2018

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Original Publication Citation

Fassbender, A. J., Bourbonnais, A., Clayton, S., Gaube, P., Omand, M., Franks, P. J. S., Altabet, M. A., & McGillicuddy Jr., D. J. (2018). Interpreting mosaics of ocean biogeochemistry. EOS, 99, https://doi.org/10.1029/2018EO109707.

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Interpreting Mosaics of Ocean Biogeochemistry

Advances in technology and modeling capabilities are driving a surge in progress in our understanding of how ocean ecosystems mix and mingle on medium to small scales.

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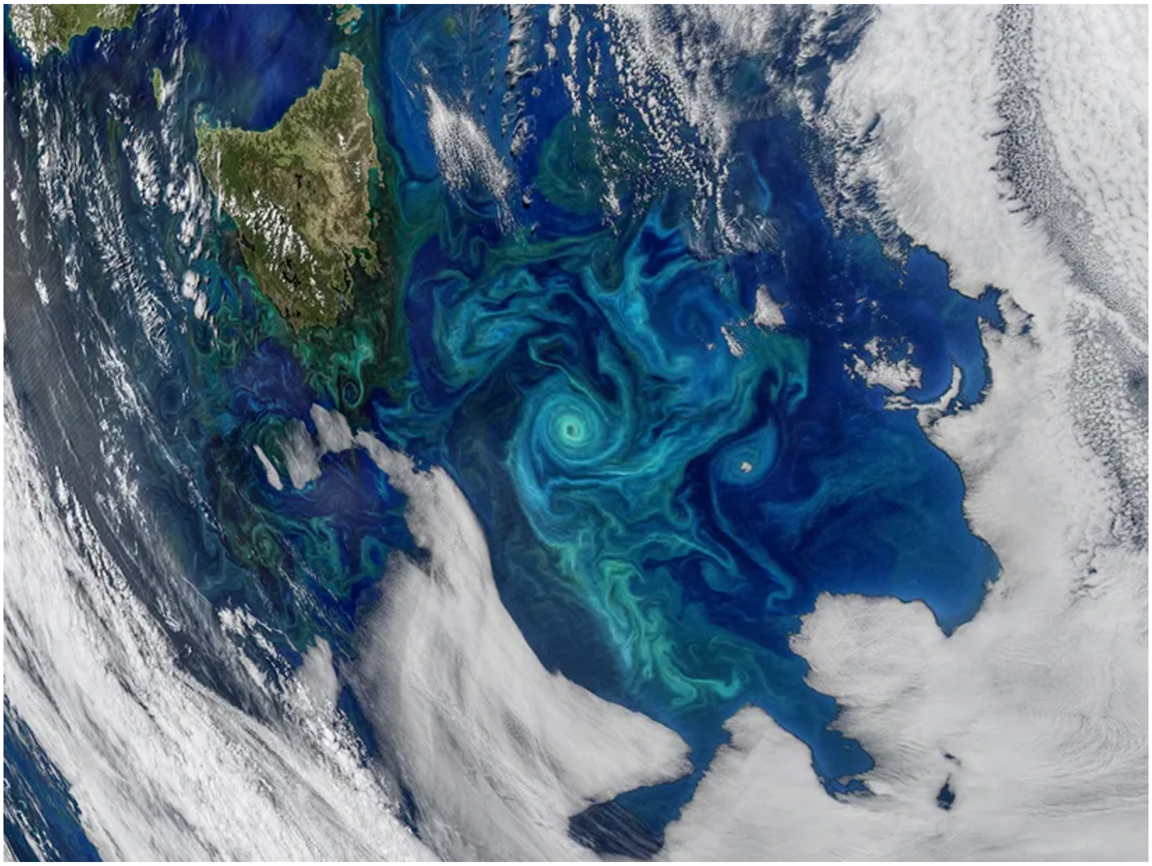
17 December 2018



Phytoplankton bloom in the Tasman Sea captured by the NASA Moderate Resolution Imaging Spectroradiometer (MODIS) instrument on the Aqua satellite on 21 November 2017. White patches are clouds. Advances in remote and in situ sensing, as well as methods for modeling and simulation, are driving an era of progress in ocean biogeochemistry research. Credit: NASA/Ocean Biology Processing Group, Goddard Space Flight Center

Sea level rise, heat transport, ocean acidification, these ocean processes, well known in the public sphere, play out on a regional to global scale. But less well known are more localized processes that bring some ecological niches together, keep others separated, and help sustain ocean life by circulating nutrients.

Physical processes in the ocean that take place over intermediate and small scales of space and time play a key role in vertical seawater exchange. They also have significant effects on chemical, biological, and ecological processes in the upper ocean.

In the past, it proved difficult to quantify the role of small-scale features in the movements of ocean chemicals and materials because of their unpredictability. Compounding that difficulty, technological limits hindered scientists’ ability to observe and model these processes.

All of this is now changing: Ocean observing tools, models, and theories have evolved significantly within the past 2 decades. Strong linkages between physics, biology, and chemistry at the small and medium scales reflect exciting opportunities for interdisciplinary research. With new tools and improved understanding of these features, the oceanographic community is now overcoming historical roadblocks to evaluate the physical mechanisms responsible for and implications of widely observed mosaics of ocean biogeochemistry.

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> ***With new tools and improved understanding, the oceanographic community is now evaluating the physical mechanisms responsible for and implications of mosaics of ocean biogeochemistry.***

From the Medium to the Small

The term “meso,” from the Greek word for middle, is often used to describe intermediate-scale processes (spanning some 10–100 kilometers, over a period of months). Physical oceanographers have been studying these mesoscale features and their contribution to the larger, ocean basin–scale distribution of chemicals and organisms since the 1970s.

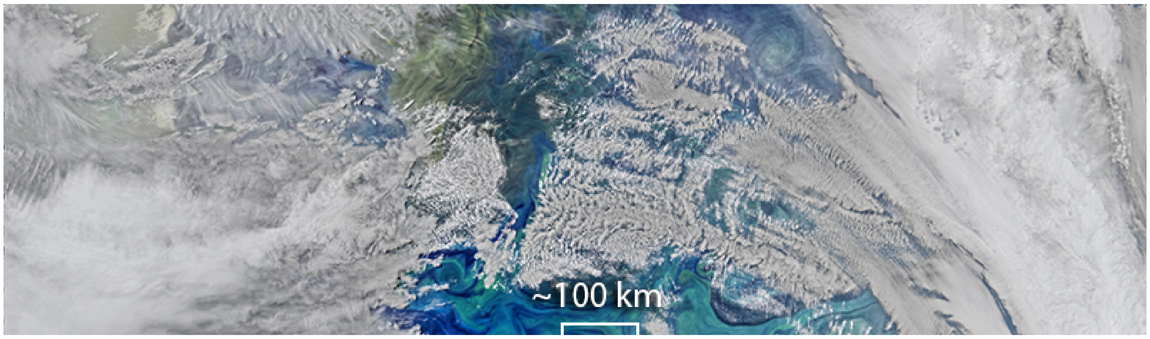
Common mesoscale features, called eddies, are rotating columns of water that extend downward hundreds of meters from the sea surface, span diameters of 50 to 200 kilometers, and can last for months. These vortices generally form as a result of various instability processes, and they can move cool water upward to the surface or push warm water to depth, depending on what direction they rotate and whether they are in the Northern or Southern Hemisphere. The spin direction is dictated by Earth’s rotation, which is accounted for in the study of fluid dynamics by what is called the Coriolis force. This force deflects water moving along a line to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. Therefore, a clockwise-rotating eddy in the Northern Hemisphere would pile water up in the eddy center, resulting in warm surface water being pushed deeper into the ocean interior. In the Southern Hemisphere, this same eddy would deflect water away from the eddy center, pulling deeper water up toward the sea surface.

> *The study of submesoscale features represents a newer scale of ocean inquiry into ephemeral processes.*

These dynamic mesoscale vortices generate mounds and depressions in the surface of the ocean itself—topographical ocean features observable in satellite records of altimetry and temperature. Such observations paved the way for rapid scientific advances at the dawn of satellite oceanography.

The study of submesoscale features represents a newer scale of ocean inquiry into ephemeral processes. These small-scale processes take place over lengths of about 1–10 kilometers, and they occur over several days. The features these processes create often evolve from the stirring, straining, and density contrasts that occur near the boundaries of mesoscale ocean features that bring unique water masses into contact, tightly linking the physical dynamics of the two scales.

Within the past 2 decades, our ability to observe and measure ocean phenomena at medium and small scales has advanced significantly. Autonomous sensors and high-resolution numerical models are now revealing the ubiquity of mesoscale and submesoscale ocean features [*Mahadevan*, 2016; *McGillicuddy*, 2016] and their interactions, stimulating new hypotheses about how ocean physics shapes ocean chemistry and ecology (Figure 1).



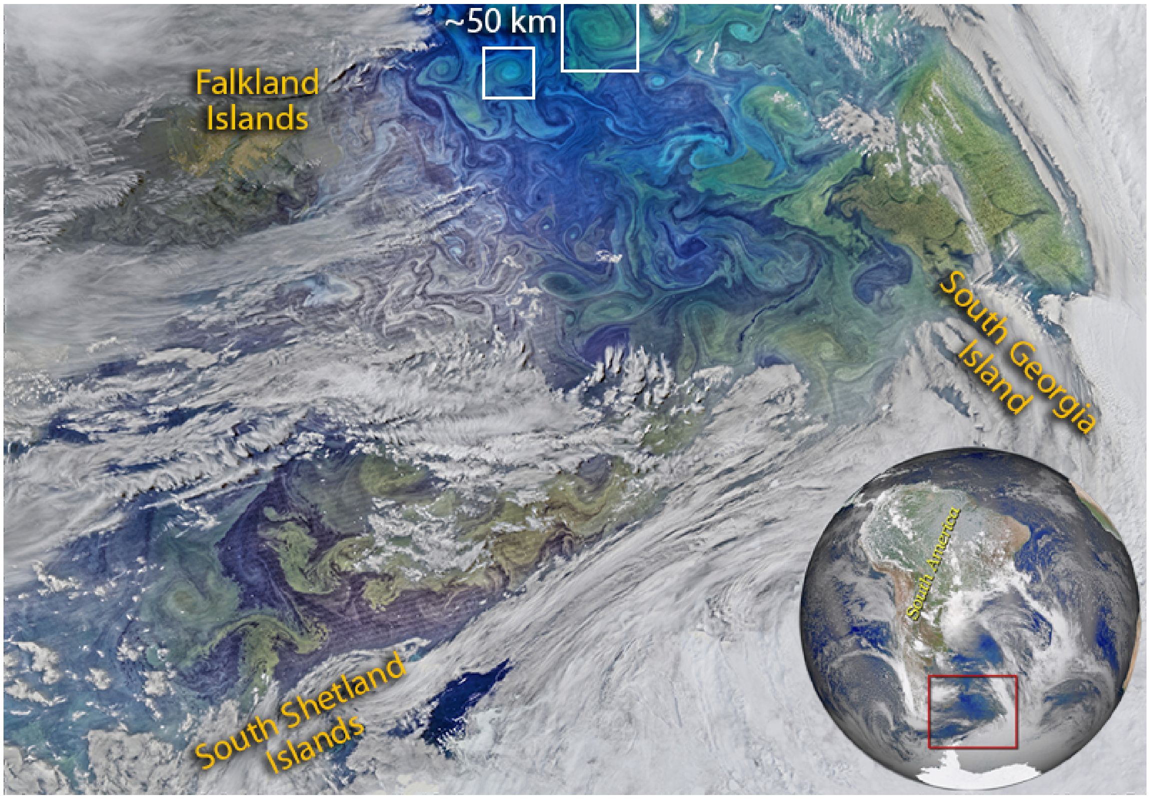


Fig. 1. Phytoplankton bloom between the Falkland Islands and South Georgia Island captured by the NASA-NOAA Suomi National Polar-orbiting Partnership (NPP) satellite on 16 November 2015. White patches are clouds. The overlaid white boxes and text provide approximate length scales for two of the mesoscale eddies pictured. Credit: NASA/Ocean Biology Processing Group, Goddard Space Flight Center.

Stirring Up Marine Ecosystems

Physical-biogeochemical ocean interactions are complex because of the fluid dynamics at play and the vast spectrum of biochemical pathways employed by competing marine organisms. Phytoplankton form the base of the oceanic food chain. These organisms span a wide range of biological classifications and functions, and they play a key role in the Earth system by mediating elemental cycles, that is, the circulation of chemical elements through an ecosystem.

The physical ocean environment is punctuated by mesoscale and submesoscale features that act not only to mix and disperse phytoplankton populations but also to modify the local environment and interactions therein. Understanding and quantifying the ways that these interactions contribute to global biogeochemical cycles remain a priority for the oceanographic community.

Mesoscale eddies, for example, are ubiquitous features colloquially referred to as “the weather of the ocean” and often produce anomalies in sea surface height that are observable from space. Automated mesoscale eddy identification and tracking programs have made it possible for scientists to use satellite data to evaluate their influence on near-surface [chlorophyll concentrations](), which are an indicator of phytoplankton activity [*Chelton et al.*, 2011; *Siegel et al.*, 2011; *Gaube et al.*, 2014]. Eddies primarily modulate near-surface chlorophyll by stirring chlorophyll gradients near the intersections of water masses with distinct characteristics (Figure 2).

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> ***Eddies entrain and trap large parcels of water, transporting entire ecosystems hundreds to thousands of kilometers.***

These eddies can also induce biological activity by lifting layers of water that contain nutrients into the sunlit region, where organisms that rely on photosynthesis live. In areas of intense mesoscale activity, such as boundary currents, eddies also entrain and subsequently trap large parcels of water, transporting entire ecosystems hundreds to thousands of kilometers, redistributing sharp gradients in chemical and biological properties into dynamic mosaics [*Gaube et al.*, 2014].

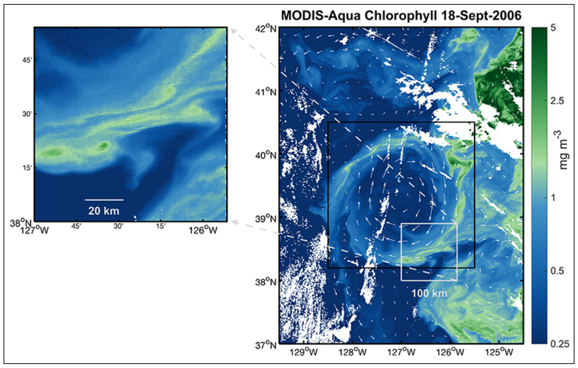

Fig. 2. Chlorophyll *a* concentrations in a mesoscale eddy

What’s Stirring Up the Plankton Communities?

Mesoscale processes can generate or influence the structuring of submesoscale ocean features, which are often responsible for small-scale biogeochemical heterogeneity (Figure 2). It can

Fig. 2. Chlorophyll *a* concentrations in a mesoscale eddy offshore of central California on 18 September 2006, as observed by NASA's MODIS instrument on the Aqua satellite. Close-up of submesoscale features (white box in the right panel) associated with the eddy (left). The anticyclonic mesoscale eddy (black box) shows elevated chlorophyll *a* levels around the perimeter (right). White arrows represent vectors of the mesoscale geostrophic current (generated from a balance between pressure gradients and Coriolis forces) estimated from sea level anomaly data. White patches indicate clouds. The logarithmic color scale represents chlorophyll *a* concentrations in milligrams per cubic meter.

therefore be challenging to determine whether heterogeneity in biogeochemical signatures reflects an active response to submesoscale physical forcing or the deformation of an existing biogeochemical gradient by mesoscale processes.

To evaluate this question, *d'Ovidio et al.* [2010] used satellite observations to investigate the organization of phytoplankton communities. These researchers showed that submesoscale filaments of chlorophyll and phytoplankton community structure were formed by simply stirring existing mesoscale (and larger) patches. This effect is particularly apparent near sharp ocean gradients. Stirring can stretch and deform distant ecosystems—usually separated by hundreds of kilometers—into swirling filaments that end up being separated by a few kilometers or less (Figure 2 and signature A in Figure 3).

Yet submesoscale processes that drive strong vertical exchanges near fronts may also cause in situ biological responses by enhancing the nutrient supply to the surface mixed layer [*Lévy et al.*, 2012]. Accurately attributing the causes of a given process will thus require researchers to deploy novel sampling platforms, such as profiling drifters, autonomous underwater vehicles, and undulating towed vehicles, to constrain three-dimensional, time-evolving biogeochemistry associated with submesoscale features.

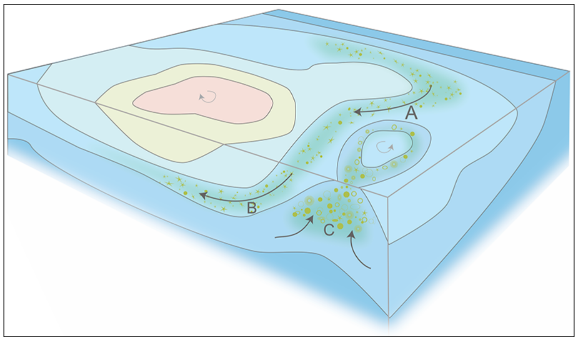

Figure 3. Mesoscale eddies and the submesoscale filaments at their peripheries can give rise to complex chemical and biological signatures, such as lateral transport of nutrient- and particle-rich water (labeled A), interleaving of water masses and variations along density surfaces (solid contours; labeled

Chemical Signatures of Small and Medium Scales

Separating stirring from other processes is also a challenge when interpreting chemical signatures at mesoscales and submesoscales. Complex patterns of seawater chemistry can develop from a suite of processes occurring over small spatial and temporal scales. Such processes include offshore transport of particle- and nutrient-

B), and nutrient enrichment and phytoplankton growth as a result of an eddy raising a density surface into the sunlit zone (labeled C). The mixing and stirring processes that are often enhanced in these regions can result in diversification of phytoplankton communities. Here a surface intensified filament near the anticyclonic eddy edge brings one community of phytoplankton into close proximity with another community of phytoplankton within a nearby cyclonic eddy.

rich coastal waters [*Barth et al.*, 2002], the development of chemical variations along density surfaces caused by the interleaving of water layers near fronts [*Nagai and Clayton*, 2017], and biological activity that occurs as an eddy raises denser, nutrient-rich water into the sunlit zone (Figure 3, signature C) [*Benitez-Nelson et al.*, 2007; *Ascani et al.*, 2013].

Not all biochemical perturbations associated with mesoscale and submesoscale dynamics produce effects at the sea surface. These subsurface processes are difficult to detect using remote sensing, which challenges our ability to quantify how these perturbations increase ocean primary production (the conversion of inorganic carbon compounds into organic compounds [*Chenillat et al.*, 2015]).

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> ***Multiple eddies in the Atlantic Ocean contain ~20% more anthropogenic carbon than surrounding waters.***

Some ocean regions exhibit consistent mesoscale and submesoscale activity that facilitates consistent chemical transport. For example, *Woosley et al.* [2016] discovered multiple eddies along 10°S latitude in the Atlantic Ocean that contained ~20% more anthropogenic carbon than surrounding waters. Relatedly, a recent modeling study by *Yamamoto et al.* [2018] found that most of the nutrients supplied to the upper layer of the Northern Hemisphere subtropical gyres originate from eddy-induced lateral transport across the Gulf Stream and Kuroshio currents.

Effects on the Bigger Picture

Ongoing changes in ocean chemistry (e.g., acidification and deoxygenation) have generated a need to evaluate how eddy transport and the associated submesoscale processes may influence large-scale distributions and gradients of chemicals, now and in the future.

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> ***Mesoscale eddies play an important role in facilitating chemical conditions that are otherwise improbable.***

But in addition to heterogeneity and transport, mesoscale and submesoscale processes can facilitate unusual chemical conditions. Multiple recent field campaigns in an oxygen-deficient zone near the coast of Peru identified intensified subsurface nitrogen loss in mesoscale eddies originating from coastal waters [*Bourbonnais et al.*, 2015; *Callbeck et al.*, 2017]. Producing these chemical signatures, which are uncommon in the water column, requires water parcel isolation. Similar findings of unlikely water chemistries within eddies have been reported in other regions, which suggests that mesoscale eddies play an important role in facilitating chemical conditions that are otherwise improbable.

The broader implications for interpreting chemical tracers, budgets, and fluxes provide new opportunities for ocean chemists, who are now applying autonomous biogeochemical sensors and platforms to study these features [e.g., *Johnson et al.*, 2009; *Inoue et al.*, 2016].

Phytoplankton Diversity

Mesoscale eddies act as natural enclaves—mesocosms—in which populations are enclosed, transported, and subject to **successional dynamics** (a sequence of ecological changes after a disturbance) over weeks or months. This isolation from the surroundings may result in reduced biodiversity as less-fit species are excluded. On the other hand, submesoscale gradients and filaments can also mix populations together, enhancing local biodiversity over short timescales.

Because of the technical challenges involved in gathering phytoplankton data that are taxonomically resolved and at the required spatial resolution, modeling studies are currently our best tool for understanding the dynamic effects of mesoscale and submesoscale processes on phytoplankton community structure. Ecological models have shown that mesoscale eddies enhance regional and annual mean biodiversity by creating more local niches for different phytoplankton species and by mixing populations together [*Clayton et al.*, 2013].

Models have also revealed the range of local impacts that eddies and fronts can impose on phytoplankton community dynamics and diversity [*Lévy et al.,* 2015]. Observational evidence that supports these models has been seen in the mingling of coastal and oceanic ecotypes of the phytoplankton species *Ostreococcus* at the Kuroshio Extension Front east of Japan [*Clayton et al.,* 2017]. Advances in automated cytometric, imaging, and sample collection technologies are starting to generate data sets that can be used to explore these questions in the field.

Carbon Export

A fundamental goal in oceanography is to quantify and understand how carbon produced by photosynthetic organisms in the surface ocean is transported to the deep sea, where it is sequestered from the atmosphere. This process of carbon export has played an important role in regulating Earth's climate over the past million years [*Sigman and Boyle,* 2000] and represents a moderately constrained (~50% uncertainty [*Siegel et al.*, 2016]) component of the modern global carbon budget.

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> ***Carbon produced by photosynthetic organisms in the surface ocean is transported to the deep sea, where it is sequestered from the atmosphere.***

Traditionally, this export of particulate organic carbon (POC) from the surface to the deep sea was thought to be driven primarily by sinking particles. Indeed, glider-based observations from the 2008 North Atlantic Bloom study showed a fast-sinking plume of particles resulting from the demise of a diatom bloom [*Briggs et al.,* 2011].

However, the observations also showed evidence of POC that would normally remain buoyant (nonsinking POC) in subsurface features coincident with elevated oxygen and chlorophyll. These features formed when POC-rich surface water was pulled beneath the surface, carrying the nonsinking POC with it (signature B in Figure 3) [*Omand et al.*, 2015].

Modeling tools helped to demonstrate that this process often coincides with enhanced downward fluxes associated with strong vertical velocities that are extremely challenging to characterize in situ. Combining observations with modeling was essential for visualizing and understanding these dynamics and may be a useful method for evaluating additional tracers and mechanisms that are presently difficult to observe at these challenging scales.

Understanding the Mosaics

The combination of existing research tools and the development of new tools is driving progress in understanding biogeochemical ocean mosaics. The integration of satellite and in situ observations continues to deliver insights, whereas high-resolution data-assimilating models present exciting opportunities to study mechanisms that help us interpret in situ and satellite observations.

These efforts are guiding the ways that the research community applies novel techniques to observe and study ocean processes from the submesoscale to the basin scale. Creative applications of small, low-power ocean sensing technologies, such as sensors that can be affixed to **marine mammals**, are informing new ways to study ocean features of interest [*Block et al.*, 2011].

In addition, burgeoning disciplines that link the chemicals found in seawater to specific marine organisms are moving us closer to relating biochemical pathways to plankton diversity for more rigorous interpretation of bulk chemical transformations. Thus, the simultaneous application of physical, biological, and chemical tools and tracers with models is rapidly accelerating our progress in unraveling the ocean mesoscales and submesoscales.

Acknowledgments

We thank the Ocean Carbon and Biogeochemistry Program (supported by the National Science Foundation) for providing a forum to discuss this topic at the 2017 Summer Workshop. Author research informing this document was supported by the National Science Foundation, NASA, the National Oceanic and Atmospheric Administration (NOAA), the Moore Foundation, the Sloan Foundation, and the Washington Research Foundation. The authors thank Nina V. Buzby and Kelly Lance for their contributions to Figure 3.

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Citation:

Fassbender, A. J.,Bourbonnais, A.,Clayton, S.,Gaube, P.,Omand, M.,Franks, P. J. S.,Altabet, M. A., and McGillicuddy Jr., D. J. (2018), Interpreting mosaics of ocean biogeochemistry, *Eos, 99*, https://doi.org/10.1029/2018EO109707. Published on 17 December 2018.