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Drift macroalgal abundance in seagrass beds: investigating large-scale associations with physical and biotic attributes

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ABSTRACT: The relationship between a suite of physical and biological factors and drift macroalgal abundance was examined in 12 seagrass sites spanning a distance of over 50 km within Tampa Bay, Florida, USA. Field sampling was conducted in December 1991, and drift algal abundance was determined by recording algal percent cover from 25 quadrants at each site. Additionally, drift macroalgae were collected from gridded plots and dry weight biomass measured. Sediment characteristics and seagrass biomass, shoot density, blade length and percent cover at each site were also determined. Likewise, position of site within Tampa Bay was categorized by spatial coordinates. Step-wise regression indicated that percent silt-clay and percent seagrass cover combined to explain 57% of the variance of drift algal cover in seagrass beds, while percent silt-clay alone explained 35% of algal biomass variance. Neither drift macroalgal cover nor biomass demonstrated any significant relationship with shoot density or aboveground biomass. Over the large spatial scale of this study, our findings suggest a link between hydrodynamic regime, as reflected by sediment characteristics, and drift macroalgal abundance in seagrass beds.

KEY WORDS: Tampa Bay, Florida · Seagrass · Macroalgae · Sediments · Scale · Hydrodynamics

INTRODUCTION

Substantial information on macroalgal ecology has been generated from studies of plants attached to hard substrata (e.g. Sousa 1979, Underwood 1980, Dayton 1985). Additionally, the importance of attached macroalgae in modifying ecosystem dynamics of soft sediment systems has been investigated in a variety of locations (e.g. Hull 1987, Rieper-Kirchner 1989). Unattached macroalgae, which exist as floating clumps (i.e. drift macroalgae) (see Norton & Mathieson 1983), present an interesting comparison to soft sediment and hard substrata systems, especially in areas with emergent vegetation because of the aboveground structure provided by rooted plants and the mobility of algal patches. Studies on drift macroalgal shading of seagrass (Holmquist 1992) and/or faunal utilization of alternative habitat (Carr 1989, Williams & Seed 1992)

as well as dynamics of drift algal invasion/retention within seagrass beds offer new perspectives on interactions among macroalgae and other ecosystem components.

Clumps of drift macroalgae in seagrass systems vary in size (typically 10 to 50 cm in diameter in Florida, USA; Holmquist 1992, S. Bell & M. Hall unpubl.), and the most typically encountered taxa include members of the Rhodophyta such as the genera *Spyridia*, *Gracilaria* and *Hypnea* (Benz et al. 1979, Dawes et al. 1985). Drift algae can originate from hard substrata located outside of seagrass beds, or alternatively break off *in situ* after epiphytic growth on seagrass blades. Regardless of their source, drift algae are moved via wind and water currents. Passive movement of drift algae implies that the hydrodynamic setting of an area may be a critical feature controlling algal retention/accumulation.

Macroalgae often display marked seasonal patterns of abundance in seagrass beds. For example, in

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Florida, both Benz et al. (1979) and Virnstein & Carbonara (1985) noted high peaks of macroalgae in spring months but a decline in summer (see also Dawes et al. 1985). Temporal abundance patterns may be related to a combination of salinity, temperature and light conditions (Dawes 1982), not only within the seagrass beds but also at off site sources.

In addition to temporal variability, macroalgae display highly aggregated distributions in seagrass beds, sometimes accumulating in the bare patches within seagrass vegetation (Cowper 1978). High variance among samples of drift macroalgae when examined on the scale of meters is commonplace (e.g. Josselyn 1977). Moreover some seagrass species may retain more drift algae than others because of morphology (Virnstein & Carbonara 1985); thus, spatial distribution of drift algae may be closely linked to seagrass species composition and zonal distribution. As one increases the spatial frame of reference to include an entire coastal system, it is unclear whether patterns of algal species composition and accumulation might vary in seagrass beds of the same species.

The purpose of our study was to examine large-scale spatial patterns of drift macroalgal abundance among numerous seagrass sites in Tampa Bay, Florida. We

examined the relationship between a suite of physical factors, including measures of vegetation structure and sediment features, and drift algal abundance in seagrass beds that represent coastal habitats extending over a 50 km distance. Sediment features were used as a surrogate measure of hydrodynamic regime because of the well-established link between descriptors of sediment characteristics and water flow. Such information not only could be useful in predicting which seagrass landscapes are likely to accumulate large amounts of algae but could also suggest whether measures of *in situ* vegetation structure can explain patterns of seagrass accumulation/retention of drift algae on a scale of kilometers.

METHODS AND MATERIALS

Field sampling. Sampling was conducted in Tampa Bay, Florida (27° 47' N, 82° 37' W) at 12 study sites (BP, CB, CBC, CK, CP, EB, FD, IK, LP, MB, SA, SK; Fig. 1) chosen because they were well established and not highly impacted and represented a broad range of sediment types. Sampling was conducted during a 6 d period in December 1991 as previous studies indicated highest algal abundance in winter-spring months (December–March) (S. Bell unpubl., M. Hall & M. Fonseca unpubl.) Shallow water (≤ 1.0 m mean low water) seagrass beds spanning a 50 km distance within Tampa Bay were utilized. *Halodule wrightii* Aschersen or *Thalassia testudinum* Banks ex Konig were the dominant seagrass species present at most sampling locations, although *Syringodium filiforme* Kutzinger was occasionally found (see Fig. 2).

At each site we established 1 transect approximately 5 m from the edge of a seagrass bed. Four additional transects were then oriented parallel to the first transect, with all transects 5 m apart. Percent cover of drift macroalgae was determined from 25 randomly selected 1 m² grids (5 per transect): each grid was divided into 16 equal quadrants and frequency of algal occurrence was recorded in each quadrant. Seagrass blade cover was similarly determined, except that a 0.25 m² grid divided into 25 equal quadrants was used. All drift macroalgae were removed from gridded plots, placed into plastic containers, and returned to the laboratory for further processing. We collected 1 core (15.7 cm diameter) of seagrass for determination of seagrass characteristics (shoot density, maximum blade length and above-ground biomass) from each of the 5 sampling transects at every site. Cores were washed over a 1.0 mm sieve in the field to remove sediments and sieve contents were returned to the laboratory. Additionally, 5 sediment cores (5.76 cm diameter) were taken to a depth of 10 cm at 1 randomly chosen position along each of 3 transects

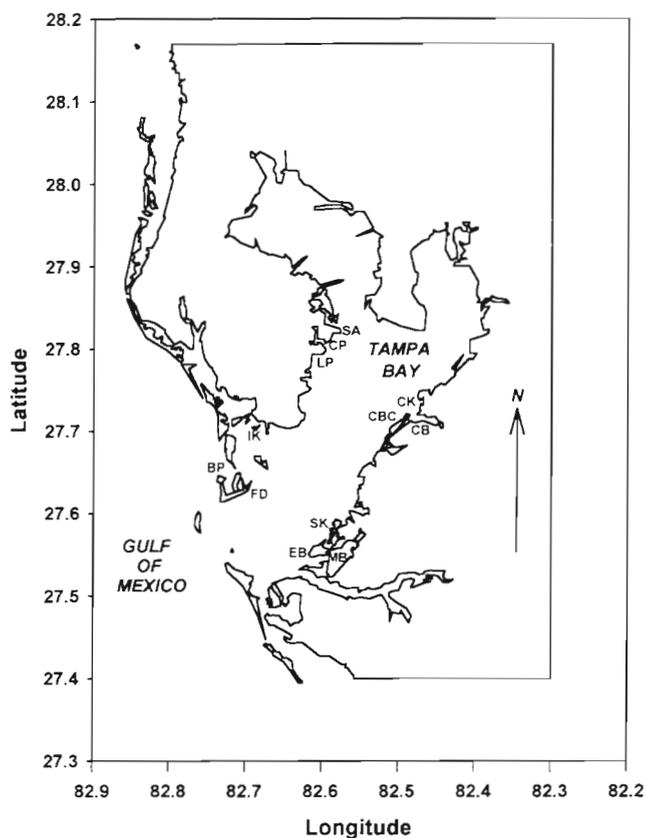


Fig. 1 Twelve sampling sites in Tampa Bay, Florida, USA

at every site, placed on ice and transported to the laboratory for further processing.

Laboratory procedures. In the laboratory, macroalgae collected from quadrants were identified to the lowest possible taxon. Biomass was then determined by drying at 60°C for 24 h. Seagrass material was identified to species, and number of shoots was recorded. Mean maximum blade length of all or up to 10 randomly selected shoots per sample was also determined. Next, seagrass aboveground structure was dried at 60°C for 24 h and biomass (g dry weight) was recorded. Percent silt-clay of each sediment core was determined from sediment grain size analysis. Likewise, organic content of sediments from each core was measured by loss upon ignition at 550°C for 24 h.

Dawes (1982) noted that the most diverse and abundant attached macroalgal communities were found in lower Tampa Bay, so we assigned a measure of approximately north-south orientation within the bay to each of the 12 sites. Using a navigational chart we measured the distance (converted to cm scale) of each site along a line placed perpendicular (approximately a north-south orientation) to one drawn across the mouth of Tampa Bay. Such 'up-down' positioning may also reflect the strong salinity gradient that exists within Tampa Bay, ranging from a median annual salinity of approx. 32‰ at the mouth of the bay to 19‰ at the uppermost site (e.g. Turner & Hopkins 1982). Additionally, we measured the east-west position of each sampling site relative to the perpendicular line within Tampa Bay, given that northeasterly winds, common during winter months, might produce heterogeneous patterns of algal transport/retention among sampling sites.

Statistical analyses. We conducted a step-wise multiple regression to investigate the relationship between macroalgal biomass or percent cover and the various physical and biotic variables measured. If variables departed from normality, we used appropriate transformations (i.e. log, sine or arcsine) to correct the deviations. All analyses were run on SAS using a 0.10 significance level as the criterion for entry into the model. Given that we were interested in a representative value for each location, mean values for each site were used in the analyses. Only single values were available for spatial coordinates of each site. Additional information on small-scale distribution of drift macroalgae within seagrass beds is available from R. Robbins, S. Bell & M. Hall (unpubl.).

Significant differences in algal abundance, as measured by percent algal cover and biomass, in seagrass beds composed of >70% *Halodule wrightii* versus those composed of >70% *Thalassia testudinum* were determined with a *t*-test if assumptions of normality were satisfied. If assumptions of normality could not be met, a Mann-Whitney Rank Sum Test was employed.

A $p < 0.05$ level of significance was utilized for these latter analyses.

RESULTS

Three seagrass species, *Thalassia testudinum*, *Halodule wrightii* and *Syringodium filiforme*, were recorded at the 12 sampling sites in Tampa Bay. Either *H. wrightii* or *T. testudinum* dominated in percent cover at almost all sites (Fig. 2). Among the 12 sampling sites, biomass of algae displayed great variability (Fig. 3A). Some sites, such as IK, LP, SA and SK, harbored little algal biomass, while biomass exceeding 150 g m⁻² was recorded at MB. Percent algal cover varied over an order of magnitude among the sampling sites, with lowest and highest values at LP and BP respectively (Fig. 3B). Neither algal biomass ($t = 0.554$, $df = 8$, $p = 0.594$) nor algal percent cover (Mann Whitney Rank Sum Test, $t = 31.0$, $p = 0.548$) differed between beds primarily composed of *T. testudinum* compared to *H. wrightii* vegetation. The largest biomass of algae was recovered from a site (MB) composed of *T. testudinum* vegetation, while algal biomass from BP, a site characterized by *H. wrightii* vegetation, ranked second in abundance. Intermediate levels of drift algal abundance were recovered from CP, which was composed exclusively of *S. filiforme*.

A total of 9 taxa of macroalgae were recovered from seagrass beds (Table 1). The BP site had the highest number of drift macroalgal species (7), while only 1 species was recorded at IK. Overall, *Hypnea* spp. and

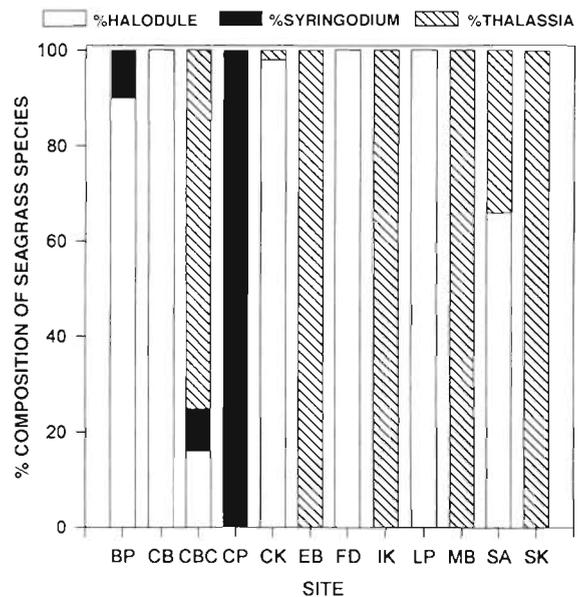


Fig. 2. Percent composition of seagrass species based upon percent cover at 12 sampling sites

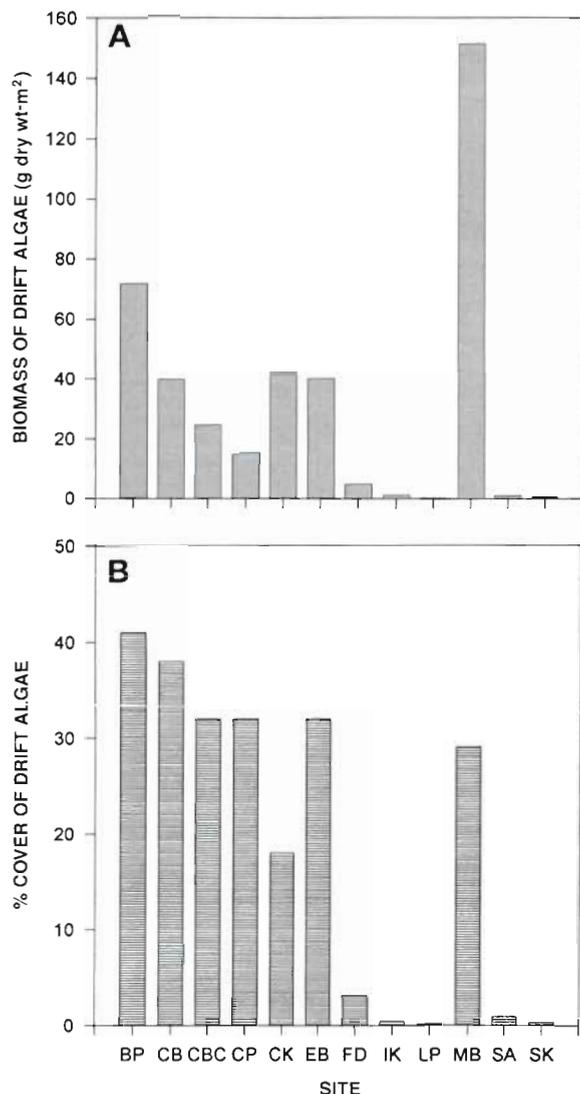


Fig. 3. (A) Drift macroalgal biomass at the 12 study sites, December 1991. (B) Percent drift macroalgal cover at the 12 sampling sites, December 1991

Gracilaria spp. were the dominant algal taxa recovered from the Tampa Bay seagrass beds. *Acanthophora spicifera* was a major component only at CP. *Spyridia filamentosa* was common at sites CB and CK and composed 40% of the drift algae at LP. Thus, differences in relative species composition of drift macroalgae (Table 1), as well as algal abundance (Fig. 3A), were evident among sites.

Using the step-wise regression analyses, we found that 2 of the 8 physical/biotic variables (from Table 2) entered into the regression model using our selection criteria. Percent silt-clay was the first variable to enter the model using algal cover as the dependent variable, and the model was improved to explain a total of 57% of the variance by adding percent seagrass cover

(Table 3). When algal biomass was used as a dependent variable, percent silt-clay once again was the first variable to enter the step-wise procedure, explaining 35% of the variance (Table 3). No other variable (i.e. position of site within the bay, seagrass shoot density or blade length, percent organics) met the 0.10 significance level for entry into the model when algal biomass was the dependent variable.

DISCUSSION

While temporal changes in algal abundance within a site are often expected (e.g. Schneider & Mann 1991), our large scale spatial study indicates that abundance of drift macroalgae may also be highly variable among sites (an order of magnitude difference) even on the same date. Factors such as salinity and prevailing wind direction, represented by site position within the estuary, did not adequately predict large scale differences in drift macroalgal abundance among sites.

Much of the among-site variation in macroalgal abundance appeared to be related to the local energy regime, given that percent silt-clay was the best predictor. The association between algae and silt-clay is a positive, but probably not a causal, one. Passive transport and deposition of both sediment particles and algal clumps may be strongly linked to the hydrodynamic regime of a particular site. The association between exposure and sediment characteristics has been well established given that wave action and current velocity are the 2 most important factors determining grain size distribution of nearshore sediments Gray (1981). Moreover, the highest percent silt-clay content of sediments in seagrass beds is typically recorded in low energy environments (M. Fonseca & S. Bell unpubl.). Accordingly, given that algal movement is strongly dictated by winds and currents, it is logical to suspect that hydrodynamically less-active environments may tend to capture/accumulate algae at a greater rate than those sites with high current velocity or extensive exposure to waves. Energy regime appeared to have little impact on algal species composition, however, with proportional representation of algal species similar in beds with both high and low percentages of silt-clay (Tables 1 & 2). Neither drift macroalgal cover nor biomass demonstrated any significant relationship with above-ground attributes of seagrass vegetation such as mean blade length, shoot density, or aboveground biomass. Note, however, that percent seagrass cover did combine with percent silt-clay to improve the predictive power of the amount of drift algal cover (Table 3). Percent cover of seagrass represents not only density but spatial arrangement of seagrass shoots and this latter feature may differen-

Table 1. Percent composition of drift macroalgal taxa (based upon algal biomass) from the 12 study sites in December 1991. Acan: *Acanthophora spicifera*; Chond: *Chondria* spp.; Dic: *Dictyota* spp.; Grac: *Gracilaria* spp.; Hypn: *Hypnea* spp.; Sar: *Sargassum* spp.; Sol: *Solaria* spp.; Spyr: *Spyridia filamentosa*; Ulva: *Ulva lactuca*

| Site | Acan | Chond | Dic | Grac | Hypn | Sar | Sol | Spyr | Ulva |
|------|------|-------|-----|-------|------|-----|-----|------|------|
| BP | 0.1 | 0.2 | 0.0 | 3.7 | 87.0 | 0.6 | 8.4 | 0.2 | 0.0 |
| CB | 0.0 | 0.0 | 0.0 | 47.3 | 22.0 | 0.0 | 0.0 | 22.0 | 9.6 |
| CBC | 0.0 | 0.1 | 0.0 | 67.8 | 29.5 | 0.0 | 0.0 | 2.4 | 0.0 |
| CP | 23.0 | 0.0 | 0.0 | 75.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 |
| CK | 0.0 | 0.0 | 0.0 | 40.0 | 32.0 | 0.0 | 1.2 | 27.0 | 0.0 |
| EB | 0.0 | 0.5 | 0.0 | 0.0 | 94.0 | 0.0 | 0.0 | 5.8 | 0.0 |
| FD | 1.1 | 2.0 | 0.0 | 0.7 | 95.8 | 0.0 | 0.0 | 0.7 | 0.0 |
| IK | 0.0 | 0.0 | 0.0 | 100.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| LP | 0.0 | 0.0 | 0.0 | 0.0 | 59.7 | 0.0 | 0.0 | 40.3 | 0.0 |
| MB | 0.0 | 0.2 | 1.6 | 3.7 | 91.6 | 0.0 | 0.0 | 2.8 | 0.0 |
| SA | 4.4 | 0.0 | 0.0 | 0.0 | 89.9 | 0.0 | 0.0 | 0.0 | 5.6 |
| SK | 0.0 | 2.4 | 0.0 | 8.9 | 88.6 | 0.0 | 0.0 | 0.0 | 0.0 |

Table 2. Mean values of physical and biological variables measured at the 12 study sites in Tampa Bay, Florida. North-South and East-West show relative spatial coordinates within the bay, where North-South shows position north of the mouth of the bay and where East-West shows position relative to a north-south line intersecting the bay, with negative values indicating 'west' (see 'Methods and materials')

| Site | Site | | % cover | Seagrass | | | Sediment | |
|------|------------------|----------------|---------|----------------------------------|------------------------|--|-------------|------------------|
| | North-South (cm) | East-West (cm) | | Shoot density (m ⁻²) | Max. blade length (cm) | Aboveground biomass (g m ⁻²) | % silt-clay | % organic matter |
| BP | 166 | -237 | 93.1 | 2741 | 12.0 | 53.9 | 8.51 | 4.5 |
| CB | 519 | 177 | 80.3 | 2258 | 4.9 | 3.1 | 6.51 | 2.6 |
| CBC | 519 | 166 | 67.5 | 596 | 9.0 | 40.4 | 1.42 | 0.5 |
| CK | 518 | 174 | 84.5 | 1404 | 6.9 | 5.8 | 7.44 | 3.4 |
| CP | 621 | -180 | 98.4 | 3830 | 12.4 | 43.2 | 0.65 | 0.7 |
| EB | 120 | 141 | 89.4 | 269 | 7.9 | 27.5 | 2.53 | 1.1 |
| FD | 169 | -122 | 89.6 | 5954 | 7.0 | 19.7 | 1.31 | 0.9 |
| IK | 326 | -222 | 92.0 | 427 | 9.5 | 69.8 | 4.89 | 2.0 |
| LP | 538 | -144 | 52.0 | 1999 | 5.7 | 3.1 | 0.87 | 0.6 |
| MB | 148 | 144 | 80.0 | 348 | 10.5 | 61.9 | 14.4 | 2.0 |
| SA | 681 | -162 | 90.0 | 1527 | 10.6 | 14.6 | 1.57 | 0.8 |
| SK | 146 | 141 | 95.6 | 550 | 11.9 | 85.7 | 2.43 | 0.7 |

tially influence capture/retain efficiencies for drift macroalgae. Some existing studies suggest that spatial arrangement of structure can impact the capture/deposition of passively dispersed particles (Eckman 1983), and such may be the case in seagrass beds. Experimental studies on macroalgal capture and movement in vegetation with varying structural characteristics and shoot dispersions will be required to explore more directly the relationship between drift macroalgal abundance and aboveground structure.

Our findings of a suggested link between hydrodynamic regime and drift macroalgal abundance may apply to other seagrass systems where drift algae are common and marked variation in tidal regime and wave exposure exists among sites. Moreover,

field experiments by Bell et al. (1995b) provide some additional perspective on what features might be important for trapping algae. By manipulating patch sizes and monitoring algal capture in experimental seagrass plots, they observed that bed shape (and associated modification of flow) may have a previously unsuspected effect on capture/retention of algae. They

Table 3. Summary of step-wise regression using forward selection procedure (with significance value $p < 0.10$ required for variable to enter model)

| Dependent variable | Independent variable | Partial r ² | p |
|------------------------|----------------------|------------------------|--------|
| % cover of drift algae | % silt-clay | 0.4319 | 0.0202 |
| % cover of drift algae | % cover of seagrass | 0.1433 | 0.1154 |
| Biomass of drift algae | % silt-clay | 0.3520 | 0.0420 |

also suggested that transport of macroalgae to sites, patch orientation relative to water transport and macroalgal availability might be critical features which operate in concert with water movement to impact algal dispersal and capture. However, other site characteristics such as nutrient levels, may need to be considered in studies that target areas where macroalgal growth occurs *in situ* (McGlathery et al. 1992) and/or drift algae are moved little from the seagrass source.

When viewed over a 50 km scale, differences in relative abundance of drift macroalgae observed among sites was not strictly related to seagrass species, although other investigations conducted over much smaller spatial scales have found a strong relationship between algal retention and seagrass species. For example, on one date, Virnstein & Carbonara (1985) charted algal biomass in 3 seagrass sites within a 15 ha area and found mean densities of algae (mainly *Gracilaria*) to be an order of magnitude higher in *Syringodium* compared to *Halodule* and *Thalassia* beds. The one seagrass bed composed of *S. filiforme* in our study harbored only intermediate levels of total algal biomass and percent cover (Figs. 2 & 3). We did find *Gracilaria* spp. in relatively high abundance at sites where *S. filiforme* was present (CBC, CP) (Fig. 2, Table 1), but this was true for a site composed only of *H. wrightii* (CB)(Fig. 2, Table 1) as well. Such results reiterate the importance of across-scale comparisons as discussed by Bell & Westoby (1986), who found little correspondence between fish response to seagrass leaf density or height in experiments repeated at different sites. Abundance of drift macroalgae within seagrass beds may represent a hierarchical set of controlling factors. Within-site differences may reflect mainly variation in seagrass morphologies (Virnstein & Carbonara 1985) and shoot arrangement and their ability to capture and retain drift macroalgae (Bell et al. 1995b), but among-site differences may reflect the additional influence of variation in physical setting.

Energy regime has been purported to be an organizing feature of seagrass systems in studies on other taxa. Bell et al. (1995a) reported that seagrass beds in North Carolina and Florida could be grouped according to the physical characteristics of percent silt-clay, wave exposure, and organic content of sediment—all indicative of hydrodynamic setting of a particular site. As an extension of this theme, Bell et al. (1995a) and Murphey & Fonseca (1995) noted that faunal characteristics varied among beds with different energy regimes and associated patchiness of beds. Thus our study adds to an emerging view that hydrodynamic regime may not only strongly control the developmental patterns of seagrasses (see Marba et al. 1994), which in turn may support correspondingly different faunal components, but also influence drift macroalgal accumulation within seagrass beds.

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