Response to comments on "Drivers of trophic amplification of ocean productivity trends in a changing climate" (bg-2014-325) by C.A. Stock, J.P. Dunne and J.G. John

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, including references to line numbers in the revised manuscript. References are provided at the conclusion of our response.

In addition to these responses, we propose a minor refinement to our zooplankton growth efficiency metric (ZGE). 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 over the three 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, just minor changes to the figures.*

__**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:

- 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.
- 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.
- 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 **(lines 25-30)** 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 **(lines 399-418)**:

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, alternative models agree on large-scale mean trends across latitudes, but these trends occur beneath substantial regional scale variations where there is less consensus (Steinacher et al., 2010; Bopp et al., 2013). Likewise, Chust et al., (2014) found broad occurrence 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 is clearly needed to further bound amplification estimates herein. There are several 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.*

We will also maintain text throughout 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 **(line 227-231)**:

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 **(lines 285-293)**:

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%, 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 below) 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 integrating an expansion of the description of exceptions to amplification with the description of the ZPC response **(lines 361-370)** and the addition of **Fig. 8**. This approach allows us to discuss exceptions without losing focus on dominant patterns of amplification:

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.***

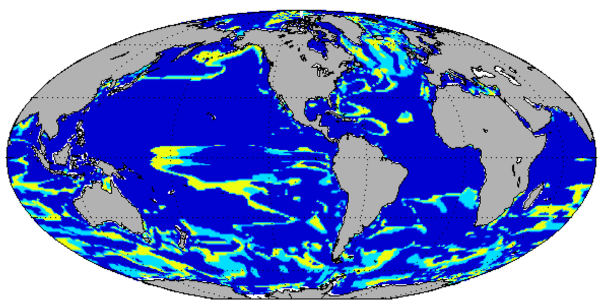


Figure 8: Areas of trophic amplification (dark blue; % MESOZP change > % NPP change and of same sign) attenuation (light blue, % MESOZP change < % NPP change and of same sign) and changes of opposite sign for NPP and MESOZP (yellow). Note that areas of trophic attenuation and changes of opposite sign 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).

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 (**Methods, line 173-176**). 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 perturbations, 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 **(lines 532-536)**, 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.

1) 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 **(lines 119-131)**:

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, 2013). 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.

<u>Reviewer #2:</u>

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 **(line 46-48)** and a focal point of our discussion **(lines 419-520)** 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.

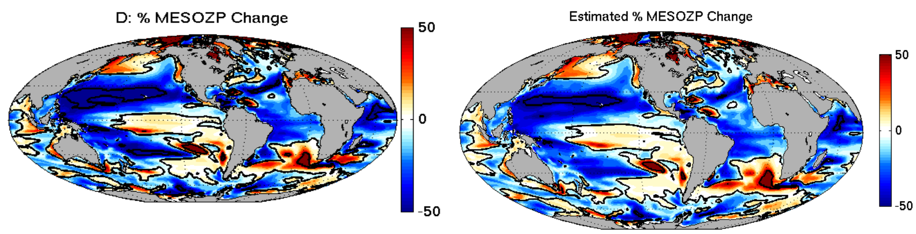
Minor points. The individual maps in figures 3 and 4 would benefit from being larger as in figure 7.

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

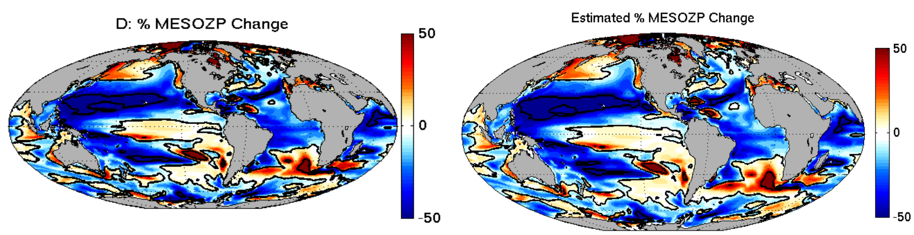
Proposed Zooplankton Growth Efficiency (ZGE) diagnostic refinement:

The zooplankton growth efficiency (ZGE) metric 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 three zooplankton groups **(line 246-248)** more evenly reflected trophic efficiencies within the food web, resulting in a slight improvement to our mesozooplankton production (MESOZP) approximation (see revised Fig. 6). Slight revisions were also required for Figs. 4 and 7. The differences are small, such that *no modifications to the text of the results or discussion were required*. 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.

Original Methodology: The exact (left) and approximate (right) % MESOZP change



Proposed refinement: The exact (left) and approximate solution (right):



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Drivers of trophic amplification of ocean productivity trends in a changing climate

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Abstract

Pronounced projected 21st century trends in regional oceanic net primary production (NPP) raise the prospect of significant redistributions of marine resources. Recent results further suggest that NPP changes may be amplified at higher trophic levels. 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. Globally, MESOZP was projected to decline by 7.9% but regional MESOZP changes sometimes exceeded 50%. Changes in three planktonic food web properties - zooplankton growth efficiency (ZGE), the trophic level of mesozooplankton (MESOTL), and the fraction of NPP consumed by zooplankton (zooplankton-phytoplankton coupling, ZPC), explain the projected amplification. Zooplankton growth efficiencies (ZGE) changed with NPP, amplifying both NPP increases and decreases. Negative amplification (i.e., exacerbation) of projected subtropical NPP declines via this mechanism was particularly strong since consumers in the subtropics have limited surplus energy above basal metabolic costs. Increased mesozooplankton trophic level (MESOTL) resulted from projected declines in large phytoplankton production. This further amplified negative subtropical NPP declines but was secondary to ZGE and, at higher latitudes, was often offset by increased ZPC. Marked ZPC increases were projected for high latitude regions experiencing shoaling of deep winter mixing or decreased winter sea ice - both tending to increase winter zooplankton biomass and enhance grazer control of spring blooms. Increased ZPC amplified projected NPP increases in the Artic and damped projected NPP declines in the Northwest Atlantic and Southern Ocean. Improved understanding of the physical and biological interactions governing ZGE, MESOTL and ZPC is needed to further refine estimates of climate-driven productivity changes across trophic levels.

Key Words: Climate Change, Trophic Amplification, Plankton Food webs, Primary Production, Mesozooplankton, fisheries

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1. Introduction

Under intensive greenhouse gas emissions scenarios (RCP8.5, Riahi et al., 2011), climate change is projected to result in a small to moderate decrease in global Net Primary Production (NPP) by the end of the 21st century (mean = -8.6%, range = 0-16%, Bopp et al., 2013). This results mainly from enhanced nutrient limitation under strengthening surface ocean stratification (Bopp et al., 2001;Doney, 2006). Projected regional NPP changes, however, can be substantially larger than global mean trends and of opposite sign (Steinacher et al., 2010;Rykaczewski and Dunne, 2010). For example, in high latitude systems - particularly those subject to very deep winter mixing or prolonged periods of sea-ice coverage - nutrients are often in surplus and enhanced stratification may increase NPP by alleviating light limitation (Doney, 2006;Bopp et al., 2001). Large regional NPP changes raise the possibility of redistributions of marine resources and significant socioeconomic consequences (Merino et al., 2012;Sumaila et al., 2011;Barange et al., 2014). Furthermore, recent results suggest that trophic amplification - or the magnification of relative biomass/productivity changes across trophic levels via food web dynamics - could lead to significantly larger changes in fisheries resources than implied by NPP changes alone (Chust et al., 2014).

Ryther (1969) hypothesized that differences in planktonic food web dynamics create much starker contrasts in fish yields across ecosystems than would be implied by more modest NPP gradients. Specifically, he posited that a relatively large number of low efficiency trophic steps in low productivity oceanic systems greatly attenuate the importance of these systems for fisheries yields. In contrast, a relatively small number of high efficiency trophic steps in upwelling systems could greatly amplify contributions to

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fisheries yields relative to what NPP alone would suggest. The corollary of this hypothesis, that NPP alone is a poor indicator of fisheries yields across global marine ecosystems, is supported by recent analysis (Friedland et al., 2012). Furthermore, inspection of the role of the food web mechanisms invoked by Ryther in sharpening higher trophic level productivity gradients between ocean ecosystems using modern data constraints supports their importance. The size of cross-ecosystem differences, however, were muted relative to the very stark differences invoked by Ryther, and cross-ecosystem contrasts in the degree of zooplankton-phytoplankton coupling was raised as an additional consideration (Stock et al., 2014).

Mechanisms leading to the amplification of spatial NPP differences may also amplify projected NPP trends in a changing climate. The present study examines the role of each of the planktonic food web factors described above - consumer growth efficiency, the length of food chains, and zooplankton-phytoplankton coupling - in amplifying projected 21st century mesozooplankton production (MESOZP) trends relative to NPP. The planktonic ecosystem model used is distinguished by extensive evaluation against observation-based energy flux estimates throughout the planktonic food web (Stock et al., 2014). We show that nearly all of the projected two-fold amplification of NPP changes for MESOZP is explained by changes in these food web factors and explicitly quantify the roles of each mechanism. Lastly, results are used to identify aspects of planktonic food web dynamics in need of further study and/or improved representation within models to build further confidence in trophic amplification estimates under climate change.

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2. Methods

2.1 ESM2M-COBALT

To conduct this analysis, the Carbon Ocean Biogeochemistry and Lower Trophics (COBALT) planktonic ecosystem model (Stock et al., 2014) was integrated with GFDL's Earth System Model ESM2M (Dunne et al., 2012;Dunne et al., 2013). ESM2M is a member of the 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;Flato et al., 2013).

ESM2M-COBALT simulations were initiated from a 2400 year pre-industrial ESM2M spin-up. An additional 1000 years of pre-industrial control was run with ESM2M-COBALT, followed by 160 years of land-use spin-up, a historical simulation from 1860-2005, and a projection to 2100 under the high emissions RCP8.5 scenario (Riahi et al., 2011). The ocean component of ESM2M is GFDL's MOM4p1 ocean model (Griffies, 2009). It has a 1^{o} horizontal grid that ramps to finer $1/3^{o}$ resolution at the equator and is tripolar above 65^{o}N (Griffies et al., 2005). It includes 50 geopotential vertical levels spaced approximately 10m apart in the top 200m with coarser resolution

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below. The atmospheric component of ESM2M is provided by GFDL's AM2 model (Anderson et al., 2004;Lin, 2004) and has a horizontal resolution of 2^{o} x 2.5^{o} resolution.

COBALT uses 33 state variables to resolve global scale cycles of nitrogen, carbon, phosphate, silicate, iron, calcium carbonate, oxygen and lithogenic material. Fig. 1 provides a distilled depiction of the planktonic food web dynamics. We note that the structure itself is similar to other intermediate complexity planktonic food web models used in global and regional physical-biological simulations (e.g., Aumont et al., 2003;Chai et al., 2002;Kishi et al., 2007) and ESM2M-COBALT exhibits similar overall fidelity to global nutrient and chlorophyll distributions as ESM2M (Dunne et al., 2013). COBALT is unique, however, in the extent to which it is has been critically assessed and calibrated against large-scale observed patterns in the flux of carbon and energy throughout the planktonic food web (Stock et al., 2014;Stock and Dunne, 2010). Most critically for the analysis herein, the model produces NPP and MESOZP estimates that are broadly consistent with observation and satellite-based estimates (Stock et al., 2014). Here we provide a brief overview of the planktonic food web dynamics in COBALT (Fig. 1), highlighting dynamics governing the food web processes central to the objectives herein. Complete details can be found in Stock et al., (2014).

Inorganic nutrients are taken up by phytoplankton falling into small and large size classes (SP and LP), where the large group is a mix of diatoms (assumed dominant when silicate is plentiful) and other phytoplankton with a nominal lower size bound of ~10 μm. Primary production is determined by light (Geider et al., 1997), the most limiting nutrient (nitrogen, phosphorous, iron) and metabolic costs (Geider, 1992;Flynn, 2005). Phytoplankton are consumed by small, medium, and large zooplankton groups (SZ, MZ,

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and LZ), where small zooplankton are microzooplankton < 200 µm in equivalent spherical diameter (ESD), medium zooplankton are small to medium bodied copepods (200 µm - 2 mm ESD), and large zooplankton are large copepods and euphausids (2 mm - 2 cm ESD). Predator-prey size ratios were chosen based on typical ratios observed for ciliates and copepods (Fuchs and Franks, 2010;Hansen et al., 1994). Feeding is modeled as a Type II saturating response with weak density-dependent switching between herbivory and carnivory (Stock et al., 2008). Higher predators (i.e., fish) enter the model as a density dependent mortality on medium and large zooplankton, reflecting an assumption that the biomass of unresolved higher predators scales with the available biomass of their zooplankton prey.

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Zooplankton consumers of phytoplankton must compete with losses due to viruses, exudation and aggregation for organic material fixed by phytoplankton. The balance of these competing rates plays a central role in determining the strength of zooplankton-phytoplankton coupling. Exudation is assumed to be 13% of primary production (Baines and Pace, 1991) and is routed to labile dissolved organic material. Viruses are assumed a minor phytoplankton loss mechanism (Suttle, 1994) and are included as a weak density-dependent loss term for small phytoplankton. This contrasts with the stronger density-dependent viral loss term imposed on bacteria, which routes 10-40% of bacterial production back to dissolved organic material (Suttle, 1994;Fuhrman, 2000). Aggregation is modeled as a density dependent loss term for small and large phytoplankton (Doney et al., 1996) calibrated for consistency with the size-specific thresholds for aggregation-based control of phytoplankton accumulation derived by Jackson (1990).

Not all the material consumed by zooplankton is realized as zooplankton production. 30% of ingested material is egested, yielding an assimilation efficiency (ae) of 70% (Carlotti et al., 2000;Nagata, 2000). An additional 30% of ingestion is allocated to active metabolism (i.e., metabolic costs associated with feeding), leaving 40% to cover basal metabolic costs and support production (i.e., growth and reproduction). Biomass-specific basal metabolic rates are assumed to scale with maximum ingestion rates (Flynn, 2005) and must be covered before any net zooplankton production is realized (Fig. 2A). The zooplankton growth efficiency (ZGE, the ratio of net zooplankton production to ingestion) is thus negative at very low ingestion rates (i.e., there is a net loss of carbon to respiration) before increasing toward an asymptotic maximum just below 40% (Fig. 2B), consistent with observations of Straile (1997) and Hansen et al. (1997). The limitations of this relatively simple approach to zooplankton energetics will be addressed in detail in Section 4.

Size-based (i.e., allometric) relationships were used to parameterize phytoplankton groups, zooplankton groups and their interactions (Stock et al., 2014). The primary trade-off for phytoplankton is that small phytoplankton can efficiently scavenge nutrients in oligotrophic systems due to their high surface area to volume ratio (Munk and Riley, 1952;Eppley et al., 1969;Edwards et al., 2012), but are susceptible to voracious small zooplankton grazing (Hansen et al., 1997). Biological rates in the model are given a Q_{10} of 1.88 (Eppley, 1972). That is, rates increase by a factor of 1.88 for a 10^{o}C change in temperature. There are two exceptions: 1) phytoplankton aggregation was assumed to be a predominantly physical process; 2) detrital remineralization was

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assumed to be modulated by mineral ballasting (Klaas and Archer, 2002;Armstrong et al., 2002). Both of these processes were thus given a Q_{10} of 1.

Calibration of the model food web dynamics involved tuning two parameters which are both highly uncertain and have a large effect on emergent food web dynamics (Stock and Dunne, 2010). Zooplankton basal metabolic rates were tuned within uncertainty ranges to ensure consistency with observed mesozooplankton biomass and productivity in sub-tropical gyres (Landry et al., 2001;Roman et al., 2002). Simultaneously, half-saturation constants for zooplankton feeding were calibrated to capture observed trends in the relationship between phytoplankton biomass and turnover times (Stock and Dunne, 2010). In both cases, tuning was done while maintaining the slope of allometric relationships across size classes (i.e., we allowed 2 degrees of freedom rather than 6).

2.2 Model Diagnostics

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.

MESOZP is the combined production of the medium and large zooplankton groups in Fig. 1. This is consistent with the definitions of Sieburth (1978) and reflects the resolution of the mesozooplankton observations that COBALT has been evaluated against (O'Brien, 2005). Production is integrated over 100m and changes in production between 50 year means (1951-2000 and 2051-2100) are considered to help filter out climate variability in favor of the century-scale climate change signal of primary interest herein (Stock et al., 2011).

Where statistics of relative changes are calculated over model grid points, we limit calculations to regions where annual average productivity during the 1951-2000 period was greater than 25 mg C m-2 day-1. This threshold, which is 10-20 times less than production in oligotrophic sub-tropical gyres, omits < 0.05% of ocean area and just 0.001% of global NPP. This is done to ensure that statistics are not skewed by a small number of grid points where extremely low contemporary productivity yields extremely large relative changes (e.g., a change from 1 mg C m-3 day-1 to 10 mg C m-3 day-1).

The zooplankton growth efficiency metric (ZGE) is calculated as the mean of the zooplankton growth efficiencies from the three zooplankton groups. It thus provides a bulk measure of consumer growth efficiency for the system.

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The mesozooplankton trophic level (MESOTL) metric is the ingestion-weighted average trophic level of medium and large zooplankton. For medium zooplankton, a trophic level of 1 was assigned to ingestion of large phytoplankton and trophic level of 2 was assigned to ingestion of small zooplankton. For large zooplankton, ingestion of large phytoplankton was assigned a trophic level of 1 and ingestion of medium zooplankton was assigned a value of 1 plus the trophic level of medium zooplankton.

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The zooplankton-phytoplankton coupling efficiency (ZPC) is the total ingestion of phytoplankton by all zooplankton groups divided by total phytoplankton production. It reflects the extent of consumer-prey coupling in the pelagic system.

3. Results

Globally, NPP in ESM2M-COBALT is projected to decline slightly, by 3.6%, between 1951-2000 and 2051-2100, from 54.7 Pg C yr^{-1} to 52.7 Pg C yr^{-1} (Fig. 3A,B). This is consistent in sign and of moderate magnitude compared with other model projections (Bopp et al., 2013;Steinacher et al., 2010). The sign of projected NPP changes also agrees with other models in regions where model consensus exists: NPP declines prevail throughout most low and mid-latitude regions (Fig. 3A,B) due to enhanced nutrient limitation. Increasing NPP is more common at higher latitudes though marked regional variability exists.

Regional NPP variations are often larger than global mean changes (Fig. 3B) and depend on detailed balances of evolving nutrient and light limitation. Full diagnosis of regional changes is beyond the objective of this contribution. It is notable, however, that a modest NPP increase is projected in the central and eastern Equatorial Pacific despite its low latitude. This has also been found in some other models (Ruggio et al., 2013) where it has been associated with increased iron in the Equatorial Undercurrent. Large portions of the interior Southern Ocean, in contrast, exhibit declining NPP in ESM2M-COBALT despite its high latitude. Very strong iron limitation and minimal iron deposition in this region place great importance on the supply of iron from depth, favoring deeper mixing for higher NPP even though light is often scarce.

Projected changes in MESOZP are highly correlated (r = 0.86) with NPP but broadly amplified in both 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.

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Globally, MESOZP declines by 7.9% from 5.35 Pg C yr^{-1} to 4.93 Pg C yr^{-1}, but regional changes can be ~50%.

Trends in planktonic food web properties are summarized in Fig. 4. ZGE changes show a strong positive correlation with NPP changes (r = 0.82, Fig. 4A,B). Like NPP, ZGE declines are ubiquitous in low and mid-latitudes. The largest ZGE declines occur within oligotrophic subtropical gyres where decreases to already low NPP further reduces small energy surpluses available for growth over basal metabolic costs. Since feeding rates are well below saturating levels, further declines in food resources are fully reflected in decreased feeding rates (Fig. 2). Likewise, increasing productivity in previously low NPP regions, such as the western Arctic Ocean, lead to pronounced ZGE increases.

Projected changes in mesozooplankton trophic level (MESOTL) are generally modest (< 0.1 acting on a range of annual mean MESOTL between 1.4-1.8, Fig. 4C,D). In lower latitudes (between 50^{o}S and 50^{o}N), there is a strong negative correlation between projected MESOTL and NPP changes (r = -0.70) that strengthens (r = -0.78) if only large phytoplankton productivity is considered (not shown). This reflects less mesozooplankton herbivory and higher MESOTL with declining phytoplankton production. The correlation breaks down poleward of 50^{o} latitude, however, where dynamic ZPC shifts that also influence the extent of herbivory are projected (Fig. 4E,F).

ZPC generally increases with climate change (Fig. 4E,F). This reflects the favorability of increased surface ocean stratification for consumer-prey coupling in the pelagic zone. ZPC changes are largest at mid and high latitudes and the largest increases are closely aligned with regions experiencing pronounced shoaling in the depth of winter

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mixing (e.g., Northwest Atlantic and many parts of the Southern Ocean, Fig. 5). In the model, shoaling winter mixed layers yield decreased winter nutrient maxima and increased winter phytoplankton and zooplankton biomass (Table 1). The particularly pronounced increase in winter zooplankton biomass combines with decreased winter nutrients to enable zooplankton to respond more effectively to the spring bloom, shifting the balance of phytoplankton loss toward zooplankton consumption and away from aggregation and direct sinking (Table 1).

In contrast to ZGE and MESOTL, ZPC changes are not significantly correlated with NPP changes. This is because decreased mixing exhibits both positive and negative effects on high latitude NPP depending on the prominence of nutrient versus light limitation while its effect on ZPC is uniformly positive.

To confirm and quantify the role of the food web factors in Fig. 4 in trophic amplification, we note that food web considerations suggest that MESOZP can be approximated as:

$$MESOZP \cong ZPC \times NPP \times ZGE^{MESOTL} \qquad (1)$$

Where $ZPC \times NPP$ is the primary production consumed by all zooplankton and ZGE^{MESOTL} accounts for the characteristic number and efficiency of trophic links separating phytoplankton and mesozooplankton. Recalculating the percent MESOZP change with this approximation yields a very close match to the exact model solution (Fig. 6 compared with Fig. 3D, r = 0.98). This confirms that changes in the planktonic food web factors used to explain contemporary spatial differences in the ratio of mesozooplankton production to primary production are also responsible for the trophic amplification of climate change driven productivity trends in Fig. 3.

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The impact of individual planktonic food web factors on MESOZP changes was estimated using Eq. (1) while holding all but one factor constant across the two time periods (Fig. 7). Changes in ZGE are the most prominent contributor to trophic amplification (Fig. 7A). Both positive and negative NPP changes are amplified by ZGE changes, but the largest impact is negative amplification (i.e., exacerbation) of subtropical NPP declines due the dynamic variation of ZGE in low food environments (i.e., Fig. 2). Increased MESOTL due to reductions in large phytoplankton productivity also amplifies subtropical declines, but its impact is secondary to *ZGE* (Fig. 7B).

Widespread ZPC increase under climate change have 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 amplication 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 join transition areas between regions 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.

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4. Discussion

Results herein demonstrate the potential for significant trophic amplification of climate change-driven NPP trends, with mean projected changes in ESM2M-COBALT MESOZP approximately twice as large as mean projected changes in NPP. While a difference between a 3.6% global NPP decline and 7.9% MESOZP decline may seem modest, results suggest that amplification may contribute to regional MESOZP changes as large as 50%. Widespread trophic amplification is explicitly attributed to changes in three planktonic food web metrics: the zooplankton growth efficiency (ZGE), mesozooplankton trophic level (MESOTL), and the strength of zooplankton-phytoplankton coupling (ZPC) - the same factors invoked to explain cross-biome differences in the transfer of energy between phytoplankton and fish (Ryther, 1969;Stock et al., 2014).

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, alternative models agree on large-scale mean trends across latitudes, but these trends occur beneath substantial regional scale variations where there is less consensus (Steinacher et al., 2010;Bopp et al., 2013). Likewise, Chust et al., (2014) found broad occurrence 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 is clearly needed to further bound amplification estimates herein. There are several impediments, however, that must be resolved for such an analysis. First, many present generation ESMs have

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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.

Focused field and laboratory research on the dynamics governing variation in ZGE, MESOTL and ZPC is also essential to refine projections. The ZGE effect was most notable for its marked negative amplification of declining NPP in many subtropical and temperate regions. The key aspect of the model structure that allows for this response is the inclusion of a basal metabolic cost that must be covered before any net production occurs. Without the inclusion of this modest rate (< 0.05 day^{-1} for medium zooplankton at 20^{o}C, Fig. 2), which is omitted in many models, no variation in ZGE and subsequent large-scale effects (Fig. 7A) would occur. As described in Section 2, the rate itself is difficult to measure and was thus calibrated to produce observed mesozooplankton production within the subtropics (Stock and Dunne, 2010). Amplification via this ZGE mechanism occurs, however, as long as basal metabolic costs are not negligibly small relative to ingestion.

A possible ZGE variation not captured herein is a decrease at high ingestion rates due to a shortened residence time of food in the gut. This can be explained as a balance between clearance of food through the gut and energy extraction from that food to maximize production (Jumars et al., 1989). This effect, however, would likely not be a factor in oligotrophic subtropical systems where ZGE-driven amplification was most

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prominent. Furthermore, maximizing production places strong constraints on how much consumers can accommodate ZGE decreases before production declines.

The spatial ZGE patterns in Fig. 4A emerge as a result of calibrating the model to recreate cross-biome trends in the ratio of mesozooplankton production to primary production while also satisfying other observation-based constraints on the planktonic food web (Stock and Dunne, 2010). Improved observational constraints on cross-biome ZGE trends could build further confidence in projected responses. Syntheses of laboratory ZGE measurements has yielded some evidence for increasing ZGE across the range of food concentrations simulated herein (~10-100 mg C m^{-3}) before dropping at very high concentrations (Straile, 1997;Hansen et al., 1997). The explanatory power of the food concentration, however, was weak ($r^2 = 0.29$) and coverage of the lowest concentrations most essential to the response herein was limited to a few studies. For heterotrophic bacteria, in contrast, syntheses of large numbers of in-situ measurements has yielded evidence for systematic trends similar in direction and magnitude to the ZGE patterns in Fig. 4A (del Giorgio and Cole, 2000). The importance of ZGE variations to trophic amplification under climate change provides further impetus for efforts to constrain cross-biome ZGE variations for zooplankton.

The relatively small contribution of MESOTL changes to trophic amplification was surprising given that diatoms and/or large phytoplankton are projected to experience sharper declines under climate change than small phytoplankton (Bopp et al., 2001). In ESM2M-COBALT under RCP8.5, large phytoplankton production declines by 6.8% while small phytoplankton production declines by 2.3%. Enhanced large phytoplankton declines arise from their higher sensitivity to declining nutrients relative to smaller cells,

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reflecting a disadvantage of the low surface area to volume ratio of large cells for nutrient scavenging. Two factors appear to minimize effects of this shift on MESOTL. First, the microbial food web (i.e., microzooplankton consuming small phytoplankton and bacteria) is prominent across all ocean biomes under contemporary ocean conditions (Calbet and Landry, 2004). A decrease in large phytoplankton production thus does not represent a binary switch from large to small phytoplankton dominance, but a more subtle shift in the relative importance of the large phytoplankton-copepod consumer link within an ocean where much of the energy flows (and is projected to continue to flow) through microzooplankton. Second, increasing ZPC compensates for decreasing large phytoplankton productivity in many of the areas experiencing the strongest increases in stratification by ensuring that a larger fraction of NPP is consumed by zooplankton (Fig. 7C).

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Dynamic ZPC changes in high latitudes within ESM2M-COBALT had simple mechanistic explanations: very deep winter mixing is conducive to high winter nutrients and smaller pre-spring bloom zooplankton populations due to combination of dilution via mixing and cumulative net losses over the unproductive winter season. This sets the stage for a large spring bloom controlled more strongly by aggregation than in less deeply mixed regions characterized by tighter coupling between phytoplankton and zooplankton consumers. A prominent aspect of mesozooplankton dynamics not resolved by ESM2M-COBALT that could influence this balance is diapause behavior in many copepod species, particularly in high latitude oceans (Mauchline, 1998). Cues initiating and terminating dormancy, however, are complex and not fully understood (Dahms, 1995;Johnson et al., 2008). A complete examination of different diapause strategies for

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ZPC is beyond the scope of this work and requires novel approaches (Record et al., 2013) applied at global scales.

The other facet of ecosystem dynamics influencing ZPC in ESM2M-COBALT is aggregation. As described in Section 2, COBALT uses a simple density dependent formulation (Doney et al., 1996) set to match theoretical size-dependent aggregation rates and critical concentrations derived by Jackson (1990). Any exploration of the impact of diapause on ZPC would thus also require consideration of more resolved formulations of particle aggregation dynamics. Particle coagulation theory provides a basis for further exploration, but significant uncertainties concerning controls on disaggregation, particle stickiness, and the production of transparent exopolymer particles (TEP) remain (Burd and Jackson, 2009). Furthermore, incorporation of highly resolved particle size spectra used by many coagulation models into long time-scale, global simulations imposes a potentially prohibitive computational burden. Strategies are thus needed to efficiently capture emergent aggregation dynamics beyond the simple density dependence presently applied in many global models while maintaining low computational cost.

Finally, we note that trophic amplification and attenuation is unlikely to end with the planktonic food web. Kearney et al. (2013) examined amplification in a fisheries food web model based on principles from the widely applied ECOPATH/ECOSIM food web modeling framework (Pauly et al., 2000). The functional form of non-predatory losses, which are intended to capture all losses not associated with consumption by other food web constituents (e.g., basal respiration, disease, cannibalism) proved an important determinant. Linear forms often used in ECOPATH/ECOSIM implementations were conducive to amplification in a manner analogous to the effect basal respiration on ZGE

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herein (Fig. 2). In contrast, strong density-dependent losses (i.e., those associated with disease and cannibalism in limited carrying capacity environments) damped the effect of NPP variations. 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.

Author Contributions: CAS, JGJ and JPD designed and carried out simulations, formulated and refined analysis and contributed to the writing of this manuscript.

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Table 1: Changes in physical and planktonic food web properties associated with regions where ZPC increases/decreases by more than 0.05. The limiting nutrient is defined as that with that imposing the greatest limitation in the annual mean sense averaged over small and large phytoplankton types.

	Max MLD	**Max Limiting Nutrient**	**Min (Winter) Phyto Biomass**	**Min (Winter) Zoop Biomass**	**Max Phyto Biomass**	**NPP change**	**Zooplankton Ingestion of Phytos**	**Phyto Aggregation Losses**
Increased ZPC Regions (> 0.05)	-275m	-36%	+35%	+67%	-5%	+4%	+29%	-11%
Decreased ZPC Regions (< -0.05)	+86m	+59%	-12%	-37%	+17%	+34%	+12%	+33%

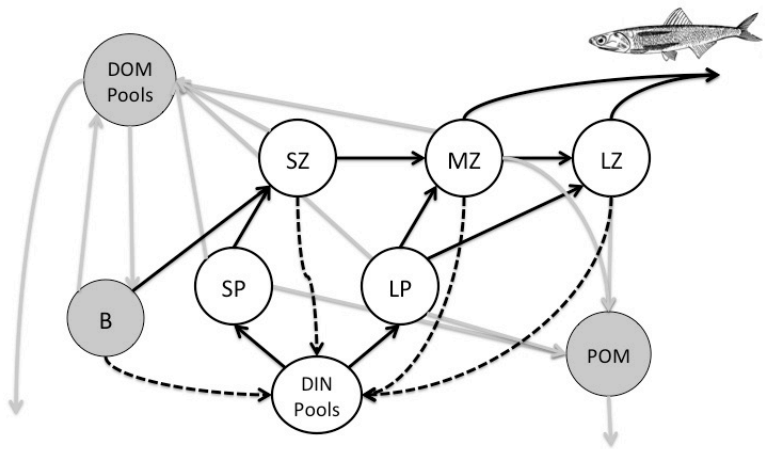

Figure 1: Simplified schematic of planktonic food web dynamics within COBALT. DIN Pools = diverse pools of dissolved organic nutrients (e.g., NH_4, NO_3, Fe, PO_4, SiO_4); SP = small phytoplankton; LP = large phytoplankton; SZ = small zooplankton (i.e., microzooplankton); MZ = medium zooplankton (i.e., small to medium-bodied copepods); LZ = large zooplankton (i.e., large copepods and euphausids/krill); DOM Pools = dissolved organic matter pools of various lability; B = free-living heterotrophic bacteria; POM = particulate organic material. Fish enter the model as a closure term on MZ and LZ. Arrows indicate exchange of material between groups. Dashed arrows are reserved for respiration/remineralization of organic matter. Downward arrows for POM indicate sinking. A downward arrow is also shown for DOM to indicate that the downward mixing of long-lived DOM can also create significant export of organic material from the euphotic zone in the model.

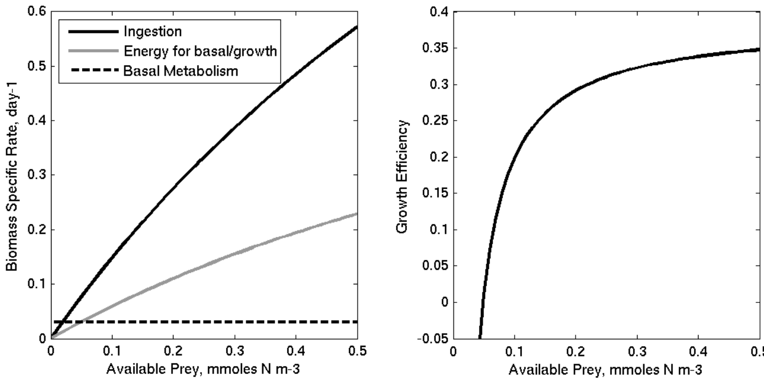

Figure 2: Summary of zooplankton feeding and growth efficiency as a function of food availability. The example shown is for a medium zooplankton at 20°C. In the left panel, the dashed line indicates the basal metabolic rate that remains constant for all levels of prey resources. The solid black line shows the grazing rate as a function of available prey resources and the solid grey line indicates the energy remaining after removing undigested food (30% of ingestion) and accounting for active metabolism (30% of ingestion). The energy available for growth is thus the difference between the grey line and the dashed line. The right panel shows the resulting growth efficiency (zooplankton production/ingestion), which is negative when the energy remaining (grey line) is less than that needed to cover basal metabolic costs and rises to a maximum value as ingestion rates become large relative to basal metabolic costs.

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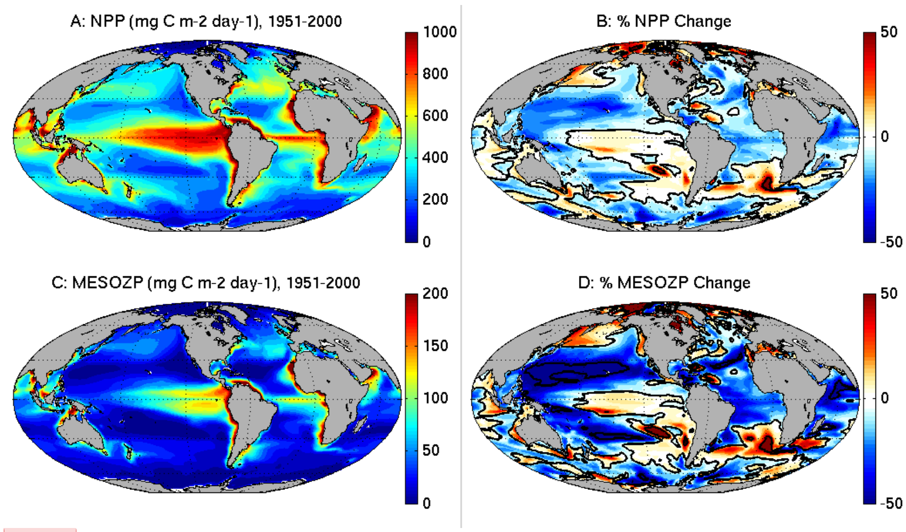

Figure 3: Contemporary (1951-2000) NPP and MESOZP (A,C) and percent changes between 2051-2100 and 1951-2000 (B,D). For regions with NPP > 25 mg C m^{-2} day^{-1} in 1951-2000 (see methods), the correlation between MESOZP change and NPP change is 0.86 and the magnitude of MESOZP changes is 2.1 times the NPP change. Contours are shown at -50%, 0 and +50%.

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Comment [1]: Will make this as big as possible in accordance with the request of reviewer #2.

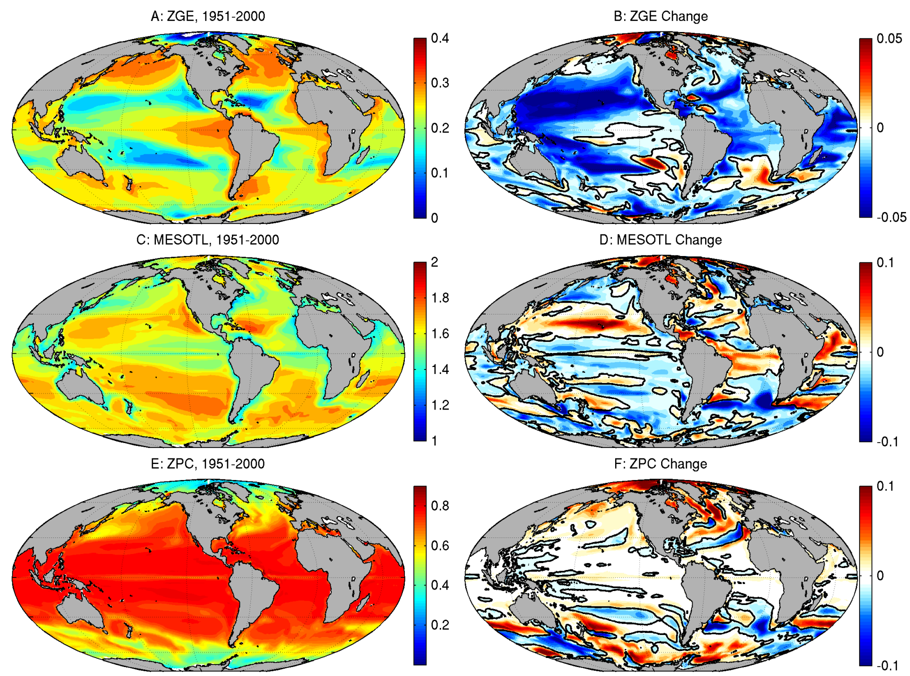

Figure 4: Contemporary (1951-2000) planktonic food web characteristics (ZGE, MESOTL, and ZPC) and changes in these properties: (2051-2100)-(1951-2000). The 0 contour is shown.

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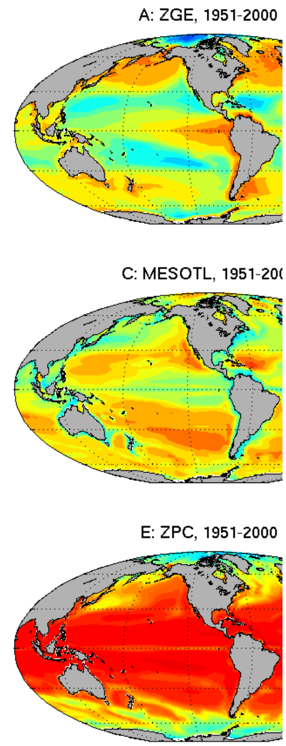

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Comment [2]: Maximized size in accordance with reviewer #2; minor change to panels A,B in accordance with the adjustment to the ZGE diagnostic.

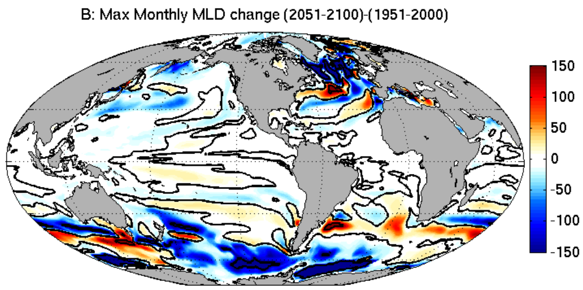

Figure 5: Change in the maximum monthly mixed layer depth (MLD, m): (2051-2100) - (1951-2000). The 0 contour is shown.

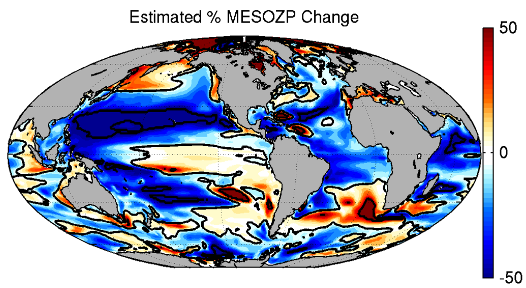

Figure 6: Estimated percent MESOZP change based on the approximation in Eq. (1). The correlation with the exact solution (Fig. 3B) is 0.98. Contours are shown at -50%, 0 and +50%.

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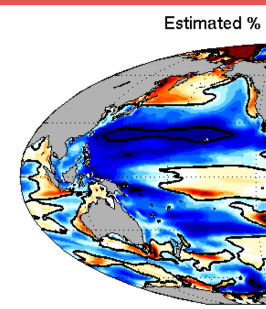

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Comment [3]: Updated in accordance with the proposed refinement to the ZGE metric.

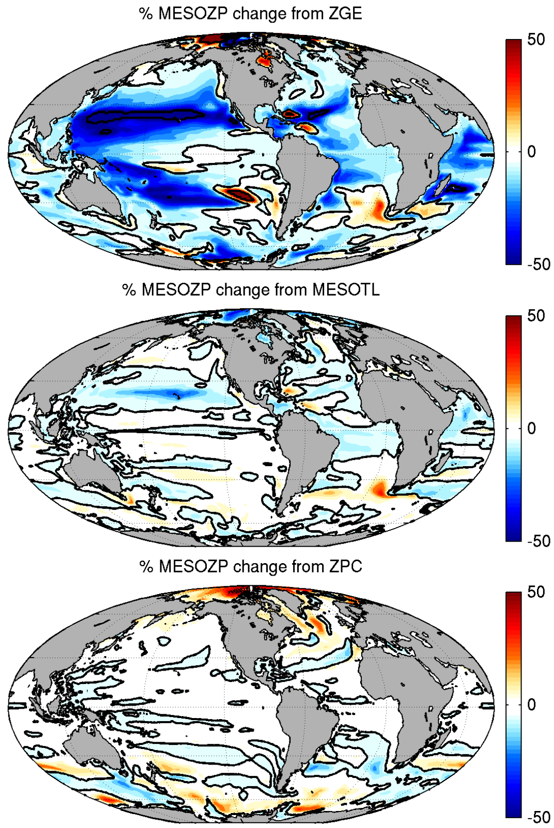

Figure 7: Contribution to percent change in MESOZP due to evolving planktonic food web properties. Adding the changes above to the percent change in NPP (Fig. 2B) yields the approximation of the percent MESOZP change in Fig. 6. The 0 contour is shown in all figures.

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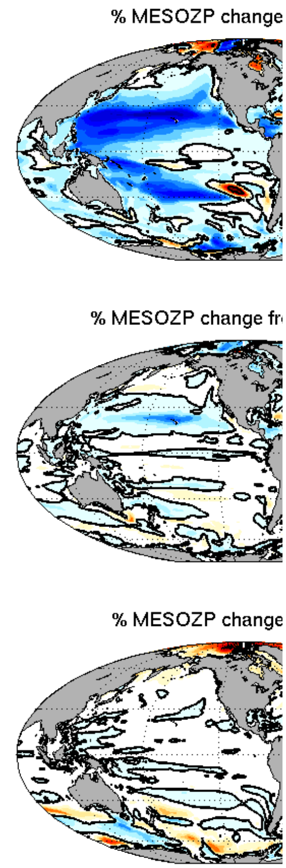

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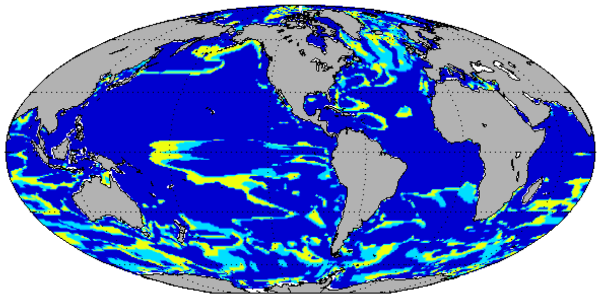

Figure 8: Areas of trophic amplification (dark blue) attenuation (light blue) and changes of opposite sign for NPP and MESOZP (yellow) in Fig. 3. Note that areas of trophic attenuation and changes of opposite sign often correspond to either a) transition regions/fringes between areas increasing and decreasing 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).

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Comment [5]: Added in response to reviewer #1

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