



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 ($\pm 20\%$) 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

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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 and 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 and 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 and 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 and 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 and 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 and Moll, 2005; Mitra and 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 (Fig. 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 (Fig. 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 = $c \cdot Z1 \cdot Z1 / (Z1 + k)$ 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 $\pm 20\%$ 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 to 2005 for most models except for HBM-ERGOM and

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