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Prochlorococcus contributes to new production in the Sargasso Sea deep chlorophyll maximum

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[1] *Prochlorococcus* is ubiquitous in tropical oceans, but its biogeochemical role is not well constrained. For example, cultured *Prochlorococcus* clones do not grow on NO_3^-, but these cultured clones may only represent 10–15% of the natural population variance resulting in a biased biogeochemical role. We report NO_3^-, NO_2^-, NH_4^+ and urea uptake rates for flow-cytometrically sorted Sargasso Sea *Prochlorococcus* populations. Reduced nitrogen substrates accounted for most, 90–95%, of the measured nitrogen uptake, but these populations also directly assimilate a significant fraction of NO_3^-, 5–10%; a finding in stark contrast to conclusions drawn from culture studies. The observed population-specific NO_3^- uptake rates compare favorably with both net *Prochlorococcus* population growth rates and diapycnal NO_3^- fluxes. We hypothesize that while reduced nitrogen supports overall high growth rates, balancing high grazing mortality, the net seasonal *Prochlorococcus* population growth is supported by NO_3^- assimilation and that *Prochlorococcus* contributes to new production in the oligotrophic ocean. **Citation:** Casey, J. R., M. W. Lomas, J. Mandecki, and D. E. Walker (2007), *Prochlorococcus* contributes to new production in the Sargasso Sea deep chlorophyll maximum, *Geophys. Res. Lett.*, *34*, L10604, doi:10.1029/2006GL028725.

1. Introduction

[2] The cyanobacterium *Prochlorococcus* is ubiquitous in oligotrophic subtropical and tropical oceans, where it can account for a significant fraction of primary production [*Partensky et al.*, 1999]. Since the first description of *Prochlorococcus*, a considerable research effort has been directed at this organism. This work has included assessments of its distribution, abundance, in-situ growth rates and primary production [e.g., *Agusti*, 2004; *Johnson et al.*, 2006]; experimental investigations of the influence of temperature, light, nutrients and trace metals on the its growth and physiology in culture and in the field [e.g., *Mann and Chisholm*, 2000; *Moore et al.*, 2002]; and molecular studies focusing on its genome and genetic diversity [e.g., *Rocap et al.*, 2003; *Zinser et al.*, 2006].

[3] Despite the global importance of *Prochlorococcus* there have been few direct studies on the nutritional ecology of natural populations [e.g., *Li*, 1994; *Zubkov et al.*, 2003]. This is especially relevant for nitrogen and phosphorus given conclusions drawn from culture and molecular studies [*Moore et al.*, 2002, 2005] and the importance of these elements as nutrients limiting oceanic primary production. In this study we quantify NO_3^-, NO_2^-, NH_4^+ and urea uptake rates in natural populations of *Prochlorococcus* collected from the Sargasso Sea DCM. We pay particular attention to the observed NO_3^- uptake as it is related to new production (sensu *Dugdale* [1967], *Dugdale and Goering* [1967]), and in contrast to conclusions drawn from culture studies.

2. Nitrogen and *Prochlorococcus* Growth in the Sargasso Sea

[4] Culture studies have shown that all ecotypes of *Prochlorococcus* grow well on NH_4^+ enriched media while only low-light ecotypes grow on NO_2^-. No currently cultured ecotypes have displayed growth in NO_3^- enriched media, and for one low-light strain, SS120, this inability to grow on NO_3^- has been confirmed by the absence of a recognizable *narB* gene [*Dufresne et al.*, 2003].

[5] Despite these growth observations in culture, maxima in *Prochlorococcus* cell densities are frequently observed coincident with the nitracline [*Partensky et al.*, 1999] (Figures 1a and 1b). Moreover, *Prochlorococcus* displays a net seasonal population growth at the nitracline in the Sargasso Sea (Figure 1c). This poses an interesting paradox: *Prochlorococcus* is associated with the presence of the most abundant nitrogen source, but is unable to assimilate it for growth; at least based upon culture studies. Recent molecular studies may shed some light on this paradox. 'Cocktails' of *Prochlorococcus* qPCR probes have been employed in the northwestern Sargasso Sea to determine depth distributions of the two genetically diverse 'light-dependent' ecotypes [*Ahlgren et al.*, 2005; *Zinser et al.*, 2006]. Zinser *et al.*, further show that below ~75 m the sum of six qPCR probes can only account for ~10–15% of the total *Prochlorococcus* population, suggesting that there may be significant ecotype(s) of *Prochlorococcus* yet to be identified that may have different abilities to assimilate oxidized nitrogen substrates. For this study we hypothesized that this (these) unidentified ecotype(s) is (are) physiologically different from those *Prochlorococcus* strains currently in culture and that NO_3^- assimilation contributes to their overall nitrogen nutrition.

3. Results and Discussion

[6] We optimized a method combining flow cytometric sorting and stable isotope tracer protocols (FLOW-SIP) for use in the oligotrophic Sargasso Sea (see auxiliary material

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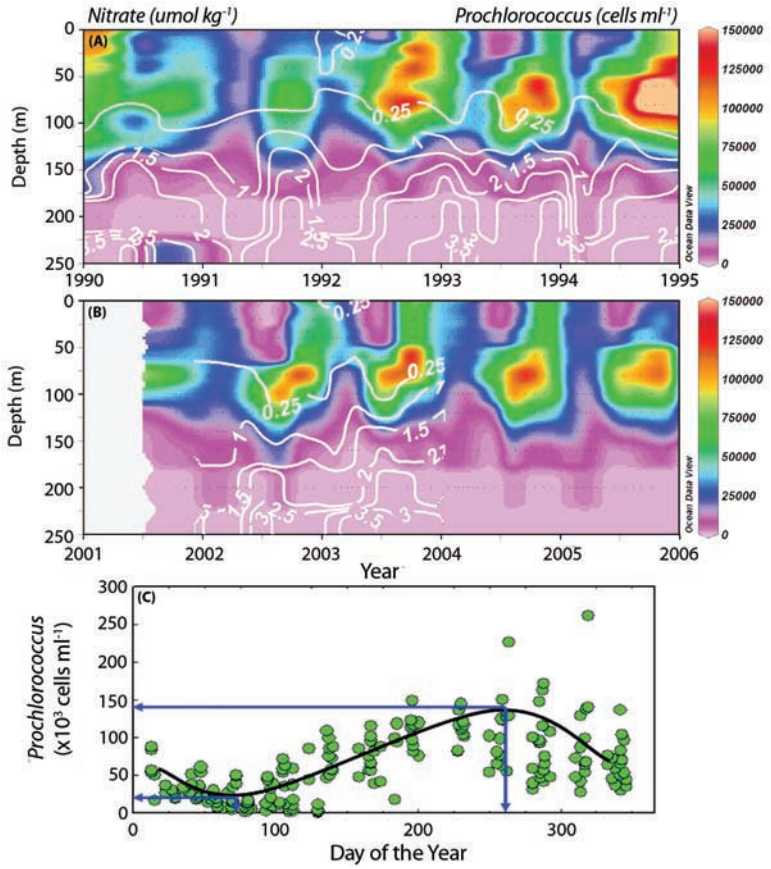

Figure 1. Time-series of *Prochlorococcus* cell density profiles in the Sargasso Sea at the Bermuda Atlantic Time-series Study (BATS) station. (a) Five year time-series contour plot from 1990 through 1994 highlighting seasonal and depth dependent patterns in *Prochlorococcus* cell densities. Overlain are NO_3^- contours as white lines, and each year is marked from January 1. (b) Same as in Figure 1a but for 2001 through 2005. Note that NO_3^- data are currently only available through 2003. (c) All data from Figures 1a and 1b at the depth closest to the DCM on each cruise plotted against day of the year. Displayed is the 'average' seasonal increase for all years that we have data. The heavy black line is an approximate fit to the seasonal cycle. The blue arrows mark the points used in calculating the seasonal net population growth presented in Table 2. Raw data for Figure 1a were kindly provided by M. Durand, R. Olson, and S. Chisholm.

Text S1 for further details).[1] The benefit of FLOW-SIP is that it permits the incubation of complete pelagic communities, allowing the determination of taxon-specific nutrient assimilation rates and thereby directly quantifies the biogeochemical ecology of the target population [*Li*, 1994; *Zubkov et al.*, 2003]. Moreover, the accuracy of measured assimilation rates for stable isotopes is significantly enhanced by the exclusion of bacterial populations and detrital nitrogen [*Lipschultz*, 1995]. We employed this technique to study nitrogen assimilation in natural *Prochlorococcus* assemblages collected from the Sargasso Sea deep chlorophyll maximum (Table 1).

[7] Oligotrophic ocean gyres are generally characterized as regenerative systems fueled by the uptake and recycling of NH_4^+ and labile organic molecules. The observed pattern in nitrogen uptake rates is consistent with this general expectation in that reduced nitrogen substrates accounted for the majority, 90–95%, of the total measured nitrogen uptake (Figure 2a). In addition, prior research has suggested that amino acid uptake also can contribute substantially to *Prochlorococcus* nutrition in natural populations [*Zubkov et al.*, 2003]. We are aware of only three other studies that have measured both NH_4^+ and urea uptake rates in the Sargasso Sea, albeit in complete assemblages [*Glibert et al.*, 1988; *Lipschultz*, 2001; *Price and Harrison*, 1988]. In contrast to the data presented here (Figure 2a), bulk urea uptake in those prior studies ranged from 30–50% of NH_4^+ rates. In all of those studies, the error bars for urea uptake are large, and although no strong conclusions can be made, our data suggest that *Prochlorococcus* may favor assimilation of labile organic molecules [*Zubkov et al.*, 2003].

[8] From the specific uptake rates measured in this study physiological growth rates can be estimated (see auxiliary material for additional details), assuming that 'instantaneous' nitrogen assimilation rates are coupled to growth rates. Moreover, these estimates of growth rate will be conservative estimates as not all nitrogen substrates that might be assimilated were measured. With these caveats, physiological growth rates are estimated to be 0.42 ± 0.17 d^{-1}; in good agreement with other growth rate estimates from natural populations (Table 2) and data from culture studies under comparable light and temperature

[1] Auxiliary materials are available in the HTML. doi:10.1029/2006GL028725.

Table 1. Sampling Station, NO_3^- Concentrations, and *Prochlorococcus* Cell Densities During Fall 2005 Sampling Efforts

Date	Site	Depth of DCM,[a] m	NO_3^-,[b] nmol L^{-1}	Cell Density,[b] 10^3cells mL^{-1}
8/31/2005	Hydrostation S	95	91.9 ± 20.7	5.6 ± 0.2
9/11/2005	Hydrostation S	85	210.0 ± 20.8	29.0 ± 2.4
9/19/2005	Hydrostation S	104	203.4 ± 29.8	21.3 ± 1.5
9/20/2005	Hydrostation S	95	162.1 ± 13.0	21.3 ± 1.5
9/21/2005	Hydrostation S	85	32.1 ± 21.2	21.3 ± 1.5
10/13/2005	Hydrostation S	105	98.1 ± 11.4	36.9 ± 2.5
11/24/2005	Hydrostation S	95‘	32.1 ± 2.9	47.6 ± 2.4
11/23/2005	BATS Spatial Station 1	98,102[c]	33.3 ± 3.6	44.9 ± 3.0
11/25/2005	BATS Spatial Station 13	104	32.2 ± 12.7	44.9 ± 3.0

[a]DCM, deep chlorophyll maximum.
[b]NO_3^- concentrations and cell densities are mean values of triplicate determinations ± s.d.
[c]GoFlo bottles were fired 4 m apart for DCM cast at BATS Spatial Station 1.

conditions [*Moore et al.*, 1995]. Moreover, these growth rate estimates are on par with grazing loss estimates from dilution experiments (Table 2). These growth rate estimates, coupled with the observation that 90–95% of the total N assimilated is from NH_4^+ and urea, suggest that natural *Prochlorococcus* populations in the Sargasso Sea are using primarily reduced nitrogen substrates to support the high gross growth rates needed to balance high grazing mortality.

[9] Although reduced nitrogen substrates accounted for the majority of the measured nitrogen uptake, these deep

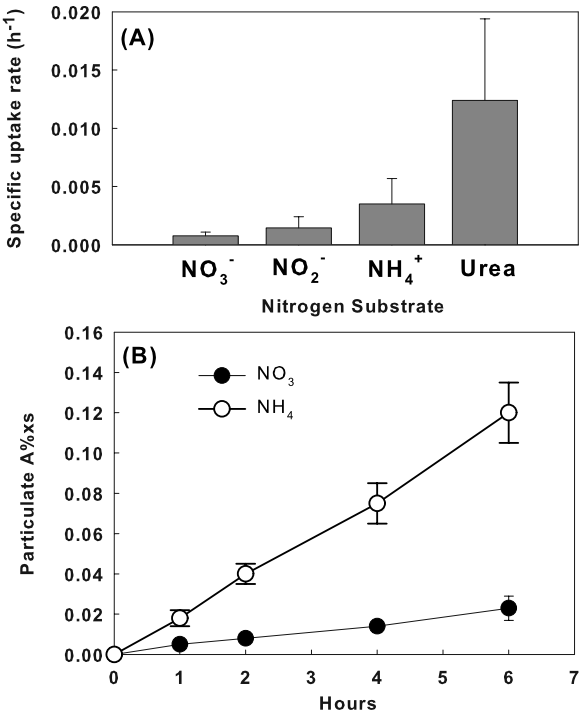

Figure 2. Nitrogen uptake by natural *Prochlorococcus* populations collected from the Sargasso Sea DCM. (a) *Prochlorococcus* uptake rates (± s.d.) for the four nitrogen substrates averaged over the entire study period. The number of independent samples in each average is - NO_3^- (13), NO_2^- (9), NH_4^+ (10), and urea (6). (b) Time course experiment, conducted 8/31/2005, for the uptake of NO_3^- and NH_4^+ by DCM *Prochlorococcus* populations. The Y-axis represents the atom percent ^{15}N excess (relative to air) in the particulate fraction. Each data point is the average (± s.d.) of triplicate samples.

populations of *Prochlorococcus* do assimilate a significant fraction of NO_3^-, ~5–10% of the total (Figure 2a). Indeed, a time course experiment of nitrogen uptake showed there was no time lag for NO_3^- uptake (Figure 2b) suggesting that there is no ‘trophic processing’ of $^{15}NO_3^-$ that would make the labeled N available for assimilation through a reduced N pathway [*Lopez-Lozano et al.*, 2002]; an important observation for relating NO_3^- uptake to new production. This observation of NO_3^- uptake is in direct contrast to conclusions drawn from cultured isolates, and has the potential to drastically alter the biogeochemical role of *Prochlorococcus* in the oceans. The canonical ratio of new (estimated from NO_3^- uptake) to total (sum of all nitrogen uptake) production for oligotrophic systems is ~10% [*Eppley and Peterson*, 1979]. This ratio represents the average for all autotrophs, and our data suggests that *Prochlorococcus* may not be different from the ‘average’ autotroph in its ability to contribute to oceanic new production; i.e., 5–10% of its measured N uptake was NO_3^-. Below we discuss additional evidence in support of *Prochlorococcus*’ contribution to new production in the Sargasso Sea DCM.

Table 2. Estimated *Prochlorococcus* Growth Rates and Nitrogen Demand for Populations Collected in the Sargasso Sea, Including Data From This Study and the Literature[a]

Method	Rate
Total Nitrogen Uptake growth rate, d^{-1}	0.42 ± 0.17[b]
Growth rate by cell-cycle analysis, d^{-1}	0.60 ± 0.10[c]
Growth rate by dilution experiment, d^{-1}	0.23 ± 0.03[d]
	0.53 ± 0.08[c]
Nitrate-specific growth rate, d^{-1}	0.01 ± 0.004[e]
Net population growth rate, d^{-1}	~0.011[f]
Estimated Nitrate influx, μmol m^{-3} d^{-1}	146 (2 – 890)[g]
Estimate Nitrate demand, μmol m^{-3} d^{-1}	126 ± 48[h]

[a]Values are the means and std errors of all measurements available, unless otherwise noted.
[b]This study, see auxiliary material for calculation details.
[c]*Worden and Binder* [2003]; samples collected from 50 m (~8% light level) and all data from southern and northern Sargasso Sea stations are combined.
[d]*Kuipers and Witte* [2000]; samples collected from ~100 m along a transect from 10° to 35°N, all data are combined.
[e]Growth rate estimated from NO_3^- uptake, see auxiliary material for calculation details.
[f]Estimated from the points denoted by the blue arrows in Figure 1c.
[g]*Lewis et al.* [1986] 95% confidence limits in parentheses.
[h]Estimated from NO_3^- uptake and cell numbers, see auxiliary material for calculation details.

[10] Despite the tight coupling between physiological growth rates and grazing losses [*Agawin and Agusti*, 2005; *Worden and Binder*, 2003], the *Prochlorococcus* DCM population in the Sargasso Sea displays a roughly five-fold seasonal increase (Figure 1c) during a time when convective nutrient inputs are at their annual minimum. This net population increase is estimated to be $\sim$0.011 d^{-1} (Figure 1c; Table 2); a very slow rate, but ecologically important. Our NO_3^- uptake data suggests a daily growth rate attributable to NO_3^- alone ranging from 0.01 to 0.018 d^{-1} (Table 2; see auxiliary material for further calculation details). The fact that these estimates agree is very encouraging, especially given that our sampling was conducted at the end of the growing season, and additional sampling during the summer might have found higher NO_3^- uptake rates. Although it does not appear that bacteria are 'processing' the added $^{15}NO_3^-$ label prior to assimilation by *Prochlorococcus* (Figure 2b), bacterial contamination in sorted samples needs to be evaluated as bacteria are known to assimilate NO_3^- [*Kirchman*, 2000]. To have the greatest confidence in the data from sorted populations a very strict sorting procedure was employed (see auxiliary material for further details), and there was negligible heterotrophic bacterial contamination (<2%) in the sorted sample due in large part to the unmistakable 'fingerprint' of *Prochlorococcus* at this depth.

[11] Beyond the importance of mesoscale eddies for nutrient fluxes in the Sargasso Sea, we also need to consider the diapycnal flux of NO_3^- at the base of the euphotic zone. *Lewis et al.* [1986] quantified vertical NO_3^- flux rates at 146 μmol NO_3^- m^{-3} d^{-1} (95% confidence interval, 2 to 890 μmol NO_3^- m^{-3} d^{-1}) assuming this flux goes into a 1 m nutristad at the base of the euphotic zone. The estimated demand for NO_3^- by *Prochlorococcus* populations in the DCM, averaged over the study period, was 126 $\pm$ 48 μmol NO_3^- m^{-3} d^{-1} (Table 2), a value at the low end of the range of the estimated diapycnal NO_3^- fluxes. In the Sargasso Sea DCM, *Prochlorococcus* and picoeukaryotes are co-dominant with respect to carbon biomass [*DuRand et al.*, 2001]. Some preliminary FLOW-SIP isotopic data for picoeukaryotes (M. W. Lomas, unpublished data, 2005) suggests that they represent a fraction of NO_3^- uptake in the DCM equal to that of *Prochlorococcus.* The sum of picoeukaryote and *Prochlorococcus* demand for NO_3^- in the DCM is well within the range of diapycnal fluxes, although a complete taxon-specific NO_3^- budget would be a very meaningful contribution to the field.

4. Potential Biogeochemical Implications

[12] With the increasing abundance of biological data on a variety of temporal and spatial scales, in particular data on functional group variability, ocean ecosystem models have become more complex by including multiple phytoplankton 'boxes'. However, our ability to properly integrate these boxes into ocean biogeochemical models is still in its infancy due to a paucity of biogeochemical ecology data [*Anderson*, 2005; *Flynn*, 2005], such as presented in this manuscript. The data discussed above lead us to conclude that *Prochlorococcus*' biogeochemical role in the DCM conforms to our current understanding of the new/regenerated production paradigm [*Dugdale and Goering*, 1967] with reduced nitrogen supporting most (>90%) of the growth N demand and NO_3^- assimilation supporting new production and, subsequently, the small net population growth. Of additional relevance to this discussion on new production is the seasonal evolution of a pronounced summer dissolved iron (dFe) minimum in the Sargasso Sea coincident with the DCM [*Sedwick et al.*, 2005]. This dFe minimum has been hypothesized to result from biological uptake and/or particle scavenging associated with the seasonal net growth of *Prochlorococcus*, although it is likely that other phytoplankton in the DCM also contribute to the removal of dFe [*Sedwick et al.*, 2005]. An important corollary hypothesis is that iron availability may constrain the rate and/or magnitude of new production by *Prochlorococcus* and other autotrophs in the Sargasso Sea DCM, through its impact on chlorophyll and ferredoxin biosynthesis. The biogeochemical implications of this corollary extend well beyond the Sargasso Sea, as subsurface minima in dissolved iron have also been observed in the subtropical North Pacific [*Boyle et al.*, 2005], and such features may be typical of the subtropical gyres during summer. Thus there is the potential for iron availability to impact new production by *Prochlorococcus* in subsurface waters over much of the subtropical ocean, providing a globally-significant linkage in the marine biogeochemical cycles of iron, nitrogen and carbon.

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