

We thank both of the referees for their close reading of the manuscript, and their thoughtful, constructive comments.

The reviewer comments are in bold, and are followed by our response and then by changes and/or additions to the text.

Anonymous Referee #1

-Page 10147, line 19: Consider rewording “has the potential to transform” to something more definite as we’re already seeing impacts of climate change on temperature distribution (e.g., Pinsky et al. 2013 Science, Walsh et al. 2015 PLoS ONE).

We have changed the sentence as follows:

Original

Anthropogenic climate change, on the other hand, has the potential to transform the ocean temperature distribution and thereby alter marine ecosystems by affecting elements of ocean circulation that drive nutrient dynamics and primary production (Doney et al., 2012).

Revised

Anthropogenic climate change, on the other hand, is already altering nutrient dynamics and primary production through its effects on ocean temperature and circulation (Doney et al., 2012), with demonstrated consequences on the distributions of several fish populations (Pinsky et al, 2013; Walsh et al., 2015).

-Page 10150, lines 24 – 26: Consider stating that these three groups are independent “species groups” and that fish don’t grow into the next larger size spectrum. In other words, “small” consists of fish that remain small throughout their life history and not the juveniles of “medium” and “large”. This becomes clear later in the paper, but it would eliminate confusion by clarifying early on.

We have changed the sentence as follows:

Original

We consider three populations of fish at every grid point, and so resolve three biomass spectra. These populations, which we refer to as groups, represent small, medium, and

large fish, and allow a very crude representation of biodiversity (Andersen and Beyer, 2006; Maury and Poggiale, 2013).

Revised

We consider three independent populations of fish at every grid point, and so resolve three biomass spectra. These populations, which we refer to as groups, are defined by their asymptotic sizes as small, medium, and large fish, which allows for a very crude representation of biodiversity (Andersen and Beyer, 2006; Maury and Poggiale, 2013). There is no growth from one group to another; in other words, the small group consists of fish that remain small throughout their life history, such as anchovies and sardines, distinct from the juveniles of the medium and large groups.

-Page 10152, first paragraph: I have trouble seeing where this paragraph is going. Is it providing support for making biomass a function of net primary production? Please clarify.

The goal of this paragraph is to place BOATS in the context of existing global fisheries modeling studies, and to provide a brief literature review of related work that employs the MVF model. We have revised the first to sentence of the paragraph to clarify this.

Original

BOATS continues on from the earlier work of Ryther (1969), who estimated global fish production and harvest based on NPP and simple trophic scaling relationships.

Revised

BOATS continues in a tradition of studies that model the global fishery by applying ecological principles to spatially-resolved environmental properties. This line of research can be traced to the work of Ryther (1969), who estimated the potential global fish production and harvest based on NPP and simple trophic scaling relationships.

-Section 2.1: Why is the time increment per second? This seems quite fast.

We use seconds as our time unit since it is the standard unit used in climate models (although it does lead to some unwieldy numbers - with no effect on the results).

-Page 10154, lines 11 – 13: What specifically prevents a buildup of biomass at the largest sizes in each spectrum? Also, would fishing mortality come into this mortality term, or would it be an additional term in eq. (1)? You don't need to go into detail about how fishing mortality is included, but it would be helpful just to note where it enters.

First part of question:

As mass approaches the asymptotic size, fish growth declines to zero, while mortality does not. This, together with the assumption that the allocation of input energy to growth, as opposed to reproduction, is strictly decreasing with increasing mass (equations 17 and 23), will prevent a buildup of biomass at the largest sizes in each group.

Second part of question, concerning harvest mortality:

The mortality due to harvest would be represented by another loss term in equation 1. However, since harvest is often assumed to be proportional to biomass, as in the BOATS framework, one could interpret the mortality $\Lambda_k(m)$ as being the sum of 2 terms, one for natural mortality and another for harvest mortality.

We have added a sentence to line 13 to describe how harvest mortality would be introduced into equation 1:

New sentence

Although we do not consider harvest mortality in this paper, in the full BOATS model (described by Carozza et al., (2016), in review) it is represented by another loss term on the right hand side of equation (1).

-Section 2.5: I'm unclear whether phytoplankton size structure influences fish size structure. How would a shift towards smaller or larger phytoplankton impact the fish spectra?

We represent phytoplankton size structure through a single representative phytoplankton mass (equation 25). This is set by the large fraction of phytoplankton production, which we calculate using the empirical relationship of Dunne et al. (2005). The only way to change the phytoplankton structure is therefore through a change in temperature or net primary production. The impacts of such changes are described in figure 5B for the intercept and in figure 5C for the slope.

The approach just described would also integrate the other impacts that a change in NPP or T would have on the system (such as through the allometric growth rate or mortality rate). An alternative approach to address this question would be to only change the representative mass, ignoring the other impacts of T and NPP.

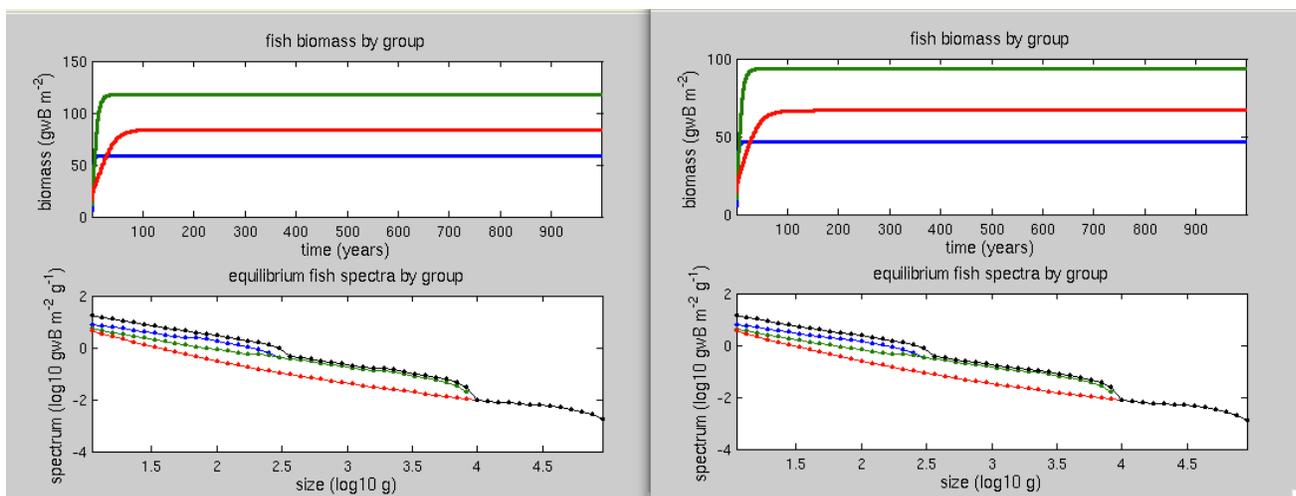
A shift to smaller (larger) phytoplankton would result in a downward (upward) shift of the fish production spectrum, but would not affect the mass dependence of the fish production spectrum. We can explain this again using equation (25). First we can rewrite equation (25) as

$$\pi(m,t) = \Pi_{\psi}(t) * m_{\psi}(t)^{-\tau} * m^{\tau - 1},$$

where $m_{\psi}(t)$ is the representative mass of phytoplankton. τ is equal to $\log_{10}(\text{trophic efficiency})/\log_{10}(\text{predator to prey mass ratio})$, and so is negative because

the trophic efficiency is < 1 and the predator to prey mass ratio is > 1 . $-\tau$ is therefore positive, and so we have m_{ψ} to the power of a positive exponent. Therefore, a shift to smaller (larger) phytoplankton would result in a shift downward (upward) of the entire fish production spectrum; that is, a reduction (increase) in the total fish production, without changes in its partitioning to different fish sizes.

This will influence the growth rate, since the shift in the fish production distribution will alter where the von Bertalanffy limit determines growth (equation 11). Moreover, the fish size structure also depends on the mortality. It would require further simulation to fully understand the details of a change in only the representative phytoplankton size. That said, as a very simple example of such a simulation, we have run the model to equilibrium with the same NPP and T values but have increased the large phytoplankton mass (parameter m_L in equation 15) by a factor of 10. The left panel consists of time series of biomass by group and equilibrium spectra for larger m_L , whereas the right panel is for a smaller m_L . At a qualitative level, there is a negligible change in the structure of the biomass spectra, but a clear positive shift in the intercepts.



-Section 2.6, final two paragraphs: I have a hard time with the lack of predation-dependent mortality, especially in a model that aims to investigate fisheries. It doesn't sound like the model is able to capture top-down impacts. For example, if there's a heavy removal of larger sizes (say, though fishing) would smaller sizes increase in abundance as a result of reduced predation? Maybe this is captured through the mechanism discussed on page 10158, lines 1 – 4? Also, the final sentence of this section seems to contradict the rest of the paragraph. Please clarify the example you're giving with a bit more detail.

The model does not capture top-down impacts. This is explicitly stated in the last paragraph on page 10165 of the manuscript. Top-down impacts are complex processes that are poorly constrained by data and difficult to implement in a manner that is both realistic and sufficiently general to be applied at the global scale. In the simplifying spirit

of the model, we decided not to include them the current version, although we certainly hope to explore them in future. In the scenario proposed by the Reviewer, if there is a strong removal of large sizes in a given group, there is no impact on the mortality of any other fish.

The mechanism discussed in Lines 1-4 on page 10158 would not capture top-down impacts. Those lines indicate that the energy input from primary production to an individual fish would increase under harvest (or another form of removal), and so that the growth rate from primary production would be higher. We have revised these sentences to clarify this.

Original Lines 1-4 on page 10158

Since we assume that the NPP that is transferred up through the trophic web is uniformly input to all individuals in a given mass class, if the biomass in a mass class falls (due to harvesting for example) then the number of individuals has fallen. This implies that more fish production is input to each individual, and so $\xi_{P,k}$ increases.

Revised

Since we assume that the NPP that is transferred up through the trophic web is uniformly input to all individuals in a given mass class, if the biomass in a mass class falls due to a removal (such as harvesting, for example) then this is equivalent to a decrease in the number of individuals in that mass class. This implies that more fish production would input to each individual, and so in such a scenario $\xi_{P,k}$ would increase.

To further clarify this point, we have added to the final sentence of section 2.3.

Original

When biomass is low enough that this equation holds, NPP no longer influences the input energy, and fish will grow at their maximum physiological rate.

Revised

When biomass is low enough that this equation holds, NPP no longer influences the input energy, and fish will grow at their maximum physiological rate, and any unused energy available to fish production is assumed to be transferred to unresolved parts of the ecosystem.

Concerning the final sentence of section 2.6, we have revised the final paragraph as follows:

Original

At the same time, since the abundance of predators does not feature in the prey mortality rate, we cannot resolve top-down trophic cascades (Andersen and Pedersen, 2010; Hessen and Kaartvedt, 2014). Since, at present, the scarcity of data prevents a formal verification of theorized trophic cascades in the open ocean, we feel this is a necessary simplifying assumption that we will further explore in the future. Through the growth formulation described in Eq. (1), however, changes in biomass due to harvesting, for example, are carried up through the trophic web.

Revised

Since the prey mortality rate does not depend on the predator biomass, we do not resolve top-down trophic cascades (Andersen and Pedersen, 2010; Hessen and Kaartvedt, 2014). At present, a scarcity of data hinders a formal verification of generalized trophic cascades in the open ocean, which would be desirable for the formulation of their impact within the BOATS framework. However, we do represent bottom-up trophic cascades through the growth formulation described in Eq. (1), since a change in biomass in one size class is carried upward through the trophic web as fish grow to larger mass classes.

-Page 10169, lines 2 – 29 and page 10170, lines 1 – 4: Consider condensing these paragraphs considerably. I don't think it's necessary to delve this far into the details of satellite estimates of NPP in this paper. After all, as you state, you could force the model with some other source. It seems sufficient to treat discussion of your NPP input as you do your discussion of temperature input.

We have made substantial changes to section 2.8. As suggested, we have removed many of the details of how NPP is estimated from satellite observations.

Revised section 2.8

The ecological model requires temperature and NPP information as forcing input to calculate the time evolution of biomass (Eq. 1). These variables can be provided by an ocean general circulation model that includes a lower trophic level model. Here, we instead use observational estimates, which would be expected to provide a more realistic simulation.

For temperature, we use the World Ocean Atlas 2005 (Locarnini et al., 2006), which brings together multiple sources of in situ quality-controlled temperature interpolated to monthly climatologies on a $1^{\circ} \times 1^{\circ}$ grid. We discuss our usage of temperature in Sect. 2.2, and as discussed above, use the average water temperature from the upper 75 m of the water column to force temperature-dependent rates.

For NPP, we take the average of three satellite-based estimates (Behrenfeld and Falkowski, 1997; Carr et al., 2006; Marra et al., 2007) to capture some of the variability

that exists in different NPP models (Saba et al., 2011). We note that satellite-based estimates suffer from a range of shortcomings, including lack of productivity sources other than phytoplankton (e.g. seagrass and corals), and biases in coastal regions and estuaries (Saba et al., 2011; Smyth, 2005). Although overall minor, these uncertainties will carry through to the modeled biomass and harvest.

-Page 10173, line 11: Your definition of the intercept here is different from that on page 10172, line 1. Is this intentional? If so, why use two different definitions?

We did not intend to use two different definitions. Since the lower boundary of the resolved biomass spectra are 10 g, this is the mass at which the intercept is defined, and that which we use for the simulations and figures. However, for the idealized continuous spectrum described in equation (30), our objective is to point out what sets the part of the curve that is not dependent on the mass of the organism, and since the actual value of the intercept assumed does not affect this, we propose the following change.

Original lines 1-3 of page 10172

On the other hand, the intercept of the spectrum (in logarithmic space, when $m = 1$) depends on a variety of parameters such as the NPP and trophic efficiency, as well as the natural mortality rate and the representative phytoplankton mass.

Revised lines 1-3 of page 10172

On the other hand, the intercept of the spectrum (in logarithmic space, when $m = m_0 = 10$ g in our case) depends on a variety of parameters such as the NPP and trophic efficiency, as well as the natural mortality rate and the representative phytoplankton mass.

-Page 10174, lines 1 – 3: The sentence beginning, “Overall. . .” is a nice summary of the influences of NPP and temperature on the biomass spectra.

Thank you.

Technical Corrections

-Throughout the paper equations are mentioned out of order. I can see why this is done in some cases, but if it's possible to address it would aid the reader. It's not critical, though.

Throughout the manuscript, we preferred to introduce the equations in logical rather than chronological order to facilitate the description and explanation of the different model components. Where appropriate, we added section numbers to the equation numbers when referring to equations that have not been introduced yet in the text.

-Page 10146, line 19: I think this should read, “determine how they change...”, not “determine how the change”.

We have made the change as suggested.

-Page 10149, final sentence: Fragment, but would be fixed by removing the word “which”.

We removed the word “which”.

-Page 10154, line 4: The closing parenthesis is missing before the period.

We corrected the error.

-Page 10154, line 13 and page 10164, line 22: Consider replacing “old age” with “senescence”.

We will make the changes as suggested.

-Page 10155, lines 17 – 18: Consider omitting “more than” for tone.

We will make the change as suggested.

-Page 10162, lines 7 – 9: I don’t think Blanchard et al. (2009) model the dynamics of the phytoplankton spectrum, but rather assume constant conditions.

We have removed this reference to Blanchard et al. (2009).

-Page 10163, lines 24 – 25: Please state how carbon is converted to wet weight, either here in the text or in Table 1.

$\text{mmolC_2_wetB} = (12 * \text{gC_2_wetB}) / 1000; \% [\text{wetB} / \text{mmolC}]$

Original lines 22-25 of page 10163

Since the model is forced with NPP data, we run the model in units of mmolC, and then convert biomass and harvest to grams of wet biomass (gwB) for analysis and presentation by assuming a constant conversion rate.

Revised

The model is forced with observations of NPP, and so we run the model in units of mmolC. For analysis and presentation, we convert to grams of wet biomass (gwB) by assuming that there are 12 gC per molC, and that there are 10 gwB for every g of dry carbon (Jennings et al., 2008).

-Page 10168, final sentence: Consider replacing “ocean general circulation model including a lower trophic level model” with “earth system model”.

See response above to changes in section 2.8.

-Page 10174, line 17: Insert “such as” before “for use in. . .”.

We will make the change as suggested.

-Page 19175, line 2: Convert “10 cm” to mass to be consistent with the body of the paper. This could be a parenthetical after the length if it’s desirable to have both measures.

We will make the change as suggested.

-Figure 5c: Are groups 1, 2, and 3 the same as small, medium, large in the other figures? If so, please change the legend for consistency.

We will make the change as suggested, and refer to the groups as small, medium, and large throughout.

-This is a somewhat picky suggestion, but blue-green-red color scheme could be hard for color-blind folks to distinguish. An easy solution would be solid, dashed, and dotted lines, differently shaded lines, or some combination thereof.

We will make the change as suggested.

Anonymous Referee #2

I want to point out just a few places where I think the simplifying assumptions may break down somewhat; not necessarily for the authors to change their approach, but to indicate that these are important assumptions that should be further explored at some point.

Firstly, the input of all NPP as a potentially exploitable resource for commercial fish species seems excessive. A substantial fraction is taken up by the many other non-commercial organisms inhabiting the oceans, for example, by export flux that goes to mesopelagics, by marine mammals, by the millions of non-commercially fished marine species. Although this is moderated somewhat when growth is constrained by allometry instead of productivity, it would make sense to have some fraction of NPP go to other groups and not be available to modelled organisms. This fraction could be a parameter, and may improve fit to data.

We assume that all NPP is transferred to commercial fish. Although difficult to constrain, we considered alternate fractions of NPP available to commercial fish (25, 50, and 75%, not shown or described in the manuscript). In those simulations, we found that globally integrated unharvested biomass, harvested biomass, and peak harvest were linear with the fraction of NPP available. From this we took that including the NPP fraction available as a parameter in the Monte Carlo analysis would not allow us to exploit another mode of variability, and so opted to not include it as a parameter.

Nevertheless, we recognize that as new approaches to estimating this parameter become available, it will be constructive to include it in future sensitivity analyses. We have revised the second paragraph on page 10157 to address these concerns.

Revised paragraph 2 p.10157

We assume that all NPP is transferred to the three commercial fish groups, and further assume that each group has access to one third of the total production. Group fish production is written as the fraction allocated to group k , $\phi_{\pi,k}$, multiplied by the fish production $\Pi(m,t)$. Although we recognize that these are strong assumptions, we feel that they are necessary simplifications given the state of current knowledge that prevents us from more formally estimating these fractions. We have examined alternative fractions of NPP transferred to the commercial groups (not shown) and find that the unharvested biomass, harvested biomass, and the peak harvest are approximately linear with the fraction. For this reason, we did not include it as a parameter when constraining the model (see Sect. 3, table 1, and Carozza et al.,2016).

Groups are independent of one another, except in that they all receive a part of NPP. Ecologically, this implies equal resource partitioning of NPP to each group, both when they are at the larval stage (through recruitment) and as juveniles and adults (through growth) (Chesson, 2000). This can be thought of as each group occupying an ecological niche that remains stable over time, and implies that excess NPP, which would result from growth-rate limitation of biomass advection, is not available to other potentially commercial groups, but rather supplied to non-commercial species. Non-commercial species could include, among others, unharvested mesopelagic fish, planktonic invertebrates such as cnidarians and fish, and benthic invertebrates such as amphipods and nematodes. By assuming that a fixed portion of NPP goes to each commercial group, all groups are assured to coexist stably.

As it stands, the model is likely biased in that for low productivity systems, most of the NPP will be taken up by commercial species (since NPP will be a strong

constraint), whereas in high productivity systems, a much larger fraction will go to other groups (since NPP constraints will be relaxed and allometry play a stronger role). The authors might want to consider any effects this will have on their results.

We note this bias on line 15 of p 10159. However, since this could also cause a bias in harvest, we will note its effect on the results in the companion paper, since such a mechanism could help to explain a bias in harvest.

New sentence at line 15 of p10159

For low productivity systems, the model could overestimate biomass, since nearly all primary production will be transferred to commercial species. However, in high productivity systems, the allometric limit is more likely to set growth rates and so a larger fraction will be transferred to the non-commercial groups. That said, the potential for this bias will depend on the particular values of the growth rates at the site in question (equation 11).

Additionally, does the fact that this model can be (is) applied to the open ocean, where depths may be great, mean that there is also an issue in deeper regions, because the export productivity going to demersal and benthic organisms will be much lower (i.e. decrease exponentially), and so the 1/3 sharing for each group also be biased?

As above, and now noted in the manuscript, the 1/3 sharing for each group is a strong assumption. Our groups are defined based on asymptotic size, and so given that at a deeper site less primary production will be delivered to benthic species, and that benthics are predominantly small and medium, then we could be overestimating benthic biomass in the open ocean.

We recognize that other variables, such as depth or the front probability index (Woodson and Litvin, PNAS, 2015, 112(6), 1710–1715), could provide for informative and alternative ways to represent important first-order processes. Although we have not included depth in this version of the model, we plan to consider it, as well as other variables, in future model development.

Secondly, having natural mortality be independent of predator biomass seems restrictive in terms of situations where it will be an appropriate assumption. For example, if all top predators are fished out, then (if I understand correctly), the mortality rate will not change, even though there are no uber-predators. Although

the authors acknowledge this, their justifications ('without necessarily losing realism', and - to paraphrase - suggesting that 'lack of data is sufficient to assume that trophic cascades in the ocean do not happen and thus this simplification is OK') seems like a stretch. I would recommend not suggesting that this is 'realistic' (which it is not), but a necessary simplification which may lead to problems with certain biomass spectra. It might also be something worth exploring in the future.

Anonymous Referee #1 made a similar comment above and we have addressed both reviewers concerns in the modifications described for the comment above.

Thirdly, no dispersal. On P10150 l15-17 'we effectively ignore nonlocal movements over spatial scales > 100x100km'. Whether this is an issue presumably depends upon the time-step of the model relative to the spatial scale. Here it is 15 days (1/2 month). For a fast region of the ocean (e.g. gulf stream, assume 6km/h, 144km/day, potentially 2160km/15 days), or even a moderate one, it does appear as if advection could move species through many grid cells and thus play a role. This should be included as a caveat, rather than saying 'we expect it to have a negligible impact on our results'. Also note that grid cells are much smaller at high latitudes on a 1 degree grid.

We have changed the paragraph.

Original lines 12-23 p10150

These are complex processes whose role in determining fish biomass are difficult to quantitatively evaluate at the global scale given present knowledge (Watson et al., 2014). For the moment, in BOATS we assume that fish are present where there is NPP to provide food. Given that the model grid points are $1^{\circ} \times 1^{\circ}$, we only effectively ignore nonlocal movements that occur over spatial scales that are larger than approximately $100 \text{ km} \times 100 \text{ km}$. However, movement induced by ocean circulation and fish behavior could be easily implemented in the future, with existing advection and diffusion algorithms (Faugeras and Maury, 2005; Watson et al., 2014). Although the location at which NPP, zooplankton (secondary) production, and fish production take place are different due to the movement of plankton by currents, we expect this to have a negligible impact on our results given our relatively coarse (approximately 100 km) spatial resolution.

Revised

These are complex processes that have been shown to play a role in determining fish biomass distributions (Watson et al., 2014). In BOATS we assume that fish are present where there is NPP to provide food. Given that the model grid cells are $1^{\circ} \times 1^{\circ}$, we only effectively ignore nonlocal movements that occur over spatial scales that are larger than approximately $100 \text{ km} \times 100 \text{ km}$. This could bias our results in parts of the ocean where the advection of fish biomass is strong, such as in the Gulf Stream, relative to the time step and spatial grid scale. This is especially true for larvae, but would likely pose less of a problem for larger fish since they swim faster than even strong oceanic currents. Due to the movement of plankton by currents, a bias could also result from the difference in the locations at which plankton and fish production occur. We expect this to have a small impact on our results given our relatively coarse spatial resolution. Movement induced by ocean circulation and fish behavior could be implemented in the future, with existing advection and diffusion algorithms (Faugeras and Maury, 2005; Watson et al., 2014).

I also think the Watson et al. paper is mis-cited here; rather than saying ‘These are complex processes whose role in determining fish biomass are difficult to quantitatively evaluate at the global scale given present knowledge’, the last line of the Watson abstract is ‘These results highlight the importance of considering movement in global-scale ecological models!’

We addressed this concern in the response to the previous question.

Other comments:

Conversion between abundance and biomass: I don’t buy that the conversion between abundance and biomass (e.g. 10153 l14-16) would not influence model dynamics. In an ideal setting (i.e. a continuous spectrum), then I think this would be the case. But here, where there are 50 mass bins, this discretization will prevent conservation of mass and abundance. If the model was run with a fixed total amount of NPP input, and all pools of biomass resulting from this measured (including respired, detritus etc), I do not think this total would remain constant, as it would in a continuous setting. This is because of fishes ‘jumping’ between the mid-points of size bins, i.e. the growth rate may only be enough to just about take them into the next size bin, but they are automatically inserted at its geometric mean, representing an instantaneous accumulation of biomass not resulting from NPP. This is simply a computational artefact, but it will clearly affect both biomass and, therefore, abundance. So while true in the limit, I don’t

think that this model will actually give the same results when run as abundance or biomass.

We have revised lines 14-16 on p. 10153:

Original

Regardless, since the abundance n and biomass f spectra are related by $f(m, t) = n(m, t)m$, using one form over the other does not influence the model dynamics.

Revised

Regardless, since the abundance n and biomass f spectra are related by $f(m, t) = n(m, t)m$, in the continuous case, using one form over the other does not influence the model dynamics. However, in the numerical implementation of the model, there will be a small difference between the two since we use the geometric mean to represent a discretized range of masses (section 2.10). Hence, as fish grow they jump from one geometric mean to next, which may result in an accumulation of biomass.

I find the notation a little cumbersome; why not drop the mass and time dependencies (where possible) as per Appendix A? It would make it easier to read.

We will keep the mass and time dependence when presenting a variable for the first time, but will remove the dependencies for successive uses. We will moreover keep the dependencies in table 2.

I was wondering where the details of parameter estimation were to be found; there is only a brief reference on p10171. This makes it hard to judge how effective the model fitting process is. Could a line or two be added to give more details (e.g. is this a Bayesian approach? If so, are flat priors being used? How many MC runs are used?

We have reorganized the two paragraphs that introduce section 3.

Revised

Here we describe the behaviour of the fish ecology model, and make use of a simplified version of the model as a reference point and initial biomass condition. We consider two model grid points that correspond to individual patches of ocean at a cold-water site in the East Bering Sea (EBS) LME (64° N, 165° W) and a warm-water site in the Benguela Current (BC) LME site (20° S, 12° E), and describe the resulting biomass

spectra and other model variables. We discuss the results from a sensitivity test that considers the role of NPP (ranging from 50 to 2000 mg C m⁻² d⁻¹) and temperature (ranging from -2 to 30 °C) on biomass. For these simulations, we use a 15-day timestep and constant forcing of annually-averaged NPP and temperature.

We do not use these sites for a thorough data-based model validation, which is difficult at this time due to a lack of suitable fish biomass data. The parameter values used here are taken from an extensive data-model comparison that employs the global implementation of the model, and is fully described in the companion paper (Carozza et al., 2015). In that study, we take a Monte Carlo approach with over 10,000 parameter sets to find parameter combinations that best fit observed harvest at the LME-scale, considering the full range of the uncertain parameter space for the 13 most important parameters. Of these 13 parameters, 2 are economic, with the remaining 11 ecological parameters being identified with a dagger symbol in table 1. Beyond the validation to harvest at the LME-scale in the companion paper (Carozza et al., 2015), more specific validation could be done in the future with suitable datasets when they become available (that is, size aggregated, regional-scale, species-comprehensive biomass assessments).

I would really like to see how precisely biomass spectra fit to data (slopes of -1.0 to -1.2 on p10173). There is nothing in the figure, and in the text it just says that ‘they are consistent with published values’, though maybe not at lower temperatures.. It would be good to get the mean values (and the confidence around that, from the MC simulations) into both the text and the figure, for comparisons sake.

We feel that such an analysis is difficult to justify given the current limitations in observations of size spectra, and so would be beyond the scope of the current work. We are currently completing another manuscript, which employs global harvest data to further examine the uncertainty in the Monte Carlo simulations that we developed (in the companion paper).

The numerical methods (Appendix C, particularly C1) are really important and should be moved to the main text (Section 3), or at least the key points, so that all details of the model (timestep, grid cell size, numerical approach used, mass bin structure) are in one place. Details of the model mass bin approach (number of bins, bin boundaries) are not numerical methods, they are model structure details like the timestep or cell size.

We will move Appendix C: Numerical Methods to become a new section 2.9, and will move Appendix C1: Group and Mass Class Structure to become a new section 2.10.

Minor editorial comments

P10148 I5-6: ‘. . . not always coupled directly with predictive models of fishing activity’. It would be good to see a reference or two for this.

We have added references to this sentence:

Original lines 5-6 P10148:

In addition, spatially-resolved models of fish production are not always coupled directly with predictive models of fishing activity.

Revised

In addition, spatially-resolved models of fish production are not always coupled directly with predictive models of fishing activity (Jennings et al., 2008; Lefort et al., 2014, Watson et al., 2014).

P10148 I10-11 ‘aims to represent the global community of marine organisms’. This is incorrect; all non-commercial species (millions!), marine mammals etc etc are left out. Please rephrase to more carefully delineate the boundaries.

We have revised the sentence on lines 9-13 of P10148.

Original

The ecological module of the BiOeconomic mArine Trophic Size-spectrum model (BOATS) aims to represent the global community of marine organisms as a suite of “super-organism” populations that grow, reproduce, and die, taking into account their dependence on local environmental variables in the framework of a two-dimensional grid of the global ocean.

Revised

The ecological module of the BiOeconomic mArine Trophic Size-spectrum model (BOATS) aims to represent commercial organisms as a suite of three super-organism populations that grow, reproduce, and die, taking into account their dependence on local environmental variables in the framework of a two-dimensional grid of the global ocean.

P10148 I11 ‘a suite of super-organism populations’ – not quite sure what is being referred to here. Is it the three size classes?

See revision to previous question.

P10148 I18-19: ‘which requires arbitrarily defining under-constrained feeding relationships’ seems a little strong, given that the present model is arbitrarily defining many things (e.g. size bins). As mentioned previously, I don’t think the authors need be so defensive.

We will remove this clause.

Revised lines 18-19 P10148.

Instead of attempting to model such species-level characteristics, we make the simplifying assumption that the overall growth of organisms within a community depends on the availability of energy from net primary production, relative to the total consumption of energy by the metabolic activity of the community.

P10151 I12-14: But there is a strong difference in how they will experience the total primary productivity input, particularly in deeper cells.

We addressed this concern in the question above concerning depth.

P10156 Eqn 5: The notation here is confusing – why not use the same symbol for formation of biomass (whether reproductive or somatic), instead of the same symbol for energetic input and somatic biomass?

We use the symbol γ to represent formation of somatic (γ_S) and reproductive (γ_R) biomass.

Original equation 5

$$\xi_{I,k}(m,t) = \gamma_k(m,t) + \xi_{R,k}(m,t),$$

Revised equation 5

$$\xi_{I,k}(m,t) = \gamma_{S,k}(m,t) + \gamma_{R,k}(m,t),$$

P10157 I8: Is there any evidence for equal partitioning of NPP among size classes? If not, this should be stated as a (fairly strong) assumption.

The revisions that we made to paragraph 2 on page 10157 that we presented above address this question.

P10170 I15-20: It would be useful to know bottom-depth at these sites.

We addressed this concern in the question above concerning depth.

P10174 I21: ‘often unconstrainable ecological processes’ – again this seems overly harsh, and not necessarily accurate.

We have changed this sentence.

Original line 21

We apply empirical relationships to simplify complex and often unconstrainable ecological processes when possible.

Revised

When possible, we apply empirical relationships to simplify complex ecological processes that are difficult to constrain.

P10175 I8: ‘Reasonably realistic’ would be more appropriate.

We will make the change as suggested.

Table 2: By variables, do you mean fitted parameters? I’m just trying to get a sense of how many parameters are actually estimated in the model – it would be good to have this value in the text somewhere as well, because right now it is just stated that there are fewer parameters than comparable models, without saying how many there actually are.

Variables refers to quantities that change in mass or time.

13 parameters are estimated in the Monte Carlo procedure described in the companion paper. 11 of these parameters are ecological, and 2 are economic. We have added this information to the introduction to section 3 (see response above). Moreover, in the section 3 introduction, as well as in the caption to table 1, we note that the dagger symbol represents a fitted parameter, which was omitted in the manuscript.

I found Fig 1 a little unintuitive – is there a clearer way of presenting this?

We have added to the figure caption.

Original

Figure 1. Schematic diagram of the main modules, components, and processes of the eco- logical module of BOATS. Solid arrows represent fluxes of biomass, whereas dashed arrows represent dependencies. Arched lines identify model components or extend a process over mass classes or groups.

Revised

Figure 1. Schematic diagram of the main modules, components, and processes of the eco- logical module of BOATS. Net primary production (NPP) and temperature (T) force the model and are used to calculate the fish production spectrum, by assuming a transfer of energy from phytoplankton to successive sizes of fish that depends on the trophic efficiency and the predator to prey mass ratio. From fish production, we calculate the size-dependent growth rate of biomass in three independent groups that represent small, medium, and large commercial fish. Mortality rates are calculated in terms of size group, and are also depend on temperature. Adult fish, the largest sizes, allocate energy to reproduction, which is returned to the spectrum at the smallest mass class. Solid arrows represent fluxes of biomass, whereas dashed arrows represent dependencies. Arched lines identify model components or extend a process over mass classes or groups.

Fig 5. ‘Note that the spectral slope does not depend on NPP’ please clarify for those just looking at the figures; also needs a clearer title for panel C.

We have changed the sentence mentioned to:

In (c), since the slopes of the biomass spectra do not depend on NPP, the results are plotted simply as lines as opposed to maps as in panels (a) and (b).

We will change the Panel C title to:

Slope of biomass spectra

We will also change the Panel B title to:

Intercept of total biomass spectra