

2 *Field Data*

INTRODUCTION

In ecology it is important to understand the dynamics of natural populations (Krebs 1978), especially if they are to be used as environmental indicators of spatio-temporal changes in the system (Landres 1992; Rapport 1992). A general property of indicators is their ability to reflect quantitative changes in an ecosystem in response to some stressor(s) (Harwell *et al.* 1990; Landres 1992; Ward 1992). Biological indicators are species or assemblages whose presence/absence and relative abundance change in response to some impact on the ecosystem (Harwell *et al.* 1990; Kelly and Harwell 1988; Friedrich *et al.* 1992; Kovacs 1992). By their presence and distribution, they can indicate the existence or abundance of particular critical factor(s) (Boyle 1984; Phillips and Rainbow 1993). Indicators can provide a means for regular monitoring of ecosystem health (Herricks *et al.* 1988; Kovacs 1992; Lovett-Doust *et al.* 1994).

The occurrence and abundance of certain macrophyte taxa can be used to indicate environmental conditions such as eutrophication (Schramm and Nienhaus 1996). Given the rapid growth rates of algae and the ease of determining presence and abundance, macroalgae may be especially good early-warning indicators and/or integrators of stress in near-shore communities (Lovett-Doust *et al.* 1994). Any changes that can be detected in the algal community may represent an early warning of a potentially adverse response in the ecosystem (Ramamoorthy and Badaloo 1995), because algae are primary producers representing the entry point for energy into the system, as well as providing habitat structure and complexity (Levine 1984; Lüning 1990).

Algal community structure is characterized by variables pertaining to species composition and abundance, biomass, and spatial distribution, and this can be evaluated through the use of indices or multivariate statistical analyses (Dennis *et al.* 1979; Abel 1996). Structural changes in algal communities occur because species loss/increases are dynamic (Rand and Petrocelli 1984). Changes in community structure in response to a stressor(s), and any subsequent recovery trajectory, are generally measured using biomass, species abundance, richness, or a variety of available diversity indices (Pearson and Rosenberg 1978; Lovett-Doust *et al.* 1994).

The major use of marine plants as indicators has been in field monitoring programs to determine the effects of stressors on community structure and function (Jensen 1984), particularly of nutrient enrichment. Thus, algae are useful aquatic indicators of changes in adjacent terrestrial landscape-function, as runoff into near-shore habitats is often associated with elevated nutrients and other stressors (sedimentation and turbidity, alteration in salinity regime, etc.). A potential community-level indication of deterioration of water quality because of eutrophication is the increased cover and abundance of macroalgae (Dennis *et al.* 1979; Hauxwell *et al.* 2001; McGlathery 2001). The accumulation of macroalgal biomass is a dynamic process regulated by the balance of plant growth rates (affected by light, temperature, nutrients, salinity, and water flow) and rates of plant removal (affected by herbivory, disease, and physical destruction by waves, currents, etc.). This study looks at community-level changes of macroalgae as an indicator of water quality in Biscayne Bay.

Gradients in salinity and nutrients across Biscayne Bay occur primarily as a result of natural and anthropogenically altered regimes of freshwater runoff and delivery into the Bay. These gradients are associated with the presence of a wide-ranging canal-drainage network, which is a conspicuous feature of the South Florida landscape (Alleman 1995). Canal discharges pose an important stressor to near-shore areas along the western (mainland) coastline of Biscayne Bay (Gentile *et al.* 2001). Three different stress regimes associated with canal discharges can be defined for Biscayne Bay: habitats directly

influenced by non-natural canal discharge, areas with natural sheet-flow runoff through mangrove-lined shores, and 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 lowered 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 (Nnaji 1988; Fatt 1989; Alleman 1995). Organisms have limited ability to adapt to acute stressors occurring at low frequencies (Ricklefs and Miller 2000), such as these low-salinity events, which have previously been realized to pose a threat to the ecological function of near-shore seagrass habitats in the Bay (Brook 1981; Montague and Ley 1993). We have shown that while the standing stock of the seagrass *Thalassia* itself is not obviously affected by the presence of canals (as reported also by Thorhaug and Roessler 1977), its primary production is greatly reduced at low-salinity sites (Irlandi *et al.* 2002). Furthermore, there are noticeable differences in the macroalgal community present in seagrass sites that are impacted by recurring low-salinity pulses.

As with any environmental indicator, a knowledge of its spatial distribution and temporal variability is needed before its application (Ward 1990; NRC 2000). Data measured on environmental changes are useful only if the observations can be related to some baseline standard (Cairns 1979). Recently such baseline information for the algal communities of the northern Florida reef tract was provided by Lirman and Biber (2000), and I now present similar information for inshore seagrass-dominated communities. This study aims to provide baseline information on the seasonal and inter-annual composition, distribution, and abundance (biomass) of macroalgae along a gradient arising from canal discharges.

METHODS

Sampling protocols

Macroalgal communities were sampled over several years along a gradient of canal-related stressors in Biscayne Bay, including seagrass beds influenced by canal discharge, sheet-flow, and oceanic inlets, as part of a program conducted to provide baseline data on *Thalassia* habitats (Irlandi *et al.* 2002). Sites on the western shoreline of the Bay were selected based on the presence of canals (disturbed sites) or the absence of canals (historic, natural sheet-flow). Salinities at canal sites are typically most variable, with the lowest salinities in summer, when large quantities of freshwater are released into the Bay (see Chapter 4). Salinity at the sheet-flow sites also drops in summer as a result of rainwater runoff, but the salinity does not drop as drastically as at the canal sites. Sites on the eastern side of the Bay are not influenced by freshwater runoff and maintain a constant salinity near 35 practical salinity units (psu) year round.

Two sites in each salinity regime 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 *Thalassia* habitats to minimize between-site habitat differences (e.g., Lapointe *et al.* 1987). The multi-year sampling program can be divided into three distinct phases, based on the methods used to sample the algal community. The three functional groups of algae that were collected were drift, rhizophytic, and epiphytic algae.

Phase 1 - In 1996-97 samples were collected in February (dry season) and August (rainy season), to allow for seasonal and inter-annual comparisons. At each site a rectangular grid of permanent buoys spaced 50 m apart was set up (Fig. 2). During each

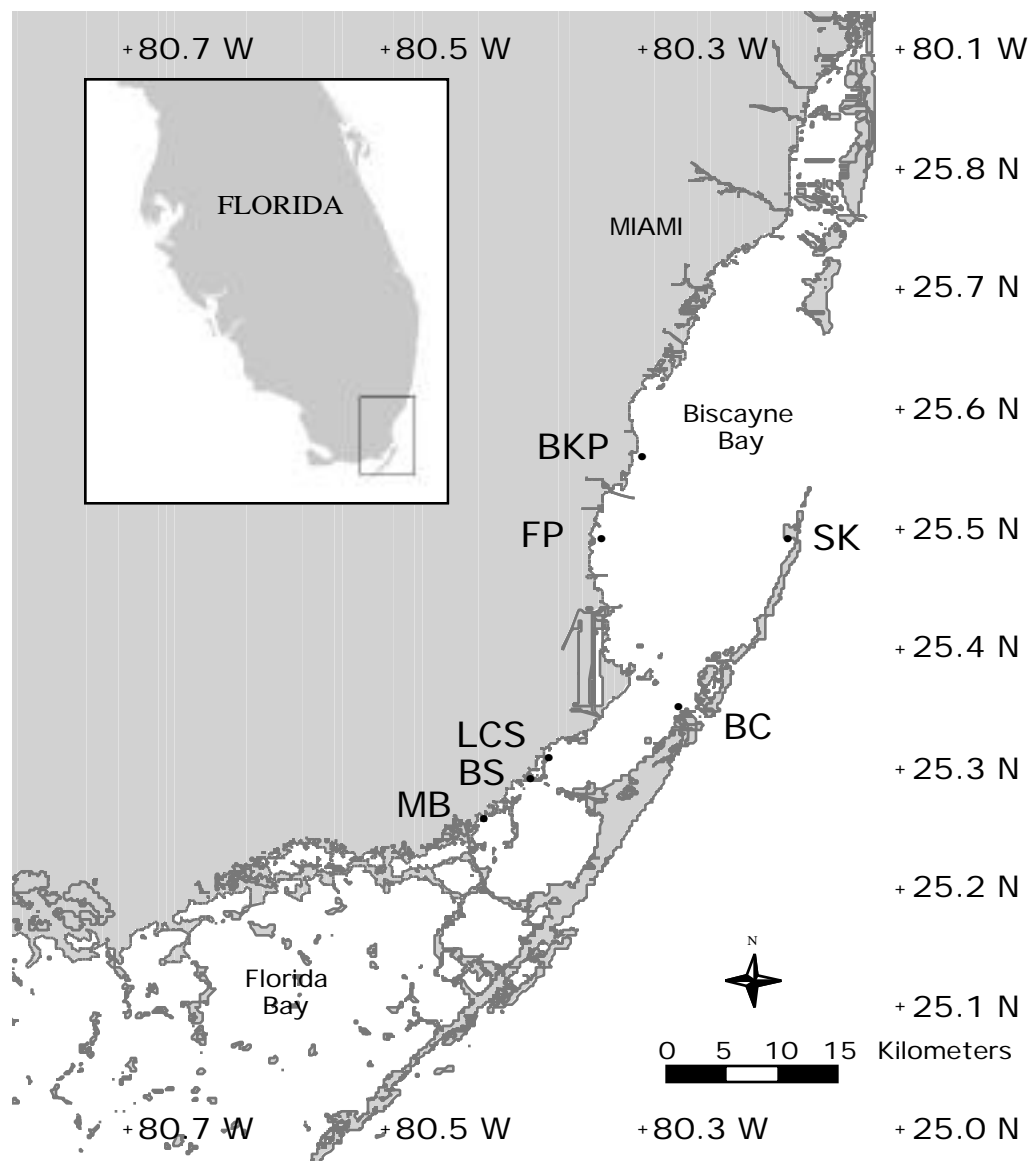


Fig. 1: Location of study sites in Biscayne Bay, Florida. Two to three sites in each salinity regime were sampled: canal sites included Fender Point (FP), Black Point (BKP), and Manatee Bay (MB); sheet-flow sites included Little Card Sound (LCS) and Barnes Sound (BS); and oceanic sites included Sands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

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 and bagged. The samples were returned to the laboratory and frozen until processing, when they were sorted to species where possible using keys provided by Taylor (1960), Woelkerling (1976), Wynne (1998), and Littler and Littler (2000). Biomass ($\text{g}\cdot\text{m}^{-2}$) was determined after drying the samples at 70°C to constant weight in a Scientific Products DK63 constant temperature oven. In addition, samples from Aug. 1997 were ashed at 500°C for 12 hours in a Thermolyne 62700 furnace and the ash-free dry weight (AFDW) determined for later regression analyses. Linear regressions of wet:dry and dry:AFDW were all forced through the origin based on theoretical considerations.

Phase II - We subsequently sampled at monthly intervals (Sept. '97 - Aug. '98) to create a time series for drift algal biomass over one annual cycle. These data were required for simulation modeling, as the biannual data was inadequate for validation comparisons of observed vs. predicted values (see Chapter 7). For this and the third phase of data collection, the Manatee Bay site was dropped in favor of a different canal site at Black Point ($25^{\circ}33.548'\text{N}$, $80^{\circ}17.959'\text{W}$) that was located closer to the area where high canal discharge volumes occur into the Bay (Fig. 1). The presence or absence of drift algae was determined from ten replicate 0.25 m^{-2} quadrats located haphazardly at each site (Fig. 2). All biomass in those quadrats that contained drift algae was collected and processed as above. Percent cover of drift algae was determined monthly in four permanent 0.25 m^{-2} plots per transect, along five transect lines ($n = 20$ quadrats). The 25 m polypropylene long transect lines were 10 m apart, marked at meter intervals, and anchored with a subsurface PVC pole at either end.

Phase III - From Aug. 1998 to Aug. 1999 photographs were taken of twelve 1 m^{-2} areas at each site. Permanent quadrats were placed out in arrays of three blocks of 4 m^{-2} ,

separated by about 50 m (Fig. 2). Every six weeks the quadrats were photographed, then digitized and % cover of drift algae determined using NIH Image version 1.61 software (National Institutes of Health, <http://rsb.info.nih.gov/nih.image/>). 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 processing as above.

Epiphytes were collected every six weeks by harvesting 10 entire *Thalassia* shoots, collected above the rhizome. These were kept in a glass jar of seawater until processing to reduce loss of epiphytes that could become detached during transport. Epiphyte biomass was determined using a modification of the method developed by Penhale (1977), whereby the seagrass blades were scraped in a shallow water-filled dish using a blunt knife to remove all epiphytes, including calcareous encrusting species. The suspended epiphytes were filtered through a pre-weighed filter paper (Whatman GF/F), which was then dried and re-weighed to determine the epiphyte dry weight. Each seagrass blade was measured for length and width, and ten blades from each sample were dried and weighed. From these data the epiphyte biomass was expressed as mg·cm⁻² seagrass surface area and mg·g⁻¹ dry wt seagrass to standardize for different blade sizes across sites and time. To re-express the epiphyte data on a spatial basis (biomass epiphytes·m⁻²) and allow comparison with other functional groups, the biomass of *Thalassia* per m² was taken from Irlandi *et al.* (2001) and epiphyte biomass·m⁻² calculated using the mean seagrass biomass determined for summer (May - November) and winter (December - April) for 1996-97 at the same six sites.

Data Exploration and Analyses

Statistical analyses were performed using JMP version 3.1.5 for Apple Macintosh from the SAS Institute Inc., Cary, N.C. Data were tested for normality and heteroscedasticity

and normalized by \ln -transformation where appropriate. Data that did not conform to parametric assumptions were analyzed using non-parametric tests.

1. Species composition: In Phase I of sampling, the species present at each site were identified, and biomass·m² entered into a genus by quadrat matrix for each site.

2. Multivariate analyses: are useful for analyzing complex datasets with multiple variables, e.g., species composition, to describe an ecological community. Multivariate techniques allow a single analysis of the data instead of a series of univariate tests (Tabachnick and Fidell 1996). For this type of data the investigator is often interested whether the units are naturally classifiable into distinct groups (Pielou 1984, Santos 1993). Exploratory data analysis to determine pattern in the genus by quadrat matrix was undertaken using Principle Components Analysis (PCA) followed by a Multivariate Analysis of Variance (MANOVA) and Canonical Variates Analysis (CVA).

Ordination by PCA was used to reduce the dimensionality of the genus by quadrat matrix. Ordination produces relationships among the data points that can more easily be recognized (Orloci 1973, Pielou 1984). An R-Type PCA was performed on the raw data following the recommendations of Pielou (1984). The data were not centered ($X_i - \bar{X}$), as species composition between sites is variable; data were not standardized ($(X_i - \bar{X})/var.$), as the most abundant species should determine the differences in sites rather than the rare species (see Pielou 1984 pp. 152-165). Ordination by PCA is considered a “success” if a large proportion of the total dispersion (scatter) of the data is parallel with the first two or three principal axes, as this concentrates the variance, thereby reducing the dimensionality of the original species space (Gauch 1982, Pielou 1984).

PCA was used to determine the dominant genera and to reduce the size of the data matrix without losing any of the inherent variation. The PCA-reduced data matrix was used in a MANOVA to test the differences between the three salinity regimes (canal, sheet-flow, ocean). The MANOVA was followed by a CVA to visualize the results, as recommended by Johnson and Field (1993).

Canonical variates analysis, sometimes also called discriminant analysis, is an ordination technique that displays differences among group means in a reduced space in which the among-group variation is maximized relative to within-group variation (Jongman *et al.* 1987). Plotting of the group centroids on the first 2-3 canonical axes graphically displays the relationship among multivariate group means determined in MANOVA (Johnson and Field 1993).

3. Linear regressions for wet:dry:AFDW relationships: Linear regressions of wet:dry weight and dry:ash-free dry weight (AFDW) were developed for the three functional groups, as well as the three most common species of drift and rhizophytic algae determined from PCA. For epiphytes, no wet:dry weight regression is reported as wet weight data could not be measured for this group because of methodological constraints.

4. Biomass across sites and seasons: Mean annual biomass, expressed in dry weight and AFDWs, of the three functional groups were determined for the three salinity regimes. Data were analyzed to determine the effects of functional group and salinity regime on biomass. From the Phase I data, the relative abundance of the three most common genera of drift algae and rhizophytic functional groups were determined for the summer wet season and winter dry season.

5. Annual time-series: the biomass data ($\text{g dw}\cdot\text{m}^{-2}$) from the three sampling phases was compiled to determine the underlying annual time-series in the three salinity regimes for each of the three functional groups.

6. Percent cover of drift algae: was used to determine if the drift algal seasonal dynamics obtained from the biomass data were consistent using another measure of abundance. Also, linear regressions of percent cover to biomass relationships, obtained from the digitized images in Phase III, were determined for each salinity regime. Analysis of Covariance (ANCOVA) was performed on these three equations to determine the significance of differences between regimes.

7. Seasonal and inter-annual comparisons: Non-parametric Wilcoxon rank-sum tests were used to analyze the seasonal and inter-annual differences in mean biomass (g dw·m⁻²) and % cover (drift algae only) for each functional group in each salinity regime. Seasonal differences in drift and rhizophytic biomass, averaged over the three sampling phases, were compared for the months of February and August (dry vs. wet season conditions). Seasonal differences in epiphytes were based on Phase III data only, comparing March 1999 with August 1998. Inter-annual differences in drift and rhizophytic algal biomass were tested using data from Phase 1, as this was the only time that the same methodology was used in collecting samples over consecutive years.

RESULTS

1. Species Composition

The influence of canal discharge as a stressor to seagrass habitats, while not particularly obvious in *Thalassia* itself (Thorhaug and Roessler 1977; Irlandi *et al.* 2002), was evident in the composition of the macroalgal community found at the three salinity regimes (Table 1).

Species present in the two canal sites were primarily rhodophytes in the genera *Chondria*, *Laurencia*, and *Polysiphonia*, all in the drift algae functional group (Table 1). *Polysiphonia* was also found growing epiphytically on *Thalassia* blades. Rhizophytic algae were uncommon, with the exception of *Penicillus capitatus*, which occupied areas that were not covered predominantly by *Thalassia*.

Species composition in the sheet-flow sites was transitional between the canal-influenced community and the oceanic community. The number of species found in this regime (sheet-flow = 34, compared with canal = 16, ocean = 36) was more than double that in the canal regime and comparable to the oceanic regime (Table 1). 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 functional

Table 1: Species composition of algal samples collected during Phase I at six sites in Biscayne Bay. Two sites in each salinity regime were sampled: canal sites included Fender Point (FP) 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). Taxonomy is based on Litter and Littler (2000). The abbreviations for the three taxonomic divisions are: chlorophyta (C), phaeophyta (P), and rhodophyta (R).

Functional Group	Tax. Div.	Canal FP	Canal MB	Sheet-flow BS	Sheet-flow LCS	Oceanic BC	Oceanic SK
Rhizophytic algae							
<i>Avrainvillea levis</i> M. Howe	C				*		*
<i>Avrainvillea nigricans</i> Descaine	C				*		
<i>Caulerpa ashmeadii</i> Harvey	C				*	*	
<i>Caulerpa cupressoides</i> (Vahl) C. Agardh	C				*		*
<i>Caulerpa mexicana</i> Sonder ex. Kützing	C						*
<i>Caulerpa paspaloides</i> (Bory de Saint-Vincent) Greville	C				*	*	
<i>Halimeda discoidea</i> Descaine	C					*	*
<i>Halimeda incrassata</i> (J.Ellis) J.V. Lamouroux	C	*		*	*	*	*
<i>Halimeda monile</i> (J.Ellis and Solander) J.V. Lamouroux	C			*	*	*	*
<i>Halimeda opuntia</i> (Linnaeus) J.V. Lamouroux	C					*	*
<i>Halimeda simulans</i> M.Howe	C						*
<i>Halimeda tuna</i> (J.Ellis and Solander) J.V. Lamouroux	C						*
<i>Penicillus capitatus</i> Lamarck	C	*	*	*	*	*	*
<i>Penicillus dumetosus</i> (J.V. Lamouroux) Blainville	C				*	*	*
<i>Rhypocephalus phoenix</i> (J.Ellis and Solander) Kützing	C				*	*	*
<i>Udotea caribaea</i> D.S. Littler and M.M. Littler	C				*	*	*
<i>Udotea flabellum</i> (J.Ellis and Solander) M. Howe	C				*	*	*
Epiphytic algae							
<i>Centroceras clavulatum</i> (C.Agardh) Montagne	R						*
<i>Ceramium cruciatum</i> Collins and Hervey	R				*		*
<i>Ceramium nitens</i> (C. Agardh) J.Agardh	R						*
<i>Fosliella</i> spp. Howe	R					*	*
<i>Herposiphonia pecten-veneris</i> (Harvey) Falkenberg	R					*	*
<i>Jania capillacea</i> Harvey	R				*	*	*
<i>Melobesia</i> spp. J.V. Lamouroux	R				*	*	*
<i>Polysiphonia echinata</i> Harvey	R	*	*	*			
<i>Polysiphonia</i> spp. Greville	R	*	*	*			
Drift algae							
<i>Acanthophora spicifera</i> (Vahl) Børgesen	R					*	*
<i>Ceramium nitens</i> (C. Agardh) J.Agardh	R						*
<i>Chondria atropurpurea</i> Harvey	R		*				
<i>Chondria cnicophylla</i> (Melville) de Toni	R	*		*	*		
<i>Chondria floridana</i> (Collins) M. Howe in W.R. Taylor	R	*	*	*			
<i>Chondria littoralis</i> Harvey	R	*		*			
<i>Chondria</i> sp. C. Agardh	R	*	*	*			
<i>Cladophora</i> spp. Kützing	C	*		*	*		
<i>Dasya baillouviana</i> (S.G. Gmelin) Montagne	R				*		*
<i>Dasya ramosissima</i> Harvey	R				*		*
<i>Dictyota caribaea</i> Hörnig and Schnetter in Hörnig et al.	P				*	*	*
<i>Digenea simplex</i> (Wulfen) C. Agardh	R	*		*	*		
<i>Gracilaria tikvahiae</i> McLachlan	R						*
<i>Hypnea spinella</i> (C. Agardh) Kützing	R						*
<i>Laurencia intricata</i> J.V. Lamouroux	R	*	*	*	*	*	
<i>Laurencia poiteaui</i> (J.V. Lamouroux) M. Howe	R	*	*	*	*	*	
<i>Polysiphonia echinata</i> Harvey	R	*	*	*			
<i>Polysiphonia</i> spp. Greville	R	*	*	*			
<i>Sargassum</i> sp. C. Agardh	P	*	*	*	*	*	
<i>Spyridia filamentosa</i> (Wulfen) Harvey in W. Hooker	R			*	*	*	*

group, while rhizophytic algae were uncommon. In contrast, the Little Card Sound site had many species of rhizophytic algae (*Avrainvillea*, *Caulerpa*, *Halimeda*, *Penicillus*, *Rhipocephalus*, and *Udotea*), as well as many of same genera of drift algae that were found at Barnes Sound, albeit in lesser abundance. Composition of the epiphyte functional group also changed, from the filamentous *Polysiphonia*'s found in the canal regime to the calcified encrusting types commonly found in the oceanic regime (such as *Melobesia* and *Jania*).

The two oceanic sites had the highest number of species of the three regimes investigated (Table 1). Species found here were predominantly members of the rhizophytic functional group including *Avrainvillea*, *Caulerpa*, *Halimeda*, *Penicillus*, *Rhipocephalus*, and *Udotea*. The *Thalassia*-epiphytes identified were also more diverse in these oceanic sites (7 species) than in the sheet-flow (3 species) and canal sites (2 species). Many other species of epiphytes were present, but were rarely large enough to be readily identified to species, and so were not included in Table 1. Drift algae were rarely encountered in the quadrats in the oceanic regime. Of this functional group, the most frequently encountered genera were *Dasya*, *Spyridia*, *Sargassum*, and *Laurencia* (Table 1).

Seagrass epiphytes were a heterogeneous assemblage of species that included diatoms, filamentous forms, and encrusting calcareous algae. The filamentous forms dominated the seagrass blades at canal sites, while crustose and calcareous forms were more abundant on seagrass occurring in oceanic conditions. This resulted in a phase-shift in epiphyte community composition between the eastern and western sides of Biscayne Bay, which mirrored the change in the drift and rhizophytic algal functional groups.

2. Multivariate Analyses

A large multi-species dataset of the type shown in Table 1 lends itself to exploratory data analysis using multivariate techniques, to elucidate patterns inherent in the data, thereby focusing subsequent analytical efforts.

The three salinity regimes fall out along three separate principle component axes (Fig. 3). Greater than 95% of the variance in the data was explained by the first principle component (PC1 in Table 2). From the eigenvector loadings (Table 2), it can be shown that the five genera that dominate the variance in the data are the two most abundant rhizophytic algae (*Halimeda* and *Penicillus*), and the three most abundant genera of drift algae (*Laurencia*, *Polysiphonia*, and *Chondria*).

Table 2: Results of Principle Components Analysis (PCA) on biomass per quadrat of all genera across all sites for data collected in 1996-97. The first Principle Component (PC1) accounts for the > 95% of the total variance. Genera marked by (R) are rhizophytic algae, the others are drift algae.

Source	PC1	PC2	PC3	PC4	PC5
Eigenvalue ():	126985.30	1910.74	397.98	189.27	109.64
Percent Variance:	97.9784	1.4743	0.3071	0.1460	0.0846
Cum. Percent Var.:	97.9784	99.4527	99.7598	99.9058	99.9904
Eigenvectors:					
<i>Halimeda</i> (R)	0.78716	-0.59050	-0.17624	-0.01823	-0.00936
<i>Penicillus</i> (R)	0.54555	0.80034	-0.23779	0.02397	-0.06618
<i>Laurencia</i>	0.21477	0.06251	0.81400	-0.49111	-0.21262
<i>Polysiphonia</i>	0.14188	0.03867	0.42808	0.86665	-0.20193
<i>Chondria</i>	0.12330	0.07181	0.25364	0.07203	0.95367

Table 3: MANOVA on the PCA-reduced species set, across all sites. Pillai's trace and the other three MANOVA statistics all indicate highly significant differences among sites.

Test	Value	F approx.	df Numer.	df Denom.	P
Wilks' Lambda	0.6521	16.8026	8	564	< 0.0001
Pillai's Trace	0.3830	16.7573	8	566	< 0.0001
Hotelling-Lawley	0.4796	16.8473	8	562	< 0.0001
Roy's Max Root	0.3005	21.2581	4	283	< 0.0001

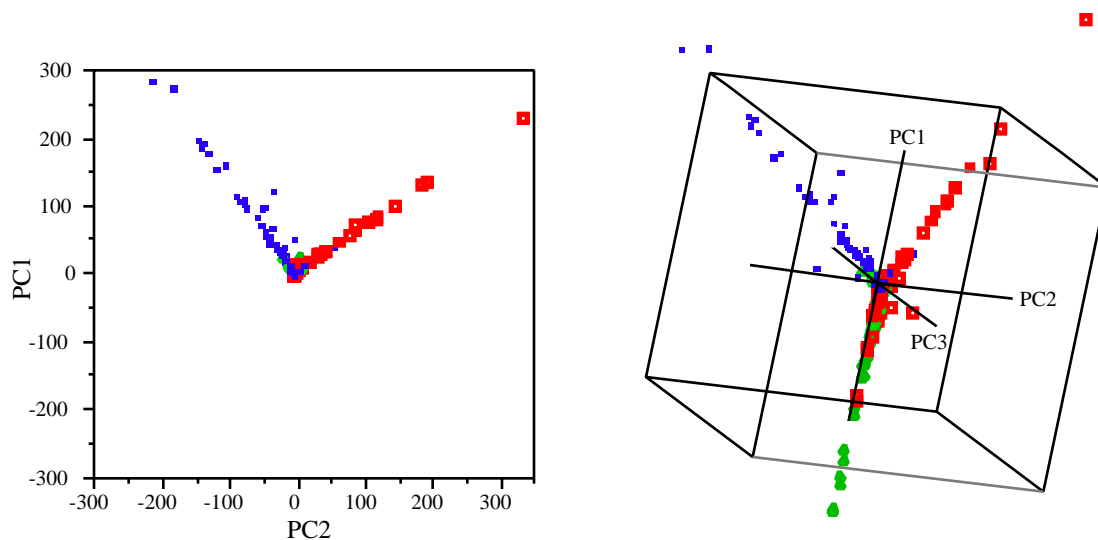


Fig. 3: Principle Components Analysis (PCA) on total algal biomass per quadrat across all sites for data collected in 1996-97 (Phase I). The quadrats from the three salinity regimes are shown in different colors: red = canal, green = sheet-flow, blue = oceanic. The 3-D plot shows the spatial separation of the quadrats in the three regimes, and shows the sheet-flow quadrats which are hidden in the first plot.

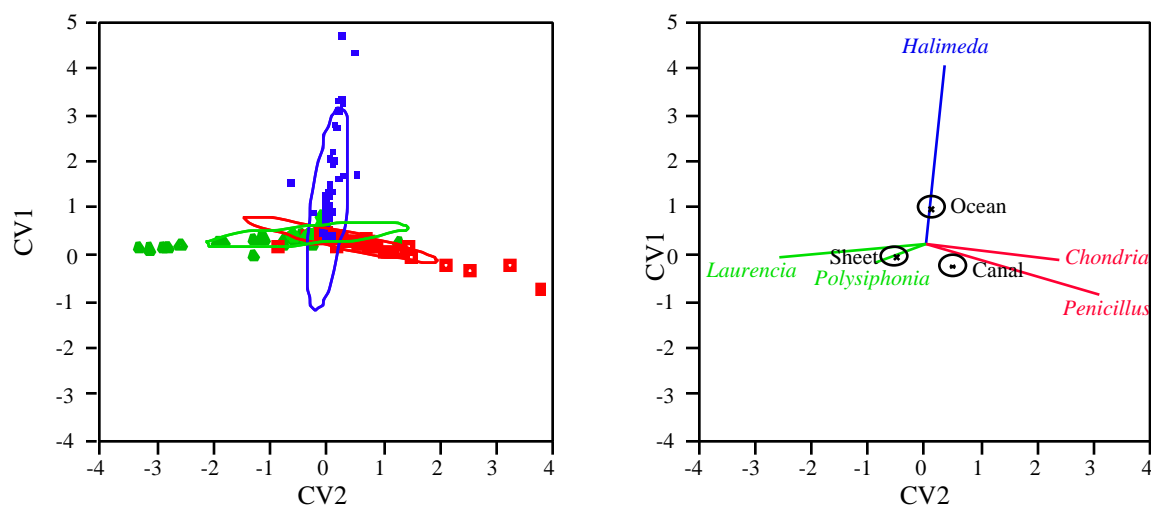


Fig. 4: Canonical Variates Analysis (CVA), a graphical representation of the MANOVA results, with the 95% confidence ellipses indicating a significant separation of the three salinity regimes. The genera responsible for the axis weightings, as well as the confidence ellipse centroids are shown in the canonical centroid plot. *Halimeda* dominates the CV1 axis, *Chondria* and *Penicillus* dominate the canal side of the CV2 axis, and *Laurencia* and *Polysiphonia* dominate the sheet-flow side of the same axis.

The MANOVA on the PCA-reduced dataset indicates that there are highly significant differences among regimes (Table 3), based on species composition. Johnson and Field (1993) recommend reporting Pillai's Trace, as they found this statistic to be the most robust to heteroscedasticity. Pillai's Trace, and the three other MANOVA statistics, all report a highly significant result (Table 3). Johnson and Field (1993) further recommended following a significant MANOVA result with a canonical analysis, as this can be considered equivalent to a graphical interpretation of the MANOVA results.

The scatter-plot of canonical variates clearly shows separation of the three salinity regimes along the first two canonical axes (Fig. 4), visually displaying the significant MANOVA result. *Halimeda* dominates the first canonical axis (CV1), which is heavily loaded by oceanic samples. The sheet-flow and canal samples are more similar in composition and separate out along CV2, with *Chondria* and *Penicillus* dominating the canal samples and *Laurencia* and *Polysiphonia* dominating toward the sheet-flow side of this axis.

Thus, these multivariate techniques demonstrate that the differences in macroalgal communities observed in the Bay among salinity regimes are indeed significant. Samples from different regimes spread out along separate axes in both PCA (Fig. 3) and CVA (Fig. 4), demonstrating the differences in community composition and abundance occurring in the different sites sampled. The graphs further show the commonality in species composition among sites, as all the axes arise from a common origin, where the samples are densely clustered. The differences between the sites are, therefore, a matter of degree (abundance) rather than of kind (composition), which is the kind of relationship that occurs when community composition changes along a gradient (Whittaker 1973; Greig-Smith 1983).

3. Linear Regressions on Biomass

Before further analysis of the biomass data can be undertaken, it is necessary to first describe the statistical relationships between the three biomass measures (wet, dry, and ash-free dry weights). From the wet:dry weight relationships, it can be seen that the drift algae all have a similar water content (Table 4). The wet:dry weight regressions for the rhizophytic algae are complicated by differing degrees of calcification among genera. *Halimeda* has the most calcified thallus (Bohm *et al.* 1978), while *Caulerpa* is uncalcified. The slope of the regression reflects that *Halimeda* has a low water content, while *Caulerpa* has a higher water content, similar to values obtained for the drift algae. A rough rule of thumb for converting dry weight data to biomass of living tissue is about a factor of ten for drift and a factor of three for rhizophytic algae, a relationship that has previously been reported by Hamm and Humm (1976, p 226).

The organic content of the thallus is indicated by the dry:AFDW relationship (Table 4). Organic content is high in the drift algae, but varies by genus. *Polysiphonia* has the lowest organic content of the drift algae, indicating a large amount of inorganic material is present. This is possibly a result of sample contamination by shells and sediment. *Polysiphonia* is highly filamentous and traps more sediments than the coarsely branched and therefore more open morphology of *Laurencia* and *Chondria*. The organic content of rhizophytic algae, such as *Halimeda* and *Penicillus*, is low as much of the dry weight is composed of calcium carbonate (Bohm *et al.* 1978). Again, for *Caulerpa* the slope of the regression is more similar to the drift algae than the rhizophytic algae, as this genus is uncalcified. Interestingly, the organic content of the epiphytes is very similar to that of the heavily calcified rhizophytic algae, potentially indicating the importance of calcified encrusting epiphytes on the total biomass measured at the oceanic sites.

Table 4: Linear regressions of wet:dry and dry:ash-free dry weights (AFDW) for drift and rhizophytic functional groups of samples collected in Phases I-III. Epiphyte samples were collected in Phase III only. Regressions forced through origin based on theoretical considerations, mean (\pm SE) of slope estimate.

Genus	n	Slope of Regression		r ²
		wet:dry		
Drift	289	dry = 0.1051 (\pm 0.0021) wet		0.975
<i>Laurencia</i>	124	dry = 0.1053 (\pm 0.0019) wet		0.990
<i>Polysiphonia</i>	43	dry = 0.1319 (\pm 0.0069) wet		0.973
<i>Chondria</i>	53	dry = 0.1049 (\pm 0.0040) wet		0.983
Rhizophytic	1144	dry = 0.2844 (\pm 0.0030) wet		0.969
<i>Halimeda</i>	446	dry = 0.3240 (\pm 0.0027) wet		0.992
<i>Penicillus</i>	620	dry = 0.2381 (\pm 0.0018) wet		0.990
<i>Caulerpa</i>	39	dry = 0.1648 (\pm 0.0049) wet		0.992
		dry:AFDW		
Drift	138	AFDW = 0.6168 (\pm 0.0162) dry		0.976
<i>Laurencia</i>	102	AFDW = 0.6427 (\pm 0.0160) dry		0.984
<i>Polysiphonia</i>	5	AFDW = 0.3335 (\pm 0.0461) dry		0.994
<i>Chondria</i>	19	AFDW = 0.5384 (\pm 0.0353) dry		0.984
Rhizophytic	1229	AFDW = 0.1633 (\pm 0.0031) dry		0.896
<i>Halimeda</i>	466	AFDW = 0.1543 (\pm 0.0022) dry		0.976
<i>Penicillus</i>	711	AFDW = 0.2924 (\pm 0.0021) dry		0.990
<i>Caulerpa</i>	32	AFDW = 0.6518 (\pm 0.0247) dry		0.990
Epiphytes	1113	AFDW = 0.1767 (\pm 0.0022) dry		0.855

4. Biomass across Sites and Seasons

After converting all biomass measures to dry weight and AFDW·m⁻², it is now possible to compare abundance of the three functional groups across salinity regimes. Abundance is defined here as the mean annual biomass pooled across sites within each salinity regime (canal, sheet-flow, ocean) and averaged across all years sampled.

Mean annual biomass across the three regimes, measured by dry weight, indicated that epiphytes were significantly more abundant than rhizophytes, which were significantly more abundant than the drift algae. When the same data was expressed in units of AFDW, then the epiphytes and drift algae were now significantly more abundant than the rhizophytes (Fig. 5). For the three functional groups, regime did not have a significant

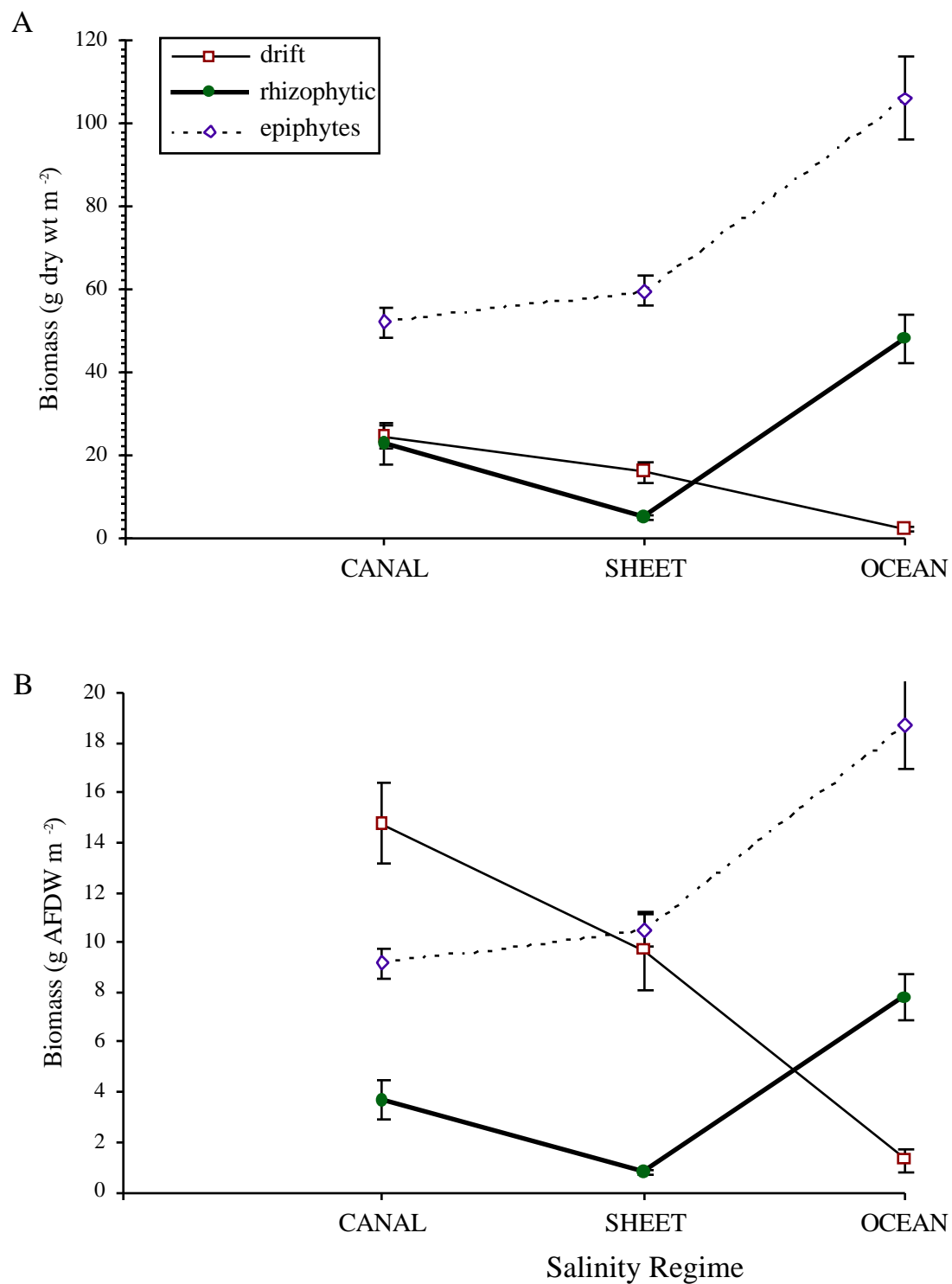


Fig. 5: Mean (\pm SE) annual biomass in A) grams dry weight \cdot m⁻² and B) AFDW \cdot m⁻² for the three functional groups of algae in each of the three salinity regimes. Note differences in Y axis values.

Table 5A: Two-way Sheirer-Ray-Hare extension of non-parametric Kruskal-Wallis tests on biomass by regime (fixed factor) and functional group (fixed factor) presented in Fig. 5. The appropriate chi-square test is SS/MS_{total} (Sokal and Rohlf 1995). Significant P values are highlighted by bold case at $\alpha = 0.05$ of significance.

Biomass	Source	df	SS	MS	χ^2	P
Dry wt	Regime (R)	2	23196.10	11598.050	1.3659	<0.75
	Group (FG)	2	3709141.80	1854570.900	218.4186	<0.001
	R x FG	4	1414299.20	353574.800	83.2832	<0.001
	Error	855	9508659.00	11121.239		
	Total	863	14655296.10	16981.803		
AFDW	Regime	2	49424.70	24712.350	2.9082	<0.10
	Group	2	3493681.30	1746840.650	205.5734	<0.001
	R x FG	4	1581820.50	395455.125	93.0767	<0.001
	Error	855	9541598.00	11159.764		
	Total	863	14666524.50	16994.814		

For dry weight the ANOVA $r^2=0.3561$, $n=95-97$; AFDW the $r^2=0.3494$, $n=95-97$.

Table 5B: Tukey's post-hoc comparisons of significant results in Table 5A indicate groups with like means by the same letter, and significantly higher biomass is highlighted.

Source	Tukey's		
Dry Weight			
<u>R x FG</u>	<u>Drift</u>	<u>Rhizo</u>	<u>Epi</u>
Canal	B	B	A
Sheet	B	C	A
Ocean	C	B	A
	<u>Canal</u>	<u>Sheet</u>	<u>Ocean</u>
Drift	A	A	B
Rhizo	B	C	A
Epiphytes	B	B	A
AFDW			
<u>R x FG</u>	<u>Drift</u>	<u>Rhizo</u>	<u>Epi</u>
Canal	A	C	B
Sheet	A	B	A
Ocean	C	B	A
	<u>Canal</u>	<u>Sheet</u>	<u>Ocean</u>
Drift	A	B	C
Rhizo	AB	B	A
Epiphytes	B	B	A

effect on mean annual biomass expressed in units of g dry wt or AFDW (Table 5A). The interaction effect of regime by functional group did have a highly significant effect on biomass (Table 5A).

Epiphytes: were the most abundant functional group (in g dw·m⁻² or AFDW·m⁻²) across all three salinity regimes, with the exception of the canal site when mean annual biomass was expressed in AFDW (Fig. 5). They were the most abundant functional group, even though they were not very noticeable in the field. Biomass in the ocean sites (106 g dw·m⁻² = 18.7 g AFDW·m⁻²) was significantly greater than at the sheet-flow (59 g dw·m⁻² = 10.5 g AFDW·m⁻²) and canal sites (52 g dw·m⁻² = 9.2 g AFDW·m⁻²) using both measures of biomass.

Drift algae: were observed to be the most conspicuous component of the macroalgal community in low-salinity canal and sheet-flow regimes. The drift algae ranked second in abundance, after the epiphytes, in the canal and sheet-flow sites when biomass was expressed as g dw. However, drift algae became the most abundant functional group in the canal regime when expressed as AFDW (Fig. 5). For both measures, biomass of drift algae was significantly lower in the oceanic (2.0 g dw·m⁻² = 1.3 g AFDW·m⁻²) regime than the canal (24 g dw·m⁻² = 14.7 g AFDW·m⁻²) and sheet-flow (15.6 g dw·m⁻² = 9.6 g AFDW·m⁻²) conditions (Tables 5A&B).

Rhizophytic algae: were the second most abundant functional group in the high-salinity, oceanic regime after the epiphytes, and the least abundant group at the canal and sheet-flow regimes (Fig. 5). Biomass of rhizophytic algae was significantly lower in the sheet-flow regime (5 g dw·m⁻² = 0.8 g AFDW·m⁻²) than the canal (23 g dw·m⁻² = 3.6 g AFDW·m⁻²) and ocean (48 g dw·m⁻² = 7.8 g AFDW·m⁻²) regimes when expressed in g dw, but not significantly less than the canal regime when expressed in AFDW units (Tables 5A&B).

The AFDW measure of biomass reflects field observations of abundance better than the dry wt measure because of the confounding impact of calcification on biomass. Even so, epiphytes were most abundant by AFDW in the oceanic and sheet-flow sites using both

measures of biomass (Fig. 5). This may be because heavier calcareous epiphytes such as *Fosliella* spp. and *Melobesia* spp. were observed to be the main epiphytes on seagrass blades in these sites. By contrast, the epiphytes observed on seagrass blades in canal sites were either diatom films or filamentous red algae, primarily *Ceramium* spp. and *Polysiphonia* spp., which have a low biomass per plant.

For those genera that were found across all or most sites (Table 1) and identified by the multivariate analyses to influence community composition, the relative abundance along the salinity gradient was plotted for the winter dry season and summer wet season (Fig. 6).

Rhizophytic algae, specifically *Halimeda* and *Penicillus*, were most abundant in the oceanic regime in both the wet and dry seasons (Fig. 6). However, *Penicillus* was also abundant in the canal regime in the dry season. In contrast, *Caulerpa* was most abundant in the sheet-flow regime, specifically at Little Card Sound (LCS). Abundance of *Caulerpa* was also higher in the dry season than the wet season (Fig. 6). For the rhizophytic functional group there was less of a discernible seasonal change in abundance than was observed for the drift algae.

Drift algae of the genera *Chondria*, *Laurencia*, and *Polysiphonia* were more abundant in the low-salinity canal and sheet-flow regimes than the oceanic regime (Fig. 6). Both *Laurencia* and *Polysiphonia* decreased in abundance during the wet season in the canal and sheet-flow regimes, whereas the abundance of *Chondria* increased in the sheet-flow regime, but decreased in the canal regime (Fig. 6). The seasonal response observed for the drift functional group appears to be one of a summer-time reduction in biomass.

5. Seasonal Patterns

The seasonal biomass-dynamics for each of the three functional groups (drift, rhizophytic algae, and epiphytes) can now be considered.

Epiphytes: were only collected over one year (Phase III), in contrast to the other two groups for which multiple years of data are available. Epiphytes were more abundant in the

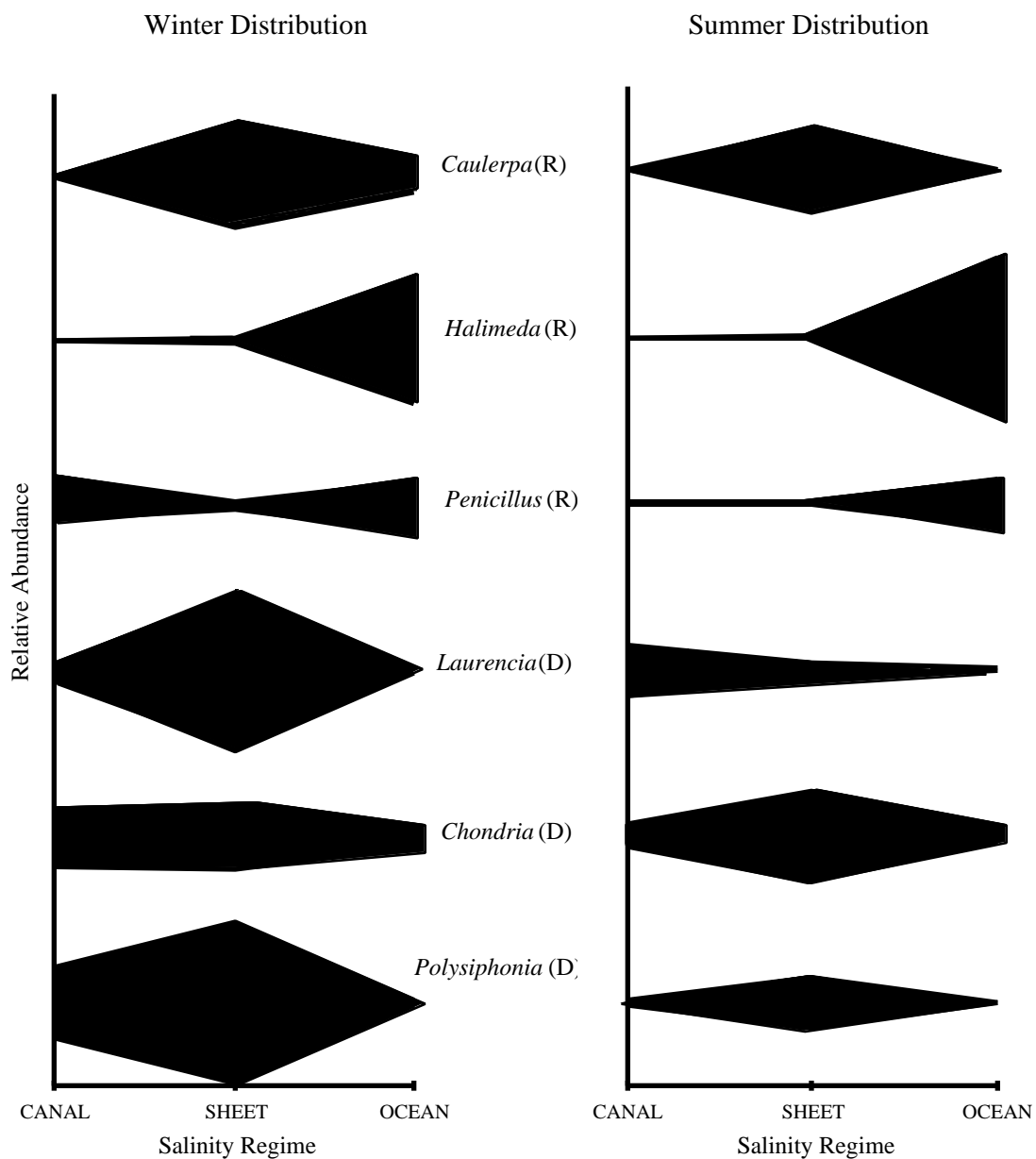


Fig. 6: Spatio-temporal distribution of common genera of macroalgae in two functional groups (drift (D) and rhizophytic algae (R)) found at the six sites in February and August of 1996-97 (Phase I). The relative abundance for each genus is plotted, so the vertical dimension is relative to the maximum abundance for each genus, and differs between the genera.

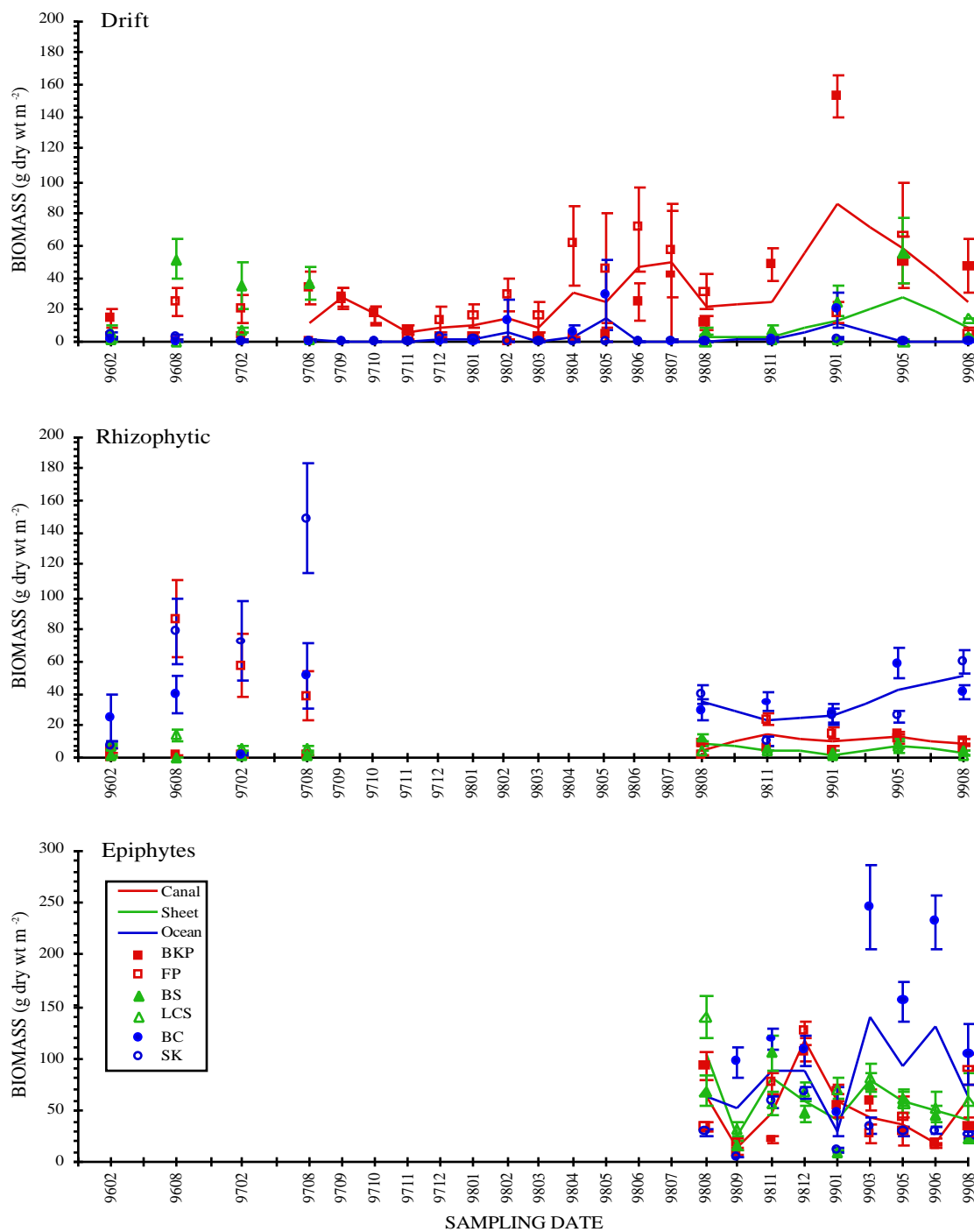


Fig. 7: Mean biomass (\pm SE) of the three functional groups for each regime over the entire study period from Feb. '96 through Aug. '99. Note lack of samples of rhizophytic algae for the sampling period of Aug. '97 through Aug. '98 (Phase II no data). Epiphytes were only sampled over one year from Aug. '98 to Aug. '99 (Phase III). Linear interpolation of data over the months not sampled was used to create a continuous time trace (solid lines). Note also different Y axis scale for the epiphyte functional group, which was the most abundant group.

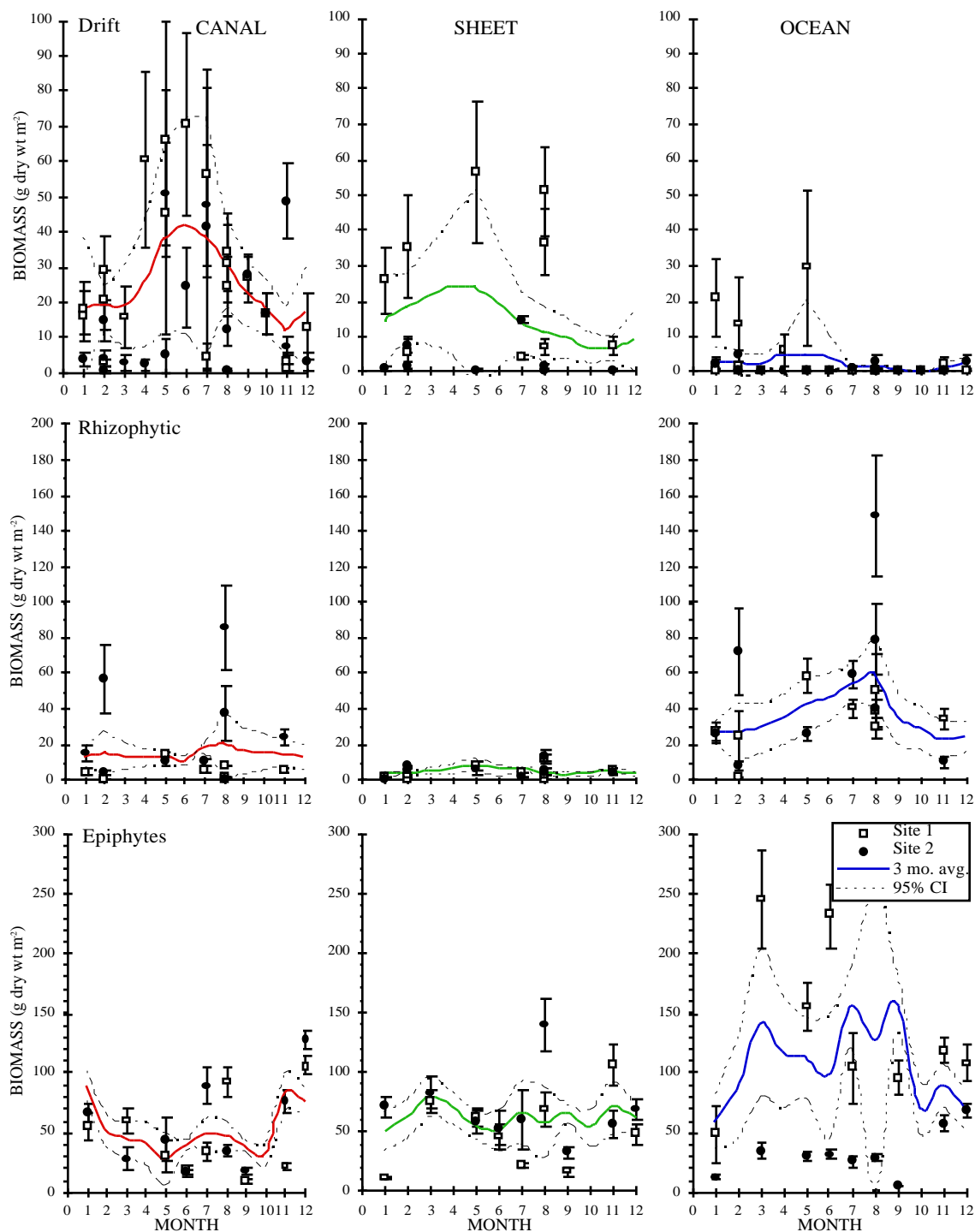


Fig. 8: Three-month moving average (colored line) of biomass ($\pm 95\%$ CI), expressed in grams dry weight per square meter, for each of the three functional groups in each of the three salinity regimes. Note the change in Y-axis scale across functional groups. The means (\pm SE) of the sample data for the two sites per regime are also shown to indicate the variability around the smoothed data trace. The drift and rhizophytic algae graphs are based on multiple years of sampling, while the epiphyte data are based on one year only (Phase III).

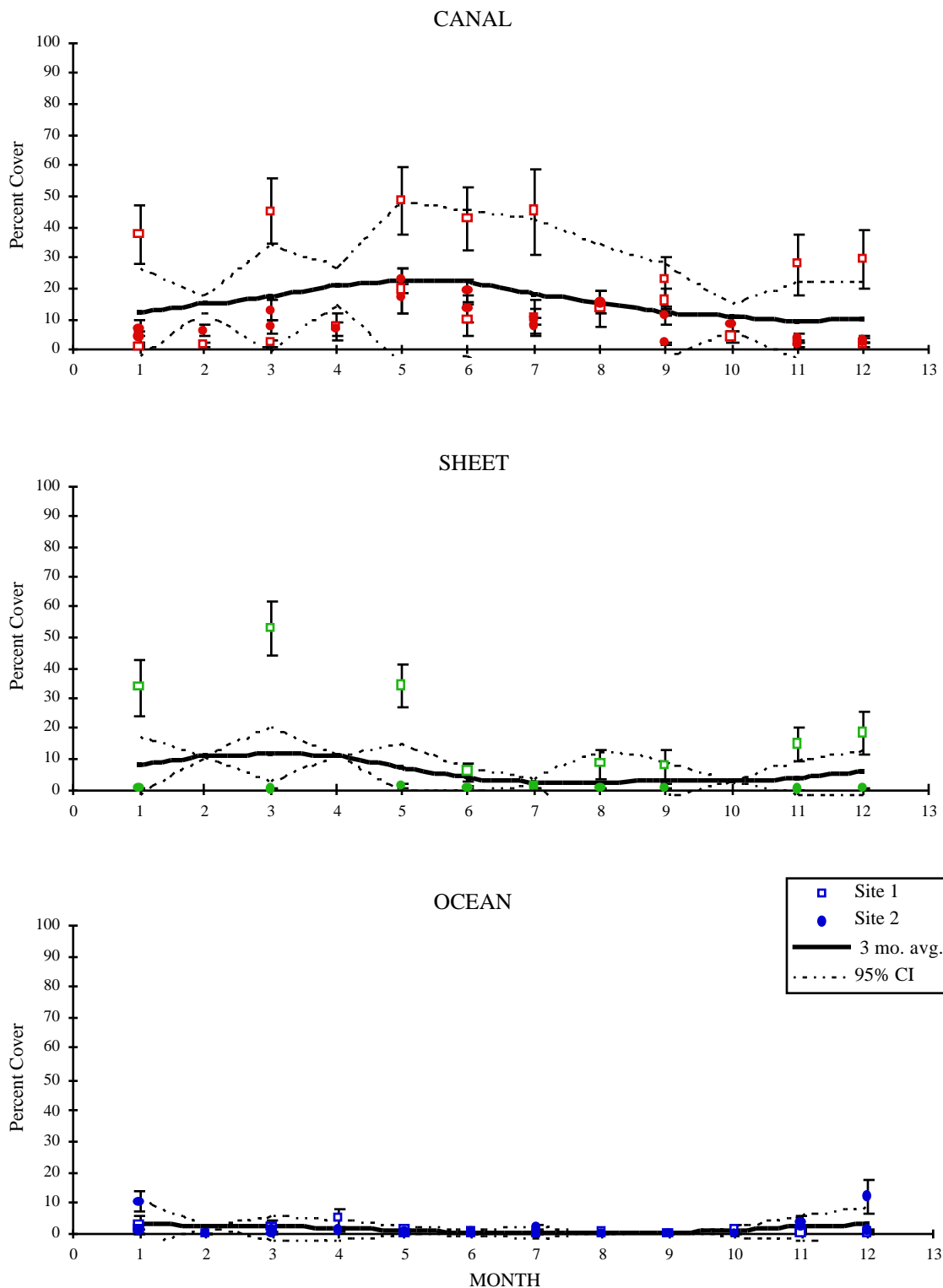


Fig. 9: Three-month moving average of percent cover of drift algae ($\pm 95\%$ CI) measured monthly from Aug. '97 to Aug. '99 (Phase II and III) in each of the three salinity regimes. The mean ($\pm SE$) of the samples collected from the two sites are also shown to indicate the variability around the smoothed data trace.

oceanic regime (mean biomass up to $250 \text{ g}\cdot\text{m}^{-2}$), than the sheet-flow and canal regimes ($<100 \text{ g}\cdot\text{m}^{-2}$) (Fig. 8). Biomass in the oceanic regime was greater during the spring and summer months than the fall and winter, while the opposite was true for the canal regime (Figs. 7&8). Epiphyte biomass remained similar throughout the year in the sheet-flow regime (Figs. 7&8). Seasonal dynamics were similar at the canal and sheet-flow regimes, with little variation ($\pm 10\text{-}30 \text{ g}$) about the mean annual value ($50\text{-}60 \text{ g}\cdot\text{m}^{-2}$) (Fig. 8). Contrast this with the oceanic regime, where there was high variability about the three month average ($\pm 15\text{-}100 \text{ g}$), and a spring/summer increase in biomass ($100\text{-}150 \text{ g}\cdot\text{m}^{-2}$), double the winter low of $70 \text{ g}\cdot\text{m}^{-2}$ (Fig. 8).

Drift algae: were most abundant in the canal regime, and least abundant in the oceanic regime (Figs. 7&8). The drift algae had a consistent seasonal dynamic across all three salinity regimes, with biomass highest in spring and summer and lowest in late fall (Fig. 8). In the canal regime mean biomass ranged from $20\text{-}40 \text{ g}\cdot\text{m}^{-2}$ with a variation of $\pm 5\text{-}35 \text{ g}$, the highest observed. At the sheet-flow and oceanic sites there was less drift biomass present (sheet = $10\text{-}25 \text{ g}\cdot\text{m}^{-2}$, ocean = $<5 \text{ g}\cdot\text{m}^{-2}$), and variability was less (sheet = $\pm 5\text{-}25 \text{ g}$, ocean = $\pm 0\text{-}10 \text{ g}$) than in the canal regime (Figs. 7&8). The oceanic regime had the lowest average standing stock, but some samples with higher biomass ($20\text{-}30 \text{ g}\cdot\text{m}^{-2}$) were present in winter and spring (Fig. 8), 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 (Figs. 7&8). Average biomass in the oceanic regime ranged from $10\text{-}25 \text{ g}\cdot\text{m}^{-2}$, the canal ($5\text{-}10 \text{ g}\cdot\text{m}^{-2}$) and the sheet-flow ($<5 \text{ g}\cdot\text{m}^{-2}$) regimes both had low biomass. Seasonal biomass dynamics were similar among the three salinity regimes; biomass was highest in summer, with a minimum occurring during the winter months (Figs. 7&8). The seasonal time-series for this functional group in the three regimes had a low mean, and variance ($< 15 \text{ g}$) due to a few high-biomass quadrats occurring in the small number of samples collected (Fig. 7).

6. Percent Cover and Biomass of Drift Algae

Percent cover of drift algae obtained in Phases II and III was used as a second measure of abundance. Average percent cover in the canal regime was 20% ($\pm 10-25\%$), with highest percent cover in the spring and summer and minimum in the fall (Fig. 9). This compares favorably with the biomass data ($20-40 \text{ g}\cdot\text{m}^{-2} \pm 5-35 \text{ g}$) for drift algae in the same regime (Fig. 8). Similarly, for the sheet-flow regime percent cover ($<10\% \pm 0-7.5\%$) and biomass measures ($10-20 \text{ g}\cdot\text{m}^{-2} \pm 5-25 \text{ g}$) are in close agreement in magnitude and seasonality (Figs. 8&9). While the magnitude of the two measures agrees favorably for the oceanic regime, the seasonality is less closely in agreement than was observed in the other two regimes, where biomass lags percent cover about one month. Across the three regimes, percent cover of drift algae increases in the spring and peaks in Mar.-May (Fig. 9), but the biomass maximum occurs in Apr.-Jun. (Fig. 8), while the minimum cover and biomass occurs in Nov.-Jan.

Linear regressions of percent cover to biomass for the drift algae were calculated for each salinity regime (Fig. 10) from the data measured in Phase III. Predicted biomass at 100% cover in the 1m^2 quadrat (= slope of the regression) was highest in the canal sites ($268 \text{ g}\cdot\text{m}^{-2}$), almost double that found in the sheet-flow sites ($137 \text{ g}\cdot\text{m}^{-2}$), with oceanic sites intermediate ($180 \text{ g}\cdot\text{m}^{-2}$). However, the low coefficient of determination (r^2) for the sheet-flow sites indicates that percent cover is not the only variable important in explaining the variation present in the biomass data in this regime (Fig. 10).

An ANCOVA on the regression relationships in Fig. 10 found significant differences in the slopes (Table 6). The canal regime had significantly higher biomass of drift algae for a given % cover than the oceanic regime, and these were higher than the sheet-flow regime (Fig. 10). The differences in the amount of biomass per % cover between regimes is indicative of the density of clumps of drift. In canal sites, drift algae were usually present in thick dense mats covering large areas of the bottom, whereas in the sheet-flow and

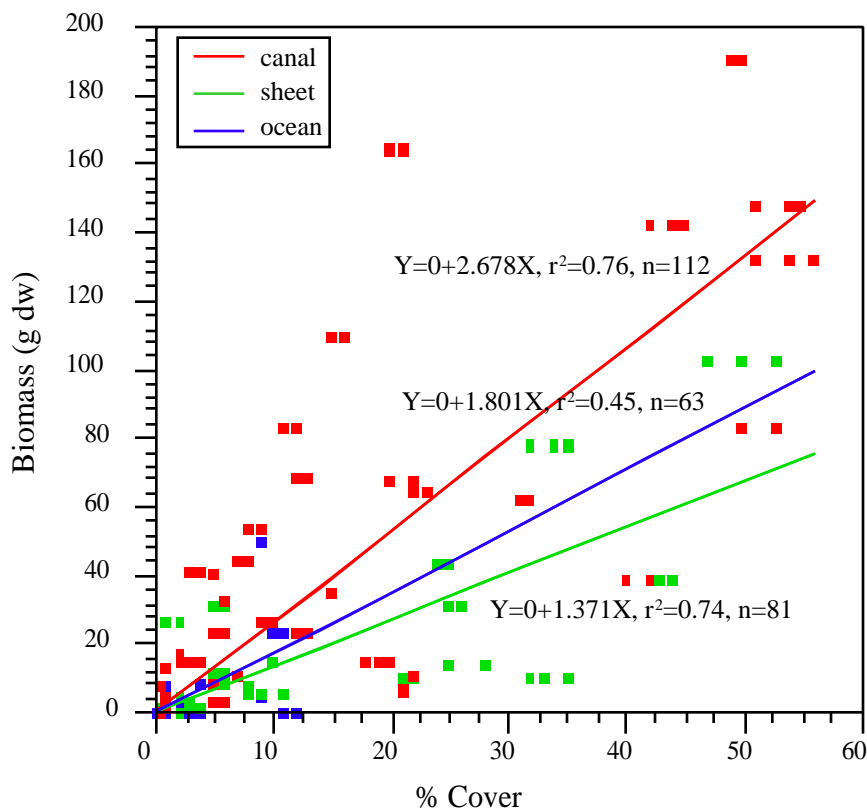


Fig 10: Regressions of drift biomass to percent cover for three salinity regimes sampled in Phase III. **B** = biomass (g dry wt), **A** = percent cover.

Table 6: ANCOVA on the three regression equations of biomass:% cover to determine significance of slopes and intercepts for the three salinity regimes, $r^2 = 0.6593$.

Source	df	SS	MS	F	P
among slopes	2	4413.42	2206.71	3.806	<0.025
sum groups	253	146690.87	579.81		
among intercepts	2	10260.29	5130.15	0.8658	n.s.
pooled groups	255	151104.29	5920.57		
total	257	161364.58			

oceanic sites, drift algae were sparse and often did not form the large extensive clumps that were present in the canal sites. The low biomass-to-cover relationship in the sheet-flow regime appears to be driven by the Little Card Sound (LCS) site, where drift algae were infrequently present, while at the Barnes Sound (BS) site drift algae occurred year-round in some abundance. The BS site in this regard is more like a “typical” canal site, with high

biomass of drift algae year-round, whereas the LCS site is more like the oceanic sites with little drift biomass (see also Chapter 6).

7. Seasonal and Inter-annual Comparisons

Seasonal differences were evident to some degree for all three functional groups (Fig. 8). Significant seasonal differences in biomass were found for the drift algae at the sheet-flow (Feb. > Aug.) and oceanic (Aug. > Feb.) sites, while there was no significant difference in drift algal biomass at the canal sites (Table 7). Similarly, significant seasonal differences in % cover were found for the drift algae at the sheet-flow (Feb. > Aug.) and canal (Aug. > Feb.) sites, while there was no significant difference in drift algal cover at the oceanic sites (Table 7). For the rhizophytic algae, the canal and oceanic sites showed significant seasonal differences, but not the sheet-flow sites (Table 7). The rhizophytic algae showed a trend across all three regimes for greater wet season biomass than dry season biomass (Fig. 8). The epiphytes did not show any significant seasonal response, except in the sheet-flow sites (Mar. > Aug.). There was a no consistent seasonal trend in epiphyte biomass across sites (Fig. 8).

The inter-annual comparisons were done on the 1996-97 data (Phase I) only, as these were the only two years in which the same sampling method was used (Fig. 2). Different sampling methods may have influenced the biomass collected. This was tested using a Wilcoxon rank-sum test in Aug. '98, when both collection methods from Phase II and III were used. The biomass collected at the two canal sites was found to be significantly higher using the Phase III methods ($\chi^2=4.803$, $df=1$, $P<0.0284$, $n=10-12$), while at the two oceanic sites there were no differences ($\chi^2=0.0044$, $df=1$, $P<0.9473$, $n=10-12$). All comparisons, with the exception of the drift algae in the oceanic regime in the wet season (Aug.), showed that biomass did not change significantly from one year to the next, suggesting that seasonal cycles were similar across years in the drift and rhizophytic

functional groups (Table 7). As epiphytes were collected for only one year, no inter-annual comparisons could be done.

Table 7: Results of separate Wilcoxon rank-sum tests for seasonal and inter-annual comparisons of biomass and % cover for three functional groups: drift, rhizophytic algae, and epiphytes. Seasonal comparisons based on multiple years for drift and rhizophytic, one year for epiphytes (dry season = Mar). Inter-annual comparison based on initial two years of sampling using the same methodology (Phase 1). P values highlighted in bold = <0.05, and italics = <0.1 level of significance.

Season	Functional Group	Location	n	df	χ^2	P
<u>Dry season (Feb.) vs.</u> <u>Wet season (Aug.)</u>	Drift - biomass	Canal	48	1	0.1357	0.7126
		Sheet	48	1	12.8214	0.0003
		Ocean	48	1	5.2103	0.0225
	Drift - % cover	Canal	107	1	3.1309	0.0768
		Sheet	54	1	42.3689	<0.0001
		Ocean	57	1	0.3960	0.5291
	Rhizo	Canal	48	1	3.2706	0.0705
		Sheet	48	1	1.1171	0.2905
		Ocean	48	1	18.1277	<0.0001
	Epi	Canal	20	1	0.3706	0.5427
Sheet		20	1	2.7232	0.0989	
Ocean		20	1	0.6586	0.4171	
<u>Feb. vs. Feb.</u> <u>1996 '97</u>	Drift	Canal	24	1	0.2276	0.6333
		Sheet	24	1	0.5859	0.4440
		Ocean	24	1	0.2040	0.6515
	Rhizo	Canal	24	1	0.6832	0.4085
		Sheet	24	1	0.0523	0.8192
		Ocean	24	1	0.1421	0.7062
<u>Aug. vs. Aug.</u> <u>1996 '97</u>	Drift	Canal	24	1	1.8406	0.1749
		Sheet	24	1	1.5207	0.2175
		Ocean	24	1	4.1120	0.0426
	Rhizo	Canal	24	1	0.1286	0.7199
		Sheet	24	1	0.1698	0.6803
		Ocean	24	1	1.4084	0.2353

DISCUSSION

The gradient across Biscayne Bay from canal inputs, correlates with a demonstrable community shift in the abundance of the dominant type of macroalgae present in the shallow *Thalassia*-dominated habitats. Drift, rhizophytic algae, and seagrass epiphytes are all recognized as important floristic components of these seagrass communities (Dawes 1987; Zieman 1982).

Drift Algae

Drift aggregations are primarily composed of red algae, division Rhodophyta (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, and *Laurencia poiteaui* was found to be the most abundant species (Bader and Roessler 1971; Josselyn 1977). More than two decades later this species remains the dominant component of the drift, indicating a long term (multi-decadal) stability of the macroalgal community.

Drift algae exhibit a distinct seasonal variation, with large spring blooms reported for many bays and estuaries along the U.S. 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 in environmental variables, the biomass of drift still tends to be greater in winter and spring than in the summer months (Bader and Roessler 1971; Josselyn 1977; Thorhaug and Roessler 1977). Proposed reasons for seasonality in drift biomass include annual light and temperature variations (Josselyn 1977). Salinity may also be 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 at canal and sheet-flow sites may be responsible for further depressing standing stock biomass of drift algae over the course of the wet season. 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).

Drift algae are often highly patchy in distribution (Josselyn 1977; Virnstein and Carbonara 1985; Bell and Hall 1997), indicated 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 varies from a few grams dry wt m⁻² (Benz *et al.* 1979, Zimmerman and Livingston 1979) to 100 g·m⁻² (Bell and Hall 1997), or even higher. In extremely dense aggregations in the Indian River lagoon, Virnstein and Carbonara (1985) reported mean drift algal biomass ranging from 164-400 g dry wt m⁻². Zieman *et al.* (1989) reported a mean biomass of 24 g dry wt m⁻² in Florida Bay, which is similar to the annual average obtained for canal sites in Biscayne Bay in this and previous studies (Bader and Roessler 1971; Josselyn 1977).

Drift algae occur mostly on the western side of the Bay as unattached mats, which can be moved around under the action of tidal currents or wind-driven wave energy (Holmquist 1994; Bell and Hall 1997). Very little drift biomass was found at the oceanic sites, which may be because of the strong tidal currents at these sites discouraging the accumulation of drift algae. The importance of flow in structuring the distribution of drift algae has been investigated previously (Zieman *et al.* 1989; Bell *et al.* 1992; Bell and Hall 1997) and has been found to be an important variable for explaining regional-scale variations of drift distribution. Hamm and Humm (1976) reported that “apparently winds favor the accumulation of loose plants and large quantities tend to move into the Bay. The water is shallow enough for light penetration and currents weak enough so that drifting masses are only occasionally washed ashore or swept out of the Bay.”

When drift algae become abundant, they have the potential to affect *Thalassia* negatively by shading the available light (Williams-Cowper 1978; Cambridge *et al.* 1986; Irlandi, unpubl. manu.). The growth of drift algae is probably enhanced by the addition of

nutrients from canals draining the South Miami agricultural zone (Meeder *et al.* 1999) and provides an important positive feedback enhancing drift algal blooms when temperature and salinity conditions are favorable for growth during the cooler dry season months.

Rhizophytic Algae

Rhizophytic algae 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 in this study were *Halimeda incrassata* and *Penicillus capitatus*, in accordance with previous reports for Biscayne Bay (Thorhaug and Roessler 1977; Bach 1979). The rhizophytic algae are unique among benthic algae for their root-like structure, which enables them to anchor in unconsolidated sediments (Dawes 1987). Therefore, rhizophytic algae can persist in areas that have quite strong tidal currents (Bach 1979), typical of oceanic inlets (or cuts) on the eastern side of Biscayne Bay. This may explain in large part why rhizophytic algae were abundant at these sites while free-floating drift algae were not.

Rhizophytic algae are highly productive and important producers of carbonate sediments, with standing stock turnover rates of approximately 4-6 weeks reported for *Penicillus* (Stockman *et al.* 1967; Wefer 1980). Standing stock biomass ranges from a few rhizophytic algae to about 100 plants per square meter (approx. 50 g dry wt 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 dry wt m⁻² (Drew and Abel 1985). However, in mixed-species seagrass beds, rhizophytic algae may be excluded (South 1983), possibly explaining the low biomass found at the sheet-flow sites.

In Card Sound, *Halimeda* and *Penicillus* were found to have maximal growth in late summer and lowest growth in midwinter (Bader and Roessler 1971; Bach 1979; Davis and

Fourqurean 2001). Similar seasonal growth cycles for *Halimeda* have been reported for Bermuda (Wefer 1980) and Pacific areas (Drew 1983; Hudson 1985; Garrigue 1991), demonstrating 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 *Laurencia*. Other rhizophytic algae, such as *Caulerpa*, have maximal growth rates in the spring and fall, with growth inhibition in summer. Winter growth is low because of reduced photosynthesis, low water temperatures, and low nutrient availability (O'Neal and Prince 1982, 1988)

In the low-salinity sites, especially Fender Point, the most abundant rhizophytic alga was *Penicillus 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 *Thalassia*. Zieman (1972) proposed these seagrass beds are present on submerged former mangrove hammocks, which eroded the bedrock because of the low pH of the peat sediments, allowing sufficiently deep sediments to accumulate in localized patches for *Thalassia* to establish. *Penicillus* can form dense aggregations in the shallow sediments surrounding the seagrass patches; however, the plants are stunted and smaller (less than 50-70mm tall) than their counterparts on the oceanic side of the Bay. This is likely a result of too little sediment depth, and 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.

Seagrass Epiphytes

Epiphytes are less well studied ecologically than the other two functional groups, with many studies offering only species lists and containing little spatial and/or temporal information (Harlin 1980). There is an increase in the number of epiphyte species as one travels south along the Florida peninsula (Humm 1964; Ballantine and Humm 1975; Hall

and Eiseman 1981). Humm (1964), in his seminal work in Biscayne Bay reported 113 species of algae occurring as epiphytes on *Thalassia*. He categorized these species of epiphytes as either year-round encrusting calcareous forms, such as *Melobesia* spp. and *Fosliella* spp., or seasonally blooming winter species, including the filamentous *Cladosiphon* spp., *Ectocarpus* spp., and *Enteromorpha* spp. Similar patterns were reported by Heijs (1985) for tropical seagrass epiphytes in Papua New Guinea. It is interesting to note that the epiphyte community was observed to phase-shift between filamentous/diatom dominated assemblages occurring on seagrass blades at the canal sites, and crustose-calcareous forms found to dominate at the oceanic sites.

Epiphyte biomass was determined using a modification of the method developed by Penhale (1977) and similar to more proficient methods proposed by both Dauby and Pollock (1995) and Frankovich and Zieman (1995). The main difference in the technique used over that proposed by Penhale (1977) is the capture of all the epiphyte biomass in the filtered sample. Biomass of epiphytes per square meter (mean = 72.56 g dw·m⁻²) fall within the range (3.93 - 869.33 g dw·m⁻²) reported previously for different seagrass habitats (Penhale 1977; Heijs 1984), including Florida Bay (Frankovich and Zieman 1994).

Epiphytes have been reported as least abundant and diverse in summer, with a gradual increase to maximal abundance toward winter (Humm 1964; Jones 1968; Hall and Eiseman 1981). This pattern was evident at the canal sites, but not at the oceanic sites where epiphyte abundance was greater in the summer. Humm (1964) attributed the seasonal trend to the slow down in growth and production of new leaves by *Thalassia* during winter. This slow-down this has also been measured recently at my study sites (Irlandi *et al.* 2002). Jones (1968) noted that in winter and spring the dominant epiphytes in the Bay consisted of red and brown algae; the summer populations, in contrast, were primarily green and red algae.

Establishment of the epiphyte community on a seagrass blade occurs over a three to six week period (Jones 1968; Heijs 1985), resulting in a greater abundance and diversity of epiphytic algae towards the apical tip of a seagrass blade (Heijs 1984, 1985; Borowitzka *et al.* 1990). The presence of calcareous coralline epiphytes may provide a favorable substrate for the filamentous forms to settle on (Humm 1964). Further, numerous drift species may initially be epiphytes, which later become detached and continue to grow amongst the seagrass until storm events transport the accumulated mats onshore or into deeper waters (Humm 1964; Benz *et al.* 1979). Epiphytes of seagrass blades have been found to play a significant role in productivity (Jones 1968; Penhale 1977; Heijs 1984, 1985, 1987; Sullivan *et al.* 1991) and food webs (Morgan and Kitting 1984; Sullivan *et al.* 1993) of these habitats.

Algae as Indicators

Algae are frequently cited as indicators of eutrophication in estuaries and nearshore waters (Laws 2000), both in temperate (Borum 1985; Lyngby *et al.* 1994) and tropical regions (Bach and Josselyn 1978; Jensen and Gibson 1986; Lapointe and O'Connell 1989). As such they have been used to assess water quality and health of a watershed by analyzing the benthic vegetation of receiving estuaries (Frithsen and Holland 1992; Dennison *et al.* 1993). Often nutrient stress is difficult to characterize chemically over large geographic areas such as Biscayne Bay because nutrient concentrations are highly variable over time and space, and nutrient inputs into oligotrophic areas are rapidly assimilated by phytoplankton or benthic plants (Falcao and Vale 1990; Kausch 1990; Valiela *et al.* 1997).

While nutrient inputs altering nearshore seagrass habitats have received much attention recently (Valiela *et al.* 1997; McGlathery 2001), including numerous South Florida locations (Lapointe 1989; Lapointe and Clark 1992; Lapointe *et al.* 1994), the importance of salinity-induced habitat alterations has been poorly reported. 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.

I have demonstrated that there are notable changes in macroalgal community composition along a gradient of stressors associated with canal discharges into Biscayne Bay. The baseline information reported on seasonal and spatial dynamics of the algae can be used to evaluate their future efficacy as indicators of seagrass ecosystem health in the Bay. Using multivariate analyses, significant differences in the composition and abundance of macroalgae were demonstrated between three different salinity regimes. These community changes are hypothesized to correlate with changes in the environmental conditions at the sites selected.

Multivariate analyses of community changes in relation to environmental gradients are frequently advocated in monitoring programs (Alden *et al.* 1997). However, potential difficulties arise in interpreting the results of these statistical approaches because of the way the tests aggregate the spatial and temporal variance components into compound axes (Smith *et al.* 1988; Jongman *et al.* 1995). Further, the use of multivariate techniques does not engender a mechanistic understanding of factors responsible for the trends being observed.

Integrated mechanistic approaches to understanding the dynamics of macroalgal communities in tropical areas in response to nutrient inputs (Lapointe *et al.* 1987) and other gradients associated with terrestrial inputs (Erfteimeijer 1994) into nearshore waters need to be more fully developed. A mechanistic understanding of processes responsible for community shifts in tropical seaweeds can be approached, in part, by using ecological simulation models. Through the development and application of these models, it is possible to determine the behavior of the system over a range of conditions (Madden and Kemp 1996; Solidoro *et al.* 1997) and to make management recommendations (Jeffrey *et al.* 1991), an approach that I will evaluate in Chapter 7 of this dissertation.