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Biogeochemical versus ecological consequences of modeled ocean physics

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Response to reviewers:

We thank the three reviewers for their helpful comments on the manuscript. We have set out our responses to the reviewers' comments below, in blue. We have also included a version of the revised manuscript with tracked changes, and a clean version of the revised manuscript. We indicate also where we have addressed the reviewers comments in the tracked changes version of the revised manuscript.

We would like to address some of the same concerns raised by Reviewers #2 and #3:

Firstly, both reviewers were unclear on what the main message of the paper is. In this study, we examined the different responses of a diverse ecosystem model to a coarse resolution and an eddying general circulation model. We found clear and unexpected differences, namely that although there were big differences in the bulk biogeochemical properties of the model solutions, the realized phytoplankton ecosystem had essentially the same structure. As pointed out by Reviewer #1, this is an interesting and unexpected result. The clear message of this paper is that the apparent decoupling in the biogeochemical and ecological responses of the model to different physical forcing can be well explained and is not a random response to the different forcing. In the discussion section of this paper, we have highlighted the mechanisms responsible for the apparent disconnected between the biogeochemical and ecological responses to the different modeled ocean physics. We should also state that this is, to our knowledge, the only study that examines the different responses of a complex ecosystem model coupled to global ocean circulation models at differing resolution. We will make these points more strongly in the revised version of the manuscript as it seems that some of the reviewers were not clear on these points.

Secondly, we would like to respond to the point raised by both Reviewers #2 and #3, that they believe that this manuscript is not sufficiently different from Clayton et al (2013) to warrant publication as a separate study. We respectfully, but very strongly disagree with their assessment of the work under discussion here. This work is based on the same set of model experiments, but that is all that it shares. This work is a stand-alone study from Clayton et al (2013). The previous paper was entirely focused on understanding the underlying physical controls (primarily transport) on modeled patterns of phytoplankton biodiversity. In fact the different resolution of the models was only a very small portion of that paper. The earlier paper does not consider any of the differences in the other ecological properties of the model results (e.g. dominant phenotype or functional group) or in the biogeochemical properties of the model. Specifically, we would draw the reviewers' and the editor's attention to the fact that there is not a single figure shared between these two manuscripts.

Thirdly, Reviewers #2 and #3 commented on what they see as a prevalence of woolly statements in the manuscript, specifically the use of the phrases "we hypothesize that…" and "may be…". We point out that we have used the phrase "we hypothesize that…"

exactly twice in this manuscript (P7, L31-32; P8, L23), and that both of these instances are found in the same section (4.2). We have used the phrase “this may…” only once to speculate on the drivers of model differences (P7, L17), at the end of section 4.1. We respectfully but strongly disagree with the reviewers: our arguments in section 4.1, 4.3 and 4.4. are strong and we have spent considerable care in laying these out. We have fully explained the mechanisms driving differences in the system in the subtropical gyres and at the gyre boundaries. We however do recognize that section 4.2 could be improved, so we have set out below (primarily in response to Reviewer #1’s comments) our improvements to that section in the revised manuscript.

Please find our responses to specific points below.

Reviewer #1

Clayton and colleagues explore the importance of model resolution on ocean ecology and biogeochemistry in two versions of ECCO. Both models were coupled to the same version of the Darwin ecosystem/biogeochemistry model with the primary difference between the two being 1deg versus 1/6 deg resolution, with the later considered ‘eddy permitting.’ The primary finding is that the phytoplankton biogeography in terms of functional type was much more stable than rates and stocks, such as primary productivity and total phytoplankton and zooplankton abundance. These conclusions are somewhat unexpected and a valuable contribution to understanding how mesoscale physics may interact with ecosystem and biogeochemical dynamics.

The manuscript addresses an important topic relevant to Biogeosciences and reaches novel conclusions. It is well written and structured. With some revision, I feel the manuscript will be a valuable contribution to Biogeosciences.

I do have some concerns regarding how the authors interpret differences between HR and CR simulations at the regional scale, particularly for the in the northern high latitudes. These concerns as well as minor comments are listed below.

General Comments:
P8-L12-32: Interpretation is primarily through a steady-state framework (i.e., R*, P*,Z*). This holds when the timescale of physics is >> timescale of biology, supply is constant, etc. My largest criticism is the attempt of the authors to explain the “Dilution-Recoupling Hypothesis” using a steady-state framework (Page 7, line 31 – Page 8 line 1). From Fig 7, it is clear that dP/dt and dZ/dt are almost never close to zero, and certainly not simultaneously zero. The hypothesis is fundamentally driven by perturbed systems where steady-state is not valid. I suggest either further justification why the authors think the Z*/P* framework is applicable here, or to use non-steady-state arguments.

Thank you for these valuable comments. We recognize that in this context, the dilution-recoupling hypothesis was not appropriate, and we have removed the reference to it in the revised manuscript.

Here, we invoke the steady state framework as a way of explaining the apparent disconnect between the similar phytoplankton biomass abundance, and simultaneously very different zooplankton abundances between simulations (in the subpolar gyres). This signal is overwhelmingly driven by the behavior of the system during the summer and autumn months, after the spring bloom. During this period, we do believe that a steady-state approximation is appropriate, as the MLDs and ecosystem properties are stable over several months (see Fig. R1, below, Fig. 6 in the revised manuscript). However, we do agree that this is not appropriate when considering either the winter months, or the entire annual cycle. We have addressed this point on P9 L11-14.

- Would not the deeper spring ML depth in HR simulations result in a greater annual S_N? The authors argue that higher Z* in CR is due to higher S_N, but present no evidence that S_N is higher in CR. If anything, it seems S_N should be higher for HR?

We have evaluated the annual mean wNO_3 at 100m, analogous to S_N. In the high latitudes, wNO_3 is 142.1 mmol NO_3 m^{-2} $year^{-1}$ in CR, and 108.1 mmol NO_3 m^{-2} $year^{-1}$ in HR (this is now on P10 L4-5). So S_N is higher in CR than HR in the high latitudes, despite the deeper MLDs in HR. This difference is due to the higher variability in vertical velocities in HR, and the asymmetry in vertical transport of nutrients. Nutrient concentrations in the surface mixed layer are lower than those below it, so higher variability in vertical velocities will result in decreased nutrient supply compared to the less variable case.

- Comparing Fig 7a and 7b along with the relationship PProd = mu*P, it seems that P growth rate is higher year-round in the CR simulation. Light limitation could explain the difference in spring, as the authors point out, but what about the rest of the year?

We have replaced Fig. 7 with a Hovmoller diagram (Fig. R1, below, Fig. 6 in the revised manuscript), which better represents seasonality. The previous version of the figure confounded seasonal and latitudinal differences between the simulations.

In the context of this model, the limiting factors on the phytoplankton growth rate are multiplicative, e.g. for a modeled phytoplankton phenotype *j*, the growth term is given by:

$$\mu_j = \mu_{MAX} \gamma_j^T \gamma_j^I \frac{R}{R + k_{Rj}}$$

where γ^T and γ^I are the temperature and light limitation terms, respectively (see P8 L31 - P9 L6)

In the Northern Hemisphere:
During the winter, when nutrients are replete (and the nutrient term goes to 1), if either the light or temperature fields experienced by the modeled phytoplankton are consistently less favourable, then μ will be lower. MLDs are consistently deeper in the HR simulation during the winter months, resulting in lower winter PP in HR than CR.

The onset of the spring bloom occurs roughly one month earlier (March-April) in the HR simulation than the CR simulation (April-May). This can be seen as higher PP in the HR simulation in March and April, followed by a reversal with higher PP in the CR simulation in May. This is driven by differences in the timing of the shoaling of the MLDs (see P9 L7-10).

Through the summer and into autumn, the MLD shoals and nutrients become limiting. Summer MLDs are deeper and there is a higher wNO_3 in CR, resulting in higher S_R and surface nitrate concentrations in CR than HR over the summer months. This explains the higher PP during early summer in the CR simulation (see P9 L11 - P10 L12)

Similar patterns can be seen in the Southern Hemisphere, where the MLD shoals earlier in the spring in the HR simulation, and PP and P biomass are both lower in the HR simulation during the summer.

Equatorial upwelling is minimally addressed. In Fig 2 there is a dramatic increase in phytoplankton stock and primary productivity in the Equatorial Pacific. It would be interesting to diagnose if there is a change in net nutrient supply from equatorial upwelling and if there is a change in subsequent meridional transport of nutrients, or if they are effectively locally trapped. The authors mention a change in equatorial productivity related to a change in poleward Ekman nutrient transport, but there is no discussion if there is any change in the supply rate from upwelling (rather than mld changes). Could the authors compare <wN> over an equatorial band between the two model resolutions?

Thank you for suggesting that we look at wN. We have evaluated the annual average wNO_3 at 100m between 5°N and 5°S for the both models. The regionally integrated mean annual vertical NO_3 fluxes (mmol NO_3 m^{-2} $year^{-1}$) evaluated at 100m for model year 1999 were 453.1 mmol NO_3 m^{-2} $year^{-1}$ and 383.7 mmol NO_3 m^{-2} $year^{-1}$, for the HR and CR simulations, respectively. There is a clear increase in vertical nutrient supply in the equatorial upwelling zone in HR that can account for the dramatic increase in phytoplankton stock and primary productivity in the Equatorial Pacific (see P8 L19-24).

Another general comment is that the model includes two Zooplankton that I believe have size specific grazing preference. It would be interesting to diagnose if the change in resolution causes any systematic changes in the efficiency of predator-prey coupling. i.e., is there any change in the average 'g' term? One might expect that higher resolution physics could disrupt predator-prey coupling. Have the authors looked into this? (This is just my curiosity, and I am fine if the authors feel the topic is beyond the scope of this manuscript).

Yes, the ecological model includes two zooplankton. Small and large zooplankton graze preferentially on small and large phytoplankton, respectively. Although this is an interesting question, we feel that it is beyond the scope of this manuscript, as we would need to re-run both models in order to diagnose the 'g' term to explore differences in it.

P8-L2-3: In equations (5) and (6) it is unclear to me why there is an 'R' term in the right side of each equation. The description of an idealized light-limited model system implies replete nutrients. Under nutrient replete conditions ($R >> k$), the $R/(R+k)$ term in Eq (1) approaches 1, and eq 5 should simplify to:

$dR/dt = - \mu_l P + S_R + \gamma m_Z Z$

I do not see the need or justification for $\mu_l RP$. In fact, there is no change in solutions for N* and Z* (Eqs. (9) and (10)). Equation (8) would then be superfluous and should be removed.

This is correct. However, we have revised our analysis in this section (4.2), and find that nutrient limitation is a more appropriate way to explain the behaviour of the system during the summer. We have updated our equations accordingly to the following:

$$\frac{dR}{dt} = -\mu_{max}\frac{RP}{R+k} + S_R$$

$$\frac{dP}{dt} = \mu_{max}\frac{RP}{R+k} - gZP$$

$$\frac{dZ}{dt} = gZP - m_z Z$$

with the following solutions for a steady system:

$$R^* = \frac{kS_R\, g}{-gS_R + \mu_{max}m_z}$$

$$P^* = \frac{m_z}{g}$$

$$Z^* = k(\frac{S_R\, g}{\mu_{max}m_z} - 1)$$

The increased S_R in the CR simulation (due to higher wN and deeper summer MLD) can account for the increased zooplankton abundance in CR in the summertime, although the summer (June - October) phytoplankton concentration remains very similar between both simulations (see P9 L11 - P10 L12).

Minor comments:
P8 L30-32: 1/6deg definitely doesn't represent the Mahadevan (2012) restratification mechanism which is fundamentally submesoscale. It might capture the McGillicuddy (2003) mechanism.

You are correct, the Mahadevan (2012) restratification mechanism is not resolved in the HR model. We had initially included that reference to give broader context on the known effects of fine sale physical dynamics, however it seems that it is superfluous in the context of this model study, so we have removed that sentence from the revised manuscript.

Figure captions:
General comment: Indicate in each figure caption if results are annual averages for 1999, or some other time period.

We have added this to each of the figure captions where it is missing in the revised manuscript.

Figure 3: The 'green' in (a) and (b) looks quite blue/teal to me

Could this be an issue with your monitor? The green colour in Fig. 3 looks green on my monitor and in my printed out version of the manuscript.

Figure 5: I would suggest that the order of (b) and (c) be switched. Also, in panel (b), it would be useful to color code by what the

Something seems to be missing in the above comment.

There are also some distracting red dots, such as south of New Zealand, that appear to be islands.

Yes, the red dots are islands, we have updated Fig. 5 in the revised manuscript to remove them.

Figure 6: Does 'higher' mean deeper? Suggest that you say Positive values indicate deeper…

Yes, thank you for pointing that out, it is a little confusing. We have changed the caption for Fig. 1 to read "Positive values indicate deeper MLD in the HR simulation, and negative values indicate deeper MLD in the CR simulation". We have removed Fig. 6 from the revised manuscript.

Figure 7: It would help interpretation to also include the seasonality of mixed layer depth for HR and CR as a separate panel (or overlay on the existing panels). Consider including seasonality of surface nitrate also.

We have replaced Figs. 6 and 7 with a Hovmoller diagram (Fig. R1, below, Fig. 6 in the revised manuscript) which now includes the seasonality of the MLD and surface nitrate.

Editorial Comments:

P5-L15: tus to thus

We have made this correction in the revised manuscript (see P6 L15).

P6-L31: μ to μ_m would be preferable, as μ alone typically refers to realized growth rate, not maximum growth rate. Also, S_N to S_R

We have modified eqs 1 and 2 to the following, and made the changes consistent through the rest of the text of section 4.1

$$\frac{dR}{dt} = -\mu_{max}\frac{RP}{R+k} + S_R$$

$$\frac{dP}{dt} = \mu_{max}\frac{RP}{R+k} - mP$$

P8-L19 "drives in an.." to "drives an.."

We have corrected this in the revised manuscript (see P8 L14).

P9-L4 Northern and Southern Pacific to North and South Pacific

We have corrected this in the revised manuscript (see P11 L20-21).

Fig 2 caption: Although 'annual' is in the text, units for primary production of g C m^{-2} y^{-1} would be preferable such that the units are consistent with a rate.

We have made that change in the caption for Fig. 2 in the revised manuscript.

Reviewer #2

This study compares the simulated biological differences in a "diverse ecosystem" model coupled to two different global physical model configurations, one that has a relatively high resolution and is eddy permitting and one that is much coarser and does not resolve eddies. This is an interesting starting point and the abstract of this manuscript is quite promising. I was very curious to read about the insights that might be gained from the study laid out there. However, the manuscript itself was rather superficial and disappointing and did not deliver on the study's potential.

There are some similarities and some difference between the two configuration, as one might have expected.

That there are differences and similarities is possibly expected, but the fact that the ecological solution of the model (phytoplankton community structure) is not affected by changes in the model physics, whereas the modeled biogeochemical properties of the model are greatly affected by changes in the model physics is striking and unexpected (see Reviewer #1's comments).

The authors do not dig deep enough in explaining the underlying reasons for the differences. In the discussion there are several occurrences of "we hypothesise that these differences result from. . ." which is rather unsatisfying in a modeling study where one can examine every process in great detail and get to the bottom of differences.

We respectfully disagree with the reviewer that we do not explain the underlying reasons. We point out that we make very definitive statements in section 4.1 about the processes that drive the differences between models in the subtropical gyres, as well as in section 4.3 about the processes that account for the geographical shifts in the boundaries between biogeographical provinces. We note that the phrase "we hypothesize that…" occurs exactly twice in the submitted manuscript (P7, L31-32; P8, L23), with both instances found in the same section (4.2). We do not believe that this can be described as "several occurrences".

However we do recognize that our discussion of the processes driving the changes in the northern hemisphere high latitudes in section 4.2 may have been a little less concrete in the submitted manuscript and we have strengthened it in with the addition of more analysis, as set out in our responses to the specific reviewer comments.

Furthermore, the mere description of differences between the two model configurations without any comparison with observations seems rather limited.

As stated in the introduction of our manuscript, the intent of this study was not to assess which model performs best with respect to reality, but rather to better understand how differences in the modeled ocean physics might affect *both* the ecological and biogeochemical properties of the model solutions. We have used versions of the CR model in several previous studies where we have compared model output more thoroughly to observations (see e.g. Follows et al 2007; Dutkiewicz et al., 2012; 2015). We feel that additional comparisons to observations would detract from the main message of the work, which explains how, in different biogeographical regions, the modeled phytoplankton community remains unchanged whereas the biogeochemical properties of the model, which are ultimately set by the phytoplankton community, vary greatly with changes in the modeled ocean physics. We also disagree that the manuscript is merely a "description" of differences. The main point of the paper is to explain the differences and similarities.

Most importantly, I don't find any broadly applicable insights articulated in the manuscript. What is the novel insight that the authors are trying to present here? Given the distinguished author list, this was a particularly disappointing read.

We are disturbed that the reviewer found no “insights articulated” in this study. We believe that we have shown that the bulk biogeochemical properties of this ecological model (*which has many similarities to other widely used biogeochemical models which also resolve multiple phytoplankton PFTs*) are more sensitive to differences in modeled ocean physics than the structure of the ecosystem itself. We would argue that this actually has profound implications for how we might think about structuring ecological and biogeochemical models. We have made this point more clearly in the conclusions of the revised version of the manuscript as it seems that it was not entirely clear to this reviewer. We have added an additional paragraph to the conclusions (see P12 L29-32):

> “We have shown that the bulk biogeochemical properties of this ecological model are more sensitive to differences in modeled ocean physics than the structure of the ecosystem itself. Given that this model has many similarities to other widely used biogeochemical models, which also resolve multiple phytoplankton PFTs, this study provides important insights into how these models might behave under different physical conditions.”

Some specific comments:
Intro, 1st paragraph: Higher ecological complexity is not necessarily because of the potential problem of overfitting. It would be appropriate to at least mention this.

We are not entirely sure what the reviewer is referring to here. As we are not constraining any of the biogeochemical or ecological fields to observations, it is hard to see how adding biological complexity could result in overfitting. Possibly the reviewer is mistaken in thinking that the biogeochemistry or ecosystem in this study is assimilated?

As the goal is to adequately represent the system under consideration, surely the level of complexity needed to represent the system will vary depending on the question being posed? We do not feel that any of our statements in the first paragraph of the introduction contradict this point.

Page 2, line 25: Reference to LeQuere et al. (2005) seems inappropriate here. This paper is not describing a global biogeochemical model, but merely a plan or idea of such.

We disagree on this point. Le Quéré et al (2005) explicitly discusses how biogeochemical models that resolve phytoplankton functional types (PFTs) behave differently to simple NPZD models. For example, their Fig. 8 shows the differences in modeled chlorophyll *a* for an NPZD model versus the PISCES model (with 3 PFTs) and the Dynamic Green Ocean Model (with 4 PFTs). We believe that this is a perfectly relevant reference in this context.

Section 2.1: What type of data assimilation was applied to the models and could this affect the results? It has been shown previously that data-assimilative physical model solutions can lead to drastically altered biogeochemical results compared to their corresponding non-assimilative model versions (see, e.g. Raghukumar et al. Progress in Oceanography, 2015).

Both physical models are data assimilation products. The ECCO-GODAE product is based on the Lagrange Multiplier method and the ECCO2 product employs a simplified Green’s function method. We have added more detail on this in the revised manuscript (P3 L21-27). However, there was no assimilation of biogeochemical or ecosystem variables in this study. It is possible that the reviewer did not appreciate this point, so we will also make this clearer to the text.

We note (though not sure that this is applicable to Raghukumar et al, 2015) that a reason for drastic alteration of biogeochemical results in data assimilative models is the use of so-called “filtering” methods that are designed for forecasting instead of “smoother” methods that are optimal for reconstruction. Filtering methods, such as the Kalman Filter (or optimal interpolation, which is an approximate form of the KF) incur so-called “analysis increments” at regular time intervals when new observations become available. At these times, a new initial condition is generated as a weighted sum of model forecast and observation, producing an “analysis”. Importantly (and not widely appreciated in the context of reconstruction), this step violates conservation of momentum, heat and salt. As a result, artificial adjustment motions are triggered, in particular in the vertical velocity field, which is crucial for vertical transport of biologically active tracers (see discussion in Wunsch and Heimbach (2013) and Stammer et al. (2016) how smoother methods can alleviate this problem). Thus we feel we should be cautious in how we attribute large changes between data-assimilative physical/biogeochemical models relative to non-assimilative models in general (again we do not know whether this is an issue in Raghukumar et al (2015) however).

REFERENCES:

- Stammer, D., M. Balmaseda, P. Heimbach, A.Koehl, and A. Weaver, 2016: Ocean Data Assimilation in Support of Climate Applications: Status and Perspectives. *Ann. Rev. Mar. Sci.*, 8, 491-518, **doi:10.1146/annurev-marine-122414-034113**
- Wunsch, C. and P. Heimbach, 2013: Dynamically and kinematically consistent global ocean circulation and ice state estimates. In: G. Siedler, J. Church, J. Gould and S. Griffies, eds.: Ocean Circulation and Climate: A 21st Century Perspective. Chapter 21, pp. 553–579, Elsevier, **doi:10.1016/B978-0-12-391851-2.00021-0**.

We thank the reviewer for bringing the Raghukumar et al (2015) paper to our attention. We notice that in that study, they used an earlier version of the same ecological model used in this work. However, we were very disappointed to see that they did not present any of the ecosystem level differences for the model solutions using different data assimilation methods. This is a shame, as we suspect that had they looked at differences in the phytoplankton community structure (e.g. dominant phenotypes and functional groups) their results would have echoed our findings, that although the bulk biogeochemical properties of the system are strongly modulated by different ocean physics, the phytoplankton community structure is more robust to those changes.

Although it is possible that some differences in the ECCO state estimates might be due to assimilation methods, as well as to differences in the resolved physical dynamics, the bottom line is that differences in the realized physical fields are responsible for driving different biogeochemical responses. We have added a comment to this effect in the third paragraph of the conclusions in our revised manuscript (see P12 L29-32).

Figures 1 and 2: I would prefer to also see the CR results, not just HR and the differences between HR and CR.

We have opted not to show the CR results in order not to overload the paper with unnecessary and repetitive extra figures. In an earlier draft of the paper we had included both and found that it was distracting as the basic patterns were so similar: *the difference plot is essential*. Since the focus of this paper is on the differences between the model solutions, we believe that it makes more sense to only show the results of one of the model configurations, along with the difference plot in the main text. We would be happy to add the CR panels to supplementary material in a revised version of the manuscript.

Page 4, line 17-18 and Page 5, line 13-14: Differences between both models (model physics as well as biogeochemistry) have previously been described by Clayton et al. (2013). I'm wondering what the new and distinct contribution of this publication is in comparison to Clayton et al. (2013).

We respectfully disagree. Clayton et al (2013) shows the difference between the following properties of the models:

- Eddy kinetic energy (Fig. 1C)
- SST variance (Fig. 1D)
- Biodiversity (Fig. 3B)
- Globally integrated annual average abundance of each modeled phenotype (Fig. 4B).

We would draw the reviewers' and the editor's attention to the fact that none of these physical or biogeochemical properties of the models are discussed (or included in figures) in the manuscript under review here. We have addressed this point above, but we would like to repeat that the manuscript under review here is a distinct contribution from the previous (2013) paper. However, we recognize that the first sentence of the results section (P4, L17) may be misleading on this point, so we have removed it from the revised manuscript and have modified the second sentence to read (P5 L5-8):

> "We describe differences in some of the physical properties of the physical circulation estimates: sea surface temperature (SST), mixed layer depth (MLD) and vertical nutrient fluxes. Differences in other physical fields between the two model configurations have previously been discussed in Clayton et al (2013), here we examine only those physical processes most directly relevant to biogeochemical processes not considered in that previous work."

Reviewer #3

In this study the authors investigate how model resolution influences simulated ecosystem and surface ocean biogeochemical properties. Two physical ocean configurations are used; a high-resolution eddy permitting model and a lower resolution version of the model that does not resolve eddies. When the same "emergent" biogeochemical ecosystem model is coupled to these different physical configurations the authors find that phytoplankton biogeography is similar, while other biogeochemical properties have much larger differences. Investigating the "biogeochemical versus ecological consequences of modeled ocean physics" is important and I was eager to read such a study. However, I was somewhat disappointed with what was presented.

The writing is clear and the analysis to show how the model results differ is mostly acceptable. However, I was not satisfied with the explanation of why there are similarities and differences between the two set-ups. The authors did not conduct a deep enough investigation and it seemed more that they were simply showing similarities and differences and then hypothesizing why this occurred. I realize that the authors made some attempts to figure out the reasons behind the similarities and differences using a resource competition framework, but they did not take this investigation far enough and instead often ended up concluding their investigation by saying things like, "we hypothesize..." or "this may...". This is rather unsatisfying since one should be able to examine the model results in detail to actually determine why any similarities or differences occurred.

We respectfully, but strongly disagree with the reviewer that we do not explain the underlying reasons for the similarities and difference. We point out that we make very definitive statements in section 4.1 about the processes that drive the differences between models in the subtropical gyres, as well as in section 4.3 about the processes which account for the geographical shifts in the boundaries between biogeographical provinces. We note that the phrase “we hypothesize that…” occurs exactly twice in the submitted manuscript (P7, L31-32; P8, L23), with both instances found in the same section (4.2). We do not feel that two occurrences of the phrase qualifies as “often”. We would also mention that there is only one instance in the text where we use the phrase “this may…” to speculate on the drivers of model differences. Again, we do not feel that this qualifies as “often”.

However we do recognize that our discussion of the processes driving the changes in the northern hemisphere high latitudes in section 4.2 may have been a little less concrete in the submitted manuscript and we have strengthened for our revised manuscript with the addition of more analysis, and have included it below.

Moreover, after reading Clayton et al., 2013 again, it seemed to me as if the authors are merely trying to extend their earlier work and publish a few new details that probably should have just been included in the earlier publication (i.e., not much seems to be new except for a few plots of biogeochemical differences). Am I wrong in this or is this a new set of experiments?

Again, we respectfully but strongly disagree. Yes, both papers use the same two model configurations, but the focus of the two papers is very different. This work stands alone from the previous paper, which was concerned with understanding the physical contributions, specifically with respect to transport, to modeled patterns of phytoplankton biodiversity. In fact the role of differing resolution plays only a very small part in our earlier paper. By contrast, this paper explicitly addresses the effects of model resolution on the biogeochemical and ecological model results.

The methods section of the paper was also lacking a few details and I had to assume that the set-up was the same as in the earlier paper based on what was stated in the results and discussion section. Without some of the critical information on how the model was spun-up and more crucially, for how long it was spun-up, I also had a difficult time interpreting some of the presented results. If the model was only run for 8 years as in Clayton et al., 2013 then, I highly doubt that steady state or even quasi-steady state conditions were reached. This makes it challenging to investigate biogeochemical properties because of model ’drift’. While it may be possible to somewhat account for such ’drift’ the authors have not attempted to do so and thus, have only provided a snapshot of a system that would likely be quite different if the simulations were run for a longer period of time. I realize that there are computational limitations that prevent high-resolution models from easily being run to steady state, but the authors need to address the issue of ’drift’ if they want to investigate differences in biogeochemistry.

Thank you for drawing our attention to the fact that the methods section would benefit from a more detailed description of the model setup, initial conditions and forcing, and the length of the simulations. We have updated the revised version of the manuscript with the information outlined below (see P4 L24-25; P4 L27-34).

We do not feel that model drift is an issue. Indeed it would take several thousands of years to fully spin up the biogeochemistry (in particular the deep nutrient concentrations) of the models. Even then the model would not be in steady state as seasonal cycling and interannual variability would only lead to what we might call a quasi-steady state. It is certainly not feasible to spin up the HR this long, nor do we feel that this would lead to insights into the specific issues we address in this study.

In several previous studies using the CR model (see e.g. Dutkiewicz et al., 2009; 2012; 2015) and in this study for both CR and HR we find that it takes only 3 years for the ecosystem to reach a stable annual cycle. And at this stage the drift in surface nutrients is very small – much smaller than the seasonal and interannual variability. We also looked at the trend in globally integrated annual average phytoplankton biomass, and found that it was in quasi-steady state (i.e. no identifiable trend) for the last few years of both simulations.

Both models were initialized with identical initial conditions and run for the same number of years. We are conducting a comparison of a snapshot of both of the models at the same point in time (i.e. for the model year 1999, at which point both models have been run out for 7 years from identical initial conditions). We have included all of this information in the revised version of the manuscript (see P4 L24-25; P4 L27-34).

This is an issue even in an idealized case where the goal is not to reproduce observations, but to only compare differences due to model resolution. Overall, I also found myself wondering what the important insights from the study were. Yes, the message is that there are some similarities and differences that could be important, but what does it mean for the marine biogeochemical modelling community? The few concluding statements are not very satisfying.

We have addressed this point above and in our specific response to the same point raised by Reviewer #2.

Specific comments:

As mentioned above, some critical information is missing from the Methods section. Information on how long the model was spun-up for is needed. More information is also needed on the biogeochemical forcing data. What biogeochemical data sets are used to initialize the model? Is this World Ocean Atlas data, etc.?

Thank you for pointing this out, we agree that the methods section as indeed too terse. We have updated the methods section with this additional information. Both of the models were initialized with identical initial conditions, forced with identical PAR fields and aerial iron dust inputs, and run for the period from 1992-1999.

The initial conditions for both model runs were as follows:

- NO_3, PO_4, SiO_2 were taken from the January climatological values given in World Ocean Atlas 2005 (Garcia *et al*., 2006), see P4 L24-25.
- Each phytoplankton and zooplankton phenotype was initialized with an identical low abundance, see P4 L21-24.

An analysis should be conducted to address the issue of model 'drift', i.e., how much drift is occurring and what it might mean for interpreting the results. The resource competition framework that is used to explain some of the differences depends on the system being at steady state to work. If this is not the case as I suspect then it's difficult to see how such a framework can be used to explain the differences. The authors will need to provide more evidence for this to be believable.

As has been stated above, both models were initialized with identical initial conditions and run for the same length of time. As alluded to by the reviewer, it is unfeasible to run a 1/6° resolution global model with ~100 biogeochemical tracers for much longer than this, so this is a useful study for what is currently the state of the art.

We have indeed considered the issue of drift in this and in previous studies, and have found that the phytoplankton community structure is robust after about 3 years' model run time, so a run of 7-8 years is sufficient to produce a repeating seasonal cycle in the modeled phytoplankton community. We also looked at the trend in globally integrated annual average phytoplankton biomass, and found that it was in quasi-steady state (i.e. no identifiable trend) for the last few years of both simulations. The nutrient drifts that are linked to slow changes in the deep nutrient concentrations are small and significantly smaller than the seasonal and interannual variability.

We would also add that the model does not need to be in steady state for the resource competition theory framework to be useful. The model is never in exact steady state (and we would argue that this is the case for all biogeochemical models). In this study we are examining the model results to ascertain whether or not the model solutions are behaving as we would expect them to under resource competition theory. Resource competition theory has previously been applied to a realization of this model (Dutkiewicz et al., 2009), and as in that study we demonstrate that the theory holds in the subtropics, where the most limiting nutrients are drawn down to the same concentration in both simulations, where the same modeled phytoplankton phenotype is also dominant. Dutkiewicz et al (2009) showed results from the 10th year of a (CR) simulation. In the work for that study the results from year 5, 10, 20 and 40 years were considered, and no discernable differences between years were found.

Given our previous studies, the stability of the ecosystem, and the lack of strong drift in nutrients, we do not feel we need further analysis on the issue of drift. However we appreciate the reviewers concern and have added a paragraph to the revised version of the manuscript to address these concerns: a more in depth detail of the model initial conditions (outlined above), a discussion of the stability of the ecosystem and mention of the tiny changes in nutrients due to drift, see P4 L27-34.

Is annual averaging the best way to evaluate the similarities and differences that are seen in Figs. 1-5? As Figure 7 shows there are striking monthly differences at higher latitudes. Perhaps it would be more informative to compare and show the key physical, ecological, biogeochemical properties in seasonal plots (e.g., winter, summer, fall, and spring)? Or maybe carefully selected Hövemoller type plots would be informative?

We do feel that the annual average plots are useful. However, we thank the reviewer for this useful suggestion. We have replaced Figs. 6 and 7 in the revised manuscript with a Hovmoller diagram showing the seasonal evolution of the MLD and biogeochemical properties of the model (Fig. R1, below, now Fig. 6 in the revised manuscript). This clearly shows differences in the seasonality of the two models.

I would be particularly interested in seeing if phytoplankton diversity and differences are more pronounced seasonally or during the progression of the spring bloom in the Atlantic.

This study does not address modeled phytoplankton diversity, so we do not see any need to add plots showing phytoplankton diversity in the annual mean or seasonally. However this would be an interesting topic for a future study.

In Figs. 1 and 2, it would be nice to see the CR results too.

As stated above in our response to Reviewer #2, we feel that adding plots of both sets of model output would add unnecessary extra figures. However, we would be happy to include the CR fields as supplementary material in a revised version of the manuscript.

Fig. 3. I find that this lone figure made it difficult to really see the differences between the model configurations and found that I had to refer to Clayton et al., 2013 to really understand what was going on. This is somewhat frustrating, as some of this information seems to be necessary to understand the study. It would be really nice to have this all in one publication.

Fig. 3 shows the distribution of the dominant phytoplankton functional groups and phenotypes (which are analogous to species), so we are unsure why the reviewer felt the need to refer to the 2013 paper that was only concerned with phytoplankton diversity. The point of this figure is to show how strikingly similar the distributions of the dominant phytoplankton phenotypes and dominant functional groups are between the two models. The differences *should* be hard to see, as the model solutions are not all that different in terms of phytoplankton community structure (which is one of the main points of the paper).

We realize that for people not used to thinking about phytoplankton community ecology, section 3.2, which describes the phytoplankton community structure may be a little terse, so we have expanded it in the revised manuscript (see P5 L25 - P6 L1).

In order to understand the results showing the dominant phytoplankton phenotypes and functional groups, it is not necessary to refer back to Clayton et al (2013). We merely include the short paragraph about the differences in biodiversity between the two models for completeness. The work in this manuscript does not address biodiversity patterns in the models, and it is not necessary to know about the patterns in biodiversity to understand any of the conclusions of this paper.

Fig. 4. What is the actual concentration? Is it realistic? I realize that the purpose of the study is not to figure out which is the ’best’ simulation, but it would still be nice to see the absolute values.

We have included a figure (Fig. R2, below) in our response which shows the annual average surface nitrate and iron fields for the ECCO2 simulation as well as the difference between the two models. The modeled concentrations are realistic. We would be happy to replace Fig. 4 with Fig. R2 in a revised version of the manuscript.

Page 5 line 15 ’tus’ needs to be ’thus’

We have made the correction in the revised manuscript (see P6 L15).

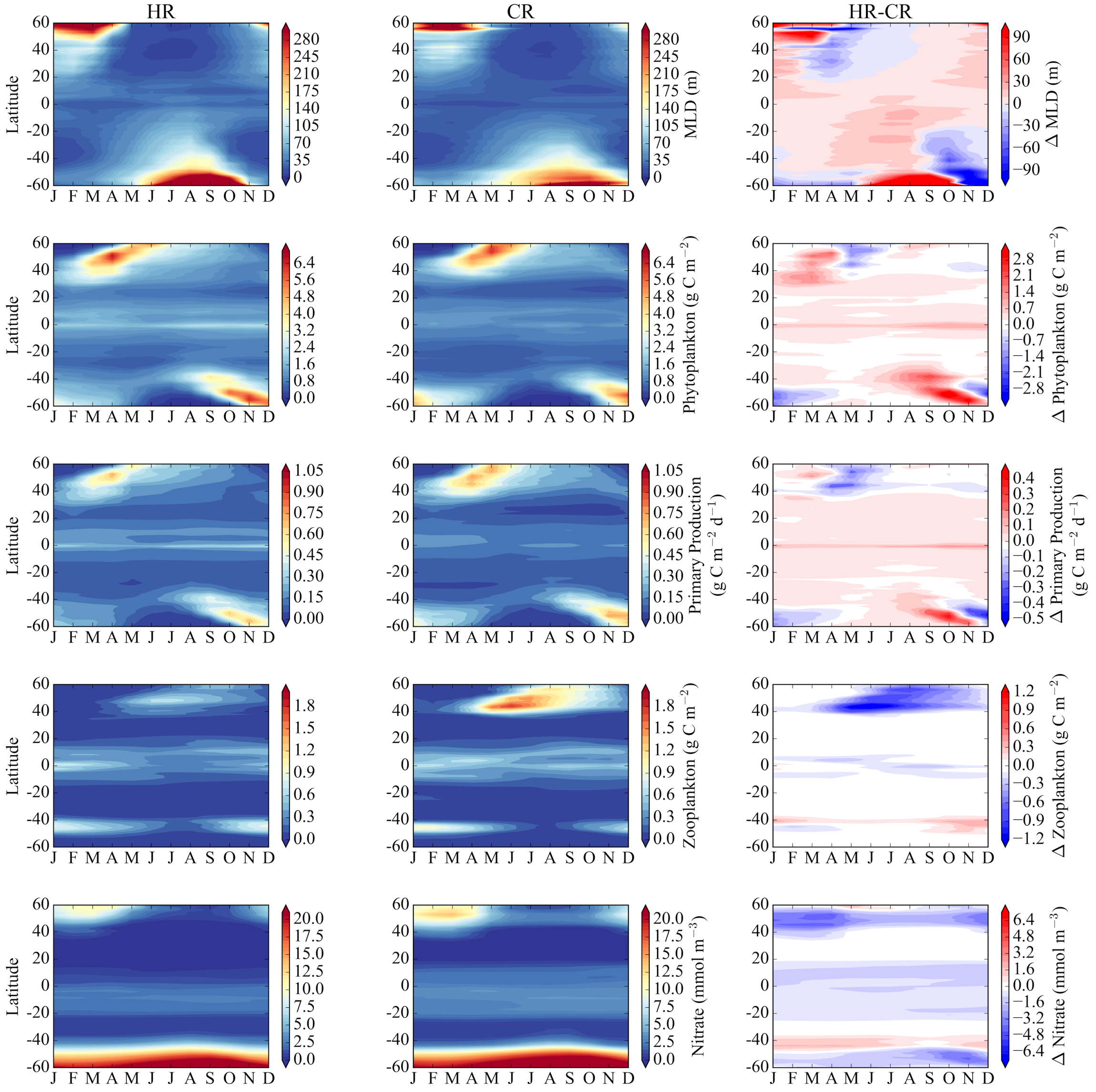

Figure R1. Hovmoller diagram showing the seasonal evolution of zonally averaged model properties for the HR simulation (left column), CR simulation (middle column) and their difference (right column). First row: mixed layer depth; second row: phytoplankton biomass; third row: primary production; fourth row: zooplankton biomass; fifth row: surface nitrate concentration. The difference is calculated as HR-CR, so positive values indicate higher values of that property in the HR simulation.

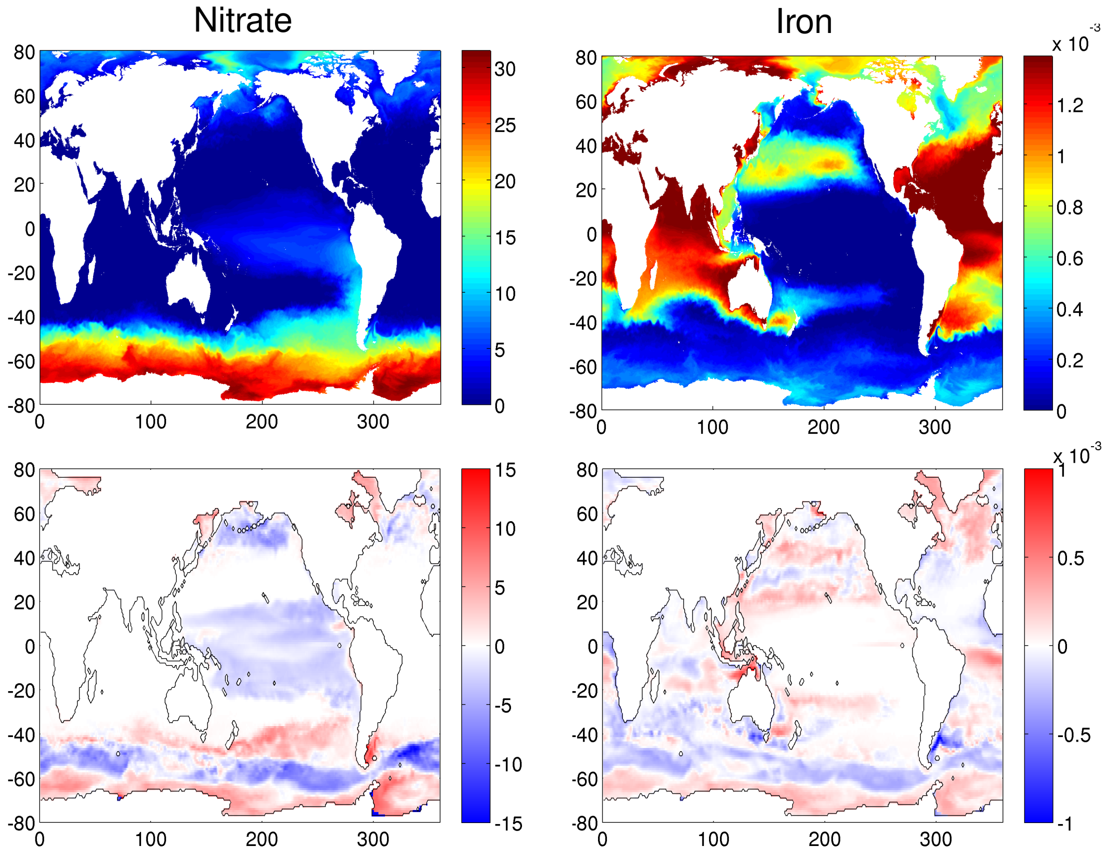

Figure R2. Top panel: Annual average surface concentrations of nitrate in mmol N m^{-3} (left) and dissolved iron in mmol Fe m^{-3} (right) in the HR model solution for model year 1999. Bottom panels: the difference in these properties between both models (HR - CR).

Biogeochemical versus ecological consequences of modeled ocean physics

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Abstract. ~~Regional and idealized modeling studies have shown that increasing the physical resolution of biogeochemical models to include mesoscale and submesoscale dynamics can result in both increases and decreases in phytoplankton biomass and primary production, as well as changes in phytoplankton community structure. Here~~ We present a systematic study of the differences generated by coupling the same ecological-biogeochemical model to a 1^o, coarse-resolution, and 1/6^o, eddy-permitting, global ocean circulation model to: a) biogeochemistry (e.g. primary production), and b) phytoplankton community structure. Surprisingly, we find that the modeled phytoplankton community is largely unchanged, with the same phenotypes dominating in both cases. Conversely, there are large regional and seasonal variations in ~~integrated~~ primary production, phytoplankton and zooplankton biomass. In the subtropics, mixed layer depths are, on average, deeper in the eddy-permitting model, resulting in higher nutrient supply driving increases primary production and phytoplankton biomass. In the higher latitudes, differences in winter mixed layer depths, the timing of the onset of the spring bloom and vertical nutrient supply result in lower primary production in the eddy-permitting model ~~deeper spring mixed layer depths in the eddy-permitting model result in increased light limitation during the spring bloom~~. Counter-intuitively, this does not drive a decrease in phytoplankton biomass, but results in lower ~~is reflected in decreased primary production and~~ zooplankton biomass. We explain these similarities and differences in the model using the framework of resource competition theory, and find that they are the consequence of changes in the regional and seasonal nutrient supply and light environment, mediated by differences in the modeled mixed layer depths. Although previous work has suggested that complex models may respond chaotically and unpredictably to changes in forcing, we find that our model responds in a predictable way to different ocean circulation forcing, despite its complexity. As our model has many similarities to other widely used biogeochemical models which also resolve multiple phytoplankton phenotypes, this study provides important insights into how these models might also behave under different physical conditions.

1 Introduction

Ocean general circulation models have proved an invaluable tool for studying the role of phytoplankton in the global biogeochemical cycles of climatically important elements. Recent advances have resulted in ever higher resolution physical models of the ocean circulation (Menemenlis et al., 2008), and more complex ecological models incorporating larger numbers of phytoplankton functional groups, and even individual phytoplankton phenotypes (Follows and Dutkiewicz, 2011). This trend for increasing resolution and complexity is aimed at creating model systems which incorporate some of the complexity seen in reality, with the hope of better resolving biogeochemical processes. In this study we explore how differences in physical resolution affect, differently, the biogeochemistry and ecosystem of a coupled model.

The physical framework of an ocean model is fundamental to accurately modeling biogeochemical cycles and phytoplankton ecology (Doney, 1999; Anderson, 2005). Observations have shown that phytoplankton biomass and community structure have characteristic temporal and spatial scales corresponding most closely with the oceanic mesoscale and submesoscale (Platt, 1972; Strass, 1992; Abbott and Letelier, 1998; Doney et al., 2003; Cotti-Rausch et al., 2016). However, most global ocean models incorporating biogeochemical and ecological processes (especially those coupled in climate studies) do not resolve scales less than ~1^o. In the ocean, the characteristic temporal and spatial scales of biology coincide with those of mesoscale and submesoscale physical dynamics. Spall and Richards (2000) showed in a high resolution model of an unstable frontal jet that spatial heterogeneity in primary production occured on scales of a few to 10s of kms, and that primary production could increase locally by up to 100%. Coarse resolution global biogeochemical models do not resolve these dynamics. Lévy (2008) and Mahadevan (2016) review the consequences of this for biogeochemical models. Previous studies, have found that neglecting to resolve the mesoscale could result in errors of up to 30% in the estimates of primary production (Lévy et al., 1998; Oschlies and Garçon, 1998; Mahadevan and Archer, 2000; McGillicuddy et al., 2003). Furthermore, Lévy et al. (2001) found discrepencies of up to 50% in integrated primary production comparing a coarse resolution model with one that resolved submesoscale dynamics. These studies found that, in the oligotrophic subtropical gyres, mesoscale (and submesoscale) dynamics drove an increased nutrient supply to the surface mixed layer, which enhanced rates of primary production. In the subpolar gyres, eddies appear to have a different effect on ocean biology, McGillicuddy et al. (2003) found in a 0.1^o resolution model of the North Atlantic that mesoscale processes drove a geostrophic adjustment to deep winter convection, which reduced nutrient supply. However, nutrients are less likely to be limiting than light in the subpolar gyres, so this may also have a positive effect on rates of primary production. Although these previous studies predict the role of the mesoscale in modulating biological and biogeochemical responses in different regional settings, it is unclear what the integrated effect will be globally, and what downstream effects might result.

The above studies, although they resolved higher resolution physics, typically employed rather simple biogeochemical models incorporating only one or two phytoplankton functional types. However, marine microbial communities are known to be incredibly diverse, and this diversity plays an important role in mediating global biogeochemical cycles. Thanks to the continuing expansion of computing resources, diversity has been included in global biogeochemical models which resolve several phytoplankton functional groups (Chai et al., 2002; Gregg et al., 2003; Quéré et al., 2005), and even several tens of phytoplankton phenotypes within mutiple functional groups have been developed (Follows et al., 2007; Ward et al., 2012). It is unknown whether a change in physical resolution will result in any changes in the emergent community structure of one of these diverse models. Sinha et al. (2010) found that an intermediate-complexity ecosystem model which resolved 5 phytoplankton functional types, run with two different physical models at similar (coarse) resolution, could result in regional changes in the modeled phytoplankton communities. However, it is unclear whether the emergent community resulting from a more complex ecosystem model will be more or less robust to changes in the physical forcing.

Here we present a process study that explores the effect of refining the physical resolution on a global, diverse ecosystem model which incorporates 78 distinct phytoplankton phenotypes. We explore both the effect on the bulk biogeochemical properties and the community structure of the model solutions. The objective of this study is not to assess which model performs best with respect to reality. Rather, we aim to examine how changes in the resolution and parameterization of subgridscale processes of the model domain alter the emergent biogeochemical and ecological properties of this diverse ecosystem model.

2 Method

This study is based upon numerical simulations of global ocean circulation, biogeochemical cycles, and diverse phytoplankton populations. We have employed the Massachusetts Institute of Technology General Circulation Model (MITgcm; Marshall et al., 1997) and biogeochemical and ecological model components as detailed in Dutkiewicz et al. (2009). Below, we describe these physical circulation and biogeochemical-ecological models in more detail.

2.1 Physical Model Configurations

We used two physical model configurations developed by the Estimating the Circulation and Climate of the Oceans (ECCO) project (Wunsch et al., 2009). Both span the period 1992 - 1999, and were constrained to be consistent with observed altimetry and hydrography. The high resolution ECCO2 configuration, with an effective resolution of 1/6^o, and horizontal grid dimensions of ~18 km (ECCO2; Menemenlis et al., 2008), is referred to as eddy-permitting, as it resolves large eddies at low latitudes, but remains below the first baroclinic Rossby radius at high latitudes (Chelton et al., 1998). We compare this high resolution configuration with the ECCO-Global Ocean Data Assimilation Experiment state estimate (ECCO-GODAE, also referred to as ECCO version 3 in the lineage of ECCO production solutions; Wunsch and Heimbach, 2007, 2013), which has a coarser grid resolution of 1^o. Both physical models are data assimilation products. The ECCO-GODAE product is based on the Lagrange Multiplier method and the ECCO2 product employs a simplified Green's function method. It should be noted that unlike most so-called ocean "reanalysis" products, both of the ECCO products are obtained using “smoother” methods, which avoid the artificial adjustment motions that can be triggered during what is called "analysis increments" in data assimilative models which use “filtering” methods (Wunsch and Heimbach, 2013; Stammer et al., 2016). Because the ECCO products are free of such artificial adjustments (expressed in particular in strong vertical adjustment motions that may confound vertical transport of biogeochemical tracers), they also conserve tracer and momentum budgets exactly.

A core focus of this study is comparing and contrasting the modeled ecological and biogeochemical behavior in a mesoscale eddy-permitting model (ECCO2) with a non-eddying model (ECCO-GODAE). Accordingly we limit our analysis latitudinally to the region between 60^{o}S and 60^{o}N. Within this latitudinal band, the first baroclinic radius of deformation (Chelton et al., 1998) is larger than the ECCO2 model horizontal resolution, and so the ECCO2 model admits corresponding mesoscale eddy dynamics. North and south of this latitude line, mesoscale eddies are not well resolved in either model, and so neither model is in a so-called large-eddy regime (Smagorinsky, 1963). In the excluded high latitude regions the two physical model mixed layers differ systematically. These differences result from the absence of parameterized mesoscale eddy dynamics in the ECCO2 model (Danabasoglu et al., 1994). This contrast in mixed layer depth, rather than behaviours due to mesoscale eddies, sets the differences in biogeochemical response seen in ice-free high latitudes. For simplicity, we will refer to the ECCO-GODAE simulation as CR, and the ECCO2 simulation as HR.

2.2 Ecological and Biogeochemical Model

The ecological model used in this study has previously been discussed in Follows et al. (2007) and Dutkiewicz et al. (2009). Briefly, we transport inorganic and organic forms of nitrogen, phosphorous, iron and silica, and resolve 78 phytoplankton phenotypes and two simple grazers. The biogeochemical and biological tracers interact through the formation, transformation and remineralization of organic matter. Excretion and mortality transfer living organic material into sinking particulate and dissolved organic detritus which are transpired back to inorganic form. The time rate of change in the biomass of each of the modeled phytoplankton types, P_j, is described in terms of a light, temperature and nutrient dependent growth, sinking, grazing, mortality and transport by the fluid flow. Many realizations of this ecological model, coupled to the ECCO-GODAE physical circulation, have been used to study a range of ecological questions, e.g. the role of top-down controls in setting patterns of phytoplankton diversity (Prowe et al., 2012; Vallina et al., 2014), the biogeography of nitrogen-fixing phytoplankton (Monteiro et al., 2011), and role of transport in setting patterns in phytoplankton diversity (Clayton et al., 2013).

In this study, the ecological model was initialized with seventy-eight phytoplankton phenotypes with a broad range of physiological attributes. Phytoplankton were assigned to one of two broad size classes by random draw at the initialization of the model, and a set of physiological trade-offs that reflect empirical observations were imposed accordingly. We stochastically assigned plausible values for the nutrient half-saturation constants (κ_N), light and temperature sensitivities within each phytoplankton functional group (*Prochlorococcus*-like, picophytoplankton, diatoms and large phytoplankton). Both the HR and CR simulations were initialized with an identical set of phytoplankton phenotypes, and initial conditions for all phytoplankton phenotypes, and in both cases the ecosystem model was forced with identical initial conditions for all variables, light forcing and dust inputs. Initial conditions for nutrients were taken from the January climatological values given in the World Ocean Atlas 2005 (Garcia et al., 2006). Interactions with the environment, competition with other phytoplankton, and grazing determine the composition of the phytoplankton communities that persist in the model solutions.

We run both models for a total of 8 years, for the period from 1992 to 1999 from the same initial conditions. Although this is a relatively short run for a biogeochemical model, it currently would not be feasible to spin up the HR simulation for much longer. In several previous studies using the CR model (Dutkiewicz et al., 2009, 2012) and in this study for both CR and HR we find that it takes only 3 years for the ecosystem to reach a stable annual cycle, so a run of 7-8 years is sufficient to produce a repeating seasonal cycle in the modeled phytoplankton community. There was no discernible trend in the globally integrated annual average phytoplankton biomass in the last few years of either of the simulations. The regional nutrient drifts that are linked to slow changes in the deep nutrient concentrations are small and significantly less than the seasonal and interannual variability.

We compare the model results for the last year (1999) from both model configurations to test the sensitivity of the ecosystem to the modeled ocean physics. The results of that comparison are described in the following section.

3 Results

~~Differences in the physical circulation estimates of these two configurations have previously been discussed in Clayton et al. (2013).~~ We describe differences in some of the physical properties most directly relevant to biogeochemical processes: sea surface temperature (SST) and mixed layer depth (MLD). Differences in other physical fields between the two model configurations have previously been discussed in Clayton et al. (2013), here we examine only those physical processes most directly relevant to biogeochemical processes not considered in that previous work. The SST patterns in both models are broadly similar, but we did find local differences in SST of up to 3^oC in some regions (Fig. 1). The HR simulation appeared to have a slight cool bias relative to the CR simulation, which is an indicator of enhanced upwelling and/or vertical mixing in the higher resolution configuration. There were marked regional patterns in the MLD differences between model configurations. Annual average MLDs were consistently deeper in the low latitudes in the HR simulation, whereas they tended to be slightly shallower in the mid-latitudes. As mentioned above, we exclude the high latitudes ($> 60^o$) from our analysis.

3.1 Primary Production and Biomass

Both model configurations result in largely similar patterns in phytoplankton biomass and primary production, with low biomass and productivity associated with the subtropical gyres, and higher biomass and productivity found in the mid-latitudes and upwelling zones. Although globally integrated primary production is very similar between both models, there are clear regional differences (Fig. 2), with higher rates of production in the low latitudes and lower rates of production in the mid latitudes, in the HR simulation. We find a ~20% global increase in the standing stock of phytoplankton biomass in the HR simulation, mostly accounted for by higher phytoplankton biomass between 40^oS and 40^oN.The largest differences in both phytoplankton biomass and primary production are associated with the western boundary currents and the equatorial upwelling zone, with higher values in the HR simulation. We also see decreases in phytoplankton biomass and productivity in the HR simulation associated with the boundaries between different biogeographical provinces.

3.2 Phytoplankton Community Structure

The ecological model represents a diverse community of phytoplankton, made up of individual phenotypes (analogous to species or ecotypes) which are defined by their nominal size, their nutrient requirements, their optimal light and temperature ranges, and their palatability to grazers. ~~subdivided into different sizes and functional groups, with different temperature, light and nutrient requirements.~~ Each phytoplankton phenotype belongs to one of four possible modeled phytoplankton functional groups. Phenotypes within each functional group have similar cell sizes and nutrient requirements, but differ in their optimal light and temperature ranges. To understand the impact of model resolution on the modeled phytoplankton community structure, we examine the regional patterns in the dominant modeled phytoplankton functional groups (Fig.3 a and b), and dominant modeled phytoplankton phenotypes (Fig.3 c and d). We find that the emergent phytoplankton community structure is remarkably similar between the two simulations. The low latitudes are dominated by *Prochlorococcus* analogues, whereas the mid-latitudes are dominated by diatoms and large phytoplankton (Fig. 3a and b), with very little difference between models. What is even more striking, is that ~~Similarly,~~ the regional patterns in the dominant phytoplankton phenotypes are largely unchanged between simulations. The only region that shows a shift in the dominant functional group and phenotype between model simulations, is the Indian Ocean, which shifts from picophytoplankton dominated in the CR simulation, to *Prochlorococcus* analogue dominated in the HR simulation, with a corresponding shift in the dominant phenotype. Other regions where the models do not agree occur mainly at the borders between different biogeochemical provinces. This suggests that changes in model resolution do not drive changes in the geographical range of dominant phenotypes, but also that they don't result in ecological shifts where different modeled phenotypes might become dominant. Given the big differences in modeled primary production and biomass described above, this is an unexpected result.

Differences in the patterns of phytoplankton biodiversity between the model simulations have previously been described in Clayton et al. (2013). Although we find an overall increase in phytoplankton biodiversity in the HR simulation (not shown here), those differences are mainly driven by the persistence of more rare species in the HR simulation with respect to CR, and are thus ~~tus~~ unlikely to have a significant effect on integrated bulk biogeochemical processes.

3.3 Nutrients and Nutrient-Limitation

Differences in model resolution are expected to drive changes in the supply of nutrients to the surface photic zone. We do find differences in the concentration of surface macro- and micro-nutrients (Fig. 4). Nitrate and dissolved iron both show marked patterns in the difference of their surface distributions between simulations. The concentration of nitrate remains unchanged in the Atlantic, the Indian Ocean, and in some parts of the North and South Pacific (Fig. 4a). However, there is a decrease in surface nitrate concentrations in the HR simulation in the mid-latitudes of the North Pacific and the Southern Ocean, and in the subtropical and equatorial Pacific. Conversely, we see an increase in surface nitrate in the HR simulation in the Brazil-Malvinas Confluence Zone, and the region of the Subantarctic Front in the Southern Ocean. Differences in surface dissolved iron concentrations exhibit markedly different patterns (Fig. 4b). The surface concentration of dissolved iron remains unchanged between model simulations in the the subtropical and equatorial Pacific, and parts of the subtropical North Atlantic. We see a general decrease in surface iron in the HR simulation in the Subantarctic Front in the Southern Ocean and the southern part of the Indian Ocean, and an increase in dissolved iron in the mid-latitudes of the North Pacific, the equatorial Atlantic, and the subpolar North Atlantic.

In addition to assessing the differences in surface nutrient concentrations, we determined the locally limiting nutrient for both models (Fig. 5). Nitrate and dissolved iron are the spatially dominant limiting nutrients in both model simulations, with almost identical regional patterns of limitation. However, we do find small but significant regions where the dominant limiting nutrients in both simulations do not correspond (Fig. 5b), primarily located at the boundaries between biogeographical provinces.

4 Discussion

In this study, we have assessed the effect of explicitly representing mesoscale dynamics in a global ocean ecological-biogeochemical model. Strikingly, we find that the realized phytoplankton communities in both simulations are remarkably similar, but that there are marked regional variations in bulk ecosystem properties such as primary production and phytoplankton biomass. We also find that although the general regional patterns of nutrient limitation remain unchanged, surface concentrations of nitrate and dissolved iron can vary markedly between simulations in some regions, but are almost completely unchanged in others. Why do we see such marked changes in the distribution of biogeochemical properties of the models, but not in the modeled phytoplankton community?

Ultimately, any differences in the biogeochemical and ecological properties between the two model solutions occur either because there are differences in the local physical fields (e.g. MLDs and transport), or because physical features of the ocean circulation such as the western boundary currents and gyre boundaries are realized in different locations. We identify three main regions that are affected in different ways by the addition of mesoscale dynamics: the tropical and subtropical regions, the subpolar gyres, and the boundaries between biogeographical provinces. We explore the linkages between the physical and biological components of the system to put these differences into context.

4.1 Tropical and subtropical regions

In the low latitudes, we found that the addition of mesoscale dynamics resulted in an overall deepening of the annual mean mixed layer depth (Fig. 1). We found an increase in phytoplankton biomass and primary production, but the dominant phytoplankton functional group and phenotypes remained unchanged. The increase in primary production and phytoplankton biomass in the HR simulation was not entirely surprising, as it has been predicted by previous regional and idealized studies on the effect of increasing model resolution on primary production (Lévy et al., 2001; Oschlies and Garçon, 1998; Mahadevan and Archer, 2000; Spall and Richards, 2000; McGillicuddy et al., 2003). However, we may have expected a large increase in the biomass of large phytoplankton thanks to more episodic eddy-driven nutrient injections to the surface mixed layer, as observed by Benitez-Nelson et al. (2007); Brown et al. (2008). In fact, the increase in phytoplankton biomass was driven by an increase in the abundance of the dominant phytoplankton functional groups, *Prochlorococcus* analogues and picophytoplankton, which are both small, gleaner types. We also found that where a particular nutrient was limiting in both model simulations, its surface concentration remained unchanged.

The subtropical gyres are steady, stable regions where seasonality is low, and phytoplankton growth is nutrient-limited. In this context, we can apply the simple resource competition framework introduced by (Tilman et al., 1982) and applied to this system by (Dutkiewicz et al., 2009) to understand the simultaneous differences and similarities in the model results. We set up a simple model system, where phytoplankton growth is nutrient-limited, and balanced by a simple linear mortality term:

$$\frac{dR}{dt} = -\frac{\mu_{MAX} RP}{R+k} + S_R \tag{1}$$

$$\frac{dP}{dt} = \frac{\mu_{MAX} RP}{R+k} - mP \tag{2}$$

where R is the limiting resource, P is the phytoplankton biomass, μ is the maximum phytoplankton growth rate, k is the resource half saturation constant, m is the phytoplankton mortality rate, and S_R~~S_N~~ is the rate of resource supply into the system. The steady state solution for this system is:

$$P^* = \frac{S_R}{m} \tag{3}$$

$$R^* = \frac{mk}{\mu - m} \tag{4}$$

In this framework, the steady state concentration of the limiting resource, R^*, is controlled not by the magnitude of the nutrient supply, but by the physiological attributes of the dominant phytoplankton phenotype. In this type of stable system, the emergent dominant phytoplankton phenotype will be the one that can draw the resource down to the lowest R^* value. As we have set the phytoplankton communities to be composed of the same phenotypes in both simulations, and R^* is set by the physiological traits of the phytoplankton (Dutkiewicz et al., 2009), we select for the same dominant phenotype in both simulations. Conversely, the steady state concentration of the phytoplankton, P^*, is a function of the resource supply, S_R~~S_N~~, as well as the mortality rate. Thus, an increase in S_R~~S_N~~ results in increased phytoplankton biomass, but not in a shift in the dominant phytoplankton type, as R^* is only a function of the physiology of the fittest phytoplankton type. Enhanced mixing in the HR simulation drives an increase in S_R~~S_N~~, but does not change the dominant phytoplankton phenotype. Rather, it results in an increase in the biomass of the dominant type, and an increase in productivity (μP^*). At the same time, the concentration of the limiting nutrient, R^*, remains unchanged (as seen in nitrate and dissolved iron, figure 4), but the non-limiting nutrients decrease due to increased removal by the increased productivity (Fig. 4). This may also result in a decrease in the supply of resources downstream from the subtropical gyres.

For instance, we see a dramatic increase in phytoplankton biomass and primary production in the Equatorial region of the HR model simulation. We evaluated the annual average vertical advective flux of nitrate (wNO_3) at 100m between 5°N and 5°S for both models. The regionally integrated mean annual vertical nitrate fluxes evaluated at 100m for model year 1999 were 453.1 mmol NO_3 m^{-2} $year^{-1}$ and 383.7 mmol NO_3 m^{-2} $year^{-1}$, for the HR and CR simulations, respectively. There is a clear increase in vertical nutrient supply in the equatorial upwelling zone in HR that can account for the dramatic increase in phytoplankton stock and primary productivity in the Equatorial Pacific.

4.2 Subpolar regions

We see a somewhat different picture in the mid to high latitudes, where there is an overall decrease in annual mean primary production, and to a lesser degree in phytoplankton biomass, in HR compared to CR (Fig. 2). Again, the dominant phytoplankton functional groups and phenotypes remain largely unchanged between models in these regions (Fig. 3). What is most striking, is the much higher abundance of zooplankton found in the Northern subpolar gyres of the CR model solution (Fig. 6). In order to explain these differences, we must look more closely at the evolution of the seasonal cycle in both models (Fig. 6).

First we consider the different behaviours of the models during the winter months. HR has deeper mixed layer depths from November through to March or April, depending on latitude. During this period, higher light limitation explains the lower primary production levels. In the context of this model, the limiting factors on the phytoplankton growth rate are multiplicative, e.g. for each modeled phytoplankton phenotype j, the growth term is given by:

$$\mu_j = \mu_{MAXj}\gamma_j^T\gamma_j^I\frac{R}{R+k_{Rj}} \tag{5}$$

where γ^T and γ^I are the temperature and light limitation terms, respectively. During the winter, when nutrients are replete (and the nutrient limiatation term approaches 1), if either the light or temperature fields experienced by the modeled phytoplankton are consistently less favourable, then μ will be decreased. Consistently deeper winter MLDs in the HR simulation during the winter months, result in lower winter primary production in HR than CR.

The onset of the spring bloom occurs roughly one month earlier (March-April) in the HR simulation than the CR simulation (April-May). This is reflected in the higher PP in the HR simulation in March and April, followed by a reversal with higher PP in the CR simulation in May. This is driven by differences in the timing of the shoaling of the MLDs, which occurs earlier in the HR model due to the action of mesoscale eddies.

During the summer and into the early autumn, the shallower mixed layer depths restrict nutrient re-supply, and nutrients become limiting. As the physical and biogeochemical properties of both models are relatively stable over several months during the summer, period, we represent them as an idealized steady-state system (see e.g. Dutkiewicz et al. (2009), Fig. 4) to better understand the processes driving the differences between the two models. In these higher latitudes, grazer dynamics become uncoupled from their prey. Thus we construct an idealized model system similar to Eq 1 and 2, but that now includes explicit grazing by zooplankton.

$$\frac{dR}{dt} = -\mu_{MAX}\frac{RP}{R+k} + S_R \tag{6}$$

$$\frac{dP}{dt} = \mu_{MAX}\frac{RP}{R+k} - gZP \tag{7}$$

$$\frac{dZ}{dt} = gZP - m_z Z \tag{8}$$

where R is the resource, P is the phytoplankton biomass, μ_{MAX} is the maximum phytoplankton growth rate, k is the nutrient half-saturation constant, g is the grazing rate of phytoplankton by zooplankton, m_z is the zooplankton mortality rate, and S_R is the rate of resource supply into the system. The steady state solution for this system is:

$$R^* = \frac{kS_Rg}{-gS_R + \mu_{MAX}m_Z} \tag{9}$$

$$P^* = \frac{m_z}{g} \tag{10}$$

$$Z^* = k(\frac{S_Rg}{\mu_{MAX}m_z} - 1) \tag{11}$$

For this system, P^*, the phytoplankton standing stock is controlled by the physiological traits of the zooplankton which are constant, so regardless of changes in S_R, phytoplankton biomass will remain the same. However, Z^*, the zooplankton standing stock is directly proportional to S_R, so increased nutrient supply results in higher zooplankton abundance. Applying this framework to our model results, we are able to explain the increase in zooplankton biomass, the roughly unchanged phytoplankton biomass and the increased primary production in the CR compared to HR. In contrast to the situation during the winter, in this case it is driven primarily by differences in nutrient supply. We evaluated the annual mean vertical nitrate supply by advection, which was 142.1 and 108.1 mmol NO_3 m^{-2} $year^{-1}$ in CR and HR, respectively. That, coupled with the deeper summer MLDs in CR result in an increased nutrient supply compared to HR. Zhang et al. (2013) find a similar response to nutrient injections at a shelfbreak front, where increases in primary production are funneled up the trophic levels and result in increased zooplankton biomass, but are not reflected in increased phytoplankton biomass. On a larger scale, Ward et al. (2012) found in a global, size-structured ecosystem model, that in regions of higher nutrient supply, top-down control drives in an increase in the biomass of larger plankton size classes relative to oligotrophic regions, rather than an unchecked increase in smaller size classes. Similar patterns can be seen in the Southern Hemisphere, where the MLD shoals earlier in the spring in the HR simulation, and PP and P biomass are both lower in the HR simulation during the summer.

~~We see a somewhat different picture in the mid latitudes, where primary production is decreased by the addition of mesoscale dynamics, but still phytoplankton biomass remains very similar in both simulations. In contrast to the subtropical gyres, these are nutrient replete regions where patterns in phytoplankton productivity and biomass are seasonally controlled, and primarily limited by light. In order to explain the differences in the annual mean distributions of phytoplankton productivity and biomass, we must examine the seasonal evolution of the system. In Fig. **??**, we show the total monthly integrated primary production, phytoplankton and zooplankton biomass for the northern hemisphere mid-latitudes for both simulations. Although in both simulations the timing and magnitude in the phytoplankton biomass at the height of the spring bloom is almost the same, we see marked differences in the magnitude of primary production, and in the seasonal abundance of zooplankton. Primary production from March to August, and zooplankton abundance over most of the year are both much lower in the HR simulation. Deeper spring MLDs in the HR simulation (Fig. **??**) result in increased light limitation during the onset of the spring bloom, reducing primary production in the HR simulation (Sverdrup, 1953). But then why do we not see a corresponding decrease in phytoplankton biomass in the HR simulation, and why is zooplankton biomass so much higher in the CR simulation? We hypothesize that this is, at least in part, a consequence of the "Dilution-Recoupling Hypothesis" (Behrenfeld, 2010), where top-down control of phytoplankton biomass by grazers resumes in spring with the shallowing of MLDs. We can explain this in the context of an idealized model system, where phytoplankton growth is a function of light, and the phytoplankton are grazed on by zooplankton:~~

~~where R is the resource, P is the phytoplankton biomass, $\mu(I)$ is the phytoplankton growth rate which is controlled by light, g is the grazing rate of phytoplankton by zooplankton, m_z is the zooplankton mortality rate, γ is a remineralization coefficient, and S_N is the rate of resource supply into the system. The steady state solution for this system is:~~

~~For this system, P^*, the phytoplankton standing stock is controlled by the physiological traits of the zooplankton which are constant, so regardless of changes in $\mu(I)$ or S_N, phytoplankton biomass will remain the same. However, Z^*, the zooplankton standing stock is directly proportional to S_N, so increased nutrient supply will translate to higher Z^*. Applying this framework to our model results explains why the higher primary production in the CR simulation results in higher zooplankton biomass,~~

~~but unchanged phytoplankton biomass. Zhang et al. (2013) find a similar response to nutrient injections at a shelfbreak front, where increases in primary production are funneled up the trophic levels and are seen in increased zooplankton biomass, but are not reflected in increased phytoplankton biomass. On a larger scale, Ward et al. (2012) found in a global, size-structured ecosystem model, that in regions of higher nutrient supply, top-down control drives in an increase in the biomass of larger plankton size classes relative to oligotrophic regions, rather than an unchecked increase in smaller size classes.~~

~~Although we can explain the decrease in primary production as a consequence of light limitation caused by deeper spring MLDs in the HR simulation, and the unchanged phytoplankton biomass as a result of top-down control, this does not account for the lower surface nutrient concentrations seen over large regions in the HR simulation (Fig. 4). We hypothesize that this could be due to the lower zooplankton biomass resulting in decreased nutrient remineralization in the surface mixed layer, but can not show this conclusively in this study. It is also possible that despite the deeper average MLDs, eddies are episodically acting to remove inorganic nutrient from the surface, as seen in McGillicuddy et al. (2003) 0.1~~ ~~^{o}~~ ~~model of the North Atlantic. They found that eddies constituted a net sink of nutrients from the surface in the subpolar gyre, counteracting the wind-driven upwelling of nutrients. Conversely, Mahadevan et al. (2012) show that eddies can help to initiate the spring bloom in the North Atlantic by stratifying the water column, and thus reducing light limitation of the phytoplankton. Neither of these mechanisms square entirely with our results, showing an increased MLD and decreased primary production in the eddy-permitting HR simulation. It is possible that at 1/6~~~~^{o}~~ ~~resolution, we still do not resolve mesoscale eddies well enough to represent either of these competing processes.~~

4.3 Boundaries between biogeographical provinces

We found marked differences in biological fields which appear to be due to differences in the geographical extent of biogeographical provinces between simulations. Differences in modeled phytoplankton biomass and primary production in the North and South Pacific subtropical gyres coincide exactly with geographical differences in regions defined by different limiting nutrients in the simulations (Fig. 2). We attribute this decrease in production and biomass to a decrease in the lateral supply of nutrients from the equatorial upwelling region. This decreased lateral supply out of the equatorial region in the HR simulation is due to more local primary production in the equatorial region (Fig. 2). Although dissolved iron is drawn down to the same concentration in both simulations, primary production and phytoplankton biomass are higher, and nitrate is much lower in the HR simulation. As discussed above, resource competition theory predicts that the concentration of the limiting nutrient, R* (in this case dissolved iron; Fig. 5) is unchanged when the phytoplankton community remains unchanged. Increased dissolved iron supply, associated with deeper MLDs would drive the increase in primary production and phytoplankton biomass observed in the in the HR simulation. However, this increase in local primary production, consuming higher levels of non-limiting macronutrients locally, reduces the Ekman transfer of non-limiting nutrients to the neighboring subtropical gyres (Dutkiewicz et al., 2005). A similar shift in biological transition zones, associated with model resolution, was found in a regional study of the California Current System. Fiechter et al. (2014) found that increasing the resolution of their model from 1/3^{o} to 1/30^{o} resulted in a marked shift in the location of the transition between near-shore outgassing and offshore absorption of CO_2. These differences in gas fluxes were driven, in their study, by different patterns in nutrient upwelling and transport offshore.

4.4 Stability of the phytoplankton community structure

As we have discussed in the previous sections, one of the most striking results of our model comparison is that despite the difference in the modeled physics, the emergent phytoplankton communities in both simulations are almost identical. We only know of one comparable study where the response of a complex ecosystem model to different model physics has been evaluated (Sinha et al., 2010). In that study, although there was a difference in resolution between the two physical models used to force the ecosystem model (1^o vs 2^o), unlike our study, both of these physical models were too coarse to resolve eddies. Although the physical models in the (Sinha et al., 2010) study were initialized and forced in essentially the same way, they were run out without being constrained to observations. This resulted in large differences in their model solutions for physical fields (e.g. seasonal SST, see their Fig. 3), which were used to force the ecosystem model. One very key difference in our study with respect to Sinha et al. (2010)'s earlier work, is that both of the physical models used to force our ecosystem model, ECCO-GODAE and ECCO2, were state estimates constrained to converge as closely as possible to observational data. Although the state estimates were constrained in different ways, and differences between them remain, compared to free-running models without any assimilation these differences are comparatively small. In the end, the differences in the ECCO state estimates used in this study are largely a consequence of whether or not they represent mesoscale dynamics.

5 Conclusions

In this study we have compared and contrasted the behavior of a complex ecological-biogeochemical model when coupled to either a mesoscale eddy-permitting high resolution physical model (HR, ECCO2), or a non-eddying coarse resolution physical model (CR, ECCO-GODAE). We found that increasing the model resolution to include mesoscale dynamics does not greatly affect the structure of our modeled phytoplankton ecosystem. However it does have a significant effect on the regional distribution of the bulk properties of the ecosystem: primary production, and phytoplankton and zooplankton biomass.

One of the most striking results of this study is the robustness of the emergent modeled phytoplankton community. We found that the dominant phytoplankton functional groups and phenotypes remained unchanged between simulations, despite differences in SST and MLDs. In contrast, we found marked regional differences in phytoplankton and zooplankton biomass, and primary production. By applying concepts from resource competition theory (Tilman et al., 1982; Dutkiewicz et al., 2009), we can explain why in the subtropical gyres, despite increased primary production, the dominant phytoplankton phenotype and the surface concentration of the limiting nutrient remain the same in both simulations. The combination of low seasonality and low grazing pressure means that despite an increased nutrient supply, phytoplankton with the lowest R^* will always be selected for in this region.

We have shown that the bulk biogeochemical properties of this ecological model are more sensitive to differences in modeled ocean physics than the structure of the ecosystem itself. Given that this model has many similarities to other widely used biogeochemical models, which also resolve multiple phytoplankton PFTs, this study provides important insights into how these models might behave under different physical conditions.

Given the complexity of our ecosystem model, which incorporates 78 individual phytoplankton types, it may seem surprising that our modeled phytoplankton community structure is so similar in both cases. This presents interesting implications for marine biogeochemical and ecological modeling. It is clear that accuracy in the representation of the physical dynamics of the environment is necessary for effectively modeling ocean biogeochemistry. The higher taxonomic resolution of our ecological model may in fact allow for subtler gradations of change in the phytoplankton community when the environment is changed, whereas in coarser ecological models, regime shifts could easily result due to larger differences between modeled phenotypes. We do not advocate simply tuning parameters to get the "right" result, but rather increasing the physiological parameter space constrained by laboratory and observational work in order to create a more robust and representative model of the phytoplankton community.

Author contributions. S. Clayton, S. Dutkiewicz and M. J. Follows designed the study. S. Dutkiewicz, O. Jahn, P. Heimbach and C. Hill implemented and ran the model simulations. S. Clayton analyzed the model outputs. S. Clayton prepared the manuscript with contributions from all co-authors. The authors declare that they have no conflict of interest.

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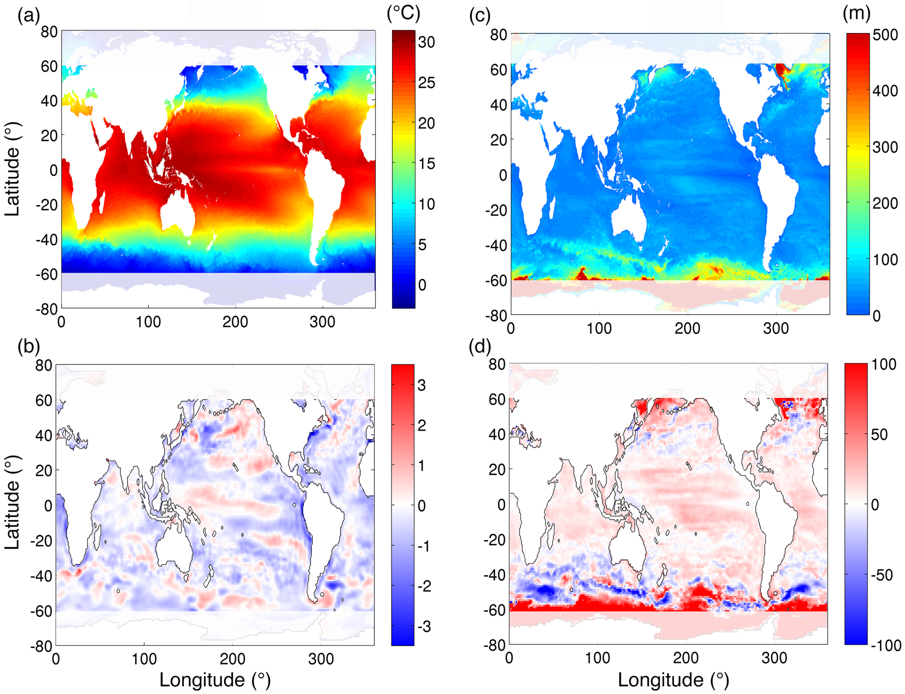

Figure 1. (a) Annual average sea surface temperature (SST), and (c) annual average mixed layer depths (MLD) in the HR simulation for the 1999 model year; (b) the difference in SST, and (d) in MLD between the two simulations. Positive values indicate deeper MLD in the HR simulation, and negative values indicate deeper MLD in the CR simulation.

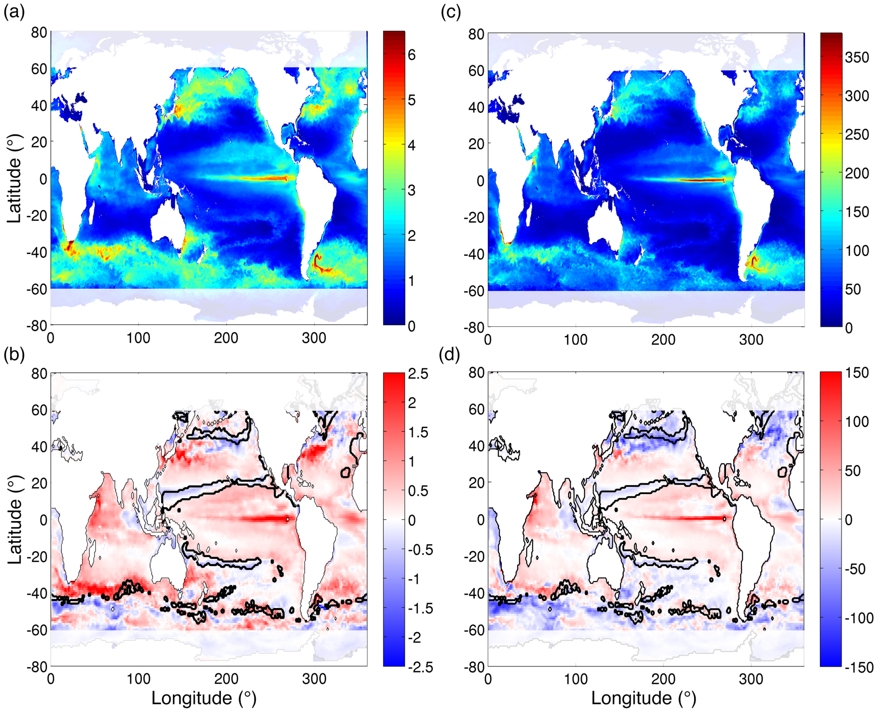

Figure 2. (a) Annual average total phytoplankton biomass in g C m^{-2}, and (c) annual primary production in g C m^{-2} y^{-1} in the HR model solution for 1999. (b) the difference in phytoplankton biomass, and (d) the difference in annual primary production. Positive values indicate higher values in the HR simulation and negative values indicate higher values in the CR simulation. The solid black contour lines in (b) and (d) indicate the region where the limiting nutrient differs between the two model simulations

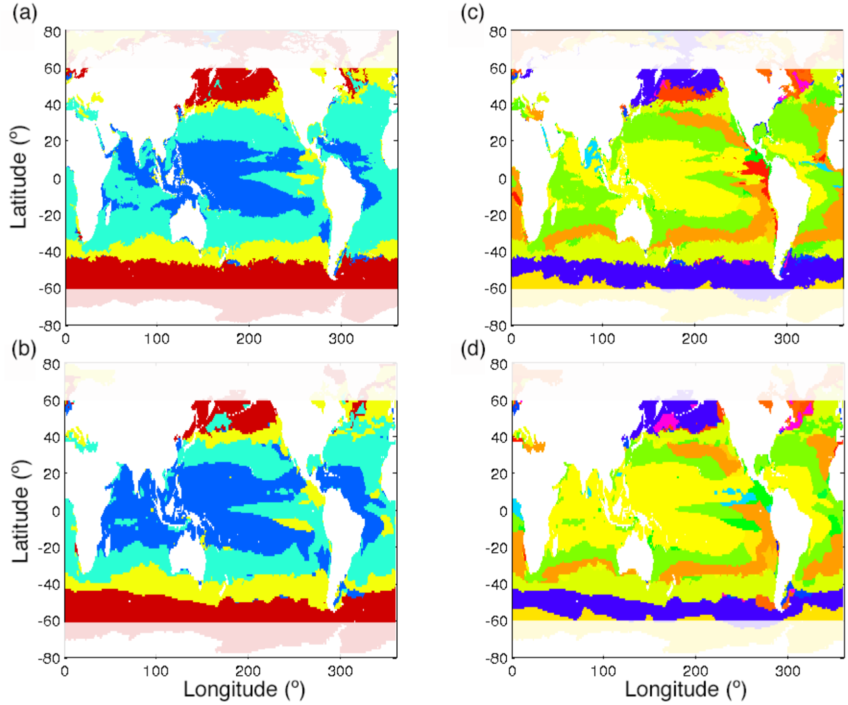

Figure 3. Dominant phytoplankton functional group (a) in the HR simulation, and (b) in the CR simulation. Diatoms are shown in red, large phytoplankton in yellow, picophytoplankton in green and *Prochlorococcus*-like phenotypes in blue. Dominant phytoplankton phenotype (c) in the HR simulation, and (d) in the CR simulation. Each color represents a different phenotype.

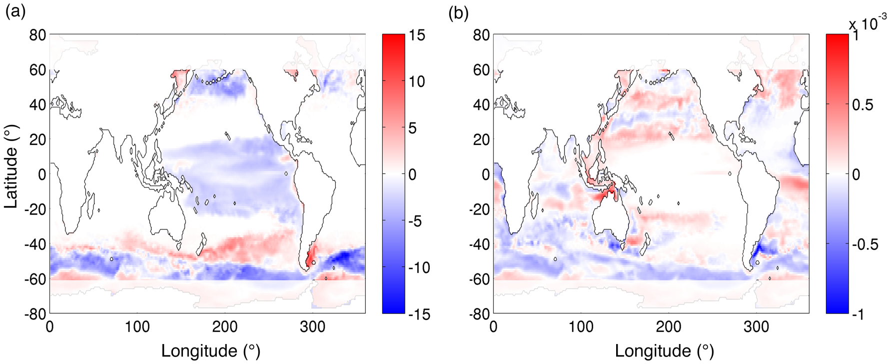

Figure 4. (a) Difference in the annual average surface concentrations of nitrate (mmol N m^{-3}) and, (b) dissolved iron (mmol Fe m^{-3}). Positive values indicate higher values in the HR simulation and negative values indicate higher values in the CR simulation.

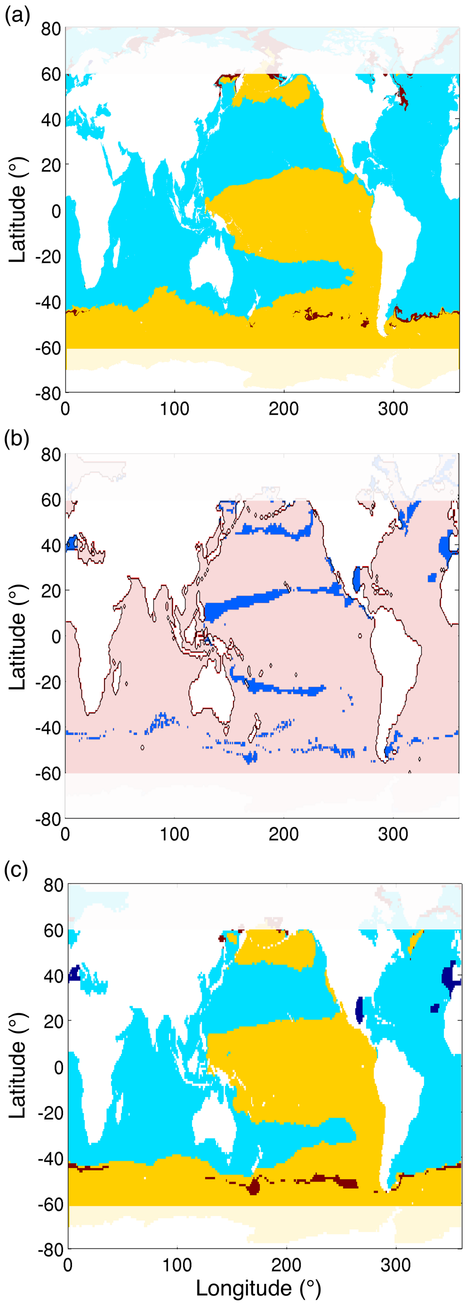

Figure 5. Limiting nutrients were assessed based on a biomass weighted average of the most limiting nutrient for each of the 78 total phytoplankton types (a) in the HR model, and (c) in the CR model. Iron-limited regions are shown in orange, nitrate-limited in light blue, phosphate-limited in dark blue, and silica-limited in red. (b) Regions where the model simulations predict different limiting nutrients are shown in dark blue, whereas pink regions have in the same limiting nutrient in both simulations.

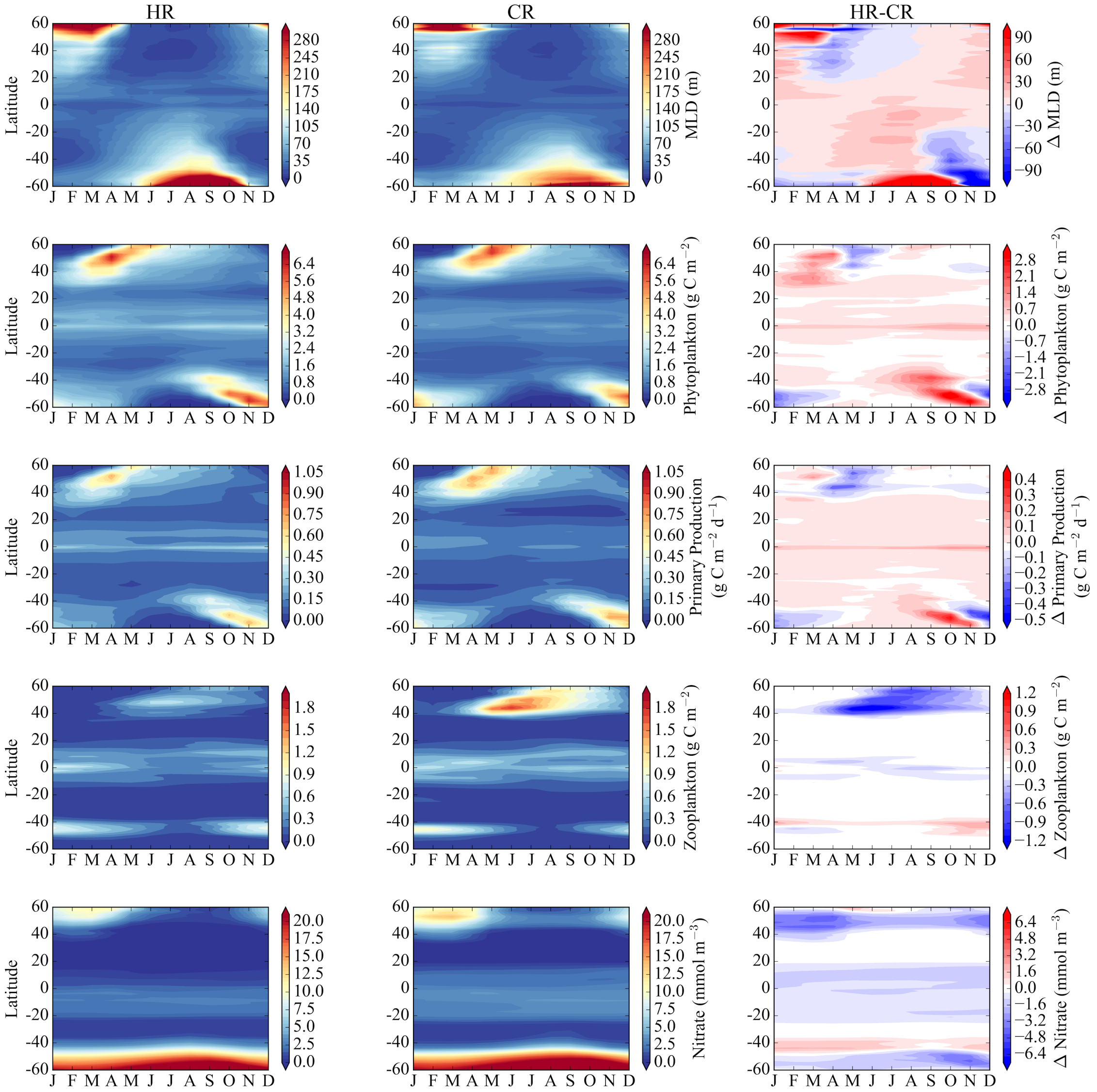

Figure 6. Hovmoller diagram showing the seasonal evolution of zonally averaged model properties for the HR simulation (left column), CR simulation (middle column) and their difference (right column). First row: mixed layer depth; second row: phytoplankton biomass; third row: primary production; fourth row: zooplankton biomass; fifth row: surface nitrate concentration. The difference is calculated as HR-CR, so positive values indicate larger values in the HR simulation.