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Local Patterns in Host-Selection by Anemone
Symbionts in Bocas Del Toro, Panama

A Thesis
Presented to
The Faculty and the Honors Program
Of the University of San Diego

By
Samantha Mercer
Environmental and Ocean Sciences
2015

Abstract

The associations made between many symbiotic cleaner shrimps and their host anemone species are influenced by local ecological factors, resulting in regional variations in symbiont-host preferences. These relationships are crucial parts of aquatic ecosystems, and as we face rapid global environmental change, understanding the local patterns of this host specificity will be essential to maintaining healthy marine environments. However, sea anemones, as well as their symbiotic relationships, from the Caribbean coasts of Panama have been poorly studied and are largely under-represented in the current literature. The purpose of this study is to identify the local host-selection patterns, specifically regarding host-size and host-species, of anemone symbionts in the Bocas del Toro, Panama region of the Caribbean. We surveyed 12 sites in this area for the presence of symbionts on the host species *Bartholomea annulata* (Corkscrew), *Bartholomea lucida* (Knobby), *Condylactis gigantea* (Giant), *Stichodactylus helianthus* (Sun), and *Lebrunia danae* (Branching). The individual symbiont species *Periclimenes yucatanicus* (Spotted Cleaner Shrimp) and *Mithrax cinctimanus* (Banded Clinging Crab), as well as symbionts overall, were found to have a significant preference in host-species and host-size. These preferences were for *S. helianthus* and larger hosts.

Keywords: Bocas del Toro, anemone symbionts, *Periclimenes yucatanicus*, *Mithrax cinctimanus*, preference, host selection, host-species, host-size

Introduction

The symbiotic relationships between anemones and crustaceans, although complex, are important aspects of marine ecosystems (Patzner 2004; Silbiger and Childress 2008; Fourzán 2012). These associations can be passive on the part of the anemone, in which associates live on

the outside of the anemone, or active on the part of the anemone, in which the anemone lives on an associated organism (Patzner 2004). Passive associations on the part of the anemone are commonly observed with symbiotic crustaceans, such as cleaner shrimp and crabs, which live within the tentacles of the anemone (Patzner 2004). These species form a mutualistic type of symbiosis, in which both species benefit. The hosts (anemones) have increased access to nutrients, and use the Nitrogen in symbiont waste as a source of food. Predation pressure is one of the greatest factors affecting decapod abundance and distribution (Guo et al. 1996; Baeza and Stotz 2003; Ory et al. 2013), and these symbiotic relationships provide protection from predation to their symbionts; many predators avoid the stinging tentacles of anemones (Patzner 2004; Silbiger and Childress 2008; Fourzán et al. 2012; Mascaró et al. 2012), while symbionts are able to acquire immunity to these stings through a process called acclimation (Crawford 1992; Fourzán et al. 2012).

Though the mechanism of acclimation is not yet fully understood, studies have shown that both cleaner shrimp and reef fish associated with anemones develop a sort of chemical camouflage that protects them from the nematocysts in their host anemones' tentacles (Levine and Blanchard 1980; Crawford 1992). Some believe this camouflage is a result of the symbiont covering itself in the anemone's mucous; reef fish associated with anemones have been shown to acclimate this way, and some believe shrimp acclimation is analogous (Levine and Blanchard 1980). Other studies suggest cleaner shrimp alter their own chemical secretions in a way that makes them immune to nematocyst stings (Crawford 1992). This chemical alteration persists through ecdysis, allowing them to remain acclimated even after they have molted (Crawford 1992). However, throughout literature there is a consensus that acclimation is temporary and symbionts lose their protection against their hosts when isolated from them (Levine and Blanchard 1980; Crawford

1992). Many individual symbiotic species also acclimate more commonly with particular host anemones (Levine and Blanchard 1980; Crawford 1992; Guo et al. 1996; Hayes and Trimm 2008; Silbiger and Childress 2008; Mascaró et al. 2012), and often symbionts are found with only some of the anemones sympatric with them (Guo et al. 1996). Furthermore, particular symbiont species have been reported to be generalists – symbionts that associate with many host species – in some areas, but specialists – symbionts that associate with only one host species – in others (Hayes and Trimm 2008; Silbiger and Childress 2008; Fourzán et al. 2012). These differences may impact how resilient local populations of these symbionts are to environmental change; specialists may be particularly vulnerable to changes in the distribution and abundance of their host species, while generalists can more effectively buffer changes in particular host species by occupying a range of species (Silbiger and Childress 2008).

Current literature also indicates that for many symbiotic cleaner shrimp species, host selection varies regionally (Levine and Blanchard 1980; Guo et al. 1996; Hayes and Trimm 2008; Silbiger and Childress 2008; Mascaró et al. 2012). Studies of anemone/cleaner-shrimp symbiosis conducted throughout the Caribbean indicate that within the species' distribution ranges, regional variations in the associations made between specific symbionts and their host species occur (Levine and Blanchard 1980; Guo et al. 1996; Hayes and Trimm 2008; Silbiger and Childress 2008; Mascaró et al. 2012). In certain regions of the Caribbean, *Periclimenes rathbunae* (Sun Anemone Cleaner Shrimp) has been found to associate with *Bartholomea annulata* (Corkscrew), yet in Jamaica, where there is a large population of *B. annulata*, *P. rathbunae* has never been found to associate with it (Levine and Blanchard 1980). Other studies throughout the Caribbean have found *P. rathbunae* to also associate with *Bunodosoma granulifera*, *Condylactis gigantea* (Giant), *Eunicea tourneforti*, *Homostichanthus duerdeni*,

Lebrunia danae (Branching), and *Stichodactylus helianthus* (Sun), though quantitative data accompanying these findings is lacking (Hayes and Trimm 2008). *Periclimenes pedersoni* (Pederson Cleaner Shrimp) has also been reported to frequently associate with *B. annulata*, as well as *C. gigantea* around the Caribbean and the Gulf of Mexico, yet in Quintana Roo, Mexico, *P. pedersoni* has never been observed in association with *C. gigantea* (Mascaro et al. 2012).

Although the mechanisms of cleaner shrimp host selection is still largely unknown, some studies have been conducted to help illuminate the many factors that could be playing a role in such varied association patterns. Lab studies conducted by Mascaro et al. (2012) indicate that while *P. pedersnoi* acclimated to *B. annulata* more frequently than to *C. gigantea*, this behavior was not a result of active choice; the difference in the frequency of acclimation to the two species was significantly similar between shrimp who were presented with alternative anemones (a choice) and shrimp that were presented with only one anemone species (no choice). This suggests that it is ecological factors, rather than active choice or preference that leads to the observed varied association patterns. Furthermore, some of these ecological factors must work at a local scale; if only larger scale factors had an effect on host selection, the regional differences in association patterns discussed throughout the literature (Levine and Blanchard 1980; Guo et al. 1996; Hayes and Trimm 2008; Silbiger and Childress 2008; Mascaró et al. 2012) would be absent (Mascaró et al. 2012). Host availability (Silbiger and Childress 2008), morphology of host (Baeza and Stotz 2003; Baeza and Thiel 2003), presence of other symbionts (Hays and Trimm 2008; Fourzán et al. 2012; Moscaró et al. 2012), and previous associations with host (Baeza and Stotz 2003; Moscaró et al. 2012; Ocampo et al. 2012; Ory et al. 2013) have all been factors reported to have an effect on symbiont host selection. Specifically, Hayes and Trimm (2008) found that multiple shrimp of the *Periclimenes spp.* often occupied the same anemone,

despite the presence of unoccupied anemones nearby, indicating that host selection is not driven by host isolation. Silbiger and Childress (2008) found that cleaner shrimp's host selection in the Florida Keys, USA, was driven in part by availability of hosts at a local spatial scale: *Periclimenes yucatanicus* (Spotted Cleaner Shrimp) were primarily found in *C. gigantea* and only inhabited *B. annulata* in areas where *C. gigantea* populations were restricted. Additionally, they found that once *P. pedersoni*, which are typically considered generalists, has selected a host, it acclimates more frequently to that host. This indicates that both generalists and species with greater specificity may alter their host selection in different environments (Silbiger and Childress 2008).

Silbiger and Childress (2008) also examined temporal variability in host selection patterns, comparing their study to one done in the same region twenty years prior (Mihalik, 1989). They found that although *P. yucatanicus* was primarily found in *C. gigantea* in their study, it had previously been primarily associated with *S. helianthus*. In 1998, *S. helianthus* comprised about 50 percent of the total anemone population in the region, and about 75 percent of these were occupied by *P. yucatanicus* (in comparison to only 32 percent and 0 percent of *C. gigantea* and *B. annulata*, respectively, occupied by *P. yucatanicus*). However, in 2006, when the Silbiger and Childress study was conducted, *S. helianthus* had declined to only one percent of the total anemone population. Interestingly, the relative proportion of anemone occupation didn't change: 100 percent of *S. helianthus*, 35 percent of *C. gigantea*, and 4 percent of *B. annulata* were occupied by *P. yucatanicus*. Additionally, the decline in the *S. helianthus* population was mirrored by a decline in the *P. yucatanicus* population. This indicates that *P. yucatanicus* largely maintained its preference for *S. helianthus* despite the decline, and did not redistribute themselves on other available hosts. Although the cause of the *S. helianthus* decline is unknown,

possible factors include eutrophication and consequent sunlight limiting algal blooms (Silbiger and Childress, 2008). The decline in *P. yucutanicus* was likely linked to the decline in *S. helianthus*, their preferred host; the host decline likely led to fewer individuals successfully settling or dispersing to an adequate anemone, resulting in a decrease in the symbiont population as well. This demonstrates the increased vulnerability specialists may exhibit in the face of environmental change. Their populations are linked to their host populations, and they lack the buffer generalists have in adapting to changing host distributions.

As development in Bocas del Toro continues, anthropogenic impacts, such as eutrophication and physical reef destruction, are expected to increase, likely affecting local marine ecosystems. However, the consequences and extent of these effects, particularly on host populations, and consequently their symbiont populations are largely unknown; the impacts felt by symbionts, as well as their resilience to changes in host distributions and populations need to be assessed (Silbiger and Childress 2008). As we face rapid environmental change, understanding the local patterns of this host specificity will be essential to maintaining healthy marine ecosystems (Silbiger and Childress 2008). However, sea anemones, as well as their symbiotic relationships, from the Caribbean coasts of Panama have been poorly studied and are largely under-represented in the current literature (Garese et al. 2009). As development in Bocas del Toro continues, anthropogenic impacts, such as eutrophication and physical reef destruction, are expected to increase, likely affecting local marine ecosystems. The symbiotic relationships between cleaner shrimp and crabs, and anemones are a vital part of this local marine ecology; a basic understanding of the distributions and mechanisms behind the regional relationships will be important to preserving these marine ecosystems. However, there is no current literature

addressing the particular host preferences of anemone shrimp in the Bocas Del Toro region of the Caribbean

As such, this study seeks to identify the local host-selection patterns of anemone symbionts in the Bocas del Toro, Panama region of the Caribbean. This will provide a baseline of local anemone-symbiont associations. Research questions include: do anemone symbionts demonstrate a preference in host species, and if they do, which symbionts prefer which hosts? Is a preference in host size present in this region, and if so, what is it?

Materials and Methods

We used snorkel to collect data at 12 different sites throughout the Bocas Del Toro archipelago in Panama. The sites were 0.5-3m deep and offshore of five islands: Isla Colón, Isla Bastimentos, Isla Popa, Isla Cristóbal, and Isla Solarte (see **Fig. 1**). The latitude and longitude of each site was recorded using GPS Garmin 60 (see **Table 1**). All data collection took place in April, 2014, between 9am and 4pm.

We used the belt-transect method to collect density and distribution data on the five sea anemones species *C. gigantea*, *S. helianthus*, *B. annulata*, *Bartholomea lucida* (Knobby), and *L. danae*. Pairs of students conducted two 50X3m transects at each site. All anemones belonging to the study species found within the transects were identified and measured for size. This size measurement was taken as the horizontal distance across the widest point of the extended anemone, tentacle tip to tentacle tip (Hayes and Trimm 2008). Each anemone was also examined for the presence of symbionts. Any that were found were identified and measured for size. For symbiotic shrimp, size was measured as carapace length. For crabs, only the width of the body at its widest point was measured. All size measurements were made to the nearest centimeter using

a ruler drawn onto an underwater slate. There were three pairs of students collecting this data, providing six transects per site and 72 transects in the whole study.

All of the data was compiled and analyzed using Microsoft Excel 2010 Version 14.0.7116.5000. Single Factor Anova tests were conducted to determine the presence of a preference in host species by symbiont species overall, as well as by the individual symbiont species *P. yucatanicus*, and *Mithrax cinctimanus* (Banded Clinging Crab). Two-tailed T-tests were used to analyze the correlation between size of anemone and the presence of symbionts; these were used to determine if there was an overall host-size preference by symbionts, as well as host-size preferences within the individual symbiont species *P. yucatanicus* and *M. cinctimanus*.

Results

We counted and measured a total of 3,534 anemones, of which 422 had symbionts (see **Fig. 2**). A total of 289 *P. yucatanicus*, 19 *Stenorhynchus seticornis* (Arrow Crab), and 177 *M. cinctimanus* were found on the host species *B. annulata*, *B. lucida*, *C. gigantea*, *L. danae*, and *S. helianthus*. A total of five *P. pedersoni* were found on *B. annulata*, and *S. helianthus* – none were found on *B. lucida*, *C. gigantea*, or *L. danae*. A total of 25 *P. rathbunae* were found on *C. gigantea*, and *S. helianthus* – none were found on *B. annulata*, *B. lucida*, or *L. danae* (see **Fig. 3**). We found two additional *Mithrax sp.*, (see **Fig. 4**) and three individuals of an unknown shrimp species (see **Fig. 5**) on two *S. helianthus*, respectively, at site nine. These symbionts were excluded from all other calculations, as they were the only ones of their kind found throughout the whole study. An overall significant preference in host species was found to be present (single factor ANOVA, $df=4$, $p=0.0005$). *P. yucatanicus* was found to have a significant preference in

host species (single factor ANOVA, $df=4$, $p \leq 0.001$); of measured *B. annulata*, *B. lucida*, *C. gigantea*, *L. danae*, and *S. helianthus*, 3%, 0%, 2%, 0%, and 39%, respectively, were occupied by *P. yucatanicus*. *M. cinctimanus* was also found to have a significant preference in host species (single factor ANOVA, $df=4$, $p=0.01$), and occupied 1%, 2%, 18%, 7%, and 17% of *B. annulata*, *B. lucida*, *C. gigantea*, *L. danae*, and *S. helianthus*, respectively (see **Fig. 6**). Of the 25 *S. helianthus* *Anemone Shrimp* found, 24 were on *S. helianthus*. An overall significant preference in host-size was found to be present (two-tailed T-test, $df=2$, $p \leq 0.001$). At every site, the average size of anemones occupied by symbionts was larger than the average size of unoccupied anemones (see **Fig. 7**). Furthermore, there was an exponential relationship between the percentage of occupied anemones for any given host size with increasing anemone size ($r^2=0.5$) (see **Fig. 8**). A significant preference in host-size was detected for specifically *P. yucatanicus* (two-tailed T-test, $df=2$, $p=0.002$) and *M. cinctimanus* (two-tailed T-test, $df=2$, $p=0.0008$). The average size of anemones occupied by *P. yucatanicus* was larger than the average size of unoccupied anemones at every site (see **Fig. 9**), and the average size of anemones occupied by *M. cinctimanus* was larger or equal to the average size of unoccupied anemones at all but one site (see **Fig. 10**).

Discussion

Our data indicate the significant preference in host species demonstrated by *P. yucatanicus* and all symbiont species combined is for *S. helianthus*. The presence of more *L. danae*, *B. lucida*, and *B. annulata* individuals, paired with the greater percentage of *S. helianthus* occupied by symbionts, indicate that this higher occupancy rate was not due to an absence of other host-species or a greater abundance of *S. helianthus*. Furthermore, while host availability has been

reported to have an effect on symbiont host selection (Baeza and Stotz 2001; Silbiger and Childress 2008), the presence of unoccupied anemones of all species indicates that this was not a contributing factor in our observed symbiont-host preferences. Instead, other ecological factors, such as level of protection from predation and potential host competitors may play a role (Guo et al. 1996). The presence of this same host-species preference in *P. yucatanicus* has also been reported in the Florida keys, USA. However, recent declines in *S. helianthus* populations have led to regional decreases in *P. yucatanicus* abundance (Silbiger and Childress 2008). This suggests that *P. yucatanicus*, as well as other symbiont species that show a strong preference for a particular host species may be particularly vulnerable to changes in host abundance and distribution. In contrast to both our results and the results of Silbiger and Childress (2008), Fourzán et al. (2012) found *P. yucatanicus* to be a generalist with no preferences for any particular host-species throughout different parts of the Caribbean. However, *S. helianthus* was not included in that study, potentially contributing to the observed differences in results. Our study also suggests a preference for *S. helianthus* by *P. rathbunae*, as all but one of these symbionts were found on this host. This symbiont was never found with *B. annulata* or *L. danae*, despite reports of such associations in other parts of the Caribbean (Levine and Blanchard 2008; Fourzán et al. 2012). A preference for *B. annulata* and *S. helianthus* by *P. Pedersoni* is suggested by its occurrence on only these two host-species. *P. Pedersoni* preference for *B. annulata* has also been reported in other parts of the Caribbean (Silbiger and Childress 2008; Fourzán et al. 2012; Mascaró et al. 2012). However, in Florida Bay, USA, this preference was found to be a result of the regional numeric dominance of *B. annulata*; there, *P. Pedersoni* demonstrated a preference for relatively abundant hosts (Silbiger and Childress 2008). This is inconsistent with our data, in which *P. Pedersoni* were not found to associate with the most numerically abundant

host, *L. danae*, at all. Our data suggest the significant preference for host-species demonstrated by *M. cinctimanus* is for *C. gigantea* and *S. helianthus*. This preference for *C. gigantea* has been reported to occur throughout the Caribbean (Fourzán et al. 2012). *S. seticornis* was found on all studied host-species, but we did not have enough data to reach any statistical conclusions regarding its host preferences. The data collected on both *P. rathbunae* and *P. Pedersoni* were also insufficient to make any statistical conclusions on their preferences, and the discussed preferences do not have statistical significance. Further research on the association patterns and preferences of these three symbionts should be conducted. Nonetheless, our results indicate symbiotic shrimp preferences in host-species that are specific to the Bocas del Toro region and support the presence of regional variation in symbiotic shrimp preferences. These results can be used to fill a current gap in the related literature (Levine and Blanchard 1980; Guo et al. 1996; Hayes and Trimm 2008; Silbiger and Childress 2008; Mascaró et al. 2012). The local preference for *S. helianthus* shared by *Periclimenes spp.* and *M. cinctimanus* in Bocas del Toro may be indicative of other shared regional preferences between symbiotic shrimps and crabs. However, there is insufficient literature on the regional associations of symbiotic crabs to determine if their preferences also vary locally. Future studies on symbiotic crab associations should be conducted around the world to determine if their host-preferences are also specific to region.

A significant preference in size of host was demonstrated by symbionts overall, as well as by the species *P. yucatanicus* and *M. cinctimanus* individually. Our results suggest this preference is for larger anemones. Ecological factors driving this preference may include the local abundance of predators, as larger anemones may provide greater protection from predation (Silbiger and Childress 2008). Other symbionts in the environment, such as reef-fish associated with cleaner-shrimps, may also contribute to this preference. Symbiotic shrimp density has been reported to

be significantly correlated with anemone size (Hayes and Trimm 2008; Fourzán et al. 2012) and higher cleaner shrimp densities have been associated with increased visitation by client fish; the local presence of symbiotic cleaner-shrimp that benefit from increased client fish visitation may drive the preference for larger host size (Fourzán et al 2012). Larger anemones may also be easier to locate (Silbiger and Childress 2008).

As environmental degradation continues to increase, understanding the factors that affect the symbiotic relationships with anemones will be essential to conserving the ecosystems they are a part of (Silbiger and Childress 2008). The significant preferences in host-species and host-size shared by *P. yucatanicus* and *M. cinctimanus* in this study raise the question of what other features of anemone symbiosis are shared between symbiotic crabs and shrimps? These shared preferences may indicate shared mechanisms of host selection, and current knowledge of one type of symbiotic decapod may be able to illuminate characteristics of others. A similar example is the shared protection of reef fishes and shrimp symbiotic with anemones; the method by which reef fish had been reported to acclimate to the anemones was tested on symbiotic shrimp, and it was found that the mechanism of acclimation is largely shared between both types of symbionts (Levine and Blanchard 1980; Crawford 1992). Realizing the similarities and differences between symbiotic shrimp and crabs will provide greater knowledge on their roles in aquatic ecosystems, as well as how they may be affected by environmental change.

Additionally, recognizing which species are likely to retain their host specificity, even in the face of declining host populations, can help predict which species will be most vulnerable to environmental change. Our results mirror the host selection and distribution patterns observed in the Florida Keys in 1989 (Silbiger and Childress, 2008). Although the factors causing the observed *S. helianthus* decline in this region are largely unknown, it is suspected that

eutrophication did play a role. As Bocas continues to develop and the surrounding marine environments are exposed to greater anthropogenic inputs, eutrophication is a very real threat. This may lead to similar declines in both *S. helianthus* and consequently *P. yucuanticus*, as was observed in Florida, likely effecting more of the local aquatic ecosystem.

Understanding the local associations of anemone symbionts helps illuminate the different patterns of associations and the factors causing them worldwide. Studies on anemone symbiont associations should continue to be conducted in areas that are underrepresented in the literature. Our study was limited in length and the time of year the study was conducted, as depth. Future studies should take place throughout different times of the year to assess the effects of seasonality, and at deeper depths to identify the host-selection patterns occurring here. The identity and distribution patterns of the two additional *Mithrax* *sp.* and the unknown shrimp species found at site nine should also be investigated, as we could not find any literature discussing the presence of these species in the Caribbean.

Acknowledgements

Special thanks to the School for Field Studies, my professor, Dr. A. Kramer, the assisting intern, M. Meilinger, and my data collection partner, O. Bourque, as well as the other members of our field team, G. Dennis, K. Rogers, C. Hughes, and C. McAleavey. Also Drs. Drew Talley and Steven Searcy for their guidance and assistance in this research.

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Appendix

GPS Coordinates of Study Sites		
Site	Latitude (N)	Longitude (W)
1	9.17.545°	82.11.664°
2	9.14.926°	82.09.907°
3	9.16.403°	82.10.685°
4	9.14.131°	82.08.787°
5	9.17.881°	82.17.368°
6	9.17.857°	82.15.954°
7	9.20.444°	82.12.639°
8	9.19.747°	82.11.372°
9	9.21.704°	82.16.754°
10	9.19.903°	82.15.264°
11	9.17.113°	82.11.456°
12	9.17.182°	82.11.676°

Table 1 GPS coordinates of the 12 sites in Bocas del Toro, Panama, used in this study. All coordinates were taken with a GPS Garmin 60

Map of Study Sites

Fig. 1 a. Map of Panama. Bocas del Toro and the region of the Caribbean where the study took place is indicated. Map courtesy of Google Maps. b. Map of the twelve sites in Bocas del Toro used in this study. Map courtesy of Google Earth

Fig. 2 The number of measured anemones compared to the number of anemones occupied by symbionts for each studied host species

Fig. 3 Percentage that the symbiont species used each study host species

Fig. 4 a. Picture of one *Mithrax sp.* found under *S. helianthus* at site nine. b. Picture of another *Mithrax sp.* found under *S. helianthus* at site nine. Both pictures courtesy of Annemarie Kramer

Fig. 5 a. Picture of unknown shrimp species under *S. helianthus*. Three individuals were found under one *S. helianthus* at site nine. b. Picture of an unknown shrimp species in a Petri dish. Both photos courtesy of Annemarie Kramer

Fig. 6 The percentage of measured anemones belonging to each studied anemone species that was occupied by the symbionts *P. yucatanicus* and *M. cinctimanus*

Fig. 7 Average size (cm) of unoccupied anemones compared to the average size of anemones occupied by any symbiont at each of the twelve study sites

Fig. 8 The exponential relationship between the size of anemones and the percentage of anemones of that particular size that are occupied by symbionts

Fig. 9 Average size (cm) of unoccupied anemones compared to the average size of anemones occupied by *P. yucatanicus* at each of the twelve study sites

Fig. 10 Average size (cm) of unoccupied anemones compared to the average size on anemones occupied by *M. cinctimanus* at each of the twelve study sites