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Response of small motile epifauna to complexity of epiphytic algae on seagrass blades

by Margaret O. Hall¹ and Susan S. Bell¹

ABSTRACT

Field collections and experiments were performed to examine the relationship between the biomass of epiphytic algae (= habitat complexity) on *Thalassia testudinum* blades and the density of associated motile epifauna. Samples collected at Egmont Key, Florida indicated a significant positive association between the density of harpacticoid copepods, the most numerous taxon on seagrass blades, and biomass of the dominant epiphyte, *Giffordia mitchelliae*. Similar results were noted for nematodes, amphipods, and crustacean nauplii.

Seagrass blades with large amounts of epiphytic algae are often older than blades with lesser amounts of algae, and have had a longer time to be colonized by epifauna. A recolonization experiment was conducted in a *T. testudinum* bed in the Indian River lagoon, Florida examining associations between the density of epifauna on blades of the "same" age (blades defaunated and replanted in the field) with various amounts of epiphytes. After 2 days a significant positive relationship between epiphyte biomass and density of dominant epifauna (copepods, crustacean nauplii, and nematodes) was recorded, suggesting that results were attributable to differential amounts of epiphytic algae since length of colonization time did not vary among blades.

Recolonization experiments in a *T. testudinum* bed at Ft. Desoto, Florida using artificial blades (polypropylene ribbon) and 3 densities (no, intermediate, and high) of artificial epiphytes (clumps of cotton-polyester thread) produced results comparable to those above within 3 days. Highest densities of dominant epifauna (copepods, nematodes, and polychaetes) were found on blades in the high epiphyte treatment. Mean numbers of copepods and also polychaetes on high and intermediate epiphyte treatments were not significantly different from each other, but were significantly higher than on blades with no epiphytes. Nematode densities declined significantly with decreasing amounts of artificial epiphytes. These results suggest that much of the relationship observed between motile epifauna and epiphytic algae on seagrass blades may be attributed to the physical structure of the algae, given the similar responses of most fauna to both living and artificial plant material.

The pattern observed for harpacticoid copepods and epiphytic algae on seagrass blades in field collections and experiments varied among species. Laophontid sp., *Harpacticus* sp., and *Diosaccus* sp. were strongly positively associated with the amount of epiphytic algae, however, *Amphiascus* sp., Ectinosomatid spp., and *Dactylopodia tisburyoides* showed little association. The results of this study demonstrate that relationships which have been shown for larger plant structure and fauna also hold for small motile epifauna and fine scale vegetative architecture.

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1. Introduction

Seagrass blades provide a substratum for a wide variety of epiphytic flora and fauna (Harlin, 1980). Investigators have suggested that algae epiphytic on seagrass blades positively influence the abundance and/or diversity of motile seagrass epifauna by increasing the habitat complexity (Nagle, 1968; Novak, 1982; Lewis and Hollingworth, 1982; Bell *et al.*, 1984; Virnstein and Curran, 1986). Increased habitat complexity has been noted to enhance the density and/or diversity of organisms in a variety of terrestrial (e.g., MacArthur and MacArthur, 1961; Southwood *et al.*, 1979; August, 1983), freshwater (e.g., Gorman and Karr, 1978; Crowder and Cooper, 1982; Gilinsky, 1984), and marine (e.g., Kohn, 1967; Abele, 1974; Heck and Orth, 1980; Stoner and Lewis, 1985) systems by providing additional habitat, increasing nutritional resources, or serving as a refuge from predation. By analogy, seagrass epiphytes may contribute to maintaining a higher density and/or diversity of seagrass epifauna by supplying more living space, food (directly, or indirectly by trapping detritus or providing attachment sites for microalgae and bacteria), or shelter from invertebrate and fish predators.

Many studies have explored the effects of habitat complexity on the abundance and/or diversity of seagrass associated macrofauna and fish (e.g., Heck and Wetstone, 1977; Virnstein, 1977; Nelson, 1979; Heck and Orth, 1980; Stoner, 1980; Gore *et al.*, 1981; Peterson, 1982; Lewis and Stoner, 1983; Stoner and Lewis, 1985; Lewis, 1987). In the aforementioned investigations, habitat complexity was measured as the surface area, biomass or density of seagrass blades or rhizomes, or the macroalgae associated with seagrass habitats. Few studies have examined the influence of smaller-sized plant structure, such as epiphytic algae, on the abundance and/or diversity of seagrass associated fauna. In addition, little emphasis has been directed towards meiofaunal-sized organisms, which are often the most numerous epifauna on seagrass blades, and frequently live among the small scale plant structure (algal filaments) attached to blade surfaces (Bell *et al.*, 1984).

Most evidence supporting the suggested positive relationship between epifauna and epiphytic algae in marine systems is descriptive, and little quantitative data are available. Previous studies by Nagle (1968), Lewis and Hollingworth (1982) and Novak (1982) report densities of both epiphytic algae and epifauna on seagrasses. Although these studies provide important information, only Nagle's (1968) data on amphipods were subjected to statistical analysis. As on seagrass blades, smaller algae that are epiphytic on rocky shore macroalgae may influence the abundance and/or diversity of associated fauna (e.g., Wieser, 1952, 1959; Hagerman, 1966; Jansson, 1974; Kangas, 1978; Gunnill, 1982; Edgar, 1983; Hicks, 1985; Johnson and Scheibling, 1987), but here, as in seagrass studies, quantification of both epiphytic algae and epifauna is generally lacking.

In the present study we examined experimentally the influence of habitat complexity on the abundance of seagrass epifauna on a much finer scale than previously

reported (see references above) by using the biomass of epiphytic algae on seagrass blades as a measure of habitat complexity (see Heck and Wetstone, 1977; Stoner, 1980; and Lewis, 1987 for examples of other studies which have used biomass of plants to measure habitat complexity). In addition, we examined species patterns of harpacticoid copepods, the numerically dominant epifaunal taxon, to assess relationships between species abundance and epiphytic algae. We addressed the following questions: 1. What is the relationship between the biomass of epiphytic algae on seagrass blades and the density of associated fauna? 2. If more animals are found on seagrass blades with higher amounts of epiphytic algae (usually older blades), do results reflect a longer colonization time rather than an association with epiphytic algal abundance? 3. If there is a relationship between epiphytic algae and epifauna, are biological attributes of epiphytic algae or characteristics of physical structure primarily responsible for the association?

2. Materials and methods

a. Field collections

Seagrass blades with various amounts of epiphytic algae were collected to examine the relationship between the abundance of epiphytes and the density of epifauna on *Thalassia testudinum* Banks ex Konig. Collections were made in a *T. testudinum* bed adjacent to the northeastern shore of Egmont Key, Florida (27°35.5'N, 82°45.3'W), a small island located outside the mouth of Tampa Bay. Egmont Key is exposed to limited wave action, has a sandy bottom, and supports an extensive seagrass bed containing pure and mixed stands of *T. testudinum* and *Syringodium filiforme* Kützing. Salinity ranges from 30 to 35 ppt and temperature from 14 to 29°C annually at the study site (Hall, unpubl. data).

Filamentous macroalgal epiphytes become abundant during the fall and early winter in this region of Florida (Hall, in prep.), and collections were made in December 1983 when seagrass blades with a range of epiphytism (Fig. 1A) and relatively high copepod densities were available. Four categories of epiphytism (negligible, low, medium, and high; see Fig. 1A) were established by visual inspection, and later quantified to satisfy the assumptions for a Model I linear regression analysis (see below). The dominant epiphytic alga by weight was a filamentous brown, *Giffordia mitchelliae* (Harvey) Hamel. Motile epifauna and epiphytic algae were quantified from five blades in each of the four categories collected from the field. A clear plastic tube covered at the end by 63 μm mesh was filled with filtered seawater by inserting it into the water mesh side down, and then corking the tube. The tube was opened and placed over a seagrass blade and stoppered, breaking the blade at the sediment surface. The contents of the tube were rinsed into a jar and preserved with 10% formalin-seawater and Rose Bengal. All animals retained on a 63 μm mesh after washing the seagrass blade were enumerated, and harpacticoid copepods were identified to the

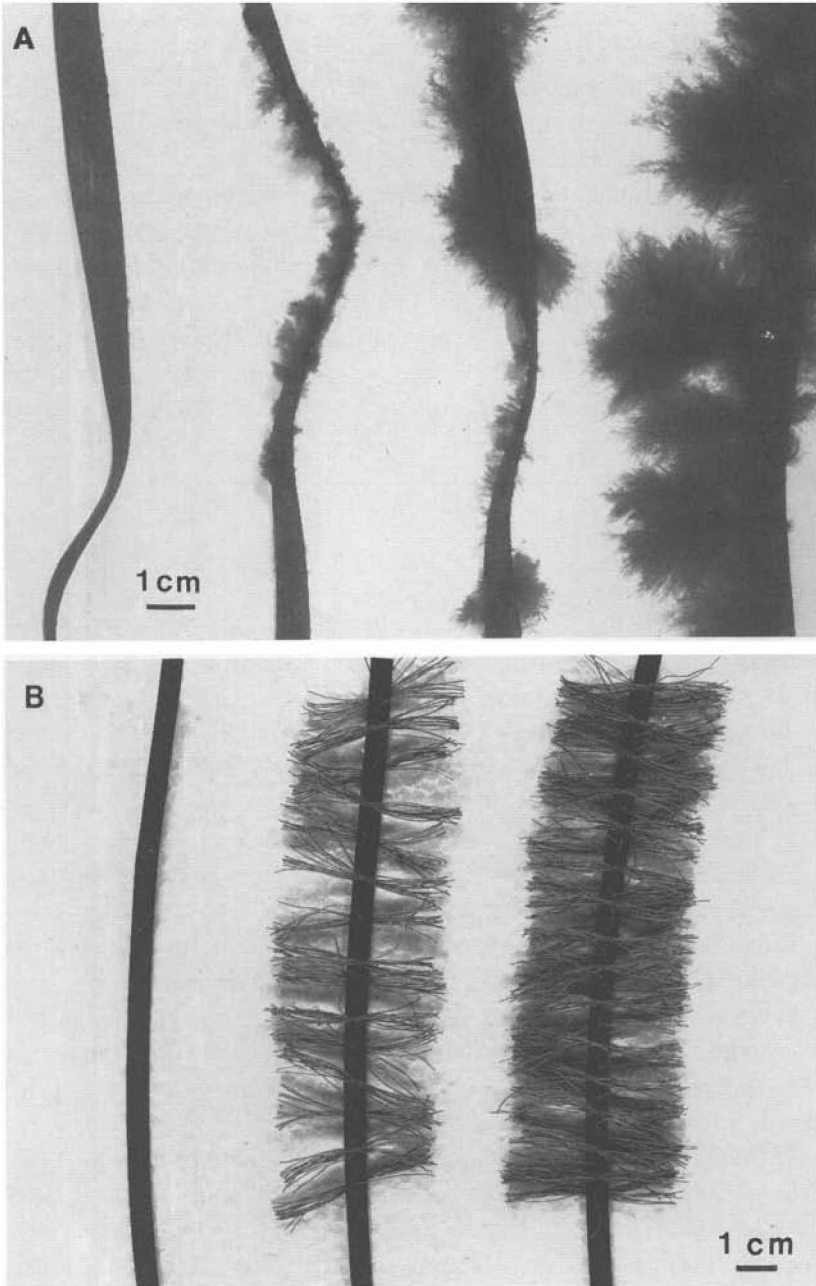


Figure 1. (A) The alga *Giffordia mitchelliae* epiphytic on *Thalassia testudinum* blades. Epiphyte abundance was categorized (from left to right) as negligible, low, moderate, and heavy. (B) Artificial epiphytic algae on artificial seagrass. Epiphyte abundance was categorized (from left to right) as none, intermediate, and high.

lowest possible taxon under a dissecting microscope. Samples with >1000 harpacticoid copepods per blade were subsampled prior to species identification using a modification of the technique developed by Sherman *et al.* (1984) for nematodes.

To quantify habitat complexity, epiphytic algae were scraped from the seagrass blades from which meiofauna were collected, dried for 24 hours at 60°C, and weighed to obtain total biomass (mg algae/cm² blade). Estimation of total biomass was chosen over percent cover, enumerating individual plants, or determining surface area (techniques previously used to estimate phytal habitat complexity; see references in introduction) for three reasons. (1) Percent cover estimates for blades epiphytized by encrusting algae could be similar to those for blades with dense growths of filamentous algae, although the amount of plant structure would be higher on the latter. (2) Distinguishing individual plants for tabulating abundance is at minimum difficult for many types of epiphytic algae. (3) Measuring the surface area of finely filamentous algae such as *G. mitchelliae* is extremely time consuming, and sometimes questionable. The surfactant method (Harrod and Hall, 1962) is inappropriate because the detergent solution does not uniformly coat the fine filaments, but becomes clogged between them (Hall, pers. obs.). Because *G. mitchelliae* was the overwhelmingly dominant epiphytic alga by weight during this investigation, differences in habitat complexity between blades could be accurately assessed by determining the total biomass of epiphytic algae on each blade.

To determine the percentage of variation in their densities attributable to variation in the amount of epiphytic algae, regression analyses were conducted for the four numerically dominant motile epifaunal taxa, and for the five most numerous harpacticoid copepod species or species groups.

b. Experiment 1—Recolonization of natural blades

Because older seagrass blades are generally more heavily epiphytized than younger seagrass blades (Harlin, 1980), a recolonization experiment was conducted in January 1984 to determine if the abundance of epiphytic algae influenced densities of seagrass epifauna when colonization time did not vary among blades. To accomplish this, we placed defaunated blades with varying amounts of epiphytic algae into the field and monitored faunal recolonization.

A *T. testudinum* bed in the Indian River lagoon on the eastern coast of Florida (27°32.1'N; 80°20.9'W) was chosen as the study site. The study area is characterized by low wave action, a silty sediment, and an extensive seagrass bed containing pure and mixed stands of *T. testudinum*, *Halodule wrightii* Ascherson, and *S. filiforme*. Salinity and temperature annually range from 20 to 30 ppt, and from 10° to 32°C, respectively (Hall and Eiseman, 1981).

The dominant epiphytic alga by weight at the time of experimentation was *G. mitchelliae*, as was true for the December field collections at Egmont Key. Three categories of blade epiphytism were visually established and later quantified. Five

blades from each of these categories were collected and washed in a $MgCl_2$ solution to remove motile epifauna. Visual estimates revealed the washing technique to be >90% efficient. Defaunated blades were clipped into wooden clothespins attached to 10 cm^2 plastic mesh squares, which were then anchored in the bed with wire stakes. Because recolonization of epibenthic substrata occurs rapidly (Bell, 1985; Virnstein and Curran, 1986; Hall, pers. obs.), recolonized seagrass blades were retrieved after 2 days. Samples were collected, processed, and statistically analyzed as described previously.

c. Experiment 2—Colonization of artificial blades

A second experiment was designed to separate the effects of factors associated with physical structure from biological aspects of epiphytic algae. Artificial mimics for *T. testudinum* and *G. mitchelliae* were constructed, and colonization by epifauna monitored. The study was conducted in May 1984 in a *T. testudinum* bed at Ft. DeSoto Park, which is located inside the mouth of Tampa Bay (27°38.2'N, 82°41.5'W), near Egmont Key. This site receives little wave action, has a silty-sand sediment and an extensive seagrass bed composed of pure and mixed stands of *T. testudinum* and *H. wrightii*. Temperature ranges from 16° to 30°C, and salinity from 28 to 35 ppt annually at the study site (Hall, unpubl. data).

Artificial seagrass blades were composed of green polypropylene ribbon approximating the dimensions of natural *T. testudinum* blades (30 cm long \times 5 mm wide). Artificial epiphytes simulating *G. mitchelliae* were constructed by sewing clumps of cotton-polyester thread onto the artificial blades (Fig. 1B). Ten replicate blades of three densities of epiphytes were established: no epiphytes, intermediate (15 clumps of epiphytes/blade), and high (30 clumps of epiphytes/blade) epiphyte density. Blades were anchored in the field as in Experiment 1, collected after 3 days, and epifauna processed as described previously. The four most abundant faunal taxa and five most abundant harpacticoid taxa were analyzed with a one-way analysis of variance and a Scheffe's multiple comparison test. In addition to the artificial blades, eight natural seagrass blades were collected to assess the effectiveness of the mimic.

3. Results

a. Major taxa

i. *Field collections.* Density of harpacticoid copepods, the numerically dominant epifaunal taxon at Egmont Key (60% of total fauna), was strongly positively associated with the amount of epiphytic algae ($r^2 = 0.86$, $p < 0.05$, Fig. 2). Numbers ranged from less than 1 copepod/ cm^2 on seagrass blades with very little epiphytism, to 48 copepods/ cm^2 on heavily epiphytized blades. Amphipod density also varied with the amount of epiphytic algae ($r^2 = 0.89$, $p < 0.05$, Fig. 2), although the abundance of amphipods was much lower than that of copepods. Crustacean nauplii and nematode densities as well were significantly associated with the amount of epiphytic algae

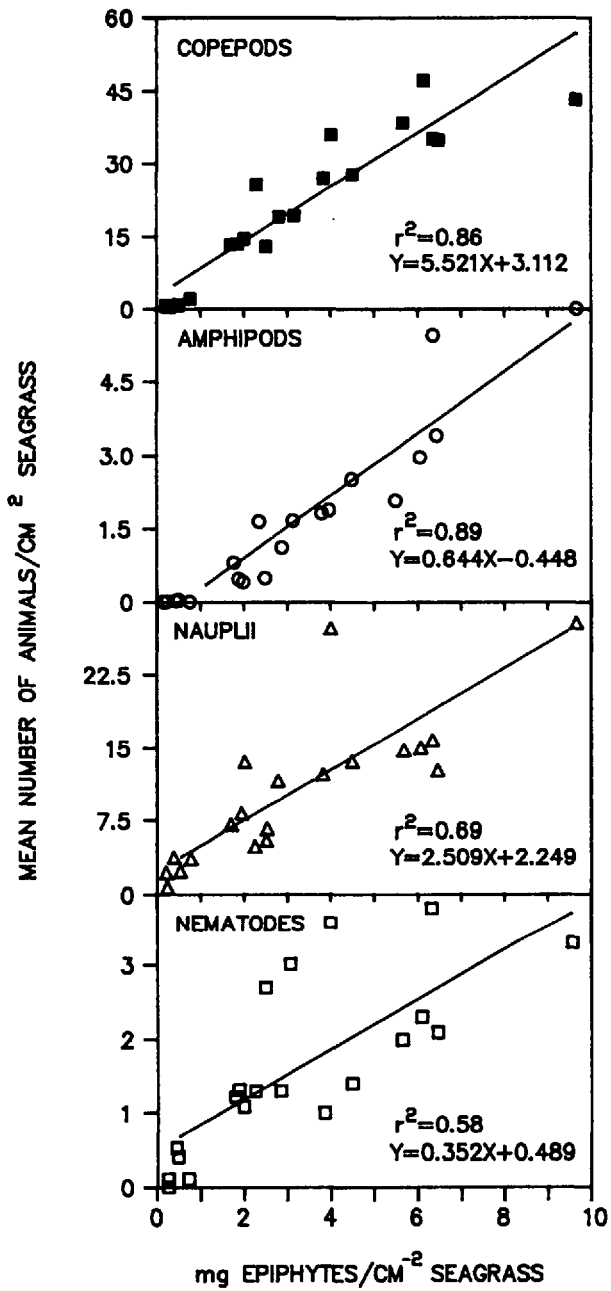


Figure 2. Linear regression of relationship between densities of the dominant motile epifaunal taxa and biomass of epiphytic algae on *Thalassia testudinum* at Egmont Key, Florida.

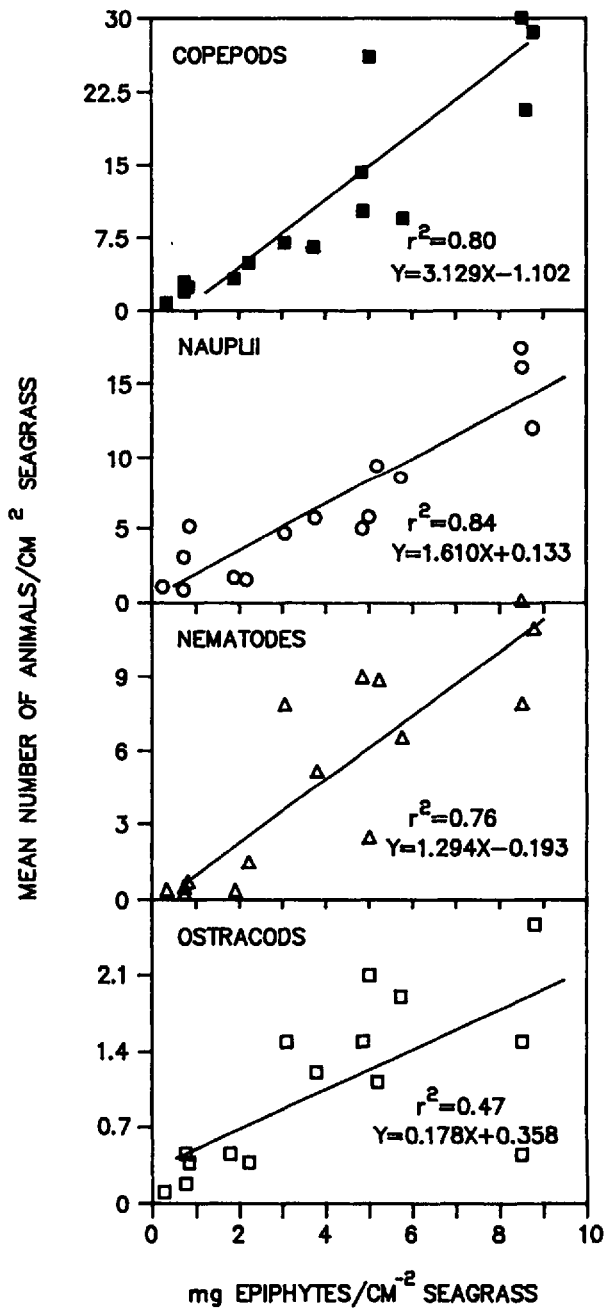


Figure 3. Linear regression of relationship between densities of the dominant motile epifaunal taxa and biomass of epiphytic algae on *Thalassia testudinum* at Indian River, Florida.

Table 1. The influence of various amounts of artificial epiphytic algae (no (0), intermediate (I), and high (H) epiphyte densities) on the abundance of the dominant motile epifaunal taxa colonizing artificial seagrass blades (30 cm long \times 0.5 cm wide) at Ft. DeSoto; Results of ANOVA and Scheffe's Multiple Range tests. Means not significantly different from each other are underlined. Data for polychaetes were $\log(Y + 1)$ transformed.

TAXON	0	I	H	F	P
Harpacticoid Copepods	60.57	<u>162.06</u>	<u>178.80</u>	21.47	<0.05
Polychaetes	1.90	<u>34.40</u>	<u>43.60</u>	94.20	<0.05
Nematodes	8.30	<u>92.40</u>	<u>128.90</u>	58.95	<0.05
Crustacean Nauplii	<u>20.10</u>	<u>31.70</u>	<u>18.70</u>	0.70	N.S.

($r^2 = 0.69$ and 0.58 respectively, $p < 0.05$, Fig. 2), but less so than harpacticoid copepods or amphipods. Other taxa present in lower abundances at Egmont Key were ostracods, polychaetes, turbellarians, bivalves, and gastropods.

ii. *Experiment 1—Recolonization of natural blades.* As on naturally colonized blades at Egmont Key, the number of harpacticoid copepods recolonizing defaunated seagrass blades in the Indian River lagoon was strongly positively associated with the amount of epiphytic algae ($r^2 = 0.80$, $p < 0.05$, Fig. 3). Copepod densities on the recolonized blades approached those recorded on nonexperimental blades at Indian River. Harpacticoid copepods were again the numerically dominant epifaunal taxon (48% of total fauna). Densities ranged from less than 1 copepod/cm² on blades with little epiphytism, to approximately 30 copepods/cm² on the most heavily epiphytized blades. Crustacean nauplii and nematode densities were also significantly associated with the amount of epiphytic algae ($r^2 = 0.84$ and 0.76 , respectively, $p < 0.05$, Fig. 3). There was less association between ostracod abundance and the amount of epiphytic algae ($r^2 = 0.47$, $p < 0.05$, Fig. 3). Amphipods, polychaetes, and gastropods were present in low numbers at the Indian River site, and were excluded from analyses.

iii. *Experiment 2—Colonization of artificial blades.* As on the natural seagrass blades collected during this study, harpacticoid copepods numerically dominated the epifauna colonizing artificial *T. testudinum* blades (47% of total fauna). The mean numbers of copepods on artificial blades with high and intermediate artificial epiphyte densities were not significantly different from each other. Numbers of copepods on both of these treatments were, however, significantly higher than on artificial blades with no epiphytes ($p < 0.05$, Table 1). Polychaetes exhibited a comparable relationship, which was again statistically significant (Table 1). While the same trend was evident with nematodes, mean densities of this second most abundant taxon were significantly different from each other on all three treatments (Table 1). In contrast to results at Egmont Key and Indian River, percent composition of crustacean nauplii was lower, and their colonization was not significantly affected by the abundance of

epiphytic algae (Table 1). Amphipods and ostracods were present at Ft. DeSoto in very low abundances.

b. Major harpacticoid taxa

i. Field collections. Laophontid sp., *Harpacticus* sp., and *Amphiascus* sp. accounted for 78.0% of the total number of harpacticoid copepods at Egmont Key. Both *Harpacticus* sp. and Laophontid sp. densities were strongly positively associated with the amount of epiphytic algae ($r^2 = 0.86$ and 0.87 , respectively, $p < 0.05$, Fig. 4), however, densities of *Amphiascus* sp. varied only slightly in relation to algal abundance ($r^2 = 0.35$, $p < 0.05$, Fig. 4). *Schizopera* sp. and *Dactylopodia tisboides* comprised 11% of the total number of copepods encountered on blades at Egmont Key. *Schizopera* sp. densities showed little ($r^2 = 0.30$, $p < 0.05$, Fig. 4), and *D. tisboides* densities showed no variation with the amount of epiphytic algae ($r^2 = 0.02$, $p < 0.05$, Fig. 4). Other taxa present at Egmont Key were *Diosaccus* sp., *Metis holothuriae*, Tegastid sp., and Ectinosomatid spp.

ii. Experiment 1—Recolonization of natural blades. *Harpacticus* sp., Laophontid sp., and *Amphiascus* sp. accounted for 80% of the total number of harpacticoid copepods at Indian River. Densities of *Harpacticus* sp. and Laophontid sp. were significantly positively associated with the amount of epiphytic algae ($r^2 = 0.74$ and 0.73 , respectively, $p < 0.05$, Fig. 5) on seagrass blades at Indian River after 2 days, while *Amphiascus* sp. density varied little with the amount of epiphytic algae ($r^2 = 0.23$, $p > 0.05$, Fig. 5). These results paralleled those from the naturally colonized blades collected at Egmont Key (Fig. 4). *Dactylopodia tisboides* abundance was more strongly associated with the amount of epiphytic algae at Indian River ($r^2 = 0.42$, $p < 0.05$, Fig. 5) than at Egmont Key (Fig. 4), however, less than 50% of the variation in density of *D. tisboides* could be attributed to the amount of epiphytic algae on *T. testudinum*. Density of Ectinosomatid spp., a group common at Indian River, was not strongly associated with the amount of epiphytic algae ($r^2 = 0.46$, $p < 0.05$, Fig. 5). Other species present at Indian River were *Mesochra schmidtii*, Tegastid sp., *Idomene forcipata*, and *Schizopera* sp.

iii. Experiment 2—Colonization of artificial blades. Laophontid sp. had the highest overall density of any copepod species on artificial blades at Ft. DeSoto, and accounted for 30% of the total number of harpacticoids. Mean numbers of Laophontid sp. on blades with intermediate and high epiphyte densities were not significantly different from each other. Numbers of Laophontid sp. on both of these treatments were, however, significantly greater than on blades with no epiphytes (Table 2). *Diosaccus* sp. and *Schizopera* sp. results were comparable to those for Laophontid sp., while *Dactylopodia tisboides* exhibited an inverse relationship, with most animals accumulating on blades with no epiphytes (Table 2). Ectinosomatid spp. were a numerically

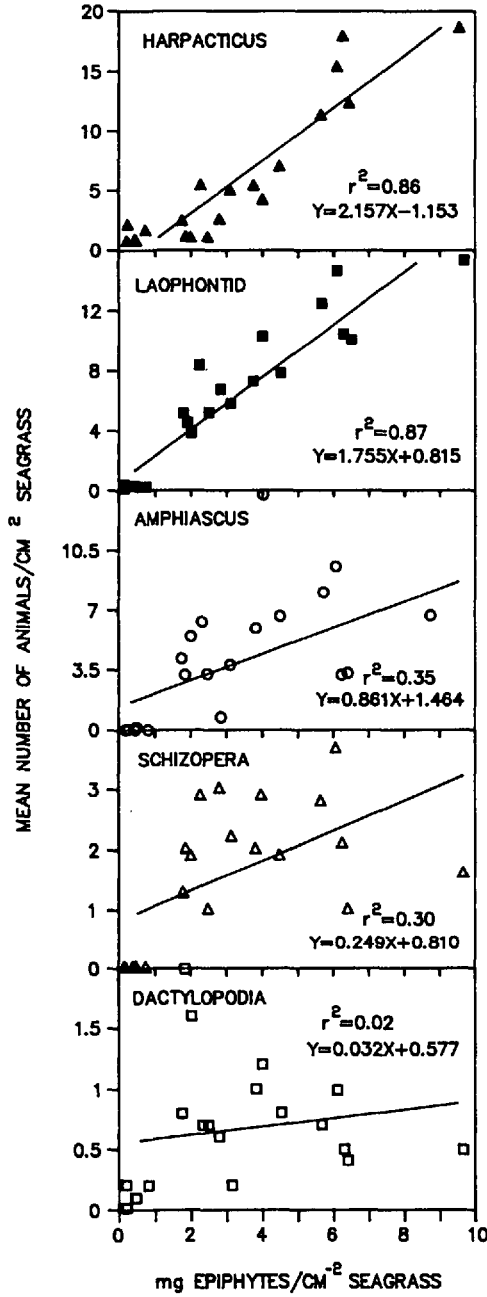


Figure 4. Linear regression of relationship between densities of the dominant harpacticoid copepod taxa and biomass of epiphytic algae on *Thalassia testudinum* at Egmont Key, Florida.

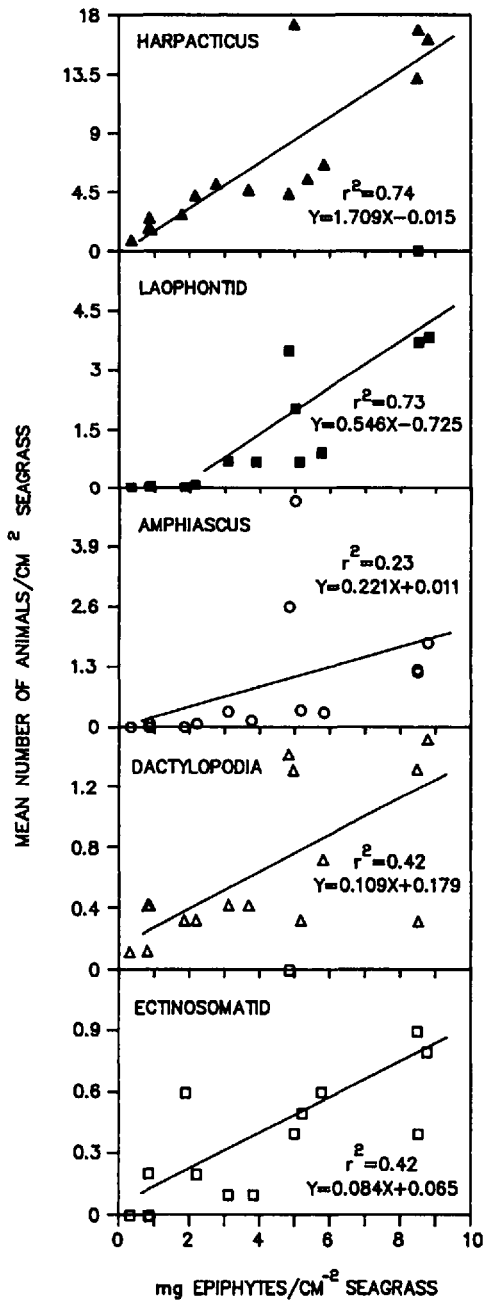


Figure 5. Linear regression of relationship between densities of the dominant harpacticoid copepod taxa and biomass of epiphytic algae on *Thalassia testudinum* at Indian River, Florida.

Table 2. The influence of various amounts of artificial epiphytic algae (no (0), intermediate (I), and high (H) epiphyte densities) on the abundance of the dominant harpacticoid copepod taxa colonizing artificial seagrass blades (30 cm long \times 0.5 cm wide) at Ft. DeSoto; Results of ANOVA and Scheffe's Multiple Range tests. Means not significantly different from each other are underlined. Data for *Schizopera* sp. were $\log(Y + 1)$ transformed.

TAXON	0	I	H	F	P
Laophontid sp.	7.44	<u>58.45</u>	<u>54.63</u>	39.50	<0.05
<i>Diosaccus</i> sp.	3.25	<u>15.54</u>	<u>17.81</u>	17.35	<0.05
<i>Schizopera</i> sp.	1.29	<u>10.11</u>	<u>19.01</u>	21.58	<0.05
<i>Dactylopodia tisboides</i>	<u>29.16</u>	<u>33.43</u>	18.08	4.46	<0.05
Ectinosomatid spp.	<u>14.03</u>	<u>18.71</u>	<u>19.43</u>	1.11	N.S.

important group of copepods at Ft. DeSoto, and there was no difference in the mean number of Ectinosomatid spp. among the three treatments (Table 2). Other species present at Ft. DeSoto were *Parapseudoleptomesochra* sp., *Mesochra pygmaea*, *Metis holothuriae*, *Idomene forcipata*, *Amphiascus* sp., Tegastid sp., and *Harpacticus* sp.

The dominant copepods from artificial epiphyte experiments at Ft. DeSoto exhibited similar responses to increased structure as copepods from natural blade collections and from experiments at Egmont Key and Indian River; i.e., more copepods were found on blades with higher amounts of epiphytic plant structure. The number of harpacticoid species present and the species composition were similar on natural blades at Ft. DeSoto and on artificial blades with no epiphytes (Sorenson's similarity index = 63.5%). These data suggest that artificial blades and epiphytes were reasonable mimics for natural *T. testudinum* and *G. mitchelliae*.

4. Discussion

Results of our study provide quantitative evidence that densities of the dominant motile epifauna on *Thalassia testudinum* are significantly associated with habitat complexity as measured by the biomass of epiphytic algae. These results were consistent for three locations on both natural and artificial seagrass blades and epiphytes. Our data support earlier suggestions from nonexperimental investigations which examined the relationship between epifauna and epiphytic algae both on seagrasses (Nagle, 1968; Lewis and Hollingworth, 1982; Novak, 1982) and various species of macroalgae (e.g., Wieser, 1952, 1959; Hagerman, 1966; Kangas, 1978; Gunnill, 1982; Edgar, 1983; Johnson and Scheibling, 1987). Thus relationships suggested for larger plant structure and fauna (e.g., MacArthur and MacArthur, 1961; Heck and Wetstone, 1977; Nelson, 1979; Southwood *et al.*, 1979; Stoner, 1980; Heck and Orth, 1980; Stoner and Lewis, 1985) are experimentally demonstrated for selected meiofauna and amphipods, and extremely fine scale vegetative architecture.

Two other important features emerge from this study. Although seagrass blades with the greatest amounts of epiphytic algae are often older and have been available for

epifaunal colonization longer than blades with lesser amounts of epiphytic algae, our data showed that biomass of epiphytic algae influenced densities of motile epifauna when length of the colonization period did not vary among blades. These results are not surprising given the rapid rates of colonization by swimming or crawling exhibited by these organisms (e.g., Bell, 1985). In addition, our results suggest that much of the relationship observed between epifauna and epiphytic algae on seagrasses may be attributable to factors associated with the physical structure rather than to biological characteristics of the algae, because similar results were obtained using both natural plants and artificial mimics.

In our study, harpacticoid copepods as a group were strongly associated with epiphytic algae. When individual species patterns were examined, however, the response to epiphytic algae was not always similar. Densities of some taxa (*Harpacticus* sp., Laophontid sp., and *Diosaccus* sp.) were much more related to the amount of epiphytic algae than others (*Amphiascus* spp., *Dactylopodia tisboides*, and Ectinosomatid spp.). Similar phenomena have been noted for amphipods which exhibit differential responses to epiphytic algae on the macrophyte *Sargassum muticum* (Norton and Benson, 1983). Close examination of copepod structure and function provides some insight into the observed variation in species utilization of plant structure. In both Laophontid sp. and *Harpacticus* sp., the endopod of the first pereopod is well developed and prehensile, and can be used efficiently in grasping algal filaments (Hicks, 1985). Thus, the morphologies of these two species may explain their close association with the abundance of epiphytic algae. Hicks (1985) reported that several Ectinosomatid spp. are suspected of using muco-polysaccharides, produced by themselves or sequestered from their algal habitats, to glue themselves to algae. Ectinosomatid spp. in our investigation were frequently observed to be coated with mucus which may have provided a means of attachment to *T. testudinum*, and could explain in part their lack of co-variation with the biomass of epiphytic algae. In related studies, Caine (1980) found that numbers of the copepod *Porcellidium sarsi*, a dorso-ventrally flattened taxon with mouthparts acting as "suction-cups," decreased as periphyton increased on *Zostera marina*. Hicks (1985) suggested that such taxa are characteristically found on plants with flat physiognomies (such as fucoid algae or *Z. marina*), because more complex plant structure most likely inhibits their attachment ability. *Idomene forcipata*, a dorso-ventrally flattened species occasionally encountered on *T. testudinum* in Tampa Bay, displayed a similar trend, as it was most often found on blades with little or no epiphytic algae (Hall, pers. obs.). Thus, the responses of epifauna to increased habitat complexity provided by epiphytic algae on seagrasses and macroalgae may vary among taxa. The kinds of resources (food, refuge, habitat) presented by epiphytic algae for epifaunal utilization are dependent on the type of epiphytic algae (microalgae, or encrusting, filamentous or fleshy macroalgae), and the ability of the epifauna to utilize the resources is dependent on their morphologies and habitat requirements.

Mechanisms by which epiphytic algae support high numbers of epifauna have not been definitively established, although protection from predation has been suggested to be important (Nagle, 1968; Edgar, 1983). Habitat complexity is frequently invoked as a feature reducing predator effectiveness in other phytal habitats (e.g., Heck and Wetstone, 1977; Virnstein, 1977; Nelson, 1979; Heck and Orth, 1980; Stoner, 1980; Coen *et al.*, 1981; Crowder and Cooper, 1982; Peterson, 1982; Coull and Wells, 1983). In the seagrass system, epiphytic algae could serve as a refuge from fish or invertebrate predators for selected epifaunal species. Epiphytic algae may also increase the amount of inhabitable space, or provide food resources either directly or indirectly by providing attachment sites for microbiota or by enhancing accumulation of sediment and detritus (see Hicks, 1985). These are by no means mutually exclusive factors (Bell, 1985). Laboratory observations, for example, have revealed that copepods spend a large portion of their time grasping or crawling along algal filaments, often moving their mouthparts. Thus, increase in the diversity of feeding surfaces could be implicated in the established relationship.

Artificial substrata have been used as valuable tools in a variety of systems to accurately quantify the habitat available to colonizing organisms, and/or to separate biological effects from factors associated with the physical structure of the natural substratum (e.g., Lund and Talling, 1957; Cattaneo and Kalff, 1977; Robinson, 1981; Bultman and Uetz, 1982; Coull and Wells, 1983; Stevenson, 1983; Creed and Coull, 1984; Virnstein and Curran, 1986). As with natural blades, most of the abundant epifaunal taxa in our study were significantly more numerous on artificial blades with artificial epiphytes than without artificial epiphytes, suggesting that factors associated with the physical structure rather than biological properties of the epiphytes were most important. The relationship between epiphytic algae and seagrass epifauna, however, may not always be due to physical structure as some differences between mimics and natural blades were noted. Crustacean nauplii, relatively abundant at all three study sites, were significantly associated with epiphytic algae on natural seagrass blades, however, artificial epiphytes did not affect their abundance. *Schizopera* sp. was significantly more abundant on blades with artificial epiphytes than without, but its density was not associated with natural epiphytes. Although copepods were significantly more abundant on artificial blades with epiphytes than without epiphytes, they were less numerous on artificial blades without epiphytes than on natural blades without epiphytes. In the present study densities of copepods and crustacean nauplii recolonizing natural blades reached ambient levels within 2 days (Hall, unpubl. data), thus the differences in faunal densities between artificial and natural blades with no epiphytes is probably not due to lack of time for copepods and crustacean nauplii to colonize. Additionally, we do not suggest that artificial seagrass blades or artificial epiphytes are always an appropriate substitute for natural seagrass and epiphytic algae. Because both seagrasses and epiphytic algae are dynamic organisms capable of rapid growth, the use of artificial structure may be inappropriate in long term studies.

In summary, the relationship between abundance of small epifauna and epiphytic algae in a seagrass habitat has been demonstrated using an experimental approach. While the physical structure of the algae seems to be responsible for much of the positive relationship observed between biomass of epiphytic algae and numbers of seagrass epifauna, the causal mechanisms behind such relationships require further scrutiny. Our findings suggest that it is necessary to examine individual species patterns to more completely understand these relationships. Furthermore, it will be crucial to consider the morphologies of both the algae and the epifaunal taxa present, and how they relate to each other, when addressing these types of questions.

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