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Nutrient gradients in the western North Atlantic Ocean: Relationship to microbial community structure and comparison to patterns in the Pacific Ocean

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Abstract

Studies of nitrogen and phosphorus dynamics in the oligotrophic surface waters of the western North Atlantic Ocean have been constrained because ambient concentrations are typically at or below the detection limits of standard colorometric methods, except during periods of deep vertical mixing. Here we report the application of high-sensitivity analytical methods—determinations of nitrate plus nitrite (N + N) by chemiluminescence and soluble reactive phosphorus (SRP) by the magnesium induced co-precipitation (MAGIC) protocol—to surface waters along a transect from the Sargasso Sea at 26°N through the Gulf Stream at 37°N, including sampling at the JGOFS Bermuda Atlantic Time-series Study (BATS) station. The results were compared with data from the BATS program, and the HOT station in the Pacific Ocean, permitting cross-ecosystem comparisons. Microbial populations were analyzed along the transect, and an attempt was made to interpret their distributions in the context of the measured nutrient concentrations.

Surface concentrations of N + N and SRP during the March 1998 transect separated into 3 distinct regions, with the boundaries corresponding roughly to the locations of the BATS station (~31°N) and the Gulf Stream (~37°N). Although N + N and SRP co-varied, the [N + N] : [SRP] molar ratios increased systematically from ~1 to 10 in the southern segment, remained relatively constant at ~40–50 between 31°N and 37°N, then decreased again systematically to ratios <10 north of the Gulf Stream. Dissolved organic N (DON) and P (DOP) dominated (≥90%) the total dissolved N (TDN) and P (TDP) pools except in the northern portion of the transect. The [DON] : [DOP] molar ratios were relatively invariant (~30–60) across the entire transect.

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Heterotrophic prokaryotes (operationally defined as "bacteria"), *Prochlorococcus*, *Synechococcus*, ultra- and nanophytoplankton, cryptophytes, and coccolithophores were enumerated by flow cytometry. The abundance of bacteria was well correlated with the concentration of SRP, and that of the ultra- and nanophytoplankton was well correlated with the concentration of N + N. The only group whose concentration was correlated with temperature was *Prochlorococcus*, and its abundance was unrelated to the concentrations of nutrients measured at the surface.

We combined our transect results with time-series measurements from the BATS site and data from select depth profiles, and contrasted these North Atlantic data sets with time-series of N and P nutrient measurements from a station in the North Pacific subtropical gyre near Hawaii [Hawaii Ocean Time-series (HOT) site]. Two prominent differences are readily observed from this comparison. The [N + N] : [SRP] molar ratios are much less than 16 : 1 during stratified periods in surface waters at the BATS site, as is the case at the HOT site year round. However, following deep winter mixing, this ratio is much higher than 16 : 1 at BATS. Also, SRP concentrations in the upper 100 m at BATS fall in the range 1–10 nM during stratified periods, which is at least one order of magnitude lower than at the HOT site. That two ecosystems with comparable rates of primary and export production would differ so dramatically in their nutrient dynamics is intriguing, and highlights the need for detailed cross ecosystem comparisons. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Sargasso Sea; Microbial community structure; Ecological stoichiometry; Redfield ratio; Nutrients

1. Introduction

A major objective of past research has been to understand the relationships among nitrogen (N), phosphorus (P) and trace element limitation of growth and production in the sea. In a comprehensive analysis of the N cycle over evolutionary time scales, Falkowski (1997) argued that the balance between dinitrogen (N_2) fixation and denitrification (bacterial formation of gaseous N) in the world ocean has been the key to biological sequestration of carbon dioxide. Falkowski cited the difference between the ratio of nitrate (NO_3^-) to soluble reactive phosphorus (SRP) in the ocean interior ($\sim$14.7 : 1; Fanning, 1992) and the N : P ratio of sinking particulate matter, which can be approximated by the Redfield ratio (16 : 1; Redfield et al., 1963), as evidence of an imbalance between denitrification and N_2 fixation. That is, for every mole of P settling out of the euphotic zone, approximately 1.3 mol of N are lost from the ocean by denitrification: the ocean is losing N (Codispoti, 1995). Because of this N deficit, Falkowski (1997) argued that the world ocean is generally N-limited, and that N_2 fixation plays a key role in re-introducing fixed N to the ocean. Furthermore, because of the high iron requirement for diazotrophs, Falkowski suggested that iron ultimately limits ocean productivity on geologic time scales. Tyrrell (1999) also argued that NO_3^- limits instantaneous growth, but in contrast, he asserted that external inputs of P ultimately control longer-term productivity in the world ocean. This debate is not new (Ryther and Dunstan, 1971; Smith, 1984; Codispoti, 1989; Codispoti, 1995), nor has it been resolved.

The ratio of NO_3^- to SRP, generally reported as nitrate plus nitrite (N + N) to SRP, has historically been used to infer limitation of new production (Dugdale and Goering, 1967): an elevated ratio (i.e., $>16:1$) would be indicative of new production that is P-limited, while a depressed ratio would be indicative of N limitation. Because the concentration of SRP in Sargasso Sea surface waters is generally below the detection limit of the standard SRP assay (i.e., <30–

50 nM; Fanning, 1992; Michaels et al., 1994; Michaels and Knap, 1996), changes in the N + N : SRP ratio in the euphotic zone have gone unmeasured for much of the year (Michaels et al., 1994; Michaels and Knap, 1996). Therefore, it has not been possible to predict what limits new production in this region based solely on the N : P ratio of the inorganic dissolved nutrients.

The original goal of this study was to examine the relationship between microbial abundance and nutrient concentrations in the western North Atlantic as a means for exploring factors regulating productivity in this region. The primary obstacle faced was the vanishingly low levels of N + N and SRP in much of the region—especially the Sargasso Sea. Thus, we employed high-sensitivity analyses for N + N and SRP along a transect allowing a comprehensive analysis of these nutrients in the euphotic zone of the western North Atlantic ecosystem. We combined an analysis of the microbial community via flow cytometry with this data set to explore relationships between nutrients and various components of the community. Finally, we contrasted the nutrient data with Bermuda Atlantic Time-series Study (BATS) and Hawaii Ocean Time-series (HOT) data to establish an Atlantic-Pacific cross ecosystem comparison.

2. Methods

2.1. Sampling and plankton analyses

Samples were collected either from a Niskin rosette equipped with a CTD, or from the ship's seawater system (intake nominally at 3 m) on a series of four cruises aboard the R/V *Oceanus* in the Atlantic Ocean (Fig. 1). The most extensive sampling occurred during March 1998 on a transect from 26°N, 70°W to the BATS site (31°40′N, 64°10′W); the cruise continued northwest to

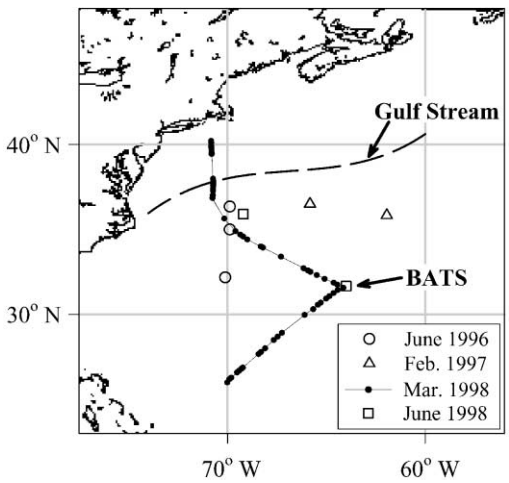


Fig. 1. Map of sampling stations in the western North Atlantic Ocean with different symbols for each of four cruises. The approximate location of the Gulf Stream is shown by a dashed line and the BATS site is denoted.

the Gulf Stream and then north towards New York. The other three cruises, two during June (1996 and 1998) and one during February 1997, included several sampling stations each (Fig. 1).

Samples were collected for nutrient, chlorophyll, and community structure analyses. Nutrient samples ($\sim$200 ml) were collected in 250 ml high density polyethylene (HDPE) bottles, which had previously been washed with Micro detergent (International Products Corporation), rinsed repeatedly, washed in 1 N HCl, and rinsed three times with the seawater to be sampled. Samples were frozen (-20°C) promptly for subsequent analysis (Dore et al., 1996). Total chlorophyll *a* (Chl *a*) samples consisted of $\sim$50 ml of seawater filtered onto GF/F (Whatman) filters, which were stored within cryovials in liquid nitrogen for later analyses. Size-fractions of Chl *a* were measured directly for the $>10\,\mu$m fraction and by difference for the <1 and 1–10 μm fractions (Cavender-Bares et al., 1999). The $>10\,\mu$m fraction was measured as the material retained on 10-μm polycarbonate membrane filters (Poretics), the $<1\,\mu$m fraction as the difference between the total Chl *a* and the material retained on a 1-μm membrane filter, and the 1–10 μm fraction as the difference between the material retained on a 1-μm membrane filter and the $>10\,\mu$m fraction. As was done with GF/F filters, membrane filters were also stored within cryovials in liquid nitrogen for later analyses. All frozen samples were measured back on land by the method of Welschmeyer (1994).

A modified EPICS V flow cytometer (Beckman Coulter; Cavender-Bares et al., 1998) was configured on land for high-sensitivity to analyze *Prochlorococcus*, *Synechococcus*, and bacteria (Fig. 2a–c), and at sea for higher sample flowrates and lower sensitivity to analyze the larger ultra- and nanoplankton (Fig. 2d–f), as described previously (Cavender-Bares et al., 1999). Note that operationally "bacteria" represent all heterotrophic prokaryotes (i.e., *Bacteria* and *Archaea* cells lacking pigment autofluorescence). Analyses conducted on land were performed on samples that had been preserved in 0.1% glutaraldehyde and frozen in liquid nitrogen (Vaulot et al., 1989). Within the ultra- and nanoplankton group, we were able to distinguish coccolithophores, because they depolarize the laser light (Fig. 2e), and cryptophytes, because they display orange fluorescence from phycoerythrin (Fig. 2f; Olson et al., 1989). Bacteria (Fig. 2c) were enumerated following the method of Marie et al. (1997) using the nucleic acid stain SYBR Green I (Molecular Probes).

2.2. Nutrient analyses

Because standard colorometric methods for N + N have been used for core measurements at the BATS site, and their detection limit is $\sim$50 nM, N + N has been detectable in the upper 100 m only during periods of deep winter mixing (Michaels et al., 1994; Michaels and Knap, 1996). We used the chemiluminescence method of Garside (1982) for our N + N analyses, which allowed us to generate a more complete picture of surface N + N concentrations for this region. The detection limit for N + N by chemiluminescence was 1–2 nM.

Much like the case of N + N, low concentrations of SRP in surface waters of the oligotrophic ocean have, in most cases, prevented SRP measurement by standard colorometric methods (detection limit $\sim$30 nM). It is clear from the BATS data set that SRP has been nearly undetectable in the upper 100 m over the past decade (Michaels et al., 1994; Michaels and Knap, 1996). To overcome the limits of this method, Ormaza-González and Statham (1991) used a 60-cm pathlength cuvette and reported SRP concentrations ranging from less than 1 to 10 nM in the

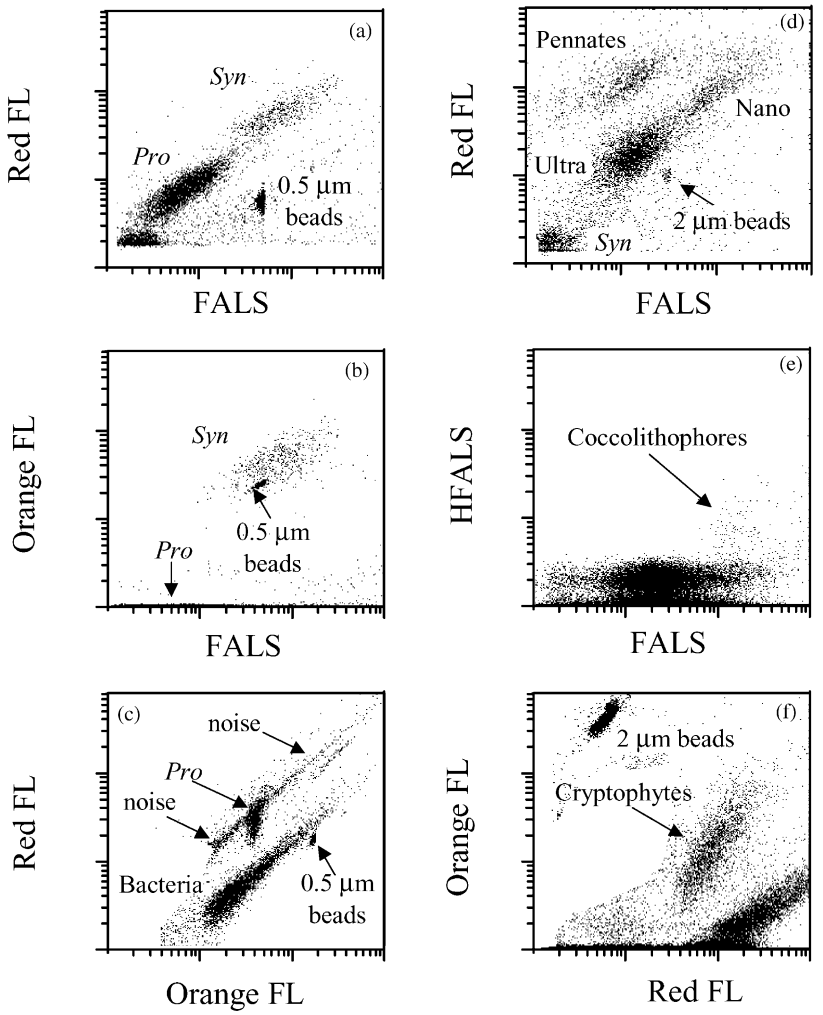


Fig. 2. Description of microbial groups enumerated by flow cytometry. (a, b) *Prochlorococcus* and *Synechococcus*; (c) bacteria visible because of their orange fluorescence after staining with SYBR Green I; (d) the ultra- and nanoplankton, shown here as individual groups, but considered as one because they were not always distinct from each other (note that pennate diatoms were included in this grouping when present); (e) coccolithophores distinguishable because they depolarize the laser beam; and (f) cryptophytes, which display orange fluorescence and can be separated from the remainder of the ultra- and nanoplankton. Note that *Synechococcus* were electronically removed (i.e., gated out) during data collection from the lower-left quadrant for the sample shown in (f). Notation: red fluorescence (Red FL), orange fluorescence (Orange FL), forward angle light scatter (FALS), horizontally-polarized forward angle light scatter (HFALS). Calibration beads shown in each panel, except (e).

upper 100 m at a single station in the Sargasso Sea near BATS. Using a $^{32}PO_4$ kinetic uptake approach, Cotner et al. (1997) set an upper limit of 10 nM on the bioavailable pool of SRP at BATS.

Another approach that has been used to improve the sensitivity of SRP analysis is the MAGIC procedure (magnesium induced co-precipitation method), which has been used extensively for

analyses at the HOT site (Karl and Tien, 1992, 1997), and which we used in the SRP analyses reported here. The advantage of this method is that SRP is concentrated prior to the addition of the analytical reagents so that only the SRP signal is amplified and not the blank.

The standard MAGIC protocol requires a 2.5% v/v addition of 1 N NaOH to initiate the formation of the mineral brucite ($Mg(OH)_2$), which is subsequently collected by centrifugation. SRP is co-precipitated and concentrated in this process and then re-solublized when the pellet is dissolved in weak acid (0.1 N HCl) prior to measurement by standard molybdate color reactions (Karl and Tien, 1992). The magnitude of SRP concentration is governed by the ratio of initial sample volume to that of the volume of the pellet dissolved in HCl; typical values range from 5- to 10-fold when starting with a 50-ml sample. Due to the exceedingly low levels of SRP (<10 nM) in the Sargasso Sea, we needed further concentration, such that SRP from a sample volume of 250 ml was concentrated to approximately 5 ml. In addition, we applied the recently modified MAGIC procedure (Thomson-Bulldis and Karl, 1998), which was designed to approximate more closely the dissolved inorganic phosphorus pool (P_i) by using only 0.25% v/v of 1 M NaOH to initiate brucite precipitation, rather than 2.5%. This latter procedure is referred to as "modified MAGIC" (Thomson-Bulldis and Karl, 1998).

Sub-samples (40 ml) of the supernatant solution from the initial centrifugation step were removed for the analyses of total N and P by uv-oxidation (N_{uv-ox}, P_{uv-ox}) (Walsh, 1989; Karl et al., 1993). As a first approximation, N_{uv-ox} and P_{uv-ox} should include both dissolved and particulate organic N (DON, PON) and P (DOP, POP) fractions. Also, dissolved inorganic nitrogen (DIN) should be present in the MAGIC supernatant and should, therefore, be included in N_{uv-ox}. As a way to constrain our interpretations, we performed modified MAGIC precipitations on three field samples, one from the equatorial Pacific and two from separate cruises in the Sargasso Sea, which had been preserved for flow cytometry following the method of Vaulot et al. (1989). We found that $<10\%$ of the bacteria and $<2\%$ of *Prochlorococcus*, *Synechococcus*, and the ultra- and nanophytoplankton were included in this supernatant (see Appendix A, Cavender-Bares, 1999). Assuming that detrital particles and any large heterotrophic organisms would also have been essentially removed from the supernatant, this suggests that N_{uv-ox} would consist primarily of DIN and DON, and P_{uv-ox} would include only DOP. Following this assumption, we represent total dissolved N (TDN) by N_{uv-ox} directly expecting that this excludes PON; total dissolved P (TDP) is equated to P_{uv-ox} plus the estimation of inorganic P (SRP) made by the modified MAGIC analysis and should exclude POP.

Note that no differences for any of the nutrients studied were found among samples taken from: the ship's seawater system, bottles from a standard rosette sampler, and trace-metal clean Go-Flo bottles (data not shown).

3. Results and discussion

This study's principal transect, which was chosen to exhibit a gradient in nutrients, was carried out during March 1998 (Fig. 1). The transect began in stratified waters of the southern Sargasso Sea (26°N, 70°W), passed through waters that were deeply mixed further north, crossed the Gulf Stream, and ended in continental shelf waters off the coast of New York.

3.1. Temperature and chlorophyll along transect

Surface temperature declined gradually from a high of 25°C at the southern extent of the transect until deeply mixed waters were reached just south of BATS, at which point water temperatures remained at about 19°C northward until the warm (23°C) waters of the Gulf Stream were reached (Fig. 3a). The northern edge of the Gulf Stream was well defined by an abrupt drop in temperature from 20°C to about 10°C followed by 5°C temperatures further northward. Total Chl *a* values ranged from 0.06 to 0.1 $\mu g l^{-1}$ in the southern portion of the transect and then increased to values ranging from 0.3 to 0.6 $\mu g l^{-1}$ just south of BATS (Fig. 3a), consistent with values reported by Michaels et al. (1994) for the spring bloom at BATS. We associate this line of latitude just south of BATS with the southern edge of the spring bloom at the time of our cruise. Chl *a* remained at these elevated levels across the Gulf Stream and increased sharply in coastal waters.

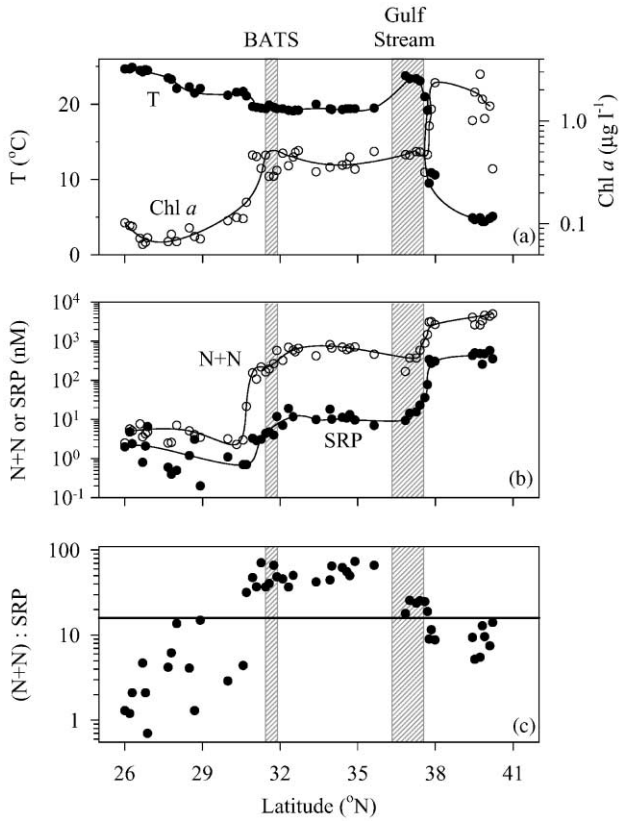


Fig. 3. Transect across Sargasso Sea, Gulf Stream, and coastal waters during March 1998. Vertical striped bars indicate the approximate location of the BATS site and the Gulf Stream. (a) Temperature and total Chl *a* as a function of latitude (see Fig. 1 for cruise track); (b) concentration of N + N and SRP as a function of latitude; (c) ratio of N + N to SRP as a function of latitude, with a solid line at a ratio of 16 : 1. All samples nominally from 3 m. Note that lines were added to plots to show trends in data.

3.2. Inorganic N and P along transect

N + N ranged from 2.5 to 7 nM in the southern region of the transect and increased steadily at the southern edge of the spring bloom, eventually reaching a mean value of 600 nM in the waters north of BATS (Fig. 3b). N + N dropped somewhat in the Gulf Stream to a mean of about 400 nM, with a steady increase at the northern edge of the Gulf Stream. This latter increase, which began at a water temperature of 23°C, persisted until leveling off at values ranging from 3 to 5 μM in the low-temperature coastal shelf waters of the North Atlantic Bight.

Changes in SRP paralleled those of N + N, however, SRP increased at the southern edge of the spring bloom by only a factor of 10 instead of the 100-fold increase for N + N (Fig. 3b). Values in the southern portion of the transect ranged from 0.5 to nearly 5 nM, with only two stations below our 0.5 nM detection limit. Subnanomolar SRP concentrations have rarely been reported for an open ocean habitat although on occasion SRP has been below the limit of detection ($\sim$1 nM) at the HOT site (Karl and Tien, 1997). In the northern portion of the Sargasso Sea, delineated by the southern edge of the spring bloom, the mean SRP value was 12 nM and ranged from 7 to 18 nM. SRP values ranged from 9 to 23 nM in the Gulf Stream, before steadily rising to a mean of 400 nM in coastal waters.

Although the recycling of N + N and SRP are generally considered to be tightly coupled in the upper ocean, variations in nutrient supply, export or net incorporation stoichiometry can result in both local and regional changes in the N + N : SRP concentration ratios. For example, in the southern portion of our transect, the N + N : SRP ratios were consistently below (mean = 4.6) the canonical Redfield molar ratio of 16N : 1P (Fig. 3c). Under these environmental conditions there would be a strong selection for the growth of diazotrophic microorganisms capable of utilizing the nearly inexhaustible supply of N_2 dissolved in seawater. Provided that there is a sufficient supply of trace elements, especially iron, the metabolic activities of N_2-fixing microorganisms would replenish fixed N and eventually elevate the N + N : SRP ratio towards the Redfield balance of average planktonic organic matter. However the supply of SRP in these hyperoligotrophic waters, which are characterized by SRP concentrations near or below 1 nM, may ultimately limit the activities of N_2-fixing microorganisms and, hence, total primary production and export. North of approximately 31°N (including the BATS station) in our March 1998 transect, the N + N : SRP ratios were higher than the Redfield ratio (mean = 51), so N_2-fixing microorganisms would not have been selected for in this region. Even further north in the Gulf Stream and the coastal waters, the N + N : SRP ratio returned to a near Redfield balance (mean = 14).

3.3. Depth profiles of inorganic N and P

Two depth profiles from this cruise were analyzed to understand how well our set of surface N + N and SRP values (Fig. 3b) represented the mixed layers along the transect. Values at the surface resembled those throughout the mixed layer at both points along the transect (26°N and BATS; Fig. 4a–d). In addition, these two nutrient profiles were similar to several others taken at various locations and times in the western Sargasso Sea. Specifically, the profiles from 26°N compare well with others taken during stratified periods at and near BATS (Fig. 4a and c), while the profile taken at BATS during March 1998 compares well with two profiles also taken during a deeply mixed period (Fig. 4b and d). Thus, surface measurements of N + N and SRP were

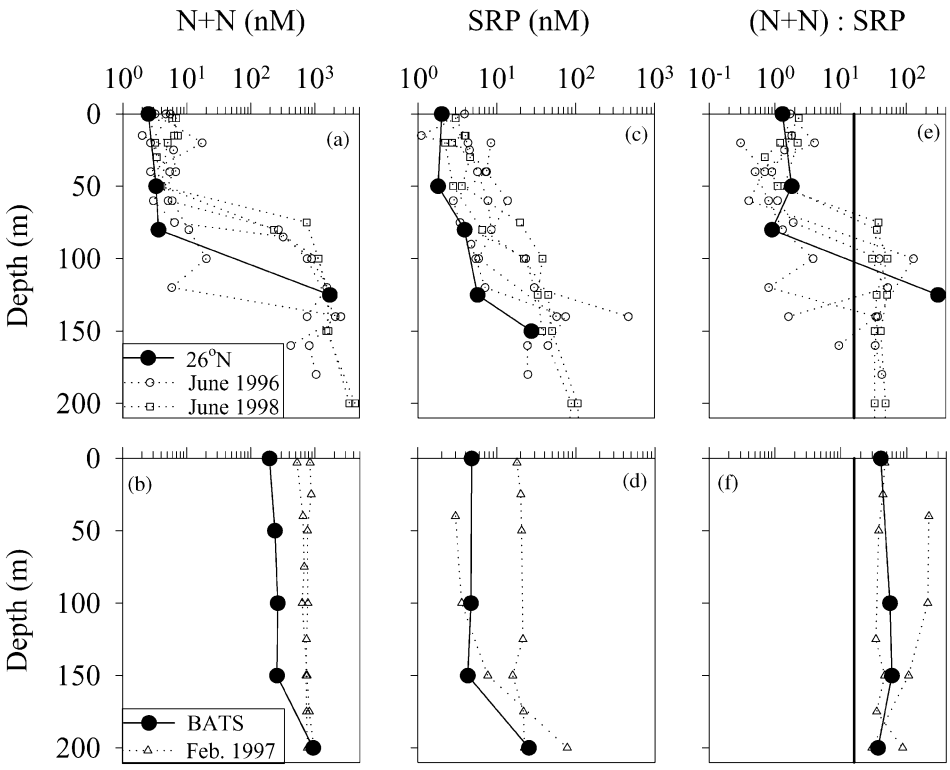


Fig. 4. Representative depth profiles of N + N, SRP, and their ratio for the Sargasso Sea. (a, c, e) oligotrophic profiles, with large filled circles for 26°N profile from the 1998 transect; (b, d, f) deeply mixed profiles, with large filled circles for BATS profile from the 1998 transect. Symbols for other cruises correspond to those in Fig. 1. Note solid lines added to panels (e) and (f) at ratios of 16 : 1.

representative of the mixed layer for the transect as well as for similar mixing regimes during other cruises.

Similar N + N and SRP values for the mixed layer during the transect resulted in rather constant ratios of N + N to SRP (Fig. 4e and f). Generally, ratios remained less than 16 : 1 in the mixed layers of stratified waters (Fig. 4e), and exceeded 16 : 1 in deeply mixed water columns (Fig. 4f), consistent with the elevated ratios reported by Michaels et al. (1994) at BATS for deeply mixed water columns; surface waters during deeply mixed periods should resemble deeper waters from which they originated.

Our values of N + N (Fig. 4a) are consistent with those reported by Garside for the Sargasso Sea (Garside, 1985; Glover et al., 1988), and our SRP values are similar to those reported by Ormaza-González and Statham (1991) using a 60-cm pathlength cuvette (ranging from 1–10 nM) for a single depth profile at Station S (32°09′N, 64°34′W), and are consistent with the values reported by Cotner et al. (1997) for BATS using a ^{32}P-bioassay technique. Moreover, other independent SRP values (Wu et al., 2000)—also measured using the modified MAGIC protocol on a portion of the same transect discussed here—are consistent with the values presented in Fig. 3.

3.4. Comparison to BATS and HOT time-series data

For a more comprehensive understanding of nutrient dynamics in open ocean habitats, we have merged our data from this study with those produced through the ongoing program of time-series measurements at BATS (data available at: http://www.bbsr.edu; Fig. 5). We contrast these data sets with those from the HOT site in the Pacific Ocean (data available at: http://hahana.soest.hawaii.edu), where high-sensitivity methods for nutrient analyses are routinely employed (Fig. 6). Following the approach of Michaels et al. (1994), Fig. 5 includes only those BATS data greater than 100 nM for both N + N and SRP, which is twice their detection limit using colorometric methods; Fig. 6 includes only those HOT data equal to or greater than twice the detection limit for N + N measured by chemiluminescence (2 nM) and SRP measured by MAGIC (1 nM). These cut-offs for the inclusion of the time-series data are shown by dotted lines in Figs. 5b, d and 6b, d.

Waters at BATS undergo seasonal stratification, which can be seen from surface temperatures that range from about 18°C during periods of deep vertical mixing up to nearly 30°C when the

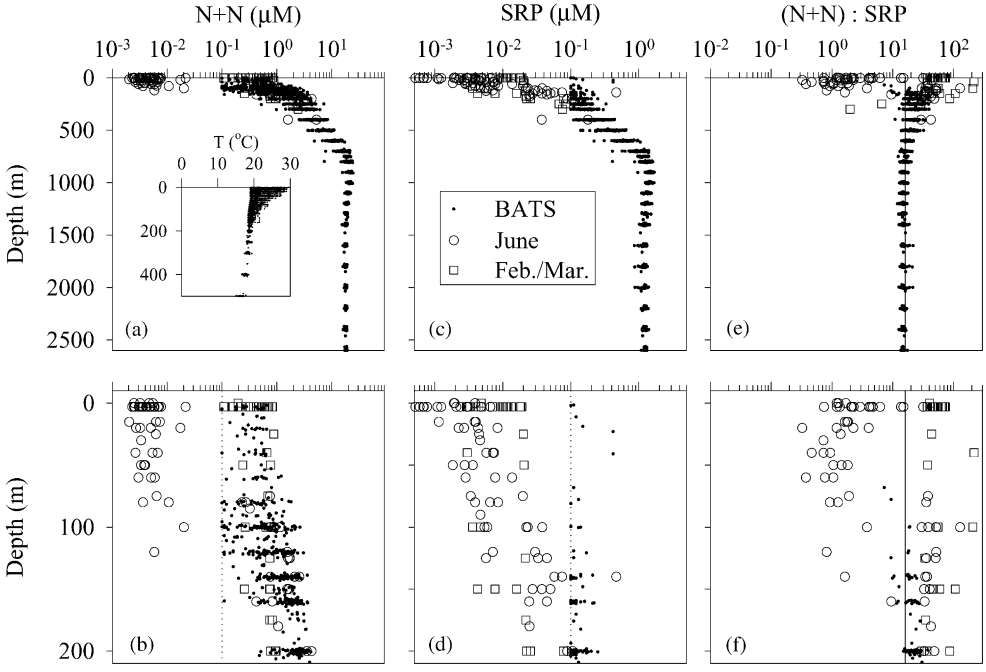


Fig. 5. Comparison of data from the BATS site with those from this study. Small filled circles for BATS data, open circles for data shown in Figs. 3b (southern portion of transect) and Fig. 4a, c and e; open squares for data shown in Fig. 3b (northern portion of Sargasso Sea) and Fig. 4b, d and f. (a) Depth profile of N + N, with an inset of temperature plotted as a function of depth; (b) depth profile of N + N on an expanded depth scale; (c) depth profile of SRP; (d) depth profile of SRP on an expanded depth scale; (e) depth profile of the ratio of (N + N) to SRP, with a solid line added for a ratio of 16 : 1; (f) depth profile of the ratio of (N + N) to SRP on an expanded depth scale. Data represent BATS cruises 17–100 (February 1990–January 1997). Note: see text for further explanation of dotted lines in (b) and (d) that represent lower cut-offs for inclusion of time-series data.

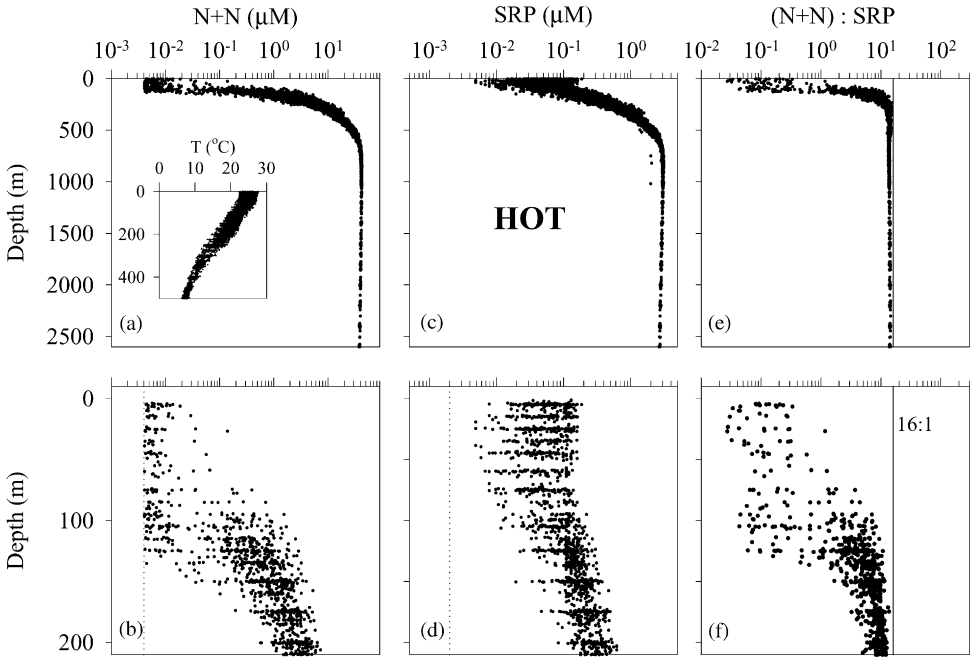


Fig. 6. Summary of nutrient data from the HOT site in the Pacific Ocean, for comparison to Fig. 5; panels labeled the same as in Fig. 5. Data from HOT cruises 1–88 (October 1988–December 1997).

water column is highly stratified (Fig. 5a, inset). The water column at the HOT site is stratified year-round (compare insets, Figs. 5a and 6a). At BATS, seasonal differences in the distribution of N + N in the upper 200 m lead to a wide range of N + N values: the lowest during stratified periods, the highest during periods of deep mixing (Fig. 5a and b). Such a pattern is absent at the HOT site, where N + N varies much less in the continually stratified waters (Fig. 6a and b).

One of the most prominent differences between the two ecosystems is that SRP is generally depleted to concentrations at BATS (1–10 nM) that are an order of magnitude lower than at the HOT site (10–100 nM; see Figs. 5c, d and 6c, d). In fact, essentially all of our SRP values shown in Fig. 5d fall below one standard deviation from the mean of SRP values from the HOT site (Fig. 7). Fanning (1989) hypothesized that the low levels of SRP in the Sargasso Sea relative to other regions of the world ocean are caused by elevated levels of nitrogen deposited aerially from heavy industrial activity in North America. He argued that higher nitrogen availability would drive plankton to reduce SRP to the undetectable levels observed. More recently, Wu et al. (2000) invoked differential rates of remineralization for DON and DOP to help explain the low SRP levels observed at BATS.

As was discussed in general for the central Atlantic by Fanning (1989, 1992) and shown in detail at the BATS site by Michaels et al. (1994), the ratio of N + N to SRP is typically in excess of 16 : 1 over a range of depths. Michaels et al. (1994) found values up to 40 : 1 at BATS over the range 200–600 m (Fig. 5e). It has been argued that the elevated ratios result ultimately from N_2 fixation

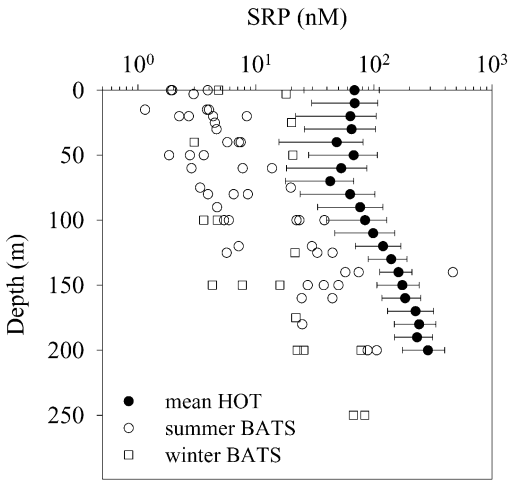


Fig. 7. Comparison of SRP values between the Sargasso Sea and the North Pacific subtropical gyre. Mean SRP values (± 1 s.d.) are shown for the HOT site (Fig. 6d). Summer (Fig. 4c) and winter (Fig. 4d) values measured at and near the BATS site are shown.

(Fanning, 1992; Michaels and Knap, 1996). It has been observed that *Trichodesmium*, a globally significant diazotroph (Capone et al., 1997), maintains elevated proportions of N relative to P (Karl et al., 1992), compared to the Redfield ratio. It has been postulated that these N-rich cells, or indirect products thereof, sink and undergo remineralization causing N + N to be elevated relative to SRP (Fanning, 1992; Michaels and Knap, 1996).

3.5. Total dissolved N and P, dissolved organic N and P

There was no prominent trend along the transect for TDN, which had a mean concentration of 6.3 μm (range 4.6–10.2 μm) at a depth of 3 m (Fig. 8a). TDP had two noticeable features, a slight depression from a mean of 0.1 μm at the southern edge of the spring bloom, and elevated values in coastal waters with a maximum of 0.7 μm (Fig. 8a). DON and DOP showed similar patterns to TDN and TDP, respectively (Fig. 8a). There is virtually no difference in the trends between dissolved and total fractions along the transect in the Sargasso Sea and the Gulf Stream. We do see, however, a clear decrease in the dissolved organic N (DON) and P (DOP) pools relative to the pools of TDN and TDP in coastal waters. As was the case with the inorganic N and P (Figs. 3 and 4), surface concentration of TDN, TDP, DON, and DOP were representative of samples taken within the upper mixed layer (data not shown). The N : P ratios of these fractions averaged about 50 over the entire cruise, with the exception of the ratio of TDN : TDP, which dropped to about 16 : 1 in coastal waters (Fig. 8b). At present, we do not know what fractions of the TDN and TDP pools are biologically available, and it is, therefore, difficult to interpret these data.

3.6. Community structure along the transect

The abundances of different groups of microorganisms are determined by both their growth rate and their mortality rate. The former is dictated by nutrients and, in some cases, photon fluxes

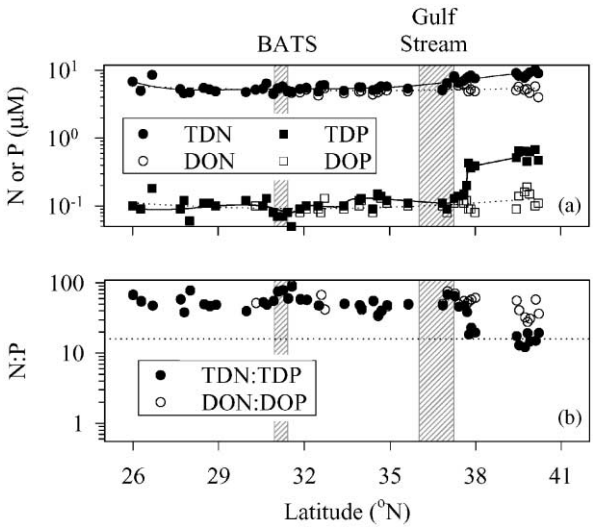


Fig. 8. Total and organic N and P along March 1998 surface transect (Fig. 3). (a) TDN, TDP (filled symbols, solid lines) and DON, DOP (open symbols, dashed lines). Vertical striped bars indicate the approximate location of the BATS site and the Gulf Stream. Note that lines were added to plots to show trends in data.

or ambient temperature. Thus, it is difficult to say much about limiting factors based solely on correlations of microbial abundances with dissolved nutrients. Nevertheless, patterns did emerge from such an analysis of this data set, which should help to focus hypotheses regarding the regulation of community structure in these ecosystems.

Patterns of the abundance of bacteria and phytoplankton in surface samples along the transect (Fig. 9) aligned with some or all of the prominent features in N + N and SRP (Fig. 3). The abundance of bacteria increased gradually along the entire transect in the Sargasso Sea and Gulf Stream, with a 25% drop in concentration near the southern edge of the spring bloom. There was an abrupt peak in bacterial numbers (9×10^5 cells ml^{-1}) just beyond the northern edge of the Gulf Stream, and concentrations receded further northward (Fig. 9a). Plotting their abundance against both nutrient concentrations (Fig. 10a) reveals a somewhat tighter relationship between SRP and abundance than N + N. Not only are R^2 values higher in the case of SRP, but N + N values fall into two groups (high and low) whereas SRP has intermediate values, demonstrating a continuous relationship between bacterial abundance and SRP. Although there could be other explanations, this is consistent with the findings of others (Cotner et al., 1997; Rivkin and Anderson, 1997) implying that bacterioplankton may be P-limited at BATS.

The smallest phytoplankter, *Prochlorococcus*, was at its highest abundance at the southern extent of the transect and declined substantially in spring bloom waters. Its abundance remained low north of BATS, but increased markedly in the Gulf Stream to levels close to those at 26°N, and then dropped below detection in coastal waters (Fig. 9b). The median concentration of *Prochlorococcus* has been observed to occur at depths close to the nitricline in the Sargasso Sea, which suggested a strong requirement for nitrate or another nutrient which co-varied with nitrate (Olson et al., 1990). Later studies indicated that this was more likely a manifestation of the ability of this group to compete successfully at low light levels (Moore et al., 1995, 1998; Moore and

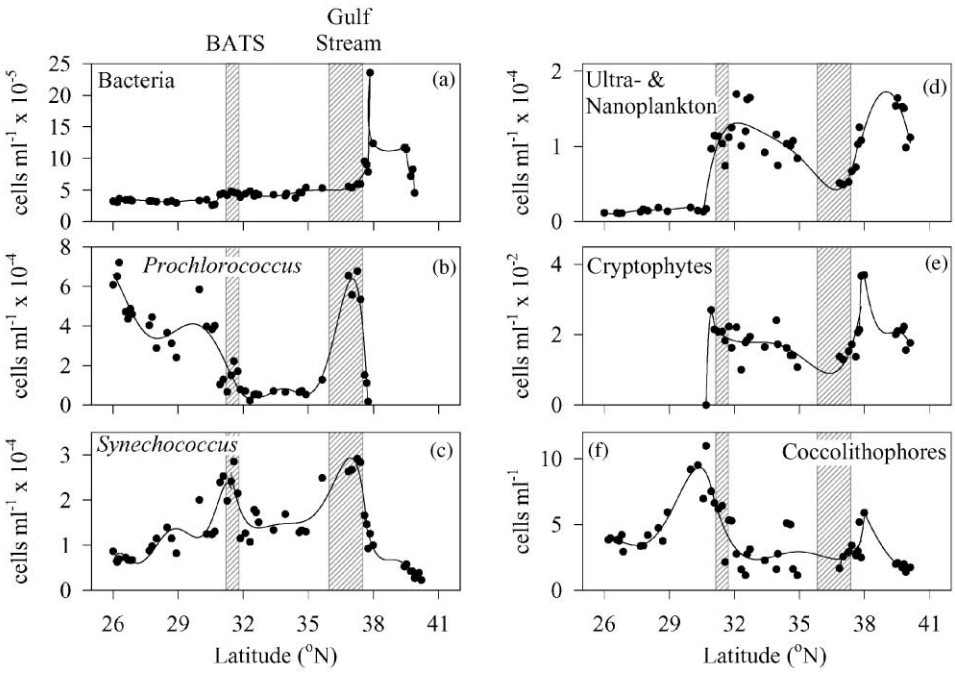


Fig. 9. Plankton abundances along March 1998 surface transect (Fig. 3). Vertical striped bars indicate the approximate location of the BATS site and the Gulf Stream. Note that lines were added to plots to show trends in data. Plankton groups correspond with those shown in Fig. 2.

Chisholm, 1999; DuRand et al., 2001). In this surface transect, however, we found that *Prochlorococcus* was actually negatively correlated with both N + N and SRP (Fig. 10b). Recent laboratory studies have shown that cultures of *Prochlorococcus* cannot utilize nitrate for growth (L.R. Moore, A. Post and S.W. Chisholm, unpublished data; Rippka et al., 2000), which is consistent with these observations, suggesting strongly that the correlation between the *Prochlorococcus* maximum and the nitricline in depth profiles has to do with light and not nitrate availability.

There are several outliers in the relationships between *Prochlorococcus* abundance and N + N and SRP (Fig. 10b), which are all from the relatively warm waters of the Gulf Stream (Fig. 9b), suggesting that temperature may be an important regulating factor for *Prochlorococcus*. Indeed, the entire data set shows a strong positive correlation between *Prochlorococcus* abundance and temperature (Fig. 11), a relationship that was not seen for any of the other groups (data not shown). This relationship is consistent with laboratory data demonstrating a temperature optimum curve for growth rates in cultures of *Prochlorococcus,* which show a positive correlation between 13°C and 24°C, an optimum at 24°C, and no growth above 28°C (Moore et al., 1995).

Even if temperature is the main controlling factor of *Prochlorococcus* abundance, the negative correlations (Fig. 10b) observed with nutrients beg for an explanation. There are several possibilities. First, their small cell size (0.5–0.7 μm diameter) could give them a growth advantage at low nutrient concentrations by reducing their threshold for diffusion limitation (Munk and Riley, 1952; Pasciak and Gavis, 1974; Chisholm, 1992). It is also possible that *Prochlorococcus* has

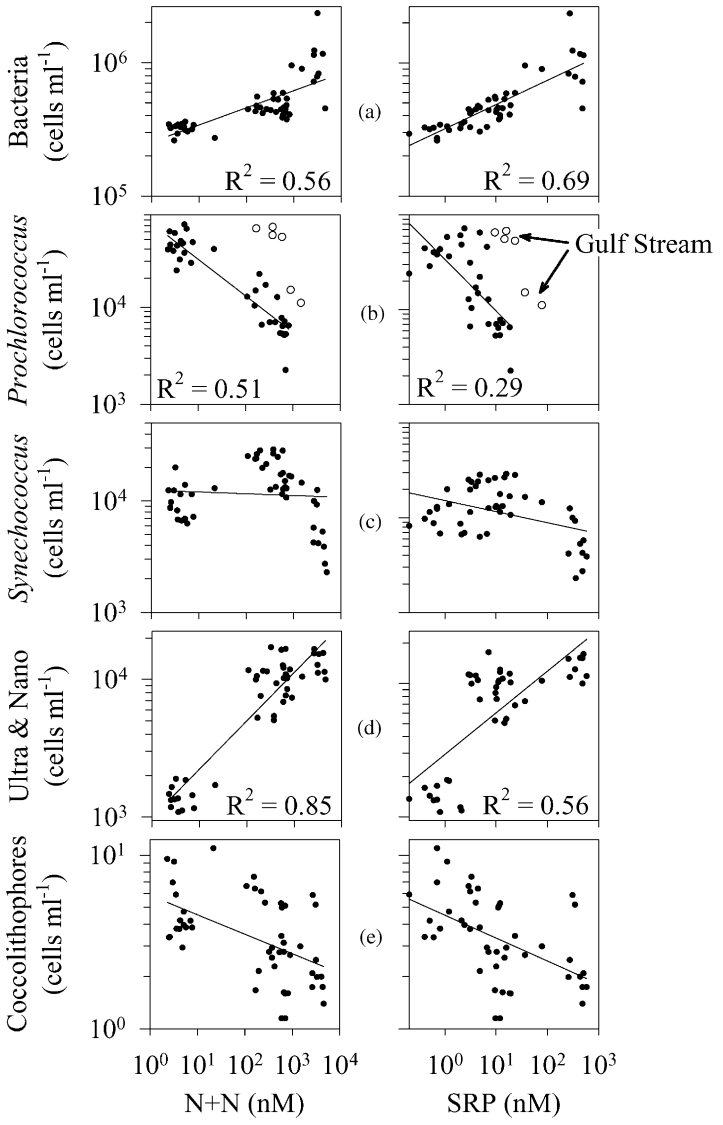


Fig. 10. Correlations between the abundance of plankton groups and nutrients along March 1998 surface transect. Left panels for N + N and right panels for SRP. In some cases correlation coefficients (R^2) are indicated. (b) Open circles are used to denote samples from the Gulf Stream.

an advantage in these low nutrient waters because it can utilize organic forms of N and P (L.R. Moore, unpublished data), which are several orders of magnitude higher in concentration (compare Figs. 3b and 8a). Third, it could be that *Prochlorococcus* is outcompeted when nutrients are abundant because they are either unavailable to them (e.g., nitrate) or their maximum growth rate is not as fast as that of some other species (e.g., *Synechococcus*—see below). We recognize that nutrient concentrations are not necessarily correlated with nutrient fluxes, and it is the latter

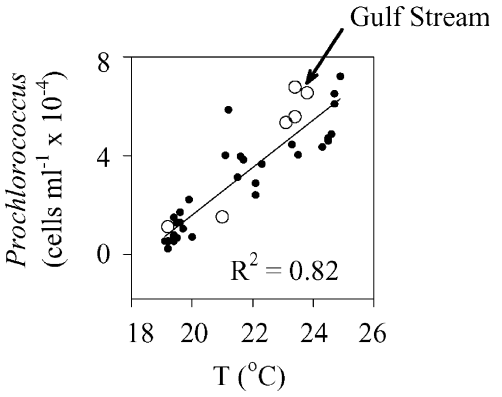


Fig. 11. Relationships between *Prochlorococcus* abundance and temperature along March 1998 transect with open circles representing Gulf Stream samples.

that is the controlling factor of phytoplankton growth. All of these hypotheses must be entertained with this in mind.

In contrast to *Prochlorococcus*, the abundance of *Synechococcus*, which *can* utilize nitrate as a nitrogen source (e.g., Waterbury et al., 1986), increased steadily from 26°N to the southern edge of the spring bloom. Beyond BATS, concentrations dropped off only to rise again in the Gulf Stream to match the highest concentrations seen at BATS. In the coastal waters, concentrations were low, but they were still detectable (Fig. 9c). Thus, the abundance of *Synechococcus* along the entire transect was not correlated with N + N or SRP (Fig. 10c). The high cell numbers at the southern edge of the spring bloom are consistent with other observations that *Synechococcus* blooms during spring (March–May, depending on year) at BATS (Gin et al., 1999; DuRand et al., 2001), and other observations of blooms of *Synechococcus* corresponding to influxes of nutrients (Glover et al., 1988).

Unlike the North Pacific subtropical gyre (NPSG), the Sargasso Sea ecosystem undergoes an annual cycle, which is characterized by a period of deep mixing in the winter and highly stratified conditions from late spring through fall; the former can be considered analogous to a chemostat culture, whereas the latter is more analogous to a batch culture. As a result, the community structure of the phytoplankton varies seasonally at BATS (Gin et al., 1999; DuRand et al., 2001). Specifically, the integrated mixed-layer abundance of the picoplankters *Prochlorococcus* and *Synechococcus* generally undergo an oscillating pattern, with one high while the other is low in abundance. In stratified waters, *Prochlorococcus* maintains a maximum near the base of the euphotic zone (Olson et al., 1990; DuRand et al., 2001), whereas *Synechococcus* is distributed more evenly. In contrast, *Prochlorococcus* always far outnumbers *Synechococcus* at HOT (Campbell and Vaulot, 1993), and their depth distribution patterns are similar.

One fundamental difference between these two groups is that the maximum growth rate in culture of *Synechococcus* is higher than that of *Prochlorococcus* (Moore et al., 1995). It could be that when nutrients are available, *Synechococcus* grows faster than *Prochlorococcus* and reaches high densities. To keep up, its protozoan predators would then increase in growth rate and numbers. Because these same predators graze on *Prochlorococcus*, this would cause high mortality

rates for *Prochlorococcus* relative to their growth rates, and abundances would decline (M.R. Landry, pers. comm.). This could both set up the oscillatory pattern in abundances of these two groups at BATS and ultimately produce the apparent negative correlation between *Prochlorococcus* abundance and nutrients. Because the NPSG is more like a chemostat, growth rates and mortality rates of the two groups are in balance and limited by the supply of nutrients, causing their abundances to remain fairly constant. *Prochlorococcus* may sustain higher cell numbers than *Synechococcus* in this system simply because they are smaller, they have lower cell quotas for nutrients, and because of their high surface to volume ratios, they should be more competitive at limiting concentrations of nutrients.

The larger phytoplankton were characterized as three groups (see Fig. 2): the ultra- and nanoplankton, cryptophytes, and coccolithophores. The first group excludes concentrations of the latter two. Ultra- and nanoplankton numbers were low (mean of 1.4×10^3 cells ml^{-1}) south of the spring bloom waters and then increased nearly 10-fold in the northern portion of the Sargasso Sea (maximum of 1.7×10^4 cells ml^{-1}). Concentrations receded in the Gulf stream, and then increased again to maximal levels in coastal waters (Fig. 9d). There was a strong positive correlation between their concentration and N + N and a weaker one with SRP (Fig. 10d).

Cryptophytes were not detected in the southern extent of the transect, but this may have been due to a limitation of our analysis. In stratified waters that were presumably low in N, cryptophytes have been observed to lack phycoerythrin (R. Olson, pers. comm.). We would not have been able to characterize such cells as cryptophytes, but rather they would have been classified within the ultra- and nanoplankton group. Cryptophytes were found at concentrations ranging from 100 to 270 cells ml^{-1} from the bloom waters northward across the Gulf Stream, and there was a sharp peak in concentration (370 cells ml^{-1}) just past the northern edge of this feature, coincident with the sharp peak in nutrients (Fig. 3b) and bacterial cell numbers (Fig. 9e). Coccolithophores had the same general pattern as the cryptophytes, but they were detectable in the southern region of the transect (mean of 4 cells ml^{-1}), and then increased in concentration slightly before the point that the cryptophytes appeared. Following this burst in cell number, they maintained low numbers north across the Gulf Stream (mean 2.6 cells ml^{-1}). There was a doubling of cell numbers coincident with the peaks for bacteria and cryptophytes in coastal waters (Fig. 9f). Coccolithophore abundance was not significantly correlated with nutrients (Fig. 10e).

Most of the cells analyzed on our instrument would have been less than about 10 μm in diameter (Cavender-Bares, 1999). This represents 75–90% of the total Chl *a* except in coastal waters, where it only accounts for roughly 40% (Fig. 12a). The drop in *Prochlorococcus* and the increase in ultra- and nanoplankton abundances in spring bloom waters (Fig. 9b and d) resulted in a redistribution of Chl *a* within the <10 μm fraction. Specifically, Chl *a* in the 1–10 μm fraction increased from about 50% to 70% of the total in spring bloom waters (Fig. 12b), while that in the <1 μm fraction dropped from about 30% to 20% of the total (Fig. 12c).

The various components of the phytoplankton community that could be characterized here did not have a uniform pattern with respect to the inorganic nutrients measured. However, it is quite interesting to note that, when phytoplankton biomass as a whole (i.e., total Chl *a*) is considered, strong correlations with both N + N and SRP result (insets Fig. 12a and c). This suggests that, as inorganic nutrients increased, fluctuations of the individual populations occurred within a framework of steadily increasing Chl *a*.

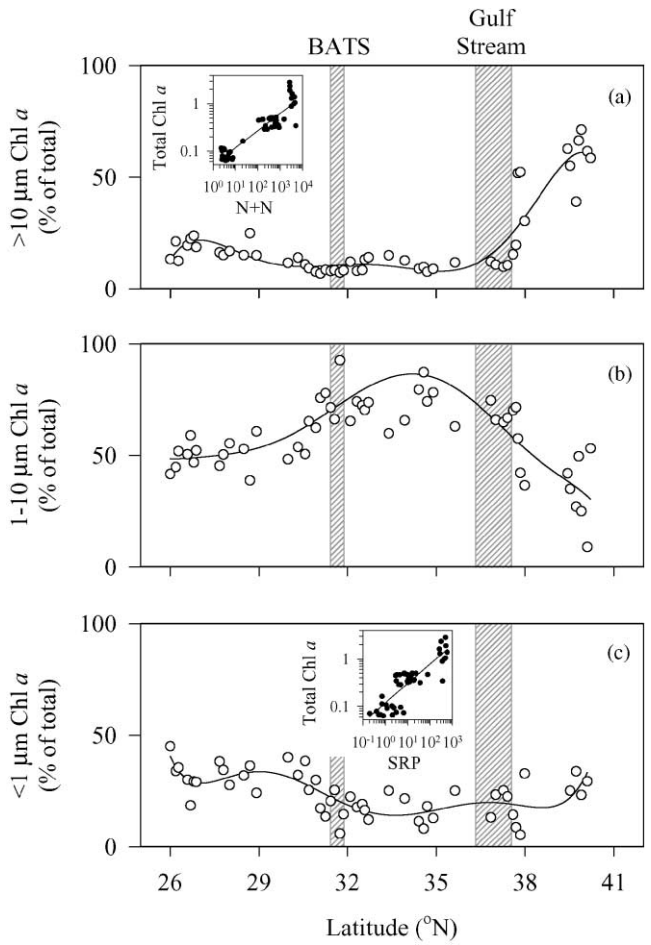


Fig. 12. Size-fractionated Chl *a* along March 1998 transect. Vertical striped bars indicate the approximate location of the BATS site and the Gulf Stream. Percent of total Chl *a* in (a) $>10\,\mu m$, (b) 1–10 µm, and (c) $<1\,\mu m$ fractions, with lines added to show trends in data. In the insets of (a) and (c) are total Chl *a* ($\mu g\,l^{-1}$) vs. N + N (nM) and SRP (nM), respectively.

3.7. Cross-ecosystem synthesis

This ocean transect conducted in early spring captured only a single snapshot of environmental conditions that are known to vary seasonally, especially at the mid-latitude sites near Bermuda. Other sampling near the BATS site (Fig. 4) and the now well-established pattern based on the 10-yr BATS program data sets (Fig. 5) indicate a seasonal progression of the near surface (0–100 m) N + N : SRP ratio of >16N : 1P in winter to <16N : 1P in summer. This implies a seasonal selection for N_2-fixing microorganisms each summer. During periods of deep winter mixing, there is an entrainment of water from >200 m which has a N + N : SRP much greater than the Redfield ratio. The spring bloom near Bermuda apparently results in the selective removal of N + N, through either export of particulate matter with N + N : SRP ratio >16N : 1P, local storage of

dissolved organic matter with non-Redfield stoichiometry or local denitrification. This results in a decrease in the N + N : SRP ratio to values less than 16N : 1P which, in turn, selects for N_2-fixing microorganisms. The local supply of fixed N eventually results in a net decrease in the ambient concentration of SRP. Provided there is an adequate supply of trace nutrients, especially iron, the ambient SRP levels will decrease to a level below which efficient P capture cannot occur. While the exact concentration may depend on species composition and other factors, it is possible that the SRP threshold is near 100 pM, as was recently found for temperate lakes (Hudson et al., 2000).

By comparison to this seasonal evolution of P limitation in the North Atlantic near Bermuda, environmental conditions at Station ALOHA in the NPSG appear to be very different. First, the N + N : SRP ratios in the surface waters (< 200 m) at Station ALOHA are always well below the Redfield ratio (mean = 3.7), so selection for the growth of N_2-fixing microorganisms would always be very strong. At the present time it appears that between 30% and 50% of the new N is derived from N_2 fixation (Karl et al., 1997). Despite this apparent relief from fixed N limitation, the surface waters near Sta. ALOHA contain "excess" SRP, nearly two orders of magnitude greater concentration than found during summer near Bermuda (Fig. 7). Furthermore, there is no strong seasonality in the North Pacific, but rather a secular decrease in SRP of nearly 50% of the inventory over the past decade (Karl, 1999). Clearly, these two otherwise similar open ocean ecosystems are fundamentally different with regard to N and P dynamics.

Karl et al. (2001) have hypothesized that the NPSG is undergoing a significant shift in its ecosystem's structure and function. Evidence resulting from the HOT study suggests that N_2 fixation rates have been increasing (Karl et al., 1997; Karl, 1999), that photosynthetically-derived dissolved organic matter is being produced in excess (Karl et al., 1998), and that the microbial community structure has shifted over the past several decades to one dominated by prokaryotic populations (Karl et al., 2001). Historically, productivity in the NPSG has been thought to be N-limited, but during the past several decades the inventory of SRP has declined significantly (Karl and Tien, 1997), which has contributed to the hypothesized shift to P-limiting conditions (Karl et al., 2001). Perhaps a multi-staged process is occurring in both ecosystems, even though they may not be synchronized. The first stage has lower than 16 : 1 N : P ratios selecting for N_2-fixing organisms because N limits production. This leads to the second stage, where N_2 is fixed, P is utilized, and N : P rises just above 16 : 1, at which point P limits production. During this stage, sinking particulate matter might have high N : P ratios leading to elevated inorganic N : P ratios in the thermocline—as is currently observed in the Sargasso Sea. The third and final stage would be a P-limited ecosystem "living" on the excess N found in the upwelling water and eventually eroding the N : P to less than 16 : 1. At this point, the cycle begins anew.

There are several testable hypotheses to account for these differences. It has been suggested that the atmospheric flux of iron to the North Atlantic greatly exceeds the flux of iron to the North Pacific (Wu et al., 2000), which results in iron control on total N_2 fixation at Station ALOHA. Production of organic matter in this oligotrophic ecosystem shows many of the key characteristics of P limitation, including non-Redfield stoichiometry of suspended and exported organic matter (Karl and Tien, 1997). Nevertheless, the net removal of P is apparently controlled by N_2 fixation and ultimately by iron delivery. Alternatively, the microbial community composition may be crucial in controlling the ambient concentrations of dissolved nutrients. It is well established that different microbial assemblages dominate at the BATS and HOT stations (Andersen et al., 1996). Eukaryotic algae and *Synechococcus* seasonally oscillate in the near surface waters at BATS

(Olson et al., 1990; DuRand et al., 2001), whereas *Prochlorococcus* dominates year round at HOT (Campbell and Vaulot, 1993). Plankton dynamics near Bermuda are more batch culture-like with significant species succession, whereas HOT species dynamics can be characterized as chemostat culture-like with single species dominance year round, but perhaps, interdecadal species succession. Laboratory studies of *Prochlorococcus* growth under P-limited conditions indicate a residual SRP concentration of 20–30 nM (Parpais et al., 1996), not the 20–100 pM measured by Hudson et al. (2000) for a variety of freshwater lakes. Consequently it is possible that *Prochlorococcus* dominance in the North Pacific is a result of one or more selection pressures other than the concentration of SRP. Eventually, other microorganisms with more efficient P-capture mechanisms should be selected for, and this would result in a decrease of the ambient SRP pool, a prediction that is consistent with the decade-long field observations at Sta. ALOHA (Karl and Tien, 1997).

The above discussions of nutrient concentrations and concentration ratios is based strictly on N + N and SRP as "preferred" forms of N and P. However, it is well known that many microorganisms including both prokaryotes and eukaryotes can use selected forms of DON or DOP for metabolism and growth.

In contrast to the systematic, regional variation in N + N : SRP ratios along the North Atlantic transect (Fig. 3), the DON : DOP ratio is relatively invariant and is consistently greater than the Redfield ratio (Fig. 8). Because the organic nutrient pools always dominated the surface water inventories (except perhaps near the coast, north of the Gulf Stream), this implies that the bioavailable N : P ratio may be substantially different from the measured N + N : SRP ratio. Unfortunately, because these organic matter pools are not yet chemically characterized, it is not possible to predict their bioavailabilities. This is clearly an important area for future research.

4. Conclusions

Investigations of nutrient inventory and dynamics, microbial community structure and succession, and rates of primary and secondary productivity are the key master variables in marine ecological research. These processes are relevant on a variety of time and space scales, and collectively determine the ocean's ability to sequester carbon dioxide from the atmosphere. Despite several decades of progressively relevant field research we are still lacking a comprehensive, mechanistic understanding of these first order biological oceanographic processes. This has been due in part to limitations imposed by the expeditionary nature of field research and by a lack of reliable methods for the measurements of nutrient inventories and fluxes.

This work highlights the following questions, which will undoubtedly be the focus of future cross-ecosystem comparisons between the Sargasso Sea and the NPSG. Data from the decade-long BATS and HOT programs indicate that rates are similar at both sites for total primary production (150–180 g C m^{-2} yr^{-1}) and total particulate matter export (5–10% of the total primary production)—why then is SRP at least an order of magnitude lower in the Sargasso Sea? Are physical or biological processes driving this difference, or is it some complex combination of processes? Are these ecosystems undergoing changes on time scales of decades such that the current conditions in the Sargasso Sea might be similar to those in the NPSG decades ago, or visa

versa? In general, how can two ecosystems with fairly similar production and carbon export differ in such striking ways?

Here we have added to the understanding of the two prominent differences between these ecosystems. First, SRP is much lower in the surface waters of the Sargasso Sea than in the NPSG. Second, our measurements confirm that the high N + N to SRP ratios in the upper thermocline extend to the surface during periods of deep mixing, but are below 16 : 1, the Redfield ratio, during stratified periods. Based on this ratio alone, new production would appear to be N-limited during stratified periods in the western Sargasso Sea. Export production is controlled by the availability of fixed N which in turn is determined by the activity of N_2-fixing microorganisms. Provided there is sufficient iron to sustain the nitrogenase enzyme system, the influx of fixed-N will eventually result in the depletion of SRP and in a shift in the ambient near surface water N + N : SRP ratio from less than the Redfield ratio following the bloom to greater than the Redfield ratio during periods of enhanced N_2 fixation.

Acknowledgements

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