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Spatio-temporal patterns and nutrient status of macroalgae in a heavily managed region of Biscayne Bay, Florida, USA

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Abstract

The coastal bays of South Florida are located downstream of the Florida Everglades, where a comprehensive restoration plan will strongly impact the hydrology of the region. Submerged aquatic vegetation communities are common components of benthic habitats of Biscayne Bay, and will be directly affected by changes in water quality. This study explores community structure, spatio-temporal dynamics, and tissue nutrient content of macroalgae to detect and describe relationships with water quality. The macroalgal community responded to strong variability in salinity; three distinctive macroalgal assemblages were correlated with salinity as follows: (1) low-salinity, dominated by *Chara hornemannii* and a mix of filamentous algae; (2) brackish, dominated by *Penicillus capitatus*, *Batophora oerstedii*, and *Acetabularia schenckii*; and (3) marine, dominated by *Halimeda incrassata* and *Anadyomene stellata*. Tissue-nutrient content was variable in space and time but tissues at all sites had high nitrogen and N:P values, demonstrating high nitrogen availability and phosphorus limitation in this region. This study clearly shows that distinct macroalgal assemblages are related to specific water quality conditions, and that macroalgal assemblages can be used as community-level indicators within an adaptive management framework to evaluate performance and restoration impacts in Biscayne Bay and other regions where both freshwater and nutrient inputs are modified by water management decisions.

Keywords: Biscayne Bay; community-level indicators; macroalgae; nutrient content.

Introduction

The coastal ecosystems of the world have experienced intense modifications in recent decades under the influence of a combination of natural and human disturbances (Orth et al. 2006, Bruno et al. 2009). High on the list of stressors that have contributed to the degraded status of coastal communities are those directly related to coastal and watershed development (Lapointe et al. 2004, 2007, Orth et al. 2006, Kleypas and Eakin 2007, Halpern 2008, Duarte et al. 2009). For example, Waycott et al. (2009) reported a global loss of 110 km^2 year^{-1} of seagrass habitat since 1980. South Florida is a peninsula with a complex hydrological configuration that includes the Florida Everglades, which receive upland effluents rich in agricultural wastes that eventually flow into Biscayne Bay, Florida Bay, and the Florida Reef Tract (Brand 2002, Lapointe et al. 2004). Coastal lagoons are also localized adjacent to large metropolitan centers (e.g., Miami, Key West, Key Largo), and thus highly susceptible to the impacts caused by over five million people living within a narrow coastal band (Meeder and Boyer 2001, Lapointe and Barile 2004, Carnahan et al. 2008, 2009).

To accommodate the water needs of a rapidly increasing population and to provide for flood control, the natural drainage of the Florida Everglades has been dramatically modified over the past 60 years by a water management system comprised of levees, canals, control structures, and pumping stations that have prevented flooding and increased the amount of arable and residential land in the Everglades (Light and Dineen 1994). As a result of these modifications, the timing, quantity, and quality of freshwater flows across the watershed into the coastal bays have been significantly modified (Brewster-Wingard and Ishman 1999, Fourqurean and Robblee 1999, Brand 2002, CERP 2005). Some of the unintended negative ecological consequences of these modifications include the mass mortality of seagrasses in Florida Bay (Robblee et al. 1991, Zieman et al. 1999, Lapointe and Barile 2004), sponge die-offs (Butler et al. 1995), and declines in pink shrimp catches (Browder et al. 1999). In response to this ecological degradation, the largest ecosystem restoration and water management program in the world, the Comprehensive Everglades Restoration Plan (CERP), was established to recapture and redistribute freshwater and restore the natural hydroperiod by increasing freshwater flows into coastal lagoons (CERP 2005). While the objective of this plan for coastal bays is clear (i.e., a return to a more natural drainage system), the effects of these projects on the abundance, diversity, and distribution of benthic organisms in littoral environments are largely unknown. Alterations to beds of seagrasses and associated macroalgae, which are key components of the coastal systems, are expected to occur as
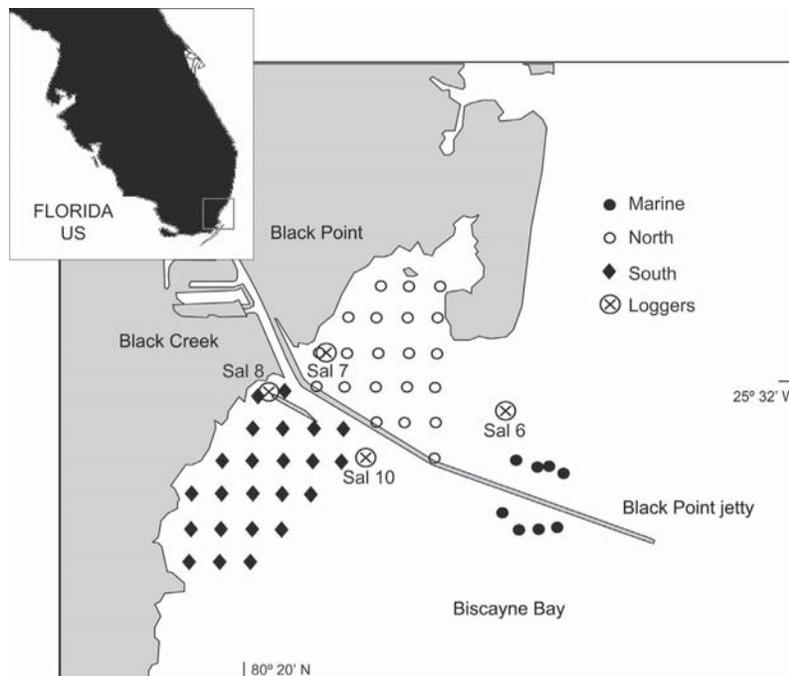
Figure 1 Map of the Black Point region of Biscayne Bay, Florida, USA, with the locations of points used for macroalgal surveys and the locations of the salinity and temperature loggers.
Data from the probes appear in Figure 2.

higher volumes of freshwater richer in nutrients will flow from the Everglades into Biscayne Bay (Lapointe et al. 1994, 2002).

The value of macroalgae as bioindicators within coastal ecosystems has been well established. Macroalgae have been widely used as indicators of pollution gradients and to document the ecological status of habitats (Fong et al. 2001, Orfanidis et al. 2001, 2003, Panayotidis et al. 2004, EPA 2008, Juanes et al. 2008, Lin and Fong 2008). In the present study, it was postulated that the spatial and temporal patterns of the structural attributes of macroalgal assemblages, and their nutrient tissue content, can be used to provide dynamic metrics to assess restoration success and serve as early-warning indicators of unexpected or undesired conditions within an adaptive management framework (Duarte et al. 2009).

Both nutrient availability and salinity patterns are known to influence macroalgal growth (Fong et al. 1994, Kamer and Fong 2000, Cohen and Fong 2004, Kamer et al. 2004, Neill 2005, Chung et al. 2007), and eutrophication has been considered as a causal factor in shifting the structure and composition of submerged aquatic vegetation (SAV) in Florida Bay and the Florida Reef Tract (Lapointe 1987, Lapointe et al. 1994, Lapointe and Barile 2004, Lapointe and Bedford 2010). Thus, under a scenario in which salinity and nutrient patterns may be impacted by water management practices, it is important to examine the combined effect of these two key variables on macroalgal abundance, distribution, and diversity. This was accomplished in this study by examining present-day patterns of algal community structure in a focal area of Biscayne Bay, Black Point, where distinct salinity and nutrient availability patterns are detectable at relatively

small spatial scales (<1 km). Specific goals of this study included: (1) evaluating seasonal and spatial patterns of macroalgal community composition and abundance; (2) exploring relationships between macroalgae and water quality parameters; and (3) measuring tissue-nutrient content patterns. The information collected can be used as an initial predictor of how and which macroalgal assemblages have the potential to expand within Biscayne Bay if freshwater patterns were modified as a result of the CERP planned practices. Similarly, this information can be used as a case study to compare with other regions within Florida and elsewhere faced with similar environmental patterns and management issues.

Materials and methods

Study area

Biscayne Bay is a coastal lagoon adjacent to the city of Miami, Florida, USA (Figure 1). The bay is affected by freshwater inputs from different sources, i.e., canals, precipitation, overland, and groundwater, each with different levels and types of nutrients (Caccia and Boyer 2007, Stalker et al. 2009). The western coastline of Biscayne Bay was selected because it is strongly influenced by the inflow of freshwater from artificial canal structures that control the spatial and temporal patterns of freshwater releases into nearshore habitats. The focal region of this study was the Black Point area (25°31.5′ N, 80°17.9′ W). One of the main canals that transports freshwater from the Florida Everglades into Biscayne

Bay is Black Creek, located in the center of the study domain (Figure 1). The pulsed discharge of freshwater from this canal creates a very dynamic environment in which salinity can be very variable; there are low-salinity events during which oceanic salinity can drop to near freshwater values within a few hours and remain low for several days. This area is also influenced by the presence of a rock jetty that extends 2.4 km into the bay, creating a physical barrier for the freshwater released from Black Creek (Figure 1). In addition, Black Point is especially susceptible to nutrient enrichment because of its close proximity to the Dade County landfill (Meeder and Boyer 2001, Caccia and Boyer 2005, 2007, Carey et al. 2011). Previous surveys in this area showed that distinct seagrass communities exist north and south of the Black Point jetty, with *Thalassia testudinum* Banks *et* Sol. ex KD Koenig dominating the northern area and *Halodule wrightii* Asch. dominating the southern area (Meeder and Boyer 2001, Lirman et al. 2008a,b).

Field surveys

Surveys of nearshore habitats of Black Point were conducted bimonthly from March 2008 to February 2009. Sampling was conducted at sites within a nearshore spatial grid divided into north and south areas. A total of 42 sites (21 sites on either side of the jetty) was sampled. In addition, eight sites were established at the end of the jetty (four north, four south) in areas with more marine conditions (further away from the inflow of freshwater) to provide a comparison with the more brackish nearshore sites (Figure 1).

Salinity, temperature, and dissolved oxygen (DO) at the bottom of the water column were measured with a YSI probe (Yellow Springs, OH, USA) at each site. Light (PAR) levels were measured at the surface and at the bottom with a LI-COR spherical sensor (Lincoln, NE, USA). To capture the dynamic characteristics of salinity and temperature, data loggers (Odyssey Corp. Burnise, Christchurch, New Zealand) were deployed at four locations along the inshore-offshore and north-south gradients of the study area. These loggers recorded salinity and temperature at the bottom at hourly intervals.

At each site, macroalgal specimens of both drift and anchored-rhizophytic macroalgae were collected. The samples were identified to the species level, and the presence/absence and frequency of observation of each taxon were recorded for each survey interval. Species were identified following taxonomic keys of Littler and Littler (2000), and Dawes and Mathieson (2008). The abundance (i.e., percent cover) of macroalgae was measured by photographing the bottom at each site using the Shallow Water Positioning System (SWaPS: http://yyy.rsmas.miami.edu/groups/SWaPS/). Ten images of the bottom were captured at each site and percent cover was estimated as the proportion of the bottom covered by each taxon, as described in detail in Lirman et al. (2008a,b). Abundance was estimated for dominant species easily distinguished from the images or growth form groups (i.e., red masses).

Nutrient content analysis

The *Laurencia-Palisada-Polysiphonia* complex forming red masses, and anchored *Chara hornemanii* were selected for nutrient analysis; the red mass complex was chosen because of its widespread distribution and *C. hornemanii* was chosen owing to its presence close to shore. Both taxa were strongly persistent throughout this study. Additional, less abundant species were also sampled to evaluate variability in tissue-nutrient content among species. Algal material collected from each site was kept in separate bags in ice and transported to the laboratory at Florida International University. Each sample was then cleaned, dried for 48 h at 6°C, then separate samples were ground and stored in individual vials for individual processing. In total, 105 samples (55 north, 38 south, and 12 marine) for CN, and 54 (25 north, 22 south, and 7 marine) for P were analyzed. Differences in the number of samples for P were due to small amount of sample or technical problems with some of them. The samples were analyzed for carbon and nitrogen content using a CHN analyzer (Fisons NA1500; Fisons Instruments, Milan, Italy). A dry-oxidation-acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration was used to determine phosphorus content (Fourqurean et al. 1992). Elemental content was calculated based on dry weight and elemental ratios were calculated on a mole:mole basis.

Statistical analyses

Principal component analyses (PCA) was conducted on the environmental data to detect parameters accounting for most of the variability, reducing the number of variables to those that were most explanatory. Box-and-whisker plots of salinity and temperature were used to represent the magnitude of spatial variability between north and south sites. Seasonal changes in salinity were explored, and the data from months with the lowest (wet season) and highest (dry season) mean salinities were used in subsequent analyses to compare macroalgal community structures during these two extreme seasons. The spatial patterns of salinity were analyzed for the dry and wet seasons by construction of Euclidian non-transformed similarity matrices and hierarchical clustering analyses to group sites; salinity maps were constructed using the results of the cluster analyses. An analysis of variance (ANOVA) was performed on the salinity data using the grouping resulting from the cluster analysis as factor to determine whether differences among groups were statistically significant. Data were tested for homogeneity of variance using Levene's test. When homogeneity assumptions were not met, a non-parametric Kruskal-Wallis test was conducted instead.

The species presence-absence data were used to compute species richness and diversity (J and H′) metrics. A PCA was performed using the presence data for the entire study period to detect species accounting for most of the variability, thus reducing the large number of variables to those that were most explanatory. Only the most common species with the highest PCA scores and highest frequencies were used
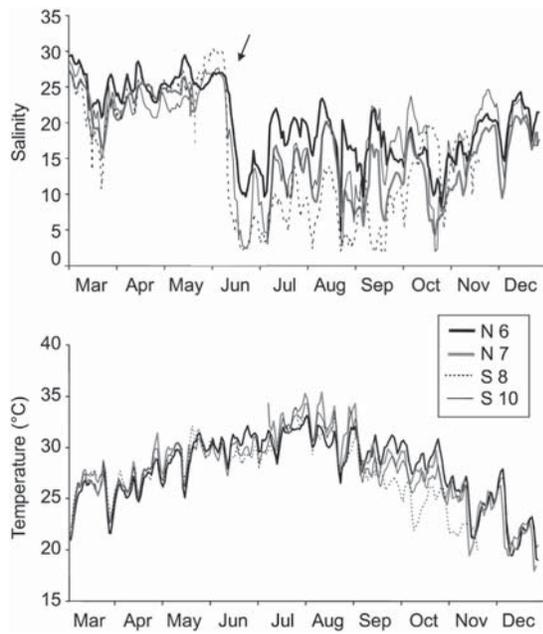
Figure 2 Salinity and temperature patterns in the Black Point area of Biscayne Bay, USA in 2008. Probes were deployed to the south (S) and north (N) of the Black Point Jetty (Figure 1) and recorded data at hourly intervals.
Probe locations appear in Figure 1. The arrow in Figure 2 indicates the timing of the first large freshwater release from Black Creek in the 2008 wet season.

for spatio-temporal analyses and for evaluating correlations with environmental factors.

Spatial patterns of macroalgal taxon distribution were analyzed using Bray-Curtis non-transformed similarity matrices and hierarchical clustering analysis using mean frequency of observation data for the most important species for the dry and wet seasons. All species similarity clusters were represented by single-linkage dendrograms, and a similarity of 75% or more was used to form groups whose statistical significance was tested by ANOSIM (Primer-E Ltd, V5 Software, Plymouth, UK). The clusters were then examined with

SIMPER to determine which species were the primary contributors to the similarity within groups. The same analysis was performed on data that included marine sites (October and December 2008, and February 2009) to find characteristic species associations.

A logistic regression analysis using species presence data (all sampling intervals) was conducted to evaluate the relationship between the physical or biological predictor variables and the probability of occurrence of frequent macroalgal taxa. A non-parametric correlation analysis (Kendall's Tau-b) was performed between the abundance (i.e., percent cover) of macroalgal categories and the key environmental variables (i.e., salinity, temperature, seagrass abundance). All multivariate analyses were performed using Primer-E V5 Software, and all univariate statistical tests were performed using SPSS V13 software (IBM Somers, NY, USA).

Results

Physical data

The shallow nearshore habitats of Biscayne Bay experienced drastic fluctuations in both temperature and salinity (Figure 2). Freshwater releases from Black Creek during the wet season caused sudden drops in salinity, and low-salinity conditions persisted for most of the summer. While both the north and south areas were influenced by pulsed releases, the south area experienced lower salinities that persisted longer (especially near the point of discharge, as shown by probe S8; Figure 2 upper panel) than in the north section. The canal empties directly to the south of the jetty, creating a physical barrier for the freshwater. Temperature fluctuations in the shallow habitats were also common and shifts of up to 6°C over a period of a few days were recorded (Figure 2 lower panel). A higher variability in both salinity and temperature occurred in the south section of the jetty compared to the north section (Figure 3).

When the physical data for each site were evaluated, the first two principal components of the PCA explained 70%
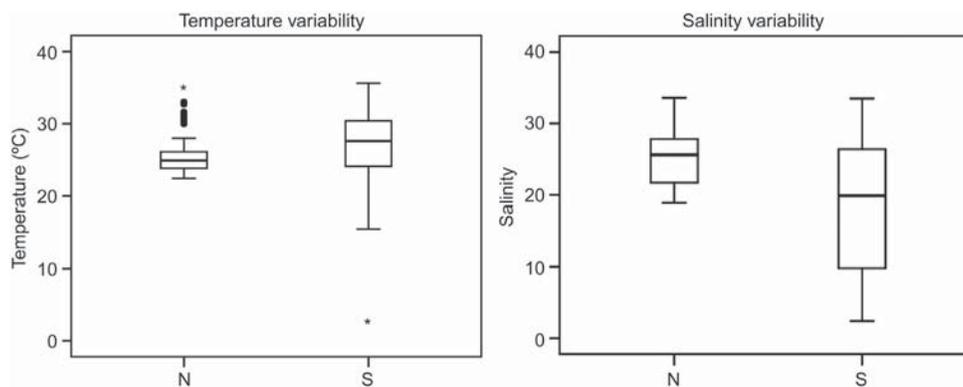

Figure 3 Box-and-whisker plots showing temperature and salinity from all 43 sites in the north and south regions of the Black Point jetty. The horizontal bar within the box represents the median, the upper and lower boundaries of the box represent the lower and upper quartile, and the whiskers represent the extreme values; circles are the outliers and asterisk the maximum extreme case.
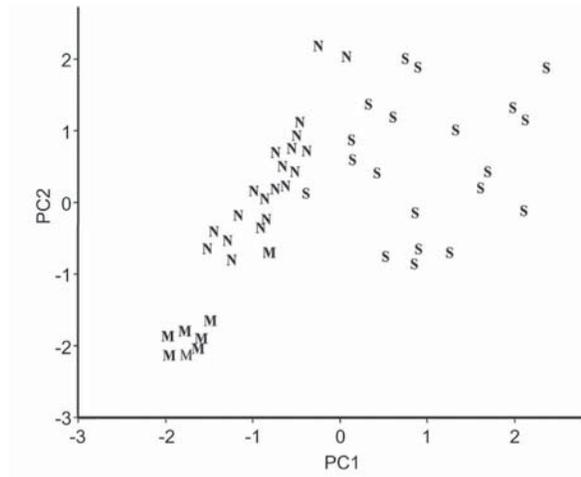
Figure 4 Principal component analyses of physical data collected at each site in the Black Point area of Biscayne Bay.
The first two principal components explained 70% of the variance. Sites labeled N are from the region north of the jetty, sites labeled S are from the region south of the jetty, sites labeled M (marine) are from the seaward end of the jetty. Each letter represents one site and one survey interval.

of the data variance. The largest loadings along PC1 were for salinity (-0.66) and DO (0.53). The variables with the largest loadings along PC2 were temperature (0.58) and DO (-0.53). Based on the physical data, sites formed mostly distinct groupings as follows (Figure 4): (1) sites south of the jetty; (2) sites to the north of the jetty; and (3) the marine sites towards the end of the jetty. Moreover, the Bray-Curtis ordination of sites based on physical parameters revealed sig-

nificant site groupings as a function of distance to shore during dry and wet seasons (ANOVA df 4, F 164.4, p<0.001) (Figure 5A), and as a function of distance to shore and section of the jetty (i.e., north, south) during the wet season (ANOVA df 3, F 1245.12, p<0.001) (Figure 5B).

The marine flora of Black Point

A total of 31 macroalgal species was identified in the Black Point area, including 12 chlorophytes, 17 rhodophytes, and two ochrophytes. Four different growth forms (carpet, film, sponge, and puff) composed of Cyanobacteria and diatoms were also found and named based on their appearance (Table 1). Out of the 31 species, seven were highly frequent and thus characterized as dominant species; two species were observed only at the marine sites (Table 1). While all 31 species were found in the south sites, only 29 were observed north of the jetty. Only a slightly higher richness (J′ index) and diversity (H′ index) were measured in the macroalgal community in the south (J′ 0.81, H′ 2.84) compared to the north (J′ 0.79, H′ 2.63).

Macroalgal growth forms included drift masses and mats, rhizophytic (attached) algae, and epiphytes here labeled as ''puff''. Drift masses of red macroalgae were composed of species in the genera *Laurencia-Palisada*, *Chondria*, *Digenea*, or *Wrightellia*. Drift red mats were commonly made up of species in the genus *Polysiphonia*, and less frequently by species of *Spyridia* or *Dasya*. Drift green mats were composed of species from the order Cladophorales, including genera such as *Cladophora*, *Cladophoropsis*, and *Chaetomorpha*. Puff was a mix of epiphytes large enough to look like a mass but still attached to the seagrass leaves; puffs included Cyanobacteria, green filamentous algae, and diatoms.
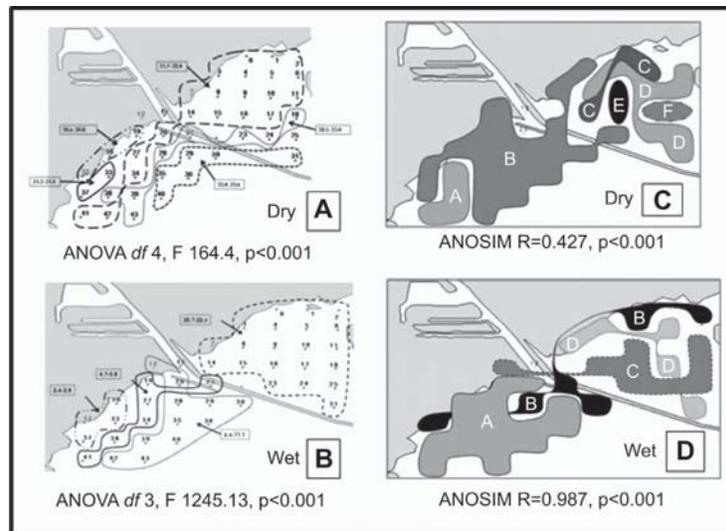
Figure 5 Groupings of sites based on patterns of similar salinities in the dry season (A) and the wet season (B).
Grouping of sites based on species frequency similarity in dry (C) and wet season (D). Species groups are represented by letters A–F in panels C and D; for specific species associations refer to text. In all four panels, the groups delimited by dashed or solid lines were identified by Bray-Curtis ordination followed by a cluster analysis. ANOVA was performed on the salinity data to determine whether differences among groups were statistically significant. ANOSIM was performed on species data to determine whether species groups with 75% or more similarity were statistically significantly different.

Table 1   Species list by phylum.

Code	Species	Authority	North	South	Marine	Dry	Wet
	Chlorophyta						
1	***Acetabularia schenckii***	K. Mobius	X	X	X	X	X
2	*Anadyomene stellata*	C. Agardh			X	X	X
3	***Batophora oerstedii***	J. Agardh	X	X	X	X	X
4	*Boodleopsis verticillata*	E.Y. Dawson		X			X
5	*Chaetomorpha gracilis*	Kützing		X		X	X
6	*Chaetomorpha brachygona*	Harvey		X		X	
7	***Chara hornemannii***	Wallm	X	X		X	X
8	*Cladophora liniformis*	Kutzing		X		X	X
9	*Cladophoropsis membranacea*	H. Bang *ex* C. Agardh	X	X	X	X	X
10	*Halimeda incrassata*	J.V. Lamouroux			X	X	X
11	*Microdictyon marinum*	P.C. Silva	X	X	X		X
12	***Penicillus capitatus***	Lamarck	X	X	X	X	X
	Rhodophyta						
13	*Anotrichium tenue*	C. Agardh	X	X	X	X	
14	*Caloglossa leprieurii*	(Montagne) G. Martens		X			
15	*Ceramium cruciatum*	Collins *et* Hervey		X	X	X	
16	*Chondria atropurpurea*	Harvey	X	X	X		
17	*Chondria capillaris*	M.J. Wayne	X	X			
18	*Dasya baillouviana*	(S.G. Gmelin) Montagne	X	X			
19	*Digenea simplex*	(Wulfen) C. Agardh	X	X	X	X	X
20	*Jania pumila*	J.V. Lamouroux	X	X	X		
21	***Laurencia intricata***	J.V. Lamouroux	X	X	X	X	X
22	*Palisada gemmifera*	Harvey	X	X	X		
23	***Palisada poiteaui (Laurencia)***	J.V. Lamouroux	X	X	X	X	X
24	***Polysiphonia echinata***	Harvey	X	X	X	X	X
25	*Polysiphonia subtilissima*	Montagne	X	X			
26	*Neosiphonia ferulacea*	Suhr *ex* J. Agardh	X	X			
27	*Wrightiella tumanowiczii*	(Gatty) F. Schmitz	X	X	X	X	
28	*Spyridia filamentosa* (JAN)	Harvey in W. Hooker					
29	*Spyridia hypnoides* subsp. *complanata*	(J. Agardh) M.J. Wynne	X		X		
	Ochrophyta						
30	*Sargassum fluitans*	Børgesen	X	X	X	X	X
31	*Sargassum natans*	(Linnaeus) Gaillon	X	X	X	X	X
	Cyanobacteria						
32	Green carpet		X	X	X	X	X
33	Green film		X	X			X
34	Green sponge		X	X	X		X
35	Green slime/puff		X	X	X	X	X

Data show seasonal and general distribution of each species. See Figure 1 for site locations. Bold species were dominant in the study site. JAN, Found in January only.

Spatial distribution patterns

When the species presence data for each site were evaluated, the first three principal components of the PCA explained 55% of the data variance. The variables with the largest loadings along PC1 included *Batophora* (-12.18), *Acetabularia* (-5.87), puff (-5.13), *Polysiphonia* (-4.38), and *Laurencia* (-2.81); while the variables with the largest loadings along PC2 included *Palisada* (-5.53), *Penicillus* (-5.08), and *Chara* (4.01). Hereafter, only these species are used for further analyses.

The south section was characterized by the presence of *Chara*, *Batophora*, and *Polysiphonia*. The north section was more complex, with isolated nearshore pockets of *Chara* and *Batophora*, and a central area dominated by masses of drift macroalgal species. Almost all sites surveyed in the south

region had drift masses as well as rhizophytic species. However, the north region was dominated by seagrasses and bare, muddy substratum where species of the genera *Penicillus* and *Palisada* were frequently found.

Bray-Curtis ordination of the species frequency per site followed by an ANOSIM showed significant differences in species assemblages among north and south areas of the jetty in both dry and wet season ($p < 0.001$, Figure 5C, D). SIMPER analysis applied to the above species assemblages showed characteristic species for each group; the south section was divided into two groups in the dry season: group A, dominated by *Batophora*, *Acetabularia*, and *Polysiphonia*, and group B, dominated by *Chara* and *Batophora*. In contrast, the north section was more complex, with several groups: group C, close to shore, had a mix of *Batophora*, *Penicillus*, and *Palisada*; group D, in the central area, was

dominated by red masses, mainly of *Palisada*; group E, also in the central area, was dominated by *Laurencia*; and group F was dominated by a mix of *Laurencia* and *Palisada*. Group B, the group closest to land, extended across the jetty to the north section and was characterized by the presence of *Chara* (Figure 5C). During the wet season (Figure 5D), group A, characterized by the presence of *Chara*, extended throughout the south section of the jetty, and group B, characterized by *Batophora*, extended to both sides of the jetty. The north section also had a central area dominated by red masses composed of *Palisada* (group D), and group C, characterized by both *Palisada* and *Batophora* (Figure 5D).

Seasonal patterns

Seasonal changes in species presence were apparent, with clear dry and wet season maxima for dominant species (Figure 6). *Acetabularia* (Figure 6A) and *Polysiphonia* (Figure 6B) were extremely rare during the peak of the rainy season, while *Palisada* followed a reverse trend, with a high at the peak of the wet, warmer season and lower values during the dry, cooler season. *Laurencia* and *Penicillus* had less marked cycles, with high peaks in the dry season and lower peaks during the wet season. *Chara* and *Batophora* were present throughout the year, with slight increases during the wet season (Figure 6A).

Species associations

Bray-Curtis ordination followed by a cluster analysis of frequency data for dominant species resulted in the following associations (Figure 7): the first group, completely separated from the rest (<25% similar), was formed by *Anadyomene* and *Halimeda*, both of which were found only in the marine sites, showing a clear separation between marine and estuarine macroalgal assemblage compositions. The other categories had <40% similarity, with a first split separating *Chara* from the rest. *Chara* is a taxon that occurred year-round, mostly close to land in freshwater-influenced environments. The next group to fall out at >40% similarity comprised the category puff, which is highly dependent on the presence of seagrasses for attachment. The rest of the taxa were split into two major groups with >50% similarity. The first association included *Acetabularia*, *Batophora*, and *Polysiphonia*. *Acetabularia* and *Batophora* depend on the presence of hard substratum for attachment and were present in a large range of salinities. However, *Acetabularia* had a sharp seasonal pattern while *Batophora* was present year-round. The final group was composed by *Palisada*, *Penicillus*, and *Laurencia*, three taxa more frequently found in the north section forming red drift masses.

Macroalgal cover patterns

Percent cover was estimated using growth-form categories and those genera easy to identify from the images. *Batophora* and the puff category (i.e., a mix of filamentous green algae, diatoms, and Cyanobacteria) were the most abundant at Black Point, followed by the red and green drift masses with
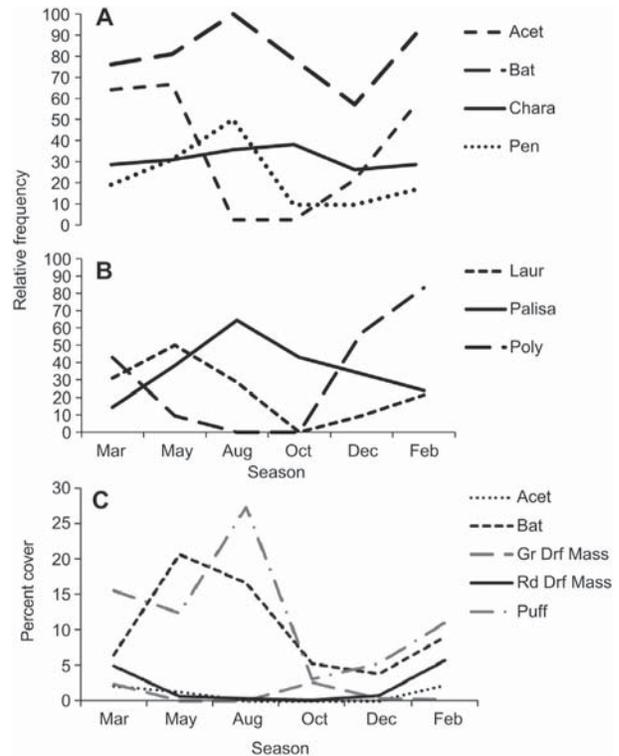

Figure 6 Seasonal relative frequency (proportion of number of sites) of (A) chlorophyte and (B) rhodophyte genera; and (C) seasonal abundance (% cover) of macroalgal genera and growth forms. Acet, *Acetabularia*; Bat, *Batophora*; Lau, *Laurencia*; Pen, *Penicillus*; Pali, *Palisada*; Poly, *Polysiphonia*; Gr Drf Mass, green drifting mass; Rd Drf Mass, red drifting mass.

lower percent cover values (Figure 6C). This general pattern differed between north and south, the north section being dominated by the puff category and the south by a mix of *Batophora* and puff. Both categories had seasonal drops dur-
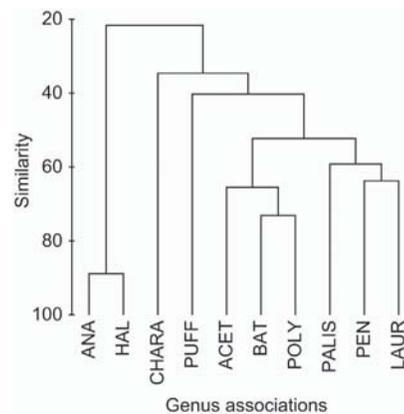

Figure 7 Cluster analysis of data in a matrix of Bray-Curtis similarities (taxon frequency data) for the time periods during which all sites (north, south, and marine) were sampled.
Clusters show genus associations. Ana, *Anadyomene*; Acet, *Acetabularia*; Bat, *Batophora*; Hal, *Halimeda*; Lau, *Laurencia*; Pen, *Penicillus*; Pali, *Palisada*; Poly, *Polysiphonia*.

Table 2 Logistic regression of presence-absence macroalgal data from the sites sampled in the Black Point area (all sampling intervals).

	Acet	*Ana*	*Bat*	*Chara*	*Hal*	*Pen*	*Lau*	*Poly*
Salinity	Neg	ns	ns	Neg	ns	Pos	ns	ns
Temperature	ns	Neg	ns	Pos	Neg	ns	ns	ns
Thalassia cover	Neg	ns	ns	Neg	ns	Pos	Pos	ns
Halodule cover	Pos	ns	ns	Pos	ns	Neg	ns	ns

Neg, Significant negative relationship between the physical or biological predictor variable and the probability of occurrence of a macroalgal taxon (p<0.05); Pos, significant positive relationship between the physical or biological predictor variable and the probability of occurrence of a macroalgal taxon (p<0.05); ns, no significant relationships documented (p>0.05). *Acet*, *Acetabularia*; *Ana*, *Anadyomene*; *Bat*, *Batophora*; *Hal*, *Halimeda*; *Pen*, *Penicillus*; *Lau*, *Laurencia*; *Poly*, *Polysiphonia*.

ing the peak of the rainy season, followed by a rapid recovery of *Batophora* and a slower one for puff.

Floristic-environment relationships

In addition to salinity and temperature, which explained a large portion of the spatial and temporal patterns observed for macroalgae in Black Point (Figure 4), seagrasses can influence macroalgal abundance and distribution by providing a physical habitat for the attachment and retention of macroalgae (especially drift mats and masses). Thus, the relationships between salinity, temperature, seagrass abundance, and the abundance and distribution of macroalgae were evaluated using both logistic regression [binary (presence-absence) data] and correlation (abundance data).

The probability of occurrence of each taxon in relationship to environmental variables was tested using logistic regression where taxa were coded within sites as either present or absent. Taxa such as *Acetabularia* and *Chara* had a higher probability of occurrence at low salinity, while *Penicillus* had a higher probability of occurrence at high salinity (Table 2). The marine genera *Anadyomene* and *Halimeda* had higher probabilities of occurrence at low temperatures. *Acetabularia* and *Chara* had lower probabilities of occurrence at higher densities of *Thalassia* and higher probabilities of occurrence at higher densities of *Halodule*. In contrast, the most marine of all estuarine species, *Penicillus*, followed a reverse trend (Table 2). Combining all factors, estuarine species such as *Acetabularia* and *Chara* had higher probabilities of occurrence at low salinities, high temperatures, low *Thalassia*, and high *Halodule* values, while marine species generally showed the reverse pattern (Table 2).

Kendall's Tau-b showed that salinity had a positive significant correlation with *Acetabularia*, red drift masses, and

Penicillus, and a negative correlation with *Halodule* (Table 3). Temperature had significant positive correlations with *Batophora*, *Penicillus*, puff, and *Halodule*, but negative correlations with red drift masses and *Thalassia*. *Thalassia* had negative correlations with *Acetabularia*, *Batophora*, drift green masses, and *Halodule*, but positive correlations with red drift masses and *Penicillus*. *Halodule* was positively correlated with *Batophora* and puff, and negatively correlated with *Penicillus* (Table 3).

Nutrient content

Nutrient content found in macroalgal tissue varied among sites, species, and seasons. Mean values for all species, seasons, and sites sampled were consistently high in percent nitrogen (%N) and low in percent phosphorus (%P); N:P values were above 30:1. High carbon to nitrogen (C:N) and very high carbon to phosphorus (C:P) ratios in the north were recorded compared with the south and marine sites (Table 4). Nutrient values, with the exception of percent carbon (%C), were significantly different among sites (Table 4), and values were higher south of the jetty compared with north and marine sites.

Species varied in their nutrient content. For example, green masses (mix of *Cladophora* and *Cladophoropsis*) and *Chara* (all green algae) had higher mean levels of both %N and %P compared with red algae. However, extreme values were still found in red masses (3.735% N and 0.204% P). All species showed very high C:P and N:P ratios, and low C:N ratios (Table 5). Red masses followed a seasonal pattern with higher values of %N in winter and lower in summer and fall; consistently, in all seasons, %N was higher in the south compared to the north (Figure 8). All nutrient values (%N, %P, C:N, C:P, and N:P) (Tables 4 and 5) demonstrate

Table 3 Correlation coefficients (Kendall's Tau-b) between macroalgal abundance (% cover) and environmental and biological variables.

	Thalassia	*Halodule*	Temperature	Salinity
Acet	-0.38	ns	ns	0.35
Bat	-0.41	0.16	0.31	ns
DGM	-0.22	ns	ns	ns
DRM	0.20	ns	-0.15	0.22
Pen	0.20	-0.17	0.16	0.21
puff	-0.37	0.15	0.23	ns

Acet, *Acetabularia*; *Bat*, *Batophora*; DGM, drifting green mass; DRM, drifting red mass; *Pen*, *Penicillus*. Only r values for significant correlations (p<0.05) are shown. ns, not significant (p>0.05).

Table 4 Average nutrient content as % of tissue dry weight.

	C (53)	N (53)	P (23)	N:P (23)	C:N (53)	C:P (23)
North						
Min/max	25.45/45.30	0.96/3.73	0.005/0.06	50.07/627.53	12.79/37.26	164/2952.62
Mean (SD)	34.51 (3.66)	1.69 (0.58)	0.016 (0.015)	377.67 (164.22)	25.37 (5.68)	1389.12 (792.24)
	C (35)	N (35)	P (14)	N:P (14)	C:N (35)	C:P (14)
South						
Min/max	25.9/37.23	1.185/2.72	0.008/0.71	61.44/464.5	13.76/34.52	152.58/491.23
Mean (SD)	33.21 (3.07)	2.015 (0.38)	0.035 (0.018)	168.94 (132.35)	20.021 (4.99)	486.22 (491.23)
	C (22)	N (22)	P (16)	N:P (16)	C:N (22)	C:P (15)
Marine						
Min/max	24.54/39.41	1.36/3.64	0.008/0.2	26.46/541.13	12.18/25.63	74.78/448.37
Mean (SD)	32.68 (4.29)	1.96 (0.48)	0.034 (0.046)	195.32 (133.51)	19.99 (3.45)	615.25 (448.36)
Kruskal-Wallis	C	N	P	N:P	C:N	C:P
χ^2	3.229	23.303	14.219	15.013	25.259	16.066
df	2	2	2	2	2	2
p	0.199	<0.01	<0.01	<0.01	<0.01	<0.01

C (n), % Carbon (no. of samples); N (n), % nitrogen (no. of samples); P, % phosphorus (no. of samples); N:P, nitrogen-phosphorus mole:mole ratio (no. of samples); C:N, carbon-nitrogen mole:mole ratio (no. of samples); C:P, carbon-phosphorus mole:mole ratio (no. of samples). Min, minimum value; Max, maximum value; SD, standard deviation. A Kruskal-Wallis test was used to compare nutrient content (% of tissue dry weight) among sites.

a strong P limitation and high N availability in this nearshore environment.

Discussion and conclusion

The macroalgal assemblage at Black Point had distinct spatial and structural patterns that were directly related to environmental gradients created by the inflow of freshwater from land and water management structures. The salinity patterns of the Black Point area were clearly dominated by the pulsed releases of freshwater through Black Creek and the presence of the jetty, which creates a physical barrier to freshwater flow out of the canal. These influences create regions of distinct physical characteristics: (1) the area south of the jetty is characterized by wide fluctuations in salinity and temperature, lower mean salinity, more persistent low-salinity periods, and higher macroalgal tissue nutrient content than the other two regions (north and marine); (2) the area north of the jetty has higher mean salinity and temperature than the south region; and (3) the area further from shore has more marine conditions, lower variability in salinity and temperature, and higher mean salinity than the other two regions. These areas, which had distinct physical patterns over a small spatial scale (<1 km), also had distinct macroalgal assemblages that paralleled the three spatial groupings (north, south, and marine). Estuarine and freshwater macroalgal species dominated nearshore environments on both sides of the jetty, but marine species (i.e., *Anadyomene*, *Halimeda*) were only found further away from shore where salinity was higher and more stable.

The highly fluctuating and often extreme character of the physical environment in Black Point is reflected in the diversity and spatial distribution of macroalgae. Species richness (31 species plus other unidentified Cyanobacteria and diatoms) in Black Point is low compared with that of other tropical coastal lagoons that commonly contain more than 70

species (Collado-Vides et al. 1995), but similar to that reported for other regions of Biscayne Bay (Biber and Irlandi 2006). The lower overall richness compared to other tropical lagoons and the dominance of only a few species may be partly linked to the extreme environmental conditions of this nearshore region, which may limit the number of species tolerant to such a wide range of fluctuations in salinity and temperature. The influence of environmental extremes at small spatial scales was also observed in the distribution of macroalgal taxa. The area south of the jetty had a more uniform spatial distribution of taxa (i.e., lower number of distinct groupings) compared to the north section of the jetty, reflecting the inhospitable nature of a rapidly fluctuating and extreme environment and its limiting impacts on the types of species that occur there on a seasonal basis.

The dominant macroalgal species had clear seasonal patterns likely related to species-specific tolerances to environmental conditions and life-history dynamics. For example, drift red masses had a general pattern of high values in winter and lower values during the summer. Seasonal peaks in abundance of drift red masses have been reported previously for Florida and elsewhere (Benz et al. 1979, Collado-Vides et al. 1995, 2005, Díaz-Pulido and Garzón-Ferreira 2002, Armitage et al. 2006, Biber and Irlandi 2006, Kopecky and Dunton 2006, Biber 2007). The drift red masses in Black Point were composed of three species, *Laurencia intricata*, *Palisada poiteaui*, and *Polysiphonia echinata*, which had distinct seasonal patterns. Drift masses were present throughout the study, but species composition varied seasonally; this seasonality and shifts within groups would not have been detected if only a growth-form approach been taken (Collado-Vides et al. 1994).

When environmental factors were considered in combination, distinct characteristic species assemblages were documented. The marine group was characterized by the presence of *Anadyomene stellata* and *Halimeda incrassata*. The latter species is a dominant taxon in South Florida coast-

Table 5   Average nutrient content as % of tissue dry weight.

Anadyomene	C (5)	N (5)	P (5)	N:P (5)	C:N (5)	C:P (5)
Mean (SD)	28.92 (3.35)	1.69 (0.07)	0.031 (0.01)	143.92 (62.89)	19.96 (2.16)	445.24 (231.82)
Batophora	C (2)	N (2)	P (0)	N:P (0)	C:N (2)	C:P (0)
Mean (SD)	37.02	1.81	–	–	24.17	–
Chara	C (11)	N (11)	P (8)	N:P (8)	C:N (11)	C:P (8)
Mean (SD)	30.05 (3.16)	2.02 (0.55)	0.05 (0.01)	111.36 (78.31)	18.50 (5.82)	254.23 (116.45)
Digenia	C (4)	N (4)	P (2)	N:P (2)	C:N (4)	C:P (2)
Mean (SD)	38.58 (0.79)	2.03 (0.31)	0.11 (0.14)	208.17 (256.97)	22.46 (2.83)	717.80 (909.37)
Green mat	C (2)	N (2)	P (2)	N:P (2)	C:N (2)	C:P (2)
Mean (SD)	29.62 (8.91)	2.23 (0.67)	0.05 (0.02)	107.74 (76.43)	15.51 (0.02)	250.36 (177.41)
Laur/Pali	C (72)	N (72)	P (32)	N:P (32)	C:N (72)	C:P (32)
Mean (SD)	33.73 (3.13)	1.60 (0.30)	0.01 (0.01)	362.16 (164.15)	25.40 (4.65)	1371.47 (758.72)
Polysiphonia	C (13)	N (13)	P (5)	N:P (5)	C:N (13)	C:P (5)
Mean (SD)	36.30 (0.45)	1.88 (0.17)	0.01 (0.001)	391.47 (60.76)	22.75 (2.31)	1389.32 (306.49)
Red mass	C (28)	N (28)	P (13)	N:P (13)	C:N (28)	C:P (13)
Mean (SD)	34.58 (4.44)	2.13 (0.77)	0.02 (0.01)	343.94 (120.68)	20.77 (6.18)	1018.6 (280.64)
Acetabularia	C (1)	N (1)	P (1)	N:P (1)	C:N (1)	C:P (1)
	24.01	0.38	0.00	187.37	73.57	2065.61
Sargassum	C (1)	N (1)	P (1)	N:P (1)	C:N (1)	C:P (1)
	28.46	1.54	0.04	86.70	21.60	280.64
Kruskal-Wallis	C	N	P	N:P	C:N	C:P
χ^2	40.79	28.83	30.09	26.60	34.18	29.24
df	7.00	7.00	6.00	6.00	7.00	6.00
p	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

C (n), % Carbon (no. of samples); N (n), % nitrogen (no. of samples); P, % phosphorus (no. of samples); N:P, nitrogen-phosphorus mole:mole ratio (no. of samples); C:N, carbon-nitrogen mole:mole ratio (no. of samples); C:P, carbon-phosphorus mole:mole ratio (no. of samples); SD, standard deviation. A Kruskal-Wallis test was used to compare nutrient content (% of tissue dry weight) among species.

al lagoons commonly associated with marine conditions (Davis and Fourqurean 2001, Collado-Vides et al. 2007). The freshwater group, found only in low-salinity habitats, was characterized by *Chara hornemanii*, a freshwater-estuarine species that is common in inland lakes and marshes in the Everglades (Montague and Ley 1993, Frankovich et al. 2011) and has been increasing in abundance and range in central Biscayne Bay and mangrove lakes in western Florida Bay (Lirman et al. 2008b, Frankovich et al. 2009) in the past few years. The presence of this taxon is a clear sign of low mean salinity and changes in its spatial distribution can be expected as lower salinity conditions are expanded in the Bay. While it was initially believed that the presence of *Chara* at Black Point was only a seasonal occurrence (Lirman et al. 2008b), the collections conducted here show a consistent background presence of this taxon in the areas closest to shore (<100 m from shore) with the lowest mean salinity. Another assemblage characteristic of the freshwater group is the category labeled here as puff, comprised of a mix of diatoms, green filamentous algae, and Cyanobacteria, which was present in low-salinity habitats of Black Point. Puff is

highly dependent on the presence of seagrasses, specifically the low-salinity tolerant species *Halodule wrightii* (Lirman et al. 2008b, Lirman and Cropper 2003, Koch et al. 2007),
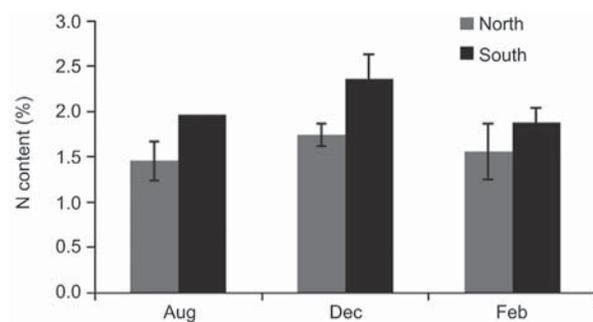

Figure 8   Seasonal changes in percent nitrogen content of red masses comparing north and south regions.
See Figure 1 for positions of north and south. Values are means±SD. (n=) August north (22), south (1), December north (3), south (8), February north (12), south (10).

for attachment and has been shown to respond quickly to changes in nutrient availability, especially phosphate (Frankovich et al. 2009). The rest of the taxa comprise the estuarine group, in which two groups were evident. The first group included *Acetabularia schenckii*, *Batophora oerstedii*, and *Polysiphonia subtilissima*. *Acetabularia schenckii* and *B. oerstedii* have been reported to occur in large ranges of salinities (Montague and Ley 1993, Collado-Vides et al. 1995, Biber 2007) and depend on the presence of hard substrata for attachment. The second group was composed of *Penicillus capitatus*, *Palisada poiteaui*, and *Laurencia intricata*. *Palisada poiteaui* and *L. intricata* commonly form drift masses within *Thalassia* beds (Virnstein and Carbonara 1985, Biber 2007), while *P. capitatus* has a widespread distribution in estuarine-marine conditions (Montague and Ley 1993, Collado-Vides et al. 1995, Biber 2007). These species assemblages provide a valuable assemblage-level indicator that can be used by managers to draw potential scenarios for the impacts of restoration activities on nearshore SAV (EPA 2008).

Increased nutrient loadings into coastal waters have been associated with a shift in dominance from seagrass and perennial macroalgae to ephemeral, bloom-forming algae in Florida and elsewhere (e.g., Lapointe et al. 1987, 1994, 2004, Duarte 1990, 1995, McGlathery et al. 1992, 2007, Lapointe 1997, McGlathery 2001). Meeder and Boyer (2001) reported high nutrient values in the water column with large seasonal and spatial variability at Black Point (NH_4^+, 0.004–26.97 ppm; NH_3 0.0–654 ppb: NO_3^{2-}, 0.002–0.415 ppm; TP, 0.002–0.94 ppm). These authors suggest that these ranges, indicative of terrestrial/groundwater nutrient loading to the canals and inshore areas of Biscayne Bay, are affecting seagrasses and macroalgal communities, facilitating the growth of fast growing microalgae and phytoplankton, and decreasing *Thalassia testudinum* populations. The tissue nutrient values found in this study had N:P ratios larger than the 30:1 Redfield ratio, indicating high N availability and P limitation (Atkinson and Smith 1983); the limitation in P is consistent with the carbonate-rich waters of Biscayne Bay (Fourqurean et al. 1992, 2003, Lapointe et al. 1992). The values found in the present study were similar to or higher than those found in algae under experimentally enriched treatments as well as those growing close to nutrient-rich mangrove areas (Lapointe et al. 1987, Lapointe 1997), but higher than those reported for enriched oceanic waters in the region (Lapointe et al. 2005). While Kopecky and Dunton (2006) did not find dissolved inorganic nitrogen (DIN) to be a reliable indicator of macroalgal abundance in the Gulf of Mexico, Armitage et al. (2006) showed that rapidly forming and ephemeral blooms of filamentous algae can develop under enriched conditions. Similarly, fast-growing green filamentous algae, diatoms, and Cyanobacteria such as those found south of the Black Point jetty may respond rapidly to fluctuations in P (Frankovitch et al. 2009). The heavy load of nutrients in the landfill adjacent to Black Point (Meeder and Boyer 2001) and the transport of these nutrients in the freshwater coming out of the Black Point canal explain the high abundance of members of the puff category in this area. Thus, the low

salinity appears to facilitate the dominance of *Halodule* over *Thalassia*, and the increase in nutrients appears to facilitate the high abundance of puff taxa that utilize *Halodule* leaves as attachment substratum. If nutrient levels keep increasing nearshore, a shift from a *Halodule-Chara*-dominated system towards an alternative one dominated by microalgae and phytoplankton can be expected (Frankovich et al. 2011).

The abundance and distribution of macroalgae at Black Point had distinct seasonal and spatial patterns related to interacting environmental factors, even at small spatial scales (<1 km). While species-to-physical factor relationships are often complex, several significant associations were revealed here that will help managers to detect changes in water quality parameters through shifts in community composition and distribution of macroalgae. Based on the modifications in hydrology and freshwater deliveries proposed under CERP, it is expected that mesohaline conditions will be expanded in both space (currently limited to areas in the immediate vicinity of canals) and time (now only observed in the wet season). Thus, shallow nearshore areas that experience changes in freshwater deliveries are expected to undergo progressive shifts from macroalgal communities dominated by morphologically complex and slow-growing species with relative low tolerance to salinity variability, towards alternative communities dominated instead by morphologically simple and fast-growing species with high tolerance to salinity variability. Similar regime shifts have already been reported in other freshwater and estuarine systems (Scheffer and van Nes 2007, Frankovich et al. 2011). If this scenario is realized, it is expected that species like *Chara* and those in the puff category (especially under high nutrient conditions) will also experience range expansions away from the immediate vicinity to shore and canals. Similarly, species associated with more marine conditions would experience reductions in range and abundance as mean salinity values decrease and mesohaline conditions expand further offshore. Thus, nutrient levels in algal tissue should be carefully monitored as the %N reported for this area is high and could eventually result on algal blooms along western Biscayne Bay, as already reported for other blooming algae in marine waters of South Florida (Lapointe et al. 2005, Lapointe and Bedford 2010). Biological indicators are useful when they integrate the cumulative effects of various stressors, and reflect current conditions as well as changes over time (EPA 2008). In this context, macroalgal community composition (assemblages) and distribution, and their nutrient content, can provide a powerful bioindicator of changes in water quality that may not be captured in water quality monitoring programs that are at present limited in spatial coverage (inshore areas are often undersampled) and frequency of observation (only quarterly water quality measurements are collected at most locations).

Acknowledgements

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