

LOCALIZED LIGHT SENSORY IN RELATION TO GRAZING ACTIVITY OF *ECHINOMETRA MATHAEI*

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Abstract. This paper offers insight on the regulation of nocturnal behavior in burrowing sea urchin *Echinometra mathaei* of the Pacific. While it is known *E. mathaei* maintains nocturnal hours of activity (primarily grazing, burrowing, and locomotion), it is unknown whether this pattern follows a circadian rhythm or responds to local conditions of darkness. Varying light treatments were tested to determine potential manipulation of active behavior and explore potential for habitat destruction. Light manipulation was used to determine the role light sensory plays in the regulation of normal behavior. First utilizing gradual manipulation and later utilizing sudden manipulation to differentiate response to light stimuli. It was determined that while *E. mathaei* maintains nocturnal activity via localized light sensory, manipulation of latent hours could not be significantly reproduced. It was found that while light manipulation can be responsible for simulating hours of activity, light manipulation cannot replicate latent hours. Upon exploration of predator response capability in *E. mathaei* following manipulation, it was found that individuals exposed to prolonged periods of artificial light had slower predation response times than individuals acclimated to a regular pattern of light exposure. These findings connect potential habitat degradation via grazing behaviors of *E. mathaei* to anthropogenic activity in Mo'orea, French Polynesia.

Key words: invertebrates; Echinometra; anthropogenic effect; tube feet; sensory mechanisms; stress response; habitat degradation; nocturnal; activity rhythm; Mo'orea; French Polynesia

INTRODUCTION

Species throughout the animal kingdom execute crucial tasks, like feeding and mating, during the night. Avoiding predation by diurnal threats allows these nocturnal species to take advantage of this temporal niche (Pizzatto, Child, and Shine, 2008). Among mammals with complex sensory systems, a 24-hour endogenous cycle called circadian rhythm manages this activity (Zee, Attarian, and Videnovic, 2013). This rhythm is maintained by a network of 'clocks' that function in the body, comprised of the interpretation of light/ dark cycles, and feeding and metabolism (Güldür and Oltu, 2016). Mammals rely heavily on the synchronization of their circadian rhythm with cycles of light and dark in the environment, a process managed by ocular photoreceptors

sending signals to the hypothalamus (Buhr and Takahashi, 2013). Observations have been made of light affecting activity rhythms of mammals (Browman, 1937). However, in invertebrates the process behind regulating a cycle of active/ latent behaviors relies on simpler mechanisms due to the absence of specified hormone receiving glands (Saigusa and Oishi, 2000).

The phylum Echinodermata is characterized in part by radial pentamerous symmetry and hydraulic structures emerging from the ventral face (Appendix A). These structures are vital for the fulfillment of most of their habitual behaviors, from sensory ability to feeding and locomotion (Arakaki, Uehara, and Indur. 1998). These structures, or "tube feet," assist in locomotion by inflating along with the contraction of a corresponding internal body

canal and providing suction to a surface (Smith, 1937). This sucking system creates the momentum needed to move across a surface and helps with adherence to substrate.

In many species, tube feet are also necessary in processes of respiration, chemoreception, cleaning, feeding, and light sensory (Kerkut, 1953). How exactly tube feet aid in these processes has been studied. However, it is relatively unknown what role light sensory plays in regulating the consolidated periods of inactivity echinometrids display (Agca, et.al., 2011). In addition, the extent of sight in different species of echinometrids is variable. There are species that, while unable to create fully resolved images, can crudely determine light levels via ossicles that use light to direct the locomotion of the animal (Johnsen and Kier, 1999, Johnsen and Blevins, 2004.). This includes species *Echinometra mathaei*, a burrowing urchin found in Indo-Pacific regions. They possess tube feet that aid in many of their habits. Unlike most Echinoderms their tube feet are not limited to the ventral surface. Instead their tube feet alternate with layered spines that provide protection and aid in locomotion (Khamala, 1971).

To avoid predation by diurnal threats, *E. mathaei* locomotes and feeds during the night (Nelson and Vance 1979). Peak hours of this behavior correspond with the darkest hours of the night, primarily around midnight (Mills, 2000). Individuals extend their tube feet to detach from their hiding places in search of food during hours of activity. The tube feet located on the ventral face are capable of sensing light and serve as threat preceptors when large dark shapes become visible, and this in turn drives a corresponding hiding response (Yerramilli and Johnsen, 2010). Due to this response they are found hidden in crevices and under rocks during daylight hours, when their predators are active in the greatest number, with light sensory controlling this behavior (Coppard and Campbell, 2005).

In areas with high concentrations of Echinoids, sea urchin grazing can become destructive to the surrounding environment (Coma, 2011). The grazing behaviors of *E. mathaei* play a pivotal role in the bioerosion of

coral reefs, and with higher urchin activity a higher rate of bioerosion is observed (Ogden, 1977). As efficient grazers, urchins can pose a threat to benthic communities when enabled to feed more often or in wider ranges (Lissner, 1980). In addition, differences in activity levels can notably affect species composition when competing for finite resources. Due to the magnitude of their isolation, oceanic islands are home to some of the most endemically biodiverse species, making them especially susceptible to anthropogenic stress (Paulay, 1994). This paper explores how light exposure directly influences the grazing and homing behaviors of *E. mathaei*, the manipulation that anthropogenically sourced light can have on these behaviors, and the resulting effect on surrounding ecosystem health. Essentially answering the question; do *E. mathaei* follow a circadian rhythm or do they respond to local conditions of darkness with activity patterns that can be manipulated or even reversed with manipulation?

METHODS

Sample sites

Individuals were collected from two sites. Both locations were within shallow lagoons on the north side of the island of Moorea, French Polynesia. Both also showed high population densities of *E. mathaei* and represented suspected nurseries, as many juveniles of species were present. Mature urchins were collected for use in this study. Individuals of test size 5-7 cm were collected by gently prying them out of crevasses under loose rocks. Test size was standardized to ensure similar feeding frequency and corresponding locomotion, as smaller individuals can be observed feeding and boring with less frequency. Purple morphotypes were favored for collection as they display the highest frequency in these sites.

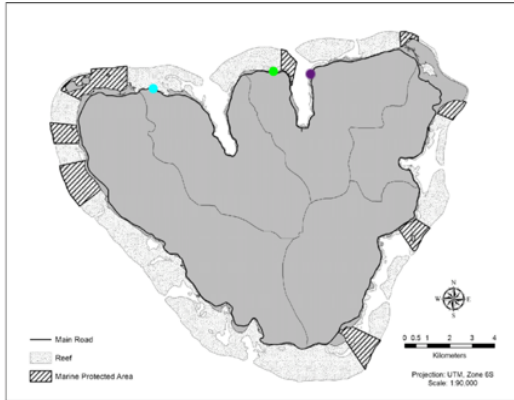


FIG. 1. Sites sampled labeled with corresponding points. *E. mathaei* collected at 'Snack Mahana' site in blue, and 'Pihaena' site in green. Crustose Coralline Algae (CCA), *Padina pavonica*, and *Sargassum sp.* for pilot experiments and feeding collected in 'Pao Pao' site, purple.

Lab study of habitual activity

In order to determine a change in nocturnal habits, first baseline patterns must be established. Thus, I conducted a preliminary aquarium study of movement. Ten individuals were collected from "Snack Mahana" site which I allowed to acclimate for three days in a large flowing tank under natural light cycles. Large rocks with algal coverage (*Padina pavonica*, *Sargassum sp.*), food sources for *E. mathaei*, were distributed evenly around the base of the tank. After the acclimation period, individuals were tagged with a dot of paint on a secondary long spine and a corresponding dot of paint was placed on their daytime hiding place. For the two following 24-hour periods, observations were made at 00:00, 03:00, 06:00, 09:00, 12:00, 15:00, 18:00, and 21:00 to count states of activity, including categories "inactive," "somewhat active," and "very active". "Inactive," was defined as being fully hidden in a corresponding cavity with no extension of tube feet, no spine movement, and no projection of Aristotle's lantern. "Somewhat active," was defined as close to a corresponding cavity with some tube feet extension and general spine movement. "Fully active," was defined as detached from the corresponding rock and actively locomoting

with the full extension of tube feet and spine movement. Upon being picked up these "very active" individuals exhibit a full projection of Aristotle's lantern, indicating active feeding or boring behavior (Black, et. al., 1984).

Activity reversal

After establishing an expected pattern for nocturnal and daytime activity, reversal of the normal activity was attempted using two methods. First, this involved a gradual reversal of light exposure. In a companion set of experiments, this involved a sudden reversal of light exposure. Both approaches were attempted to determine whether or not local light sensory is responsible for maintaining the observed activity patterns, and if so, what is necessary to alter these behaviors. In reversed light conditions, mammals like deer mice have exhibited "(reversal in) their activity rhythms." (Browman, 1937). Following the success of experiments like this, reversed light conditions were tested.

Ten acclimated urchins were placed in an aquarium with flow, shelter, and food sources (*Padina*, algal coverage on rock). A box was constructed to fit over the top of the aquarium, with a hole for flow, and a halogen light was rigged to hang above the aquarium. To begin gradual light reversal, the lamp was turned on at 18:00 and left on until 19:00, giving the population one extra hour of light. The constructed light deprivation box was then placed over the tank. The following morning the box was removed, and the light switched on at 07:00. Following this system, the tank received 12-hour intervals of light and darkness offset by one hour every nychthemeron. The process was repeated every night for twelve nights, gradually offsetting natural sunrise and sunset by an hour every nychthemeron until complete reversal was achieved. Following the twelve-day period, the tank received direct light from 18:00 to 06:00, and darkness from 06:00 to 18:00, a complete reversal from natural sunrise and sunset preceding the experiment.

On the thirteenth day of gradual reversal, a light impermeable tarp was hung around the aquarium. During simulated "night," or the 12-

hour period of darkness, the box was removed and urchin activity was observed using a red light under the tarp. The red light and tarp maintained the conditions of simulated nighttime while allowing quantification of activity using the aforementioned categories of activity: "inactive" "somewhat active" and "very active". Two 24-hour periods of observations were recorded and averaged to compare effectiveness of the gradual reversal, at 00:00, 03:00, 06:00, 09:00, 12:00, 15:00, 18:00, and 21:00.

Following gradual reversal, sudden reversal was tested to determine if there would be a "jet lag" effect or if localized light exposure directly controlled hours of activity. A new population of ten *E. mathaei* was collected from the "Snack Mahana" site and acclimated as previously described. An identical aquarium was set up as in the first reversal experiment. After acclimation, the light deprivation box was placed over the aquarium just before sunrise (05:00) and left over the tank until sunset, when the box was removed, and the light turned on. The 24-hour period following the switch, observations were taken following the same categories as before: i.e., "inactive" "somewhat active" and "very active." Only one day and night of resulting activity patterns were recorded to best reflect the immediate effect of light reversal, instead of the adjusted effect over time.

Predation response under prolonged exposure

After classifying light exposure as having a direct effect on the activity of *E. mathaei*, prolonged exposure to light and dark were tested for the effect of each manipulation on overall health via stress response. Two samples of ten urchins each (test size 5-7cm) were acclimated to natural light in a large aquarium. Spinal response time of *E. mathaei* was recorded after being prodded with a foreign object to gauge stress response prior to treatment. Two samples of ten *E. mathaei* each were placed in identical sterile aquariums with segments of clean PVC pipe for shelter and controlled food input. Urchins were then maintained on separate prepared diets to control grazing rates under each treatment. This ensured the only

variable difference was the variation in light exposure through the trials. The populations under each extended light treatment received a diet of 103.1 grams of cleaned CCA (Crustose Coralline Algae), and 50.3 grams of *Sargassum sp.*, collected from Pao Pao, Moorea. (Coralline algae were cleaned by removing other algae's, sediment, and inverts with tweezers and rinsing clean with salt water. Cleaning preceded wet weighing; weight reflects only that of coralline algae.) Population one was then placed under direct light for 1 week, and population two was covered with the light deprivation box from previous trials for five days. After each period of extended exposure manipulation, predation response was gauged to determine lights effect on the stress response of populations. This was done by repeating the spinal response time test. A metal poker was placed against the side of the test, roughly equidistant from the aboral and ventral poles on the lateral side. 'Spine response' was timed as the time it took each individual to close the immediately surrounding spines about the foreign object used to mimic predation. This response was tested to gauge threat identification ability of populations post treatments. This test was also replicated in the field. I tested 30 individuals to gauge predation response of healthy individuals in the wild under natural light. (Fig. 5)

Statistical analysis

I plotted the average frequency of activity to visualize the general reversal of activity corresponding to a reversal of light exposure. Both sudden and gradual light reversal were included in this plot. I then tested how well reversal data fit with expected distribution using a chi-square goodness of fit test with $\alpha = 0.05$. This allowed me to test the likelihood of the outcome of activity reversal for each treatment attempted when compared to activity pre-treatment.

RESULTS

Chi² test of goodness of fit

Statistical analysis was performed to determine the effectiveness of each reversal treatment. Using the program PAST, a Chi² test was applied to compare the expected hours of latent behavior with observed hours of latent behavior after gradual reversal in 12-hour periods. The comparison of latent behavior under conditions of darkness gave a P value of .041 after a gradual switch of light exposure, which was less than alpha = 0.05. Latent behavior under conditions of light had a P value of 0.41, again after gradual reversal. The same test was used to compare latent behavior after sudden reversal in the same 12-hour periods of expected active and latent behavior. The comparison of latent behavior under conditions of darkness gave a P value of .02 under a sudden switch of light exposure. The P value for latent behavior under light exposure was 2.36 after sudden reversal. Following the Chi² test of goodness of fit, both treatments showed significance in manipulation of active behavior, but insignificant reversal of latent behavior.

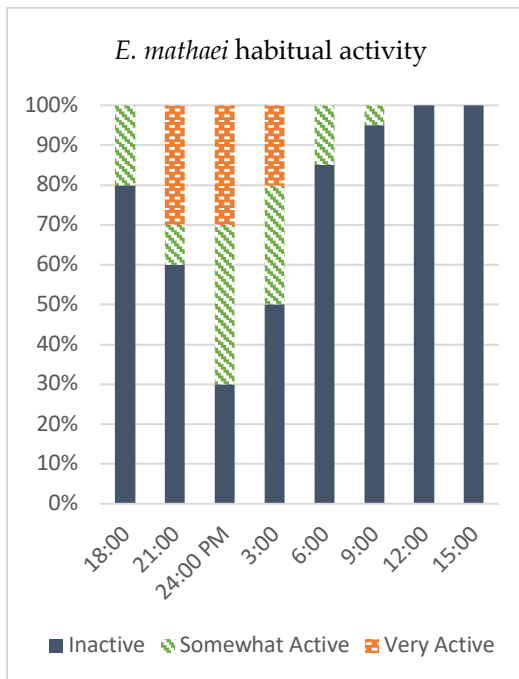


FIG. 2. *E. mathaei* average activity over a 24-hour period, from lab study of nocturnal movement following acclimation and habitat replication.

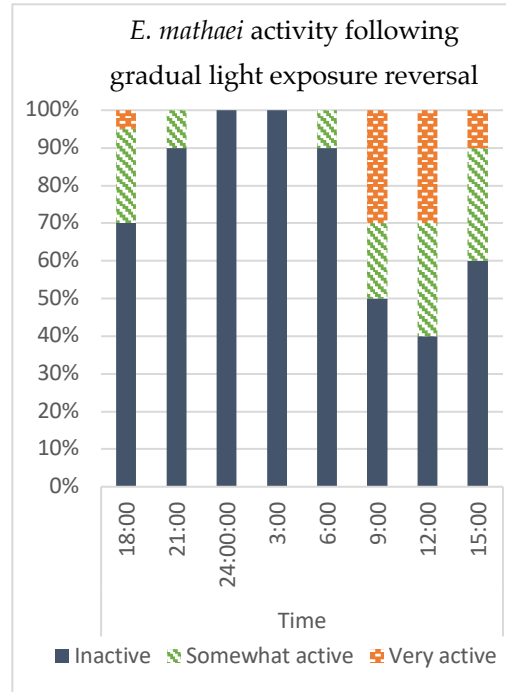


FIG. 3. *E. mathaei* average activity over a 24-hour period following gradual light exposure reversal, as observed on three-hour intervals representing activity.

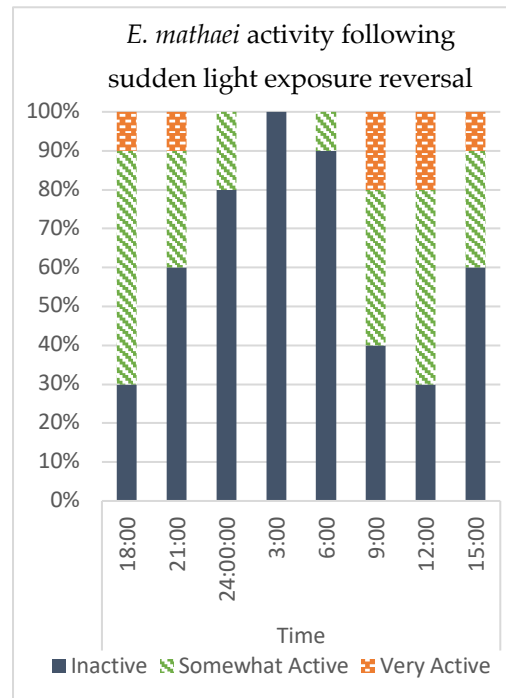


FIG. 4. *E. mathaei* activity over a 24-hour period after sudden light exposure reversal.

Evidence of artificial light on predator response was quantifiable. The effects of prolonged exposure to light and dark conditions as well as human handling were reported to gauge the effect of each treatment. Individuals taken from constant daytime input (direct light, 24+ hours) displayed the slowest response time. Individuals from constant night

input (total darkness, 24+ hours) displayed the fastest response time. From the averaged response times it is shown that handling and removal from habitat can slow stress response time. Handling is represented by 'lab survey post acclimation,' as populations tested were acclimated to natural light in man-made conditions after a period of handling.

TABLE 1. Mean response time to foreign object on test in varying conditions mimicking anthropogenic alteration of habitat, including human handling and prolonged exposure to manipulated light and dark conditions.

Survey type	Mean response time
Field survey	2.7 sec
Lab survey post-acclimation	4.3 sec
Lab survey post prolonged light treatment	7.8 sec
Lab survey post prolonged dark treatment	4.1 sec

DISCUSSION

The initial perceived outcome of both activity reversal attempts was complete reversal of activity. The histograms (Fig. 2, 3, 4) show this in a general reversal of activity during hours of both light and darkness. Upon statistical analysis, this was shown to be the case for darkness treatments of manipulation, and not the case for light. Prolonged light treatments, while not driving a reversal of behavior, caused stress responses in *E. mathaei*, including increased spinal breakage and a slower defensive response to predation.

Gradual light reversal was conducted to gauge response to a slow light change, designed to mimic the slow adjustment exhibited in mammals after a misalignment of time and circadian rhythm. (Burgess, et. al. 2003) This effectively switched light exposure over the course of 12 days, so day and night were completely reversed in terms of light exposure. A previous light manipulation study in *Drosophila* found activity to be "synchronized with the environment via light or temperature cycles," and that these cycles necessitate daily resets of the internal clock. (Peschel. et. al. 2009) This indicates that in

organisms with a lack of specialized hormone receiving glands, like *Drosophila* and *E. mathaei*, light sensory must play a direct role in regulating hours of activity. This was partially true from the results of the gradual light reversal experiment.

It was found that the degree of light exposure was directly related to hours of activity in *E. mathaei*. Rather than follow a circadian rhythm, urchins under light manipulation responded to localized light. The activity under manipulated darkness showed a significant p value under both gradual and sudden conditions. This indicates conditions of excess darkness correspond to hours of activity, defined by grazing and locomotion. To test the immediate effect of localized light sensory in maintaining nocturnal activity, sudden light reversal was performed.

Immediately reversing hours of dark and light and a consequent observation of activity displayed the significance of localized light sensory in grazing behaviors. $P = 0.02$ after sudden light reversal indicated the successful promotion of full active behaviors under manipulated darkness. The result of activity during this time was significant, as was the result after the gradual switch. In both cases,

provided darkness promoted grazing in the same pattern as normally occurs during the night. The likeness of these two outcomes promotes the resulting increased activity under manipulated darkness was stimulated by the darkness. From these results it follows that artificial conditions of darkness occurring in the natural habitat of *E. mathaei* could yield excess hours of activity. However, latent hours under prolonged light exposure was not significant by these same metrics. While manipulated hours of darkness corresponded with significant activity, complete reversal of activity was not achieved. Manipulated hours of light failed to replicate latent hours under natural conditions, meaning, while grazing behaviors can be manipulated with light input, latent hours cannot.

Implications of excess darkness promoting grazing are damage to fringing reef ecosystems. Reports of excess grazing following a change in habitat have been recorded in habitats from sea grass to fringing coral communities, similar to those on the island of Moorea, French Polynesia. (Qui, et. al. 2014. and Camp, et. al. 2009). Urchin have proved to be highly destructive grazers in multiple studies conducted after an alteration to their immediate environment, proving them to be highly opportunistic feeders with an incredible capacity for destruction of habitat.

The promotion of over-grazing in species like *E. mathaei* is the causation behind catastrophic habitat damage, as has been recorded in the degradation of California's kelp beds, where *Strongylocentrotus purpuratus* has driven destruction of kelp beds (Mann. 1977). Following the link of darkness to grazing hours, and with the possibility of a rise in ecotourism, over water construction in *E. mathaei* habitat should be surveyed for its effect on immediate reef health. On the island of Moorea, French Polynesia, this necessitates a survey of over water bungalows and other resort construction that provides excess hours of darkness, as it likely promotes destructive grazing behavior in *E. mathaei*. A survey of population abundancy of *E. mathaei* and coral health should be conducted in the areas as well.

In addition to effects on grazing activity, manipulated light exposure results in

predation response that is varied from that displayed under natural light. Excess stress observed after prolonged exposure of light indicated a slower threat response after prolonged light exposure. This result implicates dock lights, which are common at hotels and resorts, as well as lighting on boats. A slower spine response is tied to a less efficient threat detection and could leave urchins more prone to predation (Millott, Yoshida, 1959). With a slower response time to contact of a foreign object with the test, urchin are less likely to be able to ward off predators using their own primary method of defense: their spines. (Blainville, 1825) The fastest recorded response time from this study was that of *E. mathaei* observed in the field. Surveyed individuals were firmly attached to crevasses and near plentiful food sources. Likely, the handling of *E. mathaei* in lab tests caused stress to the individuals, serving to slow their response time. The individuals least prone to predation were those removed from light pollution, man-made sources of cover, and interference by handling, as was shown by spine response (Fig. 5). The individuals with the slowest recorded response time were those kept in the lab for a week long prolonged light exposure experiment. A combination of handling, less ideal habitat, and direct and constant light exposure discouraging grazing is likely the cause. These individuals were the most prone to predation based on the stress response recorded, which was over double that of individuals tested in the field.

Future research

Further responses to anthropogenic stress should be observed to establish the extent of these potential negative effects. Following occurrences of habitat destruction following uncontrolled grazing in other parts of the world, this is of interest. Another stress response of sea urchin is the loss of pigment and appendages, primarily longer spines that serve as protection, which should be monitored for species health in changing conditions. (Giese and Farmanfarmanian, 1963). Longer extended exposure to light conditions should show more advanced signs of stress, as

individuals are not signaled with darkness to graze have a slower response to predation. The converse should be done to determine the extent that over the water construction is capable of manipulating active behaviors of *E. mathaei*, inadvertently causing destruction via grazing and burrowing.

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APPENDIX A

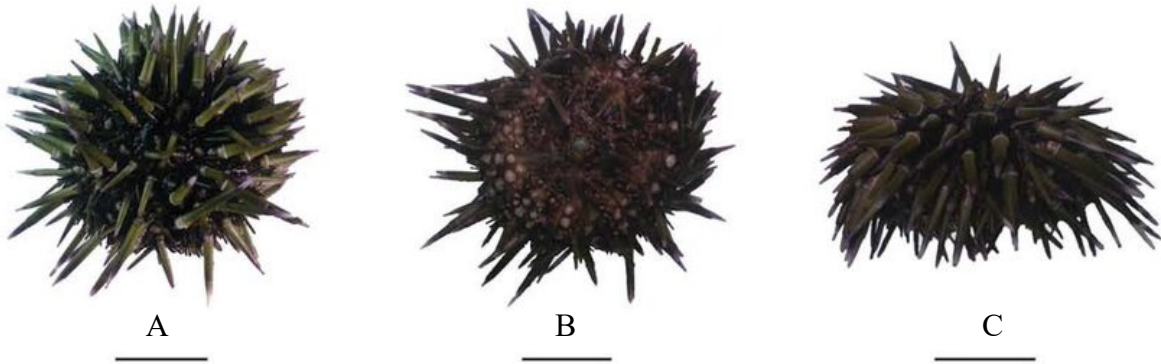


Image: Lee and Shin, 2012.

FIG. A1. *Echinometra mathaei* depicted in three views. A. image of the aboral side, with the anus centered, light sensing tube feet extend from this pole when active. B. the ventral side, no projection of Aristotle's Lantern, which is projected when feeding or burrowing behaviors are occurring. C. lateral side of individual *E. mathaei* (Lee and Shin, 2012).

APPENDIX B

TABLE B1. Ethogram classifying activity of *E. mathaei* as observed in natural activity patterns with no treatment. These behaviors were used as a basis of differentiation between active and latent states as they are associated with grazing, boring, and locomotion.

Classified behavior	Behavior description
Locomotion	Secondary spines moving, and tube feet extended to propel the animal
Feeding	Aristotle's Lantern projected for feeding or boring substrate
Active sensing	Tube feet partially or fully extended for sensory interpretation of surrounding environment