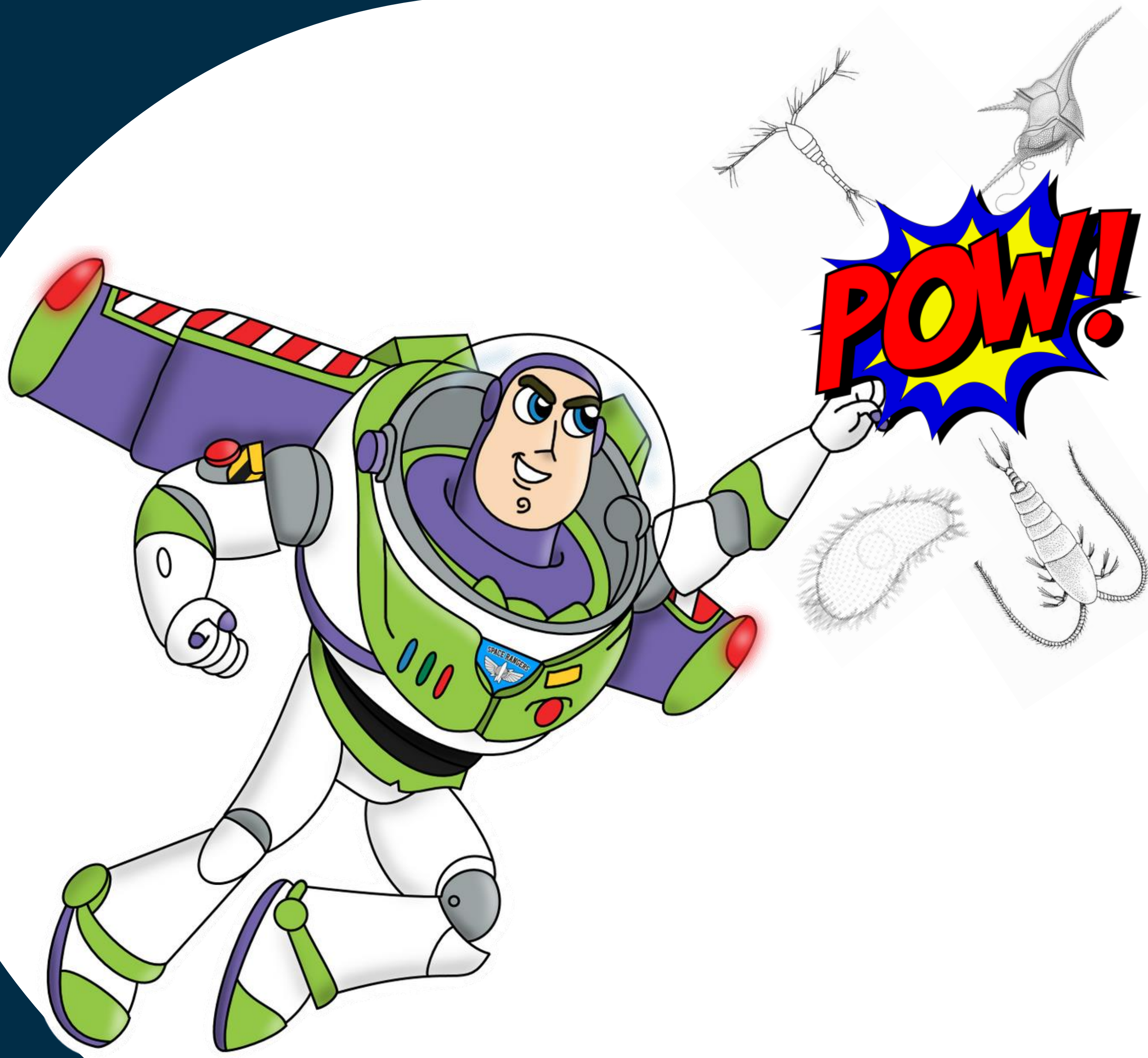
Beyond closure: Towards a world where grazing is constrained in biogeochemical models

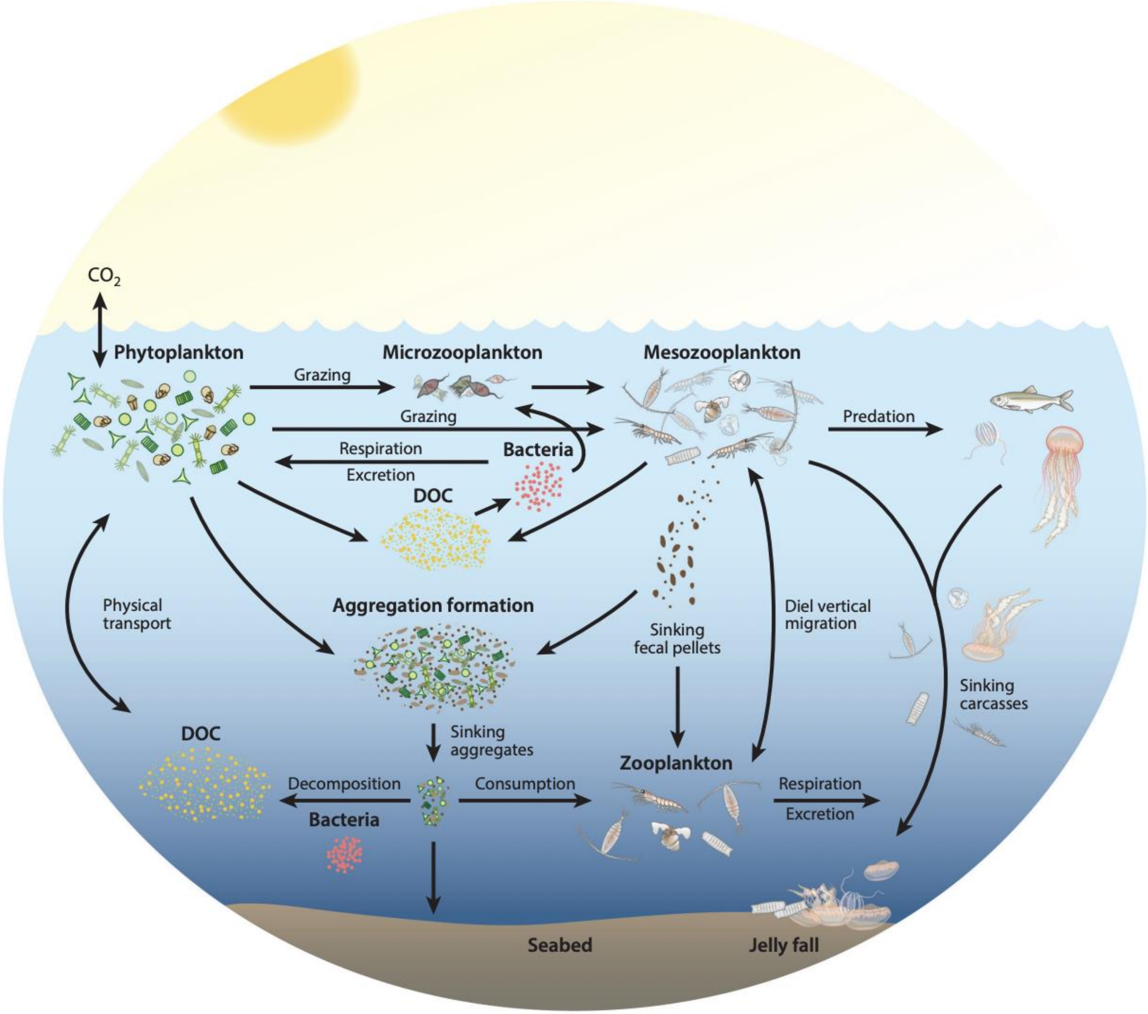


Tyler Rohr

ARC DECRA Fellow

IMAS – Lecturer in SO Biogeochemical Modelling

Zooplankton and the Marine Carbon Cycle



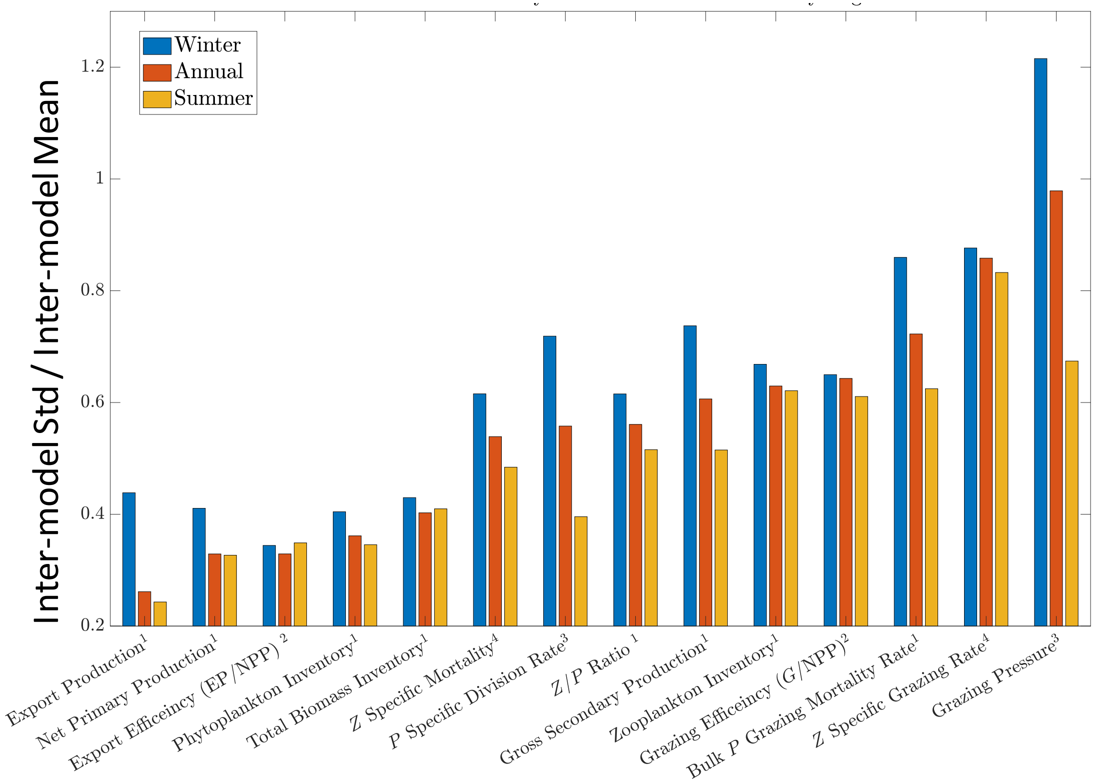
Steinberg & Landry, An. Review of Marine Science (2017)

Overview

1\. **Zooplankton grazing is the largest source of uncertainty for marine carbon cycling in CMIP6 models**

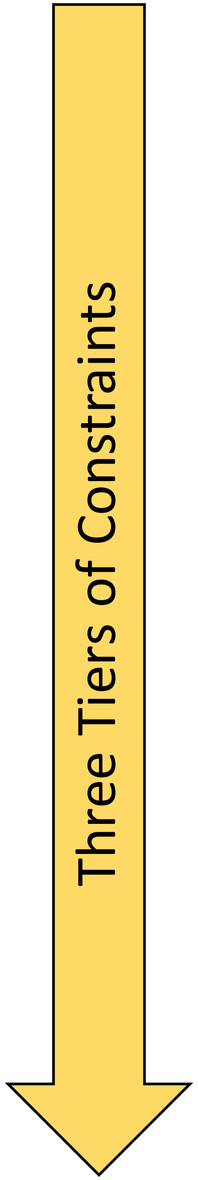
Tyler Rohr, Anthony J. Richardson, Andrew Lenton, Matthew A. Chamberlain & Elizabeth H. Shadwick

Sources of Uncertainty in
CMIP6 Marine Carbon Cycle



Rohr et al. Comm. Earth & Env (2023)

2\.



1. <u>Prescribed Properties</u>
   Compare parameters and equations to empirical observations

   e.g. $K_{1/2}$, g_{max}, <u>PGI</u>

2. <u>Emergent Properties</u>
   Compare emergent properties of model output to observed properties

   e.g. Zooplankton Biomass, <u>Grazing Pressure</u>

3. <u>Emergent Relationships</u>
   Compare emergent relationships in model to observed relationships

   e.g <u>Community-integrated functional response</u>

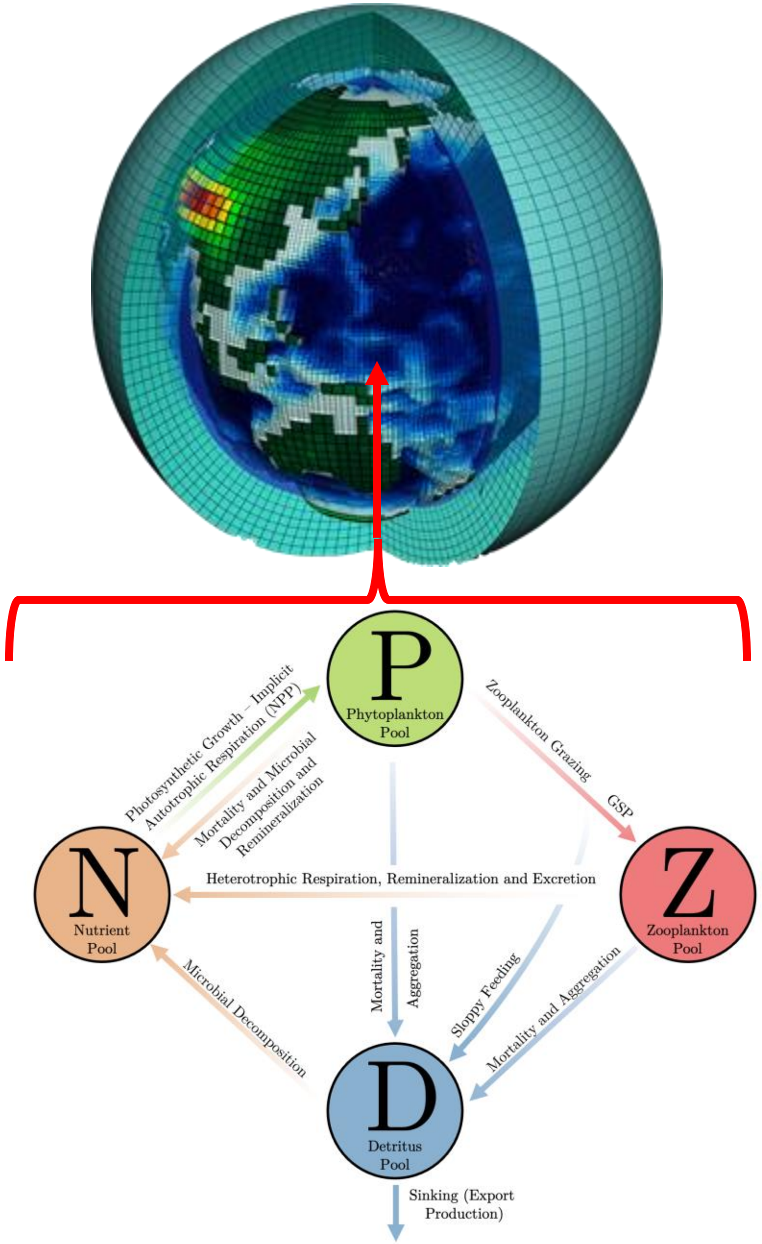
Appendix 1 – Models

Earth System Models

- Slice the Earth up into heaps of little boxes
- Solve some of differential equations
- Transform and move mass/energy around

Marine Biogeochemical (BGC) Models

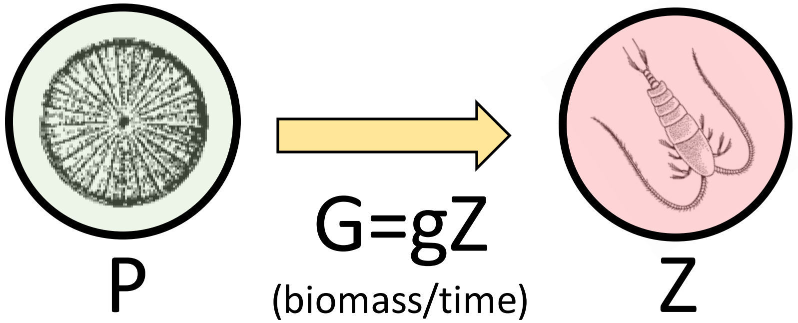
- The bit that determines how 'stuff' in the ocean biologically and chemically transforms.
- Which then gets tossed about by physics
- And allow for 2-way climate-biogeochemical feedbacks



Appendix 2 – Grazing Rate Semantics

Bulk phytoplankton loss rate to grazing (G)

- Rate all phytoplankton are killed by zooplankton
- ~Gross Secondary Production w/o the sloppy feeding



Zooplankton (specific) grazing rate (g)

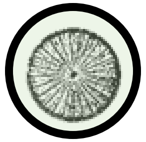
- Rate ‘individual’ zooplankton graze phytoplankton
- Phytoplankton grazed per unti zooplankton per time

g = G/ 

(1/time)

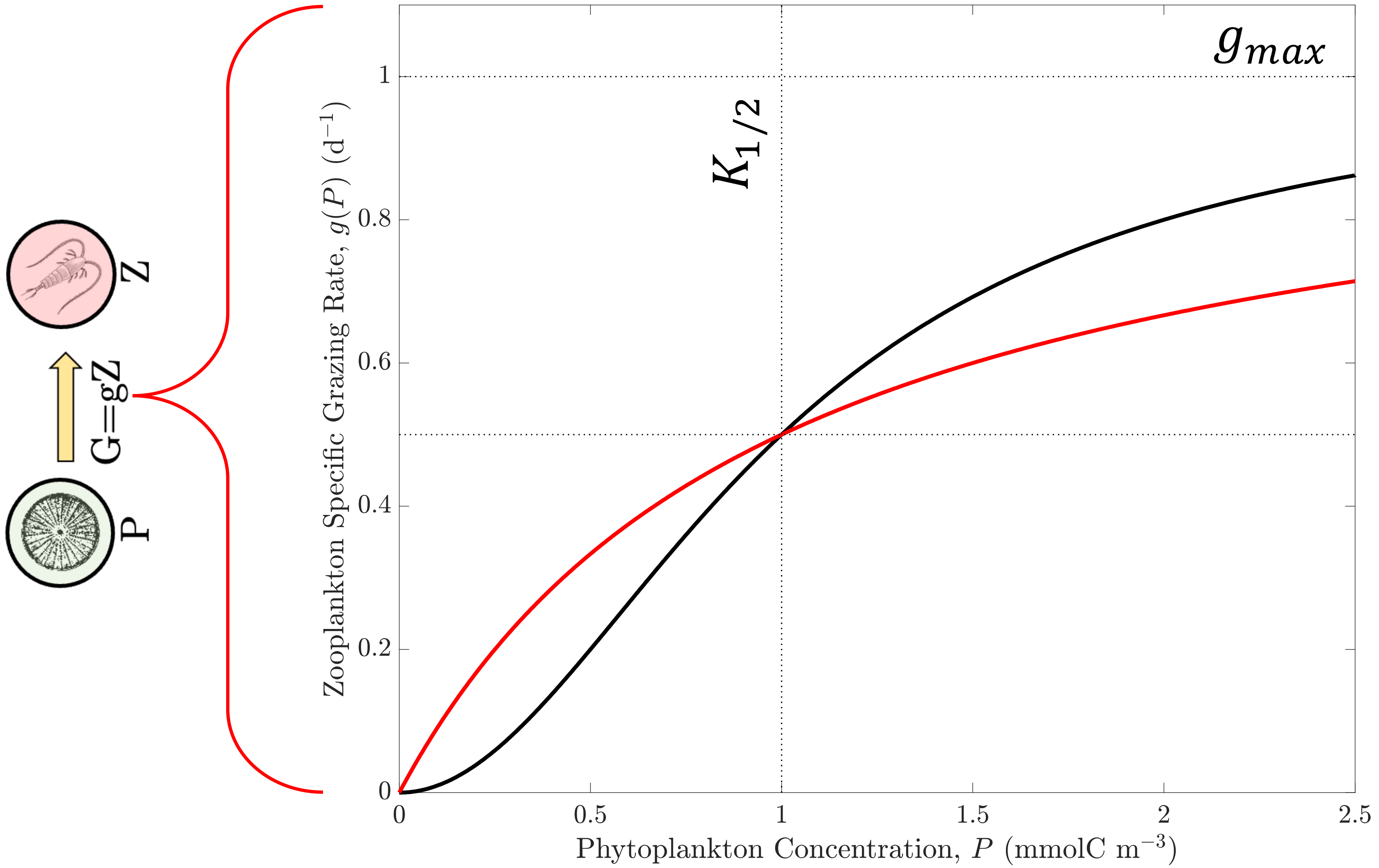
Grazing Pressure (GP)

- The phytoplankton specific loss rate to grazing
- Phytoplankton grazed per unit phytoplankton per time
- Increases with zooplankton biomass and their specific grazing rate

GP = G/ 

(1/time)

Appendix 3 – The Functional Response Curve



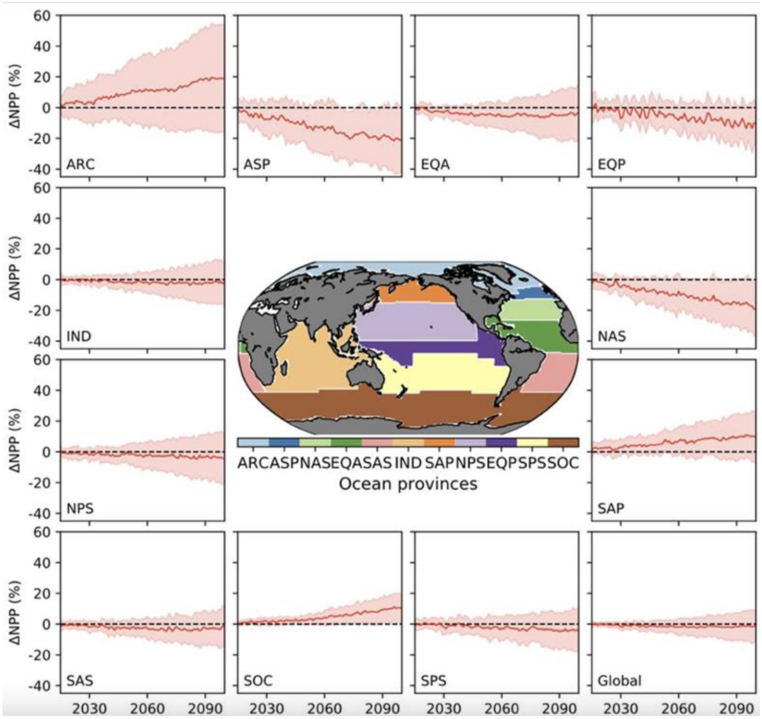
Food-replete, metabolism/digestion limited grazing rate

Food-scarce, Prey-limited grazing

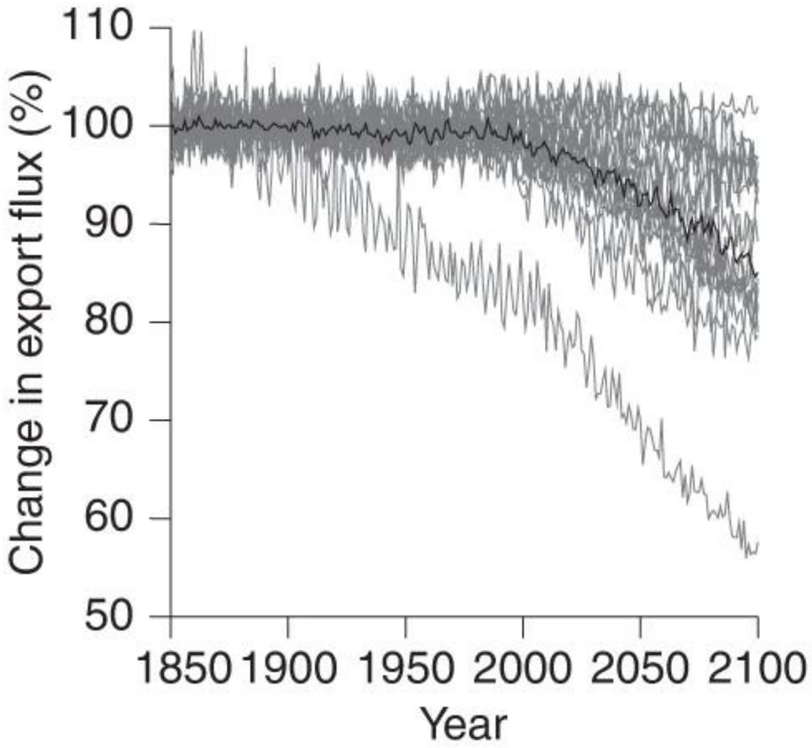
The Motivation

CMIP6 projections show persistent uncertainty in:

NPP & Export Production



Tagliabue et al., Front. in Climate (2021)



Henson et al., Front. in Climate (2021)

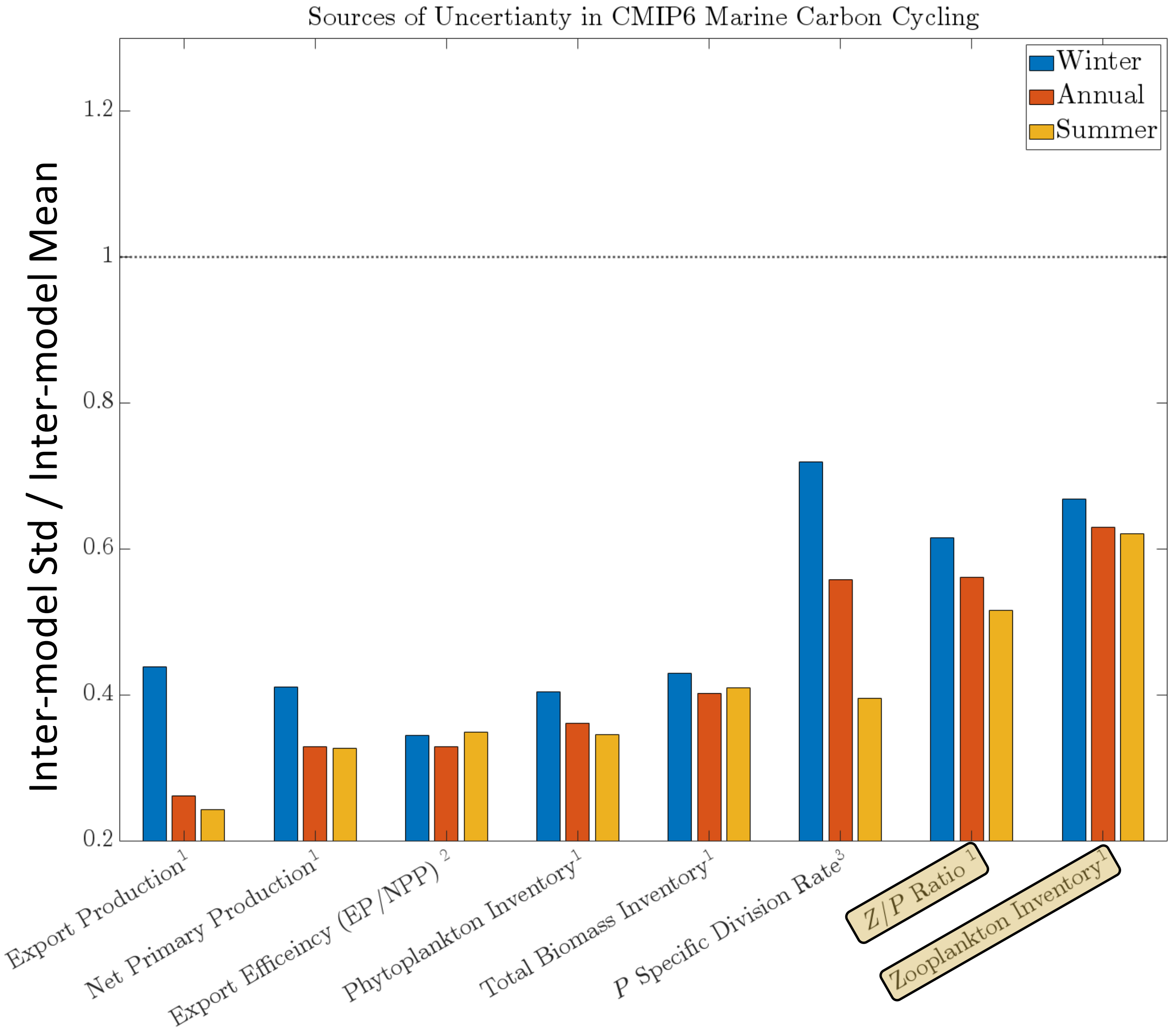
Compromising our ability to predict/prepare for future climate state and evaluate climate intervention technologies

1. The Problem

Sources of Uncertainty in CMIP6 Marine Carbon Cycle

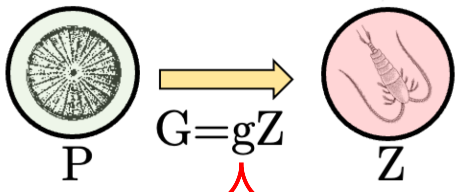
Uncertainty in projections, given the same forcing scenario, must come from uncertainty in the mechanistic meat of the model

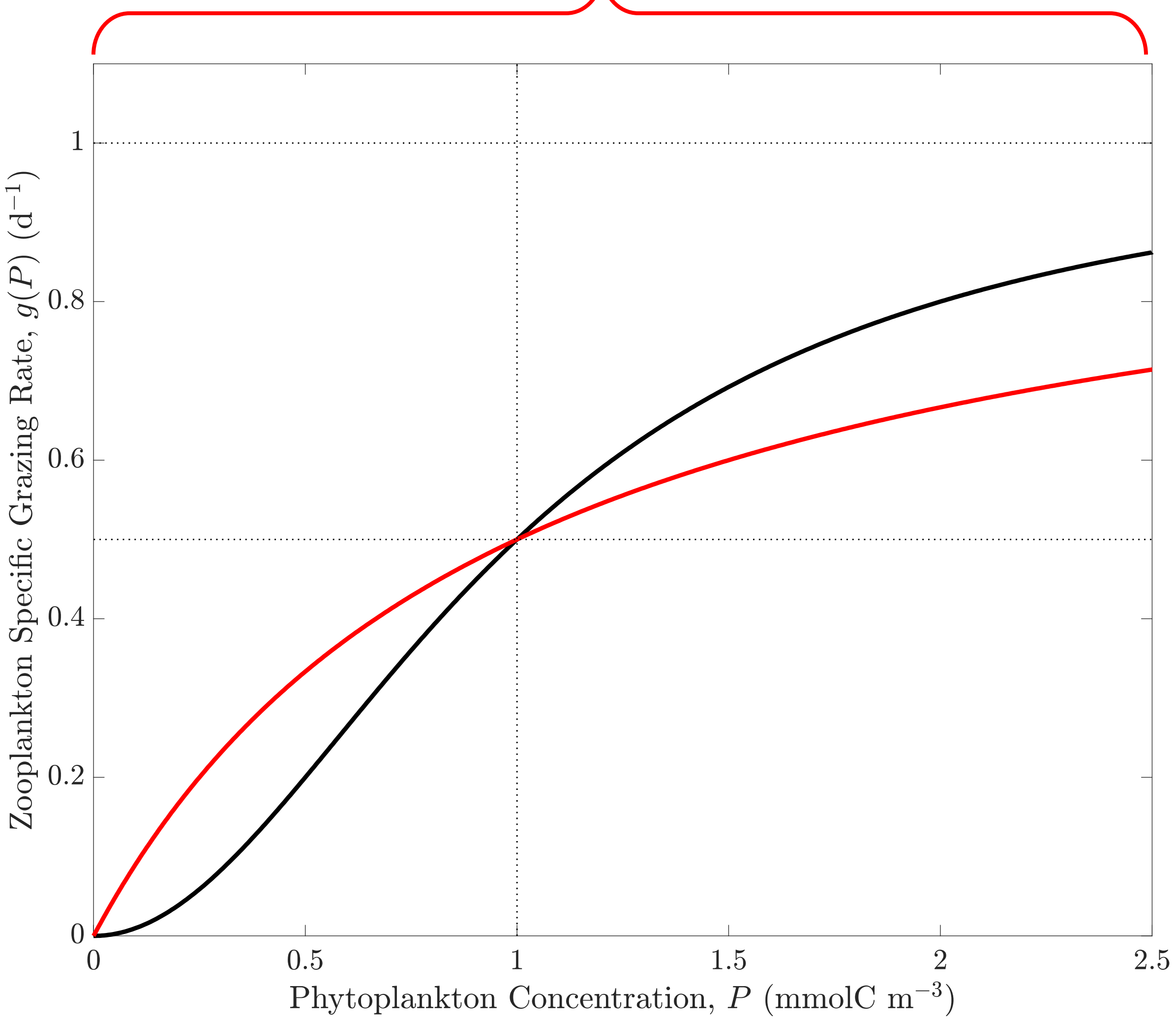
To diagnose the problem, it is useful to compare their historical runs and see how other aspects of marine carbon cylcing differ



Already, terms involving zooplankton biomass have the most uncertainty, but most models don't save any information about grazing

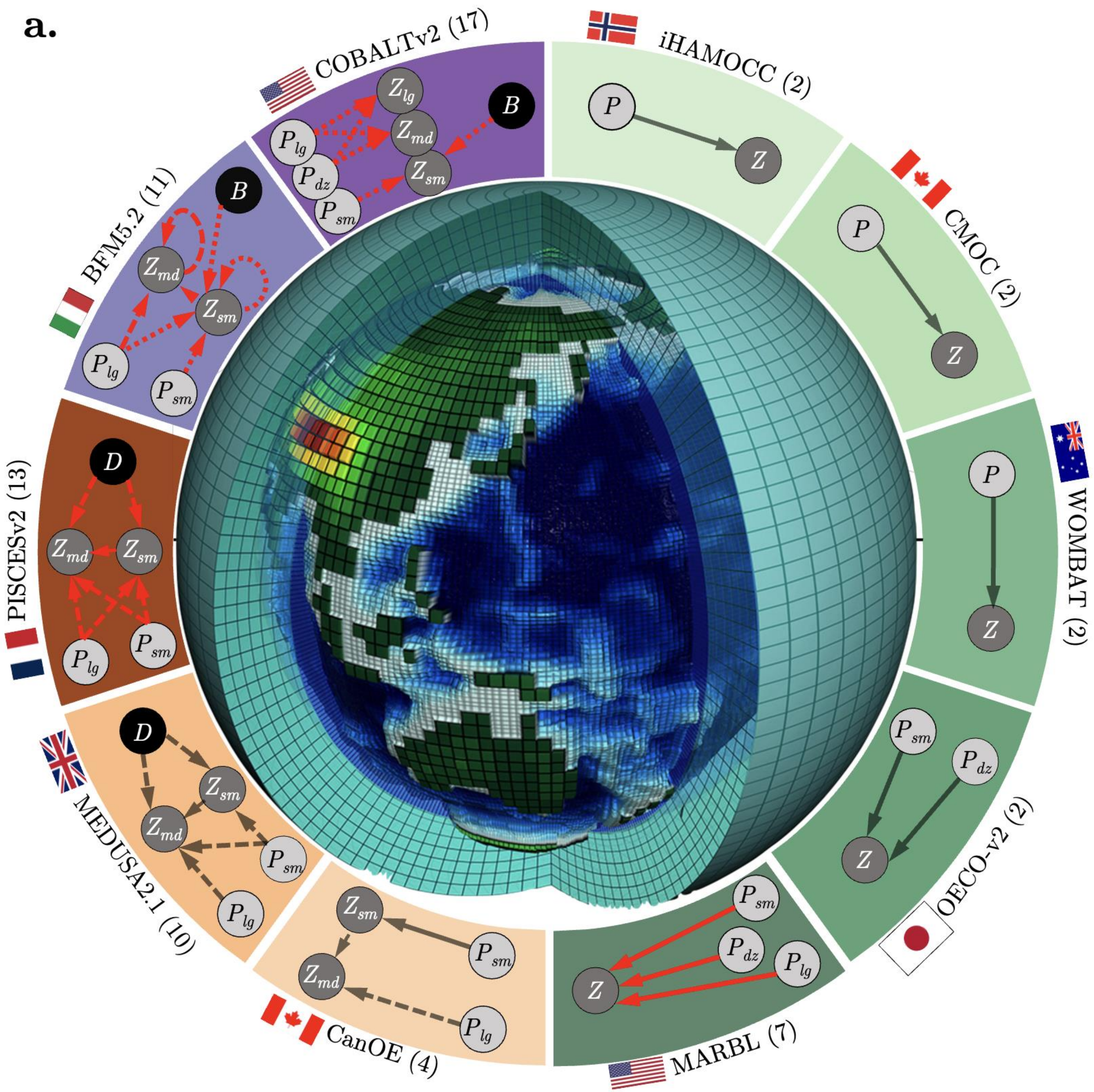
Computing Diagnostic Grazing Pressure





Computing Diagnostic Grazing Pressure

But most models aren't so simple.

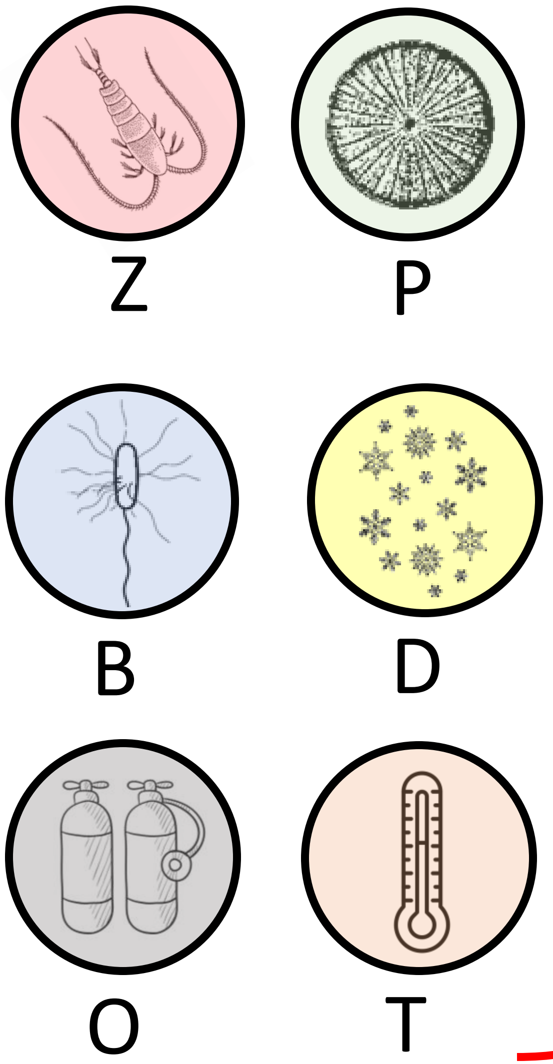


Zoo/Phytoplankton biomass is split into different size classes and…

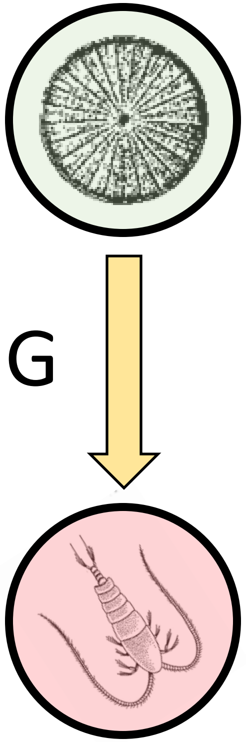
Each arrow in more complex food webs can have different parameters

Computing diagnostic grazing rates

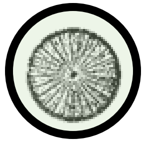
Monthly Output



	BGC Model; Earth System Model	Food Web Schematic	Zoo. Groups	Prey Options (i) Preference (p_i) for Prey i	Grazing Formulation: Functional Response for Grazing on Prey Option i	Grazing Formulation: Parameter Values [A]	Prescribed Grazing Index (w/ ±25% Prey)
	iHAMOCC NorESM2-LM		Zoo. (Z)	Phytoplankton (P) —	$\frac{\mathrm{g}_i(P_i-\mathrm{P}_{\mathrm{th}})}{\mathrm{K}_i+(P_i)}$	$\mathrm{g}_i=1.20$ $\mathrm{K}_i=9.76$ $\mathrm{P}_{\mathrm{th}}=0.001$	0.089 (0.068,0.109)
	CMOC; CanESM5		Zoo. (Z)	Phytoplankton (P) —	$\frac{\mathrm{g}_iP_i^2}{\mathrm{K}_i^2+P_i^2}$	$\mathrm{g}_i=2.00$ $\mathrm{K}_i=1.33$	0.520 (0.330,0.708)
	WOMBAT; ACCESS ESM1.5		Zoo. (Z)	Phytoplankton (P) —	$\frac{\mathrm{g}_iP_i^2}{\mathrm{K}_i^2+P_i^2}$	$\mathrm{g}_i=1.58$ $\mathrm{K}_i=6.57$ [B]	0.022 (0.013,0.034)
	OECO-v2; MIROC-ES2L		Zoo. (Z)	Non-Diazatrophs (P_{sm}), Diazatrophs (P_{dz}) —	$\frac{\mathrm{g}_iP_i^2}{\mathrm{K}_i^2+P_i^2}$	$\mathrm{g}_i=2.00$ $\mathrm{K}_i=9.37$ [B]	0.014 (0.008,0.022)
	MARBL; CESM2		Zoo. (Z)	Small Phyto. (P_{sm}), Diatoms (P_{lg}), Diazatrophs (P_{dz}) —	$T_{Lim}\frac{\mathrm{g}_i(P_i-\mathrm{P}_{\mathrm{th}})}{\mathrm{K}_i+(P_i-\mathrm{P}_{\mathrm{th}})}$ $\mathrm{T}_{Lim}=1.7^{(T-30)/10}$	$\mathrm{g}_{Psm,Plg}=2.20$ $\mathrm{g}_{Pdz}=3.15$ $\mathrm{K}_i=1.20$ $\mathrm{P}_{\mathrm{th}}=f(z,T,i)$ [C] $=0.00-.02$	0.637 (0.499,0.761)
	CanOE; CanESM5-CanOE		Microzoo. (Z_{sm})	Small Phytoplankton (P_{sm}) —	$\mathrm{g}_i(1-e^{-\lambda_iP_i})$	$\mathrm{g}_i=1.70$ $\lambda_i=0.25$	0.125 (0.095,0.155)
			Mesozoo. (Z_{md})	Large Phytoplankton (P_{lg}), Microzooplankton (Z_{sm}) —	$\mathrm{g}_i(1-e^{-\lambda_i\Sigma P_i})\left(\frac{P_i}{\Sigma P_i}\right)$	$\mathrm{g}_i=0.85$ $\lambda_i=0.25$	
	MEDUSA2.1; UKESM1-0-LL		Microzoo. (Z_{sm})	Non-Diatoms (P_{sm}), Detritus (D) $\mathrm{p}_{Psm}=0.75,\ \mathrm{p}_D=0.25$	$\frac{\mathrm{g}_i\mathrm{p}_iP_i^2}{\mathrm{K}_i^2+\Sigma\mathrm{p}_iP_i^2}$	$\mathrm{g}_i=2.00$ $\mathrm{K}_i=5.30$	0.009 (0.005,0.014)
			Mesozoo (Z_{md})	Non-Diatoms (P_{sm}), Diatoms (P_{lg}), Detritus (D), Micro Zoo. (Z_{sm}) $\mathrm{p}_{Psm,D}=0.15,\ \mathrm{p}_{Plg,Zsm}=0.35$	$\frac{\mathrm{g}_i\mathrm{p}_iP_i^2}{\mathrm{K}_i^2+\Sigma\mathrm{p}_iP_i^2}$	$\mathrm{g}_i=0.50$ $\mathrm{K}_i=1.99$	
	PISCESv2; IPSL-CM6a-LR & CNRM-ESM2.1		Microzoo. (Z_{sm})	Nanophyto. (P_{sm}), Diatoms (P_{lg}), POC (D) $\mathrm{p}_{Psm}=1,\ \mathrm{p}_{Plg}=0.5,\ \mathrm{p}_D=0.1$	$T_{Lim}F_{Lim}\frac{\mathrm{g}_i\mathrm{p}_i(P_i-\mathrm{P}_{\mathrm{th}})}{\mathrm{K}_i+\Sigma\mathrm{p}_iP_i}$ $T_{Lim}=1.079^T$	$\mathrm{g}_i=3.00$ $\mathrm{K}_i=20.00$ $\mathrm{P}_{\mathrm{th}}=0.001$ [D]	0.116 (0.080,0.153)
			Mesozoo. (Z_{md})	Nanophyto. (P_{sm}) , Diatoms (P_{lg}), POC (D), Micro Zoo. (Z_{sm}) $\mathrm{p}_{Psm,D}=0.30,\ \mathrm{p}_{Plg,Zsm}=1$	$T_{Lim}F_{Lim}\frac{\mathrm{g}_i\mathrm{p}_i(P_i-\mathrm{P}_{\mathrm{th}})}{\mathrm{K}_i+\Sigma\mathrm{p}_iP_i}$ $T_{Lim}=1.079^T$	$\mathrm{g}_i=0.75$ $\mathrm{K}_i=20.00$ $\mathrm{P}_{\mathrm{th}}=0.001$ [D]	
	BFM5.2; CMCC-ESM2		Microzoo. (Z_{sm})	Nanoflagellates (P_{sm}), Diatoms (P_{lg}), Bacteria (B), Micro Zoo. (Z_{sm}) $\mathrm{p}_i=\phi_i\frac{P_i}{P_i+1.67}$ $\phi_{Psm}=1,\ \phi_D=0.01,\ \phi_{B,Zsm}=0.2$	$\frac{\mathrm{g}_i\mathrm{p}_iP_i}{\mathrm{K}_i+\Sigma\mathrm{p}_iP_i}$ $T_{Lim}=2^{(T-10)/10}$	$\mathrm{g}_i=3.00$ $\mathrm{K}_i=1.67$	0.184 (0.122,0.253)
			Mesozoo. (Z_{md})	Diatoms (P_{lg}), Micro Zoo. (Z_{sm}), Meso Zoo (Z_{md}) $\mathrm{p}_{Plg,Zmd}=1,\ \mathrm{p}_{Zsm}=0.5$	$\frac{\mathrm{g}_i\mathrm{p}_iP_i}{\mathrm{K}_i+\Sigma\mathrm{p}_iP_i}$ $T_{Lim}=2^{(T-10)/10}$	$\mathrm{g}_i=2.00$ $\mathrm{K}_i=6.66$ [B]	
	COBALTv2; GFDL-ESM4.1		Small Zoo. (Z_{sm})	Small Phyto. (P_{sm}), Bacteria (B) $\mathrm{p}_i=\frac{\phi_i(P_i-\mathrm{P}_{\mathrm{th}})}{\sqrt{\Sigma(\phi_i(P_i-\mathrm{P}_{\mathrm{th}}))^2}}$ $\phi_{Psm}=1,\phi_B=0.25$	$T_{Lim}\frac{\mathrm{g}_i\mathrm{p}_i(P_i-\mathrm{P}_{\mathrm{th}})}{\mathrm{K}_i+\Sigma\mathrm{p}_i(P_i-\mathrm{P}_{\mathrm{th}})}$ $T_{Lim}=e^{.063T}$	$\mathrm{g}_i=1.28$ $\mathrm{K}_i=8.28$ $\mathrm{P}_{\mathrm{th}}=0.001$	0.105 (0.075,0.136)
			Medium Zoo. (Z_{md})	Large Phyto. (P_{lg}), Diazatrophs (P_{dz}), Small Zoo. (Z_{sm}) $\mathrm{p}_i=\frac{\phi_i(P_i-\mathrm{P}_{\mathrm{th}})}{\sqrt{\Sigma(\phi_i(P_i-\mathrm{P}_{\mathrm{th}}))^2}}$ $\phi_i=1$	$T_{Lim}\frac{\mathrm{g}_i\mathrm{p}_i(P_i-\mathrm{P}_{\mathrm{th}})}{\mathrm{K}_i+\Sigma\mathrm{p}_i(P_i-\mathrm{P}_{\mathrm{th}})}$ $T_{Lim}=e^{.063T}$	$\mathrm{g}_i=0.57$ $\mathrm{K}_i=8.28$ $\mathrm{P}_{\mathrm{th}}=0.001$	
			Large Zoo. (Z_{lg})	Large Phyto. (P_{lg}), Diazatrophs (P_{dz}), Medium Zoo. (Z_{md}) $\mathrm{p}_i=\frac{\phi_i(P_i-\mathrm{P}_{\mathrm{th}})}{\sqrt{\Sigma(\phi_i(P_i-\mathrm{P}_{\mathrm{th}}))^2}}$ $\phi_i=1$	$T_{Lim}\frac{\mathrm{g}_i\mathrm{p}_i(P_i-\mathrm{P}_{\mathrm{th}})}{\mathrm{K}_i+\Sigma\mathrm{p}_i(P_i-\mathrm{P}_{\mathrm{th}})}$ $T_{Lim}=e^{.063T}$	$\mathrm{g}_i=0.23$ $\mathrm{K}_i=8.28$ $\mathrm{P}_{\mathrm{th}}=0.001$	

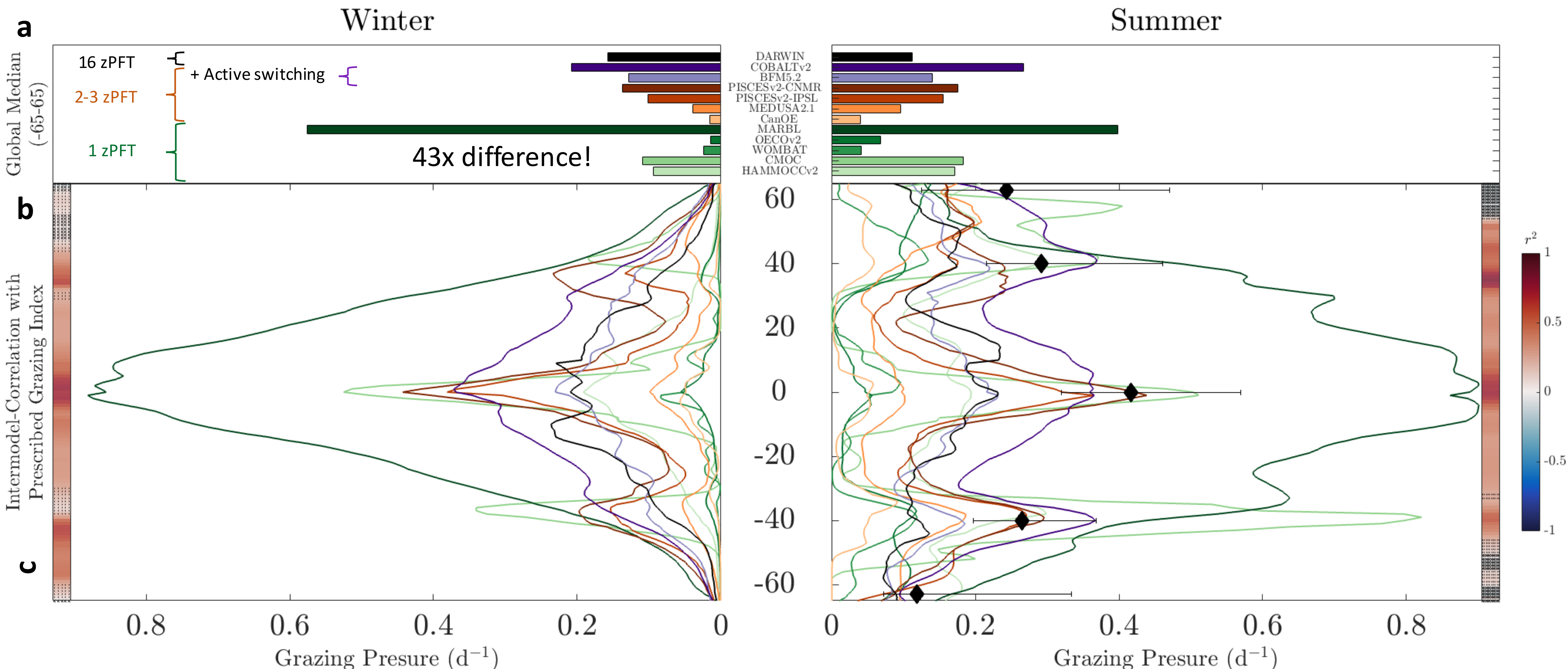


g = G/ 

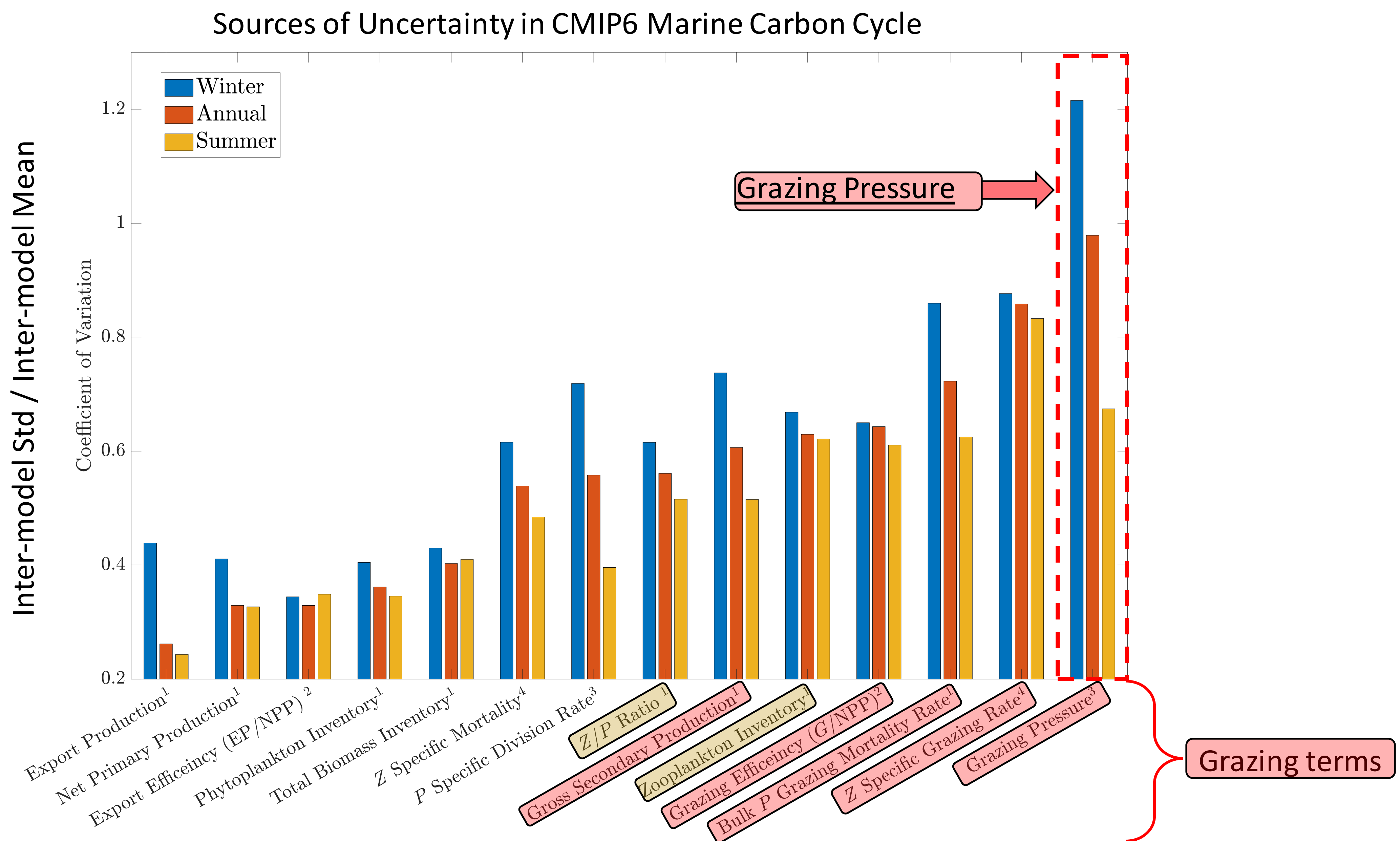
GP = G/ 

Inter-model Variation in Emergent Grazing Pressure

- Emergent grazing pressure is the **phytoplankton specific loss rate to grazing**
- It accounts for the simulated grazing rate, prey field and zooplankton population size



This is not Normal!



2. (A path to) the solution

Three Tiers of Constraints

1. <u>Prescribed Properties</u>
   Compare parameters and equations to empirical observations

   e.g. $K_{1/2}$, g_{max}, <u>PGI</u>

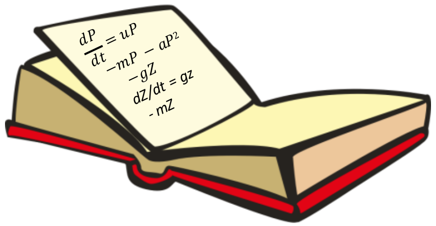
2. <u>Emergent Properties</u>
   Compare emergent properties of model output to observed properties

   e.g. Zooplankton Biomass, <u>Grazing Pressure</u>

3. <u>Emergent Relationships</u>
   Compare emergent relationships in model to observed relationships

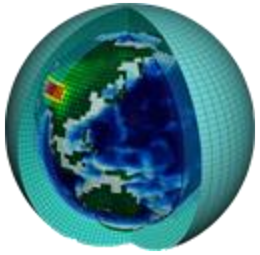
   e.g <u>Community-integrated functional response</u>

<u>Model Code</u>

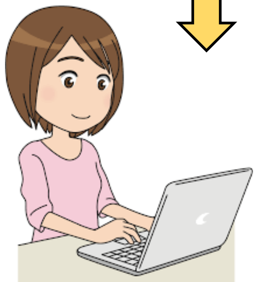


Run Model

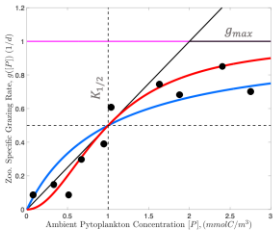
<u>Model Output</u>



Analyze Output



<u>Model Diagnostics</u>



2.1 Prescribed Properties

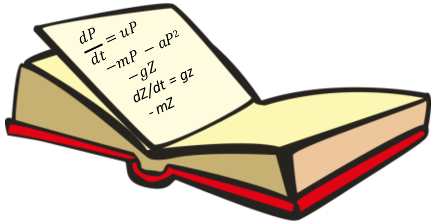
Three Tiers of Constraints

1. <u>Prescribed Properties</u>

   Compare parameters and equations to empirical observations

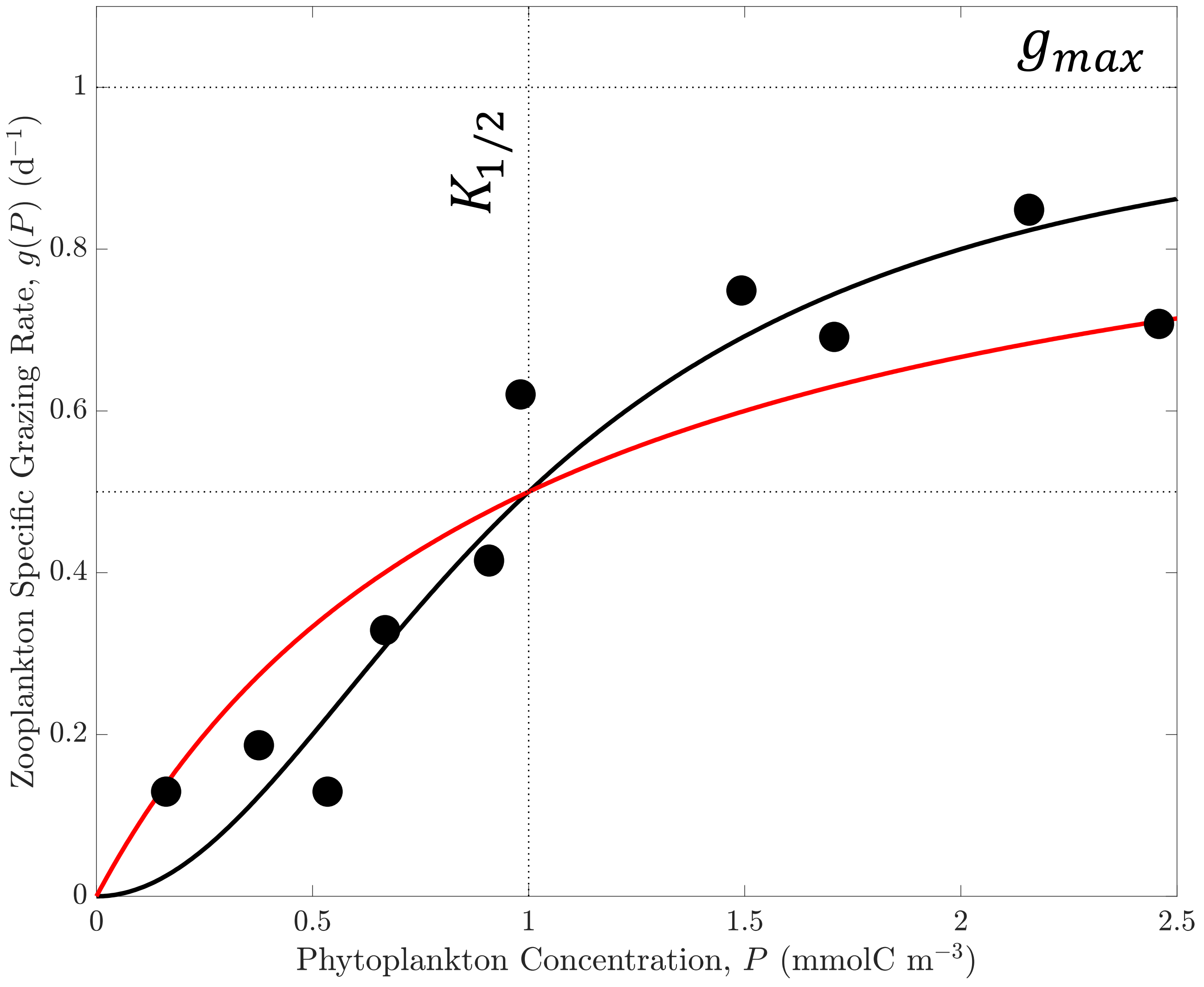
   e.g. $K_{1/2}$, g_{max}, PGI

Model Code



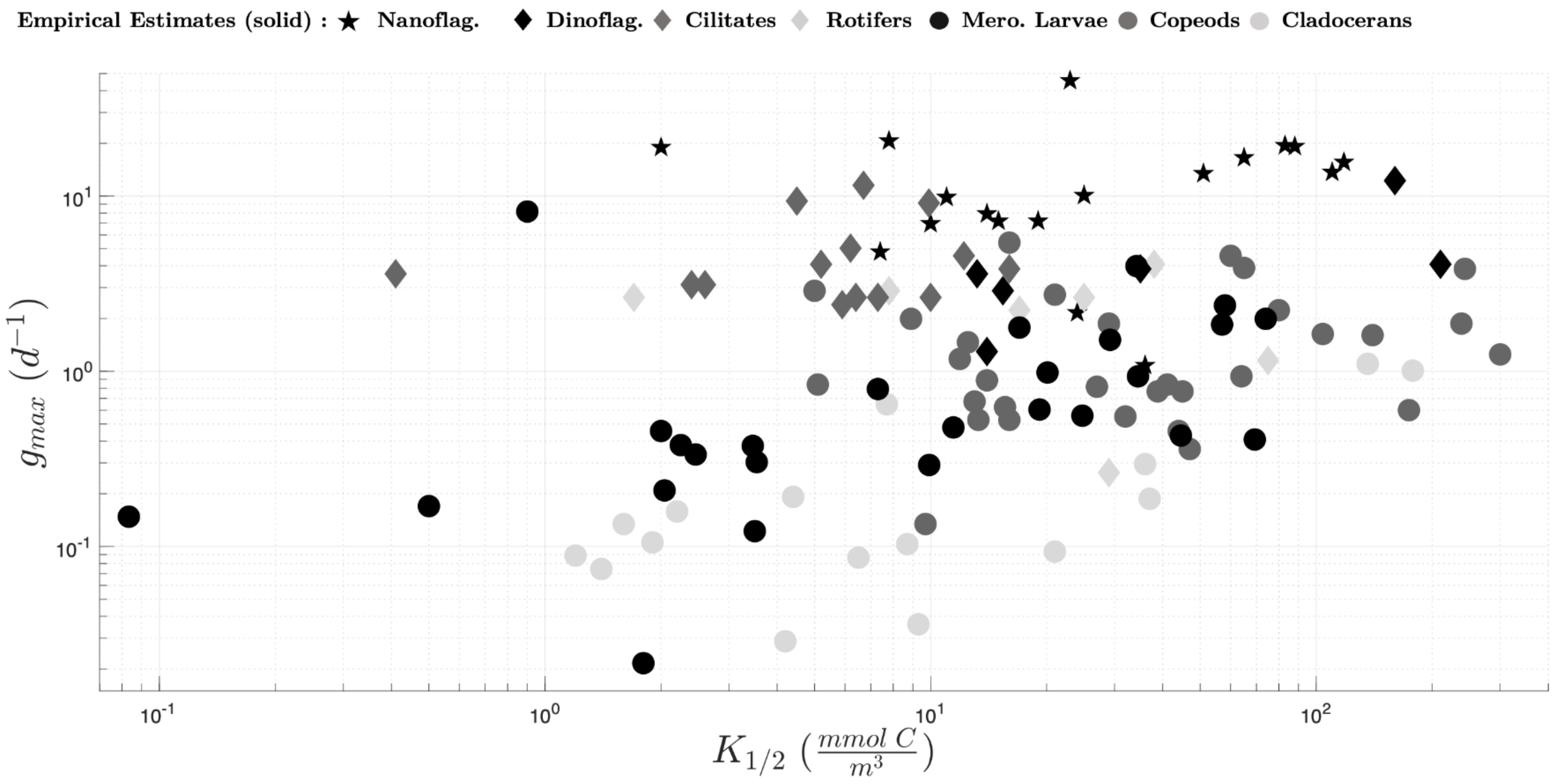
2.1 Prescribed Properties

Functional response can be measured empirically in laboratory dilution experiments



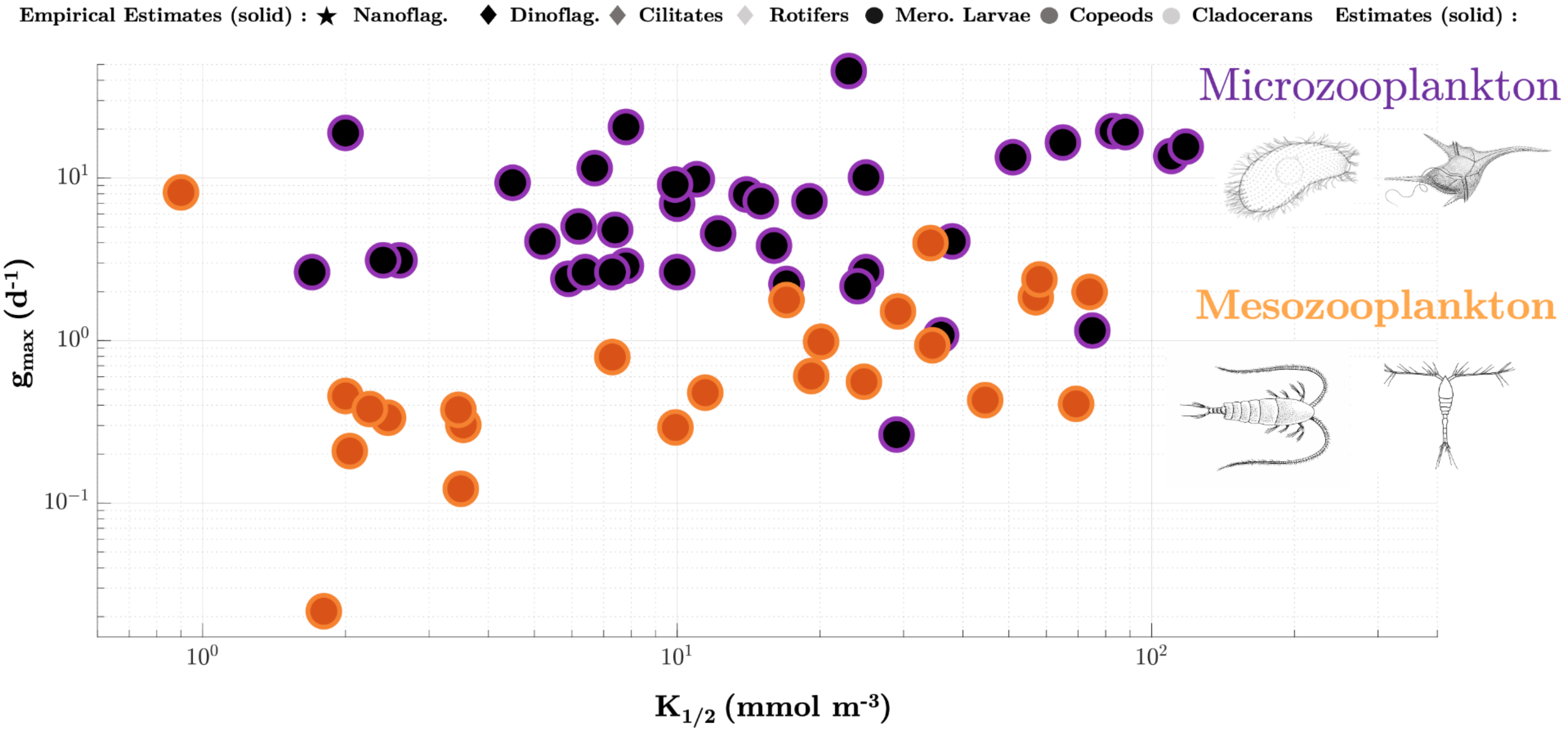
2.1 Prescribed Constraints

Giving us a range of realistic parameters. However, this range is about 3 orders of magnitude, and varies with zooplankton species, size and age,



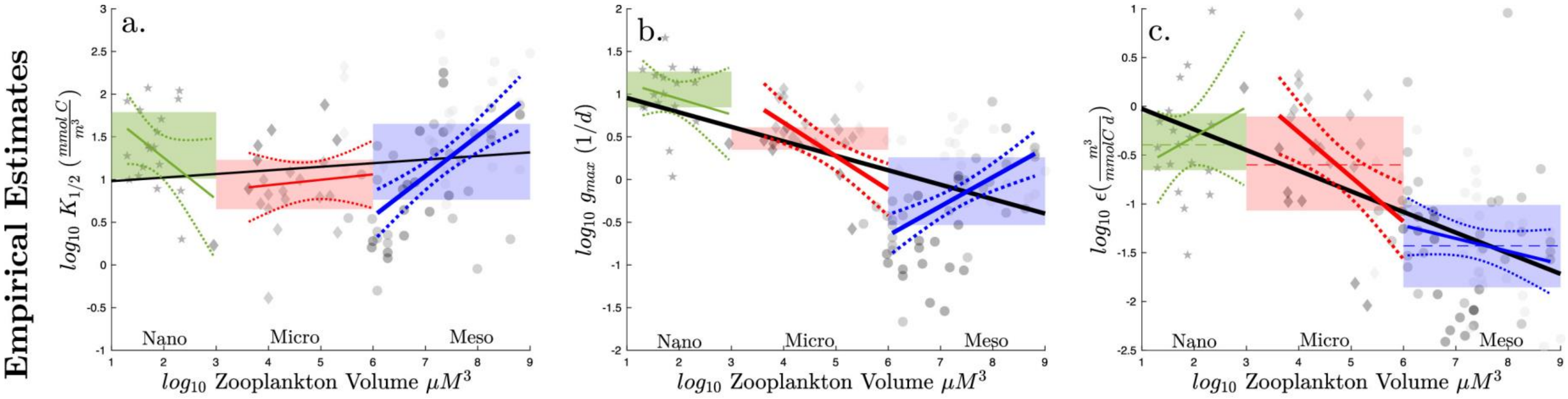
2.1 Prescribed Constraints

Although, we can begin to constrain this range if we group zooplankton in functional groups, as they are grouped in models, which represent the mean state of many species/ages/size



2.1 Prescribed Constraints

Allowing us to quantify the statistical properties of Zooplankton groups that might be included in models



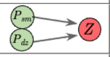
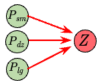
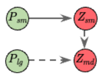
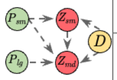
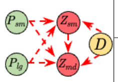
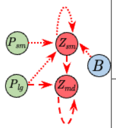
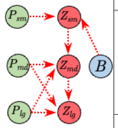
b) Empirical Estimates: Sample Statistics by Size Class

Size Class	$K_{1/2}$ $(mmolC/m^3)$				g_{max} $(1/d)$				ϵ $(m^3/mmolC/d)$			
	mean	med.	range	IQR	mean	med.	range	IQR	mean	med.	range	IQR
All zooplankton n=119	40	16	$8.3e^{-2}$ 500	6.4 43	3.7	1.6	$2.1e^{-2}$ 46	0.46 3.8	0.49	$8.4e^{-2}$	$3.4e^{-3}$ 9.5	$2.1e^{-2}$ 0.27
Nanozooplankton n=19	37	23	1.7 120	10 62	13	10	1.1 46	7.0 19	1.1	0.40	$3.0e^{-2}$ 9.5	0.22 0.85
Microzooplankton n=30	25	8.9	0.41 210	4.5 17	3.6	3.0	0.11 12	2.2 4.1	0.71	0.25	$9.1e^{-3}$ 8.8	$9.0e^{-2}$ 0.78
Mesozooplankton n=64	45	18	$8.0e^{-2}$ 500	5.8 45	1.3	0.77	$2.0e^{-2}$ 8.2	0.29 1.8	0.24	$4.0e^{-2}$	$3.4e^{-3}$ 9.1	$1.0e^{-2}$ 0.10

Rohr et al. Progress in Oceanography (2022)

2.1 Prescribed Constraints

Model Grazing Formulation

BGC Model; Earth System Model	Food Web Schematic	Zoo. Groups	Prey Options (i) Preference (p_i) for Prey i	Grazing Formulation: Functional Response for Grazing on Prey Option i	Grazing Formulation: Parameter Values [A]	Prescribed Grazing Index (w/ ±25% Prey)
iHAMOCC NorESM2-LM		Zoo. (Z)	Phytoplankton (P) —	$\frac{g_i(P_i - P_{th})}{K_i + (P_i)}$	$g_i = 1.20$, $K_i = 9.76$, $P_{th} = 0.001$	0.089 (0.068,0.109)
CMOC; CanESM5		Zoo. (Z)	Phytoplankton (P) —	$\frac{g_i P_i^2}{K_i^2 + P_i^2}$	$g_i = 2.00$, $K_i = 1.33$	0.520 (0.330,0.708)
WOMBAT; ACCESS ESM1.5		Zoo. (Z)	Phytoplankton (P) —	$\frac{g_i P_i^2}{K_i^2 + P_i^2}$	$g_i = 1.58$, $K_i = 6.57$ [B]	0.022 (0.013,0.034)
OECO-v2; MIROC-ES2L		Zoo. (Z)	Non-Diazatrophs (P_{sm}), Diazatrophs (P_{dz}) —	$\frac{g_i P_i^2}{K_i^2 + P_i^2}$	$g_i = 2.00$, $K_i = 9.37$ [B]	0.014 (0.008,0.022)
MARBL; CESM2		Zoo. (Z)	Small Phyto. (P_{sm}), Diatoms (P_{lg}), Diazatrophs (P_{dz}) —	$T_{Lim}\frac{g_i(P_i - P_{th})}{K_i + (P_i - P_{th})}$, $T_{Lim} = 1.7^{(T-30)/10}$	$g_{Psm,Plg} = 2.20$, $g_{Pdz} = 3.15$, $K_i = 1.20$, $P_{th} = f(z,T,i)$ [C] $= 0.00 - .02$	0.637 (0.499,0.761)
CanOE; CanESM5-CanOE		Microzoo. (Z_{sm})	Small Phytoplankton (P_{sm}) —	$g_i(1 - e^{-\lambda_i P_i})$	$g_i = 1.70$, $\lambda_i = 0.25$	0.125 (0.095,0.155)
		Mesozoo. (Z_{md})	Large Phytoplankton (P_{lg}), Microzooplankton (Z_{sm}) —	$g_i(1 - e^{-\lambda_i \Sigma P_i})\left(\frac{P_i}{\Sigma P_i}\right)$	$g_i = 0.85$, $\lambda_i = 0.25$	
MEDUSA2.1; UKESM1-0-LL		Microzoo. (Z_{sm})	Non-Diatoms (P_{sm}), Detritus (D), $p_{Psm} = 0.75$, $p_D = 0.25$	$\frac{g_i p_i P_i^2}{K_i^2 + \Sigma p_i P_i^2}$	$g_i = 2.00$, $K_i = 5.30$	0.009 (0.005,0.014)
		Mesozoo (Z_{md})	Non-Diatoms (P_{sm}), Diatoms (P_{lg}), Detritus (D), Micro Zoo. (Z_{sm}), $p_{Psm,D} = 0.15$, $p_{Plg,Zsm} = 0.35$	$\frac{g_i p_i P_i^2}{K_i^2 + \Sigma p_i P_i^2}$	$g_i = 0.50$, $K_i = 1.99$	
PISCESv2; IPSL-CM6a-LR & CNRM-ESM2.1		Microzoo. (Z_{sm})	Nanophyto. (P_{sm}), Diatoms (P_{lg}), POC (D), $p_{Psm} = 1$, $p_{Plg} = 0.5$, $p_D = 0.1$	$T_{Lim}F_{Lim}\frac{g_i p_i(P_i - P_{th})}{K_i + \Sigma p_i P_i}$, $T_{Lim} = 1.079^T$	$g_i = 3.00$, $K_i = 20.00$, $P_{th} = 0.001$ [D]	0.116 (0.080,0.153)
		Mesozoo. (Z_{md})	Nanophyto. (P_{sm}), Diatoms (P_{lg}), POC (D), Micro Zoo. (Z_{sm}), $p_{Psm,D} = 0.30$, $p_{Plg,Zsm} = 1$	$T_{Lim}F_{Lim}\frac{g_i p_i(P_i - P_{th})}{K_i + \Sigma p_i P_i}$, $T_{Lim} = 1.079^T$	$g_i = 0.75$, $K_i = 20.00$, $P_{th} = 0.001$ [D]	
BFM5.2; CMCC-ESM2		Microzoo. (Z_{sm})	Nanoflagellates (P_{sm}), Diatoms (P_{lg}), Bacteria (B), Micro Zoo. (Z_{sm}), $p_i = \phi_i \frac{P_i}{P_i + 1.67}$, $\phi_{Psm} = 1$, $\phi_D = 0.01$, $\phi_{B,Zsm} = 0.2$	$\frac{g_i p_i P_i}{K_i + \Sigma p_i P_i}$, $T_{Lim} = 2^{(T-10)/10}$	$g_i = 3.00$, $K_i = 1.67$	0.184 (0.122,0.253)
		Mesozoo. (Z_{md})	Diatoms (P_{lg}), Micro Zoo. (Z_{sm}), Meso Zoo (Z_{md}), $p_{Plg,Zmd} = 1$, $p_{Zsm} = 0.5$	$\frac{g_i p_i P_i}{K_i + \Sigma p_i P_i}$, $T_{Lim} = 2^{(T-10)/10}$	$g_i = 2.00$, $K_i = 6.66$ [B]	
COBALTv2; GFDL-ESM4.1		Small Zoo. (Z_{sm})	Small Phyto. (P_{sm}), Bacteria (B), $p_i = \frac{\phi_i(P_i - P_{th})}{\sqrt{\Sigma(\phi_i(P_i - P_{th}))^2}}$, $\phi_{Psm} = 1, \phi_B = 0.25$	$T_{Lim}\frac{g_i p_i(P_i - P_{th})}{K_i + \Sigma p_i(P_i - P_{th})}$, $T_{Lim} = e^{.063T}$	$g_i = 1.28$, $K_i = 8.28$, $P_{th} = 0.001$	0.105 (0.075,0.136)
		Medium Zoo. (Z_{md})	Large Phyto. (P_{lg}), Diazatrophs (P_{dz}), Small Zoo. (Z_{sm}), $p_i = \frac{\phi_i(P_i - P_{th})}{\sqrt{\Sigma(\phi_i(P_i - P_{th}))^2}}$, $\phi_i = 1$	$T_{Lim}\frac{g_i p_i(P_i - P_{th})}{K_i + \Sigma p_i(P_i - P_{th})}$, $T_{Lim} = e^{.063T}$	$g_i = 0.57$, $K_i = 8.28$, $P_{th} = 0.001$	
		Large Zoo. (Z_{lg})	Large Phyto. (P_{lg}), Diazatrophs (P_{dz}), Medium Zoo. (Z_{md}), $p_i = \frac{\phi_i(P_i - P_{th})}{\sqrt{\Sigma(\phi_i(P_i - P_{th}))^2}}$, $\phi_i = 1$	$T_{Lim}\frac{g_i p_i(P_i - P_{th})}{K_i + \Sigma p_i(P_i - P_{th})}$, $T_{Lim} = e^{.063T}$	$g_i = 0.23$, $K_i = 8.28$, $P_{th} = 0.001$	

But grazing is not as simple as single-prey functional response curve.

Simulated zooplankton often have a variety of prey options, often with prey preferences, active switching and generally more complex response curves with >2 parameters.

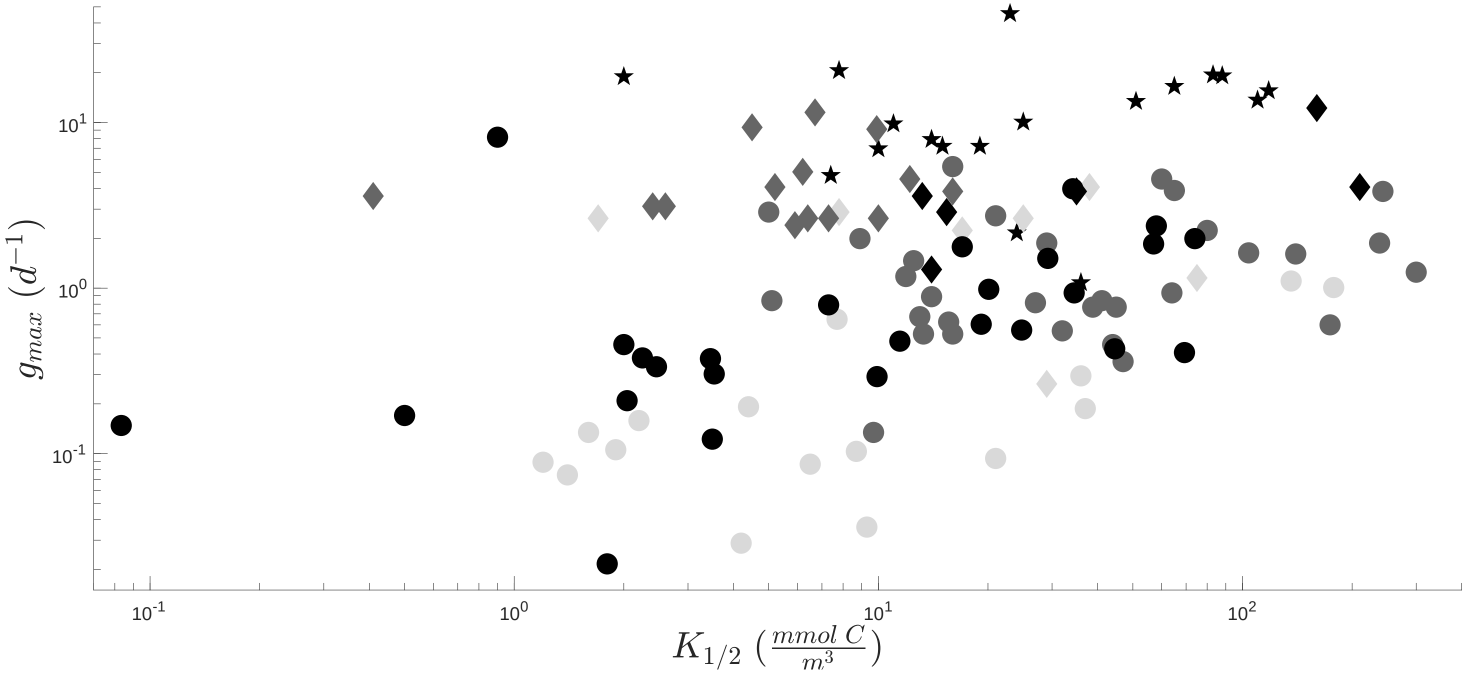
These feature help models provide prey refuge and co-existence across simplified food webs.

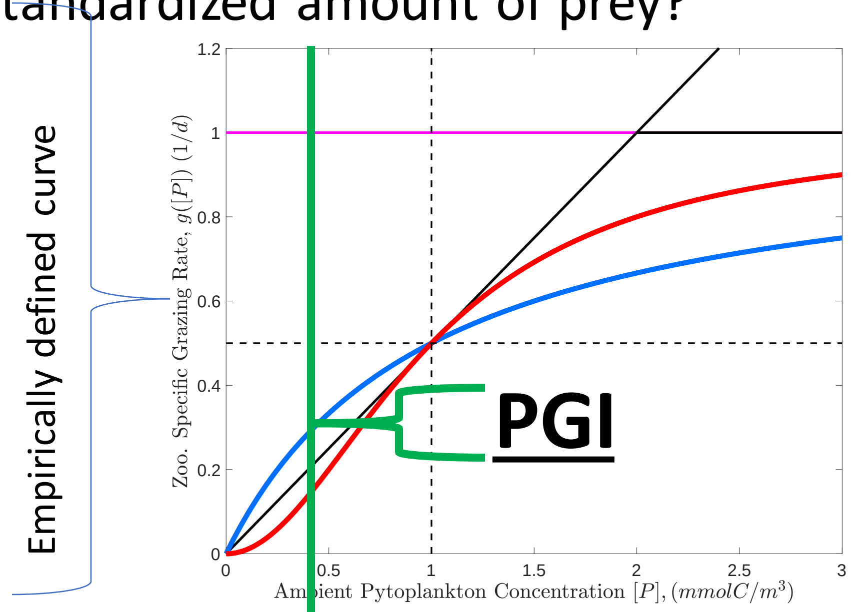
But, obfuscate the direct translation of laboratory measured parameters to what goes into a model.

Introducing The Prescribed Grazing Index (PGI)

- The PGI takes into account ALL aspects of the grazing formulation and (/but) reduces the dimensionality of the functional response curve to 1

- How fast would each of these zooplankton graze on a standardized amount of prey?





Global Median Surface Biomass Concentration

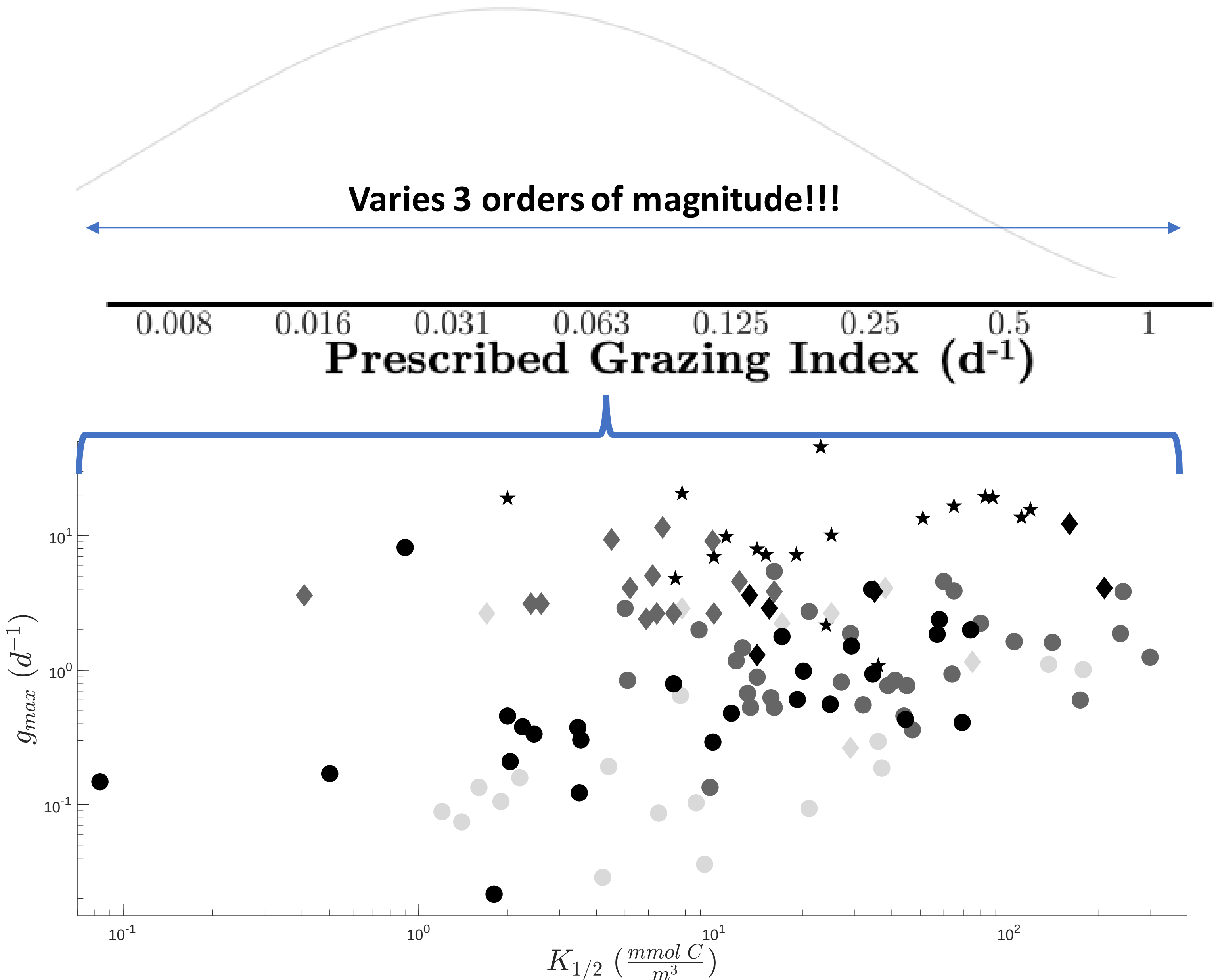
MAREDAT: towards a world atlas of MARine Ecosystem DATa

E. T. Buitenhuis, M. Vogt, R. Moriarty, N. Bednaršek, S. C. Doney, K. Leblanc, C. Le Quéré, Y.-W. Luo, C. O'Brien, T. O'Brien, J. Peloquin, R. Schiebel, and C. Swan

0.46 mmolC m^{-3}

The Prescribed Grazing Index (PGI)

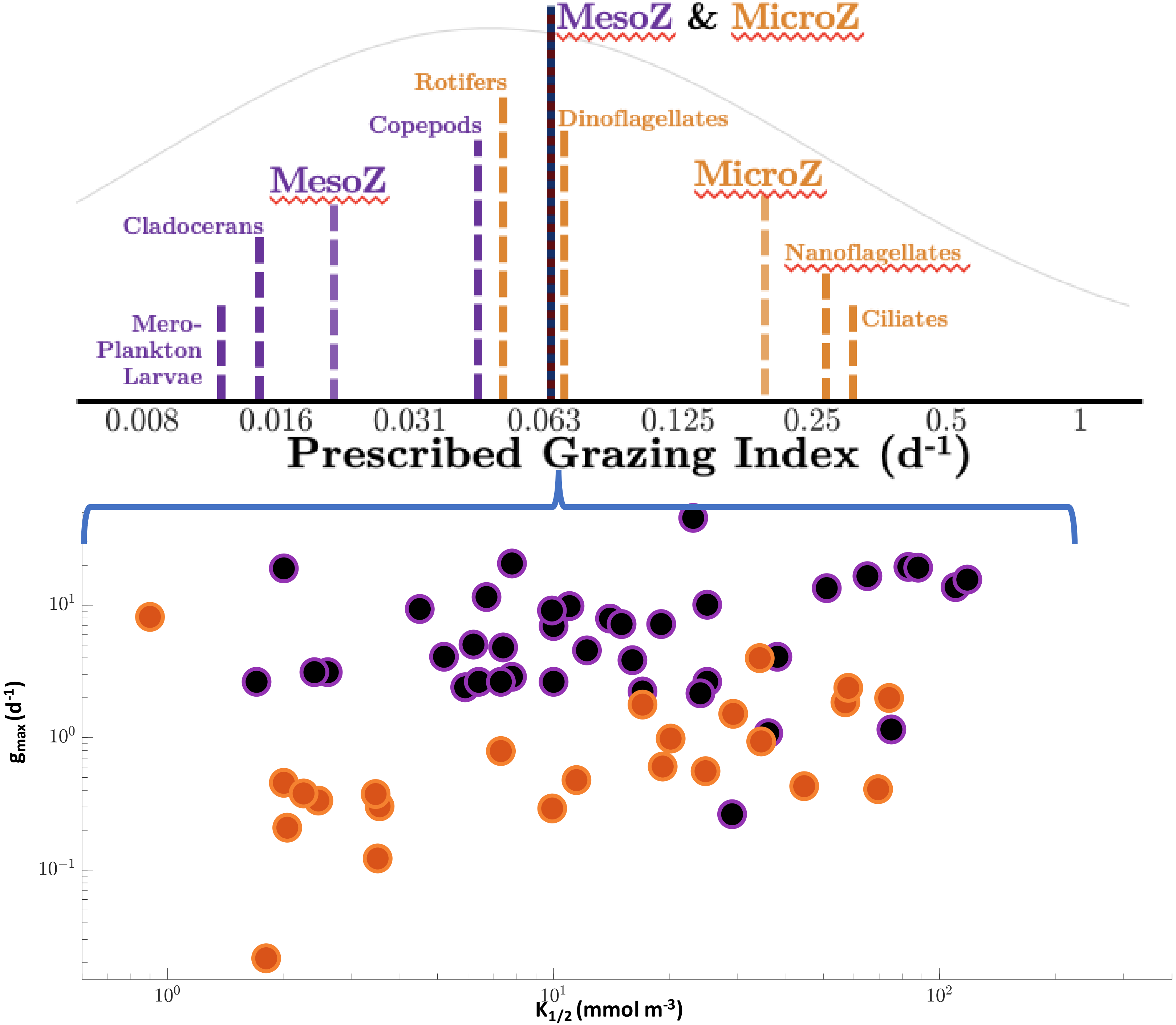
Different zooplankton graze on the same amount of phytoplankton at tremendously different rates!



The global Zoo. population is very diverse. The PGI varies across species, age, and size.

But models are tasked with only representing the mean state…

Range is still large , but gets smaller when you group into functional types.

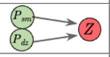
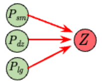
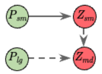
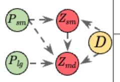
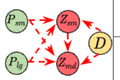
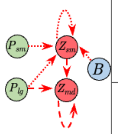
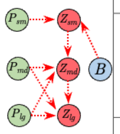


Ideally, in models with 1-3 functional types, it should get even smaller, as these represent mean properties of diverse global community

So how can we define the PGI in models to compare?

Introducing the Prescribed Grazing Index (PGI)

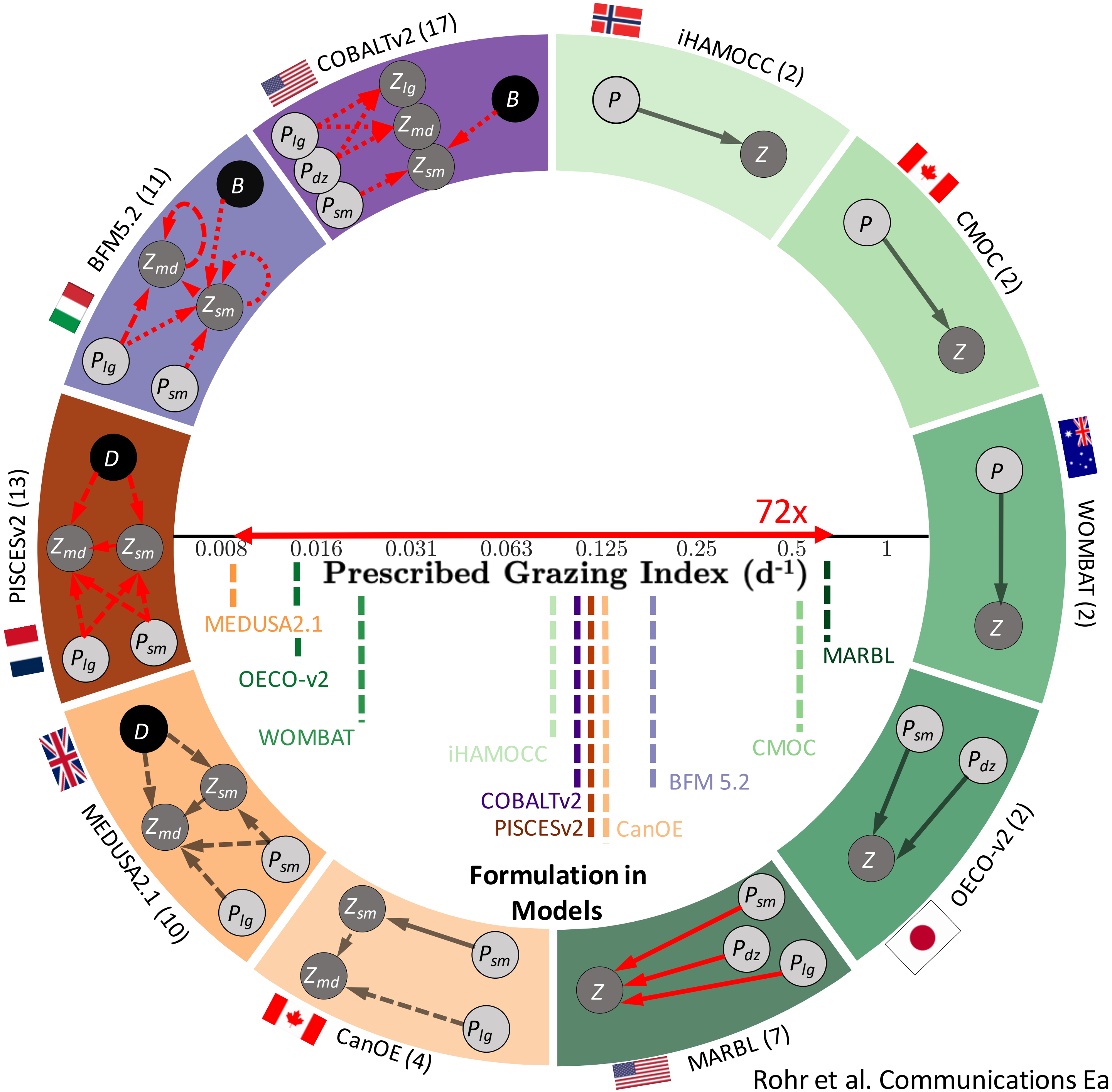
Model Grazing Formulation

	BGC Model; Earth System Model	Food Web Schematic	Zoo. Groups	Prey Options (i) Preference (p_i) for Prey i	Grazing Formulation: Functional Response for Grazing on Prey Option i	Grazing Formulation: Parameter Values [A]	Prescribed Grazing Index (w/ ±25% Prey)
	iHAMOCC NorESM2-LM		Zoo. (Z)	Phytoplankton (P) —	$\frac{g_i(P_i - P_{th})}{K_i + (P_i)}$	$g_i = 1.20$, $K_i = 9.76$, $P_{th} = 0.001$	0.089 (0.068,0.109)
	CMOC; CanESM5		Zoo. (Z)	Phytoplankton (P) —	$\frac{g_i P_i^2}{K_i^2 + P_i^2}$	$g_i = 2.00$, $K_i = 1.33$	0.520 (0.330,0.708)
	WOMBAT; ACCESS ESM1.5		Zoo. (Z)	Phytoplankton (P) —	$\frac{g_i P_i^2}{K_i^2 + P_i^2}$	$g_i = 1.58$, $K_i = 6.57$ [B]	0.022 (0.013,0.034)
	OECO-v2; MIROC-ES2L		Zoo. (Z)	Non-Diazatrophs (P_{sm}), Diazatrophs (P_{dz}) —	$\frac{g_i P_i^2}{K_i^2 + P_i^2}$	$g_i = 2.00$, $K_i = 9.37$ [B]	0.014 (0.008,0.022)
	MARBL; CESM2		Zoo. (Z)	Small Phyto. (P_{sm}), Diatoms (P_{lg}), Diazatrophs (P_{dz}) —	$T_{Lim} \frac{g_i(P_i - P_{th})}{K_i + (P_i - P_{th})}$, $T_{Lim} = 1.7^{(T-30)/10}$	$g_{Psm,Plg} = 2.20$, $g_{Pdz} = 3.15$, $K_i = 1.20$, $P_{th} = f(z,T,i)$ [C] $= 0.00 - .02$	0.637 (0.499,0.761)
	CanOE; CanESM5-CanOE		Microzoo. (Z_{sm})	Small Phytoplankton (P_{sm}) —	$g_i(1 - e^{-\lambda_i P_i})$	$g_i = 1.70$, $\lambda_i = 0.25$	0.125 (0.095,0.155)
			Mesozoo. (Z_{md})	Large Phytoplankton (P_{lg}), Microzooplankton (Z_{sm}) —	$g_i(1 - e^{-\lambda_i \Sigma P_i}) \left(\frac{P_i}{\Sigma P_i}\right)$	$g_i = 0.85$, $\lambda_i = 0.25$	
	MEDUSA2.1; UKESM1-0-LL		Microzoo. (Z_{sm})	Non-Diatoms (P_{sm}), Detritus (D), $p_{Psm} = 0.75$, $p_D = 0.25$	$\frac{g_i p_i P_i^2}{K_i^2 + \Sigma p_i P_i^2}$	$g_i = 2.00$, $K_i = 5.30$	0.009 (0.005,0.014)
			Mesozoo (Z_{md})	Non-Diatoms (P_{sm}), Diatoms (P_{lg}), Detritus (D), Micro Zoo. (Z_{sm}), $p_{Psm,D} = 0.15$, $p_{Plg,Zsm} = 0.35$	$\frac{g_i p_i P_i^2}{K_i^2 + \Sigma p_i P_i^2}$	$g_i = 0.50$, $K_i = 1.99$	
	PISCESv2; IPSL-CM6a-LR & CNRM-ESM2.1		Microzoo. (Z_{sm})	Nanophyto. (P_{sm}), Diatoms (P_{lg}), POC (D), $p_{Psm} = 1$, $p_{Plg} = 0.5$, $p_D = 0.1$	$T_{Lim} F_{Lim} \frac{g_i p_i (P_i - P_{th})}{K_i + \Sigma p_i P_i}$, $T_{Lim} = 1.079^T$	$g_i = 3.00$, $K_i = 20.00$, $P_{th} = 0.001$ [D]	0.116 (0.080,0.153)
			Mesozoo. (Z_{md})	Nanophyto. (P_{sm}) , Diatoms (P_{lg}), POC (D), Micro Zoo. (Z_{sm}), $p_{Psm,D} = 0.30$, $p_{Plg,Zsm} = 1$	$T_{Lim} F_{Lim} \frac{g_i p_i (P_i - P_{th})}{K_i + \Sigma p_i P_i}$, $T_{Lim} = 1.079^T$	$g_i = 0.75$, $K_i = 20.00$, $P_{th} = 0.001$ [D]	
	BFM5.2; CMCC-ESM2		Microzoo. (Z_{sm})	Nanoflagellates (P_{sm}), Diatoms (P_{lg}), Bacteria (B), Micro Zoo. (Z_{sm}), $p_i = \phi_i \frac{P_i}{P_i + 1.67}$, $\phi_{Psm} = 1$, $\phi_D = 0.01$, $\phi_{B,Zsm} = 0.2$	$\frac{g_i p_i P_i}{K_i + \Sigma p_i P_i}$, $T_{Lim} = 2^{(T-10)/10}$	$g_i = 3.00$, $K_i = 1.67$	0.184 (0.122,0.253)
			Mesozoo. (Z_{md})	Diatoms (P_{lg}), Micro Zoo. (Z_{sm}), Meso Zoo (Z_{md}), $p_{Plg,Zmd} = 1$, $p_{Zsm} = 0.5$	$\frac{g_i p_i P_i}{K_i + \Sigma p_i P_i}$, $T_{Lim} = 2^{(T-10)/10}$	$g_i = 2.00$, $K_i = 6.66$ [B]	
	COBALTv2; GFDL-ESM4.1		Small Zoo. (Z_{sm})	Small Phyto. (P_{sm}), Bacteria (B), $p_i = \frac{\phi_i(P_i - P_{th})}{\sqrt{\Sigma(\phi_i(P_i - P_{th}))^2}}$, $\phi_{Psm} = 1, \phi_B = 0.25$	$T_{Lim} \frac{g_i p_i (P_i - P_{th})}{K_i + \Sigma p_i (P_i - P_{th})}$, $T_{Lim} = e^{.063T}$	$g_i = 1.28$, $K_i = 8.28$, $P_{th} = 0.001$	0.105 (0.075,0.136)
			Medium Zoo. (Z_{md})	Large Phyto. (P_{lg}), Diazatrophs (P_{dz}), Small Zoo. (Z_{sm}), $p_i = \frac{\phi_i(P_i - P_{th})}{\sqrt{\Sigma(\phi_i(P_i - P_{th}))^2}}$, $\phi_i = 1$	$T_{Lim} \frac{g_i p_i (P_i - P_{th})}{K_i + \Sigma p_i (P_i - P_{th})}$, $T_{Lim} = e^{.063T}$	$g_i = 0.57$, $K_i = 8.28$, $P_{th} = 0.001$	
			Large Zoo. (Z_{lg})	Large Phyto. (P_{lg}), Diazatrophs (P_{dz}), Medium Zoo. (Z_{md}), $p_i = \frac{\phi_i(P_i - P_{th})}{\sqrt{\Sigma(\phi_i(P_i - P_{th}))^2}}$, $\phi_i = 1$	$T_{Lim} \frac{g_i p_i (P_i - P_{th})}{K_i + \Sigma p_i (P_i - P_{th})}$, $T_{Lim} = e^{.063T}$	$g_i = 0.23$, $K_i = 8.28$, $P_{th} = 0.001$	

Observed Median Plankton Community

Field	MAREDAT Group	Observed Global Median Prey Field
Phytoplankton (mmolC m^{-3})		
Small	Picophytoplankton	0.46
Large	Diatoms + Phaeocystis	0.33
Diazatrophs	Diazatrophs	2.5e-3
Total	Pico+Diat +Phae+Diat	0.79
Zooplankton (mmolC m^{-3})		
Small	Microzooplankton	0.26
Medium	Mesozooplankton	0.23
Large	Macrozooplantkon	0.02
Total	Micro+Meso+Macro	0.51
Other Carbon Reservoirs (mmolC m^{-3})		
Bacteria	Picoheterotrophs	0.55
Detritus	-	2.65
Temperature (°C)		
SST	-	15.30

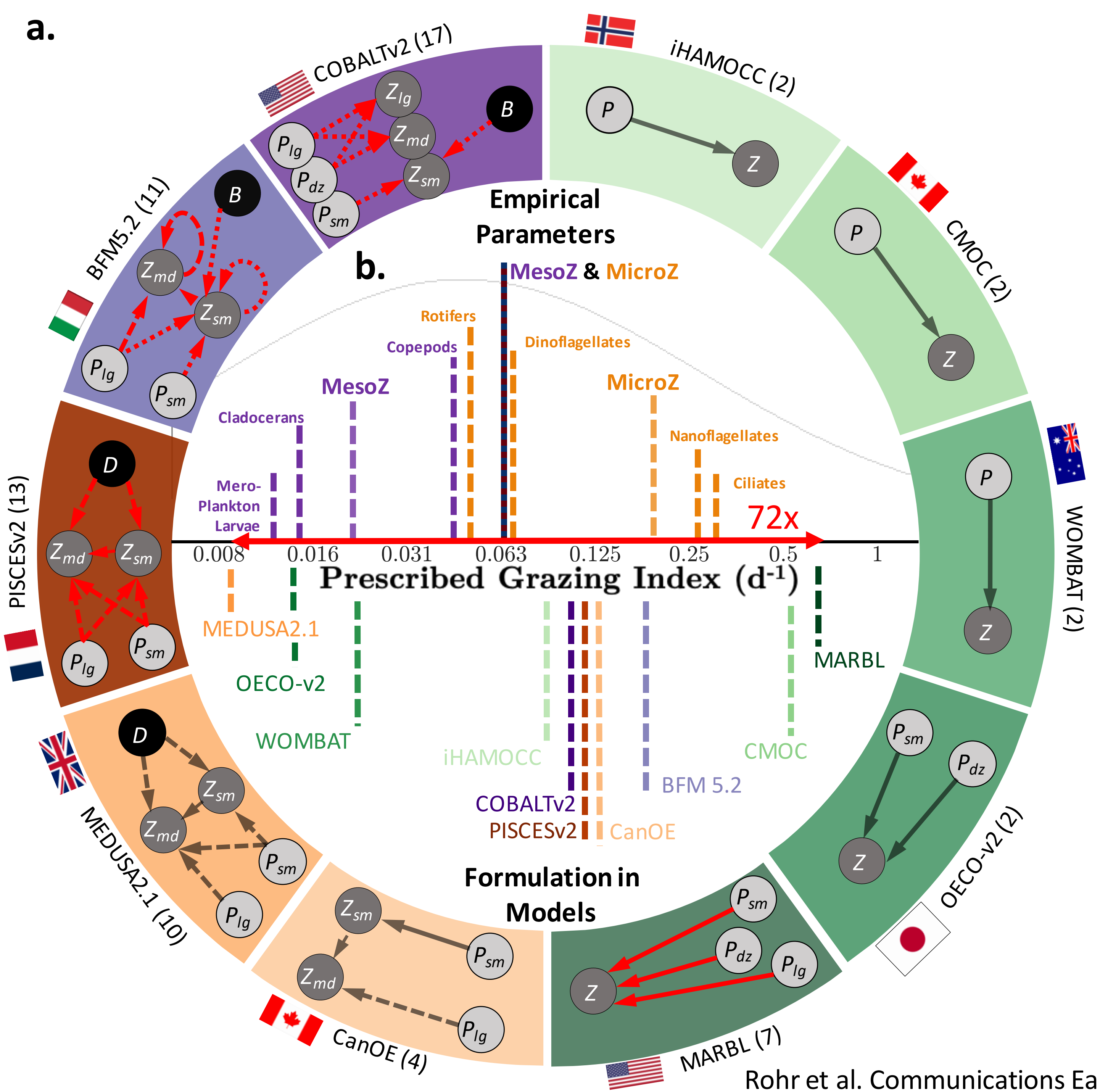
The PGI tells us how fast the average zooplankton in a given model would graze on the global median plankton community



…And varies by nearly 2 orders of magnitude!

Rohr et al. Communications Earth & Env (2023)

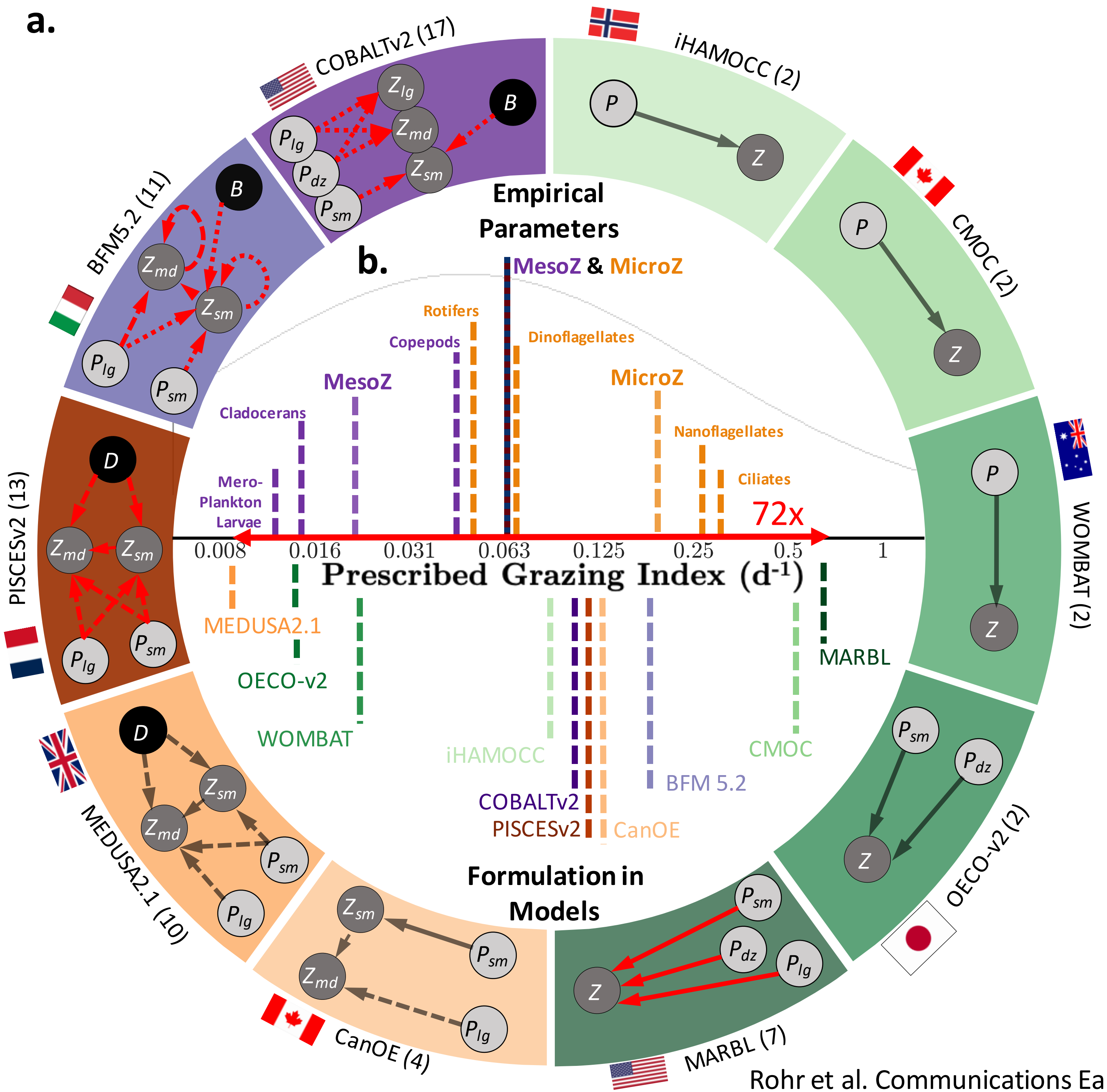
The PGI range across all surveyed CMIP6 models, is roughly as large as the middle 80% of all surveyed zooplankton species (0.005–0.55 d^{-1}),



… And greater than the range of observed Zooplankton functional Types

Rohr et al. Communications Earth & Env (2023)

Statistically, this means some BGC models assume an ocean filled with rapidly grazing ciliates, and others with slow grazing Larvae!



Rohr et al. Communications Earth & Env (2023)

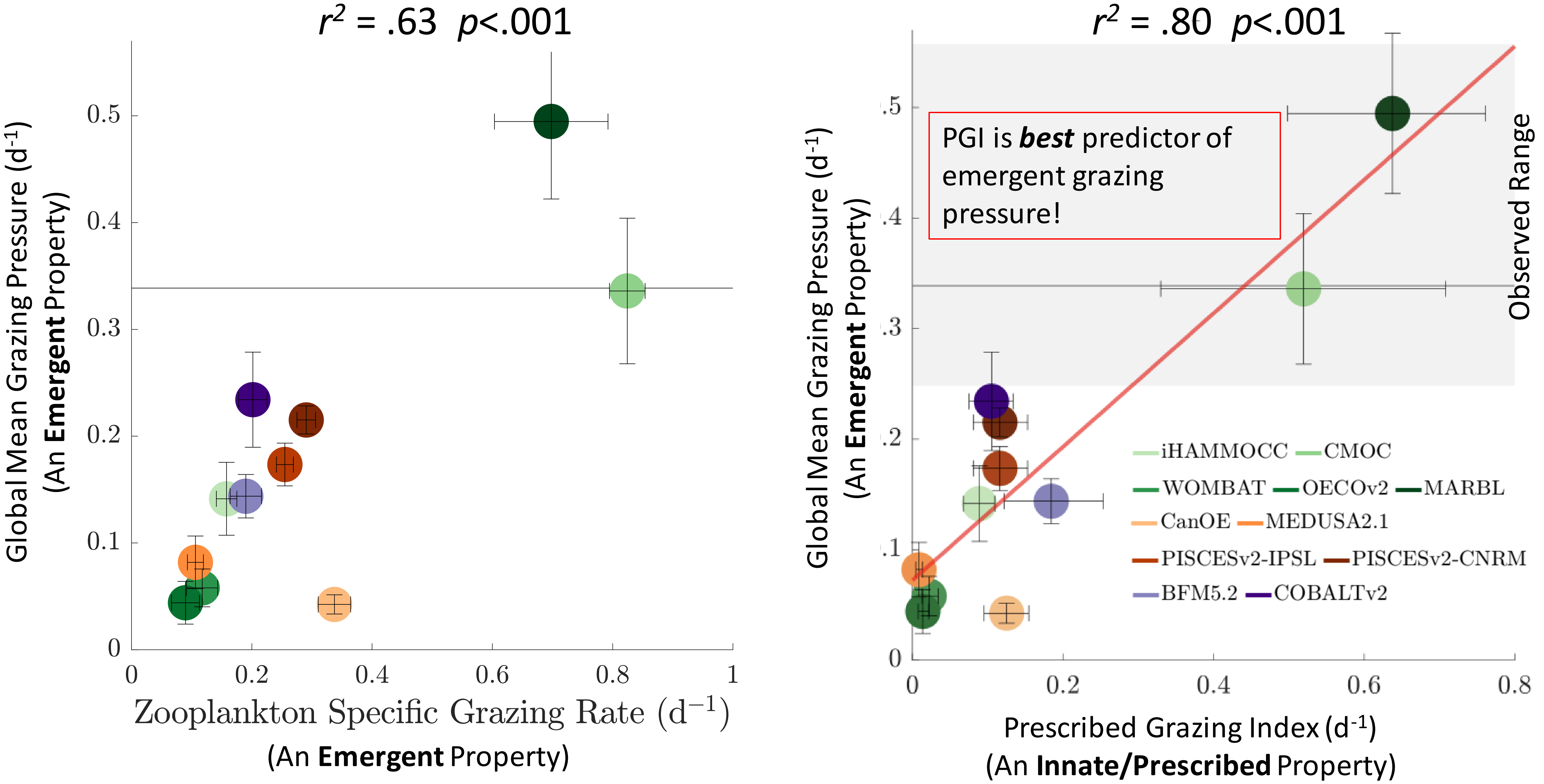
But, is that really fair?

The PGI reduces a highly multi-variate function into a single number.

And could be compensated for by zooplankton mortality rates

So doesn't it must miss a lot…?

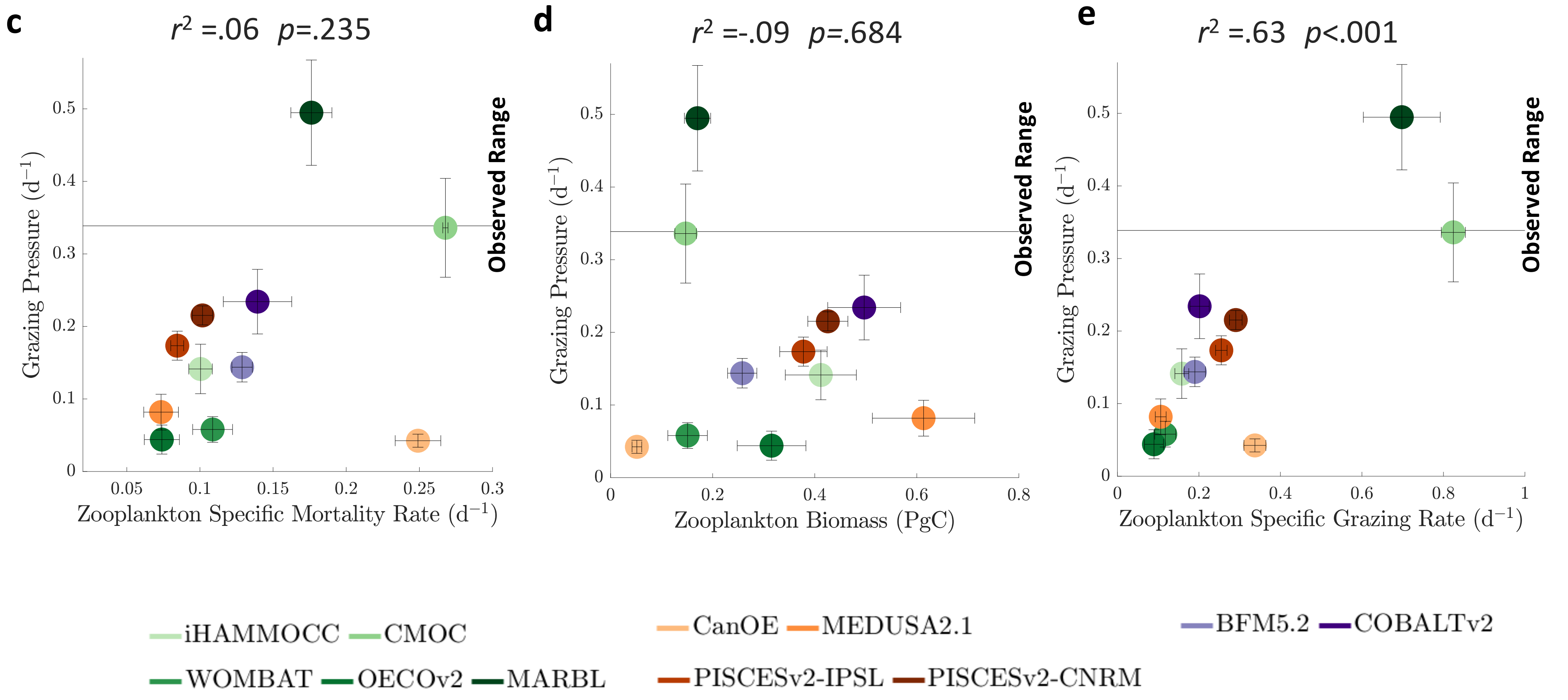
Grazing Pressure is best predicted by the PGI



…And Much Better than Biomass or Mortality

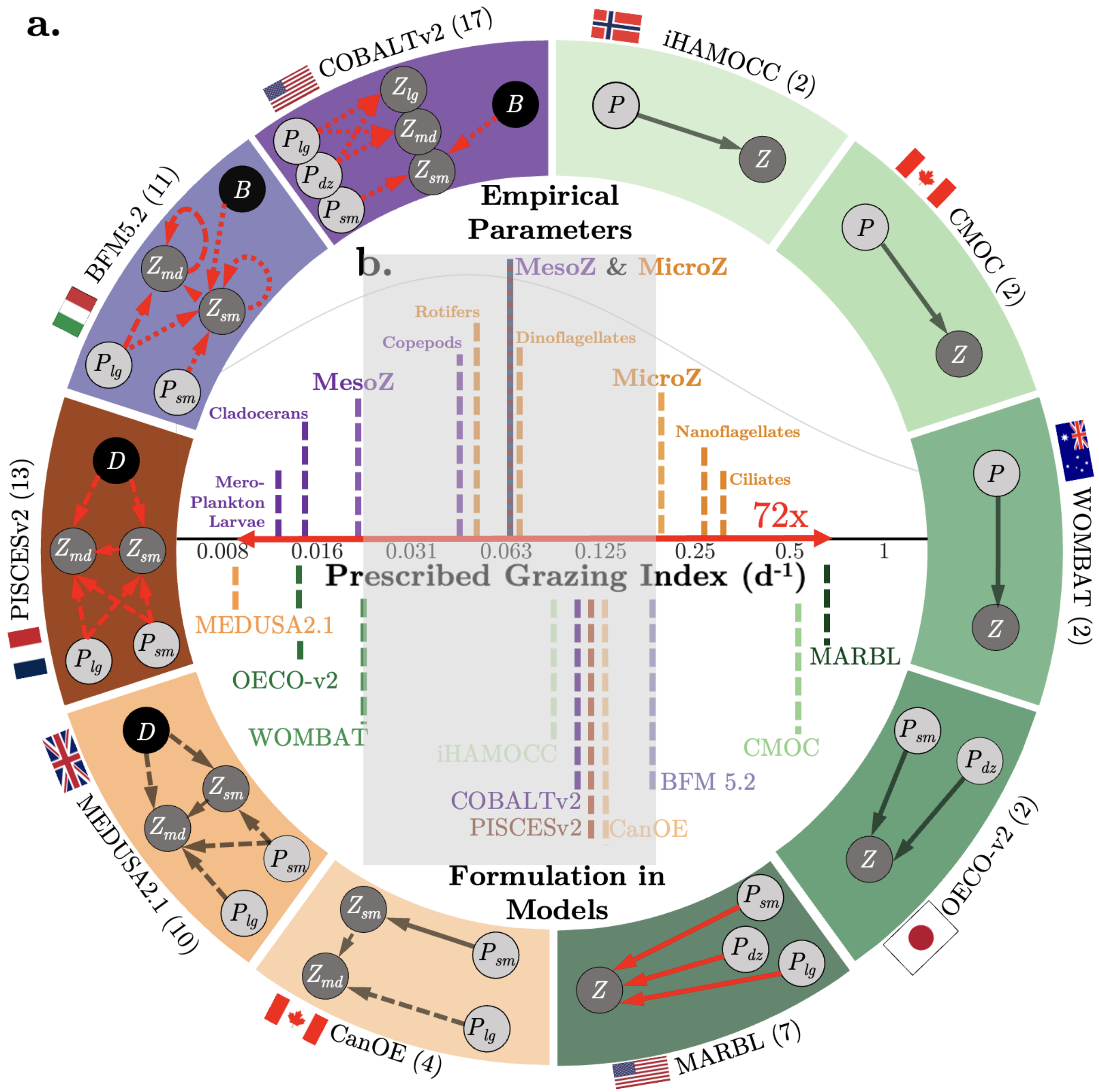
- Across models, differences in emergent grazing pressure appears mostly driven by differences in specific grazing rates, rather than zooplankton biomass or mortality

- So from phytoplankton perspective, what matters most is how fast individual zooplankton are grazing, not how many zooplankton there are or how fast they are dying.



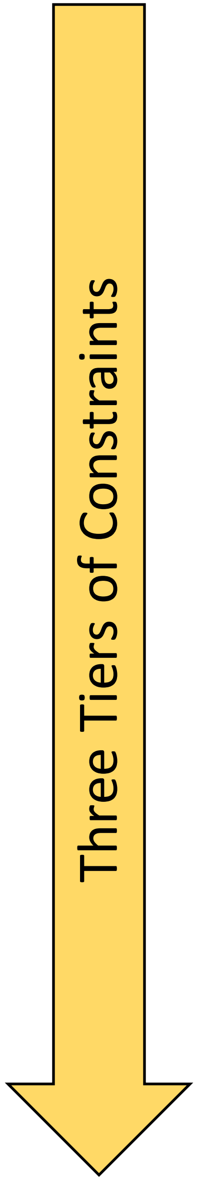
2.1 Prescribed Constraints

So before running a single simulation, modeler should make sure they are prescribing a reasonable PGI



Rohr et al. Communications Earth & Env (2023)

2.2 Emergent Properties



1. Prescribed Properties

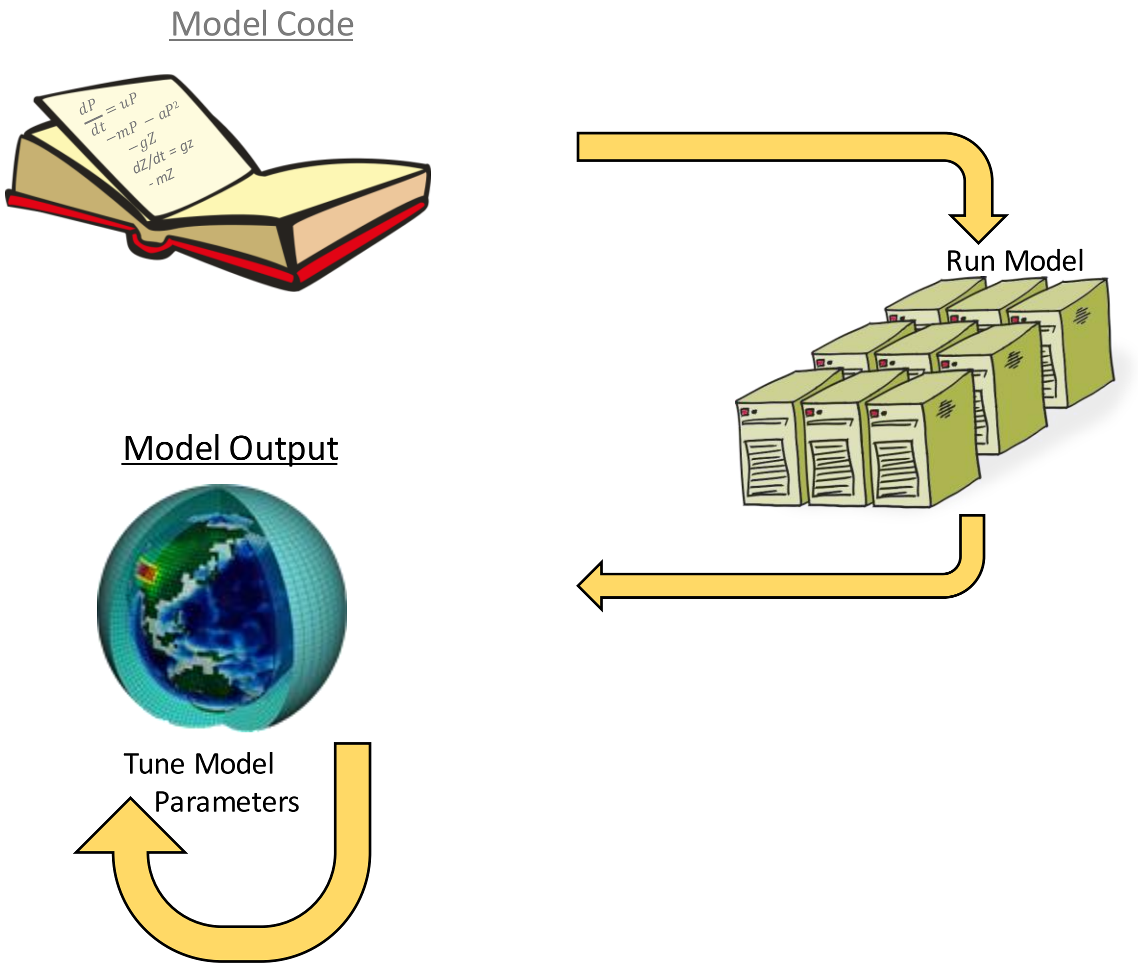
   Compare parameters and equations to empirical observations

   e.g. $K_{1/2}$, g_{max}, PGI

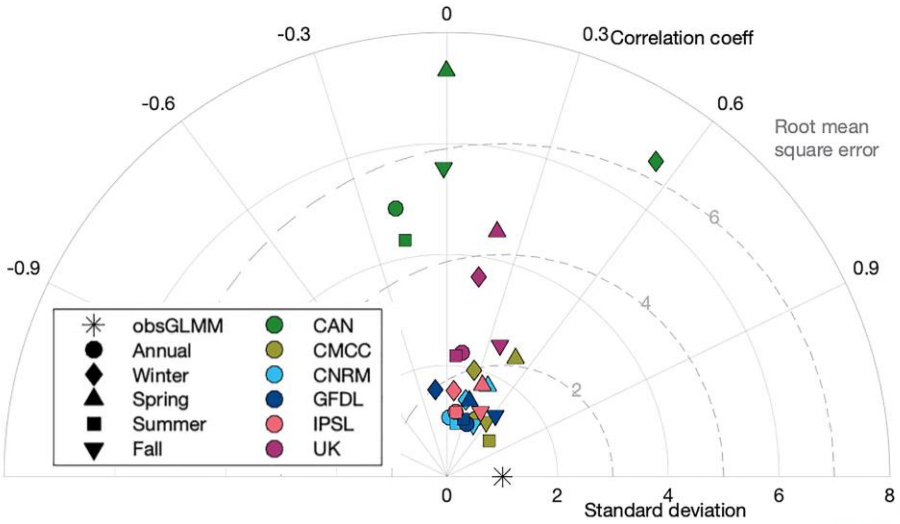
2. Emergent Properties

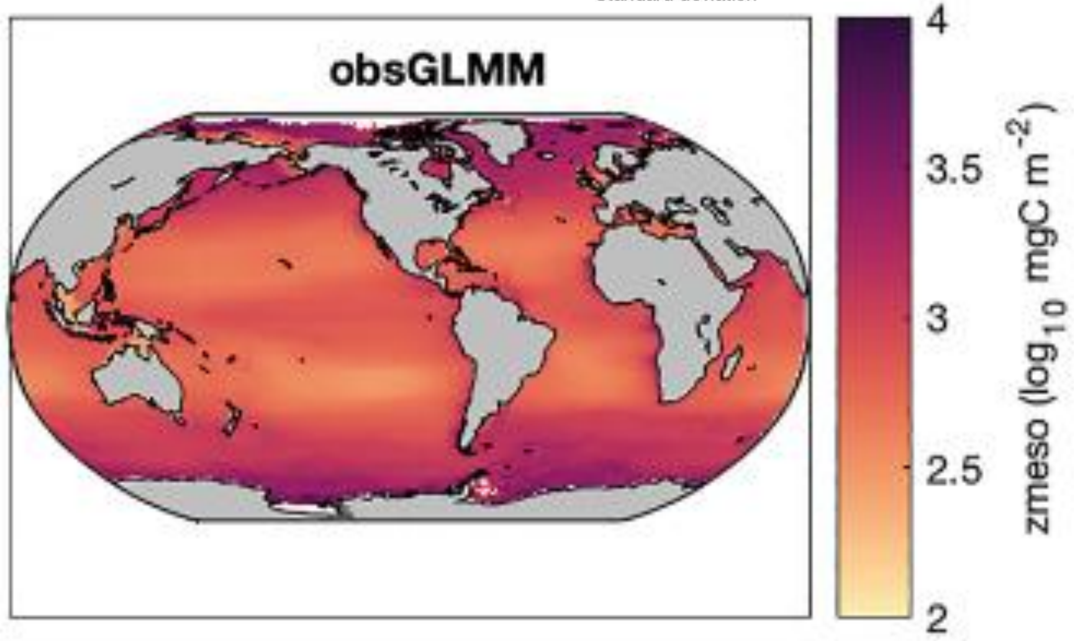
   Compare emergent properties of model output to observed properties

   e.g. Zooplankton Biomass, Grazing Pressure



Zooplankton Biomass

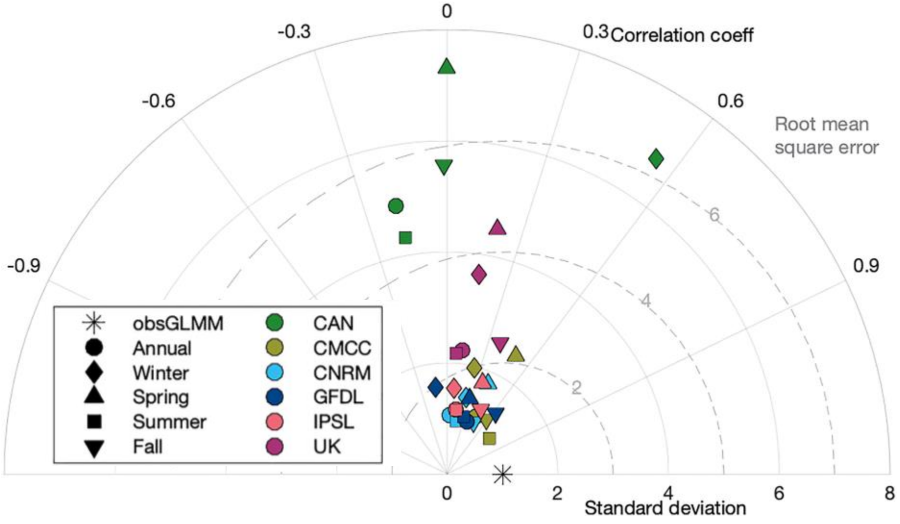




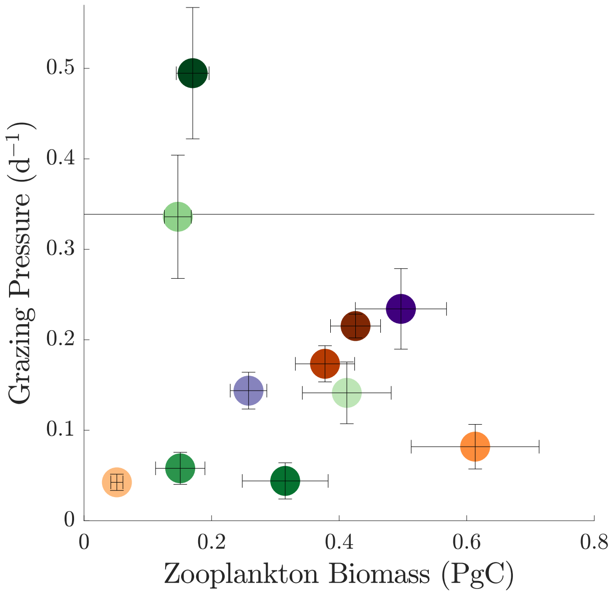
Statistical estimates of zooplankton biomass distributions can, and should be used to tune models

Petrick et al. GBC (2022)

Zooplankton Biomass



r^2 =-.09 p=.684



Statistical estimates of zooplankton biomass distributions can, and should be used to tune models

But, isn't a strong driver of grazing pressure, so can't do the whole job without information about grazing rates

'Observed' Grazing Pressure

$$\frac{dP}{dt} = uP - mP - aP^2 - Entrainment - gZ$$

Time-rate of change of phytoplankton biomass

NPP

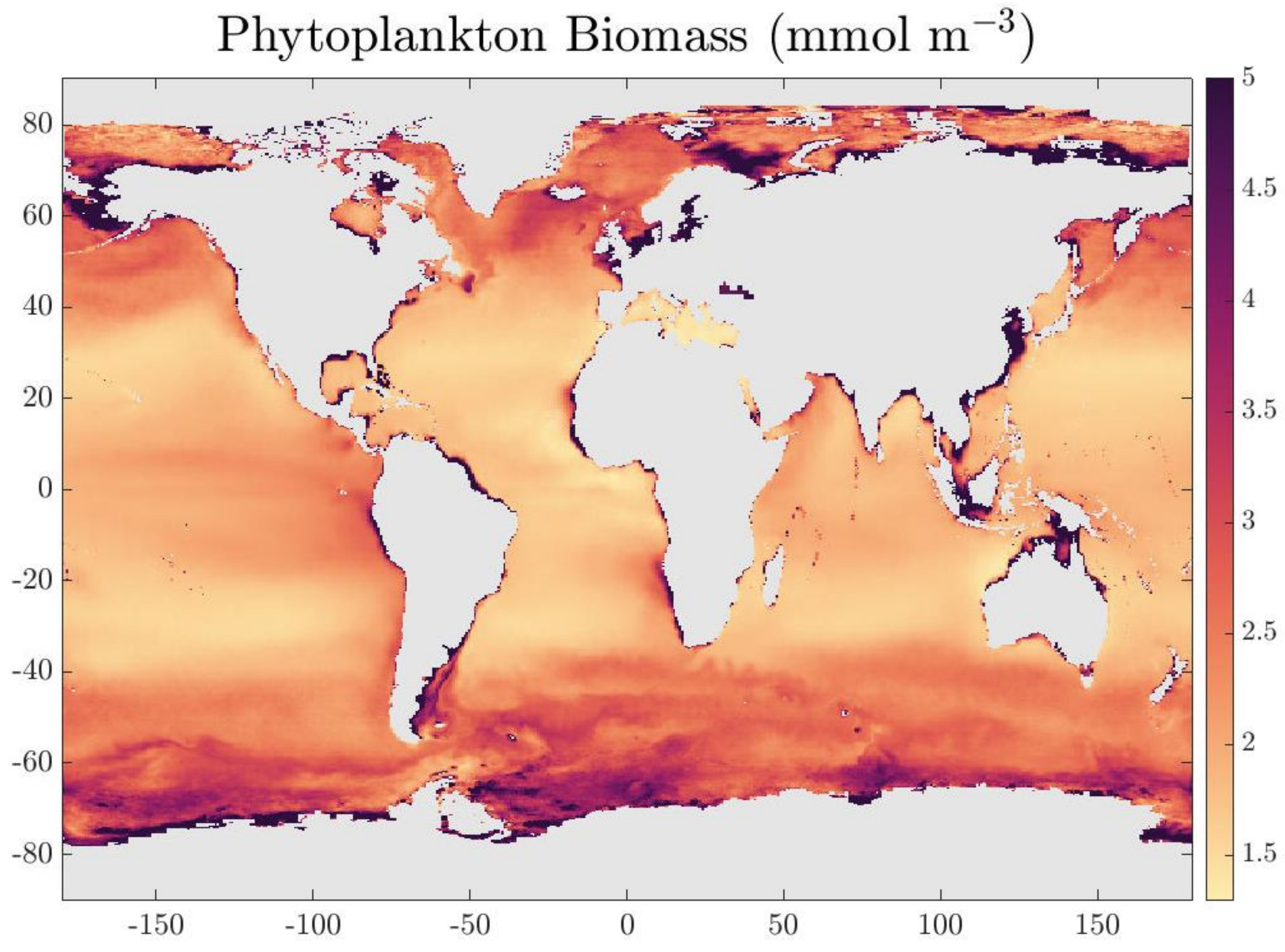
Linear + Non-linear Non-grazing losses

Physical dilution/entrainment of biomass below MLD during when MLD deepens

<u>Grazing Losses</u>
(GP =gZ/P)

‘Observed’ Grazing Pressure

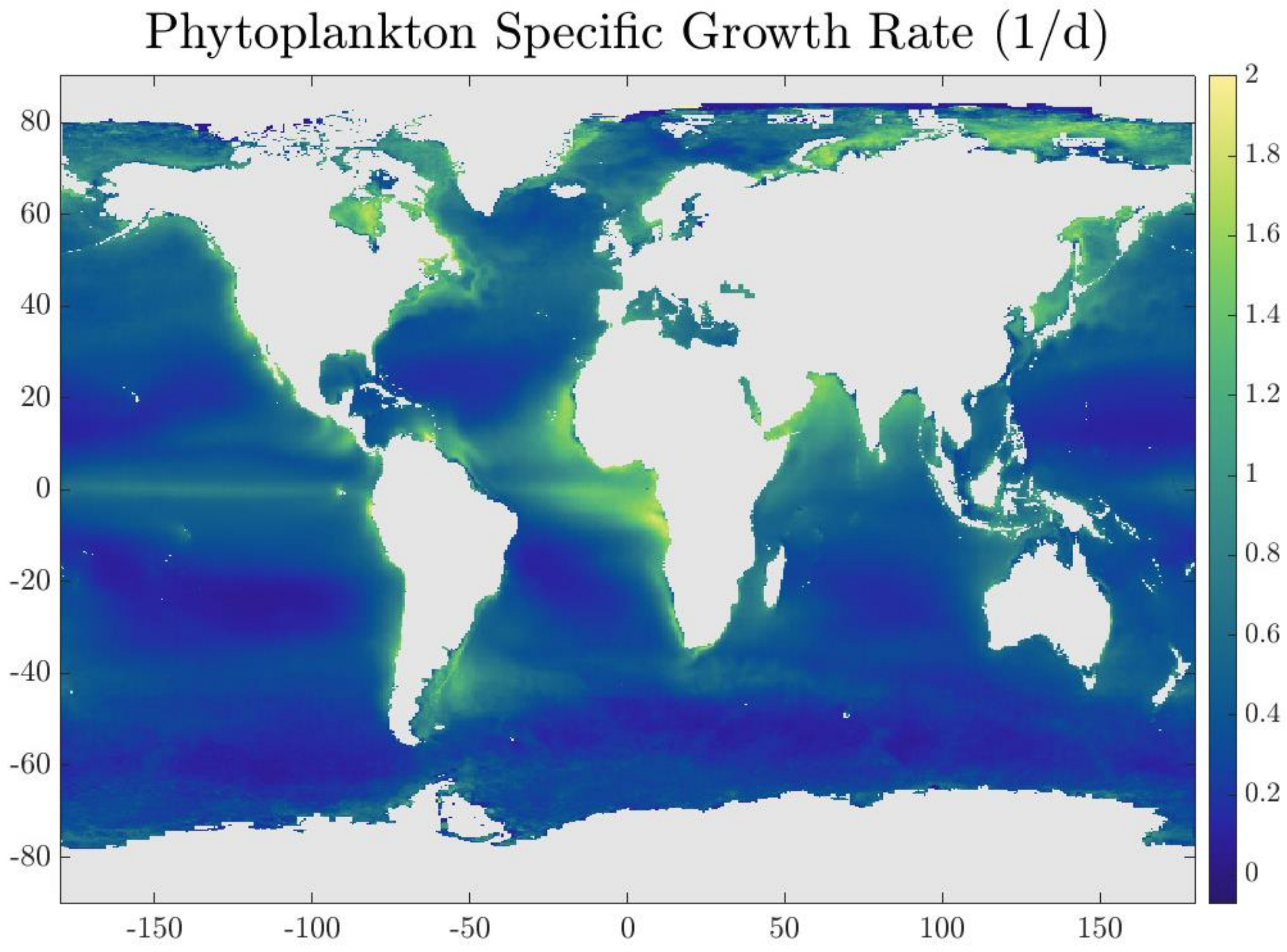
$$\frac{dP}{dt} = uP - mP - aP^2 - Entrainment - gZ$$



Optical backscattering + Empirical Relationship to phytoplankton biomass (Graff et al., 2015)

‘Observed’ Grazing Pressure

$$\frac{dP}{dt} = \boldsymbol{u}P \; - mP \; - aP^2 - Entrainment - gZ$$



Carbon-based Prod. Model
f(C:Chl, SST, Nutrients)

‘Observed’ Grazing Pressure

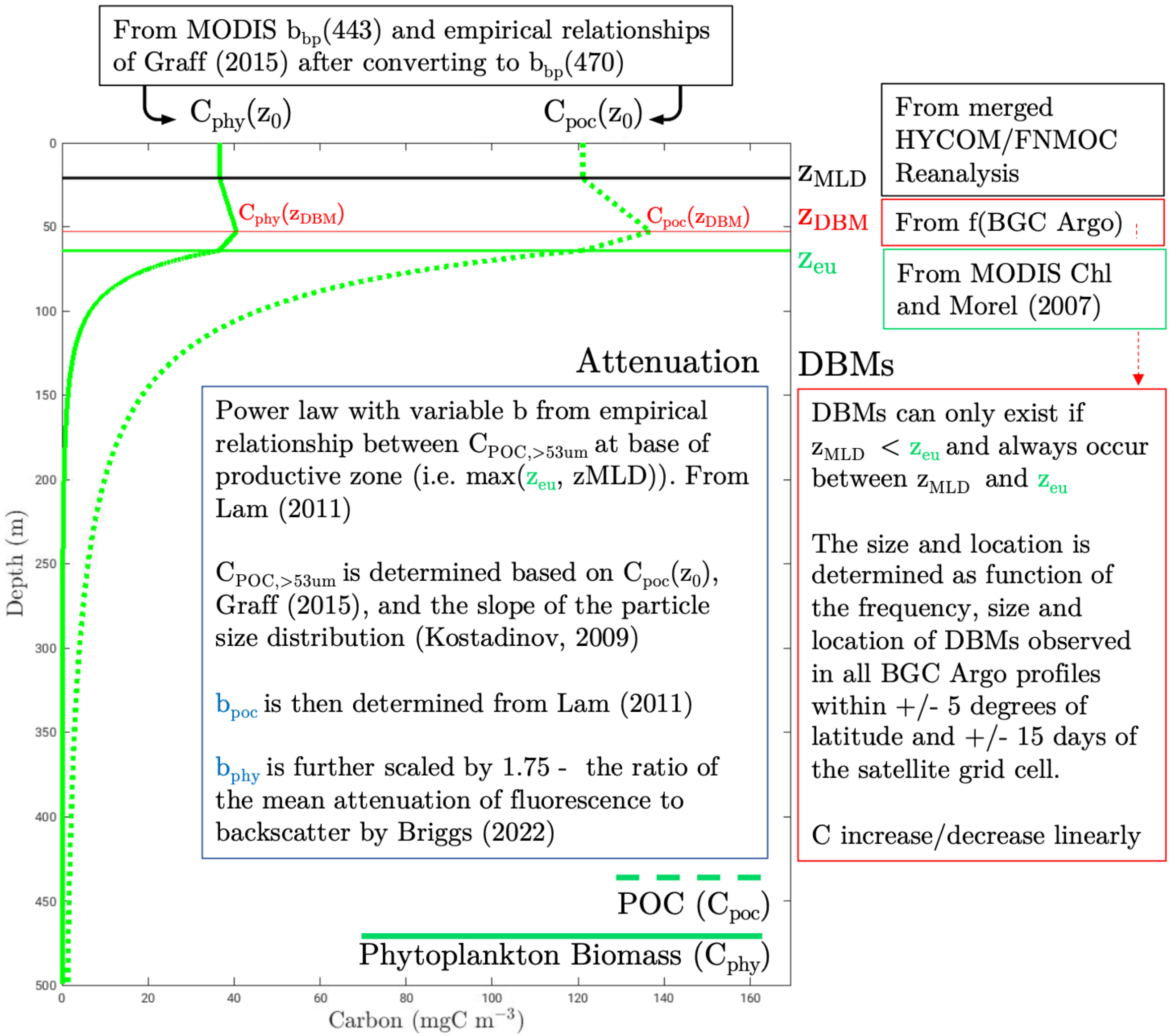
$$\frac{dP}{dt} = uP - \boldsymbol{mP} - \boldsymbol{aP^2} - Entrainment - gZ$$

BGC Model; Earth System Model	Phytoplankton Group	Non-Grazing Mortality Rate	Parameters
iHAMOCC NorESM2-LM	Phy. (P)	$(\mathrm{m}_1 + \mathrm{m}_2)P$	$\mathrm{m}_1 = 0.004$ $\mathrm{m}_2 = .004$
CMOC; CanESM5	Phy (P)	$\mathrm{m}P + \alpha P^2$	$\mathrm{m} = .05$ $\alpha = .015$
WOMBAT; ACCESS ESM1.5	Phy. (P)	$\mathrm{m}1.066^T P + \alpha P^2$	$\mathrm{m} = 0.04$ $\alpha = 0.038$
OECO-v2; MIROC-ES2L	Small Phytoplankton (P_{sm})	$\mathrm{m}P + \alpha P^2$	$\mathrm{m} = .05$ $\alpha = .0075$
	Large Phytoplankton (P_{lg})	$\mathrm{m}P$	$\mathrm{m} = .025$
MARBL; CESM2	Small Phytoplankton (P_{sm})	$\mathrm{m}1.7^{(T-30)/10}P + \alpha P^{1.75}$	$\mathrm{m} = .1$ $\alpha = .01$
	Diazatrophs (P_{dz})	$\mathrm{m}1.7^{(T-30)/10}P + \alpha P^{1.75}$	$\mathrm{m} = .1$ $\alpha = .01$
	Diatoms (P_{lg})	$\mathrm{m}1.7^{(T-30)/10}P + \alpha P^{1.75}$	$\mathrm{m} = .1$ $\alpha = .01$
CanOE; CanESM5-CanOE	Small Phytoplankton (P_{sm})	$\mathrm{m}P + \alpha P^2$	$\mathrm{m} = .05$ $\alpha = .06$
	Large Phytoplankton (P_{lg})	$\mathrm{m}P + \alpha P^2$	$\mathrm{m} = .1$ $\alpha = .06$
MEDUSA2.1; UKESM1-0-LL	Small Phytoplankton (P_{sm})	$\mathrm{m}_1 P + \mathrm{m}_2 \frac{P}{k+P} P$	$\mathrm{m}_1 = .02$ $\mathrm{m}_2 = .1$ $\mathrm{k} = .076$
	Large Phytoplankton (P_{lg})	$\mathrm{m}_1 P + \mathrm{m}_2 \frac{P}{k+P} P$	$\mathrm{m}_1 = .02$ $\mathrm{m}_2 = .1$ $\mathrm{k} = .076$

BGC Model; Earth System Model	Phytoplankton Group	Non-Grazing Mortality Rate	Parameters
PISCESv2; IPSL-CM6a-LR & CNRM-ESM2.1	Small Phytoplankton (P_{sm})	$\mathrm{m}_1 \frac{P}{k+P} P + \alpha P^2$	$\mathrm{m}_1 = .01$ $\mathrm{k} = .2$ $\alpha = .01$
	Large Phytoplankton (P_{lg})	$\mathrm{m}_1 \frac{P}{k+P} P + \alpha P^2$	$\mathrm{m}_1 = .01$ $\mathrm{k} = .2$ $\alpha = .025$
BFM5.2; CMCC-ESM2	Small Phytoplankton (P_{sm})	$\mathrm{m}_1 \frac{P}{k+P} P + \mathrm{m}_N P + \mathrm{rsp} + \mathrm{exu}$	$\mathrm{m}_1 = \mathrm{NA}$ $\mathrm{k} = \mathrm{NA}$ $\mathrm{m}_N = \mathrm{f(nuts)}$
	Large Phytoplankton (P_{lg})	$\mathrm{m}_1 \frac{P}{k+P} P + \mathrm{m}_N P + \mathrm{rsp} + \mathrm{exu}$	$\mathrm{m}_1 = \mathrm{NA}$ $\mathrm{k} = \mathrm{NA}$ $\mathrm{m}_N = \mathrm{f(nuts)}$
COBALTv2[C]; GFDL-ESM4.1	Small Phytoplankton (P_{sm})	$\beta\mathrm{NPP} + \mathrm{m}_1 e^{kT} P^2 + \alpha f(\mu) P^2$ $f(\mu) = (1 - max(1, \frac{\mu}{.25 * \mu_{max}}))^2$	$\mathrm{m}_1 = .03$ $\mathrm{k} = .063$ $\alpha = .015$ $\beta = .13$
	Diazatrophs (P_{dz})	$\beta\mathrm{NPP}$	$\beta = .13$
	Large Phytoplankton (P_{lg})	$\beta\mathrm{NPP} + \alpha f(\mu) P^2$	$\alpha = .045$ $\beta = .13$
Siegel et al. (2014)	Small Phytoplankton (P_{sm})	$\mathrm{m}P$	$\mathrm{m} = .1$
	Large Phytoplankton (P_{lg})	$\mathrm{m}P + \beta\mathrm{NPP}$	$\mathrm{m} = .1$ $\beta = .01$

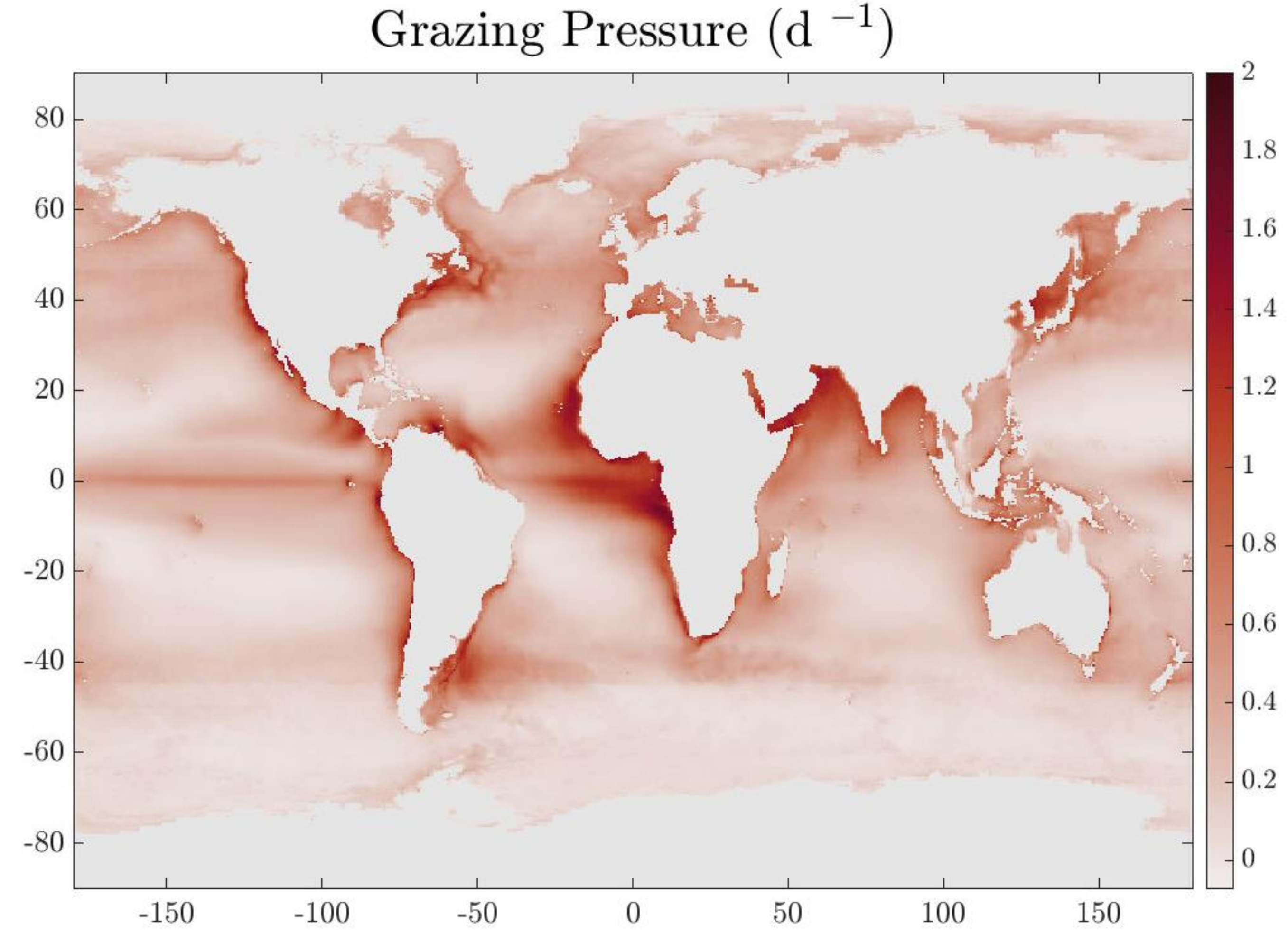
'Observed' Grazing Pressure

$$\frac{dP}{dt} = uP - mP - aP^2 - \boldsymbol{Entrainment} - gZ$$



‘Observed’ Grazing Pressure

$$\frac{dP}{dt} = uP - mP - aP^2 - Entrainment - \boldsymbol{gZ}$$

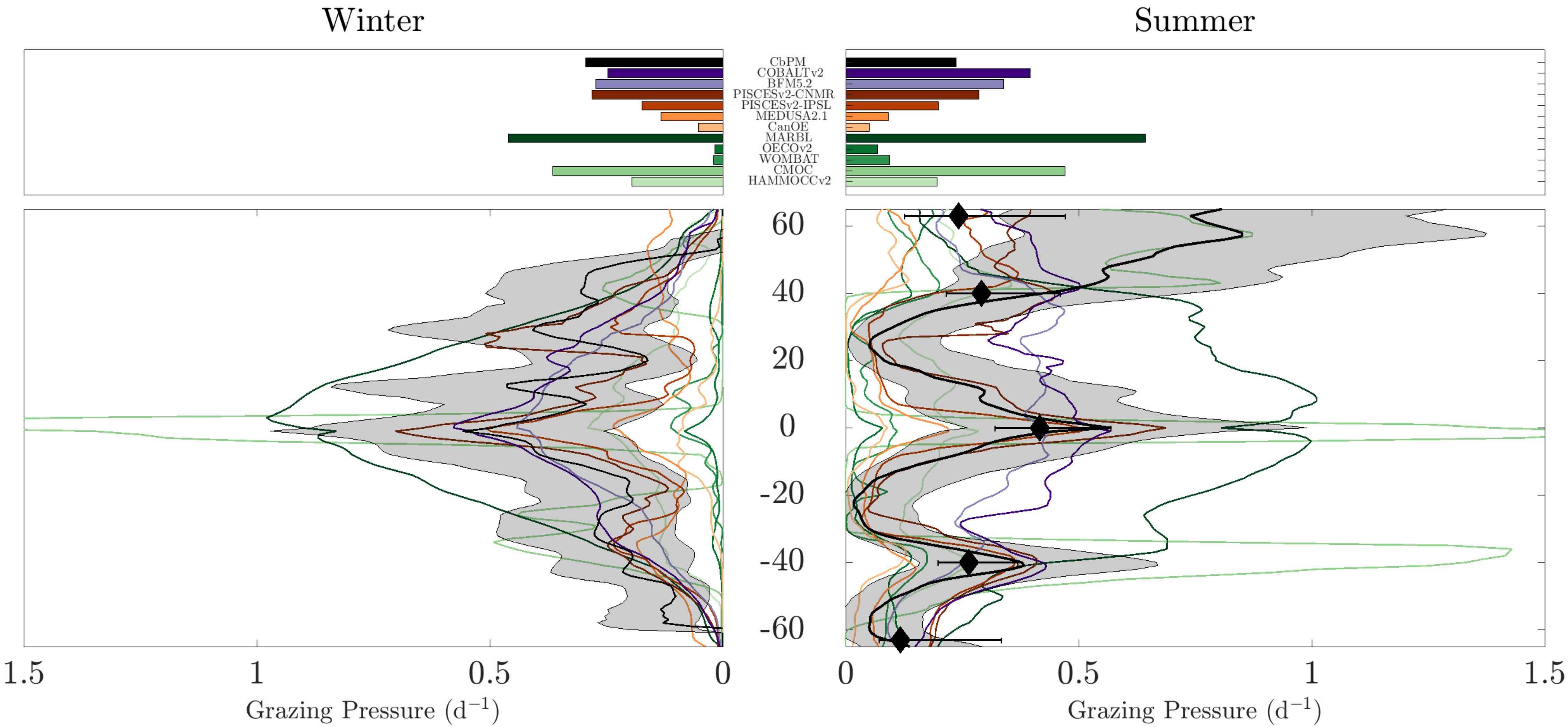


Algebra!

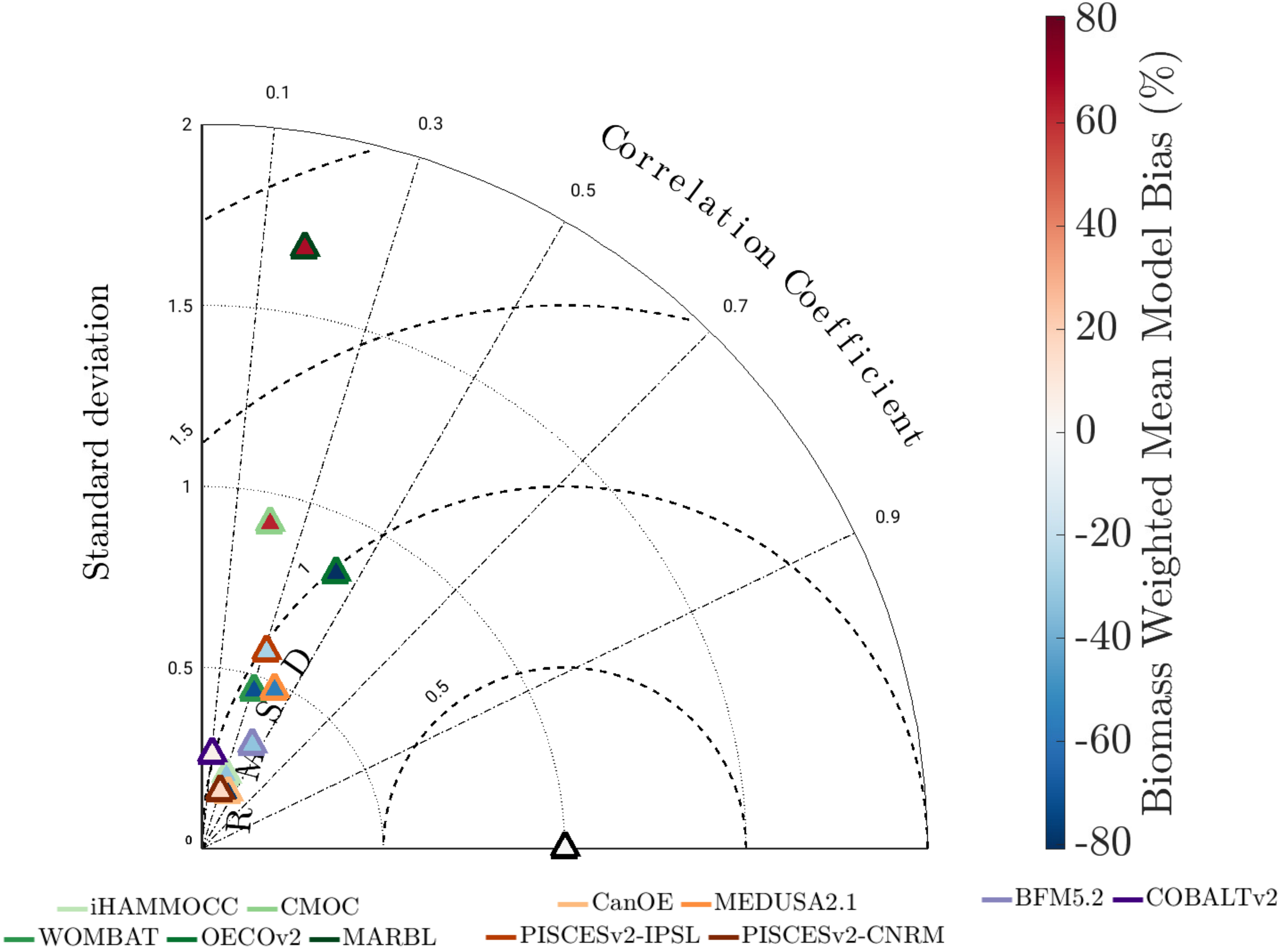
Grazing Pressure = gZ/P

‘Observed’ Grazing Pressure

$$\frac{dP}{dt} = uP - mP - aP^2 - Entrainment - \boldsymbol{gZ}$$



‘Observed’ Grazing Pressure



2.3 Emergent Relationships

Three Tiers of Constraints

1. Prescribed Properties

   Compare parameters and equations to empirical observations

   e.g. $K_{1/2}$, g_{max}, PGI

2. Emergent Properties

   Compare emergent properties of model output to observed properties

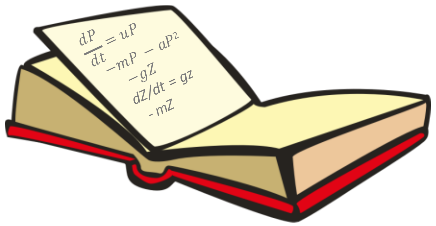
   e.g. Zooplankton Biomass, Grazing Pressure

3. Emergent Relationships

   Compare emergent relationships in model to observed relationships

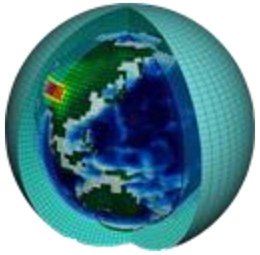
   e.g Community-integrated functional response

Model Code

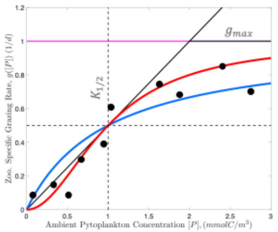


Run Model

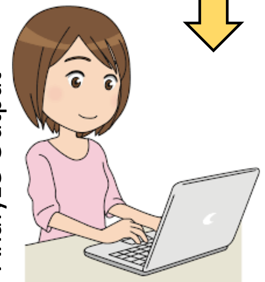
Model Output



Model Diagnostics

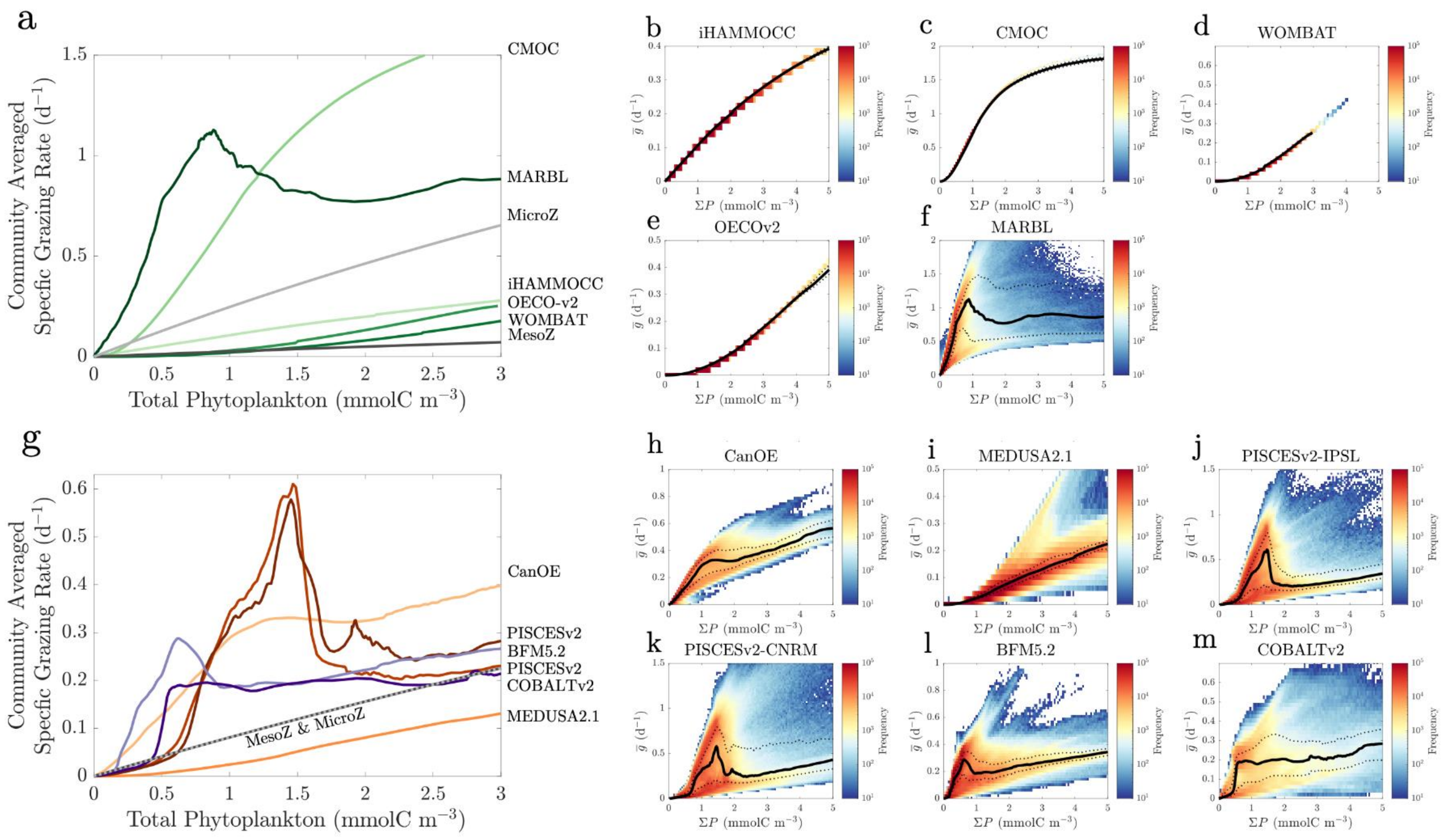


Analyze Output



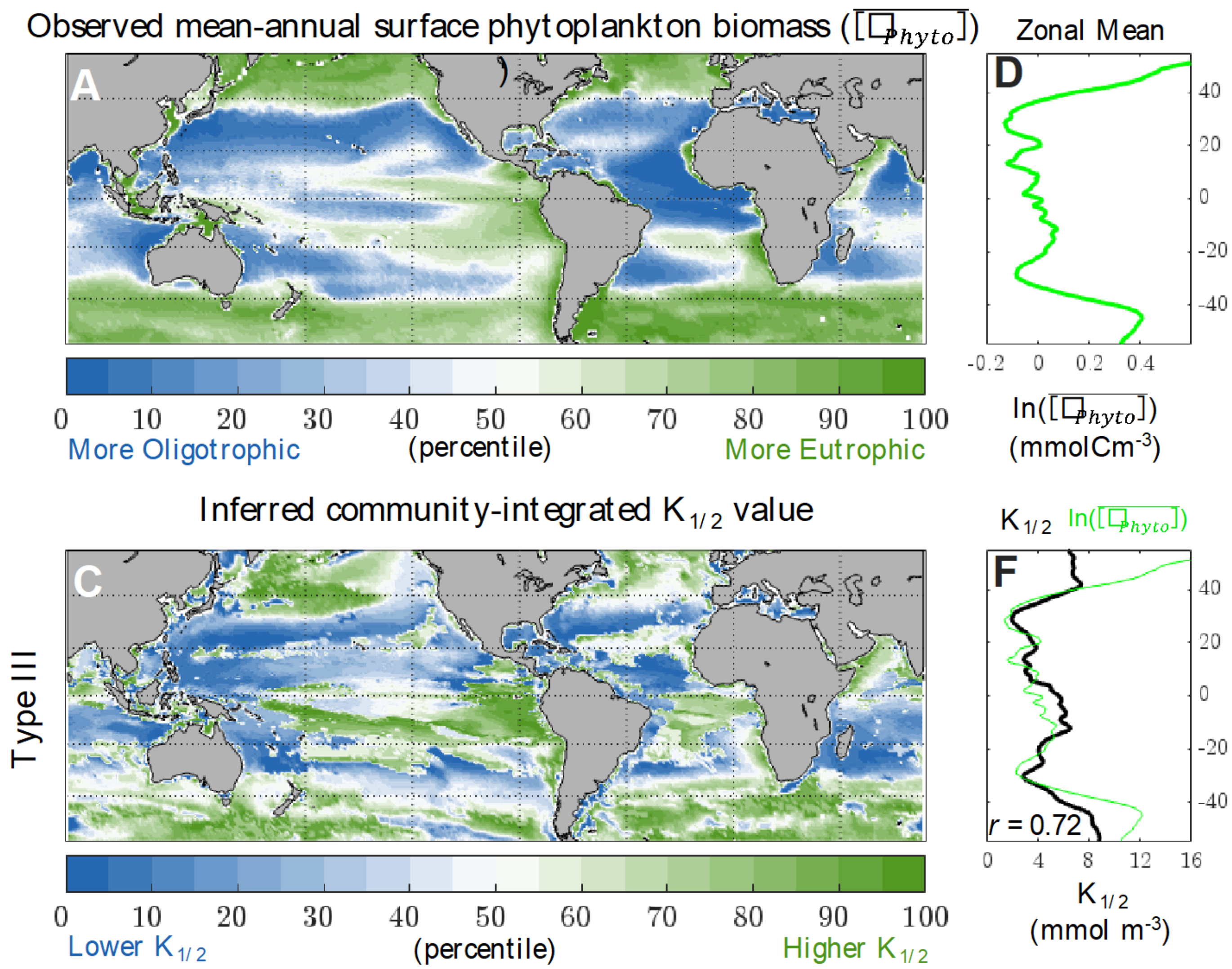
The Apparent Functional Response

In CMIP6 Models



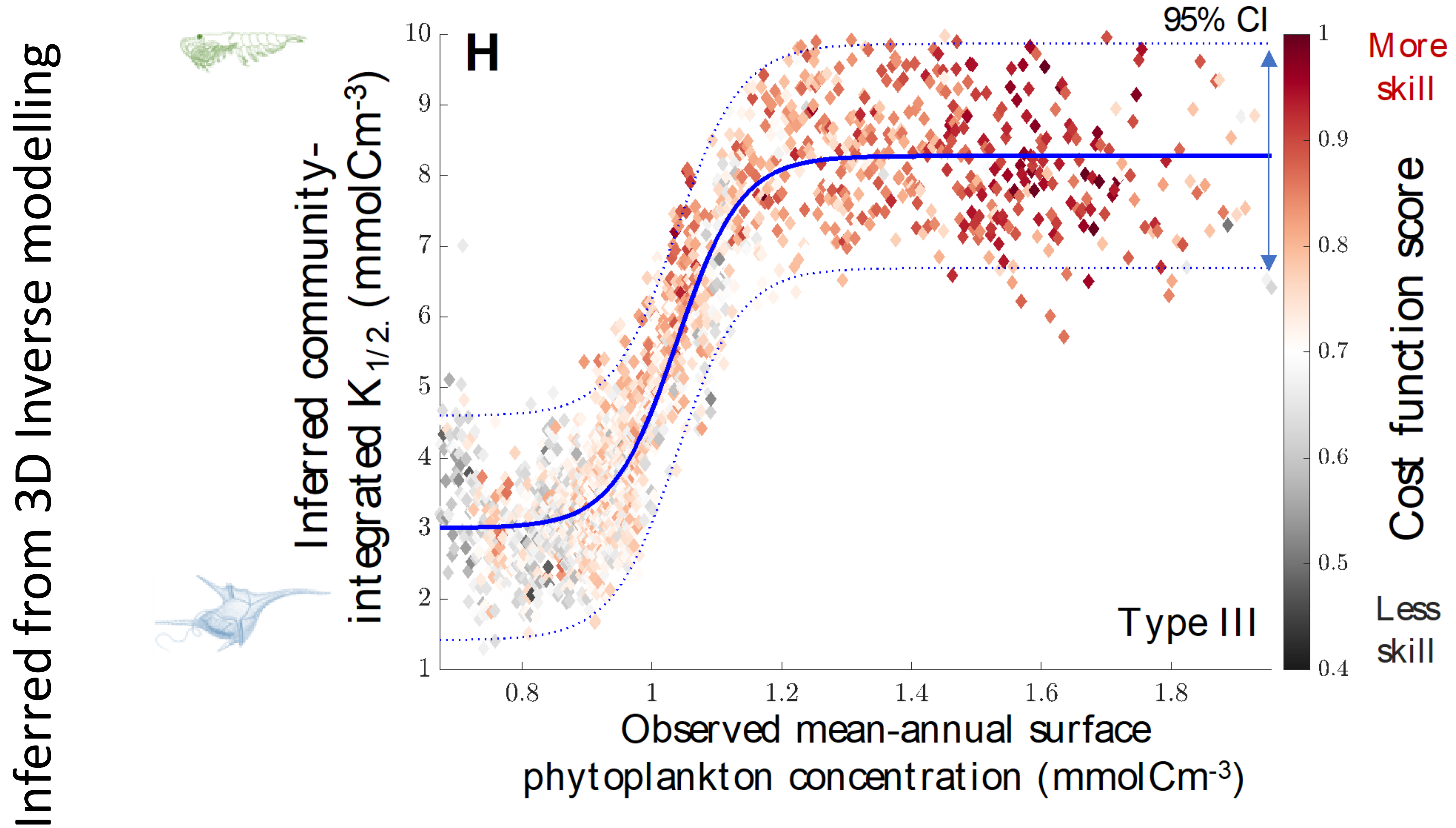
The Apparent Functional Response

Inferred from 3D Inverse modelling



Rohr et al. GRL (2024)

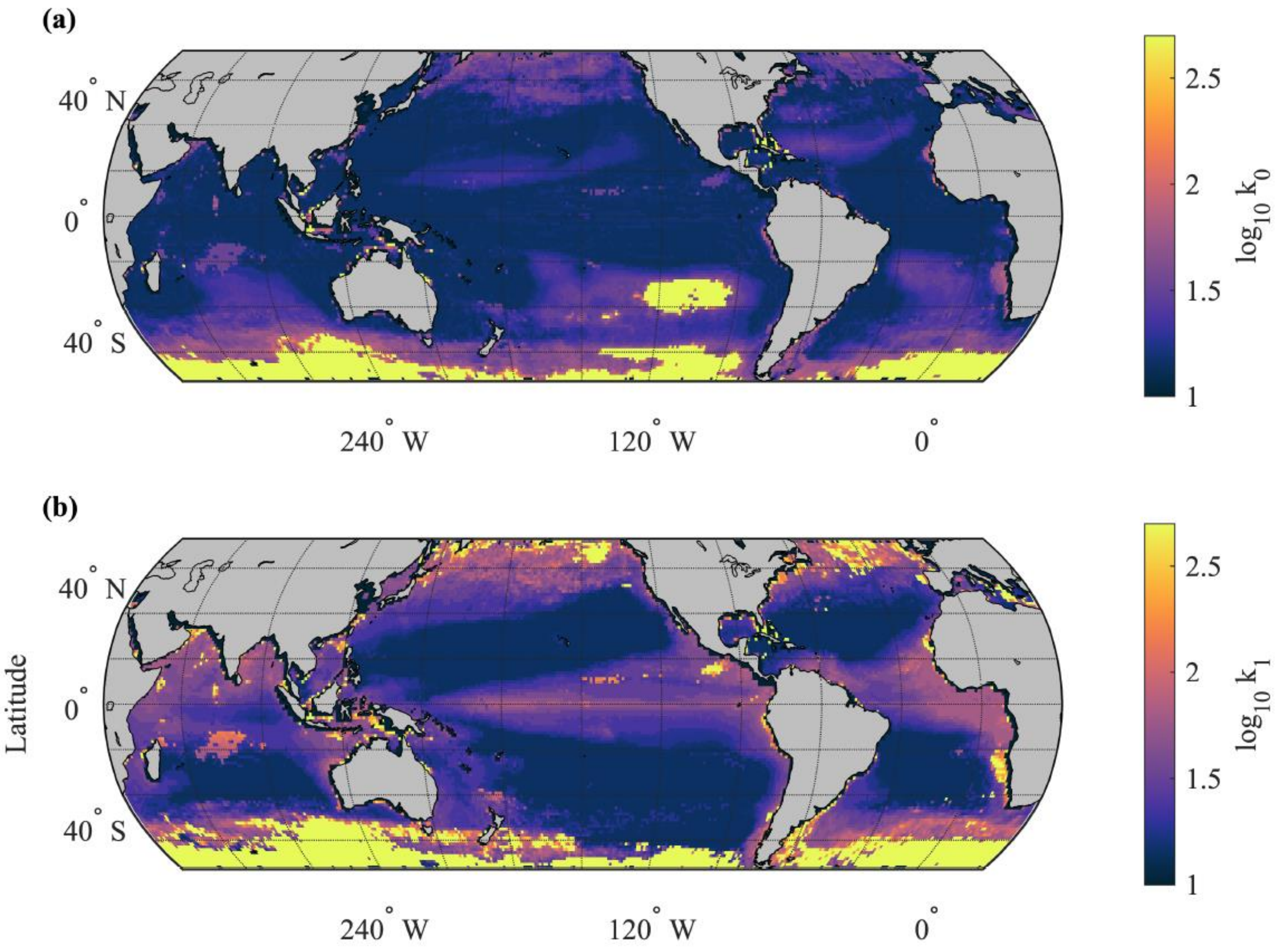
The Apparent Functional Response



Rohr et al. GRL (2024)

The Apparent Functional Response

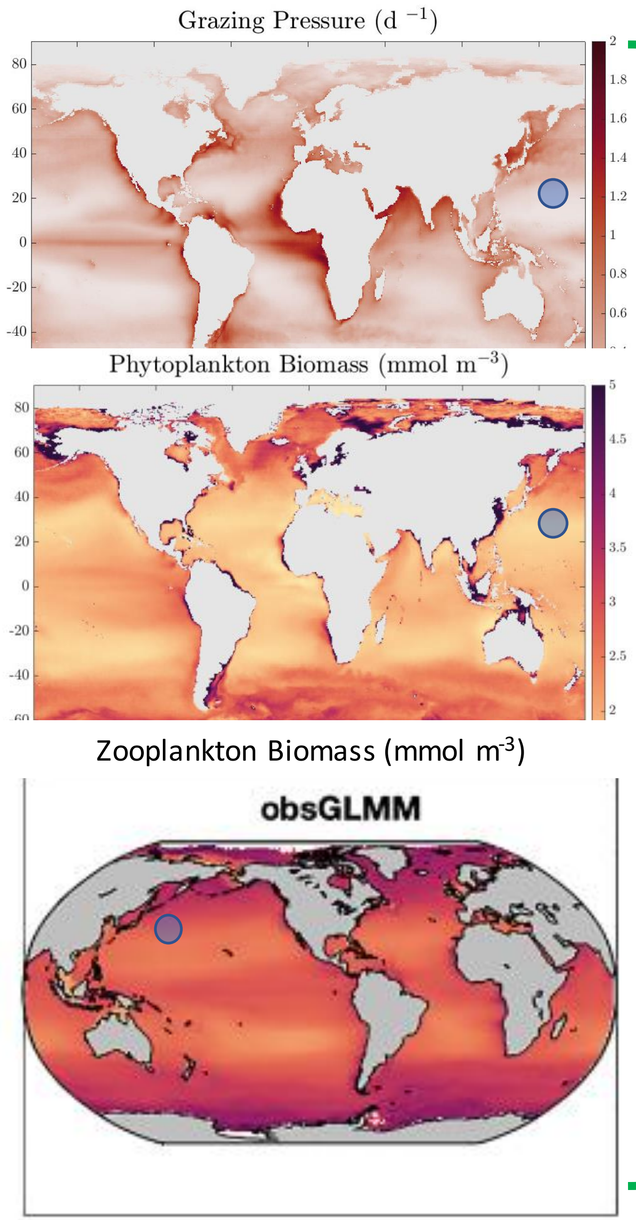
Inferred from 0D Inverse modelling



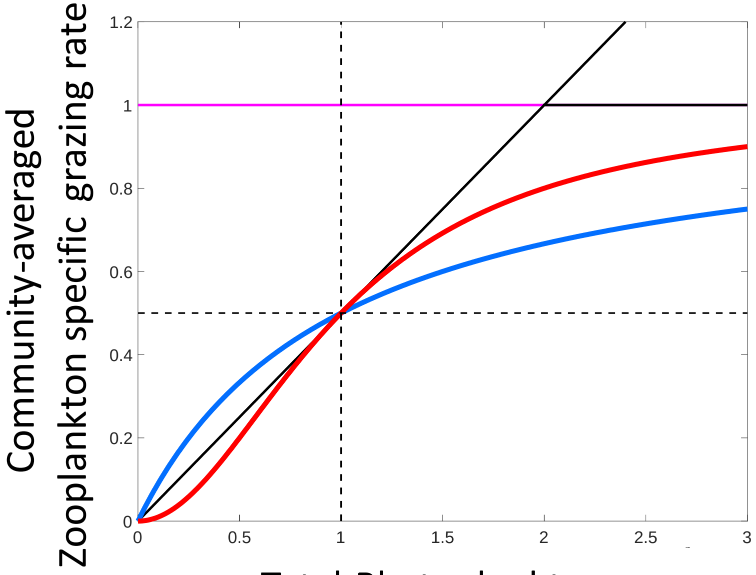
Meyers et al. GBC (Under Review)

The Apparent Functional Response

Remote Sensing 'observations'



Community – Integrated $K_{1/2}$



Total Phytoplankton Concentration

Yunzhe (Leo) Liu (PhD)

Putting It All Together In ACCESS

Three Tiers of Constraints

1. Prescribed Properties

   Compare parameters and equations to empirical observations

   e.g. $K_{1/2}$, g_{max}, PGI

2. Emergent Properties

   Compare emergent properties of model output to observed properties

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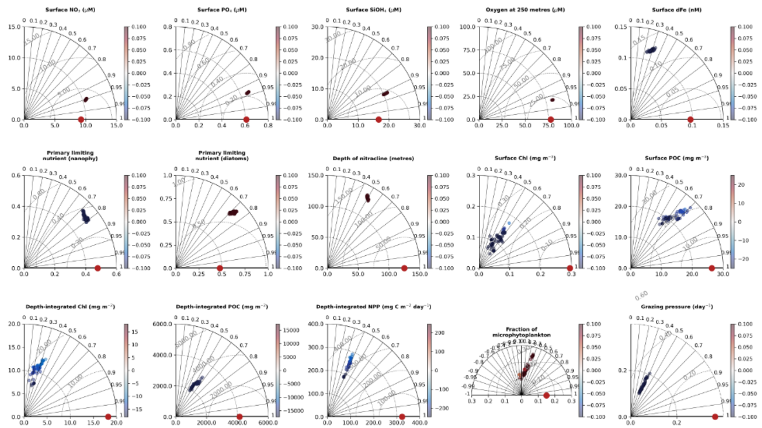
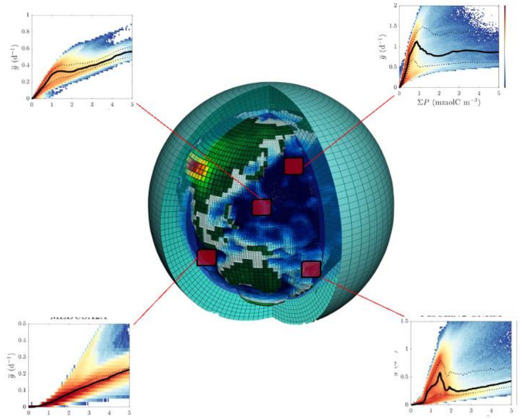
   Compare emergent relationships in model to observed relationships

   e.g Community-integrated functional response

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
1	zoogmax	mesgmax	epszoo	epsmes	zprefdia	zprefdet	zprefpoc	mprefphy	mprefdet	mprefpoc	zooexcr	mesqmor	g_mic	g_mes	g_mic_phy	g_mic_dia	g_mes_phy	g_mes_dia	pgi
2	1.66	0.35	0.47	0.05	0.32	0.18	0.24	0.51	0.19	0.18	0.05	0.48	0.39	0.07	0.04	0.01	0	0	0.13
3	1.52	0.35	0.47	0.05	0.32	0.18	0.24	0.51	0.19	0.18	0.05	0.48	0.38	0.07	0.04	0.01	0	0	0.13

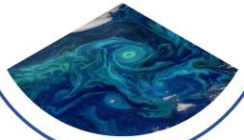
Buchanan et al. (in prep)





Yunzhe (Leo) Liu (PhD)

Thank You and Questions



Elizabeth Shadwick, Andrew Lenton, Anthony Richardson, Matthew Chamberlain