Remote sensing of new production fuelled by nitrogen fixation

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[1] Climatological satellite observations in the tropical North Atlantic generally show a wintertime surface chlorophyll-a (Chl-a) maximum except over a broad region in the western North Atlantic that has a summer Chl-a maximum. This region also shows decoupling between Chl-a and vertical nutrient flux, based on the positive relationship between sea surface height anomaly (SSH), sea surface temperature, and Chl-a. An analogous summer Chl-a maximum is simulated in a model including a dynamic representation of *Trichodesmium* and N_2-fixation, but not in runs without. These results suggest that the growth is fuelled by N_2-fixation. Using the observed summertime increase in Chl-a and the model efficiency for N_2-fixation transfer to phytoplankton biomass, we calculate a nitrogen fixation rate of 220 μmol N $m^{-2}day^{-1}$ in this region. This constitutes the first satellite observation of the effect of nitrogen fixation on Chl-a, and may ultimately provide a means of deriving new global N_2-fixation estimates. INDEX TERMS: 4275 Oceanography: General: Remote sensing and electromagnetic processes (0689); 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 4842 Oceanography: Biological and Chemical: Modeling; 4845 Oceanography: Biological and Chemical: Nutrients and nutrient cycling. **Citation:** Coles, V. J., C. Wilson, and R. R. Hood (2004), Remote sensing of new production fuelled by nitrogen fixation, *Geophys. Res. Lett.*, *31*, L06301, doi:10.1029/2003GL019018.

1. Introduction

[2] Diazotrophic cyanobacteria, such as *Trichodesmium*, may provide as much as (20–40 Tg N/y) [*Gruber and Sarmiento*, 1997; *Michaels et al.*, 1996] of atmospheric nitrogen to the ocean, which may be comparable locally to the vertical flux of nitrate [*Capone et al.*, 1997; *Karl et al.*, 1997]. Unlike the vertical nitrate flux, N_2-fixation is independent of dissolved carbon fluxes from the deep ocean and so can potentially drive a net uptake of CO_2 and export of carbon [*Hood et al.*, 2000]. However, global rate estimates are hindered by few available observations, and efforts to detect *Trichodesmium* globally using satellites have not yet succeeded [*Subramanium et al.*, 2002]. In principle, N_2-fixation driven phytoplankton growth could be distinguished from production due to vertical nitrate fluxes because diazotrophs generally grow at the surface in warm, stratified waters [*Capone et al.*, 1997] that preclude vertical mixing of nitrogen. Here, using climatological satellite

datasets, we demonstrate a summer phytoplankton maximum apparently driven by N_2-fixation. The bloom occurs under stratified conditions in the western tropical North Atlantic when sea surface height anomaly (SSH) is elevated, suggesting that the nutricline is deep. Model simulations with *Trichodesmium* reveal an analogous phytoplankton maximum that is absent in runs without N_2-fixation. These results indicate that it may be possible to detect global patterns of N_2-fixation from their influence on phytoplankton biomass.

[3] This study was motivated by the unexpected relationship between satellite surface chlorophyll-a (Chl-a), and SSH in the tropical Atlantic (Figure 1a). In general, Chl-a and phytoplankton biomass are negatively correlated with SSH [*Wilson and Adamec*, 2002]. When SSH is high, the thermocline is deep [*Siegel et al.*, 1999], implying stratified, nutrient-poor surface conditions. As the thermocline shoals and SSH falls, nutrient-rich water is brought nearer the euphotic zone. In regions where phytoplankton are macronutrient limited (much of the subtropical and tropical oceans) [*Tyrrell*, 1999], Chl-a is anti-correlated with SSH because SSH variations reflect this nutrient supply to the euphotic zone. However, in the tropical Atlantic between 5°N and 25°N there are regions of positively correlated SSH and Chl-a that are not understood (Figure 1a).

[4] To investigate this relationship, we construct monthly satellite climatologies from SeaWiFS (Sea-viewing Wide Field-of-view Sensor) ocean color data and SSH (measured by the TOPEX/Poseidon altimeter). We used empirical orthogonal function (EOF) analysis [*Preisendorfer*, 1988] to isolate the largest spatial and temporal trends in the Chl-a fields. Each mode is made up of a spatial and temporal component, which describes the evolution of the spatial pattern with time. The first mode (Figure 1b) reflects aspects of the large-scale annual cycle of Chl-a. In the western tropical North Atlantic where SSH and Chl-a are positively correlated, the Chl-a maximum occurs in July when the water column is most stratified. Over the rest of the basin, the maximum is in January–February when vertical mixing supplies nutrients to the upper ocean.

[5] We similarly analyze results from a climatologically forced, biological-physical model [*Coles et al.*, 2004; *Hood et al.*, 2004]. The primitive equation Miami Isopycnal Coordinate Ocean Model is coupled to a biological model [*Hood et al.*, 2001] with representation of phytoplankton, heterotrophs, nitrate, dissolved organic nitrogen, detritus, and *Trichodesmium*. Iron and phosphorus constraints are not included. We compare simulations with *Trichodesmium* (TRICHO) to simulations without *Trichodesmium* (NOTRICHO) [*Coles et al.*, 2004].

[6] The leading modes for the NOTRICHO and TRICHO runs are shown in Figures 1c and 1d. An important discrepancy between the simulations arises in the western tropical North Atlantic, where a summer Chl-a maximum occurs in

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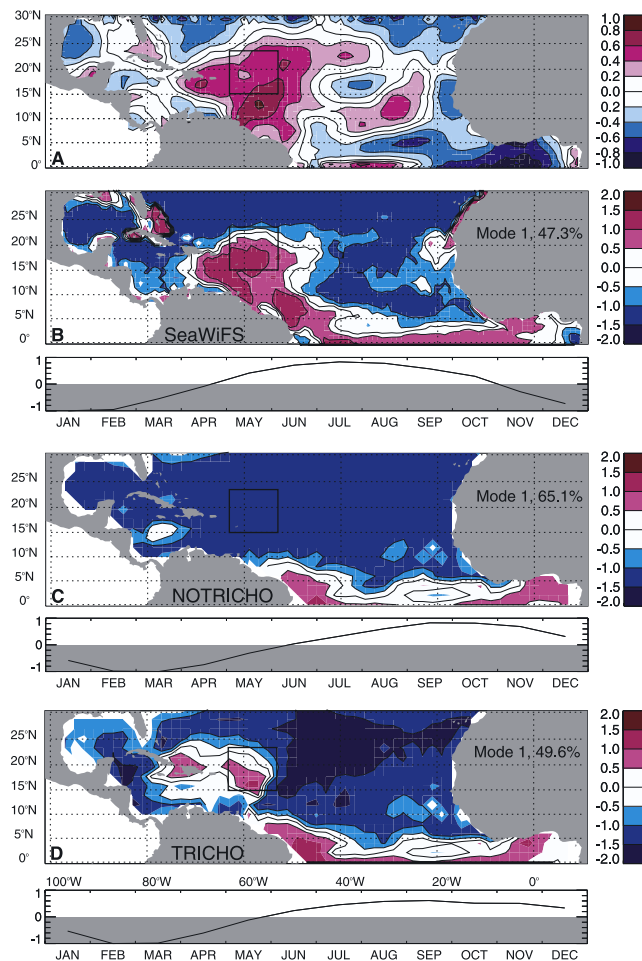
Figure 1. Chl-a and SSH correlation, and Chl-a first EOF modes. (a) Correlation between satellite SSH and Chl-a. (b) First EOF mode for the satellite Chl-a. (c) First EOF mode from the NOTRICHO run, (d) First EOF mode from the TRICHO run. Maps 1b–1d show the spatial pattern of Chl-a variance. The time-series below each panel gives the evolution over the annual cycle. Multiplying the time-series by the spatial distribution gives the magnitude of the normalized Chl-a variance at a given time. Boxes indicate the region over which data are averaged in Figure 3.

the TRICHO simulation but not in the NOTRICHO run. The maximum corresponds to the area in Figure 1a where observed SSH and Chl-a are positively correlated, suggesting low vertical nitrate flux. In the satellite data and the TRICHO run, maximum Chl-a occurs in late summer (July–September) (Figures 1b and 1d). In the NOTRICHO run, this signal is absent, and the Chl-a maximum is in winter. Given the indications of deep nutricline and stratified watercolumn, we suggest that the mechanism fuelling the climatological summer phytoplankton maximum observed in the western tropical North Atlantic is nitrogen fixation by diazotrophs. The Chl-a maximum occurs under conditions that favor *Trichodesmium* growth [*Capone et al.*, 1997], which ultimately drives production (and increased phytoplankton biomass) as bio-available nitrogen cycles through the ecosystem. *Trichodesmium* occurs in the western tropical North Atlantic, and observations from this area [*Carpenter and*

Romans, 1991] are used to tune the model nitrogen fixation rate [*Hood et al.*, 2004; *Coles et al.*, 2004]. Furthermore, indirect geochemical estimates of N_2-fixation show maxima in the western North Atlantic [*Gruber and Sarmiento*, 1997; *Lee et al.*, 2002]. Thus we expect this region to support "echo" phytoplankton blooms, but they have not been observed outside the Gulf of Mexico [*Walsh and Steidinger*, 2001].

[7] To show the temporal evolution of the biology and physics, time-series of Chl-a, SST and SSH for the winter and summer bloom regimes in the North Atlantic are shown in Figures 2 and 3. In Figure 2, the Chl-a maximum occurs in late winter when the mixed layer reaches its maximum depth, cooling SST, decreasing SSH, and injecting nutrients into the euphotic zone. This is the classic "winter bloom" observed in subtropical waters [*Campbell and Aarup*, 1992]. The observations (Figure 2a), and both model runs (Figure 2b), show similar patterns for this winter bloom although the details differ.

[8] In contrast, the western tropical North Atlantic (Figure 3a) observations show a very different pattern. Here, the Chl-a maximum occurs in late summer after a period of stratification with shallow mixed layer and elevated SST and SSH. This growth is fuelled in the model by nitrogen recycled from *Trichodesmium* production. There is also a weak winter (January) bloom in the observations and model (stronger in the model), when the mixed layer deepens.

[9] Although the observations and TRICHO run both have a late summer phytoplankton bloom that is not captured in the model without N_2-fixation, there could be other explanations for a bloom in summertime stratified conditions. This region is influenced by a number of physical factors that could stimulate phytoplankton growth including African dust deposition, the Amazon and Orinoco river plumes, and North Brazil Current eddies.
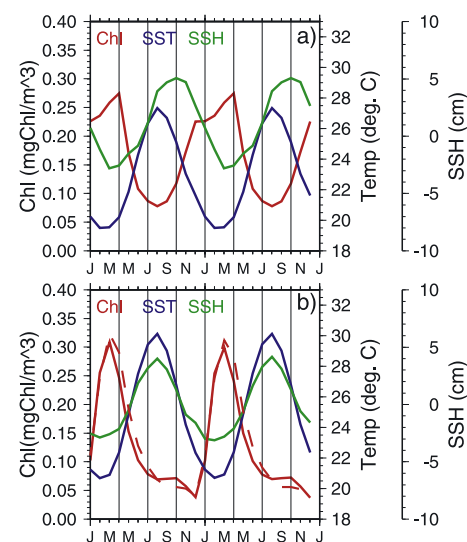
Figure 2. Evolution of Chl-a, SST, and SSH. Properties averaged spatially over the following regions: (a) Satellite data from the region of 34–35°N, 63–53°W. (b) Model mixed layer fields from 25–30°N, 63–53°W. The averaging regions are chosen to illustrate a winter bloom scenario. The solid red line is Chl-a from the TRICHO run, the dashed line is from the NOTRICHO run.
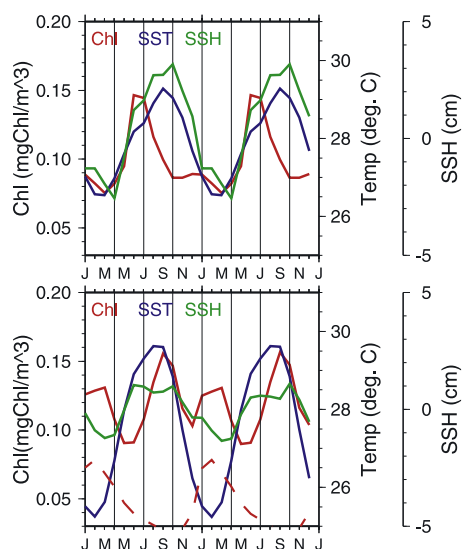
Figure 3. Evolution of Chl-a, SST, and SSH. Properties averaged spatially over 15−23°N, 63−53°W (a) Satellite data. (b) Model mixed layer fields. The solid red line is Chl-a from the TRICHO run, the red dashed line is Chl-a from the NOTRICHO run.

[10] African dust and aerosol deposition tend to be maximum during summer [*Cakmur et al.*, 2001], coincident with the Chl-a maximum. However, the greatest dust concentrations occur in the eastern Atlantic. Dust and aerosols are known to influence satellite chlorophyll retrievals [*Stegmann and Tindale*, 1999] and act as a nutrient source, however these influences should be manifest primarily in the eastern Atlantic which is inconsistent with the western tropical Atlantic pattern reported here. Furthermore, adding Fe via dust deposition would not stimulate phytoplankton growth directly because they occur in an area that is stratified and nutrient depleted [*Sañudo-Wilhelmy et al.*, 2001]. Dust deposition could however enhance nitrogen fixation if diazotrophs are Fe limited in these waters [*Walsh and Steidinger*, 2001]. Dust is not included in either of the model simulations.

[11] The Amazon plume has a seasonal cycle with maximum flood occurring in April−July, and northward transport in February−May acting as a freshwater source to the western tropical North Atlantic [*Müller-Karger et al.*, 1995]. The Orinoco has a similar cycle, but effects dominate within the Caribbean [e.g., *Bidigare et al.*, 1993]. Salinity studies indicate the northward limit of the freshwater

influence at 15°N [*Pallier et al.*, 1999], well south of the northern edge of the signal observed here. If nutrient addition from the Amazon plume enhances the southern edge of the phytoplankton maximum, we would expect to see a connection between the outflow and this area. This is seen with the satellite data (Figures 1a and 1b), but not in the model (Figures 1c and 1d). The model does not include nutrient sources with the Amazon freshwater input, which may explain why the simulated Chl-a maximum does not extend as far south. Recent observations in this area highlight the role that recycling in the shallow plume mixed layer plays in maintaining high surface phytoplankton biomass [*Corredor et al.*, 2003]. Our results have a spatial pattern that is not limited to the frontal region, and so are not necessarily in conflict with this result.

[12] As the North Brazil Current retroflection intensifies in summer, eddies shed and propagate northwest toward the Caribbean. Some eddies advect into the Caribbean, while others pass northward outside the islands [*Goni and Johns*, 2001]. These eddies may be a significant interocean exchange mechanism, however they are anti-cyclonic (downwelling) eddies, so they do not represent a significant nutrient source.

[13] If the summer biomass peak arises from nutrient input by diazotrophs, then we can use the observed summertime increase in Chl-a with modelled rates to estimate an observed nitrogen fixation rate. We calculate the rate of phytoplankton biomass change at 11 μmol N m^{-2}day^{-1} (from Figure 3a, using a carbon:Chl-a ratio of 50, Redfield stoichiometry and a 20 m mixed layer depth). This net change in biomass is probably only a small fraction of the production that results from N$_2$-fixation. The observed "bloom" (Figures 1 and 3) builds up over a period of 90 days. This slow evolution indicates that the ecosystem is close to steady state over the buildup, with losses only slightly lower than production.

[14] We use the model to estimate the nitrogen fixation rate that would result in a biomass change of the magnitude observed. The rate of phytoplankton biomass change in the model (Figure 3b) is 9.7 μmol N m^{-2}day^{-1}. We know however, that the model nitrogen fixation rate that gives rise to this signal averaged over the same area and over the euphotic zone is 192 μmol N m^{-2}day^{-1}, which is comparable to observed rates in this area (Table 1). In the model, the rate of enhancement of phytoplankton biomass is therefore 5% of the nitrogen fixation rate, which implies a rather low efficiency for conversion of di-nitrogen gas into accumulated phytoplankton biomass. Using the model effi-

Table 1. Nitrogen Fixation Rates From Various Sources and Methods

Method for estimating nitrogen fixation rate	Nitrogen fixation rate(μmol N m^{-2}day^{-1})
Shipboard estimates[a]	53−898, 288 avg.
Other observed estimates[b]	41−108
Indirect geochemical estimate[c]	197−268
Satellite estimate of the summer bloom[d]	220
Model[e]	192

[a]From *Capone et al.* Nitrogen fixation by *Trichodesmium* spp.: An important source of new nitrogen to the tropical North Atlantic Ocean, *Science*, submitted [2004], range computed as the minimum-maximum from their Table 1 and their average.

[b]Rates from *Goering et al.* [1966] recalculated by *Capone et al.* Nitrogen fixation by *Trichodesmium* spp.: An important source of new nitrogen to the tropical North Atlantic Ocean, *Science*, submitted [2004].

[c]Rate obtained from basinwide geochemical estimates of the imbalance between nitrate and phosphate at depth [*Gruber and Sarmiento*, 1997], using their Figure 18 and N:P stoichiometries of 125:1 and 50:1.

[d]Calculated based on change in Chl-a (Figure 3a, see text).

[e]Direct calculation of model rate.

ciency, the nitrogen fixation rate estimate calculated from satellite biomass change is 220 μmol N m^{-2}day^{-1} for this region in summer. Table 1 lists rates calculated using other methods, which bracket this estimate.

[15] Satellite observations of Chl-a in the western tropical North Atlantic, coupled with the model results, suggest that nitrogen fixation drives an increase in phytoplankton biomass, or an "echo bloom". This in turn provides an explanation for the positive relationship between SSH and Chl-a in the satellite-derived fields. The nitrogen fixation rate associated with this bloom is estimated from remote sensing biomass change and a model derived efficiency estimate, and is consistent with the rate estimates from in situ measurements (Table 1).

[16] The approach that we have used here—of combining multiple satellite data sets with or without model simulations—may provide a means for estimating patterns of nitrogen fixation, as well as its impact on phytoplankton biomass and ultimately carbon sequestration, on global scales. This work provides a new observational basis for evaluating the global significance of nitrogen fixation to new production and the carbon cycle. If diazotrophs have the potential to shift the ocean from nitrogen to phosphorus limitation [*Karl et al.*, 1997] and alter global climate through changes in the biological pump [*Michaels et al.*, 2001; *Sañudo-Wilhelmy et al.*, 2001], then improving our understanding of their spatial and temporal patterns and production is essential.

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