Comparing food web structures and dynamics across a suite of global marine ecosystem models

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ABSTRACT

Dynamic Green Ocean Models (DGOMs) include different sets of Plankton Functional Types (PFTs) and equations, thus different interactions and food webs. Using four DGOMs (CCSM-BEC, PISCES, NEMURO and PlankTOM5) we explore how predator–prey interactions influence food web dynamics. Using each model's equations and biomass output, interaction strengths (direct and specific) were calculated and the role of zooplankton in modeled food webs examined. In CCSM-BEC the single size-class adaptive zooplankton preys on different phytoplankton groups according to prey availability and food preferences, resulting in a strong top-down control. In PISCES the micro- and meso-zooplankton groups compete for food resources, grazing phytoplankton depending on their availability in a mixture of bottom-up and top-down control. In NEMURO macrozooplankton controls the biomass of other zooplankton PFTs and defines the structure of the food web with a strong top-down control within the zooplankton. In PlankTOM5, competition and predation between micro- and meso-zooplankton along with strong preferences for nanophytoplankton and diatoms, respectively, leads to their mutual exclusion with a mixture of bottom-up and top-down control of the plankton community composition. In each model, the grazing pressure of the zooplankton PFTs and the way it is exerted on their preys may result in the food web dynamics and structure of the model to diverge from the one that was intended when designing the model. Our approach shows that the food web dynamics, in particular the strength of the predator–prey interactions, are driven by the choice of parameters and more specifically the food preferences. Consequently, our findings stress the importance of equation and parameter choice as they define interactions between PFTs and overall food web dynamics (competition, bottom-up or top-down effects). Also, the differences in the simulated food-webs between different models highlight the gap of knowledge for zooplankton rates and predator–prey interactions. In particular, concerted effort is needed to identify the key growth and loss parameters and interactions and quantify them with targeted laboratory experiments in order to bring our understanding of zooplankton at a similar level to phytoplankton.

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1. Introduction

Changes in marine ecosystem structure and functioning, due to anthropogenic greenhouse gas emissions and climate change, have created a need for more detailed marine ecosystem models in order to forecast potential climate and ocean acidification impacts (e.g., changes in biogeochemical cycles, carbon dioxide sinks and sources, biological community composition, Doney et al., 2009a, 2012). Dynamic Green Ocean Models (DGOMs) were developed from the need to understand how changing conditions affect lower trophic marine food-webs (i.e., plankton), and the biogeochemical cycles organisms are linked to. The inclusion of biological complexity and functional diversity has been achieved through the use of Plankton Functional Types (PFTs) for both phytoplankton (pPFT) and zooplankton (zPFT) (Falkowski et al., 2000; Moore et al., 2004; Le Quéré et al., 2005). A PFT can be defined by the role it

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plays in the biogeochemical cycle of specific elements (e.g., diatoms and the silica cycle), and in processes such as remineralization (e.g., bacteria), grazing and export mediated through size class (e.g. microzooplankton versus mesozooplankton PFTs, (Le Quéré et al., 2005)).

Model output (e.g. PFT biomass, distribution, export) is often sensitive to small changes in model parameters (Woods and Thomas, 1999; Fussmann and Balsius, 2005) and the modeled functional forms (Anderson, 2005). In comparison to phytoplankton–zooplankton–nutrient models (NPZD; Fasham et al., 1993), DGOMs present an increase in complexity through a larger number of compartments as well as explicit biogeochemical cycles (e.g. C, N, P, Si). Consequently, there are a greater number of equations and parameters that have to be chosen carefully so as to describe best the group of organisms they represent. Formulations for zooplankton are particularly important in this regard due to their effect on several processes: phytoplankton mortality due to zooplankton grazing, export of carbon through feces production, food sources for higher trophic levels (e.g., larger zooplankton, fish, marine mammals, birds).

However, PFTs and size class are loose guidelines and deciding on the optimal structure of the food web and the functional responses is left to the modeler judgement; this lead to a variety of DGOMs. To understand and map the variety of the existing DGOMs, the MARine Ecosystem Intercomparison Project (MAREMIP, http://maremip.uea.ac.uk) aims at comparing food web functioning in different DGOMs. The DGOMs available in the first stage of the project are CCSM-BEC (Moore et al., 2004; Doney et al., 2009b), PISCES (Aumont and Bopp, 2006), NEMURO (Kishi et al., 2007) and PlankTOM5 (Buitenhuis et al., 2010). The four DGOMs describe marine ecosystems using different PFTs, equations and parameters, which, as stated earlier, significantly impact model outputs (e.g. PFT biomass, export, respiration). As such we have four different ecosystem structure and different ocean physics. We are comparing different integrated systems.

Even when concentrating on the biological part, the definition of PFTs within a model creates flexibility in how they are defined. This is especially true for zooplankton, where generic size class regroup a variety of organisms and behavior. Consequently comparison of zooplankton between models is made difficult by the lack of common metrics. The smallest common denominator for zooplankton is the functional response (grazing equation and parameter value), which impact the model dynamics. However, this was never explored in details as long as the modeled primary production and export are comparable to observations. Thus, comparing both the equations and the outputs of DGOMs is bound to improve our understanding of zooplankton parameterization and its influence on model results beyond agreement with observations.

The goal of this paper is to compare zooplankton and their trophic interactions as well as how they shape the model food web using three model aspects: (i) model parameterization (formulation, maximal rates and food preferences); (ii) the relationship of simulated predator and prey biomasses; and (iii) the interaction strength between PFTs with a focus on predator–prey interactions. The intent is not to establish a ranking of the available models, but look at them with a new set of tool.

2. Methods

2.1. Data

We use PFT biomasses from the available DGOMs (CCSM-BEC, Moore et al., 2004; Doney et al., 2009a,b; PISCES, Aumont and Bopp, 2006; PlankTOM5, Buitenhuis et al., 2010; and NEMURO, Aita

et al., 2007). Data are regridded onto a 360×180 pixels grid and binned into 5×5 degree bins. Annual means of surface data are used to compare PFT biomass. We also use observations of biomass for microzooplankton and mesozooplankton from Buitenhuis et al. (2006, 2010). Detrital particulate organic carbon (POC) is also a food source for zooplankton, but this compartment is neglected, since food preferences for POC are lower than those for pPFT or other zPFT in all models.

2.2. Holling type and Ivlev grazing functional forms

The DGOMs use different grazing functional forms. CCSM-BEC uses a Holling type III (sigmoidal equation; Eq. (1)); PISCES and PlankTOM5 use a Holling type II (Monod equation; Eq. (2)) and NEMURO an Ivlev equation (Eq. (3)):

$$G_{H_3} = g \times T_f \times \frac{F^2}{k^2 + F^2} \tag{1}$$

$$G_{H_2} = g \times T_f \times \frac{F}{k + F} \tag{2}$$

$$G_{Ivlev} = g \times T_f \times (1 - e^{(-F/k)}) \tag{3}$$

G is the specific grazing rate (d^{-1}), g is the maximal grazing rate (d^{-1}) at a reference temperature, T_f is a temperature function, k is the half saturation concentration (mmol C m^{-3}) and F the prey concentration (mmol C m^{-3}). For each of these equations grazing starts to saturate at a prey concentration of about $2k$. The Holling type III equation creates what is called a refuge from grazing at low prey concentration that is absent in the Holling type II equation. The equations used are shown in their basic forms, and additional parameters can be used to include prey preference, grazing threshold or toxicity of the prey (Gentleman et al., 2003).

2.3. DGOMs: equation and parameters

Each of the DGOMs analyzed here includes at least 2 phytoplankton PFTs (Table 1): nanophytoplankton (S, all DGOMs) and diatoms (D, all DGOMs); additional pPFTS are diazotrophs (N, CCSM-BEC) and coccolithophores (C, PlankTOM5). CCSM-BEC only has a single generic zooplankton (Z_G), while PISCES ad PlankTOM5 have two zooplankton PFTs: microzooplankton (Z) and mesozooplankton (M); NEMURO has a third zooplankton PFT: predatory zooplankton or macrozooplankton (P). An analysis of the phytoplankton distribution, dominance patterns and ecological niches is presented in Vogt et al. (in preparation) and an analysis of spring bloom dynamics in Hashioka et al. (under review). Note that the food web structure of each DGOM can be seen in Fig. 12a.

2.3.1. CCSM-BEC

In CCSM-BEC the specific grazing rate equation for Z_G on all three pPFTs (F) uses a Holling type III function (Table 2). CCSM-BEC's zooplankton is generic and food preferences are expressed in the different g^F values depending on pPFT. The scaling factor (f^F) for grazing on diatoms lowers the concentration at which grazing on diatoms reaches its maximum. According to g^F and f^F, zooplankton food preference decreases from nanoflagellates, to diatoms and then diazotrophs.

2.3.2. PISCES

The grazing equation for specific grazing rate (d^{-1}) in PISCES is a Holling type II with prey preferences; the formulation is independent of the prey (F, Table 2). Microzooplankton has a higher maximal grazing rate than mesozooplankton, so at equal biomass the grazing impact of microzooplankton on phytoplankton is higher than that of mesozooplankton. Also, microzooplankton