Limnology and Oceanography FLUIDS & ENVIRONMENTS

ORIGINAL ARTICLE

Dispersal, eddies, and the diversity of marine phytoplankton

Sophie Clayton, Stephanie Dutkiewicz, Oliver Jahn, and Michael J. Follows

Abstract

We examined the role of physical dispersal in regulating patterns of diversity of marine phytoplankton in the context of global ocean simulations at eddy-permitting and coarse resolutions. Swifter current speeds, faster dispersal, and increased environmental variability in the higher-resolution model enhanced local diversity almost everywhere. In the numerical simulations, each resolved phytoplankton type was characterized as "locally adapted" at any geographical location (i.e., having net local biological production and physical export) or "immigrant" (i.e., net local biological loss but a population sustained by immigration via physical transport). Immigrants accounted for a higher fraction of the total diversity in the equatorial and subtropical regions, where the exclusion timescale is long relative to the physical transport between "provinces." Hotspots of diversity were associated with western boundary currents and coastal upwelling regions. The former had high locally adapted diversity within the core of the current system, maintained by confluence of upstream populations and the induction of nutrient resources, as well as environmental variability associated with mesoscale eddies. Downstream of strong nutrient sources, convergence of populations led to immigrant-dominated diversity. The numerical simulations provide testable predictions of patterns in diversity and hypotheses regarding the mechanisms that control them. Molecular approaches to characterizing diversity in microbial populations will provide a means to test these hypotheses.

Keywords: plankton, biodiversity, hotspots

Introduction: Dispersal and Diversity in the Ocean

[1] Phytoplankton diversity is important for the stability and functioning of the oceanic ecosystem and ocean biogeochemical cycles (Ptacnik et al. 2008). However, patterns of phytoplankton diversity remain poorly constrained due to the effort and expense of gaining appropriate data sets by traditional microscopic methods (Irigoien et al. 2004). As a consequence, mechanisms regulating patterns of phytoplankton biodiversity remain largely unexplored. Here we examine numerical simulations of global phytoplankton populations to develop testable hypotheses of both the patterns of diversity and their underlying causes.

[2] In this study, we focus on the role of physical transport and dispersal, which has long been recognized as a population-structuring mechanism in ecosystems (MacArthur and Wilson 1967; Shmida and Wilson 1985; Chesson 2000). Recent studies have examined the role of dispersal in sustaining and enhancing regional biodiversity of organisms in a range of aquatic

Limnology and Oceanography: Fluids and Environments • 3 (2013): 182–197 • DOI 10.1215/21573689-2373515 © 2013 by the Association for the Sciences of Limnology and Oceanography, Inc.

Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, USA

Correspondence to Sophie Clayton, sclayton@mit.edu and terrestrial environments (Loreau and Mouquet 1999; Cadotte 2006; Gilbert 2012). However, mesocosm studies indicate that the role of dispersal strongly depends on the specific circumstances. Small-scale experimental studies have found that, depending on the local environment, dispersal may or may not influence the local community structure (Matthiessen and Hillebrand 2006; Vanormelingen et al. 2008). The impact of dispersal depends upon the relative timescales of immigration, exclusion, and speciation. (In the models studied here we will assume that speciation rates are much slower.) With regard to marine phytoplankton, the role of transport and connectivity has received significant attention in shelf and coastal environments (Palmer and Strathmann 1981; Cowen et al. 2006; Aiken and Navarrete 2011). Few studies have addressed similar issues in the open ocean, although, notably, Chust et al. (2013) found in their analysis of Atlantic Meridional Transect taxonomic data that phytoplankton communities along the transect could be explained by both niche differentiation and dispersal limitation.

[3] Though large-scale surveys of open-ocean marine phytoplankton diversity are still relatively scarce, microscope-based taxonomic analyses of transects in the Atlantic basin (Cermeño et al. 2008) and North Pacific (Honjo and Okada 1974) suggest hotspots of high diversity associated with productive regions off the west coast of North Africa, in the Patagonian shelf region, and in the Kuroshio Extension. These hotspots, identified from in situ data, are consistent with interpretation of phytoplankton functional groups from remote observations (D'Ovidio et al. 2010), as well as in numerical simulations of the global ocean (Barton et al. 2010), both arguing that the confluence of biomes maintains hotspots of enhanced phytoplankton diversity in the global ocean. An idealized model (Adjou et al. 2012) supports the inference that physical transport acts rapidly enough to be significant in shaping the diversity of planktonic ecosystems.

[4] Hotspots of phytoplankton diversity are associated with regimes of instability and enhanced eddy kinetic energy (EKE) (although the mesoscale was not resolved in the study of Barton et al. [2010]). This is consistent with the view that intermediate levels of disturbance facilitate the maintenance of diversity (Connell 1978; Huisman 2010), as shown in field experiments (Paine and Vadas 1969; Flöder and Sommer 1999). Here we use a finer resolution ocean model to examine the impact of meso- and finer-scale phenomena. Other recent modeling studies have focused on the role of mesoscale eddies with horizontal scales on the order of 10-100 km, and submesoscale features O(<1 km), in setting rates of productivity (Lévy et al. 2001; Rivière and Pondaven 2006) and organizing community structure (Bracco et al. 2000; Lima et al. 2002; Perruche et al. 2011), though they explicitly resolve a limited number of phytoplankton types. Bracco et al. (2000) noted that two competing phytoplankton types were able to coexist in an eddying domain, where ringlike eddy structures provided a refuge for a type that would otherwise be excluded, consistent with in situ observations of plankton communities in, for example, a North Atlantic cold-core ring (Ring Group 1981) and the interpretations of remotely sensed communities (D'Ovidio et al. 2010).

[5] Mesoscale and submesoscale features are also associated with narrower, swifter currents and strong shear, which can increase the efficiency with which populations are mingled. Thus fine-scale features may enhance regional or local diversity by enhancing the niche space and/or by enhancing the mixing of populations. At the same time, the intermittent nutrient supplies, which are associated with such features, can also drive down diversity by strongly selecting for the fastest-growing opportunist (Levin and Paine 1974; Barton et al. 2010). Consequently, the net effect of mesoscale and submesoscale motions on diversity is not clear.

[6] We used global simulation of ocean circulation, nutrient cycles, and phytoplankton communities to investigate the role of transport and mesoscale motions in regulating patterns of diversity in the phytoplankton. We quantified the contribution of biological processes and physical transport in maintaining patterns of diversity in the simulations. By comparing simulations that are identical in all respects except for the physical resolution of the ocean circulation, we examined how mesoscale features affect global patterns of diversity.



^{© 2013} by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689

Methods

[7] Central to this study are numerical simulations of global ocean circulation, biogeochemical cycles, and diverse plankton populations, based on the Massachusetts Institute of Technology general circulation model (MITgcm; Marshall et al. 1997) incorporating biogeochemical and ecological components as detailed in Dutkiewicz et al. (2009).

Physical Configurations

[8] We used two configurations of the physical model developed by the Estimating the Circulation and Climate of the Oceans (ECCO) project. The first, ECCO2, employs a cubed-sphere grid with horizontal grid dimensions of $\sim 18 \text{ km}$ (Menemenlis et al. 2008), which resolves mesoscale features in the tropics and is eddy permitting in subpolar regions where the radius of deformation is comparable to the grid scale. To elucidate the role of the resolved mesoscale motions we compared with the coarser $(1^{\circ} \times 1^{\circ} \text{ horizontal})$ resolution ECCO-Global Ocean Data Assimilation Experiment (GODAE) state estimate (Wunsch and Heimbach 2007). Both physical configurations were integrated from 1992 to 1999 and constrained to be consistent with observed hydrography and altimetry. Here we refer to the higher-resolution simulation ECCO2 as HR, and the coarser-resolution ECCO-GODAE simulation as CR.

Biogeochemical and Ecological Model

[9] The model transports inorganic and organic forms of nitrogen, phosphorous, iron, and silica and resolves 78 phytoplankton types and two simple grazers (Dutkiewicz et al. 2009). The biogeochemical and biological tracers interact through the formation, transformation, and remineralization of organic matter. Excretion and mortality transfer living organic matterial into sinking particulate and dissolved organic detritus, which are transpired back to inorganic form. The time rate of change in the biomass of each of the modeled phytoplankton types, P_j , is described in terms of a lighttemperature-, and nutrient-dependent growth, sinking, grazing, mortality, and transport by the fluid flow.

[10] Seventy-eight phytoplankton types were initialized with a broad range of physiological attributes and were randomly assigned to one of two broad size classes. Larger cells were assumed to be "opportunists" with higher maximum growth rates but lower nutrient affinities in oligotrophic conditions. Small size class cells were assumed to be "gleaners" with the opposite characteristics. Additional characteristics were assigned stochastically and included light and temperature sensitivities of growth. Each of the 78 types was initialized at low, identical biomass in the physical-biogeochemical model in which explicit competition selected for the regionally varying community structure over the course of a few years of simulation. To ensure that the ecological components of the fine- and coarse-resolution calculations were identical, we initialized the populations and biogeochemical forcing (incident photosynthetically active radiation, aerial iron dust inputs) identically. The physiological parameters of the 78 seeded phytoplankton types were also set to be identical in both integrations. In both cases, the model was integrated for 8 yr from 1992 to 1999, and the ecological analysis was performed on the solution from the final year of integration.

[11] Variations of this ecological model, configured with ECCO-GODAE physics, have already been used to study a range of questions in phytoplankton ecology, for example, the organization of the biogeography of diazotrophic phytoplankton (Monteiro et al. 2011; Dutkiewicz et al. 2012) and the role of top-down controls in regulating phytoplankton diversity (Prowe et al. 2012).

Results

[12] The circulation state estimates differ reflecting model resolution: EKE and the variance of sea surface temperature (SST) were elevated in the HR solution, compared with the CR simulation (Fig. 1). The greatest differences in both SST variance and EKE were found in the temperate mid and high latitudes. Notably, western boundary currents were narrower and swifter in the finer resolution configuration, as was the equatorial Pacific upwelling.

Modeled Phytoplankton Diversity

[13] We mapped the modeled phytoplankton taxonomic richness, α (Figs. 2A and 3A), measured as the total



^{© 2013} by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689



Fig. 1 A — Annual eddy kinetic energy (EKE) ($m^2 s^{-2}$). B — Sea surface temperature (SST) variance ($^{\circ}C^2$) in the high-resolution (HR) model. White contour lines indicate phytoplankton diversity (α) hotspots ($\alpha > 10.2$ for HR and $\alpha > 7.5$ for the coarse-resolution model [CR], where α is expressed in terms of taxonomic richness). The bottom panels show the difference in EKE (C) and SST (D) variance between the two models (HR–CR).

number of distinct phytoplankton types persisting with an annual average biomass that exceeded a threshold of 0.001% of the total biomass in that grid cell following Barton et al. (2010). There was a strong qualitative agreement between models in the large-scale patterns of α indicating that, for this system, resolving mesoscale motions did not change the first-order, large-scale controls relative to coarser simulations (e.g., Barton et al. 2010; Prowe et al. 2012). In both simulations there was a background, meridional gradient with low α in the highly seasonal, subpolar oceans and intermediate α in the low-seasonality, subtropical, and tropical regimes (see Barton et al. 2010). This was overlain by hotspots of relatively high α associated with the Gulf Stream and the Kuroshio Current, upwelling regions off the west coasts of Africa, South America, and North America, and the Agulhas Retroflection and Brazil–Malvinas Confluence zones.

© 2013 by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689





Fig. 2 A — Annual average diversity (α) in the surface layer of the high-resolution (HR) configuration. Diversity is defined as the total number of phytoplankton types with biomass greater than 0.001% of the total phytoplankton biomass. Black contour lines indicate phytoplankton diversity hotspots ($\alpha > 10.2$, where α is expressed in terms of taxonomic richness). B — Annual average Shannon–Weaver index of diversity (H') in the surface layer of the HR configuration.

[14] We also calculated the Shannon–Weaver index of biodiversity, H':

$$H' = -\sum_{j=1}^{n} p_j \ln p_j,$$
 (1)

where p_i is the proportion of biomass of phytoplankton type P_i with respect to the total phytoplankton biomass in each grid cell, summed over the total number of phytoplankton types, n. H' is a measure of both the phytoplankton type richness and the evenness of the phytoplankton community in each grid cell. The patterns in H' for the HR configuration (Fig. 2B) were in agreement with the global patterns of local diversity (α). Differences between these two quantities highlight regions where the evenness of the community may be high, despite low diversity, or vice versa. The diversity hotspots were evident in both maps of α and H', suggesting that these are regions not only of high species richness, but also relative evenness. Conversely, bands of high H' were present in the Southern Ocean, where α was low, highlighting a community with relatively low richness but high evenness.

[15] For the purposes of comparison between the two model configurations, we focus mostly on the modeled phytoplankton richness α . Although the Shannon-Weaver index is a useful metric for diversity and community structure, this also makes it somewhat harder to interpret differences between the model configurations as it reflects differences in both species richness and evenness of the community as a whole. Despite the qualitative agreement in pattern, α was significantly enhanced almost everywhere when mesoscale motions were resolved in the HR configuration (Fig. 3B) which had global mean \pm standard deviation $\alpha = 6.9 \pm 3.4$, compared with 5.3 ± 2.3 in the CR case. On a regional basis, α was enhanced by as much as a factor of two in the higher-resolution integration. The largest enhancement was associated with the hotspots, which we defined (somewhat arbitrarily) as regions where α was greater than the mean α plus one standard deviation (in practice, $\alpha > 10.2$ in HR and $\alpha > 7.5$ in CR) as contoured in Figs. 2A and 3A.

[16] The enhanced local diversity throughout the HR simulation did not occur because it supported more, or different, phytoplankton phenotypes in the global sense. Indeed, the global scale–simulated phytoplankton community structure was remarkably similar between the two resolutions. Of the many tens of potentially viable phenotypes seeded into each integration the same subset dominated the biomass of both solutions. This is illustrated in Fig. 3, which shows the rank of

```
© 2013 by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689
```





Fig. 3 A — Annual average diversity in the surface layer of the coarse-resolution (CR) configuration. Black contour lines indicate phytoplankton diversity hotspots ($\alpha > 7.5$, where α is expressed in terms of taxonomic richness). B — Difference in annual average diversity between the high-resolution (HR) and CR configurations (HR–CR).

global, annually averaged, abundance of phytoplankton types in the two simulations. The differences were remarkably small; although the key players do not have identical ranking of global abundance in both cases, the global phytoplankton community, which contributes to biomass above the threshold criterion, was composed of exactly the same subset of 32 types (of a possible 78). These 32 types represented the global diversity, γ , of the global phytoplankton community in both model configurations. Thus global phytoplankton diversity, γ , was unaffected by the enhanced resolution in this system.

[17] It is perhaps surprising that, in the HR simulation, a different subset of phenotypes was not selected for, since it potentially resolves a wider range of environmental regimes and niches. Instead, it modified the biogeography of the same global set of phenotypes that was selected for in the CR simulation. We note that this could be an artifact of the somewhat simple model of phytoplankton physiology used in the simulation. Alternatively, regardless of the physiological model, our jump in resolution from 1° to 1/6° may not have been sufficient to result in a change in the global phytoplankton community (Fig. 4).

[18] β -diversity, calculated using additive partitioning (Lande 1996; Veech et al. 2002) so that

 $\beta = \gamma - \alpha$, represents the number of phytoplankton types present in the global pool that were not represented in a given grid cell. This provides a relative measure of local and global diversity. Increasing the ocean model's physical resolution did not change simulated γ diversity while α diversity increased almost everywhere, and thus β decreased locally and the community composition became more homogeneous on a grid cell-to-grid cell basis in the HR configuration. This virtual ocean system behaved consistently with predictions from ecological theory that, as rates of dispersal increase, α diversity will increase while β diversity decreases (Cadotte 2006). In this system, the increase in physical resolution enhances dispersal rates by narrowing and swiftening boundary currents and by explicitly resolving swift transports associated with eddy stirring.

Quantifying the Role of Transport

[19] We used the ocean simulations, which can be analyzed comprehensively and quantitatively to ask whether rapid immigration, overpowering competitive exclusion, causes the model's hotspots of diversity. Within a control area (here a model grid cell), any particular phytoplankton type will persist because it either has a net biological source balanced by physical export or

```
© 2013 by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689
```





Fig. 4 A — The ranking of globally integrated, annual average abundance of phytoplankton types in A — the high-resolution (HR) and C — coarse-resolution (CR) simulations. B — The difference between HR and CR simulations.

there is a source due to immigration balanced by a net biological loss. We can formally quantify these possibilities in the numerical model since the rate of change of the biomass of phytoplankton type j, P_j , in a grid cell is defined by the prognostic equation

$$\frac{\partial P_j}{\partial t} = \underbrace{\mu_{\text{NET}_j}(I, T, N, Z)P_j}_{\text{net growth}} - \underbrace{\mathbf{u}. \nabla P_j + \nabla.(K \nabla P_j)}_{\text{advection and mixing}}.$$
 (2)

Here $\mu_{\text{NET}_{I}}$ (*I*,*T*,*N*,*Z*) represents the net local growth rate of phytoplankton *j*, which is a function of light levels (*I*), temperature (T), limiting nutrients (N), grazing by zooplankton (Z), and other sources of mortality. The transport term combines advection by currents (**u**) and subgrid scale mixing, which is parameterized as a down-gradient diffusion where *K* is the eddy diffusivity. Both net growth and transport can be either positive or negative, but over sufficiently long timescales a steady state is achieved such that, in the long-term average, $\partial P/\partial t = 0$. Here we examine the annual mean contributions over the last year of the integration. For most phytoplankton types, the long-term drift in abundance is small relative to the contributions from net growth and transport. In this case, sources/sinks of phytoplankton biomass from physical processes

diffusion are balanced by sinks/sources of biomass generated by local net growth. By quantifying the time-mean of $\mu_{\rm NET_i}$ for each modeled phytoplankton type we can separate them into two categories at each location, or grid cell, identified spatially by (x, y): *immi*grant types, defined as those phytoplankton with $\mu_{\text{NET}_i}(x, y) < 0$, and *local*ly adapted types defined as those phytoplankton with $\mu_{\text{NET}_i}(x, y) > 0.$ Immigrant types are maintained by a source due to transport from elsewhere, but

including transport and

are not best adapted to local environmental conditions. The source is balanced by a loss due to competitive exclusion, and if transport were shut off they would disappear from the local population. Conversely, locally adapted types thrive in the local environment, which leads to a net population growth, balanced by an export by advection or mixing. The total annually averaged richness at any location, $\alpha(x, y)$ is the sum of contributions from α_{I} , the richness of immigrant types, and α_{LA} , the richness of locally adapted types; $\alpha(x, y) = \alpha_{I}(x, y) + \alpha_{LA}(x, y)$, and we can characterize the relative contributions of these categories to diversity at any grid cell. In the same way, we can determine the contributions of immigrant and locally adapted types to H' such that $H'(x, y) = H'_{I}(x, y) + H'_{LA}(x, y)$.

Global Distributions of α_{LA} and α_{I}

[20] Global distributions of α_{LA} and α_{I} in the ocean model revealed some clear large-scale patterns (Fig. 5): α_{LA} is generally low in the subtropics and tropics but elevated in the temperate and high northern latitudes, and α_{I} was generally low in the subpolar and polar oceans but elevated over large regions of the tropics and eastern subtropical gyres. The distribution of α_{I}



^{© 2013} by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689



Fig. 5 Taxonomic diversity of locally adapted types (α_{LA} ; A) and immigrant types (α_i ; B) in the high-resolution (HR) run and the difference between the HR and coarse resolution (CR) runs (C and D, respectively). Black contour lines on the upper panels indicate the phytoplankton diversity hotspots ($\alpha > 10.2$, where α is expressed in terms of taxonomic richness).

(Fig. 5B) shows that the model's tropical and subtropical diversity was maintained almost entirely by dispersal, where co-occurrence was facilitated by immigration and a majority of the types present had negative biological population growth. The converse was true in the model's subpolar regions. The hot spots apparent in total diversity, α , were evident in both α_{LA} and α_{I} distributions; those associated with western boundary currents were generally high α_{LA} regimes, and those associated with eastern boundaries and upwellings were mostly regions of high α_{I} . The richness of immigrant

types, α_{I} , was greater almost everywhere in the HR than in the CR solution. There were also marked differences in α_{LA} , but these were more localized and strongly associated with diversity hot spots. These patterns were also evident in the global distributions of H'_{LA} and H'_{I} (Fig. 6), and there was good qualitative agreement between the partitioned Shannon–Weaver index and partitioned diversity. However, a smaller contribution of immigrant types to H' was observed downstream of the western boundary currents. This suggests that, although many immigrant phytoplankton types were present in these

© 2013 by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689





Fig. 6 Shannon – Weaver index of diversity for locally adapted types (H'_{LA}: A) and immigrant types (H'_i; B) for the high-resolution (HR) model configuration.

regions (as shown by α_I), the community of immigrants was less even than that of locally adapted types.

Discussion

[21] The results of this study raised several questions. First, what drives the dominance of $\alpha_{\rm I}$ throughout the subtropical regions of the model ocean? Second, why do the hotspots fall into two groups—one dominated by dispersal, as anticipated by Barton et al. (2010) and D'Ovidio et al. (2010), and the other dominated by local growth? Third, how do mesoscale eddies enhance disturbance and diversity—that is, what are the relative roles of enhanced transport and environmental heterogeneity?

Why Does Dispersal Dominate Diversity in the Subtropics?

[22] The oligotrophic subtropical oceans are populated by predominantly small cell types adapted to existence at low subsistence concentrations of nutrients, with tightly coupled losses due to rapid predation. This was captured in the simulations, where the subtropical phytoplankton populations were dominated by the most effective gleaners, which have similar fitness as measured by R^* , the subsistence concentration of the limiting nutrient (Dutkiewicz et al. 2009; Barton et al. 2010). This leads to competitive exclusion timescales that are long relative to transport timescales, so any given phytoplankton type only thrives (i.e., has positive μ_{NET}) in a small region. However, it will be efficiently transported away from this source region and contribute to local diversity nearby due to the long exclusion timescale. Hence diversity in the subtropics of the numerical simulation was dominated by α_{I} (Fig. 7), consistent with the interpretation of Barton et al. (2010). In this case, we are not referring to intergyre dispersal of phytoplankton types, but rather an intragyre dispersal of phytoplankton types adapted to the region. In effect, our result agrees with the findings of Chust et al. (2013) that phytoplankton communities in the subtropics are controlled predominantly by niche segregation rather than by largescale dispersal.

What Governs the Pattern and Intensity of Hotspots?

[23] The hotspots fell into two broad categories: those associated with western boundary currents and similar features (Gulf Stream, Kuroshio, Malvinas–Brazil, and Agulhas), which were dominated by locally adapted types ($\alpha_{LA} > \alpha_I$) (Fig. 5); and those associated with eastern boundary currents and associated upwellings, which were generally dominated by immigrant types ($\alpha_I > \alpha_{LA}$). The hotspots can be understood as a combination of three mechanisms: the confluence of water masses that mingles populations from diverse upstream provinces, the injection of nutrient resources into this



^{© 2013} by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689



Fig. 7 Proportion of the total diversity (γ) in the high-resolution (HR) simulation that can be attributed to immigrant types (α_i). The black contour lines indicate the diversity hotspot regions where $\alpha > 10.2$. (α is expressed in terms of taxonomic richness.)

confluent region, which further stimulates the growth of the mixture of phenotypes, and disturbance in the form of spatial and temporal variability of the environment.

Locally Driven Hotspots

[24] The four western boundary regions are confluences of different water masses and their resident phytoplankton populations (Yamamoto et al. 1988; Lillibridge et al. 1990; D'Ovidio et al. 2010). The Gulf Stream and Kuroshio mix together waters of subtropical and subpolar origin. The Malvinas-Brazil current brings together waters from the subtropical Atlantic and the Antarctic circumpolar region. The Agulhas region is a confluence of Indian and Southern Ocean waters. We might expect that the swift currents that feed these confluences have transported phytoplankton types far from their region of origin, to which they are adapted and that their populations would be declining in the confluence region. However, in these regions, the dominance of α_{LA} (the sum of types for which $\mu_{\text{NET}} > 0$), suggests that most of these immigrants thrive in the confluence region. The question remains as to why this is so.

[25] The growth of the disparate immigrant phytoplankton was increased by an enhanced supply of nutrient resources associated with the confluence. For example, the Gulf Stream and Kuroshio Extension regimes are regions where (in the annual mean) there is a vigorous source of macronutrients due to the outcropping of subsurface nutrient streams (Pelegri et al. 1996; Williams et al. 2006). These are strong, polewardflowing "rivers" of nutrients associated with the western boundary currents, bringing nutrient-rich water masses originating in southern hemisphere, sub-Antarctic mode-water formation, to northern mid-latitudes. At the intergyre boundary, the nutrient-rich density surfaces outcrop in the winter, fueling local productivity (Williams et al. 2006), coincident with the region of lateral confluence of biomes in the associated jet. Similarly, the Brazil-Malvinas current confluence coincides with the outcropping of macronutrient-rich waters originating in the Pacific basin, as well as essential iron transported in the atmosphere from the South American continent (Jickells et al. 2005). The Agulhas hotspot region is fueled by nutrient-rich Southern Ocean water (Chapman et al. 1987). Thus all these "locally driven" hotspot regions are defined by a confluence of "seed" phytoplankton populations coincident with a region of enhanced nutrient supply. Additionally, high environmental variability in all of these regions (Fig. 1) ensures that the local net growth rates of phytoplankton types with very different temperature requirements could be intermittently favored.

Dispersal-Driven Hotspots

[26] The dispersal-driven hotspots (Fig. 5) appeared further offshore of the locally driven hotspots in the western boundary currents and also near key eastern upwelling regions (e.g., North Africa and North and South America). Two examples are illustrated in Fig. 8: one in the Kuroshio Extension, and another from an upwelling region off the coast of Peru and northern Chile. In both cases we found that the dispersal-driven hotspot was driven by the transport and convergence of phytoplankton types from different regions. As illustrated, they were downstream of locally driven diversity hotspots, enhanced by high nutrient supply. In the Kuroshio region, the high diversity from the locally driven hotspot was transported by the jet beyond the region of high nutrient induction, and the downstream diver-



^{© 2013} by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689



Fig. 8 The black arrows show the mean surface velocity for the Kuroshio Extension region (A) and the Chile and Peru coastal upwelling zone (B). Both panels show immigrant types (α_{li} , color map), with black contour lines indicating the region where α_{LA} (locally adapted types) ≥ 6 .

sity was maintained only by transport; most phytoplankton types are immigrants ($\mu_{\text{NET}} < 0$) here. It is worth noting that we found a somewhat different pattern in H'_{I} for the western boundary current regions. Although the richness of phytoplankton in these regions was relatively high, H'_{I} was low, suggesting that the immigrant phytoplankton types did not represent an equal proportion of the total biomass. Offshore of Peru (Fig. 8B) the locally adapted species thriving in the upwelling region are transported offshore. As the rate of nutrient supply declines, the net growth rate of most types shifts from positive to negative, driving α_{I} up at the expense of α_{LA} . The immigrant populations also converge upon, and mingle with, the local, subtropical species, thus generating an immigrant-driven hotspot.

An Idealized Model of Hotspots

[27] We explored the mechanisms underpinning the locally adapted and dispersal-driven hotspots with a simple box model, depicted in Fig. 9A, and described in detail in the appendix. Briefly, we represented two provinces (A and B), each populated by a single phytoplankton type, P_1 and P_2 , respectively. These populations were fed by lateral volume flow (ψ_A , ψ_B) into a confluence zone (C) that could also receive an



Fig. 9 A — Schematic box model of confluence region in the surface ocean. Boxes A and B represent upstream biomes which are fed by lateral transport (with volume flows ψ_A and ψ_B) into a confluence region C, where water masses intermingle. An additional external source of nutrients may also feed into the confluence region, associated with volume flux ψ_C , representing induction from deeper waters. See the appendix for model details. B — Immigration ensures coexistence in the equilibrium population of region C for any case where ψ_A and ψ_B are positive. The steady state model solutions result in three distinct regimes: where both populations exhibit positive net biological growth, where the net biological growth of one is positive and the other negative, and finally where both have negative net biological growth.

© 2013 by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689



additional volume flow $(\psi_{\rm C})$ bringing a nutrient resource, representing induction of nutrients from below the euphotic zone. We integrated the model numerically to a steady-state solution (Fig. 9B) by using a range of parameter values plausible for the oceanic environment, with particular respect to western boundary and eastern boundary current systems.

[28] Regimes of the equilibrium population in the confluence region C are mapped as a function of the ratio of the volume fluxes through the system, referenced to ψ_A in Fig. 9B. (Model equations and parameter values are given in the appendix.) The *x*-axis measures the relative volume flow from provinces A and B into the confluence region C, thus indicating the relative delivery rates of P_1 and P_2 . The *y*-axis measures ψ_C/ψ_A and thus indicates the relative rate of delivery of additional resource by induction into the confluence region C.

[29] As long as ψ_A and ψ_B are both into box C (i.e., $\psi_B > 0$ and $\psi_A > 0$), then P_1 and P_2 coexist, though P_2 may be at extremely low abundance, maintained only by immigration. Three regimes of the solution are indicated, and they depend largely on the delivery of additional resources to the confluence region, and thus ψ_C/ψ_A . When the injection of nutrients to the confluence region is low (ψ_C/ψ_A is small), then neither P_1 nor P_2 has a positive net growth rate ($\mu_{\text{NET}} < 0$). With an intermediate nutrient input to C, the most competitive phytoplankton type, P_1 , will have positive net growth rate, whereas the weaker competitor, P_2 , persists in C only through transport and has a negative net growth rate. Finally, when the nutrient supply to C is high, both phytoplankton types have positive net growth rates.

[30] This idealized system reinforces our interpretation of the global ocean model, where regions of confluence of biomes are diversity hotspots. Those that coincide with induction of resources from below (e.g., Gulf Stream and Kuroshio Extension) are stimulated and dominated by locally adapted types. Those that do not (e.g., downstream of the eastern boundary upwellings) are dominated by immigrant types.

Enhancement of Diversity by Resolved Mesoscale Dynamics

[31] Resolved mesoscale dynamics also shaped the simulated phytoplankton community in two distinct

ways. The first was due to the increased environmental spatial and temporal variability associated with mesoscale eddies (e.g., disturbance; Huisman 2010), which acted to increase the number of potential niches and locally adapted types within a given region. The second was by enhanced dispersal, due to the swifter narrower currents that resulted from resolving the mesoscale, which increased the role of immigration. Regions of elevated α_{I} in the higher-resolution model were thus more intense and more localized and were associated with regions of mesoscale activity and enhanced EKE (see Figs. 1 and 5).

Significance to Aquatic Environments

[32] The question of why phytoplankton populations are so diverse in aquatic environments is long-standing (Hutchinson 1961), and the causes and consequences of patterns of biodiversity are the subject of much discussion in the broader context of ecology (Levin 2000). In marine phytoplankton, several mechanisms may be acting to enhance or suppress biodiversity. In our model, we explicitly represented several of these processes, particularly niche differentiation (Tilman et al. 1982; Johnson et al. 2006), neutral coexistence (Chust et al. 2013; Barton et al. 2010), disturbance (Huisman 2010), and dispersal by ocean currents. The model also included grazing by zooplankton, but such top-down control, which is known to affect diversity (Armstrong 1994; Prowe et al. 2012; Ward et al. 2012), was weak. We did not, however, resolve direct interspecific interactions, which may also play an important role in shaping patterns of diversity (e.g., via allelopathy; Legrand et al. 2003; Hulot and Huisman 2004), particularly during phytoplankton blooms.

[33] Here we have used an explicit simulation of ocean currents and diverse plankton populations to focus on the role of transport by ocean circulation and mesoscale eddies. The numerical simulations captured observed features, notably key hotspots associated with western boundary currents (Honjo and Okada 1974; Cermeño et al. 2008; D'Ovidio et al. 2010) and allowed us to explicitly quantify the relative roles of physical transport and biological growth and loss in regulating local community composition and diversity. Our analysis suggests that physical transport is important in



supplying diverse "seed populations" to the hotspot regions as hypothesized by Barton et al. (2010) and D'Ovidio et al. (2010) and consistent with the enhanced role of immigration inferred by Chust et al. (2013). However, we also found that the simulated hotspots were enhanced when the confluence was associated with high rates of nutrient supply and environmental variability.

[34] The confluence regions were associated with swift, baroclinically unstable regimes (i.e., regions where the gradients in pressure were mismatched with the gradients in fluid density), characterized by enhanced eddy activity. When resolved at finer spatial scales, mesoscale eddies provided additional spatial and temporal disturbance, enhancing the intensity of the hotspots over coarse resolution simulations. Consistent with the arguments of Huisman (2010), disturbance played an important role in maintaining the patterns of diversity, though other factors such as dispersal were also important.

[35] The ability to quantify any state variable or flux makes numerical simulations a powerful tool for examining mechanisms and interpreting patterns. The numerical simulations presented here have enabled us to develop some clear predictions of patterns of diversity in the marine phytoplankton, as well as testable hypotheses to explain those patterns. Such predictions and hypotheses provide a context, and highlight the need for, further observations of large-scale patterns of phytoplankton diversity in the ocean. Classical taxonomic observations, using microscopy, have provided invaluable resources in this regard, for example, the microscopic analyses along the Atlantic Meridional Transect discussed by Irigoien et al. (2004) and Cermeño et al. (2010) and in the North Pacific discussed by Honjo and Okada (1974). However, such data sets are extremely labor intensive and expensive to acquire. Hence they are likely to remain scarce. However, new molecular approaches to evaluating diversity and community structure (e.g., for bacterioplankton, Fuhrman et al. 2008; Pommier et al. 2007), as well as activity (Hunt et al. 2013), provide a possible avenue for systematic surveys addressing the predictions and hypotheses arising from numerical simulations, as presented here, and the analysis of existing taxonomic surveys.

Acknowledgments We thank Patrick Heimbach and Chris Hill for technical help with the ECCO-GODAE and ECCO2 physical models. We are grateful for support from National Science Foundation, National Oceanic and Atmospheric Administration, National Aeronautics and Space Administration, and the Gordon and Betty Moore Foundation.

Appendix: Confluence, Nutrient Streams and Diversity—Box Model

[A1] We represent two large, upstream provinces (A and B), which feed a confluence region (C) where the two water masses are intermingled and may receive an additional injection of nutrient resources (Fig. 9A). The populations of A and B, representing subpolar and subtropical biomes, are maintained by volume throughflow (dilution) of ψ_A and ψ_B , respectively, which delivers a resource N and exports phytoplankton, P1 and P2, which exclusively populate A and B, respectively. The outflows of A and B pass into box C, importing the equilibrium resource concentration from each of the upstream boxes as well as their attendant phytoplankton populations. The organisms are intermingled in C and compete for the single resource, which can also be delivered by an independent volume flow, $\psi_{\rm C}$, which represents the induction of nutrients from a subsurface nutrient stream (Pelegri et al. 1996) into the confluence region. Thus region C has a total volume through flow of $\psi_A + \psi_B + \psi_C$. The physiology of P_1 and P_2 is described by Monod kinetics, limited by resource N, and constructed such that P1 has a lower subsistence resource concentration $(R_N^*; e.g., Tilman et al. 1982)$ and so, in the absence of immigration would exclude P_2 in C. The model, depicted in Fig. 9, is described by the following prognostic equations:

$$V_{\rm A} \frac{dN_{\rm A}}{dt} = -\psi_{\rm A} \left(N_{\rm A} - N_{\rm A}^{\rm in} \right) - V_{\rm A} \mu_1 \frac{N_{\rm A}}{N_{\rm A} + K_1} P_{\rm A,1} \tag{A1}$$

$$V_{\rm A} \frac{dP_{\rm A,1}}{dt} = -\psi_{\rm A} P_{\rm A,1} + V_{\rm A} \mu_1 \frac{N_{\rm A}}{N_{\rm A} + K_1} P_{\rm A,1} - m_1 P_{\rm A,1} \qquad (A2)$$

$$V_{\rm B} \frac{dN_{\rm B}}{dt} = -\psi_{\rm B} \left(N_{\rm B} - N_{\rm B}^{\rm in} \right) - V_{\rm B} \mu_2 \frac{N_{\rm B}}{N_{\rm B} + K_2} P_{\rm B,2}$$
(A3)

$$V_{\rm B} \frac{dP_{\rm B,2}}{dt} = -\psi_{\rm B} P_{\rm B,2} + V_{\rm B} \mu_1 \frac{N_{\rm B}}{N_{\rm B} + K_2} P_{\rm B,2} - m_2 P_{\rm B,2}$$
(A4)

$$V_{\rm C} \frac{dN_{\rm C}}{dt} = \psi_{\rm A} N_{\rm A} + \psi_{\rm B} N_{\rm B} + \psi_{\rm C} N_{\rm C}^{\rm in} - (\psi_{\rm A} + \psi_{\rm B} + \psi_{\rm C}) N_{\rm C,1}$$

$$N_{\rm C} N_{\rm C}$$

$$+ V_{\rm C} \mu_1 \frac{N_{\rm C}}{N_{\rm C} + K_1} P_{\rm C,1} - V_{\rm C} \mu_2 \frac{N_{\rm C}}{N_{\rm C} + K_2} P_{\rm C,2} \qquad (A5)$$

$$V_{\rm C} \frac{dP_{\rm C,1}}{dt} = \psi_{\rm A} P_{\rm A,1} - (\psi_{\rm A} + \psi_{\rm B} + \psi_{\rm C}) P_{\rm C,1} + V_{\rm C} \mu_1 \frac{N_{\rm C}}{N_{\rm C} + K_1} P_{\rm C,1} - V_{\rm C} m_1 P_{\rm C,1}$$
(A6)

$$V_{\rm C} \frac{dP_{\rm C,2}}{dt} = \psi_{\rm B} P_{\rm B,2} - (\psi_{\rm A} + \psi_{\rm B} + \psi_{\rm C}) P_{\rm C,2} + V_{\rm C} \mu_2 \frac{N_{\rm C}}{N_{\rm C} + K_2} P_{\rm C,2} - V_{\rm C} m_2 P_{\rm C,2}, \qquad (A7)$$

© 2013 by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689



I

Parameter	Description	Units	Value
P _{i,1}	Phytoplankton abundance	μ mol N L ⁻¹	State variable
P _{i,2}	Phytoplankton abundance	μ mol N L ⁻¹	State variable
Ni	Nutrient concentration	mol N L ⁻¹	State variable
V _A	Volume	L	$1.5 imes 10^{18}$
V _B	Volume	L	$1.5 imes 10^{18}$
V _c	Volume	L	$1.0 imes 10^{17}$
ψ_{A}	Volume flux	Sv (10 ⁶ m ³ s ⁻¹)	5
ψ_{B}	Volume flux	Sv	Variable
ψ_{C}	Volume flux	Sv	Variable
μ_1	Max growth rate	d ⁻¹	0.6
μ_2	Max growth rate	d ⁻¹	0.5
К ₁	Half-saturation	mol N L ⁻¹	0.2
К2	Half-saturation	mol N L ⁻¹	0.2
<i>m</i> ₁	Mortality	d ⁻¹	0.05
<i>m</i> ₂	Mortality	d ⁻¹	0.05
N ⁱⁿ A	Incoming resource concentration	μmol N L⁻¹	4.0
N ⁱⁿ B	Incoming resource concentration	μmol N L ^{−1}	4.0
N ⁱⁿ _C	Incoming resource concentration	μ mol N L ⁻¹	1.0

 Table A1
 Definitions and parameter values for the box model depicted in Fig. 9. Subscripts *i* indicate association with region A, B, or C. The volume of the confluence region, C, is assumed to be much smaller than the volumes of the upstream biomes, A and B.

where *V* is the volume of each box, N^{in} is the supply of *N* into the box, μ is the phytoplankton maximum growth rate, *K* is the half-saturation constant, and *m* is the phytoplankton mortality. We solved numerically for the equilibrium solution of this system, integrating to a steady state. This was done for a range of values of ψ_{B} and ψ_{C} , keeping ψ_{A} constant (Fig. 9B). Variables and parameters are described in Table A1, along with chosen parameter values.

References

- Adjou, M., J. Bendtsen, and K. Richardson. 2012. Modeling the influence from ocean transport, mixing and grazing on phytoplankton diversity. Ecol. Modell. **225**: 19–27. doi:10.1016/j .ecolmodel.2011.11.005.
- Aiken, C. M., and S. A. Navarrete. 2011. Environmental fluctuations and asymmetrical dispersal: Generalized stability theory for studying metapopulation persistence and marine protected areas. Mar. Ecol. Prog. Ser. 428: 77–88. doi:10.3354 /meps09079.
- Armstrong, R. A. 1994. Grazing limitation and nutrient limitation in marine ecosystems: Steady state solutions of an ecosystem model with multiple food chains. Limnol. Oceanogr. 39: 597–608. doi:10.4319/lo.1994.39.3.0597.
- Barton, A. D., S. Dutkiewicz, G. Flierl, J. Bragg, and M. J. Follows. 2010. Patterns of diversity in marine phytoplankton. Science 327: 1509–1511. doi:10.1126/science.1184961.
- Bracco, A., A. Provenzale, and I. Scheuring. 2000. Mesoscale vortices and the paradox of the plankton. Proc. Biol. Sci. 267: 1795–1800. doi:10.1098/rspb.2000.1212.

- Cadotte, M. W. 2006. Dispersal and species diversity: A meta-analysis. Am. Nat. 167: 913–924. doi:10.1086/504850.
- Cermeño, P., S. Dutkiewicz, R. P. Harris, M. Follows, O. Schofield, and P. Falkowski. 2008. The role of nutricline depth in regulating the ocean carbon cycle. Proc. Natl. Acad. Sci. USA 105: 20344–20349. doi:10.1073/pnas.0811302106.
- Cermeño, P., C. de Vargas, F. Abrantes, and P. G. Falkowski. 2010. Phytoplankton biogeography and community stability in the ocean. PLoS ONE. 5: e10037. doi:10.1371/journal.pone .0010037.
- Chapman, P., C. M. Duncombe Rae, and B. R. Allanson. 1987. Nutrients, chlorophyll and oxygen relationships in the surface layers at the Agulhas Retroflection. Deep-Sea Res. 34: 1399–1416. doi:10.1016/0198-0149(87)90134-8.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. **31**: 343–366. doi:10.1146/annurev.ecolsys.31.1.343.
- Chust, G., X. Irigoien, J. Chave, and R. P. Harris. 2013. Latitudinal phytoplankton distribution and the neutral theory of biodiversity. Glob. Ecol. Biogeogr. 22: 531–543. doi:10.1111/geb .12016.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310. doi:10.1126/science.199.4335.1302.
- Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. Science 311: 522–527. doi:10. 1126/science.1122039.
- D'Ovidio, F., S. De Monte, S. Alvain, Y. Dandonneau, and M. Lévy. 2010. Fluid dynamical niches of phytoplankton types. Proc.
- © 2013 by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689



Natl. Acad. Sci. USA 107: 18366-18370. doi:10.1073/pnas .1004620107.

- Dutkiewicz, S., M. J. Follows, and J. G. Bragg. 2009. Modeling the coupling of ocean ecology and biogeochemistry. Global Biogeochem. Cycles **23**: GB4017. doi:10.1029/2008GB003405.
- Dutkiewicz, S., B. A. Ward, F. Monteiro, and M. Follows. 2012. Interconnection of nitrogen fixers and iron in the Pacific Ocean: Theory and numerical simulations. Global Biogeochem. Cycles 26: GB4017. doi:10.1029/2011GB004039.
- Flöder, S., and U. Sommer. 1999. Diversity in planktonic communities: An experimental test of the intermediate disturbance hypothesis. Limnol. Oceanogr. 44: 1114–1119. doi:10.4319 /lo.1999.44.4.1114.
- Fuhrman, J. A., J. A. Steele, I. Hewson, M. S. Schwalbach, M. V. Brown, J. L. Green, and J. H. Brown. 2008. A latitudinal diversity gradient in planktonic marine bacteria. Proc. Natl. Acad. Sci. USA 105: 7774–7778. doi:10.1073/pnas.0803070105.
- Gilbert, B. 2012. Joint consequences of dispersal and niche overlap on local diversity and resource use. J. Ecol. **100**: 287–296. doi:10 .1111/j.1365-2745.2011.01908.x.
- Honjo, S., and H. Okada. 1974. Community structure of coccolithophores in the photic layer of the mid-Pacific. Micropaleontology 20: 209–230. doi:10.2307/1485061.
- Huisman, J. 2010. Comment on "Patterns of diversity in marine phytoplankton." Science **329**: 512–512. doi:10.1126/science .1189880.
- Hulot, F., and J. Huisman. 2004. Allelopathic interactions between phytoplankton species: The roles of heterotrophic bacteria and mixing intensity. Limnol. Oceanogr. **49**: 1424–1434. doi:10 .4319/lo.2004.49.4_part_2.1424.
- Hunt, D. E., Y. Lin, M. J. Church, D. M. Karl, S. G. Tringe, L. K. Izzo, and Z. I. Johnson. 2013. Relationship between abundance and specific activity of bacterioplankton in open ocean surface waters. Appl. Environ. Microbiol. **79**: 177–184. doi:10.1128 /AEM.02155-12.
- Hutchinson, G. 1961. The paradox of the plankton. Am. Nat. 95: 137–145. doi:10.1086/282171.
- Irigoien, X., J. Huisman, and R. P. Harris. 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. Nature **429**: 863–867. doi:10.1038/nature02593.
- Jickells, T. D., et al. 2005. Global iron connections between desert dust, ocean biogeochemistry, and climate. Science **308**: 67–71. doi:10.1126/science.1105959.
- Johnson, Z., E. Zinser, A. Coe, N. McNulty, E. Woodward, and S. Chisholm. 2006. Niche partitioning among *Prochlorococcus ecotypes* along ocean-scale environmental gradients. Science 311: 1737–1740. doi:10.1126/science.1118052.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos **76**: 5–13. doi:10.2307/3545743.
- Legrand, C., K. Rengefors, G. O. Fistarol, and E. Granéli. 2003. Allelopathy in phytoplankton-biochemical, ecological and evol-

utionary aspects. Phycologia **42**: 406–419. doi:10.2216/i0031-8884-42-4-406.1.

- Levin, S. A. 2000. Multiple scales and the maintenance of biodiversity. Ecosystems (N.Y.) **3**: 498–506. doi:10.1007/s100210000044.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. USA. 71: 2744–2747.
- Lévy, M., P. Klein, and A.-M. Tréguier. 2001. Impact of sub-mesoscale physics on production and subduction of phytoplankton in an oligotrophic regime. J. Mar. Res. 59: 535–565. doi:10.1357 /002224001762842181.
- Lillibridge, J. L. III, G. Hitchcock, T. Rossby, E. Lessard, M. Mork, and L. Golmen. 1990. Entrainment and mixing of shelf/slope waters in the near-surface Gulf Stream. J. Geophys. Res. 95 (C8): 13065-13087. doi:10.1029/JC095iC08p13065.
- Lima, I. D., D. B. Olson, and S. C. Doney. 2002. Biological response to frontal dynamics and mesoscale variability in oligotrophic environments: Biological production and community structure. J. Geophys. Res. **107** (C8): 3111. doi:10.1029 /2000JC000393.
- Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. Am. Nat. **154**: 427–440. doi:10 .1086/303252.
- MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton Univ. Press.
- Marshall, J., C. Hill, L. Perelman, and A. Adcroft. 1997. Hydrostatic, quasi-hydrostatic, and nonhydrostatic ocean modeling.
 J. Geophys. Res. 102 (C3): 5733-5752. doi:10.1029 /96JC02776.
- Matthiessen, B., and H. Hillebrand. 2006. Dispersal frequency affects local biomass production by controlling local diversity. Ecol. Lett. **9**: 652–662. doi:10.1111/j.1461-0248.2006.00916.x.
- Menemenlis, D., J. Campin, P. Heimbach, C. Hill, T. Lee, A. Nguyen, M. Schodlok, and H. Zhang. 2008. ECCO2: High resolution global ocean and sea ice data synthesis. Mercator Ocean Q. Newslett. 31: 13–21.
- Monteiro, F., S. Dutkiewicz, and M. Follows. 2011. Biogeographical controls on the marine nitrogen fixers. Global Biogeochem. Cycles **25**: GB2003. doi:10.1029/2010GB003902.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus spp.*, on benthic algal populations. Limnol. Oceanogr. 14: 710–719. doi:10.4319/lo.1969.14.5 .0710.
- Palmer, A. R., and R. R. Strathmann. 1981. Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. Oecologia 48: 308–318. doi:10.1007/ BF00346487.
- Pelegri, J. L., G. T. Csanady, and A. Martins. 1996. The North Atlantic nutrient stream. J. Oceanogr. 52: 275–299. doi:10.1007 /BF02235924.
- Perruche, C., P. Riviere, G. Lapeyre, X. Carton, and P. Pondayen. 2011. Effects of surface quasi-geostrophic turbulence on phy-



^{© 2013} by the Association for the Sciences of Limnology and Oceanography, Inc. / e-ISSN 2157-3689

toplankton competition and co-existence. J. Mar. Res. **69**: 105–135. doi:10.1357/002224011798147606.

- Pommier, T., B. Canbäck, L. Riemann, K. Boström, K. Simu, P. Lundberg, A. Tunlid, and Å. Hagström. 2007. Global patterns of diversity and community structure in marine bacterioplankton. Mol. Ecol. 16: 867–880. doi:10.1111/j.1365-294X.2006 .03189.x.
- Prowe, A. E. F., M. Pahlow, S. Dutkiewicz, M. Follows, and A. Oschlies. 2012. Top-down control of marine phytoplankton diversity in a global ecosystem model. Prog. Oceanogr. 101: 1–13. doi:10.1016/j.pocean.2011.11.016.
- Ptacnik, R., A. G. Solimini, T. Andersen, T. Tamminen, P. Brettum, L. Lepistö, E. Willén, and S. Rekolainen. 2008. Diversity predicts stability and resource use efficiency in natural phytoplankton communities. Proc. Natl. Acad. Sci. USA 105: 5134–5138. doi:10.1073/pnas.0708328105.
- Ring Group. 1981. Gulf Stream Cold-Core Rings: Their physics, chemistry, and biology. Science **212**: 1091–1100. doi:10 .1126/science.212.4499.1091.
- Rivière, P., and P. Pondaven. 2006. Phytoplankton size classes competitions at sub-mesoscale in a frontal oceanic region. J. Mar. Syst. **60**: 345–364. doi:10.1016/j.jmarsys.2006.02.005.
- Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. J. Biogeogr. 12: 1–20. doi:10.2307/2845026.
- Tilman, D., S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology: The role of limiting nutrients. Annu. Rev. Ecol. Syst. 13: 349–372. doi:10.1146/annurev.es.13.110182.002025.

- Vanormelingen, P., K. Cottenie, E. Michels, K. Muylaert, W. Vyverman, and L. De Meester. 2008. The relative importance of dispersal and local processes in structuring phytoplankton communities in a set of highly interconnected ponds. Freshw. Biol. 53: 2170–2183. doi:10.1111/j.1365-2427.2008.02040.x.
- Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: Recent revival of an old idea. Oikos **99**: 3–9. doi:10.1034/j.1600-0706.2002 .990101.x.
- Ward, B. A., S. Dutkiewicz, O. Jahn, and M. J. Follows. 2012. A sizestructured food-web model for the global ocean. Limnol. Oceanogr. 57: 1877–1891. doi:10.4319/lo.2012.57.6.1877.
- Williams, R. G., V. Roussenov, and M. J. Follows. 2006. Nutrient streams and their induction into the mixed layer. Global Biogeochem. Cycles 20: 1–18. doi:10.1029/2005GB002586.
- Wunsch, C., and P. Heimbach. 2007. Practical global oceanic state estimation. Physica D 230: 197–208. doi:10.1016/j.physd .2006.09.040.
- Yamamoto, T., S. Nishizawa, and T. Taniguchi. 1988. Formation and retention mechanisms of phytoplankton peak abundance at the Kuroshio front. J. Plankton Res. 10: 1113–1130. doi:10 .1093/plankt/10.6.1113.

Received: 10 April 2013 Amended: 24 June 2013 Accepted: 9 July 2013



