Biogeographical controls on the marine nitrogen fixers

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[1] We interpret the environmental controls on the global ocean diazotroph biogeography in the context of a three-dimensional global model with a self-organizing phytoplankton community. As is observed, the model's total diazotroph population is distributed over most of the oligotrophic warm subtropical and tropical waters, with the exception of the southeastern Pacific Ocean. This biogeography broadly follows temperature and light constraints which are often used in both field-based and model studies to explain the distribution of diazotrophs. However, the model suggests that diazotroph habitat is not directly controlled by temperature and light, but is restricted to the ocean regions with low fixed nitrogen and sufficient dissolved iron and phosphate concentrations. We interpret this regulation by iron and phosphate using resource competition theory which provides an excellent qualitative and quantitative framework.

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1. Introduction

[2] Diazotrophs, or nitrogen fixers, provide the major source of fixed nitrogen to the global ocean [*Galloway et al.*, 2004; *Gruber*, 2004] and play a critical role in maintaining global ocean productivity. Marine diazotrophs include the photo-autotrophs filamentous cyanobacterium *Trichodesmium*, unicellular cyanobacteria, and diatom-diazotroph associations (DDA), as well as some heterotrophic, microbial nitrogen fixers [*Carpenter et al.*, 1999; *Zehr et al.*, 2000; *Karl et al.*, 2002; *LaRoche and Breitbarth*, 2005; *Monteiro et al.*, 2010]. Here we discuss the photo-autotrophic types.

[3] The distribution of marine diazotrophs is largely restricted to warm subtropical and tropical waters of the global ocean [*Carpenter*, 1983; *Church et al.*, 2008; *Langlois et al.*, 2008], suggesting a control by oligotrophy and temperature. *Trichodesmium* and unicellular diazotrophs have maximum growth rates about an order of magnitude less than other marine phytoplankton [*Falcon et al.*, 2005; *Fu et al.*, 2005; *LaRoche and Breitbarth*, 2005; *Breitbarth et al.*, 2008; *Goebel et al.*, 2008], probably related to the energy-demanding process of breaking the N_2 triple bond. With a slower growth rate, diazotrophs are poor competitors in environments replete with fixed nitrogen. Laboratory and theoretical experiments also demonstrate that *Trichodesmium* and unicellular diazotrophs have warm optimal temperatures for growth [*Breitbarth et al.*, 2007; *Falcon et al.*, 2005; *Staal et al.*, 2003; *Stal*, 2009], and subsequently, it is frequently assumed that diazotrophs grow only in oligotrophic waters warmer than 15°–20°C [*Capone and Carpenter*, 1982;

Capone et al., 1997; *Needoba et al.*, 2007; *Boyd et al.*, 2010]. However, heterocystic diazotrophs are observed in the much colder environments of the Baltic Sea and some polar lakes [*Staal et al.*, 2003; *Pandey et al.*, 2004; *Stal*, 2009], so the role of temperature is not so clear.

[4] These oligotrophy and temperature relationships to diazotroph abundance are probably tightly intertwined with other significant regulating factors [*Karl et al.*, 2002; *Langlois et al.*, 2005; *LaRoche and Breitbarth*, 2005; *Langlois et al.*, 2008], including light harvesting, availability of phosphorus and iron, and top-down controls. Culture experiments show *Trichodesmium* and unicellular diazotrophs to be adapted to high light environments [*Carpenter and Roenneberg*, 1995; *LaRoche and Breitbarth*, 2005; *Masotti et al.*, 2007; *Goebel et al.*, 2008]. In addition, phosphorus has been noted to limit diazotrophs in the North Atlantic Ocean [*Wu et al.*, 2000; *Sanudo-Wilhelmy et al.*, 2001; *Mills et al.*, 2004]. Iron availability also exerts an important control on these nitrogen-fixing organisms in many places of the ocean [*Falkowski*, 1997; *Berman-Frank et al.*, 2001; *Moore et al.*, 2009]. Iron is an essential constituent of nitrogenase resulting in nitrogen fixers to have high iron requirement. The Fe:P ratio of *Trichodesmium* and unicellular diazotroph varies between 7 and more than 1000 mmol:mol, while for other phytoplankton this ratio ranges between about 0.3 and 500 mmol:mol [*Ho et al.*, 2003; *Quigg et al.*, 2003; *Finkel et al.*, 2006]. Finally, some *Trichodesmium* species are observed to have fewer predators and produce toxins [*Capone et al.*, 1997; *LaRoche and Breitbarth*, 2005].

[5] Parameterizations of marine diazotrophs in regional and global ocean models have typically been based only on characteristics of *Trichodesmium*. These models have captured the distribution of *Trichodesmium* and nitrogen fixation in the ocean assuming (independently or in combination) regulation by temperature, the availability of fixed nitrogen, light environment, and phosphorus and iron limitations

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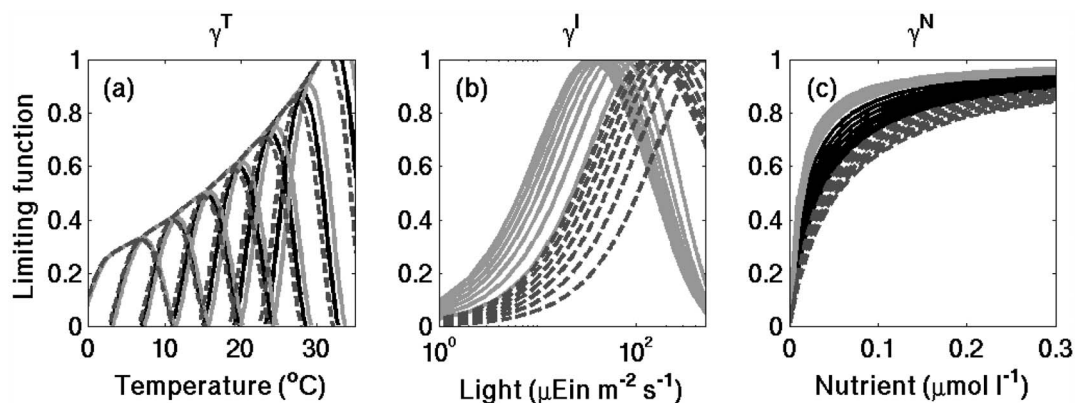
Figure 1. Limiting functions of phytoplankton growth ($\mu = \mu_{max}\gamma^T\,\gamma^I\,\gamma^N$; see equation (1)). Dark grey dashed lines indicate large phytoplankton (including *Trichodesmium* and diatom-diazotroph associations). Light grey lines indicate small phytoplankton that cannot use nitrate (*Prochlorococcus* analogs) while black lines indicate those that can (including unicellular diazotrophs). All parameters are randomly assigned from reasonable ranges. (a) Temperature-limiting function (γ^T; see equation (2)) showing the generation of optimal temperatures for all phytoplankton types. (b) Light-limiting function (γ^I). (c) Nutrient-limiting function (γ^N; see equation (3)).

[*Fennel et al.*, 2002; *Coles et al.*, 2004; *Hood et al.*, 2004; *Moore et al.*, 2004].

[6] Recently, the global modeling studies have focused on the relationship of marine nitrogen fixation to the availability of iron [*Moore et al.*, 2004, 2006; *Tagliabue et al.*, 2008; *Krishnamurthy et al.*, 2009], where sensitivity studies have consistently shown a positive response of nitrogen fixation to increases in the iron supply.

[7] Here we reexamine the relationships between these potential controlling factors, the biogeography of diazotrophs, and nitrogen-fixing rates in the context of a global ocean circulation, biogeochemistry, and self-assembling ecosystem model. Our aim is to provide a clear and simple theoretical interpretation of the key controlling factors. We use the model results of *Monteiro et al.* [2010] (hereafter MFD) which successfully reproduce a diverse population of marine autotrophic diazotrophs of *Trichodesmium*, unicellular diazotrophs, and DDAs. Section 2 provides a brief description of the model. We subsequently explore the role of temperature, light, and nutrient regulations on the distribution of the total marine diazotroph population and use a simple theoretical framework to provide clear delineation of diazotroph habitat (section 3). An additional sensitivity experiment on the iron supply is finally discussed in section 4.

2. Model Description

[8] We employ the global model of MFD which combines a three-dimensional ocean circulation model (MITgcm; *Marshall et al.* [1997]) with biogeochemical and ecological parameterizations [*Follows et al.*, 2007] and explicitly represents diverse marine phytoplankton, including multiple diazotrophs. Analogs of *Trichodesmium*, unicellular diazotrophs, and DDAs persist in the model. MFD present an extensive model-data comparison indicating that the distribution, abundances, and activity of these three types are realistic in the model for the Atlantic, Pacific, and Indian oceans, as well as in the China Sea. In particular, the

modeled lack of diazotrophs in the southeast Pacific Ocean compares well to the observations from two cruises [*Mague et al.*, 1974; *Bonnet et al.*, 2008, 2009] that did not find any evidence of nitrogen fixers in this region (except for a small pocket at 26°S). The model does underestimate *Trichodesmium* analogs in the west Pacific Ocean and coastal areas and DDA analogs globally. Recently published data [*Moisander et al.*, 2010], not included in MFD, also suggest that unicellular diazotrophs are underestimated in the model southwest Pacific Ocean. We believe that modeled iron supply to the western Pacific Ocean is too low (see MFD and section 4 for more discussion).
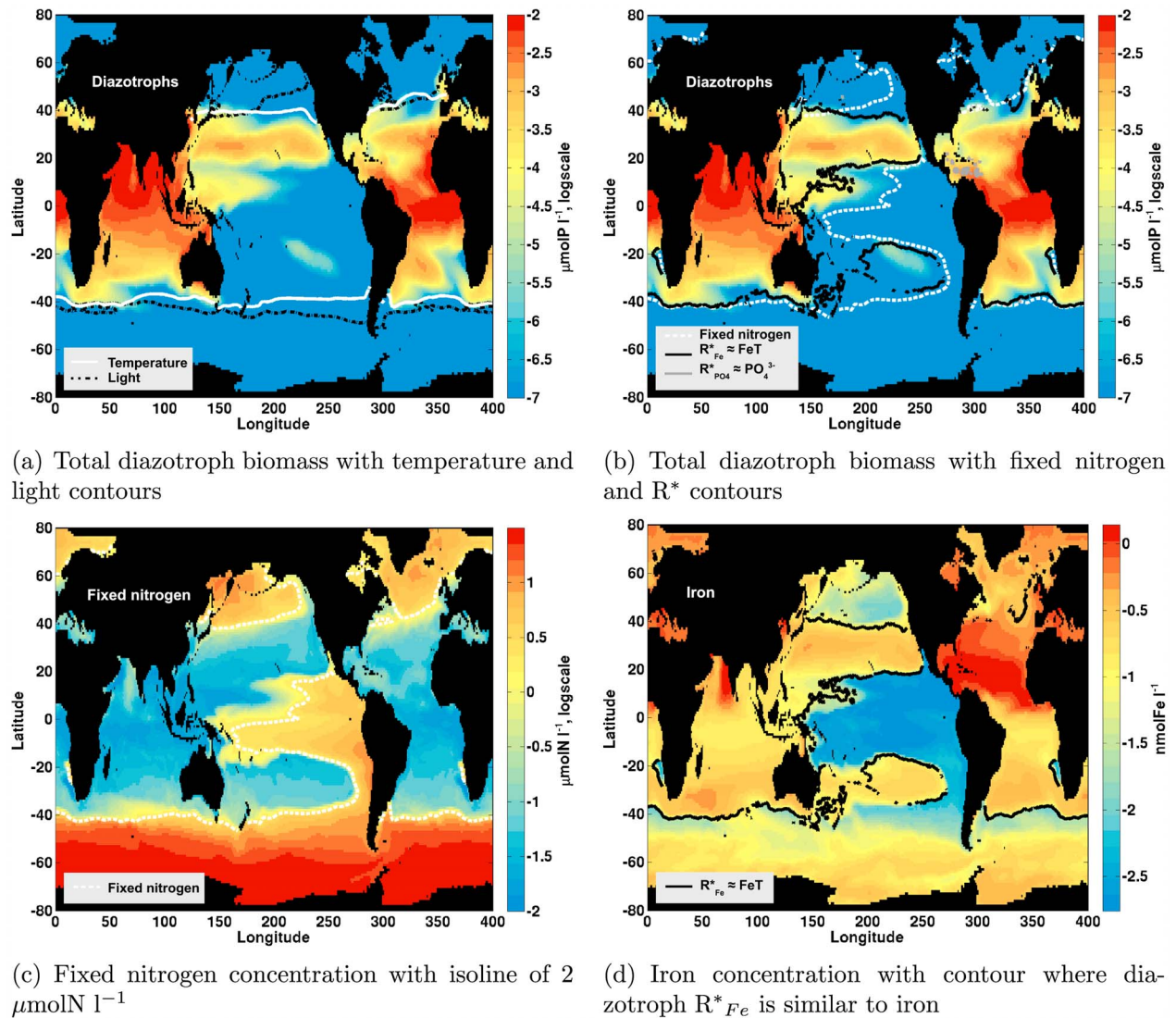
[9] The key parameters that control the growth rates of the autotrophs are assigned randomly from reasonable ranges (see *Follows et al.* [2007] for more details), and the model community self-assembles from the fittest phytoplankton in the many physical and chemical environments. Diazotrophs in the model are assumed to be free of nitrogen limitation, acquiring all of their nitrogen by fixation, but with trade-offs of lower maximum growth rate and high N:P (= 40) and Fe:P (30 times bigger than nondiazotroph phytoplankton) similar to MFD. The prognostic equation of the modeled diazotrophs (*Diaz*) is

$$\frac{dDiaz}{dt} = \underbrace{\mu_{max}\gamma^T\gamma^I\gamma^N Diaz}_{\text{Growth}} - \underbrace{mDiaz}_{\text{Mortality}} - \underbrace{\sum_k g_k Z_k}_{\text{Grazing}} - \underbrace{\frac{\partial w_{sink} Diaz}{\partial z}}_{\text{Sinking}} \quad (1)$$

where the growth term includes maximum growth rate (μ_{max}), and limiting functions for temperature (γ^T), light (γ^I) and nutrient (γ^N). The dependence of growth on temperature (Figure 1a) is defined as

$$\gamma^T = 1/\tau_1\left[A^T e^{-B\left(T - T_{opt}\right)^c} - \tau_2\right] \quad (2)$$

T is the local temperature while A, B, T_{opt}, and c regulate the form of the temperature modification function. A accounts for the Eppley curve [*Eppley*, 1972] while T_{opt} corresponds

(a) Total diazotroph biomass with temperature and light contours

(b) Total diazotroph biomass with fixed nitrogen and R* contours

(c) Fixed nitrogen concentration with isoline of 2 μmolN l^{-1}

(d) Iron concentration with contour where diazotroph R*$_{Fe}$ is similar to iron

Figure 2. Relevant concentrations of the marine ecosystem for the Reference case (iron solubility of 0.8%). Concentrations are shown for the tenth year, annually averaged and for the first 50 m depth of the water column. (a) Total biomass of diazotroph analogs (μmol P L^{-1}, log scale) with temperature (15°C white continuous line) and light (100 μE m^{-2} s^{-1}, black dashed line) contours. (b) Total biomass of diazotroph analogs (μmol P L^{-1}, log scale) with fixed nitrogen contour (2 μmol N L^{-1}, white dashed line) and R* contours (resource:R* = 0.75, black line for FeT and grey line for PO$_4^{3-}$). (c) Fixed nitrogen concentration (μmol N L^{-1}, log scale) with nitrogen contour (2 μmol N L^{-1}, white dashed line). (d) Total dissolved iron concentration (nmol Fe L^{-1}, log scale) with R*$_{Fe}^{Diaz}$ contour (FeT:R*$_{Fe}^{Diaz}$ = 0.75, black line).

to the optimal temperature for growth. Coefficients τ_1 and τ_2 normalize the maximum value. The dependence of growth on light (γ^I; see Figure 1b) reflects empirically determined relationships, and the range of possible values for coefficients includes an accounting for the packaging effect on larger cells. The dependence of growth on external nutrients (γ^N; see Figure 1c) is based on simple Monod-kinetics where the law of the minimum determines the limiting nutrient:

$$\gamma^N = \min\left\{\frac{PO_4^{3-}}{PO_4^{3-} + K_{PO_4^{3-}}}; \frac{FeT}{FeT + K_{FeT}}; \frac{Si}{Si + K_{Si}}\right\} \quad (3)$$

Represented loss terms include a nonspecific linear mortality (m for the rate), grazing by two dynamic predators (Z_k), and sinking (w_{sink} for the rate). Grazing is described by the function g_k which accounts for grazing rate and diazotroph palatability (see *Dutkiewicz et al.* [2009] and *Monteiro et al.* [2010] for more details).

[10] As in MFD's paper, we present averaged results from an ensemble of ten simulations, each differing in the randomization of the initialized population of phytoplankton. The ensemble average distribution of the total diazotroph biomass in the tenth year of integration is illustrated in Figure 2, and we refer to this as the "Reference case". A second ensemble in which the solubility of atmospheric
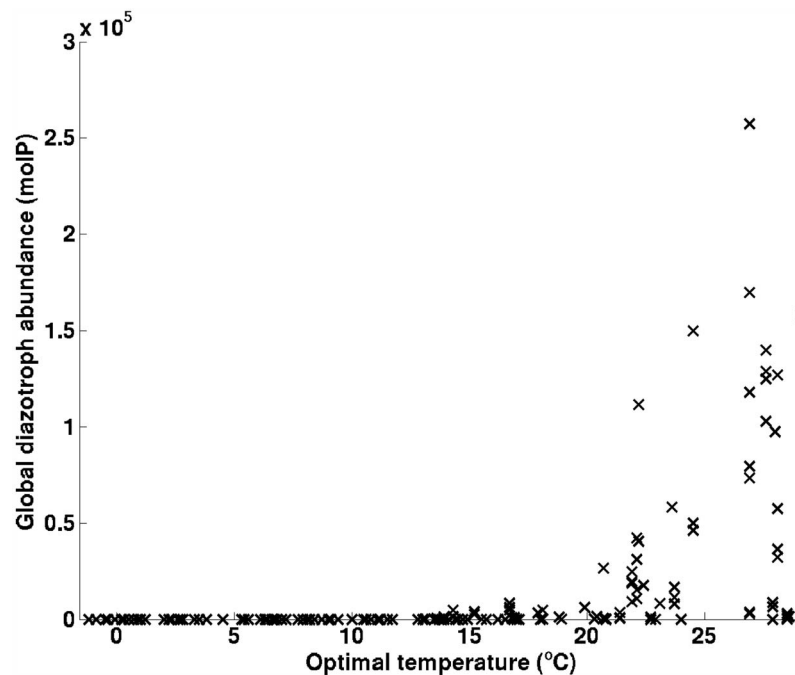
Figure 3. Total abundances (mol P) of diazotroph analogs generated for the Reference case as a function of their optimal temperature (T_{opt}, °C), for the tenth year. Though some diazotroph analogs are initialized with low T_{opt}, only the ones with T_{opt} generated above 15°C survive.

iron dust is increased by a factor of 5 (from 0.8% to 4%) will be referred to as the "High iron solubility case".

3. Biogeographical Controls

[11] We explore the factors that control the biogeography of the total population of autotrophic diazotrophs for the global ocean model, in particular temperature (section 3.1), light (section 3.2), and nitrogen oligotrophy (section 3.3), as well as the availability of iron and phosphate (sections 3.4 and 3.5).

[12] In the Reference case (Figure 2, ensemble mean of total diazotroph population), autotrophic diazotrophs are distributed over most of the oligotrophic warm subtropical and tropical waters but excluded from the high latitudes and southeastern Pacific Ocean, in agreement with observations [e.g., *Carpenter*, 1983; *Church et al.*, 2008; *Bonnet et al.*, 2009] (full summary in MFD).

3.1. Temperature Control

[13] The lack of diazotroph analogs in the high latitudes (>45°; concentrations smaller than 10^{-7} μmol P L^{-1}) are consistent with observations which have been interpreted to suggest that diazotrophs require warm temperature to undertake the energetically expensive process of nitrogen fixation [e.g., *Capone et al.*, 1997; *Langlois et al.*, 2005; *LaRoche and Breitbarth*, 2005; *Needoba et al.*, 2007]. In the model, diazotroph analogs are initialized with optimal temperatures (T_{opt}) ranging between −2°C and 30°C such that they could be adapted to either warm or cold environments. However, only the diazotrophs adapted to warm waters ($T_{opt} > 15$°C) persist at the end of the simulations, rapidly selected by other aspects of the model ocean environment (Figure 3). The selection for warm optimal tem-

peratures of the modeled diazotrophs is consistent with culture experiment results indicating *Trichodesmium* and unicellular diazotrophs to have optimal temperature between 20°–34°C [*Breitbarth et al.*, 2007] and 26°–30°C [*Falcon et al.*, 2005], respectively. We note that this model result is not due to the Eppley curve (where diazotrophs with warmer optimal temperature grow quicker than those at colder temperatures; see equation (2) and Figure 1), because the temperature function (γ^T) at any location of the model is always larger than the combined mortality and grazing terms. Thus, though the model does not require warm adapted diazotrophs, their habitat is bounded at high latitudes by the 15°C contour (continuous white line in Figure 2a). However, this contour does not follow the regions where diazotrophs are excluded in the low latitudes.

3.2. Light Control

[14] Culture experiments show that marine diazotrophs are adapted to high light environments, with high light requirement as well as lower light inhibition [*Carpenter and Roenneberg*, 1995; *Masotti et al.*, 2007; *Goebel et al.*, 2008]. *Hood et al.* [2004] used light and nitrate competition as the main differentiation between diazotrophs and non-diazotrophs and successfully generated reasonable distributions of *Trichodesmium* in a model of the Atlantic Ocean. We plot on the map of diazotroph concentration a light contour (here 100 μE m^{-2} s^{-1} of PAR; see black dashed line in Figure 2a). This light contour also captures the high-latitude boundaries of diazotroph biogeography (though not the finer-scale low-latitude distribution). As with temperature, we did not a priori assign high light requirement to diazotrophs. Nor did we find significantly different results when a higher light requirement was assigned to them.

[15] The model results may reflect the fact that warm temperature and high light environments are intertwined with such other factors to limit the distribution of diazotrophs, as previously suggested [Karl et al., 2002; Langlois et al., 2005; LaRoche and Breitbarth, 2005; Langlois et al., 2008].

3.3. Trade-Off Between N₂ Fixing and Slow Maximum Growth

[16] The trade-off between freedom from nitrogen limitation and slow growth rate results in diazotrophs populating oceanic waters that are oligotrophic and nitrogen-limited, as revealed when we plot the modeled fixed nitrogen contour of 2 μmol L^{-1} over the diazotroph concentration (white dashed line, Figures 2b and 2c). This contour delimits the high-latitude boundary of the diazotroph biogeography and, due to the correlation of macronutrient concentrations and temperature, mostly coincides with the 15°C temperature contour (white dashed line, Figure 2a). The nitrogen contour catches more details of the modeled diazotroph distribution than the temperature and light contours, especially in the eastern equatorial Pacific Ocean. This trade-off between N₂ fixing and slow maximum growth can explain why diazotrophs (even those initialized adapted to cold waters) are excluded from the high latitudes: in regions where fixed nitrogen is high, the diazotrophs are outcompeted by non-diazotrophs. Nevertheless, other features of the diazotroph biogeography cannot be simply explained by oligotrophic and nitrogen-limited environments. In the South Pacific Ocean, for instance, the concentration of fixed nitrogen is low, but diazotrophs do not populate this region of the model. This particular point is explored in more details in section 4.

3.4. Iron Regulation

[17] Marine diazotrophs are observed to have a higher relative iron requirement than other phytoplankton to satisfy the demand for nitrogenase. Here we demonstrate that simple constructs from resource competition theory [Tilman, 1977, 1982] provide a powerful qualitative and quantitative framework in which to organize and interpret the relationship between diazotrophs, iron, and other resources.

[18] Consider the rate of change of diazotroph biomass (Diaz) as a balance of the diazotroph growth and loss rates in an iron-limited environment. Growth is thus controlled by the light and temperature functions given in section 2, ($\mu_{\max}\gamma^I \gamma^T$) with simple Monod kinetics for iron-limited growth ($\gamma^N = \frac{FeT}{FeT+K_{FeT}}$), whereas losses are due to mortality, grazing (G), and sinking (S):

$$\frac{1}{Diaz}\frac{dDiaz}{dt} = \mu_{\max}\gamma^I\gamma^T\frac{FeT}{FeT+K_{FeT}} - m$$
$$- \underbrace{\frac{\sum_k g_k Z_k}{Diaz}}_{=G} - \underbrace{\frac{1}{Diaz}\frac{\partial w_{sink}Diaz}{\partial z}}_{=S} \quad (4)$$

If physical transport of the organisms can be neglected, the ambient iron concentration FeT in equilibrium with a population of diazotrophs can be described by R*$_{Fe}^{Diaz}$ such that

$$\text{R*}_{Fe}^{Diaz} = FeT_{(dDiaz/dt=0)} = \frac{K_{FeT}}{\frac{\mu_{\max}\gamma^I\gamma^T}{m+G+S}-1} \quad (5)$$

R* only depends on the organism growth and loss characteristics. According to the resource competition theory, organisms with the lowest R* outcompete others and set the ambient concentration of the limiting nutrient (down to their R*). Consequently, organisms with a higher R* than the ambient limiting-nutrient concentration are expected to be excluded. Following this approach, we compare the R* for iron as a limiting nutrient of the diazotrophs (equation (5)) to the actual environmental concentration (FeT, which may be regulated by other organisms or processes) to determine the regions where diazotrophs might be iron-excluded.

[19] We evaluate R*$_{Fe}$ of the modeled diazotroph population following the study by Dutkiewicz et al. [2009] (which did not consider diazotrophs) to diagnose the lowest annually averaged R*$_{Fe}^{Diaz}$ of the surviving diazotroph population. We note that this model analysis is noisy since it calculates the smallest R* for the diazotroph population separately at each grid point of the model. The contour where the lowest diazotroph R*$_{Fe}^{Diaz}$ is close to the ambient FeT (FeT:R*$_{Fe}^{Diaz}$ = 0.75; black contour, Figure 2b) approximately follows the boundaries of the diazotroph habitat over most of the global ocean. This R* contour provides a much more faithful description of diazotroph habitat than the temperature, light, or fixed nitrogen contours.

[20] The close match between the lowest R*$_{Fe}^{Diaz}$ and the ambient concentration of iron at the boundary of the diazotroph habitat indicates that the assumption of a tight balance between growth and loss is valid and that the resource competition framework is useful for interpreting this complex model. This framework also strongly supports the notion of a dominant role for iron in regulating the biogeography of diazotrophs and nitrogen fixation in the oceans. We note that this iron "regulation" (as defined by the ecological theory of R*) is not the same as iron "limitation" (as defined by Monod's kinetics in equation (3)). Here we define regulation as delineating the ocean region where an organism can exist, while limitation characterizes how iron affects the growth rate.

3.5. Phosphate Regulation

[21] Phosphate regulation of diazotrophs appears to be particularly important in the North Atlantic Ocean [Sanudo-Wilhelmy et al., 2001; Mills et al., 2004; Sohm et al., 2008; Hynes et al., 2009]. Following the analysis with regard to iron in section 3.4, we diagnose a diazotroph R* with respect to phosphorus. Assuming phosphate limitation in equations (1) and (3), we get

$$\text{R*}_{PO4}^{Diaz} = PO_4^{3-}{}_{(dDiaz/dt=0)} = \frac{K_{PO4}}{\frac{\mu_{\max}\gamma^I\gamma^T}{m+G+S}-1} \quad (6)$$

The contour where the minimum R*$_{Fe}^{Diaz}$ is close to the ambient concentration of phosphate is represented in grey in Figure 2b. Inside this contour, the simple theory predicts that phosphate is drawn down lower than required by diazotrophs and they should be outcompeted. In the Reference case model, the region where phosphate availability regulates the presence of diazotroph is limited to the western tropical North Atlantic Ocean (small area). Here diazotrophs are not totally excluded due to nonnegligible advection from surrounding areas where their abundance is high. Never-
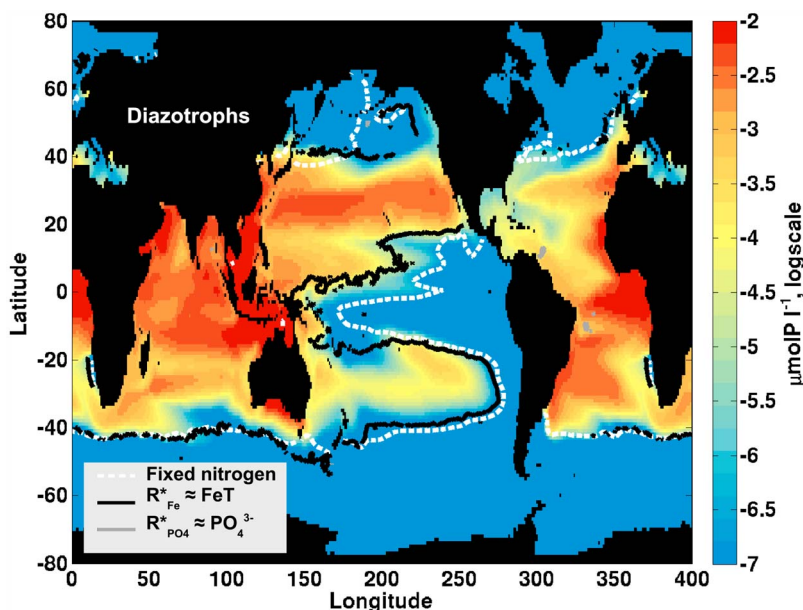
Figure 4. Total diazotroph biomass (μmol P L^{-1}, log scale) for the high iron solubility case (iron solubility of 4%) with fixed nitrogen isoline (2 μmol N L^{-1}, white dashed line) and R* contours (resource:R* = 0.75, black line for FeT and grey line for PO$_4^{3-}$). Concentrations are shown for the tenth year, annually averaged and for the first 50 m depth of the water column.

theless, it suggests that diazotrophs should be more sensitive to changes in phosphate availability in this region. Observations in the vicinity of the Amazon river show that the river input of phosphate influences DDA concentrations to be much higher there than further offshore [*Carpenter et al.*, 1999; *Foster and Zehr*, 2006; *Foster et al.*, 2007].

4. Discussion

[22] As previously noted [*Falkowski*, 1997; *Falkowski et al.*, 1998; *Moore et al.*, 2006, 2009], our model study shows that high iron requirement (and Fe:P ratio) of marine diazotrophs causes iron to be a controlling factor on the distribution of nitrogen fixation in much of the ocean. However, many aspects of the global iron cycle are not well understood, in particular the amount of atmospheric iron dust which is soluble and bioavailable. Iron solubility is observed to vary over the global ocean between 0.01% to 80%, though mostly in the low end of the range [*Chen and Siefert*, 2004; *Mahowald et al.*, 2009] but increasing with the distance from its source [*Luo et al.*, 2005; *Baker et al.*, 2006; *Waeles et al.*, 2007].

[23] We explore the sensitivity of our model and our theoretical framework ability to describe marine diazotroph biogeography by increasing the solubility of atmospheric dust iron five-fold (from 0.8% in the Reference case to 4% in the High iron solubility case in Figure 4). With higher iron solubility, dissolved iron is enriched globally, relieving diazotrophs of much of the iron limitation. The global nitrogen fixation rate increases from 60 $\pm$ 15 TgN yr^{-1} (Reference case) to 80 $\pm$ 30 TgN yr^{-1}, consistent with previous model sensitivity studies [*Moore et al.*, 2002, 2004, 2006].

[24] Diazotroph concentrations are enhanced in the Pacific and South Indian oceans (Figure 4) expanding their habitat to largely fill the regions defined by the fixed nitrogen

contour of 2 μmol L^{-1} (section 3.3) including the subtropical gyre of the South Pacific Ocean. The R*$_{Fe}^{Diaz}$ contour (Figure 4) still follows the diazotroph distribution boundaries closely, emphasizing the close relationship between diazotroph biogeography and iron availability.

[25] Within plausible ranges of the solubility of dust atmospheric iron dissolved and surface ocean iron distributions, modeled diazotrophs can be absent or present in the subtropical gyre of the southwest Pacific Ocean. In addition, while the Reference case underestimates nitrogen fixation in the southwest Pacific Ocean, it compares well to observations in the North Atlantic Ocean (the region which has the most observations). On the other hand, the high iron solubility case has more realistic nitrogen fixer distribution in the southwest Pacific region, but too little nitrogen fixation in the North Atlantic Ocean. Given the paucity of observations of both iron concentrations and diazotrophs in the ocean, it is difficult to discriminate at this point which solution is more realistic. Probably the parameterization of the iron supply to include variable iron solubility as well as sedimentary and hydrothermal sources would produce a result somewhere between these two cases.

5. Concluding Remarks

[26] We have used numerical models and simple ecological theory to assess what controls the biogeography of marine diazotrophs in the global ocean. In a numerical model of ocean circulation, biogeochemistry, and ecosystem, diazotrophs occupy most of the oligotrophic warm subtropical and tropical waters and are excluded from the high latitudes and iron-depleted southeast Pacific Ocean, in accord with observations.

[27] We have shown that the rich surface nutrient concentrations suppress modeled diazotrophs at the higher latitudes, rather than low temperatures. Because nitrogen fixation pro-

vides an independent source of nitrogen but at a higher energy demand, diazotrophsare successful only in the nitrogen-limited and oligotrophic environments, such as the (sub) tropical regions of the modern ocean which have selected only for diazotrophs adapted to warm temperatures.

[28] Inside the region where surface fixed-nitrogen concentrations are low, there is a finer-scale regulation of the diazotroph biogeography by the availability of dissolved iron and phosphate. Resource competition theory [*Tilman*, 1977, 1982] provides a powerful framework by which to define the regions of these iron and phosphorus regulations. Iron regulation is particularly important in the eastern tropical Pacific Ocean, while phosphate potentially regulates the diazotroph distribution in the tropical Atlantic Ocean.

[29] While temperature and light are often used in models and field studies to explain or regulate the biogeography of diazotrophs, we find here that nutrient resource availability is the primary control. Diazotrophs require water with low fixed nitrogen, but sufficient iron and phosphate to a level described by simple ecological theory. We hypothesize that this nutrient control sets the distribution of marine diazotrophs and that high light and temperature requirements are adaptations to these particular environments.

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