

AN ABSTRACT OF THE THESIS OF

Kaitlin Mae McConnell, for the degree of Master of Science in Microbiology
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Title: Reef Microbiomes of Mo'orea, French Polynesia, a Socio-Ecological Island System

Abstract approved:

Andrew R. Thurber

At a time of rapid global change, a socio-ecological system (SES) approach can provide a framework through which to quantify and communicate the risks and uncertainties of coupled human-natural systems. Islands, and tropical coral reef islands in particular, can be excellent models for SES research since they may be considered as both closed and open systems, where agents-- both human and non-human-- and their interactions, may be considered at a variety of spatial and temporal scales and with diverse levels of complexity. Bacteria and Archaea communities are the executants of biochemical cycling in systems, and alterations in the structure of microbial communities can provide indications of system-wide metabolic shifts driven by natural and human forces.

In this thesis, I first present patterns of spatial and temporal variability in microbial communities across a tropical coral island reefscape, where I hypothesized: Microbiome host, habitat and sampling location will house distinct microbiomes (beta diversity) that differ between seasons. Microbiomes were primarily host specific, and host specificity varied with structural scale: microbiomes of reef sediment, seawater and corals were different from each other. Zooming in, the three species of corals examined also had distinct microbial communities associated with them. These host-

specific microbiomes varied differentially across spatial scale, such as island side, reef habitat (fore, back and fringing reefs) and sampling locations.

The structure of coral microbiomes supported evidence of a core microbiome with low species richness and a less-abundant but greatly richer resident microbiome or environmentally responsive community. Of 476 taxonomic families identified in our samples, sequences of the Family Endozoicomonaceae dominated all coral microbiomes, representing between 68-80% of the relative abundance of bacteria and archaea depending on species and varying less than 1% across reef habitats. Considering all coral species together, this meant that the bulk of coral microbiome richness made up less than 13% of the total microbiome. The top ten most relatively abundant families in each coral species across habitats and seasons showed that each host- and spatially distinct microbiome experienced seasonality differently.

These shifts were contextualized within the scope of the Mo'orea Island Socio-Ecological system. Because coral microbiomes are sensitive to biophysical fluxes, coral microbiome diversity estimates (Chao1) were interpolated into an island-wide heatmap. By comparing and locating areas of anomalous microbiome diversity with locations of biophysical anomalies around the island, such as increased nitrogen concentrations, we found that locations of convergent anomalies were situated near to areas of increased human activity, although uncertainty exists as to at what extent and whether human activity is a directly causative effect. However, our maps do provide evidence for the integration of human and natural systems at local to microbial scales.

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Reef Microbiomes of Mo'orea, French Polynesia, a Socio-Ecological Island System

by
Kaitlin Mae McConnell

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APPROVED:

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Kaitlin Mae McConnell, Author

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DEDICATION

Dedicated to my grandfather, John McConnell, who in 1969 designed the “authentic” Earth Flag, inspired by the view of the Earth from space.

Dedicated also to the Micronesian islanders who, earlier this year, showed me the flag of the “Pacific Alternative,” a new Earth Flag depicting the Earth adorned with symbolic regalia on a background of stars and galaxies.

CONTRIBUTION OF AUTHORS

Chapter 1

Andrew R Thurber advised this thesis. He also conceived of the Mo'orea Virus Project from which the samples analyzed in this thesis were derived, participated in data collection, assisted in the data analysis and interpretation, and reviewed manuscripts. Rebecca Vega Thurber conceived of the Mo'orea Virus Project, participated in data collection and provided conceptual guidance as a member of the thesis committee. Adrienne Correa conceived of the Mo'orea Virus Project, participated in data collection. Carsten Grupstra completed the temperature analysis at each sampling location, participated in data collection. Emily Schmeltzer developed laboratory methods and participated in data collection. Sarah Seabrook participated in data collection.

Chapter 2

Risako Sakai collected social data and participated in the data synthesis, analysis and interpretation. Bran Black made and synthesized all maps of biophysical parameters and participated in the data analysis and interpretation. Aaron Weinstock synthesized nutrient concentrations for a map and quantified analysis confidence. Adriana Messyasz collected bacterial and virus count data, synthesized microbial datasets and participated in the data analysis and interpretation. All authors wrote a combined Transdisciplinary Report.

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1. INTRODUCTION

1.1 Risk and Uncertainty in Socio-Ecological Systems under Rapid Global Change

With the rise of the Anthropocene, in tandem with widespread innovation there have also developed new risks to, and uncertainties in, our futures (Crutzen 2006; O'Connor et al., 1999; Steffen et al., 2011). A skyrocketing human population continues to add Earth-warming greenhouse gasses into the atmosphere (Tett et al., 1999; Wigley 1997; Mitchell et al., 1995), over-exploit natural resources and pollute vanishing habitats. These activities are contributing to a loss of regional ecosystem services worldwide and a Sixth Mass Extinction (IPCC 2013; Ravindranath & Sathaye, 2002; Ceballos & Ehrlich, 2018), keeping in mind that the risks of future climate scenarios are accompanied by uncertainties (Hulme et al., 1999). In this way, rapid climate change might also be considered a matter of social and environmental justice: not only is the human population dependent on Earth's natural resources, but the communities, people groups, and other organisms that share the planet with humans that are more vulnerable to the current rapid changes are in many cases the least responsible for it (Levy et al., 2018; Thomas et al., 2005).

One approach to quantifying, communicating and considering these risks and uncertainties is via a Socio-Ecological Systems (SES) perspective, which views an “ecological system [as] intricately linked with and affected by one or more social systems” (Anderies et al., 2004). An SES approach may be particularly relevant and applicable for scientists, policy makers, community members, consumers and other stakeholders, offering spatial and temporal conceptual frameworks with which to untangle human and non-human agents and their interactions at varying scales, while accounting for the possibility of change through time and multiple stable states (Anderies & Janssen, 2013; Avriel-Avni & Dick, 2019; Berrouet et al., 2018; Holling, 2001).

Additionally, there is an expanding literature base, not limited to Ecosystem-Based Management (Silva et al., 2019; Uy & Shaw, 2012), that integrates the values of human agents in SES systems in concert with their perceptions of local and global

risks and uncertainties (Biedenweg & Gross-Camp, 2018; Cervený et al., 2017; Perrings et al., 2019). Simultaneously, there is movement towards practicing co-production of knowledge and co-management of resources that value inclusion of local and regional stakeholders in science, policy and governance in order to enhance the inclusion of diverse perspectives, and cultivate resilience and adaptive capacity (Adger, 2005; Avriel-Avni & Dick, 2019). Although vulnerable communities are often characterized as having relatively little capacity to absorb or adapt to climate change, they often are advantaged with the potential and motivation to create sweeping change at local scales and inspire change at broader scales (Cigliana & Ballard, 2017; Levy & Patz, 2018; Petridis et al., 2017), a testament to their resilience (Ruiz-Mallén & Corbera, 2013)

1.2 Coral Reefs

Islands are frequent subjects of SES research, representing model systems that can be considered as simultaneously closed and open (Aswani & Allen, 2009; Banos-González et al., 2015; Schmitz et al., 2018). In other words, human-habited islands provide an opportunity to examine coupled human and natural systems at varying scales of complexity and interaction, from local to global spheres, acute to gradual timescales and diverse mental models of perception and decision making (Liu et al., 2007; Kronen et al., 2010).

Islands with coral reefs are particularly well suited for tracking dynamic spatial and temporal socio-ecological patterns. Indeed, coral reefs cover less than 1% percent of the Earth's surface and they are home to 34% of known marine biodiversity, with more yet to be discovered (Reaka-Kudla, 2001).

Corals are a foundational species in coral reef ecosystems, growing in massive reef structures which can be seen from space and that support biodiverse communities, including humans (Dikou, 2010). The current decline of coral reefs during the Anthropocene is dismantling many long-standing, interdependent biological relationships from microbial to global scales (Hughes et al., 2017). Coral reefs worldwide are currently facing rapid decline due to anthropogenically induced increases in global temperatures, pollution in the form of excess nutrients in the water

(Wang et al., 2018a) or debris such as plastic (Ryan et al., 2009), changing ocean chemistry (Coronad et al., 2019) and overfishing, amongst several other perturbing forces (Camp et al., 2019; Hoegh-Guldberg, 2004).

Coral reefs have been estimated to provide \$352,915 of natural capital and services to the world per hectare per year (Costanza et al., 1997; de Groot et al., 2012; Costanza et al., 2014), and support approximately 500 million people who live both near to and far from reefs (Hoegh-Guldberg, 2011). Within these numbers are an estimated 6 million people who directly depend on coral reefs as a primary resource for subsistence and income (Cinner, 2014; Teh et al., 2013).

People make important cultural, spiritual and emotional connections with coral reefs as well. In a case study comparing resident and tourist perceptions and attitudes towards coral reefs and reef decline on the Great Barrier Reef in Australia, people reported feeling widespread feelings of deep loss. Termed “Reef Grief,” such research adds to an expanding global phenomenon that psychologists, ethicists and environmental scientists refer to as Ecological Grief have colloquially coined as “Global Mourning” (Marshall et al., 2019).

Embodying such transcendent value for local and global socio-ecological well-being, the costs associated with the risk of losing coral reefs is great. At the time of publication in 2003, Pandolfi et al. (2003) estimated that coral reefs from 14 regions worldwide were between 30-80% degraded and with continued trajectories for increased degradation. Additionally, a study of 100 reefs worldwide found that environmental anomalies causing coral bleaching are occurring at increasing frequency which no longer allow corals sufficient time to recover (Hughes et al., 2018).

Herein, the following two chapters seek to add to the rapidly expanding and increasingly important field of coral reef research using molecular ecological tools and multidisciplinary interpretations. First, as a thesis in partial fulfillment of the Master of Science in Microbiology at Oregon State University (OSU), I will introduce the spatial and temporal patterns of the microbial reefscape around the tropical island of Mo’orea, French Polynesia. Then, in partial fulfillment for OSU’s requirements for the Graduate Minor in Risk and Uncertainty Analysis and

Communication in Marine Science and National Science Foundation Research Traineeship (NRT) Fellowship, the risks and uncertainties in the socio-ecological system of Mo'orea Island will be framed from a multidisciplinary perspective.

2. SPATIAL AND SEASONAL VARIATION IN CORAL REEF MICROBIOMES OF MO'OREA, FRENCH POLYNESIA

2.1 ABSTRACT

The coral microbiome has been an integral component of holobiont persistence throughout the evolution of Scleractinian corals, but the speed of global change during the Anthropocene currently challenges the limits of holobiont resilience. To characterize island-wide reef microbiome variability, we tracked microbiome diversity across nested spatial scales of island side, reef habitat, site-specific sampling location, and within host species during one dry and one wet season around the island of Mo'orea, French Polynesia. Water, sediment and coral microbiomes of *Pocillopora verrucosa*, *Porites lobata* and *Acropora hyacinthus* were distinct to host type, including coral host species, and all shared taxa. Each host-specific microbiome varied across spatial scales and expressed seasonal microbiome shifts differently, if at all. The family Endozoicamonaceae, though it represented 75% of coral microbiome relative abundance overall, was comprised of 93 Amplicon Sequence Variants (ASVs). 9595 ASVs, representing 99.04% of total coral microbiome richness, made up the remaining 25%. Shifts in relative abundances of host-specific taxa were observed across habitats, though variation in individuals between seasons were specific to the coral colony, providing an indication that host-specific microbiomes are flexible between individuals and environmental conditions and may thus play a role in holobiont resilience.

2.2 INTRODUCTION

In order to recognize indications of change, quantify anthropogenic impacts and provide options for action, an essential challenge arises to understand spatial and temporal patterns of variance within systems, their underlying driving mechanisms and, in turn, their effects on the system (Graham et al., 2010; Lindenmayer et al., 2012). Integrated within their hosts and hosting environment, microbial communities are ideal candidates by which to track such changes. Often the foundation of food webs, assemblages of bacterial, archaeal and eukaryotic microbes (and viruses) are the omnipresent executants of biochemical cycling in Earth systems, exhibiting both sensitivity and resilience to acute and gradual alterations within their sphere of influence (Martiny et al., 2006; Thompson et al., 2017). As such, microbial communities can be described at endless spatial scales spanning micro-habitats (Hernandez-Agreda et al., 2017; Martiny et al., 2006; Ramirez et al., 2014) to whole oceans (Ladau et al., 2013a) and beyond (Imshenetsky et al., 1976; Napier, 2004). Tracking patterns existing within and between them may provide insightful indications into changing or stable environments (Doropoulos et al., 2013; Ladau et al., 2013a; Lesser & Slattery, 2011; Röthig et al., 2016).

Coral Microbiomes

Coral reefs cover just 0.2% percent of the Earth's surface and are home to 34% of known marine biodiversity, with more yet to be discovered (Reaka-Kudla, 2001). Coral reefs have been estimated to provide \$352,915 of natural capital and services to the world per hectare per year (Costanza et al., 1997; de Groot et al., 2012; Costanza et al., 2014), and support approximately 500 million people who live both near to and far from reefs (Hoegh-Guldberg, 2011). Within these numbers are an estimated 6 million people who directly depend on coral reefs as a primary resource for subsistence and income (Cinner, 2014; Teh et al., 2013). The corals that comprise the tropical coral reefs of the world are meta-organisms, thriving in oligotrophic waters and sustained by a rich consortia of symbionts. The term coral holobiont, or

“whole organism,” refers to the calcifying coral cnidarian, its photosynthetic symbiont (commonly a dinoflagellate belonging to the family *Symbiodiniaceae*) and a bacterial, viral and fungal microbiome that is distributed throughout the corals’ skeleton, tissue and mucus (Amend et al., 2012; Rohwer et al. 2002; Sweet & Bythell, 2017; Sweet et al., 2011). As the critical agents for biogeochemical cycling both within corals and between corals and their environment, the coral microbiome is sensitive to change and an important indication of metabolic potential (Gast, 2015; Nelson et al., 2016; Ramirez et al., 2014; Thompson et al., 2017).

Shifts in coral hosts’ environment can cause a pronounced shift in beta (between corals) and alpha diversity (biodiversity within a coral) of the microbial communities coexisting within the corals (Vega Thurber et al., 2014). Such shifts have been observed to follow progressions with increased levels of stress. For example, Maher et al. (2019) observed the increased abundance of opportunistic taxa in microbiomes of Mo’orean *Pocillopora meandrina* that were subjected to elevated temperature, nutrient enrichment, and simulated predation. Such community shifts, identified as a change in beta diversity, increased with one stressor and were somewhat counteracted by a second added stressor, then increased again with a third added stressor. This study raised questions as to the influence of the coral’s immune response to react to one stressor, tolerate a second and be overcome by a third.

When describing shifts between healthy and stressed microbiomes, The Anna Karenina Principle (AKP) proposes that stressed microbiomes exhibit dysbiosis (Zaneveld et al., 2017). Derived from Tolstoy and adapted to microbial ecology, AKP posits that ‘all healthy microbiomes are similar; each dysbiotic microbiome is dysbiotic in its own way.’ In other words, stressed coral microbiomes will increase in dispersion in comparison to non-stressed.

Natural systems present a plethora of contrasting habitats in which species may exist. In order to recognize potential disturbances in reef microbiomes, an understanding of typical variance must first be established. Here, we elucidate the spatial and temporal variance of microbiomes of three species of coral, reef sediment, and water and contrast the microbiomes of each of those groups across three reef habitats, within 8 sites, distributed across the North, East and West sides of Mo’orea,

French Polynesia. Then, we determine the seasonal coral microbiome variance of individual corals through ordination and dispersion analysis of repeatedly sampled coral colonies over two seasons. This spatially discrete data set around the island allows us to address the overarching question, “*What is the spatial and temporal variability in microbiome composition?*” with the following hypothesis:

1. Microbiome host, habitat and sampling location will house distinct microbiomes (beta diversity) that differ between seasons.

2.3 METHODS

Study Design

We tested for variation in coral microbiome beta diversity within and between hosting environments of five nested spatial scales each within a dry and wet season of one year by taking samples of reef sediment, seawater and three coral species around the island of Mo’orea, French Polynesia (Tables 2.1 and 2.2). We then visualized seasonal microbiome shifts with nonmetric multidimensional scaling (nMDS) ordination and tested whether beta dispersion was different between seasons.

Study System

Mo’orea, French Polynesia (17.490° S, 149.826° W), is a tropical high island with a 134 km² footprint lying just west of Tahiti. Like many islands in the South Pacific, Mo’orea has a rich history of Polynesian culture, foreign colonization and modern development, today supporting a gradually increasing population of over 16,000 residents. Two scientific research stations, the Centre de Recherches Insulaires et Observatoire de l’Environnement (CRIOBE, France) and Gump Station (UC Berkeley, United States), are situated in the northern Opunohu and PaoPao bays, respectively. Field work for this study was based from Gump Station, and sampling coincided within established long term monitoring sites of the National Science Foundation’s (NSF) Mo’orea Coral Reef Long Term Ecological Research (MCR LTER) location, established in 2004.

Table 2.1: Sampling times and locations			
Season	Island Side	Sampling Location	
		Site	Habitat
Dry, Wet	North	0, 1, 2	Fore, Back, Fringing
	East	3, 3.5, 4	Back, Fringing
	West	5, 5.5, 6	Back, Fringing

Table 2.2: Samples taken at each Sampling Location				
Sample Types and Replicates				
Sediment	Water	Coral		
Enough to fill a 2ml snap-cap tube	750 mL from 1m above the benthos	<i>Pocillopora verrucosa</i>	<i>Porites lobata</i>	<i>Acropora hyacinthus</i>
		6 different colonies	6 different colonies	6 different colonies

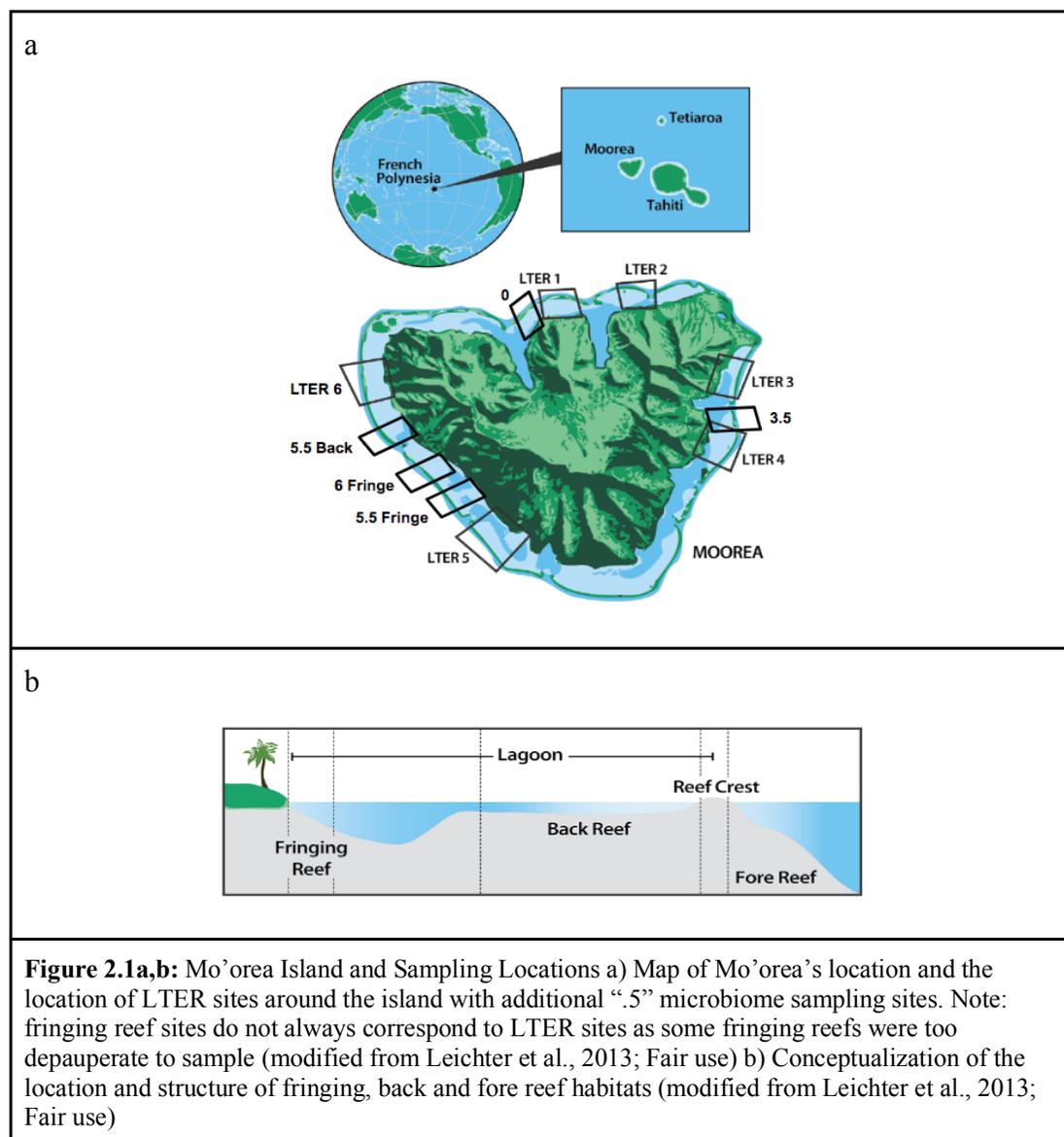
Mo'orea experiences a wet and a dry season. During the wet season, generally November through April, air temperatures are 23-31°C with over 200mm monthly average precipitation. During the dry season of May through October, average temperatures range are 22-29°C with less than 100mm monthly average precipitation. Average ocean temperatures range from 26°C degrees in the wet season and 28°C in the dry season. Inshore oceanographic circulation is wave driven (Leichter et al., 2012), and the north side of the island has higher nitrogen and sediment concentrations than the west and east sides (Carpenter 2008; Weinstock ID Chapter, Oregon State University, 2019).

In addition to gradual effects, such as warming temperatures that contribute to increased frequencies of coral bleaching events (Pratchett et al., 2013), Mo'orea's reef communities have experienced considerable disturbances within the last 15 years. These include: a corallivorous crown of thorns (COT) sea star outbreak from 2006-2010; a mass bleaching event in 2007; and cyclone Oli in 2010, which reduced coral cover and marked the end of the COT outbreak (Pratchett et al., 2011). Coral recovery post-cyclone was likely more rapid on the north shore of the island where reefs experienced the strongest impact of the cyclone, where dead coral skeletons left by the COT outbreak were cleared (Holbrook et al., 2018).

We took samples from three reef types because each experiences temperature, nutrient availability and depth differently (Figure 2.1a,b). They also occur at different distances from land (Figure 2.1b). A barrier reef punctuated by several deep passes surrounds the island, creating distinct marine habitats inshore and offshore of the reef crest. Inside the reef crest, an area commonly referred to the lagoon, fringing and back reefs occur. Fringing reefs are reefs that grow adjacent to the coastline and, although daily tidal fluctuations are nearly negligible, can become exposed during the highest high and lowest low tides of the year. A steeply sloping, deeper fore reef extends beyond the barrier reef crest. Waves break over the reef crest, flushing cooler water from the fore reef onto the back reef and into the lagoon. We measured the temperature at each sampling location during the study year using HOBO pendants (Onset, Cape Cod, MA), and estimated nitrogen concentrations around the island from LTER data derived from the carbon to nitrogen ratio of local reef macroalgae (Carlson, 2019). Microbiome sampling occurred once during the dry season (September 2017) and once in the wet season (March 2018).

Research from the last decade has shown that the microbial community of seawater inside Mo'orea's lagoons is both distinct from open ocean communities and remarkably voracious in its capability to utilize labile and semi-labile organic nutrients (Payet et al., 2014). Also, microbial diversity across all domains is different between back, fore and fringing reefs, and between inshore and offshore to 160km (Haßler et al., 2019; McCliment et al., 2012).

We took sediment, seawater and coral samples from around the West, North and East sides of Mo'orea Island (Figure 2.1a). Six of the sites corresponded with MCR LTER sites 0-6, plus an extra site on each of the East and West sides to increase geographic coverage and replication of the microbiome surveys (sites 3.5 and 5.5).



Sampling Procedure

At each site and habitat, snorkelers or SCUBA divers wore nitrile gloves and used bone cutters to snip or scrape a small quantity ("just as much as a parrotfish eats") of coral skeleton, tissue and mucus from six individuals of the island's three

most prolific genera of corals: *Pocillopora verrucosa*, *Porites lobata*, and *Acropora hyacinthus*. To monitor change in microbiomes through time, each coral individual was tagged at the first (September 2017) sampling point to ensure that each individual would be resampled at each subsequent sampling occasion. At sites on back and fringing reefs, coral individuals were chosen within a 100m² area while fore reef corals were selected along a 50m semi-permanent transect. Sampling on the west and east sides of the island occurred only within back and fringing reefs, due to logistical constraints, and *A. hyacinthus* was not sampled on fringing reefs due to its low abundance. Water samples were taken within each sampling location 1m above the benthos using two, new 750ml whirl pack bags (Sigma-Aldrich, St. Louis, MO). Sediment samples were collected from each sampling location in 2ml snap cap tubes.

Collected coral and sediment material was immediately put into 15ml falcon tubes prefilled with DNA/RNA shield (Zymo Research, Irvine, CA, USA) and garnet and ceramic beads for later “beating,” then stored with the water samples on Techni-ice (~-40°C) during transport back to GUMP field station. Upon arrival, water samples were immediately vacuum filtered through a 0.1µm polycarbonate filter which was then placed into a prepped 15ml tube filled with DNA/RNA Shield. Coral, sediment and the water sample filter were then set to vortex for twenty minutes in bead beat tubes, turning the material into a preserved slurry that was distributed into four 1200µl archival aliquots and prepared for transport to laboratories in the United States for further processing.

Extraction, Amplification, Library Preparation, Sequencing

Once received at Oregon State University or Rice University, DNA and RNA were extracted using ZymoBIOMIC DNA/RNA miniprep kits (Zymo Research, Irvine, CA, USA). Extracted material was barcoded according to Earth Microbiome Project protocols for 16S Illumina Amplicons. We amplified the V4 region of the 16S rRNA gene using 515f/806r primers (Caporaso et al., 2012; Thompson et al., 2017), cleaned the product with QIAquick PCR Purification Kit (QIAGEN, Venlo, Netherlands), and quantified produced material with a Qbit 4 Fluorometer (ThermoFisher Scientific, Waltham, MA). Sample libraries were then prepared for

sequencing with equal molar concentration and submitted to the Center for Genomic Research and Biocomputing (CGRB) at Oregon State University. There, host contamination was removed using the Blue Pippin™ DNA Size-Selection system (Sage Science, Beverly, MA). Remaining material was sequenced on the Illumina MiSeq at the CGRB with 5-10% added PhiX.

Quality control and filtering

Raw 2x250bp sequences were trimmed to 230 bp and quality filtered using dada2 using parameters: maxN=0, maxEE=2.2, trunQ=2, truncLen=230 (Callahan et al., 2016). Remaining sequences were separated into amplicon sequence variants (ASVs) using single-nucleotide differences, then taxonomically annotated using Greengenes version 13.8 (DeSantis et al., 2006). Resultant ASV and taxonomy tables were combined with sample metadata and analyzed using the R package phyloseq (McMurdie & Holmes, 2013). After removing mitochondria, chloroplasts and singletons, 209 of 707 total samples had fewer than 1000 reads; therefore, we chose to omit samples with less than 1000 reads and rarefy to the shallowest sequencing depth of one of our samples that was still greater than 1000 reads (1028 reads, set seed = 711). Downstream analyses were conducted using phyloseq, vegan (Oksanen et al., 2019) and visualized with ggplot2 (Wickham, 2009) and plotly (Sievert 2008).

Statistical Analyses

To analyze the spatial-temporal patterns of the microbiomes around the island we visualized differences using multidimensional ordination methods and tested the significant drivers of the microbiomes using permutation based statistical routines. We tested if sediment, water and coral samples had distinct microbiomes using a Permutational Analysis of Variance (PERMANOVA, permutations=999; Anderson, 2017), and then tested for the combined effect of Season, Island Side, Habitat, Sampling Location and Coral Species using pairwise comparisons adjusted with a Bonferroni correction. To uncover which taxa were driving the dissimilarity between sample types, ASVs were agglomerated by the Family taxonomic rank and a SIMPER analysis conducted. These analyses were repeated for sediment, water, all

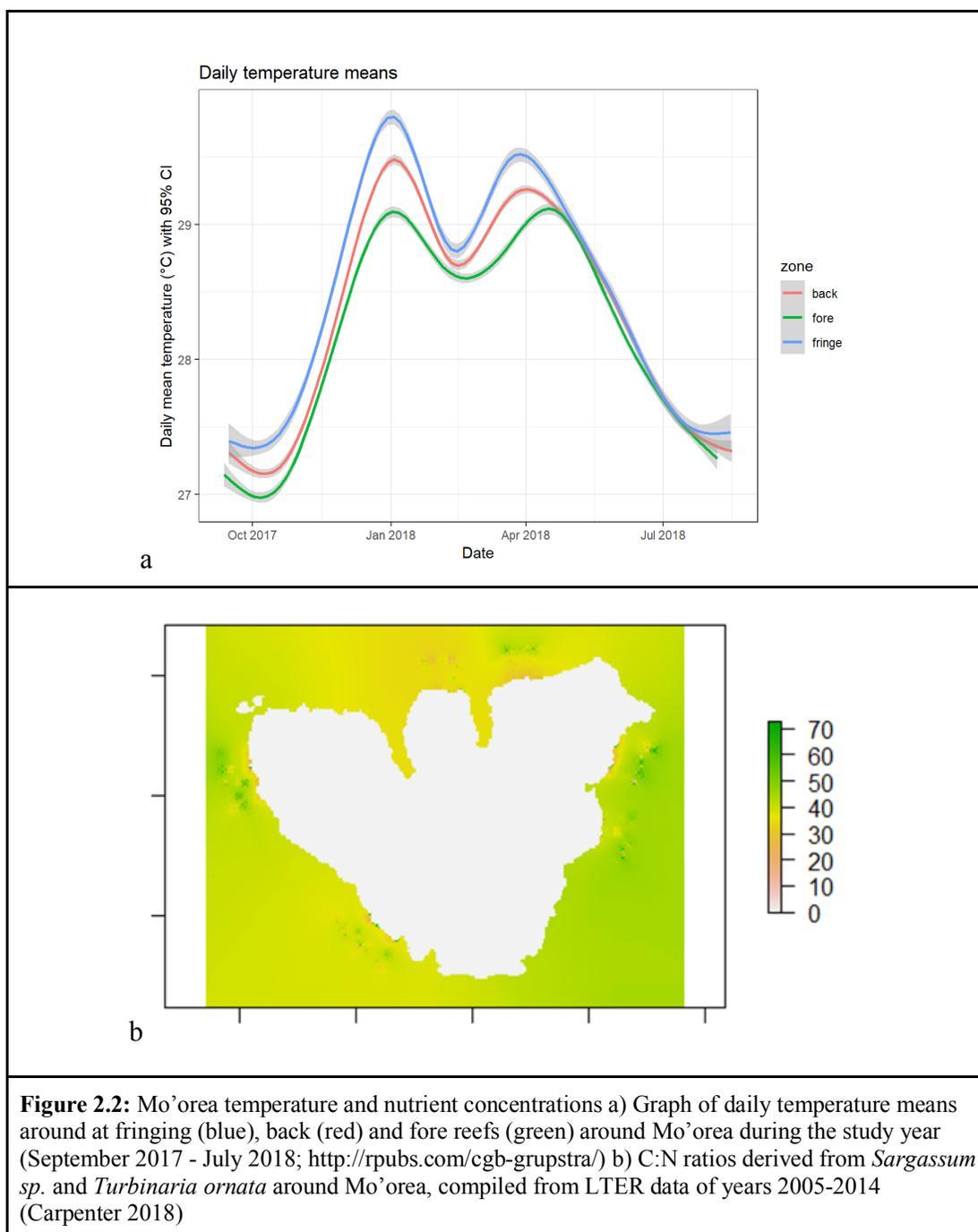
coral samples, and each coral species separately. To aid interpretations of microbial community shifts between seasons at each hosting scale and host species, we plotted the relative abundances of the top ten most relatively abundant families shared by all samples. These were then examined across habitats and seasons for each coral species.

To compare how individual coral colonies experience microbiome shifts between the seasons, we plotted repeatedly sampled individuals from each season in 2D NMDS plots and traced their position in the ordination through time from the dry (September 2017) to the wet season (March 2018). We then quantified dispersion through perm.disp, a permutation based analysis that measures whether there was a difference in the variability within these coral communities between season.

2.4 COMBINED RESULTS AND DISCUSSION

Sampling Location Data

According to temperature data collected by HOBO pendants at each sampling location during the study, and from geographically interpolated maps of C:N ratios (Carpenter 208; Weinstock ID Chapter, Oregon State University 2019), reef habitats differed in both temperature and relative nitrogen availability. Fringing reefs experienced greater daily temperature ranges sometimes greater than 2°C, while back reefs varied ~1°C and fore reefs <1°C daily (monthly averages of daily temperature ranges; Carsten Grupstra, pers. comm), and were subject to higher concentrations of nitrogen in the seawater (Figure 2.2). Over the sampling year, fringing reefs also had significantly greater mean temperatures than back and fore reefs, reaching a 31.4°C maximum temperature at site 5 Fringe in January 2018. Fore reefs temperatures, near to where sampling occurred at 10m depth, with temperatures that increased 1.2-1.3°C over the course of the year in comparison to back and fringing reefs whose temperatures ranged 2.2-3.3°C and 2.7-4.6°C, respectively. Temperature measurements on the back and fringing reefs were taken between 1-3m.



Sediment, Water and Coral Microbiomes

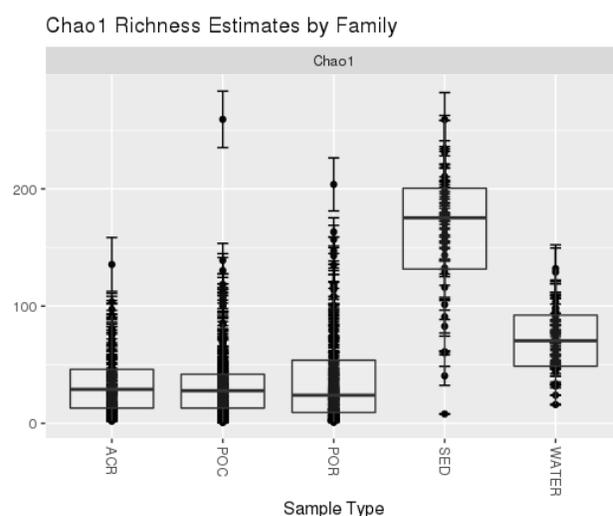
Remaining 476 quality-filtered and rarefied samples contained a total 16,996 ASVs. The bacterial and archaeal communities of water, sediment, and corals were different from each other (one-way PERMANOVA, $p=0.001$; Table 2.5; Figure 2.5) and each coral species' microbiome was significantly different than the others,

indicating host-specificity (Table 2.5; Table 2.12). Chao1 richness estimates between coral, sediment and water samples were significantly different (ANOVA $p=0.001$), as was Chao1 richness in microbiomes of each coral species (ANOVA $p=0.005$). All coral microbiomes had lower richness than sediment and water samples (Table 3, Figure 2.3).

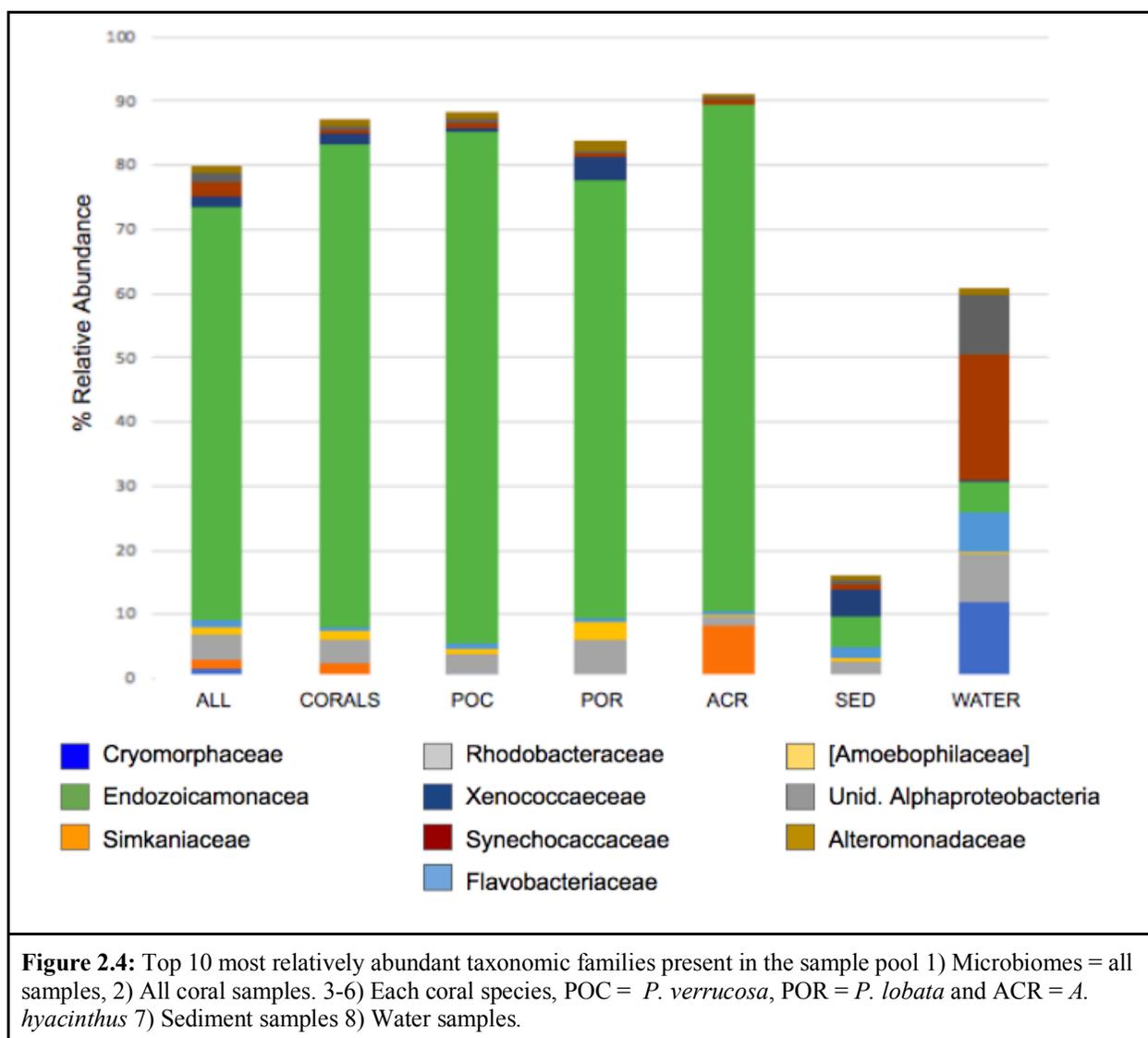
Table 2.3: Quantities of samples remaining post quality filtering, by factor					
Season	n	Island Side	n	Habitat	n=
Wet	213	W	184	Fore	98
Dry	263	N	239	Back	280
		E	53	Fringing	148
Sampling Location	n=		n=		n=
0Fore	20	2Back	27	4Fringe	4
0Back	34	2Fringe	20	5Back	32
0Fring	21	3Back	15	5Fringe	23
1Fore	33	3Fringe	7	5.5Back	28
1Back	23	3.5Back	9	5.5Fringe	29
1Fring	16	3.5Fringe	10	6Back	54
2Fore	45	4Back	8	6Fringe	28

Table 2.4, Figure 2.3: Chao1 richness estimate distributions by Sample Type. Green= skewed left, Red= skewed right. Estimates made from samples rarefied to 1028 total sequences. ACR = *A. hyacinthus*, POC = *P. verrucosa*, POR = *P. lobata*, SED = sediment.

Sample Type	n =	Min	Median	Mean	Max
ACR	87	2	29.00	34.17	135.50
POC	162	1	27.85	34.92	259.29
POR	154	1	24.00	37.95	203.80
All Corals	403	1	40.50	86.28	259.29
SED	36	8	175.3	161.4	259.1
Water	37	16	70.43	70.21	132.00
All	476	1	32.21	48.08	259.1



We found that although microbiomes were specific to each type of reef sample, each sample type shared similar taxa, which is consistent with research that has found shared taxa between coexisting microbiomes (Ainsworth et al., 2015; Hernandez-Agreda et al., 2018). Of 508 total Families, 16% of sequences in sediment samples, 61% in water and 87% in coral microbiomes included just ten bacterial Families (Figure 2.4). The top ten most relatively most abundant taxa were Endozoicamonaceae (64.3%), Rhodobacteraceae (3.86%), Synecococcaceae (2.17%), Xenococcaceae (1.70%), Simkaniaceae (1.46%), Cryomorpaceae (1.46%), Flavobacteriaceae (1.24%), [Amoebophilaceae] (1.23%), Alteromonadaceae (1.16%), and an unidentified Alphaproteobacteria (1.21%). This means that the remaining microbiome, occupying less than 13% of the total microbiome composition in the case of corals, accounted for 98% of the total family richness. Brief descriptions of each can be found in Table 2.14 after the discussion of microbiomes in each coral species.



Sediment, water and coral microbiomes were significantly different (PERMANOVA; $p=0.001$, Table 2.5), and coral microbiomes were further distinguished by host species (PERMANOVA; $p=0.001$; Table 5; Figures 2.5 & 2.6). Pairwise comparisons between water, sediment and coral samples were also significant ($p=0.003$, Table 2.5). Microbiomes of all sample types, considered together, were not affected by season at any spatial scale ($p=0.113$ - $.950$, Table 2.5), although spatial scales such as side of the island, sampling location and sample type were significant ($p=0.001$, 0.001 and 0.002 , respectively, Table 2.5). Furthermore, microbiomes of each sample type had an interactive effect with Habitat ($p=0.001$,

Table 2.5), indicating that they were each responding differently to the factor. As these two factors cannot be separated we will treat each species independently from this point forward. This also provides an indication of niche specificity where microbiomes of the same host-type are at once variable and similar within host-types, and also vary between habitats with distinct conditions.

When evaluating the overall spatial structure of the microbiomes (i.e. not separating species nor type) on the north side of the island were different from both the east and the west sides ($p=0.015$ and 0.003 , respectively; Table 2.5), which were similar to each other ($p=0.159$; Table 2.5). Fringing reef microbiomes were different than both back and fore reef microbiomes, which were also significantly different from one another. Pairwise comparisons of sampling locations (i.e. specific site within a habitat on an island side), did not result in any significant differences even though this factor was significant in the model (Supplementary Table 1); this is likely due to limited power within site compounded by the highly conservative nature of the Bonferroni correction applied. Overall, this suggests that with increased per site replication or application of a less conservative correction for multiple comparisons that we may be able to better resolve total reef microbiome spatial variability to the level of local reefscape. Regardless, reef microbiomes within fringing reefs on the north side are distinct from other habitats and from fringing reefs on other sides of the island. However, sites within that same north fringing reef are not currently distinguishable at a microbial level.

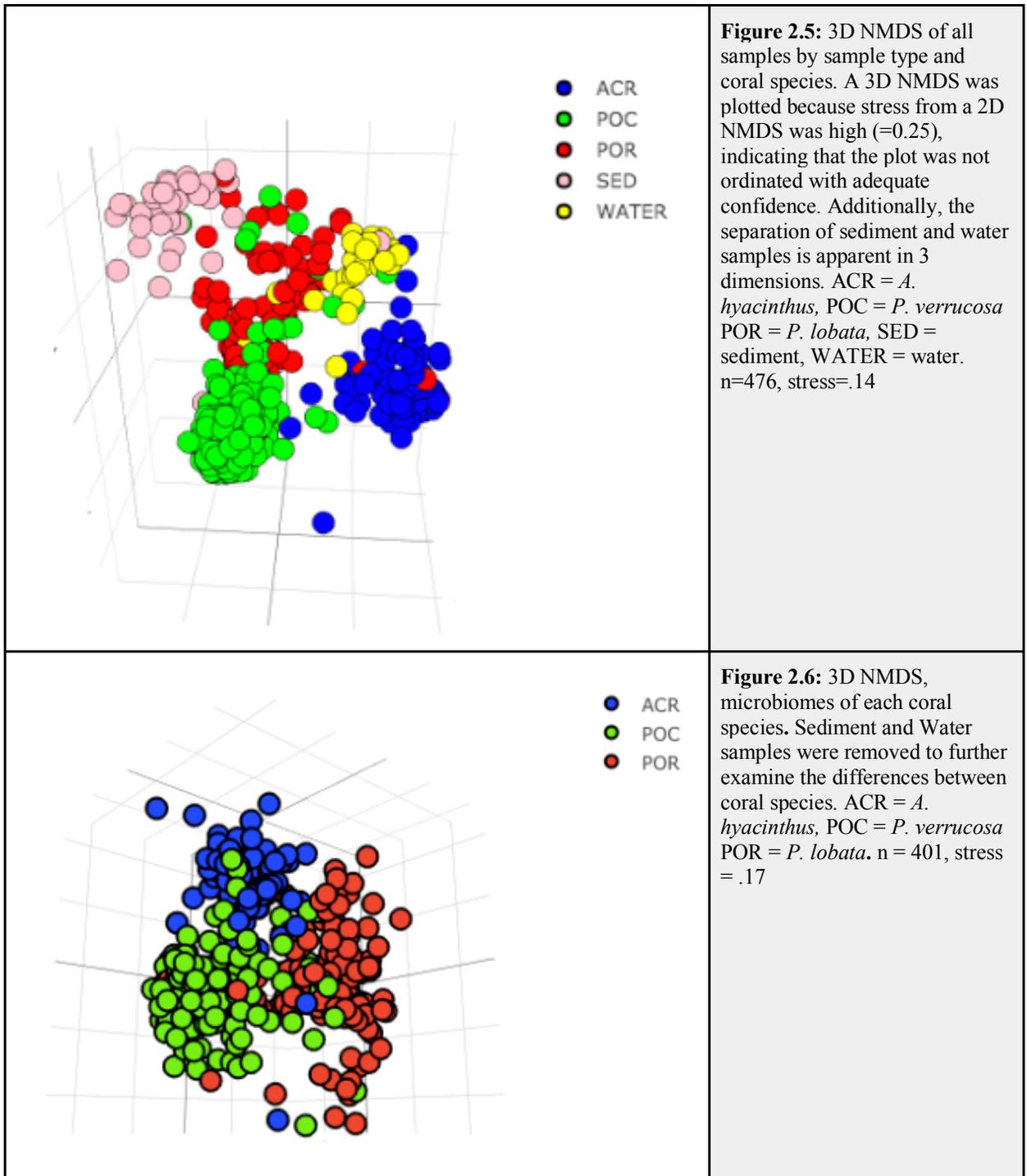


Table 2.5 PERMANOVA of microbiomes by Season, Island Side, Habitat, Sampling Location and Sample Type							
PERMANOVA of microbiomes by Season, Island Side, Habitat, Sampling Location and Sample Type based on ASVs rarified to 1028 sequence per sample.							
		Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
SEASON		1	0.621	0.6210	1.8059	0.00329	0.088
ISLAND SIDE		2	2.658	1.3289	3.8645	0.01409	0.001 *
HABITAT		2	6.408	3.2038	9.3167	0.03398	0.001 *
SAMPLING LOCATION		18	8.549	0.4750	1.3812	0.04533	0.002 *
SAMPLE TYPE		2	18.702	9.3508	27.1927	0.09917	0.001 *
SEASON:ISLAND SIDE		2	0.368	0.1841	0.5354	0.00195	0.951
SEASON:HABITAT		2	0.603	0.3013	0.8762	0.00320	0.549
SEASON:SAMPLING LOCATION		17	4.697	0.2763	0.8035	0.02491	0.950
SEASON:SAMPLE TYPE		2	0.842	0.4209	1.2240	0.00446	0.233
ISLAND SIDE:SAMPLE TYPE		4	1.873	0.4682	1.3615	0.00993	0.113
HABITAT:SAMPLE_TYPE		4	3.246	0.8114	2.3596	0.01721	0.001 *
SAMPLING LOCATION:SAMPLE TYPE		30	8.549	0.2850	0.8287	0.04533	0.984
SEASON:ISLAND SIDE:SAMPLE TYPE		4	0.936	0.2340	0.6806	0.00496	0.917
SEASON:HABITAT:SAMPLE TYPE		4	1.067	0.2668	0.7758	0.00566	0.808
SEASON:SAMPLINGLOCATION:SAMPLETYPE		17	4.292	0.2525	0.7342	0.02276	0.993
Sample Type, One-Way ANOVA							
		Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
SAMPLE_TYPE		2	19.581	9.7903	27.401	0.10383	0.001 ***
Island Sides, Post hoc comparisons							
	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted sig
1	W vs N	1	1.7456369	4.461625	0.010486552	0.001	0.003 *
2	W vs E	1	0.8667464	2.289702	0.009649396	0.053	0.159
3	N vs E	1	1.1533098	2.831992	0.009671046	0.005	0.015 *
Habitat, Post hoc comparisons							
	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted sig
1	BAK vs FRG	1	4.242262	10.969818	0.028347994	0.001	0.003 *
2	BAK vs FOR	1	1.159467	2.959477	0.008996478	0.011	0.033 *
3	FRG vs FOR	1	4.973133	13.400339	0.052060300	0.001	0.003 *
Sampling Location, Post hoc comparisons							
See Supplementary Table 1							
Sample Type, Post hoc comparisons							
	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted sig
1	CORAL vs WATER	1	12.387689	34.84757	0.07369725	0.001	0.003 *
2	CORAL vs SEDIMENT	1	7.615093	20.62699	0.04507382	0.001	0.003 *
3	WATER vs SEDIMENT	1	7.215619	24.43912	0.25607026	0.001	0.003 *

Distinguishing taxa in microbiomes of each reef type

A SIMPER analysis was conducted between sample types in order to identify which taxonomic families were driving sample dissimilarity. Some of the taxa that distinguished sediment, water and coral microbiomes from each other were part of the list of top 10 most abundant families, while others were not. All proceeding values refer to the cumulative sum of their contribution to dissimilarity (cumsum) unless otherwise noted.

The Families that contributed most to the difference between corals and other sample types were Endozoicamonas (coral vs. water= .40; coral vs. sediment =.40; Table 2.6) while the cyanobacterial family Synechocaccaceae was the leading distinguishing Family between water and coral microbiomes (.12; Table 2.6). Endozoicamonas was still a top contributor to water and sediment sample dissimilarity (.29; Table 2.6), behind Synechocaccaceae.

Other contributors to Water-Sediment dissimilarity were driven by Crymorphaceae (cumsum=.18; Table 2.6), an unidentified Alphaproteobacteria (.24), Endozoicamonaceae (.29), Halomonadaceae (.33; a putative coral symbiont observed to diminish in white band disease infected corals; Certner & Vollmer, 2018), Pirellulaceae (.37; commonly found in deep sea corals, hypothesized core coral microbiome member; Kellogg, 2019; Lawler et al., 2016; Glasl et al. 2016), Pelagibacteraceae (.41; found in fresh coral mucus and associated with low temperatures in coral reef ecosystems; Glasl et al., 2016, 2019), Rhodobacteraceae (.44), Rhodospirillaceae (.48) and Flavobacteriaceae (.50; Table 2.6).

Besides Endozoicamonaceae (cumsum = .40), Cyanobacteria of the family Synechocaccaceae were also outstanding contributors to Coral-Water dissimilarity (.51), along with Crymorphaceae (.58), an unidentified Alphaproteobacteria (.63), Rhodobacteraceae (.67), Halomonadaceae (.71), Pelagibacteraceae (.75), Flavobacteriaceae (.78), OC155 (.79; Phylum Actinobacteria; Class Acidimicrobiia), and an unidentified Proteobacteria (.81; Order Oceanospirales; Table 2.6).

Other distinguishing families of Coral-Sediment microbiomes included Pirellulaceae (.45), Rhodospirillaceae (.53), Xenococcaceae (.51), Piscirickettsiaceae (.53; a known fish pathogen, also associated with early life stages of corals and

increased abundance during inter-tidal exposure events; Bernasconi et al., 2019, Sweet et al., 2017), Rhodobacteraceae (.56), Desulfobacteraceae (.58; a proposed sulfur-reducing bacteria, Yang et al., 2019), an unidentified Gammaproteobacteria (.61; Order Chromatiales), and Ectothiorhodospiraceae (.62; a free-living sulfur-oxidizing Alphaproteobacteria commonly found in coral reef sponges; Gauthier et al., 2016; Table 2.6).

Table 2.6: SIMPER analyses between each sample type. Bolded names are also one of the ten most abundant taxa found.					
Coral vs. Water		Coral vs Sediment		Water vs. Sediment	
Family	cumsum	Familiy	cumsum	Family	cumsum
Endozoicamonaceae	0.4038	Endozoicamonaceae	0.4057	Synechocaccaceae	0.1152
Synechocaccaceae	0.5121	Pirellulaceae	0.4455	Crymorphaceae	0.1837
Crymorphaceae	0.5776	Rhodospirillaceae	0.479	unidentified Alphaproteobacteria	0.2352
unidentified Alphaproteobacteria	0.628	Xenococcaceae	0.5072	Endozoicamonaceae	0.2857
Rhodobacteraceae	0.672	Piscirickettsiaceae	0.5325	Halomonadaceae	0.3294
Halomonadaceae	0.7139	Rhodobacteraceae	0.5569	Pirellulaceae	0.3711
Pelagibacteraceae	0.7497	Desulfobacteraceae	0.5802	Pelagibacteraceae	0.4088
Flavobacteriaceae	0.78	Unidentified Gammaproteobacteria; o_Chromatiales	0.601	Rhodobacteraceae	0.4431
OCS155; p_Actinobacteria; c_Acidimicrobiia	0.7943	Ectothiorhodospiraceae (Alphaproteobacteria)	0.6177	Rhodospirillaceae	0.4753
unidentified Proteobacteria; o_Oceanospirales	0.807	unidentified Acidobacteria ; c_Sva075; o_Sva0725	0.6329	Flavobacteriaceae	0.5017

Beta Diversity: Sediment Samples

At the level of ASV, sediment microbiomes were highly spatially variable, displaying distinct microbiomes across all tested spatial scales: Island Side, Habitat and Sampling Location ($p=0.001-0.002$, Table 2.7). Season was also a significant factor ($p=0.026$, Table 2.7) and sediment samples at all spatial scales interacted with season ($p=0.006-0.014$, Table 2.7). This provided indication that the microbial reefscape is affected by season, but seasonality is experienced by microbiomes of different hosts differently at varying spatial scales. In post hoc comparisons, microbiomes of sediment samples were specific to each reef habitat ($p=0.003-0.006$, Table 2.6), providing additional evidence for microbiome niche specificity. Pairwise comparisons between sampling locations were not significantly different ($p=1.000$), but only one sediment sample per sampling location per time point was collected.

TABLE 2.7 PERMANOVA of sediment microbiomes by Season, Island Side, Habitat, and Sampling Location						
PERMANOVA of sediment microbiomes by Season, Island Side, Habitat, and Sampling Location based on ASVs rarified to 1028 sequence per sample.						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
SEASON	1	0.3502	0.35024	1.6056	0.02634	0.026 *
ISLAND SIDE	2	0.8626	0.43128	1.9771	0.06487	0.002 *
HABITAT	2	1.2377	0.61884	2.8370	0.09308	0.001 *
SAMPLING LOCATION	15	5.8450	0.38967	1.7864	0.43958	0.001 *
SEASON:ISLAND SIDE	2	0.7618	0.38091	1.7462	0.05729	0.006 *
SEASON:HABITAT	2	0.6806	0.34032	1.5601	0.05119	0.014 *
SEASON:SAMPLOC	10	3.3407	0.33407	1.5315	0.25124	0.009 *
Residuals	1	0.2181	0.21813		0.01641	
Total	35	13.2968			1.00000	
Island Side, Post hoc comparisons						
pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted sig
1 W vs N	1	0.4528885	1.202198	0.04419489	0.064	0.192
2 W vs E	1	0.4259007	1.169453	0.05798139	0.098	0.294
3 N vs E	1	0.4035303	1.038203	0.04710922	0.334	1.000
Habitat, Post hoc comparisons						
1 BAK vs FRG	1	0.6029000	1.627380	0.05145479	0.001	0.003 *
2 BAK vs FOR	1	0.7458163	2.271218	0.10677424	0.002	0.006 *
3 FRG vs FOR	1	0.6858111	1.773381	0.09446252	0.002	0.006 *
Sampling Location, Post hoc comparisons						
See supplementary Table 2						

Beta Diversity: Water Samples

At the ASV level within water samples, season, island side, and habitat resulted in distinct inshore microbiomes (PERMANOVA $p=0.001-0.017$, Table 2.7). There was no seasonal effect interacting with any spatial scale ($p=0.182-0.623$, Table 2.7), providing an indication that microbiomes in the water column do not experience the seasons differently at different spatial scales. Only one water sample per sampling location was collected during each season, so we do not have the power to identify site differences given the low replication.

Notably, the microbial community in seawater at fringing reefs habitats were different than back and fore reefs ($p=0.003, 0.024$, Table 2.7) while back and fore reefs were not different from each other ($p=0.642$, Table 2.7). Since fringing reefs line the coastline of the island, these patterns might be explained by fringing reefs' proximity to the island, which, in the case of Mo'orea, is impacted by human presence and activity.

Because tests of temporal and spatial variation on coral microbiomes dissimilarity resulted in a suite of interacting factors, driven in part because *A. hyacinthus* was not sampled on fringing reefs, we will consider *P. verrucosa*, *P. lobata* and *A. hyacinthus* separately in the next sections. Also, further analyses involving coral microbiomes used ASVs that were agglomerated by Family. This was done to provide more insight into the identity of microbes since many ASVs were not annotated beyond the Family level.

TABLE 2.8 PERMANOVA of water microbiomes by Season, Island Side, Habitat, and Sampling Location							
PERMANOVA of water microbiomes by Season, Island Side, Habitat, and Sampling Location based on ASVs rarified to 1028 sequence per sample.							
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)	
SEASON	1	0.5632	0.56324	4.1454	0.07347	0.007 *	
ISLAND SIDE	2	0.7858	0.39288	2.8916	0.10250	0.017 *	
HABITAT	2	1.5321	0.76606	5.6382	0.19986	0.001 *	
SAMPLING LOCATION	15	2.5928	0.17285	1.2722	0.33822	0.234	
SEASON:ISLAND_SIDE	2	0.2614	0.13069	0.9619	0.03410	0.504	
SEASON:HABITAT	2	0.4086	0.20431	1.5037	0.05330	0.182	
SEASON:SAMPLOC	8	0.9785	0.12232	0.9002	0.12765	0.623	
Residuals	4	0.5435	0.13587		0.07090		
Total	36	7.6659			1.00000		
Island Side, Post hoc comparisons							
pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1 W vs N	1	0.4088166	1.892832	0.06786088	0.044	0.132	
2 W vs E	1	0.3670785	2.070811	0.09827866	0.091	0.273	
3 N vs E	1	0.3865353	1.855823	0.07466351	0.057	0.171	
Habitat, Post hoc comparisons							
pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1 BAK vs FRG	1	1.4919435	9.232247	0.2353229	0.001	0.003	*
2 BAK vs FOR	1	0.2279439	1.239797	0.0644392	0.214	0.642	
3 FRG vs FOR	1	0.5640972	3.068711	0.1330248	0.008	0.024	*
Sampling Location, Post hoc comparisons							
See Supplementary Table 3							

Beta Diversity: *Pocillopora verrucosa*

At the Family level, *P. verrucosa* microbiomes were distinguished by habitat (PERMANOVA $p=0.001$; Table 2.9), though not every habitat housed distinct *P. verrucosa* microbiomes: Fringing reefs were significantly different than back and fore reefs ($p=0.03$, 0.033 ; Table 2.9) while back and fore reefs were not different ($p=0.177$; Table 2.9). Season did not impact the microbiome of *P. verrucosa* (PERMANOVA $p=0.384$, Pairwise $p=0.43$; Table 2.9), this could mean that this coral's microbiome is able to maintain relative stability at the level of taxonomic family. There were no differences between the microbiome of *P. verrucosa* across the

different sides of the island ($p=0.201-0.819$; Table 2.9) nor sampling location (Supplementary Table 2.4).

TABLE 2.9 PERMANOVA of <i>Pocillopora verrucosa</i> microbiomes by Season, Island Side, Habitat and Sampling Location						
PERMANOVA of <i>Pocillopora verrucosa</i> microbiomes by Season, Island Side, Habitat, and Sampling Location based on ASVs rarified to 1028 sequence per sample.						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr (>F)
SEASON	1	0.1617	0.16166	1.0143	0.00569	0.384
ISLAND_SIDE	2	0.5447	0.27233	1.7087	0.01917	0.056
HABITAT	2	1.4549	0.72746	4.5644	0.05122	0.001 *
SAMPLING_LOCATION	18	4.4284	0.24602	1.5437	0.15590	0.005 *
SEASON:ISLAND_SIDE	2	0.2649	0.13245	0.8311	0.00933	0.610
SEASON:HABITAT	2	0.3099	0.15497	0.9724	0.01091	0.471
SEASON:SAMPLOC	13	1.9570	0.15054	0.9446	0.06889	0.563
Residuals	121	19.2846	0.15938		0.67889	
Total	161	28.4062			1.00000	
Island Side, Post Hoc comparisons						
pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted sig
1 W vs N	1	0.2942301	1.617145	0.01118225	0.114	0.342
2 W vs E	1	0.1707693	1.173426	0.01427987	0.273	0.819
3 N vs E	1	0.3586738	1.885686	0.01966598	0.067	0.201
Habitat, Post Hoc comparisons						
pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted sig
1 BAK vs FRG	1	0.9725469	5.435474	0.04265276	0.001	0.003 *
2 BAK vs FOR	1	0.2626399	1.876351	0.01707694	0.059	0.177
3 FRG vs FOR	1	0.6187739	3.141483	0.03446820	0.011	0.033 *
Sampling Location, Post Hoc comparisons						
See Supplementary Table 4						

Beta Diversity: Porites lobata

Porites lobata microbiomes differed by season, island side, habitat and sampling location ($p=0.001-0.007$; Table 2.10). Interestingly, there was no interacting effect of season with spatial scales ($p=0.163-0.710$). North side *P. lobata* microbiomes were more different than East and West sides ($p=0.003$), which were not different from each other ($p=0.618$). Differences between fringing and back reefs were not significant ($p=0.153$) while fore reefs were distinct from both back and

fringing reefs ($p= 0.003$). Positive results that *P. lobata* microbiomes are significantly different across at every tested spatial scale provides evidence for a *P. lobata* microbiome that is adaptable to specific habitats and environmental conditions. Studies observed that this mounding coral exhibits high resilience to bleaching due in part to its ability to utilize dissolved organic carbon during recovery (Levas et al., 2013; Ziegler et al., 2019). Since Endozoicomonaceae is a heterotroph and the dominant member of *P. lobata*'s microbiome perhaps a key aspect of this site-specific difference is a metabolic specificity to the carbon sources available at each of the site facilitated by the microbiome flexibility.

TABLE 2.10 PERMANOVA of <i>Porites lobata</i> microbiomes by Season, Island Side, Habitat, and sampling location						
PERMANOVA of <i>Porites lobata</i> microbiomes by Season, Island Side, Habitat, and sampling location based on ASVs rarified to 1028 sequence per sample.						
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
SEASON	1	0.710	0.70967	3.5121	0.01807	0.004 *
ISLAND SIDE	2	5.376	2.68799	13.3027	0.13686	0.001 *
HABITAT	2	1.763	0.88137	4.3618	0.04488	0.001 *
SAMPLING LOCATION	17	5.022	0.29540	1.4619	0.12784	0.007 *
SEASON:ISLAND_SIDE	2	0.297	0.14833	0.7341	0.00755	0.710
SEASON:HABITAT	2	0.536	0.26776	1.3251	0.01363	0.163
SEASON:SAMPLOC	14	2.745	0.19609	0.9705	0.06989	0.546
Residuals	113	22.833	0.20206		0.58128	
Total	153	39.281			1.00000	
Island Side, Post hoc comparisons						
pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted sig
1 W vs N	1	4.67114680	19.426429	0.12418892	0.001	0.003 *
2 W vs E	1	0.08907534	1.173935	0.01626536	0.206	0.618
3 N vs E	1	2.03560272	6.558067	0.06521672	0.001	0.003 *
Habitat, Post hoc comparisons						
pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted sig
1 FRG vs BAK	1	0.4879136	2.334644	0.01833471	0.051	0.153
2 FRG vs FOR	1	3.5460470	15.611831	0.14923580	0.001	0.003 *
3 BAK vs FOR	1	2.4986046	9.046017	0.09321369	0.001	0.003 *
Sampling Location, Post hoc comparisons						
See Supplementary Table 5						

Beta Diversity: Acropora hyacinthus

Unlike, *P. lobata*, island side, reef habitat, and sample location contributed to the differences within the microbiome composition of *A. hyacinthus* ($p=0.001-0.002$; Table 2.11); season did not have an effect ($p=0.231$; Table 2.11) or interactive effect with any spatial scale tested (Table 2.11). The west side of the island housed distinct *A. hyacinthus* microbiomes ($p=0.012, .048$), while the East and North sides of the Island were not significantly different from each other ($p=0.261$). Back reefs microbiomes were significantly different from Fore reef microbiomes ($p=0.005$) and *A. hyacinthus* was not sampled on the fringe reefs.

TABLE 2.11 PERMANOVA of <i>Acropora hyacinthus</i> microbiomes by Season, Island Side, Habitat, and Sampling Location								
PERMANOVA of <i>Acropora hyacinthus</i> microbiomes by Season, Island Side, Habitat, and Sampling Location based on ASVs rarified to 1028 sequence per sample.								
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)		
SEASON	1	0.1442	0.14421	1.3258	0.01087	0.231		
ISLAND SIDE	2	0.9976	0.49880	4.5856	0.07519	0.001 *		
HABITAT	1	1.7615	1.76154	16.1940	0.13277	0.001 *		
SAMPLING LOCATION	7	1.6978	0.24254	2.2297	0.12796	0.002 *		
SEASON:ISLAND SIDE	2	0.4875	0.24373	2.2406	0.03674	0.057		
SEASON:HABITAT	1	0.0964	0.09641	0.8863	0.00727	0.448		
SEASON:SAMPLOC	6	0.9034	0.15057	1.3842	0.06809	0.135		
Island Side, Post hoc comparisons								
	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1	W vs N	1	0.6245953	4.426576	0.05181732	0.004	0.012	*
2	W vs E	1	0.4362087	3.982867	0.09718371	0.016	0.048	*
3	N vs E	1	0.3446147	1.902032	0.03664658	0.087	0.261	
Habitat, Post hoc comparisons								
	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1	BAK vs FOR	1	0.5835476	3.910513	0.04398258	0.005	0.005	*
Sampling Location, Post hoc comparisons								
See supplementary Table 6								

Beta diversity: All three coral species

To identify how the species of corals (in contrast to all samples discussed in above) we compared and contrasted the microbiomes of the three species. The microbiomes of all three coral species were distinguishable by season, island side, habitat and species ($p=0.001-0.01$; Table 2.12). In contrast to sediment samples, and in likeness to water samples, the microbiomes of coral did not have an interactive effect of season with each spatial scale ($p=0.109-0.321$; Table 2.12). However, coral host species did interact with season, island side, habitat and sampling location ($p=0.001-0.02$; Table 2.12), indicating that the microbiomes of specific hosts may be capable of fine-scale habitat specificity. The north side of the island again distinguished itself from the west and east ($p=0.003, 0.006$ respectively; Table 2.12), which were again similar to each other ($p=0.777$; Table 2.12). Fringing, back and fore reefs also housed distinct coral microbiomes ($p=0.003-0.03$; Table 2.12). Pairwise comparisons between all three species were also significant ($p=0.003$; Table 2.12) which further support host-specificity as a characteristic of these coral microbiomes.

Endozoicomonas was dominant in all three species of coral, representing 80% of sequences found in *P. verrucosa*. Since the next greatest family, Rhodobacteraceae, was only 3% relatively abundant, this means that the 20% sequences in *P. verrucosa* that were not Endozoicomonas were made up of Families that had $\leq 3\%$ relative abundance. Alteromonadaceae was the next least abundant family (1.05%), followed by Flavobacteraceae (0.86%). Similar trends emerged in *P. lobata* and *A. hyacinthus*, wherein Endozoicomonaceae represented 68% and 79% relative abundance in each coral species, respectively. In *P. lobata*, the next less relatively abundant Families after Endozoicomonaceae were Rhodobacteraceae (6%), Xenococaceae (4%) and [Amoebopillaceae] (2.6%). Simkaniaceae (8%), and Rhodobacteraceae (6%), and Xenococaceae (4.1%) followed Endozoicomonaceae in relative abundance in *A. hyacinthus*. After these, the relative abundance of subsequent Families in all three species of coral quickly drops to 1% or less.

Coral microbiome composition dissimilarity.

Endozoicomonaceae in *P. verrucosa*, *P. lobata* and *A. hyacinthus* formed a significant proportion of the microbiome (respectively 80%, 68% and 79%) relative

TABLE 2.12 PERMANOVA of *Acropora hyacinthus* microbiomes by Season, Island Side, Habitat, and Sampling LocationPERMANOVA of *Acropora hyacinthus* microbiomes by Season, Island Side, Habitat, and sampling location based on ASVs rarified to 1028 sequence per sample.

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
SEASON	1	0.542	0.5419	3.298	0.00366	0.010 *
ISLAND SIDE	2	2.798	1.3992	8.515	0.01890	0.001 *
HABITAT	2	6.977	3.4887	21.230	0.04713	0.001 *
SAMPLING LOCATION	18	7.887	0.4382	2.667	0.05328	0.001 *
SPECIES	2	59.696	29.8479	181.641	0.40325	0.001 *
SEASON:ISLAND_SIDE	2	0.366	0.1828	1.113	0.00247	0.312
SEASON:HABITAT	2	0.456	0.2281	1.388	0.00308	0.168
SEASON:SAMPLING_LOCATION	16	3.155	0.1972	1.200	0.02131	0.109
SEASON:SPECIES	2	0.730	0.3652	2.222	0.00493	0.026 *
ISLAND_SIDE:SPECIES	4	4.784	1.1960	7.278	0.03232	0.001 *
HABITAT:SPECIES	3	2.076	0.6921	4.212	0.01403	0.001 *
SAMPLING_LOCATION:SPECIES	24	5.242	0.2184	1.329	0.03541	0.010 *
SEASON:ISLAND_SIDE:SPECIES	4	0.562	0.1406	0.856	0.00380	0.630
SEASON:HABITAT:SPECIES	3	0.553	0.1845	1.123	0.00374	0.332
SEASON:SAMPLOC:SPECIES	17	2.913	0.1713	1.043	0.01968	0.347
Residuals	300	49.297	0.1643		0.33301	
Total	402	148.035			1.00000	

Island Side, Post hoc comparisons

pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1 W vs N	1	2.0352481	5.567709	0.01502481	0.001	0.003	*
2 W vs E	1	0.4242438	1.264591	0.00650963	0.259	0.777	
3 N vs E	1	1.2950533	3.398664	0.01384956	0.002	0.006	*

Habitat, Post hoc comparisons

pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1 BAK vs FRG	1	4.669462	13.318794	0.04094075	0.001	0.003	*
2 BAK vs FOR	1	1.243060	3.394285	0.01176960	0.011	0.033	*
3 FRG vs FOR	1	5.802322	17.485509	0.07930457	0.001	0.003	*

Sampling Location, Post hoc comparisons

See Supplementary Table 7

Coral Species, Post hoc comparisons

pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1 POC vs POR	1	36.35174	168.6360	0.3494062	0.001	0.003	*
2 POC vs ACR	1	34.26202	203.0700	0.4511965	0.001	0.003	*
3 POR vs ACR	1	29.10847	132.3908	0.3564731	0.001	0.003	*

to other taxa and were almost equal in proportion of the coral microbiome across reef habitats (74.7-75.6%, less than one percent difference). Endozoicamonaceae has been described as part of the stable coral microbiome in other systems (Hernandez-Agreda et al., 2018; Pollock et al., 2018) making it intriguing that Endozoicamonaceae was simultaneously the top contributor to microbiome dissimilarity between seasons (SIMPER cumsum=.42; Supplementary Table 2.8), island side (cumsum = .42-.44, Supplementary Table 2.9), habitat (cumsum= .42-.44, Supplementary Table 2.10) and coral species (cumsum= .42-.43, Supplementary Table 2.11). The six preceding distinguishing families in comparisons of each island side were of the same identity, in order with cumsum values reported: Rhodobacteraceae (.48-.52), Simkaniaceae (.52-.53), Xenococcaceae (.57-.61) [Amaeophilaceae, Genus SGUS912](.60), and Alteromonadaceae (Genus Alteromonas, .62-.66).

Temporal and Spatial variation in coral microbiomes

Endozoicamonas dominance was constant in all corals across habitats but does show signs of host-specific shifts. For example, it decreased from 86% - 75% relative abundance with proximity to shore in *P. verrucosa*, increased from 45% to 75% in *P. lobata* individuals (higher relative proportion at fringing reefs), and decreased from 93% to 73% between the Fore and Back reefs in *A. hyacinthus*. While season was a significant factor for *P. lobata*, Endozoicamonaceae was the taxa that most separated the seasonal microbiome in each coral species (SIMPER, Table 2.13).

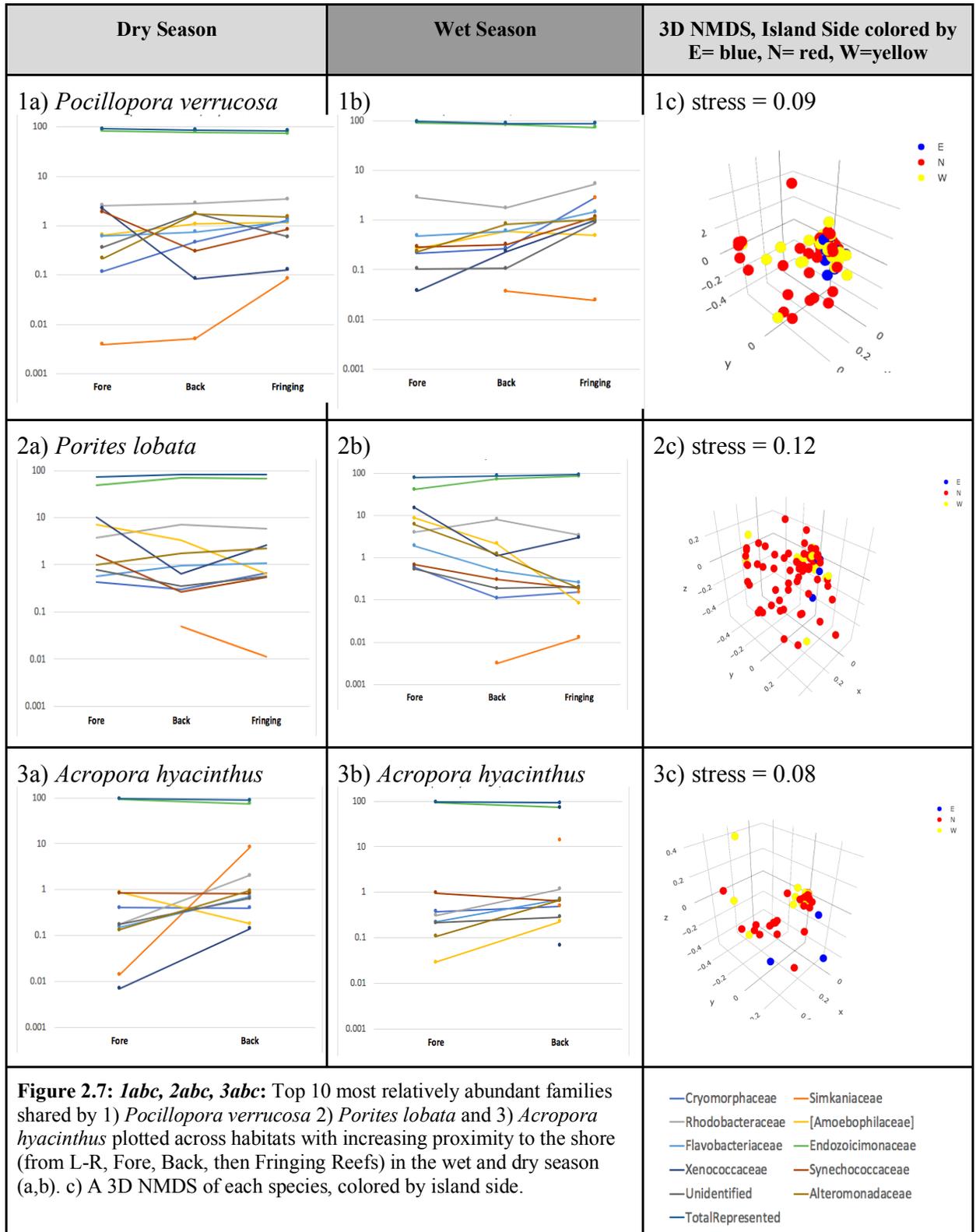
Host species and habitat were distinguishing factors between coral microbiomes (Table 2.12) and the microbiomes of each species show different patterns of increasing or decreasing relative abundances of prominent families across reefscapes (Figure 7, Supplementary Figure 2.1). More stark shifts in the relative abundances across fore, back and fringing reef habitats were visible when plotted on a log scale, and differences in relative abundances in coral microbiomes between the dry and wet season are different for each coral in each habitat, although these differences are not significant (Figure 2.8). Except for *P. lobata*, the total representation of the ten most abundant families decreases towards shore in both

summer and winter (*P. verrucosa*: 92.3-83.9% dry season, 95.5-88.0% wet season, fore to fringing reefs; *A. hyacinthus*: 95.9-88.0% dry season, 95.1-91.0% wet season, fore to back reefs). The most represented families in *P. lobata*, in comparison, increased from 73.8% to 82.0% in the dry season (fore to fringing reefs) and from 77.8-91.3% in the wet season.

Besides Endozoicomonaceae, Simkaniaceae was one of the most relatively abundant taxa but showed different temporal and spatial patterns in each coral. This family (Order Chlamydiales), is not well described in corals although it is often found in their microbiomes (Table 2.14). In Mo'orea, Simkaniaceae increased with proximity to shore in *P. lobata* and *A. hyacinthus*, which is contrary to findings from Ziegler et al. (2019), who observed the opposite trend in Red Sea Corals, especially in the presence of pollution. Simkaniaceae did increase in abundance in *P. lobata* from fringing to back reefs before disappearing from fore reef corals (i.e. it was no longer one of the ten most abundant families).

There appeared to be a significant role of Simkaniaceae and Rhodobacteraceae in separating the coral species' microbiomes from each other. Although the literature cites Simkaniaceae as taxa that decrease in abundance near to pollution, and Rhodobacteraceae as one that increases, our data has the opposite trend if we are considering fringing reefs as habitats with elevated nutrients in comparison to other habitats (Table 2.14). Further adding to this perplexing trend, ASVs within the nitrogen-fixing cyanobacteria Xenococaceae and Cryomorpaceae both increased towards shore in *P. lobata*, although we suggest that these habitats have greater nitrogen availability compared to the more offshore sites.

It was in the SIMPER analyses of coral microbiomes that presence of Vibrionaceae emerged as contributors to microbiome dissimilarity. Although they were not one of the ten greatest families amongst all reef microbiomes sampled, they are prominent characters in coral ecology and referenced frequently as potential coral pathogens (Ben-Haim et al., 1999, 2003; Cervino et al., 2008).



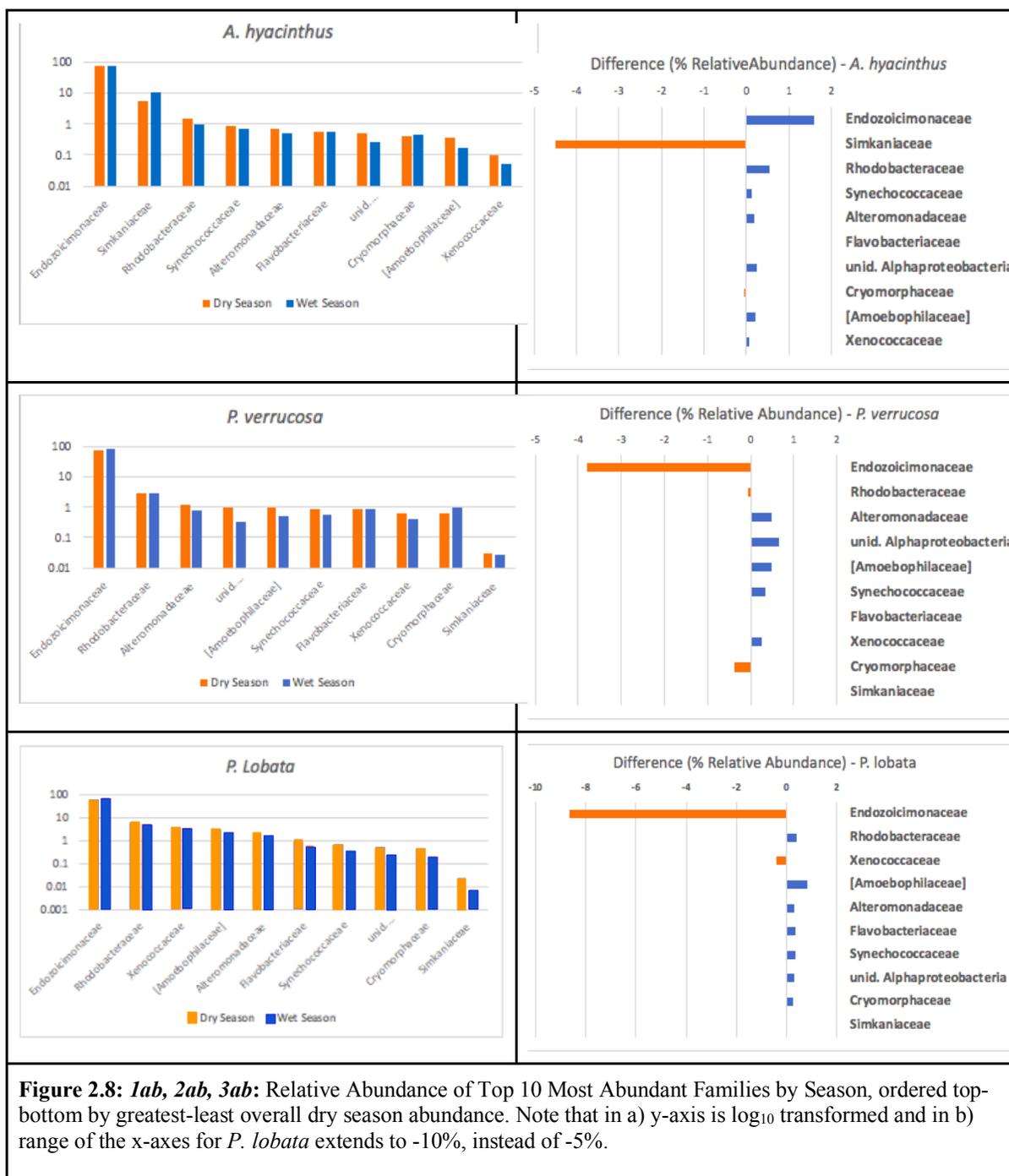


Table 13: SIMPER analysis of which taxa drive dissimilarity between coral microbiomes of each species in the Dry vs Wet Seasons					
<i>P. verrucosa</i>		<i>P. lobata</i>		<i>A. hyacinthus</i>	
Family	cumsum	Family	cumsum	Family	cumsum
Endozoicimonaceae	0.4273	Endozoicimonaceae	0.4186	Endozoicimonaceae	0.4203
Rhodobacteraceae	0.5069	Rhodobacteraceae	0.5203	Simkaniaceae	0.6548
Alteromonadaceae; g__Alteromonas	0.5348	Xenococcaceae	0.5888	Rhodobacteraceae	0.686
Vibrionaceae; g__Vibrio	0.5591	[Amoebophilaceae]; g__SGUS912	0.6353	Vibrionaceae; g__Vibrio	0.7108
Cryomorphaceae	0.5822	Alteromonadaceae; g__Alteromonas	0.6647	Cyanobacteria; c__Synechococcophycidaea e; o__Pseudanabaenales; f__Pseudanabaenaceae; g__Halomicronema	0.7264
unid. Alphaproteobacteria	0.6036	unid. Epsilonproteobacteria; o__Campylobacterales	0.6897	Alteromonadaceae; g__Alteromonas	0.7419
Flavobacteriaceae	0.6247	Flammeovirgaceae	0.7083	Flavobacteriaceae	0.7551
Synechococcaceae; g__Synechococcus	0.6452	Rhodospirillaceae; g__Roseospira	0.7219	Synechococcaceae; g__Synechococcus	0.7677
Saprospiraceae; g__Saprospira	0.6654	Saprospiraceae; g__Saprospira	0.7352	Flammeovirgaceae	0.779
[Amoebophilaceae]; g__SGUS912	0.6846	Vibrionaceae; g__Vibrio	0.7477	Saprospiraceae; g__Saprospira	0.7901

Table 2.14: Descriptions of the top ten most relatively abundant taxa in all microbiomes sampled			
Family	Phylum, Class, Order	Notes	References
Endozoicimonaceae	Proteobacteria Gammaproteobacteria Oceanospirillales	Frequently reported in high abundance in corals, especially <i>Pocillopora</i> sp. Proposed obligate symbiont because of high prevalence of carbohydrate and protein cycling genes.	(Neave, Apprill, Ferrier-Pagès, & Voolstra, 2016; Neave, Michell, Apprill, & Voolstra, 2017; Pogoreutz et al., 2018)
[Amoebophilaceae]	Bacteroidetes Cytophagia Cytophagales	Cytophagales is a proposed opportunist in coral microbiome dynamics. Also a proposed symbiont, perhaps interacting with <i>Endozoicomonas</i> , " <i>Candidatus Amoebophilus</i> " has been observed to be prevalent in the tissues of three Caribbean reef building corals and forms monophyletic lineages with symbionts in other host types.	(Pollock et al., 2018; Apprill et al 2016)
Xenococcaceae	Cyanobacteria Oscillatoriothycideae Chroococcales	Xenococcaceae is prevalent in temperate Scleractinians. Observed as a rare species only in summer in two tropical Scleractinian corals (Florida Keys).	(Pratte & Richardson, 2018; Sharp, Pratte, Kerwin, Rotjan, & Stewart, 2017)
Alteromonadaceae	Proteobacteria Gammaproteobacteria Alteromonadales	Possibly associated with sulfur-cycling (dimethyl sulfide) in corals. Observed as a rare species only in summer in two tropical Scleractinian corals (Florida Keys).	(Pratte & Richardson, 2018; Raina, Tapiolas, Willis, & Bourne, 2009)
Simkaniaceae	Chlamydiae Chlamydiai Chlamydiales	Observed large (70%) increase in relative abundance from larval to juvenile stage in <i>Acropora digitifera</i> . One of the most commonly observed taxa in corals, function unknown. Found to be in less abundance in <i>Pocillopora verrucosa</i> corals near to polluted (sewage & sediment) sites.	(Bernasconi, Stat, Koenders, Papparini, et al., 2019; Ziegler et al., 2019)
Flavobacteriaceae	Bacteroidetes Flavobacteriia Flavobacteriales	More prevalent in reef water than coral microbiomes. Especially common near to polluted (sewage & sediment) sites. Described as part of core microbiome of <i>Acropora hemprichii</i> . Identical to Flavobacteriaceae sp. Family potentially includes coral pathogens.	(Sunagawa et al., 2009; Ziegler et al., 2019) GenBank MK216896.1

Synechococcaceae	Cyanobacteria Synechococcophycideae Synechococcales	Possible coral mutualist and nitrogen-fixer observed to be suppressed in corals with increased algae cover. Found more commonly in reef water than in coral and sediment microbiomes in Thailand. Relative abundance in seawater found to be greater in wet season than dry season.	(Bulan et al., 2018; M. P. Lesser, 2004; Zaneveld et al., 2016a)
Rhodobacteraceae	Proteobacteria Alphaproteobacteria Rhodobacteraceae	Especially common near to polluted (sewage & sediment) sites. Observed with coral white plague disease. Found to increase in corals more algae cover. 100% identical to <i>Roseovarius</i> sp. in GenBank	(C. E. Nelson et al., 2013; Roder, Arif, Daniels, Weil, & Voolstra, 2014; Ziegler et al., 2019) GenBank NR_108232.1
Unidentified Alphaproteobacteria	Proteobacteria Alphaproteobacteria N/A	Alphaproteobacteria may be associated with increased nutrients, having been observed in increased numbers near to sewage-impacted sites.	(Sekar, Kaczmarzsky, & Richardson, 2008)
Cryomorphaceae	Bacteroidetes Flavobacteriia Flavobacteriales	Observed fluctuations in abundance with season (Florida Keys). Found to increase under conditions of increased algae cover on corals. May also be common in reef seawater.	(Bulan et al., 2018; C. E. Nelson et al., 2013; Pratte & Richardson, 2018)

Seasonality

Seasonal shifts in the microbiomes of coral individuals from the same species and habitat are variable for each individual, although dispersion area is not significantly different between seasons (Figure 2.9; beta.disp permutest $p=0.16-0.23$). To fully assess these shifts, continued repeated monitoring of the microbiomes of the same individuals would be valuable in order to verify if microbiomes would return to a similarly ordinated configuration in the following summer or would continue with stochastic trajectories. The inclusion of spring and summer sampling may also provide insights into island-wide coral microbiomes when their temperatures are not at their peak highs and lows. Also, since habitats would be under similar temperature

conditions, microbiomes across habitats could potentially cluster more closely during those times.

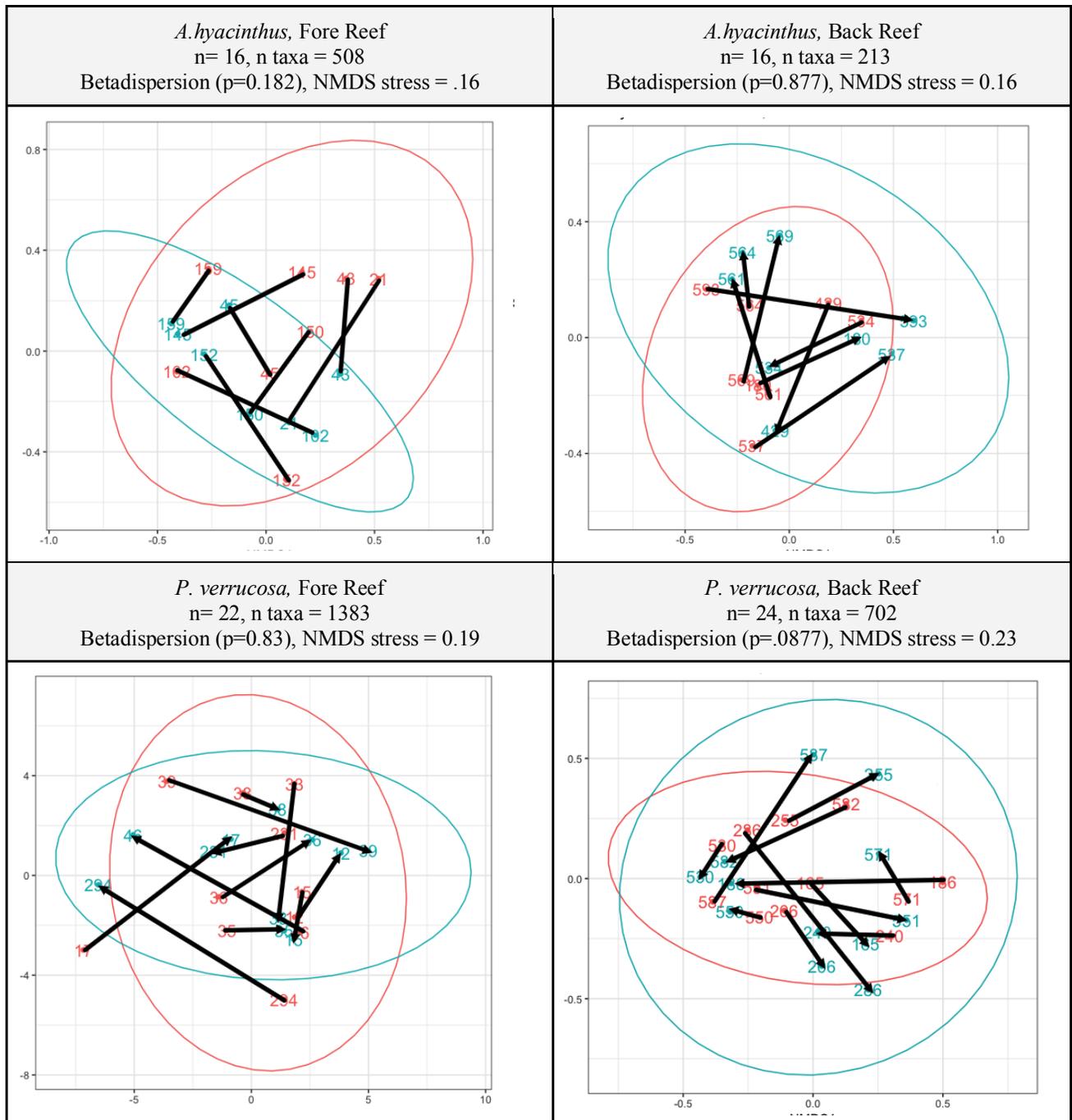


Figure 9 Continued

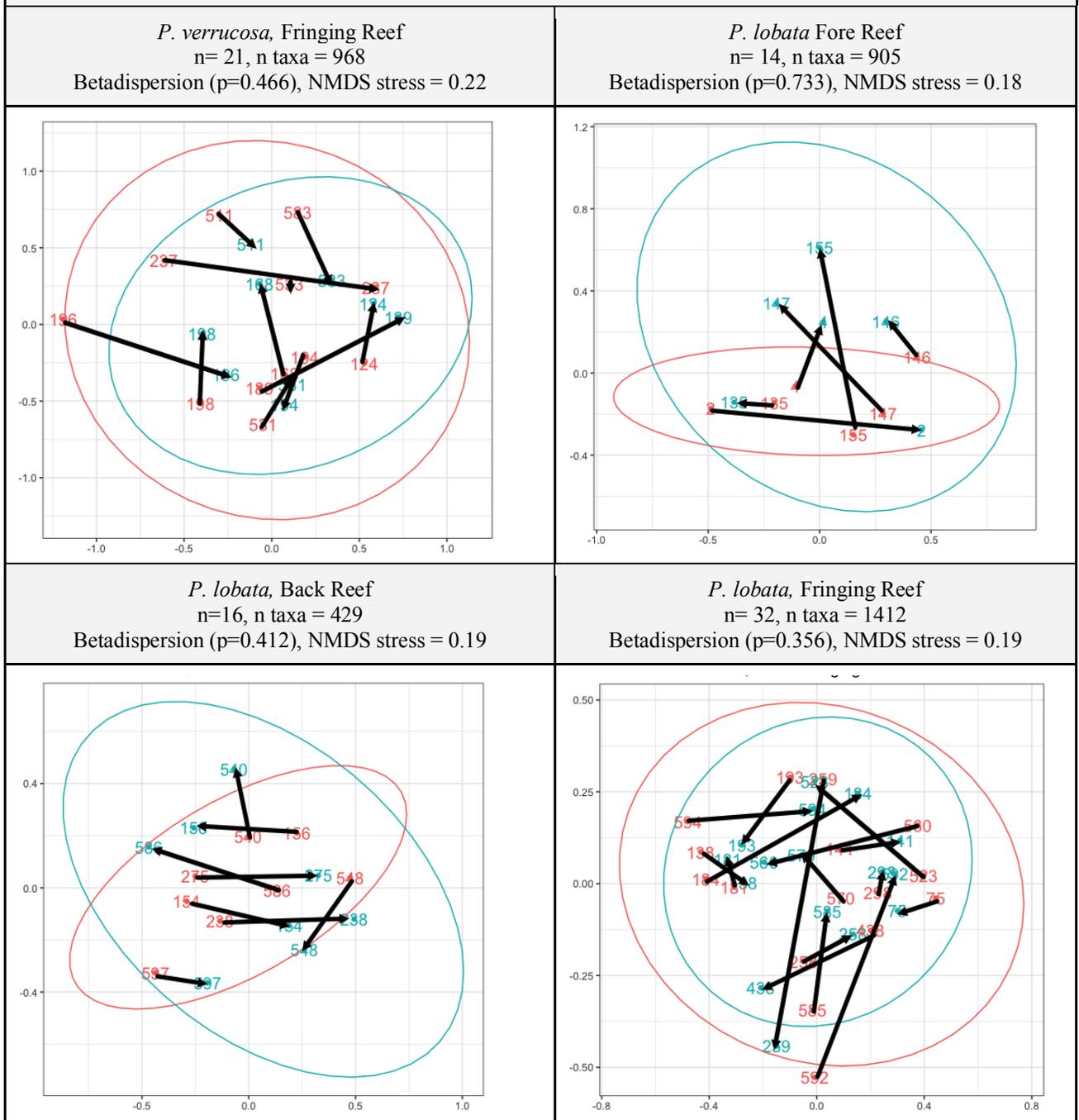


Figure 2.9: Each individual coral microbiomes' diversity shifts differently than others in the same location between seasons. The difference in dispersion from the centroid was not significantly different between seasons, although the trajectories of the shifts appear to be stochastic in nature. Arrows draw from dry season (red) to wet season (blue). All samples presented here are from the north side of the island.

2.5 CONCLUDING DISCUSSION

Mo'orea's microbiome hosts, habitats and sampling locations were home to distinct microbiomes that varied between seasons and locations in different ways although all shared common microbiome taxa. In all three coral hosts, small-scale shifts in abundance of low abundance taxa across the reefscape and between seasons may point towards coral holobionts that are both flexible to a niche habitat and stable within hosts and through time. That is, for a given group of corals there are a few core taxa constant in the same host species across all habitats, with many more that are specific to just one habitat or shared between a few (Hernandez-Agreda et al., 2017), and distinct microbiomes arise in specific locations that are the product of discrete environmental influences. Such plasticity is thought to have enabled coral holobionts to persist and diversify throughout their evolutionary life time (Putnam et al., 2017; Stolarski et al., 2011).

The north side of the island was home to distinct microbiomes. Fringing reef seawater microbiomes were different than back and fore reefs. Given that, island side did not distinguish between water microbiomes. All reef microbiomes shared certain microbial taxa, such as *Endozoicomonas*. Though shared, *Endozoicomonas* also distinguished coral microbiomes from other sample types, while *Synechococaceae*, a cyanobacteria, distinguished between Sediment and Water microbiomes. Further research could detail the shared and interacting members of these microbiome groups more thoroughly. For example, several studies have investigated the interaction between coral and seawater microbiomes (Ainsworth et al., 2015; Ochsenkühn et al., 2018), coral and sediment (Glasl et al., 2019), coral and algae (Lesser & Slattery, 2011; Vega Thurber et al., 2012), or reef fish and the effects of overfishing (Doropoulos et al., 2013; Leingang & Dixon, 2017; Zaneveld et al., 2016a). Furthermore, the bulk of coral microbiome richness was made primarily of taxa occupying less than 13% of the total microbiome but accounted for 98% of total richness (in terms of family), and changes in the abundances of non-*Endozoicomonaceae* taxa occur oftentimes in increments of less than one percent. In a recent study, Dunphy et al. (2019) also observed distinct coral microbiomes at

varying spatial scales, and further measured their dissimilarity as a function of geographical distance from each other. To test this further, an investigation into coral microbiome similarity around and between the islands of remote atolls could be made. An additional comparison could be made between human-habited and uninhabited islands of the same atoll to test for potential anthropogenic signatures in the coral microbiome, including the rare microbiome, such as has been documented in fish and benthic communities in Micronesian reefs by Crane et al. (2017).

Untangling seasonal effects on microbiomes is challenging because of the combined effect of host specificity and habitat/niche specificity. For example, only the microbiome of *P. lobata* displayed distinct seasonal microbiomes although variation in the structure of the top ten most prolific families was nearly undetectable between seasons in terms of relative abundance. It could be that there are even more shifts occurring at scales smaller than what the present study investigated that could present as increases in beta dispersion or changes in rank abundance of microbial agents (Sharp et al., 2017). Particularly, this study did not discriminate between the coral host tissue, skeleton and mucus microbiomes, which have been shown to be distinct (Pollock et al., 2018; Sweet et al., 2011; Weiler, Verhoeven, & Dufour, 2018) and vary with seasons (Li et al., 2014). Furthermore, the inclusion of spring and autumn coral microbiomes could provide insights into shifts associated with seasonal physiological changes in the host. In *Astrangia poculata* corals, a non-reef forming coral, sampled from 1-5m depth off of Rhode Island, USA, Sharp et al. (2017) found that coral microbiomes sampled in the spring were distinct from microbiomes in summer, fall and winter and contributed to the seasonal effect overall. However, those corals experience much greater temperature ranges (4-29° C over one year) than Mo'orean corals.

Future research that aims to assess coral health could include additional metrics of health that are represented by other agents in whole coral metaorganism, such as shifts in *Symbiodinium* clades. For example, Mo'orean coral microbiomes were found to host a suite of distinct *Symbiodinium* clades that varied at spatial and temporal scales that were host-specific (Rouzé et al., 2019). Quantifying the density of *Symbiodinium* cells in zooxanthellae as a measure for coral "bleached-ness" could

also provide linkages for coral health assessments (Mieog et al., 2009), or measurements of accumulated heat stress (Chung et al., 2019; Kayanne, 2017), or paying closer attention to host physiology and life history (Hernandez-Agreda, et al., 2019).

However, known for its large capacity for carbohydrate and protein production (Neave et al., 2016), perhaps even slight decreases in *Endozoicomonas* abundance significantly alters the amount of available nutrition to a microbiome that exists in an already nutrient scarce environment. In this way, it could be that shifts in *Endozoicomonas* abundance drive shifts in the rest of the microbiome although as we quantified shifts as a percentage basis, it is hard to disentangle changes in abundance from shifts in relative abundance. On the other hand, the microbiome might be responding to ambient changes, creating community-wide metabolic shifts that affect *Endozoicomonas* in such a way that it affects their abundance. For example, Haas et al., (2013) reported that exudates from both coral and macroalgae influenced the metabolism of the reef waterscape differentially, depending on spatial scale, in Mo'orea. Further, Nelson et al. (2013) found that exudates from different macroalgae resulted in both a more rapid increase in bacterioplankton and uptake of dissolved organic matter than coral exudates. Although interpreted via a literature search of the biology of top most abundant bacterial families present in the study, a more in-depth look into metabolic potential of the coral microbiome through space and time via a meta-transcriptomic analysis would be insightful (Arotsker et al., 2016; Ryu et al., 2019). Continued and consistent monitoring of individual holobionts through time may untangle more host-specific trends.

3. CORAL MICROBIOMES IN THE SOCIO-ECOLOGICAL MO'OREA ISLAND SYSTEM

This chapter was completed in partial fulfillment of the OSU-NRT program in Risk and Uncertainty quantification in marine science and policy.

3.1 ABSTRACT

Islands are model systems from which to examine change through time as they represent systems that are at once closed, within themselves, and open to global influences. Although rapid global change is putting socio-ecological dependencies at risk, local actions have the potential to enhance regional resilience and inspire changes across broader scales. As part of a Transdisciplinary Research project conducted by five graduate students from multiple disciplines at Oregon State University, this Interdisciplinary Chapter examines coral microbiome diversity shifts in the context of the local human footprint. Working with other team members, visualizations of Carbon:Nitrogen ratios around the whole island derived from LTER core data were compared with spatial patterns of coral microbiome diversity in order to highlight areas of biophysical convergence and points of interest. We found that elevated concentrations of Nitrogen coincided with elevated coral microbiome diversity on the north shore, and that patterns of decreasing microbial diversity with increasing distance from shore are consistent with previous research results (BIOCODE Project, McCliment et al., 2012). These findings were contextualized within the Mo'orea Island Socio-Ecological System via interviews with local residents and reviews of local newspapers, which revealed that local communities are concerned about diminishing water quality in watersheds on the north side of the island due to the expansion of agriculture. Although further research is needed to determine the source of the elevated nitrogen patterns on the north shore, the

inclusion of diverse datasets and using data from long-term time scales increased the breadth and depth of the research, and provided opportunities for local applications.

3.2 INTRODUCTION

Coral Reefs and Their Importance

Islands are frequent subjects of Socio-Ecological Systems (SES) research, representing model systems that can be considered as simultaneously closed and open (Aswani & Allen, 2009; Banos-González et al., 2015; Schmitz et al., 2018). In other words, human-habited islands provide an opportunity to examine coupled human and natural systems at varying scales of complexity and interaction, from local to global spheres, acute to gradual timescales and diverse mental models of perception and decision making (Liu et al., 2007; Kronen et al., 2010).

Islands with coral reefs are model systems for tracking dynamic spatial and temporal socio-ecological patterns. Indeed, coral reefs cover just 0.2% percent of the Earth's surface and they are home to 34% of known marine biodiversity, with more yet to be discovered (Reaka-Kudla, 2001). Coral reefs have been estimated to provide \$352,915 of natural capital and services to the world per hectare per year (Costanza et al., 1997; de Groot et al., 2012; Costanza et al., 2014), and support approximately 500 million people who live both near to and far from reefs (Hoegh-Guldberg, 2011). Within these numbers are an estimated 6 million people who directly depend on coral reefs as a primary resource for subsistence and income (Cinner, 2014; Teh et al., 2013). People make important cultural, spiritual and emotional connections with coral reefs as well. In a case study comparing resident and tourist perceptions and attitudes towards coral reef decline on the Great Barrier Reef in Australia, people reported feeling widespread feelings of deep loss. Termed "Reef Grief," such research adds to an expanding global phenomenon known as Environmental-based Grief (Willox 2012), or Ecological Grief (Cunsolo & Ellis, 2018): one that that psychologists, ethicists and environmental scientists have colloquially coined as "Global Mourning" (Marshall et al., 2019). Embodying such transcendent value for local and global

socio-ecological well-being, the costs associated with the risk of losing coral reefs is great.

Today, islands are at high-risk due to local and global changes that are occurring more rapidly than in previous eras of Earth's history (Field et al., 2012; Tompkins, 2005). For the last fifty years, coral reefs worldwide have been facing rapid decline due to anthropogenically induced increases in global temperatures, pollution in the form of excess nutrients in the water or debris (such as plastic), changing ocean chemistry and overfishing, amongst several other forces (Camp et al., 2019; Hoegh-Guldberg, 2004; Hughes et al., 2018ab, 2019; Camp et al., 2019). For example, global high-temperature thermal anomalies are now occurring at increasing rates and intensities that are making it impossible for corals to recover from bleaching, contributing to massive losses of coral reefs worldwide (Hughes & Tanner, 2000; Lough et al., 2018). Such pressures can spark a shift from a coral-dominated to an algal dominated reefscape, a state associated with a loss of ecosystem services (Leemput et al., 2016).

Coral Biology

The term coral holobiont is used to describe the whole coral meta-organism which includes the calcifying coral cnidarian animal, its single-celled photosynthetic dinoflagellate symbiont, and the entire microbiome of bacteria, archaea, viruses and marine fungi (Amend et al., 2012; Rohwer et al., 2002; Sweet & Bythell, 2017). Coral health and survival depends on the sustained functioning relationships between these biological agents within a particular environment (Bernasconi et al., 2019; Braverman, 2018), and are tightly connected to both the natural and social dimensions they exist in (Glasl et al., 2019; Sharp et al., 2017).

Warm water corals thrive in high light, oligotrophic (nutrient poor) waters. Changes in these conditions can lead to changes in the coral holobiont (Teplitski et al., 2016; van Oppen & Lough, 2009). For example, bleaching is a visual symptom of disease usually caused by thermal stress. The dinoflagellate is expelled from the coral's tissues and without the presence of the photosynthetic pigments of the dinoflagellate the coral appears white, or bleached (Oakley & Davy, 2018). Although

corals can eventually recover from bleaching, resilience during bleaching is severely reduced and corals have only a limited amount of time which they can survive without photosynthetic symbionts providing necessary carbohydrates and other nutrients (Baker, 2004; van Oppen & Lough, 2008).

Additionally, nutrient pollution in oligotrophic coral reef ecosystems alters important trophic dynamics within the reef ecosystem (Silveira et al., 2017). The addition of nutrients can impact trophic interactions among corals, fish, and algae in ways that negatively impact coral health, resilience, and recovery (Bellwood et al., 2006; Shaver et al., 2017; Zaneveld et al., 2016a). For example, nutrient enrichment can increase algal growth to a level that herbivores cannot keep up with, causing algae overgrowth and resulting in multiple negative effects such as inhibition of coral recruitment and growth (Burkepile & Hay, 2006).

Coral Microbiology

A stable coral microbial community, or microbiome, is also critical for coral holobiont health (Pollock et al., 2019). The destabilization of mutualistic coral microbial communities has been linked to coral disease, such as tissue loss and decay, white band disease, and yellow band disease (Holzman, 2009; Kline et al., 2011; Vega Thurber et al., 2009). Several viruses have been associated with coral bleaching and disease, and corals exposed to elevated nutrient levels also undergo increased viral infections (Vega Thurber et al., 2008, 2012; Correa et al., 2016). The coral microbiome might also protect the coral holobiont from invading pathogens (Teplitski et al., 2016; Welsh et al., 2016).

We also know that coral microbial communities are important mediators of biogeochemical cycling both within the holobiont and between the holobiont and its environment (Leichter et al., 2013; Rådecker et al., 2015). However, the coral microbiome is sensitive to environmental changes (Brown et al., 2019; Glasl et al., 2019ab; Roitman et al., 2018, Brown et al., 2019). For example, overfishing and nutrient pollution changes the coral microbiome, increasing the amount of putative bacterial pathogens and increasing rates of coral disease and death (Shaver et al., 2017; Zaneveld et al., 2016a). Furthermore, tracked microbiome diversity shifts have

been attributed to coral holobiont resilience and reef health (Brown et al., 2019; Glasl et al., 2019; Roitman et al., 2018), but questions remain as to the extent that the microbiome can tolerate change before the community's composition becomes unsuitable for coral holobiont health (Bourne et al., 2016; Rosado et al., 2019).

A transdisciplinary approach

One approach to studying Mo'orean reefs is via a Socio-Ecological Systems (SES) perspective, which views an "ecological system [as] intricately linked with and affected by one or more social systems" (Anderies et al., 2004). An SES approach may be particularly relevant and applicable for scientists, policy makers, community members, consumers and other stakeholders. It offers spatial, temporal, and conceptual frameworks as a means to enable better understanding of human and non-human agents and their interactions at varying scales, while accounting for the possibility of change through time (Anderies & Janssen, 2013; Anderies et al., 2013; Avriel-Avni & Dick, 2019; Berrouet et al., 2018; Holling, 2001). Previous coral reef research stresses the importance of using spatial data that incorporates human and natural drivers of reef change (Donovan et al., 2018; Wedding et al., 2018). Since changes in microbial community diversity have been shown to respond to changes in the environment (Ladau et al., 2013b), this work endeavors to highlight convergent locations of anomalies in microbial diversity with indications of anthropogenic activity around the island of Mo'orea, French Polynesia, by synthesizing and mapping existing datasets, with the purpose of aiding the prioritization of future research and informing practical management strategies.

To provide insight into microbiological indicators of coral health in the Mo'orea Island SES, this chapter represents a multidisciplinary contribution to a transdisciplinary group report (TD report) made by a team of Oregon State University graduate students from multiple disciplines: Anthropology, Environmental Science, Geography, Microbiology, and Statistics. Multidisciplinary data included in this chapter represents one of several map layers which contributed to the team's full, final interpretation that, when synthesized, blurred the lines between disciplinary

specializations and created an emergent perspective (Mo'orea Team TD Report, Oregon State University, 2019).

To highlight locations around Mo'orea that are potential biophysical and anthropogenic points of interest, we synthesized datasets from the last 10 years into geospatial map layers and visually inspected them for points of convergence. Appearances of highlighted areas were then interpreted within the socio-ecological context of Mo'orea at both local and extra-local spatial scales. The present paper is guided by the hypothesis:

1. Changes to coral microbiome diversity and elevated nitrogen concentrations will coincide with locations near to where human activity is greatest.

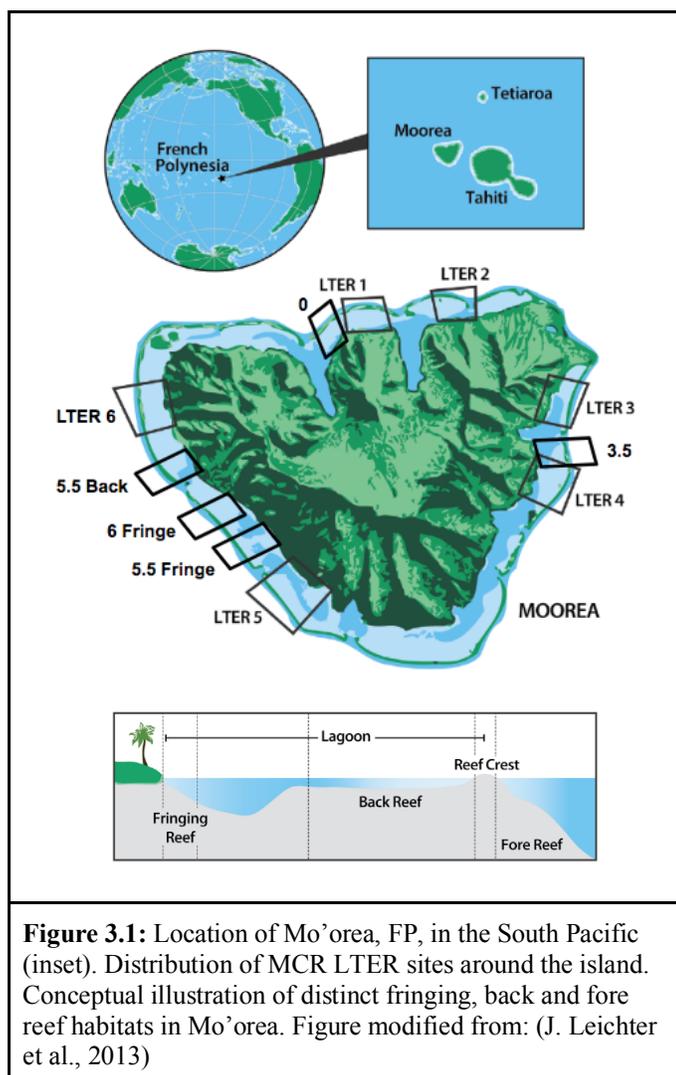
3.3 METHODS

Study system, Mo'orea's Coral Reefs

Mo'orea (17°32'S, 149°50'W) is a tropical high island with an area of 134 km² situated just west of Tahiti in the Society Islands chain in the South Pacific Ocean. A coral barrier reef punctuated by several deep passes surrounds the island, creating distinct marine habitats that harbor a diverse reef community of fish (Planes et al., 1993), macroinvertebrates (Naim, 1988; Planes et al., 1993) and microbes (Carlson, 2019; Crossland, 1928; Vénec-Peyré, 1991). A steeply sloping, deeper fore reef extends beyond the barrier reef crest which protects back and fringing reefs from large swells which seasonally affect south side of the island with stronger intensity (Leichter et al., 2013).

Although there are nearly negligible tidal fluctuations, yearly king tides can create extreme lows which will temporarily expose stretches of dry reef. More constantly, waves from predominant south swells wash over the reef crest, bathing the shallow back and fringing reefs with cooler water and creating longshore currents that eventually meet the deep channels and return to sea again through the reef passes (Leichter et al., 2013). During the wet season (November-April), precipitation can

average approximately 300mm per month, while the dry season (May-October) will receive on average <100mm per month. Precipitation can affect the composition and volume of terrestrial groundwater discharge into the nearshore marine environment, impacting fringing reefs first (Adjeroud, 1997; Haßler et al., 2019; Kneet et al., 2016).



Research from the last decade has shown that the microbial community of the seawater inside Mo'orea's lagoons is distinct from open ocean communities (McCliment et al., 2012) and that the viral community here, in particular, is remarkably voracious in its capability to utilize labile and semi-labile organic nutrients (Payet et al., 2014). However, studies on the microbial diversity of corals in

Mo'orea have only recently begun and our understanding of how microbial trends in Mo'orean reefs are tied to coral health around the island is still underdeveloped.

Gradually warming ocean temperatures around Mo'orea are contributing to increased coral bleaching, mortality, and reef degradation over time (Payet et al., 2014; Pratchett et al., 2013). Reef decline was exacerbated by an outbreak of corallivorous Crown of Thorns sea stars (COT) which was followed by Cyclone Oli in 2010. Holbrook et al. (2018) found that five years post disturbance, the coral cover of the northern outer reef (>10m depth) returned to pre-disturbance levels. When analyzing other metrics of coral resilience, there was a reduced population of *Acropora hyacinthus*, and an increased dominance of *Pocillopora verrucosa* and *Porites lobata* corals across all reef types. It is still unclear how successional shifts in the distributions of coral species may impact reef diversity in the Mo'orean system in the future (Holbrook, 2018).

Mo'orea's People and the Reefs

Today, Mo'orea supports a population of over 16,100 people in five provinces. Though colonized by Europeans since the 17th century and formally annexed by France in the 19th century, Mo'orean islanders are to this day closely connected to the reefs through fishing and to the land through agriculture. However, the use of Mo'orea reefs for fishing has significantly changed over the last century. During this time, Mo'orea shifted from a small-scale farming and fishing subsistence-based economy to an economy based on cash cropping and tourism (Risako Sakai, TD team member and Anthropology PhD candidate, personal communication). Therefore, predominant fishing practices also changed from being subsistence driven to being more recreational or to uphold cultural traditions. Fishing and farming practices still rely on a traditional lunar calendar, called *tarena*, and the preferred method of fishing is spearfishing at night. The fishing population is composed of 69% recreational, 20% subsistence, and 11% commercial although these categories are not mutually exclusive (Leenhardt et al., 2016; Thiault et al., 2018).

Mo'orea has no central fish markets, fishers instead share catches with their family and community, then sell surplus on the side of the road in the mornings and

afternoons (Holbrook et al., 2019; Rassweiler et al., 2019). Recent interviews of fishers on the island revealed an interesting disconnect between western-science based ecological observations of changes in fish assemblages and abundance, and fishers' perceptions of such changes. For example, Rassweiler et al. (2019) found that after the 2009 COT disturbance and 2010 cyclone that followed, ecological data showed significant changes in taxonomic assemblages of reef fishes but no significant changes in overall fish biomass. Data also showed that the taxonomic composition of fish catches (from roadside surveys) also shifted after the disturbance. However, interviews with fishers revealed that they did not perceive a significant change in the types of fish they caught, but instead the behavior of the fish and/or their location on the reef. The researchers concluded that, among many reasons, this discrepancy could be due to the different ways locals and western scientists conceptualize ecosystem changes in the reef habitat. This highlights how reef health may be perceived in contrasting ways due to differing mental models that are influenced by cultural and societal backgrounds and relationships to the reef (Rassweiler et al., 2019). This also provides impetus for greater inclusion of local perspectives in local research.

Mo'orea's Research Stations

There are two scientific research stations on Mo'orea: Gump station (University of California Berkeley, United States of America) and CRIOBE (University of Perpignan, France). For this report, we will focus on the data available from Gump station, which has established six Long-Term Ecological Research (LTER) sites around the island (Figure 1). Since 2004, reef data such as water temperature, nutrient concentrations, coral cover, fish diversity and abundance have been collected from the LTER sites (<http://mcr.lternet.edu/data>).

Socio-Ecological Coral Reef Systems in Mo'orea

Mo'orea, French Polynesia, is an island with a rich history of indigenous culture and fishing and farming practices, foreign colonization and modern development. For the purposes of our study, we are considering Mo'orea Island as a human-altered landscape, since the first humans most likely arrived to Mo'orea

several hundred years ago and are still closely connected to the reefs today (Galzin, 2016). In the last 20 years, land use has increased on Mo'orea in the form of agricultural expansion, such as pig farms, into the island's interior valleys (Duane 2006). Such changes may affect the natural processes of nutrient cycling around the island and pose risks to the surrounding reefs and the people that are tied to them.

To highlight locations in Mo'orea that are potential biophysical and anthropogenic points of interest, we compared locations of elevated nitrogen concentrations with distributions of chao1 diversity of 16s rRNA gene bacterial and archaeal microbial communities in corals from around the island. Both of these layers were included in a composite map in the Mo'orea Transdisciplinary Report.

Nitrogen Concentrations

Measurements of C:H:N ratios that were derived from the macroalgae *Turbinaria ornata* (Class: Phaeophyceae) during the year 2013 (LTER core data, Carpenter 2018) were interpolated onto a map of Mo'orea. The C:N ratio is used as a proxy for nitrogen availability on the reefscape allowing us to compare the amount of nitrogen present across the sides of the island (Weinstock, ID chapter 2019).

Coral Microbiomes

Diversity of microbial taxa (based on the V4 region of the 16S rRNA gene; Chapter 2) was estimated from three species of prominent corals (*Acropora hyacinthus*, *Pocillopora verrucosa*, and *Porites lobata*) spanning the west, north and east sides of the island and the fore back and fringing reefs between September 2017 and March 2018 (Figure 3.1). For each georeferenced sample, Chao1 diversity was provided in quartiles which were used by TD team member and Geography PhD candidate Bran Black to scale impact and color code the heatmap in the final TD report. An ANOVA was used to test for differences in coral microbiome diversity between the west, north and east sides of the island. Post hoc comparisons were made with Tukey's HSD.

This microbial map layer was combined with additional layers for visual comparison in our team's Transdisciplinary Report (NRT Mo'orea Team TD report):

island-wide terrestrial slope change, predicted offshore particle transport; land use classification changes in the last decade (such as clear-cutting and increased development); and the aforementioned C:H:N concentrations. All team members visually inspected the completed maps for convergent areas of high or low microbial diversity, high or low C:H:N ratios, land use change in close proximity to watersheds, with special attention paid to locations of terrestrial discharge to the sea. Risako Sakai provided her insights and further contextualized map data within the scope of human presence and activity, and grounded our interpretation and discussions of future research and management priorities within local and regional stakeholder values.

Additional Datasets Guide Interpretations

Additional 16S rRNA gene-based microbial data from the Mo'orea BIOCODE Project (Field & Davies, 2015; McCliment et al., 2012) was compared with nitrogen and coral microbiome diversity distributions around the island. There were several differences in methodology between McCliment 2012 and those provided in Chapter 2. First, BIOCODE microbiome surveys were conducted in Mo'orea's seawater, while we have mapped coral microbiome diversity and provided water microbiome diversity for comparison. Also, sampling was achieved in January 2008 (wet season) and May of 2009 (early dry season) in the BIOCODE study. Sampling locations were very near to those presented in Chapter 2, though sampling was conducted on the north shore only. Estimates were made from sequencing V6 region of the 16S rRNA gene, a different area on the same gene amplified in Chapter 2. Furthermore, richness estimates from the McCliments et al. study were made at the level of operational taxonomic units (OTUs) that were created by clustering at 97% sequence similarity. In Chapter 2, richness was estimated from amplicon sequence variants (ASVs) made from single-nucleotide differences. Taxonomic descriptions were made at 97% sequence similarity using the Greengenes 13.8 database. Richness estimates from McCliment 2012 were made using CatchAll (Bunge, 2011). Furthermore, Chapter 2 estimates were made from samples rarefied to 1028 sequences.

In order to find a common denominator between the two datasets, data from Chapter 2 was subset to both coral and water samples taken from the north side of the island in the wet season only (March 2018). A boxplot of Chao1 diversity estimates was created and compared with that of the BIOCODE project, but direct comparisons between the two datasets cannot be made because of differences in methodology. Only general trends (greater, lower) between habitats are considered here.

3.4 RESULTS AND DISCUSSION

Nitrogen Concentrations

The north side of the island harbored elevated nitrogen concentrations compared to the west and east sides (TD team member and Statistics MS student Aaron Weinstock, ID chapter 2019). Fringing reefs coinciding with LTER sites 5 and 6 were also more orange in color, indicating higher nitrogen levels and a lower C:N ratio. Reef habitats overall were also distinct: Fringing reefs displayed elevated N concentrations when compared with back and fore reefs. And, an apparent green-yellow delineation between highlighted the line of the barrier reef crest, which marks the boundary between fore and back reef habitats.

Coral Microbiomes

Coral microbiome diversity was significantly different among sides of the island (ANOVA $p=0.001$, $DF=2$, $F_{stat}=9.135$, $n=401$). Post hoc pairwise comparisons showed the North side to be significantly different than the west ($p=0.001$, Tukey's HSD), but not the east ($p=0.12$, Tukey's HSD), and that the east and west sides were not different from each other ($p=0.89$, Tukey's HSD). Overall coral microbiome diversity did not differ between reef zones (Figure 3.2a; ANOVA $p=0.181$).

Both the means and ranges of coral microbiome diversity were elevated on the north shore, coinciding with elevated levels of nitrogen (Figure 2b). Interestingly, diversity on the fringing reef at site 5 (west side) does not appear to be increased in range or mean, even though this site falls within a bright patch indicating high

nitrogen. East side microbiomes are near to areas of bright patches that indicate high nitrogen. Overall, the lack of difference between fringe and fore reef sites, in addition to the high diversity in areas of high N on the west side, suggest that N itself is not the sole deterministic factor in the diversity of the coral holobiont.

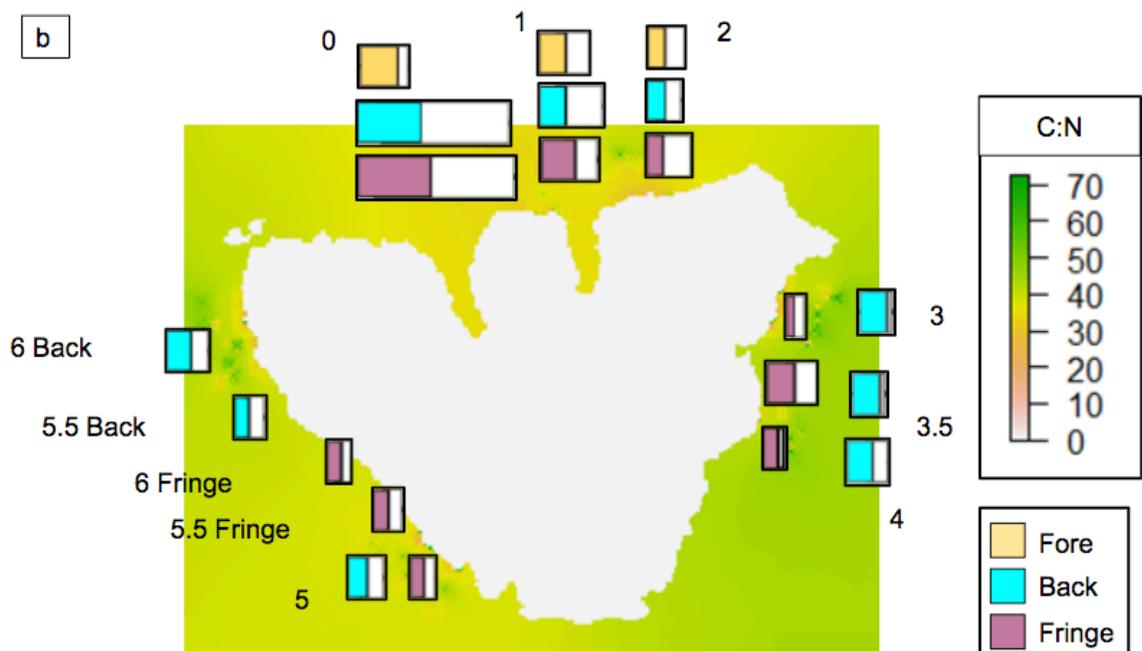
Additional datasets to guide interpretations

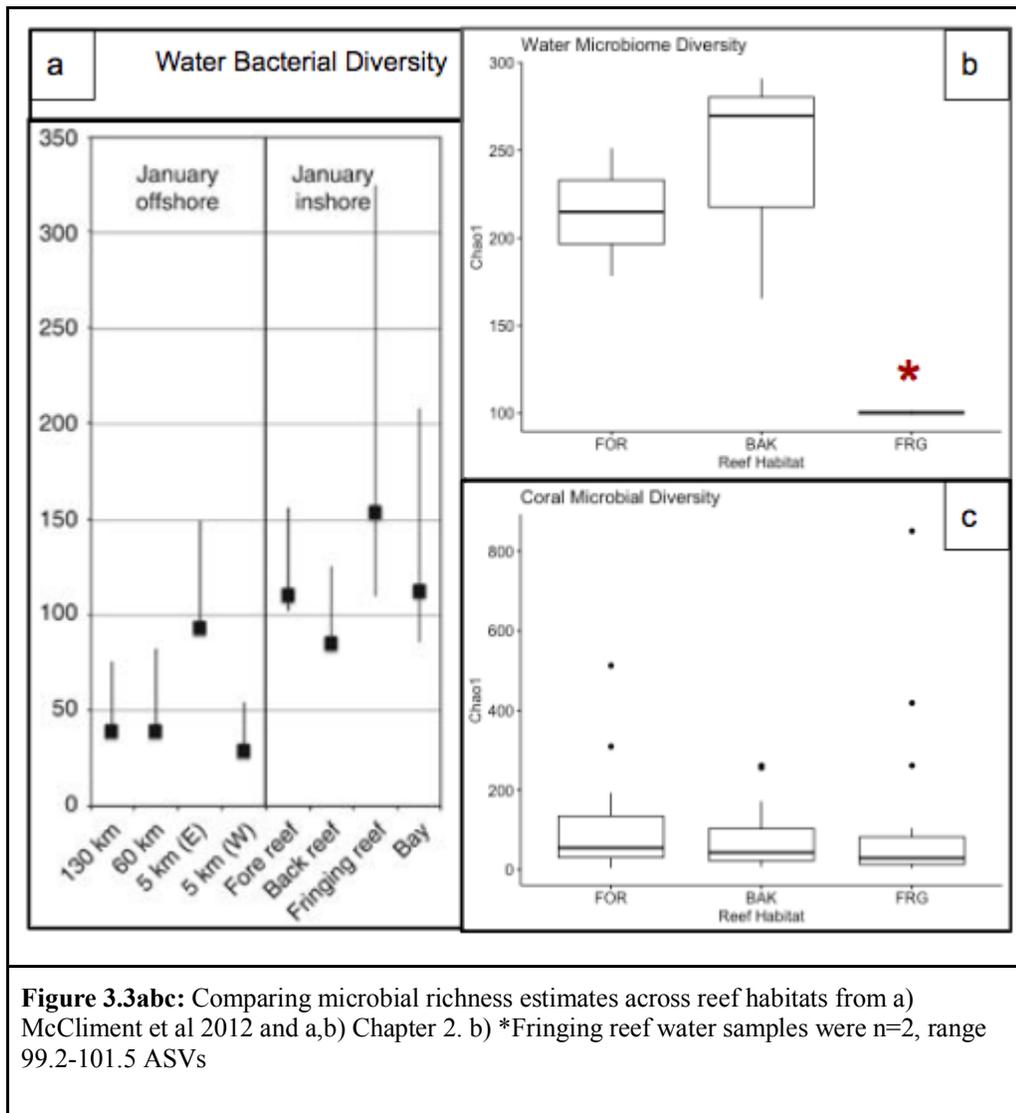
In general, comparisons between fore reef and back reef diversity indicate a decrease occurs beyond the reef crest (Figure 3.3). However, replication of water samples is low from Chapter 2: two fore reef, three back reef and two fringing reef samples were available because only one water sample was collected per season at each site and habitat, for which there are three (sites, habitats) on the north side of the island. Interestingly, estimates from Chapter 2 and McCliment et al. 2012 see contrasting trends between back reefs and fringing reefs: where McCliments reports a high mean and range, Chapter 2 estimates were at their lowest. It is interesting to consider the drop in microbial diversity in offshore environments that the BIOCODE project reports, and this could be considered when examining maps of offshore particle transport (TD team report). There appears to be no relationship, abundance-wise, between the water samples of each study with coral microbiome diversity, although coral and water microbiomes share taxa (Chapter 2). Coral microbiome diversity was less on the East and West sides of the island, though select fringing reef sites were elevated, such as 3.5, which is near to the ferry port on the East side of the island.

Figure 3.2ab

a) Coral microbiome diversity (Chao1) at each sampling location. Location names are given in site number (i.e. 0-6) and reef location/habitat type (i.e. Fore reef = FOR, Back reef = BAK, Fringing reef = FRG). Sites by island side are: 0-2, North; 3-4 East; 5-6 West.

b) Microbial diversity means (colored bar) and third quartiles (clear bar) of each sampling location overlaid on a map of C:N ratios (data from Carpenter 2018; visualization from Weinstock ID chapter 2019). Low C:N ratio (warm colors) indicated higher levels of Nitrogen in the water column.





The north shore of Mo'orea is a potential region of interest for future research and strategic management planning because of the apparent footprint of human activity there. Both nitrogen levels and shifts in microbial diversity coincide geographically on the north side of the island, where human activity is more pronounced. Similarly, fringing reefs of the East side of the island were another area of nitrogen and coral microbial diversity convergence. Those sites are situated adjacent to the ferry port at Vai'Are, and a golf course at Tama'e is situated north

from there which might also contribute to the observed biochemical patterns (King et al., 2008; Starrett, n.d.). Furthermore, Opunohu Bay also includes a shrimp aquaculture farm from which discharge could be another source of elevated nutrients and impacts to the reefs as has been reported in other places (Alonso-Rodríguez & Páez-Osuna, 2003; Hopkins et al., 1995).

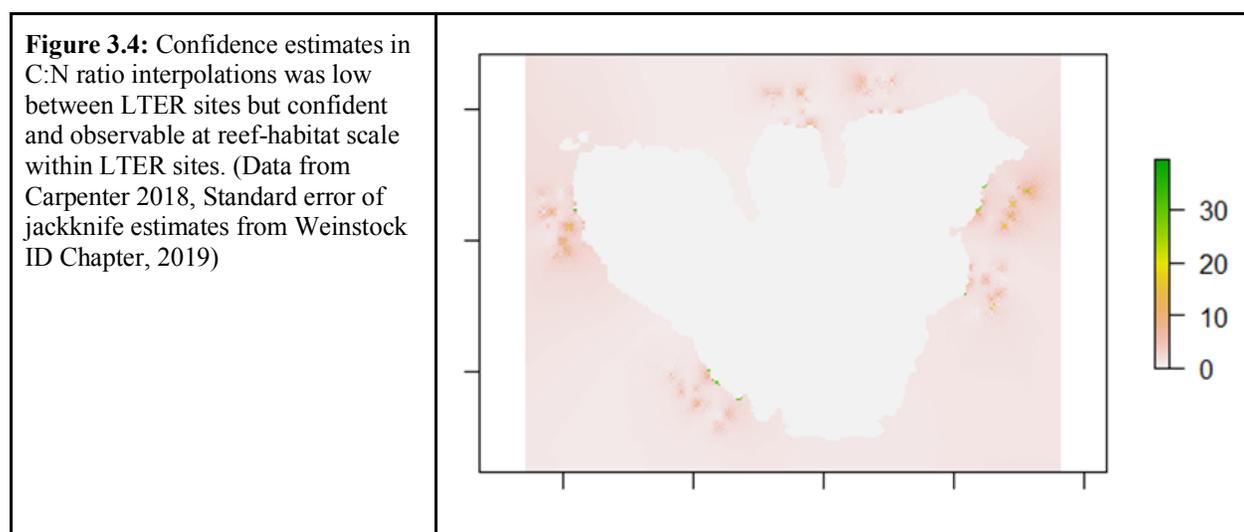
Land use change over the last two decades was noticeable inside the back valleys of Opunohu and Pao Pao bays (TD report), which might be attributed to an increase in pig farms (Duane 2006). Major watersheds drain from these valleys directly into the northern bays, and agricultural could be introducing pollution into the rivers, which are further changing nutrient profiles in the downstream Opunohu and Pao Pao bays. Indeed, local residents report an increase in observed littering and pollution along the river and the degradation of multi-generation cultural traditions that value clean rivers in Mo'orea as sacred and oftentimes religious sites (K. Neumann, UC Santa Barbara, pers. comm.; R. Sakai, Oregon State University, pers. comm). We posit that such impacts to the reefs could potentially be higher during the wet season, when heavy precipitation causes increased runoff. Additionally, the effect of runoff may be exacerbated with the expansion of clear cut lands for agriculture. However, until the effect of local added nutrient concentrations on coral holobiont physiology and reef ecosystem community structure is traced to the source, uncertainties remain as to the extent of which added inputs are affecting the local marine environment.

Quantifying uncertainties

Although elevated nitrogen levels and coral microbiome diversity were near to each other geographically, it should be noted that the interpolated map of C:N ratios had low overall confidence (Figure 3.4). But, higher resolution and confidence does exist within LTER sites, and the replication of three sites on each island side increases the confidence of island-wide analyses. In this way, LTER data, and long term ecological monitoring in general, may be considered a valuable and worthwhile endeavor. Although expanding the coverage of such estimates may increase fine-scale confidence, feasibility and funding perhaps play the role of limiting factors.

A critical hurdle when comparing data from Chapter 2 and the BIOCODE project was that Chapter 2 estimates came from reads of samples that were rarefied to 1028 sequences, whereas the BIOCODE project used non-rarefied data. Also, when reviewing McCliment et al 2012, it was found that one of their bay sites almost exactly coincided with a fringing reef site 1 from Chapter 2. This might explain why both their bay measurements and our fringing measurements tended to be lower than the next-distant-from-shore habitat.

Comparing and synthesizing datasets from diverse sources is a prime challenge for scientists today. We found similar trends microbiome richness decreasing with distance from shore in both studies compared here, and in both water and corals. This observation offered some connection to the map of probable offshore sediment and particle transport of our TD report, as it may be that microbial diversity drops out with terrestrial particles that flow outward beyond the reef passes with inner-island circulation (Schrimm et al., 2002).



3.5 CONCLUSION

Although highly confident conclusions are a challenge to draw when synthesizing diverse datasets created with differing methodologies, common ground can still be found and communicated with carefully considered uncertainties. The

inclusion of wide ranges of data sources can expand the breadth and depth of the research, and consistent and well-planned long term monitoring both increases confidences and provides a framework by which to detect trends and anomalies otherwise undetectable within shorter time scales (Lindenmayer et al., 2012). Such methods are not only useful for local and regional applications, but are one of the primary approaches for identifying extra-local influences on the system, such as increasing temperatures (L. Hughes, 2000).

As an island, Mo'orea is at once a self-contained system and part of an interactive global sphere. Amidst Mo'orea's regional natural environment is a human footprint that, with the aid of geographic visualizations, is recognizable in its surrounding seas and in the microbiomes of its coral reefs. Then, information from residents assists in contextualizing the current state of nutrients and pollution in local communities. Because distinct coral microbiomes with elevated levels of diversity coincided with regions of elevated nitrogen in the sea, future research directions could be applied towards identifying the sources of said nutrients and their additional impacts to reef and human health. This presents an additional opportunity to investigate the effect of nutrients to a naturally oligotrophic system *in-situ*, and could build upon previous research examining coral microbiomes' responses to such stressors (Rädecker et al., 2015; Shaver et al., 2017; Vega Thurber et al., 2014; Wang et al., 2018b; Zaneveld et al., 2016b).

4. CONCLUSIONS

The ability of organisms to accommodate change is essential to their persistence through short-term perturbations and longer-term change. At a time of rapid global change, human signatures are unmistakable across sea and landscapes, and are integrated within ecosystems at regional and global scales. As microbial communities are ubiquitous in Earth systems and sensitive to change, they are prime candidates for focused monitoring efforts to identify signatures of change in a system. Furthermore, as prominent agents of biochemical cycling in ecosystems, tracking microbial communities through time can provide insights into regional-scale functional shifts (Glasl et al., 2019).

What is remarkable is that the idea of a “system” can be applied at a variety of scales. From socio-ecological Earth-systems, to coral reefs, and even a microbiome within a single coral holobiont, the scale at which systems are considered reveals intricate biophysical interactions that are either specific to that scale only, or present across multiple scales.

Trends such as these were observed in reef microbiomes around Mo’orea, French Polynesia, which were both specific to their host and flexible to their environment, whether they belonged to a particular location on the reef or a broader island-side-wide area. In corals, each host was home to microbiomes that were dominated by 93 ASVs of Endozoicamonaceae, however the remaining 99% of species richness was made of taxonomic families that occupied less than 25% of the total relative abundance of coral-associated sequences of bacteria and archaea, pointing towards the existence of a consistent core microbiome in Mo’orean corals that is accompanied by a diverse array of low abundant taxa, such has been described in other coral systems (Hernandez-Agreda et al., 2017). Although the consistent dominance of Endozoicamonas was observed in *Pocillopora verrucosa*, *Porites lobata* and *Acropora hyacinthus* across habitats, the overall composition of each microbiome in each habitat was distinct. These distinctions were primarily caused by fluctuations in the abundances of Endozoicamonas in tandem with shifts in the relative abundances of taxa that were low (less than 6%) in relative abundance. This

provides evidence that the relationship between corals and their microbiomes is flexible. That is, since corals and their symbionts depend on each other, a certain level of stability must be maintained for the holobiont to persist; however, microbiome variability between specific habitats and with environmental changes, such as seasons, is tolerated by corals (Dunphy et al., 2019; Ziegler et al., 2019). Such a symbiotic relationship is thought to have enabled Scleractinian corals to persist and evolve throughout several mass extinctions since their emergence during the late Triassic (Hernandez-Agreda et al., 2017; Stanley, 2003).

The limits of such tolerance is the focus of much research into the influence of coral microbiome composition in coral and reef resilience (Bourne et al., 2016; Putnam et al., 2017). If stress may be considered as a response to change, then the changes in environmental conditions that come with the seasons might be considered a type of stressor in biological systems. Mo'orea's coral microbiomes, for example, were affected by seasons at broad spatial scales, such as across island sides and reef habitats. However, corals live with seasonal changes throughout their lifetimes, and the rapid environmental changes occurring today may be too drastic for the holobiont to keep up with, as evidenced by increases in mass coral bleaching with rising global temperatures. Continued monitoring can provide insights into the futures of these symbiotic relationships, both within holobionts and between holobionts and their environments.

Just as a coral holobiont may be considered as both its own system of symbiotic relationships (Rohwer et al., 2002) and an emergent entity within a broader Earth system, so too are islands simultaneously closed and open systems. In Mo'orea, global changes such as anthropogenically induced global warming threatens the island's coral reefs (Pratchett et al., 2013) and, in turn, the well-being of its human inhabitants who rely on Mo'orean reefs for food, black pearls and markets that attract tourism (Risa Sakai, Oregon State University, pers. comm.). However, the effects of regional-scale human behavior were apparent in non-human natural dimensions. Increased human activity on the north side of the island coincided with elevated nitrogen concentrations and altered patterns of diversity in coral microbiomes in the surrounding seas, in particular fringing reefs which are in closest proximity to the

coastline. Although land-cover classification maps revealed an expansion of agriculture into watershed valleys (Bran Black, TD report) and Duane (2006) identified mismanaged pig farms runoff as a risk to water quality, further research could be directed towards identifying the source of the nutrients and applied towards local management initiatives. Although Mo'orea is vulnerable to global changes that it may not be able to directly control on its own, the island may have the capacity to manage local environmental stressors and thereby promote environmental stewardship at scales that span beyond its shores. In doing so, and by considering humans as not separate from their Earth system, the collective efforts of biological communities of diverse ecosystems worldwide may perhaps rediscover a means of living within a planet that does not dismantle its own life supporting relationships, and thereby adapt to the new age of the Anthropocene. As Folke (2006) posits, "In a resilient social-ecological system, disturbance has the potential to create opportunity for doing new things, for innovation and for development." As can be seen in coral microbiomes, the breadth of a system can be defined at varying spatial and scales, from individual coral niches to island-wide patterns of biophysical distributions. Why not, too, the whole Earth meta-system? For, what is our Earth, but an island?

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6. SUPPLEMENTARY TABLES AND FIGURES

Table 1: Microbiomes, Pairwise comparison by Sampling Location, with Bonferroni Correction								
	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1	5BAK vs 5FRG	1	1.1603780	3.3939361	0.060182642	0.021		1.000
2	5BAK vs 6FRG	1	1.0016886	2.7369686	0.045062648	0.022		1.000
3	5BAK vs 5.5BAK	1	0.1465935	0.3875323	0.006637244	0.897		1.000
4	5BAK vs 5.5FRG	1	0.8593306	2.3298532	0.045389828	0.048		1.000
5	5BAK vs 6BAK	1	0.1449198	0.3853071	0.004566044	0.880		1.000

6	5BAK vs 1BAK	1	0.9512068	2.4769386	0.044648076	0.034	1.000
7	5BAK vs 1FOR	1	0.4228496	1.0977925	0.017126838	0.336	1.000
8	5BAK vs 0FRG	1	1.3910110	3.7389034	0.068304317	0.002	0.506
9	5BAK vs 0BAK	1	0.9061428	2.3007141	0.034701197	0.043	1.000
10	5BAK vs 0FOR	1	0.5139277	1.3370050	0.026043689	0.216	1.000
11	5BAK vs 1FRG	1	1.0992010	2.9172186	0.059635824	0.015	1.000
12	5BAK vs 2FRG	1	0.5069366	1.3160679	0.025646312	0.234	1.000
13	5BAK vs 3.5FRG	1	0.7110752	1.8622006	0.044484059	0.088	1.000
14	5BAK vs 2FOR	1	0.4586224	1.2673473	0.021383567	0.272	1.000
15	5BAK vs 4FRG	1	0.7294090	1.9176211	0.053389423	0.090	1.000
16	5BAK vs 2BAK	1	0.5796856	1.4852643	0.025395530	0.174	1.000
17	5BAK vs 3BAK	1	0.4628312	1.1944463	0.025856925	0.271	1.000
18	5BAK vs 3FRG	1	0.6681643	1.7639927	0.045505961	0.121	1.000
19	5BAK vs 4BAK	1	0.4325951	1.1287794	0.028847804	0.307	1.000
20	5BAK vs 3.5BAK	1	0.5593075	1.4700636	0.036324718	0.191	1.000
21	5BAK vs ENRICHED	1	1.4471457	4.1106262	0.095350649	0.002	0.506
22	5BAK vs CONTROL	1	0.9072777	2.4988804	0.061702457	0.047	1.000
23	5FRG vs 6FRG	1	0.3521639	1.0749897	0.021467597	0.295	1.000
24	5FRG vs 5.5BAK	1	0.9975212	2.9154999	0.056158564	0.029	1.000
25	5FRG vs 5.5FRG	1	0.2518905	0.7811731	0.019155238	0.487	1.000
26	5FRG vs 6BAK	1	1.2230412	3.4720738	0.044245980	0.011	1.000
27	5FRG vs 1BAK	1	1.4562426	4.2214105	0.087542245	0.003	0.759
28	5FRG vs 1FOR	1	1.4334689	4.0545194	0.069839858	0.004	1.000
29	5FRG vs 0FRG	1	1.1474297	3.4924156	0.076769183	0.009	1.000
30	5FRG vs 0BAK	1	2.2296657	6.1218635	0.100158326	0.002	0.506
31	5FRG vs 0FOR	1	1.5737486	4.5942230	0.100763269	0.002	0.506
32	5FRG vs 1FRG	1	0.8463572	2.5757190	0.065083314	0.037	1.000
33	5FRG vs 2FRG	1	0.4333777	1.2615470	0.029850943	0.238	1.000
34	5FRG vs 3.5FRG	1	0.5668293	1.7399398	0.053144259	0.127	1.000
35	5FRG vs 2FOR	1	1.9120984	5.9246890	0.107869322	0.001	0.253
36	5FRG vs 4FRG	1	0.8442737	2.7207237	0.098147642	0.050	1.000
37	5FRG vs 2BAK	1	1.0889193	3.0616713	0.059960264	0.018	1.000
38	5FRG vs 3BAK	1	0.5842861	1.7154010	0.045482772	0.150	1.000
39	5FRG vs 3FRG	1	0.5137925	1.6273962	0.054928762	0.161	1.000
40	5FRG vs 4BAK	1	0.7103371	2.1941875	0.070339626	0.082	1.000
41	5FRG vs 3.5BAK	1	0.3252224	1.0096635	0.032559641	0.365	1.000
42	5FRG vs ENRICHED	1	1.1322899	3.9705734	0.116882732	0.015	1.000
43	5FRG vs CONTROL	1	0.5471534	1.8403523	0.059673516	0.145	1.000
44	6FRG vs 5.5BAK	1	0.7695939	2.0913286	0.037284347	0.068	1.000
45	6FRG vs 5.5FRG	1	0.2083535	0.5858253	0.012851040	0.715	1.000
46	6FRG vs 6BAK	1	1.1401297	3.0892206	0.037179559	0.013	1.000
47	6FRG vs 1BAK	1	1.3081423	3.5055405	0.066765154	0.002	0.506
48	6FRG vs 1FOR	1	1.3318226	3.5398217	0.056601084	0.003	0.759
49	6FRG vs 0FRG	1	0.8234697	2.2893633	0.046447411	0.026	1.000
50	6FRG vs 0BAK	1	1.8196028	4.7184192	0.072906898	0.002	0.506
51	6FRG vs 0FOR	1	1.3529954	3.6287980	0.073118797	0.002	0.506
52	6FRG vs 1FRG	1	0.6115425	1.6826591	0.038520069	0.115	1.000
53	6FRG vs 2FRG	1	0.3782836	1.0122050	0.021530685	0.338	1.000
54	6FRG vs 3.5FRG	1	0.2478015	0.6755366	0.018419269	0.629	1.000
55	6FRG vs 2FOR	1	1.8686819	5.3333027	0.089887170	0.001	0.253
56	6FRG vs 4FRG	1	0.6333686	1.7489358	0.055086440	0.123	1.000
57	6FRG vs 2BAK	1	0.8338179	2.1900915	0.039682695	0.054	1.000
58	6FRG vs 3BAK	1	0.3604444	0.9615868	0.022915882	0.367	1.000
59	6FRG vs 3FRG	1	0.3502992	0.9676325	0.028486897	0.394	1.000
60	6FRG vs 4BAK	1	0.5184164	1.4106695	0.039837413	0.179	1.000
61	6FRG vs 3.5BAK	1	0.3222815	0.8833199	0.024616449	0.460	1.000
62	6FRG vs ENRICHED	1	1.2511256	3.7549885	0.096890456	0.010	1.000
63	6FRG vs CONTROL	1	0.6946945	2.0138627	0.055919099	0.072	1.000
64	5.5BAK vs 5.5FRG	1	0.7373212	1.9847259	0.042241939	0.082	1.000
65	5.5BAK vs 6BAK	1	0.2057888	0.5444480	0.006759597	0.736	1.000
66	5.5BAK vs 1BAK	1	0.9111746	2.3501392	0.045766949	0.031	1.000
67	5.5BAK vs 1FOR	1	0.5204921	1.3403649	0.022213404	0.226	1.000

68	5.5BAK vs 0FRG	1	1.1916040	3.1788019	0.063349498	0.002	0.506
69	5.5BAK vs 0BAK	1	0.8690596	2.1862143	0.035155932	0.025	1.000
70	5.5BAK vs 0FOR	1	0.5828988	1.5009825	0.031598977	0.161	1.000
71	5.5BAK vs 1FRG	1	0.9457468	2.4861295	0.055885498	0.026	1.000
72	5.5BAK vs 2FRG	1	0.4556355	1.1706442	0.024817219	0.291	1.000
73	5.5BAK vs 3.5FRG	1	0.6184156	1.5995381	0.042541430	0.116	1.000
74	5.5BAK vs 2FOR	1	0.6014413	1.6542216	0.029723202	0.139	1.000
75	5.5BAK vs 4FRG	1	0.7331997	1.8999502	0.059559661	0.063	1.000
76	5.5BAK vs 2BAK	1	0.5038190	1.2781714	0.023548535	0.221	1.000
77	5.5BAK vs 3BAK	1	0.3157189	0.8049361	0.019254571	0.545	1.000
78	5.5BAK vs 3FRG	1	0.6227986	1.6234931	0.046889928	0.136	1.000
79	5.5BAK vs 4BAK	1	0.3876036	0.9977927	0.028510160	0.400	1.000
80	5.5BAK vs 3.5BAK	1	0.4851982	1.2595420	0.034736843	0.273	1.000
81	5.5BAK vs ENRICHED	1	1.3481591	3.8131455	0.098243660	0.002	0.506
82	5.5BAK vs CONTROL	1	0.8265998	2.2589597	0.062300730	0.041	1.000
83	5.5FRG vs 6BAK	1	0.9529961	2.5657853	0.034877427	0.029	1.000
84	5.5FRG vs 1BAK	1	1.0272758	2.7157149	0.063576481	0.015	1.000
85	5.5FRG vs 1FOR	1	0.9556318	2.5090168	0.047782590	0.027	1.000
86	5.5FRG vs 0FRG	1	0.5807064	1.6046987	0.040517886	0.097	1.000
87	5.5FRG vs 0BAK	1	1.4307107	3.6512185	0.066809461	0.004	1.000
88	5.5FRG vs 0FOR	1	1.1129174	2.9419409	0.073655431	0.006	1.000
89	5.5FRG vs 1FRG	1	0.4341217	1.1829722	0.034607061	0.262	1.000
90	5.5FRG vs 2FRG	1	0.2134178	0.5625454	0.014976232	0.784	1.000
91	5.5FRG vs 3.5FRG	1	0.2628096	0.7059595	0.025480422	0.593	1.000
92	5.5FRG vs 2FOR	1	1.4919511	4.2583103	0.086448567	0.003	0.759
93	5.5FRG vs 4FRG	1	0.5474043	1.4909573	0.066291413	0.165	1.000
94	5.5FRG vs 2BAK	1	0.6936904	1.7928925	0.039152201	0.095	1.000
95	5.5FRG vs 3BAK	1	0.3599102	0.9429165	0.028622740	0.429	1.000
96	5.5FRG vs 3FRG	1	0.2792562	0.7622714	0.030783582	0.579	1.000
97	5.5FRG vs 4BAK	1	0.5527525	1.4794234	0.055870680	0.163	1.000
98	5.5FRG vs 3.5BAK	1	0.2905605	0.7856559	0.029331217	0.545	1.000
99	5.5FRG vs ENRICHED	1	1.0838700	3.3124651	0.113005342	0.016	1.000
100	5.5FRG vs CONTROL	1	0.5657480	1.6495462	0.061897722	0.141	1.000
101	6BAK vs 1BAK	1	0.9163178	2.3986044	0.030990280	0.033	1.000
102	6BAK vs 1FOR	1	0.4451606	1.1619528	0.013485683	0.283	1.000
103	6BAK vs 0FRG	1	1.8561397	4.9683721	0.063722917	0.002	0.506
104	6BAK vs 0BAK	1	1.0134465	2.6013078	0.029359700	0.028	1.000
105	6BAK vs 0FOR	1	0.4805731	1.2574220	0.017164432	0.245	1.000
106	6BAK vs 1FRG	1	1.3921760	3.6935025	0.051517953	0.007	1.000
107	6BAK vs 2FRG	1	0.6130003	1.6015816	0.021760152	0.160	1.000
108	6BAK vs 3.5FRG	1	0.8124471	2.1369187	0.033318076	0.062	1.000
109	6BAK vs 2FOR	1	0.5439968	1.4859717	0.018235921	0.178	1.000
110	6BAK vs 4FRG	1	0.7465215	1.9690738	0.033967661	0.075	1.000
111	6BAK vs 2BAK	1	0.7240587	1.8726765	0.023155862	0.099	1.000
112	6BAK vs 3BAK	1	0.5239744	1.3641389	0.019954013	0.243	1.000
113	6BAK vs 3FRG	1	0.7977339	2.1093576	0.034517751	0.065	1.000
114	6BAK vs 4BAK	1	0.3884154	1.0193992	0.016706149	0.374	1.000
115	6BAK vs 3.5BAK	1	0.4643828	1.2243637	0.019676597	0.279	1.000
116	6BAK vs ENRICHED	1	1.3032101	3.6088196	0.055856454	0.009	1.000
117	6BAK vs CONTROL	1	0.7842424	2.1296414	0.034277382	0.060	1.000
118	1BAK vs 1FOR	1	0.4827383	1.2224441	0.022136726	0.247	1.000
119	1BAK vs 0FRG	1	1.7647636	4.6233070	0.099163001	0.001	0.253
120	1BAK vs 0BAK	1	0.5080428	1.2550174	0.022309430	0.216	1.000
121	1BAK vs 0FOR	1	0.4479994	1.1284412	0.026785734	0.285	1.000
122	1BAK vs 1FRG	1	1.4055851	3.6139253	0.088982419	0.001	0.253
123	1BAK vs 2FRG	1	0.9524270	2.3931129	0.055149602	0.016	1.000
124	1BAK vs 3.5FRG	1	0.8478176	2.1312651	0.064327912	0.031	1.000
125	1BAK vs 2FOR	1	0.8066672	2.1902403	0.042786287	0.066	1.000
126	1BAK vs 4FRG	1	0.5576412	1.3954179	0.052865914	0.161	1.000
127	1BAK vs 2BAK	1	0.6486922	1.6129487	0.032510639	0.101	1.000
128	1BAK vs 3BAK	1	0.7983197	1.9827458	0.052201223	0.043	1.000
129	1BAK vs 3FRG	1	0.9297566	2.3510981	0.077463363	0.018	1.000

130	1BAK vs 4BAK	1	0.3949019	0.9854612	0.032864634	0.388	1.000
131	1BAK vs 3.5BAK	1	0.4524059	1.1408966	0.036636600	0.300	1.000
132	1BAK vs ENRICHED	1	0.7064447	1.9645504	0.061460286	0.052	1.000
133	1BAK vs CONTROL	1	0.4349736	1.1620952	0.038528331	0.270	1.000
134	1FOR vs 0FRG	1	1.6158568	4.2128246	0.074944190	0.002	0.506
135	1FOR vs 0BAK	1	0.5557168	1.3798646	0.020787397	0.180	1.000
136	1FOR vs 0FOR	1	0.3032458	0.7659840	0.014797053	0.619	1.000
137	1FOR vs 1FRG	1	1.2000626	3.0814980	0.061529668	0.007	1.000
138	1FOR vs 2FRG	1	0.6802737	1.7149275	0.032532105	0.104	1.000
139	1FOR vs 3.5FRG	1	0.7680932	1.9385643	0.045147394	0.059	1.000
140	1FOR vs 2FOR	1	0.3494773	0.9389481	0.015665074	0.411	1.000
141	1FOR vs 4FRG	1	0.5995996	1.5093824	0.041342315	0.155	1.000
142	1FOR vs 2BAK	1	0.7688973	1.9207819	0.032055354	0.066	1.000
143	1FOR vs 3BAK	1	0.6118240	1.5289021	0.032167840	0.149	1.000
144	1FOR vs 3FRG	1	0.7741779	1.9630971	0.049122746	0.055	1.000
145	1FOR vs 4BAK	1	0.4413144	1.1079574	0.027624378	0.340	1.000
146	1FOR vs 3.5BAK	1	0.4981682	1.2604532	0.030548699	0.273	1.000
147	1FOR vs ENRICHED	1	1.0325983	2.8096005	0.065630151	0.016	1.000
148	1FOR vs CONTROL	1	0.6766230	1.7868746	0.043810039	0.079	1.000
149	0FRG vs 0BAK	1	1.9212396	4.8755241	0.084241555	0.001	0.253
150	0FRG vs 0FOR	1	1.7749522	4.6465158	0.106457886	0.001	0.253
151	0FRG vs 1FRG	1	0.2185177	0.5878112	0.016517207	0.886	1.000
152	0FRG vs 2FRG	1	0.4851800	1.2667028	0.031457823	0.230	1.000
153	0FRG vs 3.5FRG	1	0.4338170	1.1486737	0.038100307	0.280	1.000
154	0FRG vs 2FOR	1	2.2573944	6.3656118	0.119283029	0.001	0.253
155	0FRG vs 4FRG	1	0.7643785	2.0416244	0.081529232	0.022	1.000
156	0FRG vs 2BAK	1	1.0032230	2.5745059	0.053001174	0.009	1.000
157	0FRG vs 3BAK	1	0.5582466	1.4471873	0.040826576	0.120	1.000
158	0FRG vs 3FRG	1	0.2572029	0.6898839	0.025848141	0.707	1.000
159	0FRG vs 4BAK	1	0.9610057	2.5334884	0.085783580	0.007	1.000
160	0FRG vs 3.5BAK	1	0.8698263	2.3158707	0.076391365	0.029	1.000
161	0FRG vs ENRICHED	1	2.0118340	5.9873198	0.176163341	0.001	0.253
162	0FRG vs CONTROL	1	1.3275018	3.7827374	0.122885024	0.001	0.253
163	0BAK vs 0FOR	1	0.4534349	1.1158544	0.021007935	0.300	1.000
164	0BAK vs 1FRG	1	1.5610550	3.8937402	0.075032946	0.001	0.253
165	0BAK vs 2FRG	1	1.1433025	2.8082080	0.051236997	0.006	1.000
166	0BAK vs 3.5FRG	1	0.9332382	2.2808198	0.051508075	0.013	1.000
167	0BAK vs 2FOR	1	0.7896268	2.0688926	0.033332198	0.050	1.000
168	0BAK vs 4FRG	1	0.5845675	1.4177230	0.037889078	0.127	1.000
169	0BAK vs 2BAK	1	0.9195846	2.2458804	0.036669901	0.024	1.000
170	0BAK vs 3BAK	1	0.8311474	2.0190111	0.041188328	0.034	1.000
171	0BAK vs 3FRG	1	0.9642135	2.3611874	0.057087031	0.010	1.000
172	0BAK vs 4BAK	1	0.4282903	1.0398955	0.025338649	0.358	1.000
173	0BAK vs 3.5BAK	1	0.7110802	1.7406263	0.040725335	0.059	1.000
174	0BAK vs ENRICHED	1	1.3369346	3.5044988	0.078744820	0.002	0.506
175	0BAK vs CONTROL	1	0.9006126	2.2933883	0.054225694	0.018	1.000
176	0FOR vs 1FRG	1	1.4505994	3.7204242	0.098631557	0.002	0.506
177	0FOR vs 2FRG	1	0.9224518	2.3086385	0.057274038	0.029	1.000
178	0FOR vs 3.5FRG	1	0.8580940	2.1456501	0.071176108	0.037	1.000
179	0FOR vs 2FOR	1	0.4496636	1.2230126	0.025898657	0.247	1.000
180	0FOR vs 4FRG	1	0.5683276	1.4117381	0.060300439	0.171	1.000
181	0FOR vs 2BAK	1	0.8374528	2.0739795	0.044057874	0.045	1.000
182	0FOR vs 3BAK	1	0.7139323	1.7633459	0.050724286	0.081	1.000
183	0FOR vs 3FRG	1	0.9119650	2.2939502	0.084046105	0.032	1.000
184	0FOR vs 4BAK	1	0.3963763	0.9827067	0.036419871	0.378	1.000
185	0FOR vs 3.5BAK	1	0.5460755	1.3699974	0.048290360	0.207	1.000
186	0FOR vs ENRICHED	1	0.9903926	2.7699238	0.093044370	0.018	1.000
187	0FOR vs CONTROL	1	0.7366302	1.9702553	0.070441089	0.064	1.000
188	1FRG vs 2FRG	1	0.3591398	0.9183220	0.026299146	0.454	1.000
189	1FRG vs 3.5FRG	1	0.3457987	0.8913141	0.035808239	0.481	1.000
190	1FRG vs 2FOR	1	1.8048314	5.0447529	0.107233061	0.001	0.253
191	1FRG vs 4FRG	1	0.6718010	1.7349406	0.087912128	0.071	1.000

192	1FRG vs 2BAK	1	0.8118325	2.0440529	0.047487463	0.050	1.000
193	1FRG vs 3BAK	1	0.4262255	1.0772502	0.035816113	0.282	1.000
194	1FRG vs 3FRG	1	0.2085955	0.5440182	0.025251473	0.877	1.000
195	1FRG vs 4BAK	1	0.8167450	2.0892344	0.086728968	0.039	1.000
196	1FRG vs 3.5BAK	1	0.6534023	1.6932444	0.068571160	0.103	1.000
197	1FRG vs ENRICHED	1	1.5969707	4.7288786	0.170539844	0.002	0.506
198	1FRG vs CONTROL	1	1.1063757	3.1069679	0.123749229	0.007	1.000
199	2FRG vs 3.5FRG	1	0.3501905	0.8725169	0.030219635	0.492	1.000
200	2FRG vs 2FOR	1	1.1072652	3.0044502	0.061309743	0.017	1.000
201	2FRG vs 4FRG	1	0.6325513	1.5641797	0.066379552	0.126	1.000
202	2FRG vs 2BAK	1	0.4620858	1.1418476	0.024746464	0.289	1.000
203	2FRG vs 3BAK	1	0.2618564	0.6448230	0.019165592	0.742	1.000
204	2FRG vs 3FRG	1	0.3058020	0.7661171	0.029733508	0.584	1.000
205	2FRG vs 4BAK	1	0.5336542	1.3180034	0.048246696	0.218	1.000
206	2FRG vs 3.5BAK	1	0.3700953	0.9250459	0.033126031	0.421	1.000
207	2FRG vs ENRICHED	1	1.2528369	3.4894130	0.114446711	0.005	1.000
208	2FRG vs CONTROL	1	0.7396542	1.9702053	0.070439431	0.060	1.000
209	3.5FRG vs 2FOR	1	1.1682041	3.2431921	0.082643433	0.014	1.000
210	3.5FRG vs 4FRG	1	0.3506134	0.8567026	0.066634703	0.561	1.000
211	3.5FRG vs 2BAK	1	0.5702075	1.4029643	0.038539836	0.185	1.000
212	3.5FRG vs 3BAK	1	0.3429303	0.8377180	0.035142542	0.547	1.000
213	3.5FRG vs 3FRG	1	0.1885868	0.4719932	0.030506297	0.834	1.000
214	3.5FRG vs 4BAK	1	0.4946213	1.2097783	0.070295985	0.237	1.000
215	3.5FRG vs 3.5BAK	1	0.3847486	0.9595296	0.053427324	0.428	1.000
216	3.5FRG vs ENRICHED	1	1.1047531	3.2900195	0.162149648	0.015	1.000
217	3.5FRG vs CONTROL	1	0.7269524	2.0139736	0.111800633	0.067	1.000
218	2FOR vs 4FRG	1	0.8495572	2.3985144	0.074031618	0.029	1.000
219	2FOR vs 2BAK	1	1.1017182	2.9283381	0.052358754	0.019	1.000
220	2FOR vs 3BAK	1	0.9620964	2.6070887	0.059785892	0.022	1.000
221	2FOR vs 3FRG	1	1.1391627	3.2107612	0.088668703	0.011	1.000
222	2FOR vs 4BAK	1	0.5637008	1.5637178	0.043969469	0.179	1.000
223	2FOR vs 3.5BAK	1	0.8377126	2.3396940	0.062659698	0.060	1.000
224	2FOR vs ENRICHED	1	1.2692228	3.8887719	0.099997293	0.012	1.000
225	2FOR vs CONTROL	1	0.8590301	2.5419071	0.069561423	0.048	1.000
226	4FRG vs 2BAK	1	0.6463636	1.5773135	0.051584438	0.125	1.000
227	4FRG vs 3BAK	1	0.5700724	1.3699578	0.074575993	0.184	1.000
228	4FRG vs 3FRG	1	0.4354380	1.0730705	0.106528636	0.328	1.000
229	4FRG vs 4BAK	1	0.4529352	1.0783099	0.097335234	0.332	1.000
230	4FRG vs 3.5BAK	1	0.4409127	1.0837185	0.089684186	0.308	1.000
231	4FRG vs ENRICHED	1	0.7443930	2.4317981	0.181047844	0.090	1.000
232	4FRG vs CONTROL	1	0.6373126	1.8558680	0.156535816	0.084	1.000
233	2BAK vs 3BAK	1	0.3793501	0.9259178	0.022624241	0.452	1.000
234	2BAK vs 3FRG	1	0.5192265	1.2814434	0.038503239	0.239	1.000
235	2BAK vs 4BAK	1	0.5344828	1.3051238	0.038044572	0.231	1.000
236	2BAK vs 3.5BAK	1	0.5430519	1.3389896	0.037889867	0.221	1.000
237	2BAK vs ENRICHED	1	1.4494896	3.8862925	0.102577798	0.003	0.759
238	2BAK vs CONTROL	1	0.9382866	2.4288877	0.068556703	0.030	1.000
239	3BAK vs 3FRG	1	0.3042437	0.7460328	0.035960263	0.584	1.000
240	3BAK vs 4BAK	1	0.4254716	1.0264527	0.046600909	0.367	1.000
241	3BAK vs 3.5BAK	1	0.3336752	0.8175039	0.035827928	0.507	1.000
242	3BAK vs ENRICHED	1	1.2091907	3.3795953	0.133161906	0.009	1.000
243	3BAK vs CONTROL	1	0.7343296	1.9426058	0.084672413	0.069	1.000
244	3FRG vs 4BAK	1	0.6554326	1.6129551	0.110378436	0.105	1.000
245	3FRG vs 3.5BAK	1	0.4747417	1.1959159	0.078699825	0.226	1.000
246	3FRG vs ENRICHED	1	1.2655867	3.9821683	0.221450953	0.012	1.000
247	3FRG vs CONTROL	1	0.8527801	2.4547280	0.158833466	0.059	1.000
248	4BAK vs 3.5BAK	1	0.2467137	0.6060866	0.038836551	0.790	1.000
249	4BAK vs ENRICHED	1	0.5733288	1.7207700	0.102912125	0.108	1.000
250	4BAK vs CONTROL	1	0.3961235	1.0950038	0.072540810	0.338	1.000
251	3.5BAK vs ENRICHED	1	0.5085599	1.5432316	0.087967348	0.203	1.000
252	3.5BAK vs CONTROL	1	0.2802002	0.7871488	0.049860102	0.532	1.000

253 ENRICHED vs CONTROL	1	0.2582796	0.9155934	0.057528073	0.419	1.000
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Table 2: Sediment; Pairwise comparison by Sampling Location, with Bonferroni Correction

	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1	6BAK vs 6FRG	1	0.3855676	1.5593053	0.3420050	0.1000000		1
2	6BAK vs 2FRG	1	0.4958687	1.5606224	0.3421950	0.1000000		1
3	6BAK vs 0BAK	1	0.3962488	1.5027592	0.3337418	0.1000000		1
4	6BAK vs 1FOR	1	0.4638704	1.9212071	0.3903935	0.1000000		1
5	6BAK vs 0FOR	1	0.4866138	1.9328930	0.3918376	0.1000000		1
6	6BAK vs 5.5FRG	1	0.5382917	2.0914689	0.4107791	0.1000000		1
7	6BAK vs 1BAK	1	0.4744284	2.0936203	0.5114349	0.2500000		1
8	6BAK vs 5FRG	1	0.5412134	1.7260878	0.3652255	0.1000000		1
9	6BAK vs 2BAK	1	0.4124152	1.6185772	0.3504493	0.1000000		1
10	6BAK vs 4FRG	1	0.3054388	1.3478807	0.4026071	0.2500000		1
11	6BAK vs 0FRG	1	0.5417201	1.7049281	0.3623707	0.1000000		1
12	6BAK vs 5.5BAK	1	0.4598536	1.8914168	0.3866808	0.1000000		1
13	6BAK vs 1FRG	1	0.4708560	1.7766981	0.3719511	0.1000000		1
14	6BAK vs 5BAK	1	0.4277446	1.7576065	0.3694308	0.1000000		1
15	6BAK vs 3BAK	1	0.3820363	1.6859002	0.4573917	0.2500000		1
16	6BAK vs 3.5BAK	1	0.4014235	1.3821946	0.3154115	0.1000000		1
17	6BAK vs 4BAK	1	0.5369799	2.1522352	0.4177284	0.1000000		1
18	6BAK vs 3.5FRG	1	0.4891561	2.1586127	0.5190704	0.2500000		1
19	6BAK vs 3FRG	1	0.5120122	2.2594753	0.5304586	0.2500000		1
20	6FRG vs 2FRG	1	0.3872575	0.9821478	0.3293424	0.6666667		1
21	6FRG vs 0BAK	1	0.3295030	1.0520157	0.3446954	0.3333333		1
22	6FRG vs 1FOR	1	0.4173902	1.4914202	0.4271672	0.3333333		1
23	6FRG vs 0FOR	1	0.4532102	1.5346358	0.4341708	0.3333333		1
24	6FRG vs 5.5FRG	1	0.4035654	1.3286007	0.3991469	0.3333333		1
25	6FRG vs 1BAK	1	0.4040250	1.3999819	0.5833302	0.3333333		1
26	6FRG vs 5FRG	1	0.4466703	1.1511719	0.3653155	0.3333333		1
27	6FRG vs 2BAK	1	0.2538847	0.8465885	0.2974046	1.0000000		1
28	6FRG vs 4FRG	1	0.2757046	0.9553403	0.4885801	0.6666667		1
29	6FRG vs 0FRG	1	0.4274868	1.0841760	0.3515286	0.3333333		1
30	6FRG vs 5.5BAK	1	0.3316134	1.1743533	0.3699504	0.3333333		1
31	6FRG vs 1FRG	1	0.3848189	1.2208102	0.3790382	0.3333333		1
32	6FRG vs 5BAK	1	0.3017790	1.0673326	0.3479677	0.6666667		1
33	6FRG vs 3BAK	1	0.3337751	1.1565597	0.5362985	0.3333333		1
34	6FRG vs 3.5BAK	1	0.3629902	1.0273494	0.3393561	0.6666667		1
35	6FRG vs 4BAK	1	0.3947141	1.3520482	0.4033499	0.3333333		1
36	6FRG vs 3.5FRG	1	0.4426548	1.5338374	0.6053417	0.3333333		1
37	6FRG vs 3FRG	1	0.3991205	1.3829873	0.5803587	0.3333333		1
38	2FRG vs 0BAK	1	0.4227588	1.0091766	0.3353664	0.3333333		1
39	2FRG vs 1FOR	1	0.4990388	1.2943075	0.3928921	0.3333333		1
40	2FRG vs 0FOR	1	0.4920726	1.2270389	0.3802368	0.3333333		1
41	2FRG vs 5.5FRG	1	0.4559986	1.1136701	0.3576712	0.3333333		1
42	2FRG vs 1BAK	1	0.3888379	0.7776758	0.4374677	1.0000000		1
43	2FRG vs 5FRG	1	0.4239099	0.8586091	0.3003591	1.0000000		1
44	2FRG vs 2BAK	1	0.3969640	0.9787204	0.3285707	1.0000000		1
45	2FRG vs 4FRG	1	0.3527104	0.7054207	0.4136344	1.0000000		1
46	2FRG vs 0FRG	1	0.3966208	0.7932416	0.2839860	1.0000000		1
47	2FRG vs 5.5BAK	1	0.4115974	1.0605908	0.3465314	0.3333333		1
48	2FRG vs 1FRG	1	0.3838677	0.9119741	0.3131807	1.0000000		1
49	2FRG vs 5BAK	1	0.4423307	1.1387221	0.3627980	0.3333333		1
50	2FRG vs 3BAK	1	0.3981151	0.7962302	0.4432785	1.0000000		1
51	2FRG vs 3.5BAK	1	0.3949464	0.8603926	0.3007953	1.0000000		1
52	2FRG vs 4BAK	1	0.4396523	1.1056504	0.3560125	0.3333333		1

53	2FRG vs 3.5FRG	1	0.4059410	0.8118821	0.4480877	1.0000000	1
54	2FRG vs 3FRG	1	0.4125072	0.8250144	0.4520591	1.0000000	1
55	0BAK vs 1FOR	1	0.3618940	1.1885680	0.3727592	0.3333333	1
56	0BAK vs 0FOR	1	0.3831519	1.1975775	0.3745265	0.3333333	1
57	0BAK vs 5.5FRG	1	0.3763146	1.1460067	0.3642735	0.3333333	1
58	0BAK vs 1BAK	1	0.4156401	1.2303262	0.5516351	0.3333333	1
59	0BAK vs 5FRG	1	0.4413040	1.0694866	0.3484252	0.6666667	1
60	0BAK vs 2BAK	1	0.3483900	1.0735894	0.3492950	0.3333333	1
61	0BAK vs 4FRG	1	0.3390026	1.0034733	0.5008668	0.6666667	1
62	0BAK vs 0FRG	1	0.3996552	0.9540255	0.3229578	0.6666667	1
63	0BAK vs 5.5BAK	1	0.3903759	1.2715923	0.3886769	0.3333333	1
64	0BAK vs 1FRG	1	0.3981052	1.1714693	0.3693775	0.3333333	1
65	0BAK vs 5BAK	1	0.3627574	1.1802386	0.3711164	0.3333333	1
66	0BAK vs 3BAK	1	0.2854609	0.8449858	0.4579904	1.0000000	1
67	0BAK vs 3.5BAK	1	0.3322576	0.8791162	0.3053424	1.0000000	1
68	0BAK vs 4BAK	1	0.3479543	1.0991873	0.3546695	0.3333333	1
69	0BAK vs 3.5FRG	1	0.4039402	1.1956934	0.5445630	0.3333333	1
70	0BAK vs 3FRG	1	0.4347708	1.2869545	0.5627373	0.3333333	1
71	1FOR vs 0FOR	1	0.2764803	0.9647282	0.3254019	0.6666667	1
72	1FOR vs 5.5FRG	1	0.4096816	1.3886568	0.4097956	0.3333333	1
73	1FOR vs 1BAK	1	0.4855992	1.7910283	0.6417091	0.3333333	1
74	1FOR vs 5FRG	1	0.4787878	1.2623550	0.3869459	0.3333333	1
75	1FOR vs 2BAK	1	0.4439791	1.5248665	0.4326026	0.3333333	1
76	1FOR vs 4FRG	1	0.4144084	1.5284563	0.6045018	0.3333333	1
77	1FOR vs 0FRG	1	0.4640504	1.2035613	0.3756948	0.3333333	1
78	1FOR vs 5.5BAK	1	0.5284942	1.9312960	0.4912619	0.3333333	1
79	1FOR vs 1FRG	1	0.4862593	1.5865737	0.4423647	0.3333333	1
80	1FOR vs 5BAK	1	0.5053277	1.8442001	0.4797357	0.3333333	1
81	1FOR vs 3BAK	1	0.3563029	1.3141465	0.5678752	0.3333333	1
82	1FOR vs 3.5BAK	1	0.4130257	1.1985839	0.3747233	0.3333333	1
83	1FOR vs 4BAK	1	0.5128524	1.8108832	0.4751873	0.3333333	1
84	1FOR vs 3.5FRG	1	0.4862992	1.7936099	0.6420402	0.3333333	1
85	1FOR vs 3FRG	1	0.5074959	1.8717893	0.6517850	0.3333333	1
86	0FOR vs 5.5FRG	1	0.4142956	1.3343706	0.4001866	0.3333333	1
87	0FOR vs 1BAK	1	0.4826544	1.5979345	0.6150788	0.3333333	1
88	0FOR vs 5FRG	1	0.4668970	1.1827917	0.3716208	0.3333333	1
89	0FOR vs 2BAK	1	0.4826464	1.5740895	0.4404169	0.3333333	1
90	0FOR vs 4FRG	1	0.4150579	1.3741410	0.5787950	0.3333333	1
91	0FOR vs 0FRG	1	0.4562666	1.1377525	0.3626011	0.3333333	1
92	0FOR vs 5.5BAK	1	0.5462237	1.8893443	0.4857745	0.3333333	1
93	0FOR vs 1FRG	1	0.4524631	1.4054094	0.4126991	0.3333333	1
94	0FOR vs 5BAK	1	0.5287573	1.8266439	0.4773488	0.3333333	1
95	0FOR vs 3BAK	1	0.3942882	1.3053786	0.5662318	0.3333333	1
96	0FOR vs 3.5BAK	1	0.3996079	1.1098528	0.3568827	0.3333333	1
97	0FOR vs 4BAK	1	0.5282553	1.7687170	0.4693154	0.3333333	1
98	0FOR vs 3.5FRG	1	0.4711450	1.5598300	0.6093491	0.3333333	1
99	0FOR vs 3FRG	1	0.4947730	1.6380556	0.6209329	0.3333333	1
100	5.5FRG vs 1BAK	1	0.4867158	1.5261787	0.6041452	0.3333333	1
101	5.5FRG vs 5FRG	1	0.4440491	1.1013868	0.3551272	0.3333333	1
102	5.5FRG vs 2BAK	1	0.4192976	1.3308895	0.3995598	0.3333333	1
103	5.5FRG vs 4FRG	1	0.3950424	1.2387214	0.5533165	0.3333333	1
104	5.5FRG vs 0FRG	1	0.4327277	1.0568365	0.3457288	0.6666667	1
105	5.5FRG vs 5.5BAK	1	0.4783726	1.6077654	0.4456402	0.3333333	1
106	5.5FRG vs 1FRG	1	0.4102052	1.2416342	0.3830272	0.3333333	1
107	5.5FRG vs 5BAK	1	0.4612125	1.5482098	0.4363355	0.3333333	1
108	5.5FRG vs 3BAK	1	0.3826823	1.1999641	0.5454471	0.3333333	1
109	5.5FRG vs 3.5BAK	1	0.4292791	1.1649802	0.3680845	0.3333333	1
110	5.5FRG vs 4BAK	1	0.4347021	1.4155203	0.4144377	0.3333333	1
111	5.5FRG vs 3.5FRG	1	0.4812455	1.5090254	0.6014389	0.3333333	1
112	5.5FRG vs 3FRG	1	0.4464399	1.3998867	0.5833137	0.3333333	1
113	1BAK vs 5FRG	1	0.4514617	0.9262006	0.4808433	1.0000000	1
114	1BAK vs 2BAK	1	0.4050369	1.3015747	0.5655149	0.3333333	1

115	1BAK vs 4FRG	1	0.3806875	0.0000000	1.0000000	1.0000000	1
116	1BAK vs 0FRG	1	0.4429496	0.8858991	0.4697489	1.0000000	1
117	1BAK vs 5.5BAK	1	0.3836016	1.3890244	0.5814191	0.3333333	1
118	1BAK vs 1FRG	1	0.4420389	1.2931202	0.5639130	0.3333333	1
119	1BAK vs 5BAK	1	0.4029772	1.4553713	0.5927296	0.3333333	1
120	1BAK vs 3BAK	1	0.3892229	0.0000000	1.0000000	1.0000000	1
121	1BAK vs 3.5BAK	1	0.3073176	0.7351026	0.4236652	1.0000000	1
122	1BAK vs 4BAK	1	0.4053525	1.3727608	0.5785500	0.3333333	1
123	1BAK vs 3.5FRG	1	0.3630714	0.0000000	1.0000000	1.0000000	1
124	1BAK vs 3FRG	1	0.4396811	0.0000000	1.0000000	1.0000000	1
125	5FRG vs 2BAK	1	0.4537209	1.1362567	0.3622971	0.3333333	1
126	5FRG vs 4FRG	1	0.3962943	0.8130214	0.4484345	1.0000000	1
127	5FRG vs 0FRG	1	0.4237436	0.8582723	0.3002766	1.0000000	1
128	5FRG vs 5.5BAK	1	0.4897444	1.2827245	0.3907500	0.3333333	1
129	5FRG vs 1FRG	1	0.4432155	1.0689252	0.3483061	0.3333333	1
130	5FRG vs 5BAK	1	0.4802680	1.2567136	0.3858840	0.3333333	1
131	5FRG vs 3BAK	1	0.4099051	0.8409448	0.4568007	1.0000000	1
132	5FRG vs 3.5BAK	1	0.4404211	0.9727744	0.3272278	0.6666667	1
133	5FRG vs 4BAK	1	0.4877264	1.2462400	0.3839026	0.3333333	1
134	5FRG vs 3.5FRG	1	0.4596567	0.9430131	0.4853354	1.0000000	1
135	5FRG vs 3FRG	1	0.4329953	0.8883157	0.4704275	1.0000000	1
136	2BAK vs 4FRG	1	0.2956746	0.9501420	0.4872168	0.6666667	1
137	2BAK vs 0FRG	1	0.4241486	1.0457444	0.3433461	0.6666667	1
138	2BAK vs 5.5BAK	1	0.2845534	0.9689299	0.3263566	0.6666667	1
139	2BAK vs 1FRG	1	0.4073675	1.2476248	0.3841653	0.3333333	1
140	2BAK vs 5BAK	1	0.2911624	0.9902144	0.3311516	0.6666667	1
141	2BAK vs 3BAK	1	0.3443338	1.1065072	0.5252805	0.6666667	1
142	2BAK vs 3.5BAK	1	0.3577734	0.9812083	0.3291311	0.6666667	1
143	2BAK vs 4BAK	1	0.3727074	1.2290991	0.3806322	0.3333333	1
144	2BAK vs 3.5FRG	1	0.4369397	1.4040933	0.5840428	0.3333333	1
145	2BAK vs 3FRG	1	0.3822404	1.2283187	0.5512312	0.3333333	1
146	4FRG vs 0FRG	1	0.3807028	0.7614057	0.4322716	1.0000000	1
147	4FRG vs 5.5BAK	1	0.3241665	1.1738097	0.5399781	0.3333333	1
148	4FRG vs 1FRG	1	0.3229228	0.9446634	0.4857722	0.6666667	1
149	4FRG vs 5BAK	1	0.3247960	1.1730161	0.5398101	0.3333333	1
150	4FRG vs 3BAK	1	0.3394303	0.0000000	1.0000000	1.0000000	1
151	4FRG vs 3.5BAK	1	0.3425739	0.8194356	0.4503790	1.0000000	1
152	4FRG vs 4BAK	1	0.3697744	1.2522726	0.5560040	0.3333333	1
153	4FRG vs 3.5FRG	1	0.3918019	0.0000000	1.0000000	1.0000000	1
154	4FRG vs 3FRG	1	0.3605888	0.0000000	1.0000000	1.0000000	1
155	0FRG vs 5.5BAK	1	0.4471973	1.1523237	0.3655474	0.3333333	1
156	0FRG vs 1FRG	1	0.4067189	0.9662628	0.3257509	1.0000000	1
157	0FRG vs 5BAK	1	0.4633577	1.1928534	0.3736011	0.3333333	1
158	0FRG vs 3BAK	1	0.3610378	0.7220757	0.4193054	1.0000000	1
159	0FRG vs 3.5BAK	1	0.4126058	0.8988638	0.3100745	1.0000000	1
160	0FRG vs 4BAK	1	0.4143122	1.0419244	0.3425215	0.6666667	1
161	0FRG vs 3.5FRG	1	0.4295211	0.8590422	0.4620886	1.0000000	1
162	0FRG vs 3FRG	1	0.4272198	0.8544395	0.4607535	1.0000000	1
163	5.5BAK vs 1FRG	1	0.4202867	1.3601397	0.4047866	0.3333333	1
164	5.5BAK vs 5BAK	1	0.2897964	1.0479827	0.3438283	0.3333333	1
165	5.5BAK vs 3BAK	1	0.3840775	1.3907479	0.5817209	0.3333333	1
166	5.5BAK vs 3.5BAK	1	0.3800185	1.0947961	0.3537539	0.3333333	1
167	5.5BAK vs 4BAK	1	0.3805671	1.3319377	0.3997487	0.3333333	1
168	5.5BAK vs 3.5FRG	1	0.4661038	1.6877655	0.6279437	0.3333333	1
169	5.5BAK vs 3FRG	1	0.3708260	1.3427640	0.5731538	0.3333333	1
170	1FRG vs 5BAK	1	0.4465598	1.4434755	0.4191915	0.3333333	1
171	1FRG vs 3BAK	1	0.3953400	1.1565093	0.5362877	0.3333333	1
172	1FRG vs 3.5BAK	1	0.3858702	1.0155818	0.3367781	0.6666667	1
173	1FRG vs 4BAK	1	0.4640870	1.4568239	0.4214342	0.3333333	1
174	1FRG vs 3.5FRG	1	0.4113319	1.2032913	0.5461336	0.3333333	1
175	1FRG vs 3FRG	1	0.4024077	1.1771848	0.5406913	0.3333333	1
176	5BAK vs 3BAK	1	0.3467162	1.2521822	0.5559862	0.3333333	1

177	5BAK vs 3.5BAK	1	0.3489620	1.0042789	0.3342829	0.6666667	1
178	5BAK vs 4BAK	1	0.3769011	1.3174391	0.3971253	0.3333333	1
179	5BAK vs 3.5FRG	1	0.4674924	1.6883711	0.6280275	0.3333333	1
180	5BAK vs 3FRG	1	0.4082223	1.4743144	0.5958476	0.3333333	1
181	3BAK vs 3.5BAK	1	0.3248333	0.7770002	0.4372538	1.0000000	1
182	3BAK vs 4BAK	1	0.3058436	1.0357656	0.5087843	0.6666667	1
183	3BAK vs 3.5FRG	1	0.4004603	0.0000000	1.0000000	1.0000000	1
184	3BAK vs 3FRG	1	0.4415074	0.0000000	1.0000000	1.0000000	1
185	3.5BAK vs 4BAK	1	0.3967507	1.1123692	0.3574027	0.3333333	1
186	3.5BAK vs 3.5FRG	1	0.3864990	0.9245043	0.4803857	1.0000000	1
187	3.5BAK vs 3FRG	1	0.4440444	1.0621526	0.5150698	0.3333333	1
188	4BAK vs 3.5FRG	1	0.4119893	1.3952369	0.5825048	0.3333333	1
189	4BAK vs 3FRG	1	0.4413447	1.4946515	0.5991424	0.3333333	1
190	3.5FRG vs 3FRG	1	0.4534706	0.0000000	1.0000000	1.0000000	1

Table 3: Water, Pairwise comparison by Sampling Location with Bonferroni correction

	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1	6BAK vs 0BAK	1	0.32016240	1.7843508	0.3084790	0.1000000		1
2	6BAK vs 2FRG	1	0.41847315	2.4324030	0.4477582	0.1000000		1
3	6BAK vs 5.5BAK	1	0.09491422	0.9103601	0.2328072	0.7000000		1
4	6BAK vs 1BAK	1	0.14786142	1.3765450	0.4076786	0.2500000		1
5	6BAK vs 5.5FRG	1	0.67842315	6.5339202	0.6853341	0.1000000		1
6	6BAK vs 1FOR	1	0.20995240	1.8748108	0.3191270	0.1000000		1
7	6BAK vs 4FRG	1	0.68353063	6.2877941	0.6769954	0.1000000		1
8	6BAK vs 6FRG	1	0.52077435	4.0600684	0.5037263	0.1000000		1
9	6BAK vs 2BAK	1	0.27621031	1.9598435	0.3951422	0.1000000		1
10	6BAK vs 3.5FRG	1	0.72260768	7.4713072	0.7135028	0.1000000		1
11	6BAK vs 2FOR	1	0.67555156	6.2891801	0.7587216	0.2500000		1
12	6BAK vs 1FRG	1	0.53449658	2.9781417	0.4981718	0.1000000		1
13	6BAK vs 0FOR	1	0.29141252	2.7129621	0.5756384	0.2500000		1
14	6BAK vs 0FRG	1	0.41746500	3.8864725	0.6602379	0.2500000		1
15	6BAK vs 3BAK	1	0.14160806	1.3901424	0.3166509	0.2000000		1
16	6BAK vs 3.5BAK	1	0.13375802	1.2452466	0.3837140	0.2500000		1
17	6BAK vs 3FRG	1	0.68916319	7.0513719	0.7015333	0.1000000		1
18	6BAK vs 5BAK	1	0.22531788	2.0976411	0.5119143	0.2500000		1
19	6BAK vs 5FRG	1	0.33534108	3.1219237	0.6095217	0.2500000		1
20	0BAK vs 2FRG	1	0.25901256	0.9662540	0.2436188	0.4000000		1
21	0BAK vs 5.5BAK	1	0.25278660	1.2621817	0.2961351	0.3000000		1
22	0BAK vs 1BAK	1	0.09550422	0.3798275	0.1596030	1.0000000		1
23	0BAK vs 5.5FRG	1	0.41154364	2.0592795	0.4070302	0.2000000		1
24	0BAK vs 1FOR	1	0.16162306	0.8783911	0.1800575	0.7000000		1
25	0BAK vs 4FRG	1	0.39806302	1.9443796	0.3932505	0.2000000		1
26	0BAK vs 6FRG	1	0.32434695	1.6194639	0.2881883	0.2000000		1
27	0BAK vs 2BAK	1	0.15470639	0.6529010	0.1787349	1.0000000		1
28	0BAK vs 3.5FRG	1	0.39539909	2.0515155	0.4061188	0.2000000		1
29	0BAK vs 2FOR	1	0.59143575	2.3521849	0.5404607	0.2500000		1
30	0BAK vs 1FRG	1	0.26192962	0.9507752	0.2406553	0.5000000		1
31	0BAK vs 0FOR	1	0.14496490	0.5765364	0.2237641	0.7500000		1
32	0BAK vs 0FRG	1	0.21064435	0.8377486	0.2952159	0.5000000		1
33	0BAK vs 3BAK	1	0.21581755	1.0906305	0.2666167	0.4000000		1
34	0BAK vs 3.5BAK	1	0.11403828	0.4535389	0.1848509	1.0000000		1
35	0BAK vs 3FRG	1	0.35556844	1.8351726	0.3795465	0.2000000		1
36	0BAK vs 5BAK	1	0.16382708	0.6515527	0.2457250	0.7500000		1

37	0BAK vs 5FRG	1	0.17959757	0.7142732	0.2631545	0.7500000	1
38	2FRG vs 5.5BAK	1	0.31526405	1.5793058	0.4412324	0.3333333	1
39	2FRG vs 1BAK	1	0.19464589	0.6460345	0.3924793	0.6666667	1
40	2FRG vs 5.5FRG	1	0.19808731	0.9955226	0.3323369	0.6666667	1
41	2FRG vs 1FOR	1	0.27625021	1.5507849	0.3407731	0.2000000	1
42	2FRG vs 4FRG	1	0.21343292	1.0346101	0.3409367	0.6666667	1
43	2FRG vs 6FRG	1	0.15559130	0.7785624	0.2060472	0.5000000	1
44	2FRG vs 2BAK	1	0.12537283	0.4923646	0.1975492	0.6666667	1
45	2FRG vs 3.5FRG	1	0.22290837	1.1837413	0.3718083	0.6666667	1
46	2FRG vs 2FOR	1	0.56041190	1.8600208	0.6503522	0.3333333	1
47	2FRG vs 1FRG	1	0.29613738	0.9478169	0.3215318	0.6666667	1
48	2FRG vs 0FOR	1	0.16854375	0.5594008	0.3587280	1.0000000	1
49	2FRG vs 0FRG	1	0.15685167	0.5205945	0.3423625	1.0000000	1
50	2FRG vs 3BAK	1	0.31699027	1.6170449	0.4470624	0.3333333	1
51	2FRG vs 3.5BAK	1	0.17071385	0.5666034	0.3616764	0.6666667	1
52	2FRG vs 3FRG	1	0.24780750	1.3053923	0.3949281	0.3333333	1
53	2FRG vs 5BAK	1	0.11602718	0.3850970	0.2780289	1.0000000	1
54	2FRG vs 5FRG	1	0.11151790	0.3701306	0.2701426	1.0000000	1
55	5.5BAK vs 1BAK	1	0.14366749	1.4667359	0.5946060	0.3333333	1
56	5.5BAK vs 5.5FRG	1	0.54136914	5.5635294	0.7355732	0.3333333	1
57	5.5BAK vs 1FOR	1	0.20696576	1.8754580	0.3846732	0.1000000	1
58	5.5BAK vs 4FRG	1	0.56204011	5.3721198	0.7287076	0.3333333	1
59	5.5BAK vs 6FRG	1	0.39588705	2.9977043	0.4998086	0.2000000	1
60	5.5BAK vs 2BAK	1	0.23615848	1.5438962	0.4356494	0.3333333	1
61	5.5BAK vs 3.5FRG	1	0.59674186	6.8878479	0.7749736	0.3333333	1
62	5.5BAK vs 2FOR	1	0.59830123	6.1082011	0.8593174	0.3333333	1
63	5.5BAK vs 1FRG	1	0.43259810	2.0524640	0.5064731	0.3333333	1
64	5.5BAK vs 0FOR	1	0.26254293	2.6803639	0.7282877	0.3333333	1
65	5.5BAK vs 0FRG	1	0.36969286	3.7742833	0.7905445	0.3333333	1
66	5.5BAK vs 3BAK	1	0.12368256	1.3107637	0.3959098	0.3333333	1
67	5.5BAK vs 3.5BAK	1	0.14165288	1.4461683	0.5911974	0.3333333	1
68	5.5BAK vs 3FRG	1	0.55954859	6.3468018	0.7603873	0.3333333	1
69	5.5BAK vs 5BAK	1	0.20860286	2.1296768	0.6804782	0.3333333	1
70	5.5BAK vs 5FRG	1	0.30425628	3.1062255	0.7564673	0.3333333	1
71	1BAK vs 5.5FRG	1	0.30249796	3.1294052	0.7578344	0.3333333	1
72	1BAK vs 1FOR	1	0.05759692	0.4941527	0.1981245	1.0000000	1
73	1BAK vs 4FRG	1	0.28216662	2.5353527	0.7171428	0.3333333	1
74	1BAK vs 6FRG	1	0.22789591	1.5282732	0.4331505	0.2500000	1
75	1BAK vs 2BAK	1	0.09432375	0.4535344	0.3120218	1.0000000	1
76	1BAK vs 3.5FRG	1	0.25633100	3.4030754	0.7728860	0.3333333	1
77	1BAK vs 2FOR	1	0.49418046	0.0000000	1.0000000	1.0000000	1
78	1BAK vs 1FRG	1	0.17926984	0.5540034	0.3565008	0.6666667	1
79	1BAK vs 0FOR	1	0.08070192	0.0000000	1.0000000	1.0000000	1
80	1BAK vs 0FRG	1	0.15264425	0.0000000	1.0000000	1.0000000	1
81	1BAK vs 3BAK	1	0.10587184	1.1664026	0.5384053	0.6666667	1
82	1BAK vs 3.5BAK	1	0.05246531	0.0000000	1.0000000	1.0000000	1
83	1BAK vs 3FRG	1	0.20019370	2.5543348	0.7186534	0.3333333	1
84	1BAK vs 5BAK	1	0.11221262	0.0000000	1.0000000	1.0000000	1
85	1BAK vs 5FRG	1	0.13694568	0.0000000	1.0000000	1.0000000	1
86	5.5FRG vs 1FOR	1	0.46469155	4.2273260	0.5849087	0.1000000	1
87	5.5FRG vs 4FRG	1	0.06265637	0.6025928	0.2315356	1.0000000	1
88	5.5FRG vs 6FRG	1	0.09807794	0.7450790	0.1989488	0.9000000	1
89	5.5FRG vs 2BAK	1	0.17556946	1.1526435	0.3656117	0.3333333	1
90	5.5FRG vs 3.5FRG	1	0.07728117	0.8986892	0.3100330	0.6666667	1
91	5.5FRG vs 2FOR	1	0.62541320	6.4700316	0.8661318	0.3333333	1
92	5.5FRG vs 1FRG	1	0.36866474	1.7544901	0.4673045	0.3333333	1
93	5.5FRG vs 0FOR	1	0.20886261	2.1607278	0.6836172	0.3333333	1
94	5.5FRG vs 0FRG	1	0.17799065	1.8413508	0.6480547	0.3333333	1
95	5.5FRG vs 3BAK	1	0.46787494	4.9925053	0.7139795	0.3333333	1
96	5.5FRG vs 3.5BAK	1	0.27267698	2.8209009	0.7382816	0.3333333	1
97	5.5FRG vs 3FRG	1	0.16889024	1.9297641	0.4910636	0.3333333	1
98	5.5FRG vs 5BAK	1	0.13066719	1.3517797	0.5747901	0.6666667	1

99	5.5FRG vs 5FRG	1	0.07602815	0.7865273	0.4402548	0.6666667	1
100	1FOR vs 4FRG	1	0.43212151	3.7640513	0.5564788	0.1000000	1
101	1FOR vs 6FRG	1	0.34029376	2.5617122	0.3904030	0.2000000	1
102	1FOR vs 2BAK	1	0.12151537	0.8264689	0.2159874	0.8000000	1
103	1FOR vs 3.5FRG	1	0.39466353	3.8386763	0.5613186	0.2000000	1
104	1FOR vs 2FOR	1	0.68205021	5.8516487	0.7452764	0.2500000	1
105	1FOR vs 1FRG	1	0.28835514	1.5539065	0.3412250	0.2000000	1
106	1FOR vs 0FOR	1	0.11462915	0.9834606	0.3296375	0.7500000	1
107	1FOR vs 0FRG	1	0.20502794	1.7590369	0.4679488	0.2500000	1
108	1FOR vs 3BAK	1	0.11492263	1.0644871	0.2618995	0.5000000	1
109	1FOR vs 3.5BAK	1	0.05743227	0.4927400	0.1976700	1.0000000	1
110	1FOR vs 3FRG	1	0.32535892	3.1335938	0.5108903	0.2000000	1
111	1FOR vs 5BAK	1	0.13644463	1.1706265	0.3692098	0.5000000	1
112	1FOR vs 5FRG	1	0.17067797	1.4643314	0.4226880	0.2500000	1
113	4FRG vs 6FRG	1	0.08286263	0.6070039	0.1682848	0.9000000	1
114	4FRG vs 2BAK	1	0.15582181	0.9761201	0.3279841	0.6666667	1
115	4FRG vs 3.5FRG	1	0.03411577	0.3656250	0.1545575	1.0000000	1
116	4FRG vs 2FOR	1	0.61730574	5.5466794	0.8472508	0.3333333	1
117	4FRG vs 1FRG	1	0.33932549	1.5605383	0.4382872	0.3333333	1
118	4FRG vs 0FOR	1	0.17391271	1.5626584	0.6097802	0.6666667	1
119	4FRG vs 0FRG	1	0.16911576	1.5195565	0.6031047	0.3333333	1
120	4FRG vs 3BAK	1	0.44356392	4.3904030	0.6870307	0.3333333	1
121	4FRG vs 3.5BAK	1	0.24707556	2.2200489	0.6894457	0.3333333	1
122	4FRG vs 3FRG	1	0.14999541	1.5816715	0.4416015	0.3333333	1
123	4FRG vs 5BAK	1	0.12850072	1.1546179	0.5358806	0.6666667	1
124	4FRG vs 5FRG	1	0.07516563	0.6753860	0.4031226	0.6666667	1
125	6FRG vs 2BAK	1	0.09351987	0.5542306	0.1559355	0.5000000	1
126	6FRG vs 3.5FRG	1	0.10602460	0.8514594	0.2210745	0.8000000	1
127	6FRG vs 2FOR	1	0.64489125	4.3246498	0.6837770	0.2500000	1
128	6FRG vs 1FRG	1	0.34491145	1.6640161	0.3567775	0.3000000	1
129	6FRG vs 0FOR	1	0.15151866	1.0160863	0.3368890	0.5000000	1
130	6FRG vs 0FRG	1	0.15096084	1.0123455	0.3360655	0.5000000	1
131	6FRG vs 3BAK	1	0.32146531	2.4791186	0.4524667	0.2000000	1
132	6FRG vs 3.5BAK	1	0.17391894	1.1663028	0.3683485	0.2500000	1
133	6FRG vs 3FRG	1	0.20483666	1.6316711	0.3522856	0.2000000	1
134	6FRG vs 5BAK	1	0.07462783	0.5004553	0.2001457	1.0000000	1
135	6FRG vs 5FRG	1	0.06372187	0.4273197	0.1760459	1.0000000	1
136	2BAK vs 3.5FRG	1	0.15668883	1.1061760	0.3561215	0.6666667	1
137	2BAK vs 2FOR	1	0.59151807	2.8441807	0.7398665	0.3333333	1
138	2BAK vs 1FRG	1	0.24054348	0.9050394	0.3115412	1.0000000	1
139	2BAK vs 0FOR	1	0.09164046	0.4406324	0.3058604	1.0000000	1
140	2BAK vs 0FRG	1	0.13834410	0.6651963	0.3994702	1.0000000	1
141	2BAK vs 3BAK	1	0.16053210	1.0747181	0.3495339	0.6666667	1
142	2BAK vs 3.5BAK	1	0.07859112	0.3778876	0.2742514	1.0000000	1
143	2BAK vs 3FRG	1	0.16942819	1.1833686	0.3717347	0.3333333	1
144	2BAK vs 5BAK	1	0.06361297	0.3058686	0.2342261	1.0000000	1
145	2BAK vs 5FRG	1	0.06998986	0.3365304	0.2517941	1.0000000	1
146	3.5FRG vs 2FOR	1	0.63832045	8.4744045	0.8944525	0.3333333	1
147	3.5FRG vs 1FRG	1	0.28496457	1.4287049	0.4166894	0.3333333	1
148	3.5FRG vs 0FOR	1	0.13897747	1.8450784	0.6485158	0.6666667	1
149	3.5FRG vs 0FRG	1	0.13240943	1.7578805	0.6374027	0.3333333	1
150	3.5FRG vs 3BAK	1	0.42263722	5.0892193	0.7178815	0.3333333	1
151	3.5FRG vs 3.5BAK	1	0.23081144	3.0642751	0.7539537	0.3333333	1
152	3.5FRG vs 3FRG	1	0.07250394	0.9434631	0.3205283	0.6666667	1
153	3.5FRG vs 5BAK	1	0.13497444	1.7919339	0.6418253	0.3333333	1
154	3.5FRG vs 5FRG	1	0.07239590	0.9611351	0.4900912	0.6666667	1
155	2FOR vs 1FRG	1	0.43420021	1.3418230	0.5729822	0.6666667	1
156	2FOR vs 0FOR	1	0.49611652	0.0000000	1.0000000	1.0000000	1
157	2FOR vs 0FRG	1	0.46935608	0.0000000	1.0000000	1.0000000	1
158	2FOR vs 3BAK	1	0.63317228	6.9757338	0.8746197	0.3333333	1
159	2FOR vs 3.5BAK	1	0.49708597	0.0000000	1.0000000	1.0000000	1
160	2FOR vs 3FRG	1	0.62445448	7.9676122	0.8884876	0.3333333	1

161	2FOR vs 5BAK	1	0.48743405	0.0000000	1.0000000	1.0000000	1
162	2FOR vs 5FRG	1	0.49611652	0.0000000	1.0000000	1.0000000	1
163	1FRG vs 0FOR	1	0.15268604	0.4718506	0.3205832	0.6666667	1
164	1FRG vs 0FRG	1	0.15683164	0.4846619	0.3264460	1.0000000	1
165	1FRG vs 3BAK	1	0.34342519	1.6576270	0.4531974	0.3333333	1
166	1FRG vs 3.5BAK	1	0.20203703	0.6243616	0.3843735	0.6666667	1
167	1FRG vs 3FRG	1	0.21373810	1.0634692	0.3471454	0.6666667	1
168	1FRG vs 5BAK	1	0.21791129	0.6734183	0.4024208	0.6666667	1
169	1FRG vs 5FRG	1	0.19854593	0.6135729	0.3802573	0.6666667	1
170	0FOR vs 0FRG	1	0.11221262	0.0000000	1.0000000	1.0000000	1
171	0FOR vs 3BAK	1	0.15724689	1.7324076	0.6340224	0.3333333	1
172	0FOR vs 3.5BAK	1	0.07419492	0.0000000	1.0000000	1.0000000	1
173	0FOR vs 3FRG	1	0.07403137	0.9445897	0.4857527	0.6666667	1
174	0FOR vs 5BAK	1	0.09495980	0.0000000	1.0000000	1.0000000	1
175	0FOR vs 5FRG	1	0.09411384	0.0000000	1.0000000	1.0000000	1
176	0FRG vs 3BAK	1	0.27749442	3.0571888	0.7535239	0.3333333	1
177	0FRG vs 3.5BAK	1	0.15971145	0.0000000	1.0000000	1.0000000	1
178	0FRG vs 3FRG	1	0.11893206	1.5174918	0.6027792	0.3333333	1
179	0FRG vs 5BAK	1	0.14104869	0.0000000	1.0000000	1.0000000	1
180	0FRG vs 5FRG	1	0.12113923	0.0000000	1.0000000	1.0000000	1
181	3BAK vs 3.5BAK	1	0.06749534	0.7436042	0.4264753	0.6666667	1
182	3BAK vs 3FRG	1	0.38330184	4.5323097	0.6938296	0.3333333	1
183	3BAK vs 5BAK	1	0.15560890	1.7143617	0.6315893	0.3333333	1
184	3BAK vs 5FRG	1	0.21021861	2.3160033	0.6984321	0.3333333	1
185	3.5BAK vs 3FRG	1	0.19365468	2.4709013	0.7118904	0.3333333	1
186	3.5BAK vs 5BAK	1	0.08994080	0.0000000	1.0000000	1.0000000	1
187	3.5BAK vs 5FRG	1	0.11923156	0.0000000	1.0000000	1.0000000	1
188	3FRG vs 5BAK	1	0.15127516	1.9301676	0.6587226	0.3333333	1
189	3FRG vs 5FRG	1	0.09501894	1.2123768	0.5479974	0.6666667	1
190	5BAK vs 5FRG	1	0.04229862	0.0000000	1.0000000	1.0000000	1

Table 4: *Pocillopora verrucosa* - Pairwise Comparison between Sampling Locations with bonferroni correction

sig	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted
1	5BAK vs 5FRG	1	0.333368969	2.7560719	0.132783888	0.0150000	1.000
2	5BAK vs 6FRG	1	0.193002242	1.1219486	0.053117664	0.2850000	1.000
3	5BAK vs 5.5BAK	1	0.134850250	0.8309995	0.046604201	0.4940000	1.000
4	5BAK vs 1FOR	1	0.166065525	1.0471230	0.052233081	0.3090000	1.000
5	5BAK vs 5.5FRG	1	0.256779209	1.2127687	0.063123055	0.2500000	1.000
6	5BAK vs 1BAK	1	0.199044937	1.4638333	0.083820846	0.2020000	1.000
7	5BAK vs 0FRG	1	1.045057121	4.1291612	0.215856886	0.0050000	1.000
8	5BAK vs 0FOR	1	0.216300726	1.0900730	0.060258075	0.2880000	1.000
9	5BAK vs 0BAK	1	0.148770188	0.7181139	0.034661162	0.7060000	1.000
10	5BAK vs 2FRG	1	0.257618837	1.1226916	0.065567474	0.3110000	1.000
11	5BAK vs 2FOR	1	0.156232135	1.0585711	0.055543044	0.3610000	1.000
12	5BAK vs 6BAK	1	0.114568841	0.6920007	0.024989192	0.6790000	1.000
13	5BAK vs 2BAK	1	0.116137105	0.7060654	0.048011850	0.6130000	1.000
14	5BAK vs 1FRG	1	0.694689747	2.8136252	0.167341971	0.0200000	1.000
15	5BAK vs 3BAK	1	0.118075336	0.6372066	0.046725599	0.6830000	1.000
16	5BAK vs 4BAK	1	0.113700759	0.5817344	0.042832118	0.7490000	1.000
17	5BAK vs 3.5BAK	1	0.128194607	0.7980714	0.057839345	0.6180000	1.000
18	5BAK vs 3.5FRG	1	0.253837793	1.3322545	0.099927175	0.1780000	1.000
19	5BAK vs 4FRG	1	0.041670208	0.2054756	0.020133861	0.9150000	1.000
20	5BAK vs 3FRG	1	0.126503296	0.6237873	0.058716091	0.4240000	1.000
21	5BAK vs ENRICHED	1	0.116840577	0.5920201	0.037969426	0.7390000	1.000
22	5BAK vs CONTROL	1	0.098595062	0.4738837	0.032740606	0.8250000	1.000

23	5FRG vs 6FRG	1	0.514072887	5.9249585	0.247647597	0.0010000	0.253
24	5FRG vs 5.5BAK	1	0.486225873	8.2885103	0.355905561	0.0010000	0.253
25	5FRG vs 1FOR	1	0.074295431	1.1132658	0.061461353	0.2690000	1.000
26	5FRG vs 5.5FRG	1	0.361598281	2.9939766	0.157627688	0.0020000	0.506
27	5FRG vs 1BAK	1	0.0342224188	1.6139639	0.103366697	0.1290000	1.000
28	5FRG vs 0FRG	1	1.527981215	10.3584031	0.443455106	0.0010000	0.253
29	5FRG vs 0FOR	1	0.319108461	3.2027422	0.175948335	0.0010000	0.253
30	5FRG vs 0BAK	1	0.454752370	3.6145205	0.167226496	0.0010000	0.253
31	5FRG vs 2FRG	1	0.243062166	1.8981667	0.119395319	0.0750000	1.000
32	5FRG vs 2FOR	1	0.158370532	3.2576130	0.169159752	0.0080000	1.000
33	5FRG vs 6BAK	1	0.271023884	2.6146117	0.094682184	0.0300000	1.000
34	5FRG vs 2BAK	1	0.108999897	3.0844866	0.204480716	0.0330000	1.000
35	5FRG vs 1FRG	1	1.033672719	7.8611433	0.395805174	0.0010000	0.253
36	5FRG vs 3BAK	1	0.320096566	6.6411612	0.376458280	0.0090000	1.000
37	5FRG vs 4BAK	1	0.379161598	6.2989793	0.364124332	0.0040000	1.000
38	5FRG vs 3.5BAK	1	0.044493907	2.3365869	0.175201267	0.0940000	1.000
39	5FRG vs 3.5FRG	1	0.447987637	10.9892868	0.523566469	0.0040000	1.000
40	5FRG vs 4FRG	1	0.029177139	1.5638678	0.163518337	0.1770000	1.000
41	5FRG vs 3FRG	1	0.115043692	6.1662359	0.435276946	0.1090000	1.000
42	5FRG vs ENRICHED	1	0.162199560	1.9494134	0.130400664	0.0270000	1.000
43	5FRG vs CONTROL	1	0.189377885	2.1976530	0.154789881	0.0280000	1.000
44	6FRG vs 5.5BAK	1	0.192242662	1.5248966	0.082316064	0.1660000	1.000
45	6FRG vs 1FOR	1	0.354732772	2.8109261	0.128876972	0.0180000	1.000
46	6FRG vs 5.5FRG	1	0.324116582	1.8256416	0.092084869	0.0890000	1.000
47	6FRG vs 1BAK	1	0.343135318	3.5190896	0.180289638	0.0030000	0.759
48	6FRG vs 0FRG	1	1.173266049	5.5327335	0.269459180	0.0020000	0.506
49	6FRG vs 0FOR	1	0.268087849	1.6525956	0.088598695	0.0850000	1.000
50	6FRG vs 0BAK	1	0.212920822	1.2070799	0.056918722	0.2400000	1.000
51	6FRG vs 2FRG	1	0.431440879	2.2588875	0.123714413	0.0430000	1.000
52	6FRG vs 2FOR	1	0.264376334	2.3314901	0.114673841	0.0190000	1.000
53	6FRG vs 6BAK	1	0.209759643	1.4692579	0.051608578	0.1660000	1.000
54	6FRG vs 2BAK	1	0.168468609	1.3978345	0.090781240	0.1680000	1.000
55	6FRG vs 1FRG	1	0.753733538	3.7141028	0.209669260	0.0120000	1.000
56	6FRG vs 3BAK	1	0.156783318	1.1364743	0.080393051	0.2430000	1.000
57	6FRG vs 4BAK	1	0.090302072	0.6097136	0.044799888	0.8320000	1.000
58	6FRG vs 3.5BAK	1	0.219674836	1.9391361	0.129802425	0.0800000	1.000
59	6FRG vs 3.5FRG	1	0.100957162	0.7250511	0.056978248	0.6140000	1.000
60	6FRG vs 4FRG	1	0.052096094	0.3688232	0.035570400	0.5800000	1.000
61	6FRG vs 3FRG	1	0.125566957	0.8889727	0.081639723	0.2370000	1.000
62	6FRG vs ENRICHED	1	0.240915487	1.5411065	0.093168286	0.1000000	1.000
63	6FRG vs CONTROL	1	0.193781705	1.1809208	0.077789803	0.2810000	1.000
64	5.5BAK vs 1FOR	1	0.304339027	2.8377477	0.150641558	0.0150000	1.000
65	5.5BAK vs 5.5FRG	1	0.480293798	2.8659074	0.160412084	0.0050000	1.000
66	5.5BAK vs 1BAK	1	0.262478287	3.8850355	0.230087495	0.0190000	1.000
67	5.5BAK vs 0FRG	1	1.195542173	5.7407300	0.323590404	0.0010000	0.253
68	5.5BAK vs 0FOR	1	0.290588001	1.9596803	0.122789448	0.0390000	1.000
69	5.5BAK vs 0BAK	1	0.184855345	1.1041745	0.060990051	0.3710000	1.000
70	5.5BAK vs 2FRG	1	0.489885626	2.6824493	0.171047852	0.0120000	1.000
71	5.5BAK vs 2FOR	1	0.148130361	1.6346619	0.098268420	0.1510000	1.000
72	5.5BAK vs 6BAK	1	0.172106669	1.3018403	0.051452397	0.2180000	1.000
73	5.5BAK vs 2BAK	1	0.132828215	1.4531411	0.116688721	0.1950000	1.000
74	5.5BAK vs 1FRG	1	0.874269913	4.4536949	0.288196118	0.0050000	1.000
75	5.5BAK vs 3BAK	1	0.065327013	0.5876768	0.055505733	0.6500000	1.000
76	5.5BAK vs 4BAK	1	0.053712608	0.4319253	0.041404179	0.8990000	1.000
77	5.5BAK vs 3.5BAK	1	0.144998607	1.8333556	0.154931171	0.0890000	1.000
78	5.5BAK vs 3.5FRG	1	0.200961873	1.8286153	0.168868804	0.0830000	1.000
79	5.5BAK vs 4FRG	1	0.038041583	0.3644412	0.049486605	0.8880000	1.000
80	5.5BAK vs 3FRG	1	0.148028949	1.4181284	0.168461241	0.3440000	1.000
81	5.5BAK vs ENRICHED	1	0.167499635	1.2085963	0.091500737	0.2610000	1.000
82	5.5BAK vs CONTROL	1	0.189303609	1.2889750	0.104888735	0.2220000	1.000
83	1FOR vs 5.5FRG	1	0.193930876	1.1908725	0.065465384	0.3080000	1.000
84	1FOR vs 1BAK	1	0.043222088	0.5722869	0.036750345	0.9320000	1.000

85	1FOR vs 0FRG	1	1.322269002	6.7226190	0.324409717	0.0030000	0.759
86	1FOR vs 0FOR	1	0.215829809	1.4817449	0.084759553	0.1400000	1.000
87	1FOR vs 0BAK	1	0.302043187	1.8508534	0.088766313	0.0860000	1.000
88	1FOR vs 2FRG	1	0.175631400	1.0021872	0.062628136	0.3330000	1.000
89	1FOR vs 2FOR	1	0.114538370	1.2065220	0.066268670	0.2380000	1.000
90	1FOR vs 6BAK	1	0.150132590	1.1388804	0.041964901	0.2620000	1.000
91	1FOR vs 2BAK	1	0.077090714	0.7953396	0.057652775	0.4720000	1.000
92	1FOR vs 1FRG	1	0.821758499	4.4255529	0.253969151	0.0100000	1.000
93	1FOR vs 3BAK	1	0.204281568	1.7943109	0.130076154	0.1160000	1.000
94	1FOR vs 4BAK	1	0.252216252	2.0202313	0.144094004	0.0750000	1.000
95	1FOR vs 3.5BAK	1	0.052450805	0.6020338	0.047772749	0.3850000	1.000
96	1FOR vs 3.5FRG	1	0.394364263	3.4880806	0.240755189	0.0310000	1.000
97	1FOR vs 4FRG	1	0.028243589	0.2579942	0.027867179	0.2780000	1.000
98	1FOR vs 3FRG	1	0.105858056	0.9669721	0.097017640	0.2020000	1.000
99	1FOR vs ENRICHED	1	0.108292782	0.7905971	0.053452684	0.5520000	1.000
100	1FOR vs CONTROL	1	0.088139897	0.6127108	0.045010195	0.5770000	1.000
101	5.5FRG vs 1BAK	1	0.295657087	2.1438162	0.132794884	0.0410000	1.000
102	5.5FRG vs 0FRG	1	0.815355614	2.9845163	0.186712957	0.0130000	1.000
103	5.5FRG vs 0FOR	1	0.268529609	1.2875283	0.079049948	0.2620000	1.000
104	5.5FRG vs 0BAK	1	0.326057213	1.5054511	0.077181047	0.1320000	1.000
105	5.5FRG vs 2FRG	1	0.141952731	0.5799729	0.039778733	0.7140000	1.000
106	5.5FRG vs 2FOR	1	0.342824183	2.2743694	0.124456793	0.0160000	1.000
107	5.5FRG vs 6BAK	1	0.384664963	2.2759480	0.083441574	0.0300000	1.000
108	5.5FRG vs 2BAK	1	0.256743586	1.4970845	0.110919103	0.1420000	1.000
109	5.5FRG vs 1FRG	1	0.381740356	1.4262722	0.106229949	0.2130000	1.000
110	5.5FRG vs 3BAK	1	0.287954175	1.4636691	0.117434853	0.1470000	1.000
111	5.5FRG vs 4BAK	1	0.305150816	1.4619424	0.117312559	0.1680000	1.000
112	5.5FRG vs 3.5BAK	1	0.242782347	1.4487735	0.116378814	0.1570000	1.000
113	5.5FRG vs 3.5FRG	1	0.347327757	1.7012944	0.145393695	0.1220000	1.000
114	5.5FRG vs 4FRG	1	0.087163981	0.3910567	0.046603986	0.7300000	1.000
115	5.5FRG vs 3FRG	1	0.105142962	0.4717185	0.055681555	0.4220000	1.000
116	5.5FRG vs ENRICHED	1	0.212556934	1.0175629	0.072591999	0.4330000	1.000
117	5.5FRG vs CONTROL	1	0.085968683	0.3866708	0.031216687	0.8020000	1.000
118	1BAK vs 0FRG	1	1.342680832	7.7084829	0.412031426	0.0010000	0.253
119	1BAK vs 0FOR	1	0.215717682	1.8784466	0.126252874	0.0410000	1.000
120	1BAK vs 0BAK	1	0.291293708	2.0595355	0.114041445	0.0630000	1.000
121	1BAK vs 2FRG	1	0.235952123	1.5808549	0.116403196	0.1200000	1.000
122	1BAK vs 2FOR	1	0.067874953	1.2242226	0.080412814	0.2830000	1.000
123	1BAK vs 6BAK	1	0.133636658	1.1868295	0.049069245	0.2570000	1.000
124	1BAK vs 2BAK	1	0.051467057	1.2183993	0.108607235	0.2530000	1.000
125	1BAK vs 1FRG	1	0.923500083	5.8588245	0.369436239	0.0030000	0.759
126	1BAK vs 3BAK	1	0.176634527	3.0077063	0.250481334	0.0380000	1.000
127	1BAK vs 4BAK	1	0.224075825	3.0532959	0.253316267	0.0260000	1.000
128	1BAK vs 3.5BAK	1	0.012393538	0.5367154	0.056278856	0.7280000	1.000
129	1BAK vs 3.5FRG	1	0.381917208	7.5251535	0.484707189	0.0090000	1.000
130	1BAK vs 4FRG	1	0.016668547	0.6775170	0.101462408	0.3610000	1.000
131	1BAK vs 3FRG	1	0.098400954	3.9996477	0.399978859	0.1250000	1.000
132	1BAK vs ENRICHED	1	0.100726336	1.0259032	0.085307787	0.3920000	1.000
133	1BAK vs CONTROL	1	0.128117709	1.2409317	0.110394027	0.2740000	1.000
134	0FRG vs 0FOR	1	1.038043860	4.0005877	0.250027546	0.0030000	0.759
135	0FRG vs 0BAK	1	0.954633379	3.6870186	0.197303737	0.0050000	1.000
136	0FRG vs 2FRG	1	0.808142476	2.6054991	0.191503383	0.0250000	1.000
137	0FRG vs 2FOR	1	1.371246736	7.4369380	0.363896880	0.0010000	0.253
138	0FRG vs 6BAK	1	1.422639229	7.4332143	0.252545107	0.0010000	0.253
139	0FRG vs 2BAK	1	1.021372674	4.4990182	0.333284845	0.0070000	1.000
140	0FRG vs 1FRG	1	0.379913286	1.0694985	0.106211695	0.3790000	1.000
141	0FRG vs 3BAK	1	0.821797122	3.0588148	0.276595175	0.0090000	1.000
142	0FRG vs 4BAK	1	0.740622114	2.5972281	0.245085606	0.0120000	1.000
143	0FRG vs 3.5BAK	1	1.069832814	4.6804484	0.369107483	0.0130000	1.000
144	0FRG vs 3.5FRG	1	0.648166460	2.2385939	0.242308941	0.0420000	1.000
145	0FRG vs 4FRG	1	0.376777157	1.0653111	0.175639980	0.5790000	1.000
146	0FRG vs 3FRG	1	0.299633538	0.8471929	0.144888827	0.8730000	1.000

147	0FRG vs ENRICHED	1	1.003839558	3.7168372	0.270968966	0.0070000	1.000
148	0FRG vs CONTROL	1	0.773633272	2.6242575	0.225757002	0.0280000	1.000
149	0FOR vs 0BAK	1	0.228572321	1.1228306	0.061956690	0.2770000	1.000
150	0FOR vs 2FRG	1	0.233351533	1.0149990	0.072422339	0.4180000	1.000
151	0FOR vs 2FOR	1	0.183567280	1.3949759	0.085085572	0.1820000	1.000
152	0FOR vs 6BAK	1	0.234935087	1.4887122	0.058406724	0.1440000	1.000
153	0FOR vs 2BAK	1	0.134561440	0.9136410	0.076688643	0.5090000	1.000
154	0FOR vs 1FRG	1	0.657252446	2.6063353	0.191553068	0.0230000	1.000
155	0FOR vs 3BAK	1	0.174378192	1.0101764	0.091749335	0.4230000	1.000
156	0FOR vs 4BAK	1	0.193046151	1.0389086	0.094113340	0.3130000	1.000
157	0FOR vs 3.5BAK	1	0.185048301	1.3166082	0.116343007	0.1600000	1.000
158	0FOR vs 3.5FRG	1	0.316312668	1.7751691	0.164746285	0.1070000	1.000
159	0FOR vs 4FRG	1	0.057982258	0.3017027	0.041319501	0.7940000	1.000
160	0FOR vs 3FRG	1	0.111328385	0.5792820	0.076429662	0.4420000	1.000
161	0FOR vs ENRICHED	1	0.143264736	0.7547918	0.059177120	0.6260000	1.000
162	0FOR vs CONTROL	1	0.165215750	0.8149287	0.068974488	0.5840000	1.000
163	0BAK vs 2FRG	1	0.324347939	1.3806339	0.079435189	0.1670000	1.000
164	0BAK vs 2FOR	1	0.225471058	1.4790574	0.075930646	0.1410000	1.000
165	0BAK vs 6BAK	1	0.186340512	1.1039251	0.039280102	0.2910000	1.000
166	0BAK vs 2BAK	1	0.155814867	0.9126573	0.061200182	0.3740000	1.000
167	0BAK vs 1FRG	1	0.664708702	2.6258158	0.157936056	0.0190000	1.000
168	0BAK vs 3BAK	1	0.144362861	0.7517987	0.054669121	0.6240000	1.000
169	0BAK vs 4BAK	1	0.099725626	0.4932685	0.036556636	0.9280000	1.000
170	0BAK vs 3.5BAK	1	0.194857018	1.1643522	0.082202999	0.2190000	1.000
171	0BAK vs 3.5FRG	1	0.196876830	0.9952601	0.076586392	0.3770000	1.000
172	0BAK vs 4FRG	1	0.050078631	0.2367368	0.023126202	1.0000000	1.000
173	0BAK vs 3FRG	1	0.111836757	0.5286862	0.050213881	0.4240000	1.000
174	0BAK vs ENRICHED	1	0.184240561	0.9067639	0.057004926	0.4500000	1.000
175	0BAK vs CONTROL	1	0.169163479	0.7893800	0.053374787	0.5280000	1.000
176	2FRG vs 2FOR	1	0.272780777	1.6808306	0.107190152	0.1240000	1.000
177	2FRG vs 6BAK	1	0.328088780	1.8469683	0.074333750	0.0570000	1.000
178	2FRG vs 2BAK	1	0.241484510	1.2588735	0.111811672	0.2560000	1.000
179	2FRG vs 1FRG	1	0.517328454	1.6839580	0.144125645	0.1110000	1.000
180	2FRG vs 3BAK	1	0.319931402	1.4223463	0.136470833	0.1920000	1.000
181	2FRG vs 4BAK	1	0.346820551	1.4475404	0.138553222	0.2100000	1.000
182	2FRG vs 3.5BAK	1	0.198439924	1.0483034	0.104326404	0.1800000	1.000
183	2FRG vs 3.5FRG	1	0.409898018	1.7241984	0.177310080	0.1100000	1.000
184	2FRG vs 4FRG	1	0.086811851	0.3169361	0.050172438	0.4980000	1.000
185	2FRG vs 3FRG	1	0.123387324	0.4504672	0.069834824	0.3860000	1.000
186	2FRG vs ENRICHED	1	0.180358388	0.7702066	0.065436963	0.5660000	1.000
187	2FRG vs CONTROL	1	0.123864542	0.4899172	0.046703629	0.7450000	1.000
188	2FOR vs 6BAK	1	0.105475810	0.8587079	0.033207688	0.4760000	1.000
189	2FOR vs 2BAK	1	0.045968223	0.6106078	0.048420169	0.6570000	1.000
190	2FOR vs 1FRG	1	0.937428621	5.4680956	0.313033299	0.0020000	0.506
191	2FOR vs 3BAK	1	0.096375141	1.0501258	0.087146461	0.3030000	1.000
192	2FOR vs 4BAK	1	0.140861981	1.3574429	0.109848201	0.2280000	1.000
193	2FOR vs 3.5BAK	1	0.035992723	0.5747962	0.049659296	0.6860000	1.000
194	2FOR vs 3.5FRG	1	0.301689476	3.4012567	0.253801323	0.0330000	1.000
195	2FOR vs 4FRG	1	0.013404547	0.1705978	0.020879472	1.0000000	1.000
196	2FOR vs 3FRG	1	0.104336848	1.3278802	0.142356053	0.3880000	1.000
197	2FOR vs ENRICHED	1	0.092638809	0.7714998	0.056021479	0.6010000	1.000
198	2FOR vs CONTROL	1	0.129784472	1.0290765	0.078983071	0.3860000	1.000
199	6BAK vs 2BAK	1	0.064278615	0.4968204	0.023111341	0.7740000	1.000
200	6BAK vs 1FRG	1	0.973816478	5.2831568	0.201009217	0.0020000	0.506
201	6BAK vs 3BAK	1	0.159180883	1.1276986	0.053375364	0.3350000	1.000
202	6BAK vs 4BAK	1	0.148490366	1.0049912	0.047845350	0.3740000	1.000
203	6BAK vs 3.5BAK	1	0.079106960	0.6322519	0.030643861	0.5800000	1.000
204	6BAK vs 3.5FRG	1	0.270054555	1.8999749	0.090908000	0.1500000	1.000
205	6BAK vs 4FRG	1	0.015658397	0.1089981	0.006370803	0.9500000	1.000
206	6BAK vs 3FRG	1	0.115404320	0.8033291	0.045122409	0.3230000	1.000
207	6BAK vs ENRICHED	1	0.126255263	0.8231001	0.036064342	0.4660000	1.000
208	6BAK vs CONTROL	1	0.140087525	0.8842325	0.040405003	0.4700000	1.000

209	2BAK vs 1FRG	1	0.742628957	3.4876643	0.303600818	0.0210000	1.000
210	2BAK vs 3BAK	1	0.112844878	1.2046289	0.146823083	0.2720000	1.000
211	2BAK vs 4BAK	1	0.134380525	1.1942205	0.145739364	0.2510000	1.000
212	2BAK vs 3.5BAK	1	0.047749766	0.9977280	0.124751425	0.3650000	1.000
213	2BAK vs 3.5FRG	1	0.245393067	2.7613461	0.315173730	0.0470000	1.000
214	2BAK vs 4FRG	1	0.007308147	0.1063773	0.025905399	1.0000000	1.000
215	2BAK vs 3FRG	1	0.097216461	1.4150821	0.261322372	0.3333333	1.000
216	2BAK vs ENRICHED	1	0.088317836	0.6584330	0.068171822	0.8850000	1.000
217	2BAK vs CONTROL	1	0.120505799	0.8313482	0.094136047	0.6840000	1.000
218	1FRG vs 3BAK	1	0.612370608	2.3688444	0.252842750	0.0540000	1.000
219	1FRG vs 4BAK	1	0.531568408	1.9165291	0.214941157	0.0480000	1.000
220	1FRG vs 3.5BAK	1	0.752483625	3.5378907	0.335730443	0.0230000	1.000
221	1FRG vs 3.5FRG	1	0.483029660	1.7179043	0.222586891	0.1210000	1.000
222	1FRG vs 4FRG	1	0.280635810	0.7857423	0.164183995	0.6666667	1.000
223	1FRG vs 3FRG	1	0.259877862	0.7276228	0.153908818	0.6666667	1.000
224	1FRG vs ENRICHED	1	0.682136595	2.6002226	0.224152818	0.0250000	1.000
225	1FRG vs CONTROL	1	0.480438954	1.6613711	0.171960179	0.1480000	1.000
226	3BAK vs 4BAK	1	0.073193884	0.4913382	0.075691358	0.8210000	1.000
227	3BAK vs 3.5BAK	1	0.102705472	1.3969097	0.188850450	0.3630000	1.000
228	3BAK vs 3.5FRG	1	0.225723640	1.7653039	0.260934900	0.1410000	1.000
229	3BAK vs 4FRG	1	0.037816574	0.2978219	0.090308664	1.0000000	1.000
230	3BAK vs 3FRG	1	0.121402245	0.9560952	0.241676497	0.4000000	1.000
231	3BAK vs ENRICHED	1	0.110529414	0.6732769	0.077626585	0.6670000	1.000
232	3BAK vs CONTROL	1	0.121970510	0.6745365	0.087892795	0.7670000	1.000
233	4BAK vs 3.5BAK	1	0.137230148	1.4367448	0.193195388	0.2180000	1.000
234	4BAK vs 3.5FRG	1	0.144158148	0.9345367	0.157474242	0.4270000	1.000
235	4BAK vs 4FRG	1	0.039791764	0.2327552	0.071999018	1.0000000	1.000
236	4BAK vs 3FRG	1	0.137101905	0.8019544	0.210932150	0.6000000	1.000
237	4BAK vs ENRICHED	1	0.140686523	0.7787372	0.088707197	0.6480000	1.000
238	4BAK vs CONTROL	1	0.142082656	0.7115842	0.092274709	0.7690000	1.000
239	3.5BAK vs 3.5FRG	1	0.280481045	4.4016244	0.468177010	0.0250000	1.000
240	3.5BAK vs 4FRG	1	0.014002956	0.6977219	0.188689663	0.8000000	1.000
241	3.5BAK vs 3FRG	1	0.096281454	4.7973926	0.615256004	0.2000000	1.000
242	3.5BAK vs ENRICHED	1	0.073123805	0.5893468	0.068613697	0.8920000	1.000
243	3.5BAK vs CONTROL	1	0.105514056	0.7815643	0.100437942	0.7880000	1.000
244	3.5FRG vs 4FRG	1	0.079438813	0.6148462	0.235136662	0.5000000	1.000
245	3.5FRG vs 3FRG	1	0.168524426	1.3043574	0.394738597	0.5000000	1.000
246	3.5FRG vs ENRICHED	1	0.280310567	1.6477756	0.190543289	0.1260000	1.000
247	3.5FRG vs CONTROL	1	0.272584740	1.4306165	0.192529983	0.1490000	1.000
248	4FRG vs 3FRG	1	0.064422342	0.0000000	1.000000000	1.0000000	1.000
249	4FRG vs ENRICHED	1	0.035948171	0.1927724	0.037123209	0.7150000	1.000
250	4FRG vs CONTROL	1	0.047237247	0.2135458	0.050680784	1.0000000	1.000
251	3FRG vs ENRICHED	1	0.110475768	0.5924272	0.105933830	0.4330000	1.000
252	3FRG vs CONTROL	1	0.107655144	0.4866775	0.108471687	0.5000000	1.000
253	ENRICHED vs CONTROL	1	0.064498278	0.3194361	0.034276329	0.8220000	1.000

Table 5: *Porites lobata* - Pairwise Comparison by Sampling Location, with Bonferroni correction

	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1	5FRG vs 5.5FRG	1	0.077234012	1.3002087	0.07976638	0.1820000		1.000
2	5FRG vs 6FRG	1	0.113436052	1.1127333	0.05032093	0.4590000		1.000
3	5FRG vs 6BAK	1	0.047794323	0.6718348	0.02838119	0.6240000		1.000
4	5FRG vs 1BAK	1	2.116228094	11.3508056	0.40036977	0.0010000		0.231
5	5FRG vs 5BAK	1	0.023783426	0.8876383	0.04962300	0.5100000		1.000
6	5FRG vs 0FRG	1	0.415144739	2.8560948	0.11972181	0.0140000		1.000
7	5FRG vs 0BAK	1	2.099349015	11.0224992	0.37979152	0.0010000		0.231
8	5FRG vs 1FOR	1	1.404994077	8.4372566	0.31914267	0.0010000		0.231

9	5FRG vs 5.5BAK	1	0.020133972	0.6109567	0.03678034	0.6880000	1.000
10	5FRG vs 1FRG	1	0.325919816	3.0993148	0.16227361	0.0160000	1.000
11	5FRG vs 2FRG	1	0.402660509	2.6091782	0.12660273	0.0140000	1.000
12	5FRG vs 3.5FRG	1	0.126165937	1.8815985	0.12643793	0.1480000	1.000
13	5FRG vs 0FOR	1	0.865691738	6.8369503	0.34465733	0.0020000	0.462
14	5FRG vs 2FOR	1	1.437690676	10.2438123	0.37600510	0.0010000	0.231
15	5FRG vs 2BAK	1	0.335713847	2.3801461	0.11678749	0.0500000	1.000
16	5FRG vs 3BAK	1	0.051736745	2.0112834	0.12561662	0.0870000	1.000
17	5FRG vs 3FRG	1	0.028893582	0.9703588	0.07481357	0.3160000	1.000
18	5FRG vs 3.5BAK	1	0.020419023	0.6082480	0.05239791	0.3840000	1.000
19	5FRG vs 4BAK	1	0.093395365	2.6312414	0.20831218	0.2500000	1.000
20	5FRG vs ENRICHED	1	1.537552152	17.8582222	0.59810065	0.0060000	1.000
21	5FRG vs CONTROL	1	1.109244979	10.7651826	0.47287926	0.0020000	0.462
22	5.5FRG vs 6FRG	1	0.097478266	0.6717026	0.04028998	0.6080000	1.000
23	5.5FRG vs 6BAK	1	0.088986471	0.8813729	0.04667949	0.3590000	1.000
24	5.5FRG vs 1BAK	1	1.352797058	4.8450032	0.28762258	0.0020000	0.462
25	5.5FRG vs 5BAK	1	0.079318632	1.4951165	0.11078944	0.0640000	1.000
26	5.5FRG vs 0FRG	1	0.170262876	0.8424798	0.05002113	0.4600000	1.000
27	5.5FRG vs 0BAK	1	1.329457570	4.7883041	0.26918272	0.0020000	0.462
28	5.5FRG vs 1FOR	1	0.867119361	3.5464670	0.21433379	0.0030000	0.693
29	5.5FRG vs 5.5BAK	1	0.074476165	1.1564621	0.09513147	0.1890000	1.000
30	5.5FRG vs 1FRG	1	0.206835129	1.2208152	0.09989638	0.2550000	1.000
31	5.5FRG vs 2FRG	1	0.222186201	0.9761586	0.06984456	0.3510000	1.000
32	5.5FRG vs 3.5FRG	1	0.091761467	0.6972718	0.08017132	0.5760000	1.000
33	5.5FRG vs 0FOR	1	0.595493071	2.6072700	0.24580029	0.0150000	1.000
34	5.5FRG vs 2FOR	1	0.933666232	4.3645821	0.26670905	0.0010000	0.231
35	5.5FRG vs 2BAK	1	0.214306845	1.0242685	0.07303543	0.2720000	1.000
36	5.5FRG vs 3BAK	1	0.077669299	1.2915027	0.12549214	0.1890000	1.000
37	5.5FRG vs 3FRG	1	0.053889284	0.7005925	0.09097904	0.3770000	1.000
38	5.5FRG vs 3.5BAK	1	0.037481761	0.4085982	0.06375782	0.7530000	1.000
39	5.5FRG vs 4BAK	1	0.094975619	0.8858497	0.15050497	0.2910000	1.000
40	5.5FRG vs ENRICHED	1	1.180594142	6.8057234	0.49296391	0.0170000	1.000
41	5.5FRG vs CONTROL	1	0.864356492	4.2681156	0.37877811	0.0140000	1.000
42	6FRG vs 6BAK	1	0.093769616	0.7337360	0.02966539	0.6120000	1.000
43	6FRG vs 1BAK	1	1.648557905	6.4503517	0.26381427	0.0010000	0.231
44	6FRG vs 5BAK	1	0.093584632	0.8929742	0.04726488	0.4670000	1.000
45	6FRG vs 0FRG	1	0.287709811	1.4118039	0.06030308	0.1630000	1.000
46	6FRG vs 0BAK	1	1.589868904	6.2165522	0.24652665	0.0020000	0.462
47	6FRG vs 1FOR	1	1.104967288	4.7409276	0.19969429	0.0020000	0.462
48	6FRG vs 5.5BAK	1	0.089829124	0.7798475	0.04386131	0.5680000	1.000
49	6FRG vs 1FRG	1	0.250525395	1.3679102	0.07447282	0.2200000	1.000
50	6FRG vs 2FRG	1	0.263926278	1.1914661	0.05900840	0.2680000	1.000
51	6FRG vs 3.5FRG	1	0.115654409	0.7031876	0.04782552	0.6180000	1.000
52	6FRG vs 0FOR	1	0.669393631	3.0456902	0.17867802	0.0460000	1.000
53	6FRG vs 2FOR	1	1.147446514	5.4113167	0.23114107	0.0020000	0.462
54	6FRG vs 2BAK	1	0.160149728	0.7665028	0.03877787	0.5050000	1.000
55	6FRG vs 3BAK	1	0.109015871	0.9130076	0.05737492	0.2900000	1.000
56	6FRG vs 3FRG	1	0.070810260	0.5147723	0.03808960	0.4300000	1.000
57	6FRG vs 3.5BAK	1	0.050248465	0.3349540	0.02715486	0.4120000	1.000
58	6FRG vs 4BAK	1	0.092589652	0.5703032	0.04929026	0.2210000	1.000
59	6FRG vs ENRICHED	1	1.296997952	6.8426705	0.34484625	0.0110000	1.000
60	6FRG vs CONTROL	1	0.922085008	4.4939276	0.25688500	0.0200000	1.000
61	6BAK vs 1BAK	1	2.037552201	9.9495202	0.33220967	0.0010000	0.231
62	6BAK vs 5BAK	1	0.058672637	0.8492064	0.04073087	0.5230000	1.000
63	6BAK vs 0FRG	1	0.405139081	2.4438127	0.09241529	0.0390000	1.000
64	6BAK vs 0BAK	1	2.041711373	9.8461027	0.31920087	0.0010000	0.231
65	6BAK vs 1FOR	1	1.362153663	7.2903128	0.25769644	0.0010000	0.231
66	6BAK vs 5.5BAK	1	0.040467611	0.5289516	0.02708551	0.7780000	1.000
67	6BAK vs 1FRG	1	0.314184491	2.2881639	0.10748526	0.0440000	1.000
68	6BAK vs 2FRG	1	0.357540944	2.0270033	0.08802723	0.0630000	1.000
69	6BAK vs 3.5FRG	1	0.132837679	1.1820883	0.06879771	0.2070000	1.000
70	6BAK vs 0FOR	1	0.792237067	4.9276549	0.23546140	0.0190000	1.000

71	6BAK vs 2FOR	1	1.355037201	8.1820314	0.29032795	0.0010000	0.231
72	6BAK vs 2BAK	1	0.269808913	1.6351204	0.07223820	0.1470000	1.000
73	6BAK vs 3BAK	1	0.076261849	1.0077749	0.05596332	0.2570000	1.000
74	6BAK vs 3FRG	1	0.047481235	0.5548437	0.03567016	0.3340000	1.000
75	6BAK vs 3.5BAK	1	0.029237222	0.3159326	0.02206860	0.3820000	1.000
76	6BAK vs 4BAK	1	0.108484637	1.1007034	0.07806018	0.1900000	1.000
77	6BAK vs ENRICHED	1	1.446206175	11.0707482	0.42464252	0.0080000	1.000
78	6BAK vs CONTROL	1	1.019456475	7.0703787	0.32035602	0.0080000	1.000
79	1BAK vs 5BAK	1	1.952723073	9.3782403	0.40115253	0.0030000	0.693
80	1BAK vs 0FRG	1	1.182172816	3.8605108	0.17659747	0.0030000	0.693
81	1BAK vs 0BAK	1	0.399126405	1.0168227	0.06348467	0.3760000	1.000
82	1BAK vs 1FOR	1	0.553788646	1.5222429	0.09213295	0.0530000	1.000
83	1BAK vs 5.5BAK	1	1.693912862	7.3726370	0.36188919	0.0010000	0.231
84	1BAK vs 1FRG	1	1.129216521	3.5440523	0.21421912	0.0050000	1.000
85	1BAK vs 2FRG	1	1.050148956	3.0076418	0.16702030	0.0090000	1.000
86	1BAK vs 3.5FRG	1	0.977303624	2.9337507	0.22682907	0.0020000	0.462
87	1BAK vs 0FOR	1	0.391281867	0.9530409	0.08701154	0.5180000	1.000
88	1BAK vs 2FOR	1	0.559104379	1.6154207	0.10345035	0.0810000	1.000
89	1BAK vs 2BAK	1	0.929166145	2.7883815	0.15675296	0.0190000	1.000
90	1BAK vs 3BAK	1	1.564319322	6.1026352	0.35682426	0.0020000	0.462
91	1BAK vs 3FRG	1	1.109479469	3.5448210	0.28257247	0.0080000	1.000
92	1BAK vs 3.5BAK	1	0.804767010	2.2758986	0.22147928	0.0220000	1.000
93	1BAK vs 4BAK	1	0.431061598	1.0720990	0.13281539	0.3420000	1.000
94	1BAK vs ENRICHED	1	0.456275833	1.1757220	0.11554187	0.3590000	1.000
95	1BAK vs CONTROL	1	0.232180298	0.5653679	0.05910571	0.9120000	1.000
96	5BAK vs 0FRG	1	0.400591930	2.5770410	0.12523866	0.0240000	1.000
97	5BAK vs 0BAK	1	1.856476884	8.7738263	0.36905403	0.0010000	0.231
98	5BAK vs 1FOR	1	1.278536080	6.9916040	0.31792151	0.0020000	0.462
99	5BAK vs 5.5BAK	1	0.020632647	0.9829382	0.07029554	0.4580000	1.000
100	5BAK vs 1FRG	1	0.307269029	2.7969895	0.17705839	0.0200000	1.000
101	5BAK vs 2FRG	1	0.382776191	2.2753177	0.13170917	0.0520000	1.000
102	5BAK vs 3.5FRG	1	0.128537502	2.0823009	0.17234308	0.0970000	1.000
103	5BAK vs 0FOR	1	0.838757297	6.0270383	0.37605440	0.0060000	1.000
104	5BAK vs 2FOR	1	1.316074169	8.6441412	0.38173853	0.0010000	0.231
105	5BAK vs 2BAK	1	0.336677067	2.2106569	0.12844698	0.1050000	1.000
106	5BAK vs 3BAK	1	0.032270263	3.3573992	0.23384452	0.0220000	1.000
107	5BAK vs 3FRG	1	0.022564497	1.9732406	0.17982296	0.1520000	1.000
108	5BAK vs 3.5BAK	1	0.016103929	1.1214872	0.12295004	0.2690000	1.000
109	5BAK vs 4BAK	1	0.091745372	6.3869876	0.47710417	0.1120000	1.000
110	5BAK vs ENRICHED	1	1.508350560	17.4314071	0.65949599	0.0070000	1.000
111	5BAK vs CONTROL	1	1.111249602	10.1837011	0.53085174	0.0110000	1.000
112	0FRG vs 0BAK	1	1.229957900	4.0495431	0.17568865	0.0030000	0.693
113	0FRG vs 1FOR	1	0.685063216	2.4375160	0.11370329	0.0190000	1.000
114	0FRG vs 5.5BAK	1	0.330440609	1.9574400	0.10325445	0.0620000	1.000
115	0FRG vs 1FRG	1	0.159334226	0.6729517	0.03807806	0.6490000	1.000
116	0FRG vs 2FRG	1	0.186277937	0.6912143	0.03510268	0.7470000	1.000
117	0FRG vs 3.5FRG	1	0.180639602	0.7868018	0.05320973	0.5880000	1.000
118	0FRG vs 0FOR	1	0.485973107	1.7057707	0.10860789	0.1090000	1.000
119	0FRG vs 2FOR	1	0.843535355	3.2111298	0.15138891	0.0020000	0.462
120	0FRG vs 2BAK	1	0.207304655	0.8068983	0.04073824	0.5130000	1.000
121	0FRG vs 3BAK	1	0.319085790	1.7709520	0.10559639	0.0760000	1.000
122	0FRG vs 3FRG	1	0.212751786	1.0244167	0.07304522	0.2130000	1.000
123	0FRG vs 3.5BAK	1	0.146657408	0.6489720	0.05130630	0.5850000	1.000
124	0FRG vs 4BAK	1	0.128064116	0.5222290	0.04532361	0.5460000	1.000
125	0FRG vs ENRICHED	1	0.979012756	3.7702187	0.22481631	0.0040000	0.924
126	0FRG vs CONTROL	1	0.738007215	2.6806496	0.17095271	0.0220000	1.000
127	0BAK vs 1FOR	1	0.589132006	1.6491333	0.09343990	0.0620000	1.000
128	0BAK vs 5.5BAK	1	1.664108799	7.1780372	0.33893779	0.0010000	0.231
129	0BAK vs 1FRG	1	1.179367787	3.7517416	0.21134499	0.0030000	0.693
130	0BAK vs 2FRG	1	1.039397465	3.0257735	0.15903551	0.0070000	1.000
131	0BAK vs 3.5FRG	1	0.968468605	2.9673920	0.21245140	0.0100000	1.000
132	0BAK vs 0FOR	1	0.439253370	1.1070794	0.09144067	0.3060000	1.000

133	OBAK vs 2FOR	1	0.638615339	1.8767005	0.11120068	0.0270000	1.000
134	OBAK vs 2BAK	1	0.956293024	2.9103995	0.15390471	0.0230000	1.000
135	OBAK vs 3BAK	1	1.469504155	5.7281009	0.32310855	0.0010000	0.231
136	OBAK vs 3FRG	1	1.042893160	3.3907455	0.25321559	0.0140000	1.000
137	OBAK vs 3.5BAK	1	0.737440406	2.1495104	0.19278967	0.0160000	1.000
138	OBAK vs 4BAK	1	0.401159766	1.0442320	0.11545834	0.4030000	1.000
139	OBAK vs ENRICHED	1	0.795776121	2.1211855	0.17499819	0.0120000	1.000
140	OBAK vs CONTROL	1	0.461293862	1.1663942	0.10445576	0.2340000	1.000
141	1FOR vs 5.5BAK	1	1.098478415	5.4635357	0.28070623	0.0010000	0.231
142	1FOR vs 1FRG	1	0.608116814	2.1444655	0.13282976	0.0530000	1.000
143	1FOR vs 2FRG	1	0.662341437	2.0921462	0.11563836	0.0220000	1.000
144	1FOR vs 3.5FRG	1	0.608616628	2.1191425	0.16153057	0.0260000	1.000
145	1FOR vs 0FOR	1	0.363138074	1.0154956	0.08451550	0.4770000	1.000
146	1FOR vs 2FOR	1	0.185950956	0.5968365	0.03826651	0.9060000	1.000
147	1FOR vs 2BAK	1	0.776279732	2.5734624	0.13855588	0.0210000	1.000
148	1FOR vs 3BAK	1	1.047117296	4.7458954	0.28340649	0.0020000	0.462
149	1FOR vs 3FRG	1	0.735261100	2.7799985	0.21752729	0.0130000	1.000
150	1FOR vs 3.5BAK	1	0.522862732	1.7712260	0.16444052	0.1010000	1.000
151	1FOR vs 4BAK	1	0.291375942	0.8821357	0.09931572	0.5480000	1.000
152	1FOR vs ENRICHED	1	0.549758355	1.6555576	0.14204019	0.0950000	1.000
153	1FOR vs CONTROL	1	0.445386506	1.2638692	0.11220560	0.1780000	1.000
154	5.5BAK vs 1FRG	1	0.265569542	2.1246695	0.15042260	0.1130000	1.000
155	5.5BAK vs 2FRG	1	0.311966848	1.6829122	0.10730865	0.1130000	1.000
156	5.5BAK vs 3.5FRG	1	0.124540959	1.6266532	0.15307296	0.1630000	1.000
157	5.5BAK vs 0FOR	1	0.750055255	4.6127729	0.33885623	0.0090000	1.000
158	5.5BAK vs 2FOR	1	1.114571120	6.5762845	0.33593119	0.0030000	0.693
159	5.5BAK vs 2BAK	1	0.270192833	1.6053981	0.10287454	0.1570000	1.000
160	5.5BAK vs 3BAK	1	0.047018794	2.6488431	0.20941386	0.0160000	1.000
161	5.5BAK vs 3FRG	1	0.032789743	1.5015715	0.15803402	0.2080000	1.000
162	5.5BAK vs 3.5BAK	1	0.019309348	0.7241501	0.09375142	0.4950000	1.000
163	5.5BAK vs 4BAK	1	0.088861601	3.0938997	0.34021705	0.2240000	1.000
164	5.5BAK vs ENRICHED	1	1.354654161	12.7413819	0.61429764	0.0090000	1.000
165	5.5BAK vs CONTROL	1	0.995267222	7.5551995	0.48570251	0.0100000	1.000
166	1FRG vs 2FRG	1	0.215289469	0.8036431	0.05428685	0.5400000	1.000
167	1FRG vs 3.5FRG	1	0.188140657	0.9180948	0.09256766	0.4610000	1.000
168	1FRG vs 0FOR	1	0.553071471	1.9008089	0.17437320	0.0840000	1.000
169	1FRG vs 2FOR	1	0.762835801	2.9527260	0.18509225	0.0110000	1.000
170	1FRG vs 2BAK	1	0.213849914	0.8525984	0.05740399	0.4840000	1.000
171	1FRG vs 3BAK	1	0.243972217	1.8305672	0.15473199	0.1590000	1.000
172	1FRG vs 3FRG	1	0.172078986	1.0350950	0.11456382	0.1280000	1.000
173	1FRG vs 3.5BAK	1	0.129388427	0.6749449	0.08794134	0.5220000	1.000
174	1FRG vs 4BAK	1	0.137566580	0.6217273	0.09389202	0.3780000	1.000
175	1FRG vs ENRICHED	1	0.793253575	3.1638147	0.28339907	0.0400000	1.000
176	1FRG vs CONTROL	1	0.743154437	2.6912192	0.25172238	0.0350000	1.000
177	2FRG vs 3.5FRG	1	0.176602057	0.6608390	0.05667165	0.7570000	1.000
178	2FRG vs 0FOR	1	0.453944484	1.3444766	0.10891322	0.1530000	1.000
179	2FRG vs 2FOR	1	0.732191569	2.4659276	0.14118504	0.0190000	1.000
180	2FRG vs 2BAK	1	0.201436045	0.6996123	0.04189392	0.7200000	1.000
181	2FRG vs 3BAK	1	0.307235401	1.5184158	0.11232202	0.1020000	1.000
182	2FRG vs 3FRG	1	0.215920241	0.8902965	0.08175136	0.2680000	1.000
183	2FRG vs 3.5BAK	1	0.151679324	0.5601110	0.05858834	0.8580000	1.000
184	2FRG vs 4BAK	1	0.137184094	0.4529591	0.05358587	0.4550000	1.000
185	2FRG vs ENRICHED	1	0.966030402	3.1151012	0.23752018	0.0040000	0.924
186	2FRG vs CONTROL	1	0.656523208	1.9867981	0.16574886	0.0590000	1.000
187	3.5FRG vs 0FOR	1	0.459358653	1.5245539	0.20261054	0.0500000	1.000
188	3.5FRG vs 2FOR	1	0.679196900	2.6659323	0.21048054	0.0090000	1.000
189	3.5FRG vs 2BAK	1	0.200860239	0.8181245	0.06922626	0.5270000	1.000
190	3.5FRG vs 3BAK	1	0.123246288	1.6530049	0.19103247	0.0050000	1.000
191	3.5FRG vs 3FRG	1	0.089784611	0.8648082	0.14745721	0.4610000	1.000
192	3.5FRG vs 3.5BAK	1	0.072855711	0.5487574	0.12063896	0.4666667	1.000
193	3.5FRG vs 4BAK	1	0.109263719	0.6343506	0.17454305	0.4000000	1.000
194	3.5FRG vs ENRICHED	1	0.958422812	4.0102727	0.44507784	0.0260000	1.000

195	3.5FRG vs CONTROL	1	0.684869591	2.4489931	0.32876834	0.0560000	1.000
196	0FOR vs 2FOR	1	0.424470453	1.2777321	0.11329690	0.1400000	1.000
197	0FOR vs 2BAK	1	0.489300559	1.5488584	0.12342624	0.1640000	1.000
198	0FOR vs 3BAK	1	0.751476476	4.0580110	0.36697477	0.0070000	1.000
199	0FOR vs 3FRG	1	0.569465214	2.2013033	0.30568124	0.0620000	1.000
200	0FOR vs 3.5BAK	1	0.430997015	1.3206273	0.24820895	0.2666667	1.000
201	0FOR vs 4BAK	1	0.292264692	0.6791028	0.18458381	0.8000000	1.000
202	0FOR vs ENRICHED	1	0.570697208	1.4489620	0.22468142	0.1760000	1.000
203	0FOR vs CONTROL	1	0.352771384	0.8118499	0.13968872	0.9160000	1.000
204	2FOR vs 2BAK	1	0.846153591	3.0113203	0.16719042	0.0100000	1.000
205	2FOR vs 3BAK	1	1.104642478	5.9677190	0.35171015	0.0010000	0.231
206	2FOR vs 3FRG	1	0.791425290	3.5030507	0.28017568	0.0060000	1.000
207	2FOR vs 3.5BAK	1	0.568429263	2.2233802	0.21747995	0.0750000	1.000
208	2FOR vs 4BAK	1	0.321277706	1.1073332	0.13658415	0.4570000	1.000
209	2FOR vs ENRICHED	1	0.644523277	2.1411313	0.19218258	0.0870000	1.000
210	2FOR vs CONTROL	1	0.419459194	1.2961884	0.12589012	0.1660000	1.000
211	2BAK vs 3BAK	1	0.279411458	1.5316609	0.11319090	0.1090000	1.000
212	2BAK vs 3FRG	1	0.192948396	0.8825441	0.08109722	0.1900000	1.000
213	2BAK vs 3.5BAK	1	0.131669195	0.5390797	0.05651275	0.6700000	1.000
214	2BAK vs 4BAK	1	0.133841584	0.4902828	0.05774634	0.3860000	1.000
215	2BAK vs ENRICHED	1	0.920796913	3.2171700	0.24340839	0.0370000	1.000
216	2BAK vs CONTROL	1	0.636642976	2.0768396	0.17196880	0.0910000	1.000
217	3BAK vs 3FRG	1	0.002504753	1.9921436	0.24926274	0.0430000	1.000
218	3BAK vs 3.5BAK	1	0.008411207	2.1564777	0.30133227	0.2820000	1.000
219	3BAK vs 4BAK	1	0.104771079	80.9418817	0.95290898	0.1666667	1.000
220	3BAK vs ENRICHED	1	1.323627771	11.6209249	0.65949574	0.0200000	1.000
221	3BAK vs CONTROL	1	0.986584045	6.6758041	0.52665725	0.0130000	1.000
222	3FRG vs 3.5BAK	1	0.008105472	1.4568675	0.32688149	0.4000000	1.000
223	3FRG vs 4BAK	1	0.095518889	80.7327379	0.97582577	0.2500000	1.000
224	3FRG vs ENRICHED	1	1.048113900	6.1600222	0.60630007	0.1000000	1.000
225	3FRG vs CONTROL	1	0.782359025	3.5404906	0.46953053	0.1000000	1.000
226	3.5BAK vs 4BAK	1	0.079503790	5.5501607	0.84733199	0.3333333	1.000
227	3.5BAK vs ENRICHED	1	0.836545216	3.6237647	0.54708536	0.2000000	1.000
228	3.5BAK vs CONTROL	1	0.621605487	2.0815999	0.40963475	0.1000000	1.000
229	4BAK vs ENRICHED	1	0.534451695	1.5760314	0.44072079	0.5000000	1.000
230	4BAK vs CONTROL	1	0.389010274	0.8825771	0.30617640	0.5000000	1.000
231	ENRICHED vs CONTROL	1	0.355998324	0.9129582	0.18582657	0.5000000	1.000

Table 6: *Acropora hyacinthus* - Pairwise Comparison by Sampling Location, with Bonferroni correction

	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1	6BAK vs 5.5BAK	1	0.299835141	2.5488230	0.09976284	0.031	1.000	
2	6BAK vs 5BAK	1	0.053250522	1.0600973	0.04230220	0.289	1.000	
3	6BAK vs 0BAK	1	0.279050631	2.5802058	0.10086728	0.021	1.000	
4	6BAK vs 1BAK	1	0.909244807	7.4346285	0.27099432	0.002	0.110	
5	6BAK vs 1FOR	1	0.037502147	0.4591181	0.01957099	0.698	1.000	
6	6BAK vs 0FOR	1	0.052024962	0.8396557	0.04232209	0.358	1.000	
7	6BAK vs 2FOR	1	0.054925182	0.8801782	0.03537669	0.527	1.000	
8	6BAK vs 2BAK	1	1.649978663	14.1161134	0.38032305	0.001	0.055	
9	6BAK vs 3BAK	1	0.607168699	5.9114281	0.25801221	0.004	0.220	
10	6BAK vs 4BAK	1	0.016938655	0.2259577	0.01484030	0.483	1.000	
11	5.5BAK vs 5BAK	1	0.314466229	3.2159985	0.15908185	0.001	0.055	
12	5.5BAK vs 0BAK	1	0.285780675	1.5530547	0.08847774	0.099	1.000	
13	5.5BAK vs 1BAK	1	0.639855259	2.8656467	0.18061960	0.026	1.000	
14	5.5BAK vs 1FOR	1	0.228079458	1.5625636	0.08897127	0.183	1.000	
15	5.5BAK vs 0FOR	1	0.251210168	1.8449097	0.13325545	0.081	1.000	
16	5.5BAK vs 2FOR	1	0.299388154	2.6041935	0.13283859	0.014	0.770	
17	5.5BAK vs 2BAK	1	1.069558470	5.4411214	0.25377038	0.003	0.165	
18	5.5BAK vs 3BAK	1	0.453038259	2.0566318	0.17058096	0.054	1.000	
19	5.5BAK vs 4BAK	1	0.078149934	0.3953988	0.04709709	0.606	1.000	
20	5BAK vs 0BAK	1	0.304594830	3.5856791	0.17418318	0.001	0.055	
21	5BAK vs 1BAK	1	0.871322912	8.6969574	0.38317723	0.001	0.055	
22	5BAK vs 1FOR	1	0.049894406	1.0153814	0.05636192	0.455	1.000	
23	5BAK vs 0FOR	1	0.025214708	2.4483115	0.15848409	0.013	0.715	
24	5BAK vs 2FOR	1	0.043941998	1.7410312	0.08819353	0.028	1.000	
25	5BAK vs 2BAK	1	1.521882269	15.7273791	0.48055724	0.001	0.055	
26	5BAK vs 3BAK	1	0.633166254	9.9110459	0.47396223	0.002	0.110	
27	5BAK vs 4BAK	1	0.010743341	1.1921698	0.11696919	0.390	1.000	
28	0BAK vs 1BAK	1	0.404087075	1.9568236	0.13083149	0.140	1.000	
29	0BAK vs 1FOR	1	0.252397999	1.9073588	0.10651257	0.058	1.000	
30	0BAK vs 0FOR	1	0.230213318	1.9512563	0.13986241	0.044	1.000	
31	0BAK vs 2FOR	1	0.280434334	2.7458664	0.13906032	0.007	0.385	
32	0BAK vs 2BAK	1	0.803706918	4.3934468	0.21543424	0.007	0.385	
33	0BAK vs 3BAK	1	0.361355117	1.8207639	0.15403099	0.059	1.000	
34	0BAK vs 4BAK	1	0.072274298	0.4242057	0.05035557	0.474	1.000	
35	1BAK vs 1FOR	1	0.716109463	4.4848117	0.25649757	0.013	0.715	
36	1BAK vs 0FOR	1	0.674922957	4.4199424	0.32935629	0.033	1.000	
37	1BAK vs 2FOR	1	0.838694296	6.9284377	0.33105375	0.001	0.055	
38	1BAK vs 2BAK	1	0.088489522	0.3986788	0.02975508	0.845	1.000	
39	1BAK vs 3BAK	1	0.456259116	1.6436314	0.19015519	0.183	1.000	
40	1BAK vs 4BAK	1	0.215362566	0.8148320	0.14012994	0.409	1.000	
41	1FOR vs 0FOR	1	0.058698361	0.8728035	0.06780213	0.375	1.000	
42	1FOR vs 2FOR	1	0.065201567	0.9831266	0.05466939	0.404	1.000	
43	1FOR vs 2BAK	1	1.262077839	8.7108311	0.35251065	0.003	0.165	
44	1FOR vs 3BAK	1	0.532562604	3.8707014	0.27905592	0.017	0.935	
45	1FOR vs 4BAK	1	0.019646862	0.2083852	0.02538687	0.282	1.000	
46	0FOR vs 2FOR	1	0.028588245	0.8724538	0.06289110	0.415	1.000	
47	0FOR vs 2BAK	1	1.065284658	7.9070786	0.39719935	0.003	0.165	
48	0FOR vs 3BAK	1	0.542470615	4.8261792	0.44578786	0.020	1.000	
49	0FOR vs 4BAK	1	0.005251404	0.3979820	0.09049195	0.500	1.000	

50	2FOR vs 2BAK	1	1.433305831	12.5785448	0.42525908	0.001	0.055
51	2FOR vs 3BAK	1	0.582926332	6.4455221	0.36946570	0.006	0.330
52	2FOR vs 4BAK	1	0.008213719	0.1980806	0.02153500	0.397	1.000
53	2BAK vs 3BAK	1	0.607959647	2.7817178	0.21763255	0.037	1.000
54	2BAK vs 4BAK	1	0.301677931	1.5431837	0.16170533	0.274	1.000
55	3BAK vs 4BAK	1	0.219473579	0.7061232	0.26093535	0.750	1.000

Table 7: All Corals - Pairwise comparisons of sampling locations with Bonferroni correction

	pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
1	5BAK vs 5FRG	1	1.2279460	3.9446551	0.077430204	0.022	1.000	
2	5BAK vs 6FRG	1	1.1360910	3.4626682	0.064767965	0.010	1.000	
3	5BAK vs 5.5BAK	1	0.1329723	0.3811071	0.007417261	0.821	1.000	
4	5BAK vs 5.5FRG	1	0.9151419	2.7663865	0.061796065	0.044	1.000	
5	5BAK vs 6BAK	1	0.1189596	0.3411793	0.004528457	0.844	1.000	
6	5BAK vs 1BAK	1	1.0035252	2.7602507	0.054378194	0.025	1.000	
7	5BAK vs 1FOR	1	0.3690102	1.0326109	0.018428748	0.353	1.000	
8	5BAK vs 0FRG	1	1.4775242	4.2798030	0.086846999	0.002	0.506	
9	5BAK vs 0FOR	1	0.4929251	1.3817138	0.030446487	0.219	1.000	
10	5BAK vs 0BAK	1	0.9445104	2.5260691	0.043161434	0.030	1.000	
11	5BAK vs 1FRG	1	1.0785881	3.1297335	0.074287997	0.026	1.000	
12	5BAK vs 2FRG	1	0.4535805	1.2601772	0.028472032	0.274	1.000	
13	5BAK vs 3.5FRG	1	0.5797990	1.6506687	0.046301199	0.190	1.000	
14	5BAK vs 2FOR	1	0.4993875	1.4427243	0.026021888	0.220	1.000	
15	5BAK vs 2BAK	1	0.6026892	1.6610894	0.032153589	0.143	1.000	
16	5BAK vs 3BAK	1	0.4060545	1.1319841	0.028206532	0.308	1.000	
17	5BAK vs 3FRG	1	0.6043234	1.7711162	0.054045037	0.131	1.000	
18	5BAK vs 4BAK	1	0.3687304	1.0414448	0.030593436	0.364	1.000	
19	5BAK vs 3.5BAK	1	0.6414731	1.8897830	0.054164368	0.157	1.000	
20	5BAK vs 4FRG	1	0.3390940	0.9634819	0.033265402	0.490	1.000	
21	5BAK vs ENRICHED	1	1.4501850	4.3736088	0.108328408	0.003	0.759	
22	5BAK vs CONTROL	1	0.9063332	2.6426793	0.070204336	0.050	1.000	
23	5FRG vs 6FRG	1	0.2817249	1.0197825	0.024269106	0.328	1.000	
24	5FRG vs 5.5BAK	1	1.0053972	3.3206876	0.073270900	0.036	1.000	
25	5FRG vs 5.5FRG	1	0.1103227	0.4129720	0.012359631	0.598	1.000	
26	5FRG vs 6BAK	1	1.2946548	4.0549766	0.057882777	0.016	1.000	
27	5FRG vs 1BAK	1	1.6366945	5.1589724	0.116827274	0.001	0.253	
28	5FRG vs 1FOR	1	1.4912369	4.7060207	0.092809900	0.006	1.000	
29	5FRG vs 0FRG	1	1.0717106	3.6894632	0.092958254	0.026	1.000	
30	5FRG vs 0FOR	1	1.6962685	5.5909909	0.137739699	0.005	1.000	
31	5FRG vs 0BAK	1	2.3326743	6.9125013	0.128217040	0.001	0.253	
32	5FRG vs 1FRG	1	0.6321610	2.2679172	0.070283966	0.101	1.000	
33	5FRG vs 2FRG	1	0.3486121	1.1398072	0.032436352	0.270	1.000	
34	5FRG vs 3.5FRG	1	0.2921432	1.0639892	0.040822191	0.326	1.000	
35	5FRG vs 2FOR	1	2.2212459	7.3424371	0.140276944	0.001	0.253	
36	5FRG vs 2BAK	1	1.0823645	3.3970996	0.076516251	0.029	1.000	
37	5FRG vs 3BAK	1	0.4362135	1.4684838	0.046665223	0.201	1.000	
38	5FRG vs 3FRG	1	0.2171571	0.8687349	0.037987888	0.276	1.000	
39	5FRG vs 4BAK	1	0.6176128	2.2439374	0.085503077	0.127	1.000	
40	5FRG vs 3.5BAK	1	0.2150097	0.8427053	0.033921641	0.376	1.000	
41	5FRG vs 4FRG	1	0.2825555	1.1239983	0.055853626	0.167	1.000	
42	5FRG vs ENRICHED	1	1.2607540	4.9632010	0.155278597	0.016	1.000	
43	5FRG vs CONTROL	1	0.6401683	2.4033808	0.084616011	0.114	1.000	
44	6FRG vs 5.5BAK	1	0.8310503	2.5808490	0.054241341	0.051	1.000	
45	6FRG vs 5.5FRG	1	0.1861237	0.6327287	0.017272223	0.545	1.000	
46	6FRG vs 6BAK	1	1.2240657	3.6969127	0.050853779	0.017	1.000	
47	6FRG vs 1BAK	1	1.5229624	4.5214511	0.097190673	0.002	0.506	
48	6FRG vs 1FOR	1	1.5209031	4.5579296	0.085102796	0.002	0.506	
49	6FRG vs 0FRG	1	0.9375473	2.9894117	0.071194417	0.025	1.000	
50	6FRG vs 0FOR	1	1.5549391	4.7679006	0.111483157	0.005	1.000	

51	6FRG vs 0BAK	1	2.0308428	5.7581380	0.103269912	0.001	0.253
52	6FRG vs 1FRG	1	0.5750917	1.8722883	0.053689860	0.120	1.000
53	6FRG vs 2FRG	1	0.4165567	1.2661286	0.033087449	0.252	1.000
54	6FRG vs 3.5FRG	1	0.1128633	0.3658290	0.012896819	0.810	1.000
55	6FRG vs 2FOR	1	2.1355765	6.6617404	0.121872087	0.002	0.506
56	6FRG vs 2BAK	1	0.9684047	2.8718160	0.061269569	0.040	1.000
57	6FRG vs 3BAK	1	0.3283302	1.0139759	0.029810566	0.331	1.000
58	6FRG vs 3FRG	1	0.2444064	0.8400719	0.032510433	0.375	1.000
59	6FRG vs 4BAK	1	0.4295731	1.3841127	0.048763641	0.243	1.000
60	6FRG vs 3.5BAK	1	0.2919002	0.9979543	0.035643829	0.320	1.000
61	6FRG vs 4FRG	1	0.2852987	0.9582037	0.041736877	0.314	1.000
62	6FRG vs ENRICHED	1	1.2626330	4.3879015	0.127600154	0.014	1.000
63	6FRG vs CONTROL	1	0.6933077	2.3111717	0.073813005	0.083	1.000
64	5.5BAK vs 5.5FRG	1	0.7492601	2.3141975	0.058864167	0.068	1.000
65	5.5BAK vs 6BAK	1	0.1915861	0.5533553	0.007843076	0.653	1.000
66	5.5BAK vs 1BAK	1	1.0105300	2.7968245	0.061070272	0.020	1.000
67	5.5BAK vs 1FOR	1	0.5227981	1.4734961	0.028626307	0.183	1.000
68	5.5BAK vs 0FRG	1	1.2816647	3.7638240	0.086003089	0.004	1.000
69	5.5BAK vs 0FOR	1	0.6136951	1.7365698	0.042629259	0.117	1.000
70	5.5BAK vs 0BAK	1	0.9604573	2.5747984	0.048059880	0.030	1.000
71	5.5BAK vs 1FRG	1	0.9384744	2.7683929	0.075292737	0.033	1.000
72	5.5BAK vs 2FRG	1	0.4260626	1.1937515	0.030457699	0.282	1.000
73	5.5BAK vs 3.5FRG	1	0.4582627	1.3252537	0.043701324	0.230	1.000
74	5.5BAK vs 2FOR	1	0.6489432	1.8953327	0.037239813	0.110	1.000
75	5.5BAK vs 2BAK	1	0.5359576	1.4863097	0.031973063	0.186	1.000
76	5.5BAK vs 3BAK	1	0.2794606	0.7868771	0.022619941	0.485	1.000
77	5.5BAK vs 3FRG	1	0.5381232	1.6150584	0.058484700	0.171	1.000
78	5.5BAK vs 4BAK	1	0.3086092	0.8845103	0.030622305	0.490	1.000
79	5.5BAK vs 3.5BAK	1	0.5558553	1.6758754	0.056472651	0.177	1.000
80	5.5BAK vs 4FRG	1	0.3245109	0.9400256	0.039265857	0.713	1.000
81	5.5BAK vs ENRICHED	1	1.3484752	4.1710168	0.118592443	0.006	1.000
82	5.5BAK vs CONTROL	1	0.8224783	2.4456578	0.075377046	0.043	1.000
83	5.5FRG vs 6BAK	1	0.9532556	2.8594891	0.044777826	0.036	1.000
84	5.5FRG vs 1BAK	1	1.1552705	3.3756754	0.090317443	0.004	1.000
85	5.5FRG vs 1FOR	1	1.0527758	3.1188773	0.070692580	0.026	1.000
86	5.5FRG vs 0FRG	1	0.6457183	2.0593139	0.062291490	0.051	1.000
87	5.5FRG vs 0FOR	1	1.2620400	3.8313749	0.113249162	0.012	1.000
88	5.5FRG vs 0BAK	1	1.6137244	4.4814956	0.096414617	0.002	0.506
89	5.5FRG vs 1FRG	1	0.3944211	1.2931251	0.049181111	0.216	1.000
90	5.5FRG vs 2FRG	1	0.2227568	0.6685874	0.022535196	0.595	1.000
91	5.5FRG vs 3.5FRG	1	0.1920257	0.6267710	0.030386289	0.617	1.000
92	5.5FRG vs 2FOR	1	1.6369957	5.0851819	0.112790537	0.002	0.506
93	5.5FRG vs 2BAK	1	0.7809680	2.2808814	0.059582782	0.075	1.000
94	5.5FRG vs 3BAK	1	0.3048005	0.9321538	0.035945870	0.395	1.000
95	5.5FRG vs 3FRG	1	0.2030464	0.7247926	0.040891460	0.488	1.000
96	5.5FRG vs 4BAK	1	0.4991990	1.6161387	0.078391922	0.165	1.000
97	5.5FRG vs 3.5BAK	1	0.2334097	0.8233092	0.041532379	0.400	1.000
98	5.5FRG vs 4FRG	1	0.2826628	0.9796642	0.065399611	0.410	1.000
99	5.5FRG vs ENRICHED	1	1.0357176	3.7221512	0.144706061	0.023	1.000
100	5.5FRG vs CONTROL	1	0.5115716	1.7359560	0.076352892	0.158	1.000
101	6BAK vs 1BAK	1	0.9862268	2.7656143	0.039641510	0.027	1.000
102	6BAK vs 1FOR	1	0.3912133	1.1093574	0.014769896	0.298	1.000
103	6BAK vs 0FRG	1	1.9588056	5.7043549	0.081836421	0.002	0.506
104	6BAK vs 0FOR	1	0.4784335	1.3614980	0.021153920	0.227	1.000
105	6BAK vs 0BAK	1	1.0615719	2.9078768	0.037324555	0.022	1.000
106	6BAK vs 1FRG	1	1.3507839	3.9405609	0.063618425	0.008	1.000
107	6BAK vs 2FRG	1	0.5153400	1.4577193	0.022971505	0.208	1.000
108	6BAK vs 3.5FRG	1	0.6169007	1.7784966	0.032467057	0.109	1.000
109	6BAK vs 2FOR	1	0.5935979	1.7241298	0.023073267	0.153	1.000
110	6BAK vs 2BAK	1	0.7456163	2.0928288	0.029437973	0.086	1.000
111	6BAK vs 3BAK	1	0.4776949	1.3560855	0.022846613	0.252	1.000
112	6BAK vs 3FRG	1	0.6801649	1.9982624	0.038429407	0.079	1.000

113	6BAK vs 4BAK	1	0.2877086	0.8254146	0.015625331	0.511	1.000
114	6BAK vs 3.5BAK	1	0.5128725	1.5116124	0.028248306	0.180	1.000
115	6BAK vs 4FRG	1	0.2765679	0.7976671	0.016688410	0.866	1.000
116	6BAK vs ENRICHED	1	1.3054007	3.9066563	0.066319438	0.009	1.000
117	6BAK vs CONTROL	1	0.7820950	2.2896811	0.040676747	0.055	1.000
118	1BAK vs 1FOR	1	0.5040180	1.3616910	0.028156398	0.185	1.000
119	1BAK vs 0FRG	1	1.9405940	5.4078091	0.127519182	0.001	0.253
120	1BAK vs 0FOR	1	0.4505803	1.2070024	0.032440194	0.236	1.000
121	1BAK vs 0BAK	1	0.4863134	1.2495793	0.025372385	0.218	1.000
122	1BAK vs 1FRG	1	1.5179388	4.2080315	0.119519078	0.001	0.253
123	1BAK vs 2FRG	1	0.9025825	2.3897375	0.063914261	0.030	1.000
124	1BAK vs 3.5FRG	1	0.8262963	2.2183452	0.078613582	0.028	1.000
125	1BAK vs 2FOR	1	0.7537028	2.1097094	0.043852050	0.065	1.000
126	1BAK vs 2BAK	1	0.7015983	1.8552140	0.042303157	0.098	1.000
127	1BAK vs 3BAK	1	0.8565378	2.2633201	0.068042518	0.034	1.000
128	1BAK vs 3FRG	1	1.0148870	2.8057277	0.108724997	0.013	1.000
129	1BAK vs 4BAK	1	0.3178094	0.8429157	0.032616897	0.500	1.000
130	1BAK vs 3.5BAK	1	0.5626378	1.5727317	0.059185924	0.148	1.000
131	1BAK vs 4FRG	1	0.2180412	0.5740549	0.027901886	0.750	1.000
132	1BAK vs ENRICHED	1	0.6448937	1.8656311	0.062467493	0.091	1.000
133	1BAK vs CONTROL	1	0.3883082	1.0757974	0.038317608	0.303	1.000
134	1FOR vs 0FRG	1	1.8261491	5.1902547	0.105513882	0.001	0.253
135	1FOR vs 0FOR	1	0.3286025	0.9032983	0.020574724	0.440	1.000
136	1FOR vs 0BAK	1	0.6144707	1.6182435	0.028581662	0.103	1.000
137	1FOR vs 1FRG	1	1.3123154	3.7253744	0.089283187	0.006	1.000
138	1FOR vs 2FRG	1	0.6370521	1.7348496	0.039667442	0.121	1.000
139	1FOR vs 3.5FRG	1	0.7499543	2.0817789	0.059340745	0.075	1.000
140	1FOR vs 2FOR	1	0.2206480	0.6274705	0.011700543	0.607	1.000
141	1FOR vs 2BAK	1	0.8383213	2.2711203	0.044296288	0.051	1.000
142	1FOR vs 3BAK	1	0.6807255	1.8562598	0.046573858	0.094	1.000
143	1FOR vs 3FRG	1	0.8428053	2.4027210	0.074151829	0.030	1.000
144	1FOR vs 4BAK	1	0.3473989	0.9559126	0.029005798	0.413	1.000
145	1FOR vs 3.5BAK	1	0.6140507	1.7627371	0.052209543	0.111	1.000
146	1FOR vs 4FRG	1	0.2788252	0.7681833	0.027664153	0.716	1.000
147	1FOR vs ENRICHED	1	0.9471077	2.7897467	0.073822847	0.048	1.000
148	1FOR vs CONTROL	1	0.6124238	1.7425763	0.048753517	0.114	1.000
149	0FRG vs 0FOR	1	1.9921894	5.7051123	0.147399450	0.001	0.253
150	0FRG vs 0BAK	1	2.0938674	5.6202398	0.111027522	0.001	0.253
151	0FRG vs 1FRG	1	0.2365834	0.7148419	0.024894508	0.680	1.000
152	0FRG vs 2FRG	1	0.5632934	1.5946602	0.047467669	0.129	1.000
153	0FRG vs 3.5FRG	1	0.4023485	1.1911512	0.049239127	0.235	1.000
154	0FRG vs 2FOR	1	2.4430886	7.2359869	0.144039907	0.001	0.253
155	0FRG vs 2BAK	1	1.1067302	3.0901375	0.073417140	0.010	1.000
156	0FRG vs 3BAK	1	0.5679199	1.6199604	0.054691511	0.092	1.000
157	0FRG vs 3FRG	1	0.2625602	0.8199934	0.039384903	0.512	1.000
158	0FRG vs 4BAK	1	0.9987028	2.9255102	0.117370122	0.014	1.000
159	0FRG vs 3.5BAK	1	1.0210318	3.1961519	0.126850796	0.017	1.000
160	0FRG vs 4FRG	1	0.5502469	1.6465951	0.088305404	0.094	1.000
161	0FRG vs ENRICHED	1	2.0440035	6.5823649	0.208419000	0.001	0.253
162	0FRG vs CONTROL	1	1.3444427	4.1208801	0.146541649	0.005	1.000
163	0FOR vs 0BAK	1	0.5083292	1.3213766	0.029155703	0.215	1.000
164	0FOR vs 1FRG	1	1.6033787	4.5915859	0.145342051	0.002	0.506
165	0FOR vs 2FRG	1	0.9019151	2.4386462	0.072928976	0.044	1.000
166	0FOR vs 3.5FRG	1	0.8822321	2.4474017	0.100108867	0.031	1.000
167	0FOR vs 2FOR	1	0.3247739	0.9292131	0.021645240	0.417	1.000
168	0FOR vs 2BAK	1	0.9344626	2.5131796	0.062033631	0.028	1.000
169	0FOR vs 3BAK	1	0.8048085	2.1778469	0.074640427	0.067	1.000
170	0FOR vs 3FRG	1	1.0180102	2.9460418	0.134240236	0.018	1.000
171	0FOR vs 4BAK	1	0.3138715	0.8591566	0.039304197	0.449	1.000
172	0FOR vs 3.5BAK	1	0.6848806	2.0004660	0.086975022	0.089	1.000
173	0FOR vs 4FRG	1	0.2619817	0.7174560	0.042916580	0.626	1.000
174	0FOR vs ENRICHED	1	0.9157164	2.7732500	0.103582867	0.029	1.000

175	0FOR vs CONTROL	1	0.6886008	1.9818183	0.079330426	0.069	1.000
176	0BAK vs 1FRG	1	1.6913077	4.4962835	0.103371671	0.002	0.506
177	0BAK vs 2FRG	1	1.0970563	2.8235970	0.061618843	0.009	1.000
178	0BAK vs 3.5FRG	1	0.9380320	2.4212372	0.066478718	0.025	1.000
179	0BAK vs 2FOR	1	0.6843303	1.8549854	0.033210739	0.094	1.000
180	0BAK vs 2BAK	1	1.0104888	2.6082409	0.049578562	0.019	1.000
181	0BAK vs 3BAK	1	0.9028015	2.3134458	0.055997407	0.031	1.000
182	0BAK vs 3FRG	1	1.0804706	2.8367892	0.083837422	0.003	0.759
183	0BAK vs 4BAK	1	0.3886670	0.9932202	0.029218186	0.395	1.000
184	0BAK vs 3.5BAK	1	0.8717262	2.3140744	0.065528389	0.038	1.000
185	0BAK vs 4FRG	1	0.3057368	0.7723278	0.026842728	0.860	1.000
186	0BAK vs ENRICHED	1	1.2389646	3.3876068	0.086006922	0.010	1.000
187	0BAK vs CONTROL	1	0.8230693	2.1768903	0.058554933	0.041	1.000
188	1FRG vs 2FRG	1	0.4128710	1.1657219	0.042911499	0.278	1.000
189	1FRG vs 3.5FRG	1	0.2892516	0.8666397	0.048506027	0.431	1.000
190	1FRG vs 2FOR	1	1.8403847	5.4812625	0.129027768	0.001	0.253
191	1FRG vs 2BAK	1	0.8566460	2.3810141	0.067296377	0.056	1.000
192	1FRG vs 3BAK	1	0.4087825	1.1647539	0.050281298	0.264	1.000
193	1FRG vs 3FRG	1	0.1717527	0.5580337	0.038331669	0.642	1.000
194	1FRG vs 4BAK	1	0.8196872	2.4218455	0.131465955	0.039	1.000
195	1FRG vs 3.5BAK	1	0.7475474	2.4246253	0.131596994	0.061	1.000
196	1FRG vs 4FRG	1	0.4880237	1.4970378	0.119791414	0.330	1.000
197	1FRG vs ENRICHED	1	1.5197008	5.0941163	0.211425737	0.004	1.000
198	1FRG vs CONTROL	1	1.0662211	3.3464528	0.156768567	0.014	1.000
199	2FRG vs 3.5FRG	1	0.2718352	0.7403404	0.034053765	0.502	1.000
200	2FRG vs 2FOR	1	1.0601123	3.0058863	0.068306461	0.034	1.000
201	2FRG vs 2BAK	1	0.4703466	1.2511427	0.032708635	0.268	1.000
202	2FRG vs 3BAK	1	0.2212049	0.5894043	0.022166886	0.709	1.000
203	2FRG vs 3FRG	1	0.2812682	0.7978378	0.042443065	0.457	1.000
204	2FRG vs 4BAK	1	0.4716554	1.2658445	0.059524771	0.238	1.000
205	2FRG vs 3.5BAK	1	0.3882202	1.1140113	0.052761707	0.337	1.000
206	2FRG vs 4FRG	1	0.3303841	0.8813911	0.055498356	0.472	1.000
207	2FRG vs ENRICHED	1	1.1409099	3.4057424	0.128977339	0.010	1.000
208	2FRG vs CONTROL	1	0.6280143	1.7777590	0.074765625	0.109	1.000
209	3.5FRG vs 2FOR	1	1.0384906	3.0417456	0.086803485	0.016	1.000
210	3.5FRG vs 2BAK	1	0.5186480	1.3997356	0.047610482	0.240	1.000
211	3.5FRG vs 3BAK	1	0.2510129	0.6856908	0.038770934	0.556	1.000
212	3.5FRG vs 3FRG	1	0.2103314	0.6734051	0.069614071	0.439	1.000
213	3.5FRG vs 4BAK	1	0.3901830	1.0956271	0.090580430	0.278	1.000
214	3.5FRG vs 3.5BAK	1	0.3469046	1.1108551	0.091723921	0.299	1.000
215	3.5FRG vs 4FRG	1	0.3066480	0.8811576	0.128053682	0.763	1.000
216	3.5FRG vs ENRICHED	1	0.9133893	3.0663271	0.179671178	0.028	1.000
217	3.5FRG vs CONTROL	1	0.5637648	1.7296931	0.117428997	0.131	1.000
218	2FOR vs 2BAK	1	1.1453579	3.2105233	0.062692647	0.015	1.000
219	2FOR vs 3BAK	1	0.9405411	2.6826247	0.067601997	0.037	1.000
220	2FOR vs 3FRG	1	1.0894032	3.3046073	0.102295233	0.021	1.000
221	2FOR vs 4BAK	1	0.4200974	1.2209227	0.037892234	0.283	1.000
222	2FOR vs 3.5BAK	1	0.8765346	2.6680891	0.079246822	0.062	1.000
223	2FOR vs 4FRG	1	0.3173447	0.9336656	0.034665374	0.507	1.000
224	2FOR vs ENRICHED	1	1.2512536	3.8960522	0.102808920	0.011	1.000
225	2FOR vs CONTROL	1	0.8736238	2.6241467	0.073662024	0.047	1.000
226	2BAK vs 3BAK	1	0.3787517	1.0061756	0.029588026	0.381	1.000
227	2BAK vs 3FRG	1	0.5256256	1.4584653	0.055122823	0.200	1.000
228	2BAK vs 4BAK	1	0.5275780	1.4080912	0.049566556	0.225	1.000
229	2BAK vs 3.5BAK	1	0.6737508	1.8882375	0.065363541	0.129	1.000
230	2BAK vs 4FRG	1	0.3663318	0.9725369	0.042334761	0.407	1.000
231	2BAK vs ENRICHED	1	1.4330768	4.1461816	0.121424458	0.006	1.000
232	2BAK vs CONTROL	1	0.9218726	2.5617426	0.081166070	0.046	1.000
233	3BAK vs 3FRG	1	0.2612842	0.7529444	0.051036887	0.507	1.000
234	3BAK vs 4BAK	1	0.3769178	1.0110839	0.059436769	0.328	1.000
235	3BAK vs 3.5BAK	1	0.4042860	1.1798981	0.068678991	0.347	1.000
236	3BAK vs 4FRG	1	0.3380050	0.8991218	0.075562033	0.530	1.000

237	3BAK vs ENRICHED	1	1.1263971	3.4421719	0.153379626	0.017	1.000
238	3BAK vs CONTROL	1	0.6569546	1.8817006	0.094644853	0.101	1.000
239	3FRG vs 4BAK	1	0.6580517	2.0625404	0.204972137	0.134	1.000
240	3FRG vs 3.5BAK	1	0.4577172	1.7688384	0.181069468	0.084	1.000
241	3FRG vs 4FRG	1	0.4657526	1.9325160	0.391791123	0.200	1.000
242	3FRG vs ENRICHED	1	1.1391632	4.4668723	0.288802561	0.018	1.000
243	3FRG vs CONTROL	1	0.7537357	2.6243139	0.207877745	0.069	1.000
244	4BAK vs 3.5BAK	1	0.1986227	0.6252921	0.058849400	0.602	1.000
245	4BAK vs 4FRG	1	0.1257894	0.3438057	0.064337230	1.000	1.000
246	4BAK vs ENRICHED	1	0.3825622	1.2714207	0.089088585	0.242	1.000
247	4BAK vs CONTROL	1	0.2461731	0.7425166	0.058270795	0.578	1.000
248	3.5BAK vs 4FRG	1	0.1063685	0.3948021	0.073181947	0.873	1.000
249	3.5BAK vs ENRICHED	1	0.3638408	1.3792461	0.095919220	0.183	1.000
250	3.5BAK vs CONTROL	1	0.1741020	0.5975679	0.047435180	0.633	1.000
251	4FRG vs ENRICHED	1	0.1094376	0.4204596	0.049933094	0.904	1.000
252	4FRG vs CONTROL	1	0.1152517	0.3753953	0.050898323	1.000	1.000
253	ENRICHED vs CONTROL	1	0.2582796	0.9155934	0.057528073	0.405	1.000

Table 8 SIMPER - All Corals	
Season	
Dry vs. Wet	
	cumsum
Endozoicomonas	0.4221
Rhodobacteraceae	0.5034
Simkaniaceae	0.5504
Xenococcaceae	0.592
Cryomorphaceae; Crocinitomix	0.6236
Alteromonadaceae	0.6497
Vibrionaceae	0.6678

Flammeovirgaceae	0.6845
unidentified Proteobacteria (c__Epsilonproteobacteria; o__Campylobacteriales)	0.7005
Flavobacteriaceae	0.7154

SIMPER - All corals					
Table 9: Island Side					
North vs. East		West vs. East		West vs. North	
	cumsum		cumsum		cumsum
Endozoicomonas	0.4178	Endozoicomonas	0.4338	Endozoicomonas	0.4403
Rhodobacteraceae	0.4891	Rhodobacteraceae	0.5032	Rhodobacteraceae	0.5209
Simkaniaceae	0.5302	p__Proteobacteria c__Gammaproteobacteria; o__Alteromonadales ;f__Alteromonadaceae; g__Alteromonas	0.5396	Simkaniaceae	0.5649
Xenococcaceae	0.5672	p__Cyanobacteria; c__Synechococcophycideae; o__Pseudanabaenales; f__Pseudanabaenaceae; g__Halomicronema	0.5743	Xenococcaceae	0.6059
c__Cytophagia; o__Cytophagales; f__[Amoebophilaceae]; g__SGUS912	0.5993	p__Proteobacteria; c__Gammaproteobacteria; o__Vibrionales; f__Vibrionaceae; g__Vibrio	0.5998	c__Cytophagia; o__Cytophagales; f__[Amoebophilaceae]; g__SGUS912	0.6378
p__Proteobacteria c__Gammaproteobacteria; o__Alteromonadales; f__Alteromonadaceae; g__Alteromonas	0.6242	unidentified Alphaproteobacteria	0.6247	p__Proteobacteria c__Gammaproteobacteria; o__Alteromonadales ;f__Alteromonadaceae ;g__Alteromonas	0.6637

p__Cyanobacteria; c__Synechococcophycidea e; o__Pseudanabaenales; f__Pseudanabaenaceae; g__Halomicronema	0.6452	Cryomorphaceae	0.6475	p__Proteobacteria; c__Gammaproteobacteria; o__Vibrionales; f__Vibrionaceae; g__Vibrio	0.6808
p__Proteobacteria; c__Alphaproteobacteria; o__Rhodospirillales; f__Rhodospirillaceae; g__Roseospira	0.6638	p__Proteobacteria; c__Alphaproteobacteria; o__Rhodospirillales; f__Rhodospirillaceae; g__Roseospira	0.6702	Unidentified: p__Proteobacteria; c__Epsilonproteobacteria; o__Campylobacteriales	0.6971
p__Proteobacteria; c__Gammaproteobacteria; o__Vibrionales; f__Vibrionaceae; g__Vibrio	0.6811	Flammeovirgaceae	0.6892	Flammeovirgaceae	0.7132
Flammeovirgaceae	0.6981	p__Bacteroidetes; c__[Saprospirae]; o__[Saprospirales]; f__Saprospiraceae; g__Saprospira	0.7082	p__Bacteroidetes c__[Saprospirae]; o__[Saprospirales]; f__Saprospiraceae; g__Saprospira	0.7279

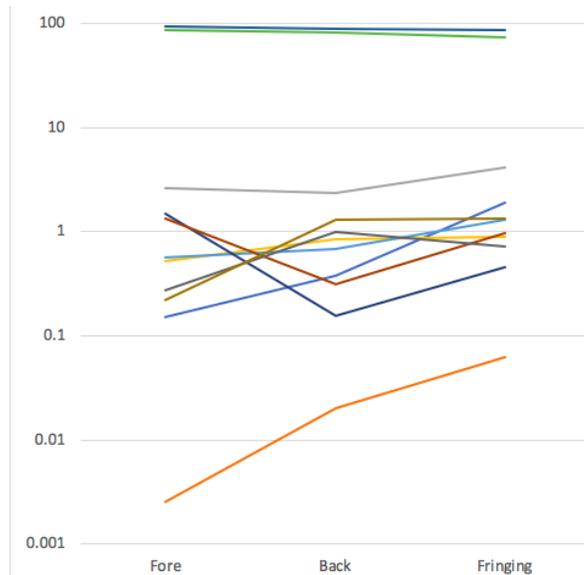
Table 10
HABITAT

BAK_FRG		BAK_FOR		FRG_FOR	
	cumsum		cumsum		cumsum
Endozoicomonas	0.4236	Endozoicomonas	0.4169	Endozoicomonas	0.4193
Rhodobacteraceae	0.5126	Rhodobacteraceae	0.4861	Xenococcaceae	0.494
Simkaniaceae	0.5595	Xenococcaceae	0.5468	Rhodobacteraceae	0.5679
Alteromonadaceae	0.5864	Simkaniaceae	0.5933	Cryomorphaceae; Crocinitomix	0.6069
Xenococcaceae	0.6128	Cryomorphaceae; Crocinitomix	0.6392	Alteromonadaceae	0.633
Cryomorphaceae; Crocinitomix	0.634	unidentified Proteobacteria c__Epsilonproteobacteria; o__Campylobacteriales	0.6671	unidentified Proteobacteria; c__Epsilonproteobacteria; o__Campylobacteriales	0.657
Vibrionaceae	0.6525	Alteromonadaceae	0.6922	Synechococcaceae; g__synechococcus	0.6766
Flammeovirgaceae	0.6697	Vibrionaceae	0.7098	Flavobacteriaceae	0.6927

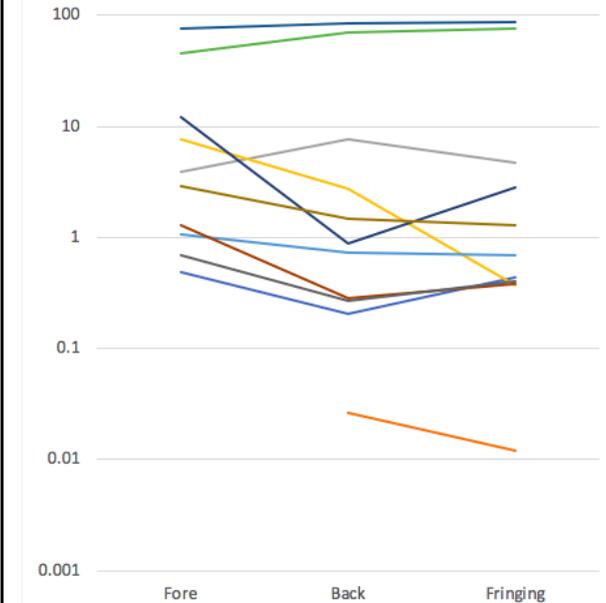
Saprosiraceae	0.6865	Flammeovirgaceae	0.726	Saprosiraceae	0.7084
Flavobacteriaceae	0.7027	Synechococcaceae; g_synechococcus	0.7417	Flammeovirgaceae	0.724
Species					
POC vs. POR		POC vs. ACR		POR vs. ACR	
	cumsum		cumsum		cumsum
Endozoicamonas	0.4292	Endozoicamonas	0.4148	Endozoicamonas	0.4163
Rhodobacteraceae	0.5195	Simkaniaceae	0.5426	Simkaniaceae	0.5129
Xenococcaceae	0.5706	Rhodobacteraceae	0.598	Rhodobacteraceae	0.5876
Cryomorphaceae; Crocinitomix	0.6082	Vibrionaceae	0.6211	Xenococcaceae	0.6322
Alteromonadaceae	0.6365	Alteromonadaceae	0.6428	Cryomorphaceae; Crocinitomix	0.6658
unidentified Proteobacteria c_Epsilonprot eobacteria;o__Campyloba cterales	0.6569	Synechococcaceae; g_synechococcus	0.6606	Alteromonadaceae	0.6891
Flammeovirgaceae	0.6746	Flavobacteriaceae	0.6774	Vibrionaceae	0.7056
Vibrionaceae	0.6906	unidentified Alphaproteobacteria	0.6934	unidentified Proteobacteria c_Epsilonproteobacteria; o_Campylobacteriales	0.7216
Saprosiraceae	0.7062	Saprosiraceae	0.7092	Flammeovirgaceae	0.7372
Flavobacteriaceae	0.7213	Pseudanabaenaceae; g_Halomiconema	0.7244	Saprosiraceae	0.7497

Supplementary Figure 1a,b,c: Percent Relative abundance of the top 10 families shared by a) *Pocillopora verrucosa* b) *Porites lobata* and c) *Acropora hyacinthus*. Endozoicomonas represents the majority of the coral microbiome. Other visible shifts at log10 scale transform across fore, back and fringing reef habitats. Incomplete lines do not represent missing data, rather an absence, or zero abundance, of the taxa at that habitat in that species.

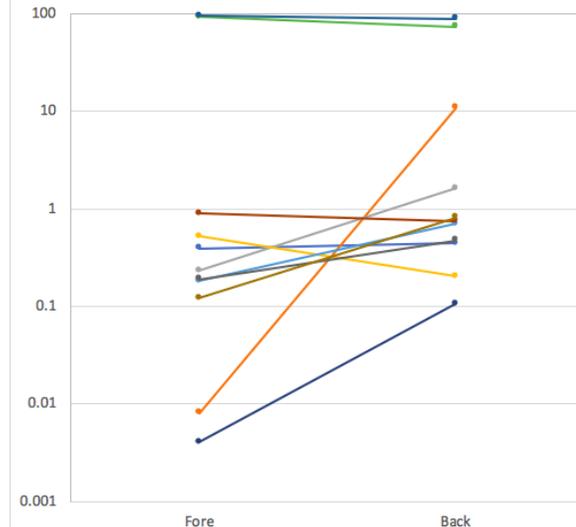
a) *Pocillopora verrucosa*



b) *Porites lobata*



c) *Acropora hyacinthus*



— Cryomorphaceae — Simkaniaceae
 — Rhodobacteraceae — [Amoebophilaceae]
 — Flavobacteriaceae — Endozoicimonaceae
 — Xenococcaceae — Synechococcaceae
 — Unidentified — Alteromonadaceae
 — TotalRepresented

TABLE 12 SIMPER analysis - Each coral species by season, full table of values

<i>P. verrucosa</i> Wet vs. Dry Season	average	sd	ratio	ava	avb	cumsum
Endozoicimonaceae	1.24E-01	1.31E-01	0.9421	803.33684	842.26866	0.4273
Rhodobacteraceae	2.31E-02	3.85E-02	0.5998	30.50526	31.22388	0.5069
Alteromonadaceae; g__Alteromonas	8.09E-03	1.98E-02	0.4084	12.89474	7.92537	0.5348
Vibrionaceae; g__Vibrio	7.06E-03	1.11E-02	0.6364	7.90526	12.32836	0.5591
Cryomorphaceae	6.68E-03	1.66E-02	0.4015	6.75789	10.50746	0.5822
unid. Alphaproteobacteria	6.22E-03	3.12E-02	0.1989	10.36842	3.52239	0.6036
Flavobacteriaceae	6.11E-03	8.97E-03	0.6814	8.95789	8.59701	0.6247
Synechococcaceae; g__Synechococcus	5.94E-03	2.01E-02	0.2949	9.33684	5.83582	0.6452
Saprospiraceae; g__Saprospira	5.86E-03	9.10E-03	0.644	8.48421	7.0597	0.6654
[Amoebophilaceae]; g__SGUS912	5.56E-03	1.15E-02	0.4848	10.18947	5.13433	0.6846
<i>P. lobata</i> - Dry vs. Wet Season						
	average	sd	ratio	ava	avb	cumsum
Endozoicimonaceae	1.97E-01	1.81E-01	1.0864	660.01205	748.73239	0.4186
Rhodobacteraceae	4.78E-02	8.88E-02	0.5386	60.96386	56.84507	0.5203
Xenococcaceae	3.22E-02	6.89E-02	0.4678	35.3253	39.57746	0.5888
[Amoebophilaceae]; g__SGUS912	2.19E-02	3.66E-02	0.5979	30.6988	22.3662	0.6353

Alteromonadaceae; g__Alteromonas	1.38E-02	3.51E-02	0.3936	18.43373	15.09859	0.6647
unid. Epsilonproteobacteria; o__Campylobacteriales	1.18E-02	2.55E-02	0.4614	15.66265	10.74648	0.6897
Flammeovirgaceae	8.75E-03	1.38E-02	0.6344	12.85542	9.25352	0.7083
Rhodospirillaceae; g__Roseospira	6.35E-03	1.45E-02	0.437	10.89157	3.8169	0.7219
Saprospiraceae; g__Saprospira	6.30E-03	8.60E-03	0.7321	10.96386	5.28169	0.7352
Vibrionaceae; g__Vibrio	5.85E-03	1.04E-02	0.5637	8.37349	7.66197	0.7477

Acropora hyacinthus, Dry vs. Wet

	average	sd	ratio	ava	avb cu	msum
Endozoicimonaceae	1.30E-01	1.41E-01	0.9215	818.2766	801.8500.	4203
ASV33356	7.25E-02	1.36E-01	0.5343	59.68085	105.9000.	6548
Rhodobacteraceae	9.64E-03	1.89E-02	0.5096	15.23404	9.7750.	6860
Vibrionaceae; g__Vibrio	7.67E-03	1.06E-02	0.7225	8.7234	15.2250.	7108
f__Pseudanabaenaceae; g__Halomicronema	4.82E-03	2.11E-02	0.2286	6.89362	3.2750.	7264
Alteromonadaceae; g__Alteromonas	4.80E-03	8.37E-03	0.573	7.21277	5.4750.	7419
Flavobacteriaceae	4.09E-03	5.82E-03	0.7036	5.59574	5.9750.	7551
Synechococcaceae; g__Synechococcus	3.87E-03	3.37E-03	1.1506	8.65957	7.4500.	7677
Flammeovirgaceae	3.49E-03	5.99E-03	0.583	4.02128	4.5500.	7790
Saprospiraceae; g__Saprospira	3.44E-03	6.18E-03	0.5572	5.29787	3.0000.	7901