Modeling the impact of *Trichodesmium* and nitrogen fixation in the Atlantic Ocean

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[1] In this paper we use a biological-physical model with an explicit representation of *Trichodesmium* to examine the influence of N_2 fixation in the Atlantic. Three solutions are examined, one where the N_2 fixation rate has been set to observed levels, one where the rate has been increased to levels comparable to geochemical estimates, and one with no N_2 fixation. All solutions are tuned to reproduce satellite surface chlorophyll concentrations, so that differences in the runs are manifested in productivity and export. Model runs with N_2 fixation have different phytoplankton production and export distributions than runs without. Over the Atlantic basin the ecosystem "fixes" nitrogen at the rate of 1.47×10^{12} mol N yr^{-1}, when tuned to observed phytoplankton and *Trichodesmium* biomass. This rate is comparable to the lower range of direct estimates of $1.3–2.2 \times 10^{12}$mol N yr^{-1} [*Capone et al.*, 1997; J. N. Galloway et al., manuscript in preparation, 2003; D. Capone et al., New nitrogen input in the tropical North Atlantic Ocean by nitrogen fixation, submitted to *Nature*, 2004, hereinafter referred to as Capone et al., submitted manuscript, 2004] but less than geochemical indirect estimates over a reduced domain (2.0×10^{12} mol N yr^{-1} [*Gruber and Sarmiento*, 1997] versus 0.55×10^{12} mol N yr^{-1} for the model). The nitrogen from N_2 fixation increases new production by 30% and total production by 5%. However, it does not supplement upwelled nitrate sufficiently to bring production and export into line with remote sensing and geochemically derived estimates. Simulations with N_2 fixation rates comparable to geochemical estimates show that reasonable phytoplankton concentrations can be maintained if export is increased. Moreover, phytoplankton productivity increases to values approaching remote-sensing-based estimates in the oligotrophic ocean. However, *Trichodesmium* biomass may be higher than observed. *INDEX TERMS:* 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4845 Oceanography: Biological and Chemical: Nutrients and nutrient cycling; *KEYWORDS:* nitrogen fixation, Atlantic, trichodesmium

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1. Introduction

[2] Understanding biologically mediated cycling of nutrients in the ocean may be important to resolving the coupled ocean-atmosphere response to climate variability. Variations in climate influence biogeochemical cycles in the ocean through changes in mixing, light and temperature, as well as potentially the delivery of micronutrients. In turn, the ocean ecosystem may provide a direct feedback to climate through modulation of the sequestration of atmospheric CO_2 [*Falkowski et al.*, 1998; *Sarmiento and LeQuere*, 1996]. Although we now know that iron and possibly even phosphorus can limit primary production in some regions of the ocean [e.g., *Coale et al.*, 1996; *Karl et al.*, 1997, 2001; *Wu et al.*, 2000], nitrogen is limiting or close to limiting over most of the global oligotrophic oceans [*Tyrrell*, 1999; *Codispoti*, 1989]. This is important because primary production supported by N_2 fixation can result in a net export of carbon from the surface waters to the deep ocean and a net draw down of atmospheric carbon dioxide and may therefore play a significant, direct role in the global carbon cycle. In fact, N_2 fixation may be the only biologically mediated process in the open ocean which drives a

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significant net export of atmospheric carbon dioxide over greater than annual timescales [*Hood et al.*, 2000]. In addition, the global difference between N_2 fixation and denitrification largely determines the degree to which the oceans are nitrogen limited. Thus global warming-induced changes in N_2 fixation could have significant long-term effects on oceanic productivity and the global carbon cycle.

[3] Despite decades of intensive study, the nitrogen budget of the oceans is still so poorly constrained that we do not know whether it is in balance. Current estimates of the major nitrogen loss term, denitrification (>300 Tg N yr^{-1}), substantially exceed recent estimates of the major source term, nitrogen fixation (200 Tg yr^{-1}) [*Codispoti et al.*, 2001; *Gruber and Sarmiento*, 1997; Capone et al., submitted manuscript, 2004], and the uncertainty in these sources and sinks is quite large. In particular, estimates of global ocean N_2 fixation vary by more than an order of magnitude, with geochemical (N* based) estimates of nitrogen fixation generally exceeding direct estimates from shipboard measurements [*Gruber and Sarmiento*, 1997; *Deutsch et al.*, 2001; Capone et al., submitted manuscript, 2004]. Despite this uncertainty, it is now clear that open ocean N_2 fixation is quantitatively significant in the global nitrogen cycle [*Karl et al.*, 1997; *Capone et al.*, 1997; Capone et al., submitted manuscript, 2004]. The conspicuous marine cyanobacterium, *Trichodesmium*, has long been recognized as an important N_2 fixer in the open ocean. Although we now know that this organism is not the only diazotroph that contributes significantly to open ocean and N_2 fixation [*Hood et al.*, 2000], *Trichodesmium* is still considered to be the dominant nitrogen source [*Capone et al.*, 1997; Capone et al., submitted manuscript, 2004]. Recent estimates, based upon direct measurements of Trichodesmium biomass and N_2 fixation rate, indicate that the input of new nitrogen from the atmosphere to the oceans due to this organism can be comparable to the upward flux of nitrogen from the deep ocean in oligotrophic tropical waters [*Karl et al.*, 1997; *Capone et al.*, 1997].

[4] We expect, therefore, that this input will have a significant impact upon phytoplankton distributions, productivity and nitrogen fluxes in the open ocean. However, only a handful of studies support this. *Karl et al.* [1997] has hypothesized that inputs of new nitrogen from N_2 fixation have given rise to a long-term (decadal) shift in ecosystem structure in the subtropical North Pacific Ocean, from a nitrogen limited system dominated by diatoms and export, to a phosphorus limited system dominated flagellates and nutrient recycling. Recent work by *Lenes et al.* [2001] and *Walsh and Steidinger* [2001] suggests that short-term inputs of new nitrogen from *Trichodesmium* blooms may be responsible for initiating harmful algal blooms in the Gulf of Mexico. Remote sensing observations of a summertime chlorophyll maximum in the western tropical North Atlantic have also been attributed to nitrogen fixation (Coles et al., submitted manuscript, 2004).

[5] Here we use a coupled biological-physical model with an explicit, dynamic representation of *Trichodesmium* to examine the influence of N_2 fixation on the nitrogen cycle in the Atlantic. In a companion paper, *Hood et al.* [2004] (hereinafter referred to as HCC) focus on model validation and understanding the mechanisms governing the distributions of *Trichodesmium* in the Atlantic. The model simulates nitrogen fixation over the tropical and subtropical Atlantic gyres, which may contribute a third of global oceanic nitrogen fixation [*Capone and Carpenter*, 1982]). Our goal is to evaluate the effects of N_2 fixation on the spatiotemporal variability of phytoplankton, and on the inorganic nitrogen concentrations and fluxes in model runs with different levels of N_2 fixation. Specifically we ask, how do phytoplankton and nitrogen concentrations differ in the Atlantic when there is no N_2 fixation compared with runs where the rates have been tuned to match directly measured rates, and the high rates implied by geochemical estimates [e.g., *Gruber and Sarmiento*, 1997]. Our model shows that different levels of N_2 fixation have major impacts on phytoplankton patterns, productivity and inorganic nitrogen fluxes.

[6] The paper is organized as follows; additional details of the model formulation are described in section 2. In section 3 we explore how nitrogen fixation impacts the ecosystem within the euphotic zone, and how it alters the nitrogen budget and exchange with the deep ocean. Then in section 4 we compare the model-derived nitrogen fixation rates with direct and indirect measurements on basin-wide scales. Finally, in section 5, the high nitrogen fixation simulation is compared to the baseline solution without nitrogen fixation, and to observations.

2. Model

[7] The physical and biological models have been discussed in detail in the work of HCC and *Hood et al.* [2001]; however, some aspects of the model formulation are addressed here. The physical model is the Miami Isopycnal Coordinate Ocean Model (MICOM), a primitive equation model configured for this study with 19 vertical layers concentrated in the tropical upper ocean to better resolve the euphotic zone. The uppermost layer is a bulk mixed layer following the formulation of *Kraus and Turner* [1967] modified by *Gaspar* [1988]. Model resolution (2° mercator projection) is coarse and does not include an accurate topography of the Caribbean Archipelago or the Mediterranean Sea outflow, which is known to be a nitrogen source to the Atlantic presumably due to N_2 fixation in the Mediterranean. At the northern and southern boundaries of the model (45°N–20°S) the inflow and outflow of water masses are parameterized in 6° "sponge" relaxation zones. Nitrogen is also relaxed to the monthly NOAA/NESDIS/NODC climatology [*Conkright et al.*, 1998] in these zones as described in the work of HCC. The model is forced with monthly climatological heat and momentum fluxes for 25 years, and the last 3 years are shown. This simple configuration allows for a large number of model experiments; however, efforts are underway to improve the model resolution and forcing.

[8] The ecosystem model has 6 state variables representing dissolved inorganic nitrogen (N), dissolved organic nitrogen (DON), phytoplankton (P), heterotrophs (H), detritus (D), and *Trichodesmium* (T). The food web is structured to predominantly represent microbial processes. A large fraction of phytoplankton growth (30%) is shunted directly to the dissolved organic nitrogen pool [*Hood et al.*, 2001]. *Trichodesmium* is differentiated from phytoplankton by the absence of DIN limitation and photoinhibition,

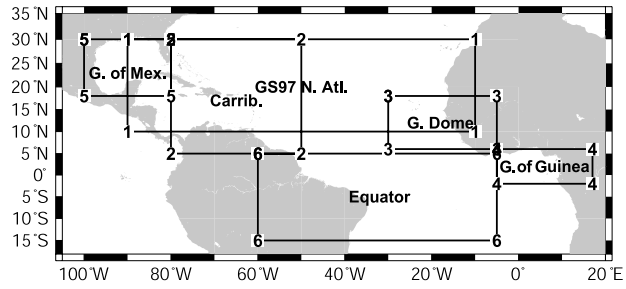

Figure 1. The regions over which nitrogen fixation rates are computed in Table 1, and shown in Figure 7. Each region is indexed by a number at the corners of the rectangular areas, this number is included in Table 1.

though *Trichodesmium* will take up DIN if it is available. In addition, *Trichodesmium* is parameterized with a higher light requirement, a slower growth rate, and much lower mortality due to predation [*Hood et al.*, 2001; HCC]. Remineralization of particulate nitrogen (D) occurs throughout the water column via the heterotroph pool which exists in all model layers, and is intended to represent primarily bacterial and microzooplankton communities [*Hood et al.*, 2001; HCC].

[9] Detritus is the only component of the ecosystem which is not advected passively, but which also has a vertical velocity (sinking rate) associated with it. Detritus is not allowed to sink out of the bottom-most layer, but remineralizes gradually, allowing a potentially unrealistic buildup of DIN in the abyssal layers. However, this is not a significant source of error for the relatively short simulations discussed in this paper and in the work of HCC.

3. Role of *Trichodesmium* in the Basin-Wide Ecosystem

[10] In this section we explore how N_2 fixation impacts the pelagic ecosystem and nutrient concentrations. This impact is quantified by comparing (differencing) model runs with and without *Trichodesmium*. Because the model physics does not differ between simulations, this difference is dominated by local changes to the ecosystem. Specifically, we compare the simulation discussed in detail in the work of HCC (TRICHO run), with the simulation where *Trichodesmium* and N_2 fixation are absent, (NOTRICHO run). In these comparisons we focus on DIN concentrations, phytoplankton concentrations, phytoplankton production, and export. These effects are described broadly within the regions shown in Figure 1. In a later section we use this same comparative approach to explore the ramifications of turning up N_2 fixation in the model to levels comparable to the high geochemical rate estimates of *Gruber and Sarmiento* [1997] (HITRICHO run).

3.1. Model Tuning

[11] The ecosystem parameters with the exception of *Trichodesmium* mortality and sinking rate are unchanged from the values used in the work of *Hood et al.* [2001]. Here the goal is to compare simulations to understand the impact of adding nitrogen fixation to the system, rather than to optimize the model by a definitive sweep of the parameter space. The tuning process minimizes differences between the surface phytoplankton fields in model runs with different levels of N_2 fixation. We assume that the new nitrogen supplied by diazotrophs is ultimately made available to phytoplankton for uptake. As such, the effects of nitrogen fixation are included in observed surface chlorophyll patterns, and they represent the best available temporal and spatial validation of the influences of the new nitrogen. All of the simulations presented here tune to observed surface chlorophyll. The different levels of new nitrogen input are accommodated (balanced) by adjusting the detrital sinking (export flux). In this way, the NOTRICHO run implicitly includes the effect of nitrogen fixation, by tuning to observed surface chlorophyll and reducing nitrogen losses uniformly over the basin. The TRICHO and HITRICHO runs explicitly simulate different levels of nitrogen fixation, and to maintain surface phytoplankton biomass at the observed levels, sinking is increased. Our goal is to determine the effects of nitrogen fixation which are linked to the explicit representation of an additional nitrogen fixing functional group with different levels of N_2 fixation.

[12] As described in the work of HCC, the tuning process for the TRICHO run begins with adjusting *Trichodesmium* biomass to observed levels by changing *Trichodesmium*'s mortality rate. In this case the observed levels are colony concentrations in the western Atlantic reported by *Carpenter and Romans* [1991] (see HCC for details). Then mixed layer chlorophyll is tuned to the observed (SeaWiFS-derived) concentrations by adjusting the sinking rate of detritus. The best fit detrital sinking rate for the TRICHO run is 6 m day^{-1}. The NOTRICHO run was tuned similarly but in this case the growth rate of *Trichodesmium* was set to zero and then the sinking rate of detritus was readjusted (to 3 m day^{-1}) to compensate for the reduced new nitrogen inputs and bring the chlorophyll concentrations back up to the observed levels. For the HITRICHO run *Trichodesmium* biomass and N_2 fixation rate is again tuned using the mortality rate parameter. In this case, however, the target is to adjust basin-wide nitrogen fixation rate to the high geochemical N_2 fixation rate estimates, rather than tuning to *Trichodesmium* biomass in the western Atlantic. The increased inputs of new nitrogen to the system are then balanced by adjusting (increasing) the sinking parameter to maintain reasonable phytoplankton concentrations. In order to achieve this balance the sinking rate must be set at a high but not unreasonable [*Parsons et al.*, 1984], value of 55 m day^{-1}.

[13] The different runs are tuned by inspection (i.e., visual comparison) to reproduce the observed seasonal cycle and spatial distribution of surface chlorophyll concentrations. These data are a SeaWiFs monthly climatology constructed from an arithmetic mean of 174 cycles from September 1997 to July 2001. Here our criteria are to maximize agreement in the oligotrophic open ocean, and to represent the seasonal cycle. In practice, tuning a single parameter improves some regions while degrading others; however, this process works well in equalizing the phytoplankton dynamics of the runs, as the basin averaged net phytoplankton production in the three runs were equivalent to within 4%, and to less than 1% in the North Atlantic tropics.

3.2. Nitrogen Fixation Impacts on the Ecosystem

[14] Figure 2 shows the model-estimated distribution of N_2 fixation due to *Trichodesmium* as a function of season

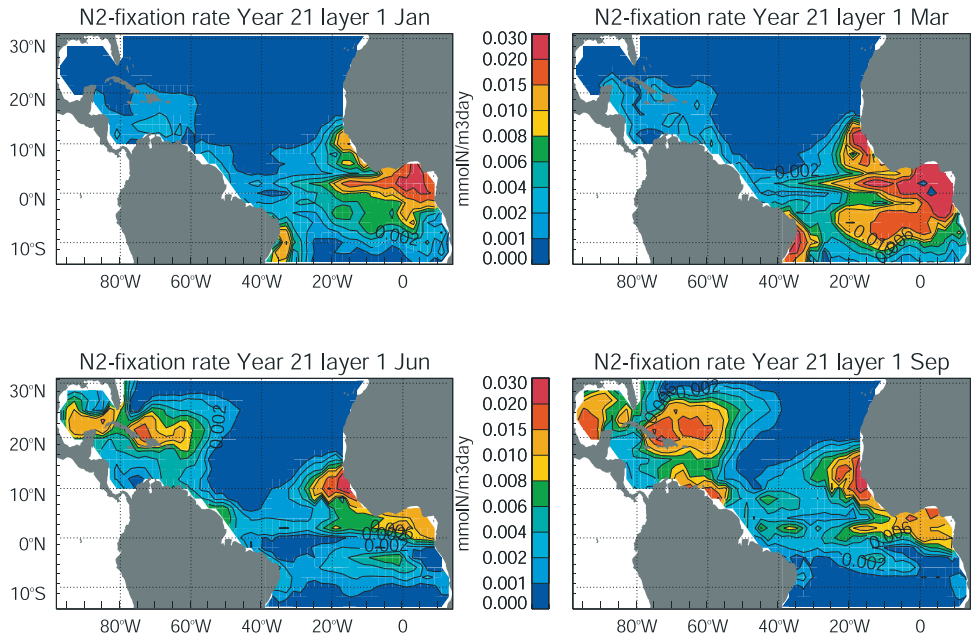

Figure 2. Model-estimated nitrogen fixation rate in the mixed layer as a function of season. The fields are synoptic, taken from the middle of the specified month. The rates are expressed in mmol N m^{-3} day^{-1}.

for the TRICHO run (see also HCC, Figure 7). The temporal and spatial variability in N_2 fixation rate follows the variability in *Trichodesmium* biomass quite closely. We assume the model is therefore reproducing the approximate observed time/space patterns of N_2 fixation rate because there are few measurements for validation.

[15] The point to point differences between maps of the mixed layer DIN and P concentrations for the TRICHO and NOTRICHO runs are shown in Figures 3 and 4, respectively. These maps show similar patterns (though the units and magnitudes differ) reflecting the tight coupling between new nutrient supply from N_2 fixation and enhanced phytoplankton biomass. As *Trichodesmium* fix dissolved nitrogen gas, the primary route to DIN in the model is through heterotroph consumption of DON and *Trichodesmium* themselves. A comparison of Figures 2 and 3 suggests that this is a fairly slow process in the model. Note, for example, that the DIN anomaly in the Caribbean due to N_2 fixation is most pronounced in the fall and winter months (Figure 3); however, the N_2 fixation rate maximum occurs earlier, in the

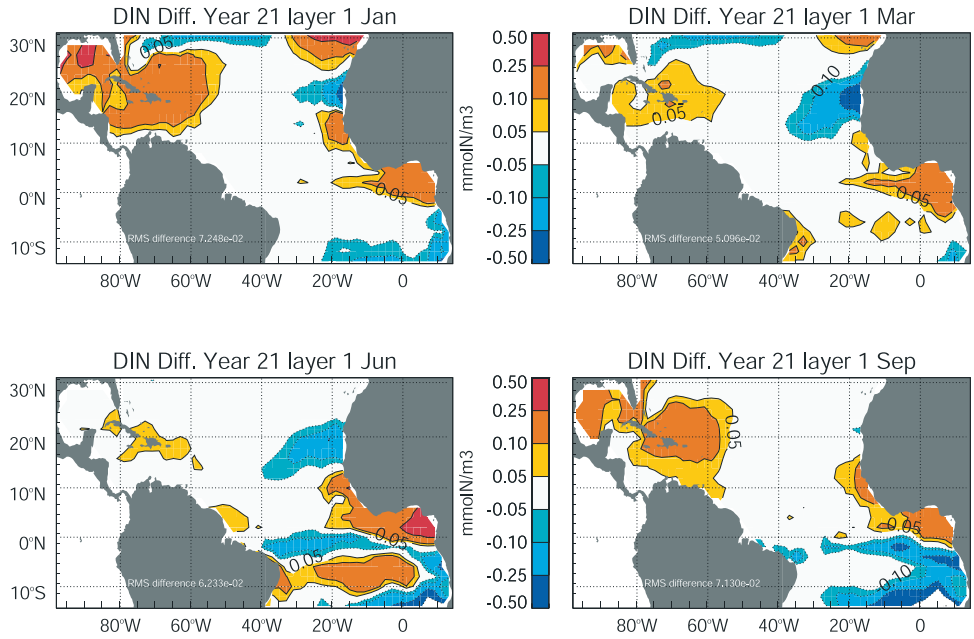

Figure 3. The point to point instantaneous difference between mixed layer DIN concentration in the NOTRICHO and TRICHO runs (mmol N m^{-3}). Positive values indicate greater DIN in the TRICHO run.

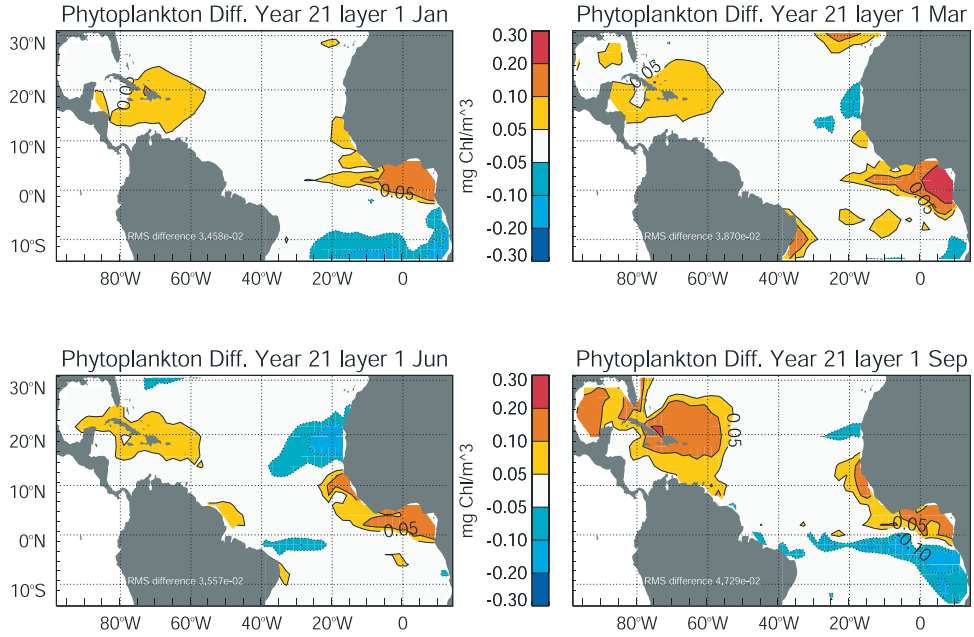

Figure 4. The point to point instantaneous difference between mixed layer phytoplankton chlorophyll in the NOTRICHO and TRICHO runs (mg Chl m^{-3}). Positive values indicate greater chlorophyll in the TRICHO run.

summer and fall (Figure 2). Thus there appears to be a time lag on the order of months before the new nitrogen due to N_2 fixation is regenerated as DIN. The development of this DIN anomaly is probably also related to suboptimal phytoplankton growth conditions in the fall and winter which inhibit nitrogen uptake, thus allowing DIN accumulation in the mixed layer.

[16] Major positive differences in Figures 3 and 4 are linked to regions where N_2 fixation is sustained at relatively high rates over part or all of the year, and those areas influenced by advection of this new nitrogen out of the high N_2 fixation regions. In March, (Figure 2), high rates are simulated in the Gulf of Guinea, Guinea Dome, and equatorial regions. This N_2 fixation leads to the development of regional DIN and P anomalies particularly in northern hemisphere spring and summer (again lagging the N_2 fixation maximum which occurs in spring). In general the tropics from 10°N to 10°S and excluding the equatorial upwelling region, exhibit weak enhancement of mixed layer P biomass as a result of the fairly stable tropical nitrogen fixation (Figure 4).

[17] The N and P difference maps (Figures 3 and 4) show a strong north-south negative-positive dipole difference centered near 15°N in the Guinea Dome region. This line marks the northern edge of the *Trichodesmium* population. North of 15°N, phytoplankton production is fueled by new nitrogen flux into the mixed layer from depth. The higher sinking flux in the TRICHO simulation keeps DIN levels lower than in the NOTRICHO simulation. South of 15°N, nitrogen fixation balances or overwhelms the increased sinking flux, and both P and DIN increase. The anomalies in DIN and P concentration in these upwelling regions are large relative to the oligotrophic gyres, but relatively small with respect to the absolute DIN and P concentrations.

[18] In the Caribbean and Gulf of Mexico regions, DIN is generally elevated in the TRICHO simulation (Figure 3), due mostly to seasonal inputs of new nitrogen from to N_2 fixation in summer and fall. Although the highest rates of N_2 fixation occur in the model in early fall (September) in these areas, the maximum DIN anomaly occurs in winter. This maximum occurs in conjunction with the deepening of the mixed layer in winter, and suggests that a significant fraction of the fixed nitrogen in this region may be mixed down into the thermocline during winter before it can be fully utilized by the phytoplankton population. The winter and fall DIN differences are roughly comparable; however, the fall P difference is greater than the winter P difference showing the impact of light limitation in the winter on the ability of the P population to grow and utilize DIN. There is residual enhancement of the surface DIN in the southern Sargasso Sea, the Caribbean and the Gulf of Mexico throughout winter and spring (Figure 3), so the winter mixing does not penetrate deeply enough here to eliminate the N_2 fixation signal. The P biomass generally remains slightly elevated throughout the year in the TRICHO run. These model results suggest that the influence of nitrogen fixation is felt throughout the year in some regions, and may lead to a general elevation of phytoplankton biomass.

[19] The negative differences in Figures 3 and 4 are due to higher sinking rates in the TRICHO simulation. In regions far from the influence of nitrogen fixation, the surface waters become more oligotrophic due to the more rapid removal of particulate matter. The effect of the model tuning is to make some regions increasingly oligotrophic to compensate for enhanced biomass and production in others.

3.3. Production Rates

[20] Figures 5 and 6 show the phytoplankton production rate for the NOTRICHO run, and the difference in production rate between the TRICHO and NOTRICHO runs, respectively. A carbon to chlorophyll mass ratio of 50:1 is used for the conversion. As expected, the spatial and

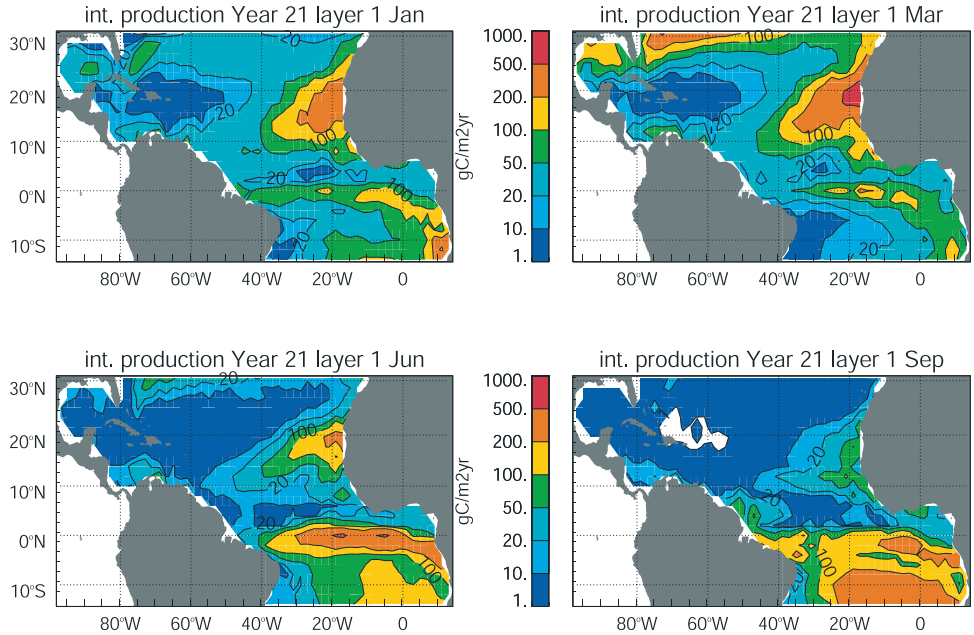

Figure 5. The instantaneous production rate integrated over the euphotic zone in the NOTRICHO model (gm C $m^{-2}yr^{-1}$).

temporal variability in production rate is very similar to phytoplankton biomass, i.e., the rates are low in the oligotrophic gyres and high at high latitudes during the spring bloom, and in upwelling areas. With the addition of N_2 fixation in the TRICHO run, production rates are significantly elevated in all of the regions where there are inputs of new nitrogen (e.g., in the Gulf of Mexico, the Caribbean, the Guinea Dome, the Gulf of Guinea, and in equatorial waters). Note that production rates are elevated throughout the year in the Caribbean where there is a distinct production rate anomaly of 10–50 g C m^{-2} yr^{-1} (Figure 6). Production rates are similarly elevated throughout the year by N_2 fixation in the Gulf of Guinea.

[21] In general, the production rates in both the TRICHO and NOTRICHO runs are comparable to remote and in situ estimates of primary production in upwelling regions, but they are low in the oligotrophic gyres, especially on the western side of the basin [*Behrenfeld and Falkowski*, 1997; *Antoine et al.*, 1996]. Although primary production is elevated in oligotrophic waters by N_2 fixation in the TRICHO run, the increases are not sufficient to bring the model into agreement with the remote and in situ estimates.

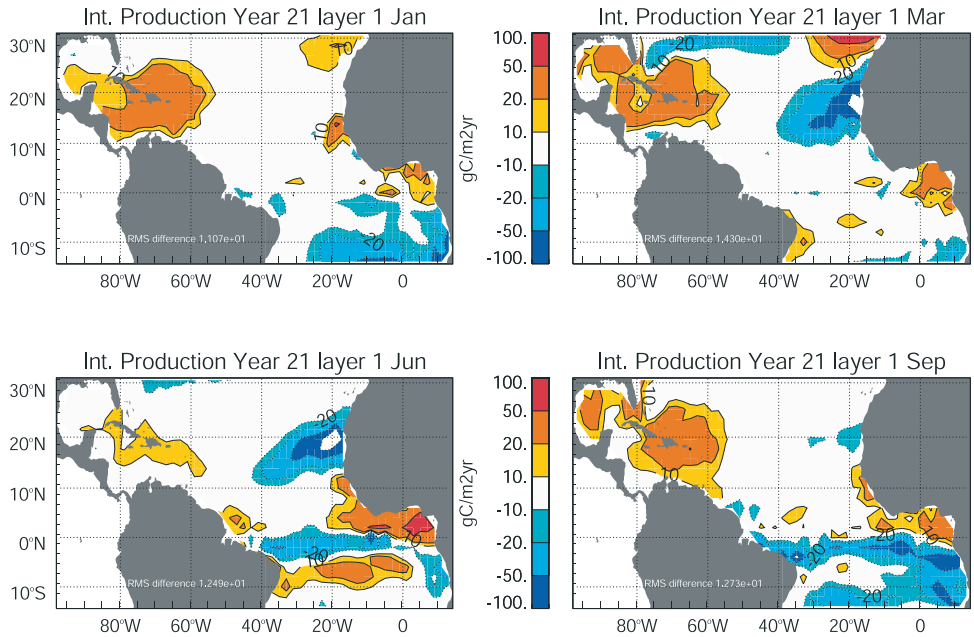

Figure 6. The point to point instantaneous difference between the integrated production (gm C $m^{-2}yr^{-1}$) in the NOTRICHO and TRICHO runs. Positive values indicate more growth in the TRICHO run.

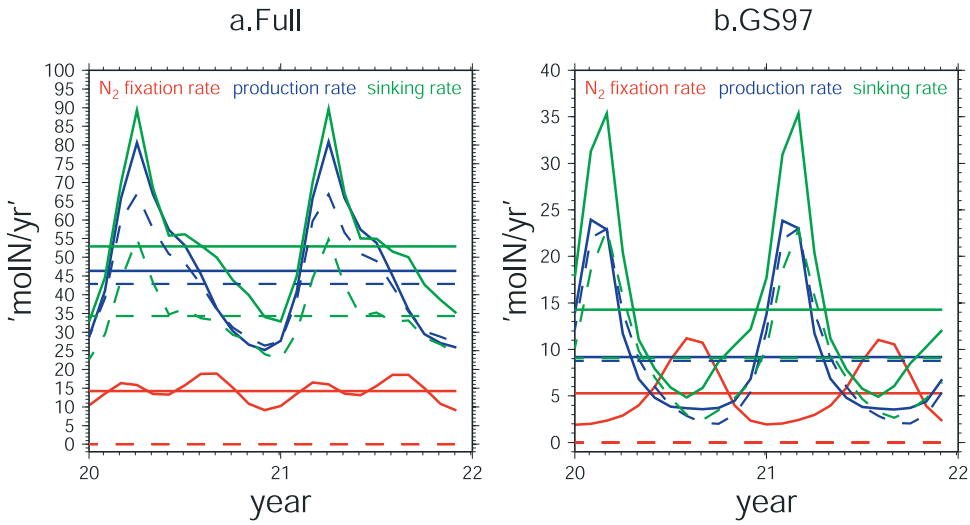

Figure 7. Spatially integrated nitrogen fixation rate (circles), phytoplankton production rate divided by a factor of 10 (plusses), and detrital sinking rate out of the euphotic zone (stars) over three annual cycles. The units are 10^{11} mol N year^{-1}. The simulation with nitrogen fixation (TRICHO) is shown in solid lines, without nitrogen fixation (NOTRICHO) is indicated with dashed lines. Regions indicated in Figures 7a–7g are shown in Figure 1. (a) Full domain shown, (b) GS97 region, (c) Gulf of Mexico region, (d) Caribbean region, (e) equatorial region, (f) Guinea Dome region, and (g) Gulf of Guinea region.

It is shown below that our model generates basin-wide N_2 fixation rates that are comparable to estimates derived from direct measurements. Thus the model suggests that N_2 fixation may not be sufficient to resolve the low-production rate problem [*McGillicuddy et al.*, 1998; *Oschlies and Garcon*, 1999]. However, it is also shown below that the higher N_2 fixation rates implied by N* anomalies in the Atlantic [*Michaels et al.*, 1996; *Gruber and Sarmiento*, 1997] are sufficient to bring the model into agreement with the remote and in situ estimates of primary production in oligotrophic waters, albeit with some negative consequences.

[22] Like the previous difference maps, Figure 6 reveals both positive and negative anomalies. The negative differences occur where the increased export in the TRICHO run is not balanced by N_2 fixation. In particular, note the negative anomalies at high latitudes and in the Guinea Dome region in the winter and spring. These are regions where N_2 fixation is always low, so increasing the sinking rate in the TRICHO run results in a net decline in production rate because it increases export without a compensatory increase in new nitrogen input. Negative anomalies (lower production in the TRICHO run) also tend to be areas where light limits primary production whereas the positive anomalies (higher production rate in the TRICHO run due to N_2 fixation) correspond to regions where nitrogen limits primary production.

3.4. Basin-Wide and Regional Rates Over the Seasonal Cycle

[23] Here we examine the temporal evolution of the ecosystem rates averaged within the regions defined above in Figure 1. We compare and contrast the seasonal cycles of N_2 fixation, primary production and sinking flux out of the euphotic zone for each region (Figure 7). The rates and fluxes are plotted over two annual cycles for the TRICHO and NOTRICHO runs, and they are integrated over the area of each region so they also show the relative magnitude of the processes in the different physical regimes. The vertical axis varies between regions and phytoplankton production rate has been divided by a factor of 10. Also the difference between the nitrogen fixation rate and sinking flux gives only a rough estimate of the vertical flux of nitrate into the euphotic zone because there are horizontal fluxes of particulate and dissolved matter in each region, as well as a changing euphotic depth.

3.4.1. Tropical North and South Atlantic

[24] According to the model, N_2 fixation in the tropical North Atlantic occurs seasonally with a large peak in the late summer and early fall (Figure 7b). In contrast, the phytoplankton production rate peaks strongly in the winter/spring. The *Trichodesmium* biomass maximum and high rates of N_2 fixation develop long after the spring phytoplankton bloom in the late summer and fall when the water column is stratified and nutrient concentrations are depleted. Thus N_2 fixation occurs when the North Atlantic is strongly nutrient but not light limited.

[25] Figure 7b demonstrates the connection over broad scales between the phytoplankton biomass and production rate. Because the NOTRICHO and TRICHO simulations were tuned to surface chlorophyll concentration, the seasonal and mean phytoplankton production rates are very similar between the runs even though the input of new nitrogen in the TRICHO run is higher due to N_2 fixation. The additional flux of nitrogen into the system in the TRICHO run is removed through the enhanced detrital sinking flux. One can, however, see some subtle differences in the seasonal production rate patterns between the two runs in Figure 7b, i.e., primary production is enhanced slightly during late summer and fall when N_2 fixation is highest, and primary production is lowered slightly as the spring bloom declines. The export flux is enhanced throughout the year, but in particular during late fall, winter and

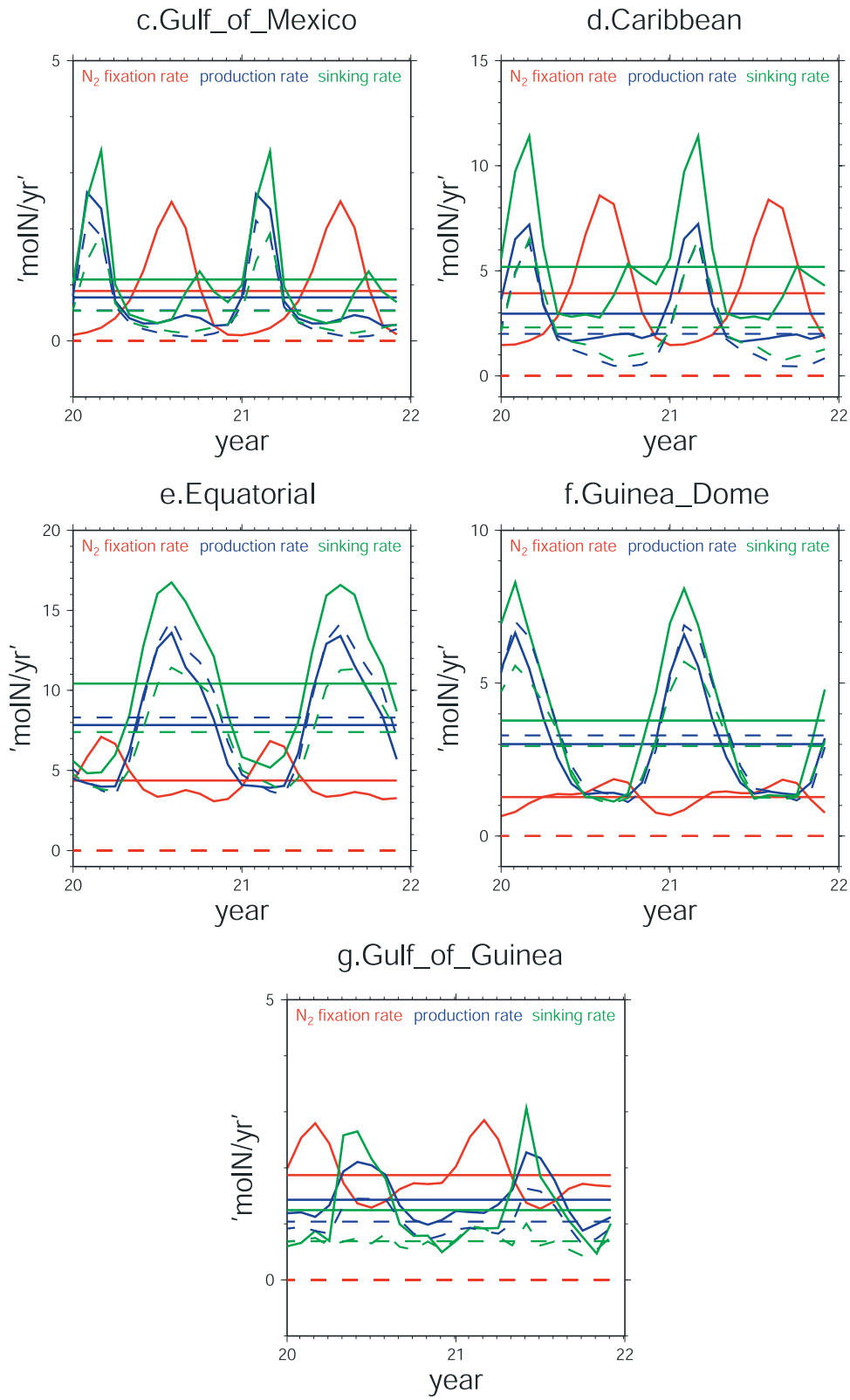

Figure 7. (continued)

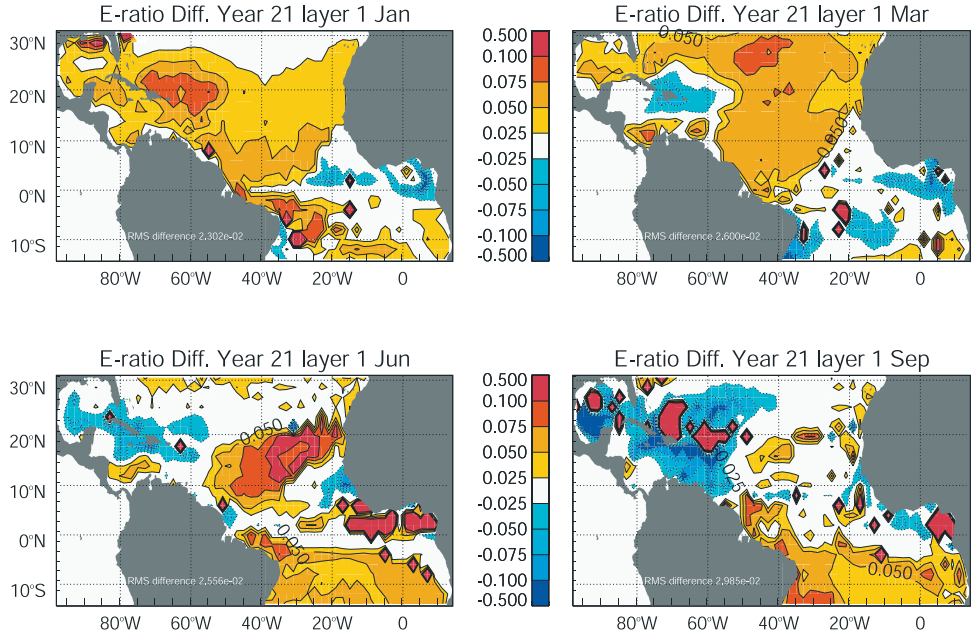

Figure 8. The point to point instantaneous difference between the e ratio in the NOTRICHO and TRICHO runs. Positive values indicate higher new production in the TRICHO run.

spring. Thus it appears that the new nitrogen that is input in late summer and fall due to N_2 fixation is exported months later, with much of it leaving the system via the spring phytoplankton bloom.

3.4.2. Gulf of Mexico

[26] The seasonal patterns in N_2 fixation, primary production, and export flux in the Gulf of Mexico (Figure 7c) are essentially similar to the patterns we see over the entire North Atlantic (Figure 7b). However, the new nitrogen supplied by N_2 fixation is much greater relative to the phytoplankton production (nearly 10%), highlighting the importance of nitrogen fixation over the region. As a result the TRICHO run has substantially more impact on primary production in the Gulf of Mexico in late summer/early fall and produces a stronger enhancement of export flux in fall and winter. As discussed in the work of HCC, observations suggest that the model underestimates N_2 fixation in the Gulf of Mexico.

3.4.3. Caribbean

[27] The seasonal patterns in N_2 fixation, primary production, and export flux in the Caribbean region (Figure 7d) are very similar to the patterns in the Gulf of Mexico. However, the magnitudes are roughly four times larger. New nitrogen inputs due to N_2 fixation constitute a large fraction of the mean phytoplankton production (slightly more than 10%), and they account for 80% of the sinking flux.

3.4.4. Equatorial Band

[28] The equatorial region (Figures 1 and 7e) encompasses a broad area from 5°N to 15°S, and from the western boundary to 5°W; however, N_2 fixation, primary production and export tend to cycle similarly over the area. The annual cycle in the rates differs substantially from the northern hemisphere regions discussed above. Peak phytoplankton production and sinking flux occurs in late summer and fall, coincident with enhanced trade winds and equatorial surface divergence that lead to shoaling of the thermocline and nutricline, and upwelling of nutrients [*Busalacchi and Picaut*, 1983; *Monger et al.*, 1997].

[29] In the TRICHO run N_2 fixation peaks in the winter and spring when upwelling and phytoplankton production is reduced and phytoplankton exhaust the nutrient supply. The timing of the peaks also reflect, to some degree, the influence of the southern hemisphere, where N_2 fixation is highest in winter and spring (i.e., the austral summer and fall). New nitrogen inputs from N_2 fixation are relatively small compared to the total primary production in the equatorial region because upwelling supplies most of the new nitrogen. As a result we do not see as large a stimulation of primary production due to N_2 fixation in the winter/spring in the TRICHO run. Note that this region is not included in *Gruber and Sarmiento*'s [1997] Atlantic N_2 fixation rate estimate, though their estimate may include effects of N_2 fixation near the equator through subsurface advection of the excess nitrogen signature into their domain.

3.4.5. Guinea Dome Region

[30] The Guinea Dome region (Figure 7f), operates under a different physical regime, despite its proximity to the equator. Ekman pumping drives the upwelling in the Guinea Dome and along the coast of NW Africa, and has a maximum intensity in winter and spring months [*Signorini et al.*, 1999; *McClain and Firestone*, 1993] (Figure 4). The N_2 fixation in this region develops over a relatively small area adjacent to the productive upwelling regions (see discussion in the work of HCC, Figure 7) and is relatively constant throughout most of the year with only a small increase in late summer and fall when primary production is low.

3.4.6. Gulf of Guinea

[31] The seasonal patterns in N_2 fixation, primary production and export flux in the Gulf of Guinea are similar to those in the equatorial region (Figure 7g). However, the inputs of new nitrogen due to N_2 fixation in the Gulf of

Table 1. Nitrogen Fixation Rates Integrated Over Space and Averaged[a]

Source	10^{12} mol N yr^{-1}	Notes
	Tropical Atlantic Domain (1), 10°N to 30°N, Based on GS97.	
Capone and Carpenter [1982]	0.09	excluding blooms, based on Caribbean observations
Carpenter and Capone [1992]	0.18	including blooms, extracted from their global estimate based on GS97 ratios
Michaels et al. [1996]	3.7–6.4	geochemical indirect estimate based largely on BATS data
Gruber and Sarmiento [1997]	2.0	geochemical indirect estimate based on N* distributions coupled with age tracers
This study	0.55	tuning to Caribbean observations and rates
This study	2.15	tuning to GS97 observations and rates
	Whole Atlantic Domain, 25°S to 45°N	
Capone et al. [1997]	1.0–1.5	derived from global estimate using GS97 ratios
Capone et al. (unpublished)	1.3	temperature >25.0°C, 0.14 mmol N m^{-2} day^{-1}
Capone et al. (unpublished)	2.2	temperature >25.0°C, 0.242 mmol N m^{-2} day^{-1}
This study	1.47	tuning to Caribbean observations and rates
This study	5.28	tuning to GS97 estimates in the North Atlantic
Active temperature	1.42	model rates × model (temperature >25.0°C) area
Passive temperature	1.5	*Capone et al.* (unpublished) rates (0.14 mmol N m^{-2} day^{-1}) × model temp >25.0°C area
Passive temperature	2.6	*Capone et al.* (unpublished) rates (0.242 mmol N m^{-2} day^{-1}) × model temp >25.0°C area
Regional Domains	10^{12} mol N yr^{-1}	See Figure 8
(1)		see tropical Atlantic domain above
(2) Caribbean	0.41	tuning to Caribbean observations and rates
(2) Caribbean	1.23	tuning to GS97 estimates
(3) Guinea Dome	0.13	tuning to Caribbean observations and rates
(3) Guinea Dome	0.44	tuning to GS97 estimates
(4) Gulf of Guinea	0.19	tuning to Caribbean observations and rates
(4) Gulf of Guinea	0.41	tuning to GS97 estimates
(5) Gulf of Mexico	0.09	tuning to Caribbean observations and rates
(5) Gulf of Mexico	0.29	tuning to GS97 estimates
(6) Equatorial	0.45	tuning to Caribbean observations and rates
(6) Equatorial	1.62	tuning to GS97 estimates

[a]GS97 are rates and spatial domain of *Gruber and Sarmiento* [1997].

Guinea are much larger relative to the upwelling flux from depth. As a result, there is a much more obvious stimulation of primary production and export by N_2 fixation. As in the other regions, most of the export of this new nitrogen is associated with the phytoplankton bloom rather than the period of maximum N_2 fixation.

[32] The regional breakdown of N_2 fixation, production rate, and sinking flux shows that the model generates temporal and spatial variability in N_2 fixation, and that different patterns arise in the regions in direct response to changes in forcing. While some regions (Caribbean, Gulf of Mexico) support a late summer nitrogen fixation maximum which stimulated a phytoplankton growth rate increase, other regions show little influence on phytoplankton growth rate from nitrogen fixation (equatorial, Guinea Dome). Still other regions (Gulf of Guinea) support year-round nitrogen fixation with enhancement of phytoplankton growth which is uniform over the annual cycle. In most of the regions we selected, the annual rate of primary production is not greatly changed by the addition of N_2 fixation because our tuning procedure increases export so as to roughly balance the additional new nitrogen inputs. However, N_2 fixation does lead to subtle changes in the seasonal primary production patterns, and the seasonal patterns in export are dramatically altered. Interestingly, in the model the export of new nitrogen from N_2 fixation tends to be associated with phytoplankton blooms that occur months after the new nitrogen is input into the system. There is reason to believe that a similar kind of lag may actually happen in nature. *Trichodesmium* colonies are often neutral or positively buoyant, and as a result blooms do not sink after their demise (D. G. Capone, personal observations, 2004). Rather, it appears that the colonies must decay and/or be consumed and recycled into other forms of particulate matter before the new nitrogen is exported.

3.5. Nitrogen Sources and Sinks

[33] As discussed above, there are two sources of nitrogen to the euphotic zone in the model interior (the model buffer zones at northern and southern boundaries also may introduce sources and sinks of nitrogen). The first source/sink results from physical processes which bring deep nitrogen to the euphotic zone through isopycnal and diapycnal advection and mixing processes. The second source is the fixation of atmospheric nitrogen gas by *Trichodesmium*. Net sinks of nitrogen out of the euphotic zone come primarily from the sinking flux of detritus, though diapycnal and isopycnal advection and mixing processes can also result in a net sink if there is a significant accumulation of mass in the surface layers relative to depth.

[34] The f ratio [*Eppley and Peterson*, 1979] specifies the fraction of phytoplankton growth that comes from new nitrogen from the deep ocean. We calculate an e ratio comparable to the f ratio by dividing the total export flux out of the euphotic zone by vertically integrated primary production for each model grid cell [*Laws et al.*, 2000]. This measure includes the new nitrogen from nitrogen fixation which is not the case for the f ratio. Because it is a ratio, the

e ratio is highly sensitive to small changes at low export and sinking flux values, which leads to a rather noisy plot on monthly timescales.

[35] Figure 8 shows the difference between the e ratio fields with and without N_2 fixation. The changes in e ratio are quite large, i.e., in many regions we see much more than a doubling or halving of the values compared to the NOTRICHO run. N_2 fixation increases the e ratio in the oligotrophic subtropical gyre and the Gulf of Mexico in fall (September) and Winter (January), and decreases it in spring (March) and summer (June). Figure 6 shows that N_2 fixation generally enhances primary production in these areas. Thus the increases in e ratio are due to the relative enhancement of export compared to production. Note, however, that there is a lag, with the greatest increases in e ratio occurring one full season later than the periods of maximum N_2 fixation (compare Figures 2 and 8). Thus it takes months for the new nitrogen from N_2 fixation to cycle through the ecosystem into the detritus pool and sink out of the euphotic zone in the model. Figure 8 also reveals substantial changes in the e ratio due to N_2 fixation off of NW Africa, the Cape Verde/Sierra Leone region, and in the Gulf of Guinea. The increased e ratio in the Guinea Dome region off of NW Africa in June is clearly associated with decreased primary production in this region (compare Figures 6 and 8), caused by the increased sinking rate in the TRICHO run. In contrast, the increases in the Cape Verde/Sierra Leone region and in the Gulf of Guinea are associated with increased primary production, so the increase in e ratio is due to a relative increase in export due to N_2 fixation.

[36] The magnitudes of these changes in e ratio are large. Direct measurements of N_2 fixation rate indicate that the input of new nitrogen from the atmosphere to the oceans due to *Trichodesmium* can be comparable to the upward flux of nitrogen from the deep ocean in oligotrophic tropical waters [*Karl et al.*, 1997; *Capone et al.*, 1997]. This would imply that N_2 fixation can double the f ratio in oligotrophic waters, but it is generally believed that increases in new production due to N_2 fixation are much smaller in more productive regions. In the model, however, we see e ratios that are increased by as much as a factor of ten by N_2 fixation, and in some cases these increases occur in very productive regions (e.g., the Cape Verde/Sierra Leone region, Figure 8). As discussed above, some of this may be due to time lags in the export signal, and this effect is particularly pronounced in synoptic maps like Figure 8. In fact, when we calculate basin averaged e ratios we get much lower values. Without N_2 fixation (NOTRICHO) we obtain a rather low (perhaps unrealistically low) new production value of 0.074 mol N $m^{-2}yr^{-1}$, which gives a basin-wide e ratio = 0.1 [c.f., *Behrenfeld and Falkowski*, 1997; *Laws et al.*, 2000]. Including N_2 fixation (TRICHO) raises the new production to 0.1 mol N m^{-2} yr^{-1} and gives an e ratio = 0.125, closer to box model and early *Eppley and Peterson* [1979] levels. Very high rates of N_2 fixation equivalent to geochemical estimates (HITRICHO run, discussed below in section 5) yield new production rates of 0.22 mol N m^{-2} yr^{-1} and give a basin-wide e ratio = 0.2.

[37] While new production is, perhaps, too low in the NOTRICHO simulation presented here, the differences in new production between the simulations with and without N_2 fixation point to the potential role that such a source may have in the nitrogen budget of the oligotrophic ocean. Realistic levels of nitrogen fixation tuned to direct measurements, as in the TRICHO run, increase new production in this simulation by 25%.

4. Impact of Nitrogen Fixation on Biogeochemistry

[38] In this section we address the question of how N_2 fixation influences regional and basin-wide nitrogen budgets and what this additional source of nitrogen may mean to the flux of organic matter out of the euphotic zone.

4.1. Comparison With Large-Scale Direct and Indirect Rates

[39] Estimates of nitrogen fixation fall into two camps, those for which relatively sparse direct observations have been extrapolated in time and space over regional areas or the global oceans [e.g., *Carpenter*, 1983; *Capone et al.*, 1997; *Carpenter and Romans*, 1991], and estimates of nitrogen fixation involving geochemical parameters or indices which integrate over long timescales and over broad spatial domains. In general, the direct observations have tended to be significantly lower (2–10 times) than the more recent indirect, geochemical estimates. However, the disparity is getting smaller because more recent direct estimates are considerably higher (see Table 1). Problems with both approaches may account for these apparent differences.

[40] Direct measurements have been generally restricted to consideration of the cyanobacterium *Trichodesmium* in its colonial form, which can be isolated and assayed. *Carpenter* [1983] scaled a cell specific rate of nitrogen fixation to global maps of its distribution. His value of about 0.09×10^{12} mol N yr^{-1} for the entire Atlantic Ocean, Table 1, is very low. More recent direct estimates scaled to the area of water warmer than 25°C in the North and South Atlantic (about 25.2×10^6 km^2) yield a range of 1.3 to 2.2×10^{12} mol N yr^{-1} (Capone et al., submitted manuscript, 2004). This estimate does not include input by free-living filaments, by blooms [e.g., *Capone et al.* manuscript], or input by other N_2 fixers.

[41] N* ("N star") is one geochemical index which has been used to estimate N_2 fixation [*Gruber and Sarmiento*, 1997; *Michaels et al.*, 1996; *Deutsch et al.*, 2001]. This index relates nitrogen to phosphorus to determine where an excess of nitrogen occurs. Excesses of nitrate above Redfield (N* > 0) exist throughout much of the tropical and subtropical North Atlantic and have been interpreted as a result of N_2 fixation. Using this approach, *Gruber and Sarmiento* [1997] derive a value for N_2 fixation of 2.0×10^{12} mol N yr^{-1} for the Atlantic between 10° and 30°N, and *Michaels et al.* [1996] estimate a range of N_2 fixation rates that are about a factor of two higher (Table 1). These estimates, however, are not without caveats. In particular, deriving a rate of N_2 fixation from integrated N* values requires assuming an N:P biomass formation ratio for the N_2 fixers in excess of Redfield [*Gruber and Sarmiento*, 1997]. The resulting rate estimate is quite sensitive to the choice of this value, which is not well constrained. *Gruber and Sarmiento* [1997] chose an N:P value of 125 based on

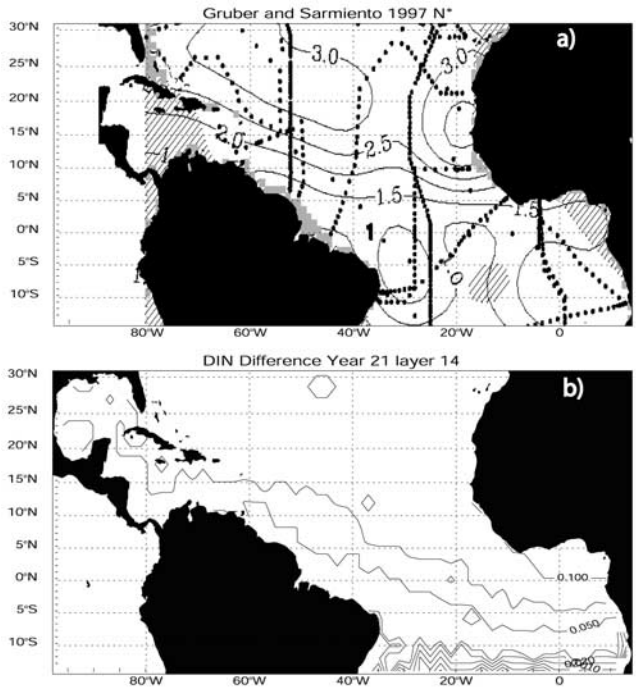

Figure 9. (a) N* adapted from *Gruber and Sarmiento* [1997] on the 27.10 sigma-theta surface. (b) The difference between the Tricho and NOTRICHO N concentration (mmol N m^{-3}) for layer 14 (27.05 sigma-theta).

observations by *Karl et al.* [1992] of the N:P ratio of surface particulate matter after a *Trichodesmium* bloom at Station ALOHA. However, direct analyses of *Trichodesmium* biomass typically yield N:P ratios of 40 to 50 [*Letelier et al.*, 1996; *Letelier and Karl*, 1998; *Krauk*, 2001]. Adopting this lower value increases the *Gruber and Sarmiento* [1997] estimate by 50%.

[42] Over the tropical Atlantic domain defined by *Gruber and Sarmiento* [1997], the TRICHO model run generates 0.55×10^{12} mol N yr^{-1} (TRICHO run), which lies within the range defined by the direct and indirect estimates (Table 1). Clearly, however, the model-generated rate is closer to the older direct estimates [*Capone and Carpenter*, 1982; *Carpenter and Capone*, 1992]. This is expected because the model was formulated using measured *Trichodesmium* growth rates from these studies [*Hood et al.*, 2001] and tuned to reproduce the observed *Trichodesmium* biomass from [*Carpenter and Romans*, 1991] from which the direct extrapolations were made.

[43] For the whole Atlantic domain (25°S to 45°N) the TRICHO model run generates 1.47×10^{12} mol N yr^{-1}, which is generally in agreement with recent direct estimates (1.3 to 2.2×10^{12} mol N yr^{-1}) (Capone et al., submitted manuscript, 2004). These newer estimates of Atlantic Ocean N_2 fixation rate are larger because, among other things, they include additional observations which incorporate *Trichodesmium* blooms. It should be noted, however, that these direct estimates may be overestimates because the observations from which they are derived are not randomly distributed, i.e., the measurements tend to be focused in areas where rates are expected to be large.

[44] Table 1 also shows the contribution that each region (Figure 1) makes to the total Atlantic nitrogen fixation budget. The total amount of N_2 fixation in the Gulf of Mexico (0.09×10^{12} mol N yr^{-1}) makes a small, but significant contribution to basin-wide N_2 fixation rate. As discussed in the work of HCC, observations suggest that the model underestimates N_2 fixation in the Gulf of Mexico. A greater fraction of the total (nearly 30%) in this model is supplied from the Caribbean ($=0.41 \times 10^{12}$ mol N yr^{-1}).

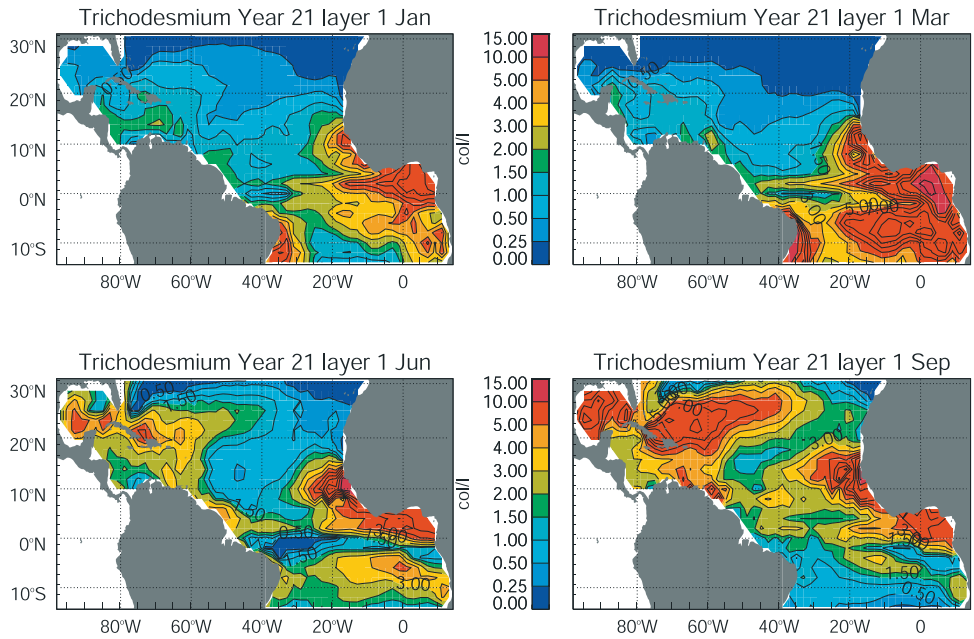

Figure 10. Simulated *Trichodesmium* (col l^{-1}) concentration in the HITRICHO model mixed layer over year 21.

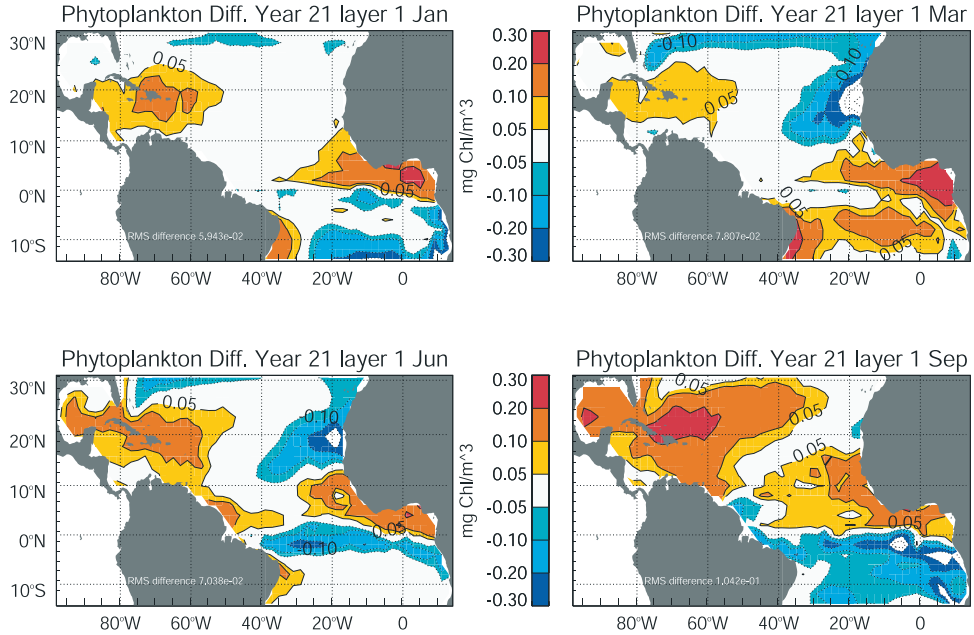

Figure 11. The point to point instantaneous difference between mixed layer phytoplankton chlorophyll in the NOTRICHO and HITRICHO runs (mg Chl m^{-3}). Positive values indicate greater chlorophyll in the TRICHO run.

The equatorial region also contributes about 30% of the total. The Guinea Dome region contributes about 9% of the total, basin-wide N_2 fixation, and the Gulf of Guinea 15%. Although the rates are high in the Gulf of Guinea, the areal extent of the nitrogen fixation is relatively small, so it doesn't contribute a large fraction of the total.

[45] The ecosystem model used here does not include a temperature dependence in the *Trichodesmium* or phytoplankton growth and remineralization terms [*Eppley and Peterson*, 1979]. Rather, in the model, *Trichodesmium* is confined to the tropics because winter mixing at higher latitudes is too deep and protracted to allow significant accumulation in the summer and fall. It is possible that the absence of a temperature constraint on *Trichodesmium* growth results in an overestimation of the area over which N_2 fixation occurs. We therefore calculated the rate that the model would yield if N_2 fixation only occurs in waters warmer than 25°C. The result (labeled active temperature in Table 1) shows that the model-estimated rate is not greatly changed by the addition of this temperature constraint. This implies that the question of whether temperature or light determines the latitudinal range of *Trichodesmium* cannot be answered from these model simulations; either limitation yields similar large-scale rates. It also indicates that the choice of the 25°C isotherm is relatively general, applying both to observational data, and to a bulk mixed layer model as a proxy for light. To determine to what extent our dynamic model contributes to our understanding of the basin-wide N_2 fixation, we also calculate the rates following the procedure of *Eppley and Peterson* [1979], but using the model-estimated surface temperature fields to determine the area over which the measured rates are applied. The resulting integrated rate (labeled passive temperature in Table 1 and calculated using either 0.14 or 0.242 mmolN m^{-2} day^{-1}) exceeds the *Capone et al.* (manuscript) estimates by about 20%, indicating that the model generally has a greater or more persistent expanse of warm (warmer than 25°C) water than the Levitus climatology used by *Capone et al.* (manuscript). If they correlate with shallow mixed layer depths, excessive high surface temperatures in the physical model may cause the ecosystem model to overestimate basin-wide N_2 fixation, with an upper bound of 20% or 0.29×10^{12} mol N yr^{-1}. The dynamic model estimate of N_2 fixation lies in the midrange of the direct estimates because N_2 fixation rates vary seasonally in the model, which is not accounted for by *Capone et al.* (manuscript).

4.2. Comparison With Geochemical or Indirect Spatial Rate Estimates

[46] In addition to the basin-wide comparisons, we can also compare the model-derived spatial patterns in N_2 fixation to the Atlantic N* distribution of *Gruber and Sarmiento* [1997]. We do not include the effects of denitrification in this model, which may alter the boundary conditions for the comparison; however, open ocean denitrification rates are thought to be quite low in the Atlantic based on relatively high dissolved oxygen concentrations.

[47] Figure 9a is adapted from *Gruber and Sarmiento* [1997, Figure 13b]. It shows the N* distribution on the 27.10 sigma-theta surface. The map shows high N* values in the North Atlantic subtropical gyre with a western intensified maximum, and isolated maxima on the eastern side of the basin at the Mediterranean outflow, and off of NW Africa in the Guinea Dome region. A sharp meridional gradient at 10°N separates the northern subtropical high values from lower values on the equator and in the South Atlantic. There is, however, some indication of weak local N* maxima extending westward from the coast of South Africa (between the equator and 20°S) and off the tip of South America (Brazil, between the equator and 10°S).

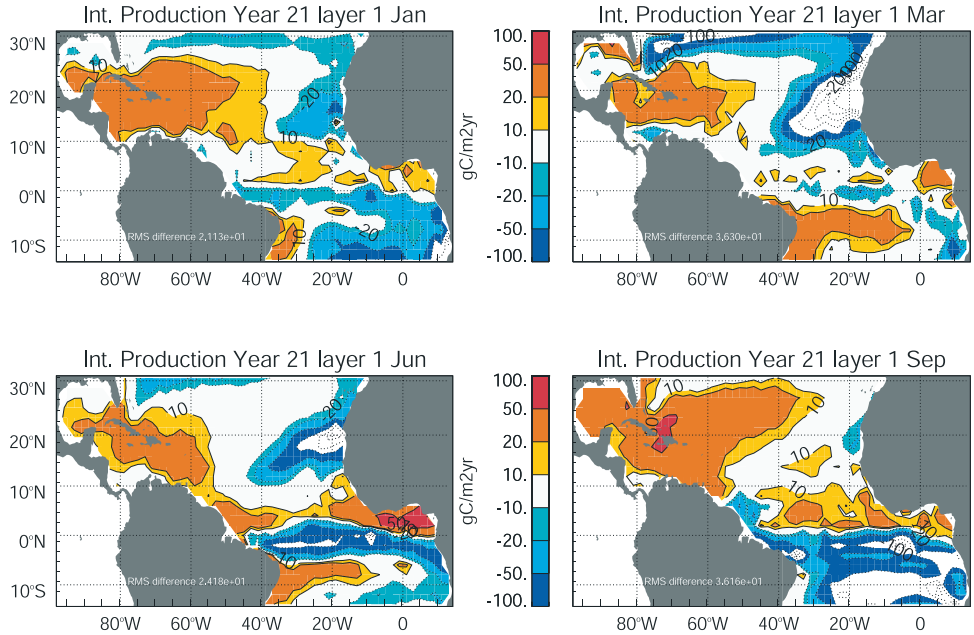

Figure 12. The point to point instantaneous difference between the integrated production in the NOTRICHO and HITRICHO runs (gC $m^{-2}yr^{-1}$). Positive values indicate more growth in the TRICHO run.

[48] The difference between the nitrate concentrations in the TRICHO and NOTRICHO model simulations (Figure 9b) is an indication of excess N resulting from nitrogen fixation, and should resemble the N* distributions in some respects. For this comparison, the simulations were run with no nitrogen relaxation on the northern boundary (which otherwise provides a large sink for excess nitrogen as though there was a region of denitrification in the North Atlantic). However, the boundary conditions for N* and the model N differences still differ, with the model having no sinks for N difference except at the southern boundary, and the data including coastal N* sinks as a result of sedimentary denitrification.

[49] The model patterns are similar to the observations; however, there is no western intensified maximum in the tropics. This is likely related to the absence of low N* water advecting southward along the eastern boundary in the model. The model and data both indicate a frontal region in the excess nitrogen signature along the eastern basin at 10°N; however, the model front dips too sharply southward in the eastern basin.

[50] In general the comparison with the N_* patterns suggests that the model overestimates rates of N_2 fixation in the eastern basin, particularly in the Gulf Guinea and waters to the south. In fact, *Gruber and Sarmiento* [1997] interpret the N* distributions as conservative southward from 10°N, assuming that only a northern source of N_2 fixation contributes to the western North Atlantic maximum. This interpretation, however, is not consistent with our model results, nor is it consistent with observations which show significant *Trichodesmium* populations in the Gulf of Guinea and the South Atlantic [e.g., *Dandonneau*, 1971; *Tyrrell et al.*, 2003]. Moreover, as discussed in the work of HCC, conditions appear to be ideal (in both the model and the observations) for *Trichodesmium* growth in the Gulf of Guinea. Some part of this discrepancy may be linked to the effect of shelf denitrification on the N* signal. Alternatively, it may be due to the paucity of nutrient data in these regions.

5. Nitrogen Fixation Tuned to Geochemical Rates

[51] In this final results section we describe our model run (HITRICHO) where the rate of N_2 fixation is increased to levels comparable to the geochemical rate estimates of *Gruber and Sarmiento* [1997]. As discussed above, we use essentially the same tuning procedure that we used to develop our NOTRICHO and TRICHO runs, i.e., we first lower the mortality rate of *Trichodesmium*, in this case to yield basin-wide N_2 fixation rates that are increased by nearly a factor of four, then we increase the sinking rate of detritus (export flux) to bring the phytoplankton concentrations into reasonable agreement with remote observations.

[52] The temporal and spatial variability of *Trichodesmium* concentrations in the HITRICHO run (Figure 10) remain qualitatively similar to the TRICHO run discussed above (see Figure 2 and HCC, Figure 6). Blooms centered in the Gulf of Mexico and the Caribbean still have their maxima in summer and fall; however, they extend over a larger area, and the concentrations are more than doubled (reaching 8.0 col l^{-1}). In the Caribbean and southern Sargasso significant colony concentrations extend all the way across the Atlantic to more than 30°W along 25°N in the HITRICHO run in the fall. In contrast, in the TRICHO run elevated *Trichodesmium* concentrations are more localized to the western Atlantic west of 60°W (see Figure 2 and also Figure 6 in HCC). In the NW African upwelling zone and the Guinea Dome region *Trichodesmium* concentrations are still highest in summer and fall in the HITRICHO run as before, but now they persist throughout the year and the

concentrations are about twice as high over most of the area (exceeding 10 col l^{-1}; compare HCC, Figures 6 and 10). Similar increases can be seen in the Gulf of Guinea, along the equator, and south of the equator in the austral summer and fall. Although the *Trichodesmium* concentrations in the HITRICHO run are distinctly elevated compared to our TRICHO run, they are not entirely inconsistent with the direct observations, except perhaps in the Caribbean and western Atlantic regions in Fall (compare HCC, Figures 5 and 10). In fact, HCC concluded that the TRICHO run has a general tendency to underestimate observed *Trichodesmium* concentrations. In particular, the *Trichodesmium* concentrations in the HITRICHO run appear to be in better agreement with observations off of the northeastern coast of South America, and in the winter months in the Caribbean, where the TRICHO run substantially underestimates observed concentrations (see discussion of HCC). The HITRICHO run also generates significant *Trichodesmium* concentrations between 20° and 30°N off of the coast of Africa as observed whereas the TRICHO run does not (see HCC).

[53] In general the differences in the phytoplankton biomass and production between the NOTRICHO and HITRICHO runs (Figures 11 and 12) are similar to the differences we see between the NOTRICHO and TRICHO runs (Figure 4 and Figure 6), i.e., increased concentrations and rates in the areas where N_2 fixation is increased and lower concentrations and rates in areas where N_2 fixation is absent. Note, however, that surface chlorophyll and primary production are increased over a broader area, especially in the eastern part of the oligotrophic subtropical gyre (east of 60°W), where the new nitrogen inputs from N_2 fixation in the HITRICHO run maintain phytoplankton concentrations of 0.1–0.15 mg Chl m^{-3} over most of the year. The regions where chlorophyll concentration and primary production are decreased are mainly in active upwelling areas (Figures 11 and 12). In these regions there is little or no N_2 fixation in the TRICHO run so there is no increase in new nitrogen inputs in the HITRICHO run, but export is increased due to the increased sinking flux. The result is a net loss of nitrogen in the upwelling regions which leads to lower biomass and primary production.

[54] In the HITRICHO run average annual primary production is still low relative to remote estimates in both the coastal upwelling regions (which are not adequately resolved) and in the interior oligotrophic ocean. Basin-wide integrated production has increased, however, from levels less than 10 gC $m^{-2}yr^{-1}$ in the NOTRICHO run to more than 20 gC $m^{-2}yr^{-1}$ in the HITRICHO run, with much of the increase coming from the oligotrophic subtropical gyre. This compares with levels of order 50–100 gC $m^{-2}yr^{-1}$ derived from remote estimates [*Behrenfeld and Falkowski*, 1997] and less than 1gC $m^{-2}yr^{-1}$ from the eddy permitting model of *Oschlies et al.* [2000]. These results suggest that the high N_2 fixation rates derived from the N* data can, indeed, support a significant fraction of the high levels of production in the open ocean that noneddy resolving numerical models with realistic stratification cannot. As discussed above, the N* data show patterns that are broadly consistent with both modeled and observed *Trichodesmium* distributions in the North Atlantic (i.e., maxima in the subtropical and tropical western Atlantic and off of NW Africa), but the implied rates are significantly higher than most direct N_2 fixation rate estimates.

[55] The HITRICHO run produces *Trichodesmium* concentrations that appear to be unrealistically high in some regions (i.e., the western Atlantic). However, *Trichodesmium* is not the only diazotroph in Atlantic waters. Moreover, observed colony concentrations may significantly underestimate the true *Trichodesmium* biomass due to the presence of free trichomes [*Orcutt et al.*, 2001] and the development of blooms that are not observed due to their patchiness in space and time. Given this and the fact that *Trichodesmium* concentrations generated by the HITRICHO run are not unrealistic in some places, we cannot rule out the possibility that the high geochemical N_2 fixation rates could be supported by *Trichodesmium* and other diazotrophic species.

6. Summary and Conclusions

[56] In this paper we examine how the inclusion of a dynamic representation of *Trichodesmium* and N_2 fixation in a coupled three-dimensional biogeochemical model impacts the pelagic ecosystem and nitrogen budgets in the tropical and subtropical Atlantic Ocean. A comparison of simulations with and without N_2 fixation shows that diazotrophs play a significant role in structuring the pelagic ecosystem. In general, input of new nitrogen via this pathway increases inorganic nitrogen concentrations, phytoplankton biomass, primary production and export flux. In the western Atlantic and Caribbean N_2 fixation rates are highest in summer and fall when the water column is stratified and phytoplankton are strongly nutrient limited. However, the impact of this new nitrogen on the rest of the ecosystem is manifested somewhat later, i.e., DIN concentrations, phytoplankton production and export are enhanced in fall and winter. We also see significant influences due to N_2 fixation off of Africa and in equatorial waters, but the timing and the magnitude of the effects varies. In general, N_2 fixation has a stronger impact on production and export in areas where upwelling is less important. According to the model, new nitrogen inputs from N_2 fixation have a particularly strong influence on the ecosystem in the Gulf of Guinea, though we have few measurements to confirm this.

[57] Because there are so few measurements of *Trichodesmium* biomass and nitrogen fixation rate, the effect of various assumptions in the biological and physical models are difficult to assess. One such assumption involves the use of climatological physical model forcing. High rates of nitrogen fixation in our model require prolonged periods of stratified surface conditions which allow *Trichodesmium* biomass accumulation. Using more realistic temporal and spatial forcing scales is likely to act to reduce the overall *Trichodesmium* biomass and the basin-wide nitrogen fixation rate estimates derived from the model. The biological model also involves a number of simplifications, including a simple linear death term that fails to represent the observed rapid disappearance of *Trichodesmium* blooms. The role of cyanophage viruses may be important to this process [*Hewson et al.*, 2004] for example, and is not represented in the model. These simplifications may lead to less patchy and more stable *Trichodesmium* populations in the model than in nature. In addition, the model does not

include other diazotrophs which may represent a significant fraction of the basin averaged nitrogen fixation [*Zehr et al.*, 2001; Capone et al., submitted manuscript, 2004]. Inclusion of these species would presumably raise the model-derived nitrogen fixation rate estimates which are derived by fitting the model to the observed *Trichodesmium* biomass in the northwestern Atlantic. Sinking is also represented very simply in the model with a constant sinking rate that is independent of particle size. However, it is not sensible to implement a more realistic sinking rate parameterization without including different size classes for the phytoplankton and heterotroph pools. We anticipate that the response to such an increase in complexity might be quite nonlinear, as sinking flux would tend to be temporally and spatially inhomogeneous, linked perhaps to upwelling regions, and the spring bloom as well as the Amazon plume area. Finally, we are actively investigating the role of phosphorus and iron in determining the distribution of diazotrophs in the ocean. In two related papers [*Hood et al.*, 2004; *Coles et al.*, 2004] we argue that these factors are not required to simulate the distribution of *Trichodesmium* biomass in the Atlantic. However, P and Fe may play a role in constraining the maximum basin-wide nitrogen fixation rate.

[58] The basin-wide N_2 fixation rate generated by our model run that was tuned to observed *Trichodesmium* biomass generally agrees with rate estimates derived from direct measurements, i.e., it fixes 1.47×10^{12} mole N yr^{-1}. This rate is significantly lower than recent geochemical (N*-based) estimates. Regionally, the Caribbean/southern Sargasso Sea and equatorial waters contribute 56% of the total N_2 fixation, with significant, but lesser contributions from the Gulf of Mexico, the Gulf of Guinea and the Guinea Dome/NW Africa regions. On basin-wide scales, N_2 fixation translates directly into increased nitrogen flux into the deep ocean which is the same magnitude as the input. However, regionally new nitrogen inputs from N_2 fixation are not generally balanced by increased export due to advective effects.

[59] When the model is tuned to reproduce observed *Trichodesmium* concentrations, the resulting N_2 fixation increases total phytoplankton production by 5% and new production by 30%. However, the increase in primary production is not enough to bring the model-generated rates into line with observed rates [e.g., *Behrenfeld and Falkowski*, 1997]. Reasonable phytoplankton concentrations can be maintained when the model is tuned to reproduce the high N_2 fixation rate estimates derived from N^* measurements [*Gruber and Sarmiento*, 1997]. With this additional input of new nitrogen, primary production in the model approaches the observed levels [e.g., *Behrenfeld and Falkowski*, 1997]. In order to achieve these high N_2 fixation rates *Trichodesmium* concentrations have to be increased to unrealistically high levels in some regions, but in other places the agreement between the modeled and observed *Trichodesmium* concentrations is improved. The increased *Trichodesmium* biomass required to achieve the high geochemical N_2 fixation rates may be also viewed as a proxy for other presently unquantified diazotrophic species.

[60] The differences between our simulations with and without a dynamic representation of N_2 fixation indicate that the role of diazotrophs cannot be parameterized as a simple enhancement of nutrient flux from the deep ocean or with a uniform surface addition of new nitrogen. The N_2 fixation has complicated spatial and temporal variability which influences nitrogen concentrations, phytoplankton production and export in a nonlinear way. Moreover, because *Trichodesmium* biomass must be consumed and cycled through the ecosystem before the fixed nitrogen is exported, it introduces significant time lags between input and export of new nitrogen from N_2 fixation. As a result, the fixation and export of the new nitrogen usually occurs at very different times and places, and the export often occurs in association with phytoplankton rather than *Trichodesmium* blooms. If open ocean N_2 fixation is as significant as recent direct and geochemical estimates suggest, then our model results suggest it may not be possible to accurately model phytoplankton production and export without a dynamic representation of N_2 fixation.

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