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THE ANTI-PREDATOR BEHAVIOR OF THE BLACK LONGSPINE URCHIN (*Diadema savignyi*): SPATIAL VISION AND THE ROLE OF LIGHT IN EMERGENCE

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Abstract. The tropical sea urchin genus *Diadema,* is considered one of the most significant and abundant. Their population dynamics greatly influence the health of coral reefs. *Diadema* have anti-predator behavior and defenses that help them to maintain a stable population. I investigated the limited spatial vision in *Diadema savignyi*, by testing their directional orientation to a target representing a crevice space used to hide from predators. This is the fourth sea urchin echinoderm to demonstrate evidence of spatial vision, the first for the genus *Diadema*. Furthermore, my results demonstrate that *D. savignyi* use their spines to filter light to improve their spatial vision. *D. savignyi* which had their spines removed lost their spatial vision. However, in starting closer to the target, *D. savignyi* still oriented without spines, suggesting spatial vision is still possible. In a field and lab study on the emergence times of *D. savignyi*, I found that *D. savignyi* may use daylight levels as a cue in their nocturnal emergence, used to avoid their diurnal predators. The pervious understanding that *Diadema* react and process light supports my evidence of the role of light in emergence. My results illustrate mechanisms for which *D. savignyi* specifically are able to avoid predators, but also suggest the presence of such mechanisms in other sea urchins. In understanding these mechanisms of defense, it is possible to better understand the maintenance of sea urchin populations and thus their role in coral reef ecosystems.

Key words: coral reefs; sea urchins; photoreceptors; vision; diel rhythms; light dark cycles; nocturnal emergence; mechanisms of defense

INTRODUCTION

Coral reefs are some of the most biologically diverse ecosystems in the world. However, their health is threatened by human actions such as overfishing and climate change (Roberts *et al*. 2002). In order to ensure the persistence of coral reefs, conservation management and a greater understanding of the functions of important reef groups and their mechanisms for maintaining reef ecology are necessary (Bellwood *et al*. 2004). Sea urchins are one of those groups. However, not much is understood about their mechanisms of defense; and how their anti-predator behavior helps to maintain their populations.

Sea urchins play an important role in the ecology of tropical reefs. Their relative numbers can greatly affect the population dynamics of coral, reef fish and algae (McClanahan *et al*. 1996). The genus of sea urchin, *Diadema,* has long been cited as one of the most significant and abundant tropical urchins (Tuya *et al. 2005;* Bellwood *et al.* 2004). *Diadema* are herbivorous grazers and one of the major forces of bioerosion in shallow tropical reefs, providing necessary nutrients

for other species of reef creatures (Muthiga and McClanahan 2007).

Depending on *Diadema*'s abundance, habitat and biogeography, they can either be considered detrimental (Tuya *et al*. 2005), or vital in maintaining and restoring coral reefs (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006). At high densities, sea urchins can threaten reefs with excessive grazing and depression of coral recruitment. (Sammarco 1980). The presence of extremely high densities of sea urchins, often due to the overfishing of their predators, can result in the break down of reef structure and loss of species diversity (Carreiro-Silva and McClanahan 2001). However, at low densities, a phase shift can occur resulting in macroalgal dominance, also, suppressing coral recruitment and growth. On the other hand, Edmunds and Carpenter (2001) established that increased densities of sea urchins, in a macroalgae dominated reef, resulted in the reduction of macroalgae, and thus an elevated level of juvenile coral. This illustrates the importance of sea urchins as a mechanism to reverse the phase shift, from the degradation of coral reefs back to a healthy reef. Thus,

when sea urchins are in balance with their ecosystem, they can help to maintain a healthy coral reef.

It has been recognized that predation on sea urchins acts as a determinant of sea urchin populations (Muthiga and McClanahan 2007). Randall *et al.* (1964) identified the predators of the genus *Diadema* as 15 different species of fish, mostly those with hard palettes. *Diadema* and sea urchins in general have evolved mechanisms for predator avoidance and defense. Two of the main strategies that sea urchins defend and protect themselves against predation are hiding in crevices and diel foraging patterns. First, *Diadema* hide in crevices with their spines pointed outward, while their tube feet and lower spines hold them in place. It has been shown that *Diadema antillarum* when presented with chemical evidence of a predator will retreat to a crevice (Park and Schulman 1986).

The second way that sea urchins avoid predation is diel foraging patterns. Foraging activity differs among species as well as within species depending on locality (Muthiga and McClanahan 2007). The evolution of diel foraging has been driven by fish predation on sea urchins (Nelson and Vance 1979, Young and Bellwood 2011). In overfished marine environments, nocturnal urchins were observed feeding diurnally (McClanahan 1988, McClanahan and Muthiga 1988). Young and Bellwood (2011) assert that nocturnal activity in sea urchins is an adaptive response to the pressures of diurnal predators. Therefore, the ability to which accurately assess day from night is vital, in avoiding predators.

It has been well documented that sea urchins react to light and shadows (Carpenter 1997, Millott and Yoshida 1960, Muthiga and McClanahan 2007, Ullrich-Luter et al. 2011). However, until recently there was little suggestion of how. Woodley (1982) suggested with his work on *Diadema antillarum* that a sea urchin's entire body acts as a complex eye, filtering light with its spines. A recent genetic study supported these suggestions, showing that there is a system of photoreceptor cells located in the base of the purple sea urchin's (*Strongylocentrotus purpuratus*) tube feet (Ullrich-Luter *et al.* 2011). Furthermore, Ullrich-Luter *et al.* (2011) showed that the whole body surface of the sea urchin was necessary for light sensing.

With this recent breakthrough, I aimed to examine the role of light in the anti-predator defenses of *Diadema savignyi*. First, I examined the sea urchin's spatial vision as related to shelter seeking behavior. To investigate the methods used to filter light, I tested the importance of *D. savignyi's* spines as related to spatial vision. Then, I investigated the role of light in the emergence times of *D. savignyi* as related to its diel forage patterns.

It has been shown that the sea urchin genus *Echinometra,* does has limited spatial vision, and is capable of detecting the direction of shelter (Blevins and Johnsen 2004). Similar to *Diadema, Echinometra* uses crevices as protection against predators. Therefore, I hypothesized that as a crevice dweller, *Diadema savignyi* will be capable of limited spatial vision as well. Furthermore, with recent work by Ullrich-Luter *et al.* (2011) , I hypothesized that *D. savignyi*'s emergence is related to light.

METHODS

All data were collected between September 23, 2011 and November 18, 2011 at the UC Berkeley Gump Research Station, Mo'orea, French Polynesia. All data were collected in studying *Diadema savignyi*, the only member of the important genus *Diadema* present in Mo'orea. *D. savignyi* were collected from Cook's Bay, Mo'orea (17°29'28.12" S 149°49'34.32" W). Individuals were collected from 20:00 to 24:00 by pushing them into a bucket with an outrigger paddle. The collected *D. savignyi* were stored with regularly filtering seawater and coral rubble in two large circular 1m-diameter tanks with a depth of .75m. All individuals were tested within a week of their collection.

Spatial Vision

In order to test *D. savignyi*'s spatial vision, an experimental arena was created (fig 1). The experimental arena was similar to the one utilized by Blevins and Johnsen in their spatial vision test (2004). My arena consisted of a white, rectangular fiberglass tank (2.10m x1m x .18m), filled with seawater directly from Cook's Bay, Mo'orea. A drain painted white was located in the far corner of the tank (fig 1). The trials were conducted in the white tank from 10:00 to 14:00 to maximize the amount of direct sunlight, to create a uniform amount of light in the tank and ensure that no shadows were present. While rain limited trials, all trials were conducted with uniform light on

the tank ensuring that no shadows were present in the experimental arena.

FIG. 1. The experimental arena used in the testing of *Diadema savignyi*'s spatial vision and spine importance. In the center is the 8cm target with specimen moving near it. In the bottom left, the drain painted white.

A square (8cm x 8cm) black plastic target representing a crevice or hiding space was positioned flat on the lower wall of the tank and held in place with fishing line (fig 1). The genus *Diadema* are crevice dwellers and return to shelter when exposed, i.e. placed in the center of a tank (Nelson and Vance 1979). Because of this shelter seeking behavior, *Diadema savignyi's* ability to accurately orient and move directionally can be tested. If orientation to the target was present, this suggests that spatial vision is the mechanism doing so (Blevins and Johnson, 2004).

Orientation was determined based on the position of the target relative to the place where the *D. savignyi* specimen touched the wall, ending the trial. The tank was divided into eight sections (Fig. 2) in which the specimen's final position could be recorded. The two sections on either side of the target and the two across from the target were considered directional. While the four perpendicular sections, on the far sides of the target were considered random. For example, in figure 2 the four sections that contain stars are considered directional, while the remaining ones are considered random. Now if an urchin were to move away from the target into those sections, it would be considered directional. This decision was based on the work of Yerramilli and Johnsen (2009), which showed that sea urchins with spatial vision might mistake the target for a predator instead of a safe hiding place. Because I was trying to determine whether *D. savignyi* do have spatial vision, and not determine their personality behavior, I choose to include those sectors as directional.

A total of eight trials were conducted for each individual. The target was placed on one of the four walls for each trial with two replicates per wall, ensuring that there was no particular preference in the testing arena. Because the tank was a rectangle, two placements of the target were 1 m from the specimen's starting position, while the other two were only 0.5 m from the starting position. This created a near distance and a farther distance (Fig. 1). This allowed the depth of *D. savignyi*'s spatial vision to be considered.

A total of 20 individuals were tested. A *D. savignyi* was removed from its holding tank, and placed in 2.10m x1m x .18m tank before it was placed under a release container (standard bucket) in the center of the testing arena. After 5 seconds, the release container would be pulled up, with the urchin in the center of the tank. The target's position was recorded as well as the section in which the individual finished the trial by touching the wall. Between trials the tank was scrubbed with fresh seawater and a brush to ensure no trail following between trials. In this intermediate period, the specimen was placed in the small holding tank (2.10m x1m x .18m). It was hypothesized that *D. savignyi* would significantly orient, suggesting spatial vision.

Statistical Methods: All statistical methods were performed in JMP, version 9. A chi-squared tested was to determine the difference between directional and random trials. Also, a chi-squared was used to understand the disparity in orientation between the two lengths of target position.
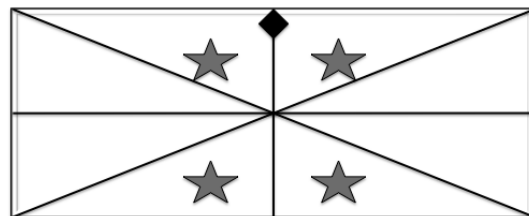

FIG. 2. The experimental arena divided in eight sectors, used to determine if *D. savignyi*'s movement was directional or random. In the shown placement of the target, the four sectors with the stars are considered directional while those lacking stars are random.

In a similar spatial vision experiment, the importance of *D. savignyi*'s spines in its possible spatial vision was tested. *D. savignyi* were tested in using the same process as stated above. However, 4 *D. savignyi* were tested for 8 trial with spines and 8 trials after their spines were removed. The spines were removed by cutting near the base within 1cm of the body, with clippers. The urchins were given an hour to acclimate before testing proceeded. By removing the spines, individual differences in spatial vision could be compared in individuals before and after their spines were removed. It was hypothesized that without spines *D. savignyi* would lose spatial vision.

Statistical Methods: A matched pairs test was used and run in JMP to determine the change in individuals with and without spines, rather than grouping them together. Furthermore, a chi-squared test was used to determine if individuals at the further distance from the target did have spatial vision.

Emergence Rhythms

To determine the relationship between light and emergence time of *D. savignyi,* a 30 x10m area centered at 17°29'25.00" S 149°49'32.41" W was surveyed. The area was located on the reef flat extending to the reef drop off near the center of the bay. The area was dominated by sand with about 30% coral rubble cover and a few live coral heads.

To determine the emergence time, the area was surveyed from 17:30 to 19:00 - a time of high emergence as determined by early observations. Individual *D. savignyi* were recorded every five minutes in the sampling period. To find individuals, all crevices and coral were searched in the sampling area. Individual's activity levels were measured by their position relative to their crevice or hiding place. Individuals that had 100%-51% of their body inside the hole were considered hiding, while those with 50% or more of their body out of the hole was considered emerging. Individuals that were fully out of their crevice were considered out.

Furthermore, information on the relative amount of light was recorded. The time of sunset, moon phase, as well as cloud cover was recorded. Cloud cover was classified into 4 levels: 1 representing no cloud cover and 4 representing complete cover. Cloud cover was only recorded once in the hour and half sample period. It was hypothesized that light was an important factor in the emergence of *D. savignyi*.

Emergence Rhythms Manipulation: Absence of Light

In order to determine if *D. savignyi* synchronized its emergence cues with light, a manipulation of natural settings was created. Five *D. savignyi* were placed in two glass control tanks (25cmx30cmx50cm) with regularly filtered seawater and coral rubble, while five other *D. savignyi* were kept in two completely dark (25cmx30cmx50cm) tanks with similar coral rubble. The dark tanks were covered with aluminum foil to prevent the entry of light. All tanks had regularly flowing seawater from Cook's Bay. The dark tanks were created to determine if emergence time would shift greatly in the absence of light. If so this would suggest that light cues play an important role in the emergence times of *D. savignyi.*

D. savignyi were observed from 18:00 to 19:00 for seven days. Observations started a day after individuals were placed in their tanks. However, added observation times (9:00, 13:00, 16:00, 17:30) were included when the emergence of dark tank individuals occurred outside the original observation times. *D. savignyi* relative position to hiding place was recorded, similar to in the field. Because crevices were not large enough to house an entire individual's body, only hiding and out could be used. Hiding was categorized as having a portion over of the body covered, while out was recorded when 100% uncovered. It was hypothesized that *D. savignyi* would emerge in the dark tanks at irregular hours compared to the control, thus illustrating the large influence of synchronizing with the daylight on emergence time.

Spatial Vision

D. savignyi were able to orient to a target resembling a dark crevice space. In 80% of the trials, *D. savignyi* were directional, meaning the urchin moved either towards or away from the target (Fig 3). It was expected that if the urchin's movement were random, the directional vs. random trials would have a proportion of .5 to .5. However, a .80 to .20 proportion of directional to random, respectively, was found (Fig 3). This shows that the overall movement of *D. savignyi* was in fact directional, as well as shows *D. savignyi*'s ability to orient (Chi Squared, x^2= 57.600, DF= 1, p< .001.). Furthermore, of the possible directions, landing directly on the target was the highest percent with 34% of the total trials.

In addition, when *D. savignyi* started relatively 'near' the target, the proportion of directional trials was much larger than at a 'far' starting distance of a full meter (Fig 4)(Chi squared, DF t_1=30.625, p<.001). Even so, at the far distance of one meter, *D. savignyi* still showed significant directional orientation, compared to that of the expected ratio of .5 directional to .5 (Chi-squared, $\chi 2$=5.00, DF=1, p<0.253). Likewise, in 19 of 80 of the far trials, *D. savignyi* moved directly to the target and ended the trial on top of it. This shows that the orientation of *D. savignyi* improves at a closer starting distance to the target; however, orientation is not lost at the further distance of one meter.

Spatial Vision Manipulation:
Spine Importance

The lack of spines negatively affected the directional orientation of *D. savignyi*. Overall, *D. savignyi* showed a decrease in directional orientation in individuals tested with and without spines (Fig 5.). When spines were present, *D. savignyi* directionally orient at a similar proportion as previously shown in figure 1. However, when spines were absent, there was no clear directional orientation (Chi-squared, T_1=0.5, p<0.4795). Even so, when the spineless *D. savignyi* started at the near distance of 0.5 m, their directional orientation was shown at a high proportion (Fig 6). However, at the further distance of 1 m, directional orientation was absent. In summary, spineless *D. savignyi* was not able to directionally orient at distances beyond .5 m.
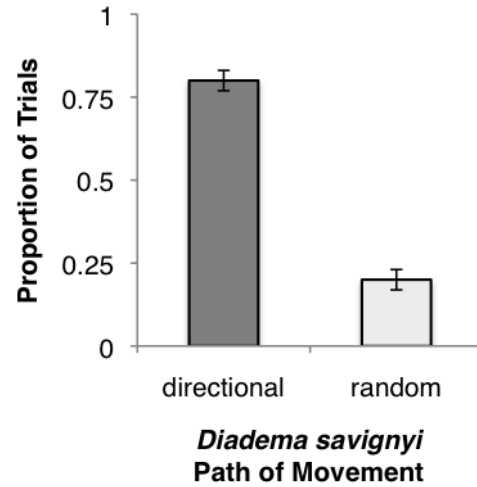

FIG. 3. The directional orientation of *Diadema savignyi* relative to a target, resembling a crevice. Data are means ± SE. Chi-squared was performed with an expected value of .5, x^2= 57.600, DF=1, p< .001.
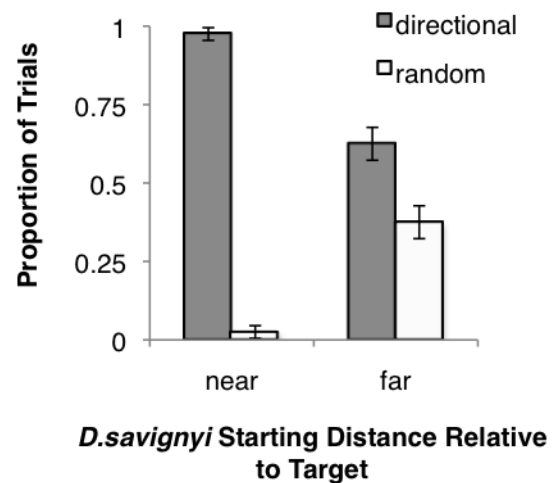

FIG. 4. The relationship between relative distance and directional orientation of *Diadema savignyi*. Tested at UCB Gump Station, Mo'orea, French Polynesia. Data are means ± SE. (Chi squared, DF t_1=30.625, p<.001).
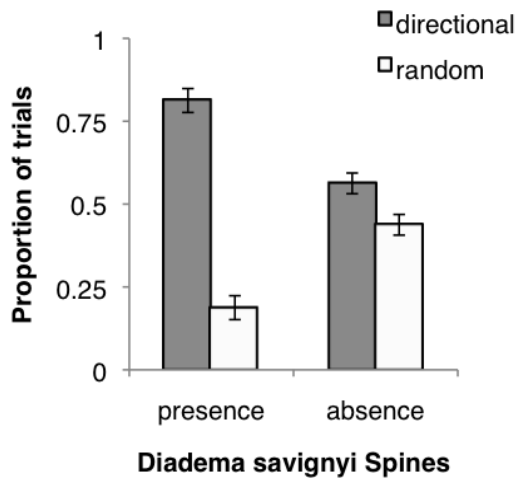
FIG. 5. The presence or absence of spines in the proportion of orienting trials of *Diadema savignyi* in testing spine importance. Data are means ± SE. A matched pairs test was performed to determine the difference between individuals with spines and without spines. Paired t-test, t-ratio = -3.592. DF=3, P >| t |=0370.
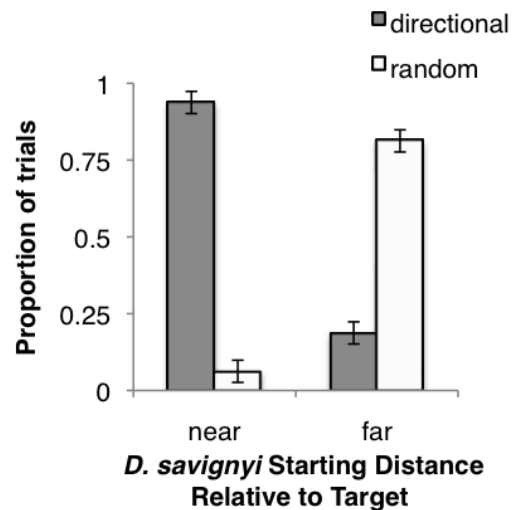
FIG. 6. The directional orientation of spineless *Diadema savignyi* starting at a 'near' target compared to a lack of directional orientation at the 'far' distance. Data are means ± SE. A Chi-squared was run for 'far' comparing directional to random with an expected value of .5. Showing the far distance is highly random. (Chi-squared, DF= 1, X^2= 18.286, P<.001).

Emergence Rhythms

The emergence of *D. savignyi* occurred on average in 30 minutes. The average first individual 'emerging' occurred at 18:09. While the average time that all of the urchins were categorized, as out was 18:39. Furthermore, the average time of the earliest individual considered out was 18:17. Cloud cover ranged from completely absent to full cloud cover, while the moon ranged from third quarter to new moon. On days where there was high cloud cover, *D. savignyi* emerged up to 10 minutes later than the average first emergence. On the other hand, on days where there were there was no cover, emergence occurred up to 11 minutes earlier than the average emergence. A similar trend was shown in the earliest individual *D. savignyi* to be classified as out. These data suggest that there may be a relationship between cloud cover and emergence time.

Emergence Rhythms Manipulation: Absence of Light

Without light, *D. savignyi* consistently emerged at earlier than the control. Over the seven-day sample period, the *D. savignyi*'s specimens kept in darkness, had fluctuated their emergence time greatly. While, the control tank had a relatively tight cluster of emergence times. The majority of control specimens emerged around 18:30. An average of all the control specimens showed that the total average emergence time was 18:26.

The *D. savignyi* in the two dark tanks emerged the first day of data collection only ten minutes prior to the control. However, on the next two days emergence occurred before data collection at 6:00. In an attempt to find the emergence time, I sampled at 5:30 for day four and five and found all five urchins out and grazing, in what was an hour before sunset. On the sixth day, I found the dark tanks compromised by a tropical storm, which ripped a large portion of the aluminum foil off of the tanks. Nonetheless, I observed the emergence of *D. savignyi* around 16:00. On the final morning of sampling, I viewed a single dark tank specimen grazing at 9:00, while the rest were hiding.

While, there is not a clear trend in the data, there is however, a major difference between the control and the dark tanks. The emergence of dark tank specimens regularly occurred before the control. Furthermore, it seems that the emergence time of dark tank specimens was getting earlier each day.

DISCUSSION

Diadema savignyi were able to orient to a target suggesting that *D. savignyi* do have spatial vision. Likewise, *D. savignyi* were better able to orient to the near target, showing that their spatial vision is limited but improves at a closer proximity. This provides evidence to support my original hypothesis that *D. savignyi* have limited spatial vision.

It could be suggested that *D. savignyi* individuals were merely trying to find any wall for protection, rather than visually sensing and moving in relation to the target. My inclusion of individuals moving away from the target as directional may have resulted in random movements being recorded as directional. This decision was based on previous spatial vision research that suggested some individuals may perceive the target as a threat, not a shelter (Yermilli and Johnsen 2009). This interesting behavioral difference is where future studies should continue. As a behavioral trait of some sea urchins, this boldness or shyness may put them at more risk of predation. Nonetheless, this inclusion of away movement as directional orientation played a very small role in the results. Instead, the most common movement was traveling directly to the target and stopping on it. This suggests that *D. savignyi* were capable of sensing the target itself and thus do have spatial vision. What is more, limited spatial vision has been demonstrated in *Strongylocentrotus purpuratus* as well as in two species of *Echinometra* (Yerramilli and Johnsen 2009, Blevins and Johnsen 2004). While these species are not in the same genus, they do share a similar ecology, the anti-predator behavior of dwelling in crevices as protection (Schoppe and Werding 1996, Verling *et al.* 2004).

Unlike other sea urchin genera, *D. savignyi* have longer length spines. *D. savignyi* or the Long Black Spine Urchin are they are commonly known, use their spines for protection like most sea urchins. Yet, it has been suggested that sea urchins also use their spines to screen adjacent light in order to improve their visual system (Woodley 1982, Blevins and Johnsen 2004). Until now, this idea has remained untested. *D. savignyi*'s overall directional orientation greatly decreased without spines, indicating that spines do play a role in spatial vision. However, *D. savignyi*'s ability to orient at a near distance remains the same with or without spines. This may have resulted from

an inability to completely remove the spines. At a close range, *D. savignyi* may have been able to use the remaining 1cm of each of its spines to aptly filter light. On the other hand, spines may only be important in improving spatial vision at further distances. This is supported by the fact that at the further distance, the ability to orient was completely lost and thus spatial vision was clearly not present. In this way, by removing the spines of *D. savignyi*, spatial vision was lost at further distances. Therefore, spines are important for spatial vision, however, they are not as necessary for all spatial vision.

The existence of spatial vision in *D. savignyi* raises the hypothesis that this functions ecologically as a mechanism to avoid predators. *D. savignyi* like many species of sea urchins use dark crevices for protection from their diurnal predators. It has been shown that without protective shelter, the mortality of urchins increases greatly (McClanahan 1988). Previously, it has been shown in the genus *Diadema* that when presented with the indication of a predator, *Diadema antillarum* would retreat to a crevice (Parker and Schulman 1986). Also, Carpenter has shown that *Diadema* spp. are able to evaluate crevice quality in terms of depth and thus quality to avoid predators (1984). Until now, there has been no evidence of the mechanism by which these anti-predator behaviors were achieved. My results, however, provide evidence for a possible mechanism by which *Diadema savignyi* are able to quickly find and evaluate crevices in attempts to evade predators.

Likewise, the evidence supporting *D. savignyi*'s spatial vision without spines at a close range is beneficial for individuals escaping nonlethal encounters with predators. Individuals that lose spines in a nonlethal encounter may still be able to escape to a nearby crevice. However, if no crevice were nearby, a *D. savignyi* would not be able to visually sense any others at a further distance. Even so, the ability to use their limited spatial vision at close ranges even after a nonlethal attack resulting in the loss of spines, is high advantageous in escaping predators.

The ability to avoid predators is linked to the population levels of sea urchins. Spatial vision as a mechanism to initially find and assess crevices or to escape nonlethal attacks, is an important anti-predator defense. Another major anti-predator defense is diel foraging. It has been widely cited that predation pressure is a key influence in the

evolution of nocturnal patterns of feeding and emergence. (Bernstein *et al.* 1981, Nelson and Vance 1979, Young and Bellwood 2011). The emergence of *D. savignyi* occurs only after the sunset. On days when darkness seems to occur earlier, my results may suggest that emergence may also occur earlier. However, on a small scale, my results are supported by a demonstrated change in diurnal emergence time, driven by predator seasonality (Bernstein *et al.* 1981). Additionally, Hernandez *et al.* (2011) showed that *Diadema* spp. were using day length in order to regulate their gonad production. While there have been impressions of emergence and other rhythms in *Diadema* spp. mechanism, none have been tested until now. The early emergence of *D. savignyi* while kept in a constant dark tank, suggests that there is a cue associated with day light levels. This can be explained by the presence of photoreceptors in sea urchins, which could enable them to accurately judge light levels and use them as an indicator to emerge (Millot and Yoshida 1960, Ullrich-Luter *et al.* 2011). My hypothesis that emergence may be caused by light, is supported by previous work showing *Diadema* spp. reaction and sensitivity to light.

In conclusion, the anti-predator defenses of *D. savignyi* are influenced by its spatial vision and ability to sense light. The ability to use spatial vision to seek out crevices and to judge their quality is vital in defending against predators. Similarly, the ability to perceive and to possibly use light as a cue in avoiding diurnal predators is important. These two abilities to avoid predators are central for individual *D. savignyi*'s existence. Because predators are the main determinant of sea urchin population, the ability to avoid predators is key in ensuring balanced population dynamics (Muthiga and McClanahan 2007). These anti-predator defenses help to ensure balanced population dynamics for *D. savignyi*. Furthermore, the genus *Diadema*'s population dynamics have been shown to be very important in the ecosystems dynamics of coral, reef fish and algae (Tuya et al. 2005, Edmunds and Carpenter 2001, Carpenter and Edmunds 2006). Finally, there is evidence showing that a balanced population of *Diadema* can maintain reef ecosystems (Edmunds and Carpenter 2001). In understanding these mechanisms of anti-predator defense and behavior, we can better understand this influential genus's position in the maintenance of their population dynamics.

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