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Discussions

Interactive comment on "Role of zooplankton dynamics for Southern Ocean phytoplankton biomass and global biogeochemical cycles" *by* C. Le Quéré et al.

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The Southern Ocean (SO) plays a key role in the ocean carbon cycle hence efforts to model its past, current and possible future impact on atmospheric CO2 levels are most worthy of discussion in a broad forum. This general rule applies particularly to this paper because the authors are prominent members of the ocean modelling community. Their message is that adding more zooplankton grazers, in this case "large, slow-growing crustacean zooplankton", to a global ocean biogeochemistry model produces phytoplankton biomass levels in the SO closer to values obtained from satellite imagery. An earlier model without the additional zooplankton components gave unrealistically high summer phytoplankton biomass values in the SO. This is a logical conclusion: plant biomass will go down if the growth rate is kept constant but the grazing pressure increased. From this straight-forward balance equation the authors conclude that grazing rate rather than iron supply is responsible for the low chlorophyll concentrations in the Southern Ocean. Since this generalisation would bring the great HNLC debate of the 1990s - is it light, iron or grazing that controls productivity? - back to square one, it is necessary to review the arguments for the case made here in order to help clear up what is probably widespread confusion in the community regarding the extent of iron limitation in HNLC regions and the capabilities of biogeochemical models to deal with the issue.

A number of questions arose in my mind whilst reading the manuscript to which I could not find the answers in the manuscript and supplementary information. If the issues have been considered they should be mentioned prominently in the main text. If, on the other hand, one or more of these issues has not been considered, then the text will need to be rewritten in the appropriate places and the conclusions modified accordingly.

Question 1: Since phytoplankton biomass is equated with chlorophyll concentrations throughout the text, I would like to know whether the following factors that affect its variability have been considered and how: a) Latitudinal variation in mixed layer depth, b) increasing C/Chl ratios with declining iron supply.

a) Mixed layer depth (MLD) The "phytoplankton biomass" of interest to food web and carbon cycle studies is the integrated stock per area of water column (in mg or g chlorophyll or carbon m-2) and not just the concentration. The difference between concentration (obtained from discrete measurements) and stock (obtained from integrating discrete values for the mixed layer) is highlighted by the differences in chlorophyll yields between the OIF experiments SEEDS I in the Subarctic Pacific and EIFEX in the SO: >20 mg Chl m-3 and ~3 mg Chl m-3 respectively. However, the mixed layer during SEEDS I was only 10 m deep but 100 m during EIFEX, so the standing stocks were

∼200 and ∼300 mg Chl m-2 respectively. As others have fallen into the MLD dilution trap before (e.g. de Baar et al. 2005), I refer to Smetacek and Naqvi (2008) and the comments to Smetacek et al. (2012) where the issue has been explained in detail. Reference to the effect of MLD on phytoplankton biomass is given only in Lines 9-12 of page 17 but the MLD values used in the model need to be explained explicitly in the text and, where appropriate, in the legends.

Only concentrations are referred to in this paper and the model results are compared with satellite images that measure concentration in the upper few metres. How the effects of much deeper MLDs in the SO as compared to the N. Pacific and N. Atlantic have been taken into account needs to be highlighted in the text and legend of figure 4. In the model, meso- and macrozooplankton biomass is derived from 200 m vertical net tows and then converted to concentration in the 200 m water column (lines 12 – 15, page 12). Phytoplankton concentrations should be treated in an equivalent fashion but for the MLD and not a standard depth as for zooplankton. It is likely that the differences in surface chlorophyll concentrations between satellite and model will reduce further when this effect is considered.

b) Chlorophyll-biomass ratios Chlorophyll synthesis is one of many biochemical pathways that are limited by iron deficiency. Providing iron to phytoplankton leads to increased production of this pigment and C/chl ratios can drop two to threefold with only a marginal increase in biomass, an effect which is particularly apparent in diatoms. So chlorophyll concentrations are an unreliable proxy for phytoplankton biomass because they can vary so much between iron-limited and iron-replete conditions. The ratio (Chl/C) has been considered as a determinant of growth rate in the model but I could not ascertain whether the “phytoplankton biomass” based on chlorophyll in the SO was also corrected for this variable. This would exacerbate the chlorophyll problem by increasing the real, carbon-based biomass.

Question 2 Why only 3 zooplankton PFTs? What would the model results look like if a fourth zooplankton PFT that included the salps was introduced: micro-feeding,

fast-growing, large zooplankton? Put in another way, why stop at the third category of zooplankton? They have many more PFTs than phytoplankton. Salps are relevant because their stocks have been increasing in the SO over the past decades concomitant with a krill decline (Atkinson et. al. 2004) so it is possible that a replacement is taking place with consequences for SO productivity. Salps differ from the category of zooplankton added here (slow-growing macrozooplankton) in that they have short generation times because they can produce individual animals by budding in the course of a day to weeks depending on temperature and presumably food supply. Their inclusion might lead to complete grazing down of the phytoplankton because nothing is known about the checks and balances on their population size. Since they swim, feed and breathe simultaneously it should be possible to model their grazing efficiency fairly easily using threshold values (particle concentration at which they starve, multiply, etc.) from the literature. If the data have not been collected yet, the model results could be used to generate interest in this question.

Question 3: Has iron recycling due to zooplankton grazing been considered in the model? The authors refer to “the dynamics of the SO zooplankton community” as being a more important determinant of low summer phytoplankton biomass than iron limitation. They mention that trophic cascades within the zooplankton have been built into the model but there is no mention of recycling of the limiting nutrient, in this case iron, by the zooplankton, i.e. a feedback loop which would stimulate net production. At the end of the abstract and in the conclusions one is reminded that zooplankton make fast-sinking faecal pellets and carry out vertical migration, implying that the more zooplankton, the more vertical flux and carbon sequestration. So, in today’s times it might be a good thing to have zooplankton around because they sink carbon, a few decades ago, before collapse of the traditional commercial fisheries, zooplankton were good because they made fish food. Since the zooplankton category introduced here are long-lived, their food supply would have to be sustainable, so one wonders what percentage of the faecal pellets produced sinks out of the mixed layer. If all were to sink out, the surface layer would soon be depleted of essential elements and the grazers would starve; so the category introduced here only evolved because most of its wastes are recycled in the surface layer. Salps on the other hand are roving grazers that can afford to let their wastes sink behind them. This is just to mention a few complications that arise when attempting to model the impact of zooplankton and nekton on the biogeochemistry of the surface layer.

General comments In order to continue improvement of biogeochemical models by exploring the impact of zooplankton dynamics on ecosystem structure and functioning, it will be necessary to develop a framework of interactions based on the evolutionary ecology of the phytoplankton/zooplankton relationship. Unfortunately this has not received the attention it deserves for various reasons (see Smetacek et al. 2004, Smetacek 2012), in particular, because the necessary, dependable, quantitative information is still lacking. To my mind this can only come from studies carried out in situ because enclosures of any sort will hamper the zooplankton and nekton. Furthermore, comprehensive measurement programmes of the same body of water will be necessary to study rates and processes within functioning ecosystems. Perturbing the system under study in order to identify shifts in the mechanisms would enhance the value of the information gained from sustained measurements of the same water mass. The whole-lake experiments carried out in the 1970s in the USA and Canada brought unsuspected trophic cascades into focus: Lakes changed their colour depending on the presence or absence of predatory fish. “Were it not for whole lake experiments, limnology would be where bio-oceanography is today, firmly entrenched in the bottom-up paradigm. It follows that bio-oceanography could be where limnology is today if more dedicated in situ experiments are carried out by the scientific community” (comments in Smetacek et al 2012). Could removal of the whales, that once lived sustainably from krill biomass equivalent to double the global commercial fish catch, have had an effect on SO chlorophyll concentrations? Such hypotheses could be tested with ocean iron fertilization (OIF) experiments that have proven themselves as the equivalent of whole-lake experiments in the sea.

All ocean iron fertilization (OIF) experiments carried out so far have shown that iron addition led to a substantial increase in the photosynthetic efficiency index (Fv/Fm) and remained higher for many weeks inside the fertilized patch than values measured concomitantly in surrounding iron-limited water. These results, bolstered with direct measurements of iron concentrations and various types of bottle experiments have unequivocally shown that phytoplankton growth rates in HNLC areas are limited by the iron supply. The conclusion of this paper: that zooplankton grazing rather than iron controls phytoplankton biomass build up would imply, framed in John Martin’s iron hypothesis, that fluctuations in the grazer populations were responsible for climate cycles. This is probably not what the authors mean so the wording of their concluding remarks needs to be properly qualified rather than presented in a simplistic sweeping statement.

Nevertheless, the improved model presented here clearly demonstrates that increasing zooplankton PFTs is an important way to nudge biogeochemical models closer to reality. The last sentences of the Conclusions focus on the possible outcome of ocean iron fertilization (OIF): “Assessments of the impact of such geoengineering will be unreliable, at least until the full ecosystem response including the grazing pathways (Landry et al., 1997) and the relationship to deep water carbon export (Smetacek et al., 2012) can be reproduced with models, which could be used to make quantitative predictions.” The authors are putting the cart before the horse here: OIF experiments are the most reliable way of achieving the assessments called for here. So far only puddles of a few weeks’ duration have been studied. Larger, longer-term experiments are needed to assess the impact of higher trophic levels on ocean biogeochemistry. The ensuing model would then permit one to extrapolate from the experimental scale to the really large-scale of relevance to the global carbon cycle, should this be deemed necessary.

References

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