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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**A R T I C L E   I N F O**

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**A B S T R A C T**

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-trophic-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. © 2016 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

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; Ehrén 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 (Epplle, 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 (Folkes 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 2D 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 dispersal 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 (MRLCOM) developed at the Meteorological Research Institute of the Japan Meteorological Agency (Tsujino et al., 2010). The rectangular model domain is 0°–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 cm2/s2. The model was forced with an idealized wind stress (Fig. 1a) and the restoring temperature at the sea surface. In August (February), the reference 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 thermostaline 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
zooplankton concentration \([\text{zoo}]\) are described by the following set of equations:

\[
\frac{\partial \text{zoo}}{\partial t} = (1 - \gamma)(F_i(T) \cdot G_i(L) \cdot H_i([\text{NO}_3],[\text{NH}_4]))p_1 - re^{k_T}p_1 - mp_1p_{\text{sum}} - ge^{k_p} \left(1 - e^{-\lambda(p_{\text{sum}} - p_1)}\right) [\text{zoo}] \frac{p_1}{p_{\text{sum}}} + \text{(advection)} + \text{(diffusion)}.
\]
Fig. 3. Dependency of photosynthetic rate on (a) temperature, (b) light, and (c) nutrient. A phytoplankton type has traits for temperature, light, and nutrient represented by one characteristic curve selected in the (a) 12 curves, (b) 5 curves, and (c) 4 curves, respectively.

\[ p_{\text{sum}} = \sum_{i=1}^{N} p_i, \]  
\[ \frac{d[ZOO]}{dt} = \beta_{\text{bio}} g_{\text{e}} k_{\text{r}} T \left( 1 - e^{-\lambda(p_{\text{sum}} - p_{\text{sum}})} \right) \left[ \text{ZOO} \right] - m_{\text{e}} e^{\alpha T} [\text{ZOO}]^2 + (\text{advection}) + (\text{diffusion}), \]  

where \( T, L, [\text{NO}_3] \), and \([\text{NH}_4] \) are the temperature, light intensity, nitrate concentration, and ammonia concentration, respectively. The constant parameters \( \gamma, r, k_r, m, g, k_p, \lambda, p_{\text{sum}}, \beta_r, m_e, \) and \( k_0 \) and their values are described in Table 1. In the phytoplankton equation (Eq. (1)), the first to fourth terms on the right-hand side represent the photosynthesis minus the extracellular excretion, respiration, mortality by the density effect, and mortality by predation, respectively. \( N \) indicates the number of phytoplankton types, and we seeded 240 types of phytoplankton in the standard experiment. They differed only in their photosynthesis rate, where their dependencies on temperature, light, and nutrient (nitrogen) are denoted by \( F_i(T), G_i(L) \), and \( H_i([\text{NO}_3], [\text{NH}_4]) \), respectively, which are given by Eqs. (A-7)–(A-9) in Appendix. We set 12 characteristic curves for \( F_i(T) \), 5 for \( G_i(L) \), and 4 for \( H_i([\text{NO}_3], [\text{NH}_4]) \) assuming a trade-off (Fig. 3), where Fig. 3c shows the \( H_i([\text{NO}_3], [\text{NH}_4]) \) when ammonium concentration is zero. The characteristic curves are an idealized representation of observed trade-off; that is, different temperature optimum for different species (Eppley, 1972; Raven and Geider, 1988), species-specific light requirements (Richardson et al., 1983), and the trade-off between the maximum nutrient uptake rate and the half-saturation constant for nutrient uptake (Litchman et al., 2007). Such idealized representations are used in the DARWIN model (Follows et al., 2007). Compared to the representations in the DARWIN model, our characteristic curves are more overlapped, and then stronger competitive exclusion is expected. The combination of the 12 × 5 × 4 characteristic curves yields the traits for the 240 phytoplankton types. The naming rule of a phytoplankton type is as follows: “phy.26Aa” has the characteristic curve “26” for its temperature dependency, “A” for its light dependency, and “a” for its nutrient dependency in Fig. 3. The temperature zones of our phytoplankton types overlap each other, and subsequently, strong competitive exclusion is expected. Note that mortality via the density effect is represented not by \( m_{\text{e}} p_{\text{bio}} \), but by \( m_{\text{e}} p_{\text{sum}} \). The predation term includes no preference, e.g., for the phytoplankton size or the kill-the-winner mechanism. Therefore, there is no mechanism for minor species to be beneficial.

The initial values of the 240 phytoplankton types and zooplankton were \( 1.0 \times 10^{-3} \) \( \mu \)molN/l and \( 1.0 \times 10^{-4} \) \( \mu \)molN/l, respectively, in all grid points. For the nutrient, while the initial values of ammonium, PON, and DON were zero, nitrate started from an idealized initial value depending on the density. To prevent a drift in the nitrate distribution due to the lack of thermohaline circulation, nitrate concentrations below 200 m were restored to the initial value during the experiment, where the restoring time constant gradually increased with depth. After the connection to the physical model, the model was integrated for 22 years in the standard experiment. A vertical section of the temperature and nitrate concentration at 10 m is shown in Fig. 1f, which shows that the vertical and latitudinal gradients of nitrate are properly represented in the model. To save computational resources, we removed the phytoplankton types whose maximum concentration in all grid points was less than \( 1.0 \times 10^{-6} \) \( \mu \)molN/l; the removal was implemented at the beginning of years 3 and 11. 174 in 240 types and 30 in 66 types are removed at year 3 and 11, respectively. Because concentration of removed phytoplankton types decreases to less than 1/10 of the initial concentration in all grid points, such types will have no chance to increase their biomass after the removal manipulation. The maximum of the total biomass in the entire model domain in the removed types is approximately smaller than \( 10^{-5} \) of the total biomass of the surviving types in year 22, and therefore the impact of removal manipulation is assumed to be very small.

2.3. 0D model experiment

An offline model (hereafter the 0-D model) was developed to estimate the potential habitat of each phytoplankton type without phytoplankton dispersion via advection and diffusion. The phytoplankton and zooplankton concentrations were the prognostic variables, and the advection and diffusion of the phytoplankton and zooplankton were set to zero. Temperature, nitrate, ammonia, and DON were given by a time interpolation of the 5-day average calculated in the online 3-D model. For the light strength, the diurnal variation in the light strength was recalculated from the daily averaged data of the online 3-D model. The traits of the initial 240 phytoplankton types were the same as those in the standard experiment. The calculation domain of the 0-D model was the upper 150 m layers. The initial values of the 240 phytoplankton types and zooplankton were the same as those in the standard experiment of the 3-D model. The 0-D model was integrated for 10 years.

2.4. Case studies

Three additional experiments using the 3-D model were implemented (Fig. 4), as listed below.

Exp. I) Each phytoplankton concentration started from the value obtained at year 10 in the 0-D model, as opposed to the standard
Table 1
Parameters and their values used in the model.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Parameter</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>γ</td>
<td>Phytoplankton extracellular excretion to photosynthesis</td>
<td>0.135</td>
<td>nodim</td>
</tr>
<tr>
<td>r</td>
<td>Phytoplankton respiration rate at 0 °C</td>
<td>0.03</td>
<td>day⁻¹</td>
</tr>
<tr>
<td>kₗ</td>
<td>Phytoplankton temperature coefficient for respiration</td>
<td>0.0519</td>
<td>°C⁻¹</td>
</tr>
<tr>
<td>m</td>
<td>Phytoplankton mortality rate</td>
<td>0.08</td>
<td>(μmolN⁻¹)⁻¹ day⁻¹</td>
</tr>
<tr>
<td>ψ</td>
<td>Phytoplankton ammonium inhibition coefficient</td>
<td>1.5</td>
<td>(μmolN⁻¹)⁻¹</td>
</tr>
<tr>
<td>kₗNH₄</td>
<td>Phytoplankton half saturation constant for ammonium</td>
<td>0.5</td>
<td>μmolN⁻¹</td>
</tr>
<tr>
<td>kₗPP</td>
<td>Phytoplankton temperature coefficient for photosynthetic rate</td>
<td>0.0693</td>
<td>°C⁻¹</td>
</tr>
<tr>
<td>Pₗ</td>
<td>Phytoplankton potential maximum light-saturated photosynthetic rate</td>
<td>0.8</td>
<td>day⁻¹</td>
</tr>
<tr>
<td>αₛ</td>
<td>Zooplankton assimilation efficiency</td>
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<td>nodim</td>
</tr>
<tr>
<td>β₣</td>
<td>Zooplankton growth efficiency</td>
<td>0.3</td>
<td>nodim</td>
</tr>
<tr>
<td>g</td>
<td>Zooplankton maximum grazing rate on phytoplankton at 0 °C</td>
<td>0.5</td>
<td>day⁻¹</td>
</tr>
<tr>
<td>kₙ</td>
<td>Zooplankton temperature coefficient for grazing</td>
<td>0.0693</td>
<td>°C⁻¹</td>
</tr>
<tr>
<td>λₙ</td>
<td>Zooplankton bλK constant</td>
<td>1.4</td>
<td>(μmolN⁻¹)⁻¹</td>
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<tr>
<td>ρₙₘₚ</td>
<td>Zooplankton threshold value for grazing on phytoplankton</td>
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<td>μmolN⁻¹</td>
</tr>
<tr>
<td>mₙ</td>
<td>Zooplankton mortality rate at 0 °C</td>
<td>0.0585</td>
<td>(μmolN⁻¹)⁻¹ day⁻¹</td>
</tr>
<tr>
<td>kₙₘ</td>
<td>Temperature coefficient for zooplankton mortality</td>
<td>0.0693</td>
<td>°C⁻¹</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>Nitrification rate at 0 °C</td>
<td>0.05</td>
<td>day⁻¹</td>
</tr>
<tr>
<td>kₙₐ</td>
<td>Temperature coefficient for nitrification</td>
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<td>°C⁻¹</td>
</tr>
<tr>
<td>kₙ₃ₐ</td>
<td>Remineralization rate of DON at 0 °C</td>
<td>0.01</td>
<td>day⁻¹</td>
</tr>
<tr>
<td>kₙ₄ₐ</td>
<td>Temperature coefficient for DON decomposition to NH₄</td>
<td>0.0693</td>
<td>°C⁻¹</td>
</tr>
<tr>
<td>dₓₙ₄ₐ</td>
<td>Dissolution length scale for PON</td>
<td>200</td>
<td>m</td>
</tr>
</tbody>
</table>

Fig. 4. Design of the experiments. The shaded and blank arrows show the experiments using the 3-D and 0-D models, respectively.

experiment where they started from a constant small value. Transport of the phytoplankton from its potential habitat was examined. A comparison with the standard experiment shows the effects of the difference in the initial phytoplankton concentration on the resulting phytoplankton density.

Exp. II) The same as Exp. I; however, the phytoplankton concentration was treated as a passive tracer. This experiment was conducted to calculate the residence time of a phytoplankton type in its potential habitat.

Exp. III) One phytoplankton type was removed from the 240 phytoplankton types to enable clear competitive exclusions. The other experimental settings were the same as those in the standard experiment.

3. Analyses

To estimate the competitive ability of each of the 240 seeded phytoplankton types, we used the specific growth rate, which is the growth rate of each phytoplankton type normalized by its biomass. The specific growth rate is determined uniquely by the oceanic environment and does not depend on the initial or present biomass of each phytoplankton type. Using Eq. (1), it is defined as the photosynthesis minus respiration per unit of phytoplankton concentration:

\[(1 - γ)(F_l(T) \cdot G_l(L) \cdot H_l([NO₃], [NH₄])) - r e_k T,\]

which is determined in every grid box. The specific growth rate was calculated at every time step in the 3-D standard experiment, corresponding to the change in the oceanic environment (temperature, light intensity, and the nutrient), and the monthly average in year 2 was stored.

We also introduced an index indicating the relative competitive ability of each of the 240 seeded phytoplankton types. First, we identified the grid boxes in which a phytoplankton type has the highest specific growth rate in the seeded 240 types, where such grid boxes satisfy the equation \(F_l G_l H_l = \max(F_l G_l H_l | 1 \leq j \leq 240)\) for a phytoplankton type \(i\). Hereafter, such grid boxes are called "the most competitive space". Second, the volume integration of such grid boxes in the entire model domain is calculated for each of the 240 types. Hereafter, the volume integration is called "the oceanic volume where a phytoplankton has the highest specific growth rate in the 240 types" or simply "the abundance in the most competitive space". In the integration of the volume, deep layers below the critical depth were excluded. The abundance of the most competitive space was calculated from the monthly average of the specific growth rate, and the annual average was used in the analysis.

4. Results

4.1. Standard experiment: surviving phytoplankton types

In the standard experiment, 29 of the 240 seeded phytoplankton types survive, where we define a surviving type as a type whose relative species abundance in the entire model domain is larger than 10⁻³% in the last year (year 22). Their annually averaged biomass in the entire model domain is in a quasi-steady state. As shown in the horizontal distributions of the phytoplankton concentration (Fig. 5), each phytoplankton type has an inherent habitat, which is slightly modified by seasonal changes and by mesoscale eddies. Both habitat segregation and habitat overlap occur, the latter of
which typically occurs around the peripheries of the habitats. The habitat distribution strongly depends on the temperature gradient (Fig. 1d), as shown by the dominant three types in the subpolar region (Fig. 5a–c), of which only the optimum temperature differs. In an exceptional case, the habitats of phy.16Ad and phy.16Ac (Fig. 5g and k), which differ only in their nutrient traits, nearly overlap. As shown by the phytoplankton names, 11 of the 12 dominant phytoplankton types have the characteristic curve “A” for the light dependency of their photosynthesis.

The relative abundance was calculated for the 29 surviving types (Fig. 6). Hereafter, this distribution is called the relative species abundance, even though it is for virtual species. Very minor phytoplankton types whose relative species abundance is less than $10^{-2}$% do not exist. The non-existence of very minor types is assumed to be an essential consequence because advection and diffusion decrease the phytoplankton biomass within its habitat and this impact is relatively strong for minor types.

4.2. 0D model experiment

Based on the results of the 0-D model experiment, the potential habitats without oceanic advection and diffusion were estimated for each phytoplankton type to prepare for the following experiments, Exps. I and II. The potential habitat for a phytoplankton type is defined as the oceanic region where the rate of the phytoplankton type in the total phytoplankton is larger than 1/1000 in December of year 10. The horizontal distribution of the potential habitat for the 12 dominant phytoplankton types in the 3-D standard experiment suggests that the habitats are basically exclusive (not shown); that is, in most of the grid points, only one phytoplankton type survives.
In the 0-D model experiment, 80 of the 240 seeded phytoplankton types survive in the entire model domain. The definition of survival in the 0-D model is that the percentage of a phytoplankton type biomass in the total phytoplankton biomass is larger than 0.1% in at least one grid point after 10 years of integration. The 80 phytoplankton types include all of the 29 types surviving in the 3-D model. The larger number of surviving types in the entire model domain in the 0-D model compared to the 3-D model indicates that advection and diffusion decrease species richness in diversity. Diversity is the total diversity in a wide area, which is the whole model domain in our case, while diversity is the diversity in sites at a more local scale (Whitaker, 1960). Our results for diversity is consistent with Lévy et al. (2014), which demonstrates that diversity increases without advection and diffusion using the DARWIN model (Follows et al., 2007) applied to the North Pacific and its 0-D version.

4.3. Traits of the surviving phytoplankton

To explore the differences between the surviving and excluded phytoplankton types, we investigated how the traits of the surviving phytoplankton types in the 3-D standard experiment are distributed in parameter space (Fig. 7). In the subpolar region with low temperature, phytoplankton types competitive under high nutrient conditions survive, while those preferring low nutrient conditions survive in the subtropical region. This result is consistent with observation-based description (Lalli and Parsons, 1997). The excluded phytoplankton types with “4a” are competitive under low-temperature and low-nutrient conditions; however, such a condition does not exist in the ocean. The 29 surviving phytoplankton types have traits fitting to oceanic environments. As a result, the traits of the surviving types are not distributed randomly in the parameter space but are concentrated within specific domains.

4.4. Abundance in the most competitive space

To explore what determines the relative species abundance (Fig. 6), we used the abundance in the most competitive space, an index indicating the relative competitive ability, which was previously defined in the Analysis section. For each of the 240 seeded phytoplankton types, the abundance in the most competitive space was calculated, where three examples of the most competitive space is displayed in Fig. 8. Then its relationship to the relative species abundance was investigated (Fig. 9). For the 29 surviving phytoplankton types (the blue markers) whose relative species abundance is larger than $10^{-3}$% at the end of year 22, the relative species abundance is nearly proportional to the abundance in the most competitive space. Compared to the surviving phytoplankton types, non-persistent phytoplankton types tend to have relatively less abundance in the most competitive space. We divided non-persistent types into two groups: the group shown by the yellow markers (the other group shown by the red markers) has relative abundance larger than (less than) $10^{-4}$% at the end of year 5. In the non-persistent types, the types with long exclusion times of over 5 years (the yellow markers) have nearly more abundance in their most competitive space than others (the red markers). Note that many non-persistent phytoplankton types are not drawn in Fig. 9 because their abundance in their most competitive spaces is less than $10^{10} \text{m}^3$, which is below the minimal value of the horizontal axis. There are 118 phytoplankton types whose abundance in the most competitive space is zero, and all of these 118 types are non-persistent. Even in the 0-D model experiment, the 118 types are not persistent. Corresponding to the distribution of the surviving and non-persistent phytoplankton types, we expediently classified the three regions as shown in the figure: in region 1, only the non-persistent types exist, both the surviving and non-persistent types exist in region 2, and only the surviving types exist in region 3. In region 2, the abundance in the most competitive space does not necessarily uniquely determine whether a phytoplankton type survives. This suggests that there is another factor related to the relative species abundance, which we presume to be the oceanic current in the habitat.
phytoplankton

Fig. 8. Horizontal distributions of the most competitive space, in which a phytoplankton type has the highest specific growth rate in the 240 types, for three selected phytoplankton types (marked in Fig. 9). The colors on each grid box show the number of months in which a phytoplankton type has the highest specific growth rate in all types.

Fig. 9. Dependence of the relative abundance of a phytoplankton type on its oceanic volume where the phytoplankton type has the highest specific growth rate in the 240 types. The blue closed circles show the 29 surviving types. The relative abundances of the 29 surviving types are the same as those in Fig. 6. The red and yellow closed circles show the non-persistent types, in which the relative abundance of the red (yellow) types is smaller than (larger than) $10^{-4}$% at the end of year 5. A relative abundance of less than $10^{-3}$% is displayed at a value of $10^{-3}$% for the red markers and $1.2 \times 10^{-5}$% for the yellow markers. Note that the non-persistent phytoplankton types whose top volume of the specific growth rate is less than the minimal value of the horizontal axis ($1.0 \times 10^{15}$ m$^3$) are not displayed in the figure. The line between region 1 and 2 (region 2 and 3) is drawn at the minimum in the surviving types (at the maximum in the extinct types) of the oceanic volume shown in the horizontal axis.

4.5. Effects of advection and diffusion on extinction

To explore the effects of oceanic currents in habitats on the survival of a phytoplankton type, we used “potential habitat without oceanic currents”, which was introduced in Section 4.2 based on the results of the 0-D model experiment, for each of the 240 seeded phytoplankton types in the 3-D model experiment. We implemented Exp. I, in which the initial concentration of a phytoplankton type was distributed only in their potential habitat and was nearly equal to zero elsewhere. The experiment can be used to investigate how the transport of a phytoplankton type from its potential habitat affects its survival. Type phy.20Ca starts from the initial value displayed in Fig. 10a, where the colored region corresponds to approximately its potential habitat (Fig. 10j). Type phy.20Ca is not persistent in the 3-D standard experiment and is located in region 2 in Fig. 9, with an abundance in the most competitive space of $4.68 \times 10^{12}$ m$^3$. A comparison of its potential habitat and the oceanic horizontal currents (Fig. 1e) shows that its potential habitat is unfortunately located along a strong jet. Over two years, the strong jet and subtropical circulation quickly transport phy.20Ca from its potential habitat to a southeastward region where phy.20Ca is an inferior competitor (Fig. 10a–i). As shown in the nutrient acquisition minus nutrient loss (Fig. 10k–r), which is

\[
(1 - \gamma)(E(T) \cdot G(L) \cdot H([NO_3], [NH_4]))p_i - re^{i\gamma}p_i - mp_ip_{sum}
\]

phy.20Ca can acquire nutrient in its potential habitat and the downstream areas, but the nutrient acquisition is insufficient for persistence. Outside its potential habitat, phy.20Ca gradually decreases in its relative abundance and is eventually excluded. In the potential habitat, the increase in its biomass within the habitat via biological processes is insufficient to compensate for the outflow of biomass from the potential habitat due to physical processes. Based on the results, we inferred that potential habitats with low horizontal current velocities are more suitable for survival than those with high horizontal current velocities, and inspected the inference by the following analysis.

We introduced the residence time during which each phytoplankton type stays in its potential habitat, where the residence time is expected to be inversely proportional to the current speed averaged in the potential habitat. We implemented Exp. II, which is the same as Exp. I except that the phytoplankton concentration is treated as a passive tracer without biological growth, to extract the effects of the physical processes. Since there is no production of new biomass and biomass outside the potential habitat is nearly equal to zero in Exp. II, biomass within the potential habitat monotonically decreases with time by the outflow from the potential habitat. In Exp. II, the residence time, $\tau$, is defined as the period
during which the biomass, $B$, of a phytoplankton type integrated within its potential habitat to drop to 1/10 of its initial value; that is, $B(t_r) = \frac{1}{10}B(t_0)$. We then estimated how the survival of a phytoplankton type depends on its residence time within its potential habitat (Fig. 11). In Figs. 9 and 11, the horizontal axes, classified regions, the 29 surviving types (the blue markers), and two non-persistent types (the yellow and red markers) are the same. Of the phytoplankton types whose abundances in the most competitive space are nearly equal, their residence times can be considerably different; for example, of the phytoplankton types whose abundance in the most competitive space ranges from $0.8 \times 10^{12}$ m$^3$ to $1.0 \times 10^{12}$ m$^3$, the residence time has a broad range from a few to a few hundred days. In region 2, the surviving phytoplankton types (the blue markers) tend to have larger residence times com-
pared to the non-persistent types (the red and yellow markers). As exceptional cases, non-persistent types with relatively long exclusion times of over 5 years (the yellow markers) have an abundance in the most competitive volume and a residence time comparable to the surviving types. For major types located in region 3, their residence times of more than a few hundred days reflect the fact that such types have broad habitat volume extending to a few hundreds of kilometers. For minor types located in region 2, whose habitat volume is fractional compared to major types, their residence time significantly influences their survival. As typically shown in the case of phy.20Ca (Fig. 10), a minor type that is rapidly transported from its habitat does not have a sufficient chance to grow, and subsequently, the increase in its concentration in its habitat by growth is not sufficient to compensate for the decrease in its concentration caused by transport from its habitat, resulting in extinction.

5. Discussion

5.1. Habitats of minor species

Our results in Fig. 11 suggested that a habitat with low current velocity is more suitable for species survival than one with high current velocity, and minor phytoplankton species tend to inhabit regions with low current velocity. The latter suggestion could be useful for observational investigations and to conserve the phytoplankton assembly.

5.2. Contributions of deterministic and random stochastic effects

Our simulations suggest that the phytoplankton assembly can be explained via deterministic processes rather than random processes because the relative species abundance is strongly dependent on the competitive ability and the residence time in the habitat, as already shown. To further explore the deterministic and random contributions, we examined the long-term trend of relative species abundance for a few decades (Fig. 12). If random processes are dominant, the order of the phytoplankton types will change with time due to random ecological drift; that is, some dominant (minor) phytoplankton types would become minor (dominant). However, almost all phytoplankton types maintain their abundances with regular seasonal cycles, and a fundamental change in the order does not occur. For example, phy.6Ad is the most dominant type at all times during the experiment. Conversely, the interannual variability found primarily in the minor phytoplankton types suggests the effect of the random activity of mesoscale eddies on the abundances of phytoplankton types via random environmental changes and the random dispersion of phytoplankton types. In the interannual variability of phy.16Ad and phy.16Ac, whose habitats exceptionally nearly overlap (Fig. 5g and k), an increase in phy.16Ad is correlated to a decrease in phy.16Ac. The sum of the two types does not show strong interannual variability (not shown). Therefore, the effects of random processes are limited and are not strong enough to change the fundamental structure of the phytoplankton assembly. Regardless of random transport occurring at a scale on each grid point, a phytoplankton assembly shows deterministic behavior at a scale on the entire model domain. Perc et al. (2007), which explored stochastic versus deterministic nature of dynamics at the cell and tissue level, proposed an interesting idea that internal stochasticity, present at the level of each individual cell, may lead to deterministic behavior often observed at the level of an organ. Their idea for interaction among different scales may be useful in considering deterministic and random effects on a phytoplankton assembly.

A comparison of the time series between the 3-D standard experiment (Fig. 12a) and Exp. I (Fig. 12b) indicates that the dependence on the initial value of a phytoplankton type is not significant because almost all phytoplankton types have similar relative abundances in the two experiments, even though the initial distributions of the phytoplankton concentrations are completely different. Furthermore, the horizontal and vertical distributions of each phytoplankton type are nearly equivalent for the two experiments (not shown). Effects of the different initial concentrations are only seen in a very minor type, phy.26Ea, which goes extinct in the 3-D standard experiment and maintains a very small abundance in Exp. I. The small dependence on the initial concentration indicates that deterministic factors are dominant in a formation of the phytoplankton assembly.

We examined why effects of random processes on relative species abundance are not significant in the oceanic phytoplankton assembly. For landscape vegetation, many studies have suggested fundamental contributions of random stochastic processes in structuring the community assembly via dispersal limitation or recruitment limitation (Hurt and Pacala, 1995; Gravel et al., 2006). Oceanic phytoplankton dispersion is a fast process, as shown in Fig. 10, in which phytoplankton are dispersed and can spread to several hundred kilometers in a few months. This figure also shows that the dispersion is not isotropic and the dispersal direction is restricted by the current direction, which can prevent the most competitive species from using their niches. The effects of dispersion on recruitment are different for oceanic phytoplankton and landscape vegetation. In landscape vegetation, where an individual occupies a site until its death and the dispersion carrier is a kernel, propagule, or spore, dispersion causes an increase in the chance of recruitment. In oceanic dispersion, where the parent itself is transported, the chance of recruitment is increased in “new frontiers” where the phytoplankton are transported; however, the chance of recruitment is decreased in “in situ” oceanic volumes.
due to the decrease in its concentration. Because phytoplankton competition is essentially for nutrient acquisition rather than for space, we propose that a recruiting limitation on oceanic phytoplankton occurs when the most competitive species at an oceanic point does not uptake enough nutrients. In Eq. (1), recruiting limitation occurs when a phytoplankton type has the highest specific growth rate \((1 - \gamma)(F_e(T) \cdot G_e(L) \cdot H_e([\text{NO}_3], [\text{NH}_4])) \cdot r_{\text{phy}}T\) among the 240 phytoplankton types, but has relatively low phytoplankton concentration \(p_i\). The above condition results in insufficient nutrient acquisition \([(1 - \gamma)(F_e(T) \cdot G_e(L) \cdot H_e([\text{NO}_3], [\text{NH}_4])) \cdot r_{\text{phy}}T \cdot p_i)\].

In Fig. 9, the extinction of non-persistent phytoplankton types whose abundance in the most competitive space is comparable to the surviving types, shown by the yellow and red markers in region 2, can be interpreted as being caused by recruiting limitations related to the low concentration of the non-persistent phytoplankton types. In this case, the recruitment limitation on the phytoplankton does not work as a mechanism contributing to rich diversity but instead works to decrease diversity.

5.3. Competition among three species

The competitive relationship of three phytoplankton types was explored using a removal experiment. Types phy.22Ca, phy.22Ba, and phy.22Aa have the same nutrient and temperature traits and differ only in their light traits. Therefore, they would inhabit vertically adjacent regions, and there would be a competitive relationship between phy.22Ba and phy.22Aa and between phy.22Ba and phy.22Ca. In the 3-D standard experiment, phy.22Ca and phy.22Aa survive (Fig. 13), while phy.22Ba does not persist and gradually decreases its concentration over several years. We implemented Exp. III, in which only phy.22Aa is removed from the original 240 types. As opposed to the 3-D standard experiment, phy.22Ba survives in Exp. III (Fig. 13e), even though the specific growth rate of phy.22Ba is the same in the two experiments. This suggests that the non-persistence of phy.22Ba in the 3-D standard experiment is caused by competitive exclusion by phy.22Aa. The competitive exclusion of phy.22Ba by phy.22Aa benefits phy.22Ca.
In the standard experiment where phy.22Ba is extinct, the biomass of phy.22Ca integrated over the entire model domain increases to 154% (157%) in year 5 (year 6) compared to Exp. III, where phy.22Ba survives. For phy.22Ca, the enemy (phy.22Aa) of my enemy (phy.22Ba) is my friend. In sessile communities, the spreading effects of a decrease in abundance of a single species on the other species at the same trophic level have been discussed in Potts and Vincent (2008), where a trade-off between the competitive and colonization abilities is assumed. In a wide variety of ecosystems, such spreading effects within a trophic level can have an essential impact on the community structure.

6. Conclusions

Observational evidence demonstrates that a huge number of species coexist in an oceanic plankton functional or taxonomical group; for example, the number of diatom species is estimated to be larger than 10,000 (Guiry, 2012). To advance our understanding of competition and coexistence within a phytoplankton functional group, we developed a phytoplankton competition model combined with an eddy-resolving OGCM. We explored how relative species abundance is structured by the interaction among spatiotemporally variant physical-biological fields, species-specific responses to these fields, and phytoplankton transport via oceanic currents. The following two significant factors were obtained.

1) A species’ relative competitive ability provides an outline of the relative species abundance. As an index of the relative competitive ability of each phytoplankton virtual species, we introduced the oceanic volume in which a phytoplankton species has the highest growth rate in all the species. This volume significantly correlated to the relative species abundance, where a larger volume results in a larger abundance of a phytoplankton species. If the volume of a phytoplankton species is zero, then the species is an inferior competitor at all grid points, and the phytoplankton species never survives.

2) The residence time in the potential habitat is also significant in structuring the relative species abundance. Of the phytoplankton species whose abundances in the most competitive space are nearly equal, the surviving species tend to have larger residence times compared to the non-persistent species.

The above results indicate the dominance of deterministic processes in phytoplankton diversity, – rather than random stochastic processes. This is also supported by the fundamental long-term invariance in the rank of a phytoplankton species in abundance and by the small dependence of the relative species abundance on the initial phytoplankton value.

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Appendix.

While Eqs. (1)–(3) for the phytoplankton and zooplankton are described in Section 2, the other equations used in our biologi-
The decomposition of DON depends on phytoplankton mortality, zooplankton mortality, and egestion:

\[
(\text{PON decompositions to DON at } k_{\text{PON}}) = \left( \sum_{k=1}^{k_{\text{PON}}} \text{PONprod}(k) \right) e^{-\Delta z(k_{\text{PON}})} \left( 1 - e^{-\Delta z(k_{\text{PON}})} \right),
\]

where \(k_{\text{PON}}\) and \(z(k)\) are the model layer and the depth of layer \(k\), respectively, and \(\Delta z(k_{\text{PON}})\) is the layer thickness at \(k_{\text{PON}}\).

The dependency of photosynthesis on temperature, light, and the nutrient nitrogen, which is different for the phytoplankton types, is described by the following set of equations.

\[
F_i(T) = \theta_{\text{e}} e^{\phi_0 T} \left( 1 - e^{-\phi_1 T} \right)^2
\]

\[
G_i(L) = \left( \frac{\beta_0}{\beta(L)} \right) \left( \frac{\phi(L)}{\phi_0} \right) e^{-\phi_1 T}
\]

\[
H_i([NO_3], [NH_4]) = V_{\text{max}}(i) \left( \frac{[NO_3]}{[NO_4] + K_{\text{NO}}(i)} e^{-\phi_3 [NH_4]} + \frac{[NH_4]}{[NH_4] + K_{\text{NH}}(i)} \right)
\]

\[
\frac{\partial [NO_3]}{\partial t} = V_{\text{NitO}} e^{\phi_0 T} [NH_4] - \sum_{i=1}^{N} \left[ 1 - \phi_4 T \right] \left( F_i(T) \cdot G_i(L) \cdot H_i([NO_3], [NH_4]) \right) p_i - \text{advection} + \text{diffusion (A-1)}
\]

\[
\frac{\partial [NH_4]}{\partial t} = \frac{\partial [NO_3]}{\partial t} e^{\phi_0 T} + \sum_{i=1}^{N} \left[ 1 - \phi_4 T \right] \left( F_i(T) \cdot G_i(L) \cdot H_i([NO_3], [NH_4]) \right) p_i - \text{advection} + \text{diffusion (A-2)}
\]

\[
\frac{\partial [DON]}{\partial t} = \sum_{i=1}^{N} \gamma (F_i(T) \cdot G_i(L) \cdot H_i([NO_3], [NH_4]) p_i - \text{advection} + \text{diffusion (A-3)}
\]

These equations represent the effect of nitrification (Eqs. (A-1) and (A-2)), zooplankton excretion (Eq. (A-2)), remineralization of DON (Eqs. (A-2) and (A-3)), and phytoplankton excretion (Eq. (A-3)).

The growth \(R_{\text{new}}(i)\) in Eqs. (A-1) and (A-2) is given by

\[
R_{\text{new}}(i) = \frac{[NO_3]}{[NO_4] + K_{\text{NO}}(i)} e^{-\phi_3 [NH_4]} + \frac{[NH_4]}{[NH_4] + K_{\text{NH}}(i)},
\]

where \(K_{\text{NO}}(i)\) is the half saturation constant for nitrate and depends on the phytoplankton type. The production of PON (\(\text{PONprod}\)) depends on phytoplankton mortality, zooplankton mortality, and egestion,

\[
(\text{PON decompositions to DON at } k_{\text{PON}}) = \left( \sum_{k=1}^{k_{\text{PON}}} \text{PONprod}(k) \right) e^{-\Delta z(k_{\text{PON}})} \left( 1 - e^{-\Delta z(k_{\text{PON}})} \right).
\]

References


