Does horizontal mixing explain phytoplankton dynamics?

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The modern era of biological oceanography arguably began in 1978 with the successful launch of the Coastal Zone Color Scanner on the Nimbus 7 satellite. Although limited by today's standards, the Coastal Zone Color Scanner provided the first glimpse of the complex, beautiful, and difficult-to-sample interactions between single-celled phytoplankton and the turbulent mixing of the surface ocean. In the intervening decades, oceanographers have made tremendous advances, with more and better ocean color sensors such as the Sea-viewing Wide Field-of-view Sensor, Moderate Resolution Imaging Spectroradiometer, and Medium Resolution Imaging Spectrometer. The PNAS report by d'Ovidio et al. (1) shows us how much further we need to go and provides a glimpse into the true complexity of the surface ocean and the mechanisms driving this ecological landscape.

Three decades of satellite ocean color measurements have led to fundamental observations and discoveries about the role of the microscopic unicellular algae in regulating the biogeochemistry of our planet. We routinely make maps of both terrestrial and ocean plant and algae biomass, using the photosynthetic pigment chlorophyll as a proxy, and link this to the biogeochemical cycling of carbon through estimates of net primary production (2). Although there is certainly room for improvement in these estimates (3), these nearly synoptic measurements show the oceans respond to basin-scale decadal oscillations, such as El Niño and the Atlantic and Pacific Decadal Oscillations (4), and have helped to identify both the short- (decadal) and long-term (centuries) response of the oceans to climate change (5, 6).

Despite the many advances in ocean color, we still rely almost exclusively on estimates of bulk biomass as chlorophyll. Unlike the most simple microscope, chlorophyll alone tells us almost nothing about the individual types of phytoplankton, or the role these groups play in the ocean ecosystem. The report by d'Ovidio et al. (1) begins to unpack this black box by applying a new ocean color method that partitions the bulk optical signal retrieved from satellites into major phytoplankton functional types using a numerical algorithm called PHYSAT (7). PHYSAT takes advantage of the subtle biooptical differences between major groups of phytoplankton, or functional types, to identify
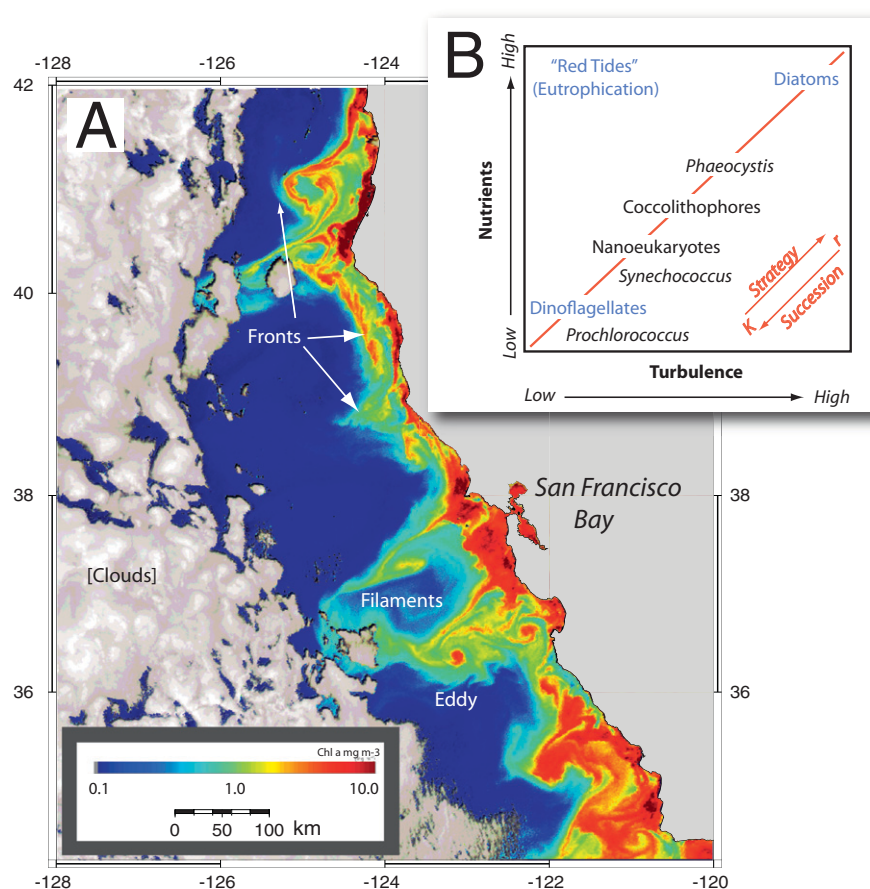
Fig. 1. The introduction of chlorophyll maps from satellites provided a view of the often-complex interactions between phytoplankton and physics in the surface ocean. The large panel (*A*) provides an example of this complexity for coastal California, depicting ocean chlorophyll concentrations from the Sea-viewing Wide Field-of-view Sensor with some typical physical features annotated. The *Inset* (*B*) is an adaptation of the Mandala of Margalef (17), who attempted to map phytoplankton functional types into physicochemical environmental space. Blue functional types were included in the original conceptual diagram. As noted by others (18), the Mandala breaks down for many phytoplankton functional types because the physicochemical control is often more complicated than two factors (i.e., dimensions) can portray. d'Ovidio et al. (1) provide a method for mapping these functional types geospatially using a combination of ocean color and satellite altimetry. This may ultimately allow researchers to move beyond simple chlorophyll maps (*A*) by tracking fluid dynamical niches that integrate the biological response of groups of phytoplankton to their environment, thereby capturing the multidimensional forcing shaping the ocean landscape.

the dominant types of phytoplankton from ocean color. Currently, these functional types include diatoms, coccolithophores, nanoeukaryotes, *Phaeocystis*, *Synechococcus*-like cyanobacteria, and *Prochlorococcus*. Other researchers have developed similar approaches for both phytoplankton size (8) and additional phytoplankton groups such as the nitrogen-fixing cyanobacteria *Trichodesmium* (9), demonstrating that this approach could be extended to at least a few more phytoplankton functional types.

d'Ovidio et al. (1) apply PHYSAT to a region of intense physical mixing, where the Brazil and Malvinas currents interact in the southern hemisphere. They combine the results of PHYSAT with altimetry data from a suite of satellite sensors to estimate sea surface height, from which

they derive the surface current structure of the ocean corresponding to the ocean color measurements. By combining these two remote sensing methods, the authors link the biological landscape from PHYSAT with the physical landscape from altimetry, allowing them to define what they call fluid dynamical niches where the phytoplankton assemblages interact with distinct physicochemical environments. It is thus possible to examine the submesoscale (i.e., tens to hundreds of kilometers) interactions between physics and biology using the synoptic capabilities of modern oceanographic satellites.

Why is this important? First, we can begin to move beyond bulk biology (chlorophyll biomass) and start to assign ecological niches to different water masses. This is important because not all phytoplankton are equal—some, such as diatoms, disproportionately contribute to fisheries and export of organic material to the ocean's depths, whereas coccolithophorids can impact the carbon chemistry of the surface ocean through the formation of calcium carbonate tests or shells. Other groups distinguished by PHYSAT such as *Phaeocystis* produce dimethyl sulfide, molecules that act as cloud condensation nuclei and thus may alter the heat balance of the surface ocean. The ability to identify these phytoplankton functional types from satellites is a tremendous step forward; coupling this to the physical landscape will provide a better understanding of what organisms bloom where, and why (Fig. 1).

Second, these results can provide observational data on spatial and temporal scales appropriate for comparison with sophisticated biological–physical models that also track or predict the distribution of major phytoplankton functional types (10, 11). Although recent models have allowed as many as 78 phytoplankton functional types to interact in a virtual (numerical) ocean (10, 12), it is difficult to validate these models using traditional

oceanographic sampling. By combining observational data such as presented by d'Ovidio et al. (1) with the results of these coupled physical–biological models, we can begin to detangle the physical and biological time scales driving phytoplankton communities, and ultimately the biogeochemistry, in the surface ocean. The combination of empirical methods with models also provides an important reality check on both sets of results. For example, both Barton et al. (12) and d'Ovidio et al. (1) identify regions of horizontal stirring as areas of high biological diversity by providing "ecological windows" for distinct phytoplankton functional types to thrive, so long as the physical landscape continues to support that biological niche.

A fundamental paradox that has challenged oceanographers for decades is how the ocean, which, superficially at least, is relatively homogenous, can support so much diversity; this concept was formalized as the "paradox of the plankton" by G. Evelyn Hutchinson (13). We now know that this paradoxical diversity is supported at least in part by spatial and temporal heterogeneity of factors influencing plankton (e.g., light, nutrients, turbulence) that result in a mosaic of shifting niches rather than a homogenous ocean (Fig. 1) (12, 14). d'Ovidio et al. (1) provide evidence for how this occurs at the mesoscale, and present a possible solution to how the interaction of physical and biological space and time scales both selects for certain types of organisms, allowing for nearly monospecific blooms and recurrent seasonal structure, and also allows for the emergence of seemingly random patterns of phytoplankton succession. The authors argue that the ocean's ecological landscape produces stable fluid dynamical niches within which there is a quasi-homogenous physicochemical environment. This allows a particular group of organisms to thrive, as the submesoscale patches are stable on the same time scale (days to weeks) as phytoplankton bloom development, but this same land-

scape will ultimately destroy these patches through mixing, resulting in competition and succession of the newly mixed phytoplankton functional types. Within this paradigm, the authors argue that previously well-studied examples of physical–biological systems with defined phytoplankton communities, such as mesoscale eddies (15), are simply a special case of the more general phenomenon described in this contribution.

The satellite-based methods used by d'Ovidio et al. (1) are not without their limitations. Currently, PHYSAT provides very coarse resolution, with only five phytoplankton functional types [versus the 78 or more groups included by Follows et al. (10) and the thousands of known marine phytoplankton species]. Analyses are limited to the spatial and temporal resolution available from satellite sensors, and more importantly, represent only the near surface of the ocean. Submesoscale variability in the vertical has also been shown to strongly influence the distribution of plankton that results from the same balance between mixing (turbulence) and the physicochemical environment (16). Nonetheless, compared with our state of knowledge before the launch of modern ocean color sensors, or to the "black box" approach of tracking bulk chlorophyll, these are exciting advances. The authors make a compelling case for tracking these tangled physical/biological fluid dynamical niches when we consider the ecological landscape and the biogeochemical consequences of phytoplankton productivity in the ocean. Techniques such as these bring us one step closer to mapping the ocean's ecological landscape at appropriate space and time scales, a necessary first step toward predicting the biogeochemical processes occurring in the world's oceans.

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