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Community Composition of Crustaceans and Gastropods on *Caulerpa prolifera*, *Halodule wrightii* and *Thalassia testudinum*

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Community Composition of Crustaceans and Gastropods on *Caulerpa prolifera*,

Halodule wrightii and *Thalassia testudinum*

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
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Community Composition of Crustaceans and Gastropods on *Caulerpa prolifera*,
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ABSTRACT

A survey was conducted in monospecific beds of two seagrasses, *Halodule wrightii* Ascherson and *Thalassia testudinum* Banks ex König and the macroalgae *Caulerpa prolifera* (Forsskål) Lamouroux in Lassing Park, Tampa Bay, Florida (USA) to examine epifauna communities and to determine factors influencing the abundances of epifauna in this area including surface area of the vegetation or amount of epiphytic algae growing on each type of vegetation. This survey addressed three questions: 1) Does the amount of epiphytic algae differ among seagrasses, *T. testudinum* and *H. wrightii*, and the macroalga, *C. prolifera*? 2) Is there a difference between community composition, measured by epifauna density or species dominance, on each type of vegetation? 3) Is there a correlation between the amount of epifauna and the amount of either epiphytic algae or blade/frond surface area for each of the three types of vegetation? Field surveys were conducted in June and October 2004 in monospecific beds of *C. prolifera*, *H. wrightii*, and *T. testudinum*. The amount of epiphytic algae on *C. prolifera* was found to be an order of magnitude lower than the amounts found on either seagrass species over both sampling dates, although the amount of *C. prolifera* surface area was roughly double that of the seagrasses in October 2004. Although all three vegetation species supported epifauna communities composed mainly of

peracarids and gastropods, there were differences in the amount of epifauna found on each type of vegetation. Three major findings of this survey include: 1) evidence for a positive relationship between the amount of epifauna and amount of blade/frond surface area, including vegetation with higher amounts of surface area supporting higher amounts of epifauna, 2) no relationship between the amount of epifauna and amount of epiphytic algae on submerged vegetation, and 3) when the amount of surface area of all vegetation species was similar the epifauna communities were similar in species composition. Together these lend support to the theory that surface area of vegetation (and therefore possibly habitat complexity) is an important factor in determining the abundance and community composition of epifauna in seagrass and macroalgae beds in Lassing Park, Florida.

Introduction

Marine epifauna in macrophyte beds act as an important link in the food web between primary producers and secondary consumers, such as small fish and crabs (Schneider and Mann 1991). Epifauna are found in vegetated habitats around the world including seagrass beds, algae beds, kelp forests, and drift algae. Different species of epifauna have developed various feeding strategies and predator avoidance tactics to adapt to the specific vegetative habitats in which they live.

One habitat in which epifauna have been widely studied is coastal seagrasses. Seagrass systems are composed of one or more species of seagrass and may have one or more species of macroalgae as well. Previous studies have shown seagrass systems to have primary production rates of 0.2 to 18.7 g C m⁻² d⁻¹ (similar to coral reefs which have primary production rates of 5 to 20 g C m⁻² d⁻¹) (Dawes 1998). Seagrass beds may also support other primary producers including attached macroalgae, microalgae, and drift algae (Klumpp et al. 1992). Epifauna have been shown to use these highly productive seagrasses and algae as a food source (Dawes 1998). Previously it was thought that epifauna of seagrass systems used seagrass detritus as their main source of food (Darnell 1967, Odum and de la Cruz 1963, Fenchel 1970). More recently, Bologna and Heck (1999) and Moncreiff and Sullivan (2001) have shown that epiphytic algae, not detritus or living seagrass blades, are the main source of food for these epifauna, although the diets of epifauna may vary by species (Morgan and Kitting 1984, Duffy and Hay 1994, Cruz-Rivera and Hay 2000, Cruz-Rivera and Hay 2003,

Sotka et al. 2003). Epiphytic algae have been shown to have primary productivity rates equal to or exceeding the primary productivity rates of the seagrass on which they live (Morgan and Kitting 1984, Jensen and Gibson 1986, Moncreiff et al. 1992, Dawes 1998, Moncreiff and Sullivan 2001). It is reasonable to assume that the epiphytic algae on submerged vegetation are sufficiently abundant enough to serve as an important food source for small consumers living in and among seagrass beds. Therefore a higher abundance of epifauna on vegetation that supports higher numbers of readily consumable epiphytic algae should be expected.

Along with using seagrass beds as a food source, epifauna also use seagrass beds as structure for protection from predators. Previous studies have shown that epifauna prefer habitats with more complex structure, such as that provided by highly branched macroalgae, seagrass short shoots with a high number of blades, or epiphytes growing on seagrass (Hacker and Steneck 1990, Knowles and Bell 1998, Boström and Mattila 1999, Edgar and Klumpp 2003). Hacker and Steneck (1990) concluded that branched and filamentous algae provide complex three-dimensional structures with many small crevices which could be used by epifauna to avoid predators while leathery-type algae lack such complexity and thus do not offer many refuges for epifauna. Therefore systems with high complexity and high productivity of seagrass and epiphytes should be the most highly utilized by epifauna species.

Two seagrasses, *Halodule wrightii* and *Thalassia testudinum*, and one type of macroalgae, *Caulerpa prolifera*, present different habitat structural complexity for epifauna based on their morphology. The two seagrasses have flat blades that grow only from the rhizomes at short shoots with *H. wrightii* producing multiple thin (around 1mm wide) blades per short shoot and *T. testudinum* producing three to seven (up to 15mm wide) blades per

short shoot (Dawes 1998). *Caulerpa prolifera* offers a structural habitat of fronds up to approximately 15mm wide that present a wavy to whirled configuration growing from both the rhizoid and also from other fronds (Dawes 1974). In a previous study Sánchez-Moyano et al. (2001) showed that fronds of *C. prolifera* provided a habitat with high structural complexity, supporting a rich community of epifauna although they did not look at a possible relationship between the amount of epifauna and epiphytic algae cover. Therefore, there are marked differences among macrophyte morphology.

Along with using the structural complexity of the vegetation as a habitat, epifauna may also take advantage of the chemical composition characteristics of the vegetation that could offer protection from predators. *Caulerpa prolifera* is known to produce a secondary compound, caulerpenyne, which may act as a defense mechanism to prevent grazing (Vest et al. 1983, Meyer and Paul 1992, Sánchez-Moyano et al. 2001). Experiments testing the effectiveness of caulerpenyne as an antiherbivory defense have had mixed results. McConnell et al. (1982) showed that caulerpenyne effectively deters sea urchins from feeding on *C. prolifera*. In contrast, Meyer and Paul (1992) found that caulerpenyne coated on algal pieces actually stimulated fish feeding. If *C. prolifera* exhibits an effective antiherbivory chemical defense against large grazers or omnivores then the epifauna that live on and among *C. prolifera* fronds may be indirectly protected from any predators that avoid grazing on *C. prolifera*.

Distributional studies have revealed that epifauna are commonly habitat generalists (Edgar and Klumpp 2003) and are able to move from one type of vegetation habitat to another (Virnstein and Curran 1986, Howard 1987). These mobile epifauna have been shown to move between different macrophytes in order to find optimal habitats for feeding and predator avoidance (Stoner 1980, Main 1987, Hacker and Steneck 1990, Duffy and Hay

1991, Bostöm and Mattila 1999, Parker et al. 2001, Edgar and Klumpp 2003). With this ability to move from one habitat to another, epifauna should be able to move from unsuitable habitats to more suitable habitats such as those with a higher availability of food and/or more protection from predators, provided either directly through structural complexity or indirectly because of reduced herbivory on the habitat macrophyte. Thus, if there is a difference in the amount of food and/or protection offered by a macrophyte species then one would expect to find more epifauna moving to, and staying within, the more suitable habitat offered by that vegetation.

Monospecific areas of *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* coexist within Lassing Park, Tampa Bay, Florida. Here I describe a survey conducted in these areas designed to answer the following questions: 1) Does the amount of epiphytic algae differ among the three dominant macrophytes: *T. testudinum*, *H. wrightii*, and *C. prolifera*? 2) Is there a difference among community composition, measured by epifauna density or species dominance, on each type of vegetation? and 3) Is there a correlation between the amount of epifauna and either epiphytic algae or the amount of blade/frond surface area for each of the three types of vegetation?

Materials and Methods

Study Site

The survey was conducted in Lassing Park, Tampa Bay, Florida (27°45'N, 82°37'W) (Figure 1). Lassing Park has a mean depth of 0.53m, the temperature ranged from 18.14°C-32.53°C and salinity ranged from 22.1‰-29.3‰ over the course of the study. Both monospecific beds and mixed areas of the seagrasses *Thalassia testudinum* and *Halodule wrightii* as well as the macroalgae *Caulerpa prolifera* are all present within this area. Further information on the study site is available in Bell et al. (1993).

Experimental Design and Data Collection

Areas of monospecific seagrasses *Thalassia testudinum*, *Halodule wrightii*, and the macroalga *Caulerpa prolifera* were located throughout Lassing Park. In order to determine if there was a difference in the amount or composition of epifauna or epiphytic algae among the three types of vegetation, fifteen samples of both vegetation and epifauna were collected from monospecific areas within each type of vegetation. These samples were collected in summer (June 3 and 4) and fall (October 9 and 10), 2004. Both the vegetation and epifauna samples were taken from the same location within the monospecific beds. First, the epifauna samples were collected using an X-sampler (Figure 2), similar to one used by Virnstein et al. (1987) consisting of two 0.5mm mesh screens fixed to frames. The two frames were configured in order to sample a consistent bottom area of 0.09m². When used

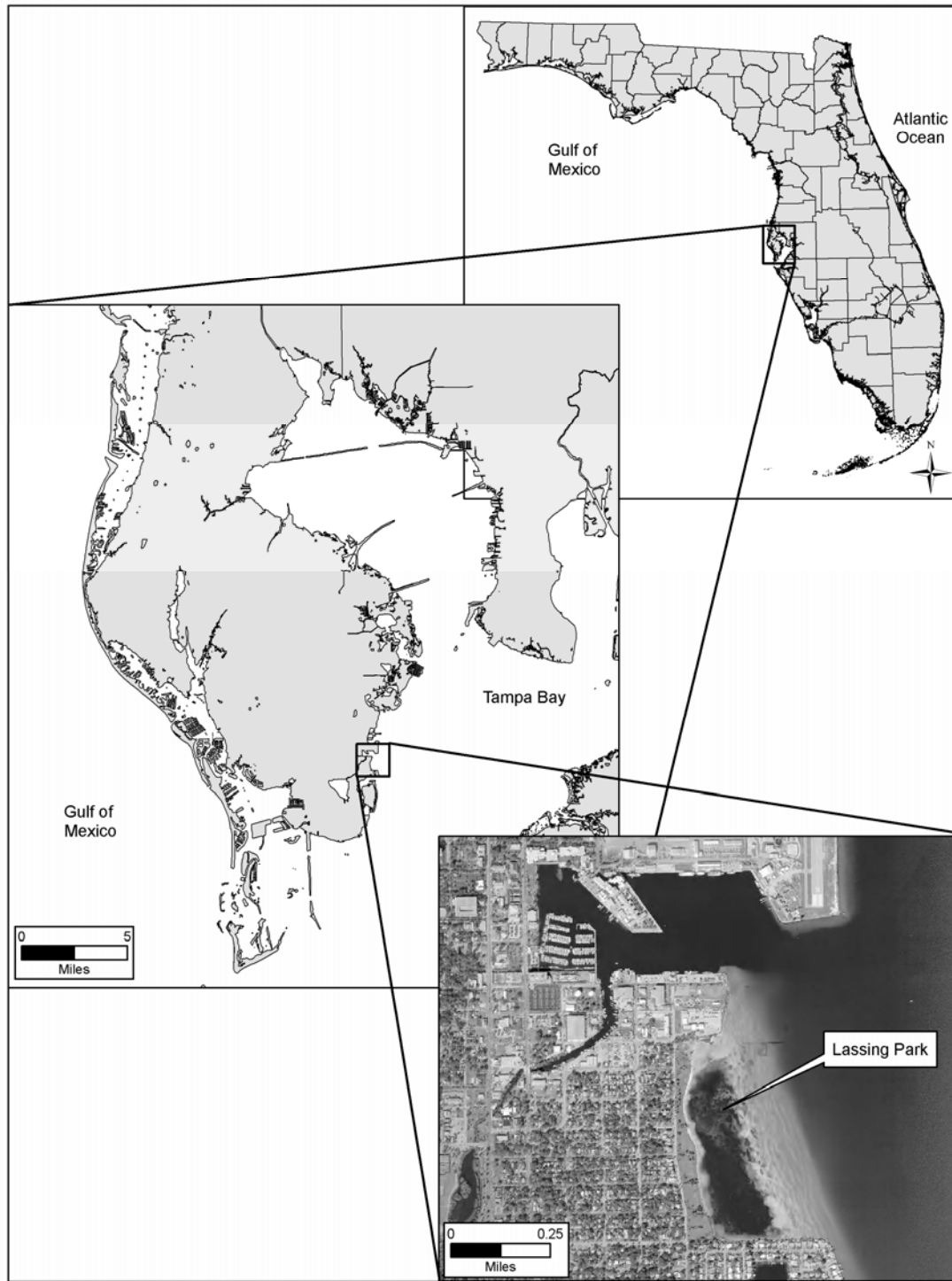


Figure 1. Map and aerial photo (LABINS 2004) showing the location of Tampa Bay, Florida and Lassing Park within Tampa Bay ($27^{\circ}45'N$, $82^{\circ}37'W$).



Figure 2. View of the X-sampler used to collect epifauna samples, in the open position.

in the field, the sampler was opened the maximum amount (encompassing a bottom area of 0.09m^2), lowered onto the monospecific vegetation, and closed to trap epifauna and vegetation between the frames. The vegetation trapped in the sampler was then clipped at its base and the trapped epifauna and clipped vegetation were rinsed into a glass jar and stored in 10% formalin with Rose Bengal. After each epifauna sample was collected a companion core of vegetation was collected using a 16cm diameter PVC corer at each site within a distance of 0.6m of the epifauna sample. The vegetation from the core was returned to the lab where the June 2004 samples were preserved in 5% formalin and the October 2004 samples were frozen until further processing.

In the laboratory the epifauna samples were rinsed over a 0.5mm sieve, sorted using a dissecting microscope, and all taxa were identified. Peracarid crustaceans and gastropods were then identified to genus, and species when possible. Each of the vegetation samples were rinsed free of sand and the surface area of all blades/fronds within the core was measured to the nearest 0.1cm^2 . Epiphytic algae on seagrass and algae blades/fronds were removed with a scalpel blade, dried at 60°C for 5 days, and weighed to the nearest 0.0001g. Thus for both summer and fall, data on the number of blades/fronds per sample (0.09m^2 bottom area), surface area of blades/fronds per sample, amount of epiphytic algae (g) per sample, and total numbers of all epifauna identified to species, when possible, per sample was available for further analysis.

Data Analysis

A two-way ANOVA was used to determine if there were significant differences in the amount of blade/frond surface area per sample, epiphytic algae per sample, and epifauna abundances between sampling dates and among vegetation types. Because early analysis revealed the dominance of one peracarid species, *Cymadusa compta*, and one gastropod species, *Bittium varium*, across all samples, all epifauna collected over both dates were divided into the following groups for statistical tests: total epifauna, total peracarids, total number of *C. compta*, total remaining peracarids (all species of peracarids except *C. compta*), total gastropods, and total number of *B. varium*. The epifauna were tested using the two-way ANOVA as abundances of epifauna per sample (0.09m² bottom area), per blade/frond surface area (cm²), and per epiphytic algae (g). Regression analysis of epifauna to vegetation surface area and epifauna to epiphytic algae was used to determine any relationship between the amount of epifauna and the amount of surface area or epiphytic algae present.

Similarities in the epifauna species assemblages among the three vegetation types, *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum*, were plotted using non-metric Multi-Dimensional Scaling (MDS) ordination using the Bray Curtis similarity measure to calculate similarities among replicate samples. One way analyses of similarities (ANOSIM) was used to test for differences in species assemblages among the three vegetation types. Similarity percentages-species contributions (SIMPER) analysis was used to determine the contribution of each epifauna species to the dissimilarity of the epifauna communities among *C. prolifera*, *H. wrightii*, and *T. testudinum*. Vegetation characteristics were included to assess their influence on the epifauna assemblages for each type of

vegetation using a Biodata-Environmental matching (BIOENV) analysis (Clarke and Warwick 2001).

Results

Vegetation and Epiphytic Algae

In June 2004 the amount of vegetation in Lassing Park as measured by total surface area per 0.09m² of bottom area was similar between all three types of vegetation ranging from 135cm² to 680cm² for *Caulerpa prolifera*, 114cm² to 474cm² for *Halodule wrightii*, and 214cm² to 713cm² for *Thalassia testudinum*. In October 2004 AVOVA revealed that the amount of *C. prolifera* was greater than in June 2004 ($p < 0.001$) while the amount of seagrasses did not change significantly. The total surface area of *T. testudinum* was significantly lower than *C. prolifera* and significantly higher than *H. wrightii* in October 2004 but not significantly different than the total surface area of *T. testudinum* in June 2004 (Figure 3). There was a significant interaction between dates and vegetation type ($p < 0.003$) (Table 1).

When compared between dates, the amount of epiphytic algae found on each of the three types of vegetation did not differ (2-way ANOVA). However, in both June and October, 2004 the mean amount of epiphytic algae found on *Caulerpa prolifera* was significantly less than that found on either seagrass ($p = 0.002$). The mean amount of epiphytic algae in June and October 2004, on *C. prolifera* was an order of magnitude lower than that recorded for *Halodule wrightii* and *Thalassia testudinum*. The mean amount of epiphytic algae found on *T. testudinum* and *H. wrightii* was similar between seagrass species and over both dates (Figure 4). There was no interaction between date and vegetation type (Table 2).

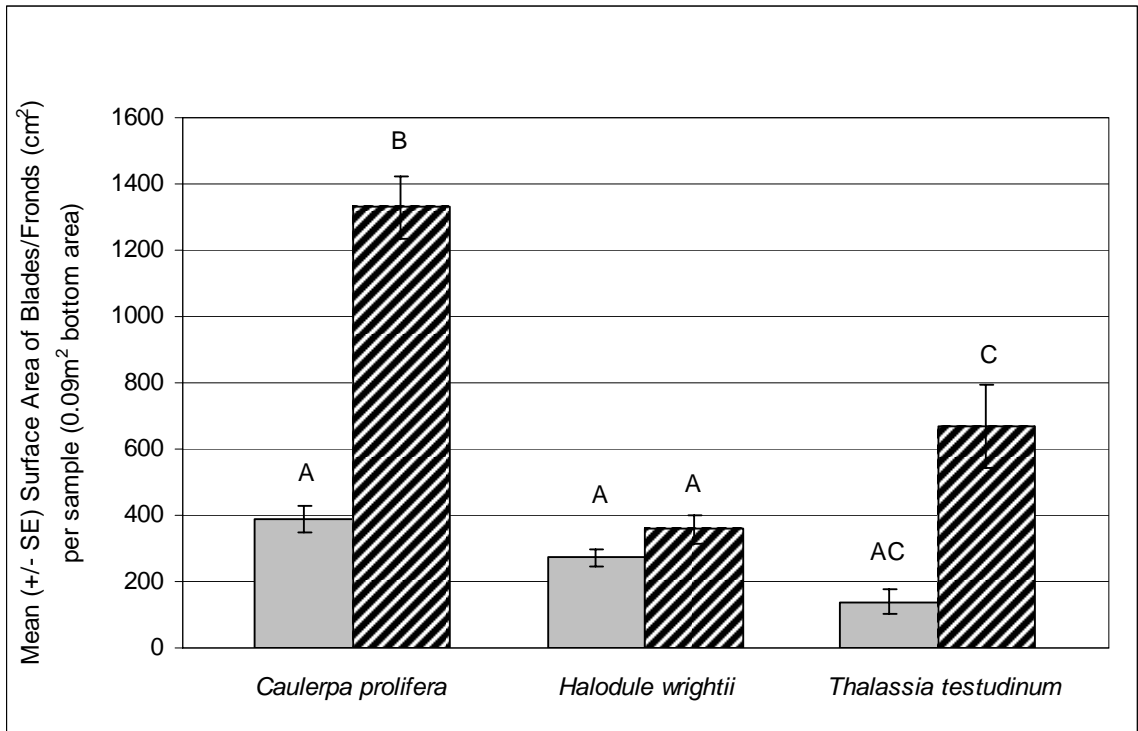


Figure 3. Mean (\pm SE) amount of surface area (cm²) of vegetation per sample (0.09m² bottom area) for June and October 2004 samples. Solid areas represent June 2004 samples, striped areas represent October 2004 samples. Results of a two-way ANOVA; means with the same letter are not significantly different ($p < 0.05$).

Table 1. Results of a two-factor ANOVA on surface area of seagrass, *Halodule wrightii* and *Thalassia testudinum*, blades and the fronds of the macroalga *Caulerpa prolifera* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	3339757.538	3339757.538	40.725	<0.001
Vegetation Species	2	3917796.28	1958898.140	23.887	<0.002
Sampling Date x Vegetation Species	2	2826253.881	1413126.940	17.231	<0.003
Residual	83	6806699.342	82008.426		
Total	88	16932890.94	192419.215		

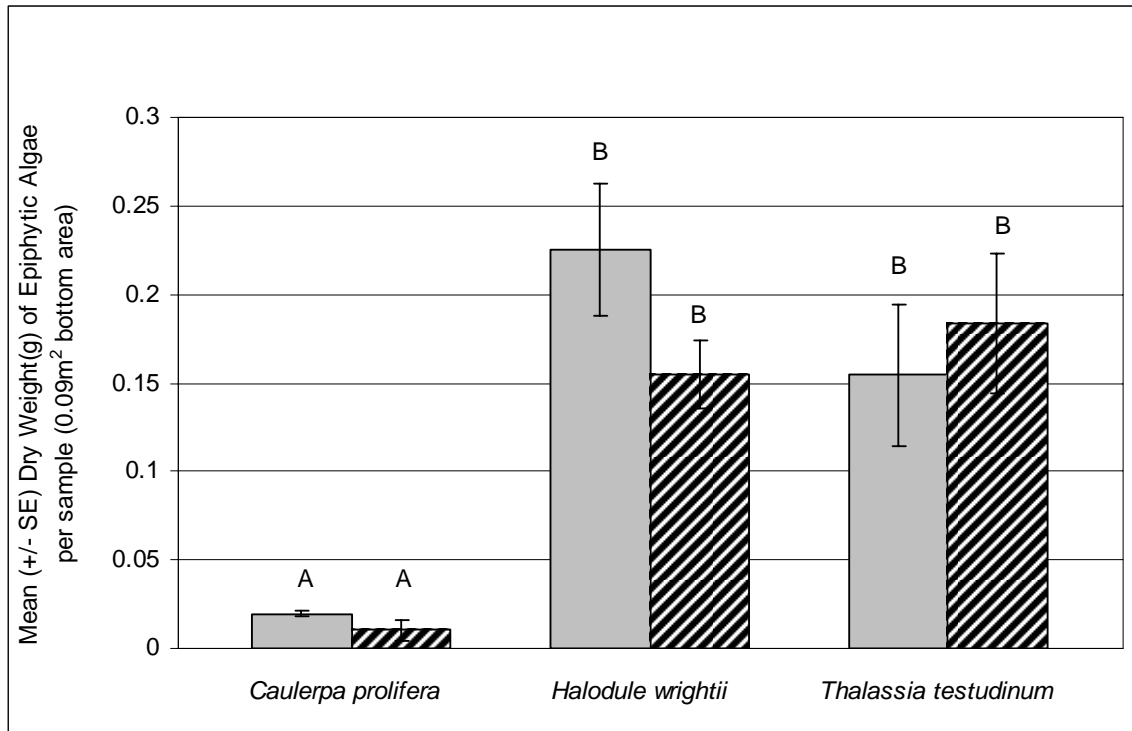


Figure 4. Mean (\pm SE) dry weight (g) of epiphytic algae per sample (0.09m² bottom area) for June and October 2004 samples. Solid areas represent June 2004 samples, striped areas represent October 2004 samples. Results of a two-way ANOVA; means with the same letter are not significantly different ($p < 0.05$).

Table 2. Results of a two-factor ANOVA on the amount of epiphytic algae found on the seagrass, *Halodule wrightii* and *Thalassia testudinum*, blades and macroalgae, *Caulerpa prolifera*, fronds for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	0.0941	0.0941	7.775	0.007
Vegetation Species	2	0.8180	0.4090	33.817	<0.001
Sampling Date x Vegetation Species	2	0.0383	0.0192	1.583	0.212
Residual	83	0.9920	0.0121		
Total	88	1.9400	0.0223		

Epifauna

Major epifauna taxa collected in this study included shrimp, crabs, bivalves, peracarids, and gastropods. Peracarids and gastropods dominated all samples from all vegetation types on both dates. These peracarid and gastropod species were grouped into five different feeding groups: herbivores that feed both micro- and macro-organisms, epifauna that are only carnivores, epifauna that are omnivores, epifauna that are only suspension feeders, and epifauna that are only detritus feeders (Table 3). The majority of epifauna (84%) found in the June and October 2004 samples were generalist herbivores that eat microalgae and/or macroalgae (Table 4). *Cymadusa compta*, an herbivore generalist, was the most abundant of the eleven peracarids present. *Bittium varium*, an herbivore generalist, was the most abundant of the seven gastropod species present in the samples.

Total epifauna per sample (0.09m² bottom area) were found in similar abundances on *Caulerpa prolifera* in June 2004, *Halodule wrightii* in June and October 2004, and *Thalassia testudinum* in June 2004 (Table 5). Both *C. prolifera* and *T. testudinum* had significantly higher abundances of total epifauna in October 2004 ($p < 0.001$ and $p = 0.008$ respectively) than in June 2004 (Figure 5). *Cymadusa compta* showed this same pattern with higher abundances found on *C. prolifera* ($p < 0.001$) and *T. testudinum* in October 2004 ($p = 0.005$) than in June 2004. Total peracarids were found in higher abundances on *C. prolifera* in October 2004 than on *C. prolifera* in June 2004 ($p < 0.001$) or either of the seagrasses over both dates. All three of these groups: total epifauna, total peracarids, and *C. compta* had a significant interaction between vegetation type and date ($p < 0.001$) (Tables 5-7). The remaining peracarids were significantly less abundant on *H. wrightii* in October 2004 than on any of the other samples

Table 3. Peracarid crustacean and gastropod species, and their feeding group (for the majority of species), collected in epifauna samples in June and October 2004 on three types of vegetation: *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum*.

Species	Feeding Group
<p>Amphipoda</p> <p><i>Cymadusa compta</i> (Smith)</p> <p><i>Ampithoe longimana</i> (Smith)</p> <p><i>Elasmopus levis</i> (Smith)</p> <p><i>Ampelisca</i> sp.</p> <p><i>Gammarus mucronatus</i> (Say)</p> <p><i>Erichthonius brasiliensis</i> (Dana)</p> <p><i>Colomastix</i> sp.</p> <p><i>Caprella</i> sp.</p>	<p>Herbivore Generalist</p> <p>Herbivore Generalist</p> <p>Omnivore</p> <p>Suspension</p> <p>Omnivore</p> <p>Detritus Only</p> <p>Unknown</p> <p>Omnivore</p>
<p>Isopoda</p> <p><i>Erichsonella attenuata</i> (Harger)</p> <p><i>Harrieta faxoni</i> (Richardson)</p>	<p>Herbivore Generalist</p> <p>Unknown</p>
<p>Tanaidacea</p> <p><i>Hargeria rapax</i> (Harger)</p>	<p>Unknown</p>
<p>Gastropoda</p> <p><i>Bittium varium</i> (Pfeiffer)</p> <p><i>Cerithium muscarum</i> (Say)</p> <p><i>Caecum pulchellum</i> (Stipson)</p> <p><i>Astyris lunata</i> (Say)</p> <p><i>Marginella bella</i> (Conrad)</p> <p><i>Nassarius vibex</i> (Say)</p> <p><i>Odostomia laevigata</i> (d'Orbigny)</p>	<p>Herbivore Generalist</p> <p>Herbivore Generalist</p> <p>Herbivore Generalist</p> <p>Carnivore</p> <p>Carnivore</p> <p>Carnivore</p> <p>Unknown</p>

Table 4. The percentage of peracarid crustacean and gastropod epifauna found in each feeding group, collected in epifauna samples in June and October 2004 on three types of vegetation: *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum*.

Feeding Group	Total Number of Epifauna	Percent of Total Epifauna
Herbivore Generalist	12670	84.38
Detritus Feeder	1027	6.84
Carnivore	731	4.87
Omnivore	553	3.68
Suspension Feeder	34	0.23

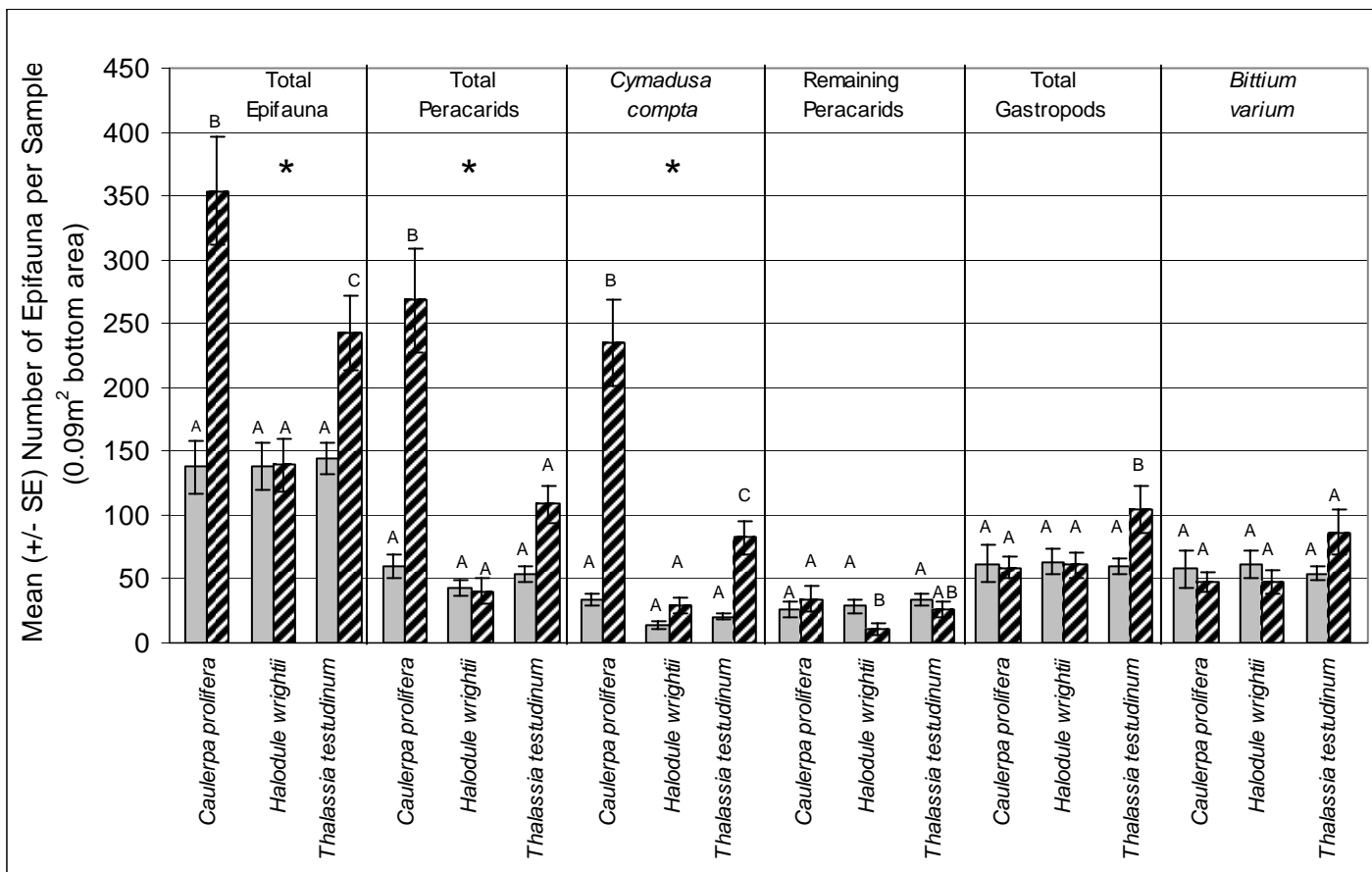


Figure 5. Mean (\pm SE) abundances of epifauna per sample (0.09m^2 bottom area) for June and October 2004 samples. Solid areas represent June 2004 samples, striped areas represent October 2004 samples. Results of a two-way ANOVA; means with the same letter are not significantly different ($p < 0.05$), presence of an asterisk in the upper center of the column represents a significant interaction between vegetation type and date for that column.

Table 5. Results of a two-factor ANOVA on the abundance of total epifauna per sample (0.09m²) on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	250588.9000	250588.9000	25.235	<.001
Vegetation Species	2	171678.156	85839.0780	8.644	<.001
Sampling Date x Vegetation Species	2	173833.8	86916.9000	8.753	<.001
Residual	84	834130.267	9930.1220		
Total	89	1430231.122	16070.0130		

Table 6. Results of a two-factor ANOVA on the abundance of total peracarids per sample (0.09m²) on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	177333.611	177333.611	30.033	<.001
Vegetation Species	2	217324.467	108662.233	18.403	<.001
Sampling Date x Vegetation Species	2	185173.489	92586.744	15.681	<.001
Residual	84	495984.533	5904.578		
Total	89	1075816.100	12087.821		

Table 7. Results of a two-factor ANOVA on the abundance of *C. compta* per sample (0.09m²) on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	193210.0000	193210.0000	56.801	<.001
Vegetation Species	2	203503.899	101751.9440	29.913	<.001
Sampling Date x Vegetation Species	2	138924.467	69462.2330	20.421	<.001
Residual	84	285730.533	3401.5540		
Total	89	821368.889	9228.8640		

except *T. testudinum* in October 2004. Total gastropods were found in significantly higher abundances on *T. testudinum* in October 2004 than on any of the other samples. No differences in abundances of *B. varium* across all vegetation types and between sample dates were noted (Figure 5).

When epifauna were standardized to the amount of vegetation surface area (Figure 6) all three vegetation types appeared to support similar numbers of total epifauna over both sampling dates. Total peracarids were also found in similar numbers on all types of vegetation during both June and October 2004 except on *Thalassia testudinum* where the total peracarids were more abundant in October 2004 than in June 2004 ($p=0.048$). *Cymadusa compta* was found in similar numbers on all three types of vegetation in June 2004 and on *Halodule wrightii* in June and October 2004. *Caulerpa prolifera* and *T. testudinum* supported significantly higher numbers of *C. compta* in October 2004 than in June 2004 ($p=0.027$ and 0.003 respectively). The remaining peracarids were found in similar abundances on all three types of vegetation over both sampling dates except on *H. wrightii* which had significantly more remaining peracarids in June 2004 than October 2004 ($p=0.001$). In June 2004 all three types of vegetation supported similar abundances of total gastropods. In October 2004 all three types of vegetation supported abundances of gastropods that were similar to those found in June 2004 although the number of total gastropods found on *C. prolifera* was significantly less than *H. wrightii* ($p=0.021$) or *T. testudinum* ($p=0.008$) (Figure 6). *Bittium varium* was found in similar abundances across all three types of vegetation and on both dates except on *C. prolifera* in October 2004, which had significantly less *B. varium* than *C. prolifera* in June 2004 ($p=0.041$) and *Thalassia testudinum* in October 2004 ($p=0.01$). The abundances of both the total gastropods (Table 8) and *B. varium* (Table 9) groups showed a significant interaction

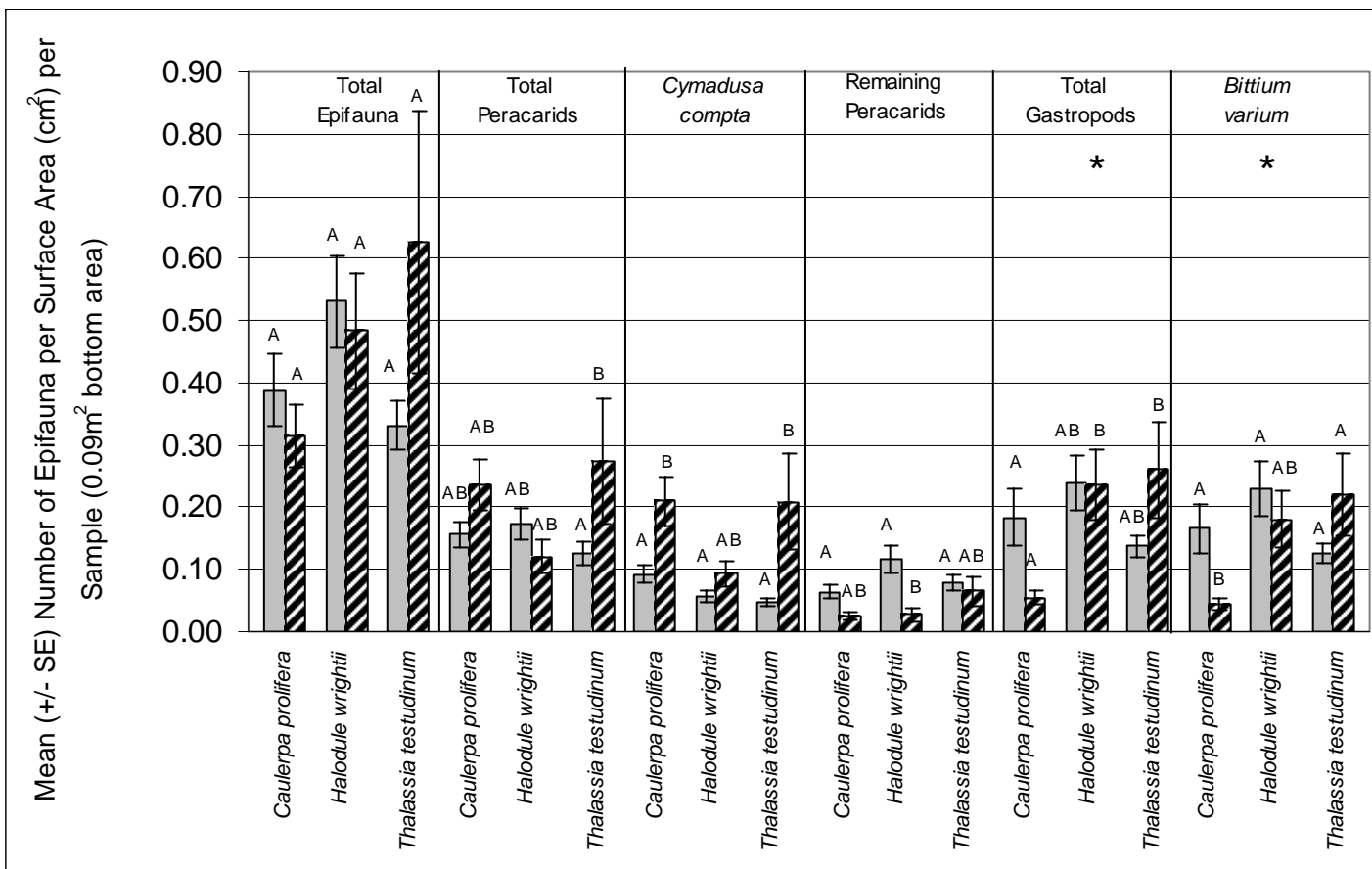


Figure 6. Mean (\pm SE) abundances of epifauna per surface area of vegetation blades/fronds (cm^2) for June and October 2004 samples. Solid areas represent June 2004 samples, striped areas represent October 2004 samples. Results of a two-way ANOVA; means with the same letter are not significantly different ($p < 0.05$), presence of an asterisk in the upper center of the column represents a significant interaction between vegetation type and date for that column.

between vegetation type and sample date ($p=0.033$ for both groups).

The epifauna of each sample were also standardized to the amount of epiphytic algae (g) found in each sample (0.09m^2 bottom area). The epifauna abundances in all groups: total epifauna, total peracarids, *Cymadusa compta*, remaining peracarids, total gastropods, and *Bittium varium* showed the same trend when compared over the three types of vegetation and both sample dates. After being standardized to the amount of epiphytic algae in each sample, abundances of all epifauna in the above mentioned groups were not statistically different on *Caulerpa prolifera*, *Halodule wrightii*, or *Thalassia testudinum* in both June and October 2004 with one exception. In October 2004, *C. prolifera* hosted significantly more epifauna per gram of epiphytic algae than either the *C. prolifera* samples from June 2004 or the seagrass samples ($p\leq 0.006$ for all comparisons involving epifauna found on *C. prolifera* in October 2004). The following groups: total epifauna, total peracarids, *C. compta*, total gastropods, and *B. varium* showed a significant interaction between vegetation type and sample date ($p\leq 0.02$) (Figure 7) (Tables 10-14).

Table 8. Results of a two-factor ANOVA on the abundance of total gastropods per blade/frond surface area of *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	Df	SS	MS	F	P
Sampling Date	1	0.000205	0.000205	0.00609	0.938
Vegetation Species	2	0.217	0.109	3.223	0.045
Sampling Date x Vegetation Species	2	0.241	0.120	3.571	0.033
Residual	83	2.796	0.0337		
Total	88	3.253	0.0370		

Table 9. Results of a two-factor ANOVA on the abundance of *Bittium varium* per blade/frond surface area of *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	0.0138	0.0138	0.539	0.465
Vegetation Species	2	0.154	0.0770	3.000	0.055
Sampling Date x Vegetation Species	2	0.183	0.0915	3.563	0.033
Residual	83	2.131	0.0257		
Total	88	2.279	0.0282		

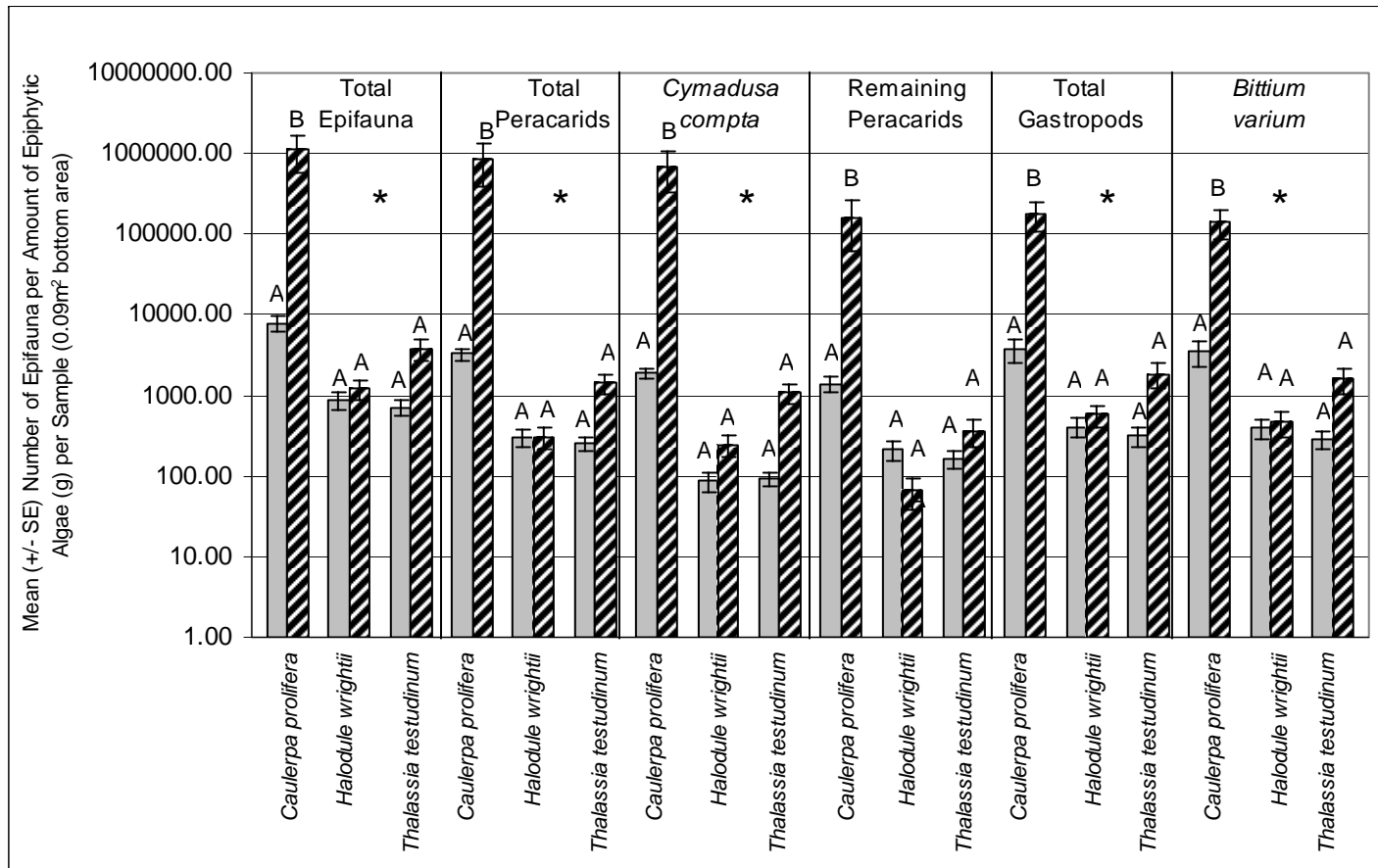


Figure 7. Mean (\pm SE) abundances of epifauna per amount of epiphytic algae (g) for June and October 2004 samples. Solid areas represent June 2004 samples, striped areas represent October 2004 samples. Results of a two-way ANOVA; means with the same letter are not significantly different ($p < 0.05$), presence of an asterisk in the upper center of the column represents a significant interaction between vegetation type and date for that column.

Table 10. Results of a two-factor ANOVA on the abundance of total epifauna per amount of epiphytic algae (g) found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	3.398x10 ¹²	3.398x10 ¹²	4.84200	0.031
Vegetation Species	2	6.862x10 ¹²	3.431x10 ¹²	4.889	0.010
Sampling Date x Vegetation Species	2	6.699x10 ¹²	3.349x10 ¹²	4.772	0.011
Residual	82	5.755x10 ¹³	7.018x10 ¹¹		
Total	87	7.397x10 ¹³	8.503x10 ¹¹		

Table 11. Results of a two-factor ANOVA on the abundance of total peracarids per amount of epiphytic algae (g) found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	2.204x10 ¹²	2.204x10 ¹²	4.06200	0.047
Vegetation Species	2	4.425x10 ¹²	2.212x10 ¹²	4.077	0.021
Sampling Date x Vegetation Species	2	4.364x10 ¹²	2.182x10 ¹²	4.021	0.022
Residual	82	4.449x10 ¹³	5.426x10 ¹¹		
Total	87	5.514x10 ¹³	6.338x10 ¹¹		

Table 12. Results of a two-factor ANOVA on the abundance of *Cymadusa compta* per amount of epiphytic algae (g) found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	1.360x10 ¹²	1.360x10 ¹²	4.231	0.043
Vegetation Species	2	2.719x10 ¹²	1.359x10 ¹²	4.228	0.018
Sampling Date x Vegetation Species	2	2.693x10 ¹²	1.346x10 ¹²	4.188	0.019
Residual	82	2.636x10 ¹³	3.215x10 ¹¹		
Total	87	3.292x10 ¹³	3.784x10 ¹¹		

Table 13. Results of a two-factor ANOVA on the abundance of total gastropods per amount of epiphytic algae (g) found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	8.299x10 ¹⁰	8.499x10 ¹⁰	7.26500	0.009
Vegetation Species	2	1.768x10 ¹¹	8.842x10 ¹⁰	7.558	<.001
Sampling Date x Vegetation Species	2	1.644x10 ¹¹	8.222x10 ¹⁰	7.028	0.002
Residual	82	9.593x10 ¹¹	1.170x10 ¹⁰		
Total	87	1.372x10 ¹²	1.577x10 ¹⁰		

Table 14. Results of a two-factor ANOVA on the abundance of *Bittium varium* per amount of epiphytic algae (g) found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

Source	df	SS	MS	F	P
Sampling Date	1	5.552x10 ¹⁰	5.552x10 ¹⁰	7.20900	0.009
Vegetation Species	2	1.166x10 ¹¹	5.831x10 ¹⁰	7.572	<.001
Sampling Date x Vegetation Species	2	1.073x10 ¹¹	5.372x10 ¹⁰	6.975	0.002
Residual	82	6.315x10 ¹¹	7.701x10 ⁹		
Total	87	9.023x10 ¹¹	1.037x10 ¹⁰		

Community Composition

In the June 2004 samples there was no apparent separation of the samples of peracarid and gastropod communities in MDS plots recorded for the three different vegetation types (Figure 8). In all three types of vegetation *Cymadusa compta* was the most dominant species of peracarid and *Bittium varium* the most dominant species of gastropod. In October 2004 there was an apparent difference (ANOSIM $p=0.001$) between the communities found on each type of seagrass (Figure 9). Based on SIMPER analysis of epifauna per sample (0.09m² bottom area) *C. compta*, the most abundant peracarid, accounted for 33.12% of the difference between the communities found on *Halodule wrightii* and *Thalassia testudinum*, 55.72% of the difference between communities on *Caulerpa prolifera* and *T. testudinum*, and 65.55% of the difference between the communities found on *C. prolifera* and *H. wrightii*.

When the vegetation characteristics (number of blades/fronds, surface area of blades/fronds, and amount of epiphytic algae per sample (0.09m² bottom area) from the June samples were included in a BIOENV analysis using the Bray Curtis similarity measure there was little difference among these factors on the epifauna found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* (Table 15). In the October 2004 samples, however, epiphytic algae were responsible for the majority of differences among the communities found on each type of vegetation (Table 16). The results of the ANOSIM analysis of the October samples indicated that the communities found on *C. prolifera* and *H. wrightii* and on *C. prolifera* and *T. testudinum* were significantly different with R statistics of 0.884 and 0.722, respectively, and significance levels of 0.01 respectively. Communities of peracarids and gastropods found on the seagrasses were more similar to each other than to

the the peracarid and gastropod communities found on *C. prolifera* with an R statistic of 0.169 and a significance level of 0.09.

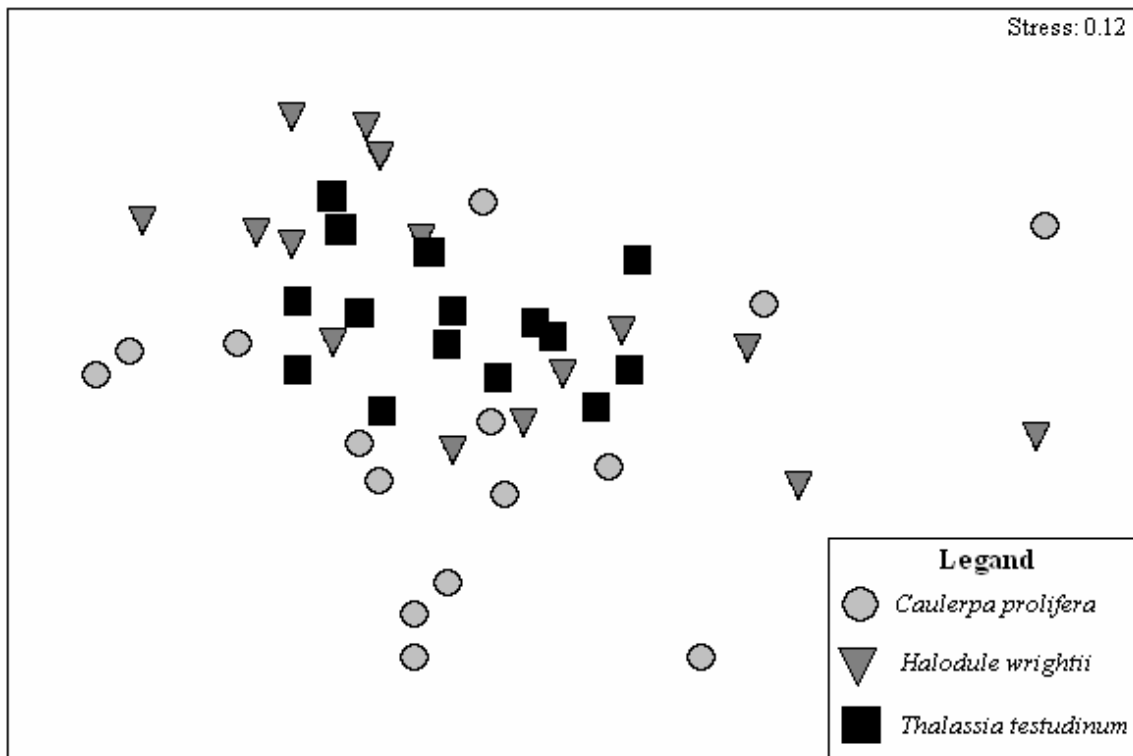


Figure 8. Multi-Dimensional Scale plot of epifauna communities found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* per sample (0.09m² bottom area), June 2004.

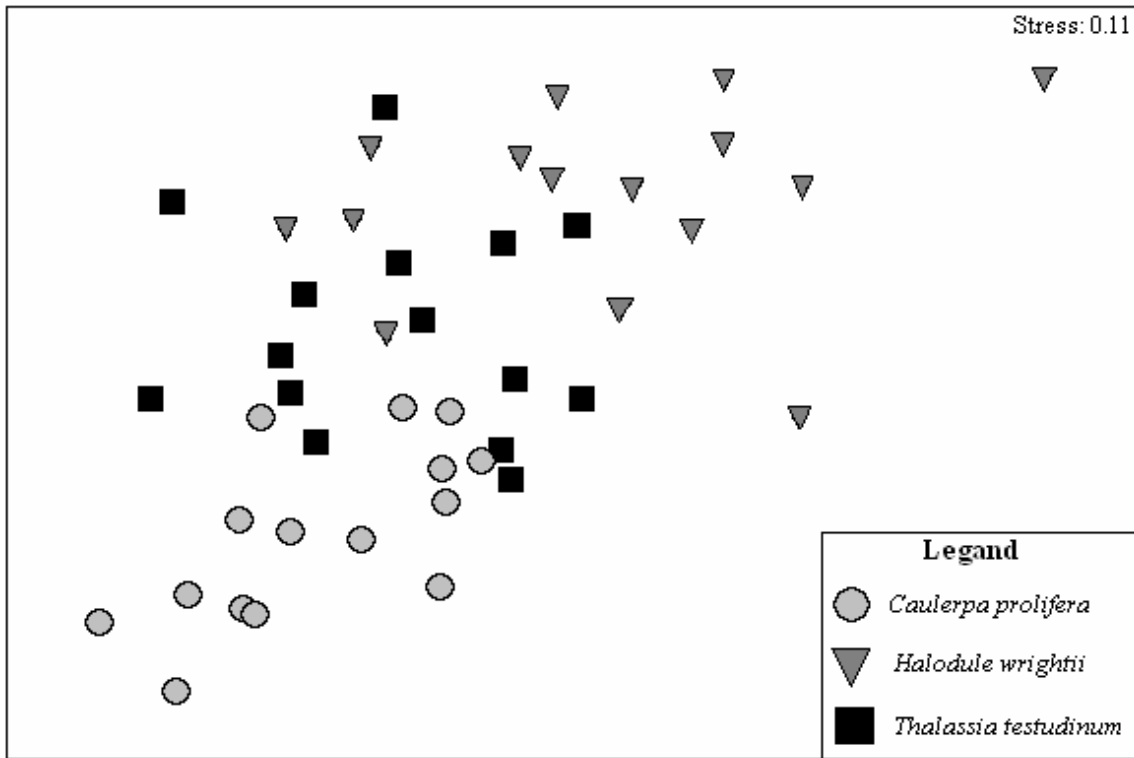


Figure 9. Multi-Dimensional Scale plot of epifauna communities found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* per sample (0.09m² bottom area), October 2004.

Table 15. Results of the June 2004 BIOENV analysis of the relative amount of influence that the three vegetation characteristics: number of blades/fronds, surface area of blades/fronds (cm²), and/or amount of epiphytic algae (g) have on the peracarid and gastropod communities found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum*.

Variable	Correlation
Surface Area of Blades/Fronds(cm ²) and Epiphytic Algae (g)	0.268
Surface Area of Blades/Fronds (cm ²)	0.267
Surface Area of Blades/Fronds (cm ²), Epiphytic Algae (g), and Number of Blades/Fronds	0.259
Number of Blades/Fronds and Surface Area of Blades/Fronds (cm ²)	0.259
Number of Blades	0.164
Number of Blades and Epiphytic Algae (g)	0.163
Epiphytic Algae (g)	0.130

Table 16. Results of the October 2004 BIOENV analysis of the relative amount of influence that the three vegetation characteristics: number of blades/fronds, surface area of blades/fronds (cm²), and/or amount of epiphytic algae (g) have on the peracarid and gastropod communities found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum*.

Variable	Correlation
Epiphytic Algae (g)	0.874
Surface Area of Blades/Fronds (cm ²), Epiphytic Algae (g), and Number of Blades/Fronds	0.067
Number of Blades/Fronds with Surface Area of Blades/Fronds (cm ²)	0.067
Number of Blades with Epiphytic Algae (g)	0.063
Surface Area of Blades/Fronds (cm ²) with Epiphytic Algae (g)	0.063
Surface Area of Blades/Fronds	0.062
Number of Blades	0.062

Relationship Between Epiphytes and Epifauna or Surface Area and Epifauna

The number of epifauna per sample (0.09m² bottom area) was compared to the amount of epiphytes per sample from the June and October 2004 samples (Figure 10). The relationship between the amount of epifauna and the amount of epiphytic algae was plotted for the epifauna found on *Caulerpa prolifera*, *Halodule wrightii* and *Thalassia testudinum* for the June and October 2004 samples. These relationships suggest there was no correlation between the amount of epiphytic algae on the vegetation and the amount of epifauna present with regression slopes ranging from -122.9 to 2761.7 and extremely low R² value (ranging from 0.0019 to 0.1561) (Table 17). When the amount of epifauna present in each sample was compared to the amount of surface area of the blades/fronds, the epifauna on *C. prolifera* and *H. wrightii* in June and October and on *T. testudinum* in October showed a small positive correlation between the number of epifauna and surface area for each of the three types of vegetation (with regression slopes ranging from -0.0235 to 0.2772) (Figure 11 and Table 18). Low R² values (ranging from 0.0047 to 0.3233), however, show a poor correlation between the amount of epifauna and surface area per sample.

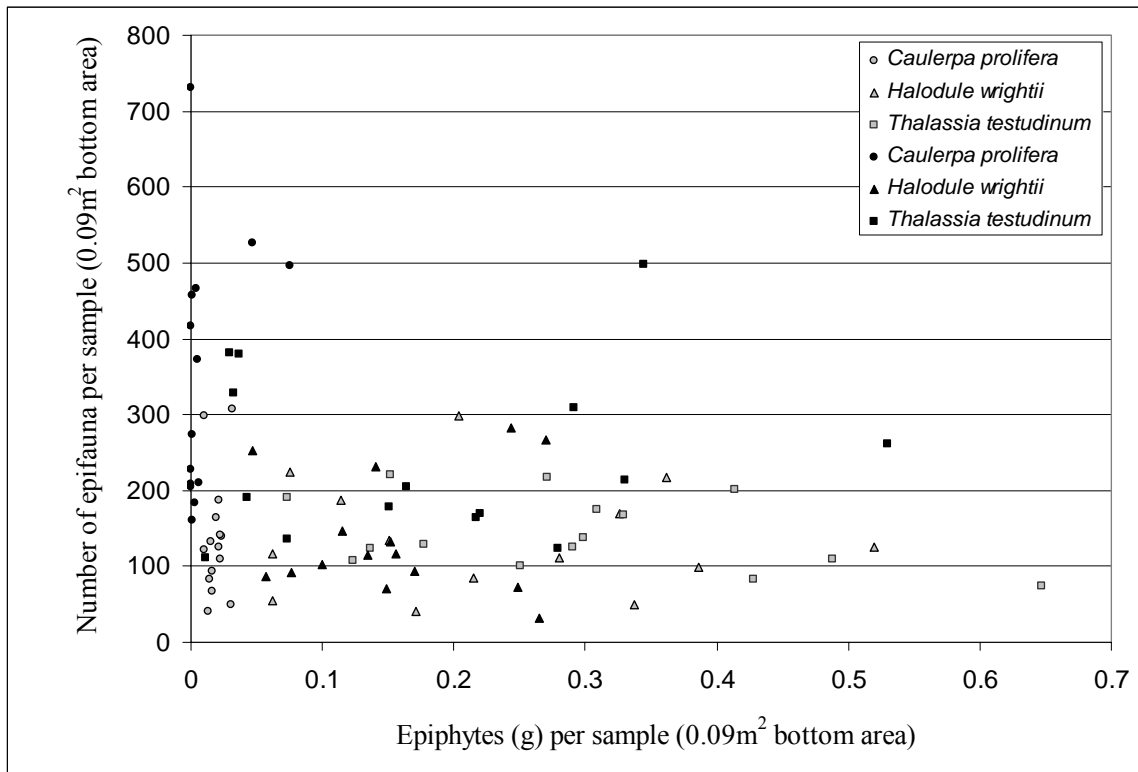


Figure 10. Number of total epifauna per sample (0.09m² bottom area) vs. dry weight of epiphytic algae (g) per sample (0.09m² bottom area) for June and October 2004 samples. Light symbols represent June 2004 samples, dark symbols represent October 2004 samples.

Table 17. Regression slopes and R² values for the relationships between the amount of epifauna and the amount of epiphytic algae (g) found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

	Regression Slope	R ² value
June		
<i>Caulerpa prolifera</i>	1662.7	0.0186
<i>Halodule wrightii</i>	-23.7	0.0019
<i>Thalassia testudinum</i>	-122.9	0.1561
October		
<i>Caulerpa prolifera</i>	2761.7	0.1321
<i>Halodule wrightii</i>	87.6	0.0065
<i>Thalassia testudinum</i>	72.8	0.0095

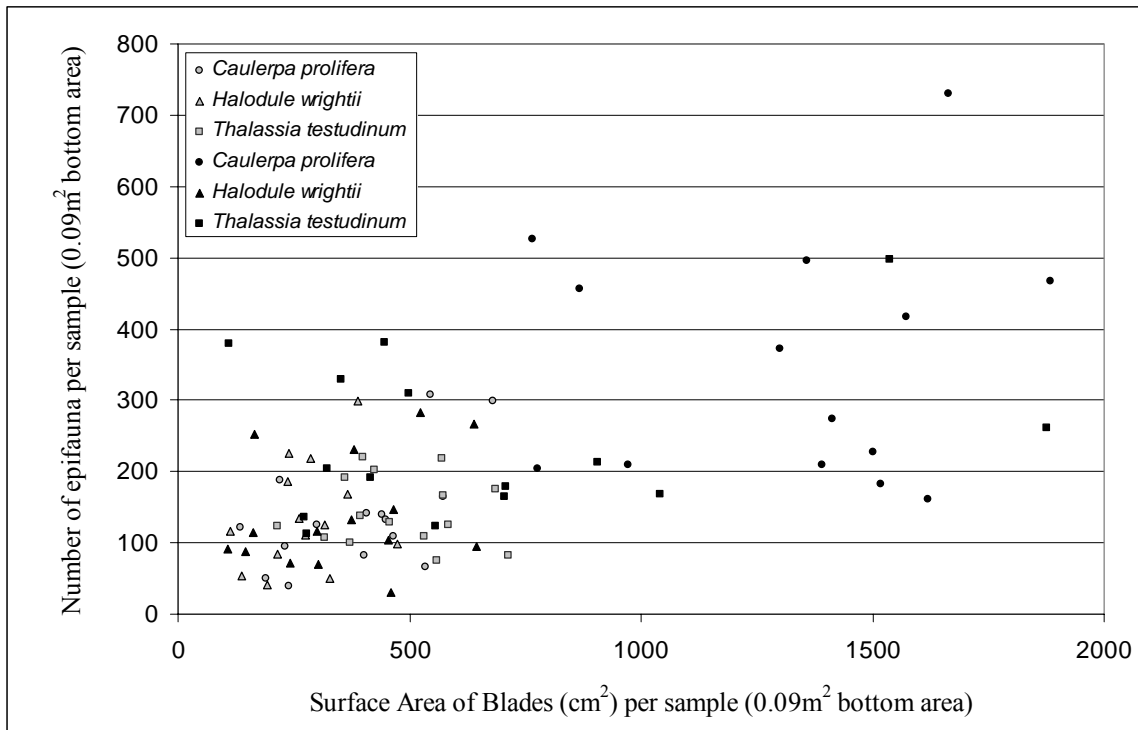


Figure 11. Number of total epifauna per sample (0.09m² bottom area) vs. surface area of blades/fronds (cm²) per sample (0.09m² bottom area) for June and October 2004 samples. Light symbols represent June 2004 samples, dark symbols represent October 2004 samples.

Table 18. Regression slopes and R² values for the relationships between the amount of epifauna and the amount of vegetation blade/frond surface area (cm²) of *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* for June and October 2004 samples.

	Regression Slope	R ² value
June		
<i>Caulerpa prolifera</i>	0.2772	0.3233
<i>Halodule wrightii</i>	0.2437	0.0997
<i>Thalassia testudinum</i>	-0.0235	0.0047
October		
<i>Caulerpa prolifera</i>	0.0439	0.0083
<i>Halodule wrightii</i>	0.1276	0.0778
<i>Thalassia testudinum</i>	0.0562	0.0602

Discussion

If the number of epifauna found on each type of vegetation was driven by habitat complexity (measured by the amount of surface area) as has been shown by previous studies (Hacker and Steneck 1990), one would expect the vegetation with the highest amount of surface area to support the highest amounts of epifauna. This was what was observed in both June and October 2004 for the majority of the epifauna groups tested. In June 2004, when the *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum* had similar amounts of surface area per sample, all of the epifauna groups tested were found in similar abundances on all three types of vegetation. In October 2004 the amount of vegetation surface area increased significantly from *H. wrightii* to *T. testudinum* to *C. prolifera*. Two groups of epifauna follow this pattern with total epifauna and *C. compta* having significantly higher abundances as amounts of vegetation increased. Total peracarids also had significantly higher abundances per sample on *C. prolifera*.

The results of the PRIMER tests combined with measures of vegetation surface area lend support to the theory that structural complexity may be a factor influencing the species composition of mobile epifauna. In June 2004 when the amount of surface area for the three types of vegetation, *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum*, was not significantly different, the epifauna communities on the three types of vegetation also showed strong similarity. In October 2004, when the amount of *C. prolifera* vegetation was greater than that of either seagrass, the epifauna communities found on the two seagrasses

were more similar to each other than either was to the epifauna community found on *C. prolifera*. The BIOENV analysis showed that the difference between the epifauna communities found on *C. prolifera* and the two seagrasses was driven equally by a combination of vegetation surface area and epiphytic algae and by vegetation surface area alone in the June 2004 samples. Overall, the abundances of epifauna for both the June and October 2004 samples support the theory that epifauna abundances may be related to the amount of habitat complexity (represented by the amount of surface area) as set forth by previous studies (Hacker and Steneck 1990, Knowles and Bell 1998, Boström and Mattila 1999, Edgar and Klumpp 2003).

Although the epifauna collected for this survey appear to be influenced by the amount of surface area of *Caulerpa prolifera*, *Halodule wrightii*, or *Thalassia testudinum*, the epifauna may also be influenced by the amount of epiphytic algae found on the vegetation. If the number of epifauna found on each type of vegetation was driven by the amount of epiphytic algae in this system as has been shown previously by Bologna and Heck (1999) and Moncreiff and Sullivan (2001) then the vegetation that supported the highest amounts of epiphytic algae should also support the highest numbers of epifauna. However, in both June and October 2004 while the amount of epiphytic algae on *C. prolifera* was an order of magnitude less than the amount found on both types of seagrass the number of epifauna per sample found on *C. prolifera* was equal to or greater than the number of epifauna found on the seagrass. When the number of epifauna were standardized to the amount of epiphytic algae found on each type of vegetation the amount of epifauna found on *C. prolifera* was one to five orders of magnitude higher than the amount of epifauna found on either of the two seagrasses. Thus, there does not seem to be a strong relationship between the amount of epifauna and epiphytic algae present in this system.

Information on individual species may add insight into the patterns exhibited by the major taxa present in this survey. After the epifauna species were categorized by feeding group one of the feeding groups, herbivores that feed on micro- and macroorganisms, accounted for 84% of all peracarids and gastropods that could be put into a feeding group (all except three of the eighteen species identified). This one feeding group consists of five species including *Cymadusa compta*, the most abundant peracarid species, and *Bittium varium*, the most abundant gastropod species. These species are most likely to be affected by the lack of epiphytes on *Caulerpa prolifera* and possibly the secondary compounds produced by *C. prolifera*, which have been shown to deter herbivory by fish and therefore be less abundant on *C. prolifera* compared to the seagrasses. Instead two of these species, *C. compta* and *B. varium*, are the most abundant species in the epifauna communities, not only on the seagrasses but also on *C. prolifera*, even though the latter had an order of magnitude less epiphytic algae compared to the seagrasses. *Cymadusa compta* is known to eat a variety of foods including macroalgae, microalgae, detritus, diatoms, vascular plants, and even tunicates (Morgan and Kitting 1984, Duffy and Hay 2001, Cruz-Rivera and Hay 2003,). Because *C. compta* is such a broad generalist it may be better able to deal with the lack of one type of food (microalgae) and survive well on *C. prolifera* while species which eat mainly microalgae cannot because of the lack of epiphytic algae. This would explain why *C. compta* was abundant on *C. prolifera* while other peracarids and gastropods which rely more on epiphytic algae were less abundant.

Overall, this study found varying amounts of evidence to support the possibility of both the amount of blade/frond surface area and the amount of epiphytic algae influence the amount and community composition found on *Caulerpa prolifera*, *Halodule wrightii*, and *Thalassia testudinum*. Evidence that supports epiphytic algae influencing the amount and

community composition of epiphytes was found in the fact that in the October 2004 the community composition of epifauna was overwhelmingly driven by epiphytic algae. However, the major findings of this survey: 1) some evidence for a positive relationship between the amount of epifauna and the amount of blade/frond surface area, including vegetation with higher amounts of surface area supporting higher amounts of epifauna, 2) no relationship between the amount of epifauna and the amount of epiphytic algae on submerged vegetation, and 3) when the amount of surface area of all vegetation species was similar the epifauna communities were similar in species composition lend support to the theory that surface area of vegetation (and therefore possibly habitat complexity) is an important factor in determining the abundance and community composition of epifauna in seagrass and macroalgae beds in Lassing Park, Florida.

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