

Temporal and spatial dynamics of macroalgal communities along an anthropogenic salinity gradient in Biscayne Bay (Florida, USA)

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Received 2 June 2005; received in revised form 19 January 2006; accepted 2 February 2006

Abstract

The seasonal and spatial dynamics of two groups of macroalgae, drift algae and rhizophytes, commonly found in tropical seagrass meadows were studied. The aim of this study was to provide insight into how freshwater discharges may be altering seagrass-dominated nearshore tropical habitats. Species composition, biomass, and percent cover of macroalgae were collected at six *Thalassia testudinum* König dominated sites within Biscayne Bay, Florida, representing three salinity regimes: canal-influenced, natural sheet-flow, and oceanic conditions. Mean annual salinities in these three regimes correspond to 10, 25 and 35 psu, respectively, with much greater variability in the canal and sheet-flow regimes, than in the oceanic condition. There were distinct changes in the composition of the macroalgal community along this salinity gradient. Drift algae (*Chondria* spp., *Laurencia* spp.) were most commonly found at canal-disturbed sites (10–85 g m⁻²), while rhizophytic calcareous green algae (*Halimeda* spp., *Penicillus* spp.) were most abundant at the higher salinity oceanic sites (20–105 g m⁻²). Seasonal patterns exhibited by the two groups differed also, with drift algae being more abundant in the cooler dry-season months, while rhizophytic algae were more abundant during the warmer wet-season months. These periods of higher abundance correlated with higher growth rates (drift = 2.3% day⁻¹, rhizophytes = 0.85% day⁻¹) measured in representative species for each group. Grazing rates on drift algae were found to be low for tropical habitats and did not differ much between canal (0.44% h⁻¹) and oceanic sites (0.42% h⁻¹).

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Keywords: Macroalgae; Salinity; Canals; Distribution; Abundance; Growth

1. Introduction

Seagrass meadows are highly productive and ecologically important habitats within South Florida's estuaries and coastal lagoons, as well as throughout the world (Zieman, 1982; Larkum et al., 1989; Bortone, 2000). In Biscayne Bay, the structural complexity of the seagrass community includes many species of macroalgae (Dawes, 1987; Zieman, 1982) that can be coarsely grouped into drift algae (e.g., *Chondria* spp., *Laurencia* spp.), and rhizophytic algae (e.g., *Caulerpa* spp., *Halimeda* spp., and *Penicillus* spp.). Macroalgae may be present in these seagrass beds as large clumps of detached drift

algae (Josselyn, 1977; Williams-Cowper, 1978; Benz et al., 1979; Vírnsstein and Carbonara, 1985; Bell and Hall, 1997) that have the potential to alter seagrass productivity and biomass by shading (Bach and Josselyn, 1978; Cambridge et al., 1986; Hauxwell et al., 2001; but see Irlandi et al., 2004). In contrast, benthic rhizophytic algae are important in stabilizing sediments and adding organic matter, thereby facilitating seagrass succession (Williams, 1990; Thayer et al., 1994). The functional roles of macroalgae in seagrass-dominated tropical systems are therefore numerous and include increased habitat complexity, primary production and trophic cycling, as well as sediment stabilization and successional facilitation (Zieman, 1982; Larkum et al., 1989). Macroalgae, like seagrasses, can however be negatively impacted by the low and variable salinity conditions typical of anthropogenic freshwater discharges (Brook, 1981; Montague and Ley, 1993).

Gradients in salinity across Biscayne Bay, Florida, occur primarily as a result of anthropogenically altered regimes of freshwater runoff and delivery into the Bay. These gradients are associated with the presence of a wide-ranging canal drainage

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network, which is a conspicuous feature of the South Florida landscape (Alleman, 1995). Canal discharges are an important management concern in Biscayne Bay, due to the unnatural timing and volumes of freshwater discharged, which pose an important stressor to near-shore areas along the western (mainland) coastline (Gentile et al., 2001). Three different stress regimes associated with canal discharges can be defined: (1) habitats directly influenced by non-natural canal discharge; (2) areas with natural sheet-flow (characterized by shallow, slow-flowing, over-land runoff percolating through mangrove-lined shores); and (3) oceanic areas far from the influence of terrestrial freshwater inputs.

Salinity varies over the course of a year at canal and sheet-flow sites because of freshwater inputs, with lower salinities occurring during the summer/fall rainy season (Alleman et al., 1995). The oceanic sites, in contrast, experience more constant salinities, near 35 practical salinity units (psu) year round. The artificial delivery of freshwater from canals results in acute low-salinity pulses, especially in the region immediately surrounding canal mouths (Chin-Fatt and Wang, 1987; Nnaji, 1987). These low-salinity events have previously been identified as a threat to the ecological function of near-shore benthic habitats, especially seagrass beds, in the Bay (Brook, 1981; Montague and Ley, 1993). Even so, seagrass beds occur both in areas of fluctuating low salinities near canals, as well as in oceanic areas where salinities are relatively high and more stable. We have previously shown that while the standing stock of the seagrass *Thalassia testudinum* König (turtlegrass) itself is not obviously affected by the presence of low-salinity water discharged from adjacent canals, as reported also by Thorhaug and Roessler (1977), its primary production is greatly reduced at low-salinity sites (Irlandi et al., 2001). Furthermore, there are noticeable differences in the macroalgal community present in seagrass habitats at canal sites that are impacted by recurring low-salinity pulses, when compared to those occurring in high salinity oceanic sites. We hypothesize that these spatial differences observed in the macroalgal community structure in these seagrass beds may occur because of the low and variable salinity imposed by anthropogenic freshwater discharges from canals. This study provides data on the composition, distribution, abundance, and growth of macroalgal groups under three different salinity scenarios with the aim to provide insight into how canal discharges may be altering seagrass-dominated nearshore tropical habitats.

2. Material and methods

Macroalgal communities were sampled over several years (1996–1999) over a range of salinity conditions, including seagrass beds influenced by canal discharge (low salinity), sheet-flow (intermediate salinity), and oceanic water (normal 35 psu salinity) as part of several independent programs conducted to provide monitoring data on *T. testudinum* habitats in Biscayne Bay (e.g., Irlandi et al., 2001). Six sites were sampled (Fig. 1): canal sites included Fender Point (25°29.643'N, 80°19.822'W) and Manatee Bay (25°15.390'N, 80°25.394'W); sheet-flow sites included Little Card Sound

(25°17.814'N, 80°22.373'W) and Barnes Sound (25°17.494'N, 80°23.246'W); and oceanic sites included Sands Key (25°30.004'N, 80°11.497'W) and Broad Creek (25°20.939'N, 80°16.316'W). All sites were located in shallow-water (<2 m depth), near-shore, mangrove-lined *T. testudinum* habitats to minimize between site habitat differences (e.g., Lapointe et al., 1987).

Macroalgae in this study were identified using keys provided by Taylor (1960), Woelkerling (1976), Wynne (1998), and Littler and Littler (2000). Macroalgae were broadly categorized into two ecological groups: drift algae (e.g., *Laurencia*, *Hypnea*) and rhizophytic algae (e.g., *Halimeda*, *Penicillus*) for further analyses (Table 1).

2.1. Physical environment

Light data were obtained from the NOAA Coastal Marine Automated Network (C-MAN) weather station at Fowey Reef (25°35.4'N, 80°06.0'W) from 1993 to 1998. Hourly readings of photosynthetically active radiation (PAR) in the 400–700 nm spectral bands were averaged to obtain daily mean, and minimum and maximum surface irradiance values. A 30-day moving average was calculated to elucidate monthly trends in surface irradiance (I_0). Attenuation coefficients (k) measured in summer and winter at a canal (FP) and an oceanic (SK) site were used to determine the average light available to benthic algae at a depth of 1 m at these two sites. Seasonally averaged light attenuation was less for oceanic ($k = 0.30 \text{ m}^{-1}$) compared to canal ($k = 0.47 \text{ m}^{-1}$) sites. Mean photon flux at 1 m depth ranged from 200 to 500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ with the highest levels observed during March and April. Summer cloud cover reduced total light availability even though higher solar irradiance occurs in the summer. Minimum irradiance occurred in December, when mean photon flux fell below the photosynthetic saturation levels of the algae studied (Josselyn, 1977; Bach, 1979; Biber, 2002).

Representative water temperature and salinity data for study sites in Biscayne Bay were obtained from hourly datasets collected over 3 years in Biscayne National Park (BNP), at a canal (25°31.637'N, 80°18.243'W) and an oceanic site (25°23.790'N, 80°15.900'W). Mean daily water temperatures and salinities, as well as minimum and maximum values were calculated for each site from this data. Daily mean water temperature at both the canal and oceanic site ranged from 18 to 32 °C over a typical year. Winter and summer temperature extremes ranged from approximately 12 to 35 °C. In summer, mean water temperatures exceeded 30 °C for 80 days at the canal site and 71 days at the oceanic site. In winter, low temperature events were associated with winter cold fronts, which caused rapid drops in water temperature (>5 °C) within 12–24 h.

The canal site had the greatest variability in salinity, with mean salinities ranging from 15 to 35 psu, while mean salinity at the oceanic site was nearly constant at 35 psu year round. The influence of freshwater discharges results in lowered mean salinity values for the canal sites (25.4 ± 9.5 psu), less than oceanic (37 ± 1.5 psu), and sheet-flow (35.9 ± 4.2 psu)

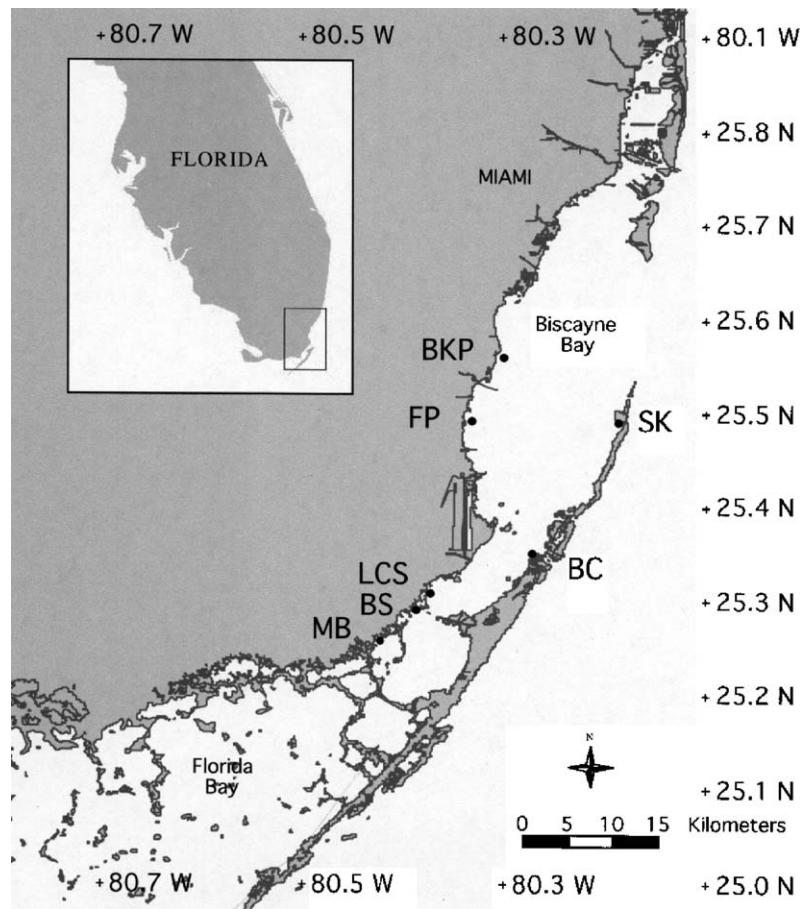


Fig. 1. Location of study sites in Biscayne Bay, FL. Two to three sites in each salinity regime were sampled: canal sites included Fender Point (FP), Black Point (BKP), and Manatee Bay (MB); sheet-flow sites included Little Card Sound (LCS) and Barnes Sound (BS); and oceanic sites included Sands Key (SK) and Broad Creek (BC).

Table 1
Species of algae collected and identified at the six study sites in Biscayne Bay, FL

Drift algae		Rhizophytic algae	
<i>Acanthophora spicifera</i> (Vahl) Børgesen	R	<i>Acetabularia crenulata</i> J.V. Lamouroux	C
<i>Ceramium nitens</i> (C. Agardh) J. Agardh	R	<i>Avrainvillea levis</i> M. Howe	C
<i>Chondria atropurpurea</i> Harvey	R	<i>Avrainvillea nigricans</i> Descaigne	C
<i>Chondria cnicophylla</i> (Melville) de Toni	R	<i>Batophora oerstedii</i> J. Agardh	C
<i>Chondria floridana</i> (Collins) M. Howe in W.R. Taylor	R	<i>Caulerpa ashmeadii</i> Harvey	C
<i>Chondria littoralis</i> Harvey	R	<i>Caulerpa cupressoides</i> (Vahl) C. Agardh	C
<i>Chondria</i> sp. C. Agardh	R	<i>Caulerpa mexicana</i> Sonder ex. Kützing	C
<i>Cladophora</i> spp. Kützing	C	<i>Caulerpa paspaloides</i> (Bory de Saint-Vincent) Greville	C
<i>Dasya baillouviana</i> (S.G. Gmelin) Montagne	R	<i>Halimeda discoidea</i> Descaigne	C
<i>Dasya ramosissima</i> Harvey	R	<i>Halimeda incrassata</i> (J.Ellis) J.V. Lamouroux	C
<i>Dictyota caribaea</i> Hörnig and Schnetter in Hörnig et al.	P	<i>Halimeda monile</i> (J.Ellis and Solander) J.V. Lamouroux	C
<i>Digenea simplex</i> (Wulfen) C. Agardh	R	<i>Halimeda opuntia</i> (Linnaeus) J.V. Lamouroux	C
<i>Gracilaria tikvahiae</i> McLachlan	R	<i>Halimeda simulans</i> M. Howe	C
<i>Hypnea spinella</i> (C. Agardh) Kützing	R	<i>Halimeda tuna</i> (J.Ellis and Solander) J.V. Lamouroux	C
<i>Jania adherens</i> J.V. Lamouroux	R	<i>Penicillus capitatus</i> Lamarck	C
<i>Jania capillacea</i> Harvey	R	<i>Penicillus dumetosus</i> (J.V. Lamouroux) Blainville	C
<i>Laurencia intricata</i> J.V. Lamouroux	R	<i>Rhypocephalus phoenix</i> (J. Ellis and Solander) Kützing	C
<i>Laurencia poiteaui</i> (J.V. Lamouroux) M. Howe	R	<i>Udotea caribaea</i> D.S. Littler and M.M. Littler	C
<i>Polysiphonia echinata</i> Harvey	R	<i>Udotea flabellum</i> (J. Ellis and Solander) M. Howe	C
<i>Polysiphonia</i> spp. Greville	R		
<i>Sargassum</i> sp. C. Agardh	P		
<i>Spyridia filamentosa</i> (Wulfen) Harvey in W. Hooker	R		

The abbreviations for the three taxonomic divisions are: chlorophyta (C), phaeophyta (P), and rhodophyta (R).

conditions. Salinity at the ocean site dropped below 25 psu for only 8 days, compared to 325 days at the canal site. At the canal site, minimum salinity of less than 10 psu was recorded on 55 days per year.

2.2. Algal biomass and percent cover

The multi-year (1996–1999) sampling program can be divided into three distinct phases, based on the methods used to sample the algal community. The reason different methods were used is that this study summarizes the results obtained from three different monitoring programs, each with different aims, that were conducted over a 4-year period. This longer time series allows us to examine temporal and spatial patterns that would not have become evident from analyzing each of the three shorter studies independently.

2.2.1. Phase I

In 1996–1997, samples were collected in February (dry season) and August (rainy season) of each year. At each of the six sites a rectangular grid of six permanent buoys spaced 50 m apart was arranged as depicted in Fig. 2. During each sampling period, meter square PVC quadrats ($n = 12$) were positioned in two random directions and distances from each buoy. Percent cover of drift and rhizophytic macroalgae was recorded and all biomass in the quadrat was collected. The samples were returned to the laboratory and frozen until processing, when they were sorted and identified to the species level when possible. Biomass (g m^{-2}) was then determined after drying the samples at 70 °C to a constant weight.

2.2.2. Phase II

For this and the third phase of sampling, the Manatee Bay site was dropped in favor of a different canal site at Black Point (25°33.548'N, 80°17.959'W) that was located closer to the area where high canal-discharge volumes flow into the Bay (Fig. 1). Sampling was performed at monthly intervals during September 1997 through August 1998. Presence or absence of drift algae was determined from ten replicate 0.25 m² quadrats located haphazardly at each site (Fig. 2). All biomass in those quadrats that contained drift algae was collected and processed as discussed above. Percent cover of drift algae was determined monthly in four permanent 0.25 m² quadrats, along five transect lines ($n = 20$ quadrats). The 25 m long polypropylene transect lines were 10 m apart, marked at 1 m intervals, and anchored with a subsurface PVC pole at either end.

2.2.3. Phase III

From August 1998 to August 1999 photographs were taken of twelve 1 m² areas at each site. Permanent quadrats were placed in arrays of three blocks of 4 m², separated by about 50 m (Fig. 2). Every 6 weeks the quadrats were photographed, then digitized, and % cover of drift algae was determined using NIH Image Version 1.61 software (National Institutes of Health, <http://rsb.info.nih.gov/nih-image/index.html>). In addition, at every other sampling interval (every 3 months), a fourth

randomly established 4 m² block was photographed and all the drift and rhizophytic biomass collected. The algal samples were returned to the laboratory for routine processing. Linear regressions of biomass to percent cover relationships were determined from this dataset for each salinity regime.

2.3. Algal growth experiments

Microcosm studies were performed to determine the growth rates of common representatives of the two functional groups: *Laurencia* (drift algae), *Halimeda*, and *Penicillus* (rhizophytic algae). Plants were collected quarterly (winter = February, spring = May, summer = August, autumn = November) from Biscayne Bay and transported back in aerated coolers to the outdoor mesocosm facilities at the University of Miami within 3 h of collection, where they were placed in flow-through holding tanks for no longer than 24 h before the start of each experiment. For each species, 10 thalli (approx. 10 g blotted wet weight) were placed inside 10 replicate 9.4 L aquaria filled with seawater at three salinities: 35 psu to represent mean oceanic salinity (control), 20 psu, the mean annual salinity in canal-influenced sites, and 10 psu, indicative of a low-salinity event observed when benthic algae are exposed to a plume of freshwater after a large discharge event. Salinities in the microcosm tubes were mixed by dilution of Bay water with reverse osmosis water and adjusted every few days by adding reverse osmosis water to compensate for evaporation losses in the greenhouse facility.

Four cylindrical aquaria (used as static growth chambers and each containing one thallus) were placed inside 120 L tanks designed as a flow-through system for temperature control. Abiotic conditions during experiments in each of the four seasons are summarized in Table 4. An air stone placed in each cylinder provided circulation to reduce boundary layer effects on nutrient uptake rates by the algae (e.g., Mann and Lazier, 1996). Drift algal thalli were weighed initially and at the end of the growth study (5–7 days). For the growth studies, growth was recorded as percent change per day using the following formula:

$$\% \text{ daily growth} = 100 \frac{[\ln(\text{wt}_{t1}/\text{wt}_{t0})]}{t}$$

where wt_{t0} = initial weight, wt_{t1} = final weight, t = time.

The rhizophytes, *Penicillus* and *Halimeda*, were stained overnight (12–14 h) prior to the experiment using Alizarin Red S (Sigma Chemicals) at a concentration of 0.2 g L⁻¹. Alizarin red has been successfully applied to determine in situ growth rates of corals (Lamberts, 1978), as well as calcified marine algae (Wefer, 1980; Payri, 1988; Davis and Fourqurean, 2001). The algae were subsequently rinsed thoroughly in flowing seawater to purge residual stain that had not been incorporated into the thallus. One individual of each genus was “planted” into a 500 mL plastic flowerpot using weathered limestone gravel to anchor the thalli in an upright position, before placing the pot and algae in a microcosm cylinder. After 1 week, the thallus was bleached for 10–20 min in a 25% bleach solution to remove chlorophyll pigments, dried at 70 °C to constant

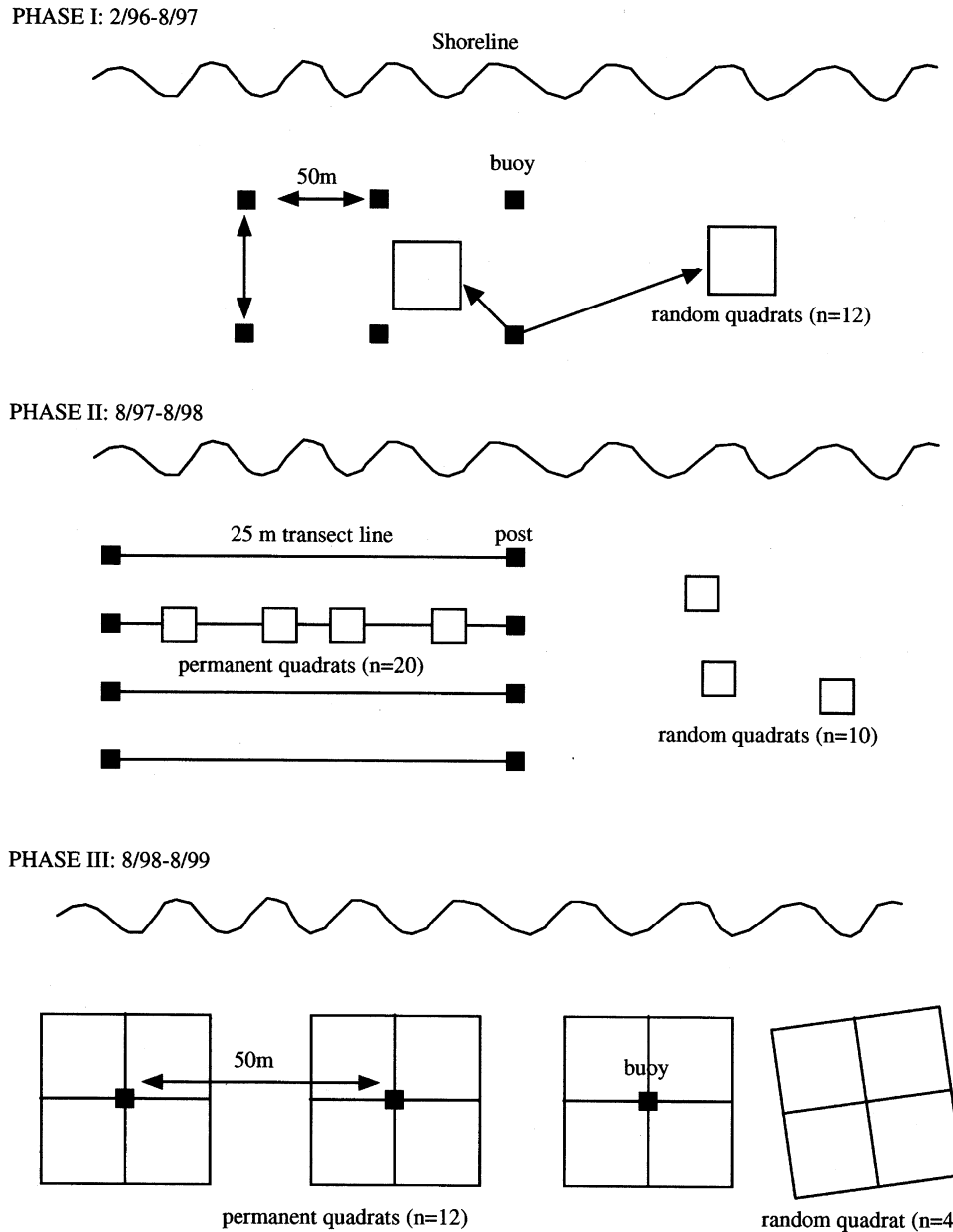


Fig. 2. Sampling designs employed during the three phases of community analysis. Buoys and posts were permanent fixtures for the duration of each sampling phase. Random quadrats were relocated during each sampling interval, so that a given area was sampled destructively only once.

weight, and any unstained tissue (US) was removed and weighed separately. This new growth was compared to the initial biomass (stained tissue = S), and daily growth rates were calculated using the formula:

$$\% \text{ daily growth} = 100 \frac{[\ln(\{S + US\}/S)]}{t}$$

2.4. Field grazing assays

Assays using the alga *Laurencia poiteau* were done to compare the intensity of grazing among sites (Hay, 1981) that may contribute to spatio-temporal patterns in abundance. Freshly collected pieces of algae were pre-weighed and woven

into 10 cm pieces of three-strand nylon rope. Two marked ropes with their associated pre-weighed algae were attached to a wooden dowel with cable ties 180° apart, and the dowels were then inserted into the sediment to anchor the ropes just above the seagrass canopy. Ten dowels, each with two clumps of algae, were placed on the bottom along each of the five permanent transect lines at each site in phase II and collected after 2 days. The remaining algal tissue was weighed. Control ropes (in cages) were also placed in the seagrass beds at the same time to determine changes in algal biomass due to growth or handling losses. Changes in biomass on grazed ropes were corrected for changes in the controls to determine losses principally due to grazing. Grazing assays were performed in October 1997, January and April 1998.

2.5. Statistics

Statistical analyses were performed using JMP Version 3.1.5 for Apple Macintosh from the SAS Institute Inc., Cary, NC. Data were tested for normality and heteroscedasticity and normalized where appropriate (Sokal and Rohlf, 1995). Non-parametric analyses were performed on those data that did not fulfill the assumptions required for parametric tests. Post-hoc tests using Tukey's HSD were performed on significant results obtained to determine groups that had statistically different means.

3. Results

3.1. Species composition

Macroalgae identified during this study included 19 species of rhizophytes (R) in 8 genera, and 22 species of drift algae (D) in 14 genera (Table 1). Of the rhizophytes, *Halimeda* had the most species (6 species), followed by *Caulerpa* (4 species), and *Avrainvillea*, *Penicillus*, and *Udotea* (2 species). In the drift algae, *Chondria* had the most species (5 species), followed by

four genera claiming 2 species each (*Dasya*, *Jania*, *Laurencia*, *Polysiphonia*). Number of species increased from the canal sites (5R + 12D = 17spp.), through the sheetflow sites (11R + 16D = 27spp.), to the oceanic sites (17R + 17D = 34spp.). Total macroalgal biomass was greater in summer (August) than winter (February) samples in all three salinity regimes (Table 2).

The dominant macroalgal species observed in the seagrass beds at the two canal sites were primarily rhizophytes in the genera *Chondria*, *Laurencia*, and *Polysiphonia*, all in the drift algae functional group (Tables 1 and 2). *Polysiphonia* was also found growing epiphytically on *T. testudinum* blades. Rhizophytic algae that were common at the canal sites included *Acetabularia crenulata*, *Batophora oerstedii* and *Penicillus capitatus*, which occupied areas that were not covered by the seagrass *T. testudinum*. *Penicillus* was the most abundant alga by dry weight in three of the four sampling months, with the exception of February 1996, when *Polysiphonia* was more abundant (Table 2).

Species richness in the sheet-flow sites was transitional between the canal-influenced community and the oceanic community (Tables 1 and 2), and this was the only regime

Table 2
Mean biomass (g DW m⁻²) of various genera of macroalgae collected during phase I from the three salinity regimes in Biscayne Bay

	Canal				Sheet-flow				Ocean			
	9602	9608	9702	9708	9602	9608	9702	9708	9602	9608	9702	9708
Rhizophytes												
<i>Acetabularia</i>	0.00	0.02		0.01	0.44	0.26	2.99	0.03		0.09		
<i>Avrainvillea</i>							0.25	0.07				
<i>Batophora</i>	3.53	0.98	0.44	0.50	2.34	0.13	0.93	0.96				
<i>Caulerpa</i>					2.75	7.13	5.15	1.68		1.46		
<i>Halimeda</i>			0.15		2.04	10.80	3.69	6.20	18.19	62.18	75.09	109.05
<i>Penicillus</i>	3.97	69.30	62.90	56.60	3.74	1.61	1.85	1.79	8.26	15.98	4.57	14.17
<i>Rhipocephalus</i>						0.46			0.12	0.30	0.12	3.12
<i>Udotea</i>				7.03	1.33	0.34	1.62	0.95		1.73	1.54	
Rhizo total	7.50	70.29	63.48	64.14	12.64	20.72	16.49	11.69	26.57	81.74	81.31	126.34
Drift												
<i>Acanthophora</i>									0.12	0.01		
<i>Amphiroa</i>						0.08				0.19		
<i>Anadyomene</i>					0.18	0.22	0.04	0.66	0.17	0.07		
<i>Ceramium</i>					0.00						0.12	
<i>Champia</i>										0.11	0.17	
<i>Chondria</i>	1.71	6.25	21.02	16.73	1.49	52.99	3.55	0.12		0.62	0.25	
<i>Cladophora</i>	0.04	0.46	0.14		2.02	4.21	0.75	0.18				
<i>Dasya</i>					0.21		0.00		0.35		0.04	
<i>Dictyosphaeria</i>										0.37		1.88
<i>Dictyota</i>										4.47	1.16	1.68
<i>Digenea</i>			0.33	0.56	0.04		1.28	1.44				
<i>Gracilaria</i>										2.69		
<i>Herposiphonia</i>									0.76		0.05	
<i>Hypnea</i>										1.45		0.01
<i>Laurencia</i>	1.11	1.93	4.82	11.47	6.37	5.08	16.44	55.51	0.51	2.48	1.05	5.38
<i>Polysiphonia</i>	14.40	6.27	1.06	0.85	37.83	1.05	10.13	0.11	1.02			0.10
<i>Sargassum</i>			0.60	0.36		0.28				0.06		
<i>Spyridia</i>							1.06			0.14	0.99	
Drift total	17.26	14.91	27.97	29.97	48.16	63.91	33.26	58.02	2.93	12.65	3.82	9.04
Total biomass	24.76	85.20	91.45	94.11	60.80	84.63	49.75	69.71	29.50	94.39	85.13	135.4

Dates are formatted as YYMM. Genus with the highest biomass in each of the two groups is indicated in bold.

where drift biomass exceeded rhizophyte biomass (Table 2). At the Barnes Sound site, drift algae in the genera *Chondria*, *Cladophora*, *Digenea*, *Laurencia*, *Polysiphonia*, *Sargassum*, and *Spyridia* were observed to be the most abundant species, while the rhizophytic algae were represented primarily by *Acetabularia* and *Batophora*. In contrast, the Little Card Sound site had many additional species of rhizophytic algae (*Avrainvillea*, *Caulerpa*, *Halimeda*, *Penicillus*, *Rhizocephalus*, and *Udotea*), as well as many of same genera of drift algae that were found at Barnes Sound, albeit in lower abundance (Table 1).

The two oceanic sites had the highest number of species of the three salinity regimes investigated (Table 1). Species found here were predominantly members of the rhizophytic functional group including *Avrainvillea*, *Caulerpa*, *Halimeda*, *Penicillus*, *Rhizocephalus*, and *Udotea*. *Halimeda* and *Penicillus* were the two most abundant genera by biomass in all four sampling periods (Table 2). Drift algae were rarely encountered in any large abundance in the quadrats in the oceanic regime (Table 2), however, the number of species encountered was greater than at the canal or sheet-flow sites (Table 1). Of this functional group, the most abundantly encountered genera were *Dictyota*, *Laurencia*, and *Polysiphonia* (Table 2).

3.2. Biomass

Biomass of drift algae was greater in samples collected from seagrass beds in the canal sites than the other two salinity regimes, with the exception of phase 1, when drift algae were more abundant in the sheet-flow sites than the canal sites. In contrast, rhizophyte biomass was always greatest in the seagrass habitats found at the oceanic sites (Table 2).

Drift algae typically had higher biomass during the spring and summer and lowest biomass in late fall (Table 2). In the canal regime, mean biomass ranged from 10 to 85 g m⁻², while at the sheet-flow (5–60 g m⁻²) and oceanic sites (<18 g m⁻²) there was less drift biomass present (Table 2). The maximum biomass of drift algae occurred in January 1999 at both the canal and oceanic sites (Table 2). The oceanic regime had the lowest average standing stock, but some samples with higher biomass (20–30 g m⁻²) were present in winter and spring, indicating temporally patchy occurrence of drift algae in this regime.

Rhizophytic algae were most abundant in the oceanic regime and least abundant in the sheet-flow regime (Table 2). Average biomass in the oceanic regime ranged from 20 to 105 g m⁻², while the canal (5–58 g m⁻²) and the sheet-flow (<13 g m⁻²) regimes both had lower rhizophyte biomass. Seasonal biomass dynamics of rhizophytes were similar among the three salinity regimes with biomass highest in summer and lower during the winter months. The maximum biomass was recorded in August 1996 and August 1997 at the sheet-flow and oceanic sites, respectively, while the lowest biomass in these two regimes occurred in January 1999 and February 1996, respectively (Table 2).

3.3. Percent cover of drift algae

Drift algae occurred in patches, and were not present in all quadrats sampled (Table 3). The number of quadrats containing drift algae varied between 35 and 95% of quadrats in the canal sites, 10 and 55% in the sheet-flow, and 0 and 40% in the oceanic sites (Table 3). In the canal regime, the average area covered by drift algae was between 5 and 40% in any given quadrat depending on month sampled; the maximum area covered frequently exceeded 75% on sampling dates after April 1998, but not before. This apparent increase in percent cover coincides with a trend for greater biomass over the same time period (Table 2). The increase in drift algae was greater at the FP than at the BKP site over this period. In the sheet-flow regime, percent cover ranged from 5 to 50% on average (Table 3) and the highest percent cover encountered was typically less than at the canal sites on any given sampling date (Table 3). The majority of the drift algae were collected at the BS site, with only a small contribution from LCS (Table 3). The oceanic regime had the lowest percent cover of drift algae, ranging from 0 to 25%, with peak cover less than 50% (Table 3). The cover of drift algae was sporadic and patchy at both oceanic sites, with occasional extensive coverage by drift algae, e.g., 44% in one quadrat at BC on January 1998 (Table 3). The trend observed in the percent cover data is in agreement with the data collected on algal biomass across the three salinity regimes, as drift algae declined in abundance from canal to oceanic sites.

Linear regressions of biomass (Y) to percent cover (X) for the drift algae were calculated for each salinity regime. Predicted biomass at 100% cover in a 1 m² quadrat (the slope of the regression) was highest in the canal sites (268 g m⁻², $r^2 = 0.76$, $n = 112$), almost double that found in the sheet-flow sites (137 g m⁻², $r^2 = 0.74$, $n = 81$), with oceanic sites intermediate (180 g m⁻², $r^2 = 0.45$, $n = 63$). However, the low coefficient of determination (r^2) for the oceanic sites indicates that percent cover is not the only variable important in explaining the variation present in the biomass data in this regime. The difference in the amount of biomass per % cover between salinity regimes is indicative of the density of clumps of drift algae. In canal sites, drift algae were usually present in thick dense mats covering large areas of the bottom, whereas in the sheet-flow and oceanic sites, drift algae were sparse and often did not form the large extensive clumps that were present in the canal sites.

3.4. Algal growth experiments

Mean growth rates of drift algae that were collected from canal sites in Biscayne Bay and kept in 9.4 L aquaria at the microcosm facility at the University of Miami ranged from 0.07 to 2.28% increase in weight per day (Table 5). Significantly higher growth rates occurred in the drift alga, *L. poiteaui*, during fall and winter when water temperatures were cooler (Table 4), and at the higher salinities of 20 and 35 psu (Tables 5 and 6).

In contrast, the rhizophytic algae (*P. capitatus* and *Halimeda incrassata*) collected from oceanic sites, exhibited higher

Table 3
Mean (\pm S.E.) percent cover of drift algae recorded at the six sites within the three salinity regimes in Biscayne Bay

	Canal		Sheet-flow		Ocean	
	FP	MB/BKP	BS	LCS	BC	SK
Phase I						
9602	0.0	0.0	0.0	14.3(2.48)	4.0	0.0
9608	0.0	15.0(6.83)	32.0	0.0	0.0	0.0
9702	13.3(4.62)	24.0	20.0(0.001)	4.0(0.001)	4.0	0.0
9708	0.0	0.0	0.0	0.0	0.0	0.0
Phase II						
9709	12.2(2.31)	24.2(4.57)			0.0	0.0
9710	12.4(2.52)	11.1(2.04)			24.0	0.0
9711	7.3(1.83)	5.5(1.14)			18.0	6.5(1.10)
9712	5.3(1.32)	3.4(0.71)			0.0	3.7(0.59)
9801	7.4(2.04)	3.6(0.75)			44.0	8.5(2.06)
9802	9.0(2.05)	6.6(1.40)			0.0	0.0
9803	13.6(2.56)	5.0(1.21)			22.5(5.85)	0.0
9804	11.7(2.01)	20.9(6.06)			16.7(4.58)	4.0(0.45)
9805	23.6(3.83)	27.9(8.32)			3.0	1.8(0.21)
9806	20.1(3.58)	26.6(7.93)			6.0(1.27)	1.0(0.00)
9807	13.3(2.43)	26.0(8.93)			7.5(1.11)	6.0
9808	19.3(3.83)	24.0(7.26)			2.2(0.29)	0.0
Phase III						
9808	32.2(9.27)	39.4(5.57)	17.1(6.35)	1.3(0.24)	0.0	0.0
9809	38.5(8.13)	4.8(0.49)	13.5(7.19)	1.1(0.07)	0.0	0.0
9811	33.3(10.09)	3.6(0.51)	22.6(5.87)	1.3	5.0	9.4(1.74)
9812	35.5(9.45)	4.3(0.71)	22.3(7.11)	1.7(0.51)	6.3	20.7(5.52)
9901	37.6(9.70)	9.3(2.35)	36.5(9.23)	2.3(0.43)	8.1(2.81)	14.2(3.29)
9903	44.9(10.77)	12.9(3.54)	53.0(8.78)	2.9	6.3(1.46)	4.6(1.45)
9905	52.8(10.49)	16.6(4.42)	37.4(6.88)	2.8(0.52)	3.0(0.35)	2.5
9906	46.6(10.28)	15.6(4.24)	8.4(3.58)	2.8(0.39)	3.8	1.8(0.50)
9907	49.2(13.83)	9.5(2.59)	4.4(1.30)	3.5(0.61)	0.0	5.0(0.85)

Three separate phases of data collection occurred from 1996 to 1999 (see Fig. 2), dates are formatted as YYMM. No sampling of drift algae was undertaken at sheet-flow sites during phase II.

growth rates in summer and fall (Table 5). Similar to drift algae, growth rates of rhizophytes were also significantly higher at 35 and 20 psu than at 10 psu (Tables 5 and 6). There was a significant season \times salinity interaction only for *H. incrassata*, with maximum growth rates occurring in warmer temperatures and higher salinity (Table 6). Mean daily growth rates for the two rhizophytic species, *P. capitatus* ($<0.84\%$ day⁻¹) and *H. incrassata* ($<0.07\%$ day⁻¹) were much less than those measured in the drift algal species *L. poiteaui* (Table 5).

3.5. Field grazing assays

Grazing rates were low, ranging from 12 to 30% of initial biomass in 48 h (Fig. 3). This is much lower than typically reported from other studies in tropical habitats, where all

biomass can be consumed in a few hours. Grazing did not differ much between canal and oceanic sites, but was higher in the canal site during two of the three assays (January, April). Grazing was higher in October and April than that measured in January in both salinity regimes (Fig. 3), possibly indicating a temperature effect.

4. Discussion

Knowledge about the physical environment, such as light, temperature, and salinity, is required to describe the conditions that may be responsible for the changes observed in macroalgal abundance in seagrass communities along a salinity range in Biscayne Bay. The values of light attenuation measured were somewhat lower than reported previously for *T. testudinum*

Table 4
Abiotic conditions experienced by macroalgae in the four seasonal growth experiments conducted in mesocosms located in a greenhouse

Season	Temperature (°C)	Irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$)	Photoperiod L:D (h)
Winter (February)	21–23	250 ^a (500 ^b)	11:13
Spring (May)	27–30	300 (650)	14:10
Summer (August)	31–33	300 (550)	14:10
Fall (November)	24–26	250 (475)	11:13

^a Daily mean photon flux.

^b Maximum photon flux averaged over 7 days.

Table 5

Mean (\pm S.E.) growth rates expressed as percent increase in weight per day for three species of macroalgae grown at three salinities and four seasons, $n = 8-9$

	10 psu	20 psu	35 psu	Mean
<i>L. poiteaui</i>				
Spring	0.00	0.53(0.243)	1.74(0.492)	0.757 B
Summer	0.07(0.069)	0.64(0.281)	0.75(0.282)	0.487 B
Fall	1.03(0.208)	2.13(0.544)	2.20(0.340)	1.787 A
Winter	0.63(0.282)	2.28(0.650)	2.16(0.499)	1.690 A
Mean	0.433 B	1.395 A	1.713 A	
<i>P. capitatus</i>				
Spring	0.00	0.01(0.009)	0.26(0.057)	0.090 B
Summer	0.00	0.32(0.062)	0.84(0.650)	0.387 A
Fall	0.07(0.073)	0.49(0.155)	0.60(0.128)	0.387 A
Winter	0.01(0.014)	0.02(0.018)	0.09(0.057)	0.040 B
Mean	0.020 B	0.210 A	0.448 A	
<i>H. incrassata</i>				
Spring	0.00 C	0.02(0.005) B	0.05(0.043) A	0.023
Summer	0.00 C	0.03(0.030) B	0.06(0.024) A	0.030
Fall	0.00(0.001) C	0.03(0.026) B	0.07(0.066) A	0.033
Winter	0.00 C	0.00 C	0.02(0.019) B	0.007
Mean	0.000	0.020	0.050	

Letters indicate means that are not significantly different by Tukey's post-hoc comparisons on the significant main or interaction effects in Table 6.

Table 6

Results of two-way ANOVA performed on daily growth rates of three species of macroalgae by season and salinity (both fixed factors), and presented in Table 5

Algae	Source	df	SS	P
<i>L. poiteaui</i> ^a	Season (Se)	3	65.237	<0.0001
	Salinity (Sal)	2	73.710	<0.0001
	Se \times Sal	6	6.144	0.8949
	Error	92	253.129	
<i>P. capitatus</i> ^b	Season	3	12509.38	<0.005
	Salinity	2	12746.93	<0.001
	Se \times Sal	6	4958.16	<0.5
	Error	90	57327.60	
	Total	101	88425.50	
<i>H. incrassata</i> ^c	Season	3	19116.37	<0.001
	Salinity	2	567.68	<0.75
	Se \times Sal	6	11598.43	<0.025
	Error	88	37643.51	
	Total	99	83325.00	

Two-way Sheirer–Ray–Hare extension of non-parametric Kruskal–Wallis tests on daily growth rates of three species of macroalgae by season (fixed factor) and salinity (fixed factor), and presented in Table 5. The appropriate chi-square test is SS/MS_{total} (Sokal and Rohlf, 1995). Significant results at $\alpha = 0.05$ are highlighted in bold.

^a Data for *Laurencia* were normal (Shapiro–Wilk's $W = 0.9781$, $P < 0.4181$) and homoscedastic (Bartlett's $F = 1.2566$, $P < 0.2430$), with $r^2 = 0.5043$ for the ANOVA, $n = 8-9$.

^b Data for *Penicillus* were analyzed by two-way Sheirer–Ray–Hare extension of the non-parametric Kruskal–Wallis test with $r^2 = 0.3517$ for the ANOVA, $n = 8-9$.

^c Data for *Halimeda* were analyzed by two-way Sheirer–Ray–Hare extension of the non-parametric Kruskal–Wallis test with $r^2 = 0.5482$ for the ANOVA, $n = 8-9$.

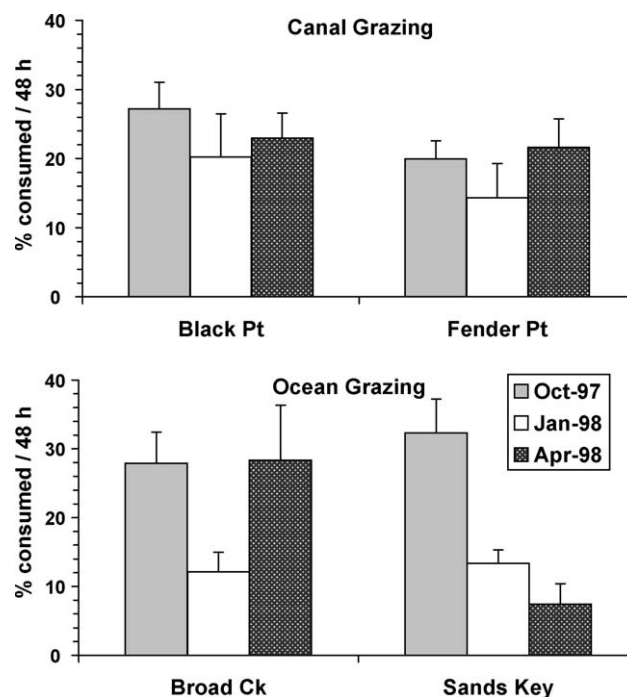


Fig. 3. Mean percent (\pm S.E.) of *Laurencia poiteaui* consumed by grazers during 48 h assays at four field sites and three dates, $n = 20$.

habitats in Florida (Dennison et al., 1993; Hanisak, 2001), indicating that light levels were generally not limiting primary production of macroalgae. The higher light levels present at Sands Key, an oceanic site, probably included a large back-scatter component, which can be a significant fraction of total irradiance in shallow-water tropical sites with reflective carbonate sediments (Gallegos et al., 1990).

Freshwater inputs to the study locations from terrestrial runoff through the canals vary seasonally. About 64% of Miami-Dade County rainfall occurs during the 5-month wet season from June to November (Duever et al., 1994; Obeyseker et al., 1999). Mean daily freshwater discharge from canals is greater during this time, with volumes during the wettest month (August = $25.7 \text{ m}^3 \text{ s}^{-1}$) almost five times the discharge occurring in the driest months (April and May = $5.4 \text{ m}^3 \text{ s}^{-1}$) (Alleman et al., 1995). There is about a 30–45-day lag period between rainfall events and discharge from the canals into the Bay (Wang et al., 2003). Measurements from the datasondes deployed near a canal mouth by Biscayne National Park show that low-salinity events from canal discharges occur as discrete pulses of freshwater delivery at frequencies of hours to days. These high-frequency fluctuations were directly related to canal-discharge management practices, with salinity fluctuating between 7 and 25 psu on a time scale of a few hours or less (J. Wang, unpublished data). Salinities measured in the canal sites at the bottom of the water column (25–30 psu) were higher than those at the surface (10–15 psu) (Biber, 2002). Often, a definite halocline was observed at the canal sites in summer. Stratification of the water column has previously been reported to occur along the western boundary of Biscayne Bay (Alleman, 1995). Canal discharges create a

layer of freshwater that covers the surface and forms a layer of high salinity water near the bottom (Chin-Fatt and Wang, 1987). The effect of this halocline and the resulting stratification on water-column light attenuation in the canal sites remains unstudied.

Canal-discharge poses an unnatural stress regime to the seagrass habitats of western Biscayne Bay. While stress effects were not particularly obvious in the standing stock biomass of the seagrass *T. testudinum* (Thorhaug and Roessler, 1977; Irlandi et al., 2001), the influence of canal discharge was evident in the composition of the macroalgal community found within seagrass beds at the three salinity regimes, in particular changes in abundance and dominance from drift algae at the canal sites to rhizophytic algae at the oceanic sites.

Drift algae dominated in the low and variable salinity canal sites, and were also commonly found in the medium salinity sheet-flow sites. Drift aggregations were primarily composed of red algae in the division Rhodophyta, which has been reported previously from other seagrass-dominated bays in the same biogeographic province (Phillips, 1961; Williams-Cowper, 1978; Benz et al., 1979). About 20 genera occur in Biscayne Bay, dominated by *Laurencia*, *Chondria*, and *Polysiphonia*. Drift algae in Biscayne Bay have previously been studied in Little Card Sound (sheet-flow site), and *L. poiteaui* was found to be the most abundant species there (Bader and Roessler, 1971; Josselyn, 1977); more than two decades later this species remains the dominant component of the drift in our study sites.

Drift algae exhibit a distinct seasonal variation, with large spring blooms reported for many bays and estuaries along the US Atlantic and Gulf coasts (Conover, 1964; Hamm and Humm, 1976; Josselyn, 1977; Benz et al., 1979; Virnstein and Carbonara, 1985). This trend continues into southern Florida, where even though there is less seasonal variation, the biomass of drift still tends to be greater during the winter and spring than in the summer months (Bader and Roessler, 1971; Josselyn, 1977; Thorhaug and Roessler, 1977). This seasonal dynamic was not observed in 1998 (phase II), but did occur in 1996, 1997 (phase I) and 1999 (phase III). Proposed reasons for seasonality in drift biomass include annual light and temperature variations (Josselyn, 1977). It is likely that synergistic effects of seasonal light and temperature, combined with reductions in salinity during the rainy season, influence the biomass of drift algae (Conover, 1964; Benz et al., 1979; Virnstein and Carbonara, 1985).

Salinity is an important variable (Hamm and Humm, 1976) in South Florida, which has a distinct wet season with high rainfall from May to November (Duever et al., 1994). Seasonally low salinities during the wet season (summer and fall) at canal and sheet-flow sites may have been responsible for further depressing standing stock biomass of drift algae over the course of the wet season in these study sites.

Part of the difficulty in assessing temporal and landscape scale dynamics of drift algae are their highly patchy distribution at the small spatial scales at which field studies are typically done (Josselyn, 1977; Virnstein and Carbonara, 1985; Bell and Hall, 1997). This small-scale patchiness is reflected by the large variation reported around mean biomass values (e.g., Williams-

Cowper, 1978; Benz et al., 1979). The range of mean biomass values reported in the literature varies from a few grams dry weight per square meter (Benz et al., 1979; Zimmerman and Livingston, 1979) to 100 g m^{-2} (Bell and Hall, 1997) or even higher, to $164\text{--}400 \text{ g DW m}^{-2}$ (Virnstein and Carbonara, 1985). Zieman et al. (1989) reported a mean biomass of 24 g DW m^{-2} in Florida Bay, which is similar to the annual average obtained for canal sites in Biscayne Bay in this study.

In contrast, rhizophytic algae were most abundant in stable high salinity conditions typical of the oceanic sites. Rhizophytes are calcareous green algae (division Chlorophyta), comprised of about 10 genera of the order Bryopsidales including: *Halimeda*, *Penicillus*, *Udotea*, *Avrainvillea*, and the non-calcified genus *Caulerpa* (Littler and Littler, 2000). The most common species observed in this study were *H. incrassata* and *P. capitatus*, in accordance with previous reports for Biscayne Bay (Thorhaug and Roessler, 1977; Bach, 1979).

Rhizophytic algae are highly productive and prolific contributors to aragonitic carbonate sediments in shallow tropical lagoons (Stockman et al., 1967), with standing stock turnover rates of approximately 4–6 weeks reported for *Penicillus* (Wefer, 1980). Standing stock biomass ranges from a few rhizophytic algae to about 100 plants per square meter (approx. 50 g DW m^{-2}) in South Florida (Stockman et al., 1967; Thorhaug and Roessler, 1977; Davis and Fourqurean, 2001). Biomass can be higher for sites containing the mat-forming alga *Halimeda opuntia*, which can be present in mats of greater than 4 kg DW m^{-2} (Drew and Abel, 1985). Similar biomass values were found at the oceanic sites in this study.

In Card Sound, *Batophora*, *Halimeda*, and *Penicillus* were found to have maximal growth in late summer and reduced growth in midwinter, as reported previously (Bader and Roessler, 1971; Bach, 1979; Morrison, 1984; Davis and Fourqurean, 2001). Similar seasonal growth cycles for *Halimeda* have also been reported for Bermuda (Wefer, 1980) and from Pacific areas (Drew, 1983; Hudson, 1985; Garrigue, 1991), with higher productivity in the summer and reduced productivity or even dormancy during the colder winter months. Bach (1979) suggested that the lower productivity of *Halimeda* in winter was related to reduced light and temperature, as well as overgrowth by mats of the drift alga, *Laurencia*. Winter growth in *Caulerpa* is low because of reduced photosynthesis, low water temperatures, and low nutrient availability (O'Neal and Prince, 1982, 1988). The growth studies suggest that the cooler winter water temperatures do reduce the growth rate of these species (see also Biber, 2002).

In the low-salinity sites, especially Fender Point, the most abundant rhizophytic alga was *P. capitatus*. This species was primarily found in areas with shallow sediment depths (<5 cm) over the limestone bedrock (Wanless, 1969) adjacent to patchily distributed beds of *T. testudinum*. *Penicillus* can form dense aggregations in the shallow sediments between these seagrass patches; however, the plants were observed to be stunted and smaller (less than 50–70 mm tall) than their counterparts on the oceanic side of the Bay. This is probably a result of stress imposed by low salinities throughout much of

the year. Stockman et al. (1967) report that *Penicillus* was found in Florida Bay in normal to hyper-saline conditions, but disappeared in brackish salinities around runoff zones.

The importance of salinity-induced habitat alterations has been poorly reported from tropical seagrass systems, indications from the few studies available (Brook, 1981; Montague and Ley, 1993), however, show this may be an important factor influencing the shift in community composition exhibited by the macroalgae investigated in this study. Macroalgal dominance changes from rhizophytes in high salinity waters to drift algae in low and variable salinity conditions typical of canal-influenced sites. This obvious shift in primary producer community structure has implications for seagrasses, which are the major habitat architects in this system. The increased abundance of drift algae can result in a reduction in seagrass plants and cause a phase-shift in primary producers, which can have potentially negative consequences for ecosystem structure and function, as has been demonstrated elsewhere (e.g., Cambridge et al., 1986; Lapointe, 1989; Dennison et al., 1993; Hauxwell et al., 2001; McGlathery, 2001).

Lirman and Biber (2000) provided data on the algal growth rates and grazing from the northern Florida reef tract, here we present similar information for the inshore seagrass-dominated communities. In comparison to the reef tract communities, growth rates were lower for the drift alga *L. poiteaui* in the seagrass. Also grazing rates were much reduced; 20% consumed per hour on the reef (Lirman and Biber, 2000) compared to 0.42% per hour in the seagrass. Growth rates of drift algae from similar systems typically range from 2 to 5% mean daily increase in biomass (Thorhaug et al., 1979; Thorhaug and Marcus, 1981; Lapointe, 1989), with peak rates up 10–12% per day (Lapointe, 1987, 1989). These growth rates have been shown to be ample to explain the seasonal dynamics of drift and rhizophyte biomass seen in the various salinity regimes using a simulation model (Biber, 2002; Biber et al., 2003). Compared to the drift algae, the rhizophytes had much lower growth rates and were found to be strongly inhibited by salinities below 20 psu. The growth of *Halimeda* and *Penicillus* in this study were low compared to field measurements reported for the same genera (Bach, 1979; Stockman et al., 1967; Delgado and Lapointe, 1994), indicating a potential drawback with transplanting these species into the experimental microcosms. Nonetheless, the seasonality of the observed growth responses, with the rhizophytic species growing faster in summer and the drift algae growing better in cooler temperatures, was as expected from their abundance in the field surveys and previous literature reports. It appears that grazing was a less important check on algal growth in the seagrass habitats studied than has been reported for the adjacent coral reefs (Lirman and Biber, 2000) despite the connectivity between these habitats by numerous fish and invertebrate species (Lindeman et al., 1999; Wang et al., 2003). This suggests that in tropical seagrass habitats grazer density may be lower or that the greater abundance of plant material is sufficient to reduce herbivory on any one plant to a much lower level than has often reported from coral reefs (e.g., Hay, 1981, 1984, 1991).

The low herbivory suggests that top-down biotic control of macroalgae in tropical seagrass habitats is less important in determining abundance than are bottom-up abiotic factors such as temperature and salinity. Seasonal temperature effects were important in establishing favorable growth rates of drift algae during winter and rhizophytes in summer, while salinity stress was important in determining differences in abundance of these two ecological groupings across Biscayne Bay. Low salinities excluded rhizophytic algae from attaining high biomass in canal-influenced sites. In contrast drift algae were better able to tolerate low and variable salinity conditions and this tolerance combined with high growth rates during the cooler winter dry season allowed this group of macroalgae to proliferate in the canal and sheet-flow regimes when salinities were higher and more stable. During and after wet-season rains in the summer/fall, low-salinity stress combined with higher water temperatures combined to drive drift algae biomass to lower levels. The importance of freshwater discharges from canals in the form of pulsed, infrequent events is a potentially important stressor to nearshore tropical seagrass-dominated communities, and has not been widely reported in the literature to date. We suggest that this form of anthropogenic stress has important effects on primary producer community composition and structure and should be further investigated in other locations.

Acknowledgements

This research was funded by U.S. Army Corps of Engineers (DACW39-94-K-0032) and NOAA Coastal Ocean Program (NA37RJO149) awards to M.A. Harwell and the Center for Marine and Environmental Analyses at the University of Miami. Appreciation is extended to R. Curry at Biscayne National Park for field support on this project. We thank B. Orlando, S. Macía, L. Kaufman, and T. Jones for their invaluable assistance. The manuscript benefited from comments by A. Szmant, L. Valdes, L. Leist and two anonymous reviewers. Portions of this research were conducted to fulfill the requirements of a Ph.D. dissertation by P.D. Biber at the University of Miami.

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