

DOES SHE HAVE A TYPE? EFFECTS OF *HETERACTIS*
MAGNIFICA COLOR MORPHOTYPE ON PREFERENCE IN
DASYLLUS TRIMACULATUS AND *AMPHIPRION*
CHRYSOPTERUS

BEN MALIT

Environmental Science Policy and Management, University of California, Berkeley, California
94720 USA

Abstract. Coral reefs contain high diversity of color, which conveys various information to the organisms that live there. *Heteractis magnifica* exhibits phenotypic variation in its color, which may influence anemonefish selection of the anemone. *Amphiprion chrysopterus* and *Dascyllus trimaculatus* are two species of anemonefish *H. magnifica* on the island of Mo'orea, French Polynesia. By classifying these distinct color morphs of *H. magnifica* and observing their fish frequencies in both the field and in a fish choice test, *D. trimaculatus* became the ideal study organism to study color preference in these mutualisms. In the field, *D. trimaculatus* preferred orange color morphs, and presence of *A. chrysopterus* influenced the number of *D. trimaculatus* present on each color morph. While different groups of anemones were found based on actual color values, not all these differences in color values were significant. I found that *D. trimaculatus* showed significant differences in frequency on yellow versus pink anemone color morphs, with yellow being the preferred morphotype. Frequency between pink versus orange anemones varied with the group size of fish, with smaller group sizes preferring pink *H. magnifica* morphotypes and larger group sizes preferring orange color morphs. However, there was no significant correlation between the principal color components of anemone morphospace with frequency of *D. trimaculatus* on *H. magnifica*. This suggests that color could possibly act as a signal of some other morphotypical character of the anemone that was not considered. Results from this study demonstrate how color can affect fish preference, which is important in the context of a changing environment.

Key words: color variation; fish vision; anemone; *Heteractis magnifica*; anemonefish; *Amphiprion chrysopterus*; *Dascyllus trimaculatus*; fish choice; color preference; Mo'orea, French Polynesia; group size; mutualisms

INTRODUCTION

Color plays an important role in the animal kingdom. Color can be used to attract mates, exhibit dominance, or deter predators (Cott 1940, Espmark *et al.* 2000). Color vision in fish is very variable and depends on the

number of single visual-bearing pigment cones (range 1-4) that each have different absorption spectrums (Neumeayer 1992, Losey *et al.* 2003, Bowmaker and Loew 2007). In general, fish possess dichromatic or trichromatic color vision, meaning they have two to three color receptors in their retina

(Lythgoe 1979, Lythgoe and Partridge 1989, Losey *et al.* 2003). As a result, fish can distinguish colors and be conditioned to develop preferences for specific colors (Siebeck 2008, Cheney *et al.* 2013, Champ *et al.* 2016). Most importantly, unlike humans, fish can see in the UV spectrum (Losey *et al.* 1999), and on reefs, vision is biased toward UV violet, blue, and green wavelengths in the ambient spectrum of these shallow broad-sunlight waters (Marshall *et al.* 2003). In addition, specific colors can confer different meanings; blue and yellow are highly contrasting in coral reef systems and are important in signaling toxicity or danger (Rudman 1991, Marshall 2000). Understanding the visual ecology of fish can help us further understand how color plays an important role in the life histories of coral reef organisms.

On Mo'orea, French Polynesia, the anemone *Heteractis magnifica* comes in a variety of colors and is host to the anemonefish *Dascyllus trimaculatus* and *Amphiprion chrysopterus* (Holbrook and Schmitt 2004). The anemone and fish live together in a symbiotic relationship (Mariscal 1970). Many different forms of symbiosis have been characterized, including mutualisms, a symbiotic relationship where both species benefit from their interactions with each other (Vandermeer and Boucher 1978). Mutualisms can either be facultative or symbiotic. Obligate mutualists require the presence of another species for survival, while facultative mutualists benefit from the presence of another species but can survive in its absence (Vandermeer and Boucher 1978). *D. trimaculatus* is facultatively mutualistic only at its juvenile stage and leave *H. magnifica* at maturity, while *A. chrysopterus* is obligatorily mutualistic with the anemone (Fautin 1986, Fautin and Allen 1992, Holbrook and Schmitt 2004). Anemonefish protect anemones from potential predators such as chaetonids. In the absence of their protectors, anemone mortality

can be as high as ninety percent (Godwin and Fautin 1992, Holbrook and Schmitt 2005). In return, anemones provide protection to the anemonefish. Anemonefish often rely on anemones for their life histories and can even follow anemones as they move throughout a habitat (Mitchell 2003).

D. trimaculatus are group-forming species and often co-occupy anemones with *A. chrysopterus* (Fautin and Allen 1992, Fishelson 1998). They have a planktonic life stage and may actually be a collection of species with smaller ranges rather than one species with a large geographic range (Holbrook and Schmitt 2003, 2004). In the genus of *Dascyllus*, ocular media of juveniles confers them some visual sensitivity to the UV spectrum (Losey *et al.* 2000). *A. chrysopterus* is a direct competitor of *D. trimaculatus*. The average number of *D. trimaculatus* on anemones occupied by *A. chrysopterus* is 9, and nearly doubles to 17 in the absence of *A. chrysopterus* (Holbrook and Schmitt 2004). However, *A. chrysopterus* is also an indirect mutualist to *Dascyllus*, as *A. chrysopterus* have a positive effect on anemone growth. The larger the size of the anemone, the more difficult it is for *A. chrysopterus* to exclude *D. trimaculatus* and control their densities (Holbrook and Schmitt 2000, 2004). On Mo'orea, it is very common to find anemones occupied by *D. trimaculatus*, sometimes co-occurring with either single or paired *A. chrysopterus*.

The Mo'orean population of *H. magnifica* exhibits color variation (pers. comm. with Daphne Cortese and Ricardo Beldade). The base is generally pinkish tan or brown, with the tentacles' tips being green, yellow, or bifurcated (Fautin and Allen 1992). However, it has been observed that even the tentacles themselves can vary in color, coming in varieties of yellow, pink, orange, and even white. *H. magnifica* often are found in beds, presumably constituting a clone (Fautin and

Allen 1992). However, in certain habitats on Mo'orea anemones exhibit a high diversity of color morphotype, such that two anemones of different color morphotypes can be clustered next to each other (Appendix C). Since such phenotypic variation can be seen in clumped distributions of anemones, it is difficult to assume that all individuals in a habitat constitute a single color morphotype clone. Variation in these characteristics of anemone morphotypes are known to be important from similar systems. Juvenile and adult anemonefish competitively exclude each other from different anemone species based on tentacle length (Huebner *et al.* 2012), and similar mutualisms with anemones and crabs have indicated that crabs detect anemone color and have preference for the color morph that is most adaptive for the individual (Baeza and Stotz 2003). Understanding if the anemone preferences in these studies are applicable to anemone color morphotype and fish preference can elucidate the role that color vision and perception in fish plays in anemone choice. Conversely, understanding the role of color morphology in showing *H. magnifica's* adaptive benefits to fish can help further the body of research on host preference in anemones.

In this study, I aim to understand the relationship between fish preference for anemones and anemone color morphotype, and what morphological character makes an anemone attractive to the anemonefish. I hypothesize that *Dascyllus trimaculatus* occurs more frequently on yellow or orange color morphotypes of *H. magnifica* over pink color morphs. I also hypothesize that there will be a difference in frequency on color morphotypes between *D. trimaculatus* and *A. chrysopterus*. I also observe the role of anemone color morphotype with respect to anemonefish behavior and selectivity. Using quantitative color analysis of the anemones used in fish-choice experiments, I hypothesize

that the color values and tentacle length significantly differ across the different color morphotypes. I predict that yellow anemones have longer tentacles, and larger tentacles will attract more fish to yellow morphs. I will investigate anemone preference by performing choice tests between two morphotypes, yellow versus pink and pink versus orange. In addition, I will explore how fish respond to different group sizes. I hypothesize that increasing the group size in *D. trimaculatus* will significantly impact their preference for any given color morphotype.

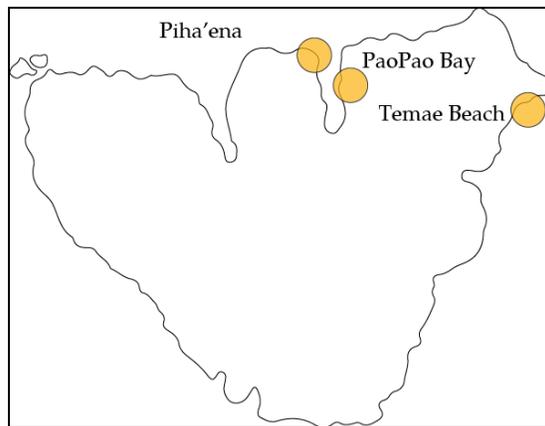


FIG. 1. Field survey sites on the island of Mo'orea, French Polynesia.

METHODS

All field and lab work was performed on the island of Mo'orea, French Polynesia (17.5388° S, 149.8295° W) from 15 October to 14 November 2018.

Study organisms

Dascyllus trimaculatus, the three spot damselfish, lives on *Heteractis magnifica*, the magnificent sea anemone (Appendix B). These fish often co-occur with *Amphiprion chrysopterus*, or the orange-fin anemonefish

(Appendix B). All three species have Indo-Pacific ranges that include the island of Mo'orea, French Polynesia (Fautin and Allen 1992). *D. trimaculatus* only inhabits *H. magnifica* during their juvenile stage (Holbrook and Schmitt 2005) while *A. chrysopterus* settle on a single or multiple anemones and remain there for the rest of their lives (pers. comm. with Daphne Cortese and Ricardo Beldade, CRIOBE). *H. magnifica* exhibit different color morphs in the field – for the purposes of this study, these are categorized as orange, pink, and yellow color morphs (Appendix C).

Field survey

Preliminary observational data of fish populations and anemone morphotypes was taken from Temae Beach, PaoPao Bay, Piha'ena Beach, Painapo Beach. These study sites were chosen because of the high density of either anemonefish and/or anemones that live there. I snorkeled at the field sites to collect preliminary observations of both the anemones and fish. Field surveys were performed at Piha'ena, Temae Beach, and PaoPao Bay (Fig. 1). An opportunistic survey was performed at each field site for two hours. The frequency of *D. trimaculatus* and *A. chrysopterus* on each anemone was recorded, alongside the color morph of *H. magnifica* it was found on. After number of fish was counted, I recorded information on the primary color (yellow, orange, or pink), maximum length of tentacles, maximum width of tentacles, color/morphology of tentacles, presence of bifurcated tentacles, foot/base color, and longest length across (LLA) for each anemone surveyed. If three or more anemones were clustered together, I considered the cluster an aggregation. The largest values for tentacle width and length in the aggregation were recorded, and the sum of all their LLAs was the final measurement

used. The anemones which *A. chrysopterus* frequented was determined based on observing the fish over multiple days and seeing which anemones they frequented consistently.

Anemone morphospace

Anemones that hosted no fish were collected from Painapo Beach (pers. comm., Suzanne C. Mills, 2018), PaoPao Bay, and Temae Beach. If they were attached to a removable rock, the anemone was taken with its rock (Häussermann 2004). If not, the anemone was removed by gently prying/"tickling" the anemone off of its substrate, as well as coaxing it off using a thin, blunt object such as a butter knife. Anemones were transported to an acclimation tank at the UC Berkeley Gump Station that was filled with rocks for them to re-attach over a period of several days.

Once they reattached, the anemones were photographed using a color wheel standard and shot with a DSLR camera, with standardized lighting across all photos. I standardized and color corrected the images using Adobe Photoshop Curves function (Stevens *et al.* 2007, Whitley *et al.* 2009). Photos were then analyzed using FIJI to convert the image into a Lab color space (Schiendelin *et al.* 2012). Lightness, a (red-green), and b (blue-yellow) values are the three components of the color space. Lab color space was used as it is considered an approximate representation of color vision in fish, as it tries to account for UV sensitivity in fish that humans cannot perceive (Martin 2013). An 800x800 pixel sample was taken haphazardly from each anemone area, where the average L, a, and b values of that sample were used in figuring out the most important components morphospace of *H. magnifica*.

Fish choice tests

I performed an initial pilot study to explore fish choice of anemones using eight *D. trimaculatus* from Temae Beach and recorded their frequencies on two anemones in a trial of pink vs yellow anemone color morph. From this I learned that there was some sort of observable preference for yellow. I then began the lab experiment, which involved testing the color preference of fish from two different group sizes (n = 2 fish and n = 16 fish). The sample sizes were chosen to test a) whether group size influenced fish preference, b) whether two fish would make the same choice or different choices, and c) to mimic the average number of *D. trimaculatus* found on an anemone in the absence of *A. chrysopterus*, which is 17 fish (Holbrook and Schmitt 2005).

For choice tests, three large blue circular tanks with continuous flow were used. A fine mesh barrier was placed in the middle of two of the tanks so that up to four anemones could be held per tank for two simultaneous trials. Fish were placed in a clear plastic container that was lowered without the lid into the experimental tank with two anemones of different colors on opposite sides of the tank. The lid was omitted to control for any chemical cues from the anemone, and because the fish were observed not swimming out beyond the limits of the lid when lowered into the tank. Fish acclimation time was 1-5 minutes, as the water used in these experiments was pumped from the same bay the fish were collected from. 1-5 minutes was also the time it took for the fish to swim out of the Tupperware if they did not have to be gently lifted and tilted out. After acclimation, the container was slowly tilted, allowing the fish to orient such that they could swim freely in the tank outside of the Tupperware. The initial choice of the fish was recorded (i.e., pink vs yellow anemone); if the fish made no choice and hid underneath the piping or rocks

in the tank, then I instead recorded that the fish made no initial choice. Fish were observed at one-hour intervals for five minutes from 5:00 to 19:00 over 48 hours. The number of visible fish on each anemone was counted after observing fish movement for one minute. The number of fish observed ranged from 1-2 (for the groups of 2) and 9-16 (for the groups of 16). This range accounts for the fact that sometimes fish died during a trial, which decreased the group size. At the same time, I recorded fish behavior, including whether the fish were observed chasing, hiding, or exploring. I also recorded if fish were observed brushing against the tentacles of the anemone at any time during the trial. Any switches between two anemones that occurred within the five-minute observation period were noted.

D. trimaculatus were collected from primarily PaoPao Bay, as well as some from Temae Beach, and were used for the anemone choice trials. No *A. chrysopterus* were collected during the laboratory experiments due to their obligate relationship with *H. magnifica* and were only observed in field surveys. All fish collected were returned to the site of collection within 4 days. All procedures were covered by the University of California, Berkeley Animal Care Protocol AUP-2018-04-11006.

Statistical analyses

All statistical tests were done using PAST. Graphs were made in both PAST and Microsoft Excel (Hammer *et al.* 2001). All data was tested for normality using a Shapiro-Wilk's test.

To test whether there was a statistical difference in frequency of both *D. trimaculatus* and *A. chrysopterus*, a chi-square test was performed to see if observed frequency of fish on color morphs significantly differed amongst one another within species.

A chi square test for independence was performed on frequency data collected on *D. trimaculatus* and *A. chrysopterus* to test if differences between the two species' inhabited anemone color morphs existed. A two-way ANOVA was performed using color morph and presence of *A. chrysopterus* to test if the interaction of both color and presence of a competitor significantly affected the average number of *D. trimaculatus* across the color morphs. Afterwards a Tukey's post-hoc was used to see on which color morphs presence of *A. chrysopterus* made a significant difference on the average frequency of *D. trimaculatus*.

To understand which morphological factors are important in *H. magnifica*, a Principal Components Analysis (PCA) was performed to see which characters explained the greatest variance in the color characters, physical characters, and the combination of both morphological characters. A PCA score plot helped to visualize whether clustering occurred in anemone morphospace based on color. It also illustrated how much of the variance in morphospace was explained by the PC 1 axis and what components had the greatest loading on this axis. A Kruskal-Wallis and one-way ANOVA performed on each of the quantitative measurements in morphospace determined if significant differences existed between the pink, orange, and yellow *H. magnifica* color morphs.

Fish choice tests were analyzed using a Mann-Whitney U test to see if significant differences between the frequency of fish on pink versus yellow color morph trials existed. The same statistics were also used for pink versus orange color morph trials. To test the importance of group size affecting fish frequency within the trials, a Kruskal-Wallis one-way ANOVA was used to test for significant differences between the two color choice tests. Afterwards a Dunn's post-hoc was used to see which color morph had significant differences in fish frequency

between group size. Finally, using the PC 1 scores from the PCA with both Lab values and physical measurements, a linear regression plotted these PC 1 scores against average frequency of fish for each anemone to see if the principal components of anemone morphospace were significantly correlated with *D. trimaculatus* frequency on the color morphs.

RESULTS

Field survey

H. magnifica color morphotype was significantly related to the number of *D. trimaculatus* present (Chi-Square Test, $X^2 = 26.207$, d.f. = 2, $P < 0.001$), with fish presence plotted against color morph category in Fig. 2. However, *H. magnifica* color morphotype was not significantly related to the number of *A. chrysopterus* present (Chi-Square Test, $X^2 = 1.35$, d.f. = 2, $P = 0.51$). Presence of both *D. trimaculatus* and *A. chrysopterus* significantly related to *H. magnifica* color morphotype (Chi-Square Test of Independence, $X^2 = 59.69$,

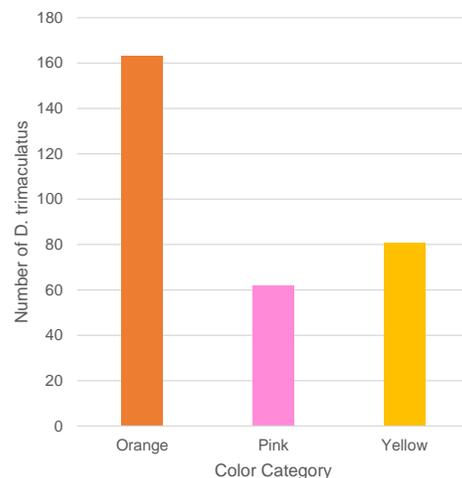


FIG. 2. Frequency of *D. trimaculatus* on different color morphs of *H. magnifica*.

d.f. = 2, Crit. Value = 5.99, $P < 0.001$). Linear

regressions of measured physical characteristics such as *H. magnifica* tentacle length, width, and Longest Length Across (LLA) versus number of fish for both species did not show a significant relationship between these physical measurements and number of fish. A Kruskal-Wallis one-way ANOVA demonstrated that there was no significant difference in the number of *D. trimaculatus* between the three different field sites. A chi-square test of independence revealed that there is no statistically significant difference between the two species' frequencies on color morphotypes.

H. magnifica color morphotype was factored alongside *A. chrysopterus* presence versus average number *D. trimaculatus* in a two-way ANOVA and shown to be significant ($F = 6.80$, $d.f. = 2$, $P = 0.0041$). Presence of *A. chrysopterus* on yellow color morphs increased the average number of *D. trimaculatus* present. Conversely, presence of *A. chrysopterus* on orange color morphs decreased the average number of *D. trimaculatus* present, as shown in Fig. 3. However, these differences between frequency

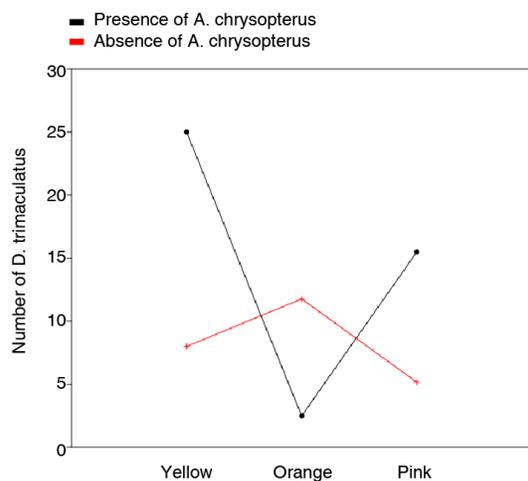


FIG. 3. Number of *D. trimaculatus* on each color morph when *A. chrysopterus* is present (black) versus absent (red).

on yellow and orange color morphs due to *A. chrysopterus* presence were not significant.

From a Principal Component Analysis (PCA) of anemone morphospace (Appendix A), the PC 1 axis explained 63% of the variance in morphology, with LLA having a large positive correlation with morphological variance. Scores for the PC 1 axis were plotted against the number of *D. trimaculatus* found on anemones, for which no significant correlation was found. A Kruskal-Wallis one way ANOVA of orange, yellow, and pink *H. magnifica* color morphs versus their average LLA measurements did not demonstrate a significant difference between the three types.

Anemone morphospace

Using the Lab colorspace values of *H. magnifica*, a color morphospace using a PCA illustrates each anemone plotted in a three-dimensional space of color values, as shown in Appendix A. Component 1 summarizes about 85% of the variance in the individuals collected from the field. Scores for the PC1 axis had a large positive correlation with mean L values. A Kruskal Wallis one-way ANOVA performed on L values amongst the three color morph categories showed that there was no significant difference between L values. However, a one-way ANOVA on a and b values showed that there were significant differences between the a ($F = 20.2$, $d.f. = 2$, $p = 0.00075$) and b ($F = 4.95$, $d.f. = 2$, $p = 0.040$) color-space values across the three color morph categories.

Appendix A shows PCA morphospace of *H. magnifica* using only physical measurements, with Component 1 summarizing about 85% of the variance in the individuals collected from the field. Scores for the PC1 axis had a large positive correlation with LLA and foot length. A one-way ANOVA of each physical measurement showed that there were no significant physical

differences between any of the *H. magnifica* color morph individuals collected, with only differences between tentacle width being marginally significant ($F = 4.15$, d.f. = 2, $p = 0.060$) amongst the three color morph categories.

The overall *H. magnifica* morphospace for all collected individuals using all measurements taken is shown in Fig. 4. The morphospace of the yellow and pink *H. magnifica* overlaps with one anemone. Component 1 summarizes about 79% of the

of Lab color space. Scores for the PC2 axis had a large positive correlation with b (blue-yellow) values and a large negative correlation with the a (red-green) values of the Lab color space, which divided the pink and yellow *H. magnifica* color morphs on the PC2 axis.

Fish color preference and group size effects

The frequency of *D. trimaculatus* found on each color morphotype differed across the different trials (Fig. 5). Pink versus yellow *H.*

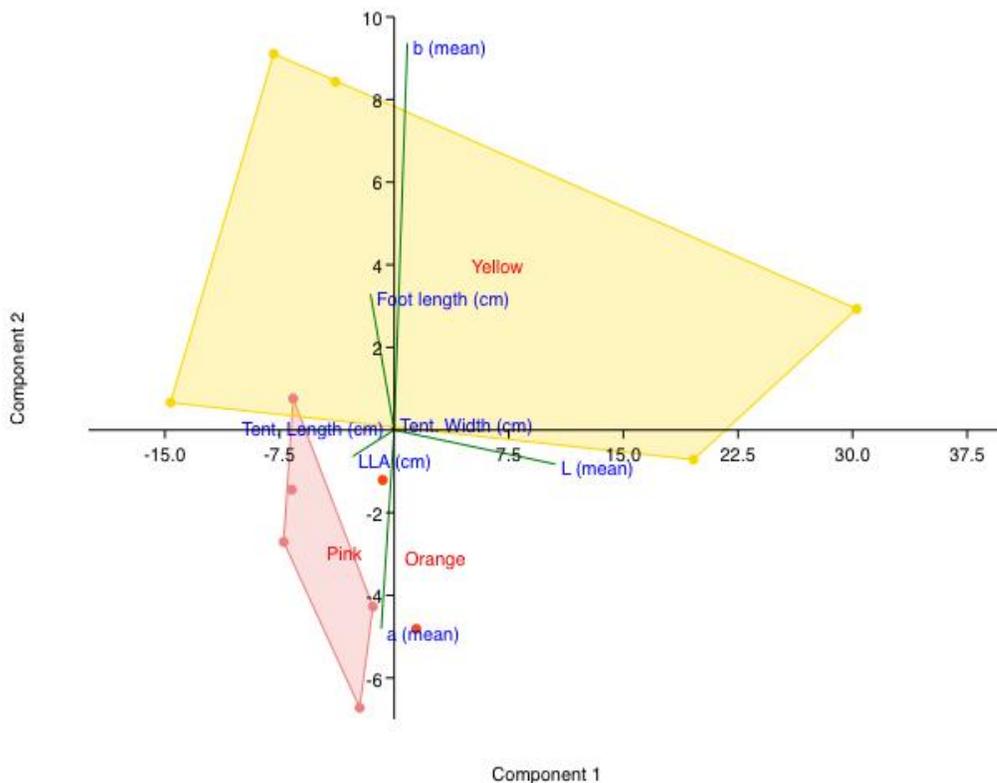


FIG 4. Principal Component Analysis of *H. magnifica* morphospace from the specimens collected for fish choice test. PC 1 axis explains 79% of the variation in this morphospace, with PC 2 axis separating pink and orange from yellow color morphs.

variance in the individuals collected from the field. Scores for the PC1 axis had a large positive correlation with the Lightness values

magnifica had significantly different mean numbers of *D. trimaculatus* on each color morph. For group sizes of sixteen fish there

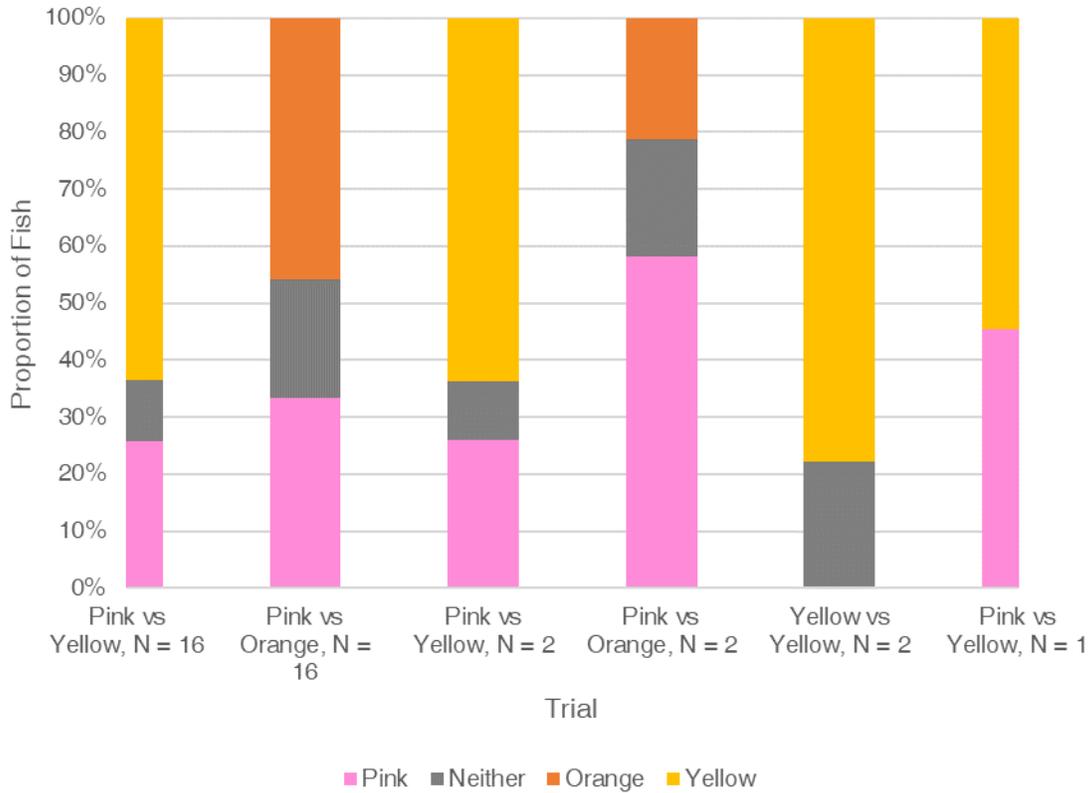


FIG 5. The frequency of fish on each anemone as represented by proportions across each trial. N equals number of fish per trial, which are the different group sizes. Yellow vs Yellow was a preliminary trial not used in the data set. Pink vs Yellow preference for one fish was recorded and originally was a two-fish trial but was not used in final data analysis.

was a significant color preference, where the mean rank of a yellow *H. magnifica* was 47.54 versus the mean rank of 24.96 for pink *H. magnifica* (Mann-Whitney test, $U = 966$, $n_1 = n_2 = 72$, $p < 0.001$). Similarly, in group sizes of two fish *D. trimaculatus* exhibited a significantly strong preference for yellow *H. magnifica*, where the mean rank of yellow was 77.79 versus 48.71 on pink (Mann-Whitney test, $U = 4273.5$, $n_1 = n_2 = 126$, $p < 0.001$). The results varied in pink versus orange *H. magnifica* trials. For group sizes of sixteen fish, there was only a marginally significant color preference between pink and orange *H. magnifica* color morphs (Mann-Whitney test, $p = 0.065$). However, for group sizes of two fish there was a statistically significant color

preference for orange *H. magnifica*, with a mean rank of 22.13 for pink color morphs versus 14.38 for orange color morphs (Mann-Whitney test, $U = 369$, $n_1 = n_2 = 36$, $p = 0.00065$).

A Kruskal-Wallis one-way ANOVA also yielded significant differences of *D. trimaculatus* frequency on pink and yellow color morphs ($H = 83.9$, d.f. = 3, $p < 0.001$), but a Dunn's post-hoc showed that there were no significant differences between the two group sizes of *D. trimaculatus* in frequency on pink and yellow color morphs. A Kruskal-Wallis one-way ANOVA showed that there was a statistically significant difference across all trials of pink and orange color morphs for *D. trimaculatus* frequency ($H = 20.72$, d.f. = 3, $p <$

0.001). Dunn's post-hoc revealed that there was a significant difference in frequency on orange *H. magnifica* color morphs between the two group sizes of fish ($p = 0.001$).

Because PC 1 explained 79% of the variance in anemone morphospace, and there were statistically significant differences in fish frequencies between color morphs, the scores for PC 1 were plotted against the average frequency of *D. trimaculatus* across the different *H. magnifica*. However, when a linear regression was performed, there was no significant correlation between PC 1 scores of *H. magnifica* individuals and the average frequency of *D. trimaculatus* found on them ($R^2 = 0.035$, $F = 1.02$, $p = 0.32$).

DISCUSSION

Field survey of anemones

Contrary to my initial hypothesis, tentacle length was not the most important physical component of *H. magnifica*, with LLA explaining 63% of the morphological variance observed amongst anemones at the different field sites. There was a lot more overlap between the physical measurements of *H. magnifica* color morphs in the field than I had expected, and there was no significant difference between the three color morphs' LLA measurements. Although I initially hypothesized that orange and yellow anemones would have longer tentacles, from conducting the field survey and collecting *H. magnifica*, in general anemone tentacle length was more dependent on size of the anemone than the color.

When measuring anemones, I noticed that some would flare their tentacles and withdraw inward in response to the ruler or caliper touching them. When doing some measurements, it was very clear that certain anemones would change their size in response to the ruler or calipers. Although the

anemones were measured as non-invasively as possible, stimulus from the ruler or calipers may have irritated the anemone and caused it to modify its size in response.

Field survey of anemonefish

There was no difference in the occurrence of *D. trimaculatus* and *A. chrysopterus* on different anemone color morphs. While *D. trimaculatus* had significant differences in frequency on color morphs, *A. chrysopterus* did not demonstrate significant differences in frequency. Orange *H. magnifica* had the highest frequency of *D. trimaculatus*. In general, orange and pink anemones had the highest frequency of *A. chrysopterus*. The average number of *D. trimaculatus* on *H. magnifica* was 9.42 fish when co-inhabited with *A. chrysopterus*, which is consistent with the results found in Holbrook and Schmitt's 2005 study.

However, when not co-inhabited with *A. chrysopterus*, the average number of *D. trimaculatus* on *H. magnifica* is 9.23 fish, which is not a huge difference compared to when *A. chrysopterus* is present. The average number of *D. trimaculatus* without *A. chrysopterus* on the anemone is inconsistent with the average in Holbrook and Schmitt, which was 17 fish. However, this inconsistency may be due to small sample size of anemones hosting *A. chrysopterus*. Although previous research has demonstrated that *A. chrysopterus* display aggression towards *D. trimaculatus* and chase them off their anemones (Lau 2010), from personal observations this is not always the case, with the aggression towards *D. trimaculatus* depending on the individual.

Interestingly, the two-way ANOVA showed that *A. chrysopterus* do significantly decrease the average number of *D. trimaculatus* on orange anemones specifically, and while there was no significant difference

between orange anemones and presence of *A. chrysopterus*, this trend was only observed on the orange anemones. The pink and yellow anemones demonstrated the opposite trend, as the average number of *D. trimaculatus* on these color morphs increased with the presence of *A. chrysopterus*. Potentially orange anemones could be the most attractive to *A. chrysopterus* and thus are guarded more and host more aggressive fish than do pink and yellow color morphs. However, no behavioral data was collected on *A. chrysopterus* with respect to the color of their host anemone, and even then, it would be unclear as to why such a behavioral difference due to anemone color would exist.

Anemone morphospace

The results of the ImageJ analysis on the anemones demonstrate that the color morphs I defined do differ in values on the Lab color space. The PCAs of physical measurements showed that PC1 explained 85% of the variation in *H. magnifica*, with LLA measurements and foot size having large positive correlations along the PC1 axis. LLA measurements explaining the variance in physical morphospace of *H. magnifica* is consistent with the PCA results from the field survey. There were no significant differences between any of the physical measurements on the three color morphs. This result was expected, since I tried to control for the actual physical characteristics of the anemone such that color would be the morphological character being varied across trials.

While there were some marginally significant differences in the tentacle length of the anemones, tentacle length did not explain most of the variation seen in the anemones. Throughout the trials, anemones demonstrated the ability to change the structure of their tentacles just from the stimulus of a ruler or hand alone (personal

observation, 2018). In addition, anemones also are capable of flaring and enlarging their tentacles when they are brushed or touched frequently by foreign objects (personal observation, 2018).

When Lab values were combined with physical measurements to analyze the sum of anemone morphospace, PC1 still explained 79% of the variance and had a large positive correlation with Lightness values in the Lab color space explained the variation between the three color morphs, which supports my hypothesis that the anemones are actually different color morphotypes.

However, when an ANOVA and Kruskal-Wallis test were performed on the Lab color space values, Lightness did not have significant differences between these three color morphs. Even though Lightness explained the majority of the variation seen in *H. magnifica* morphospace, there was no significant difference in those values amongst the three color morphs. The values for a (red-green) and b (blue-yellow) did significantly differ between the three color morphs, but did not account for the majority of variation seen between the anemones.

Fish color preference

There is a statistically significant difference in the frequency of *D. trimaculatus* between pink and yellow color morphs of *H. magnifica*. Even without considering the results of the Mann-Whitney U test, on average across trials of both group sizes of fish, roughly 60% of fish preferred the yellow color morph while 20-25% of fish preferred the pink color morph. The choice tests between the pink and orange color morphs had more varied results. There was only marginal significance in the group size of 16 fish, whereas trials with two fish had statistically significant differences in the number of fish on the two color morphs. Interestingly, although

in the trials with only two fish, the pink color morph had a higher frequency than the orange color morph. Conversely, while the trials with sixteen fish exhibited marginally significant results, the orange color morph had a higher frequency of fish than the pink color morph.

This color preference is in line with previous work on anemone color morph preference done in crabs, wherein the amount of camouflage conferred by each color morph affected the choice of the crab (Baeza and Stotz 2003). However, the strong preference for yellow anemones across both trials is inconsistent with the results of the field survey for *D. trimaculatus* frequency, like the inconsistency between lab and field anemone preference seen in Baeza and Stotz's study. They inferred that this difference was due to homochromy-related preferences differing between a lab setting and the heterogeneous habitat where the anemones and crabs were found. Prior studies have shown that when viewed from a distance, complementary colors on fish blur together into a dull gray and form inconspicuous coloration on reefs (Kinney *et al.* 1967, Marshall *et al.* 2003). However, it is unknown if the structural blue coloration on the white spots of *D. trimaculatus* provides some form of camouflage to the fish when present on *H. magnifica* yellow color morphs.

Group size effects

While the results are consistent with prior research demonstrating anemone preference in fish of the family Pomacentridae (Huebner *et al.* 2012), the question of group size had not yet been tested. When comparing the effect of group size, the choice test between the pink and yellow color morphs of *H. magnifica* did not have statistically significant differences between group sizes. However, for the choice test between orange and pink color morphs, a Dunn's post-hoc of a Kruskal-Wallis test

showed that there was a statistically significant difference of orange anemone frequency between the two group sizes, suggesting that preference for orange color morphs may be density-dependent, compared to the density-independent preference for yellow color morphs.

Although past research has shown that fish use schooling and group behavior to circumvent territoriality between conspecifics (Robertson *et al.* 1976), in the group sizes of 16 *D. trimaculatus* would often have individuals hiding within the anemone tentacles to avoid competition. This was because in group sizes of 16, sometimes individual fish displayed high levels of aggression towards conspecifics. In general, from behavioral observations, the groups of 16 fish had a strong preference in the first 6 hours of the trial; however, after the fish became more adjusted to the tank, movement between the two anemones was oftentimes observed. A prior study in the Mo'orea class showed that average boldness in *D. trimaculatus* increases with group size (Parkhouse 2011). It was observed that larger individuals were more exploratory of the tank and two anemones and would often be bolder than other individuals.

Behavioral observations

D. trimaculatus in PaoPao Bay were observed brushing against the tentacles of yellow *H. magnifica* in both the field and laboratory settings. While some brushing also occurred in the orange anemones as well, across all trials of pink versus yellow, brushing behavior occurred. Previously it was reported that *Dasyllus* develop a protein in their own slime coat that is not present prior to contact with the anemone (Foster 1975), which suggests that physical contact is important in maintaining immunity from the toxins of *H. magnifica*. Although a prior study in the Mo'orea class reported that *D.*

trimaculatus do not nestle in the tentacles of the anemone and only swim around the anemone (Lau 2010), the fish consistently brushed the tentacles regularly during the fish choice tests and during observations in the field.

Although *A. chrysopterus* have a larger impact on the health and size of the anemone (Holbrook and Schmitt 2004), shoals of *D. trimaculatus* have also been suggested to have a positive impact on *H. magnifica* size and health in the Red Sea (Brolund *et al.* 2004). Species within the *Dascyllus* genus are also shown to have positive impacts on the pocilloporid coral *Stylophora pistillata*, increasing the reproductive output and growth of the coral compared to unoccupied coral heads (Lieberman *et al.* 1995). However, there was no clear positive correlation between the number of *D. trimaculatus* and any of the physical measurements taken in the field.

Time, place, and occasion

While *D. trimaculatus* exhibited preference for yellow color morphs in *H. magnifica*, how much of that preference is due to anemone color and not anemone locality remains unclear. The linear regression that plotted PC 1 axis scores against average proportion of *D. trimaculatus* on anemones found little correlation between the two, suggesting that *H. magnifica* color is not totally responsible for the color preference seen. Because anemones host photosynthetic zooxanthellae (Fautin 1992) and lose their color when they bleach, it is possible that color morphs may act as an indicator of some information on health to the fish. In addition, it could be possible that the color morphs of anemones signal the level of toxicity and thus level of protection an anemone can provide. Yellow colors on reefs are known to be aposematic and signal toxicity (Rudman 1991,

Marshall 2000), so it is possible that color morphs can also indicate some information on the attractiveness of an anemone. However, there was no analysis of concentrations of zooxanthellae or nematocysts amongst the three color morphs, and there could potentially be other information conveyed in anemone color that the fish are perceiving. In addition, other morphological characters, such as number and distribution of tentacles, may change the composition of anemone morphospace and explain more of the variance than Lab values.

Locality of fish could potentially be skewing the results of the study. Because both anemones and fish were collected from PaoPao Bay, the location and familiarity of fish with local anemones may have been more important than the color. The anemones were taken from different color locations, with only one color morph taken from each location to control for morphological differences due to location. The pilot study using sixteen fish from Temae Beach also showed that the fish had a general preference for yellow over pink anemone morphotypes, even though neither anemone was from Temae. Trials with orange versus pink anemones were conducted to additionally control for the issue of locality, as fish for those trials were never caught from Temae or Painapo Beach.

Orange anemones were difficult to obtain at Temae Beach, so fewer trials were conducted with that color morph. As a result, the data for trials with pink versus orange color morphs may be skewed due to the small sample size, as only two trials were done for each group size. Due to time constraints and difficulty in capturing orange anemones, no fish choice tests of yellow versus orange color morphs were conducted.

Because there were only statistically significant differences between a and b values of the collected anemones, it was assumed that the anemones were all similar enough to each

other, with color being the significantly changing morphological character. However, differences between color morphs of *H. magnifica* do not have to be statistically significant for the fish to perceive differences between anemones. Even if Lightness was not significantly different across anemones, it explained most of the variation seen in anemone color morphospace.

Improvement and implications for future research

Although I found that my defined groups of pink, orange, and yellow *H. magnifica* color morphs had different measurements that separated them in anemone morphospace, the actual a and b color values significantly differed between them while the L values did not. To better understand if the anemones collected were an accurate representation of this variation and clustering in anemone morphospace based on color, ImageJ analysis of color morphs should be used to obtain Lab color space values for field anemones. In addition, incorporating more color morphs would be beneficial for better understanding of color morphotypes of *H. magnifica*. Unbleached white anemones with *D. trimaculatus* were observed at Snack Mahana and could provide more interesting conclusions on color preference in *D. trimaculatus*. A higher sample size of anemones and more replicates of pink versus orange trials would allow for stronger conclusions to be drawn from this study.

Testing for the threshold in group sizes and at what group size of fish the effect on anemone choice becomes statistically significant would help the understanding of these animals' life histories. Yellow versus orange fish choice tests would help explain the discrepancy between *D. trimaculatus* field frequency on orange morphs and lab preference for yellow morphs. In the future,

an equal number of anemones of each color morph, with the same color morphs from different sites, would be better for controlling for the issue of locality. Using groups of fish from different sites would also help control for locality.

Understanding the effects of *H. magnifica* color morphology on the preference of *A. chrysopterus* and *D. trimaculatus* can help elucidate why such phenotypic variation exists on reef. This can be especially true with respect to the preference for yellow color morphs of *H. magnifica*, as blue and yellow colors account for 30% of coloration on reefs and are often complementary to one another (Marshall and Yorobyev 2003). The diversity of color on coral reefs is not entirely understood, especially as to what 'colors' are actually displayed by organisms on coral reefs (Losey 2003). Understanding the importance of color in these systems is essential to conservation efforts, especially in the context of photosynthetic organisms such as corals and anemones.

As sea temperatures continue to rise, the frequency and severity of these coral reef bleaching events is expected to increase over the next 30 to 50 years, with severe bleaching events expected to become commonplace by the year 2020 (Baker *et al.* 2008). Because corals and anemones lose their color when they expel zooxanthellae during a bleaching event (Brown 1997), to which anemonefish are especially sensitive to (Saenz-Agudelo *et al.* 2011, Beldade *et al.* 2017, Norin *et al.* 2018), understanding the importance of color morphology in fish preference can help us understand how climate change will affect these mutualisms, not only in the context of anemonefish health but also anemonefish host choice. Besides the ecological importance, charismatic and colorful fauna like anemones and anemonefishes have economic importance on tropical islands such as Mo'orea. On similar island systems such as Hawai'i,

tourism largely depended on the state of coral reefs, with 85% of its value coming from tourism (Cesar and Bukering 2004). Future research into how anemone color morphology affects anemonefish mutualisms will help further our understanding of color perception in these fish, how color may be affected by climate change, and how this interaction can maintain its primary ecological and economic value.

CONCLUSIONS

Overall, the goal of this study aimed to understand how color morphology affects the choice of *D. trimaculatus* and whether differences exist between frequency of *D. trimaculatus* and *A. chrysopterus* on these color morphs. No differences between the two species exist, but there were significant differences between *D. trimaculatus* on different color morphs. Lab values were principal components that explained most of the variance seen in *H. magnifica*, but Lightness did not significantly differ between anemones of different color morphs, while the a red-green and b blue-yellow values in Lab color space did. *D. trimaculatus* significantly occurred at higher frequencies on yellow color morphs for *H. magnifica* irrespective of group size. However, selectivity based on anemones available to *D. trimaculatus* in PaoPao Bay may be a confounding variable in the preference exhibited in these fish. This study elucidates a greater understanding of the symbiosis between *D. trimaculatus* and *Heteractis magnifica*, and contributes to the overall body of knowledge about this highly charismatic relationship.

ACKNOWLEDGMENTS

I would like to thank Professors Cindy Looy, Vince Resh, and especially Stephanie Carlson and Ivo Duijnsteer for helping me with

my methods and statistics, and being a great teaching team. Thank you to Daphne Cortese and Ricardo Beldade for meeting with me at CRIOBE and providing me invaluable expertise and advice on my project. Thank you to Eye Sirison, Emma Reich, Sally Dowd, Mary Cozy, and Kylie Tuitaviki for their patience with me in the field and assistance as I spent hours catching fish. Many thanks to Heather McCandless and Jac Jogula for being field buddies at Temae as I tried searching for a collectible orange anemone over the course of days. ImageJ analysis would not have been possible without Stavi Tannenbaum, who alongside GSIs James LaChance, Renske Kirchkotles, and Clay Noss provided invaluable advice and guidance on this project.

In addition, I want to thank the entire Mo'orea Class of 2018 for the entire experience and memories to last a lifetime. It wouldn't have been the same without all of you. To Daisy Stock and Wendy Lin, thank you for your patience in my cooking group and being awesome chefs. I would also like to thank the entire staff at Gump Station and the volunteers at the Attitia Center for their generosity throughout the entire trip. Finally, thank you to my family for their love and support for me. Mauruuru roa. Nana!

LITERATURE CITED

- Baeza, J.A, and W. Stotz. 2003. Host-use and selection of differently colored sea anemones by the symbiotic crab *Allopetrolisthes spinifrons*. *Journal of Experimental Marine Biology and Ecology* **284**:25–39.
- Baker, A.C., P.W. Glynn, and B. Reigl. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* **80**:435-471.

- Beldade, R., A. Blandin, R. O'Donnell, and S.C. Mills. 2012. Cascading fitness effects of anemone bleaching on associated anemonefish hormones and reproduction. *Nature Communications* **8**.
- Bowmaker, J.K., and E.R. Loew. 2007. *Vision in fish. The senses: a comprehensive reference*. Elsevier, Amsterdam, Netherlands.
- Brolund, T.M., A. Tychsen, L.E. Neilsen, and M. Arvedlund. 2004. An assemblage of the host anemone *Heteractis magnifica* in the northern Red Sea, and distribution of the resident anemonefish. *Journal of the Marine Biological Association of the United Kingdom* **84**:671-674.
- Cesar, H.S.J., and P.J.H. van Beukring. 2004. Economic valuation of the coral reefs of Hawai'i. *Pacific Science* **58**: 231-242.
- Champ, C.M., M. Vorobyev, and N.J. Marshall. 2016. Colour thresholds in coral reef fish. *Royal Society Open Science* **3**.
- Cheney, K. L., C. Newport, E.C. McClure, and N.J. Marshall. 2013. Colour vision and response bias in a coral reef fish. *Journal of Experimental Biology*. **216**: 2967-2973.
- Cott, Hugh. B. 1940. *Adaptive coloration in animals*. Methuen, London, UK.
- Espmark, Y., T. Amundsen, and G. Rosenqvist. 2000. *Animal signals: signalling and signal design in animal communication*. Tapir Academic Pres, Trondheim, Norway.
- Fishelson, L. 1998. Behaviour, socio-ecology and sexuality in damselfishes (Pomacentridae). *Italian Journal of Zoology* **65**:397-398.
- Fautin, D.G. 1986. Why do anemonefishes inhabit only some host actinians? *Environmental Biology of Fishes* **15**:171-180.
- Foster, M.A. 1975. The comparative acclimation behavior of several pomacentrid fishes to tropical sea anemone. Master's thesis, University of Hawai'i, Honolulu, Hawai'i, USA.
- Godwin, J., and D.G. Fautin. 1992. Defense of host actinians by anemonefish. *Coepia* **1992**:902-908.
- Hammer, Ø., D.A.T Harper, and P.D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**:1-9.
- Holbrook, S.J., and R.J. Schmitt. 2000. Habitat-limited recruitment of coral reef damselfish. *Ecology* **71**:3479-3494.
- Holbrook, S.J., and R.J. Schmitt. 2003. Mutualism can mediate competition and promote coexistence. *Ecology Letters* **8**: 898-902.
- Holbrook, S.J., and R.J. Schmitt. 2004. Population dynamics of a damselfish: effects of a competitor that also is an indirect mutualist. *Ecology* **85**: 979-985.
- Holbrook, S.J., and R.J. Schmitt. 2005. Growth, reproduction and survival of a tropical sea anemone (Actiniaria): benefits of hosting anemonefish. *Coral Reefs* **24**: 67-73.
- Häussermann, V. 2004. Identification and taxonomy of soft-bodied hexacorals exemplified by Chilean sea anemones; including guidelines for sampling, preservation and examination. *Journal of the Marine Biological Association of the United Kingdom* **84**:931-936.
- Huebner, L.K., B. Dailey, B.M Titus, M. Khalaf, and N.E. Chadwick. 2012. Host preference and habitat segregation among Red Sea anemonefish: effects of sea anemone traits and fish life stages. *Marine Ecology Progress Series* **464**:1-15.
- Hurley, T.A, and S.D. Healey. 1996. Memory for flowers in rufous hummingbirds: location or visual cues? *Animal Behavior* **51**:1149 -1157.
- Kinney, J.A.S., S.M. Luria, and D.O. Weitzman. 1967. Visibility of colors underwater. *Journal of the Optical Society of America* **57**:802-809.

- Lau, S.I. 2010. The territorial agonistic behaviors of two anemonefish: *Dascyllus trimaculatus* and *Amphiprion chrysopterus*. "Biology and Geomorphology of Tropical Islands" class, University of California, Berkeley: Student Papers. [http://www.moorea-ucb.org/uploads/6/6/8/3/6683664/laufinalpaper.pdf - accessed 13 December 2018]
- Liberman, T., A. Genin, and W. Loya. 1995. Effects on growth and reproduction of the coral *Stylophora pistillata* by the mutualistic damselfish *Dascyllus marginatus*. *Marine Biology* **124**:741-746.
- Losey, G.S. 2003. Crypsis and communication functions of UV-visible coloration in two coral reef damselfish, *Dascyllus aruanus* and *D. reticulatus*. *Animal Behavior* **66**:299-307.
- Losey, G.S., Cronin, T.W., Goldsmith, T.H., Hyde, D., Marshall, N.J., McFarland, N. T. 1999. The UV visual world of fishes: a review. *Journal of Fish Biology* **54**: 921-943.
- Losey, G.S., P.A. Nelson, and J.P. Zamzow. 2000. Ontogeny of Spectral Transmission in the Eye of the Tropical Damselfish, *Dascyllus albisella* (Pomacentridae), and Possible Effects on UV Vision. *Environmental Biology of Fishes* **59**:21-28.
- Losey, G.S., W. N. McFarland, E. R. Loew, J. P. Zamzow, P. A. Nelson, and N. J. Marshall. 2003. Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. *Copeia* **2003**:433-454.
- Lythgoe, J. N. 1979. *The ecology of vision*. Oxford: Clarendon Press, Oxford, UK.
- Lythgoe, J. N., and J.C. Partridge. 1989. Visual pigments and the acquisition of visual information. *Journal of Experimental Biology* **146**:1-20.
- Marsical, R.N. 1970. The nature of the symbiosis between Indo-Pacific anemone fishes and sea anemones. *Marine Biology* **6**:58-65.
- Marshall, N. J. 2000. The visual ecology of reef fish colours. *Animal signals. Adaptive significance of signalling and signal design in animal communication*. Tapir Publishers. Trondheim, Norway.
- Marshall, N.J., K. Jennings, L. McFarland, E.R. Loew, and G.S. Loey. 2003. Visual Biology of Hawaiian Coral Reef Fishes. III. Environmental Light and an Integrated Approach to the Ecology of Reef Fish Vision. *Copeia* **2003**:467-480.
- Marshall, N. J., and M. Vorobyev. 2003. Sensory processing in aquatic environments. Pages 194-203 *in* Collin, Shaun P., Marshall, N.J., editors. *Sensory processing in aquatic environments*. Springer-Verlag, New York City, New York, USA.
- Martin, C.. 2013. Strong assortative mating by diet, color, size and morphology but limited progress toward sympatric speciation in a class example: Cameroon crater like cichlids. *Evolution* **67**:2114-2123.
- Mitchell, J.S. 2003. Mobility of *Stichodactyla Gigantea* Sea Anemones and Implications for Resident False Clown Anemonefish, *Amphiprion Ocellaris*. *Environmental Biology of Fishes* **66**:85-90.
- Norin, T. S.C. Mills, A. Crespel, D. Cortese, S.S. Killen, and R. Beldade. 2018 Anemone bleaching increases the metabolic demands of symbiont anemonefish. *Proc. R. Soc. B* **285**.
- Neumeyer, C. 1992. Tetrachromatic color vision in goldfish: evidence from color mixture experiments. *Journal of Comparative Physiology A* **171**:639-649.
- Parkhouse, T.A. 2011. Behavioral syndromes in juvenile *Dascyllus trimaculatus* (Three-spot dascyllus) in Mo'orea, French Polynesia: Individual variation in shyness and boldness. "Biology and

- Geomorphology of Tropical Islands" class, University of California, Berkeley: Student Papers. [http://www.moorea-ucb.org/uploads/6/6/8/3/6683664/parkhouse_finalpaper.pdf - accessed 13 December 2018]
- Robertson, D.R., H.P.A. Sweatman, E.A. Fletcher, and M.G. Cleland. 1976. Schooling as a Mechanism for Circumventing the Territoriality of Competitors. *Ecology* **57**:1208-1220.
- Rudman, W. B. 1991. Purpose in Pattern: The Evolution of Colour in Chromodorid Nudibranchs. *Journal of Molluscan Studies* **57**:5-21.
- Schindelin, J., I. Arganda-Carreras, E. Frise, V. Kaynig, M. Longair, T. Pietzsch, S. Preibisch, C. Rueden, S. Saalfeld, B. Schmid, J.Y. Tinevez, D.J. White, V. Hartenstein, K. Eliceiri, P. Tomancak, and A. Cardona. 2012. Fiji: an open-source platform for biological-image analysis. *Nature methods* **9**:676-682.
- Saenz-Agudelo, P., G.P. Jones, S.R. Thorrold, and S. Planes. 2011. Detrimental effects of host anemone bleaching on anemonefish populations. *Coral Reefs* **30**:497-506.
- Siebeck, U.E., G.M. Wallis, and L. Lutherland. 2008. Color vision in coral reef fish. *Journal of Experimental Biology* **211**:354-360.
- Stevens, M., C.A. Parraga, I.C. Cuthill, J.C. Partridge, and T.S. Troscianko. 2007. Using digital photography to study animal coloration. *Biological Journal of the Linnean Society* **90**:211-237.
- Whiteley, A.R., S.M. Gende, A.J. Gharrett, and D.A. Tallmon. 2009. Background matching and color-change plasticity in colonizing freshwater sculpin populations following rapid deglaciation. *Evolution* **63**:1519-1529.
- Vandermeer, J.H., and D.H. Boucher. 1978. Varieties of Mutualistic Interaction in Population Models. *Journal of Theoretical Biology* **74**:549-558.

APPENDIX A

Principal Component Analyses of field anemones, and separate Lab color space and physical measurements in fish choice test anemones.

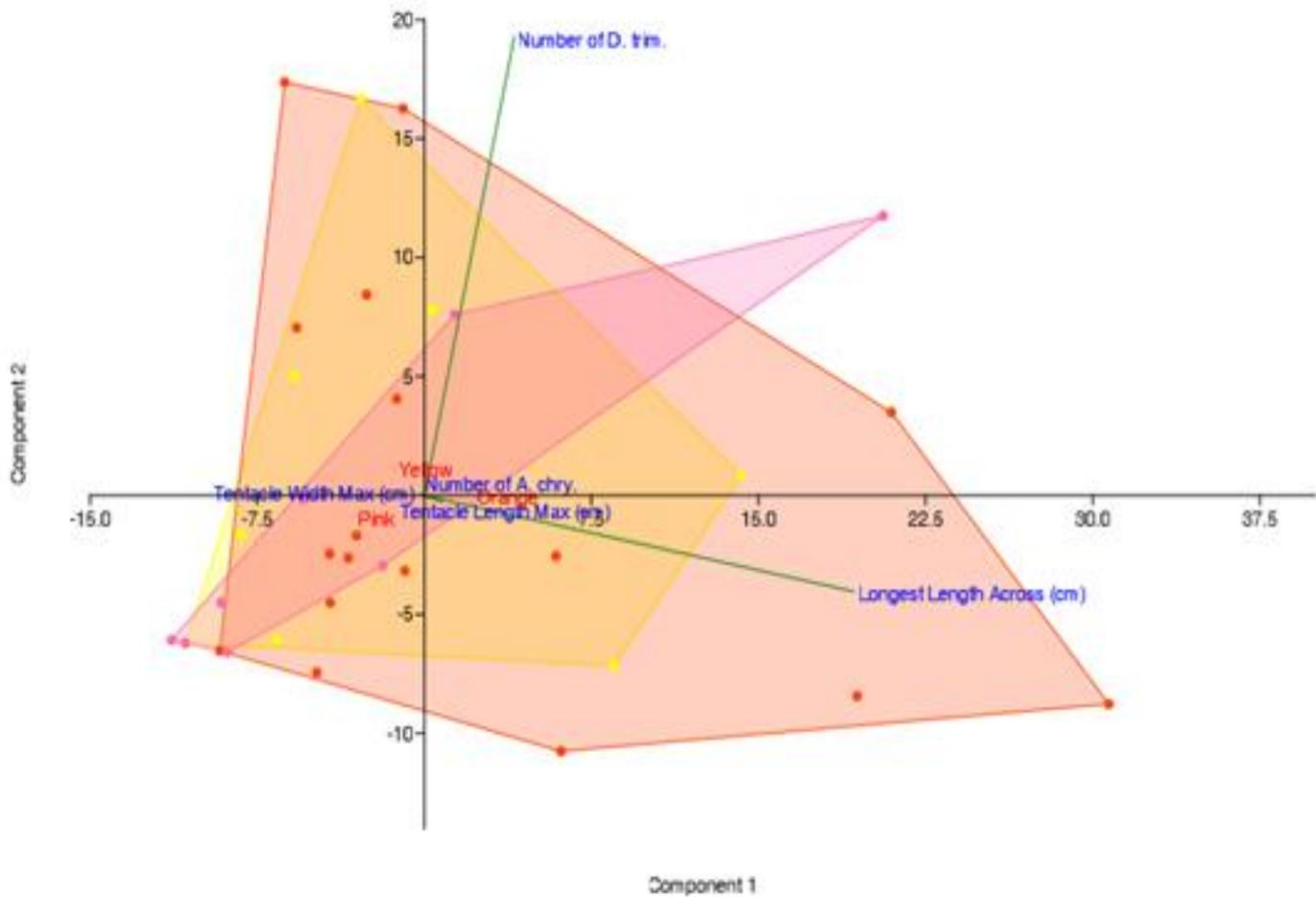


FIGURE 1. Principal Component Analysis of *H. magnifica* morphospace in the field. PC 1 axis explains 63% of the variation in this morphospace, with overlap between the three color morphs in the space.

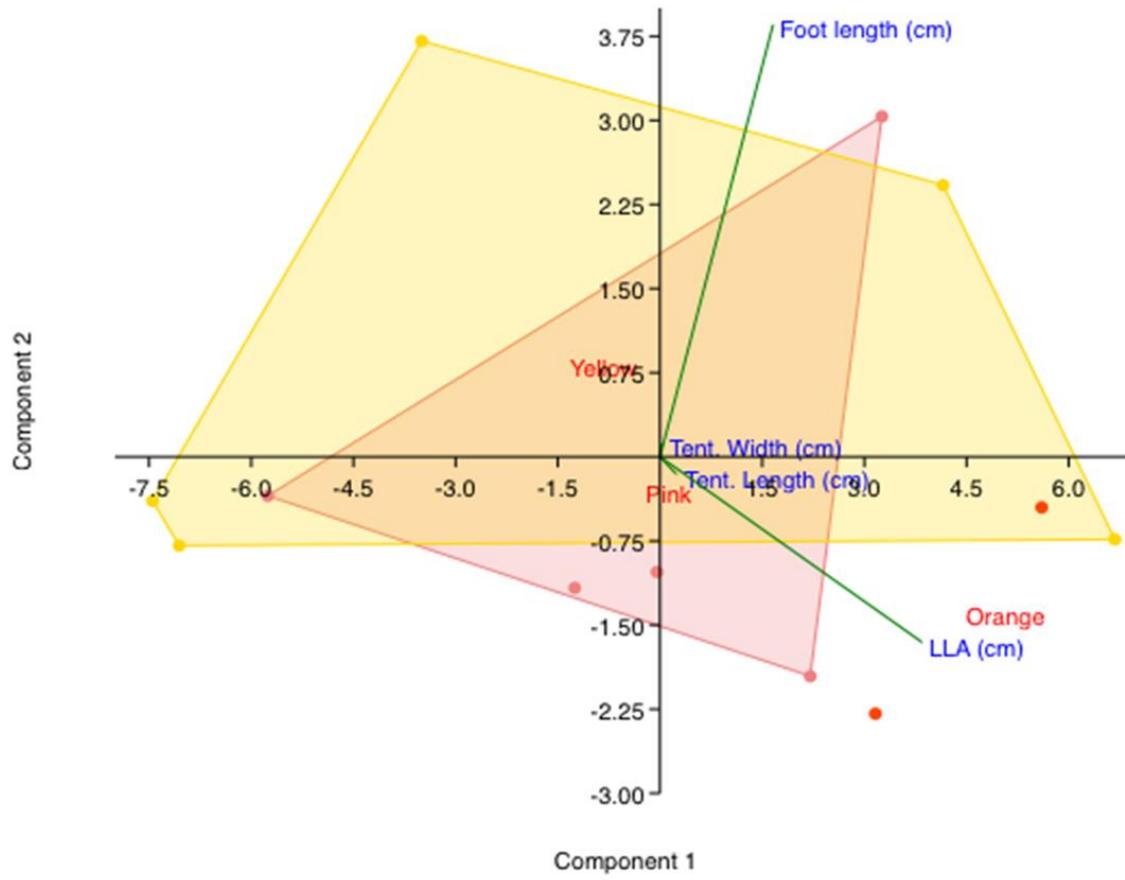


FIGURE 2. Principal Component Analysis of *H. magnifica* morphospace in the lab of physical measurements. PC axis 1 explained 85% of the variance seen in anemone morphospace. Longest length across (LLA) had a large positive correlation with the PC1 axis.

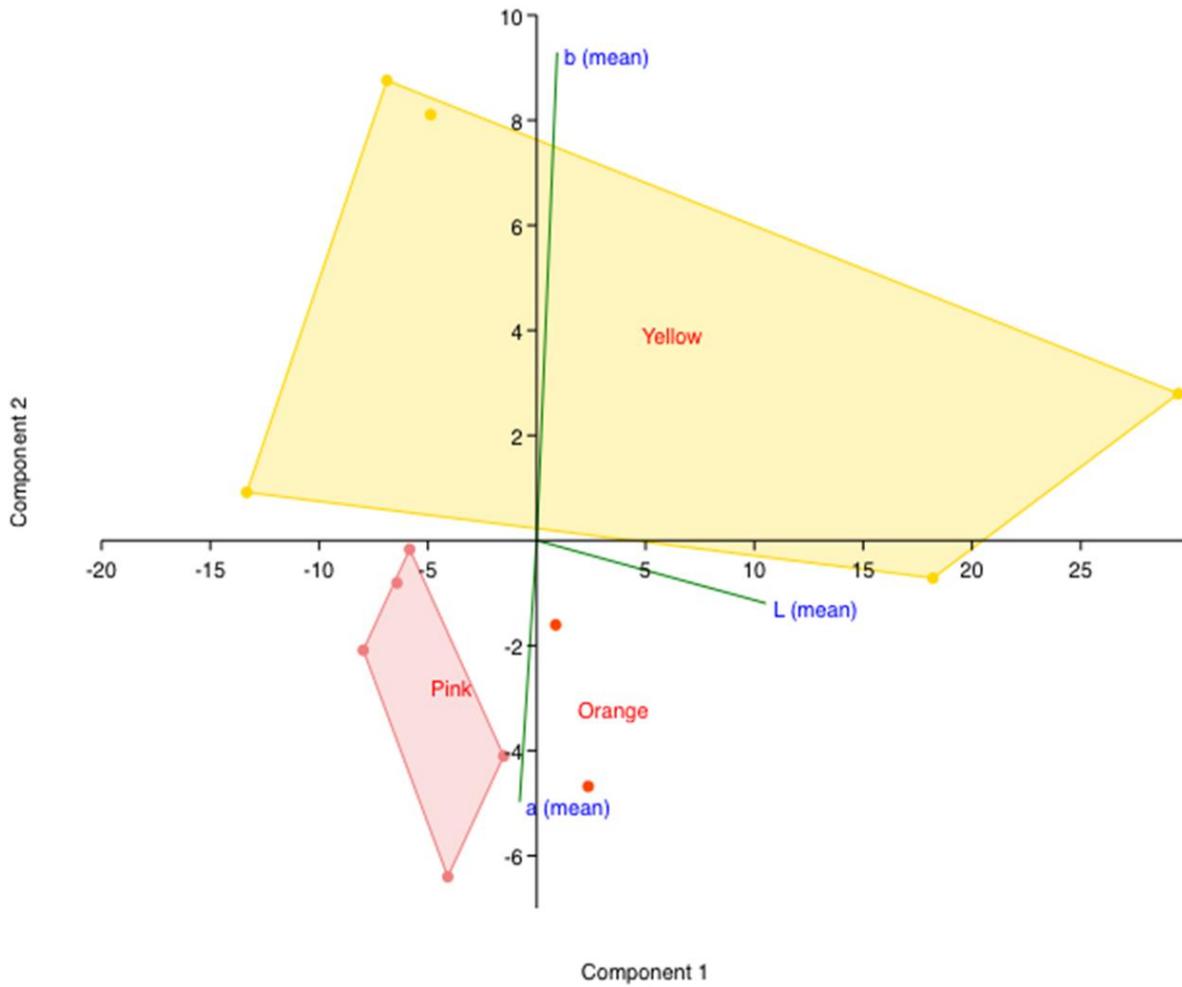


FIGURE 3. Principal Component Analysis of *H. magnifica* morphospace in the lab of physical measurements. PC axis 1 explained 85% of the variance seen in anemone morphospace. Longest length across (LLA) had a large positive correlation with the PC1 axis.

APPENDIX B

Photographs of *Amphiprion chrysopterus* with *Dascyllus trimaculatus* and color morphs of *Heteractis magnifica*.



Photos of *Dascyllus trimaculatus* (left) and *Amphiprion chrysopterus* (right). *D. trimaculatus* is on a yellow color morph of *Heteractis magnifica*, while *A. chrysopterus* is on an orange color morph of *H. magnifica*.



Photo (left) of *Amphiprion chrysopterus* chasing *Dascyllus trimaculatus* above a coral head of *Porites*. Photo (right) of *Dascyllus trimaculatus* hiding and brushing against the tentacles of a yellow *Heteractis magnifica* color morph.

APPENDIX C

Photos of color morphotypes observed in *Heteractis magnifica* on the island of Mo'orea, French Polynesia.



Going clockwise from bottom right: a pink color morph of *H. magnifica* (Temae Beach), an orange color morph of *H. magnifica* (Temae Beach), a yellow color morph of *H. magnifica* (PaoPao Bay), and an orange and yellow color morph occurring right next to each other at Temae Beach, Mo'orea, French Polynesia.