

LOOK OUT: GIANT CLAM (*TRIDACNA MAXIMA*) DEFENSE RESPONSE TO VISUAL STIMULI IN MO'OREA, FRENCH POLYNESIA

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Abstract. Predator detection is key for survival in sessile marine organisms such as the giant clam (*Tridacna maxima*). *T. maxima* have several protective adaptations, primarily the development of a hard shell surrounding their soft tissue and the ability to burrow into coral and coral rubble. They also have hundreds of small, rudimentary eyespots on their mantle surface. Prior research has shown that these pinhole eyes are developed enough to detect shadows and may have the ability to detect nearby movement in a way that evokes discernable defense reactions. This study aimed to explore how the visual system of the giant clam generates different predator defense responses, while considering eyespot number and eyespot density on their mantle surface. Through testing *T. maxima* response to visual stimuli, a correlation between eyespot number and a more pronounced defense response was established. Eyespot distribution did not reveal a similar trend, but potentially has implications for the role energetic optimization plays in *T. maxima* defense response and morphological development. Clams displaying a teal color morphotype were seen to have an increased number of eyespots and eyespot density, as well as a shallower growth depth. Additionally, a proxy method for counting eyespots was developed. Overall these results indicate that predation is a key factor driving changes in clam morphology and may generate differences in eyespot growth.

Keywords: *giant clams; Tridacna; Tridacna maxima; Mo'orea; French Polynesia; motion response; eyespots; eyes; eyespot number; eyespot distribution; color morphology; defense; predator adaptation*

INTRODUCTION

The need to avoid predators in marine ecosystems directly correlates with survivorship and increased reproductive potential. Therefore, predation drives many evolutionary advances for marine organisms (Neo and Todd 2011). A few adaptations that are commonly present in invertebrates in shallow marine environments include vibrant cryptic coloration, burrowing, and protective shells (Vermeij 1978). Giant clams of the genus *Tridacna* exhibit several of these traits.

Giant clams produce acid that dissolves coral rubble, a carbonate rock, in order to burrow into these types of matrix (Hill *et al.* 2018), and protect their soft tissue by producing a hard shell (Vermeij 1978). *Tridacna spp.* are brightly colored to match their vibrant reef environment, and display cryptic patterning (Merilaita *et al.* 2001, Merilaita and Lind 2005, Stegall 2013). Some of this coloration comes from photosynthetic

zooxanthellae symbionts that inhabit that mantle surface (Ozog 2009). These algae provide the majority of the clam's energy and create a need for light sensitivity in order to expose the mantle surface to as much solar radiation as possible (Norton *et al.* 1992, Ozog 2009). This corresponds with the clam's ability to open and close their shell in reaction to environmental stimuli, including changes in light levels (Vermeij 1978, Johnson *et al.* 2016). (Merilaita *et al.* 2001, Merilaita and Lind 2005, Ozog 2009).

The large number of small eyespots in their mantle surface that are for rudimentary visual perception distinguish *Tridacna* from certain other bivalve species (Dougherty *et al.* 2017). Their eyes are a simple pinhole eye that consists of a pupil which focuses light at the bottom of a chamber that is lined with receptor cells (Land 2002). Despite their basic eye structure, the pinhole eye is useful for detecting light orientation and basic shadow perception (Land 2002, Dougherty *et al.* 2017).

This ability is key to preventing *Tridacna* from inhabiting an area without enough sunlight, and allowing them to them to react in time to prevent predation (Wilkins 1986).

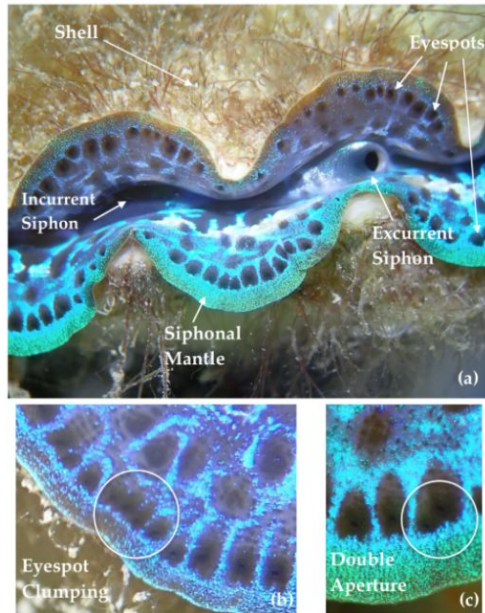


FIG. 1. (a). *T. maxima* siphonal mantle surface showing incurrent and excurrent siphons and eyespots. Closeup image displaying eyespot clumping, cluster of four eyespots on teal clam surface. Also visible are internal mantle eyespots, indicated by arrows. (c). Closeup image of double aperture near siphonal mantle edge.

There are generally three observed eyespot distributions in *Tridacna*: located solely around the mantle edge, clustered in patches throughout the mantle, or scattered randomly on the mantle (Dougherty *et al.* 2017). Eyespots are primarily located along the outermost mantle edges to allow for maximum sight range even if the mantle is partially retracted, however some clams display eyespots deeper into the mantle and around the siphonal tissue (Dougherty *et al.* 2017). Most variants tend to modifications of the mantle-edge eye arrangement (Dougherty *et al.* 2017). Different eyespot distributions may lead to differences in their ability to detect predators and react to their surroundings, as well as mantle patterning and coloration.

Some species of chitons, urchins and bivalves have been shown to see objects and motion rather than a reduction in light above their photoreceptors (Frossard 2011, Speiser 2011, Dougherty *et al.* 2017). This indicates a more complex visual apparatus that is able to detect more than simple shadows. Lon Wilkins (1986) found that several species of *Tridacna* exhibit prominent responses to shadows moving across their surface. These reactions differ between individuals, but the primary components are siphonal retraction, mantle retraction, and shell movement. Land (2002) found that *Tridacna maxima* have differentiable reactions to moving gratings of different sizes. Land's study used dissections to ascertain the angle of acceptance created in the clam's eyes, and tested basic movement towards the clam. Land's results show that the specimens exhibit full mantle retraction to larger spots that subtended a larger portion of their vision field, implicating a stronger response as an object or predator approaches.

Additional factors that may impact *Tridacna* sight capabilities include the size of the clam, mantle coloration, and how buried the clam is in the site. As clams develop, their mantle grows both in surface area and thickness, allowing them to accumulate more zooxanthellae (Wilkins 1986). A larger mantle leads to a higher amount of available energy, which may impact their reaction time. Zooxanthellae presence is also correlated with mantle color, which can dictate the amount of light the clam requires and the depth which it lives (Ozog 2009). Additionally, larger mantle surface area increases rates of exposure and vulnerability to predation.

T. maxima are commonly found in the shallow reef regions around the island of Moorea, French Polynesia (Gilbert *et al.* 2006). *T. maxima* live to a depth of up to twenty-five meters, and can display a variety of mantle colorations (Fatherree 2012). Their natural color variation is dependent on the species of zooxanthellae inhabiting their mantle (Ozog 2009). Algal symbiont species vary with depth, as different species require different amounts of solar radiation for survival (Norton *et al.* 1992).

The primary goal of this study is to survey the reactions of *T. maxima* to visual stimuli and determine the correlation between their predator response and their eyespot location.

This is done by exploring potential relations between their defense response and their

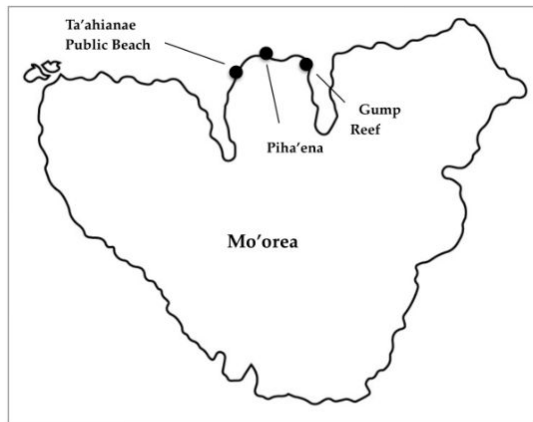


FIG. 2. Map of Mo'orea, French Polynesia displaying collection and research sites used for *T. maxima* motion response testing.

eyespot number, density, and distribution on the mantle surface. The primary hypothesis is that *T. maxima* will react to moving objects rather than purely shadows cast on their mantle. In addition, I hypothesize that the eyespot number in relation to mantle size and the eyespot distribution plays a role in the accuracy of movement detection. More specifically, more eyespots and an increased incidence of clumping would allow for an increased reaction to stimuli. Other research questions are whether the clam's response is correlated with mantle color and amount of light reaching the mantle, which are both indicators of zooxanthellae species inhabiting the clam's mantle. This would impact the number of eyespots and their distribution as the amount of available sunlight determines how well their eyes will detect movement.

METHODS

This study was conducted on Mo'orea, French Polynesia (Fig. 2). All experimentation was done with *Tridacna maxima*, a species of giant clam that occurs naturally in French Polynesia and is the most widespread species of *Tridacna* globally (Gilbert *et al.* 2006). Preliminary lab trials were conducted with six collected *T. maxima* specimens. Once this work

was completed, a broader field study was conducted on twenty-five more specimens using the same procedures developed in lab.

Pilot Study

As part of an initial lab-based study, a group of six *T. maxima* were collected on Mo'orea, French Polynesia from Gump Reef (-17.488867, -149.826082), Piha'ena (-17.485061, -149.831642), and Ta'ahiana'e Public Beach (-17.491160, -149.850562) (Fig. 2). All of these sites are centered around Cook's Bay and neighboring regions with similar water quality and weather. At each location, large numbers of *Tridacna* were observed in both blue and white-brown color morphs, as well as common combinations of these colorations. Two clams were collected from each site, one predominantly blue and one predominantly brown in order to avoid color bias. Clams collected for the pilot study were between 2-6cm in shell length. To remove the specimens from their habitat, the clams were selected for minimal rock obstruction over their shell surface and tested for grip strength. Full extraction was done by gripping the clam firmly on both sides of the shell and pulling until the pedal mantle released from the rock surface. This minimized tissue damage to the organism. All collected clams were placed in a holding tank at the UC Gump Research Station and provided with suitable rock substrate to re-attach onto.

Trials conducted with collected *T. maxima* were used to assess the distance and the speed the motion testing apparatus (Fig. 3) should be at to evoke a consistent defense response. The distance used in this experiment was 10 cm from the closest part of the mantle surface. The movement speed was established to be approximately three seconds of total motion across the track over the clam's surface (Land 2002). Once these parameters were optimized in lab, they were applied to *T. maxima* in the field in order to obtain a larger data sample size.

Additionally, the pilot study was integral to developing methods for eyespot count and density measurements as accurate eyespot number was counted. A dissecting microscope was used to count eyespots and photograph eyespot distribution types. This allowed for categorization of different eyespots densities

and distributions as mantle edge, inner mantle, clumped, and double aperture. Once these standards were established they could be applied to images taken of *T. maxima* in the field using an Olympus TG-5 Waterproof Camera. These photographs are not as accurate as viewing the clams through a microscope but allow a more convenient way of analyzing clam eyespots.

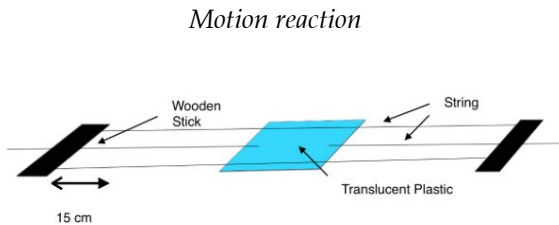


FIG. 3. Motion Response Testing Apparatus

To measure motion reaction, I moved a standardized object across each individual's mantle surface (following Wilkens 1986) and recorded their defense reaction type. The stimuli consisted of a 15x15cm semi-translucent blue plastic square on a track of two strings tied between wooden sticks (Fig. 3). The square was pulled over the clam at a steady speed several times, until the organism acclimated to the stimuli and no longer reacted consistently.

The testing procedure was developed using six collected clams in a pilot study, and then applied to the field once this was completed. Field studies were conducted between October 20th and November 15th, 2018 on Gump Reef at times near low tide in both the morning and afternoon. Twenty-five individuals were used. The average clam growth site depth was 67cm.

T. maxima response was categorized based on the amount of surface closure presented and physical reaction to movement. During the trials three categories were established (once the individuals response appeared consistent): shell closure, mantle and siphonal retraction, and no response. Shell closure was defined as mantle retraction combined with shell movement or full closure. This was the most extreme reaction consistently observed. Mantle and siphonal retraction response consisted of pronounced mantle and siphonal

movement to the point where the siphon was no longer visible. No response was defined as minimal mantle motion, no shell movement, and no or little siphonal retraction.

Eyespot number and distribution

Two techniques were used to ascertain eyespot number and the distribution of eyespots. The method for eyespot count and density calculations were initially developed during the in-lab pilot study using the six collected clams. The clams were photographed using an Olympus TG-5 Waterproof Camera, and eyespot number was assessed using the multi-point tool in ImageJ (Fig. 4b). All images were standardized by photographing clams with incurrent and excurrent siphons visible. This software was also used to assess mantle surface area and eyespot distribution across the mantle.

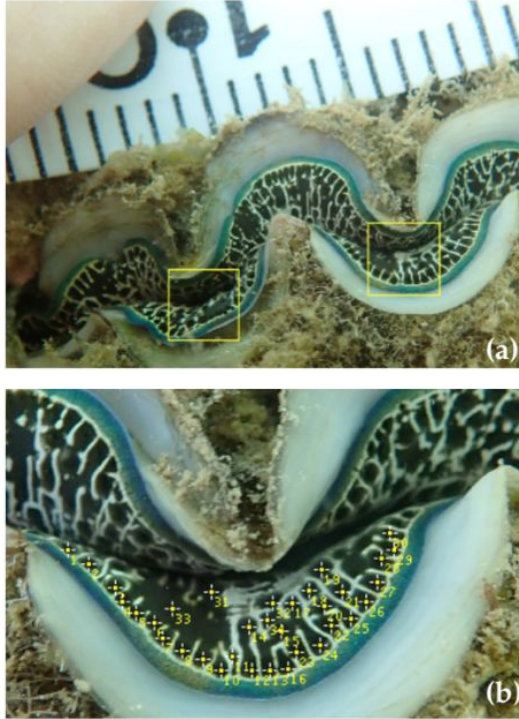
Relative eyespot number to mantle surface area was then calculated for all individuals. Distribution, calculated using the Nearest Neighbor Distance (NND) tool, was also compared among regions using the NND average for two 0.5x0.5cm regions of the mantle, with one taken at the mantle center and one a quarter from the shell edge, as the response variable (Fig. 4a). Once this procedure was established in the pilot study the same methods were applied to the twenty-five field clams studied.

FIG. 4. ImageJ Eyespot Analysis Example (a). Two 0.5x0.5 cm square selections of *T. maxima* mantle on one individual for eyespot count averaging (one approx. ¼ from mantle edge, one approx. center of mantle). (b). Eyespot selection using multi-point tool. NND can be calculated using this technique, as well as patch eyespot number.

Statistical Analysis

All statistical mathematics were done using the software PAST. The data was found to be non-parametric using the Shapiro-Wilk normality test, and an alpha value of 0.05 was used. To test the hypothesis that increased eyespot number and density would positively affect *Tridacna maxima* reaction strength The Kruskal-Wallis test was used to analyze differences between means, followed by Dunn's post-hoc test to see if data was

significantly different. In these tests the independent variable was eyespot number or density and the response variable was *T. maxima* response type.



Additional testing on clam color and growth depth was analyzed using chi square as well as a series of Kruskal-Wallis analyses combined with Dunn's post-hoc tests in order to assess the hypothesis that *T. maxima* eyespot number and distribution is influenced by coloration or depth. The alpha value used was 0.05. Coloration and depth were measured as the independent variable, while eyespot number, eyespot density and defense response type were all used as response variables for comparison to see if any or all of these factors are influenced by coloration.

RESULTS

Eyespot Counting Method Analysis

Two methods were used to assess eyespot number: manually counting and an approximation using ImageJ to assess surface area and extrapolate eyespot number. Both data collected by counting eyespot number directly and data collected through the

estimated proxy was established to be non-parametric using the Shapiro-Wilk normality test ($p=0.00679$). For each proxy measurement two sample squares were counted per individual (Fig. 4). A total of 22 *T. maxima* specimens were used for the eyespot proxy analysis. The accuracy of the proxy method was assessed using Pearson's chi square test in PAST, which showed a χ^2 value of 77.5 and a p value of 2.861×10^{-8} . Due to this, the proxy and observed values are correlated. Based on Fig. 5 the correlation may be direct, and the proxy eyespot mean is offset by a factor of approximately 16 eyespots from the observed eyespot mean. As most clams of this size have 60-100 or more eyespots on their mantle surface, this is accurate enough to provide a consistent estimation of eyespot number.

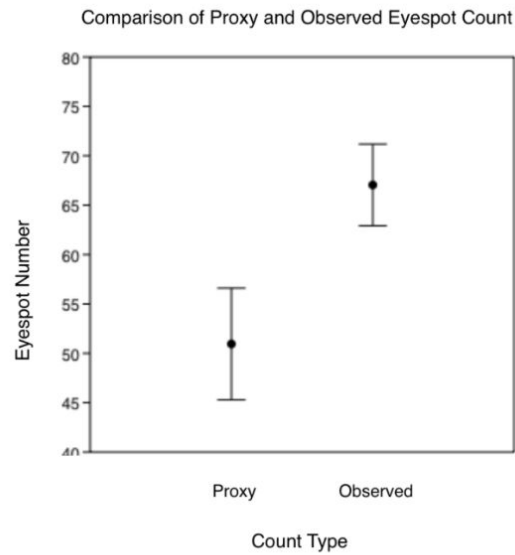


FIG. 5. Eyespot Count Comparison with x-axis displaying eyespot count method (proxy or manually observed and counted). The y-axis enumerates the eyespot count on half of the mantle surface.

Eyespot Number in Comparison With Reaction Type

Assessment of a potential eyespot number-dependency of *T. maxima* reaction types was done in PAST statistical analysis software. The data was found to be

non-parametric and a Kruskal-Wallis test was used to check for differences in eyespot number between defense reaction types. It was found that there was a significant difference between eyespot number for different reactions ($p=0.01789$). Using Dunn's post-hoc, it was shown that this difference is between the Full Shell Closure response category and the other two response categories (Small/No reaction and Mantle Retraction; $p=0.02265$ and $p=0.01123$ respectively). A Full Shell Closure response is correlated with a larger number of eyespots on the mantle surface proportional to mantle surface area (Fig. 6). *T. maxima* displaying a Full Shell Closure response also had more variance in eyespot number than those displaying Small/No response or a Mantle Retraction response (Fig. 6).

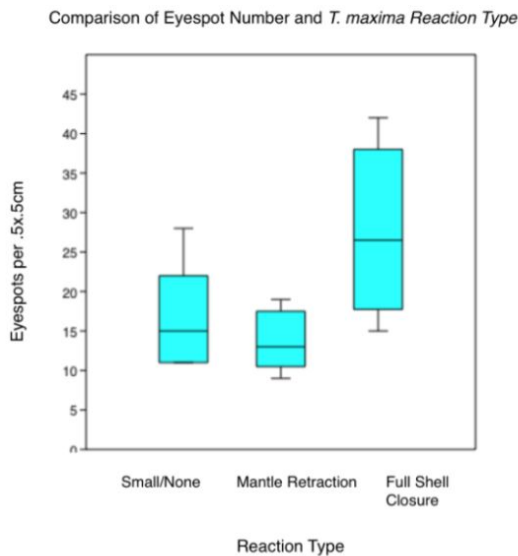


FIG. 6. Eyespot Distribution and Reaction Data with x-axis displaying with x-axis displaying *T. maxima* reaction type: Small/No Reaction, Mantle Retraction, and Full Shell Closure. The y-axis enumerates the eyespot count in 0.5x0.5cm of the mantle surface. This value is calculated from total eyespot count and the mantle surface area found in ImageJ.

Eyespot Distribution in Comparison With Reaction Type

Data analysis correlating eyespot distribution and *T. maxima* reaction was found

to be non-parametric. Analysis was conducted using Kruskal-Wallis in PAST and no significant difference between means was found ($p=0.2784$). However, clams exhibiting a Mantle Retraction response were seen to have a broader range of eyespot distribution than those displaying other response types (Fig. 7). Additionally, clams displaying No/Small reaction tended to exhibit the smallest eyespot distribution, meaning that their eyes are closest together and display the highest incidence of clumping.

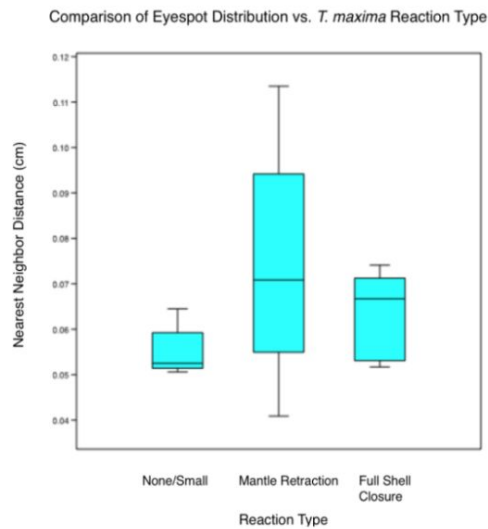


FIG. 7. Eyespot Distribution and Reaction Data with x-axis displaying with x-axis displaying *T. maxima* reaction type: Small/No response, Mantle Retraction, and Full Shell Closure. The y-axis contains the eyespot distribution amount per 0.5x0.5cm of the mantle surface. This value is an average of two 0.5x0.5cm squares from different mantle locations, and is calculated using the NND function in ImageJ.

Color in Comparison With Eyespot Number, Density and Depth

T. maxima coloration and depth was recorded to ascertain connection between these factors and eyespot number and distribution. Collected data for each of these comparisons was non-parametric and no significant difference between means was found using a Kruskal-Wallis test. When graphed, the data showed that teal color

morph *T. maxima* display higher eyespot number and density than other color morph individuals (Fig. 8, 9).

Additionally, they tend to inhabit more shallow depths than other color morph *T. maxima* studied (Fig. 10). While this difference is not statistically significant it is pronounced.

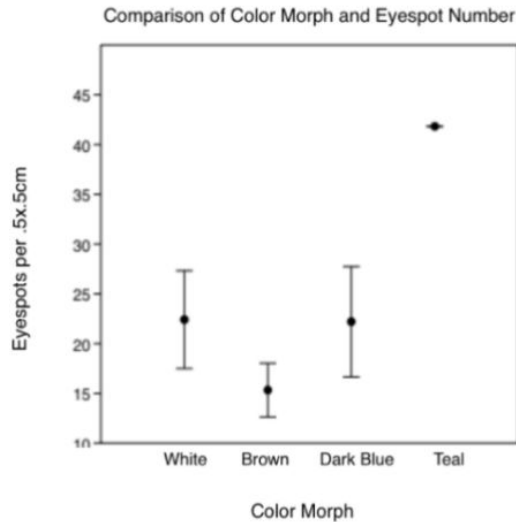


FIG. 8. Comparison of *T. maxima* Color and Eyespot Density with the x-axis displaying color morph and the y-axis displaying clam eyespot count averaged for two 0.5x0.5cm squares on each *T. maxima* mantle surface.

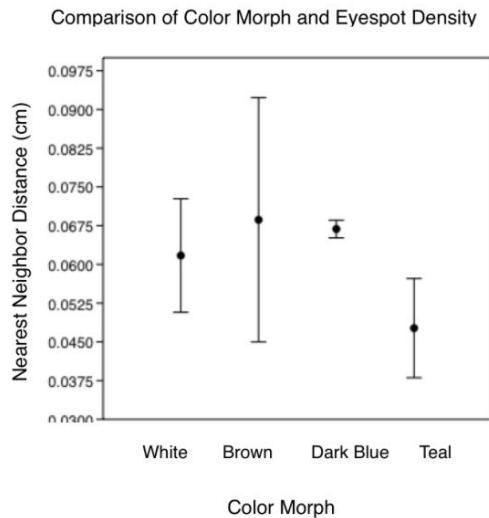


FIG. 9. Comparison of *T. maxima* Color and Eyespot Density with the x-axis displaying color morph and the y-axis displaying clam eyespot distribution averaged for two

0.5x0.5cm squares on each *T. maxima* mantle surface.

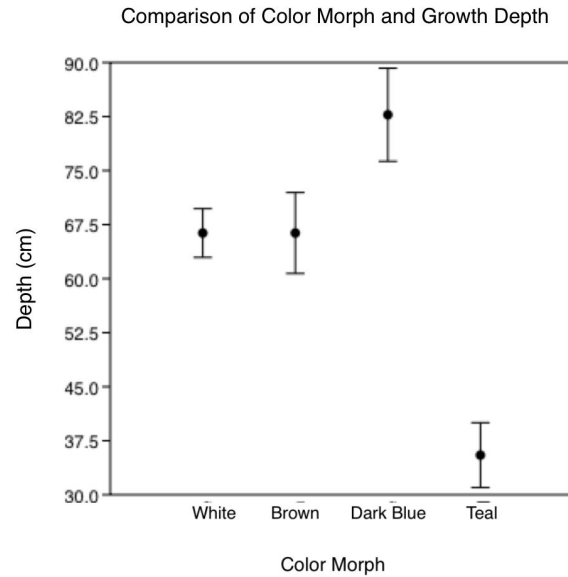


FIG. 10. Comparison of *T. maxima* Color and Growth Depth with the x-axis displaying color morph and the y-axis displaying clam growth depth.

DISCUSSION

Visual detection of predators is a key adaptation that allows *Tridacna spp.* to exhibit a defense response and increases their survival rate (Wilkins 1986, Morton 2001, Gilbert 2006). Overall, the results of my research suggest increased likelihood of *T. maxima* exhibiting a Full Shell Closure defense response if the individual has a larger number of eyespots on the mantle. *T. maxima* displaying a Mantle Retraction defense response were shown to have the broadest range in average distance between eyespots.

Additionally, a proxy was established for counting eyespots using ImageJ rather than counting each manually. When looking at growth depth and coloration in comparison with eyespot number and density it was expected that darker color morphs inhabited deeper locations (Ozog 2009). It was seen, however, that teal color morph *T. maxima* differ from other color morphs in growth depth as well as eyespot density and number.

One of the main goals of my study was to explore how clams respond to disturbance.

To explore this question required developing a method for rapidly estimating eyespot number along the edge of the mantle. I tackled this issue by taking photos to estimate the number of eyespots and compared the manual counts for eyespot amounts to estimated numbers using ImageJ so that an accurate estimation of the total eyespots on each *T. maxima* specimen could be achieved. This proxy was established to develop a more rapid method for counting eyespots using ImageJ rather than counting each manually. The proxy method was shown to be effective, however it is less accurate than counting each eyespot manually and tends to reflect a lower amount of eyespots (found to be approx. 16 fewer on average) than the actual number on the mantle surface. Results using eyespot count relied on the manual counting method for increased accuracy, although the proxy method is statistically sound enough for scientific use.

Comparison of eyespot number on the mantle of each tested *T. maxima* revealed a positive correlation between the number of eyespots on the mantle surface. *T. maxima* displaying a Full Shell Closure response were found to have a statistically larger number of eyespots on their mantle while individuals that responded to the presented motion stimuli with No/Small response or a Mantle Retraction response tended to have fewer eyespots on their mantle on average. A Full Shell Closure response is an example of an increased muscle reaction resulting in substantial shell movement or closure. This is a strong reaction that provides more full protection of the clam's soft tissue than the other two reaction types. If a clam develops more eyespots on its mantle surface there may be more accurate visualization of its surroundings, particularly to reductions of light and motion nearby. This is advantageous in that it generates sensitivity to potential predators.

In arc clams (*Arca spp.*) and polychaete worms (*Sabella spp.*), which respectively display upwards 300 and 240 compound eyes, an increased number of eyespots is beneficial in detecting motion from any direction as opposed to simple shadow detection that is only seen when an object passes in front of a light source (Nilsson 1994, Bok *et al.* 2016). However, the eyes of *Sabella spp.* and *Arca spp.*

do not contain lenses and are therefore incapable of focusing the objects they detect into meaningful images (Nilsson 1994, Bok *et al.* 2016).

The eye structure of *Tridacna spp.* is considered a simple pinhole eye, consisting of an oval 390 μm deep chamber lined at the bottom with two layers of receptor cells, reduced to one layer on the lower sides (Land 2002). Light is focused through a pupil located approximately 400 μm from the receptors, allowing for an acceptance angle of 16.5° (Land 2002). This eye structure is morphologically distinct from the compound eyes displayed on other bivalves, but the placement of their eyespots along the edge of the mantle is similar to that of scallops (Speiser & Johnson 2008, Audino *et al.* 2015, 2017), and ark clams (Nilsson 1994). This similarity implies an importance in eyespot location along the edge of the mantle, as well as possessing larger numbers of eyespots relative to mantle size for bivalves and polychaetes.

Although *T. maxima* possess a simple nervous system that is predicted to be incapable of processing image data from a large number of eyespots, visual data may be simplified to essentially capture contrast or a "yes/no" system for each eyespot that is comparable to the alarm system theory presented by Bok *et al.* (2001) and Nilsson (1994). A larger number of eyes across the mantle and along the edge may be what separates *T. maxima* that exhibit the Full Shell Closure response from those that do not, a factor that potentially gives them an advantage when it comes to predator detection and avoidance.

Eyespot distribution was not found to have a significant impact on *T. maxima* reaction to motion stimuli. All three response categories (No/Small response, Mantle Retraction, and Full Shell Closure) were found to exhibit roughly the same eyespot density based on the NND values calculated in ImageJ. This contradicts my hypothesis that a smaller distance between eyespots, essentially a denser eyespot distribution, would allow the clam to see better and generate a stronger defense response.

Interestingly, *T. maxima* exhibiting a Mantle Retraction defense response appear to have a larger spread of eyespot distribution

values than those exhibiting the other two response types. This could be due to a Mantle Retraction defense response being advantageous regardless of eyespot density. When considering the amount of energy that goes into a Full Shell Closure response and the limited protection afforded by the Small/No response type, a Mantle Retraction response is a happy medium. Enough of the *T. maxima*'s soft tissue is protected inside the shell to limit predator attack, while energy expenditure is minimized.

For *T. maxima* energy availability is determined by the photosynthetic zooxanthellae inhabiting their mantle surface. Since this can be one of several morphologically different species of algae, this often determines mantle coloration and patterning. Mantle color tends to vary with depth as different species of zooxanthellae thrive best with at specific light levels (Wilkens 1986, Ozog 2009). Light attenuates with depth, so clams located at different depths are exposed to different levels of solar radiation of different wavelengths. The relative amount of light impacts the sight capability of clam (Wilkens 1986, Morton 2001, Gilbert 2006), and so a correlation between clam depth, coloration, and overall eyespot arrangement was expected.

While collecting data on eyespot number and distribution in order to correlate it with *T. maxima* defense reaction type, measurements on mantle color and growth depth were recorded. They were then compared to the response variables of eyespot number and distribution in PAST. Statistical analysis of these factors did not reflect any significant results, but graphical representations showed that teal color morph *T. maxima* may be morphologically distinct from white, brown, or dark blue clams sampled. When comparing color morph with eyespot number it was seen that teal clams sampled tend to have a higher number of eyespots per surface area (Fig. 8). This is reflected when examining color morph and eyespot density comparisons, which show that teal *T. maxima* tend to have a higher density of eyespots across their mantle when compared to other commonly seen color morphs (Fig. 9). I initially hypothesized that these factors would be correlated with a deeper growth depth as more eyespots would allow for an

increased amount of light receptivity which is beneficial at depths where less overall light reaches. Contrary to this, however, teal *T. maxima* are shown to inhabit shallower regions (Fig. 10). In other bivalve species such as scallops and arc clams, the eyespot number is suggested to correspond with habitat depth, with deeper dwelling organisms having fewer eyes. (Nilsson 1994, Audino *et al.* 2015). This is consistent with my findings in terms of teal *T. maxima*, although my study was based on a relatively small number of teal color morph individuals. As they differed from other color morph *T. maxima* it is possible that future work could be used to substantiate these findings enough to provide statistical significance.

Similar to the energy expenditure balance theorized to be the basis of clams exhibiting a Mantle Retraction defense response, teal color morph *T. maxima* are essentially a mid-tone color on the spectrum of clam coloration (Stegall 2013). With white and brown *T. maxima* on the light end of the spectrum and dark blue clams on the dark end, there may be something that distinguishes teal clams in terms of cryptic coloration or zooxanthellae type (Stegall 2013). This may drive the trend toward shallower growth depths and increased eyespot number. Further study comparing coloration and reaction, as well as broader survey of teal *T. maxima*, is needed to understand these results.

In summary, protective defense responses are key predation survival mechanisms for marine invertebrates (Vermeij 1978). The ability of *T. maxima* to retract their siphonal mantle tissue and close their shells acts as a prominent means of avoiding predation by protecting their soft mantle tissue (Vermeij 1978). The development of a relatively refined visual system that is capable of shadow and motion detection and triggers a defense response when nearby predator movement is detected is beneficial to survival. The number of eyes on the *T. maxima*'s mantle appear to trigger a distinct motion response as displayed in Land (2002) and Wilkens (1986) when testing was completed using the motion response apparatus (Fig. 3) without casting a shadow over the mantle surface. This was shown to generate a variety of mantle retractions, however, a larger number of eyespots on the mantle surface proportional to

size tends to trigger a Full Shell Closure response in small *T. maxima* individuals. Quantification of these reactions is still needed in order to discern the nuances of reaction angle and timing, as well as the response threshold for the Full Shell Closure response.

Additional study could also expand this project to larger *T. maxima* specimens at a variety of depths in order to further characterize their defense reactions. This study focused on small (2–6cm), easily collectable individuals in order to optimize field procedures in the laboratory. The average size of *T. maxima* ranges from 15–25cm, which is substantially larger than the individuals used. Larger clams were also observed to display an increased number of eyespots and a larger variety of color morphs, possibly due to their mantle's accumulating more zooxanthellae with age (Wilkens 1986). These may play into their vision capabilities, and could provide basis for future study of predator defense response to motion in *T. maxima* and other marine invertebrates.

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