

1 **Effects of mesozooplankton growth and reproduction**
2 **on plankton and organic carbon dynamics in a marine**
3 **biogeochemical model**

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12 **Key Points:**

- 13 • Incorporating mesozooplankton growth and reproduction alters carbon cycling path-
14 ways, reducing carbon export at 100 m by 10%.
- 15 • Cohort dynamics lead to significant variations in seasonal dynamics across meso-
16 zooplankton size classes without affecting export seasonality.
- 17 • Statistical predictive models demonstrate consistency between modeled and ob-
18 served mesozooplankton dynamics globally.

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Abstract

Marine mesozooplankton play an important role for marine ecosystem functioning and global biogeochemical cycles. Their size structure, varying spatially and temporally, heavily impacts biogeochemical processes and ecosystem services. Mesozooplankton exhibit size changes throughout their life cycle, affecting metabolic rates and functional traits. Despite this variability, many models oversimplify mesozooplankton as a single, unchanging size class, potentially biasing carbon flux estimates. Here, we include mesozooplankton ontogenetic growth and reproduction into a 3-dimensional global ocean biogeochemical model, PISCES-MOG, and investigate the subsequent effects on simulated mesozooplankton phenology, plankton distribution, and organic carbon export. Utilizing an ensemble of statistical predictive models calibrated with a global set of observations, we generated monthly climatologies of mesozooplankton biomass to evaluate the simulations of PISCES-MOG. Our analyses reveal that the model and observation-based biomass distributions are comparable ($r_{pearson}=0.40$, total epipelagic biomass: 137TgC from observations vs. 232TgC in the model), with similar seasonality ($r_{pearson}=0.25$ for the months of maximal biomass). Including ontogenetic growth in the model induced cohort dynamics and variable seasonal dynamics across mesozooplankton size classes and altered the relative contribution of carbon cycling pathways. Younger and smaller mesozooplankton transitioned to microzooplankton in PISCES-MOG, resulting in a change in particle size distribution, characterized by a decrease in large particulate organic carbon (POC) and an increase in small POC generation. Consequently, carbon export from the surface was reduced by 10%. This study underscores the importance of accounting for ontogenetic growth and reproduction in models, highlighting the interconnectedness between mesozooplankton size, phenology, and their effects on marine carbon cycling.

1 Introduction

Mesozooplankton are heterotrophic plankton that span a size range of 10^2 - 10^4 μm and play a central role in marine biogeochemical cycles (Calbet, 2001; Steinberg & Landry, 2017). Mesozooplankton hold an intermediate position in marine trophic webs, as they mediate the energy transfer from phytoplankton and small zooplankton to larger organisms such as fish and large marine mammals (Steinberg & Landry, 2017; Dupont et al., 2023). They regulate the efficiency and intensity of the soft-tissue biological carbon pump (BCP; Steinberg and Landry (2017); Boyd et al. (2019)). Recent model-based studies estimated that mesozooplankton contribute to a quarter of the total carbon sequestered by the biological carbon pump (Pinti, DeVries, et al., 2023). Due to trophic amplification, mesozooplankton are highly vulnerable to changes in marine ecosystem structure caused by climate change (Chust et al., 2014; Kwiatkowski et al., 2019; Clerc, Aumont, & Bopp, 2023). Hence, quantifying their contribution to biogeochemical processes is key to accurately understanding how changes in mesozooplankton abundance and distribution threaten ecosystem functioning and global biogeochemical cycling. Accurately quantifying the effects of mesozooplankton on ecosystem functions and the carbon cycle necessitates a nuanced understanding of the trade-offs associated with various functional traits exhibited by mesozooplankton, including their feeding mechanisms, life histories, and mortality rates (Kjørboe, 2011; Hébert et al., 2017; Steinberg & Landry, 2017; Kjørboe et al., 2018).

The expression of most plankton functional traits is linked to body size (Litchman et al., 2013; Andersen et al., 2016). Changes in body size throughout the life history of an individual are a primary driver of zooplankton ecology, as body size controls the performance of the "fundamental Darwinian missions" organisms strive to maximise (feeding, growth, reproduction, survival) (Litchman et al., 2013). In this context, the traits and life histories of mesozooplankton largely differ from those of the smaller microzooplankton, which are mainly composed of protozoans and share many similarities with phytoplankton, except for their trophic mode. Recent observations even suggest that a

71 significant amount of unicellular marine organisms are mixoplankton (i.e., they can per-
72 form both phototrophy and phagotrophy, Mitra et al. (2023)). Microzooplankton size
73 variations are generally limited to a doubling or halving of their biovolume, resulting in
74 marginal fluctuations of their metabolic rates throughout their life cycle. On the con-
75 trary, mesozooplankton often undergo size changes spanning multiple orders of magni-
76 tude. Consequently, these changes in body size contribute to the emergence of distinct
77 phenologies between micro- and mesozooplankton, influencing the seasonality of biogeo-
78 chemical functions driven by zooplankton. Using a chemostat-like zero-dimensional bio-
79 geochemical model, Clerc et al. (2021) showed that a size-based formulation, including
80 explicit reproduction and ontogenetic growth, significantly impacts the seasonal dynam-
81 ics of mesozooplankton. Indeed, compared to a standard model version in which meso-
82 zooplankton are represented as a single and nonvarying size class, the new model ver-
83 sion resulted in a delayed response of mesozooplankton to an increase in food availabil-
84 ity (i.e., a phytoplankton bloom) by a few months. In addition, mesozooplankton in the
85 new model version started to display cohort dynamics, namely the propagation of suc-
86 cessive waves of biomass from small to larger organisms, controlled by the dependency
87 of the ingestion rate on body size. However, this simplified zero-dimensional framework
88 did not allow for the quantification of the spatial variability of this specific temporal dy-
89 namic across different regions of the ocean, nor the corresponding impacts on carbon cy-
90 cling.

91 Global models strive to increase the ecological realism in their representation of the
92 marine plankton community. A range of recent global marine ecosystem models now in-
93 cludes the size spectrum of particles (Serra-Pompei et al., 2020), phytoplankton (Serra-
94 Pompei et al., 2020; Heneghan et al., 2020; Blanchard et al., 2014), zooplankton (Heneghan
95 et al., 2020) or even upper trophic levels (Maury, 2010; Dupont et al., 2023). Cohort dy-
96 namics are a common emergent pattern in these size spectrum models (Pope et al., 1994;
97 Maury et al., 2007; Zhou et al., 2010). However, the seasonal patterns of the zooplank-
98 ton size structure are usually not analysed in such global models, with very few excep-
99 tions (e.g., Datta and Blanchard (2016)). In parallel, recent developments in global bio-
100 geochemical models introduced additional zooplankton functional types (e.g. cnidarians
101 in Wright et al. (2021), pelagic tunicates in Luo et al. (2022); Clerc, Bopp, et al. (2023);
102 Clerc, Aumont, and Bopp (2023), crustacean macrozooplankton in Clerc, Bopp, et al.
103 (2023); Luo et al. (2022)) and new processes (e.g., diel vertical migration in (Aumont
104 et al., 2018), grazing parameterization in (Rohr et al., 2023)) known to impact the ma-
105 rine biological carbon pump, leading to a better quantification of BCP pathways (Boyd
106 et al., 2019). In this context, modeling studies offer a valuable framework for investigat-
107 ing the influence of plankton-mediated pathways on biogeochemical processes. However,
108 existing biogeochemical models often overlook mesozooplankton size variation and re-
109 production, resulting in a lack of quantification regarding the effects of these processes
110 on carbon cycling (Clerc et al., 2021). One limitation to such an implementation is the
111 difficulty of evaluating mesozooplankton phenology on a global scale due to the sparsity
112 of field observations necessary for model evaluation, even though satellite-based zooplank-
113 ton indicators are under active development (Strömberg et al., 2009; Basedow et al., 2019;
114 Druon et al., 2019).

115 In this study, we develop and use PISCES-MOG (Mesozooplankton ontogenetic growth),
116 a new version of PISCES-v2 (Aumont et al., 2015), the standard marine biogeochem-
117 istry component of NEMO (Nucleus for European Modelling of the Ocean) (Madec, 2008).
118 In PISCES-MOG, mesozooplankton are now represented similarly as in Clerc et al. (2021)
119 and the new mesozooplankton module accounts for ontogenetic growth and reproduc-
120 tion. We first explore the global structure of simulated mesozooplankton phenology and
121 characterise the presence and drivers of the emergent cohort dynamics. To evaluate how
122 PISCES-MOG performs in simulating mesozooplankton seasonality, we derive a global
123 mesozooplankton monthly climatology by training an ensemble of biomass distribution
124 models (BDMs) based on the MAREDAT mesozooplankton biomass dataset (Moriarty

125 & O'Brien, 2013) in combination with the recent predictive modelling framework of (Knecht
 126 et al., 2023). We also evaluate the skill of PISCES-MOG in reproducing the seasonal pat-
 127 terns in mesozooplankton size-structure by comparing the model-based seasonal cycles
 128 to those observed at two well-studied time series (the Hawaii ocean time series, HOT (Sheridan
 129 & Landry, 2004), and the Bermuda Atlantic time series study, BATS (Steinberg et al.,
 130 2001). We then investigate how the simulated cohort dynamics affect the biogeochem-
 131 ical properties of the total mesozooplankton to answer the following questions: Does the
 132 inclusion of ontogenetic growth and reproduction induce a change in mesozooplankton
 133 seasonality and biomass distribution, compared to that simulated by a model with a sin-
 134 gular and nonvarying size representation (as in PISCES-v2)? Does this affect the phenol-
 135 ogy and distribution of other living ecosystem and non-living particle components, and
 136 how do all these factors influence the carbon fluxes associated with the BCP?

137 2 Materials and method

138 2.1 Model description

139 2.1.1 Model structure

140 The marine biogeochemical model used in the present study is a revised version of
 141 PISCES-v2 (grey boxes in Fig. 1, Aumont et al. (2015)). It includes five nutrient pools
 142 (Fe , NH_4^+ , Si , PO_4^{3-} and NO_3^-), two phytoplankton groups (Diatoms and Nanophy-
 143 toplankton, denoted D and N), two zooplankton size classes (Micro- and Mesozooplank-
 144 ton, denoted \mathcal{Z} and \mathcal{M}) and an explicit representation of dissolved and particulate or-
 145 ganic matter, reaching a total of 24 prognostic variables (tracers). A full description of
 146 the model is provided in Aumont et al. (2015).

147 PISCES-MOG includes a subdivision of the zooplankton to explicitly represent dif-
 148 ferent metazoan size classes, mesozooplankton sexual reproduction, and ontogenetic growth.
 149 Zooplankton representation in PISCES-MOG has been updated from PISCES-v2 based
 150 on the size-structured model outlined in Clerc et al. (2021) (Figure 1). In PISCES-MOG,
 151 we consider a subdivision of the metazoan zooplankton into N_s size classes of equal width
 152 in logarithmic space. The centre of each size class is defined as follows: $l_s = l_{min} \left(\frac{l_{max}}{l_{min}} \right)^{\frac{2s+1}{2N_s}}$
 153 where $s \in [0, N_s - 1]$. The width of each size class is $\Delta \ln(l_s) = \frac{1}{N_s} \ln \left(\frac{l_{max}}{l_{min}} \right)$ in loga-
 154 rithmic space and is therefore constant. Microzooplankton \mathcal{Z} is now divided into strictly
 155 heterotrophic protists U and the $\frac{N_s}{2}$ first metazoan size classes, representing juvenile meta-
 156 zoan zooplankton, J_i with $i \in [0, \frac{N_s}{2} - 1]$. The remaining $\frac{N_s}{2}$ size classes, representing
 157 adult metazoan zooplankton, A_i with $i \in [0, \frac{N_s}{2} - 1]$, form the mesozooplankton com-
 158 partment \mathcal{M} in PISCES-MOG. The adult metazoan size class of maximum size is de-
 159 noted as A_{max} .

160 2.1.2 Metazoans and protists dynamics

161 The newly introduced adult metazoan groups aim to represent the same commu-
 162 nity as mesozooplankton in PISCES-v2, for which the parameterisation is mainly based
 163 on copepods (Aumont et al., 2015). Juvenile metazoans and unicellular protists aim to
 164 represent the same community as microzooplankton in PISCES-v2. Thus, the tempo-
 165 ral evolution of the N_s metazoan zooplankton groups is computed according to PISCES-
 166 v2 micro- and mesozooplankton equations, in which we introduced ontogenetic growth

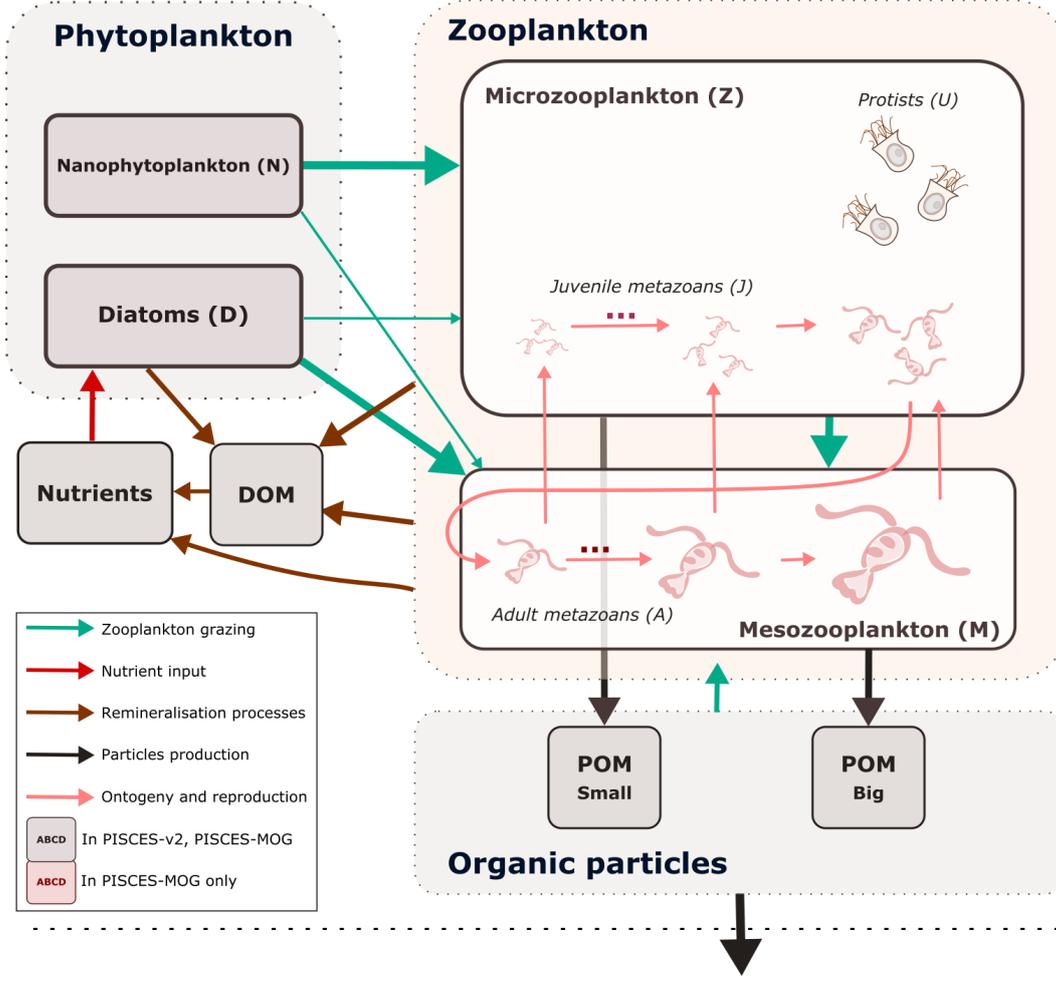


Figure 1. Architecture of the PISCES-MOG (mesozooplankton ontogenetic growth) model in the study This figure illustrates the living and non-living organic components of the model (boxes) and their interactions (arrows). This diagram emphasizes trophic interactions (i.e., turquoise arrows, the width representing the preference of the predator for the prey) as well as particulate organic matter production (i.e., black arrows), two processes impacted by the introduction of metazoan reproduction (vertical upward pink arrows) and ontogenetic growth (other pink arrows) in PISCES-MOG. POM = Particulate Organic Matter; DOM = Dissolved Organic Matter.

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and reproduction terms (derived from (Clerc et al., 2021)):

$$\begin{aligned}
 G_X &= e^X g_X (1 - \Delta(O_2)) f_X(T) \\
 r_X &= r^X f_X(T) \left(\frac{X}{K_m + X} + 3\Delta(O_2) \right) \\
 m_X &= m^X f_X(T) (1 - \Delta(O_2)) X^2 \\
 \frac{\partial J_0}{\partial t} &= \left[\underbrace{(1-v)G_{J_0}}_{\text{growth and transition}} - \underbrace{g_M^Z \mathcal{M}}_{\text{predation}} - \underbrace{m_{A_0} Z - r_{J_0}}_{\text{mortality}} \right] \cdot J_0 + \underbrace{wG_{A_0} A_0}_{\text{reproduction}} \\
 \frac{\partial J_s}{\partial t} &= \left[\underbrace{(1-v)G_{J_s}}_{\text{growth and transition}} - \underbrace{g_M^Z \mathcal{M}}_{\text{predation}} - \underbrace{m_{J_s} Z - r_{J_s}}_{\text{mortality}} \right] \cdot J_s + \underbrace{vG_{J_{s-1}} J_{s-1}}_{\text{transition}} + \underbrace{wG_{A_s} A_s}_{\text{reproduction}} \\
 \frac{\partial A_0}{\partial t} &= \left[\underbrace{(1-w)(1-v)G_{A_0}}_{\text{growth, reproduction and transition}} - \underbrace{m_{A_0} \mathcal{M} - r_{A_0}}_{\text{mortality}} \right] \cdot A_0 + \underbrace{vG_{J_{\frac{N_s}{2}-1}} J_{\frac{N_s}{2}-1}}_{\text{transition}} \\
 \frac{\partial A_s}{\partial t} &= \left[\underbrace{(1-w)(1-v)G_{A_s}}_{\text{growth, reproduction and transition}} - \underbrace{m_{A_s} \mathcal{M} - r_{A_s}}_{\text{mortality}} \right] \cdot A_s + \underbrace{(1-w)vG_{A_{s-1}} A_{s-1}}_{\text{transition}}
 \end{aligned}$$

168 X is a metazoan compartment, T is temperature and O_2 is dissolved oxygen con-
 169 centration. Grazing (G_X), quadratic (m_X) and linear mortalities (r_X) parameterisations
 170 are identical to that of micro- and mesozooplankton in PISCES-v2. Food preference is
 171 constant for each major zooplankton compartment (microzooplankton and mesozooplank-
 172 ton): all zooplankton groups feed on diatoms, nanophytoplankton, and small POC. In
 173 addition, mesozooplankton feed on heterotrophic protists, juveniles, and large POC. For
 174 mesozooplankton, in addition to conventional suspension feeding based on a Michaelis-
 175 Menten parameterisation without switching and a threshold, flux feeding is also repre-
 176 sented (Jackson, 1993; Stukel et al., 2019). e^X is the growth efficiency. All terms in this
 177 equation were given the same temperature sensitivity $f_X(T)$ using a Q10 of 2.14 (Eq.
 178 25a and 25b in Aumont et al. (2015)), as for mesozooplankton in PISCES-v2 and accord-
 179 ing to Buitenhuis et al. (2006). Growth rate and quadratic mortality are reduced and
 180 linear mortality is enhanced at very low oxygen levels, as we assume that mesozooplank-
 181 ton are not able to cope with anoxic waters ($\Delta(O_2)$ is an anoxia parameterisation that
 182 varies between 0 in fully oxic conditions and 1 in fully anoxic conditions, see Eq. 57 in
 183 Aumont et al. (2015)). Linear mortality is also enhanced at high organism concentra-
 184 tions (K_m is the half-saturation constant for mortality).

185 Similarly to (Clerc et al., 2021), for each mature mesozooplankton A_s , part of the
 186 assimilated food w is allocated to reproduction and is transferred to the juvenile sub-
 187 compartment J_s . This representation assumes that we represent a community of meta-
 188 zoan individuals with a mean egg-to-adult ratio of 1/20. The remainder of the assimi-
 189 lated food is used for growth, resulting in a transfer between adjacent size classes at a
 190 rate v . The value of this parameter depends on the number of size classes and the as-
 191 sumed size distribution within each size class (see Table 1 and (Clerc et al., 2021)). For
 192 the largest size class of mature mesozooplankton A_{max} , no size growth is possible.

193 Protists, U , follow the same dynamics as microzooplankton in PISCES-v2, except
 194 for predation by mesozooplankton and quadratic mortality which are now scaled to the
 195 full PISCES-MOG microzooplankton compartment ($\mathcal{Z} = U + \sum J$) to keep equiva-
 196 lency between PISCES-v2 and PISCES-MOG microzooplankton compartments.

$$\frac{\partial U}{\partial t} = \left[\underbrace{G_U}_{\text{growth}} - \underbrace{g_{\mathcal{M}}^{\mathcal{Z}} \mathcal{M}}_{\text{predation}} - \underbrace{m_U \mathcal{Z} - r_U}_{\text{mortality}} \right] \cdot U$$

197 All of the other 22 biogeochemical tracers that are common to PISCES-v2 and PISCES-
 198 MOG are driven by the exact same equations, which are fully detailed in Aumont et al.
 199 (2015).

200 *2.1.2.1 Size-based parameterisation* The maximum ingestion and quadratic mor-
 201 tality rates of the different zooplankton classes are set according to the allometric rela-
 202 tionship proposed by Hansen et al. (1997). The half-saturation constant used in the graz-
 203 ing parameterisation is supposed constant as observations suggest no significant varia-
 204 tions with size (Hansen et al., 1997). The transition rate v between the different size classes
 205 was computed by assuming that the slope of the biomass size spectrum within each size
 206 class is constant in a log-log space. It is set to -3 following the seminal study of Sheldon
 207 et al. (1972), which corresponds to an approximate constant biomass in logarithmically
 208 equal size intervals. The expressions for the transition rate and for the maximum inges-
 209 tion rate are shown in Table 1. The size-dependent formulations used in our standard
 210 model configuration are listed in Table 1.

Term	Value	Description
l_{min}		Minimal metazoan zooplankton body length
l_{max}		Maximal metazoan zooplankton body length
v	$= \frac{N_S}{3 \ln \frac{l_{max}}{l_{min}}}$	Transition rate between the mesozooplankton size-classes
g_M		Geometric mean of the maximum adult metazoans ingestion rate
g_Z		Geometric mean of the maximum juveniles metazoans ingestion rate
$L(J_s)$	$= \frac{2s+1}{2N_S^s}$	Length factor of juvenile size-classes J_s
$L(A_s)$	$= \frac{N_S^s + 2s+1}{2N_S^s}$	Length factor of mature size-classes A_s
$L(U)$	$= \frac{1}{4}$	Length factor for generic microzooplankton U
$\ln g_s$	$= \ln g_Z + \alpha(L(U) - L(X_s)) \ln \left(\frac{l_{max}}{l_{min}} \right)$	Maximum ingestion rate of the zooplankton size-class X_s
$\ln m_s$	$= \ln m_Z + \alpha(L(U) - L(X_s)) \ln \left(\frac{l_{max}}{l_{min}} \right)$	Quadratic mortality rate of the zooplankton size-class X_s

Table 1. Parameters and equations used in the size-based parameterizations To parameterize size in the equations, we introduce a length factor L for each size class. It ranges from 0 (minimum length) to 1 (maximal length) and varies linearly with the logarithm of the length.

Parameter	Default	Unit	Description	Range	Source
N_S	20	-	Number of mesozooplankton size-classes		
g_M	0.5	d^{-1}	Geometric mean of the adult metazoans ingestion rate	0.13-0.97	(Buitenhuis et al., 2006)
g_Z	2.0	d^{-1}	Geometric mean of the maximum juveniles metazoans ingestion rate	0.55-4.1	See table 1
m_M	1.5×10^4	$L \text{ mol}^{-1} d^{-1}$	Geometric mean of adult metazoans quadratic mortality		(Aumont et al., 2015)
m_Z	5.0×10^3	$L \text{ mol}^{-1} d^{-1}$	Geometric mean of juveniles metazoans quadratic mortality		See table 1
w	0.3	-	Fraction of the assimilated food allocated to reproduction	0.2-0.8	(Kooijman, 2013)
v	1.1	-	Transition rate across metazoan size-classes		(Clerc et al., 2021)
l_{min}	10	μm	Minimal metazoan zooplankton body length		
l_{max}	4000	μm	Maximal metazoan zooplankton body length		
α	0.48	-	Allometric parameter	0.42-0.54	(Hansen et al., 1997)

Table 2. Parameter values of the default configuration.

2.2 Numerical experiments

2.2.1 Reference simulation

PISCES-MOG is run in offline mode with dynamic fields identical to those used in Aumont et al. (2015). These climatological dynamic fields (as well as the input files) can be obtained at www.nemo-ocean.eu and were produced using an ORCA2-LIM configuration (Madec, 2008). The spatial resolution is about 2° by $2^\circ \cos(\phi)$ (where ϕ is the latitude) with a meridional resolution enhanced to 0.5° at the equator. The model has 30 vertical layers with increasing vertical thickness from 10 m at the surface to 500 m at 5000 m. PISCES-MOG was initialised from the quasi-steady-state simulation presented in Aumont et al. (2015). N_S , the number of metazoan size classes was set to 20 to achieve a reasonable discretization of a metazoan size-spectrum while limiting the computational cost to a doubling compared to PISCES-v2. The initial concentrations of the 21 zooplankton groups were set to a small uniform value of $10^{-9} \text{ mol CL}^{-1}$. The model was then integrated for the equivalent of 100 years, forced with 5-day averaged ocean dynamic fields and with a three-hour integration time step. All the analyses are performed on the last year of the simulation. When not specified, the parameter values are identical to those of PISCES-v2 (Aumont et al., 2015). The other parameter values are given in Table 2.

2.2.2 Sensitivity experiments

Here, microzooplankton include 10 juvenile metazoan size classes and one protist size class. Mesozooplankton include 10 adult metazoan size classes. Quadratic mortalities and maximum ingestion rates vary with size following the allometric relationship proposed by Hansen et al. (1997). To investigate the influence of each new mesozooplank-

233 ton feature (e.g., reproduction, ontogenetic growth, and size structure) on the model's
 234 behavior, we conducted sensitivity experiments based on three alternative model versions.
 235 The resulting biogeochemical model properties are compared with those of the standard
 236 model, PISCES-MOG.

237 The first alternative model version simply corresponds to the PISCES-v2 standard
 238 model. Here, metazoans are represented by a single mesozooplankton compartment, while
 239 the microzooplankton only include one protist size class. Thus, juvenile and mature meta-
 240 zoan organisms are assumed to have the same metabolic rates and the same predation
 241 behaviour. In this model, the representation of both microzooplankton and mesozooplank-
 242 ton is similar and corresponds to a formalism used for protists whose reproduction mode
 243 is based on cell division. This model serves as a reference representing the most com-
 244 mon mesozooplankton formulation in the biogeochemical components of Earth System
 245 Models (Kearney et al., 2021).

246 In the second alternative model version, PISCES-MOG-2LS ("Two-life-stage"), the
 247 representation of metazoan zooplankton is limited to two size classes: juveniles and ma-
 248 ture organisms (microzooplankton include one juvenile metazoan size class and one pro-
 249 tist size class; mesozooplankton include one adult metazoan size class only). As a result,
 250 the computing cost of PISCES-MOG-2LS is reduced by a factor of two compared to PISCES-
 251 MOG. PISCES-MOG-2LS was built to investigate the effect of a full-size spectrum rep-
 252 resentation of metazoans (in PISCES-MOG but not in PISCES-MOG-2LS) on the spa-
 253 tiotemporal dynamics of the system.

254 In the third alternative model version, PISCES-MOG-CM ("Constant Mortality"),
 255 zooplankton compartmentation is identical to the one in PISCES-MOG, but quadratic
 256 mortality rates are constant across all size classes of each zooplankton compartment. In-
 257 deed, in the chemostat-like model presented in Clerc et al. (2021), the allometric scal-
 258 ing was only applied to maximum ingestion rates and not to quadratic mortality rates.
 259 Thus, PISCES-MOG-CM serves as a reference representing the zooplankton dynamics
 260 from Clerc et al. (2021)'s model. The resulting system dynamics are very similar to those
 261 of PISCES-MOG and subsequently will not be presented in this paper. A figure compar-
 262 ing PISCES-MOG and PISCES-MOG-CM outputs is available in the supplementary
 263 material (Fig. S1 and S2).

264 *2.2.3 Metrics to evaluate the seasonality of different plankton functional* 265 *groups*

266 Given the high dimensionality of the biomass outputs of PISCES-MOG (space, time,
 267 and size), summary metrics are needed to describe the global metazoan seasonality. To
 268 this end, we designed a set of four phenological metrics inspired by (Lort et al., 2015):
 269 (i) Relative Seasonal Amplitude is computed as the difference between the annual min-
 270 imal and maximal biomass, normalised by the yearly average. (ii) Bloom Apex refers to
 271 the time of year when biomass reaches its maximum (iii) Bloom Climax refers to the time
 272 of year when population growth (derivative of the biomass) is maximal. (iv) Bloom du-
 273 ration is defined as the period spent within the 75th percentile of the yearly seasonal cy-
 274 cle, indicating the length of the bloom period.

275 **2.3 Observations-based products**

276 We used two distinct observations-based products for model evaluation: (i) a global
 277 monthly climatology of mesozooplankton biomass was used to evaluate how the model
 278 performs in simulating the seasonality of global mesozooplankton distribution (Moriarty
 279 & O'Brien, 2013), and (ii) monthly climatologies from local time series are used to eval-
 280 uate the model performance in reproducing the size-structure of mesozooplankton biomass
 281 and seasonality (Steinberg et al., 2001; Sheridan & Landry, 2004).

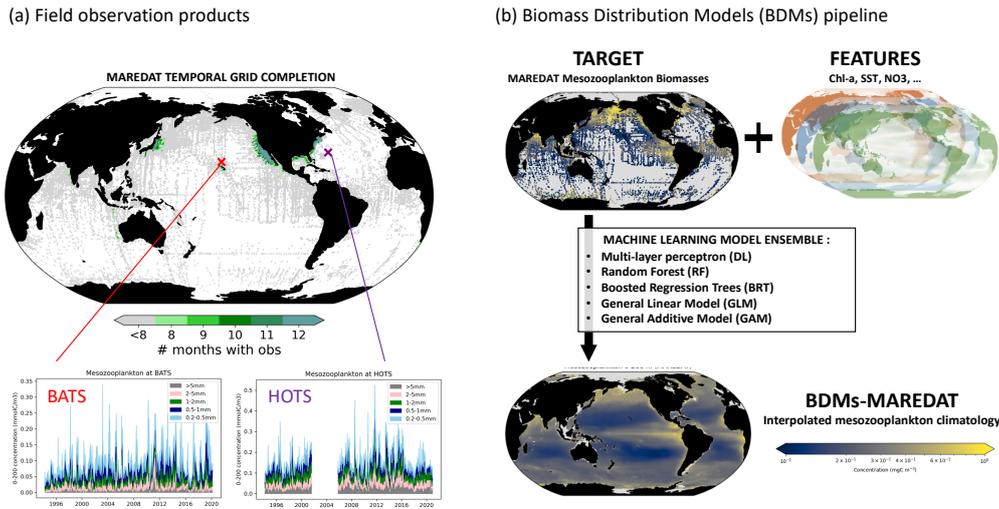


Figure 2. Description of the fields observation and biomass distribution models (BDMs) datasets. (a) Spatio-temporal coverage of mesozooplankton biomass field observations from MAREDAT global monthly climatologies (Moriarty & O’Brien, 2013) and from the BATS and HOT time-series stations (Steinberg et al., 2001; Sheridan & Landry, 2004) (b) BDMs pipeline trained on the MAREDAT monthly climatology of mesozooplankton biomass integrated over the top 200 m (Moriarty & O’Brien, 2013)

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2.3.1 Global mesozooplankton monthly climatology

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To be able to compare the mesozooplankton biomass distribution simulated by PISCES-MOG to observational data, we relied on observational monthly mesozooplankton biomass fields from the MARine Ecosystem DATA (MAREDAT) (Moriarty & O’Brien, 2013) in combination with climatological fields of the environmental predictors of mesozooplankton biomass (Strömberg et al., 2009; Knecht et al., 2023; Benedetti et al., 2021) to make use a new habitat modelling pipeline for continuous target variables (Knecht et al., 2023) that enable us to estimate monthly fields of mesozooplankton biomass in model units of mmol C m^{-3} for the global epipelagic ocean.

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MAREDAT mesozooplankton biomass product The MAREDAT mesozooplankton biomass field consists of 153,163 field measurements of mesozooplankton biomass concentrations and was extracted from the Coastal and Oceanic Plankton Ecology, Production, and Observation Database (COPEPOD, <http://www.st.nmfs.noaa.gov/copepod>). These measurements were quality controlled, standardised across different sampling and measurement methods and then aggregated into global climatological biomass concentration values (for more information about the treatment and standardisation of data in COPEPOD, see O’Brien (2010) (<http://www.st.nmfs.noaa.gov/copepod/2010>)) and (Moriarty & O’Brien, 2013). After re-gridding, the MAREDAT biomass fields comprise 42,245 data points on the WOA grid ($1 \times 1 \times 12$ months \times 33 depths), expressed in $\mu\text{mol C L}^{-1}$ (Moriarty & O’Brien, 2013). In our study, these standardised monthly values are converted into mmol m^{-3} and are vertically integrated between 0 and 200 m to be representative of the epipelagic zone which is where most of the zooplankton organisms are concentrated. The resulting climatology encompasses 27% of the epipelagic ocean area and shows an uneven distribution between the hemispheres. The spatial coverage is 40%

306 in the northern hemisphere and 16% in the southern hemisphere. Moreover, the dataset
 307 has limited temporal coverage, as only 1% of the grid cells contain data for at least 8
 308 distinct months (i.e., including observations that span at least three seasons), mostly con-
 309 centrated near the coasts of Japan and the US (Fig. 2(a)). To address this spatiotem-
 310 poral bias, we employ an ensemble of statistical data-driven models to predict mesozoo-
 311 plankton biomass concentration as a function of biologically relevant environmental pre-
 312 dictors and map it onto a global monthly 1×1 grid (Knecht et al. (2023)). Such a sta-
 313 tistical modelling framework is widely used in community ecology and biogeography to
 314 predict the spatial distribution of species and emerging diversity patterns based on en-
 315 vironmental covariates (Melo-Merino et al., 2020). In our study, we adapt the concept
 316 of species distribution modelling to model mesozooplankton biomass as a continuous tar-
 317 get variable (as opposed to the binary presence-absence data commonly used in the fields
 318 of community ecology and biogeography Guisan and Zimmermann (2000); Elith and Leath-
 319 wick (2009); Righetti et al. (2019); Benedetti et al. (2021); Waldoek et al. (2022)).

320 *Biomass Distribution Models (BDM)-ensemble* We used the ensemble of monthly
 321 climatologies of environmental variables from Knecht et al. (2023) to identify the set of
 322 potential environmental predictors that explain a substantial variance in the biomass data,
 323 in order for these predictors to be used in training the BDMs. These climatologies were
 324 selected as potentially relevant for modelling the biomass of pteropods and foraminifers,
 325 two important mesozooplankton functional groups that share similar predictors with cope-
 326 pods (Benedetti et al., 2023). Where necessary, these environmental predictor fields were
 327 averaged and re-gridded to monthly climatologies on a $1 \times 1^\circ$ resolution. We followed
 328 a similar approach as described in (Knecht et al., 2023) to select the set of predictors
 329 used in training the BDMs. Initially, using univariate Generalised Additive Models (GAM)
 330 and Generalized Linear Models (GLM), we evaluated the percentage of deviance explained
 331 by each selected predictor at various spatial aggregation levels (Knecht et al., 2023). We
 332 retained all predictors that explained 5% of the variability at any of the spatial aggre-
 333 gation levels. We used a Pearson correlation coefficient threshold ($|r| \geq 0.7$) to iden-
 334 tify clusters of collinear variables, which cannot reliably be discerned by our statistical
 335 models (Dormann et al., 2013). Then, we used univariate tests to identify the predic-
 336 tor displaying the highest predictive skill within those collinearity clusters. These top-
 337 ranking predictors were selected to represent all the candidate predictors in the cluster
 338 to which they belong. The resulting set of predictors includes surface chlorophyll-*a*, mixed
 339 layer depth (MLD), nitrate concentrations averaged over the MLD, partial pressure of
 340 CO_2 , total alkalinity, eddy kinetic energy (EKE) and photosynthetically active radia-
 341 tion (PAR). Note that Chlorophyll-*a*, EKE, MLD and nitrate concentration were log-
 342 transformed, so their distribution is closer to a Gaussian distribution. The final set of
 343 predictors is consistent with the predictors that were retained to model global zooplank-
 344 ton habitat suitability patterns in other SDM-based studies (Knecht et al., 2023; Benedetti
 345 et al., 2021; Strömberg et al., 2009).

346 We train an ensemble of five BDMs with the selected environmental predictor vari-
 347 ables and gridded, depth-integrated mesozooplankton biomass, using a 75%:25% train-
 348 test split and five-fold cross-validation following the method detailed in (Knecht et al.,
 349 2023). The five BDMs include a GLM, a GAM, a Random Forest (RF), a Gradient Boost-
 350 ing Machine (GBM), and a Neural Network/Deep Learning Model (DL; see Figure 2).
 351 Model parameter tuning for the RF, GBM, and DL was performed using grid search (see
 352 supplementary table ?? for the list of tuned hyperparameters). The statistical modelling
 353 framework was conducted in the R coding environment (R Core Team, 2022) based on
 354 the h2o 3.36.0.3 R package (H2O.ai, 2021).

355 We applied the BDMs to predict monthly mesozooplankton biomass values for the
 356 epipelagic layer globally. These projections were made for each grid cell and month with
 357 available data for all the predictors included in the BDMs. Statistical predictive mod-
 358 els including too many complex features can suffer from limited transferability into novel

environmental conditions due to non-linear response curves (Bell & Schlaepfer, 2016; Elith et al., 2010; Qiao et al., 2019). To address this issue, we evaluated whether the environmental conditions for each grid cell fell within the range of the training dataset or were non-analogue states, using a Multivariate Environmental Similarity Surfaces (MESS) analysis (Elith et al., 2010). This allows us to flag those locations of the ocean where our spatial predictions of mesozooplankton biomass are more uncertain due to model extrapolation into non-analogue conditions.

We assessed the performance of each BDM based on three metrics. The root mean squared error (RMSE) is an error metric estimating the deviation between predicted and true values. Pearson’s coefficient of correlation, R^2 indicates the magnitude of correspondence between trends in the predicted and observed values. Finally, the Nash-Sutcliffe efficiency (NSE; Nash and Sutcliffe (1970)) compares the model performance to a null model, that is, the mean of all observations. Positive NSE values indicate that the assessed model performs better than the null model. Each performance metric was calculated on both the training and the testing set of the data. The models perform reasonably well (Table S1), with the RF model showing the best performance across all metrics (RMSE = 0.22, R^2 = 0.52, NSE = 0.52 on the test set), followed by the GBM and then the DL model. Chlorophyll-*a* concentration was found to be the most important predictor as it explains 42.1% of the model’s predictive power on average. This finding supports the models’ ability to capture the responses of zooplankton biomass to large-scale gradients of plankton productivity (Strömberg et al., 2009). The supplementary materials include annually averaged mesozooplankton biomass maps for the five models, seasonal maps, and the Partial Dependency Plots (PDP) that show the response learnt by the BDMs to the gradients of predictors included (Fig. S3, S4 and S5).

To evaluate the global mesozooplankton biomass of PISCES-MOG, model outputs were vertically integrated over the top 200 m and horizontally re-gridded to match the grid of the BDMs predictions. Then, annually averaged fields were computed and PISCES-MOG outputs were compared against the BDM outputs based on relevant quantitative statistics (see Table 3).

2.3.2 *Size-structured mesozooplankton climatologies at BATS and HOT*

To compare the size-specific seasonal dynamics of metazoan simulated by PISCES-MOG to in situ observations, we used two widely-studied times series of size-structured mesozooplankton biomass (the Hawaii ocean time series, HOT; Sheridan and Landry (2004), and the Bermuda Atlantic time series study, BATS; Steinberg et al. (2001)). Mesozooplankton at HOT and BATS have been collected biweekly to monthly since 1994 at day time and night time through two replicate oblique net tows equipped with a 200 m mesh net, in the top 200 m of the water column. The samples were divided into two halves, and one half underwent successive wet sieving with nested sieves of various mesh sizes (5.0, 2.0, 1.0, 0.5, and 0.2 mm). The resulting fractions were placed on nets with a 0.2 mm mesh size, frozen, thawed, blotted, and then analysed for dry weight on shore (Madin et al., 2001). Thus, dry weight mesozooplankton time series, in mg m^{-2} , are available for five size classes: 200-500 μm , 500 μm - 1 mm, 1-2 mm, 2-5 mm, and ≥ 5 mm. We downloaded the 1994-2019 mesozooplankton biomass times series at <https://bats.bios.asu.edu/bats-data/bats.bios.asu.edu> for BATS (last access: 02/01/2024) and <https://hahana.soest.hawaii.edu/hot/hot-dogs/documentation/mextraction.html> for HOT (last access: 02/01/2024). Note that there is a measurement gap in the HOT mesozooplankton biomass time series between 2002 and 2005.

Prior to comparing PISCES-MOG outputs with the time series observations, the latter underwent a series of post-processing steps. First, we only retained the night-time observations (18:00-7:00). Indeed, the version of PISCES used here does not represent diel vertical migration (DVM). Consequently, simulated mesozooplankton do not migrate

410 down to the mesopelagic zone during the day, contrary to observed behavior. Thus, we
 411 posit that PISCES, operating with a 3-hourly time step and constant light forcing, pri-
 412 marily captures nighttime mesozooplankton vertical distribution across all time steps.
 413 This assumption is based on the hypothesis that variations in light exert minimal influ-
 414 ence on diurnal variations in epipelagic zooplankton biomass compared to DVM. Then
 415 we converted the dry weights (mg m^{-2}) to carbon molar concentration (mg C m^{-3}) by
 416 dividing by the maximal tow depth (200 m) and multiplying by a single dry weight-to-
 417 carbon mass conversion factor of 0.35 (as per Madin et al. (2001)). For the HOT time
 418 series, both dry weight and carbon biomass were available, allowing us to validate the
 419 use of the conversion factor at both stations (see Fig. 4(b)). Subsequently, we averaged
 420 the time series to create monthly daytime size-resolved mesozooplankton carbon concen-
 421 tration climatologies at both stations.

422 First, to compare the observed and modelled size structure of mesozooplankton com-
 423 munity, we computed the mean annual size spectrum at both stations by dividing the
 424 mean annual concentration of each size class by its width. Then, to analyse the size de-
 425 pendency of seasonality strength, we computed the relative seasonal amplitude for each
 426 mesozooplankton size class. This was done by calculating the difference between the max-
 427 imum and minimum biomass of each year, normalised by the annual mean. The mean
 428 and standard deviation of the relative amplitude were then computed for each size class
 429 across the available years. Lastly, to further explore size-driven differences in temporal
 430 dynamics, we calculated a seasonal cycle for each year and each size class. To do so, we
 431 normalised each month by the mean of that year and averaged the monthly normalized
 432 values over the years, for the five size classes, at both stations.

433 3 Results

434 3.1 Simulated ecosystem structure and phenology

435 3.1.1 Global mesozooplankton biomass and community dynamics

436 The total integrated annual mean biomass of all living compartments simulated by
 437 PISCES-MOG is 1.2 Pg C for the upper 200 m of the global ocean (Table 4). Primary
 438 producers account for 48% of this biomass, with the remaining 52% consisting of zoo-
 439 plankton, divided into unicellular protists (36%), juvenile metazoans (27%), and adult
 440 metazoans (37%, mesozooplankton). The contribution of each metazoan size class ranges
 441 from 3 (J_1) to 36 TgC (A_{max}), with a mean normalized biomass size spectrum (NBSS)
 442 slope of -0.80 ± 0.05 , close to the theoretical size spectrum slope of -1 (Sheldon et al.,
 443 1972). The spatial distribution of the NBSS slopes indicates steeper spectra in less pro-
 444 ductive areas (e.g. -0.9 in oligotrophic gyres vs -0.7 in the upwelling systems, see fig. S17),
 445 consistent with previous studies about the plankton size spectrum (see (Sprules & Barth,
 446 2016) and references within).

447 Spatially, simulated mesozooplankton concentration is high (\bar{i} 0.25 mmol C m^{-3})
 448 in the subpolar and upwelling regions and low (\bar{j} 0.25 mmol C m^{-3}) in the oligotrophic
 449 gyres and at high latitudes (Fig. 3(a)). This results in a clear zonal pattern in both hemi-
 450 spheres: low concentrations below 30° and above 70° latitude, and high concentrations
 451 between 30° and 60° latitude (Fig. 3(b)). This pattern seems to be driven by primary
 452 producers, as all plankton compartments show the same zonal pattern (Fig. 3(b)). The
 453 same zonal pattern also emerges for all adult metazoan size classes within the mesozoo-
 454 plankton (Fig. 3(c)).

455 The phenology of mesozooplankton significantly differs from that of microzooplankton
 456 and phytoplankton, both of which exhibit shorter and earlier blooms (Table 5, Fig.
 457 3(e)). On average, phyto- and microzooplankton bloom apexes occur 133 days after the
 458 start of the year (1st of January in the Northern Hemisphere, 1st of July in the South-
 459 ern Hemisphere), whereas mesozooplankton peak one month later (Table 5). Bloom cli-

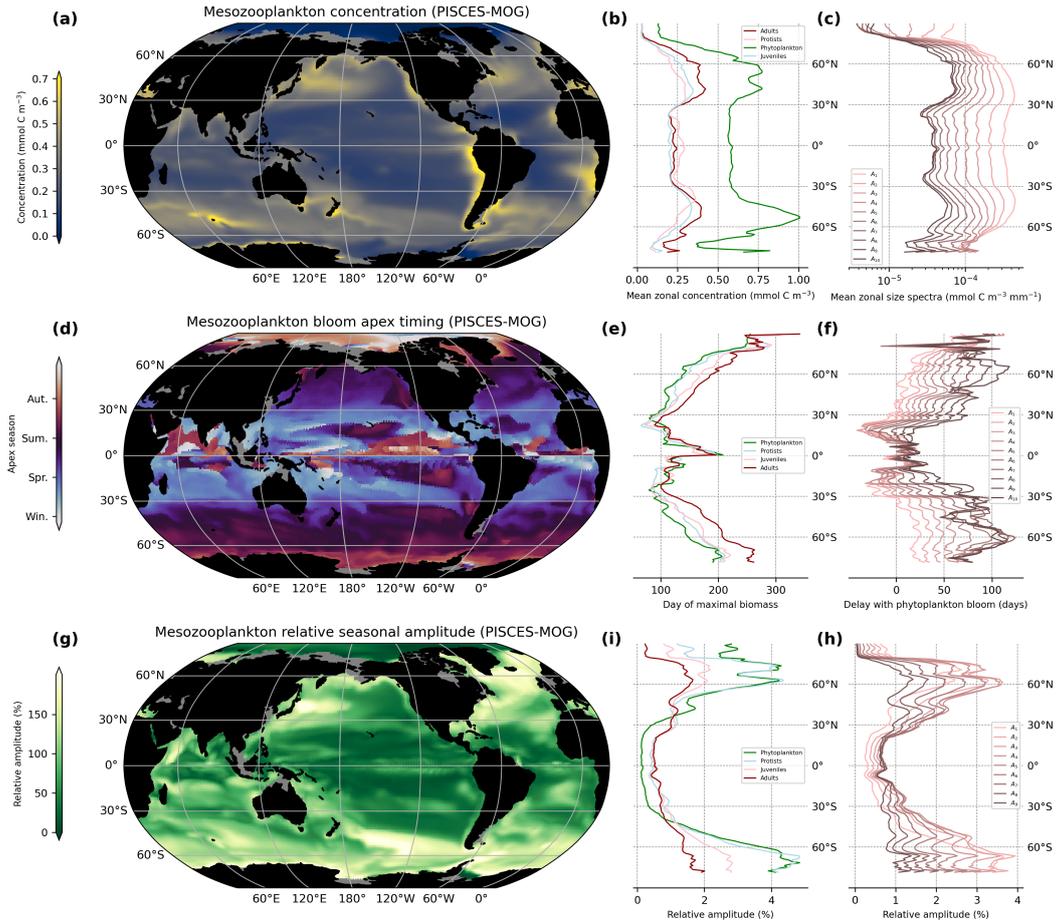


Figure 3. Global and zonally averaged epipelagic (0-200 m) plankton biomass and seasonality simulated by PISCES-MOG (a) Global average of epipelagic adult metazoans (mesozooplankton) concentration (mmol C m^{-3}). (b) Zonal mean of adult (red) and juvenile (pink) metazoans, unicellular protists (light blue), and total phytoplankton (green) concentrations (mmol C m^{-3}). (c) Mean zonal size spectra (biomass over size class width, $\text{mmol C m}^{-3} \text{mm}^{-1}$) for the 10 adult metazoans size-classes. (d) Global average of epipelagic mesozooplankton bloom apex (day of maximal abundance). (e) Zonal mean plankton groups bloom apexes (days, same colors as above) (f) Mean zonal delay (days) between the bloom apex of the 10 adult metazoans size classes and the bloom apexes of phytoplankton. (g) Global average of epipelagic mesozooplankton relative seasonal amplitude (%) (h) Zonal mean plankton groups relative seasonal amplitude (%), same colours as above). (i) Mean zonal relative seasonal amplitude (%) for the 10 adult metazoan size classes.

460 max is synchronous with the bloom apex for phytoplankton, occurs two weeks before the
 461 bloom apex for microzooplankton, and happens a month before the bloom apex for meso-
 462 zooplankton (Table 5). Phytoplankton and microzooplankton show sharp but short blooms
 463 (mean duration: 64 and 70 days resp.), while mesozooplankton are characterized by longer
 464 blooms that lasts 86 days on average (Table 5). Lastly, the relative seasonal amplitude
 465 of biomass is more than 25% smaller for mesozooplankton than for microzooplankton
 466 and phytoplankton (Table 5).

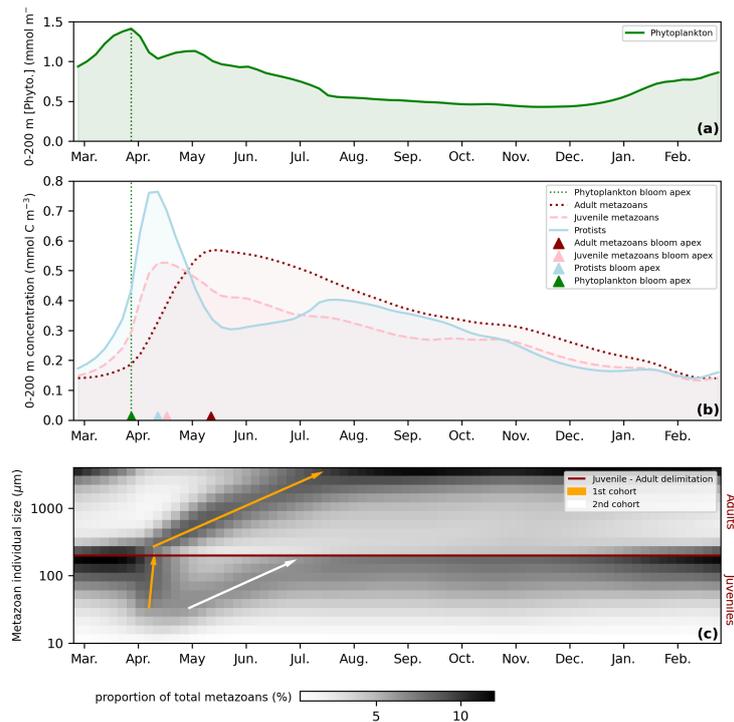


Figure 4. Seasonal dynamics of the epipelagic (0-200 m) ecosystem simulated by PISCES-MOG in the North Atlantic (46.4°N , 19.9°W). The coordinates are chosen to match the location of the North Atlantic Bloom Experiment (NABE), a pilot process study of the spring phytoplankton bloom conducted by JGOFS in 1989-1990 (Ducklow & Harris, 1993). Time evolution of (a) the phytoplankton and (b) the zooplankton concentrations (mmol C m^{-3}) over one year. Triangles indicate the bloom apexes of the plankton groups. (c) Change in size-class composition of metazoans over the year. The y-axis represents the 20 size classes ordered by increasing size. The grey levels correspond to the proportion of total metazoans (juvenile + adults) in each size classes for each time-step. Thus, for each time step, the proportions of the 20 size classes sums to 100. The arrows indicate cohorts, namely the propagation of successive waves of biomass from small to large organisms.

467 As latitude increases poleward, mesozooplankton phenology exhibits a later (Fig.
 468 3(d)) and more pronounced (Fig. 3(g)) bloom (approximately +3 days delay and +5%
 469 in relative amplitude per degree poleward in PISCES-MOG). A similar pattern is sim-
 470 ulated for the phytoplankton (Fig. 3(e,i)), suggesting that primary producers' phenol-
 471 ogy drives the simulated zonal pattern in mesozooplankton's phenology.

472 3.1.2 Cohort dynamics

473 Globally, all mesozooplankton size classes exhibit a zonal seasonality pattern sim-
 474 ilar to the one shown for total mesozooplankton. There is a strong latitudinal gradient
 475 in seasonality, with bloom apex (Fig. 3(e,f)) and bloom climax (Fig. S6(d,e,f)) occur-
 476 ring later as latitude increases poleward. The relative seasonal amplitude of mesozoo-
 477 plankton biomass increases poleward (Fig. 3(h)).

478 Moreover, PISCES-MOG simulations reveal a size class dependency of mesozoo-
 479 plankton dynamics: larger size classes peak later than smaller ones, with the largest size

480 classes peaking up to 3 months later than the smallest one (Fig 3(f)). This trend aligns
 481 with the temporal trend of other metrics: larger size classes have a later bloom climax
 482 (Fig. S6(f)) and a longer bloom duration (Fig. S6(c)), along with a lower seasonal am-
 483 plitude (Fig 3(j)). Note that a similar size class dependency is simulated for juvenile meta-
 484 zoans dynamics (Fig. S7 and S8). These size-dependent variations in bloom metrics indi-
 485 cate a cohort dynamics, a phenomenon in which biomass spreads across the size spec-
 486 trum due to synchronous growth and/or reproduction. This behaviour is extensively de-
 487 scribed in the chemostat model of plankton dynamics by Clerc et al. (2021). The bio-
 488 geochemical conditions driving metazoan cohort dynamics in Clerc et al. (2021) aim to
 489 replicate those in the North Atlantic, where zooplankton phenology is influenced by a
 490 strong phytoplankton spring bloom. To further characterise this pattern in PISCES-MOG,
 491 we analyse the temporal dynamics of plankton at a grid point representative of the well-
 492 studied North Atlantic bloom system: NABE (46.4°N, 19.9°W).

493 As expected, PISCES-MOG simulates a phytoplankton bloom in early spring at
 494 NABE, reaching its peak in early April (Fig. 4(a)). This triggers a zooplankton bloom:
 495 microzooplankton (protists and juvenile metazoans) peak around 15 days later, while meso-
 496 zooplankton peak 45 days later (Fig. 4(b)). The temporal evolution of the metazoan com-
 497 position shows a wave signal driven by a cohort dynamic, as demonstrated in Clerc et
 498 al. (2021). Before the phytoplankton spring bloom, biomass is distributed similarly in
 499 both juvenile and adult metazoan groups; larger organisms are more abundant than smaller
 500 ones (Fig. 4(c)). The bloom triggers an increase in food availability, leading to popu-
 501 lation growth. Smaller organisms, that are characterised by higher maximal grazing rates,
 502 experience a faster increase in concentration than larger organisms, resulting in a higher
 503 proportion of biomass accumulating in smaller size classes at the beginning of April (Fig.
 504 4(c)). Ontogenetic growth results in the transfer of this biomass to the larger juvenile
 505 size classes (orange arrow) and then to adults (orange arrows in Fig. 4(c)). This char-
 506 acterises the formation of a first cohort. Reproduction of the adults from this first co-
 507 hort results in a second cohort, for which the signal is lost in the adult size classes (white
 508 arrow, Fig. 4(c)). Note that a comparable cohort pattern also emerges under the oligo-
 509 trophic conditions prevalent at BATS (Fig. S9) and at HOT even though the signal is
 510 weaker there (Fig. S10).

511 3.2 Comparison of PISCES-MOG outputs to observations

512 Next, we focus on the evaluation of the key new component of the PISCES-MOG
 513 model (absent in PISCES-v2): the size-structured mesozooplankton compartment. In
 514 the supplementary material, we present an evaluation of nitrate and chlorophyll distri-
 515 butions (Fig. S11) and chlorophyll dynamics (Fig. S12). For these tracers, note that the
 516 performance of PISCES-MOG is similar to that of PISCES-v2 (Aumont et al., 2015).

517 3.2.1 Evaluation of simulated total mesozooplankton biomass and sea- 518 sonality against observation-based products

519 The annual mean distribution of total mesozooplankton biomass as well as the dis-
 520 tribution of the four seasonality metrics defined in section 2.2.3 are compared to the BDMs-
 521 based climatology. Overall, the quantitative statistical evaluation shows that PISCES-
 522 MOG successfully simulates mesozooplankton biomass and phenology at the global scale
 523 (Table 3) and zonally 5.

524 We find that both biomass distributions align in their overall order of magnitude
 525 (total epipelagic biomass: 137 TgC in the BDMs-based climatologies vs. 322 TgC in the
 526 PISCES-MOG outputs). PISCES-MOG and BDMs-based global mesozooplankton biomasses
 527 are significantly correlated (Pearson $r = 0.4$, p -value $\leq 10^{-15}$, Table 3 and Fig. S13). In
 528 productive systems, such as upwelling areas, and less productive systems, such as oligo-
 529 trophic gyres, both observed and modeled climatologies consistently depict higher and

	Corr	RMSE	Bias	Mean		Standard deviation	
				Obs.	Model	Obs.	Model
average biomass (mmol/m ³)	0.40	0.14	0.09	0.18	0.27	0.10	0.11
bloom apex (days)	0.25	75	-15	158	144	57	56
bloom climax (days)	0.32	77	0	87	87	60	57
bloom duration (days)	0.04	50	14	75	89	37	32
relative amplitude (%)	0.52	42%	-3%	82%	79%	43%	46%

Table 3. Evaluation metrics computed to compare the model-based and the observation-based mesozooplankton biomass monthly climatologies. *Obs* refers to the BDMs-MAREDAT product, *Model* here refers to the PISCES-MOG mesozooplankton outputs. With the exception of correlation coefficients, metric units are the same as the units of the evaluated variable. *Corr* is the correlation coefficient between the BDM-based and the PISCES-MOG-based fields of mesozooplankton biomass. For the average concentration, the bloom duration and the relative amplitude, the metric corresponds to the Pearson correlation coefficient. For the bloom climax and bloom duration, the metric corresponds to the circular version of the Pearson correlation coefficient (Jammalamadaka & SenGupta, 2001), since those are periodic metrics (with a period of 1 year). The periodicity of those metrics is also accounted for in the computation of root mean square error (RMSE) and Bias. All metrics are weighted by the area of each ocean grid cell and averaged over the top 200 m of the ocean. Seasonality metrics are also weighted. Note that a visualisation of the comparison between PISCES-MOG and BDMs-MAREDAT mesozooplankton metrics is available in Fig. S13.

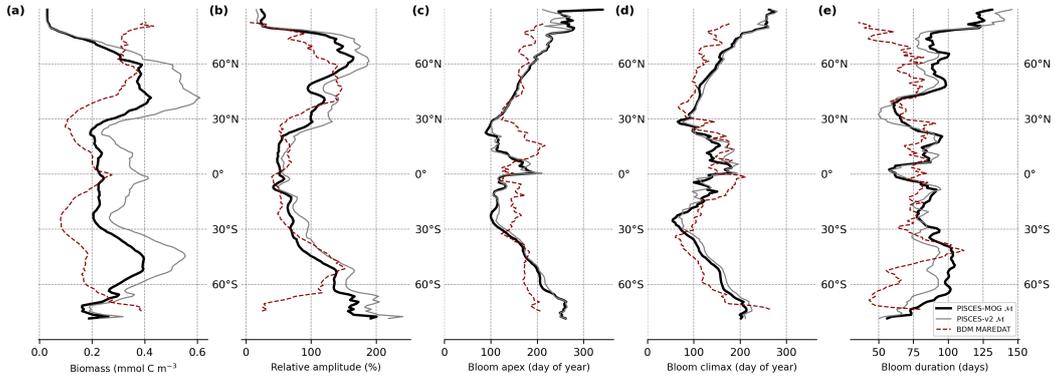


Figure 5. Model-data comparison of the mesozooplankton biomass and its seasonality. For each of the five evaluated metrics, we compare the zonal mean of the metric computed on the mesozooplankton distribution simulated by PISCES-v2 (grey line), PISCES-MOG (black line) and interpolated from observation (BDMs-MAREDAT, dotted red line). The five metrics evaluated are (a) biomass (mmol C m⁻³), (b) relative seasonal amplitude (%), (c) bloom apex (day of the year), (d) bloom climax (day of the year) and (e) bloom duration (days). The metrics are defined in the methods section 2.2.3.

530 lower biomass levels, respectively (Fig. 5(a), Fig. S13). Spatial variability is also con-
 531 sistent between the model-based outputs and observations (Table 3).

532 The seasonality metrics and their standard deviations are consistent between PISCES-
 533 MOG outputs and observation-based fields on a global scale (Table 3, Fig. S13), with
 534 biases lower than 20%. However, PISCES-MOG tends to simulate earlier and longer meso-
 535 zooplankton blooms than computed from the BDMS-based climatology (Table 3, Fig. 5(c,d)).
 536 The spatial distribution of bloom climax and bloom duration is consistent across the model-
 537 based and the BDMS-based outputs ($r^2 = 0.23$ and 0.32 , Table 3, Fig. 5(c,d), with the
 538 dominant pattern being a later bloom as latitude increases poleward (approximately +3
 539 days per degree poleward in PISCES-MOG, +2 days per degree poleward in the BDMS-
 540 based climatology, Fig. 5(c,d)). In the tropical band (i.e., between 30°S and 30°N), where
 541 the seasonal signal is low (<80%, Fig. 5(b)), the bloom apex and bloom climax distribu-
 542 tion are patchy in both the model-based and the BDMS-based fields (Fig. 5(c,d), Fig.
 543 3(d), S14(d), S6(d), S15(d)), as intra-annual variations are not driven by seasonality in
 544 these regions at the first order. In contrast, bloom duration is poorly correlated between
 545 the model-based and the BDMS-based fields ($r = 0.04$, Table 3, Fig. 5(e)). No clear large-
 546 scale pattern emerges from the model and observation for this metric, as bloom dura-
 547 tion seems to be uniformly patchy across the global ocean (Fig. S15(a), Fig. S6(a)). Rel-
 548 ative biomass amplitudes are spatially consistent between the model-based and the BDMS-
 549 based fields ($r = 0.52$, table 3, Fig. 5(b)), with the dominating pattern being an increase
 550 in relative amplitude towards the poles (Fig. 3(g) and S16(a)). Therefore, PISCES-MOG
 551 consistently simulates large-scale mesozooplankton spatial and intra-annual variability,
 552 even though bloom duration is poorly constrained due to its patchiness.

553 *3.2.2 Evaluation of modelled mesozooplankton size structure against time-* 554 *series data*

555 To our knowledge, no global monthly climatologies of mesozooplankton size struc-
 556 ture based on field observation are currently available. Thus, our evaluation of mesozoo-
 557 plankton size structure is limited to the observations from the two time series stations,
 558 BATS and HOT. Note that observed mesozooplankton time-series were not available at
 559 NABE, where we described an emergent metazoan cohort dynamics in PISCES-MOG
 560 (section 3.2.2). However, PISCES-MOG simulates a cohort pattern at HOT and BATS
 561 that is similar to the one simulated for NABE (see supp fig. S9 and S10).

562 We divided the evaluation of the seasonal patterns in mesozooplankton size struc-
 563 ture at the HOT and BATS stations into three parts: (i) the comparison of the size spec-
 564 tra aims to evaluate the size structure of the mean annual biomass (Fig. 6(a,b)), (ii) the
 565 comparison of relative seasonal amplitudes investigates the size-dependent variations in
 566 seasonal biomass (Fig. 6(c,d)), and (iii) the comparison of normalised seasonal cycles eval-
 567 uates the relationship between size and the temporal structure of seasonality (Fig. 6(e,f)).

568 Consistent with Sheldon's theoretical hypothesis (Sheldon et al., 1972), the slope
 569 of the spectrum is not significantly different from -1 (p-values > 0.05) for the model-based
 570 outputs and the observations at both stations (modelled resp. observed, size spectrum
 571 slopes are -0.92 resp. -0.84 at BATS, -1.12 resp. -0.61 at HOT, Fig. 6(a,b)). Note that,
 572 for the time series observations, the size spectrum's normalised biomass (NBSS) value
 573 (Fig. 6(a,b)) is likely underestimated for the small size class due to the detection limit
 574 corresponding to the net mesh size (202 μm). This explains the misalignment of the smaller
 575 size class point in both field-based size spectra. The model overestimates biomass at BATS
 576 by a factor of 4 (Fig. 6(a)) but performs well at HOT (mean model over obs. ratio < 1.5,
 577 Fig. 6(b)). As a result, a simple parameterization of mesozooplankton allows the intro-
 578 duction and evaluation of a consistent size-spectrum structure in PISCES-MOG, which
 579 was absent in PISCES-v2 (indicated by the black dot).

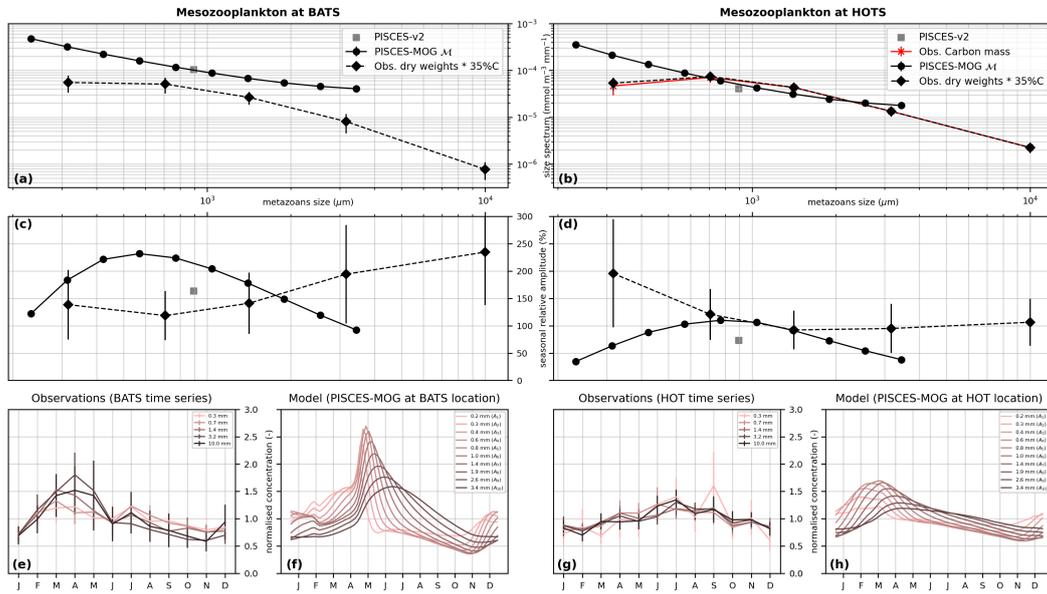


Figure 6. Model-data comparison of mesozooplankton biomass and seasonality at BATS ($32.1^{\circ}\text{N } 64.0^{\circ}\text{W}$, left panels) and HOT ($25.1^{\circ}\text{N } 158.0^{\circ}\text{W}$, right panels). (a,b) (resp. (c,d)) Size spectra comparison (concentration/width class, in $\text{mmol m}^{-3} \mu\text{m}^{-1}$), (resp. relative seasonal amplitude, in % of yearly average biomass). The time series of the ten adult metazoan size classes simulated by PISCES-MOG are represented by black lines with round dots. The squared grey dot refers to the PISCES-v2 total mesozooplankton time series. Black dotted lines with lozenge dots represent observed mesozooplankton dry weight time series converted to carbon concentrations for the five size classes (see section 2.3.2). Note that for the larger observed size class, the mean individual size is arbitrarily set to 10 mm since the upper size limit is unknown, but is not considered when computing size spectrum slopes. For (b), the red line indicates the size spectrum computed from carbon content values, available only for the HOT time series, illustrating the consistency of our dry-weight to carbon conversion. Error bars in observations represent inter-annual variability. (e-h) Normalised seasonal cycle for each observed and modelled mesozooplankton biomass time-series by size class. Normalisation is based on yearly average biomass, with error bars indicating inter-annual variability of the normalized seasonal cycle. The colour represents the mean size of the class (light pink for smaller sizes to dark brown for larger size classes). Note that error bars are absent for model outputs in all panels (a-h) since PISCES is forced with a 1-year climatology.

	Ecosystem					Biological carbon pump		
	Nanophyto. (PgC)	Diatoms (PgC)	Microzoo. (PgC)	Mesozoo. (PgC)	Total (PgC)	NPP (PgC yr ⁻¹)	EP100 (PgC yr ⁻¹)	pe-ratio (-)
PISCES-MOG	0.378	0.174	0.394	0.232	1.178	42.32	7.13	0.168
PISCES-v2	0.430	0.158	0.326	0.322	1.236	43.31	7.89	0.182
Anomaly MOG - v2 (%)	-11.9%	+9.6%	+20.8%	-27.9%	-4.7%	-2.3%	-9.6%	-7.7%
PISCES-MOG-2LS	0.366	0.168	0.427	0.232	1.194	44.80	7.02	0.157
Anomaly MOG-2LS - v2 (%)	-14.8%	+6.3%	+30.9%	-27.8%	-3.4%	+3.4%	-11.0%	-13.7%

Table 4. Global biomass of the simulated living compartments and associated carbon export. All biomass values are computed over the top 200m. NPP100 is the Net Primary Production over the top 100 m. EP100 is the particulate organic carbon export at 100 m. pe-ratio is defined as EP100/NPP100.

580 The relative seasonal amplitude of mesozooplankton biomass is comparable between
581 the model and observations at both stations, albeit with a consistently reduced mean
582 amplitude at HOT compared to BATS. (Fig. 6(c,d)). Although PISCES-MOG exhibits
583 a clear bell-shaped size structure in relative seasonal amplitude, with lower seasonal am-
584 plitudes for the smallest and largest size classes, the inter-annual variability of the ob-
585 servations is too high to delineate differences in seasonality across size classes (Fig. 6(c,d)).

586 The comparison of the observed and modelled mesozooplankton temporal dynam-
587 ics is limited by the inter-annual variability in the observations. PISCES-MOG predicts
588 a bloom that occurs between one and two months later than the ones reported at BATS
589 (April-July vs. March-May, Fig. 6(e)). It also predicts a marked shift in the timing of
590 maximum biomass with increasing size that is consistent with a cohort process (Fig. 6(e),
591 see section 3.1.2). A similar pattern appears in the observations, but the high inter-annual
592 variability makes it difficult to discern a significant pattern. At HOT also, a cohort pat-
593 tern is observed in the model, with bloom peaks occurring between February and April
594 (Fig. 6(f)). However, analysing the seasonality in observations at HOT is even more chal-
595 lenging than at BATS due to the high inter-annual variability and the low seasonal vari-
596 ability (Fig. 6(g)).

597 In summary, while the evaluation of mesozooplankton size structure and season-
598 ality showed that PISCES-MOG performs reasonably well, evaluating the size structure
599 of the seasonal signal remains challenging. Yet, we note that both BATS and HOT are
600 stations located in oligotrophic gyres, where both productivity and seasonality are known
601 to be low all year long. This could explain why observations have a low seasonal signal
602 versus inter-annual variability ratio.

603 3.3 Biogeochemical impacts of the representation of mesozooplankton 604 ontogenetic growth and reproduction

605 In order to quantify the impacts of mesozooplankton ontogenetic growth and re-
606 production, in this section we compare PISCES-MOG and PISCES-v2. We first com-
607 pare the ecosystem structure and phenology between the two models, and then show how
608 these differences between models induce different carbon fluxes.

609 3.3.1 Impacts on the ecosystem structure

610 The simulated total living epipelagic biomass is similar in both PISCES-v2 and PISCES-
611 MOG, with an estimated amount of 1.18 and 1.24 GtC, respectively, over the top 200
612 m (Table 4). The inclusion of mesozooplankton ontogenetic growth in PISCES-MOG re-
613 sults in juvenile metazoans biomass redistribution from the mesozooplankton biomass
614 pool to the microzooplankton pool. Consequently, total mesozooplankton biomass is 28%
615 lower and total microzooplankton 21% higher in PISCES-MOG compared to PISCES-

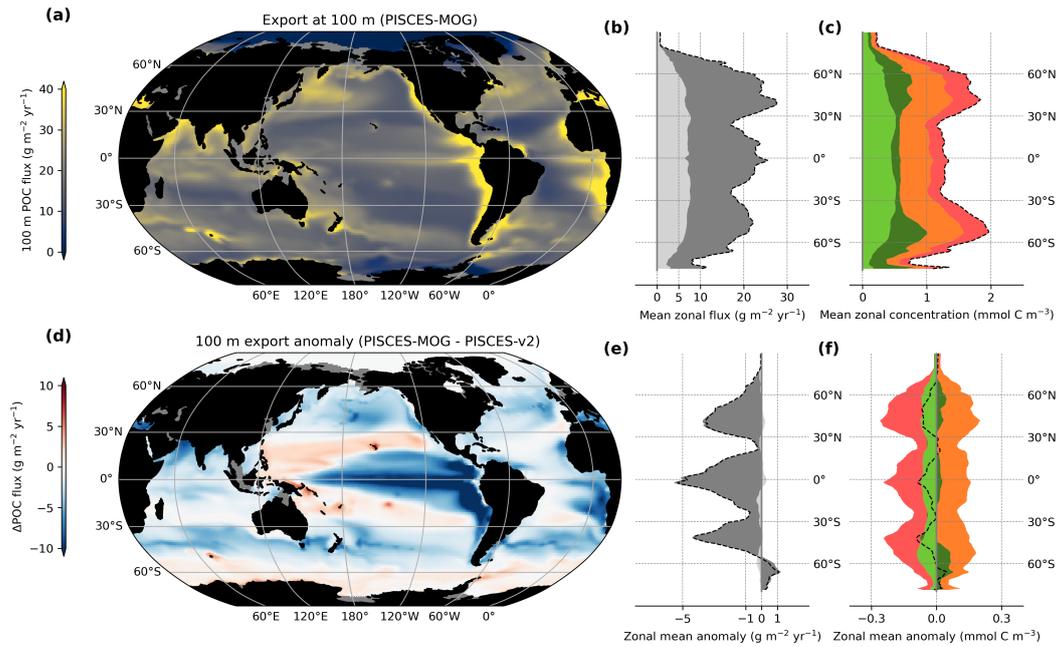


Figure 7. Global particulate organic carbon (POC) flux estimates, particle composition and biological drivers in PISCES-MOG and PISCES-v2. (a) Global distribution of POC export at 100 m ($\text{gC m}^{-2} \text{yr}^{-1}$) simulated in PISCES-MOG and (d) relative anomaly compared to PISCES-v2 (b) Zonal mean POC export at 100 m ($\text{gC m}^{-2} \text{yr}^{-1}$) and (e) relative anomaly compared to PISCES-v2. The dashed line shows the total POC. The fill colours show the contribution of the different components of the POC: small particles in light grey, large particles in dark gray. (c) Zonal mean community composition (mmol C m^{-3}) in PISCES-MOG and (f) relative anomaly compared to PISCES-v2. The dashed line shows the total simulated living concentration. The fill colours show the different groups of organisms: nanophytoplankton in light green, diatoms in dark green, microzooplankton in orange and mesozooplankton in pink.

616 v2 (Table 4). Thus, while total zooplankton (i.e., micro- and mesozooplankton together)
 617 biomass is only slightly affected by the inclusion of a more complex mesozooplankton
 618 representation (-3.4% in PISCES-MOG compared to PISCES-v2, Table 4), the repar-
 619 tition within size-based compartments is different (i.e., mesozooplankton represents 50%
 620 of total zooplankton in PISCES-v2, 38% in PISCES-MOG, Table 4).

621 These changes in biomass distribution impact the overall ecosystem structure sig-
 622 nificantly. As zooplankton exert a top-down control on primary producers through graz-
 623 ing, changes in zooplankton composition modify predation pressure and thus impact phy-
 624 toplankton composition. Indeed, PISCES includes an explicit representation of two phy-
 625 toplankton groups: nanophytoplankton that are mainly grazed by microzooplankton, and
 626 diatoms that are mainly grazed by mesozooplankton. As a consequence of this top-down
 627 control by zooplankton, a decrease of 12% of nanophytoplankton biomass is simulated
 628 in PISCES-MOG compared to PISCES-v2 due to an increase in predation pressure me-
 629 diated by an increase in microzooplankton (Table 4). Similarly, an increase of 10% in
 630 diatom biomass is simulated in PISCES-MOG due to a relaxation of predation pressure
 631 by mesozooplankton (Table 4). These effects on the epipelagic ecosystem structure are
 632 qualitatively similar across latitudes (Fig. 7(f))

		Phytoplankton	Microzoo.	Mesozoo.
Relative seasonal amplitude (%)	PISCES-MOG	121%	107%	93%
	PISCES-v2	115%	132%	111%
	Anomaly MOG - v2	6%	-25%	-18%
Bloom apex (day)	PISCES-MOG	133	133	159
	PISCES-v2	133	129	161
	Anomaly MOG - v2	0	4	-2
Bloom climax (day)	PISCES-MOG	117	124	130
	PISCES-v2	116	124	133
	Anomaly MOG - v2	1	0	-3
Bloom duration (days)	PISCES-MOG	64	70	86
	PISCES-v2	62	60	80
	Anomaly MOG - v2	2	10	6

Table 5. Global seasonality metrics of the simulated living compartments. Variables are defined in section 2.2.3 of the methods. All values are computed over the top 200m. Global averages are weighted by the corresponding plankton biomass distribution simulated in PISCES-MOG (the same weights are applied to PISCES-v2 and PISCES-MOG for consistency in the anomaly computation. Note that applying weights from PISCES-v2 would result in similar averages).

633 *3.3.2 Impacts on plankton phenology*

634 We evaluate the differences in seasonal patterns between PISCES-v2 and PISCES-
635 MOG for latitudes beyond 20 degrees based on 5-day-average time series (Table 5).

636 Differences in seasonality are small between PISCES-MOG in PISCES-v2 (Table
637 5). The timing of the bloom apex and bloom climax varies by a few days in the two mod-
638 els for micro- and mesozooplankton (Table 5, Fig. 5). The impacts on phytoplankton
639 phenology are even smaller (i.e., ± 2 days). However, annual absolute amplitudes are af-
640 fected consistently with the change in absolute biomass: mesozooplankton seasonal am-
641 plitude is reduced by 39%, while it is increased by 6% for microzooplankton (Table 5).
642 More interestingly, while absolute amplitudes show opposite patterns for meso- and mi-
643 crozooplankton, relative amplitudes are reduced by more than a quarter in both groups
644 (Table 5). This can be explained by the subdivision into classes that have differential
645 seasonality (cohort pattern, see section 3.1.2), which flattens the seasonal signal of the
646 whole group. This is confirmed by the bloom duration, which increases by 17% for mi-
647 crozooplankton and 8% for mesozooplankton in PISCES-MOG compared to PISCES-
648 v2 (Table 5).

649 Therefore, while the introduction of ontogenetic growth in PISCES-MOG modi-
650 fies the ecosystem structure and the seasonal amplitude of total mesozooplankton sig-
651 nificantly, its impact on total mesozooplankton biomass seasonality remains limited, even
652 if there are large intra-compartment variations in biomass seasonality due to cohort dy-
653 namics (see section 3.1).

654 *3.3.3 Impacts on the carbon cycle*

655 The efficiency of carbon transfer to the deeper layers strongly relies on the sink-
656 ing speed of particles which is highly size-dependent (Cael et al., 2021). In both PISCES
657 versions, POC is split into two groups: small organic carbon particles, which sink at a
658 speed of 2 m d^{-1} , and large particles, which sink at a speed of 50 m d^{-1} . Consequently,
659 for an identical remineralisation rate, carbon contained in large particles will be exported
660 25 times more efficiently than carbon contained in small POC. Moreover, while meso-
661 zooplankton particle production is mainly directed towards large POC, microzooplankton-

662 produced particles are considered small particles. As a direct consequence of simulated
 663 changes in zooplankton composition in PISCES-MOG compared to PISCES-v2, POC
 664 flux at 100 m is reduced by 10% in PISCES-MOG. This change is mainly driven by the
 665 decrease in the flux associated to large particles (97%) caused by the decrease in meso-
 666 zooplankton biomass. The net primary production being similar in PISCES-v2 (43.3 PgC
 667 yr⁻¹) and PISCES-MOG (42.3 PgC yr⁻¹), this reduced export in PISCES-MOG is as-
 668 sociated to a 8% lower pe-ratio.

669 Spatially, the changes in export are driven by changes in mesozooplankton biomass
 670 in the productive regions, since maxima in mesozooplankton decline at around 40° lat-
 671 itude and at the Equator (7(f)) correlate with peaks in large particles' decline at the same
 672 latitudes (7(e)). As a result, the equatorial upwelling and the sub-polar productive zones
 673 contribute the most to the decline in 100 m export when accounting for mesozooplank-
 674 ton reproduction and ontogenetic growth (7(d)).

675 While the introduction of mesozooplankton ontogenetic growth and reproduction
 676 into PISCES significantly reduces the mean annual export of particulate organic carbon
 677 (POC) at 100 meters depth in the ocean, its impact on the seasonality of this flux is lim-
 678 ited. Changes of less than 5 days in the global average for particles bloom apexes and
 679 climaxes, not presented here, indicate this limited effect. This expected behaviour re-
 680 sults from the limited influence of mesozooplankton ontogenetic growth and reproduc-
 681 tion on the seasonal timing of various organism groups (3.3.2).

682 ***3.3.4 Relative contributions: the relative role of reproduction and*** 683 ***ontogenetic growth versus that of the representation of size***

684 The addition of explicit reproduction and ontogenetic growth versus the addition
 685 of a full size spectrum could have differential effects on the behaviour of PISCES-MOG.
 686 To disentangle their relative importance, we compare PISCES-MOG vs PISCES-v2 anoma-
 687 lies to PISCES-MOG-2LS vs PISCES-v2 anomalies (Table 4, models defined in section
 688 2.2.2). We identified three possible scenarios: i) If PISCES-MOG anomalies are similar
 689 to PISCES-MOG-2LS anomalies, the size spectrum representation has little impact on
 690 the behaviour of PISCES-MOG. In this case, the simulated differences between PISCES-
 691 MOG and PISCES-v2 are driven by the introduction of ontogenetic growth and repro-
 692 duction. ii) If there is a lower absolute anomalies in PISCES-MOG-2LS compared to PISCES-
 693 MOG, the impact of reproduction and ontogenetic growth on the model behaviour is am-
 694 plified when representing the size spectrum. iii) If there is a higher absolute anomaly in
 695 PISCES-MOG-2LS compared to PISCES-MOG, the size spectrum representation actu-
 696 ally dampens the effect of representing ontogenetic growth and reproduction.

697 Based on these scenarios, we disentangle the relative effect of reproduction and on-
 698 togenetic growth versus that of the representation of size. PISCES-MOG-2LS and PISCES-
 699 MOG show consistent biomass anomaly signs across all plankton groups (Table 4). How-
 700 ever, micro- and nanophytoplankton anomalies are 30-50% higher, while diatom anoma-
 701 lies are 30% lower in PISCES-MOG-2LS compared to PISCES-MOG (Table 4). Con-
 702 sequently, diatoms and mesozooplankton are less abundant in PISCES-MOG-2LS, lead-
 703 ing to a 20% higher absolute export flux anomaly (Table 4). In PISCES-MOG-2LS, NPP
 704 shows an opposite anomaly compared to PISCES-MOG, resulting in a doubling of the
 705 PE-ratio anomaly. Thus, the effect of metazoan ontogenetic growth and reproduction
 706 representation on the intensity and efficiency of the BCP is dampened by the represen-
 707 tation of a size spectrum. Spatially, both models show similar anomaly distributions for
 708 most plankton groups, except for diatoms in the Southern Ocean (Fig. S1). Despite this
 709 difference, the resulting export flux anomaly distribution is similar in both models for
 710 most ocean regions (Fig. S2). Thus, in PISCES-MOG, metazoan reproduction and on-
 711 togenetic growth representation primarily drive differences with PISCES-v2 behaviour.

712 4 Discussion

713 4.1 Changes in plankton biomasses and carbon export estimates

714 Incorporating a detailed representation of mesozooplankton ontogenetic growth and
 715 reproduction into a biogeochemical component of an earth system model did not alter
 716 the realism of PISCES biogeochemical global properties. Indeed, in PISCES-MOG, spa-
 717 tial patterns are primarily related to the global gradient in primary productivity. This
 718 results in high biomasses in high-latitude regions and low biomasses in oligotrophic gyres,
 719 consistent with observations (Hatton et al., 2021). Net primary production (NPP, 42 PgC
 720 yr^{-1}) and carbon export estimates at 100 m (EP100, 7.1 PgC yr^{-1}), fall within the range
 721 of the literature (EP100: 5.8 PgC yr^{-1} in Clements et al. (2023), 6.6 PgC yr^{-1} in (Siegel
 722 et al., 2014) and 9.1 PgC yr^{-1} in (DeVries & Weber, 2017), NPP: 35-77 PgC yr^{-1} ; Field
 723 et al. (1998); Westberry et al. (2023)).

724 However, incorporating mesozooplankton ontogenetic growth and reproduction led
 725 to significant changes in annual biomass distribution within plankton compartments rel-
 726 ative to the standard version of the model. As anticipated in Clerc et al. (2021), zoo-
 727 plankton biomass was partly redistributed toward microzooplankton because adult meta-
 728 zoans allocate a portion of their energy towards reproduction. This behaviour enhances
 729 the realism of PISCES. Indeed, *Copepoda*, recognised as the most abundant mesozoo-
 730 plankton group (Moriarty & O'Brien, 2013; Drago et al., 2022), can represent a signif-
 731 icant portion of microzooplankton at their nauplii stages (up to 30%; Quevedo and Anadón
 732 (2000); Safi et al. (2007)). In addition, PISCES-MOG simulated mesozooplankton biomass
 733 distributions are closer to our present BDMS-based biomass estimates compared to the
 734 distributions simulated by PISCES-v2 (Fig. 6), suggesting that PISCES-MOG simula-
 735 tions are closer to field observations. Thus, PISCES-MOG simulates zooplankton more
 736 accurately than PISCES-v2, which may lead to increased realism in biogeochemical fluxes.

737 As a consequence of the changes in zooplankton structure, the particle size distri-
 738 bution shifted toward smaller particles (section 3.3.3). Consequently, the export at 100
 739 meters was 10% lower in PISCES-MOG compared to PISCES-v2. This finding suggests
 740 that zooplankton-driven carbon export may be overestimated in many biogeochemical
 741 components of Earth System Models, as these often represent mesozooplankton as a sin-
 742 gle and constant size class (Kearney et al., 2021). However, adding a more complex rep-
 743 resentation of the mesozooplankton would increase the computational cost by a factor
 744 of 2 or even more in fully coupled Earth System Models experiments, where physical and
 745 biogeochemical processes interact in both ways (such as in the Climate Model Intercom-
 746 parison Project (CMIP) exercises; Eyring et al. (2016); Taylor et al. (2012)). In paral-
 747 lel, the sensitivity experiment based on PISCES-MOG-2LS, where the representation of
 748 metazoan zooplankton is limited to two size classes instead of 20 (one juvenile compart-
 749 ment and one mature organism compartment, section 2.2.2) resulted in similar changes
 750 in biomass distribution and changes in carbon export compared to the changes observed
 751 when comparing PISCES-MOG to PISCES-v2 (section 3.3.4). Therefore, mesozooplank-
 752 ton ontogenetic growth and reproduction could be included in biogeochemical models
 753 without inducing a significant increase in computational cost by simply including a ju-
 754 venile metazoan compartment in the microzooplankton. This simple addition would likely
 755 suffice to influence the dynamics of carbon export in a manner similar to adding a com-
 756 plete representation of mesozooplankton ontogenetic growth and reproduction.

757 4.2 Cohort-driven impacts on plankton and carbon cycling

758 To our knowledge, this is the first study to specifically diagnose potential shifts in
 759 zooplankton phenology induced by incorporating of full size spectrum representation in
 760 a global biogeochemical model. By representing metazoan size classes the same way as
 761 in the 0D chemostat model of Clerc et al. (2021), we successfully introduced cohort dy-
 762 namics for metazoans in PISCES-MOG. Indeed, the seasonal behaviour of each size class

763 showed a globally consistent pattern: larger metazoans peak later and their blooms last
764 longer. These cohort dynamics is consistent with patterns previously evidenced in the
765 field (Mackas et al., 2012) and in models (McCauley & Murdoch, 1987; Persson et al.,
766 1998; Pope et al., 1994; Maury et al., 2007; Zhou et al., 2010). They emerge because ju-
767 veniles display a competitive advantage over adults right after a phytoplankton bloom
768 thanks to their higher mass-specific ingestion rates (Persson et al., 1998; De Roos & Pers-
769 son, 2003; De Roos et al., 2008; Persson & de Roos, 2013).

770 We expected cohort dynamics to induce a temporal delay in the peak of mesozoo-
771 plankton biomass within the year, compared to the peak simulated by a model without
772 cohorts (Clerc et al., 2021). Surprisingly, the inclusion of mesozooplankton ontogenetic
773 growth and reproduction did not significantly modify the temporal dynamics of meso-
774 zooplankton biomass in the 3-D implementation of the Clerc et al. (2021) model (Ta-
775 ble 5). To explain this, we argue that the metazoan population size structure right be-
776 fore the phytoplankton bloom (i.e., pre-bloom conditions) plays a determining role in
777 the simulated temporal dynamics. In Clerc et al. (2021) the pre-bloom metazoan pop-
778 ulation consisted of mature adult stages only. Due to the lower growth rate of mature
779 adults compared to other smaller metazoan size classes, this population structure resulted
780 in a slow formation of the first cohort, significantly contributing to the simulated delay
781 in the peak of mesozooplankton compared to the model without ontogenetic growth and
782 reproduction. In PISCES-MOG, pre-bloom metazoan size classes are more evenly dis-
783 tributed among juveniles and adults (Fig. 4). This structure led to a faster cohort for-
784 mation than in Clerc et al. (2021) and eliminated the delay in the peak of mesozooplank-
785 ton biomass between PISCES-MOG and PISCES-v2 (Table 5).

786 Including mesozooplankton ontogenetic growth also had limited impact on the sea-
787 sonality of carbon export (section 3.3.3). However, we argue that the effects on carbon
788 flux seasonality are underestimated because the particles produced by any mesozooplank-
789 ton size class are all directed to the same particle pool. We hypothesise that represent-
790 ing a particle size spectrum in PISCES-MOG would delay the annual peak in carbon ex-
791 port, because particles produced by each mesozooplankton size class would be allocated
792 to distinct particle size classes. Small metazoans, that peak earlier (section 3.1.2), would
793 produce small particles that sink slowly (Cael et al., 2021). Large metazoans, that peak
794 later (section 3.1.2), would produce large particles, that sink fast. Thus, by introducing
795 a particle size spectrum, the particle export efficiency would increase over time after the
796 phytoplankton bloom, and consequently POC flux export peak would be delayed. Us-
797 ing a numerical model representing a particle size spectrum, Serra-Pompei et al. (2022)
798 showed that size-spectrum slope and trophic levels of copepods (that can be linked to
799 the size) are important drivers of carbon export and carbon export efficiency (pe-ratio),
800 respectively. This supports our hypothesis that including particles size spectrum in PISCES-
801 MOG would result in changes in POC flux seasonality when accounting for mesozooplank-
802 ton ontogenetic growth.

803 **4.3 Evaluating mesozooplankton phenology and size structure in ma-** 804 **rine biogeochemical models**

805 We emphasise that new observation-based BDMs provide valuable insights into the
806 seasonal patterns of global zooplankton biomass, as they unlock spatial and temporal
807 scales that are not covered by the previous observations. Observations-based biomass
808 products from MAREDAT (Moriarty & O'Brien, 2013) (or subset, such as COPEPOD,
809 O'Brien (2005)) are often used to evaluate the predictions made by marine ecosystem
810 models for various plankton functional types in point-by-point comparisons (Le Quéré
811 et al., 2005; Aumont et al., 2015; Stock et al., 2014; Clerc, Bopp, et al., 2023). This eval-
812 uation is limited by the restricted spatiotemporal scales covered by these observational
813 data. Here, we benefit from novel approaches established to develop distribution mod-
814 els based on continuous abundance and derived biomass observations (Drago et al., 2022;

815 Waldock et al., 2022; Knecht et al., 2023). Indeed, for the first time to our knowledge,
816 we were able to evaluate the skill of a global biogeochemical model in predicting the phe-
817 nology and the seasonal production patterns of zooplankton against an observation-based
818 product. BDMs can thus successfully extract and extrapolate biomass patterns in space
819 and time, and substantially reduce the noise levels in biological data, enabling their com-
820 parison with biogeochemical model outputs. Our work represents a key step towards im-
821 proving the assessment of zooplankton functional groups in Earth System Models, as we
822 anticipate that further versions of such data-driven extrapolated biomass distribution
823 products will emerge for multiple plankton functional types (PFT), like those developed
824 for crustaceans and radiozoa based on imaging data (Drago et al., 2022) and those for
825 pteropods and foraminifers based on traditional net data Knecht et al. (2023).

826 Unlike previous versions of PISCES, a new feature requiring evaluation against field
827 observations is the mesozooplankton size spectrum. However, we identified only two open-
828 ocean time series that provided sufficient information to assess both the zooplankton size
829 spectrum and its seasonality. While modeled and observed zooplankton size spectra ex-
830 hibited similarities, both time series displayed significant inter-annual variation in sea-
831 sonality, precluding the identification of size-dependent seasonal patterns. In this con-
832 text, zooplankton community monitoring using imaging methodology (e.g., Lombard et
833 al. (2019)) paired with machine learning and BDM techniques are promising tools to (a)
834 increase the number of observations, and (b) extrapolate between measurements at a global
835 scale. Specifically, Under Vision Profiler 6 (UVP6) images are expected to significantly
836 contribute to constraining zooplankton size spectrum dynamics globally (Picheral et al.,
837 2022). Indeed, particle size distribution can be extracted from the images with novel ma-
838 chine learning tools that enable the quantification and monitoring of zooplankton func-
839 tional traits from a wealth of in situ imaging observations (Irisson et al., 2022; Orenstein
840 et al., 2022). Thus, the integration of imaging-derived in situ zooplankton size observa-
841 tions with machine learning and BDM techniques would enable the evaluation of size-
842 structured zooplankton global dynamics simulated by our model.

843 4.4 Model caveats

844 The extraordinary diversity of zooplankton life histories leads to complex responses
845 to environmental conditions and seasonal successions between different organisms (Romagnan
846 et al., 2015; Kenitz et al., 2017). In contrast, the way we incorporated mesozooplank-
847 ton ontogenetic growth and reproduction remains simplified due to computational con-
848 straints and does not account for all sources of intra- and interspecific variability within
849 the mesozooplankton life histories (Mauchline, 1998). First, we assumed that all adult
850 metazoans can reproduce. However, large species can reach a size considered as adult
851 in PISCES-MOG before reaching sexual maturity (Hartvig et al., 2011). A consequence
852 of that assumption is that the biomass and pool of reproductive organisms is overesti-
853 mated, leading to a likely overestimate of simulated reproduction rates. A more realis-
854 tic representation of reproduction would necessitate multiple size spectra organized based
855 on maximum size (Hartvig et al., 2011) or to make coarse assumptions about the max-
856 imum reproduction rates (Baird & Suthers, 2007), and this would likely reduce the dif-
857 ferences in annual biomass and POC fluxes between PISCES-MOG and PISCES-v2.

858 Second, zooplankton are assumed to be "income breeders" (Sainmont et al., 2014)
859 in PISCES-MOG, meaning that a portion of the grazing flux is instantaneously allocated
860 to reproduction (section 2.2.2). However, some organisms adopt an alternative repro-
861 duction strategy called "capital breeding" (Varpe et al., 2009), according to which an
862 individual may allocate energy to reserves which are used later in the year for reproduc-
863 tion. For example, certain copepod species undergo one or more diapause stages through-
864 out their life cycle to overcome unfavourable conditions (Hirche, 1996; Baumgartner &
865 Tarrant, 2017). This pause in biological development can occur at various life stages, in-
866 cluding eggs, embryos, juveniles, and adults and lead to synchronous metazoan life cy-

cles (Brun et al., 2016). Consequently, representing this additional process in PISCES-MOG could affect the pre-bloom metazoan population size structure by delaying the peak of mesozooplankton biomass between PISCES-MOG and PISCES-v2, in an even further fashion than presently modelled (see section 4.2). Capital breeding being the dominant reproductive strategy for marine copepods Sainmont et al. (2014) in regions characterised by strong seasonality, implementing this strategy in PISCES-MOG would alter our results. In this case, the impact of reproduction and ontogenetic growth on mesozooplankton seasonality and on metazoan-driven carbon export seasonal dynamics would be higher than currently simulated in high latitude regions.

Another caveat is that our model misses part of the complex processes through which mesozooplankton interact with the BCP (Steinberg & Landry, 2017). In particular, (Boyd et al., 2019) estimated the contribution of five additional mechanisms to the gravitational carbon pump, referred to as "particle injection pumps". Two of these mechanisms are directly linked to zooplankton: (i) the mortality of specific zooplankton groups undertaking seasonal migration to hibernate in the deep ocean (the "seasonal lipid pump" (Jónasdóttir et al., 2015; Pinti, DeVries, et al., 2023)), and (ii) the active transport of organic carbon by organisms that feed in surface layers and excrete in deeper layers by performing diel vertical migration (DVM) (the "mesopelagic-migrant pump"). As a result, the gravitational pump alone exports between 4 to 9 PgC yr⁻¹, whereas incorporating the "particle injection pumps" would increase this export flux up to 5 to 16 PgC yr⁻¹ (Boyd et al., 2019). Notably, DVM alone would contribute several petagrams of carbon per year (Boyd et al., 2019; Pinti, Jónasdóttir, et al., 2023; Aumont et al., 2018). Thus, in a model also accounting for both migration (i.e., DVM and hibernation) and reproduction processes, representing DVM and hibernation would increase the export of particles whereas reproduction would decrease it (see section 3.3.3). Yet, it remains difficult to hypothesise how the combination of these two processes would impact total export, since they have opposing effects on these fluxes. So far, these processes have been evaluated independently in different models (Jónasdóttir et al., 2015; Aumont et al., 2018), including ours, but no global biogeochemical model currently integrates all these processes in its representation of zooplankton. The ongoing developments in zooplankton observation systems (Lombard et al., 2019; Irsson et al., 2022) and the emergence of more spatially explicit data products of group-specific plankton biomass (Drago et al., 2022; Knecht et al., 2023) will facilitate the development of such integrative models and they will help to better constrain BCP estimates in a context of climate change.

5 Conclusions

Our study provides new insights into the impact of a more realistic representation of mesozooplankton biology on community structure, plankton functional type dynamics, and the export of organic carbon to depth in a global model. The inclusion of ontogenetic growth and reproduction shifts the structure of the zooplankton community toward smaller organisms (more mesozooplankton, less microzooplankton) and thus toward smaller organic particles, compared to that simulated by a model with a single and nonvarying size representation (as in PISCES-v2). This shift increases the grazing pressure on the nanophytoplankton while relaxing it for larger phytoplankton (diatoms), thus influencing the structure of the phytoplankton community size inversely to that of zooplankton. The net effect of mesozooplankton ontogeny and reproduction on total particles is a shift towards smaller particles, significantly reducing organic carbon export below 100 meters depth compared to a previous version of PISCES. This suggests that the contribution of zooplankton to the Biological Carbon Pump (BCP) export may be overestimated in many biogeochemical components of Earth System Models (ESMs).

Surprisingly, despite the partial representation of zooplankton life histories in our model that induced cohort dynamics, the emergent impact of this representation on the phenology of living ecosystem and non-living particle components is limited, even though

919 it was important for their mean annual distribution. However, we could benefit from the
920 cohort behaviour that emerges in PISCES-MOG to improve the understanding of zooplankton-
921 driven carbon flux dynamics and BCP seasonality. This would require new model de-
922 velopments, such as incorporating mesozooplankton capital breeding at high latitude or
923 representing the size spectrum of non-living particles and could be the subject of fur-
924 ther studies.

925 We emphasise that the observations-based mesozooplankton biomass climatology
926 provide valuable insights into the seasonal patterns of global zooplankton biomass as they
927 unlock spatial and temporal scales that were not covered by the previous observations.
928 New model development and data-based product presented in this study contribute to
929 improve model-observation synergies to understand the role of mesozooplankton on the
930 biological carbon pump, and to characterize the level of abstraction necessary to accu-
931 rately estimate its contribution to carbon fluxes.

932 Finally, here, we focused of the biogeochemical impacts of the mesozooplankton re-
933 production and ontogenetic growth. Given that mesozooplankton serve as food for many
934 predators, understanding their life cycles and ontogenetic growth could also regulate the
935 dynamics of higher trophic levels. Therefore, it would be relevant to study the effects
936 of these characteristics in a model explicitly representing the top of the trophic chain,
937 e.g. APECOSM (Maury, 2010; Dupont et al., 2023). In particular, the size structure of
938 zooplanktivorous predators could be influenced by the cohort pattern. Smaller preda-
939 tors would be favoured at the beginning of the cohort when smaller metazoans dominate,
940 while larger ones would emerge later along with larger metazoans.

941 **6 Open Research**

942 The authors declare no competing interests

943 **Author contributions**

944 CC, LB and OA conceived the study. CC, OA and LB developed the model for this
945 study. CC processed model outputs and time-series and performed the analysis. CC, NK
946 and FB processed and evaluated the interpolated observation product for this study. CC
947 draw the first draft. All authors (CC, LB, FB, NK, MV, OA) contributed to the manuscript
948 text with initial contributions from CC, LB and OA. The authors declare no compet-
949 ing interests.

950 **Availability statement**

951 The codes, datasets and model outputs needed to reproduce the figures, are openly
952 available in Zenodo at [10.5281/zenodo.10720907](https://zenodo.org/doi/10.5281/zenodo.10720907).

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