

Overall, this is a well written and interesting study linking a classic NPZD model to a single fish compartment. As a fisheries modeller and ecosystem modeller familiar with OSMOSE and Atlantic frameworks, I found the approach useful, however as the authors acknowledge, simplistic in its treatment of fish and fisheries. There is no mention of the impact that fisheries have on the ecosystem until the results section. There should be some introductory material about this as they are the biggest impact on fish populations, as many fisheries reduce more than half of fish biomass as a goal.

Daewel et al: As our model is formulated, fisheries can only be targeted in a very simplistic way. In particular species specific fish stock information are not possible through our functional group type approach. That is the reason why fisheries has not been addressed more extensively in the ms. However, we agree with the reviewer that fishing indeed plays an important role for the fish biomass in both ecosystems, North Sea and Baltic Sea, and that given additional consideration to the topic might become an additional component of the model (see conclusion). That is why we will follow the reviewer's suggestion and add some relevant sentences to the introduction. "The two systems also differ substantially in terms of ecosystem dynamics. The North Sea is known as a highly productive area inhabited by more than 26 zooplankton taxa (Colebrook et al., 1984) and over 200 fish species (Daan et al., 1990), with highest biomasses distributed among demersal gadoids, flatfish, clupeids and sandeel (*Ammodytes marinus*) (Daan et al., 1990). Consequently the North Sea is economically highly relevant with nine nations fishing in the area with landings of currently about 2 million tons (ICES, 2018b). Compared to the North Sea, species composition in the Baltic Sea is primarily limited by the low salinities and encompasses only a few key players for zooplankton (Möllmann et al., 2000) and fish (Fennel, 2010). Thus, compared to the North Sea, commercial fishing in the Baltic Sea includes only a few stocks with total landings of over 0.6 million tons (ICES, 2018a). Both regions have in common that landings peaked in the 1970s and have substantially (ca 50%) decline since then. Thus fishing has a substantial impact on the overall fish biomass in the region."

I would also like to see a more quantitative approach to calibrating the model to observed biomass of fish and fisheries catches. This data is spatially available, and a difference plot or map showing how well predicted vs observed fish biomasses compare in a spatially explicit analysis would be useful.

Daewel et al: We have deliberately avoided an active calibration of the model. For the following reasons: i) The emerging pattern for fish from our model cannot fully represent the actual observed fish biomass due to the specific restriction applied to the functional group in our model (see methods p6110-15). Therefore a quantitative calibration to observed pattern would not necessarily improve the models parameterization. ii) Other than the reviewer implies, we do not think that the relevant data (spatial distribution of total fish biomass) actually are available, even if our model were to simulate the real overall fish distribution. However, we agree with the reviewer that a spatial comparison to fish distribution is desirable. Therefore we chose to estimate fish biomass from the IBTS surveys (Figure 10a-c), which is the only long-term, consistently sampled dataset on fish available in the region and compared those sampled distributions qualitatively to our estimated distribution (Fig. 10 & discussion in paragraph 3.3). Fisheries catch data are probably not applicable since fishery mortality is not explicitly parameterized in the model. It is quite possible that there are relevant datasets available that we are not aware of and we would be grateful if the reviewer would share this information with us.

I'm also a bit concerned about the huge seasonality in biomass of the macrobenthos, much of which I presume is dominated by macroinvertebrates which don't vary in biomass as much as plankton communities do seasonally. & (page 13, line 11 - Is it reasonable for macrobenthos to vary that much annually? I would have expected there to be a much more constant standing stock similarly to fish. I'm thinking about the macro invertebrate community which doesn't vary that much through time.)

Daewel et al: See also comment above. We think that the reviewer's concern is valid in the way that the one functional group for MB might not adequately address all processes responsible for MB variation. However a comparison to observed seasonality shows that the seasonality for MB can be quite high in both systems. We will thus add a discussion at the respective position in the manuscript.: "This is in line with observations on seasonality of benthic infauna at three different locations in the North Sea published by Reiss and Krönke (2005), who found maximum biomass in late summer. Although the observed seasonality showed the highest magnitude in the German Bight the seasonality was clear at all three locations. The authors concluded that of the potential relevant factors (food availability/quality, water temperature, predation, hydrodynamic stress) food quality plays the major role for infauna seasonality, thus is strongly related to primary production. They also suggest food limitation and predation pressure to be the main processes for decrease in

abundance during winter. The same authors also looked at seasonality in the epibenthic community (Reiss and Krönke, 2004) showing that the epifaunal biomass varies less seasonally, especially in the off shore region, and that the main processes causing seasonal variations are related to migratory behaviour, which is not covered by our model. For the Baltic Sea only very local studies in seasonality of MB are available of which some indicate locally strong seasonality (Anders and Möller, 1983), while in other regions no seasonal changes in biomass were observed due to the dominance of long-lived species (Persson, 1983). In general the comparison to observations indicates that on the one hand the model is able to represent the main seasonality in MB even though epi- and infauna are not separated. On the other hand in future study the consideration of an additional functional group encompassing longer-lived species will be required for addressing MB seasonality more correctly.“

It's not clear to me why the Baltic and North Seas were combined into one model, as they exhibit very different environmental and fish production regimes.

Daewel et al: two reasons: First: Other than species specific models like OSMOSE and ATLANTIS, the methods we propose is based on a generic approach and shall be able to describe in a general way the transfer of matter and energy to the higher trophic levels. The specific advantage is, that it does not depend on species-specific information and the application to two systemically different regimes is in principle possible and a good test to the method and assumptions made here. Second: Even though North Sea and Baltic Sea are very different systems both in physical as well as in biological characteristics, they are dynamically tightly coupled to each other. On the one hand the Baltic Sea dynamics strongly determine the conditions in the Norwegian trench and are thus relevant for simulating the northern North Sea dynamics. On the other hand, the coupling to the North Sea is essential to simulate timing and characteristic of the Major Baltic Inflow events and hence is relevant for the dynamics in the Baltic Sea. Since the model setup used here is computationally relatively cheap and runs quickly, there is no need to separate two systems that are closely interlinked.

I think the closure terms where a lot of fish migration could be happening would be more important to focus on than connecting the two domains.

Daewel et al: As we commented on in the conclusions (ms P19 L5 et sqq.) we are aware that the assumption of “no migration” is a shortcoming of the method and needs to be addressed in continuative studies. It is however beyond the scope of this ms.

I would also like to see a more detailed treatment of fisheries mortality in the model, as this data is readily available and will be a huge driver of fish biomass given the very long exploitation history of the North Sea.

Daewel et al: A better representation of fisheries mortality is desirable but requires developmental work for integrating a dynamical representation of fisheries mortality and is thus beyond the scope of this ms (also see conclusion ms P19 L20 et sqq.).

Intro - You don't describe how this component contributes to the model and how the macrobenthos communities vary in the North and Baltic Seas.

Daewel et al: We agree that this has not been sufficiently addressed in the introduction.

Action: We will add additional information on macrobenthos in the North Sea and Baltic Sea to the introduction section.

Results and Discussion - I suggest separating out your results first and then comparing to other studies. The way the two sections are intertwined makes it difficult to follow.

Daewel et al: We understand the reviewer's opinion. However, it is quite common in complex modeling studies to combine the results and discussion section, to avoid a repetition of major results in a separate discussion section. We thought carefully about the structure and still think that a combined section is more appropriate for this study.

page 2, lines 6-8 - the most common ecosystem models are Ecosim with Ecopath models which organize fish based on a combination of functional groups, species groups, and age-structured of species groups (see Tittensor et al. 2018 GMD).

Daewel et al: Right! A short paragraph on EwE will be included in the introduction.

page 3, lines 16-18 - How can questions about food webs be tested when there is only one fish functional

group? There are different trophic levels of fish that are harvested which exert different controls on the macro food web. For example, forage fish have been shown to be important prey for many higher trophic levels and their exploitation has different effects than harvesting top predators (see Smith et al. 2010 Science).

Daewel et al: We agree that this kind of food-web interactions cannot be addressed by the current formulation of the model. However, the model presented in the ms is a first approach that can be further developed to represent a more complex food web (by e.g. distributing the fish group into separate feeding guilds), which can then be used to address this kind of question. We will make this more clearly in a revised version of the manuscript.

page 4, line 1 - Awkward start to the sentence, suggest restructuring.

Daewel et al: Will be changed to: “Here we present a functional-type, E2E modelling approach, which relates food availability to potential fish growth and biomass distributions. In this manuscript we introduce...”

page 4, lines 16-17 - Awkward sentence, suggest combining with previous sentence in parentheses. – will be changed.

page 6, line 25 - What are the constraints for vertical fish movement based on oxygen and temperature limitations? This is one constraint of using only one fish group as there is a lot of variability among fish species in sensitivity to environmental conditions.

Daewel et al: Fish consumption is constrained by oxygen availability such the fish would not migrate into low oxygen regions. This information was missing in the ms and will be added to the method section. Temperature only plays a role for metabolic rates.

The advantage of the generic functional group approach used in the model is that we simplify a complex community structure (also for phytoplankton and zooplankton) and reduce the information to the basic common features thus avoiding a huge parameter set and data requirements. Still the model is able to simulate relevant ecosystem dynamics.

We will add an additional explanation to the manuscript for clarification.

page 7, lines 17-18 - This sentence can be combined with the previous sentence. –will be changed

page 8, lines 1-12 - What about fisheries mortality on the fish compartment? Was this not included in the model? For the North Sea, this would comprise a significant proportion of total mortality.

Daewel et al: Fisheries has not been included in the reference simulation where mortality accounts for natural mortality and predation losses, which allows us to estimate the undisturbed “fish production potential”. We will clarify this in a revised version of the manuscript. To understand and clarify the impact of additional fisheries mortality we have additionally included the “fisheries scenarios” in the ms.

page 10, lines 11-16 - This is the first mention of fisheries, if they are a component of the model, then they should have been included much earlier in the manuscript. How was the loss rate calculated? Much greater detail about the fisheries data that was used and how this was applied need to be included.

Daewel et al: Since simulating and understanding fisheries impacts on the ecosystem is not (and cannot be, due to the model simplifications applied) the primary research question addressed by the model, fisheries has not been addressed in the reference simulation (see comment above).

Therefore we included the scenarios to understand the effect of fisheries on the results. From estimated biomass and reported fisheries landings (see below our response to *page 12, line 28 - page 13, line 9*) we see that biomass losses due to fisheries are in both regions in the range of 20%-50% of the fish biomass per year. For convenience we decided to receive the fisheries mortality rate by scaling the natural mortality rate ($=0.001\text{d}^{-1}=0.365\text{yr}^{-1}$) with 0.5, 1 & 2. Thus receiving mortality rates that are representative for the bandwidth of the observed fisheries loss rates.

We will add a related explanation to a revised version of the manuscript.

page 10, lines 18-23 - How was this value of 20% less loss rate derived? Any empirical data that supports this value?

Daewel et al: See explanation in the methods section (P7 and paragraph below)

page 12, lines 24-26 - This is a reason why it is important to consider functional groups/species/age classes/size classes when including fish in ecosystem models.

Daewel et al: As in many other models this depends on the research question that should be addressed with the model. If the main aim is indeed to estimated species-specific stock biomass or fisheries landings we agree that the model requires a much greater detail than what we presented

here. On the other hand if the question is related to the overall productivity of the ecosystem, energy and matter transfer processes and long-term variation of the latter, which is aimed for here, a more simplified approach with less data requirements and low computational costs is a helpful method. Of course that causes difficulties when comparing to observations. However, all models (also those that actually resolve species/age/size) are simplifications in a way and a large number of groups comes with a high degree of uncertainty in parameter settings and large computational costs.

page 12, line 28 - page 13, line 9 - How do the fish biomass estimates compare to reported fisheries landings from the regions? Is there enough biomass to support known landings?

Daewel et al: Following ICES, fisheries during the 1980's were in the range of 0.7-1. Million tons in the Baltic Sea and 2-3 million tons in North Sea. Despite that the model underestimates fish production due to the no horizontal migration assumption and no fish migration over the lateral boundaries, the models estimates of fish biomass in the North Sea 5.13-10.27 mill tons and 3.47-6.93 mill tons would support the fisheries landing during that time. We will add explanations in the revised manuscript.

page 14, line 13 - You haven't introduced this analysis in the methods section to describe what it is.

Daewel et al: We understand the need for a more detailed description of the method. Since the method has been in detail introduced in an earlier manuscript, we suggest adding the method description to the ms as follows: The EOF analysis is a statistical method to understand major modes of variability in multidimensional data fields. A detailed description on how this method has been applied is given in Daewel et al. (2015): "The annual values of the spatially explicit variable field form a $N \times M$ matrix χ (N : number of years; M : number of wet grid points). The empirical modes are given by the K eigenvectors of the covariance matrix with non-zero eigenvalues. Those modes are temporally constant and have the spatially variable pattern $p_k(m=1, \dots, M)$ where $k=1, \dots, K$. The time evolution $A_k(t=1, \dots, N)$ of each mode can then be obtained by projecting $p_k(m)$ onto the original data field χ such that $\chi(t, m) = \sum_{k=1}^K p_k(m) A_k(t)$. In the following we will refer to $A_k(t)$ as the principal components (PC) and to $p_k(m)$ as empirical orthogonal function (EOF). The percentage of the variance of the field χ explained by mode k is determined by the respective eigenvalues and is referred to as the global explained variance $\eta_g(k)$. Before using the method to analyse the spatiotemporal dynamics of the field, the data were demeaned (to account for the variability only) and normalized (to allow an analysis of the variability independent of its amplitude). The identified modes are not necessarily equally significant in all grid points of the data field. Thus, the local explained variance $\eta_{local,k}(m)$ could provide additional information about the regional relevance of an EOF mode and the corresponding PC in percent:

$$\eta_{local}^k(m) = \left[1 - \frac{\text{Var}(\chi(m,t) - p^k(m)A^k(t))}{\text{Var}(\chi(m,t))} \right] \cdot 100, \quad (12)$$

where $\text{Var}(X) = \sum_{t=1}^N (\bar{X} - X(t))^2$ denotes the variance of the field $X(t)$."

New references

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