The Global Distribution and Drivers of Grazing Dynamics Estimated from Inverse Modelling

Tyler Weaver Rohr¹, Anthony Richardson², Andrew Allan Lenton³, Matthew A Chamberlain⁴, and Elizabeth H. Shadwick⁵

¹University of Tasmania ²University of Queensland, Australia ³Commonwealth Scientific and Industrial Research Organisation (CSIRO) Oceans and Atmosphere ⁴CSIRO Marine and Atmospheric Research ⁵CSIRO Oceans & Atmosphere

May 25, 2023

Abstract

We use inverse modelling to infer the distribution and drivers of community-integrated zooplankton grazing dynamics based on the skill with which different grazing formulations recreate the satellite-observed seasonal cycle in phytoplankton biomass. We find that oligotrophic and eutrophic biomes require more and less efficient grazing dynamics, respectively. This is characteristic of micro- and mesozooplankton, respectively, and leads to a strong sigmoidal relationship between observed mean-annual phytoplankton biomass and the optimal grazing parameterization required to simulate its seasonal cycle. Globally, we find Type III rather than Type II functional response curves consistently exhibit higher skill. These new observationally-based distributions can help constrain, validate and develop next-generation biogeochemical models.

The Global Distribution and Drivers of Grazing **Dynamics Estimated from Inverse Modelling**

Tyler Rohr^{1,2}, Anthony Richardson^{3,4}, Andrew Lenton⁵, Matt Chamberlain⁵, **Elizabeth Shadwick** 2,5

²Institute for Marine and Antarctic Science, University of Tasmania, Hobart, Tasmania, 7000, Australia ²Australian Antarctic Partnership Program, Hobart, Tasmania, 7000, Australia ³School of Environment, The University of Queensland, St Lucia, 4072, Queensland, Australia ⁴Commonwealth Scientific and Industrial Research Organisation (CSIRO) Environment, BioSciences Precinct (QBP), St Lucia, Queensland, 4067, Australia ⁵Commonwealth Scientific and Industrial Research Organisation (CSIRO) Environment, Hobart, Tasmania, 7000 Australia

Key Points:

1

2

3

4

9 10

11

12

| 13 | • | Oligotrophic (eutrophic) biomes exhibit more (less) efficient community-integrated |
|----|---|--|
| 14 | | grazing, characteristic of micro- (meso-) zooplankton. |
| 15 | • | We find a strong link between observed mean-annual phytoplankton biomass and |
| 16 | | the grazing dynamics required to recreate its seasonal cycle. |
| 17 | • | A type III functional response does a consistently better job recreating observed |
| 18 | | phytoplankton seasonal cycles than a type II response. |

Corresponding author: Tyler Rohr, tyler.rohr@utas.edu.au

19 Abstract

We use inverse modelling to infer the distribution and drivers of community-integrated 20 zooplankton grazing dynamics based on the skill with which different grazing formula-21 tions recreate the satellite-observed seasonal cycle in phytoplankton biomass. We find 22 that oligotrophic and eutrophic biomes require more and less efficient grazing dynam-23 ics, respectively. This is characteristic of micro- and mesozooplankton, respectively, and 24 leads to a strong sigmoidal relationship between observed mean-annual phytoplankton 25 biomass and the optimal grazing parameterization required to simulate its seasonal cy-26 cle. Globally, we find type III rather than type II functional response curves consistently 27 exhibit higher skill. These new observationally-based distributions can help constrain, 28

²⁹ validate and develop next-generation biogeochemical models.

³⁰ Plain Language Summary

To improve predictions of our ocean's ability to feed a growing human population 31 and buffer a changing climate, we need to improve our understanding of what happens 32 to carbon once it is absorbed into the ocean. One of the largest gaps in marine carbon 33 cycling is the role of zooplankton grazing. The rate at which zooplankton graze phyto-34 plankton modifies the size and seasonal evolution of phytoplankton populations and in 35 turn the associated rates of net primary production at the base of the food web, secondary 36 production of grazers (an indicator of fisheries potential) and export production (the bi-37 ological sequestration of carbon). However, regional differences in grazing, which are dif-38 ficult to measure outside of a laboratory setting, remain poorly constrained by obser-39 vations and thus difficult to model. Here, we run a suite of model simulations, each of 40 which simulate grazing in a different way, then compare the results to infer which type 41 of grazing dynamics match observations. We find that there is dramatic spatial variabil-42 ity in how zooplankton, as a community, appear to be grazing and that this variability 43 maps well onto observed phytoplankton concentrations, suggesting that the type of zoo-44 plankton present may be determined by the amount of prey available. 45

46 **1** Introduction

Marine net primary production (NPP) supports the biological export (EP) of car-47 bon (de la Rocha, 2006) and forms the base of the marine food web (Armengol et al., 48 2019). Although oceanographers have historically focused on light (Sverdrup, 1953) and 49 nutrients (Howarth, 1988), increasing experimental (Lima-Mendez et al., 2015; Guidi et 50 al., 2016), observational (Behrenfeld et al., 2013) and modelling (Hashioka et al., 2013; 51 Prowe et al., 2012; Laufkötter et al., 2015; Vallina & Le Quéré, 2011; Chenillat et al., 52 2021) work has highlighted zooplankton grazing as a critical control on NPP. However, 53 grazing dynamics remain poorly constrained across modern biogeochemical (BGC) mod-54 els, including those used by the IPCC in climate projections (Rohr et al., 2023). This 55 likely contributes to persisting uncertainty in projections of NPP (Tagliabue et al., 2021; 56 Laufkötter et al., 2015), EP (Laufkötter et al., 2016; Fu et al., 2016), zooplankton biomass 57 (Petrik et al., 2022) and fisheries catch (Tittensor et al., 2021). 58

The parameterization of relatively coarse global models implicitly requires an un-59 derstanding of the mean dynamics of many species averaged across a patchy ocean, which 60 may diverge dramatically from the dynamics of individual zooplankton (Rohr et al., 2022; 61 Morozov, 2010). Although empirical laboratory experiments have shown that grazing 62 dynamics (i.e. the manner in which zooplankton-specific grazing rates increase with prey 63 concentration) vary substantially across zooplankton species, ages, and sizes (Hansen et 64 al., 1997; Hirst & Bunker, 2003), most laboratory studies consider the idealized behav-65 ior of a single species in a well-mixed environment. 66

Field-based dilution experiments help average across some of this variability (Morrow et al., 2018; Landry et al., 2009, 2008; Landry et al., 2000) and have been used to estimate grazing dynamics in natural microzooplankton assemblages (Chen et al., 2014). However, these experiments are limited in their spatial scope and resolution (Schmoker et al., 2013) and can be biased by trophic cascades (Calbet et al., 2011), the presence of mixotrophs (Calbet et al., 2012) and the exclusion of mesozooplankton and macrozooplankton (Schmoker et al., 2013).

In the absence of direct, global, high-resolution measurements, community-integrated grazing rates and dynamics could theoretically be backed-out from zooplankton biomass budgets. However, disparate methods for shipboard observation make it difficult to describe time-evolving global distributions without large levels of statistical inference (Everett et al., 2017; Heneghan et al., 2020; Ratnarajah et al., 2023) and algorithms for satellite observation are limited (Druon et al., 2019; Strömberg et al., 2009).

Yet, while zooplankton grazing dynamics and biomass are difficult to observe directly, phytoplankton loss rates (Mojica et al., 2021; Deppeler & Davidson, 2017) and population dynamics (Gentleman & Neuheimer, 2008; Truscott et al., 1994; Steele, 1974) are largely driven by grazing. Thus the most viable option to estimate community-integrated grazing dynamics at scale may be inference from the remote sensing record of phytoplankton biomass (Westberry et al., 2008).

Here, we infer the global distribution of community-integrated grazing dynamics 86 using an inverse modelling approach. We run a suite of simulations in a coupled ocean-87 BGC model, parameterized with a wide range of grazing dynamics, and determine the 88 optimal parameters required to recreate the observed phytoplankton seasonal cycle. We 89 map the distribution of optimal parameters, examine how they appear driven by regional 90 variability in phytoplankton biomass (Sec. 3.1), and explain mechanistically how graz-91 ing dynamics can shape the seasonal cycle (Sec. 3.2). Finally, we discuss the limitations 92 of this work (Sec. 4.1), as well its potential utility from a ecological (Sec. 4.2) and mod-93 elling perspective (Sec. 4.3). 94

95 **2** Materials and methods

2.1 Grazing in BGC models

108

The simplest BGC models include one zooplankton grazing on one phytoplankton. 97 The relationship between specific grazing rates $(g; d^{-1})$ and prey abundance is typically 98 described by a type II or III functional response curve (Gentleman & Neuheimer, 2008; 99 Rohr et al., 2022). The primary difference between response curves is that the type II 100 response increases linearly at low phytoplantkon concentrations ($[C_{phyto}]$; mmolC m⁻³), 101 while the type III increases quadratically (**Figure 1**). Both curves, $g([C_{phyto}])$, can be 102 parameterized with a saturation grazing rate $(g_{max}; d^{-1})$, which describes the rate when 103 prey is non-limiting, and a half saturation concentration $(K_{1/2}; \text{ mmolC m}^{-3})$, which de-104 scribes how much prey is required to get there (i.e. $g([K_{1/2}]) = 0.5 * g_{max}$). Here we 105 focus on $K_{1/2}$ because it has been shown to have a stronger influence on population dy-106 namics (Rohr et al., 2022) and marine carbon cycling (Rohr et al., 2023) than g_{max} . 107

2.2 Grazing and population dynamics

Grazing dynamics can influence the seasonal cycle of phytoplankton biomass via the curvature of the functional response, which has either a stabilizing or destabilising influence on phytoplankton population dynamics depending on its concavity (Steele, 1974; Truscott et al., 1994; Gentleman & Neuheimer, 2008; Rohr et al., 2022). If the functional response is concave upward, then phytoplankton-specific loss rates to grazing increase with the size of the phytoplankton population. This creates a negative feedback loop which dampens changes in the size of the phytoplankton population, thereby exerting a stabilizing influence. Alternatively, downward concavity means phytoplankton-specific loss
rates to grazing decline with population growth, creating a destabilizing, positive feedback which amplifies changes in the size of the phytoplankton population.

The shape and stabilizing influence of the functional response is determined by its 119 response type (II or III) and parameters (particularly $K_{1/2}$). While the parameter val-120 ues determine the magnitude of curvature and thus the strength of the stabilizing influ-121 ence, the response type determines the direction. A type II response is always concave 122 123 downward and thus always destabilizing. A type III response has upward concavity below $K_{1/2}$ and thus stabilizing properties at low phytoplankton concentrations. In turn, 124 the grazing formulation exerts a strong influence on the size, shape, and propensity of 125 phytoplankton blooms, sub-seasonal oscillations, and extinction events (Dunn & Hovel, 126 2020; Adjou et al., 2012; Hernández-García & López, 2004; Malchow et al., 2005; Rohr 127 et al., 2022). 128

While a type II response is typically found in laboratory experiments (Hansen et 129 al., 1997), a type III response can be justified as the implicit representation of more com-130 plex behavior such as active prey switching (Prowe et al., 2012; Vallina et al., 2014) or 131 the mean state of a patchy ocean (Morozov & Arashkevich, 2010; Rohr et al., 2022). Thus, 132 in any given region, the true shape of the apparent functional response (i.e. the spatially-133 integrated relationship between total prey and community-averaged zooplankton-specific 134 grazing rates) is determined by the community-composition, prey preferences, spatial dis-135 tributions and physiology of resident zooplankton. Using inverse modelling to match the 136 spatially-averaged and community-integrated phytoplankton record observed from satel-137 lites helps average out spatial, species-level, and behavioral complexities that many global 138 models do not explicitly resolve. 139

140

155

2.3 Model configuration

We use a global, ocean-BGC model to determine which $K_{1/2}$ values and response 141 types are required to best match the observed phytoplankton seasonal cycle. Simulations 142 are run with the Whole Ocean Model of Biogeochemistry and Trophic-dynamics (WOM-143 BAT) (Law et al., 2017), part of the Australian Earth Systems Model (ACCESS-ESM1.5) 144 (Ziehn et al., 2020), which has been studied and validated extensively (Mortenson et al., 145 2021; Kwiatkowski et al., 2020; Ziehn et al., 2017; Oke et al., 2013). The ocean model 146 is the global configuration of Modular Ocean Model version 5 (Griffies, 2012). WOM-147 BAT has a relatively simple structure, with one phytoplankton and one zooplankton group. 148 While more complex models include multiple zooplankton grazing on multiple phyto-149 plankton (Rohr et al., 2023), we are interested here in estimating community-integrated 150 grazing dynamics. These can be inferred most directly by tuning WOMBAT's single-prey 151 grazing formulation, which implicitly represents the community-integrated behavior of 152 all zooplankton groups, towards the satellite-observed phytoplankton seasonal cycle, which 153 explicitly integrates across all phytoplankton groups. 154

2.4 Model experiments

We ran a total of 36 global simulations, each with a different grazing formulation. 156 To isolate the influence of grazing, all simulations were initialized from the same state, 157 embedded in an identical repeat-climatological physical ocean, and forced with identi-158 cal surface flux and freshwater runoff from the Japanese 55-year atmospheric reanaly-159 sis surface dataset (Tsujino et al., 2020). After initialisation, each run was spun up for 160 5 years to a quasi-steady state, long enough to equilibrate with changes to the grazing 161 formulation. Output is reported from the fifth year and can be considered climatolog-162 ical. 163

We ran two suites of experiments, using a type II and III functional response. Within each suite, we tested 18 different parameters combination: $K_{1/2} = 0.5$, 1, 2, 4, 8, 16 (*mmolC* m^{-3}) and $g_{max} = 0.5$, 1, 2 (d^{-1}). These values are consistent with the range that has been derived empirically and used in models historically (Rohr et al., 2022). All other parameters were kept constant and identical to Law et al. (2017).

2.5 Model skill assessment

We used two metrics to evaluate the model's ability to recreate the observed phy-170 toplankton seasonal cycle: the correlation coefficient (CC) and the coefficient of vari-171 ation (CV). The CC measures the co-variability between the simulated and observed 172 climatologies, while the CV measures the magnitude of variability separately in each cli-173 matology relative to its annual mean $(CV = \frac{std}{mean})$. Together they capture the shape (CC) and strength (CV) of the seasonal cycle. Both metrics are largely agnostic to the 174 175 size of mean-annual phytoplankton population (i.e. CC independent to mean; CV nor-176 malized by mean). This is to help isolate the influence of grazing dynamics on the qual-177 itative shape of the seasonal cycle rather than mean-state NPP which could be biased 178 by many other model attributes. 179

For each metric, the seasonal cycle of simulated surface phytoplankton biomass was 180 compared to an 18-year remote sensing climatology (July 2002 - April 2021) from the 181 Carbon-based Productivity Model (CbPM) (Westberry et al., 2008). The remote sens-182 ing record was interpolated onto the model grid and all time series were centered on the 183 summer solstice. We use the observed carbon product, which is derived from back-scatter, 184 instead chlorophyll because WOMBAT does not resolve chlorophyll. However, we repeated 185 the analysis comparing model carbon to satellite chlorophyll (Sathyendranath et al., 2019) 186 and found similar results (Supporting Text 1). 187

The cost function for model skill was quantified for each run in each grid-cell by subtracting the absolute difference between the modelled (CV_{mod}) and observed (CV_{obs}) coefficient of variation from the correlation coefficient $(CC_{mod,obs})$,

Model Skill =
$$norm(CC_{mod,obs}) - norm(|CV_{mod} - CV_{obs}|)$$
 (1)

Both metrics are normalized across all grid cells from all 36 model runs, such that they are equally weighted and cost function scores can be directly compared across all experiments.

For each response type, we considered three sets of six runs. Each run in a set used a different $K_{1/2}$ value but constant g_{max} value. Within each set, the cost function score was interpolated between $K_{1/2}$ values at each grid cell using a piece-wise cubic polynomial (**Figure 2**). The $K_{1/2}$ value with the maximum score was identified and averaged across all three sets to infer the optimal value. Regions below 55°S or above 55°N with limited remote sensing coverage were excluded.

200 **3 Results**

201

169

3.1 Global distribution and drivers of grazing dynamics

The distribution of observed mean-annual surface phytoplankton biomass estimated from CbPM (**Figure 1A**) has a striking co-variability with the distribution of grazing dynamics inferred by the optimal $K_{1/2}$ value required to match the observed seasonal cycle (**Figure 1B, C**). We find that more oligotrophic regions with mean-annual phytoplankton biomass lower than the global median require smaller $K_{1/2}$ values to best match the observed phenology (**Figure 1A-C; more blue**). Alternatively, eutrophic regions with mean-annual phytoplankton biomass above the global median, including HNLC re²⁰⁹ gions, require larger $K_{1/2}$ values (Figure 1A-C; more green). Qualitatively, this pat-²¹⁰ tern generally holds regardless of whether a type II (Figure 1B) or III (Figure 1C) ²¹¹ functional response is used to described grazing dynamics and whether biomass (Figure ²¹² 1A) or chlorophyll (Supporting Figure 1) is used to described the observed seasonal ²¹³ cycle.

Plotting the optimal $K_{1/2}$ value against the corresponding observed mean-annual 214 surface biomass reveals a clear sigmoidal relationship (Figure 1D, E). Regardless of func-215 tional response type, larger $K_{1/2}$ values are required to recreate the seasonal cycle of biomes 216 217 with higher mean-annual phytoplankton biomass, but appear to be bound asymptotically by a minimum and maximum viable $K_{1/2}$ value. Switching from a type II (Figure 218 **1D**) to type III (Figure 1E) response or decreasing g_{max} (Supporting Figure 2) de-219 creases the value of both asymptotes, but neither substantively influence the shape of 220 the curve. Thus, while other assumptions about the grazing formulation influence the 221 specific quantitative estimates of the optimal $K_{1/2}$ (Supporting Table 1), the qual-222 itative relationship is consistent: higher biomass regions appear to be populated with 223 zooplankton with higher community-integrated $K_{1/2}$ values. 224

Finally, regardless of biome, using a type III response consistently recreates the observed phytoplankton seasonal cycle better than a type II response, with 30% more model skill on average (**Figure 1**). Moreover, the type III response performs better regardless of whether the observed seasonal cycle is quantified with carbon or chlorophyll or which g_{max} value is used (**Supporting Figures 1, 2**).

230

3.2 Mechanistic influence of the grazing dynamics

Importantly, our estimations of model skill do not include any metric for mean model bias. Thus, the correct interpretation of these results is not that more or less grazing leads to less or more phytoplankton biomass, respectively, but rather that the dynamical properties of the functional response curve can shape of the seasonal evolution of phytoplankton accumulation in a way that appears more or less consistent with observations.

For example, when $K_{1/2}$ is large, phytoplankton tend to exhibit a stronger, well-236 defined seasonal cycle with less high frequency variability (Figure 2; green lines). This 237 is because the grazing formulation does not heavily influence the stability of the system, 238 allowing bloom dynamics to be driven primarily by bottom-up controls, such as light and 239 nutrients, which generally exhibit strong seasonality following seasonal cycles in verti-240 cal mixing and day length. In turn, phytoplankton population dynamics are not as sen-241 sitive to the whether a type II (Figure 2C, D) or III (Figure 2A, B) response is used. 242 However, as $K_{1/2}$ decreases, the grazing formulation has a stronger influence on the sta-243 bility on the system. This influence is stabilizing if a type III response is used but desta-244 bilizing if a type II response is used (Supporting Text 2; Supporting Figure 3), re-245 sulting in substantively different seasonal cycles (Figure 2; blue tracers). We consider 246 two case studies, in the Subantarctic zone (SAZ) and Sargasso sea, which are generally 247 representative of the seasonal variability in more eutrophic and oligotrophic biomes, re-248 spectively. 249

In the SAZ (Figure 2A, C) the observed evolution of biomass (black line) exhibits 250 a strong seasonal cycle with an amplitude $\sim 20\%$ greater than its mean and relatively 251 little sub-seasonal variability. It is best recreated using larger $K_{1/2}$ values and exhibits 252 slightly more model skill when a type III response is used. With a type III response (Figure 253 **2A**), lower $K_{1/2}$ values reduce the mean biomass but do not systematically modify the 254 255 CV, leaving the ratio of summer to winter biomass roughly proportional. Alternatively, with a type II response (Figure 2C), decreasing $K_{1/2}$ delays bloom initiation but am-256 plifies its acceleration once initiated, leading to smaller, shorter, sharper features and sys-257 tematically higher CVs. The initiation is delayed because the type II response dispro-258 portionately increases grazing rates at low biomass concentrations compared to a type 259



Figure 1. The distribution and drivers of grazing dynamics. A) The observed climatological mean-annual phytoplankton biomass concentration plotted as a percentile of the full spatial distribution. Below, the corresponding optimal $K_{1/2}$ parameter required to best recreate the observed phytoplankton seasonal cycle using a B) type II or C) type III response function plotted as a percentile for direct qualitative comparison. Beside each is an example functional response curve for their respective (bolded) response types, both parameterized with the same $K_{1/2}$ and g_{max} . Below A) a schematic of the characteristic phytoplankton associated with low and high biomass waters and below C) a schematic of zooplankton associated with low and high $K_{1/2}$ values. The optimal $K_{1/2}$ found with a D) type II and E) type III response are plotted against the observed mean-annual phytoplankton biomass. Each point represents the mean of roughly 30 grid cells, binned based on their percentile biomass, with the top and bottom 5% percent removed. Points are colored by their mean cost function score, with red indicating more model skill. All values are averaged across three experiment suites, with each using a different g_{max} value. Results from individual experiment suites are shown in **Supporting Figure 2**. Data is fit to a sigmoidal curve (solid blue), shown with 95% confidence bounds (dashed blue).



Figure 2. Influence of $K_{1/2}$ and response type on phytoplankton seasonal cycle. Phytoplankton biomass climatologies and model skill evaluations are provided from A, C the SAZ and B, D Sargasso Sea, showing the emergent seasonal cycle from runs using six $K_{1/2}$ values with a A, B Type III and C, D type II functional response. All simulations shown use identical g_{max} values $(1 d^{-1})$. In the upper panel of each subplot, the observed (black) and simulated (blue-green) seasonal cycles are plotted with the simulation that best matches the observed phenology in bold. In the lower panel, the cost function scoring is demonstrated for each simulation, with the corresponding CC and CV shown above the total cost function score. Red and blue shading indicates better and worse model skill, respectively. The optimal $K_{1/2}$ value is determined by the maximum (red line) interpolated model skill (black line). In the inset map (top-right corner) the distribution of optimal $K_{1/2}$ values is shown with the example location marked in red. Note, these distributions are qualitatively identical to gigure 1, with the same percentile-based colorbar. However, they only consider runs with $g_{max} = 1$ to be consistent with the traces, rather than the mean of all three g_{max} sets.

III response. The bloom is a sharper because lowering $K_{1/2}$ in a type II response destabilizes the system, allowing phytoplankton biomass to accumulate rapidly until bottomup factors respond (i.e. nutrient limitation, self-shading) and rapidly terminate the bloom.

In the Sargasso Sea (Figure 2B, D), the observed evolution of biomass (black line) 263 exhibits a weaker seasonal cycle, with an amplitude less than half the size of its mean. 264 It is best recreated using smaller $K_{1/2}$ values and a type III response. With a type III 265 response (Figure 2B), highly-stable lower $K_{1/2}$ values dampen seasonality in bottom-266 up controls and prevent a bloom. Increasing $K_{1/2}$ allows an unrealistic late-winter/early-267 spring bloom to emerge, systematically increasing the CV and decreasing model skill. 268 While the emergent seasonal cycle is nearly identical between response curves when us-269 ing high $K_{1/2}$ values (Figure 2D), the Type II response diverges substantially when us-270 ing low $K_{1/2}$ values. Here, decreasing stability introduces unstable predator-prey dynam-271 ics which drive higher-frequency oscillations. Thus, the model cannot eliminate the un-272 natural early-spring bloom without inducing unnatural sub-seasonal spikes, neither of 273 which are observed. 274

275 4 Discussion

276 4.1 Limitations

The largest limitation of these results likely stems from the accuracy of non-grazing 277 attributes in the BGC-ocean model we have optimized. Despite running experiments in 278 an identical physical ocean, if their is a systematic bias in the simulated seasonal light 279 and nutrient cycle, then it is possible that the 'wrong' grazing dynamics could combine 280 with the 'wrong' bottom-up controls to produce the correct seasonal cycle, leading us 281 to infer unnatural grazing dynamics. This could be the case along the equator where there 282 is a disproportionately large bias in phytoplankton biomass relative to NPP (Supporting 283 Figure 4), suggesting simulated phytoplankton-specific growth rates are systematically 284 low. This may explain why we inferred higher $K_{1/2}$ values in the equatorial Indian, At-285 lantic, and Pacific basins (Figure 1B; greener) than we would have expected from the 286 low mean-annual phytoplankton biomass observed there (Figure 1A; bluer). If the model 287 is misrepresenting the seasonal cycle in bottom-up controls as too weak, it makes sense 288 that higher $K_{1/2}$ values are needed to not damp out all seasonal variability and recre-289 ate the observed seasonal cycle. Additional biases may stem from the remote sensing prod-290 ucts, which are limited by clouds and the solar inclination angle, the exact nature of the 291 link between trophic controls and bloom phenology (Behrenfeld et al., 2013; Rohr et al., 292 2017), and our ability to accurately quantify the fidelity of the seasonal cycle. Collec-293 tively then, our results our best understood qualitatively, rather than as specific quan-294 titative predictions of the apparent $K_{1/2}$ value in any specific location. 295

296

4.2 Ecological Perspectives

Nevertheless, our inferred distribution of community-integrated grazing dynamics 297 is consistent with the biogeography of community composition which we would expect 298 to inhabit each respective biome (Barton et al., 2013; Heneghan et al., 2020; Décima, 2022; 299 Brandão et al., 2021). Ecologically, the value of $K_{1/2}$ at a fixed g_{max} is related to the 300 rate at which zooplankton can capture (rather than consume) prey (Rohr et al., 2022). 301 Physiologically, the zooplankton with fastest prey capture rates are typically rapidly-grazing 302 microzooplankton and filter feeders (Hansen et al., 1997). However, these zooplankton 303 species are generally unable to consume anything larger than small flagellates, ciliates 304 and cyanobacteria, exactly the sort of phytoplankton that tend to dominate more olig-305 otrophic regions such as the gyres (Calbet & Landry, 2004). On the other hand, slowly-306 grazing euphausiids, copepods and macrozooplankton tend to have much slower capture 307 rates but are capable of consuming much larger prey, such as dinoflagellates and diatom 308

assemblages, which tend to dominate more eutrophic coastal and higher-latitude regions
 (San Martin et al., 2006).

The sigmoidal relationship between phytoplankton biomass and inferred community-311 integrated $K_{1/2}$ values implies the importance of two end-member communities in the 312 most oligotrophic and eutrophic regions. The location of each asymptotes implies a com-313 munity integrated $K_{1/2}$ value of 3 mmolC m⁻³ for ecosystems dominated by faster-grazing 314 microzooplankton and filter feeders and $8.3 \text{ mmolC} \text{ m}^{-3}$ for ecosystems dominated by 315 slower-grazing mesozooplankton and macrozooplantkon. While these values are lower 316 than the median empirical $K_{1/2}$ values measured by Hansen et al. (1997) in individual 317 microzooplankton (8.9 mmolC m⁻³) and mesozooplantkon (18 mmolC m⁻³), the appar-318 ent $K_{1/2}$ of spatially-averaged, community-integrated dynamics is expected to be much 319 lower than that of any individual species measured in well-mixed laboratory medium (Rohr 320 et al., 2022). 321

However, despite two prominent asymptotes, the region of monotonically increas-322 ing $K_{1/2}$ values between them (~.85-1.2 mmolC m⁻³) encompasses over 50% of the ocean 323 area in our domain (55°S-55°N) and 43% of the global ocean. This suggests a critical 324 role for more heterogeneous zooplankton communities and the co-existance of diverse func-325 tional groups therein. This steady increase in $K_{1/2}$ across intermediate mean-annual phy-326 toplankton concentrations is consistent with the positive relationship between empiri-327 cally estimated microzooplankton $K_{1/2}$ values and in-situ chlorophyll concentrations mea-328 sured across shipboard dilution experiments (Chen et al., 2014). Note, while these re-329 sults strongly imply slower zooplankton-specific grazing rates in more productive biomes, 330 they can be consistent with observations of bulk ingestion rates and phytoplankton-specific 331 grazing mortality increasing with primary productivity (Schmoker et al., 2013; Calbet, 332 2001) due to differences in phytoplankton and zooplankton abundance. 333

Finally, while community-integrated $K_{1/2}$ values exhibit large regional variability, 334 the spatially integrated dynamics of all biomes are consistently best described by a type 335 III versus type II response (Figure 1, Supporting Table 1). Although dynamic instabil-336 ities are not necessarily unnatural (McCauley & Murdoch, 1987), when averaged across 337 a relatively large area the destabilizing properties of a type II response appear to lead 338 to sharper, more delayed blooms than observed in eutrophic regions and more sub-seasonal 339 variability than observed in eutrophic regions (Figure 2). This is consistent with obser-340 vational (Morozov et al., 2008; Kiørboe, 2018), modelling (Nissen et al., 2018; Prowe et 341 al., 2012; Chenillat et al., 2021), and theoretical (Rohr et al., 2022; Morozov, 2010) work 342 suggesting that the downward concavity, prey refuge, and stabilizing properties associ-343 ated with a type III response may be a better empirical representation of the mean state 344 of a patchy ocean and complex food web, even if a type II response is typically measured 345 for individual species in a well-mixed laboratory medium (Hansen et al., 1997; Hirst & 346 Bunker, 2003). 347

348

4.3 Modelling Perspectives

Considering the sensitivity of simulated carbon cycling to the representation of zoo-349 plankton grazing dynamics (Rohr et al., 2023; Chenillat et al., 2021; Prowe et al., 2012; 350 Laufkötter et al., 2015, 2016; Dupont et al., 2023), it is critical for models to accurately 351 recreate the distribution community-integrated grazing dynamics and allow it to respond 352 to environmental change. As warming, stratification, and stronger winds transform the 353 surface ocean, the ensuing balance of light and nutrients may reshape marine ecosystems 354 (Pörtner et al., 2019), favouring different zooplankton species, in different places, with 355 vastly different grazing dynamics. For instance, a shift toward smaller phytoplankton, 356 which have higher light but lower nutrient requirements (Pörtner et al., 2019; Bopp et 357 al., 2005) would precipitate a shift towards microzooplankton, salps and larvaceans. Al-358 ready a southward shift of salps into regions previously dominated by euphausiids has 359

been observed (Henschke & Pakhomov, 2019; Steinberg & Landry, 2017). Such shifts should
be captured in BGC models if Earth system and ecosystem models hope to predict changes
in the oceans capacity to buffer a changing climate and feed a growing population.

Fortunately, the validation of zooplankton biomass in BGC models is receiving in-363 creasing attention (Petrik et al., 2022; McGinty et al., 2023). However, given large un-364 certainties in the parameterization of grazing within ostensibly similar zooplankton func-365 tional groups across models (Rohr et al., 2022, 2023), a further validation of zooplankton-366 specific grazing rates is required to determine if a model is accurately simulating graz-367 ing pressure (i.e. the phytoplankton-specific mortality rate to grazing), which may be 368 the single largest source of uncertainty in CMIP6 representations of marine carbon cy-369 cling (Rohr et al., 2023). While direct field measurements of grazing rates are typically 370 limited to the role of microzooplankton (Schmoker et al., 2013; Calbet & Landry, 2004; 371 Landry & Calbet, 2004) our results implicitly reflect the integrated grazing dynamics 372 of the entire zooplankton community, averaging over the distribution and behavior of 373 individual species. 374

First off, it appears clear that modellers should use a type III over type II response. 375 especially if explicitly resolving a limited food web with relatively coarse spatial reso-376 lution. Further, although our exact quantitative estimates of $K_{1/2}$ are limited and vary 377 with other model parameters (Supporting Table 1), there is a consistent qualitative 378 pattern in apparent $K_{1/2}$ values which models ought to recreate. At minimum, it is clear 379 a priori that models with a single zooplankton and prey option (e.g. Tjiputra et al. (2020); 380 Zahariev et al. (2008); Law et al. (2017)) cannot simulate the established spatial vari-381 ability in community-integrated grazing dynamics (as the single zooplankton will graze 382 with the same $K_{1/2}$ everywhere). In turn, bottom-up controls are likely over-tuned to 383 compensate for unrealistic top-down homogeneity. While many CMIP6-class models in-384 clude 2-3 zooplankton groups (Kearney et al., 2021; Rohr et al., 2023), it is critical to 385 know if competition between them is sufficient to drive a realistic emergent distribution 386 in community-integrated grazing dynamics. Thus, we encourage modellers to confirm 387 whether the distribution of community-integrated $K_{1/2}$ values is qualitatively consistent 388 with **Figure 1**. This can be done by fitting a curve between the mean zooplankton-specific 389 grazing rate and total prey concentration in different regions or grid cells to diagnosti-390 cally compute the apparent functional response and associated community-integrated 391 $K_{1/2}$ value. Significant disagreement from **Figure 1** would likely imply that additional 392 zooplankton groups, such as macrozooplankton (Le Quéré et al., 2016), salps (Luo et al., 393 2020), larvaceans, euphausiids, chaetognaths, jellyfish (Heneghan et al., 2020, 2023) may 394 be required. 395

Finally, if explicit competition between limited functional groups is insufficient to 396 resolve the emergent distribution of community-integrated grazing dynamics and a suf-397 ficiently complex food web is not computationally tractable with high-resolution projec-398 tions (Neelin et al., 2010), then modellers might consider parameterizing zooplankton 399 community composition using the relationship described in **Figure 1**. That is, modellers 400 could implicitly represent changes in zooplankton community composition by modify-401 ing $K_{1/2}$ of a single group as a function of phytoplankton abundance (Supporting Ta-402 ble 1). This could allow allow the mean attributes of the zooplankton community to re-403 spond dynamically to changing environmental conditions without explicitly resolving each 404 of its constituent species. While potentially powerful, implementing such a parameter-405 ization would require several important assumptions and careful calibrations (Supporting 406 Text 3). 407

408 5 Conclusions

These results present a novel, observationally-informed, map of global communityintegrated grazing dynamics (i.e $K_{1/2}$ values). Further refining the observed distribution and drivers of grazing, and how to replicate them in models, will require close collaboration with zooplankton ecologists, but presents an exciting new frontier in oceanography focused on a rigorous understanding of how NPP is controlled from the top-down.
Moreover, improving the representation of zooplankton could realize dramatic improvements in marine BGC models and our predictions of future ocean states.

416 6 Open Research

All relevant model output and documentation can be found at https://doi.org/10.25919/wn096j31. Remote sensing products were downloaded at http://orca.science.oregonstate
.edu/2160.by.4320.8day.hdf.carbon2.m.php. Please address any questions to Tyler
Rohr, at tyler.rohr@utas.edu.au.

421 Acknowledgments

This research was supported by the Australian Antarctic Program Partnership through
 the Australian Government's Antarctic Science Collaboration Initiative.

424 **References**

| 425 | Adjou, M., Bendtsen, J., & Richardson, K. (2012, January). Modeling the influence |
|-----|---|
| 426 | from ocean transport, mixing and grazing on phytoplankton diversity. <i>Ecologi</i> - |
| 427 | cal Modelling, 225, 19–27. doi: 10.1016/j.ecolmodel.2011.11.005 |
| 428 | Archibald, K. M., Siegel, D. A., & Doney, S. C. (2019). Modeling the Impact of Zoo- |
| 429 | plankton Diel Vertical Migration on the Carbon Export Flux of the Biological |
| 430 | Pump. Global Biogeochemical Cycles, 33(2), 181–199. Retrieved 2022-02-03, |
| 431 | <pre>from https://onlinelibrary.wiley.com/doi/abs/10.1029/2018GB005983</pre> |
| 432 | doi: 10.1029/2018GB005983 |
| 433 | Armengol, L., Calbet, A., Franchy, G., Rodríguez-Santos, A., & Hernández-León, |
| 434 | S. (2019, February). Planktonic food web structure and trophic transfer ef- |
| 435 | ficiency along a productivity gradient in the tropical and subtropical Atlantic |
| 436 | Ocean. Scientific Reports, $9(1)$, 2044. (Publisher: Nature Publishing Group |
| 437 | tex.copyright: 2019 The Author(s)) doi: $10.1038/s41598-019-38507-9$ |
| 438 | Barton, A. D., Pershing, A. J., Litchman, E., Record, N. R., Edwards, K. F., |
| 439 | Finkel, Z. V., Ward, B. A. (2013). The biogeography of marine plank- |
| 440 | ton traits. $Ecology Letters, 16(4), 522-534.$ Retrieved 2023-01-19, from |
| 441 | https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12063 doi: |
| 442 | 10.1111/ele.12063 |
| 443 | Behrenfeld, M. J., Doney, S. C., Lima, I., Boss, E. S., & Siegel, D. A. (2013). An- |
| 444 | nual cycles of ecological disturbance and recovery underlying the subarctic |
| 445 | Atlantic spring plankton bloom. Global Biogeochemical Cycles, 27(2), 526–540. |
| 446 | Retrieved 2022-03-08, from https://onlinelibrary.wiley.com/doi/abs/ |
| 447 | 10.1002/gbc.20050 doi: 10.1002/gbc.20050 |
| 448 | Bopp, L., Aumont, O., Cadule, P., Alvain, S., & Gehlen, M. (2005). Response of |
| 449 | diatoms distribution to global warming and potential implications: A global |
| 450 | model study. Geophysical Research Letters, $32(19)$. Retrieved 2023-03-26, from |
| 451 | https://onlinelibrary.wiley.com/doi/abs/10.1029/2005GL023653 doi: |
| 452 | 10.1029/2005GL023653 |
| 453 | Brandão, M. C., Benedetti, F., Martini, S., Soviadan, Y. D., Irisson, JO., Ro- |
| 454 | magnan, JB., Lombard, F. (2021, August). Macroscale patterns of |
| 455 | oceanic zooplankton composition and size structure. Scientific Reports, $11(1)$, |
| 456 | 15714. Retrieved 2022-03-07, from https://www.nature.com/articles/ |
| 457 | $a^{1598-021-94615-5}$ doi: 10.1038/ a^{1508} .021.04615.5 |
| | S41330 021 94013 5 doi: 10.1030/S41330-021-94013-5 |
| 458 | Calbet, A. (2001). Mesozooplankton grazing effect on primary production: |

| 460 461 | <i>Oceanography</i> , 46(7), 1824–1830. Retrieved 2023-02-20, from https://onlinelibrary.wiley.com/doi/abs/10.4319/lo.2001.46.7.1824 doi: |
|------------|--|
| 462 | 10.4319/lo.2001.46.7.1824 |
| 463 | Calbet, A., & Landry, M. R. (2004). Phytoplankton growth, microzooplankton |
| 464 | grazing, and carbon cycling in marine systems. Limnology and Oceanography, |
| 465 | 49(1), 51-57. Retrieved 2023-02-02, from https://onlinelibrary.wiley |
| 466 | .com/doi/abs/10.4319/10.2004.49.1.0051 doi: 10.4319/lo.2004.49.1.0051 |
| 467 | Calbet, A., Martínez, R. A., Isari, S., Zervoudaki, S., Nejstgaard, J. C., Pitta, P., |
| 468 | Ptacnik, R. (2012, August). Effects of light availability on mixotrophy |
| 469 | and microzooplankton grazing in an oligotrophic plankton food web: Evi- |
| 470 | dences from a mesocosm study in Eastern Mediterranean waters. Journal |
| 471 | of Experimental Marine Biology and Ecology, 424-425, 66–77. Retrieved |
| 472 | 2023-02-20, from https://www.sciencedirect.com/science/article/pii/ |
| 473 | $C_{1} = \frac{1}{2} \sum_{i=1}^{2} \sum_{j=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}{2} \sum_{j=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}{2} \sum_{j=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}{2} \sum_{j=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}$ |
| 474 | Calbet, A., Saiz, E., Almeda, R., Movilla, J. I., & Alcaraz, M. (2011, May). Low |
| 475 | nicrozoopiankton grazing rates in the Arctic Ocean during a Finebocystis |
| 476 | Lowrnal of Plankton Research 32(5) 687-701 Botrioved 2023 02 20 from |
| 477 | https://doi.org/10.1093/plankt/fbg142.doi: 10.1093/plankt/fbg142 |
| 478 | Chon B Laws F A Lin H & Huang B (2014) Estimating microzoonlank |
| 479 | ton grazing half-saturation constants from dilution experiments with non- |
| 400 | linear feeding kinetics Limnology and Oceanography 59(3) 639–644 doi: |
| 482 | 10.4319/lo.2014.59.3.0639 |
| 483 | Chenillat, F., Rivière, P., & Ohman, M. D. (2021, May). On the sensitivity of plank- |
| 484 | ton ecosystem models to the formulation of zooplankton grazing. <i>PLOS ONE</i> . |
| 485 | 16(5), e0252033. Retrieved 2021-05-27, from https://journals.plos.org/ |
| 486 | plosone/article?id=10.1371/journal.pone.0252033 doi: 10.1371/journal |
| 487 | .pone.0252033 |
| 488 | de la Rocha, C. L. (2006). Chapter 5. The Biological Pump. In The Oceans and Ma- |
| 489 | rine Geochemistry - 1st Edition (1st Edition ed.). Pergamon. |
| 490 | Deppeler, S. L., & Davidson, A. T. (2017). Southern Ocean Phytoplankton in a |
| 491 | Changing Climate. Frontiers in Marine Science, 4. doi: 10.3389/fmars.2017 |
| 492 | .00040 |
| 493 | Druon, JN., Hélaouët, P., Beaugrand, G., Fromentin, JM., Palialexis, A., & |
| 494 | Hoepffner, N. (2019, March). Satellite-based indicator of zooplankton dis- |
| 495 | tribution for global monitoring. Scientific Reports, $9(1)$, 4732. Retrieved |
| 496 | 2023-01-19, from https://www.nature.com/articles/s41598-019-41212-2 |
| 497 | doi: 10.1038/s41598-019-41212-2 |
| 498 | Dunn, R. P., & Hovel, K. A. (2020, January). Predator type influences the fre- |
| 499 | quency of functional responses to prey in marine habitats. Biology Letters, |
| 500 | 16(1), 20190758. (Publisher: Royal Society) doi: $10.1098/rsb1.2019.0758$ |
| 501 | Dupont, L., Le Mézo, P., Aumont, O., Bopp, L., Clerc, C., Ethé, C., |
| 502 | & Maury, O. (2023). High trophic level feedbacks on global |
| 503 | ocean carbon uptake and marine ecosystem dynamics under climate Cl_{1} between Cl_{2} |
| 504 | https://onlinelibrory.viley.com/doi/obs/10.1111/geb.16559 |
| 505 | (https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.16558) doi: 10.1111/ |
| 507 | geb 16558 |
| 507 | Décima M (2022 June) Zooplankton trophic structure and ecosystem produc |
| 500 | tivity Marine Ecology Progress Series 692 23-42 Retrieved 2022-05-04 |
| 510 | from https://www.int-res.com/abstracts/mens/v692/p23-42/ doi: |
| 511 | 10.3354/meps14077 |
| 512 | Everett, J. D., Baird, M. E., Buchanan, P., Bulman, C., Davies, C., Downie, R., |
| 513 | Richardson, A. J. (2017). Modeling What We Sample and Sampling What We |
| 514 | Model: Challenges for Zooplankton Model Assessment. Frontiers in Marine |

| 515 | Science, 4, 77. Retrieved 2021-10-19, from https://www.frontiersin.org/ |
|--|--|
| 516 | article/10.3389/Imars.2017.00077 doi: 10.3389/Imars.2017.00077 |
| 517 | Fu, W., Randerson, J. T., & Moore, J. K. (2016, September). Climate change |
| 518 | impacts on net primary production (NPP) and export production (EP) |
| 519 | regulated by increasing stratification and phytoplankton community struc- ture in the CMIDE model. P_{i} and P_{i} (18) [11] [170] Detrieved |
| 520 | ture in the CMIP5 models. Biogeosciences, $13(18)$, $5151-5170$. Retrieved |
| 521 | 2022-02-01, from https://bg.copernicus.org/articles/13/5151/2016/ |
| 522 | bg-13-5151-2016.ntml doi: 10.5194/bg-13-5151-2016 |
| 523 | Gentleman, W. C., & Neuheimer, A. B. (2008, November). Functional responses |
| 524 | and ecosystem dynamics: How clearance rates explain the influence of satia- |
| 525 | tion, food-limitation and acclimation. Journal of Plankton Research, $30(11)$, |
| 526 | 1215–1231. doi: 10.1093/plankt/fbn0/8 |
| 527 | Griffies, S. M. (2012). Elements of MOM5, GFDL Ocean Group Technical |
| 528 | Report No. 7 (Tech. Rep.). NOAA/Geophysical Fluid Dynamics Labo- |
| 529 | ratory. Retrieved from https://mom-ocean.github.io/assets/pdfs/ |
| 530 | MUM5_manual.pdf |
| 531 | Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Gorsky, |
| 532 | G. (2016, April). Plankton networks driving carbon export in the oligotrophic |
| 533 | ocean. Nature, 532(7600), 465–470. doi: 10.1038/nature16942 |
| 534 | Hansen, P. J., Bjørnsen, P. K., & Hansen, B. W. (1997). Zooplankton grazing and |
| 535 | growth: Scaling within the 2-2,-Mm body size range. Limnology and Oceanog- |
| 536 | raphy, 42(4), 687-704. doi: 10.4319/10.1997.42.4.0687 |
| 537 | Hashioka, T., Vogt, M., Yamanaka, Y., Le Quéré, C., Buitenhuis, E. T., Aita, |
| 538 | M. N., Doney, S. C. (2013, November). Phytoplankton competition |
| 539 | during the spring bloom in four plankton functional type models. Bio- |
| 540 | geosciences, 10(11), 6833–6850. Retrieved 2023-01-31, from https:// |
| 541 | bg.copernicus.org/articles/10/6833/2013/bg-10-6833-2013.html doi: |
| | |
| 542 | 10.5194/bg-10-6833-2013 |
| 542 543 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. |
| 542 543 544 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines |
| 542 543 544 545 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27. |
| 542 543 544 545 546 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1028/s41558-023-01630-7 |
| 542 543 544 545 546 547 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 |
| 542 543 544 545 546 547 548 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, M., Wang, M., Wang, |
| 542 543 544 545 546 547 548 549 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum |
| 542 543 544 545 546 547 548 549 550 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. |
| 542 543 544 545 546 547 548 549 550 551 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https:// |
| 542 543 544 545 546 547 548 549 550 551 551 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/i.acalma.cdl 2020.100265 |
| 542 543 544 545 546 547 548 549 550 551 552 553 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 |
| 542 543 544 545 546 547 548 549 550 551 552 553 554 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni |
| 542 543 544 545 546 547 548 550 551 552 553 554 555 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2020 lapse |
| 542 543 544 545 546 547 548 550 551 552 553 554 555 556 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno |
| 542 543 544 545 546 547 554 550 551 552 553 554 555 556 556 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061) |
| 542 543 544 545 546 547 550 551 552 553 554 555 556 557 558 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061) doi: 10.1002/lno.11061 |
| 542 543 544 545 547 548 549 550 551 552 553 554 555 556 557 558 559 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 doi: 10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms |
| 542 543 544 545 547 548 550 551 553 555 555 555 555 556 557 558 559 560 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/i.econew.2004.002 |
| 542 543 544 545 547 548 550 551 552 555 556 555 556 557 558 559 560 551 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64 (2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. <i>Ecological Complexity</i>, 1 (3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 |
| 542 543 544 545 548 549 550 551 555 556 557 558 559 560 561 562 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64 (2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. <i>Ecological Complexity</i>, 1 (3), 253-259. doi: 10.1016/j.ecocm.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic cope- |
| 542 543 544 545 546 547 548 549 550 551 552 555 556 557 558 559 560 561 562 563 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and be diversity. Linguage and Oceanography and planktonic copepods: Clobal rates and patterns in relation to chlorophyll a, temperature, and be diversity. Linguage and Oceanography and planktonic copepods: Slobal rates and patterns in relation to chlorophyll a, temperature, and be diversity. Linguage and the planktonic copepods: Clobal rates and patterns in relation to chlorophyll a, temperature, and be diversity. Linguage and the planktonic copepods: Clobal rates and patterns in relation to chlorophyll a, temperature, and be diversity. Linguage and the principle complexity. Accounted and patterns in relation to chlorophyll a, temperature, and be diversity. |
| 542 543 544 545 547 548 549 550 551 555 556 557 558 559 560 561 562 563 563 564 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. <i>Ecological Complexity</i>, 1(3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. <i>Limnology and Oceanography</i>, 48(5), 1988-2010. doi: 10.4210/0.2024.8.5.108 |
| 542 543 544 545 546 547 548 550 551 555 556 557 558 559 560 561 562 563 564 564 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography, 48(5), 1988-2010. doi: 10.4319/lo.2003.48.5.1988 |
| 542 543 544 545 547 548 550 551 555 556 555 556 557 558 559 560 561 562 563 564 565 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography, 48(5), 1988-2010. doi: 10.4319/lo.2003.48.5.1988 Howarth, R. W. (1988, November). Nutrient limitation of net primary production in marine growsteme. Annual Review of Ecology and Systems and System |
| 542 543 544 545 546 547 548 549 550 551 555 556 557 556 560 561 562 563 564 566 567 567 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061) doi: 10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/j.ecocm.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography, 48(5), 1988-2010. doi: 10.4319/lo.2003.48.5.1988 Howarth, R. W. (1988, November). Nutrient limitation of net primary production in marine ecosystems. Annual Review of Ecology and Systematics, 19(1), 89-110. (Publisher: Annual Review) dei: 10.1146/onnurse.cc. 10.11048.005142 |
| 542 543 544 545 548 549 550 551 555 556 557 558 559 560 561 562 563 564 565 566 567 568 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64 (2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1 (3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography, 48(5), 1988-2010. doi: 10.4319/lo.2003.48.5.1988 Howarth, R. W. (1988, November). Nutrient limitation of net primary production in marine ecosystems. Annual Review of Ecology and Systematics, 19(1), 89-110. (Publisher: Annual Review) doi: 10.1146/annurev.es.19.110180.00513 |

| 570 | A. J., Woodworth-Jefcoats, P. A. (2021). Using Global-Scale Earth System |
|-----|--|
| 571 | Models for Regional Fisheries Applications. Frontiers in Marine Science, 8, |
| 572 | 1121. Retrieved 2021-10-21, from https://www.frontiersin.org/article/ |
| 573 | 10.3389/fmars.2021.622206 doi: 10.3389/fmars.2021.622206 |
| 574 | Kiørboe, T. (2018). A Mechanistic Approach to Plankton Ecology. Princeton Uni- |
| 575 | versity Press. Retrieved 2023-01-31, from https://www.degruyter.com/ |
| 576 | document/doi/10.1515/9780691190310/html?lang=en doi: 10.1515/ |
| 577 | 9780691190310 |
| 578 | Kiørboe, T., & Hirst, A. G. (2014, April). Shifts in Mass Scaling of Respiration, |
| 579 | Feeding, and Growth Rates across Life-Form Transitions in Marine Pelagic |
| 580 | Organisms. The American Naturalist, 183(4), E118–E130. Retrieved 2022- |
| 581 | $11-25,\mathrm{from}https://www.journals.uchicago.edu/doi/10.1086/675241$ |
| 582 | (Publisher: The University of Chicago Press) doi: 10.1086/675241 |
| 583 | Kwiatkowski, L., Torres, O., Bopp, L., Aumont, O., Chamberlain, M., Christian, |
| 584 | J. R., Ziehn, T. (2020, July). Twenty-first century ocean warming, acid- |
| 585 | ification, deoxygenation, and upper-ocean nutrient and primary production |
| 586 | decline from CMIP6 model projections. $Biogeosciences, 17(13), 3439-3470.$ |
| 587 | Retrieved 2022-03-19, from https://bg.copernicus.org/articles/17/3439/ |
| 588 | 2020/ (Publisher: Copernicus GmbH) doi: 10.5194/bg-17-3439-2020 |
| 589 | Landry, Ondrusek, M., Tanner, S., Brown, S., Constantinou, J., Bidigare, R., |
| 590 | Fitzwater, S. (2000, August). Biological response to iron fertilization in the |
| 591 | eastern equatorial Pacific (IronEx II). I. Microplankton community abundances |
| 592 | and biomass. Marine Ecology-progress Series - MAR ECOL-PROGR SER, |
| 593 | 201, 27-42. doi: $10.3354/meps201027$ |
| 594 | Landry, M. R., Brown, S. L., Ru, Y. M., Selph, K. E., Bidigare, R. R., Yang, E. J., |
| 595 | & Simmons, M. P. (2008, May). Depth-stratified phytoplankton dynam- |
| 596 | Us in Cyclone Opal, a subtropical mesoscale eddy. Deep Sea Research Part |
| 597 | 11: 10pical Studies in Oceanography, 55(10), 1548–1559. Retrieved 2025- |
| 598 | 02-02, non netps.//www.sciencedifect.com/science/article/pii/ S0967064508000921 doi: 10.1016/j.dsr2.2008.02.001 |
| 599 | Landry M R & Calbet A (2004 January) Microzoonlankton production in the |
| 601 | oceans ICES Journal of Marine Science 61(4) 501–507 Betrieved 2023-03- |
| 602 | 26. from https://doi.org/10.1016/j.jcesims.2004.03.011 doi: 10.1016/j |
| 603 | icesims.2004.03.011 |
| 604 | Landry, M. R., Ohman, M. D., Goericke, R., Stukel, M. R., & Tsyrklevich, K. (2009. |
| 605 | December). Lagrangian studies of phytoplankton growth and grazing rela- |
| 606 | tionships in a coastal upwelling ecosystem off Southern California. Progress |
| 607 | in Oceanography, 83(1), 208–216. Retrieved 2023-02-02, from https:// |
| 608 | www.sciencedirect.com/science/article/pii/S0079661109000846 doi: |
| 609 | 10.1016/j.pocean.2009.07.026 |
| 610 | Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., |
| 611 | Völker, C. (2015, December). Drivers and Uncertainties of Future Global Ma- |
| 612 | rine Primary Production in Marine Ecosystem Models. $Biogeosciences, 12(23),$ |
| 613 | 6955–6984. doi: $10.5194/bg-12-6955-2015$ |
| 614 | Laufkötter, C., Vogt, M., Gruber, N., Aumont, O., Bopp, L., Doney, S. C., |
| 615 | Völker, C. (2016, July). Projected Decreases in Future Marine Export Pro- |
| 616 | duction: The Role of the Carbon Flux through the Upper Ocean Ecosystem. |
| 617 | Biogeosciences, $13(13)$, $4023-4047$. doi: $10.5194/bg-13-4023-2016$ |
| 618 | Law, R. M., Ziehn, T., Matear, R. J., Lenton, A., Chamberlain, M. A., Stevens, |
| 619 | L. E., Vohralik, P. F. (2017, July). The carbon cycle in the Australian |
| 620 | Community Climate and Earth System Simulator (ACCESS-ESM1) – Part 1: |
| 621 | Model description and pre-industrial simulation. Geoscientific Model Develop- |
| 622 | ment, $10(7)$, $2567-2590$. doi: $10.5194/\text{gmd}-10-2567-2017$ |
| 623 | Le Quéré, C., Buitenhuis, E. T., Moriarty, R., Alvain, S., Aumont, O., Bopp, L., |
| 624 | Vallina, S. M. (2016, July). Role of Zooplankton Dynamics for Southern Ocean |

| 625 | Phytoplankton Biomass and Global Biogeochemical Cycles. Biogeosciences, |
|-----|--|
| 626 | 13(14), 4111-4133. doi: $10.5194/bg-13-4111-2016$ |
| 627 | Lima-Mendez, G., Faust, K., Henry, N., Decelle, J., Colin, S., Carcillo, F., Raes, |
| 628 | J. (2015, May). Determinants of community structure in the global plankton |
| 629 | interactome. Science, $348(6237)$. doi: 10.1126/science.1262073 |
| 630 | Luo, J. Y., Condon, R. H., Stock, C. A., Duarte, C. M., Lucas, C. H., Pitt, |
| 631 | K. A., & Cowen, R. K. (2020). Gelatinous Zooplankton-Mediated Car- |
| 632 | bon Flows in the Global Oceans: A Data-Driven Modeling Study. Global |
| 633 | Biogeochemical Cycles, $34(9)$, e2020GB006704. Retrieved 2022-07-20, from |
| 634 | https://onlinelibrary.wiley.com/doi/abs/10.1029/2020GB006704 doi: |
| 635 | 10.1029/2020GB006704 |
| 636 | Malchow, H., Hilker, F. M., Sarkar, R. R., & Brauer, K. (2005, November). Spa- |
| 637 | to the transformation of the second |
| 638 | inflection. Mathematical and Computer Modelling, $42(9)$, 1035–1048. doi: 10.1016/j.m.m. 2004.10.027 |
| 639 | 10.1016/J.mcm.2004.10.025 |
| 640 | McCauley, E., & Murdoch, W. W. (1987, January). Cyclic and Stable Populations: |
| 641 | Plankton as Paradigm. <i>The American Naturalist</i> , 129(1), 97–121. Retrieved |
| 642 | 2021-06-20, from fittps://www.journais.ucfficago.edu/doi/abs/10.1000/ |
| 643 | McCinty N Irwin A I Finkel 7 V & Duthievier S (2023) Using acaleri |
| 644 | cal partitions to assess zooplankton biogeography and seasonality. <i>Eroptiers in</i> |
| 645 | Marine Science 10 Retrieved 2023-05-04 from https://www.frontiersin |
| 647 | .org/articles/10.3389/fmars.2023.989770 |
| 648 | Mojica, K., Behrenfeld, M., Clay, M., & Brussaard, C. (2021, August). Spring Ac- |
| 649 | cumulation Rates in North Atlantic Phytoplankton Communities Linked to |
| 650 | Alterations in the Balance Between Division and Loss. Frontiers in Microbiol- |
| 651 | ogy, 12. doi: 10.3389/fmicb.2021.706137 |
| 652 | Morozov, A. (2010). Emergence of Holling type III zooplankton functional response: |
| 653 | Bringing together field evidence and mathematical modelling. Journal of Theo- |
| 654 | retical Biology, 265(1), 45–54. doi: 10.1016/j.jtbi.2010.04.016 |
| 655 | Morozov, A., & Arashkevich, E. (2010, January). Towards a correct description |
| 656 | of zooplankton feeding in models: Taking into account food-mediated unsyn- |
| 657 | chronized vertical migration. Journal of Theoretical Biology, 262(2), 346–360. |
| 658 | Retrieved 2022-04-21, from https://www.sciencedirect.com/science/ |
| 659 | article/pii/S0022519309004536 doi: 10.1016/j.jtbi.2009.09.023 |
| 660 | Morozov, A., Arashkevich, E., Reigstad, M., & Falk-Petersen, S. (2008, Oc- |
| 661 | tober). Influence of spatial heterogeneity on the type of zooplankton |
| 662 | functional response: A study based on field observations. Deep Sea Re- |
| 663 | search Part II: Topical Studies in Oceanography, $55(20)$, $2285-2291$. doi: |
| 664 | Mumar D. M. Ohman M. D. Charisha D. Kalla T. D. Charland, D. M. S. |
| 665 | Studiel M. P. (2018 October) CCE V. Drimowy production mesoscoplank |
| 666 | ton grazing and the biological pump in the California Current Ecosystem: |
| 669 | Variability and response to El Niño Deen Sea Research Part I: Oceano- |
| 669 | araphic Research Papers, 1/0, 52–62. Betrieved 2023-02-02, from https:// |
| 670 | www.sciencedirect.com/science/article/pii/S096706371830013X doi: |
| 671 | 10.1016/j.dsr.2018.07.012 |
| 672 | Mortenson, E., Lenton, A., Shadwick, E. H., Trull, T. W., Chamberlain, M. A., |
| 673 | & Zhang, X. (2021, December). Divergent trajectories of ocean warming |
| 674 | and acidification. Environmental Research Letters, 16(12), 124063. Re- |
| 675 | trieved 2022-03-19, from https://doi.org/10.1088/1748-9326/ac3d57 doi: |
| 676 | 10.1088/1748-9326/ac3d57 |
| 677 | Neelin, J. D., Bracco, A., Luo, H., McWilliams, J. C., & Meyerson, J. E. (2010, De- |
| 678 | cember). Considerations for parameter optimization and sensitivity in climate |
| 679 | models. Proceedings of the National Academy of Sciences, 107(50), 21349– |

| 680 | 21354. Retrieved 2021-10-13, from https://www.pnas.org/content/107/50/ |
|-----|---|
| 681 | 21349 (Publisher: National Academy of Sciences Section: Physical Sciences) |
| 682 | doi: 10.1073/pnas.1015473107 |
| 683 | Nissen, C., Vogt, M., Münnich, M., Gruber, N., & Haumann, F. A. (2018, |
| 684 | November). Factors controlling coccolithophore biogeography in the |
| 685 | Southern Ocean. Biogeosciences, 15(22), 6997–7024. Retrieved 2023-03- |
| 686 | 26, from https://bg.copernicus.org/articles/15/6997/2018/ doi: |
| 687 | 10.5194/bg-15-6997-2018 |
| 688 | Oke, P. R., Griffin, D. A., Schiller, A., Matear, R. J., Fiedler, R., Mansbridge, |
| 689 | J., Ridgway, K. (2013, May). Evaluation of a near-global eddy- |
| 690 | resolving ocean model. Geoscientific Model Development, 6, 591–615. doi: |
| 691 | 10.5194/gmd-6-591-2013 |
| 692 | Petrik, C. M., Luo, J. Y., Heneghan, R. F., Everett, J. D., Harrison, C. S., & |
| 693 | Richardson, A. J. (2022). Assessment and Constraint of Mesozooplank- |
| 694 | ton in CMIP6 Earth System Models. Global Biogeochemical Cucles, 36(11). |
| 695 | e2022GB007367. doi: 10.1029/2022GB007367 |
| 696 | Prowe A E F Pahlow M Dutkiewicz S Follows M & Oschlies A (2012 Au- |
| 607 | gust) Top-down control of marine phytoplankton diversity in a global ecosys- |
| 608 | tem model Progress in Oceanography 101(1) 1–13 doi: 10.1016/i pocean |
| 699 | 2011 11 016 |
| 700 | Pörtner H. Roberts, D. Masson-Delmotte, V. Zhai, P. Tignor, M. Poloczanska |
| 700 | E Wever N (2019) IPCC Special Report on the Ocean and Cruosphere |
| 701 | in a Changing Climate (Tech Ben) IPCC |
| 702 | Retnerajeh I. Abu-Alhajia R. Atkinson A. Batten S. Bay N. I. Bernard |
| 703 | K S Vebra I. (2023 February) Monitoring and modelling ma- |
| 704 | 1/(1) |
| 705 | 564 Retrieved 2022-03-08 from https://www.neture.com/articles/ |
| 706 | s/1467-023-36241-5doi: 10.1038/s/1467-023-36241-5 |
| 707 | Bichardson A I (2008 April) In hot water: zooplankton and climate change |
| 708 | ICES Journal of Marine Science 65(3) 270–205 Retrieved 2021-10-10 from |
| 709 | https://doi org/10.1093/icesimg/fsn028 doi: $10.1093/icesimg/fsn028$ |
| 710 | Pohr T. Long M. T. Kayanaugh M. Lindsay K. & Doney S. (2017 May) Vari |
| 711 | ability in the Machanisms Controlling Southern Ocean Phytoplankton Bloom |
| 712 | Phonology in an Ocean Model and Satellite Observations — Clabal Biogeochemi |
| 713 | cal Cucles 21 doi: 10.1002/2016gb005615 |
| 714 | Pohr T. Dichardson A. Lonton A. Chambarlain M. I. Shadwight F. (2022) |
| 715 | Zooplanlitan grazing is the largest source of 1 uncertainty for maxima carbon |
| 716 | avaling in CMIP6 IPCC 2 models — Communications Forth and Environment |
| 717 | Under Bowiew See 'Polated Manuscript' |
| 718 | Debry T. Dichardson A. L. Lonton A. & Chadwidt E. (2022 Nevershor) Dec |
| 719 | Konr, I., Kichardson, A. J., Lenton, A., & Snadwick, E. (2022, November). Rec- |
| 720 | on the formulation of grazing in marine biogeochemical and |
| 721 | 2022 04 24 from https://www.sciencediweet.com/science/outicle/mii/ |
| 722 | 2023-04-24, Ifold https://www.sciencedirect.com/science/article/pii/ |
| 723 | S0079001122001379 doi: 10.1010/J.pocean.2022.102878 |
| 724 | Roy, S., Sathyendranath, S., Bouman, H., & Platt, I. (2013, December). The |
| 725 | global distribution of phytoplankton size spectrum and size classes from |
| 726 | ing of Environment 120, 185, 107 Detrieved 2022 11 25 from https:// |
| 727 | my of Environment, 159, 160–197. Refrieved 2022-11-25, from https:// |
| 728 | www.sciencedifect.com/science/artificie/pii/s0034425/15002629 doi: |
| 729 | 10.1010 (J.180.2013.00.004 Son Montin E Honnig D D & Inimizer V (2006 Intro) I attactional interval |
| 730 | in plankton size spectra in the Atlantic Occor Deve Co. Deve 1 Deve |
| 731 | III prankton size spectra in the Atlantic Ocean. Deep Sea Research Part |
| 732 | 11. 10picul situlies in Oceanography, 33(14), 1300–1372. Retrieved 2023- |
| 733 | 04-20, HOHI HUUPS://WWW.SCIENCEGIFECT.COM/SCIENCE/ATTICLE/P11/ SOOGTOGAEOGOO124X doi: 10.1016/j.dom2.2006.05.006 |
| 734 | 5050700450000124A dui. 10.1010/J.ds12.2000.05.000 |

| 735 | Sathyendranath, S., Brewin, R. J. W., Brockmann, C., Brotas, V., Calton, B., |
|-----|---|
| 736 | Chuprin, A., Platt, T. (2019, January). An Ocean-Colour Time Series |
| 737 | for Use in Climate Studies: The Experience of the Ocean-Colour Climate |
| 738 | Change Initiative (OC-CCI). Sensors, 19(19), 4285. doi: 10.3390/s19194285 |
| 739 | Schmoker, C., Hernández-León, S., & Calbet, A. (2013, July). Microzooplank- |
| 740 | ton grazing in the oceans: impacts, data variability, knowledge gaps and |
| 741 | future directions Journal of Plankton Research 35(4) 691–706 Re- |
| 742 | trieved $2023-02-02$ from https://doi org/10_1093/plankt/fbt023doi: |
| 743 | 10 1093/plankt/fbt023 |
| 744 | Steele I (1074) Stability of plankton access tems In M B Usher k |
| 744 | M H Williamson (Edg.) Ecological Stability (np. 170–101) Boston MA: |
| 745 | M. H. Williamson (Eds.), Ecological Stability (pp. 179–191). Doston, MA. |
| 746 | Springer U.S. doi: $10.1007/976-1-4099-0956-0-12$ |
| 747 | stelliberg, D. K., & Landry, M. R. (2017). Zoopiankton and the Ocean Carbon Cy- |
| 748 | cie. Annual Review of Marine Science, 9(1), 413–444. Retrieved 2022-03-07, |
| 749 | ITOIN https://doi.org/10.1146/annurev-marine=010814=015924 (001:10 |
| 750 | .1140/annurev-marine-010814-015924 |
| 751 | Steinberg, D. K., Ruck, K. E., Gleiber, M. R., Garzio, L. M., Cope, J. S., Bernard, |
| 752 | K. S., Ross, R. M. (2015, July). Long-term (1993–2013) changes in |
| 753 | macrozooplankton off the Western Antarctic Peninsula. Deep Sea Re- |
| 754 | search Part I: Oceanographic Research Papers, 101, 54–70. Retrieved 2021- |
| 755 | 11-25, from https://www.sciencedirect.com/science/article/pii/ |
| 756 | S0967063715000412 doi: 10.1016/j.dsr.2015.02.009 |
| 757 | Strömberg, K. H. P., Smyth, T. J., Allen, J. I., Pitois, S., & O'Brien, T. D. |
| 758 | (2009, August). Estimation of global zooplankton biomass from satellite |
| 759 | ocean colour. Journal of Marine Systems, $78(1)$, 18–27. Retrieved 2023- |
| 760 | 01-19, from https://www.sciencedirect.com/science/article/pii/ |
| 761 | S0924796309000669 doi: 10.1016/j.jmarsys.2009.02.004 |
| 762 | Sverdrup, H. U. (1953, January). On Conditions for the Vernal Blooming of Phy- |
| 763 | toplankton. ICES Journal of Marine Science, 18(3), 287–295. doi: 10.1093/ |
| 764 | icesjms/18.3.287 |
| 765 | Tagliabue, A., Kwiatkowski, L., Bopp, L., Butenschön, M., Cheung, W., Lengaigne, |
| 766 | M., & Vialard, J. (2021). Persistent Uncertainties in Ocean Net Primary |
| 767 | Production Climate Change Projections at Regional Scales Raise Challenges |
| 768 | for Assessing Impacts on Ecosystem Services. Frontiers in Climate, 3. Re- |
| 769 | trieved 2022-02-07, from https://www.frontiersin.org/article/10.3389/ |
| 770 | fclim.2021.738224 |
| 771 | Tittensor, D. P., Novaglio, C., Harrison, C. S., Heneghan, R. F., Barrier, N., |
| 772 | Bianchi, D., Blanchard, J. L. (2021, October). Next-generation ensem- |
| 773 | ble projections reveal higher climate risks for marine ecosystems. Nature |
| 774 | Climate Change, 1-9. Retrieved 2021-10-25, from https://www.nature.com/ |
| 775 | articles/s41558-021-01173-9 doi: $10.1038/s41558-021-01173-9$ |
| 776 | Tjiputra, J. F., Schwinger, J., Bentsen, M., Morée, A. L., Gao, S., Bethke, I., |
| 777 | Schulz, M. (2020, May). Ocean biogeochemistry in the Norwegian Earth Sys- |
| 778 | tem Model version 2 (NorESM2). Geoscientific Model Development, 13(5), |
| 779 | 2393-2431. Retrieved 2022-03-08, from https://gmd.copernicus.org/ |
| 780 | articles/13/2393/2020/ doi: 10.5194/gmd-13-2393-2020 |
| 781 | Truscott, J. E., Brindley, J., Brindley, J., & Gray, P. (1994, June). Equilibria, |
| 782 | stability and excitability in a general class of plankton population models. |
| 783 | Philosophical Transactions of the Royal Society of London. Series A: Physical |
| 784 | and Engineering Sciences, 347(1685), 703–718. (Publisher: Royal Society) doi: |
| 785 | 10.1098/rsta.1994.0076 |
| 786 | Tsujino, H., Urakawa, S., Nakano, H., Small, R. J., Kim, W. M., Yeager, S. G., |
| 787 | Yamazaki, D. (2020). input4MIPs.CMIP6.OMIP.MRI.MRI-JRA55- |
| 788 | do-1-5-0. Retrieved 2022-03-19, from https://doi.org/10.22033/ESGF/ |
| 789 | input4MIPs.15017 (Publisher: Earth System Grid Federation Type: dataset) |
| | |

| 790 | doi: $10.22033/\text{ESGF/input}4MIPs.15017$ |
|-----|---|
| 791 | Vallina, S. M., & Le Quéré, C. (2011, March). Stability of complex food webs: |
| 792 | Resilience, resistance and the average interaction strength. Journal of The- |
| 793 | oretical Biology, 272(1), 160–173. Retrieved 2023-01-23, from https:// |
| 794 | www.sciencedirect.com/science/article/pii/S0022519310006387 doi: |
| 795 | 10.1016/j.jtbi.2010.11.043 |
| 796 | Vallina, S. M., Ward, B. A., Dutkiewicz, S., & Follows, M. J. (2014, January). |
| 797 | Maximal feeding with active prey-switching: A kill-the-winner functional |
| 798 | response and its effect on global diversity and biogeography. Progress |
| 799 | in Oceanography, 120, 93–109. Retrieved 2023-01-17, from https:// |
| 800 | www.sciencedirect.com/science/article/pii/S0079661113001468 doi: |
| 801 | 10.1016/j.pocean.2013.08.001 |
| 802 | Westberry, T. K., Behrenfeld, M. J., Siegel, D. A., & Boss, E. S. (2008, June). |
| 803 | Carbon-Based Primary Productivity Modeling with Vertically Resolved |
| 804 | Photoacclimation. Global Biogeochemical Cycles, $22(2)$. doi: 10.1029/ |
| 805 | 2007 GB003078 |
| 806 | Zahariev, K., Christian, J. R., & Denman, K. L. (2008, April). Preindustrial, Histor- |
| 807 | ical, and Fertilization Simulations Using a Global Ocean Carbon Model with |
| 808 | New Parameterizations of Iron Limitation, Calcification, and N 2 Fixation. |
| 809 | Progress in Oceanography, 77, 56–82. doi: 10.1016/j.pocean.2008.01.007 |
| 810 | Ziehn, T., Chamberlain, M. A., Law, R. M., Lenton, A., Bodman, R. W., Dix, M., |
| 811 | Srbinovsky, J. (2020, August). The Australian Earth System Model: |
| 812 | ACCESS-ESM1.5. Journal of Southern Hemisphere Earth Systems Science, |
| 813 | 70(1), 193-214. Retrieved 2021-05-27, from https://www.publish.csiro.au/ |
| 814 | es/ES19035 doi: 10.1071/ES19035 |
| 815 | Ziehn, T., Lenton, A., Law, R., Matear, R., & Chamberlain, M. (2017, July). The |
| 816 | carbon cycle in the Australian Community Climate and Earth System Simu- |
| 817 | lator (ACCESS-ESM1) – Part 2: Historical simulations. Geoscientific Model |
| 818 | Development, 10, 2591-2614. doi: $10.5194/gmd-10-2591-2017$ |

The Global Distribution and Drivers of Grazing **Dynamics Estimated from Inverse Modelling**

Tyler Rohr^{1,2}, Anthony Richardson^{3,4}, Andrew Lenton⁵, Matt Chamberlain⁵, **Elizabeth Shadwick** 2,5

²Institute for Marine and Antarctic Science, University of Tasmania, Hobart, Tasmania, 7000, Australia ²Australian Antarctic Partnership Program, Hobart, Tasmania, 7000, Australia ³School of Environment, The University of Queensland, St Lucia, 4072, Queensland, Australia ⁴Commonwealth Scientific and Industrial Research Organisation (CSIRO) Environment, BioSciences Precinct (QBP), St Lucia, Queensland, 4067, Australia ⁵Commonwealth Scientific and Industrial Research Organisation (CSIRO) Environment, Hobart, Tasmania, 7000 Australia

Key Points:

1

2

3

4

9 10

11

12

| 13 | • | Oligotrophic (eutrophic) biomes exhibit more (less) efficient community-integrated |
|----|---|--|
| 14 | | grazing, characteristic of micro- (meso-) zooplankton. |
| 15 | • | We find a strong link between observed mean-annual phytoplankton biomass and |
| 16 | | the grazing dynamics required to recreate its seasonal cycle. |
| 17 | • | A type III functional response does a consistently better job recreating observed |
| 18 | | phytoplankton seasonal cycles than a type II response. |

Corresponding author: Tyler Rohr, tyler.rohr@utas.edu.au

19 Abstract

We use inverse modelling to infer the distribution and drivers of community-integrated 20 zooplankton grazing dynamics based on the skill with which different grazing formula-21 tions recreate the satellite-observed seasonal cycle in phytoplankton biomass. We find 22 that oligotrophic and eutrophic biomes require more and less efficient grazing dynam-23 ics, respectively. This is characteristic of micro- and mesozooplankton, respectively, and 24 leads to a strong sigmoidal relationship between observed mean-annual phytoplankton 25 biomass and the optimal grazing parameterization required to simulate its seasonal cy-26 cle. Globally, we find type III rather than type II functional response curves consistently 27 exhibit higher skill. These new observationally-based distributions can help constrain, 28

²⁹ validate and develop next-generation biogeochemical models.

³⁰ Plain Language Summary

To improve predictions of our ocean's ability to feed a growing human population 31 and buffer a changing climate, we need to improve our understanding of what happens 32 to carbon once it is absorbed into the ocean. One of the largest gaps in marine carbon 33 cycling is the role of zooplankton grazing. The rate at which zooplankton graze phyto-34 plankton modifies the size and seasonal evolution of phytoplankton populations and in 35 turn the associated rates of net primary production at the base of the food web, secondary 36 production of grazers (an indicator of fisheries potential) and export production (the bi-37 ological sequestration of carbon). However, regional differences in grazing, which are dif-38 ficult to measure outside of a laboratory setting, remain poorly constrained by obser-39 vations and thus difficult to model. Here, we run a suite of model simulations, each of 40 which simulate grazing in a different way, then compare the results to infer which type 41 of grazing dynamics match observations. We find that there is dramatic spatial variabil-42 ity in how zooplankton, as a community, appear to be grazing and that this variability 43 maps well onto observed phytoplankton concentrations, suggesting that the type of zoo-44 plankton present may be determined by the amount of prey available. 45

46 **1** Introduction

Marine net primary production (NPP) supports the biological export (EP) of car-47 bon (de la Rocha, 2006) and forms the base of the marine food web (Armengol et al., 48 2019). Although oceanographers have historically focused on light (Sverdrup, 1953) and 49 nutrients (Howarth, 1988), increasing experimental (Lima-Mendez et al., 2015; Guidi et 50 al., 2016), observational (Behrenfeld et al., 2013) and modelling (Hashioka et al., 2013; 51 Prowe et al., 2012; Laufkötter et al., 2015; Vallina & Le Quéré, 2011; Chenillat et al., 52 2021) work has highlighted zooplankton grazing as a critical control on NPP. However, 53 grazing dynamics remain poorly constrained across modern biogeochemical (BGC) mod-54 els, including those used by the IPCC in climate projections (Rohr et al., 2023). This 55 likely contributes to persisting uncertainty in projections of NPP (Tagliabue et al., 2021; 56 Laufkötter et al., 2015), EP (Laufkötter et al., 2016; Fu et al., 2016), zooplankton biomass 57 (Petrik et al., 2022) and fisheries catch (Tittensor et al., 2021). 58

The parameterization of relatively coarse global models implicitly requires an un-59 derstanding of the mean dynamics of many species averaged across a patchy ocean, which 60 may diverge dramatically from the dynamics of individual zooplankton (Rohr et al., 2022; 61 Morozov, 2010). Although empirical laboratory experiments have shown that grazing 62 dynamics (i.e. the manner in which zooplankton-specific grazing rates increase with prey 63 concentration) vary substantially across zooplankton species, ages, and sizes (Hansen et 64 al., 1997; Hirst & Bunker, 2003), most laboratory studies consider the idealized behav-65 ior of a single species in a well-mixed environment. 66

Field-based dilution experiments help average across some of this variability (Morrow et al., 2018; Landry et al., 2009, 2008; Landry et al., 2000) and have been used to estimate grazing dynamics in natural microzooplankton assemblages (Chen et al., 2014). However, these experiments are limited in their spatial scope and resolution (Schmoker et al., 2013) and can be biased by trophic cascades (Calbet et al., 2011), the presence of mixotrophs (Calbet et al., 2012) and the exclusion of mesozooplankton and macrozooplankton (Schmoker et al., 2013).

In the absence of direct, global, high-resolution measurements, community-integrated grazing rates and dynamics could theoretically be backed-out from zooplankton biomass budgets. However, disparate methods for shipboard observation make it difficult to describe time-evolving global distributions without large levels of statistical inference (Everett et al., 2017; Heneghan et al., 2020; Ratnarajah et al., 2023) and algorithms for satellite observation are limited (Druon et al., 2019; Strömberg et al., 2009).

Yet, while zooplankton grazing dynamics and biomass are difficult to observe directly, phytoplankton loss rates (Mojica et al., 2021; Deppeler & Davidson, 2017) and population dynamics (Gentleman & Neuheimer, 2008; Truscott et al., 1994; Steele, 1974) are largely driven by grazing. Thus the most viable option to estimate community-integrated grazing dynamics at scale may be inference from the remote sensing record of phytoplankton biomass (Westberry et al., 2008).

Here, we infer the global distribution of community-integrated grazing dynamics 86 using an inverse modelling approach. We run a suite of simulations in a coupled ocean-87 BGC model, parameterized with a wide range of grazing dynamics, and determine the 88 optimal parameters required to recreate the observed phytoplankton seasonal cycle. We 89 map the distribution of optimal parameters, examine how they appear driven by regional 90 variability in phytoplankton biomass (Sec. 3.1), and explain mechanistically how graz-91 ing dynamics can shape the seasonal cycle (Sec. 3.2). Finally, we discuss the limitations 92 of this work (Sec. 4.1), as well its potential utility from a ecological (Sec. 4.2) and mod-93 elling perspective (Sec. 4.3). 94

95 **2** Materials and methods

2.1 Grazing in BGC models

108

The simplest BGC models include one zooplankton grazing on one phytoplankton. 97 The relationship between specific grazing rates $(g; d^{-1})$ and prey abundance is typically 98 described by a type II or III functional response curve (Gentleman & Neuheimer, 2008; 99 Rohr et al., 2022). The primary difference between response curves is that the type II 100 response increases linearly at low phytoplantkon concentrations ($[C_{phyto}]$; mmolC m⁻³), 101 while the type III increases quadratically (**Figure 1**). Both curves, $g([C_{phyto}])$, can be 102 parameterized with a saturation grazing rate $(g_{max}; d^{-1})$, which describes the rate when 103 prey is non-limiting, and a half saturation concentration $(K_{1/2}; \text{ mmolC m}^{-3})$, which de-104 scribes how much prey is required to get there (i.e. $g([K_{1/2}]) = 0.5 * g_{max}$). Here we 105 focus on $K_{1/2}$ because it has been shown to have a stronger influence on population dy-106 namics (Rohr et al., 2022) and marine carbon cycling (Rohr et al., 2023) than g_{max} . 107

2.2 Grazing and population dynamics

Grazing dynamics can influence the seasonal cycle of phytoplankton biomass via the curvature of the functional response, which has either a stabilizing or destabilising influence on phytoplankton population dynamics depending on its concavity (Steele, 1974; Truscott et al., 1994; Gentleman & Neuheimer, 2008; Rohr et al., 2022). If the functional response is concave upward, then phytoplankton-specific loss rates to grazing increase with the size of the phytoplankton population. This creates a negative feedback loop which dampens changes in the size of the phytoplankton population, thereby exerting a stabilizing influence. Alternatively, downward concavity means phytoplankton-specific loss
rates to grazing decline with population growth, creating a destabilizing, positive feedback which amplifies changes in the size of the phytoplankton population.

The shape and stabilizing influence of the functional response is determined by its 119 response type (II or III) and parameters (particularly $K_{1/2}$). While the parameter val-120 ues determine the magnitude of curvature and thus the strength of the stabilizing influ-121 ence, the response type determines the direction. A type II response is always concave 122 123 downward and thus always destabilizing. A type III response has upward concavity below $K_{1/2}$ and thus stabilizing properties at low phytoplankton concentrations. In turn, 124 the grazing formulation exerts a strong influence on the size, shape, and propensity of 125 phytoplankton blooms, sub-seasonal oscillations, and extinction events (Dunn & Hovel, 126 2020; Adjou et al., 2012; Hernández-García & López, 2004; Malchow et al., 2005; Rohr 127 et al., 2022). 128

While a type II response is typically found in laboratory experiments (Hansen et 129 al., 1997), a type III response can be justified as the implicit representation of more com-130 plex behavior such as active prey switching (Prowe et al., 2012; Vallina et al., 2014) or 131 the mean state of a patchy ocean (Morozov & Arashkevich, 2010; Rohr et al., 2022). Thus, 132 in any given region, the true shape of the apparent functional response (i.e. the spatially-133 integrated relationship between total prey and community-averaged zooplankton-specific 134 grazing rates) is determined by the community-composition, prey preferences, spatial dis-135 tributions and physiology of resident zooplankton. Using inverse modelling to match the 136 spatially-averaged and community-integrated phytoplankton record observed from satel-137 lites helps average out spatial, species-level, and behavioral complexities that many global 138 models do not explicitly resolve. 139

140

155

2.3 Model configuration

We use a global, ocean-BGC model to determine which $K_{1/2}$ values and response 141 types are required to best match the observed phytoplankton seasonal cycle. Simulations 142 are run with the Whole Ocean Model of Biogeochemistry and Trophic-dynamics (WOM-143 BAT) (Law et al., 2017), part of the Australian Earth Systems Model (ACCESS-ESM1.5) 144 (Ziehn et al., 2020), which has been studied and validated extensively (Mortenson et al., 145 2021; Kwiatkowski et al., 2020; Ziehn et al., 2017; Oke et al., 2013). The ocean model 146 is the global configuration of Modular Ocean Model version 5 (Griffies, 2012). WOM-147 BAT has a relatively simple structure, with one phytoplankton and one zooplankton group. 148 While more complex models include multiple zooplankton grazing on multiple phyto-149 plankton (Rohr et al., 2023), we are interested here in estimating community-integrated 150 grazing dynamics. These can be inferred most directly by tuning WOMBAT's single-prey 151 grazing formulation, which implicitly represents the community-integrated behavior of 152 all zooplankton groups, towards the satellite-observed phytoplankton seasonal cycle, which 153 explicitly integrates across all phytoplankton groups. 154

2.4 Model experiments

We ran a total of 36 global simulations, each with a different grazing formulation. 156 To isolate the influence of grazing, all simulations were initialized from the same state, 157 embedded in an identical repeat-climatological physical ocean, and forced with identi-158 cal surface flux and freshwater runoff from the Japanese 55-year atmospheric reanaly-159 sis surface dataset (Tsujino et al., 2020). After initialisation, each run was spun up for 160 5 years to a quasi-steady state, long enough to equilibrate with changes to the grazing 161 formulation. Output is reported from the fifth year and can be considered climatolog-162 ical. 163

We ran two suites of experiments, using a type II and III functional response. Within each suite, we tested 18 different parameters combination: $K_{1/2} = 0.5$, 1, 2, 4, 8, 16 (*mmolC* m^{-3}) and $g_{max} = 0.5$, 1, 2 (d^{-1}). These values are consistent with the range that has been derived empirically and used in models historically (Rohr et al., 2022). All other parameters were kept constant and identical to Law et al. (2017).

2.5 Model skill assessment

We used two metrics to evaluate the model's ability to recreate the observed phy-170 toplankton seasonal cycle: the correlation coefficient (CC) and the coefficient of vari-171 ation (CV). The CC measures the co-variability between the simulated and observed 172 climatologies, while the CV measures the magnitude of variability separately in each cli-173 matology relative to its annual mean $(CV = \frac{std}{mean})$. Together they capture the shape (CC) and strength (CV) of the seasonal cycle. Both metrics are largely agnostic to the 174 175 size of mean-annual phytoplankton population (i.e. CC independent to mean; CV nor-176 malized by mean). This is to help isolate the influence of grazing dynamics on the qual-177 itative shape of the seasonal cycle rather than mean-state NPP which could be biased 178 by many other model attributes. 179

For each metric, the seasonal cycle of simulated surface phytoplankton biomass was 180 compared to an 18-year remote sensing climatology (July 2002 - April 2021) from the 181 Carbon-based Productivity Model (CbPM) (Westberry et al., 2008). The remote sens-182 ing record was interpolated onto the model grid and all time series were centered on the 183 summer solstice. We use the observed carbon product, which is derived from back-scatter, 184 instead chlorophyll because WOMBAT does not resolve chlorophyll. However, we repeated 185 the analysis comparing model carbon to satellite chlorophyll (Sathyendranath et al., 2019) 186 and found similar results (Supporting Text 1). 187

The cost function for model skill was quantified for each run in each grid-cell by subtracting the absolute difference between the modelled (CV_{mod}) and observed (CV_{obs}) coefficient of variation from the correlation coefficient $(CC_{mod,obs})$,

Model Skill =
$$norm(CC_{mod,obs}) - norm(|CV_{mod} - CV_{obs}|)$$
 (1)

Both metrics are normalized across all grid cells from all 36 model runs, such that they are equally weighted and cost function scores can be directly compared across all experiments.

For each response type, we considered three sets of six runs. Each run in a set used a different $K_{1/2}$ value but constant g_{max} value. Within each set, the cost function score was interpolated between $K_{1/2}$ values at each grid cell using a piece-wise cubic polynomial (**Figure 2**). The $K_{1/2}$ value with the maximum score was identified and averaged across all three sets to infer the optimal value. Regions below 55°S or above 55°N with limited remote sensing coverage were excluded.

200 **3 Results**

201

169

3.1 Global distribution and drivers of grazing dynamics

The distribution of observed mean-annual surface phytoplankton biomass estimated from CbPM (**Figure 1A**) has a striking co-variability with the distribution of grazing dynamics inferred by the optimal $K_{1/2}$ value required to match the observed seasonal cycle (**Figure 1B, C**). We find that more oligotrophic regions with mean-annual phytoplankton biomass lower than the global median require smaller $K_{1/2}$ values to best match the observed phenology (**Figure 1A-C; more blue**). Alternatively, eutrophic regions with mean-annual phytoplankton biomass above the global median, including HNLC re²⁰⁹ gions, require larger $K_{1/2}$ values (Figure 1A-C; more green). Qualitatively, this pat-²¹⁰ tern generally holds regardless of whether a type II (Figure 1B) or III (Figure 1C) ²¹¹ functional response is used to described grazing dynamics and whether biomass (Figure ²¹² 1A) or chlorophyll (Supporting Figure 1) is used to described the observed seasonal ²¹³ cycle.

Plotting the optimal $K_{1/2}$ value against the corresponding observed mean-annual 214 surface biomass reveals a clear sigmoidal relationship (Figure 1D, E). Regardless of func-215 tional response type, larger $K_{1/2}$ values are required to recreate the seasonal cycle of biomes 216 217 with higher mean-annual phytoplankton biomass, but appear to be bound asymptotically by a minimum and maximum viable $K_{1/2}$ value. Switching from a type II (Figure 218 **1D**) to type III (Figure 1E) response or decreasing g_{max} (Supporting Figure 2) de-219 creases the value of both asymptotes, but neither substantively influence the shape of 220 the curve. Thus, while other assumptions about the grazing formulation influence the 221 specific quantitative estimates of the optimal $K_{1/2}$ (Supporting Table 1), the qual-222 itative relationship is consistent: higher biomass regions appear to be populated with 223 zooplankton with higher community-integrated $K_{1/2}$ values. 224

Finally, regardless of biome, using a type III response consistently recreates the observed phytoplankton seasonal cycle better than a type II response, with 30% more model skill on average (**Figure 1**). Moreover, the type III response performs better regardless of whether the observed seasonal cycle is quantified with carbon or chlorophyll or which g_{max} value is used (**Supporting Figures 1, 2**).

230

3.2 Mechanistic influence of the grazing dynamics

Importantly, our estimations of model skill do not include any metric for mean model bias. Thus, the correct interpretation of these results is not that more or less grazing leads to less or more phytoplankton biomass, respectively, but rather that the dynamical properties of the functional response curve can shape of the seasonal evolution of phytoplankton accumulation in a way that appears more or less consistent with observations.

For example, when $K_{1/2}$ is large, phytoplankton tend to exhibit a stronger, well-236 defined seasonal cycle with less high frequency variability (Figure 2; green lines). This 237 is because the grazing formulation does not heavily influence the stability of the system, 238 allowing bloom dynamics to be driven primarily by bottom-up controls, such as light and 239 nutrients, which generally exhibit strong seasonality following seasonal cycles in verti-240 cal mixing and day length. In turn, phytoplankton population dynamics are not as sen-241 sitive to the whether a type II (Figure 2C, D) or III (Figure 2A, B) response is used. 242 However, as $K_{1/2}$ decreases, the grazing formulation has a stronger influence on the sta-243 bility on the system. This influence is stabilizing if a type III response is used but desta-244 bilizing if a type II response is used (Supporting Text 2; Supporting Figure 3), re-245 sulting in substantively different seasonal cycles (Figure 2; blue tracers). We consider 246 two case studies, in the Subantarctic zone (SAZ) and Sargasso sea, which are generally 247 representative of the seasonal variability in more eutrophic and oligotrophic biomes, re-248 spectively. 249

In the SAZ (Figure 2A, C) the observed evolution of biomass (black line) exhibits 250 a strong seasonal cycle with an amplitude $\sim 20\%$ greater than its mean and relatively 251 little sub-seasonal variability. It is best recreated using larger $K_{1/2}$ values and exhibits 252 slightly more model skill when a type III response is used. With a type III response (Figure 253 **2A**), lower $K_{1/2}$ values reduce the mean biomass but do not systematically modify the 254 255 CV, leaving the ratio of summer to winter biomass roughly proportional. Alternatively, with a type II response (Figure 2C), decreasing $K_{1/2}$ delays bloom initiation but am-256 plifies its acceleration once initiated, leading to smaller, shorter, sharper features and sys-257 tematically higher CVs. The initiation is delayed because the type II response dispro-258 portionately increases grazing rates at low biomass concentrations compared to a type 259



Figure 1. The distribution and drivers of grazing dynamics. A) The observed climatological mean-annual phytoplankton biomass concentration plotted as a percentile of the full spatial distribution. Below, the corresponding optimal $K_{1/2}$ parameter required to best recreate the observed phytoplankton seasonal cycle using a B) type II or C) type III response function plotted as a percentile for direct qualitative comparison. Beside each is an example functional response curve for their respective (bolded) response types, both parameterized with the same $K_{1/2}$ and g_{max} . Below A) a schematic of the characteristic phytoplankton associated with low and high biomass waters and below C) a schematic of zooplankton associated with low and high $K_{1/2}$ values. The optimal $K_{1/2}$ found with a D) type II and E) type III response are plotted against the observed mean-annual phytoplankton biomass. Each point represents the mean of roughly 30 grid cells, binned based on their percentile biomass, with the top and bottom 5% percent removed. Points are colored by their mean cost function score, with red indicating more model skill. All values are averaged across three experiment suites, with each using a different g_{max} value. Results from individual experiment suites are shown in **Supporting Figure 2**. Data is fit to a sigmoidal curve (solid blue), shown with 95% confidence bounds (dashed blue).



Figure 2. Influence of $K_{1/2}$ and response type on phytoplankton seasonal cycle. Phytoplankton biomass climatologies and model skill evaluations are provided from A, C the SAZ and B, D Sargasso Sea, showing the emergent seasonal cycle from runs using six $K_{1/2}$ values with a A, B Type III and C, D type II functional response. All simulations shown use identical g_{max} values $(1 d^{-1})$. In the upper panel of each subplot, the observed (black) and simulated (blue-green) seasonal cycles are plotted with the simulation that best matches the observed phenology in bold. In the lower panel, the cost function scoring is demonstrated for each simulation, with the corresponding CC and CV shown above the total cost function score. Red and blue shading indicates better and worse model skill, respectively. The optimal $K_{1/2}$ value is determined by the maximum (red line) interpolated model skill (black line). In the inset map (top-right corner) the distribution of optimal $K_{1/2}$ values is shown with the example location marked in red. Note, these distributions are qualitatively identical to gigure 1, with the same percentile-based colorbar. However, they only consider runs with $g_{max} = 1$ to be consistent with the traces, rather than the mean of all three g_{max} sets.

III response. The bloom is a sharper because lowering $K_{1/2}$ in a type II response destabilizes the system, allowing phytoplankton biomass to accumulate rapidly until bottomup factors respond (i.e. nutrient limitation, self-shading) and rapidly terminate the bloom.

In the Sargasso Sea (Figure 2B, D), the observed evolution of biomass (black line) 263 exhibits a weaker seasonal cycle, with an amplitude less than half the size of its mean. 264 It is best recreated using smaller $K_{1/2}$ values and a type III response. With a type III 265 response (Figure 2B), highly-stable lower $K_{1/2}$ values dampen seasonality in bottom-266 up controls and prevent a bloom. Increasing $K_{1/2}$ allows an unrealistic late-winter/early-267 spring bloom to emerge, systematically increasing the CV and decreasing model skill. 268 While the emergent seasonal cycle is nearly identical between response curves when us-269 ing high $K_{1/2}$ values (Figure 2D), the Type II response diverges substantially when us-270 ing low $K_{1/2}$ values. Here, decreasing stability introduces unstable predator-prey dynam-271 ics which drive higher-frequency oscillations. Thus, the model cannot eliminate the un-272 natural early-spring bloom without inducing unnatural sub-seasonal spikes, neither of 273 which are observed. 274

275 4 Discussion

276 4.1 Limitations

The largest limitation of these results likely stems from the accuracy of non-grazing 277 attributes in the BGC-ocean model we have optimized. Despite running experiments in 278 an identical physical ocean, if their is a systematic bias in the simulated seasonal light 279 and nutrient cycle, then it is possible that the 'wrong' grazing dynamics could combine 280 with the 'wrong' bottom-up controls to produce the correct seasonal cycle, leading us 281 to infer unnatural grazing dynamics. This could be the case along the equator where there 282 is a disproportionately large bias in phytoplankton biomass relative to NPP (Supporting 283 Figure 4), suggesting simulated phytoplankton-specific growth rates are systematically 284 low. This may explain why we inferred higher $K_{1/2}$ values in the equatorial Indian, At-285 lantic, and Pacific basins (Figure 1B; greener) than we would have expected from the 286 low mean-annual phytoplankton biomass observed there (Figure 1A; bluer). If the model 287 is misrepresenting the seasonal cycle in bottom-up controls as too weak, it makes sense 288 that higher $K_{1/2}$ values are needed to not damp out all seasonal variability and recre-289 ate the observed seasonal cycle. Additional biases may stem from the remote sensing prod-290 ucts, which are limited by clouds and the solar inclination angle, the exact nature of the 291 link between trophic controls and bloom phenology (Behrenfeld et al., 2013; Rohr et al., 292 2017), and our ability to accurately quantify the fidelity of the seasonal cycle. Collec-293 tively then, our results our best understood qualitatively, rather than as specific quan-294 titative predictions of the apparent $K_{1/2}$ value in any specific location. 295

296

4.2 Ecological Perspectives

Nevertheless, our inferred distribution of community-integrated grazing dynamics 297 is consistent with the biogeography of community composition which we would expect 298 to inhabit each respective biome (Barton et al., 2013; Heneghan et al., 2020; Décima, 2022; 299 Brandão et al., 2021). Ecologically, the value of $K_{1/2}$ at a fixed g_{max} is related to the 300 rate at which zooplankton can capture (rather than consume) prey (Rohr et al., 2022). 301 Physiologically, the zooplankton with fastest prey capture rates are typically rapidly-grazing 302 microzooplankton and filter feeders (Hansen et al., 1997). However, these zooplankton 303 species are generally unable to consume anything larger than small flagellates, ciliates 304 and cyanobacteria, exactly the sort of phytoplankton that tend to dominate more olig-305 otrophic regions such as the gyres (Calbet & Landry, 2004). On the other hand, slowly-306 grazing euphausiids, copepods and macrozooplankton tend to have much slower capture 307 rates but are capable of consuming much larger prey, such as dinoflagellates and diatom 308

assemblages, which tend to dominate more eutrophic coastal and higher-latitude regions
 (San Martin et al., 2006).

The sigmoidal relationship between phytoplankton biomass and inferred community-311 integrated $K_{1/2}$ values implies the importance of two end-member communities in the 312 most oligotrophic and eutrophic regions. The location of each asymptotes implies a com-313 munity integrated $K_{1/2}$ value of 3 mmolC m⁻³ for ecosystems dominated by faster-grazing 314 microzooplankton and filter feeders and $8.3 \text{ mmolC} \text{ m}^{-3}$ for ecosystems dominated by 315 slower-grazing mesozooplankton and macrozooplantkon. While these values are lower 316 than the median empirical $K_{1/2}$ values measured by Hansen et al. (1997) in individual 317 microzooplankton (8.9 mmolC m⁻³) and mesozooplantkon (18 mmolC m⁻³), the appar-318 ent $K_{1/2}$ of spatially-averaged, community-integrated dynamics is expected to be much 319 lower than that of any individual species measured in well-mixed laboratory medium (Rohr 320 et al., 2022). 321

However, despite two prominent asymptotes, the region of monotonically increas-322 ing $K_{1/2}$ values between them (~.85-1.2 mmolC m⁻³) encompasses over 50% of the ocean 323 area in our domain (55°S-55°N) and 43% of the global ocean. This suggests a critical 324 role for more heterogeneous zooplankton communities and the co-existance of diverse func-325 tional groups therein. This steady increase in $K_{1/2}$ across intermediate mean-annual phy-326 toplankton concentrations is consistent with the positive relationship between empiri-327 cally estimated microzooplankton $K_{1/2}$ values and in-situ chlorophyll concentrations mea-328 sured across shipboard dilution experiments (Chen et al., 2014). Note, while these re-329 sults strongly imply slower zooplankton-specific grazing rates in more productive biomes, 330 they can be consistent with observations of bulk ingestion rates and phytoplankton-specific 331 grazing mortality increasing with primary productivity (Schmoker et al., 2013; Calbet, 332 2001) due to differences in phytoplankton and zooplankton abundance. 333

Finally, while community-integrated $K_{1/2}$ values exhibit large regional variability, 334 the spatially integrated dynamics of all biomes are consistently best described by a type 335 III versus type II response (Figure 1, Supporting Table 1). Although dynamic instabil-336 ities are not necessarily unnatural (McCauley & Murdoch, 1987), when averaged across 337 a relatively large area the destabilizing properties of a type II response appear to lead 338 to sharper, more delayed blooms than observed in eutrophic regions and more sub-seasonal 339 variability than observed in eutrophic regions (Figure 2). This is consistent with obser-340 vational (Morozov et al., 2008; Kiørboe, 2018), modelling (Nissen et al., 2018; Prowe et 341 al., 2012; Chenillat et al., 2021), and theoretical (Rohr et al., 2022; Morozov, 2010) work 342 suggesting that the downward concavity, prey refuge, and stabilizing properties associ-343 ated with a type III response may be a better empirical representation of the mean state 344 of a patchy ocean and complex food web, even if a type II response is typically measured 345 for individual species in a well-mixed laboratory medium (Hansen et al., 1997; Hirst & 346 Bunker, 2003). 347

348

4.3 Modelling Perspectives

Considering the sensitivity of simulated carbon cycling to the representation of zoo-349 plankton grazing dynamics (Rohr et al., 2023; Chenillat et al., 2021; Prowe et al., 2012; 350 Laufkötter et al., 2015, 2016; Dupont et al., 2023), it is critical for models to accurately 351 recreate the distribution community-integrated grazing dynamics and allow it to respond 352 to environmental change. As warming, stratification, and stronger winds transform the 353 surface ocean, the ensuing balance of light and nutrients may reshape marine ecosystems 354 (Pörtner et al., 2019), favouring different zooplankton species, in different places, with 355 vastly different grazing dynamics. For instance, a shift toward smaller phytoplankton, 356 which have higher light but lower nutrient requirements (Pörtner et al., 2019; Bopp et 357 al., 2005) would precipitate a shift towards microzooplankton, salps and larvaceans. Al-358 ready a southward shift of salps into regions previously dominated by euphausiids has 359

been observed (Henschke & Pakhomov, 2019; Steinberg & Landry, 2017). Such shifts should
be captured in BGC models if Earth system and ecosystem models hope to predict changes
in the oceans capacity to buffer a changing climate and feed a growing population.

Fortunately, the validation of zooplankton biomass in BGC models is receiving in-363 creasing attention (Petrik et al., 2022; McGinty et al., 2023). However, given large un-364 certainties in the parameterization of grazing within ostensibly similar zooplankton func-365 tional groups across models (Rohr et al., 2022, 2023), a further validation of zooplankton-366 specific grazing rates is required to determine if a model is accurately simulating graz-367 ing pressure (i.e. the phytoplankton-specific mortality rate to grazing), which may be 368 the single largest source of uncertainty in CMIP6 representations of marine carbon cy-369 cling (Rohr et al., 2023). While direct field measurements of grazing rates are typically 370 limited to the role of microzooplankton (Schmoker et al., 2013; Calbet & Landry, 2004; 371 Landry & Calbet, 2004) our results implicitly reflect the integrated grazing dynamics 372 of the entire zooplankton community, averaging over the distribution and behavior of 373 individual species. 374

First off, it appears clear that modellers should use a type III over type II response. 375 especially if explicitly resolving a limited food web with relatively coarse spatial reso-376 lution. Further, although our exact quantitative estimates of $K_{1/2}$ are limited and vary 377 with other model parameters (Supporting Table 1), there is a consistent qualitative 378 pattern in apparent $K_{1/2}$ values which models ought to recreate. At minimum, it is clear 379 a priori that models with a single zooplankton and prey option (e.g. Tjiputra et al. (2020); 380 Zahariev et al. (2008); Law et al. (2017)) cannot simulate the established spatial vari-381 ability in community-integrated grazing dynamics (as the single zooplankton will graze 382 with the same $K_{1/2}$ everywhere). In turn, bottom-up controls are likely over-tuned to 383 compensate for unrealistic top-down homogeneity. While many CMIP6-class models in-384 clude 2-3 zooplankton groups (Kearney et al., 2021; Rohr et al., 2023), it is critical to 385 know if competition between them is sufficient to drive a realistic emergent distribution 386 in community-integrated grazing dynamics. Thus, we encourage modellers to confirm 387 whether the distribution of community-integrated $K_{1/2}$ values is qualitatively consistent 388 with **Figure 1**. This can be done by fitting a curve between the mean zooplankton-specific 389 grazing rate and total prey concentration in different regions or grid cells to diagnosti-390 cally compute the apparent functional response and associated community-integrated 391 $K_{1/2}$ value. Significant disagreement from **Figure 1** would likely imply that additional 392 zooplankton groups, such as macrozooplankton (Le Quéré et al., 2016), salps (Luo et al., 393 2020), larvaceans, euphausiids, chaetognaths, jellyfish (Heneghan et al., 2020, 2023) may 394 be required. 395

Finally, if explicit competition between limited functional groups is insufficient to 396 resolve the emergent distribution of community-integrated grazing dynamics and a suf-397 ficiently complex food web is not computationally tractable with high-resolution projec-398 tions (Neelin et al., 2010), then modellers might consider parameterizing zooplankton 399 community composition using the relationship described in **Figure 1**. That is, modellers 400 could implicitly represent changes in zooplankton community composition by modify-401 ing $K_{1/2}$ of a single group as a function of phytoplankton abundance (Supporting Ta-402 ble 1). This could allow allow the mean attributes of the zooplankton community to re-403 spond dynamically to changing environmental conditions without explicitly resolving each 404 of its constituent species. While potentially powerful, implementing such a parameter-405 ization would require several important assumptions and careful calibrations (Supporting 406 Text 3). 407

408 5 Conclusions

These results present a novel, observationally-informed, map of global communityintegrated grazing dynamics (i.e $K_{1/2}$ values). Further refining the observed distribution and drivers of grazing, and how to replicate them in models, will require close collaboration with zooplankton ecologists, but presents an exciting new frontier in oceanography focused on a rigorous understanding of how NPP is controlled from the top-down.
Moreover, improving the representation of zooplankton could realize dramatic improvements in marine BGC models and our predictions of future ocean states.

416 6 Open Research

All relevant model output and documentation can be found at https://doi.org/10.25919/wn096j31. Remote sensing products were downloaded at http://orca.science.oregonstate
.edu/2160.by.4320.8day.hdf.carbon2.m.php. Please address any questions to Tyler
Rohr, at tyler.rohr@utas.edu.au.

421 Acknowledgments

This research was supported by the Australian Antarctic Program Partnership through
 the Australian Government's Antarctic Science Collaboration Initiative.

424 **References**

| 425 | Adjou, M., Bendtsen, J., & Richardson, K. (2012, January). Modeling the influence |
|-----|---|
| 426 | from ocean transport, mixing and grazing on phytoplankton diversity. <i>Ecologi</i> - |
| 427 | cal Modelling, 225, 19–27. doi: 10.1016/j.ecolmodel.2011.11.005 |
| 428 | Archibald, K. M., Siegel, D. A., & Doney, S. C. (2019). Modeling the Impact of Zoo- |
| 429 | plankton Diel Vertical Migration on the Carbon Export Flux of the Biological |
| 430 | Pump. Global Biogeochemical Cycles, 33(2), 181–199. Retrieved 2022-02-03, |
| 431 | <pre>from https://onlinelibrary.wiley.com/doi/abs/10.1029/2018GB005983</pre> |
| 432 | doi: 10.1029/2018GB005983 |
| 433 | Armengol, L., Calbet, A., Franchy, G., Rodríguez-Santos, A., & Hernández-León, |
| 434 | S. (2019, February). Planktonic food web structure and trophic transfer ef- |
| 435 | ficiency along a productivity gradient in the tropical and subtropical Atlantic |
| 436 | Ocean. Scientific Reports, $9(1)$, 2044. (Publisher: Nature Publishing Group |
| 437 | tex.copyright: 2019 The Author(s)) doi: $10.1038/s41598-019-38507-9$ |
| 438 | Barton, A. D., Pershing, A. J., Litchman, E., Record, N. R., Edwards, K. F., |
| 439 | Finkel, Z. V., Ward, B. A. (2013). The biogeography of marine plank- |
| 440 | ton traits. $Ecology Letters, 16(4), 522-534.$ Retrieved 2023-01-19, from |
| 441 | https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12063 doi: |
| 442 | 10.1111/ele.12063 |
| 443 | Behrenfeld, M. J., Doney, S. C., Lima, I., Boss, E. S., & Siegel, D. A. (2013). An- |
| 444 | nual cycles of ecological disturbance and recovery underlying the subarctic |
| 445 | Atlantic spring plankton bloom. Global Biogeochemical Cycles, 27(2), 526–540. |
| 446 | Retrieved 2022-03-08, from https://onlinelibrary.wiley.com/doi/abs/ |
| 447 | 10.1002/gbc.20050 doi: 10.1002/gbc.20050 |
| 448 | Bopp, L., Aumont, O., Cadule, P., Alvain, S., & Gehlen, M. (2005). Response of |
| 449 | diatoms distribution to global warming and potential implications: A global |
| 450 | model study. Geophysical Research Letters, $32(19)$. Retrieved 2023-03-26, from |
| 451 | https://onlinelibrary.wiley.com/doi/abs/10.1029/2005GL023653 doi: |
| 452 | 10.1029/2005GL023653 |
| 453 | Brandão, M. C., Benedetti, F., Martini, S., Soviadan, Y. D., Irisson, JO., Ro- |
| 454 | magnan, JB., Lombard, F. (2021, August). Macroscale patterns of |
| 455 | oceanic zooplankton composition and size structure. Scientific Reports, $11(1)$, |
| 456 | 15714. Retrieved 2022-03-07, from https://www.nature.com/articles/ |
| 457 | $a^{1598-021-94615-5}$ doi: 10.1038/ a^{1508} .021.04615.5 |
| | S41330 021 94013 5 doi: 10.1030/S41330-021-94013-5 |
| 458 | Calbet, A. (2001). Mesozooplankton grazing effect on primary production: |

| 460 461 | Oceanography, 46(7), 1824–1830. Retrieved 2023-02-20, from https:// onlinelibrary.wiley.com/doi/abs/10.4319/lo.2001.46.7.1824 doi: |
|------------|--|
| 462 | 10.4319/lo.2001.46.7.1824 |
| 463 | Calbet, A., & Landry, M. R. (2004). Phytoplankton growth, microzooplankton |
| 464 | grazing, and carbon cycling in marine systems. Limnology and Oceanography, |
| 465 | 49(1), 51-57. Retrieved 2023-02-02, from https://onlinelibrary.wiley |
| 466 | .com/doi/abs/10.4319/10.2004.49.1.0051 doi: 10.4319/lo.2004.49.1.0051 |
| 467 | Calbet, A., Martínez, R. A., Isari, S., Zervoudaki, S., Nejstgaard, J. C., Pitta, P., |
| 468 | Ptacnik, R. (2012, August). Effects of light availability on mixotrophy |
| 469 | and microzooplankton grazing in an oligotrophic plankton food web: Evi- |
| 470 | dences from a mesocosm study in Eastern Mediterranean waters. Journal |
| 471 | of Experimental Marine Biology and Ecology, 424-425, 66–77. Retrieved |
| 472 | 2023-02-20, from https://www.sciencedirect.com/science/article/pii/ |
| 473 | $C_{1} = \frac{1}{2} \sum_{i=1}^{2} \sum_{j=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}{2} \sum_{j=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}{2} \sum_{j=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}{2} \sum_{j=1}^{2} \frac{1}{2} \sum_{i=1}^{2} \frac{1}$ |
| 474 | Calbet, A., Saiz, E., Almeda, R., Movilla, J. I., & Alcaraz, M. (2011, May). Low |
| 475 | nicrozoopiankton grazing rates in the Arctic Ocean during a Finebocystis |
| 476 | Lowrnal of Plankton Research 32(5) 687-701 Botrioved 2023 02 20 from |
| 477 | https://doi.org/10.1093/plankt/fbg142.doi: 10.1093/plankt/fbg142 |
| 478 | Chon B Laws F A Lin H & Huang B (2014) Estimating microzoonlank |
| 479 | ton grazing half-saturation constants from dilution experiments with non- |
| 400 | linear feeding kinetics Limnology and Oceanography 59(3) 639–644 doi: |
| 482 | 10.4319/lo.2014.59.3.0639 |
| 483 | Chenillat, F., Rivière, P., & Ohman, M. D. (2021, May). On the sensitivity of plank- |
| 484 | ton ecosystem models to the formulation of zooplankton grazing. <i>PLOS ONE</i> . |
| 485 | 16(5), e0252033. Retrieved 2021-05-27, from https://journals.plos.org/ |
| 486 | plosone/article?id=10.1371/journal.pone.0252033 doi: 10.1371/journal |
| 487 | .pone.0252033 |
| 488 | de la Rocha, C. L. (2006). Chapter 5. The Biological Pump. In The Oceans and Ma- |
| 489 | rine Geochemistry - 1st Edition (1st Edition ed.). Pergamon. |
| 490 | Deppeler, S. L., & Davidson, A. T. (2017). Southern Ocean Phytoplankton in a |
| 491 | Changing Climate. Frontiers in Marine Science, 4. doi: 10.3389/fmars.2017 |
| 492 | .00040 |
| 493 | Druon, JN., Hélaouët, P., Beaugrand, G., Fromentin, JM., Palialexis, A., & |
| 494 | Hoepffner, N. (2019, March). Satellite-based indicator of zooplankton dis- |
| 495 | tribution for global monitoring. Scientific Reports, $9(1)$, 4732. Retrieved |
| 496 | 2023-01-19, from https://www.nature.com/articles/s41598-019-41212-2 |
| 497 | doi: 10.1038/s41598-019-41212-2 |
| 498 | Dunn, R. P., & Hovel, K. A. (2020, January). Predator type influences the fre- |
| 499 | quency of functional responses to prey in marine habitats. Biology Letters, |
| 500 | 16(1), 20190758. (Publisher: Royal Society) doi: $10.1098/rsb1.2019.0758$ |
| 501 | Dupont, L., Le Mézo, P., Aumont, O., Bopp, L., Clerc, C., Ethé, C., |
| 502 | & Maury, O. (2023). High trophic level feedbacks on global |
| 503 | ocean carbon uptake and marine ecosystem dynamics under climate Cl_{1} between Cl_{2} |
| 504 | https://onlinelibrory.viley.com/doi/obs/10.1111/geb.16559 |
| 505 | (https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.16558) doi: 10.1111/ |
| 507 | geb 16558 |
| 507 | Décima M (2022 June) Zooplankton trophic structure and ecosystem produc |
| 500 | tivity Marine Ecology Progress Series 692 23-42 Retrieved 2022-05-04 |
| 510 | from https://www.int-res.com/abstracts/mens/v692/p23-42/ doi: |
| 511 | 10.3354/meps14077 |
| 512 | Everett, J. D., Baird, M. E., Buchanan, P., Bulman, C., Davies, C., Downie, R., |
| 513 | Richardson, A. J. (2017). Modeling What We Sample and Sampling What We |
| 514 | Model: Challenges for Zooplankton Model Assessment. Frontiers in Marine |

| 515 | Science, 4, 77. Retrieved 2021-10-19, from https://www.frontiersin.org/ |
|--|--|
| 516 | article/10.3389/Imars.2017.00077 doi: 10.3389/Imars.2017.00077 |
| 517 | Fu, W., Randerson, J. T., & Moore, J. K. (2016, September). Climate change |
| 518 | impacts on net primary production (NPP) and export production (EP) |
| 519 | regulated by increasing stratification and phytoplankton community struc- ture in the CMIDE model. P_{i} and P_{i} (18) [11] [170] Detrieved |
| 520 | ture in the CMIP5 models. Biogeosciences, $13(18)$, $5151-5170$. Retrieved |
| 521 | 2022-02-01, from https://bg.copernicus.org/articles/13/5151/2016/ |
| 522 | bg-13-5151-2016.ntml doi: 10.5194/bg-13-5151-2016 |
| 523 | Gentleman, W. C., & Neuheimer, A. B. (2008, November). Functional responses |
| 524 | and ecosystem dynamics: How clearance rates explain the influence of satia- |
| 525 | tion, food-limitation and acclimation. Journal of Plankton Research, $30(11)$, |
| 526 | 1215–1231. doi: 10.1093/plankt/fbn0/8 |
| 527 | Griffies, S. M. (2012). Elements of MOM5, GFDL Ocean Group Technical |
| 528 | Report No. 7 (Tech. Rep.). NOAA/Geophysical Fluid Dynamics Labo- |
| 529 | ratory. Retrieved from https://mom-ocean.github.io/assets/pdfs/ |
| 530 | MUM5_manual.pdf |
| 531 | Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Gorsky, |
| 532 | G. (2016, April). Plankton networks driving carbon export in the oligotrophic |
| 533 | ocean. Nature, 532(7600), 465–470. doi: 10.1038/nature16942 |
| 534 | Hansen, P. J., Bjørnsen, P. K., & Hansen, B. W. (1997). Zooplankton grazing and |
| 535 | growth: Scaling within the 2-2,-Mm body size range. Limnology and Oceanog- |
| 536 | raphy, 42(4), 687-704. doi: 10.4319/10.1997.42.4.0687 |
| 537 | Hashioka, T., Vogt, M., Yamanaka, Y., Le Quéré, C., Buitenhuis, E. T., Aita, |
| 538 | M. N., Doney, S. C. (2013, November). Phytoplankton competition |
| 539 | during the spring bloom in four plankton functional type models. Bio- |
| 540 | geosciences, 10(11), 6833–6850. Retrieved 2023-01-31, from https:// |
| 541 | bg.copernicus.org/articles/10/6833/2013/bg-10-6833-2013.html doi: |
| | |
| 542 | 10.5194/bg-10-6833-2013 |
| 542 543 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. |
| 542 543 544 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines |
| 542 543 544 545 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27. |
| 542 543 544 545 546 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1028/s41558-023-01630-7 |
| 542 543 544 545 546 547 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 |
| 542 543 544 545 546 547 548 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, M., Wang, M., Wang, |
| 542 543 544 545 546 547 548 549 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum |
| 542 543 544 545 546 547 548 549 550 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. |
| 542 543 544 545 546 547 548 549 550 550 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https:// |
| 542 543 544 545 546 547 548 549 550 551 551 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/i.acabmed.el.2020.100265 |
| 542 543 544 545 546 547 548 549 550 551 552 552 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 |
| 542 543 544 545 546 547 548 550 551 552 553 554 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni |
| 542 543 544 545 546 547 548 550 551 552 553 554 555 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64 (2), 575-584. Retrieved 2021 la 25 from https://article/pii/science/ar |
| 542 543 544 545 546 547 548 550 551 552 553 554 555 556 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno |
| 542 543 544 545 546 547 554 550 551 552 553 554 555 556 556 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061) |
| 542 543 544 545 546 547 554 550 551 552 553 554 555 556 557 558 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 deprint: https://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.11061 deprint: https://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.11061 |
| 542 543 544 545 547 548 550 551 552 553 554 555 556 555 556 558 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms |
| 542 543 544 545 547 548 550 551 553 555 555 556 555 556 557 558 559 560 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/i.econew.2004.002 |
| 542 543 544 545 546 547 548 550 551 552 555 556 557 558 559 560 561 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64 (2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. <i>Ecological Complexity</i>, 1 (3), 253-259. doi: 10.1016/j.ecocm.2004.05.002 Hirst A. C. & Burghar, A. L. (2002) |
| 542 543 544 545 547 548 550 551 552 555 555 555 555 555 555 555 555 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64 (2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. <i>Ecological Complexity</i>, 1 (3), 253-259. doi: 10.1016/j.ecocm.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic cope-network. |
| 542 543 544 545 547 548 549 550 551 552 555 556 557 558 559 560 561 562 563 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64 (2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1 (3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and back wright. |
| 542 543 544 545 547 548 550 551 555 555 555 555 555 555 556 555 556 555 556 559 560 561 562 563 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. <i>Ecological Modelling</i>, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. <i>Limnology and Oceanography</i>, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. <i>Ecological Complexity</i>, 1(3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. <i>Limnology and Oceanography</i>, 48(5), 1988-2010. doi: 10.4210/0.2002.48.5.108 |
| 542 543 544 545 546 547 548 550 551 555 556 557 556 559 560 561 562 563 564 564 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography, 48(5), 1988-2010. doi: 10.4319/lo.2003.48.5.1988 |
| 542 543 544 545 546 547 548 550 551 555 556 557 556 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1–8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography, 48(5), 1988-2010. doi: 10.4319/lo.2003.48.5.1988 Howarth, R. W. (1988, November). Nutrient limitation of net primary production in marine growstems. Annual Review of Ecology and Systems and System |
| 542 543 544 545 548 549 550 551 555 556 557 558 559 560 561 562 563 564 565 566 567 567 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64(2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061) doi: 10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1(3), 253-259. doi: 10.1016/j.ecocm.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography, 48(5), 1988-2010. doi: 10.4319/lo.2003.48.5.1988 Howarth, R. W. (1988, November). Nutrient limitation of net primary production in marine ecosystems. Annual Review of Ecology and Systematics, 19(1), 89-110. (Publisher: Annual Review) dei: 10.1146/onnurse.cc. 10.11048.005142 |
| 542 543 544 545 548 549 550 551 552 555 556 557 558 559 560 561 562 563 564 565 566 567 568 | 10.5194/bg-10-6833-2013 Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023, March). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nature Climate Change, 1-8. Retrieved 2023-03-27, from https://www.nature.com/articles/s41558-023-01630-7 doi: 10.1038/s41558-023-01630-7 Heneghan, R. F., Everett, J. D., Sykes, P., Batten, S. D., Edwards, M., Takahashi, K., Richardson, A. J. (2020, November). A functional size-spectrum model of the global marine ecosystem that resolves zooplankton composition. Ecological Modelling, 435, 109265. Retrieved 2021-08-10, from https://www.sciencedirect.com/science/article/pii/S0304380020303355 doi: 10.1016/j.ecolmodel.2020.109265 Henschke, N., & Pakhomov, E. A. (2019). Latitudinal variations in Salpa thompsoni reproductive fitness. Limnology and Oceanography, 64 (2), 575-584. Retrieved 2022-11-25, from https://onlinelibrary.wiley.com/doi/abs/10.1002/lno.11061 Hernández-García, E., & López, C. (2004, September). Sustained plankton blooms under open chaotic flows. Ecological Complexity, 1 (3), 253-259. doi: 10.1016/j.ecocom.2004.05.002 Hirst, A. G., & Bunker, A. J. (2003). Growth of marine planktonic copepods: Global rates and patterns in relation to chlorophyll a, temperature, and body weight. Limnology and Oceanography, 48(5), 1988-2010. doi: 10.4319/lo.2003.48.5.1988 Howarth, R. W. (1988, November). Nutrient limitation of net primary production in marine ecosystems. Annual Review of Ecology and Systematics, 19(1), 89-110. (Publisher: Annual Review) doi: 10.1146/annurev.es.19.110180.00513 |

| 570 | A. J., Woodworth-Jefcoats, P. A. (2021). Using Global-Scale Earth System |
|-----|--|
| 571 | Models for Regional Fisheries Applications. Frontiers in Marine Science, 8, |
| 572 | 1121. Retrieved 2021-10-21, from https://www.frontiersin.org/article/ |
| 573 | 10.3389/fmars.2021.622206 doi: 10.3389/fmars.2021.622206 |
| 574 | Kiørboe, T. (2018). A Mechanistic Approach to Plankton Ecology. Princeton Uni- |
| 575 | versity Press. Retrieved 2023-01-31, from https://www.degruyter.com/ |
| 576 | document/doi/10.1515/9780691190310/html?lang=en doi: 10.1515/ |
| 577 | 9780691190310 |
| 578 | Kiørboe, T., & Hirst, A. G. (2014, April). Shifts in Mass Scaling of Respiration, |
| 579 | Feeding, and Growth Rates across Life-Form Transitions in Marine Pelagic |
| 580 | Organisms. The American Naturalist, 183(4), E118–E130. Retrieved 2022- |
| 581 | $11-25,\mathrm{from}https://www.journals.uchicago.edu/doi/10.1086/675241$ |
| 582 | (Publisher: The University of Chicago Press) doi: 10.1086/675241 |
| 583 | Kwiatkowski, L., Torres, O., Bopp, L., Aumont, O., Chamberlain, M., Christian, |
| 584 | J. R., Ziehn, T. (2020, July). Twenty-first century ocean warming, acid- |
| 585 | ification, deoxygenation, and upper-ocean nutrient and primary production |
| 586 | decline from CMIP6 model projections. $Biogeosciences, 17(13), 3439-3470.$ |
| 587 | Retrieved 2022-03-19, from https://bg.copernicus.org/articles/17/3439/ |
| 588 | 2020/ (Publisher: Copernicus GmbH) doi: $10.5194/bg-17-3439-2020$ |
| 589 | Landry, Ondrusek, M., Tanner, S., Brown, S., Constantinou, J., Bidigare, R., |
| 590 | Fitzwater, S. (2000, August). Biological response to iron fertilization in the |
| 591 | eastern equatorial Pacific (IronEx II). I. Microplankton community abundances |
| 592 | and biomass. Marine Ecology-progress Series - MAR ECOL-PROGR SER, |
| 593 | 201, 27-42. doi: $10.3354/meps201027$ |
| 594 | Landry, M. R., Brown, S. L., Rii, Y. M., Selph, K. E., Bidigare, R. R., Yang, E. J., |
| 595 | & Simmons, M. P. (2008, May). Depth-stratified phytoplankton dynam- |
| 596 | ics in Cyclone Opal, a subtropical mesoscale eddy. Deep Sea Research Part |
| 597 | 11: 10pical Studies in Oceanography, 55(10), 1348–1359. Retrieved 2023- |
| 598 | 02-02, non nucles: //www.sciencedirect.com/science/article/pii/ S0967064508000921 doi: 10.1016/j.dsr2.2008.02.001 |
| 599 | Landry M R & Calbet A (2004 January) Microzoonlankton production in the |
| 601 | oceans ICES Journal of Marine Science 61(4) 501–507 Betrieved 2023-03- |
| 602 | 26 from https://doi.org/10.1016/j.icesims.2004.03.011 doi: 10.1016/j. |
| 603 | icesims.2004.03.011 |
| 604 | Landry, M. R., Ohman, M. D., Goericke, R., Stukel, M. R., & Tsyrklevich, K. (2009. |
| 605 | December). Lagrangian studies of phytoplankton growth and grazing rela- |
| 606 | tionships in a coastal upwelling ecosystem off Southern California. <i>Progress</i> |
| 607 | in Oceanography, 83(1), 208–216. Retrieved 2023-02-02, from https:// |
| 608 | www.sciencedirect.com/science/article/pii/S0079661109000846 doi: |
| 609 | 10.1016/j.pocean.2009.07.026 |
| 610 | Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., |
| 611 | Völker, C. (2015, December). Drivers and Uncertainties of Future Global Ma- |
| 612 | rine Primary Production in Marine Ecosystem Models. <i>Biogeosciences</i> , 12(23), |
| 613 | 6955–6984. doi: $10.5194/bg-12-6955-2015$ |
| 614 | Laufkötter, C., Vogt, M., Gruber, N., Aumont, O., Bopp, L., Doney, S. C., |
| 615 | Völker, C. (2016, July). Projected Decreases in Future Marine Export Pro- |
| 616 | duction: The Role of the Carbon Flux through the Upper Ocean Ecosystem. |
| 617 | Biogeosciences, $13(13)$, $4023-4047$. doi: $10.5194/bg-13-4023-2016$ |
| 618 | Law, R. M., Ziehn, T., Matear, R. J., Lenton, A., Chamberlain, M. A., Stevens, |
| 619 | L. E., Vohralik, P. F. (2017, July). The carbon cycle in the Australian |
| 620 | Community Climate and Earth System Simulator (ACCESS-ESM1) – Part 1: |
| 621 | Model description and pre-industrial simulation. Geoscientific Model Develop- |
| 622 | ment, $10(7)$, 2567–2590. doi: 10.5194/gmd-10-2567-2017 |
| 623 | Le Quéré, C., Buitenhuis, E. T., Moriarty, R., Alvain, S., Aumont, O., Bopp, L., |
| 624 | Vallina, S. M. (2016, July). Role of Zooplankton Dynamics for Southern Ocean |

| 625 | Phytoplankton Biomass and Global Biogeochemical Cycles. Biogeosciences, |
|-----|---|
| 626 | 13(14), 4111-4133. doi: $10.5194/bg-13-4111-2016$ |
| 627 | Lima-Mendez, G., Faust, K., Henry, N., Decelle, J., Colin, S., Carcillo, F., Raes, |
| 628 | J. (2015, May). Determinants of community structure in the global plankton |
| 629 | interactome. Science, $348(6237)$. doi: 10.1126/science.1262073 |
| 630 | Luo, J. Y., Condon, R. H., Stock, C. A., Duarte, C. M., Lucas, C. H., Pitt, |
| 631 | K. A., & Cowen, R. K. (2020). Gelatinous Zooplankton-Mediated Car- |
| 632 | bon Flows in the Global Oceans: A Data-Driven Modeling Study. Global |
| 633 | Biogeochemical Cycles, $34(9)$, e2020GB006704. Retrieved 2022-07-20, from |
| 634 | https://onlinelibrary.wiley.com/doi/abs/10.1029/2020GB006704 doi: |
| 635 | 10.1029/2020GB006704 |
| 636 | Malchow, H., Hilker, F. M., Sarkar, R. R., & Brauer, K. (2005, November). Spa- |
| 637 | to the transmission of the second se |
| 638 | inflection. Mathematical and Computer Modelling, $42(9)$, 1035–1048. doi: 10.1016/j.m.m. 2004.10.025 |
| 639 | 10.1016/J.mcm.2004.10.025 |
| 640 | McCauley, E., & Murdoch, W. W. (1987, January). Cyclic and Stable Populations: |
| 641 | 2021 08 20 from https://www.icumple.uchicome.edu/doi/ohg/10_1086/ |
| 642 | 2021-06-20, from https://www.journais.uchicago.edu/doi/abs/10.1000/ |
| 643 | MaCinty N Irwin A I Finkel 7 V & Dutkiewicz S (2023) Using acalogi |
| 644 | cal partitions to assess zooplankton biogeography and seasonality <i>Frontiers in</i> |
| 645 | Marine Science 10 Retrieved 2023-05-04 from https://www.frontiersin |
| 647 | .org/articles/10.3389/fmars.2023.989770 |
| 648 | Mojica, K., Behrenfeld, M., Clay, M., & Brussaard, C. (2021, August). Spring Ac- |
| 649 | cumulation Rates in North Atlantic Phytoplankton Communities Linked to |
| 650 | Alterations in the Balance Between Division and Loss. Frontiers in Microbiol- |
| 651 | ogy, 12. doi: 10.3389/fmicb.2021.706137 |
| 652 | Morozov, A. (2010). Emergence of Holling type III zooplankton functional response: |
| 653 | Bringing together field evidence and mathematical modelling. Journal of Theo- |
| 654 | retical Biology, 265(1), 45–54. doi: 10.1016/j.jtbi.2010.04.016 |
| 655 | Morozov, A., & Arashkevich, E. (2010, January). Towards a correct description |
| 656 | of zooplankton feeding in models: Taking into account food-mediated unsyn- |
| 657 | chronized vertical migration. Journal of Theoretical Biology, $262(2)$, $346-360$. |
| 658 | Retrieved 2022-04-21, from https://www.sciencedirect.com/science/ |
| 659 | article/pii/S0022519309004536 doi: 10.1016/j.jtbi.2009.09.023 |
| 660 | Morozov, A., Arashkevich, E., Reigstad, M., & Falk-Petersen, S. (2008, Oc- |
| 661 | tober). Influence of spatial heterogeneity on the type of zooplankton |
| 662 | functional response: A study based on field observations. Deep Sea Re- |
| 663 | search Part II: Topical Studies in Oceanography, $55(20)$, $2285-2291$. doi: |
| 664 | Mumar D. M. Ohman M. D. Charisha D. Kalla T. D. Charland, D. M. S. |
| 665 | Styled M P (2018 October) CCE V. Drimery production measurements |
| 666 | ton grazing and the biological pump in the California Current Ecosystem: |
| 669 | Variability and response to El Niño Deen Sea Research Part I: Oceano- |
| 669 | araphic Research Papers, 1/0, 52–62. Retrieved 2023-02-02, from https:// |
| 670 | www.sciencedirect.com/science/article/pii/S096706371830013X doi: |
| 671 | 10.1016/j.dsr.2018.07.012 |
| 672 | Mortenson, E., Lenton, A., Shadwick, E. H., Trull, T. W., Chamberlain, M. A., |
| 673 | & Zhang, X. (2021, December). Divergent trajectories of ocean warming |
| 674 | and acidification. Environmental Research Letters, 16(12), 124063. Re- |
| 675 | trieved 2022-03-19, from https://doi.org/10.1088/1748-9326/ac3d57 doi: |
| 676 | 10.1088/1748-9326/ac3d57 |
| 677 | Neelin, J. D., Bracco, A., Luo, H., McWilliams, J. C., & Meyerson, J. E. (2010, De- |
| 678 | cember). Considerations for parameter optimization and sensitivity in climate |
| 679 | models. Proceedings of the National Academy of Sciences, 107(50), 21349– |

| 680 | 21354. Retrieved 2021-10-13, from https://www.pnas.org/content/107/50/ |
|-----|---|
| 681 | 21349 (Publisher: National Academy of Sciences Section: Physical Sciences) |
| 682 | doi: 10.1073/pnas.1015473107 |
| 683 | Nissen, C., Vogt, M., Münnich, M., Gruber, N., & Haumann, F. A. (2018, |
| 684 | November). Factors controlling coccolithophore biogeography in the |
| 685 | Southern Ocean. Biogeosciences, 15(22), 6997–7024. Retrieved 2023-03- |
| 686 | 26, from https://bg.copernicus.org/articles/15/6997/2018/ doi: |
| 687 | 10.5194/bg-15-6997-2018 |
| 688 | Oke, P. R., Griffin, D. A., Schiller, A., Matear, R. J., Fiedler, R., Mansbridge, |
| 689 | J., Ridgway, K. (2013, May). Evaluation of a near-global eddy- |
| 690 | resolving ocean model. Geoscientific Model Development, 6, 591–615. doi: |
| 691 | 10.5194/gmd-6-591-2013 |
| 692 | Petrik, C. M., Luo, J. Y., Heneghan, R. F., Everett, J. D., Harrison, C. S., & |
| 693 | Richardson, A. J. (2022). Assessment and Constraint of Mesozooplank- |
| 694 | ton in CMIP6 Earth System Models. Global Biogeochemical Cucles, 36(11). |
| 695 | e2022GB007367. doi: 10.1029/2022GB007367 |
| 696 | Prowe A E F Pahlow M Dutkiewicz S Follows M & Oschlies A (2012 Au- |
| 697 | gust) Top-down control of marine phytoplankton diversity in a global ecosys- |
| 608 | tem model Progress in Oceanography 101(1) 1–13 doi: 10.1016/i pocean |
| 699 | 2011 11 016 |
| 700 | Pörtner H. Roberts, D. Masson-Delmotte, V. Zhai, P. Tignor, M. Poloczanska |
| 700 | E Wever N (2019) IPCC Special Report on the Ocean and Cruosphere |
| 701 | in a Changing Climate (Tech Ben) IPCC |
| 702 | Retnerajeh I. Abu-Alhajia R. Atkinson A. Batten S. Bay N. I. Bernard |
| 703 | K S Vebra I. (2023 February) Monitoring and modelling ma- |
| 704 | 1/(1) |
| 705 | 564 Retrieved 2022-03-08 from https://www.neture.com/articles/ |
| 706 | s/1467-023-36241-5doi: 10.1038/s/1467-023-36241-5 |
| 707 | Bichardson A I (2008 April) In hot water: zooplankton and climate change |
| 708 | ICES Journal of Marine Science 65(3) 270–205 Retrieved 2021-10-10 from |
| 709 | https://doi org/10.1093/icesimg/fsn028 doi: $10.1093/icesimg/fsn028$ |
| 710 | Pohr T. Long M. T. Kayanaugh M. Lindsay K. & Doney S. (2017 May) Vari |
| 711 | ability in the Machanisms Controlling Southern Ocean Phytoplankton Bloom |
| 712 | Phonology in an Ocean Model and Satellite Observations — Clabel Biogeochemi |
| 713 | and Cucles 21 doi: 10.1002/2016gb005615 |
| 714 | Debry T. Dichardson A. Lonton A. Chambarlain M. & Shadwick F. (2022) |
| 715 | Zooplanlitan maring is the langest source of 1 uncentainty for marine contain |
| 716 | auding in CMID6 IDCC 2 models — Communications Forth and Environment |
| 717 | Under Deview See 'Poloted Manuscript' |
| 718 | Dahn T. Dishandara A. L. Luntar, A. & Chadmids E. (2002) Manuscher) Dec |
| 719 | Konr, I., Richardson, A. J., Lenton, A., & Snadwick, E. (2022, November). Rec- |
| 720 | ommendations for the formulation of grazing in marine biogeochemical and |
| 721 | ecosystem models. Progress in Oceanography, 208, 102878. Retrieved |
| 722 | 2023-04-24, from https://www.sciencedirect.com/science/article/pii/ |
| 723 | S0079661122001379 doi: 10.1010/J.pocean.2022.102878 |
| 724 | Roy, S., Sathyendranath, S., Bouman, H., & Platt, T. (2013, December). The |
| 725 | global distribution of phytoplankton size spectrum and size classes from |
| 726 | their light-absorption spectra derived from satellite data. Remote Sens- |
| 727 | ing of Environment, 139, 185–197. Retrieved 2022-11-25, from https:// |
| 728 | www.sciencedirect.com/science/article/pii/S0034425/13002629 doi: |
| 729 | 10.1010/J.ISE.2010.00.004 |
| 730 | San Martin, E., Harris, K. P., & Irigoien, A. (2006, July). Latitudinal variation |
| 731 | III plankton size spectra in the Atlantic Ocean. Deep Sea Research Part |
| 732 | 11: 10pical Studies in Oceanography, 53(14), 1560–1572. Retrieved 2023- |
| 733 | 04-20, Irom https://www.sciencedirect.com/science/article/pii/ |
| 734 | 5096706450600124X doi: 10.1016/J.dsr2.2006.05.006 |

| 735 | Sathyendranath, S., Brewin, R. J. W., Brockmann, C., Brotas, V., Calton, B., |
|-----|---|
| 736 | Chuprin, A., Platt, T. (2019, January). An Ocean-Colour Time Series |
| 737 | for Use in Climate Studies: The Experience of the Ocean-Colour Climate |
| 738 | Change Initiative (OC-CCI). Sensors, 19(19), 4285. doi: 10.3390/s19194285 |
| 739 | Schmoker, C., Hernández-León, S., & Calbet, A. (2013, July). Microzooplank- |
| 740 | ton grazing in the oceans: impacts, data variability, knowledge gaps and |
| 741 | future directions Journal of Plankton Research 35(4) 691–706 Re- |
| 742 | trieved $2023-02-02$ from https://doi.org/10.1093/plankt/fbt023 doi: |
| 742 | 10 1093/plankt/fbt023 |
| 744 | Steele I (1074) Stability of plankton accosystems In M B Usher k |
| 744 | M H Williamson (Eds.) Ecological Stability (np. 170–101) Boston MA: |
| 745 | Springer US_doi: 10.1007/078.1.4800.6038.5.12 |
| 746 | Springer U.S. doi: $10.1007/976-1-4099-0936-0-12$ |
| 747 | steinberg, D. K., & Landry, M. R. (2017). Zoopiankton and the Ocean Carbon Cy- |
| 748 | Cie. Annual Review of Marine Science, $9(1)$, $415-444$. Reineved 2022-05-07, |
| 749 | from https://doi.org/10.1146/annurev-marine=010814=015924 doi: 10 |
| 750 | .1140/annurev-marine-010814-015924 |
| 751 | Steinberg, D. K., Ruck, K. E., Gleiber, M. R., Garzio, L. M., Cope, J. S., Bernard, |
| 752 | K. S., Ross, R. M. (2015, July). Long-term (1993–2013) changes in |
| 753 | macrozooplankton off the Western Antarctic Peninsula. Deep Sea Re- |
| 754 | search Part I: Oceanographic Research Papers, 101, 54–70. Retrieved 2021- |
| 755 | 11-25, from https://www.sciencedirect.com/science/article/pii/ |
| 756 | S0967063715000412 doi: 10.1016/j.dsr.2015.02.009 |
| 757 | Strömberg, K. H. P., Smyth, T. J., Allen, J. I., Pitois, S., & O'Brien, T. D. |
| 758 | (2009, August). Estimation of global zooplankton biomass from satellite |
| 759 | ocean colour. Journal of Marine Systems, $78(1)$, 18–27. Retrieved 2023- |
| 760 | 01-19, from https://www.sciencedirect.com/science/article/pii/ |
| 761 | S0924796309000669 doi: 10.1016/j.jmarsys.2009.02.004 |
| 762 | Sverdrup, H. U. (1953, January). On Conditions for the Vernal Blooming of Phy- |
| 763 | toplankton. ICES Journal of Marine Science, 18(3), 287–295. doi: 10.1093/ |
| 764 | icesjms/18.3.287 |
| 765 | Tagliabue, A., Kwiatkowski, L., Bopp, L., Butenschön, M., Cheung, W., Lengaigne, |
| 766 | M., & Vialard, J. (2021). Persistent Uncertainties in Ocean Net Primary |
| 767 | Production Climate Change Projections at Regional Scales Raise Challenges |
| 768 | for Assessing Impacts on Ecosystem Services. Frontiers in Climate, 3. Re- |
| 769 | trieved 2022-02-07, from https://www.frontiersin.org/article/10.3389/ |
| 770 | fclim.2021.738224 |
| 771 | Tittensor, D. P., Novaglio, C., Harrison, C. S., Heneghan, R. F., Barrier, N., |
| 772 | Bianchi, D., Blanchard, J. L. (2021, October). Next-generation ensem- |
| 773 | ble projections reveal higher climate risks for marine ecosystems. Nature |
| 774 | Climate Change, 1-9. Retrieved 2021-10-25, from https://www.nature.com/ |
| 775 | articles/s41558-021-01173-9 doi: $10.1038/s41558-021-01173-9$ |
| 776 | Tjiputra, J. F., Schwinger, J., Bentsen, M., Morée, A. L., Gao, S., Bethke, I., |
| 777 | Schulz, M. (2020, May). Ocean biogeochemistry in the Norwegian Earth Sys- |
| 778 | tem Model version 2 (NorESM2). Geoscientific Model Development, 13(5), |
| 779 | 2393-2431. Retrieved 2022-03-08, from https://gmd.copernicus.org/ |
| 780 | articles/13/2393/2020/ doi: 10.5194/gmd-13-2393-2020 |
| 781 | Truscott, J. E., Brindley, J., Brindley, J., & Gray, P. (1994, June). Equilibria, |
| 782 | stability and excitability in a general class of plankton population models. |
| 783 | Philosophical Transactions of the Royal Society of London. Series A: Physical |
| 784 | and Engineering Sciences, 347(1685), 703–718. (Publisher: Royal Society) doi: |
| 785 | 10.1098/rsta.1994.0076 |
| 786 | Tsujino, H., Urakawa, S., Nakano, H., Small, R. J., Kim, W. M., Yeager, S. G., |
| 787 | Yamazaki, D. (2020). input4MIPs.CMIP6.OMIP.MRI.MRI-JRA55- |
| 788 | do-1-5-0. Retrieved 2022-03-19, from https://doi.org/10.22033/ESGF/ |
| 789 | input4MIPs.15017 (Publisher: Earth System Grid Federation Type: dataset) |
| | |

| 790 | doi: $10.22033/\text{ESGF/input}4MIPs.15017$ | | | | | | |
|-----|---|--|--|--|--|--|--|
| 791 | Vallina, S. M., & Le Quéré, C. (2011, March). Stability of complex food webs: | | | | | | |
| 792 | Resilience, resistance and the average interaction strength. Journal of The- | | | | | | |
| 793 | oretical Biology, 272(1), 160–173. Retrieved 2023-01-23, from https:// | | | | | | |
| 794 | www.sciencedirect.com/science/article/pii/S0022519310006387 doi: | | | | | | |
| 795 | 10.1016/j.jtbi.2010.11.043 | | | | | | |
| 796 | Vallina, S. M., Ward, B. A., Dutkiewicz, S., & Follows, M. J. (2014, January). | | | | | | |
| 797 | Maximal feeding with active prey-switching: A kill-the-winner functional | | | | | | |
| 798 | response and its effect on global diversity and biogeography. Progress | | | | | | |
| 799 | in Oceanography, 120, 93–109. Retrieved 2023-01-17, from https:// | | | | | | |
| 800 | www.sciencedirect.com/science/article/pii/S0079661113001468 doi: | | | | | | |
| 801 | 10.1016/j.pocean.2013.08.001 | | | | | | |
| 802 | Westberry, T. K., Behrenfeld, M. J., Siegel, D. A., & Boss, E. S. (2008, June). | | | | | | |
| 803 | Carbon-Based Primary Productivity Modeling with Vertically Resolved | | | | | | |
| 804 | Photoacclimation. Global Biogeochemical Cycles, $22(2)$. doi: 10.1029/ | | | | | | |
| 805 | 2007 GB003078 | | | | | | |
| 806 | Zahariev, K., Christian, J. R., & Denman, K. L. (2008, April). Preindustrial, Histor- | | | | | | |
| 807 | ical, and Fertilization Simulations Using a Global Ocean Carbon Model with | | | | | | |
| 808 | New Parameterizations of Iron Limitation, Calcification, and N 2 Fixation. | | | | | | |
| 809 | Progress in Oceanography, 77, 56–82. doi: 10.1016/j.pocean.2008.01.007 | | | | | | |
| 810 | Ziehn, T., Chamberlain, M. A., Law, R. M., Lenton, A., Bodman, R. W., Dix, M., | | | | | | |
| 811 | Srbinovsky, J. (2020, August). The Australian Earth System Model: | | | | | | |
| 812 | ACCESS-ESM1.5. Journal of Southern Hemisphere Earth Systems Science, | | | | | | |
| 813 | 70(1), 193-214. Retrieved 2021-05-27, from https://www.publish.csiro.au/ | | | | | | |
| 814 | es/ES19035 doi: 10.1071/ES19035 | | | | | | |
| 815 | Ziehn, T., Lenton, A., Law, R., Matear, R., & Chamberlain, M. (2017, July). The | | | | | | |
| 816 | carbon cycle in the Australian Community Climate and Earth System Simu- | | | | | | |
| 817 | lator (ACCESS-ESM1) – Part 2: Historical simulations. Geoscientific Model | | | | | | |
| 818 | Development, 10, 2591-2614. doi: $10.5194/gmd-10-2591-2017$ | | | | | | |

Supporting Information for "The Global Distribution and Drivers of Grazing Dynamics Estimated from Inverse Modelling"

Tyler Rohr^{1,2}, Anthony Richardson^{3,4}, Andrew Lenton⁵, Matt Chamberlain⁵,

Elizabeth Shadwick^{2,5}

²Institute for Marine and Antarctic Science, University of Tasmania, Hobart, Tasmania, 7000, Australia

²Australian Antarctic Partnership Program, Hobart, Tasmania, 7000, Australia

³School of Environment, 4072, The University of Queensland, St Lucia, Queensland, Australia

⁴Commonwealth Scientific and Industrial Research Organisation (CSIRO) Environment, BioSciences Precinct (QBP), St Lucia,

Queensland, 4067, Australia

 5 Commonwealth Scientific and Industrial Research Organisation (CSIRO) Environment, Hobart, Tasmania, 7000 Australia

Contents of this file

- 1. Supporting Text 1 to 3
- 2. Supporting Figures 1 to 4
- 3. Supporting Table 1

Corresponding author: Tyler Rohr, Australian Antarctic Partnership Program, Hobart, Tasmania, 7000, Australia. (tyler.rohr@utas.edu.au)

X - 2

Supporting Text 1. Distribution and drivers of grazing dynamics using the VIIRS chlorophyll record

In Figure 1 we use phytoplankton carbon biomass estimated remotely from the Carbonbased Productivity Model (Westberry et al., 2008) to compare directly to prognostic phytoplankton biomass resolved in the simulation. However, estimating carbon biomass from space using particle back-scattering involves a different set of assumptions than traditional estimates of phytoplankton abundance which infer chlorophyll concentrations from ocean color. To confirm these differences did not influence our results we repeated the analysis comparing the seasonal cycle of modelled phytoplankton carbon to that of remotely sensed chlorophyll from VIIRS (Sathyendranath et al., 2019). The results were largely consistent (Supporting Figure 1).

The primary difference is that the two clear asymptotes apparent when using CbPM biomass as an indicator of phytoplankton abundance are now not as well defined, with the lower asymptote disappearing entirely. Note, while we use a sigmoidal function to fit the relationship for consistency and direct comparison, it may be better described with a rectangular hyperbole. It is not entirely clear why there is no lower asymptote for chlorophyll but it may have to do with the detection threshold for ocean colour versus backscatter, the fact that at low phytoplankton concentrations the particle back scatter signal may no longer be dominated by phytoplankton, or variability in the carbon to chlorophyll ratio as a result of community composition or photo-adaptation. Never the less, our two most important results remain consitent: 1. The type III response consistently outperforms the type II response (**Supporting Figure 2, Supporting Table 1**) and 2. the seasonal

cycle in more eutrophic regions is better described using larger $K_{1/2}$ values (Supporting

Figures 1, 2

Note, model skill scores appear higher for VIIRS than CbPM (**Supporting Table 1**); however, model skill was normalized across all runs using chlorophyll (VIIRS) and all run using carbon (CbPM) independently. Thus, the higher scores for VIIRS do not necessarily mean the modelled seasonal phytoplankton cycle better reflects observed chlorophyll compared to carbon, but rather that the difference between the model skill achieved with the optimal $K_{1/2}$ values compared to sub-optimal $K_{1/2}$ values is larger when comparing to observed chlorophyll.

Supporting Text 2. First order stability of the functional response

The shape of the functional response curve, $g([C_{phyto}])$, influences the shape of the seasonal cycle of phytoplankton biomass primarily through its stabilizing or destabilizing influence on phytoplankton population dynamics (Gentleman & Neuheimer, 2008). The stabilizing influence of grazing is determined by how clearance rates ($Cl = g([C_{phyto}])/[C_{phyto}]$) change in response to changing phytoplankton biomass. If phytoplankton accumulation decreases clearance rates, thereby promoting further population growth, that is a positive feed back with a destabilizing influence. Alternatively, if phytoplankton accumulation increases clearance rates, thereby damping further population growth, that is a negative feed back with stabilizing influence. The stabilizing influence of the functional response at a given phytoplankton concentration can thereby be quantified by the first derivation of the clearance rate with respect to the phytoplankton concentration (i.e. $\frac{dCl}{d[C_{phyto}]}$). The value of $\frac{dCl}{d[C_{phyto}]}$ is determined both the shape of $g([C_{phyto}])$ as

well as the prognostic phytoplankton concentration which determines where on the curve $\frac{dCl}{d[C_{phyto}]}$ is evaluated.

To capture a mean sense of the stabilizing influence of the functional response across a complete model run and many different phytoplankton concentrations, we define the mean first order stability as the value of $\frac{dCl}{d[C_{phyto}]}$ at the mean annual $[C_{phyto}]$ in a given grid cell of a given run. The mean first order stability of our experiments was consistently negative (destabilizing) when a type II response was employed (**Figure S3B**) and positive (stabilizing) when a type III response was employed (**Figure S3A**). Note, while it is not possible to have positive first order stability when a type II response is used, it is possible to have negative first order stability stability when a type III response is used. The latter is possible in model configurations with a very low g_{max} or very strong bottom-up growth conditions that could buoy phytoplankton populations above $K_{1/2}$.

Regardless of response type, large $K_{1/2}$ values stretch out the response curve, leading to the depression and linearization of the functional response at low (but common) prey concentrations, slow and steady clearance rates, and very little influence on the stability of the system. Decreasing $K_{1/2}$ with a type II response monotonically decreases the first order stability by both directly altering the shape of the functional response curve and indirectly decreasing the prognostic phytoplankton population via increased grazing pressure. Decreasing $K_{1/2}$ with a type III response monotonically increases the first order stability of the system. This occurs because decreasing $K_{1/2}$ increases grazing pressure and, without suitably strong bottom-controls, keeps the annually-averaged phytoplankton concentration below $K_{1/2}$, where the first order stability increases as $K_{1/2}$ decreases.

Supporting Text 3. Challenges and potential of parameterizing zooplankton community composition

By invoking the equations descried in Figure 1 or Supporting Table 1 modellers could implicitly resolve changes in zooplankton community composition by driving changes in the community-integrated functional attributes (i.e. $K_{1/2}$) of a single zooplankton group with changes in prey abundance. However, experimenting with this parameterization warrants careful consideration of several factors.

Ecologically, such a parameterization requires assuming that a) bulk phytoplankton biomass co-varies with phytoplankton community composition in a systematic way, with less productive waters inhabited by smaller phytoplankton (Roy et al., 2013), and b) zooplankton community composition is determined by the composition of the prey field in a systematic way, with more efficient grazing able to dominate when prey options are smaller (Kiørboe & Hirst, 2014). While both assumptions are generally well supported by observations and together are consistent with the emergent relationship between observed phytoplankton biomass and the inferred grazing dynamics required to best recreate its seasonal cycle (**Figure 1**), implementing the associated relationship introduces additional challenges.

First off, the specific parameters listed in **Supporting Table 1** and **Figure 1** would likely need to be tuned-up to the bottom-up configuration and physical dynamics of each particular model in which they are embedded. Secondly, it is not obvious what space and time scales one should assume that specific grazing rates should change due to the influence of food scarcity on individual zooplankton versus the influence of zooplankton community

composition on mean grazing dynamics. That is, while the value of $K_{1/2}$ determines the instantaneous response of zooplankton grazing rates to food scarcity, it should take longer for $K_{1/2}$ itself to evolve. This is because $K_{1/2}$ reflects the mean physiological characteristics of the entire zooplankton community and can only change at the rate with which community composition can evolve. This timescale likely varies globally and as a function of other environmental drivers such as temperature (Richardson, 2008). For example, much shorter time periods are needed in communities dominated by asexuallyreproducing zooplankton such as salps compared to those dominated by zooplankton with complex, multi-year, life histories, such as euphausiids (Steinberg et al., 2015). Finally, the best implementation of this parameterization would require further constraining the relationship between phytoplankton biomass and $K_{1/2}$ in addition to the strength and covariability of other drivers of zooplankton bio-geography such as temperature (Brandão et al., 2021) or the relative distribution of prey in models with multiple phytoplankton groups.

Despite the challenges, properly implementing such a parameterization could realize dramatic improvements in BGC models and our predictions of changes to marine carbon cycling. Extending from the assumption that a given optimal $K_{1/2}$ reflects the mean behavior of a particular zooplankton community, other attributes of that community could be additionally parameterized. For instance, crustaceans associated with slower grazing (and larger $K_{1/2}$ values) are typically stronger swimmers. They tend to vertically migrate on daily and seasonal timescales, allowing them to actively transport carbon much faster than microzooplantkon (Steinberg & Landry, 2017). This could be represented by

increasing the flux of carbon from zooplankton into the sinking detritus pool (i.e. POC) at low $K_{1/2}$ values, without explicitly including the important role of Diel-vertical migration in carbon transport (Archibald et al., 2019). Other important BGC attributes that vary with zooplankton community composition include the recalcitrance of their detritus and thus the remineralization rates of what they contribute to export production, their sensitivity to temperature, their stoichiometry and carbon content, and their response to seasonal change in the depth of the surface mixed layer.



Figure S1. Identical to Figure 1, except using VIIRS chlorophyll instead of CbPM carbon biomass to track the observed phytoplankton phenology.



Observed Mean-annual Phytoplankton Concentration (mmolC m⁻³)



Figure S2. Identical to Figure 1 D, E and Supporting Figure 2 D, E, expect now showing results from individual experiment suites (each using a different g_{max} value) instead of averaging optimal values across experiment suites.



Figure S3. Sensitivity of ecosystem stability to $K_{1/2}$. Global distributions of the meanannual first order stability is plotted for all $K_{1/2}$ values, each with a consistent $g_{max} = 1$, and a **A**) type III and **b**) type II functional response.



Figure S4. The mean annual model bias is plotted for the A) mixed layer depth (MLD) relative to HYCOM reanalysis, B) Phytoplankton biomass relative to CbPM and C) NPP relative to CbPM.

| D | g _{max} | Parameters of Sigmoidal Fit (95% Confidence) $K_{+,\alpha} = L + \frac{U - L}{U - L}$ | | | | Mean | |
|------------------|--------------------|--|---------------------------------|-----------------------|----------------------|------|--|
| Response Type | (d ⁻¹) | | 1/2 2 · 1 + e | Model Skill | | | |
| туре | | L | U | α | β | | |
| Type II | 0.5 | 4.89 (4.77-5.00) | $11.17 \\ (11.05-11.29)$ | 1.10 (1.09-1.10) | 0.30 (0.28-0.33) | 0.57 | |
| Type II | 1 | 6.19 (6.10-6.28) | 13.98 (13.88-14.09) | 1.07 (1.06-1.08) | 0.20 (0.18-0.21) | 0.61 | |
| Type II | 2 | 8.479 (8.24-8.7) | $14.53 \\ (14.36\text{-}14.69)$ | 1.076 (1.06-1.09) | 0.5 (0.45-0.57) | 0.56 | |
| Type II | Mean | 6.68 (6.59-6.76) | $13.16 \\ (13.07-13.24)$ | 1.08 (1.08-1.09) | 0.28 (0.27-0.30) | 0.57 | |
| Type III | 0.5 | 1.96 (1.86-2.04) | 6.65 (6.57-6.78) | 1.06 (1.05-1.06) | 0.26 (0.23-0.28) | 0.75 | |
| Type III | 1 | 2.90 (2.80-3.00) | 6.65 (8.18-8.35) | 1.034 (1.03- 1.04) | 0.23 (0.21- 0.25) | 0.74 | |
| Type III | 2 | 4.20 (4.11-4.29) | 9.91 (9.8-10.00) | 1.027 (1.02-1.03) | 0.16 (0.14-0.17) | 0.73 | |
| Type III | Mean | 3.0 (2.92-3.10) | 8.279 (8.20-8.36) | 1.038 (1.03-1.04) | 0.22 (0.20-0.23) | 0.74 | |

A Optimal $K_{1/2}$ (mmolC m⁻³) vs. Mean-annual Observed Phytoplankton Biomass (mmolC m⁻³)

Optimal $K_{1/2}$ (mmolC m⁻³) vs. Mean-annual Observed Chlorophyl (mg m⁻³)

в

| | | Parameters of Sigmoidal Fit (95% Confidence) | | | | |
|----------------|---------------------------------|---|--|-----------------------|-------------------------------|------------------------|
| Response | ${f g_{ m max} \over (d^{-1})}$ | $K_{1/2} = L + \frac{U - L}{1 + \exp\left(\frac{[Chl] - \alpha}{\beta}\right)}$ | | | | Mean Model Skill |
| - <i>J</i> P C | | L | U | α | β | |
| Type II | 0.5 | -1.01 (-3.55-1.54) | $\begin{array}{c} 10.54 \\ (10.35\text{-}10.73) \end{array}$ | 0.06 (0.04-0.09) | $0.25 \\ (0.2102, \\ 0.2897)$ | 0.65 |
| Type II | 1 | 0.23 (-6.58-7.04) | 12.2 (12.04-12.36) | 12.2 (12.04-12.36) | 0.20 (0.15-0.24) | 0.64 |
| Type II | 2 | -855 (-1.4e+06- 1.48e+06) | $11.61 \\ (10.74-12.47)$ | -0.81 (-240-240) | 0.60 (-1.14-2.34) | 0.47 |
| Type II | Mean | -3.446 (-16.04-9.15) | $11.34 \\ (11.19-11.49)$ | 0.00 (-0.09-0.08) | 0.27 (0.20-0.33) | 0.59 |
| Type III | 0.5 | 1.10 (0.43-1.77) | 5.78 (5.66-5.90) | 0.10 (0.08-0.11) | 0.17 (0.14-0.20) | 0.79 |
| Type III | 1 | 2.378 (1.74-3.01) | 7.42 (7.29-7.55) | 0.10 (0.09-0.11) | 0.15 (0.12-0.17) | 0.81 |
| Type III | 2 | 2.28 (0.73-3.83) | 8.84 (8.69-8.98) | 0.08 (0.06-0.09) | 0.15 (0.12-0.18) | 0.85 |
| Type III | Mean | 2.00 (1.21-2.79) | 7.34 (7.21-7.45) | 0.09 (0.08-0.10) | 0.15 (0.12-0.18) | 0.82 |

Table S1. The relationship between mean annual phytoplankton abundance and the $K_{1/2}$ parameter required to best recreate its seasonal cycle. Different relationships refer to different response functions (II,III), g_{max} values (0.5,1,2) and observed phytoplankton variables (Carbon, Chlorophyll). Mean model skill refers to the average cost function score of the optimal $K_{1/2}$ across all grid cells in a given configuration