AUTOTOMIZED ARM BEHAVIOR OF THE BRITTLE STAR *MACROPHIOTHRIX LONGIPEDA* (ECHINODERMATA: OPHIUROIDEA) IN MOOREA, FRENCH POLYNESIA

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Abstract. Autotomy is a unique process that involves the voluntary release of one or more appendages usually as a defense mechanism to escape lethal predation. Many organisms that display autotomy can later regrow the fragmented body part(s) which is seen in all five classes of echinoderms (Candia-Carnevali et al. 2007). It has also been shown that for many autotomizing organisms such as geckos, lizards, and crickets, the dropped body parts can function for a period of time after they have been dropped. Although there has been extensive research done on autotomy itself as well as autotomizing organisms and their regenerative capacity, little work has been done on the functionality and behavior of the limbs or appendages after an autotomy event. This research aims to study why and how the dropped arms of the brittle star *Macrophiothrix longipeda* (Lamarck 1816) in Moorea, French Polynesia can function post-autotomy. This study will look at autotomy frequencies in the field by both size and exposure type: exposed, burrowed, or partially burrowed. In addition, this study will specifically aim to take a deeper look into arm behavior post-autotomy by examining the arms' ability to find their way under a physical object or shade for a three-day period after they have been dropped. The results of this study can better inform us on the benefits of autotomy as well as what makes this a successful defense mechanism for many organisms. It can also provide information for future research into why autotomy has evolved in many organisms.

Key words: autotomy; autotomized arms, brittle star; Echinodermata; Ophiuroidea; Moorea; French Polynesia; predation; regeneration; Macrophiothrix longipeda; Ophiocoma dentata

INTRODUCTION

Many organisms have evolved the capacity to autotomize partial or full limbs in order to escape lethal predation under stressful conditions (Shaeffer 2016). Autotomy is a unique process in which an organism voluntarily discards one or more of its own appendages, usually as a self-defense mechanism to either elude a predator's grasp or to distract a predator and escape (Shaeffer 2016). Oftentimes, these organisms can regrow the lost body part later or in some cases, a new individual can grow from the autotomized body segment (Candia-Carnevali 2006). Autotomy is common among many phyla including: annelids, arthropods, cnidarians, echinoderms, and molluscs (Pomory and Lawrence 1999). The process and effect of autotomy is especially studied in echinoderms, as this very unique and effective process occurs among all five classes, namely the asteroidea, ophiuroidea, holothuroidea, echinoidea, and crinoidea (Candia-Carnevali *et al.* 2007). The brittle stars (Ophiuroidea) are among the most popular organisms to study in regards to regeneration as they are known to have a very high regenerative capacity (Bowmer and Keegan 1983). According to a study by Carnevali (2006), regeneration among ophiuroids is so common that "specimens collected in natural environments almost always have two or more regenerating arms at different regrowth stages" (Candia-Carnevali 2006). There have also been several studies showing that a majority of ophiuroids are able to autotomize their arms at any given intersegment, thus making autotomy as a defense mechanism extremely effective and beneficial for these organisms (Emson and Wilkie 1980, Candia-Carnevali *et al.* 1998).

Ophiuroids are primarily filter feeders, a sub-group of suspension feeders, making them extremely vulnerable to predation. They suspend their arms into the water column to trap microorganisms such as plankton or bacteria and use the mucous strands between the spines on each arm to carry them into their mouths (Warner and Woodley, 2009). Because they are vulnerable to predation by significantly larger organisms such as crabs, shrimp, and various fish, they will often suspend only one or two arms to feed and use the others to anchor themselves. If predation does occur on the vulnerable arms while feeding that is when autotomy is likely to occur, giving the rest of the organism time to quickly distract and escape the predator (Warner and Woodley 2009).

Although autotomy and regeneration of ophiuroid limbs has long been a topic of scientific interest (Dinsmore 1991, Wilkie 2001, Sides 1987, DuPont and Thorndyke 2006, Sköld & Rosenberg 1996, Bowmer and Keegan 1983), little work has been done on the functionality and behavior of the arms themselves after an autotomization event. It is known that for several species of autotomizing organisms, the dropped limbs or fragmented body parts are able to function several days or even weeks after they have been autotomized (Candia-Carnevali 2006).

The main goal of this study is to describe the behavior of the autotomized arms of the brittle star *Macrophiothrix Longipeda* in order to understand how arm length correlates to arm behavior and functionality over time. Another aim of this research is to understand the correlation between brittle star size and autotomy frequencies across the species *M. Longipeda* (Lamarck 1816) at the site Pihaena in Moorea, French Polynesia. Specifically, the objectives of this project are to: 1) describe how the diameter of the brittle star's central disc correlate to the number of arms autotomized at any given time, 2) understand how brittle star arms are able to function independent of their central disc following an autotomization event, and 3) to compare autotomy frequencies between individuals that are burrowed, partially burrowed, or exposed during both high and low tide. I aimed to take a closer look at brittle star arm behavior by testing whether the arms are able to physically find their way under suitable habitat (rock/coral rubble/coraline algae) and if they are able to continuing using their light sensory nerves on their arms to find their way under shade and away from light. I expect to find a positive relationship between brittle star size and autotomy frequency due to higher predation pressure and vulnerability to predators during feeding. Based on preliminary studies done in the lab, I hypothesize that the longer autotomized arms (dropped closer to the central disc) would be able to function significantly longer than the shorter ones. Since more energy and nutrients are more likely stored in the larger arms following autotomization, I hypothesize that the larger arms may find their way under habitat and shade more efficiently and frequently than the shorter arms. I also predict that brittle stars that are either burrowed or partially burrowed are more likely to autotomize due to greater chances of escaping predation by continuing to burrow into the sand or crevices of the rocks.

METHODS

Study site

Moorea is a small volcanic island located in the Southern Pacific Ocean (17° 30′ S, 149° 50′ W). It is ~1.5 million years old making it the second youngest island in French Polynesia's Society Island Archipelago next to Tahiti. The Pihaena Jetty (17° 29.110′ S, 149° 49.893′ W, Fig.1) is located on Moorea between Cooks Bay and Opunohu Bay, approximately 100 meters from the Richard B. Gump Station. Pihaena consists of a jetty extending ~30 meters into the ocean and is comprised of primarily concrete, rocks, and rubble. Perpendicular to the jetty is a small beach with a shallow rocky shoreline comprised of abundant brittle stars, sea urchins, sea cucumbers, and gastropods.

FIG. 1. Map of Moorea, French Polynesia from Google Earth with the primary field site, Pihaena circled.

System

Macrophiothrix longipeda is a large and fairly common brittle star that is widely distributed in the Indo- West Pacific (Davie, 1998). They can be found in shallow depths of < 5 meters in the tropics and have been previously observed on the shore of Pihaena in

Moorea, French Polynesia under rocks and coral rubble (Chinn 2006, West 2012).

Field Survey

Macrophiothrix longipeda were surveyed along a 30 meter transect placed along the shore of Pihaena beach on October 16, October 25, and October 29, 2018. Each time an individual was encountered along the transect, I measured the diameter of each brittle star's central disc, the number of autotomized arms (including regrowing arms), and the type of habitat they were found under: rock, coral rubble, or algae which were all recorded. To ensure double counting of individuals did not occur during the survey, all brittle stars that were found within a 30-minute time frame were first collected. Once they were all collected, each individual was then measured, processed, and released.

A second survey was also conducted at Pihaena, in this case recording the state each individual brittle star was found in during the time of observation including whether they were exposed, burrowed, or partially burrowed. I classified individuals as "exposed" if their full central disc and all arms are visible; "partially burrowed" as some arms being exposed and some arms and/or the central disc being completely burrowed; and "fully burrowed" when the majority of the brittle star was found under its preferred habitat type with very little of the organism exposed. I also recorded the depth of the water for each observed brittle star as well as how many arms were autotomized/ actively autotomizing at the time of observation. I did this survey twice during both high and low tide at Pihaena beach on November 7, 2018 and November 10, 2018.

Experimental design

Upon encountering *Macrophiothrix longipeda* in the field, some individuals autotomized arms, which were then collected for lab experiments back at the Richard B. Gump Station. Each individual arm was measured prior to the start of each experiment. Two small tanks (24 x 22) were set up and filled with 15 centimeters of water to replicate the shallow environments the animals would typically be found in the wild. In each of the two tanks, a circle was created out of black electrical tape with a circumference of 96 cm and a radius of 18 cm. Five pieces of black electrical tape were then evenly spread along the inside of the circle extending halfway toward the center of the circle. Each piece of tape was about 19 cm apart from one another allowing enough space for each arm to not touch. In one tank, a piece of rock, coraline algae, or coral rubble was placed in the center of the circle, depending on which habitat the arms were found under in the field at the time of collection (Fig. 2). In the second tank, a shadow was created covering the center of the circle using a small plastic lid and string tied to the top of the tank (Fig. 3).

Because physical vs. sensory behavior after an autotomization event was the primary focus of these experiments, it was critical that the arms in the sensory tank were not able to touch anything including the lid and the string. Five arms from the same survey were placed along the outside of each circle at 9:30am where the five black markings were located. The arms were observed every four hours at 10:00, 14:00, and 18:00 for three consecutive days. At each observation, the location of each individual arm was recorded (initial position, under the physical object, under the shade, etc.) and arm length was measured. At each observation, it was also noted where in the tank the ones that did not find their way under were (i.e. corner of tank, on black electrical tape, etc). Because close detail of arm behavior was observed and the water was shallow (~15 cm deep), there was no consistent water flow in the tanks during the experiments. To account for this, sea water from Cooks Bay was switched out each morning upon the beginning of each new trial starting at 10:00am.

FIG. 2. Five autotomized arms several minutes after being placed in the tank. Testing whether they are able to physically find their way under their preferred habitat.

FIG. 3. Five autotomized arms several minutes after being placed in the tank. Testing whether they can still use their light sensory nerves to find their way under shade.

Statistical analysis

To test whether or not there was a significant relationship between the size of the brittle star and autotomy frequency, a linear regression analysis was done using the statistical analysis software PAST 3. This test was done using counts of individuals found at Pihaena beach during the field survey.

In order to understand if autotomy frequency varied between individuals that were burrowed, partially burrowed, or exposed, a chi square one-sample test was used for goodness of fit also using the statistical analysis software PAST 3. This test was done to assess autotomy frequencies of individuals by exposure type at both high and low tide using counts of individuals located in each of the three habitats in the field.

To test whether or not longer arms were able to find their way under rock or shade more quickly or more often than the shorter arms (dropped further from the central disc), a logistic regression analysis was used to assess how quickly the arms were able to find their way under the physical object or shade over time. Additionally, this test used a binomial distribution and was also done using the software PAST 3.

Lastly, a Mann- Whitney-U test was used to compare the median time it took individuals to find their way under rock versus under shade. The statistical analysis software PAST 3 was also used for this test. All tests were done with an alpha value = 0.05 (statistical convention).

RESULTS

Size vs. autotomy frequency field survey

Macrophiothrix longipeda was the dominant species of brittle star found at the site Pihaena between Cooks and Opunohu Bay. Another species of brittle star, *Ophiocoma dentata*, was also found at Pihaena however in much smaller quantities than *M. longipeda*. Both species were found either under rock or coral rubble on the shore of Pihaena beach. Each individual brittle star that was observerd along the 30 m transect at Pihaena beach was found in depths no greater than one meter of water either burrowed, partially burrowed, or fully exposed. Often times, many of the juvenile and smaller brittle stars were found inside the rocks and coral rubble and not immediately visible to the naked eye. *Macrophiothrix longipeda* were often found with two or more arms regenerating at the time of observation (Fig. 4) which has been observed in several previous studies (West 2012, Chinn 2006). There was no obvious correlation between the size of the central disc and the number of arms autotomized during the survey (Fig. 4), as also illustrated by the results of the linear regression analysis. The results of this analysis revealed a potential slope around zero and an exceptionally poor fit. A total of seventy-seven brittle stars were observed in this survey with diameter sizes ranging from 0.1 to 3.81 cm. There was substantial variation between the number of autotomized arms per individual with size not being a causing factor.

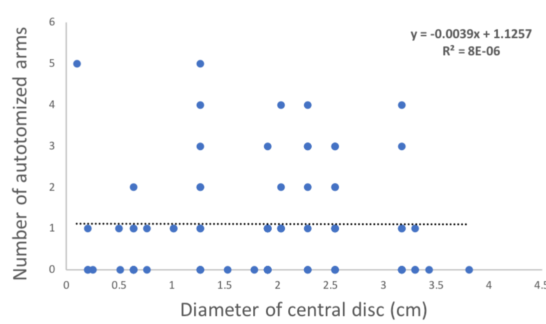

FIG. 4. Number of autotomized arms per individual brittle star versus diameter of the central disc of *Macrophiothrix longipeda* at Pihaena in Moorea, French Polynesia.

Exposure field survey

There was not a significant difference between exposure type (burrowed, partially burrowed, or exposed) during high tide or low tide proven by the chi square test for goodness of fit done for the distribution of individuals observed at both high and low tide. For both high and low tide, more individuals were found burrowed or partially burrowed as opposed to exposed. However, significantly more individuals were found exposed during high tide than low tide (Fig. 5). A total of 65 individuals were found burrowed during the survey, 76 partially burrowed, and 31 exposed. However, twice as many individuals were found exposed during high tide with 21 exposed during high tide and only 10 exposed during low tide. A chi square test of independence between two or more samples was done to assess differences between the distributions by exposure type at both high and low tide. The test gave me a chi square value of 1.7161 with a p value of 0.421888 which is significantly greater than the $\alpha<0.05$. From these results, I can conclude that there is no significant difference between the number of individuals observed burrowed, partially burrowed, or exposed at high tide versus low tide.

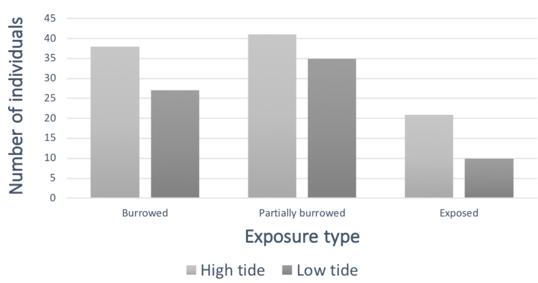

FIG. 5. Distribution of the number of individuals found burrowed, partially burrowed, or exposed during both high and low tide.

Autotomy frequency by exposure type

In order to assess the distribution frequency between those individuals who autotomized and did not autotomize by exposure type (burrowed, partially burrowed, exposed), I conducted a chi-squared one-sample test for goodness of fit for individuals observed at high tide and individuals observed at low tide. To test whether individuals autotomized more frequently by exposure type during high tide, I used the number of individuals observed exposed, burrowed, or partially burrowed during the high tide surveys at Pihaena beach. The results of this test showed a chi-squared value of 6.971 and a p-value of 0.030393 which concluded that there was in fact a significant difference among individuals who autotomized and did not autotomize at each exposure type (Fig. 6). For the low tide survey, a similar test was conducted in which I got a chi-squared value of 13.583 and a p-value of 0.0011231. This concluded that there was also a significant difference among autotomy frequencies by exposure type at low tide (Fig. 7). Similar results were shown across both high tide and low tide with more than 50% of individuals observed burrowed or partially burrowed during the surveys. Additionally, more than half of the individuals (66% at high tide, 63% at low tide) were found actively autotomizing across all exposure types with "exposed" being the only category in which more individuals were found not actively autotomizing during the time of observation (Fig.6 and Fig. 7).

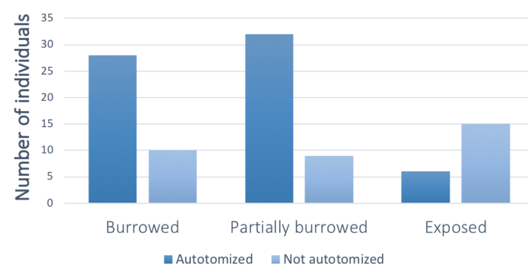

FIG. 6. A simple bar graph showing the number of individuals that autotomized arms and did not autotomize arms based on exposure type during high tide.

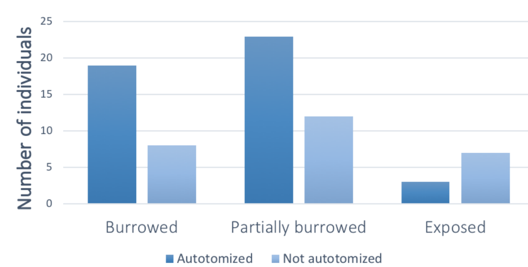

FIG. 7. A simple bar graph showing the number of observed individuals that autotomized arms based on exposure type during low tide.

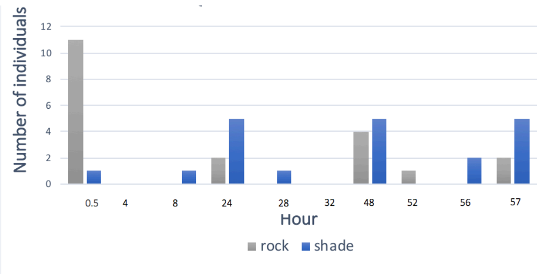

FIG. 8. Bar chart summarizing the count of individuals that found their way under both rock and shade at each hour of observation.

A Mann Whitney-U test was used to assess if there was a significant difference in the median time it took for individuals to find their way under rock and shade. This test proved a significant difference (Mann-Whitn U=104.5, p(same med)=0.008). Of the 20 individuals that found there way under rock (Fig. 8.), more than half (11/20) found their way under at the very first observation time at 10:00am (listed as hour 0.5, Fig.8) whereas the median time it took individuals to find their way under shade was 48 hours into the study. Additionally, more individuals in total found their way under the physical object than the shade indicated by hour 57 (reference Fig.8) which represents individuals who never made their way under.

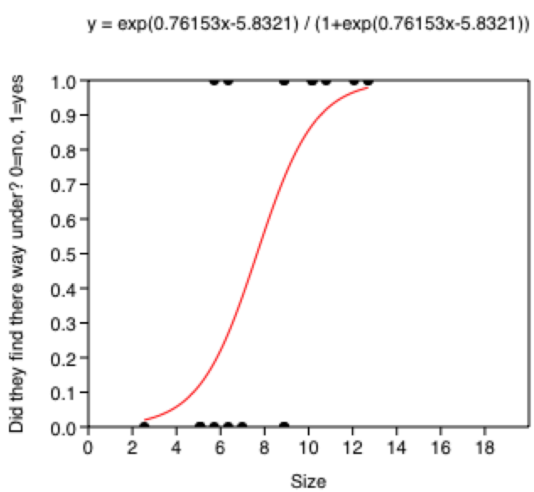

FIG. 9. A regression analysis used to display the relationship between size and how often individuals were able to find their way under rock/shade represented by the equation y=exp(0.76153x-5.8321)/(1+exp(0.76153x-5.8321)).

A logistic regression analysis was used to determine whether there was a significant difference between the length of autotomized arms and their ability to find their way under both rock and shade. The results showed that shorter arms found their way under both rock and shade substantially less often than the longer arms (Fig. 9). These results suggest that there was a significant difference between the length of the autotomized arms and their ability to function after they have been dropped (p(slope=0): 0.00083008, $\alpha<0.05$).

DISCUSSION

The overall goals of this study were to explore the factors influencing arm autotomization in brittle stars using field observations and a laboratory study. From my field observational study, I found that the number of arms autotomized in the field was unrelated to the diameter of the brittle star's central disc. However, arm automization was related to exposure type and, in particular, whether the individual was burrowed, partially burrowed, or exposed during high and low tide. I found that individuals were likely to autotomize when burrowed or partially burrowed during both high and low tide (88%). However, when exposed, more individuals were likely to autotomize during high tide than low tide, and significantly more individuals were found exposed during high tide. The final objective of this study was to understand arm behavior after an autotomization event has occurred, and whether behavior correlated with arm length. I found that that longer arms were able to find their way under both the physical object (i.e. rock, rubble, coraline algae, etc.) and shade much quicker than the shorter arms. However more arms on average, despite arm length, were able to find their way under the physical object than the shade.

Two species of brittle stars were found on the shore of Pihaena Beach in Moorea- *Macrophiothrix longipeda* and *Ophiocoma dentata*. A total of 77 individuals were observed during the field survey comparing brittle star size and autotomy frequency. Contrary to my hypothesis, the finding was that there was no significant correlation between autotomy frequency and brittle star size. This result supports an earlier study done that showed very little evidence that time to autotomize a limb was dependent upon body mass for the autotomizing species, *G. bimaculatus* (Bateman and Fleming 2008). Together, these results suggest that size plays less of a role in autotomy frequency when compared to other factors such as predation pressure or exposure during time of predation, or in this case, handling. Brittle stars frequently autotomize when handled which may be a primary reason for autotomization despite size (pers. obs., Price *et al.* 2014). In addition, defense mechanisms such as autotomization may be less influenced by changes in body size and more likely an automatic response that is species-specific (Bateman et al., 2008). Although not enough individuals of the species *Ophiocoma dentata* were found during my study to show significant differences between the two species, this may be something interesting to look at in future studies. Additionally, a key aspect of autotomy is the individual's willingness to lose an appendage at its own discretion (Bateman & Fleming, 2008). Because the survey required me to handle the brittle stars, hence inducing the autotomization process, it may not have been an accurate representation for natural autotomy rates in the wild. For example, for the species *Gryluss bimaculatus*, "unmated females are less 'willing' to shed legs when entrapped compared with mating females" (Bateman & Fleming, 2006). Thus, brittle stars may have other significant reasons or mechanisms to autotomize that may influence natural autotomy frequencies in the wild (i.e. gender, reproductive stage, etc. Fleming *et al.* 2007). These are all factors that could be considered in future studies.

Significantly more brittle stars were found burrowed or partially burrowed during both high tide and low tide at the Pihaena Beach field site. This aligns with an observation made in a previous study done in Moorea showing that brittle stars were often found exposing only one or two arms at a time (West 2012). The brittle stars that were burrowed or partially burrowed autotomized much more frequently than the ones that were found exposed. In fact, the organisms that were found exposed rarely autotomized, which contrasts with my original hypothesis that individuals would be more likely to autotomize when they are fully exposed. This could suggest that predation pressure may be low at this site and organisms are less inclined to autotomize when actively feeding. During my observations, I noticed that when the brittle stars are exposed they are usually not feeding but rather moving themselves to a new location. When feeding, they are usually partially burrowed with some of the body anchored beneath the substrate. In the future, it would be interesting to look at autotomy frequencies of *M. longipeda* across different sites in Moorea and compare autotomy frequencies by exposure type in these various environments. Additionally, it would be interesting to study autotomy frequencies by exposure type across several different species of brittle stars in Moorea in order to compare populations in different predation environments as well as explore species-specific differences as previously mentioned in a paper by Bateman *et al.* (2008).

My experimental studies revealed that autotomized arms continue to function several days after they have been dropped from the organism. Not only do they continue to move, they appear to have the capability to find their way under habitat and shade just like the whole organism would do in the wild if it was fully intact. Although not a lot of research has been done on the fate of the arms after they have been dropped, one potential reason they can still move days after being released from the organism may be to confuse predators into thinking that it is the actual organism itself giving the brittle star time to successfully escape. Another reason for the arms being able to move several days after autotomization may be that since brittle stars experience increased risk of predation following an autotomization event (Price *et al.* 2014), the moving arms may distract predators, and allow the organism time to escape, recover and, regenerate. Since the loss of a locomotor structure can significantly impair the brittle star's ability to escape future predation, moving arms may buy the organism time to recover and regenerate increasing the likelihood of survival (Shaeffer, 2016).

Many organisms, including all five classes of echinoderms, have successfully developed the ability to autotomize full or partial limbs to escape lethal predation (Candia-Carnevali *et al.* 2007). Understanding arm behavior post autotomy can give us greater insight into why ophiuroids in particular have developed the ability to autotomize and what makes it such an effective strategy to escape predators. Although autotomy and regeneration has been widely studied, not much work has been done on limb behavior or functionality post autotomization. For many organisms that autotomize, such as geckos and brittle stars, dropped limbs are able to function and move several hours of even days after they have been dropped (Jagnandan *et al.* 2014). The results of my study align with prior research that dropped limbs from autotomizing organisms can in fact move for a period of time after they have been dropped from the organism.

Overall this study revealed that size does not correlate with autotomy frequency, individuals at Pihaena beach are more likely to autotomize when burrowed or partially burrowed at both high and low tide, and individual arms are able to find their way under a physical object both quicker and more often. For future research, it would be interesting to look more in depth at the specific movements of individual arms post amputation to see if they move in the same way as intact arms. Work on this topic in geckoes has been done for changes in behavior and movement of the organism itself once it has dropped an appendage (Jagnandan and Higham 2017). However, behavior and functionality of the dropped limb(s) themselves has never been studied. Similarly, it would also be interesting to observe autotomized arms in the field and compare their behavior to that in a controlled lab setting like the one done in this study to understand how their behavior may differ under natural conditions and if those results are similar to results from the lab.

ACKNOWLEDGMENTS

I would like to thank Professors Cindy Looy, Ivo Duijnstee, Vince Resh, and Stephanie Carlson for their constant guidance and mentorship throughout the duration of the course. I would also like to thank graduate student instructors James LaChance, Clay Noss, and Renske Kirchholtes for going beyond their duties and always making themselves available to help with our research both in Moorea and in Berkeley. Thank you to all of my classmates, especially Heather McCandless, for making Moorea such a fun and memorable experience. Also, I'd like to acknowledge Heather and Kim for the hours spent helping me turn over rocks and rubble to find brittle stars for my surveys and experiments. Thank you to the Richard B. Gump station and its staff for their hospitality during our stay and for sharing their knowledge of the island with us. Lastly, thank you to the University of California, Berkeley for offering such an amazing and transformative experience for its undergraduate students.

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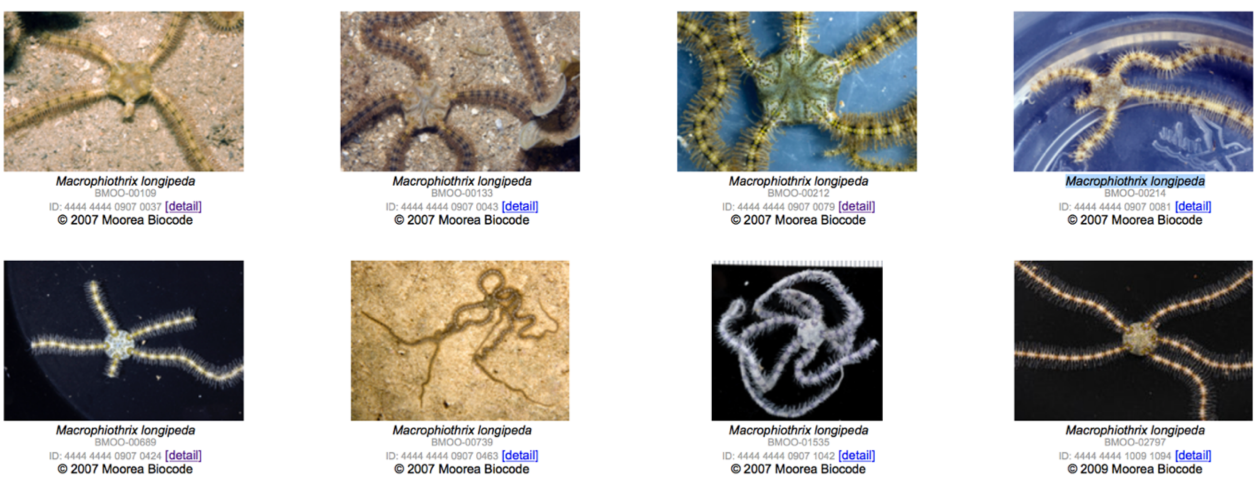
APPENDIX A



Color variation among the brittle star, *Macrophiothrix longipeda,* on Moorea, French Polynesia. Moorea Biocode.