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MOTILE EPIFAUNA OF MARINE MACROPHYTES IN THE
INDIAN RIVER LAGOON, FLORIDA.
II. COMPARISONS BETWEEN DRIFT ALGAE AND THREE
SPECIES OF SEAGRASSES

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ABSTRACT

Within each of three adjacent monospecific beds of seagrasses (*Halodule wrightii* Aschersen, *Syringodium filiforme* Kutzing, and *Thalassia testudinum* Banks ex König) in the Indian River lagoon, Florida, the motile epifauna of seagrass and drift algae (*Gracilaria* sp.) were quantitatively sampled. In spite of sometimes large and significant differences in abundance of many epifaunal species, the lists of species on all substrata were similar, with an average of 75% of 47 species in common, mostly gastropods and peracarid crustaceans. Similarity analysis grouped faunas by substratum type (i.e., either algae or seagrass) rather than by site. At each site, the majority of the top 15 species had significant differences in abundance between seagrass and algae, both in terms of individuals per unit plant biomass and per unit plant surface area. Gastropod species were usually significantly more abundant on seagrass than on algae, whereas crustaceans were more abundant on algae. Both plant biomass and plant surface area were poor predictors of epifaunal abundances across substratum types, contrary to earlier predictions. These strong plant-animal associations may be due to differential survivorship and/or active habitat selection. The former may be particularly important in determining relative abundance of gastropods and crustaceans. When locally abundant, drift algae can be an important component of seagrass systems, and may provide superior refuge, food and habitat over seagrasses for associated epifauna.

In the majority of studies concerned with seagrass-dominated ecosystems, the seagrasses themselves are implied to be the sole macrophyte providing structural complexity to the habitat (e.g., see reviews in Phillips and McRoy, 1980). Nevertheless, many seagrass systems, particularly those at low latitudes, typically do not possess a homogeneous macrophyte structure and may contain variable amounts of macroalgae (and other substrata of complex morphology). Macroalgae may be very abundant in many coastal seagrass systems (Conover, 1958; 1964; Bader and Roessler, 1971; Thorhaug and Roessler, 1977; Cowper, 1978; Zimmerman and Livingston, 1979; Lewis, 1982; Harlin, 1983; Thorne-Miller et al., 1983), at times rivaling the abundance of seagrasses themselves. High densities of trophically important epifauna have been found associated with such algae (Gore et al., 1981; Kulczycki et al., 1981; Lewis, 1982; 1987), suggesting that this habitat may provide food, living space, and refuge from predators in a manner comparable to that traditionally ascribed to seagrasses.

In the Indian River lagoon, Florida, unattached (drift) macroalgae are at times extremely abundant, covering hectares of lagoon bottom in densities of >400 g dry weight m^{-2} (Virnstein and Carbonara, 1985). Here drift algae provide potentially major additional or alternative habitats for macrophyte-associated fauna.

One would predict highly similar species compositions and abundances of epifauna on drift macroalgae and seagrasses if both types of substrata provide comparable habitats. Alternatively, one would predict strong habitat selection and/or differential survivorship if these morphologically distinct macrophytes provide differing quality of habitat, based on their provision of food, living space and predator refuge. These differences in habitat selection and/or survivorship would

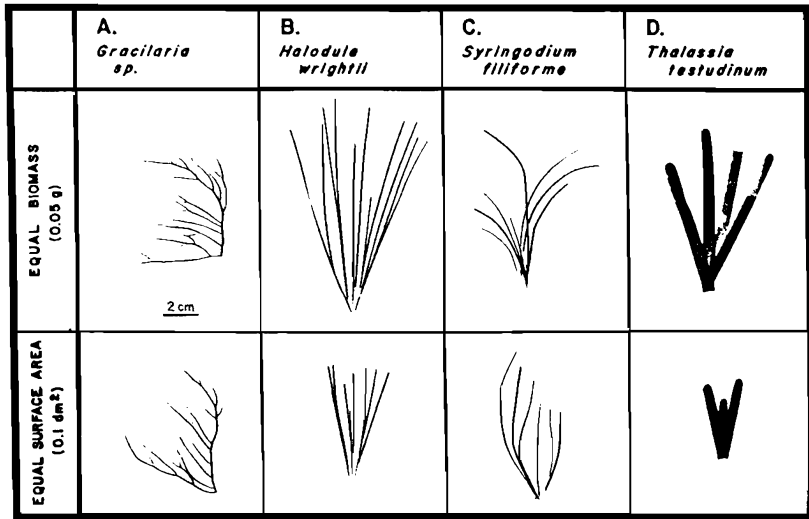


Figure 1. Equal biomass (0.05 g dry) and equal surface area (0.1 dm²) of each of the four macrophytes sampled: (A) Drift algae and (B–D) three species of seagrasses. Constant scale throughout.

be detectable as differences in species composition and relative abundance of epifaunal species.

Because of their trophic importance and capability to respond behaviorally to differences in plant architecture, the motile macro-epifauna are appropriate for studying plant-animal interactions. Based on field collections of algae and seagrasses at each of three sites, we assess whether the epifaunal communities associated with algae and three species of seagrasses are qualitatively and quantitatively similar.

STUDY SITE

The Indian River lagoon is a bar-built, estuarine lagoon extending 182 km along the central east coast of Florida, USA (for more detailed description, see Gilmore, 1977; Gore et al., 1981). The study area at Link Port (27°32.2'N, 80°20.9'W) is described in Virnstein and Carbonara (1985), with distributional maps of seagrasses and drift algal abundance. Generally, at this site and throughout the lagoon, *Halodule wrightii* is dominant in shallow water (subtidal to 0.4 m), and *Syringodium filiforme* is dominant in deeper water (0.5 to <1 m). *Thalassia testudinum* occurs throughout as scattered patches.

Three sampling sites were established—one in each of three monotypic stands of seagrass. All sites were subtidal, 0.4 to 0.8 m deep and 50 to 60 m apart within a single contiguous seagrass meadow. The *Halodule* site was shallowest, about 50 m from shore. The *Syringodium* site was ~50 m further from shore, and the *Thalassia* site was ~60 m from each of the other two sites, at an intermediate depth. At the time of sampling, water temperature was 29°C and salinity was 30‰.

METHODS

Sampling Collections.—At each of the three sites, quantitative samples were taken of the animals associated with (1) seagrass and (2) clumps of drift algae (Fig. 1) within the seagrass beds. Individual clumps of drift algae (*Gracilaria* sp.) judged to be of similar size were carefully collected with a 0.5-mm mesh dip net. Seagrass epifaunal samples were collected with a sampler designed to quantitatively collect seagrass blades and associated animals and exclude sediment-associated animals (Virnstein and Howard, 1987).

Samples were collected on 19 April 1982 in midday. Eight replicate samples of drift algae and six

Table 1. Above-ground plant biomass, based on 0.1-m² replicate quadrats at each of the three seagrass sites ($\bar{x} \pm s_x$)

Site	N	Above-ground biomass (g dry weight m ⁻²)	
		Seagrass	Algae
<i>Halodule</i>	5	128.5 ± 6.3	14.7 ± 2.4
<i>Syringodium</i>	8	40.1 ± 9.0	191.2 ± 41.7
<i>Thalassia</i>	5	278.4 ± 13.1	19.1 ± 8.5

of seagrass were collected at each of the three sites. Samples were fixed in a Formalin-seawater mixture with rose bengal stain added.

In the laboratory, animals were separated from the plants by washing with freshwater onto a 0.5-mm mesh sieve. Animals were identified to species in most cases and counted. Included in the analyses here are the motile macroepifauna; we excluded (1) taxa normally considered as meiofauna (e.g., nematodes and harpacticoid copepods, which were abundant in some samples, but not adequately sampled by our 0.5-mm mesh), (2) polychaetes, (3) bivalves, and (4) attached, strictly sessile species (e.g., barnacles, tunicates and bryozoans). Plant material from each replicate was washed, dried at 60°C, and weighed. Any drift algae present in seagrass samples was dried and weighed separately.

Although we tried to keep the amount of plant material in each sample roughly equal, mean drift algal sample size was 3.5, 3.9 and 4.1 g dry weight of algae from the *Syringodium*, *Halodule*, and *Thalassia* sites, respectively. Mean seagrass sample size was 2.8, 4.4 and 10.8 g dry weight of *Syringodium*, *Halodule*, and *Thalassia*, respectively. See Figure 1 for an illustration of plant morphology and an indication of sample size.

Analyses.—Because sample size (plant biomass) varied, we standardized abundances of animals, both with respect to plant biomass and plant surface area as follows. For each species, the number of individuals in each replicate was divided by the respective plant biomass in that replicate. However, an additional correction was first necessary for those seagrass samples which contained some algae, especially for samples collected from the *Syringodium* site, where drift algae was most abundant (Table 1). Drift algal biomass comprised a mean of 20.6%, 4.8% and 0.2% of total plant biomass in samples from the *Syringodium*, *Halodule*, and *Thalassia* sites, respectively. The number of animals estimated to be associated with the algal fraction was subtracted from the total number in the sample in order to calculate the number of animals associated with the seagrass only. The estimated number of individuals associated with the algae in each seagrass sample was calculated as: (grams of algae in the seagrass sample) × (mean number of individuals per gram of algae, as calculated from the eight drift algal samples from that site). These calculations were made separately for each species in each seagrass replicate.

Numbers of animals per plant surface area (individuals per square decimeter, =individuals 100 cm⁻²) were calculated as the product of individuals per plant biomass and the surface area-to-biomass ratios for these plants from the same locality (Stoner, 1980).

Similarity of species assemblages from the six different collections was measured by two similarity indices, one qualitative and one quantitative. The qualitative, presence-absence quotient of similarity (QS) measures the mean proportion of species common to two samples (Sørensen, 1948). The quantitative, relative-dominance index rho (van Belle and Ahmad, 1974), which heavily weights dominance, considers the relative proportion of species in two samples and is thus not affected by sample size. For each collection, totals of the replicates were used, eliminating those species occurring as single individuals. See Virnstein and Howard (1987) for more detailed descriptions of indices. Group-average clustering strategy (Lance and Williams, 1967) was used to group collections for the construction of dendrograms.

RESULTS

Plant Biomass at the Three Sites.—*Thalassia* had the highest seagrass biomass, while the *Syringodium* site had the lowest seagrass biomass and the highest biomass of drift algae (Table 1).

DOMINANT TAXA. Although relative abundance ranks differed, species lists of all six collections (three each of drift algae and seagrass) were similar. Only nine species included the top five species in all collections (Table 2) and comprised

Table 2. Species list and rank abundance in each of the three algae and three seagrass collections. Based on mean number of individuals per plant biomass. Unranked = not present. *Hal* = *Halodule*, *Syr* = *Syringodium*, *Tha* = *Thalassia*

Overall rank	Species	Type*	Rank							
			Algae				Seagrass			
			<i>Hal</i>	<i>Syr</i>	<i>Tha</i>	\bar{x}	<i>Hal</i>	<i>Syr</i>	<i>Tha</i>	\bar{x}
1	<i>Crepidula convexa</i>	G	1	8	8	5.7	1	3	1	1.7
2	<i>Bittium varium</i>	G	2	1	3	2.0	2	1	2	1.7
3	<i>Cymadusa compta</i>	A	5	2	1	2.7	7	2	3	4.0
4	<i>Astyris lunata</i>	G	6	5	2	4.3	4	4	6	4.7
5	<i>Erichsonella attenuata</i>	I	4	3	6	4.3	5	9	—	14.7
6	<i>Cymodoce faxoni</i>	I	3	4	4	3.7	9	13	21	14.3
7	<i>Hippolyte pleuracanthus</i>	S	7	7	5	6.3	6	5	14	8.3
8	<i>Modulus modulus</i>	G	9	13	11	11.0	3	8	5	5.3
9	<i>Corophium baconi</i>	A	8	6	7	7.0	17	6	16	13.0
10	<i>Ampithoe longimana</i>	A	18	12	9	13.0	8	7	4	6.3
11	<i>Hargeria rapax</i>	T	10	11	15	12.0	14	10	17	13.7
12	<i>Pagurus macclaughlinae</i>	C	11	10	10	10.3	17	14	12	14.3
13	Nemertinea	—	—	—	—	—	16	11	11	12.7
14	<i>Mysidopsis bigelowi</i>	M	—	16	—	21.7	11	12	19	14.0
15	Turbellaria	—	17	22	—	20.0	15	19	8	14.0
16	<i>Elysia catula</i>	G	—	20	—	23.0	—	—	7	17.7
17	<i>Ercolania fuscata</i>	G	13	—	13	16.7	17	16	23	18.7
18	<i>Paracaprella tenuis</i>	A	23	16	12	17.0	—	22	21	21.7
19	<i>Cerithium muscarum</i>	G	24	—	16	21.3	—	17	10	16.3
20	<i>Okenia impexa</i>	G	19	9	—	16.3	—	—	—	—
21	<i>Caecum pulchellum</i>	G	—	18	—	22.3	—	—	9	18.3
22	<i>Cratena pilata</i>	G	11	15	17	14.3	—	—	—	—
23	<i>Penaeus duorarum</i>	S	—	—	—	—	10	20	—	20.0
24	<i>Corophium bonnellii</i>	A	—	20	—	23.0	—	15	18	18.3
25	" <i>Odostomia</i> " engonia	G	—	—	—	—	—	20	13	18.3
26	" <i>Odostomia</i> " sp. A	G	—	14	—	21.0	12	—	—	22.0
27	Pycnogonida	—	14	—	14	17.3	—	—	—	—
28	<i>Palaemonetes intermedius</i>	S	19	—	—	21.3	17	18	23	19.3
29	<i>Gammarus mucronatus</i>	A	16	—	18	19.3	—	—	20	22.0
30	<i>Corophium simile</i>	A	—	—	—	—	—	—	15	20.3
31	<i>Turbonilla incisa</i>	G	—	—	—	—	13	—	—	22.3
32	<i>Gitanopsis tortugae</i>	A	19	19	—	19.7	—	—	—	—
33	<i>Syngnathus scovelli</i>	F	15	—	—	20	17	—	—	—
34	<i>Neritina virginea</i>	G	19	—	—	21.3	—	—	—	—
35-47†										

* A = Amphipod, C = Crab, F = Fish, G = Gastropod, I = Isopod, M = Mysid, S = Shrimp, T = Tanaid.

† Less-abundant species, in decreasing rank order: *Pyrgocythara plicosa*, *Phyllaplysia smaragda*, *Acteocina canaliculata*, *Polycera chiluna*, *Hippocampus zosterae*, *Phascolion cryptus*, Xanthidae, *Costoanachis avara*, *Erichthonius brasiliensis*, *Corophium acherusicum*, *Crepidula plana*, *Boonea impressa* and *Callinectes* sp.

94% of total individuals in all six collections. Of the top 12 species overall, only the isopod *Erichsonella attenuata* did not occur in all six collections.

Gastropods and peracarid crustaceans together comprised the top 7 species in all collections and 35 of the total 47 species collected. The top 10 species overall consisted of four gastropods, three amphipods, two isopods, and one caridean shrimp. Species dominant in all six collections (within the top eight species) include the gastropods *Crepidula convexa*, *Bittium varium*, and *Astyris lunata* and the amphipod *Cymadusa compta*. *Bittium varium* was the most consistently abundant species, ranging in rank only from 1 to 3 in all six collections. *Cymadusa compta* was the dominant crustacean in both the drift algae and seagrass collections.

The largest variability in rank between seagrass and algae was exhibited by the two isopods *Erichsonella attenuata* and *Cymodoce faxoni*—both had a mean rank of 4.0 in the three drift algal collections (range = 3 to 6), but only a mean rank of 14.5 in seagrass (range = 5 to 25).

Site differences in rank abundance were not uniform. High abundance of a given species on a particular seagrass rarely corresponded to high abundance on drift algae collected from that site.

Similarity Analysis.—Within-substratum presence-absence quotient of similarity (QS), i.e., within-seagrass and within-algae ($\bar{x} = 0.79$, $N = 6$), was significantly greater ($P = 0.02$, t -test) than between-substrata QS, i.e., between seagrass and algae, ($\bar{x} = 0.72$, $N = 9$) (Fig. 2A). Like QS, within-substratum rho ($\bar{x} = 0.87$) was greater ($P = 0.02$, t -test) than between-substrata rho ($\bar{x} = 0.73$).

Cluster analysis using QS values produced a weak separation into two groups—drift algae and seagrasses (Fig. 2B). However, the algal collection from the *Syringodium* site (a-S in Fig. 2) was weakly grouped with the seagrass collections.

Cluster analysis using the dominance-weighted index rho produced stronger separation of groups than QS, again forming two groups—drift algae and seagrasses (Fig. 2). However, the fauna of *Syringodium* (s-S in Fig. 2) was more similar to that of drift algae than to that of either of the other two seagrasses.

Community Totals.—Mean number of species per replicate varied from 11.0 on algae from the *Syringodium* site to 17.5 on *Thalassia* (Fig. 3). Within-site, mean number of species was significantly greater on *Syringodium* and *Thalassia* than on algae from their respective sites, but mean sample size (=plant biomass) of the *Thalassia* samples was more than twice the size of the algal samples. However, mean number of species on *Syringodium* was significantly greater ($P < 0.01$) than on drift algae from the same site, even though the mean size of the seagrass samples (2.8 g dry weight) was less than that of the drift algal samples (3.5 g) from this site. When replicates were rarefied to the smallest number of individuals in any single replicate (Heck et al., 1975), estimated numbers of species could then be compared more equitably. Mean number of expected species on seagrass was less than that on drift algae at the *Halodule* site, more than that on drift algae at the *Thalassia* site, and not significantly different at the *Syringodium* site (Fig. 3).

Abundance of total epifauna per plant biomass varied from 22.2 individuals g^{-1} on drift algae from the *Syringodium* site to 69.8 individuals g^{-1} on *Halodule* (Fig. 3). Abundance of total epifauna per plant surface area varied from 4.6 to 19.0 individuals dm^{-2} on *Thalassia* and *Syringodium*, respectively.

Gastropods and crustaceans comprised roughly equal proportions and had similar abundances on algae at all three sites (Fig. 3). On seagrasses, however, gastropods were much more abundant than crustaceans (mean gastropod : crustacean ratio = 7), especially on *Halodule* (ratio = 16), where *Crepidula convexa* and *Bittium varium* together comprised 86% of the total individuals.

Comparing epifaunal abundances on algae vs. seagrass within-site, the pattern of total abundance was variable. At the *Halodule* and *Syringodium* sites, individuals per plant biomass and per plant surface area were twice as abundant on seagrass as on algae from the same site, primarily due to the far greater abundance of gastropods on the seagrasses (Fig. 3). The opposite trend was found at the *Thalassia* site. Here, abundances of gastropods were not significantly different on the two substrata, whereas crustaceans and total individuals per plant biomass and per plant surface area were greater on the drift algae (Fig. 3). At the *Thalassia* site, crustaceans were 4.6 \times as abundant per plant biomass and 8.7 \times as abundant per plant surface area on drift algae as on seagrass (Fig. 3).

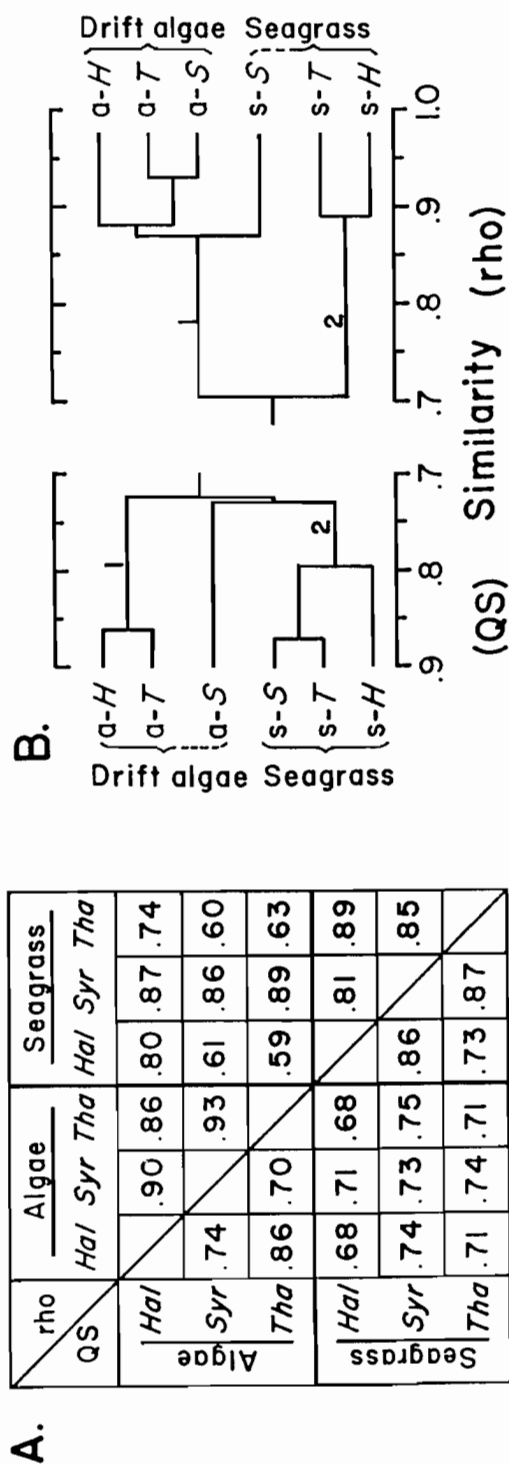


Figure 2. (A) Matrix of similarity coefficients. Below diagonal: Sørensen's presence-absence quotient of similarity (QS). Above diagonal: the dominance-weighted index rho. (B) Dendrograms grouping collections, based on both QS and rho, using group-average clustering strategy. Sample labels refer to collections of drift algae (a) or seagrass (s) from three seagrass sites: H = *Halodule*, T = *Thalassia*, S = *Syringodium*.

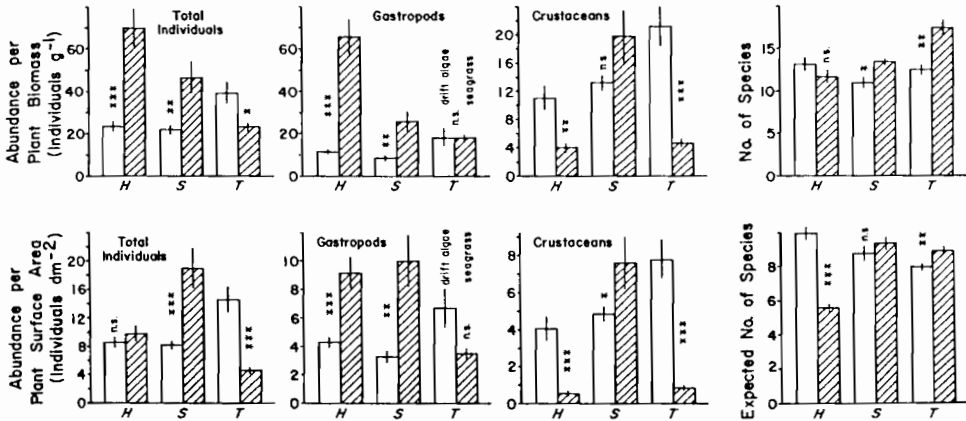


Figure 3. Algae-seagrass comparisons of community totals at each of the three sites. *H* = *Halodule* site, *S* = *Syngodium* site, *T* = *Thalassia* site. Open bars are drift algae; hatched bars are seagrass. Total number of individuals, and numbers of gastropods and crustaceans per plant biomass (indiv. g^{-1} dry weight) and per plant surface area (indiv. dm^{-2}), and actual and expected (rarefied to a sample size of 37 individuals) numbers of species. All values are means ($N = 8$ for algae, 6 for seagrasses) $\pm s_e$. Significant algae-seagrass comparisons are indicated: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, n.s. = not significant ($P > 0.05$).

Individual Patterns, Top 15 Taxa.

INDIVIDUALS PER PLANT BIOMASS. Again reflecting the high species similarity of algal and seagrass fauna, the same top 10 species made up 95.4% and 95.6% of the total number of individuals in the drift algal and seagrass collections, respectively.

Comparing abundances between the two substratum types at each of the three sites, seven species had significantly different abundances between seagrass and algae at the *Halodule* site (Fig. 4). The gastropods *Crepidula convexa*, *Bittium varium*, and *Modulus modiolus* and the crustaceans *Ampithoe longimana* and *Mysidopsis bigelowi* were more abundant on seagrass. Only two species, the crustaceans *Cymadusa compta* and *Cymodoce faxoni*, were more abundant on algae.

At the *Syngodium* site, seven taxa (three gastropods, three crustaceans, and nemerteans) were all more abundant on seagrass (Fig. 4). No taxa were more abundant on algae.

At the *Thalassia* site, 10 taxa (three gastropods, five crustaceans, nemerteans, and turbellarians) had significantly different abundances between substratum types (Fig. 4). Five were more abundant on seagrass and five were more abundant on algae.

Over all three sites, one-third of the taxa demonstrated consistent patterns of abundance with respect to the seagrass-algae comparison. *Crepidula convexa*, *Modulus modiolus* and *Ampithoe longimana* were more abundant on seagrass at all three sites. No taxon was more abundant on algae at all sites. Two species, the crustaceans *Hargeria rapax* and *Pagurus maclaughlinae*, had non-significant differences in abundance at all sites.

INDIVIDUALS PER PLANT SURFACE AREA. At the *Halodule* site, eight species (two gastropods and six crustaceans) had significantly different abundances between substratum types (Fig. 5). Five were more abundant on algae, and three were more abundant on seagrass.

At the *Syngodium* site, eight taxa (four gastropods, three crustaceans, and

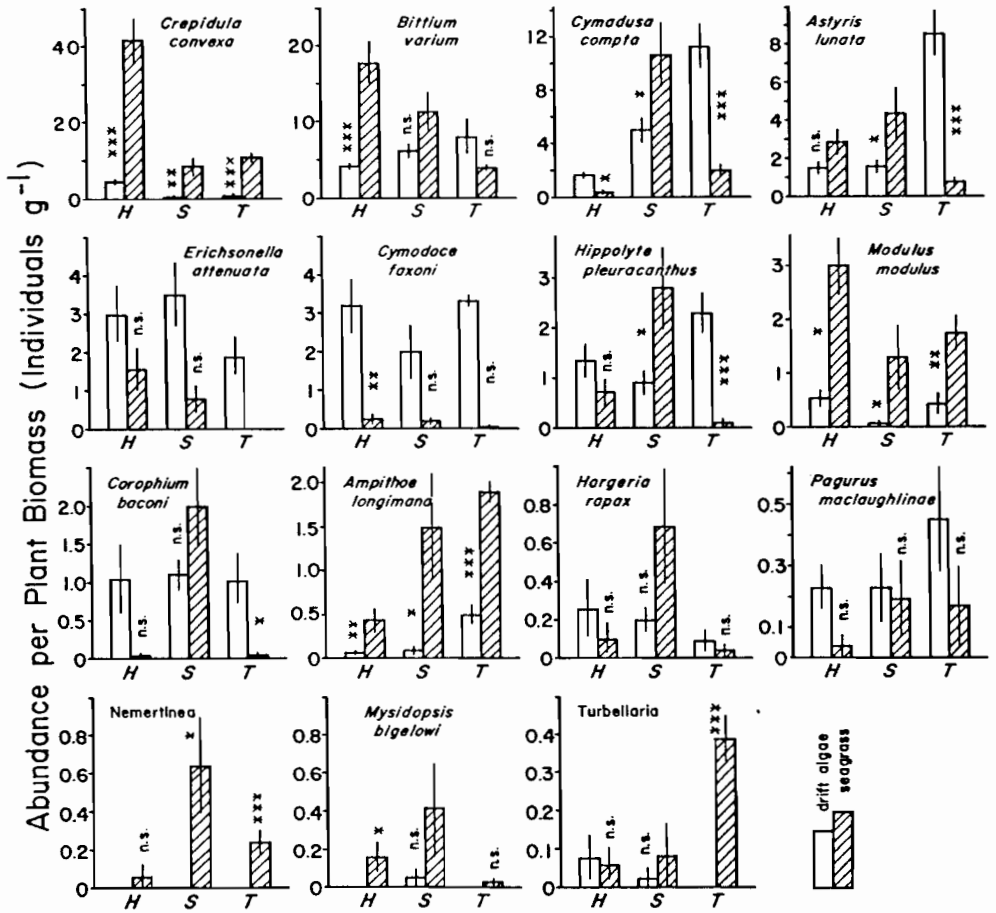


Figure 4. Abundance per plant biomass (individuals g⁻¹ dry weight) of the 15 top-ranked species, at each of the three sites. H = *Halodule* site, S = *Syringodium* site, T = *Thalassia* site. Open bars are drift algae; hatched bars are seagrass. All values are means (N = 8 for algae, 6 for seagrasses) ± s.e. Note changes in scales. Significant algae-seagrass comparisons are indicated: * = P < 0.05, ** = P < 0.01, *** = P < 0.001, n.s. = not significant (P > 0.05).

nemertean) had significantly greater abundance on seagrass (Fig. 5). Only a single species, the isopod *Erichsonella attenuata*, was more abundant on algae.

At the *Thalassia* site, four taxa (*Crepidula convexa*, *Ampithoe longimana*, nemertean, and turbellarians) were more abundant on seagrass (Fig. 5). Six species (two gastropods and four crustaceans) were more abundant on algae.

Over all three sites, two species had significantly higher abundance on a single substratum type: *Crepidula convexa* on seagrass and *Erichsonella attenuata* on algae (Fig. 5). *Hargeria rapax* and *Pagurus maclaughlinae* showed non-significant differences in abundance between seagrass and algae at all three sites.

Summary of Algae-seagrass Comparisons.—The number of occurrences of significant differences in the abundance of epifaunal taxa on the two substratum types (Table 3) was fairly consistent across sites. Number of significant differences was highest at the *Thalassia* site, both in terms of individuals per plant biomass

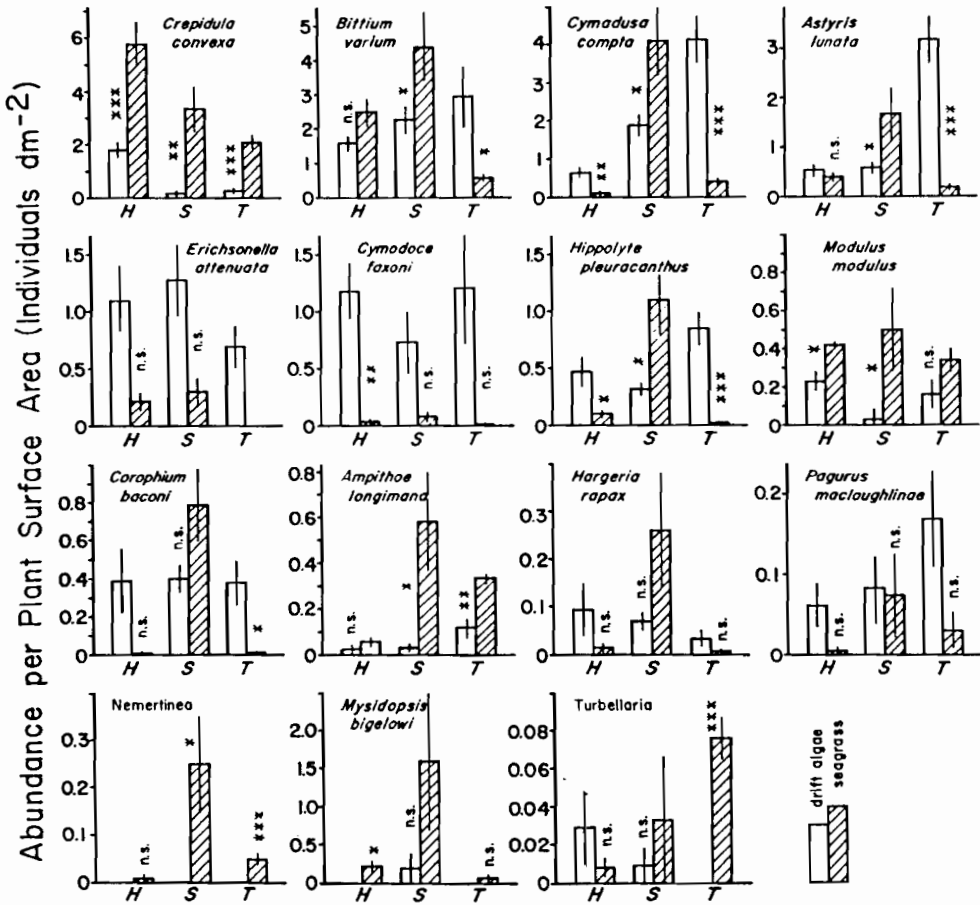


Figure 5. Abundance per plant surface area (individuals dm^{-2}). Algae-seagrass comparisons of the 15 top-ranked species, at each of the three sites. H = *Halodule* site, S = *Syringodium* site, T = *Thalassia* site. Open bars are drift algae; hatched bars are seagrass. All values are means ($N = 8$ for algae, 6 for seagrasses) \pm s.e. Note change in scales. Significant algae-seagrass comparisons are indicated: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, n.s. = not significant ($P > 0.05$).

and individuals per plant surface area. Two-thirds of the top 15 species showed significant differences between epifaunal abundance on seagrass and drift algae at the *Thalassia* site. The total number of significant seagrass-algae differences was not reduced when abundances per plant biomass were converted to abundances per plant surface area, 24 and 27, respectively (Table 3). Considered over all sites, taxa were more often significantly more abundant on seagrass than they were on drift algae (17 vs. 7 taxa for individuals per plant biomass and 15 vs. 12 taxa for individuals per plant surface area). This result was due mainly to the strong trend toward higher abundances on seagrass at the *Syringodium* site.

Overall, gastropod species were more often significantly more abundant on seagrass than on algae (final column of Table 3). Crustacean species more often occurred in greater abundance on drift algae than on seagrass. Total gastropod abundance was greater on seagrass than on drift algae, whereas total crustacean abundance was greater on drift algae (Fig. 3).

Table 3. Summary of the total number of taxa showing significantly higher abundance per plant biomass and per plant surface area on one substratum type (seagrass or drift algae) for the 15 most abundant taxa at each of three sites. Totals are partitioned into gastropods (G) and crustaceans (C)

Substratum type	Number of significant differences in abundance			Total
	<i>Halodule</i>	<i>Syringodium</i>	<i>Thalassia</i>	
A. Per plant biomass				
On seagrass	5	7	5	17 (8G, 6C)
On drift algae	2	0	5	7 (1G, 6C)
Total	7	7	10	24
B. Per plant surface area				
On seagrass	3	8	4	15 (7G, 5C)
On drift algae	5	1	6	12 (2G, 10C)
Total	8	9	10	27

DISCUSSION

In spite of sometimes large and significant differences in abundance, the list of species of mobile epifauna on all substrata was similar, with an average of 75% of the species in common with each other (Fig. 2). Dominance similarity values were higher *within* substrata (within algae and within seagrass) than *between* algae and seagrass. Thus there is some affinity of epifauna for substratum type that overrides spatial (site) differences, except at the *Syringodium* site. Here, the *Syringodium*-associated fauna was more similar to that of algae than to that of the other seagrasses. Because the abundance of drift algae was far greater at this site than at the *Halodule* or *Thalassia* sites (Table 1), epifauna-*Syringodium* associations may have been masked by the abundant epifauna associated with drift algae at that site, although the epifaunal associates of abundant *Thalassia* did not overwhelm the epifauna of algae, which comprised only 0.2% of *Thalassia* biomass at this site. Alternatively, the similar faunas may be due to similar plant morphologies; both *Syringodium* blades and *Gracilaria* branches are cylindrical with similar diameters (Fig. 1).

The fact that either drift algae or any of the seagrasses can serve as habitat for most species of epifauna may in part reflect the high mobility of epifauna, as measured by the rapid rate of turnover of individuals. By in situ staining of the animals within 0.6-m² patches of seagrass, Howard (1985) found that 37% of the crustacean and 16% of gastropod individuals were exchanged with non-stained individuals within a 6-h period. Turnover was even more rapid on individual clumps of drift algae (Virnstein, unpubl.). Also, various defaunated plants and artificial substrata are colonized rapidly (hours to days) by similar suites of species (Virnstein and Curran, 1986). Given such rapid turnover of individuals, it is surprising that some of the plant-animal associations are so strong; 13 of the top 15 species had significant differences in abundance between substrata at one or more sites.

However, the demonstration that these strong plant-animal associations exist does not per se reveal the mechanisms of these associations. Such differences in abundance of certain species of mobile epifauna on various macrophytes may be ascribed to a variety of processes. Among these, two processes—differential survivorship and/or active selection—have been previously acknowledged as important in macrophyte-dominated communities.

Two lines of evidence support the contention that differential survivorship may explain part of the algal-seagrass difference in relative abundance of epifaunal

species. Firstly, structurally complex macroalgae may provide certain epifaunal species with greater protection from predators than does seagrass (Heck, 1979; Heck and Thoman, 1981; Edgar, 1983; Stoner, 1985; Stoner and Lewis, 1985). This refuge may be particularly effective for small nestling crustaceans which are capable of occupying small spaces between branches of algae. Secondly, small crustaceans, especially amphipods, are preyed upon more heavily than the more abundant gastropods by major predators (pinfish, *Lagodon rhomboides*, and pink shrimp, *Penaeus duorarum*) in this seagrass system (Young and Young, 1978; Nelson, 1979; 1981a; 1981b; Nelson et al., 1982; Stoner, 1979; 1983a; 1983b; Virnstein et al., 1983; Leber, 1983; 1986). Shells of gastropods presumably offer some degree of predator protection which frees them from a strong dependence on complex vegetational cover. Hence the refuge value of vegetation may be far more critical to survival of "predator-vulnerable" crustaceans (Virnstein et al., 1984).

Active habitat selection on the part of the epifauna might also be operating, via the potentially important attributes of food and physical structure provided by macrophytes. *Cymadusa compta*, the dominant crustacean on both algae and seagrass, prefers to feed on macroalgae (Zimmerman et al., 1979); however, it showed an inconsistent pattern of abundance on algae compared to that on seagrass (Figs. 4, 5). *Bittium varium*, the dominant gastropod on algae, feeds by rasping loosely adhering epiphytes and trapped surface material on macrophyte surfaces (van Montfrans et al., 1982). Yet *Bittium* abundance was greater on algae than on seagrass at the *Thalassia* site (Fig. 5), even though visible epiphyte abundance clearly was far greater on all seagrasses than on algae (personal observations). Differences in microscopic attached algae, however, have not been examined. *Cymadusa* and *Bittium* are dominant colonizers (in hours to days) of clean artificial seagrass (Virnstein and Curran, 1986) which presumably offers no food resources. It is apparent that abundance of food, by itself, cannot explain the relative abundance of epifaunal species. Quality of food resources, especially of epiphytic algae, may also be important, and may be influenced by differences in chemical and physical structure of the host macrophyte.

Active selection for habitat might instead be based on the physical structure of the macrophyte. Stoner (1980) stated that amphipods selected habitats of high surface area and that the equal abundances per plant surface area in his laboratory experiments suggested uniform or random distribution over surface area. From our field collections, however, nine of the top 10 species had significant associations with either algae or seagrass at one or more of the sites (Figs. 4, 5), indicating that selection for surface area is not the overriding factor determining field distributions. Therefore, we argue that surface area alone is not an accurate predictor of epifaunal abundance.

Part of this discrepancy arises because two aspects of habitat structure should be distinguished: (1) *amount* of space or surface area available for occupancy and (2) the *type* of structure (plant form, often called "architecture"), meant to be a measure of habitat quality. Three examples suggest that plant form is important. The seagrass *Syringodium* and the drift alga *Gracilaria* sp. are round in cross section, while the two other seagrasses have flat, strap-shaped leaves (Fig. 1). The epifauna of *Syringodium* was quantitatively more similar to that of the morphologically similar drift algae than to that of the other two seagrasses (Fig. 2). Secondly, *Thalassia* blades are $\sim 5\times$ as wide as the other seagrasses or algae (Fig. 1), and algal-seagrass differences in epifaunal abundance are greatest at the *Thalassia* site (Figs. 2-5). Thirdly, a probable case of mismatch between plant architecture and animal size is that of *Thalassia* and *Erichsonella attenuata*, which

was not collected on *Thalassia*, despite ranking within the top nine species in each of the other five collections (Table 2). *Erichsonella*, an idoteaid isopod measuring approximately 1 by 10 mm as an adult, grips opposing edges of surfaces approximately equal to its body width, and may find *Thalassia* blades too wide to grasp. Lewis (1984) found a similar relationship for *Erichsonella filiformis* abundance on *Thalassia* and *Halodule*, which he also attributed to differences in plant morphology. Thus plant form or "architecture" appears important in determining the associated animal community.

Although both differential survivorship and active selection appear important, neither is sufficient by itself to explain differential patterns of epifaunal distribution. Competitive displacement may also be important (Coen et al., 1981), but has been little studied. These and other factors presumably act simultaneously, both as proximate and ultimate causes. The relative importance of these factors has yet to be determined.

The apparently desirable attributes provided by macroalgae, together with their high abundance in many seagrass systems, suggest that macroalgae are indeed important components of seagrass systems. On a local scale, their importance to the mobile epifauna may surpass that of seagrass itself. Drift algal biomass in the Indian River lagoon can be extremely high (to 500 g dry weight m^{-2}) in winter and spring, when seagrass biomass is low (Virnstein and Carbonara, 1985). In a manner traditionally ascribed to seagrasses (Thayer et al., 1975; McRoy and Helfferich, 1977; Phillips and McRoy, 1980), abundant and structurally complex macroalgae also provide habitat, food and refuge for an abundance and diversity of epifauna. At the least, for trophically important epifauna, especially small crustaceans, drift algae provide an alternative habitat.

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