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Host-plant specialization by a non-herbivorous amphipod: advantages for the amphipod and costs for the seaweed

Abstract Studies of factors affecting host plant specialization by herbivores commonly highlight the value of the plant as both food and habitat, but often cannot distinguish the relative importance of these plant traits. A different approach is to study non-herbivorous animals that specialize on particular plants but do not feed on tissue from these plants. Such animals will not be affected directly by the nutritional, chemical, or morphological traits that determine the value of the plant as a food. This study reports on a filter-feeding amphipod, *Ericthonius brasiliensis*, that lives in domiciles it constructs by curling terminal segments of the green, calcified, and chemically defended seaweed *Halimeda tuna*. We examined the temporal (1850s–1990s) and spatial (Caribbean, Mediterranean, and Pacific regions) scale of the association, the factors that may select for specialization on *H. tuna*, and the effect of the amphipod on growth of its host. Sampling along 125 km of coral reefs in the Florida Keys (USA) indicated that almost all populations of *H. tuna* had been colonized by this amphipod. Infested plants occurred on nine of ten reefs that supported *H. tuna* populations, with between 8 and 75% of the plants on those reefs colonized by the amphipod. For infested plants, 2–23% of all segments on each plant had been curled by the amphipod. Common co-occurring congeners of *H. tuna* (*H. opuntia* and *H. goreaui*) were never used for domicile construction.

A survey of 1498 *Halimeda* specimens collected during the last 140 years and archived in the U.S. National Museum of Natural History (Smithsonian Institution, Washington, D.C.) indicated that the association has existed for >100 years and occurs throughout the Caribbean region, never in the Indo-Pacific or Mediterranean, and only on *H. tuna*. Predation by fishes could select for amphipod specialization on *H. tuna*. Laboratory experiments demonstrated that amphipods inhabiting curled segments of *H. tuna* were relatively immune from fish predation while those on the exterior surface of the plant or in open water were rapidly eaten. Segments of *H. tuna* are large enough to provide full protection from predators, while those of the co-occurring congeners *H. goreaui* and *H. opuntia* are of a size that may provide only partial protection. Experimental addition of *E. brasiliensis* to *H. tuna* plants in the field significantly decreased segment accumulation on infested relative to uninfested control plants. Whether this negative effect was a direct or indirect consequence of amphipod occupancy is unclear. Rolling plant portions into domiciles could directly decrease host growth by increasing shading and decreasing exposure of plant surface area to water column nutrient flux. Amphipod occupancy could indirectly slow net host growth if fishes selectively feed on plant sections occupied by amphipods. Underwater video showed that herbivorous fishes did not graze infested plants more than uninfested plants, but small predatory fishes did prefer feeding from infested plants. These non-herbivorous fishes may slow host growth by damaging the terminal meristematic tissues of plants during attacks on amphipods. This study demonstrates that habitat specialists can negatively impact hosts without consuming them and that specialization on a plant can occur due to its habitat value alone (as opposed to its value as a food).

Key words Host-plant specialist · Amphipod · *Halimeda* · Plant-animal interactions · Coral reef fishes

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Introduction

Factors influencing the evolution of specialization among small herbivores have been explored in terrestrial systems for decades (Berenbaum 1996) and in marine systems only recently (Hay 1992; Hay and Steinberg 1992; Hay and Fenical 1996). In both terrestrial and marine systems, the value of potential host plants as refuges from consumers, parasites, or pathogens can affect the distribution of some specialist herbivores (Hay et al. 1987; Bernays and Graham 1988; Bernays 1989; Hay 1992, 1997b). But because specialist herbivores both consume and live on their hosts, the values of a plant as food versus habitat are usually confounded. For example, if a herbivore has a high growth rate or fecundity on a host that also acts to reduce other selective pressures (e.g., predation risk, susceptibility to pathogens), it may be unclear which factor, or interaction of factors, generates and maintains the association. By manipulating the system experimentally, one may demonstrate the importance of one factor or another, but their relative importance often remains incompletely understood. A different approach is to study animals that are specialized on particular plants but do not consume their hosts. For these habitat specialists, food quality will not play a direct role in host choice. This allows other selective pressures to be explored without the potentially confounding influence of the food value of the plant.

Habitat specialists that do not consume their host need not have any effect on host fitness, and there are numerous associations described within natural history literature where this seems to be the case (e.g., spiders that spin webs on only a few host plants). However, the effects of these types of specialists on host fitness have rarely been assessed. When habitat specialists do affect their hosts, the interactions may operate indirectly through other species or other trophic levels. In previous studies that have reported an effect of habitat specialists on their host plants, the specialists appeared to increase rather than decrease host plant fitness by consuming competitors (e.g., coralline algal mutualisms with limpets, chitons, or crabs: Steneck 1982; Littler et al. 1995; Stachowicz and Hay 1996) and/or by protecting the plant from herbivores (e.g., *Acacia*-ant mutualism: Janzen 1966; Bentley 1977). It is possible that mutualistic associations have been viewed as more interesting or more publishable than neutral interactions and are thus over-reported in the literature; however, from the current literature, it appears that habitat specialists are commonly mutualists that enhance host fitness via indirect effects. These more complex and indirect interactions are of current interest to ecologists, because they are less well understood than many direct, two-species interactions but may have large effects on community structure (Wootton 1994).

This study investigates a novel association between the amphipod *Ericthonius brasiliensis* and its host seaweed *Halimeda tuna*. The amphipod is a filter-feeder and thus does not eat macroalgae. It curls segments of *H. tuna* into domiciles, dwells in these, and filter-feeds from the water column. Seaweeds in the genus *Halimeda* are among the most widespread and abundant seaweeds on tropical reefs. They are relatively resistant to reef herbivores due to their heavily calcified thallus and potent chemical defenses (Hay 1984; Paul and Hay 1986; Paul and Van Alstyne 1988a; Hay et al. 1994; Schupp and Paul 1994). They are also unusual in that they grow at night, producing thin uncalcified new segments when herbivorous fishes are not active (Hay et al. 1988).

We address the following questions regarding this amphipod-seaweed association. (1) Are populations of *E. brasiliensis* restricted to *H. tuna*? (2) What is the spatial and temporal scale of the association between *E. brasiliensis* and *H. tuna*? (3) Is the curled segment in which the amphipod dwells created by the amphipod and, if so, does curling occur at night before new segments calcify or can the amphipods curl mature, calcified segments? (4) Do these domiciles provide a refuge from predation for *E. brasiliensis*? (5) Does the experimental addition of *E. brasiliensis* to *H. tuna* plants affect net growth of *H. tuna* in the field? (6) Does *H. tuna* become more attractive to herbivorous or predatory fishes when it is infested by these domicile-building amphipods?

Materials and methods

Study organisms

In the Atlantic, *E. brasiliensis* occurs from Cape Cod, Mass., USA south to Brazil and throughout the Caribbean (Bousfield 1973; Myers and McGrath 1984). Though *E. brasiliensis* has been described as cosmopolitan, recent work suggests that some specimens in Pacific, Indian, and Mediterranean waters may have been mis-identified (Barnard and Karaman 1991). Outside the Caribbean, the filter-feeding amphipod is considered a habitat generalist; for example, it was found abundantly on five algal species (two brown and three red algal species) on a North Carolina subtidal jetty (Duffy 1989). Within the Caribbean, the extent of the distribution of the amphipod is relatively unknown, though it has been noted on drifting rafts of algae (J. Thomas, personal observation). As with all members of the family Corophidae, *E. brasiliensis* is tubiculous and sometimes in the process of making a tube will roll an algal frond over itself (Bousfield 1973; E. Cruz-Rivera, personal communication).

Green seaweeds in the genus *Halimeda* are among the most abundant seaweeds in tropical oceans worldwide (Hillis-Colinvaux 1980) and, as such, generate a significant proportion of the carbonate in tropical marine systems (Milliman 1974; Davies and Marshall 1985). *Halimeda* species are among the least palatable upright seaweeds in the tropics (Hay 1981, 1984, 1985; Lobel and Ogden 1981; Littler et al. 1983; Lewis 1985; Paul and Hay 1986). Low susceptibility to herbivores is due to the deterrent effects of noxious secondary metabolites (Paul and Fenical 1983; Targett et al. 1986; Hay et al. 1988; Paul and Van Alstyne 1988a), the relatively high concentrations of $CaCO_3$ in algal tissues (Hay 1984; Paul and Hay 1986), the synergistic or additive effects of these two traits (Hay et al. 1994; Schupp and Paul 1994; but see Pennings and Paul 1992), and to nocturnal growth, which allows these algae to produce their most herbivore-susceptible tissues during short

periods when herbivorous fishes are not feeding (Hay et al. 1988; Hay 1997c).

Morphological and chemical traits vary among species of *Halimeda*, including those used in this study. The highly deterrent diterpenoids, halimedatrial and halimedatetraacetate, are present in *H. tuna* and *H. opuntia* but absent from *H. goreaui* (Paul and Fenical 1983; Paul and Hay 1986; Paul and Van Alstyne 1988a; Hay et al. 1994); the concentrations of ash and $CaCO_3$ are generally lower in *H. tuna* than in either *H. opuntia* or *H. goreaui* (Hillis-Colinvaux 1980; Paul 1985). However, despite these morphological and chemical differences, assays using natural assemblages of herbivorous reef fishes on numerous reefs scattered throughout the Caribbean suggest that the three congeners are all low-preference foods for herbivorous fishes (Hay 1984; Paul and Hay 1986).

Field survey

To quantify the distribution and abundance of the *E. brasiliensis* domiciles on species of *Halimeda*, individuals of *H. tuna*, *H. opuntia*, and *H. goreaui* (the three species that were common to the reefs visited) were collected from a variety of forereefs along a 125-km stretch of the Florida Keys. At most sites and depths visited (Table 1), a 25 m transect was stretched on hard substrata along the chosen depth contour. The initial point and bearing of the transect were selected haphazardly by the diver. At 1 m away from the initial point, a 1-m^2 quadrat was centered on the transect. All congeneric *Halimeda* plants common to the reefs visited were randomly collected as follows. For *H. tuna*, the 1-m^2 quadrat was divided into four 0.25-m^2 subquadrats, and all individuals were collected from the lower-left subquadrat. If there were less than five individuals of *H. tuna* in that subquadrat, then all individuals were collected from the next subquadrat encountered when moving counter-clockwise. This continued until at least five individuals were collected. *H. opuntia* and *H. goreaui* were less abundant than *H. tuna*. If either of these two species occurred in a quadrat, up to five individuals of each species were gathered haphazardly. Our sample sizes for *H. tuna* were larger than for the other two congeners because it was more abundant and because initial observations suggested that amphipod domiciles were found only on *H. tuna*. All plants from each 1-m^2 quadrat were sealed in separate plastic bags. The quadrat was moved 3 m away and the procedure repeated until a total of five to eight quadrats had been collected. Plants from two sites (Carysfort and a reef halfway between Pickles and Conch) were gathered haphazardly by the divers, and no plants were collected at the two sites at which *H. tuna* was absent (Sombrero and Looe).

In the laboratory [National Oceanographic and Atmospheric Administration's National Undersea Research Center (NOAA/NURC) in Key Largo, Fla., USA], the number of plants, the presence and absence of domiciles, and the total number of domiciles and segments per plant were recorded. To distinguish plant segments curled by *E. brasiliensis* from segments curled by other processes, a curled segment had to contain the amphipod or display evidence of a mucus tube built by the amphipod in order to be counted as a domicile. These criteria seem appropriate given that we closely inspected over 700 plants but never encountered a species other than *E. brasiliensis* living in a curled segment of *H. tuna*. By grouping all plants of a species at a given site, we calculated the percentage of individuals with domiciles and also the mean number of domiciles per infested plant.

Herbarium specimen survey

Because *Halimeda* plants are heavily calcified, they maintain their integrity when pressed onto paper. Thus, it was possible to survey dry herbarium collections to obtain some indication of the worldwide distribution and recent history (< 140 years) of the *E. brasiliensis*-*H. tuna* association, as well as the presence of the domiciles on *Halimeda* congeners in locations other than our study sites. We examined 1498 specimens pressed onto herbarium paper and catalogued at the Smithsonian Institution's National Museum of Natural History in Washington, D.C., USA. All pressed specimens of *Halimeda* species available were examined, regardless of species or location of collection. We did not attempt to validate that each specimen had been identified correctly; we simply accepted the identifications as given. This prevented us from using taxonomic uncertainties to bias our sample; however herbaria collections can be biased due to factors such as collector, collection method, or habitats sampled. Evidence of a mucus tube or the fusion of the segment around a tube distinguished domiciles from segments that were incidentally folded during the pressing procedure. It is possible that animals other than *E. brasiliensis* could curl segments of *H. tuna*. This seems unlikely, however, because we never observed this during any of our field assays and collections and because this behavior is not known for any other species.

Amphipod additions to *H. tuna*: field experiment

To demonstrate that *E. brasiliensis* adults actively roll segments of *H. tuna* and to evaluate whether they do this during the day or during the night, domicile-free plants were enclosed with amphi-

Table 1 A summary of the Florida keys forereefs visited during this study (arranged from north to south). At most sites, the algal species present were collected using a transect-and-quadrat method. Plants at two sites were collected haphazardly, and no plants were collected at two sites at which *Halimeda tuna* was absent

Reef	Depth (m)	Date (in 1996)	Number of quadrats	Transect or haphazard	Number of plants collected		
					H. goreaui	*H. opuntia*	*H. tuna*
Carysfort	6	02 October	–	Haphazard	Not collected	Not collected	20
French	6	27 September	8	Transect	38	40	51
Molasses	6	26 September	8	Transect	7	23	102
Pickles	5	26 July	8	Transect	27	28	102
Pickles	9	22 July	8	Transect	0	42	73
Pickles/Conch[a]	6	06 October	–	Haphazard	Not collected	Not collected	49
Conch	5	24 July	7	Transect	12	37	90
Conch	14	24 July	8	Transect	32	48	78
Alligator	9	09 October	6	Transect	0	4	57
Sombrero	12	28 September	–	Transect	Not collected	Not collected	Not present
Looe	6	29 September	–	Transect	Not collected	Not collected	Not present
Middle Sambo	5	29 September	5	Transect	0	25	51
Total					116	247	673

[a] This site was approximately halfway between Pickles and Conch Reefs

pods in the field either overnight or during the day. Just before sunset, when newly forming and uncalcified segments are beginning to be produced (see Hay et al. 1988), 20 pairs of *H. tuna* plants were chosen so that members of a pair (1) were within approximately 1 m of each other, (2) were similar in size, (3) had a similar number of newly forming segments (small white terminal tips), and (4) had no domiciles. Different pairs were separated by at least 1.5 m. An enclosure cage (approximately 10 cm in diameter and 25 cm tall), constructed with a wire frame and shrouded with a nylon sock, was placed over each individual plant and fastened around the stipe using cable ties. Ten adult amphipods were collected from the same forereef where the experiment was conducted and added to one of the cages in each pair. Amphipods were not added to the other cage in the pair (= control). The next morning (12 h after amphipod addition), the cages were removed and the presence or absence of domiciles on each plant was recorded.

A second experiment was performed to determine if amphipods created domiciles during daylight hours when uncalcified new segments would be less available. We utilized the same procedures as the first experiment, with two differences. First, the cages were placed on the plants early in the morning and removed in the evening (10 h after amphipod addition). Second, plants were chosen so that each plant in a pair (total number of pairs = 16) contained a similar number of poorly calcified segments that appeared to have been produced the previous night. Differences in the frequency of domicile construction were analyzed using a chi-square test.

Effects on plant growth: field experiment

A second amphipod addition experiment was performed to assess the impact of amphipods on the net growth of *H. tuna*. Artificially infested plants (methods described above) and their uninfested, paired controls were stained with alizarin red within 24 h of amphipod addition. These plants remained in the field until recovery 5 days later. Alizarin red stain is deposited into the calcareous skeleton of the segments during photosynthesis, giving a reference point in time from which new plant growth (measured as number of new segments) can be measured (Wefer 1980). In this experiment, 9 of the 14 pairs of plants had a segment curled on the amphipod addition plant. To stain these 9 pairs of plants, plastic bags were placed over the plants and fastened to the stipe using cable ties. An alizarin red solution was injected into the bags using a syringe to create a concentration of approximately 45 mg/l within the liter-sized bags. The next morning (14 h later), the bags were removed. After 5 days, the plants were sealed in plastic bags and returned to the laboratory. To remove the natural pigments and reveal the dye, the plants were rinsed with seawater, placed in a 20% bleach solution for 2 min, rinsed with seawater again, and then dried at approximately 25°C overnight. Whitened segments that appear distal to the reddened segments were assumed to be new (Wefer 1980). Net relative growth was calculated as the number of new segments divided by the total number of segments on each plant. Data were analyzed with a paired *t*-test.

Segment versus amphipod size

Because segment size could affect how well amphipods in rolled segments are defended from consumers, we determined how completely domiciles made from each of the three *Halimeda* species could potentially encompass the amphipod. The height of apical segments of *Halimeda* congeners (*H. goreaui*, *H. opuntia*, and *H. tuna*) were measured from a sample of specimens ($n = 15$) located at the Smithsonian herbarium and collected from throughout the Caribbean. A one-way ANOVA was used to determine if apical segment sizes differed among species. We also measured the length of ten adult amphipods by adding the lengths of the head, peraeon, abdomen, and telson. This estimate

did not include antennule length and thus may be conservative. A Dunnett's test evaluated mean amphipod length versus the mean maximum segment size of each *Halimeda* species to determine which species of *Halimeda* might provide the best refuge for the amphipod.

Predation risk: laboratory experiment

To determine if inhabiting a domicile provided greater protection from predation than inhabiting the plant surface or the water column, we performed a series of laboratory assays with two species of fishes that readily consume small invertebrates and that co-occur with the amphipod in the field. Slippery dicks (*Halichoeres bivittatus*) and bluehead wrasses (*Thalassoma bifasciatum*) were collected from backreef areas near Pickles Reef (Florida Keys), kept at the NOAA/NURC facility for a week before the experiment, and fed daily with cultured brine shrimp.

The experiment took place in 1.2-l plastic tubs filled with seawater. While each amphipod treatment was being installed, each fish was restrained by a mesh screen so that it could not attack the amphipod until we removed the screen. In the first treatment, the amphipod was placed in the water column using a pipette. In the second treatment, a *H. tuna* branch approximately 5 cm long (= three to five segments) without curled segments was placed in the tub, and an amphipod was placed onto the surface of the plant using a pipette. The amphipod did not move appreciably once it settled on the algal surface, even in the presence of a fish predator. In the third treatment, a similarly sized plant with one curled segment and a single amphipod in the domicile was placed in the tub. The order of treatment presentation was randomized. Before and after each replicate assay, a brine shrimp was offered to the fish in order to gauge hunger level. In no case did a fish refuse to eat the brine shrimp. The fate of the amphipod (alive or dead) was recorded after 120 s. Each replicate represents one fish exposed to each of the three treatments ($n = 10$ for slippery dicks and $n = 8$ for bluehead wrasses). The presence of a difference among treatments was determined using a chi-square test. Multiple pairwise comparisons between treatments were analyzed using adjusted chi-square tests [i.e., the adjusted *P*-value is $\alpha' = 1 - (1 - \alpha)^{1/k}$, where $k = b(b-1)/2$ and b is the number of treatment types (Sokal and Rohlf 1981, pp. 728–729)].

Fish activity: field assay

Many herbivores are nitrogen limited and will thus opportunistically consume animals when possible (Mattson 1980; Dearing and Schall 1992; White 1993). *Halimeda* segments containing amphipods should be more valuable nutritionally than those without amphipods, and this might increase herbivory by fishes on *H. tuna*. Underwater video monitoring of fish bites on *H. tuna* individuals with and without domiciles was performed at Pickles Reef at a depth of about 6 m. Equal volumes (200 ml) of *H. tuna* plants with and without domiciles were strung into separate three-strand polypropelene ropes and paired within a 0.25-m² quadrat. Because epiphytes may alter herbivore preferences for hosts (Wahl and Hay 1995), we selected relatively unfouled plants for this assay. On two occasions in the early afternoon (1 and 7 August 1996), four Hi-8 video cameras in underwater housings were placed on stands that held the cameras approximately 1 m above each quadrat. Cameras taped feeding on the plants for an hour in the absence of divers. One camera ran for only 0.5 h, so we excluded that replicate. The resolution of Hi-8 video allowed for accurate identification of fish species and quantification of fish bites. Comparisons were analyzed using a paired *t*-test. When trophic or taxonomic groups of fishes were analyzed (e.g., carnivorous fishes), only those replicates receiving bites from that group of fishes were used.

Results

Throughout the Florida Keys, *H. tuna* was heavily infested by the amphipod *E. brasiliensis* while co-occurring congeners were uninfested. *E. brasiliensis* had rolled *H. tuna* segments on nine of the ten reefs supporting *H. tuna*, with 8–75% of the plants at each of these nine sites being affected (Fig. 1). Amphipod-infested plants had a mean of 2–23% of their total number of segments rolled (Fig. 2); this equals about two to ten rolled segments per infested plant. No amphipod domiciles were found on the 247 *H. opuntia* and 116 *H. goreaui* plants examined throughout these same sites. We occasionally found what appeared to be rolled segments on *H. opuntia*; however, close examination indicated that these curled segments did not contain the mucus-lined tubes that are characteristic of tubiculous amphipods. These rare instances of curled segments on *H. opuntia* may occur naturally; there was no indication that they were rolled by amphipods.

To provide a broader geographic and temporal perspective on this amphipod-*Halimeda* association, we also examined 1498 pressed specimens of *Halimeda* in the herbarium at the Smithsonian Institution's National Museum of Natural History. The collections examined were made between 1854 and 1990. They included specimens from the Caribbean Sea, Mediterranean Sea, and Pacific Ocean, and represented 14 species of *Halimeda*. Amphipod domiciles were present almost exclusively on *H. tuna* (Tables 2, 3). The sole exception was a single *H. copiosa* plant from Belize, and it is possible that this plant was misidentified. Amphipod domiciles on *H. tuna* occurred only in the Caribbean,

with 20% of all Caribbean *H. tuna* plants being occupied by the amphipod. The frequency of amphipods occupying plants ranged from 0% for Costa Rica to over 50% for Belize. There were no domiciles found on any *Halimeda* species, including *H. tuna*, in the Pacific Ocean or in the Mediterranean Sea. The association is at least a century old in the Caribbean region; rolled segments could be observed on *H. tuna* plants collected from 1898 onward.

Amphipods curled only newly produced terminal segments of *H. tuna* and did this almost exclusively at night. When amphipods were caged with unoccupied plants for 10 h starting shortly after sunrise, curled segments occurred on none of the 16 treated plants and on 1 of 16 control plants; thus the frequency on amphipod addition versus control plants did not differ (Fig. 3). When amphipods were caged with unoccupied plants for 12 h starting shortly before nightfall, curled segments occurred on 12 of 20 treated plants and on only 3 of 20 control plants. Frequency of segment rolling thus increased significantly on treatment plants only at night (Fig. 3). Domiciles varied in number from one to six per infested plant and were always made from terminal, never subterminal, segments. The presence of curled segments on control plants is likely due to either error in choosing uninfested plants underwater or to amphipods being on the plants before they were caged.

Five days after plants were experimentally infested, the alizarin red staining technique indicated that plants with segments curled by amphipods were accumulating new segments at only one-third the rate of uninfested plants (Fig. 4). Of the nine experimental pairs, two were removed from analysis because no stain could be detected on one of the plants in the pair. Although

Fig. 1 Frequency of *Ericthonius brasiliensis*-infested *Halimeda tuna* plants on forereefs of the Florida Keys. *Numbers above bars* represent the number of plants collected at each location
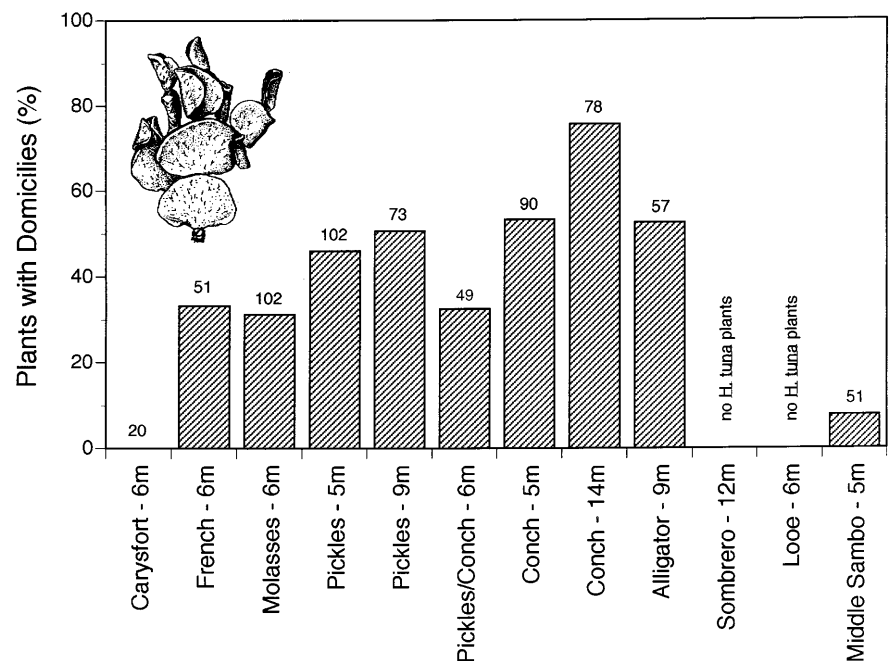
476

Fig. 2 Mean percentage of segments (+1 SE) that had been curled into domiciles on *Ericthonius*-infested plants. Only infested plants were used. *Numbers above bars* represent the number of infested plants
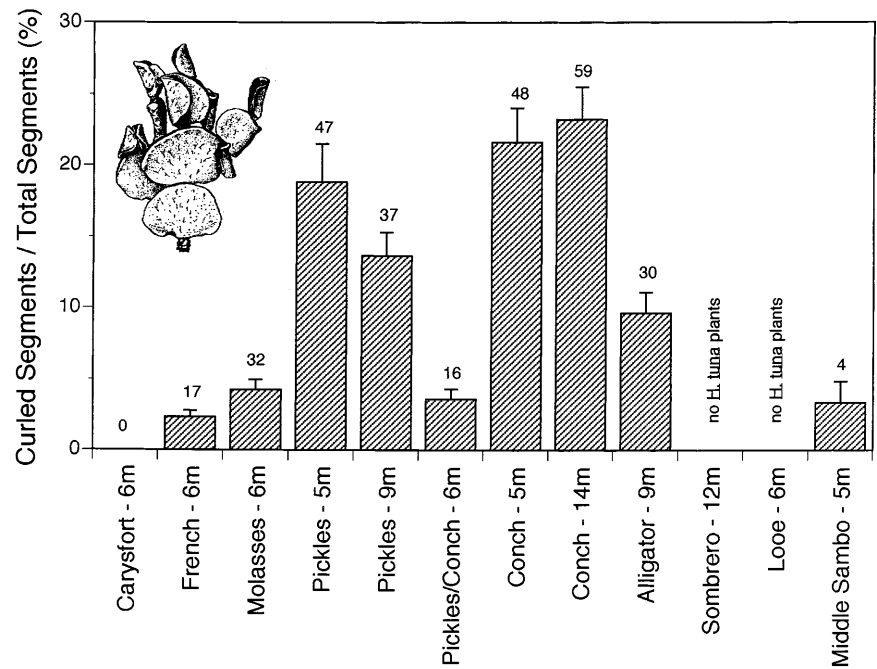

Table 2 A summary of *Halimeda* specimens examined at the Smithsonian Institution, Washington, D.C. The number of plants that held at least one amphipod domicile over the total number of plants examined is recorded for three major regions: the Pacific Ocean, the Mediterranean Sea, and the Caribbean Sea
[a] *H. opuntia* is known to be present in the Mediterranean
[b] 136 of 150 Mediterranean plants were from Tunisia

Species	All plants (totals)	Pacific Ocean (total)	Mediterranean (total)	Caribbean Sea (total)
H. copiosa	23	0/6	–	1/17 = 6.8%
H. cuneata	13	0/13	–	–
H. discoidea	233	0/103	–	0/130
H. goreaui	47	–	–	0/47
H. gracilis	25	0/17	–	0/8
H. lacunalis	12	0/12	–	–
H. macroloba	88	0/88	–	–
H. macrophysa	24	0/24	–	–
H. opuntia	402	0/97	No plants[a]	0/305
H. scabra	27	0/1	–	0/26
H. simulans	75	0/2	–	0/73
H. taenicola	65	0/65	–	–
H. tuna	454	0/50	0/150[b]	50/254 = 19.7%
H. velasquezii	10	0/10	–	–
Grand total	1498			

amphipods significantly reduced the net growth of *H. tuna*, domicile production did not prevent further growth of the meristematic tissue located in these distal segments. We found some plants in the Florida Keys with as many as seven sequential segments that were all rolled to make domiciles.

Lower net growth of *H. tuna* due to amphipod activity could result from direct effects of domicile construction, or might result indirectly if segments harboring an amphipod are selectively removed by herbivorous fishes opportunistically consuming amphipods. Video assays of fish feeding in the field revealed that fishes as a group bite plants with domiciles significantly more often than plants without domiciles (Fig. 5A). However, carnivorous fishes were responsible

for most of this pattern (Fig. 5B); neither parrotfishes, surgeonfishes, nor all herbivorous fishes combined showed a significant preference for plants with versus without domiciles (Fig. 5C). Thus, carnivorous fishes selectively forage on *H. tuna* plants containing amphipods, but herbivorous fishes could not be demonstrated to prefer infested plants.

Despite small predatory fishes focusing on curled plants as foraging sites in the field, when exposed to two species of predatory wrasses (slippery dick, *H. bivittatus*, and bluehead wrasse, *T. bifasciatum*) for up to 2 min in the laboratory, the amphipods were always consumed when in the water column, were consumed approximately half the time when on an uncurled plant, and were almost never consumed when

Table 3 A summary of the *Halimeda* specimens examined at the Smithsonian Institution, Washington, D.C., that were from the Caribbean region only

Species	Bahamas	Belize	Bermuda	Costa Rica	Honduras	Florida	Panama	Lesser Antilles	Puerto Rico	Other
H. copiosa	—	1/9 = 11.1%	—	—	—	—	0/4	—	—	0/4
H. discoidea	0/3	0/8	—	0/24	—	0/34	0/7	—	0/9	0/45
H. goreaui	0/4	0/10	—	—	0/2	0/10	—	—	0/1	0/20
H. gracilis	—		—	—	—	—	—	—	—	0/8
H. opuntia	0/6	0/29	—	0/1	0/4	0/58	0/94	0/10	0/40	0/63
H. scabra	0/10		—	—	—	0/7	—	—	—	0/9
H. simulans	0/6		0/3	—	0/9	0/16	0/19	—	0/6	0/14
H. tuna	6/28 = 21.4%	25/46 = 54.3%	1/27 = 3.7%	0/9	2/15 = 13.3%	7/51 = 13.7%	4/38 = 10.5%	0/11	3/9 = 33.3%	2/20 = 10.0%

Fig. 3 Domicile-building activities of *E. brasiliensis* when added to uninfested plants during the day (**A**) or during the night (**B**). The experiment was conducted in the field using attached plants. *P*-values are from χ^2-tests
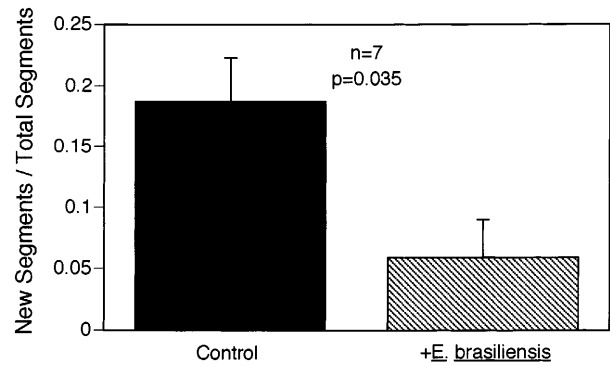

Fig. 4 Net growth (mean + 1 SE) of experimentally infested *H. tuna* plants. *P*-value is from a paired *t*-test

in the domicile (with 1 exception in 18 replicates; Fig. 6A,B). If the amphipod in a treatment was attacked by either species (i.e., one or more fish bites), the amphipod never survived the attack when in the water column or on an uncurled plant, but nearly always survived when in a domicile (Fig. 6C,D). Thus, when attacked, the plant provided the amphipod significantly greater protection from predatory wrasses when curled domiciles were present than when they were absent, and an uncurled plant provided no greater protection than being in the water column with no plant cover at all.

Segment size could restrict *E. brasiliensis* to those species of *Halimeda* with segments sufficiently large to encompass the amphipod (Fig. 7). Apical segments of *H. goreaui* were a significant 50% shorter than the

Fig. 5 Fish bites on *H. tuna* as recorded by underwater video cameras. The mean (+1 SE) number of bites in an hour assay on curled and uncurled plants is indicated for all fishes (**A**), carnivorous fishes and the most common species of carnivorous fish, the slippery dick (*Halichoeres* bivattus) (**B**), and all herbivorous fishes and two types of herbivorous fishes (**C**). *P*-values were generated from a paired *t*-tests
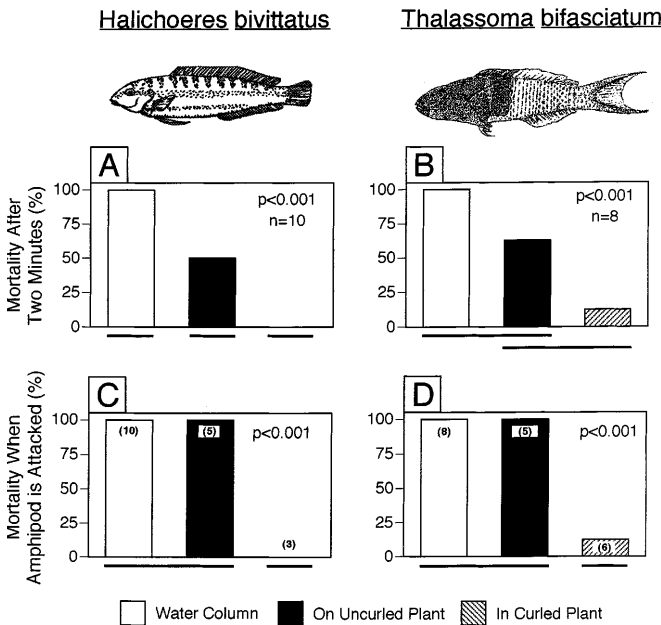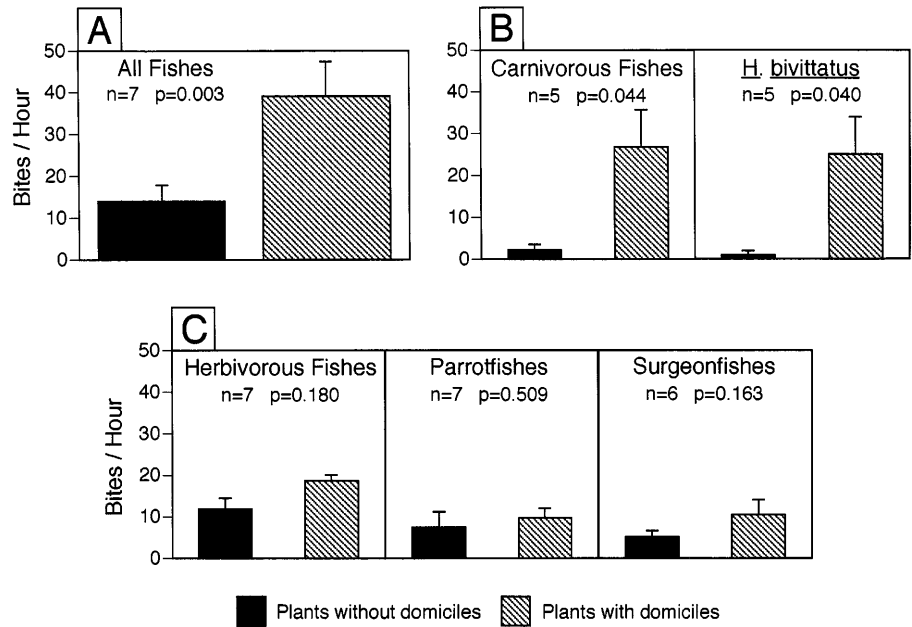

Fig. 6 Laboratory assay of amphipod mortality in the water column, on uncurled plants, and in curled plants after 2 min exposure to predators. *Lines beneath bars* connect pairs of treatments with no significant difference ($P > 0.017$) as determined by multiple pairwise comparisons (see Materials and methods for details). Shown are mortality due to slippery dick predation (**A**) or bluehead wrasse predation (**B**) (considers both attacked and unattacked amphipods), and mortality when the amphipod was attacked by a slippery dick (**C**) or a bluehead wrasse (**D**) *P*-values are from χ^2-tests. *Numbers in parentheses* within the bars in (**C,D**) are sample sizes for these treatments

Fig. 7 The mean height (+1 SE) of apical segments of *Halimeda* congeners and the body length of the amphipod *E. brasiliensis*. A one-way ANOVA contrasted the three *Halimeda* species. A Dunnett's test was then used to compare plant segment height of each species with amphipod length. A *star* indicates segment heights that differ significantly ($P < 0.01$) from amphipod length; *ns* no significant difference ($P > 0.05$)

Discussion

Specialization by *E. brasiliensis*

The filter-feeding amphipod *E. brasiliensis* does not eat *H. tuna*, yet both field and herbarium surveys indicate that it specializes on *H. tuna* as a host plant. It should thus be added to the small, but growing list of marine animals that specialize on morphologically and/or chemically defended algae for food or habitat (Steneck 1982; Paul and Van Alstyne 1988b; Hay et al. 1989, 1990a,b; Littler et al. 1995; Hay and Fenical 1996; Stachowicz and Hay 1996, in press). Amphipod domiciles were found abundantly on nine of the ten forereefs in the Florida Keys at which *H. tuna* occurred (Figs. 1, 2), and

length of the amphipod. *H. opuntia* segments were statistically indistinguishable in size from the amphipod and segments of *H. tuna* were a significant 46% larger than the amphipod.
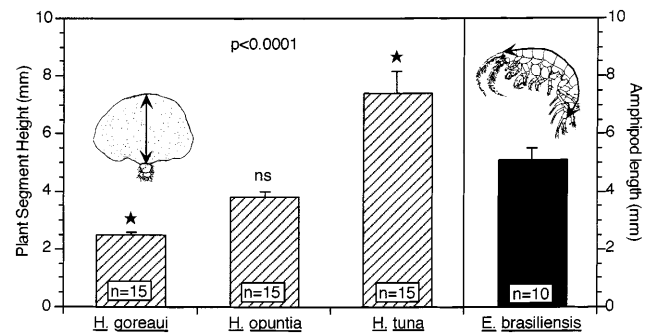
were never found on any of the 363 congeneric *Halimeda* plants that occurred on the same reefs (Table 1). In a survey of 1498 herbaria specimens covering 14 species of *Halimeda* from the Caribbean, the Indo-Pacific, and the Mediterranean, amphipod domiciles were found only in the Caribbean and, with the exception of a single *H. copiosa* plant, only on *H. tuna* (Tables 2, 3).

The amphipod takes advantage of the nocturnal growth pattern of Halimeda to curl *H. tuna* segments into domiciles. Newly formed tips (<12 h old) are curled by the amphipod overnight; in contrast, the newest segments available during the day (approximately 12–17 h old) are not curled by the amphipod (Fig. 3). While it is possible that nocturnal construction of domiciles occurs simply because *E. brasiliensis* may be more active at night than during the day (see Brawley 1992 for examples in other amphipod species), the present evidence suggests that the amphipod preferentially curls the youngest, uncalcified and more malleable segments that are available only at night. Older, partially calcified segments that are available both day and night were never used.

Because *E. brasiliensis* is a filter-feeder, the fitness of the amphipod is not influenced directly by the nutritional quality of the plant. Thus, the amphipod-*H. tuna* association illustrates that an animal can specialize on a plant for traits unrelated to food quality (Bernays and Graham 1988 and other papers in that volume; Hay 1992; Stachowicz and Hay, in press). This separates the present system from other plant-animal associations (e.g., insect herbivores or marine mesograzers and their hosts) where the value of the host plant as food and as habitat are potentially confounded. For instance, when a herbivore preferentially consumes a host plant that also gives it protection from predators, it may be difficult to determine the relative importance of host nutrition versus habitat value in selecting for host preference or specialization (Duffy and Hay 1991, 1994).

It is likely that the decreased predation risk associated with inhabiting a domicile constructed of *H. tuna* helps maintain this association (Fig. 6A–D). *Halimeda* species are among the least palatable of all upright seaweeds on coral reefs (see citations in Study organisms), and many organisms appear to associate with this well-defended genus as a means of avoiding predation (Hay 1997a). However, relative palatability of potential host plants alone does not adequately explain why the amphipod is limited to *H. tuna*. Several *Halimeda* congeners are also avoided by fishes and might thus provide equivalent protection from incidental predation by larger omnivores (Hay 1984, 1997a; Paul and Hay 1986). These co-occurring congeners also grow nocturnally and produce young, uncalcified and malleable tips that could be curled by the amphipod (Hay et al. 1988). Additionally, even though *Halimeda* species differ considerably in segment size, this may not fully explain the host specificity either. Of the three co-occurring congeners

surveyed in the Florida Keys, *H. tuna* had the largest segments, and domiciles constructed from *H. tuna* could easily encompass at least one large adult amphipod (Fig. 7). We sometimes found domiciles containing a pair of adults and numerous offspring. *H. goreaui* segments are shorter than the average adult *E. brasiliensis*, while the height of the largest *H. opuntia* segments equals the length of the amphipod. Thus, the full refuge value of domiciles may best be realized on *H. tuna*, because domiciles on this plant would be large enough to permit full enclosure of one or more amphipods, enabling them to minimize predation by both omnivorous and predaceous consumers. There are, however, other species of *Halimeda* in the Caribbean with segment size similar to, or larger than that of *H. tuna* (e.g., *H. discoidea*), yet these species show no evidence for the presence of *E. brasiliensis* domiciles (Tables 2, 3). Thus, neither relative palatability of the plant nor segment size alone can fully explain the specificity for *H. tuna*. Abundance, predictability of occurrence, and other factors may also be important in affecting this association.

There appears to be geographic variability in the association between the amphipod and *H. tuna*. In the western Atlantic, the species presently understood as *E. brasiliensis* extends from Cape Cod to Brazil, while *H. tuna* is limited to the Caribbean. In areas of non-sympatry, the amphipod does not specialize on any single alga. For example, at a North Carolina rocky subtidal jetty, the amphipod was common on five macroalgal species surveyed (two brown and three red algal species; Duffy 1989). Even in areas of sympatry, the association does not appear robust. Within the Caribbean, the amphipod is found on drifting rafts of algae, suggesting that there are Caribbean populations that do not specialize on *H. tuna* (J. Thomas, personal observation). Additionally, although both the amphipod and *H. tuna* are reported from the Pacific and Mediterranean, the Smithsonian herbarium specimens show no evidence of their association in these regions (Table 2). These observations raise the question of whether the Caribbean populations limited to *H. tuna* (1) are locally specialized due to ecological factors ("ecological specialization" sensu Fox and Morrow 1981), (2) have developed behavior unique to the species, or (3) represent an unrecognized cryptic species. Transplant experiments coupled with breeding and allozyme studies that compared Caribbean "habitat specialist" populations with both sympatric generalist populations and non-sympatric populations would help to elucidate the relative genetic and environmental contribution to the observed specialist behavior as well as the taxonomic state of the populations. A number of terrestrial and marine invertebrate species once thought to be singular were later identified as a group of multiple subspecies or full sibling species (Mayr 1970; Knowlton 1993). *E. brasiliensis* may turn out to be another of these organisms.

Amphipod impact on the host-plant *H. tuna*

Although not herbivorous, this habitat specialist decreases net growth of its host under field conditions (Fig. 4). However, our data do not demonstrate the mechanism by which these amphipods reduce segment accumulation in *H. tuna*. In principle, curling a segment decreases its surface area by up to 50%, which could decrease light capture, nutrient uptake, and thus photosynthesis and growth. However, there is some evidence that photosynthesis of *H. tuna* is rarely light limited at depths comparable to those in this study (Littler et al. 1988). Alternatively, if the host is nutrient limited, as has been suggested for other populations of *H. tuna* in the Caribbean (Littler et al. 1988), then amphipod excretions could act to increase growth rates by increasing nutrient availability to the plant (Taylor and Rees 1998).

Amphipods might indirectly decrease net production of new segments on *H. tuna* by increasing the susceptibility of the plant to herbivory by fishes. Amphipods are a higher source of protein relative to the surrounding plant tissue; thus, herbivorous fishes, which are generally nitrogen limited (Horn 1989), might prefer an infested over an uninfested plant. However, neither parrotfishes, surgeonfishes, nor both of these fish types grouped together demonstrated a significant preference for infested *H. tuna* plants (Fig. 5C). Surgeonfishes tended to bite infested plants more often, but calcification in *Halimeda* strongly deters consumers like surgeonfishes that have acid-mediated digestion (Schupp and Paul 1994), so it is unlikely that they are removing *Halimeda* tissue. Their feeding is more likely to be focused on the amphipods or on *Halimeda* epiphytes. Thus, direct herbivory by fishes appears to be an inadequate explanation for the decrease in net growth of infested *H. tuna* plants. In contrast, carnivorous fishes overwhelmingly preferred infested over non-infested *H. tuna* plants (Fig. 5B). Videos revealed that carnivorous fishes may incidentally bite and pull on terminal segments while attacking filter-feeding amphipods in their domiciles (M.E. Hay and E.E. Sotka, personal observation). Since terminal segments contain the plant meristem, it is possible that incidental bites by carnivorous fishes damage meristematic tissue and slow production of new segments.

Previous research on host-plant specialists that rarely, or never, consume host tissue has often demonstrated a positive or neutral effect of these animals on their host. For example, some ants that are habitat specialists on particular host plants have become classic examples of mutualism (Janzen 1966; reviewed in Bentley 1977). These host plants provide specialized shelters and extrafloral nectaries that attract the ants; in return ants defend the host from herbivores and competing plant species. Even herbivorous specialists that can feed on host tissues can function as mutualists for their hosts. As examples, a herbivorous limpet, chiton and crab that use coralline algae as refuges from predation benefit their hosts by preventing host overgrowth by epiphytes (Steneck 1982; Littler et al. 1995; Stachowicz and Hay

1996). To our knowledge, negative effects on the host of habitat specialists that do not consume host tissues have rarely, if ever, been demonstrated. Our study of the amphipod-*H. tuna* association demonstrates that plant specialists can negatively impact the growth of their host without consuming it. Although we only assessed effects of amphipods on host growth, growth should be a good predictor of fitness for *Halimeda* because plants in this genus reproduce by turning their entire cytoplasm into gametes, releasing these synchronously over a period of only a few minute, and then dying (Clifton 1997). Thus, any decrease in vegetative mass should lower gamete production.

Habitat specialists that do not consume host tissue may increase (e.g., the ants cited earlier), decrease (e.g., this study), or have no measurable effect upon host growth, survivorship, or fitness. Similarly, plant specialists that consume host tissue may increase (e.g., herbivorous limpets and chitons: Black 1976; Steneck 1982; Littler et al. 1995), decrease, or have no effect (see Caughley and Lawton 1981; Crawley 1983) on host fitness. These observations suggest that simplistic generalizations on the effects of plant-animal interactions may ignore a wider spectrum of potential outcomes.

Conclusion

The association between the seaweed *H. tuna* and the amphipod *E. brasiliensis* demonstrates that specialization on a plant for its habitat value alone is possible and that habitat specialists can negatively impact hosts without consuming them. To construct domiciles, Caribbean populations of this filter-feeding amphipod curl young, uncalcified, and chemically rich segments of *H. tuna*; they do not use other co-occurring algal congeners. Because the amphipod is a filter-feeder and does not consume the plant, nutritional quality should play no role in maintaining the specialization. Rather, by associating with this unpalatable seaweed, the amphipod reduces incidental predation by herbivorous fishes, and by constructing domiciles, the amphipod reduces predation risk due to carnivorous fishes. Of the *Halimeda* species that are common on forereefs of the Florida Keys, only *H. tuna* segments are large enough to completely enclose the amphipod, allowing the full refuge benefit of domicile construction to be realized. The presence of the amphipod decreases net growth of the host; however, the mechanism by which this occurs is uncertain.

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