Title: Coral color and depth drive symbiosis ecology of *Montipora capitata* in Kāne‘ohe Bay, O‘ahu, Hawai‘i

Running Page Head: Coral color and symbiosis ecology

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**ABSTRACT**

Scleractinian corals form symbioses with diverse photosynthetic dinoflagellates (genus *Symbiodinium*) that confer varying levels of performance and stress-tolerance to their hosts. Variation in thermal stress susceptibility (i.e. bleaching) among conspecific corals is linked to variability in symbiont community composition, yet factors driving dissimilar symbiont associations within a population are poorly understood. To investigate potential drivers, we characterized *Symbiodinium* communities in *Montipora capitata* (N = 707 colonies) across the biophysical regions, reef types, and depth range of Kāne‘ohe Bay (Hawai‘i, USA), where this dominant reef-builder associates with *Symbiodinium* in clade C (C31) and/or D (D1a), and occurs as brown and orange color morphs. The distribution of these traits was primarily influenced by depth: orange, D-dominated colonies were more prevalent in shallow, high light environments (<2 m), whereas brown, C-dominated colonies were more prevalent with increasing depth and light attenuation. Though either color morph could be dominated by either symbiont, brown colonies were almost exclusively C-dominated, while orange colonies were more likely to be D-dominated above 4.3 m, and C-dominated below, revealing a significant interaction between color morph and symbiosis ecology. The distribution of orange, D-dominated colonies extended deeper on patch reefs, where light penetrates deeper, compared to the more turbid, fringing reefs, further supporting light as the driver of these patterns. This work reveals that symbiont community variability may arise either from holobiont phenotypic plasticity or differential survival across light gradients, with implications for predicting coral bleaching responses and informing management applications such as selective breeding of robust corals.

**INTRODUCTION**

The persistence of coral reefs is essential to sustain ecosystem services worth billions of dollars annually, including shoreline protection, critical habitat formation, and support of tourist economies (Barbier et al. 2011). Reef construction is made possible by corals’ mutualistic endosymbioses with photosynthetic dinoflagellates (*Symbiodinium* spp.; Muscatine & Porter 1977), yet the vulnerability of these symbioses to collapse at high temperatures (coral ‘bleaching’; Jokiel & Coles 1977) forecasts a bleak future for coral reefs in warming oceans (Hoegh-Guldberg et al. 2007).  
 However, significant variability exists in coral susceptibility to thermal stress, even among individual colonies. Indeed, one colony may bleach severely while neighboring conspecifics appear unaffected, which in many cases is due to association with different types of *Symbiodinium* (Glynn et al. 2001, Jones et al. 2008, Cunning et al. 2016)*.* Heterogeneous symbiont associations are observed among individuals in many, but not all, coral populations including *Pocillopora* spp. in the eastern Pacific (Glynn et al. 2001), *Orbicella* spp. in the Caribbean (Thornhill et al. 2006), *Acropora* spp. in Taiwan (Chen et al. 2005) and Australia (Jones et al. 2008), and *Montipora capitata* in Hawai‘i (Stat et al. 2011, Cunning et al. 2016). Different *Symbiodinium* types (Pochon & Gates 2010) display different capacities to utilize light energy (Iglesias-Prieto et al. 2004, Rowan 2004) and nutrients (Baker et al. 2013), which may lead to differences in photosynthate supplied to the host (Cantin et al. 2009), coral growth (Little et al. 2004), and thermal bleaching susceptibility (Glynn et al. 2001). Therefore, identifying the factors that drive symbiont community assembly within—and variability among—individuals is critical to understanding coral performance and function.

In coral populations where multiple *Symbiodinium* types are observed, they often co-occur in individual colonies, where one type is numerically dominant with background populations of the other(s) (Silverstein et al. 2012). The presence of multiple symbionts implies a potential for ‘shuffling’ (i.e., temporal change in the relative abundance of symbionts) in response to changing environmental conditions (Rowan & Knowlton 1995, Jones et al. 2008), and suggests that a colony’s symbiont community structure may reflect competition or differential performance of symbionts under prevailing abiotic conditions. Indeed, temperature and light may influence which symbiont establishes dominance in a mixed community (Cunning et al. 2015), and thus spatial variability in symbiont dominance within populations may reflect variability in the external environment (Sampayo et al. 2007, Bongaerts et al. 2015, Ezzat et al. 2017).

However, frequent occurrence of neighboring coral conspecifics with dissimilar symbionts (Iglesias-Prieto et al. 2004, Cunning et al. 2016) suggests factors other than the environment are also important. In some cases, a colony’s symbionts may reflect vertical transmission of cells from parent to offspring (Baird et al. 2009, Padilla-Gamiño et al. 2012), or may be otherwise genetically determined (Poland & Coffroth 2016). Alternatively, the symbiont community may reflect an emergent interaction of abiotic and biotic factors, as particular host traits may directly or indirectly influence symbiont community dynamics. One such trait is colony color morph, which may arise from host-produced fluorescent proteins (Kelmanson & Matz 2003) that modify intracellular light environments (Salih et al. 2000) with the potential to affect the physiological performance and association patterns of *Symbiodinium* (Frade et al. 2008, LaJeunesse & Thornhill 2004).

Here, we investigate potential biotic and abiotic drivers of *Symbiodinium* community variability in *Montipora capitata* inKāne‘ohe Bay (Hawaiʻi, USA), where this dominant reef-builder may harbor clade C (C31; bleaching-susceptible) and/or D (D1a; bleaching-resistant) symbionts (LaJeunesse & Thornhill 2011, Stat et al. 2011, Cunning et al. 2016) and occur as distinct brown and orange color morphs (LaJeunesse &Thornhill et al. 2004). The mosaic of patch and fringing reefs in Kāne‘ohe Bay occurs across regions of varying oceanic influence, water turnover time, and freshwater and nutrient input (Smith et al. 1981, Bahr et al. 2015), while shallow depths and high turbidity produce strong vertical irradiance clines. These environmental gradients create an ideal study system to explore the interactions of environment, color morph, and *Symbiodinium* community variability. Elucidating these patterns may provide significant insight into symbiosis ecology and the power to predict distributions of individuals with differential responses to environmental change.

**MATERIALS AND METHODS**

*Study Design and Sampling*

Colonies of *Montipora capitata* in Kāne‘ohe Bay were tagged and sampled between 7 June and 12 August 2016. Sampling effort was distributed among three bay regions (north, central, and south) and across five patch reefs and three fringing reefs within each region. At each reef, 10 colonies from the windward slope, reef top, and leeward slope (patch reefs only) were sampled, for a total of 30 samples from each patch reef and 20 samples from each fringe reef. Additional colonies below ~ 10 m were targeted across all sites to increase replication in deeper environments, and a deeper submerged patch reef was also sampled south of the Hawai‘i Institute of Marine Biology (HIMB) (*n* = 25 reefs; Fig. 1). In total, 16 patch reefs and 9 fringing reefs were sampled across Kāne‘ohe Bay resulting in 25 collection sites and a sample size of 707 colonies.

To ensure random sampling within each targeted area (e.g. reef top, reef slopes), weights with attached floats were thrown from the surface across a distance of approximately 20 m. The closest colony of *M. capitata* to each float was tagged and sampled, and colony depth was recorded using a depth gauge. Photographs with color standard were taken of each colony to later assess color morph of each colony (Fig. 2). A tissue biopsy (< 1 cm2) was collected from the upper surface of each colony.

*Sample Processing*

Tissue biopsies were placed in 500 μL DNA buffer (5M NaCl, 0.5M EDTA) with 1% sodium dodecyl sulfate, and DNA was extracted following a CTAB-chloroform protocol (dx.doi.org/10.17504/protocols.io.dyq7vv) at HIMB. The relative abundances of clades C and D *Symbiodinium* within each DNA sample were measured using quantitative PCR assays targeting actin loci specific to each symbiont clade (Cunning & Baker 2013). All samples were assayed in duplicate 10 μL reactions for 40 cycles on a StepOnePlus platform (Applied Biosystems) with a fluorescence threshold of 0.01 and a baseline interval of cycles 15 - 22. The ratio of clade C to D in each sample was calculated by the formula C:D = 2^(CTD-CTC), where CTD and CTC are the threshold cycles for clade D and C amplifications, normalized for fluorescence intensity and locus gene copy number (Cunning et al. 2016). Symbiont clades detected in only one technical replicate were not considered as present in a colony.

*Data Analysis*

Each colony was categorized as C- or D-dominated based on its numerically most abundant symbiont clade from qPCR analysis. Colony color morph (brown or orange) was visually assigned by five independent observers using *in situ* photographs taken during collection. The majority assignment for each colony determined color morph designation, and colonies with ambiguous color (only three out of five observers in agreement) were excluded from analyses involving color. *In situ* depths recorded for each sampled colony were corrected for tidal variation using NOAA tide data at 6-minute intervals for Moku o Lo‘e (Station ID: 1612480) retrieved through the CO-OPS API using custom R code. Generalized linear models (GLMs) with binomial errors were used to model the probability of symbiont dominance (D vs. C) and colony coloration (orange vs. brown) as a function of depth, reef type (patch vs. fringe), and bay area (north, central, south) as fully crossed factors, which were evaluated for significance using likelihood ratio tests (LRTs). A binomial GLM was also used to model D-dominance as a function of depth and color morph. Spatial autocorrelation in the distribution of color morph and dominant symbiont associations (based on Bray-Curtis dissimilarity) was assessed by a mantel test after a multinomial logistic regression was performed to account for the influence of depth. All analyses were performed in R v.3.2.2 (R Core Team 2016). R code to execute and reproduce all of the analyses and figures presented in the manuscript is available in the accompanying data repository (doi: PENDING).

**RESULTS**

*Prevalence of Symbionts and Color Morphs*

Samples of *Montipora capitata* contained *Symbiodinium* clades C and D either exclusively or in combination. Across all samples, 53.2 % contained only clade C, 1.3 % contained only clade D and 45.5 % contained a mixture of clades C and D. Clade C was the dominant symbiont in 61.4 % of colonies, and of these C-dominated colonies, most (86.6 %) occurred without background clade D. The remaining 38.6 % of colonies were dominated by clade D, which, in striking dissimilarity, rarely occurred without background clade C (3.3 % of D-dominated colonies; Fig. 3, Fig. 4).

Of all colonies sampled, 53.0 % were orange and 47.0% were brown. There was a significant correlation between color and dominant symbiont (*p* < 0.001), with clade C-dominance in 96.9 % of brown colonies but only 24.5 % of orange colonies. Moreover, the probability of orange coloration increased with the proportion of clade D in mixed symbiont assemblages (Fig. 4). The relative abundance of all four color-symbiont combinations among colonies sampled throughout Kāneʻohe Bay was 45.5 % Brown-C, 40.0 % Orange-D, 13.0 % Orange-C, and 1.5 % Brown-D.

*Spatial Distribution*

Depth proved to be the most significant predictor of symbiont dominance (*p* < 0.001) and color morph (*p* < 0.001) among colonies of *M. capitata* (Fig. 5). Overall, colonies were more likely to be D-dominated shallower than 1.3 m, and C-dominated when deeper (Fig. 5A). A higher prevalence of orange colonies was also observed shallower than 2.7 m, whereas brown colonies were more prevalent below 2.7 m (Fig. 5B). However, depth profiles differed between reef types for both color (*p* < 0.05) and symbiont dominance (*p* < 0.01), such that orange and D-dominated colonies extended deeper on patch reefs compared to fringe reefs (Fig. 5A-B). A significant interaction between depth and color (*p* < 0.05) also affected the dominant symbiont type: brown colonies were more likely to be dominated by clade C *Symbiodinium* across all depths, but orange colonies were more likely to be dominated by clade D when shallower than 4.3 m and clade C when deeper (Fig. 5C). Bay region did not affect either color morph or symbiont type, and after adjusting for the influence of depth, no spatial autocorrelation in the distribution of these traits was detected within Kāne‘ohe Bay (*p* = 0.22; Fig. 6).

**DISCUSSION**

*Symbiodinium* communities in colonies of *Montipora capitata* were highly variable with some hosting clade C or clade D exclusively, and others hosting mixtures of both clades in different relative proportions. Most mixtures were heavily dominated by one clade with low ‘background’ levels of the other (Fig. 4), though more evenly mixed assemblages also occurred. While C and D each dominated colonies relatively frequently (61 and 39 %, respectively), they showed very different patterns at ‘background’ levels: clade D was usually absent from C-dominated colonies, while clade C was almost always present in D-dominated colonies. This distribution may indicate that clade C often competitively excludes clade D (Baker et al. 2013), but clade D rarely excludes clade C. Such a competitive dynamic is consistent with observations in other coral species that associate with both C- and D-types, where the C-type is more competitive than the D-type in photosynthate production and nutrient utilization (Cantin et al. 2009, Baker et al. 2013). Nevertheless, the presence of D-dominated colonies suggests D may outperform C under certain conditions or in discrete microenvironments (e.g., high light), and forms a stable relationship with the coral host once becoming established.

Differential performance of these symbionts is also supported by the contrasting depth distributions of C- and D-dominance (Fig. 5). While colonies dominated by either symbiont were found at all depths, shallow colonies were more likely to be D-dominated (~ 70 % < 1 m), whereas deeper colonies were much more likely to be C-dominated (~ 99 % > 10 m). While this depth zonation correlates with gradients in temperature and freshwater lensing, vertical light attenuation is likely to be the strongest driving factor. Indeed, particular *Symbiodinium* types may be adapted to particular light regimes (Iglesias-Prieto et al. 2004, Ezzat et al. 2017), and clade D specifically may better tolerate high light at shallow depths (Cooper et al. 2011, Yuyama et al. 2016). Thus, the relative physiological performance of C and D types may change along a vertical light gradient, leading to differential outcomes in symbiont dominance. A similar displacement of clade A *Symbiodinium* in shallow colonies by clade C in deeper colonies of *Stylophora pistillata* in the Red Sea was attributed to greater carbon fixation by clade C at low irradiance (Ezzat et al. 2017).

While depth zonation in symbiont dominance has been observed in many coral species across tens of meters (Cooper et al. 2011, Bongaerts et al. 2015), the shallow transition from a higher frequency of D- to C-dominated colonies observed here (1.3 m) likely reflects the high seawater turbidity and rapid attenuation of light in Kāne‘ohe Bay (Grigg 1965). Irradiance measurements during October – November 2016 showed that the daily integrated irradiance at 0.5 m is attenuated by ~ 60 % at 2 m depth and 85 % at 7 m depth (CB Wall, unpublished data). Moreover, light attenuates with depth more rapidly at inshore, fringing reef sites in Kāneʻohe Bay compared to patch reefs further from shore (Jacobson 2005), which may explain the more rapid transition from D- to C-dominated colonies (and orange to brown color morphs) observed at fringing reefs (Fig. 5A-B).

While depth alone was a significant predictor of clade C- or D-dominance, there was also a significant interactive effect of depth and colony color morph. While deeper colonies (10 m) of both color morphs had < 4 % chance of being D-dominated, this probability rose to 84 % at 1 m for orange colonies, but remained < 4 % for brown colonies. Thus, symbiont community structure may be more responsive to environmental conditions in orange colonies compared to brown. Alternatively, differential survival of different morph color-symbiont pairings across a depth gradient may give rise to these distributions. Overall, these patterns do not support a fixed relationship between color morph and symbiont type (LaJeunesse et al. 2004), but reveal complex interactions between the environment, colony color, and symbiont community structure (Frade et al. 2008).

After accounting for the strong influence of depth on symbiont distributions, no significant spatial differences were observed across regions of the bay, individual reefs, or reef types, consistent with the lack of spatial variation in *Symbiodinium* ITS2 types previously observed across Kāneʻohe Bay (Stat et al. 2011). The lack of spatial structure in color and symbiont dominance across bay regions occurs despite considerable differences in oceanic influence and seawater residence time (Smith et al. 1981, Lowe et al. 2009), although surface temperature and light are relatively similar (Ritson-Williams & Gates 2016 a & b). Overall, a lack of variability across the bay but strong influence of depth on these distributions supports the conclusion that light is the most important factor driving the distribution of symbiont dominance and color in *M. capitata*.

Color morph variation in other species has been linked to differential expression of fluorescent proteins (Kelmanson & Matz 2003), indicating the possibility for epigenetic or environmental control. In this way, differences in irradiance may drive differential expression of fluorescent pigments (Takabayashi & Hoegh-Guldberg 1995), creating an internal spectral niche (Salih et al. 2000) that favors a particular symbiont (Frade et al. 2008). Alternatively, different light levels may directly mediate the competitive dominance of one symbiont over another, with symbiont composition then influencing coral color through symbiont-derived pigments (Oswald et al. 2007, Padilla-Gamiño et al. 2012), or by mediating host pigment expression (DeSalvo et al. 2012). Moreover, other microbial members of the holobiont may contribute to color. Indeed, recent evidence suggests bacterial communities can differ between orange and brown morphs of *M. capitata* (Shore-Maggio et al. 2015), and cyanobacterial phycoerithrin has been linked to orange coloration in *Montastraea cavernosa* (Lesser et al. 2004).

Disentangling the complex relationships between the environment, symbiont communities, and color will require additional experimental effort, particularly to address whether these traits are plastic and dynamic within individuals. This information is critical to determine whether the primary mechanism driving the ecological distributions of these traits occurs at the colony level, where dynamic color and symbiont communities within each colony are shaped by the environment (phenotypic plasticity, or ‘polyphenism’), or at the population level, where genetically constrained color and symbiont dominance drive differential survival across environmental gradients (‘polymorphism’, *sensu* Kelmanson & Matz 2003). A third possibility, in which these traits are environmentally-determined in early ontogeny (e.g., during gamete or larval development or settlement) and remain fixed throughout a colony’s lifetime, involves both of these scenarios, and potentially implicates epigenetic control and/or alternate phenotypic stable states. We suggest that observations of mixed symbiont assemblages in varying proportions (Fig. 4) are more consistent with phenotypic plasticity, and although direct evidence for temporal dynamism in these traits in *M. capitata* individuals is currently lacking, colonies of other coral species have shown environmentally-induced changes in both symbiont dominance (Baker 2001) and color (Todd et al. 2002).

The ecological distributions of color and symbiont dominance identified here suggest that multiple symbiont types may compete within individual corals with outcomes determined interactively by attributes of the host (color) and the abiotic environment (light). Understanding the drivers of symbiont dominance and variability within and among colonies helps predict disturbance ecology and bleaching susceptibility; the high probability of clade C dominance in deeper, brown colonies suggests that these are likely to be most sensitive in response to a given level of environmental stress, while shallow, orange colonies may be the most robust. However, shallow, brown, C-dominated colonies, as ecological outliers, may also be specially adapted to high light environments. These patterns can inform management practices such as selective breeding efforts by helping to identify the most robust individuals.

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**Figure Legends**

Figure 1. Reef locations at which colonies of *Montipora capitata* were sampled in Kāne‘ohe Bay, O‘ahu, Hawai‘i, USA. The three targeted bay regions and reef types are indicated by color and shape, respectively.

Figure 2. Color morphs of *Montipora capitata* colonies: orange (left) and brown (right) (photo credit: Raphael Ritson-Williams).

Figure 3. Proportion of C- and D-dominated colonies that contain single symbiont or mixed symbiont assemblages.

Figure 4. Histogram of the number of *M. capitata* colonies with varying mixtures of *Symbiodinium* in clade C and/or D. Bar colors indicate colony color morph.

Figure 5. (A) Bars indicate the proportion of clade-dominance in all colonies grouped by 1 m depth intervals. Line indicates the probability of clade D-dominance as a function of depth. (B) Bars indicate the proportion of occurrence of each color morph in all colonies grouped by 1 m depth intervals. Line indicates the probability of occurrence of the orange color morph as a function of depth. (C) Probability of clade D-dominance for colonies of each color morph as a function of depth

Figure 6. Spatial distribution of the dominant symbiont type and color morph of *Montipora capitata* colonies across Kāne‘ohe Bay, O‘ahu, Hawai‘i, USA. Proportions of each phenotype are the adjusted means calculated at the overall mean sampling depth (2.5 m) based on a fitted multinomial model including depth and reef location as predictors.