

Recommendations for the Formulation of Grazing in Marine Biogeochemical and Ecosystem Models

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Key Points:

- We provide a detailed derivation for the functional response equations, in an explicitly aquatic context.
- When describing zooplankton grazing, parameter values vary by 3 to 4 order of magnitude, both in models and experiments.
- We recommend using a type III functional response, a Michaelis-Menten parameter scheme, and testing a wide range of $K_{1/2}$ values, particularly low ones.

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Abstract

For nearly a century, the functional response curves, which describe how predation rates vary with prey density, have been a mainstay of ecological modelling. While originally derived to mechanistically describe specific, terrestrial interactions on a two dimensional plane, they have more recently been adopted to characterize the mean state of three dimensional aquatic systems in marine biogeochemical, size-spectrum, and population models. This translation, however, has further abstracted the functional response from first principles and led to a large divergence in its formulation across models. Marine ecological modellers disagree over the qualitative shape of the curve (e.g. Type II vs. III), whether its parameters should be mechanistically or empirically defined (e.g. disk vs. Michaelis-Menten scheme), and the most representative value of those parameters. This leaves modellers with little sense of best practice and models liable to bias. As a case study, we focus on marine biogeochemical models, providing a comprehensive theoretical, empirical, and numerical road-map for interpreting, formulating, and parameterizing the functional response when used to prescribe zooplankton specific grazing rates on phytoplankton. After providing a detailed derivation of each of the canonical functional response types explicitly for aquatic systems, we review the literature describing their parameterization. We find that empirical values and those used in models vary hugely, ranging over three to four orders of magnitude. Next, we conduct a suite of 0-D NPZ simulations to isolate the sensitivity to phytoplankton population size and stability to the grazing formulation. We find that the disk parameterizations scheme is much less sensitive to its parameterization than the Michaelis-Menten scheme, and confirm that the Type II response is susceptible to instabilities and extinction events. Finally, after considering the numerical sensitivity of the functional response in the context of ecological reality, we recommend using a type III rather than the type II response, employing a Michaelis-Menten rather than disk parameter scheme, and testing a large range of values to parameterize the half saturation concentration in optimization search routines. While we focus specifically on the grazing formulation in marine biogeochemical models, we believe these recommendations are robust across a much broader range of ecosystem models when seeking to represent the mean state of a complex trophic system constrained by limited observations.

1 Introduction

In the late 1950s, Buzz Holling began studying the predation of sawfly cocoons by small mammals (Holling, 1959a) to better understand how predation rates varied with prey density, a relationship coined a decade earlier as the functional response (Solomon, 1949). Holling observed that individual predators consumed more prey at higher prey densities, but found that this relationship was not necessarily linear or consistent across species. Over the course of three seminal papers, Holling went on to develop a theoretical framework to describe how different assumptions about the rates at which predators captured and consumed their prey could explain observed nonlinearities and variability in the shape of functional response curve (Holling, 1959a, 1959b, 1965). Using this mechanistic approach, Holling derived three qualitatively distinct response types to describe differences in predator-prey interactions and their associated rates. In the ensuing decades, these equations have been further generalized (Real, 1977, 1979) and cemented into the bedrock of ecological modelling (Beardsell et al., 2021; Denny, 2014).

Although the functional response was originally developed for terrestrial applications (Holling, 1959a), the equations are also common in marine ecological modelling (Evans & Parslow, 1985; Fasham, 1995; Franks, Wroblewski, & Flierl, 1986). In the ocean, the functional response equations are now routinely used to link trophic dynamics in marine biogeochemical (Law et al., 2017; Moore, Lindsay, Doney, Long, & Misumi, 2013), size spectrum (Heneghan et al., 2020), and population models (Alver, Broch, Melle, Bagøien, & Slagstad, 2016). They are used to simulate both the rate at which heterotrophic zoo-

70 plankton graze on autotrophic phytoplankton (Evans & Parslow, 1985; Fasham, Duck-
71 low, & McKelvie, 1990; Franks et al., 1986) as well as the transfer of mass and energy
72 further up the food chain in ecosystem (Butenschön et al., 2016) and fisheries models
73 (Maury, 2010; Tittensor et al., 2018, 2021). However, although Holling’s canonical equa-
74 tions remain fairly ubiquitous across marine applications they have become somewhat
75 abstracted from the first principles on which they were founded. Modellers must trans-
76 late equations derived to described specific interactions between individual species on
77 a two-dimensional, terrestrial plane into a three-dimensional, aqueous medium in which
78 observations are sparse and the mean state of diverse communities must be represented
79 by a limited number of equations.

80 In turn, there remains a great deal of uncertainty surrounding the formulation of
81 the functional response. For example, trade offs between the ecological veracity and nu-
82 merical stability of different response types (Gismervik, 2005; Morozov, 2010; Morozov,
83 Arashkevich, Reigstad, & Falk-Petersen, 2008) have led to disagreement over which is
84 best suited for rapidly growing, easily excitable, microbial systems common in marine
85 ecology (Fasham, 1995; Flynn & Mitra, 2016; Gentleman & Neuheimer, 2008). Even amongst
86 mathematically identical curves, there is not a consensus on how to define their param-
87 eters, no less prescribe them. While some modellers opt for a parameter scheme that mir-
88 rors the Michaelis–Menten (Johnson & Goody, 2011) and Monod (Monod, 1949) equa-
89 tions developed to describe enzyme kinetics and bacterial growth rates (e.g. Aumont and
90 Bopp (2006); Dutkiewicz et al. (2015); Moore et al. (2013); Vichi, Pinardi, and Masina
91 (2007)), others use a parameter scheme that mirrors the disc equation (Holling, 1959b,
92 1965)) developed by Holling to describe specific terrestrial interactions (e.g. Fasham (1995);
93 Laws, Falkowski, Smith, Ducklow, and McCarthy (2000); Oke et al. (2013); Schartau and
94 Oschlies (2003b)). Disagreement over the chemostat-like, biogeochemical and mechanis-
95 tic, ecological flavours of these equations can confuse inter-model comparisons and in-
96 fluence the parameter space considered in optimization schemes, especially if there are
97 not robust observations to bound them.

98 Here, we focus on the formulation of grazing in marine biogeochemical models, which
99 are a critical component of coupled climate models (Eyring et al., 2016; Flato et al., 2013;
100 Taylor, Stouffer, & Meehl, 2012) and often used to drive fisheries models (Maury, 2010;
101 Tittensor et al., 2018, 2021), but are increasingly under constrained and over parame-
102 terized (Doney, 1999; Mearns, 1995; Schartau et al., 2017; Ward, Friedrichs, Anderson,
103 & Oschlies, 2010). Accurately representing grazing is critical to both climate and fish-
104 eries models, as it mediates the biological transport of carbon fixed via net primary pro-
105 duction (Behrenfeld, Doney, Lima, Boss, & Siegel, 2013; Laufkötter et al., 2015) and trans-
106 ported to higher trophic levels via secondary production (Brander, 2007; Scherrer et al.,
107 2020). Still, despite the growing recognition that biogeochemical models are highly sen-
108 sitive to the grazing formulation (Adjou, Bendtsen, & Richardson, 2012; Anderson, Gen-
109 tleman, & Sinha, 2010; Chenillat, Rivière, & Ohman, 2021; Fasham, 1995; Flynn & Mi-
110 tra, 2016; Fussmann & Blasius, 2005; Gentleman & Neuheimer, 2008; Gross, Ebenhöf,
111 & Feudel, 2004), we lack adequate observations to constrain it (Chen, Laws, Liu, & Huang,
112 2014). Parameters inferred empirically vary across zooplankton species and age (Hansen,
113 Bjørnsen, & Hansen, 1997; Hirst & Bunker, 2003), lack a robust allometric relationship
114 (Hansen et al., 1997), and can not be validated against robust global distributions (Mori-
115 riarty, Buitenhuis, Le Quéré, & Gosselin, 2013; Moriarty & O’Brien, 2012).

116 Given the uncertainty in the governing dynamics, it is useful to clarify and con-
117 solidate a theoretically, mathematically, empirically, and numerically sound understand-
118 ing of how the functional response is employed and how it could best be implemented
119 in marine ecological models to represent grazing. We begin with a derivation of each func-
120 tional response type in an explicitly aquatic context (**Section 2**), before reviewing their
121 mathematical influence on population stability (**Section 3**). Next, we survey the litera-
122 ture to assess the range of parameter values that have been estimated empirically and

123 used prescriptively in models (**Section 3**). Finally, we conduct a suite of simulations to
 124 isolate the sensitivity of phytoplankton population size and stability to the parameter-
 125 ization of the functional response using four different combinations of response type (i.e.
 126 II vs. III) and parameter scheme (i.e. disk vs. Michaelis-Menten) (**Section 4**). We con-
 127 clude with a set recommendations for the formulation of grazing based on the evidence
 128 presented (**Section 5**). These recommendations are tailored to the representation of graz-
 129 ing in marine biogeochemical models, but are broadly applicable to much wider usage
 130 of the functional response across most marine and many terrestrial applications.

131 2 Derivation of the grazing formulation

132 In marine biogeochemical modelling, the rate at which phytoplankton are grazed
 133 by zooplankton is generally expressed as the grazing rate (G) in units of phytoplankton
 134 concentration lost per unit time (e.g. $\frac{mmolC}{m^3d}$). This grazing rate is equal to the prod-
 135 uct of the ambient zooplankton concentration, $[Z]$, and the zooplankton specific graz-
 136 ing rate (g), often referred to as the ingestion rate (Franks et al., 1986; Gentleman & Neuheimer,
 137 2008), which describes the concentration of phytoplankton grazed per unit zooplankton
 138 per unit time, reducing to units of one over time (e.g. $1/d$), such that

$$G = g[Z] \quad (1)$$

139 To account for the intuitive fact that grazing is easier when phytoplankton are more
 140 abundant, the zooplankton specific grazing rate, g , must vary with the ambient phyto-
 141 plankton concentration, $[P]$. The mathematical formula that describes these relation-
 142 ships is known as the functional response.

143 Buzz Holling originally derived the functional response by assuming there was a
 144 fixed time interval, T , over which predator and prey were exposed (e.g. same location,
 145 same time, predator is awake), and that predators were assumed to exclusively be cap-
 146 turing (e.g. searching, encountering, hunting, attacking) (T_{cap}) or consuming (e.g. killing,
 147 handling, processing, eating, digesting) prey (T_{con}) during this interval (Holling, 1959a),
 148 such that

$$T = T_{cap} + T_{con}. \quad (2)$$

149 The canonical type I, II, and III functional responses (**Fig. 1a**) were consequently
 150 derived (**Fig. 1b**) from different assumptions (**Fig. 1c**) about the efficiency of the cap-
 151 ture and consumption processes, the associated total time needed to capture and con-
 152 sume a given amount of prey, and how those rates and times vary with prey density (see
 153 **Table 1** for a catalogue of terms). However, prey density was originally expressed in dis-
 154 crete units of prey over a given circular area (or disk). Here, we instead provide a deriva-
 155 tion of the type I (**Section 2.2**), II (**Section 2.3**), and III (**Section 2.4**) responses ex-
 156 plicitly for aquatic systems, with example units of $mmolC$ biomass per meter cubed ($mmol/m^3$)
 157 for phytoplankton and zooplankton concentrations and days (d) for time. Further, we
 158 show how each functional response can be described by two sets of parameters, an eco-
 159 logically flavored set, in which the consumption and capture processes are explicitly pre-
 160 scribed (disk parameter scheme), and a biogeochemically flavored set, in which the sat-
 161 uration rate and half saturation concentration of the curve are explicitly prescribed (Michaelis-
 162 Menten scheme).

163 For each derivation, consider some concentration of phytoplankton, $[P_G]$ ($mmol/m^3$),
 164 that is grazed (i.e. captured and consumed) by the ambient zooplankton population, $[Z]$ ($mmol/m^3$),
 165 over the fixed grazing (or exposure) interval, T (d), at a grazing rate of $G = \frac{[P_G]}{T}$ and
 166 a zooplankton specific (i.e. considering the amount of predator present) grazing rate of

167 $g = \frac{[P_C]}{[Z]T}$. To derive each functional response type, $g([P])$, we must solve for g ($1/d$)
 168 in terms of the ambient phytoplankton population, $[P]$ ($mmol/m^3$), considering their
 169 respective assumptions regarding capture and consumption rates.

170 2.1 Type 0 response

171 A type 0 functional response is described by a straight horizontal line in which a
 172 zooplankton specific grazing rate is invariant to the ambient phytoplankton population
 173 ($g([P]) = constant$, **Fig. 1**; magenta). A type 0 response is not ecologically realistic
 174 for any species, nor does it appear in any models, but for pedagogical purposes assumes
 175 that the capture process is unaffected by prey scarcity and that the consumption pro-
 176 cess is negligible.

177 2.2 Type I response

178 A type I functional response is described by a straight line (Holling, 1959b), in which
 179 the zooplankton specific grazing rate ($g([P])$) increases linearly with the ambient phy-
 180 toplankton concentration (**See Fig. 1**; black). Ecologically, a type I response assumes
 181 that zooplankton capture prey faster when it is more abundant and that the time needed
 182 to consume it is negligible compared with the time needed to capture it ($T_{cap} \gg T_{con}$).
 183 Accordingly, zooplankton can spend all of their time capturing prey, such that

$$T = T_{cap}. \quad (3)$$

184 The time, T_{cap} (d), that it takes to capture some concentration of phytoplankton,
 185 $[P_{Cap}]$ ($mmol/m^3$), can be related to the capture rate, C ($\frac{mmol/m^3}{d}$), or the concen-
 186 tration of phytoplankton captured per unit time, by the equation

$$T_{cap} = \frac{[P_{Cap}]}{C}, \quad (4)$$

187 The capture rate can then be decomposed into the product of the ambient zooplank-
 188 ton concentration, $[Z]$ ($mmol/m^3$), and the zooplankton specific capture rate, E ($1/d$),
 189 which describes the concentration of phytoplankton captured per unit zooplankton per
 190 unit time, such that

$$C = E[Z]. \quad (5)$$

191 Depending on the zooplankton in question, the zooplankton specific capture rate,
 192 E ($1/d$), can represent a passive encounter rate (e.g. filter feeding) or an active search
 193 and attack rate (e.g. hunting), but does not include the time required to consume phy-
 194 toplankton once captured. Either way, E ($1/d$) is assumed to increase linearly with the
 195 ambient phytoplankton concentration, $[P]$ ($mmol/m^3$), to account for the fact that zoo-
 196 plankton are stochastically more likely to encounter and capture phytoplankton at higher
 197 ambient phytoplankton concentrations. The rate (per unit phytoplankton) at which the
 198 zooplankton specific capture rate increases with the ambient phytoplankton concentra-
 199 tion can be considered the prey capture efficiency, ϵ ($\frac{1}{(mmol/m^3)d}$), such that

$$E = \epsilon[P]. \quad (6)$$

200 The prey capture efficiency can be thought of as the fraction of the ambient phytoplank-
 201 ton concentration captured per unit zooplankton per unit time, in which units of $\frac{(mmol/m^3)}{(mmol/m^3)^2 d}$

THE FUNCTIONAL RESPONSE OF THE GRAZING FORMULATION

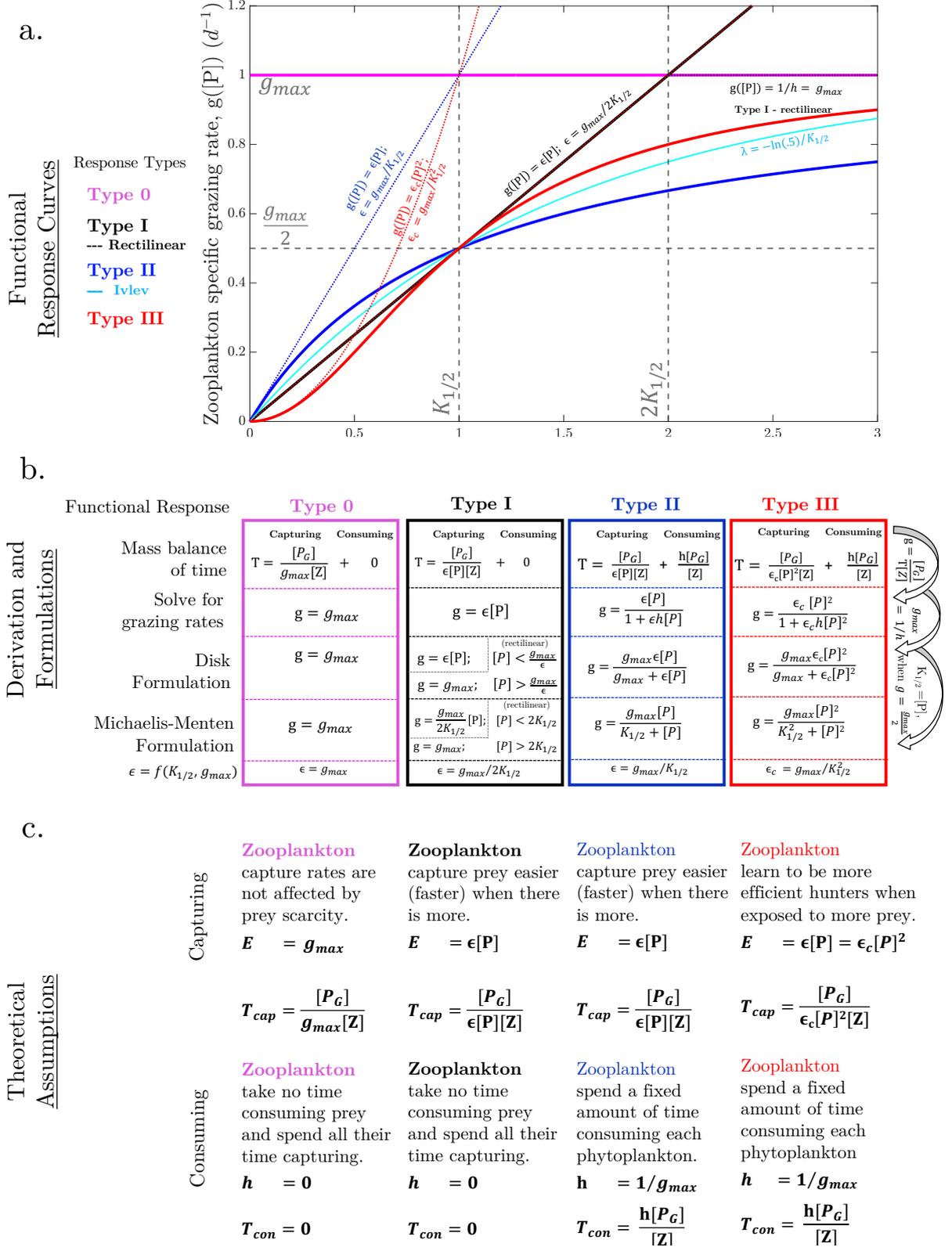


Figure 1. The functional response of the grazing formulation. **a)** The zooplankton specific grazing rate (or ingestion rate) as a function of prey density, known as the the functional response curve is plotted for type 0, I, II, Ivlev and III response types, along with notes on the associated **b)** derivation and **c)** underlying assumptions. Each response type is parameterized such that the maximum specific grazing rate, g_{max} , and the half saturation concentration, $K_{1/2}$ are equal to one. Note, this requires different parameters for the disk parameter scheme.

Variable	Notation	Conceptual Units	Reduced Units	Relevant Relationships	Description
Phytoplankton concentrations	$[P], [P_c], [P_{cap}], [P_{con}]$	$[P]$	$\frac{mmolC}{m^3}$	$[P_c] = GT = g[Z]T$ $[P_c] = [P_{cap}] = [P_{con}]$	Concentration of ambient, grazed (i.e. captured and consumed), captured, and consumed phytoplankton over the exposure period, respectively
Zooplankton concentration	$[Z]$	$[Z]$	$\frac{mmolC}{m^3}$	-	Concentration of Zooplankton biomass
Functional response	$g([P])$	-	-	$g([P]) = c[P]$ (I) $= \frac{g_{max}}{2K_{1/2}}P$ (I-Rect) $g([P]) = \frac{g_{max}c[P]}{g_{max} + c[P]}$ (II) $= \frac{g_{max}[P]}{K_{1/2} + [P]}$ $g([P]) = g_{max}(1 - e^{-\lambda[P]})$ (II-IV) $g([P]) = \frac{g_{max}c_c[P]^2}{g_{max} + c_c[P]^2}$ (III) $= \frac{g_{max}[P]^2}{K_{1/2}^2 + [P]^2}$	Functional description of how the zooplankton specific grazing rate varies with the phytoplankton concentration
Half saturation concentration	$K_{1/2}$	$[P]$	$\frac{mmolC}{m^3}$	$K_{1/2} = \frac{g_{max}}{c}$ (II-R) $K_{1/2} = \frac{2c}{g_{max}}$ (II) $K_{1/2} = -\ln(.5) \frac{1}{\lambda}$ (II-IV) $K_{1/2} = \sqrt{\frac{g_{max}}{c_c}}$ (III)	Phytoplankton concentration where $g = \frac{g_{max}}{2}$
Saturation grazing rate	g_{max}	$\frac{[P]}{[Z]time}$	$\frac{1}{d}$	$g_{max} = \frac{1}{h}$	Rate of phytoplankton consumption per unit zooplankton when food is replete
Grazing rate	G	$\frac{[P]}{time}$	$\frac{mmolC}{m^3 d}$	$G = \frac{[P_c]}{T}$ $G = g[Z]$	Rate at which phytoplankton are grazed by the zooplankton population
Phytoplankton specific grazing loss rate	l	$\frac{[P]}{[P]time}$	$\frac{1}{d}$	$l = \frac{G}{[P]}$	Phytoplankton specific rate at which phytoplankton are lost to grazing
Zooplankton specific grazing rate (i.e. ingestion rate)	g	$\frac{[P]}{[Z]time}$	$\frac{1}{d}$	$g = \frac{G}{[Z]}$	Zooplankton specific rate at which phytoplankton are grazed. The way in which g varies with $[P]$ is the functional response
Clearance rate	Cl	$\frac{[P]}{[P][Z]time}$	$\frac{m^3}{mmolC d}$	$Cl = \frac{G}{[P][Z]}$ $Cl = \frac{g}{[P]}$	Phytoplankton specific rate at which phytoplankton are grazed per unit zooplankton
Exposure period	T	$time$	d	$T = T_{cap} + T_{con}$	Fixed period over which zooplankton and phytoplankton are exposed
Capture period	T_{cap}	$time$	d	$T_{cap} = \frac{[P_c]}{[Z]c[P]}$	Time spent capturing phytoplankton
Consumption period	T_{con}	$time$	d	$T_{con} = 0$ (I) $T_{con} = \frac{h[P_c]}{[Z]}$ (II, III)	Time spent consuming phytoplankton
Capture rate	C	$\frac{[P]}{time}$	$\frac{mmolC}{m^3 d}$	$C = \frac{[P_{cap}]}{T_{cap}}$ $C = E[Z]$ (II) $C = c_c[Z]^2$ (III)	Rate at which phytoplankton are captured by the zooplankton population
Zooplankton specific capture rate	E	$\frac{[P]}{[Z]time}$	$\frac{1}{d}$	$E = \frac{C}{[Z]}$ $E = c[P]$	Specific rate at which phytoplankton are captured per unit zooplankton
Prey capture efficiency	c	$\frac{[P]}{[P][Z]time}$	$\frac{m^3}{mmolC d}$	$c = c_c[P]$ (III)	Rate at which the zooplankton specific capture rate increases with the ambient phytoplankton concentration
Prey capture efficiency coefficient	c_c	$\frac{[P]}{[P]^2[Z]time}$	$\frac{m^6}{mmolC^2 d}$	-	Rate at which the prey capture efficiency increases with the ambient phytoplankton concentration
Consumption time	h	$\frac{[Z]time}{[P]}$	d	-	Time it takes for one unit of zooplankton to eat one unit of phytoplankton
Consumption rate	$\frac{1}{h}$	$\frac{[P]}{[Z]time}$	$\frac{1}{d}$	-	Rate of phytoplankton consumption per unit zooplankton
Ivlev parameter	λ	$\frac{1}{[P]}$	$\frac{m^3}{mmolC d}$	-	Used to parameterize Ivlev equation which is qualitatively similar to a type II

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Table 1. List of terms relevant to the derivation, parameterization and context of the functional response.

202 reduce to $\frac{1}{(mmol/m^3)d}$, and reflects the efficiency with zooplankton can capture the prey
 203 they are exposed to. Note that the prey capture efficiency is variously referred to as the
 204 prey capture rate (Schartau & Oschlies, 2003b) or attack rate (Gentleman & Neuheimer,
 205 2008) and is qualitatively similar to the search area defined by Holling (1959b), but not
 206 identical for concentration-based rates.

207 Substituting **eqs. 5 & 6** into **eq. 4** yields,

$$T_{cap} = \frac{[P_{Cap}]}{[Z]\epsilon[P]}. \quad (7)$$

208 Next, we can substitute T for T_{cap} because of our assumption that no time is needed
 209 for zooplankton to consume phytoplankton (i.e. $T_{con} = 0$), and substitute $[P_G]$ for $[P_{Cap}]$
 210 because the entire concentration of phytoplankton lost to grazing, $[P_G]$, must first be cap-
 211 tured, $[P_{Cap}]$. Finally, we solve for G as a function of $[P]$,

$$G([P]) = \frac{[P_G]}{T} = \epsilon[P][Z], \quad (8)$$

212 and divide by $[Z]$ to yield the zooplankton specific grazing rate, g ($1/d$), as a function
 213 of the ambient phytoplankton concentration $[P]$, such that,

$$g([P]) = \frac{[P_G]}{T[Z]} = \epsilon[P]. \quad (9)$$

214 With **eq. 9** we have arrived at the type I functional response, wherein $g([P])$ in-
 215 creases linearly with the ambient phytoplankton concentration, $[P]$, at a rate described
 216 by the prey capture efficiency, ϵ . This type of response is akin to a food-limited system
 217 in which it takes much longer to find and capture prey than it takes to consume it, and
 218 is analogous to the classic Lotka-Volterra equations (Lotka, 1910; Volterra, 1927) used
 219 to describe simple predator-prey dynamics. Note that here the grazing rate is identical
 220 to the capture rate ($G = C$) and the zooplankton specific grazing rate is identical to
 221 the zooplankton specific capture rate ($g = E = \epsilon[P]$). This is because the entire graz-
 222 ing process is assumed to be described by the capture process; however, this is not the
 223 case for higher order functional responses, in which zooplankton are assumed to spend
 224 a non-trivial amount of time consuming phytoplankton in addition to capturing them.

225 A standard type I response may be characteristic of passive filter feeders (Jeschke,
 226 Kopp, & Tollrian, 2004), but can overestimate the zooplankton specific grazing rate of
 227 mesozooplankton such as copepods (Gentleman & Neuheimer, 2008) by over an order
 228 of magnitude compared to observations (Frost, 1972; Hansen et al., 1997) because it does
 229 not account for predator satiation at high prey densities. To account for predator sati-
 230 ation, the type I response can be extended to a rectilinear response (Chen et al., 2014;
 231 Frost, 1972; Hansen, Bjørnsen, & Hansen, 2014; Mayzaud, Tirelli, Bernard, & Roche-
 232 Mayzaud, 1998), in which $g([P])$ reaches some maximum rate, g_{max} (d^{-1}) such that

$$\begin{aligned} g([P]) &= \epsilon[P] & \text{if } [P] < \frac{g_{max}}{\epsilon} \\ g([P]) &= g_{max} & \text{if } [P] > \frac{g_{max}}{\epsilon}, \end{aligned} \quad (10)$$

233 where $\frac{g_{max}}{\epsilon}$ ($\frac{mmolC}{m^3}$) describes the prey concentration required to reach the saturation
 234 zooplankton specific grazing rate, g_{max} , for a given prey capture efficiency, ϵ .

235 Solving for $[P]$ when $g([P]) = \frac{g_{max}}{2}$ returns the half saturation concentration, $K_{1/2} =$
 236 $\frac{g_{max}}{2\epsilon}$. Note that parameterizing **eq. 10** with $K_{1/2}$ allows one to explicitly define the lo-
 237 cation of satiation using a single variable (as opposed to $\frac{g_{max}}{\epsilon}$); however, changing $K_{1/2}$
 238 for a given g_{max} implicitly alters assumptions about the prey capture efficiency.

239 2.3 Type II response

240 A type II functional response assumes a more gradual transition to satiation by em-
 241 ploying a rectangular hyperbola with downward concavity (Holling, 1959b), in which the
 242 zooplankton specific grazing rate ($g([P])$) saturates towards a maximum asymptote at
 243 high phytoplankton concentrations (**See Fig. 1**; blue). Ecologically, a type II response
 244 assumes that zooplankton capture prey faster when it is more abundant and that a fixed,
 245 non-trivial, amount of time is needed to consume it ($T_{con} > 0$), allowing for gradual
 246 predator satiation as the prey density increases and more time is need to consume all
 247 of it (Jeschke et al., 2004). Note, all assumptions about the capture process and zooplank-
 248 ton specific capture rate ($E = \epsilon[P]$) from the type I response are held.

249 The time it takes to consume the captured phytoplankton is parameterized by the
 250 consumption time, h (d), also commonly referred to as the handling time (Holling, 1959b,
 251 1965), which is assumed to be equal to the fixed amount of time it takes for one unit of
 252 zooplankton to eat one unit of phytoplankton. The total time, T_{con} (d), needed for con-
 253 sumption of the entire captured phytoplankton concentration, $[P_{Cap}]$ ($mmol/m^3$), by
 254 the ambient zooplankton concentration, $[Z]$ ($mmol/m^3$), can then be expressed as the
 255 consumption time, h , multiplied by the ratio of the concentration of phytoplankton cap-
 256 tured relative to the ambient concentration of zooplankton capturing them ($\frac{[P_{Cap}]}{[Z]}$), such
 257 that

$$T_{con} = \frac{h[P_{Cap}]}{[Z]}. \quad (11)$$

258 Remembering that all phytoplankton grazed must first be captured (i.e. $[P_G] = [P_{Cap}]$)
 259 and substituting T_{cap} and T_{con} into **eq. 2** yields

$$T = T_{cap} + T_{con} = \frac{[P_G]}{[Z]\epsilon[P]} + \frac{h[P_G]}{[Z]}. \quad (12)$$

260 Solving for the concentration of phytoplankton lost to grazing, $[P_G]$, yields the aquatic
 261 analogue to familiar disk equation, originally derived by Holling (1959b) for terrestrial
 262 predation on a planar disk,

$$[P_G] = \frac{\epsilon[P][Z]T}{1 + \epsilon h[P]}, \quad (13)$$

263 where dividing by T returns the grazing rate,

$$G = \frac{[P_G]}{T} = \frac{\epsilon[P][Z]}{1 + \epsilon h[P]}, \quad (14)$$

264 and dividing again by Z returns the zooplankton specific grazing rate, which is equiv-
 265 alent to the type II functional response,

$$g([P]) = \frac{[P_G]}{[Z]T} = \frac{\epsilon[P]}{1 + \epsilon h[P]}. \quad (15)$$

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Note that by factoring out $\epsilon[P]$ from the denominator and rearranging **eq. 15** as

$$g([P]) = \frac{1}{\frac{1}{\epsilon[P]} + h}, \quad (16)$$

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it becomes clear that the type II disk equation reduces to a type I linear Lotka-Volterra functional response when food is limiting. If the consumption rate ($\frac{1}{h}$) is much faster than the zooplankton specific capture rate ($E = \epsilon[P]$), such that $\frac{1}{h} \gg \epsilon[P]$ or equivalently $h \ll \frac{1}{\epsilon[P]}$, then **eqs. 15 & 16** reduce to $g([P]) = \epsilon[P]$ (i.e. **eq. 9**). This occurs when the consumption time, h , is very fast (i.e. type I, **Section 2.1.1**), or the phytoplankton concentration, $[P]$, is very low (i.e. a food-limited system).

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Alternatively, we see that **eqs. 15 & 16** saturate towards $g([P]) = 1/h$ when the consumption rate ($\frac{1}{h}$) is much slower than the zooplankton specific capture rate ($E = \epsilon[P]$), such that $\frac{1}{h} \ll \epsilon[P]$ or equivalently $h \gg \frac{1}{\epsilon[P]}$. This is typical of a food replete system (high $[P]$), where more food is captured as soon as the previous prey item has been consumed. The saturation grazing rate, g_{max} ($1/d$), can now be defined by the consumption rate, or one over the consumption time, such that $g_{max} = \frac{1}{h}$. Accordingly, the disk equation (**eq. 13**) can be simplified by substituting the parameter $g_{max} = \frac{1}{h}$ into **eq. 15** and multiplying by $\frac{g_{max}}{g_{max}}$ to arrive at

$$g([P]) = \frac{g_{max}\epsilon[P]}{g_{max} + \epsilon[P]} \quad (17)$$

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Henceforth, this will be referred to as the disk parameter scheme.

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Finally, **eq. 17** can be rewritten as the familiar Michaelis–Menten equation originally derived for enzyme kinetics (Johnson & Goody, 2011) (or Monod equation derived for bacterial growth (Monod, 1949)) by defining the half-saturation concentration, $K_{1/2}$ ($mmol/m^3$), in terms of parameters g_{max} and ϵ . Setting $g([P]) = \frac{g_{max}}{2}$ and solving for $[P]$, we find,

$$[P] = K_{1/2} = \frac{g_{max}}{\epsilon}. \quad (18)$$

286

Substituting $\epsilon = \frac{g_{max}}{K_{1/2}}$ into **eq. 17** and rearranging yields the familiar form,

$$g([P]) = \frac{g_{max}[P]}{K_{1/2} + [P]}. \quad (19)$$

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Henceforth, this will be referred to as the Michaelis–Menten parameter scheme.

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Eq. 19 is mathematically identical to **eq. 17**. That is, for all parameter sets $\{g_{max}, \epsilon\}$, there exists a parameter set $\{g_{max}, K_{1/2}\}$ that can identically describe $g([P])$. As with the type I response (**eq. 10**), the difference is that $\{g_{max}, \epsilon\}$ are ecologically independent, while $\{g_{max}, K_{1/2}\}$ more directly define the shape of the curve. For example, increasing g_{max} in **eq. 17** does not affect the prey capture efficiency, ϵ , but it does increase the half-saturation concentration. This makes sense ecologically, as it should require a higher phytoplankton concentration for a faster consumption time (i.e. higher g_{max}) to become limiting, given a constant prey capture efficiency. On the other hand, increasing g_{max} in **eq. 19** does not change the location of $K_{1/2}$, but implicitly assumes that the prey capture efficiency, ϵ , increases in order to maintain a constant $K_{1/2}$.

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Note, another common formulation that is qualitatively similar to the type II response is the Ivlev equation (Ivlev, 1961), where

$$g([P]) = g_{max}(1 - e^{-\lambda[P]}) \quad (20)$$

300 (Anderson et al., 2010; Edwards, Batchelder, & Powell, 2000; Franks & Chen, 2001; Shigemitsu
 301 et al., 2012). However, the Ivlev formulation is strictly empirical and cannot be derived
 302 mechanistically, but is qualitatively similar to the type II response (**See Fig. 1a**; cyan).
 303 All else being equal, the Ivlev equation will yield faster grazing rates below the half sat-
 304 uration concentration and slower grazing rates above the half saturation concentration.
 305 The half saturation point can be related to the Ivlev parameter, λ ($\frac{1}{mmol/m^3}$) as

$$K_{1/2} = \frac{-\ln(.5)}{\lambda}. \quad (21)$$

306 2.4 Type III response

307 A type III functional response is described by a sigmoidal curve (Jeschke et al., 2004),
 308 in which the zooplankton specific grazing rate ($g([P])$) increases exponentially at low phy-
 309 toplankton concentrations (**Fig. 1**; red). Ecologically, a type III response further assumes
 310 that the prey capture efficiency, ϵ ($\frac{1}{(mmol/m^3)d}$), increases with prey density. That is,
 311 the zooplankton specific capture rate, $E = \epsilon[P]$, does not just increase due to a stochas-
 312 tic increase in the likelihood of encountering phytoplankton as the ambient phytoplank-
 313 ton concentration increases, but zooplankton additionally become more efficient graz-
 314 ers as well, capturing an increasing fraction of the ambient phytoplankton concentration.

315 Mathematically, this change in behavior can be represented by assuming the prey
 316 capture efficiency, ϵ ($\frac{1}{(mmol/m^3)d}$), is a function of the ambient phytoplankton concen-
 317 tration, $[P]$. In a type III response this function is assumed to be linearly proportional
 318 to some prey capture efficiency coefficient, ϵ_c ($\frac{1}{(mmol/m^3)^2d}$), such that,

$$\epsilon = \epsilon_c[P], \quad (22)$$

319 and

$$E = \epsilon_c[P]^2. \quad (23)$$

320 By assuming that the prey capture efficiency, ϵ , increases linearly with the phyto-
 321 plankton concentration at a rate described by the prey capture efficiency coefficient, ϵ_c ,
 322 we are in turn assuming that the zooplankton specific grazing rate, E , increases quadrat-
 323 ically with the phytoplankton population (i.e. $E = \epsilon_c[P]^2$). Note that higher order func-
 324 tional responses can be achieved by modifying the relationship between the prey cap-
 325 ture efficiency and the phytoplankton concentration (e.g. $\epsilon = \epsilon_c[P]^2$).

326 Replacing **eq. 6** with **eq. 23**, and following the same derivation as **Section 2.3**
 327 yields the disk parameterization of the type III functional response,

$$g([P]) = \frac{g_{max}\epsilon_c[P]^2}{g_{max} + \epsilon_c[P]^2}. \quad (24)$$

328 As for the type II response, $g([P])$ reduces to the zooplankton specific capture rate ($E =$
 329 $\epsilon_c[P]^2$) at low phytoplankton densities and saturates towards the consumption rate ($1/h$)
 330 at high phytoplankton densities. Now, however, because the zooplankton specific cap-
 331 ture rate, E , is described by a quadratic function of $[P]$, the functional response, $g(P)$,
 332 is sigmoidal in shape (**Fig. 1a**).

333 The prey capture efficiency, ϵ , in **eq. 17** has been replaced with the prey capture
 334 efficiency coefficient, ϵ_c , in **eq. 24**, which describes how ϵ varies with $[P]$. Units of ϵ_c are
 335 non-intuitive, but can be considered as the fraction of the phytoplankton population cap-
 336 tured per unit zooplankton, per unit phytoplankton, per unit time, which reduces to $\frac{1}{(mmol/m^3)^2 d}$.

337 Finally, following identical logic to the type II response, **eq. 24** can be transformed
 338 to the Michaelis–Menten function by setting $g([P])$ equal to $\frac{g_{max}}{2}$, solving for $[P]$ to find
 339 $K_{1/2}$, and substituting the ensuing value of $K_{1/2}$ into **eq. 24**. The result is the Michaelis–Menten
 340 parameterization of the type III functional response,

$$g([P]) = \frac{g_{max}[P]^2}{K_{1/2}^2 + [P]^2}, \quad (25)$$

341 where,

$$K_{1/2} = \sqrt{\frac{g_{max}}{\epsilon_c}}. \quad (26)$$

342 Note that the Michaelis–Menten parameter scheme employs the same parameters in each
 343 response type ($K_{1/2}, g_{max}$), while the disk scheme requires a slightly different paramete-
 344 ter set in a type II (ϵ, g_{max}) and III (ϵ_c, g_{max}) response.

345 **3 Stability of the grazing formulation**

346 When these theoretical relationships are embedded into numerical models and inte-
 347 grated forward in time, the shape of the functional response curve influences the nu-
 348 merical stability of the solution (**Fig. 2**), and in turn the propensity for phytoplankton
 349 extinction (Adjou et al., 2012; Dunn & Hovel, 2020; Steele, 1974) and excitation (i.e. blooms)
 350 (Hernández-García & López, 2004; Malchow, Hilker, Sarkar, & Brauer, 2005; Truscott
 351 & Brindley, 1994; Truscott, Brindley, Brindley, & Gray, 1994). Mathematically, the first
 352 order stability of the grazing formulation ($\frac{dCl}{d[P]}$) is equal to the first derivative of the clear-
 353 ance rate (Cl), which is equal to the the functional response ($g([P])$) normalized by the
 354 ambient phytoplankton concentration (i.e. $Cl = g([P])/[P]$) (Franks et al., 1986; Gen-
 355 tleman & Neuheimer, 2008; Oaten & Murdoch, 1975). This is equivalent to the phyto-
 356 plankton specific loss rate to grazing per unit zooplankton (see **Table 1**). Ecologically,
 357 the clearance rate can be thought of as the volume of water completely cleared of phy-
 358 toplankton per unit time, per unit zooplankton, implying that at higher clearance rates
 359 individual zooplankton are either spending less time consuming their prey or more ef-
 360 ficiently capturing it.

361 In a type I functional response (**Fig. 2a-c**, black trace), clearance rates (**Fig. 2b**)
 362 are constant because it is assumed that the prey capture efficiency (ϵ) is constant and
 363 the consumption time is negligible (thus constant). In a type II response (**Fig. 2b**, blue
 364 trace), clearance rates decrease with increasing prey density because the consumption
 365 rate is no longer assumed negligible, meaning the more zooplankton graze, the more time
 366 they need to consume their food, leaving less time to capture it. In a type III response
 367 (**Fig. 2b**, red trace), clearance rates first increase, then decrease with prey density based
 368 on the balance between increasing consumption time and increasing prey capture effi-
 369 ciency.

370 First order stability is negative (**Fig. 2c**) when clearance rates decrease with in-
 371 creasing prey density ($\frac{dCl}{d[P]} < 0$), meaning that growing (decaying) phytoplankton pop-
 372 ulations are subject to decreasing (increasing) per capita grazing pressure, creating a desta-
 373 bilizing positive feedback that amplifies changes in phytoplankton growth (decay). There
 374 is negative first order stability at all prey densities in type II formulation, but only above

STABILITY OF THE GRAZING FORMULATION

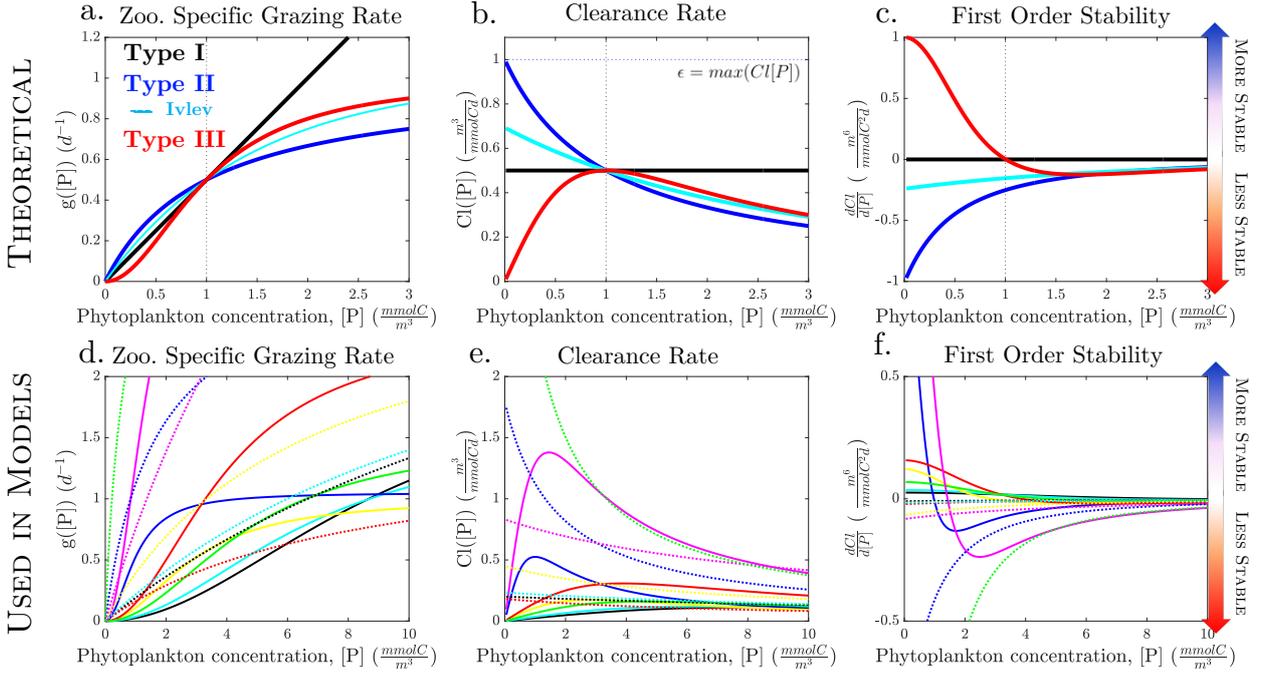


Figure 2. The stability of the grazing formulation. **a.** The zooplankton specific grazing rate ($g([P])$), **b.** clearance rate ($Cl([P]) = \frac{g([P])}{[P]}$), and **c.** first order stability ($\frac{dCl([P])}{d[P]}$) are plotted against prey density for four (**a-c**) functional response types and (**d-f**) fourteen formulation used in models. Colors corresponds to references in **Table 2**.

375 $K_{1/2}$ in type III formulations (Gentleman & Neuheimer, 2008). First order stability is
 376 positive (**Fig. 2c**, red trace) when clearance rates decrease with increasing prey density
 377 ($\frac{dCl}{d[P]} < 0$), meaning that growing (decaying) phytoplankton populations are subject
 378 to increasing (decreasing) per capita grazing pressure, creating a stabilizing negative feed-
 379 back that buffers changes in phytoplankton growth (decay). Positive first order stabil-
 380 ity only occurs below $K_{1/2}$ in type III formulations (Gentleman & Neuheimer, 2008; Oaten
 381 & Murdoch, 1975). A type I response, in which clearance rates are constant ($\frac{dCl}{d[P]} = 0$),
 382 has no first order influence on stability (**Fig. 2c**, black trace).

383 In a prognostic simulation, the first order stability of the ecosystem depends on the
 384 grazing formulation, as well as where the time-evolving phytoplankton population stands
 385 relative to $K_{1/2}$. Accordingly, the parameterization of the functional response can mod-
 386 ify first order stability directly, by changing the shape of the curve, and indirectly, by
 387 driving the size of the phytoplankton population. Increasing g_{max} or decreasing $K_{1/2}$
 388 act to both increase the non-linearity of the response curve, thereby increasing the desta-
 389 bilizing (stabilizing) influence of a type II (III) response at low $[P]$, while simultaneously
 390 increasing grazing pressure and driving phytoplankton concentrations down towards low
 391 $[P]$. At high $[P]$, above the half saturation concentration, decreasing $K_{1/2}$ reduces the
 392 first order influence on stability, but faster grazing rates associated with lower $K_{1/2}$ val-
 393 ues make it unlikely high $[P]$ will be realized. Note, in a disc scheme, $K_{1/2}$ is not param-
 394 eterizaed directly and its location varies with both parameters.

4 Parameters of the grazing formulation

4.1 Empirical estimates

Parameters of the functional response have been empirically described for a myriad of zooplankton species based on laboratory incubation and dilution experiments. Hansen et al. (1997) summarizes the findings from over > 60 zooplankton species, and Hirst and Bunker (2003) constitute a global dataset of copepods, which comprise 80% of global mesozooplankton biomass (Kiørboe, 1997). All reviewed empirical studies were fit to a type II response and parameterized with a Michaelis-Menten scheme. Combining both data sets (**Fig. 3**; filled markers), it is clear that empirical estimates of $K_{1/2}$ and g_{max} vary dramatically.

Empirical estimates of the half saturation concentration ($K_{1/2}$) vary by nearly four orders of magnitudes, ranging from $.08 - 500 \text{ mmolC}/\text{m}^3$ across zooplankton species. Estimates even vary by two to three orders of magnitude within a given species and do not exhibit a consistent allometric relationship. For example, Hansen et al. (1997) and Hirst and Bunker (2003) together reported a range of $.41 - 75 \text{ mmolC}/\text{m}^3$ in microzooplankton (e.g. ciliates and dinoflagellates) and slightly larger (and lower) range of $.08 - 74 \text{ mmolC}/\text{m}^3$ in mesozooplankton (e.g. copepods). These values extend well beyond the range of $1 - 7 \text{ mmolC}/\text{m}^3$ for microzooplankton (Gismervik, 2005; Montagnes & Lessard, 1999) and $2.5 - 25 \text{ mmolC}/\text{m}^3$ for mesozooplankton (Anderson et al., 2010) that have been reported elsewhere, and are not consistent with work suggesting that $K_{1/2}$ should increase with predator size (Ray et al., 2011). Together, it is clear that $K_{1/2}$, both at the species and population level, is very poorly constrained by even laboratory-scale observations of specific interaction, which are unlikely to translate directly to the mean state of the open ocean or models designed to replicate it (Dutkiewicz et al., 2015).

Empirical estimates of the saturation grazing rate (g_{max}), which are mathematically easier to fit to a curve, still range by three orders of magnitude, but are slightly better constrained than $K_{1/2}$. Across all species, estimates of g_{max} range from 0.02 to $45.6 \text{ (d}^{-1}\text{)}$; however, the middle 50% range from $.46$ to $3.8 \text{ (d}^{-1}\text{)}$, consistent with commonly reported values of $1 \text{ (d}^{-1}\text{)}$ for mesozooplankton (Hansen et al., 1997; Lancelot et al., 2005) and $2 - 4 \text{ (d}^{-1}\text{)}$ for microzooplankton (Edwards et al., 2000; Gismervik, 2005; Hansen et al., 1997; Leising, Gentleman, & Frost, 2003; Strom & Morello, 1998). Further, at the species level, estimates vary, on average, by half an order of magnitude less than the corresponding range of $K_{1/2}$ values (Hansen et al., 1997; Hirst & Bunker, 2003), and more importantly, do exhibit an allometric relationship (Hansen et al., 1997) consistent with the conventional wisdom that g_{max} decreases with predator size (Moloney & Field, 1989; Peters & Downing, 1984; Saiz & Calbet, 2007; Wirtz, 2013).

While the surveyed empirical studies report the parameters g_{max} and $K_{1/2}$, $K_{1/2}$ alone is not an ecologically meaningful value, but rather a mathematical description of the curve, relating the consumption and capture rates of zooplankton (see **Section 2**). It is the prey capture efficiency (ϵ) that explicitly constrains the physiological boundaries of how fast zooplankton can capture their prey. That is, for a fixed saturation grazing rate, g_{max} , $K_{1/2}$ can only decrease if ϵ increases, because zooplankton must be able to capture prey more efficiently to reach food replete conditions (i.e. saturation) at lower prey densities. Assuming a type II response, as explicitly stated by Hansen et al. (1997), the reported range of ϵ values also spans 4 orders of magnitude (**Fig. 3**; blue contours), from as slow as $\sim .003 \frac{\text{m}^3}{\text{mmolC d}}$ in some large cladocerans ($\sim 10^8 \mu\text{m}^3$) to as fast as $\sim 10 \frac{\text{m}^3}{\text{mmolC d}}$ in nanoflagellates ($\sim 10^2 \mu\text{m}^3$) as well as much larger copepods ($\sim 10^8 \mu\text{m}^3$).

4.2 Values used in models

Over 50 independent grazing formulations from 36 modelling studies were surveyed (**Table 2**, **Fig. 2d-f**, **3**; empty markers) to gauge the range of commonly prescribed pa-

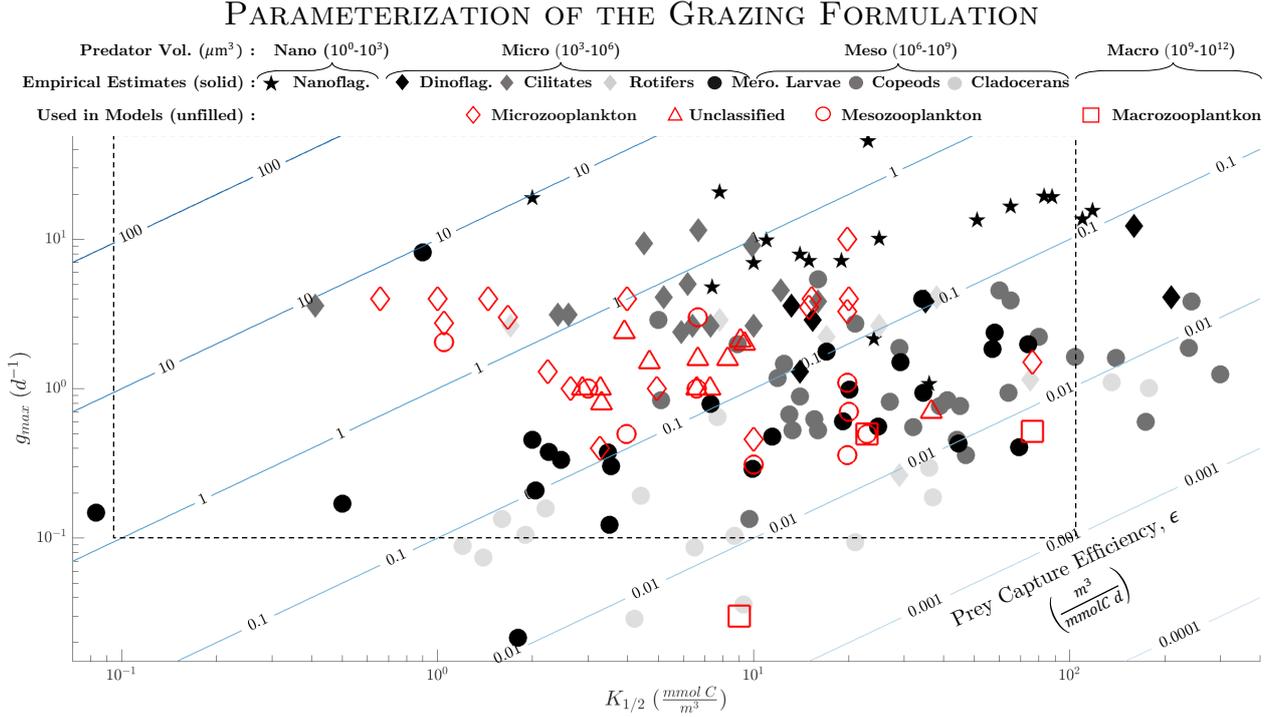


Figure 3. The parameters of the grazing formulation. Empirical estimates of parameters for >60 zooplankton species (Hansen et al., 1997; Hirst & Bunker, 2003) are plotted with filled markers. Parameters used in 36 modelling studies (**Table 2**) are plotted with empty markers. Contours for the corresponding prey capture efficiency (assuming type-II response) are overlaid. Dashed lines bound the parameter space tested in **Section 5**.

parameter values and see if they systematically vary with other aspects of the grazing formulation. A large sampling of prominent modelling studies, from canonical 0-dimensional theoretical work (Evans & Parslow, 1985; Franks et al., 1986), through slightly more sophisticated NPZD models (Fasham, 1995; Fasham et al., 1990), to state of the art climate models (Aumont & Bopp, 2006; Moore et al., 2013; Oke et al., 2013), were included. All units were converted to carbon using a standard Redfield ratio of 106:16:1, and $K_{1/2}$ was derived algebraically (see **Table 1**) when not explicitly prescribed. This survey is not comprehensive, but is sufficient to demonstrate that there is little consensus in the parameterization of prominent biogeochemical models.

While the range of g_{max} across the surveyed models is fairly well constrained between 0.5-4 ($1/d$), the range of $K_{1/2}$ spans over two order of magnitude, from as low as 0.66 mmol C/m^3 (Leising et al., 2003) to above 70 mmol C/m^3 (Newberger, Allen, & Spitz, 2003; Spitz, Newberger, & Allen, 2003). Values of $K_{1/2}$ vary with the size of zooplankton the modellers intended to represent despite no such empirical allometric relationship (Hansen et al., 1997), as well as the functional response curve and parameterization scheme they used to represent it.

Averaging across modelling studies in **Table 2** (and **Fig. 3**) that describe the size of zooplankton as microzooplankton, mesozooplankton (or copepods), or macrozooplankton, respectively, the value of g_{max} decreases with predator size from ~ 3.1 to 1.0 to $0.4 \text{ } 1/d$, while the value of $K_{1/2}$ increases with size from ~ 11 to 13 to 46 mmol C/m^3 . This is consistent with empirical observations of g_{max} in > 60 species of zooplankton, but

466 no such allometric relationship was shown for $K_{1/2}$ (Hansen et al., 1997). Zooplankton
 467 tracers without a specified size have, on average, a g_{max} of 1.4 and a $K_{1/2}$ of 7.9, lower
 468 than any specified size class. Unsurprisingly, most simulations that prescribe multiple
 469 size classes of zooplankton decrease g_{max} with predator, but lack consensus on how they
 470 treat $K_{1/2}$. Many simulation do not vary $K_{1/2}$ at all (Moore et al., 2013; Newberger et
 471 al., 2003; Spitz et al., 2003; Stock, Dunne, & John, 2014), while others vary both param-
 472 eters (Anderson et al., 2010; Denman & Peña, 2002; Le Quéré et al., 2016) or even just
 473 $K_{1/2}$ alone (Edwards et al., 2000).

474 Averaging across models that employ different functional response choices, the value
 475 of $K_{1/2}$ is, on average, three times as high in non-sigmoidal (i.e. type II or Ivlev) response
 476 types ($17.5 \text{ mmolC}/\text{m}^3$) as those with a type III response ($6.2 \text{ mmolC}/\text{m}^3$). This may
 477 be necessary to compensate for faster grazing rates at low prey concentrations without
 478 the downward concavity of the type III response. For example, the zooplankton specific
 479 grazing rate at phytoplankton concentrations of $\sim 1 \text{ mmolC}/\text{m}^3$ is roughly the same
 480 in the type II formulation of Stock, Powell, and Levin (2008) and the type III formula-
 481 tion of Hauck et al. (2013), despite the former employing $K_{1/2}$ value 2.5 times as large
 482 (**Table 2, Fig 2d**). The difference is exacerbated when considering only models with
 483 an Ivlev response which, on average, employ a $K_{1/2}$ of $42 \text{ mmolC}/\text{m}^3$, likely because the
 484 Ivlev parameter is further abstracted from an mechanistically meaningful value or in-
 485 tuitive characteristic of the curve (Gentleman & Neuheimer, 2008).

486 Averaging across models that use different parameterization schemes, but a math-
 487 ematically identical type III response, those with a disk parameter scheme have $K_{1/2}$ val-
 488 ues twice as large ($\sim 12 \text{ mmolC}/\text{m}^3$) as those that have a Michaelis–Menten param-
 489 eterization scheme ($\sim 6 \text{ mmolC}/\text{m}^3$). One explanation for this is in a disk scheme, $K_{1/2}$
 490 is dependent on two parameters (ϵ_c, g_{max}) that modify $K_{1/2}$ in opposite directions, such
 491 that low $K_{1/2}$ values are only considered with (often unrealistically) low g_{max} values. For
 492 example, in their parameter optimization routine, Schartau and Oschlies (2003a) implic-
 493 itly use a range of $K_{1/2} = 0.825 - 52 \text{ (mmolC}/\text{m}^3)$, but $K_{1/2} = 0.825$ was only tested
 494 with $g_{max} = 0.025$ yet selected the lowest possible value of $K_{1/2}$ ($6.625 \text{ (mmolC}/\text{m}^3)$)
 495 given the selected value of g_{max} ($1.575 \text{ 1}/d$).

Reference	Dimensions (P,Z tracers)	Location	$K_{1/2}$ ($mmol\ C/m^3$)	$K_{1/2}$ Relationship	Functional Response	Zooplankton Size Class	Other Parameters	
							g_{max} (1/d)	μ_{max} (1/d)
Wroblewski (1977)	2 (1P1Z)	Coastal Upwelling	76.18 ⁿ	$-ln(.5)/\lambda$	II ^t	macro	.52	2
Evans and Parslow (1985)	0 (1P1Z)	N. Atlantic	7.28 ⁿ	$K + P_{0,.66}$	II ^t	herb.	1	2
P. J. S. Franks et al. (1986)	0 (1P1Z)	-	2.25-45.7 ⁿ	$-ln(.5)/\lambda$	II ^t	copepods	.16-1.5	-
Fasham et al. (1990)	0 (1P1Z)	Bermuda (S)	6.6 ⁿ	K	II ^m	copepod	1	2.9
Frost (1993)	1 (1P1Z)	Station P	2.23	$K + P_{0,.83}$	II ^t	micro (P)	1.01-1.6	0.47-1.38
Truscott and Brindley (1994)	0 (1P1Z)	Coastal (red tide)	36.6 ⁿ	K	III ^m	-	.7	.3
Fasham (1995)	0 (1P1Z)	Station P	6.6 ⁿ , 3.82 ⁿ	$g_{max}/\epsilon, \sqrt{g_{max}/\epsilon}$	II ^d , III ^d	herb.	1	1.2
P. J. S. Franks and Chen (1996)	2 (1P1Z)	Georges Bank	22.9 ⁿ	$-ln(.5)/\lambda$	II ^t	copepods	.5	2
P. J. S. Franks and Walstad (1997)	2 (1P1Z)	-	22.9 ⁿ	$-ln(.5)/\lambda$	II ^t	copepods	.5	2
Denman and Peña (1999)	1 (1P1Z)	Station P	2.64 ⁿ	K	III ^m	micro	1	2
Edwards et al. (2000)	2 (1P1Z)	Coastal Upwelling	15.3 ⁿ , 22.9 ⁿ	$-ln(.5)/\lambda$	II ^t	micro, macro	4	2
P. J. S. Franks and Chen (2001)	3 (1P1Z)	Georges Bank	22.9 ⁿ	$-ln(.5)/\lambda$	II ^t	copepods	.5	2
Denman and Peña (2002)	1 (2P2Z)	Station P	4.95 ⁿ , 3.96 ⁿ	K	III ^m	micro, meso	1, .5	1.5
Leising et al. (2003)	0 (1P1Z)	HNLC eq. Pac.	.66 ⁿ , 1.45 ⁿ , 3.98 ⁿ , 1.45 ⁿ	$K, K + P_{0,.79},$ K, K	II ^m , II ^t , II ^m , III ^m	micro	4	1.4
Newberger, Allen, and Spitz (2003)	0 (1P1Z)	Coastal Upwelling	76.18 ⁿ	$-ln(.5)/\lambda$	II ^t	micro, macro	1.5, .52	2
Schartau and Oschlies (2003b)	3 (1P2Z)	N. Atlantic	6.672 ⁿ	$\sqrt{g_{max}/\epsilon}$	III ^d	herb	1.58	.27
Spitz, Newberger, and Allen (2003)	2 (1P1Z)	Coastal Upwelling	76.18 ⁿ	$-ln(.5)/\lambda$	II ^t	micro, macro	1.5, .52	2
Aumont and Bopp (2006) (PISCES)	3 (2P2Z)	global	20	K	II ^m	micro, meso	4, .7	.6
Vichi, Pinardi, and Masina (2007) (PELAGOS)	3 (3P3Z)	global	1.67	K	II ^m	micro	3	2
Vichi et al. (2007) (PELAGOS)	3 (3P3Z)	global	6.67	K	II ^m	meso	3	2
W. C. Gentleman and Neuheimer (2008)	0 (1P1Z)	-	4.68 ⁿ	$K, K, -ln(.5)/\lambda,$ $K + P_{0,1.3}$	III ^m , II ^m , II ^t , II ^t	-	1.5	2
Stock, Powell, and Levin (2008)	0 (3P4Z)	Low, Mid, High Productivity	3	K	II ^m	micro(10,100 μ m) meso(1e3,1e4 μ m)	10,3,3, 1.1, .36	1.1,26, .42
Sinha et al. (2010)	3 (3P2Z)	global	15	K	II ^m	micro	3.5	2,4,6
T. Anderson et al. (2010)	3 (3P2Z)	global	1.3	$K, K, -ln(.5)/\lambda$	III ^m , II ^m , II ^t	micro, meso	4.1	2,4,6
Adjou, Bendtsen, and Richardson (2012)	0 (2P1Z)	Station P	6.6 ⁿ	$K, \sqrt{g_{max}/\epsilon}$	II ^m , III ^d	herb.	1	1,2,5
Kriest, Oschlies, and Khatiwala (2012)	3 (1P1Z)	global	9.38 ^P	K	III ^m	-	2	2
Shigemitsu et al. (2012) (MEM)	3 (2P3Z)	N. Pacific	3.26 ⁿ	K	II ^t	micro	0.4	1.4
Dunne et al. (2013) (TOPAZ)	3 (1P0Z)	global	-	-	II ^t	implicit	.19	1.3
Hauck et al. (2013) (RECOM2)	3 (2P1Z)	global	3.9	\sqrt{K}	III ^m	herb	2.4	3
Moore, Lindsay, Doney, Long, and Misumi (2013) (BEC)	3 (3P1Z)	global	1.05	K	III ^m	herb.	2.05, 2.75	3
Oke et al. (2013) (WOMBAT)	3 (1P1Z)	global	9.1 ⁿ	$\sqrt{g_{max}/\epsilon}$	III ^d	herb	2.1	.6
Stock, Dunne, and John (2014) (COBALT)	3 (3P3Z)	global	8.28 ⁿ	$\sqrt{g_{max}/\epsilon}$	II ^m	sm, md, lrg	1.42, .57, .23	1.125, 1.25, .5
Dutkiewicz et al. (2015) (Darwin)	3 (8P2Z)	global	2.87	K	III ^m	sm, lrg	1	2
Le Quéré et al. (2016) (PlankTOM10)	3 (6P3Z)	S. Ocean	10,10,9	K	II ^m	proto, meso, macro	.46, .31, .03	.05, .26, .35, .44, .68, .7
Law et al. (2017) (WOMBAT)	3 (1P1Z)	global	6.57 ⁿ	$\sqrt{g_{max}/\epsilon}$	III ^d	herb (A)	1.58	1.83
Totterdell (2019) (diat-HadOCC)	3 (1P1Z)	global	3.3 ⁿ	K	II ^m	herb.	0.8	1.5

Table 2. The parameterization of the grazing formulation in biogeochemical models. The half saturation concentration, alongside other relevant information, is reported for > 50 independent grazing formulations from 36 modelling studies. Units of $K_{1/2}$ are converted to carbon from nitrogen where required using a Redfield ratio of 106:16:1 (C:N:P) and noted with the superscript ⁿ. The $K_{1/2}$ relationship algebraically relates the mathematical half saturation concentration ($g(P) = g_{max}/(2 + g(P)/K)$) to the parameters specified in the model. $P_{0,x}$ denotes a prey threshold of $g(P) = 0$ below $x\ mmol/m^3$. Michaelis-Menten (^m), disk (^d), Ivlev (ⁱ), and threshold(^t) parameterization schemes are noted in superscript above each functional response type. When an individual study includes multiple simulations or zooplankton classes with different formulations, each associated value is included in the relevant columns. Color coded rows correspond to **Fig. 2d-f**

a. The Grazing Formulation					b. Other Parameters			
	Response Type	Parameter Scheme	Parameters	Sensitivity Range		Parameter	Value	Sensitivity Range
$g([P])$	II	disk	ϵ g_{max}	$100 - 0.1 \left(\frac{m^3}{mmolCd} \right)$ $0.1 - 100 \left(d^{-1} \right)$	α	Grazing efficiency	0.7	0.35, 1.0
	III	disk	ϵ_c g_{max}	$100 - 0.1 \left(\frac{m^6}{mmolC^2d} \right)$ $0.1 - 100 \left(d^{-1} \right)$	μ_{max}	Phytoplankton maximum specific growth rate	$2 d^{-1}$	1, 4 d^{-1}
	II	Michaelis-Menten	$K_{1/2}$ g_{max}	$100 - 0.1 \left(\frac{mmolC}{m^3} \right)$ $0.1 - 100 \left(d^{-1} \right)$	m_p	Phytoplankton mortality rate	$0.1 d^{-1}$.05, 0.2 d^{-1}
	III	Michaelis-Menten	$K_{1/2}$ g_{max}	$100 - 0.1 \left(\frac{mmolC}{m^3} \right)$ $0.1 - 100 \left(d^{-1} \right)$	m_z	Zooplankton mortality rate	$0.2 d^{-1}$	0.1, 0.4 d^{-1}
					K_N	Nutrient uptake half-saturation constant	$1 \frac{mmol}{m^3}$	0.5, 2 $\frac{mmol}{m^3}$
					N_0	Nutrient density initial condition	$1.6 \frac{mmol}{m^3}$.8, 3.2, 9.6 $\frac{mmol}{m^3}$
					P_0	Phytoplankton density initial condition	$0.2 \frac{mmol}{m^3}$	0.1, 0.4 $\frac{mmol}{m^3}$
					Z_0	Zooplankton density initial condition	$0.2 \frac{mmol}{m^3}$	0.1, 0.4 $\frac{mmol}{m^3}$

Table 3. List of **a.** grazing formulations and **b.** other parameters used in NPZ (eq. 27) sensitivity analysis **Section 5.**

5 Sensitivity of the grazing formulation

To isolate the sensitivity of phytoplankton population dynamics to the functional response and its parameterization, we extend the sensitivity analysis conducted by Gentleman and Neuheimer (2008), who accessed the change in numerical stability when switching between a type II and III response or doubling/halving $K_{1/2}$ and g_{max} . In addition to the both response types, we test both parameter schemes (disk, Michaelis-Menten) and a much larger range of grazing parameters in an identical, idealized, 0-dimensional Nutrient-Phytoplankton-Zooplankton (NPZ) box model. Nutrient transfer between N, P and Z pools is described by

$$\begin{aligned}
 \frac{dN}{dT} &= (1 - \alpha)g([P])Z - \mu_{max} \frac{N}{K_N + N}P + m_pP + m_zZ, \\
 \frac{dP}{dT} &= \mu_{max} \frac{N}{K_N + N}P - g([P])Z - m_pP, \\
 \frac{dZ}{dT} &= \alpha g([P])Z - m_zZ,
 \end{aligned} \tag{27}$$

where α is the grazing efficiency, μ_{max} is the phytoplankton maximum specific growth rate, K_N is the nutrient uptake half saturation constant, m_p is the phytoplankton mortality rate, m_z is the zooplankton mortality rate, and $g([P])$ is the grazing formulation (i.e. eq. 17, 18, 24, or 25). Sampled grazing parameters are log-spaced, span 3 orders of magnitude (Table. 3a) and are representative of those that have been estimated empirically and used in previous models (Fig. 3). Non-grazing parameters are identical to Gentleman and Neuheimer (2008) (Table. 3b). We integrated each solution for 5 years and examine the final year to explain how the choice of response type, parameter scheme, and parameter values influences prescribed grazing rates (Section 5.1) and in turn drives the size (Section 5.2) and stability (Section 5.3) of the phytoplankton population. The sensitivity of our results to non-grazing parameters and initial conditions is also examined (Table 3b; Section 5.4).

5.1 Sensitivity of grazing rates

Modellers can prescribe faster grazing rates by increasing ϵ , ϵ_c , and/or g_{max} in a disk parameter scheme, or decreasing $K_{1/2}$ and/or increasing g_{max} in a Michaelis-Menten parameter scheme. However, the sensitivity of the shape of the curve (Fig. 4) and as-

521 sociated grazing rates (**Fig. 5**) to these parameters varies with the parameter scheme,
 522 response type, and the prey density (or location on the curve) in question.

523 When using a disk scheme (**Fig. 4**, green), regardless of response type, grazing rates
 524 are determined almost entirely by prey capture rates when food is scarce (Low $[P]$; **Fig.**
 525 **4**, middle row) and by consumption rates when food is replete (High $[P]$; **Fig. 4**, bot-
 526 tom row). This means that g_{max} has almost no bearing on the shape of the curve at low
 527 $[P]$ (**Fig. 4f, h**) and ϵ (or ϵ_c) has little influence on the shape of the curve at high $[P]$;
 528 (**Fig. 4i, k**). Moving from a type II (**Fig. 4**, left side) to III (**Fig. 4**, right side) response
 529 switches the description of prey capture rates from a linear to quadratic function of $[P]$
 530 (see **Section 2**), which decreases the sensitivity of grazing rates to ϵ_c (relative to ϵ), espe-
 531 cially at low $[P]$ (**Fig. e, g**).

532 When using a Michaelis-Menten parameter scheme (**Fig. 4**, magenta), grazing rates
 533 are substantially more sensitive to the parameterization of the response curve, partic-
 534 ularly in a type III response. In a type II response (**Fig. 4a, b**), grazing rates are pro-
 535 portionally, but inversely, affected by changes in $K_{1/2}$ compared to ϵ in a disk scheme
 536 (**Fig. 4a, e, i**); however, in a type III response, grazing rates are substantially more sen-
 537 sitive to $K_{1/2}$ than ϵ_c , (**Fig. 4c, g, k**), particularly at low prey densities (**Fig. 4g**). More-
 538 over, in both a type II and III response, the Michaelis-Menten scheme is dramatically
 539 more sensitive to g_{max} at low prey densities (**Fig. 4f, h**). This is because faster (slower)
 540 prey capture rates (and thus a larger prey capture efficiency, ϵ) are implicitly required
 541 for the curve to saturate at a faster (slower) grazing rate with the same half saturation
 542 concentration.

543 Computing the mean grazing rate across low ($0-0.1 \frac{mmolC}{m^3}$) and high ($2-4 \frac{mmolC}{m^3}$)
 544 phytoplankton concentrations ($[P]$) for all grazing formulations considered in our sensi-
 545 tivity analysis (**Table 3**) confirms these trends (**Fig. 5**). In a type II disk formulation,
 546 grazing rates at low $[P]$ are almost entirely unaffected by g_{max} , especially when ϵ is low
 547 (**Fig. 5a**), whereas grazing rates at high $[P]$ are almost entirely driven by g_{max} , espe-
 548 cially when ϵ is large (**Fig. 5b**). Introducing the concavity of a Type III response in-
 549 creases this disparity. In turn, the mean grazing pressure at low $[P]$ increases with ϵ_c but
 550 is effectively invariant across 3 orders of magnitude change in g_{max} (**Fig. 5c**). Alterna-
 551 tively, mean grazing rates at high $[P]$ are almost entirely described by g_{max} unless ϵ_c is
 552 so low that our definition of ‘high $[P]$ ’ no longer falls above the half saturation point of
 553 the curve (**Fig. 5d**).

554 Using a Michaelis-Menten scheme increases the sensitivity of grazing rates to both
 555 parameters (**Fig. 5e-h**), such that g_{max} has much more influence at low $[P]$ (**Fig. 5e,**
 556 **g**) and $K_{1/2}$ has more influence at high $[P]$ (**Fig. 5f, h**). However, in a type III response,
 557 grazing rates are still more sensitive to $K_{1/2}$ than g_{max} at low $[P]$ (**Fig. 5g**) and more
 558 sensitive to g_{max} than $K_{1/2}$ at high $[P]$ (**Fig. 5h**). Increased parameter sensitivity in
 559 the Michaelis-Menten scheme means that a greater variety of curve shapes and associ-
 560 ated grazing rates can be described with an equivalent range of parameter values, albeit
 561 with lower resolution.

562 5.2 Sensitivity of phytoplankton population size

563 The mean size of the phytoplankton population ($\overline{[P]}$) is largely driven by the shape
 564 of the curve at low phytoplankton concentrations and unaffected by what the curve looks
 565 like once it begins to saturate at high phytoplankton concentrations, particularly in a
 566 type III response (**Fig. 6**, left column). Considering all stable (see **Section 5.3**) solu-
 567 tions to the type III response (**Fig. 6d, j**), $\overline{[P]}$ has a much stronger correlation with mean
 568 grazing rates at low $[P]$ ($r^2 = 0.79$) than high $[P]$ ($r^2 = -0.20$). Accordingly, the sensi-
 569 tivity of $\overline{[P]}$ to the grazing formulation qualitatively mirrors the sensitivity of mean graz-
 570 ing rates at low $[P]$ to the grazing formulation (**Fig. 5, 6**, left columns). Ecologically,
 571 this implies that the size of phytoplankton populations is limited by zooplankton cap-

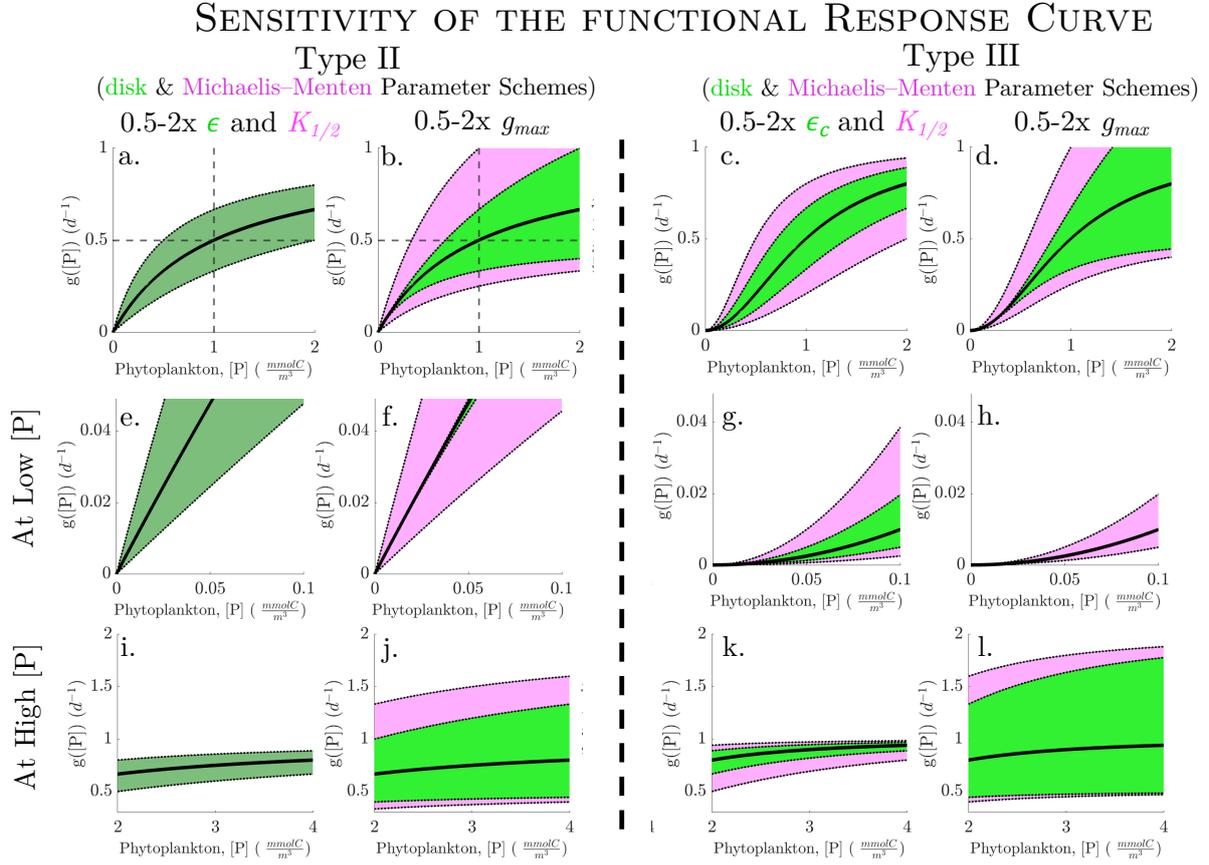


Figure 4. Sensitivity of the functional response curve to its parameters. A type II (a,b) and III (c,d) response curve is plotted in black with colored windows depicting how the curve varies with proportional changes to its parameters. Initial parameters were chosen such that the disk and Michaelis-Menten parameter schemes yield mathematical identical curves ($g_{max} = 1$, $K_{1/2} = 1$, $\epsilon = 1$, $\epsilon_c = 1$). Colored windows show how the curve varies when its parameters are individually halved or doubled within a disk (green) or Michaelis-Menten (magenta) parameter scheme. Close ups of the same curves are shown below for (e-h) low and (i-l) high phytoplankton concentrations. Note, the dark green shading in (a,e & f) indicates a complete overlap in the variability window for both parameter schemes.

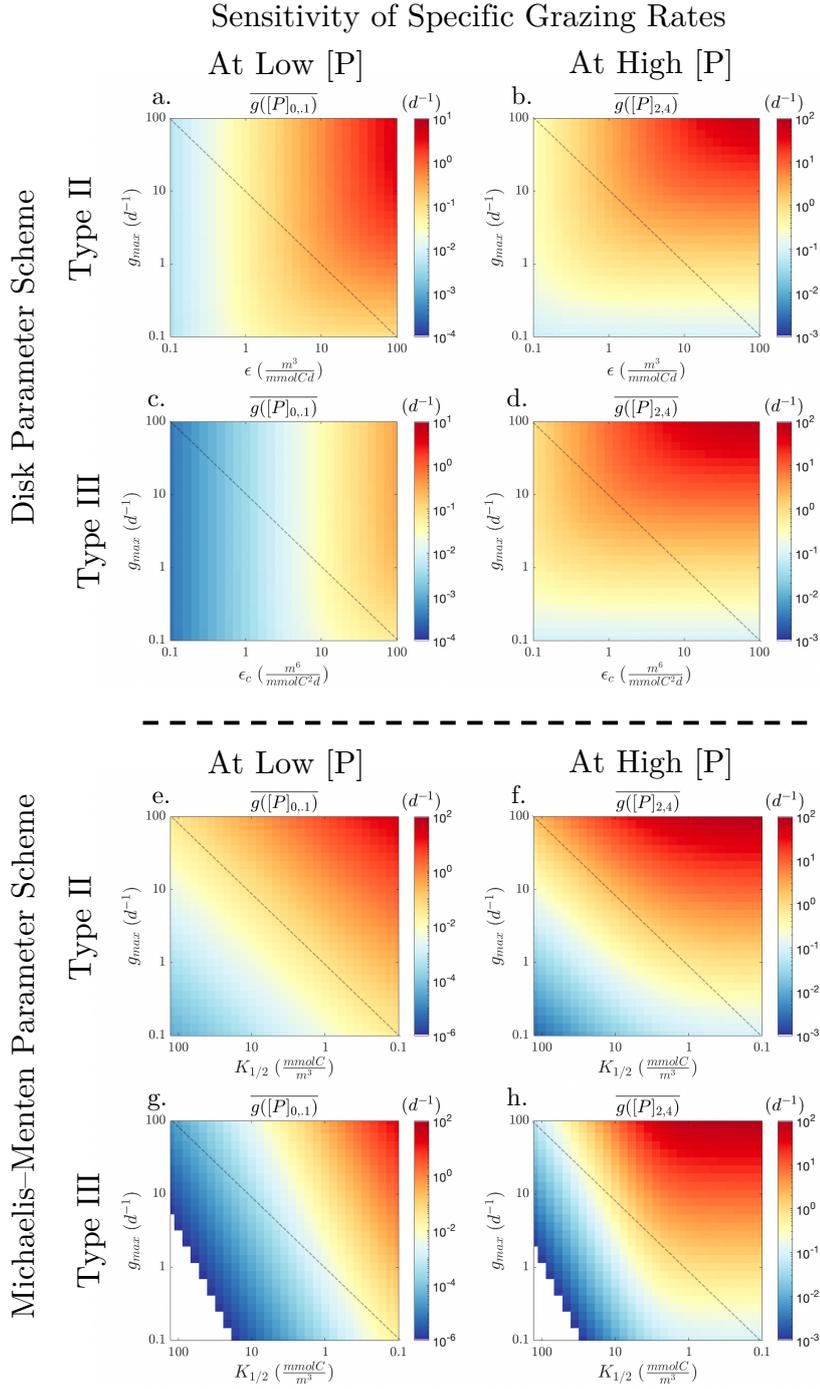


Figure 5. Sensitivity of specific grazing rates. Variability in the mean zooplankton specific grazing rate averaged across **(a, c, e, g)** low ($[P] < 0.1 \frac{mmolC}{m^3}$) and **(b, d, f, h)** high ($2 < [P] < 4 \frac{mmolC}{m^3}$) phytoplankton concentrations ($[P]$) is shown as a function of the parameters of the functional response curve using a **(a, b, e, f)** Type II and **(c, d, g, h)** Type III response type as well as a **(a-d)** disk and **(e-h)** Michaelis-Menten parameter scheme. A dashed 1-1 line is included to assess the relative parameter sensitivity.

Sensitivity of Phytoplankton Population Dynamics

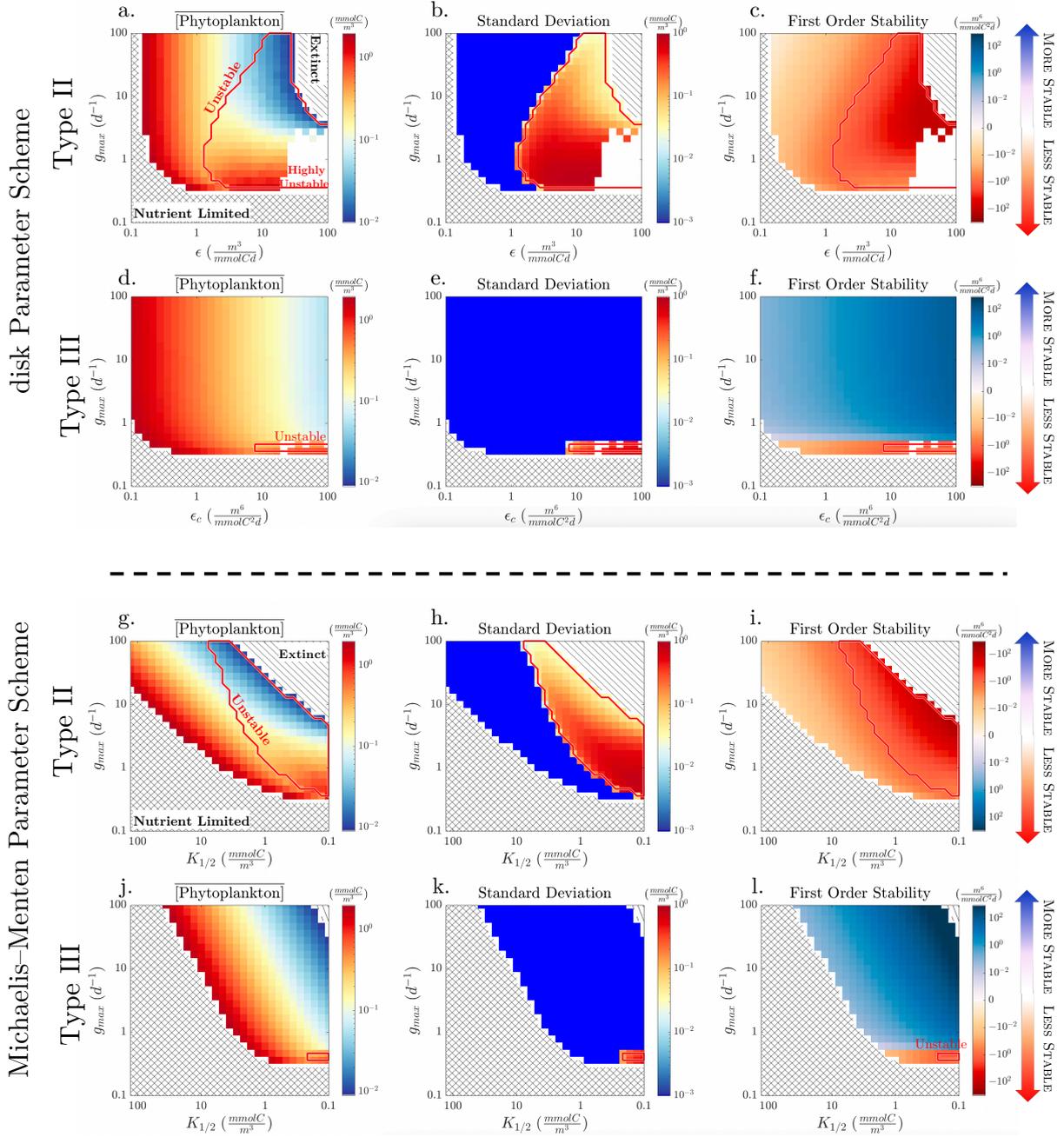


Figure 6. Sensitivity of phytoplankton population dynamics. Variability in the (a, d, g, j) mean annual phytoplankton concentration, (b, e, h, k) standard deviation, and (c, f, i, l) first order stability of the mean annual phytoplankton concentration is plotted against the parameterization of the functional response curve using a (a-c, g-j) Type II and (d-f, j-l) Type III response type as well as a (a-f) disk and (g-l) Michaelis-Menten parameter scheme. Parameter schemes that yield complete nutrient utilization or phytoplankton extinction are hatched out with cross or single lines, respectively. Numerically unstable regions are bounded with a red contour. Highly unstable regions, which yield a stiff solution, are plotted in white.

572 ture rates, which dominate when prey is scarce and the zooplankton population is small,
 573 not consumption rates, which dominate when phytoplankton is replete and the zooplank-
 574 ton population is large and therefore able to exert strong grazing pressure, regardless of
 575 the speed of zooplankton specific grazing rates.

576 In turn, $\overline{[P]}$ is most sensitive to the parameterization of the response curve when
 577 the response type and parameter scheme allow for those parameters to most efficiently
 578 describe the bottom of the response curve. This means $\overline{[P]}$ is less sensitive to the param-
 579 eterization of the functional response in a disk than Michaelis-Menten parameter scheme.
 580 For example, phytoplankton in a type III disk scheme only experienced extinction or com-
 581 plete nutrient utilization in 20% of the tested parameter space (**Fig. 6d**), compared to
 582 50% when using a type III Michaelis-Menten scheme (**Fig. 6j**). The size of the inter-
 583 mediate solution space will vary with other parameter choices and the size of the nutri-
 584 ent pool; however, the fact remains that a smaller range of parameters is needed to span
 585 from extinction to complete nutrient utilization in a Michaelis-Menten than disk scheme.
 586 Similarly, when using a type III response, $\overline{[P]}$ is more sensitive to $K_{1/2}$ and ϵ_c than g_{max}
 587 in both parameter schemes because they more directly define the shape of the response
 588 curve when prey is scarce (**Fig. 4g, h**). Together, the value g_{max} has almost no influ-
 589 ence on the size of the phytoplankton population in a type III disk scheme.

590 5.3 Sensitivity of phytoplankton population stability

591 In the simplified NPZ model, which is not forced with seasonality in light, mixing
 592 or other growth conditions, phytoplankton populations tend to quickly reach a season-
 593 ally invariant steady state. However, when a type II response is used, instabilities in the
 594 functional response often trigger sub-annual oscillations in the phytoplankton popula-
 595 tion, leading to dozens of blooms per year, and in some cases intractably stiff solutions.
 596 The strength of these oscillations can be approximated by the standard deviation of the
 597 phytoplankton population (**Fig. 6b, e, h, k**) and the stabilizing (or destabilizing) in-
 598 fluence of the function response can be approximated by first order stability of the mean
 599 phytoplankton population (**Fig. 6c, f, i, l**; see **Section 3**).

600 The phytoplankton population remains stable, with a near zero standard deviation
 601 (**Fig. 6b, e, h, k**, blue shading), when the first order stability of the mean phytoplank-
 602 ton concentration is positive or slightly negative (**Fig. 6c, f, i, l**). However, the phy-
 603 toplankton population begins to oscillate, exhibiting much larger standard deviations once
 604 the first order stability becomes sufficiently negative. Oscillations never occur when the
 605 first order stability is positive. However, it is possible for negative first order stability
 606 to produce a stable solution if other factors that can dominate the destabilizing feedback
 607 associated with grazing provide a stabilizing feedback on the phytoplankton population.
 608 These factors include nutrient limitation and the size of the zooplankton population, which
 609 both dampen phytoplankton population growth as phytoplankton biomass accumulates,
 610 even as specific grazing rates decline.

611 When using a type II response, first order stability is always negative and 30% of
 612 tested solutions exhibited a standard deviation greater than 0.5% of the total nutrient
 613 pool and were deemed unstable (**Fig. 6**; rows 1 & 3, red contour). This fraction increased
 614 to 40% when including solutions that were nominally stable but the phytoplankton pop-
 615 ulation went extinct (**Fig. 6**; single hatching). Increasing g_{max} and decreasing $K_{1/2}$ both
 616 decrease stability; however, when using a Michaelis-Menten parameter scheme, the first
 617 order stability is, on average, ~ 5 times more sensitive to changes in $K_{1/2}$ than g_{max}
 618 due to its greater influence on the curvature of the functional response. In a disk scheme,
 619 however, first order stability is only 25% more sensitive to ϵ than g_{max} , because both pa-
 620 rameters influence the location of $K_{1/2}$. Because the stability of the population is much
 621 more sensitive to g_{max} than the size of the population, relatively small changes in g_{max}
 622 can trigger sudden instabilities with little warning.

When using a type III response, first order stability is rarely negative. Only 2% of tested solutions were deemed unstable (**Fig. 6**; rows 2 & 4, red contour) and less than 1% led to phytoplankton extinction (compared to 10% with a type II). First order stability becomes increasingly stable with increasing g_{max} and decreasing $K_{1/2}$ because increasing grazing pressure drives $[P]$ below $K_{1/2}$ where the downward concavity of the response curve provides stability and protects against extinction. This holds even though decreasing $K_{1/2}$ simultaneously lowers the threshold for instability. There is only negative first order stability and oscillations in the phytoplankton population when both $K_{1/2}$ and g_{max} are very low. This occurs because as the g_{max} approaches the zooplankton mortality rate, zooplankton net population growth slows, decoupling $[P]$ and $[Z]$ and allowing $[P]$ to escape grazing pressure and exceed a low $K_{1/2}$ value.

5.4 Influence of other parameters

The sensitivity of phytoplankton population size to the grazing formulation does not appear to be qualitatively influenced by the selection of other non-grazing parameters or initial conditions (see **Table 3b**); however, these choices do influence the size of the stable solution space. Nutrient limitation is described by a type II Michaelis-Menten curve and thus has similar, but qualitatively opposite, stabilizing properties to the grazing formulation. The difference is that the saturation of nutrient uptake provides a negative, rather than positive, feedback on phytoplankton population growth. In turn, increasing the maximum phytoplankton specific division rates (μ_{max}) or decreasing the half saturation concentration for nutrient uptake (K_N) both increase the stability of the system and reduce the number of unstable solutions. On the other hand, limiting zooplankton population growth by either increasing zooplankton mortality (m_Z) or reducing grazing efficiency (α) can destabilize a type III response if $m_Z > \alpha g_{max}$, thereby decoupling specific grazing rates from bulk grazing pressure (i.e. $g[Z]$). Reallocating the initial distribution of nutrients between the $[N]$, $[P]$, and $[Z]$ pools has little effect, however, increasing the total nutrient pool increases the number of unstable solutions by diminishing the stabilizing effect of nutrient limitation.

6 Recommendations for modellers

6.1 Functional Response Choice

Use a type III rather than a type II functional response

Numerically, there is little reason to employ a type II over III response, as the type II response is more likely to trigger phytoplankton extinction or instability (**Section 5.3**). While these dynamics are not necessarily ecologically impossible for specific, regional interactions (McCauley & Murdoch, 1987), they are unlikely to characterize the mean state of many interactions in coarse, global, models, which are trained to match the mean chlorophyll concentration observed over large areas from space. To avoid complete ecosystem collapse or unnatural oscillations when a type II response is used, parameter optimization schemes are likely to favor other stabilizing processes (Edwards et al., 2000; Gentleman & Neuheimer, 2008) or large, less destabilizing $K_{1/2}$ values (**Fig. 6**). In turn, optimization schemes may also favor slower photosynthetic phytoplankton growth parameters to compensate for slower grazing, yielding a system with the correct NPP but unrealistically slow turnover, which could bias estimations of carbon transport (Henson, Le Moigne, & Giering, 2019).

Additionally, some models require a type III response to produce realistic blooms (rather than unstable oscillations) (Hernández-García & López, 2004; Malchow et al., 2005; Morozov, 2010; Truscott & Brindley, 1994; Truscott et al., 1994). This is because bloom initiation must be preceded by slow rates of wintertime net primary production to starve zooplankton and decrease their biomass (Evans & Parslow, 1985), allowing sub-

672 sequent springtime changes in phytoplankton growth rates to outpace increasing graz-
 673 ing pressure from a growing zooplankton population as the bloom develops (Behrenfeld
 674 et al., 2013). The stabilizing properties of a type III response prevent the extinction of
 675 a very small phytoplankton seed population, while starving the zooplankton population,
 676 subsequently permitting a bloom at the onset of rapid changes in bottom-up growth con-
 677 ditions.

678 Ecologically, there is disagreement on whether a type II (Hansen et al., 1997; Hirst
 679 & Bunker, 2003; Jeschke et al., 2004) or type III (Chow-Fraser & Sprules, 1992; Frost,
 680 1975; Gismervik & Andersen, 1997; Sarnelle & Wilson, 2008) response is more appro-
 681 priate. Individual interactions in laboratory dilution experiments are often better fit
 682 empirically by a type II response (Hansen et al., 1997; Hirst & Bunker, 2003), while a type
 683 III response is typically justified by more complex behavior, such as changes in prey refuge,
 684 (Wang, Morrison, Singh, & Weiss, 2009), predator learning (Holling, 1965; van Leeuwen,
 685 Jansen, & Bright, 2007), predator effort, (Gismervik, 2005), or prey switching (Gentle-
 686 man, Leising, Frost, Strom, & Murray, 2003; Oaten & Murdoch, 1975; Uye, 1986). Un-
 687 fortunately, this behavior is difficult to replicate in a lab (Leising et al., 2003) and large-
 688 scale field experiments are challenging and rare, meaning it is difficult to say definitively
 689 if zooplankton are more likely to exhibit type II or III behavior in their natural environ-
 690 ment. Moreover, dilution experiments are tailored to particular interactions in a particu-
 691 lar environment, making them less tractable to explain the statistical relationship be-
 692 tween the mean state of a limited number of zooplankton and phytoplankton functional
 693 groups represented in most marine ecosystem models.

694 There is, however, a strong mathematical justification for the use of a type III func-
 695 tional response to represent the mean state of grazing dynamics in marine biogeochemi-
 696 cal models (Englund & Leonardsson, 2008; Morozov, 2010; Morozov et al., 2008; Nach-
 697 man, 2006). Global phytoplankton distributions are highly heterogeneous at scales well
 698 below the typical resolution of even eddy-resolving ocean models (Ohman, 1990; Ray-
 699 mont, 2014). Moreover, phytoplankton and zooplankton populations are typically log-
 700 normally distributed (??), such that an increase in the mean plankton concentration is
 701 likely associated with a disproportionate increase in smaller areas of high productivity,
 702 surrounded by large oligotrophic swaths. As the relative proportion of phytoplankton
 703 in highly productive subgrid-scale patches increases, so will that of the zooplankton feed-
 704 ing in them (either via local growth or migration). This means that as the mean grid
 705 cell phytoplankton concentration increases, the mean specific grazing rate will increase
 706 multiplicatively with an increasing proportion of zooplankton grazing at increasingly fast
 707 specific rates, leading to an exponential increase at low $[P]$. Therefore, even if individ-
 708 uals are assumed to exhibit a sub grid-scale type II response, their spatially-averaged dy-
 709 namics are better described by a type III response without invoking any associated change
 710 in foraging behavior (Morozov, 2010). This is particularly relevant in the vertical direc-
 711 tion when implicitly representing diurnal vertical migration (Morozov, 2010), which zoo-
 712 plankton may use to look for better feeding opportunitites (?), but applies to horizontal
 713 distributions as well. In this way, a type III response is an ecologically justifiable way
 714 to account for coarse model resolution.

715 of the zooplankton population feeding in highly productive subgrid-scale patches
 716 is likely to increase with the productivity of those patches, either via local growth or mi-
 717 gration, the

718 Although models are largely split in their use of a type II (or Ivlev) (Aumont &
 719 Bopp, 2006; Dunne et al., 2013; Le Quéré et al., 2016; Shigemitsu et al., 2012; Stock et
 720 al., 2014; Totterdell, 2019; Vichi et al., 2007) or type III functional response (Dutkiewicz
 721 et al., 2015; Hauck et al., 2013; Law et al., 2017; Moore et al., 2013; Oke et al., 2013),
 722 there appears to ample reason to prefer a type III response. The numerical benefits of
 723 a type III response *do not* appear to be undermined by sufficient ecologically uncertainty,
 724 as there is in-situ and theoretical evidence that a type III functional response can do a

725 better job of replicating the mean state of a complex, patchy ocean, even if individual
 726 interactions are better represented by a type II response (Morozov, 2010; Morozov et al.,
 727 2008; Nachman, 2006). Note that this argument does not extend to type II response func-
 728 tions with an imposed feeding threshold, which behave more like a type III response (Leis-
 729 ing et al., 2003) and were not considered explicitly here.

730 6.2 Parameter Scheme

731 *Use a Michaelis–Menten rather than a disk parameter scheme*

732 Throughout the literature, the type II and type III functional response appear in
 733 two distinct, but mathematically equivalent, forms (**Table 2**): the disk parameter scheme
 734 (**eq. 17, 24**) (e.g. Fasham (1995); Adjou et al. (2012); Fasham (1995); Law et al. (2017);
 735 Oke et al. (2013); Schartau and Oschlies (2003b)) and the Michaelis–Menten paramete-
 736 ter scheme **eq. 19, 25** (e.g. Aumont and Bopp (2006); Le Quéré et al. (2016); Stock et
 737 al. (2014); Totterdell (2019); Vichi et al. (2007); Dutkiewicz et al. (2015); Hauck et al.
 738 (2013); Moore et al. (2013)). Both parameter schemes can describe identical response
 739 curves given the right parameterization, but use different information to do so. This dis-
 740 tinction would be irrelevant if we had robust knowledge of the real parameters or infi-
 741 nite computational power to sample them all in multivariate parameter optimization schemes.
 742 Unfortunately, observations span several orders of magnitude (**Section 4**; Hansen et al.
 743 (1997)) and computational limitations exist (Matear, 1995; Neelin, Bracco, Luo, McWilliams,
 744 & Meyerson, 2010), meaning that modellers must pick a limited subset of parameters
 745 without confidence that it is inclusive of the actual values. The parameter scheme they
 746 use influences this choice.

747 When considered as two orthogonal bases, the disk parameter scheme rotates the
 748 axes to load more variance in phytoplankton population size on a single parameter, ϵ_c ,
 749 than the Michaelis–Menten scheme, which favors $K_{1/2}$, but not as dramatically. This is
 750 because phytoplankton population dynamics are primarily driven by the speed of graz-
 751 ing rates at low concentrations (**Section 5.2**), where phytoplankton predominately oc-
 752 cur (Anderson et al., 2010) and must pass through to reach higher ones. In the mech-
 753 anistically defined type III disk scheme, consumption rates (prescribed by g_{max}) have
 754 essentially no bearing on grazing rates at low $[P]$, when food is scarce; where as, in the
 755 empirically defined type III Michaelis–Menten scheme, g_{max} and $K_{1/2}$ both influence graz-
 756 ing rates at low $[P]$, because both implicitly modify ϵ_c (**Section 2.4**), although $K_{1/2}$ does
 757 so more efficiently (**Section 5.1**). Given the over parameterized and under constrained
 758 nature of marine biogeochemical models (Doney, 1999; Matear, 1995; Schartau et al.,
 759 2017; Ward et al., 2010), there is an initial appeal to the disk scheme, which consolidates
 760 variance on one of two parameters. However, there are strong mathematical and ecolog-
 761 ical arguments in favor of a Michaelis–Menten scheme.

762 Mathematically, ϵ_c , and thus phytoplankton accumulation, is actually more sen-
 763 sitive to proportional changes to $K_{1/2}$ in a Michaelis–Menten scheme than direct changes
 764 in a disk scheme (**Section 5.3**). This is because ϵ_c implicitly varies with the square of
 765 $K_{1/2}$ in a Michaelis–Menten scheme ($\epsilon_c = \frac{g_{max}}{K_{1/2}^2}$). In turn, the disk scheme is less sen-
 766 sitive to its parameterization, meaning it requires a larger range of parameters to be tested
 767 to cover the same range of solutions. For example, a conservative range of observed ϵ_c
 768 values, from $.0001-1 \frac{m^6}{mmolC^2d}$, can be span with $K_{1/2} \frac{mmolC}{m^3}$ values from 1-100 at a fixed
 769 g_{max} (**Fig. 3**). The trade off is increased precision in the disk scheme; however, the over-
 770 whelming lack of consensus on what these parameters actually are (**Section 4**), espe-
 771 cially for the mean state of the entire ocean (Moriarty et al., 2013; Moriarty & O’Brien,
 772 2012), suggests that it is more valuable to consider a wider, but lower resolution, set of
 773 parameters to avoid inadvertently constraining the parameter space, rather than trying
 774 to narrow in on an impossibly exact value. For example, the parameter search used by
 775 Schartau and Oschlies (2003a), who use a disk scheme, chose both parameter values at

776 the boundary of their search space, suggesting a wider range might have found a bet-
 777 ter solution. Practically speaking, this problem could be addressed by careful conver-
 778 sion. Modellers using a disk scheme could sub sample a wider set of coarser resolution
 779 ϵ_c values in optimization search schemes; however, modellers must select a search range
 780 for dozens, if not hundreds, of parameters, and are less likely to mistakenly constrain the
 781 parameter space if using a Michaelis-Menten scheme, which has a narrower range of real-
 782 istic parameters and much more intuitive units.

783 More importantly though, the Michaelis-Menten scheme is a more ecologically de-
 784 fensible way to describe the mean state of subgrid-scale heterogeneity. Ostensibly,
 785 the primary advantage of using a disk scheme is that it maintains the mechanistic in-
 786 tegrity of two ecologically independent rate parameters (**Section 2**). This may be valid
 787 when using a type II response to represent a specific interaction between homogeneously
 788 distributed populations, but is not when using a type III response to represent the mean
 789 state of large swaths of open ocean (per **Section 6.1**), for several reasons. First, unlike
 790 the prey capture efficiency (ϵ) used to parameterize a type II disk response, the prey cap-
 791 ture efficiency coefficient (ϵ_c) used to parameterize a type III disk response is not derived
 792 mechanistically (**Section 2**), but rather is an empirical estimate of the net influence of
 793 various possible behaviours (Gismervik, 2005; Oaten & Murdoch, 1975; van Leeuwen et
 794 al., 2007; Wang et al., 2009). Second, even in well mixed, laboratory studies, observa-
 795 tional estimates of both ϵ and ϵ_c are typically inferred empirically and fit to a Michaelis-
 796 Menten parameter scheme, not measured directly (Hansen et al., 1997; Hirst & Bunker,
 797 2003). Last, even if ϵ_c did mechanistically describe specific interactions at the species
 798 level and could be measured directly, any representation of the mean state of many het-
 799 erogeneously distributed interactions is necessarily empirical. This is important because
 800 the mechanistic assumptions underpinning the disk scheme preclude g_{max} from influenc-
 801 ing grazing rates at low $[P]$ (**Section 5.1**), where they are most important (**Section 5.2**).
 802 This makes sense in a well-mixed, mechanistic framework, because consumption rates
 803 should not influence grazing rates when capture rates are much lower (see **eq. 16**), as
 804 there is nothing to consume if it cannot first be caught. However, in a more realistic rep-
 805 resentation of the open ocean, many zooplankton are likely concentrated in small patches
 806 of high biological activity where they can graze at saturation, even when the mean grid
 807 cell phytoplankton concentration is driven down by large surrounding swaths of oligotrophic
 808 water. In turn, when representing subgrid-scale heterogeneity in an ecologically realis-
 809 tic way, changes in g_{max} should influence the mean state of grazing rates at low grid cell
 810 $[P]$, even if they don't for individual interactions. This is only possible in a Michaelis-
 811 Menten scheme.

812 Moving forward, it makes sense to converge on a best practice parameter scheme
 813 to avoid confusion in inter-model comparisons. The Michaelis-Menten scheme requires
 814 a smaller search range, uses more intuitive units, is more directly comparable to empir-
 815 ical observations, and more realistically represents the mean state of patchy biology in
 816 the open ocean.

817 6.3 Parameter Search Range

818 *Consider a wide range of $K_{1/2}$ values.*

819 Given the uncertainty in empirically estimated parameter values, it is necessary to
 820 choose a range of parameters to test in optimization routines. While population dynam-
 821 ics are less sensitive to the value of g_{max} (**Section 5.2**) and it has been better constrained
 822 by observations between $\sim 0.5-2$ ($1/d$) (**Section 3**), it is necessary to test a much
 823 wider range of $K_{1/2}$ values, which are far less constrained by observations (**Section 3**),
 824 yet more important in driving ecosystem dynamics (**Section 5.2**). Yet, when using a
 825 Michaelis-Menten parameterization, it is reasonable to ask how large a range is appro-
 826 priate, lest implicitly imposing ecologically unrealistic prey capture rates. However, there

827 are insufficient empirical, ecological, and mathematical arguments to heavily restrict the
 828 range of grazing parameters, and $K_{1/2}$ values as low as 0.1 ($\frac{mmolC}{m^3}$) and as high as 100
 829 ($\frac{mmolC}{m^3}$) should be considered.

830 Empirically, reported estimates of $K_{1/2}$ and g_{max} fit to a type II response function
 831 by Hansen et al. (1997); Hirst and Bunker (2003) combine to yield a range of ϵ that spans
 832 4 orders of magnitude, from .003 to $10 \frac{m^3}{mmolC d}$ (**Section 3.1; Fig. 3**). Moreover, if a
 833 type III response had been assumed, $K_{1/2}$ estimates would remain similar while the range
 834 of ϵ_c would increase to nearly 7 orders of magnitude, from .00001 to $21 \frac{m^6}{mmolC^2 d}$, or roughly
 835 1 order of magnitude slower and 3 orders of magnitude faster than the range tested in
 836 the parameter optimization search of Schartau and Oschlies (2003a) ($0.00056 < \epsilon_c <$
 837 $.0364$). At the species level, the range of plausible $K_{1/2}$ values appears largely uncon-
 838 strained by empirical estimates of ϵ_c .

839 Ecologically, we simply do not have a firm understanding of how myriad complex
 840 interactions combine across innumerable zooplankton species and evolve over time to yield
 841 a reasonable approximation of the mean state. For instance, juvenile zooplankton have
 842 different metabolic rates (Clerc, Aumont, & Bopp, 2021) and graze with $K_{1/2}$ an order
 843 of magnitude smaller than adults (Hirst & Bunker, 2003; Richardson & Verheye, 1998),
 844 suggesting the apparent $K_{1/2}$ of the community could be substantially lower during spawn-
 845 ing events. On the other hand, filter feeders, such as salps and larvaceans, that are typ-
 846 ically common in low chlorophyll waters, have a much smaller $K_{1/2}$ than euphausiids and
 847 copepods that graze in high chlorophyll waters (Hansen et al., 1997; Hirst & Bunker, 2003).
 848 If species with slower $K_{1/2}$ values dominate in more productive ecosystems, such that
 849 $K_{1/2}$ increases with chlorophyll (Chen et al., 2014), that would effectively raise the ap-
 850 parent global mean $K_{1/2}$ value. In turn, the community-wide $K_{1/2}$ value probably varies
 851 spatially and temporally depending on the zooplankton community present and whether
 852 it is dominated by juveniles or adults, such that the mean state of a population with shift-
 853 ing age and species distributions could have an apparent $K_{1/2}$ value much different than
 854 any individual within.

855 Mathematically, it is not just the ecosystem complexity that is poorly resolved in
 856 models, but also its spatial heterogeneity. The ocean is notoriously patchy (Ohman, 1990;
 857 Raymond, 2014), meaning that the phytoplankton concentration in many of the areas
 858 within a grid cell is likely to be much lower than the most productive regions within it.
 859 This means that the phytoplankton density the average zooplankton experiences is larger
 860 than the grid cell mean, which is averaged across many square kilometers of implicitly
 861 less productive water (??). In turn, the mean grazing rate is largely responding to the
 862 activity in small but productive regions, while the mean phytoplankton concentration
 863 is diluted by large, less productive regions, effectively decreasing the spatially averaged
 864 $K_{1/2}$ value well below what might be expected for any individual. This further increases
 865 the range of possible $K_{1/2}$ values below even the fastest prey capture rates inferred from
 866 dilution experiments with homogeneous phytoplankton concentrations.

867 Together, there appears to be little empirical, ecological, or mathematical evidence
 868 to constrain the parameterization of $K_{1/2}$ on the basis of implied unrealistic ϵ_c values.
 869 We thus recommend testing a broad range of $K_{1/2}$ values, particularly lower end, in pa-
 870 rameter optimization routines.

871 **6.4 Implications for other models**

872 We focus on grazing in marine biogeochemical models, but these recommendations
 873 apply to a much broader range of marine and terrestrial ecological models. Most mod-
 874 els in marine and terrestrial systems that involve predator-prey interactions use type I,
 875 type II or type III functional responses. We found that when trying to implicitly rep-
 876 resent subgrid-scale heterogeneity, a type III (**Section 6.1**) Michaelis-Menten response

(**Section 6.2**) parameterized with a lower than-expected $K_{1/2}$ value (**Section 6.3**) is the most ecologically defensible way to describe the mean state of patchy predator and prey populations, even if individual interactions are best described by a type II disk response, parameterized with higher $K_{1/2}$ values. In the ocean, this would apply to most higher trophic levels simulated in size spectrum (Heneghan et al., 2020; ?), population (Alver et al., 2016), ecosystem (Butenschön et al., 2016; ?) and fisheries models (Maury, 2010; Tittensor et al., 2018, 2021). Fish, for instance aggregate in schools and feed on sparse, but consolidated, patches of prey. These distribution are in turn reflected in global fishing effort (Kroodsma et al., 2018). On land, plants and animals are also patchy in time and space, with high prey concentration rare. Most abundance data for marine and terrestrial species are overdispersed and/or have an excess of zeros, implying there is a long tail to the right of low abundances (?). The mean state of any of these systems, is likely best represented by a low- $K_{1/2}$, type III, Michael-Menten response; however, the range of possible $K_{1/2}$ considered should increase with the number of unique species, interactions, and stages of life history being averaged into individual pools.

On the other hand, specific, well understood interactions in local, well mixed systems, may be better represented by a type II disk response, provided there is a low amount of implicit averaging at the species and spatial level. At the species level, this may include models of simple systems with fewer species, such as lakes or polar regions rather than rain forests or coral reefs, or models of more complex systems, but with many explicitly resolved predator groups. At the spatial level, this may include the oligotrophic gyres in the ocean and grasslands or boreal forests on the land. Still, modellers should consider how much implicit averaging is baked into their model and consider if it warrants a more empirical approach before choosing a mechanistic framework (disk) or response type (II) better suited for specific interaction.

7 Conclusions

In marine biogeochemical and ecological modelling, the transfer of carbon and nutrients between trophic groups, particularly from phytoplankton to zooplankton via grazing, is typically represented with one of two functional response curves, originally derived to described terrestrial predatory-prey interactions. However, we find that there is little consensus across biogeochemical models regarding: **I**) which response type to use (II vs. III); **II**) whether to describe that curve with mechanistic (disk scheme) or empirical parameters (Michaelis-Menten scheme); and **III**) what parameter values to use.

To converge on a set of best practices with theoretical clarity, we derived the functional response equations explicitly for a 3-dimensional marine system. Next, we surveyed the literature and found little convergence in the formulation or parameterization of these equations, both when estimated empirically in experiments and when employed prescriptively in models, with values ranging over 3 to 4 order of magnitude. To address the extensive uncertainties in the formulation of the functional response, we ran a suite of sensitivity experiments in an idealized, NPZ, box-model to illustrate how the sensitivity of population dynamics to the parameterization of the functional response varies with the response type and parameter schemes that is used.

Collectively, we conclude that **I**) there is no ecological basis to prefer a type II response if you want to represent the mean state of multiple interaction across a diverse ecosystem distributed across a patchy ocean. Moreover, a type II response is numerically unstable when prescribed with strong grazing pressure and apt to introduce unnatural, sub-seasonal oscillations in population dynamics. Avoiding such solutions likely biases parameter optimization schemes towards slower grazing and photosynthetic division rates. **II**) Using a disk parameter scheme provides more precision, but requires a greater range of parameterizations to describe the same breadth of curves compared to the Michaelis-Menten scheme. Considering the large uncertainty in parameter values it is probably bet-

928 ter to use a coarser brush, rather than risk constraining the solution space. Moreover,
 929 it probably does not make sense to be beholden to the mechanistically defined param-
 930 eters in a disk scheme when describing the mean state of myriad interactions, which even
 931 at an individual level, are almost exclusively understood empirically. **III)** In a type III
 932 Michaelis-Menten response, phytoplankton population size and stability is more sensi-
 933 tive to the parameterization of $K_{1/2}$ than g_{max} , which is also better constrained empir-
 934 ically than $K_{1/2}$. While there is too much uncertainty in the observed parameter space
 935 to make specific parameter recommendations, parameter optimization search schemes
 936 could focus on the value of $K_{1/2}$, rather than g_{max} . Further, we recommend testing a
 937 large range of $K_{1/2}$ values without fear of invoking unrealistic prey rapture rates,
 938 noting that spatial heterogeneity will lower the apparent value of the grid cell mean.

939 Together we recommend using Type III response with Michaelis-Menten param-
 940 eter scheme, and testing a large range of $K_{1/2}$ values, particularly low ones. These rec-
 941 ommendations apply specifically to the formulation of grazing in marine biogeochem-
 942 ical models, but also apply to any effort to describe the mean state of multiple interac-
 943 tions across a large grid cell with populations assumed to have heterogeneous sub-grid
 944 cell distributions.

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