Response to Reviewers

Manuscript Title: Role of diatoms reproductive dynamics in plankton trophic webs

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Response to Reviewer #1

We thank the reviewer for the careful and prompt reading of the manuscript and for the constructive and very interesting comments. For clarity, all figures and tables included in this response are identified using the prefix R1- (e.g., Fig. R1-1, Table R1-1) to distinguish them from those in the revised manuscript.

Major Comment 1

Reviewer Comment:

> *1. Central elements of the methodology are missing or are unclear (section 2.3):*
>
> *a) how does the ratio between the size of new sexually reproduced cells (large) and the size of sexual reproduction (small) enter into the model? It seems as if all cells become smaller, regardless of their species, until they reach a lower limit (50 um), where there is a flux from the smallest size class towards the largest one. That rate of sexual reproduction is only described loosely as being proportional to NPP. Further, if that is correctly understood, then the diatom model essentially models a fictive species that has a ratio between new cells and sexually reproducing cell of a factor 10 (the size range of diatom cells) which is much larger than the ratio in individual species (50/20). If that is correctly understood, then the sexual reproduction model does not faithfully represent the sexual reproduction dynamics of the diatoms. The implication of this approximation should be discussed.*

Response:

We thank the Reviewer for this important comment, which touches on the conceptual scope of the proposed modelling framework. The objective of the present model is not to reproduce the reproductive cycle of all the individual diatom species, but rather to investigate whether reproduction-induced restructuring of the diatom size spectrum can influence plankton community dynamics at the ecosystem scale. Accordingly, the model represents the diatom community as a continuum of size classes and describes the aggregate redistribution of biomass associated with repeated cycles of size reduction and sexual size restoration.

As a consequence of this coarse-grained representation, the modeled size-reduction–restitution cycle spans a broader size interval than is typically observed for individual species and should therefore not be interpreted as the life cycle of a single taxon. Instead, it provides an effective description of community-level biomass redistribution across the diatom size spectrum, allowing us to isolate and quantify the ecological consequences of reproductive size restructuring within a marine ecosystem model.

Nevertheless, we agree that it is important to assess the sensitivity of our conclusions to this modelling assumption. To this end, in the revised manuscript we will implement an alternative formulation in which the diatom community is partitioned into two representative size groups, each characterized by an independent size-reduction–restitution cycle and a distinct minimum size threshold (Fig. R1-1).

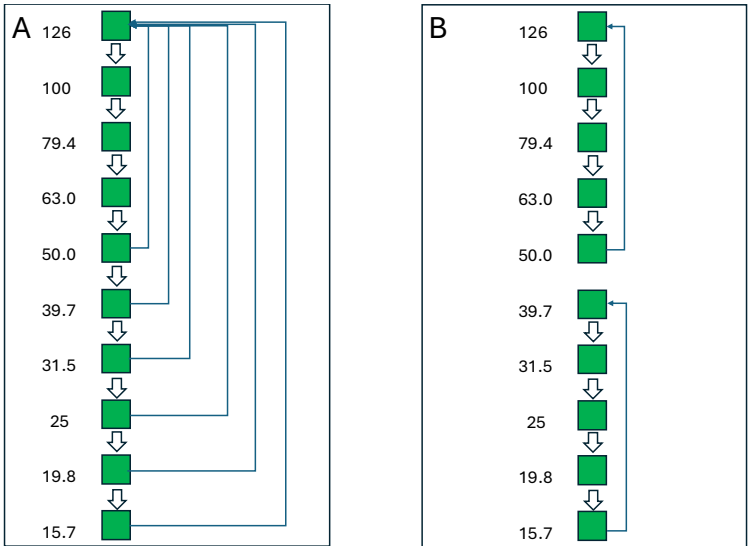

Figure R1-1: Alternative schemes for diatom reproduction dynamics. Scheme A represents the formulation currently adopted in the manuscript, while Scheme B is the additional framework proposed in response to the Reviewer's comment, accounting for stricter mother/daughter size ratios during the CSRR. In Scheme B, diatoms are separated into two classes, corresponding to larger and smaller cells.

This formulation introduces an explicit size constraint between the mother cell and the auxospore, leading to a more realistic representation of the reproductive cycle.

Regarding the rate of sexual reproduction, quantitative observational constraints are currently lacking. For this reason, we assumed it to be proportional to primary production. To account for the associated uncertainty, the proportionality coefficient was systematically perturbed in the sensitivity experiments.

Reviewer Comment:

> *b) How is the growth rate rho (or is it a division rate?) modeled? I miss a description of the physiological model of the diatoms: which resources do the use? What are the affinities (and how do they scale with size)? What is the maximum growth rate (a unimodal size dependency is alluded to, but it should be shown). Are there any density-dependent terms? Here I miss equations for the full diatom model and figures that show the data that the size-based relations have been fitted to.*

Response:

We thank the Reviewer for this helpful comment. The base model, including its governing equations and allometric relationships, was published previously [1] and is referenced throughout the manuscript. The objective of the present work is not to re-derive the allometric scaling relationships from the original experimental measurements. These empirical relationships were established and validated in the studies from which they were adopted and constitute the foundation of the published model. Instead, the objective of the present study is to extend the existing framework by introducing the explicit representation of diatom reproductive dynamics. For this reason, the manuscript reports the original sources and references from which the allometric parameterizations were adopted.

Nevertheless, we agree that the presentation can be made more transparent. In the revised manuscript, we propose to include a figure summarizing the principal allometric scaling relationships employed in the model (Fig.R1-2). In addition, we have prepared a comprehensive table (Tab.R1-1) reporting the analytical expressions of all scaling laws, together with their parameter values and the corresponding literature sources. We believe these additions will sub-

stantially improve the transparency, readability, and reproducibility of the model while avoiding unnecessary duplication of material already presented in the original model description.

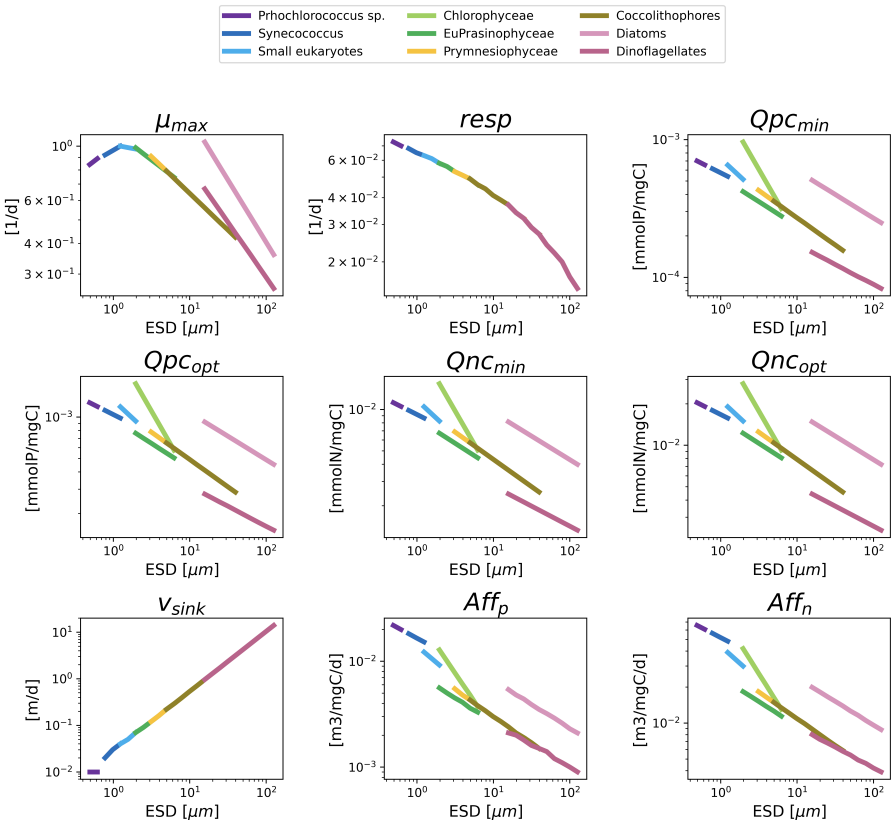

Figure R1-2: Allometric relationships between equivalent spherical diameter (ESD) and the main physiological parameters adopted for the different phytoplankton functional groups. Panels show the maximum growth rate ($\mu_{\max}$), respiration rate ((resp)), minimum and optimal phosphorus quotas (Qpc_{min}, Qpc_{opt}), minimum and optimal nitrogen quotas (Qnc_{min}, Qnc_{opt}), sinking velocity (v_{sink}), and phosphorus and nitrogen affinities (Aff_p, Aff_n). Colors identify the different phytoplankton groups considered in the model.

Following Major Comment 1e by Reviewer 1, we will improve the description of diatom physiology in the revised manuscript by explicitly summarizing the physiological processes represented in the model. To further improve transparency, we will provide an explicit reference to the complete BFM manual, either through an online link or by including the relevant documentation as supplementary material with the revised manuscript.

Table R1-1: Allometric relationships used to derive BFM parameters from cell size. Volume is denoted by V and equivalent spherical diameter by ESD. For brevity, allometric parameters are reported only for diatoms when the same relationships were used for the other phytoplankton classes.

PFT	Parameter	Allometric relationship	Unit	Source	BFM parameter
P1 – Diatoms					
	Maximum growth rate ($\mu_{\max}$)	$3.8\,V^{-0.17}$	day^{-1}	[2, 3]	p_sum
	Basal respiration rate (resp)	$0.063 - 0.008\log_{10}(V)$	day^{-1}	[4]	p_srs
	Optimum internal phosphate quota ($\mathrm{QPC_{opt}}$)	$10^{-0.29}V^{0.767}/2$	fmol cell^{-1}	[5]	p_qpcPPY
	Minimum internal phosphate quota ($\mathrm{QPC_{min}}$)	$0.55\,QPC_{\mathrm{opt}}$	fmol cell^{-1}	–	p_qplc
	Optimum internal nitrogen quota ($\mathrm{QNC_{opt}}$)	$QPC_{\mathrm{opt}} \times 0.0126/0.000786$	fmol cell^{-1}	–	p_qncPPY

PFT	Parameter	Allometric relationship	Unit	Source	BFM parameter
	Minimum internal nitrogen quota (QNC_{min})	$0.55\,QNC_{opt}$	fmol cell^{-1}	–	p_qnlc
	Membrane affinity for phosphorus (AffP)	$10^{-8.1}V^{0.73}$	L cell^{-1} d^{-1}	[6]	p_qup
	Membrane affinity for nitrogen (AffN)	$10^{-8.2}V^{0.75}$	L cell^{-1} d^{-1}	[6]	p_qun
	Settling velocity (v_{sink})	$0.024V^{0.37}$	m d^{-1}	[7]	p_res
	Carbon content (C)	$10^{-0.933}V^{0.881}$	pg C cell^{-1}	[8]	used for unit conversions
P4 – Dinoflagellates					
	Maximum growth rate (μ_{max})	$2.1V^{-0.15}$	day^{-1}	[2, 3]	p_sum
	Carbon content (C)	$10^{-0.353}V^{0.864}$	pg C cell^{-1}	[8]	used for unit conversions
P2 – Prymnesiophyta and P5 – Coccolithophores					
	Maximum growth rate (μ_{max})	$1.2V^{-0.10}$	day^{-1}	[9]	p_sum
	Carbon content (C)	$10^{-0.642}V^{0.899}$	pg C cell^{-1}	[8]	used for unit conversions
P7 – Chlorophyceae					
	Maximum growth rate (μ_{max})	$1.1V^{-0.08}$	day^{-1}	[9]	p_sum
	Carbon content (C)	$10^{-1.026}V^{1.088}$	pg C cell^{-1}	[8]	used for unit conversions
P8 – Prasinophyceae					
	Maximum growth rate (μ_{max})	$1.1V^{-0.08}$	day^{-1}	[9]	p_sum
	Carbon content (C)	$10^{-0.545}V^{0.886}$	pg C cell^{-1}	[8]	used for unit conversions
P3 – Small eukaryotes					
	Maximum growth rate (μ_{max})	$1.0V^{-0.02}$	day^{-1}	[9]	p_sum
	Carbon content (C)	$10^{-0.665}V^{0.939}$	pg C cell^{-1}	[8]	used for unit conversions
P9 – Synechococcus					
	Maximum growth rate (μ_{max})	$1.0V^{0.06}$	day^{-1}	[9]	p_sum
	Carbon content (C)	$10^{-0.583}V^{0.860}$	pg C cell^{-1}	[8]	used for unit conversions
P6 – Prochlorococcus					
	Maximum growth rate (μ_{max})	$1.05V^{0.08}$	day^{-1}	[9]	p_sum
	Carbon content (C)	$10^{-0.583}V^{0.860}$	pg C cell^{-1}	[8]	used for unit conversions
Z3–Z6 Zooplankton					
	Maximal productivity	$26\,ESD^{-0.4}$	d^{-1}	[10]	p_sum
	Optimum prey size (PreyESD)	$ESD/10$	μm	[11, 12]	used to compute preferences
	Prey preference	$\exp\left[-\left(\frac{\log_{10}(D)-\log_{10}(\text{PreyESD})}{0.20}\right)^2\right]$		[13]	supreyX

Reviewer Comment:

c) How is the central equation (9) derived? I miss a description of all the parameters and relations that enter into this relationship.

Response:

Equation (9) is obtained by integrating the continuous size-structured transport equation over the size interval $[S_{A_i}, S_{B_i}]$. The transport term

$$\frac{\partial}{\partial s}\big(\rho(s)\,n\big)$$

reduces to the net flux across the class boundaries,

$$\frac{\mathrm{d}}{\mathrm{d}t}\int_{S_{A_i}}^{S_{B_i}} n(t,s)\,ds = \cdots + \left[\rho(s)\,n(t,s)\right]_{S_{A_i}}^{S_{B_i}}.$$

Introducing the discrete concentration

$$n_i(t) = \int_{S_{A_i}}^{S_{B_i}} n(t,s)\,ds,$$

the boundary density is approximated assuming that the concentration is nearly uniform within each logarithmically spaced size class,

$$n\big(t, S_{A_i}\big) \approx \frac{n_i(t)}{S_{B_i} - S_{A_i}}.$$

Accordingly, the shrinking flux through the lower interface is approximated as

$$\Phi_{S_{A_i}} \approx \rho\big(S_{A_i}\big)\, \frac{n_i(t)}{S_{B_i} - S_{A_i}}.$$

which corresponds to a first-order finite-volume (upwind) approximation of the transport flux, where the transport velocity is evaluated at the interface S_{A_i}. Therefore, the evaluation of ρ at the lower class boundary is a numerical approximation introduced by the discretization rather than a direct consequence of the continuous formulation. ρ was formerly expressed in splitting cycle assuming one splitting per day: in the updated version of the theoretical and numerical model, the shrinking flux has been further corrected by replacing the modulation factor f_{NPP} with $F_{\mathrm{NPP}} \ln(2)$. The additional factor $\ln(2)$ accounts for the splitting velocity associated with binary cell division. The revised expression therefore reads

$$\Phi_{S_{A_i}} \approx F_{\mathrm{NPP}} \ln(2)\, \rho\big(S_{A_i}\big)\, \frac{n_i(t)}{S_{B_i} - S_{A_i}}.$$

Reviewer Comment:

> *d) It would be great to see an analysis of the diatom model in isolation and in an idealized setting. E.g. solving for the size distribution under a specific light and nutrient environment. How does the distribution look?*

Response:

We thank Reviewer 1 for the useful comment. Yes, the analysis proposed by the reviewer can be carried out using the model introduced in the theoretical section, by integrating it in isolation and adopting the same growth term used in the realistic simulations presented in the numerical section.

Specifically, we consider the characteristic equation,the ODE along the characteristic curve in s-space, with an additional saturation term representing the integrated effect of the ecosystem:

$$\frac{\mathrm{d}n}{\mathrm{d}s} = \left[\left(\mu(s) - \delta(s) - \beta(s)\right) n - n^2/K\right]/\rho(s)$$

The solution shown in Fig. R1-3 illustrates the evolution of an isolated diatom cohort initially introduced at a large cell size (120 μm). As the cohort ages, cell size progressively decreases and the population relaxes toward the equilibrium distribution, represented by the dotted green line. Within the characteristic framework, this temporal relaxation can be mapped onto the size dimension, as shown by the lower x-axis (cell size) and the upper x-axis (cohort age). In this example, the parameter ω is relatively large: the auxospore reaches its equilibrium concentration within approximately 10 days, Fig.R1-3c, with the characteristic and numerical solutions closely overlapping both each other and the analytical equilibrium solution. As a consequence, the cohort is unable to fully exploit the favorable conditions associated with the local maximum in carrying capacity around 120 μm. On the contrary, for lower values of ω, the relaxation toward equilibrium becomes slower, allowing the cohort to partially exploit the favorable region associated with the higher carrying capacity around 120 μm (Fig. R1-4). In this regime, the timescale of sexual reproduction becomes comparable to, or longer than, the ecological timescale,

leading to a transient accumulation of biomass at large cell sizes before the population converges toward the equilibrium distribution.

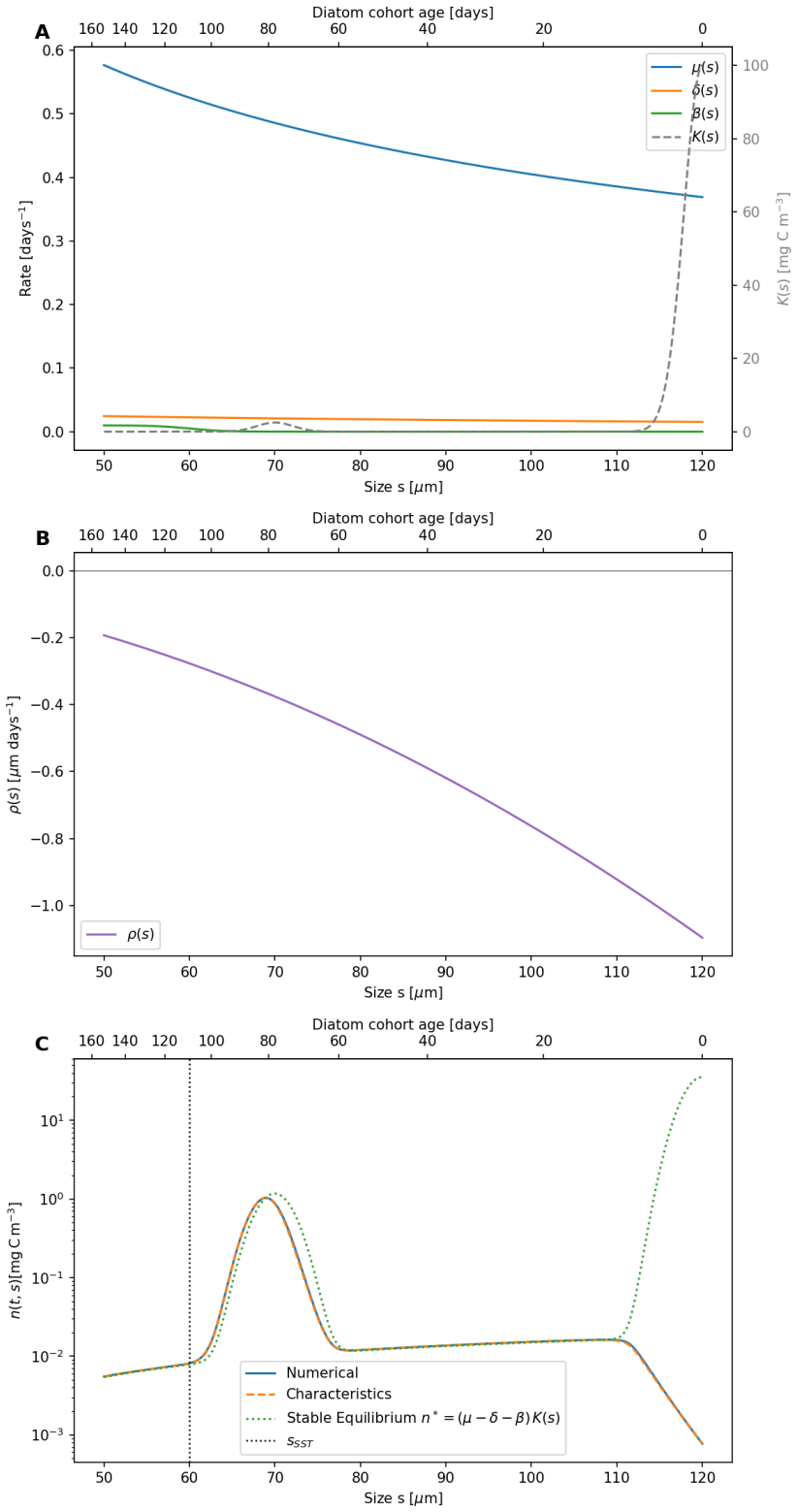

Figure R1-3: A) Size-dependent growth $\mu(s)$, mortality $\delta(s)$, sexual reproduction $\beta(s)$, and carrying capacity $K(s)$ used in the characteristic formulation of the diatom population model. The upper axis reports the corresponding cohort age associated with each cell size. (B) Characteristic velocity $\rho(s)$ governing the evolution of the population along the size coordinate, highlighting the progressive reduction in cell size during vegetative reproduction, $\omega = 0.5\ 10^{-4}\ \mu\text{m}^{-\frac{3}{2}}\ \text{d}^{-1}$. (C) Comparison between the numerical solution of Eq. (1), the solution obtained from the characteristic formulation, and the analytical stable equilibrium $n_*(s) = (\mu - \delta - \beta)K(s)$. The vertical dotted line indicates the sexual-size threshold S_{SST}. The close agreement between the numerical and characteristic solutions demonstrates the consistency of the characteristic approach and confirms convergence toward the equilibrium distribution over most of the size spectrum. The two abundance maxima correspond to regions of reduced effective losses and enhanced population accumulation, associated with the interplay between size-dependent demographic rates and carrying capacity.

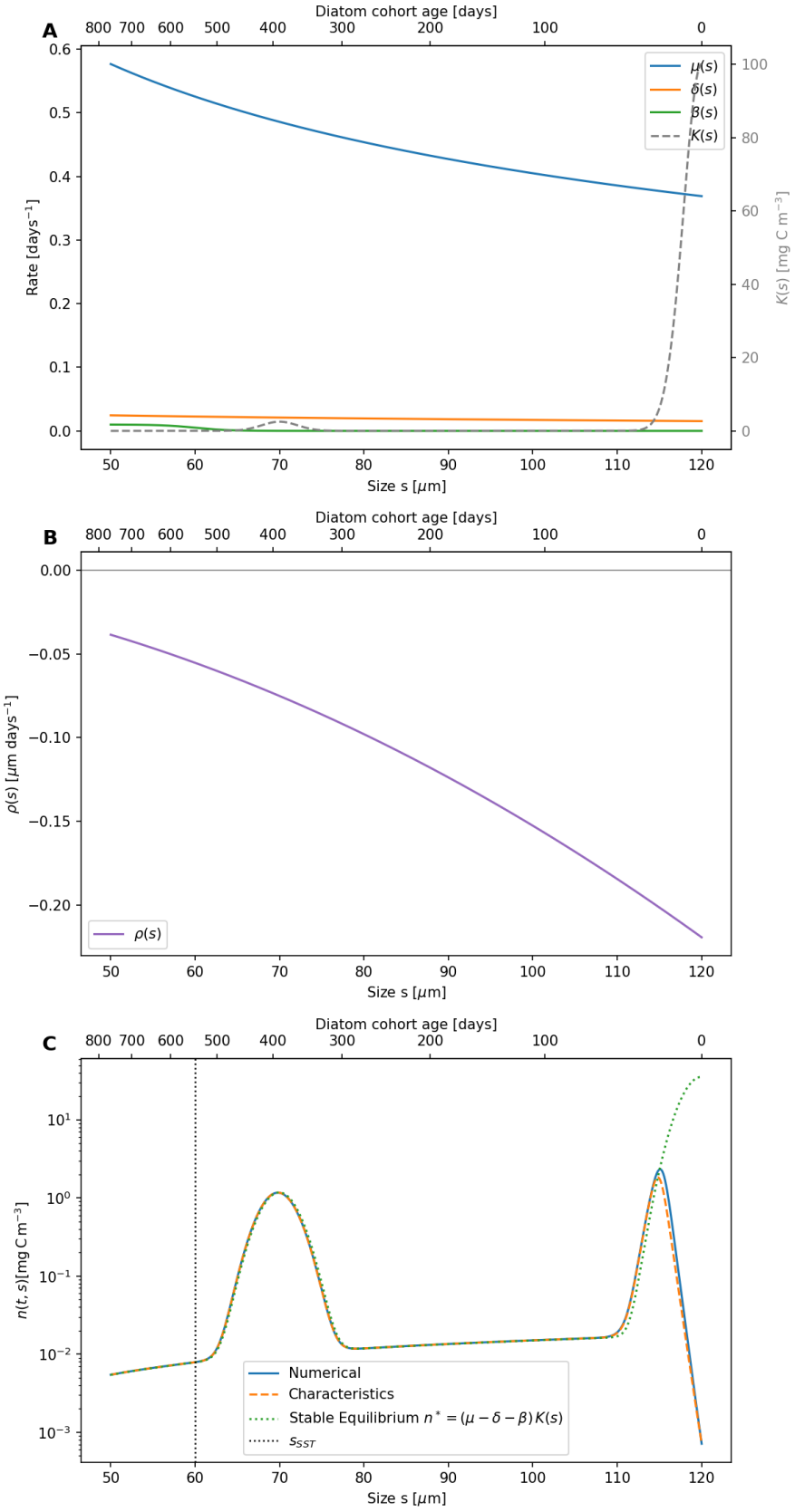

Figure R1-4: Same as Fig. R1-3, but for $\omega = 10^{-5}$ $\mu\text{m}^{-\frac{3}{2}}$ d^{-1} .

Reviewer Comment:

> *e) Lastly, I miss a better description of the "mother-model". It is described as a "optical" model, however, the optical-related traits play no role in the present manuscript. Specifically, I miss a description of the main principles and the main governing equations, with a full set of equations and parameters in the appendix (parameters and equations for the new diatom model could go in the main text).*

Response:

We agree with the Reviewer's suggestion that the equations directly related to diatoms, which are currently described in the online manual, should be included in the main manuscript. In the revised version, we will therefore report the terms that are strictly relevant to the processes examined in this study, while referring the reader the available online manual or evaluate to attach a copy of the manual in the supplementary material (amounting to approximately 30 pages). We also plan to include a more explicit description of diatom physiology:" In the Biogeochemical Flux Model (BFM), phytoplankton functional types are represented within a common physiological framework in which growth and metabolic rates are regulated by environmental forcing and intracellular state variables. For diatoms, physiological processes depend on light, temperature, and nutrient availability, with silicate (Si) explicitly represented as an essential nutrient required for frustule formation. Photoacclimation follows the dynamic chlorophyll-to-carbon (Chl:C) formulation of Geider et al. (1998), allowing flexible adjustment of pigment content to changing light conditions. Light absorption is computed from chlorophyll-specific absorption cross sections, while primary production is described through a standard production–irradiance (P–I) relationship. Growth is regulated by an internal nutrient quota formulation, enabling nitrogen (N), phosphorus (P), and silicate (Si) limitation to emerge from cellular stoichiometry rather than external concentrations alone. A fraction of primary production is released as dissolved organic carbon (DOC), whereas the remaining particulate organic matter supports higher trophic levels through zooplankton grazing. In the present model implementation, grazing represents the only explicit mortality process acting on diatoms."

Major Comment 2

Reviewer Comment:

> *2. The theoretical analysis (section 2.2) feel very disjoint from the rest of the manuscript. It uses the methods of characteristics to calculate the size trajectories of diatoms (fig 1). However, this is done with an idealized division rate, which is different from the emergent division rates in the rest of the paper. Further, these trajectories could have been calculated without entering into the entire discussion of characteristics by just integrating (4) directly; the abundances (3) are never used. Finally, the central result does not appear to be used in the rest of the manuscript (perhaps it is, but then I did not find it). As it is, the manuscript would be sharper without this section.*

Response:

We thank the Reviewer for the useful comments. The introduction and analysis of the equations provide a simplified theoretical framework to better understand diatom reproduction dynamics, in particular the role of the term (ρ) in controlling the trajectory of diatom cohorts along the size space.

We agree that Eq. 4 could be integrated directly. However, the theoretical formulation is important because it clarifies the meaning and why Eq. 4 enters the game and highlights the role of the characteristic equation in describing the evolution of the system.

To better connect the theoretical and numerical sections, we additionally provide an explicit integration of the characteristic equation as explained in reply to Major comment 1d.

This additional analysis illustrates the behavior of the model along the characteristics and provides a direct comparison with the numerical solutions presented in the manuscript.

Major Comment 3

Reviewer Comment:

> *3) The model contains a sensitivity analysis, which is nice. However, I miss a comparison of the new model with sexual reproduction to the original model without sexual reproduction. Essentially addressing the questions: how important is it to add sexual reproduction to resolve community dynamics.*

Response:

We thank the Reviewer for this insightful comment. We agree that it is important to clarify how the extended model relates to the original formulation without explicit sexual reproduction.

As shown in Fig. 4 of the manuscript, the lower-left corner of the parameter space (i.e., small values of the reproductive parameters controlling the size-restitution process) corresponds to a regime in which the model progressively approaches the original formulation ("Mother Model" in the Reviewer's terminology). In this limit, the influence of sexual reproduction becomes negligible, and the simulated community dynamics closely resemble those obtained with the original model. In particular, the reference configuration, characterized by the calibrated size-reduction velocity, produces results that are very similar to those of the original model while maintaining good agreement with the available observational data (Fig.3 original manuscript). This is also evident from the sensitivity analysis (Fig.R1-5, reproduced from Fig. 4j of the submitted manuscript), where the high-diatom-biomass (yellow) region is contiguous between the reference parameterization and the limiting case located in the lower-left corner of the parameter space. This continuity indicates that, as both the sexual and asexual reproduction dynamics are progressively weakened, the extended model converges smoothly towards the original ("Mother") model without exhibiting abrupt changes in the simulated diatom biomass.

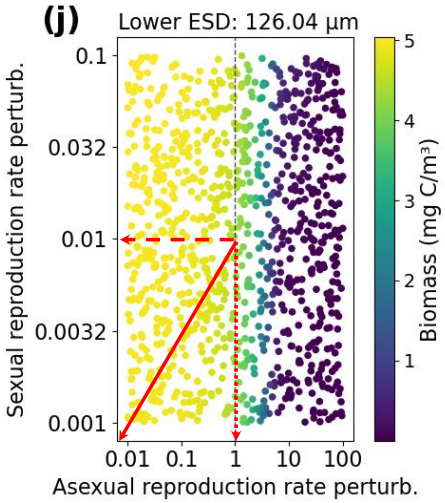

Figure R1-5: Sensitivity of the simulated diatom biomass to perturbations of the asexual reproduction rate (horizontal axis) and sexual reproduction rate (vertical axis) for the largest diatom size class (Lower ESD = 126.04 μm). Colors represent the simulated diatom biomass (mgCm^{-3}). The dashed horizontal red arrow indicates the reduction of the sexual reproduction rate while maintaining a constant asexual reproduction rate. The dashed vertical red arrow indicates the reduction of the asexual reproduction rate while maintaining a constant sexual reproduction rate. The solid red arrow represents the simultaneous reduction of both sexual and asexual reproduction rates, illustrating the overall decrease in diatom reproductive dynamics and the transition towards the limiting case represented by the original ("Mother") model.

The advantage of the extended formulation becomes evident through the sensitivity analysis. Rather than simply reproducing the original behaviour, it reveals that the reference configuration lies close to a critical transition. As the reproductive parameter ω is increased, the system undergoes a shift from a diatom-dominated regime toward one in which dinoflagellates become dominant. Therefore, the explicit representation of sexual reproduction does not merely add biological realism; it introduces a dynamical mechanism capable of generating alternative community states that cannot be explored with the original model.

To make this point clearer, we will explicitly discuss in the revised manuscript that the original model can be interpreted as a limiting case of the new formulation and that the sensitivity analysis quantifies how increasing the strength of the reproductive dynamics drives the system away from this limit toward a different ecological regime.

Minor Comment 1

Reviewer Comment:

Line 12. "...secondary modulator". Please be more specific

Response:

We intended to indicate that this process has a secondary role rather than being a primary driver of the system dynamics. We propose to revise the text accordingly to avoid ambiguity.

Minor Comment 2

Reviewer Comment:

Line 16. Is biodiversity a "mechanism"? would it be better to describe as a "property"?

Response:

We thank the Reviewer for pointing this out. We agree that biodiversity is more appropriately described as a property of ecological communities rather than a mechanism. We will amend the text accordingly.

Minor Comment 3

Reviewer Comment:

Line 18. Perhaps better to remove "coarse" because FR type of representations can actually be quite complex.

Response:

We agree to remove "coarse".

Minor Comment 4

Reviewer Comment:

Line 29 and 33: "e.g." instead of "i.e."

Response:

Agree.

Minor Comment 5

Reviewer Comment:

Line 43. "... as abundance increases".

Response:

Agree.

Minor Comment 5

Reviewer Comment:

Line 52-58. This paragraph feels a bit out of place here. It might work better before the previous paragraph.

Response:

Agree.

Minor Comment 6

Reviewer Comment:

> *Line 53. I would add "affinitiy to light and nutrient uptakes" as other properties that are influenced by cell size.*

Response:
Agree.

Minor Comment 7

Reviewer Comment:

> *Line 75: 50-20% in mass or diameter?*

Response:
We thank the Reviewer for pointing this out. The reported 20–50% reduction refers to cell diameter, not biomass. We will clarify this explicitly in the revised manuscript to avoid ambiguity.

Minor Comment 8

Reviewer Comment:

> *Line 76: What does "this" refer to in "... departing from this theoretical..."?*

Response:
"this" refers to sexual reproduction. We will clarify in the revised manuscript.

Minor Comment 9

Reviewer Comment:

> *Line 77. "mechanisms are " => "as"*

Response:
Agree.

Minor Comment 10

Reviewer Comment:

> *Line 79-83. Why is this information relevant here?*

Response:
Agree, we can remove this part.

Minor Comment 11

Reviewer Comment:

Line 87. Remove "with a method"

Response:
Agree.

Minor Comment 12

Reviewer Comment:

Line 95. Is S really defined all the way down to a size zero?

Response:
In the revised version of the model, which introduces two decoupled SRRC cycles representing large and small diatoms, we have also incorporated a minimum cell size for each cycle.

Minor Comment 13

Reviewer Comment:

Eq 1 (and elsewhere): The differential "d" is an operator and should not be in italics.

Response:
Agree.

Minor Comment 14

Reviewer Comment:

Line 115 (and elsewhere): Units should not be in italics.

Response:
Agree.

Minor Comment 15

Reviewer Comment:

Section 2.3.1: The optical traits appears to be of secondary importance to this manuscript. Perhaps just move to a supplementary.

Response:
We agree that the description of the optical traits is not central to the objectives of the present study. In the revised manuscript, we will shorten this section and retain only the information necessary to understand the model formulation, while referring the reader to the BFM documentation for a more detailed description of the optical parameterization.

Minor Comment 16

Reviewer Comment:

Line 211. Is there a reference that describes the site?

Response:

We agree, we will add information related to the site ([14], https://boussole.imev-mer.fr/html/home/home.pl

Minor Comment 17

Reviewer Comment:

Fig 4. All panels should have the same colour scale so it is easy to see which parameters matters compared to the others. Font size on axes should be increased.

Response:

We thank the Reviewer for this helpful suggestion. We agree that using a common colour scale across all panels will facilitate the comparison of the relative influence of the different parameters. In the revised manuscript, we will adopt a uniform colour scale for all panels of Fig. 4 and increase the font size of the axis labels and tick marks to improve the overall readability of the figure. We will also explore alternative ways of presenting the results, with the aim of condensing the information and reducing the number of panels where possible, thereby increasing the overall size and readability of the individual plots.

References

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