

L'Institut Agro Rennes-Angers

Site d'Angers Site de Rennes

<p>Année universitaire : 2022 - 2023</p> <p>Spécialité : Ingénieur Agronome</p> <p>Spécialisation (et option éventuelle) : Sciences Halieutiques et Aquacoles (option Ressources et Écosystèmes Aquatiques)</p>	<p>Mémoire de fin d'études</p> <p><input checked="" type="checkbox"/> d'ingénieur de l'Institut Agro Rennes-Angers (Institut national d'enseignement supérieur pour l'agriculture, l'alimentation et l'environnement)</p> <p><input type="checkbox"/> de master de l'Institut Agro Rennes-Angers (Institut national d'enseignement supérieur pour l'agriculture, l'alimentation et l'environnement)</p> <p><input type="checkbox"/> de l'Institut Agro Montpellier (étudiant arrivé en M2)</p> <p><input type="checkbox"/> d'un autre établissement (étudiant arrivé en M2)</p>
---	--

Étude de la structure du zooplancton dans le golfe de Gascogne à l'aide d'un modèle structuré en taille et impact sur la croissance de la sardine

Par : Raphaëlle HUARD



Soutenu à Rennes le 15 septembre 2023

Devant le jury composé de :

Président : Olivier LE PAPE

Maître de stage : Martin HURET,
Mathilde CADIER et Thomas GORGUES

Enseignant référent : Olivier LE PAPE

Autres membres du jury (Nom, Qualité)

Pablo BROSSET (Enseignant-chercheur, Institut Agro Rennes-Angers)

Mathieu DORAY (Chercheur, Ifremer HALGO-EMH)

Les analyses et les conclusions de ce travail d'étudiant n'engagent que la responsabilité de son auteur et non celle de l'Institut Agro Rennes-Angers

Ce document est soumis aux conditions d'utilisation «Patrimoine-Pas d'Utilisation Commerciale-Pas de Modification 4.0 France» disponible en ligne <http://creativecommons.org/licenses/by-nc-nd/4.0/deed.fr>



Fiche de confidentialité et de diffusion du mémoire

Confidentialité

Non Oui si oui : 1 an 5 ans 10 ans

Pendant toute la durée de confidentialité, aucune diffusion du mémoire n'est possible ⁽¹⁾.

Date et signature du **maître de stage** ⁽²⁾ : 15/09/2023
(ou de l'étudiant-entrepreneur)



A la fin de la période de confidentialité, sa diffusion est soumise aux règles ci-dessous (droits d'auteur et autorisation de diffusion par l'enseignant à renseigner).

Droits d'auteur

L'auteur ⁽³⁾ Nom Prénom Huon Raphaëlle

autorise la diffusion de son travail (immédiatement ou à la fin de la période de confidentialité)

Oui Non

Si oui, il autorise

la diffusion papier du mémoire uniquement ⁽⁴⁾

la diffusion papier du mémoire et la diffusion électronique du résumé

la diffusion papier et électronique du mémoire (joindre dans ce cas la fiche de conformité du mémoire numérique et le contrat de diffusion)

(Facultatif) accepte de placer son mémoire sous licence Creative commons CC-BY-NC-Nd (voir Guide du mémoire Chap 1.4 page 6)

Date et signature de l'auteur :

Autorisation de diffusion par le responsable de spécialisation ou son représentant

L'enseignant juge le mémoire de qualité suffisante pour être diffusé (immédiatement ou à la fin de la période de confidentialité)

Oui Non

Si non, seul le titre du mémoire apparaîtra dans les bases de données.

Si oui, il autorise

la diffusion papier du mémoire uniquement ⁽⁴⁾

la diffusion papier du mémoire et la diffusion électronique du résumé

la diffusion papier et électronique du mémoire

Date et signature de l'enseignant :

15/9/23
Raphaëlle



(1) L'administration, les enseignants et les différents services de documentation de l'Institut Agro Rennes-Angers s'engagent à respecter cette confidentialité.

(2) Signature et cachet de l'organisme

(3) Auteur = étudiant qui réalise son mémoire de fin d'études

(4) La référence bibliographique (= Nom de l'auteur, titre du mémoire, année de soutenance, diplôme, spécialité et spécialisation/Option) sera signalée dans les bases de données documentaires sans le résumé

Remerciements

Tout d'abord, je souhaiterais remercier mes encadrants, Mathilde, Martin et Thomas, de m'avoir sélectionnée puis accompagnée tout au long de mon stage. J'ai beaucoup appris à vos côtés !

Ensuite, merci à Nina Grandrémy et Jean-Baptiste Romagnan d'avoir accepté de nous partager vos données de mésozooplancton dans le golfe de Gascogne et de votre aide dans le calcul des spectres de taille. C'était très généreux de votre part !

Je remercie aussi l'ensemble de l'équipe du DTU Aqua travaillant sur le modèle NUM, en particulier Ken Haste Andersen, avec qui nous avons fait plusieurs réunions pour discuter de l'avancée de mon stage. Ce fut toujours enrichissant !

Merci à mes colocataires : Alice, Baptiste, Perrine, et Patricia (la coloc du weekend) pour les sorties qu'on a faites ensemble et le soutien au quotidien ! Merci aussi de votre aide sur le plan des choix de vie, notamment avec les candidatures de thèse.

Merci aussi aux belles rencontres que j'ai faites à DYNECO : Léa, Pierre, Lola, Julie, pour les nombreux fous rires surtout et pour l'aide que vous avez aussi pu m'apporter sur le plan des choix de vie. Un grand merci également à l'ensemble des équipes PELAGOS et LEBCO, dont les membres ont toujours été bienveillants et accueillants, et qui m'ont aussi aidée à certains points de mon stage, en particulier merci à Claire et à Martin.

Enfin, un grand merci à l'ensemble de l'équipage et des scientifiques du Thalassa avec qui j'ai embarqué lors de la campagne PELGAS. C'était super et j'ai hâte de repartir !

CONTENTS

Remerciements

List of Acronyms

INTRODUCTION	1
MATERIALS AND METHODS	3
1. <i>Study area</i>	3
1.1. <i>Description of the Bay of Biscay</i>	3
1.2. <i>Selection of contrasted stations based on the mesozooplankton community</i>	3
2. <i>Modelling approach</i>	4
2.1. <i>Environmental forcing</i>	4
2.2. <i>Plankton compartment : the NUM model</i>	6
2.2.1. <i>Simulation setup</i>	6
2.2.2. <i>The NUM Framework</i>	6
2.2.3. <i>Overview of the parameters used in the NUM model</i>	9
2.2.4. <i>Post-processing of NUM outputs</i>	9
2.3. <i>Small pelagic fish compartment : the DEB model</i>	10
3. <i>Comparison with in situ data</i>	11
3.1. <i>PELGAS sampling scheme</i>	11
3.2. <i>Computation of Normalized Biomass Size Spectra and indicators derivation</i>	12
RESULTS	14
1. <i>Environmental contrasts between the stations selected in the Bay of Biscay</i>	14
2. <i>The structure of the plankton community in the Bay of Biscay</i>	15
2.1. <i>Biomass and trophic composition</i>	15
2.2. <i>Biomass and size structure of the plankton community</i>	17

2.3. Focus on the copepods biomass and size structure	18
2.3.1. Comparing the NUM model outputs in May with PELGAS in situ data	18
2.3.2. Copepods biomass and size structure over a year obtained from NUM outputs	19
3. <u>Effect of copepods biomass and size structure on sardine growth</u>	20

DISCUSSION _____ 22

1. <u>How do environmental spatial gradients impact the planktonic community in the Bay of Biscay ?</u>	22
1.1. Seasonal variations of the plankton biomass	22
1.2. Spatial variations of the plankton biomass	22
2. <u>What is the copepods size structure in the Bay of Biscay ?</u>	23
2.1. Comparing NUM outputs with in situ PELGAS data in May	23
2.2. Extrapolating copepods size structure over a year with NUM	24
3. <u>How do the spatial variations in copepod biomass and size structure impact sardine growth ?</u>	24
4. <u>Is there a transfer in size structure through the trophic chain in the Bay of Biscay ?</u>	25

CONCLUSION _____ 27

REFERENCES

APPENDICES

List of Acronyms

DEB - Dynamic Energy Budget

ESD - Equivalent Spherical Diameter

MLD - Mixed Layer Depth

NBSS - Normalised Biomass Size Spectra

NUM - Nutrient Unicellular Multicellular

PELGAS - Pelagic ecosystem survey in the Bay of Biscay

0D - 0 Dimension

INTRODUCTION

Small pelagic fishes are key species in most coastal ecosystems around the globe (Peck et al., 2020). Indeed, they provide large ecological and socio-economic functions. Located at an intermediate level of the trophic chain, they represent an essential link in marine ecosystems (Brosset et al., 2017). Economically, they constitute a valuable resource, with a high proportion of the catches being used to produce fishmeal and fish oil for aquaculture (FAO, 2022). In 2021, sardines were the second species declared in fish auctions by French fleets, with 15 169 tons sold (FranceAgriMer, 2022). Sardine is also of social importance, with the use of specific fishing techniques such as bolinche (Duhamel et al., 2011), as well as with a developed sardine can industry representing a significant cultural heritage in Brittany (Celton and Oulhen, 2019).

Over the last decades, the average weight of sardines in the Bay of Biscay has decreased sharply (Doray et al., 2018a), along with their total length and body condition (Véron et al., 2020). A major scientific issue is to understand the processes at work behind these declines. Several hypotheses have been put forward to explain them. This phenomenon might be the result of fishing pressure, which could induce a selection by fishing sardines above a certain length. Nevertheless, in the Bay of Biscay, the observed size reduction of sardines catches has occurred even at low fishing pressure, so this may not be the main driver (Boëns, 2022). Another hypothesis to explain this size decrease is the existence of a top-down control by predators on prey populations. In the same way as fishing, top predators could select sardines above a certain length and this selection could impact on life history traits such as growth. The strength of this impact has not been quantified yet in the Bay of Biscay (Véron et al., 2020), but was considered negligible in the Gulf of Lion where the decreasing trend of sardine size was similar (Saraux et al., 2019). Another hypothesis to explain this size decline is the existence of a bottom-up control of small pelagic fish populations by their planktonic preys. Indeed, a modification of abundance and/or composition of plankton communities could directly impact sardines phenotypes such as size through a change in their food quantity and/or quality (Menu et al., 2023). In the present work, the focus is made on this bottom-up control hypothesis.

Small pelagic fish populations are strongly influenced by the structure and dynamics of lower trophic levels, i.e. plankton communities, themselves influenced by environmental gradients in physical and biogeochemical conditions. Consequently, the observed changes in phenotypes and population dynamics of small pelagic fishes are often representative of regime shifts occurring in marine ecosystems (Chust et al., 2022). In the Bay of Biscay, adult sardines mainly feed on mesozooplankton communities (Bachiller, 2012; Bertrand et al., 2022), which are at 80% dominated by copepods (Chouvelon et al., 2015; Dessier et al., 2018). Therefore, it is considered in this study that copepods account for most of the energy intakes of *Sardina pilchardus*. The quantity and quality of sardine's preys exhibit temporal and spatial variability in the Bay of Biscay (Vandromme et al., 2014; Grandrémy, 2023), with some areas being more beneficial energetically than others (Dessier et al., 2018). The nutritional quality of zooplanktonic preys can be assessed in different ways, for instance through fatty acid profiles or digestibility measurements (Colombo-Hixson et al., 2011). As a proxy for small pelagic fish resource quality, the present study chose to use copepod body size. Indeed, size is a master trait in marine ecosystems as it characterises the capabilities and limitations of individuals in terms of physiology and trophic strategy (Andersen et al., 2016).

For instance, the prey-predator relationship is ruled by the size ratio (Andersen and Beyer, 2006). Through an experimental design, Queiros et al. (2019) highlighted the impact of food size itself on sardine growth. This study reveals that fishes fed with food having a similar energy content but with pellets of various sizes had different growth rates, with an advantage conferred by larger pellets.

In the Bay of Biscay, a decline in the mean size of mesozooplanktonic organisms has also been noticed over the last decade. Moreover, the mesozooplankton assemblages exhibit time-consistent spatial patterns, characterised by gradients from coastal to offshore areas and from north to south in terms of abundance, species composition and size structure (Grandrémy et al., 2023). The distribution of mesozooplankton in the Bay of Biscay seems to be driven by geographical features that reflect the hydrological conditions and the availability of phytoplanktonic prey (Irigoiien et al., 2011; Dessier et al., 2018). For this study, it was chosen to focus on the spatial variability of plankton biomass and size structure over a year, rather than to study the inter-annual variability, which is an objective of an ongoing PhD.

One scientific objective of this study is to explore how environmental gradients drive the planktonic community structure in the Bay of Biscay. The second focus of this work is to determine if the variability of copepods biomass and size structure impacts on sardine growth.

To achieve these objectives, we use mechanistic modelling approaches that rely on physical equations. The zooplankton compartment is usually represented in a simple way in fisheries models (Heneghan et al., 2020). The plankton model we use in this study is a mechanistic size-based model called NUM (Nutrient Unicellular Multicellular). It has the advantage of explicitly representing both unicellular plankton and copepods with a large number of size classes. In the NUM framework, unicellular plankton is characterised by its size and trophic strategy with inclusion of autotrophic, mixotrophic and heterotrophic cells. Copepods are represented by several populations with different adult sizes and are simulated with an explicit life cycle. The abundance and size structure of copepods is already well described in the Bay of Biscay but mainly during springtime, thanks to data sampled during the PELGAS oceanographic cruise. The use of a modelling approach allows to resolve the abundance and the size structure of copepods during the whole year, including a seasonal variability.

NUM outputs in terms of copepods biomass and size structure at springtime is compared to in situ data acquired during the PELGAS oceanographic cruise. Then, indicators on copepods biomass and on their size structure are derived from NUM size spectra to force a bioenergetic DEB model (Dynamic Energy Budget) of sardine. The DEB model describes the processes of energy allocation between different compartments of an organism. The objective with the use of the DEB model in this study is to assess the spatial variability of sardine growth at contrasted stations of the Bay of Biscay. The modelling framework that is used here is a first step to model the transfer of the size structure of copepod preys to sardine predators through the trophic chain.

MATERIALS AND METHODS

1. *Study area*

1.1. *Description of the Bay of Biscay*

The Bay of Biscay is a gulf located in the eastern North Atlantic Ocean, offshore the French and Spanish coasts and between the cities of Brest and La Coruña. The bay has a narrow continental shelf in its southern part, which becomes wider in the north. The hydrological conditions in the Bay of Biscay are quite complex, with coastal upwellings, seasonal currents, and river runoffs from the Loire, the Gironde, and to a lesser extent from the Vilaine, the Adour and the Charente. These inputs strongly impact the physical and biogeochemical characteristics of the Bay of Biscay (Lassalle et al., 2011). There is a strong haline stratification from February to June and a thermal stratification between May and mid September (Guillaud et al., 2008). These seasonal stratifications limit the plankton vertical distribution.

In the Bay of Biscay, the main phytoplanktonic bloom occurs in spring and is mostly composed of microphytoplankton, ranging from 20 to 200 μm (Houliez et al., 2021). There are also winter phytoplankton blooms, mainly composed of diatoms, that are generated by the presence of short anticyclonic conditions in the outer part of the estuaries (Labry, 2001). As their resource, these primary producers drive the dynamics of zooplankton communities (Dessier et al., 2018; Grandrémy et al., 2023).

1.2. *Selection of contrasted stations based on the mesozooplankton community*

The biomass and size structure of the mesozooplankton communities exhibit spatial gradients in the Bay of Biscay. Coastal areas are known to display high zooplankton abundance with a predominance of smaller individuals. In contrast, offshore areas show a relatively higher proportion of large zooplankton, but with lower abundances (Sourisseau and Carlotti, 2006; Vandromme et al., 2014; Grandrémy et al., 2023). Recently, Grandrémy et al. (2023) emphasised the existence of a time-consistent spatial pattern of the mesozooplankton community in the Bay of Biscay, structured by three main clusters (*Figure 1*). These clusters differ in terms of taxonomic composition and biomass.

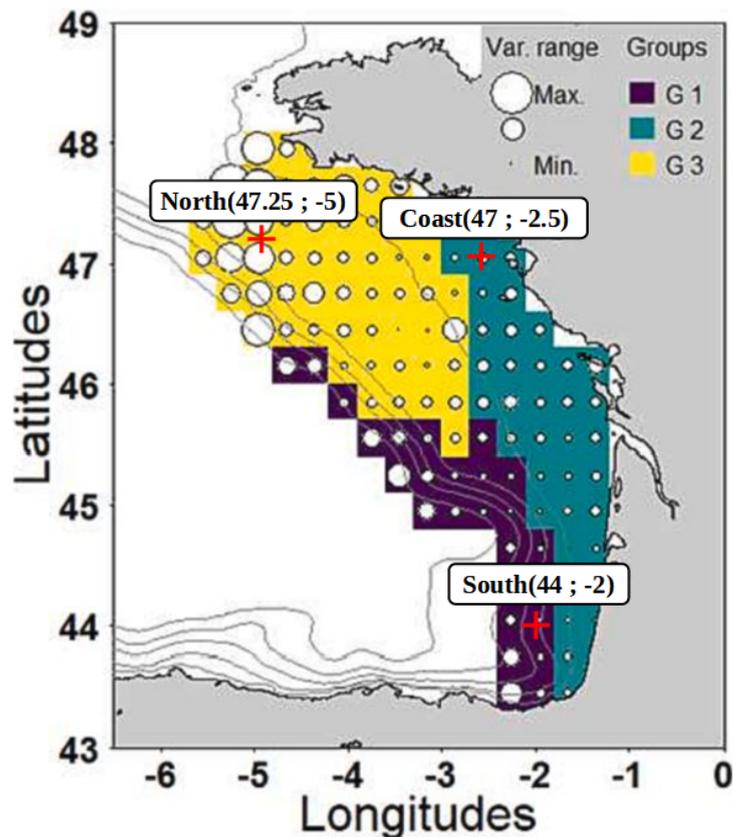


Figure 1 – Time-consistent spatial pattern of the mesozooplankton community in the Bay of Biscay (Grandrémy et al., 2023) and contrasted stations North, Coast and South

To conduct this study, three stations were selected based on their location within each of the clusters defined by Grandrémy et al. (2023) : North(47.25, -5), Coast(47, -2.5) and South(44, -2). The choice of these stations is also arising from the contrasted values they exhibit in terms of nitrates concentration and temperature.

2. Modelling approach

2.1. Environmental forcing

The version of the plankton model used in this study is forced by nitrates ($\mu\text{g.L}^{-1}$), temperature ($^{\circ}\text{C}$) and light ($\mu\text{E.m}^{-2}.\text{s}^{-1}$). Temperature and nitrates are extracted from the existing outputs of the physico-biogeochemical ECO-MARS3D model for the Bay of Biscay. To compute a climatology for these variables, temperature and nitrates are averaged daily between 2012 and 2019. The available light L is computed using *Equation 1*. The light flux at surface swhf (W.m^{-2}) is extracted from the atmospheric reanalysis ERA5 and the attenuation coefficient k_w (m^{-1}) is also extracted from the ECO-MARS3D outputs.

$$L(t, \sigma) = \text{EinConv} * \text{PARfrac} * \text{swhf}(t) * e^{-k_w(t, \sigma) * \text{depth}(t, \sigma)} \quad \text{Equation 1}$$

L is calculated regarding time t in days and vertical sigma level σ ranging from 1 (bottom) to 30 (surface). The conversion factor $E_{inConv} = 4.57$ converts $W.m^{-2}$ into μmol of $photon.s^{-1}.m^{-2}$. The fraction of total irradiance that is available for photosynthesis is noted PARfrac and equals 40%. Light is computed daily for each year between 2012 and 2019, and averaged daily in the same way as temperature and nitrates.

In order to have a vertical layer representative of the plankton development zone, it was decided to average the environmental forcing over the mixed layer depth (MLD). The MLD refers to the depth above which the physical and biogeochemical properties of the water column are relatively well-mixed and uniform. This depth varies seasonally and spatially depending notably on temperature, freshwater inputs, or winds. In this study, the MLD is calculated based on the vertical temperature gradient. The MLD is computed daily for each year between 2012 and 2019 and a MLD climatology is then derived by averaging between each day of the years over that period (*Figure 2*).

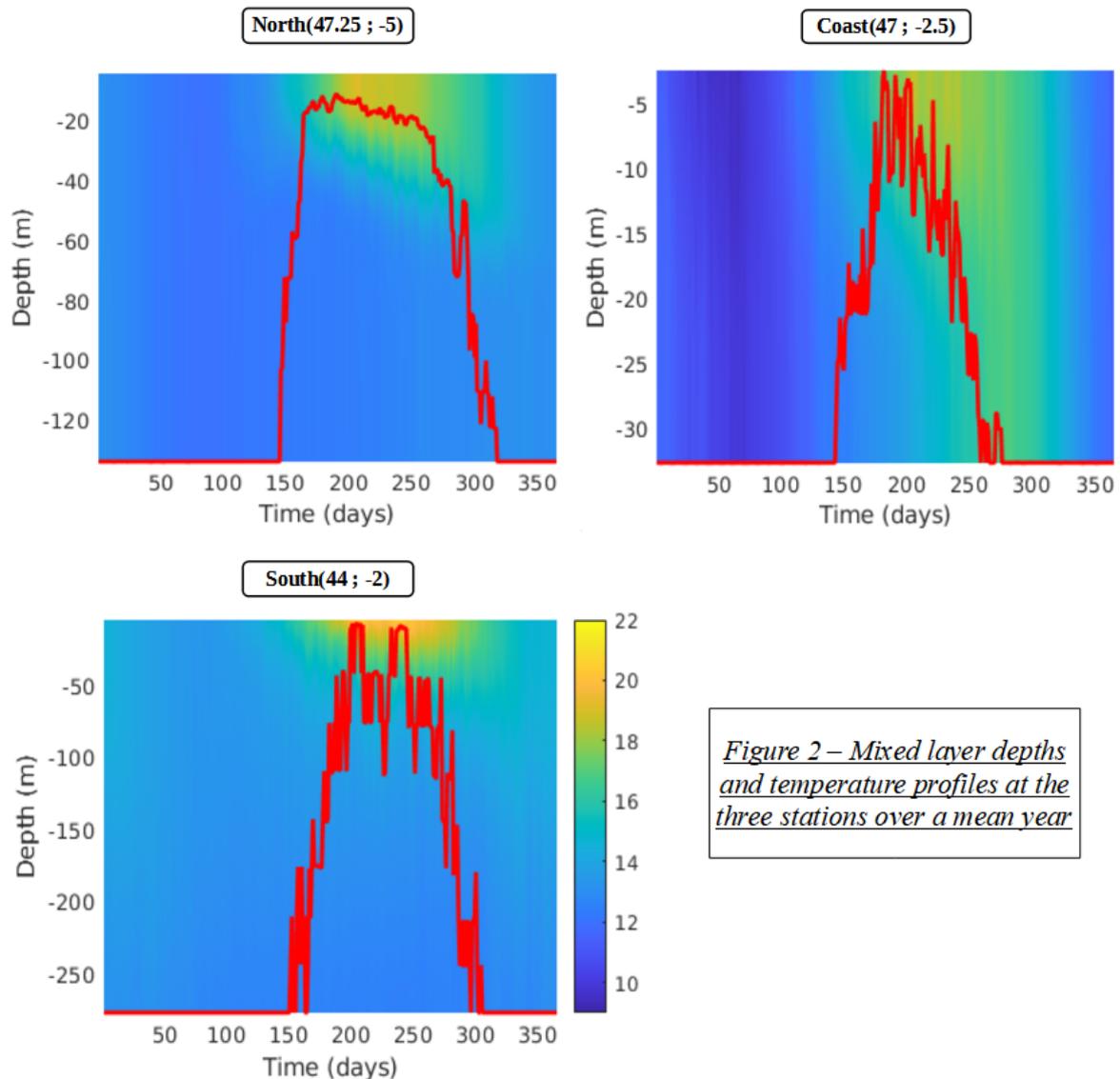


Figure 2 – Mixed layer depths and temperature profiles at the three stations over a mean year

2.2. Plankton compartment : the NUM model

2.2.1. Simulation setup

To meet the objectives of this study, the NUM plankton model is adapted for a local use in the Bay of Biscay. The model is set up in a 0D (0 dimension) configuration. This type of test run considers a system aggregated in a single point, without considering spatial variations along a dimension. A 0D simulation of the NUM model is made for each of the three preselected stations North, Coast and South. At every station, the 0D simulation of NUM loops over a spin-up of 10 years and only the last year is represented in the results. This operation ensures a certain stability of the simulation as the seasonal dynamics is reproducible.

The core equations of the NUM model are written in Fortran and interfaced with Matlab through a library. Matlab 2022a is used for model modification and post-processing of its outputs.

2.2.2. The NUM Framework

The model used to represent the planktonic community is called NUM, which stands for Nutrient Unicellular Multicellular. It includes a pool of dissolved nitrogen N, a pool of dissolved organic carbon DOC, a size-structured community of unicellular plankton named the generalists G and a defined number of size-structured copepod populations C (see [Figure 3](#)). A closure variable, called mHTL, is set to 0.1 per day to implement a mortality by higher trophic levels on copepods above a size corresponding to 1 μgC .

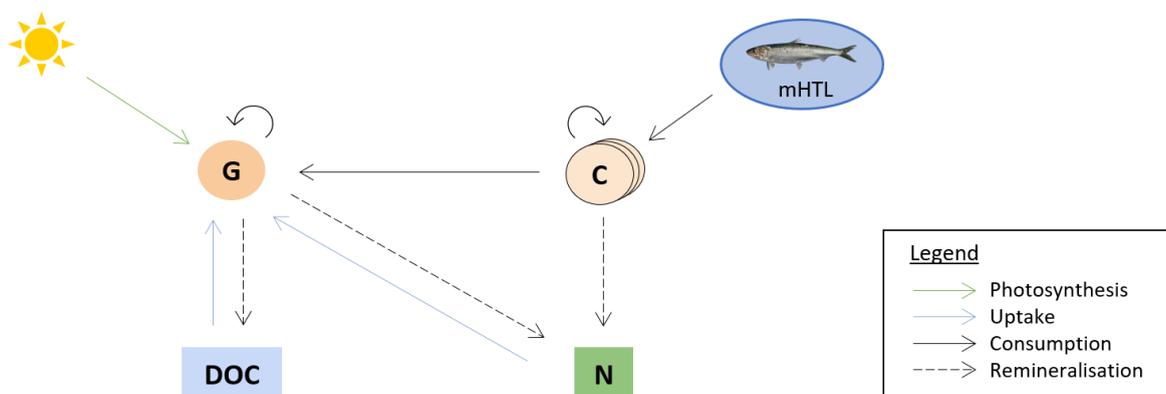


Figure 3 – Schematic representation of the ecosystem processes modelled by the NUM model in this study, adapted from (Serra-Pompei et al., 2020; Kandylas, 2022)

The generalists cover a panel of potential mixotroph protists that are able to optimise their trophic strategy according to their size and resources availability. They can be osmotrophs and grow on DOC uptake, phototroph and growth through photosynthesis and N uptake, and/or fed on smaller protists preys. The unicellular compartment of the NUM model was created and developed by Chakraborty et al., 2017; Cadier et al., 2020; Andersen and Visser, 2023. The generalists are divided in 10 size classes ranging from $3,16 \cdot 10^{-9}$ to 1 μgC .

The dynamic of their biomass is defined by their division rate δ_G and their mortality μ_G (see [Equation 2](#)). The mortality μ_G includes the mortality due to viral lysis and the predation mortality from larger generalists and from copepods.

For a size class i of generalists G ,
$$\frac{dG_i}{dt} = \delta_{G,i} \times G_i - \mu_{G,i} \times G_i$$
 Equation 2

The copepods are modelled as active feeders and can feed on generalists or smaller copepods. The multicellular compartment of the model was further developed by (Serra-Pompei et al., 2020). Five populations of copepods were defined by an implemented adult size ; respectively 0.1, 1, 10, 100 and 1000 μgC . These sizes range between 200 and 4000 μm ESD (Equivalent Spherical Diameter ou inverse) according to [Equation 3](#) (Vandromme et al., 2014). This interval encompasses the mesozooplankton size range in the Bay of Biscay, comprised between 200 and 2000 μm ESD (Vandromme et al., 2014).

For carbon content cc in μgC and equivalent spherical diameter ESD in μm ,

$$ESD = \sqrt{\frac{4}{\pi} \times \left(\frac{cc}{0.447 \times 43.38} \right)^{\frac{1}{154}}}$$
 Equation 3

Each copepod population is divided into 10 logarithmically spaced size classes, corresponding to several life stages : nauplii, eight copepodite stages and adult. The food available for a given life stage, noted s , depends on the concentration of prey. Prey selection is based on a prey/predator size ratio. [Equation 4](#) represents size predation preference of predators d on preys y , noted $\theta_{d,y}$; m_d stands for the mass of the predator, m_y is the mass of the prey, β is the preferred predator/prey size ratio, and σ represents the width of the preference function.

$$\theta_{d,y} = \exp\left(\frac{\ln\left(\frac{m_d}{\beta m_y}\right)^2}{2\sigma^2}\right)$$
 Equation 4

The dynamic process of the evolution of the copepod populations is represented in [Figure 4](#). It includes the following terms : C represents the biomass of copepod of a defined stage $s \in [1;S]$, γ describes the transfer of biomass between size classes due to somatic growth, g is a coefficient of biomass accumulation within a size class, μ is the mortality of a defined life stage and b is the birth rate of the adult copepods. The mortality μ includes the mortality by starvation, and the predation by larger copepods or higher trophic levels (Kandylas, 2022).

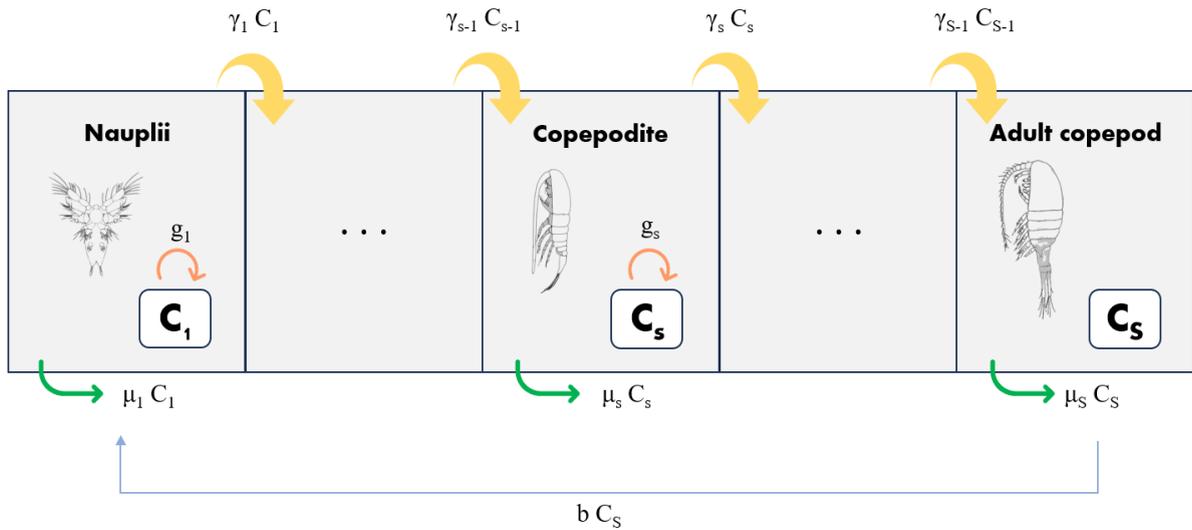


Figure 4 – Schematic representation of the copepods biomass dynamic process, adapted from (Serra-Pompei et al., 2020; Kandylas, 2022)

The process represented in *Figure 4* can be summarised with the following equations :

For the nauplii stage $s=1$,
$$\frac{dC_1}{dt} = b C_S + g_1 C_1 - \gamma_1 C_1 - \mu_1 C_1$$
 Equation 5.a

For a copepodite stage s ,
$$\frac{dC_s}{dt} = \gamma_{s-1} C_{s-1} + g_s C_s - \gamma_s C_s - \mu_s C_s$$
 Equation 5.b

For an adult copepod stage S ,
$$\frac{dC_S}{dt} = \gamma_{S-1} C_{S-1} - \mu_S C_S$$
 Equation 5.c

2.2.3. Overview of the parameters used in the NUM model

Table 1 – Parameters used in our set up of the NUM model

Symbol	Description	Value	Unit
δ_G	Division rate of the generalists		day ⁻¹
μ_G	Mortality of the generalists		day ⁻¹
G	Generalists biomass		$\mu\text{gC.L}^{-1}$
C	Copepods biomass		$\mu\text{gC.L}^{-1}$
γ	Coefficient describing the biomass transfer between copepods size classes		day ⁻¹
g	Coefficient of biomass accumulation within a copepod size class		day ⁻¹
μ	Copepods mortality		day ⁻¹
b	Birth rate of adult copepods		day ⁻¹
μ_{HTL}	Part of the copepods mortality imposed by higher trophic levels	0.1	day ⁻¹
m_{HTL}	Copepods size at which μ_{HTL} starts	1	μgC
mAdult	Adult sizes of the 5 copepods populations	[0.1 1 10 100 1000]	μgC
nYear	Time length of the NUM simulation	10	year

2.2.4. Post-processing of NUM outputs

The NUM model's output structure contains especially the biomass of generalists and copepods (in $\mu\text{gC.L}^{-1}$), their sizes (in μgC), and the values of the fluxes (in day^{-1}) transferred in and out of the system. These variables are used to construct several plots : evolution of the biomass of generalists and copepods regarding time, evolution of the biomass regarding time and size, trophic strategies regarding time and size, and the Normalised Biomass Size Spectra (NBSS) for copepods. In a first part, the focus is made on the whole planktonic community, including generalists and copepods. Then, the emphasis is on the copepods to explore the trophic link between copepods and sardines. For copepods, NBSS are computed daily and averaged during the month of May in order to be compared to the data sampled during the PELGAS survey. The method used to implement NBSS is similar to the method used to compute them from the PELGAS data and is detailed in part 3.2..

What is a Normalised Biomass Size Spectrum ?

A size spectrum is a graphical representation that illustrates the link between biomass concentration and body size of organisms. To construct a biomass size spectrum, measurements of biomass are distributed among successive logarithmic size bins (*Figure 5*). To build a Normalised Biomass Size Spectrum, the biomass value within each bin is divided by the width of the corresponding size bin. Therefore, the obtained NBSS becomes independent of the specific size class definition used.

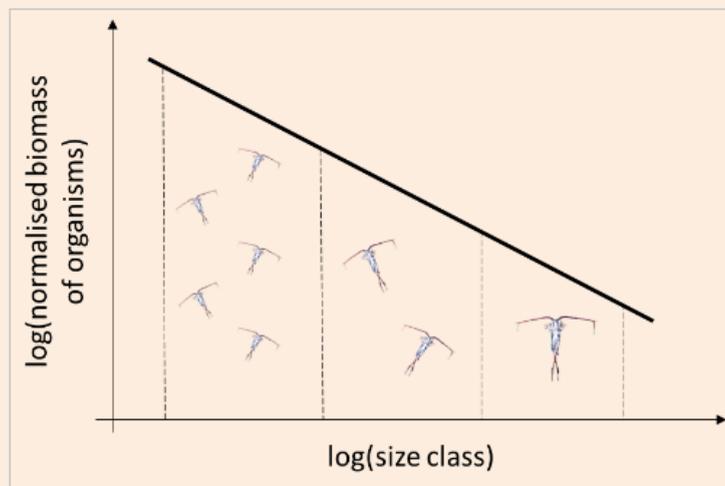


Figure 5 – Schematic representation of a NBSS for copepods

The NBSS has the theoretical characteristic of being a straight line. The slope is therefore a characteristic feature of the NBSS. This slope provides information about the proportion of small organisms compared with larger organisms. A flatter slope is interpreted as indicating an increase in the proportion of organisms in the largest size classes.

Adapted from (Andersen and Beyer, 2006; Sprules and Barth, 2016; Grandr my, 2023)

2.3. Small pelagic fish compartment : the DEB model

The Dynamic Energy Budget theory was developed by Kooijman (2010). This framework describes the repartition of the energy fluxes from the food intake of an individual to its use for growth, reproduction and maintenance. The DEB model comprises 4 state variables characterising an organism, namely reserve, structure, and maturity or reproduction depending on the life stage (*Figure 6*). The energy from the assimilated part of the ingested food is stored in the reserve compartment. Then, this reserve energy is either allocated to the individual's structure or to its maturity or reproduction. Once the individual is mature, the energy that was previously allocated to maturity switches to reproduction. A part of the assimilated energy is used to maintain the organism, through somatic and maturity maintenance. The DEB model allows to study the energy allocation within an organism at

different stages of the life cycle (larvae, juvenile, adult) and at different seasons throughout the year (Gatti, 2016; Queiros, 2019).

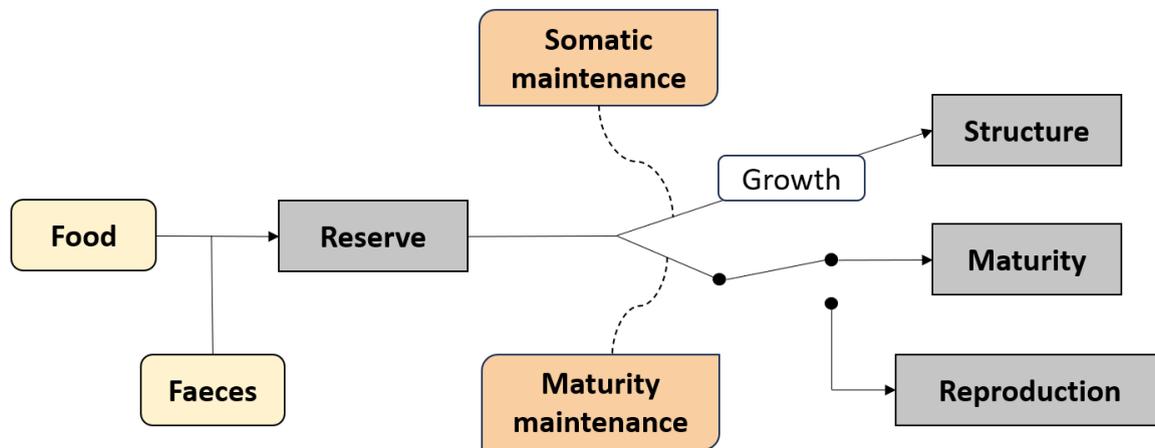


Figure 6 – Representation of the bioenergetic process modelled with DEB, adapted from (Gatti, 2016; Menu et al., 2023)

This study uses the DEB model for sardine developed by Gatti, 2016 and then Menu et al., 2023. Three average individuals are defined for each preselected stations North, Coast and South. Their whole life cycle is modelled, from larvae to juvenile and finally adults up to 7 years. At each station, daily temperature, copepods biomass and their size structure were extracted from the NUM model to be used as inputs of the DEB model. The copepods size structure is provided in a synthetic way, through the slope of the daily Normalized Biomass Size Spectra. The daily slopes are computed from linear regressions adjusted on the NBSS obtained each day over the last year of the NUM simulation spin up. For a given biomass of copepods, different slopes are possible that distribute the biomass differently among size classes. This size information is important for sardines as they prey upon selected size classes, depending on their own size.

3. Comparison with in situ data

3.1. PELGAS sampling scheme

The PELGAS survey covers the French continental shelf and takes place in May each year since 2000 on board the RV “Thalassa”. It is designed to monitor the spring pelagic ecosystem of the Bay of Biscay, with a scientific crew divided into four teams : an acoustic team, a fishing team, a hydrobiology team and a megafauna team (Doray et al., 2018b). The hydrobiology team samples the data we are interested in to compare to our model outputs. At night, WP2 zooplankton nets of 200 μm mesh, equipped with a mechanical flowmeter, are deployed up to 100 m deep, or up to 5 m above the seabed for coastal shallow stations (Doray et al., 2018b). The WP2 net quantitatively samples objects whose equivalent spherical diameter is between 400 and 2500 μm (Vandromme et al., 2014). Until 2016, the zooplankton samples were preserved with 4% buffered formaldehyde and identified manually on land using a ZooScan. From 2017 onwards, the WP2 samples are directly digitised and analysed

on board using a ZooCAM (Grandrémy et al., 2023). The ZooCAM allows a time-efficient gross taxonomic identification of the zooplankton organisms using the Ecotaxa semi-identification procedure (Colas et al., 2018). Grandrémy et al. (In Press) constituted a database combining the data obtained from the ZooScan and the ZooCAM between 2004 and 2019. The data obtained from both instruments are comparable (Colas et al., 2018). A subset of this database, selecting only the copepods sampled between 2012 and 2019, is used in this study.

3.2. Computation of Normalized Biomass Size Spectra and indicators derivation

The copepods Normalized Biomass Size Spectra (NBSS) obtained from NUM are expressed in $\log(\mu\text{gC.L}^{-1} / \mu\text{gC})$ with respect to the size of the organisms, expressed in $\log(\mu\text{gC})$. To obtain comparable results, the NBSS computed from PELGAS data is calculated from the individual carbon content of copepods sampled in May between 2012 and 2019. The individual carbon content (in μgC) is calculated from the available data `object_area` (in pixel) following the methodology described in [Figure 7](#).

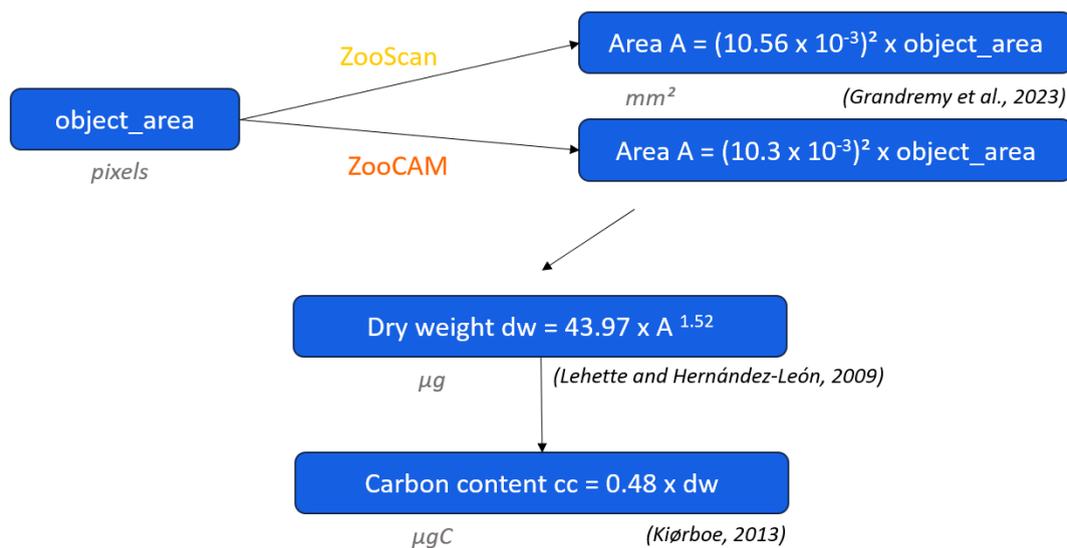


Figure 7 – Methodology used to compute the individual carbon content of copepods

To construct the NBSS, the individual carbon contents are organised in size classes. The spectrum is computed on 21 size classes, logarithmically spaced, and ranging from 0.001 μgC to 1048.576 μgC to cover all the copepods sizes of the dataset and in line with the NUM size classes defined for copepods. The middle points of these size classes are represented on the x-axis of the NBSS, in $\log(\mu\text{gC})$.

The normalised biomass is represented on the y-axis of the NBSS. This biomass is computed from the sum of the carbon content by size class and weighted by the sampled volume. Then, the obtained biomass is normalized by the width of the size class, so the obtained spectrum does not depend on the definition of the size classes. The unit of the plotted normalised biomass is in $\log(\mu\text{gC.L}^{-1} / \mu\text{gC})$, which is consistent with the NUM model's representation.

The size spectra are calculated at the three stations and characterised by their slope a and intercept b . These indicators are computed from a log-linear regression, following the *Equation 6* (Huret et al., 2012; Vandromme et al., 2014). B_i represents the copepods biomass of the size class i in $\mu\text{gC.L}^{-1}$, Δ_i is the width of the size class i in μgC and w_i represents the mid of the size class i in μgC .

$$\log\left(\frac{B_i}{\Delta_i}\right) = a \times \log(w_i) + b$$

Equation 6

In the Bay of Biscay, the mesozooplankton size range is between 200 and 2000 μm ESD (Vandromme et al., 2014). This interval corresponds to the size classes comprised between -2.40 and 5.22 $\log(\mu\text{gC})$ according to *Equation 3*. The linear regressions are calculated on this interval.

RESULTS

1. Environmental contrasts between the stations selected in the Bay of Biscay

The evolution of nitrates throughout a climatology year exhibits a seasonality, with lower values during summer and higher values at wintertime due to a higher mixing at this period. Moreover, the coastal station has much higher nutrient values, linked to river runoffs (*Figure 8-a*). In terms of temperature, the seasonality is also marked, and there is a spatial variability with a warmer South station and a colder Coast station (*Figure 8-b*). The light values seem less contrasted but the South station is brighter compared to the North station (*Figure 8-c*). The three stations chosen present contrasting forcing for our NUM model, with a nutrient rich and colder Coast station, a relatively nutrient poor and light limited North station, and a relatively nutrient poor, warmer and brighter South station.

Furthermore, the period and timing of the seasonal pattern varies between stations. For the stations North and Coast, the environmental variables undergo a sudden shift around day 150, i.e. at the end of May for light and temperature. The South station experiences the same shifts but later, around day 170, i.e. in the second part of June. The duration of these shifts also varies between stations. This seasonal variability is associated with the calculation of the mixed layer depth, which exhibits pronounced seasonal variations.

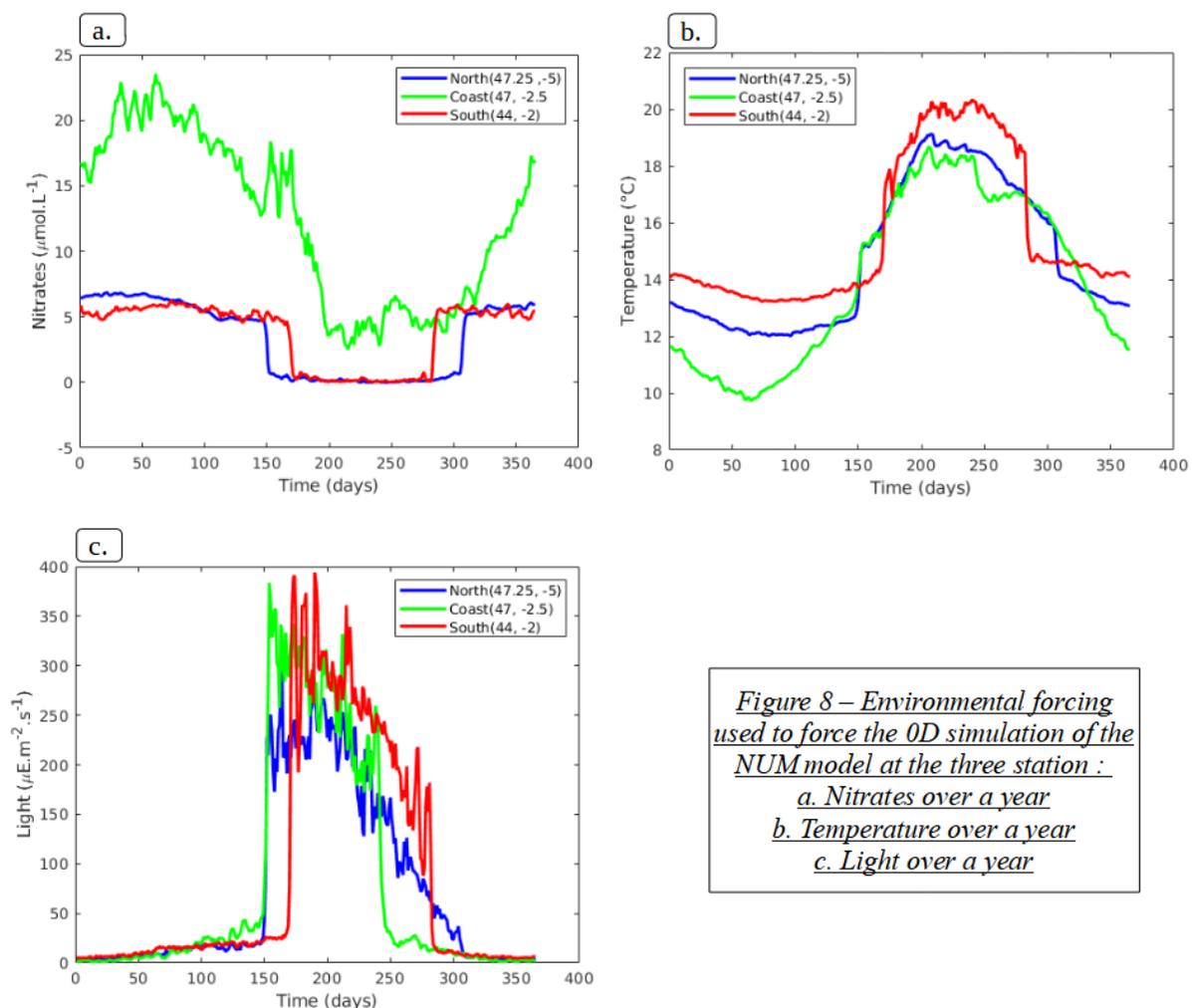


Figure 8 – Environmental forcing used to force the 0D simulation of the NUM model at the three station :
a. Nitrates over a year
b. Temperature over a year
c. Light over a year

2. The structure of the plankton community in the Bay of Biscay

2.1. Biomass and trophic composition

At the three stations, the NUM outputs in terms of biomasses of generalists and copepods exhibit a seasonal pattern (*Figure 9*), following the variations of the environmental forcing. The timing of the bloom starts around day 100, i.e. in the first part of April. At this time, the environmental conditions are right for the development of the generalists. Then, the copepod community grows, feeding on smaller organisms. In the first half of the bloom, until day 200, the biomass levels of each group follow the size structure, with the smallest organisms having the highest biomass, and the larger the organism, the lower their biomass. This is the classic structure of biomass in a trophic chain. From the second half of the bloom, at the North and South stations, the largest copepods, whose adult size is 1000 μgC , become more abundant than copepods of 10 and 100 μgC . This phenomenon occurs later at Coast, around day 250. At the coastal station, a steady state between copepods growth and mortality seems to be reached during a period of around 50 days, with constant values of copepods biomasses for sizes higher than 0.1 μgC .

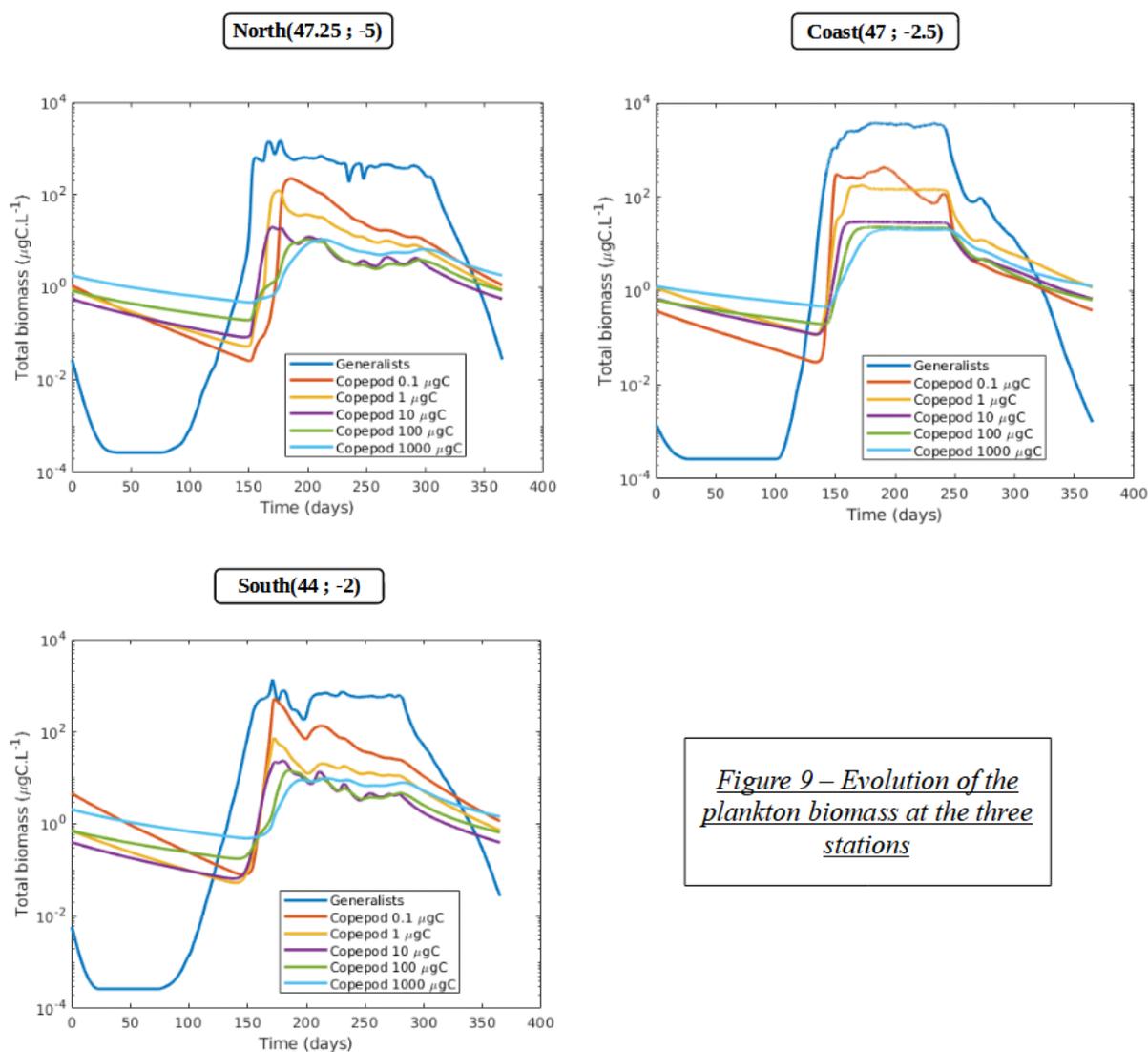


Figure 9 – Evolution of the plankton biomass at the three stations

The *Figure 10* represents the trophic strategies of the generalists regarding time and size in μgC . Sizes range from 10^{-9} to $1 \mu\text{gC}$, which corresponds to a size range for unicellular plankton comprised between 0.6 and $500 \mu\text{m}$ ESD. The first pattern of the year is green, which corresponds to photoautotroph organisms. Then, the coastal station especially is characterised by a blue pattern of small osmoheterotroph organisms such as bacteria that fed on nutrient uptakes. The red pattern corresponds to heterotrophy and the other colours represent various degrees of mixotrophy. After the development of phytoplanktonic organisms, all stations are characterised by mixotroph unicellular organisms.

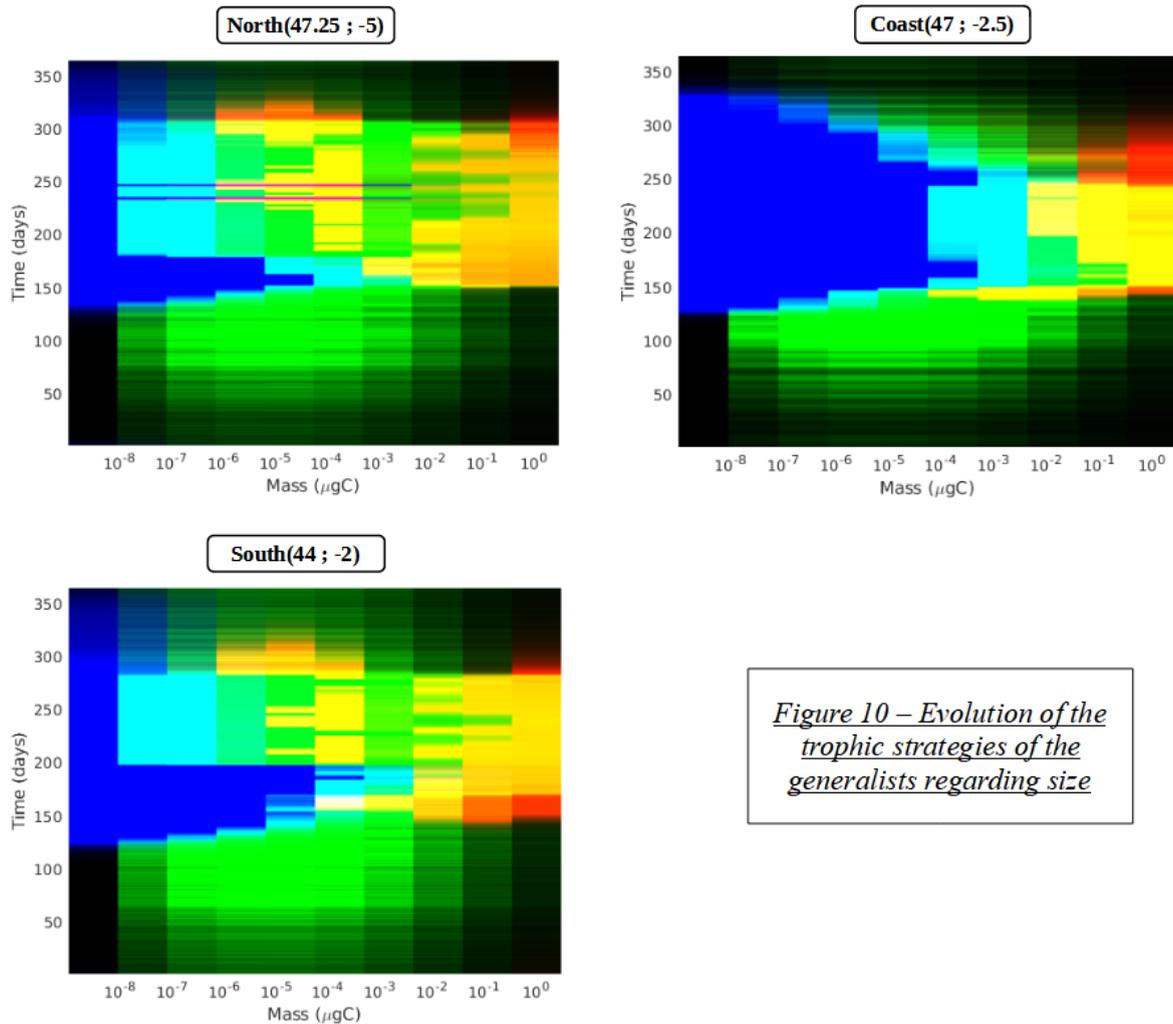


Figure 10 – Evolution of the trophic strategies of the generalists regarding size

2.2. Biomass and size structure of the plankton community

At the North and South stations, a bloom of small plankton (10^{-8} μgC), likely corresponding to osmotrophic bacteria, can be observed (*Figure 11*). At the northern station, this bloom initiates around the 170th day (mid-June), while at South, a first peak is noted starting from the 150th day (late May), followed by a second, longer peak from the 200th day (mid-July). The remaining patterns, excluding the smallest bacteria, obtained for the stations North and South are quite similar whereas the Coast station displays a more abundant plankton bloom. Indeed, plankton biomasses at Coast remain higher throughout the summer compared to North and South, for both generalists and copepods. The size range covered by plankton patterns (excluding bacteria) differs at each station : at North, sizes start at 10^{-5} μgC , at Coast, from 10^{-6} μgC , while at South, they start from 10^{-4} μgC . For each station, the five copepod populations can be distinguished by vertical bands as they have been defined discretely. The trophic cascading from abundant small copepods to less abundant large copepods is noticed at each station.

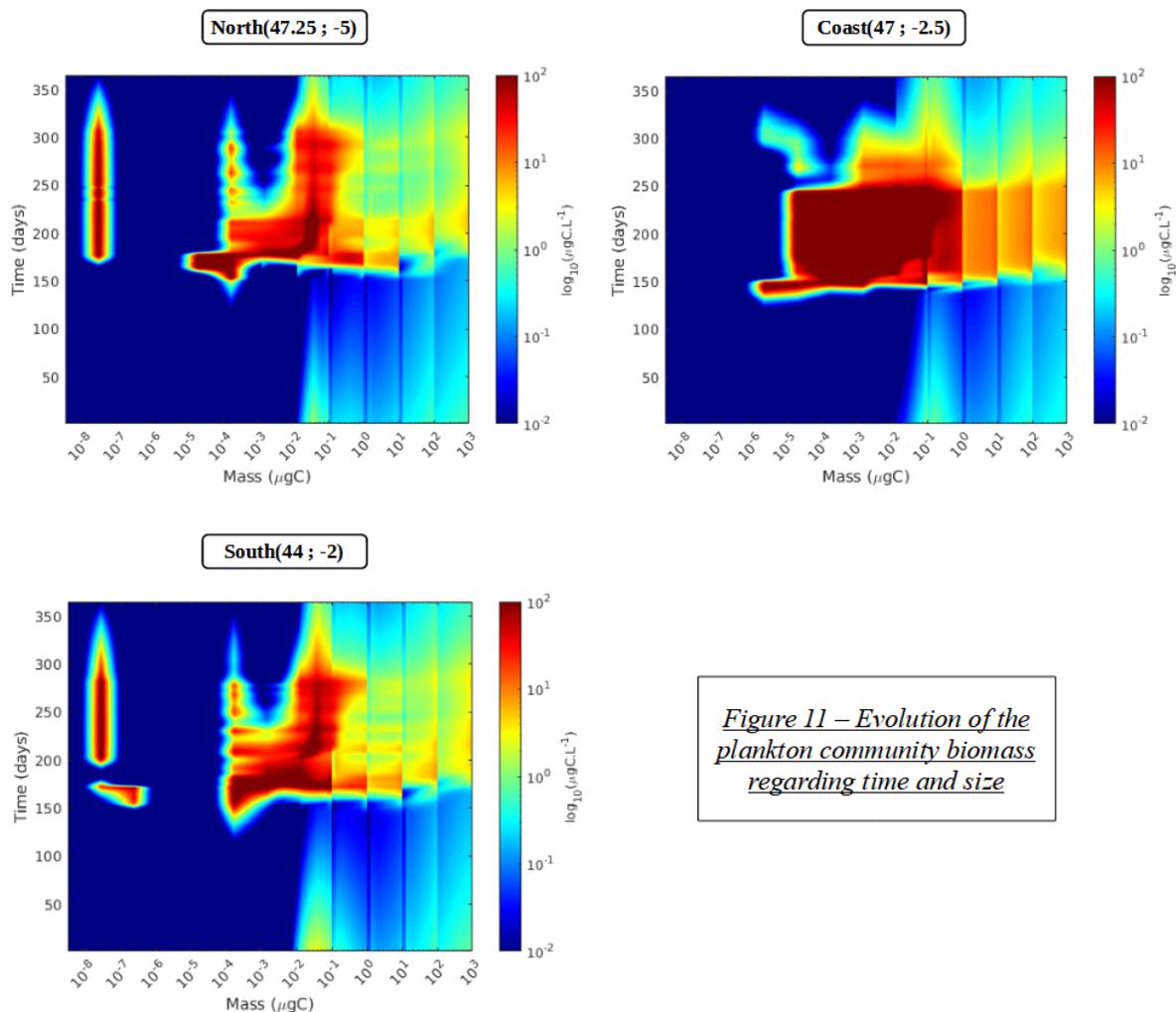


Figure 11 – Evolution of the plankton community biomass regarding time and size

2.3. Focus on the copepods biomass and size structure

2.3.1. Comparing the NUM model outputs in May with PELGAS in situ data

The comparison of the NBSS obtained from NUM (*Figure 12.a*) reveals dissimilarities between stations. Notably, the Coast station exhibits a steeper slope than the North and South stations that seem more similar. The slope of the linear regression informs on the balance between smaller and larger organisms. A flatter slope indicates an increase in biovolume within the larger size classes (Grandrémy, 2023). The intercept can be seen as an indirect indicator of the biomass level. Thus, during the month of May, the Coast station displays a higher biomass of smaller organisms whereas the North and South stations exhibit lower biomasses of larger organisms.

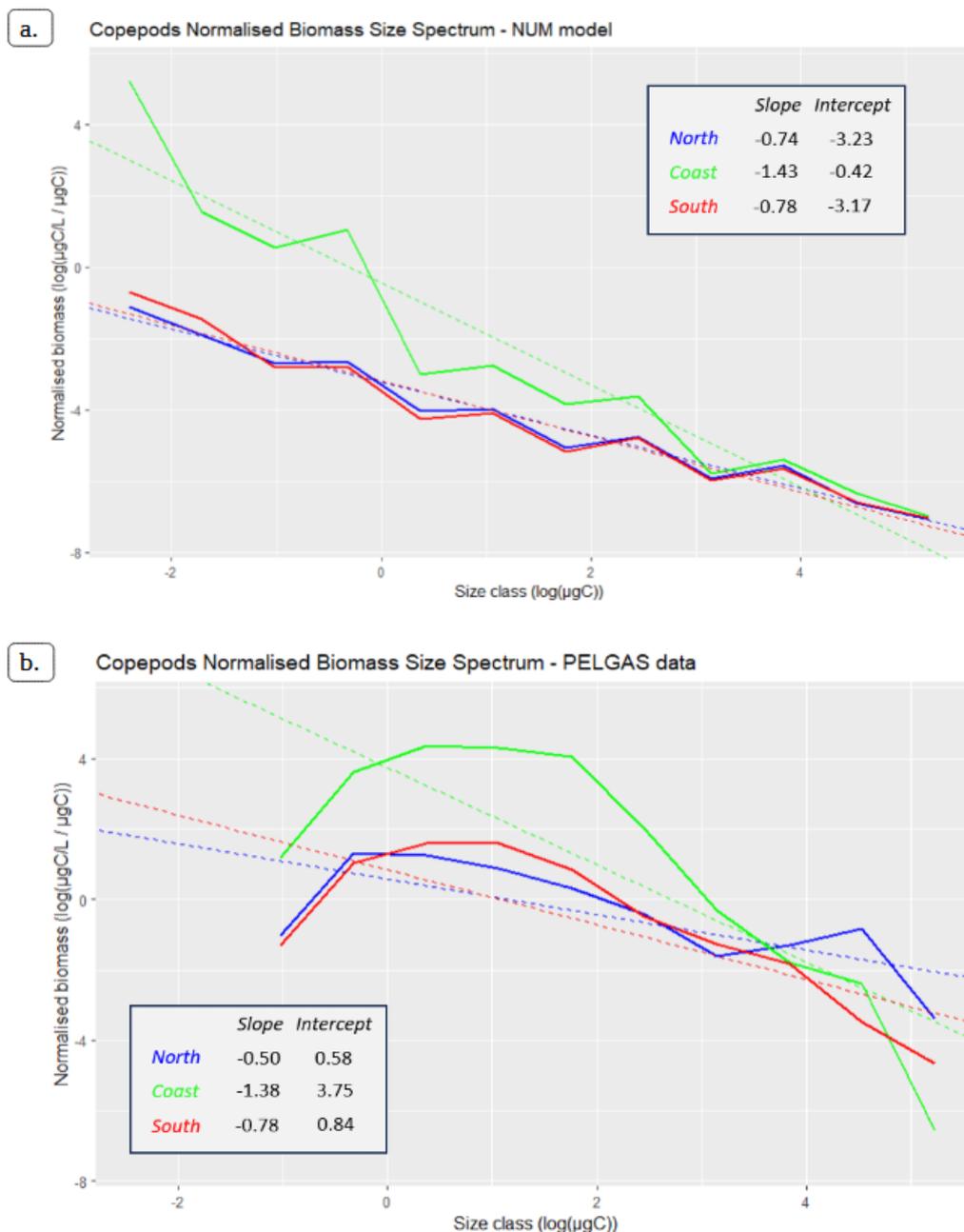


Figure 12 – Comparison of the copepods Normalised Biomass Size Spectra obtained from the NUM model for the month of May (a.) and obtained from PELGAS in situ data (b.)

The NBSS computed from PELGAS data also displays inter-station variability (*Figure 12.b*). Indeed, the Coast station exhibits a steeper slope than the North and South stations. By comparing the NUM spectra results with those from PELGAS, one can notice that they exhibit relatively comparable slopes, suggesting that the NUM model aptly captures the copepods size structure in May in the Bay of Biscay.

2.3.2. Copepods biomass and size structure over a year obtained from NUM outputs

The computation of the daily size spectra over a year with the NUM model reveals that the copepods abundances are higher at Coast all over the year (*Figure 13*). The stations North and South are more similar, with a noteworthy peak of biomass at South around day 170 (mid June).

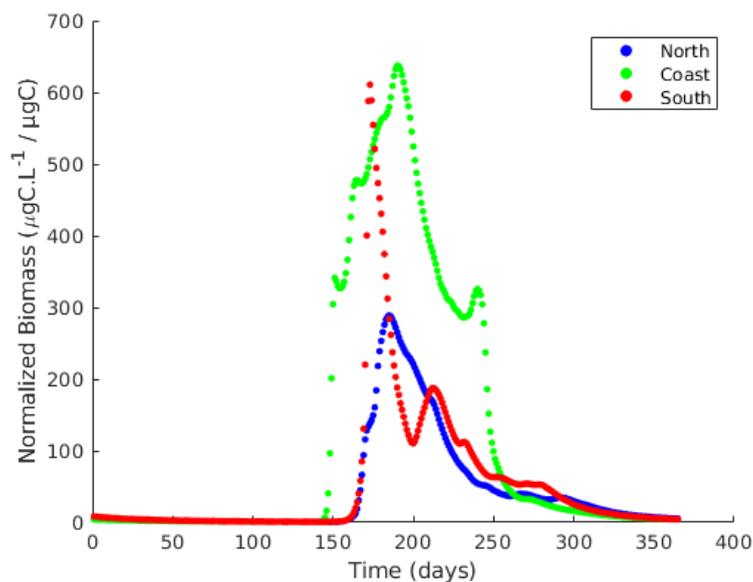


Figure 13 – Total daily biomass of copepods for each station as simulated by the NUM model

Figure 14 displays the daily slopes and intercepts estimated from linear regressions computed on daily NBSS derived from the NUM model. Throughout the year, the Coast station exhibits steeper slopes than the North and South stations. Therefore, the coastal point tends to display smaller organisms all over the year, whereas the offshore stations tend to display larger organisms all over the year. Around day 170, this trend is reversed over a very short period.

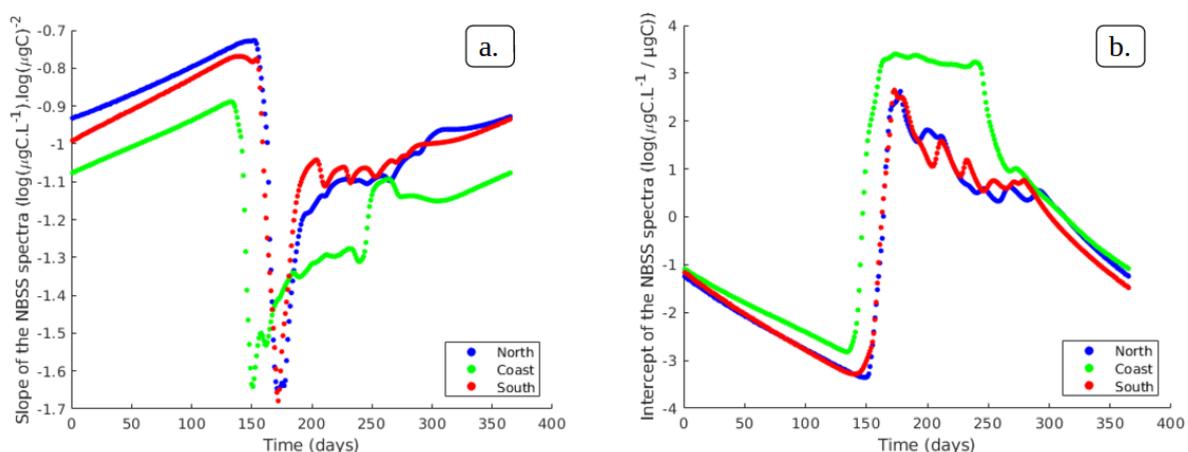
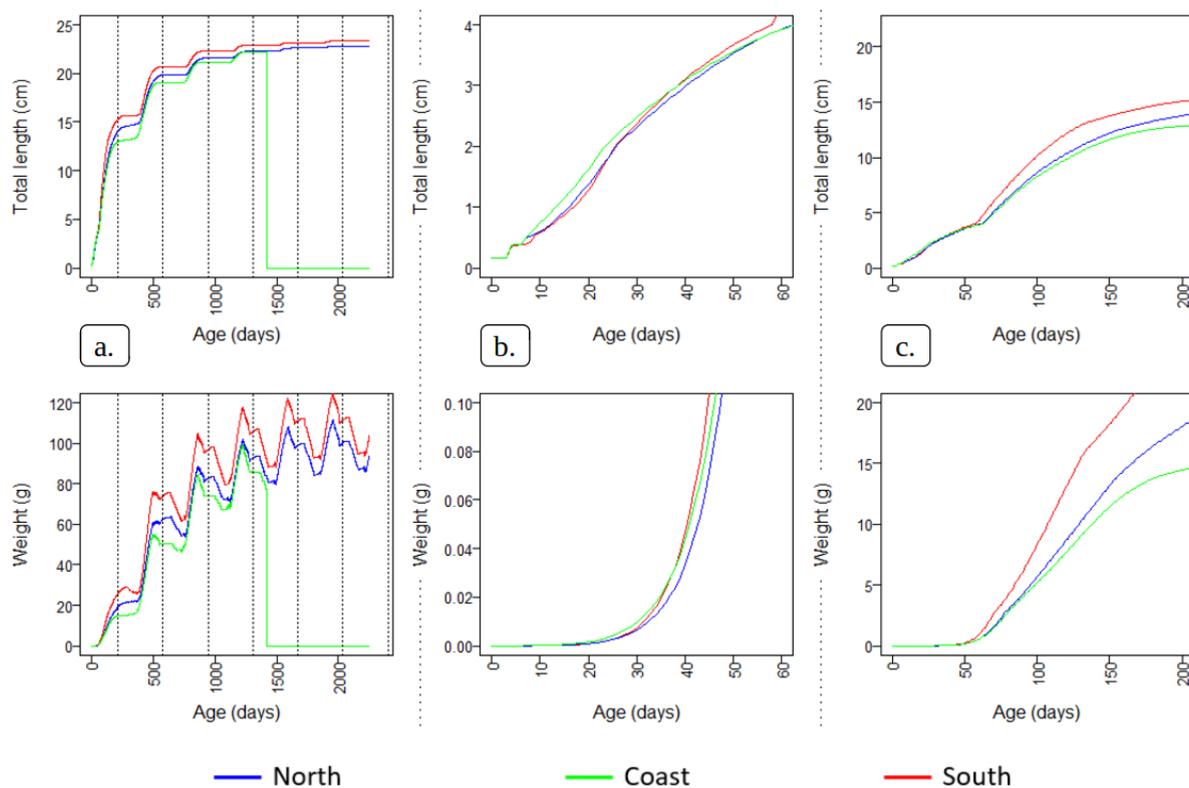


Figure 14 – Daily Normalised Biomass Size Spectra slopes (a.) and intercepts (b.) for each stations

3. Effect of copepods biomass and size structure on sardine growth

The results of *Figure 13* and *Figure 14*, i.e. the copepods biomass and size structure under the form of the slope of the NBSS, are used as inputs of a DEB model for sardine. Between stations, the growth curves are quite different. During the 40 first days, one can notice a faster growth for sardine at Coast than at North and South (*Figure 15.b.*). Then, this pattern reverses. The high biomass of small copepods displayed at Coast seems to be favourable to very young sardine stages, whereas the lower abundance but with larger copepods (North and South) seems to be more beneficial to older sardine stages. The South station displays the most beneficial conditions for juvenile and adult sardine growth (*Figure 15.a.*). At Coast, at age 4-5 the growth curve decreases to 0, which means that the individual dies.



*Figure 15 – Sardine growth curves obtained from the DEB model at our three stations :
a. Representation on 7 years, b. Representation of the 60 first days of sardine development,
c. Representation of the 200 first days of sardine development*

To determine whether these results mainly stem from variations in the biomass or variations in the size structure of copepods, another DEB simulation is run with only the slopes varying between each station (*Figure 16*). The temperature and the copepods biomass are set to the Coast values. In this second simulation, the differences previously observed for the South station no longer appear. Therefore, the observed variations in sardine growth between the stations North and South *Figure 15* is mainly due to differences in biomass at those stations.

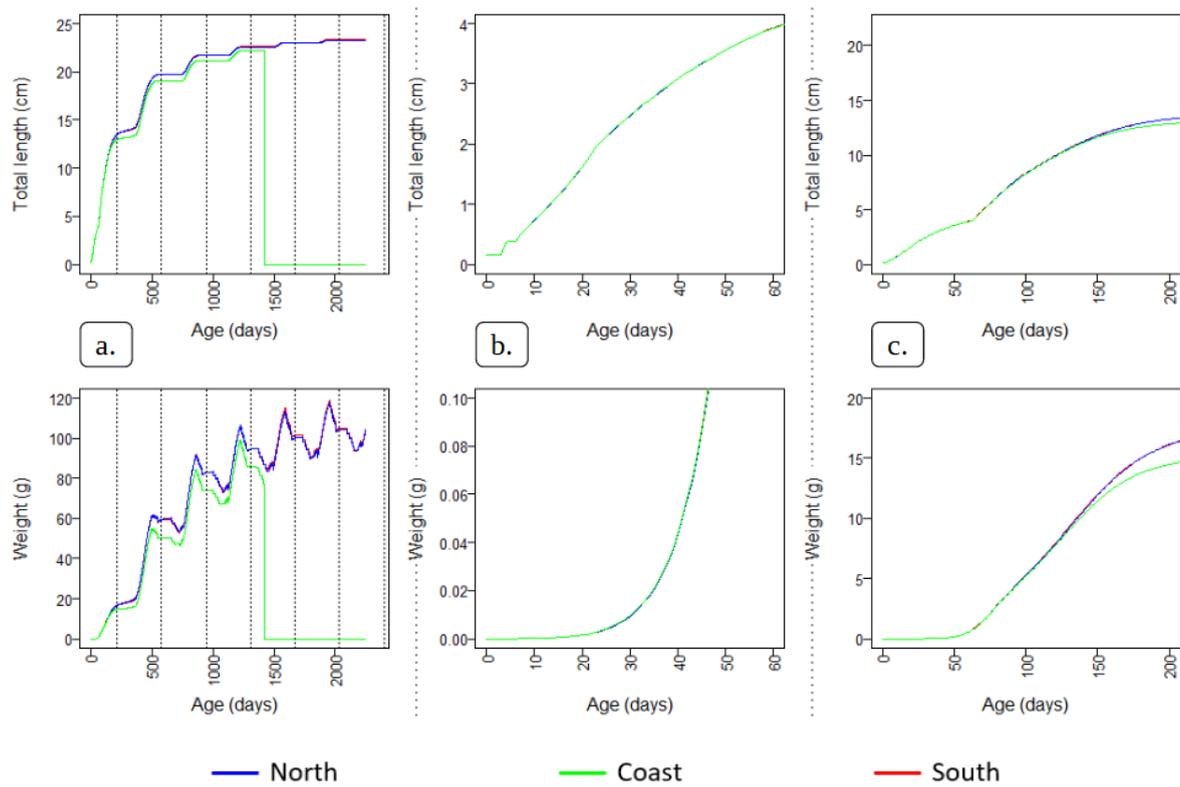


Figure 16 – Sardine growth curves with only copepods size structure varying between stations : a. Representation on 7 years, b. Representation of the 60 first days of sardine development, c. Representation of the 200 first days of sardine development

For both simulations, adult sardine of age 4-5 dies at the Coast station. The predominance of smaller copepods at this coastal station therefore seems to be detrimental to the development of the adult stages of sardines.

DISCUSSION

1. How do environmental spatial gradients impact the planktonic community in the Bay of Biscay?

1.1. Seasonal variations of the plankton biomass

For each of the three stations, the plankton biomass obtained from the NUM model shows strong seasonal variations. In fact, the first part of the year is characterised by rather low biomasses of generalists and copepods. An initial bloom of generalists begins in April/May, followed a few days later by a bloom of copepods, whose concentrations maintains relatively high throughout summer, especially at the Coast station. These variations in plankton biomass are mainly the result of seasonal variations in environmental forcing in terms of nitrates, temperature and light. These seasonal changes in environmental forcing are themselves closely linked to the seasonal variability of the mixed layer depth over which they have been averaged. The computation of the MLD is satisfactory for the purposes of this study, as it provides a plankton development zone that varies seasonally and spatially, between the three stations. However, the mixed layer depths obtained can be criticised. For example, at the coastal station, the MLD values obtained around day 180 are very shallow (< 5 m). At the South station, very shallow values were also obtained around days 200 and 240. To take the study further, the calculation of the MLD could be improved by revisiting the algorithm used. For example, instead of calculating it on the basis of a temperature gradient, it could be calculated on the basis of a density gradient, which would make it possible to include vertical variations in salinity and obtain a more accurate stratification.

1.2. Spatial variations of the plankton biomass

Comparison of the biomasses obtained at the three stations North, Coast and South revealed some disparities. The North and South stations are fairly similar in terms of generalist and copepod biomass. The Coast station exhibits higher biomasses for both generalists and copepods. This seems to be linked to the nitrate input at each station. In fact, the coastal station is rich in nitrates, while the two stations further offshore seem to be more nutrient-limited. These gradients in biomass from the coast to the open sea are in line with the observations made in spring for mesozooplankton in the Bay of Biscay: biomasses are higher at the coast whereas they tend to be lower in the offshore area (Sourisseau and Carlotti, 2006; Bachiller, 2012; Vandromme et al., 2014; Grandrémy et al., 2023). In the literature, this coast-offshore biomass gradient is less obvious for generalists, since they include bacteria, phytoplankton and small zooplanktonic organisms. Marquis et al (2011) compared the phytoplankton and nano-microzooplankton biomasses of a coastal station located in the Gironde estuary and an offshore station. The biomasses recorded at the coast were higher than those obtained offshore, which could partly confirm our model outputs for generalists.

2. *What is the copepods size structure in the Bay of Biscay ?*

2.1. *Comparing NUM outputs with in situ PELGAS data in May*

A comparison of the NBSS from the NUM model with the NBSS from the PELGAS data emphasises that the model correctly reproduces the differences in slope between the stations. In fact, whether using the model or the data, the coastal station has a steeper slope than the North and South stations, which are further offshore. These differences in slope can be interpreted as a prevalence of small copepods at the Coast and a higher proportion of large copepods at the North and South stations. The size structure of the copepods obtained from the NUM model in May is also in line with the literature relating in situ observations made in spring: prevalence of small organisms at the coast and a larger proportion of bigger organisms offshore (Sourisseau and Carlotti, 2006; Vandromme et al., 2014; Grandrémy, 2023). The coast-offshore size gradient can be seen on the map of slopes obtained by Grandrémy (2023) from PELGAS in situ data (*Figure 17*). To produce this map, NBSS was calculated using biovolumes (mm³). The slopes we obtained are quite different as they are calculated on the basis of carbon content (µgC).

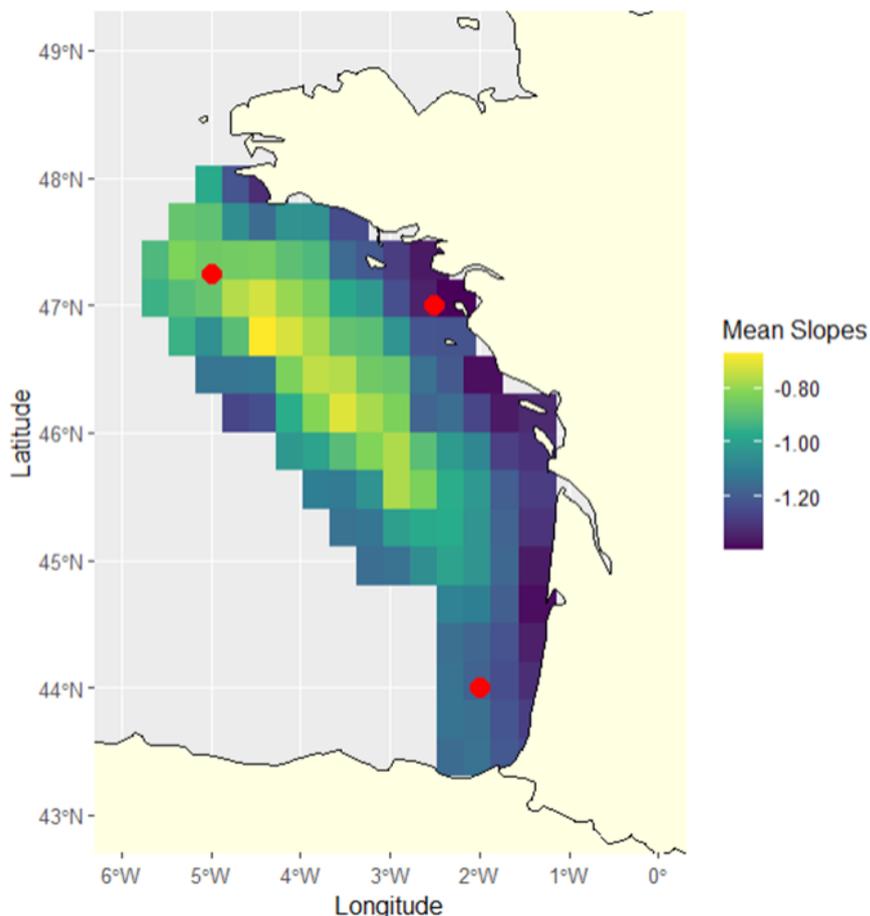


Figure 17 – Mean NBSS slopes obtained from PELGAS data between 2012 and 2019, red dots represent our three stations North, Coast and South. (Grandrémy, 2023)

2.2. *Extrapolating copepods size structure over a year with NUM*

NUM outputs over the last year of the spin-up year reveal variations in biomass and size structure between stations. The Coast station has an overall higher biomass over the year, with a dominance of small copepods. The North and South stations are fairly similar to each other. They display lower biomasses over the year, with a higher proportion of large copepods. Therefore, according to the NUM simulations, the spatial gradient in copepods size observed at springtime is the same all over the year. This result is an important contribution of the model compared with data sampled during the oceanographic cruises since it provides information for the whole year.

3. *How do the spatial variations in copepod biomass and size structure impact sardine growth ?*

The Coast station has an overall higher biomass over the year, with a dominance of small copepods. The North and South stations exhibit lower biomasses over the year, with a higher proportion of large copepods. Using these NUM outputs to force a DEB model for sardine revealed inter-station differences. The coastal station, with a high biomass of small copepods, seems to be more favourable to very young sardine stages. The DEB simulation relying only on the size spectra slopes highlighted the very unfavourable size structure of copepods at the Coast station for adult sardines, while the size structure of copepods at stations further offshore seems to be more favourable to them. According to observations made in the Bay of Biscay on anchovy, a similar small pelagic species in terms of ecology, larvae and juveniles are indeed mainly concentrated in coastal areas (Cotano et al., 2008; Boyra et al., 2013). There is also a coast-offshore size gradient, with young, small sardines at coast and older, larger sardines offshore (Véron, 2020). These findings are in line with the DEB model outputs. Indeed, we have a coastal station, with small organisms, more favourable to young stages and offshore stations favouring older sardines, and presenting larger copepods.

However, these results should be interpreted with caution, as adult sardines are also capable of filter-feeding on small prey thanks to their gill rakers. In fact, although the size range of catchable prey increases with the size of the predator, the diet of adult sardines does not exclude small planktonic organisms (Bachiller, 2012; Gatti, 2016). In this study, sardines were considered to feed mainly on copepods throughout their lives. An interesting perspective could be to implement variable dietary intakes for sardines depending on their life cycle. For the time being, the size of copepods varies according to life stage. However, adult sardines have better filtration capacities than juveniles and are also able to feed on small phytoplankton prey (Bachiller, 2012; Gatti, 2016). It would be possible to envisage a supply of generalist prey and not only copepods for adult sardines.

4. Is there a transfer in size structure through the trophic chain in the Bay of Biscay ?

In the Bay of Biscay over the last few decades, the size at age of sardines has decreased (Véron et al., 2020). At the same time, a decline in the average size of mesozooplankton, which makes up the bulk of sardines' diet (Bachiller, 2012), has been observed in the same area (*Figure 18*). In fact, small mesozooplanktonic organisms tend to be smaller and more numerous, and the size of larger organisms has also declined (Grandrémy, 2023).

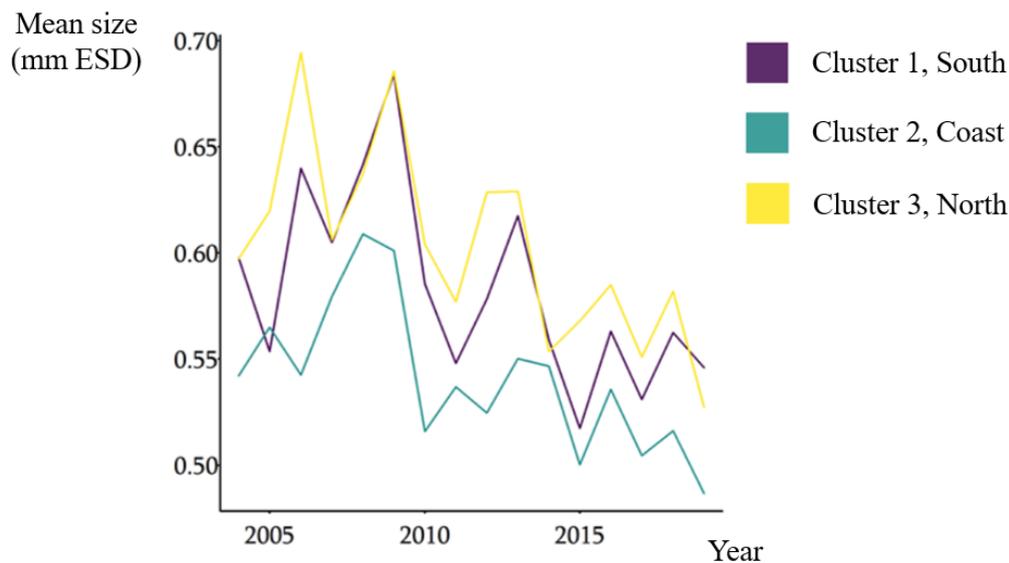


Figure 18 - Time series of mean mesozooplankton size (mm Equivalent Spherical Diameter) constructed by clusters between 2004 and 2019, the location of the stations used in this study are written in the legend, next to the clusters, (Grandrémy, 2023)

In the Mediterranean sea, a decline in the size of sardines has also been observed since 2008. This decrease in size seems to have coincided with a shift in the diet of sardines, from a high proportion of large copepods between 1994 and 2007, to a dominance of small copepods in 2011 and 2012 (Brosset et al., 2016). Smaller organisms generally have a lower energy content than larger organisms (Zarubin et al., 2014; Barroeta et al., 2017). Independently from energy content, it has been shown that food size alone influences sardine growth. The consumption of small particles seems to be less favourable to predators than that of larger particles. The hypothesis put forward to explain this phenomenon is that sardines consuming smaller preys expend more energy to filter feed than sardines hunting larger preys (Queiros, 2019). A reduction in the average size of mesozooplankton could therefore be unfavourable to predators such as sardines. The results obtained in this study show that the reduction in zooplankton size would a priori be favourable to sardine juveniles but not to adult stages. This could explain the fact that there have been good recruitments over the last few decades and, at the same time, a reduction in the size of adult sardines in the Bay of Biscay.

In addition, the reduction in zooplankton size is sometimes associated with a reduction in the size of primary producers. Indeed, the reduction in algal cell size has an impact on the size structure of microzooplankton (Labry, 2001; Marquis et al., 2011). Yet, the

hypothesis of a transfer of size structure within the trophic chain must be treated with caution, as the reduction in the size of mesozooplankton has not been directly linked to a reduction in the size of its prey (Grandrémy, 2023).

In order to explore this hypothesis, it would be interesting to obtain a finer size structure for generalists from the NUM model in order to better understand the impact of the size structure of generalists on the size structure of copepods. Moreover, since our results showed a significant dependency of the sardine growth towards the copepods size structure (see DEB simulation relying on the size spectra slopes), it would be also enriching to study interannual variability in addition to the spatial aspect. This would make it possible to determine whether the NUM model can reproduce the decrease in mesozooplankton size over the last few decades and to better understand the impact of this decrease on variations in sardine growth over time.

CONCLUSION

In conclusion, the NUM model appears to capture well the impact of spatial and seasonal variability in environmental conditions on plankton biomass in the Bay of Biscay. Throughout the year, the station close to the coast has high biomasses of small copepods, while the stations further offshore have lower biomasses of larger organisms. This spatial size structure in the Bay of Biscay is confirmed by in situ observations from springtime scientific surveys. Spatial variations in copepod resources have an impact on sardine growth. Using the DEB model, the size structure of copepods in the coastal station appears to be favourable for very young sardine stages, whereas it is highly unfavourable for adult stages.

REFERENCES

- Andersen KH, Berge T, Gonçalves RJ, Hartvig M, Heuschele J, Hylander S, Jacobsen NS, Lindemann C, Martens EA, Neuheimer AB, et al** (2016) Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. *The Annual Review of Marine Science* 8: 3.1-3.25. doi: <https://doi.org/10.1146/annurev-marine-122414-034144>
- Andersen KH, Beyer J** (2006) Asymptotic Size Determines Species Abundance in the Marine Size Spectrum. *The American Naturalist* 168: 54–61. doi: <https://doi.org/10.1086/504849>
- Andersen KH, Visser AW** (2023) From cell size and first principles to structure and function of unicellular plankton communities. *Progress in Oceanography*. doi: <https://doi.org/10.1016/j.pocean.2023.102995>
- Bachiller E** (2012) Trophic ecology of small pelagic fish in the Bay of Biscay: ecological effects of trophic interactions. Thèse de Doctorat. Universidad del País Vasco
- Barroeta Z, Olivar P, Palomera I** (2017) Energy density of zooplankton and fish larvae in the southern Catalan Sea (NW Mediterranean). *Journal of Sea Research* 124: 1–9. doi: <https://doi.org/10.1016/j.seares.2017.04.008>
- Bertrand M, Brosset P, Soudant P, Lebigre C** (2022) Spatial and ontogenetic variations in sardine feeding conditions in the Bay of Biscay through fatty acid composition. *Marine Environmental Research*. doi: <https://doi.org/10.1016/j.marenvres.2021.105514>
- Boëns A** (2022) Compromis croissance-survie : mortalité sélective et diminution des tailles-aux-âges chez deux poissons pélagiques (l’anchois *Engraulis encrasicolus* et la sardine *Sardina pilchardus*). Thèse de Doctorat. Université de Nantes
- Boyra G, Martinez U, Cotano U, Santos M, Irigoien X, Uriarte A** (2013) Acoustic surveys for juvenile anchovy in the Bay of Biscay: abundance estimate as an indicator of the next year’s recruitment and spatial distribution patterns. *ICES Journal of Marine Science* 70: 1354–1368. doi: <http://dx.doi.org/10.1093/icesjms/fst096>
- Brosset P, Fromentin J-M, Van Beveren E, Lloret J, Marques V, Basilone G, Bonanno A, Carpi P, Donato F, Čikeš Keč V, et al** (2017) Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Progress in Oceanography* 151: 149–162. doi: <https://doi.org/10.1016/j.pocean.2016.12.002>
- Brosset P, Le Bourg B, Costalago D, Bănaru D, Van Beveren E, Bourdeix J-H, Fromentin J-M, Ménard F, Saraux C** (2016) Linking small pelagic dietary shifts with ecosystem changes in the Gulf of Lions. *Marine Ecology Progress Series* 554: 157–171. doi: <https://doi.org/10.3354/meps11796>
- Cadier M, Hansen AN, Andersen KH, Visser AW** (2020) Competition between vacuolated and mixotrophic unicellular plankton. *Journal of Plankton Research* 42: 425–439. doi: <https://doi.org/10.1093/plankt/fbaa025>

Celton Y, Oulhen C (2019) La conserverie Le Gall de Loctudy, des conserves de sardines à la conservation d'un patrimoine. In Situ. doi: <https://doi.org/10.4000/insitu.26961>

Chakraborty S, Nielsen LT, Andersen KH (2017) Trophic Strategies of Unicellular Plankton. *American Naturalist* 189: 77–90. doi: <https://doi.org/10.1086/690764>

Chouvelon T, Violamer L, Dessier A, Bustamante P, Mornet F, Pignon-Mussaud C, Dupuy C (2015) Small pelagic fish feeding patterns in relation to food resource variability: an isotopic investigation for *Sardina pilchardus* and *Engraulis encrasicolus* from the Bay of Biscay (north-east Atlantic). *Mar Biol* 162: 15–37. doi: <https://doi.org/10.1007/s00227-014-2577-5>

Chust G, González M, Fontán A, Revilla M, Alvarez P, Santos M, Cotano U, Chifflet M, Borja A, Muxika I, et al (2022) Climate regime shifts and biodiversity redistribution in the Bay of Biscay. *Science of the Total Environment*. doi: <https://doi.org/10.1016/j.scitotenv.2021.149622>

Colas F, Tardivel M, Perchoc J, Lunven M, Forest B, Guyader G, Danielou M-M, Le Mestre S, Bourriau P, Antajan E, et al (2018) The ZooCAM, a new in-flow imaging system for fast onboard counting, sizing and classification of fish eggs and metazooplankton. *Progress in Oceanography* 166: 54–65. doi: <https://doi.org/10.1016/j.pocean.2017.10.014>

Colombo-Hixson SM, Olsen RE, Milley JE, Lall SP (2011) Lipid and fatty acid digestibility in *Calanus* copepod and krill oil by Atlantic halibut (*Hippoglossus hippoglossus* L.). *Aquaculture* 313: 115–122. doi: <https://doi.org/10.1016/j.aquaculture.2010.12.020>

Cotano U, Irigoien X, Etxebeste E, Alvarez P, Zarauz L, Mader J, Ferrer L (2008) Distribution, growth and survival of anchovy larvae (*Engraulis encrasicolus* L.) in relation to hydrodynamic and trophic environment in the Bay of Biscay. *Journal of Plankton Research* 30: 467–481. doi: <http://dx.doi.org/10.1093/plankt/fbn011>

Dessier A, Bustamante P, Chouvelon T, Huret M, Pagano M, Marquis E, Rousseaux F, Pignon-Mussaud C, Mornet F, Bréret M, et al (2018) The spring mesozooplankton variability and its relationship with hydrobiological structure over year-to-year changes (2003–2013) in the southern Bay of Biscay (Northeast Atlantic). *Progress in Oceanography* 166: 76–87. doi: <http://dx.doi.org/10.1016/j.pocean.2018.04.011>

Doray M, Petitgas P, Huret M, Duhamel E, Romagnan JB, Authier M, Dupuy C, Spitz J (2018a) Monitoring small pelagic fish in the Bay of Biscay ecosystem, using indicators from an integrated survey. *Progress in Oceanography* 166: 168–188. doi: <https://doi.org/10.1016/j.pocean.2017.12.004>

Doray M, Petitgas P, Romagnan JB, Huret M, Duhamel E, Dupuy C, Spitz J, Authier M, Sanchez F, Berger L, et al (2018b) The PELGAS survey: Ship-based integrated monitoring of the Bay of Biscay pelagic ecosystem. *Progress in Oceanography* 166: 15–29. doi: <http://dx.doi.org/10.1016/j.pocean.2017.09.015>

Duhamel E, Laspougeas C, Fry A (2011) Rapport final du programme d'embarquement à bord des bolincheurs travaillant dans le Parc naturel marin d'Iroise. 41. <https://archimer.ifremer.fr/doc/00065/17593/>

FAO (2022) The State of World Fisheries and Aquaculture 2022. Rome, FAO. doi: <https://doi.org/10.4060/cc0461en>

FranceAgriMer (2022) Chiffres-clés des filières pêche et aquaculture en France en 2022.

Gatti P (2016) Une approche bioénergétique pour la comparaison des traits d’histoire de vie de l’anchois et de la sardine du golfe de Gascogne. Thèse de Doctorat. Université de Rennes 1

Grandrémy N (2023) Dynamiques spatio-temporelles du zooplancton, en lien avec l’habitat et les petits poissons pélagiques, dans le Golfe de Gascogne. Thèse de Doctorat. Université de Nantes

Grandrémy N, Bourriau P, Daché E, Danielou M-M, Doray M, Dupuy C, Forest B, Jalabert L, Huret M, Le Mestre S, et al (In Press) Metazoan zooplankton in the Bay of Biscay: 16 years of individual sizes and abundances from the ZooScan and ZooCAM imaging systems. Earth System Science Data. doi: <https://doi.org/10.5194/essd-2023-187>

Grandrémy N, Romagnan JB, Dupuy C, Doray M, Huret M, Petitgas P (2023) Hydrology and small pelagic fish drive the spatio-temporal dynamics of springtime zooplankton assemblages over the Bay of Biscay continental shelf. Progress in Oceanography. doi: <https://doi.org/10.1016/j.pocean.2022.102949>

Guillaud J-F, Aminot A, Delmas D, Gohin F, Lunven M, Labry C, Herbland A (2008) Seasonal variation of riverine nutrient inputs in the northern Bay of Biscay (France), and patterns of marine phytoplankton response. Journal of Marine Systems 72: 309–319. doi: <http://dx.doi.org/10.1016/j.jmarsys.2007.03.010>

Heneghan RF, Everett JD, Sykes P, Batten SD, Edwards M, Takahashi K, Suthers IM, Blanchard JL, Richardson AJ (2020) A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling. doi: <https://doi.org/10.1016/j.ecolmodel.2020.109265>

Houliez E, Lefebvre S, Dessier A, Huret M, Marquis E, Bréret M, Dupuy C (2021) Spatio-temporal drivers of microphytoplankton community in the Bay of Biscay: do species ecological niches matter? Progress in Oceanography 194: 16. doi: <https://doi.org/10.1016/j.pocean.2021.102558>

Huret M, Vandromme P, Petitgas P, Pecquerie L (2012) Connectivity patterns of anchovy larvae in the Bay of Biscay from a coupled transport-bioenergetic model forced by size-structured zooplankton. ICES CM E:14:. doi: <https://doi.org/10.1016/j.pocean.2021.102558>

ICES (2022) ICES Advice on fishing opportunities, catch and effort - Sardine (*Sardina pilchardus*) in divisions 8.a-b and 8.d (Bay of Biscay).

Irigoién X, Chust G, Fernandes JA, Albaina A, Zarauz L (2011) Factors determining the distribution and beta diversity of mesozooplankton species in shelf and coastal waters of the Bay of Biscay. Journal of Plankton Research 33: 1182–1192. doi: <https://doi.org/10.1093/plankt/fbr026>

Kandylas A (2022) What is the global biogeography of copepod biomass, body size and POM production?

Kjørboe T (2013) Zooplankton body composition. *Limnology and Oceanography* 58: 1843–1850. <https://doi.org/10.4319/lo.2013.58.5.1843>

Kooijman S (2010) *Dynamic Energy Budget Theory for Metabolic Organisation*. Cambridge University Press

Labry C (2001) Dynamique du phosphore et rôle comme facteur limitant de la production planctonique dans le panache de la Gironde sur le plateau continental Sud Gascogne. Thèse de Doctorat. Université de la Méditerranée

Lassalle G, Lobry J, Le Loc'h F, Bustamante P, Certain G, Delmas D, Dupuy C, Hily C, Labry C, Le Pape O, et al (2011) Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: Implications for ecosystem management. *Progress in Oceanography* 91: 561–575. doi: <http://dx.doi.org/10.1016/j.pocean.2011.09.002>

Lehette P, Hernández-León S (2009) Zooplankton biomass estimation from digitized images: a comparison between subtropical and Antarctic organisms. *Limnology and Oceanography : Methods* 7: 304–308. doi: <https://doi.org/10.4319/lom.2009.7.304>

Marquis E, Niquil N, Dupuy C (2011) Does the study of microzooplankton community size structure effectively define their dynamics? Investigation in the Bay of Biscay (France). *Journal of Plankton Research* 33: 1104–1118. doi: <https://doi.org/10.1093/plankt/fbr009>

Menu C, Pecquerie L, Bacher C, Doray M, Hattab T, Van der Kooij J, Huret M (2023) Testing the bottom-up hypothesis for the decline in size of anchovy and sardine across European waters through a bioenergetic modeling approach. *Progress in Oceanography*. doi: <https://doi.org/10.1016/j.pocean.2022.102943>

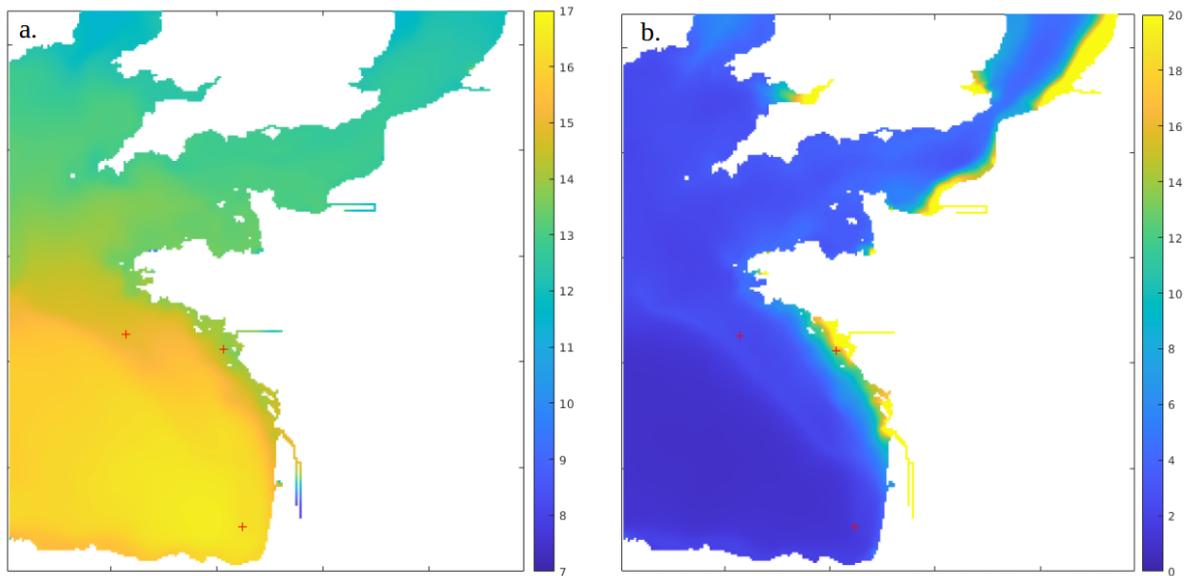
Peck MA, Alheit J, Bertrand A, Catalan IA, Garrido S, Moyano M, Rykaczewski RR, Takasuka A, Van Der Lingen CD (2020) Small pelagic fish in the new millennium: A bottom-up view of global research effort. *Progress in Oceanography* 191: 102494. doi: <https://doi.org/10.1016/j.pocean.2020.102494>

Queiros Q (2019) Mechanisms underlying the bottom -up control of sardine populations in the Gulf of Lions: insights from experiments and modeling. Thèse de Doctorat. Université de Montpellier

Queiros Q, Fromentin J-M, Gasset E, Dutto G, Huiban C, Metral L, Leclerc L, Schull Q, McKenzie DJ, Saraux C (2019) Food in the Sea: Size Also Matters for Pelagic Fish. *Frontiers in Marine Science*. doi: <https://doi.org/10.3389/fmars.2019.00385>

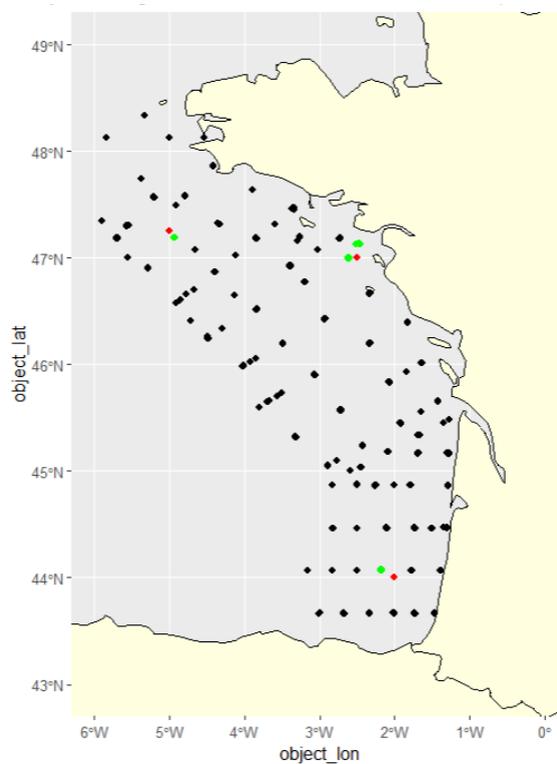
Saraux C, Van Beveren E, Brosset P, Queiros Q, Bourdeix J-H, Dutto G, Gasset E, Jac C, Bonhommeau S, Fromentin J-M (2019) Small pelagic fish dynamics: A review of mechanisms in the Gulf of Lions. *Deep-Sea Research Part II* 159: 52–61. doi: <https://doi.org/10.1016/j.dsr2.2018.02.010>

-
- Serra-Pompei C, Soudijn F, Visser AW, Kiørboe T, Andersen KH** (2020) A general size- and trait-based model of plankton communities. *Progress in Oceanography*. doi: <https://doi.org/10.1016/j.pocean.2020.102473>
- Sourisseau M, Carlotti F** (2006) Spatial distribution of zooplankton size spectra on the French continental shelf of the Bay of Biscay during spring 2000 and 2001. *Journal of Geophysical Research*. doi: <https://doi.org/10.1029/2005JC003063>
- Sprules WG, Barth LE** (2016) Surfing the biomass size spectrum: some remarks on history, theory, and application. *Canadian Journal of Fisheries and Aquatic Sciences* 73: 477–495. doi: <https://doi.org/10.1139/cjfas-2015-0115>
- Vandromme P, Nogueira E, Huret M, Lopez-Urrutia A, Gonzalez-Nuevo GG, Sourisseau M, Petitgas P** (2014) Springtime zooplankton size structure over the continental shelf of the Bay of Biscay. *Ocean Science* 10: 821–835. doi: <https://doi.org/10.5194/os-10-821-2014>
- Véron M** (2020) Variabilité de traits d’histoire de vie et implications pour la modélisation des dynamiques de population : application au stock de sardines du golfe de Gascogne. Thèse de Doctorat. Université de Bretagne Occidentale
- Véron M, Duhamel E, Bertignac M, Pawlowski L, Huret M** (2020) Major changes in sardine growth and body condition in the Bay of Biscay between 2003 and 2016: Temporal trends and drivers. *Progress in Oceanography* 182: 102274 (14p.). doi: <https://doi.org/10.1016/j.pocean.2020.102274>
- Zarubin M, Farstey V, Wold A, Falk-Petersen S, Genin A** (2014) Intraspecific Differences in Lipid Content of Calanoid Copepods across Fine-Scale Depth Ranges within the Photic Layer. *PLoS ONE* 9(3): e92935. doi: <https://doi.org/10.1371/journal.pone.0092935>



*Appendix 1 – a. Map of annual surface temperature ($^{\circ}\text{C}$) between 2012 and 2020 ;
b. Map of annual surface nitrates ($\mu\text{mol.L}^{-1}$) between 2012 and 2020*

Note that the colour scale is set to a maximum value of $20 \mu\text{mol.L}^{-1}$ of nitrates but the values in rivers can go up to almost $400 \mu\text{mol.L}^{-1}$.



Appendix 2 – Map of the hydrobiological stations sampled during the PELGAS oceanographic cruise (in black), with the North, Coast and South stations (in red) and the stations chosen to compute the NBSS

	Diplôme : Ingénieur Spécialité : Ingénieur Agronome Spécialisation / option : Sciences Halieutiques et Aquacoles / Ressources et Écosystèmes Aquatiques Enseignant référent : Olivier LE PAPE
Auteur(s) : Raphaëlle Huard Date de naissance* : 10/08/1999	Organisme d'accueil : Ifremer, Unité DYNECO, Laboratoire PELAGOS Adresse : Centre Ifremer Bretagne
Nb pages : 26 Annexe(s) : 1	ZI Pointe du Diable
Année de soutenance : 2023	CS 10070 29280 PLOUZANÉ Maîtres de stage : Mathilde CADIER, Martin HURET, Thomas GORGUES
Titre français : Étude de la structure du zooplancton dans le golfe de Gascogne à l'aide d'un modèle structuré en taille et impact sur la croissance de la sardine	
Titre anglais : Study of zooplankton structure in the Bay of Biscay using a size-structured model and impact on sardine growth	
Résumé (1600 caractères maximum) : Au cours des dernières décennies, un déclin de la taille des sardines a été observé dans le golfe de Gascogne. Plusieurs hypothèses ont été mises en avant afin d'expliquer cette diminution de taille, notamment celle d'un contrôle bottom-up. En effet, une modification de l'abondance et/ou de la composition des communautés de plancton pourrait expliquer les variations phénotypiques subies par les sardines. On modélise la biomasse et la structure en taille du plancton à l'aide d'un modèle mécaniste nommé NUM (Nutrient Unicellular Multicellular), appliqué à plusieurs stations contrastées du golfe de Gascogne. Les résultats obtenus sont comparés aux données issues de la campagne océanographique PELGAS. La biomasse ainsi que la structure en taille du zooplancton obtenue avec NUM est ensuite utilisée pour forcer un modèle bioénergétique DEB (Dynamic Energy Budget) pour la sardine afin d'analyser la variabilité de sa croissance à différentes stations contrastées du golfe de Gascogne.	
Abstract (1600 caractères maximum) : In recent decades, a decline in the size of sardines has been observed in the Bay of Biscay. Several hypotheses have been put forward to explain this reduction in size, including that of a bottom-up control. A change in the abundance and/or composition of plankton communities could explain the phenotypic variations experienced by sardines. The biomass and size structure of the plankton are modelled using a mechanistic model called NUM (Nutrient Unicellular Multicellular), applied to several contrasted stations in the Bay of Biscay. The results obtained are compared with data from the PELGAS oceanographic campaign. The biomass and size structure of zooplankton obtained with NUM is then used to force a DEB (Dynamic Energy Budget) bioenergetic model for sardines in order to analyse the variability of their growth at different stations in the Bay of Biscay.	
Mots-clés : <i>Copepoda</i> , <i>Sardina pilchardus</i> , modèle NUM (Nutrient Unicellular Multicellular), modèle DEB (Dynamic Energy Budget), structure en taille, chaîne trophique, golfe de Gascogne Key Words: <i>Copepoda</i> , <i>Sardina pilchardus</i> , NUM (Nutrient Unicellular Multicellular) model, DEB (Dynamic Energy Budget) model, size structure, trophic chain, Bay of Biscay	