biomass and a continuous decrease through summer to winter. However, the difference between two models of the same scenario (POLCOMS ERSEM and NEMO MEDUSA in rcp 8.5) is more pronounced than that observed between the two scenarios (rcp 4.5 and rcp 8.5) of the same model POLCOMS ERSEM (Figure 13). NEMO MEDUSA shows a higher biomass during winter but the increase is less substantial than in POLCOMS ERSEM rcps. Variability between models is highest in spring and lowest in winter. The density has also decreased in all projections compared to the 2006-2015 period (Table 3). For POLCOMS ERSEM, the average density per year decrease of 5% for 4.5 rcp and 6.2% for 8.5 rcp. For NEMO MEDUSA, the decrease is more significant with -14.5%.

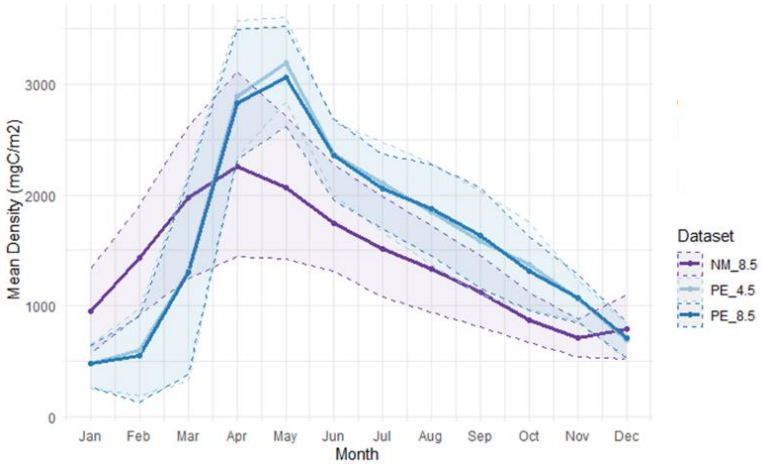


Figure 13: Mean month Zooplankton biomass density between 2040 and 2049 with first and third quantiles according to projections models

Table 3: Mean annual density between the actual period and projections period, according to forecast models:

Model	***Mean density 2006-2015 (mgC/m²)***	***Mean density 2040-2049 (mgC/m²)***	***Evolution (%)***
POLCOMS ERSEM 4.5	1664.0	1576.8	- 5.24
POLCOMS ERSEM 8.5	1671.3	1567.4	- 6.22
NEMO MEDUSA 8.5	1691.8	1445.7	- 17.0

1.2.2 Spatial pattern in projections

The two POLCOMS ERSEM rcp's scenarios show few spatial differences between them, but these differences are more marked with the reanalysed version. In fact, the coast/offshore gradient is pressent in all the POLCOMS ERSEM models, but seems stronger in the reanalysed version, particularly visible in July (refer to Figure 10 for reanalysed and Appendice D for POLCOMS ERSEM rcp 4.5 projections). Also in rcp 8.5, NEMO MEDUSA shows a different spatial pattern than POLCOMS ERSEM 8.5. The major difference lies in the north to south gradient which is positive for POLCOMS ERSEM rcp 8.5 but negative for NEMO MEDUSA rcp 8.5 (Figure 14).

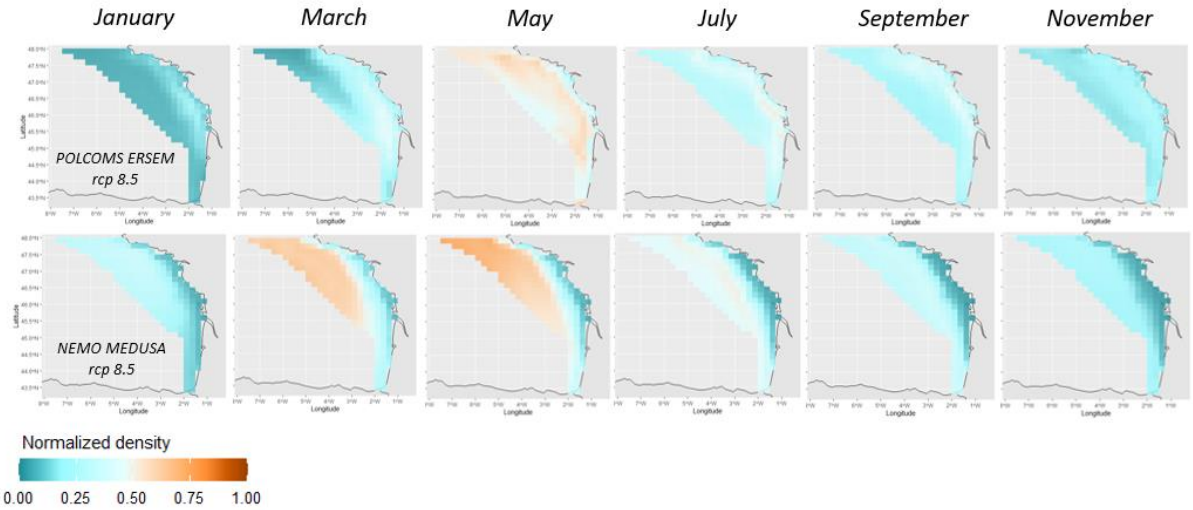


Figure 14: Annual spatial distribution normalized of Zooplankton mean biomass according to POLCOMS ERSEM rcp 8.5 and NEMO MEDUSA rcp 8.5 between 2040 and 2049 on the continental shelf.

1.2.3 Size ratio evolution through projections

The variation in this average ratio over the years available here gives an overall picture of all the models. NEMO MEDUSA shows a higher ratio of mesozooplankton than all the models (50-60%), followed by NEMO PISCES between 45 and 50% (Figure 15). Then NEMO ERSEM and POLCOMS ERSEM rcps are between 40 and 45% of mesozooplankton when we look between 2000 and 2020. The lowest ratio is given by the reanalysis version of POLCOMS ERSEM with a ratio around 40%. The differences in average ratios are both marked between models and also between scenarios such as POLCOMS ERSEM rcps 4.5 and 8.5. Furthermore, the ratio in the projections tends to decrease regardless of the model or scenario. Between actual period (2006-2015) and forecast period (2040-2049), the ratio decrease by 14.3 % for POLCOMS ERSEM 4.5, 9.8% for POLCOMS ERSEM 8.5 and 7.1% for NEMO MEDUSA 8.5.

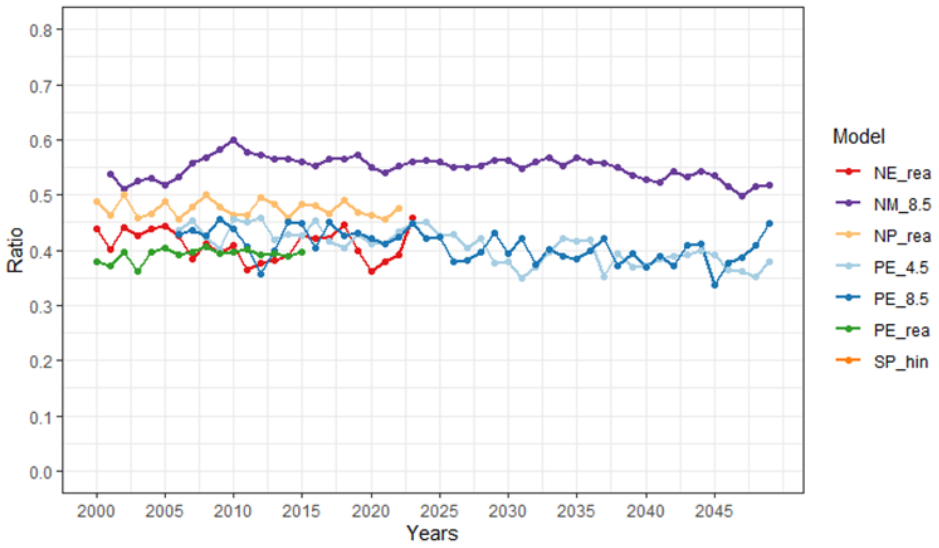


Figure 15: Interannual variations of the annual mean proportion of Mesozooplankton biomass between 2000 and 2049 according to models

1.3 Environment explanations for models differences

We are also looking at variations in the seasonal dynamics of parameters reflecting environmental conditions. Abiotic parameters comes from the hydrodynamic model, fitted on satellites. Sea Surface Temperature (SST) is one of parameters that supposed to be identic through model because coming from field data. Phytoplankton is assumed to vary between different LTL models, because even if the chlorophyll measurement comes from observations, the estimate biomass of the different phytoplankton compartments are represented by the biological model.

Variations in SST between models remain marginal, but two blocks stand out between July and October where major differences occur (Figure 16). During this period, POLCOMS ERSEM reanalysis and NEMO MEDUSA are almost identical with 2°C higher than the others whereas NEMO MEDUSA has lower average temperatures than POLCOMS ERSEM reanalysis in winter and spring. Projections models show an increase of SST, visible in summer, due to forcing by rcp scenario supposing to increase CO2 emissions and the average temperature.

Furthermore, when we look on interannual mean of temperature in the whole water column, models show differences (Figure 17). NEMO ERSEM is the model showing the fewer mean temperature whereas other models seem to be quite agree on values for the actual period. The temperature also increase in projections. Average temperature in NEMO MEDUSA will rise between 2030 and 2040, surpassing the two POLCOMS ERSEM rcp versions.

The absence of SEAPODYM is explained by the data available. Although temperature data is given, it is an average temperature along the first layer, which for SEAPODYM can extend from the surface to a depth of more than 150m. This average is therefore lower than a SST and can't be compared.

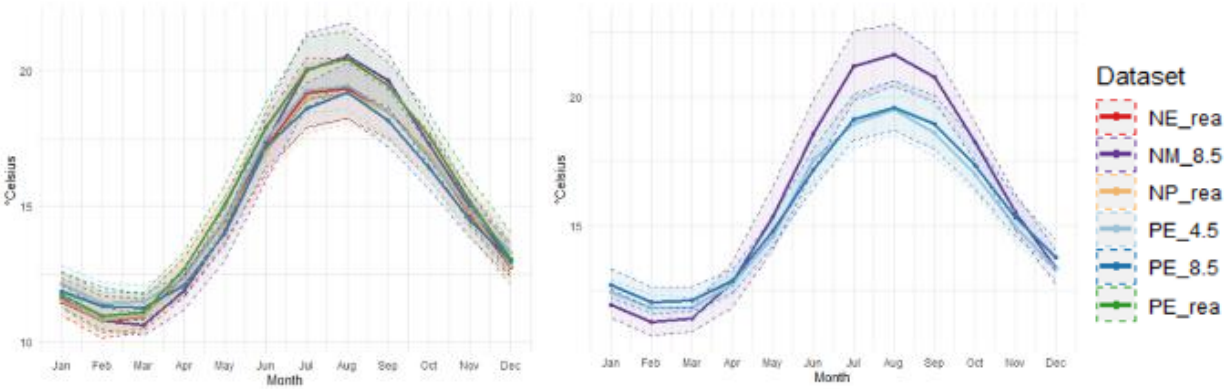


Figure 16: SST seasonality between 2006 and 2015 (left) and 2040 and 2049 (right) with standard deviation

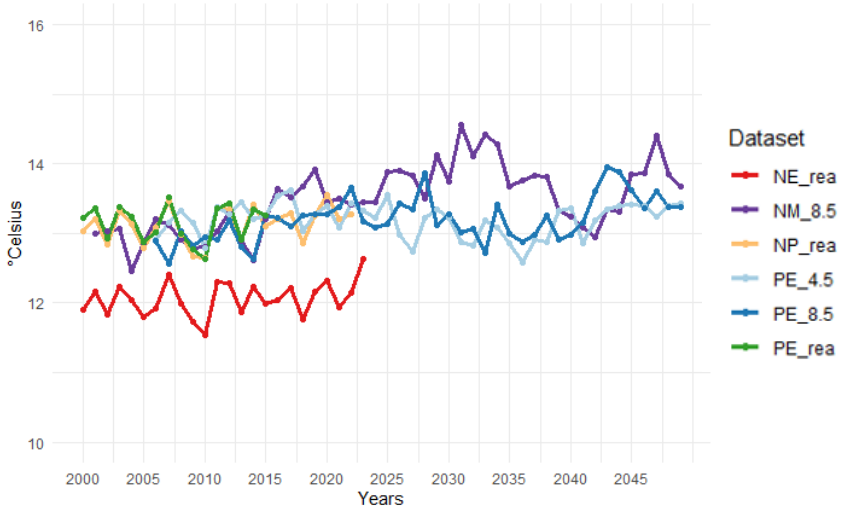


Figure 17: Annual mean evolution of SST between 2000 and 2049

Phytoplankton appears to be more uncertain according to models than the SST. As with zooplankton, the models show a strong seasonal pattern for phytoplankton, with a biomass peak during spring (Figure 18). The bloom is clearly visible in the different versions of POLCOMS ERSEM. For NEMO MEDUSA and NEMO PISCES, the biomass is smoother over the year but showing an increase during spring. Finally, NEMO ERSEM shows an increase in biomass in summer that persists for several months, unlike the other models.

In projections, the seasonality pattern didn't change, but phytoplankton biomass has decreased in both NEMO MEDUSA and POLCOMS ERSEM. The decrease is more marked in POLCOMS ERSEM whatever the scenario (the peak decrease from 6500 mgC/m² between 2006 and 2015 to 5700 mgC/m²).

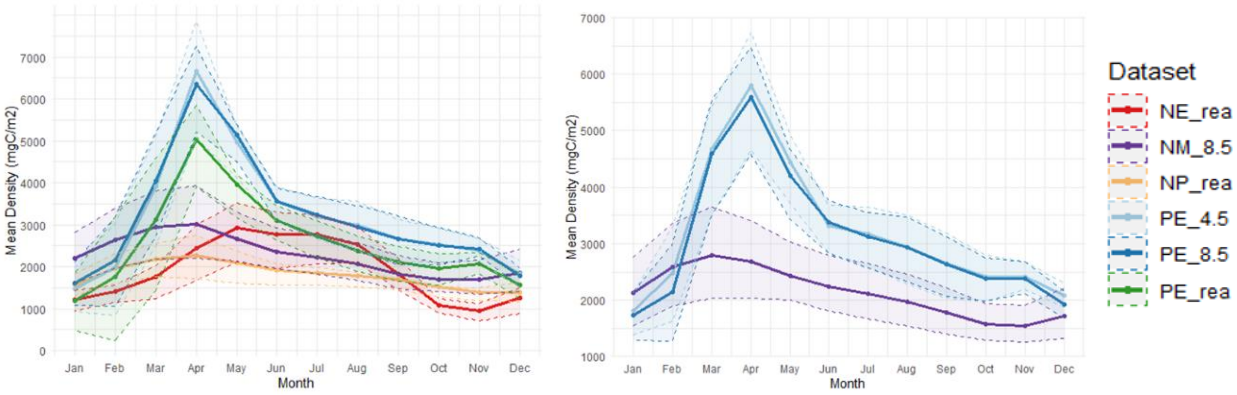


Figure 18: Phytoplankton biomass seasonality between 2006 and 2015 (left) and 2040 and 2049 (right) with standard deviation

2. Effects of plankton dynamics on OSMOSE outputs

After comparing the zooplankton dynamics of the different LTL models, they were used to force a configuration of the OSMOSE model. This second part presents the model results according to the LTL forcing models.

2.1. Biomass

The comparison of pelagic biomass (mackerel, sardine, anchovy, sprat and horsemackerel) between models and runs shows a clear difference in biomass simulated by OSMOSE according to the forcing model (Figure 19). Furthermore, a systematic and significant decrease in biomass was observed when zooplankton is divided into two compartments (micro and mesozooplankton). The difference in biomass between models, is ranging from multiplying by two to multiplying by 6 between NEMO ERSEM and SEAPODYM, but is not very different between the other models.

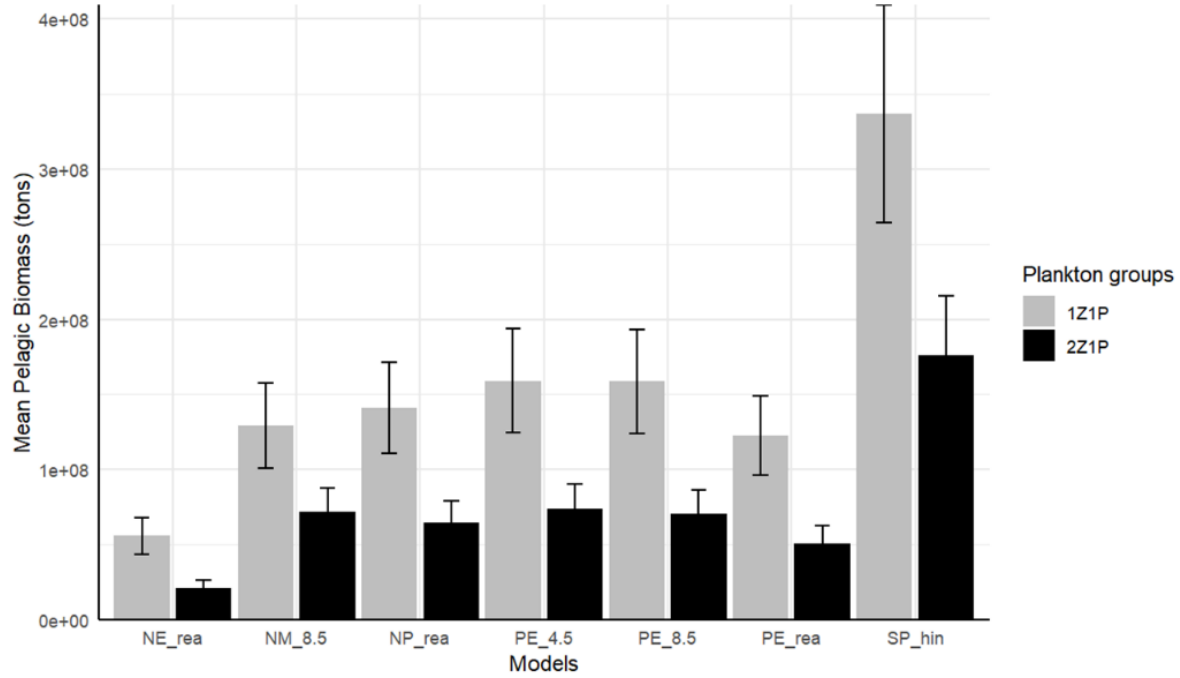


Figure 19: Mean pelagic Biomass according to the different models LTL forcing and runs (means between 2006-2015)

Among all pelagic species, we focus on sardine, anchovy and mackerel dynamics. Those three species show different seasonnals patterns (Figure 20). When the biomass of anchovy reach a peak in April, sardine are slowly increasing and the peak is during autumn. Mackerel biomass increase and decrease sharply during spring and also decrease sharply after summer. There are no much differences in seasonal trends between simulations with one or two compartments of zooplankton but the scale of the biomass changed for all pelagic species, with a higher biomass when we only consider one global functional group of zooplankton.

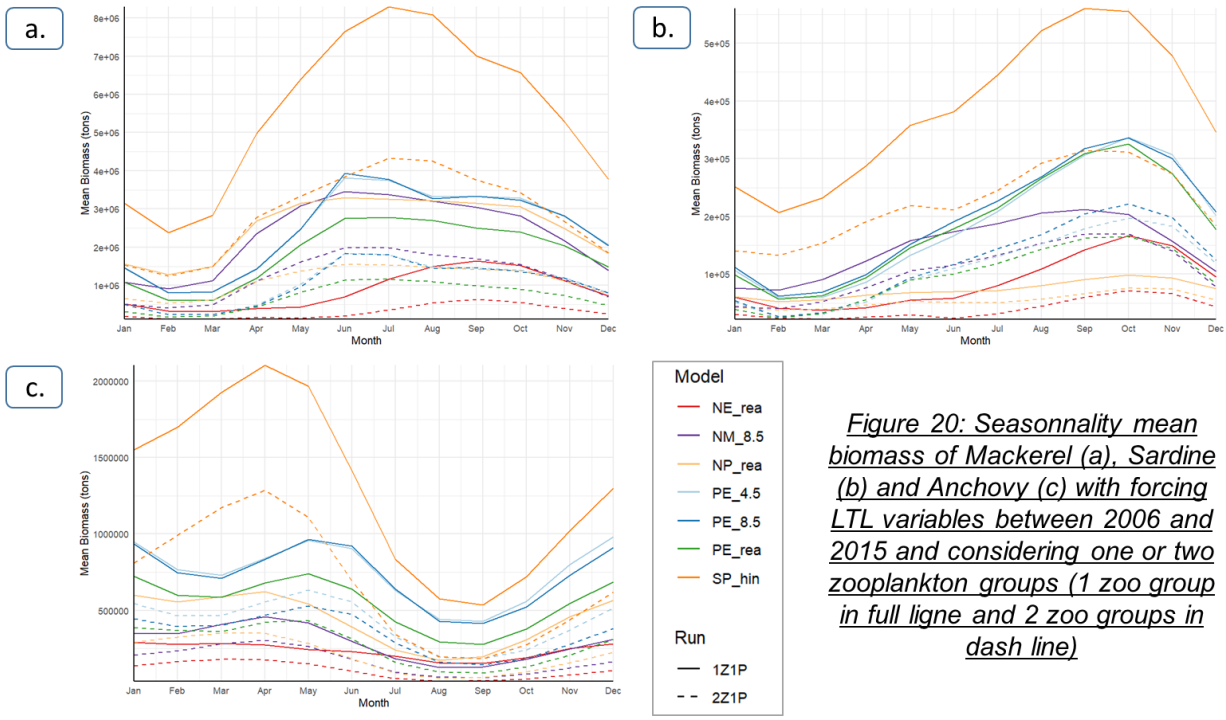


Figure 20: Seasonnality mean biomass of Mackerel (a), Sardine (b) and Anchovy (c) with forcing LTL variables between 2006 and 2015 and considering one or two zooplankton groups (1 zoo group in full ligne and 2 zoo groups in dash line)

Variations in the biomass of pelagic species therefore seem to depend on the LTL forcing model given as input. The figure 21 resumes relationships between the pelagic biomasses and zooplankton given as input according to the different models and the different runs. The horizontal differences concerning zooplankton biomass of NEMO ERSEM and the POLCOMS ERSEMs with one or two functional groups runs are due to the presence of the nanozooplankton compartment in models, which the biomass was not considered in the different runs because nanozooplankton is not part of the size range accessible to fish.

Both POCLOMS ERSEM rcps versions are confused, in connection with the identical zoo biomass in these models. The increase of biomass is clearly visible between dividing zooplankton group in two. It seems like POLCOMS ERSEM rcps, NEMO MEDUSA and NEMO PISCES, which has similar zooplankton biomass, the increase in fish biomass is more important in POLCOMS ERSEM rcps, followed by NEMO PISCES and MEDUSA. SEAPODYM shows significant increase in fish biomass, but in line with the increases in the other models.

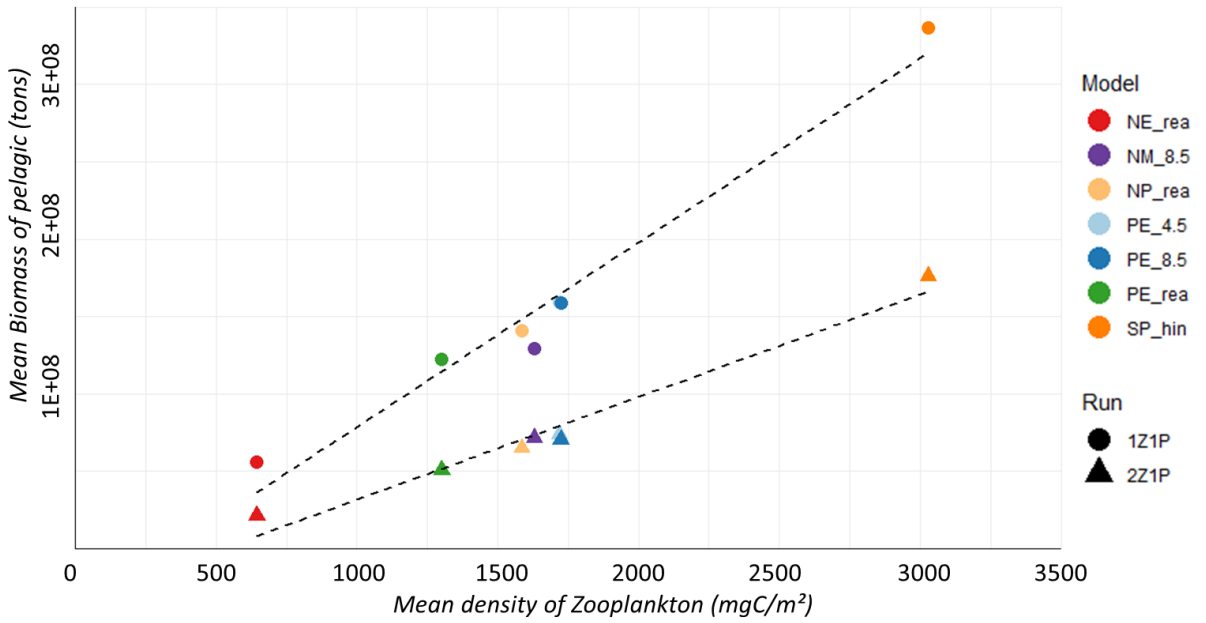


Figure 21: Relationship between Zooplankton biomass and Pelagic fishes biomass according to models and runs (1Z1P = one zoo and phytoplankton group, 2Z1P = two groups of zooplankton and one group of phytoplankton)

2.2. Size at Age

Size at first ages in pelagic fish varies little between LTL forcing models when considering one zooplankton group (Figure 22). They express similar trends but show discrepancies at certain times of the year. For anchovies (Figure 23 c.), the size at age 0 is sensitive to the model used for forcing during the first few months of the year (March-June), whereas the trends are almost identical from July to February. In addition, mean size is greater under rcp model forcing than under reanalysed models. For mackerel (Figure 23 a.) and sardine (Figure 23 b.), the 0 age is the most stable with few uncertainties between models and age 1 provides more differences between models. Considering two zooplankton groups, size-at-age pattern doesn't change a lot but for anchovy, uncertainty increased at ages 0 and 1 (results in Appendice E). This parameter followed biomass trends, which is supporting the analysis. In addition, changes in size show different seasonality according to species. Mackerel are growing during early winter and spawning just after, whereas it's the opposite for sardines, spawning during late autumn and growing during summer. Anchovies spawn during spring and grow during autumn and winter.

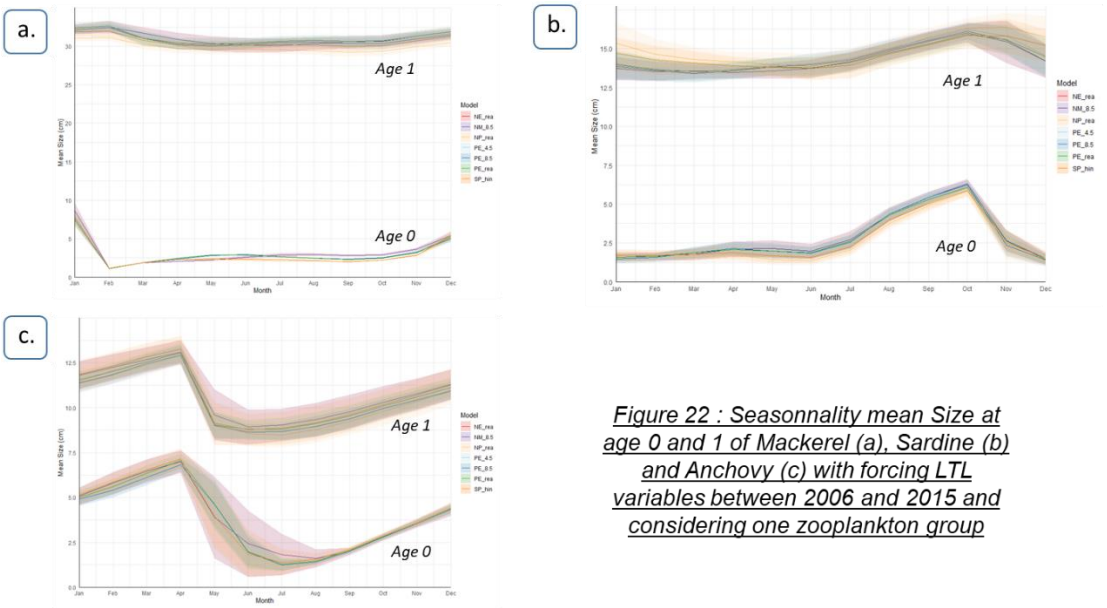
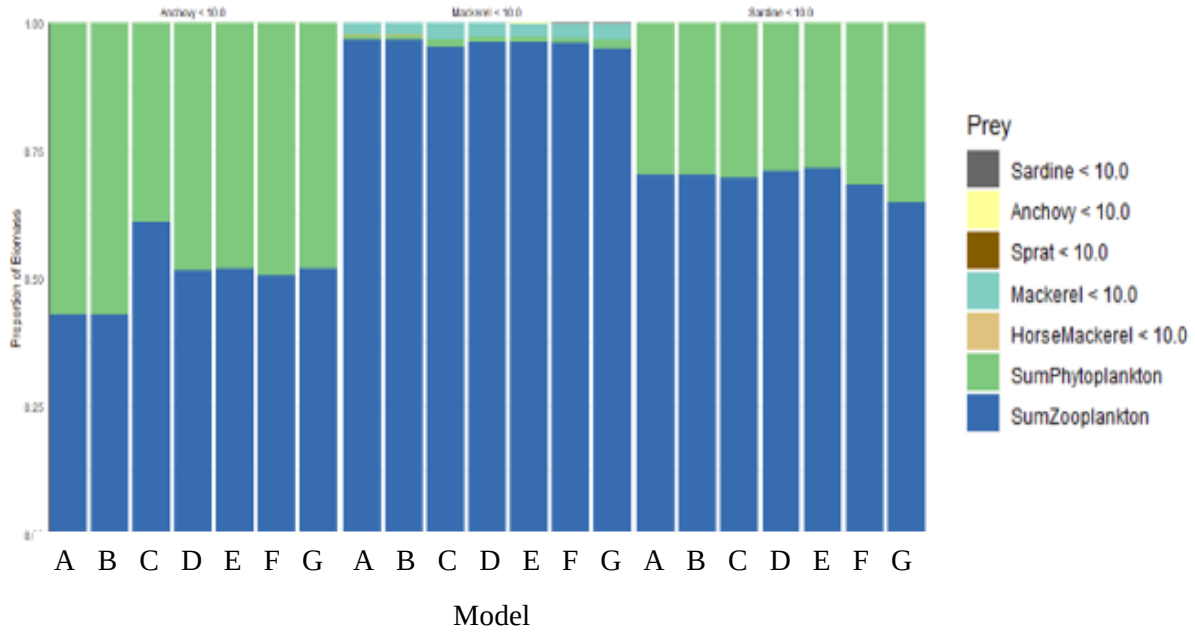


Figure 22 : Seasonnality mean Size at age 0 and 1 of Mackerel (a), Sardine (b) and Anchovy (c) with forcing LTL variables between 2006 and 2015 and considering one zooplankton group

2.3. Diet matrix

The study of diets provides additional information for identifying species that are more or less dependent on zooplankton resources. For early life stages (species < 10 cm), diets focus on phytoplankton and zooplankton (Figure 23). Mackerel feed exclusively on zooplankton, whereas small sardines and anchovies alternate between zooplankton (50-60%) and phytoplankton. After reaching 10 cm, mackerel shift their diet to small fish (25% small mackerel and 10% small anchovies), with zooplankton accounting for only 50% of their diet. Beyond 10 cm, sardines and anchovies consume zooplankton exclusively. These trends are consistent across all models, even when zooplankton is divided into two size ranges. The proportion allocated to phytoplankton remains relatively unchanged, but there is a predominance of mesozooplankton in the diet of these species, regardless of their size, with microzooplankton representing less than 15% of the diet when pelagic fish measure less than 10 cm (results available in Appendix F).



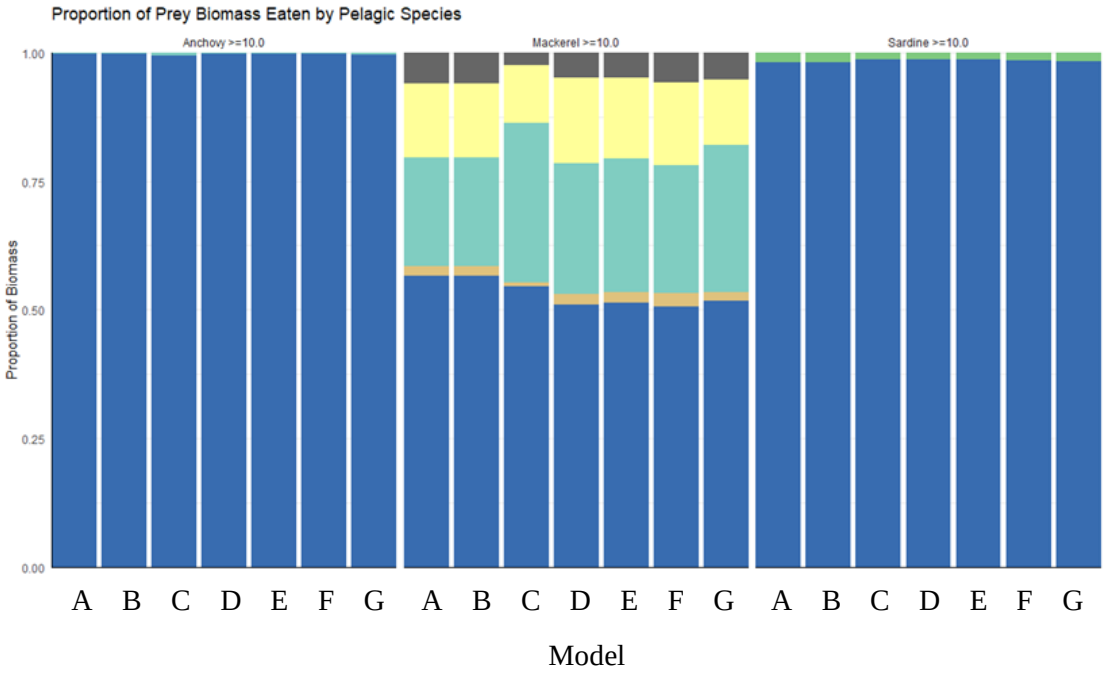


Figure 23: Proportion of prey consumption according to three pelagic species (Anchovy, Mackerel and Sardine) and LTL forcing models between 2006 and 2015 considering one zooplankton group (in order from left to right : A) NEMO ERSEM reanalysis, B) NEMO MEDUSA rcp 8.5, C) NEMO PISCES reanalysis, D) POLCOMS ERSEM rcp 4.5, E) POLCOMS ERSEM rcp 8.5, F) POLCOMS ERSEM reanalysis and G) SEAPODYM hindcast)

DISCUSSION

1. *What factors contribute to the variations observed in zooplankton dynamics across different models?*

1.1. Hydrodynamic considerations

The observation of SST data exhibits minimal variation between models, however, slight variations appears during May which represent the primary peak in plankton biomass (Poulet, Laabir, et Chaudron 1996). The versions of NEMO ERSEM and NEMO PISCES that were used were reanalysed with SST data from satellites. This implies that those models are supposed to have a good modelling of SST (O'Dea et al. 2012; Sotillo et al. 2015). Moreover, it would be beneficial to undertake a comparative analysis of the SST from the SEAPODYM model, which was also sourced from a reanalysed database (European Union-Copernicus Marine Service 2021, as detailed in the User Manual). On the other hand, as SEAPODYM is not a coupled model, the transmission of uncertainty from abiotic factors to biological compartments may be subject to different processes.

The first source of uncertainty identified in the models is the representation of hydrodynamics and the modelling of matter cycles and abiotic factors. In addition to environmental factors, the modelling of geophysical characteristics such as bathymetry and marine currents represents a significant source of uncertainty. To illustrate, in all the models examined here, bathymetry values exhibited variability at the local level, particularly in in proximity to the coast or at the periphery of the continental shelf. The determination of the extent of the continental shelf was found to be contingent upon the spatial resolution of the physical models. The vertical movement of water and the speeds of currents, particularly in areas of high nutrient input and mixing of water phenomena, exert an influence on primary production and consequently, on the dynamics of zooplankton (Ramirez-Romero et al. 2020). Furthermore, previous studies have demonstrated the existence of local differences between the physical parameters of the POLCOMS and NEMO models, leading to errors in the estimation of these parameters (O'Neill et al. 2012). In order to adopt a more comprehensive approach of uncertainties quantification, it is necessary to take the hydrodynamic part into account.

Other potential sources of uncertainty that may contribute to the observed differences in spatio-temporal dynamics may originate from biological models. As with zooplankton, phytoplankton, are categories as compartments and estimated using trophic equations. Similarly, reanalysis version are intended to provide the most accurate representation of reality. However, the biomass data for phytoplankton are derived from satellite observations, which may contains errors. The same is true of model simulations, in particular with regard to the conversion equations (Everett et al. 2017).

1.2. Biological compartments

Regarding to the phytoplankton biomass, the principal differences are observed between the POLCOMS ERSEM versions and the alternative models, which appear to be associated with the physical models POLCOMS and NEMO. This is consistent with the establish fact that phytoplankton dynamics are dependent on the physical parameters of temperature, oxygen and marine currents. Furthermore, the POLCOMS versions demonstrate annual biomass differences between 2006 and 2015 that are four times greater than those observed in the NEMO PISCES and two times greater than those observed in the NEMO ERSEM (ΔPOLCOMS ERSEM reanalysis = 4279 mgC/m², ΔNEMO ERSEM = 2182 mgC/m², ΔNEMO PISCES = 1024 mgC/m²), indicating that the POLCOMS ERSEM model allows for greater flexibility in capturing seasonal variations than the NEMO versions. In May, the rivers contribute a substantial input of nutrients, resulting in a peak in phytoplankton biomass. In addition, there is an increase in the surface temperature and biomass from the northern to the southern regions.

The distribution of phytoplankton is influenced by abiotic factors, including salinity, temperature and stratification (Zarauz et al. 2007). To go further, the spatial dynamics of phytoplankton according to models could be explored.

The analysis of temporal dynamics in zooplankton biomass revealed significant differences between all the models. The gap between the models is at its greatest during the spring and lowest during the summer. In both cases, the model with the lowest biomass is NEMO ERSEM, while the model with the highest biomass is SEAPODYM. The seasonal variability of zooplankton has been demonstrated in previous studies and scientific field surveys (Benedetti et al. 2019; Cataletto et Fonda Umani 1994). This phenomenon is well represented in the different models. However, the NEMO ERSEM model does not appear to fit with this pattern, exhibiting a biomass peak during the summer months. The difference in the modelling results may be attributed to the differing hydrodynamic approaches employed by the NEMO hydrodynamic model, as the biological model is the same (ERSEM). Furthermore, the NEMO ERSEM model shows the lowest biomass quantity in comparison to the other models. Conversely, SEAPODYM shows a greater quantity of biomass than all other models. This discrepancy may be attributed to differences in the methodology employed for the measurement of abiotic parameter, given that SEAPODYM is not a coupled model. However, this difference may also be attributed to the manner in which SEAPODYM models the zooplankton compartment, which considers a single zooplankton group, whereas the other models encompass two to three zooplankton compartments. Additionally, this variability is contingent upon inputs from the principal estuaries (Loire, Gironde), which is susceptible to change. Moreover, POLCOMS ERSEM versions, which exhibited a more expansive seasonal range of phytoplankton biomass than the NEMO versions, also demonstrated a broader range of zooplankton biomass throughout the year. This lends further support to the explanation proposed by the number of zooplankton functional groups as well as by the physical model and the reanalysis version.

The investigation of the spatial distributions of zooplankton between models revealed a diverse range of pattern. In January, while the models concur on a low plankton density, some models show contrasting coast/offshore gradients. The NEMO PISCES and the NEMO MEDUSA models both indicate a higher density off the Gulf, whereas the other models suggest an increase in plankton density in coastal regions. This trend is sustained throughout the year and become increasingly pronounced in spring. Furthermore, a north-south was observed to vary between models, for example between NEMO ERSEM and NEMO PISCES. NEMO MEDUSA also exhibit a very pronounced gradient. A comparison of the outputs with a reanalysis version would have been a valuable addition to this model. It is challenging to ascertain a singular spatial pattern for the distribution of zooplankton across all the studied models. It is however, well documented that field data has demonstrated a higher biomass of plankton in coastal areas, due to their dependence on coastal plumes (Poulet, Laabir, et Chaudron 1996; Vandromme et al. 2014; Albaina et Irigoien 2007; Grandremy 2023). It is therefore intriguing to observe the emergence of inverted coast/offshore patterns in certain models such as NEMO PISCES. This phenomenon can be attributed to the inherent complexity of accurately representing trophic compartments at precise scales, such as the Bay of Biscay, where the model was originally developed for a global scale. The spatial pattern of mesozooplankton exhibited no significant divergence from that of zooplankton, suggesting that mesozooplankton plays a pivotal role in shaping the community. As demonstrated by Albaina et Irigoien (2004), the vertical distribution of zooplankton in the Bay of Biscay is important and has not been explored in this study.

1.3. Comparison method

In order to facilitate the exploration and comparison of all models outputs, which are subject to a number of differences, the data were integrated both vertically and spatially.

The horizontal resolution of the various models employed differences in the representation of coastal boundaries. It should be noted that data for the Loire and Gironde estuaries for example, are only

available in NEMO PISCES (see Figure 7), SEAPODYM and NEMO ERSEM. POLCOMS ERSEM, despite an equivalent resolution, does not model these areas (see Figure 1). However, these locations exhibited very high concentration of zooplankton, despite the relatively shallow depths. Furthermore, the OSMOSE model lacks the requisite resolution to adequately represent these areas. Consequently, during the process of interpolation, it is possible that some biomasses may have been partially diluted, or even no longer represented. The challenge in modelling coastal areas lies in the capacity of the models to represent the transitional zones between land and sea that are occupied by species that are ubiquitous in these environments.

2. *How zooplankton dynamics influence Osmose runs on pelagic fish?*

2.1. LTL models forcing influence on pelagic species

In order to examine the influence of the couplings between LTL and OSMOSE, we first look at the pelagic fish biomasses as they are presented in the model outputs. Figure 21 provides a summary of the differences in pelagic biomass according to the LTL model used for forcing. The biomass of pelagic fish in relation to the quantity of accessible zooplankton exhibits a linear correlation ($R^2 = 0.97$ for both of 1Z1P and 2Z1P), as demonstrated by Van De Wolfshaar et al. 2021. The different forcings result in significant seasonal variations in biomass for pelagic species (see Figure 20), with some discernible pattern. In addition, the differences between the models are most pronounced when the pelagic biomass reaches its maximum and are smallest when there is a decline in biomass. Therefore, the sensitivity of the LTL models is reflected in the HTL model. However, the differences in zooplankton biomass between SEAPODYM and NEMO ERSEM averaged 4.7 over the 2006-2015 period, while the divergence in pelagic biomass between these same models over the same period was 6. It thus appears that LTL/HTL coupling has amplified these differences.

In order to understand these variations in biomass, an analysis of size-at-age could provide insights into fish growth seasonality, maturation and reproduction cycle. Body size is a determining factor in many ecological processes (predation, colonisation) and energetic processes like productivity (Stemmann et Boss 2012). Early life ages are a sensitive period of survival in pelagic fish, depending a lot of the environmental conditions (Menu et al. 2023) and food availability. Lack of prey during early ages can be the source of large variations in biomass (Chevillot et al. 2017). This is why it is important to regard at diet matrix. Pelagic are consuming both zooplankton and phytoplankton before 10 cm which corresponds to age 0. Also, models outputs illustrate peak zooplankton biomass in May (spring period) and in April for phytoplankton. Anchovies increase their size during spring, which is matching prey availability. The increase of uncertainty of size-at-age 0 may be explain by some models illustrating summer peak of biomass like NEMO ERSEM, allowing the mean size-at-age to decrease slower than other model even during spawning period. Mackerel is less dependent of zooplankton after 10cm, eating small fish that may explain the little variations between models for this specie.

It should be noted that the OSMOSE model used here is not calibrated. It represents a naïve state of the ecosystem, which may result in significant variations in biomass depending on the forcing used. It is therefore difficult to draw conclusions about the robustness of the different pelagic species according to the prey fields forcing. Furthermore, the calibration is based on LTL model data. To be completely accurate, the OSMOSE model would need to be calibrated for each LTL model tested. This would be a time-consuming step. So the advantage of using a non-calibrated version ensures that there is no bias linked to calibration.

2.2. Influence of the number of zooplankton compartments

The ability of choosing the number of compartments according to size in the OSMOSE model is an ecological advantage. For fish species, size of the jaw determines the size of prey they can consume (Y.-

J. Shin et Cury 2011). In addition, the structuration of zooplankton community encompasses a wide size range (from 2 mm to 20 µm). With two compartments, planktivorous species have access to less biomass, but this is more realistic. Indeed, the results show that the pelagic biomass is greater when there is only one zooplanktonic compartment given as input, but when there is two compartments, there is an reduction in the range. This may be due to the OSMOSE model. It is based on opportunistic predation that has a tendency to attenuate differences. These results agreed with similar study conducted in the North Sea by Van De Wolfshaar et al. 2021, accuenting the bottom-up effect already described in ecosystems (Daewel et al. 2014; Vandromme et al. 2014).

If there is less mesozooplankton, pelagic may change their diet to smaller prey. However, size prey dependancy in pelagic fish diets is real, pealgic are not gonna eat plankton which is in in a different size range. A reduction of mesozooplankton proportion in plankton community is going to be unfavourable for adult but may be favourable for juveniles, or also projections show a decrease in global zooplankton biomass which is supposed to affect pelagic fish and in terms fisheries.

3. How ecosystem is supposed to evolve according to model projections?

The results show that the projections in the rcp models (POLCOMS ERSEM and NEMO MEDUSA) show changes in biomass (zooplankton and small pelagic), in the structure of the zooplankton community and in environmental conditions. Spatial and temporal pattern are also affected but to a lesser extent.

The SST is supposed to increase (Tinker et al. 2016) and salinity decreases. The phytoplankton biomass is also decreasing. Chust et al. (2014) shows that a warming of the oceans leads to a higher ocean stratification which conduct to a reduction in the biomass of phytoplankton and zooplankton in the Bay of Biscay, but beyond the continental shelf, plankton biomass is supposed to increase. This spatial part was not explored in this study, according with the horizontal resolution of the OSMOSE model, and also because dynamics between the open sea and the continental shelf are different.

The drop in the mesozooplankton ratio is greater in the 4.5 rcp than in the 8.5 rcp. The decrease is also variable between both projection models which may be due to difference in the number of zooplankton functional groups modelled (two NEMO MEDUSA and three for POLCOMS ERSEM) but also to the fundamental differences between these models. Garzke et al. (2015) have shown that copepods size decrease in warmer oceans. This is consistent with the decrease observed in the proportion of mesozooplankton coupled with an overall decrease in zooplankton in the projections.

CONCLUSION

In conclusion, there are as many representations of zooplankton dynamics as there are LTL models. However, some temporal and spatial pattern are more robust and vary little between models. The contribution of the re-analysed models offers other insights that can be compared to see whether the projections appear realistic. Furthermore, even the re-analysed versions show discrepancies, indicating that the differences in modelling and the scale of the ecosystem considered are fundamental and affect the representation of zooplankton dynamics. Regional scale sharply increases the number of variables whereas global scaleSpatial and temporal variations in zooplankton are therefore more variable between models than between versions of the same model.

The HTL model OSMOSE also shows that the choice of the number of plankton compartment is important in simulating fish biomasses. Adding compartments makes the model more realistic in term of prey-predator interactions, but requires more accurate zooplankton data from LTL models.

The trade-off between precision and complexity applies both LTL models and HTL models.

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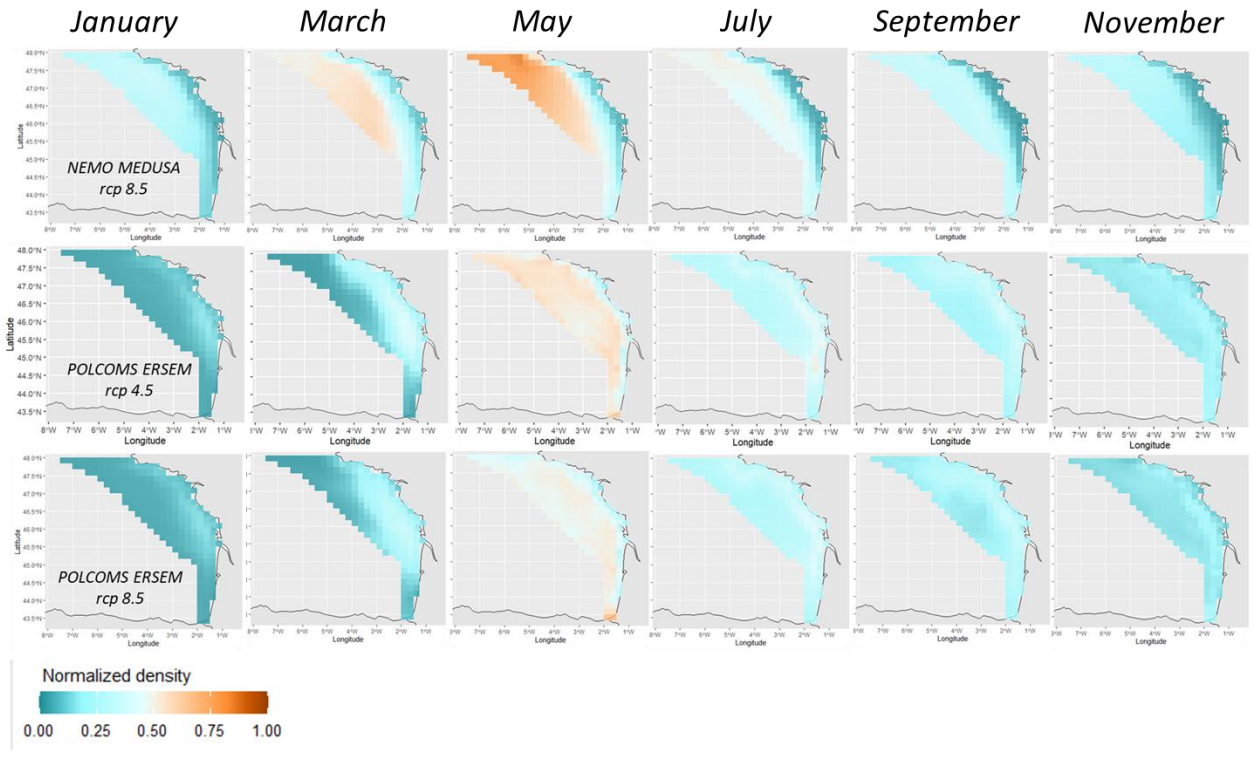
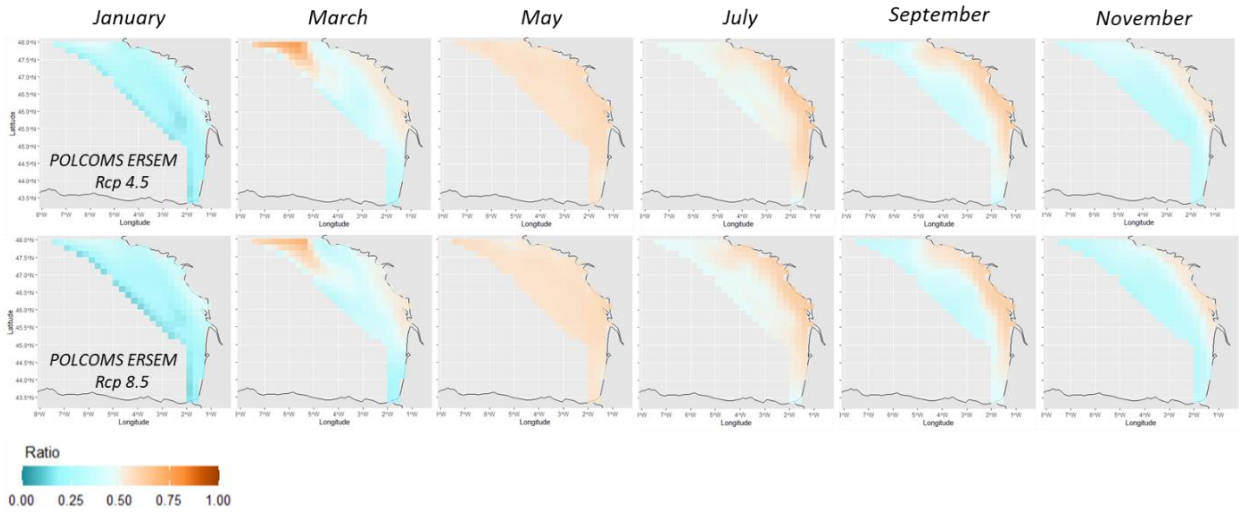
APPENDICES

Model / Month	POLCOMS ERSEM	NEMO ERSEM	NEMO PISCES	SEAPODYM
Jan	0.518	0.852	0.423	0.598
Feb	0.499	0.865	0.390	0.585
Mar	0.558	0.729	0.419	0.568
Apr	0.581	0.397	0.488	0.489
May	0.616	0.339	0.541	0.499
Jun	0.650	0.420	0.520	0.530
Jul	0.642	0.483	0.488	0.538
Aug	0.624	0.515	0.484	0.541
Sep	0.598	0.516	0.479	0.531
Oct	0.549	0.522	0.476	0.516
Nov	0.488	0.639	0.447	0.524
Dec	0.489	0.761	0.437	0.563

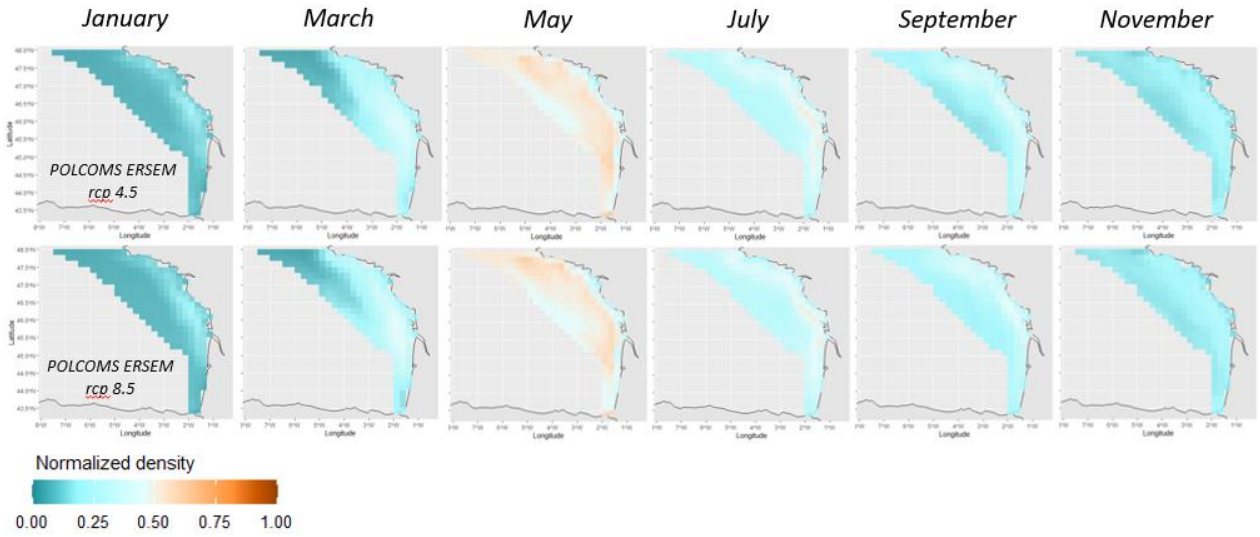
Appendice A: Monthly mean ratio meso/dens_zooplankton calculated in reanalysis models POLCOMS ERSEM, NEMO ERSEM and NEMO PISCES between 2006 and 2015



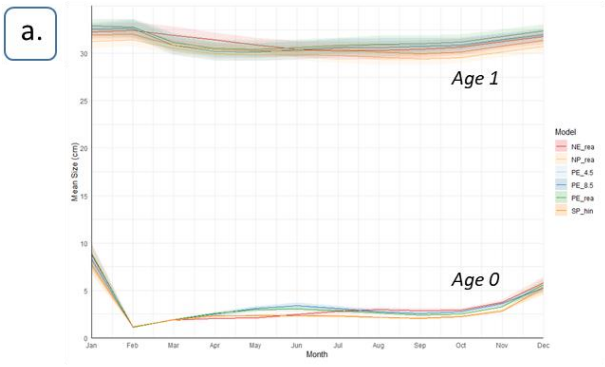
Appendice B: Spatial mean biomass of zooplankton between 2006 and 2015 according to models

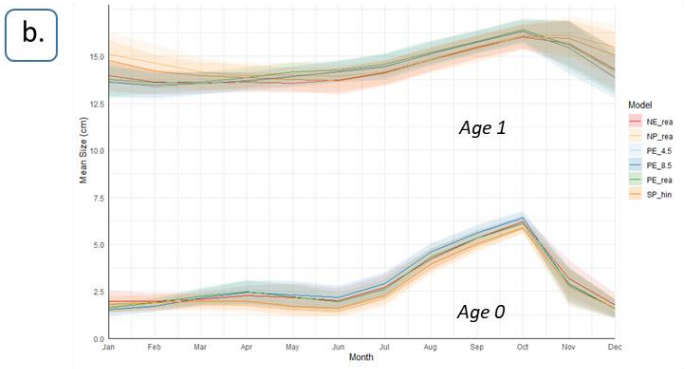


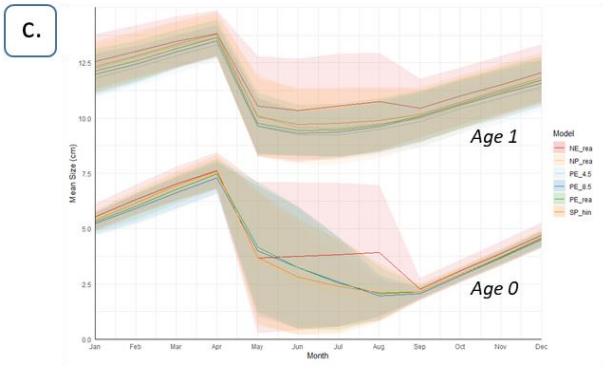
Appendice C: Spatial mean biomass of zooplankton between 2006 and 2015 according to models



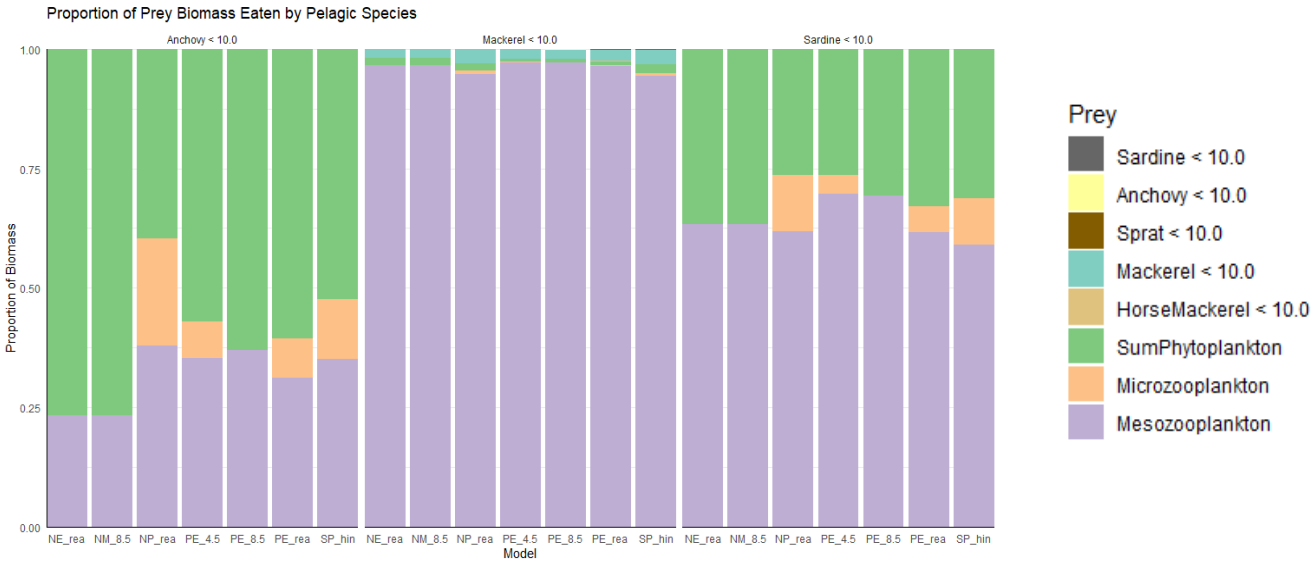
Appendice D : Annual spatial distribution normalized of Zooplankton mean biomass according to rcps POLCOMS ERSEM, rcp 4.5 and rcp 8.5 between 2040 and 2049 on the continental shelf.

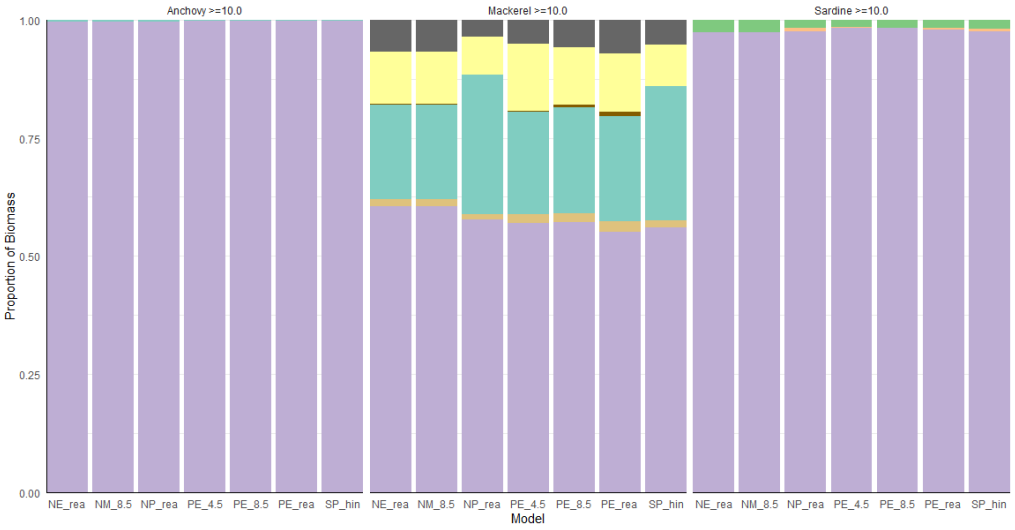






Appendice E: Seasonnality mean Size at age 0 and 1 of Mackerel (a), Sardine (b) and Anchovy (c) with forcing LTL variables between 2006 and 2015 and considering two zooplankton group (Meso and Micro)





Appendice F: Proportion of prey consumption according to three pelagic species (Anchovy, Mackerel and Sardine) and LTL forcing models between 2006 and 2015 considering two zooplankton groups

L'INSTITUT agro Rennes Angers	Diplôme : Ingénieur en agronomie Spécialité : Sciences Halieutiques et Aquacoles Spécialisation / option : Modélisation des Ecosystèmes Aquatiques Enseignant référent : Etienne RIVOT

Auteur(s) : Lucia DOTTIN Date de naissance* : 08/04/1999	Organisme d'accueil : Ifremer, Centre Atlantique Adresse : 65 rue de l'Ile d'Yeu 44 000 Nantes cedex
Nb pages : 36 Annexe(s) : oui Année de soutenance : 2024	Maîtres de stage : Morgane TRAVERS TROLET, Maël GERNEZ

Titre français : Influence des caractéristiques des modèles de Bas Niveaux Trophiques sur les dynamiques de poissons simulées par le modèle OSMOSE appliqué au Golfe de Gascogne

Titre anglais : Importance of low trophic levels' characteristics for simulation of fish community dynamics with OSMOSE model applied to the Bay of Biscay

Résumé (1600 caractères maximum) : Depuis plus de trente ans, les modèles écosystémiques sont largement développés et utilisés pour estimer l'état des écosystèmes, des producteurs primaires aux grands prédateurs. La modélisation du plancton dans ces modèles est souvent limitée, alors que le plancton est un élément clé des réseaux trophiques et représente une source importante d'incertitudes dans le contexte du changement climatique. Ici, nous évaluons les différences dans les dynamiques spatiales et temporelles, ainsi que dans la structure de la communauté zooplanctonique du golfe de Gascogne, simulées par plusieurs modèles de bas niveaux trophiques (LTL) pour divers scénarios climatiques entre 2000 et 2049. Les sorties sont homogénéisées pour servir de forçages au modèle de poissons OSMOSE. Nous nous intéressons aux variations des simulations des pélagiques en fonction des champs de proies des modèles. Les résultats montrent peu de différences entre les scénarios climatiques d'un même modèle, mais les différences sont importantes entre les différents modèles LTL, tant sur le plan spatial que temporel. Les simulations d'OSMOSE selon les différents modèles LTL montrent des différences importantes selon les modèles et les scénarios. Les résultats soulignent également l'importance de la compartimentation en taille du compartiment planctonique dans le fonctionnement du modèle OSMOSE. Le choix du modèle LTL utilisé pour forcer un modèle de poissons est donc déterminant dans l'estimation de l'état des écosystèmes.

Abstract (1600 caractères maximum): For more than thirty years, ecosystem models have been extensively developed and used to estimate the state of ecosystems, from primary producers to top predators. The modelling of plankton in these models is often limited, despite plankton being a key component of trophic networks and a significant source of uncertainty in the context of climate change. Here, we evaluate the differences in spatial and temporal dynamics, as well as in the structure of the zooplankton community in the Bay of Biscay, simulated by several lower trophic level (LTL) models for various climate scenarios between 2000 and 2049. The outputs are standardised to serve as forcings for the OSMOSE fish model. We focus on variations in pelagic simulations according to the prey fields of the models. The results show few differences between climate scenarios within the same model, but significant differences between the different LTL models, both spatially and temporally. OSMOSE simulations based on the different LTL models exhibit significant differences depending on the models and scenarios. The results also highlight the importance of size compartmentalisation within the planktonic compartment in the functioning of the OSMOSE model. The choice of LTL model used to force a fish model is therefore crucial in estimating the state of ecosystems.

Mots-clés : modèles écosystémiques, zooplancton, niveaux trophiques, taille, dynamiques

Key Words : ecosystems models, zooplankton, trophic levels, size, dynamics

* *Elément qui permet d'enregistrer les notices auteurs dans le catalogue des bibliothèques universitaires*

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