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Interactive comment on "Drivers of trophic amplification of ocean productivity trends in a changing climate" *by* C. A. Stock et al.

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We would like to thank the two reviewers for their constructive comments that we feel have helped to improve our submission. We've provided detailed responses that we hope address their concerns. Reviewer comments are in bold. These are followed by our response in plain type, and proposed modifications to the text in italics. References are provided at the conclusion of our response.

In addition to these responses, we propose a minor refinement to our zooplankton growth efficiency (ZGE) diagnostic. It results in a small improvement to the analysis in this paper and, more importantly, will provide a more robust metric for future applications. The change would be a switch from an ingestion-weighted characteristic growth efficiency to the mean of the zooplankton growth efficiencies across the zooplankton groups. The former approach skews the ZGE metric toward the lowest trophic level consumer, while the latter provides a more even measure of consumer efficiency across trophic levels. For mesozooplankton analyzed in this paper, the difference is small (described below), but it will be more significant for anticipated future applications that include fish. *The proposed adjustment, which we describe after our response to the reviewers, results in no changes to the text of the results or discussion of the paper.*

Reviewer 1:

General comments: The manuscript (bg-2014-325) addresses a key issue to anticipate the impacts of global warming in the ocean ecosystem and fish stocks: the potential causes and patterns of trophic amplification in lower trophic levels under climate change using a global coupled model of the ocean biogeochemical system. It is also well written and structured.

Thank you for the positive assessment and useful comments. We've provided detailed responses that we hope address your concerns.

I have some minor comments:

1) the study uses a single model, while consensus in climate change projections is to use an ensemble of models (eg. Steinacher et al.,2010 Biogeosciences 7:979–1005.; and Bopp et al., 2013 Biogeosciences 10:6225–6245). I suggest including in the discussion this limitation and that findings are subjected to be confirmed by using other models.

We agree with the reviewer that ensemble approaches are ultimately essential to quantifying uncertainty in projected climate change trends. Our decision to begin with a detailed analysis of one model rests on several considerations:

1. The Steinacher et al., (2010) and Bopp et al., (2013) examples both rest on the mechanistic underpinnings established through detailed analysis of single models in earlier work (e.g., Bopp et al., 2001). Our intent here is to establish similar mechanistic

underpinnings for changes in secondary production that would support an eventual global ensemble analysis. This is reflected in our choice of title, which emphasizes drivers.

2. Most CMIP5/AR5 Earth System Model projections described in Steinacher et al., (2010) and Bopp et al., (2013) have highly idealized representations of zooplankton dynamics that have not been rigorously assessed against observation-based planktonic food web constraints.

3. Pragmatically, the diagnostics used to understand the response are not provided for other models.

Lastly, while we agree with the reviewer that there is great value to ensemble approaches, there is also community recognition of the continued need for detailed diagnosis of individual models to elucidate mechanisms. See, for example, recommended practices and priority developments in the community synthesis "On the use of IPCC-class models to assess the impact of climate on living marine resources" Stock et al. (2011).

We propose the following changes to address your concerns. First, we will add text to the abstract making it clear that we are looking at only one model:

Here, we elucidate the role of planktonic food web dynamics in driving projected changes in mesozooplankton production (MESOZP) found to be, on average, twice as large as projected changes in NPP by the latter half of the 21st century under a high emissions scenario in the Geophysical Fluid Dynamics Laboratory's ESM2M-COBALT Earth System Model.

Second, we will add the following as the second paragraph in the discussion:

The potential for stark regional changes in ocean productivity has implications for food security. An important caveat, however, is that results herein reflect only one model. For NPP, different Earth System Models agreed on large-scale mean trends across latitudes, but these trends occur beneath substantial regional scale variations where there is less agreement (Steinacher et al., 2010; Bopp et al., 2013). Likewise, Chust et al., (2014) found broad occurrences of trophic amplification under climate change across a suite of mainly regional physical-biological modeling frameworks, but the degree of amplification was highly variable. Analysis of a global ensemble (e.g., Bopp et al., 2013) is clearly needed to further bound amplification estimates herein. There are several key impediments, however, that must be resolved for such an analysis. First, many present generation ESMs have highly simplified representation of planktonic food web dynamics that are incapable of resolving the interactions described herein (e.g., Dunne et al., 2005). Second, most biogeochemical models in present ESMs have not undergone detailed assessments against a holistic suite of available observation-based planktonic food constraints (Stock et al., 2014). Third, standard outputs lack the key diagnostics (e.g., ZGE, MESOTL, and ZPC) required to understand inter-model differences. In addition to addressing these issues, focused field and laboratory research on the dynamics governing variation in ZGE, MESOTL and ZPC is also essential to refine projections.

We will also maintain text in the results comparing projected NPP changes in ESM2M-COBALT with the CMIP5 ensemble NPP changes described in Bopp et al. (2013).

2) The way to assess negative and positive amplification should be explicitly explained in methods.

We will expand our description of our treatment of amplification in the methods:

To assess trophic amplification within the planktonic food web, we compare the magnitudes of projected relative (i.e., percent) changes in mesozooplankton production (MESOZP) against projected relative changes in primary production (NPP). Larger percent MESOZP increases (decreases) in areas of increasing (decreasing) NPP indicate positive (negative) amplification.

You can find also proportional effects, which threshold have you used?

While we considered extensive classification schemes, such as those of Chust et al. (2014) and Kearney et al. (2013), we strongly feel that Fig. 3 and the associated statistics most effectively communicate the clear, dominant pattern of amplification that motivates the paper:

Projected changes in MESOZP are highly correlated (r = 0.86) with NPP but broadly amplified in both the positive and negative directions (Fig. 3C,D). The mean magnitude of percent changes in MESOZP is 2.1 times the percent change in NPP and approximately equal in both the positive (2.2 times) and negative (2.0 times) directions. Globally, MESOZP declines by 7.9% compared with a 3.6% for NPP, but regional MESOZP changes can be $>$ 50%.

We do recognize, however, that there are exceptions - areas of trophic attenuation and changes of NPP and MESOZP of opposite sign account for 20% of ocean area. Most of these are associated with either the transitions between areas of positive and negative NPP change (see Figure 1 of this response) or areas where dynamics shifts in zooplankton-phytoplankton coupling (ZPC) counteract the amplifying effects of ZGE and MESOTL on NPP decreases (Fig. 4F, 7 of initial submission). Areas of strictly (or nearly) proportional change were thin "ribbons" in the transition areas.

Since ZPC is a main driver of these exceptions, we propose an expansion (bold face) of the description of exceptions within the section of Results describing the damping ZPC response, including the Figure 1 of this document as Fig. 8. This approach allows us to discuss exceptions without losing focus on dominant patterns:

Widespread ZPC increase under climate change has a positive influence on MESOZP changes (Fig. 7C, i.e., it exerts a stimulatory effect on mesozooplankton production). The effect, however, is only large in high latitude regions experiencing large changes in winter mixing or ice coverage. Increasing ZPC plays a large role in the positive amplification of NPP increases in the Arctic but counteracts amplification in most other regions. In regions where sharp decreases in winter mixing are associated with declining productivity (e.g., the Northwest Atlantic, many interior portions of the Southern Ocean, Figs. 3-5), increased ZPC counteracts negative amplification from ZGE and MESOTL effects. In other regions of the Southern Ocean where strongly enhanced winter mixing is associated with increasing NPP, declining ZPC attenuates MESOZP increases. It is thus not surprising that regions with sharp ZPC shifts (Fig. 4F) join transition areas between region of positive and negative productivity changes to account for most of the 20% of ocean regions exhibiting trophic attenuation or opposing NPP and MESOZP changes (Fig. 8). The damping influence of ZPC in these regions, however, was not large enough to offset the dominant global pattern of trophic amplification.

Amplification is bottom up control, what about top-down control?

COBALT uses a density dependent (specifically, quadratic) "higher predation closure" that is ubiquitous across planktonic food web models (noted in methods, p. 6, lines 6-9 of the original submission). As discussed in Steele and Henderson (1992), use of this closure reflects an assumption that the biomass of unresolved higher predators (e.g., fish) respond positively to the biomass of their zooplankton prey. Prevailing "Bottom-up control" is thus an underlying assumption in COBALT and, to our knowledge, nearly all planktonic food web models that have not been explicitly linked to fish food webs. Changes in MESOZP and NPP of opposite sign (yellow regions in Fig. 8) are thus not indicative of top-down control, but likely subtle differences in sign transitions for NPP and MESOZP in advective environments (e.g., observations of White et al. (1995) describing the aliasing of temporal response lags into spatial offsets in the equatorial Pacific).

We will re-iterate limitation associated with the higher predation closure in the Discussion, noting that linkages with fish food web models would be needed for such an analysis:

Integration of fish and planktonic food webs (e.g., Rose et al., 2010) would also allow exploration of top-down perturbations that cannot be captured with simple higher *predation closures used by planktonic food web models. Holistic accounting for amplification effects throughout the marine food web is needed to fully understand the implications of climate change for fisheries yields.*

3) The author refers to Dunne et al. 2012 for a comprehensive evaluation of the climate model ESM2M. I suggest providing a brief model evaluation description.

We will add the following text to address this comment:

ESM2M is a member of this latest generation of coupled-carbon-climate Earth System Models used for the Coupled Model Intercomparison Project Phase 5 (CMIP5; Flato et al., 2013) which has informed the 5th assessment report of the Intergovernmental Panel on Climate Change (IPCC-AR5). Its physical origin is GFDL's CM2.1 climate model (Delworth et al, 2006). ESM2M has moderate transient and equilibrium climate sensitivities of 1.5 C and 3.2 C (Winton et al., 2013) compared to the assessed likely range among climate models of 1-3 C and 2-4.5 C, respectively (Meehl et al., 2007). It captures regional surface climate patterns (Reichler and Kim, 2008), modes of interannual variability (Guilyardi et al., 2009) and historical climate change (Hegerl et al., 2007; Figures 9.7 and 9.8 in Flato et al., 2013).

Specific comments: Line 1 Page 11340. The following sentence is vague "Planktonic food web properties exhibit temporal trends and spatial patterns suggestive of a role in the trophic amplification apparent in Fig. 3."

This sentence was both vague and not necessary, we have removed it.

Reviewer 2:

Trophic amplification (or attenuation) is a measure of the propagation of a hydroclimatic signal up the food web, causing magnification (or depression) of biomass values between trophic levels. Ocean warming can modify the ecophysiology and distribution of marine organisms, and relationships between species, with nonlinear interactions between ecosystem components potentially resulting in trophic amplification.

The paper by Stock et al describes a global numerical modelling study which explores the impact of climate induced change in net primary production on higher trophic levels. It shows how changes in NPP may be amplified (either positivity or negatively) as reflected in the production of mesozooplankton. In this respect is it similar to the recently published work by Chust et al GBC 2014) but the paper goes beyond the analysis of Chust by considering the role of three key planktonic foodweb properties, zooplankton growth efficiency (ZGE), the trophic level of meso-zooplankton and the coupling between zooplankton and phytoplankton (fraction of NPP consumed by zooplankton).

The paper is well constructed and well written and is based on one of the best global model systems around. While one can always argue about ecosystem model foodweb structure and process descriptions (and modellers frequently do) I believe that in this respect COBALT is appropriate for the task at hand.

The key result is that zooplankton growth efficiencies change with NPP amplifying increases and decreases in NPP as illustrated in figure 2. The work is to my mind quite thought provoking as it highlights the importance of zooplankton in mediating the transfer of energy from phytoplankton to both higher trophic levels and to carbon export. It makes the crucial point that it's not always just about the changes in the physical environment. As zooplankton physiology (e.g. assimilation efficiency, respiration) is thought to be sensitively to climate drivers (e.g. T, pH), it is clear that further research effort should be made in this area.

Thank you for the encouraging review. We are indeed hopeful that this paper's analysis will spur improved understanding of and constraints on physical and biological factors governing planktonic food web properties (ZGE, MESOTL, and ZPC) shown herein to influence trophic amplification. We will maintain this as a closing message in our abstract and a focal point of our discussion through the revision process. While this work shows the potential for these factors to contribute to pronounced regional productivity shifts under climate change, much work remains to refine and build confidence in these projections.

Minor points. The individual maps in figures 3 and 4 would benefit from being larger as in figure 7.

We will make these maps as large as possible in the final submission.

Proposed Zooplankton Growth Efficiency (ZGE) diagnostic refinement:

The zooplankton growth efficiency (ZGE) formulation in our initial submission was defined as the total zooplankton production across all three zooplankton groups divided by the total ingestion by zooplankton across all three groups. This resulted in an "ingested-weighted" metric that most strongly reflected small zooplankton. We found an alternative definition of ZGE as the mean efficiency of the zooplankton groups more evenly reflected trophic efficiencies within the food web, resulting in a slight improvement to our mesozooplankton production (MESOZP) approximation (figures 2 and 3 of this document). The difference is small, such that *the change results in no modifications to the results or discussion*. Moving forward, however, the revised metric will be more robust for applications to fish and other higher trophic levels organisms. We thus feel this would be a worthwhile improvement for the final manuscript.

Figure 1: Areas of trophic amplification (dark blue; % MESOZP change $>$ % NPP change and of same sign) attenuation (light blue, % MESOZP change $<$ % NPP change and of same sign) and changes of opposite sign for NPP and MESOZP (yellow). Note that areas of trophic attenuation and changes of opposite sign correspond to either a) transition regions/fringes between areas of increasing and decreasing NPP, or b) areas with dynamic changes in ZPC that counteract the amplifying effects of ZGE and MESOTL (e.g., Sub-polar North Atlantic, Parts of the Southern Ocean).

Figure 2: Original ZGE Methodology: The exact (left) and approximate (right) %

MESOZP change

Figure 3: Proposed ZGE refinement: The exact (left) and approximate (right) % MESOZP change

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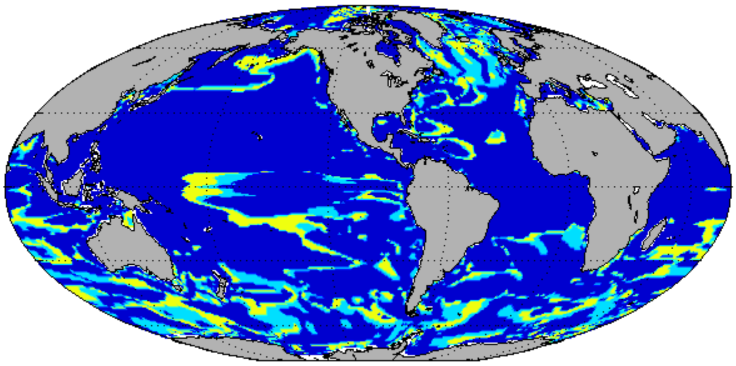

Fig. 1.

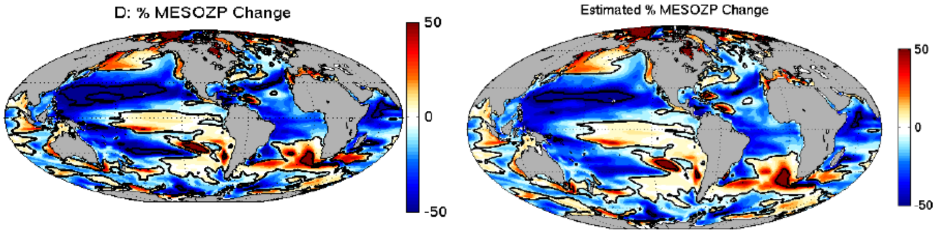
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Fig. 2.

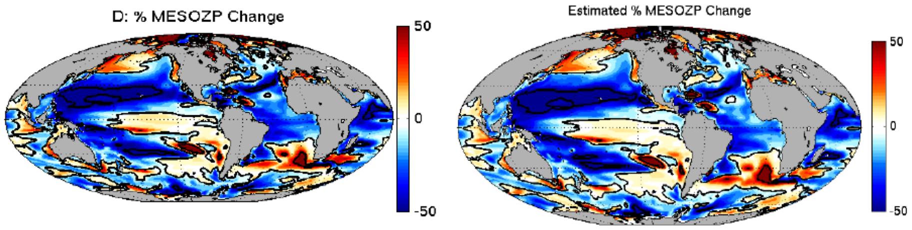
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Fig. 3.