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ASSOCIATIONS BETWEEN THE HERMIT CRAB *DARDANUS PEDUNCULATUS* AND ITS COMMENSAL SEA ANEMONE *CALLIACTIS TRICOLOR* ON MOOREA, FRENCH POLYNESIA

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Abstract. Crabs of the species *Dardanus pedunculatus* form a symbiotic relationship with *Calliactis tricolor* anemones on Moorea, French Polynesia. Crabs actively collect anemones for protection against octopus predation, while simultaneously giving the anemones a better habitat, defense against predators, and food as a result of the crab's messy eating. In a laboratory setting, crabs will compete for anemones with larger crabs winning competitions. This paper examined crabs' field collection patterns, and found that larger crabs collect more anemones, cover a greater percentage of their dorsal side with anemones, and carry a larger volume of anemones than smaller individuals. An experiment was designed to determine collection preference when unimpeded by field restrictions, and found that larger crabs show similar collection patterns as in the field, while smaller crabs cover a greater percentage of their dorsal side with anemones than in the field. This implies that abundance of anemones limits collection for this population, and that smaller crabs are being out-competed for anemones in the field. Additional behavioral experiments were designed to determine individual anemone preference patterns. Crabs show no preference for anemones they had been associated with in the field, but did show a significant preference for larger anemones. Gaining a better understanding of this symbiosis adds to the much-needed literature on the fragile coral reef ecosystem.

Key words: *Moorea, French Polynesia, hermit crab, Dardanus pedunculatus, Calliactis tricolor, size preference, mutualism, symbiosis*

INTRODUCTION

Symbiotic relationships are a vital part of the reef ecosystem. An important example of this is the association between zooxanthellae and coral, which forms the backbone of the reef ecosystem (Moberg 1999). A symbiotic relationship is said to be mutualistic if both organisms receive benefit from the association (Boucher 1982). In these relationships, the organisms involved often receive nutrition or protection from each other (Cushman and Beattie, 1991). A well-known example of this type of relationship can be seen in the interaction between goby fish and shrimp. The goby warns the blind shrimp of possible predators, while the shrimp builds a burrow that they both inhabit (Helfman 1997). Many species of crabs are also involved in a wide variety of mutualistic relationships. For example, the spider crab will decorate its carapace with algae for camouflage, while simultaneously providing the algae with a better environment (Wicksten 1993). Shedding more light on symbioses like these will allow us a better understanding of the complex reef system.

Many species of hermit crabs, ranging from the Pacific Ocean to the Mediterranean, are involved in a mutualistic relationship with sea anemones (Ross 1960). Molecular data show that this interaction has evolved independently at least twice (Gusmao and Daly 2010). In this association, the anemone gains a better environment by being able to move with the crab, and receives nutrition as a result of the crab's messy eating (Ross 1961). It has also been demonstrated that the crab will actively defend its commensal anemones against certain would-be predators such as fire-worms (Brooks 1993). The hermit crab decorates the outer wall of its shell with certain species of anemones for protection against octopus predation (Cutress and Ross 1968). It has been shown that when an octopus comes into contact with the anemone, the octopus will recoil in a seemingly painful response (Ross 1970). The degree of protection received from the mutualism seems to be dependent upon how many anemones the hermit crab is able to collect; in two separate lab experiments, with *Dardanus arrosor* crabs used in one and *Pagurus pollicaris* in the other, it was shown that hermit crabs with no

anemones were eaten first, followed by crabs with one and then three anemones, and that crabs with full anemone coverage seemed to receive complete protection against octopus predation (Brooks 1988, Ross 1971). In addition, *Pagurus pollicaris* individuals that place anemones close to the shell aperture survive longer in a lab setting (Brooks 1988). Interestingly, when *Dardanus arrosor* crabs are kept in artificial habitats for extended periods of time, they stop actively collecting anemones; however, when an octopus is introduced to the habitat the hermit crabs will resume anemone collection (Balasch and Mengual 2009).

Anemone placement on the crab's shell is nonrandom; the most significant factor influencing anemone placement by *Pagurus pollicaris* seems to be balance (Brooks 1989). With *Dardanus venosus* crabs, large anemones seem to be preferred over small anemones, with small anemones often eaten by the crab (Brooks 1991). In the Aegean Sea, larger species of crabs carry a greater biomass of anemones than smaller species (Vafeiadou et al. 2011). In addition, under starvation conditions in a laboratory setting, *Dardanus pedunculatus* has been shown to eat its commensal anemones (Imafuku et al. 2009).

On Moorea, French Polynesia, the hermit crab *Dardanus pedunculatus* has a mutualistic relationship with the anemone *Calliactis tricolor* and the small white anemone *Sagartiomorphe*. *C. tricolor* is larger, and generally found on the outside of the shell, while *Sagartiomorphe* anemones are generally found along the shell aperture and sometimes even inside the shell (Ross and Sutton 1961). Members of *D. pedunculatus* will compete for and steal *C. tricolor* anemones from each other, with larger crabs generally winning (Giraud 2011). However, the implications of this in the field have not been assessed. If collection were limited by anemone abundance, it would imply that smaller crabs are able to collect fewer anemones and cover a smaller percentage of their shells with anemones.

This paper examined *D. pedunculatus* crabs' field anemone collection along with anemone choice in a lab setting in order to test four hypotheses: (1) small crabs in the field will be out-competed for anemones by larger crabs, and thus will be associated with fewer anemones and have a lower percent anemone coverage; (2) *D. pedunculatus* individuals will prefer large anemones over small anemones; (3) *D. pedunculatus* crabs will have no preference for anemones they were associated

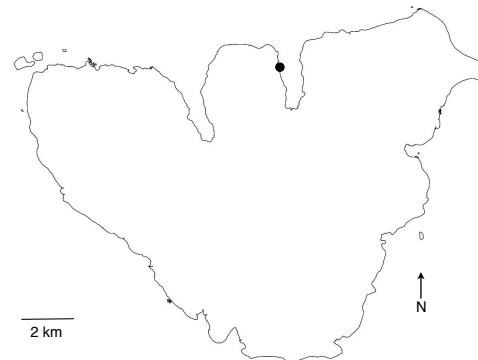


FIG. 1. Map of Moorea with location of collection site (Gump Research Station), 17°29'23.10"S, 149°49'31.78"W

with in the field over other *C. tricolor* anemones; (4) when anemone limitation and competition do not influence crabs' collection, large crabs will not deviate from anemone collection patterns found in the field while small crabs will collect more than in the field.

METHODS

Collection of hermit crabs

Crabs from one population of the species *Dardanus pedunculatus* (Appendix A) were studied in this paper. Crabs were collected off of the University of California Gump Research Station (Figure 1) by night snorkeling using a dive lamp. Night snorkeling took place between the hours of 6:30 and 11pm, and at a depth between 0.2 and 2.5m. Individuals were placed in a zipped mesh bag during snorkeling and taken to the Gump Research Station within one hour of collection. Crabs were then placed in open-circulating seawater aquariums for an acclimation period of 24 hours. Because of limited aquarium space, a maximum of six crabs were collected in any night, and aquariums were divided into two compartments so that each could accommodate two crabs.

After the 24-hour acclimation period was over, dorsal-view photographs and measurements were taken. The cheliped size of each crab was recorded to the nearest 0.1mm with calipers, as well as the number of *Calliactis tricolor* anemones on each crab and the presence or absence of *Sagartiomorphe* anemones. Cheliped size was used as a proxy for crab size. Each *C. tricolor* was also measured along the widest pedal disc diameter to the nearest 0.1mm. Crabs were

then placed back into original open-circulating seawater tanks.

After a second 24 hours had passed (total of 48 hours from original collection), all *C. tricolor* anemones were gently removed from each crab by sliding a thin piece of metal under the pedal disc. Anemones were allowed to settle on pieces of coral rubble for three hours. During this time, the crabs and their anemones were kept separately on the same open-circulating seawater table so that chemoreceptive cues, if used by the crab, were still available. Two crabs were kept on each table.

Behavioral experiments began after anemones had settled for the three-hour period. Behavioral experiments were always done in the same order, with preference for field-associated anemones tested 48 hours after collection from the field, and size preference examined 72 hours after collection from the field. In accordance with other behavioral studies on anemone-collecting hermit crabs, the crabs were not fed. 48 hours was chosen before proceeding with behavioral experiments because most experiments in the literature starved crabs for 48 hours before running any behavioral tests. Only one anemone choice experiment was done in a night for any individual crab.

Crabs' field anemone collection

The dorsal-view photograph of each crab was analyzed in ImageJ (Rashband, 2012). Percentage cover of anemones was determined by measuring the total area in the dorsal-view photograph filled with anemones vs area of bare shell (Appendix B). This measurement was decided upon to standardize among the different sizes of anemones and shells. Only the dorsal view was analyzed as previous placement studies only considered this angle.

Regression analyses were run using cheliped size as the explanatory variable and various parameters including percentage cover of anemones, number of anemones, and anemone volume as response variables. Analyses were performed in JMP (SAS Institute, 2012). All analyses in this paper define statistical significance as $p < 0.05$. T-tests were run between size classes of crabs to determine if percentage cover of anemones was significantly different between small and large crabs. Crabs were broken into two different groups based on cheliped size: 0-2mm and greater than 2.01mm.

Experiment 1: Crabs' preference for own anemone

Three hours after anemones were removed, crabs were placed in rectangular enclosures with one anemone that had been on the crab's shell in the field, hereafter called the field anemone, and another anemone of the same species (Figure 2). Only one of the crab's field anemones was used for the experiment, with the largest chosen if possible. The other anemone had never been in the same tank with the crab, to ensure that the crab would never have become accustomed to it. The two anemones were as close to the same size as possible. The crab's field anemone was placed on the left in half of the experiments, and on the right in the others. A dim red light was placed above the enclosure to minimize disturbance to the crab and to other organisms in the area. Crabs were only used once for each experiment, but because of limited numbers and ability to collect and house crabs, individuals were used in more than one of each of the four experiments.

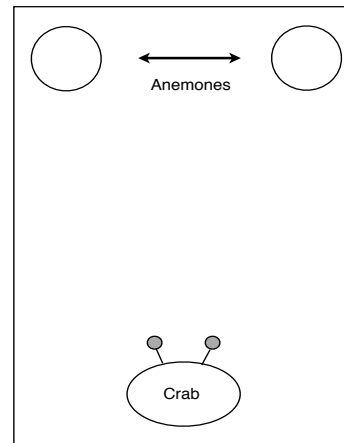


FIG. 2. Choice and size preference experimental setup for experiments 1 and 2

All experiments were done at night, when *D. pedunculatus* is most active. The crab was placed at the opposite end of the tank from the two anemones, and allowed 30 minutes to place an anemone on its shell. Any crab that did not collect in this time period was not counted. The anemone chosen first was marked as preferred. If an anemone was chosen by the crab but abandoned before placement, the trial was not counted. Data

from this experiment was analyzed using a binomial test.

Experiment 2: Size preference

Crab's preference for anemone size was tested in the same manner as was used in experiment 1. Two anemones of different sizes were placed in two corners of a rectangular enclosure (Figure 2). The larger anemone was placed on the left in half of the experiments, and on the right in the others. The crab was placed on the opposite side, and allowed 30 minutes to collect an anemone. The anemone collected first was marked as preferred.

Results of this experiment were also analyzed using a binomial test.

Experiment 3: Anemone collection under excess *C. tricolor*

To determine the difference between the crab's anemone collection in the field and without competition or anemone limitation, crabs were given more anemones than they were found with in the field, and allowed 12 hours overnight for collection and placement. The number of anemones offered to any crab was determined by the number of anemones that crab had collected in the field. Most crabs were given 6 anemones. However, crabs that were collected from the field with no anemones were given 2, while crabs that were collected with 6 anemones were given 8. To ensure that crabs were offered anemones that were appropriate for the crab's size, anemones were chosen to be of similar size to the crab's field anemone. At the end of the 12-hour period, dorsal-view photographs were taken and percentage cover was analyzed in ImageJ.

Results from this experiment were compared with field data for each crab. Data points were obtained by subtracting percentage anemone cover in the field from percentage anemone cover after the experiment for each crab. This resulted in positive values signifying that a greater percentage of the crab's dorsal view was covered by anemones in the lab than in the field for the crab in question.

T-tests were run between the two different size classes of crabs, 0-2cm and greater than 2.01cm, in JMP to gauge significance.

Release

Crabs were kept for a maximum of seven

days. Each crab was given an opportunity to collect anemones before release. Because a wide selection of anemone sizes was needed for behavior experiments, some anemones were kept up to a two-week period.

RESULTS

Crabs' field anemone collection

40 *Dardanus pedunculatus* individuals were collected, with 95% (38 out of 40) carrying *Calliactis tricolor* anemones.

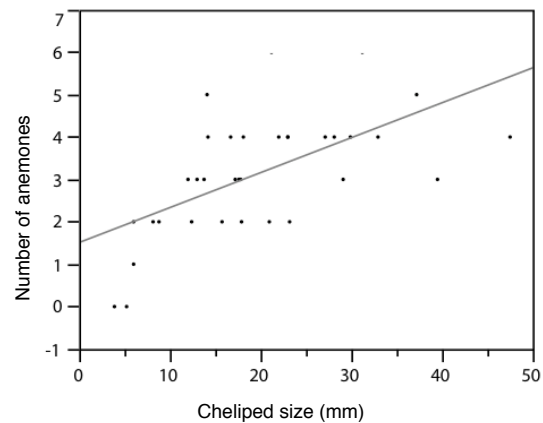


FIG. 3. Positive correlation between cheliped size (mm) and number of anemones. $R^2=0.36$; $p=0.0002$; $n=33$; $y = 0.0825x + 1.5113$. Larger crabs carried more anemones than smaller individuals.

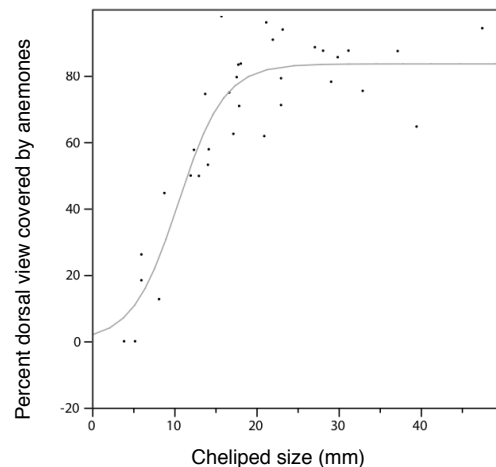


FIG. 4. Percent dorsal view covered by anemones by cheliped size fit to a logistic growth model. $n=33$; $R^2=0.848$, Growth rate= 0.37 (95% 0.23-0.49), Inflection 10.51 (95% 9.25-11.77), Asymptote= 83.55 (95% 77.8-89.29). Smaller crabs cover a smaller percent of their dorsal size with anemones.

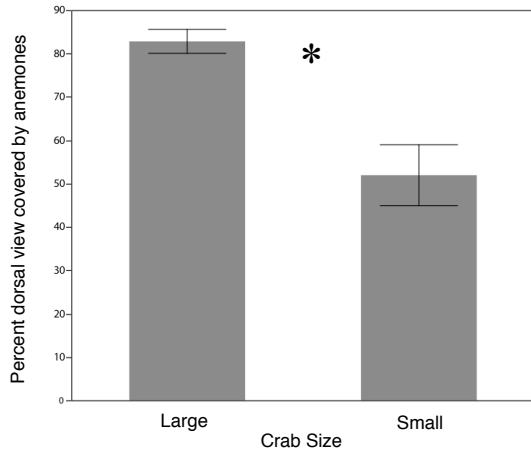


FIG. 5. Percent dorsal view covered by anemones by crab size (same data as Fig. 4) divided into crab size classes. T-test $p=0.0002$. $n=33$. Error bars show one standard error from the mean. Large crabs carry significantly more anemones than small crabs.

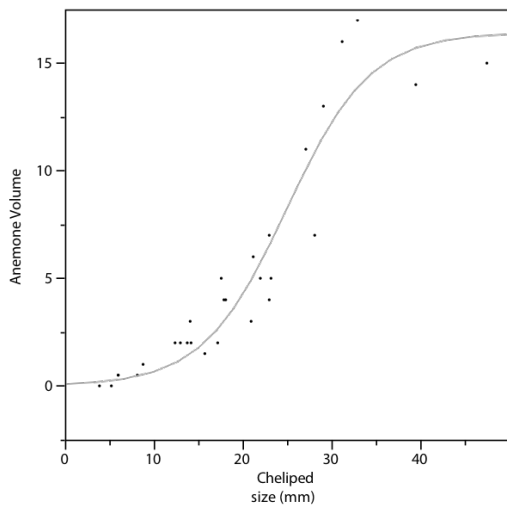


FIG. 6. Anemone volume by cheliped size fit to a logistic growth model. $R^2=0.91$; $n=21$; growth rate=0.21 (95%: 0.14-0.28), Inflection=24.96 (95%: 22.72-27.2) Asymptote= 16.42 (95%: 13.9-18.94). Smaller crabs carry a smaller volume of anemones.

Sagartiomorphe anemones were carried near the shell's aperture, with parts or whole anemones often inside of the shell, by 92.5% of crabs (37 out of 40). Crabs ranged in cheliped size from 3.9mm to 47.5mm.

The number of anemones carried by a *D. pedunculatus* individual in the field was found to positively correlate with the crab's

cheliped size (Figure 3). Smaller crabs generally carried fewer anemones than larger crabs. The number of anemones carried by a single crab ranged from zero to six.

Through a Spearman's ρ test, $p<0.0001$, it was determined that there was a correlation between cheliped size and percent dorsal view covered by anemones. The data best fit a logistic growth model (Figure 4). Smaller crabs had a lower percentage of their shell covered than larger crabs. Percent cover ranged from 12% to 96%, with an asymptote at 85%. When broken down into size classes, a statistically significant difference was found between the percent cover of small and large crabs (Figure 5).

A Spearman's ρ test determined that there was a correlation between anemone volume and cheliped size with $p<0.0001$. The trend was again best fit by a logistic growth model, with an asymptote of about 16 ml of anemone volume. (Figure 6). Larger crabs were found to carry a greater volume of anemones.

Experiment 1: Crab's preference for own anemone

No significant preference was found for a crab's field anemones over other anemones of the same species. Nine crabs chose their own anemone, while six chose the other anemone (Figure 7).

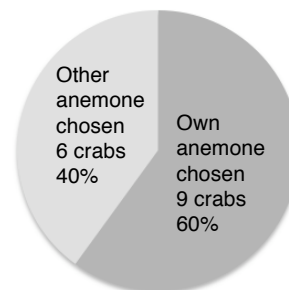


FIG. 7. Experiment 1: Preference for own anemone. $n=15$. Binomial test $p= 0.3$. No preference was found for a crab's field anemone.

Experiment 2: Size preference

In size preference tests, crabs chose the larger anemone with statistical significance (Figure 8). Out of 17 tested crabs, 13 chose the larger anemone.

Experiment 3: Anemone collection under excess C. tricolor

In general, small crabs had a positive percent change in percent anemone cover, meaning more anemones were collected under experimental conditions, while large crabs had a negative percent change (Figure 9). However, with a p value of 0.07, this trend was not statistically significant.

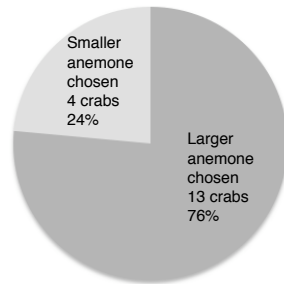


FIG. 8. Experiment 2: Anemone size preference. n=17, 13 crabs chose larger anemone. Binomial test p=0.02

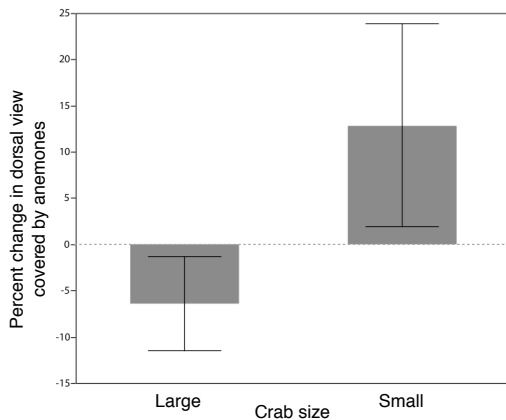


FIG. 9. Experiment 3: collection under no competition or anemone limitation. n_{total}=15; n_{small}=6; n_{large}=9. T-test p=0.07. Error bars constructed using one standard error from the mean

DISCUSSION

Crabs' field anemone collection

Dardanus pedunculatus individuals in the field display significant differences in anemone collection patterns when small and

large crabs are compared. Large crabs collected more anemones (Figure 3) and were able to cover a greater percentage of their dorsal side with anemones (Figures 4 and 5). This suggests that *C. tricolor* may be a limiting resource for this population of *D. pedunculatus* on Moorea, similar to gastropod shells in many locations (Fotheringham 1976). In fact, no *C. tricolor* individuals were found separate from the shells of *D. pedunculatus* individuals, further supporting this claim. The results also suggest that intraspecific competition for *Calliactis tricolor* is not limited to a lab setting.

In addition, the volume of anemones carried by small crabs was consistently smaller than the volume carried by larger crabs. These results agree with a previous study, which found that larger species of crabs carry a larger anemone biomass (Vafeiadou et al. 2011). A tradeoff may exist between protection gained from collecting more anemones and the ability to maneuver properly. This is consistent with results found by Brooks, showing that the most significant factor in anemone placement was balance (Brooks 1989). As anemones appear to be fairly large when compared to crab size, it can be assumed that carrying anemones incurs significant drag. With enough drag, locomotion in water can be significantly altered, reducing the speeds and confining the positions an animal may exhibit (Martinez 2001). This may explain why an asymptote was found; perhaps at this volume of anemones an optimal balance is achieved between protection and maneuverability.

Experiment 1: Crab's preference for own anemone

As was expected, crabs showed no preference for anemones they had carried in the field over other anemones of *C. tricolor* species. While some organisms, such as Clown Fish, do form individual bonds with anemones (Dunn 1981), *D. pedunculatus* will chose any available anemone. This may be related to the proposed anemone limitation and competition between individuals for anemones.

Experiment 2: Size preference

D. pedunculatus individuals showed a strong preference for large anemones over small anemones. This study is in agreement with the experiment by Brooks showing that *Dardanus venosus* individuals also show a preference for larger anemones (Brooks 1991).

This may simply be because larger anemones are more conspicuous and are noticed by the crab first. However, crabs often passed over a small anemone in favor of collecting a larger one. Since more than one species of anemone-collecting crabs show a preference for large anemones over small anemones, it is likely that there is an underlying biological reason for this preference. It is possible that one large anemone provides more nematocysts and better protection against predation than having smaller anemones.

*Experiment 3: Anemone collection under excess
C. tricolor*

When given a large number of *C. tricolor*, collection on average changed for both small and large crabs. The mean collection for large individuals was slightly lower than in the field. This may simply be because the pedal disc is retracted after being so recently manipulated. As the anemones become acclimated to the new placement, percentage cover would probably be more similar to field data. The results suggest that large crabs are already carrying the desired number of anemones in the field. However, small crabs covered a greater percentage of their shell with anemones under non-limiting conditions. The fact that average collection is greater when given an excess of *C. tricolor* suggests that small crabs do not have the optimal number of anemones in the field. These results provide further evidence that anemones are a limiting resource for this population of *D. pedunculatus* individuals. Hermit crabs extensively compete for quality shells, which is generally a limiting resource (Arnott 2007). *D. pedunculatus* individuals most likely compete for anemones in the field in a similar manner, with small crabs out-competed for anemones by larger individuals. While the difference between small and large crabs was not significant in this paper, this may simply be because of the limited number of individuals tested.

Conclusion

While much research has gone into studying the symbiotic relationship between anemone-collecting hermit crabs and their commensal sea anemones, the vast majority of this research has focused on lab-setting behavior research (Ross 1971, Imafuku 2000, Brooks 1995, Brooks 1993, Brooks 1988, Balasch 1974). This paper serves to fill in a gap

in the literature about what characterizes this symbiosis in the field, supplemented with lab-setting behavior research. While different locations will undoubtedly provide different results because of differences in populations of both the hermit crabs and the anemones, the population in Cooks Bay on Moorea is an interesting piece of the puzzle and provides valuable insight into the symbiosis. Mutualistic relationships such as these have been shown to enhance diversity (Schmitt and Holbrook 2003), and so are especially important in the coral reef ecosystem. Understanding how symbiotic relationships characterize themselves in different field environments is crucial, especially with the projected decline in reef communities around the world.

ACKNOWLEDGMENTS

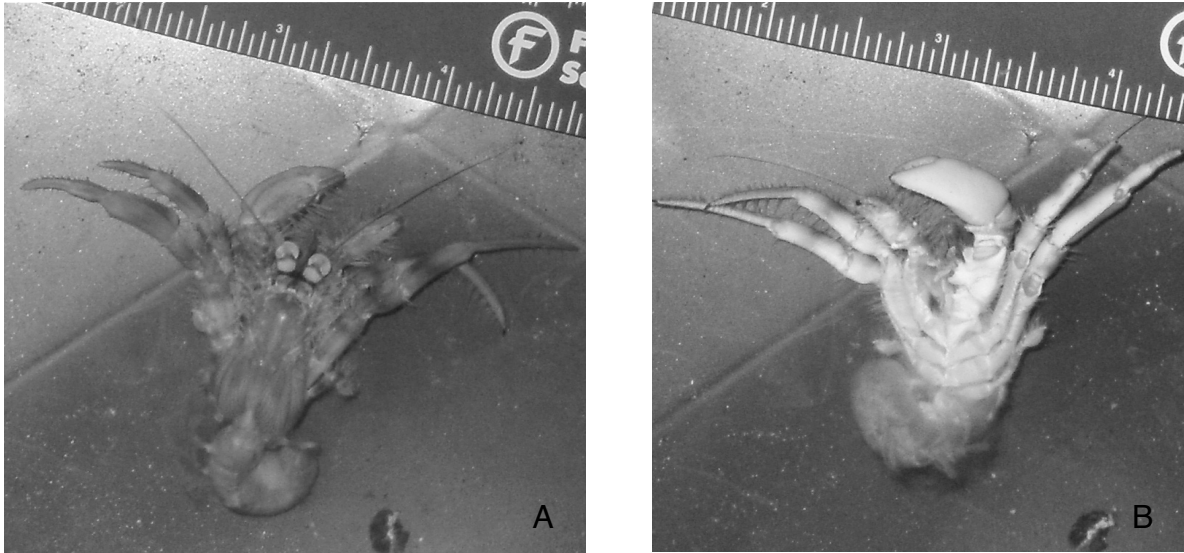
I would like to thank professors Brent Mishler, Vincent Resh, George Roderick, and Jonathon Stillman, as well as GSI's Darcy Kato Ernst, Rosemary Romero, and Matthew Luskin for their invaluable support and guidance throughout the semester. I would also like to thank the entire Moorea class of 2012, with special appreciation to the many that helped me with night-time crab collection.

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APPENDIX A



A *Dardanus pedunculatus* individual is shown in the above two pictures, removed from its shell. Image A shows the crab's dorsal side, while image B shows the crab's ventral side. The ruling measurements shown in both pictures are in inches. Out of a total of 40 individuals collected, 38 carried *Calliactis tricolor* anemones, and 37 carried *Sagartiomorphe* anemones. Crabs ranged in color from cream to orange-red, with distinctive green eyes.

APPENDIX B

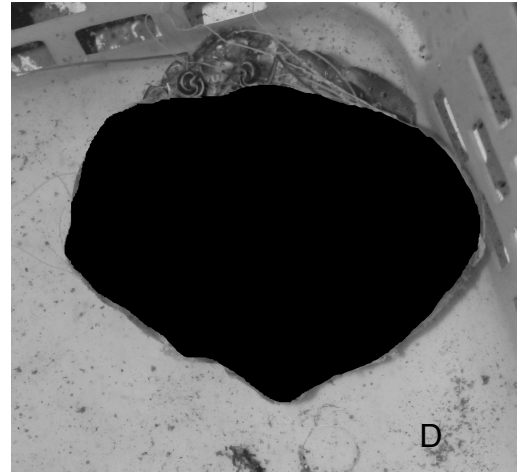
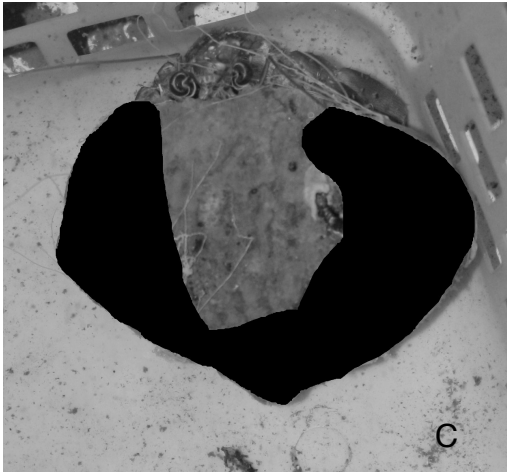
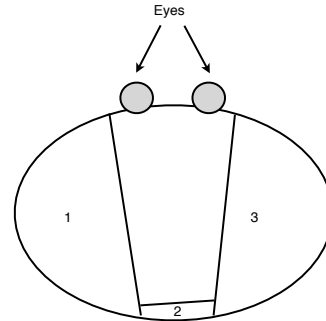
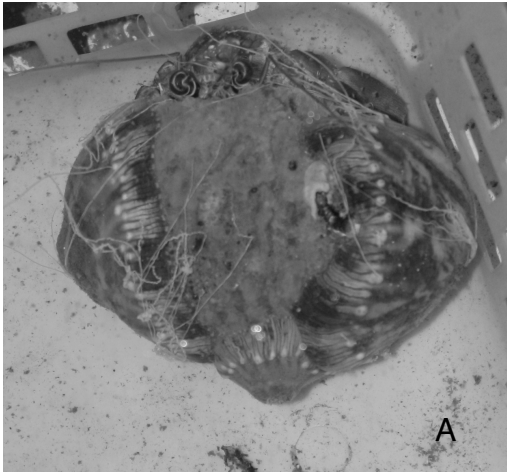


Image A shows the dorsal-view photograph of a *Dardanus pedunculatus* individual to be used in calculating percentage change in anemone cover. Image B attempts to clarify image A, showing the location of the crab's eyes as well as the location of anemones, labeled 1, 2, and 3. Image C shows the total dorsal-view area covered by anemone. Anemone area that extends beyond the shell boundary was included because it extends the area that can be seen by a predator and because the crab actively added the anemones. Image D shows the total dorsal-view area. The calculation for percent dorsal-view area covered by anemone used C/D.