

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

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5 **J. W. Fourqurean<sup>1,2</sup>, S. A. Manuel<sup>3</sup>, K. A. Coates<sup>3</sup>, W. J. Kenworthy<sup>4</sup> and J. N. Boyer<sup>2,\*</sup>**  
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7 [1] Marine Science Program, Department of Biology, Florida International University, Miami,  
8 Florida, USA

9 [2] Southeast Environmental Research Center, Florida International University, Miami, Florida,  
10 USA

11 [3] Applied Ecology Section, Department of Conservation Services, Bermuda Ministry of  
12 Environment and Sports, Smiths, Bermuda

13 [4] Beaufort, North Carolina, USA

14 [\*] now at: Center for the Environment and Department of Environmental Science and Policy,  
15 Plymouth State University, Plymouth, New Hampshire, USA

16  
17 Correspondence to: J. W. Fourqurean (jim.fourqurean@fiu.edu)

18  
19 **Abstract**

20 Striking spatial patterns in stable isotope ratios (isoscapes) and elemental ratios (stoichioscapes)  
21 of seagrass leaves and the water column nutrients indicate general P-limitation of both water  
22 column and benthic primary productivity on the Bermuda Platform, and they highlight the role of  
23 the Bermuda Islands as a source of N and P. We found consistent differences among the four  
24 seagrass species (*Syringodium filiforme*, *Thalassia testudinum*, *Halodule* sp. and *Halophila*  
25 *decipiens*) in the N, P,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of leaf tissues. The  $\delta^{15}\text{N}$  of seagrass leaves was especially

1 variable, with values from -10.1 to 8.8 ‰, greatly expanding the reported range of values for all  
2 seagrass species globally. Spatial patterns from both the water column and the seagrass leaves  
3 indicated that P availability was higher near shore, and  $\delta^{15}\text{N}$  values suggest this was likely a result  
4 of human waste disposal. Spatially-contiguous areas of extremely depleted seagrass  $^{15}\text{N}$  suggest  
5 unique N sources and cycling compared to other seagrass-dominated environments. Seagrass N:P  
6 values were not as far from the stoichiometric balance between N and P availability as in the water  
7 column, and there were no strong relationships between the water column N:P and the seagrass  
8 N:P. Such isoscapes and stoichioscapes provide valuable ecogeochemical tools to infer ecosystem  
9 processes as well as provide information that can inform food web and animal movement studies.

10

## 11 **1 Introduction**

12

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

20 Seagrasses are rooted plants; for a single location they can provide an integrated picture of water  
21 quality attributes, such as nutrient availability, chlorophyll *a* (CHL*a*), and turbidity that affect their  
22 growth. For example, ratios of the abundance of the major elements of carbon (C), nitrogen (N)  
23 and phosphorus (P) in seagrass tissues provide indications of the relative availability of light, N  
24 and P (Atkinson and Smith, 1983; Abal et al., 1994; Grice et al., 1996). Stable C isotopic  
25 composition of seagrass leaves serves as an indicator of light availability (Campbell and  
26 Fourqurean, 2009; Cooper, 1989; Cooper and DeNiro, 1989; Udy and Dennison, 1997) and stable  
27 N isotopic composition is used as a tracer of environmental  $\delta^{15}\text{N}$  values, which can indicate human  
28 sewage pollution (Cabana and Rasmussen, 1996) as well as internal cycling within the ecosystem  
29 (Fourqurean et al., 2005; Fourqurean et al., 1997; Lamb et al., 2012). Landscape-scale spatial

1 pattern in stable isotopic composition (termed the “isoscape”, Bowen, 2010) and in elemental  
2 content (which we can similarly call “stoichioscapes”) of the seagrass “canaries” can be very useful  
3 in elucidating ecosystem-scale patterns in sources of materials and processes affecting elemental  
4 cycling (Burkholder et al., 2013; Fourqurean et al., 2005; Fourqurean et al., 2007; Fourqurean et  
5 al., 1997; Fourqurean and Zieman, 2002; Fourqurean et al., 1992a).

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

21 Since the 1990’s, there has been a loss of about 23% of the spatial extent of seagrass meadows  
22 across the Bermuda platform, and the density of seagrass in many of the remaining meadows has  
23 decreased from historic conditions (Murdoch et al., 2007). Interestingly, most of this decline has  
24 occurred in the offshore areas, distant from any direct anthropogenic nutrient sources. While it has  
25 become clear that grazing by the large population of green sea turtles that use Bermuda as  
26 developmental juvenile habitat has contributed to the decline (Fourqurean et al., 2010), the role  
27 that nutrient availability plays in controlling seagrass distribution and health across the platform is  
28 still unknown. Globally, the majority of seagrass declines documented since the beginning of the  
29 20<sup>th</sup> century have been related to decreases in water quality caused by anthropogenic nutrient  
30 loading (Short and Wyllie-Echeverria, 1996). This suggests that understanding the current state of

1 water quality and its relationship to seagrass vitality is important for a more complete  
2 understanding of the recent trajectory of Bermuda's seagrasses. In addition, given their restriction  
3 to areas of very high bottom light availability compared to other more tropical areas (Manuel et  
4 al., 2013), the potential exists for even small changes in water quality to impact the distribution of  
5 seagrasses. The stoichioscapes and isoscapes of Bermuda's seagrasses should reflect the mean  
6 state of the environment and provide clues about the factors controlling their distribution and  
7 trajectory. Further, species-specific isotopic differences and isoscapes could also provide tools for  
8 understanding the movements of the green turtle herbivores that may be contributing to seagrass  
9 declines.

10 In this paper, we present an extensive data set describing the water quality of the Bermuda  
11 platform. If land-based sources of nutrients are impacting the marine environment of the Bermuda  
12 Platform, then we hypothesize there will be a distinct spatial pattern of decreasing concentrations  
13 of inorganic nutrients, organic matter and  $CHL_a$  with distance from the shoreline. Further, we test  
14 whether the isoscape and stoichiосscape of seagrasses across the Bermuda platform are  
15 representative of this long-term water quality dataset. Specifically, we hypothesize that the C:N:P  
16 of seagrass will approach seagrass Redfield ratios (SRR, defined as N:P of 25-30 for plants  
17 growing with a relative abundance of both N and P compared to light availability, Atkinson and  
18 Smith, 1983; Duarte, 1990; Ferdie and Fourqurean, 2004), and given the importance of light  
19 availability in determining seagrass distribution across the Bermuda platform (Manuel et al.,  
20 2013), we also expect seagrass tissues to have C:N:P near SRR and a decrease in  $\delta^{13}C$  of the  
21 seagrass in low-light environments. Because of the influence of human wastewater on the isotopic  
22 content of nitrogen in sewage effluent (Cabana and Rasmussen, 1996), we expect water quality to  
23 be a determinant of  $\delta^{15}N$  of seagrasses and for the isoscape of seagrass  $\delta^{15}N$  to trend from high  
24 values close to shore to lower values further from human influence. Also, given our knowledge of  
25 the distribution of seagrass species across the Bermuda platform (Manuel et al., 2013) we expected  
26 species identity could influence our interpretations of seagrass isoscapes and stoichioscapes.

27

## 28 **2 Methods**

### 29 **2.1 Study Site**

1 Despite its high latitude, the shallow platform surrounding the mid-Atlantic island chain of  
2 Bermuda (32.4° N) has coral reefs, seagrasses, and macroalgal beds formed by tropical species  
3 (Coates et al., 2013). Coral cover on Bermuda's reefs is very high compared to most locations in  
4 the Caribbean (Sheppard, 2013; Riegl and Dodge, 2008). Seagrass meadows are widespread on  
5 the Bermuda Platform and are found at about 24% of randomly-selected sites inside the fringing  
6 coral reef (Manuel et al., 2013); many of the larger beds are in nearshore locations. *Syringodium*  
7 *filiforme* is the most often encountered seagrass, followed in order of prevalence by *Halophila*  
8 *decipiens*, *Thalassia testudinum* and *Halodule* sp. (There is uncertainty about the taxonomic  
9 identity of the *Halodule* that is currently found in Bermuda, Manuel et al., 2013). Owing to the  
10 relatively high latitude of Bermuda compared to the rest of the range of these tropical plants,  
11 seagrasses are restricted to areas of shallower water and higher mean light transmittance to the  
12 bottom in Bermuda; this is likely a consequence of low insolation during winter months (Manuel  
13 et al., 2013).

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

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

## 1   **2.2   Seagrass surveys, collection and analysis**

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

10   Seagrasses were present at all of the 17 permanent monitoring sites, but only at 168 of the 516  
11   random sites. If seagrasses were present, multiple intact short shoots of each seagrass species were  
12   haphazardly collected along the 50m transect line. In order to assure sufficient sample for all  
13   subsequent analyses, we collected five short shoots of the larger *T. testudinum*, 30 short shoots of  
14   *S. filiforme*, 40 short shoots of *Halodule* sp. and ca. 300 leaves of *H. decipiens*. In the lab, seagrass  
15   shoots were washed free of sediment, and all green leaves from each species at each site were  
16   pooled into a common sample. Leaf material was gently cleaned of epiphytes using a razor blade,  
17   dried to a constant weight at 50°C, and ground to a fine powder. C and N content of leaf material  
18   was analyzed in duplicate using a CHN analyzer (Fisons NA1500). Leaf P content was determined  
19   through a dry oxidation and acid hydrolysis extraction followed by a colorimetric analysis  
20   (Fourqurean et al., 1992b). Elemental content was calculated on a dry weight basis (i.e., mass of  
21   element/dry weight of sample × 100%); all elemental ratios were calculated on a molar basis.  
22   Stable isotope ratios of C and N were analyzed using standard elemental analyzer isotope ratio  
23   mass spectrometer (EA-IRMS) procedures. The EA was used to combust the organic material and  
24   to reduce the formed gases into N<sub>2</sub> and CO<sub>2</sub>, which were measured on a Finnigan MAT Delta C  
25   IRMS in a continuous flow mode. Isotopic ratios (R) were reported in the standard delta notation  
26   (‰):  $\delta$  (‰) =  $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ . These results are presented with respect to the  
27   international standards of atmospheric N (AIR, N<sub>2</sub>) and Vienna Pee Dee belemnite (V-PDB) for  
28   C. Analytical reproducibility of the reported  $\delta$  values, based on sample replicates, was better than  
29   ± 0.2‰ for  $\delta^{15}\text{N}$  and ± 0.08‰ for  $\delta^{13}\text{C}$ .

## 30   **2.3   Water quality measurements**

1 Water quality parameters were measured on a monthly basis at the 17 permanent monitoring sites,  
2 over a period of 1-3 days. For detailed description of the water quality methods and data, please  
3 see the Supplementary Material. As water quality data were collected monthly at each site for the  
4 period 2007-2012, the period of water quality data collection began one year later and continued  
5 3 years after our collection of seagrass elemental and isotopic content data. We tested the water  
6 quality data for long-term monotonic trends from 2006-2012; when these trends were lacking, we  
7 assumed that the means of the water quality data could be applied to the analyses of the  
8 relationships among seagrass and water quality variables, and we then subsequently compared the  
9 average water quality data to seagrass data from the three years of record.

## 10 **2.4 Submarine light regime in seagrass beds**

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

## 17 **2.5 Statistical methods**

18 Prior to statistical analyses, data were tested for their adherence to assumptions of the statistical  
19 techniques; we used parametric methods if the data were normally distributed and homoscedastic.  
20 If data did not meet these assumptions we used non-parametric methods. We tested for long-term  
21 monotonic trends in the water quality data using linear regression with time as the independent  
22 variable. Relationships between water quality measurements and seagrass elemental and stable  
23 isotopic content were elucidated by analyzing bivariate correlations; a general lack of normality in  
24 the water quality data resulted in using Spearman's  $\rho$  rank correlation coefficient as a test of  
25 monotonic relationships among water quality variables. Seagrass elemental and isotopic content,  
26 as well as the water quality parameters N:P and % $I_0$  met the assumptions for parametric statistical  
27 analysis, so we assessed relationships with Pearson's correlation coefficient,  $r$ . Analysis of  
28 Variance (ANOVA) with Student-Newman-Keuls post-hoc tests were used to assess differences  
29 in elemental and isotopic content among seagrass species. Differences in elemental and isotopic

1 content among co-occurring seagrasses were tested using paired t-tests, pairing species within  
2 sites.

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

13

### 14 **3 Results**

#### 15 **3.1 Water quality on the Bermuda platform**

16 Reflecting its small size and position in the central Atlantic Ocean, water quality surrounding  
17 Bermuda reflected the influence of the ocean endmember, with generally high water clarity and  
18 low nutrient concentrations (See Supplementary Material). Linear regressions yielded no  
19 significant trends in time in platform-averaged average water quality measurements.

20 In comparison to N, P concentrations were very low; soluble reactive phosphorous (SRP)  
21 concentrations averaged  $0.048 \pm 0.001 \mu\text{M}$  and total phosphorus (TP) concentrations averaged  
22  $0.136 \pm 0.002 \mu\text{M}$ . Both the dissolved inorganic nitrogen (DIN):SRP and N:P ratios were much  
23 higher than Redfield, and the total organic carbon (TOC):N ratio lower than Redfield, suggesting  
24 that, in general, the waters around Bermuda are P-limited. CHL $a$  concentrations were positively  
25 correlated with temperature (Table 1), suggesting seasonal, summertime increases in  
26 phytoplankton biomass; high CHL $a$  was also correlated with higher  $\text{NO}_2^-$ ,  $\text{NO}_3^-$ , TP, SRP, TOC,  
27 dissolved organic carbon (DOC) and  $\text{SiO}_2$ . On the contrary, there was no correlation between total  
28 nitrogen (TN) and CHL $a$  (Table 1), further suggesting N availability does not generally limit  
29 phytoplankton around Bermuda.



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

### 7 **3.2 Seagrass elemental content and stoichiometry**

8 Seagrass leaves exhibited a wide range of values for N and P content (Figure 3, Table 2). N content  
9 ranged from 1.40 % to 3.91 % and P content ranged from 0.058 % to 0.465%. When data were  
10 pooled from all sites by species, there were significant differences among species in N content  
11 (ANOVA,  $F_{3,376} = 11.8$ ,  $p < 0.001$ ) and P content (ANOVA,  $F_{3,376} = 18.4$ ,  $p < 0.001$ ). Post-hoc tests  
12 indicated that there were no significant differences in N content between *S. filiforme* and *H.*  
13 *decipiens*, but *T. testudinum* and *Halodule* sp. were different from all other species. In contrast,  
14 there was more overlap among the species in P content: there was no significant difference between  
15 *S. filiforme* and *Halodule* sp. nor between *Halodule* sp. and *T. testudinum*, while P content of *H.*  
16 *decipiens* was distinct. While there was a significant difference in N:P among species (ANOVA,  
17  $F_{3,375} = 5.8$ ,  $p = 0.001$ ), *H. decipiens* was the only species with different N:P ratios from the other  
18 species. N:P of the larger-bodied seagrasses (*S. filiforme*, *T. testudinum* and *Halodule* sp.) were  
19 greater than 30:1, indicative of P limitation. N:P of the smaller, faster-growing, and low light-  
20 adapted *H. decipiens* indicated P limitation in approximately 80% of the samples, but N:P was <  
21 30: in about 20% of the samples, suggesting potential N-limitation at some sites.

22 Comparisons of global means of elemental content data (Table 2) do not fully capture the actual  
23 differences among species driven by their physiology and morphology, since the distributions of  
24 the species across the platform are different (Manuel et al., 2013) and there also were gradients in  
25 availability of N and P in the water column across the platform (Figure 1). To control for this  
26 variation, we compared species pairwise based on co-occurrence at individual sampling sites. At  
27 the 66 sites where they co-occurred, *S. filiforme* had N content  $0.23 \% \pm 0.06 \%$  higher than *T.*  
28 *testudinum* (paired  $t = 3.9$ ,  $df = 65$ ,  $p < 0.001$ ). *S. filiforme* had N content  $0.22\% \pm 0.06$  higher ( $p <$   
29  $0.001$ ) than *Halodule* sp. and  $0.39 \% \pm 0.14 \%$  higher ( $p = 0.013$ ) than *H. decipiens*. *T. testudinum*  
30 had significantly lower N content (by  $0.14 \% \pm 0.06 \%$ ,  $p = 0.038$ ) than *Halodule* sp.. On a single

1 occasion, *T. testudinum* was found co-occurring with *H. decipiens*. There were no significant  
2 differences in the N content of *Halodule* sp. and *H. decipiens* at the 15 sites where they co-  
3 occurred.

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

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

### 21 **3.3 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of seagrass leaves**

22 In a manner similar to elemental content, seagrass leaves were found with a broad range of  $\delta^{13}\text{C}$   
23 and  $\delta^{15}\text{N}$  values (Table 3 and Figure 5).  $\delta^{13}\text{C}$  values ranged from  $-12.9\text{‰}$  to  $-3.3\text{‰}$ ; and  $\delta^{15}\text{N}$   
24 values ranged from  $-10.1\text{‰}$  to  $8.8\text{‰}$ . When data were pooled from all sites, there were species-  
25 specific differences in  $\delta^{13}\text{C}$  (ANOVA,  $F_{3,369} = 262.7$ ,  $p < 0.001$ ), but not in  $\delta^{15}\text{N}$  ( $F_{3,370} = 1.8$ ,  $p =$   
26  $0.148$ ). The mean  $\delta^{13}\text{C}$  was lowest for *Halodule* sp. ( $-9.6\text{‰} \pm 0.1\text{‰}$ ), followed in increasing  
27 order by *H. decipiens* ( $-8.3\text{‰} \pm 0.2\text{‰}$ ), *T. testudinum* ( $-7.3\text{‰} \pm 0.04\text{‰}$ ) and *S. filiforme* ( $-4.6$   
28  $\text{‰} \pm 0.01\text{‰}$ ).

1 Analyses of differences between species pairs at sites where the species co-occurred corroborate  
2 the interspecific differences in  $\delta^{13}\text{C}$ , with all possible pairwise comparisons significantly different  
3 (paired t-tests,  $p \leq 0.001$  for all comparisons). When found at the same site,  $\delta^{13}\text{C}$  of *S. filiforme*  
4 averaged  $2.3\text{‰} \pm 0.01\text{‰}$  higher than *T. testudinum*,  $4.15\text{‰} \pm 0.08\text{‰}$  higher than *Halodule* sp. and  
5  $1.3\text{‰} \pm 0.2\text{‰}$  higher than *H. decipiens*. *T. testudinum* averaged  $1.9\text{‰} \pm 0.2\text{‰}$  higher than *Halodule*  
6 sp.. We had insufficient data to compare isotopic signatures of *T. testudinum* and *H. decipiens*.  
7 *Halodule* sp. averaged  $2.8\text{‰} \pm 0.2\text{‰}$  higher than *H. decipiens*. In these pairwise analyses, there  
8 were no significant differences in the  $\delta^{15}\text{N}$  of *S. filiforme* and either *T. testudinum* or *Halodule* sp.,  
9 nor were there significant differences in the  $\delta^{15}\text{N}$  of *T. testudinum* or *Halodule* sp. However, there  
10 were significant differences in the  $\delta^{15}\text{N}$  of co-occurring *S. filiforme* and *H. decipiens* ( $t = 3.18$ , d.f.  
11  $= 16$ ,  $p = 0.006$ ) and co-occurring *Halodule* sp. and *H. decipiens* ( $t = 2.98$ , d.f.  $= 13$ ,  $p = 0.11$ ). *H.*  
12 *decipiens* had  $\delta^{15}\text{N}$  on average  $2.3\text{‰} \pm 0.8\text{‰}$  higher than *Halodule* sp. and  $1.7\text{‰} \pm 0.5\text{‰}$  higher  
13 than *S. filiforme*.

14 Given that there were no differences in the  $\delta^{15}\text{N}$  of *S. filiforme*, *T. testudinum* or *Halodule* sp., the  
15 spatial pattern in the  $\delta^{15}\text{N}$  from all sites where any of these species occurred indicates a striking  
16 spatial pattern in the  $\delta^{15}\text{N}$  of the seagrasses from across the platform (Figure 6).  $\delta^{15}\text{N}$  on the  
17 platform distant from the Bermuda Islands was distinctly depleted in  $^{15}\text{N}$ , with some areas  
18 exhibiting  $\delta^{15}\text{N}$  values as low as  $-10.1\text{‰}$ . As distance from land decreased,  $\delta^{15}\text{N}$  values increased,  
19 with values higher than  $8\text{‰}$  in the semi-enclosed Hamilton Harbor and in enclosed Harrington  
20 Sound. The spatial gradients in  $\delta^{15}\text{N}$  were very steep, with  $\delta^{15}\text{N}$  changing as rapidly as  $1.8\text{‰ km}^{-1}$   
21 from Hamilton Harbor to the center of the platform.

### 22 **3.4 Relationships among seagrass elemental content and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values**

23 Given the differences among species in N:P ratios and  $\delta^{13}\text{C}$ , we analyzed the relationships among  
24 elemental and stable isotopic composition of seagrasses by species (Table 3). For all seagrass  
25 species, there was a significant positive correlation between C:N and C:P, but N:P was in all cases  
26 correlated with C:P, and only weakly correlated with C:N for *Halodule* sp. ( $r=0.243$ ,  $p=0.032$ ).  
27 There were also strong positive correlations between C:N and  $\delta^{15}\text{N}$  for all species, which indicated  
28 that plants with low N content had relatively enriched  $\delta^{15}\text{N}$  values. With one exception,  $\delta^{13}\text{C}$  was  
29 positively correlated with both C:P and N:P, indicating that plants with low P content tended to

1 have stable carbon composition more enriched in  $^{13}\text{C}$ ; for *H. decipiens* there was no significant  
2 correlation between  $\delta^{13}\text{C}$  and N:P. There were some exceptions to the general correlation patterns:  
3 for *T. testudinum* only, there was a significant positive correlation between C:P and  $\delta^{15}\text{N}$ ; and N:P  
4 was significantly, negatively correlated with  $\delta^{15}\text{N}$  for *S. filiforme* and *H. decipiens*, but not for *T.*  
5 *testudinum* or *Halodule* sp.

### 6 **3.5 Water quality as a predictor of seagrass elemental content and $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$** 7 **values**

8 There were no simple linear relationships between seagrass elemental and isotopic content and  
9 water quality that applied across all four seagrass species. There were differences in the ranges of  
10 light availability at sites where the different species occurred: %I<sub>0</sub> at sites supporting *T. testudinum*  
11 averaged  $70 \pm 1\%$ , compared to  $59 \pm 2\%$ ,  $55 \pm 2\%$  and  $44 \pm 2\%$  for *S. filiforme*, *Halodule* sp., and  
12 *H. decipiens*, respectively. At sites that supported *S. filiforme* and *T. testudinum*, there was a  
13 significant negative relationship between water column N:P and the amount of light reaching the  
14 bottom (%I<sub>0</sub>, a function of water quality and depth), but there was no significant relationship  
15 between these environmental parameters at sites that supported *Halodule* sp. and *H. decipiens*  
16 (Table 3, italic font). %I<sub>0</sub> was significantly and positively correlated with the C:N, C:P, N:P and  
17  $\delta^{13}\text{C}$  of *S. filiforme* and *Halodule* sp, suggesting that high light availability leads to decreases in N  
18 and P content in seagrass leaves, an increase in the relative amount of N with respect to P, and  
19 enrichment with  $^{13}\text{C}$  relative to  $^{12}\text{C}$  for these species. The  $\delta^{15}\text{N}$  of *S. filiforme* and *H. decipiens*  
20 were both significantly positively correlated with %I<sub>0</sub>. Interestingly, there were only weak  
21 relationships between the water column N:P and seagrass elemental and isotopic content. *Halodule*  
22 sp. C:N was higher when water column N:P was higher, but *H. decipiens* C:P and N:P were higher  
23 when the water column N:P was higher.  $\delta^{15}\text{N}$  of *S. filiforme* and *T. testudinum* were correlated  
24 with water column N:P, but there were no similar significant correlations for *Halodule* sp and *H.*  
25 *decipiens*.

26 Interspecific differences in the distributions of species and elemental content and isotopic  
27 composition necessitated analyses of the relationships between water quality and seagrass  
28 elemental and isotopic content be done individually for each species. The multiple bivariate  
29 correlations among the water quality and seagrass variables (Tables 2 and 4) resulted in robust  
30 extraction of composite variables in PCA that explained between 73.1 and 82.7% of the original

1 variation in the species-specific data sets (Table 4). For all four species, PCA revealed strong,  
2 positive relationships between the water quality variables CHL<sub>a</sub>, DOC, TP and TN and the  $\delta^{15}\text{N}$   
3 of seagrass leaves which loaded strongly onto the first principal component (PCI) which explained  
4 between 31.3 and 36.7% of the variation in the original dataset. There were species-specific  
5 differences in the subsequently extracted PCs, For *S. filiforme*: PCII was strongly related to high  
6 %I<sub>0</sub> and seagrass N:P and  $\delta^{13}\text{C}$ ; PCIII was strongly correlated with high water column TP and low  
7 water column TN:TP; and PCIV was related to high C:N and C:P in seagrass leaves. For *T.*  
8 *testudinum*: PCII was positively correlated with high C:P, N:P and  $\delta^{13}\text{C}$  of seagrass leaves; PCIII  
9 was negatively correlated with %I<sub>0</sub> but positively correlated with water column TN and TN:TP;  
10 and PCIV was associated with high seagrass C:P and C:N. Only three significant PCs were  
11 extracted for *Halodule* sp; with PCII strongly correlated with high %I<sub>0</sub> and seagrass C:P, C:N and  
12 N:P; and PCIII positively correlated with water column TN and TN:TP. For *H. decipiens*: PCII  
13 was positively correlated with seagrass C:P and N:P; PCIII was associated with high seagrass C:N  
14 and  $\delta^{13}\text{C}$ ; and PCIV was influenced strongly by high water column TN:TP.

15

## 16 **4 Discussion**

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

### 29 **4.1 “Stoichioscapes” as indicators of ecosystems processes**

1 C:N:P stoichiometry of the water column strongly suggests general P-limitation of the nearshore  
2 waters of Bermuda, with the vast majority of the measurements of water column N:P well in excess  
3 of the 16:1 of the Redfield Ratio (Redfield, 1958). Furthermore, the spatially-coherent patterns in  
4 water column TP, TOC and CHL<sub>a</sub> clearly demonstrate that the islands of Bermuda are a source of  
5 the limiting nutrient to the nearshore marine waters. Our findings based on C:N:P stoichiometry  
6 of the P-limited nature of the phytoplankton community on the Bermuda platform agree with  
7 recent studies finding generalized P-limitation of plankton production in the ocean surrounding  
8 Bermuda – the source waters for the Bermuda Platform (Ammerman et al., 2003; Lomas et al.,  
9 2004; Salihiglu et al., 2008). Stoichiometry of seagrass tissues is also consistent with P limitation  
10 across much of the Bermuda platform, with most N:P values greater than the “seagrass Redfield  
11 ratio” (SRR) of 30:1 (Atkinson and Smith, 1983; Duarte, 1990).

12 The strength of seagrass P-limitation, as assessed by the degree of N:P deviation from SRR, is not  
13 as severe as documented in other parts of these species range, like south Florida (Fourqurean and  
14 Zieman, 2002; Fourqurean et al., 1992a) and seagrass N:P values were are not as far from the  
15 stoichiometric balance between N and P availability as in the water column. In fact, there was no  
16 significant relationship between the water column and seagrass N:P across the Bermuda Platform.  
17 These conditions likely arise because of relatively low light availability on the bottom compared  
18 to the more tropical locations of the centers of the ranges of these seagrass species (Manuel et al.,  
19 2013). When growing in light-limited conditions, a consequence of strong seasonality of insolation  
20 in Bermuda, nutrients are not limiting to seagrass production (Fourqurean and Zieman, 2002),  
21 hence the seagrass elemental content tends towards the SRR. Light limitation could ameliorate the  
22 degree of P limitation in Bermuda’s seagrasses as suggested by other studies for the relationship  
23 between light availability and nitrogen limitation (Abal et al., 1994; Grice et al., 1996; Zimmerman  
24 et al., 1987). This is consistent with our results for *Halophila decipiens*, which grew in the deepest  
25 and lowest-light environments on the Bermuda Platform (Manuel et al., 2013) and had a mean N:P  
26 the closest to the SRR of the four Bermuda seagrasses.

27 In addition to the differences in the mean N:P of *H. decipiens* compared to the other species that  
28 arise as a consequence of differences in the mean depths at which these species are found,  
29 biological differences among species led to consistent differences in N:P within sites. N:P is an  
30 integrated measure of the balance of light, N, and P availability for seagrass growth (Fourqurean  
31 and Rutten, 2003), and availability is determined by the balance between resource supply and the

1 demand for that resource by the plants. Making the assumption that the supply of resources is  
2 constant within sites, then the species with the highest demand, i.e., the highest relative growth  
3 rate, should experience the lowest relative availability and exhibit greatest resource limitation  
4 (Tilman, 1980), as has been shown by comparing N:P of co-occurring seagrasses in other locations  
5 (Campbell and Fourqurean, 2009; Fourqurean et al., 1995). The relative N:P of Bermudian  
6 seagrasses likewise follow the pattern expected by comparing their relative growth rates. The  
7 relative growth rates (%d<sup>-1</sup>) are higher for *H. decipiens*, intermediate for *Halodule* sp. and *S.*  
8 *filiforme*, and lowest for *T. testudinum* (Duarte, 1991; Gallegos et al., 1994; Kenworthy et al.,  
9 1989); resulting in, when co-occurring, relative N:P of seagrasses of *H. decipiens* > (*S. filiforme*  
10 and *Halodule* sp.) > *T. testudinum*. Since *S. filiforme* and *Halodule* sp. were similar in N:P and  
11 widely distributed across the Platform we were able to use their common stoichiometry to indicate  
12 the nutrient status of the different environments.

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

#### 24 **4.2 Isoscapes as indicators of ecosystem processes**

25 The striking spatial pattern in  $\delta^{15}\text{N}$  serves as an informative isoscape (Bowen, 2010) for generating  
26 hypotheses and testing models about biogeochemical processes on the Bermuda platform. Human  
27 wastewater can contain DIN with  $\delta^{15}\text{N}$  values as high as 40‰ (Tucker et al., 1999), and plants in  
28 close proximity to wastewater outflows often exhibit high  $\delta^{15}\text{N}$  (Cabana and Rasmussen, 1996).  
29 The very near shore, <sup>15</sup>N-enriched  $\delta^{15}\text{N}$  signatures of seagrasses, and the rapid decline of seagrass  
30  $\delta^{15}\text{N}$  offshore at the rate of 1.8 ‰ km<sup>-1</sup>, suggest that sewage-influenced groundwater transports

1 nutrients into the nearshore marine environment, and that those nutrients are rapidly processed by  
2 both the water column and the benthos. Hence, the influence of sewage-derived nutrients on the  
3 benthos is currently limited in spatial extent in Bermuda; it is clear that the zone of  $\delta^{15}\text{N}$  of  
4 seagrasses  $> 0$  corresponds with the zones of enhanced TOC, TN, TP and CHL $a$  in the water  
5 column.

6 To our knowledge, the  $\delta^{15}\text{N}$  values we report from all four seagrass species occurring in Bermuda  
7 greatly expand the known range of values previously reported for each species. For example, the  
8 published range of  $\delta^{15}\text{N}$  values for *T. testudinum* encompasses -4.3‰ to 9.4‰ (Fourqurean et al.,  
9 2005); our data expands this range to a new minimum of -10.1‰.  $\delta^{15}\text{N}$  values  $< 0$  have rarely been  
10 reported for seagrasses, and the mechanisms that would lead to plant tissues more depleted than  
11 atmospheric N need to be elucidated. Large spatially-contiguous zones of  $\delta^{15}\text{N}$  values between -  
12 4.3‰ and 0‰ in the Florida Keys are hypothesized to be a result of either an isotopically depleted  
13 source pool of DIN, or maximum fractionation of DIN on uptake in regions of very high N  
14 availability (Fourqurean et al., 2005). Additionally, the process of ammonification produces  $\text{NH}_4^+$   
15 that has  $\delta^{15}\text{N}$  values lower than the values of the source organic matter (Mobius, 2013); further,  
16 when DIN is available in excess compared to plant demand, plants discriminate against  $^{15}\text{N}$  uptake  
17 (Fourqurean et al., 2005; Yoneyama et al., 1991; Evans, 2001; Koba et al., 2010). Indeed,  
18 experimental N additions have been shown to increase fractionation of nitrogen isotopes upon  
19 uptake when nitrogen supply exceeds demand (Udy and Dennison, 1997). In fact, the only report  
20 of seagrass  $\delta^{15}\text{N}$  values as low as we observed in the center of the Bermuda platform are from  
21 experimental N addition experiments with very fast-growing, high N-demanding seagrasses (Udy  
22 and Dennison, 1997).

23 The strong correlation we found between  $\delta^{15}\text{N}$  and C:N for all four species of seagrass are  
24 consistent with enhanced fractionation of the source pool in regions of high N availability, but  
25 such a fractionation may not be sufficient to explain the large negative  $\delta^{15}\text{N}$  values. It is likely  
26 that benthic processing of N in the middle of the Bermuda platform is creating uniquely  
27 isotopically-depleted DIN that is being incorporated into seagrasses. The depleted  $^{15}\text{N}$  on the  
28 Bermuda platform is consistent with the input of new N to the region by  $\text{N}_2$  fixation (Montoya et  
29 al., 2002), additional processes must be involved to generate the observed negative  $\delta^{15}\text{N}$ . High  
30 rates of ammonification could partly explain why DIN would be depleted in  $^{15}\text{N}$  (Mobius, 2013).



### 1 **4.3 $\delta^{13}\text{C}$ of seagrasses in Bermuda**

2 We expected to find that  $\delta^{13}\text{C}$  of seagrass tissues would be a function of light availability, because  
3 in high light environments there is less fractionation of dissolved inorganic carbon (DIC) upon  
4 photosynthetic uptake. In essence, seagrasses are more isotopically enriched in  $^{13}\text{C}$  if light  
5 availability does not limit photosynthesis (Campbell and Fourqurean, 2009; Fourqurean et al.,  
6 2005; Hu et al., 2012) and therefore C demand is high relative to availability. We did find this  
7 expected relationship across the platform for *S. filiforme* and *Halodule* sp., but not for *T.*  
8 *testudinum* or *H. decipiens*. The lack of these relationships for *T. testudinum* and *H. decipiens*  
9 could be owing to the more restricted ranges of light availability at which these species were found:  
10 *T. testudinum* is generally restricted to high light environments, *H. decipiens* to low-light  
11 environments, and the other two species are found from high light to low light environments.  
12 Additionally, lower light availability at Bermuda's latitude could decrease the dependence of  $\delta^{13}\text{C}$   
13 on light compared to more tropical locations with higher light. Interestingly, for all four seagrasses,  
14 plants with higher  $\delta^{13}\text{C}$  had lower P content, similar to previous reports from south Florida  
15 (Fourqurean et al., 2005), suggesting that plants from high light environments experience greater  
16 P-limitation than plants from low light environments.

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

### 24 **4.4 Stoichioscapes and isoscapes as important tools to study marine ecological** 25 **processes**

26 The spatial patterns of elements and their ratios, which we can call a stoichioscape, and the stable  
27 isotopic composition of widespread seagrasses (an isoscape) specifically point to: 1) generalized  
28 P limitation of both the water column and the benthos; 2) land-based sources of both N and P, and  
29 3) locations within the more generally P-limited seascape that are light- or N-limited. The  
30 substantial impact of light availability on seagrass distribution, elemental content and stable

1 isotopic composition did not obscure the spatial patterns. Further, our results have generated new  
2 hypotheses about the nature of N cycling on the Bermuda platform that will guide research of local  
3 processes but also of the role of the coastal ocean in global biogeochemical cycles.

4 Bermuda presents a unique opportunity to examine the use of elemental and isotope content of  
5 organisms to help explain ecological processes, in particular the large decline of seagrasses on the  
6 outer platform. Although the isoscape of nutrients implicates land based sources of nitrogen and  
7 phosphorus, we can't attribute the decline of seagrasses to degraded water quality and have  
8 hypothesized that seagrass losses are the result of overgrazing by green turtles (Fourqurean et al.  
9 2010). Our isoscapes and stoichioscapes can be used as tools in ecogeochemistry where the  
10 elemental and isotope content are used as natural markers to help understand trophic ecology and  
11 population structure. Ecogeochemistry is providing new insights on animal movements in marine  
12 ecosystems (see McMahon et al., 2013 for review) and has long been used to study food web  
13 structure. Pronounced patterns in isotopic composition of plants across an area like the Bermuda  
14 platform can help interpret the distribution of stable isotope ratios among individuals in a  
15 population of consumers. For example, large variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of green sea turtles within  
16 a population has been interpreted as individual diet specialization, with some individuals feeding  
17 on seagrasses, others on macroalgae and still others with a carnivorous diet (e.g. Burkholder et al.,  
18 2011). Given the very large ranges in isotopic composition of seagrasses we found on the Bermuda  
19 platform, a similar variability in the isotopic composition of green sea turtles could be driven by  
20 spatial variation in the isotopic composition (and species identity) of seagrasses and restricted  
21 home ranges of individual turtles in the population, and indeed variation in stable isotopic  
22 composition of sea turtles has been used to infer differences in provenance of sea turtles in other  
23 locations (Pajuelo et al., 2012). Only with knowledge of the relationship between the isoscapes  
24 and stoichioscapes and the home ranges of individuals can variation of ecogeochemical tags within  
25 a population be properly interpreted.

26

## 27 **Author contribution**

28 All authors designed the study. J.W.F., S.A.M., K.A.C. and W.J.K. collected field samples; J.W.F.  
29 analyzed plant samples for elemental and isotopic content and J.N.B analyzed water samples. J.  
30 W. F prepared the manuscript with contributions from all co-authors.

1

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11

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13

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

4

	NO <sub>3</sub> <sup>-</sup>	NO <sub>2</sub> <sup>-</sup>	NH <sub>4</sub> <sup>+</sup>	TN	TP	SRP	TOC	DOC	Si	CHL <sub>a</sub>	SAL	TEMP	DO%
NO <sub>3</sub> <sup>-</sup>		.042	-.023	.072*	.092**	.028	-.025	-.022	.186**	.109**	-.142**	-.055	-.008
NO <sub>2</sub> <sup>-</sup>	.192		.051	.079*	.040	.039	.103**	.050	.097**	.090**	-.001	.013	-.055
NH <sub>4</sub> <sup>+</sup>	.474	.107		-.118**	.049	.105**	.210**	.208**	-.014	.052	.061	.086**	-.017
TN	.024	.013	.000		.050	-.063	.158**	.198**	.076*	.053	.134**	.196**	.107**
TP	.004	.205	.121	.114		.181**	.071*	.048	.120**	.109**	-.029	.292**	.015
SRP	.385	.221	.001	.051	.000		.137**	.144**	.069*	.138**	.003	.079*	.018
TOC	.429	.001	.000	.000	.026	.000		.888**	-.040	.247**	.048	.382**	.059
DOC	.487	.118	.000	.000	.135	.000	0.000		-.031	.256**	.109**	.358**	.104**
Si	.000	.003	.656	.017	.000	.033	.213	.343		.119**	.068*	.011	-.042
Chl-a	.001	.008	.127	.118	.001	.000	.000	.000	.001		-.030	.317**	-.115**
Sal	.000	.965	.054	.000	.369	.933	.132	.001	.036	.384		.161**	.130**
Temp	.087	.687	.007	.000	.000	.014	.000	.000	.723	.000	.000		-.145**
DO	.797	.089	.609	.001	.651	.586	.068	.001	.197	.001	.000	.000	

5

6

1 Table 2. Nitrogen and Phosphorus content, N:P,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of seagrass leaves from  
 2 the Bermuda platform. Superscripts indicate homogenous groups as indicated by Student-  
 3 Newman-Keuls post hoc tests in ANOVA of data grouped by species, significant differences at  $\alpha$   
 4 = 0.05.

Parameter	Mean	SE	Minimum	Maximum	n
N content (% of dry wt)					
<i>Syringodium filiforme</i>	2.69 <sup>a</sup>	0.05	1.67	3.72	139
<i>Thalassia testudinum</i>	2.31 <sup>b</sup>	0.05	1.57	3.38	86
<i>Halodule sp.</i>	2.51 <sup>c</sup>	0.05	1.59	3.87	78
<i>Halophila decipiens</i>	2.66 <sup>a</sup>	0.06	1.40	3.91	77
P content (% of dry wt)					
<i>Syringodium filiforme</i>	0.158 <sup>a</sup>	0.004	0.079	0.301	139
<i>Thalassia testudinum</i>	0.136 <sup>b</sup>	0.005	0.058	0.259	86
<i>Halodule sp.</i>	0.144 <sup>a,b</sup>	0.005	0.065	0.306	78
<i>Halophila decipiens</i>	0.192 <sup>c</sup>	0.009	0.067	0.465	77
N:P (molar)					
<i>Syringodium filiforme</i>	39.1 <sup>a</sup>	0.7	20.2	63.6	139
<i>Thalassia testudinum</i>	40.6 <sup>a</sup>	1.2	21.1	78.5	86
<i>Halodule sp.</i>	40.8 <sup>a</sup>	1.1	23.3	68.5	78
<i>Halophila decipiens</i>	34.6 <sup>b</sup>	1.5	13.6	77.8	76

$\delta^{13}\text{C}$ (‰)					
<i>Syringodium filiforme</i>	-5.5 <sup>a</sup>	0.01	-8.8	-3.3	138
<i>Thalassia testudinum</i>	-7.3 <sup>b</sup>	0.1	-9.7	-5.5	85
<i>Halodule sp.</i>	-9.6 <sup>c</sup>	0.1	-12.4	-7.2	78
<i>Halophila decipiens</i>	-8.3 <sup>d</sup>	0.2	-12.9	-5.7	72
$\delta^{15}\text{N}$ (‰)					
<i>Syringodium filiforme</i>	1.3 <sup>a</sup>	0.33	-7.7	8.8	138
<i>Thalassia testudinum</i>	2.2 <sup>a</sup>	0.4	-10.1	8.0	86
<i>Halodule sp.</i>	1.6 <sup>a</sup>	0.4	-8.9	5.6	78
<i>Halophila decipiens</i>	2.2 <sup>a</sup>	0.2	-1.2	7.5	72

1

Table 3. 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).

*Italics indicate water column parameters.*

	n		C:N	C:P	N:P	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	<i>Water N:P</i>	<i>%I<sub>0</sub></i>
<i>Syringodium filiforme</i>	139	C:N		<b>0.626</b>	-0.064	0.129	<b>0.384</b>	<i>0.097</i>	<b>0.214</b>
<i>Thalassia testudinum</i>	86			<b>0.497</b>	0.048	-0.037	<b>0.203</b>	<i>0.122</i>	<i>-0.033</i>
<i>Halodule</i> sp.	78			<b>0.704</b>	<b>0.243</b>	0.106	<b>0.306</b>	<b>0.337</b>	<b>0.315</b>
<i>Halophila decipiens</i>	77			<b>0.328</b>	-0.027	0.300	<b>0.455</b>	<i>0.056</i>	<i>0.149</i>
<i>Syringodium filiforme</i>	139	C:P	< <b>0.001</b>		<b>0.725</b>	<b>0.224</b>	0.129	<i>0.093</i>	<b>0.335</b>
<i>Thalassia testudinum</i>	86		< <b>0.001</b>		<b>0.866</b>	<b>0.280</b>	<b>0.243</b>	<i>-0.071</i>	<i>0.028</i>
<i>Halodule</i> sp.	78		< <b>0.001</b>		<b>0.849</b>	<b>0.244</b>	0.117	<i>0.212</i>	<b>0.406</b>
<i>Halophila decipiens</i>	77		<b>0.004</b>		<b>0.928</b>	<b>0.227</b>	-0.216	<b>0.321</b>	<i>0.031</i>
<i>Syringodium filiforme</i>	139	N:P	0.453	< <b>0.001</b>		<b>0.210</b>	<b>-0.198</b>	<i>0.065</i>	<b>0.238</b>
<i>Thalassia testudinum</i>	86		0.659	< <b>0.001</b>		<b>0.364</b>	0.189	<i>-0.074</i>	<i>0.013</i>
<i>Halodule</i> sp.	78		<b>0.032</b>	< <b>0.001</b>		<b>0.251</b>	-0.089	<i>0.046</i>	<b>0.318</b>
<i>Halophila decipiens</i>	77		0.818	< <b>0.001</b>		0.138	<b>-0.390</b>	<b>0.338</b>	<i>-0.017</i>
<i>Syringodium filiforme</i>	139	$\delta^{13}\text{C}$	0.132	<b>0.008</b>	<b>0.013</b>		-0.161	<i>0.150</i>	<b>0.230</b>
<i>Thalassia testudinum</i>	86		0.736	<b>0.009</b>	<b>0.001</b>		-0.158	<i>0.176</i>	<i>-0.135</i>

<i>Halodule</i> sp.	78		0.357	<b>0.032</b>	<b>0.026</b>			-0.016	0.086	<b>0.301</b>
<i>Halophila decipiens</i>	77		<b>0.010</b>	<b>0.050</b>	0.247			-0.073	0.015	0.158
<i>Syringodium filiforme</i>	139	$\delta^{15}\text{N}$	<b>0.012</b>	0.131	<b>0.020</b>	0.059			<b>-0.341</b>	<b>0.241</b>
<i>Thalassia testudinum</i>	86		<b>0.050</b>	<b>0.024</b>	0.081	0.148			<b>-0.340</b>	0.091
<i>Halodule</i> sp.	78		<b>0.006</b>	0.308	0.439	0.888			-0.015	0.205
<i>Halophila decipiens</i>	77		<b>&lt;0.001</b>	0.068	<b>0.001</b>	0.542			-0.181	<b>0.320</b>
<i>Syringodium filiforme</i>	139	Water column N:P	0.256	0.275	0.445	0.079		<b>&lt;0.001</b>		<b>-0.324</b>
<i>Thalassia testudinum</i>	86		0.263	0.516	0.497	0.108		<b>0.001</b>		<b>-0.404</b>
<i>Halodule</i> sp.	78		<b>0.003</b>	0.062	0.692	0.456		0.898		-0.163
<i>Halophila decipiens</i>	77		0.627	<b>0.005</b>	<b>0.003</b>	0.673		0.129		-0.187
<i>Syringodium filiforme</i>	139	%I <sub>0</sub>	<b>0.012</b>	<b>&lt;0.001</b>	<b>0.005</b>	<b>0.007</b>	<b>0.004</b>		<b>&lt;0.001</b>	
<i>Thalassia testudinum</i>	86		0.764	0.801	0.906	0.217	0.405		<b>&lt;0.001</b>	
<i>Halodule</i> sp.	78		<b>0.005</b>	<b>&lt;0.001</b>	<b>0.005</b>	<b>0.007</b>	0.072		0.154	
<i>Halophila decipiens</i>	77		0.196	0.788	0.887	0.184	<b>0.006</b>		0.102	

Table 4. 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
<i>Syringodium filiforme</i>						<i>Halodule</i> sp.				
%I <sub>0</sub>	0.205	<b>0.515</b>	0.480	0.198		%I <sub>0</sub>	0.100	<b>0.569</b>	-0.483	
Water column CHL <sub>a</sub>	<b>0.893</b>	-0.059	0.167	-0.051		Water column CHL <sub>a</sub>	<b>0.915</b>	0.055	0.039	
Water column DOC	<b>0.948</b>	-0.085	0.219	-0.008		Water column DOC	<b>0.954</b>	0.119	0.012	
Water column TP	<b>0.682</b>	-0.176	<b>0.608</b>	-0.039		Water column TP	<b>0.856</b>	-0.043	-0.383	
Water column TN	<b>0.846</b>	0.003	-0.459	0.034		Water column TN	<b>0.616</b>	0.383	<b>0.602</b>	
Water Column TN:TP	-0.111	0.093	<b>-0.961</b>	0.064		Water Column TN:TP	-0.259	0.347	<b>0.854</b>	
Seagrass C:P	-0.047	0.076	-0.007	<b>0.632</b>		Seagrass C:P	-0.267	<b>0.900</b>	-0.147	
Seagrass C:N	0.051	0.041	-0.045	<b>0.980</b>		Seagrass C:N	0.259	<b>0.729</b>	0.161	
Seagrass N:P	-0.137	<b>0.882</b>	0.008	-0.050		Seagrass N:P	-0.191	<b>0.697</b>	-0.320	
Seagrass δ <sup>13</sup> C	-0.092	<b>0.547</b>	-0.120	0.020		Seagrass δ <sup>13</sup> C	-0.096	0.386	-0.226	
Seagrass δ <sup>15</sup> N	<b>0.753</b>	-0.142	0.284	0.425		Seagrass δ <sup>15</sup> N	<b>0.706</b>	0.380	0.140	
% of Variance explained	32.1	17.4	17.3	14.5		% of Variance explained	32.2	23.4	17.5	



<i>Thalassia testudinum</i>					<i>Halophila decipiens</i>				
%I <sub>0</sub>	-0.004	-0.103	<b>-0.663</b>	0.042	%I <sub>0</sub>	0.330	0.240	0.384	-0.405
Water column CHL <sub>a</sub>	<b>0.879</b>	-0.038	0.014	-0.260	Water column CHL <sub>a</sub>	<b>0.925</b>	-0.092	-0.061	-0.129
Water column DOC	<b>0.957</b>	0.025	0.065	-0.183	Water column DOC	<b>0.938</b>	-0.176	-0.039	-0.209
Water column TP	<b>0.670</b>	0.303	-0.488	0.062	Water column TP	<b>0.791</b>	-0.225	-0.046	-0.480
Water column TN	<b>0.617</b>	-0.107	<b>0.712</b>	-0.068	Water column TN	<b>0.921</b>	-0.086	-0.038	0.229
Water Column TN:TP	-0.352	-0.027	<b>0.886</b>	0.045	Water Column TN:TP	-0.054	0.254	0.055	<b>0.921</b>
Seagrass C:P	0.078	<b>0.796</b>	-0.072	<b>0.544</b>	Seagrass C:P	-0.170	<b>0.921</b>	0.222	0.136
Seagrass C:N	0.229	0.070	0.004	<b>0.915</b>	Seagrass C:N	0.148	0.018	<b>0.857</b>	0.122
Seagrass N:P	0.228	<b>0.888</b>	-0.009	0.142	Seagrass N:P	-0.218	<b>0.955</b>	-0.077	0.109
Seagrass δ <sup>13</sup> C	-0.254	<b>0.723</b>	0.117	-0.297	Seagrass δ <sup>13</sup> C	-0.343	-0.106	<b>0.668</b>	-0.098
Seagrass δ <sup>15</sup> N	<b>0.788</b>	0.030	-0.085	0.436	Seagrass δ <sup>15</sup> N	<b>0.710</b>	-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 captions

Figure 1. Isopleths of period-of-record averages for Total Nitrogen (TN,  $\mu\text{M}$ ), Total Phosphorus (TP,  $\mu\text{M}$ ) and the molar ratio of N:P in the water column on the Bermuda platform. The blue line is the 20m 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,  $\mu\text{M}$ ) and Chlorophyll-a (Chl-a,  $\mu\text{g L}^{-1}$ ) in the water column on the Bermuda platform. The blue line is the 20m 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  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of seagrasses collected on the Bermuda Platform, by species.

Figure 6.  $\delta^{15}\text{N}$  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-occurring species is shown.

Figure 1.

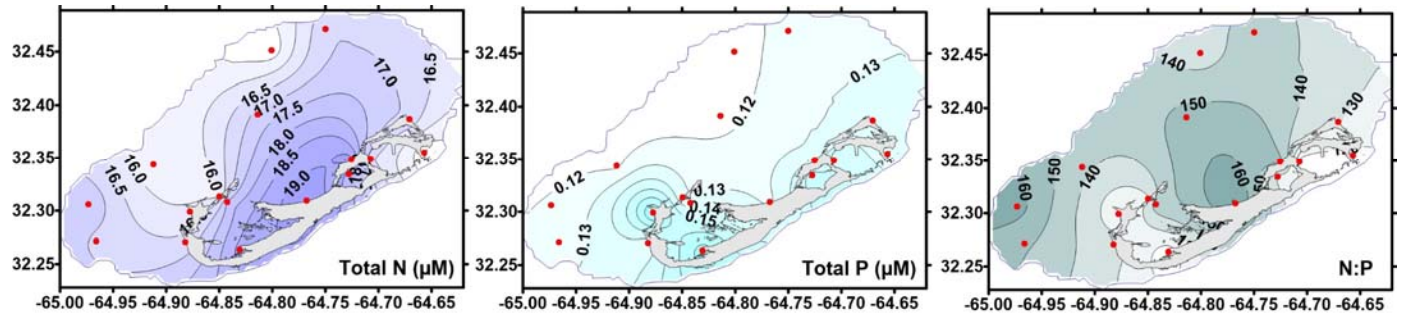


Figure 2.

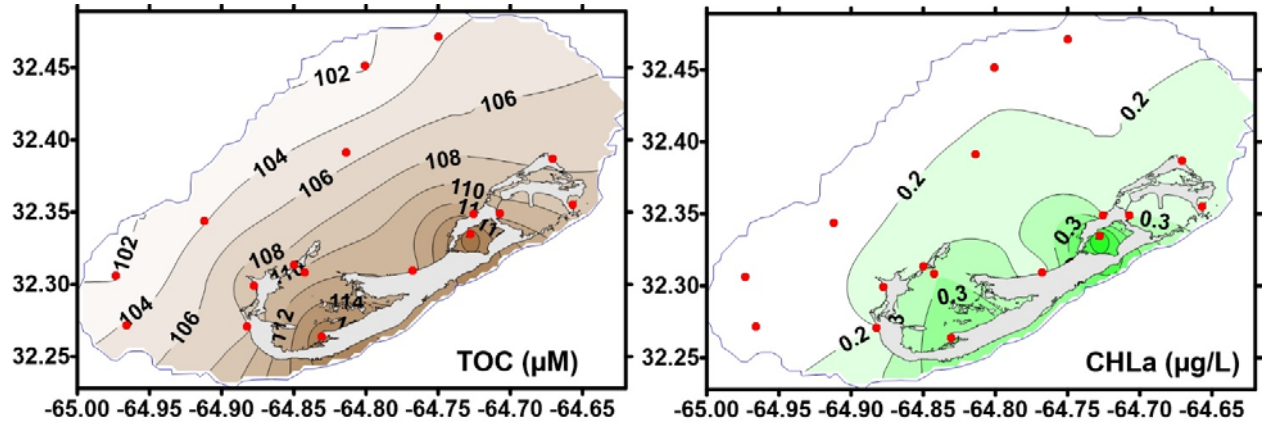


Figure 3.

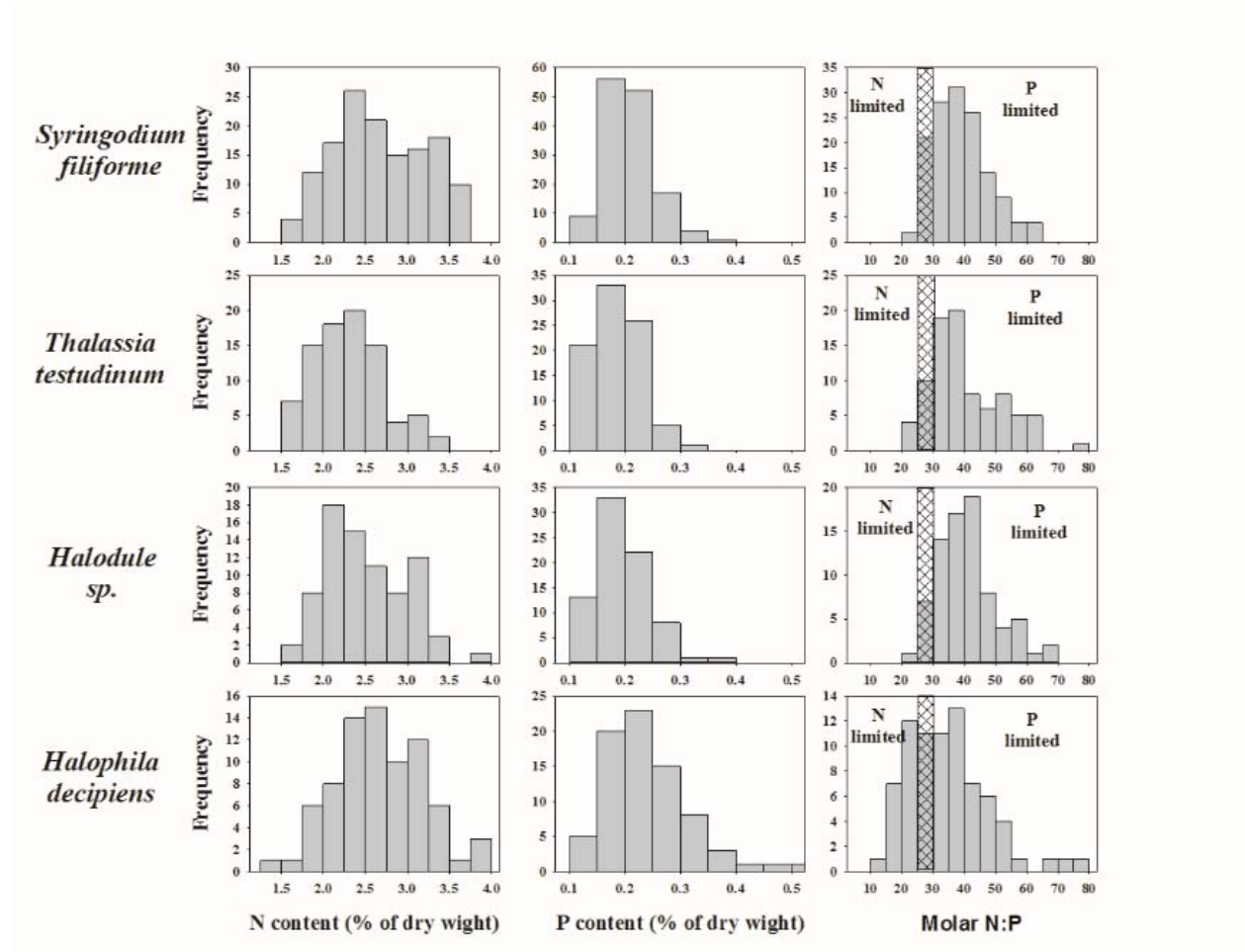


Figure 4.

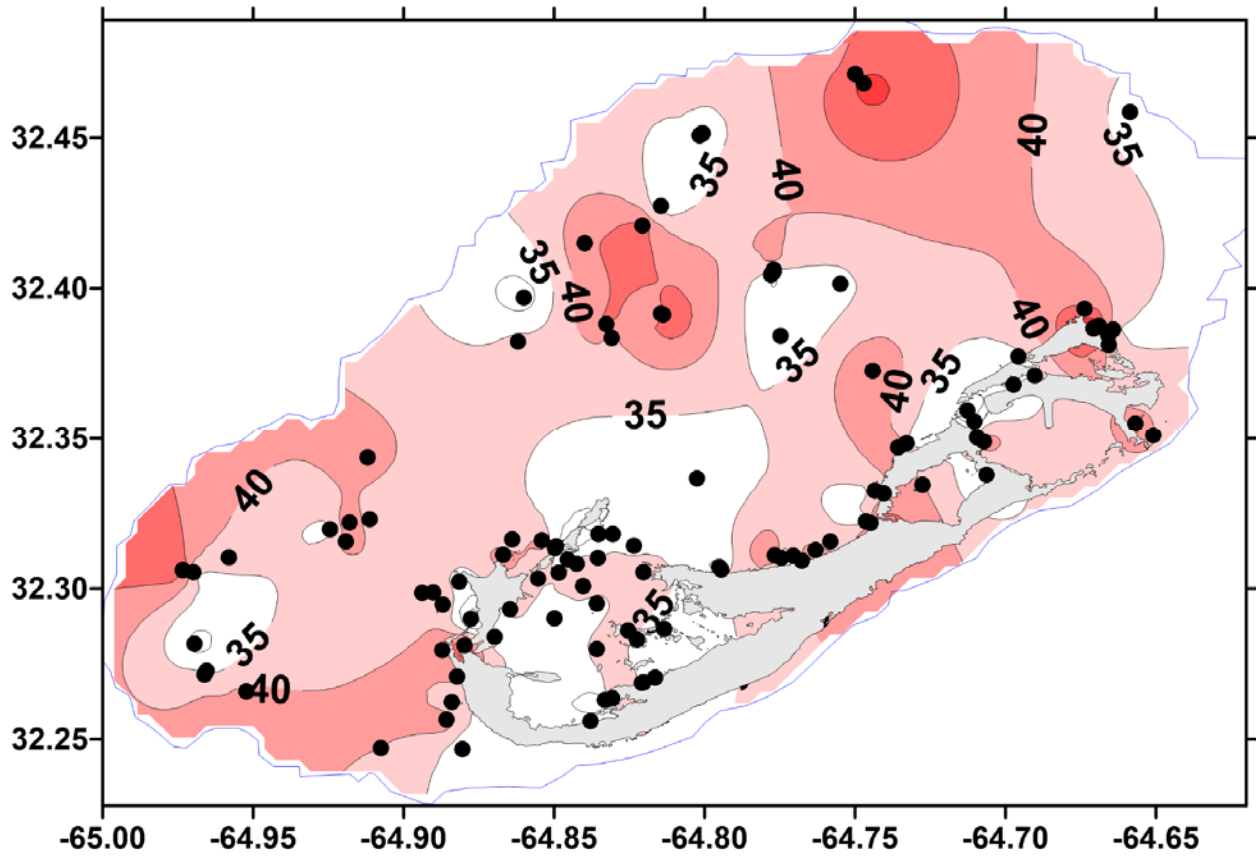


Figure 5.

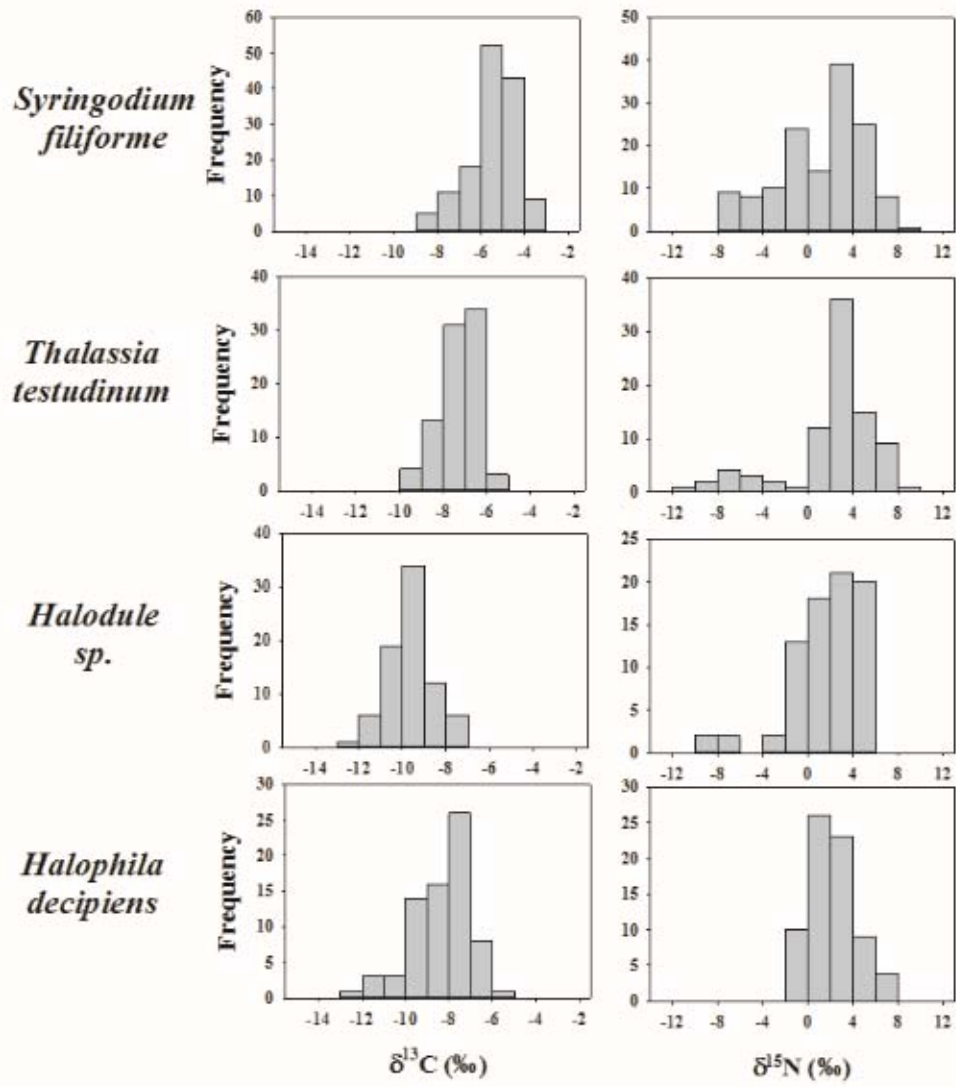


Figure 6.

