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High N₂ Fixation in and Near the Gulf Stream Consistent with a Circulation Control on Diazotrophy

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Key Points:

- The stoichiometry of nutrient supply predicts high N_2 fixation rates in/near Gulf Stream
- Measured N_2 fixation rates in surface waters match expectations from a P^* budget (order 10 nmol $N L^{-1} day^{-1}$)
- Molecular analyses and microscopy confirm robust diazotrophy, with gradients possibly caused by convergent flow

Supporting Information:

- Supporting Information S1

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High N_2 Fixation in and Near the Gulf Stream Consistent with a Circulation Control on Diazotrophy

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Abstract The stoichiometry of physical nutrient supply may provide a constraint on the spatial distribution and rate of marine nitrogen (N_2) fixation. Yet agreement between the N_2 fixation rates inferred from nutrient supply and those directly measured has been lacking. The relative transport of phosphate and nitrate across the Gulf Stream suggests that 3–6 Tg $N year^{-1}$ must be fixed to maintain steady nutrient stoichiometry in the North Atlantic subtropical gyre. Here we show direct measurements of N_2 fixation consistent with these estimates, suggesting elevated N_2 fixation in and near the Gulf Stream. At some locations across the Gulf Stream, we measured diazotroph abundances and N_2 fixation rates that are 1–3 orders of magnitude greater than previously measured in the central North Atlantic subtropical gyre. In combination, rate measurements and gene abundances suggest that biogeochemical budgets can be a robust predictive tool for N_2 fixation hot spots in the global ocean.

Plain Language Summary Marine photosynthetic organisms face a unique challenge: They are confined to the ocean's near-surface layer where there is sufficient light for photosynthesis, yet the nutrients needed for growth are rapidly stripped from these layers. In response to this nutrient scarcity, some microorganisms, called diazotrophs, evolved the ability to tap into alternative resources: They convert the nitrogen gas that comprises a majority of the atmosphere and is abundantly dissolved in seawater into ammonium needed for growth. Diazotrophs regulate the rate of new nitrogen input to the ocean, which influences the productivity of marine fisheries, as well as how carbon dioxide is partitioned between the atmosphere (where it contributes to the greenhouse effect) and the ocean (where it does not). Therefore, understanding the controls on diazotrophy is a key oceanographic objective. It was previously hypothesized that the Gulf Stream region could be a hot spot of nitrogen fixation. In this work, we tested this hypothesis by measuring nitrogen fixation rates and diazotroph abundances across the Gulf Stream. We found robust diazotrophy, far exceeding that previously measured in the subtropical North Atlantic. Understanding the linkages between ocean circulation and N_2 fixation helps us assess the vulnerability or stability of ocean biology and chemistry to future change.

1. Introduction

Nitrogen is an essential element to all living organisms. However, over much of the surface ocean, bioavailable nitrogen is in scarce supply. Some microorganisms, called diazotrophs, have adapted to this scarcity by fixing N_2 gas dissolved in seawater to its bioavailable forms. In so doing, diazotrophs replenish the global ocean reservoir of fixed nitrogen compounds and exert a key control on marine productivity and the ocean's biological carbon pump (Tyrrell, 1999). Despite this important role in the Earth system, the rates and spatial distribution of biological N_2 fixation are highly uncertain (Landolfi et al., 2018). A quantification of N_2 fixation rates in the subtropical North Atlantic, along with questions about the sources of non-nitrogenous nutrients, such as phosphorus (P) and iron (Fe), needed to fuel such fixation, have provoked extensive debate (Capone et al., 2005; Gruber & Sarmiento, 1997; Mahaffey et al., 2005; Marconi et al., 2017; Palter et al., 2011). Moreover, biogeochemical cycles in the North Atlantic can take on global importance, since this is

the basin in which large-scale ocean circulation unites the nutrients subducted in the Southern Ocean with aeolian iron mobilized from the Northern Hemisphere land masses and deposited at the ocean's surface (Moore et al., 2009).

Because N_2 fixation is energetically costly, diazotrophs are thought to have a competitive advantage only where the supply of bioavailable nitrogen compounds (N) is low relative to that of P and Fe with respect to the demands of non-diazotrophs (Falkowski, 1997; Landolfi et al., 2015; Ward et al., 2013). If non-diazotrophs can exhaust P or Fe before N begins to limit their growth, then there may be no niche for N_2 fixing organisms. Given that the P:N ratio is very low in the subsurface waters of the subtropical North Atlantic (Palter et al., 2011), the phosphate that gets mixed vertically into the euphotic zone is accompanied by more than enough nitrate to be completely consumed by non-diazotrophs before any niche is created for N_2 fixing organisms (Ward et al., 2013). These subsurface nutrient ratios imply that N_2 -fixing organisms in the central gyre may depend on dissolved organic phosphorus to support their growth (Landolfi et al., 2015).

However, conditions near the Gulf Stream are distinct from the broader subtropical North Atlantic. North of the Gulf Stream, phosphate concentrations are in excess of the average non-diazotrophic biological nitrate demand, as indicated by positive values of the metric $P^* = PO_4^{3-} - NO_3^-/16$. Assuming that the average community N:P ratio is 16 (Deutsch et al., 2007; Gruber & Sarmiento, 1997), a niche for N_2 fixers may be created in or near this region. Hydrographic sections occupied across the Gulf Stream consistently show positive P^* north of the current (Palter et al., 2011). Likewise, recent measurements have also shown that the Slope Sea, between the Gulf Stream and North American shelf, has elevated concentrations of dissolved iron relative to the subtropical gyre, so that the Fe:N ratio may exceed the cellular requirements of non-diazotrophs near the Gulf Stream (Conway et al., 2018). Finally, along its path from the Florida Strait to an offshore position of 60°W, 38°N, the Gulf Stream transports water with temperatures exceeding 20°C all year, and 23°C for all but the coldest months. Therefore, the transport of P- and Fe-rich waters from the Slope Sea across the warm Gulf Stream may alleviate the nutrient limitation of diazotrophy and mitigate any potential temperature effect of the cooler wintertime subtropical water masses.

A cross-Gulf Stream supply of P^* and Fe would also help explain satellite-based indications (Westberry & Siegel, 2006) and enigmatic video footage (Davis & McGillicuddy, 2006) of elevated abundances of the marine N_2 fixing organism *Trichodesmium* along the southern fringe of the Gulf Stream. Here, we present direct observations of N_2 fixation across the Gulf Stream, along with gene copy abundances of *Trichodesmium* and UCYN-A2, and microscopic observations of *Trichodesmium* and *Richelia*. With these data, we lend evidence in support of the hypothesis that the region in and near the Gulf Stream fosters high abundances of N_2 fixing organisms and robust rates of N_2 fixation.

2. Methods

2.1. Overview of Sampling and Data Collection

The majority of the data presented here were collected during EN596, a 6-day cruise aboard the R/V Endeavor from 25–30 April 2017, which occupied a high-resolution section across the Gulf Stream (Figure 1). Additional opportunistic sampling was also conducted on a subsequent leg, EN597, from 1–7 May 2017 between Morehead City, NC, and Fort Lauderdale, Florida. The Gulf Stream was identified from satellite sea surface temperature (SST) data, and the hydrographic section on EN596 was intended to cross the Gulf Stream perpendicular to its local trajectory at 74°W. On this hydrographic section, seawater samples were collected at approximately 24 discrete depth intervals from the surface to 1,000 m, and the distance between stations was approximately 10 km.

Here we give an overview of the sampling and data collection, with all of the methodological details explained in Text S1 in the supporting information. Water samples were collected and analyzed for nutrients, nitrogen isotopes, and chlorophyll *a* at each of the hydrographic stations. Particulate material for DNA extractions was also collected at each hydrographic station and during transits between stations using an automated custom-made seawater sampler (based upon the design of Holser et al., 2011) connected to the ship's uncontaminated seawater system, drawing seawater from a nominal depth of 5 m. The filtration system was programmed to iteratively redirect water through tubing connected to filter holders in order to sample at a high spatial resolution along the cruise track (Figure 1).

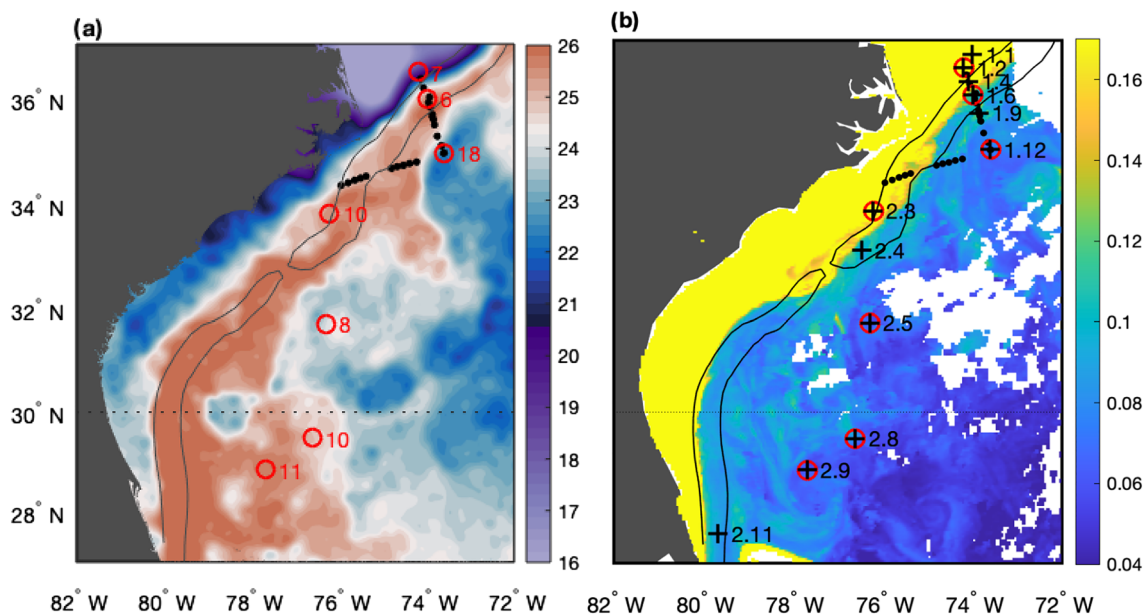


Figure 1. Sea surface properties and the EN596 and 597 cruise stations. (a) The sea surface temperature ($^{\circ}\text{C}$, background colors) on 27 April 2017 from NASA JPL Multi-scale Ultra-high Resolution Foundation Temperature. The surface geostrophic speed of 90 cm s^{-1} from altimetry (black contour) marks the Gulf Stream path on 27 April 2017. The black dots show the locations of the DNA extractions from the underway autosampler. The red circles show the locations of the $25\text{ m }^{15}\text{N}_2$ -enriched incubations, and the red numbers give the mean of the duplicate or triplicate N_2 fixation rates in $\text{nmol L}^{-1}\text{ d}^{-1}$ (uncertainty and limits of detection are provided in Table S1). (b) The MODIS Aqua 4 km satellite chlorophyll (mg m^{-3} ; colors), averaged over 1–8 May 2017, which is the 8-day average closest to the cruise dates with reasonably cloud-free view of the cruise region. Cloud covered pixels are white. The crosses are stations where qPCR was performed on bottle samples collected at various depths and reported in Table S2. The numbers next to the crosses are the leg and station numbers (labeled as leg.station). Bottles were collected to a depth of 1,000 m for the analysis of nutrients and natural abundance of $\delta^{15}\text{N}$ of nitrate at 12 stations between stations 1.1 and 1.12. All other symbols are the same as in panel a.

On Leg 1, at Stations 2, 6, and 12 (Figure 1), the entire volume of a PVC rosette bottle (from a depth of 25 m) was gravity filtered through a 47-mm diameter, $10\text{ }\mu\text{m}$ pore size, black polycarbonate filter with a Sterlitech polyester drain disk as per the protocol of White et al. (2018) in order to enumerate large cell-sized diazotrophic taxa. At these same stations, as well as Station 12 on Leg 1 and Stations 5, 8, and 9 on Leg 2, N_2 and carbon fixation rates were measured via the modified bubble release $^{15}\text{N}_2$ -tracer method of Jayakumar et al. (2017) and via traditional ^{13}C methods of Legendre and Gosselin (1997).

3. Results and Discussion

3.1. Oceanographic Context

As is evident in Figure 1a, the high-resolution section crossed the Gulf Stream where its ribbon of warm ($>25^{\circ}\text{C}$), surface waters separates the cold ($<19^{\circ}\text{C}$) Slope Sea waters to the north from the subtropical spring mixed layer (22°C and 23°C) to the south. The Slope Sea is much richer in chlorophyll than the Gulf Stream or subtropical gyre (Figure 1b). Eddies and filaments of elevated chlorophyll concentrations extend hundreds of kilometers southward and eastward from the Gulf Stream into the more oligotrophic central gyre. These warm, high chlorophyll features show how water is stirred across the Gulf Stream and stretched into coherent structures.

Finite Size Lyapunov Exponents (FSLE), calculated from the altimetric surface geostrophic velocity field and made freely available from the AVISO group (d'Ovidio et al., 2004), identify regions where the mesoscale velocity field stretches tracer into thin tendrils (Figure 2). More specifically, the large-magnitude ridges of the backward FSLE (Figure 2) indicate convergent flow lines (Liu et al., 2018) and partition the flow field into regions that have come from a similar origin. Many studies have shown that these ridges correspond with filaments of chlorophyll and other tracers in the ocean, consistent with their convergent nature (e.g., Hernández-Carrasco et al., 2018; Lehahn et al., 2007). The fact that many of these ridges coincide with

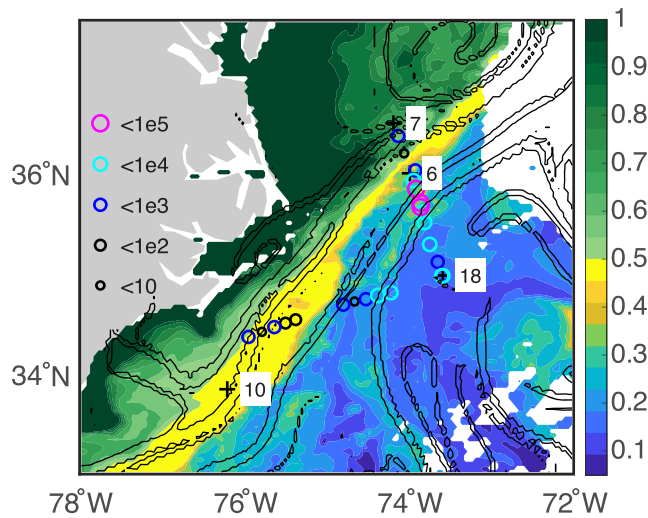


Figure 2. *Trichodesmium* gene abundance (gene copies L^{-1} , shown as colored circles, with legend on land) and N_2 fixation rates from incubations (black crosses and numbers in $nmol L^{-1} day^{-1}$) on the high-resolution Gulf Stream sections. The background colors are chlorophyll (as in Figure 1b). The black contours are the ridges of the backwards Finite Size Lyapunov Exponents (d'Ovidio et al., 2004), calculated from the surface geostrophic velocity field deduced from the satellite altimetry on 27 April 2017. FSLE are related to the exponential rate of separation between two neighboring particles over time and accordingly have units of day^{-1} . These ridges generally align with regions of convergent flow and therefore coincide with elevated chlorophyll in the subtropical gyre. For reference, the station which averaged an N_2 fixation rate of $6 nmol L^{-1} day^{-1}$ is at the center of the Gulf Stream.

elevated chlorophyll and SST structures on the subtropical side of the Gulf Stream (Figure 1) suggests that these features have been, at least in part, passively advected by the surface circulation. An illustration of such a feature is the tongue of high chlorophyll extending southeastward from the Gulf Stream at $74^\circ W$ and about $35^\circ N$ to $33^\circ N$, along a clear ridge of the backward FSLE (Figure 2), a feature that is also visible as a tongue of warm SST (Figure 1a).

3.2. Diazotroph Abundance and N_2 Fixation Rates

Figure 2 shows the distribution of N_2 fixation rates and *Trichodesmium nifH* gene copy abundances across the Gulf Stream. This section is shown versus latitude in Figure 3, along with the *nifH* gene copy abundances of the unicellular cyanobacterium UCYN-A2, above the Gulf Stream velocity as a function of depth and latitude. The highest *Trichodesmium* and UCYN-A2 *nifH* gene abundances are found very near the swiftest velocities of the Gulf Stream, while the highest N_2 fixation rate was measured at a station more than 10 km south of the zero velocity isotach and, therefore, outside of the Gulf Stream. The satellite chlorophyll concentration and FSLE ridges (Figure 2) indicate that the high *Trichodesmium* and UCYN-A2 abundances coincide with regions of lateral convergence, suggesting that the circulation field may passively accumulate the cells. *Trichodesmium* is known to be positively buoyant and may be prone to accumulate while it floats in convergent surface circulation (Detoni et al., 2016; Walsby, 1975). Indeed, diazotroph gene abundance was much higher at 5 m than any other depth (Table S3), consistent with the hypothesis of passive accumulation of the cells, but also typical of the vertical distribution of cyanobacterial diazotrophs (decreasing with depth). Cell counts determined via epifluorescence microscopy at 25 m were much lower (≤ 14 *Trichodesmium* cells L^{-1} and ≤ 437 *Richelia* heterocysts L^{-1}) but did independently confirm the presence of these large cell-sized diazotrophs.

We note that due to known polyploidy and limitations in qPCR assays we would not expect 1:1 relationship with gene copies and cell counts (White et al., 2018).

While vertical profiles of gene copies could suggest physical accumulation of at least *Trichodesmium*, we cannot rule out the possibility that conditions within the Gulf Stream fostered active *Trichodesmium* growth at locations where its abundance was high, as there were no incubations or microscopic observations precisely colocated with the highest gene abundances. From the underway data at 5 m, *Trichodesmium* showed as the most consistently dominating diazotroph in the area. Its abundances were measured at 10^4 *nifH* gene copies L^{-1} at all the stations both within the Gulf Stream and south of its swiftest central velocity (Figures 2 and 3). UCYN-A2 abundances were up to 5,000 gene copies L^{-1} in the Gulf Stream, with the notable exception of the station closest to the center of the current measuring 60,000 gene copies L^{-1} . UCYN-A2 has often been considered a coastal phylotype, but the understanding of its global distributions is evolving (Thompson et al., 2014). The g24774A11 diazotroph phylotype was found consistently at 'detected but not quantifiable' (DNQ) levels along the high resolution sampling transect, with the exception of the northernmost stations beyond the Gulf Stream north wall, where it was not detected in the samples. The g24774A11 distributions thus support the idea that Gulf Stream waters are enhancing diazotroph fitness.

One hypothesis to explain the disconnect between the N_2 fixation rates and gene abundances is that in the areas where highest rates were measured, the diazotrophic cells experienced conditions more favorable for fixation, resulting in greater N_2 fixation activities per cell. Conversely, in areas with reduced N_2 fixation rates, the diazotroph cells may have been senescent. Alternatively, a relatively fast local reduction in cell-specific N_2 fixation rates could have been induced by a local injection of dissolved inorganic nitrogen (DIN) to the system. *Trichodesmium* can switch to nitrate uptake when it becomes available, while reducing its N_2 fixation rates (e.g., Holl & Montoya, 2005). In addition, it is possible that such disconnect between rates and gene abundances may arise by changing diazotroph community composition across the transect. In this

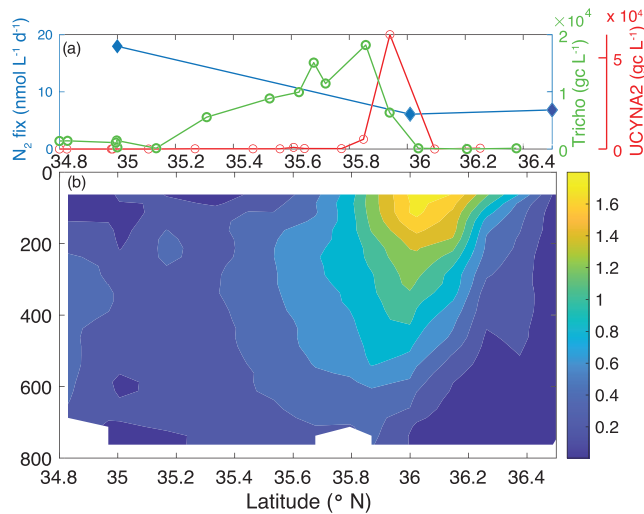


Figure 3. N₂ fixation rates, diazotroph gene abundances, and velocity on the high-resolution cross section of the Gulf Stream at approximately 74°W. (a) N₂ fixation rates at 25 m (left axis, nmol L⁻¹ d⁻¹) in blue diamonds, *Trichodesmium* gene copies (inner right axis, gc L⁻¹) in green circles, and UCYN-A2 (outer right axis, gc L⁻¹) in red circles. The standard deviations of the triplicate N₂ fixation incubation measurements are 7.8, 0.5, and 2.5 nmol L⁻¹ d⁻¹ from south to north. (b) The Gulf Stream velocity (m s⁻¹) as a function of depth and latitude from the ship's hull-mounted ADCP. In Figure 4, the location of the highest depth-averaged velocity (36.1°N) is taken as the center of the Gulf Stream, and the horizontal distance axis is transformed to be perpendicular to the current direction at this location.

study we screened for the presence of the known key oceanographic diazotroph groups; yet it is possible that some of the active diazotrophs were missed. Amplicon sequencing data (not shown) targeting the *nifH* gene containing communities was processed from the stations and showed presence of many non-cyanobacterial (presumably heterotrophic) diazotrophs in addition to the ones quantified with qPCR. These groups could have potentially contributed to rates, although evidence is scarce in terms of their actual contributions to N₂ fixation activity in the oceanic surface waters (e.g., Moisaner et al., 2017).

In the global diazotroph abundance databases of Luo et al. (2012) and Tang and Cassar (2019), there are no samples of *nifH* gene abundance measurements directly in the Gulf Stream. In the central subtropical gyre (i.e., near Bermuda, about 32°N), *Trichodesmium* and UCYN-A abundances are generally below 100 gene copies L⁻¹ and often not detectable at any depth (c.f. Tang & Cassar, 2019, their Figures S1 and S2). Thus, the peak measured gene copies here are 1–3 orders of magnitude above those typically measured in the central North Atlantic subtropical gyre, though they are several orders of magnitude smaller than frequently measured in the tropical Atlantic.

The N₂ fixation rates reported here are also between a factor of two and ten higher than nearby open ocean measurements: with rates between 6 and 18 nmol L⁻¹ day⁻¹ during this April cruise (Figure 1, Table S1), compared to rates consistently below 4 nmol L⁻¹ day⁻¹ measured in the open ocean subtropical North Atlantic gyre in August (Tang et al., 2019). These rates are consistent with those newly reported for the northwestern gyre (Tang et al., 2020).

3.3. Comparing Measured Rates to Inferences from Biogeochemical Budgets

The strong gradients across the Gulf Stream are a reflection of its role as a sharp dynamical and biogeochemical divide, with high nutrient layers outcropping at the sea surface to the north of the current and near-zero concentrations to the south (Figure 4). As has been observed on six previous cross-Gulf Stream nutrient sections (Marshall et al., 2009; Palter et al., 2011), P* is enriched on the northern side of the current (Figure 4b). Additionally, a Geotraces cruise (GA03) recently revealed that the Slope Sea is enriched in iron relative to the Sargasso Sea (Conway et al., 2018). Therefore, the environment near the Gulf Stream has many of the nutrient elements required for diazotrophs to thrive. Moreover, down-front winds and a rich spectrum of mesoscale eddies associated with the Gulf Stream drive a down-gradient flux of P* and iron into the subtropical gyre (Conway et al., 2018; Letscher et al., 2016; Palter et al., 2011; Roussenov et al., 2006; Williams & Follows, 2003; Williams et al., 2011; Yamamoto et al., 2018).

To maintain steady state nutrient ratios in the Sargasso Sea, any net P* supply must be consumed (Deutsch et al., 2007). The most likely P* sink is diazotrophic N₂ fixation, which consumes water column phosphate without drawing down nitrate. The steady state budget equation for P* can be rearranged to solve for N₂ fixation, $J_{fix}(N)$, integrated over the annual maximum mixed layer of depth, H , as in (Palter et al., 2011):

$$\int_{-H}^0 J_{fix}(N) \partial z = \lambda \left[\int_{-H}^0 \left(\overbrace{-u \cdot \nabla P^*}^1 + \overbrace{A_h \nabla^2 P^*}^2 \right) \partial z + \overbrace{w P^*|_{z=-H}}^3 - \overbrace{A_v \frac{\partial P^*}{\partial z}|_{z=-H}}^4 - \overbrace{\frac{F_{atm}(N)}{16}}^5 \right]. \quad (1)$$

Here, the P* supply terms include (1) advection across a P* gradient by the horizontal velocity field u and (2) the lateral mixing of the P* gradient with horizontal mixing coefficient A_h , both integrated above the depth H . The third term is the vertical advection of P* across the base of the layer with vertical velocity, w , and the fourth term is the turbulent mixing across a gradient in P* at the base of the layer with vertical mixing coefficient A_v . The supply of fixed nitrogen by atmospheric deposition (the fifth term on the right hand side)

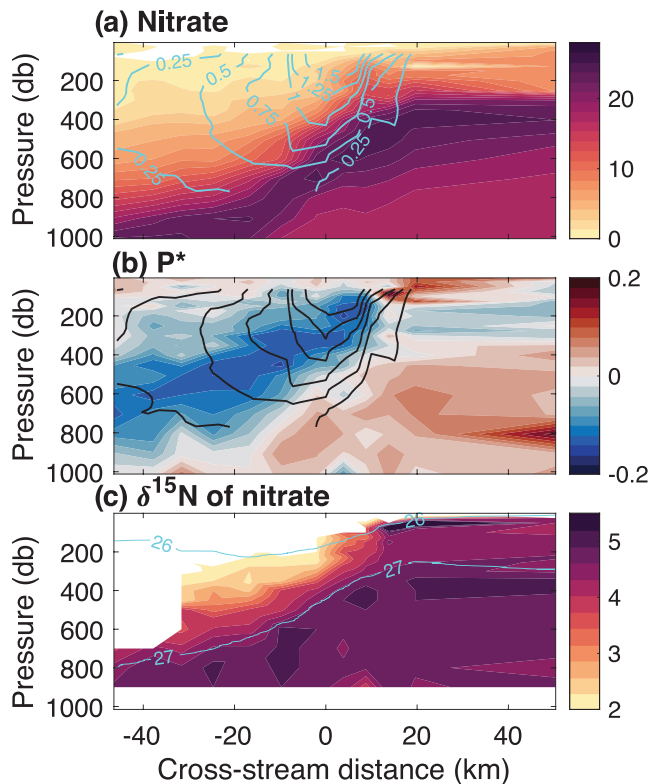


Figure 4. Properties as a function of distance across the Gulf Stream and pressure. (a) Nitrate concentration, (b) P^* concentration (μM); (c) $\delta^{15}\text{N}$ of nitrate (‰). White regions in the bottom panel are shown where the low nitrate concentrations and small volume of the samples precluded the isotopic analysis. The top two panels show velocity contours from the shipboard ADCP, with the contours labeled in m s^{-1} in panel a. The bottom panel shows two isopycnals, labeled with their potential density anomaly (potential density referenced to the sea surface in kg m^{-3} , minus 1,000). As in Thomas and Joyce (2010), the horizontal axis is distance from the center of the Gulf Stream, with geographical coordinates (x_o, y_o) . The Gulf Stream center is defined as the location of the maximum depth-averaged horizontal velocity from the shipboard ADCP, (\bar{U}, \bar{V}) . The direction of the velocity vector at (x_o, y_o) , that is, $\phi = \tan^{-1}(\bar{V}/\bar{U})|_{x_o, y_o}$, sets the cross-stream coordinate.

(Letscher et al., 2016) and observation-based estimates of the Ekman convergence (Palter et al., 2011) suggest these lateral transports may elevate productivity and/or N_2 fixation in a large area of the northwestern gyre. If so, the per-area fixation rate inferred from the biogeochemical budget would be approximately $0.1 \text{ mol m}^2 \text{ year}^{-1}$, or an average volumetric rate of $10 \text{ nmol L}^{-1} \text{ day}^{-1}$ spread over the top 25 m of the water column, in line with the measured N_2 fixation rates in the incubations. If robust diazotrophy were to extend throughout a deeper layer or was heightened at the ocean's surface relative to that measured at 25 m, it would imply the P^* budget could be balanced by a higher areal rate of N_2 fixation over a smaller region. In addition, it is important to recognize that the P^* budget assumes a steady state over an annual cycle, whereas our incubations measure daily rates during a single week in April at just a few stations in a turbulent ocean. We would expect that such fixation would be patchy in space and time, perhaps tracking the mesoscale features that deliver P^* - and Fe-rich water to the subtropics. Higher-resolution data would be needed to test whether rates we measured represent an average over this larger region.

The $\delta^{15}\text{N}$ of nitrate is also frequently used to investigate the integrated rate and spatial distribution of N_2 fixation (e.g., Knapp et al., 2008) and is defined as

reduces the amount of N_2 fixation required to balance the physical supply of P^* . The factor λ represents the number of moles of N that must be fixed to balance each mole of P^* supplied to the region (Deutsch et al., 2007). For oligotrophic systems like the Sargasso Sea with low fractions of organic material exported from the mixed layer, λ predominantly reflects the N:P ratio for non- N_2 fixing organisms, and is often elevated above 16 (Mills & Arrigo, 2010; Moreno & Martiny, 2018; Weber & Deutsch, 2010). Thus, a choice of $\lambda = 16$ should yield a conservative estimate of the N_2 fixation required to balance the estimated P^* supply. An upper bound of the N:P ratio for the subtropical North Atlantic has been estimated at 25 (Galbraith & Martiny, 2015). If we were to use this higher estimate for λ , all of the N_2 fixation rates from the P^* budget calculations would be revised upwards by a factor of approximately 1.5.

Using the average P^* gradients from six cross-Gulf Stream nutrient sections, similar to those shown in Figure 4b, together with satellite winds and mixing coefficients taken from the literature, Palter et al. (2011) estimated the physical supply of P^* by transport across the Gulf Stream, as in Equation 1. A scale analysis showed that atmospheric nitrogen deposition and vertical mixing and advection were small P^* sink terms, and were essentially negligible in the budget. Thus, the budget simplified to a balance between the P^* lateral transport convergence (Term 1) and the biological N_2 fixation that consumes it ($J_{\text{fix}}(\text{N})$). This budget calculation suggested the cross-Gulf Stream mixing and advection of P^* could support subtropical gyre N_2 fixation rates of $4.7 \pm 1.6 \text{ Tg N year}^{-1}$. The new hydrographic and nutrient data collected during EN596 are consistent with these estimates, because the cross-stream P^* gradients are very close to the averages reported in Palter et al. (2011). A comparison of the P^* transport during EN596 to the earlier work is included in Text S2.

The N_2 fixation rates measured in the incubations (Figure 1, Table S1) agree with those that would be inferred from the P^* budget, if the P^* convergence were evenly distributed over an area $3 \times 10^{12} \text{ m}^2$ (i.e., the northwestern gyre with a zonal extent of approximately 30° longitude and meridional extent of 10° latitude). We do not know the precise area over which the lateral P^* transport converges, since our observations permit the quantification of only the cross-stream transport, which moves P^* from the north side of the Gulf Stream toward its swiftly flowing center. The Gulf Stream then advects the P^* further downstream, and much of it likely recirculates over a broad region in the northwest gyre. Models

$$\delta^{15}\text{N}(\text{vs. air}) = \left[\frac{\left(\frac{^{15}\text{N}}{^{14}\text{N}} \right)_{\text{sample}}}{\left(\frac{^{15}\text{N}}{^{14}\text{N}} \right)_{\text{N}_2 \text{ in air}}} - 1 \right] \times 1,000. \quad (2)$$

Newly fixed N has a $\delta^{15}\text{N}$ that is similar to that of atmospheric N_2 , approximately -2‰ to 0‰ (e.g., Carpenter et al., 1997). In contrast, nitrate $\delta^{15}\text{N}$ in the North Atlantic north of $\sim 30^\circ\text{N}$ and within/beneath the thermocline is typically above 4‰ , as documented in Marconi et al. (2017) and in Figure 4c. Therefore, the light isotopic values (2‰ and 3‰) measured on the southern fringe of the Gulf Stream are suggestive of N_2 fixation, though it is unclear whether the isotopically light nitrate is added locally or is advected with the Gulf Stream from the tropics. Preliminary evidence that local N_2 fixation within the subtropical gyre is at least partly responsible for the isotopic signature of these water masses is provided by the fact they have potential densities between $1,026$ and $1,027 \text{ kg m}^{-3}$ (Figure 4c). Water mass analysis suggests that these density classes in the Gulf Stream are comprised almost entirely of recirculated subtropical water, with little contribution from the throughput of tropical or Southern Hemisphere sourced water in the Atlantic Meridional Overturning Circulation (Palter & Lozier, 2008; Schmitz & McCartney, 1993; Schmitz & Richardson, 1991; Schmitz et al., 1993).

The total subtropical N_2 fixation inferred from the P^* budget and verified with the incubation measurements agrees with a recent analysis by Marconi et al. (2017), who estimate the N_2 fixation in the Atlantic from the divergence of the nitrate $\delta^{15}\text{N}$ transport between two latitudes. Their method takes advantage of the requirement for isotope mass balance, and the assumption that the divergence in $\delta^{15}\text{N}$ meridional transport is principally driven by the addition of isotopically light nitrate due to biological N_2 fixation. The difference between the estimated meridional transport of $\delta^{15}\text{N}$ across 24°N and 48°N suggests that $3\text{--}5 \text{ Tg N year}^{-1}$ must be fixed between these latitudes, similar to the total N_2 fixation potentially supported by the cross-Gulf Stream supply of P^* (Palter et al., 2011). If these fixation rates were distributed evenly over the entire Atlantic between 24°N and 48°N and above 25 m , it would imply volumetric fixation rate of only $1 \text{ nmol L}^{-1} \text{ day}^{-1}$, about an order of magnitude lower than the incubation results reported herein. Thus, this comparison suggests the likelihood of a region of elevated N_2 fixation in the northwestern subtropical gyre under the influence of the Gulf Stream and its recirculations.

However, we caution that the apparent agreement between the North Atlantic N_2 fixation rate estimates of Marconi et al. (2017) and those estimated by Palter et al. (2011) may be coincidental. Because $\delta^{15}\text{N}$ was never measured on the zonal sections used in the divergence estimates, Marconi et al. (2017) used $\delta^{15}\text{N}$ values from cross-over points between the zonal sections and a meridional section in the eastern Atlantic where $\delta^{15}\text{N}$ data were available. This practice neglects the likelihood that the Gulf Stream, which is the conduit of almost all the northward volume transport at these latitudes (Rayner et al., 2011), could have a different nitrate $\delta^{15}\text{N}$ concentration than in the eastern basin, even on the same isopycnals. Indeed, the average Gulf Stream $\delta^{15}\text{N}$ we measured at approximately $36^\circ\text{N}/74^\circ\text{W}$, weighted by velocity and nitrate concentration in each grid cell, is 4.2‰ , which is lighter than the purported 4.9‰ of the northward transport at both 24° and 48° from the cross-over point method of Marconi et al. (2017). The inference of N_2 fixation from the $\delta^{15}\text{N}$ transport divergence is extraordinarily sensitive to small differences in the $\delta^{15}\text{N}$ of the northward and southward transport. Therefore, it is crucial that $\delta^{15}\text{N}$ of nitrate be measured at the same time and location as the velocity field to accurately deduce the net meridional transport of the isotope and the implied N_2 fixation rate.

4. Conclusions

Advection and mixing across the Gulf Stream supply P^* and iron to the northwest subtropical gyre (Conway et al., 2018; Palter et al., 2011). A quantification of the P^* supply led to the hypothesis that there is likely elevated N_2 fixation in and near the Gulf Stream (Palter et al., 2011). Here we report the results from a cruise designed to test this hypothesis by measuring N_2 fixation and the abundance of diazotrophs in this region. The measurements made on this cruise confirmed the presence of diazotrophs and reveal rates of N_2 fixation in and near the Gulf Stream 1–3 orders of magnitude greater than those previously measured in the central and southern subtropical gyre. These N_2 fixation rates are on the order of $10 \text{ nmol L}^{-1} \text{ day}^{-1}$, consistent with estimates of the fixation needed to balance P^* supply, if that supply were consumed within a broad region in

the northwestern subtropical gyre. The high resolution measurements also show sharp gradients in diazotrophic abundance that would be missed from more typical station spacing. The patchiness in *Trichodesmium* abundance possibly indicated that the cells accumulated along convergent structures in the surface circulation, though more sampling would be needed to confirm this speculation.

The sources and sinks of fixed nitrogen in the ocean are thought to be tightly coupled, thereby stabilizing the ocean nitrogen reservoir (Deutsch et al., 2007). One mechanism behind this hypothesized homeostasis is that denitrifying bacteria create a niche for diazotrophs by decreasing nitrogenous nutrients to concentrations that limit non-diazotrophic competitors. However, the scarcity of iron can decouple denitrification and N_2 fixation (Bonnet et al., 2017), contributing to the mismatch between N_2 fixation inferred from a model-based P^* budget and that measured in incubations and estimated from nitrogen isotopes in the tropical Pacific (Knapp et al., 2016). The separation between P^* supply and consumption can have important implications for the time scale over which a perturbation to the ocean nitrogen budget might persist. For instance, Moore et al. (2009) proposed that nitrogen fixed in the North Atlantic, where there is relatively abundant iron, is added to the North Atlantic Deep Water; this fixed nitrogen helps balance nitrogen lost in the denitrifying, sub-oxic zones of the Indo-Pacific. In this paradigm, a perturbation to either the removal or inputs of nitrogen could persist over centuries to a millennium, the average time scale over which a parcel of water makes a circuit through the global-scale circulation pathways connecting these distant regions.

These considerations reveal the importance of understanding the rate and spatial distribution of Atlantic N_2 fixation and how phosphate and iron are supplied to support it. Circulation features, like the Gulf Stream, that transport water masses from distant locales into new biogeographical regions, play an important role in these nutrient cycles. Expanding our observations to quantify the mean N_2 fixation rates in and near the Gulf Stream, their spatial and temporal variability, the diazotrophic communities responsible, and the phosphate and iron sources that sustain these communities will ultimately help uncover the stability or variability of the oceans fixed nitrogen reservoir.

Data Availability Statement

Sea surface temperature and MODIS chlorophyll data were downloaded from the NASA JPL site: <https://podaac.jpl.nasa.gov>. Biological and hydrographic data are archived in the Biological and Chemical Oceanography Data Management Office (BCO-DMO), <http://lod.bco-dmo.org/id/dataset/774288>.

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