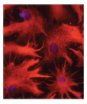
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Andrew D. Barton *et al.*

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Patterns of Diversity in Marine Phytoplankton

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Spatial diversity gradients are a pervasive feature of life on Earth. We examined a global ocean circulation, biogeochemistry, and ecosystem model that indicated a decrease in phytoplankton diversity with increasing latitude, consistent with observations of many marine and terrestrial taxa. In the modeled subpolar oceans, seasonal variability of the environment led to competitive exclusion of phytoplankton with slower growth rates and lower diversity. The relatively weak seasonality of the stable subtropical and tropical oceans in the global model enabled long exclusion time scales and prolonged coexistence of multiple phytoplankton with comparable fitness. Superimposed on the decline in diversity seen from equator to pole were "hot spots" of enhanced diversity in some regions of energetic ocean circulation, which reflected lateral dispersal.

In both marine and terrestrial environments, many taxa exhibit a decline in species diversity with increasing latitude (*1*, *2*), and this pattern has important implications for ecosystem structure and function (*3*). The extent to which and why marine phytoplankton may follow such patterns is not yet clear, although it has been argued that the biogeography of microbes is governed by a similar set of processes as for macroorganisms (*4*). There is some evidence of latitudinal diversity gradients among certain taxa of marine microbes, including bacterioplankton (*5*, *6*) and coccolithophorids (*7*, *8*), although the generality of these patterns, particularly in the open ocean, is, as yet, equivocal (*9*, *10*).

In a recent study, a three-dimensional and time-varying global ocean circulation, biogeochemistry, and ecosystem model was initialized with a relatively large number (78) of virtual phytoplankton types whose traits were assigned stochastically from plausible ranges of possibilities (*10*–*12*). The modeled phytoplankton communities "self assembled" according to the relative fitness of the phytoplankton types in the regionally and seasonally varying resource and predatory environment. The emergent phytoplankton populations captured the observed large-scale oceanic patterns in the distribution of phytoplankton biomass and community structure, including the observed niche differentiation among ecotypes of the cyanobacterium *Prochlorococcus* in the Atlantic Ocean (*11*).

Here, we have studied an ensemble of 10 integrations of the global model, each member having a different, stochastically seeded selection of phytoplankton types, to examine and interpret the emergent patterns of phytoplankton diversity. In each of the solutions, after a decade of integration, a dozen or so phytoplankton types account for more than 99% of the total global phytoplankton biomass. Others persist at low abundance or with limited geographic distribution, and some decline toward virtual extinction. Fast-growing "opportunist" phytoplankton tend to dominate the biomass of the variable high latitudes, whereas "gleaners" (those best able to survive on minimal resources) dominate the stable, low-latitude seas (*12*, *13*). There is also a degree of local coexistence among phytoplankton types. On an annual, vertically averaged basis, the phytoplankton diversity in the euphotic zone (here assumed to be 0- to 260-m depth) is lower in the polar and subpolar oceans and higher in tropical and subtropical latitudes (Fig. 1A). This meridional gradient is clearly seen in the zonally averaged view (Fig. 1B) and is consistent with numerous observations of marine and terrestrial ecosystems (*1*, *2*), including the sparse observations of marine microbial diversity (*5*–*8*). Superimposed on the model's meridional gradient are "hot spots" of highest diversity, which are generally associated with regions of energetic circulation such as the western boundary currents. The Atlantic Ocean hot spots appear to be consistent with observations of increased diatom diversity near the North African and South American coasts (*8*).

The mechanisms for maintaining the diversity of life on Earth have long interested ecologists (*14*, *15*), and the explanations for the meridional diversity gradient have been classified as historical, evolutionary, or ecological in nature (*6*, *16*). Historical explanations invoke events and changes in Earth history, such as Milankovitch cycles, in setting current species diversity. Evolutionary explanations examine the rates of speciation and extinction and their balance through time (*17*, *18*). These processes are not resolved in

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this model, yet diversity gradients are still apparent. Thus, we seek ecological explanations for the model diversity gradients, acknowledging that some real-world processes are not being considered. Niche differentiation, including seasonal succession, plays a role in determining the regional and seasonal habitats of phytoplankton types, adding to, but not fully explaining, the spatial diversity patterns (*10*). We find dispersal and temporal variability of the environment to be the most important ecological controls on phytoplankton diversity gradients in this model, whereas other factors are of lesser importance or not resolved (*10*).

Resource competition theory (*12*, *13*, *19*–*21*) provides a useful framework for illustrating the role of temporal variability in the global model. Consider an idealized system with a single, limiting nutrient, where the rate of change of biomass is determined by the balance between growth and mortality and the rate of change of the nutrient is determined by consumption by phytoplankton and its environmental resupply (*10*). At equilibrium in this system, the phytoplankton type with the lowest environmental nutrient concentration at which the growth and mortality are in balance (designated as R^*) (*10*) is expected to outcompete other phytoplankton types over time (*12*, *20*). This limit is relevant to the subtropical oceans, which are characterized by a relatively weak seasonal cycle, and a strongly stratified, oligotrophic surface ocean. An emergent feature of the global model solutions was the coexistence of multiple physiologically distinct phytoplankton types with similarly low R^* in the tropical and subtropical regions (Fig. 1C) (*12*), at least for the time scale of the model integrations. Because the R^* for each phytoplankton type depends on imposed physiological characteristics and mortality, there are, in theory, many possible combinations that can achieve the same maximal fitness (lowest R^*). Moreover, the emergent, coexisting community of physiologically distinct but R^*-equivalent organisms is consistent with studies of laboratory populations of manipulated bacteria (*22*) and the hypothesis that such a mechanism may be important in maintaining the diversity of marine phytoplankton (*21*). This model outcome itself points to a possible explanation for enhanced phytoplankton diversity at lower latitudes and echoes the neutral theory of ecology and the hypothesis of ecological equivalence (*23*).

We analyzed the diversity dynamics within the idealized resource competition framework for the special case where all phytoplankton types have identical R^*. In support of the emergent pattern in the global model, the idealized simulations indicate that the relatively steady environmental conditions in the tropical and subtropical oceans enable the prolonged coexistence of many phytoplankton with equivalent fitness (equal R^*) and enhanced diversity (Fig. 2A) (*10*). However, the oceans are constantly perturbed by atmospheric forcing and internal physical phenomena

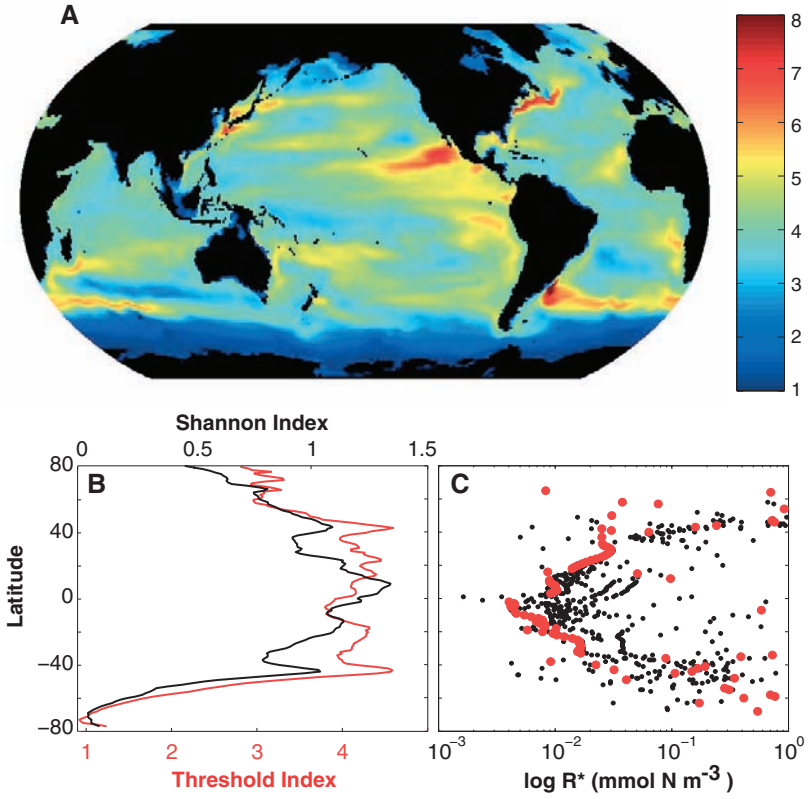


Fig. 1. (**A**) Diversity of modeled phytoplankton types in the uppermost 260 m, averaged annually across 10 ensemble members. Diversity is defined as the number of phytoplankton types comprising greater than 0.1% of the total biomass. (**B**) Zonal mean diversity, as well as the Shannon Index (*10*), for the map shown in (A). (**C**) Annual mean R^* (small black dots) of all phytoplankton types with a concentration above 10^{-12} mmol N m^{-3} along a meridional transect through the Atlantic Ocean at 20°W in an idealized global model with a single limiting nutrient (*12*). The large red dots show the R^* for only the most abundant type in each latitude.

across a vast range of spatial and temporal scales. Introducing a time-varying, periodic nutrient source to the idealized simulations eventually leads to competitive exclusion of all but the single phytoplankton type that grows fastest under optimal conditions (Fig. 2B), even if the equivalence of R^* is imposed. The slower-growing phytoplankton types need a higher time-averaged nutrient concentration to compete with the faster growers and are excluded over time (*10*). Environmental variability creates a competitive structure such that the number of extant phytoplankton types can be reduced through competitive exclusion. Indeed, in the higher latitude, strongly seasonal marine environments where the global model solution exhibits lower diversity (Fig. 1), high growth rate, and not low R^*, is the most appropriate measure of organismal fitness (*12*).

Using the idealized experimental system, we investigated a range of natural frequencies and amplitudes of variability in nutrient supply and defined the time taken until one phytoplankton type accounts for more than 90% of the total biomass as the time scale of competitive exclusion, or τ_{CE}. This time scale can exceed a thousand years when the environmental variability has either short (hours to days) or long (annual and longer) periodicity (Fig. 3). In contrast, when the environment varies with a period of months, competitive exclusion occurs within a few years or less. Large amplitude variations promote rapid exclusion, whereas small amplitude variations allow for extended coexistence. Therefore, in the subtropical and tropical oceans, where seasonality is relatively weak, we expect the time scale of competitive exclusion to be long (centuries or more, which is long relative to the length of global model integrations) for phytoplankton types with equivalent R^* (Fig. 2A). In contrast, the subpolar and polar oceans are subject to strong seasonal variations, including changes in the mixed layer depth that regulate light and nutrient availability. Here, opportunism is favored and the exclusionary pressure by the fastest growing phytoplankton on those with lesser growth rates is strong (Fig. 3). The exclusion time scale here may be as short as several years, and the long-term coexistence of many phytoplankton types is not sustained. Variability in growth rate, which is sensitive to changes in temperature and light, led to similar results (*10*).

The time scale of competitive exclusion is set by the character of environmental variability, but local diversity in the global model is ultimately a

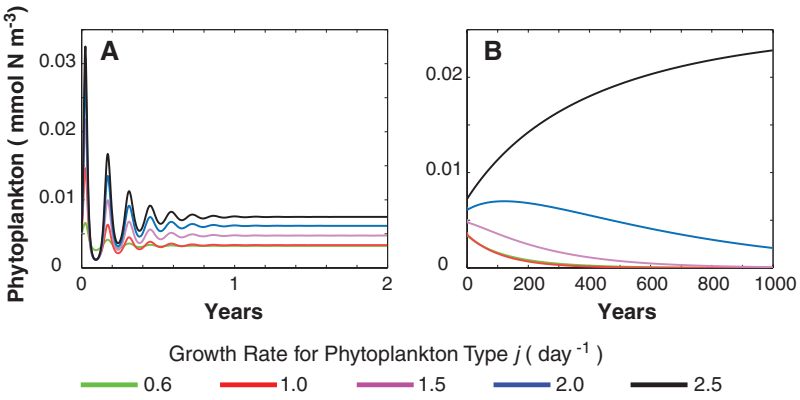


Fig. 2. Abundances for five hypothetical phytoplankton types with a constant (**A**) and periodically varying (**B**) nutrient source (ω^{-1} = 365 days, and the amplitude is 0.5). Colors represent phytoplankton with different maximum growth rates (μ). Data in (B) were annually averaged.

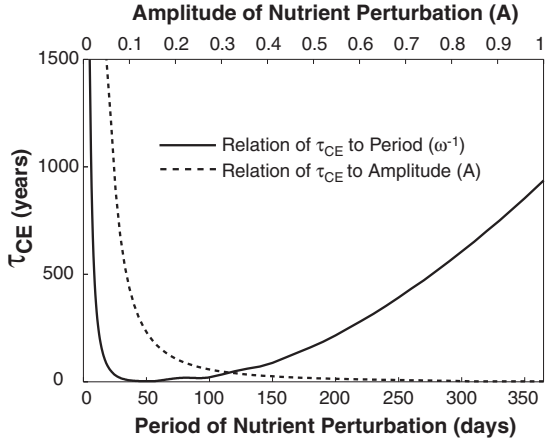


Fig. 3. The relationship between exclusion time scale (τ_{CE}) and the period (ω^{-1}, solid line) and amplitude (A, dashed line) of the external nutrient source in the idealized model (*10*). We considered a system to be in a state of competitive exclusion when one species comprises greater than 90% of the total biomass.

balance between the removal of species by exclusion and the replenishment of phytoplankton types through physically mediated dispersal (*17*). The rate of long-range dispersal of phytoplankton types in the ocean can be fast in swift currents (weeks to months) but is generally slower (decades to centuries) within and between ocean gyres (*24*). In the high latitudes, exclusion is generally rapid relative to dispersal and intergyre exchange, and diversity is consequently lower. In the tropical and subtropical oceans, the exclusion time scale is typically long relative to the redistribution of phytoplankton by dispersal. Here, a higher diversity of similar R^* types can be maintained.

In the "hot spots" of highest phytoplankton diversity, ocean dynamics, such as lateral advection and stirring due to planetary waves, mix organisms from different habitats. For example, the elevated diversity in the region of the Gulf Stream reflects the rapid poleward and eastward advection of organisms adapted to tropical and subtropical environments, as has been observed (*25*). As the boundary current transports away the subtropical communities and their environments, the transported waters are mixed and their phytoplankton intermingled with locally adapted organisms and eventually outcompeted. The exclusion time scale here is long relative to the advective time scale, and the transported population contributes to the local total biomass and diversity (Fig. 1A). Similar processes are responsible for the enhanced diversity in the tropical Eastern Pacific. In contrast, the energetic Antarctic Circumpolar Current region has low diversity because the near-zonal circumpolar flow acts as a barrier to, and not an agent of, communication between marine provinces.

Although the global model presented here is a simplified system, the emergent patterns of diversity show features generally consistent with the sparse observations of marine microbial diversity. The model's diversity patterns primarily reflect a balance between dispersal and competitive exclusion, with the latter modulated by environmental variability. Both neutral coexistence and niche differentiation play important roles in regulating the diversity and biogeographies of model phytoplankton (*26*). Such a modeling approach might be extended to explicitly reflect a broader spectrum of marine organisms, such as heterotrophic microbes and zooplankton, and enable comparison with more observational data sets. The roles of other processes, including speciation and climate change, should also be explored. Further laboratory or mesocosm experiments might be designed to address the potential for coexistence of microbes with equal fitness. New, molecular approaches (*5*, *6*) will enable efficient, systematic surveys in the near future, and we suggest that a targeted survey of phytoplankton diversity (prokaryotes and eukaryotes), crossing from a subpolar regime, across a boundary current, dispersal-dominated region (the model hot spots), and into the interior of a subtropical gyre, could provide a valuable test of the hypothesized patterns and mechanisms that emerge from this study.

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