Bridging the Spatiotemporal Gap in Diazotroph Activity and Diversity With High-Resolution Measurements

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The biological fixation of dinitrogen (N_2) by marine microbes called "diazotrophs" sustains ∼50% new production in the ocean, boosting CO_2 absorption by photoautotrophs and thus contributing to the mitigation of climate change. New environmental conditions sustaining N_2 fixation have been revealed in recent years, enabling more accurate forecasting of future nitrogen inputs and localized hot spots. However, at present the paucity and biased geographical coverage of N_2 fixation and diazotroph diversity measurements impede attempts to reconcile global nitrogen budgets with observed rates. Most studies have been conducted at disparate spatiotemporal scales, including: (i) discrete and short duration measurements in small seawater volumes isolated from the environment, and (ii) spatial extrapolations and global models of diazotrophy projected over decades to centuries. We argue that this knowledge gap lies at the fine scales: dynamic seawater structures < 200 km wide and < 2 months lifetime. However, the spatiotemporal resolution of conventional oceanographic cruises, with stations separated by tens to hundreds of kilometers, is too poor to resolve fine scale processes. Bridging this gap requires leveraging high spatiotemporal resolution measurements. Here we present and discuss the advantages and disadvantages of contemporary methods and equipment able to provide high-resolution measurements at sea. We also provide insights into high-resolution sampling approaches to be developed in the near future. Increasing the spatiotemporal resolution of diazotroph activity and diversity will provide more realistic quantifications of nitrogen fluxes in the dynamic ocean.

Keywords: diazotrophs, fine scale dynamics, physical-biological coupling, cyanobacteria, N_2 fixation

THE GAP IN OCEANIC N_2 FIXATION

Nitrogen is considered the predominant nutrient limiting primary production in the ocean (Tyrrell, 1999). Most of the ocean surface is too remote to benefit from land and atmospheric inputs but can receive from dinitrogen (N_2) fixation: the reduction of N_2 to ammonia carried out by specialized types of microbes called "diazotrophs." Diazotrophs play a crucial role in ocean biogeochemistry: they sustain ∼50% of marine new production (Mahaffey et al., 2005) and can contribute > 70% to carbon sequestration in the vast oligotrophic regions of the ocean (Karl et al., 2012; Caffin et al., 2018).

Our current knowledge of diazotroph diversity and activity (diazotrophy) is derived from disparate spatiotemporal scales (**Figure 1**). At smaller spatiotemporal scales, diazotrophs are studied by manipulating communities in incubation bottles with restricted volumes (typically < 5 L). Such incubations require a physical isolation from their environment, which can lead to exposure to well known "bottle effects" that introduce bias in our results (Zobell and Anderson, 1936). These small scale discrete incubations as well as local nutrient climatologies can be used to extrapolate rates of N_2 fixation regionally (e.g., Hansell et al., 2004; Luo et al., 2012). On larger scales, the isotopic composition of dissolved and particulate nitrogen are used to infer regional N_2 fixation rates (e.g., Bates and Hansell, 2004; Knapp et al., 2016). Mathematical models allow the extrapolation of diazotroph and N_2 fixation rate distribution patterns up to the global scale (Ward et al., 2013; Dutkiewicz et al., 2014; Gruber, 2016). Current estimates of fixed nitrogen inputs to the ocean via small or large scale approaches vary by dozens of Tg N y^{-1} (Luo et al., 2012; Landolfi et al., 2018). These discrepancies are perhaps not surprising given the spatiotemporal variation between these approaches.

Flow instabilities such as mesoscale (10–200 km, weeks) and submesoscale (1–10 km, days) structures—here collectively referred to as "fine scales"—control major processes fundamental to microbial physiology, including nutrient advection and export (Falkowski et al., 1991; Johnson et al., 2010; Guidi et al., 2012). Despite their importance, there is currently a spatiotemporal gap between small- and large-scale approaches in typical oceanographic research, limiting our understanding of microbial dynamics at fine scales (**Figure 1**). The inherent dynamic and sporadic character of fine scale structures makes them difficult to observe on individual oceanographic cruises (Mahadevan, 2016; McGillicuddy, 2016). Satellite ocean color data enables the observation of how fine scale dynamics accumulate or disperse chlorophyll, and even specific groups of phytoplankton (reviewed in Lehahn et al., 2017a). These approaches have formed a solid foundational understanding of physical-biological interactions in the ocean. However, *in situ* sampling remains imperative to measure changes in distributions at depth and microbial processes, which cannot be captured by satellite oceanography. Typical oceanographic cruises transect geographic locations separated by hundreds to a few thousand kilometers. With a regular navigation speed of ∼18 km h^{-1} (or 10 kn) and sampling operations that last several hours, such approaches result in poor spatiotemporal resolution sampling, incapable of resolving fine scale dynamics for most chemical and biological processes (Lévy et al., 2012).

As the physical features that create biogeochemical conditions dictating microbial activity, fine scale structures should be a focus, but they require a sampling scale that matches the structure of interest (Lévy et al., 2012). Recent technological advances have significantly improved this resolution. In this perspective, we provide an overview of the role of fine scale processes in structuring diazotrophic communities, the available tools to measure diazotrophic activity, abundance and diversity at high spatiotemporal resolution, and provide recommendations for future developments in the field.
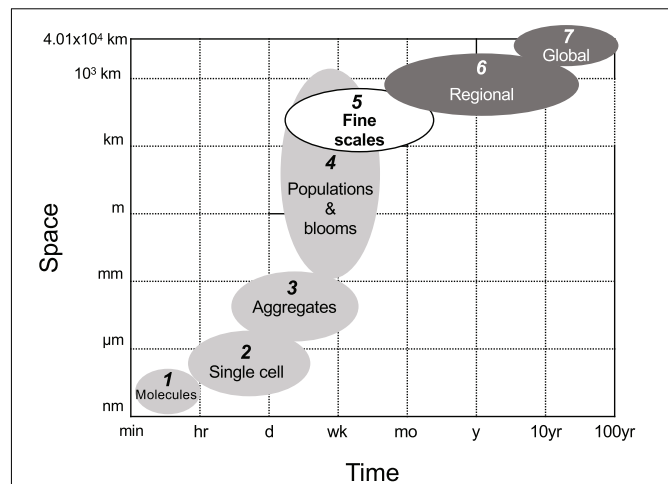

FIGURE 1 | The spatiotemporal scales of diazotrophy studies in the ocean ranging from minutes to 100 years in time and from nm to 4.01 × 10⁴ km (the circumference of the Earth) in space. Light and dark gray ellipsoids depict the spatiotemporal scales of diazotrophy studied to date, i.e., lower and larger scales in light and dark gray, respectively. The white ellipsoid depicts the current gap in knowledge: the fine scales. This gap can only be filled by developing novel methods capable of measuring diazotroph community composition, abundance and activity at high spatiotemporal resolution. (1) We refer as "molecules" to molecular processes covered in transcriptomic studies. Gene transcription typically takes place in a time range of minutes. (2) The interaction between molecules and cells is approached by nano- to microscale techniques exploring chemical microenvironments with microsensors (e.g., Eichner et al., 2017, 2019), substrate uptake using nanoscale secondary ion mass spectrometry (e.g., Finzi-Hart et al., 2009; Thompson et al., 2012; Bonnet et al., 2016), or molecular marking targeting proteins (e.g., Lin et al., 1998; Foster et al., 2006; Hynes et al., 2009) at the single-cell level. This spatiotemporal scale ranges in space from the size of intracellular compartments visible with those techniques to the maximum size of a single diazotroph cell. In time, this spatiotemporal scale reaches the maximum incubation time used in such studies, i.e., usually up to 72 h. (3) The localization of substrates or sub-cellular structures of interest in colonies and or aggregates can be approached with the techniques included in (2). The size, shape and horizontal/vertical distribution of aggregates in the ocean is usually resolved with microscopy (e.g., White et al., 2018), bench flow cytometry (Bombar et al., 2013; McInnes et al., 2014), field semiautomated flow cytometry (Dugenne et al., 2020), or automated underway devices such as the video plankton recorder (Davis and McGillicuddy, 2006). The size of this spatiotemporal scale ranges from tens of microns to several mm. The time range is considered to range between several hours and a few weeks, although the fate of aggregates in the ocean or how long they remain intact or alive is uncertain. (4) The composition and distribution of diazotroph populations is usually approached by discrete sampling along oceanographic cruise transects spanning hundreds to a few thousands of km. Such studies cover a time range from a few days to several weeks and depict communities using microscopy and/or molecular analyses such as quantitative PCR (e.g., Moisander et al., 2010; Bonnet et al., 2015; Benavides et al., 2016; Shiozaki et al., 2017). *Trichodesmium* blooms can cover extensions of hundreds to thousands of square km and are studied with customized algorithms applied to satellite products such as SeaWiFS or MODIS (Hood et al., 2002; Subramaniam et al., 2002; Rousset et al., 2018). (5) Submesoscale (1–10 km, days) structures such as filaments, and mesoscale (10–200 km, several weeks) structures including fronts and eddies (here collectively referred to as "fine scales," see section "How Fine Scale Processes May Affect Diazotrophs" of the main text). Studies seeking to link fine scales to diazotrophy have conducted discrete sampling along the central edge of mesoscale eddies at stations situated tens of km apart at best (e.g., Fong et al., 2008; Zhang et al., 2011; Löscher et al., 2016; Liu et al., 2020). In these studies, the distribution

(Continued)

HOW FINE SCALE PROCESSES MAY AFFECT DIAZOTROPHS

Although there are a limited number of diazotroph taxa, their ecologies are very distinct (referred to here as "ecotypes"; Thompson and Zehr, 2013), with different morphologies, activities and physiological constraints which dictate their biogeographical and seasonal distribution globally (Zehr and Capone, 2020). Due to the high variability of physical and chemical factors at the fine scale, the extent to which physical features affect diazotrophs will depend on how the resulting physicochemical changes affect each ecotype's physiology and metabolism (Lévy et al., 2012). Due to the range of factors contributing to the relative success of each ecotype, rates alone cannot provide enough information to model diazotrophy. It is necessary to collect rates while quantifying the organism(s) responsible to better characterize the bottom-up controls on distributions and activities of each ecotype.

Fine scales comprise a wide range of structures including filaments, fronts and eddies, with different physical dynamics that influence their biogeochemical properties. For example, vertical transport in submesoscale fronts causes rapid injections of deep nutrient rich waters, enhancing phytoplankton growth locally (Mahadevan, 2016). It is uncertain to which extent diazotrophs may benefit from such rapid inputs given their slow growth rates. Horizontal stirring strains fine scale features into thinner filaments, distributing phytoplankton niches (d'Ovidio et al., 2010) and regulating the access to limiting nutrients and mortality due to grazing and viral infection (Lehahn et al., 2017b). The success of a given species will depend on the balance between physical and biological time scales, e.g., when nutrient

delivery promotes sufficient growth to overcome grazing and viral pressure (Lehahn et al., 2017b).

Eddy trapping can isolate planktonic assemblages in Lagrangian coherent structures where lateral exchange with surrounding waters is limited (Lehahn et al., 2011). Such structures may act as a shield impeding dilution of nutrients permitting phytoplankton growth, or as a trap if a given species gets "trapped with the enemy" (i.e., predator; Bracco et al., 2000; Lehahn et al., 2014). Mills and Arrigo (2010) argued that non-Redfield usage of nutrients by non-diazotrophic phytoplankton lowers N:P ratios, creating diazotroph niches. Following this logic, we hypothesize that non-diazotrophic phytoplankton thrive in coherent eddies until the nitrogen trapped within them is depleted. While non-diazotrophic phytoplankton thrive, diazotrophs would be outcompeted (likely with the exception of UCYN-A, as discussed below). Once nitrogen is depleted diazotrophs may succeed, benefiting from a decrease in competition for phosphorus and trace metals with non-diazotrophic phytoplankton. This balance is likely further set by grazing and viral infection on diazotrophs. Indeed, Dugenne et al. (2020) observed higher growth rates and lowered grazing pressure on *Crocosphaera* inside a lower-biomass anticyclonic eddy as compared to a cyclonic eddy.

Eddy pumping is postulated to explain differences in diazotroph abundance and/or N_2 fixation rates, i.e., anticyclonic eddies deepen isopycnals, lowering nutrient availability and promoting diazotroph development, while the reverse occurs in cyclonic eddies. For example, *Trichodesmium* is sensitive to dissolved inorganic nitrogen (Knapp et al., 2012) and accumulates in anticyclonic eddies (Davis and McGillicuddy, 2006; Fong et al., 2008). However, anticyclones do not only hamper the upwelling of nitrate, but also of dissolved inorganic and organic phosphorus which exert an important control in the growth and diazotrophic activity of *Trichodesmium* (e.g., Dyhrman et al., 2006; Hynes et al., 2009).

Trichodesmium harbors gas vesicles that provide them with buoyancy control (Villareal and Carpenter, 2003). *Trichodesmium* may be thus treated as buoyant particles accumulating at frontal structures (Taylor, 2018). Forced accumulation at surface frontal structures may increase nutrient limitation in *Trichodesmium* colonies while increasing sunlight exposure, potentially inducing cell mortality via autocatalytic death pathways and thereby vertical export (Berman-Frank et al., 2004). The unicellular diazotroph *Crocosphaera watsonii* can be found as small (2–3.5 μm) and large (4–5 μm) cell types (Bench et al., 2016). While the oligotrophic conditions that promote *Trichodesmium* in anticyclonic eddies similarly contribute to the proliferation of *C. watsonii* (Fong et al., 2008; Liu et al., 2020), physical accumulation at high density frontal areas is less likely for non-floating unicellular diazotrophs. The large cell type may be more prone to accumulation aided by the excretion of extracellular polymeric substances and formation of aggregates, a characteristic not described for the small cell type (Webb et al., 2009; Sohm et al., 2011) and implied previously to explain their distinct vertical distributions at the edge of an anticyclone (Bench et al., 2016). Wilson et al. (2017) quantified an 11% contribution to net community production attributed

to N_2 fixation by abundant *Crocosphaera* near an anticyclonic eddy, and an increased contribution of N_2 fixation to particulate nitrogen export flux.

The uncultivated unicellular diazotroph UCYN-A is a small (<1 μm) cyanobacterium in obligate symbiosis with a prymnesiophyte host to whom they provide fixed nitrogen in exchange for fixed carbon (Thompson et al., 2012). While widely distributed in warm low latitude seas (Moisander et al., 2010), UCYN-A also thrives in nutrient-rich and cold waters such as coastal upwelling ecosystems and polar seas (Agawin et al., 2014; Harding et al., 2018; Moreira-Coello et al., 2019). Both UCYN-A and its host are dependent on N_2 fixation for their nitrogen needs even in the presence of abundant inorganic nitrogen, which has been found to stimulate N_2 fixation (Mills et al., 2020). Such tolerance makes UCYN-A a good candidate to benefit from the biogeochemical conditions provided by eddy pumping in cyclonic eddies. However, abundant UCYN-A have been reported in anticyclones but not cyclones (Fong et al., 2008; Robidart et al., 2014; Liu et al., 2020). Perhaps driven by Ekman pumping of deep nutrient-rich waters in anticyclonic eddies (Anderson et al., 2011), as proposed to explain higher abundances of *Trichodesmium* in cyclonic eddies in the North Atlantic (Olson et al., 2015). Counter to expectations, episodic nutrient advection at the periphery of an anticyclonic eddy has previously been found to contribute to lower *nifH* transcription from both UCYN-A and *Crocosphaera* (Robidart et al., 2019).

Non-cyanobacterial diazotrophs (bacteria and archaea) cannot photosynthesize, which renders them dependent on organic matter to fulfill their energy and carbon needs (Bombar et al., 2016) although other metabolisms such as chemolithoautotrophy are plausible (Riemann et al., 2010). Their prevalence in anticyclonic eddies has been attributed to the accumulation of organic matter within the core (Löscher et al., 2016), while a separate study finding higher abundances in cyclonic eddies predicted that is was due to the alleviation of phosphorus stress (Zhang et al., 2011). Finally, diatom-diazotroph associations (DDAs) dominate in low salinity and high silicate waters of river mouths such as the Mekong and the Amazon river plumes (Foster et al., 2007; Bombar et al., 2011). As the plume dilutes, the diazotrophic community shifts toward unicellular diazotroph ecotypes, indicating that the dispersion of the plume ultimately determines their geographical distribution (Grosse et al., 2010). In the oligotrophic North Pacific, Harke et al. (2019) measured coordinated gene expression between the *Richelia-Rhizosolenia* DDA over the same anticyclonic transect as *Crocosphaera* and *Trichodesmium* high-resolution metatranscriptomes mentioned previously (Wilson et al., 2017; Frischkorn et al., 2018, respectively). Comparative analysis of these metatranscriptomes within the dynamic physical environmental context may reveal conserved mechanisms of response associated with N_2 fixation.

As discussed above, fine scale structures may affect diazotroph ecotypes in different ways according to their autoecology and physiology as well as trophic interactions within the planktonic community. The biogeochemical characteristics and trophic interactions taking place within these structures change between formation and dissipation. We thus predict that the impacts on diazotrophs evolve over the lifetime of these structures.

TOOLS FOR HIGH-RESOLUTION DIAZOTROPH SAMPLING

Fine scale structures are dynamic and ephemeral, making instrumentation for high-resolution measurements indispensable for their study. This instrumentation must be capable of providing activity, abundance and diversity data at spatiotemporal resolutions equal to or smaller than that of the physical and biological processes under study (Lévy et al., 2012). Below we present currently available technology to address the dynamics of diazotroph assemblages embedded in dynamic fine scale structures.

The studies that have sought to understand the role of fine scales on structuring diazotrophic communities or modulating N_2 fixation rates have used traditional sampling approaches consisting of CTD-rosette casts at discrete stations. These approaches may suffice when applying a Lagrangian sampling strategy, i.e., following a given water mass at the pace it moves. However, ephemeral submesoscale structures associated with eddies are not easily quantified or characterized with traditional sampling (Johnson et al., 2010). In the past decade, technological developments have allowed the quantification of diazotroph ecotypes at a higher frequency than that provided by conventional sampling. The first study to do so used a towed video plankton recorder to continuously visualize *Trichodesmium* colonies across the North Atlantic, finding clear associations with anticyclones (Davis and McGillicuddy, 2006). Using an ecogenomic sensor, Robidart et al. (2014) found that diazotroph abundances changed over three orders of magnitude in less than 2 days and 30 km in the North Pacific. Most recently, a microbiological autosampler collected 1 sample/h over a transect in the North Atlantic, showing record abundances of UCYN-A in cold coastal regions and less abundant *Trichodesmium* in warmer waters offshore (Tang et al., 2020). In the same region, another study with a spatial resolution of 1 sample each $\sim$5 km found peak abundances of *Trichodesmium* coinciding with steep gradients of current velocity at the edge of the Gulf Stream (Palter et al., 2020).

Geochemical approaches to measure N_2 fixation include the N* parameter, which measures the concentration of nitrate in excess (or deficit) of that expected from the remineralization of phosphate at Redfield stoichiometries (Gruber and Sarmiento, 1997). This method has been used to study diazotrophy within mesoscale eddies in the eastern tropical South Pacific (Löscher et al., 2016). The $\delta^{15}N$ approach measures the relative $^{14}N/^{15}N$ isotope signature and relates low values ($\delta^{15}N\sim0.6$‰) to diazotrophic activity (Karl et al., 2002). Geochemical methods have the disadvantage that N_2 fixation signatures (N* > 2.5 μmol kg^{-1} or low $\delta^{15}N$ values) can be caused by processes other than N_2 fixation (Hastings et al., 2003; Zamora et al., 2010), but have the advantage that they can be used in large oceanic regions and are incubation-independent.

The most common biological method to measure N_2 fixation rates is using stable isotope tracers in 24 h incubations

(Montoya et al., 1996; White et al., 2020). *In situ* stable isotope incubations have been previously adapted to surface drifters (the Submersible Incubation Device, or SID), with 4×24 hour incubations per deployment (Bombar et al., 2015). Indirect methods such as hydrogen production measurements or the acetylene reduction assay allow working with smaller volumes and shorter incubation times, thus providing a faster measurement alternative for high spatiotemporal resolution studies. Hydrogen production measurements are based on the principle that N_2 reduction produces hydrogen (H_2) in an equimolar reaction, so that every mole of H_2 produced can be equated to a mole of N_2 fixed (Wilson et al., 2010b). However, uptake hydrogenase enzymes are also present in diazotrophs to re-assimilate H_2 and recover energy, altering the ratio of N_2 reduced to H_2 released, which in practice varies between 0.2 and 13 (Wilson et al., 2010b; Wilson et al., submitted). This method yields rates every ∼20 min, and can be used in diel cycle studies (Wilson et al., 2010a,b) or on high-frequency measurements over oceanographic cruise transects (Moore et al., 2014, 2018).

The acetylene reduction assay is based on the ability of the nitrogenase enzyme to reduce other triple-bonded molecules such as acetylene, which is reduced to ethylene and converted to N_2 fixation rates using a ratio of 3:1 or 4:1 depending on if hydrogen re-assimilation is considered or not (Stal, 1988; Capone, 1993), but just as with hydrogen measurements, empirically determined ratios vary widely (Mulholland et al., 2004, 2006). Recently, this assay has been adapted to measure continuous N_2 fixation in underway seawater systems (Cassar et al., 2018; Tang et al., 2020). Indirect methods measure gross N_2 fixation rates, i.e., how much N_2 has been reduced by the nitrogenase enzyme, independent of whether it is channeled to diazotroph biomass or released extracellularly as dissolved nitrogen compounds. Because diazotrophs are known to release significant amounts of fixed N_2 extracellularly (Mulholland et al., 2004; Benavides et al., 2013; Berthelot et al., 2015; Bonnet et al., 2016), gross N_2 fixation measurements may provide better estimates of fixed N_2 inputs to the ocean.

FUTURE PERSPECTIVES

In situ DNA sensors, samplers and rate measurements have provided abundance or activity data at an unprecedented spatiotemporal resolution. Understanding how fine scales shape diazotroph communities requires the combination of diazotroph identification, enumeration and N_2 fixation measurements at high, 4-dimensional spatiotemporal resolution.

Directed sampling within fine scale structures can be challenging, requiring the inspection of hydrographic variables and Lagrangian structures prior to the cruise (Nencioli et al., 2011; Doglioli et al., 2013). Following Lagrangian coherent structures requires the deployment of floats or vehicles capable of geolocalizing a moving water parcel. Fronts and mesoscale eddies are easier to characterize than ephemeral structures such as submesoscale filaments. Importantly, synoptic measurements of physical and chemical variables including horizontal and vertical current speed, vorticity, vertical turbulent microstructure and inorganic and organic nutrient diffusion are needed to comprehensively understand how fine scale processes affect diazotrophs.

Recent advances in vehicles and sensors will contribute to our understanding of physical-chemical-biological interactions *in situ*. Measurements of turbulence are becoming more frequent on seagliders (e.g., Fernández-Castro et al., 2020). Deployed nutrient sensors with nanomolar limits of detection (Beaton et al., 2012) can facilitate the observation of episodic or small-scale events in oligotrophic mixed layers. Autonomous vehicles capable of Lagrangian drift can follow specific water masses, sampling the microbial community in its environmental context (Birch et al., 2019) and autonomous orientation using chlorophyll concentrations allows targeted sampling of structures within the water column (Zhang et al., 2019). Deployments of combined sensors will enable a more thorough understanding of diazotroph – environmental interactions on fine scales, to be integrated across water masses for larger scale understanding. Measurements of flux, although currently providing data at higher resolution (Bombar et al., 2015; Tang et al., 2019; Wilson et al., submitted) currently require ship-based manipulations and/or analysis and are not yet capable of *in situ* deployment. Integrated, cross-disciplinary field-based efforts are crucial to resolve effects of short spatiotemporal scale dynamic processes fundamental to microbial activity.

RECOMMENDATIONS

Providing detailed sampling procedures to study the effects of fine scale structures on diazotrophs is challenging since dedicated high-resolution sampling devices are not widely available nor standardized for the oceanographic community. Nevertheless, dedicated study of fine scale processes is required in order to connect biological processes to underpinning physical and biogeochemical drivers. Below we provide a list of recommendations hoping to inspire microbial oceanographers to embrace such studies in their research programs.

(1) Fine scales are dynamic and ephemeral, requiring Lagrangian sampling approaches. Prior geolocalization of structures with satellite products is required for targeted sampling. Post-cruise satellite-derived data such as altimetry and ocean color aid description of underlying physical processes. In addition, *in situ* measurements of current speed and vertical mixing are highly recommended to better constrain fine scale structures.

(2) High-resolution measurements within large eddies can deliver the same diazotroph dynamics observed via long-term Eulerian measurements in time-series station data (McGillicuddy et al., 1999; Robidart et al., 2014). Since comprehensive time-series stations cannot be implemented across the global oceans, strategic observations targeting fine scale features should be implemented in representative oceanic provinces to capture biogeochemical variability over short field programs.

(3) Diazotroph abundance and diversity measurements should be measured synoptically with N_2 fixation measurements. Fine scales comprise a wide array of structures which may affect different diazotroph phylotypes in disparate ways. Coupling activity and abundance/diversity measurements will provide insights into passive (accumulation) versus active (N_2 fixation activity stimulation) effects on diazotrophs.

(4) Growth and mortality measurements should be implemented (e.g., Dugenne et al., 2020). While few studies have attempted to measure *in situ* growth of diazotroph phylotypes, redistribution of assemblages by fine scale structures may alter the balance between growth, mortality and predator pressure.

DATA AVAILABILITY STATEMENT

All datasets presented in this study are included in the article/supplementary material.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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