Title: Depth-mediated interactions between color and *Symbiodinium* in *Montipora capitata* in Kāne‘ohe Bay, O‘ahu, Hawai‘i

Running Page Head: Distribution of *Symbiodinium* and Color

Authors: T. Innis1, R. Cunning2, R. Ritson-Williams2, C. B. Wall2, R. D. Gates2

1Northeastern University, Marine Science Center, 430 Nahant Rd, Nahant, MA 01908, USA

2University of Hawai‘i at Mānoa, Hawai‘i Institute of Marine Biology, PO Box 1346, Kāne‘ohe, HI 96744, USA

\*Corresponding author: teegan.innis@gmail.com

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**ABSTRACT**

Scleractinian corals form mutualistic symbioses with genetically and functionally diverse photosynthetic dinoflagellates in the genus *Symbiodinium* that confer varying levels of performance and stress-tolerance to their hosts. Variation in bleaching susceptibility among conspecifics is linked to symbiont community variability, yet the factors driving dissimilar symbiont associations within a population are poorly understood. To investigate potential drivers, we characterized symbiont 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* clades C (C31) and/or D (D1a) and occurs as two color morphs (brown and orange). The prevalence of C- and D-dominated colonies (61 vs. 39 % of colonies respectively) did not vary across bay regions, reef types or among individual reefs. However, there was a significant influence of depth on both symbiont-dominance and color. Orange, D-dominated colonies were more prevalent in shallower, high-light environments, whereas brown, C-dominated colonies were more prevalent with increasing depth and light attenuation. Though either color morph could be dominated by either clade, brown colonies were more likely to be C-dominated regardless of depth, while orange colonies were more likely to be D-dominated above 3.63 m and C-dominated below, revealing a significant interaction between host color and symbiosis ecology. This work reveals that symbiont community variability may arise either from holobiont phenotypic plasticity or differential survival across light gradients, with significant implications for predicting coral responses to climate change stressors and informing potential 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 (Rowan 2004; Iglesias-Prieto et al. 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, understanding the factors that drive symbiont community assembly within (and variability among) individuals is critical to understand coral performance and function.

In coral populations where multiple *Symbiodinium* types are observed, they often co-occur in individual colonies, where one type is typically 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 symbiont types) 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).

However, frequent occurrence of neighboring conspecifics with dissimilar symbionts (Cunning et al. 2016) suggests factors other than the environment are also important. In corals where symbionts are maternally derived (i.e., vertical-transmission), a colony’s symbionts may reflect which cells were transmitted into unfertilized eggs (Padilla-Gamiño et al. 2012) and brooded larva (Baird et al. 2009) in addition to exogenous sources (Byler et al. 2013), 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 arises from host-produced fluorescent proteins (Kelmanson & Matz 2003) that modify intracellular light environments (Salih et al. 2000) with the potential to affect patterns in coral-*Symbiodinium* associations (Frade et al. 2008; LaJeunesse & Thornhill 2004) and physiological performance.

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 of 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 2016 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.

*Color Morph Assessment*

Five independent observers visually assigned color morph, either brown or orange, to each sample colony using *in situ* photographs taken during collection. The majority’s opinion for each colony was ultimately the color morph assigned. Uncertainty in color, meaning the number of agreements per five observers, was tested using Chi-Squared analyses across color morphs, geographic scales and symbiont community composition.

*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^(CTC-CTD), where CTC and CTD are the threshold cycles for clade C and D 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. The proportions of clades C and D present in colonies dominated by each clade and color morph were compared using Chi-Squared analyses. Chi-Squared tests were then used to assess the relationship between dominant symbiont clade, color morph (orange vs. brown), and one vs. two symbiont clade assemblages between bay regions (northern, central and southern), reef types (patch vs. fringe), and each individually sampled reef. Logistic regressions were used to model the probability of C- vs. D-dominance and orange vs. brown color as a function of depth. *In situ* recorded depths were corrected for differences in mean sea level using daily tide tables for Moku o Lo‘e, Kāne‘ohe Bay at 6-minute intervals (NOAA, "Tide Predictions - MOKU O LOE 1612480 Tidal Data Daily View - NOAA Tides & Currents", 2016). Spatial autocorrelation among reefs in the composition of color morph and dominant symbiont association (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).

**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 % contained only clade C, 1.2 % contained only clade D and 45.8 % contained a mixture of clades C and D. Clade C was the dominant symbiont in 61 % of colonies, and of these C-dominated colonies, most (86.6 %) occurred without background clade D. The remaining 39 % of colonies were dominated by clade D; but in striking dissimilarity, D rarely occurred without background clade C (3.3 % of D-dominated colonies; Fig. 3, Fig. 4).

Of all colonies sampled, 52 % were orange and 48 % were brown. There was a significant correlation between color and dominant symbiont (*p* < 0.001), with clade C-dominance in 92.4 % of brown colonies but only 32.5 % 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 44.4 % Brown-C, 34.9 % Orange-D, 16.9 % Orange-C, and 3.8 % Brown-D.

*Color Morph Uncertainty*

Uncertainty in color morph varied significantly between reef areas (p < 0.05), colony color morph (p < 0.001) and dominant symbiont (p < 0.001). Colonies on reef slopes had more discrepancies in their color assignment between observers than did colonies on the reef tops. Orange colonies had more agreements in color assignment between observers than did brown colonies.

*Spatial Distribution*

Depth proved to be the significant driving factor for symbiont dominance (*p* < 0.001) and color morph (*p* < 0.001) among colonies of *M. capitata*. Colonies were more likely to be C-dominated at depths below 1.31 m, while D-dominated colonies were more common at depths above 1.31 m. A higher probability of a colony being orange was observed in colonies at depths < 2.93 m, whereas brown color morphs were more prevalent at depths > 2.93 m. 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 at depths shallower than 3.63 m and clade C at depths deeper than 3.63 m (*p* < 0.001; Fig. 5).

The proportion of colonies that were C- vs. D-dominated did not differ among regions of the bay (*p* = 0.14), individual reefs (*p* = 0.07) or between patch and fringing reef types (*p* = 0.37) initially. However, after adjusting for the influence of depth on spatial patterns, bay region was a significant predictor of a colony’s likelihood of being C- or D-dominated and brown or orange in coloration simultaneously (*p* < 0.01; Fig. 6). D-dominated brown colonies were more abundant in the southern (*n* = 9) bay area than they were central (*n* = 3) and northern (*n* = 3) regions, though this trend is likely due to the trifling subset of samples with only 15 brown colonies dominated by clade D.

**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 D almost never excludes C, resulting in greater occurrences of mixed symbiont assemblages when D is the dominant symbiont. 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 a more beneficial symbiont than the D-type under favorable conditions (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, and clade D is capable of establishing 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, freshwater lensing, or suspended particles, vertical light attenuation is likely to be the strongest driving factor given the intense loss of light across a small vertical scale. Indeed, particular *Symbiodinium* types may be adapted to particular light regimes (Iglesias-Prieto et al. 2004), and clade D specifically may better tolerate high light (Yuyama et al. 2016). Thus, the relative performance of C and D types in *M. capitata* may change along a light gradient, leading to differential outcomes in symbiont dominance. While depth zonation in symbiont dominance has been observed in many coral species across tens of meters (Bongaerts et al. 2015), the shallow transition from a higher frequency of D- to C-dominated colonies observed here (1.31 m) likely reflects the seawater turbidity and rapid attenuation of light in Kāne‘ohe Bay (Grigg 1965).

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 80 % at 1 m for orange colonies, but only to 12 % 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 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, little spatial variability in color or symbiont composition was evident. No significant spatial differences were observed across regions of the bay, individual reefs, or reef types, consistent with the lack of spatial variation in symbiont prevalence previously observed across sites and regions (Stat et al. 2011). The prevalence of different color-symbiont pairings did not vary throughout the bay despite considerable differences in oceanic influence and seawater residence time (Smith et al. 1981; Lowe et al. 2009). Previous studies have shown temperature and light are relatively similar across the bay (Ritson-Williams & Gates 2016 a & b), although higher irradiance in the south end of the bay correlated with a slightly higher abundance of brown-D colonies (Cunning et al. 2016). Moreover, there were no interactions between geography and depth on symbiont dominance or color morph, indicating that the strong influence of depth on these patterns was consistent throughout the bay. Overall, the overwhelming influence of depth on these distributions suggests light is the most important factor driving the relationship between symbiont dominance and color.

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), which may subsequently create an internal spectral niche (Salih et al. 2000) favorable to certain symbionts (Frade et al. 2008). Alternatively, different light levels may directly mediate the competitive dominance of a symbiont over another, which may subsequently result in modified colony 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, bacterial communities may 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 manipulative and experimental work, 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 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 CAPTIONS**

Fig 1. Collection reef locations in Kāne’ohe Bay, O’ahu, Hawai’i, USA

Fig. 2. *Montipora capitata* colonies of both color morphs: orange (left) and brown (right). Photo credit: Raphael Ritson-Williams

Fig. 3. Proportion of occurrence of *Symbiodinium* clades C and D in *Montipora capitata* colonies per dominant symbiont clade

Fig. 4. Percentage of clade D in all colonies of *Montipora capitata*. Bar colors indicate colony color morph

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

Fig. 6. Latitudinal geographic distribution of *Symbiodinium* and color morph in *Montipora capitata* across Kāne’ohe Bay, O’ahu, Hawai’i, USA