Competition and community assemblage dynamics within a phytoplankton functional group: Simulation using an eddy-resolving model to disentangle deterministic and random effects

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ABSTRACT

To advance our understanding of competition and coexistence in phytoplankton species within a functional group, such as a diatom group, we developed a numerical model composed of 240 within-tropic-level virtual species that can actually or potentially compete. We then explored how the phytoplankton assembly is structured by deterministic or stochastic processes, where the former process is typically represented using the traditional niche theory and the latter process is highlighted using the neutral theory. Because we used eddy-resolving resolution, phytoplankton dispersion and the resultant dispersal limitation were explicitly represented, where the dispersal limitation prevents the most competitive species from using its appropriate niche and subsequently enhances stochastic effects. In the simulation results, all surviving species have an oceanic volume in which the phytoplankton species has the highest specific growth rate in all the 240 species. The abundance in the most competitive space has a strong positive correlation with the relative species abundance. Moreover, of the phytoplankton types whose abundances in the most competitive space are nearly equal, the survival of a species is affected by its residence time within its habitat; the surviving phytoplankton species tend to have larger residence times compared to the non-persistent species. These results led us to conclude that deterministic processes had significant contributions to a formation of phytoplankton assembly. This was supported by the result that a structure of phytoplankton assembly represented by species rank in abundance was invariant with time and hardly dependent on initial conditions of phytoplankton composition.

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1. Introduction

In marine phytoplankton communities, a broad diversity of taxonomic groups and high species diversity in a taxonomic group have been revealed by observational studies. A conservative approach estimates that there are 72,500 algal species and 12,000 described species of diatoms with a further 8000 diatom species to be discovered (Guiry, 2012). In the ecology community, ecologists have explored how relative species abundances are structured, which can be a useful index to represent the within-trophic-level diversity of a biological community that actually or potentially competes for the same resources. It has long been debated whether deterministic or random processes contribute to relative species abundance in natural communities. In the traditional niche theory

(Gause, 1934; Macarthur, 1970; Levin, 1970), all species differ in important ways, and hence, each species is limited by a unique set of factors. The resource ratio hypothesis (Tilman, 1985) demonstrates that the difference in the nutrient utilization ration among species enables species to coexist, where the upper limit of the number of coexisting species is determined by the number of nutrients. Chesson and Warner (1981) demonstrated the storage effect, where different species-specific responses in time-varying environments result in species coexistence. Following the niche theory, relative species abundance is governed by deterministic processes. Conversely, an emphasis on random stochastic processes is typically represented in the neutral theory of biodiversity (Hubbell, 2001). The neutral theory considers ecological communities as a continuously changing, non-equilibrium assemblage of species with their relative abundances governed by random stochastic processes. Dispersal limitation, or recruiting limitation (Tilman, 1994; Ehrlén and Eriksson, 2000), is thought to play a significant role (Hurtt and Pacala, 1995; Hubbell, 2001; Gravel et al., 2006) in determining the

relative contribution of deterministic and random processes. In the example case of a forest, a site released by the death of an individual is not necessarily occupied by the most competitive species if a seed of the most competitive species does not reach that site. Therefore, if dispersal limitation is strong, random processes become important rather than the deterministic processes primarily caused by species competition. It is likely that both deterministic and random processes contribute to relative species abundances, and their relative contribution will be different for a wide variety of biological communities including plants, animals, and oceanic planktons.

In studies of phytoplankton diversity, deterministic processes are usually focused on rather than random processes. Deterministic mechanisms enabling coexistence have been proposed in previous studies (Litchman and Klausmeier, 2008), e.g., species-specific responses to temperature (Eppley, 1972; Raven and Geider, 1988) and zooplankton prey preferences, including the kill-the-winner mechanism (Thingstad and Lignell, 1997; Thingstad, 2000) and size-selective grazing (Armstrong, 2003; Petchey et al., 2008; Fuchs and Franks, 2010; Wirtz, 2013). Plankton functional type group models represent the coexistence of several functional groups (Moore et al., 2004; Aumont and Bopp, 2006; Aita et al., 2007; Buitenhuis et al., 2010), and a typical model is composed of small phytoplankton, diatoms, and nitrogen fixers. Nitrogen fixers can coexist with other taxonomic groups because of the differences in the requisite nutrients in a multinutrient environment. The coexistence of diatoms and small phytoplankton has been achieved in multiple models, even though the mechanisms for their coexistence differ between models (Hashioka et al., 2013). The DARWIN model (Follows et al., 2007; Dutkiewicz et al., 2009; Barton et al., 2010; Clayton et al., 2013) offers a basis for a comprehensive description of global oceanic phytoplankton diversity and is composed of 78 seeded phytoplankton types across several taxonomic groups and two zooplanktons. The model simultaneously simulates coexistence across both phytoplankton functional groups, as in plankton functional models, and within each functional group.

We focused on the competition and assemblage dynamics within a phytoplankton functional type. Our approach is a step toward understanding the competition and coexistence of the over-10,000 diatom species (Guiry, 2012) or among the vast numbers of species in other taxonomical groups. In an oceanic phytoplankton community, at the same trophic level competing for common resources, how is the relative species abundance structured by deterministic or random process? To answer this question, we developed a simple model composed of a few hundred phytoplankton belonging to a common functional group with only one nutrient and one predator, which does not include coexistence mechanisms caused by different requisite nutrients in a multinutrient environment or multiple predators with grazing preferences. That is, the prescribed coexisting mechanisms as in a plankton functional model were excluded, where such mechanisms enable phytoplankton to coexist in a 0D homogeneous environment. We concentrated on how different species-specific responses to spatiotemporally varying physical and biological conditions structure the phytoplankton assembly and tried to find general rules regulating the relative species abundances. The other significant characteristic of our model is that it has eddy-resolving resolution, and subsequently, can explicitly represent the dispersion processes of phytoplankton via advection and diffusion. As mentioned in the previous paragraph, dispersion processes are crucial in determining whether a biological community is a niche or random assembly. If the dispersal of phytoplankton is not unlimited, a phytoplankton species would not fully use its appropriate niche, and subsequently, be dominated by random processes. These random processes are represented in our model because the mesoscale eddies disperse the phytoplankton species in random directions. Note that oceanic dispersion has no trade-off between competitive ability and disper-

sal ability, while in landscape vegetation, a trade-off (Tilman, 1994; Levine and Rees, 2002) related to seed size (Ehrlén and Eriksson, 2000) exists.

2. Model and design of the experiments

2.1. Physical model

An idealized subtropical and subpolar circulation with seasonal temperature variability was simulated in our model. We used an OGCM, Meteorological Research Institute Community Ocean Model (MRI.COM) developed at the Meteorological Research Institute of the Japan Meteorological Agency (Tsujino et al., 2010). The rectangular model domain is 0° E–30° E, 25° N–55° N with a flat bottom at a depth of 2000 m. The horizontal resolution is 0.1° by 0.1° to permit the explicit representation of mesoscale eddies. An idealized simple model was used instead of a realistic global model for the following reasons. First, we needed to reconcile a few hundred variables representing phytoplankton with explicit representations of phytoplankton dispersion by mesoscale eddies, where the huge computational costs preclude a global eddy-resolving model with a few hundred phytoplankton. Second, for our research interest in the competition and coexistence of phytoplankton, a few hundred phytoplankton were needed to exhibit the different responses to the physically and biologically variable environments, and such a spatiotemporal environmental variation is sufficiently represented in our simple model, which does not require a realistic geometry. The model has 40 vertical layers, of which the upper 20 layers have the same thickness of 10 m under the condition that the sea surface height variation is zero. Salinity was constant at 34.5 psu. The horizontal viscosity was calculated using the biharmonic Smagorinsky scheme (Griffies and Hallberg, 2000). For the vertical viscosity, the K-profile parameterization of Large et al. (1994) was applied with a constant background diffusion coefficient of $0.1\ cm^2/s^2$. The model was forced with an idealized wind stress (Fig. 1a) and the restoring temperature at the sea surface. In August (February), the referral temperature was 28 °C (25 °C) at 25° N and 10 °C (0 °C) at 55° N, with a restoring time constant of 20 days. To prevent temperature drift due to the lack of thermohaline circulation, we used a temperature restoration that was weak in the upper layers and increased with depth. The model started from a steady state with an idealized stratification (Fig. 1b), and after 15 years of spin-up, it was connected to the biological model. Year 1 was defined as starting after the connection. As shown in the sea surface height, temperature, and velocity in Fig. 1c–e, the model appropriately represents the subtropical and subpolar gyres with a strong westerly boundary current and vigorous mesoscale eddy activity. Such a double gyre model with a rectangular closed basin is traditionally and frequently used in physical oceanography (Holland, 1978; Figueroa and Olson, 1994).

2.2. Biological model

A biological model in which a few hundred phytoplankton types compete under common rules was developed referring to NEMURO (Kishi et al., 2007) and MEM (Shigemitsu et al., 2012). In this subsection, we explain the differences between the phytoplankton types with a brief overview of the biogeochemical cycle. See the Appendix for the detailed biogeochemical cycle. The model treats a single nutrient, that is, only the nitrogen cycle is represented. The model components are a few hundred phytoplankton types, one zooplankton, dissolved organic nitrogen (DON), particulate organic nitrogen (PON), nitrate, and ammonia (Fig. 2). The rate of change of the phytoplankton concentration, p_i, for a phytoplankton type i and the