

On the example of the North and Baltic Sea, the authors present a very simple way to extend a lower trophic level model (marine biogeochemistry) to an end-to-end model. Two state variables have to be added, both of them two-dimensional (only horizontally resolved). These are the biomasses of fish and macrozoobenthos.

Since these two "upper trophic levels" influence especially the mortality of zooplankton, the result is a spatially heterogenous mortality which replaces the previously uniform closure term of the LTL model. A comparison to a study for the North Sea where fish predation mortality is estimated from observed distributions of planktivorous fish shows, as the authors state, that the correct spatial patterns emerge. In this way, the model outlines a rather simple way to include, to a first order, higher trophic level effects onto the lower trophic food web. Compared to the previous study, this approach has much lower data requirements, which is an advantage not pointed out well enough.

When it comes to overall model performance, the authors could show a slight benefit when adding the two state variables as they compare lower trophic level variables such as nutrient concentrations and oxygen. At least for the North Sea, the authors could also show that fish and macrozoobenthos spatial patterns were similar to observations.

From my point of view, the largest benefit of the model is the opportunity to gain more realistic zooplankton mortality values. I would like this point to be more highlighted. Especially I would like to see the spatial patterns of zooplankton mortality as they emerge from this model compared to those of Maar et al. (2014). Contrary to what the authors state in the caption of Fig. 9, fish production is not a suitable indicator for zooplankton predation mortality, but only the ratio between fish production and zooplankton biomass gives the predation mortality. The comparison should be done to Fig. 10C+D in Maar et al., not to Fig. 4, and it would be very useful if the comparison was shown in this article.

Daewel et al: We agree that this comparison is necessary. We have compiled biomass specific mortality based on our model results as an average from 1980-1989 and separated the year into 1st and 2nd half as done in Maar et al. (2014) (see suppl. Figure 1a). The results are around the same magnitude as calculated by Maar et al. (2014) and the structure resembles the structure they had calculated for the first half of the year 2001. The results from Maar et al (2014) showed a clear difference between half-year 1 and half-year 2 with decreased biomass specific mortality in the second half-year in the central North Sea. This difference between the 1st and 2nd half-year is not evident in our model results. However we found a clear difference in magnitude when comparing winter and summer season (not shown). The reasons for the discrepancies between our model results and Maar et al (2014) are presumably related to interannual variations in fish consumption, which are not considered in a 10 year average, the fact that migration is not considered in the model and thus restrict the spatial variation, and that our functional group cannot resolve species and stage specific spatial and temporal variations like e.g. the increase in larval biomass in spring and changes in species composition. On the other hand, the approach from Maar et al. (2014) reveals uncertainties due to the fact that only parts of the North Sea fish assemblage is considered and that the fish biomass is prescribed and not dynamically coupled to zooplankton biomass. Considering the uncertainties in both approaches the comparison is actually quite good in both magnitude and spatial structure.

Action: We suggest adding Suppl. Figure 1, (which also shows biomass specific zooplankton mortality due to macrobenthos), and a related discussion to the manuscript.

The discussion and conclusions sound reasonable to me, I would support them. The only

exception is that I would not present total fish biomass as a model result, since it might be quite sensitive to the feeding efficiency which is poorly confined for the “average fish” I guess? I would rather interpret fish biomass as a tuning parameter which you have to fit to ensure that the ratio between predation mortality and background mortality is reasonable. In this way, quite simple measured quantities like total fish biomass and fishing mortality can be used to confine the zooplankton mortality, which was an arbitrary closure term before your extension.

Daewel et al.: We agree that showing total fish biomass as a model result is a bit critical in this context. On the other hand this is one of the few possibilities to confirm that the model is able to estimate reasonable results in terms of magnitude and distribution, otherwise it will certainly be difficult to show that the approach actually improves the formulation of the predation mortality for zooplankton. So we would rather leave that part in the ms. We have added the scenarios simulations to the manuscript to identify the sensitivity of the results. However, we suggest clarifying the uncertainty of the variable more thoroughly in the ms, together with the response to general remark 1 below.

General remarks:

1.) You say you can interpret the fish functional group as a “fish production potential”. In principle it is clear what you mean: Where there is food, there will be fish who eat it. You are not interested in where they will migrate afterwards, but you keep the fish biomass locally as a kind of bookkeeping of what the fish consumed here. However, see a few issues with this interpretation:

· Zooplankton or macrobenthos will not be consumed if the fish just “potentially” grow.

So, the loss terms for these functional groups contradict this interpretation.

· Consumption of food by fish is limited by local fish biomass in the model. A “fish production potential” in reality could be larger, since fish from remote locations could migrate towards a spot of high prey abundance, which might lead to more efficient food consumption. I would like a clearer discussion of why neither of the two interpretations (fish biomass / fish production potential) is entirely correct.

Daewel et al.: Yes we agree with the reviewer, this needs to be clarified in the ms. We will add the following explanation to the method section: “In the following, we will thus refer to “fish” as a functional group that comprises the fish biomass that emerges based on the lower trophic production at each horizontal grid cell. For clarification it needs to be noted that, even when called “fish production potential”, the fish biomass is a state variable in the model that interacts dynamically with the lower trophic level components and that will be used in the following to confirm the model's ability to simulate spatial and temporal pattern of carbon transfer to higher trophic levels. On the other hand by constraining the horizontal migration capabilities of the fish group to one grid cell we will likely underestimate the local fish production potential by confining it to the locally available fish biomass.”

2.) Your extension has a very low computational cost. Not only is it just two state variables that are added, but also these are 2-d only which saves their advection, and the advection of the state variables is the most time consuming step. So your extension is especially suitable for LTL models which are simple by purpose, e.g. because they are used in long-term climate simulations where computational load is critical. You could highlight that even more.

Daewel et al.: Yes thank you. We will add this more clearly to the conclusion section.

3.) You mix up British and American English, e.g. P1L20: “analysed”, P1L24: “summarizes”. Please be consistent. –will be changed

4.) Also, please be consistent with “3d” vs. “3-d” / “end-to-end” vs. “End-to-End”. –will be changed

5.) Please capitalise “Figure 4” etc. – will be changed

6.) Commas are often missing in sentences which do not start with the subject, please add them. – we will correct where commas are missing

Specific comments:

P1L20: “the observed pattern” -> “the observed patterns”? -ok

P1L26: “pattern agree” -> “patterns agree”? -ok

P2L10: “The differentiation of trophic levels” -> hard to understand what exactly you mean, can you rephrase? – Right! Changed to : “the separation of trophic levels ...”

P2L11: Citation missing in reference list. - added

P2L26: Please explain “foodweb models” as opposed to end-2-end models

Daewel et al: Here, a food web model is a model that resolves a complex food web on the basis of species or very specific functional groups. In principle a food web model does not necessarily need to be End-2-End. However the model Atlantis is both a food web model and End-2-End. We will make that more clear in the ms.

P2L31: “based on environmental condition” -> “based on environmental conditions”? –will be changed

P2L31: “excluded” -> “excludes”? - will be changed

P3L25: “relative low” -> “relatively low”? - will be changed

P4L16-17: This is not a complete sentence. –combined with previous sentence

P4L21-22: Please cite Neumann and Schernewski (2008) who invented this approach in the model world. – will be added to the ms

P5L2-3: “with additional restriction as” -> “with the additional restriction that”?- will be changed

P5L8,10: Please use different symbols for the velocity vector and its vertical component. – will be changed

P5L10: A_v needs italics here. Actually, italics are missing a few times in this section when variables appear in the text. Please check. – will be changed

P5L15: “RC” needs formatting. -will be changed

P5L25: “the MB menu” -> “the MB diet”? – will be changed

P6L2: I suggest the use of X' instead of X to make clear it has nothing to do with the X in line 1. – The X in line 2 is the same X as in line 1. However, X was not clarified in the text. We suggest modifying the text as follows:

“Grazing rates GMB on prey type X ($X \in [Z_1; Z_2; P_1; P_2; DET; DOM; SED1]$) are estimated using ...”

P6L29: To be precise, the vertical integral of equation 1 reduces to the equation given in the text. Equation 1 itself would still keep a vertical migration term ($C w_m(z)$), even if the vertical migration velocity $w_m(z)$ is only known implicitly.

Daewel et al: Yes right that is not explained correctly. We suggest changing the sentence to: “Following those three principles implies that equation 1 is simplified to $\frac{\partial C_{Fi}}{\partial t} + w_m(z) \frac{\partial C_{Fi}}{\partial z} = R_{Fi}$, where $w_m(z)$ is the vertical migration speed, which is given implicitly by the dynamical vertical distribution of the fish biomass in dependence of the vertical prey distribution. ...”

P7L13: Does this consumption even occur in anoxic layers? – No, fish consumption is confined to oxic conditions. We will add the information to the ms.

P7L14: There is no respiration of fish in the model? You rather treat fish respiration as an excretion and subsequent detritus mineralisation? Could you state this explicitly?

Daewel et al: The term excretion loss is related to respiration of MB and fish does not include fecal excretion. It is considered directly as a source of dissolved inorganic nutrient (PO_4/NH_4 in principle also DIC if that were a state variable of

the model)(see table 4 in the ms). See also explanation to P13L30-31 below. We will clarify that in the ms.

P7L20: In your formulation, TK is always equal to 1/273.15 because T/T cancels out. This is certainly not correct.

Daewel et al: You are right. Thanks for pointing this out. The equation given here is not correct. Will be changed to: $\epsilon_{Fi} = \mu_{Fi} e^{\left(\frac{\theta_{Fi}}{k} * TK\right)}$; $TK = \frac{T-T_0}{T * T_0}$ with T is given in °K and $T_0=273.15$ °K.

P7L28-29: Which food web did the study consider? I assume this value differs a lot between different seas/regions. – The food web of the North Sea is considered in the study. - information will be added to the ms

P7L31: “is considerable higher” -> “is considerably higher with”? –will be changed

P7L31: Please state more explicitly that intraguild predation in zooplankton does not need to be represented in the model since it is not stage-resolving. – will be added to the ms.

P8L21-27: Could you add a reference to the hydrodynamic model you used and the atmospheric forcing dataset? – We will add more details to the setup paragraph.

P9L2: “at each of the location” -> “at each location” / “at each of the locations”? - will be changed

P9L9: “on” -> “onto” - will be changed

P10L6: “equals” -> “equals to” -changed

P13L9: “concrete” -> “actual”? -changed

P13L12: “relative small” -> “relatively small”? –changed

P13L11-13: Could you give relative values (in % of average mass)?

Daewel et al: Yes we will give these values. Following a suggestion by reviewer 2 we will also add a discussion on the MB seasonality to a revised version of the ms.

P13L15: A minimum never falls, does it? A function of time falls until it reaches the minimum. – Yes, right. Will be changed to “reaches”

P13L30-31: Macrozoobenthos and fish can feed on their own excretions, since the energy contained in the carbon is not considered, correct? Also, there is no MB or fish respiration in the model, which would convert the organic carbon to DIC. So, there can be an infinite loop in the model where MB feeds and excretes, feeds and excretes, with no need to add energy from primary production. In Section 4 where you discuss future model improvements, could you comment on how to prevent this? I see, besides the way of explicitly defining “nutritional value classes” in detritus, the possibility to limit detritus consumption to ensure that at least a specific percentage of the total diet is fresh (non-detrital) material.

Daewel et al: We understand your concern, but we cannot agree on this conclusion, and fear that the model description might be a bit unclear in that respect. On the one hand only parts of what is consumed can be assimilated while the rest can be considered as fecal excretion (this is probably what the reviewer is referring to). On the other hand the additional loss term for both fish and MB consists of a mortality and an excretion term. The mortality loss and fecal excretion contributes to the detritus pool, while the excretion loss is related to respiration of MB and fish and is considered directly as a source of dissolved inorganic nutrient (PO_4/NH_4 in principle also DIC if that were a state variable of the model)(see table 4 in the ms). Thus the feeding cycle features two specific loss term; i) the excretion term and ii) the remineralization of the dead organic matter, which would prevent the occurrence of such a self-containing feeding chain.

Action: We will clarify these details in the model description of the ms. We also found an error in the last equation of table 4, which will be corrected

P13L33: This is because the North Sea is a tidal sea, correct? I would consider it as helpful for the non-European readers to state this difference here.

Daewel et al: Right, although the differences have been explained in the introduction, it is probably good to make that clear at this point.

Action: we suggest changing the sentence to: " ... presumably due to the fact that a higher percentage of detritus is re-suspended in the tidal influenced, highly turbulent areas of the North Sea."

P13L33: "Zooplankton and Phytoplankton is included" -> "Zooplankton and phytoplankton are included"? - will be changed

P15L5: "zooplankton form" -> "zooplankton forms"? - will be changed

P16L6-9: I would consider this as the main benefit of your model: You can obtain reasonable spatial patterns in zooplankton mortality without requiring data on planktivorous fish abundance. I would point this out already in the abstract and see it as the main point why your approach should be used.

Daewel et al: Thanks for pointing that out. We will follow the suggestion and add this more prominent to the abstract of the revised ms.

P16L12-16: Couldn't you split your model fish into pelagic and demersal "feeding groups" based on their diet-dependent vertical distribution and then compare the spatial patterns?

Daewel et al: We have tried to do so by differentiating between biomass in the water column and in the bottom layer (Suppl. Figure 2). However, clearly this is not directly comparable to the observation, where demersal and pelagic biomass is separated by species not actually by vertical appearance. Additionally the fish in our model has the chance to feed on all food sources at each time step.

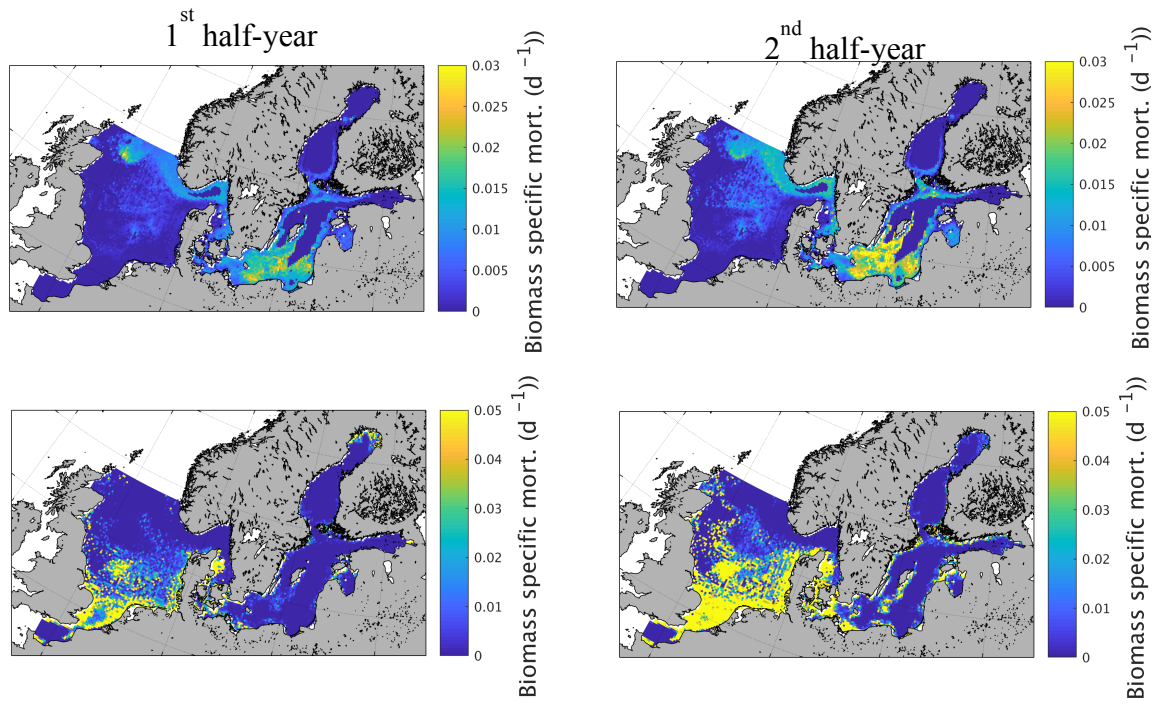
Nonetheless we agree that this comparison can be helpful and thus will include it in a revised version of the manuscript together with a discussion. One thing that becomes quite apparent is, as already suggested in the discussion, that the pelagic fish biomass is underrepresented by the model, since, in contrast to the observations, the bottom biomass exceeds that of the water column biomass. On the other hand, similar to the observation, both stocks contribute to the latitudinal gradient in biomass.

Note that there was a unit error in the original version of the Figure 10d that was corrected in the new figure (Suppl. Figure 2).

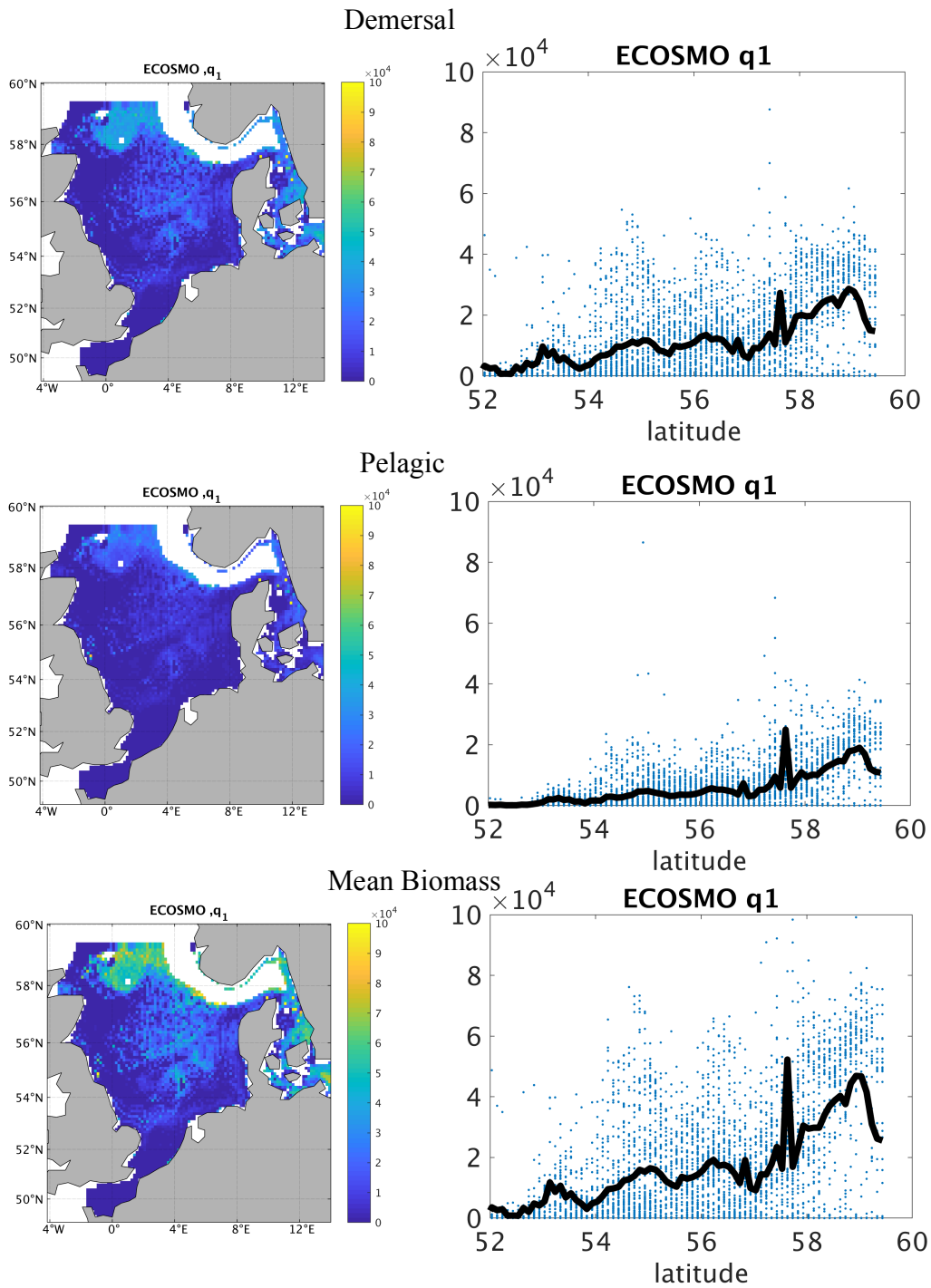
P16L25: What is zero at which boundary? - Here we mean that no fish enters the area through the open boundaries to the North Atlantic by e.g. migration. Action: will be clarified in the ms

P17L8: "fish and MB is resolved" -> "are resolved"? - will be changed

P17L12: "for e.g." -> "e.g.", P18L31: the same - will be changed



Suppl. Figure 1 Half-annually averaged biomass specific mortality (d^{-1}) of zooplankton due to fish predation (upper panels) and macrobenthos predation (lower panels).



Suppl. Figure 2 Mean (1980-1989) total fish biomass as estimated from ECOSMO E2E . For biomass in the bottom layer a), in the pelagic water layers b), and the combined biomass. Left panels: spatial distribution of fish biomass. Right panels: Biomass versus latitude and the mean of biomass at latitude (black line).