Response to Reviewers

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

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Journal: Biogeosciences

Manuscript ID: egusphere-2026-1437

Response to Reviewer #2

We thank the reviewer for the careful reading of the manuscript and for the constructive comments. For clarity, all figures and tables included in this response are identified using the prefix R2- (e.g., Fig. R2-1, Table R2-1) to distinguish them from those in the revised manuscript.

Major Comment 1

Reviewer Comment:

> *The model description would benefit from more explanations. I found the theoretical background sometimes difficult to understand.*

Reviewer Comment:

> *a) Line 91: functional diversity biogeochemical model – the calculation of the growth rate and mortality rate were difficult to understand.*
>
> *If I understand well, grazing pressure is a function of the prey size selectivity of predators (Lines 151-152), however the relation between the polynomial delta(s) (after Eq. 4) and the size-dependent predation risk was unclear?*

Response:

We agree that the notation used in the original manuscript could lead to confusion because it combines two different formulations of the growth loss term. In the theoretical model, the function ($\delta(s)$) was introduced following the simplified formulation in [1], whereas the numerical model computes grazing losses using the full predator–prey formulation, in which grazing pressure emerges from predator size selectivity and prey availability.

To remove this ambiguity, in the revised manuscript we adopt the same allometric formulation used in the numerical model also in the simplified theoretical framework. Consequently, predation is represented through the same size-dependent growth loss term employed in the numerical simulations. The population dynamics along a characteristic curve is expressed as

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

where μ is the allometry based maximum growth rate used for the numerical model [2] and we added a density-dependent quadratic term represents the combined effect of ecological interactions to enable direct comparison with the numerical model. The definition of K(s) includes in the example below two maximal values corresponding to the numerical results where diatoms pick are observed i.e. at 50 μm and 126 μm.

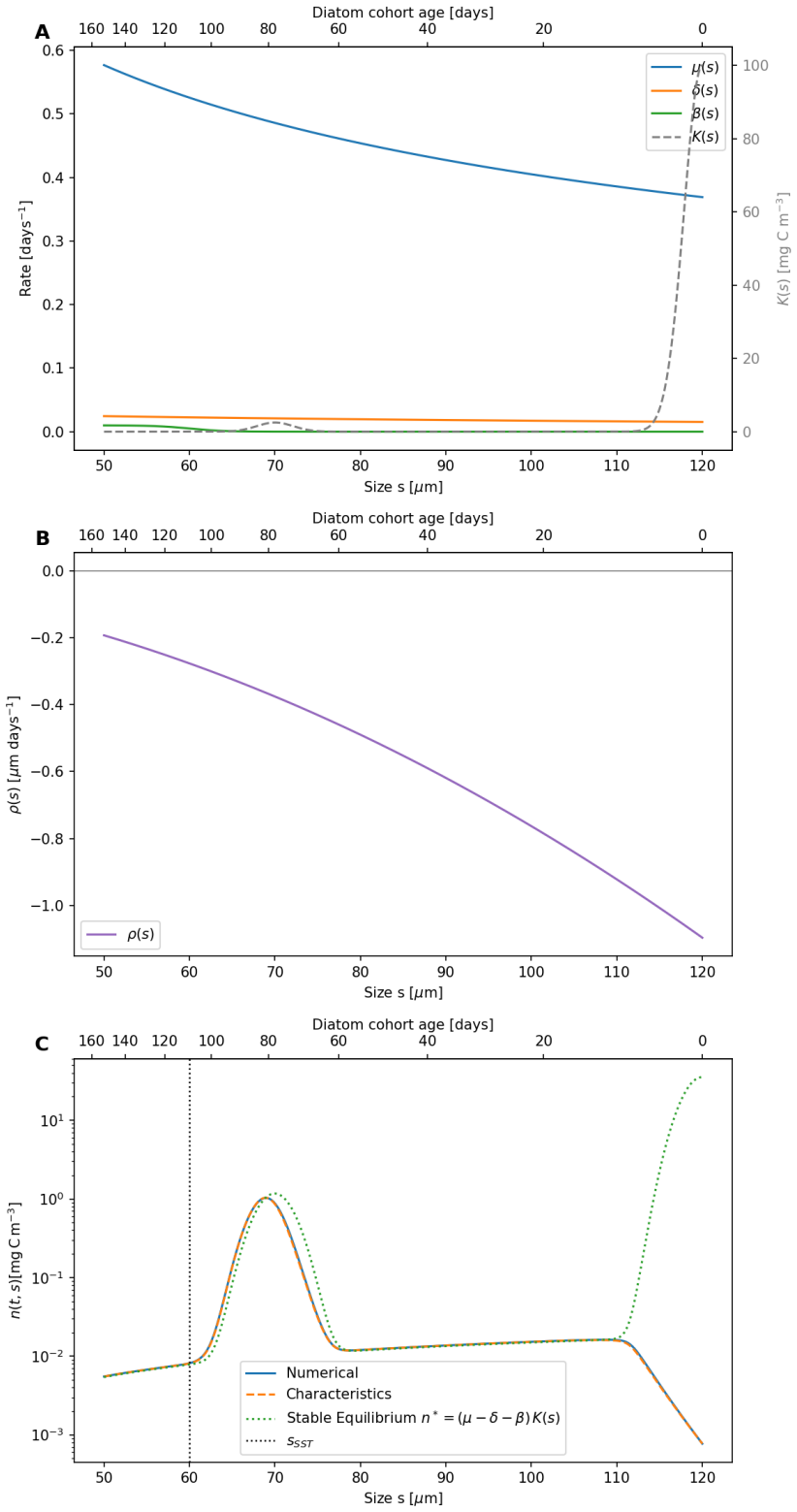

Figure R2-1: A) Size-dependent growth $\mu(s)$, mortality $\delta(s)$, sexual reproduction $\beta(s)$, and carrying capacity $K(s)$ used in the characteristic formulation of the diatom population model. The upper axis reports the corresponding cohort age associated with each cell size. (B) Characteristic 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.

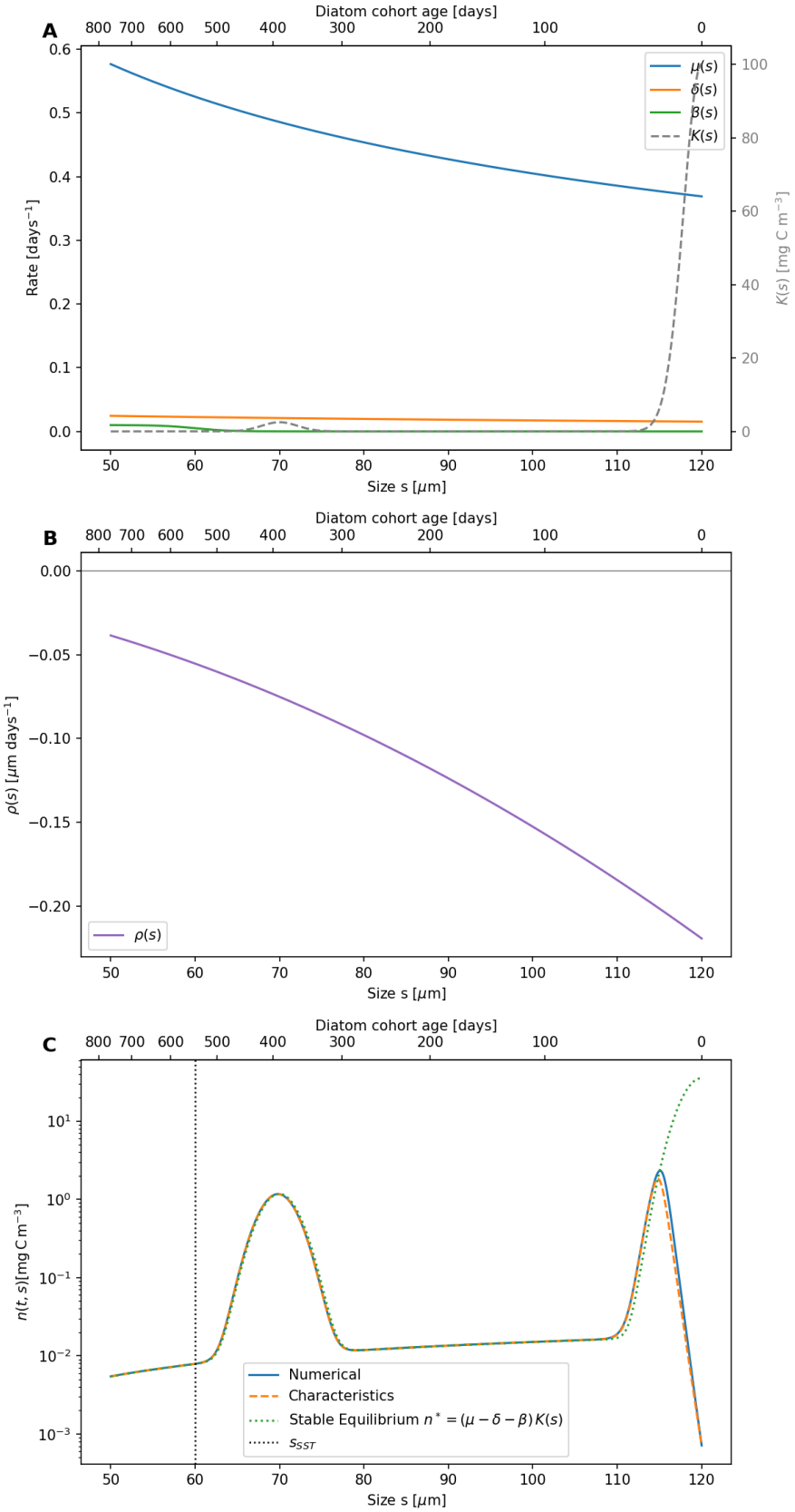

Figure R2-2: Same as Fig. R2-1, but for $\omega = 10^{-5}$ $\mu\text{m}^{-\frac{3}{2}}$ d^{-1}.

This revised formulation also clarifies the relationship between the ecological and reproductive dynamics. The analysis shows that when the size-reduction velocity is sufficiently small, the

ecological dynamics rapidly approach a quasi-equilibrium with respect to growth and grazing. Only when the size-reduction flow becomes sufficiently fast do the reproductive dynamics interact strongly with predator–prey dynamics, leading to departures from the quasi-equilibrium regime. This fast–slow behaviour is now explicitly discussed in the revised manuscript and illustrated through the new analytical and numerical results.

Reviewer Comment:

> *b) Eq. (6) gives the boundary condition for the maximum size of diatoms. The text would benefit from a clearer description of the equation.*
>
> *The relation between Eq. (6) and lines 127-128 was not clear to me.*
>
> *Line 127: what is b(s) referencing to? I could not find it anywhere else in the text.*

Response:

We thank the Reviewer for pointing out this lack of clarity. We agree that the original description of Eq. (6) was not sufficiently explicit. In particular, the function ($\beta(s)$) appears in the boundary condition before being properly defined, which may cause confusion.

In the revised manuscript, we will introduce ($\beta(s)$) before Eq.(6) and explicitly define it as the size-dependent sexual reproduction rate. In the present formulation, ($\beta(s) = \beta_0$) is assumed constant for cells with sizes below the sexualization size threshold (SST) and zero otherwise. We will also clarify the biological interpretation of the boundary condition: the integral in Eq. (6) represents the total production of newly restored large diatom cells generated through sexual reproduction by all cells with sizes below the SST. This total reproductive flux constitutes the boundary condition at (S_{MAX}), where newly formed large cells re-enter the size spectrum. The revised text will explicitly connect Eq. (6) with the definition of the SST and explain how the boundary condition closes the size-reduction–restitution cycle. We also note that this boundary condition is intentionally formulated in a simple manner because quantitative information on the size dependence of the reproductive flux is currently limited. Consequently, we assume a constant sexual reproduction rate below the SST. Therefore, already in the original manuscript to account for the uncertainty associated with this assumption, we performed a dedicated sensitivity analysis on the sexual reproduction rate parameter, allowing us to assess the robustness of the model predictions over a broad range of plausible values.
We corrected the typo in line 127: $b(s) \rightarrow \beta(s)$.

Reviewer Comment:

> *c) Section 2.3.: "Predation interactions are parametrized through allometric relations" (Line 151).*
>
> *It is unclear which process is defined by an allometry. Is it the predation risk of diatoms, the prey preference of predators, or the ingestion rate?*
>
> *If the prey size preference follows an allometry of the predator's body size, the authors might want to discuss this assumption in the text. Some herbivorous plankton, such as dinoflagellates https://doi.org/10.1007/s00227-022-04102-2, can show an optimal prey size that is independent of their body size.*

Response:

The total carbon ingestion by zooplankton is computed using a Holling Type-II functional response [3],

$$\left.\frac{dX_c}{dt}\right|_{Z_c}^{\mathrm{prd}} = f_Z^T r_Z^0 \delta_{Z,X} e_{Z,X} \frac{X_c}{F_c} \frac{F_c}{F_c + h_Z^F} Z_c,$$

where

$$h_Z^F = \frac{r_Z^0}{v_Z},$$

is the predator-specific search volume.

Allometric scaling enters the ingestion dynamics at two distinct levels. First, it regulates the grazing rate through the predator-specific search volume, (v_Z), whose maximum grazing rate (r_Z^0)scales with predator body size according to an allometric power-law relationship. This scaling determines the overall ingestion capacity of each zooplankton functional group and reflects the increase in feeding capability with organism size.

Second, allometry determines prey size selectivity through the prey availability coefficient, ($\delta_{Z,X}$). The total food available to predator (Z) is defined as

$$F_i = \sum_X \delta_{Z,X} e_{Z,X} X_i, \; e_{Z,X} = \frac{X_c}{X_c + \mu_Z}$$

where ($\delta_{Z,X}$) represents the availability of prey (X) to predator (Z), while ($e_{Z,X}$) denotes the capture efficiency. Following the formulation of [4], prey availability is determined by the relative sizes of predator and prey through allometric relationships describing encounter and handling processes. Consequently, the coefficient ($\delta_{Z,X}$) is not constant but varies with predator and prey size, controlling the spectrum of prey that can be efficiently exploited. Therefore, allometric scaling influences both the magnitude of grazing, through the predator-specific search volume, and the size selectivity of predation, through the prey availability function.

Table R2-1: Allometric relationships used to derive BFM parameters from cell size. Equivalent spherical diameter by ESD.

PFT	Parameter	Allometric relationship	Unit	Source	BFM parameter
Z3–Z6 Zooplankton					
	Potential specific growth rate (r_Z^0)	$26\,ESD^{-0.4}$	d^{-1}	[5]	p_sum
	Optimum prey size (PreyESD)	$ESD/10$	μm	[4, 6]	used to compute preferences
	Preference fo prey of size D	$\exp\left[-\left(\frac{\log_{10}(D)-\log_{10}(\text{PreyESD})}{0.20}\right)^2\right]$		[7]	supreyX

We agree that prey size preference can be more complex than the allometric formulation adopted in the present model. The assumption that prey size scales with predator body size provides a simple, mechanistic, and computationally efficient framework that has been widely adopted in marine ecosystem models. Nevertheless, we recognize that this assumption does not capture the full diversity of feeding strategies observed in plankton communities.

We agree that this limitation should be discussed more explicitly. In the revised manuscript, we will expand the Discussion section to acknowledge this assumption, and highlight that alternative prey selection formulations represent an important direction for future model developments.

Reviewer Comment:

d) The manuscript is discussing the cascading effects of size dynamics of diatoms, related to sexual reproduction, on the food web.

It would be helpful to have a table or figure showing the trophic relationships between trophic levels, such as the prey preferences of grazers and predators. The lack of description of the trophic linkages makes it difficult to understand the results.

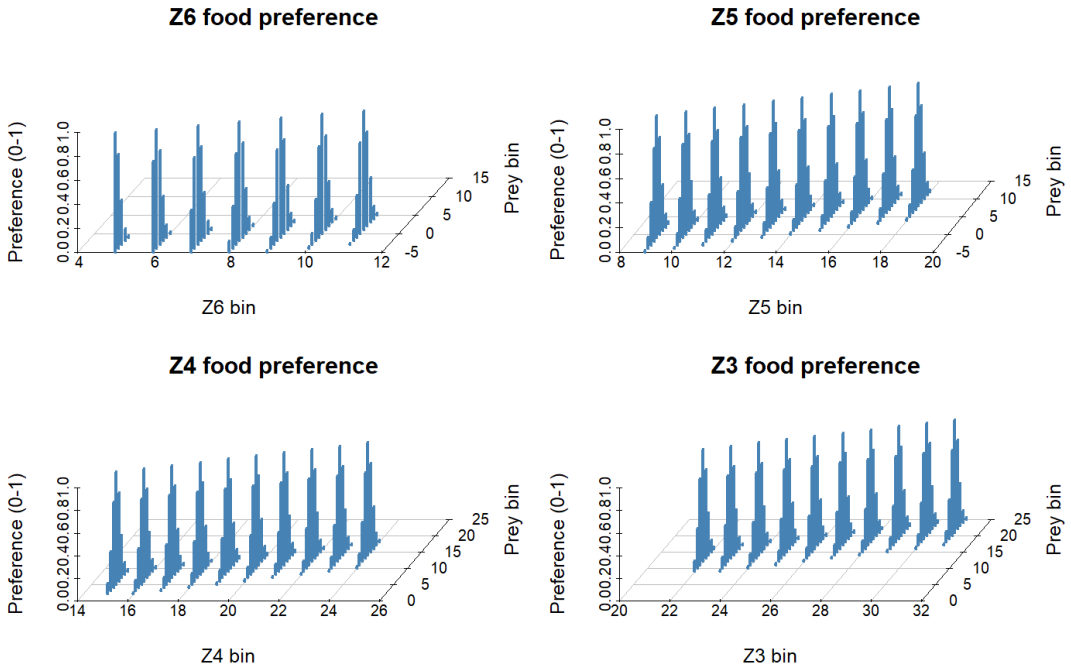

Figure R2-3: Three-dimensional representation of the prey preference matrices $\delta_{Z,X}$ for the four zooplankton functional groups (Z3–Z6). Each panel displays the normalized prey preference (0–1) as a function of predator size bin (x-axis) and prey size bin (y-axis). The preference coefficients are computed following the allometric formulation of [4]

Response:

We explored different approaches to visualize the zooplankton prey preference matrices. The first option consists of a three-dimensional representation (Fig. R2-3), which provides a compact overview of the size-dependent feeding preferences of each zooplankton functional group and is therefore better suited for inclusion in the main manuscript. As an alternative, we generated a more detailed set of two-dimensional histograms (e.g., Fig. R2-4, shown here for the mesozooplankton functional group Z3), where the prey preference profile is presented separately for each predator size class. Although the 2D histograms provide a more comprehensive representation of the preference matrices, they require a considerably larger number of panels and are therefore better suited for the Supplementary Material. Owing to the high density of information, the individual panels necessarily contain relatively small fonts and labels, making them more appropriate for digital visualization, where zooming allows the detailed inspection of the prey preference patterns.

Reviewer Comment:

> *e) Section 2.3.1 – It is unclear how the optical trait is related to diatoms size. The text would benefit from a description of the size – optical trait relationships in the model.*

Response:

We thank the Reviewer for this observation. The optical traits adopted in the model were derived and calibrated in a dedicated study for the Mediterranean Sea, [8], and are independent of the phytoplankton size traits considered in the present work. Since the optical parameterization is not central to the objectives of this study, and following the suggestion of Reviewer 1, we will shorten this section in the revised manuscript, retaining only the information necessary

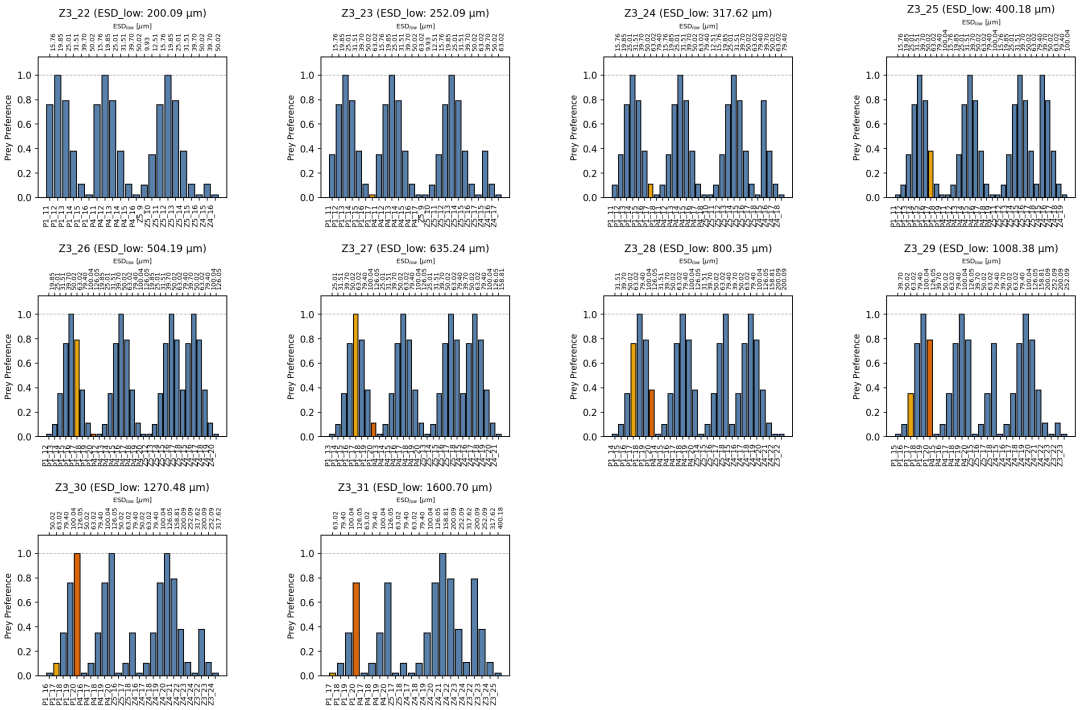

Figure R2-4: Two-dimensional representation of the prey preference matrix for the mesozooplankton functional group Z3. Each panel corresponds to a predator size class (indicated by the lower equivalent spherical diameter, ESD(low) and reports the normalized prey preference coefficient ($\delta Z, X$) for all potential prey groups included in the model. The upper axis indicates the lower ESD of each prey size class. Blue bars represent the complete prey preference spectrum. The orange and vermilion bars highlight the preference coefficients associated with the two diatom size classes corresponding to the biomass peaks observed in the reference simulation, with equivalent spherical diameters of approximately 60 μm (orange) and 126 μm (vermilion), respectively. The preference coefficients are computed following the allometric formulation of [4]), illustrating how prey selectivity varies with predator size.

to understand the model formulation and referring the reader to the original publication for a detailed description.

Reviewer Comment:

> *f) Line 258: "... indicating a competitive displacement as dinoflagellates become increasingly dominant under enhanced asexual reproduction ..." Could the authors explain why? Are the dinoflagellates feeding on small diatoms?*

Response:

We thank the Reviewer for raising this important point. Dinoflagellates do not feed on the smaller diatoms. In the present model, the observed shift results primarily from indirect competition for resources and the combined effects of grazing rather than from direct trophic interactions between dinoflagellates and diatoms.

As illustrated in Fig.R2-1, increasing the size-reduction velocity causes diatoms to move more rapidly through the size spectrum under non-equilibrium conditions. Consequently, they spend less time within the size ranges characterized by the most favourable growth conditions, represented in the simplified theoretical model by higher values of the carrying capacity parameter (K(s)). This reduces the ability of diatoms to fully exploit these favourable regions of the size space, thereby weakening their competitive advantage. Dinoflagellates, which are not subject to the size-reduction–restitution cycle, are therefore able to exploit the available resources more effectively, leading to an increase in their relative biomass.

We stress that, unlike the simplified theoretical model, the full numerical ecosystem model does not assume a static carrying capacity for diatoms. Instead, the effective ecological conditions experienced by each phytoplankton size class emerge dynamically from the coupled interactions among nutrients, light, grazing, and competition. Consequently, the mechanism should be interpreted as a dynamic redistribution of ecological advantage rather than as movement across a fixed carrying-capacity landscape, that we introduced as illustrative mechanisms in the theoretical model.

To avoid this ambiguity, we will revise the manuscript to clarify that the increase in dinoflagellate biomass arises from indirect competition for resources together with grazing-mediated effects, rather than from direct trophic interactions with diatoms.

Reviewer Comment:

> *g) Are the dinoflagellates autotrophs or mixo/heterotrophs? From the text, it is unclear if dinoflagellates are strictly autotrophs or mixotrophs. The authors might want to specify it.*

Response:

In the current model formulation, dinoflagellates are represented as strictly autotrophic phytoplankton functional types; mixotrophic strategies are not included. We will clarify this explicitly in the revised manuscript to avoid any misunderstanding. We agree that mixotrophy represents an important ecological process for many dinoflagellate species and constitutes a promising direction for future developments of the model.

Reviewer Comment:

> *h) Line 260-263: "Smaller phytoplankton groups ... show limited sensitivity to the asexual reproduction perturbation ... suggesting that their dynamics are primarily controlled by processes other than direct reproduction rate modulation in this parameter regime ..."*

This paragraph refers to phytoplankton other than diatoms. However, in this sentence, it seems that the asexual reproduction rate perturbation is applied to all phytoplankton groups. Is it true?

Response:

We thank the Reviewer for pointing out this ambiguity. The asexual reproduction rate perturbation is applied only to the diatom functional group. The other phytoplankton groups are not directly affected by this parameter. Instead, the analysis examines how changes in the diatom size-reduction–restitution dynamics propagate through the ecosystem via competition for resources, grazing interactions, and nutrient recycling. Consequently, the response of the smaller phytoplankton groups reflects indirect ecosystem effects rather than a direct modification of their own reproductive dynamics. We will revise the text to make this distinction explicit.

Minor Comment 1

Reviewer Comment:

a) Line 241-244: Panels g and j show strong transition zones. Interestingly, panels h and i show a similar pattern as in d-f. Do the authors have an idea why?

Response:

We thank the Reviewer for this interesting observation. We believe that the similar patterns observed in panels h and i arise from the progressive shift of diatom biomass towards smaller size classes as the size-reduction (shrinking) velocity increases. As illustrated in Fig.R2-1, increasing the shrinking velocity causes diatom cohorts to move more rapidly through the size spectrum, resulting in a leftward displacement of the biomass accumulation peak. Consequently, the transition pattern observed for the dominant size classes (in Fig.R2-1 at 60 μm) also appears in the adjacent smaller size classes, producing similar sensitivity patterns in panels h and i. We will expand the discussion in the revised manuscript to clarify this interpretation.

Minor Comment 2

Reviewer Comment:

b) Line 275-279: It might be useful to also plot the contribution of large sizes.

Response:

Thanks for the comment, we will add the contrivution for larger sizes.

Minor Comment 3

Reviewer Comment:

Line 31: "... especially in multicellular zooplankton ..."

Response:

Agree to amend.

Minor Comment 4

Reviewer Comment:

> *Line 43: "... whole diatom community as small cells becomes more abundant ..." It is not clear what this becomes is.*

Response:

Minor Comment 5

Reviewer Comment:

> *Line 44: "... the original size, a common strategy is sexual reproduction ..."*

Response:
Agree to amend.

Minor Comment 6

Reviewer Comment:

> *Line 47: "... showed that newborn cells shrinking below their sexualization*

Response:
Agree to amend.

Minor Comment 7

Reviewer Comment:

> *size threshold (SST) acquire sexual competence ..."*

Response:
Agree to amend.

Minor Comment 8

Reviewer Comment:

> *Line 78-79: The sentence "In the asexual part of the reproduction cycle one of the two daughter cells is smaller than the other by two times the frustule width" was unclear to me. Could the authors reformulate?*

Response:
We thank the Reviewer for pointing out this lack of clarity. The purpose of this sentence was to highlight that vegetative (asexual) cell division in diatoms is inherently asymmetric: following mitosis, one daughter cell inherits the larger parental frustule and retains approximately the same size, whereas the other inherits the smaller theca and is reduced in diameter by approximately twice the frustule thickness. In the present model, however, this asymmetry

is not represented explicitly. Instead, the progressive reduction in cell size is described through a continuous size-reduction process, following the approach by [1], which provides a symmetric simplified representation of the cumulative effect of successive asymmetric divisions. We will reformulate this sentence in the revised manuscript to make this point clearer. This aspect was mentioned in the discussion section of the original manuscript.

Minor Comment 9

Reviewer Comment:

> *Line 123: "... conditions are required. At t0 the distribution ..."*

Response:
Agree to amend.

Minor Comment 10

Reviewer Comment:

> *Line 133: "... newly generated ... composed of clones, evolve ..."*

Response:
Agree to amend.

Minor Comment 11

Reviewer Comment:

> *Line 138-139: "... abiotic regulations of growth predation ..." This sentence is unclear, could the authors reformulate? Maybe some commas are missing.*

Response:
We thank the Reviewer for pointing out this ambiguity. Our intention was to indicate that, in the simplified theoretical model, the maximum growth rate is assumed to be constant and is therefore not modulated by abiotic environmental factors such as light, temperature, or nutrient availability. The theoretical framework is designed to isolate the effects of size reduction, reproduction, and predation, whereas the full numerical model explicitly accounts for environmental regulation of phytoplankton growth. We will reformulate this sentence in the revised manuscript to make this distinction clearer.

Minor Comment 12

Reviewer Comment:

> *Line 141: "... and in particular in term of cohorts time scale evolution as shown in Fig.1" Do the authors mean the evolution timescale of cohorts?*

Response:

We thank the Reviewer for pointing out this ambiguity. Our intention was not to refer to the characteristic timescale of cohort evolution, but rather to the trajectory followed by a diatom cohort through the size spectrum. Specifically, Fig. 1 (in the submitted manuscript) illustrates how a cohort progressively moves from larger to smaller cell sizes during successive vegetative divisions until it reaches the sexualization size threshold (SST), where sexual reproduction restores the maximum cell size. We will reformulate the sentence in the revised manuscript to make this interpretation explicit.

Minor Comment 13

Reviewer Comment:

Line 146: "... on the BFM98 model (Álvarez et al. 2025)."

Response:

Agree to amend.

Minor Comment 14

Reviewer Comment:

Line 151: "Predation interactions ..."

Response:

Agree to amend.

Minor Comment 15

Reviewer Comment:

Line 196: "... ni (t) represents the concentration ..."

Response:

Agree to amend.

Minor Comment 16

Reviewer Comment:

Line 206: "... of 50 μm ..."

Response:

Agree to amend.

Minor Comment 17

Reviewer Comment:

Line 222: "phasing" Do the authors mean "dynamics"?

Minor Comment 18

Reviewer Comment:

Line 229: "... reproduction rates with constant multiplicative factors ..."

Response:
Agree to amend.

Minor Comment 19

Reviewer Comment:

Line 256: "... perturbations below unity ..." Do the authors mean below 1? Please also check Line 269. The word "unity" is unclear.

Response:
We thank the Reviewer for pointing this out. We agree that the term "unity" is inappropriate in this context and may be misleading. In the revised manuscript, we will replace "below unity" with "below 1" (and similarly for Line 269) to improve clarity.

Minor Comment 20

Reviewer Comment:

Line 269: This sentence is unclear. Could the authors reformulate?

Response:
Microzooplankton show only a modest decline in biomass for perturbation factors larger than one. This limited response is consistent with their prey preference, which includes little or no direct grazing on diatoms. Consequently, the shift in community composition from diatoms toward dinoflagellates has a comparatively small indirect effect on microzooplankton biomass.

Minor Comment 21

Reviewer Comment:

Line 302: "... coherently with previous results ..." Do the authors mean "in accordance with" or "in coherence with" previous results?

Response:
Yes, we agree to amend.

Minor Comment 22

Reviewer Comment:

Line 317: "... pathways, damping high-frequency ..." Do the authors mean "dampening"?

Response:
Yes, we agree to amend.

Minor Comment 23

Reviewer Comment:

Line 333: "... changes in the Shannon index reflect ..."

Response:
We agree to amend.

Minor Comment 24

Reviewer Comment:

Line 375: The sentence is unclear. Could the authors reformulate?

Response:
We thank the Reviewer for pointing out this lack of clarity. The purpose of this section is to derive the evolution equation for the perturbation around the steady-state solution. Specifically, we decompose the solution as

$$n(s,t) = \bar{n}(s) + \delta n(s,t),$$

where $(\bar{n}(s))$ denotes the steady-state solution and $(\delta n(s,t))$ is a small perturbation. Since the steady-state solution is independent of time, it satisfies

$$0 = \omega s^{\alpha} \frac{\partial \bar{n}}{\partial s} + M(s)\bar{n}.$$

Substituting the decomposition and subtracting the steady-state equation yields the governing equation for the perturbation,

$$\frac{\partial \delta n}{\partial t} = \omega s^{\alpha} \frac{\partial \delta n}{\partial s} + M(s)\delta n.$$

We will reformulate this section accordingly to make the derivation clearer.

Minor Comment 25

Reviewer Comment:

Line 389: "... depends on ..."

Response:
We agree to amend.

3 – Suggestions

Please find below a list of suggestions aimed at improving the text and figures. Elements in this section are optional for the review of the manuscript, but I think it would improve the overall clarity of the text.

a) In Fig. 2: What is the reason behind choosing the numbers for the trophic levels? They do not correspond to the ESD or the size classes described below, which makes it more difficult to compare the figure and the caption.

Response:

We thank the Reviewer for this observation. The notation and numbering of the plankton functional types (e.g., P1, P2, ..., Z3, Z4) follow the original BFM implementation by ERSEM and have been retained here for consistency with the existing model formulation and previous publications. We agree, however, that this notation does not directly convey the corresponding size classes (ESD), making the figure more difficult to interpret. In the revised manuscript, we will revise Fig. 2 to make the correspondence between the functional group labels and their associated size classes more explicit, thereby improving the readability of both the figure and its caption.

b) Fig. 4: The authors might want to increase the fontsize of the figure, if possible.

Response:

We thank the Reviewer for this helpful suggestion. We agree that the readability of Fig. 4 can be improved. In the revised manuscript, we will increase the font size of the labels, axes, and annotations and reorganize the figure layout to enhance its overall readability. This suggestion is consistent with a similar recommendation made by Reviewer 1, and we will revise the figure accordingly.

References

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[8] Eva Álvarez, Paolo Lazzari, and Gianpiero Cossarini. "Phytoplankton diversity emerging from chromatic adaptation and competition for light". en. In: *Progress in Oceanography* 204 (June 2022), p. 102789. ISSN: 00796611. DOI: 10.1016/j.pocean.2022.102789. URL: https://linkinghub.elsevier.com/retrieve/pii/S0079661122000507 (visited on 11/19/2025).