# RECRUITMENT BIOLOGY OF THE STOMATOPOD *PULLOSQUILA;* THE EFFECTS OF CONSPECIFIC DENSITY AND LUNAR CYCLE

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*Abstract.* The process of settlement requires many marine organisms to use different biotic and abiotic cues. In this study, the effects of the lunar cycle and conspecific density were examined as potential settlement cues. I hypothesized that the stomatopod *Pullosquila* larvae congregate in some time across the lunar cycle. I also hypothesized that conspecific density (*P. thomassini*) negatively correlates with settlement time. The results showed that as conspecific density increased, settlement time decreased. The survey of the *Pullosquilla* larval abundance showed that the larvae congregated one to three days after the first observed full moon, but this result was not repeated during the second lunar cycle.

*Key words: stomatopod; light trap;* Pullosquila thomassini*; lunar cycle; settlement*

## INTRODUCTION

Understanding the factors that control population abundance is an important aspect of ecology. Many organisms' reproductive and developmental successes are highly dependent on the quality and quantity of resources. Evolutionarily, a favorable habitat will increase the fitness of the developing young. There are many indicators of a good habitat such as the presence of food, shelter, or potential mates (Hunt and Scheibling 1997). Different biotic and abiotic cues can be used by organisms to evaluate the potential quality of an environment (Hunt and Scheibling 1997). Many marine organisms that metamorphose use habitat cues to initiate physiological changes (Hunt and Scheibling 1997).

Most marine invertebrates have a planktonic phase where the larvae live in open waters (Pawlik 1992). In contrast, the adults are often benthic, settling into the bottom of the ocean once they metamorphose (Olson 1989). Large quantities of larvae are produced by marine invertebrates because of the high mortality rate that occurs in the plankton stage (Booth and Brosnan 1995). The high mortality rate in zooplankton is due to predation, starvation, or inability to find appropriate habitat to settle (Booth and Brosnan 1995). The process of settlement may involve either attaching to a substrate or finding shelter in a substrate (Booth and Brosnan 1995).

Settlement is a critical stage for these pre-recruits because the larvae must metamorphose at a site that ensures shelter, food, and, ultimately a mate (Hunt and Scheibling 1997). The drastic physiological changes at metamorphosis often put the organism in a vulnerable state, thus many organisms settle during the night in order to avoid predators (Booth and Brosnan 1995). Settlement of plankton is not well documented because most planktons are morphologically transparent in color and settle at night (Booth and Brosnan 1995). Both biotic and abiotic factors in a habitat act as cues for these pre-recruits (Booth and Brosnan 1995). Looking at patterns of recruitment is important for understanding population dynamics of marine invertebrates.

Many studies have found that the presence of conspecifics act as signals for recruitment (Crisp 1974). The larvae of damselfish selected corals with resident adult conspecifics; dissolved chemical cues caused the damselfish to choose or avoid settlement sites (Sweatman 1988). Slattery (1992), showed that larvae of the red abalone *Haliotis rufescens* will settle on substrates with mucus secreted by conspecifics. That study also suggested that the presence of conspecific mucous acts as an inductive cue for settlement and metamorphosis. Settling near conspecifics is advantageous because of the presence of refuge, food, and opportunities for mating (Sweatman 1988). The presence of adult conspecifics indicates that resources are sufficient for survival since the last settlement season, thus the presence of a conspecific may

often be a good habitat indicator (Sweatman 1988).

The larval distribution of marine organisms is highly complex and poorly understood (Metaxas 2001). The timing of larval release is usually consistent but varies across taxa and is often unknown (Metaxas 2001). The abundance of zooplankton varies with the lunar cycle and the lunar cycle is tightly linked to the cycle of tides (Kobervig 2009). This adaptive variation across the lunar cycle is thought to increase chances of mating and fertilization and help distribute larvae to adult habitat (Omori 1995). The lunar cycle provides organisms with a physical cue to allow synchronous breeding (Omori 1995). Organisms may be able to control larval distribution based on current tidal height predicted by the different moon phases (Omori 1995). Variation across the lunar cycle can affect the larval abundance, which can in turn affect when the larvae settle on a substrate.

Mantis shrimps (order Stomatopoda) are crustaceans that have a planktonic larvae stage and a benthic adult stage. The developmental history of stomatopod larvae is understudied, mainly due to the difficulty of rearing stomatopod larvae in the lab (Schram *et.al.*, 2013). Little is known about the settlement process of stomatopods (Schram *et.al.*, 2013) – a key life history transition for understanding their dynamics. Stomatopod larvae are important predators on the plankton community (Porter 2002), and the spatial distribution of the late-larvae is important because it connects directly to the distribution of the adult population (Hadfield and Koehl 2004).

The transition from the highly mobile larval stage to the benthic burrowed-dwelling adults is a complete change in lifestyle (Porter 2002), which makes settlement an interesting area of research. Stomatopods settle in rock crevices or sand burrows (Hadfield and Koehl 2004); there is a strong selection for stomatopod larvae that can choose a favorable reef flat habitat to settle (Wood 2002). The pre-recruit stomatopods often actively congregate at habitats that provide the optimal quality for adults (Porter 2002). A series of requirements must be met before these larvae metamorphose to the adult form, suggesting that initial habitat selection has long-term effects on the individual's performance. Factors such as the lunar cycle and the presence of conspecifics will be explored to test the temporal and spatial preference for these pre-recruits as settlement cues.

In a crest net survey done in Rangioria, it was found that the pulse of some stomatopod species were greatest around the new moon and last quarter of the lunar cycle (Santos *et.al.*, 2011). In Moorea, most zooplankton peaked in abundance 6-11 days after full moon (Endo 2008). Although many studies were done on larval abundance across the lunar cycle, the exact pulse peaks of many stomatopod species remain unknown (Santos *et.al.*, 2011).

Most adult stomatopods are solitary and territorial creatures (Christy and Salmon 1991) with little social interaction except when searching for a mate (Caldwell and Dingle 1972). Sexually matured stomatopod will briefly leave its burrow to search for a mate (Caldwell and Dingle 1972), but time spent outside the burrow places the stomatopod in a highly vulnerable position. Predation on mate-searching stomatopods are extremely high (Christy and Salmon 1991); therefore, finding a potential mate is an important aspect that can affect settlement. Pattern of settlement will affect the distribution of the adult individuals, which may in turn affect pairing opportunities (Wright 2013).

As the population density increases, the drive for resources also increases, often causing intraspecific competition. Limiting resources, such as access to favorable burrowing sites, will often cause competition between stomatopod individuals (Caldwell 1979). The presence of conspecifics can be a good indicator of food availability and possible mates; therefore choosing an optimal habitat is a fine balance between available resources and intraspecific competition. In the final larval stage, stomatopods are strong swimmers and can thus actively choose where to settle and burrow (Porter 2002). There may be a correlation between conspecifics density and settlement time.

Despite the lack of social interaction of most stomatopods, the genus *Pullosquilla* is unique because it is the only known monogamous marine crustacean that provides biparental care to its embryo (Wright, 2013). The social interaction of *Pullosquilla* is especially interesting because the presence of conspecifics may play a significant role in recruitment. In Moorea, two species of *Pullosquilla* are commonly found burrowed within the sandy lagoon – *Pullosquilla thomassini* and *Pullosquilla litoralis* (Wright 2013).

In this study I focused on the late larvae of *Pullosquilla thomassini,* commonly found in the water column of Cook's Bay at night. Upon capture, the late instar larvae readily settle, molt, and burrow (Wood 2002). The goal of this study was to explore settlement time in relation to conspecific density. I hypothesized that there was a negative relationship between the density of *P. thomassini* and settlement time (time it took for larva to burrow). The prediction was that settlement time would decrease as the conspecific density increased because the presence of conspecifics may serve as cues for available resources. The negative correlation between settlement time and density of conspecifics was predicted to be lowest at a certain density; after that point, intraspecific competition may override the effects of density on settlement, with settlement time starting to increase as density continues to increase.

This study also surveyed the abundance of *Pullosquilla* over the lunar cycle (*P. litoralis* and *P. thomassini* are indistinguishable at pre-recruit stage). I hypothesized that the lunar cycle had an affect on larvae abundance, in which the number of *Pullosquilla* larvae congregate around the full moon quarter of the lunar cycle, as shown by Santos *et.al. (2011)* in Rangioria for other species of stomatopods.

## METHODS

### *Study site*

Data for this project were collected on the island of Moorea, French Polynesia in Cook's Bay (Fig. 1). Data were collected over a period of 33 days from October 20 to November 23, 2013, which included one full lunar cycle. The light traps were tied off the dock of Berkeley Gump Station (17°29'27.02"S,149°49'33.92"W).

### *Study Animal*

The organism for this experiment was a lysiosquilloid, the stomatopod *Pullosquilla thomassini*. The adults live in sand burrows and the larvae are found all throughout Cook's Bay (Porter 2002). The late instar pelagic larvae of *Pullosquilla* are readily identifiable from other zooplankton because of their distinct long rostral spine with the pink tip at the end (Wood 2002; Fig. 2). The *Pullosquilla* larvae have a transparent body with pigmented eyes (Fig. 2). The adult molt of *P. thomassini* are readily distinguishable from other stomatopods because *P. thomassini* have numerous sharp spines on the midventral surface of the telson (Manning 1978; Fig. 3).

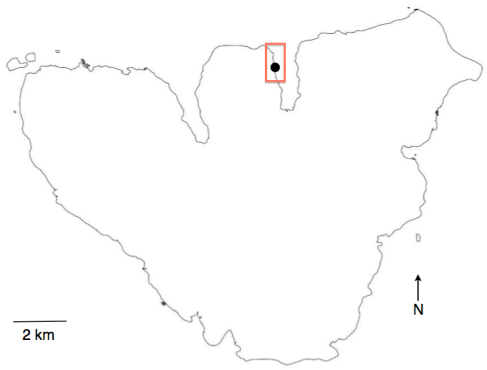


FIG. 1. Study site (black dot = Gump Station). Base map courtesy of the Geospatial Innovation Facility, University of California, Berkeley

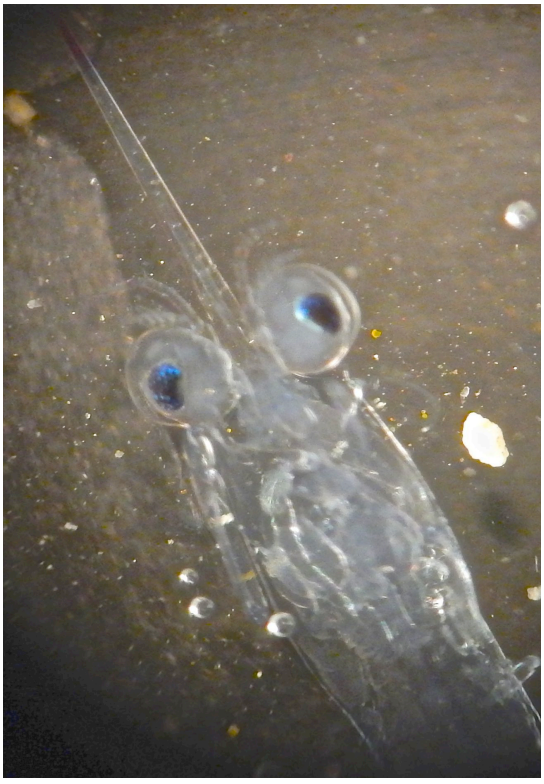

FIG. 2. The *Pullosquilla* larva (~12mm in length). Photo by E.Hsiao.

FIG. 3. Spines on the telson of *Pullosquilla thomassini*. Photo by E.Hsiao.

*Abundance of larvae and Collection*

Both species of *Pullosquilla* larvae were collected for analyzing the larval abundance over the lunar cycle. This is because *P. thomassini* and *P. litoralis* are indistinguishable in the larval stage. Only *P. thomassini* was used to analyzed conspecific density as a settlement cue.

To collect stomatopod larvae, I used two light traps (Appendix A). Each light trap was constructed using a translucent plastic 5L water bottle as the body of the trap and holes were cut and attached with funnels to guide zooplankton into the body of the trap. A dive light was attached to one end to serve as an attractant because only the very early and late larval instars of stomatopod larvae expresses positively to phototaxis (Porter 2002). Complete details on light trap construction can be found in Appendix A.

Each light trap was tied to the dock off the UC Berkeley Gump Field Station (17°29'27.02"S,149°49'33.92"W) and was submerged completely in water just below the surface of the water. The light traps were set out each night for ~3 hours from 1930 h to 2230h (± 1 hour). After retrieving each light trap, the samples were placed in a bucket and the number of *Pullosquilla* larvae collected were counted.

*Settlement time in presence of conspecifics*

To examine the effect of conspecific density on *P. thomassini* stomatopod settlement time, captured stomatopods were transferred in buckets from the capture site to the laboratory at the UC Berkeley Gump Field Station.

The experiment included four treatments to which a pre-recruit *P. thomassini* larva was added and settlement time was measured. Each treatment had a different number of post-recruit stomatopod larvae present, which were hypothesized to affect settlement time. The experiment tested the hypothesis that a higher density of stomatopods would lead to a shorter settlement time. Treatment A had no post-recruit stomatopods (control), Treatment B had 2, Treatment C had 4, and Treatment D had 10 (Fig. 4). The post-recruit stomatopods used in all experimental designs were allowed to burrow for at least 12 hours prior to the experiment. For all treatments, one single pre-recruit *P. thomassini* larva was added to the cup, together with the post-recruits already present as part of the treatment (except the Treatment A cup, which had no post-recruits present).

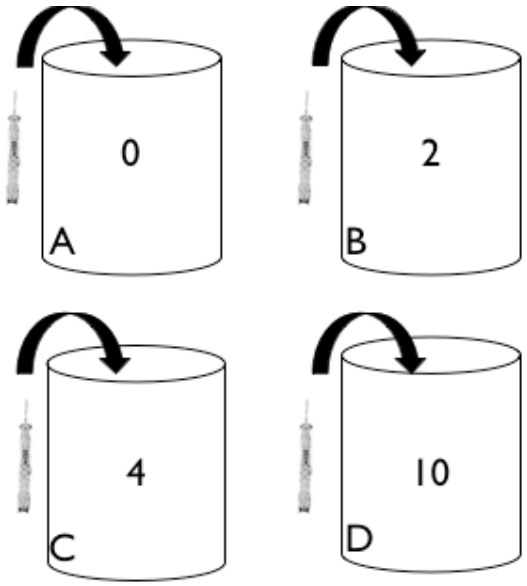


FIG. 4. Experimental design to test the effects of conspecific density on settlement time. Each cup had varying amount of conspecifics present (A=0, B=2, C=4, D=10). One single pre-recruit late larvae was added to each of the treatment cups. The settlement time was determined. Photo by R. Caldwell

Each hour after the larva had been placed into the treatment (up to 12 hours), the settlement of the larva was determined visually by the author (in water column = not settled, not in water column = settled). The number of hours it took for the larva to burrow was recorded as the settlement time. If the stomatopod larva did not burrow after 12 hours, it was considered "not settled". When this occurred, the data was not counted because the larva may have halted settlement due to stress from being captured. Each treatment was repeated a total of 12 times.

The treatment cups were filled with 500mL of sand and 500mL of sea water. Equal size 1000mL cups were used throughout the experiment. The sand was collected from the Vaipahu back-reef in Cook's Bay. Any experimental subjects that died within 24 hours upon capture were excluded from the study. This protocol was used to minimize the possibility of stress affecting the results. The experiments were run from 00:00h to 12:00h the night that the larvae were captured. The post-larvae that successfully settled in the sand were removed to determine the species.

*Pullosquilla litoralis* and *Pullosquilla thomassini* are indistinguishable at the larval stage; therefore the larvae were identified after they molted. The experimental containers with *P. litoralis* were disregarded, only *P. thomassini* settlement time was recorded for the experiment.

### *Statistical Approach*

All analyses were conducted using "R" version 3.0.1. (R Developement Core Team 2013). The Shapiro-Wilk test was used to determine the normality of my data (the effects of conspecific density on setlement time). The results from data were not normally distributed, therefore the Spearman's Rank Correlation test was used. The Spearman's Rank Correlation test was used to examine the correlation between the settlement and conspecific density.

To determine whether or not the distribution of stomatopod larvae over the lunar cycle was significant or randomly distributed, a generalized linear model (poisson) was used.

## RESULTS

### *Settlement time in presence of conspecifics*

The Spearman's Rank Correlation test showed that there was a significant relationship between conspecific density and settlement time ($S=29583.14$ , $p<0.001$, $R^2= -0.61$). Using the regression analysis, it showed that the density of stomatopod was negatively correlated with conspecific density (Fig. 5).

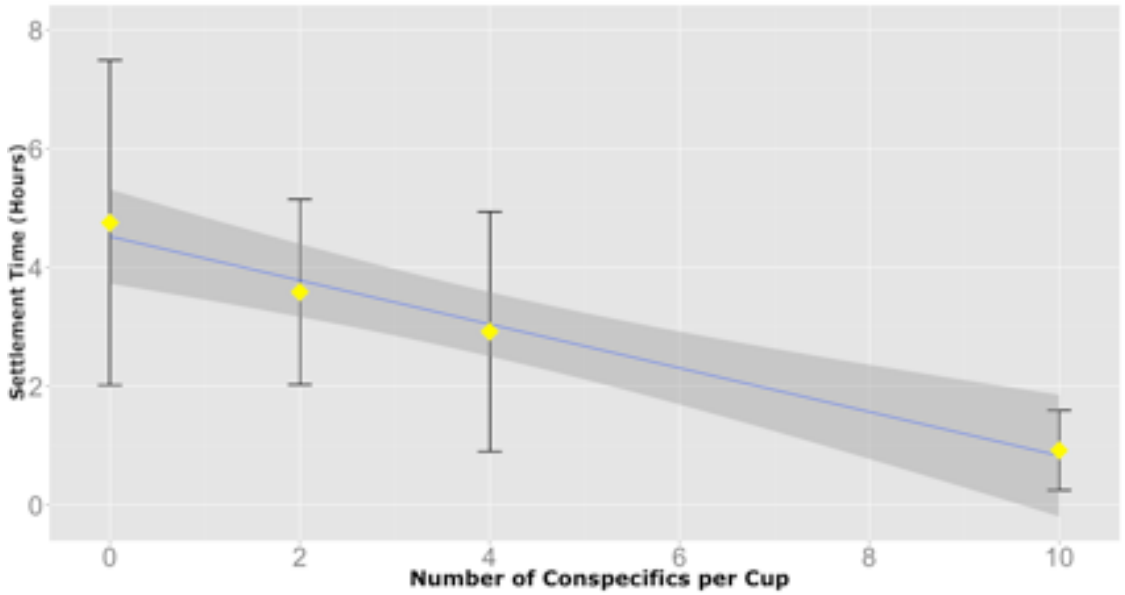


FIG. 5. The settlement time of *P. thomassini* as conspecific density increases. The Y-axis is the time (in hours) it took for the larvae to settle or burrow. The X-axis is the conspecific density, number of conspecifics per cup (1000mL). The yellow diamond is the average settlement time of each treatment. The error bar represents the standard error.

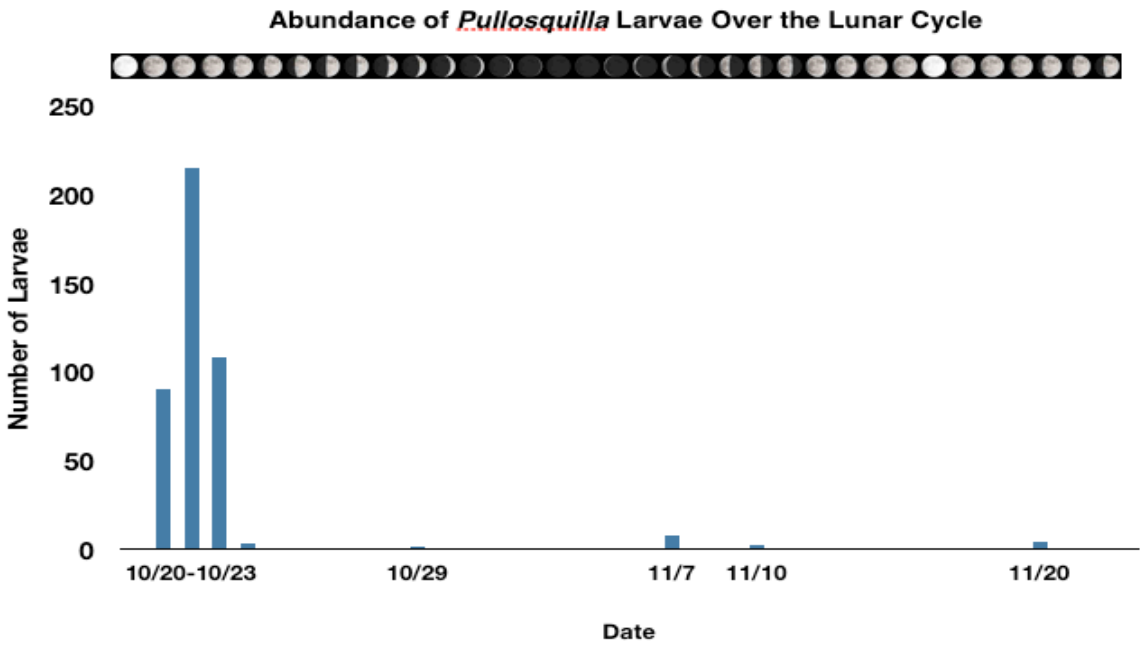


FIG. 6. The abundance of *Pullosquilla* late larvae over the course of 33 days. X-axis is the phase of the lunar cycle. Y-axis is the number of individual larvae. Moon Phases used by permission of The University of Texas McDonald Observatory

*Abundance of larvae*

A total of 431 *Pullosquilla* late larvae were collected over the course of 33 sampling days. A total of 66 light trap samples were collected. Over the course of 33 days, the *Pullosquilla* larvae had a first pulse of high larval abundance 1-3 days after the first full moon (Fig. 6). After the second full moon, no peak of larval abundance was observed. There was a significant variation in *Pullosquilla* larval supply with the lunar cycle (GLM (poisson), $X^2 = 1306.2$, Df=1, $p < 0.001$).

## DISCUSSION

*Stomatopod Settlement*

My results showed that on average, as conspecific density increased settlement time decreased (Fig. 5). Settlement time was defined as the time it took for a stomatopod larva to burrow in the sand. The presence of conspecifics in *Pullosquilla thomassini* may act as a settlement cue. For example, the presence of conspecifics may be an indicator of certain resources such as potential mate and food. I hypothesized that this negative correlation would continue to a point of the densest stomatopod population with the least amount of required settlement time for a single larva. After this point, competition may occur and settlement time may start to increase. From the results, it showed that population density did negatively correlate with the settlement time.

Due to time constraints, I did not reach a population density in which competition occurred. By increasing the population density to higher density than ten stomatopods per cup, competition may occur and settlement time may have a positive correlation with conspecific density. Further research is required to test the density in which intraspecific competition outweighs the settlement cue of conspecifics' presence.

*Lunar Cycle and Larvae Abundance*

The results showed that in the first full moon an aggregation of late-larvae occurred from one day after the full moon till three days after the full moon. The pulse of stomatopod larvae did not occur in the second observed full moon cycle (Fig. 6). My results

agreed with past studies done, in which stomatopod species synchronously breed and are congregated in some time across the lunar cycle (Reaka 1976). Synchronize settlement time may allow for greater reproductive fitness for these species (Endo 2008).

There may be various reasons for the observed difference in the *Pullosquilla* larval pulse during the two full moon quarters. *Pullosquilla* larvae have been observed to pulse one to two weeks after full moon (per. com. Caldwell). The first pulse of stomatopod late-larvae may had been triggered by the strong storm that occurred on 20 October, 2013, which may had caused the larval peak to be early. The strong wind and waves may have caused the larvae to be carried from the deep waters onto the surface water column. There may be different biotic and abiotic reasons why the second pulse did not occur within the allotted time frame. Future research can focus on understanding the additional factors that affect larval abundance across the lunar cycle.

The lunar cycle is known to cause changes in tidal height and current, which may indirectly affect dispersal of these larvae (Endo 2008). New moon and full moon create larger tidal variations due to the alignment of the sun and moon during these time (Morgan and Christy 1995). The spring tides found during full and new moon may provide larger currents that may assist the larval in dispersion. This may be one reason why the *Pullosquilla* larval congregation was during the full moon quarter.

The larvae collected from the light trap were composed mainly of *Pullosquilla thomassini*, but there were a few individuals that I was unable to identify due to death before the larvae molted. Previous studies showed that *P. litoralis* and *P. thomassini* were both found in the waters of Cook's Bay (Wood 2002). A mixture of *P. thomassini* and *P. litoralis* were found when I collected my preliminary sample with the plankton tow. This may be due to uneven distribution of *Pullosquilla* within Cook's Bay.

The single species by the dock may be the result of a variety of factors. For example, off the Gump Station dock, there may be a congregated population of *Pullosquilla thomassini* late larvae, because a monogamous pair of *Pullosquilla* adults will produce successive clutches of 130-140+ eggs (Porter 2002). There may be a patchy distribution of *Pullosquilla thomassini* and *Pullosquilla litoralis* to explain why only *P. thomassini* were found in the light trap.

*Pullosquilla thomassini* will settle successfully in deep water (Jutte 1997). The dock may provide a deep sandy water habitat in which these stomatopod can settle. The light traps were set out on the east and south side of the dock (the deep channel side). In contrast, the preliminary plankton tows were done in shallower areas in which the kayak can be anchored; therefore this may be the reason why both populations of *P. thomassini* and *P. litoralis* were found in the preliminary plankton tows.

Another possible explanation for why only *P. thomassini* were found off the Gump dock may be because *P. thomassini* and *P. litoralis* follow different moon phases within the lunar cycle. Future research can explore when *P. litoralis* and *P. thomassini* are congregated across the lunar cycle, which can help to determine the temporal variation of the larval abundance.

## CONCLUSION

The presence of conspecific and the lunar cycle are both abiotic and biotic factors that can potentially affect settlement pattern, which may in turn affect the distribution of the adult population. Many settlement cues, such as the lunar cycle and the presence of conspecifics, may contribute to the settlement pattern of stomatopod larvae both temporally and spatially. Understanding the population dynamic of recruitment and how it compares to adult stomatopod population will give us a greater understanding of larval ecology.

Pursuing research on the factors the effect settlement and recruitment can help contribute to the ongoing debate over recruitment as a limiting factor in the marine environment. My study showed that conspecific density and the lunar cycle has potential effects on stomatopod settlement. Understanding the population dynamic of recruitment will give us a better picture of the spatial distribution, competition, and the adult population size of these stomatopods.

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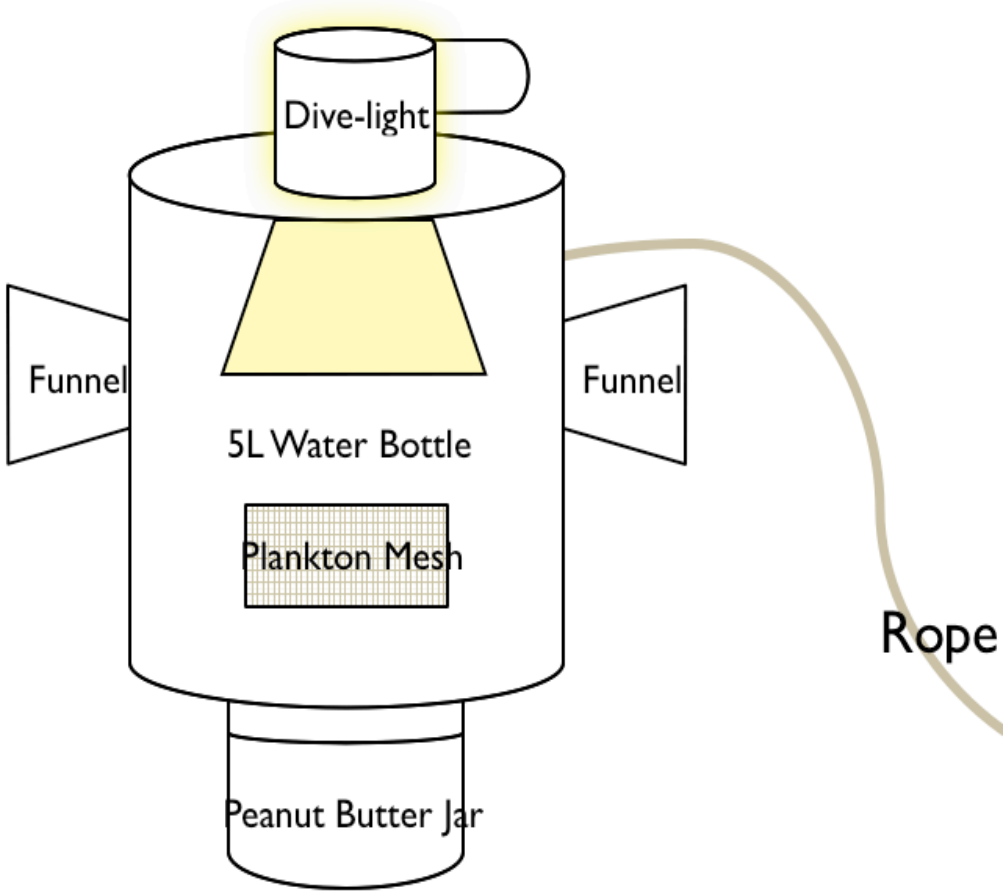
**APPENDIX A**

*Detailed light trap design*

Before starting the experiment, two light trap prototypes were tested for their ability to capture zooplankton. The model most successful at capturing zooplankton was used and replicated for the experiment. A translucent plastic 5L water container formed the body of the trap (5L Tahiti Springs Premium Water). Two circular holes were cut on two opposite sides of the plastic water container and funnels were silicon glued onto the holes. The circular holes were ~20mm in diameter, and the circular holes were placed 15cm below the cap of the bottle. The translucent funnels were 20mm at the narrow end and 160mm at the wider end. One rectangular hole about 9cm in width and 5cm in height was made in the side panel without the funnels. The hole was made 3.5cm above the bottom of the plastic water container. This hole was covered up with plankton mesh (210 $\mu$m) and sealed with silicon sealant to avoid planktons from escaping. A circular hole with 7.5cm in diameter was cut off at the top of the water container along with the bottle's cap, this was to attach the dive light. The dive light (Princeton Tec MiniwaveII) was duct-taped onto the light trap with the light facing directly towards the bottom of the light trap. The dive light was removed daily to recharge the C batteries, and the dive light was duct-taped back on each day. In order for the light trap to be bottom heavy, 250mL of epoxy (Splash Zone 2-Part Epoxy) were glued to the bottom of the skippy jar. A 5 meter rope was tied to the pre-existing handle that comes with the 5L water bottle to tie the light trap unto the dock. At the bottom panel of the translucent water bottle, a hole of 5cm in diameter was cut out. The same 5cm diameter hole was cut out from a skippy peanut butter jar's lid (Skippy Creamy Peanut Butter 16.3 oz). The lid was then glued onto the bottom of the translucent 5L water container. After all the glue dries, the skippy peanut butter jar was screw back on the lid, this was where the plankton will collect. Only the lid of the catchment was attach to the trap and the skippy jar can freely detach to pour out the plankton. When removed from the sea, the majority of the salt water drained out the plankton mesh and the plankton drained into the catchment (Skippy jar). This design was a variation of the light trap used in Porter (2002).



## APPENDIX B

List of other organisms collected by light traps
- Unidentified fish larvae
- Gastropod larvae
- Polycheate worms
- Ostracods
- Unidentified worms
- Crab zoea
- Crab megalopes
- Copepods
- Eel snakes
- Sea jellies
- Octopus paralarvae
- Squid paralarvae
- Shrimps
- Small fishes
- Small needle fish
- Mysid shrimps
- Spanish dancer flat worms
- Other flat worms

List of other stomatopod larvae collected by light traps
- *Roulserena*
- *Acanthosquilla*
- *Squilla*
- *Alima*
- *Lysiosquillina*