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PRIMARY RESEARCH PAPER

Seasonal changes in the abundance and distribution of submerged aquatic vegetation in a highly managed coastal lagoon

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Abstract The inflow of fresh water into coastal lagoons is a key factor influencing the structure and function of these ecosystems. Biscayne Bay, a coastal lagoon adjacent to the city of Miami, is located downstream of the Everglades ecosystem where the extensive water management system now in place has modified the historical hydrology, replacing groundwater and overland flows with pulsed releases from canals. In areas where canals discharge directly into littoral habitats, an environment with low-mean salinity and high-salinity variability is created. In this study, we characterize the salinity patterns of nearshore habitats (<500 m from shore) and document patterns of seasonal abundance and distribution of submerged aquatic vegetation (SAV) to evaluate the impacts of water management practices. Seagrasses were the principal component of the SAV community during the 2005 dry season (mean cover = 25.5%), while macroalgae dominated during the wet season (mean cover = 33.4%). The distribution and abundance of SAV were directly related to the tolerance of each taxon to salinity patterns. Seagrass species with high tolerance to low and variable salinity such as *Halodule wrightii* and *Ruppia maritima* were found only in canal-influenced areas and increased in abundance and spatial distribution in the wet season when freshwater inflow is highest. The dominance of rhizophytic macroalgae during the wet season was determined by the appearance and high abundance of *Chara*, a taxon commonly associated with freshwater environments. *Thalassia testudinum*, the most abundant seagrass species, was found throughout the study region, but decreased in abundance in the canal-influenced areas during the wet season when lower, more variable salinity resulted in lowered productivity. The data presented here showed a significant relationship between salinity patterns and the seasonal abundance and distribution of SAV. These findings support the use of SAV as appropriate indicators of changes in water quality resulting from future restoration projects associated with the Everglades Restoration Plan, which will once again modify the delivery of fresh water into littoral habitats with unknown ecological consequences.

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Introduction

Coastal lagoons and estuaries play a pivotal role as centers of high productivity, nursery habitats for fishes and invertebrates, foci of human recreational activities, and nutrient and sediment sinks. However, the proximity of these important ecosystems to large urban developments has influenced their dramatic decline in condition in recent history. Submerged aquatic vegetation (SAV) communities are keystone components of coastal lagoons and estuaries, and significant patterns of decline and shifts in community structure have been documented for these communities worldwide. In a recent study, Lotze et al. (2006) documented declines of 65% of seagrasses and 48% of other SAV taxa in 12 coastal systems in the past 150–300 years. Among the main causes of the decline in SAV are chemical pollution, eutrophication, physical impacts, and modifications to the trophic structure (Duarte, 2002; Orth et al., 2006; Short et al., 2006). Worldwide, significant management efforts are underway to restore the extent and quality of estuarine systems and to recover productivity and habitat value of these important ecosystems. To guide the successful management of estuarine systems located downstream of large population centers, a better understanding of the influence of human activities on water quality as well as the relationship between physical and biological factors and the structure and function of SAV communities is needed. In this study, we evaluate the patterns of distribution and seasonal abundance of SAV within the littoral habitats of Biscayne Bay, a shallow (<4 m), subtropical coastal lagoon adjacent to the city of Miami, to test the hypothesis that the seasonal and spatial dynamics of nearshore benthic communities are significantly influenced by patterns of freshwater releases from man-made structures in this managed system.

The coastal lagoons of South Florida are an integral part of a linked regional hydroscape that includes upland habitats, the Florida Everglades, Biscayne Bay, Florida Bay, and the Florida Reef Tract (Davis & Ogden, 1994). The hydrology of the South Florida ecosystem is presently managed by an extensive water management system that controls water flows among the different system compartments and the release of fresh water into coastal habitats mainly through canals (Browder & Ogden, 1999). Canal drainage and associated point-source releases of fresh water into nearshore habitats have altered historical sheet and groundwater flows and have created nearshore environments that now experience rapid fluctuations in salinity, nutrients, and contaminants (Sklar et al., 2002).

Biscayne Bay supports extensive recreational and commercial fishing activities and provides essential habitat for numerous fish and invertebrate species (Ault et al., 1999a, b; Serafy et al., 2003). Benthic habitats of central and southern Biscayne Bay are dominated by seagrass and hardbottom communities. Seagrass communities are composed of four seagrass species (i.e., *Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrigthii*, *Ruppia maritima*) (Lirman & Cropper, 2003), while hardbottom communities are composed of hard and soft corals and sponges (Cropper et al., 2001; Lirman et al., 2003). Moreover, both of these community types have highly productive macroalgal components that provide essential habitat for associated fish and invertebrates (Zieman, 1982; Irlandi et al., 2004).

The location of Biscayne Bay, downstream of the Florida Everglades and the coastal canal system, has made this lagoon susceptible to water management decisions that are based mainly on urban and agricultural water needs and flood control, with limited consideration for the potential impacts on nearshore natural resources. In the recent past, the modification of the historical sheet flow patterns of drainage into coastal habitats has resulted in adverse impacts to seagrass communities (Robblee et al., 1991; Zieman et al., 1999), sponges (Butler et al., 1995), and pink shrimp catches (Browder et al., 1999) in nearby Florida Bay. Such adverse impacts have not been documented yet for Biscayne Bay, but considering the potential future impacts of the recently approved Comprehensive Everglades Restoration Plan (CERP), which will once again modify the regional hydrology (Davis & Ogden, 1994; Steinman et al., 2002), it is important to understand present-day linkages between species abundance and distribution patterns and freshwater drainage patterns so that the future impacts of the restoration activities on the existing biota may be fully ascertained.

Abundance and distribution of seagrasses and macroalgae are known to be influenced by multiple biotic and abiotic factors that can vary significantly seasonally and spatially. Light, temperature, and nutrient availability are usually recognized as key abiotic factors, whereas herbivory, and intra- as well as interspecific competition are recognized as key biotic factors influencing marine plant productivity (Larkum et al., 2006 and references therein). In addition to these factors, human activities can introduce both physical (e.g., dredging, boating impacts) and chemical (e.g., heavy metals, oil, and fuel) sources of disturbance that can influence productivity and species distribution patterns (Ralph et al., 2006). The focus of this study, however, is on the relationship between salinity patterns and the seasonal dynamics of submerged aquatic vegetation (SAV) in the nearshore habitats of a coastal lagoon presently influenced by water management practices and the release of fresh water from canals. Our approach was to focus on the littoral habitats most susceptible to water management practices by implementing a stratified random field sampling design, which captured seasonal and spatial variation in SAV species composition, distribution, and abundance, and relate these patterns to simulated and observed salinity patterns.

Materials and methods

Field surveys

In 2005, surveys of the nearshore habitats (<500 m from shore) of western Biscayne Bay were conducted using the Shallow Water Positioning System (SWaPS), a video-based benthic survey technology developed by scientists from NOAA's National Geodetic Survey (Lirman et al., in press) to document seasonal species composition, distribution, and abundance of submerged aquatic vegetation. This methodology has been shown to be a rapid and cost-effective way to survey shallow habitats that, due to shallow depths (<30 cm–1 m), limit the access of larger vessels and the deployment of divers. In addition, a calibration exercise conducted to compare the data obtained by divers and the SWaPS method revealed no significant differences in estimates of percent cover of SAV collected at the same sites using these two methods (Lirman et al., in press). Surveys were limited to the area <500 m from shore because this is area most likely to be directly affected by the proposed Everglades Restoration projects on the watershed and where the influence of freshwater inflow from canals is highest (RECOVER, 2004).

The SWaPS method uses a Global Positioning System (GPS) receiver attached to a camera installed in a shallow-draft boat (14-ft Carolina skiff). To improve taxonomic classification, images of the bottom were obtained using a high-resolution digital SLR camera (7.0 megapixels). The GPS receiver was centered over the camera that was suspended over a glass enclosure that provided a down-looking view of the bottom. Each image recorded was stamped with time, date, depth, and position information and the images were analyzed to determine percent cover and spatial distribution of SAV.

Surveys to document benthic community patterns along latitudinal and inshore–offshore gradients were conducted using a stratified random sampling design based on the US EPA's EMAP sampling protocol (Jackson et al., 2000). The sampling methodology consisted of the following steps: (1) a shoreline map of the study region was extracted from 3-m Digital Ortho-Quarter Quad photography (Fig. 1); (2) a shoreline vector was delineated, and five 100-m buffers were created; (3) buffers were divided into cells of equal size using the fishnet function in Xtools (ArcGIS extension); and (4) one survey point was generated within each subdivision of the buffer at a random location using Hawth's Tools (ArcGIS extension). Survey sites were selected using this method (80 sites within the buffer at <100 m from shore and 40 sites in each of the remaining buffers, $n = 240$ sites), and the same sites were surveyed during the dry season (March–April) and the wet season (July–August) to provide a seasonal comparison. The GPS coordinates for each site were exported to a portable GPS unit for navigation in the field.

For each survey location (i.e., a transect <25 m along the survey track), 10 non-overlapping geo-referenced images were analyzed. This approach was chosen to be consistent with the methods used by existing SAV monitoring programs in the region where multiple sites are sampled visually using 0.25 m^2-quadrats (Durako et al., 2002; Fourqurean et al., 2002). For each image (i.e., the sample unit for

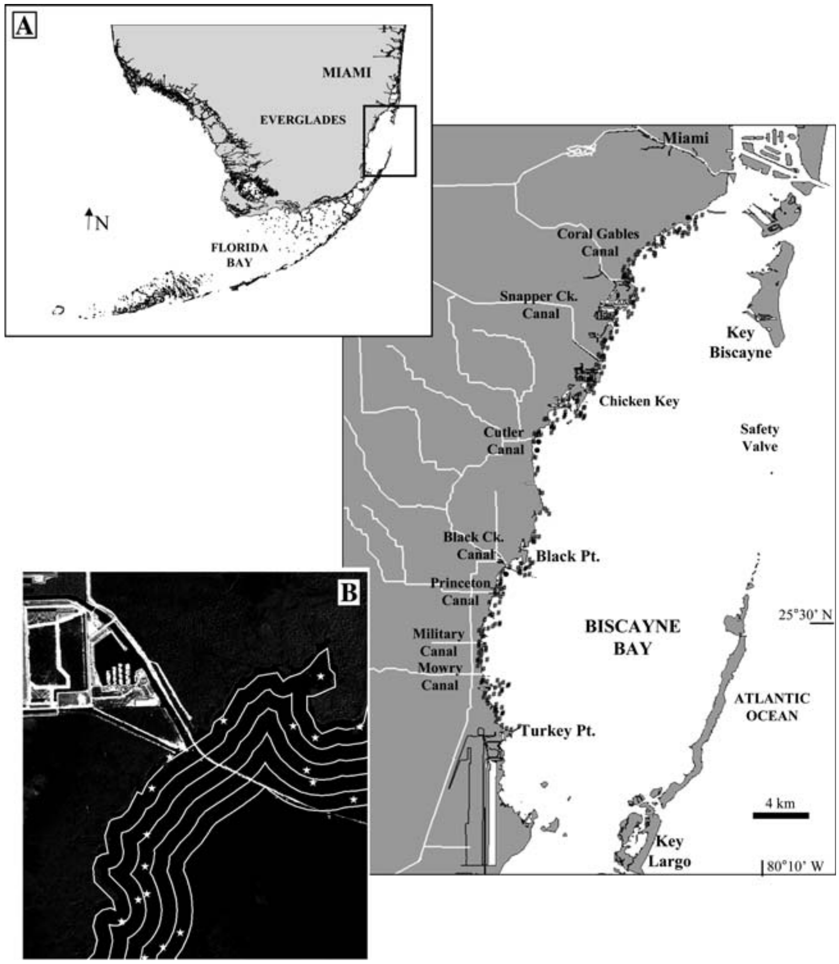

Fig. 1 (**A**) Map of the study area and the location of the study sites (n = 240 sites surveyed each season). (**B**) Photograph of the Black Point area showing the survey buffers. Sites (stars) were located randomly within each sub-section of the five buffers

that site), community type, species list, and abundance (percent cover) were recorded from a computer monitor. Percent cover was determined as the fraction of each frame occupied by each taxon. Seagrasses were identified to species while macroalgae were identified to species or functional form (Collado-Vides et al., 2005). Two main macroalgal functional groups, attached (rhizophytic) and unattached (drift) macroalgae, were identified in this study (Biber & Irlandi, 2006). The benthic coverage data obtained for each frame were averaged for each site and used to develop percent cover surface contours using the ArcView Spatial Analyst software and applying the Inverse Distance Weighted interpolation procedure. Differences in percent cover were calculated as [(% cover wet season − % cover dry season)/% cover dry season] and these values were used to develop change contour plots. The mean cover of each taxon was compared between seasons using t-tests and among buffers and between seasons using a 2-way ANOVA with season and buffer as main factors. Coverage data were arcsin-transformed to conform to the normality assumption of the statistical tests employed (Sokal & Rohlf, 1995).

Water quality patterns

The salinity patterns of nearshore habitats of Biscayne Bay are influenced spatially and seasonally by the release of fresh water from canals, with smaller contributions from precipitation, groundwater, and overland flows. Previous research has indicated that the areas in the vicinity of canals are characterized by low-mean salinity and high-salinity variability, while areas removed from these sources of fresh water, located in the northern section of the study area directly adjacent to The Safety Valve, are influenced by the influx of oceanic waters and are characterized by higher-mean salinity and less-variable salinity patterns (Wang et al., 2003).

Water quality data collected by Biscayne National Park and the SERC-FIU Water Quality Monitoring Network (Caccia & Boyer, 2005) provide broad-scale information on water quality parameters in Biscayne Bay, but have limited coverage in the nearshore habitats where benthic surveys were conducted. In this study, the Biscayne Bay salinity and hydrodynamic model (Wang et al., 2003) was used to provide a high-resolution temporal and spatial characterization of the salinity patterns at nearshore environments of western Biscayne Bay at a scale commensurate with the benthic surveys. The two-dimensional hydrodynamic and salinity transport numerical model is based on a triangular finite element grid with 6,364 elements and 3,407 nodes, with an average grid point spacing of 500 m. The model was run using wind data and freshwater inputs for a four-year period (1995–1998) to obtain hourly salinity values for each one of the benthic survey points. Hourly data were simulated for each site (n = 240 sites) for 1995–1998 and averaged by day, month, and season. The monthly mean salinity and salinity variability (S.D.) for each simulation site were used in a hierarchical cluster analysis using Ward's minimum variance method to determine the spatial distribution of sites with similar salinity patterns (Fig. 2). Finally, the salinity simulated for each point was related to the presence-absence of seagrasses and macroalgae using logistic regression to assess the probability of occurrence of each taxon in relationship to salinity values.

In addition to the data simulated by the hydrodynamic model, salinity and temperature data were collected in the field during 2005 at eight locations where water quality probes (YSI Environmental 6,600 Series) were deployed by Biscayne National Park. Data from eight probes (two from within each salinity cluster) were measured at 15-min intervals and averaged by day and season. The data collected in the field was compared to the data simulated by the model at the locations closest to the field probes. The mean monthly salinity calculated for each probe (n = 8) was correlated to the monthly salinity values obtained for the salinity model nodes at the same locations to evaluate the performance of the model in predicting salinity patterns of nearshore habitats.

Results

Salinity patterns obtained using the Biscayne Bay salinity model showed clear spatial and seasonal patterns in mean salinity and salinity variability. A

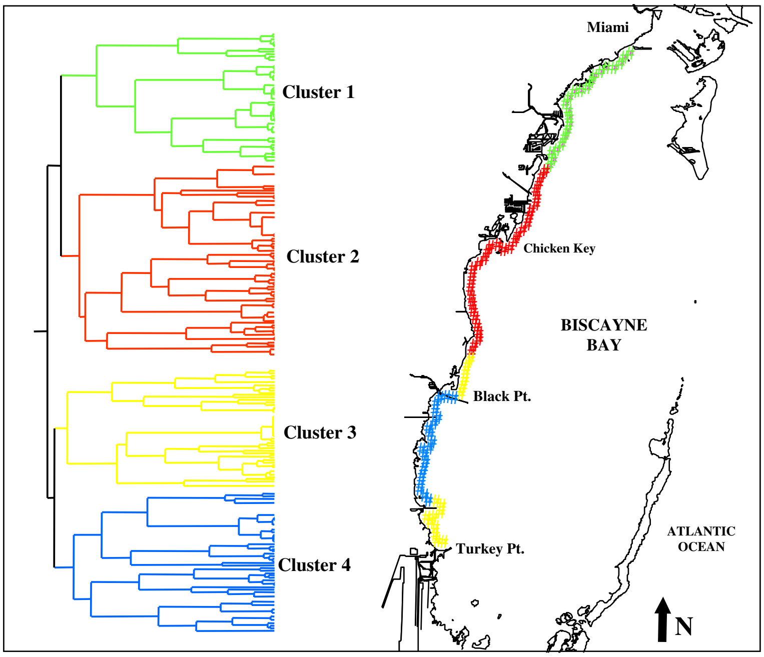

Fig. 2 Classification of sites based on salinity patterns obtained from the Biscayne Bay salinity model. The data for each site (e.g., mean monthly salinity and standard deviation) simulated for 1995–1998 were used in a hierarchical cluster analysis to determine site groupings. The dendrogram (left panel) and the site map (right panel) share the same color scheme to represent the spatial distribution of sites with similar salinity patterns

negative correlation ($r = -0.95$) was found between mean salinity and the standard deviation of salinity, highlighting the fluctuating nature of freshwater inflow through canals and groundwater sources. The cluster analysis arranged the SAV sites into four main clusters (Fig. 2). Cluster 4, comprising the sites most heavily influenced by canal outflow, is characterized by low mean salinity and high salinity variability, especially in the wet season (Table 1). The northern section of the study area (north of Black Point) has higher mean salinity and lower salinity variability in both the dry and wet season compared to the area to the south where canal discharge is highest. Mean salinity values for the dry season were >30 psu in the northern region (clusters 1 and 2), while mean salinity was 27–30 psu in the southern region of the study area (clusters 3 and 4). During the wet season, mean salinity values were >23 psu in the northern region, while mean salinity was 17–23 psu in the southern region (Table 1).

The data obtained from field probes in 2005 showed patterns similar to those obtained using the salinity model. Salinity values (mean and median) were higher and salinity variability lower in the northern section, while lower-mean salinity and higher-salinity variability were measured in cluster 4 where canal influences prevail (Table 2). Moreover, salinity decreased in all clusters from the dry season to the wet season, but the decrease was more pronounced in the southern section of the study area. In contrast, temperature patterns showed clear seasonal patterns but no spatial patterns. Mean temperature increased by up to 8°C between seasons but temperature patterns were consistent among the four salinity clusters (Table 2). Lastly, salinity showed a general decrease with distance to shore in all clusters in both seasons, with the exception of cluster 4 in the dry season where mean salinity showed a slight increase (1 psu) with increasing distance to shore (Table 2). When the mean monthly

Table 1 Seasonal salinity patterns in Western Biscayne Bay

Salinity clusters	1		2		3		4	
Season	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Mean Sal (psu)	33.4 (2.2)	29.4 (3.1)	32.4 (3.6)	26.6 (4.6)	30.0 (5.3)	22.9 (6.5)	27.0 (7.5)	17.1 (8.2)
Min–Max Sal (psu)	26–37	20–36	23–37	13–36	14–37	6–37	10–38	2–33
Median Sal (psu)	34.0	29.6	33.6	26.7	31.4	22.1	28.8	16.3

The data were obtained from Biscayne Bat's hydrodynamic model for 1995–1998. Daily salinity values were averaged for all sites within each cluster (see Fig. 2 for the location of the salinity clusters)

Table 2 Salinity (psu) and temperature (°C) patterns from nearshore habitats of Western Biscayne Bay documented for the dry and wet seasons of 2005

Sal cluster	Dist. to shore (m)	Mean temp (S.D)		Min–max temp		Median temp		Mean salinity (S.D)		Min–max sal		Median sal	
		Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
1	680	22.8 (2.5)	30.5 (1.5)	18.1–27.8	26.8–32.7	23.3	30.9	34.5 (0.7)	29.8 (2.3)	33.1–35.6	19.6–32.3	34.6	30.0
1	2000	22.7 (2.3)	30.3 (1.5)	18.4–27.2	27.1–32.3	23.2	30.6	36.6 (1.0)	33 (2.6)	34.5–39.1	25.7–38.4	36.7	33.1
2	110	22.8 (2.5)	30.4 (1.5)	17.0–27.8	26.9–32.8	23.3	30.9	32.3 (2.1)	18.2 (8.5)	25.0–36.0	0.3–35.5	32.6	20.1
2	360	23.7 (2.6)	31.4 (2.1)	17.8–28.7	26.6–35.7	24.2	32.1	33.1 (1.9)	21.2 (7.1)	27.9–37.8	1.1–34.5	33.4	23.3
3	140	22.9 (2.5)	30.4 (1.6)	17.3–27.7	26.5–32.7	23.3	30.8	32.8 (3)	16.3 (6.3)	27.1–38.7	1.9–32.2	33.1	17.6
3	340	23.0 (2.7)	30.7 (1.8)	15.5–28.4	25.9–33.5	23.5	31.2	32.9 (2.8)	17.4 (6.2)	27.3–38.4	2.4–33.1	33.1	18.3
4	52	22.7 (2.7)	30.8 (1.3)	19.0–27.6	27.4–32.5	23.1	31.2	29.7 (2.9)	12.9 (6.6)	24.9–35.2	2.5–33.1	28.5	12.8
4	296	23.3 (2.6)	31 (1.9)	16.1–28.2	25.6–33.9	23.6	31.4	28.7 (4.0)	13.3 (6.7)	21.8–34.8	2.1–33.3	27.7	12.7

Data were collected at 15-min intervals with water quality probes (YSI Environmental 6600 Series) deployed by Biscayne National Park. The data were averaged by day and season. The data presented are from representative probes deployed at increasing distance from shore within the salinity clusters determined using Biscayne Bay's hydrodynamic model in this study (Fig. 2) salinity values from each salinity probe (n = 8, 2 sites within each salinity cluster) were compared to values simulated by the hydrodynamic model for the same locations, a significant correlation was obtained at each location between the two data sources ($P < 0.01$, r = 0.90–0.98), indicating that the output from the salinity model can be adequately used to simulate salinity patterns within nearshore habitats of western Biscayne Bay.

Submerged aquatic vegetation dominates the nearshore benthic communities of central and southern Biscayne Bay. The mean cover of SAV in 2005 (all taxa combined) was 41.3% (S.D. = ±34.8) in the dry season and 66.1% (35.2) in the wet season. Only 17% of sites in the dry season and 15% of sites in the wet season were completely devoid of SAV. These sites were found mainly in the northern section of the study region (north of Shoal Point) in areas where dredging activities have taken place and depth is >2 m. Seagrasses were the principal component of the SAV community during the dry season, while macroalgae dominated during the wet season (Table 3). *Thalassia testudinum*, the most abundant seagrass species, was found at 68% of sites in the dry season and 63% of sites in the wet season. The highest abundance levels of *T. testudinum* were found north of the Cutler Canal in the Chicken Key area and north of Black Point, while the lowest abundance of this species was recorded in the northernmost section of the study area and south of Black Point, and directly opposite Military canal (wet season) and Mowry canal (dry season) (Figs. 3, 4). The overall abundance and distribution of *T. testudinum* remained consistent between seasons (Table 3), with general increases in percent cover north of the Cutler Canal and comparable decreases in the southern region of the study area (Fig. 5).

In contrast to the wide distribution of *Thalassia*, *H. wrightii*, *S. filiforme*, and *R. maritima* had lower abundance and more patchy spatial distribution (Table 3, Fig. 3). *Halodule wrightii* had high-abundance foci in the areas in the immediate vicinity of canals throughout the study domain (Figs. 3, 4), *S. filiforme* was restricted to the northern section of the survey area (Fig. 3), and *R. maritima* was restricted to the southern region in areas directly influenced by freshwater inflows from canals (Fig. 3). Both *H. wrigthii* and *S. filiforme* experienced significant increases in percent cover in the wet season and an expansion in the number of sites where these species were observed (Table 3). *Ruppia maritima* did not show a significant change in cover between seasons (Table 3). The spatial patterns of change in percent cover of *H. wrightii* were the opposite of those of *T. testudinum*: the mean cover of *H. wrightii* generally increased in the area south of the Cutler Canal and decreased in the area north of this canal (Fig. 5).

Attached macroalgae (*Halimeda* spp., *Caulerpa* spp., *Penicillus* spp., *Batophora* spp., *Acetabularia* sp.) and drift (*Laurencia* spp., *Chondria* spp., *Dictyota* spp) were found throughout the study region (Table 3) and showed the largest seasonal changes in percent cover of any taxa (Fig. 5). The cover of drift macroalgae decreased significantly (from 12.5 to 4.4%), and attached macroalgae had a six-fold

Table 3 Percent cover (S.D.) and percentage of sites where SAV was found in Western Biscayne Bay in the 2005 Dry (March–April) and Wet (July–August) seasons

	% Sites dry season	% Sites wet season	% Cover dry season	% Cover wet season	P values
T. testudinum	68	63	19.9 (28.0)	19.2 (28.3)	ns
H. wrightii	38	50	1.4 (8.3)	4.0 (13.2)	<0.01
S. filiforme	15	21	4.2 (9.8)	5.2 (12.2)	<0.05
R. maritime	4	5	0.03 (0.2)	0.01 (0.1)	ns
Attached algae	64	66	4.0 (10.4)	29.0 (33.4)	<0.01
Drift algae	69	43	12.5 (18.7)	4.4 (10.4)	<0.01
Seagrass	78	80	25.5 (30.1)	28.4 (30.8)	ns
Macroalgae	77	74	16.5 (20.8)	33.4 (35.5)	<0.01

The mean cover of each taxon was compared between the dry and wet seasons using a t-test. ns = no significant differences between seasons. n = 240 sites each season

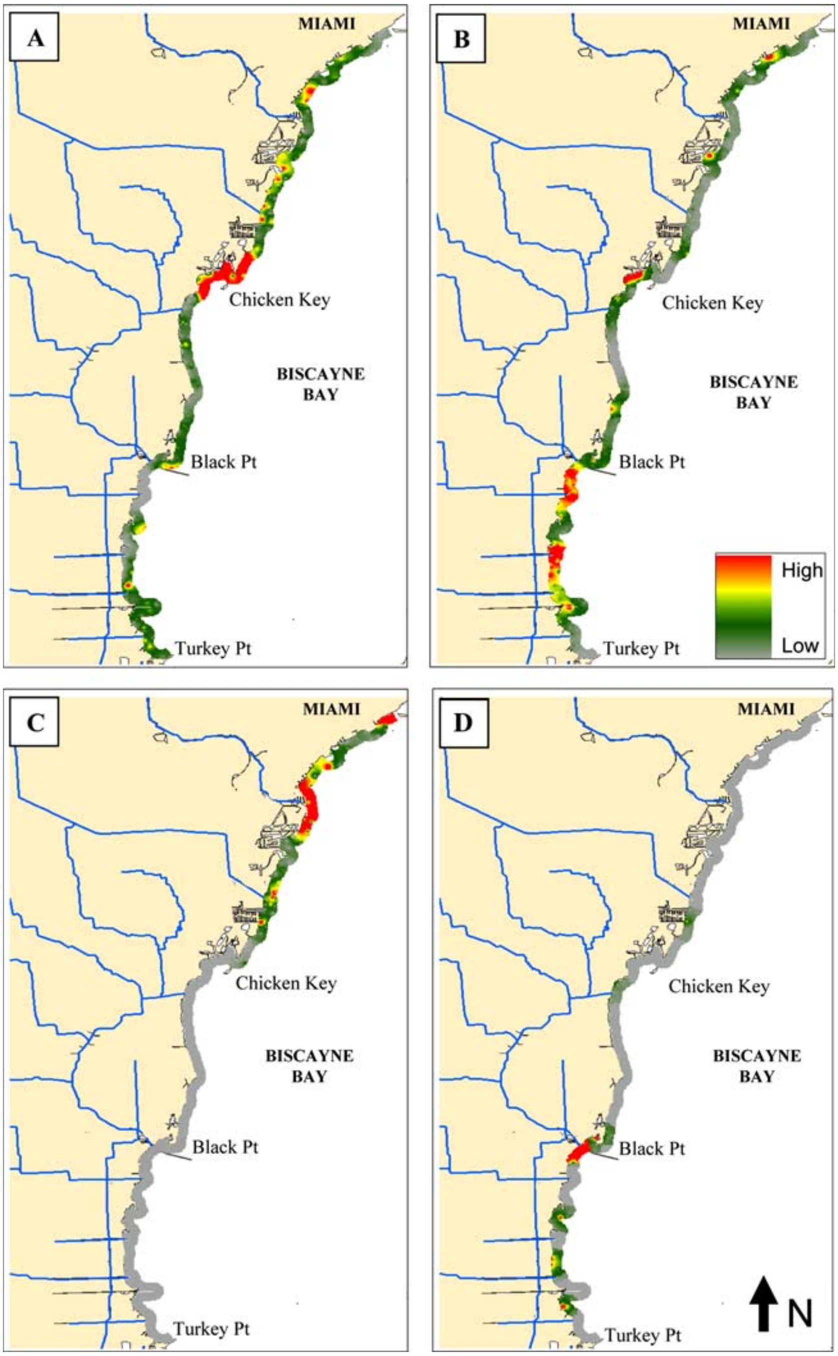

Fig. 3 Abundance and distribution patterns of seagrasses in western Biscayne Bay. The color scheme represents the minimum–maximum percent cover of each taxon. These contours are intended to highlight the spatial patterns of distribution of taxa that are not observable when displayed when using the full scale (0–100%). (**A**) *Thalassia testudinum*, (**B**) *Halodule wrightii*, (**C**) *Syringodium filiforme*, (**D**) *Ruppia maritima*. Data are from the 2005 wet season

increase in cover from the dry to the wet season. Drift macroalgae decreased in percent cover throughout the study domain between the dry and wet seasons. Attached macroalgae coverage decreased in the area north of the Cutler Canal, but increased in the region south of this canal between the dry and wet seasons. The large increase in biomass and percent cover documented for attached macroalgae in the southern section of the study region was caused by the appearance of *Chara* and the expansion of *Batophora* documented in areas influenced by canals.

The abundance and distribution of SAV were clearly influenced by season and location with respect to sources of fresh water and connectivity to the open

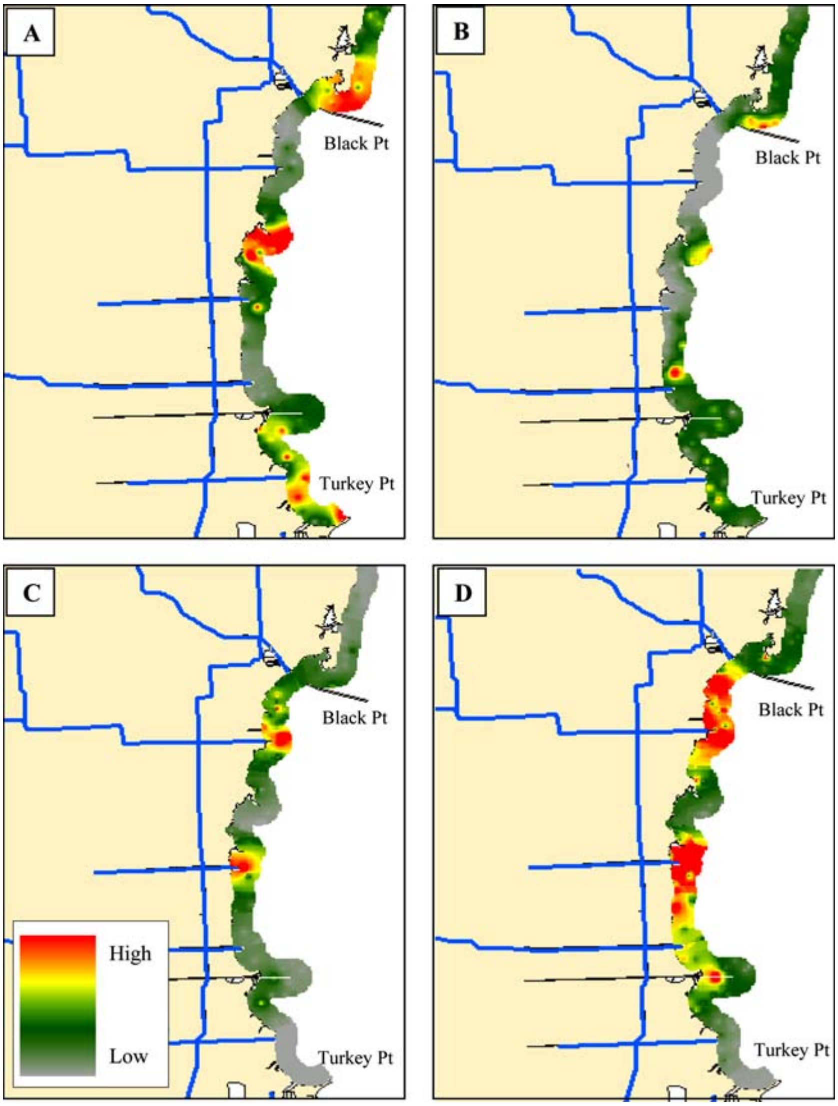

Fig. 4 Abundance of seagrasses in western Biscayne Bay in the area with the greatest inflow of fresh water through water management canals. The color scheme represents the minimum–maximum percent cover of each taxon. (**A**) *Thalassia testudinum* (dry season), (**B**) *T. testudinum* (wet season), (**C**) *Halodule wrightii* (dry season), (**D**) *H. wrightii* (wet season)

ocean. The abundance of each of the taxa encountered was significantly influenced by salinity patterns within the four distinct salinity clusters recognized ($P < 0.05$, 2-way ANOVA, Table 4). Significant changes in abundance with respect to season were only observed for drift macroalgae (lower cover in the wet season) and *S. filiforme* and attached macroalgae (higher cover in the wet season for both taxa) ($P < 0.05$, 2-way ANOVA, Table 4) (Fig .6).

At a smaller spatial scale, SAV communities showed significant patterns in percent cover with respect to distance to shore, especially in areas influenced by canals (Table 5). The cover of *T. testudinum* increased significantly with increasing distance from shore, while *S. filiforme* reached its highest value at the 300-m buffer. Decreases in the mean cover of *H. wrightii* and *R. maritima* were observed with increasing distance from shore, but the low and variable cover of these species reduced the power to detect statistically different patterns (power < 0.3). The abundance of attached and drift macroalgae were significantly influenced by both season and distance to shore (Table 5). Peaks in percent cover of attached macroalgae were recorded close to shore (100-m buffer) in the wet season due to the high abundance of *Chara* and *Batophora*.

In light of the significant spatial patterns of association documented between salinity and the

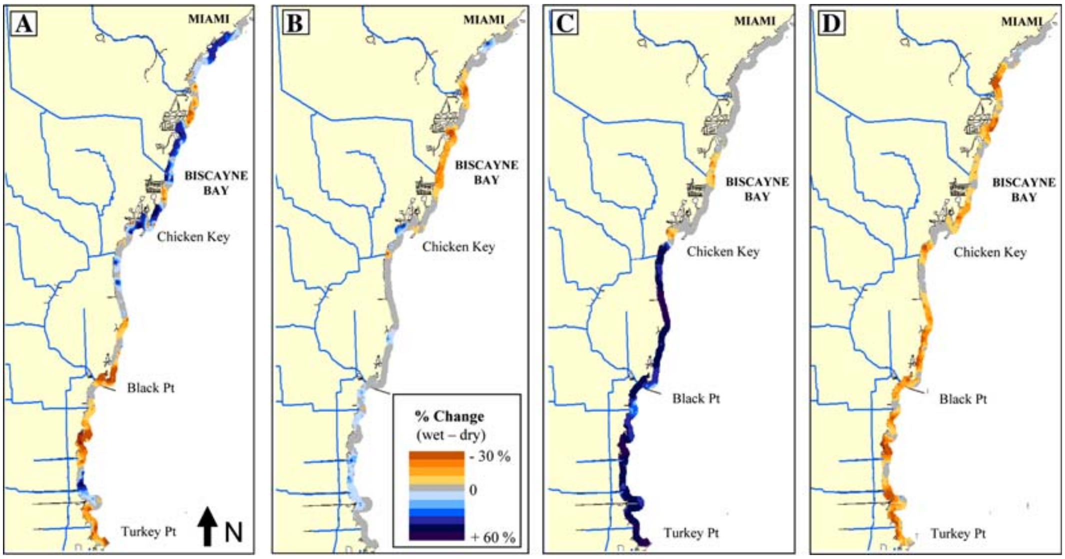

Fig. 5 Seasonal change in the abundance and distribution of SAV in western Biscayne Bay. The amount of change in percent cover for each site was obtained for each taxon by calculating the percent change with respect to the Dry Season value (% change = (% cover wet season − % cover dry season)/(% cover dry season). (**A**) *Thalassia testudinum*, (**B**) *Halodule wrightii*, (**C**) Rhizophytic Macroalgae, (**D**) Drift Macroalgae

abundance of SAV, the probability of occurrence of each taxon in relationship to salinity was tested using logistic regression where taxa were coded within sites as either present or absent. The response curves (logistic regression, $P < 0.05$ for all 5 taxa tested) showed general agreement with the observed SAV distribution patterns. Taxa like rhizophytic algae, *Halodule*, and, to a lesser extent, drift algae, have a higher probability of occurrence at low mean salinity. In contrast, taxa like *Thalassia* and *Syringodium* have a higher probability of occurrence at high mean salinity. The steep salinity tolerance curves displayed by attached algae and *Syringodium* contrast with the broader tolerance to salinity exhibited by *Halodule*, drift algae and, to a lesser extent, *Thalassia*.

Discussion and conclusions

The inflow of fresh water into estuaries and coastal lagoons has been identified as one of the key factors influencing the structure and function of these ecosystems worldwide (Cross & Williams, 1981; Sklar & Browder, 1998). In Biscayne Bay, water quality and more specifically salinity fields are significantly influenced by the drainage of fresh water from the Florida Everglades through water management canals. In areas where canals discharge directly into littoral habitats, an environment with low mean salinity and high salinity variability is created. This environment is where those seagrass species commonly associated with low and variable salinity like *H. wrightii* (McMahan, 1968; Montague & Ley, 1993) and *R. maritima* (Lazar & Dawes, 1991; Bird et al., 1993) reach their highest abundance. In contrast, the northern area of the study region, where higher mean salinity and lower salinity variability prevail, is where *S. filiforme*, a species commonly associated with deeper, oceanic conditions (Fourqurean et al., 2002) reaches its maximum abundance. *T. testudinum*, a seagrass species with a wide salinity tolerance and maximum growth at salinity between 25 and 40 psu (Zieman et al., 1989; Lirman & Cropper, 2003) is the dominant component of the seagrass community throughout the study area. The relationships documented in this study between the probability of occurrence of *Thalassia*, *Halodule*, and *Syringodium* and salinity agree well with the reported tolerance of these species to salinity (Fong & Harwell, 1994; Lirman & Cropper, 2003) and highlight the influence of this abiotic factor on the abundance and distribution of SAV within the near-shore habitats of Biscayne Bay. The influence of human activities and freshwater inflow on the relative

Table 4 Mean percent cover (S.D.) of SAV in Western Biscayne Bay in 2005

Salinity clusters	1		2		3		4		2-Way ANOVA		
Season	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Cluster	Season	Interaction
T. testudinum	16.9 (24.2)	21.4 (26.3)	25.7 (31.9)	34.6 (37.6)	31.7 (25.0)	17.5 (14.1)	18.1 (30.9)	10.3 (19.7)	<0.05	ns	<0.05
H. wrightii	5.6 (10.3)	5.0 (10.8)	6.2 (13.5)	4.1 (12.0)	2.1 (4.4)	4.6 (9.3)	6.0 (10.2)	11.9 (17.1)	<0.05	ns	<0.05
S. filiforme	8.1 (19.7)	25.5 (28.6)	0.4 (2.5)	3.4 (9.4)	0.2 (0.5)	0.1 (0.4)	0.1 (0.1)	0.4 (1.8)	<0.05	<0.05	<0.05
R. maritime	–	–	0.03 (0.2)	0.01 (0.02)	0.08 (0.4)	0.04 (0.2)	0.01 (0.02)	0.01 (0.05)	<0.05	ns	ns
Attached algae	0.5 (1.2)	0.8 (2.3)	6.4 (15.9)	24.0 (34.0)	4.8 (7.9)	55.2 (24.1)	5.6 (9.8)	49.6 (29.6)	<0.05	<0.05	<0.05
Drift algae	10.0 (17.8)	1.7 (3.9)	8.1 (13.9)	1.4 (3.7)	25.1 (22.1)	14.3 (16.3)	17.8 (19.9)	4.5 (10.9)	<0.05	<0.05	ns

SAV survey sites were grouped based on the clusters determined from the salinity patterns (Fig. 2). The mean cover of each taxon was compared among salinity clusters and between the dry and wet seasons using a 2-way Analysis of Variance with cluster and season as main factors. ns = no significant differences

abundance of different macrophyte communities was simulated for South African estuaries (Wortmann et al., 1997). In this case, it was shown that a reduction in riverine flow caused by freshwater impoundment can result in higher mean salinities and the population expansion of the seagrass *Zostera capensins*, a species that thrives in salinity around 30 psu and can displace more brackish communities under increased salinity scenarios. The opposite pattern (i.e., the removal of *Zostera*) was observed in a Mediterranean lagoon due to an increase in freshwater flow from a hydroelectric plant (Bernard et al., 2005). Salinity was also found to be one of the main factors influencing the distribution, productivity, and competitive interactions between native and invasive macrophytes in King's Bay, a spring-fed system in Florida's Gulf Coast (Frazer et al., 2006). In this system, increases in salinity due to drought conditions and storms that enhance saltwater intrusion can provide the salinity-tolerant native macrophyte *Vallisneria americana*, a competitive advantage over the less tolerant invasive species *Myriophyllum spicatum* and *Hydrilla verticillata*.

Macroalgae, an important component of the benthic community of Biscayne Bay, also showed spatial and seasonal patterns influenced by salinity. Experimental studies showed that drift macroalgae have a higher tolerance for lower salinity and faster growth rates in the fall and winter seasons when temperatures are lower. In contrast, rhizophytic macroalgae have a limited tolerance for low salinity (<20 psu) and faster growth rates in the summer when water temperatures are higher (Biber & Irlandi, 2006). In this study, the spatial and seasonal distribution and abundance of drift macroalgae in western Biscayne Bay agreed with the growth data of Biber and Irlandi (2006). Drift macroalgae were more abundant in the cooler dry season and had a higher abundance in the canal-influenced southern region of Biscayne Bay. Seasonal peaks in high abundance of drift macroalgae during cooler periods have also been observed in other estuaries (Benz et al., 1979). In contrast, no clear seasonal patterns in the abundance of drift macroalgae were detected by Riegl et al. (2005) in subtropical Indian River Lagoon, Florida, and by Kopecky and Dunton (2006) in two Texas estuaries.

The increase in cover of rhizophytic algae in the warmer wet season is consistent with previous reports of maximal growth in the summer for calcareous

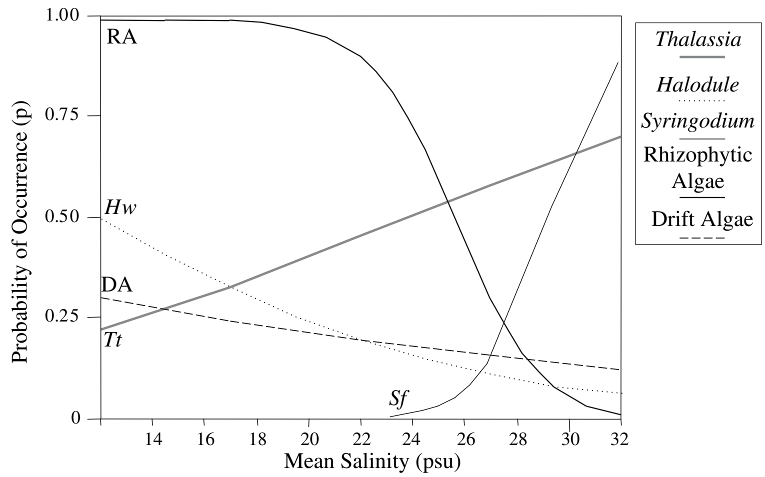

Fig. 6 Probability of occurrence of SAV taxa in relation to mean salinity during the wet season fitted with logistic regression. The low abundance of *Ruppia* precluded this species from being included in this analysis

green macroalgae including *Halimeda*, *Penicillus*, and *Udotea* (Bach, 1979; Collado-Vides et al., 2005; Biber & Irlandi, 2006). However, the significant increase in abundance of this functional group in the canal-influenced region during the wet season when salinity is lowest is contrary to the predictions of Biber et al. (2003) and the field observations of Stockman et al. (1967) and Biber and Irlandi (2006) who reported a reduced abundance of this stenohaline functional group in areas with low and variable salinity. The rhizophytic algae in Biscayne Bay represent a heterogeneous group composed of species with distinct susceptibility to salinity patterns. While the calcareous green genera within this group (i.e., *Halimeda*, *Penicillus*) have been shown to have reduced growth and abundance under low salinity conditions (Biber & Irlandi, 2006), other genera such as *Chara* and *Batophora* are commonly associated with low and variable salinity (Montague & Ley, 1993). In fact, the large increase in biomass of rhizophytic algae documented in the wet season in the canal-influenced region of western Biscayne Bay was due mainly to the high abundance of *Chara* and *Batophora*. These results agree with Collado-Vides et al. (2005), who suggested that while the functional-group approach simplifies the documentation of large-scale patterns of abundance by grouping similar species together, it might not be adequate when the species within a functional group respond differently to environmental factors.

The significant relationship between salinity patterns and the spatial and seasonal changes in abundance of SAV observed in this study does not discount the influence of other factors such as temperature, light, nutrient availability, and grazing that commonly influence macrophyte abundance and distribution (Larkum et al., 2006). Indeed, the influence of multiple physical factors was demonstrated by Fourqurean et al. (2003) who analyzed both water quality and seagrass distribution patterns in Florida Bay and concluded that mean salinity and salinity variability alone could be used to correctly classify 16.7% of stations, but the predictive capabilities of their discriminant function increased to >55% after the inclusion of irradiance, sediment depth, and nutrient and organic carbon availability in the model.

Seasonal patterns of SAV growth are influenced by temperature and, even in the subtropical climate of South Florida, it was expected that the seasonal productivity would be higher in the warmer wet season (Fong & Harwell, 1994; Biber et al., 2003). The temperature patterns documented during 2005 showed a significant increase in mean seawater temperature (up 8°C) between seasons that can account for the increase in biomass for some SAV taxa in the wet season but, unlike salinity, temperatures did not show distinct spatial patterns that could explain the observed spatial patterns of SAV distribution and abundance. The influence of salinity on the ecological niche (Rotenberry et al., 2006) that a species can occupy is especially evident when the expectation of higher biomass in the wet season is considered. Namely, increases in abundance and spatial extent of seagrasses in the warmer wet season were only observed in the areas where salinity

Table 5 Percent cover (S.D.) of benthic organisms in Western Biscayne Bay in the 2005 Dry (March–April) and Wet (July–August) seasons

Buffer (m)	100		200		300		400		500		*P* value		
Depth (m)	0.5 (0.3)		0.7 (0.3)		0.9 (0.3)		1.0 (0.3)		1.0 (0.3)				
Season	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Season	Buffer	Interaction
T. testudinum	14.1 (25.5)	12.6 (25.2)	11.8 (17.1)	19.9 (28.3)	28.3 (33.4)	21.5 (27.0)	23.2 (24.0)	26.8 (31.3)	31.3 (36.2)	27.0 (32.1)	ns	<0.05	ns
H. wrightii	3.5 (7.9)	7.5 (10.2)	4.1 (3.9)	7.0 (8.2)	5.7 (16.2)	2.5 (23.7)	6.7 (5.1)	2.2 (13.9)	1.9 (0.6)	1.5 (7.6)	ns	ns	ns
S. filiforme	1.0 (8.3)	2.2 (15.1)	0.9 (8.6)	2.1 (14.9)	4.6 (15.9)	10.6 (5.1)	0.9 (10.6)	6.2 (5.5)	0.1 (3.8)	2.8 (3.3)	<0.05	<0.05	ns
R. maritime	0.05 (0.3)	0.02 (0.1)	0.06 (0.4)	0.01 (0.04)	0	0	0	0	0	0.01 (0.04)	ns	ns	ns
Attached algae	3.4 (20.4)	39.4 (7.7)	3.5 (21.0)	22.0 (8.4)	2.5 (16.2)	24.4 (12.4)	7.4 (14.4)	20.4 (14.6)	3.6 (18.1)	23.7 (10.5)	<0.05	<0.05	<0.05
Drift algae	11.5 (8.4)	2.1 (38.2)	14.7 (8.9)	3.2 (28.7)	12.1 (5.3)	5.6 (30.5)	9.6 (18.4)	8.3 (27.3)	15.0 (7.9)	7.9 (27.9)	<0.05	<0.05	ns

Survey sites were distributed among 100-m buffers at increasing distance from shore. The mean cover of each taxon was compared among buffers and between the dry and wet seasons using a 2-way Analysis of Variance with season and buffer as main factors. ns = no significant differences

patterns were within the tolerance range of each species. *Syringodium filiforme* increased in abundance and spatial distribution only in the area with limited influence of canal discharge, while *H. wrightii* experienced significant increases in both abundance and spatial distribution only in the region of canal influence. In the wet season, as the area of low and variable salinity expands due to the higher flow of fresh water, so does the ecological niche that can be occupied by *H. wrightii*. Moreover, *T. testudinum*, the seagrass species with the widest distribution showed increases in abundance in the northern region (area with higher-salinity and lower-salinity variability) and corresponding decreases in the southern, canal-influenced region where lower, more variable salinity resulted in lowered productivity.

Detailed information on other abiotic (e.g., light, nutrients, pollutants) and biotic (e.g., grazing) factors known to influence SAV productivity is presently lacking for nearshore habitats of Biscayne Bay and the documentation of these additional factors at a scale commensurable with the benthic monitoring program is needed to develop better predictive capabilities in support of future habitat restoration efforts (Dennison et al., 1993). A limited number of water quality stations (n = 25) have been surveyed quarterly since 1994 in Biscayne Bay but none of these stations are located in nearshore habitats (<500 m from shore); thus the patterns documented at these locations are not fully representative of nearshore environments (Caccia & Boyer, 2005). Nevertheless, relationships were established between salinity and nutrient patterns, with higher nutrient concentrations associated with lower salinity values. The significant spatial and temporal correlation between freshwater input and nutrient availability suggests that nutrients may play a role in determining the abundance and distribution patterns of SAV documented in this study. However, experimental studies need to be performed in the future to accurately evaluate the relative influence of salinity and nutrients on SAV communities of nearshore habitats. The main sources of N and P, the South Dade agricultural basins, the Black Point Landfill and Sewage treatment plant, and freshwater canals, are all located in the southern portion of the study region (Caccia & Boyer, 2005) and the dominance of early successional species like *H. wrightii*, which are able to thrive and outcompete the competitive dominant

T. testudinum under high-nutrient conditions (Fourqurean et al., 1995), in the vicinity of canals highlights the interactive role between salinity and nutrients. Low canal discharge, better connection to the open ocean, and lower water residence times combine to keep nutrient concentrations lower in northern region of the study area where *Syringodium* and *Thalassia* coexist. Chlorophyll a content and turbidity exhibited minor seasonal variations but very limited spatial trends between the north and south areas of the study region (Caccia & Boyer, 2005) suggesting that light requirements may play a secondary role in determining species distribution in the shallow habitats of nearshore western Biscayne Bay.

The Comprehensive Everglades Restoration Plan (CERP), approved by the US Congress in 2000, is the largest environmental restoration project in the world and the role of freshwater distribution within the system plays a central role within this program. One of the main objectives of this engineering project is to recapture and redistribute fresh water now "lost to tide" to restore the natural hydroperiod and increase flows into coastal habitats. The modification of freshwater flows into coastal lagoons has been the focus of restoration efforts not only in the United States, but in countries such as Mexico (Herrera-Silveira et al., 2000) and South Africa (Wortmann et al., 1997) as well**.** The principal restoration goals for Biscayne Bay are to: (1) restore quantities and timing of freshwater flows into littoral habitats; (2) modify the present drainage system by replacing point-sources of freshwater inflow to the shoreline through canals with an upstream spreader system that would restore a more natural overland flow through coastal wetlands; and (3) reduce nutrient loads by allowing the uptake of nutrients by wetland vegetation prior to discharge (USACE & SFWMD, 1999; CERP, 2005). While the future impacts of the proposed activities on SAV and associated organisms are not known, performance measures that are based explicitly on the relationship between salinity patterns and the abundance and distribution of seagrasses and macroalgae have been proposed. More specifically, it is expected that the modification of freshwater deliveries will result in an increase in the abundance and an expansion in the spatial distribution of taxa with tolerance for lower salinity like *Chara*, *Halodule*, and *Ruppia*, and a reduction in the dominance of *Thalassia* (RECOVER, 2004). These predictions were tested for Florida Bay by Fourqurean et al. (2003) who showed, through simulation modeling, that a decrease in salinity by one-half of current values and an increase in salinity variability would indeed expand the range of *Halodule* and *Ruppia* while decreasing the extent of *Thalassia*.

The data presented here showed a significant relationship between salinity patterns (i.e., mean value, variability) and the seasonal abundance and spatial distribution of SAV in western Biscayne Bay, which supports the use of SAV as appropriate indicators of changes in water quality resulting from restoration projects. Nevertheless, it should be noted that the patterns reported were obtained for only a single year and that interannual variability in SAV abundance and distribution need to be fully documented to be able to discern the impacts of the restoration projects and evaluate restoration performance. The health of its coastal ecosystems is vital to the ecology and economy of Florida and it is important that the habitat value of the littoral environment be conserved or enhanced in the face of increasing human pressure. The role of these habitats as essential nursery habitat for estuarine and reef organisms is highly dependent on the extent and condition of the SAV (e.g., Jackson et al., 2001; Dahlgren et al., 2006), and, therefore, it is recommended that spatially and temporally resolved monitoring should be continued so that early-warning signals of unexpected or undesirable patterns can be detected in time and remediation steps implemented.

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