

THE EFFECTS OF LUNAR CYCLING AND FISH PREDATION ON DECAPOD LARVAL ABUNDANCES

BRANDON P. ENDO

Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Planktonic larvae of many marine organisms have been known to cycle in abundance according to lunar phases. It is unknown, however, if these cycles are caused by timed release of larvae by the adults in accordance with lunar cues or if predation pressure on the larvae varies across the lunar cycle. Larvae of some invertebrate taxa are capable of predator detection and avoidance, suggesting that predation on meroplankton is lower than dispersal models predict. This study tracked lunar cycling of decapod larvae from Oct. 6, 2008 to Nov. 13, 2008 in Moorea, French Polynesia. Predator avoidance capabilities of the larvae and relative predation pressure during each phase of the moon were also tested in a laboratory setting. Larval abundances on the reef were highest during the new moon period and lowest during quarter and full moons, suggesting predation does affect lunar abundance cycling. Decapod megalops stage larvae were found to be capable of predator avoidance but younger stage zoeas were not. Predation pressure was also found to correlate directly with light intensity. Results of this study suggest predation does affect larval population cycling, however it is possible that both predation and larval release timing play a role in shaping larval abundances and dispersal.

Key words: *lunar cycling; meroplankton; larvae; decapod; predation; larval behavior; Moorea, French Polynesia*

INTRODUCTION

A microscopic, planktonic larval phase is characteristic of a variety of megafaunal marine organisms. Although this is among the most important stages in an organism's life history, many aspects of larval biology are not well studied. Larval distributions of marine invertebrates can be highly complex and are poorly understood in many locations (Metaxas 2001). The timing of larval release is often consistent but the planktonic period of larvae among many taxa can be variable and is also largely unknown (Metaxas 2001). Observations of larval abundances synchronized with lunar phases have been made for a long time. Reproductive behavior in many marine organisms is often seen in lunar (29.5 days)

or semi-lunar (14.8 days) cycles, especially in marine invertebrates (Korringa 1947). The adaptive significance of this is thought to be to 1) increase the rate of mating 2) increase the rate of fertilization 3) help retain free-living larvae in nursery sites 4) help to spread free-living larvae over some adult habitats 5) decrease predator pressure on free-living larvae and increase reproductive success by the direct influence of environmental effects such as moonlight (Omori 1994).

Lunar cycling provides organisms with a physical cue (light intensity) to males and females of a given species to allow synchronization of reproductive behavior (Omori 1994). The moon may also indirectly affect dispersal through its control of tidal height variations and thus currents.

Organisms may be able to control their larval distribution based on probable current strength from a given tidal height predictable by the stage of the lunar cycle. As a result, a variety of marine taxa are observed to have patterns of larval release following lunar cycles and their associated cues (Naylor 2001).

Planktonic stage larvae are thought to simply float with ocean currents without much control over their own distribution (Roughgarden 1985). Previous studies have found large variations in temporal and spatial larval recruitment, which has led to a common assumption that planktonic larvae cannot behaviorally control their fate (Morgan 2001). As a result, many dispersal models treat planktonic larvae as free floating organisms, without swimming capabilities (Porter 2002). Due to an abundance of planktivorous organisms in marine ecosystems and the larvae's limited mobility, previous studies have also assumed high larval mortality rates from predation (Metaxas & Burdett-Coutts 2005). Predictive larval dispersal models are thus created with predation serving as a large parameter.

Observed lunar cycling patterns could thus be a product of variations in predation pressure rather than lunar timing of larval release. It is likely that both factors play a role in controlling planktonic larval abundances, however the relative weight of each factor is not known. Some studies argue predation is very high among planktonic larvae. Variations in predation pressure across the lunar cycle may cause fluctuations in larval populations despite relatively constant release rates.

Since many planktivorous organisms, such as a variety of fish, are thought to be visual predators, predation pressure will depend on the amount of ambient light produced by the moon. Therefore predation pressure will be highest during a full moon and lowest during a new moon (Dawidowicz et al. 1990). Gliwicz 1986

found lunar fluctuations of planktonic cladocerans that were attributed to predation pressure variations in a tropical lake environment. Larval release was found to be relatively constant in a laboratory study, however, gut content analysis of planktivorous fish revealed patterns of feeding according to moonlight intensities that could completely account for cladoceran population fluctuations.

Other studies have argued larval population fluctuations are more heavily attributable to the adult's timing of larval release rather than predation. Augusto et al. 2006 attributed larvae population increases during full and new moons to the timing of larval release in various species of tropical shore crabs. Timing release according to full and new moons may increase dispersion of larvae due to increased tidal fluctuations during these times. Also, recent studies have suggested that many larvae have swimming capabilities and can position themselves in the water column to take advantage of currents for a desired directional movement. Crustacean larvae in particular are strong swimmers and are thought to use vertical positioning for dispersal purposes. Decapod megalops, for example, are found near the surface most prevalently during night flood tides to facilitate dispersal and are thought to position themselves there by swimming (Queiroga & Blanton 2005).

It has been suggested that larvae can also use swimming behaviors to escape or avoid predation. Some larvae have shown abilities to detect a nearby predator and behave accordingly. Although out-swimming a predator is improbable, they may be able to position themselves in a current to be carried away, similar to their dispersal mechanism. Due to such behavioral escape mechanisms, it has been suggested that predation rates are generally low with natural densities of larvae (Metaxas & Burdett-Coutts 2005). This suggests release rate fluctuations may control larval populations. Metaxas &

Burdett-Coutts 2005 have also shown that echinoplutei change vertical position within the water column in response to a predator while gastropod veligers do not. This may suggest variability in predator avoidance capabilities, and thus variability in larval population controlling factors, across various taxonomic groups.

Understanding the effects of lunar cycling and predation on larvae provides important insight into species distribution and recruitment abilities. Processes that control early life history determine size and composition of adult assemblages as well (Rooker et al. 1996). Many decapod species are commercially fished for human consumption. Thus larval studies of these species are of economic interest as well (Naylor 2001). Larval studies are also important for understanding the spread of invasive species, designing marine reserves, and providing insight into the adaptation and disappearance of species as the global climate continues to change (Morgan 2008). Meroplankton is also an important food source for many higher trophic level animals. Larval cycles are thus important for sustaining populations and diversity of its predators as well as its own species.

As tested by previous studies, I hypothesize that larval abundances will vary according to lunar cycles, though the expected pattern is uncertain. If timing of larval release has more influence on larval populations, one might expect to find greater abundances during full and new moons, when tidal variations are greatest, which aids in larval transport and dispersion. If predation pressure is a greater influence, one might expect to find the highest larval populations during new moons and the lowest populations during full moons due to higher ambient moonlight aiding visual predators. Predator avoidance capabilities of larvae appear to be mixed across taxa, therefore there are no expectations for decapod response to predators. Planktivorous fish have been

shown to be visual predators so I hypothesize that light intensity and predation pressure will correlate directly, with higher light increasing predation.

METHODS

Research structure and rationale

This study looked specifically at decapod meroplanktonic larvae to gain insight into their reproduction and dispersal behaviors as well as the factors controlling their populations. Diversity and populations were tracked across a temporal scale to show patterning of populations of various species of decapod larvae according to cyclic lunar or tidal cues. Larvae are also likely to vary spatially according to the adult's preferred habitat and the amount of dispersal, whether it is current or behaviorally driven. A second site was subsequently measured to compare two different sites across the same time frames. To test behavioral predator avoidance capabilities, measurements of movement in response to the presence of a predator were quantified in a laboratory setting from two different larval stages. Predation pressure under different ambient light conditions simulating lunar phasing was also measured for the decapod larvae collected.

Lunar cycling

Light trap design and construction: To track lunar cycling of abundances of decapod larvae, samples were collected at night with a light trap (Fig. 1). The light trap was constructed with a clear plastic, 5 liter mineral oil bottle. Two funnels were placed in the sides of the bottle, one on each side. Each funnel measured 11 cm in diameter on its outward facing opening and 1 cm in diameter on the inside opening. The funnels were sewn into the mineral oil bottle with 16.4 lb test fishing line and sealed around the edges with aquarium sealant. A 1 L

Nalgene™ bottle was attached through a 3 cm diameter hole cut in the bottom of the mineral oil bottle to serve as a detachable capture bottle. The top of the cap of the Nalgene™ bottle was removed and the threaded sides of the cap were sewn into the bottom of the mineral oil bottle with the fishing line. The edges of the cap were sealed with aquarium sealant. The bottom of the Nalgene™ bottle was removed. A subsequent 2.5 cm section of the bottom of the Nalgene™ bottle was cut off and glued back together with a layer of 133 micrometer mesh in between. A 450 g lead plate was hung from the bottom of the trap with fishing line to serve as a weight to properly orient the trap underwater. Two small holes, 1 mm in diameter were drilled into the top of the top of the trap for air release. An empty 500 ml Tropical Fanta™ bottle was attached 15 cm above the trap with fishing line to serve as a float. An Underwater Kinetics™ MiniQ40 eLED underwater flashlight was placed in spout of the mineral oil bottle at the top of the trap, pointing down, to serve as the trap's light source. This design is a variation of the light trap used in Hickman 2007.

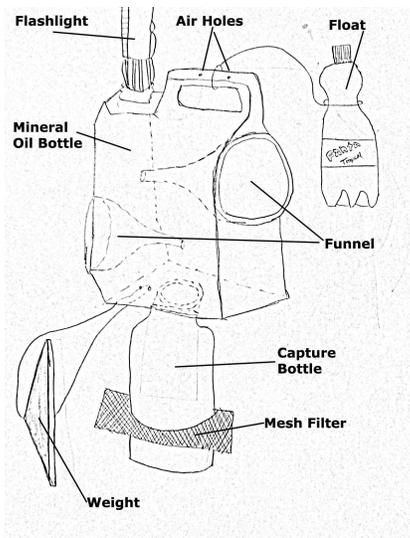


FIG. 1. Schematic of the light trap used in this study.

Sampling sites and protocol: Two sites were chosen to track larval abundances across a temporal scale: a location on the fringing reef of Cook's Bay and a location in Cook's Bay in Moorea, French Polynesia. The reef site was located in Zone 6 South N0199879, W8063923 and the bay site was located in Zone 6 South N0199986, W8064002. GPS points were taken with map datum WGS84 in UTM coordinates (Fig. 2). Sampling took place the day before, the day of, and the day after each lunar phase (quarter moon, full moon, three quarter moon, and new moon). Six consecutive lunar phases were sampled, accounting for one and a half complete lunar cycles. This corresponds to sampling dates of October 6, 7, 8, 13, 14, 15, 20, 21, 22, 27, 28, 29 and November 5, 6, 7, 11, 12, 13 in 2008. On these dates, a light trap was placed at the reef site around 10pm for 20 minutes and at the bay site around 11pm for 20 minutes.

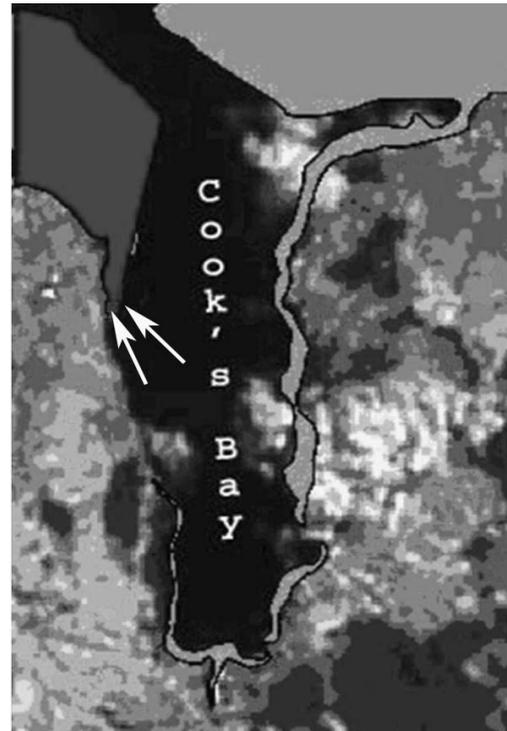


FIG. 2. Map of Cook's Bay. Each arrow points to a sampling site. One is over the reef and one is in the bay near the edge of the reef.

After the 20 minute sampling period, the light trap was removed from the water by the top handle, forcing the water to drain through the collection bottle and trapping plankton on the mesh inside the bottle. The capture bottle was removed from the trap and inverted over a plastic collection cup. Sea water was poured over the filter mesh from the outside to wash trapped plankton into the collection cup.

Collected plankton samples from each site were immediately killed and stored by adding 15 ml of 90% ethanol. Plankton samples were then concentrated into a volume of 40 ml and a subset of 5 ml was removed for counting. On dates 10/20/08 and 10/21/08, plankton was concentrated to 80 ml due to a large amount of holoplanktonic shrimp caught in the trap and a subset of 10 ml was removed for counting. Specimens identified as decapod larvae were separated based on physical characters into morphospecies and counted. Each morphospecies was drawn, photographed with a Leica™ EZ4D microscope camera, and a few were saved as voucher specimens in 90% ethanol. Vouchers are deposited in the invertebrate wet collection in the University of California Museum of Paleontology and images of the 22 morphospecies are provided in Appendix B. Preserved specimens have also been provided to Christopher P. Meyer (Smithsonian Institution) for molecular sequencing in anticipation of identifying larvae by matching sequences with those of adult Moorean species.

Total larval abundances were plotted against lunar phases for both the bay and reef sites. Post hoc ANOVA tests were run to test statistical significance of cycling trends found in each site. Data values were transformed using the formula $\sqrt{(X+0.5)}$ to improve normality of the distribution. Tukey-Kramer HSD tests were run on plots of abundance in the bay and reef sites to establish significant differences between each phase of the lunar cycle.

Larval response to fish predators

Larvae movement was measured with and without the presence of a predatory fish to test their predator avoidance capabilities. Larvae were observed from the side of a fish tank (40 cm wide, 23 cm tall, 3 cm deep) with a white grid serving as the back wall of the tank. A rectangular mesh bag (9 cm X 13 cm) was used as a cage for the predator and was placed in the top left corner of the tank. Larvae were introduced in the middle of the tank, 20 cm from the left side and 11 cm from the surface of the tank. Position of the larvae on the grid was measured every 30 seconds for a total of five minutes. Decapod zoea and megalops larval stages were both tested. For each group, 10 trials were run in the presence of the predator in the mesh cage and 10 trials with only the mesh bag present. The predator, the damselfish *Abudefduf sexfasciatus*, was drawn from a pool of 7 individuals. They ranged in length from 3 cm to 5 cm long. Complete water changes in the experiment tank were done between predator and no predator trials.

Both vertical and horizontal positions in the tank were plotted separately against each 30 second time interval. A Repeated Measures ANOVA test was used to compare predator and no predator trials and test statistical differences between them. All data points were first transformed using the formula $\sqrt{(X+0.5)}$ to improve normality of the distribution.

Predation pressure

To estimate relative predation pressure across lunar phases, a series of feeding experiments were conducted. The predator fish, *A. sexfasciatus*, was kept on a diet of 0.3 ml of plankton per night. The fish were then starved for 24 hours prior to testing. A single fish was placed in a 4 L fish tank and the tank was covered with a black plastic trash bag. The tank was then placed in an area where light penetrating the trash bag

was 0 lux, 0.5 lux, or 1 lux as measured by an Extech™ EA40 light meter. These light intensities correspond to moonlight intensity during the four different lunar phases at which samples were taken. 0 lux corresponds to a new moon, 0.5 lux corresponds to a one quarter and three quarter moons, and 1 lux corresponds to a full moon (Bunning and Moser 1968). Fish were allowed to acclimate to their light conditions for at least 15 minutes prior to testing. At this time, 20 zoeas were placed in the tank and the fish were allowed to feed. After 30 minutes of feeding, the fish was removed from its tank. The tank water was filtered with 133 micrometer mesh to remove the remaining zoeas which were subsequently counted. 10 trials were run for each of the three light conditions with a predator and one without a predator to estimate the number of zoeas that were not eaten but escaped recapture.

The percent of recaptured zoeas were plotted against light intensity. A post hoc ANOVA test was used to test the overall significance of the trend found in the recapture data. A Tukey-Kramer HSD test was also used to test significant differences in recapture between each of the light intensity trials and the absent predator negative control. All data points were first transformed using the formula $\arcsin(X)$ to improve normality of the distribution. All statistical tests were performed using JMP® 4.0.

RESULTS

Lunar cycling

Patterns of decapod larval abundances were found to vary significantly across the lunar cycle. Of the six lunar phases sampled during this study, the most abundant lunar phase of the reef sampling site was found to be the new moon with an average abundance of 1796. The second most abundant phase was the three quarter moon

with an average of 717. The quarter moon and the full moon were both found to be much less abundant than the other two phases with averages of 317 and 56 respectively (Fig. 3). These trends were significant (ANOVA, $p \leq 0.0138$, $df=5$, $F\text{-ratio}=4.848$), however only the new moon was significantly different from the quarter and three quarter moon (Table 1). Although only 1.5 lunar cycles were measured, preliminary observations of decapod abundances that took place during the two lunar phases prior to this study were also found to hold this same pattern. The three quarter moon phase has a relatively larger standard deviation due to a sudden increase in abundances found during the night following the three quarter lunar phase.

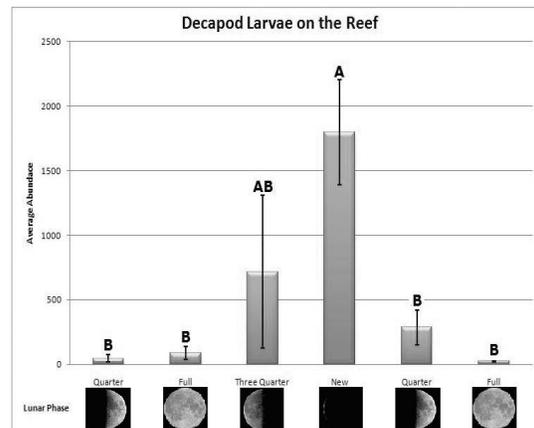


FIG. 3. Abundances of decapod larvae collected on the reef during each lunar period. Abundances were averaged across the three sampling days (before, during and after the night of each lunar period). The black bars represent ± 1 standard error. The letters compare phases through a Tukey-Kramer HSD test.

Decapod larvae were generally found to be much less abundant in the bay than the reef. Larval abundances also showed a different pattern in the bay as compared to the reef. Both the full moon and the new moon had higher averages of 11 and 17 respectively. Comparatively, the quarter

and three quarter moon averaged 4.9 and 4.6 respectively. The quarter and three quarter phases both had similar abundances to each other (Fig. 4). This trend was nearly significant (ANOVA, $p \leq 0.0763$, $df=5$, $F\text{-ratio}=2.736$) but each phase was not significantly different from each other (Table 1).

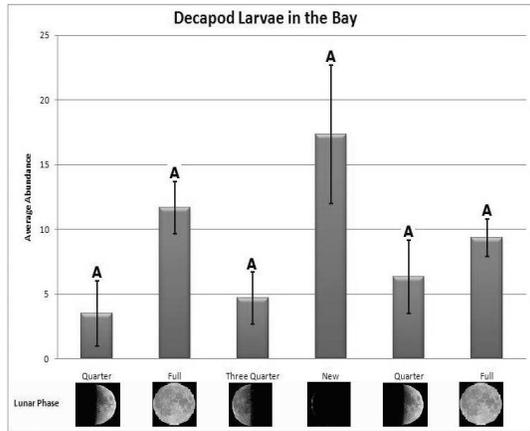


FIG. 4. Abundances of decapod larvae collected in the bay during each lunar period. Abundances were averaged across the three sampling days (before, during and after the night of each lunar period). The black bars represent ± 1 standard error. The letters compare phases through a Tukey-Kramer HSD test

Larval response to fish predators

Decapod zoeas did not show any observable differences in their pattern of movement in the presence of a predator as compared to the same experimental setup without a predator. Zoeas were found to position themselves on average between 7 cm and 11 cm from the surface throughout the 5 minute time interval allotted for each trial. There were no observable differences in the average vertical position of the zoeas between trials with and without predators (Fig. 5). There were also relatively large standard error values for both trials suggesting a wide range of vertical positions and unpredictability of movement. Vertical position values ranged from the surface to

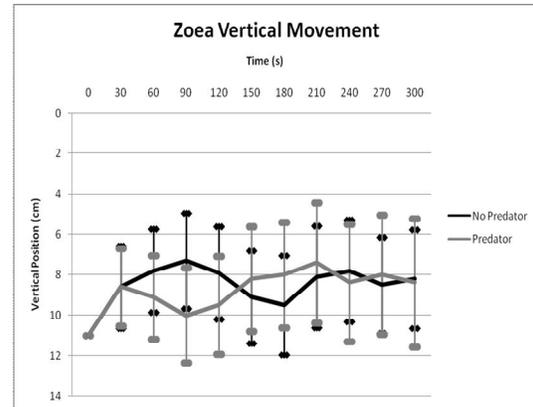


FIG. 5. Average vertical position of the zoeas measured from the surface of the water. The grey line represents trials performed in the presence of a predator while the black line represents trials in the absence of a predator. Vertical bars represent ± 1

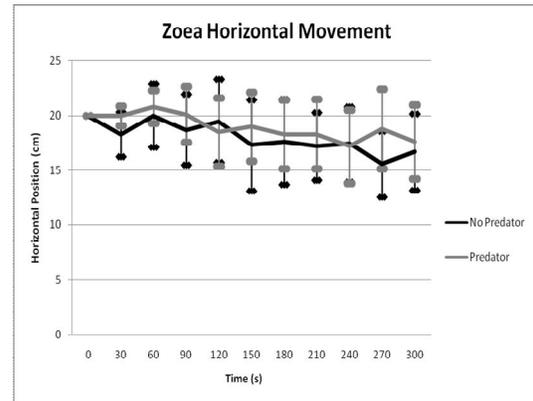


FIG. 6. Average horizontal position of the zoeas measured from the left edge of the tank where the predator cage is. The grey line represents trials performed in the presence of a predator while the black line represents trials in the absence of a predator. Vertical bars represent ± 1 standard error for the line of its corresponding color.

the bottom in most time intervals tested. There were also no observable trends found between predator and no predator trials in horizontal position in the experiment tank (Fig. 6). Horizontal position averaged between 15cm and 21cm from the left edge of the tank. Each time interval also showed large standard error values suggesting wide ranges of movement. There were no

significant differences found between predator and no predator trials in zoea vertical (ANOVA, $p \leq .9317$, $df=1$, $ExactF=.0075$) and horizontal (ANOVA, $p \leq .7987$, $df=1$, $ExactF=.0674$) movements (Table 2).

The slightly more developed megalops stage of decapod larvae did show differences in vertical positioning between trials with and without predators. Megalops averaged a position 4.8cm deeper in the tank throughout the 5 minute time interval with a predator present as compared to no predator trials. Predator trials also averaged a standard deviation 2.5 less than no predator trials suggesting movements in the presence of a predator may not be as random. The average position at every time interval was deeper for predator trials versus non-predator trials (Fig. 7). Horizontal position also showed differences in trends between the two trials. Megalops averaged 16.3 cm further from the left edge of the tank for the whole 5 minute interval. Also the average standard deviations for each position taken in the 30 second time intervals were 2.7 lower for predator trials, maybe again suggesting less random

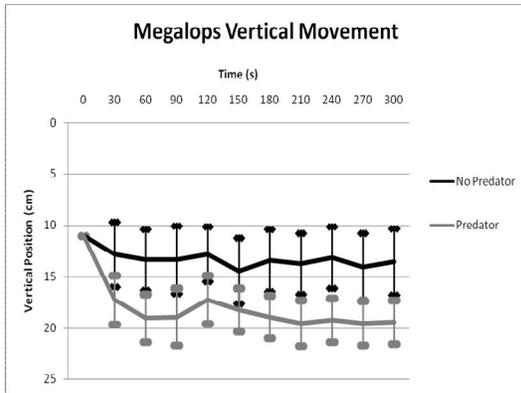


FIG. 7. Average vertical position of the megalops measured from the surface of the water. The grey line represents trials performed in the presence of a predator while the black line represents trials in the absence of a predator. Vertical bars represent ± 1 standard error for the line of its corresponding color.

movements with a predator present. Average positions at every time interval were farther left for predator trials versus non-predator trials (Fig. 8). The megalops vertical movement trials were not found to be significantly different (ANOVA, $p \leq .1817$, $df=1$, $ExactF=1.93$) but horizontal movement was significantly different (ANOVA, $p < .0001$, $df=1$, $ExactF=23.01$) in comparison of predator and no predator trials (Table 2).

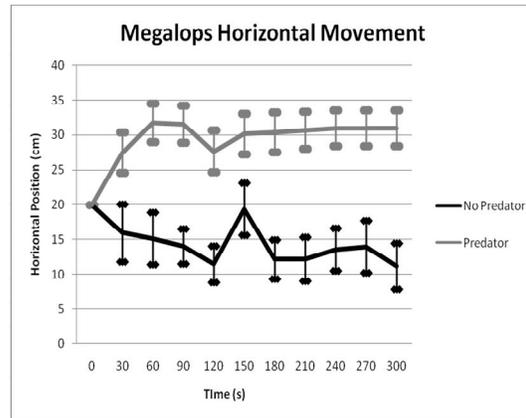


FIG. 8. Average horizontal position of the zoeas measured from the left edge of the tank where the predator cage is. The grey line represents trials performed in the presence of a predator while the black line represents trials in the absence of a predator. Vertical bars represent ± 1 standard error for the line of its corresponding color.

Predation pressure

As light intensity increased, the percent of recovered larvae decreased. In the absence of a predators, larval recovery was higher than in all trials with a predator (Fig. 9). No predator trials averaged 84.3% recovery, 0 lux trials averaged 77.5% recovery, .5 lux trials averaged 13% recovery, and 1 lux trials averaged 6.1% recovery. Standard errors were similar among all conditions tested. This pattern of correlation between light level and % recapture is highly significant (ANOVA, $p < .0001$, $df=4$, $F\text{-ratio}=224.4$) (Table 1). No predator and 0 lux trials are both

significantly different from all other conditions. 0.5 lux and 1 lux trials are significantly different from no predator and 0 lux trials but not from each other.

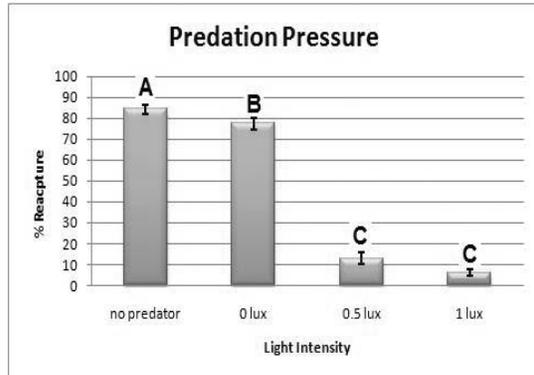


Figure 9- Average % recapture of zoeae under various light intensities. Black bars represent ± 1 standard error. The letters compare the light conditions through a Tukey-Kramer HSD test.

DISCUSSION

Lunar cycling

The higher abundances during the new moon and lower abundances during full moon supports the hypothesis that predator pressure has a large effect on the population cycling of decapod larvae. Predator pressure is thought to be highest during the full moon and lowest during the new moon due to the lunar light intensity during these phases (Dawidowicz et al. 1990). The brighter moonlight during full moons allows for efficient activity of visual planktivorous organisms, thus decreasing planktonic larvae populations during this time. The absence of moonlight during the new moon prevents visual predation, causing much larger abundances of plankton during new moon periods.

The three quarter moon period showed higher abundances than quarter moons, which is not explained by predation from moonlight. Both of these phases have

essentially the same light availability so based on visual predation one would expect similar larval abundances during these two lunar periods. Higher abundances during the three quarter moon may be caused by a larger release of larvae during this time. There was a sudden increase in larval abundance following the night of the third quarter moon. This increase in larval release may be advantageous for adults seeking to reduce predation of their offspring.

Although decapod molting and metamorphosis rates are species dependent, a typical zoea will metamorphose into a higher level megalops stage in 4-6 days, which may be delayed up to 8 days if nutrients or other environmental conditions are not optimal (McConaughy 1985). By releasing larvae following the third quarter moon, zoeas are present in their initial, vulnerable state as moonlight is waning and predation pressure is decreasing. This provides the time necessary, even if conditions are not optimal, for metamorphosis into the megalops stage before the light levels of the quarter and full moons are reached. Decapods in the megalops stage are thought to possess greater behavioral control and may escape predation better than younger zoea stages (Queiroga & Blanton 2005).

The higher larval abundances of the bay site found during the full and new moon and lower relative abundances during quarter and three quarter moons may not be a product of predation or timed larval release. Larger tidal variations, spring tides, are created by combined gravitational forces from alignment of the sun and moon during full and new moons while smaller variations, neap tides, are created from the opposing gravitational forces of the sun and moon (Christy 1977). Spring tides found during full and new moon periods provide larger currents that may carry larvae from the reef nursery ground to farther offshore bay sites. During the quarter and three quarter moon, when neap tides occur,

currents moving offshore are weaker and larvae may not be dispersed. Zoeas of shore crabs have been shown to purposely take advantage of heightened currents during spring tides for dispersal purposes.

Zoeas have been shown to follow endogenous cycles of positioning themselves higher in the water column during ebb tides and lower during flood tides, facilitating seaward transport (Zeng & Naylor 1996). Transport would be greater during full and new moons when tidal height variation is greater. Zoeas ascending to catch the current would be transported in top water layers where the sampling trap was placed in the bay each night, creating patterns of relatively higher abundances during full and new moons.

Larval response to fish predators

Decapod zoeas did not show any trends in comparison of vertical and horizontal positioning in the presence and absence of a fish predator. Movements throughout the tank were seemingly random with large standard error values at each sampling period. Many decapod species are known to possess large rostral spines in their zoea stage; some reach several times their body length. Although the function of these spines remains debated, it has been suggested that they serve as an anti-predator device. They have been found to significantly deter predation by planktivorous animals, including fish (Morgan 1989). Protection from their spines may eliminate the need to behaviorally detect and avoid nearby predators.

Perhaps zoeas are simply in a developmental stage that lacks the sensory and motor systems necessary for predator detection and avoidance. Decapod larvae are known to be released in extremely large numbers (McConaugha 1992). This r-select species approach to reproduction may provide sufficient recruitment levels even though predation may be high. The inability

to avoid predators supports the hypothesis that larval predation is high and may control population cycling.

Decapod megalops stage larvae tended to position themselves deeper and farther away from the predator during behavioral trials. Although only horizontal positioning was significant, both horizontal and vertical measurements showed trend of positioning. Megalops are known to possess relatively strong swimming capabilities for water column positioning and dispersal (Queiroga & Blanton 2005). It is possible they can also detect the presence of a predator and use their swimming capabilities to position themselves farther from predators or escape.

The results of the larvae behavioral analysis may also help explain the lunar cycling of larval abundances observed in this study. Initial zoea stage larvae were not found to be able to respond to predators while later stage megalops were. Perhaps zoeas are released just before and during the new moon phase because they are defenseless against planktivorous organisms and this phase has the lowest associated predation pressure. This allows sufficient time required for zoea metamorphosis into megalops before the heavier predation from the cycle's movement toward the full moon. By this time of higher predation pressure, larvae have developed into megalops that are capable of predator detection and escape.

Predation pressure

Planktivorous fish are thought to track prey mainly through visual cues (Hairston 1982). Thus, higher light intensities would be expected to increase a predatory fish's ability to find plankton. The pattern of predation pressure observed in the results of this study was consistent with predicted predation pressure based on light intensities, where higher light intensity yielded higher predation. All trials performed in the presence of a predator

differed significantly from trials without a predator assuring that the results were not an artifact of sampling technique.

Predation trials carried out in no light conditions likely yielded significantly higher recapture rates of zoeas, possibly due to the predator's limited visibility. Predation trials carried out under 0.5 lux and 1 lux also showed this pattern where increasing light intensity increases predation pressure. Predators may have been able to better track larval prey with higher levels of light availability.

Although recapture rates in 0.5 lux and 1 lux trials followed expected trends, these two trials were not significantly different from one another. This suggests that there is a threshold light intensity level above which predatory fish can track prey and predation pressure remains constantly high, rather than a linear relationship between light intensity and predation pressure. Additional research with larger sample sizes would be necessary to distinguish between these two situations.

Polynesians have known about lunar cycling of marine life for generations. Every year, a Tahitian lunar fishing calendar is produced predicting larval abundances and fishing activity for the rest of the year. In addition to a traditional solar calendar, Tahitians also have a lunar calendar with different names for each lunar month and each lunar day within the month. For any given day, one can use the calendar to find out the current position in the lunar cycle as well as what larvae are abundant, which fish species are most active, expected weather conditions, and even what crops to plant. This lunar calendar is produced only in Tahitian and much of it does not have a direct translation to English. General patterns expressed by the calendar are that the most larvae are released around the new moon and fishing for reef fish species is best done around the full moon (pers. com. Auzepy 2008, pers. com. Murphy 2008). These patterns are supported by the results

of this study because the largest abundances of decapod larvae were found during the new moon. Also, this study suggests increased light during a full moon increases predation pressure from planktivorous reef fish, which may explain why fishing is better during full moons as fish are actively feeding.

ACKNOWLEDGEMENTS

This project would not have been possible without the help and support from all of the professors and GSI's for the class. I would like to thank Brent Mishler, Jere Lipps and Chris Meyer for their help in developing a project, Jaime Bartolome for help with experimental setup, George Roderick for help with statistical analysis, and Carole Hickman for her guidance and advice throughout the entire process. I would like to thank Molly Wright, Kari Roesch Goodman, and Jennifer Imamura for their help in all aspects of this project. I would also like to thank all my classmates for making this an amazing experience.

LITERATURE CITED

- Augusto, A.V.F., A.C.A. Mazzuco, and M. Bueno. 2007. A field study to describe diel, tidal and semilunar rhythms of larval release in an assemblage of tropical rocky shore crabs. *Marine Biology*. **151**: 1989-2002
- Auzepy, Patrick. 2008. *Personal communication*
- Bünning, E., and I. Moser. 1968. Interference of moonlight with the photoperiodic measurement of time by plants, and their adaptive reaction. *Botany*. **62**: 1018-1022
- Christy, J. H., 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: A Hypothesis. *Science*. **199**: 453-455

- Dawidowicz, P., J. Pijanowska, and K. Ciechomski. 1990. Vertical migration of *Choaborus* larvae is induced by the presence of fish. *Limnology and Oceanography*. **35**: 1631-1637
- Gliwicz, M. 1986. A lunar cycle in zooplankton. *Ecology*. **67**: 883-897
- Hairston, N.G., K.T. Li, and S.S. Easter. 1982. Fish vision and the detection of planktonic prey. *Science*. **218**: 1240-1242
- Hickman, C.S. and S.S. Porter. 2007. Nocturnal swimming, aggregation at light traps, and mass spawning of scissurellid gastropods (Mollusca: Vetigastropoda). *Invertebrate Biology*. **26(1)**: 10-17
- Korringa, P. 1947. Relations between the Moon and Periodicity in the Breeding of Marine Animals. *Ecological Monographs*. **17**: 347-381
- McConaughy, J. R., 1985. Nutrition and larval growth. In Wenner, A. M. (ed.), *Larval Growth*. *Crustacean Issues*. **2**: 127-154
- McConaughy, J.R., 1992. Decapod Larvae: Dispersal, Mortality, and Ecology. A Working Hypothesis. *American Zoologist*. **32(3)**: 512-523
- Metaxas, A. 2001. Behaviour in flow: perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Canadian Journal of Fish and Aquatic Science*. **58**: 86-98
- Metaxas, A., and V. Burdett-Coutts. 2006. Response of invertebrate larvae to the presence of the ctenophore *Bolinopsis infundibulum*, a potential predator. *Journal of Experimental Marine Biology and Ecology*. **334**: 187-195
- Morgan, S.G. 2001. The larval ecology of marine communities, *in*: Bertness, M.D. *et al.* (Ed.). *Marine Community Ecology*. 159-181
- Morgan, S.G. 1989. Significance of spination in estuarine crab zoeae. *Ecology*. **70**: 464-482
- Morgan, S.G., and J.R. Anastasia. 2008. Behavioral tradeoff in estuarine larvae favors seaward migration over minimizing visibility to predators. *PNAS*. **105**: 222-227
- Murphy, Hinano. 2008. *Personal communication*
- Naylor, E. 2001. Marine animals behaviour in relation to lunar phases. *Earth, Moon and Planets*. 85-86: 291-302
- Omori, K. 1995. The adaptive significance of a lunar or semi-lunar reproductive cycle in marine animals. *Ecological Modeling* **82**: 41-49
- Porter, S.S. 2002. A light trap survey of stomatopod larvae at Cook's Bay, Moorea. *UC Berkeley - Moorea Student Research Papers*. 11: 135-152
- Queiroga, H., Blanton, J.O., 2005. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustaceans larvae: an overview. *Advances in Marine Biology*. **47**: 107-214
- Robertson, D.R., D.G. Green, and B.G. Victor. 1988. Temporal Coupling of Production and Recruitment of Larvae of a Caribbean Reef Fish. *Ecology*. **69**: 370-381
- Rooker, J.R., G.D. Dennis, and D. Goulet. 1996. Sampling larval fishes with a nightlight lift-net in tropical inshore waters. *Fisheries Research*. **26**: 1-15
- Roughgarden, J., Y. Iwasa, C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology*. **66**: 54-67
- Smith, DeBoyd & K.B. Johnson. 1996. A guide to marine coastal plankton and marine invertebrate larvae. Kendall/Hunt. Dubuque, Iowa.
- Zeng, C. and E. Naylor. 1996. Endogenous tidal rhythms of vertical migration in field collected zoea-1 larvae of the shore crab *Carcinus maenas*: implications for ebb tide offshore dispersal. *Marine Ecology Progress Series*. **132**: 71-82

Appendix A

Experiment	DF	Sum of Squares	F-Ratio	Prob>F
Cycling of larvae abundances (Reef)	5	7052584	4.848	.0138
Cycling of larvae abundances (Bay)	5	367.93137	2.7362	0.0763
Recapture rates (Predation Pressure)	4	2252.475	224.425	<.0001

TABLE 1- Post hoc ANOVAs for abundance cycling in the bay, in the reef, and predation pressure experiments.

Experiment	Exact F	NumDF	DenDF	Prob>F
Zoea vertical movement	0.0075	1	1	0.9317
Zoea horizontal movement	0.0674	1	18	0.7981
Megalops vertical movement	1.93	1	18	0.1817
Megalops horizontal movement	23.0108	1	18	<0.0001

TABLE 2- Repeated measures ANOVAs for all larval behavior trials.

Appendix B
(Photos or drawings of all larval decapod morphospecies encountered during this study)

