

We thank G. C. Small and an anonymous referee for their detailed and constructive comments. All comments have been taken into consideration. For the sake of clearness, we formatted comments from the referees in normal fonts, our responses in italic fonts, and additional or removal sentences to the manuscript in quote and bold.

Responses to the comments of reviewer #1 - G. C. Small

A. General Comments

This paper extends Tyrrell's model of N and P cycling in the global ocean to explore the potential importance of nutrient recycling by herbivores, using Sterner's model of consumer nutrient recycling (CNR). The resulting model illustrates that CNR can control total primary productivity (by supplying P) and affect competitive interactions between N-fixers and non-fixers. The model was parameterized using available data, and model results are largely consistent with empirical values. This paper makes a convincing case for the potential importance of CNR affecting TPP, phytoplankton dynamics, and concentrations of dissolved nutrients in the ocean, and should spur further empirical research investigating these nutrient pathways and further constraining important parameters. This study represents an important contribution linking food webs, physiology, and the biogeochemistry of the global ocean.

The importance of these homeostatic herbivores stems from their potential to recycle nutrients through excretion at N:P ratios that are different than ambient ratios. One point that may deserve further emphasis is that the importance of N:P excretion ratios depends on the fate of the nutrients that are bound in consumer biomass, a point that is not always considered in empirical studies of CNR. In a steady state model, if all of the herbivore biomass was eventually remineralized and became available for uptake by phytoplankton, the differential ratios by which herbivores excrete nutrients would be canceled out by the N:P ratios of herbivore biomass remineralization. In this model, a fraction of detritus is removed from the system through settling, allowing for herbivore excretion ratios to affect dissolved N:P ratios at steady state.

[Response] A short paragraph in the conclusion of the paper has been added to the revised manuscript, emphasising the point raised by the reviewer:

“Here, the importance of the N:P resupply ratio from herbivores depended on the fate of nutrients that are bound into consumer biomass. If all of the herbivore biomass was eventually remineralised in the surface layer and became available for uptake by phytoplankton, the differential ratios by which herbivores excrete nutrients would be cancelled out by the N:P ratios of herbivore biomass remineralisation. In our model however, the nutrient resupply ratio from herbivores affected the dissolved inorganic N:P ratios at steady state through two processes: a fraction of detritus was removed from the surface of the ocean through settling, and a fraction of herbivore excretion occurred in the deep ocean.”

B. Specific Comments

[Comment 1] 6:4 Could use additional explanation. Why does this assumption imply that non-fixers are N-limited?

[Response] Equation (3) describes that non-fixers are potentially N- or P-limited. However, in Tyrrell's model (1999), N_2 -fixers and non-fixers have the same specific mortality (M_0). At steady state (when $dO/dt=0$ and $dNF/dt=0$), it follows that for N_2 -fixers (Eq. 2)

$$\frac{dNF}{dt} = \mu'_{NF} \frac{P_S}{K_P + P_S} NF - M_0 NF = 0$$

that is

$$\mu'_{NF} \frac{P_S}{K_P + P_S} = M_0.$$

Similarly, for non-fixers (Eq. 3)

$$\frac{dO}{dt} = \mu'_O \min\left(\frac{P_S}{K_P + P_S}, \frac{N_S}{K_N + N_S}\right) O - M_0 O = 0$$

that is

$$\mu'_O \min\left(\frac{P_S}{K_P + P_S}, \frac{N_S}{K_N + N_S}\right) = M_0.$$

Thus, at steady state

$$\mu'_O \min\left(\frac{P_S}{K_P + P_S}, \frac{N_S}{K_N + N_S}\right) = \mu'_{NF} \frac{P_S}{K_P + P_S}. \quad \text{Eq.(A)}$$

As N_2 -fixers have a lower maximal growth rate than non-fixers ($\mu'_{NF} < \mu'_O$), the only solution for Eq. (A) is $\mu'_O \frac{N_S}{K_N + N_S} = \mu'_{NF} \frac{P_S}{K_P + P_S}$, that is non-fixers are N-limited and N_2 -fixers are P-limited. For the sake of clarity, the following sentence has been removed from the revised version:

“...This assumption implies that N_2 -fixers are P-limited while non-fixers are N-limited (Tyrrell, 1999).”

[Comment 2] 13.16 This is an interesting result, that N-supply does not affect total phytoplankton biomass but does control herbivore biomass. I am not sure whether this is an artifact of the model or a real result; further explanation here might be helpful.

[Response] In the model herbivores graze on a mixed assemblage of phytoplankton species (non-fixers and N_2 -fixers) which have different N:P ratios. If herbivores have a N:P ratio of 25:1, and non-fixers have a N:P ratio of 16:1, then N is in deficit compared to zooplankton requirement. In this case, increasing N inputs to the ocean stimulated non-fixers growth and eventually zooplankton growth. In the revised manuscript, the paragraph has been modified as follow (to take into account the comment of the reviewer)

“...Therefore, in the model, both N and P limitation of primary production **travelled** up the food chain up to herbivores. **Indeed, when herbivores fed on a phytoplankton pool with a low N content compared to their requirement, such as non-fixers which had a N:P ratio of 16 (Table 1), N was the limiting element of herbivore growth. In this case, increasing N inputs from either atmosphere or rivers increased non-fixers biomass (Eq. 14), which in turn increased herbivore biomass (Eq. 17a). This effect was however partly counterbalanced by a decrease in N₂-fixation when external N inputs increased (Eq. 15). All in all, increasing N inputs to the ocean by a factor of two, for example, led to a slight increase of herbivore biomass (~1%, Eq. (17b)).**”

[Comment 3] 14.21 I understand the rationale for the model, although I wonder about the implications of modeling herbivory as a constant fraction of a constant phytoplankton mortality rate. Would the dynamics be different if, say, herbivory was depended on biomass of both herbivores and phytoplankton?

[Response] We agree that modelling herbivory as a constant fraction of phytoplankton mortality rate is a simplification. However, in the model, the dynamic is mainly controlled by bottom-up forces, through the delivery of nutrients to the ocean. If grazing was made dependant on the biomass of both phytoplankton and herbivore, the model behaviour did not profoundly change. For this purpose, model equations were also solved numerically. It was found that some oscillations appeared at the beginning of the simulation, but these oscillations disappeared after some time, and the model solutions converged towards a stable steady state. It should be noted however that if this model was used to simulate a seasonal cycle for example, then modelling herbivory as a constant fraction of phytoplankton mortality rate would be effectively an oversimplification.

C. Technical Comments

There are several instances where word choice may be improved:

[Comment 4] 2:19 Change “contributes” to “accounts”

[Response] corrected.

[Comment 5] 8:15 Change “is” to “in”

[Response] corrected.

[Comment 6] 10:17 Change “higher” to “lower” (?)

[Response] corrected.

[Comment 7] 22:22 Change “converged towards” to “was set at” (?)

[Response] Rephrased as

“...Here, we found that when the N:P ratio in herbivores (R_{org}^Z) increased above Redfield stoichiometry, $[R_{\text{org}}^O]_{\text{fix}}$ converged towards a constant value of ~4-5, **while $[R_{\text{org}}^O]_{\text{fix}}$ increased sharply when R_{org}^Z decreased below Redfield stoichiometry.**”

[Comment 8] Fig. 1 “Phosphorus” is misspelled

[Response] corrected.

[Comment 9] Fig. 2 Egestion arrow is backwards (?)

[Response] corrected.

[Comment 1] Fig. 4 Legend: “using the following set of assimilation efficiencies” (?)

[Response] Rephrased as

“...(c) Gross growth efficiency of N (GGE_N) and P (GGE_P) plotted against the N:P ratio in non-fixers (R_{org}^O) **using the following set of parameters: assimilation efficiencies, $\beta_1^N = 0.69$ and $\beta_1^P = 0.80$, maximum accumulation efficiency, $L_m=0.9$, and N:P ratio in herbivores, $R_{org}^Z=20$.**”