

UNDERSTANDING DRIVERS OF DIVERSITY: AN INVESTIGATION OF COLOR MORPHS IN THE GIANT CLAM *TRIDACNA MAXIMA*

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Abstract. This study investigates the role of color morphs of the giant clam, *Tridacna maxima*, in Moorea, French Polynesia to determine if color polymorphism (morphs) possess a beneficial adaptation. Environmental factors were observed through field surveys to determine if they benefit certain color morphs. No environmental factors were deemed preferential. However, the adaptation of cryptic coloration pertains to color morphs as the clam R, G, and B color values correlate to the substrate R, G, and B color values. Additionally, color was analyzed on multiple levels to compare cryptic ability amongst color morphs. A more adapted color morph was identified and this finding is further paralleled in results on abundance and size distribution throughout the population. Understanding the selective pressures that cause for phenotypic diversity allows insight into conservation and how human actions can either drive or stabilize the gene pools of organisms.

Key words: *color morph, Tridacna maxima, cryptic coloration, phenotypic diversity*

INTRODUCTION

The first evolutionary account of cryptic coloration was Edward Poulton's classic work, *The Colours of Animals* (1890). It gives an account of moths that adopt color patterns of leaves, twigs, and bark to reduce the efficiency of predatory search (Bond 2007). Polymorphism is an adaptive response to the behavior of visual predators and results in frequency-dependent, apostatic selection with higher mortality among abundant prey types, thus stabilizing prey polymorphism (Bond 2007). Cryptic (concealing) coloration allows prey to blend into the background and reduce vulnerability to visually searching predators (Cott and Hugh 1952, Edmunds 1976, Bond 2007).

Color polymorphism is the co-occurrence of multiple discrete color morphs within a single population (Cox and Rabosky 2013). Examining color morphs can provide insight into ways that phenotypic diversity originated and is maintained, as well as facilitates understanding of drivers of diversity (Cox and Rabosky 2013). Studying the mechanisms that drive color polymorphisms may explain whether certain polymorphisms are beneficial adaptations, rather than random genetic drift fixing neutral alleles (Fisher 1930, Epling and Dohzansky 1942).

Heterogeneous areas with large patches of diverse habitats promote evolution of specialist morphs through selection for crypsis (Endler 1978, Bond 2007, Surmacki et al. 2013).

In homogenous areas that have a mixture of small macrohabitats, generalist polymorphism occurs through species evolving multiple distinctive morphs (Van Vallen and Levins 1968, Bond 2007). According to the apostatic selection theory, crypsis of all morphs should be similar within one microhabitat (Surmacki et al. 2013).

Moorea, French Polynesia has a barrier reef encircling the majority of the island, creating a lagoon. The reef exemplifies a homogeneous area that contains a mixture of microhabitats with each coral head representing an isolated habitat. The bivalve *Tridacna maxima* has a variety of color morphologies which may possibly be explained through habitat preference as certain habitats provide more camouflage.

Marine bivalves exemplify the importance of habitat selection because post settlement they are immobile (Richards et al. 1999). High mortality of bivalves (>98%) occurs from the pelagic larval phase to the benthic juvenile phase (Roegner and Mann 1995, Gosselin and Qian 1997, Hunt and Scheibling 1997). They are broadcast spawners with high fecundity but poor early life survivorship (Heslinga and Fitt 1987). For the species *Tridacna maxima*, the planktonic phase is approximately 9 days and the larvae have high dispersal capability, which facilitates connectivity among populations (Crawford et al. 1988). Due to having poor early survivorship, processes that increase survivorship are crucial.

Three main processes control population structure: individual growth and mortality, recruitment, and the variability of these in time and space (Levitan 1991). The local density, population structure, and spatial distribution of adults play roles in settlement processes, reproductive outputs, and individual growth patterns that shape the population (Roegner and Mann 1995). The population of adult residents has a dual role with respect to settling juveniles as they supply larvae through reproduction while also limiting available space and food via intraspecific competition, therefore having pre- and post-dispersal effects (Morsan et al. 2011).

Because larvae and juvenile mortality is so high, it is very difficult to distinguish settlement patterns from the effects of early post settlement mortality (Connell 1985). Research on larvae development and cultivation of *Tridacna maxima* has become important as it's populations have declined throughout the Indo-Pacific region due to overharvesting and habitat degradation (Crawford et al. 1986, Lucas et al. 1989). Multiple studies on preferential spawning and larvae development have been completed. It is established that there can be rational management of *T. maxima* as a resource (Gwyther and Munro 1981). The environment that *T. maxima* inhabits is vital to its reproduction as larvae settle during days 7-9 but they have a extremely low survival rate until ages 2-3 years (Waters et al. 2013). *Tridacna maxima* larvae settlement is crucial to its survival because the organism must inhabit an area that allows it to grow until it is large enough to escape harm. Until it reaches an estimated size of 3 cm, it is highly susceptible to predation and trauma from water turbulence (Waters et al. 2013).

The factors that have been addressed for cultivation of larvae and juvenile development are: light intensity, substrate roughness, water turbidity, and algae growth as a result of silty water. These factors play an influential and critical role for *T. maxima* settlement and vitality. After settlement, various adaptations may exist that increase the survival of *T. maxima*.

The present study examined the color morphologies of *T. maxima* to determine if they provide a beneficial adaptation through cryptic coloration and addressed the question: why does *Tridacna maxima* have such a wide variety and intensity of colors in the mantle? Correlations among the variables habitat, size,

color morphs, depth, and zooxanthellae count have been previously studied on Moorea (Wagner 2001; Ozog 2009), thus this project expanded upon those studies by relating color morphs to size, distance from reef crest, depth (as a proxy for light intensity), substrate preferences, algae and coral proximity, and proximity to like color morphs. It is hypothesized that evolutionary processes have positively selected for a color morph that prefers certain environmental factors that facilitate settlement and recruitment. Additionally it exhibits cryptic coloration more successfully than others and thus is highest in abundance.

METHODS

Study Site

A survey of the color morphologies of *Tridacna maxima* was conducted on Moorea, French Polynesia. Observations were conducted on the back reef of the UC Berkeley Gump Station, starting at 17°28'56.46"S, 149°49'28.26"W (Fig. 1). This habitat is isolated by a lagoon and consists primarily of sand surrounding isolated coral heads. The climate of Moorea during the month of November (when most of the data were collected) varied between highs of 83°F and lows of 72°F, with on average 7 inches of precipitation.

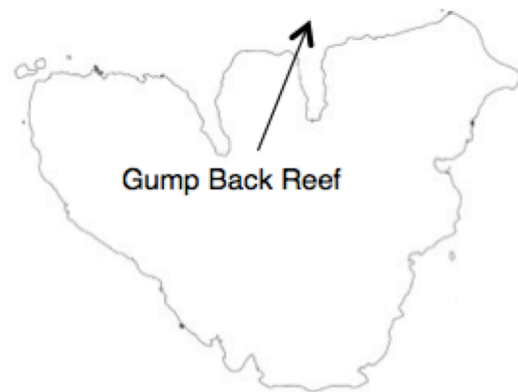


Fig. 1. Map of Moorea, French Polynesia showing survey site.

Tridacna maxima are found throughout the entire reef of the island. This specific site was chosen due to its high density of *T. maxima* and calm current. Other sites Temae and Haapiti were analyzed and deemed not suitable for this study as they lacked these two qualities. Additionally this site was chosen due to being a marine protected area, which

eliminated the confounding variable of human predation on *T. maxima*.

Field Survey

The reef was surveyed from the lagoon to the back reef, encompassing a total area of 17,920 m². Observations were made between 9:00 to 13:00 hours in roughly 2 hour increments. Data on a total of 197 clams were collected. The tide was taken into account for the time of day the data was collected. If current or wind were strong enough to create white caps, observations were not made. Surveys were conducted starting at the proximal coral head to the end of the previous survey. Each coral head observed was marked with flagging tape to ensure that no measurements are done twice. All flagging tape was removed at the end of the project. At the end of taking various measurements and notes on size, depth, color and habitat, as well as photographs, a waypoint of the latitude and longitude was taken.

All statistical analysis was conducted in the program R (R Development Core Team, version 3.0.2, 2013). In order to determine both color morph and microhabitat abundance, a χ^2 test for independence was run between the abundance of clams and these two variables. The measured environmental factors were analyzed with a Pearson χ^2 goodness of fit test to determine correlation to the mantle color of *T. maxima*.

A one way ANOVA test was used to determine if color morphs differed in size. This provides information on population structure of the color morphs.

To analyze spatial pairing between the color morphs a Pearson pairwise correlation was performed between the color morphs on each coral head. This test was again replicated in 5x5 meter quadrants and 10x10 meter quadrants.

Tridacna Color and Microhabitat

Photos were taken with a Nikon COOLPIX AW110 with zero zoom, on macro setting. An L shaped black and white striped (1cm increments) white standard was held at a 45° angle to the mantle of the clam and against the substrate to determine color morph and pattern of mantle. Photos were then taken with a Succhi disc held at the depth of the clam and at the surface as a comparison of light intensity. However, during data analysis,

little variation was found in regards to the difference in light intensity and so this data was not analyzed in the results. Percent algae and live coral cover were determined through photos taken of a .5 x .5 m quadrant centered over the clam and then counting the grids that coral and algae occupied.

Clam size was measured by taking the distance across the curved edge of the mantle and depth was recorded as distance from the highest part of the clam to the surface of the water. Distance from the reef crest was measured on Google Earth (Google Earth, 2013) using the ruler tool.

The microhabitat was recorded according to the five categories of rubble, dead coral in rubble, live coral in sand, dead coral in sand, and adjacent to live coral in sand. Notes on the edge color, main mantle color, and spot pattern were made to categorize into color morphs.

Color Measurement and Analysis

Color of *T. maxima* was analyzed using Photoshop (Adobe Photoshop CS5.1) by attaining red, green, and blue (RGB) intensity values. RGB values of the white standard, substrate, edge of the mantle, main color of the mantle, and spots of the mantle were measured through the tool "Replace Color". All values were then adjusted according to the average RGB values of the white standard to account for varying light intensities. All RGB values were taken in the center of the mantle, found using the ruler tool. The value taken from the white standard was done in the same spot in each photo. The point taken from the substrate was done in the center of the clam, a mantle widths distance away.

Analysis of the spot percent cover of the mantle was conducted using the program Image J (Rasband, 2012). A square encompassing one fold of the mantle was used so the same proportion of the clam mantle was taken each time. The number and average size of spots was analyzed as a type 8-Bit image with the threshold adjusted to maximize contrast. Then the tool "Analyze Particles" was used in pixel range from 0-5000.

Color morphs were grouped based on analysis of color pattern. Color pattern was defined as the relation between the edge color of the clam, the main color, and the proportion of spot coverage of the mantle (FIG. 2). A Generalized Linear Model (GLM) was used to



Fig. 3. Microhabitat Preference of *T. maxima* color morphs. Chi-squared Test for Independence was not significant.

test the relation of how color pattern affected size. The model contained the predictor variables spot percent coverage of mantle, main color, and edge color. P values were obtained through different pairings of χ^2 tests. Analysis determined a relation between main color and edge color. From this finding, morphotypes were categorized. Twenty different color morphs were created.

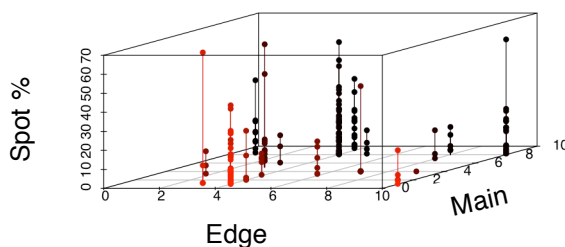


Fig. 2. Color Pattern shown through the relation between the spot % cover of the mantle, edge color, and main color.

Evidence for Cryptic Coloration

A Pearson correlation test was additionally used to analyze the RGB values of the clam in comparison to the RGB values of the substrate to determine if certain color morphs exhibit cryptic coloration. It was performed between the grouping of edge, main, and spot points against the substrate RGB values. Then the edge RGB, main RGB,

and spot RGB were run individually against the substrate RGB values. Furthermore the RGB values of the edge of the clam were categorized by color (e. g. blue, brown, green, etc) and compared with substrate RGB. The same procedure was repeated for the colors of the main mantle.

RESULTS

Field Survey

Based off of the categorized microhabitats, a Pearson χ^2 test of goodness of fit was run to determine microhabitat preference in regards to all *T. maxima* and to the color morphs. *T. maxima* prefers a microhabitat of dead coral (Pearson χ^2 test for goodness of fit $\chi^2=584.4$, $df=4$, $p<0.001$). However it displayed no significant preference between the color morphs (Fig. 3, Pearson χ^2 test for goodness of fit $\chi^2= 62.4$, $df= 76$, $p=0.87$).

Categorization of color morphs was done through analysis of color pattern. A Generalized Linear Model determined a relation between main and edge color as both significantly contributed to the affect of color pattern on size (Table 1). The relation of spot percent coverage of the mantle to size was not significant (Fig. 4). Color morphs were then grouped accordingly to the edge and main colors. The spot percent cover of the mantle was insignificant. However, main color was $F_{8, 187} = 47.864$

$p < 0.001$ and so was edge color $F_{9, 188} = 44.453$ $p = 0.002$.

TABLE 1. Results of Generalized Linear Model (quasipoisson) testing the affect of Color Pattern on Size.

Spot relation to Edge and Main	$F_{17, 179} = 20.272$ $p = 0.8237$
Main relation to Spot and Edge	$F_{8, 187} = 47.864$ $p < 0.001$
Edge relation to Spot and Main	$F_{9, 188} = 44.453$ $p = 0.002$

The abundance of observed color morphs varied (Figure 5). A Chi-squared test for goodness of fit was used to determine the highest abundance of color morphs. Color morph C was significantly the highest ($\chi^2 = 197.41$, $df = 19$, $p\text{-value} < 0.001$).

The population structure of the color morphs was determined based on a one way ANOVA test to analyze the size distribution of color morphs throughout the population (Fig. 6). The size distribution among color

morphs is significant, ANOVA $F_{19, 177} = 4.83$ $p < 0.001$.

A Tukey FSD test was used and determined a significant size difference between color morph G with E, A, H, and K, the color morph D with C, N, and Q, color morph Q with E and K, N with H and K, and K with F.

To test for any environmental adaptations the relation between each measured environmental factor and color was determined through a Pearson correlation. A Pearson correlation was run between each factor and the RGB values taken from the edge, main of the mantle, and spots in the mantle (Table 2). The B value taken from the edge of the clam was correlated to the location of the clam as distance from the reef crest (Pearson $t = 2.26$, $df = 195$, $p = 0.025$). The main mantle B value was correlated to the percent algae proximity (Pearson, $t = 1.98$, $df = 195$, $p = 0.049$). The G value for the main mantle color and algae percent proximity were almost significant (Pearson, $t = 1.95$, $df = 195$, $p = 0.053$). Additionally the R value of spots and depth were almost significant (Pearson, $t = 1.8502$, $df = 195$, $p = 0.066$).

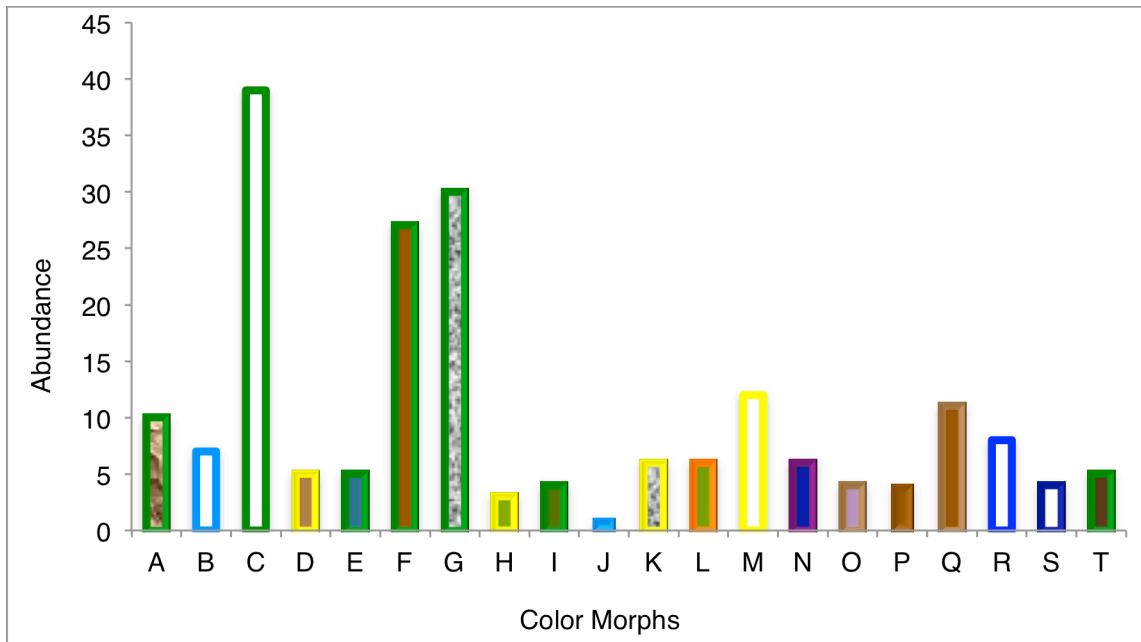


Fig. 5. Abundance of *T. maxima* for each color morph, Chi-square test for goodness of fit, $\chi^2 = 197.41$, $df = 19$, $p\text{-value} < 0.001$

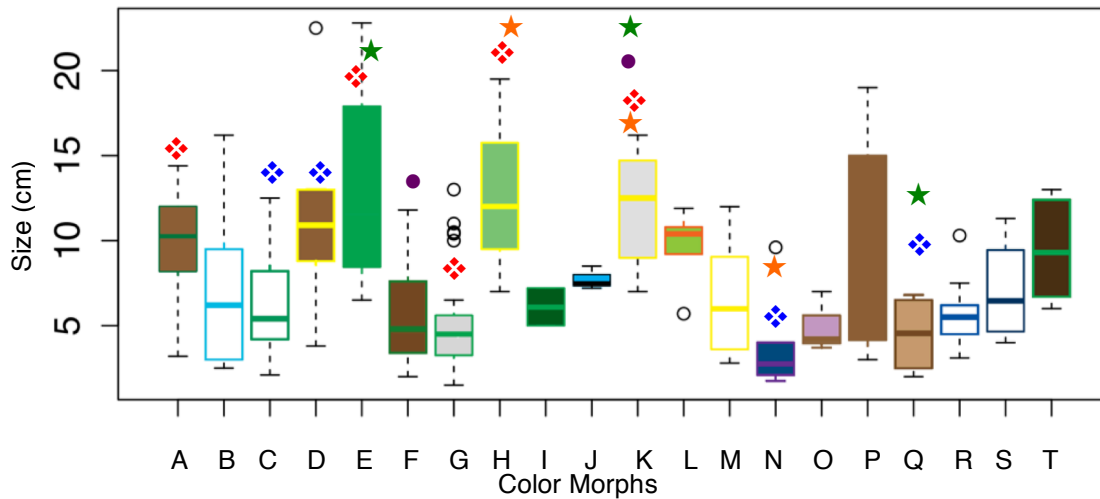


Fig. 6. Size distribution of each color morph. ANOVA $F_{19, 177} = 4.83$ $p < 0.001$, TukeyFSD < 0.05 . The size distribution of G is significantly different than A, E H, and K. D is different from C, N, and Q. Q is different from E and K. N is different than H and K. And K is different from F.

TABLE 2. Report of Pearson correlation test statistics for RGB values of *T. maxima* correlated to environmental factors. Only significant values were reported. Insignificant values include the variables Coral % proximity, Depth (cm) and Microhabitat measured against the area of the mantle spot and Color RGB values.

Area Mantle	Color	Distance from Reef	Algae % proximity
Edge	B Value	Pearson, $t = -2.26$, $df = 195$, $P = 0.025$	
Main	B Value		Pearson, $t = 1.98$, $df = 195$, $p = 0.049$

To further investigate the correlation between Edge B value and distance from reef crest, a Spearman test was ran between the color morph and distance from reef crest ($df = 197$, $p = 0.002$, $r_s = 0.215$).

Spatially Paired Color Morphs

Pair wise Pearson correlation tests were run between each color morphs on each coral head to determine if there is a spatial pairing to them ($n = 49$). The r value and p value were recorded in a matrix between each possible pairing of color morph. Significant p values were found for coral head pairing between C with H and K, D with K, and F with M (Table 3). Significant pairings in 5x5 meter quadrants and 10x10 meter quadrants were identical to the pairings among coral heads

TABLE 3. Report of Spearman correlation p values for spatial pairing between coral heads.

	F	H	I	O	Q
Q	.025				
S			.927		
T	.001	.043		.034	.02

Evidence for Cryptic Coloration

A multitude of Pearson correlation tests were conducted between the RGB values of the clam and the RGB values of the substrate to measure the ability of the clam's mantle to exhibit cryptic coloration. A Pearson correlation test between the RGB values of the combined edge, main, and spots of the clam to the RGB values of the substrate

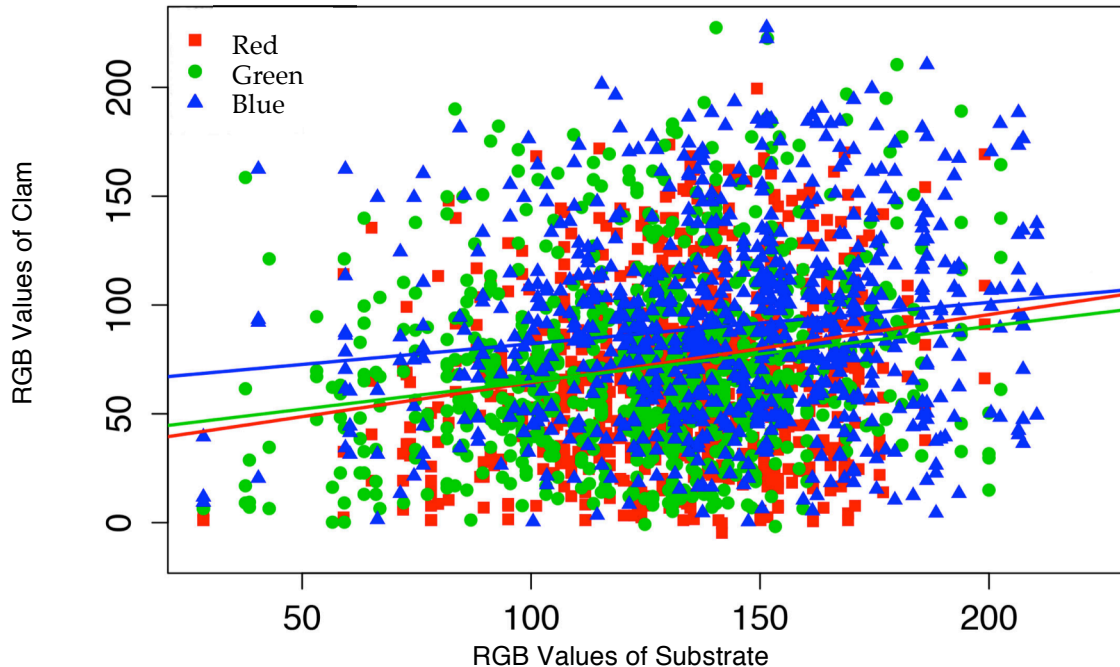


Fig. 7. Correlation between the RGB values of *T. maxima* versus the RGB values of the substrate. Pearson correlation tests were significant for red, green, and blue values. Red: $t=7.44$, $df=585$, $p<0.001$, Green: $t=7.78$, $df=585$, $p<0.001$, and Blue: $t=2.18$, $df=585$, $p<0.001$

proved significant (Fig. 7). The red values correlated by $t=7.44$, $p<0.001$, the green values correlated by $t=7.78$, $p<0.001$, and the blue values correlated by $t=2.18$, $p<0.001$.

Pearson tests were then ran between RGB values taken from the edge, main, and spots independently (in contrast to the previous test which ran them combined). All tests proved significant except the B value of spots was almost significant (See Table 3 in Appendix A) $t=1.87$, $df=195$, $p=0.06$).

In order to determine which color morphs exhibit the most successful cryptic coloration, the RGB values of the edge where then clumped into 7 categories based off of their color to the naked eye: blue, brown, green, indigo, orange, teal, and yellow. Pearson correlation tests were run in accordance to each color category and the RGB values of the substrate. The edge colors brown, green, and yellow proved to have the highest correlation to the substrate as all RGB values were significant (see Table 4 in Appendix A). Additionally the B value of indigo was significant.

In parallel the RGB values of the main color of the mantle were divided into 8 categories and a Pearson test was ran between each and the RGB values of the substrate. White was the only color to be significant for R, G, and B (See Table 4 in

Appendix A). The G value of green was significant as well, $t=4.01$, $df=11$, $p<0.01$).

DISCUSSION

Thus the previously stated research findings conclude color morphs do possess a beneficial adaptation. Through cryptic coloration, they camouflage with substrate and decrease chances for predation. The adaptation of cryptic coloration is key to sedentary animals as they lack defenses to ward off predators.

Field Survey

By investigating relations between environmental factors and color, one can extrapolate which factors are beneficial to *T. maxima*. Beneficial environmental factors may serve to support recruitment by enhancing survivorship until *T. maxima* reaches reproductive maturity. *T. maxima* is hermaphroditic at 5 cm in size (Wagner 2001). However, no adaptations have yet to be discovered regarding certain color morphs and environmental factors. No factors were measured that were directly related to settlement and recruitment. Additionally no significant findings were made that certain color morphs prefer to

settle in certain microhabitats. All color morphs prefer to settle on the substrate dead coral.

The only beneficial relations present between environmental factors and *T. maxima* were those that provided camouflage. A positive relationship between the blue intensity of the edge color of the mantle and distance from the reef crest may be due to an increase in depth. As depth increases, the blue color of the ocean intensifies, which may serve to camouflage blue edge clams better than other colors from a view point above the water (therefore camouflaging *T. maxima* from human predation). Additionally as distance from the reef crest increases, the proportion of blue color morphs significantly increases. Thus blue color morphs thrive at deeper depths. This data is consistent with a previous study that also found clams of blue color morphs to be significantly deeper than green color morphs (Ozog, 2009).

Moreover, the strong correlation between the algae percent cover in proximity to the clam and B value of the main color of the mantle is unexpected, for the blue color value was found significant and not green. It would be expected that green macro-algae would camouflage green clams. Regardless, this relation may assist in camouflaging the clams as macroalgae, such as *Turbinaria*, can visually block the clam from predators. For example, presence of *Turbinaria* may explain the high abundance of color morph F (green edge, brown) as this color morph would easily be camouflaged by it. Further research should be done to determine if there is a maximum threshold for algae cover, for it could block zooxanthellae access to sunlight.

Other environmental factors do not correlate significantly to clam color. The environment's lack of influence on clam color supports clam color to be independent from the environment. The color of *T. maxima* is due to a structural reason. Its mantle consists of platelets iridocytes that have different forms of stacking (Griffiths et al. 1992). Through these different formations, wavelengths of sunlight refract differently through the mantle and thus reflect different colors (Huxley, 1968; Land 1972). Since the color of the clam offers no relation to the environment, it can be assumed that color does not provide a beneficial adaptation to environmental processes.

Spatially Paired Color Morphs

Analysis of the spatial pairing of color morphs on coral heads further supports that *T. maxima* exhibits cryptic coloration. Analysis of spatial pairing within 5x5 meter quadrants and 10x10 meter quadrants yielded the same results as pairing among coral heads. Thus coral heads must cause for the pairing, and not environmental factors of the microhabitat, which would prove consistent throughout the space of the quadrant. The pairing of color morphs consists of the clams having the same edge color or having the same main mantle color. This consistency in color makes it highly likely that these color morphs blended into the substrate the best and thus eluded predators during the early juvenile stage (1-3 cm) when they are most vulnerable (Waters et al. 2013). Additionally, pairings existed between clams of the same edge and main color, but with differences in spot patterns. Spot coverage of the mantle may decrease throughout the clam's lifetime. The role that color pattern plays in cryptic coloration is unknown, but the pattern with smaller spot coverage area at a higher density may create the visual effect of a rough texture that would match the texture of the dead coral and better blend the color morph into the substrate.

Evidence for Cryptic Coloration

The ability to exhibit cryptic coloration differs among the color morphs. Analysis of the individual colors for the edge and main colors proves that certain color morphs are more cryptic than others. The color morphs with the edge colors of brown, green yellow, and indigo (only the blue value was significant) and main mantle colors white and green (only green value was significant) are more cryptic from predators. This includes four color morphs (C, F, M and K) being deemed as the best at this adaptation and two other color morphs (E and S) deemed the second most successful. C and F are similar in edge and main colors but differ in spot patterns. The same is true for M and K.

By analyzing the cryptic ability of the edge of the mantle one may extrapolate the ability of the clam to camouflage itself at its most vulnerable state. *T. maxima* can sense changes in sunlight exposure and current.

When it does, it reflexively closes its mantle. When the clam is in this state, the edge of the mantle is the only portion of the clam that may be seen. Thus the color of the mantle edge may prove to be more significant to cryptic coloration than the color of the main of the mantle.

Cryptic ability may explain for the population's size distribution. The smallest color morphs are those with indigo edge and green edge mantles, two colors that exhibit cryptic coloration. A higher percentage of the younger clams in the population may be these color morphs, because they have higher survival rates as juveniles. Cryptic coloration increases their chance of surviving, which would result in an increase in fecundity and thus increase abundance.

The abundance of color morphs reflects cryptic ability. Color morph C is the highest in abundance and, being green edge white main color morph, is successful at cryptic coloration as well. Other green and brown edge color morphs also are high in abundance. The color morphs that are blue in main or edge color are lower in abundance. This holds consistent to findings by Stosh Ozog in 2009. This study is built upon those findings by extrapolating color morph abundance rather than grouping the clams into two categories.

CONCLUSION

The ability of clams to exhibit cryptic coloration may be due to selective pressures occurring over time. Color morphs that benefit thorough camouflage have higher chances of surviving and thus, greater fecundity. These color morphs then would a greater proportion of the population as they have become naturally selected for. Additionally, they will constitute a larger proportion of the younger clams, as they are less likely to be preyed on as juveniles.

Selective pressures from humans also may result in changing the color morphs population structure. Since *T. maxima* is eaten when it reaches a substantial size, this may cause a lower proportion of adults in the population. This then may cause a future population collapse, as clams of reproductive age will have been removed from the population. It is important to maintain conservation efforts to even out the abundance and size distribution of the color morphs and balance the population.

FUTURE RESEARCH

Future research could be done to measure changes in density over time as a proxy of survivorship and to compare this among color morphs. Thus one would be able to analyze which color morphs reach reproductive age. This would further provide insight onto the population structure of the color morphs. Additionally the color pattern of the color morphs could be observed throughout their lifetime to determine the changes in spot percent cover of the mantle.

Mantle scars could be counted to determine predation rates of the different color morphs. Moreover time-lapse videos can be taken to observe interactions with predators. For this analysis the visual abilities of the predators should be taken into account.

Finally if one is able to manipulate the clams to spawn, larvae and color development could be observed and compared between the color morphs.

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APPENDIX A

TABLE 3. Pearson correlation results for RGB values taken from different areas of the mantle versus the RGB values taken from the substrate. All were significant except for B spot.

	Edge correlation to Substrate
R Edge	Pearson, $t=5.79$, $df=193$, $p<0.001$
G Edge	Pearson, $t=30.897$, $df=193$, $p<0.001$
B Edge	Pearson, $t=4.009$, $df=193$, $p<0.001$
	Main correlation to Substrate
R Main	Pearson, $t=3.8198$, $df=195$, $p<0.001$
G Main	Pearson, $t=2.3643$, $df=195$, $p=0.019$
B Main	Pearson, $t=4.009$, $df=193$, $p=0.0059$
	Spot correlation to Substrate
R Spot	Pearson, $t=4.6941$, $df=195$, $p<0.001$
G Spot	Pearson, $t=4.112$, $df=195$, $p<0.001$
B Spot	Pearson, $t=1.8713$, $df=195$, $p=0.0628$

TABLE 4. Report of Pearson correlation test statistics between the colors of the edge and main of the clam versus the substrate background. Only significant findings were included. Other colors tested and not found significant were for edge: blue, orange, and teal and for main: brown, dark brown, indigo, light brown, mauve, and teal.

Edge	R	G	B
Brown	Pearson, $t=4.38$, $df=16$, $p<0.001$	Pearson, $t=2.54$, $df=16$, $p=0.02$	Pearson, $t=3.78$, $df=15$, $p<0.001$
Green	Pearson, $t=3.93$, $df=117$, $p<0.001$	Pearson, $t=3.02$, $df=117$, $p<0.01$	Pearson, $t=2.53$, $df=117$, $p=0.012$
Indigo			Pearson, $t= -5.26$, $df=2$, $p=0.03$
Yellow	Pearson, $t=3.41$, $df=21$, $p<0.01$	Pearson, $t=3.25$, $df=21$, $p<0.01$	Pearson, $t=3.9$, $df=21$, $p<0.001$

Main	R	G	B
Green		Pearson, $t=4.01$, $df=11$, $p<0.01$	
White	Pearson, $t=3.98$, $df=106$, $p<0.001$	Pearson, $t=3.59$, $df=106$, $p<0.001$	Pearson, $t=2.61$, $df=106$, $p=0.01$

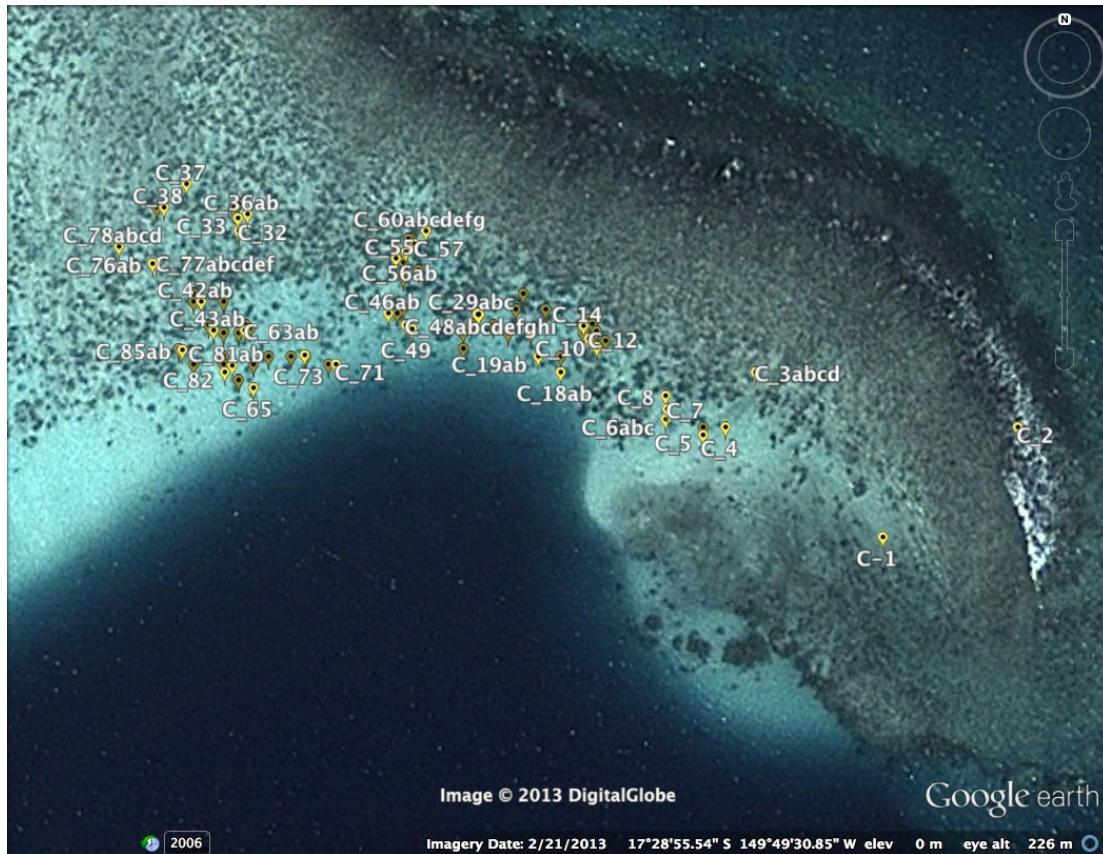


Fig. 8. Map of Coral Heads surveyed. Google Earth 2013.

Appendix B

Color Morph Key

A: Green edge, brown main, dark spots



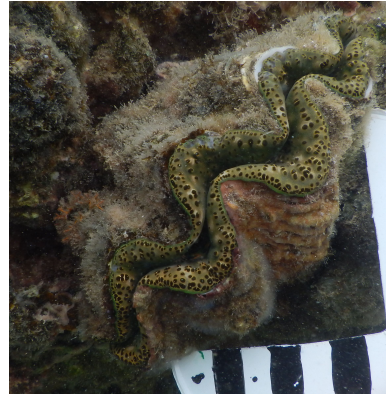
B: Teal edge white main, no pattern



C: Green edge, white main, pattern



D: Yellow edge, brown main, large spots



E: Green edge, green main, small spots



F: Green edge, brown main, less patterned



G: Green edge, white main, highly patterned



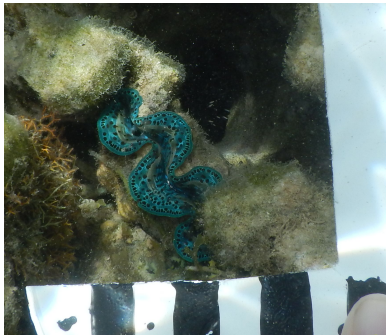
H: Blue edge, green main



I: Green edge, brown main, no spots



M: Yellow edge, white mantle with large spots



J: Teal edge, teal main



N: Purple edge, indigo main



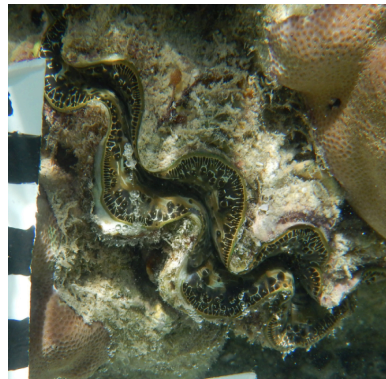
K: Yellow edge, white main, highly patterned small spots



O: Brown edge, mauve main



L: Green edge, orange main



P: brown edge, brown main



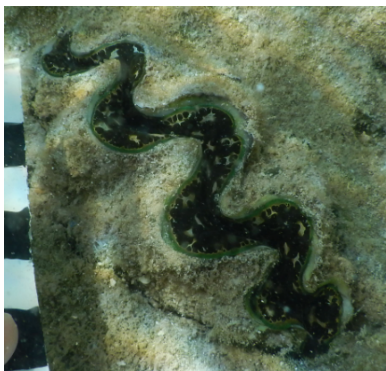
Q: Brown edge, light brown main



R: Blue edge, white main, highly spotted



S: Indigo edge, white main



T: Green edge, dark brown main