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Feeding by coral reef mesograzers: algae or cyanobacteria?

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Abstract Marine studies on herbivory have addressed the role of algae as food and shelter for small consumers, but the potential of benthic cyanobacteria to play similar roles is largely unknown. Here, feeding preferences were measured for eight invertebrate consumers from Guam, offered four common macroalgae and two cyanobacteria. The survivorship of another consumer raised on either macroalgae or cyanobacteria was also assessed. From the choices offered, the sacoglossans *Elysia rufescens* and *E. ornata* consumed the green macroalga *Bryopsis pennata*. The crab *Menaethius monoceros* preferred the red alga *Acanthophora spicifera*. The amphipods *Parhyale hawaiiensis* and *Cymadusa imbroglia* consumed macroalgae and cyanobacteria in equivalent amounts, with *C. imbroglia* showing less selectivity among diets. In contrast to these patterns, in these assays the gastropods *Stylocheilus striatus*, *Haminoea cymbalum*, *H. ovalis*, and *Haminoea* sp. fed exclusively, or survived only, on cyanobacteria. Preferences for different cyanobacteria varied. Field surveys of cyanobacteria-associated species yielded 34 different invertebrate taxa and suggested different degrees of specificity in these associations. Tropical mesograzers exploit considerably different food resources, with some species adapted to consume cyanobacterial mats. Benthic cyanobacteria may play important roles as food and shelter for marine consumers and may indirectly influence local biodiversity through their associated fauna.

Keywords Cyanobacteria · Mesograzers · Marine herbivory · Food choice · Invertebrate epifauna

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Introduction

Benthic marine herbivores encounter a diversity of potential foods that vary in nutritional quality, structure, and chemical composition over spatial and temporal scales (Neighbors and Horn 1991; John et al. 1992; Paul 1992; Kaehler and Kennish 1996; Cruz-Rivera and Hay 2001, 2003; McClintock and Baker 2001). In some coral reefs, both eukaryotic macroalgae and large filamentous benthic cyanobacteria are important components of the benthos (Thacker et al. 2001; Thacker and Paul 2001). These benthic cyanobacteria form large mats that can occupy a significant portion of the available substrate and, thus, constitute an available resource for marine consumers. However, studies on herbivory have traditionally considered only the roles of eukaryotic algae as food and habitat for marine grazers (Paul et al. 2001). This is likely because community studies that consider cyanobacteria, particularly in freshwater systems, have focused mainly on explaining the factors controlling cyanobacterial blooms. Because cyanobacterial blooms have often been related to eutrophication, disturbance and anthropogenic habitat degradation (Paerl 1988; Dennison et al. 1999; Lapointe 1999; Oliver and Ganf 2000; but see Thacker and Paul 2001), the persistence of cyanobacteria in aquatic environments has been viewed as “abnormal” rather than as a normal component of the community.

In areas of intense grazing, such as coral reefs, algae often persist by using structural or chemical deterrents that reduce attack from large and abundant herbivores like urchins and fishes (Hay and Fenical 1988; Duffy and Hay 1990; Hay and Steinberg 1992; Hay 1997; Paul et al. 2001). These algae are colonized by smaller herbivores (mesograzers) that may gain “enemy-free space” by associating with defended hosts (Stoner 1985; Hay 1992; Hay and Steinberg 1992; Duffy and Hay 1994; Paul et al. 2001). Although some mesograzers feed primarily on epiphytes (Brawley 1992; Stachowicz and Hay 1996; Mancinelli and Rossi 2001) or on palatable algae that

may not constitute a safe refuge (Taylor and Steinberg 2005), a variety of these small herbivores are resistant to chemical and structural defenses of host algae (e.g., Duffy and Hay 1994; Littler et al. 1995) and feed directly on their host (Hay 1992; Hay and Steinberg 1992; Paul et al. 2001).

More recent studies suggest that some benthic tropical cyanobacteria might play similar ecological roles as those of eukaryotic macroalgae by serving as food and shelter for marine mesograzers (Paul et al. 2001; Cruz-Rivera and Paul 2002). For example, the small sea hare *Stylocheilus striatus* (= *longicauda*, Rudman 1999; Yonow 2000) (Gastropoda: Opisthobranchia) inhabits cyanobacterial mats, feeds preferentially on cyanobacteria in the genus *Lyngbya* when presented simultaneously with macroalgae and cyanobacteria, and will grow better on *Lyngbya majuscula* (= *Microcoleus lyngbyaceus* in Paul and Pennings 1991; Cruz-Rivera and Paul 2002) than on macroalgae. *Lyngbya majuscula* mats are commonly 30–50 cm high or more (E. Cruz-Rivera, personal observation), thus providing complex three-dimensional structures for small epifauna to colonize. While chemical defenses of *Lyngbya* will deter feeding by macrograzers such as fishes and the urchin *Echinometra mathaei*, feeding by *S. striatus* often is not deterred, and sometimes is stimulated, by cyanobacterial secondary metabolites and extracts (Nagle et al. 1998; Cruz-Rivera and Paul 2002; Capper et al. 2006). However, the feeding preference of *Stylocheilus* for cyanobacteria is rare among sea hares, which are largely macroalgal grazers (Carefoot 1987; Pennings et al. 1993; Rogers et al. 1995). Other studies have suggested a preference for cyanobacteria by certain mesograzers (Renaud 1976; D'Antonio 1985; Mukai and Iijima 1995; Yamamuro 1999; Capper et al. 2005) but these patterns have not been assessed adequately.

If benthic cyanobacteria play important roles parallel to those of eukaryotic algae on coral reefs, it is necessary to demonstrate that they are utilized as food and shelter by diverse organisms. While differences in the utilization of cyanobacteria between macrograzers and *Stylocheilus* have been demonstrated (Cruz-Rivera and Paul 2002), no studies have compared the relative use of cyanobacteria among different mesograzers. Recent surveys found 43 invertebrate species associated with seven cyanobacteria from Guam and Palau (Cruz-Rivera and Paul 2002), suggesting a potential for broader utilization of benthic cyanobacteria by small tropical consumers. However, most of these organisms could be transient residents of cyanobacterial mats that do not graze on cyanobacteria. In this study, patterns of food utilization for nine tropical mesograzers from Guam when exposed to cyanobacteria versus eukaryotic macroalgae are compared. The following questions were asked: (1) Are cyanobacteria readily consumed by tropical mesograzers? If so, (2) are certain consumers specialized on cyanobacteria? Experimental observations are complemented with epifaunal species records from various cyanobacterial collections over the span of 3 years.

These records provide additional information on patterns of host use for various mesograzers.

Materials and methods

Animals, macroalgae, and cyanobacteria were collected from reef flats at Pago Bay and Piti Bomb Holes in Guam, Mariana Islands (13°30'N, 144°45'E). Six of the most abundant algae and cyanobacteria at these two sites were collected. These species, and their most frequently associated mesograzers, were used in feeding experiments. Field observations showed that some of the grazers (some cephalaspideans) were more active at night, so both day and night collections were conducted by snorkeling around reef flats. The green alga *Bryopsis pennata*, the brown algae *Padina tenuis* and *Sargassum cristaefolium*, the red alga *Acanthophora spicifera*, and the cyanobacteria *L. majuscula* and *Tolypothrix* sp. were sealed inside plastic bags and brought to the lab where they were sorted by hand to collect associated epifauna. Animals from these collections were sorted to species and kept in separate tubs with bubbled air and a mixture of algae and cyanobacteria for food before the start of the assays. One of the mesograzers, *Haminoea* sp., was found in very low abundance in the field, but populations of this species recruited into flow-through tanks at the University of Guam Marine Laboratory. The tanks received unfiltered water from the adjacent Pago Bay and a variety of algae and invertebrates readily and continuously recruited. For this species, both field and tank-collected individuals were used (see below).

Using multiple-choice assays, the feeding preferences of two sacoglossan gastropods (*Elysia rufescens* and *E. ornata*), one majid crab (*Menaethius monoceros*), two gammaridean amphipods (*Parhyale hawaiiensis* and *Cymadusa imbroglia*), one sea hare (*S. striatus*—previously *S. longicauda*, Rudman 1999; Yonow 2000), and two cephalaspidean snails (*Haminoea cymbalum* and *H. ovalis*) found in collections were studied. While some of these animal species (e.g., *Elysia* spp. and *Stylocheilus*) might attain larger sizes than what are typically considered for mesograzers (Brawley 1992), animals collected in the field were considerably smaller than their maximum size (E. Cruz-Rivera, personal observation). Brawley (1992) has pointed out that many macrograzers pass through a mesograzers stage. For the purposes of this work, experimental animals were in the general size range of typical mesograzers (0.5–2.0 cm).

Fresh macroalgae and cyanobacteria were collected before the beginning of the multiple-choice experiments. Epiphyte-free pieces of all algae and cyanobacteria were manually cleaned of mobile epifauna and sediment, spun in a salad spinner (i.e., centrifuge) to eliminate excess water, weighed, and placed in individual circular plastic dishes (16 cm diameter, 6 cm height) with fresh seawater. The amounts of each food used per replicate varied (50 mg–2 g) depending on the size of the mesograzers tested and the density of the alga or cyanobacterium, but

animals were always fed in excess of what they could consume of each diet during the experiments. Despite the weight differences related to food densities, each replicate received algal and cyanobacterial portions of similar size to ensure that consumers had similar likelihood of finding all foods offered.

Replicate experimental dishes ($n = 4\text{--}12$) received 1–5 individuals of each grazer species depending on their size and availability. When noticeable size differences between conspecifics were noted, equalizing the average mass for that consumer in the replicates was attempted. Thus, 1 *E. rufescens*, *E. ornata*, or *S. striatus*; 1–3 *H. cymbalum*, *H. ovalis*, or *M. monoceros*; and 3–5 *C. imbroglia* per replicate were used. For *P. hawaiiensis*, ten individuals per replicate were used. This was because the average size of these amphipods was small and because a portion of individuals would invariably form precopulatory pairs. Mate guarding could influence feeding, so in this way the number of unpaired individuals that would feed normally within the replicates was maximized. Interspersed among the replicates receiving mesograzers, an equal number of dishes received algae and cyanobacteria, but no animals, and served as controls for autogenic changes in mass of the treatment foods (Peterson and Renaud 1989). Animals were allowed to feed for a maximum of 2 days. Upon termination of the experiments, algae and cyanobacteria were spun in a salad spinner and weighed. Amount eaten of each species was calculated using the formula $[T_i(C_f/C_i)] - T_f$, where T_i and T_f are the initial and final masses of the algae or cyanobacteria in the containers with mesograzers and C_i and C_f the initial and final masses of the same species in the control dishes. Data were analyzed using the non-parametric Friedman's test and corresponding post hoc analyses (Conover 1999), which allow for comparisons among multiple non-independent treatments based on ranks. For *E. ornata* there were fewer replicates than the number of treatments, which negated the analysis of data with these tests. These data are presented for comparison purposes.

In addition to the consumer species mentioned above, a third undescribed haminoid cephalaspidean species (*Haminoea* sp.) was also studied. Preliminary assays showed that the amount eaten by this small cephalaspidean was too small to be reliably quantified with the methods explained previously. Instead, the survivorship and growth of this species were measured when cultured on monospecific diets of algae or cyanobacteria. The undescribed status of this cephalaspidean was confirmed by C. Carlson and corresponds to *Haminoea* c86 in Carlson and Hoff (2003). Although few individuals could be obtained from algal collections (see above), animals that recruited into outdoor flow-through tanks could be used. Animals were gently blotted dry on absorbent paper to reduce excess water, weighed, and placed individually in small 260 ml plastic cups (filled approximately to the 250 ml mark with seawater). Animals ($n = 11$, for a total of 77 individuals) were

randomly assigned to one of seven treatments: a starvation control, the algae *Ulva clathrata* (green), *P. tenuis* (brown), and *A. spicifera* (red), and the cyanobacteria *Symploca* sp., *L. majuscula*, and *Tolypothrix* sp. Treatments and starvation controls were interspersed to account for microspatial differences in light and temperature.

Shell size of these cephalaspideans did not exceed 5 mm and thus, only small pieces of algae or cyanobacteria (ca. 2 cm) were needed to provide food in excess of feeding rates. This was important as larger or denser cyanobacterial mats would have turned anoxic at night, potentially inducing mortality in those treatments. Food and water in the cups were renewed every 2–3 days. As with previous assays, cups were kept from direct sunlight at ambient temperature and followed natural day:night cycles. With these methods, any substantial degradation of the foods and the accumulation of exudates that could foul the water in the cups were minimized. Number of survivors was recorded daily. The experiment was terminated after 16 days, when surviving individuals were weighed and mass gain was calculated. Survivorship data for this experiment were analyzed using a contingency table analysis on the numbers of individuals alive in each treatment at day 16.

As part of the ongoing work, cyanobacteria-associated fauna in various collections from Guam between 1998 and 2001 was documented. Although faunal surveys from specific cyanobacterial species from Guam and Palau have been documented previously (Cruz-Rivera and Paul 2002), the observations herein do not include those data. The purpose is to provide information on the specificity or generality of cyanobacterial host use for both the species studied in these experiments and other species that have been encountered. Because cyanobacterial species varied in abundance, and sampling was not standardized to account for this, only qualitative observations on the abundance of these organisms are provided. Observations come from various collections (ca. 30 collections ranging approximately from 20 to 300 g) of 13 cyanobacterial species over the course of 3 years. The focus was on mesoconsumers and did not account for cyanobacterial microfauna such as very small nematodes, harpacticoid copepods, and ostracods that were often abundant. Organisms are not grouped by taxonomic affinity at any particular level and are qualified as abundant (found consistently in large numbers), common (found consistently in low numbers), rare (uncommonly found even if occasionally occurring in high numbers), and very rare (uncommonly encountered and in very low numbers). This information should be treated as species records rather than absolute measurements of species diversity in cyanobacterial mats. The cumulative number of taxa in each of 14 cyanobacteria from Guam is presented as the total number of taxa encountered and is not standardized by cyanobacterial mass. Thus, these descriptive data are not analyzed statistically.

Results

Naturally, feeding experiments only present a limited amount of all potential foods found in nature, but these experiments targeted algal and cyanobacterial species that are common and abundant in a variety of environments in Guam. Feeding preferences on eukaryotic macroalgae versus cyanobacteria differed markedly among mesograzers during the assays (Fig. 1). From the choices offered, the sacoglossans *E. rufescens* and *E. ornata* fed exclusively on *B. pennata* ($P = 0.007$ for *E. rufescens*). Although the low replication precluded statistical analysis of the data from *E. ornata*, patterns of feeding were strong and consistent for all four animals tested.

The three crustacean mesograzers, the majid crab *M. monoceros* and the amphipods *P. hawaiiensis* and *C. imbroglio*, demonstrated a more generalized diet than the sacoglossans. The crab consumed the red alga *A. spicifera* significantly more than any other food ($P = 0.002$), but consumed the other five diets in similar amounts, and consumption of these diets was statistically different than zero. *Parhyale hawaiiensis* consumed the algae *B. pennata*, *P. tenuis*, and the cyanobacterium *L. majuscula* in equivalent amounts and preferred these three diets significantly ($P < 0.001$) to other foods. Although on average *C. imbroglio* consumed more of the green alga *Bryopsis* and the cyanobacterium *Tolypothrix* than all other diets, variance in consumption for this amphipod was high among treatment diets. For this species, there were no statistical differences in preference among macroalgae or cyanobacteria.

The sea hare *S. striatus* and the cephalaspideans *H. cymbalum* and *H. ovalis* consumed only cyanobacteria, but differed in their relative preferences for the cyanobacteria offered. While *S. striatus* fed on the cyanobacterium *L. majuscula* ($P < 0.001$), *H. cymbalum* fed on *Tolypothrix* ($P < 0.001$). *Haminoea ovalis* fed similarly on both these cyanobacteria but did not consume any of the macroalgae offered ($P = 0.009$).

Because it was not possible to quantify food choice, survivorship and growth of the small cephalaspidean *Haminoea* sp. on six monospecific diets and a starvation control (Fig. 2) were measured. After 16 days, survivorship of individuals feeding on *L. majuscula* was significantly higher ($P < 0.001$) than on all other treatments. In fact, only one animal in the *Tolypothrix* treatment was alive at the end of the experiment and no survivors were observed on any of the other five treatments. Animals in the *Acanthophora*, *Padina*, *Enteromorpha*, and *Symploca* treatments died at similar rates as those in the starvation control, while death rates in the *Tolypothrix* treatment were lower (Fig. 2). Animals cultured on *L. majuscula* showed a 17% increase in mass during the experiment. Because this was the only treatment producing a large number of survivors, growth rates among treatments could not be compared.

Cyanobacterial collections between 1998 and 2001 yielded 34 mobile invertebrate species (Fig. 3, Table 1).

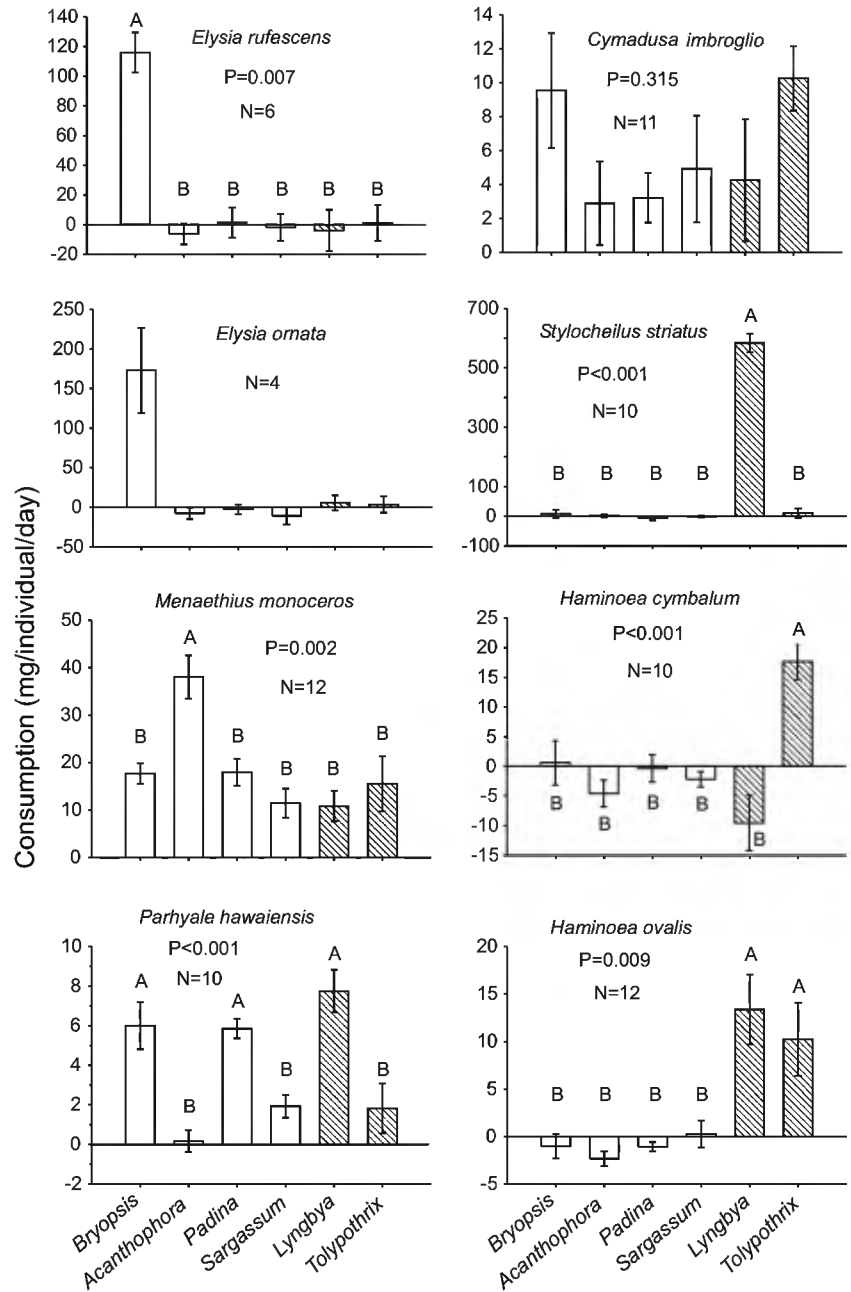
In general, the cyanobacterium *L. majuscula* contained the most diverse epifauna, whereas congeneric species such as *L. bouillonii* and others, as well as various *Symploca* spp., only yielded 1–2 animal taxa (Fig. 3). However, it should be noted that, because of its abundance, collections of *L. majuscula* tended to be larger over the years than for other cyanobacteria. Nevertheless, a comparison between *L. majuscula* and *L. bouillonii*, both of which were collected extensively during these studies, might be more equitable and suggests a strong difference between the number of taxa supported (Fig. 3). Records also suggest different degrees of specialization in the use of cyanobacteria by some of the collected organisms. For example, the sea hare *S. striatus*, the amphipod *C. imbroglio*, the cephalaspidean *Diniatys dentifera* and the tanaid *Leptocheilia dubia* were found in collections of 5–9 different cyanobacteria, even if they were not similarly abundant in all of them (Table 1). In contrast, cyanobacteria-associated shrimps and crabs, as well as some of the less abundant cephalaspideans, were found only in 1–3 cyanobacterial hosts even when the animals were abundant in the field (e.g., *Alpheus frontalis*, Table 1). Surprisingly, no noticeable polychaetes were found during these surveys, although polychaetes have been found associated with cyanobacteria in both Guam and Palau during previous studies (Cruz-Rivera and Paul 2002).

Discussion

Experiments showed marked differences in the use of macroalgae versus cyanobacteria as food for the nine mesograzers tested. Of these consumers, three showed significant preferences for at least one macroalga, two preferred some macroalgae and cyanobacteria in equivalent amounts, and four fed on, or survived exclusively on, cyanobacteria (Figs. 1, 2). These interspecific differences in food preference suggest different degrees of trophic specialization among these consumers which are often grouped together in functional groups or feeding guilds due to the lack of information on their feeding behavior (Cruz-Rivera and Hay 2000a, b). Larger consumers like the crab *Grapsus albolineatus* are known to graze on cyanobacteria during certain times of the year (Kennish et al. 1996) and some gastropods will graze on cyanobacterial films (Mak and Williams 1999). However, in these examples, the size of the grazers relative to their foods does not allow the potential to exploit cyanobacteria as shelter.

From the foods offered during the experiments, the two sacoglossans, *E. rufescens* and *E. ornata*, fed exclusively on the green alga *B. pennata*. This is consistent with previous works showing that most species of *Elysia* are consumers of green macroalgae occasionally having very restricted diets (Williams and Walker 1999; Trowbridge 1992; Hirose et al. 2003). Some *Elysia* species have also been reported to sequester functional chloroplasts (Williams and Walker 1999) and the species

Fig. 1 Feeding preferences of eight mesograzers on macroalgae (*open bars*) and cyanobacteria (*hatched bars*) from Guam offered simultaneously. Bars represent means (± 1 SE). Analyses are by Friedman's tests. *Same letters above bars* indicate statistically equivalent means after post hoc tests, when necessary. *Negative numbers* indicate mass gain by the algae in the presence of the mesograzers. Data from *Elysia ornata* were not analyzed due to the low replication (see [Materials and methods](#))



studied here sequester defensive secondary metabolites from *Bryopsis* which function as acquired defenses against predators (Hamann and Scheuer 1993; Hamann et al. 1996; Horgen et al. 2000; Becerro et al. 2001).

In contrast to this more specialized tendency, the small spider crab (Majidae) *M. monoceros* and the amphipods *P. hawaiiensis* and *C. imbroglia* showed a more generalized diet that included macroalgae and cyanobacteria to different degrees. *Menaethius* showed a strong preference for the red alga *A. spicifera* which was a low preference food for all other mesograzers (Fig. 1). However, individuals in assays also consumed an average of 10–20 mg of all other algae and cyanobacteria offered, roughly 25–50% of the amount eaten from their

preferred food. This pattern could arise if the crabs systematically sampled all foods offered when encountered or mixed foods in different amounts to balance dietary requirements or dilute noxious metabolites (Freeland and Janzen 1974; Pennings et al. 1993). During collections, *Menaethius* individuals were found on *Acanthophora* but were most abundant on *S. cristaeifolium*. In Guam, this crab is also found on a variety of cyanobacteria (Table 1) and macroalgae (E. Cruz-Rivera, personal observation) including chemically defended algae such as *Caulerpa* spp. and *Portieria hornemanii* (Ginsburg and Paul 2001; Paul et al. 2001). *Menaethius* is highly variable in color and often matches its host alga in a fashion similar to that

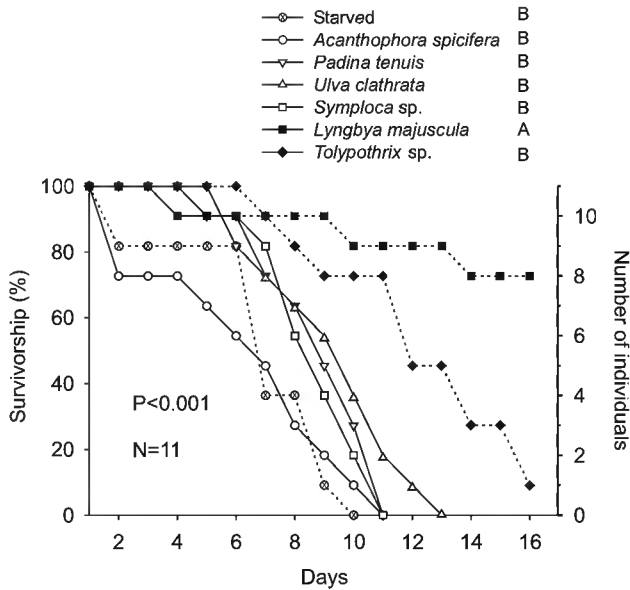


Fig. 2 Survivorship of the cephalaspidean *Haminoea* sp. on macroalgae, cyanobacteria, and a starvation control treatment. Single individuals were confined to either one of the diets or a control containing no food (see [Materials and methods](#)). Chi-square analyses were used for main effects and significant groupings. Same letters to the right of the legend represent treatment producing statistically equivalent survivorship

described for other majid crabs that sequester algal pigments and become cryptic on their hosts (Wilson 1987; Woods and McLay 1996). These patterns suggest that this crab is a relatively generalized grazer with the potential to exploit very different resources.

For the two amphipods tested, consumption of macroalgae was matched by consumption of at least one

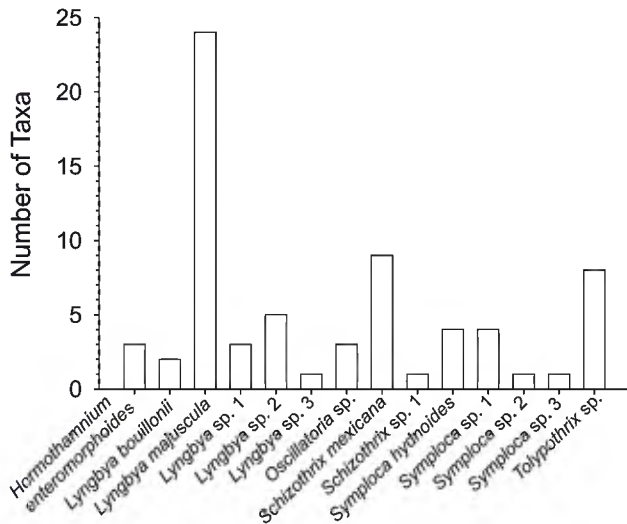


Fig. 3 Distribution of epifaunal taxa in 14 cyanobacterial species collected in Guam between 1998 and 2001. Because times of collections and amounts of each cyanobacterium varied, data are not analyzed. Bars represent total taxa found and numbers are not standardized by cyanobacterial mass (see Table 1)

cyanobacterium tested. However, *P. hawaiiensis* preferred *Bryopsis*, *Padina*, and *Lyngbya* in similar amounts and above other foods, whereas *C. imbroglia* did not show a statistical preference for any diet (although average consumption was higher on *Bryopsis* and *Tolypothrix*). *Parhyale* appears to have a broad distribution and diet, feeding on algae and detritus (Myers 1985; Poovachiranon et al. 1986; Barnard and Karaman 1991; Serejo 1999; Pereira et al. 2000). Interestingly, *P. hawaiiensis* was never observed in any of the cyanobacterial collections, although it was found on macroalgae from Pago Bay.

Extensive search in various databases (e.g., Web of Science, ASFA) suggests that this is the first study on the natural diet of *C. imbroglia*. Feeding by this amphipod can be deterred by certain *L. majuscula* extracts and metabolites when placed in artificial diets (Capper et al. 2006; Cruz-Rivera and Paul, unpublished). Other *Cymadusa* species are found on algae and seagrasses and readily feed on diverse macroalgae; however, their use of cyanobacteria has not been tested (Brawley 1992; Hay et al. 1994; Cruz-Rivera and Hay 2000b). A few studies have observed cyanobacterial grazing by benthic marine amphipods with contrasting results (D’Antonio 1985). D’Antonio (1985), Mukai and Iijima (1995), and Yamamuro (1999) reported that species of *Ampithoe*, a genus in the same family as *Cymadusa*, fed on cyanobacterial epiphytes. However, these studies either did not provide amphipods with various potential foods to choose from or the experimental design makes data difficult to interpret.

The sea hare *S. striatus* and the cephalaspideans *H. cymbalum*, *H. ovalis*, and *Haminoea* sp. only consumed cyanobacteria in the assays (Figs. 1, 2), suggesting that some tropical mesograzers have evolved to consume primarily benthic cyanobacteria instead of algae. *Stylocheilus* consumed *L. majuscula*, the same cyanobacterium that caused high survivorship in *Haminoea* sp. (Figs. 1, 2). In contrast *H. cymbalum* fed only on *Tolypothrix*. In fact, *Lyngbya* offered to *H. cymbalum* increased noticeably in mass during these experiments (note negative value in Fig. 1). The cephalaspidean *H. ovalis* was less selective for different cyanobacteria and consumed equivalent amounts of *Lyngbya* and *Tolypothrix*, but did not feed on macroalgae. Although these four consumers appear adapted to feed primarily on cyanobacteria, they varied in their selectivity for different cyanobacterial species. It is possible that some cyanobacterial consumers have a degree of trophic specialization similar to that found in certain mesograzers groups that feed on macroalgae (Hay 1992; Williams and Walker 1999). For example, in Micronesia, the abundant snapping shrimp *A. frontalis* only occurs on the cyanobacterium *L. bouillonii* (Table 1; Cruz-Rivera and Paul 2002), which the shrimp uses as food and to build a tube in which it lives (Banner and Banner 1982; Cruz-Rivera and Paul, unpublished).

Stylocheilus strongly preferred *L. majuscula* in assays, and previous studies showed this sea hare attains high

Table 1 Mobile epifauna associated with cyanobacteria from Guam

Taxa	Cyanobacteria	Number of hosts	Locations	Abundance
Gastropods				
Anaspidea: "sea hares"				
<i>Stylocheilus striatus</i>	<i>Hormothamnium enteromorphaeoides</i> , <i>Lyngbya majuscula</i> , <i>L. bouillonii</i> , <i>Lyngbya</i> sp. 1, <i>Oscillatoria</i> sp., <i>Schizothrix mexicana</i> , <i>Symphloca</i> , <i>hydnoidea</i> , <i>Symphloca</i> sp. 1, <i>Tolypothrix</i> sp.	9	Apaca Point, Asan Beach, Bile Bay, Cocos Lagoon, Fingers Reef, Pago Bay, Piti Bomb Holes, Piti Channel, Tanguisson	Abundant on <i>L. majuscula</i> , common to very rare on other species
Cephalaspidacea: "bubble snails and allies"				
<i>Aglaia orientalis</i>	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Very rare
<i>Diniatys dentifer</i>	<i>Hormothamnium enteromorphaeoides</i> , <i>Lyngbya majuscula</i> , <i>Lyngbya</i> sp. 2, <i>Oscillatoria</i> sp., <i>Schizothrix mexicana</i> , <i>Symphloca</i> sp. 1, <i>Tolypothrix</i> sp.	7	Apaca Point, Apra Harbor, Asan Beach, Bile Bay, Cocos Lagoon, Pago Bay, Piti Bomb Holes, Piti Channel, Tanguisson	Abundant
<i>Diniatys dubia</i>	<i>Lyngbya</i> sp. 2	1	Apra Harbor	Rare
<i>Diniatys monodonta</i>	<i>Lyngbya majuscula</i> , <i>Lyngbya</i> sp. 2	2	Apra Harbor, Piti Bomb Holes	Very rare
<i>Hamiinoa nigropunctatum</i>	<i>Lyngbya majuscula</i> , <i>Tolypothrix</i> sp.	2	Piti Bomb Holes, Tanguisson	Common
<i>Hamiinoa ovalis</i>	<i>Hormothamnium enteromorphaeoides</i> , <i>Lyngbya majuscula</i> , <i>Schizothrix</i> <i>mexicana</i> , <i>Tolypothrix</i> sp.	4	Asan Beach, Bile Bay, Cocos Lagoon, Piti Bomb Holes	Common
<i>Liloa curta</i>	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Very rare
<i>Metaruncina setoensis</i>	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes, Cocos Lagoon	Abundant
<i>Mnesitia villica</i>	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes, Cocos Lagoon	Common
<i>Phanerophthalmus smaragdinus</i>	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Very rare
Hamiinoeid sp. 1 (C7)	<i>Lyngbya majuscula</i> , <i>Oscillatoria</i> sp., <i>Symphloca</i> sp. 1	3	Piti Bomb Holes	Common
Hamiinoeid sp. 2 (C46)	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Rare
Hamiinoeid sp. 3 (C24)	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Very rare
Echinoderms				
Gnathostomata: "sand dollars and sea biscuits"				
Unidentified	<i>Lyngbya</i> sp. 2	1	Apra Harbor	Common
Ophiura: "brittle stars"				
Unidentified small ophiuroid	<i>Lyngbya majuscula</i> , <i>Lyngbya</i> sp. 2	2	Apra Harbor, Piti Bomb Holes	Rare
Crustaceans				
Amphipoda: "(gammaridean) amphipods"				
<i>Cymadusa imbroglia</i>	<i>Lyngbya majuscula</i> , <i>Lyngbya</i> sp. 3, <i>Schizothrix mexicana</i> , <i>Symphloca</i> <i>hydnoidea</i> , <i>Tolypothrix</i> sp.	5	Bile Bay, Cocos Lagoon, Pago Bay, Piti Bomb Holes, Piti Channel, Tanguisson, Tumon Bay	Abundant to common
Gammarid sp. 1	<i>Lyngbya majuscula</i>	1	Cocos Lagoon	Very rare
Isopoda: "isopods"	<i>Schizothrix mexicana</i>	1	Piti Bomb Holes	Very rare
<i>Carpas</i> cf. <i>algicola</i>				
Tanaidacea: "tanaids"	<i>Lyngbya majuscula</i> , <i>Tolypothrix</i> sp., <i>Symphloca hydnoidea</i> , <i>Symphloca</i> sp. 1, <i>Schizothrix mexicana</i>	5	Bile Bay, Cocos Lagoon, Pago Bay, Piti Bomb Holes, Tanguisson	Abundant
<i>Leptocheila</i> cf. <i>dubia</i>	<i>Schizothrix mexicana</i>	1	Piti Bomb Holes	Common

Table 1 (Contd.)

Taxa	Cyanobacteria	Number of hosts	Locations	Abundance
Cumacea				
<i>Namastacus</i> sp.	<i>Schizothrix mexicana</i>	1	Piti Bomb Holes	Rare
Decapoda				
Dromiidae: "sponge crabs"				
Unidentified dromiid	<i>Schizothrix</i> sp.	1	Piti Bomb Holes	Very rare
Majidae: "decorator crabs"				
<i>Achaetus laeviculus</i>	<i>Symploca</i> sp. 3	1	Tanguisson	Very rare
<i>Menaethius monoceros</i>	<i>Lyngbya majuscula</i> , <i>Schizothrix mexicana</i> , <i>Tolypothrix</i> sp.	3	Cocos Lagoon, Piti Bomb Holes	Common
<i>Pseudomicippe eldredgei</i>	<i>Lyngbya</i> sp. 1, <i>Symploca hydrooides</i>	3	Fingers Reef, Pago Bay, Tanguisson	Rare
Portunidae: "swimming crabs"				
<i>Thalamita corrugata</i>	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Common
<i>Thalamita integra</i>	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Common
<i>Thalamita miniscula</i>	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Common
Alpheidae: "snapping shrimp"				
<i>Alpheus frontalis</i>	<i>Lyngbya bouillonii</i>	1	Cocos Lagoon, Fingers Reef, Hospital Point, Piti Bomb Holes	Abundant
<i>Alpheus</i> sp. 2	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes	Rare
<i>Alpheus</i> sp. 3	<i>Lyngbya</i> sp. 1	1	Pago Bay	Very rare
<i>Alpheus</i> sp. 4	<i>Lyngbya</i> sp. 2	1	Apra Harbor	Common
Worms				
Nematoda: "roundworms"				
Unidentified large nematode	<i>Lyngbya majuscula</i> , <i>Tolypothrix</i> sp.	2	Cocos Lagoon, Piti Bomb Holes	Common
Nemertea: "ribbon worms"				
Banded nemertean	<i>Lyngbya majuscula</i>	1	Piti Bomb Holes, Cocos Lagoon	Abundant

Abundance is provided as a qualitative assessment (see [Materials and methods](#)) based on collections from 1998 to 2001. Codes in parentheses correspond to Carlson and Hoff (2003). Number of hosts (third column) states the number of cyanobacterial species where the taxon was recorded

growth on monospecific diets of this cyanobacterium (*M. lyngbyaceus* in Paul and Pennings 1991). However, *Stylocheilus* associates with other cyanobacteria and will readily consume other species of *Lyngbya* (Table 1; Cruz-Rivera and Paul 2002). *Stylocheilus* is not deterred by certain cyanobacterial metabolites that deter feeding in larger consumers (Nagle et al. 1998; Cruz-Rivera and Paul 2002; Capper et al. 2006), which parallels patterns found for various macroalgal mesograzers that specialize on chemically defended macroalgae (Hay 1992; Hay and Steinberg 1992; Paul et al. 2001; Cruz-Rivera and Paul 2002). But despite the apparent tolerance for cyanobacterial compounds, higher concentrations of cyanobacterial metabolites will deter *Stylocheilus* (Pennings and Paul 1993; Nagle et al. 1998). Pennings and Paul (1993) suggested that the broad dispersal of *Stylocheilus* during its planktonic phase precluded local adaptation to the metabolite concentrations in *Lyngbya* populations. It is possible that the unpredictability of cyanobacterial patches (e.g., Thacker et al. 2001; Thacker and Paul 2001) may also select against this local adaptation. In this sense, the sea hare will benefit from associating with cyanobacteria of lower preference until the preferred host becomes available. This could explain why *Stylocheilus* was found in at least nine different cyanobacterial hosts (Table 1), including species that support little growth for this sea hare (Cruz-Rivera and Paul, unpublished).

It is interesting to note that all other cyanobacterial grazers in this study are haminoidean cephalaspideans ("bubble snails"). In fact, cephalaspideans have consistently been the most diverse group associated with cyanobacterial collections (Table 1). It is possible that cyanobacterial grazing is widely spread in this group. Under the microscope, other species such as *H. nigropunctatus* and *D. dentifer* have been observed grazing on cyanobacterial filaments on various occasions (E. Cruz-Rivera, unpublished), but feeding has never been quantified (but see Capper et al. 2005, 2006). The fact that the species shown here to feed on cyanobacteria (and those observed to do so) are closely related suggests this behavior could be restricted to particular phylogenetic lineages within the Cephalaspidea.

Studies on mesograzers or herbivory in general have seldom considered coral reef cyanobacteria as a potentially important food resource (Paul et al. 2001; Cruz-Rivera and Paul 2002), probably because cyanobacteria are mostly noted during periods of blooms and regarded as indicators of disturbance and poor reef health. Some benthic marine cyanobacteria can form extensive blooms that can potentially have detrimental effects on benthic communities (Nagle and Paul 1998; Dennison et al. 1999; Thacker et al. 2001; Thacker and Paul 2001; Paul et al. 2005), and certain marine cyanobacterial compounds can also cause respiratory and skin problems in humans, constituting a health hazard when benthic cyanobacteria containing the harmful compounds bloom (Moore 1984; Dennison et al. 1999). Cyanobacteria can also be pathogenic to

corals (e.g., Rützler and Santavy 1983; Feingold 1988). As has been the case for freshwater systems (Paerl 1988; Perona et al. 1998; Oliver and Ganf 2000), cyanobacteria in marine systems have been treated as indicators of eutrophication (Dennison et al. 1999; Lapointe 1999). However, in Guam, benthic cyanobacteria are typical members of the benthic community, occur in densities similar to those of other benthic organisms, and follow similar population dynamics compared to other sessile organisms (Thacker et al. 2001; Thacker and Paul 2001). Furthermore, a variety of invertebrates associate with these benthic cyanobacteria (Cruz-Rivera and Paul 2002; Fig. 3, Table 1). This study demonstrates that some tropical benthic cyanobacteria are preferred foods for different specialized consumers and suggests that a diverse fauna may depend on cyanobacterial mats. Although mesograzers are often grouped within the same feeding guild, the differential use of algae and cyanobacteria by these consumers argues for a higher degree of complexity in mesograzers resource utilization. The differential distribution of benthic algae or cyanobacteria will likely indirectly affect benthic biodiversity by influencing the populations of particular mesograzers groups.

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