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A comparison of nutrient-limited productivity in *Sargassum natans* from neritic vs. oceanic waters of the western North Atlantic Ocean

Abstract—Physiological studies and seawater nutrient analysis showed that the productivity of the macroalga *Sargassum natans* was significantly enhanced by higher N and P availability in neritic compared to oceanic waters of the western North Atlantic Ocean (17–40°N). The initial slope of the P vs. I curve (α), photosynthetic capacity ($P_{\max}$), dark respiration, and the light saturation irradiance (I_s) were all significantly greater in neritic compared to oceanic populations. The higher productivity of neritic *S. natans* correlated with higher levels of tissue N and P; C:N, C:P, and N:P ratios averaged 27.9, 347, and 10.2 in neritic populations compared to 49.4, 877, and 18.1 in oceanic populations. Lower alkaline phosphatase activity in neritic vs. oceanic populations corroborated the higher P limitation in oceanic waters. Experimental pulses with dissolved inorganic N, DIN (NO_3^-), and soluble reactive phosphate, SRP (PO_4^{3-}), significantly enhanced net $P_{\max}$ and dark respiration of oceanic but not neritic *S. natans,* demonstrating that increased N and P availability enhances productivity of nutrient-depleted *S. natans.* Higher DIN and SRP concentrations within *Sargassum* windrows along shelf fronts in neritic regions explained the higher productivity and suggest that chronic nutrient limitation in oceanic regions is related to highly patchy nutrient supply.

For almost five centuries, the pelagic *Sargassum* community of the North Atlantic Ocean has been a subject of lively debate among explorers and scientists alike. Columbus first described the vegetation, which is comprised largely of two holopelagic species—*Sargassum natans* and *Sargassum fluitans*—that propagate by vegetative fragmentation. Phycologists have long thought that these plants grow primarily in the Sargasso Sea, where Winge (1923) suggested they grow at "a lively rate." Parr (1939) was similarly impressed that the entire vegetation seemed vigorous in the central area of the Sargasso Sea. Of the 7–10 × 10^6 t of pelagic *Sargassum* in the Sargasso Sea, ~90% is *S. natans* with the remainder consisting of *S. fluitans* and several species of benthic *Sargassum* recruited from neritic waters of the Caribbean, Gulf of Mexico, Straits of Florida, and the West Indies (Parr 1939).

The precept that pelagic *Sargassum* flourishes in surface waters of the Sargasso Sea is a paradox in biological oceanography (Ryther 1956). Primary productivity in this oligotrophic gyre is characteristically low due to limited vertical nutrient flux to surface waters (Ryther and Menzel 1960). The possible importance of nitrogen fixation by epiphytic cyanobacteria has been considered (Carpenter 1972), although incorporation of fixed nitrogen by *Sargassum* has not been demonstrated. Nitrogen fixation in the oceans can be limited by P, organic matter, and trace metals (Paerl et al. 1987), all of which are of relatively low availability in the nutrient-poor surface waters of the Sargasso Sea. Significant rates of N fixation occur in *Trichodesmium* in the Sargasso Sea and Caribbean (Carpenter and Price 1977) and N fixation by *Trichodes-*

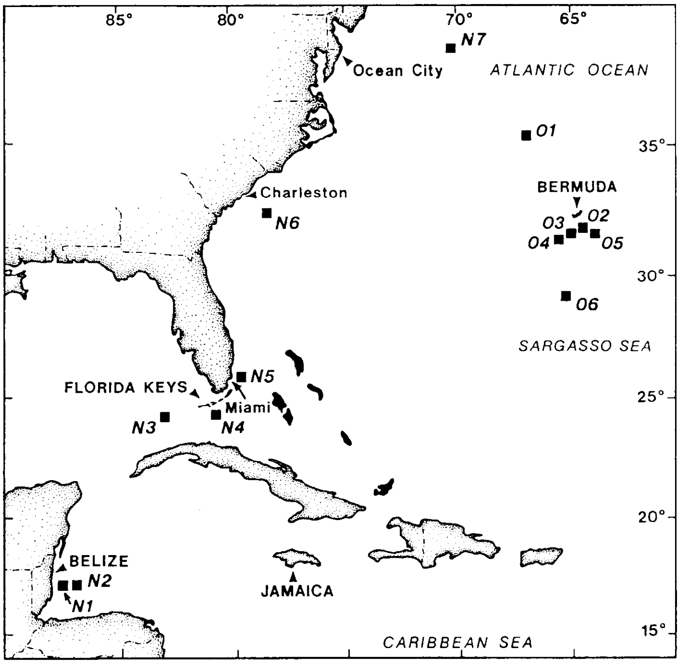

Fig. 1. Locations of neritic (N1–N7) and oceanic (O1–O6) stations where *Sargassum natans* populations were sampled.

mium alone is about a fourth of the total in the oceans (Capone and Carpenter 1982).

Few studies have assessed relationships between nutrient availability and productivity of pelagic *Sargassum*. Carpenter and Cox (1974) found that *Sargassum* productivity was 2-fold greater in the northern Sargasso Sea compared to the southern; however, because seawater nutrient concentrations did not significantly correlate with productivity of *Sargassum,* nutrient regulation of productivity was not apparent. Enrichment bioassays with pelagic *Sargassum* offshore the Florida Keys and Bahamas showed increased productivity with nutrient enrichment, indicating the importance of nutrient availability (Lapointe 1986). The high irradiance experienced by *Sargassum* on the ocean surface likely interacts with the generally low nutrient availability in these oligotrophic surface waters, intensifying the degree of nutrient limitation (Lapointe and Duke 1984).

Considering the broad distribution of *Sargassum* between the nutrient-poor waters of the Sargasso Sea and neritic waters of the Caribbean, Gulf of Mexico, Florida Straits, and Gulf Stream, significant large-scale spatial patterns in nutrient-limited productivity might exist. For example, nutrient enrichment of *Sargassum* could occur in neritic waters at midshelf or shelf-break fronts—areas known to have elevated biological productivity. Standing crops of phytoplankton are higher in the vicinity of such fronts (Pingree et al. 1974) due to elevated nutrient fluxes resulting from increased vertical and lateral mixing (Olson and Backus 1985). I hypothesized that neritic *Sargassum* populations, especially those associated with frontal features, would be significantly enriched with N and P compared to oceanic populations that lack such direct continental influence; if significant neritic enrichment occurs, it should also enhance the productivity of neritic *Sargassum* populations.

As a test of my hypothesis, I performed this study between March 1986 and September 1987 in neritic and oceanic regions of the western North Atlantic. Neritic stations as defined here were those either within continental shelf or slope waters; oceanic stations were those within the generally defined boundaries of the Sargasso Sea (Fig. 1). Windrows of *S. natans,* which result from Langmuir circulation that aligns *Sargassum* parallel with the wind direction (Ryther 1956), were encountered at various locations during the research cruises. Plant samples were collected by divers with an inflatable boat and dipnets. During collection, observations were made by divers as to the abundance and composition of associated fauna, especially fish. The plants were held in a cooler during return to the ship where they were placed into 48-liter polycarbonate aquaria that received continuous flowing seawater pumped from the ocean surface (2 m). Following collection of *S. natans,* two composite samples (~6–10 apical thalli each) were cleaned of macroscopic epizoa and epiphytes, rinsed briefly (3 s) in deionized water, oven-dried at 70°C for 48 h, powdered, and frozen until analysis. Total C and N were determined on a Carlo-Erba CHN analyzer and total P was determined by persulfate digestion followed by analysis for soluble reactive P, SRP (Menzel and Corwin 1965).

Water samples were hand-collected by divers from the water column (0.5-m depth) within the *Sargassum* windrows into clean, high-density polyethylene Nalgene bottles. The water samples were immediately filtered through combusted Gelman 0.45-μm GF/F filters and placed on ice in the dark until shipboard analysis within ~48 h. Concentrations of DIN (dissolved inorganic N) (NH_4^+, NO_3^- + NO_2^-) were determined with a Technicon AutoAnalyzer II and SRP concentrations were measured with a Bausch and Lomb Spectronic 88 fitted with a 10-cm cell for maximum sensitivity. CTD casts were made at several neritic and oceanic stations to characterize the water column for salinity, temperature, and density adjacent to the *Sargassum* windrows. This instrument was calibrated with Copenhagen seawater according to standard published techniques.

The productivity of *Sargassum* was determined by critical analysis of P vs. I curves measured by changes in dissolved oxygen with an Orbisphere (model 2610) oxygen measurement system. Apical thalli (<1 g wet wt) were incubated 24–48 h after collection in clean, 1-liter Wheaton widemouth bottles (that were mixed and cooled via water-driven magnetic stirrers) on the ship's deck under full natural irradiance (I_0) on clear, sunny days between 1000 and 1400 hours. Net photosynthesis (at seven different irradiance levels) and dark respiration were determined in triplicate by methods described by Lapointe and O'Connell (1989). Temperature ranged from 18 to 30°C during these studies (Table 1).

Photosynthetic capacity (net P_{max}) was estimated from the six highest photosynthetic rates in a particular P vs.

Table 1. Locations, dates, temperatures, and dissolved nutrient concentrations ($N = 4$) associated with pelagic *Sargassum* windrows. Nutrient concentrations are in μM, SRP—soluble reactive phosphorus.

Geographic region	Location		Temp. (°C)	NH_4^+	$NO_3^- + NO_2^-$	SRP	N:P
		Neritic					
N1: Carrie Bow Cay, Belize	16°48.5'N, 88°02.0'W	14 May 87	29	1.57±0.52	0.22±0.13	0.14±0.05	12.8
N2: Glovers Reef, Belize	17°10.6'N, 87°53.8'W	25 May 87	29	0.43±0.25	0.16±0.05	0.06±0.03	9.8
N3: Dry Tortugas, Florida Current	24°30.0'N, 82°27.1'W	25 Mar 86	24	0.34±0.21	0.14±0.06	0.07±0.06	6.9
N4: Looe Key, Florida Current	24°35.4'N, 81°24.2'W	15 Mar 86	26	0.29±0.22	0.17±0.08	0.05±0.04	9.2
N5: Miami, Gulf Stream	25°50.8'N, 79°45.9'W	13 Aug 86	30	0.35±0.12	0.17±0.08	0.04±0.03	13.3
N6: Charleston, Gulf Stream	32°10.3'N, 79°28.1'W	15 Aug 87	30	3.32±1.30	0.26±0.13	0.30±0.15	11.9
N7: Ocean City, Gulf Stream	39°50.5'N, 70°10.0'W	18 Aug 87	27	4.27±1.62	0.19±0.04	0.42±0.14	10.6
		Oceanic					
O1: Northern Sargasso Sea	35°10.5'N, 67°29.5'W	23 Aug 87	27	0.21±0.12	0.13±0.07	0.03±0.01	11.3
O2: Central Sargasso Sea	32°10.0'N, 64°60.0'W	28 Apr 86	23	0.23±0.12	0.12±0.06	0.04±0.03	8.8
O3: Central Sargasso Sea	32°33.5'N, 65°27.7'W	19 Aug 86	29	0.12±0.10	0.10±0.04	0.03±0.02	7.3
O4: Central Sargasso Sea	32°33.5'N, 65°27.7'W	19 Aug 86	29	0.19±0.07	0.08±0.05	0.03±0.02	9.0
O5: Central Sargasso Sea	32°04.0'N, 64°22.0'W	28 Feb 87	18	0.15±0.10	0.11±0.05	0.03±0.02	8.7
O6: Southern Sargasso Sea	28°48.1'N, 65°03.3'W	26 Aug 87	28	0.15±0.14	0.12±0.04	0.04±0.03	6.8

I curve; these rates were typically between 0.33 and 0.60 I_0. Gross P_{max} was calculated as the sum of net P_{max} and dark respiration. The initial slope of the P vs. I curve, α, was estimated by least-squares linear regression of the linear portion of the P vs. I curve at low irradiance (i.e. <200 μmol photons m^{-2} s^{-1}). The half-saturation irradiance, I_k, was estimated as

$$I_k = P_{max}/\alpha.$$

I_s was estimated by differentiation of Steele's (1962) equation as

$$I_s = 2.72 I_k.$$

The compensation irradiance, I_c, was determined as the irradiance where the initial slope (α) intersected the abscissa.

Effects of nutrient enrichment on net P_{max} and dark respiration of *S. natans* were also assessed directly through nutrient-enrichment assays. The assays consisted of enriching apical *S. natans* tissue overnight (12 h) for 3 consecutive days with nutrient treatments that included DIN, SRP, DIN+SRP, and a control (no enrichment). Nightly "pulses" of these nutrients were provided by stopping seawater flow to the 48-liter flowing-seawater aquaria and spiking the aquaria to achieve concentrations of 160 μM for DIN (provided as $NaNO_3$) and 16 μM for SRP (provided as NaH_2PO_4).

During the overnight pulses, the *Sargassum* was gently aerated to provide mixing to aid nutrient uptake. After the overnight pulses, seawater flow to the *Sargassum* was restored to high flow rates (100 tank volumes d^{-1}) to minimize tank effects. After 4–5 d of this protocol, P vs. I curves of *Sargassum* were measured. Previous nutrient pulsing studies with tropical macroalgae (Lapointe 1989) have demonstrated the utility of this experimental approach as an assay for nutrient-limited productivity.

Freshly collected *Sargassum* from neritic and oceanic stations was also assayed for alkaline phosphatase activity (APA), an exoenzyme that allows algae to use dissolved organic P pools as a source of phosphate (Kuenzler and Perras 1965). APA is an index of P limitation in macroalgae and was measured by the method of Lapointe (1989).

The P vs. I parameters, tissue C:N:P ratios, and APA data from neritic and oceanic stations were compared with nonparametric statistical tests (Wilcoxon's signed-rank test). Two-way ANOVA was used to analyze effects of the nutrient enrichment assays on the P vs. I parameters. Significance reported below indicates that the probability of the null hypothesis is <0.05.

Populations of *S. natans* were sampled at seven neritic and six oceanic stations (Fig. 1, Table 1). Nutrient concentrations in the water column of the *Sargassum* windrows were higher in neritic compared to oceanic stations (Table 1). The NH_4^+ and SRP concentrations were higher in neritic waters compared to concentrations in oceanic waters (Table 1). $NO_3^- + NO_2^-$ concentrations were also higher in neritic waters compared to concentrations in oceanic waters (Table 1).

Gross P_{max} values of *S. natans* were significantly ($P <$ 0.001) higher in neritic [mean of 2.38 mg C (g dry wt)$^{-1}$ h^{-1}] compared to oceanic populations [mean of 1.17 mg C (g dry wt)$^{-1}$ h^{-1}; Fig. 2]. Gross P_{max} values were highest in neritic populations of the western Caribbean (N1 and N2—Belize Barrier Reef), the Gulf of Mexico (N3—Dry Tortugas) and at shelf frontal zones off the eastern United States (e.g. off Charleston, South Carolina—N6, and Ocean City, New Jersey—N7; Fig. 2). CTD casts within the *S. natans* windrow on the Charleston front showed the presence of lower salinity, higher temperature, and lower density modified shelf water to a depth of ~4 m (Fig. 3A); a CTD cast 0.5 km southeast of that windrow in more offshore blue water showed a relatively uniform water

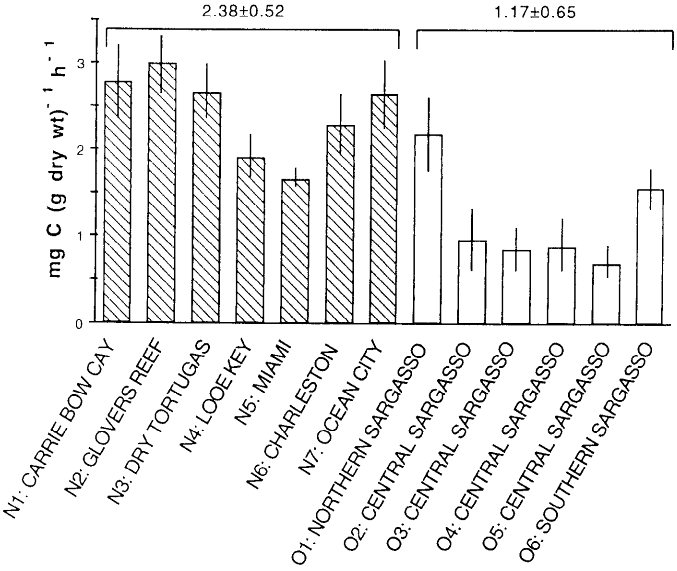

Fig. 2. Gross productivity (gross P_{max}) of *Sargassum natans* determined from P vs. I curves at neritic (N1–N7) and oceanic (O1–O6) stations. Each station value represents a mean ±1 SD ($n = 6$).

column (Fig. 3B) that lacked the continental influence associated with the *Sargassum* windrow.

Lower gross P_{max} values were typical of oceanic populations in the Sargasso Sea. The highest values [~2 mg C (g dry wt)$^{-1}$ h^{-1}] were in populations from the northern Sargasso Sea with the lowest values [< 1 mg C (g dry wt)$^{-1}$ h^{-1}] from those in the central Sargasso Sea. Anomalously high gross productivity [~1.5 mg C (g dry wt)$^{-1}$ h^{-1}] of *S. natans* was associated with a thermal front south of Bermuda in the southern Sargasso Sea (O6; Fig. 2). CTD casts along a 200 km north–south transect (163° heading) showed the presence of 19°C water within 30 m of the surface near this station (O6, corresponding to Sta. 1 in Fig. 4).

Net P_{max} of *S. natans* averaged 1.87±0.42 mg C (g dry wt)$^{-1}$ h^{-1} in neritic waters, significantly ($P < 0.001$) greater than the mean of 0.86±0.48 for oceanic waters. However, the C.V. for net P_{max} of *S. natans* was greater in oceanic waters (56) compared to neritic waters (22). Dark respiration of *S. natans* averaged 0.51±0.13 mg C (g dry wt)$^{-1}$ h^{-1} in neritic waters, significantly ($P < 0.001$) higher than the mean of 0.31±0.18 for oceanic waters. The C.V. for dark respiration was also higher in oceanic waters (60) compared to neritic waters (26).

α values averaged 0.005 mg C (g dry wt)$^{-1}$ h^{-1} μmol m^{-2} s^{-1} in neritic waters compared to a significantly ($P < 0.001$) lower mean of 0.003 in oceanic waters. Values of I_k, I_s, and I_c averaged 359, 976, and 85.8 μmol photons m^{-2} s^{-1} in neritic regions—values significantly ($P = 0.004$) higher than the values of 257, 700, and 64.3 in oceanic waters. Photoinhibition occurred at irradiance levels above saturation in oceanic *S. natans*, as shown in the plots of averaged P vs. I curves for neritic and oceanic waters (Fig. 5).

S. natans had lower N and P relative to C in oceanic

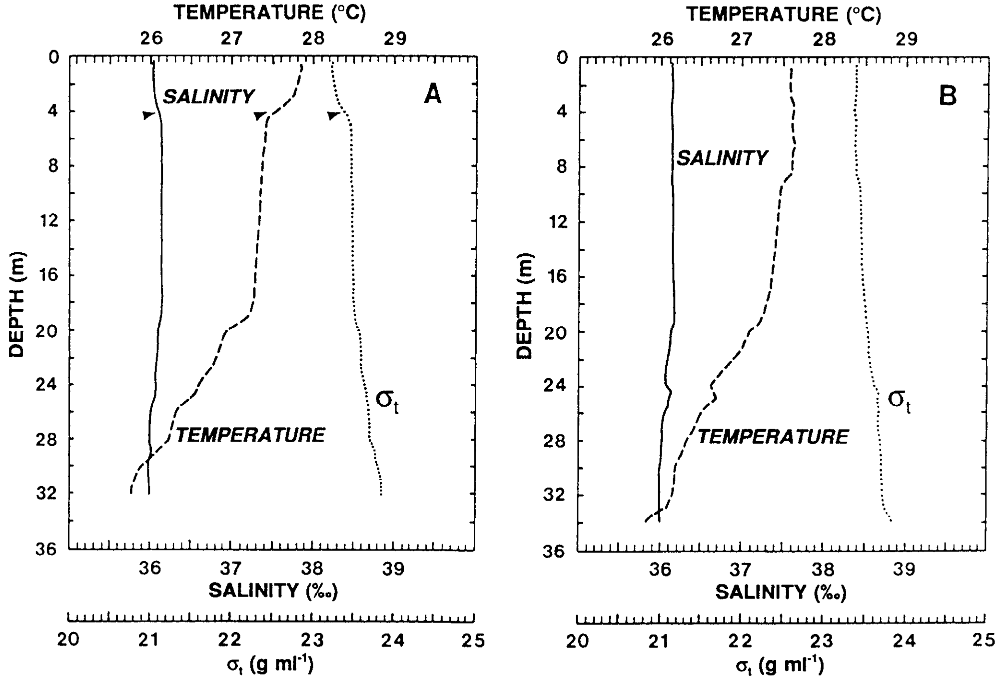

Fig. 3. A. Profile of salinity, temperature, and density (σ_t) of the water column associated with a pelagic *Sargassum* windrow at a midshelf front off Charleston, South Carolina. Note lower salinity and density but higher temperature of surface (<4 m) water associated with *Sargassum*. B. As panel A, but of the water column 0.7 km offshore the frontal zone in blue water; note lack of surface water modification as shown in panel A.

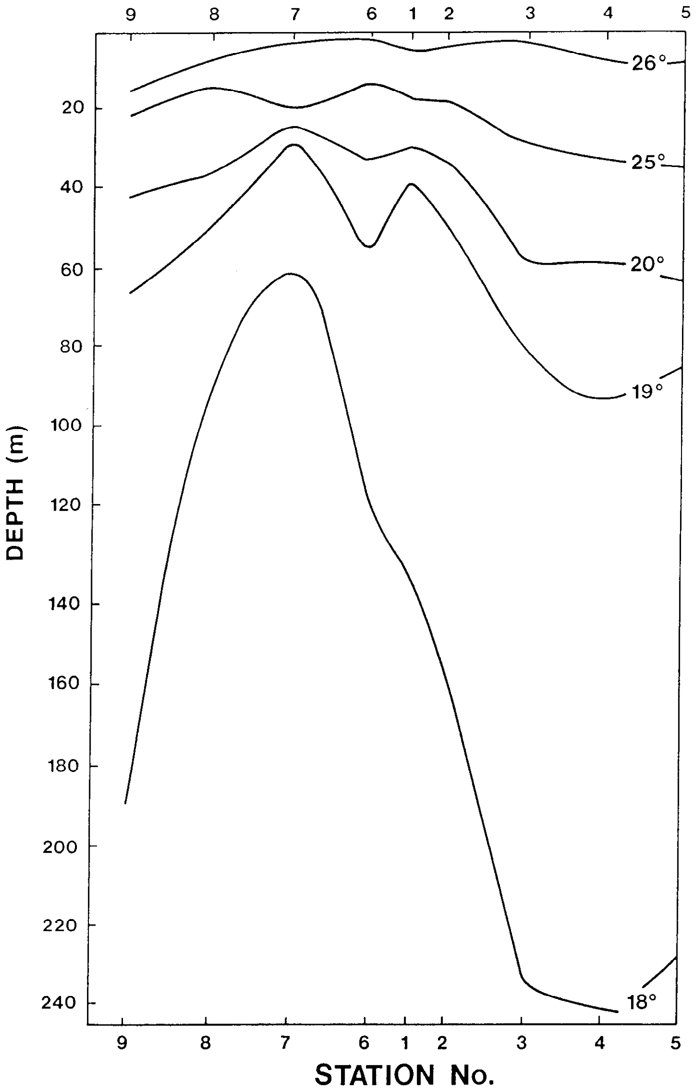

Fig. 4. Thermal front in the southern Sargasso Sea ~240 km southeast of Bermuda. The isotherms were measured by CTD casts along a 112-km transect (163° heading) and show the presence of 19°C water within 30 m of the surface; large windrows of *Sargassum natans* were centered at Sta. 1.

waters compared to neritic waters. The mean C : N ratio of *S. natans* was 49.4 in oceanic waters—significantly ($P = 0.003$) higher than the mean of 27.9 in neritic waters; however, oceanic *S. natans* did have low C : N ratios during a late winter sampling in the central Sargasso Sea off Bermuda (O5; Fig. 6). The mean C : P ratio of *S. natans* was 877 in oceanic waters—significantly ($P = 0.003$) higher than the mean of 347 in neritic waters; oceanic *S. natans* also had a low C : P ratio during one late winter sampling off Bermuda (O5; Fig. 6). The mean N : P ratio of *S. natans* was 10.2 in neritic waters—significantly ($P = 0.006$) lower than the mean of 18.1 in oceanic waters. This higher tissue N : P ratio paralleled a significantly ($P < 0.001$) higher mean APA of *S. natans* [from 10.7±1.9 μM PO_4^{3-} (g dry wt)$^{-1}$ h^{-1} in neritic waters to 28.6±9.3 in oceanic waters].

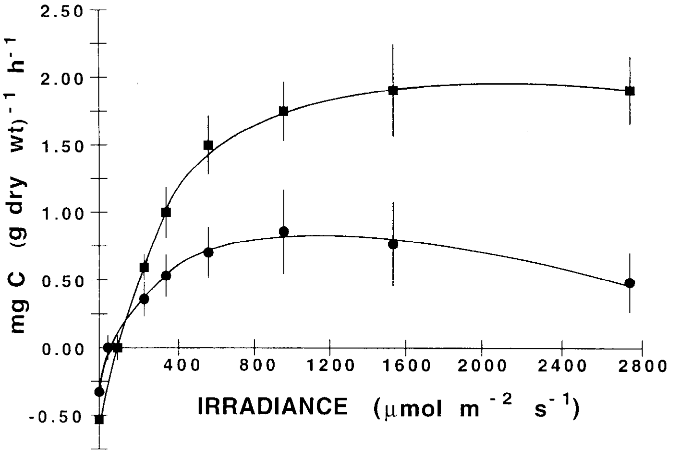

Fig. 5. *P* vs. *I* curves for neritic (■) and oceanic (●) *Sargassum natans*. Data points represent mean values ± SD ($n = 20$).

Experimental nutrient pulses enhanced the net P_{max} of oceanic *S. natans* with more significant effects for N ($P = 0.007$) than P ($P = 0.021$); in contrast, effects of nutrient enrichment were not highly significant for neritic *Sargassum*, although the effects of N were significant at $P = 0.079$. Dark respiration was significantly enhanced by N enrichment ($P = 0.047$) in oceanic waters and P enrichment ($P = 0.002$) in neritic waters.

The mean gross productivity (gross P_{max}) of oceanic *S. natans* in the present study—1.17±0.65 mg C (g dry wt)$^{-1}$ h^{-1} ($n = 42$)—is 34% higher than previous estimates by Carpenter and Cox (1974), who measured a mean gross O_2 productivity of 0.87±0.45 ($n = 34$) for populations from the northern, central, and southern Sargasso Sea. The higher values in my study likely reflect different methodologies. Carpenter and Cox used whole plants of unreported weight in 2.9 liter Fernbach flasks; I used ~0.1 g dry wt plants in 1-liter bottles. I used this method specifically to optimize incubation biomass : volume ratios to <0.1 (g dry wt) liter^{-1}, above which bottle effects cause nonlinearity (due to C limitation, self-shading, etc.) that reduce the apparent productivity in macroalgal assays (Littler 1979).

Gross productivity of neritic *S. natans* was significantly higher than that of oceanic populations in my study and also higher than previously published values for neritic populations. A few measurements of gross productivity by Carpenter and Cox (1974) in continental shelf and Gulf Stream waters averaged 1.27±0.24 mg C (g dry wt)$^{-1}$ h^{-1} ($n = 4$), less than my mean gross P_{max} of 2.38±0.52 ($n = 36$). My mean net P_{max} value for *Sargassum* was 1.87 mg C (g dry wt)$^{-1}$ h^{-1} ($n = 36$), ~400% higher than mean values of net community productivity reported by Blake and Johnson (1976) at Dry Tortugas. Their measurements used entire clumps of *Sargassum* that included epiphytes and associated fauna and their incubation biomass : volume ratio was not reported. My estimate of net P_{max} for neritic *Sargassum* is similar to that reported for *Sargassum polyceratium* in coastal waters of the Florida

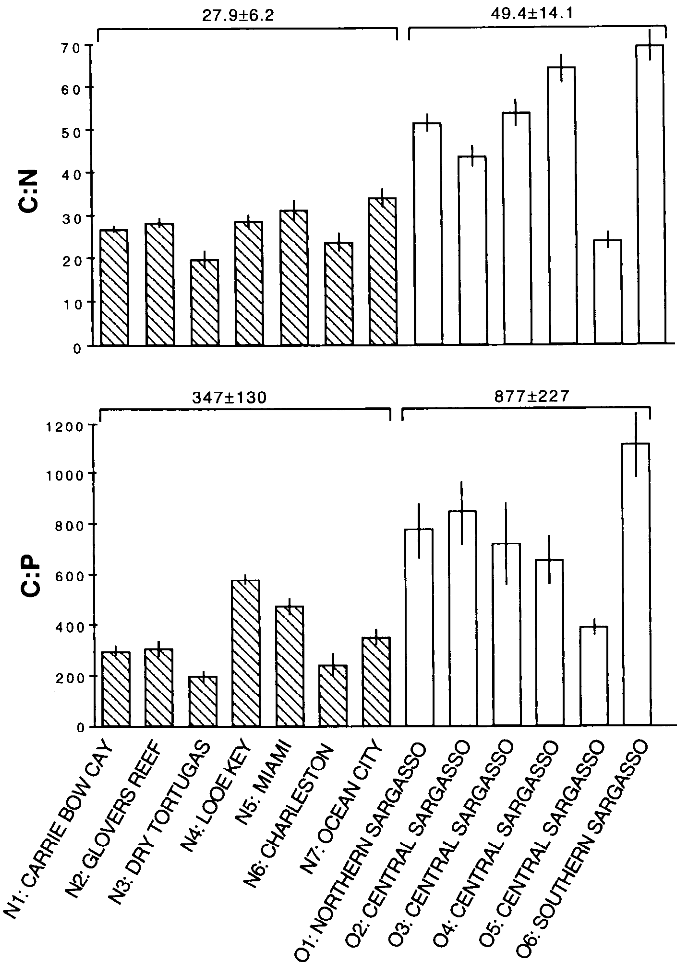

Fig. 6. C : N and C : P ratios of *Sargassum natans* at neritic (N1–N7) and oceanic (O1–O6) stations in the western North Atlantic. Values represent means ±1 SD ($n = 6$).

Keys [e.g. ~2.0 mg C (g dry wt)$^{-1}$ h^{-1}, Kilar et al. 1989], indicating that the light-saturated productivity of pelagic *Sargassum* in neritic waters is of similar magnitude to that of related benthic species. These findings confirm previous suggestions (Lapointe 1986) that productivity (and growth rate) of pelagic *Sargassum* may be greater than previously thought as based on studies of low productivity oceanic plants.

The 65% higher respiration of *Sargassum* in neritic waters during my study agrees with the results of Smith et al. (1973) who found that respiration of the *Sargassum* community was 42% higher in slope-water populations offshore New Jersey compared to oceanic populations southeast of Bermuda. Most (54%) of that increase was attributed to microbial activity, although respiratory contributions from macrofauna (24%) and *Sargassum* (20%) were also significant. Pomeroy and Johannes (1968) also noted higher respiration of ultraplankton in slope water off North Carolina compared to the Sargasso Sea. The higher respiration of *S. natans* in neritic waters is attributable to the increased nutrient availability and assimilation (Syrett 1953) needed to support the higher productivity in these waters.

Several lines of evidence indicated that elevated nutrient availability supported the enhanced productivity of neritic *Sargassum* populations. First, higher net $P_{\max}$ in neritic waters was associated with higher water-column nutrient concentrations within *Sargassum* windrows. Second, experimental N and P pulses significantly increased net $P_{\max}$ and respiration of oceanic but not neritic *S. natans,* demonstrating chronic nutrient-limited productivity of oceanic populations; overall, the effects of N enrichment were more significant than P enrichment in stimulating productivity. Third, the mean C : N and C : P ratios (49.4 and 877) of oceanic *Sargassum* are well above the mean values for marine macrophytes (22 and 700; Atkinson and Smith 1983), suggesting both N- and P-limited productivity. In neritic waters, the mean C : P ratio (347) of *Sargassum* was lower than that of marine macrophytes, suggesting P sufficiency; however, the mean C : N ratio (27.9) of neritic *S. natans* was higher than the mean for marine macrophytes, supporting my observations of weak N limitation in the neritic enrichment assays.

That the C : N ratio of oceanic *S. natans* was elevated more than the C : P ratio over the mean values for marine macrophytes suggests that N limitation is quantitatively more important than P limitation in these oceanic waters. Exceptions to the chronic nutrient limitation in oceanic waters were the anomolously low C : N and C : P ratios during the February 1987 sampling (Sta. O5), which coincided with a winter storm and strong westerly wind patterns. This wind forcing could have transported enriched neritic *Sargassum* into the northern and central Sargasso Sea (Kirwin et al. 1975) and also increased vertical mixing of nutrients to near-surface waters in the Sargasso (Ryther and Menzel 1960). Overall, oceanic *S. natans* populations had high C : N ratios—even those populations associated with the thermal front in the southern Sargasso Sea. These high C : N ratios suggest that atmospheric N_2 fixation by cyanobacterial epiphytes is quite limited as a source of N to *Sargassum* in these waters. P availability, organic matter, and trace metals are factors potentially limiting N_2 fixation in the open ocean (Paerl et al. 1987) and the decrease in tissue N : P of *Sargassum* in neritic waters may reflect an increased ability for N_2 fixation. Carpenter and Cox (1974) noted that the biomass of the cyanobacterial N_2-fixing algal epiphyte *Dichothrix fucicola* was greatest on *Sargassum* in continental shelf waters, followed by northern Sargasso Sea populations, and least on southern Sargasso Sea populations.

P limitation of oceanic *Sargassum* productivity was corroborated by the higher APA in oceanic vs. neritic populations. APA correlates with the degree of P limitation in phytoplankton (Kuenzler and Perras 1965) because it provides PO_4^{3-} via hydrolysis of organic P monoesters. For phytoplankton, Healy (1975) suggested that APA values <1 μM PO_4^{3-} released (g dry wt)$^{-1}$ h^{-1} indicate P deficiency whereas values >2 are likely to be associated with P-sufficient algae. The relatively high APA in *Sargassum* enables this macroalga to sequester PO_4^{3-} from dissolved organic P compounds—a characteristic of adaptive value to growth in oligotrophic oceanic surface waters. McCarthy and Carpenter (1979) noted that although *Trichodesmium* has a very high potential for hydrolyzing phosphomonoesters, it also has a low affinity for SRP uptake ($K_s = 9.0\ \mu M$ SRP). Thus, hydrolysis of sea-surface organic phosphomonoesters, which are concentrated in windrows by Langmuir circulation (Sutcliffe et al. 1963), may result in the buildup of SRP that I observed in neritic *Sargassum* windrows.

Elevated N and P availability in neritic waters enhances productivity of *Sargassum* through a variety of physiological mechanisms that increase photosynthetic performance. The higher α values in neritic compared to oceanic *S. natans* are likely related to nutrient-mediated increases in pigment contents, α values, and photosynthetic efficiency. Although pigment levels were not measured in this study, oceanic plants typically appeared golden-yellow, whereas neritic plants were a darker golden-brown; such differences in seaweed pigment contents are directly related to nutritional status (Lapointe and Duke 1984). Ironically, the "enhanced appearance" and "vigorous growth" of pelagic *Sargassum* noted by Parr (1939) describes the bright-yellow, low-productivity plants that are typical of the nutrient-depleted Sargasso Sea populations. The α values of *S. natans* were low compared to other macroalgae, which range from 0.018 mg C (g dry wt)$^{-1}$ h^{-1} μmol m^{-2} s^{-1} for the optically thick *Codium fragile* to 0.129 for the optically thin *Ulva rigida* (Arnold and Murray 1980). This difference may reflect "sun acclimation" in *Sargassum* that would reduce α values via a reduction in the density or size of algal photosynthetic units (Falkowski 1980).

Nutrient-mediated increases in I_s and $P_{\max}$ values of *S. natans* in neritic waters also allow these populations to more fully use the high irradiance encountered in this pelagic habitat. Arnold and Murray (1980) reported saturation irradiances $<100\ \mu$mol m^{-2} s^{-1} for five species of subtidal temperate green macroalgae. Levavasseur et al. (1991) showed that light saturation irradiances increased up to $\sim500\ \mu$mol m^{-2} s^{-1} for *Ulva rotundata* when sun acclimated. Accordingly, the high I_s values of *S. natans* in my study (ranging from 700 to 976 μmol m^{-2} s^{-1}) reflects sun acclimation. In addition, my nurient pulsing studies showed that N or P enrichment enhanced the $P_{\max}$ of oceanic *S. natans,* confirming that the higher $P_{\max}$ values in neritic populations are a predictable response to increased nutrient availability. Nutrient-limited productivity of oceanic *S. natans* was also associated with photoinhibition, which results in decreased productivity at high irradiance. The dark reactions of photosynthesis that regulate $P_{\max}$ and affect I_s are enzymatically controlled by ribulose bisphosphate carboxylate-oxygenase (RuBPCase)—an N-rich cellular component and a probable rate-limiting step in photosynthesis in macroalgae (Lapointe and Duke 1984).

The nutrient-enhanced productivity of *S. natans* in neritic waters may result, in part, from nutrients excreted from associated fish schools. The highest NH_4^+ and SRP concentrations were measured at Sta. N1, N6, and N7 where dense schools of the filefish *Stephanolepsis hispidus* and *Cantherhines macroceros,* the triggerfish *Xanthichthys ringens,* and juvenile jacks—*Caranyx bartholomaei* and *Caranyx ruber*—were associated with *S. natans*. Fish are attracted to floating objects (Hunter and Mitchell 1968), and dense fish schools are a well-known feature of neritic *Sargassum* (Dooley 1972). I found fewer and less abundant fish schools in oceanic waters—an observation that parallels the lower macrofauna biomass observed in the *Sargassum* community in the Sargasso Sea compared to shelf waters (Smith et al. 1973). In the Pacific Ocean, Leis and Miller (1976) found that larval fish recruitment decreases with increasing distance from shore. Thus, nutrient inputs from fish schools may be an asset to pelagic *Sargassum,* as noted for reef corals (Meyer et al. 1983).

On a larger scale, a variety of nutrient inputs to the coastal waters contribute to nutrient enrichment. Continental runoff via rivers (Meybeck 1982), submarine groundwater discharge (Johannes 1980), shelf-break upwelling (Atkinson et al. 1984), benthic sediment regeneration (Rowe et al. 1975), and atmospheric inputs (Graham and Duce 1979) are all recognized sources of nutrient input. Human influences on several of these nutrient sources have increased in the past century and are increasing coastal ocean productivity, especially along midshelf fronts adjacent to coastlines undergoing agricultural and urban development (Walsh et al. 1981). The recent proliferation of agricultural fertilizer use in the U.S. has correlated with increased nutrient loads to the Gulf of Mexico from the Mississippi River (Turner and Rabalais 1991), as have nutrient inputs from human wastewaters (Peierls et al. 1991) and atmospheric pollution (Fanning 1989). Such inputs may be linked to the unusually large accumulations of *Sargassum* biomass that have fouled shorelines adjacent to the Mississippi River outflow between north Florida and Texas during the past decade (K. Steidinger pers. comm.).

In addition to stranding on coastlines, a significant amount of "new" neritic *Sargassum* production, including tissue nutrients stored by luxury consumption, could be transported horizontally into the Sargasso Sea. Prevailing westerly wind directions and storm tracks over the North American continent (Galloway and Whelpdale 1987) are consistent with transport of *Sargassum* from shelf waters off the southeastern U.S. easterly across the Gulf Stream; interaction of drifting *Sargassum* with northerly flowing surface currents of the Gulf Stream would transport *Sargassum* at a modified vector angle (Kirwin et al. 1975) toward the central and northern Sargasso Sea. Cold-core rings could also enrich *Sargassum* with shelf water as well as transport it to the Sargasso Sea (Ring Group 1981). Such a neritic-oceanic coupling, although as yet an untested hypothesis, could represent a unique phenomenon that has facilitated the adaptation and growth of pelagic *Sargassum* in nutrient-poor surface waters of the Sargasso Sea.

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