

# SYMBIOSIS OF THE SEA STAR SHRIMP (*PERICLIMENES SOROR*) AND CUSHION STAR (*CULCITA NOVAEGUINEAE*): HOST FIDELITY, HOST FINDING, AND BENEFITS

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*Abstract.* Symbioses play an integral role in community structure and act as significant selective forces in evolution; hence these relationships have been the subject of much scientific interest. The symbiosis between the pontonine shrimp, *Periclimenes soror* (family Palaemonidae) and the Cushion Star, *Cucita novaeguineae* (family Oreasteridae) was investigated using field observations as well as laboratory experimentation. Host fidelity, host-seeking behavior, and benefits imparted to shrimp symbionts were examined. A mark-recapture study indicated that shrimp populations on individual sea stars change frequently, suggesting a dynamic relationship between *P. soror* and *C. novaeguineae*. Results from a Y-maze experiment revealed that *P. soror* appears to actively orient to its hosts, and that chemical cues play a role in the orientation process. Results from a survivorship experiment suggest that *P. soror* may be an obligate associate of its host and likely receives alimention through its relationship with *C. novaeguineae*. Results from a hiding experiment and color-match experiment indicate that *P. soror* may also obtain protection from predators through this association by both behaviorally hiding on its host, and also actively changing color to reside cryptically on *C. novaeguineae*. The findings of this study provide insight into the relationship between *P. soror* and *C. novaeguineae* as well as help contextualize this association with symbioses in general.

*Key words:* symbiosis; shrimp; sea star; *Periclimenes soror*; *Cucita novaeguineae*, host fidelity; orientation; cryptic coloration; protection from predators; alimention; Mo'orea, French Polynesia

## INTRODUCTION

Symbiotic relationships are biological associations in which individuals of different species engage in close and often long-term interaction with one another. These interactions may be beneficial to both parties (mutualism), beneficial to one party and neutral to the other (commensalism), or beneficial to one party but detrimental to the other (parasitism). Due to the fact that symbioses play an integral role in community structure and act as significant selective forces in evolution, these associations have been the subject of much scientific interest (Leung and Poulin 2008). In ecosystems with exceptionally high levels of biodiversity, such as coral reefs, understanding the intricate relationships among species is essential to our comprehension of ecosystem structure.

In the marine environment, Crustacea are of notable interest when examining symbioses because they have been documented in a prolific number of inter- and intra-phyla symbiotic associations (Green 1961). Shrimps,

in particular, are often found in symbiotic relationships with a diverse group of organisms, including sponges, cnidarians, echinoderms, and fish (Fautin 1995, Duris *et al.* 2008, Wear 1976, Poulin and Grutter 1996, Crandall *et al.* 2008). Analysis of the stomach contents of several species of sponge-inhabiting pontonine shrimp including *Typton carneus*, *Periclimenaeus caraibicus*, and *Onycocharis spinosa* revealed that the spongiobionts often interact parasitically with their hosts by feeding directly on sponge tissue. It is thought that these shrimp colonize their host during the postlarval stage and subsequently live permanently on their host as either a solitary individual or in a male-female pair. The shrimps' large chelae are hypothesized to be utilized in repelling conspecifics that would compete for limited host resources (Duris *et al.* 2008). *Periclimenes pedersoni*, a pontonine associate of the anemone *Bartholomea annulata*, places itself in a prominent location on or near its host and sways back and forth while whipping its antennae in order to attract reef fish, which are

subsequently cleaned by the shrimp. *P. pedersoni* is generally found in pairs, but also occurs solitarily, and can be found in groups of up to five. The relationship between *P. pedersoni* and *B. annulata* is thought to be relatively dynamic, as *P. pedersoni* has been observed to frequently switch between host anemones (Limbaugh *et al.* 1961).

In Mo'orea, French Polynesia, the pontonine shrimp *Periclimenes soror*, is commonly found on the cushion star (*Culcita novaeguineae*). Little is known about the relationship between these two species. Gontang (1999) found that the number of shrimp symbionts found on the host stars was not correlated to star diameter. Additionally, she determined that *P. soror* did not exhibit host preference among individuals of *C. novaeguineae* in a laboratory setting. Both organisms display a wide variety of colors (Gontang 1999, personal observation), and it is thought that *P. soror* is able to color match its host (Crandall *et al.* 2008), although this has yet to be documented with empirical data.

This study aims to further investigate the symbiotic relationship between *P. soror* and *C. novaeguineae*. In order to better understand this symbiosis and place it in the context of other symbioses, it is important to examine host fidelity in the natural environment, whether the organisms actively seek one another, and the various costs or benefits imparted to the involved organisms. This study will explore these topics by addressing the following questions: Do populations of *P. soror* on individual sea stars change over time? Does *P. soror* actively seek out host sea stars, and if so, do chemical cues play a role in the orientation process? Does *P. soror* obtain any metabolic benefits through its association with *C. novaeguineae*? Does *P. soror* obtain protection from predators through associating with *C. novaeguineae* by both behaviorally hiding on the sea stars and actively changing color to match its host?

## METHODS

### *Study site*

Field experiments and surveys were conducted in Cook's Bay, Mo'orea on the reef flat adjacent to and just north of the UC Berkeley Gump Research Station (17°29'22.76"S, 149°49'33.12"W). The site was chosen due to the high density of *C. novaeguineae* individuals in this area.

### *Study organisms*

The sea star shrimp (*Periclimenes soror*) is an asteroid echinoderm symbiont widely distributed in the Pacific Ocean, Indian Ocean, as well as the Red Sea (Bruce 1978). *P. soror* has been recorded in symbioses with over 25 species of sea stars in the tropical Pacific Ocean alone (Crandall *et al.* 2008). Although the shrimp's relationship with its hosts has been previously described as commensal (Wear 1976, Gontang 1999), the exact nature of the symbioses remains unknown (Crandall *et al.* 2008, AJ Bruce, personal communication).

The cushion star (*C. novaeguineae*) is an asteroid corallivore present on coral reefs in the western and central Pacific Ocean, as well as the eastern Indian Ocean. *C. novaeguineae* is known to feed selectively on certain species of coral, and is thus presumed to have the ability to affect coral community structure (Glynn and Krupp 1986).

### *Pilot study*

A general survey was conducted of *C. novaeguineae* and its symbiotic associates at the study site from 11 Oct. 2011 – 19 Oct. 2011. Various types of data were collected about each *C. novaeguineae* individual encountered while snorkeling, including sea star color, sea star depth, and the number, size, color and location of any *P. soror* associates. To ensure that the location of *P. soror* on its host was accurately determined, the aboral surfaces of the sea stars were inspected for about 30 seconds before the sea stars were turned over to expose any *P. soror* individuals located on the oral surface. In order to minimize disruption of the symbiosis, the sea stars were handled very gently so as not to dislodge any shrimp from their hosts.

### *Consistency of P. soror associates on C. novaeguineae*

In order to assess the consistency of *P. soror* populations on *C. novaeguineae* individuals, 58 sea stars were marked in situ by superficially etching a design onto their aboral surfaces with a small blade during the pilot study. Additionally, pictures were taken of the oral and aboral surfaces of each individual in order to assist in identifying individuals if the marks became indistinguishable. For a 10-day period, the number, color, and size of shrimp associates on marked sea stars were recorded as the sea

stars were opportunistically encountered while snorkeling. As it was difficult to measure the shrimp using a ruler, shrimp were placed in a size class (small, medium, large) using visual estimation. In analyzing the data, a change in the *P. soror* population was defined as the appearance or disappearance of either one shrimp in the large or medium size classes, or two shrimp in the small size class. The appearance or disappearance of a single shrimp in the small size class was not considered to be a change because these shrimp tended to be mostly transparent, and the appearance or disappearance of a single small shrimp may have been the result of faulty recording. This definition of change is thought to be conservative, for it is possible that shrimp joined and left marked starfish between sightings. Additionally, because it is difficult to distinguish among shrimp in the same size class, it is possible that different shrimp were recorded to be the same individual on separate sightings.

#### *Collection and housing of study organisms*

All shrimp and sea stars used in the experiments described below were opportunistically encountered while snorkeling at the study site and collected using one-liter Ziploc bags. After being transported back to the wet laboratory at the Gump Station, the organisms were housed in large, circular tanks supplied with a constant flow of ocean water.

#### *Chemical orientation to *C. novaeguineae**

Because data from the pilot survey suggested that *P. soror* may frequently switch between hosts, an experiment was designed to test whether *P. soror* actively orients to its host using chemical cues. *P. soror* individuals were manually isolated from their hosts using 50 ml. falcon tubes and placed into a Y-maze (Figure 1). One arm of the Y-maze was pumped with water from a separate 4.5 liter tub containing a *C. novaeguineae* individual, and the other arm of the maze was pumped with regular ocean water, also flowing from a 4.5 liter tub. All shrimp were placed in the same location at the base of the Y-maze, and their movement in relation to the different water flows was recorded. If the shrimp swam 15 cm or more into the arm of the Y-maze containing the stimulus, it was considered to have oriented to its host. If the shrimp did not

move, or moved more than 15 cm into the arm of the Y-maze without the stimulus, it was considered to have not oriented. The same *C. novaeguineae* individual was used for every trial. The experiment was carried out with 28 large, purple *P. soror* individuals, none of which were originally found on the *C. novaeguineae* individual used in the experiment. Each shrimp was used in two trials, one in which the stimulus was pumped into the left arm of the Y-maze, and another in which the stimulus was pumped into the right arm of the maze. Switching water flows ensured that the data was not biased by preference for a particular arm of the Y-maze.



FIG. 1. Y-maze used in the chemical orientation experiment. Both arms of the Y-maze were 30 cm long, and the base was 26 cm long. The Y-maze was 5 cm wide and 4 cm deep.

#### *Alimentation and survivorship*

*P. soror* individuals on their hosts were examined with a hand lens in order to view any possible feeding behaviors of the shrimp. Additionally, a survivorship experiment was conducted to examine whether *P. soror* receives alimentation through its association with *C. novaeguineae*. A total of 27 shrimp were used in the experiment. The experiment comprised three treatments: isolated-unfed, isolated-fed, and not isolated. In the isolated-unfed treatment, nine shrimp were isolated from their hosts using 50 ml. falcon tubes and divided into three three-liter Tupperwares equipped with bubblers. The ocean water in these Tupperwares was filtered with a plankton net to remove any potential sources of food. In the fed-isolated treatment, nine shrimp were isolated from their hosts using 50 ml. falcon tubes and divided into three three-liter Tupperwares equipped with bubblers. The water in these Tupperwares was supplemented with plankton every four days. In the not isolated treatment, nine shrimp

were isolated from their original hosts and divided evenly among three sea stars of similar size and color. The sea stars were placed in clear tanks (40 cm. X 30 cm. X 30 cm.) equipped with bubblers. The water in these tanks was also supplemented with plankton every four days. Plankton supplements in the fed-isolated treatment and the not isolated treatment were obtained using a plankton net attached to a 100 ml bottle. During plankton supplementation, approximately 1/3 of the contents of the bottle were administered to each of the three groups in the two treatments that received supplementation. The tanks and Tupperwares were cleaned every four days, three days after the plankton supplements were administered. The tanks and Tupperwares were examined twice a day, once in the morning, and once in the evening, and any deaths were recorded. The experiment ended after 13 days once all of the shrimp in two of the three treatments had expired.

#### *Hiding on C. novaeguineae*

A laboratory experiment was used to observe the hiding behavior of *P. soror* on *C. novaeguineae* and examine whether this behavior differed on sea stars of different colors. For these observations, shrimp hiding was divided into two categories: "locational" and "camouflage". Locational hiding was defined as either situating on the bottom or side of the oral surface of the sea star, where the shrimp could not be seen from the side or above. Camouflage hiding was defined as situating on the side or aboral surfaces of the sea stars in a location where the shrimp blended in with its background. A total of 20 *P. soror* individuals were used in this experiment, and all were dark purple in color. Shrimp were isolated from their original hosts using 50 ml. falcon tubes and placed onto the top of a sea star, which was located in a clear plexiglass tank (40 cm X 30 cm X 30 cm). The tank was elevated so as to allow viewing of the oral surface of *C. novaeguineae*. The shrimp were given five minutes to situate themselves, after which their picture was taken. Additionally, the shrimps' location and extent of camouflage were recorded. Camouflage was recorded on a three-point scale (0 = no color match, .5 = partial color match, 1 = full color match). When analyzing the data, only shrimp that were recorded as a full color match were considered to be camouflage hiding. Each shrimp was used in two trials. In

one trial, the shrimp was placed on a sea star with a purple aboral surface and a cream-colored oral surface. In the other trial, the shrimp was placed on a sea star with an orange aboral surface and a yellow oral surface. Sea stars of different colors were used to see if the shrimp situated themselves in different locations on their host depending on where they were better able to blend into their background. The same two sea stars were used throughout the course of the experiment.

#### *Host color-matching*

Two laboratory experiments were conducted to examine the ability of *P. soror* to "color-match" its host. In the first experiment, three yellow shrimp were transplanted from their original host onto a dark purple *C. novaeguineae* individual. Because only three yellow shrimp were found during the time of experimental implementation, there was not a sufficient number of shrimp to create a control group, in which yellow shrimp would have been transplanted to a yellow sea star. In the second experiment, there were two treatments: color-switch and control. In the color-switch treatment, nine purple shrimp were evenly divided among three yellow sea stars. In the control treatment, three purple shrimp were placed on a purple star. For both experiments, standardized photographs of the shrimp were taken every other day for a seven-day period. The color of the shrimp was quantified and recorded through analyzing RGB values of the photographs in the computer program ImageJ. All sea stars were contained in large, blue, circular tanks supplied with a constant flow of ocean water.

#### *Statistical methods*

In order to examine consistency of *P. soror* populations on individual sea stars, a logistic regression was used to determine the effect of interval of time between sightings on the likelihood of shrimp population change. To determine whether *P. soror* actively orients to its host using chemical cues, a chi-square test was used to test whether the number of shrimp that oriented to the arm of the Y-maze containing the stimulus was more than would be expected by a hypothetical ratio of 1:1. To determine whether *P. soror* may receive alimentation through its relationship with *C. novaeguineae*, a t-test was used to test differences in mortality among the different treatments in the survivorship experiment. To

look at differences in the hiding behaviors of *P. soror* on hosts of different colors, a chi-square test was used to compare *P. soror*'s relative use of different hiding types on purple and yellow sea stars. To examine whether *P. soror* may gain protection from predators through actively changing colors to achieve cryptic coloration on its host, a paired t-test was used to test the difference in the average RGB values of shrimp in the two treatments of the second color-match experiment. All statistical tests were done using JMP (version 9.0.0).

## RESULTS

### *Pilot study*

The 58 marked sea stars had anywhere between 0 and 10 shrimp associates of various size classes, with a mean value of 2.25 shrimp per sea star. Smaller shrimp were consistently more transparent, and larger shrimp were consistently more solid in color. Almost all shrimp encountered had a purple hue, although several shrimp were orange, yellow, or red. Orange, yellow, and red shrimp were found on sea stars that were primarily orange, yellow, and red in color. All shrimp were found on either the bottom or side of the oral surface of the sea stars.

### *Consistency of P. soror populations on C. novaeguineae*

Populations of *P. soror* on individual sea stars changed frequently during the initial

survey. Increased time between sightings meant increased likelihood of change (logistic regression,  $\chi^2 = 9.99$ ,  $df = 1$ ,  $P = 0.002$ ; Figure 2). For example, there was a 30.8% chance of change occurring in a shrimp population when time between sightings was about 24 hours, and an 82% chance of change occurring when time between sightings was 6 days or more.

### *Chemical orientation to C. novaeguineae*

In both trial one and trial two, *P. soror* swam against the current and entered the arm of the Y-maze being pumped with water containing *C. novaeguineae* chemical cues significantly more often than would be expected by a hypothetical ratio of 1:1. (Chi-square Test, trial 1:  $\chi^2 = 9.71$ ,  $df = 1$ ,  $P = 0.003$ ; trial 2:  $\chi^2 = 19.74$ ,  $df = 1$ ,  $P = 0.0001$ ; Figure 3). In the majority of trials, the isolated shrimp immediately swam towards the orienting arm of the Y-maze and stopped at the tube that was pumping water that contained *C. novaeguineae* chemical cues. In several instances, the shrimp entered the non-orienting arm of the Y-maze, stopped just past the split in the Y, and then swam backwards in order to enter the orienting arm (personal observation).

### *Alimentation and survivorship*

There were significant differences in the mortality of shrimp in the isolated and not isolated treatments. Over the 13-day

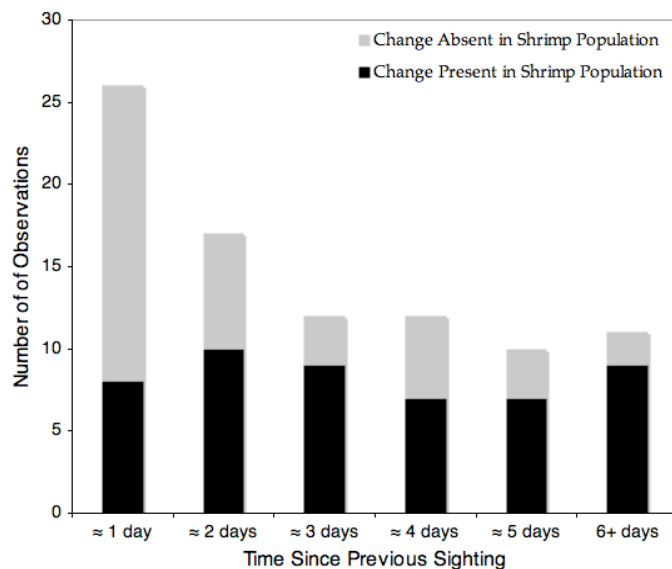


FIG. 2. Presence and absence of change in *P. soror* populations on wild sea stars for different time intervals. A change in shrimp population was defined as the appearance or disappearance of either one shrimp in the large or medium size classes, or two shrimp in the small size class.

experiment, shrimp in both the fed-isolated and unfed-isolated treatments experienced 100% mortality, while shrimp in the no isolation treatment experienced 0% mortality. Although average time until death was shorter in the unfed-isolated treatment than in the fed-isolated treatment, this was not significant (t-test,  $t = -1.75$ ,  $df = 16$ ,  $P = 0.10$ ; Table 1). Additionally, *P. soror* was observed on its host through a hand lens and appeared to be placing items found on the sea star into its mouth.

#### Hiding on *C. novaeguineae*

*P. soror* individuals consistently hid on purple and yellow sea stars in the hiding experiment (Figure 4). In 34 out of 40 trials, *P. soror* situated on either the bottom or side of its host's oral surface, and was thus considered to be hiding by means of location. In 4 trials, *P. soror* situated itself on the aboral or side surfaces of its host, but in a location where it matched its background, and was

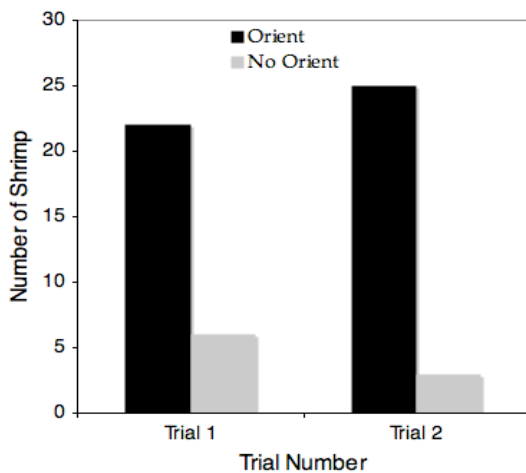


FIG. 3. Shrimp responses to the chemical orientation experiment in a Y-maze. Shrimp were considered to have oriented after swimming 15 cm. into the arm of the Y-maze containing the stimulus. Shrimp were considered not to have oriented if they did not orient after 10 minutes. Each shrimp was tested in two trials, one in which the stimulus was on the right side of the maze, and another in which the stimulus was on the left side. For 14 shrimp, the stimulus was in the left side of the maze in trial 1 and in the right side of the maze for trial 2. For the other 14 shrimp, the stimulus was on the right side of the maze in trial 1 and on the left side of the maze in trial 2.

thus considered to be hiding by means of camouflage. There was no significant difference in the hiding behaviors of *P. soror* on different colored hosts (Chi-square Test,  $\chi^2 = 1.12$ ,  $df = 2$ ,  $P = 0.57$ ).

#### Host color-matching

*P. soror* individuals changed colors when transplanted to hosts of a color different from their own (Figure 5). In Experiment 1, three yellow shrimp were placed on a purple star, and after the 7-day experiment, they had become purple (Average RGB  $\approx 50$ ). In Experiment 2, the nine purple shrimp in the color switch treatment became lighter in color after being placed on yellow sea stars, although they still retained a purple rather than yellow hue. The three purple shrimp in the control treatment stayed purple after being placed on a purple sea star. There was a significant difference between the two treatments in Experiment 2 (paired t-test,  $t = -4.07$ ,  $df = 3$ ,  $P = .03$ ).

## DISCUSSION

#### Pilot study

Results from the pilot study indicate that *P. soror* is commonly found as an ectosymbiont on *C. novaeguineae*. Although most shrimp had a purple hue, the fact that

TABLE 1. Percent mortality and average length of time until death of *P. soror* individuals in three different treatments in a survivorship experiment. Shrimp in the unfed-isolated treatment were isolated from their hosts and placed in filtered ocean water. Shrimp in the fed-isolated treatment were isolated from their hosts and placed in ocean water supplemented with plankton. Shrimp in the not isolated treatment were not separated from their hosts and were supplemented with plankton.

|  | Unfed-Isolated Treatment | Fed-Isolated Treatment | Not Isolated Treatment |
|--|--------------------------|------------------------|------------------------|
| Percent Mortality                          | 100%                     | 100%                   | 0%                     |
| Average Length of Time Until Death (hours) | 160.22                   | 221.25                 | No Death               |

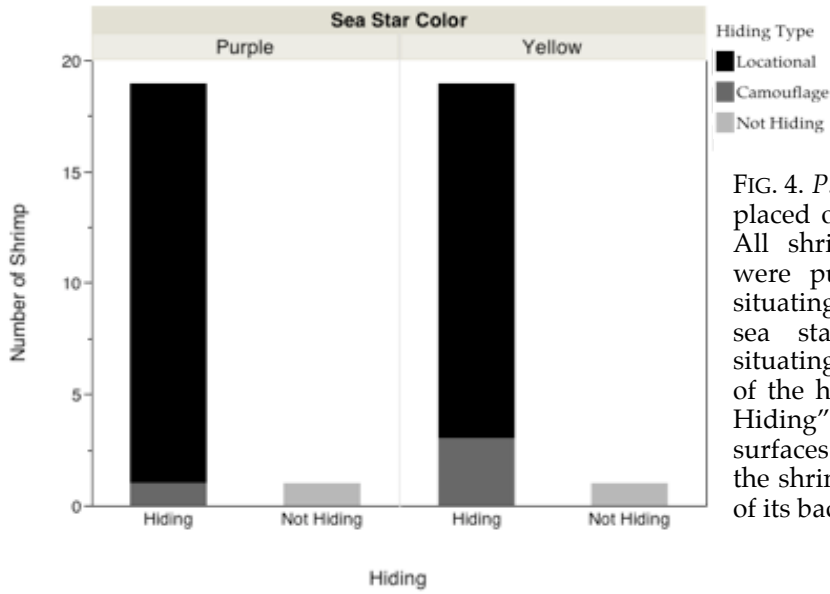


FIG. 4. *P. soror*'s hiding behaviors when placed on sea stars of different colors. All shrimp used in the experiment were purple. "Locational" hiding is situating on the underside of the host sea star. "Camouflage" hiding is situating on the aboral or side surfaces of the host in a cryptic location. "Not Hiding" is situating on the oral or side surfaces of the host in a location where the shrimp's color contrasted with that of its background.

orange, yellow, and red shrimp were found on similarly colored sea stars supports the notion that *P. soror* may be able to color-match its host, and thus may benefit from the symbiosis by residing cryptically on its host to avoid predators. Cryptic coloration is a defense mechanism employed by many other biological organisms (Krupa and Geluso 2000, Lawrence and Willhoft 1958, Moreira 1974). Additionally, all shrimp were observed on

either the bottom or side of the oral surfaces of sea stars. In both locations, the shrimp are not visible from above. Although it is unknown what predates *P. soror*, residing in such a location would seem to enable it to hide from potential predators in the water column. Protection from predators is a symbiotic benefit commonly associated with commensal and mutualistic relationships (Mariscal 1966, Reeves and Brooks 2001, Fautin *et al.* 1995).

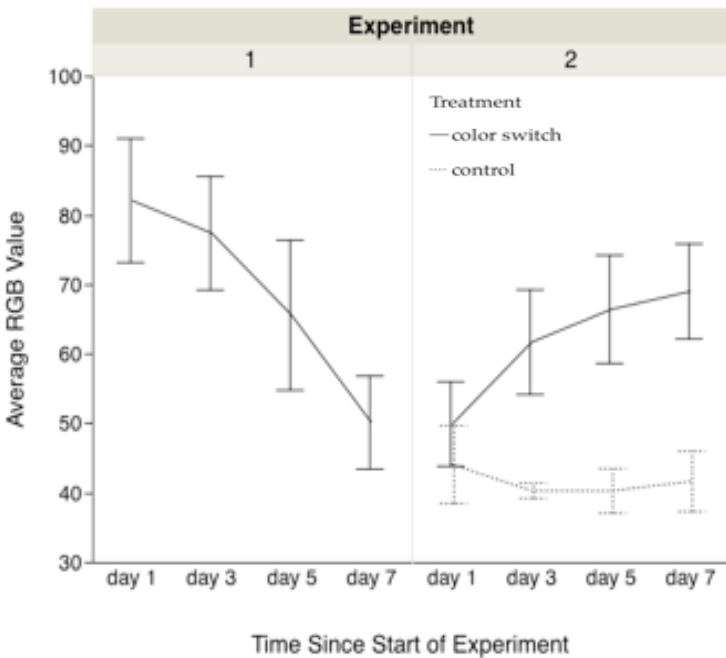


FIG. 5 Color change in shrimp after being transplanted to hosts of different colors. In Experiment 1, three yellow shrimp were placed on a purple sea star. In Experiment 2, nine purple shrimp were placed on yellow sea stars in the color-switch treatment, and three purple shrimp were placed on a purple star in the control treatment. Error bars are standard error.

### *Consistency of P. soror populations on C. novaeguineae*

The rapid changes in shrimp populations on individual sea stars demonstrate a dynamic relationship between *P. soror* and *C. novaeguineae* (Figure 2). Wear (1976) reported that *P. soror* presumably reproduces with individuals on the same host. Therefore, one reason shrimp may change hosts is to locate potential mates. This explanation for symbiont host switching has been well documented in other systems (Grove and Woodin 1996, Bandilla *et al.* 2008). Future studies should examine whether *P. soror* immediately seeks a new host after disassociating with a *C. novaeguineae* individual, and if so, how these hosts differ from one another (e.g. sea star species, number and sex of shrimp associates).

### *Chemical orientation to C. novaeguineae*

The results suggest that *P. soror* actively orients to *C. novaeguineae*, probably by means of chemical cues. Personal observations of *P. soror*'s consistent orienting behaviors in the Y-maze demonstrate the shrimps' acute ability to perceive and respond to chemical cues released by its host. The importance of chemical cues in the ability of marine organisms to locate and identify one another has been well documented in previous literature (Moore and Lepper 1997, Elliott 1995, Orihuela *et al.* 1992, Dos Santos *et al.* 2004).

### *Alimentation and survivorship*

The 100% mortality rates in the fed-isolated and unfed-isolated treatments in comparison to the lack of mortality in the not isolated treatment suggests that *P. soror* receives alimentary benefits from its relationship with *C. novaeguineae*. Because the shrimp used in this experiment were in the absence of predators, mortality was most likely caused by the lack of sustenance. Shrimp in the fed-isolated and unfed-isolated treatments experienced similar mortality rates, which suggests that the supplemental plankton was either too inadequate to create a significant difference between the fed-isolated and unfed-isolated treatments, or was not utilized as a food source at all. Although shrimp in the fed-isolated and not isolated treatments were provided with similar amounts of supplemental plankton, differences in mortality were striking. This

indicates that isolation from host, rather than the presence of supplementary plankton, was responsible for differences in mortality rates.

Thus, it appears that one benefit *P. soror* receives in this relationship is alimentation by means of a food source made available through association with *C. novaeguineae*. This notion is corroborated by personal observation of *P. soror* placing items found on the sea star into its mouth. Although these results suggest that *P. soror* is an obligate associate of *C. novaeguineae*, it is possible that *P. soror* obtains sustenance from non-planktonic aquatic organisms separate from its host. Analysis of the stomach contents of *P. soror* coupled with examination of the shrimps' chelae morphology would be greatly beneficial in determining if and how the shrimp benefit metabolically through their relationship with *C. novaeguineae*, as well as clarify whether this relationship can be classified as a mutualism, commensalism, or parasitism. Similar to other symbionts living on larger hosts, *P. soror* may feed on its hosts' ectoparasites, in which case *C. novaeguineae* would also benefit from this biological association (Nunn 2011, Limbaugh 1961, Poulin and Grutter 1996). Alternatively, *P. soror* may be parasitically feeding directly on host tissue, a phenomena that has been documented in other shrimp symbioses (Fautin *et al.* 1995, Duris *et al.* 2011). Another possibility is that *P. soror* may be feeding on detritus that settles on its host, in which case *C. novaeguineae* may be neither positively nor negatively affected by this relationship.

### *Hiding on C. novaeguineae*

Results from the hiding experiment indicate that another advantage *P. soror* obtains from its relationship with *C. novaeguineae* is protection from predators, a symbiotic benefit that has been documented in many other biological associations (Mariscal 1996, Reeves and Brooks 2001, Fautin *et al.* 1995). These results are consistent with in situ observations of *P. soror* made during the pilot study. After being placed on top of *C. novaeguineae*, almost all *P. soror* individuals situated themselves in locations where they would be difficult to detect from the side or above. Although one might expect purple *P. soror* individuals to behave differently when placed on a purple as opposed to yellow host because the shrimp are camouflaged regardless of location, this was not the case (Figure 4). This may be explained by the fact



that *P. soror* appears to be frequently switching among hosts, and situating on the underside of *C. novaeguineae* would be a reliable way to evade predators when arriving at a new host regardless of host color.

#### *Host color-matching*

Experimental evidence indicates that *P. soror* changes color based on the color of its host, but is limited in its ability to undergo rapid physiological color change (i.e. color change in the span of minutes or hours). Because the initial survey demonstrated that *P. soror* may be frequently switching among host sea stars, it appears that the shrimp would be unable to rely on color-matching their hosts for cryptic defense when initiating a new association. However, if the shrimp reside on their host for an extended period of time (i.e. > 1 week), they may enhance the benefit of protection from predators by means of cryptic coloration. Indeed, many organisms utilize crypticity as a means to improve fitness (Krupa and Geluso 2000, Lawrence and Willhoft 1958, Moreira 1974). Although Gontang (1999) suggested that *P. soror* does not display host-specificity because it is able to rapidly color-match any *C. novaeguineae* individual, these results refute this hypothesis. Lack of host-specificity may be attributed to the fact that *P. soror* appears to primarily rely on locational hiding rather than camouflage hiding, and can thus benefit from protection from predators on any *C. novaeguineae* host.

#### *Conclusion*

These observations and experiments have provided insight into various aspects of the relationship between *P. soror* and *C. novaeguineae*. It appears that *P. soror* may be an obligate associate of its host and benefits from this relationship through both alimantation and protection from predators. However, *P. soror* seems to be frequently moving between hosts, suggesting that this relationship is not an individual-specific symbiosis. *P. soror* actively orients to *C. novaeguineae*, which is not surprising given the associated benefits of this relationship, and chemical cues appear to play a role in the orientation process.

The relationship between *P. soror* and the *C. novaeguineae* provides insight into important biological and ecological concepts, including cryptic coloration, chemical ecology, and the various ways in which symbiotic relationships may improve species' fitness.

Additionally, this relationship demonstrates the intricacy of the interspecific associations that structure ecological communities and maintain the biodiversity of complex ecosystems such as coral reefs.

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