



# Tropical species at the northern limit of their range: Composition and distribution in Bermuda's benthic habitats in relation to depth and light availability



Sarah A. Manuel<sup>a</sup>, Kathryn A. Coates<sup>a</sup>, W. Judson Kenworthy<sup>b,1</sup>, James W. Fourqurean<sup>c,\*</sup>

<sup>a</sup> Department of Conservation Services, P.O. Box FL 588, Smiths Parish, FL BX, Bermuda

<sup>b</sup> Center for Coastal Fisheries and Habitat Research, NCCOS, NOS, NOAA, 101 Pivers Island Rd, Beaufort, NC 28516 USA

<sup>c</sup> Marine Science Program, Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, North Miami, FL 33199, USA

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## ABSTRACT

Surveys were undertaken on the shallow Bermuda marine platform between 2006 and 2008 to provide a baseline of the distribution, condition and environmental characteristics of benthic communities. Bermuda is located in temperate latitudes but coral reefs, tropical seagrasses and calcareous green algae are common in the shallow waters of the platform. The dominant organisms of these communities are all living at or near their northern latitudinal range limits in the Atlantic Ocean. Among the major benthic autotrophs surveyed, seagrasses were most restricted by light availability. We found that the relatively slow-growing and long-lived seagrass *Thalassia testudinum* is restricted to habitats with much higher light availability than in the tropical locations where this species is commonly found. In contrast, the faster growing tropical seagrasses in Bermuda, *Syringodium filiforme*, *Halodule* sp. and *Halophila decipiens*, had similar ecological compensation depths (ECD) as in tropical locations. Increasing sea surface temperatures, concomitant with global climate change, may either drive or allow the poleward extensions of the ranges of such tropical species. However, due to latitudinal light limitations at least one abundant and common tropical autotroph, *T. testudinum*, is able to occupy only shallower depths at the more temperate latitudes of Bermuda. We hypothesize that the poleward shift of seagrass species ranges would be accompanied by restrictions to even shallower depths of *T. testudinum* and by very different seagrass community structures than in tropical locations.

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## 1. Introduction

Bermuda provides an opportunity to explore the ecology of tropical marine communities at the poleward extent of their current geographic ranges. It is a shallow oceanic platform with a subtropical climate, located in the northern West Atlantic (32.4°N, 64.8°W) that supports extensive reefs of hermatypic corals, meadows of tropical seagrasses, beds of tropical and subtropical calcareous green algae, and small mangrove forests. Major primary producers of the benthic communities of Bermuda are the seagrasses *Thalassia testudinum* Banks ex König, *Syringodium filiforme* Kützting, *Halodule* sp., and *Halophila decipiens* Ostenfeld (Manuel, 1986), diverse species of macroalgae and microalgae (Cavaliere and Sterrer, 1998), and zooxanthellate hard and soft corals (Cairns et al., 1986). Bermuda is

the northern limit of the distributions of the seagrasses *T. testudinum*, *S. filiforme* and *H. decipiens*, whereas *Halodule wrightii* is found on the North American continent as far north as North Carolina (35° N) (Green and Short, 2003). The species of *Halodule* occurring in Bermuda is problematic: it may be *H. wrightii*, or it may be another *Halodule* species (den Hartog and Kuo, 2006; Waycott et al., 2006; KAC, unpublished data). Bermuda also represents the current northern range limits of the corals and tropical macroalgae occurring in Bermuda (Sterrer, 1986).

Fluctuations in global climate have been implicated in observed changes in the geographic distributions of plants and animals in coastal oceans (Occhipinti-Ambrogi, 2007; Ling et al., 2009; Dillon et al., 2010) and are predicted to drive further changes to primary producer communities including seagrasses (Short and Neckles, 1999). Climate related changes in the distribution of a species may be directly caused by changes in temperature maxima and minima, seasonality, dissolved gas concentrations in seawater (CO<sub>2</sub> is the primary example) and pH ranges. Frequent correlations of distributional changes to sea surface temperature changes (Harley et al., 2006) have led to suggestions that a poleward extension in

\* Corresponding author. Tel.: +1 305 348 4084; fax: +1 305 348 4096.

E-mail addresses: [smanuel@gov.bm](mailto:smanuel@gov.bm) (S.A. Manuel), [kacoates@gov.bm](mailto:kacoates@gov.bm) (K.A. Coates), [jud.kenworthy@gmail.com](mailto:jud.kenworthy@gmail.com) (W.J. Kenworthy), [jim.fourqurean@fiu.edu](mailto:jim.fourqurean@fiu.edu) (J.W. Fourqurean).

<sup>1</sup> Current address: 109 Holly Lane, Beaufort, NC 28516, USA.

the ranges of many species may be expected (for example Hiscock et al., 2005). Other factors such as light and nutrient availability are also important determinants of the suitability of habitat for marine autotrophs and may ultimately control both local and global distributions. Recognizing the primary determinants of local distribution patterns of species at the poleward limits of their ranges may aid in predicting changes in the geographic range of a species as sea surface temperatures rise. As temperate waters warm, will tropical species expand poleward and occupy the same environments as they occupy in lower latitudes? Or will other factors, such as decreased light availability, control depth and habitat ranges of tropical species in more temperate latitudes?

A benthic mapping, monitoring and assessment programme was implemented on the Bermuda platform in 2006 after a major loss of seagrass habitat in the 1990s was recognized (Murdoch et al., 2007). The cause of this loss remains poorly understood due to a general lack of baseline information about distribution and condition of benthic communities and about their physical and chemical environment. Primary goals of the ongoing monitoring programme are to acquire a data set that allows: recognition of changes, identification of possible causes of recent changes, and determination of limiting factors on the platform. In this paper, we use data collected from 2006 through 2008 to describe the distribution of macrobenthic primary producers across the Bermuda platform, in relation to depth and light availability. Understanding distributional limits and the environmental factors affecting the limits allows the recognition of imminent threats to benthic habitats in Bermuda. We then use these relationships to determine local depth distributions and compare these local distributions to those found in more tropical latitudes to help predict how tropical species will be distributed if poleward expansions of their ranges occur.

## 2. Materials and methods

### 2.1. Study site description

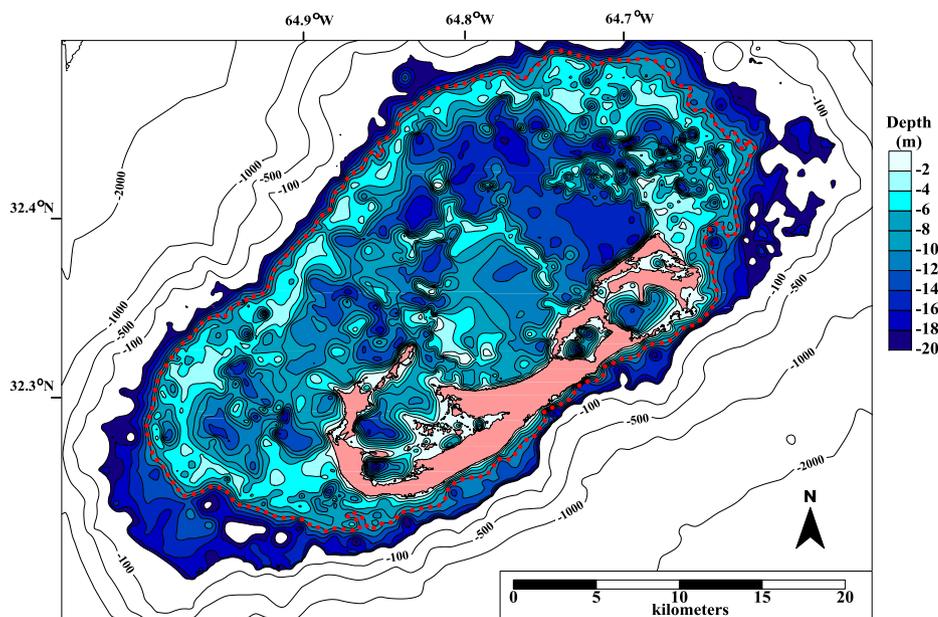
The total area of the Bermuda platform to the 10 m depth contour line outside the rim reefs is 555 km<sup>2</sup>, including approximately

53 km<sup>2</sup> of islands near the southern edge (Fig. 1). There are water depths >10 m inside the rim, especially in the Great Sound, Harrington Sound and the North Lagoon. The submarine environment consists of outer, descending, terrace and shallow rim reefs and semi-enclosed lagoons with patches of reef intermixed with unconsolidated carbonate sediments (Logan and Murdoch, 2011).

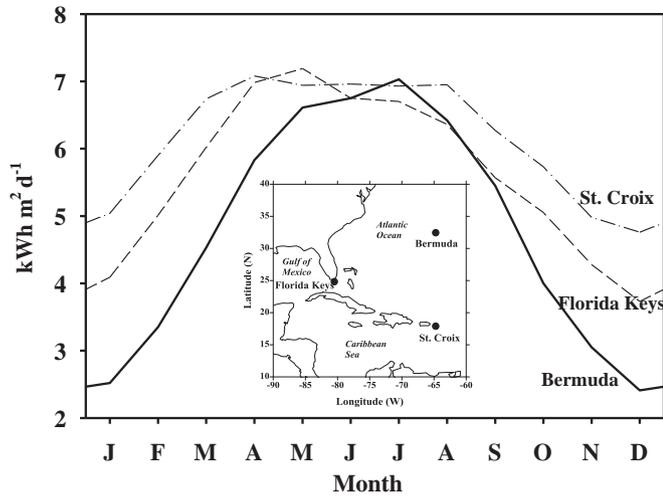
Due to the influence of major oceanographic and climatic features, Bermuda has a subtropical climate despite its temperate latitude. The mean annual water temperature on the platform is near 23 °C; monthly means range from a low of 17.3 °C in February to a high near 28.0 °C in August (Morris et al., 1977; Smith, 1998; Marine Environmental Program, 2006, 2007). Annual ranges at individual sites can be as great as 19 °C (SAM, KAC, unpub. obs.) with extreme temperatures of about 13.5 °C (February 2009) and 32.6 °C (August 2009). Surface salinities on the platform have been reported to range annually from about 36.1–36.9 (Practical Salinity Scale) but precipitation on the shallow platform can strongly influence salinity at specific locations, with an extreme measured minimum of 33.9 at the outflow of the only existing wetland with a surface outlet to the sea (Marine Environmental Program, 2007).

Incident solar radiation (measured as global horizontal radiation, which takes into account cloud cover) in Bermuda shows a large annual range, in a pattern typical of temperate rather than subtropical latitudes. It ranged from a monthly mean of about 2.53 kW h m<sup>-2</sup> day<sup>-1</sup> in December to 7.03 kW h m<sup>-2</sup> day<sup>-1</sup> in July for the years 1983–2005 (Darnell et al., 1996; N.A.S.A., 2010) (Fig. 2). Mean yearly integrated solar irradiance during the same period was 1767 kW h m<sup>-2</sup> in Bermuda, much less than the amount received at more southerly latitudes supporting tropical seagrass and coral reef communities. In the Florida Keys (ca. 24.4°N), for example, mean annual integrated solar irradiance was 2062 kW h m<sup>-2</sup>, and St. Croix in the U.S. Virgin Islands (ca. 17.5°N) received 2261 kW h m<sup>-2</sup>. There is little difference in the peak summer irradiances at these three locations, and the annual difference is driven by decreased winter irradiance at the more northern latitudes (Fig. 2).

Bermuda has generally high water column clarity, due to generally low turbidity (Jones, 2009) and low concentrations of



**Fig. 1.** Bathymetry of the Bermuda platform, based on a combination of chart data (Clarke, 1997) and diver depth gauge data. See mapping methods. Depth shallower than 20 m indicated by blue-filled contours. The red dotted line represents the 10 m isobath on the outer edge of the reef rim, which demarcated the sampling area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



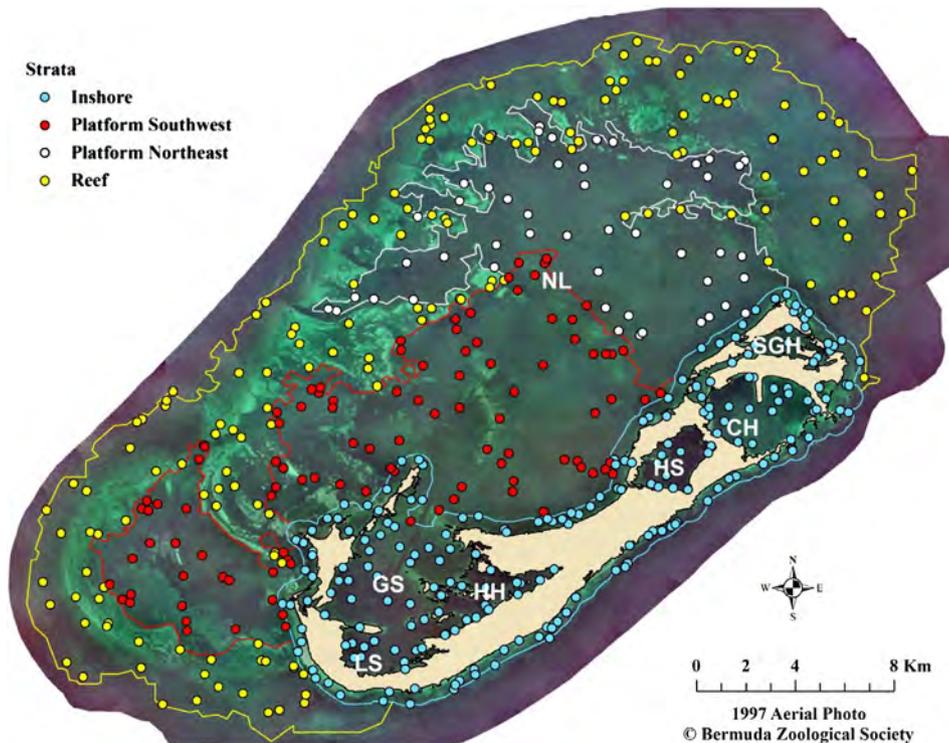
**Fig. 2.** Monthly averaged daily insolation based on a 22 year record of satellite observations for the 1° square grid cell containing Bermuda and for two other island locations with extensive coral reef and seagrass ecosystems. Data are from the N.A.S.A. insolation calculator <http://eosweb.larc.nasa.gov/sse/>. Inset map indicates the relative geographic positions of Bermuda, (32.4°N latitude), the Florida Keys (24.5°N), and St. Croix (17.5°N).

nitrogen (N) and phosphorous (P) (Beers and Herman, 1969). The deep waters surrounding Bermuda typically have attenuation coefficients ( $K_d$ ) < 0.1 m<sup>-1</sup> (Morris et al., 1977; calculated from secchi depths). Water on the platform is less clear than the surrounding open ocean, with  $K_d$  generally from 0.13 to 0.57 m<sup>-1</sup>, but with most sites having annual mean  $K_d$  between 0.19 and 0.33 m<sup>-1</sup> (Morris et al., 1977; calculated from secchi depths; McGlathery, 1995). Ratios of N:P suggest general P limitation to planktonic growth in the water column (Beers and Herman, 1969). In contrast, sediment pore

water N:P ratios are reported from 6:1 to 4:1 (McGlathery et al., 1992) and this, and experimental studies (McGlathery, 1995), suggest strong N limitation to algal and seagrass growth.

2.2. Sampling design

We surveyed the species composition and relative abundance of conspicuous epibenthic sessile autotrophs and the environmental characteristics of the Bermuda platform using a stratified random protocol, modified from Fourqurean et al. (2001), to distribute our sample sites. The sampling area was the entire Bermuda platform to a depth of 10 m outside the rim reef (Figs. 1 and 3). This area was subdivided into four spatial strata: 1) inshore, extending from the shoreline to 500 m from the shore but including all of any largely enclosed bodies of water and extending along the entire South Shore, 2) reef, which was delimited by the shoreward reef boundaries and the 10 m depth contour seaward of the shallow reef rim, 3) platform southwest, and 4) platform northeast (Fig. 3). The division of the platform into two zones was based on local knowledge of the biogeophysical zonation of the platform. A grid of rectangle-based sampling units was created and grid density was adjusted relative to the believed frequency of occurrence of seagrass in each stratum (Murdoch et al., 2007); inshore stratum ( $n = 67$  grid units), reef ( $n = 54$ ), platform southwest ( $n = 34$ ), and platform northeast ( $n = 16$ ); fewer units in a stratum generally correspond to an increase in unit size. This design allowed for the sampling of the entire platform, whether it was suspected seagrasses were present or not. One site within each grid unit was surveyed annually from 2006 through 2008 so that about 171–180 sites were observed in each year (Fig. 3). The locations for the survey sites were generated independently within each sampling unit and for each year using the ESRI ArcGIS V. 9 algorithm for random number generation. In the field, the sampling sites were located with GPS (Garmin GPS Map 276C) by navigating in a small vessel to the predetermined



**Fig. 3.** Aerial photographic mosaic of the Bermuda platform showing sample locations within sampling strata; lighter greenish areas in the image are shallow reefs and inter-reef sand patches. CH = Castle Harbour, GS = Great Sound, HH = Hamilton Harbour, HS = Harrington Sound, LS = Little Sound, NL = North Lagoon, SGH = St Georges Harbour.

locations, over which the boat anchor was dropped. The anchor was used as our survey/transect starting point. Water depths at time of sampling were recorded to the nearest 0.3 m and were not corrected for tidal height.

The sampling period in each year was slightly different. In 2006, we sampled from August 11 to December 6, in 2007 from May 22 to September 5, and in 2008 from May 29 to August 22.

### 2.3. Environmental parameters

#### 2.3.1. Salinity, water temperature, dissolved oxygen

Beginning in May 2007, surface measurements, approximately 0.2 m below the water surface (referred to as surface, hereafter), of salinity, temperature ( $^{\circ}\text{C}$ ), and dissolved oxygen (DO) were made at all sites during each sampling event. Salinity was measured with a YSI 30 salinity, temperature and conductivity instrument and DO with a YSI 550A. Starting in 2008, measurements about 1 m below the surface (referred to as  $-1$  m hereafter) and bottom readings of salinity, temperature and DO were also made with a YSI 600XL sonde equipped with an optical DO sensor model YSI 6150.

#### 2.3.2. Water clarity

Profiles of photosynthetically active radiation (PAR, 400–700 nm) at depth were obtained at 396 stations during 2006 through 2008, using a  $4\pi$  submerged spherical quantum sensor (LiCor model LI-193SA). PAR was measured at either 0.5 m or 1 m intervals from the water surface to the bottom, so that a minimum of 4 or 5 readings per depth profile were obtained at each site. PAR at depth was recorded as a ratio of incident PAR measured with a  $2\pi$  quantum sensor (LiCor model LI-190) deployed on the deck of the vessel. The diffuse attenuation coefficient,  $K_d$ PAR, was calculated from the profiles of light intensity at depth by fitting the Lambert–Beer law ( $I_z = I_0 e^{-K_d z}$ ) to ln-transformed profile data and solving for  $K_d$  using linear regression. We accepted all determinations of  $K_d$  from these analyses as long as the probability of the slope differing from zero was greater than 95% (i.e.,  $p \leq 0.05$ ). No correction was attempted for sun angle, as there was no spatial pattern in the time of day that readings were taken across the platform.

Secchi depth (m) (0.2 m diameter disc) and water depth (m) were recorded for all years; if the secchi depth was equal to the bottom depth, this was noted as 100% secchi depth. During 2007 and 2008, water samples were collected from approximately 0.1 m below the surface at 369 sites and analysed for turbidity (nephelometric turbidity units, NTU) with a portable turbidimeter (Hach model 2100P). Further, to investigate seasonal patterns in water clarity, we collected turbidity data monthly from March 2007 through April 2011 at 17 permanent stations distributed across the platform.

#### 2.3.3. Benthic habitat characterization

At each site a team of SCUBA divers laid out a 50 m line running along the bottom in a south to north direction. At 10 pre-selected random points along the line, a 0.5 m by 0.5 m quadrat was placed on the bottom. Water depth ( $\pm 1$  m) was recorded at each quadrat, and benthic plants and sessile animals were identified to a meaningful and reliable taxonomic level. Seagrasses were identified to species with the exception of *Halodule* sp. because of the aforementioned uncertainty of the taxonomic identity of this species in Bermuda. Macroalgae were identified to genus and other higher categories. Seagrasses and macroalgal genera, as well as Phylum Porifera (sponges), Subclass Octocorallia (octocorals or soft corals) (on the Bermuda platform these are all in Order Alcyonacea) and hard corals (comprised of Order Scleractinia [stony corals] plus Order Anthoathecata, Family Milleporidae [fire corals]), were each

assigned a cover ranking according to a modified Braun–Blanquet scale (Fourqurean et al., 2001). Cover was defined as the fraction of the total quadrat area obscured by the species, genus or group when observed by a diver from directly above, and cover categories were 0 = no specimens present, 0.1 = solitary individual present with <5% cover, 0.5 = few individuals with <5% cover, 1.0 = many individuals with <5% cover, 2.0 = 5–25% cover, 3.0 = 25–50% cover, 4.0 = 50–75% cover, and 5.0 = 75–100% cover.

### 2.4. Data analyses

#### 2.4.1. Occurrence estimates of benthic organisms

We determined taxon presence directly from our quadrat observations for each site. Braun–Blanquet density values ( $D$ ) were calculated for each taxon as the mean cover scores for all quadrats at a site; then the percentage of sites that supported each taxon within specified  $D$  intervals was calculated.

#### 2.4.2. Mapping

**2.4.2.1. Light and depth.** The point estimates of  $K_d$ PAR collected during 2006–2008 were used to generate a surface that described the spatial variability in water clarity across the study area. To interpolate the  $K_d$ PAR data, we used a kriging routine with a linear variogram and assuming isotropy (Surfer V. 8, Golden Software).

A bathymetric map of the platform was created by merging the water depth data measured at each site by the divers with data from a digitized navigational chart (Clarke, 1997), using the 3D Analyst extension in ESRI ArcGIS V.9 to create a bathymetric triangulated irregular network (TIN) surface. The  $K_d$ PAR and bathymetry surfaces were then sampled at ca. 8000 points using a rectangular grid with 250 m spacing. The amount of light entering the water column that reached the bottom ( $\%I_0$ ) at these points was calculated as  $\%I_0 = e^{-K_d z} \times 100\%$ ; these 8000 points were then used to generate a map of the fraction of insolation reaching the bottom across the study area employing the same kriging routine as above. Areas of the platform receiving defined levels of  $\%I_0$  were calculated using map analysis software (Surfer V. 8, Golden Software). We used the measured site depths at the time of sampling to calculate  $\%I_0$  without correcting the depths to a chart datum. This introduces little error into our calculations of light reaching the bottom given the observed water depths, low tidal amplitude in Bermuda (0.76 m), and low measured  $K_d$ PAR values.

The minimum amount of surface irradiance necessary to sustain seagrass communities has been called the ecological compensation depth (ECD, Gallegos and Kenworthy, 1996). We used our measurements of  $\%I_0$  and species distribution data to define the realized ECD for benthic autotrophs in our study area. ECD for a taxon was defined as minimum  $\%I_0$  calculated among all of the sites supporting that particular taxon.

**2.4.2.2. Benthic fauna and flora.** Maps of presence and absence were generated from transect data for genera of calcareous green algae, hard corals and octocorals, and each of the four seagrass species using Surfer V. 8.

## 3. Results

### 3.1. Environmental parameters and physical habitat characterization

#### 3.1.1. Salinity, water temperature, dissolved oxygen

Details of these environmental parameters are provided as supplementary data (Supplementary Figs. S1 and S2). Maximum summer temperatures were just over  $30^{\circ}\text{C}$  in August 2007 and 2008; deeper and offshore sites experienced a smaller increase in

temperature over the summer season, for both surface and bottom temperatures. Surface salinities ranged from 34.4 to 37.0, which slightly expands the range of reported salinities on the platform (36.1–36.9, Marine Environmental Program, 2007). DO, as % saturation, was high at all locations and depths within our survey area, with few exceptions. DO in bottom water was below saturation at five sites in summer 2008, all of which had depths of 9.5 m or more; lowest DO saturations of about 64% and 57% were measured in August.

### 3.1.2. Water clarity

Water clarity across our study area was generally high; about 39% of sites had Secchi depths greater than the water depth, with the maximum Secchi depth measured being >20.7 m. The range of Secchi depths at sites where the disc was not visible on the bottom was from 2.4 to 14.9 m, with a mean of 6.6 m and median of 6.4 m.

Turbidity at 369 sites ranged from 0.14 NTU to 4.23 NTU, with a mean value of 0.57 NTU and a median of 0.52 NTU (Fig. 4a). The most turbid sites were in harbours and bays. There was no seasonal pattern in turbidity at the 17 permanent monitoring stations (Fig. 5). Light attenuation ( $K_d$ PAR) at 396 sites in 2006–2008 exhibited a skewed distribution with a tail towards higher values (Fig. 4b); the minimum measured  $K_d$ PAR was  $0.01\text{ m}^{-1}$  and the maximum was  $0.56\text{ m}^{-1}$ ; the mean value was  $0.13\text{ m}^{-1}$  and the median value was  $0.12\text{ m}^{-1}$ . Our measured  $K_d$ PAR values were generally similar to full spectrum  $K_d$  values reported in the literature for Bermuda (Morris et al., 1977; McGlathery, 1995); it is

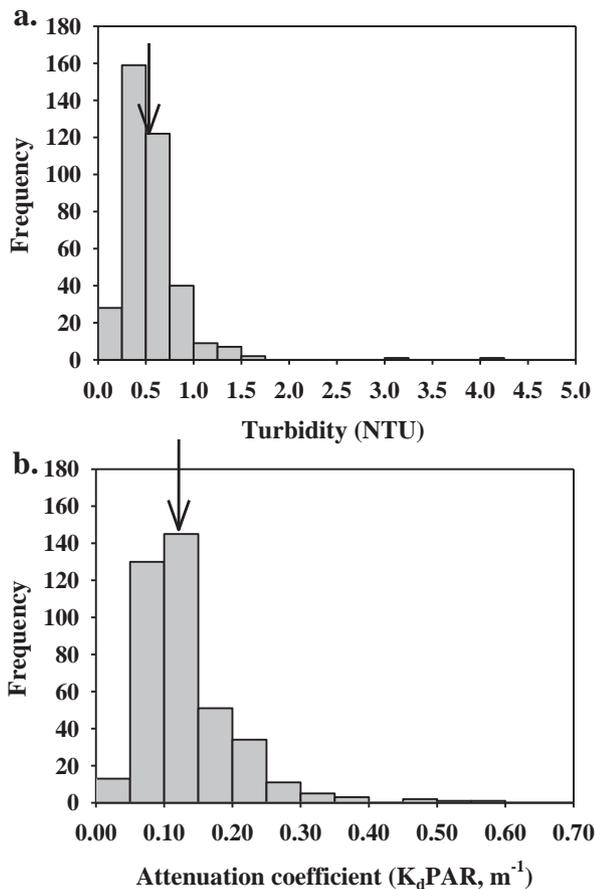


Fig. 4. Water column turbidity and light attenuation on the Bermuda platform in 2007 and 2008. a. Frequency distribution (number of observations) of turbidity values (NTUs); b. Frequency distribution (number of observations) of  $K_d$ PAR. Arrows indicate median values.

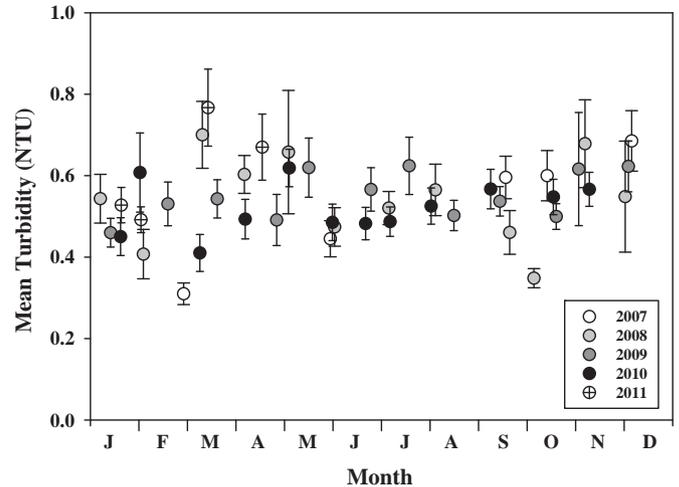


Fig. 5. Water column turbidity at 17 permanent monitoring stations during the period March 2007 through April 2011. Values are the mean NTU values for all 17 stations during each sampling interval. Error bars indicate one standard error.

possible that the relatively few determinations of very low  $K_d$ PAR could have been influenced by reflection of light off of the bottom.

### 3.1.3. Depth

The depths for 533 survey sites ranged from 0 m to 22.9 m, with a median depth for all sites of 10.1 m. Twelve percent of the benthic survey sites were <4 m deep, 75% of the sites surveyed were distributed fairly evenly between 4 and 16 m and 13% of the sites were deeper than 16 m (Table 1). Our deepest sites were in the northeastern region of the North Lagoon and in Little Sound (21 m), Harrington Sound (18 m) and Castle Harbour (15 m) (Fig. 3). The shallowest subtidal regions of the platform are in the harbours at Hamilton and St. Georges, around the islands of Castle Harbour and Great Sound, in the western region of the platform generally, and over the reefs (Fig. 1). The seafloor topography of the Bermuda platform is complex (Figs. 1 and 3) with shallow reefs distributed not only along the rim of the platform but also throughout the North Lagoon and across the shallower western and eastern ledges of the platform.

### 3.1.4. Mapping depth and light

In general,  $K_d$ PAR was highest nearshore, particularly along the north shores of the Bermuda islands in enclosed harbours and sounds (Fig. 6a).  $K_d$ PAR values across most of the platform were  $<0.15\text{ m}^{-1}$ , with spatially cohesive areas of differing  $K_d$ PAR. Even given these generalities, the spatial pattern of  $K_d$ PAR on the platform is as complex as the seafloor topography and cannot be described as a simple trend from offshore sites to inshore sites.

As a consequence of the clear water, indicated by generally low  $K_d$ PAR, and the relatively shallow depth of the entire study area, most of the bottom on the platform received more than 20% of  $I_0$  (Fig. 6b); only in deeper basins and in some of the more turbid bays and harbours did  $<10\%$  of the light entering the water column reach the bottom (Fig. 6b).

## 3.2. Benthic habitat characterization

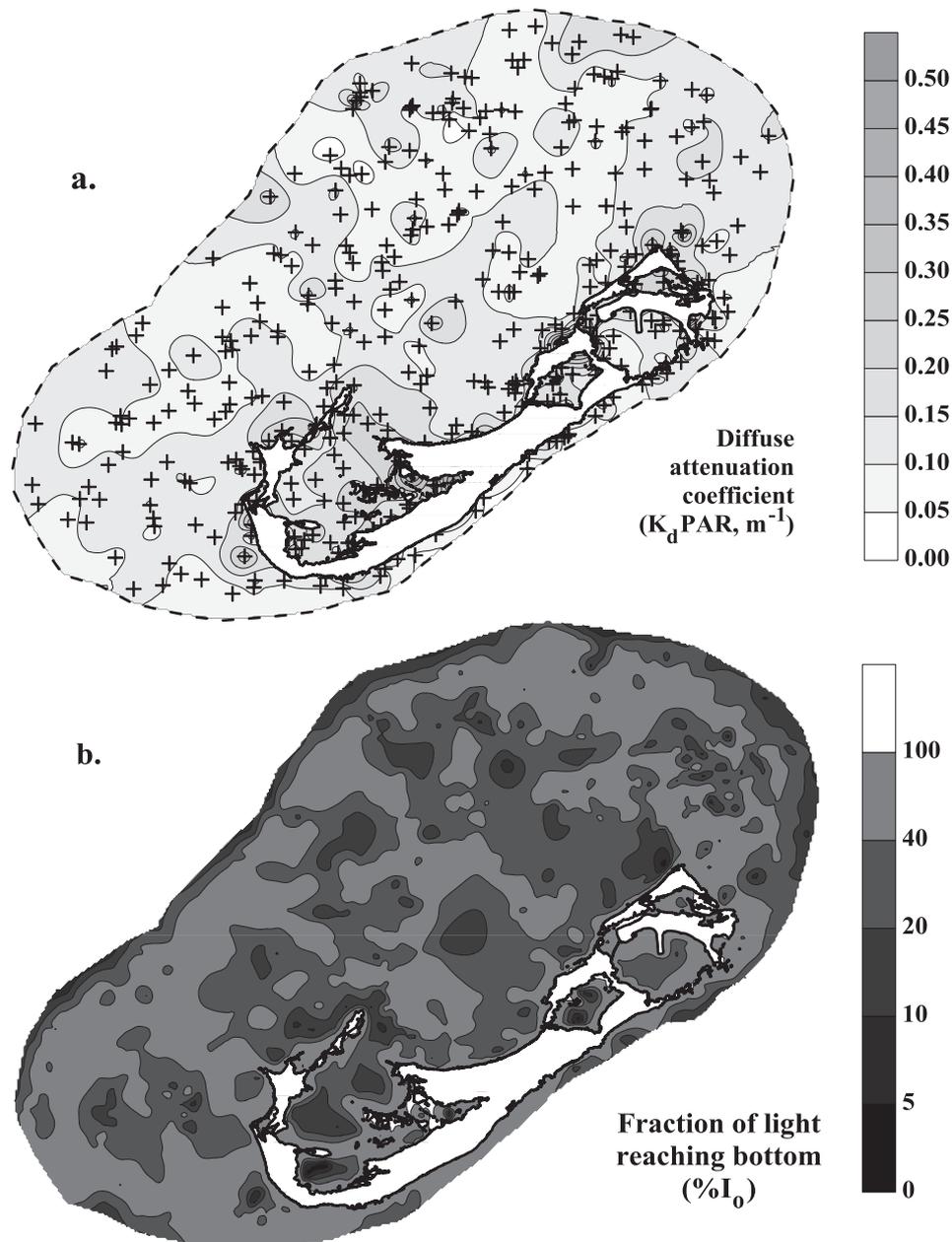
### 3.2.1. Taxonomic composition and spatial distribution

The benthic habitats at 533 sites were characterized. At least one seagrass species was found at about 24% of the sites, with *S. filiforme* being the most commonly encountered (12% of sites), followed by *H. decipiens* (10%), *T. testudinum* (7%) and *Halodule* sp. (6%) (Table 2).

**Table 1**

Depth distribution intervals of sites and taxa, indicating number of sites sampled, and percentage of sites where a taxon was found for each interval.

Depth interval (m)	Number of sites	Any seagrass	<i>Thalassia testudinum</i>	<i>Syringodium filiforme</i>	<i>Halodule</i> sp.	<i>Halophila decipiens</i>	<i>Acetabularia</i> spp	<i>Halimeda</i> spp	<i>Neomeris</i> sp.	<i>Udotea</i> spp	<i>Penicillus</i> spp	Octocorals	Hard corals
0–2	19	52.6	52.6	36.8	15.8	0.0	57.9	42.1	21.1	0.0	36.8	0.0	5.3
2–4	44	38.6	31.8	20.5	13.6	2.3	39.5	39.5	30.2	18.6	32.6	48.8	51.2
4–6	63	25.4	12.7	20.6	12.7	6.3	18.3	31.7	23.3	15.0	25.0	55.0	66.7
6–8	68	30.9	8.8	23.5	7.4	4.4	21.4	27.1	24.3	25.7	32.9	48.6	54.3
8–10	66	30.3	1.5	16.7	9.1	13.6	25.8	43.9	22.7	39.4	48.5	30.3	43.9
10–12	76	23.7	0.0	3.9	3.9	19.7	7.9	25.0	17.1	39.5	50.0	28.9	35.5
12–14	60	15.0	0.0	3.3	1.7	13.3	8.6	12.1	3.4	25.9	55.2	22.4	25.9
14–16	65	10.8	0.0	1.5	0.0	9.2	1.5	4.4	7.4	29.4	63.2	13.2	19.1
16–18	39	10.3	0.0	0.0	0.0	10.3	5.3	2.6	7.9	21.1	47.4	18.4	28.9
18–20	22	4.5	0.0	0.0	0.0	4.5	0.0	0.0	0.0	21.7	60.9	13.0	13.0
20–22	10	10.0	0.0	0.0	0.0	10.0	0.0	0.0	0.0	9.1	36.4	27.3	27.3
22–24	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0



**Fig. 6.** Light attenuation ( $K_d$ PAR) and estimated bottom light distribution patterns for the Bermuda platform. a. Map of  $K_d$ PAR; b. Map of  $\%I_0$  at depth for the Bermuda platform. Crosses indicate survey sites.

**Table 2**Taxon presence and density; percentages of 533 sampled sites that supported each taxon at the indicated Braun–Blanquet density categories (*D*).

Taxon	<i>D</i> = 0	0 < <i>D</i> ≤ 0.1	0.1 < <i>D</i> ≤ 0.5	0.5 < <i>D</i> ≤ 1	1 < <i>D</i> ≤ 2	2 < <i>D</i> ≤ 3	3 < <i>D</i> ≤ 4	4 < <i>D</i> ≤ 5
<i>Thalassia testudinum</i>	92.3	1.3	0.9	1.1	1.3	1.3	0.7	0.6
<i>Syringodium filiforme</i>	88.0	2.1	3.6	1.5	1.5	2.1	0.9	0.0
<i>Halodule</i> sp.	93.6	1.9	1.5	1.5	0.6	0.4	0.2	0.0
<i>Halophila decipiens</i>	89.9	2.8	4.1	1.5	1.3	0.0	0.0	0.0
<i>Halimeda</i> spp	76.8	8.8	7.3	2.8	3.0	0.7	0.2	0.0
<i>Udotea</i> spp	73.5	12.1	6.2	2.2	3.2	1.7	0.6	0.2
<i>Penicillus</i> spp	54.8	15.0	16.1	8.4	4.9	0.6	0.0	0.0
<i>Acetabularia</i> spp	83.7	11.4	4.1	0.4	0.0	0.0	0.0	0.0
<i>Neomeris</i> sp.	83.6	12.3	3.6	0.2	0.0	0.0	0.0	0.0
Sum of calcareous green macroalgae	43.0	14.2	20.6	8.0	9.0	3.7	0.9	0.2
<i>Caulerpa</i> spp	62.6	9.7	17.0	6.4	3.9	0.0	0.0	0.0
<i>Batophora</i> sp.	97.0	2.1	0.6	0.0	0.0	0.0	0.0	0.0
<i>Avrainvillea</i> sp.	96.3	2.6	0.6	0.2	0.0	0.0	0.0	0.0
<i>Dasycladus</i> sp.	97.9	0.7	0.7	0.0	0.2	0.0	0.0	0.0
Other green macroalgae	58.7	10.1	20.7	6.7	2.6	0.6	0.2	0.0
Drift red macroalgae	98.3	0.4	0.7	0.2	0.0	0.0	0.0	0.0
<i>Laurencia</i> spp	57.9	15.1	16.1	7.7	2.8	0.0	0.0	0.0
Calcareous red algae	65.0	8.0	12.3	7.3	6.4	0.6	0.0	0.0
Other attached red macroalgae	28.4	8.6	24.1	13.8	20.4	3.7	0.6	0.0
<i>Sargassum</i> spp	98.7	0.6	0.4	0.0	0.0	0.0	0.0	0.0
<i>Dictyota</i> spp	62.4	8.8	10.8	9.9	7.3	0.4	0.0	0.0
<i>Padina</i> spp	92.3	6.5	0.7	0.0	0.0	0.0	0.0	0.0
Other brown macroalgae	85.8	4.7	6.0	2.6	0.6	0.0	0.0	0.0
Sponges	45.6	15.0	26.9	9.2	3.0	0.0	0.0	0.0
Octocorals	68.8	3.6	10.7	4.5	9.2	3.0	0.0	0.0
Hard corals	61.9	4.9	10.7	5.4	6.9	7.9	2.1	0.0

Seagrass was found in the lagoon on the north side of the islands, nearshore, in bays and harbours, and offshore in the west and the north where it was associated with reefs (Fig. 7a). No seagrass was observed on the exposed South Shore. About 63% of the 124 sites where seagrass beds were observed consisted of just one seagrass species while 25% had two species and 12% had three (Fig. 8a). There were no sites where all four seagrasses were present; *H. decipiens* was never found along a transect line where all the other three species of seagrass also occurred, however, all other possible combinations of these species were found.

Calcareous green algae were found at 57% of the 533 sites (Table 2). At 43% of sites where calcareous green algae occurred only a single genus was recorded, but it was fairly common to find 2 or 3 genera at a site, 24% and 22% of sites, respectively, with even greater generic richness (4 or 5 genera) found at about 10% of sites (Fig. 8b). *Penicillus* was the most commonly observed genus of calcareous green algae, followed by *Udotea* and *Halimeda* (Table 2). Calcareous green algae were found across the platform but were rarely observed on the South Shore (Fig. 7b).

Non-calcareous green algae occurred at more than 41% of the sites (Table 2). *Caulerpa* was the most abundant genus occurring at 37% of the sites. All other identified genera of non-calcareous green algae each occurred at <4% of the sites (Table 2). The most commonly observed macroalgae taxon was attached red macroalgae. *Laurencia* spp occurred at 42% of the sites, followed by calcareous red macroalgae (35%) and other attached red macroalgae (72%). Other than *Dictyota* spp (38%), brown algae were not common.

Sponges, hard corals and octocorals were present at 55%, 38% and 31% of the sites, respectively (Table 2). Hard corals were distributed along the coastline, in patches throughout the lagoon, and at the boundary of our sampling area (Fig. 7c). The distribution of octocorals was similar to that of the hard corals except for a relatively infrequent occurrence along the north shoreline and in harbours and sounds (Fig. 7c).

### 3.2.2. Depth distribution

The maximum depth of the most common seagrass species, *S. filiforme*, was 15.3 m (Table 3). In any given depth interval from 0 to

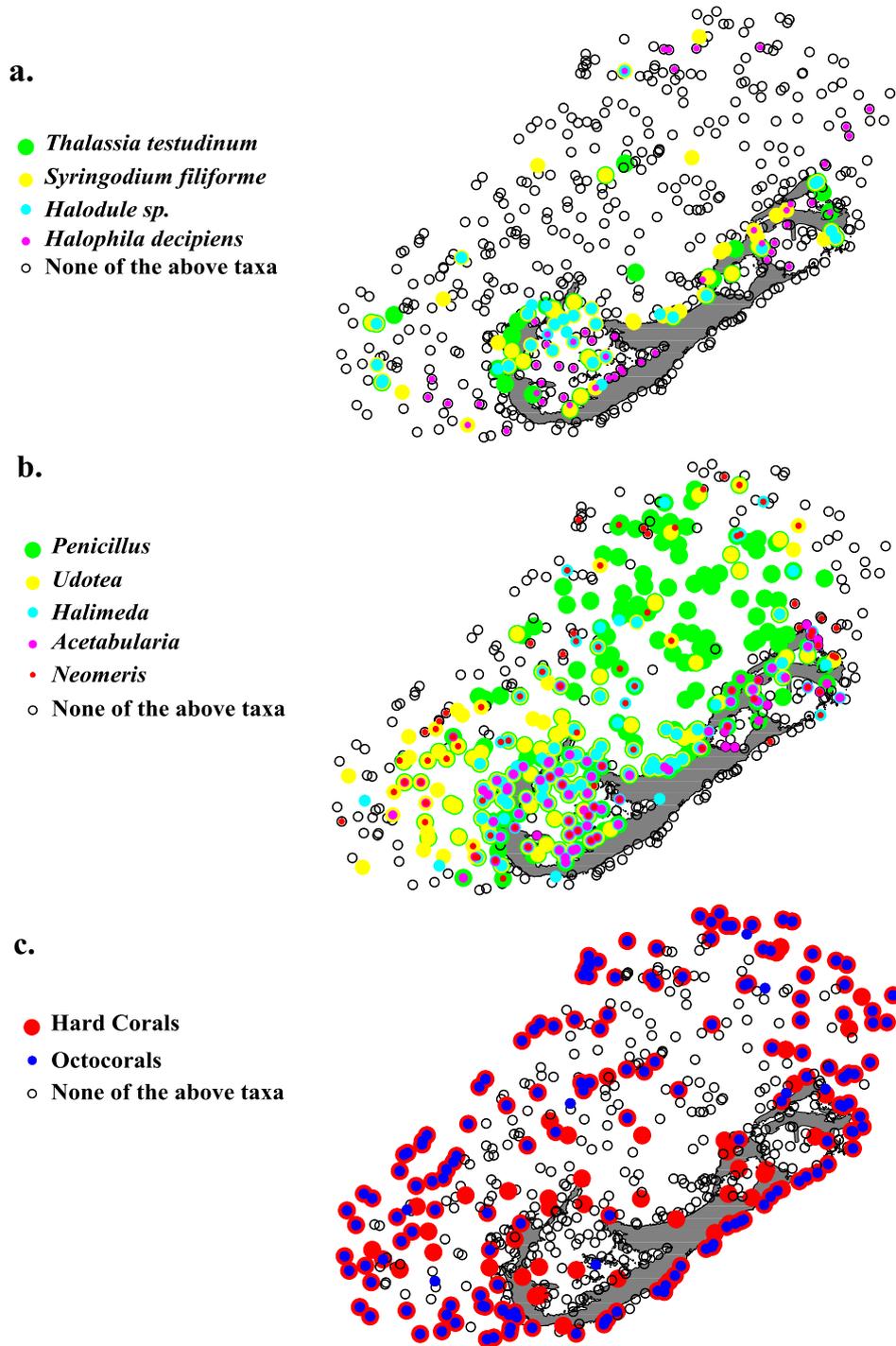
10 m, *S. filiforme* occurred at more than 10% of our sites (Table 1) and the mean depth of all sites at which it was observed was 6.3 m (Table 3), much shallower than its maximum depth. The maximum depth for *T. testudinum* was 9.1 m (Table 3), but it only occurred at more than 10% of sites with depths <6 m; of 19 sites in the shallowest depth interval (0–2 m) it occurred at 10 and it occurred at almost 40% of sites with depths of 2–4 m, so that it was the most common seagrass at the shallowest sites (Table 1). For the 39 sites at which *T. testudinum* was observed (7% of all sites), the mean depth was 3.7 m (Table 3). The maximum depth for *Halodule* sp. was 12.9 m, but it was commonly observed at sites shallower than 6 m, with a mean depth of occurrence of 6.1 m (Tables 1 and 3). The majority of sites where *H. decipiens* was observed were those with depths between 8 and 18 m, with a mean depth of 11.2 m, but the maximum depth at which *H. decipiens* was observed was 20.2 m and it was the only seagrass growing deeper than *S. filiforme* (Tables 1 and 3).

Calcareous green algae were distributed across all depths except the deepest sites, 22–24 m (Table 1). All the genera of calcareous green algae we identified were observed to depths >16 m (Tables 1 and 3). However, there were differences among the genera in their frequencies for different depth intervals; with some more common at deeper sites than others. *Penicillus* occurred at 25% or more of all sites with depths up to 22 m and *Udotea* at more than 25% of all sites between 6 and 16 m; whereas, *Halimeda*, *Acetabularia* and *Neomeris* sp. were only observed at more than 25% of sites with shallower depths, <10–12 m, <4 m and <2–4 m plus 8–10 m, respectively.

Hard corals were observed at sites at all depths except the deepest 2 m interval surveyed; however, they extend well below our sampling depth limit on the outer reef and the maximum depth observed is simply that of the deepest reef surveyed (Tables 1 and 3). Octocorals were encountered at all depth intervals apart from the shallowest and the deepest. Both hard corals and octocorals were present at more than 50% of the sites in the 2–8 m depth range.

### 3.2.3. Depth distribution and light availability at depth

3.2.3.1. Seagrass. At the 22 sites that supported *T. testudinum*, and for which  $K_d$ PAR was measured, %  $I_0$  estimated at the sea bottom ranged from 34.1% to 80.7%, with a median of 54.2% (Table 4). Of the

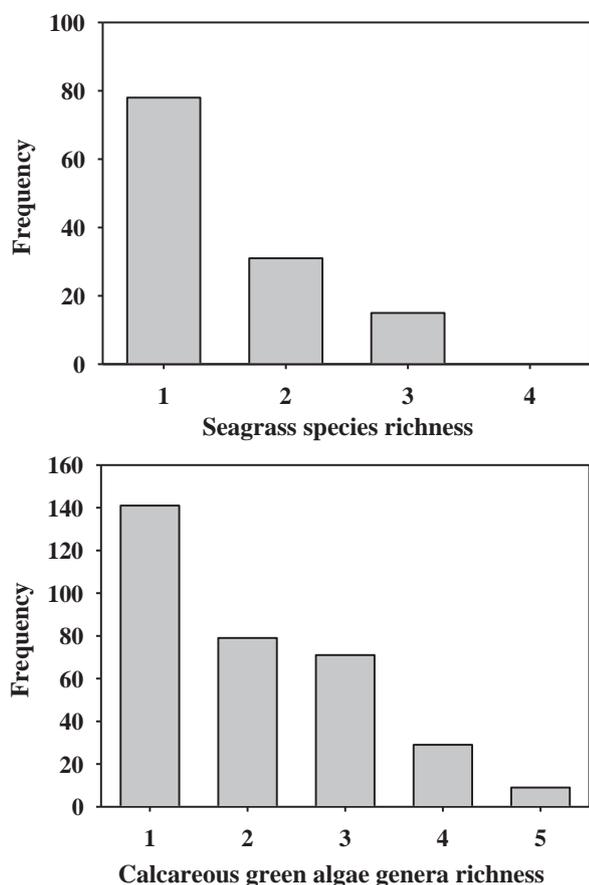


**Fig. 7.** Taxon presence and absence at survey sites in 2006, 2007 and 2008. a. Seagrass species; b. Genera of calcareous green algae; c. All corals, hard corals (Order Scleractinia [stony corals] plus Family Milleporidae [fire corals]) and octocorals (Subclass Octocorallia).

sites at which *T. testudinum* was found, the minimum light reaching the bottom was 34.1% of  $I_0$ . We interpreted this amount of light as the ECD for *T. testudinum*, since this species was found at no sites that received less than 34.1% of  $I_0$ . We computed ECDs for the other species similarly. ECDs for *S. filiforme* and *Halodule sp.* were the same (17.7% of  $I_0$ ), about one-half that of *T. testudinum*; whereas *H. decipiens* had a much lower ECD; it was found at sites with %  $I_0$  as low as 1.6%. The mean and median values of %  $I_0$  for sites where *H. decipiens* was found were less than half of those for sites with the other seagrass species.

The range of depths and %  $I_0$  for both *Halodule sp.* and *S. filiforme* are substantially broader than for *T. testudinum* (Tables 1, 3 and 4), and their distributions are skewed towards the low light end of their ranges, even though they have similar mean and median values to *T. testudinum*. Thus we see both *Halodule sp.* and *S. filiforme* more frequently than *T. testudinum* in relatively lower light environments.

The entire 502 km<sup>2</sup> of the area surveyed received  $\geq 1.6\%$  of surface irradiance at the bottom (Figs. 6b and 9) and, therefore, received enough light to support *H. decipiens*. About 92%, or



**Fig. 8.** Taxon richness by site. a. Frequency distribution (number of observations) among sites of species richness for seagrasses; b. Frequency distribution (number of observations) among sites of generic richness for calcareous green algae.

462 km<sup>2</sup>, of our survey area received  $\geq 17.7\%$  of surface irradiance, and had enough light to support all of *S. filiforme*, *Halodule* sp. and *H. decipiens*. A much smaller proportion, only 59%, 296 km<sup>2</sup>, of the area received  $\geq 34.1\%$  of the surface irradiance and therefore could potentially support *T. testudinum* as well as the other seagrass species. Note that there were many places where %  $I_0$  was higher than the minimum measured for each taxon from which the taxon was absent (Fig. 9), suggesting that factors other than light (e.g., substrate, herbivory, disturbance, lack of propagules, etc.) also limit the distribution of seagrasses on the Bermuda Platform.

**Table 3**

Depth distribution characteristics for seagrasses, calcareous green algae, octocorals and hard corals.

	n	Depth (m)			
		Minimum	Maximum	Mean	Median
<i>Thalassia testudinum</i>	39	0.5	9.1	3.7	3.2
<i>Syringodium filiforme</i>	62	0.5	15.3	6.3	6.2
<i>Halodule</i> sp.	32	1.7	12.9	6.1	6.0
<i>Halophila decipiens</i>	52	2.6	20.2	11.2	10.8
<i>Acetabularia</i> spp	85	0.5	16.3	6.5	6.3
<i>Halimeda</i> spp	122	0.5	17.2	7.4	7.7
<i>Neomeris</i> sp.	86	1.0	17.5	7.7	7.6
<i>Udotea</i> spp	140	2.6	20.7	10.6	10.7
<i>Penicillus</i> spp	240	0.5	21.8	11.2	11.2
Octocorals	165	2.3	21.3	8.7	7.7
Hard corals	202	2.0	21.3	8.8	8.0

**Table 4**

Percentage of surface irradiance reaching the bottom (%  $I_0$ ) at sites where a taxon occurred.

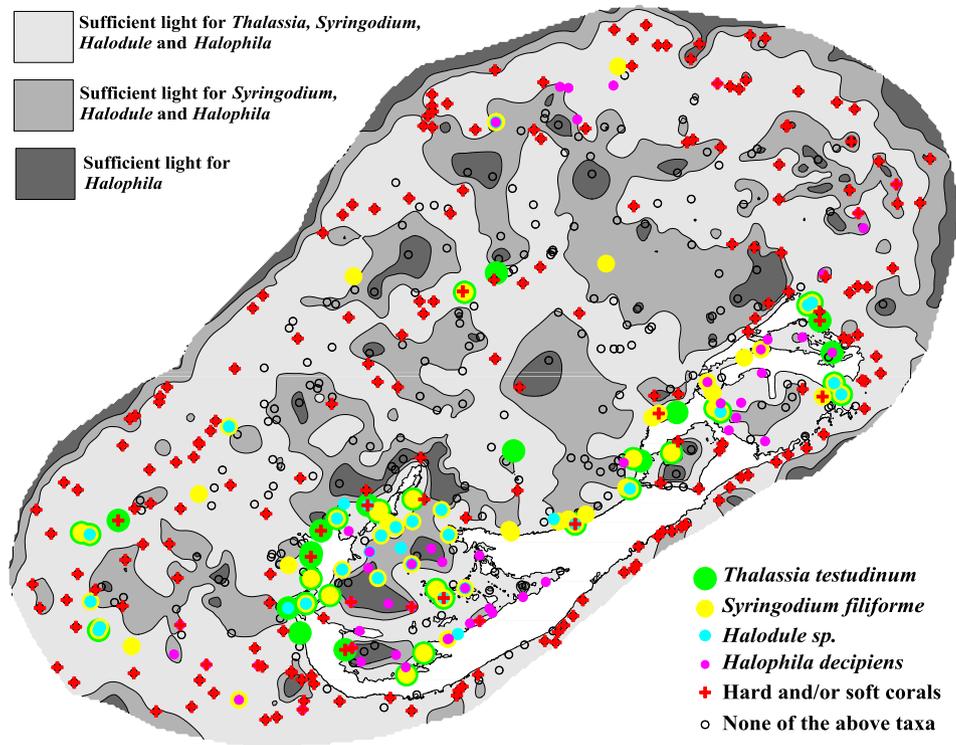
	n	Percent of surface irradiance reaching bottom			
		Minimum	Maximum	Mean	Median
<i>Thalassia testudinum</i>	22	34.1%	80.7%	56.6%	54.2%
<i>Syringodium filiforme</i>	47	17.7%	88.9%	46.6%	46.8%
<i>Halodule</i> sp.	32	17.7%	88.2%	46.2%	49.5%
<i>Halophila decipiens</i>	52	1.6%	55.1%	22.2%	18.8%
<i>Acetabularia</i> spp	68	9.2%	89.0%	39.6%	40.8%
<i>Halimeda</i> spp	84	9.2%	89.0%	39.6%	39.3%
<i>Neomeris</i> sp.	73	3.9%	84.6%	40.0%	42.2%
<i>Udotea</i> spp	96	2.0%	78.3%	25.3%	28.4%
<i>Penicillus</i> spp	191	2.0%	89.0%	26.5%	30.0%
Octocorals	116	3.7%	84.9%	40.6%	41.0%
Hard corals	138	3.7%	84.9%	39.8%	40.1%

3.2.3.2. *Other taxa.* The two most commonly encountered genera of calcareous green algae, *Penicillus* and *Udotea*, were found at sites with %  $I_0$  as low as 2.0% and as high as 89.0% (mean 26.5%, median 30.0%) and 78.3% (mean 25.3%, median 28.4%), respectively (Table 4). The other genera of calcareous green algae had higher mean and median values for %  $I_0$ , but these were lower than for the seagrasses, other than *H. decipiens*. Octocorals and hard corals were found at a minimum of 3.7%  $I_0$  up to 84.9%  $I_0$  with means and medians around 40%.

#### 4. Discussion

In these first comprehensive surveys of the distribution of the benthic communities on the Bermuda platform we documented tropical seagrasses, calcareous green algae, and both hard corals and octocorals to be widely distributed. Seagrass beds occur in harbours, nearshore, and as reef-associated features across the platform, and infrequently in the North Lagoon (Murdoch et al., 2007), and contrary to the generally held belief that *T. testudinum* is the most common seagrass in Bermuda (Thomas and Logan, 1992), *S. filiforme* and *H. decipiens* are more common at present. Extensive beds of calcareous green algae occur along the shore and near reefs but are also prominent and widespread features of deeper and more turbid basins. Neither of these plant groups is very common along the South Shore of Bermuda and this appears to be unrelated to water clarity and light penetration. The South Shore is a higher energy environment than the North Lagoon and has highly mobile, coarse sediments (unpub. obs., SAM, KAC), which are not conducive for the establishment of these plants. The species composition, density and the relative abundance of various taxa, including hard corals, octocorals, and sponges of the benthic communities on the Bermuda platform have subtropical and tropical characteristics similar to more southerly latitudes in the Caribbean and western Atlantic (Bermuda – Sterrer, 1986; south Florida – Fourqurean et al., 2001; global – Green and Short, 2003; Caribbean – Ballantine et al., 2008; Gulf of Mexico – Hine et al., 2008; Florida Keys – Jaap et al., 2008).

Bermuda has a unique combination of environmental conditions and subtropical climate that allows all these tropical autotrophic communities to exist on the relatively small Bermuda platform at a temperate latitude. The platform is shallow with an abundance of unconsolidated substrate overlain by generally clear water. There is minimal fresh water input so that salinity is consistently high and optimum for marine species. Stressful conditions associated with low dissolved oxygen are rare and the entire water column remains well-oxygenated throughout the year; with the exception of bottom waters at a few sites in the harbours and



**Fig. 9.** Area of benthic habitat with sufficient light to support the four species of seagrass, indicated by isopleths of median values for %  $I_0$  found for seagrass species in Bermuda; and distribution of reef (hard and soft coral [=octocorals]) habitat and seagrass species by survey site. Shades of grey indicate different light regimes, and symbols indicate taxa found at each location.

sounds, all with depths >9 m, DO levels do not fall much below saturation levels.

Although most of the Bermudian seagrass beds are mono-specific, mixed beds are not uncommon with the species sometimes completely intermixed in a single quadrat, although with very different cover values. More often, however, at sites with more than one species, they are found in discrete patches with both *Halodule* sp. and *S. filiforme* dominating at disturbed, excavated, locations, such as in blowouts and below eroding edges of *T. testudinum* rhizosphere. South (1983) reported that *T. testudinum* and *S. filiforme* grew intermixed in Whalebone Bay, but that in Ferry Reach, *T. testudinum* was shallower and *S. filiforme* deeper, forming two separate zones. These different small scale distribution patterns are probably related to the different light requirements of these species, different water quality and depth characteristics of the sites, and colonization and growth patterns of the species. *H. decipiens* tends to occur alone and occupies sites in deeper and more turbid water than the other species found in Bermuda, similar to its reported distribution in other subtropical and tropical ecosystems (St. Croix – Kenworthy et al., 1989; southeast Florida – Kenworthy, 2000; Gulf of Mexico – Hammerstrom et al., 2006; Fonseca et al., 2008).

Where suitable substrate is available and there are no other significant limiting biophysical factors (e.g., grazers, Fourqurean et al., 2010), one of the most important parameters controlling the distribution and abundance of benthic primary producers is the correspondence between the availability of sufficient light to support photosynthesis and the light requirements of a plant species. On the Bermuda platform the depth limits of the different primary producers indicated taxon-specific minimum light requirements for seagrass species and genera of calcareous green macroalgae. Seagrasses had the narrowest light distribution ranges and, with exception of *H. decipiens*, the highest minimum light requirements.

In general, calcareous green macroalgae were more widely distributed than the seagrasses and were found in areas where as little as 2.0% of surface irradiance penetrated; but there were notable differences among the genera we recorded with *Penicillus* and *Udotea* being on average “lower-light” genera and *Neomeris*, *Acetabularia* and *Halimeda*, relatively and on average, “higher-light” genera. The calcareous green macroalgae are important producers of the calcium carbonate particles that form the sediments of the Bermuda platform which support seagrass beds and other soft-bottom ecological communities (Wefer, 1980). Both hard corals and octocorals include a high diversity of species and were encountered even more commonly than seagrasses or calcareous green macroalgae. Among the diverse assemblage of corals found in Bermuda there are known low-light species (Fricke and Meischner, 1985) as well as other species that dominate shallow reefs. However, even though they were found in areas where as little as 3.7% incident light reached the bottom, the median %  $I_0$  at sites where hard and soft corals occurred was around 40%, indicating, the coral communities most often occur in higher light environments.

Our estimates of ECD were made based on calculations of the fraction of the sun’s energy that entered the water column that was transmitted to the bottom (%  $I_0$ ), one of the most commonly encountered and practical field based measurements used for estimating and comparing seagrass light requirements (e.g., Buesa, 1974; Wiginton and McMillan, 1979; Iverson and Bittaker, 1986; Duarte, 1991a; Kenworthy and Haunert, 1991; Kenworthy and Fonseca, 1996; Gallegos and Kenworthy, 1996; Biber et al., 2008; Duarte et al., 2007). The water clarity data ( $K_d$ ) used for measuring %  $I_0$  and calculating ECD were largely restricted to collection in the summer months. Since we found no difference in turbidity (NTU) on a seasonal basis, we believe that our estimates of %  $I_0$  and the relative differences in ECD between species are applicable to the rest of the year. We recognize that the lower sun angles in winter

could increase the amount of light reflected off the surface of the water and decrease the total photon flux in winter even with seasonally invariant %  $I_0$ . Ideally, if continuous measurements of underwater photon flux were acquired throughout the year we could avoid this uncertainty, but this would be impractical to do at the scale of the Bermuda platform. Due to the difficult logistical problems, very few studies have actually attempted continuous light measurements in seagrass systems, but in the rare instance where they have, the data indicated a close correspondence between %  $I$  and total photon flux (Dunton, 1994; Czerny and Dunton, 1995). However, most estimates of ECD have been made using water clarity based analyses similar to our methods and we restrict our comparisons for the different species to these.

For seagrasses, the relative pattern among species for ECD from our surveys was as expected from studies in other tropical and subtropical regions. The smallest seagrass, *H. decipiens*, had the lowest ECD and was found in deeper and more turbid areas receiving as little as 1.6% of surface irradiance (Kenworthy et al., 1989; Kenworthy, 2000; Hammerstrom et al., 2006; Fonseca et al., 2008). *Halodule* sp. and *S. filiforme*, the two intermediate-sized and relatively fast growing opportunistic species, had a higher light requirement and were found at intermediate depths that received at least 17.7% of surface irradiance. This ECD was less than the range established for both of these species in the Indian River Lagoon (20%–37%: Kenworthy and Fonseca, 1996; Gallegos and Kenworthy, 1996), but higher than values of 10% reported in the Gulf of Mexico (Iverson and Bittaker, 1986) and 7% in the back-reef environments of the Florida Keys (JWF, unpublished data). It was, however, similar to the ECD reported for *Halodule* sp. in St. Croix, U.S. Virgin Islands (17%–18%: Wiginton and McMillan, 1979) and Laguna Madre in the Gulf of Mexico (18%: Dunton, 1994; 15%: Onuf, 1991, 1994). Values for *S. filiforme* in Bermuda were similar to those found in St. Croix (11%–17%: Wiginton and McMillan, 1979) and Cuba (19.2%: Buesa, 1974).

As found elsewhere, *T. testudinum* had the highest ECD among the seagrass species found in Bermuda. However, although the relative ECD and depth distribution patterns for the seagrasses observed on the platform were as expected, we would not have predicted such a high light requirement for *T. testudinum* in Bermuda. *T. testudinum*, which in Bermuda has an ECD of 34.1% of incident light, has been documented to have an ECD as low as 10% of surface irradiance in the Gulf of Mexico (Iverson and Bittaker, 1986) and south Florida (JWF, unpublished data). In coastal regions of Florida, the ECD of *T. testudinum* has been established as 20% in Florida Bay (Fourqurean et al., 2003), 23.3% in Lemon Bay (Tomasko et al., 2001), and 20% in Tampa Bay (Dixon, 2000; Johansson and Greening, 2003). The ECD for this species was found to be as low as 17.5% in St. Croix, U.S. Virgin Islands (Wiginton and McMillan, 1979) and 21.5% in Cuba (Buesa, 1974). If reflection off the bottom caused us to underestimate  $K_d$ PAR, this would lead to an overestimation %  $I_0$  at some sites. Such an overestimation would only make the contrasts between the ECDs measured in Bermuda and elsewhere in the ranges of these taxa more pronounced. Thus, although the depth limits of seagrasses are controlled in large part by the attenuation of light in the water column, our data suggest water clarity is not the only important factor limiting occurrence in Bermuda, especially for *T. testudinum*. We suspect factors like herbivory (Fourqurean et al., 2010), absence of suitable unconsolidated sediment, lack of propagules and disturbance history play a large part in determining seagrass distributions in addition to light availability.

In oligotrophic subtropical and tropical marine environments of the western hemisphere *T. testudinum* is often the dominant seagrass species (Williams, 1990). Despite its relatively slower rate of asexual reproduction and rhizome growth compared to other

tropical Atlantic species (Duarte, 1991b), *T. testudinum* has the highest proportion of non-photosynthetic below-ground biomass, and requires a large amount of light in order to support respiratory demands of the non-photosynthetic tissues (Fourqurean and Zieman, 1991). We propose that the ECD for this larger, slower spreading and long-lived seagrass is higher than elsewhere in its range because, at the relatively high latitude of Bermuda, total annual insolation is low due to low winter light levels. Multiple stressors can have synergistic effects on seagrasses (Orth et al., 2006), and we believe the combination of low winter irradiance and cold temperatures contributes to the higher ECD as well. Water clarity (Fig. 5) and insolation (Fig. 2) in Bermuda are high in summer when water temperatures are ideal for seagrass growth, however, low insolation combined with colder temperatures slows the production and growth of photosynthetic tissues of this species in winter without a reduction in the mass and demands of non-photosynthetic biomass. We expected to see a similar change in ECD in Bermuda compared to the rest of their ranges among all the species, but we did not. Since the other environmental factors that the species are responding to should also be similar, then it seems we are looking at something intrinsic to the species – growth form, distribution of biomass, reproductive patterns, life history differences, etc – and how those intrinsic features interact with seasonality in light to determine ECD. Those other species usually have both lower light requirements and faster rates of growth (Gallegos et al., 1994), as well as a smaller proportion of their biomass in below-ground, non-photosynthetic tissues. Further, *H. decipiens* is unique among the four seagrass species occurring in Bermuda because it is an annual, with high rates of seed set and seeds that can lay dormant in the sediments in winter until conditions are right for germination and growth during the Bermuda summer (Kenworthy, 2000; Hammerstrom et al., 2006; Fonseca et al., 2008; Bell et al., 2008); there is no non-photosynthetic tissue to support through the low-light winters.

Generalizing from these observations, we suggest that long-lived tropical autotrophs such as *T. testudinum* may expand their ranges poleward as seas warm, but these species will be restricted to shallower depths in the more poleward parts of their new ranges because of low light levels in the winter. This will be compounded by the potential for increased respiration rates associated with increased temperatures. Smaller species with more opportunistic life history characteristics and lower biomass respiratory demands, like *Halodule* sp., *S. filiforme* and *H. decipiens*, may be able to occupy consistent depths as they expand poleward. If this hypothesis is true, then it would lead to the prediction that one of the consequences of global warming for tropical seagrasses may be a shift in the dominance of species at intermediate and deeper depths at latitudes poleward of their current ranges. Species with lower light requirements and different growth strategies than *T. testudinum* may gain a distinct competitive advantage at more northern latitudes. The overall structure and function of seagrass communities formed by successful expansion into temperate habitats could be very different from the tropical communities that now exist.

## 5. Conclusions

The grid and random site-based protocol used in our studies allowed the first platform-wide compilation of abundance and condition of all benthic communities in Bermuda; in particular the deeper-growing seagrasses (especially *H. decipiens*) and the distribution of calcareous green macroalgae were fully documented for the first time. More broadly, this study provides significant comparative data to similar benthic communities in more tropical locations. Our results show that one of four tropical seagrasses found in Bermuda, *T. testudinum*, has a notably higher light

requirement than has been found in more tropical locations. We suggest this may be related to seasonality of insolation in Bermuda and therefore propose that any poleward range extensions of tropical seagrass communities may be accompanied by significant differences in community structure and depth distribution compared to tropical locations. Our light and depth limit data also indicate that for habitat to remain available to *T. testudinum* at higher latitudes, including in Bermuda, very high water clarity is required, much higher than tropical studies have indicated. Thus, in situ studies of tropical species at their poleward limits are potential sources of data that are relevant to predictions about distributional range changes related to global warming.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.marenvres.2013.05.003>.

## References

- Ballantine, D.L., Appeldoorn, R.S., Yoshioka, P., Weil, E., Armstrong, R., Garcia, J.R., Otero, E., Pagan, F., Sherman, C., Hernandez-Delgado, E.A., Bruckner, A., Lileystrom, C., 2008. Biology and ecology of Puerto Rican coral reefs. In: Riegl, B.H., Dodge, R.E. (Eds.), *Coral Reefs of the World*, vol. 1. Coral Reefs of the USA. Springer, U.S.A., pp. 375–406.
- Beers, J.R., Herman, S.S., 1969. The ecology of inshore plankton populations in Bermuda. Part one – seasonal variations in hydrography and nutrient chemistry. *Bulletin of Marine Science* 19, 253–278.
- Bell, S.S., Fonseca, M.S., Kenworthy, W.J., 2008. Dynamics of a subtropical seagrass landscape: links between disturbance and mobile seed banks. *Landscape Ecology* 23, 67–74.
- Biber, P., Gallegos, C., Kenworthy, W.J., 2008. Calibration of a bio-optical model in the North River, North Carolina (Albemarle-Pamlico Sound): a tool to evaluate water quality impact on seagrasses. *Estuaries and Coasts* 31, 177–191.
- Buesa, R.J., 1974. Population and biological data on turtle grass (*Thalassia testudinum* König, 1805) on the northwestern Cuban shelf. *Aquaculture* 4, 207–226.
- Cairns, S., den Hartog, C., Arneson, C., Rützler, K., 1986. Class Anthozoa (corals, anemones). In: Sterrer, W. (Ed.), *Marine Fauna and Flora of Bermuda: a Systematic Guide to the Identification of Marine Organisms*. Wiley, New York, U.S.A., pp. 159–194.
- Cavaliere, A.R., Sterrer, W., 1998. Bermuda's Seashore Plants and Seaweeds. Bermuda Zoological Society, Bermuda, p. 269.
- Clarke, J.P., 1997. North Atlantic Ocean: Bermuda. In: Admiralty Chart 334. Hydrographic Office, Admiralty Charts and Publications, Taunton, U.K.
- Czerny, A.B., Dunton, K.H., 1995. The effects of in situ light reduction on the growth of two subtropical seagrasses *Thalassia testudinum* and *Halodule wrightii*. *Estuaries* 18, 418–427.
- Darnell, W.L., Staylor, W.F., Rithcey, N.A., Gupta, S.K., Wilber, A.C., 1996. Surface Radiation Budget: A Long-term Global Dataset of Shortwave and Longwave Fluxes. American Geophysical Union. [http://www.agu.org/eos\\_elec/95206e.html](http://www.agu.org/eos_elec/95206e.html).
- den Hartog, C., Kuo, J., 2006. Taxonomy and biogeography of seagrasses. In: Larkum, A.W.D., Orth, R.J., Duarte, C. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Springer, Dordrecht, pp. 1–23.
- Duarte, C.M., 1991a. Seagrass depth limits. *Aquatic Botany* 40, 363–377.
- Duarte, C.M., 1991b. Allometric scaling of seagrass form and productivity. *Marine Ecology Progress Series* 77, 289–300.
- Duarte, C.M., Marba, N., Krause-Jensen, D., Sanchez-Camacho, M., 2007. Testing the predictive power of seagrass depth limit models. *Estuaries and Coasts* 30, 652–656.
- Dillon, M.E., Wang, G., Huey, R.B., 2010. Global metabolic impacts of recent climate warming. *Nature* 467, 704–707.
- Dixon, L.K., 2000. Establishing light requirements for the seagrass *Thalassia testudinum*: an example from Tampa Bay, Florida. In: Bortone, S.A. (Ed.), *Seagrasses: Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton, U.S.A., pp. 9–32.
- Dunton, K.H., 1994. Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. *Marine Biology* 120, 479–489.
- Fonseca, M.S., Kenworthy, W.J., Griffith, E., Hall, M.O., Finkbeiner, M., Bell, S.S., 2008. Factors influencing landscape pattern of the seagrass *Halophila decipiens* in an oceanic setting. *Estuarine Coastal and Shelf Science* 76, 163–174.
- Fourqurean, J.W., Zieman, J., 1991. Photosynthesis, respiration and whole plant carbon budget of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 69, 161–170.
- Fourqurean, J.W., Willis, A.W., Rose, C.D., Rutten, L.M., 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology* 138, 341–354.
- Fourqurean, J.W., Boyer, J.N., Durako, M.J., Hefty, L.N., Pederson, B.J., 2003. Forecasting responses of seagrass distributions to changing water quality using monitoring data. *Ecological Application* 13, 474–489.
- Fourqurean, J.W., Manuel, S., Coates, K.A., Kenworthy, W.J., Smith, S.R., 2010. Effects of excluding sea turtle herbivores from a seagrass bed: overgrazing may have led to loss of seagrass meadows in Bermuda. *Marine Ecology Progress Series* 419, 223–232.
- Fricke, H., Meischner, D., 1985. Depth limits of Bermuda scleratinian corals: a submersible survey. *Marine Biology* 88, 175–187.
- Gallegos, C.L., Kenworthy, W.J., 1996. Seagrass depth limits in the Indian River Lagoon (Florida, USA): application of an optical water quality model. *Estuarine Coastal and Shelf Science* 42, 267–288.
- Gallegos, M.E., Merina, M., Rodriguez, A., Marba, N., Duarte, C.M., 1994. Growth patterns and demography of pioneer Caribbean seagrasses *Halodule wrightii* and *Syringodium filiforme*. *Marine Ecology Progress Series* 109, 99–104.
- Green, E.P., Short, F.T., 2003. *World Atlas of Seagrasses*. University of California Press, Berkeley, California, U.S.A., p. 298.
- Hammerstrom, K.K., Kenworthy, W.J., Fonseca, M.S., Whitfield, P.E., 2006. Seed bank, biomass and productivity of *Halophila decipiens*, a deep water seagrass on the west Florida continental shelf. *Aquatic Botany* 84, 110–120.
- Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9, 228–241.
- Hine, A.C., Halley, R.B., Locker, S.D., Jarrett, B.D., Jaap, W.C., Mallinson, D.J., Ciembronowicz, K.T., Ogden, N.B., Donahue, B.T., Naar, D.F., 2008. Coral reefs, present and past, on the West Florida Shelf and platform margin. In: Riegl, B.H., Dodge, R.E. (Eds.), *Coral Reefs of the World*, vol. 1. Coral Reefs of the U.S.A., Springer, U.S.A., pp. 127–173.
- Hiscock, K., Baker, G., Crump, A., Jefferson, R., 2005. Marine Life Topic Note. Climate Change and Marine Life Around Britain and Ireland. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme [on-line]. Marine Biological Association of the United Kingdom, Plymouth. <http://www.marlin.ac.uk>.
- Iverson, R.L., Bittaker, H.F., 1986. Seagrass distribution and abundance in eastern Gulf of Mexico coastal waters. *Estuarine Coastal Shelf Science* 22, 577–602.
- Jaap, W.C., Szmant, A., Jaap, K., Dupont, J., Clarke, R., Somerfield, P., Ault, J.A., Bohnsack, J.A., Kellison, S.G., Kellison, G.T., 2008. A perspective on the biology of Florida Keys coral reefs. In: Riegl, B.H., Dodge, R.E. (Eds.), *Coral Reefs of the World*, vol. 1. Coral Reefs of the U.S.A., Springer, U.S.A., pp. 75–125.
- Johansson, J.O.R., Greening, H.S., 2003. Seagrass restoration in Tampa Bay: a resource-based approach to estuarine management. In: Bortone, S.A. (Ed.), *Seagrasses: Monitoring, Ecology, Physiology and Management*. CRC Press, Boca Raton, U.S.A., pp. 279–293.
- Jones, R.J., 2009. Environmental Effects of Sediment Re-suspension by Cruise Ships in Bermuda. BIOS Technical Report FEB 2009 to the Bermuda Ministry of Environment and Sport. Bermuda Aquarium, Museum, and Zoo Pub #2271, p. 44.
- Kenworthy, W.J., 2000. The role of sexual reproduction in maintaining populations of *Halophila decipiens*: implications for the biodiversity and conservation of tropical seagrass ecosystems. *Pacific Conservation Biology* 5, 251–259.
- Kenworthy, W.J., Haunert, D.E., 1991. The light requirements of seagrasses. In: Proceedings of a Workshop to Examine the Capabilities of Water Quality Criteria, Standards, and Monitoring Programs to Protect Seagrasses. National Oceanic and Atmospheric Administration. Technical Memorandum NMFS-SEFC-287.
- Kenworthy, W.J., Fonseca, M.S., 1996. Light requirements of seagrasses *Halodule wrightii* and *Syringodium filiforme* derived from the relationship between diffuse light attenuation and maximum depth distribution. *Estuaries* 19, 740–750.
- Kenworthy, W.J., Currin, C.A., Fonseca, M.S., Smith, G., 1989. Production, decomposition, and heterotrophic utilization of the seagrass, *Halophila decipiens* in a submarine canyon. *Marine Ecology Progress Series* 51, 277–290.
- Ling, S.D., Jonson, C.R., Ridgway, K., Hobday, A.J., Haddon, M., 2009. Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Global Change Biology* 15, 719–731.
- Logan, A., Murdoch, T.J.T., 2011. Bermuda. In: Hopley, D. (Ed.), *Encyclopedia of Modern Coral Reefs*. Encyclopedia of Earth Sciences Series, Part 2. Springer, Dordrecht, pp. 118–123.
- Manuel, E.A., 1986. Phylum Anthophyta (=Angiospermae) (flowering plants). In: Sterrer, W. (Ed.), *Marine Fauna and Flora of Bermuda: A Systematic Guide to the Identification of Marine Organisms*. Wiley, New York, U.S.A., pp. 79–91.

- Marine Environmental Program, 2006. Annual Report: 2005–2006. Annual report submitted by the Bermuda Institute of Ocean Sciences to the Bermuda Department of Environmental Protection, Ministry of Environment and Sport. Bermuda Aquarium, Museum, and Zoo Pub #2282, p. 128.
- Marine Environmental Program, 2007. Annual Report: 2006–2007. Annual report submitted by the Bermuda Institute of Ocean Sciences to the Bermuda Department of Environmental Protection, Ministry of Environment and Sport. Bermuda Aquarium, Museum, and Zoo Pub #2230, p. 128.
- McGlathery, K.J., 1995. Nutrient and grazing influences on a subtropical seagrass community. *Marine Ecology Progress Series* 122, 239–252.
- McGlathery, K.J., Howarth, R.W., Marino, R., 1992. Nutrient limitation of macroalga, *Penicillus capitatus*, associated with subtropical meadows in Bermuda. *Estuaries* 15, 18–25.
- Morris, B., Barnes, J., Brown, F., Markham, J., 1977. The Bermuda Environment. In: Special Publication 15. Bermuda Biological Station for Research, Bermuda, p. 120.
- Murdoch, T.J.T., Glasspool, A.F., Outerbridge, M., Ward, J., Manuel, S., Nash, A., Coates, K.A., Pitt, J., Fourqurean, J.W., Barnes, P.A.G., Vierros, M., Holzer, K., Smith, S.R., 2007. Large-scale decline in offshore seagrass meadows in Bermuda. *Marine Ecology Progress Series* 339, 123–130.
- N.A.S.A., 2010. Surface Meteorology and Solar Energy. A Renewable Energy Resource Website (Release 6.0). Stackhouse, P.W. Jr., Whitlock, C.H., Kusterer, J.M. (Administrators). <http://eosweb.larc.nasa.gov/sse/>.
- Occhipinti-Ambrogi, A., 2007. Global change and marine communities: alien species and climate change. *Marine Pollution Bulletin* 55, 342–352.
- Onuf, C.P., 1991. Light requirements of *Halodule wrightii*, *Syringodium filiforme*, and *Halophila engelmannii* in a heterogeneous and variable environment inferred from long-term monitoring. In: Kenworthy, W.J., Haunert, D. (Eds.), *The Light Requirements of Seagrasses: Proceedings of a Workshop to Examine the Capability of Water Quality Criteria, Standards, and Monitoring Programs to Protect Seagrasses*. N.O.A.A. Technical Memorandum, NMFS-SEFC-287.
- Onuf, C.P., 1994. Seagrasses, dredging and light in Laguna Madre, Texas, U.S.A. *Estuarine and Coastal Shelf Science* 39, 75–91.
- Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. *BioScience* 56, 987–996.
- Smith, S.R., 1998. Bermuda. In: Kjerfve, B. (Ed.), *UNESCO 1998 CARICOMP – Caribbean Coral Reef, Seagrass and Mangrove Sites. Coastal Region and Small Island Papers 3*. UNESCO, Paris, pp. 247–257.
- Short, F.T., Neckles, H.A., 1999. Effects of global climate change on seagrasses. *Aquatic Botany* 63, 169–196.
- South, G.R., 1983. A note on two communities of seagrasses and rhizophytic algae in Bermuda. *Botanica Marina* 26, 243–248.
- Sterrer, W. (Ed.), 1986. *Marine Fauna and Flora of Bermuda: a Systematic Guide to the Identification of Marine Organisms*. John Wiley and Sons, New York, p. 742.
- Thomas, M.L.H., Logan, A., 1992. *A Guide to the Ecology of Shoreline and Shallow-water Marine Communities of Bermuda*. Wm. C. Brown, Dubuque, p. 346.
- Tomasko, D.A., Bristol, D.L., Ott, J.A., 2001. Assessment of present and future nitrogen loads, water quality, and seagrass (*Thalassia testudinum*) depth distribution in Lemon Bay, Florida. *Estuaries* 24, 926–938.
- Waycott, M., Procaccini, G., Les, D.H., Reusch, T.B.H., 2006. Seagrass evolution, ecology and conservation: a genetic perspective. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Springer, Dordrecht, pp. 25–50.
- Wefer, G., 1980. Carbonate production by algae *Halimeda*, *Penicillus* and *Padina*. *Nature* 285, 323–324.
- Wiginton, J.R., McMillan, C., 1979. Chlorophyll composition under controlled light conditions as related to the distribution of seagrasses in Texas and the U.S. Virgin Islands. *Aquatic Botany* 6, 171–184.
- Williams, S.L., 1990. Experimental studies of Caribbean seagrass bed development. *Ecological Monographs* 60, 449–469.