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Title: Responses of summer phytoplankton biomass to changes in top-down forcing: Insights from comparative modelling

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Abstract: The present study describes the responses of summer phytoplankton biomass to changes in top-down forcing (expressed as zooplankton mortality) in three ecosystems (the North Sea, the Baltic Sea and the Nordic Seas) across different 3D ecosystem models. In each of the model set-ups, we applied the same changes in the magnitude of mortality (±20%) of the highest trophic zooplankton level (Z1). Model results showed overall dampened responses of phytoplankton relative to Z1 biomass. Phytoplankton responses varied depending on the food web structure and trophic coupling represented in the models. Hence, a priori model assumptions were found to influence cascades and pathways in model estimates and, thus, become highly relevant when examining ecosystem pressures such as fishing and climate change. Especially, the different roles and parameterizations of additional zooplankton groups grazed by Z1, and their importance for the outcome, emphasized the need for better calibration data. Spatial variability was high within each model indicating that physics (hydrodynamics and temperature) and nutrient dynamics also play vital roles for ecosystem responses to top-down effects. In conclusion, the model comparison indicated that changes in top-down forcing in combination with the modelled food-web structure affect summer phytoplankton biomass and, thereby, indirectly influence water quality of the systems

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To the editor of Ecological Modelling

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Submission of revised research article

Please receive the revised manuscript entitled “Responses of summer phytoplankton biomass to changes in top-down forcing: Insights from comparative modelling” by the authors Marie Maar (MM), M. Butenschön (MB), U. Daewel (UD), A. Eggert (AE), W. Fan (WF), S.S. Hjøllo (SSH), M. Hufnagl (MH), M. Huret (MHU), R. Ji (RJ), G. Lacroix (GL), M.A. Peck (MAP), H. Radtke (HR), S. Sailley (SS), M. Sinerchia (MS), M.D. Skogen (MDS), M. Travers-Trolet (MTT), T. Troost (TT), and K. van de Wolfshaar (KW).

We thank the referee’s and editor for their constructive suggestions and we have accordingly revised the manuscript. The major changes are highlighted below and further detailed replies can be found in the attached document:

- The highlights have been modified to better describe the innovations of the study
- The conceptual diagrams of all models are shown in figure 2
- Equations/forcing variables have been better explained to the reader
- Result and discussion sections have been separated
- The new discussion is more clearly comparing the results with other studies on trophic cascades
- A new table 2 is now included giving an overview of the previous data and time periods used for model validation and the findings are discussed

The manuscript is original and not under consideration in any other journal. There are no conflicts of interest. We have tried to accommodate all the suggested changes and hope the revised manuscript will be considered for publication.

Kind regards

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Reply to reviews MS No ECOMOD 17-700.

We have highlighted ours answers as red text in the sections below.

Reply to reviewer 1:

MS No ECOMOD 17-700

RESPONSES OF SUMMER PHYTOPLANKTON BIOMASS TO CHANGES IN TOP DOWN FORCING: INSIGHTS FROM COMPARATIVE MODELLING.

The paper considered four types of food web models (applying the same zooplankton mortality across seven models covering three different domains) and studied the response of summer phytoplankton biomass to changes in top -down forcing on lower trophic levels. For these the authors mainly used three different equations. The following questions/discussions/clarifications are needed to be solved: thank, we have tried to clarify the points below.

a) **On page 10, state the derivation of eqn. 1, in at least some lines clearly, for example, mentioning i) parameter SCE is what for etc.** This is already stated in the line above the equation in section 2.5: 'The response of each PFT was estimated as the relative change (ΔC) in biomass between the scenarios (*SCE*) and the Baseline (*B*) normalized by the change in forcing (*F*=0.20)', **ii) why B in the denominator etc.** because the equation '(SCE-B)/B' is the difference in biomass between the scenario (SCE) and the Baseline (B) relative to the biomass in B **, iii) why biomass of Z1 directly affect the forcing** The Z1 group corresponds to the highest trophic level, and constitutes the group for which the +/- 20% change in background mortality was applied in the "top-down" scenarios-therefore Z1 is directly affected by the change in forcing as already explained in lines 57-61, p.7 (submitted version). We have now clarified this further by modifying the following line in section 2.5: 'For the zooplankton group Z1, the relative change of biomass will inform on the direct effect of the change of the forcing (mortality of Z1)'. **& iv) for other groups these values indirectly effect the forcing F?** Because they were not directly affected by the change in mortality of the highest trophic level Z1, but only indirectly through changes in fx grazing pressure from Z1. We have now modified the following line in section 2.5: 'For other groups, these values will inform about the indirect effect of the forcing (fx change in grazing pressure from Z1) and the dampening role of the food web structure complexity'.

On page 11, i) negative values of L-ratios of eqn. 2 indicate a top-down forcing via skipped level transmission, then how they are related to parameter F in eqn. 1 -'F' was used to normalise 'the relative change of biomass' to the constant change in mortality of Z1 (F='0.20', without a sign) in eq.1. Hence, there is no relation between L-ratios and F. It is already stated that: 'L-ratios were used to estimate the ratios of ΔCs between each predator and its prey for all trophic links' (which all were normalised by F in eq.1). **, ii) in case of direct gazing what will be the value of L** in most cases negative due to direct grazing pressure from Z1 on different phytoplankton groups (P1, P2 etc), but in some cases positive for some of the phyto-PFTs (but not all), if there is competition between several phytoplankton groups for nutrients, which is beneficial for one of the phytoplankton groups, eg in DELFT3D (figure 2A). This was discussed in line 22, p. 14 (submitted version). We have now modified the following lines in section 2.5: 'Hence, food web type 1 models with one zoo-PFT (1 trophic link) can only show a direct grazing response, which in most cases would lead to a negative $L_{P,Z}$-ratio.

However, it is possible that changes in grazing pressure on different phytoplankton groups competing for a limiting nutrient will favor certain phytoplankton groups and in this case result in a positive $L_{P,Z}$-ratio (Wollrab et al. 2012)'**., iii) it is not clear from eqn. 3, how for negative TC-ratios , Z1 & PHY change in opposite direction. Similarly clarify the other statements below the eqn. 3.** ΔC_{PHY} and ΔC_{Z1} were estimated from eq. 1 and therefore have a sign according to their change. If ΔC_{PHY} was positive and ΔC_{Z1} was negative, the TC-ratio will be negative. If both ΔC_{PHY} and ΔC_{Z1}were positive, the TC-ratio was positive and so on. We have modified the following lines in section 2.5: 'Finally, the trophic cascade (*TC*) -ratio was used to estimate the cascade strength of total phytoplankton biomass (*PHY*) in relation to changes in the highest zooplankton trophic level (*Z1*) based on the estimated ΔC_{PHY} and ΔC_{Z1} from eq. 1.'

b) **Page 12, how it follows from eqn. 3 that TC-ratios is negative, when both Z1 & PHY are negatives. –**yes, good point. This is complicated and has to do with averaging procedure and none-linearity of model responses. When you calculate the TC-ratio for each month and each grid cell and then take the average, you may get another value when calculating the TC-ratio from the overall mean of ΔC_{PHY} and ΔC_{Z1}. This is only the case with the ECOSMO model, but as you can see in figure 5D, this model has a very patchy response and this causes the negative TC-ratio (although the overall mean of Z1 and PHY are both negative and would give a positive overall mean TC-ratio). However, we think it is more appropriate to estimate the TC-ratio for each month/grid cell and then take the average, because it is a more direct estimate and also reflects the spatial patterns. We have inserted the following lines in the result section 3.1: 'ECOSMO-NS (P20) also gave a negative *TC*-ratio during the averaging procedure (months and grid cells) despite the negative signs of both ΔC_{Z1} and ΔC_{PHY} on total average (Table 4) probably due to non-linear responses in the food web'.

c) **Page 13, trophic cascades is due to negative TC -ratios, whereas on page 11, trophic cascade is due to negative L-ratios. So, there is some relation between them and what is that?** The L-ratios are the changes between each trophic link (Z's and P's) and the number of links varies between the models. The TC-ratio is the change of total phytoplankton biomass (= P1+P2+P3+P4) relative to the change of Z1, and hence a measure of the trophic cascade from highest to lowest trophic level. The TC-ratio depends on the strength of the individual L-ratios, because some of them will reinforce and others will attenuate the overall phytoplankton biomass response to changes in Z1 mortality.

d) **On page 16, as spatial variability of phytoplankton responses varies with different areas, then it may possible to write down some equations involving L, F, T, or nutrient N.** It would probably be possible to do a further analysis of the driving factors behind the different spatial responses. However, it is important to remember that the applied models are mechanistic descriptions of ecosystem dynamics and the observed patterns are responses to complex interactions of nutrient inputs, grazing interactions, etc. and not like statistical models, where the responses are based on simple empirical relationships. Hence, it would be a substantial task outside the scope of the current study and something that should be considered in a new, separate study.

For complex food web models like types 3 & 4, by parameters in eqns. 1 to 3, it seems not possible to predict the impact of human-induced pressures on the trophodynamics of ecosystems locally or globally, then the conclusion of the present study how far be valid whenever most ecosystems consist of 4 or more food web types including higher trophic levels is a serious question. Still the present study indicates this is also important. Moreover, it is

revealed in this paper that the dynamics of second or more zooplanktons are important factors for top-down forcing impact on lower trophic levels. Yes, we agree. It is not straightforward to predict these changes to human-induced pressures and the model structure (eg the second zooplankton group) is important for the outcome.

Reply to reviewer 2:

- We excuse for the problems with line numbering, but this is due to the editorial system and not something we could change during the submission
- Highlights: we have tried to modify the highlights and hope there is more innovation of the study now
- Abstract: we have deleted the part of the sentence with positive/negative responses.
- Introduction, the first paragraph is now divided into two new sections as suggested.
- Latin abbreviations have been corrected to italics except for citations (*et al*.), because this will be automatically corrected during the editorial process.
- Introduction: the reference to Table 1 has been deleted.
- M&M: the time periods for all models are described on p.5, line 16 (submitted version). The years are 2002-2004 or 2003-2005, hence the years are similar and should not affect the conclusions of the model scenarios. It is said in the M&M section 2.1: 'The modelled period in Baseline and top-down scenarios covered a period of 3 years from 2003-2005 for most models except for HBM-ERGOM and POLCOMS-ERSEM using the years 2002-2004'.
- M&M: the reviewer ask for more background information about the model assumptions concerning the validation. We have therefore added a new table 2 explaining the kind of data used in the previous model validations and time periods for the validations. This was an interesting exercise and the results from the new table is now discussed in relation to the difference in zooplankton PFTs between models. We have inserted the following lines in section 4.1: 'An accurate model parameterization of this PFT is challenging without the necessary calibration data. This issue is also reflected in the relatively few attempts to validate the biomass of different zoo-PFTs based on available national monitoring-, research- and 'other' data sets (Table 2). For the Z1-PFT (often assumed to represent copepods), more data sets from e.g. the Continuous Plankton Recorder (Pitois & Fox 2006), national monitoring data and research data were available allowing a validation of Z1 biomass in most models (Table 2).'
- Results & discussion sections are now separate according to the suggestions.
- Figure 4 now has colours as suggested.

Highlights

- We applied the same change in top-down forcing to different 3D ecosystem models
- Phytoplankton showed dampened responses compared to the highest trophic level
- The roles of different zooplankton groups were important for the outcome
- Environmental conditions affected the spatial variability of phytoplankton responses
- Summer phytoplankton biomass was affected by changes in top-down forcing
- A priori model assumptions should be considered when examining ecosystem pressures

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Responses of summer phytoplankton biomass to changes in top-down forcing: Insights from comparative modelling

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Key words: plankton functional types; trophic cascades; zooplankton mortality; phytoplankton; ensemble modelling

Running head: Phytoplankton responses to top-down forcing

Abstract

The present study describes the responses of summer phytoplankton biomass to changes in top-down forcing (expressed as zooplankton mortality) in three ecosystems (the North Sea, the Baltic Sea and the Nordic Seas) across different 3D ecosystem models. In each of the model set-ups, we applied the same changes in the magnitude of mortality (±20%) of the highest trophic zooplankton level (Z1). Model results showed overall dampened responses of phytoplankton relative to Z1 biomass. Phytoplankton responses varied depending on the food web structure and trophic coupling represented in the models. Hence, a priori model assumptions were found to influence cascades and pathways in model estimates and, thus, become highly relevant when examining ecosystem pressures such as fishing and climate change. Especially, the different roles and parameterizations of additional zooplankton groups grazed by Z1, and their importance for the outcome, emphasized the need for better calibration data. Spatial variability was high within each model indicating that physics (hydrodynamics and temperature) and nutrient dynamics also play vital roles for ecosystem responses to top-down effects. In conclusion, the model comparison indicated that changes in top-down forcing in combination with the modelled food-web structure affect summer phytoplankton biomass and, thereby, indirectly influence water quality of the systems.

1. **Introduction**

Overfishing, pollution or destruction of habitats combined with climate change impose pressures on marine food webs and it is challenging to predict how changes in the strength of these human-induced pressures will impact on the trophodynamic structure and function of ecosystems (Polis et al. 2000, Shurin et al. 2002, Heath et al. 2014). Top-down forcing is defined as the regulation of lower food-web components by an upper-level predator (Pace et al. 1999). Trophic cascades occur when pressures change the biomass of one trophic level and thereby the strength of the top-down forcing across more than one trophic link in a food web (Cury et al. 2003, Huse et al. 2012). The strong decline in populations of large top-predators observed in coastal and oceanic waters and corresponding changes in top-down forcing may have severe consequences for ecosystem function (Myers & Worm 2003, Scheffer et al. 2005). Examples of top-down controlled systems are the Black Sea, the Eastern Scotian shelf off Canada and the Baltic Sea, where overfishing of the top predators directly affected the whole food web from planktivorous fish to primary producers and resulted in higher summer phytoplankton biomass (Frank et al. 2005, Casini et al. 2008, Möllmann et al. 2008, Llope et al. 2011).

High phytoplankton biomass is normally a sign of eutrophication caused by nutrient enrichment (bottom-up control) and summer phytoplankton biomass is used as an indicator of water quality in the HELCOM Baltic Sea Action Plan (HELCOM 2013). Top-down forced trophic cascades may thereby contribute to the eutrophication status and work against the goal to achieve a good ecological status in coastal and open waters according to the EU Water Framework Directive (2000/60/EC) and the EU Marine Strategy Framework Directive (2008/56/EC). On the other hand, it has been suggested that changes in fishing pressure on selected species could in turn decrease summer phytoplankton biomass and improve water clarity, as seen in lakes and some coastal ecosystems (Carpenter et al. 1985, Hansson et al. 1998, Lindegren et al. 2010, Petersen et al. 2017). Hence, knowledge on trophodynamics is important when formulating guidelines to sustainably manage fisheries as well as meet other management goals such as to maintain high water quality (Frank et al. 2007).

Responses to changes in top-down forcing often emerge as ‘skipped-level-transmission’, *i.e.* different directions of change between adjacent trophic levels (Casini et al. 2008, Heath et al. 2014). The strength of the response is often dampened by each trophic level due to various compensatory mechanisms that regulate internal food-web dynamics and structure (McCann et al. 1998a, Pace et al. 1999, Shurin et al. 2002, Andersen & Pedersen 2010). The compensatory mechanisms include replacement of the affected species, regulation through density-dependent grazing pressure and loss of energy due to respiration, cannibalism and other types of mortality (Mccann et al. 1998b, Andersen & Pedersen 2010). Trophic cascades are transitory and dynamic phenomenon and, hence, exhibit variation in their strength and duration both within and between systems, the latter due to ecosystem-specific differences in food web dynamics and structure (Cury et al. 2003).

Food web models have become an important tool in examining how reductions in specific predators or prey impact on other ecosystem components (Travers et al. 2007, Daewel et al. 2014, Peck et al. 2018). A general framework and theoretical description of the different types of food web responses that can be expected in relation to changes in trophodynamic controls was provided by Cury et al. (2003). Further, theoretical modelling has produced simple rules for how perturbations at upper trophic levels can affect the strength of potential trophic cascades within specific ecosystems (Mccann et al. 1998b, Leibold et al. 2004, Wollrab et al. 2012, Heath et al. 2014). Although these models take into account trophic complexity, they do not account for any local spatio-temporal variability of the ecosystem, which may affect predator-prey interactions and, hence, trophic cascades (Frank et al. 2007, Schulz et al. 2007, Travers & Shin 2010). To fully and more realistically resolve the emergence of trophic responses in the plankton community, spatially- and temporally-explicit models are required which include both hydrodynamics and biogeochemical processes.

Ecosystem models of lower trophic levels depict nutrient cycling and dynamics of plankton functional types (PFTs) including primary producers and grazers with different life strategies and sizes (Blackford et al. 2004, Daewel et al. 2014). In these models, the zooplankton community ranges from unicellular fast-growing microorganisms to multicellular meso- and macrozooplankton (*e.g*. copepods, krill) with longer generation times, but the community is often reduced to one or a few zoo-PFTs (Maar et al. 2011, Butenschön et al. 2016). Mesozooplankton (carnivorous or omnivorous) represents, in most cases, the highest trophic level and mortality on this group represents a closure term for nutrient and carbon fluxes. A background mortality (encompassing natural mortality, predation, cannibalism, diseases, etc.) is often applied as a linear, quadratic or saturation function assuming that *e.g.* higher densities of zooplankton will lead to more or less strong habitat limitation effects, might attract potential predators or will increase the likelihood of infections (Edwards & Yool 2000, Fulton et al. 2003). Although different 3D ecosystem models may seem very similar, there can be important differences in their assumptions (*e.g.* food web structure, physiological rates, prey preferences, mortality terms) and underlying hydrodynamics, which may lead to different responses of the PFTs to changes in forcing (Fulton et al. 2003, Skogen & Moll 2005, Mitra & Davis 2010, Sailley et al. 2013). Most previous ecosystem model inter-comparisons have focused on changes in environmental drivers such as nutrient loads and climate change on water quality (e.g. Lenhart et al. 2010, Meier et al. 2012a, Skogen et al. 2014). A few studies have focused on the sensitivity of lower trophic levels to different formulations of predator-prey interactions, and the strength and complexity of zooplankton grazing dynamics (Anderson et al. 2013, Hashioka et al. 2013, Sailley et al. 2013, Le Quéré et al. 2016). These studies showed that food web dynamics, especially the predator-prey interactions, are very sensitive to the model formulations and gave different results of phytoplankton biomass within the same area. However, to our knowledge, there has not been a comprehensive model inter-comparison study of lower trophic level responses to the same change of mortality at the highest zooplankton trophic level.

In a first step towards using ecosystem models to describe potential trophic cascades at the base of the food web induced by changes in top-down forcing, the present study applied the same zooplankton mortality scenarios across seven, previously validated 3D ecosystem models. The ecosystem models represented four types of food webs based on their trophic structure and interactions and covered three areas. The aim of the study was to predict the response of summer phytoplankton biomass to changes in top-down forcing i) among models within the same area (the North Sea or the Baltic Sea) and ii) across areas using the same model (*i.e.* the North Sea versus the Baltic Sea and the North Sea versus the Nordic Seas). The variability was expected to be high within areas due to differences in model formulation and across areas due to differences in ecosystem dynamics.

2. Methods and Material

2.1. Approach

We compared simulation results across seven different 3D models covering three different domains in the NE Atlantic Ocean (Figure 1) yielding 10 model set-ups in total (Table 1). The models considered in this study have been thoroughly described and validated in the list of papers given in Table 1. The data sources and time periods used for model validations are shown in Table 2. Hence, only the directly relevant features concerning the model food-web structure are outlined here (Figure 2). The models were set-up for a “Baseline” (corresponding to the published set-ups) and two “top-down” scenarios representing changes in the background mortality (model closure term) of the highest trophic level named ‘Z1’. The background mortality term encompasses a range of processes and was described either as: linear = $c \cdot Z1$, quadratic = $c \cdot Z1^2$, and saturation = $c \cdot Z1 \cdot Z1/(\mathrm{Z1}+k)$ functions, where c is the closure term constant and *k* is the mortality half-saturation constant (Table 1). The closure term constant (*c*) was changed by +/- 20% in the P20 and M20 scenarios, respectively, which is within the natural variability of zooplankton mortality (Ji et al. 2013, Maar et al. 2014). In some models, other mortality terms such as cannibalism or death due to anoxia were explicitly described, but remained at their baseline values in the scenarios. The modelled period in Baseline and top-down scenarios covered a period of 3 years from 2003-2005 for most models except for HBM-ERGOM and POLCOMS-ERSEM using the years 2002-2004. The spin-up time varied from 2 to 10 years depending on the model.

2.2. Study areas

The three different domains covered by the models were: A) the North Sea (Delft3D-GEM, NORWECOM-NS, MIRO&CO, ECOSMO-NS, HBM-ERGOM-NS, POLCOMS-ERSEM), B) the Baltic Sea (MOM-ERGOM, ECOSMO-BS, HBM-ERGOM-BS) and C) the Nordic Seas (NORWECOM-NO) (Figure 1). Hence, the North Sea was covered by six models, the Baltic Sea by three models and the Nordic Seas by one model. The domains of the North Sea models were not identical, but outputs were estimated for the same area corresponding to the model domain of DELFT3D-GEM (-3.2-9.0°E, 49.3 -56.7°N) except for the MIRO&CO model, which only covered the southern part of the North Sea (extracted for 49.3-52.5°N). The model results for the Baltic Sea were extracted from the same area (11.0-30.3°E, 54.0-65.9°N). The Nordic Seas model domain covered the Greenland Sea, the Iceland Sea, the Norwegian Sea and the Barents Sea (-30.0-60.0°E, 61.3-80.0°N).

2.3. Model descriptions

For simplicity and ease of comparison among model responses to changes in top-down forcing, we only considered phyto- and zoo-PFTs and ignored grazing on bacteria and detritus in the analysis (Figure 2). The zoo-PFTs and phyto-PFTs were labelled as Z1-3 and P1-4, respectively, depending on the number of PFTs in each model. The Z1 group corresponds to the highest trophic level, and constitutes the group for which the +/- 20% change in background mortality was applied in the “top-down” scenarios. Nutrient uptake by the phyto-PFTs was also simplified to competition for one resource (*e.g.* nitrogen or phosphorous) in the schematic representations in Figure 2. In all models, the diet of each zoo-PFT was determined dynamically by the relative abundances of its prey, but weighted with statically defined food preference factors (Table 3). In most models, there were no differences in the quality (C:N:P-ratio) of prey for zooplankton growth; in the Delft3D-GEM and POLCOMS-ERSEM, however, prey stoichiometry could vary with time, space and/or species, which could influence zooplankton growth. Complexity of the models was defined by i) the number of trophic links (L) per number of PFTs (L/S) and ii) connectance ($C=L/S^2$) *i.e.* the ratio of trophic links over the number of possible links (Dunne et al. 2002). Among the models, four types of food webs were depicted based on the trophic structure and interactions (Figure 2, Table 1):

Food web type 1: One zoo-PFT (Z1) grazes on several phyto-PFTs with low L/S and low connectance in DELFT3D-GEM and MOM-ERGOM (Figure 2A).

In Delft3D-GEM (the North Sea), zooplankton (Z1) feeds on diatoms (P1), photoautotrophic flagellates (P2), the colony-forming *Phaeocystis* (P3) and dinoflagellates (P4) with different prey preferences (Table 3). The background mortality is a saturation function of the Z1 biomass.

In MOM-ERGOM (the Baltic Sea), zooplankton (Z1) feeds on diatoms (P1) and photoautotrophic flagellates (P2) with equal prey preferences and on diazotophic cyanobacteria (P3) with lower preference (Table 3). The background mortality is a quadratic function of the Z1 biomass and a loss term due to hypoxia is expressed as increased respiration.

Food web type 2: Two zoo-PFTs and several phyto-PFTs interact with low L/S and low connectance as applied in the models NORWECOM (-NO, -NS) and MIRO&CO (Figure 2B).

In NORWECOM (the North Sea and the Nordic Seas), omnivorous mesozooplankton (Z1) feeds on diatoms (P1) and microzooplankton (Z2), while microzooplankton feeds on photoautotrophic flagellates (P2), all with equal prey preferences (Table 3). The background mortality is a saturation function of the Z1 biomass.

In MIRO&CO (the southern North Sea), omnivorous mesozooplankton (Z1) feeds on diatoms (P1) and microzooplankton (Z2), while microzooplankton feeds on photoautotrophic nanoflagellates (P2), all with equal prey preferences (Table 3). *Phaeocystis* colonies (P3) are not grazed, but can be disrupted into single edible cells (P2). The background mortality is a quadratic function of the Z1 biomass.

Food web type 3: Two zoo-PFTs and three phyto-PFTs interacts with intermediate *L*/*S* and high connectance in the models ECOSMO and HBM-ERGOM (Figure 2C).

In ECOSMO (the North Sea and Baltic Sea), omnivorous zooplankton feeds on diatoms (P1), photoautotrophic flagellates (P2), diazotophic cyanobacteria (P3) and on herbivorous zooplankton (Z2), while Z2 feeds on all phyto-PFTs with different prey preferences (Table 3). The background mortality is a linear function of the Z1 biomass.

In HBM-ERGOM (the North Sea and the Baltic Sea), omnivorous mesozooplankton feeds on diatoms (P1), photoautotrophic flagellates (P2), diazotophic cyanobacteria (P3) and microzooplankton (Z2), while Z2 grazes on the three phyto-PFTs. Prey preferences are lower for diazotophic cyanobacteria and Z2 than for the other PFTs (Table 3). Background mortality is described as a saturation function of the Z1 biomass and mortality due to cannibalism and hypoxia was explicitly described for both zoo-FTPs.

Food web type 4: Three zoo-PFTs and four phyto-PFTS interact with high *L*/*S* and intermediate connectance in POLCOMS-ERSEM (Figure 2D).

POLCOMS-ERSEM (the North Sea) includes omnivores mesozooplankton (Z1), microzooplankton (Z2) and heterotrophic flagellates (Z3), diatoms (P1), microphytoplankton (P2), nanophytoplankton (P3) and picophytoplankton (P4) with complex predator-prey interactions and different prey preferences (Table 3, Figure 2D). The background mortality is a linear function of the Z1 biomass and cannibalism is explicitly resolved as part of the predation for all three zoo-FTPs.

2.5. Model output

Average plankton biomass was calculated from model outputs for the summer period (June to September) in the upper 50 m of the water column. The response of each PFT was estimated as the relative change (Δ*C*) in biomass between the mortality scenarios (*SCE*) and the Baseline (*B*) with respect to the Baseline value and normalized by the change in forcing (*F*=0.20) (Petersen et al. 2017):

$$\Delta C_{PFT} = \frac{(SCE - B)}{B \times F} \qquad (1)$$

An absolute value <1 indicates that the response is smaller than the impact, whereas an absolute value >1 means that the impact is amplified by the system. For the zooplankton group Z1, the relative change of biomass will inform on the direct effect of the change of the forcing (mortality of Z1). For other groups, these values will inform about the indirect effect of the forcing (fx change in grazing pressure from Z1) and the dampening role of the food web structure complexity. Total summer phytoplankton biomass (PHY) was estimated as the sum of all phyto-PFTs (P1+P2+P3+P4). In addition, for an inter-model and inter-region comparison, we aggregated the individual model values of ΔC_{PHY} for i) the same area over different models and ii) the same model over different areas. From that, we calculated the median ΔC_{PHY} (due to skewness of data) as a measure for the typical food web response and the data range (=maximum-minimum) as a measure of the variability of ΔC_{PHY} between individual models or regions.

In order to evaluate the major responses to changes in top-down forcing (Figure 2), we estimated the ratios of Δ*Cs* (from eq. 1) between each predator and its prey for all trophic links:

$$L_{P,Z} = \frac{\Delta C_{prey}}{\Delta C_{predator}} \qquad (2)$$

We identified those direct links where the ratio was negative (*i.e.* opposite responses of predator and prey), which indicates a top-down forcing via skipped-level transmission (Casini et al. 2008, Heath et al. 2014). These links and their strengths are shown in Figure 2 for each model. The food web response was termed as 'direct grazing' if only 1 trophic link was involved, as a 'trophic cascade' if subsequent trophic links (*e.g.* Z1-Z2-P2) all responded with negative $L_{P,Z}$ –ratios or as 'combined' if it exhibited both direct grazing and trophic cascades. Hence, food web type 1 models with one zoo-PFT (1 trophic link) can only show a direct grazing response, which in most cases would lead to a negative $L_{P,Z}$-ratio. However, it is possible that changes in grazing pressure on different phytoplankton groups competing for a limiting nutrient will favor certain phytoplankton groups and result in a positive $L_{P,Z}$-ratio for some (but not all) phyto-PFTs (Wollrab et al. 2012).

Finally, the trophic cascade (*TC*) -ratio was used to estimate the cascade strength of total phytoplankton biomass (*PHY*) in relation to changes in the highest zooplankton trophic level (*Z1*):

$$TC = \frac{\Delta C_{PHY}}{\Delta C_{Z1}} \qquad (3)$$

based on the estimated ΔC_{PHY} and ΔC_{Z1} from eq. 1. When the *TC*-ratio is negative, *Z1* and *PHY* change in the opposite direction (positive or negative) and vice versa. If the *TC*-ratio is close to one (absolute numbers), the cascade strength is strong with little or no dampening. If the *TC*-ratio is close to zero (*i.e.* low change of ΔC_{PHY}), the cascade is dampened quickly, while a *TC*-ratio larger than one indicates that the cascade is amplified.

3. Results

3.1. Overall responses to top-down forcing

The impact of changes in top-down forcing on summer phytoplankton biomass and different PFTs was analyzed using a high diversity of ecosystem models with different representations of the structure and function of lower trophic levels. First, the highest trophic level, *i.e.* the zoo-PFT Z1 directly impacted by the change in forcing, showed expected responses in the opposite direction than the change in the background mortality across all models (Figure 3A). The global median ΔC_{Z1} value was -0.65 in P20 and 0.73 in M20 for all models and regions (Table 4). The absolute value of ΔC_{Z1} was less than 1 in most model results (14 out of 20) indicating an attenuation of the impact strength despite the direct impact on Z1. Amplification of the Z1-response was found in the type 3 models, *i.e.* ECOSMO-NS-BS (P20 and M20) and HBM-ERGOM-NS-BS (M20).

Second, the indirect effects of changes in top-down forcing were analyzed for trophic levels lower than Z1. Conversely to the direct responses, changes in total summer phytoplankton biomass (ΔC_{PHY}) varied between the models for each scenario, both in direction (positive/negative) and magnitude (Figure 3B). The ΔC_{PHY} showed generally an opposite response direction to that of Z1 except for NORWECOM-NS-NO and ECOSMO-NS (P20). The median of ΔC_{PHY} was 0.10 (range: -0.36 to 0.64) in P20 and -0.11 (range: -0.35 to 0.34) in M20 across all models (Table 4). When comparing zooplankton and phytoplankton relative changes in biomass, the *TC*-ratio (eq. 3) was negative in most cases (*i.e.* opposite responses) except for the NORWECOM models (Figure 3C). ECOSMO-NS (P20) also gave a negative *TC*-ratio during the averaging procedure (months and grid cells) despite the negative signs of both ΔC_{Z1} and ΔC_{PHY} on total average (Table 4) probably due to non-linear responses in the food web. The median *TC*-ratio was

-0.14 (range: -0.67 to 0.48) in P20 and -0.18 (range: -0.58 to 0.32) in M20 (Table 4) and overall -0.17 in both scenarios. Hence, there was a general dampening of the signal from Z1 to phytoplankton biomass.

3.2. Inter-model comparison: The North Sea

3.2.1. Responses between models and food web types

The North Sea was covered by six models (DELFT3D, NORWECOM-NS, MIRO&CO, ECOSMO-NS, HBM-ERGOM-NS and POLCOMS-ERSEM) representing four different types of food webs with median ΔC_{PHY} of 0.06 and -0.15 in P20 and M20, respectively (Table 5). The inter-model variability of ΔC_{PHY} (range=1.00) was high in comparison with the other areas and the overall model variability (Table 5).

In the food web type 1 model (DELFT3D-GEM), there was only one zoo-PFT (Z1) grazing mainly on P1 (diatoms) or P4 (dinoflagellates) with negative $L_{P,Z}$ -ratios (Figure 2A, Table 4). The other two phyto-PFTs (P2 and P3) showed, on the other hand, a positive $L_{P,Z}$ –ratios, because they were influenced by the differentiated grazing pressure and competition for a limiting nutrient. The ΔC_{PHY} values had the same response direction as the North Sea median values, but were slightly higher with 0.23 and -0.25 in P20 and M20, respectively (Table 4, Figure 3A).

The food web type 2 models (NORWECOM-NS and MIRO&CO, Figure 2B) showed the strongest responses in terms of ΔC_{PHY} values and *TC*-ratios (Figure 3B-C). This food web type was characterized by two branches that were looped through the top consumer (Z1) and had a low connectance. Opposed to the other North Sea models, the *TC*-ratios in NORWECOM-NS were positive with 0.32 and 0.48 in P20 and M20, respectively (Table 4). The positive ratios could be explained by a strong trophic cascade in the Z1-Z2-P2 branch (causing the same response direction for Z1 and PHY) compared to a weaker grazing effect in the Z1-P1 branch, probably due to the high overlap of Z2 and P2 biomasses during summer (Figures 2B, 3, 4). The other type 2 model, MIRO&CO in the southern North Sea, showed on the contrary the most negative *TC*-ratios among all the models with -0.58 and -0.67 in P20 and M20, respectively (Table 4). Here, the grazing response observed in the Z1-P1 branch was stronger than in the Z1-Z2-P2 branch (Figure 2B), probably because the P1 (diatom) biomass was higher than for P2 (flagellates) (Figure 4B). There was indication of a bottom-up effect (competition for nutrients) in the P2-Z2 branch, because both were affected in the same direction as Z1 (Figure 2B).

The food web type 3 models were characterized by having two zoo-PFTs and high connectance. ECOSMO-NS showed skewed responses of ΔC_{PHY} with negative values in both scenarios (-0.18 and -0.19 in P20 and M20, respectively) (Table 4). The Z1 PFT (omnivorous zooplankton) dominated the total summer zooplankton biomass (97%) and P2 (flagellates) the total summer phytoplankton biomass (96%) (Figure 4), which allowed different types of model responses to changes in top-down forcing. When the grazing impact by Z1 decreased (P20), this allowed Z2 (herbivorous zooplankton) to increase considerably (ΔC_{Z2}=5.76) and initiated a strong trophic cascade in the Z1-Z2-P2 branch leading to negative ΔC_{PHY} values (same direction between Z1 and PHY). In the opposite situation (M20), the increased grazing pressure by Z1 reduced both Z2 (ΔC_{Z2}=-2.60), P1 and P2 leading to negative ΔC_{PHY} values (opposite direction between Z1 and PHY) (Figure 3, Table 4). In the other food web type 3 model, HBM-ERGOM-NS, the resultant ΔC_{PHYs} were 0.10 and -0.11 in P20 and M20, respectively, and hence less strong than for ECOSMO-NS (Table 4). The major grazer pathways (Z1 grazing on P2 and Z2) were similar to the M20 response in ECOSMO-NS (Figure 3C). The zoo-PFTs were also subject to cannibalism. The Z1 (mesozooplankton) biomass (69% of total zoo-PFTs) and P2 (flagellates) biomass (73% of total phyto-PFTs) also dominated the summer plankton biomasses, but to a lesser extent than in ECOSMO-NS (Figure 4).

In the food web type 4 model (POLCOMS-ERSEM), the predator-prey interactions were the most complex with several major grazer pathways in the scenarios compared to the other food webs (Figure

2D). There was a direct grazing response between Z1 and P2 in addition to trophic cascades in the branches Z1-Z2-P3 and Z1-Z2-Z3, both involving the Z2 group (Figure 3D). In addition, the three zoo-PFTs were subject to cannibalism. The different responses counteracted each other and overall resulted in a weak ΔC_{PHY} of 0.03 and -0.03 in P20 and M20, respectively (Table 4).

3.2.2. Spatial patterns of phytoplankton biomass changes in the North Sea

Spatial patterns of responses (magnitude and direction) in summer phytoplankton biomass (ΔC_{PHY}) to changes in top-down forcing in the North Sea were highly variable between the models (Figure 5). In five of the six North Sea models (DELFT3D-GEM, NORWECOM-NS, MIRO&CO, HBM-ERGOM-NS and POLCOMS-ERSEM), 87-100% of the area showed the same response direction of ΔC_{PHY} in P20 and M20 (Table 6), but with opposite response direction for NORWECOM-NS (as explained before). ECOSMO-NS showed, on the other hand, the highest spatial heterogeneity of ΔC_{PHY} with only 67% and 76% in P20 and M20, respectively, of the areas showing the same (negative) response direction (Figure 5D). The high spatial variability in ECOSMO-NS was due to the competition between two pathways in the food web (Z1-P2 or Z1-Z2-P2), which had different outcomes in different areas. Hence, local areas could have either negative or positive values within the same model and scenario and, hence, not necessarily in the same response direction as the area-averaged result (Figure 3B-C). The strongest responses (either negative or positive) were observed in the German Bight and the English Channel (southeastern shallowest parts) in most models except for POLCOMS-ERSEM with lowest responses in this area.

3.3. Inter-model comparison: The Baltic Sea

The Baltic Sea was covered by three models (MOM-ERGOM, ECOSMO-BS and HBM-ERGOM-BS), which represented two different types of food webs (1 and 3) with ΔC_{PHY} median of 0.11 and -0.11 in P20 and M20, respectively (Table 5). Despite their differences, the three models provided similar results of zooplankton and total phytoplankton changes in the Baltic Sea (Figure 3). The variability of ΔC_{PHY} was relatively low (range=0.33) compared to the North Sea and the overall model variability (Table 5). The overall *TC*-ratios were negative (from -0.09 to -0.19), *i.e.* the opposite response between Z1 and phytoplankton biomass (Table 4). The direct grazing response by Z1 on different phytoplankton prey dominated the models, whereas the trophic cascade through Z2 (food web type 3 models) was weaker (Figures 2A and C). Spatially, the responses were in the same direction in MOM-ERGOM and HBM-ERGOM-BS, whereas in ECOSMO-BS the response was more diverse (Table 6, Figure 6). However, in all three models, the highest changes (ΔC_{PHY}) were estimated in the high productive coastal and shallow areas and in the same response direction (Figure 6).

3.4. Inter-regional model comparison

Three of the models covered two areas; NORWECOM-NS-NO, ECOSMO-NS-BS and HBM-ERGOM-NS-BS. The internal model variability expressed as the range of ΔC_{PHY} within each model (including the two areas) was highest for NORWECOM with the range= 0.70 followed by ECOSMO with the range= 0.38 and lowest for HBM-ERGOM with the range= 0.21 (Table 5). NORWECOM exhibited four to five times stronger responses of ΔC_{PHY} in the North Sea than for the Nordic Seas (Figures 3B, C). The inter-regional variability of ΔC_{PHY} in NORWECOM was lower than the inter-model variability of the North Sea models, but higher than for the Baltic Sea models (Table 5). In ECOSMO, the internal variability of ΔC_{PHY} was higher than for the Baltic Sea models, but lower than for the North Sea models (Figure 3, Table 4). In HBM-ERGOM, variability of ΔC_{PHY} was generally lower than for the Baltic Sea and North Sea models (Figure 3B, C).

4. Discussion

4.1. Top-down mediated trophic cascades

The present study provides new knowledge on the role of top-down mediated trophic cascades and its parameterization in lower trophic level ecosystem models by applying the same top-down scenarios to a wide range of 3D dynamic ecosystem models. The top-down scenarios were expressed as a change in the background mortality of the highest trophic level, Z1, which showed opposite responses to the change in forcing (Figure 3A). In most cases, there was an attenuation of the response by Z1 due to a dilution effect at the open boundaries, other mortality terms (*e.g.* anoxia, cannibalism) or complex food web interactions (*e.g.* bottom-up effects) counterbalancing the top-down effects (Wollrab et al. 2012). Amplification of the Z1-response was found in the type 3 models (*i.e.* ECOSMO and HBM-ERGOM) probably due to positive feedback mechanisms from the trophic cascades in the food web (Wollrab & Diehl 2015). Overall, there was a general dampening of the signal from the highest trophic level (Z1) to phytoplankton biomass (*i.e.* an absolute *TC*-ratio less than one, Figure 3C), which is a common feature of aquatic food webs due to internal trophic interactions (Shurin et al. 2002, Andersen & Pedersen 2010, Heath et al. 2014). However, phytoplankton responses varied in both magnitude and direction (positive/negative) relative to the change in Z1 depending on the food web structure and trophic coupling represented in the models (Figures 2, 3B).

The model results emphasized that the second zooplankton group (Z2) played an important role as mediator of trophic cascades. In most cases, the Z2 exhibited opposite grazing pressures on the phyto-PFTs compared to Z1 (Figure 2, Table 4) and thereby dampened the total phytoplankton biomass responses to changes in Z1 (*i.e*. less negative *TC*-ratio). In NORWECOM, the trophic cascades in the Z1-Z2-P2 branch even overruled the direct grazing pressure by Z1 on phytoplankton biomass and caused a positive *TC*-ratio. The Z2-PFT covers a wide range of species with different sizes, growth rates, prey preference, mixotrophy and feeding strategies (Hansen 1991), which makes it difficult to define them as a functional group and to parameterize the general physiological processes (Anderson et al. 2013, Sailley et al. 2013). According to our model results from NORWECOM, MIRO&CO and HBM-ERGOM, Z2 had a biomass similar to Z1 (31-77% of total), whereas in ECOSMO, Z2 comprised 3% of the zooplankton biomass (Figure 4A). However, the Z2-PFT plays different roles in different models as *e.g.* herbivorous zooplankton in ECOSMO, ciliates and heterotrophic dinoflagellates in HBM-ERGOM and a broader range of microzooplankton in NORWECOM. POLCOMS-ERSEM included both microzooplankton (Z2) and heterotrophic flagellates (Z3), comprising 16% and 28%, respectively, of total zooplankton biomass (Figure 4A). Consequently, a direct comparison of Z2 between models is complicated by the lack of common metrics (Sailley et al. 2013). There is, to our knowledge, no coherent data set on microzooplankton (Z2) for the North Sea and the Baltic Sea (Quéré et al. 2005, Bils et al. 2017). An accurate model parameterization of this PFT is challenging without the necessary calibration data. This issue is reflected in the relatively few attempts to validate the biomass of different zoo-PFTs based on available national monitoring-, research- and ‘other’ data sets (Table 2). For the Z1-PFT (often assumed to represent copepods), more data sets from e.g. the Continuous Plankton Recorder (Pitois & Fox 2006), national monitoring data and research data were available allowing a validation of Z1 biomass in most models (Table 2).

4.2. Effects on summer phytoplankton biomass

The change in summer phytoplankton biomass showed overall opposite responses relative to the change of Z1. Hence, a higher mortality of Z1 (scenario P20) was shown to increase the summer phytoplankton biomass and thereby affect the water quality negatively in marine waters as suggested by previous studies (Frank et al. 2005, Casini et al. 2008, Llope et al. 2011). In the North Sea, a previous model study using size-selective predation by Atlantic herring (*Clupea harengus*), four zoo-PFTs and two phyto-PFTs also found that top-down control should be present in the system (Koslow 1983). However, analysis of field data from 50 years showed no sign of top-down forced trophic cascades affecting the phytoplankton despite intense fishing activities in the North Sea (Koslow 1983, Reid et al. 2000). These studies suggested that trophic cascades in the North Sea disappeared due to ecosystem-wide fishing on most species, that zooplankton was more food limited than predation limited or that complex food web interactions dampened the response (Koslow 1983, Reid et al. 2000, Andersen & Pedersen 2010). For the Baltic Sea, the scenarios results in P20 (decrease of Z1) are consistent with field data over a 30-year period showing that overfishing of cod population directly affected its main prey, European sprat (*Sprattus sprattus*), and indirectly caused a reduction in summer zooplankton and higher summer phytoplankton biomass (Casini et al. 2008, Möllmann et al. 2008). The responses were analyzed with respect to the summer period, but will probably be different other times of the year due the seasonal plankton community succession (*e.g.* the spring diatom bloom) and change in environmental conditions (*e.g.* light, nutrient levels).

4.3. Inter-model comparison: the North Sea

The highest inter-model variability was found for the North Sea covered by six models (Table 5). The inter-model median for the North Sea predicted that changes in top-down forcing could affect the summer phytoplankton biomass although the responses varied in magnitude and direction both spatially and between models. The high variability in model responses was mainly due to the food web type 2 models (NORWECOM-NS and MIRO&CO, Figure 2B), which showed the strongest responses in terms of ΔC_{PHY} values and *TC*-ratios (Figures 3B-C). These models with two branches were very sensitive to top-down forcing, because it was possible for one of the two branches to dominate the response depending on the spatial-seasonal overlap of predator-prey distributions. A dominant trophic cascade response in one of the branches is consistent with theoretical models for an odd-length food chain (McCann et al. 1998a, Cury et al. 2003, Wollrab et al. 2012, Heath et al. 2014). In the food web type 1 model DELFT3D-GEM, the differentiated grazing pressure and competitive ability for a shared nutrient favored some phyto-PFTs on behalf of others in agreement with theoretical models (Wollrab et al. 2012). In food web type 3 models, ECOSMO-NS and HBM-ERGOM-NS, the different model parameterizations of grazing interactions (*e.g.* grazing rates, prey preferences and cannibalism) resulted in a different sensitivity of the lower trophic levels to changes in top-down forcing in P20, whereas the responses in M20 were more similar. The missing trophic cascade in HBM-ERGOM-NS was due to internal attenuation of the signal from top-down forcing by the prescribed cannibalism within Z2 (not present in ECOSMO-NS) indicated by the lower ΔC_{Z2} compared to ECOSMO-NS (Table 4). It was previously demonstrated that inclusion of zooplankton interference (*e.g.* cannibalism) weakened trophic interactions in a theoretical food web model and better matched the patterns found in nature (Mccann et al. 1998b). Hence, the food web type 3 responses were more complex than the more rigid food web types 1 and 2 models and therefore more difficult to predict in relation to changes in top-down forcing. In the food web type 4 model (POLCOMS-ERSEM), the more complex and compensating food web interactions dampened the response to changes in top-down forcing. This is in agreement with previous studies, which showed that increased complexity in model structures stabilized the system with a higher resistance to perturbations (Mccann et al. 1998b, Vallina & Le Quéré 2011, Vallina et al. 2017).

In top-down scenarios, the skipped-level-transmission complicates the prediction of responses at various trophic levels and the choice of model parameters and food web structure becomes even more important and should be appropriate for the study area. In comparison, ecosystem models are expected to give more similar results in bottom-up scenarios (*e.g.* changes in nutrient inputs), because of the direct link between nutrients and phytoplankton and responses typically will be in the same direction as the forcing (Cury et al. 2003, Heath et al. 2014). In addition to the food web definition, additional model components, such as the choice of nutrient cycles, remineralization rates and benthic-pelagic coupling would be indirectly affected by changes in the Z1 mortality and additionally lead to response variability among different ecosystem models. Hence, a priori assumptions on food web structure and parameterization will influence cascades and pathways in model estimates and, thus, become highly relevant when examining ecosystem pressures such as fishing and climate change.

4.4. Spatial patterns

Spatial variability of the phytoplankton responses was generally high in the North Sea and the Baltic Sea indicating that not only the specification of trophic links, but also temperature and nutrient dynamics play vital roles for ecosystem response to top-down effects. Strong horizontal gradients of temperatures and nutrient concentrations are typically found at the interface between coastal and offshore areas. Especially in the North Sea, bathymetric features and strong tides result in the formation of mixed, stratified and frontal regions that are characterized by very different hydrographic features (Otto et al. 1990). Higher temperatures can strengthen trophic interactions since zooplankton respiration increases faster with warming than primary production (Scheffer et al. 2001, Maar & Hansen 2011, Svensson et al. 2017). Likewise, higher nutrient concentrations may strengthen or weaken different grazer pathways and thereby interact with the top-down forced trophic cascades (Wollrab & Diehl 2015, Petersen et al. 2017). Furthermore, spatial variations in top-down responses are also caused by spatial patterns in background mortality in the field (Fulton et al. 2003, Travers et al. 2009, Maar et al. 2014), a feature that could not be investigated by our experimental set-up. These diverse spatial responses make it difficult to support a coherent management plan with respect to sustainable fishing and water quality.

4.5. Inter-regional model comparisons

Strongest responses of NORWECOM were found in the shallow, well-mixed and highly productive southern North Sea (Figure 5C), whereas the phytoplankton responses were lower and more homogenously distributed in the Nordic Seas (Figure 6D). This difference could be related to the higher nutrient inputs and higher temperatures in the North Sea that can strengthen trophic interactions compared to the more nutrient limited, colder and less productive Nordic Seas (Frank et al. 2007, Wollrab & Diehl 2015, Svensson et al. 2017). Hence, the higher variability of the North Sea models and partly the Baltic Sea models compared to the internal model variability still indicates that *a priori* assumptions in the food web structure and dynamics will influence trophic cascades and pathways arising from the same change in top-down forcing (Sailley et al. 2013, Heath et al. 2014). In principle, the model response of a single model can be highly variable in different regions, indicating that ecosystem functioning and hydrographic characteristics, and not only model formulations, were driving the responses to top-down forcing.

4.6. Conclusions

There was a high variability in the responses across models, especially in the North Sea, due to the different food web structures and trophic couplings represented in the models. Especially the role of the zoo-PFTs seems important for the resulting model response to top-down forcing and highlights a challenge in ecosystem modelling. The model-dependent responses to the same forcing demonstrate the uncertainty that arises from simplifying real-world ecosystems into numerically tractable model systems. This needs to be taken into account when confronting models tuned to present-day dynamics using what-if scenarios, *e.g.* by discussing their outcome as a possible, rather than a predicted, reaction of the ecosystem. In the present state of model development, an ensemble of model simulations seems as a reasonable approach to reduce inherent uncertainty in model estimates and provide weight of evidence (Lenhart et al. 2010, Meier et al. 2012b, Queiros et al. 2016, Yun et al. 2017). The behavior of the relatively simple ecosystem models used here, should be compared to potentially more complex behavior and trophic responses of trait-based models, which can include many more groups (or a blending across groups in terms of size-spectrum models) to better understand how changes in top-down forcing may cascade through the plankton community. For a better representation of trophic cascades, the ecosystem models could be coupled to higher trophic level models (*e.g.* fish production models) or provide input to 'End-to-End' models considering food web interactions for all trophic levels including human pressures (Fulton 2010, Shin et al. 2010, Utne et al. 2012).

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Table 1. Overview of the applied models and their domains, food web types (see Figure 2), number of zoo-PFTs, number of total PFTs (*S*) *i.e.* not including resources, number of trophic links (*L*), links per PFT (L/S), connectance (*C*=L/S^2), mesozooplankton background mortality function and model references. The model domains are the North Sea (NS), the Baltic Sea (BS) and the Nordic Seas (NO).

Model name	Model domain	Food web type	Zoo-PFTs	*S*	*L*	*L/S*	*L/S*^{2}	Background mortality	References
DELFT3D-GEM	NS	1	1	5	4	0.80	0.16	saturation	(Los et al. 2008, Blauw et al. 2009, Los & Blaas 2010)
MIRO&CO	S. NS	2	2	5	4	0.80	0.16	quadratic	(Lancelot et al. 2005, Lacroix et al. 2007)
NORWECOM	NS, NO	2	2	4	3	0.75	0.19	saturation	(Aksnes et al. 1995, Skogen et al. 1995, Skogen et al. 2007, Skogen & Mathisen 2009, Hjøllo et al. 2012)
ECOSMO	NS, BS	3	2	5	7	1.40	0.28	linear	(Schrum et al. 2006, Daewel & Schrum 2013, Daewel et al. 2015)
HBM-ERGOM	NS, BS	3	2	5	7	1.40	0.28	saturation	(Maar et al. 2011, 2014, 2016, Petersen et al. 2017)
POLCOMS-ERSEM	NS	4	3	7	12	1.71	0.24	linear	(Lewis et al. 2006, Holt et al. 2012, Saux Picart et al. 2012, Butenschön et al. 2016)
MOM-ERGOM	BS	1	1	4	3	0.75	0.19	quadratic	(Neumann et al. 2002, 2015, 2017)

Table 2. Data sources used for model validation of nutrient concentrations, biomass of different phyto-PFT's, Chl *a* concentration, primary production, biomass of different zoo-PFT's and Z1 biomass. I=ICES data, H=HELCOM data, N=National monitoring data, C=Continuous Plankton Recorder (CPR) data, W=World Ocean Atlas, R= research projects, RS = remote sensing data, L=literature values and O=other data (e.g. PhD project). The last column shows the validation period for the different variables. Validation references are shown in Table 1.

Model name	Nutrients[a]	Phyto-PFT's[b]	Chl a[c]	Primary production[d]	Zoo-PFT's[e]	Z1 biomass[f]	Validation period
DELFT3D-GEM	N, R	N, R	N, R, RS	-	Not relevant	L	a,c) 1975-2012 b) 1998 f) 2008
MIRO&CO	N, R, O	R, O	N, R, O, RS	-	R, O	R, O	a,b,c,e,f) 1989-1999 and a,b,c) 1991-2003
NORWECOM-NS	I, N, R	-	I, N, R	L, R, O	-	-	a, c) 1980-2006, d) 1985-1994
NORWECOM-NO	-	-	N, RS	L	-	N, L	c) 1981-2007, d) 1981-2006, f) 1997-2007
ECOSMO	I, H	I, W	I	L	-	R, C	a,d) 1970-2008, b,c,f) 1984-1986 and f) 1995
HBM-ERGOM	I, H, N, W	-	I, H, N	N	N	N, C	a) 2001-2006, c-d) 2001-2010, e) 2010 and f) 2001-2004
POLCOMS-ERSEM	I, W	C	I, RS, W	L	-	C	a, c) 1970-2004 (I), a, c) 1981-2004 (W), c) 2003-2004 (RS), d) bulk values and b, f) 1988-1989
MOM-ERGOM	I, H, N, R	-	I, H, N	-	Not relevant	-	a) 2008-2013 and b) 1970-2008

Table 3. Prey preferences of the different zoo-PFTs in the food web models (see Figure 2). In some models, the zoo-PFTs are subject to cannibalism.

Predator	Type				Z1							Z2					Z3	
prey		P1	P2	P3	P4	Z1	Z2	Z3	P1	P2	P3	P4	Z2	Z3	P3	P4	Z3
DELFT3D-GEM	1	0.85	0.50	0.10	0.30	-	-	-	-	-	-	-	-	-	-	-	-
MOM-ERGOM	1	1.00	1.00	0.20	-	-	-	-	-	-	-	-	-	-	-	-	-
NORWECOM	2	1.00	0.00	-	-	0.00	1.00	-	0.00	1.00	-	-	0.00	-	-	-	-
MIRO&CO	2	1.00	0.00	0.00	-	0.00	1.00	-	0.00	1.00	0.00	-	0.00	-	-	-	-
ECOSMO	3	0.85	0.10	0.30	-	0.00	0.15	-	0.25	0.70	0.30	-	0.00	-	-	-	-
HBM-ERGOM	3	1.00	1.00	0.20	-	0.40	0.40	-	1.00	1.00	0.20	-	0.40	-	-	-	-
POLCOMS-ERSEM	4	0.15	0.15	0.05	0.00	0.25	0.25	0.05	0.15	0.10	0.15	0.15	0.15	0.20	0.15	0.25	0.15

Table 4. The ΔC for each PFT and TC-ratios in scenarios P20 (top) and M20 (bottom) averaged from June to September in the upper 50 m and the median for all models.

P20 scenario	Domain	Food web type	ΔC_{Z1}	ΔC_{Z2}	ΔC_{Z3}	ΔC_{ZOO}	ΔC_{P1}	ΔC_{P2}	ΔC_{P3}	ΔC_{P4}	ΔC_{PHY}	TC-ratio
DELFT3D-GEM	NS	1	-0.70	-	-	-0.70	0.47	0.17	-0.39	0.10	0.23	-0.24
MIRO&CO	S. NS	2	-0.21	-0.50	-	-0.24	3.90	-0.86	-1.28	0.18	0.64	-0.67
NORWECOM	NS	2	-0.60	0.59	-	-0.01	0.16	-0.43	-	-	-0.36	0.48
ECOSMO	NS	3	-1.50	5.76	-	-1.01	2.51	-0.41	0.00	-	-0.18	-0.03
HBM-ERGOM	NS	3	-0.89	0.50	-	-0.45	0.06	0.12	0.00	-	0.10	-0.12
POLCOMS-ERSEM	NS	4	-0.22	0.29	-0.10	-0.09	0.02	0.21	-0.09	-0.05	0.03	-0.21
MOM-ERGOM	BS	1	-0.49	-	-	-0.49	-0.10	0.18	0.12	-	0.11	-0.29
ECOSMO	BS	3	-1.75	2.18	-	-1.71	2.90	-0.91	3.62	-	0.19	-0.16
HBM-ERGOM	BS	3	-0.91	0.38	-	-0.40	0.05	0.12	0.12	-	0.09	-0.10
NORWECOM	NO	2	-0.59	0.07	-	-0.09	0.05	-0.08	-	-	-0.07	0.13
P20 median	All		-0.65	0.44	-0.10	-0.42	0.11	0.02	0.01	0.10	0.10	-0.14

M20 scenario	Domain	Food web type	ΔC_{Z1}	ΔC_{Z2}	ΔC_{Z3}	ΔC_{ZOO}	ΔC_{P1}	ΔC_{P2}	ΔC_{P3}	ΔC_{P4}	ΔC_{PHY}	TC-ratio
DELFT3D-GEM	NS	1	0.81	-	-	0.81	-0.08	0.27	0.99	-0.18	-0.25	-0.21
MIRO&CO	S. NS	2	0.29	0.36	-	0.19	-1.72	1.62	1.26	-0.05	-0.35	-0.58
NORWECOM	NS	2	0.54	-0.41	-	0.01	-0.12	0.42	-	-	0.34	0.32
ECOSMO	NS	3	1.85	-2.60	-	1.40	-2.93	-0.11	0.00	-	-0.19	-0.33
HBM-ERGOM	NS	3	1.21	-0.63	-	0.61	-0.07	-0.13	0.00	-	-0.11	-0.10
POLCOMS-ERSEM	NS	4	0.23	-0.27	0.09	0.09	-0.01	-0.21	0.09	0.06	-0.03	-0.18
MOM-ERGOM	BS	1	0.65	-	-	0.65	0.19	-0.19	-0.14	-	-0.11	-0.18
ECOSMO	BS	3	2.86	-2.68	-	2.75	-2.26	1.60	-1.49	-	-0.14	-0.19
HBM-ERGOM	BS	3	1.29	-0.49	-	0.56	-0.07	-0.14	-0.05	-	-0.11	-0.09
NORWECOM	NO	2	0.64	-0.07	-	0.10	-0.07	0.10	-	-	0.08	0.14
M20 median	All		0.73	-0.45	0.09	0.58	-0.08	-0.01	0.00	-0.05	-0.11	-0.18

Table 5. Aggregated ΔC_{PHY} results. The number (*N*) of all results (P20 and M20), the number of models, the median for P20 and M20 and the range=maximum-minimum values for both P20 and M20 for i) each model area and ii) for the models covering two areas.

	N	Number of models	Median P20	Median M20	P20+M20 range
North Sea	12	6	0.06	-0.15	1.00
Baltic Sea	6	3	0.11	-0.11	0.33
Nordic Seas	2	1	-0.07	0.08	0.15
NORWECOM	4	1	-0.21	0.21	0.70
ECOSMO	4	1	0.00	-0.17	0.38
HBM-ERGOM	4	1	0.10	-0.11	0.21
All	20	10	0.10	-0.11	1.00

Table 6. The % of grid cells in the model domains with negative values of ΔC_{PHY} and *TC*-ratio.

Model	Domain	P20 ΔC_{PHY}	M20 ΔC_{PHY}	P20 *TC*-ratio	M20 *TC*-ratio
DELFT3D-GEM	NS	5	95	94	94
MIRO&CO	NS	1	93	86	86
NORWECOM	NS	97	3	6	10
ECOSMO	NS	67	76	32	71
HBM-ERGOM	NS	0	100	100	100
POLCOMS-ERSEM	NS	9	87	91	87
MOM-ERGOM	BS	0	100	100	100
ECOSMO	BS	17	68	83	68
HBM-ERGOM	BS	1	99	99	100
NORWECOM	NO	99	2	2	2

Figure

Figure 1. Maps showing the study areas in the NE Atlantic Ocean (A) and the bathymetry of B) the Nordic Seas (NO), C) the North Sea (NS) and D) the Baltic Sea (BS). Bathymetry was obtained from GEBCO (www.gebco.net) and Natural Earth (www.naturalearthdata.com) datasets.

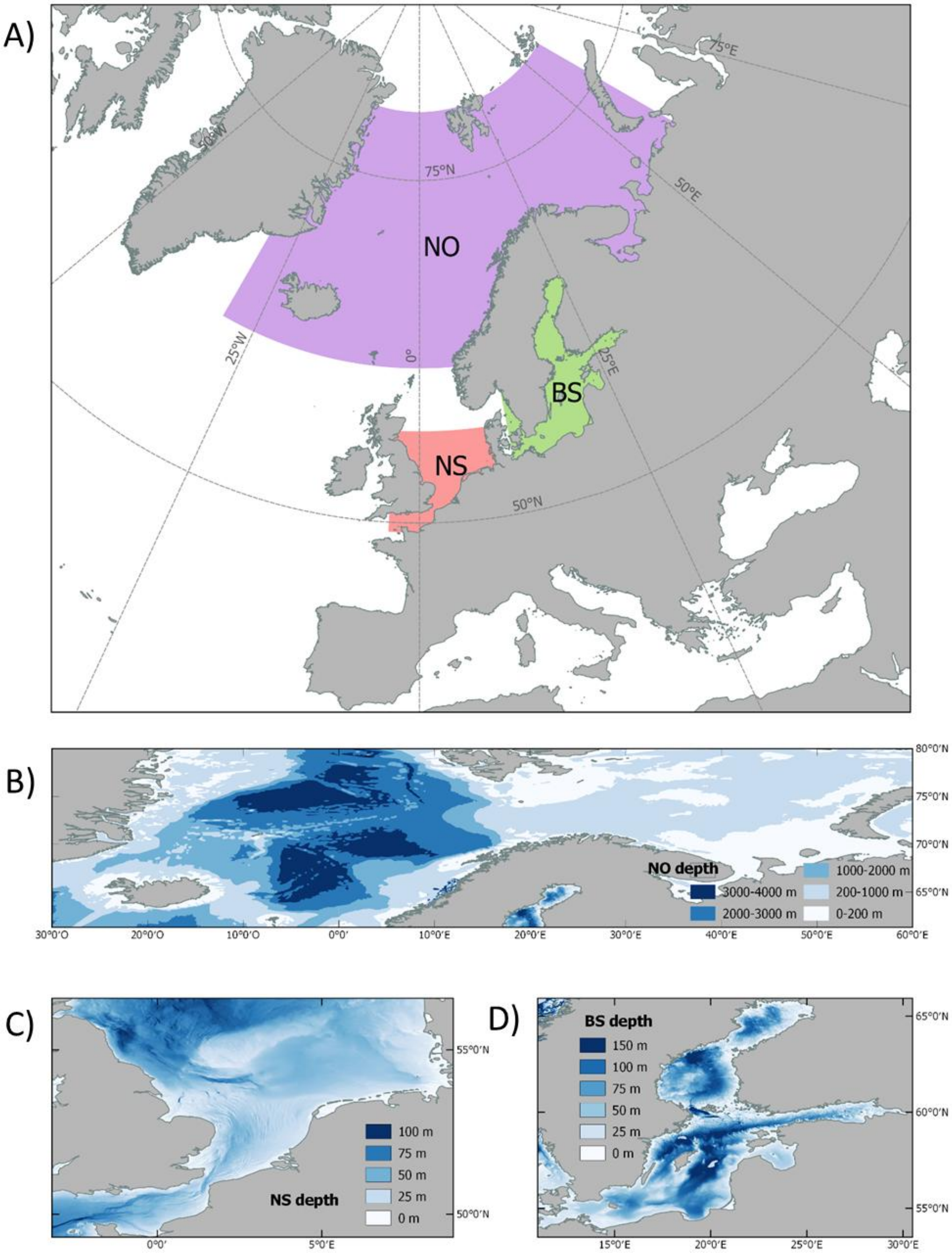

Figure 2. Conceptual diagrams of the four (A-D) food web types applied in the models. Circles indicate the nutrient resource (R) and the different zoo- (Z) and phyto- (P) plankton functional types (PFTs). Arrows show the direction of the energy transfer. The grey arrow at the top indicates the modified background mortality of the highest trophic level (Z1). PFTs and trophic links with highest responses to changes in Z1 mortality are highlighted in bold. PFT responses opposite to that of Z1 are highlighted with grey background.

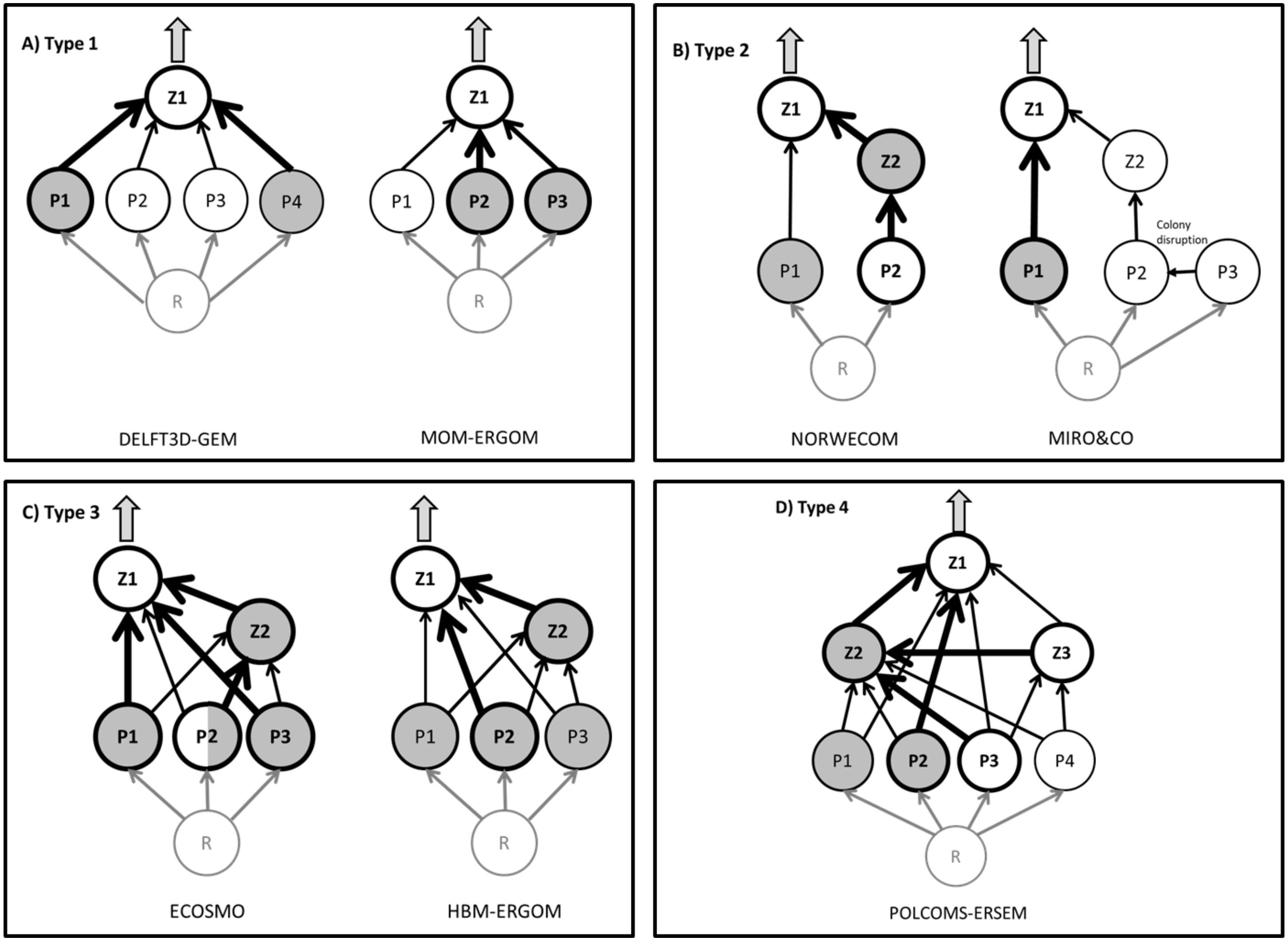

Figure 3. Summer means of A) relative change in the biomass of the highest trophic level (*ΔC_{Z1}*), B) relative change of total phytoplankton biomass (*ΔC_{PHY}*) and C) the *TC*-ratio for the two scenarios (P20 and M20). The vertical separations indicate the different areas and the bottom numbers in A) indicate the food web type.

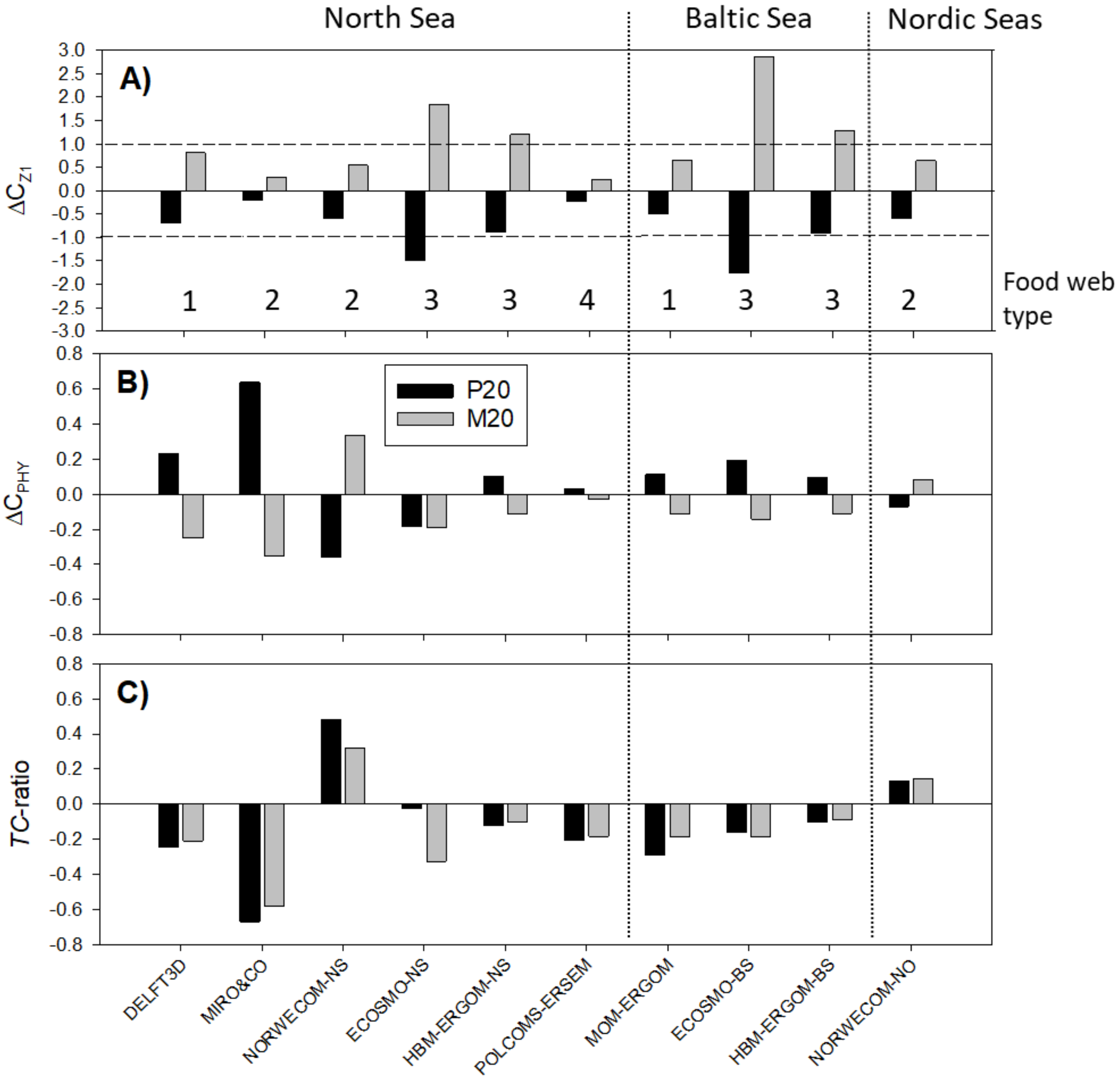

Figure 4. The %-contributions of the different PFTs to total summer biomass of either zooplankton (A) or phytoplankton (B). The vertical separations indicate the different areas.

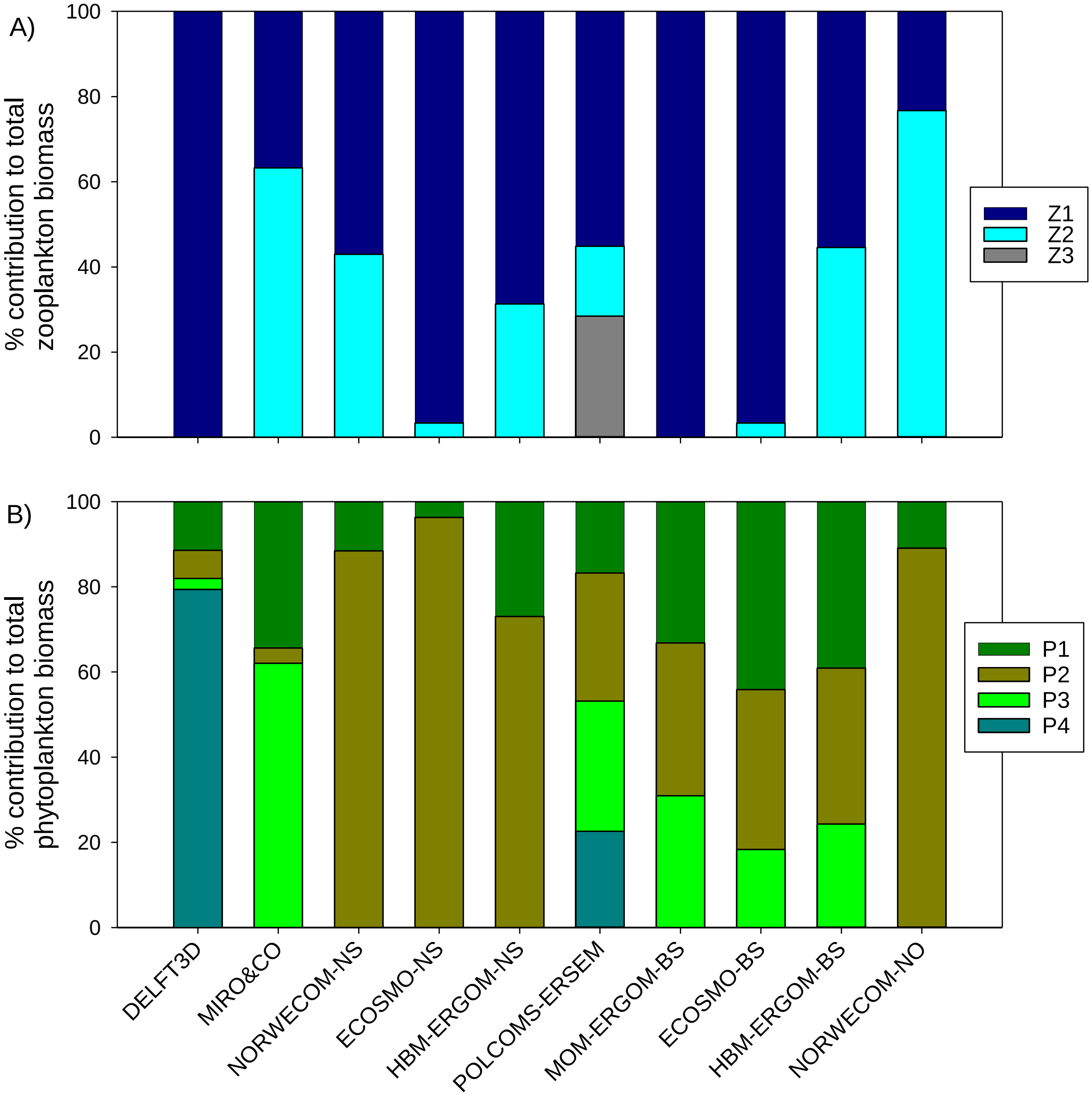

Figure 5. Spatial patterns of ΔC_{PHY} (total summer phytoplankton biomass) in the North Sea models; A) DELFT3D-GEM, B) MIRO&CO, C) NORWECOM-NS, D) ECOSMO-NS), HBM-ERGOM-NS and POLCOMS-ERSEM for the scenarios P20 (left) and M20 (right). Please note the different scales.

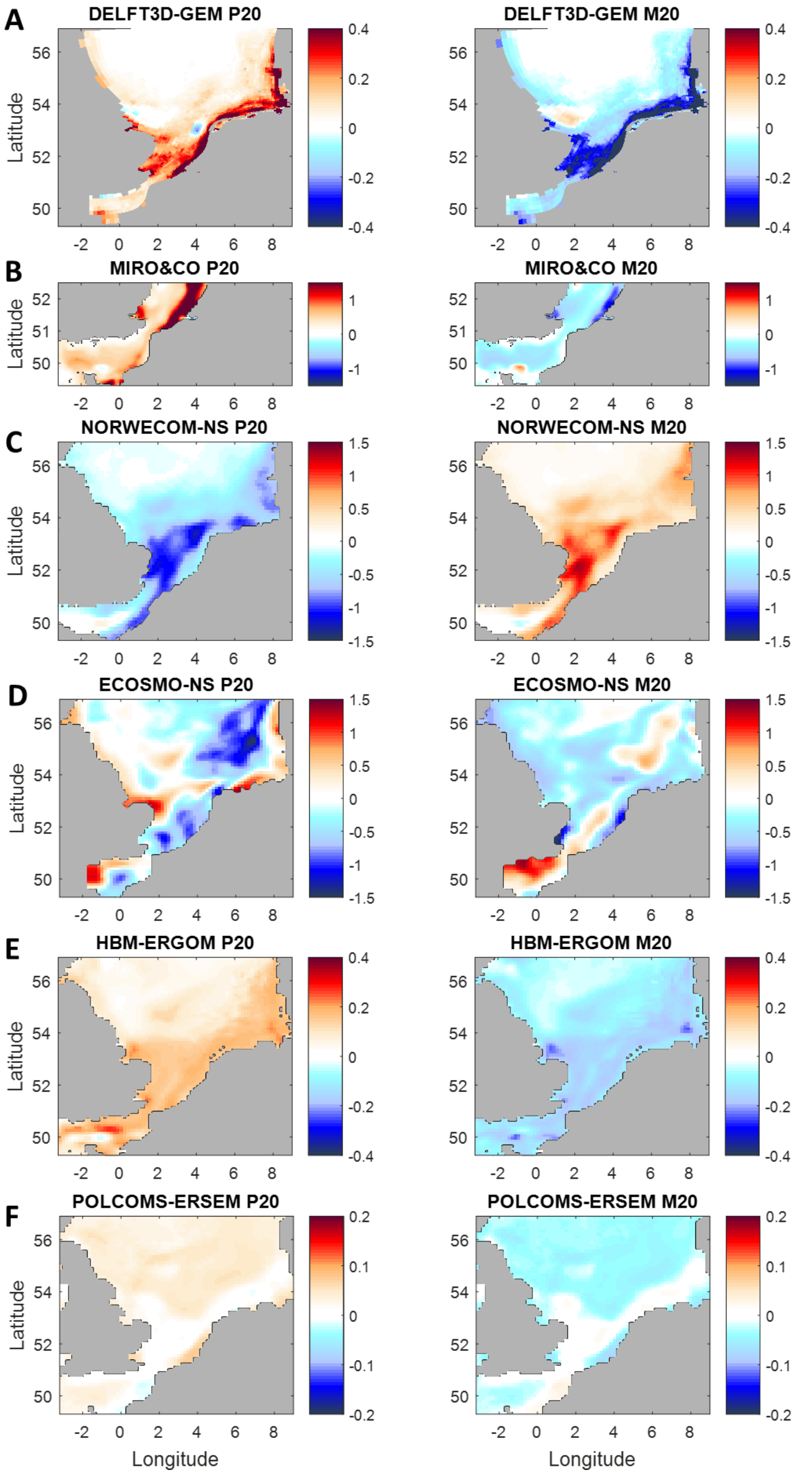

Figure 6. Spatial patterns of ΔC_{PHY} (total summer phytoplankton biomass) in the Baltic Sea models; A) MOM-ERGOM, B) ECOSMO-BS, C) HBM-ERGOM-BS and the Nordic Seas D) NORWECOM-NO for the scenarios P20 (left) and M20 (right). Please note the different scales.