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Ryther revisited: nutrient excretions by fishes enhance productivity of pelagic *Sargassum* in the western North Atlantic Ocean

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ABSTRACT

The sustained biomass of pelagic *Sargassum* in nutrient-poor waters of the Sargasso Sea has long been a paradox in biological oceanography. To better understand the mechanisms supporting growth of *Sargassum* over its broad geographic range in the western North Atlantic, we measured growth rate, gross productivity, and C:N:P ratios of both *Sargassum natans* and *Sargassum fluitans* from a variety of neritic (Caribbean Sea, Straits of Florida, Gulf Stream) and oceanic (Sargasso Sea) locations. In neritic areas, the abundance of associated fishes was quantified with a purse seine net designed to minimize fish avoidance of sampling gear. Abundant fish species were also collected for measurements of ammonium and soluble reactive phosphorus excretion rates. Low growth rates and productivity of both *S. natans* and *S. fluitans* were associated with high C:N and C:P ratios in oceanic populations in the Sargasso Sea, confirming strong nutrient-limitation in this oligotrophic gyre. In comparison, both species from the neritic areas had higher productivity and growth rates and lower C:N and C:P ratios, indicating relatively nutrient-enriched growth. *Sargassum* windrows in neritic locations had high abundances of associated fishes (mean of 128 fishes/kg wet weight *Sargassum*), especially juvenile filefish *Stephanolepsis hispidus* (Monacanthidae) and jacks (Carangidae). High excretion rates of ammonium and soluble reactive phosphorus were associated with these mutualistic fishes, which can provide nutrients needed to sustain growth and biomass of *Sargassum*. These findings suggest that new production of *Sargassum* occurs in neritic waters of the western North Atlantic Ocean and Gulf of Mexico, where mutualistic relationships with fishes, especially juvenile filefishes and carangids, contribute to nutrient supply and growth.

1. Introduction

The pelagic *Sargassum* vegetation of the western North Atlantic Ocean represents a unique feature of the global ocean. This floating vegetation is comprised of two holopelagic species (Fig. 1a) – *Sargassum natans* (Linnaeus) Gaillon and *Sargassum fluitans* (Børgesen) Børgesen – that propagate by vegetative fragmentation (Børgesen, 1914; Meyen, 1838) and sustain a biomass estimated at 7–10 × 10^6 tons (Butler and Stoner, 1984; Parr, 1939). Both species are characterized by numerous blades, a highly branched thallus, and air bladders (pneumatocysts), which together create a floating habitat at the ocean surface. These *Sargassum* mats (Fig. 1b–d) often form linear "weedlines" that accumulate at convergence zones in parallel windrows as a result of wind-driven Langmuir circulation (Ryther, 1956). In addition to wind, surface currents (e.g., Loop Current and Gulf Stream) also transport pelagic *Sargassum* throughout the western North Atlantic Ocean, linking populations in the Sargasso Sea with the Caribbean Sea and Gulf of Mexico (Butler et al., 1983; Parr, 1939). *Sargassum* has also been observed sinking in the Sargasso Sea (Johnson and Richardson, 1977; Schoener and Rowe, 1977), providing about 10% of the total particulate organic matter (POM) transfer to the deep-sea community (Rowe and Staresinic, 1979).

Pelagic *Sargassum* is widely recognized as a keystone taxon that provides habitat for a diverse assemblage of invertebrates, fishes, sea turtles, pelagic birds, and marine mammals (Butler et al., 1983; Casazza and Ross, 2008; Haney, 1986; Witherington et al., 2012; Fig. 1e–k). At least 145 species of sessile and motile invertebrates and over 100 species of fish are found in or associated with the *Sargassum* community, many of which are endemic (Bortone et al., 1977; Butler et al., 1983; Casazza and Ross, 2008; Dooley, 1972; Wells and Rooker, 2004). These fish species range from the Sargassum fish (*Histrio histrio*), which are obligate, to juvenile jacks (*Caranx* spp.) and the planehead filefish (*Stephanolepsis hispidus*) that form common and abundant shoals in *Sargassum* mats (Butler et al., 1983; Casazza and Ross, 2008; Coston-Clements et al., 1991; Dooley, 1972). These, and other larval and juvenile fishes, in turn, provide forage for commercially and recreationally important species. These include dolphin fish, tuna, mackerels, barracudas, swordfish, sailfish and marlin

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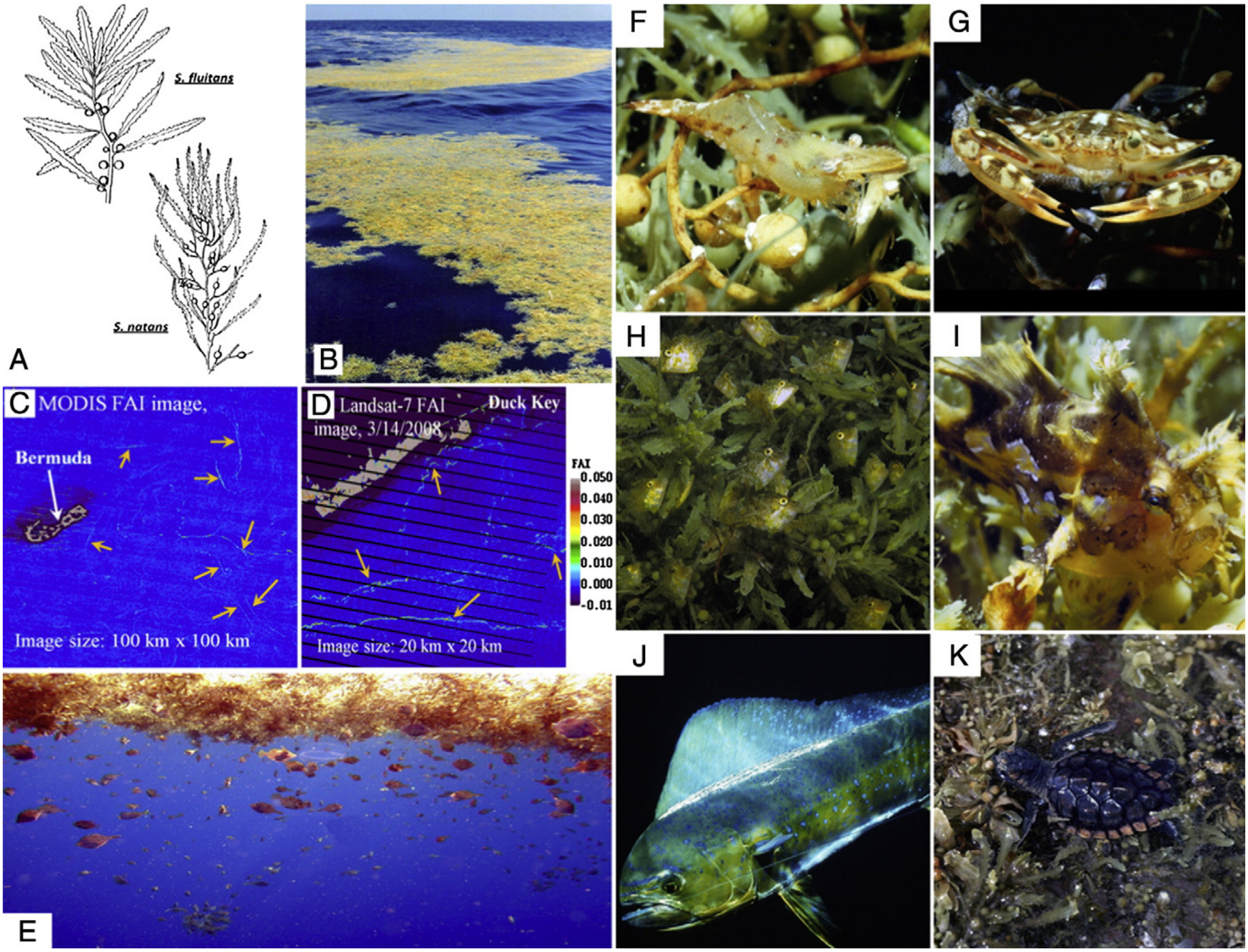

Fig. 1. Images of pelagic *Sargassum* and the diversity of invertebrates and vertebrates commonly associated with pelagic *Sargassum*. A) Two holopelagic species of *Sargassum*, B) typical *Sargassum* mat weedline, C and D) satellite images of *Sargassum*-like features in the Sargasso Sea near Bermuda at 32.30°N 64.77°W (C) and in the Straits of Florida near Duck Key in the Florida Keys at 24.77°N 80.91°W (D), E) diverse biological communities supported by *Sargassum*, F) Sargassum shrimp, *Latreutes fucorum*, G) Sargassum crab, *Portunus sayi*, H) planehead filefish, *S. hispidus*, I) Sargassum fish, *H. histrio*, J) common dolphin fish, *Coryphaena hippurus*, and K) loggerhead sea turtle, *Caretta caretta*. The MODIS/Terra image in (C) has a ground resolution of 250 m while the Landsat-7 image in (D) has a ground resolution of 30 m. Prominent features are annotated with brown arrows. Figure credits: B, K) Brian Lapointe; E) NOAA; F, G, and I) Larry Lipsky; H) Stephen Frink; J) Don DeMaria.

(Coston-Clements et al., 1991; Wells and Rooker, 2004). Juvenile fishes from *Sargassum* mats have been found in the stomachs of dolphin and tuna associated with these floating mats (Dooley, 1972; Manooch and Mason, 1983; Manooch et al., 1984). Larger patches of *Sargassum* contain higher numbers and diversity of fish species (Casazza and Ross, 2008), underscoring the importance of *Sargassum* in providing physical habitat in offshore waters otherwise devoid of physical structure. As a result of their importance to pelagic food webs and endangered species, pelagic *Sargassum* mats were designated as Essential Fish Habitat (EFH) by the National Marine Fisheries Service (NOAA, 1996).

Geographic differences in diversity and abundance of fishes associated with pelagic *Sargassum* have been observed in the western North Atlantic Ocean but the significance of this pattern has not been established. Dooley (1972) reported decreasing fish diversity in collections from neritic waters off Florida to oceanic waters of the Sargasso Sea; some 54 species of fish from 23 families were in this assemblage in neritic waters of the Gulf Stream, compared to only 14 species from 11 families in the Sargasso Sea. Other researchers have made similar observations of either decreasing fish diversity and/or abundance from the Gulf of Mexico (GOM) and Gulf Stream to the Sargasso Sea (Fine, 1970; Stoner and Greening, 1984). The abundance of juvenile fishes observed in the Loop Current and Gulf Stream suggests that the majority of fishes recruit to the *Sargassum* community in neritic (continental shelf and slope) waters in the Loop Current (GOM), Florida Current, and Gulf Stream. The strong association of small, juvenile fishes and their shoaling behavior in the *Sargassum* indicate that this habitat provides shelter from predation. The increasingly close association of fishes to *Sargassum* with decreasing fish size further demonstrates a strong role of this habitat in mitigating predation (Casazza and Ross, 2008). While the benefits of the *Sargassum* habitat have been recognized to reduce predation and increase prey availability for fishes, other potential ecological benefits of fish shoals to *Sargassum* have not been documented. On tropical coral reefs, dense schools of grunts increase nutrient supply to adjacent hermatypic corals through nutrient excretion, increasing pigment content and productivity of their host corals (Meyer and Schultz, 1985a, 1985b; Meyer et al., 1983). Accordingly, increased abundance and species richness of associated fishes in neritic locations (Casazza and Ross, 2008) could hypothetically provide significant nutrient enrichment to *Sargassum* during its circulation towards the Sargasso Sea.

Although *Sargassum* is distributed throughout the western North Atlantic Ocean, oceanographers have long thought that these plants grow primarily from within the Sargasso Sea. Winge (1923) suggested it grows there "at a lively rate" and Parr (1939), similarly impressed with the vigorous appearance of *Sargassum* in the Sargasso Sea, concluded this alga propagates within its boundaries. However, the precept that *Sargassum* flourishes in the Sargasso Sea became a paradox during the 1950s. Due to the very low nutrient concentrations in the surface waters of this oligotrophic central gyre, Ryther (1956) described the Sargasso Sea as a "biological desert" and raised the questions "where do these plants come from and how do they grow?" Indeed, subsequent productivity studies showed relatively low *Sargassum* productivity in the Sargasso Sea compared to continental shelf and Gulf Stream waters, a phenomenon assumed to result from stratification and nutrient limitation in the Sargasso Sea (Carpenter and Cox, 1974; Mann et al., 1980; Ryther and Menzel, 1960). Experimental nutrient-enrichment studies confirmed that both nitrogen (N) and phosphorus (P) potentially limit growth and productivity of *Sargassum* in the Sargasso Sea (Lapointe, 1986, 1995). However, recent advances in satellite remote sensing show abundant *Sargassum*-like features not only in the Sargasso Sea, but also the Straits of Florida and Gulf of Mexico (Gower and King, 2011; Gower et al., 2006; Hu, 2009; Fig. 1c, d), posing the question of how nutrients are supplied to support *Sargassum* growth in these contrasting environments.

Considering the continuous circulation of *Sargassum* by boundary currents in the western North Atlantic Ocean and GOM, we hypothesized that a mutualistic relationship exists between fish shoals and *Sargassum*, whereby nutrient excretion from abundant fishes, particularly in neritic waters, enhances productivity and growth. This hypothesis was tested by: 1) measuring growth rates and gross photosynthesis of *S. natans* and *S. fluitans* in neritic and oceanic waters of the western North Atlantic, 2) using tissue carbon:nitrogen:phosphorus (C:N:P) ratios to gauge the type and degree of nutrient limitation of *S. natans* and *S. fluitans* in neritic and oceanic waters, and 3) determining the abundance and excretion rates of fishes associated with *Sargassum* in neritic waters.

2. Materials and methods

2.1. Measuring growth and productivity of pelagic Sargassum

A series of research cruises was conducted to study the productivity and nutrition of *S. natans* and *S. fluitans* at a variety of neritic and oceanic locations in the western North Atlantic Ocean and Caribbean Sea between March 1986 and June 1990. Because previous reports from this research focused only on *Sargassum natans* (Lapointe, 1995), the present study provides comparative data for both *S. natans* and *S. fluitans*, as well as data on abundance and nutrient excretion rates of associated fishes. This research was conducted in either the U.S. Exclusive Economic Zone (EEZ) or international waters where no clearance or research permits were required. Growth rate and productivity of *Sargassum* were sampled at neritic and oceanic sites, including the Caribbean Sea (Twin Cays and Glovers Reef off the coast of Belize), Straits of Florida (offshore Dry Tortugas, Looe Key in the Florida Keys and Miami), Gulf Stream (offshore Charleston, South Carolina, Cape Fear, North Carolina and Ocean City, New Jersey), northern Sargasso Sea, several stations near Bermuda, and the southern Sargasso Sea (Fig. 2). At each location *S. natans* and *S. fluitans* were collected with dip nets from a rigid inflatable boat, placed in coolers and returned to the research vessel. Associated fauna from these collections, such as invertebrates and fishes, were immediately released back to the sea. The *Sargassum* plants were placed in a flowing-seawater culture system used for the growth and productivity studies. A plastic impeller pump and hull-mounted seawater intake system provided high volumes of surface seawater to a series of clear, 48-liter polycarbonate aquaria used for culturing the *Sargassum* under natural irradiance (I_o). Small populations (5–6 individual thalli, ~20 g wet weight) of *S. natans* and *S. fluitans* were wet-weighed, placed in 35-mm Vexar mesh cages ($n = 6$ per species), and held in the flowing seawater aquaria for four to six days before a final wet weight was measured on a top-loading electronic balance to calculate growth rate (doublings · day^{-1}). Light attenuation by the Vexar mesh did not reduce irradiance <0.6 I_o and was assumed to have insignificant effects on photosynthesis and growth of *Sargassum*, which becomes light-saturated at irradiances >0.33 I_o (Lapointe, 1995). Growth rate data from both *S. fluitans* and *S. natans* from neritic and oceanic waters were analyzed using two-way ANOVA.

Gross productivity (net photosynthesis + dark respiration) of *Sargassum* was determined by critical analysis of photosynthesis vs. irradiance (P vs. I) curves measured by changes in dissolved oxygen with an Orbisphere Model 2610 oxygen measurement system. To avoid the potential confounding effects of fouling by hydroids, bryozoans and barnacles that are common on older *Sargassum* tissue, young apical thalli (<1 g wet weight) of *S. natans* and *S. fluitans* lacking macroscopic epiphytes and epizoa were incubated 24–48 h after collection in clean, 1-liter Wheaton wide-mouth bottles that were mixed and temperature-controlled by seawater-driven magnetic stirrers on the ship's deck. The measurements were recorded between 1000 and 1400 h under full natural irradiance (I_o) on clear, sunny days. Net photosynthesis was measured at seven different irradiance levels ($n = 3$ per irradiance level) using different levels of fiberglass window screening and dark respiration ($n = 3$) was determined in dark bottles. Net photosynthesis was calculated as net $P_{max,}$ which was estimated from the six highest individual photosynthetic rates that typically occurred between 0.33 and 0.57 I_o. Gross photosynthesis was calculated as the sum of net P_{max} and dark respiration ($n = 6$ per location). Because these studies were conducted over a broad range of latitude and season in the western North Atlantic Ocean (Lapointe, 1995), temperature was quite variable, ranging between 18 and 30 °C during the productivity studies. Gross productivity data from both *S. fluitans* and *S. natans* from neritic and oceanic waters were analyzed using a two-way ANOVA.

2.2. Measuring C:N:P of Sargassum tissue

As a test of the neritic nutrient enrichment hypothesis, we collected samples of *S. natans* and *S. fluitans* from the nine neritic and nine oceanic locations during research cruises in 1986 and 1987 (Fig. 2) for tissue C:N:P analysis. Freshly collected composite samples (6–10 apical thalli per species) of *S. natans* and *S. fluitans* were cleaned of macroscopic epizoa and epiphytes, rinsed briefly (3–5 s) in deionized water, dried in a laboratory oven at 70 °C for 48 h, and powdered with a mortar and pestle (Lapointe et al., 1992). Total C and N were determined ($n = 2$ per species for each location) on a Carlo-Erba CHN Analyzer and total P was determined by persulfate digestion followed by analysis for soluble reactive phosphorus (Menzel and Corwin, 1965). The resulting tissue % C, N and P data were used to calculate molar C:N:P ratios to allow comparison with other published data for macroalgae as well as the Redfield Ratio (106:16:1; Redfield, 1934). Calculated molar C:N:P ratios of *S. fluitans* and *S. natans* in neritic and oceanic waters were analyzed using a two-way ANOVA.

2.3. Quantifying the abundance of associated fishes and their nutrient excretions

To quantitatively assess the abundance of fishes associated with pelagic *Sargassum*, we designed and constructed a miniature purse seine to capture pelagic juvenile and adult fishes in *Sargassum* windrows (Hunter et al., 1966). The net was set from a small rigid inflatable boat and used to sample *Sargassum* windrows during research cruises in May 1989 and May 1990 at three neritic locations in the Caribbean region (two samplings near Saba in the eastern Caribbean; one sampling in the Straits of Florida near Dry Tortugas; one sampling near Glovers Reef, Belize; Fig. 2). At each location, a large *Sargassum* mat (~3–4 m across) was approached, a sea anchor attached to the purse seine deployed on the downwind side, and the *Sargassum* encircled in a clockwise direction. The net was closed and pursed as quickly as

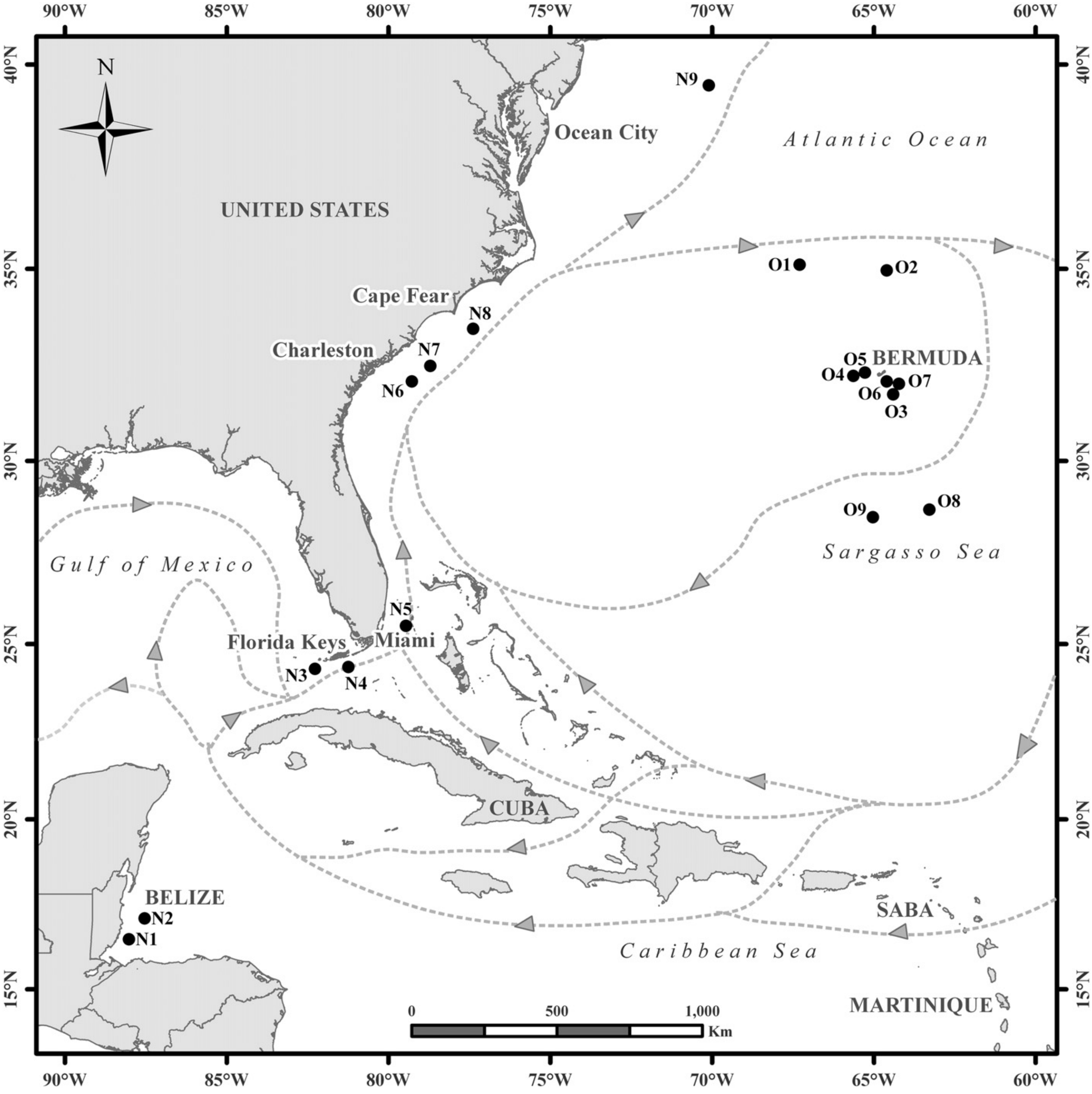

Fig. 2. Map showing neritic (N) and oceanic (O) locations used for these studies of pelagic *Sargassum*. Major currents and flow direction involved with transport of *Sargassum* among the Caribbean, Gulf of Mexico, and Sargasso Sea regions indicated by dashed lines and arrows.

possible. The contents were placed into large PVC coolers and sorted immediately; the *Sargassum* was wet-weighed using a spring scale and returned to the sea. The fishes captured in the cod end of the net were euthanized (by freezing), preserved using formalin and ethanol, and subsequently identified, counted, and measured.

The close spatial relationship between juvenile fishes and pelagic *Sargassum* suggests that nutrient excretion could be readily available for uptake by the algae. To quantify nutrient excretion, we captured abundant, non-protected species of fish from *Sargassum* windrows during early morning hours by carefully using a dip-net and transferring the fishes into large coolers filled with seawater and small floating *Sargassum* plants for transport back to the research vessel. The excess *Sargassum* and associated invertebrates were returned to the sea. We measured excretion rates of ammonium (NH4+) and soluble reactive phosphorus (SRP) by *S. hispidus* ($n = 10$), *Cantherhines pullus* ($n = 8$), *Caranx ruber* ($n = 5$), and *Caranx bartholmaei* ($n = 5$). Single fish (~0.2–0.5 g dry wt.) were transferred into clean, 1-liter Wheaton wide-mouth bottles that were filled with 10 μm-filtered seawater, held in a flowing seawater bath for temperature control, and covered at the top with fiberglass screening to allow exposure to the atmosphere for gas exchange. Fishes were out of the water for no more than four seconds during transfer and showed no signs of injury from handling. Control bottles lacking fishes were also used. *Sargassum* was placed around the bottles to mimic natural conditions within *Sargassum* windrows. Water samples were removed from the bottles at 1-hour intervals with a syringe and immediately analyzed shipboard for NH4+ using a

Technicon AutoAnalyzer II and for SRP using a Bausch and Lomb Spectronic 88 fitted with a 10-cm cell for maximum sensitivity (Lapointe, 1995). Upon termination of the experiments, the fishes were removed from the bottles, euthanized (by freezing), dried in a laboratory oven at 70 °C for 48 h, and weighed on a top-loading electronic balance in the laboratory.

3. Results

3.1. Growth, productivity and C:N:P ratios of *Sargassum*

The shipboard culture studies showed significantly ($p < 0.0001$; Table 1) higher growth rates in neritic compared to oceanic waters (Fig. 3). In neritic waters, growth rates for both *S. natans* and *S. fluitans* were statistically similar (average ~0.06 doublings · day^{-1}) and ranged from 0.041 to 0.091 doublings · day^{-1} and 0.031 to 0.093 doublings · day^{-1}, respectively ($p = 0.9811$; Table 1). The highest growth rates for both species were observed at Dry Tortugas and Looe Key in the Straits of Florida, which could reflect highly productive populations from the GOM being advected by the Loop Current around the Florida Keys and towards the Gulf Stream and Sargasso Sea. Growth rates were only measured for *S. natans* in oceanic waters, which ranged from 0.005 to 0.020 doublings · day^{-1}.

Gross productivity of pelagic *Sargassum* was also significantly higher in neritic compared to oceanic populations ($p < 0.0001$; Table 1, Fig. 4), with no significant difference between *S. fluitans* and *S. natans* ($p = 0.4271$; Table 1). In neritic waters, gross productivity of *S. natans* and *S. fluitans* averaged 2.37 ± 0.40 and 2.53 ± 0.45 mgC · g dry wt. · h,$^{-1}$ ranging from 1.84 to 2.81 mgC · g dry wt. · h^{-1} and 1.89 to 3.2 mgC · g dry wt. · h^{-1}, respectively. In oceanic waters, lower gross productivity rates of *S. natans* and *S. fluitans* averaged 1.15 ± 0.67 and 1.36 ± 0.64 mgC · g dry wt. · h^{-1}, ranging from 0.55 to 1.59 mgC · g dry wt. · h^{-1} and 0.61 to 1.91 mgC · g dry wt. · h^{-1}, respectively.

Table 1
Summary of main effects and interactions from two-way ANOVA of carbon:nitrogen (C:N), carbon:phosphorus (C:P), nitrogen:phosphorus (N:P), growth rates, and gross productivity data. Factors included location (neritic vs. oceanic) and species (*S. natans*, *S. fluitans*).

Source	Sum of squares	*df*	Mean square	*F*	*P*
C:N					
Location	1.67819676	1	1.67819676	11.2	0.0024
Species	0.0277902	1	0.0277902	0.19	0.6702
Location × species	0.07148128	1	0.07148128	0.48	0.4957
Error	4.04715465	27	0.14989462		
C:P					
Location	8.52044841	1	8.52044841	50.96	<0.0001
Species	0.13976247	1	0.13976247	0.84	0.3687
Location × species	0.15169591	1	0.15169591	0.91	0.3493
Error	4.51442591	27	0.16720096		
N:P					
Location	2.67299833	1	2.67299833	68.58	<0.0001
Species	0.04319811	1	0.04319811	1.11	0.3018
Location × species	0.01599173	1	0.01599173	0.41	0.5272
Error	1.05241788	27	0.03897844		
Growth rates					
Location	6.60508656	1	6.60508656	33.45	<0.0001
Species	0.00011499	1	0.00011499	0	0.9811
Location × species	0	0			
Error	2.36959859	12	0.19746655		
Gross productivity					
Location	3.61226253	1	3.61226253	25.73	<0.0001
Species	0.0922791	1	0.0922791	0.66	0.4271
Location × species	0.02312951	1	0.02312951	0.16	0.6892
Error	2.80823888	20	0.14041194		

Tissue analysis for C:N:P contents of pelagic *Sargassum* supported the hypothesis of nutrient enrichment in neritic waters. The C:N:P ratios for *Sargassum* were all significantly lower in neritic compared to oceanic waters (C:N, $p = 0.0024$; C:P, $p < 0.0001$; N:P, $p < 0.0001$; Table 1), with no difference between *S. fluitans* and *S. natans* (C:N, $p = 0.6702$; C:P, $p = 0.3687$; N:P, $p = 0.3018$; Table 1). In neritic waters, C:N ratios for *S. natans* and *S. fluitans* averaged 27 ± 7 and 27 ± 6, ranging from 29 to 35 and 17 to 34, respectively. In comparison, oceanic C:N ratios averaged 47 ± 14 and 46 ± 32, ranging from 24 to 72 and 16 to 108, respectively (Table 1, Fig. 5). The highest C:N ratios for *S. natans* and *S. fluitans* were 72 and 108, respectively, both observed in the southern Sargasso Sea. In neritic waters, C:P ratios for *S. natans* and *S. fluitans* averaged 271 ± 111 and 268 ± 82, ranging from 189 to 483 and 133 to 413, respectively. In comparison, oceanic C:P ratios for *S. natans* and *S. fluitans* averaged 875 ± 254 and 719 ± 416, ranging from 369 to 1113 and 399 to 1551, respectively (Fig. 6). The highest C:P ratios for *S. natans* and *S. fluitans* were 1113 and 1551, respectively, both observed in the southern Sargasso Sea. In neritic waters, N:P ratios for *S. natans* and *S. fluitans* both averaged 10 ± 2 and ranged from 8.4 to 14 and 7.6 to 12.4, respectively. In comparison, oceanic N:P ratios averaged 19 ± 4 and 17 ± 4, ranging from 12.5 to 24.9 and 12.6 to 24.2, respectively (Fig. 7). The highest N:P ratios for *S. natans* and *S. fluitans* were 24.9 and 24.2, values observed in the southern and northern Sargasso Sea, respectively.

3.2. Abundance and excretion rates of associated fishes

The quantitative fish sampling in this study supported previous observations of abundant shoals of juvenile filefishes and jacks in neritic *Sargassum* windrows. In the Caribbean Sea and Straits of Florida, juvenile *C. ruber* (bar jack) and *S. hispidus* (planehead filefish) were the most abundant fish species collected with a mean of 50 ± 25 and 45 ± 27 individuals kg^{-1} wet weight *Sargassum*, respectively (Fig. 8). In the eastern Caribbean Sea near Saba, shoals of juvenile *C. ruber* were more abundant compared to shoals in the Straits of Florida and western Caribbean Sea, with a mean of 183 ± 64 and 40 ± 22 individuals kg^{-1} *Sargassum*, respectively. Conversely, larger numbers of juvenile *S. hispidus* were collected in the Straits of Florida and western Caribbean Sea compared to the eastern Caribbean Sea, with a mean of 161 ± 28 individuals kg^{-1} *Sargassum*, respectively. Visual fish counts made by divers along *Sargassum* windrows during the seine hauls confirmed that dense shoals, up to a hundred fish or more kg^{-1} of *Sargassum*, were common. Other fish species, including the pipefish *Syngnathus pelagicus*, the orange-spotted filefish *C. pullus*, and the Sargassum fish *H. histrio*, were also collected in significant numbers (Fig. 8).

Individual fish excretion rates for NH4+ ranged from 3.8 to 107 μM · g dry wt.$^{-1}$ · h^{-1}, with the lowest mean rate (18 μM · g dry wt.$^{-1}$ · h^{-1}) in *S. hispidus* and the highest mean rate (70 μM · g dry wt.$^{-1}$ · h^{-1}) in *C. bartholmaei* (Fig. 9). Individual excretion rates of SRP by fishes ranged from 0.08 to 4.30 μM · g dry wt.$^{-1}$ · h^{-1}, with the lowest mean rate (0.43 μM · g dry wt.$^{-1}$ · h^{-1}) in *C. ruber* and the highest (1.24 μM · g dry wt.$^{-1}$ · h^{-1}) in *S. hispidus* (Fig. 9).

4. Discussion

The results of these studies support the hypothesis that fish shoals contribute substantial nutrients to pelagic *Sargassum*, enhancing growth and productivity, especially in neritic locations where fish shoals are common. This hypothesis was supported by multiple lines of evidence, including: 1) increased growth rate and productivity in neritic waters, 2) lower C:N:P ratios in *S. natans* and *S. fluitans* in neritic compared to oceanic waters, and 3) abundant juvenile fishes in neritic waters, which excrete substantial amounts of NH4+ and SRP into the pelagic *Sargassum* habitat.

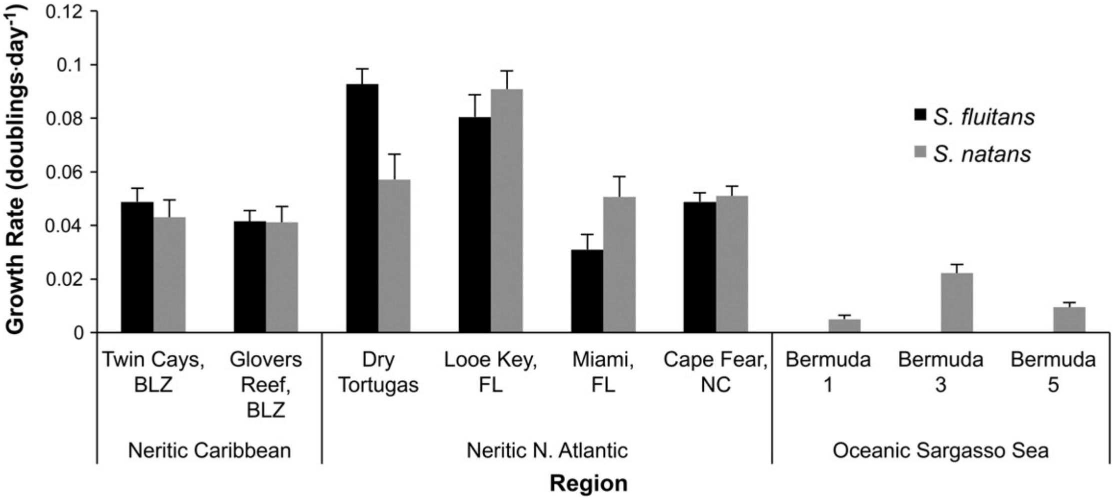

Fig. 3. Growth rates of *Sargassum*. Measured as doublings · day^{-1} of *S. fluitans* and *S. natans* in neritic [Caribbean (Belize) and North Atlantic] and oceanic (Central Sargasso Sea) waters. Values represent means ± S.E. (n = 6). Growth rates for *S. fluitans* were not measured at oceanic locations and should not be interpreted as zero values.

4.1. Geographic variability in growth, productivity and C:N:P contents

Our findings support previous observations of higher *Sargassum* productivity in more nutrient-enriched neritic waters compared to oceanic waters of the Sargasso Sea (Lapointe, 1995), which have long been considered a "biological desert" (Ryther, 1956). Based on growth rates ranging from 0.02 doublings · d^{-1} (oceanic waters) to 0.09 doublings · d^{-1} (neritic waters), our data suggest that *S. natans* and *S. fluitans* could double their biomass in as little as ~11 days in neritic waters compared to ~50 days or more in the Sargasso Sea. Our maximal growth rates are in close agreement with laboratory growth studies of *S. natans* and *S. fluitans*, which reported maximal growth rates of 0.07 and 0.10 doublings · d^{-1}, respectively, between 24 and 30 °C (Hanisak and Samuel, 1987). Our doubling time estimate for the Sargasso Sea populations is in close agreement with those of Carpenter and Cox (1974), who used ^{14}C-based techniques and reported C turnover times of ~40 days for the Sargasso Sea. The higher gross productivity values in neritic waters are also comparable to reported *Sargassum* photosynthesis measurements of 2.4 mgC · g dry wt. · h^{-1} for the eastern Bahamas Bank (Lapointe, 1986) and 5.5 mgC · g dry wt. · h^{-1} for outer shelf waters off the coast of North Carolina (Howard and Menzies, 1969). The lower gross productivity values we found in oceanic waters of the Sargasso Sea are similar to values ranging from 0.13 to 1.04 mgC · g dry wt. · h^{-1} for the western Sargasso Sea (Carpenter and Cox, 1974).

However, one exception to the general spatial pattern in *Sargassum* productivity was apparent. Anomalously high levels of gross productivity (>1.5 mgC · g dry wt. · h^{-1}) were observed for both *S. natans* and *S. fluitans* at a station south of Bermuda in the southern Sargasso Sea (Fig. 4). A series of CTD casts along a 200-km long transect (163° heading) showed the presence of 19 °C water within 30 m of the surface during the sampling, indicating vertical mixing at this location (Lapointe, 1995). These observations are consistent with mixed-layer thermocline models that show upward flux of nitrate in pulse-like injections to the euphotic zone, which can account for estimates of new production in the Sargasso Sea (Jenkins and Goldman, 1985; Michaels and Knap, 1996).

The growth and productivity measurements suggest that traditional views of pelagic *Sargassum* sustaining itself in the Sargasso Sea (Parr, 1939) may not be entirely accurate. The low growth rates and productivity of *S. natans* and *S. fluitans* in the Sargasso Sea as measured in this study, and others (Carpenter and Cox, 1974), support the view

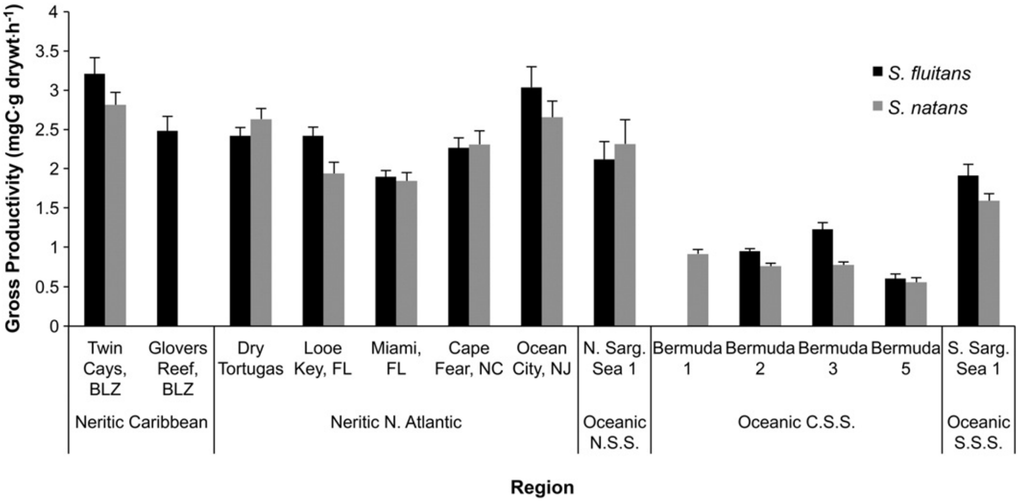

Fig. 4. Gross productivity of *Sargassum*. Measured as mgC · g dry wt. · h^{-1} of *S. fluitans* and *S. natans* in neritic [Caribbean (Belize) and North Atlantic] and oceanic (Northern Sargasso Sea, Central Sargasso Sea, and Southern Sargasso Sea) waters. Values represent means ± S.E. (n = 6). Gross productivity for *S. natans* at the Glovers Reef neritic location and *S. fluitans* at the Bermuda 1 oceanic location was not measured and should not be interpreted as zero values.

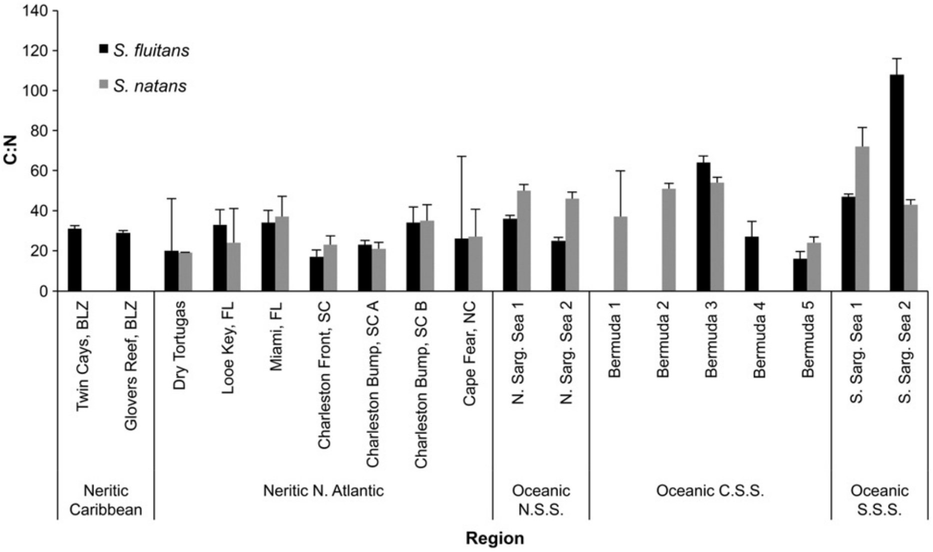

Fig. 5. C:N ratios of *Sargassum*. Carbon:nitrogen (C:N) ratios of *S. fluitans* and *S. natans* in neritic [Caribbean (Belize) and North Atlantic] and oceanic (Northern Sargasso Sea, Central Sargasso Sea, and Southern Sargasso Sea) waters. Values represent means ± S.E. (n = 2). C:N for *S. natans* at the Twin Cays, Glovers Reef, and Bermuda 4 locations, as well as *S. fluitans* at the Bermuda 1 and 2 oceanic locations were not measured and should not be interpreted as zero values.

that this nutrient-poor gyre has limited capacity to support oceanic productivity due to limited vertical mixing and nutrient supply (Børgesen, 1914; Cavender-Bares et al., 2001; Ryther, 1956; Ryther and Menzel, 1960). Hypothetically, higher growth rates and productivity of *Sargassum* from continuous, long-term circulation through the Caribbean Sea, GOM, Straits of Florida, and Gulf Stream provide nutrient enrichment and new production via advection from neritic areas. The concept of new production, originally developed by Dugdale and Goering (1967), distinguishes between new inputs of nitrogen, such as nitrate from vertical mixing, and regenerated sources, such as ammonium and SRP from fish or zooplankton excretions. We extend the concept herein to distinguish between vertically mixed nutrients within the Sargasso Sea from those such as excretions from abundant fish shoals, shelf-break upwelling, river discharges, and atmospheric deposition that could result in relatively nutrient enriched *Sargassum* in shelf or slope waters in neritic regions, especially along frontal zones (Franks, 1992).

Compared to the Redfield Ratio (106:16:1) based on particulate matter in the oceans, the C:N:P data suggest that both N and P potentially limit growth of pelagic *Sargassum*, especially in nutrient-poor waters of the Sargasso Sea. The Redfield proportions of C:N (6.6) and C:P (106) are considerably lower than the values observed in pelagic *Sargassum*, due in part to the relatively greater production of carbon-rich compounds in *Sargassum* compared to phytoplankton. In a global survey of benthic marine macroalgae and seagrasses, the mean C:N:P contents were 700:35:1, resulting in a mean C:N of 20 and C:P of 700 (Atkinson and Smith, 1983). The corresponding C:N ratios for pelagic *Sargassum* averaged 27 and 47 in neritic and oceanic waters, respectively, suggesting these pelagic populations are more N-limited than benthic macroalgae and seagrasses globally. Previous studies suggested that ~44% of the *Sargassum* N demand may be met through N_2-fixation associated with epiphytic N_2-fixing cyanobacteria (Carpenter, 1972; Hanson, 1977; Phlips and Zeeman, 1990). However, the elevated C:N values we observed, especially in oceanic waters,

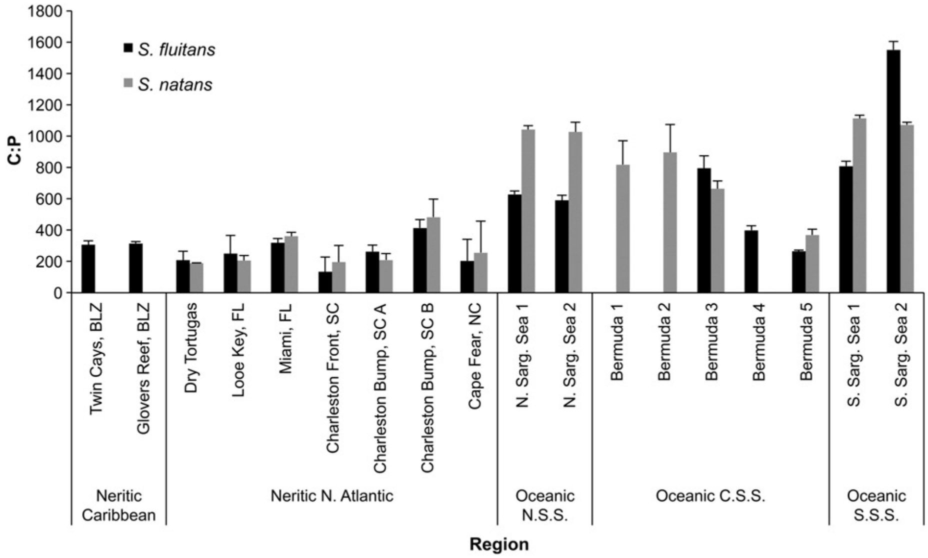

Fig. 6. C:P ratios of *Sargassum*. Carbon:phosphorus (C:P) ratios of *S. fluitans* and *S. natans* in neritic [Caribbean (Belize) and North Atlantic] and oceanic (Northern Sargasso Sea, Central Sargasso Sea, and Southern Sargasso Sea) waters. Values represent means ± S.E. (n = 2). C:P for *S. natans* at the Twin Cays, Glovers Reef, and Bermuda 4 locations, as well as *S. fluitans* at the Bermuda 1 and 2 oceanic locations were not measured and should not be interpreted as zero values.

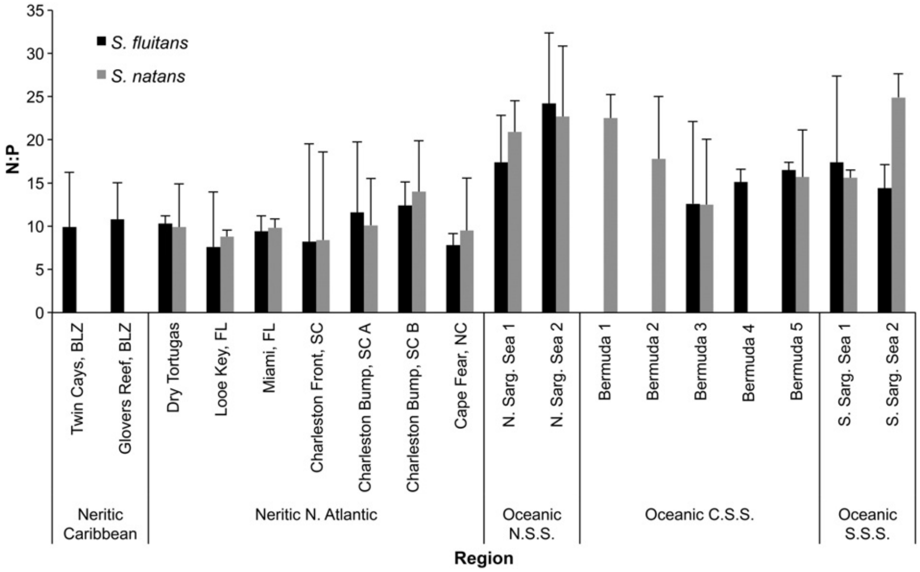

Fig. 7. N:P ratios of *Sargassum*. Nitrogen:phosphorus (N:P) ratios of *S. fluitans* and *S. natans* in neritic [Caribbean (Belize) and North Atlantic] and oceanic (Northern Sargasso Sea, Central Sargasso Sea, and Southern Sargasso Sea) waters. Values represent means ± S.E. (n = 2). N:P for *S. natans* at the Twin Cays, Glovers Reef, and Bermuda 4 locations, as well as *S. fluitans* at the Bermuda 1 and 2 oceanic locations were not measured and should not be interpreted as zero values.

indicate that pelagic *Sargassum* may have limited access to this N source that would be available to *Sargassum* through nutrient cycling within the community. Furthermore, the strong N-limitation of *Sargassum* we observed in oceanic waters is consistent with current biogeochemical models that recognize limitations on oceanic N-fixation by aeolian Fe-rich dust and P inputs from fluvial sources in coastal regions (Falkowski et al., 1998). Alternatively, our results showed that dense fish shoals have the capacity to substantially increase NH4+ concentrations in the seawater surrounding *Sargassum*, which would be immediately available for uptake. N-limited brown seaweeds do have high uptake rates of NH4+, especially when supplied as pulses similar to those of fish excretions as observed in this study (Rosenberg et al., 1984).

Likewise, the high C:P ratios in pelagic *Sargassum* indicate strong P-limitation, especially in oceanic waters of the Sargasso Sea. Although the mean C:P ratio of ~270 in neritic locations was below the global average of 700, the mean of ~797 for *Sargassum* in oceanic waters supports previous observations of strong P-limitation in the Sargasso Sea (Lapointe, 1986, 1995). This is further supported by the significant increase in N:P ratios of *Sargassum* from 10 in neritic waters to 18 in oceanic waters, illustrating how the degree of P-limitation (relative to N) increased in more offshore, P-depleted waters of the Sargasso Sea. Whereas the N:P ratios of *Sargassum* in oceanic waters – 18 – were above Redfield proportions of 16, they were much lower than values ranging from 42 to 79 for benthic *Sargassum* on shallow, N-enriched and P-limited coral reefs on the north coast of Jamaica (Lapointe et al., 2011). Nevertheless, the relatively higher degree of P-limitation in oceanic waters correlates with three-fold higher alkaline phosphatase activity of *S. natans* in oceanic versus neritic waters, which allows these oceanic P-limited populations to sequester SRP from dissolved organic P pools (Lapointe, 1995). Our findings of significant increases in N:P ratios of *Sargassum* from neritic to oceanic waters, together with N:P values ranging up to ~25 in the Sargasso Sea, are consistent with a growing body of evidence suggesting primary P-limitation in open ocean waters (Downing, 1997).

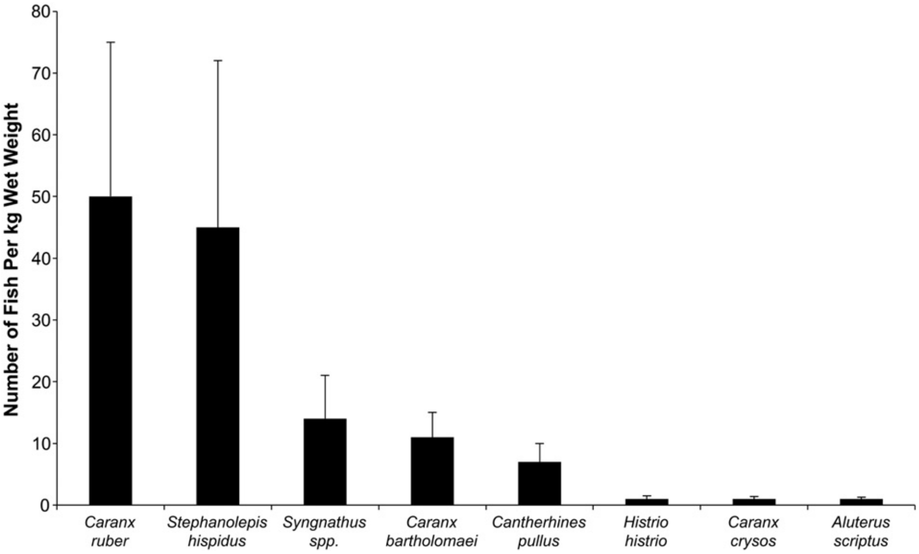

Fig. 8. Abundance of various fish species associated with pelagic *Sargassum*. Values represent means ± S.E. (n = 4) kg^{-1} wet weight of *Sargassum*.

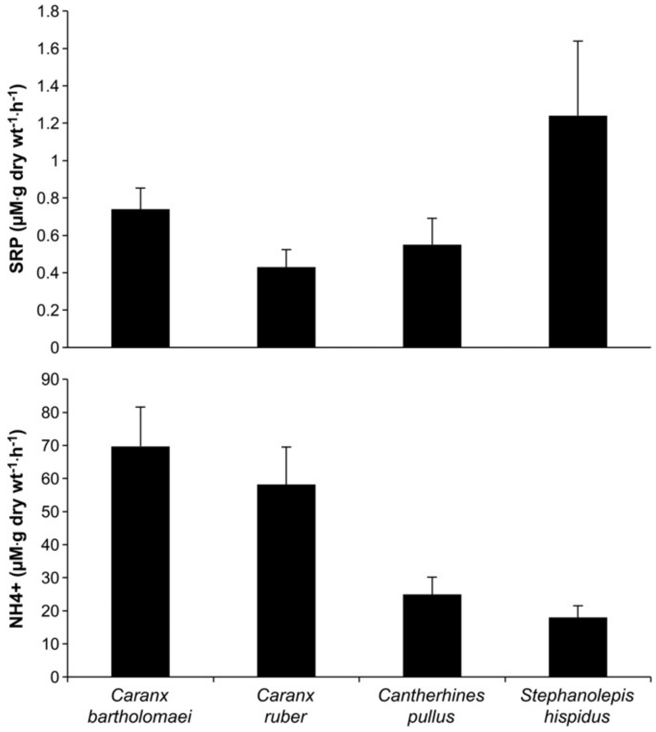

Fig. 9. Excretion rates of soluble reactive phosphorus and ammonium by fishes associated with pelagic *Sargassum*. Measured as $\mu M \cdot g$ dry wt $\cdot\ ^{-1} \cdot h^{-1}$ for *S. hispidus* (n = 10), *C. pullus* (n = 8), *C. ruber* (n = 5), and *C. bartholmaei* (n = 5), all of which are commonly associated with *Sargassum*.

4.2. Importance of fishes as a nutrient source

The patterns of abundance for dominant fish species observed (overall mean of 128 fishes kg^{-1} wet weight of *Sargassum*) were similar to previous collections from pelagic *Sargassum* off North Carolina, Florida and the GOM, where *S. hispidus* and carangids dominated the fish assemblages (Casazza and Ross, 2008; Dooley, 1972; Wells and Rooker, 2004). The high abundance of juveniles in the fish assemblages, and their behavior in maintaining a close spatial relationship to the *Sargassum*, indicate that this habitat provides shelter from predation (Casazza and Ross, 2008). Assemblages of juvenile fishes associated with *Sargassum* are more diverse and abundant in neritic waters, and their NH4+ and SRP excretions can potentially account for much of the nutrient demand of *Sargassum*. Based on the spatial and functional relationships between fish abundance and the productivity and nutrition of pelagic *Sargassum*, we propose that the *Sargassum*-fish relationship we studied represents a heretofore unrecognized mutualism. Within this *Sargassum*-fish mutualism, nutrients that normally become easily dispersed in oligotrophic waters are provided to *Sargassum* by closely associated fishes through dissolved and highly reactive metabolic byproducts (ammonium, SRP). In return, *Sargassum* provides these fishes a nursery habitat and potential protection from predation (Casazza and Ross, 2008; Wells and Rooker, 2004). In the case of the Sargassum fish, *H. histrio*, which has a more intimate relationship with *Sargassum*, such a relationship would constitute a symbiosis. Many symbioses and/or mutualisms in the marine environment are thought to involve nutrient transfer between partners and have been documented in a wide range of organisms including fishes to kelp (Bray et al., 1986), sponge to rhodophyte (Davy et al., 2002), fishes to coral (Holbrook et al., 2008; Meyer and Schultz, 1985a, 1985b), and anemonefishes to anemone (Fautin, 1991; Roopin et al., 2008). Other studies have shown the importance of *Sargassum* in mediating predation (Brooks et al., 2007).

Dissolved nutrient excretions from fishes are significant sources of nutrients in coral reef ecosystems (Meyer and Schultz, 1985a, 1985b; Meyer et al., 1983) and kelp beds (Bray et al., 1986), but their importance to pelagic *Sargassum* has not been previously quantified. The nutrient excretion rates in this study, combined with the measured fish abundances (mean of 128 fishes kg^{-1} wet weight *Sargassum*), indicate that juvenile fishes can potentially account for a large fraction of the nutrient demand of pelagic *Sargassum*. The NH4+ excretion rates we measured are higher than other published values for fishes, which range from 2.0 to 12.5 $\mu M \cdot g$ dry $wt.^{-1} \cdot h^{-1}$ for adult reef fishes (Meyer and Schultz, 1985a). The higher rates of NH4+ excretion in our study would result from the small size of fishes in our experiments (<50 mm SL) that are typical of the *Sargassum* community (Casazza and Ross, 2008); weight-specific excretion rates are inversely correlated with body size (Meyer and Schultz, 1985a). The highest NH4+ excretion rates were those of the juvenile carangids, *C. ruber* and *C. bartholmaei*, which is likely related to the high metabolic rates in these fishes. Fish supply of NH4+ was highest from *S. hispidus* and the total fish supply of NH4+, combined from *S. hispidus*, *C. ruber*, *C. bartholmaei*, and *C. pullus*, could potentially support more (280%) than the N demand of *Sargassum*, assuming a C:N ratio of 27, gross productivity of $3 mgC \cdot g$ dry wt $^{-1} \cdot h^{-1}$, and that all excreted NH4+ is available for uptake by *Sargassum*. SRP supplied by *S. hispidus* was also the highest of all fish species, and using the same assumptions, total SRP from all four fish species could potentially be much (70%) of the *Sargassum* demand. The importance of nutrient enrichment by abundant fishes (and other members of the assemblage) is supported by 2–3 times higher SRP concentrations within mats of *Sargassum* as compared with *Sargassum*-free surface water (Culliney, 1970). Higher dissolved NH4+ and SRP concentrations have also been reported in neritic versus oceanic *Sargassum* windrows, with concentrations in neritic waters up to 4.27 μM and 0.42 μM, respectively (Lapointe, 1995).

5. Conclusions

The historical view that pelagic *Sargassum* sustains itself in oligotrophic waters of the Sargasso Sea (Børgesen, 1914; Parr, 1939) needs revision in light of these findings. The low growth rates of pelagic *Sargassum* in the Sargasso Sea, combined with relatively low gross productivity and high C:N and C:P ratios, indicate strong nutrient limitation by both N and P. Significantly lower C:N and C:P ratios in neritic waters reduce nutrient limitation, resulting in higher gross productivity and rapid growth of *Sargassum*. The fastest growth rates for both *S. natans* and *S. fluitans* were observed near Dry Tortugas and Looe Key in the Straits of Florida, which could reflect highly productive, nutrient-enriched populations advected from the GOM. This was supported by the relatively low C:N and C:P ratios of *S. natans* and *S. fluitans* at the Dry Tortugas, which suggests nutrient enrichment in the GOM. These findings are consistent with recent C and N isotope analysis of *Trichodesmium* in neritic and oceanic regions of the GOM, which similarly reported significant N-enrichment associated with river discharges and terrestrial runoff (Dorado et al., 2012). *Sargassum* populations advected by the Loop Current and transported around the Florida Keys could also be retained in the Tortugas Gyre, where recruitment of juvenile fishes and additional nutrient enrichment of *Sargassum* could occur (Lee et al., 1994). The Florida Current would transport these enriched *Sargassum* communities northwards to the Gulf Stream and into the northern Sargasso Sea. This physical connectivity is supported not only by our observations, but also those of Carpenter and Cox (1974) who observed the most productive *Sargassum* populations of the Sargasso Sea occur in the northern region where relatively nutrient-enriched *Sargassum* populations are found.

Accordingly, we hypothesize that populations of pelagic *Sargassum* in the Sargasso Sea may rely on sustained inputs of new production that occurs during circulation between the Caribbean, GOM, Straits of Florida, and Gulf Stream, which is facilitated by a mutualism involving nutrient excretions by abundant juvenile fishes. The significant nutrient inputs from fishes and other inhabitants suggests that these mutualistic relationships have evolved over time and explains the paradox of how these highly diverse and productive communities sustain themselves in what has long been considered a "biological desert" (Ryther, 1956). This model is supported by recent interpretation of satellite remote sensing that shows seasonal transport of *Sargassum* from the GOM to the Sargasso Sea during the late spring and summer (Gower and King, 2011). These findings indicate that seasonal and year-to-year variability in physical, chemical and biological dynamics in the GOM may play a critical role in sustaining biomass of pelagic *Sargassum* in the linked populations in the Straits of Florida, Gulf Stream and Sargasso Sea.

Acknowledgements

We dedicate this paper to the memory of John H. Ryther (1922–2006), whose seminal research on nutrients and primary production in the Sargasso Sea inspired this research. We thank the captains and crews of the RV *Columbus Iselin*, RV *Calanus*, RV *Weatherbird*, and RV *Cape Hatteras* for their support of the shipboard studies. Julie Bishop, Luigi Ferrer, Richard Brown, Barbara Brown, Mark Clark and William Matzie provided technical assistance. Ken Lindeman is gratefully acknowledged for help with the design and construction of the purse seine net. An early draft of this paper was improved by Laura Herren, Margaret Vogel and the comments of several anonymous reviewers. This research was supported by NSF grants OCE 85–15492 and OCE 88–12055 and a Red Wright Fellowship from the Bermuda Biological Station. This is contribution number 1919 from the Harbor Branch Oceanographic Institute at Florida Atlantic University. **[SS]**

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