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On nitrogen fixation and preferential remineralization of phosphorus

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[1] Regional and global nitrogen fixation rates are often estimated from geochemical tracers related to N^* ($= NO_3^- - 16PO_4^{3-}$). However the patterns of this tracer reflect the influence of numerous processes including nitrogen fixation, denitrification, remineralization of organic matter, variable stoichiometry, atmospheric deposition and physical transport. Here we have used idealized models to illustrate how preferential remineralization of organic phosphorus may explain observed features of N^* distribution in the North Atlantic Ocean, including a subsurface maximum and an increased temporal variability in the mid-thermocline. If preferential remineralization of phosphorus is key in shaping the oceanic distribution of N^* , published estimates of nitrogen fixation may be underestimating the marine nitrogen fixation rate by as much as a factor of three. **Citation:** Monteiro, F. M., and M. J. Follows (2012), On nitrogen fixation and preferential remineralization of phosphorus, *Geophys. Res. Lett.*, 39, L06607, doi:10.1029/2012GL050897.

1. Introduction

[2] Nitrogen fixation, the biological assimilation of dinitrogen gas into organic nitrogen, is the major external source of nitrogen to the modern global ocean, counterbalanced by denitrification and anammox [Gruber, 2004]. Marine nitrogen fixation is achieved by phytoplanktonic diazotrophs, *Trichodesmium* and unicellular cyanobacteria [Monteiro *et al.*, 2010], with unquantified contributions from diazotroph-diatom associations and heterotrophic diazotrophs [Langlois *et al.*, 2005].

[3] Rates of nitrogen fixation have been estimated on basin and global scales using compilations of direct measurements and model results, and interpretations of the patterns of geochemical tracers [Gruber, 2004; Moore *et al.*, 2004; Capone *et al.*, 2005]. Direct and model estimates suffer from the infrequency of observations of marine diazotrophs mostly restricted to the *Trichodesmium* community and the North Atlantic region. In this region, direct estimates range from 15 to 35 TgN yr⁻¹ [Lipschultz and Owens, 1996; Capone *et al.*, 2005], and modeled estimates from 8 to 30 TgN yr⁻¹ [Coles and Hood, 2007; Monteiro *et al.*, 2010]. On the other hand, geochemically-based estimates use the larger database of inorganic nitrogen and phosphorus measurements and integrate the activity of the entire diazotroph community. Geochemical tracers such as N^* ($= NO_3^- - 16PO_4^{3-}$) [Gruber and Sarmiento, 1997; Hansell *et al.*, 2007; Weber and Deutsch,

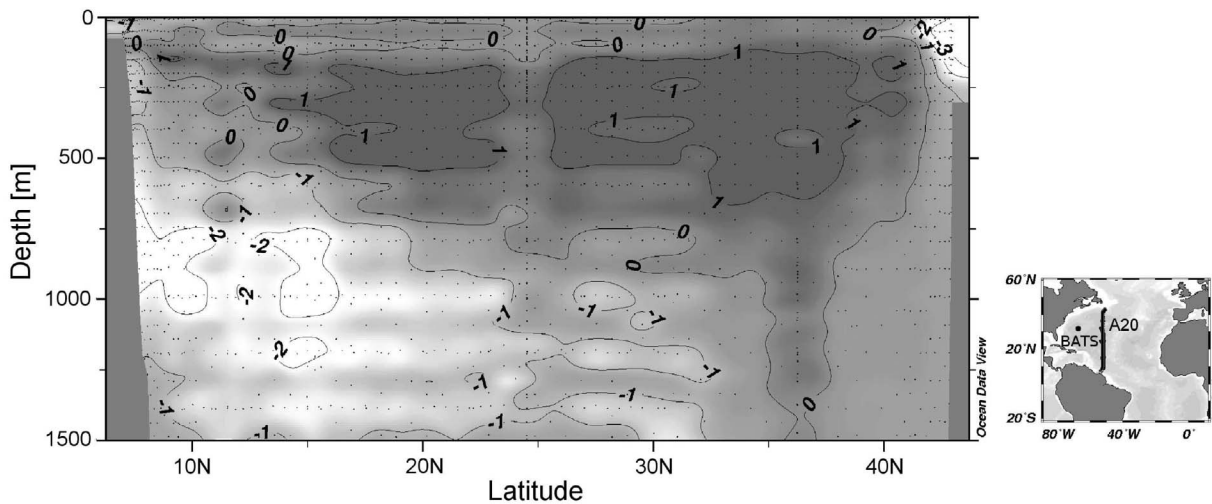
2010] measure the excess of dissolved inorganic nitrogen relative to the Redfield molar ratio of 16:1. In general, N^* increases with nitrogen fixation as diazotrophs fix new nitrogen into the ocean, and decreases with denitrification/anammox as microbes consume fixed nitrogen to oxidize organic matter when oxygen is low. The rate of accumulation of N^* along isopycnals is used to infer the integrated contribution of nitrogen fixation and denitrification in each density surface. This technique estimates nitrogen fixation rates of the North Atlantic Ocean to range between 4 to 30 TgN yr⁻¹ [Gruber and Sarmiento, 1997; Hansell *et al.*, 2007; Landolfi *et al.*, 2008]. The range of estimates is mainly due to uncertainties in the volume of water over which the integration is made [Hansell *et al.*, 2004]. Such estimates have been extrapolated to evaluate global nitrogen fluxes [Gruber and Sarmiento, 1997; Gruber, 2004].

[4] However, the tracer N^* here specifically $NO_3^- - 16PO_4^{3-}$ [Weber and Deutsch, 2010]) has some notable characteristics in the North Atlantic Ocean. In this region, N^* has a subsurface maximum in the thermocline between 100 m and 1000 m (Figure 1a). This pattern is counter-intuitive if one expects most of the N-rich organic matter derived from diazotrophs to be remineralized in the upper ocean; this would lead to a maximum of N^* in the near surface waters. Besides, observations from the Bermuda Atlantic Time-series Study (BATS) indicate that temporal variability of N^* is weaker in the mixed layer and upper thermocline (i.e., shallower than 200 m or so) than in the main thermocline (i.e., around 500 m) where there are strong N^* variations between 1 and 4 $\mu\text{mol l}^{-1}$ on annual and longer timescales (Figure 1b). We might expect though that near surface N^* should be more variable and closely coupled to the variability in diazotrophy because of local remineralization of organic matter, whereas thermocline N^* should integrate and “smooth out” the variations of the source.

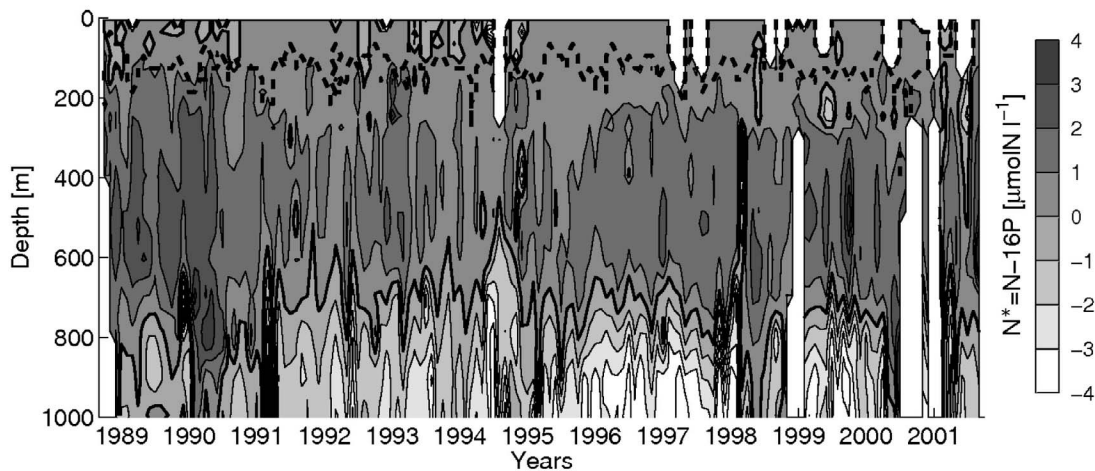
[5] The distribution of N^* may then not only reflect processes of nitrogen fixation and denitrification. Important other processes include physical transport of N^* in and out of the domain of interest, variable phytoplankton stoichiometry [Weber and Deutsch, 2010], atmospheric deposition [Hansell *et al.*, 2007], and different remineralization rates for organic phosphorus and nitrogen [Coles and Hood, 2007; Landolfi *et al.*, 2008; Zamora *et al.*, 2010]. There is considerable evidence that phosphorus is remineralized from organic detritus faster than nitrogen [e.g., Clark *et al.*, 1998]. Notably Dyhrman and Palenik [1999] observed that when phosphate is limiting phytoplankton produce an alkaline-phosphatase enzyme which is used to break down dissolved organic phosphorus compounds, providing an additional source of phosphate. Finally Wu *et al.* [2000] and Mahaffey *et al.* [2004] suggested that phosphorus is more labile than nitrogen in dissolved organic matter.

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(a) Vertical distribution of N^* along the transect A20 (see map)



(b) Time series of N^* at station BATS (see map)

Figure 1. Observations of $N^* = \text{NO}_3^- - 16\text{PO}_4^{3-}$ ($\mu\text{molN l}^{-1}$) in the North Atlantic Ocean. (a) N^* distribution along WOCE transect A20 from the GLODAP data compilation [Key *et al.*, 2004]. Contours and shading represent N^* while black dots indicate sample points. A subsurface maximum of N^* is present between 100–1000 m depth. (b) N^* time series at the Bermuda Atlantic Time-series Station near Bermuda (<http://bats.bbsr.edu>). Observations have been averaged for each month and linearly interpolated with depth. The dashed line indicates the detection limit of N^* based on analytical methods for nitrate and phosphate using detection limits of $0.05 \mu\text{molN l}^{-1}$ and $0.03 \mu\text{molP l}^{-1}$ respectively. The thick black continuous line indicates the zero contour of N^* . Temporal variability of N^* in the mixed layer and upper thermocline is much weaker than in the main thermocline.

[6] Here we use idealized models, re-visiting and extending the framework of Gruber and Sarmiento [1997], to investigate and illustrate how differential remineralization may shape the distribution and temporal variability of N^* , in particular of what is observed in the North Atlantic Ocean. We also evaluate the possible error in N^* -based estimates of nitrogen fixation when preferential remineralization of phosphorus is not accounted for.

2. Idealized N^* Dynamics of the North Atlantic Ocean

[7] We generalize the framework laid out by Gruber and Sarmiento [1997] for the development of N^* in the North Atlantic Ocean, by explicitly introducing the effects of phytoplankton uptake and differential remineralization of

organic phosphorus and nitrogen. In the open North Atlantic Ocean, concentrations of phosphate (P) and fixed nitrogen (N , including nitrate, nitrite and ammonium) change due to the combined effects of photosynthesis, remineralization of organic matter and nitrogen fixation. Here we neglect N^* sinks from denitrification because the region is well oxygenated. Since our focus is on differential remineralization, we also neglect N^* sources from atmospheric deposition though these have been estimated to account for up to 13–38% of the N^* signal in the region [Hansell *et al.*, 2007; Zamora *et al.*, 2010]. We represent two broad classes of phytoplankton; diazotrophs (*Diaz*) and all other phytoplankton (*Phy*) with respective primary production pd and pp . *Diaz* are assumed to use dinitrogen gas as their sole source of nitrogen and to have a relatively high N:P ratio [LaRoche

and *Breitbarth*, 2005], while *Phy* are assumed to have a Redfield stoichiometry (N:P = 16). Under these assumptions, the variations of *P* and *N* are then:

$$\frac{dP}{dt} = \underbrace{\lambda_P TOP}_{\text{Remineralization}} - \underbrace{(pp + pd)}_{\text{Total phytoplankton uptake of P}} \quad (1)$$

$$\frac{dN}{dt} = \lambda_N TON - 16pp \quad (2)$$

d/dt equals $\partial/\partial t + \mathbf{u} \cdot \nabla + \mathbf{D}$; the time rate of change, advection and diffusion. λ_P and λ_N are the constant coefficients for the remineralization terms of *P* and *N*, which are represented by a first-order decay of organic matter. *TOP* and *TON* represent the concentrations of total organic phosphorus and nitrogen which originate from organic detritus, including both particulate and dissolved forms. Equations (1) and (2) describe how, following a water parcel, phosphate and fixed nitrogen concentrations increase with remineralization and decrease with phytoplankton uptake. Combining these two equations and using $N^* = N - 16P$ lead to a Lagrangian, prognostic expression of the geochemical tracer N^* :

$$\frac{dN^*}{dt} = \underbrace{16pd}_{\text{Diaz uptake of P}} + \underbrace{\lambda_N TON - 16\lambda_P TOP}_{\text{Remineralization}} \quad (3)$$

We see that along the water trajectory, N^* can change with either the uptake of phosphate by diazotrophs or remineralization. The latter takes effect only if the N:P ratio of the organic matter is non-Redfield or if $\lambda_N \neq \lambda_P$ (i.e., differential remineralization). In the limit when $pd = 0$ and $\lambda_P = \lambda_N$, equation (3) is equivalent to the expression given by *Gruber and Sarmiento* [1997].

2.1. Why Is There a Subsurface Maximum of N^* in the North Atlantic Ocean?

[8] For a subsurface maximum, N^* must increase with depth from the surface. In the idealized system described by equation (3), this can be achieved by either diazotrophs consuming phosphate or remineralization of N-rich organic matter ($dN^*/dt > 0$). For the former, diazotrophic uptake needs to occur at the depth of the N^* maximum (100–1000 m, Figure 1a). This is unlikely because most diazotrophic phytoplankton inhabit the sunlit uppermost 200 m of the ocean (even for those that can migrate vertically [*Villareal and Carpenter*, 2003]). Heterotrophic diazotrophs might be present at depth but we expect them to be most abundant where organic matter is most concentrated, i.e., in the surface mixed layer [*Langlois et al.*, 2005]. Thus the subsurface maximum of N^* in the North Atlantic Ocean is more likely the result of remineralization of N-rich organic detritus from diazotrophs [e.g., *Gruber and Sarmiento*, 1997; *Hansell et al.*, 2004].

[9] To characterize how remineralization of N-rich organic matter can affect the N^* depth profile, we rewrite the remineralization term of equation (3):

$$\frac{dN^*}{dt} = 16pd + 16\lambda_N TOP \left(\frac{R}{16} - \frac{\lambda_P}{\lambda_N} \right) \quad (4)$$

where *R* is the N:P ratio of the organic matter (*TON:TOP*) which is assumed to be greater than 16 due to the diazotroph

contribution. Observations show that organic matter has maximum concentration in the mixed layer where it is produced and mainly respired [*Martin et al.*, 1987]. In the idealized framework of equation (4), if organic nitrogen and phosphorus are remineralized with equal rate constants ($\lambda_P = \lambda_N$), the maximum rate of remineralization of N-rich organic matter, and thus concentration of N^* , would occur in the mixed layer: When the rates are equal, the distribution of N^* is determined directly by the distribution of organic matter (dN^*/dt evolves the same way as *TOP* when $R/16 > \lambda_P/\lambda_N$).

[10] If phosphorus is remineralized more efficiently than nitrogen, $\lambda_P/\lambda_N > 1$, a local reduction of N^* in the mixed layer and upper thermocline can develop ($dN^*/dt < 0$, provided $\lambda_P/\lambda_N > R/16$). This reduction potentially damps the signature of diazotrophy at the source and enriches the relative nitrogen content of the remaining organic matter sinking or being transported away from the source (*R* increases). This in turn would enhance the net source of N-rich matter downstream or at depth ($R/16 - \lambda_P/\lambda_N$ increases), creating a N^* maximum away from the diazotroph growth region.

[11] This simplified analysis suggests that preferential remineralization of phosphorus relative to nitrogen could be responsible for a maximum of N^* in the thermocline. A more rigorous analysis of this framework, considering sinking particles and dissolved organic material independently, leads to the same conclusion (see auxiliary material).¹ We also illustrate this point in the context of a 3D circulation and biogeochemistry model characteristic of the North Atlantic Ocean (Figure 2). Beside, similarly to recent published basin-scale simulations [*Coles and Hood*, 2007; *Zamora et al.*, 2010], our model simulations suggest that both differential remineralization and nitrogen fixation may be necessary to produce a N^* maximum in the thermocline.

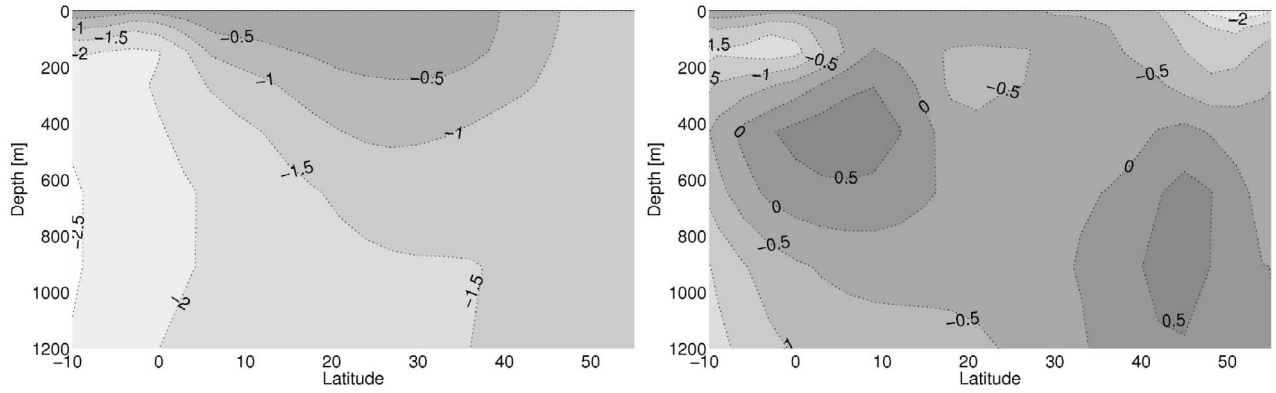
2.2. Why Is the Temporal Variability of N^* Smaller in the Mixed Layer and Upper Thermocline Than at Depth?

[12] Time-series observations at BATS station show that the temporal variability of N^* in the uppermost 200 m (and still above the detection limit) of the water column is smaller than deeper in the thermocline (Figure 1b). To understand why the variability is smaller nearer to the surface, we consider the time-dependent case of equation (4) and neglect physical transport: $\partial N^*/\partial t \approx 16pd + 16\lambda_N TOP (R/16 - \lambda_P/\lambda_N)$. Assuming that low temporal variability is similar to steady state ($\partial/\partial t \approx 0$), the diazotrophic uptake of phosphate is tightly coupled to the remineralization of N-rich organic matter:

$$pd \approx (\lambda_P/\lambda_N - R/16)\lambda_N TOP \quad (5)$$

By definition *pd* is positive and if diazotrophs are present, $R \geq 16$. As a result, the balance of equation (5) is possible only if preferential remineralization of phosphorus exists, $\lambda_P > \lambda_N$. In other words, preferential remineralization can dampen the variability of N^* in the upper ocean. This analysis does not however imply that differential remineralization enhances the variability in the main thermocline which may result from variations in the physical transport and/or N-rich source.

¹Auxiliary materials are available in the HTML. doi:10.1029/2012GL050897.



(a) Modeled N* with equal remineralization rate (b) Modeled N* with differential remineralization rate

Figure 2. Meridional section of modeled N* through a North Atlantic-like basin, without and with preferential remineralization of phosphorus. The model is a sector configuration of the MITgcm ocean model (see details in the auxiliary material). (a) Equal remineralization rate ($\lambda_P = \lambda_N = 0.03 \text{ d}^{-1}$). (b) Faster remineralization rate for phosphorus relative to nitrogen ($\lambda_P = 1.5\lambda_N$).

[13] These simple models suggest that differential remineralization could be a significant process in the North Atlantic basin where it may contribute to the observed thermocline maximum of N* and the relatively low temporal variability of near-surface N*. If differential remineralization is an important process in shaping the N* distribution of the North Atlantic Ocean, how might it affect estimates of nitrogen fixation rate based on N*?

3. Underestimation of Nitrogen Fixation Rates From N*

[14] We evaluate the potential error of neglecting the effect of preferential remineralization of phosphorus on basin-wide or global estimates of nitrogen fixation rates which are based on N* anomalies. Following Gruber and Sarmiento [1997], we consider the N* equation (3) below the mixed layer where $pd = 0$. In addition, organic matter originates from either Phy or Diaz, so that $TOP = TOP^{Phy} + TOP^{Diaz}$ and $TON = TON^{Phy} + TON^{Diaz}$, and equation (3) becomes:

$$\frac{dN^*}{dt} \approx \lambda_N(TON^{Diaz} + TON^{Phy}) - 16\lambda_P(TOP^{Diaz} + TOP^{Phy}) \quad (6)$$

Following Gruber and Sarmiento [1997], we define the nitrogen source from diazotrophs as $J_{NF} = \lambda_N TON^{Diaz}$, and N:P ratios as $TON^{Phy} : TOP^{Phy} = 16$ and $TON^{Diaz} : TOP^{Diaz} = R^{Diaz}$. Rewritten as a function of J_{NF} , N* varies along the trajectory of a water parcel as

$$\frac{dN^*}{dt} \approx J_{NF} \left[1 - \frac{16}{R^{Diaz}} \frac{\lambda_P}{\lambda_N} + \frac{16}{R^{Diaz}} \left(1 - \frac{\lambda_P}{\lambda_N} \right) \frac{TOP^{Phy}}{TOP^{Diaz}} \right] \quad (7)$$

This expression is reworked to describe the rate of nitrogen fixation for both cases: equal and differential remineralization

$$J_{NF(\lambda_P=\lambda_N)} \approx \frac{R^{Diaz}}{R^{Diaz} - 16} \frac{dN^*}{dt} \quad (8)$$

$$J_{NF(\lambda_P \neq \lambda_N)} \approx \frac{R^{Diaz}}{R^{Diaz} - 16\lambda_P/\lambda_N + 16(1 - \lambda_P/\lambda_N)TOP^{Phy}/TOP^{Diaz}} \frac{dN^*}{dt} \quad (9)$$

Equation (8) is equivalent to the expression used by Gruber and Sarmiento [1997] and Hansell et al. [2007] to evaluate nitrogen fixation rates. The difference between equations (8) and (9) reveals the error inferred when differential remineralization is unaccounted for: $\varepsilon = (J_{NF(\lambda_P \neq \lambda_N)} - J_{NF(\lambda_P=\lambda_N)})/J_{NF(\lambda_P \neq \lambda_N)}$. Using equations (8) and (9),

$$\varepsilon = -\frac{16}{R^{Diaz} - 16} \left(\frac{\lambda_P}{\lambda_N} - 1 \right) \left(1 + \frac{TOP^{Phy}}{TOP^{Diaz}} \right) \quad (10)$$

Because ε is negative, evaluating rates from N* assuming equal remineralization rates underestimates nitrogen fixation

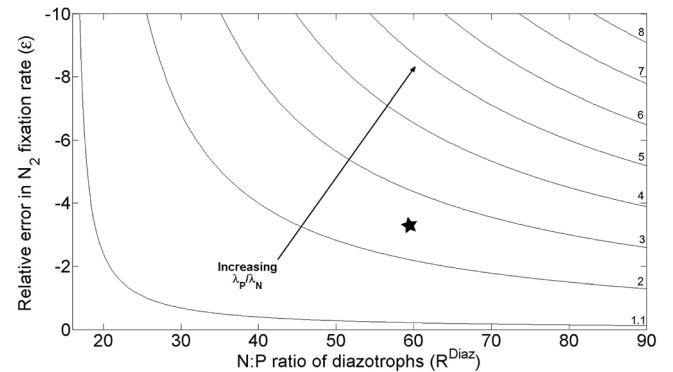


Figure 3. Underestimation (ε) of nitrogen fixation rate inferred from N* if preferential remineralization of phosphorus relative to nitrogen is not taken into account. ε is plotted for $OP^{Phy}/OP^{Diaz} = 5$ as a function of R^{Diaz} and for different values of λ_P/λ_N , ranging from 1.1 to 8 (indicated on each line). The star represents the “typical” value of ε , suggesting that nitrogen fixation rate could be underestimated by about of factor three when using N*-estimates with equal remineralization rate.

rates. The sensitivity of the incurred error is plotted as a function of R^{Diaz} and λ_P/λ_N (Figure 3). The magnitude of the underestimation ε increases along with the degree of preferential remineralization λ_P/λ_N and with lower N:P ratio of diazotrophs.

[15] Relatively few observations exist to constrain ε , but a simple analysis of observed changes in particulate and dissolved organic nitrogen and phosphorus concentrations with depth (auxiliary material) suggests that λ_P/λ_N ranges between 1.1 and 6.6 in subtropical oceans. Observations of R^{Diaz} range between 30 and 90 [LaRoche and Breitbarth, 2005] and of the relative contributions of non-diazotrophs and diazotrophs to biomass (and thus organic detritus) between 1 and 10 in the subtropical North Atlantic Ocean [Carpenter *et al.*, 2004]. Taking the “typical” values from these ranges suggests an underestimation of nitrogen fixation by a factor of about three, but with very large uncertainty (ε ranging from -0.05 to -70) when preferential remineralization is occurring but is not accounted for.

4. Concluding Remarks

[16] Observations in the North Atlantic Ocean of the geochemical tracer N* show a subsurface maximum (100–1000 m) and an increasing temporal variability with depth at station BATS. We used idealized models, extending the framework developed by Gruber and Sarmiento [1997], to seek explanations for these observations. While these models are not comprehensive, and may exclude some other important processes, our analysis suggests three potentially significant results. Firstly, the observed subsurface maximum of N* present in the thermocline of the North Atlantic Ocean can be explained as a result of the faster remineralization rate of organic phosphorus relative to nitrogen. Secondly, preferential remineralization of phosphorus can explain the weak temporal variability of N* observed in the mixed layer and upper thermocline at BATS. The faster recycling of phosphorus relative to nitrogen damps the signal of nitrogen fixation in the mixed layer reducing the remineralization source of N-rich matter. Thirdly, if the process of differential remineralization is not taken into account, indirect estimates of nitrogen fixation based on the accumulation N* along isopycnals may lead to a significant underestimation of nitrogen fixation rates, perhaps as much as several fold. The error in nitrogen fixation rate is not well constrained as there is little information on the difference of remineralization rates for organic nitrogen and phosphorus.

[17] The geochemical tracer of total nitrogen excess, TN_{xs} ($= N^* + TON - 16TOP$ [Landolfi *et al.*, 2008; Monteiro and Follows, 2009]) provides a good alternative to N* with which to assess marine nitrogen fixation and denitrification rates because of its conservative properties with respect to differential remineralization. However, information on the distribution of the organic components in the ocean are still relatively sparse. We conclude that continued efforts to characterize the relative rates of remineralization of these elements in the laboratory and field, and to characterize the basin- and global-scale distributions of organic forms of phosphorus and nitrogen, should be encouraged and supported.

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