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Functional Significance of Decorating and Associated Behaviors in the Crab *Microphrys bicornutus* (Decapoda, Brachyura)

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Abstract

Organisms employ varying strategies to procure resources and defend themselves from competitors and potential predators. Decorating behavior, or attaching biotic and abiotic materials to the body, by majid crabs can potentially assist in this regard and may be influenced by factors such as algal substrate composition and social interactions among the crabs. To determine these potential functions and factors we created a baseline catalog of behaviors (ethogram) exhibited by the decorating crab *Microphrys bicornutus*. Decorating by this crab involved a complex set of behaviors that begins when a crab approaches an algal substrate, removes, then manipulates pieces resulting in the attachment of algae to specialized hooked setae on the exoskeleton of its body. In general, once decorated, the crab remained motionless on the substrate for considerable periods of time compared to other behavioral acts. In addition to the decorating behaviors exhibited when solitary, crabs were involved in limited agonistic behaviors during encounters with conspecifics. Specifically, crabs showed aggressive behaviors including active strikes and displays that apparently served as warning to conspecifics. Crabs also showed a concomitant decrease in motility (when not actively engaged with another individual) during these conspecific encounters. Such behaviors may help crabs maintain dispersed distributions around algal substrate sources thereby decreasing intraspecific encounters. Overall, data from these trials suggest that *Microphrys bicornutus* shows a generalist tactic and uses algae based on abundance rather than preference for an algal species. Decorating by these crabs, and others, provide excellent opportunities to explore community-level interactions in marine ecosystems.

Keywords: Camouflage, Decorating behavior, Decorator crab, majid crab crab

Introduction

Basic requirements for organisms are to procure resources and defend themselves from competitors and potential predators. One strategy used by some animal species is to attach materials from their environment to their body surface, sometimes facilitated by specialized morphological structures. This behavior has been called many things (e.g., covering, ornamenting, masking, hatting, carrying, shield-carrying, or trash-carrying), but is most referred to as decorating [1]. Decorating occurs in 25% of animal phyla and is common in at least nine families of brachyuran crustaceans; it is especially common in the Superfamily Majoidea [2].

Decorating is a multifaceted behavior that generally begins by a crab selecting a piece of material of appropriate size from its surrounding [3]. One of the chelae then transfers the decorating material to the area near the front of the crab where the maxillae (or mouthparts) chew the material to the appropriate size and shape [4,5].

Maxillary glands (associated with the mouthparts) might also assist the process by producing a glue-like substance to adhere the material onto the crab's carapace [6,7]. However, studies that involved the removal of these glands have shown that they primarily serve a digestive purpose, and that crabs are still capable of decorating when the glands have been removed [8-10]. Once materials have been chewed to an appropriate shape and size, they are ready for attachment. The crab takes the material from its mouthparts using one of the chelae and rubs it against the area of the carapace covered with hooked setae until the material is securely attached (i.e., the rigid hooks pierce into the material similar to Velcro) [11-13]. Hooked setae are unique to the superfamily Majoidea [14], and are generally found on the rostrum, on the carapace, and on the pereopods, with distribution in these areas varying among species. Decorator crabs typically decorate anteriorly from the rostrum, and subsequently place materials laterally and posteriorly to the remaining portions of the carapace and legs [15,16]. Decorating behavior by majid crabs may serve several functions including protection [17-20], food source [21,22] and influencing intraspecific interactions [23,24], and may be influenced by factors such as algal substrate composition [25] and social interactions among the crabs. *Microphrys bicornutus* is a majid crab ideal for studying functional aspects of decorating as it is omnivorous (90% of diet is composed of vegetation) and a medium-heavy decorator that attaches algae to its exoskeleton [26,27]. The objectives of this study with this crab species were the following:

1) Create ethogram of behaviors exhibited by crabs when presented with potential algal sources.
2) Determine if interactions with conspecifics will modify behaviors associated with decorating.
3) Determine if different algal species affect crab decorating behavior.

Materials and Methods

Animal collection and maintenance

Microphrys bicornutus specimens were collected from algal assemblages found in shallow-water banks off Tavernier Key and

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Long Key in the Florida Keys at depths ranging from 0.5-3.0 m. Algal assemblages were composed of several species, including (*Halimeda* sp., *Laurencia* sp., *Acanthophora* sp., and *Dictyota* sp.). Algal assemblages of various sizes were collected using snorkeling equipment and transported back to shore using a floating device that prevented the escape of crabs during transport. Once back on land, the algal assemblages were sorted, and crabs were removed and placed in a cooler with natural seawater and a portable air supply. Algae found in assemblages were sorted and placed separately from the crabs in a cooler with natural seawater and a portable air supply. Crabs and algae were then transported to the laboratory at Florida Atlantic University. Three hours after collection (time of transport between the collection sites and FAU), crabs and algae were separately transferred to 37.9 L aquaria (with filtration and air supply) containing seawater (35 psu salinity), and maintained at 27 °C with a 12L: 12D photoperiod. Crabs were continuously supplied with algae before and after trials to emulate their natural habitat. Individual crabs were used only once for trials. Algal assemblage substrates for experimental trials were prepared by combining pieces of algae (~ 1 x 5 cm) to a lead weight. Clear monofilament was used to tie one end of the algal mats to the lead weight, emulating algae attached to rock.

Decorating behavior

A baseline ethogram of decorating and associated behavioral acts displayed by *M. bicornutus* crabs was first established. Specifically, crabs were stripped of their decoration materials (using forceps), weighed (after blotting dry), and individually placed in a rectangular aquarium (15.5 x 21.5 x 30 cm) containing an algal assemblage composed of *Halimeda* sp., *Dictyota* sp., *Acanthophora* sp., and *Laurencia* sp. After a 30 min acclimation period, behavioral acts and their durations exhibited by each crab were observed for 1 h during daytime periods (i.e., when the laboratory lights were on). The minimum duration of each behavior recorded in all trials was 1 sec measured using a stopwatch.

Specific behavioral categories observed and documented for this study were defined as follows:

Feeding: Crab tears a piece of alga with the chelae and brings it to the maxillae where the alga is then chewed and all or portions of the sample are consumed.

Masking: Crab takes material from the substrate, using its chelae, and attaches the material to hooked setae on the exoskeleton.

Motionless: Crab remains still.

Picking: Crab picks at the algae using its chelae but does not tear, consume, or use the algae for decoration.

Walking: Crab moves on the substrate using its pereopods.

After 1h, crabs were reweighed to quantify the amounts of algae added to the exoskeleton using the following equation:

Weight of algae added to exoskeleton = Final weight of the crab - Initial weight of the crab

Additionally, algae added to the exoskeleton were removed, sorted by species, and weighed.

Kruskal-Wallis One Way ANOVA on Ranks and a Mann Whitney Rank Sum Test were used to analyze the data. Data were also collected and analyzed similarly for the following trials described below.

Influence of conspecifics on decorating behavior

To determine if decorating and associated behavioral acts displayed by *M. bicornutus* were influenced by interactions with conspecifics, behaviors were first observed and documented for isolated crabs (as described in the previous section). Crabs (n=10) were stripped of their decoration and reweighed. Each of these crabs was then placed individually in the rectangular aquarium containing an algal assemblage (with the same 4 algal species mentioned above) and another crab of the same size (within 1 mm carapace width (CW)). Specific behavioral categories observed for these 20 crabs (i.e., 10 paired crabs) included feeding, masking, motionless, picking, and walking. Additionally, aggressive behaviors were observed and described as either "active" or "display" - these additional behaviors were defined as follows:

Aggressive behavior

Active: Crab physically approaches a conspecific and attacks using its chelae.

Display: An act that involves both threatening and submissive behavior; this includes retreating from a conspecific, approaching a conspecific, raising of the chelipeds, and raising of the pereopods.

Influence of different algal species on decorating behavior

To determine if decorating and associated behavioral acts displayed by *M. bicornutus* were influenced by different algal species available, individual crabs (n=10) were stripped of their decoration materials and weighed. Crabs were placed in a rectangular aquarium (15.5 x 21.5 x 30 cm) containing an algal assemblage composed of one of the following species: *Halimeda* sp., *Dictyota* sp., *Acanthophora* sp., *or Laurencia* sp. Behavioral observations of crabs were recorded with each of the 4 algal species (n=10 crabs per algal species).

Results

Decorating behaviors

Specific decorating behavior we labeled as "masking" in *M. bicornutus* and begins when a crab approaches an algal substrate and selects a piece of algae using its chelae. One of the chelae then transfers the piece of alga to the area near the front of the crab where the maxillae, or mouthparts, chew the algae to an appropriate size and shape for attachment. The crab then takes the algae from its mouthparts using one of the chelae and rubs it against the area of the carapace covered with hooked setae until it is securely attached. The algal patch or mat is attached to the hooks using mechanical manipulation (i.e., the rigid hooks pierce into the material like Velcro). The crab begins by attaching larger pieces of algae anteriorly, on the rostrum and subsequently places algae posteriorly and laterally, with smaller pieces of algae attached to the pereopods.

More broadly we identified 5 behavioral acts for isolated crabs, including feeding, masking, motionless, picking, and walking. Average frequencies of each behavior are summarized in **Table 1**. Overall, isolated crabs spent a significant amount of time feeding, picking, and walking compared to masking ($P \leq 0.050$; Mann Whiney Rank Sum Test) **(Figure 1)**. Additionally, isolated crabs spent a significant amount of time motionless when compared to all active behaviors ($P<0.001$; t-test, Mann Whitney Rank Sum Test); specifically, crabs also remained motionless more frequently than masking ($P=0.008$; Mann Whitney Rank Sum Test). Isolated crabs did not show a preference for one algal species over another while decorating ($P=0.261$; Kruskal-Wallis One Way ANOVA).

Influence of conspecifics on decorating behavior

A total of 7 behavioral acts were recorded for crabs paired with conspecifics, including feeding, masking, motionless, picking, walking, "active" aggressive behavior and aggressive behavioral "displays."

	Feeding	Masking	Motionless	Picking	Walking	Aggressive "Active"	Aggressive "Display"
Crab Alone	5.2	1.9	11.4	8.1	3.6	NA	NA
Crab+Conspecific	4.1	0.4	18.8	4.3	3.2	2.0	3.6

Table 1: Average frequency (number of times behavior occurred per hour) of behavioral acts by individual (i.e., alone) crabs and crabs with another conspecific of the same size (n=10 trials for both conditions) during a 1 h observation period with an algal mound constructed of the following 4 algae: *Acanthophora sp., Laurencia sp., Halimeda sp., and Dictyota sp.* Isolated crabs spent a significant amount of time feeding, picking, and walking compared to masking (P≤0.050; Mann Whiney Rank Sum Test), but motionless was the most frequent behavior observed (P<0.001; t-test, Mann Whitney Rank Sum Test). Aggressive behaviors were observed for crabs with conspecifics; however, the frequencies of the remaining 5 behaviors were not statistically different from frequencies observed for isolated crabs (P≥ 0.050; Mann Whitney Rank Sum Test).

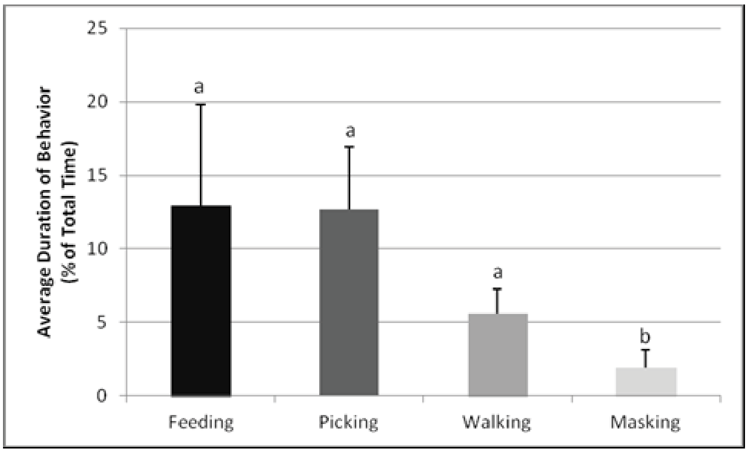

Figure 1. Histograms represent average durations of behavioral acts by crabs observed individually (n=10) during a 1 h observation period with an algal mound constructed to include the following 4 algae: *Acanthophora* sp., *Laurencia* sp., *Halimeda* sp., and *Dictyota* sp. Error bars represent the standard error. Motionless activity, which occurred typically over 60% of the time, was not included in the figure. Letters above bars indicate statistically similar and dissimilar groups at P ≤ 0.050 (Mann Whitney Rank Sum test).

Average frequencies of each behavior are summarized in **Table 1**. Paired crabs spent a significant amount of time motionless when compared to all active behaviors (P<0.001; Mann Whitney Rank Sum Test). There was no significant difference in the amount of time (i.e., duration) paired crabs invested in each of the individual active (i.e., excluding motionless) behaviors (P=0.232; Kruskal-Wallis One Way ANOVA) **(Figure 2)**. Time spent on active versus display aggressive behaviors among conspecifics were also statistically similar (P=0.845; Mann Whitney Rank Sum Test) **(Figure 2)**.

There was also no significant difference in the amount of time crabs invested in feeding, masking, and picking when paired with a conspecific versus isolated crabs (P ≥ 0.050; Paired t-test) **(Figure 3)**. Crabs with conspecifics did, however, show a significant decrease in the amount of time spent walking compared to isolated crabs (P=0.048; Paired t-test) **(Figure 3)**. Paired crabs and isolated crabs statistically spent the same amount of time motionless (P=0.519; Paired t-test). Finally, statistically, time spent on active versus display aggressive behaviors among conspecifics were similar (P=0.845; Mann Whitney Rank Sum Test).

Influence of different algal species on decorating behavior

The 5 non-aggression, behavioral acts documented in the previous section were also observed here for individual crabs given access to single-species algal mounds constructed of one each of the following four algal species: *Acanthophora* sp., *Dictyota* sp., *Halimeda* sp., and *Laurencia* sp. Average frequencies (i.e., number of times occurred) of each behavior are summarized in **Table 2** for crabs with each of the four algae. There were no significant changes in the frequencies of picking, masking, walking, and remaining motionless by the crabs with the single-species algal mounds (P ≥ 0.050; Kruskal-Wallis One Way Analysis of Variance). However, crabs did feed at a significantly lower frequency when with *Halimeda* sp. exclusively compared to the other 3 species. (P < 0.05; Mann Whitney Rank Sum Test).

Crabs spent a significant amount of time motionless with all single-species algal mounds (P ≤ 0.050; t-test/Mann Whitney Rank Sum Test). When comparing all active behaviors exhibited within a single-species algal mound, there was no significant difference in the amount of time crabs invested in each of the behavioral acts for *Acanthophora* sp., *Dictyota*sp., and *Laurencia* sp. (P ≥ 0.050; Kruskal-Wallis One Way Analysis of Variance) **(Figure 4)**. A statistically significant difference was detected with *Halimeda sp.* (P=0.001; Kruskal-Wallis One Way Analysis of Variance). Specifically, crabs invested less time in feeding, masking, and picking than in walking (P ≤ 0.050; Mann Whitney Rank Sum test) **(Figure 4)**.

Crabs also showed a significant decrease in activity (and concomitant increase in inactivity) with the single species algal mounds composed of *Halimeda* sp. when compared to a control (i.e., 4 species mixed algal mounds used in previous trials with individual crabs) (from 66% to 94%; P=0.006; Mann Whitney Rank Sum test) **(Figure 5)**. Crabs did not show a significant difference in the amount of each individual algal species used for decoration (P ≥ 0.050; Friedman Repeated Measures Analysis of Variance on Ranks) **(Figure 6)**.

Discussion and Conclusion

Animals that decorate have been looked at primarily from the standpoint of using this strategy for camouflage, with the typical assumption of defense against predators, etc. However, studies focusing on the effects of social interactions and species of decorating material on the specific behaviors involved in decorating are rare. Such focus on these potential effects is especially important given that the decorating materials may additionally serve as a significant source of food for the animals. This is especially true for crabs in the

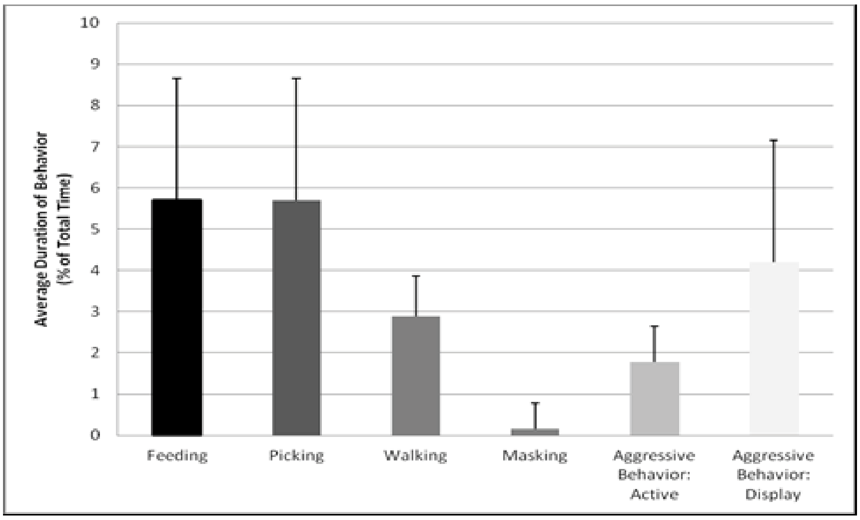

Figure 2. Histograms represent the average durations of behavioral acts (4 observed in previous trials, excluding motionless, and 2 additional behaviors of active and display associated with aggressive, intraspecific interactions) by crabs (n=10) during 1 h observation periods. Error bars represent the standard error. Motionless activity, which occurred typically over 70% of the time, was not included in the figure. None of the behaviors shown occurred significantly more than others. (P $\geq$ 0.050, Kruskal-Wallis One Way ANOVA), including a separate analysis of time spent on active *versus* display aggressive behaviors among conspecifics (P=0.845; Mann Whitney Rank Sum Test).

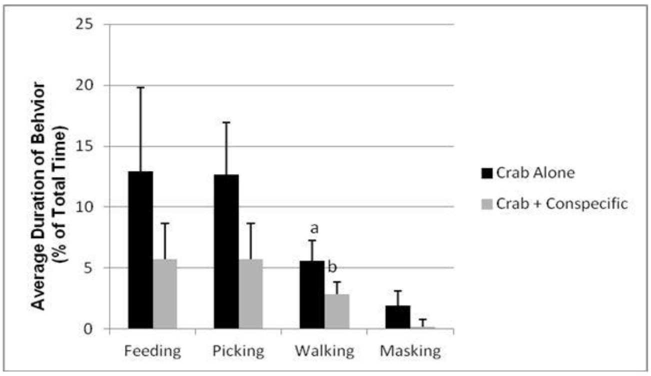

Figure 3. Histograms represent a comparison of the average durations of behavioral acts by crabs (n = 10) during 1 h observation periods alone versus 1 h observation periods paired with crabs of the same size ($\pm$1.0 mm carapace width; n = 20). Error bars represent the standard error. The durations of feeding, picking, and masking were not significantly different based on the presence of a conspecific (P $\geq$ 0.050, Paired t-test). Walking decreased in the presence of a conspecific (indicated by different letters above the histograms) (P = 0.048, Paired t-test).

	Feeding	Masking	Motionless	Picking	Walking
***Acanthophora* sp.**	2.2	1.5	4.9	2.7	3.2
***Dictyota* sp.**	2	1.1	4.1	2.4	2.5
***Halimeda* sp.**	0	0	3.8	1.2	0.9
Laurencia sp.	2	1.8	3.2	4.4	3.1

Table 2: Average frequency (number of times behavior occurred per hour) of behavioral acts by isolated crabs (n=10) during 1 h observation periods with a single-species algal mound constructed with one of the following four algal species: *Acanthophora* sp., *Dictyota* sp., *Halimeda* sp., and *Laurencia* sp. There were no significant changes in the frequencies of masking, picking, walking, and remaining motionless by the crabs with the single-species algal mounds (P≥ 0.050; Kruskal-Wallis One Way ANOVA). However, crabs did feed at a significantly lower frequency with *Halimeda* sp. compared to the other 3 species. (P<0.05; Mann Whitney Rank Sum Test).

superfamily Majoidea as they are morphologically well adapted for decorating behavior, e.g., having hooked setae that are unique to this superfamily. Herein, we studied the majid crab *Microphrys bicornutus* not only with the focus on the decorating behaviors but additionally how these behaviors related to social interactions with conspecifics and potential algal preferences for decorating by this crab species. Isolated crabs demonstrated 5 distinct behaviors during the 1h observation periods and 2 additional behaviors during the 1 h observation periods with a conspecific present. These behaviors included feeding, masking, motionless, picking, walking, and aggressive behaviors (active and displays). Motionless was considered a behavioral display, as this is part of the crab's cryptic methods. On average crabs remained motionless for 66% of the solitary observation periods, and 75% of the observation periods with a conspecific. Collectively, durations of this behavior were significantly higher than any other behavior documented within the 1h observation periods, which were made during daylight periods.

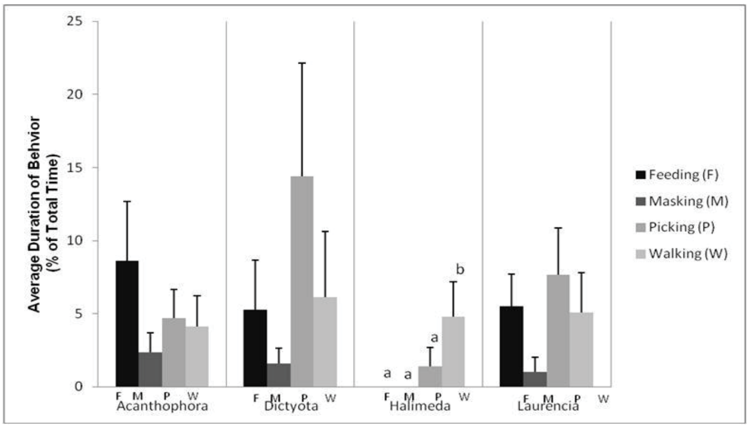

Figure 4. Histograms represent average durations of behavioral acts by crabs during 1 h observation periods with an algal mound constructed with one of the following four algal species: *Acanthophora* sp., *Dictyota* sp., *Halimeda* sp., and *Laurencia* sp. Thus, behaviors were observed for crabs in 4 different trials (n=10 crabs per algal species). Error bars represent the standard error. Motionless activity, which occurred typically over 70% of the time, was not included in the figures. The only significant differences (indicated by different letters above the histograms) in behaviors by crabs occurred with *Halimeda* sp. where feeding, masking, and picking behaviors were lower in duration than walking (P = 0.001, Kruskal-Wallis One Way ANOVA).

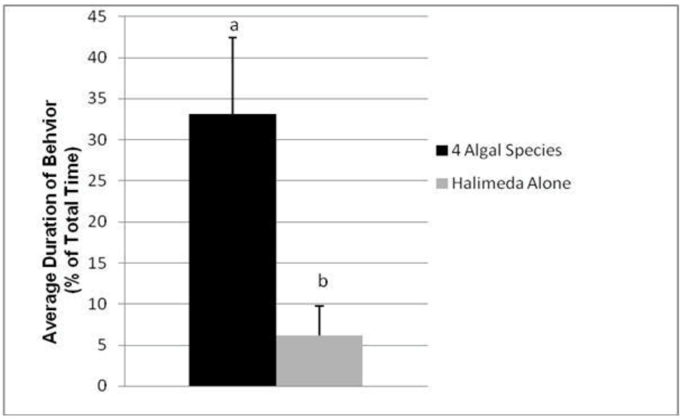

Figure 5. Black histogram represents pooled durations of feeding, masking, picking and walking from trials where individual crabs (n=10) were given access to algal mounds constructed with 4 algae: *Acanthophora* sp., *Dictyota* sp., *Halimeda* sp., and *Laurencia* sp. Grey histogram represents pooled frequencies of the same 4 behaviors, but crabs had only *Halimeda* sp. present on the algal mound. Error bars represent the standard error. Different letters above bars indicate statistically different groups at $P \leq 0.050$ (Mann Whitney Rank Sum test). Total activity of the crabs decreased in the presence of *Halimeda* sp. Concomitantly, motionless activity (not shown on figure) increased significantly in the presence of *Halimeda* sp. (from 66% to 94% P = 0.006; Mann Whitney Rank Sum test).

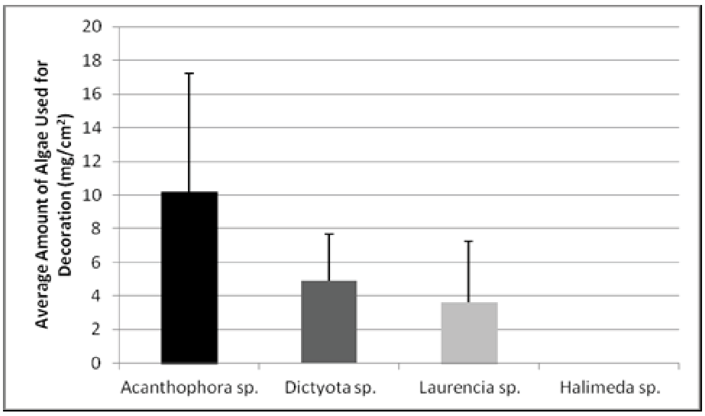

Figure 6: Histograms represent average amounts of algae used for decoration during 1 hour observation periods where crabs (n=10) were given access to an algal mound constructed with one of the following four algal species: *Acanthophora* sp., *Dictyota* sp., *Laurencia* sp., and *Halimeda* sp. The amount of algae used by the crab for decorating was measured in 4 different trial types. Error bars represent the standard error. The amounts of each algal species used for decoration were not significantly different based on the algal type ($P \geq 0.050$, Friedman Repeated Measures ANOVA on Ranks).

In general, majids and many decapods are more active nocturnally. Camouflage among decorator crabs is not only dependent on physical appearance but on behavioral adaptations. In general, predator avoidance is a key factor driving variation in behavior, and tradeoffs between energetic costs and anti-predator benefits of decoration thereby shape the evolution of camouflage. During daylight periods when presumably algal resources are also most easily located (at least visually), simultaneously, crabs are potentially most vulnerable to predators. Establishing a behavioral repertoire involving long periods of being stationary could be advantageous in that limited crab movement, and thus also the attached algae, more closely mimics the stationary nature of natural mats of algae and other benthic materials that might be attached to enhance the camouflage effect. For *M. bicornutus*, agonistic displays are typically initiated when crabs come within chela lengths of each other with the behavior solicited from a conspecific playing an important role in the crab's reaction. When interacting with conspecifics in the present study, crabs spent only 4% of the observation periods involved in agonistic displays and 2% of the observation periods involved in fighting or active aggression with conspecifics. In addition to the relatively low amount of time invested in agonistic behaviors, crabs showed a decrease in the amount of time walking while paired with a conspecific. Crabs may show a decrease in motility during such interactions to avoid confrontations that could result in conflicts with conspecifics. In general, it has been shown for this species that sex, color phase, size and hunger state have little effect on the crab's behavior when exposed to a conspecific. Our results are comparable in that conspecific interactions had little effect on the behaviors associated with decorating. Perhaps abundant supplies of the algal species also minimized the need for potential competitive interactions. Based on resource utilization patterns, decorator crabs may be categorized as specialist or generalist. *M. bicornutus* did not, in general, show much change in the duration of behavior between the different individual algal substrates when presented individually. Crabs did show a decrease in feeding and activity with *Halimeda* sp. compared to a control in which they had simultaneous access to all 4 algal species. *Halimeda* sp. is a calcified alga; thus, the decrease in activity with this algal species may be related to difficulty by crabs to both manipulate and attach it to the exoskeleton and ingest and digest the hardened algal thallus. Crabs, however, did not show a significant difference in the amounts of each algae used for decoration, including *Halimeda*. Overall, data from these trials suggest that *M. bicornutus* shows a generalist tactic and uses algae based on abundance rather than preference for an algal species. However, the data also show that some species of algae may require greater handling times and adjustments in behavior by the crabs. Future directions for study could involve exploring in more depth the primary functional role(s) of decorating in this crab based on varying levels of predation pressure. High levels may shift the decisions made by crabs for decorating to materials that maximize defensive attributes whereas low levels of predation pressure may shift the function to allow crabs to have a readily available algal food source attached to their exoskeletons. Additionally, population densities of this crab may influence availability of algal resources thereby increasing conspecific interactions. Such potential scenarios show that decorating by these crabs, and others, provide excellent opportunities to explore community-level interactions in marine ecosystems. Finally, while the focus of most studies has been on the crabs, algae are also functionally facultative symbionts. Little is known about the potential biological impacts of such associations on these algal species. In terms of cost/benefit ratios, it is possible that the algae benefit significantly from these associations, too.

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