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Decadal Monitoring in Bermuda Shows a Widespread Loss of Seagrasses Attributable to Overgrazing by the Green Sea Turtle *Chelonia mydas*

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Abstract

The condition of seagrass habitat and the marine environment on the Bermuda Platform, a mid-oceanic shallow water habitat in the northwest Atlantic, has been monitored since 2006. The overall oceanic climate of the Platform is subtropical; the Platform supports communities of tropical marine seagrasses, including *Thalassia testudinum*, *Syringodium filiforme*, *Halodule* sp., and *Halophila decipiens*. At the beginning of the study, the general condition of seagrass beds at 17 permanent offshore and nearshore sites indicated that 14 were healthy, complex, and thriving communities, and three represented offshore beds, which had declined precipitously prior to the initiation of study. Over the period of the study, seagrass beds declined at all 17 sites; three beds disappeared, and there was no recovery at the sites known to have declined prior to 2006. Over the same period, there was no apparent negative change in the water quality overlying the seagrass beds. Assessments of elemental content, stable isotopic composition, and leaf morphology indicated that grazing by the green turtle (*Chelonia mydas*) is driving the decline of the seagrasses of Bermuda. Given the feeding behavior of these turtles on the Bermuda Platform, human intervention may be required to mitigate the decline of seagrass in Bermuda.

Keywords Ecological indicators · Herbivory · Stable isotopes · Stoichiometry · Plant morphology · Time series

Introduction

Seagrass meadows are among the most highly valued of the world's ecosystems because of the many goods and services they provide (Costanza et al. 2014; de Groot et al. 2012). They are also among the world's most productive ecosystems. Seagrasses are essential habitat and support high fishery yields both within the meadows (Norlund et al. 2018) as well as in adjacent offshore ecosystems (Blandon and zu Ermgassen 2014). They also regulate water quality and reduce erosion (Beck et al. 2001; Hemminga and Duarte 2000; Orth et al. 2006), and are hotspots for carbon fixation and storage (Duarte et al. 2010; Fourqurean et al. 2012). A number of charismatic, endangered, or threatened species rely on seagrasses for habitat and food, including a number of species of seahorses (Vincent et al. 2011), sirenians (Preen 1995), and green sea turtles (Bjorndal et al. 2000).

These important ecosystems have been in decline since at least the early twentieth century; it is estimated that the current extent of seagrasses globally is at most 71% of historical values and seagrass losses continue at a rate of at least 1.5% per year (Waycott et al. 2009). Seagrass losses have been primarily driven by anthropogenic deterioration of water quality (Short and Wyllie-Echeverria 1996). Even though they are taxonomically diverse, the species of seagrasses share a requirement for high light, so that they are very sensitive to decreases in ambient water clarity (Duarte 1995). Decreases in water transparency that lead to seagrass declines are often

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caused by eutrophication and poor management of runoff from urban and agricultural watersheds (Short and Wyllie-Echeverria 1996).

Because of the warm ocean waters that surround the islands, Bermuda hosts tropical marine ecosystems even at a temperate latitude of 32.3° N (Coates et al. 2013). The seagrasses of Bermuda are composed of species with subtropical to tropical distributions. However, at the relatively high latitudes of Bermuda, there is marked seasonality in light availability, similar to temperate rather than tropical locations, restricting seagrasses in Bermuda to shallower water depths with higher penetration of sunlight compared to more tropical locations within the species' ranges (Manuel et al. 2013). This could result in Bermuda's seagrasses being especially susceptible to eutrophication and impaired water clarity.

Spatial patterns in stable isotope and elemental ratios of seagrass leaves and water column nutrients indicate general phosphorus (P) limitation of both pelagic and benthic primary productivity on the Bermuda Platform, and they highlight the role of the Bermuda islands as a source of nitrogen (N) and P to nearshore waters (Fourqurean et al. 2015). Spatial patterns from both the water column and the seagrass leaves indicated that P availability is higher nearer the islands, while sewage biomarkers and δ^{15}N values indicate that human waste disposal influences nutrient availability (Baker et al. 2017; Fourqurean et al. 2015; Jones et al. 2011), and may be altering some benthic communities in nearshore waters (Lapointe and O'Connell 1989; McGlathery et al. 1992). Despite this human influence, Bermuda's waters remain oligotrophic and clear enough to allow high light penetration to the bottom across the entire Bermuda Platform (Manuel et al. 2013). These studies suggest that light availability is not the factor limiting seagrass distribution on the Platform, since many sites with appropriate sediments and high light penetration do not support seagrasses (Manuel et al. 2013; Murdoch et al. 2007).

Recently, seagrass declines were reported in locations distant from the Bermuda islands' nutrient sources (Murdoch et al. 2007), suggesting that factors other than water quality degradation could be responsible for the declines. Offshore declines were first documented between 1996 and 1998 (Fourqurean et al. 2010) as part of the CARICOMP monitoring program (van Tussenbroek et al. 2014), and by 2004 nearly 25% of the island's known seagrass beds had been lost (Murdoch et al. 2007). It was suggested that a possible driver of these declines was overgrazing by herbivorous fish and sea turtles. Preventing grazing by green sea turtles has been demonstrated to stop decline in offshore seagrass meadows in Bermuda (Fourqurean et al. 2010). Given the possible roles of sea turtle overgrazing and documentation of anthropogenic eutrophication in some of Bermuda's nearshore waters (Lapointe and O'Connell 1989; McGlathery et al. 1992; Murdoch et al. 2007), a monitoring program for seagrasses and water quality was initiated in 2006 (Fourqurean et al. 2015; Manuel et al. 2013).

Many aspects of the seagrass communities and the plants themselves are indicators of water quality and nutrient availability in the overlying water and the overall health of the seagrass community (Fourqurean and Rutten 2003; McMahon et al. 2013), including taxonomic composition, elemental content, and stable carbon (C) and N isotope ratios (Table 1). Further, herbivore grazing elicits morphological and chemical changes in seagrasses. Intense grazing leads to increases in N and P content, and seagrass leaves that are both shorter and narrower compared to ungrazed seagrasses. It was our aim in this work to monitor simultaneously water quality and seagrass indicators of stress (Table 1) to evaluate the status of the seagrass meadows of Bermuda and attempt to identify factors responsible for any changes in their status. We present the results from a decade of monitoring at 17 locations distributed across the Bermuda Platform. The Bermuda monitoring program was specifically designed to assess causes of seagrass change. Monitored indicators were chosen because of their applicability to assessing drivers of change, and were selected based on the foundational literature listed in Table 1, as well as a decade of monitoring of seagrass communities in south Florida (Fourqurean and Rutten 2003). We examined evidence of two alternative drivers of the loss of seagrasses: changes in water quality and high grazing pressure by sea turtles. We hypothesized that if water quality was deteriorating and light was becoming limiting over time, we would see (1) increases in water column nutrients, chlorophyll-*a* (Chl-*a*), and turbidity; (2) increased light attenuation in the water column coupled with trends in C/N/P stoichiometry of seagrass leaves; (3) decreases in the δ^{13}C of the seagrass leaves; and (4) increasing δ^{15}N of the leaves as an indicator of increasing wastewater influence. Alternatively, if increased grazing pressure was driving seagrass losses, we expected to find no discernible correspondence in water quality and seagrass condition accompanied by four indicators of grazing: (1) seagrass morphological changes (leaf length, width, and area), (2) increased N and P content of the seagrass leaves, (3) no decrease in leaf δ^{13}C, and (4) no increases in leaf δ^{15}N.

Methods

Site Selection

A stratified random procedure was used to select 17 monitoring sites across the Bermuda Platform (Manuel et al. 2013; Fig. 1). These permanent monitoring sites were established in December 2006 and repeatedly sampled until August 2017.

Water Quality Assessment

Surface measurements of salinity (PSU), temperature (°C), and oxygen (DO) were made regularly at the 17 monitoring

Table 1 Proposed indicators of seagrass ecosystem status and the stressor each indicates

Property	Indicative of	References
Species composition	Light availability: species-specific light requirements	Wiginton and McMillan 1979
	Nutrient availability: higher nutrient availability favors faster growing taxa	Powell et al. 1989, 1991; Fourqurean et al. 1995
	Selective herbivory: most herbivores prefer high-nutrient, faster-growing taxa	Mariani and Alcoverro 1999; Armitage and Fourqurean 2006; Kelkar et al. 2013;
	Herbivory: herbivores create conditions that favor faster-growing species	Hernández and van Tussenbroek 2014
Elemental stoichiometry (C/N/P)	Relative availability of nutrients and light: high light drives increases in C/N and C/P, higher nutrient availability drives decreases in C/N, C/P	Duarte 1990; Fourqurean and Rutten 2003; Campbell and Fourqurean 2009
	Herbivory: herbivores remove older tissues lower in nutrients, leading to decreases in C/N and C/P in grazed plants	Thayer et al. 1984; Moran and Bjorndal 2007; Burkholder et al. 2012; Holzer and McGlathery 2016; Mutchler and Hoffman 2017
$\delta^{13}C$	Light availability: seagrasses from high light environments have less negative $\delta^{13}C$	Cooper and DeNiro 1989; Abal et al. 1994; Hu et al. 2012; Campbell and Fourqurean 2009
$\delta^{15}N$	N source: wastewater pollution leads to increased $\delta^{15}N$; fertilizer pollution can decrease $\delta^{15}N$	McClelland et al. 1997
Leaf length	Herbivory: shortens leaves	Fourqurean et al. 2010
Leaf width	Herbivory: leaves become narrower on grazed plants	Thayer et al. 1984; Zieman et al. 1984; Moran and Bjorndal 2005; Fourqurean et al. 2010; Holzer and McGlathery 2016;
Area per short shoot	Herbivory: grazed plants have less area per shoot	Fourqurean et al. 2010

sites. Measurements were made between 0.2 and 1 m below the water using electronic sensors (salinity and temperature: either a YSI 30 instrument or a YSI 600XL sonde; DO: either a YSI 550A instrument or a YSI 600XL sonde). Over the course of the monitoring program, instruments were replaced and regularly calibrated. Profiles of photosynthetically active radiation (PAR, 400 to 700 nm) at depth were obtained at most water quality sampling events using a 4π submerged spherical quantum sensor (LiCor model LI-193SA). Light profiles and site depth were used to calculate the fraction of incident irradiation reaching the bottom, $\%I_0$ (Manuel et al. 2013).

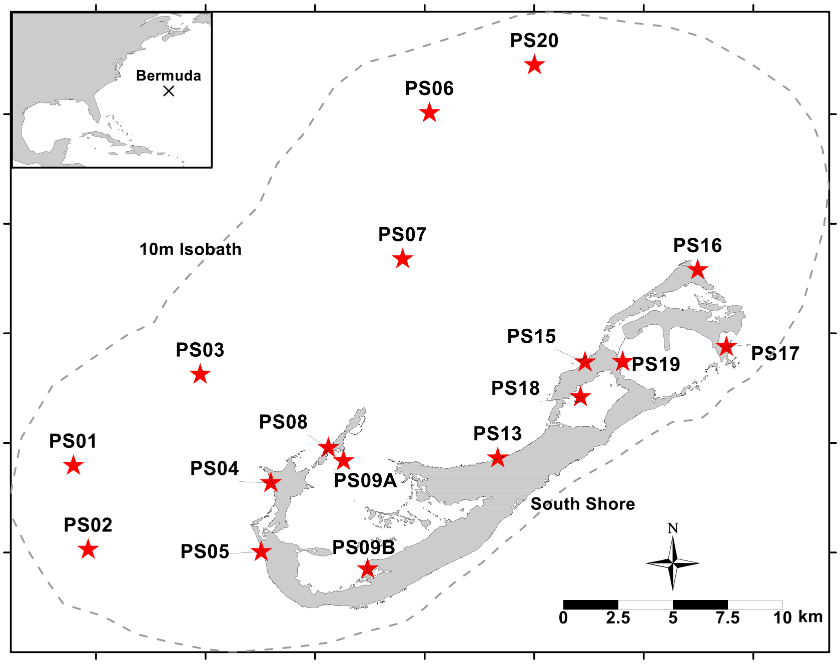


Fig. 1 Station location for water quality and seagrass monitoring inside the 10-m isobath that defines the top of the Bermuda Platform. For site selection criteria, see Manuel et al. 2013

Surface water samples were collected and analyzed for nutrient and Chl-*a* concentrations, monthly from September 2007 until September 2012, and then again in August and November 2013 and February and May 2014. Unfiltered water samples were assessed for total organic carbon (TOC), total nitrogen (TN), total phosphorus (TP), silicate (SiO_4^{4-}), and turbidity. Water was filtered in the field through GFF glass fiber filters, and the material retained on the filters was analyzed for Chl-*a* concentration. The filtrate was analyzed for nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), and soluble reactive phosphorus (SRP). For more detailed descriptions of the water quality methods and data, please see Online Resource 1.

Seagrass Monitoring

Individual and community characteristics of seagrass habitat were measured at the 17 sites during quarterly transect surveys, each completed by scuba divers over approximately three consecutive days, beginning in March 2007 until September 2016. One survey set was also done in August 2017. The full suite of seagrass metrics collected and what they indicate are shown in Table 1. Abundance and species composition of selected benthic taxa, including four seagrass species, were estimated at each of the 17 monitoring sites using modified Braun-Blanquet surveys composed of 10 randomly placed 0.25-m^2 quadrats along a 50-m fixed transect at each site (Fourqurean et al. 2001). For each taxon present in each quadrat, a Braun-Blanquet score (BB) was assigned by the scuba diver according to the cover that taxon represented, with 0 = absent, 0.1 = less than 5% cover by a single individual or short shoot, 1 = less than 5% cover with many individuals/shoots, 2 = > 5 to 25% cover, 3 = > 25 to 50% cover, 4 = > 50 to 75% cover, and 5 = > 75 to 100% cover. The observations from each quadrat were used to estimate seagrass abundance, as a Braun-Blanquet density score (D), for each taxon i using the observations from the 10 quadrats (q) on each transect as:

$$D_i = \sum_{q=1}^{10} \mathrm{BB}_i$$

We used the D_i scores for the seagrasses to calculate the relative importance of the slowest-growing seagrass for each survey, expressed as a species composition index (SCI):

$$\mathrm{SCI} = \frac{D_{\mathrm{Thalassia}}}{\sum\left(D_{\mathrm{Thalassia}}, D_{\mathrm{Syringodium}}, D_{\mathrm{Halodule}}, D_{\mathrm{Halophila}}\right)}$$

During each survey, seagrass plants were collected for morphological assessment (length and width) and analysis of elemental content (C, N, and P) and stable isotope ratios $\delta^{13}C$ and $\delta^{15}N$ of the leaves. For each seagrass species present, multiple intact short shoots were haphazardly collected along the 50-m transect line. In order to assure adequate samples for all subsequent analyses, we collected five to seven short shoots of the larger *Thalassia testudinum* (K.D.Koenig, 1805), 30 short shoots of *Syringodium filiforme* (Kützing, 1860), 40 short shoots of *Halodule* sp., and ca. 300 leaves of *Halophila decipiens* (Ostenfeld, 1902). Seagrass plants were first collected at the monitoring sites in December 2006.

Seagrass shoots were held on ice after collection and then frozen until processed for morphological and nutrient and isotope analyses. In the lab, the shoots were thawed, washed free of sediment, and the number of leaves attached to each short shoot was counted, and each leaf within a sample was measured for length for *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule* sp. Width was also determined for *T. testudinum* leaves, and we calculated the one-sided leaf area as length × width. All green leaves from each species at each site were then pooled into a common sample. Leaf material was gently cleaned of epiphytes using a razor blade, dried at 50 °C, and ground to a fine powder. C and N content of leaf material was analyzed in duplicate using a CHN analyzer (Fisons NA1500). Leaf P content was determined through dry oxidation and acid hydrolysis extraction followed by colorimetric analysis (Fourqurean et al. 1992). 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 (‰): δ (‰) = $[(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1000$‰. 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.

Small subsets of our transect monitoring and water quality data have been analyzed in previous publications (Manuel et al. 2013, Fourqurean et al. 2015). Specifically, those publications used averages of summertime values of water quality, seagrass abundance, nutrient stoichiometry, and stable isotope ratios for the period 2006–2008 to describe the general distribution of benthic communities across the Bermuda Platform and their relationships to light availability and water quality. The analyses for this current paper use data collected during all seasons of the year from 2006 to 2017.

Statistical Analyses

For all analyses, confidence in estimates of means is given as ± 1 standard error (SE) throughout. We used principal component analysis (PCA) to explore the structure of the water quality dataset and to define how the measured variables were correlated. Prior to PCA, variables were standardized by calculating the *Z* scores of all observations so that all variables had similar means and variances. We used the correlation matrix to extract the principal components (PCs) that had eigenvalues > 1, and Varimax rotation to aid in the interpretation of the resultant PCs.

Using linear regression, we tested for monotonic trends, first platform-wide and then by individual sampling site, in the component water quality variables identified with the PCA as well as in Chl-*a* and TOC. The assumptions of normality and homoscedasticity were tested prior to linear regression analyses. We also tested for monotonic trends in seagrass abundance at the monitoring sites using linear regression with date as a predictor of the average *D* for each seagrass species and SCI. Despite the non-linear nature of the BB scores that inflates the importance of relatively low *D*, the assumptions of linear regression were met for these analyses as *D* values were normally distributed and homoscedastic. To calculate net change over the monitoring period, we summed the *D* scores for all seagrasses at each site and computed average summed *D* values for the years 2007 and 2017, and we calculated the net change, Δ:

$$\Delta = \frac{D_{2017}–D_{2007}}{D_{2007}} \times 100\%.$$

Note that since Braun-Blanquet scores upweight the importance of low abundance sites, this approach would produce conservative (i.e., less negative) Δ values at sites with $D < 1$.

Results

Water Quality Analyses

The water quality dataset analyzed for this work expands by 4 years a previously published dataset (Fourqurean et al. 2015), but the generally superior water quality and low nutrient concentrations reported earlier continued to be expressed in the data (Table 2). In comparison to N, water column P concentrations were very low; SRP concentrations averaged 0.048 ± 0.001 μM, and TP concentrations averaged 0.14 ± 0.002 μM. Both the dissolved inorganic nitrogen (DIN)/SRP and N/P ratios were much higher than Redfield, suggesting that, in general, the waters around Bermuda are P-limited. The relatively high availability of N was indicated by TOC/TN ratios that were generally lower than Redfield.

Our PCA identified seven composite PCs that described 71.8% of the original variance in the water quality data set. Factor loadings on the individual PCs indicated that some of the measured variables were indeed highly correlated (Table 3). PC1 described the greatest portion of the original variation, and was strongly associated with high TN and total organic nitrogen (TON), and therefore also positively correlated with TN/TP and negatively correlated with TOC/TON. Hence, we interpret PC1 as an indicator of N abundance in the water column. Ammonium (NH_4^+) generally dominated the DIN, so we interpret the factor loadings on PC2 as a general indicator of NH_4^+ abundance. PC3 was strongly correlated with TOC and dissolved organic carbon (DOC) abundance. PC4 was positively correlated with TP and negatively correlated with TOC/TP; hence, we interpret PC4 as an indicator of P abundance. Both measures of water clarity (TURB and K_d) were highly correlated with PC5. Only SRP concentrations were strongly correlated with PC6, while PC7 was correlated with high NO_2^- and low DO. Chl-*a* was not strongly correlated with any of the PCs; Chl-*a* had its highest loading onto the organic carbon (OC) and P abundance PCs.

When data from all sites collected throughout the sampling period were combined, there were significant long-term monotonic trends in many of the water quality principal components, as well as Chl-*a* and TOC (Table 4). Nitrogen abundance (PC1), ammonium concentrations (PC2), water clarity (PC5), and SRP concentrations (PC6) all decreased platform-wide. Organic carbon abundance (PC3), Chl-*a* concentration, and TOC concentration all increased. There was also a significant decrease in PC7, correlated with a decrease in NO_2^- and an increase in DO. However, inspection of the data on a site-wise basis suggested that water quality showed different long-term trends at different sites, with significant trends at individual sites, while most sites had no significant trends.

Except for PC3 (OC abundance), there were very few significant long-term monotonic trends (as indicated by significant linear regressions) in any of the water quality composite variables when examined on a site-wise basis. There was a significant long-term increase in water clarity (PC5) at PS02 (slope = 0.078 ± 0.031 year^{-1}, $r^2 = 0.095$, $p = 0.015$). This increase can be seen in the time series of TURB and K_d at this site (Online Resource 2 Figure OR2.2). At two sites (PS01 and PS02), SRP abundance (PC6) decreased (PS01: slope = − 0.236 ± 0.074 year^{-1}, $r^2 = 0.150$, $p = 0.002$; PS02: slope = − 0.204 ± 0.068 year^{-1}, $r^2 = 0.115$, $p = 0.004$) (see Online Resource 2 Figures OR2.1 and OR2.2). PC7, indicative of high NO_2^- and low [O_2], decreased significantly over the time period of PS15 (slope = − 0.184 ± 0.081 year^{-1}, $r^2 = 0.079$, $p = 0.027$).

Table 2 Summary of water quality data collected from the 17 permanent monitoring stations, 2006–2016. SE = standard error of the mean

	Number	Mean	SE	Median	Minimum	Maximum
Temperature (°C)	1620	23.5	0.1	22.8	15.1	31.3
Salinity (PSU)	1621	36.6	0.0	36.6	32.6	40.0
Turbidity (NTU)	1615	0.65	0.01	0.58	0.16	7.45
Diffuse attenuation coeff. K_d (m^{-1})	1366	0.183	0.003	0.160	0.027	1.219
Dissolved O_2 (mg L^{-1})	1584	7.5	0.0	7.5	5.3	12.1
Dissolved O_2 (% saturation)	1582	107.7	0.2	106.8	55.4	178.7
Chlorophyll-*a* (μg L^{-1})	917	0.25	0.01	0.21	0.00	2.79
NH_4^+ (μM)	1052	1.39	0.04	1.05	0.06	10.03
NO_2^- (μM)	1052	0.02	0.00	0.02	0.00	0.25
NO_3^- (μM)	1050	0.47	0.02	0.27	0.01	14.52
DIN (μM)	1052	1.88	0.04	1.51	0.19	15.12
TON (μM)	1050	14.70	0.62	9.72	0.02	178.93
TN (μM)	1052	16.55	0.61	11.62	3.30	179.73
SRP (μM)	1044	0.048	0.001	0.043	0.000	0.278
TP (μM)	1052	0.14	0.00	0.13	0.02	1.47
SiO_4^{4-} (μM)	1035	0.25	0.01	0.12	0.00	2.29
TOC (μM)	1052	108.8	0.7	106.4	57.8	227.9
DOC (μM)	1052	101.9	0.7	100.7	27.1	197.3
TOC/TN	1052	9.5	0.1	8.9	0.6	30.1
TOC/TP	1052	881.2	10.2	835.1	67.2	4541.7
TN/TP	983	138.5	5.4	96.0	10.7	1932.8
DIN/SRP	981	57.7	2.5	36.2	2.0	846.1

At all sites, there were significant long-term trends in PC3, the abundance of OC, with rates of increase of 0.168–0.299 year^{-1} ($p < 0.042$ for all 17 stations), but there was a lot of variation around the long-term trend lines as the r^2 values for these regressions ranged from 0.06 to 0.14. A composite plot of water column TOC for all observations at all sites through time illustrates this general pattern (Fig. 2). Averaged across all sites, TOC increased at a rate of 2.98 ± 0.40 μM year^{-1} ($r^2 = 0.050, p < 0.001$), although there was significant inter-year variability around the long-term trend. There were significant trends in Chl-*a* at two of the 17 permanent sites, with Chl-*a* increasing at a rate of 0.021 ± 0.008 μg L^{-1} year^{-1} ($r^2 = 0.121, p = 0.010$) at site PS05 and at a rate of 0.022 ± 0.009 μg L^{-1} year^{-1} ($r^2 = 0.098$, $p = 0.021$) at PS17 (Online Resource 2 Figures OR2.5 and OR2.14).

Water depths at the 17 monitoring sites ranged from 1.2 m at PS17 to 12.1 m at PS06 (Table 5). The average K_d for the period of record at the sites ranged from 0.076 m^{-1} at the clearest offshore site (PS20) to 0.372 m^{-1} at the most turbid inshore site (PS09B). At the deepest site, 38.9% of incident solar radiation (%I_0) penetrated to the benthos, and over 50% on incident radiation reached the bottom at 16 of the 17 sites.

Seagrass Monitoring Data

Syringodium filiforme was found at 15 of the 17 sites while *Thalassia testudinum* was found at 14, *Halodule* sp. at 10, and *Halophila decipiens* at two (Tables 5 and 6). At 11 of the 15 sites where it occurred, the abundance of *S. filiforme* (as assessed by *D*) declined significantly from 2007 to 2017 (Table 6), and there were no significant trends at the remaining four sites. *Thalassia testudinum* abundance declined significantly at all but one of the sites where it occurred. The one site that had no significant decline (PS07) had very low initial *D* but had an extensive network of still intact and mostly dead *T. testudinum* rhizomes in the sediment. This site was established near (~ 1.8 km west of) one of the CARICOMP Bermuda seagrass monitoring sites that had been a dense *T. testudinum* meadow at the beginning of the CARICOMP program in 1993, but had declined to much less than 1% cover between 1994 and 2000 (Fourqurean et al. 2010). The other two seagrass species (*Halodule* sp. and *Halophila decipiens*) encountered at the monitoring sites were always found with $D \leq 1$, corresponding to less than 5% cover, and as many sites saw minor increases in abundance as experienced declines of these relatively small-bodied, sparser species. The net result of almost universal declines in the two larger, more abundant species and mixed trends in the sparse, smaller species was a severe net decline in total seagrass abundance (*D*) at all sites over the period 2007–2017 (Fig. 3). PS04 experienced the least decline at 24%, while there was 100% loss of seagrasses at three sites (PS03, PS18, and PS20; the last had a very low *D* at the beginning of the monitoring program). Losses were

Table 3 Factor loadings resulting from principal component analysis of water quality data. Factor loadings are the correlation between the standardized variable value and the extracted principal components following Varimax rotation. The seven extracted principal components explained a cumulative 71.8% of the variation in Z scores of the original data. Italic type is used to indicate high correlation ($r > 0.500$) between the standardized variables and the principal components

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
% of variance explained	17.6	12.2	12.0	8.9	7.7	7.0	6.4
Interpretation	N abundance	NH_4^+ abundance	OC abundance	P abundance	Water clarity	PO_4^{3-} abundance	High NO_2^-/low $[O_2]$
Original variable							
TN	*0.972*	−0.026	0.144	0.034	−0.001	−0.013	−0.015
TON	*0.969*	−0.091	0.136	0.029	0.002	−0.015	−0.021
N/P	*0.930*	−0.074	0.099	−0.176	0.013	−0.064	0.014
TOC/TON	*−0.708*	−0.022	0.371	−0.060	−0.026	−0.061	0.070
TIN	−0.054	*0.968*	0.097	0.062	−0.023	0.018	0.058
NH_4^+	−0.130	*0.869*	0.167	−0.049	0.052	0.108	−0.168
DIN/SRP	−0.052	*0.617*	0.014	−0.042	−0.009	−0.605	0.086
TOC	0.031	0.099	*0.938*	−0.079	−0.062	0.049	0.035
DOC	0.102	0.129	*0.913*	−0.075	−0.058	0.060	−0.056
TOC/TP	0.035	−0.017	0.366	*−0.838*	0.076	−0.076	−0.012
TP	−0.005	0.037	0.131	*0.807*	−0.071	0.135	0.103
K_d	0.017	0.066	0.032	0.087	*−0.779*	0.047	0.146
Turbidity	−0.082	−0.051	0.078	0.044	*−0.729*	0.054	0.042
SRP	−0.078	0.056	0.105	0.203	−0.093	*0.837*	−0.029
NO_2^-	0.108	0.130	−0.007	−0.341	−0.082	0.346	*0.568*
Dissolved O_2 (% saturation)	0.108	0.005	0.035	−0.019	−0.488	−0.064	*−0.502*
Chl-*a*	0.004	−0.006	0.391	0.254	−0.131	0.039	0.447
Salinity	0.107	0.122	0.003	−0.083	0.080	0.197	−0.434
NO_3^-	0.127	0.403	−0.104	0.226	−0.142	−0.170	0.421

ubiquitous across the Bermuda Platform, at sites both close to land and ones distant from land-based anthropogenic influence.

Seagrass Indicator Data

There was no significant trend in SCI of the seagrasses of the Bermuda Platform when data from all sites were pooled (linear regression, $F = 0.21$, $p = 0.64$), but this platform-wide analysis obscured site-specific trends (Table 7). At sites PS02, PS07, PS08, and PS09B, SCI increased, indicating that the relative importance of *Thalassia testudinum* to the seagrass community increased. Conversely, the relative importance of *T. testudinum* decreased at PS05, PS13, PS16, PS17, PS18, and PS19, and the remainder of the sites had no significant trends in the SCI.

Table 4 Platform-wide water quality trends, 2006–2017. Note that subsequent analyses reveal that these apparent platform-wide trends were often influenced by significant trends at a subset of sites

Water quality parameter (units)	Trend, ± 1 SE	Interpretation
PC1 (unitless)	$-0.112 \pm 0.023^{***}$	Decreasing total N
PC2 (unitless)	$-0.089 \pm 0.023^{***}$	Decreasing DIN
PC3 (unitless)	$0.229 \pm 0.022^{***}$	Increasing OC
PC4 (unitless)	-0.034 ± 0.023	No trend in TP
PC5 (unitless)	$-0.042 \pm 0.019^{*}$	Decreasing water clarity
PC6 (unitless)	$-0.060 \pm 0.022^{**}$	Decreasing DIP
PC7 (unitless)	$-0.043 \pm 0.021^{*}$	Decreasing NO_2^- and increasing DO
Chl-*a* ($\mu g\ L^{-1}$)	$0.015 \pm 0.004^{***}$	Increasing phytoplankton abundance
TOC (μM)	$2.982 \pm 0.400^{***}$	Increasing TOC

Probability that the reported slope was significantly different from 0: $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$

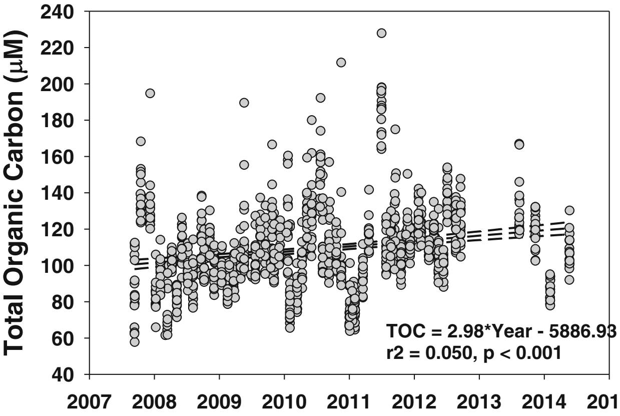


Fig. 2 Time series of TOC collected at all 17 sites during the period 2007–2014. Linear regression plotted, dashed lines indicate 95% confidence interval

When averaged across all sites for the duration of the monitoring program, C/N of seagrass leaves ranged from 15.0 ± 0.5 for *Halophila decipiens* to 20.1 ± 0.2 for *Thalassia testudinum* (Table 8). C/P means ranged among species from 752.7 ± 45.8 for *H. decipiens* to 1001.6 ± 25.6 for *Halodule* sp. N/P ranged from 43.8 ± 0.9 for *T. testudinum* to 49.8 ± 3.5 for *H. decipiens*. The δ^{13}C values encompassed a broad range, from − 21.2‰ for a *Halodule* sp. sample to − 4.0‰ for a *Syringodium filiforme* sample. The range in δ^{15}N observations was broad as well, ranging from − 9.3 to 9.2‰. Similarly, there was a wide range in plant morphology as assessed by leaf width, leaf length, number of leaves per short shoot, and leaf area per shoot.

The time series of all the measured indicators for all seagrass species can be found in Online Resource 3. For each of the indicators of the *Thalassia testudinum* status, the significant linear temporal trends had the same implications for seagrass status (Table 7). At six of the monitoring locations, N content (as indicated by decreases in C/N) increased linearly over the monitoring period, with no significant changes at the remaining eight sites at which this species occurred in 2007. At one site, there was a significant linear increase in C/P, and only at this site was there also a significant long-term linear increase in N/P. δ^{13}C of leaves exhibited a significant linear increase at only one station. In contrast, δ^{15}N significantly decreased at half of the 14 sites at which *T. testudinum* occurred. At nine sites, *T. testudinum* leaves became significantly narrower during the monitoring period, and there were significant decreases in leaf length at six sites. The number of leaves per short shoot also decreased at four sites. At eight sites, total leaf area per short shoot decreased.

Compared to *Thalassia testudinum*, there were fewer significant linear temporal trends in *Syringodium filiforme* indicators over the period 2007–2017 (Table 9). At three of the 15 sites that supported this species, there were significant increases in N content (as indicated by decreases in C/N), but no significant trends

Table 5 Description of seagrass monitoring stations in 2007 at the beginning of the monitoring program. Water depth, diffuse attenuation coefficients, and the fraction of incident irradiance reaching the bottom (%I$_o$) are the means recorded at each site from 2006 to 2016. Dense in this table indicates > 25% cover (density > 3). Sparse indicates < 25% cover ($D < 3$). Seagrass species present listed in order of decreasing abundance within a site

Site	Depth (m)	K_d (m^{-1})	%I$_o$	Site characteristics at beginning of monitoring program
PS01	5.9	0.097	57.5	Dense *T. testudinum* meadow with sparse *S. filiforme* and *Halodule* sp. intermixed. Canopy height = 11.7 cm
PS02	3.9	0.119	63.5	Dense mixed species meadow dominated by *T. testudinum* and *Halodule* sp., with sparse *S. filiforme*. Canopy height = 10.7 cm
PS03	3.3	0.095	73.5	Sparse *S. filiforme* and *Halodule* sp. meadow with occasional *H. decipiens*. Canopy height = 8.8 cm
PS04	2.2	0.219	62.6	Dense *T. testudinum* meadow. Canopy height = 9.6 cm
PS05	1.6	0.210	72.5	Dense *T. testudinum* meadow with sparse *S. filiforme*. Canopy height = 8.0 cm
PS06	12.1	0.080	38.9	Sparse *S. filiforme* and *H. decipiens* meadow with occasional *Halodule* sp. Canopy height = 6.5 cm
PS07	5.0	0.087	65.0	Sparse *S. filiforme* and *T. testudinum* meadow. Canopy height = 3.3 cm
PS08	3.4	0.194	52.2	Dense *T. testudinum* and *S. filiforme* meadow. Canopy height = 15.5 cm
PS09A	5.6	0.165	40.5	Dense *S. filiforme* meadow with sparse *Halodule* sp. Canopy height = 10.5 cm
PS09B	1.5	0.372	58.1	Dense *T. testudinum* and *S. filiforme* meadow. Canopy height = 20.3 cm
PS13	3.6	0.160	56.8	Sparse *T. testudinum* meadow mixed with *Halodule* sp. and *S. filiforme*. Canopy height = 11.3 cm
PS15	1.3	0.276	70.5	Dense *T. testudinum* meadow. Canopy height = 12.7 cm
PS16	2.5	0.191	62.7	Sparse mixed-species meadow of *T. testudinum*, *S. filiforme* and *Halodule* sp. Canopy height = 5.5 cm
PS17	1.2	0.329	68.7	Dense *T. testudinum* and *S. filiforme* meadow mixed with sparse *Halodule* sp. Canopy height = 11.8 cm
PS18	2.0	0.209	66.4	Sparse *T. testudinum* and *S. filiforme* meadow. Canopy height = 7.5 cm
PS19	1.8	0.254	64.0	Dense mixed-species meadow of *T. testudinum*, *S. filiforme*, and *Halodule* sp. Canopy height = 13.7 cm
PS20	9.2	0.076	51.4	Sparse mixed-species meadow of *T. testudinum, S. filiforme*, and *Halodule* sp. Canopy height = 5.4 cm

Table 6 Initial Braun-Blanquet density (*D*) (average scores for the first year of the monitoring in 2007) for each seagrass species at each site. Trends in *D* are the slopes calculated using linear regression. If a species was not found at a site (i.e., $D = 0$), no slope is reported

Site	*Thalassia testudinum*		*Syringodium filiforme*		*Halodule* sp.		*Halophila decipiens*	
	Initial *D*	Trend D $year^{-1}$	Initial *D*	Trend D $year^{-1}$	Initial *D*	Trend D $year^{-1}$	Initial *D*	Trend D $year^{-1}$
PS01	2.71 ± 0.15	-0.226^{***}	0.18 ± 0.03	-0.032^{**}	0.02 ± 0.02	− 0.002	0	
PS02	1.96 ± 0.17	-0.221^{***}	0.62 ± 0.08	-0.112^{***}	1.07 ± 0.11	-0.150^{***}	0	
PS03	0		0.04 ± 0.01	-0.013^{*}	0.29 ± 0.10	-0.120^{***}	0.004 ± 0.003	− 0.002
PS04	2.96 ± 0.09	-0.064^{*}	0		0		0	
PS05	2.55 ± 0.20	-0.343^{***}	0.25 ± 0.04	0.057^{***}	0		0	
PS06	0		0.14 ± 0.02	-0.015^{*}	0.01 ± 0.01	-0.004^{*}	0.128 ± 0.052	-0.039^{*}
PS07	0.01 ± 0.01	− 0.001	0.02 ± 0.01	− 0.003	0		0	
PS08	1.39 ± 0.12	-0.183^{***}	0.94 ± 0.13	-0.204^{***}	0		0	
PS09A	0		1.99 ± 0.13	-0.209^{***}	0.54 ± 0.07	0.055^{*}	0	
PS09B	3.97 ± 0.12	-0.142^{***}	1.07 ± 0.08	-0.094^{***}	0		0	
PS13	1.89 ± 0.10	-0.143^{***}	0.19 ± 0.03	0.003	0.33 ± 0.04	− 0.008	0	
PS15	3.48 ± 0.13	-0.186^{***}	0		0		0	
PS16	2.07 ± 0.14	-0.221^{***}	1.10 ± 0.08	− 0.050	0.96 ± 0.11	0.107^{**}	0	
PS17	1.89 ± 0.16	-0.256^{***}	1.37 ± 0.09	-0.110^{***}	0.96 ± 0.09	0.106^{***}	0	
PS18	0.55 ± 0.08	-0.100^{***}	0.44 ± 0.06	− 0.002	0		0	
PS19	2.48 ± 0.13	-0.202^{***}	1.95 ± 0.08	-0.070^{**}	0.61 ± 0.07	− 0.036	0	
PS20	0.01 ± 0.00	-0.003^{*}	0.01 ± 0.01	-0.006^{*}	0		0	

Probability that the reported slope was significantly different from 0: $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$

in C/P or N/P were observed. At only one site, $\delta^{13}C$ increased significantly, while at seven sites $\delta^{15}N$ decreased. At seven sites, leaf length decreased, and there were no significant trends in the number of leaves per shoot.

For *Halodule* sp., which occurred at 10 sites, N content increased at three sites, while P content increased at one site (Table 10). There were no linear trends in N/P. At one site, there was a significant linear increase in $\delta^{13}C$, and $\delta^{15}N$

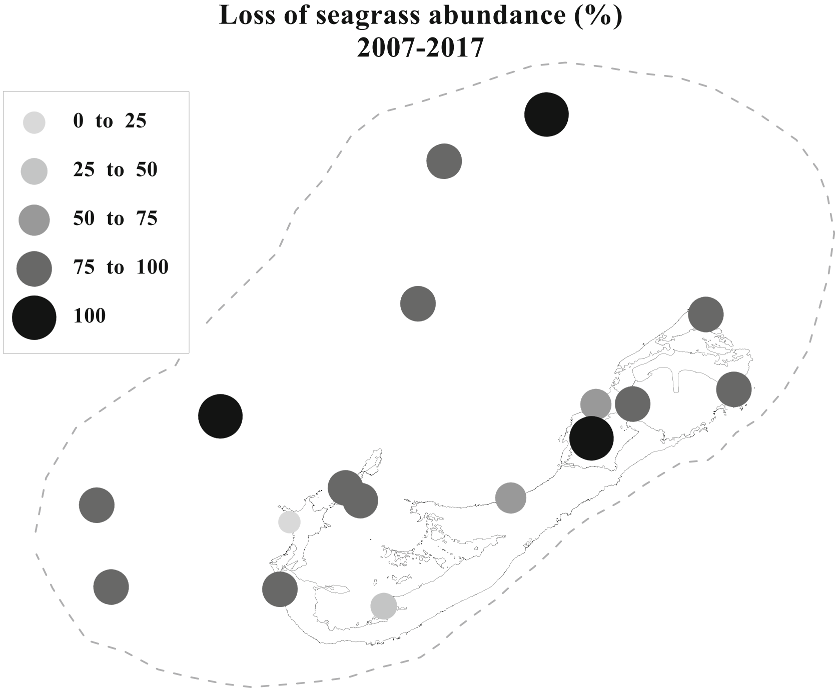


Fig. 3 Net change in total seagrass abundance (Δ as $-100\% * (D_{2017} - D_{2007})/D_{2017})$) over the period 2007–2017 across the Bermuda Platform. Symbols are scaled to the observed net decline in seagrass abundance. Dashed line indicates the 10 m isobath that defines the top of the Bermuda Platform

Table 7 Linear trends in *Thalassia testudinum* indicators by site. Trends are the slopes calculated using linear regression. If *Thalassia testudinum* was not found at a site, no slope is reported

Site	SCI (year^{-1})	C/N (year^{-1})	C/P (year^{-1})	N/P (year^{-1})	δ^{13}C (‰ year^{-1})	δ^{15}N (‰ year^{-1})	Leaf width (mm year^{-1})	Leaf length (mm year^{-1})	Leaves per short shoot (year^{-1})	Leaf area per short shoot (mm^2 year^{-1})
PS01	0.007	−0.258	2.080	0.218	0.089	−0.065	−0.269***	−3.151	−0.132*	−187.2**
PS02	0.017*	−0.591*	−30.586	−0.131	0.055	−0.303**	−0.301***	−3.396	−0.075*	−123.7*
PS03										
PS04		−0.375***	−28.914	−0.290	0.005	−0.164*	−0.296***	−3.396*	−0.085	−130.1***
PS05	−0.400***	−0.692***	−40.543	−0.284	0.014	−0.959***	−0.257***	−2.899**	−0.042	−64.9***
PS06										
PS07	0.004	−0.299	41.886**	3.551**	0.004	0.008	0.020	6.080***	0.024	32.7
PS08	0.035***	−0.012	−9.941	−0.338	0.013	−0.290**	−0.227***	−5.432***	−0.078	−125.4***
PS09A										
PS09B	0.008*	0.013	−5.994	−0.365	0.132***	0.021	−0.108	−2.438	0.049	−46.7
PS13	−0.014*	−0.167	−5.763	0.164	0.043	0.066	−0.167*	−2.331	0.062	−54.9
PS15	0.000	0.032	2.809	0.074	−0.015	−0.045	0.026	−0.496	0.059	38.9
PS16	−0.023*	−0.368*	−16.834	−0.141	0.029	−0.254***	−0.225***	0.388	−0.041	−34.7*
PS17	−0.042***	−0.838***	−21.723	−0.295	−0.020	−0.138*	−0.368***	−4.473***	−0.078*	−132.0***
PS18	−0.052**	−0.059	19.011	1.129	0.168	0.026	0.001	0.813	0.016	30.4
PS19	−0.011*	−0.318***	18.851	1.804	0.036	−0.079	−0.144***	−2.761**	0.016	−43.9**
PS20	0.169	−0.929	62.728	−3.808	10.313	−1.207*	−0.191	−4.747	−2.80**	−138.9

Probability that the reported slope was significantly different from 0: $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$

significantly decreased at three. At three sites, leaves became shorter, and at two sites the number of leaves per short shoot decreased.

Discussion

Seagrass abundance declined drastically at 16 of the 17 monitoring locations spread across the Bermuda Platform during the period 2007–2017. Three of the four seagrass species found in Bermuda, *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule* sp., decreased in abundance at most of the sites at which each species was found. The only site where there was not a significant decline was site PS07 which had already lost most of its seagrass during the period 1994–2000 (Fourqurean et al. 2010), and there has been no recovery at this site. Declines occurred to a greater degree at sites distant from land compared to nearshore sites, although extensive declines also occurred at nearshore sites, and the location and magnitude of the declines did not correspond to any discernible changes in water quality or the amount of light reaching the bottom. In situ observations by divers made during the transect monitoring indicated that seagrasses were disappearing despite very clear water (Fig. 4). Light reaching the bottom exceeded the reported light requirements of all of the seagrass species (see Manuel et al. 2013).

In general, seagrass leaves became narrower and shorter over the monitoring period, resulting in smaller individual shoots, while changes in elemental stoichiometry and stable isotopes of C and N of the seagrass leaves showed no indication of decreased light availability or relaxation of the general P limitation of seagrass biomass typical of the Bermuda Platform. We interpret these results to support our hypothesis that seagrass losses cannot be attributed to degradation of water quality across the Bermuda Platform.

Water Quality Trends in Relation to Seagrass Trajectories

Our assessment of the water quality in Bermuda is in line with earlier observations (Fourqurean et al. 2015; Manuel et al. 2013) that water column nutrient concentrations were low and water clarity high. There were two sites with significant, but small in magnitude, long-term increases in water column Chl-*a* over the course of our study; both of these (PS05 and PS17) are very close to shore in shallow water (< 2 m deep). Interestingly, neither of these sites displayed significant trends in water clarity or the abundance of P, which has been identified as the element limiting phytoplankton biomass in Bermuda's clear waters (Ammerman et al. 2003; Fourqurean et al. 2015; Lomas et al. 2004; Salihiglu et al. 2008). At both of these sites, the amount of light reaching the bottom was far above the locally derived ecological compensation depths for

Table 8 Mean values of indicators of seagrass status for all sites for the period 2007–2017. n.d. = no data. SE = standard error of the mean

Indicator		*Thalassia testudinum*	*Syringodium filiforme*	*Halodule sp.*	*Halophila decipiens*
C/N	*n*	364	362	220	34
	Mean ± SE	21.0 ± 0.2	18.1 ± 0.2	20.9 ± 0.2	15.0 ± 0.5
	Min–max	12.0–31.0	11.1–29.4	12.7–32.2	6.5–21.1
C/P	*n*	345	362	222	34
	Mean ± SE	918.2 ± 19.8	810.8 ± 18.8	1001.6 ± 25.6	725.7 ± 45.8
	Min–max	306.6–2840.3	292.9–2723.3	389.1–2684.6	368.6–1546.6
N/P	*n*	345	362	221	34
	Mean ± SE	43.8 ± 0.9	45.2 ± 1.1	48.3 ± 1.2	49.8 ± 3.5
	Min–max	15.7–150.1	21.7–186.1	20.5–155.8	27.9–121.1
δ^{13}C (‰)	*n*	351	353	221	31
	Mean ± SE	−7.5 ± 0.1	−6.3 ± 0.01	−9.8 ± 0.1	−8.4 ± 0.2
	Min–max	−10.9–(−4.2)	−17.8–(−4.0)	−21.2–(−4.8)	−11.7–(−6.1)
δ^{15}N (‰)	*n*	352	369	221	31
	Mean ± SE	2.7 ± 0.2	1.5 ± 0.2	1.3 ± 0.2	0.3 ± 0.3
	Min–max	−9.2–9.2	−9.2–9.1	−9.3–6.9	−5.0–4.8
Leaf width (mm)	*n*	394	n.d.	n.d.	n.d.
	Mean ± SE	5.7 ± 0.3	n.d.	n.d.	n.d.
	Min–max	2.2–10.0	n.d.	n.d.	n.d.
Mean leaf length (mm)	*n*	394	405	244	n.d.
	Mean ± SE	64.6 ± 1.4	67.0 ± 1.2	43.8 ± 0.8	n.d.
	Min–max	3.91–189.1	23.5–213.8	19.6–90.1	n.d.
Leaves per short shoot	*n*	394	405	244	n.d.
	Mean ± SE	2.7 ± 0.1	1.3 ± 0.0	2.5 ± 0.0	n.d.
	Min–max	1.2–6.8	1.0–2.1	1.4–6.0	n.d.
Leaf area per short shoot (mm^2)	*n*	394	n.d.	n.d.	n.d.
	Mean ± SE	1111.7 ± 43.9	n.d.	n.d.	n.d.
	Min–max	86.0–5843.5	n.d.	n.d.	n.d.

all seagrass species growing in Bermuda (1.6% I_0 for *Halophila decipiens*, 17.7% I_0 for *Halodule* sp. and *Syringodium filiforme*, and 34.1% I_0 for *Thalassia testudinum*) (Manuel et al. 2013). Furthermore, epiphyte abundance was also quite low compared to many locations where these species are found (authors' personal observations), suggesting that the factors influencing the increase in phytoplankton abundance at these sites have yet to lead to adverse conditions for the seagrasses. However, the seagrass abundance of the originally dense *Thalassia*-dominated seagrass bed at PS05, where Chl-*a* increased, decreased by 84% and the abundance of the dense meadow that started as a mix of *T. testudinum*, *S. filiforme*, and *Halodule* sp. at PS17 decreased by 75% where Chl-*a* also increased.

In contrast to the increases in phytoplankton abundance at PS05 and PS17, water quality improved at PS01 and PS02, yet these two sites that started as dense, mixed-species seagrass beds in 2007 saw declines in seagrass abundance of 79% and 97%, respectively. At PS01, P abundance decreased during the monitoring period and water clarity increased at both PS01 and PS02. While these two sites were deeper (at 5.9 m and 3.9 m deep, respectively) than the inshore sites at which phytoplankton abundance had increased, both had light availability reaching the bottom at > 63% of I_0, well above the ecological compensation depth for all the Bermudian seagrasses.

At the remaining 12 monitoring stations that experienced seagrass declines, there were no significant long-term trends in any of the water quality parameters except for organic carbon in the water column, which trended up significantly across the Platform at about 3% per year. Given that this increase was not accompanied by increases in N, P, Chl-*a*, and turbidity, it is unlikely to have been driven by general eutrophication of the water around Bermuda and it is also unlikely that the increase in TOC is driving declines in seagrasses across the Platform. Whether TOC is increasing in response to changes in the local Bermuda environment, part of some larger oceanic phenomenon, or a result of a methodological artifact all merit further investigation.

Wastewater Impacts on Water Quality

Stable isotope, tracer, and stoichiometric evidence suggests that wastewater from human sources has had impacts on the

Table 9 Linear trends in *Syringodium filiforme* indicators by site. Trends are the slopes calculated using linear regression. If *Syringodium filiforme* was not found at a site, no slope is reported

Site	C/N (year^{-1})	C/P (year^{-1})	N/P (year^{-1})	δ^{13}C (‰ year^{-1})	δ^{15}N (‰ year^{-1})	Leaf length (mm year^{-1})	Leaves per short shoot (year^{-1})
PS01	−0.135	9.973	0.178	−0.010	−0.021	−3.937**	−0.005
PS02	−0.621**	−15.956	0.569	0.111	−0.710***	−2.571*	0.007
PS03	−0.026	9.935	0.787	−0.194	0.154	0.039	0.027
PS04							
PS05	−1.212***	−71.75	−0.892	−0.020	−0.959***	−5.297***	0.006
PS06	0.072	15.074	0.808	0.096	−0.025	1.259	−0.014
PS07	−0.120	0.673	−0.271	0.065	0.239	−0.491	0.024
PS08	−0.314	6.955	1.068	−0.018	−0.252***	−4.339***	−0.015
PS09A	−0.229*	−0.280	0.518	0.084	−0.468***	−1.593	0.001
PS09B	0.062	5.564	0.081	0.163*	0.010	−1.629	0.004
PS13	−0.013	12.959	0.752	0.076	−0.093	−0.991	0.005
PS15							
PS16	−0.212	−18.707	−0.425	0.140	−0.263*	−2.292**	0.007
PS17	−0.325	−32.737	−1.648	−0.058	0.012	−3.973***	−0.003
PS18	−0.011	6.692	0.490	0.210	−0.093	−0.892	−0.022
PS19	−0.184	−11.697	−0.391	−0.080	−0.105	−2.304*	0.002
PS20	−0.231	−22.987	−0.566	0.016	0.106	−4.215	−0.014

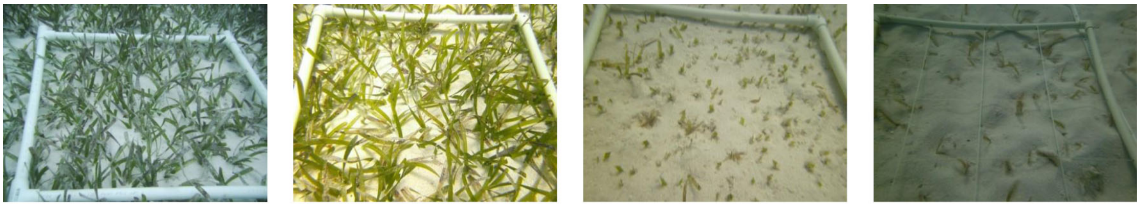
Probability that the reported slope was significantly different from 0: $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$

shallow marine environments along Bermuda's coastline (Jones et al. 2011; Lapointe and O'Connell 1989; McGlathery et al. 1992). Marine plants and animal collected from nearshore in Bermuda are enriched with ^{15}N compared to those from farther offshore, which has been interpreted to indicate that wastewater-derived nutrients are detectable in Bermuda's coastal zone (Baker et al. 2017; Fourqurean et al. 2015). Further, δ^{15}N from museum specimens of soft corals show an increase in δ^{15}N over the period 1956 to 1978, suggesting worsening sewage pollution over that interval (Baker et al. 2017). In contrast, we observed no statistically significant increases in the δ^{15}N of seagrasses during our study.

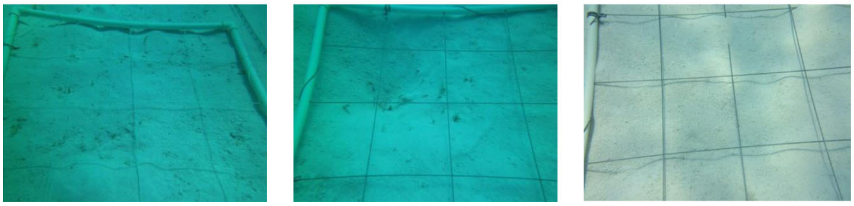
Table 10 Linear trends in *Halodule sp.* indicators by site. Trends are the slopes calculated using linear regression. If *Halodule* sp. was not found at a site, no slope is reported

Site	C/N (year^{-1})	C/P (year^{-1})	N/P (year^{-1})	δ^{13}C (‰ year^{-1})	δ^{15}N (‰ year^{-1})	Leaf length (mm year^{-1})	Leaves per short shoot (year^{-1})
PS01	−0.655*	−11.802	0.655	0.044	−0.635***	−1.224	−0.093***
PS02	−0.381	−7.168	0.356	0.034	−0.564***	0.211	−0.047
PS03	−1.747	−54.453	1.508	0.012	−1.634	−0.790	−0.083
PS04							
PS05							
PS06	0.396	116.433	3.452	0.319	0.818	−0.404	0.082
PS07							
PS08							
PS09A	−0.306	19.971	1.595	0.122*	−0.370***	−1.653*	−0.045*
PS09B							
PS13	0.236	37.522	1.112	0.054	0.149	1.101	−0.005
PS15							
PS16	−0.368*	−40.384*	−0.930	0.027	0.008	0.151	0.027
PS17	−0.512*	−5.083	−0.134	0.074	0.023	−1.269*	−0.004
PS18							
PS19	−0.259	−33.133	−1.376	−0.118	−0.132	−1.537*	−0.009
PS20	−0.835	−45.471	−0.612	−0.416	−1.391	−2.710	−0.013

Probability that the reported slope was significantly different from 0: $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$



June 2007 June 2011 September 2013 December 2014



September 2015 October 2016 August 2017

Fig. 4 Time series of typical quadrat photographs at PS01. Note *Thalassia testudinum* shoots cropped 0.5 cm above the sediment surface in September 2013 and December 2014. Quadrat size = 50 cm × 50 cm. Mean site depth is 5.9 m

Rather, we found significant decreases in δ^{15}N in three seagrass species from nine of 17 sites, with no significant trends at the remaining eight sites; hence, we found no evidence for increasing sewage pollution during our monitoring period.

Seagrass Indicators of Eutrophication

When growing in an environment with ample nutrients to meet demands for growth, seagrass leaves have N/P of 25–30 (Atkinson and Smith 1983; Duarte 1990); N/P > 30 indicates a deficit in P availability with respect to N. Our sampling, as well as previous work on marine primary producers on the Bermuda Platform (Fourqurean et al. 2015; Lapointe and O'Connell 1989; McGlathery et al. 1992), indicates general P limitation of seagrass biomass. Seagrasses in Bermuda had on average, by species, N/P values ranging from 43.8 to 49.8. The N content of seagrasses did increase (as indicated by significant linear decreases in C/N) where each species occurred: in *Thalassia testudinum* at six of the 14 sites, in *Syringodium filiforme* at three of the 15 sites, and in *Halodule* sp. at three of the 10 sites. There were no significant decreases in N content for any species at any site. P content decreased in *T. testudinum* at one site and increased in *Halodule* sp. at another site. While there were changes in N and P content in some species at some sites, there was only a trend in N/P at PS07, where a remaining rhizome mat and studies at similar nearby CARICOMP sites indicated that seagrasses had declined drastically prior to our monitoring program. At no sites did N/P decline, as would be expected if the relative availability of the limiting nutrient P had increased over the period of monitoring.

There were no significant trends of decreasing δ^{13}C of any species of seagrass from any of the 17 monitoring sites. In fact, there were a few long-term increases in δ^{13}C. Seagrass species differ in the δ^{13}C of their leaf tissues owing to differences in carbon uptake physiology and leaf morphology (Campbell and Fourqurean 2009), but within a species, δ^{13}C is a function of light availability. Seasonality in light availability leads to relatively lower δ^{13}C in winter compared to summer, even in subtropical locations (Campbell and Fourqurean 2009; Fourqurean et al. 2005). Further, experimental shading studies and sampling along depth gradients show that seagrass δ^{13}C becomes lower when light reaching the leaves is reduced (e.g., Abal et al. 1994; Campbell and Fourqurean 2009; Cooper and DeNiro 1989; Fourqurean et al. 2007; Grice et al. 1996). Indeed, it has been proposed that δ^{13}C of seagrasses can be used as an integrating indicator of light availability (Hu et al. 2012). At site PS09B, the δ^{13}C of both *Thalassia testudinum* and *Syringodium filiforme* increased during the monitoring period, and at PS09A the δ^{13}C of *Halodule* sp. also increased suggesting that light availability reaching through the canopy to the plants actually increased at these two sites.

Changes in Species Composition of Seagrass Beds

A decrease in the relative importance of slower growing species and an increase in the importance of faster-growing taxa is often a consequence of eutrophication, and a decrease in the relative importance of *Thalassia testudinum* in seagrass meadows of the Western Atlantic is an indicator of increased nutrient availability (Fourqurean and Rutten 2003). On a platform-wide scale, our SCI showed no long-term trend, but there were some sites at which the relative importance of *T. testudinum* increased, and some where it decreased. The rates of decline in seagrasses among sites were not correlated with our trends in SCI. In addition to nutrient availability, selective grazing by herbivores has the potential to change the SCI, since herbivores often prefer to graze on the faster-growing taxa with generally higher nutrient content (Armitage and Fourqurean 2006; Burkholder et al. 2012; Kelkar et al. 2013; Mariani and Alcoverro 1999). In this study, SCI did not provide compelling indication of the potential pressures leading to seagrass decline.

Herbivory Is Driving Seagrass Losses

Our water quality and indicator data clearly show that eutrophication, the driver of most historic losses of seagrass globally (Short and Wyllie-Echeverria 1996; Waycott et al. 2009), was not associated with the Platform-scale decline in the seagrass ecosystems of Bermuda. Seagrasses in Bermuda are also largely protected from direct dredging, and there is no intense fishing activity that disturbs the benthos and would lead to seagrass loss. Yet, our data suggest that the sustainability of seagrasses in Bermuda is in serious jeopardy. The trends in the seagrass indicators, especially the trend in declining abundance, decreasing leaf widths and shoot area, and increasing N content that occurred in parallel with seagrass loss are consistent with overgrazing of seagrasses by green sea turtles. Experimental work shows that sea turtle grazing leads to increased N content of *Thalassia testudinum* leaves because of the loss of older, nutrient-depleted leaves (Bjorndal 1997; Fourqurean et al. 2010; Moran and Bjorndal 2007) as well as to reductions in leaf width and leaf area of intensely grazed seagrasses (Fourqurean et al. 2010).

Consequences of Seagrass Declines

Bermuda is an important developmental habitat for green turtles originating from many nesting populations throughout the western Atlantic (Meylan et al. 2011). Juvenile turtles that arrive on the Bermuda Platform have an omnivorous diet based on macroalgae and animals, and after 7–9 years 70% of their diets is seagrass (Burgett et al. 2018). Turtles spend another 11 to 13 years (about 20 years total) resident in Bermuda, grazing on seagrass and growing to subadult size of 65–75 cm SCL, then depart to join breeding populations across the tropical western Atlantic (Meylan et al. 2011).

There is scant evidence that the larger turtles in Bermuda are shifting their diet away from seagrasses (Burgett et al. 2018), even though green turtles in other locations have more diverse, seagrass-independent diets when seagrasses are scarce (e.g., Cardona et al. 2009; Hatase et al. 2006; Howell et al. 2016; Santos et al. 2015; Shimada et al. 2014) or predation risk in seagrass meadows is high (Burkholder et al. 2011). If the trends in seagrass abundance we documented here continue, the turtles' primary food source will become limiting. If turtle grazing is the primary cause of seagrass loss, which seems likely, the losses could decrease if the turtles switched to reliance on macroalgal or animal foods.

While still rare, reports of major structural changes in marine ecosystems due to seagrass overgrazing by green turtles are increasing. Overgrazing has been reported in the US Virgin Islands (Williams 1988), Bermuda (Fourqurean et al. 2010), India (Lal et al. 2010), Indonesia (Christianen et al. 2014), and Mexico (Hernandez and van Tussenbroek 2014; Lacey et al. 2014). It has been hypothesized that overgrazing could be a consequence of the conservation measures aimed at protecting herbivores in ecosystems that have no effective top-down control (Heithaus et al. 2014). Because of overfishing, top predators (i.e., sharks) are no longer a natural control of these herbivore populations. Similarly, protection of other herbivores in Bermuda has been linked to other unintended consequences in the marine environment. Protection of herbivorous parrotfish and the reintroduction and protection of a large, intertidal, herbivorous snail in the latter half of the twentieth century may have resulted in the extirpation of several large and formerly abundant seaweed species from Bermuda (Schneider and Flook 2017).

The loss of seagrasses is likely to have serious implications for the nearshore marine environment on the Bermuda Platform. In addition to being responsive to water quality, seagrasses themselves can regulate water quality and stabilize sediments (e.g., Austin et al. 2017; Lamb et al. 2017; Moore 2004). Sediment resuspension could also become an issue, as it is quite likely that loss of seagrass cover will lead to an overall decrease in water clarity in Bermuda as both water column nutrients and suspended particles increase. A loss of fisheries' income and declines in biodiversity may also result as a number of commercially and culturally important marine species of Bermuda, including black grouper (*Mycteroperca bonaci*, Poey 1860) and the Queen Conch (*Lobatus gigas*, Linnaeus 1758), rely on seagrass meadows as critical habitat during some phase of their lives.

Conclusions

Perhaps Bermuda is not a sustainable developmental habitat for green turtles in the Anthropocene without some form of directed human intervention informed by research designed to better understand the sea turtle–carrying capacity of the Bermuda Platform. Given little evidence of the large turtles responding to a decrease in their primary food, human action seems necessary to reverse the losses of seagrass habitat in Bermuda and to protect the populations of turtles that use Bermuda as a developmental habitat. This study suggests that addressing nutrient pollution, an important activity for many reasons, will not reverse the seagrass decline. The P-limited nature of Bermuda's seagrasses may actually lead to a lack of resilience to repeated grazing (Holzer and McGlathery 2016), so it is possible that incidental or intentional P fertilization to the nearshore marine environment could help those meadows withstand grazing. As a nod to this possibility, seagrass meadows far from coastal nutrient sources declined sooner and faster than those close to shore. It is also possible that the earlier and more rapid offshore declines could be a result of more intense grazing in areas where turtles were not disturbed by human activities. Nearshore losses may have accelerated recently if turtles have begun grazing inshore as the offshore beds disappear, but we have no data confirming changes in grazing sites.

Clearly, green turtle populations in Bermuda have expanded beyond the current carrying capacity and reducing grazing on seagrasses could slow losses. Experimental exclusion of sea turtles in both the US Virgin Islands (Williams 1988) and Bermuda (Fourqurean et al. 2010) reversed the negative impacts of grazing. Reducing grazing could also encourage propagule recruitment of the early-successional seagrasses that initiate the process of seagrass meadow recovery. During our monitoring, seedlings of *Syringodium filiforme* were regularly found along the transect lines, but no plants became established (surviving from one year to the next), except under experimental turtle exclusion cages (SAM, personal observations, unpublished data). Thus, solutions to overgrazing might include temporarily excluding turtles from declining meadows, in the same way that ranchers control access to pastures by their herds and flocks in the terrestrial environment to allow those meadows to recover (Teague et al. 2013). If overpopulation of turtles in response to lack of predators is the ultimate driver of seagrass losses, reestablishing turtle predators (like tiger sharks, *Galeocerdo cuvier*) could prove effective (Heithaus et al. 2014). Another possibility for reducing the population of Bermuda turtles might be relocation, although this would not reduce the rate of recruitment of small turtles. Culling of the green sea turtle population through a responsible and well-regulated fishery could also be employed to control sea turtle populations and their impact on seagrass meadows. The management targets for such a fishery would need to be informed by research designed to determine the current sea turtle–carrying capacity of the Bermuda Platform.

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