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Water quality, isoscapes and stoichioscapes of seagrasses indicate general P limitation and unique N cycling in shallow water benthos of Bermuda

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Abstract

Striking spatial patterns in stable isotope ratios (isoscapes) and elemental ratios (stoichioscapes) of seagrass leaves and the water column nutrients indicate general P-limitation of both water column and benthic primary productivity on the Bermuda Platform, and they highlight the role of the Bermuda Islands as a source of N and P. We found consistent differences among the four seagrass species (*Syringodium filiforme*, *Thalassia testudinum*, *Halodule* sp. and *Halophila decipiens*) in the N, P, δ^{13}C and δ^{15}N of leaf tissues. The δ^{15}N of seagrass leaves was especially variable, with values from −10.1 to 8.8 ‰, greatly expanding the reported range of values for all seagrass species globally. Spatial patterns from both the water column and the seagrass leaves indicated that P availability was higher near shore, and δ^{15}N values suggest this was likely a result of human waste disposal. Spatially-contiguous areas of extremely depleted seagrass δ^{15}N suggest unique N sources and cycling compared to other seagrass-dominated environments. Seagrass N : P values were not as far from the stoichiometric balance between N and P availability as in the water column, and there were no strong relationships between the water column N : P and the seagrass N : P. Such isoscapes and stoichioscapes provide valuable ecogeochemical tools to infer ecosystem processes as well as provide information that can inform food web and animal movement studies.

1 Introduction

Water quality in coastal environments can be episodic and ephemeral, such that it requires high frequency sampling or a long time series to adequately characterize spatial and temporal patterns in water quality. However, the long life span of seagrass tissues, relative to the temporal scale of environmental variability, allows seagrasses to integrate this variable signal of environmental quality through time. Single or low frequency samples of seagrasses can clearly indicate prevailing water quality conditions as well as indicate the effects of extreme events. Thus seagrasses are biological sentinels of conditions in the coastal zone, or "coastal canaries" (Orth et al., 2006).

Seagrasses are rooted plants; for a single location they can provide an integrated picture of water quality attributes, such as nutrient availability, chlorophyll *a* (Chl *a*), and turbidity that affect their growth. For example, ratios of the abundance of the major elements of carbon (C), nitrogen (N) and phosphorus (P) in seagrass tissues provide indications of the relative availability of light, N and P (Atkinson and Smith, 1983; Abal et al., 1994; Grice et al., 1996). Stable C isotopic composition of seagrass leaves serves as an indicator of light availability (Campbell and Fourqurean, 2009; Cooper, 1989; Cooper and DeNiro, 1989; Udy and Dennison, 1997) and stable N content is used as a tracer of environmental δ^{15}N ratios, which can indicate human sewage pollution (Cabana and Rasmussen, 1996) as well as internal cycling within the ecosystem (Fourqurean et al., 2005, 1997; Lamb et al., 2012). Landscape-scale spatial pattern in stable isotopic content (termed the "isoscape", Bowen, 2010) and in elemental content (which we can similarly call "stoichioscapes") of the seagrass "canaries" can be very useful in elucidating ecosystem-scale patterns in sources of materials and processes affecting elemental cycling (Burkholder et al., 2013; Fourqurean et al., 2005, 2007, 1997, 1992a; Fourqurean and Zieman, 2002).

Seagrasses are a polyphyletic group of plants and therefore it should not be surprising that they have different morphology, growth rate and biochemical pathways that can lead to interspecific differences in stoichiometry and elemental content (Campbell and Fourqurean, 2009; Fourqurean et al., 2007), so differences in species distribution could complicate interpretations of isoscapes and stoichioscapes if these species differences are not appreciated. Additionally, interspecific difference in elemental and isotopic composition of seagrasses can complicate stable isotope-based food web studies, since even when such studies are conducted in areas with relatively high seagrass species diversity, a few seagrass samples are often assumed to represent the possible range in isotopic content of all seagrasses within the range of the herbivores being studied (e.g. Davis et al., 2014; Vander Zanden et al., 2013, as recent examples). Spatial pattern in the isoscape of a single seagrass species and interspecific variation among seagrasses could actually provide refined signals to be used to determine foraging location and food preferences of herbivores. Such approaches have proven to be informative in terrestrial ecosystems (Rubenstein and Hobson, 2004) and, when coupled with knowledge of marine species distributions and isoscapes, could prove equally useful in the ocean (McMahon et al., 2013).

Since the 1990's, there has been a loss of about 23 % of the spatial extent of seagrass meadows across the Bermuda platform, and the density of seagrass in many of the remaining meadows has decreased from historic conditions (Murdoch et al., 2007). Interestingly, most of this decline has occurred in the offshore areas, distant from any direct anthropogenic nutrient sources. While grazing by the large population of green sea turtles that use Bermuda as developmental juvenile habitat has contributed to the decline (Fourqurean et al., 2010), the role that nutrient availability plays in controlling seagrass distribution and health across the platform is still unknown. Globally, the majority of seagrass declines documented since the beginning of the 20th century have been related to decreases in water quality caused by anthropogenic nutrient loading (Short and Wyllie-Echeverria, 1996). This suggests that understanding the current state of water quality and its relationship to seagrass vitality is important for a more complete understanding of the recent trajectory of Bermuda's seagrasses. In addition, given their restriction to areas of very high bottom light availability compared to other more tropical areas (Manuel et al., 2013), the potential exists for even small changes in water quality to impact the distribution of seagrasses. The stoichioscapes and isoscapes of Bermuda's seagrasses should reflect the mean state of the environment and provide clues about the factors controlling their distribution and trajectory. Further, species-specifc isotopic differences and isoscapes could also provide tools for understanding the movements of the green turtle herbivores that may be contributing to seagrass declines.

In this paper, we present an extensive data set describing the water quality of the Bermuda platform. If land-based sources of nutrients are impacting the marine environment of the Bermuda Platform, then we hypothesize there will be a distinct spatial pattern of decreasing concentrations of inorganic nutrients, particulate matter and Chl *a* with distance from the shoreline. Further, we test whether the isoscape and stoichioscape of seagrasses across the Bermuda platform are representative of this long-term water quality dataset. Specifically, we hypothesize that the C : N : P of seagrass will approach seagrass Redfield ratios (SRR, defined as N : P of 25–30 for plants growing with a relative abundance of both N and P compared to light availability) (Atkinson and Smith, 1983; Duarte, 1990; Ferdie and Fourqurean, 2004), and given the importance of light availability in determining seagrass distribution across the Bermuda platform (Manuel et al., 2013), we also expect seagrass tissues to have C : N : P near SRR and a decrease in δ^{13}C of the seagrass in low-light environments. Because of the influence of human wastewater on the isotopic content of nitrogen in sewage effluent (Cabana and Rasmussen, 1996), we expect water quality to be a determinant of δ^{15}N of seagrasses and for the isoscape of seagrass δ^{15}N to trend from high values close to shore to lower values further from human influence. Also, given our knowledge of the distribution of seagrass species across the Bermuda platform (Manuel et al., 2013) we expected species identity could influence our interpretations of seagrass isoscapes and stoichioscapes.

2 Methods

2.1 Study site

Despite its high latitude, the shallow platform surrounding the mid-Atlantic island chain of Bermuda (32.4° N) has coral reefs, seagrasses, and macroalgal beds formed by tropical species (Coates et al., 2013). Coral cover on Bermuda's reefs is very high compared to most locations in the Caribbean (Sheppard, 2013; Riegl and Dodge, 2008). Seagrass meadows are widespread on the Bermuda Platform and are found at about 24 % of randomly-selected sites inside the fringing coral reef (Manuel et al., 2013);

many of the larger beds are in nearshore locations. *Syringodium filiforme* is the most often encountered seagrass, followed in order of prevalence by *Halophila decipiens*, *Thalassia testudinum* and *Halodule* sp. (There is uncertainty about the taxonomic identity of the *Halodule* that is currently found in Bermuda, Manuel et al., 2013). Owing to the relatively high latitude of Bermuda compared to the rest of the range of these tropical plants, seagrasses are restricted to areas of shallower water and higher mean light transmittance to the bottom in Bermuda; this is likely a consequence of low insolation during winter months (Manuel et al., 2013).

Phytoplankton primary production (PP) and biomass in the Sargasso Sea surrounding Bermuda are limited by the supply of P to the photic zone (Ammerman et al., 2003; Lomas et al., 2004; Salihiglu et al., 2008). It is believed that PP in the shallow water benthos on the Bermuda platform is also P-limited. Given the nutrient-limited state of the marine ecosystem surrounding Bermuda, there exists the potential for land-based sources of nutrients to influence those marine ecosystems. In one embayment on the north shore of Bermuda, experimental work indicates a general P-limitation of seagrass growth offshore with a lessening of that P-limitation inside the eutrophic embayment (McGlathery et al., 2001) while at the same locations macroalgae can be N-limited (McGlathery et al., 1992).

The total land area of Bermuda is quite small, just 53.6 km^2, but the shoreline of the more than 150 islands is relatively long, ca. 296 km (Meyer, 2012), and the nearshore area extensive. Bermuda is densely populated with no comprehensive wastewater collection system; many households dispose of wastewater in septic systems or cesspits that sit in a highly vuggy karst bedrock. Molecular markers of human enterococci and coprostanol indicate that some sewage makes its way through the groundwater to the nearshore ocean (Jones et al., 2011). This contaminated groundwater contains high concentrations of nutrients (Simmons and Lyons, 1994) and some eutrophication of enclosed, P-limited bays has been demonstrated (Lapointe and O'Connell, 1989).

2.2 Seagrass surveys, collection and analysis

We surveyed seagrass abundance and collected seagrass leaves for analysis of elemental content and stable isotope ratios of C and N from 516 sites distributed across the Bermuda platform during the summer months of 2006–2008 using a stratified-random protocol to locate the sites (see Manuel et al. (2013) for a detailed description of seagrass abundance on the Bermuda platform). In addition, we used summer 2007 data from 17 permanent monitoring sites established in existing seagrass beds (Fig. 1). We estimated seagrass abundance at each of these 533 sites using modified Braun–Blanquet surveys composed of 10 randomly placed 0.25 m^2 quadrats along a 50 m transect (Fourqurean et al., 2001).

Seagrasses were present at all of the 17 permanent monitoring sites, but only at 168 of the 516 random sites. If seagrasses were present, multiple intact short shoots of each seagrass species were haphazardly collected along the 50 m transect line. In order to assure sufficient sample for all subsequent analyses, we collected five short shoots of the larger *T. testudinum*, 30 short shoots of *S. filiforme*, 40 short shoots of *Halodule* sp. and ca. 300 leaves of *H. decipiens*. In the lab, seagrass shoots were washed free of sediment, and all green leaves from each species at each site were pooled into a common sample. Leaf material was gently cleaned of epiphytes using a razor blade, dried to a constant weight at 50 °C, and ground to a fine powder. C and N contents of leaf material were analyzed in duplicate using a CHN analyzer (Fisons NA1500). Leaf P content was determined through a dry oxidation and acid hydrolysis extraction followed by a colorimetric analysis (Fourqurean et al., 1992b). Elemental content was calculated on a dry weight basis (i.e., mass of element/dry weight of sample × 100 %); all elemental ratios were calculated on a molar basis. Stable isotope ratios of C and N were analyzed using standard elemental analyzer isotope ratio mass spectrometer (EA-IRMS) procedures. The EA was used to combust the organic material and to reduce the formed gases into N_2 and CO_2, which were measured on a Finnigan MAT Delta C IRMS in a continuous flow mode. Isotopic ratios (R) were reported in the standard delta notation (‰): $\delta(‰) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$. These results are presented with respect to the international standards of atmospheric N (AIR, N_2) and Vienna Pee Dee belemnite (V-PDB) for C. Analytical reproducibility of the reported δ values, based on sample replicates, was better than ±0.2 ‰ for δ^{15}N and ±0.08 ‰ for δ^{13}C.

2.3 Water quality measurements

Water quality parameters were measured on a monthly basis at the 17 permanent monitoring sites, over a period of 1–3 days. From September 2007 to 2008, salinity (practical scale salinity) was measured using a handheld salinity, temperature and conductivity instrument (YSI 30, calibrated using a 50 mS cm^{-1} conductivity standard). Dissolved oxygen (DO) was also measured using a handheld instrument (YSI 550A, calibrated using 100 % water-saturated air). DO (mg L^{-1}) was corrected for temperature, ambient salinity and altitude. All measurements were surface readings (probe suspended at about 20–30 cm below the water surface). From June 2008 on, salinity, temperature (YSI 6560 conductivity/temperature probe, calibrated using a 50 mS cm^{-1} conductivity standard), and DO (YSI 6150 ROX optical DO sensor, calibrated using 100 % water-saturated air) were also measured using a YSI 650 MDS with YSI 600 XL sonde. DO was automatically corrected for salinity, temperature and barometric pressure. Field readings using the sonde system were done at approximately 1 m depth, and calibrations of the instruments were performed at the beginning of each monthly sampling trip.

Unfiltered water was collected directly into pre-acidified 250 mL HDPE sample bottles. For chlorophyll *a* (Chl *a*), 140 mL of water was collected via syringe and filtered by hand through 25 mm Whatman GF/F glass fiber filters. The filters were then placed in 1.8 mL plastic centrifuge tubes, capped, and kept frozen in a dark Nalgene bottle until analysis. Turbidity was measured within 12 h of sample collection using a Hach portable turbidimeter (model 2100P) and reported in NTU.

Unfiltered water samples were analyzed for total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), and dissolved silicate (SiO_2). TOC was measured by direct injection onto hot platinum catalyst in a Shimadzu TOC-5000 after first acidifying to $pH < 2$ and purging with CO_2-free air. TN was measured using an ANTEK 7000N Nitrogen Analyzer using O_2 as carrier gas to promote complete recovery of the nitrogen in the water samples (Frankovich and Jones, 1998). TP was determined using a dry ashing, acid hydrolysis technique (Solórzano and Sharp, 1980). SiO_2 was measured using the molybdosilicate method (Strickland and Parsons, 1972). Filtrate was analyzed for nitrate + nitrite (NO_x^-), nitrite (NO_2^-), ammonium (NH_4^+), and soluble reactive phosphorus (SRP) by flow injection analysis (Alpkem model RFA 300, APHA, 1999).

Filters for Chl *a* ($\mu g\,L^{-1}$) to which 1.5 mL of 90 % acetone/water were added (Strickland and Parsons, 1972) were allowed to extract for a minimum of 2 days at −20 °C before analysis. Extracts were analyzed using a Gilford Fluoro IV Spectrofluorometer (excitation = 435 nm, emission = 667 nm). Some parameters were not measured directly but were calculated by difference. Nitrate (NO_3^-) was calculated as $NO_x^- - NO_2^-$, dissolved inorganic nitrogen (DIN) as $NO_x^- + NH_4^+$, and total organic nitrogen (TON) defined as TN − DIN. All elemental ratios discussed were calculated on a molar basis. Percent DO saturation in the water column (DO_{sat}) was calculated using the equations of Garcia and Gordon (1992).

As water quality data were collected monthly at each site for the period 2007–2012, the period of water quality data collection began one year later and continued 3 years after our collection of seagrass elemental and isotopic content data. By averaging all water quality measurements collected at a site for the period of record of the water quality data, and comparing them to seagrass data from 3 years before the water quality data were collected, we have implicitly assumed that there were no long-term trends in water quality from 2006–2012.

2.4 Submarine light regime in seagrass beds

At each site from which seagrass leaves were collected, we estimated the fraction of solar radiation reaching the bottom, as a percentage of sunlight entering the water column ($\%I_0$), by interpolating the maps of $\%I_0$ in Manuel et al. (2013). These maps were generated using site-specific water depth and an interpolated map of attenuation coefficients, k_d. As $\%I_0$ is a function of both k_d as well as depth, it more accurately represents the influence of light availability on seagrasses than would be evident by water depth alone.

2.5 Statistical methods

Prior to statistical analyses, data were tested for their adherence to assumptions of the statistical techniques; we used parametric methods if the data were normally distributed and homoscedastic. If data did not meet these assumptions we used non-parametric methods. Relationships between water quality measurements and seagrass elemental and stable isotopic content were elucidated by analyzing bivariate correlations; a general lack of normality in the water quality data resulted in using Spearman's ρ rank correlation coefficient as a test of monotonic relationships among water quality variables. Seagrass elemental and isotopic content, as well as the water quality parameters N : P and $\%I_0$ met the assumptions for parametric statistical analysis, so we assessed relationships with Pearson's correlation coefficient, r. Analysis of Variance (ANOVA) with Student–Newman–Keuls post-hoc tests were used to assess differences in elemental and isotopic content among seagrass species. Differences in elemental and isotopic content among co-occurring seagrasses were tested using paired t tests, pairing species within sites.

Spatial pattern in measured variables was visualized by creating contour maps using a point kriging algorithm assuming a linear variogram and isotropic conditions (SURFER 9, Golden Software, Inc, Golden, Colorado, USA). We used the water quality contour plots to estimate water quality at sites from which seagrass was collected, which were often different from the water quality stations, by sampling the water quality fields at the locations of the seagrass sampling. Relationships between the mean value of water quality variables, as assessed by this spatial interpolation of the mean data fields, and seagrass elemental and isotopic content was further explored using Principal Component Analysis (PCA) with varimax rotation of the solution to facilitate interpretation of the composite variables (IBM SPSS Statistics 21, IBM Corporation, Armonk, New York, USA). Before PCA, all data were standardized by computing Z-scores.

3 Results

3.1 Water quality on the Bermuda platform

Reflecting its small size and position in the central Atlantic Ocean, water quality surrounding Bermuda reflected the influence of the ocean endmember, with generally high water clarity and low nutrient concentrations (Table 1). There was little variability in salinity compared to more coastal continental locations, with a total range of 36.0 to 37.5. Turbidity averaged 0.57 ± 0.01 (±SE) NTU, and Chl *a* in the water column ranged between 0.0 and 2.8 $\mu g L^{-1}$, with a mean of 0.24 ± 0.01 $\mu g L^{-1}$.

NH_4^+ was the dominant form of DIN in the water column, with a mean concentration of 1.44 ± 0.04 µM, which was approximately 3× the mean of the sums of the concentrations of NO_3^- and NO_2^-. TN concentrations in the water column were ca. 10× as high as the sum of the concentrations of the DIN, indicating that the majority of N in the water column was in the form of organic N. In comparison to N, P concentrations were very low; SRP concentrations averaged 0.048 ± 0.001 µM and TP concentrations averaged 0.136 ± 0.002 µM. Both the DIN : SRP and N : P ratios were much higher than Redfield, and the TOC : N ratio lower than Redfield, suggesting that, in general, the waters around Bermuda are P-limited. Chl *a* concentrations were positively correlated with temperature (Table 2), suggesting seasonal, summertime increases in phytoplankton biomass; high Chl *a* was also correlated with higher NO_2^-, NO_3^-, TP, SRP, TOC, DOC and SiO_2. On the contrary, there was no correlation between TN and Chl *a* (Table 2), further suggesting N availability does not generally limit phytoplankton around Bermuda.

The islands of Bermuda exhibited a marked influence over water quality on the Platform. Station-averaged TN and TP generally declined with distance from the island (Fig. 1). The pattern in station-averaged N : P was more complex, with generally lower N : P (ca. 130 : 1) in the enclosed waters of the sounds and harbors, compared to higher values in the more open waters of the platform. There were also strong gradients in TOC concentrations and Chl *a* across the platform, with higher values close to shore that decreased with distance north of the island (Fig. 2).

3.2 Seagrass elemental content and stoichiometry

Seagrass leaves exhibited a wide range of values for N and P content (Fig. 3, Table 3). N content ranged from 1.40 to 3.91 % and P content ranged from 0.058 to 0.465 %. When data were pooled from all sites by species, there were significant differences among species in N content (ANOVA, $F_{3,376} = 11.8$, $p < 0.001$) and P content (ANOVA, $F_{3,376} = 18.4$, $p < 0.001$). Post-hoc tests indicated that there were no significant differences in N content between *S. filiforme* and *H. decipiens*, but *T. testudinum* and *Halodule* sp. were different from all other species. In contrast, there was more overlap among the species in P content: there was no significant difference between *S. filiforme* and *Halodule* sp. nor between *Halodule* sp. and *T. testudinum*, while P content of *H. decipiens* was distinct. While there was a significant difference in N : P among species (ANOVA, $F_{3,375} = 5.8$, $p = 0.001$), *H. decipiens* was the only species with different N : P ratios from the other species. N : P of the larger-bodied seagrasses (*S. filiforme*, *T. testudinum* and *Halodule* sp.) were greater than 30 : 1, indicative of P limitation. N : P of the smaller, faster-growing, and low light-adapted *H. decipiens* indicated P limitation in approximately 80 % of the samples, but N : P was < 30: in about 20 % of the samples, suggesting potential N-limitation at some sites.

Comparisons of global means of elemental content data (Table 3) do not fully capture the actual differences among species driven by their physiology and morphology, since the distributions of the species across the platform are different (Manuel et al., 2013) and there also were gradients in availability of N and P in the water column across the platform (Fig. 1). To control for this variation, we compared species pairwise based on co-occurrence at individual sampling sites. At the 66 sites where they co-occurred, *S. filiforme* had N content 0.23 ± 0.06 % higher than *T. testudinum* (paired $t = 3.9$, df = 65, $p < 0.001$). *S. filiforme* had N content 0.22 ± 0.06 % higher ($p < 0.001$) than *Halodule* sp. and 0.39 % ± 0.14 % higher ($p = 0.013$) than *H. decipiens*. *T. testudinum* had significantly lower N content (by 0.14 ± 0.06 %, $p = 0.038$) than *Halodule* sp. On a single occasion, *T. testudinum* was found co-occurring with *H. decipiens*. There were no significant differences in the N content of *Halodule* sp. and *H. decipiens* at the 15 sites where they co-occurred.

There were no significant differences in the P content of *T. testudinum* and either *S. filiforme* (co-occurred at 66 sites, $p = 0.151$) or *Halodule* sp. (co-occurred at 39 sites, $p = 0.139$); however the P content of *S. filiforme* was 0.012 ± 0.005 % higher than *Halodule* sp. (69 sites, $p = 0.015$). *S. filiforme* had P content 0.046±0.015 % higher (19 sites, $p = 0.005$) than *H. decipiens*. *Halodule* sp, had P content on average 0.045 ± 0.013 % higher than *H. decipiens* (15 sites, $p = 0.004$).

For all possible 2-species comparisons except *S. filiforme* and *Halodule* sp., seagrass species had distinct N : P ratios ($p \leq 0.02$ for all comparisons). N : P of *S. filiforme* was 4.9 ± 1.4 greater than N : P of *T. testudinum*, and 7.1 ± 2.7 less than *H. decipiens*. N : P of *Halodule sp*. was 6.6 ± 1.8 higher than *T. testudinum*, and N : P of *Halodule* sp. was 7.7 ± 2.9 less than *H. decipiens*. As there were no systematic differences in the N : P of leaves of *S. filiforme* and *Halodule sp.* and these two species are widespread across the Bermuda Platform, we mapped the spatial pattern in N : P of these two species. When both species were present at a site, we averaged their N : P ratios. The resultant spatial pattern (Fig. 4) indicates broad-scale P-limitation across the platform for these species (i.e. N : P > 30), with only a few locations very close to shore near the west end of the island and in an enclosed cove near the northeastern part of the island with N : P ratios indicative of light limitation. Interestingly, no sites where *S. filiforme* or *Halodule* sp. occurred had N : P < 25 that would indicate N-limitation.

3.3 δ^{15}N and δ^{13}C content of seagrass leaves

In a manner similar to elemental content, seagrass leaves were found with a broad range of δ^{13}C and δ^{15}N values (Table 4 and Fig. 5). δ^{13}C values ranged from −12.9 to −3.3 ‰ ; and δ^{15}N values ranged from −10.1 to 8.8 ‰. When data were pooled from all sites, there were species-specific differences in δ^{13}C (ANOVA, $F_{3,369} = 262.7$, $p < 0.001$), but not in δ^{15}N ($F_{3,370} = 1.8$, $p = 0.148$). The mean δ^{13}C was lowest for *Halodule* sp. (−9.6 ± 0.1 ‰), followed in increasing order by *H. decipiens* (−8.3 ± 0.2 ‰), *T. testudinum* (−7.3 ± 0.04 ‰) and *S. filiforme* (−4.6 ± 0.01 ‰).

Analyses of differences between species pairs at sites where the species co-occurred corroborate the interspecific differences in δ^{13}C, with all possible pairwise comparisons significantly different (paired *t* tests, $p \leq 0.001$ for all comparisons). When found at the same site, δ^{13}C of *S. filiforme* averaged 2.3 ± 0.01 ‰ heavier than *T. testudinum*, 4.15 ± 0.08 ‰ heavier than *Halodule* sp. and 1.3 ± 0.2 ‰ heavier than *H. decipiens*. *T. testudinum* averaged 1.9 ± 0.2 ‰ heavier than *Halodule* sp. We had insufficient data to compare isotopic signatures of *T. testudinum* and *H. decipiens*. *Halodule* sp. averaged 2.8 ± 0.2 ‰ heavier than *H. decipiens*. In these pairwise analyses, there were no significant differences in the δ^{15}N of *S. filiforme* and either *T. testudinum* or *Halodule* sp., nor were there significant differences in the δ^{15}N of *T. testudinum* or *Halodule* sp. However, there were significant differences in the δ^{15}N of co-occurring *S. filiforme* and *H. decipiens* ($t = 3.18$, d.f. = 16, $p = 0.006$) and co-occurring *Halodule* sp. and *H. decipiens* ($t = 2.98$, d.f. = 13, $p = 0.11$). *H. decipiens* had δ^{15}N on average 2.3 ± 0.8 ‰ heavier than *Halodule* sp. and 1.7 ± 0.5 ‰ heavier than *S. filiforme*.

Given that there were no differences in the δ^{15}N of *S. filiforme*, *T. testudinum* or *Halodule* sp., the spatial pattern in the δ^{15}N from all sites where any of these species occurred indicates a striking spatial pattern in the δ^{15}N of the seagrasses from across the platform (Fig. 6). δ^{15}N on the platform distant from the Bermuda Islands was distinctly depleted in ^{15}N, with some areas exhibiting δ^{15}N values as light as −10.1 ‰. As distance from land decreased, δ^{15}N values increased, with isotopically enriched δ^{15}N values over 8 ‰ in the semi-enclosed Hamilton Harbor and in enclosed Harrington Sound. The spatial gradients in δ^{15}N were very steep, with δ^{15}N changing as rapidly as 1.8 ‰ km^{-1} from Hamilton Harbor to the center of the platform.

3.4 Relationships among seagrass elemental, δ^{15}N and δ^{13}C content

Given the differences among species in N : P ratios and δ^{13}C, we analyzed the relationships among elemental and stable isotopic content of seagrasses by species (Table 4). For all seagrass species, there was a significant positive correlation between C : N and C : P, but N : P was in all cases correlated with C : P, and only weakly correlated with C : N for *Halodule* sp. ($r = 0.243$, $p = 0.032$). There were also strong positive correlations between C : N and δ^{15}N for all species, which indicated that plants with low N content had relatively enriched δ^{15}N values. With one exception, δ^{13}C was positively correlated with both C : P and N : P, indicating that plants with low P content tended to have more enriched δ^{13}C; for *H. decipiens* there was no significant correlation between δ^{13}C and N : P. There were some exceptions to the general correlation patterns: for *T. testudinum* only, there was a significant positive correlation between C : P and δ^{15}N; and N : P was significantly, negatively correlated with δ^{15}N for *S. filiforme* and *H. decipiens*, but not for *T. testudinum* or *Halodule* sp.

3.5 Water quality as a predictor of seagrass elemental, δ^{15}N and δ^{13}C content

There were no simple linear relationships between seagrass elemental and isotopic content and water quality that applied across all four seagrass species. There were differences in the ranges of light availability at sites where the different species occurred: $\%I_0$ at sites supporting *T. testudinum* averaged 70±1 %, compared to 59±2 %, 55±2 %

and 44 ± 2 % for *S. filiforme*, *Halodule* sp., and *H. decipiens*, respectively. At sites that supported *S. filiforme* and *T. testudinum*, there was a significant negative relationship between water column N : P and the amount of light reaching the bottom (%I_0, a function of water quality and depth), but there was no significant relationship between these environmental parameters at sites that supported *Halodule* sp. and *H. decipiens* (Table 4, cells in italic). %I_0 was significantly and positively correlated with the C : N, C : P, N : P and δ^{13}C of *S. filiforme* and *Halodule* sp, suggesting that high light availability leads to decreases in N and P content in seagrass leaves, an increase in the relative amount of N with respect to P, and enrichment with ^{13}C relative to ^{12}C for these species. The δ^{15}N of *S. filiforme* and *H. decipiens* were both significantly positively correlated with %I_0. Interestingly, there were only weak relationships between the water column N : P and seagrass elemental and isotopic content. *Halodule* sp. C : N was higher when water column N : P was higher, but *H. decipiens* C : P and N : P were higher when the water column N : P was higher. δ^{15}N of *S. filiforme* and *T. testudinum* were correlated with water column N : P, but there were no similar significant correlations for *Halodule* sp. and *H. decipiens*.

Interspecific differences in the distributions of species and elemental and isotopic content necessitated analyses of the relationships between water quality and seagrass elemental and isotopic content be done individually for each species. The multiple bivariate correlations among the water quality and seagrass variables (Tables 2 and 4) resulted in robust extraction of composite variables in PCA that explained between 73.1 and 82.7 % of the original variation in the species-specific data sets (Table 5). For all four species, PCA revealed strong, positive relationships between the water quality variables Chl *a*, DOC, TP and TN and the δ^{15}N of seagrass leaves which loaded strongly onto the first principal component (PCI) which explained between 31.3 and 36.7 % of the variation in the original dataset. There were species-specific differences in the subsequently extracted PCs, For *S. filiforme*: PCII was strongly related to high %I_0 and seagrass N : P and δ^{13}C; PCIII was strongly correlated with high water column TP and low water column TN : TP; and PCIV was related to high C : N and C : P in seagrass leaves. For *T. testudinum*: PCII was positively correlated with high C : P, N : P and δ^{13}C of seagrass leaves; PCIII was negatively correlated with $\%I_0$ but positively correlated with water column TN and TN : TP; and PCIV was associated with high seagrass C : P and C : N. Only three significant PCs were extracted for *Halodule* sp; with PCII strongly correlated with high $\%I_0$ and seagrass C : P, C : N and N : P; and PCIII positively correlated with water column TN and TN : TP. For *H. decipiens*: PCII was positively correlated with seagrass C : P and N : P; PCIII was associated with high seagrass C : N and δ^{13}C; and PCIV was influenced strongly by high water column TN : TP.

4 Discussion

The striking spatial pattern in water quality on the Bermuda platform clearly demonstrates the impact of the island and platform on water quality, and strong relationships between the long-term water quality data and the one-time sampling of seagrass tissues indicates that seagrasses really do serve as a long-term, integrating "canary" for environmental conditions. Stoichiometry of both the water column and the seagrasses that grow across the platform are consistent with general P-limitation of primary producers close to the island. However, the lack of clear relationships between the N : P in the water column and the N : P in the seagrasses suggests that benthic processes act to modify the N : P available to the benthos compared to the water column. Strong spatial patterns in the δ^{15}N of seagrasses are consistent with a signature of sewage-derived N influencing waters very close to shore, but large areas of severely depleted ^{15}N signatures in the seagrasses of the Bermuda platform suggest a very active role of the nearshore benthos in processing land-based sources of N.

4.1 “Stoichioscapes” as indicators of ecosystems processes

C : N : P stoichiometry of the water column strongly suggests general P-limitation of the nearshore waters of Bermuda, with the vast majority of the measurements of water column N : P well in excess of the 16 : 1 of the Redfield Ratio (Redfield, 1958). Furthermore, the spatially-coherent patterns in water column TP, TOC and Chl *a* clearly demonstrate that the islands of Bermuda are a source of the limiting nutrient to the nearshore marine waters. Our findings based on C : N : P stoichiometry of the P-limited nature of the phytoplankton community on the Bermuda platform agree with recent studies finding generalized P-limitation of plankton production in the ocean surrounding Bermuda – the source waters for the Bermuda Platform (Ammerman et al., 2003; Lomas et al., 2004; Salihiglu et al., 2008). Stoichiometry of seagrass tissues is also consistent with P limitation across much of the Bermuda platform, with most N : P values greater than the “seagrass Redfield ratio” (SRR) of 30 : 1 (Atkinson and Smith, 1983; Duarte, 1990).

The strength of seagrass P-limitation, as assessed by the degree of N : P deviation from SRR, is not as severe as documented in other parts of these species range, like south Florida (Fourqurean and Zieman, 2002; Fourqurean et al., 1992a) and seagrass N : P values were are not as far from the stoichiometric balance between N and P availability as in the water column. In fact, there was no significant relationship between the water column and seagrass N : P across the Bermuda Platform. These conditions likely arise because of relatively low light availability on the bottom compared to the more tropical locations of the centers of the ranges of these seagrass species (Manuel et al., 2013). When growing in light-limited conditions, a consequence of strong seasonality of insolation in Bermuda, nutrients are not limiting to seagrass production (Fourqurean and Zieman, 2002), hence the seagrass elemental content tends towards the SRR. Light limitation could ameliorate the degree of P limitation in Bermuda’s seagrasses as suggested by other studies for the relationship between light availability and nitrogen limitation (Abal et al., 1994; Grice et al., 1996; Zimmerman et al., 1987). This is consistent with our results for *Halophila decipiens*, which grew in the deepest and lowest-light environments on the Bermuda Platform (Manuel et al., 2013) and had a mean N : P the closest to the SRR of the four Bermuda seagrasses.

In addition to the differences in the mean N : P of *H. decipiens* compared to the other species that arise as a consequence of differences in the mean depths at which these species are found, biological differences among species led to consistent differences in N : P within sites. N : P is an integrated measure of the balance of light, N, and P availability for seagrass growth (Fourqurean and Rutten, 2003), and availability is determined by the balance between resource supply and the demand for that resource by the plants. Making the assumption that the supply of resources is constant within sites, then the species with the highest demand, i.e., the highest relative growth rate, should experience the lowest relative availability and exhibit greatest resource limitation (Tilman, 1980), as has been shown by comparing N : P of co-occurring seagrasses in other locations (Campbell and Fourqurean, 2009; Fourqurean et al., 1995). The relative N : P of Bermudian seagrasses likewise follow the pattern expected by comparing their relative growth rates. The relative growth rates ($\% \mathrm{d}^{-1}$) are higher for *H. decipiens*, intermediate for *Halodule* sp. and *S. filiforme*, and lowest for *T. testudinum* (Duarte, 1991; Gallegos et al., 1994; Kenworthy et al., 1989); resulting in, when co-occurring, relative N : P of seagrasses of *H. decipiens* > (*S. filiforme* and *Halodule* sp.) > *T. testudinum*. Since *S. filiforme* and *Halodule* sp. were similar in N : P and widely distributed across the Platform we were able to use their common stoichiometry to indicate the nutrient status of the different environments.

Despite our observations of general P-limitation of seagrasses across the platform, on occasion our sampled seagrasses had N : P < SRR, indicative of N-limitation (Fig. 4). Because the island is karstic with no natural streams, nutrients emanating from the island that could influence water quality and phytoplankton abundance in nearshore waters travel through groundwater to the sea. Recent studies of the importance of N and P in groundwater in controlling the primary production of benthic macroalgae in cave pools point to spatial and species-specific differences, with some macroalgae species being P-limited at some sites and other species being N-limited or light-limited at others (Maloney et al., 2011). Localized differences in N : P in groundwater may be responsible for this variation in the identity of the limiting nutrient in cave pools, and thus the groundwater. This could help explain why N-limitation of benthic marine plants very close to shore has been observed (McGlathery et al., 1992).

4.2 Isoscapes as indicators of ecosystem processes

The striking spatial pattern in δ^{15}N serves as an informative isoscape (Bowen, 2010) for generating hypotheses and testing models about biogeochemical processes on the Bermuda platform. Human wastewater can contain DIN with δ^{15}N values as high as 40 ‰ (Tucker et al., 1999), and plants in close proximity to wastewater outflows often exhibit high δ^{15}N (Cabana and Rasmussen, 1996). The very near shore, ^{15}N-enriched δ^{15}N signatures of seagrasses, and the rapid decline of seagrass δ^{15}N offshore at the rate of 1.8 ‰ km^{-1}, suggest that sewage-influenced groundwater transports nutrients into the nearshore marine environment, and that those nutrients are rapidly processed by both the water column and the benthos. Hence, the influence of sewage-derived nutrients on the benthos is currently limited in spatial extent in Bermuda; it is clear that the zone of δ^{15}N of seagrasses > 0 corresponds with the zones of enhanced TOC, TN, TP and Chl *a* in the water column.

To our knowledge, the δ^{15}N values we report from all four seagrass species occurring in Bermuda greatly expand the known range of values previously reported for each species. For example, the published range of δ^{15}N values for *T. testudinum* encompasses −4.3 to 9.4 ‰ (Fourqurean et al., 2005); our data expands this range to a new minimum of −10.1 ‰. δ^{15}N values < 0 have rarely been reported for seagrasses, and the mechanisms that would lead to plant tissues more depleted than atmospheric N need to be elucidated. Large spatially-contiguous zones of δ^{15}N values between −4.3 and 0 ‰ in the Florida Keys are hypothesized to be a result of either an isotopically depleted source pool of DIN, or maximum fractionation of DIN on uptake in regions of very high N availability (Fourqurean et al., 2005). Additionally, the process of ammonification produces NH_4^+ that has δ^{15}N values lower than the values of the source organic matter (Mobius, 2013); further, when DIN is available in excess compared to plant demand, plants discriminate against ^{15}N uptake (Fourqurean et al., 2005; Yoneyama et al., 1991; Evans, 2001; Koba et al., 2010). Indeed, experimental N additions have been shown to increase fractionation of nitrogen isotopes upon uptake when nitrogen supply exceeds demand (Udy and Dennison, 1997). In fact, the only report of seagrass δ^{15}N values as depleted as we observed in the center of the Bermuda platform are from experimental N addition experiments with very fast-growing, high N-demanding seagrasses (Udy and Dennison, 1997).

The strong correlation we found between δ^{15}N and C : N for all four species of seagrass are consistent with enhanced fractionation of the source pool in regions of high N availability, but such a fractionation may not be sufficient to explain the large negative δ^{15}N values. It is likely that benthic processing of N in the middle of the Bermuda platform is creating uniquely isotopically-depleted DIN that is being incorporated into seagrasses. The depleted ^{15}N on the Bermuda platform is consistent with the input of new N to the region by N_2 fixation (Montoya et al., 2002), additional processes must be involved to generate the observed negative δ^{15}N. High rates of ammonification could partly explain why DIN would be depleted in ^{15}N (Mobius, 2013).

4.3 δ^{13}C of seagrasses in Bermuda

We expected to find that δ^{13}C of seagrass tissues would be a function of light availability, because in high light environments there is less fractionation of dissolved inorganic carbon (DIC) upon photosynthetic uptake. In essence, seagrasses are more isotopically enriched in ^{13}C if light availability does not limit photosynthesis (Campbell and Fourqurean, 2009; Fourqurean et al., 2005; Hu et al., 2012) and therefore C demand is high relative to availability. We did find this expected relationship across the platform for *S. filiforme* and *Halodule* sp., but not for *T. testudinum* or *H. decipiens*. The lack of these relationships for *T. testudinum* and *H. decipiens* could be owing to the more restricted ranges of light availability at which these species were found: *T. testudinum* is generally restricted to high light environments, *H. decipiens* to low-light environments, and the other two species are found from high light to low light environments. Additionally, lower light availability at Bermuda's latitude could decrease the dependence of δ^{13}C on light compared to more tropical locations with higher light. Interestingly, for all four seagrasses, plants with higher δ^{13}C had lower P content, similar to previous reports from south Florida (Fourqurean et al., 2005), suggesting that plants from high light environments experience greater P-limitation than plants from low light environments.

Differences in morphology and carbon uptake produce species-specific differences in the δ^{13}C of co-ocurring seagrasses. It has been shown that, when occurring together in south Florida, the relative δ^{13}C of *Halodule* sp. < *T. testudinum* < *S. filiforme* (Campbell and Fourqurean, 2009). Our data corroborate these relative differences, and add information about *Halophila decipiens*, which we frequently found growing in the same sites with other seagrasses in Bermuda, whereas in south Florida it rarely is found growing together with other seagrasses (Fourqurean et al., 2002). *H. decipiens* in Bermuda has δ^{13}C values intermediate between *Halodule* sp. and *T. testudinum*.

4.4 Stoichioscapes and isoscapes as important tools to study marine ecological processes

The spatial patterns of elements and their ratios, which we can call a stoichioscape, and the stable isotopic composition of widespread seagrasses (an isoscape) specifically point to: (1) generalized P limitation of both the water column and the benthos, (2) land-based sources of both N and P, and (3) locations within the more generally P-limited seascape that are light- or N-limited. The substantial impact of light availability on seagrass distribution, elemental content and stable isotopic composition did not obscures the spatial patterns. Further, our results have generated new hypotheses about the nature of N cycling on the Bermuda platform that will guide research of local processes but also of the role of the coastal ocean in global biogeochemical cycles.

Bermuda presents a unique opportunity to examine the use of elemental and isotope content of organisms to help explain ecological processes, in particular the large decline of seagrasses on the outer platform. Although the isoscape of nutrients implicates land based sources of nitrogen and phosphorus, we can not attribute the decline of seagrasses to degraded water quality and have hypothesized that seagrass losses are the result of overgrazing by green turtles (Fourqurean et al., 2010). Our isoscapes and stoichioscapes can be used as tools in ecogeochemistry where the elemental and isotope content are used as natural markers to help understand trophic ecology and population structure. Ecogeochemistry is providing new insights on animal movements in marine ecosystems (see McMahon et al. (2013) for review) and has long been used to study food web structure. Pronounced patterns in isotopic composition of plants across an area like the Bermuda platform can help interpret the distribution of stable isotope ratios among individuals in a population of consumers. For example, large variation in δ^{13}C and δ^{15}N of green sea turtles within a population has been interpreted as individual diet specialization, with some individuals feeding on seagrasses, others on macroalgae and still others with a carnivorous diet (e.g. Burkholder et al., 2011). Given the very large ranges in isotopic composition of seagrasses we found on the Bermuda platform, a similar variability in the isotopic composition of green sea turtles could be driven by spatial variation in the isotopic composition (and species identity) of seagrasses and restricted home ranges of individual turtles in the population, and indeed variation in stable isotopic composition of sea turtles has been used to infer differences in provenance of sea turtles in other locations (Pajuelo et al., 2012). Only with knowledge of the relationship between the isoscapes and stoichioscapes and the home ranges of individuals can variation of ecogeochemical tags within a population be properly interpreted.

Author contributions. All authors designed the study. J. W. Fourqurean, S. A. Manuel, K. A. Coates and W. J. Kenworthy collected field samples; J. W. Fourqurean analyzed plant samples for elemental and isotopic content and J.N.B analyzed water samples. J. W. Fourqurean prepared the manuscript with contributions from all co-authors.

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Table 1. Summary of water quality data collected across the Bermuda platform, based on monthly sampling from 17 sites during the period 2007–2012. Sampling locations are indicated in Fig. 1. SE = standard error of the mean.

Parameter	Mean	SE	Minimum	Maximum	*n*
Temperature (°C)	23.3	0.1	15.0	31.2	1019
Salinity (PSU)	36.70	0.01	36.00	37.50	1020
Turbidity (NTU)	0.57	0.01	0.16	2.70	983
Dissolved O_2 (% saturation)	107.6	0.3	55.4	178.7	983
Chlorophyll *a* ($\mu g\,L^{-1}$)	0.24	0.01	0.00	2.79	866
Total Organic Carbon (µM)	108.6	0.7	57.8	227.9	984
Dissolved Organic Carbon (µM)	102.7	0.7	27.1	197.3	984
NH_4^+ (µM)	1.44	0.04	0.06	10.03	984
NO_2^- (µM)	0.02	< 0.01	< 0.01	0.25	984
NO_3^- (µM)	0.48	0.02	0.01	14.54	984
Total Nitrogen (µM)	17.0	0.7	0.2	179.7	984
SRP (µM)	0.048	0.001	< 0.001	0.278	984
TP (µM)	0.136	0.002	0.020	1.474	984
SiO_2 (µM)	0.25	0.01	< 0.01	2.292	984
TOC : N	9.2	0.1	0.6	28.7	984
TOC : P	895.9	10.6	67.2	4541.7	984
DIN : SRP	57.7	2.5	2.0	846.1	983
N : P	138.5	5.4	10.7	1932.8	983

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Table 2. Pearson's correlation of water quality data, correlation coefficient (ρ) above the diagonal, 2-tailed test of significance of the correlation (p) below the diagonal. The number of observations for each quantity are in Table 1; in general ($n \approx 1000$).

	NO_3	NO_2	NH_4	TN	TP	SRP	TOC	DOC	Si	Chl *a*	SAL	TEMP	DO%
NO_3		0.042	−0.023	0.072^a	0.092^b	0.028	−0.025	−0.022	0.186^b	0.109^b	-0.142^b	−0.055	−0.008
NO_2	0.192		0.051	0.079^a	0.040	0.039	0.103^b	0.050	0.097^b	0.090^b	−0.001	0.013	−0.055
NH_4	0.474	0.107		-0.118^b	0.049	0.105^b	0.210^b	0.208^b	−0.014	0.052	0.061	0.086^b	−0.017
TN	0.024	0.013	0.000		0.050	−0.063	0.158^b	0.198^b	0.076^a	0.053	0.134^b	0.196^b	0.107^b
TP	0.004	0.205	0.121	0.114		0.181^b	0.071^a	0.048	0.120^b	0.109^b	−0.029	0.292^b	0.015
SRP	0.385	0.221	0.001	0.051	0.000		0.137^b	0.144^b	0.069^a	0.138^b	0.003	0.079^a	0.018
TOC	0.429	0.001	0.000	0.000	0.026	0.000		0.888^b	−0.040	0.247^b	0.048	0.382^b	0.059
DOC	0.487	0.118	0.000	0.000	0.135	0.000	0.000		−0.031	0.256^b	0.109^b	0.358^b	0.104^b
SiO_2	0.000	0.003	0.656	0.017	0.000	0.033	0.213	0.343		0.119^b	0.068^a	0.011	−0.042
Chl *a*	0.001	0.008	0.127	0.118	0.001	0.000	0.000	0.000	0.001		−0.030	0.317^b	-0.115^b
Sal	0.000	0.965	0.054	0.000	0.369	0.933	0.132	0.001	0.036	0.384		0.161^b	0.130^b
Temp	0.087	0.687	0.007	0.000	0.000	0.014	0.000	0.000	0.723	0.000	0.000		-0.145^b
DO	0.797	0.089	0.609	0.001	0.651	0.586	0.068	0.001	0.197	0.001	0.000	0.000	

[a] $p < 0.05$
[b] $p < 0.005$

Table 3. Nitrogen and phosphorus content, N : P, δ^{13}C and δ^{15}N content of seagrass leaves from the Bermuda platform. Superscripts indicate homogenous groups as indicated by Student–Newman–Keuls post hoc tests in ANOVA of data grouped by species, significant differences at $\alpha = 0.05$.

Parameter	Mean	SE	Minimum	Maximum	*n*
N content (% of dry wt)					
Syringodium filiforme	2.69^{a}	0.05	1.67	3.72	139
Thalassia testudinum	2.31^{b}	0.05	1.57	3.38	86
Halodule sp.	2.51^{c}	0.05	1.59	3.87	78
Halophila decipiens	2.66^{a}	0.06	1.40	3.91	77
P content (% of dry wt)					
Syringodium filiforme	0.158^{a}	0.004	0.079	0.301	139
Thalassia testudinum	0.136^{b}	0.005	0.058	0.259	86
Halodule sp.	$0.144^{a,\,b}$	0.005	0.065	0.306	78
Halophila decipiens	0.192^{c}	0.009	0.067	0.465	77
N : P (molar)					
Syringodium filiforme	39.1^{a}	0.7	20.2	63.6	139
Thalassia testudinum	40.6^{a}	1.2	21.1	78.5	86
Halodule sp.	40.8^{a}	1.1	23.3	68.5	78
Halophila decipiens	34.6^{b}	1.5	13.6	77.8	76
δ^{13}C (‰)					
Syringodium filiforme	-5.5^{a}	0.01	-8.8	-3.3	138
Thalassia testudinum	-7.3^{b}	0.1	-9.7	-5.5	85
Halodule sp.	-9.6^{c}	0.1	-12.4	-7.2	78
Halophila decipiens	-8.3^{d}	0.2	-12.9	-5.7	72
δ^{15}N (‰)					
Syringodium filiforme	1.3^{a}	0.33	-7.7	8.8	138
Thalassia testudinum	2.2^{a}	0.4	-10.1	8.0	86
Halodule sp.	1.6^{a}	0.4	-8.9	5.6	78
Halophila decipiens	2.2^{a}	0.2	-1.2	7.5	72

Table 4. Relationships among elemental content and stable isotope ratios for seagrasses from the Bermuda platform. Values above the diagonal are Pearson's correlation coefficients (r), below the diagonal is the 2-tailed test of the significance of the correlation (p). *Values in italics indicate water column parameters*.

	n		C : N	C : P	N : P	δ^{13}C	δ^{15}N	Water N : P	%I_0
Syringodium filiforme	139	C : N		**0.626**	−0.064	0.129	**0.384**	*0.097*	***0.214***
Thalassia testudinum	86			**0.497**	0.048	−0.037	**0.203**	*0.122*	*−0.033*
Halodule sp.	78			**0.704**	**0.243**	0.106	**0.306**	***0.337***	***0.315***
Halophila decipiens	77			**0.328**	−0.027	0.300	**0.455**	*0.056*	*0.149*
Syringodium filiforme	139	C : P	**< 0.001**		**0.725**	**0.224**	0.129	*0.093*	***0.335***
Thalassia testudinum	86		**< 0.001**		**0.866**	**0.280**	**0.243**	*−0.071*	*0.028*
Halodule sp.	78		**< 0.001**		**0.849**	**0.244**	0.117	*0.212*	***0.406***
Halophila decipiens	77		**0.004**		**0.928**	**0.227**	−0.216	***0.321***	*0.031*
Syringodium filiforme	139	N : P	0.453	**< 0.001**		**0.210**	**−0.198**	*0.065*	***0.238***
Thalassia testudinum	86		0.659	**< 0.001**		**0.364**	0.189	*−0.074*	*0.013*
Halodule sp.	78		**0.032**	**< 0.001**		**0.251**	−0.089	*0.046*	***0.318***
Halophila decipiens	77		0.818	**< 0.001**		0.138	**−0.390**	***0.338***	*−0.017*
Syringodium filiforme	139	δ^{13}C	0.132	**0.008**	**0.013**		−0.161	*0.150*	***0.230***
Thalassia testudinum	86		0.736	**0.009**	**0.001**		−0.158	*0.176*	*−0.135*
Halodule sp.	78		0.357	**0.032**	**0.026**		−0.016	*0.086*	***0.301***
Halophila decipiens	77		**0.010**	**0.050**	0.247		−0.073	*0.015*	*0.158*
Syringodium filiforme	139	δ^{15}N	**0.012**	0.131	**0.020**	0.059		***−0.341***	***0.241***
Thalassia testudinum	86		**0.050**	**0.024**	0.081	0.148		***−0.340***	*0.091*
Halodule sp.	78		**0.006**	0.308	0.439	0.888		*−0.015*	*0.205*
Halophila decipiens	77		**< 0.001**	0.068	**0.001**	0.542		*−0.181*	***0.320***
Syringodium filiforme	139	*Water column N : P*	*0.256*	*0.275*	*0.445*	*0.079*	***<0.001***		***−0.324***
Thalassia testudinum	86		*0.263*	*0.516*	*0.497*	*0.108*	***0.001***		***−0.404***
Halodule sp.	78		***0.003***	*0.062*	*0.692*	*0.456*	*0.898*		*−0.163*
Halophila decipiens	77		*0.627*	***0.005***	***0.003***	*0.673*	*0.129*		*−0.187*
Syringodium filiforme	139	*%I_0*	***0.012***	***<0.001***	***0.005***	***0.007***	***0.004***	***<0.001***	
Thalassia testudinum	86		*0.764*	*0.801*	*0.906*	*0.217*	*0.405*	***<0.001***	
Halodule sp.	78		***0.005***	***<0.001***	***0.005***	***0.007***	*0.072*	*0.154*	
Halophila decipiens	77		*0.196*	*0.788*	*0.887*	*0.184*	***0.006***	*0.102*	

Table 5. Principal Components Analysis of the relationship among water quality and seagrass environmental and isotopic composition, by seagrass species. Values are the correlations between the original variables and the extracted principal components. Values in bold type have the largest loadings within a principal component.

	PCI	PCII	PCIII	PCIV		PCI	PCII	PCIII	PCIV
Syringodium filiforme					*Halodule* sp.				
%I_0	0.205	**0.515**	0.480	0.198	%I_0	0.100	**0.569**	−0.483	
Water column Chl *a*	**0.893**	−0.059	0.167	−0.051	Water column Chl *a*	**0.915**	0.055	0.039	
Water column DOC	**0.948**	−0.085	0.219	−0.008	Water column DOC	**0.954**	0.119	0.012	
Water column TP	**0.682**	−0.176	**0.608**	−0.039	Water column TP	**0.856**	−0.043	−0.383	
Water column TN	**0.846**	0.003	−0.459	0.034	Water column TN	**0.616**	0.383	**0.602**	
Water Column TN : TP	−0.111	0.093	**−0.961**	0.064	Water Column TN : TP	−0.259	0.347	**0.854**	
Seagrass C : P	−0.047	0.076	−0.007	**0.632**	Seagrass C : P	−0.267	**0.900**	−0.147	
Seagrass C : N	0.051	0.041	−0.045	**0.980**	Seagrass C : N	0.259	**0.729**	0.161	
Seagrass N : P	−0.137	**0.882**	0.008	−0.050	Seagrass N : P	−0.191	**0.697**	−0.320	
Seagrass δ^{13}C	−0.092	**0.547**	−0.120	0.020	Seagrass δ^{13}C	−0.096	0.386	−0.226	
Seagrass δ^{15}N	**0.753**	−0.142	0.284	0.425	Seagrass δ^{15}N	**0.706**	0.380	0.140	
% of Variance explained	32.1	17.4	17.3	14.5	% of Variance explained	32.2	23.4	17.5	
Thalassia testudinum					*Halophila decipiens*				
%I_0	−0.004	−0.103	**−0.663**	0.042	%I_0	0.330	0.240	0.384	−0.405
Water column Chl *a*	**0.879**	−0.038	0.014	−0.260	Water column Chl *a*	**0.925**	−0.092	−0.061	−0.129
Water column DOC	**0.957**	0.025	0.065	−0.183	Water column DOC	**0.938**	−0.176	−0.039	−0.209
Water column TP	**0.670**	0.303	−0.488	0.062	Water column TP	**0.791**	−0.225	−0.046	−0.480
Water column TN	**0.617**	−0.107	**0.712**	−0.068	Water column TN	**0.921**	−0.086	−0.038	0.229
Water Column TN : TP	−0.352	−0.027	**0.886**	0.045	Water Column TN : TP	−0.054	0.254	0.055	**0.921**
Seagrass C : P	0.078	**0.796**	−0.072	**0.544**	Seagrass C : P	−0.170	**0.921**	0.222	0.136
Seagrass C : N	0.229	0.070	0.004	**0.915**	Seagrass C : N	0.148	0.018	**0.857**	0.122
Seagrass N : P	0.228	**0.888**	−0.009	0.142	Seagrass N : P	−0.218	**0.955**	−0.077	0.109
Seagrass δ^{13}C	−0.254	**0.723**	0.117	−0.297	Seagrass δ^{13}C	−0.343	−0.106	**0.668**	−0.098
Seagrass δ^{15}N	**0.788**	0.030	−0.085	0.436	Seagrass δ^{15}N	**0.710**	−0.238	0.447	−0.087
% of Variance explained	31.3	18.8	18.2	14.1	% of Variance explained	36.7	18.6	14.5	12.9

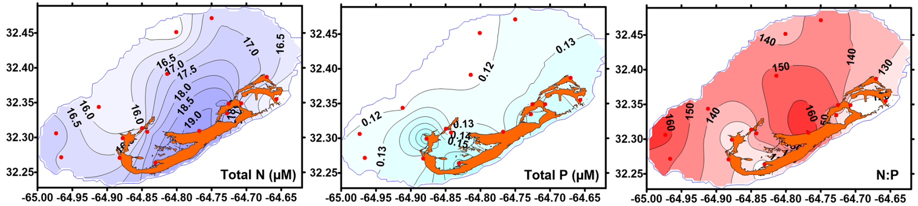

Figure 1. Isopleths of period-of-record averages for Total Nitrogen (TN, µM), Total Phosphorus (TP, µM) and the molar ratio of N : P in the water column on the Bermuda platform. The blue line is the 20 m isobaths on the rim of the platform. Red dots indicate locations of the 17 permanent sampling locations.

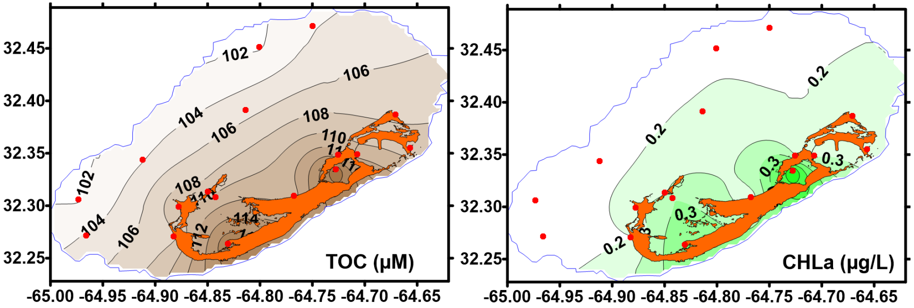

Figure 2. Isopleths of period-of-record averages for Total Organic Carbon (TOC, µM) and Chllorophyll *a* (Chl *a*, µg L^{-1}) in the water column on the Bermuda platform. The blue line is the 20 m isobaths on the rim of the platform. Red dots indicate locations of the 17 permanent sampling locations.

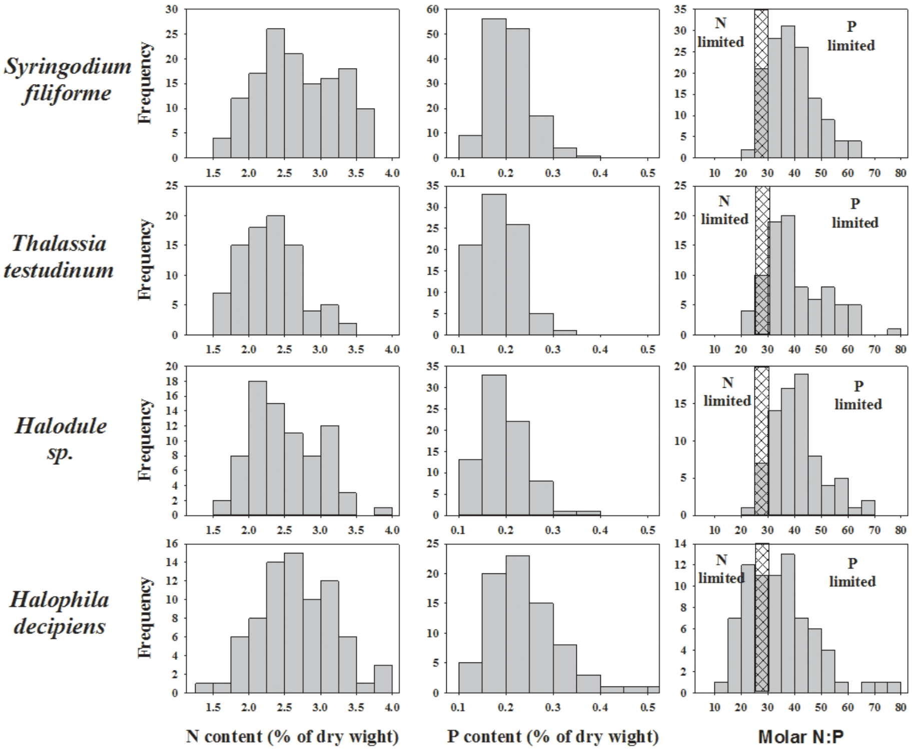

Figure 3. Frequency distribution of the measured carbon, nitrogen and phosphorus content of seagrasses collected on the Bermuda Platform, by species. The cross-hatched region on the molar N : P plots indicates the Seagrass Redfield Ratio of 25–30; N : P less than this indicates N-limitation, while N : P greater than this indicates P-limitation.

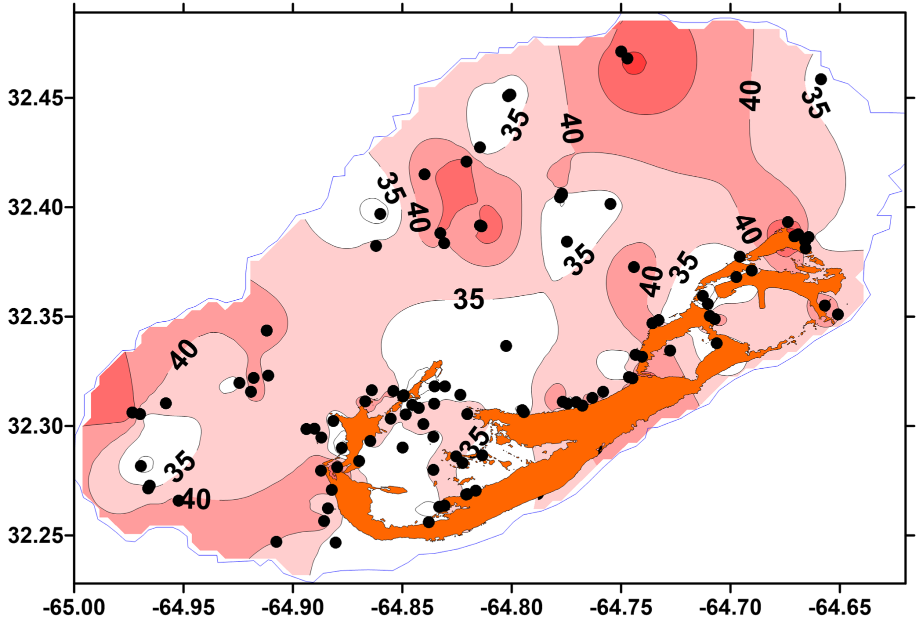

Figure 4. Isopleths of the N : P of leaves of the seagrasses *Syringodium filiforme* and *Halodule* sp. Black dots indicate sampling locations.

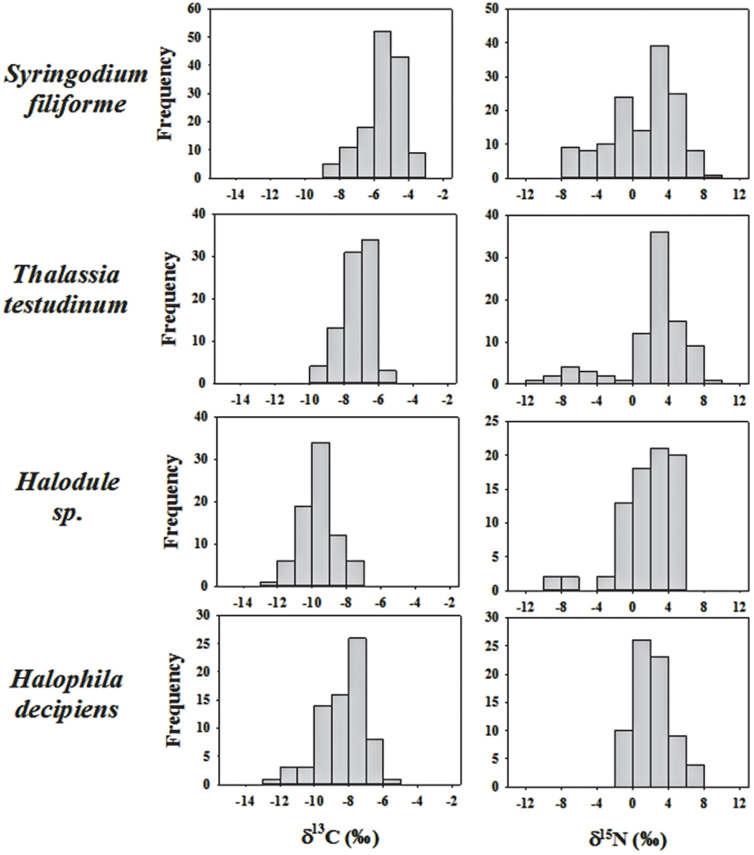

Figure 5. Frequency distribution of the measured δ^{13}C and δ^{15}N of seagrasses collected on the Bermuda Platform, by species.

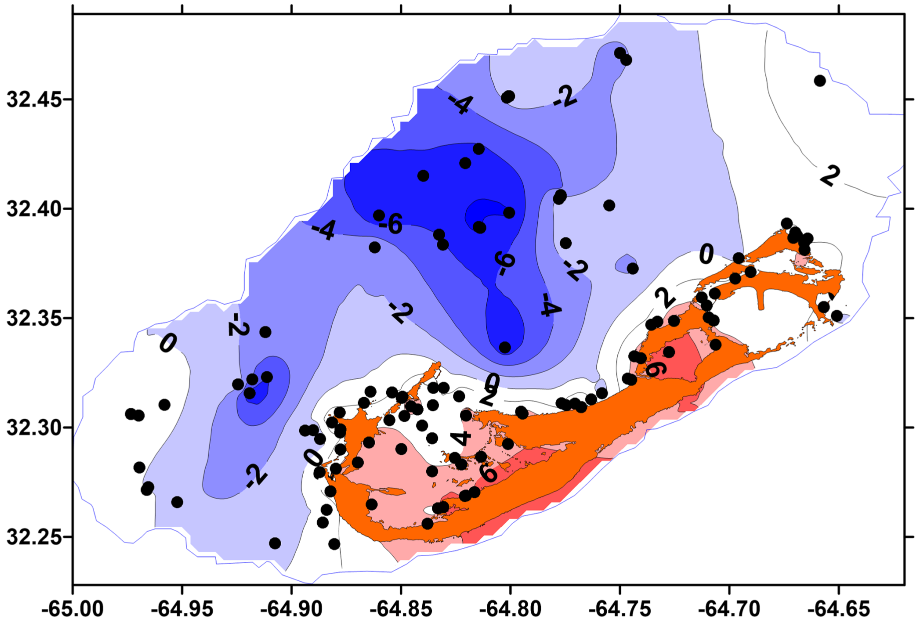

Figure 6. δ^{15}N of seagrass leaves from the Bermuda platform. Black dots indicate sites where at least one of the seagrasses *Syringodium filiforme*, *Thalassia testudinum* or *Halodule* sp. occur. If more than one species occurred at a site, the average value for all co-occuring species is shown.