

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

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Key Points:

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

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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.

Plain Language Summary

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

1 Introduction

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

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

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 using an inverse modelling approach. We run a suite of simulations in a coupled ocean-BGC model, parameterized with a wide range of grazing dynamics, and determine the optimal parameters required to recreate the observed phytoplankton seasonal cycle. We map the distribution of optimal parameters, examine how they appear driven by regional variability in phytoplankton biomass (**Sec. 3.1**), and explain mechanistically how grazing dynamics can shape the seasonal cycle (**Sec. 3.2**). Finally, we discuss the limitations of this work (**Sec. 4.1**), as well its potential utility from an ecological (**Sec. 4.2**) and modelling perspective (**Sec. 4.3**).

2 Materials and methods

2.1 Grazing in BGC models

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

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

115 dampens changes in the size of the phytoplankton population, thereby exerting a sta-
 116 bilizing influence. Alternatively, downward concavity means phytoplankton-specific loss
 117 rates to grazing decline with population growth, creating a destabilizing, positive feed-
 118 back which amplifies changes in the size of the phytoplankton population.

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

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

140 **2.3 Model configuration**

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

155 **2.4 Model experiments**

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

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 phytoplankton seasonal cycle: the correlation coefficient (CC) and the coefficient of variation (CV). The CC measures the co-variability between the simulated and observed climatologies, while the CV measures the magnitude of variability separately in each climatology 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 size of mean-annual phytoplankton population (i.e. CC independent to mean; CV normalized by mean). This is to help isolate the influence of grazing dynamics on the qualitative shape of the seasonal cycle rather than mean-state NPP which could be biased by many other model attributes.

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

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 ($CC_{mod,obs}$),

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

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.

3 Results

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 re-

209 regions, 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.

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

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

230 3.2 Mechanistic influence of the grazing dynamics

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

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

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

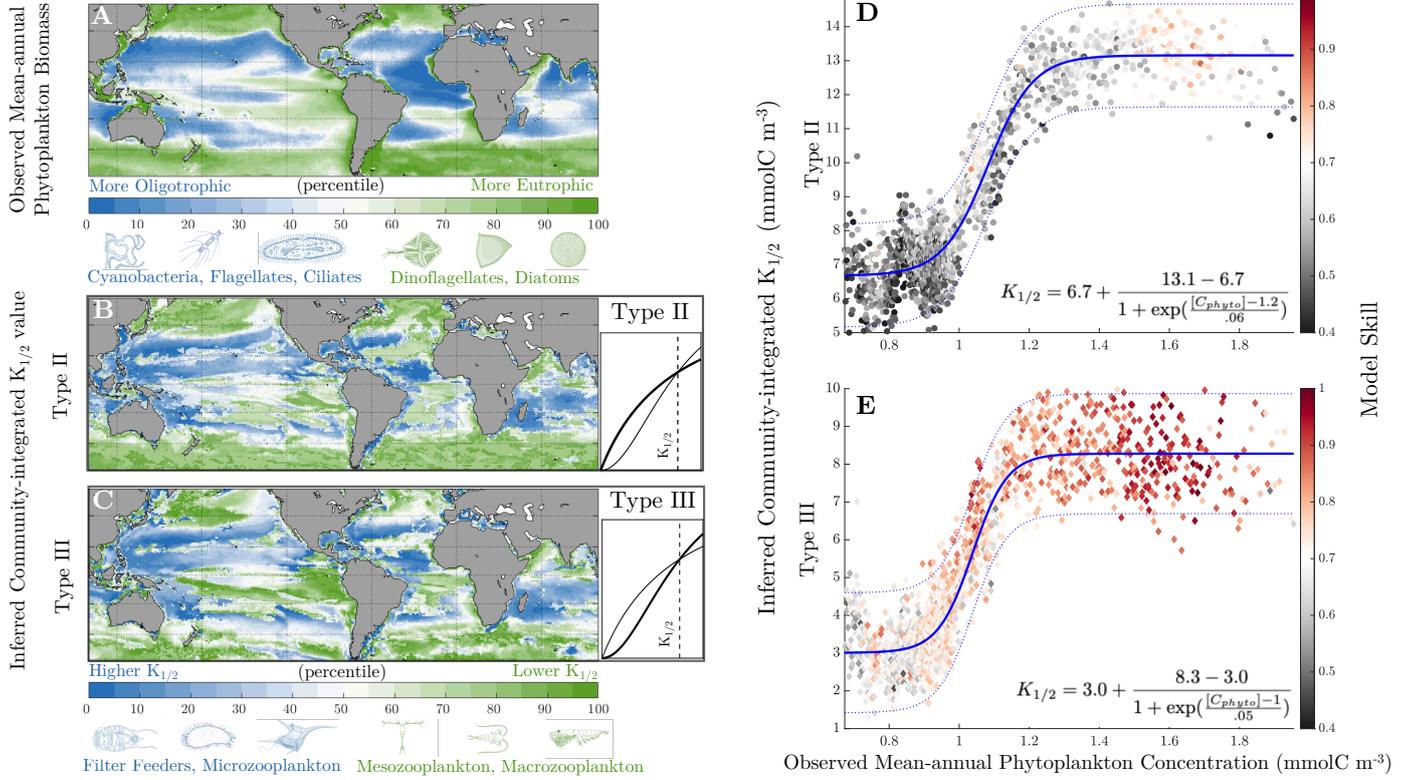


Figure 1. The distribution and drivers of grazing dynamics. **A)** The observed climatological mean-annual phytoplankton biomass concentration plotted as a percentile of the full spatial distribution. Below, the corresponding optimal $K_{1/2}$ parameter required to best recreate the observed phytoplankton 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).

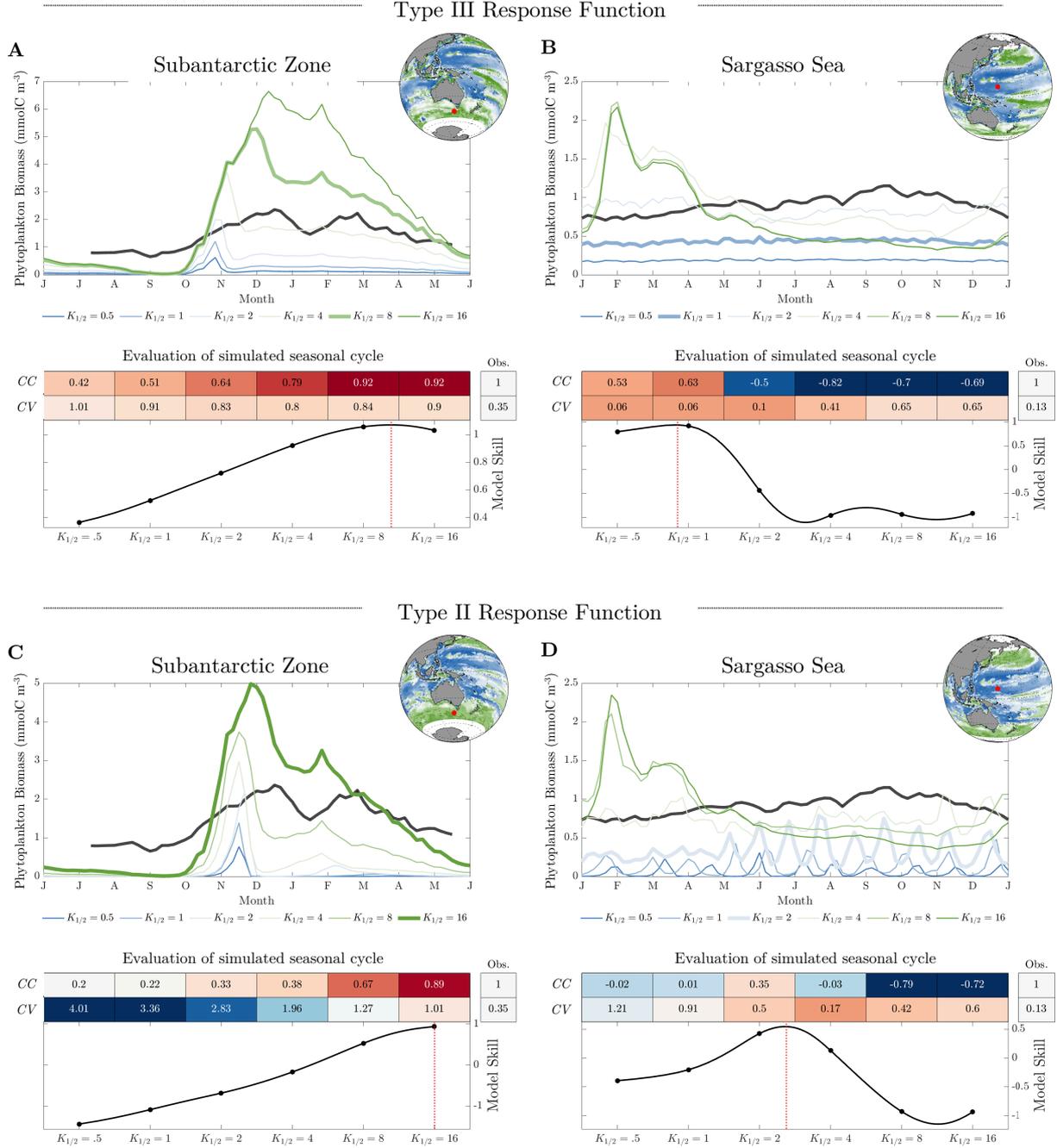


Figure 2. Influence of $K_{1/2}$ and response type on phytoplankton seasonal cycle. Phytoplankton biomass climatologies and model skill evaluations are provided from **A, C** the SAZ and **B, D** Sargasso Sea, showing the emergent seasonal cycle from runs using six $K_{1/2}$ values with a **A, B** Type 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 Figure 1, with the same percentile-based color-bar. 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.

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

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

275 4 Discussion

276 4.1 Limitations

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

296 4.2 Ecological Perspectives

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

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

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

322 However, despite two prominent asymptotes, the region of monotonically increas-
323 ing $K_{1/2}$ values between them ($\sim 0.85\text{-}1.2 \text{ mmolC m}^{-3}$) encompasses over 50% of the ocean
324 area in our domain ($55^\circ\text{S-}55^\circ\text{N}$) and 43% of the global ocean. This suggests a critical
325 role for more heterogeneous zooplankton communities and the co-existence of diverse func-
326 tional groups therein. This steady increase in $K_{1/2}$ across intermediate mean-annual phy-
327 toplankton concentrations is consistent with the positive relationship between empiri-
328 cally estimated microzooplankton $K_{1/2}$ values and in-situ chlorophyll concentrations mea-
329 sured across shipboard dilution experiments (Chen et al., 2014). Note, while these re-
330 sults strongly imply slower zooplankton-specific grazing rates in more productive biomes,
331 they can be consistent with observations of bulk ingestion rates and phytoplankton-specific
332 grazing mortality increasing with primary productivity (Schmoker et al., 2013; Calbet,
333 2001) due to differences in phytoplankton and zooplankton abundance.

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

348 4.3 Modelling Perspectives

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

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

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

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

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

408 5 Conclusions

409 These results present a novel, observationally-informed, map of global community-
 410 integrated grazing dynamics (i.e $K_{1/2}$ values). Further refining the observed distribu-

411 tion and drivers of grazing, and how to replicate them in models, will require close col-
 412 laboration with zooplankton ecologists, but presents an exciting new frontier in oceanog-
 413 raphy focused on a rigorous understanding of how NPP is controlled from the top-down.
 414 Moreover, improving the representation of zooplankton could realize dramatic improve-
 415 ments in marine BGC models and our predictions of future ocean states.

416 6 Open Research

417 All relevant model output and documentation can be found at [https://doi.org/10.25919/wn09-](https://doi.org/10.25919/wn09-6j31)
 418 [6j31](https://doi.org/10.25919/wn09-6j31). Remote sensing products were downloaded at [http://orca.science.oregonstate](http://orca.science.oregonstate.edu/2160.by.4320.8day.hdf.carbon2.m.php)
 419 [.edu/2160.by.4320.8day.hdf.carbon2.m.php](http://orca.science.oregonstate.edu/2160.by.4320.8day.hdf.carbon2.m.php). Please address any questions to Tyler
 420 Rohr, at tyler.rohr@utas.edu.au.

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