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 Anonymous Referee #2**

I enjoyed reading this article and, with some clarification of some issues, I think it will make a good contribution to the scientific literature. The extension of Tyrrell's box modelling approach to include the stoichiometry of grazers is interesting and topical given current interest in the role of multi-nutrients in structuring ecosystems and the impacts on associated biogeochemistry. I very much liked the main conclusion: Levels of global primary production were higher particularly when herbivores had higher N:P ratios than phytoplankton. This higher primary production was triggered by a low N:P resupply ratio from herbivores, which in turn favoured the P-limited $N_2$-fixation.

[Comment 1] I did however find reading the ms hard going at times. My main criticism, which I think the authors must address, is that it the stoichiometric model of herbivores is poorly described in terms of text accompanying the equations. It is based on a relatively old model of Sterner's. The authors need to do far more in terms of describing, in plain text accessible to modellers and non-modellers alike, the basic assumptions and parameterization of this model, and say why they are justified for their application of it. Let me give a few examples: 1) Page 117, line 19: What is an "accumulation efficiency"? How do accumulation efficiencies affect the balance of N and P cycling, and how are they parameterized (given that they appear to be calculated, not fixed)?

*[Response] The model of Sterner (1990) has been explained in more details in the revised version of the manuscript. The new version of the text which can be found in the revised manuscript is:*

**"We used Sterner's model (1990) which describes the fate of N and P from primary producers to consumers, assuming strict homeostasis of the N:P ratio in consumers. In this model, the flux of N and P entering the herbivore pool occurs at a rate equals to the per capita mortality rate of phytoplankton as a result of grazing ($\varepsilon_0 M_0$, Fig. 2). The fraction of N and P removed from phytoplankton which passed the gut wall is called the *assimilation efficiency* ($\beta_1^N$ or $\beta_1^P$, Figs. 2 and 3). The unassimilated fraction is then egested as fecal pellets (1-$\beta_1^N$ or 1-$\beta_1^P$).** It should be noted that Sterner (1990) did not explicitly consider the assimilation efficiency and the production of fecal pellets. **A fraction of N and P which has passed the gut wall is used to build herbivore biomass. In Sterner's model, this fraction is called the *accumulation efficiency* ($a_N$ for N and $a_P$ for P, Figs. 2 and 3). Using Eq. (1), it follows that $GGE_N = a_N \beta_1^N$ and $GGE_P = a_P \beta_1^P$. The fraction which is not accumulated in herbivore biomass is released (excreted) as dissolved products (Figs. 2 and 3).**

**In the model, $\beta_1^N$ and $\beta_1^P$ are kept constant (see Sect. 2.3). On the other hand, $a_N$ and $a_P$ are variable and calculated as a function of the difference between the N:P ratio of**

**phytoplankton ($R^{i}_{org}$, with *i* = NF or O) and that of the herbivore ($R^{Z}_{org}$). Before calculating $a_N$ and $a_P$, Considering that differential assimilation efficiency for N and P can modify the N:P stoichiometry in the algal food after the gut passage is essential. To take into account this effect, $a_N$ and $a_P$ are calculated using the N:P ratio of food which has passed the gut wall as:**

$$R^{i}_{org} \cdot \frac{\beta_1^N}{\beta_1^P} . \qquad (4)$$

**Two cases have then to be considered (Fig. 3), following Sterner (1990): When $R^{i}_{org} \cdot \beta_1^N / \beta_1^P < R^{z}_{org}$, there is an excess of P and a deficit of N in the assimilated food compared to herbivore requirement. In this case, the accumulation efficiency of the limiting element, N, is maximal, i.e. $a_N = L_m$ (the value of the constant $L_m$ is discussed in Sect. 2.3). Conversely, the accumulation efficiency of the nutrient in excess, P, is lower and proportional to the difference between the N:P ratio in the algal pool and that of the herbivore, i.e. $a_P = L_m \left(R^{i}_{org} \cdot \beta_1^N / \beta_1^P\right) / R^{z}_{org}$.**

**Using these parameterisations, strict homeostasis of the N:P ratio in herbivore biomass is maintained. Indeed, considering a flux of N and P entering the herbivore pool ($I_N$ and $I_P$ respectively, mmol m$^{-3}$ yr$^{-1}$), the N:P ratio in the fraction of nutrients accumulated in herbivore biomass can be written:**

$$\frac{I_N}{I_P}\frac{GGE_N}{GGE_P} = \frac{I_N}{I_P}\frac{a_N \beta_1^N}{a_P \beta_1^P}, \qquad (5a)$$

**with $a_N = L_m$, $a_P = L_m \left(R^{i}_{org} \cdot \beta_1^N / \beta_1^P\right) / R^{z}_{org}$, and $I_P = I_N / R^{i}_{org}$, this yields**

$$\frac{I_N}{I_P}\frac{GGE_N}{GGE_P} = R^{Z}_{org} . \qquad (5b)$$

**The second case is when $R^{i}_{org} \cdot \beta_1^N / \beta_1^P > R^{z}_{org}$, nitrogen is in excess compared to herbivore requirement and its accumulation efficiency is lower than its maximal value, i.e. $a_N = L_m \cdot R^{z}_{org} / \left(R^{i}_{org} \cdot \beta_1^N / \beta_1^P\right)$. Conversely, phosphorus becomes the limiting element and its accumulation efficiency is maximal, i.e. $a_P = L_m$. Here again, strict homeostasis of the N:P ratio in herbivore biomass is maintained.**"

[Comment 2a] 2) State the conditions under which N and P will be limiting. Looking at Fig 4 (c) and (d), it appears that the threshold elemental ratio is at an algal N:P ratio of about 24. So how has this come about (which parameters is it determined from)? How sensitive are the overall results and conclusions to this TER?

*[Response] The TER was indeed close to 24 (23.188) as rightly pointed out by the reviewer in the figure. In the revised version of the manuscript, the calculation of TER has been detailed as follow:*

"…**This threshold ratio corresponded to the case where** $R_{org}^{O} \cdot \beta_1^N / \beta_1^P = R_{org}^{Z}$ **, that is** $R_{org}^{O} = R_{org}^{Z} \cdot \beta_1^P / \beta_1^N$ **(see model description, Eq. (4)). Using** $R_{org}^{Z}$ **=20,** $L_m$**=0.90,** $\beta_1^P$ **=0.80 and** $\beta_1^N$ **=0.69, this threshold ratio is equal to 23.188 (Fig. 4c). This was a condition** for which the growth of herbivores shifted from N to P limitation. Below this threshold ratio, the excess of P in the phytoplankton pool compared to the herbivore requirement was excreted at a N:P ratio lower than that of phytoplankton (Fig. 4b). In parallel, $GGE_P$ was lower than its maximal value, while, on the other hand, $GGE_N$ was maximal (Fig. 4c). Conversely, above this threshold ratio, phytoplankton nitrogen content was in excess of the herbivore requirement, the N:P ratio of the excreted products increased (Fig. 4b), and $GGE_P$ is maximal while $GGE_N$ decreased exponentially (Fig. 4c). **In Fig. 4c, it should also be noted that** $GGE_N$ **and** $GGE_P$ **reached simultaneously their maximal value when the N:P ratio is the algal pool reached the threshold ratio of 23.188, that is when the N:P ratio of algal food which has passed the gut wall matched the N:P ratio of herbivore.**"

[Comment 2b] Likewise, GGEs were 52% and 33% for N and P (page 131, line 11). Make it far easier for the reader to understand how this has come about. What is actually predicted to be limiting the herbivores, and what were the consequences for nutrient excretion.

*[response] GGEs were calculated using the default parameter set listed in Table 1 (with some parameters having different values than those used in the sensitivity analyses section discussed above). We have detailed how these numbers has come about in the revised manuscript as follow:*

"In the model, excretion by herbivores depended on the N and P assimilation and accumulation efficiencies. **Using the parameters values in Table 1, when zooplankton fed on non-fixers (** $R_{org}^{O}$ **= 16), the predicted zooplankton GGE for N and P were**

$$GGE_N = a_N \beta_1^N = L_m \beta_1^N = 0.52,$$

**And,**

$$GGE_P = a_P \beta_1^P = L_m \frac{R_{org}^{O} \beta_1^N / \beta_1^P}{R_{org}^{Z}} \beta_1^P = 0.33.$$

**Conversely, when zooplankton fed on $N_2$ fixers (** $R_{org}^{NF}$ **= 33), GGE for N and P were**

$$GGE_N = a_N \beta_1^N = L_m \frac{R_{org}^{Z}}{R_{org}^{NF} \beta_1^N / \beta_1^P} \beta_1^N = 0.45,$$

**And,**

$$GGE_P = a_P \beta_1^P = L_m \beta_1^P = 0.60."$$

[Comment 3] 3) Some statements confused me. E.g. (p. 122, line 14): "In the model, a total of 56.5% of gross intake was released as either NH4+ or DON." But surely the release should be variable, according to the N:P ratios of predator and prey? Indeed, on p. 131 (line 10) there is: "In the model, herbivores' excretion depended on the N and P assimilation and accumulation efficiencies."

*[Response] We agree with the referee's comments that the sentence p.122, line 14 was indeed confusing especially in the use of the terms "in the model".* In fact, the terms "*in the model*" *referred to the study by Vincent et al. (2007), which was not to our model. The main purpose*

*of these sentences was to give ranges for the assimilation efficiencies. For the sake of clarity, we have modified this paragraph as followed:*

"As mentioned above, the assimilation efficiency for N and P by herbivores ($\beta^N$ and $\beta^P$) were not explicitly considered in Sterner's model. Here we included these parameters because sinking fecal pellets can be a significant component of export to the deep ocean. **Nitrogen assimilation efficiencies for copepods are in the ranges 0.70–0.99 (Daly, 1997; Landry et al., 1984; Vincent et al., 2007). For those of P, they range from 0.4 to 0.77 for copepods (Butler et al., 1970; Corner et al., 1972), and from 0.54 to 0.82 for cladocerans (Peters and Rigler, 1973; Hessen and Andersen, 1990).** A compilation of all these values suggests that N and P assimilation efficiencies are in the ranges 0.70–0.99 and 0.4–0.82, respectively. In the standard simulation, we assigned a slightly **lower** assimilation efficiency for N ($\beta^N$ = 69%) than for P ($\beta^P$ = 80%) following Anderson et al. (2005)."

[Comment 4] I've only given a few examples. But in general I found the model impenetrable, which was a shame. The model description does, I suggest, require a major overhaul.

*[Response] We have thoroughly modified the description of the model. We hope that the basic assumptions and parameterization of Sterner's model are now much clearer.*

[Comment 5] The only other major criticism I have relates to iron. Tyrrell himself received criticism for not including iron in his model, given that it likely mediates the competition between nitrogen fixers and other phytoplankton. Given that iron cycling in the ocean is a topical issue, I am surprised that I could find no mention of it in this ms. The authors do suggest, for example, that N2-fixers are P-limited. Interesting, but surely this should be set in context of current views of this group being limited by Fe?

*[Response]The referee raised an important issue about the influence of iron. We have inserted the paragraph below related to the influence of CNR on iron cycling.*

"**Considering the influence of CNR in driving marine ecosystem functioning, an important issue which would need further investigations is the influence of CNR on iron cycle in the Ocean. Iron limits primary production in several oceanic environments (Martin and Fitzwater, 1988; Hutchins and Bruland, 1998), and $N_2$-fixers are known to have high Fe-requirement compared to other algae (Finkel et al., 2010). Thus, the influence of CNR on $N_2$-fixation could be triggered not only by P but also by Fe resupply from herbivores. Several studies have suggested that grazing by herbivores enhances iron recycling (Barbeau et al., 1996, 2001; Twining et al., 2004a; Sato et al., 2007; Sarthou et al., 2008). Barbeau et al. (1996, 2001) found for example that digestion of colloidal iron in the acidic food vacuoles of protozoan grazers may be a mechanism for the regeneration of bioavailable iron from the refractory iron phases. Similarly, a study of the impact of grazing on Fe regeneration in a naturally iron-fertilised area also revealed that copepod grazing resulted in a 1.7–2.3-fold increase in Fe regeneration (Sarthou et al., 2008). It was also found that Fe regeneration accounted for 42–61% of the total Fe demand, and the presence of copepods increased Fe regeneration by 48%. Sato et al. (2007) have suggested that organic Fe-binding ligand formation during microzooplankton and copepod grazing on phytoplankton may be responsible for the observed increase of Fe regeneration.**

**Applying CNR theory principles to iron implies that enhanced iron recycling from grazing should result from Fe-excess in the phytoplankton pool compared to the herbivore requirement. To our knowledge, few things are known about the iron requirement of zooplankton. Twining et al. (2004b) measured the C:P:Fe stoichiometry of individual cells of heterotrophic flagellates ($H_{flag}$) during the Southern Ocean Iron experiment. They found that $H_{flag}$ and phytoplankton had similar Fe:P ratios under low Fe-conditions, while $H_{flag}$ had lower Fe:P ratios than phytoplankton under high-Fe conditions. Low Fe:P ratio in the consumer pool compared to the algal pool would be consistent with enhanced iron recycling from herbivores. This influence of CNR on iron cycling would need further investigations, especially regarding the Fe requirement of consumers.**“