The supply of excess phosphate across the Gulf Stream and the maintenance of subtropical nitrogen fixation

Jaime B. Palter, M. Susan Lozier, Jorge L. Sarmiento, and Richard G. Williams

Received 7 September 2010; revised 1 August 2011; accepted 30 August 2011; published 3 November 2011.

[1] The subtropical North Atlantic is considered a hot spot for biological nitrogen fixation, with estimated rates between 1 and \(20 \times 10^{11}\) mol nitrogen fixed annually. However, the region’s nutrient reservoir beneath the euphotic zone is so enriched in nitrate relative to phosphate that it is perplexing how fixation might be sustained there. Here, we investigate whether the physical transport of excess phosphate into the subtropical gyre is sufficient to sustain nitrogen fixation in the gyre. Specifically, we assess the Ekman advection and isopycnal mixing of excess phosphate to the subtropical North Atlantic, using detailed hydrographic and nutrient sections occupied across the Gulf Stream combined with satellite wind data. Ekman advection and along-isopycnal mixing provide a source of approximately \(2 \times 10^{10}\) mol yr\(^{-1}\) of excess phosphate in the northwestern subtropics, a physical mechanism that has the potential to support more than \(3 \times 10^{11}\) mol yr\(^{-1}\) of biological nitrogen fixation, after accounting for alternative sinks of excess phosphate. This excess phosphate supply across the gyre’s northern boundary and high nitrogen fixation there offers a mechanism that can explain both the maintenance of subtropical North Atlantic nitrogen fixation in a phosphate-poor environment and help account for the weak gradients in the proxies of fixation observed along interior circulation pathways of the gyre.


1. Introduction

[2] Biological nitrogen fixation is thought to add fixed nitrogen to the subtropical North Atlantic at rates of 1–20 \(\times 10^{11}\) mol N per year [Gruber and Sarmiento, 1997; Capone et al., 2005; Mahaffey et al., 2005; Hansell et al., 2007]. However, the nutrient in the region is so enriched in nitrate relative to phosphate, it would appear that non-N\(_2\) fixing phytoplankton should have more than enough nitrate to fully consume all available phosphate [Wu et al., 2000; Sañudo-Wilhelmy et al., 2001]. Under such circumstances, it is believed that the energetically costly process of N\(_2\) fixation is discouraged [Redfield et al., 1963; Tyrrell, 1999; Ganeshram et al., 2002; Deutsch et al., 2004], even though other requirements for nitrogen fixation such as low surface nitrate concentrations and relatively high inputs of iron are met. Thus, it is puzzling that N\(_2\) fixation should occur in the North Atlantic subtropical gyre at all, and even more so that it should proceed at the robust rates estimated by various studies (see Mahaffey et al. [2005] for a detailed review).

[3] One possible solution to this puzzle is that phosphate in excess of the biological nitrate demanded by non-N\(_2\) fixing phytoplankton is transported across the subtropical gyre’s boundaries, which delimit the phosphate-depleted region (Figure 1a). N\(_2\) fixing organisms could then consume this physical supply of excess phosphate without the accumulation of a measurable phosphate pool. If the nitrogen fixation occurred preferentially near the gyre’s boundaries, this scenario would also help explain the perplexing results from studies of the isotopic proxy of N\(_2\) fixation (depleted \(\delta^{15}\)N) [Knapp et al., 2005, 2008]. These studies detect little isotopic transformation, and therefore little indication of biological N\(_2\) fixation, at Bermuda and between Bermuda and Puerto Rico; yet, in these same waters, the isotopic signature suggests that approximately 50% of the nitrate in the subtropical upper thermocline is due to “recent” biological N\(_2\) fixation. Knapp et al. [2008] use the term “recently-fixed” nitrogen to mean nitrogen that was biologically fixed in the tropical and/or subtropical North Atlantic, which they distinguish from nitrogen that is imported from outside the basin. Thus, there is an apparent paradox in that high concentrations of recently fixed nitrogen are measured in the gyre interior where local rates of fixation are low. We hypothesize that fluxes of excess phosphate at the gyre’s boundaries may sustain nitrogen.
Nitrogen fixation near its edges, creating a signal of nitrogen fixation that is then transferred into the gyre interior. Here, we take advantage of new high-resolution, in situ nutrient and velocity data to diagnose the advection and mixing of the phosphate capable of fueling such nitrogen fixation near the gyre’s northern boundary, the Gulf Stream. We then extend this analysis over the whole gyre using nutrient and wind climatologies. We begin by first reviewing the definition of excess phosphate.

\[ P^* = \text{PO}_4^{3-} - \frac{\text{NO}_3^-}{16} \]

Communities of non-nitrogen-fixing organisms typically consume both nitrate and phosphate in a proportion that approximately conserves \( P^* \), whereas nitrogen-fixing organisms consume water column phosphate and atmospheric dinitrogen gas to drive residual euphotic zone concentrations toward lower \( P^* \) values. Making the basic assumption that the \( \text{NO}_3^- : \text{PO}_4^{3-} \) ratio is in a

\[ \frac{\text{NO}_3^-}{\text{PO}_4^{3-}} = 16 \]

Figure 1. Spatial and temporal variability of \( P^* \) concentrations (mmol m\(^{-3}\)) in the subtropical North Atlantic. (a) Annual mean \( P^* \) on the 1026.4 kg m\(^{-3}\) potential density surface in color with the depth of that density surface in contours. This map was constructed from the gridded World Ocean Atlas 2005 nutrient data and was interpolated to the depth of the isopycnals using gridded density data. White shading reflects the annual mean outcrop of that density surface. The location of the A22 section is marked by a white line, the BATS hydrographic station as a black and white square, and the CLIMODE stations used in this analysis as white circles. An enlargement of the CLIMODE region appears in Figure 2. (b) \( P^* \) (colors) and potential density (contours) as a function of pressure and latitude from WOCE section A22, occupied in 1997. WOCE section data was accessed from the corrected GLODAP database [Key et al., 2004]. (c) \( P^* \) (colors) and potential density (contours) versus pressure and time at BATS (31.93°N, 64.18°W). The color bar applies to all of Figure 1.
steady state on time scales of a year or more, the net divergence of $P^*$ to the euphotic zone over an annual cycle must be balanced by a source of fixed nitrogen with no corresponding source of phosphate or a sink of phosphate with no corresponding sink of nitrate (in either case, a sink of $P^*$) [Deutsch et al., 2007]. Given that biological nitrogen fixation is one important $P^*$ sink, the physical supply of $P^*$ can be used to infer the rate of nitrogen fixation, after accounting for all other sinks. A complicating factor is the potential for non-$N_2$-fixing organisms to consume nitrate and phosphate at ratios that differ from the canonical Redfield Ratio of 16:1 [Mills and Arrigo, 2010; Weber and Deutsch, 2010], a point we return to in Section 4.

2. Nutrient Concentrations in the Subtropical North Atlantic

Phosphate is strongly depleted relative to nitrate beneath the North Atlantic subtropical euphotic zone, as illustrated by the negative climatological mean $P^*$ on the 26.4 isopycnal (Figure 1a), in the mode water of the subtropical gyre (equivalent to the 1026.4 kg m$^{-3}$ potential density surface) [Worthington, 1976]. The phosphate-depleted status of the interior gyre extends from the base of the euphotic zone to a depth of more than 700 m (Figure 1b). Additionally, the thermocline’s negative $P^*$ signature appears to persist over time. At the Bermuda Atlantic Time Series station, only one year out of sixteen (2003) shows a possible vertical supply of $P^*$ (Figure 1c). Since the $P^*$ is negative at depth, the supply rate of nitrate through vertical processes should exceed that of $16P\text{O}_4^-$ and remineralization of the products of nitrogen fixation in the gyre interior should drive the system toward ever-increasing N:P ratios. Indeed, phosphorus appears to be crucial to photosynthesis in the gyre: nutrient addition bioassay experiments in the region have shown that phosphorus and nitrogen likely co-limit phytoplankton photosynthesis [Moore et al., 2008; Davey et al., 2008], while iron and phosphorus likely co-limit nitrogen fixation [Saito-Wilhelmy et al., 2001; Mills et al., 2004]. As for the lateral supply of $P^*$ to the interior gyre, horizontal advection and mixing of excess phosphate should be confined to the flanks of the subtropical gyre, because $P^*$ is negative throughout the interior gyre (Figure 1a).

Beyond all of the boundaries of the subtropical gyre, phosphate is elevated relative to nitrate (Figure 1). Relatively $P^*$-rich water is carried to the tropics (Figures 1a and 1b; Figure S1 in the auxiliary material) in the shallow limb of the Gulf Stream [Deutsch et al., 2007]. This $P^*$ continues its northward journey in the Gulf Stream, enriching the gyre’s northern boundary [Williams et al., 2006; Palter and Lozier, 2008; Moore et al., 2009]. This northern biogeochemical boundary is further maintained by an influx of $P^*$-rich water from the Arctic, where denitrification in the anoxic shelf environment removes nitrate from Pacific waters [Yamamoto-Kawai et al., 2006]. In addition, denitrification in the shelf sediments of the Middle Atlantic Bight may contribute an important nitrate removal process for the subtropical North Atlantic [Fennel et al., 2006; Fennel, 2010].

Thus, there may be an important supply of $P^*$ across all of the gyre’s boundaries. Because the CLIMODE field program occupied the first wintertime nutrient and velocity sections across the Gulf Stream [Marshall et al., 2009] (Figure 2), we take advantage of this unique opportunity to evaluate the $P^*$ transport across the gyre’s northern boundary directly from these detailed observations.

The sharp front between the phosphate-deficient waters of the subtropics and the excess-phosphate waters within and to the north of the Gulf Stream is visible in the map of climatological $P^*$ (Figure 1a), the WOCE section (Figure 1b), and every CLIMODE section (Figures 2c and S1). Of the six complete cross-stream sections, we have chosen to illustrate the spatial pattern of $P^*$ across the Gulf Stream using the fourth section occupied in the January 2006 cruise (Figure 2), and made the other sections available in Figure S1. We first use the CLIMODE sections and satellite observations of wind stress to estimate cross-stream Ekman $P^*$ transport (Section 3), the dominant $P^*$ supply term and the one evaluated most directly from observational data. Next, we quantify the remaining terms in the $P^*$ conservation equation for the Gulf Stream region (Section 4). In evaluating the dominant terms in this equation, we diagnose the biological nitrogen fixation required to balance the cross-stream $P^*$ transport. We then place this estimate in the context of previous inferences of $N_2$ fixation rates and observations of the spatial distribution of $N_2$-fixing organisms (Section 5).

3. The CLIMODE Sections and the Cross-Stream Ekman Advection of $P^*$

In the region of the detached Gulf Stream (i.e., the predominantly eastward-flowing portion of the Gulf Stream downstream of its separation point from the shelf break at Cape Hatteras), the time-mean wind stress is westerly and oriented along the front. This along-front wind drives an Ekman velocity ($v_{E_k}$) directed southward across the Gulf Stream (Figure 2b), which, integrated over the Ekman layer of depth $H_{ek}$, can be calculated from the wind stress as:

$$\int_{-H_{ek}}^{0} v_{E_k} dz = -\frac{\tau_{x}}{\rho_0 f} \quad (1)$$

Here, $\tau_{x}$ is the along-stream wind stress, calculated from a satellite wind product averaged over the month of the cruise (this wind product is a version of the QuikScat mean wind field processed and gridded at half-degree resolution by the Centre European Remote Sensing Satellite (ERS) d’Archivage et de Traitement (CERSAT) available online at http://www.ifremer.fr/cersat/); $\rho_0$ is a reference density; and $f$ is the Coriolis parameter. Using ocean current velocity data from a ship-mounted Acoustic Doppler Current Profiler (ADCP), all hydrographic and wind stress data have been rotated into a stream-wise coordinate system as by Thomas and Joyce [2010]. In this coordinate system the origin is the location of the maximum vertically averaged current velocity, and the cross-stream direction is normal to the maximum current. Such a coordinate system allows the explicit calculation of the cross-Gulf Stream Ekman flux at the center of our hypothesis. We neglect relative vorticity in the calculation, because we found that including it did not significantly change the
average magnitude of Ekman volume transport, despite its influence on the transport’s submesoscale variability [Thomas and Lee, 2005].

[9] The resultant Ekman transport sweeps elevated P* southward across the Gulf Stream (Figures 2a–2c). For the section depicted in Figure 2c, a signal of this P* transport is revealed by positive P* penetrating at least 100 km into the interior gyre (the limit of our observations). The cross-stream Ekman P* transport is a maximum on the northern side of the Gulf Stream (Figure 2d) with a mean maximum value from the six sections of $-0.27 \pm 0.13 \text{ mmol m}^{-1} \text{s}^{-1}$, calculated as the product of the vertically integrated Ekman velocity from equation (1) times the average P* concentration in the upper 50 m. This southward Ekman P* transport rapidly weakens within and south of the Gulf Stream (Figure 2d) leading to a convergence of the P* transport in the northern half of the Gulf Stream in all sections (Figure 2d). This convergence is due to P* concentrations approaching zero within the Gulf.
Stream, since the Ekman volume transport extends beyond the southern limit of every section (Figure 2). Accordingly, the convergence of the Ekman P* transport provides a supply of P*, potentially sustaining nitrogen fixation. Because climatological mean winter wind stress in the Gulf Stream region is a factor of 1.7 stronger than the annual average [Risien and Chelton, 2008], we divide our observed wintertime Ekman P* supply by this factor to estimate an annual mean P* supply equal to $1.5 \pm 0.8 \times 10^{10} \text{ mol yr}^{-1}$. To arrive at this rate, we have also assumed that the cross-stream transport is constant along the length of the separated Gulf Stream between Cape Hatteras and 45ºW (3000 km using a linear path).

[10] Does this cross-stream P* transport, which largely converges within the Gulf Stream, influence nutrient budgets in the subtropical gyre? The answer depends on whether the southward-advected P* reaches the subtropical side of the Gulf Stream or gets carried along in the North Atlantic Current extension of the Gulf Stream.

[11] The P* supply estimated from the discrete CLIMODE sections and contemporaneous monthly wind data is complemented by an analysis of the climatological mean Ekman P* transport convergence, calculated using a mean monthly satellite wind stress product [Risien and Chelton, 2008] and the monthly World Ocean Atlas nutrient climatology [Conkright et al., 2002] (Figure 4). The climatological analysis affords a greater spatial context for the Ekman supply terms and resolves the annual cycle that the CLIMODE wintertime sections cannot. Such analysis confirms that there is a net P* supply to the gyre in the CLIMODE region over an annual cycle, and suggests additional regions of Ekman P* supply across the gyre’s southern boundary (Figure 4). However, there are several limitations with the climatological

Figure 3. P* concentration and transport plotted against temperature versus salinity for all CLIMODE cruises. Dots are colored by (a) P* concentration in mmol m$^{-3}$ and (b) Ekman P* transport in mmol m$^{-1}$ yr$^{-1}$ (in the Ekman layer only). Cross-stream Ekman P* transport in mmol m$^{-1}$ yr$^{-1}$, represented by colored dots, are available for the Ekman layer only and have been interpolated to a new grid based on the cross-stream coordinate system. Black points represent all temperature and salinity measurements. Contours are potential density referenced to the surface. The red arrow indicates the direction of the Ekman transport in temperature and salinity space. For an approximate indication of the spatial distribution of the points, the temperature and density can be compared to the section shown in Figure 2b.
data. First, using the 1° resolution climatological data comes at the expense of resolving the sharpness of the flux convergence. For example, averaging over the Gulf Stream’s large meander envelope smears the current of Excess Phosphate 4. Quantifying All Remaining Sources and Sinks

Figure 4. The Ekman P* transport convergence, \( \frac{\partial U_{Ek}P^*}{\partial y} = \frac{\partial V_{Ek}P^*}{\partial z} \), where \( U_{Ek} \) and \( V_{Ek} \) are the Ekman transports (m2 s\(^{-1}\)) computed using mean climatological wind stress data from Risien and Chelton [2008] and nutrient data from the World Ocean Atlas [Conkright et al., 2002]. The black contour is the largest closed contour of sea surface height (in 1 cm increments) from the AVISO mean absolute dynamic topography [Rio and Hernandez, 2004] and is meant to represent the boundary of the closed recirculation of the subtropical gyre. The short black lines show the locations of the CLIMODE sections.

The Ekman P* transport convergence is shown in Figure 4. The Ekman P* transport convergence is given by the largest closed contour of sea surface height (in 1 cm increments) from the AVISO mean absolute dynamic topography [Rio and Hernandez, 2004] and is meant to represent the boundary of the closed recirculation of the subtropical gyre. The short black lines show the locations of the CLIMODE sections.

4. Quantifying All Remaining Sources and Sinks of Excess Phosphate

The \( \text{N}_2 \) fixation, \( J_{\text{fix}}(N) \), sustained by the total convergence of the P* transport can be estimated by evaluating each term in the steady state conservation equation for P*. This analysis is pursued to gain insight into the dominant terms in the P* budget (summarized in Table 1 and schematized in Figure 5) and relies on order-of-magnitude approximations for several terms. The P* conservation equation is:

\[
\frac{\text{DP}^*}{\text{Dt}} = \frac{\partial (A_\text{t} \text{DP}^*)}{\partial y} + \frac{\partial (A_t \text{DP}^*)}{\partial z} - \frac{F_{\text{a,t}}(N)}{\lambda} - J_{\text{fix}}(N)
\]

where the material derivative is equal to the change in P* following a fluid parcel \( \frac{\text{DP}^*}{\text{Dt}} = \frac{\text{DP}^*}{\text{dy}} + u \cdot \nabla P^* \). Here, \( u \) is the three-dimensional advection and \( y \) is the cross-stream coordinate. The diapycnal and along-isopycnal turbulent exchange coefficients are represented by \( A_t \) and \( A_n \), respectively. \( F_{\text{a,t}}(N) \) is the atmospheric supply of fixed nitrogen to the surface ocean, which provides a non-biological sink of P* in the region and is spread over the surface mixed layer of depth \( H \). Here, we have assumed that the atmosphere deposits only nitrogen and no phosphorus, a good assumption given that the N:P ratio in atmospheric dust is almost 10,000:1 according to Baker et al. [2010]. The final term, \( J_{\text{fix}}(N) \) is the nitrogen fixation supported by the P* supply. The factor, \( \lambda \), represents the number of moles of N that must be fixed to balance each mole of excess P supply. This factor is defined as, \( \lambda = r_f[1 - \gamma_e(1 - \gamma_r)]^{-1} \) where \( r_f \) is the N:P ratio of \( \text{N}_2 \) fixers, \( r_n \) is the average N:P ratio of all other phytoplankton, and \( \gamma_e \) is the fraction of organic matter that sinks below the base of the wintertime mixed layer (see Deutsch et al. [2007] for a detailed derivation of this factor). Because the fraction of material sinking out of the mixed layer is very low in the oligotrophic North Atlantic, \( \gamma_e \) is below 0.1 [Dunne et al., 2005], and the quantity in brackets is close to 1 in the study region. Therefore, \( \lambda \) predominantly reflects the choice of N:P ratio for non-\( \text{N}_2 \) fixing organisms, \( r_n \). If \( r_n \) were below 16, then non-\( \text{N}_2 \) fixing organisms would consume P* and reduce that which
Table 1. The Size of the Physical P* Terms in Equation (3)

<table>
<thead>
<tr>
<th>Term</th>
<th>Method</th>
<th>Rate (mol P* yr⁻¹), Narrow Region</th>
<th>Rate (mol P* yr⁻¹), Wide Region</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cross-stream Ekman advection</td>
<td>Winds and hydrographic data</td>
<td>1.5 ± 0.8 × 10¹⁰</td>
<td>1.5 ± 0.8 × 10¹⁰</td>
</tr>
<tr>
<td>Cross-stream (up-gradient) eddy advection</td>
<td>Scaling argument (see text)</td>
<td>−1.5 × 10⁹</td>
<td>−1.5 × 10⁹</td>
</tr>
<tr>
<td>Along isopycnal mixing</td>
<td>Estimated as $\frac{\partial \Delta P^*}{\partial y}$</td>
<td>1.1 ± 10⁹</td>
<td>1.1 ± 10⁹</td>
</tr>
<tr>
<td>Diapycnal mixing</td>
<td>Estimated as $\frac{\partial \Delta P^*}{\partial y}$</td>
<td>−9 × 10⁸</td>
<td>−1.8 × 10⁸</td>
</tr>
<tr>
<td>Vertical advection</td>
<td>$wP^*$ at the depth of wintertime mixing,</td>
<td>−6 × 10⁷</td>
<td>−1.2 × 10⁷</td>
</tr>
<tr>
<td>Atmospheric nitrogen deposition</td>
<td>From Baker et al. [2010]</td>
<td>−1.2 × 10⁸</td>
<td>−2.3 × 10⁹</td>
</tr>
<tr>
<td>Total P* supply</td>
<td>2.4 ± 0.8 × 10¹⁰</td>
<td>2.0 ± 0.8 × 10ⁱ⁰</td>
<td></td>
</tr>
<tr>
<td>Implied N₂ fixation (mol N yr⁻¹)</td>
<td>3.9 ± 1.3 × 10¹⁵</td>
<td>3.3 ± 1.3 × 10¹⁵</td>
<td></td>
</tr>
<tr>
<td>Implied N₂ fixation per unit area (mol N m⁻² yr⁻¹)</td>
<td>2.6</td>
<td>0.11</td>
<td></td>
</tr>
</tbody>
</table>

¹Positive numbers represent P* supply, negative numbers represent P* removal.
²Rates are for a region 50 km wide separating the Gulf Stream along its 3000 km journey after separating from the shelf break.
²Rates are for a broader region, 1000 km x 3000 km, encompassing the northwestern gyre.
⁴These terms represent fluxes across the box’s northern boundary and therefore do not depend upon the width of the box.
⁵These terms represent fluxes across the surface of box or the base of the mixed layer and are larger when integrated over a larger region.

is available for biological N₂-fixation [Mills and Arrigo, 2010]. In practice, however, the average N:P ratio for phytoplankton in oligotrophic regions is typically elevated above the traditional Redfield ratio, and the nitrogen fixed for a given supply of P* is thought to be at least 16 [Mills and Arrigo, 2010; Weber and Deutsch, 2010]. If this ratio is indeed above 16 for the CLIMODE region, our choice of $\lambda = 16$, will result in a conservative estimate of the nitrogen fixation required to balance the estimated P* supply.

[13] In formulating equation (2), mixing in the along-stream direction is neglected, a convenient choice motivated by the small gradients in P* along the length of the Gulf Stream compared to those across the current. However, because the along-stream velocities are so great (up to 2 m s⁻¹), even small changes in P* concentrations and/or velocities in the along-stream direction can give rise to large divergences of the Gulf Stream’s P* transport. Therefore, it is likely that the Ekman P* convergence could be swept along in a swiftly flowing Gulf Stream that accumulates excess phosphate. In an effort to evaluate the along-stream accumulation of P*, we compared P* concentrations in CLIMODE sections at various positions along the length of the stream (not shown). Unfortunately, this comparison did not lead to any straightforward conclusions: as a function of downstream distance, P* concentrations do not uniformly increase in the upper Gulf Stream. Thus, we cannot resolve the degree to which the southward advected P*:

\[ \int_{-H}^{0} J_{\beta}(N) d\zeta = \lambda \left[ \int_{-H}^{0} \left( -\frac{\partial (\mu P^*)}{\partial x} - \frac{\partial (w P^*)}{\partial y} + \frac{\partial (A_h \partial P^*)}{\partial y} \right) d\zeta + wP^*|_{z=-H} - A_h \frac{\partial P^*}{\partial x} |_{z=-H} - \frac{F_{\text{atm}}(N)}{16} \right] \quad (3) \]

(a) crosses the Gulf Stream into the northern fringes of the gyre (as in Figure 2c); (b) accumulates in the Gulf Stream and is swept downstream in the subtropical recirculation gyre; or (c) enters the Gulf Stream and is partially consumed within the current by nitrogen fixation. In the first two scenarios, the physical supply of excess phosphate fuels nitrogen fixation within the northern subtropical gyre; in the third scenario, the recirculating waters carry only the signature of fixation, including its nitrogen isotopic signature and depressed P* concentrations.

[14] Regardless of the precise region where the cross-front P* flux converges, this flux convergence term influences the nutrient budget of the subtropical waters and must be balanced by removal processes in these same waters. As we have seen, the spatial scale over which the physical P* convergence is balanced is an open question. P* might be consumed in a narrow band within the Gulf Stream and along its southern flank or, alternatively, P* might be transferred over the broader recirculation region in the northwestern gyre. The analysis that follows (summarized in Table 1) considers the leading terms in the conservation equation for two scenarios: first, that the physical supply of P* is consumed in a 50 km by 3000 km box encompassing the Gulf Stream after it separates from the shelf break, and; second, that the P* is consumed in a region that encompasses the northwestern region of the subtropical gyre, an area 1000 km by 3000 km. These two scenarios are meant to represent two extremes, with the middle ground revealed in Figure 6.

[15] Rearranging equation (2) to solve for the biological nitrogen fixation $J_{\beta}(N)$, assuming steady state, and integrating over the wintertime mixed layer of depth H to avoid complications arising from the vertical redistribution of nutrients over a seasonal cycle [Williams and Follows, 1998], we arrive at the expression:

With this formulation, the nitrogen fixation rate per unit area is estimated over the annual cycle. This budget is schematized in Figure 5, where fluxes of nitrate and phosphate are represented by separate arrows (red for phosphate, blue for nitrate). When the red phosphate arrows are larger than the blue nitrate arrows, the P* flux is positive. Thus, a convergent P* flux is signaled by a bigger phosphate arrow entering the box than leaving the box, accompanied by a
corresponding pair of nitrate arrows that do not suggest nitrate convergence, as is depicted for the northern and southern boundaries of the box. The physical supply terms in this conservation equation are due to P* fluxes across the region’s lateral boundaries (terms 1 through 3 on the right hand side), across the region’s bottom boundary (i.e., the base of the wintertime mixed layer, terms 4 and 5), and across the ocean’s surface (term 6).

[16] The first two terms on the right hand side of equation (3) are the convergences of the P* lateral advective transport. The lateral advection can be broken into three components: 1) Ekman advection, primarily directed across the Gulf Stream from high P* toward low. This Ekman advection, discussed in detail above, supplies $1.5 \pm 0.8 \times 10^{10}$ mol yr$^{-1}$ Stream from high P* toward low. This Ekman advection, primarily directed across the Gulf Stream and along its southern flank (as depicted here) and/or throughout a larger region in the recirculation gyre. The black arrows represent the Gulf Stream volume transport; they are not colored because it remains unclear the degree to which P* accumulates in the Gulf Stream along its pathway before recirculating. The size of the colored arrows is meant to represent the size of the nutrient transport relative to a ratio of N:P = 16:1. (b) A map of the region depicted in the schematic (black box) and the larger area over which the P* supply may be consumed (dotted box) overlaid on the P* concentration (as in Figure 1a) and the schematized streamlines of the Gulf Stream and the subtropical gyre. The white arrows represent the cross-Gulf Stream advection and diffusion of P*.


deep than expected for the Ekman depth. 2) The time-mean geostrophic advection, which is predominantly directed along the Gulf Stream and along the P* contours. Our data does not allow a meaningful quantification of the divergence of this along-stream transport and is the motivation for the calculating the budget terms over both a narrow region near the Gulf Stream and a broader region, thus accounting for the convergence of this flux wherever it may occur. 3) The time-varying advection, which is mainly due to mesoscale motion and gives rise to a P* flux directed across the Gulf Stream, from low P* to high, discussed next.

[17] The P* advection due to mesoscale motion is due to the temporal correlation between anomalies of the thickness of an isopycnal layer and the velocity anomalies on that layer [Gent et al., 1995]. Transport arising from mesoscale motion tends to flatten sloping isopycnals and therefore opposes the Ekman transport, which raises isopycnals in regions of Ekman divergence [Lee and Williams, 2000]. Our observations do not resolve such eddy advection and we therefore rely on scaling arguments to assess its importance. The mean velocity due to mesoscale motion is often parameterized as

$$v_{edd} = \frac{\partial H}{\partial y}$$

where $h$ is the mean thickness of the isopycnal layer, and $\Delta z$ is the change in depth of the isopycnal over the distance $\Delta y$ [Gent et al., 1995]. The divergence of the eddy P* transport integrated over the annual mixed layer depth,

$$\int_0^H \frac{\partial}{\partial y} \text{P*}_x \, dz,$$

therefore scales as $\Delta z \frac{\partial P^*}{\partial y}$, We apply an $A_h$ of 250 m$^2$ s$^{-1}$, appropriate for the Gulf Stream region [Bower et al., 1985], and consider an isopycnal layer that is 100 m thick and situated at a mean depth of 100 m on the light side of the Gulf Stream. Over a cross-stream distance of 50 km, this layer thins to 50 m and shoals to an average depth of 25 m (Figure 2b). Given that the cross-stream change in P* is $0.06$ mmol m$^{-3}$ (Figure 2c), the convergence of the eddy P* advection is on the order of $-0.01$ mol P* m$^{-2}$ yr$^{-1}$ an order of magnitude smaller than the Ekman convergence and of opposite sign. Assuming, as we did for the Ekman advection, that the cross-stream eddy P* transport is constant along the length of the Gulf Stream, this term removes P* at a rate of $-1.5 \times 10^6$ mol P* yr$^{-1}$. This estimate is independent of the region over which we calculate the budget (Table 1).
In addition to advecting tracers, mesoscale motions also diffuse tracers, and this diffusion is directed predominantly along isopycnals. Along-isopycnal diffusion is represented by the third term on the right hand side of equation (3), and scales as $-\frac{\partial \overline{c} \delta \rho}{\partial D}$, where $D$ is the depth scale of the wintertime mixed layer (taken as 350 m), and $L$ is the horizontal length scale over which the change in $P^*$ is observed. Using the same coefficient of diffusion, change in $P^*$, and length scale of 50 km as in the estimate of the eddy advection, the isopycnal mixing adds 0.07 mol $P^*$ m$^{-2}$ yr$^{-1}$ to the mixed layer. Again, integrating over the 50 km x 3000 km band near the Gulf Stream where this diffusion is acting, yields a total $P^*$ supply of $1.1 \times 10^{10}$ mol yr$^{-1}$ (Table 1). This diffusive $P^*$ supply is almost an order of magnitude greater than the removal due to eddy advection, and is nearly as large as the estimate for the Ekman supply. The dominance of the down-gradient tracer diffusion over the up-gradient tracer advection for nutrients that are rapidly consumed at the ocean’s surface was first proposed by Lee and Williams [2000], a result recently bolstered by an independent modeling approach [Pasquero, 2005]. Because both eddy advection and diffusion transport $P^*$ only at the gyre’s boundaries, the integral of their contributions are independent of the size of the gyre area.

The vertical advection of $P^*$, the fourth term on the right hand side of equation (3), is estimated by multiplying the $P^*$ at the depth of the maximum annual mixed layer by an estimate of the Ekman pumping velocity, which is proportional to the wind stress curl. The curl of the satellite wind stress in the northwestern gyre leads to an average Ekman pumping velocity smaller than $-10$ m yr$^{-1}$ directed downward, and $P^*$ at the base of the annually mixed depth is below 0.04 mmol m$^{-3}$ (Figures 1 and 2). Hence, vertical advection of $P^*$ amounts to $-4 \times 10^{-9}$ mol m$^{-2}$ yr$^{-1}$, representing a loss over the mixed layer. This term is even smaller in the narrow region hugging the Gulf Stream because the wind stress curl vanishes at the northern boundary of the gyre; we estimate that it accounts for the removal of no more than $10^7$ mol yr$^{-1}$ in that narrow region. Over the larger area encompassing the north-west recirculation gyre, the loss term due to vertical pumping is roughly $-10^9$ mol $P^*$ yr$^{-1}$, and removes up to 5% the cross-Gulf Stream advective-diffusive $P^*$ supply (Table 1).

Diapycnal mixing at the base of the mixed layer, the fifth term on the right hand side of equation (3), also acts as a sink of $P^*$ by transporting a phosphate deficit upwards from the pycnocline to the mixed layer. The diapycnal mixing is estimated as $-\frac{\Delta P^*}{D}$, where $\Delta P^*$ is the change in $P^*$ over the vertical length scale, $D$. Applying a value for $A_o$ of $10^{-3}$ m$^2$ s$^{-1}$ from tracer release studies [Ledwell et al., 1998] and $\Delta P^* = 0.07$ mmol m$^{-3}$ over a depth of $D = 350$ m (Figure 2), the diapycnal mixing removes $6.3 \times 10^{-9}$ mol $P^*$ m$^{-2}$ yr$^{-1}$ from the mixed layer. For the narrow Gulf Stream region, diapycnal mixing removes only $10^7$ mol yr$^{-1}$, three orders of magnitude less than the supply of $P^*$ by along-isopycnal mixing in the region near the Gulf Stream (Table 1). Though the coefficient of diapycnal mixing in the turbulent Gulf Stream environment may be slightly higher than the coefficient given for the gyre interior from tracer release studies, only unrealistically high mixing in the Gulf Stream ($>10^{-3}$ m$^2$ s$^{-1}$) would lead to the removal of $P^*$ from diapycnal mixing being comparable to the supply of $P^*$ due to Ekman advection and along-isopycnal mixing. Integrating over the larger region encompassing the northwestern gyre, diapycnal diffusion removes about $2 \times 10^9$ mol $P^*$ yr$^{-1}$, still two orders of magnitude smaller than the lateral supply across the region’s northern boundary (Table 1).

The final term on the right hand side of our conservation equation is the $P^*$ sink due to the deposition of atmospheric fixed nitrogen, $F_{amp}(N)$, which adds between 0.012 and 0.016 mol N m$^{-2}$ yr$^{-1}$ at the surface of the subtropical gyre [Prospero et al., 1996; Baker et al., 2010]. This nitrogen input is divided by 16 and multiplied by the area of each region to find the corresponding sink of $P^*$. The deposition of atmospheric nitrogen represents a $P^*$ sink equal to $1.1-1.5 \times 10^8$ mol $P^*$ yr$^{-1}$ in the Gulf Stream region and $2.2-3 \times 10^9$ mol $P^*$ yr$^{-1}$ for the larger region, and therefore offsets no more than 10% of the advective-diffusive supply across the Gulf Stream (Table 1).

Up to now, we have discussed only the contribution of phosphate and nitrate to the $P^*$ budget, but there are also dissolved organic pools of both nutrients in the subtropical North Atlantic. The transformation of these dissolved organic nutrients to their inorganic counterparts could create a $P^*$ source or sink term. A paucity of dissolved organic nutrient data in the Gulf Stream region precludes the direct evaluation of the sources and sinks of $P^*$ stemming from transformations between the inorganic and organic nutrient pools. Several studies argue that cycling of dissolved organic phosphorus may sustain nitrogen fixation at a rate of approximately $6 \times 10^{-3}$ mol N m$^{-2}$ yr$^{-1}$ in the subtropical North Atlantic [Mahaffey et al., 2004; Roussenov et al., 2006; Mather et al., 2008; Torres-Valdés et al., 2009]. The DOP supply mechanism for sustaining North Atlantic nitrogen fixation is complementary to the cross Gulf Stream supply of excess phosphate proposed here: the DOP cycling appears to be important at the southern and eastern edges of the oligotrophic gyre, close to productive, upwelling systems on the eastern side of ocean basins [Roussenov et al., 2006; Torres-Valdés et al., 2009], while the transfer of excess phosphate across the Gulf Stream is limited to the northwest corner of the basin.

To summarize, the budget analysis suggests a net physical supply of $P^*$ to the northwestern subtropical gyre of approximately $2 \times 10^{10}$ mol $P^*$ yr$^{-1}$ (Table 1), which for a balanced budget, requires biological nitrogen fixation of more than $3 \times 10^{11}$ mol yr$^{-1}$. The fixation sustained by the cross-Gulf Stream supply of $P^*$ decreases with increasing area over which the $P^*$ is consumed, because the physical loss terms (vertical advection and diffusion and atmospheric deposition of nitrogen) are proportional to the size of this area, while the physical supply terms are not. In Figure 6, a full range of areas is considered along with several previous estimates of $N_2$ fixation rates. From this view it becomes clear that varying the area over which the cross-Gulf Stream $P^*$ supply is consumed from one as large as the subtropical gyre (approximately $6 \times 10^{11}$ m$^2$) to one as narrow as the Ekman convergence zone (50 km wide along the length of the 3000 km Gulf Stream) changes the total integrated nitrogen fixation by only 25%. However, the $N_2$ fixation rate per unit area for the scenario where $P^*$ is consumed over a narrow band is much higher than has been measured in biological
surveys (Figure 6), which suggests that the cross-stream P* supply is consumed over a broader region of at least several hundreds of kilometers.


Over the last three decades, many attempts to assess N\textsubscript{2} fixation rates in the North Atlantic have yielded a range of estimates spanning two orders of magnitude (see Mahaffey et al. [2005] for a detailed review). Direct biological measurements of N\textsubscript{2} fixation at discrete locations have yielded per-area rates of 0.001 – 0.08 mol N m\textsuperscript{-2} yr\textsuperscript{-1}, which have been extrapolated to gyre-wide rates ranging over 0.1 – 16 × 10\textsuperscript{11} mol N yr\textsuperscript{-1} [e.g., Capone and Carpenter, 1982; Lipschultz and Owens, 1996; Orcutt et al., 2001; Davis and McGillicuddy, 2006]. Using a method refined from Michaels et al. [1996] that quantified the increase in excess nitrate (N* = NO\textsubscript{3}\textsuperscript{-} − 16PO\textsubscript{4}\textsuperscript{3−}) along isopycnals on hydrographic sections, Gruber and Sarmiento [1997] arrived at an estimate of 20 × 10\textsuperscript{11} mol N yr\textsuperscript{-1} over the region from 10 to 50\degree N, 25 – 95\degree W, an area of 28 × 10\textsuperscript{12} m\textsuperscript{2}. The cross-Gulf Stream supply of P* calculated here will likely influence the nutrient budgets and proxies of N\textsubscript{2} fixation in the subtropical gyre on the western side of the basin, an area of approximately 6 × 10\textsuperscript{12} m\textsuperscript{2}. Scaling the estimate from Gruber and Sarmiento [1997] for this smaller region, yields a nitrogen fixation rate of 4.3 × 10\textsuperscript{11} mol yr\textsuperscript{-1}, which agrees well with a recent re-evaluation of North Atlantic N\textsubscript{2} fixation from N* gradients along sections in the western subtropical region [Hansell et al., 2007]. The scaled-down estimate from Gruber and Sarmiento [1997] and the revised estimate from Hansell et al. [2007] are similar to our assessment of the N\textsubscript{2} fixation sustained by the P* flux across the Gulf Stream if it converges within a zone on the order of 1000 km wide (Figure 6).

Although nitrogen fixation rates in these studies were estimated using various methods [Mahaffey et al., 2005], none addressed the phosphate necessary to sustain the fixation. However, a recent study [Deutsch et al., 2007] inferred fixation rates from the convergence of P*, the same technique used here, but with transports computed in an

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**Figure 6.** The relationship between the nitrogen fixation sustained by the cross-Gulf Stream P* supply versus the area over which that P* supply is consumed. The black line (inner vertical axis) represents the total nitrogen fixation in the gyre (10\textsuperscript{11} mol N yr\textsuperscript{-1}). The red line (outer vertical axis) is the total inferred N\textsubscript{2} fixation divided by the area of the gyre, giving an N\textsubscript{2} fixation rate per unit area (mol N m\textsuperscript{2} yr\textsuperscript{-1}). Crosses mark the fixation rates for the scenarios given in Table 1. Red dashed lines indicate biologically based estimates of N\textsubscript{2} fixation per unit area of Capone et al. [2005] (0.08 mol N m\textsuperscript{2} yr\textsuperscript{-1}), Orcutt et al. [2001] (0.015 mol N m\textsuperscript{2} yr\textsuperscript{-1}), and Davis and McGillicuddy [2006] (0.02 mol N m\textsuperscript{2} yr\textsuperscript{-1}, calculated in that reference from observed colony abundances and models of light-dependent fixation rates per colony). The black dashed lines indicate the biogeochemical estimate of N\textsubscript{2} fixation from Hansell et al. [2007] (3–4 × 10\textsuperscript{11} mol N yr\textsuperscript{-1}), which was calculated as a gyre-integrated value, and the model-derived value of Deutsch et al. [2007] (2.6 × 10\textsuperscript{11} mol N yr\textsuperscript{-1}, which we integrated over the region of North Atlantic anticyclonic circulation). The Gruber and Sarmiento [1997] estimate (20 × 10\textsuperscript{11} mol N yr\textsuperscript{-1}) is for the entire North Atlantic, a region much larger than we expect is influenced by the cross-Gulf Stream P* supply.
Table 2. Nitrate Supply and Demand in the North Atlantic Subtropical Gyre*

<table>
<thead>
<tr>
<th>Supply Mechanism</th>
<th>Area-Average Gyre Supply Rate (mol N m² yr⁻¹)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atmospheric deposition</td>
<td>0.012 – 0.016</td>
<td>Prospero et al. [1996]; Baker et al. [2010]</td>
</tr>
<tr>
<td>Ekman transport of nitrate across gyre boundaries</td>
<td>0.03</td>
<td>Williams and Follows [1998]</td>
</tr>
<tr>
<td>Diapycnal diffusion</td>
<td>0.05 – 0.08</td>
<td>Lewis et al. [1986]</td>
</tr>
<tr>
<td>Mesoscale and submesoscale upwelling</td>
<td>0.05 – 0.24</td>
<td>McGillicuddy et al. [1998]; Oechsles and Garcon [1998]</td>
</tr>
<tr>
<td>$N₂$ fixation at BATS from direct measurement</td>
<td>0.004 – 0.015</td>
<td>Orecutt et al. [2001]</td>
</tr>
<tr>
<td>$N₂$ fixation in the western Sargasso inferred from colony abundances</td>
<td>0.02</td>
<td>Davis and McGillicuddy [2006]</td>
</tr>
<tr>
<td>$N₂$ fixation in the southwestern North Atlantic from incubation experiments</td>
<td>0.08</td>
<td>Capone et al. [2005]</td>
</tr>
<tr>
<td>$N₂$ fixation sustained by cross Gulf Stream Ekman and mixing fluxes of excess phosphate</td>
<td>0.03 – 0.07</td>
<td>This study</td>
</tr>
<tr>
<td>Total known supply</td>
<td>0.15–0.45</td>
<td>Jenkins [1982] Dunne et al. [2007]</td>
</tr>
<tr>
<td>Biological nitrate demand</td>
<td>0.5 (at Bermuda) 0.4 (averaged over gyre)³</td>
<td></td>
</tr>
</tbody>
</table>

*Nitrate demands per unit area given here are for the gyre as a whole (i.e., the total cross-stream supply term is divided by the $6 \times 10^{12}$ m² area of the gyre).

²The summed total of the nitrogen in the narrow Gulf Stream region and the northwestern gyre calculated in Section 3 ($3 - 3.9 \times 10^{11}$ mol yr⁻¹) has been divided by the total area of the subtropical gyre ($6 \times 10^{12}$ m²) to calculate the supply of fixed nitrogen, averaged over the gyre interior.

³The low end of the estimate reflects the sum of all of the lowest estimates for each supply term and vice versa for the high end.

°This biological nitrate demand averaged over the gyre was calculated using an estimate of the export of particulate organic nutrients from the euphotic zone. This estimate was provided by John Dunne from his work using empirical relationships to deduce the global export of organic matter from satellite data [Dunne et al., 2007]. We propagate the export of organic matter from the base of the euphotic zone to the base of the annual maximum mixed layer depth with an empirical formulation for particle flux [Martin et al., 1987], also used in the Ocean Carbon Model Intercomparison Project (OCMIP2) protocol: $F(z) = F_{75}*(H/75)$, where $F$ is the flux of particulate organic nitrogen and $H$ is the mixed layer depth. We assume the export at the base of the euphotic zone is not appreciably different from the export at 75 m. The size of the flux was averaged over the subtropical gyre, as defined by the maximum closed contour of Sea Surface Height (see Figure 4).

Ocean circulation model. We integrated the simulated nitrogen fixation from the model run of Deutsch et al. [2007] over the region of the anticyclonic circulation in the modeled North Atlantic to find an $N₂$ fixation rate of $2.6 \times 10^{11}$ mol yr⁻¹, which falls within the range of our estimates (Figure 6).

[26] In situ data and satellite observations that are independent from the biogeochemical data support the view that the northwestern region of the subtropical gyre may be an important site of nitrogen fixation. First, a trans-Atlantic survey with a towed underwater digital microscope revealed that the colony abundances of *Trichodesmium* are greatest in the northwestern part of the gyre, trending toward sparser populations with distance from the Gulf Stream [Davis and McGillicuddy, 2006]. This spatial distribution of the *Trichodesmium* agrees with our inference of fixation in the northwestern gyre. However, the quantitative estimates of $N₂$ fixation rates from the colony abundances reached a maximum of 0.02 mol N m⁻² yr⁻¹ in the northwestern gyre, a factor of 5 lower than our estimate from the lateral $P^{*}$ supply, even if that supply is consumed over a region 1000 km wide (Table 2).

[27] Evidence from satellite data also agrees with the inference of $N₂$ fixation near the gyre’s northern boundary. Ocean color data suggest that in the subtropical North Atlantic, *Trichodesmium* blooms are found primarily in a band south of the Gulf Stream [Westberry and Siegel, 2006]. However, the satellite analysis of Westberry and Siegel show the *Trichodesmium* blooming primarily in summer and fall, while our analysis suggests the largest $P^{*}$ flux occurs during the winter months when the wind stress is maximized. This discrepancy may be explained by seasonal variability and the accumulation of $P^{*}$ on time scales shorter than a year. In wintertime, the Gulf Stream region is likely too cold and with mixed layers too deep for nitrogen fixation to effectively compete with the physical supply of $P^{*}$, which peaks in this season due to the strengthening along-front wind stress. Therefore, the wintertime $P^{*}$ convergence is unlikely to be offset locally in wintertime by $N₂$ fixation; rather, the $P^{*}$ may be consumed downstream and/or after the mixed layer shoals in spring.

[28] In the warmer seasons, the location where the $P^{*}$ Ekman transport converges (i.e., where the $P^{*}$ concentration goes to zero in the Gulf Stream) might possibly be influenced by the requirements of the $N₂$-fixing organisms themselves. The marine $N₂$-fixing cyanobacterium, *Trichodesmium* grows in culture only at temperatures above 20°C and achieves its optimal growth rate at temperatures between 24 and 30°C [Breitharth et al., 2007]. These temperature conditions are achieved just south of the Gulf Stream’s north wall throughout most of the year except during the time of deepest mixing in the winter (Figure 3). Deep mixing can inhibit biological nitrogen fixation [Satius-Wilhelmy et al., 2001], so that the strongly stratified Gulf Stream may be an ideal location for nitrogen fixers to drawdown $P^{*}$ as it is transported across the current. This possibility will remain speculative until $N₂$ fixation rates are measured in this region, ideally in winter as well as summer.

[29] A related paradox at Bermuda is that mixed layer carbon is removed in summertime with no known supply of nitrate, prompting the hypothesis that biological nitrogen fixation fuels the carbon drawdown [Karl et al., 2003]. However, because the lateral $P^{*}$ gradients are so weak near Bermuda and because the isotopic signal of $N₂$ fixation is...
not detected there [Knapp et al., 2005], biological fixation is not likely to directly resolve this paradox. On the other hand, the DON and DOP created by nitrogen fixing organisms may be advected and mixed to the interior where they can fuel primary productivity, so long as they are not exported beneath the seasonal boundary layer [Lomas et al., 2009]. The influence of the dissolved organic nutrients may extend over much of the subtropical gyre, as is thought to be the case for nitrate advected in the Ekman layer across the Gulf Stream, converted to DON a short distance from the Stream, and advected throughout the gyre’s geostrophic interior [Williams and Follows, 1998]. Accounting for this supply in the nutrient budgets at Bermuda might help reconcile the discrepancy between estimated rates of primary productivity and the physical supply of nutrients (Table 2), though a fully closed budget remains elusive.

6. Concluding Remarks

This work quantifies the physical mechanisms that transfer excess phosphate into the North Atlantic subtropical gyre, with a particular emphasis on processes that flux P* across the gyre’s northern boundary. Physical transport processes give rise to a net supply of P* to the gyre of roughly $2.4 \times 10^{10}$ mol P* yr$^{-1}$, because Ekman transport and along-isopycnal diffusive supplies of P* across the Gulf Stream are larger than physical removal processes such as downwelling and atmospheric deposition throughout the gyre interior. Thus, for steady state conditions, the physical supply of P* must be removed by a biogeochemical process, most likely biological N$_2$ fixation. This budget analysis leads to an inferred gyre-integrated rate of N$_2$ fixation of $3.3 - 3.9 \times 10^{11}$ mol N yr$^{-1}$, which is similar to recent estimates (Figure 6). To arrive at N$_2$ fixation rates per unit area in the range of what has been measured in the past [Capone et al., 2005], the P* supply must be consumed over an area as wide as the Gulf Stream and several hundred kilometers in north–south extent (Figure 6). Assuming that the nitrogen fixed to balance the P* supply is ultimately advected and mixed across the entire subtropical gyre, N$_2$ fixation would provide 0.06 to 0.07 mol N m$^{-2}$ yr$^{-1}$ of the subtropical nitrate budget, up to 15% of the biological nitrate demand (Table 2). In a similar manner, southeasterly trade winds blowing over a meridional P* gradient at the southern boundary of the subtropical gyre might provide an influx of P* at the southern boundary of the subtropical gyre (Figures 1a, 1b, and 4). An alternative source of excess phosphorus that could possibly augment the supply of P* and maintain N$_2$ fixation is provided by the cycling and transport of semi-labile DOP, which can be produced in upwelling zones and then transported by a combination of the gyre and eddy circulations to the flanks of the gyre interior; see model experiments by Roussenov et al. [2006] and observational diagnostics by Mahaffey et al. [2004], Mather et al. [2008], and Torres-Valdés et al. [2009].

Understanding the pathways that allow excess phosphate to enter the subtropical North Atlantic helps resolve the puzzle of how nitrogen fixation may persist in an environment where the nutrient reservoir is vastly enriched in nitrate relative to phosphate. Our analysis suggests that a large P* transport enters the subtropical gyre at its northern boundary, possibly sustaining high rates of fixation in the northwestern sub tropics. Such an interpretation provides a testable hypothesis that could be evaluated in future field experiments in which nitrogen fixation rates are directly measured at the gyre’s northern flanks.

Acknowledgments. We thank R.T. Barber, E.D. Galbraith, C.M. Moore, D.M. Sigman, A. N. Knapp, and two anonymous reviewers for useful comments. We are grateful to C. Deutsch for making his model output available to us and to J. Dunne for providing the estimate of particulate nutrient export. We thank all members of the CLIMODE project for their help collecting samples. Funding for the CLIMODE project was provided by the U.S. National Science Foundation. JBP gratefully acknowledges funding from the Discovery Program of the National Sciences and Engineering Research Council of Canada. RGW also gratefully acknowledges support from NERC grant NE/D011108/1.

References


M. S. Lozier, Division of Earth and Ocean Sciences, Nicholas School of the Environment, Box 90227, Duke University, Durham, NC 27708, USA.

J. B. Palter, Department of Atmospheric and Oceanic Science, McGill University, 945 Burnside Hall, 805 Sherbrooke St. West, Montreal, QC H2X 1C4, Canada. (jaime.palter@mcgill.ca)

J. L. Sarmiento, Atmosphere and Ocean Sciences Program, Princeton University, Princeton, NJ 08544-0710, USA.

R. G. Williams, School of Environmental Sciences, University of Liverpool, Liverpool L69 3GP, UK.