DEEP-SEA CORAL BIOGEOGRAPHY AND COMMUNITY STRUCTURE IN TROPICAL SEAMOUNT ENVIRONMENTS

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ABSTRACT

As the largest and most poorly environment on Earth, the deep-sea is facing global threats from climate change and anthropogenic disturbance further compounded by the lack of critical baseline data on seafloor species composition and community structure. Many data-deficient regions include those in geographically-isolated offshore environments, like low-latitude seamounts, where sampling and surveys have been limited, resulting in critical knowledge gaps that do not allow for effective conservation measures to be realized. This work seeks to characterize the coral fauna of tropical seamount environments greater than 150 m depth and understand the environmental controls on species distribution and community assembly for long-lived, ecologically-important species, primarily from the Octocorallia, Antipatharia, Stylasteridae, and Scleractinia. Methodologies for accomplishing this research have included analysis of remotely operated vehicle (ROV) video surveys and identification of collected voucher specimens to understand biogeographic patterns within coral communities on seamounts and other rugged seafloor features in 3 different regions: the tropical western Atlantic (Anegada Passage), the equatorial central Pacific (Phoenix Islands), and the tropical eastern Pacific (Costa Rica). These regions represent vastly different oceanographic regimes in terms of biological productivity and water column structure resulting in differential effects on deep-sea coral communities. Evidence from these three regions has shown significant effects of the role that oceanic water masses have on structuring deep-water coral biodiversity and suggests that these features, along with other abiotic environmental variables, are important indicators for understanding species distribution

patterns, community structure, and global biogeographic patterns. More broadly, the results of this work have demonstrated the capabilities of exploratory ROV surveys, across multiple platforms, to add practical knowledge to coral species inventories and identify bathyal biogeographic patterns in remote regions of the deep sea. The results of this work, serving as baseline coral biodiversity surveys for each area, are also germane to evaluating the effects of human-mediated disturbance and global climate change in the deep ocean. These disturbances also include ocean acidification, ocean deoxygenation, deep-sea mining, and bottom-contact fishing, all of which have been identified as threats to the seamount benthos.

For Eneko and Amaia

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CHAPTER 1

INTRODUCTION

Few environments on Earth evoke as much mystery as the deep sea and the organisms that inhabit it. It is a place of extremes including pressure, temperature, oxygen, and carbon resources, among many others, testing the adaptability and evolutionary potential of life on Earth. Composed of two broadly defined realms, the pelagic and benthic zones, they occupy more than 90% of the volume that life can inhabit on Earth (Ramirez-Llodra et al., 2010; Dawson, 2012). However, fundamental patterns concerning the distribution and diversity of deep-sea species relative to environmental variables in those zones remain poorly understood. The ability to test broad scale hypotheses regarding these patterns and underlying processes in the deep ocean also remains difficult, largely owing to the lack of exploration, both in space and time. The deep-sea benthic environment specifically, composing about 91.5% of all seafloor area (Watling et al., 2013), hosts substantial biodiversity (Hessler & Sanders, 1967; Grassle et al., 1975; Rex, 1981) including species that are likely still unknown to science (Ramirez-Llodra et al., 2010; Menegotto & Rangel, 2018). Among the most poorly studied benthic environments are offshore seamounts (Clark et al., 2010) and other similarly isolated open-ocean features like islands and atolls. Hard substrate deep-sea environments compose the majority of these features, many of which have volcanic origins (Wessel, 2007), and are potential hotspots for biodiversity (Rowden et al., 2010a) and long-lived species (Roark et al., 2009), and vulnerable to anthropogenic disturbance (Rogers, 2018). This work will examine newly explored offshore seamount environments in the Atlantic and Pacific Ocean testing hypotheses on the drivers of species distribution and community assembly of deep-water corals, important inhabitants and generators of biodiversity on seamount hard substratum (Rogers et al., 2007).

Determining global biogeographic patterns of benthic megafauna at the species level are critical to advancing our understanding of biodiversity and connectivity in the deep ocean. It is clear that biogeographic ranges in the deep sea are filtered through major geological, physical, and chemical events across evolutionary time (McClain & Hardy, 2010). Long-held understanding that deep-sea species are homogenously distributed and dominated by cosmopolitan fauna (Bruun, 1957) have been largely unsubstantiated (Ekman, 1953; Vinogradova, 1997) by increased sampling effort and technological developments in taxonomy (Cairns & Chapman, 2001; Dawson, 2002; McClain & Hardy, 2010). In the Gulf of Mexico, recent work has indicated biogeographic barriers can exist between sites that are several hundred kilometers distant as well as between different depth strata in a single locality (Quattrini et al., 2013; Doughty, Quattrini & Cordes, 2014). Biogeographic patterns on seamounts are particularly difficult to assess owing to taxonomic or spatial sampling biases (Pante et al., 2015). Recently, this has led to biogeographic provinces being identified by modelling of oceanographic proxies, rather than directly through species composition (Watling et al., 2013). Such proposed biogeographic provinces would greatly benefit from ground truthing analysis of collected voucher specimens. Nevertheless, identifying oceanographic and environmental variables (e.g. depth, temperature, dissolved oxygen, water masses, surface productivity) coincident with species distribution patterns is vitally important important to establishing and refining biogeographic provinces as more information becomes available.

For the purposes of this work, the deep sea will be defined in bathymetric terms as greater than 200 m depth, typically identified as beyond the depth of the continental shelf (Carney, 2005). Within these limits I will largely focus on bathyal depths between 200-3000 m (Zezina, 1997; Watling et al., 2013). Not explicitly studied here, but relevant to broader interpretation, abyssal depths will be defined as between 3000-6000 m and followed by hadal at depths greater than 6000 m (Watling et al., 2013).

1.1 Biology and ecology of deep-sea corals

Deep-sea corals (likewise referred to as cold-water corals or deep-water corals) are groups of solitary and colonial marine metazoans within the phylum Cnidaria that secrete skeletal elements and typically occur below 50 m depth (Cairns, 2007). In this work, the definition of deep-sea corals will focus on six taxonomic groups: the Alcyonacea and Pennatulacea (Williams, 2011) within the Octocorallia (Watling et al., 2011), the Scleractinia (Kitahara et al., 2010), Antipatharia (Wagner, Luck & Toonen, 2012), and Zoantharia (Carreiro-Silva et al., 2017) within the Hexacorallia, and the calcified hydrozoan family Stylasteridae (Cairns, 2011) (Table 1.1). With over 5100 described species, more than half occur at depths greater than 50 m (Cairns, 2007). While members of the Zoantharia may not have always been recognized as deep-water corals (Cairns, 2007), some species (e.g. *Kulamanamana haumeaae* (Sinniger, Ocaña & Baco, 2013)) are capable of producing thin skeletal secretions after parasitizing other coral hosts, while many other species are epizoic (Carreiro-Silva et al., 2017).

Table 1.1 Taxonomic classification of major deep-water coral groups. Common name designations for orders (bold) are indicated in parentheses.

- Domain: Eukaryota
  - Kingdom: Animalia
    - Phylum: Cnidaria
      - Class: Hydrozoa
        - **Order: Stylasterina (Lace corals)**
      - Class: Anthozoa
        - Subclass: Octocorallia
          - **Order: Pennatulacea (Sea pens)**
          - **Order: Alcyonacea (Soft corals and sea fans)**
            - Suborder: Calcaxonia
            - Suborder: Scleraxonia
            - Suborder: Holaxonia
            - Suborder: Stolonifera
        - Subclass: Hexacorallia
          - **Order Antipatharia (Black corals)**
          - **Order Scleractinia (Stony corals)**
          - **Order Zoantharia (Gold corals)**

Many deep-sea corals are characteristically long-lived and slow growing (Roark et al., 2009; Houlbrèque et al., 2010). Unlike their shallow water relatives (Veron, 2011), deep-sea corals are entirely azooxanthellate (Cairns, 2007) and food resources are considered to be derived entirely from capture of particulate organic matter (POM) or small zooplankton in the water column (but see Kellogg, 2019; Vohsen et al., 2020) through suspension feeding (Lewis, 1978). Dense coral communities are more likely to occur in areas where POM supply is enhanced, for example by topographically-induced currents (Genin et al., 1986). Reproductive processes remain understudied for many cold-water coral species, but additional insights have been gained in recent years (Cordes et al., 2001, Waller & Feehan, 2013; Feehan & Waller, 2015; Rossin, Waller & Försterra, 2017). Reproduction is considered to be semi-synchronous with seasonal food falls acting as a stimulus to initiate gametogenesis (Waller, 2005; Rossin, Waller & Försterra, 2017).

Most species are gonochoristic with entire colonies producing only male or female gametes, however hermaphroditism is present in some solitary scleractinian species (Waller, Tyler & Gage, 2005).

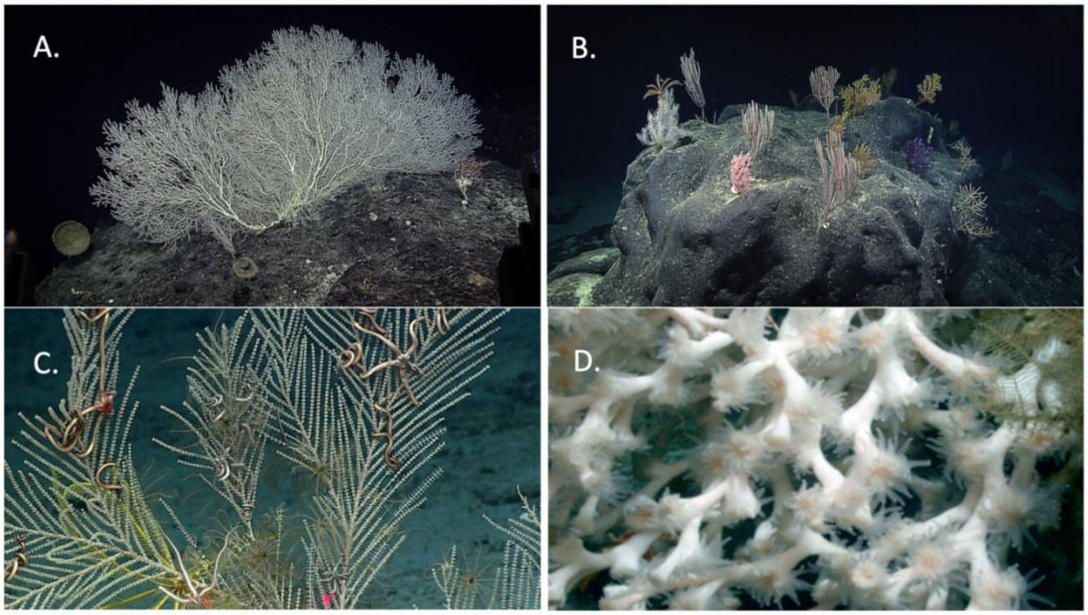


Figure 1.1 Diversity of deep-water corals and associated fauna. **A.** A massive, 2.5 m tall bamboo coral in the family Isididae (Keratoisidinae) in the Pacific Remote Islands Marine National Monument (Demopoulos et al., 2018). **B.** A diverse octocoral knoll on Titov Seamount in the central Pacific. Representatives from 4 families are present including the Plexauridae, Primnoidae, Coralliidae, and Victorgorgiidae. **C.** *Callogorgia cracentis* Cairns 2017 from the Phoenix Islands with numerous asteroschematid brittle star associates (Auscavitch et al., 2020a). **D.** Framework-forming reef-builder, *Lophelia pertusa* Linnaeus 1758, in the Gulf of Mexico.

Over the past several decades it has become increasingly clear that deep-water corals as a group are neither restricted to the deep-sea, nor occur exclusively in cold water, but rather are eurybathic and can be found from inshore environments to the high seas (Cairns, 2007, 2016; Häussermann & Försterra, 2007; Roberts et al., 2009). Abiotic environmental and oceanographic variables can be important indicators of species distribution patterns as many species have large geographic and bathymetric ranges. Coral species distributions appear to be strongly influenced by a few key environmental variables like depth (Thresher et al., 2014; Quattrini et al., 2015), temperature (Brooke et al., 2013), dissolved oxygen (Hanz et al., 2019; Hebbeln et al., 2020), overlying water masses (Miller et al., 2011; Buhl-Mortensen et al., 2014; Radice et al., 2016; Auscavitch & Waller, 2017; Victorero et al., 2018; Auscavitch et al., 2020a; Puerta et al., 2020), pH (Georgian et al., 2016b,a), and carbonate saturation state (Roberts et al., 2009; Georgian et al., 2016a; Auscavitch et al., 2020b; Puerta et al., 2020). On offshore seamounts, additional variables like seafloor topography, particulate organic material export to the benthos (Duineveld, Lavaleye & Berghuis, 2004; Baco et al., 2017), and current flow also have great importance on coral density and distribution (Genin et al., 1986; Genin & Dower, 2007; Morgan et al., 2019; Bashah et al., 2020). Among the stylasterid hydrocorals, sedimentation rate is important, as they are often excluded from heavily sedimented continental margins, yet are prevalent on offshore seamounts and in tropical oligotrophic seas (Cairns, 1992). For mixed assembalges of soft corals and other coral taxa, particularly dense and diverse communities, termed coral gardens (Stone, 2006), can be observed on continental margins (Auster et al., 2013) or in offshore environments (Fig. 1.1). On continental margins and some seamounts at higher latitudes (Tracey et al., 2011), framework-forming stony coral species (Fig. 1.1D) can form extensive reefs (Davies et al., 2015). Such reefs are largely absent from low-latitude seamounts worldwide (but see observations in Auscavitch et al., 2020c), but still many tropical and equatorial seamounts remain underexplored (Kennedy et al., 2019).

Cold-water corals are ecosystem engineers (*sensu* Jones, Lawton & Shachak, 1994) as well as indicator species for vulnerable marine ecosystems (VMEs) (FAO, 2009; Watling & Auster, 2017). As ecosystem engineers, some reef-forming corals are capable of altering their physical environment by modifying local topography which can result in hydrographic and productivity changes in the above-lying water column (Soetaert et al., 2016). Some of these effects can remain long after death in the form of skeletal rubble or debris which can act as persistent sources of habitat heterogeneity (Buhl-Mortensen et al. 2010). Both classifications make studying deep-sea corals critical for understanding the degree of anthropogenic impacts on deep-sea benthic environments (Davies, Roberts & Hall-Spencer, 2007; Ragnarsson et al., 2017). For seamounts in particular, the use of bottom-contact fishing gear has been observed to reduce structural complexity of benthic habitats which support high deep-sea biodiversity and biomass (Althaus et al., 2009).

Environmental changes resulting from climate drivers can have manifold effects on deep-water corals and the ecosystems they support. The broadest reaching and most impactful of these include warming deep ocean waters (Barnett et al., 2005; Yasuhara & Danovaro, 2016; Brito-Morales et al., 2020), ocean acidification (Jiang et al., 2015; Pérez et al., 2018), and ocean deoxygenation (Stramma et al., 2010). Increased seawater temperature has been found to have marked effects on distribution of relatively stenotherm (Brooke et al., 2013) deep-water coral species and substantially altering physiological and metabolic responses (Dodds et al., 2007; Hennige et al., 2014).

Expansion of oxygen minimum zones (Stramma et al., 2008) and open-ocean deoxygenation (Levin, 2018) resulting from warming waters and changing ocean circulation both are critical (Oschlies et al., 2018) processes in determining future habitable zones for deep-water corals. The sensitivity of some framework-forming species to low oxygen has been observed to result in rapid mortality effects (Lunden et al., 2014) in the present and across geological timescales (Fink et al., 2012).

Many deep-water coral species that produce aragonitic or calcitic calcium carbonate skeletal elements are susceptible to changes in ocean carbonate chemistry (Feely et al., 2004; Lunden et al., 2014; Roberts & Cairns, 2014). As ocean pH and buffering capacity decreases with increasing dissolution of atmospheric CO2 into the ocean, coral species may respond with the potential for adaptation (Kurman et al., 2017) or extirpation. One abiotic variable that can be used to determine habitat suitability of corals (Guinotte et al., 2006; Davies & Guinotte, 2011) is the saturation state of the calcium carbonate minerals aragonite or calcite (Feely et al., 2012). These values indicate the solubility of carbonate minerals that corals can use to secrete a skeleton at a given temperature and pressure (Feely et al., 2004). The carbonate saturation state and location of corals relative to a shoaling aragonite and calcite saturation depth are known to be controls on distribution for some of the most common species (Guinotte et al., 2006). Decreasing saturation states can lead to energetic stress on calcifying corals or active dissolution of skeletal material or biogenic undergrowth (Maier et al., 2012; Lunden et al., 2014; Hennige et al., 2015; Gómez et al., 2018). These stressor effects can also be observed on coral metabolism and in gene expression (Glazier et al., 2020). Loss of suitable habitat through multiple stressors on cold-water coral species may lead to declining species diversity and population fragmentation (Danovaro et al., 2008). However, some environments in the deep-sea, like isolated seamounts (Tittensor et al., 2010), may act as refugia for some groups of cold-water corals (Henry et al., 2014), but not others like solitary cup corals that might lack strong population connectivity (Miller et al., 2011).

1.2 Seamounts and similar rugged seafloor features

Seamounts are broadly defined as large, steep undersea mountains rising at least 1000 m above the surrounding seafloor (Menard, 1964). Many isolated offshore seamounts are formed as a result of intraplate hotspot volcanism (Wessel, 2007), but they can also be fomed from tectonic uplift of seafloor crust (Schmidt & Schmincke, 2000). Guyots, or flat-topped seamounts, will not be examined separately here and are included in the definition of a seamount. Shallow or deep-water seamounts may also be capped in carbonate rock, indicating historical coral atoll or reef existance and subsequent subsidence (Darwin, 1851; Grigg, 1982; Terry & Goff, 2013). It has been estimated that fewer than 300 seamounts (>1000m in height) world-wide have been visually or physically sampled (Rowden et al., 2010a) out of the recently estimated 33,000 or more thought to exist worldwide (Yesson et al., 2011).

Whereas abyssal seafloor is often thought to be heavily sedimented and relatively featureless, seamounts, with abundant hard bottom habitat, have been found to be oases of biodiversity and abundance in the deep-sea (Rowden et al., 2010b; Thresher et al., 2011). Compared to adjacent continental shelf and slope environments, seamounts have been shown to support higher epibenthic megafaunal biomass (Rowden et al., 2010b).

Additionally, open ocean lower bathyal and abyssal depths (>3000m) are often dominated by muddy or soft bottom sediments prohibiting the attachment of hard-substrate suspension or filter feeders (but see (Riehl et al., 2020)). Abundant hard substrate, coupled with prominent topographically-induced flows create locally consistent food resources for suspension and filter feeding organisms (Genin et al., 1986).

Hydrodynamic processes, including Taylor columns (Beeston, Cragg & Linse, 2018), create the potential to retain planktonic coral larvae within the seamount environment enhancing local recruitment (Mullineau & Mills, 1997). However, processes that might contribute to connectivity of populations between seamounts continue to be considered from a range of geographic areas and across taxonomic groups (Baco & Shank, 2005; Thoma et al., 2009; Cho & Shank, 2010; Miller et al., 2011; Baco & Cairns, 2012). One example using microsatellites indicated significant genetic differentiation among precious corals (*Hemicorallium lauuense* Bayer, 1956) in the Hawaiian archipelago; however, a lack of locus heterozygosity was identified which indicated possible inbreeding (Baco & Shank, 2005). Such findings may support the hypothesis that seamount communities are largely self-recruiting and potentially harbor higher than average numbers of endemic species, but still little evidence broadly supports these ideas to date (Thoma et al., 2009; Rowden et al., 2010a).

Among the most widely accepted hypotheses about seamount ecology is the vulnerability of their communities to anthropogenic disturbance and resource exploitation. These threats largely come from deep-sea bottom contact fishing (Watling & Norse, 1998), marine debris (Amon et al., 2020), and new technologies like mineral crust mining (Miller et al., 2018). As major targets for fishing in areas beyond national jurisdiction (Clark et al., 2006), seamounts have been (Waller et al., 2007) and are being exploited by high-seas fishing vessels using destructive bottom contact gear (Gianni, 2004; Parker, Penney & Clark, 2009). Studies of affected seamount features show megaepibenthic community resilience is extremely low (Althaus et al., 2009), with little known about recovery trajectories after disturbance (Clark et al., 2016; Baco, Roark & Morgan, 2019). These circumstances, combined with strategies to maintain biological diversity, population integrity, and habitat quality has led to the proposition that seamounts be classified as vulnerable marine ecosystems (VMEs) (Watling & Auster, 2017). Marine reserves with special attention to excluding or minimizing fishing are one approach to conservation in the deep sea. In order to maintain fish and invertebrate population integrity and connectivity, marine reserves within national jurisdictions that exclude fishing, like recently created large-scale marine protected areas in the Pacific Ocean (Friedlander et al., 2016), need to consider the potential scales of dispersal for all benthic fauna potentially affected (Hilario et al., 2015; Baco et al., 2016; Taboada et al., 2018).

Development of new technologies for mining of cobalt-rich ferromanganese crusts has become another potentially significant distbance facing seamount fauna in the near future. In the deep-sea, metal-rich crusts precipitate from the water column onto hard substrate at rates of 1-5 mm per million years resulting potentially exploitable deposits of concentrated metal ores (Hein et al., 2000, 2013). Diverse benthic communities composed of corals and sponges are known to occur on features with significant crust accumulations but community composition and crust accumulation rates are not uniform across seamount landscapes (Schlacher et al., 2014; Morgan et al., 2015).

Additionally, holdfasts of attached seafloor fauna are also thought to modulate crust accretion rates, but these processes need to be further studied (Verlaan, 1992).

Seamount benthos and nearby pelagic communities are considered to lack resilience to disturbance by deep-sea mining, potentially resulting in significant detrimental effects over time (Gollner et al., 2017; Drazen et al., 2020). For example, physical seabed disturbance during crust removal and subsequent disposal of mine tailings in the water column are likely to impact deep-sea species across vast spatial and temporal scales (Miller et al., 2018; Drazen et al., 2020). Compounded by the stressors of climate change already being experienced by deep-sea fauna (Brito-Morales et al., 2020), policies regulating the exploration and exploitation of seamount mineral resources are critical to effective ecosystem conservation (Levin, Amon & Lily, 2001; Levin et al., 2020). Some seamounts in the central and northern Pacific ocean occur in an area called the Pacific Prime Crust Zone where areas of thicker crusts can be observed (Hein et al., 2013), owing in part to the older age of the Pacific seafloor compared to the relatively young eastern Pacific or Atlantic Ocean. Biological communities in Pacific MPAs, including the Phoenix Islands Protected Area (PIPA) and parts of the Pacific Remote Islands National Marine Monument (PRIMNM), benefit from these protections and may serve as baseline reference communities for impacted seamounts within nearby national jurisdicitions or on the high seas. While it is still not yet certain what effects seamount crust mining will have as the technologies and methods are still in development (Du et al., 2017), there is consensus that there will be lasting negative consequences to seafloor biota (Gollner et al., 2017) and the precautionary approach should be applied moving forward (Durden et al., 2017).

1.3 Objectives and aims

This work will address major knowledge gaps concerning deep-water coral species distribution, diversity, community structure, and biogeography on seamounts in three regions of the Atlantic and Pacific Oceans. The areas for investigation are based on recent exploration of deep-sea habitats in the Anegada Passage in the northeast Caribbean Sea, the Phoenix Islands Protected Area (PIPA) in the equatorial central Pacific, and offshore Costa Rica seamounts in the eastern tropical Pacific. In addition to testing hypotheses specific to each chapter, for each locality I will: 1) characterize deep-sea coral communities on seamounts and other similar rugged submarine features by identifying corals to species from video survey transects and associated collections, 2) identify major oceanographic and environmental drivers of change in patterns of diversity and community structure across the bathyal depths, and 3) add biogeographic context to the distribution of deep-sea coral species to better understand the biogeography of bathyal depths. While species-level identifications are often difficult data to obtain in deep-sea exploration owing to technological or methodological constraints (Clark, Consalvey & Rowden, 2016), a strength of this work includes the use of species-level coral identifiers as they have been found to be better descriminators of change in community structure than higher level taxon rankings in the deep sea (Narayanaswamy, Nickell & Gage, 2003). The final chapter (Chapter 5) will focus on a summary of major findings, additional concerns, and future directions applicable to deep-sea corals and seamount ecological research.

CHAPTER 2

DISTRIBUTION OF DEEP-WATER SCLERACTINIAN AND STYLASTERID CORALS ACROSS ABIOTIC ENVIRONMENTAL GRADIENTS ON THREE SEAMOUNTS IN THE ANEGADA PASSAGE

2.1 Abstract

In the Caribbean Basin, the distribution and diversity patterns of deep-sea scleractinian corals and stylasterid hydrocorals are poorly known compared to their shallow water relatives. In this study, we examined species distribution and community assembly patterns of scleractinian and stylasterid corals on three high-profile seamounts within the Anegada Passage, a deep-water throughway linking the Caribbean Sea and western North Atlantic. Using remotely operated vehicle surveys conducted on the E/V *Nautilus* by the ROV *Hercules* in 2014, we characterized coral assemblages and seawater environmental variables between 162-2157 m on Dog Seamount, Conrad Seamount, and Noroît Seamount. In all, 13 morphospecies of scleractinian and stylasterid corals were identified from video with stylasterids being numerically more abundant than both colonial and solitary scleractinians. Cosmopolitan framework-forming species including *Madrepora oculata* and *Solenosmilia variabilis* were present but occurred in patchy distributions among the three seamounts. Framework-forming species occurred at or above the depth of the aragonite saturation horizon with stylasterid hydrocorals being the only coral taxon observed below Ω_{arag} values of 1. Coral assemblage variation was found to be strongly associated with depth and aragonite saturation state, while other environmental variables exerted less influence. This study enhances our understanding of

the factors that regulate scleractinian and stylasterid coral distribution in an underreported marginal sea and establishes a baseline for monitoring future environmental changes due to ocean acidification and deoxygenation in the tropical western Atlantic.

2.2 Introduction

Global and regional modelling efforts in parallel with observational studies have contributed to our understanding of the distribution of framework-forming azooxanthellate corals in the deep sea (>200 m depth). However, a significant number of data deficient localities persist, most often hindered by a lack of records from direct seafloor observation and *in situ* environmental data. A number of environmental variables have been observed to control the distribution of deep-water azooxanthellate scleractinian corals and stylasterid hydrocorals, including parameters linked to depth, terrain, hydrography, and seawater chemistry (Guinotte et al., 2006; Cairns, 2007; Davies & Guinotte, 2011). In the tropical western Atlantic, a center for deep-water scleractinian diversity (Cairns, 2007), additional direct observational data are needed to validate modelling efforts.

The growth of a scleractinian coral colony and formation of the aragonitic calcium carbonate skeleton are generally dependent upon the ambient seawater aragonite saturation state (Ω_{arag}) being greater than 1, or supersaturated. However, some deep-water scleractinian corals, including the cosmopolitan species *Solenosmilia variabilis* and *Enallopsammia rostrata*, have been reported well below the saturation horizon (the depth at which $\Omega_{arag} = 1$) on the Tasmanian Seamounts (Thresher et al., 2011). A more recent survey of seamounts in the Northwestern Hawaiian Islands and Emperor Seamounts documented living colonial scleractinian reefs at Ω_{arag} as low as 0.71 (Baco et al., 2017). Previous studies lend support for targeted observational surveys in underexplored regions in order to delineate species distribution patterns with respect to aragonite saturation and other environmental variables. These efforts are particularly salient in light of potential and ongoing anthropogenic impacts to deep-sea coral ecosystems (Ragnarsson et al., 2017), including global climate change and ocean acidification (Gleckler et al., 2016; Pérez et al., 2018), deep-water drilling and resource extraction (Cordes et al., 2016), bottom-contact fishing (Watling & Norse, 1998), and deep-sea crust mining (Miller et al., 2018).

The Greater-Lesser Antilles transition zone is one of the most sparsely surveyed yet biogeographically important deep-water entries from the western Atlantic Ocean into the Caribbean Basin. Topographic features, such as seamounts and other submarine banks associated with deformation along tectonic plate boundaries, are important contributors to the environmental complexity of the deep-sea benthos. In the Anegada Passage, Dog Seamount, Conrad Seamount, Noroît Seamount, and Barracuda Bank are some of the most prominent of the large (> 2km in height above the surrounding seafloor) seamounts and banks present, ranging from abyssal to mesophotic depths. Typical environmental characteristics of seamounts, including substrate heterogeneity, enhanced productivity and carbon flux, and variable currents (Rogers, 2018), create the potential for deep-water biodiversity hotspots in the region and elevated species abundance relative to the adjacent continental margins and slopes. Previous studies indicate that at depths > 200 m, azooxanthellate corals generally prefer hard substrata that exhibit topographic complexity (Roberts et al., 2009; Georgian, Shedd & Cordes, 2014). As such, seamounts are one example of topographically complex deep-water features that provide ideal hard substrate for corals (Rogers, 1994). Yet very few seamount benthic communities in the Caribbean region have been characterized with respect to these important abiotic gradients.

Throughout the tropical western Atlantic, scleractinian species diversity and distributions are relatively well-known from shallow waters but the extent of their distribution below 150 m is poorly understood. For deep-water azooxanthellate corals, 81 species have been reported at depths greater than 50 m for the Greater and Lesser Antilles (Cairns, 2007). As with scleractinians, stylasterid hydrocorals are reportedly diverse from the Lesser Antilles (Cairns, 1986), can occur in high densities in the tropical western Atlantic (Messing, Neumann & Lang, 1990), and are composed of rigid, primarily aragonitic coralla (Cairns & Macintyre, 1992). Additionally, three-dimensional structures produced by deep-water stylasterids provide habitat for fishes (Love, Lenarz & Snook, 2010) and invertebrate fauna (Braga-Henriques et al., 2011; Reed et al., 2013). Efforts have also been made to understand the biogeographic context of Caribbean ecoregions using deep-water corals in order to support conservation strategies (Cairns & Chapman, 2001; Miloslavich et al., 2010; Hernández-Ávila, 2014). In the Caribbean Basin, patterns in deep-sea coral beta diversity (e.g., species turnover) between ecoregions have been attributed to topography and oceanography (Hernández-Ávila, 2014). Within the insular Caribbean, the Greater Antilles and Lesser Antilles regions are found to diverge into two ecoregions, one encompassing the Greater Antilles islands and the other the Lesser Antilles islands, at continental slope depths (200-2000 m) (Hernández-Ávila, 2014). At larger biogeographic scales and evolutionary time, deep-water currents or water masses have been hypothesized as distribution pathways for constraining cosmopolitan habitat-forming corals like *Lophelia pertusa* in the western Atlantic (Arantes et al., 2009; Henry, 2011). While widespread seamount surveys from the Caribbean Basin remain rare, the effect of environmental variables like temperature, dissolved oxygen, and water mass has been demonstrated for demersal fishes on seamounts in the Anegada Passage (Quattrini et al., 2017).

The present study focuses on describing patterns in the distribution of deep-water scleractinians and stylasterid corals on three prominent seamounts in the northeastern Caribbean Sea. In addition to the primary abiotic oceanographic variables including temperature, salinity, and dissolved oxygen, we explore the distribution of aragonitic corals in the region with respect to the aragonite saturation state in this region of the western Atlantic Ocean. As a suspected driver of change in deep-water coral community structure, we also examine the relationship between water mass structure and community similarity in the bathyal zone, hypothesizing that different water masses would have distinct coral assemblages. Finally, we aim to identify abiotic oceanographic variables that most strongly influence the presence of hard corals and their contribution to changes in community similarity for this locality.

2.3 Methods

2.3.1 ROV surveys

This study examined sites within the Anegada Passage in the northeastern corner of the Caribbean Sea (Fig. 2.1). Three seamounts of varying summit depths were surveyed in September 2014 using the ROV *Hercules* during E/V *Nautilus* cruise NA052

(Table 2.1). Three dives were conducted on Dog Seamount (276 to 1035 m depth), two were conducted on Conrad Seamount (162 to 1314 m depth), and two were conducted on Noroît Seamount (949 to 2206 m depth). Efforts were made to cover similar depth ranges on each feature for direct comparison as permitted by the bathymetry.

The ROV was deployed to a maximum target depth on each seamount and generally moved to shallower depths up slope. The ROV continuously traversed the seafloor as near to the bottom as practical at a slow, steady speed (~0.1-0.2 knots, ~0.1 m/s); however, transects were occasionally interrupted by stopping the ROV for sampling and detailed camera zooms. The ROV was equipped with a high-definition camera and paired scaling lasers (10 cm apart). During the dives, the forward-facing cameras were set on wide-angle view, but frequent snap-zooms (up to 20 sec) were conducted to aid in species identification. The ROV was also equipped with a Seabird FastCAT 49 conductivity-temperature-depth (CTD) logger and an Aanderaa oxygen optode to measure dissolved oxygen (DO). The ROV was tracked on the seafloor using an ultra-short baseline (USBL) tracking system as well as a Doppler Velocity Log (DVLNAV).

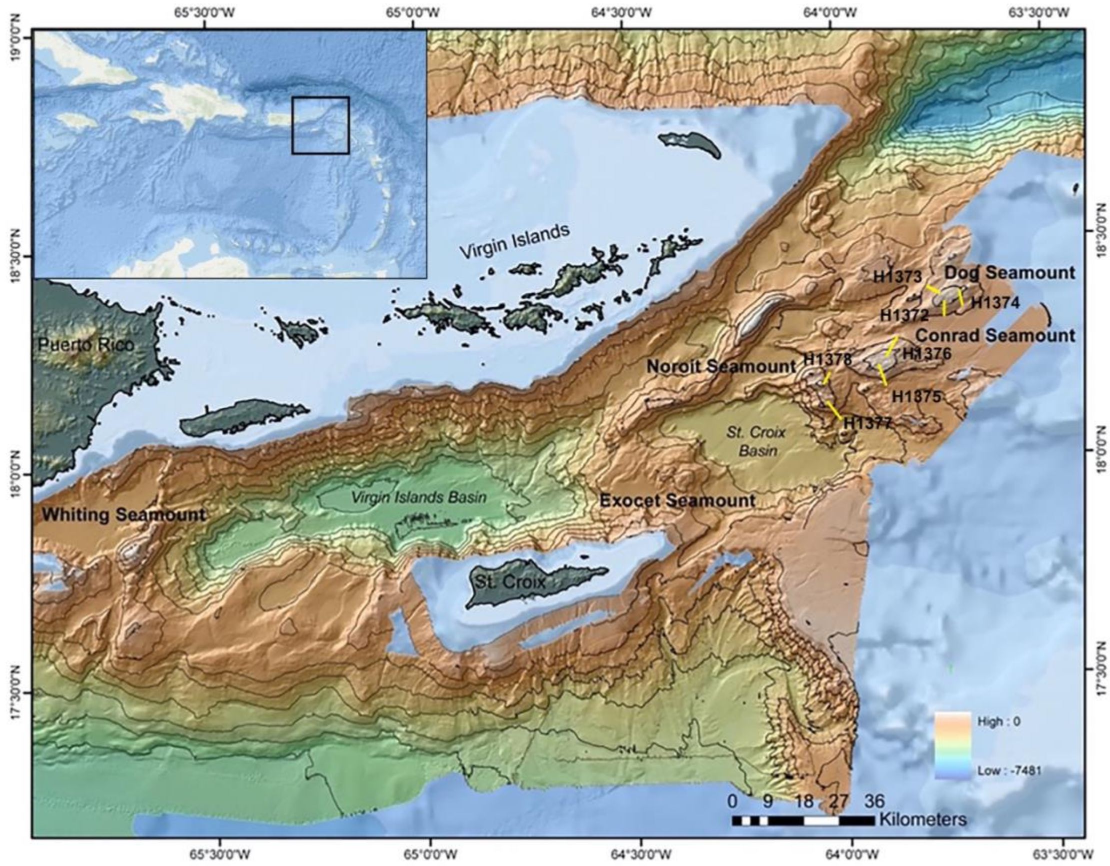


Figure 2.1 Multibeam bathymetric map of the Anegada Passage seamounts. The locations of Dog, Conrad, and Noroît Seamount are indicated in bold. Dive locations are overlaid in yellow and labeled by dive number. The bathymetry color ramp in the lower right indicates depth values measured in meters. Transect segments lengths are not drawn to scale.

Table 2.1 ROV dive transect details for 2014 surveys of the Anegada Passage seamounts. Start and end coordinates for each transect, time spent in visual contact with the seafloor, and number of water samples collected at depth over the dive interval are indicated.

Dive	Seamount	Start Coordinates	End Coordinates	Depth Range (m)	Number of Niskin Bottle Samples	Total Bottom Time (hh:mm)
H1372	Dog	18°18.7385 N 63°46.0896 W	18°19.6177 N 63°46.1645 W	717-1035	6	07:56
H1373	Dog	18°22.6480 N 63°46.1953 W	18°21.9711 N 63°45.9306 W	503-784	6	11:09
H1374	Dog	18°20.4464 N 63°43.6091 W	18°21.9311 N 63°43.5024 W	276-601	5	09:58
H1375	Conrad	18°10.5420 N 63°53.1020 W	18°13.0029 N 63°53.3459 W	162-876	5	31:40
H1376	Conrad	18°16.4904 N 63°52.3364 W	18°14.2223 N 63°52.9767 W	344-1267	6	22:38
H1377	Noroît	18° 05.4657 N 64° 00.1741 W	18° 07.0695 N 64° 01.1760 W	881-2157	6	17:10
H1378	Noroît	18° 09.6969 N 64° 01.3606 W	18° 09.4122 N 64° 01.8888 W	949-1035	2	06:01

2.3.2 Seawater collection and carbonate chemistry analysis

Seawater samples (n = 34) were collected both in the water column and at the benthos using Niskin bottles mounted to the ROV *Hercules*. On bottom, seawater samples were collected within 1-2 meters of the benthos and usually co-occurred with the observation of scleractinian colonies on the seafloor. For all seawater samples, co-located physical data (pressure, temperature, salinity, and oxygen) were obtained using vehicle mounted conductivity-temperature-depth (Paroscientific Digiquartz, SBE 49Plus) and oxygen (Aanderaa Optode 3830) sensors, respectively. Upon recovery of the ROV, samples were immediately transferred to 500 mL high-density polyethylene (HDPE) containers according to Best Practices for Ocean CO_2 measurements (Dickson, Sabine & Christian, 2007). While HDPE containers are suitable for long-term storage of seawater for total alkalinity analyses (Huang, Wang & Cai, 2012), they are not suitable for long-term storage for pH or dissolved inorganic carbon analyses as they are permeable to CO_2. Accordingly, pH was measured within 1 hour of collection onboard the vessel. Immediately following pH measurement, samples were poisoned with 100 µL saturated mercuric chloride solution and stored in a cool, dark location. Total alkalinity was measured in the laboratory in triplicate according to methods previously described (Lunden, Georgian & Cordes, 2013; Georgian et al., 2016a), and final Ω_{arag} values were computed using CO2calc (Robbins et al., 2010). Due to the logistical challenge of pairing a discrete water sample with each individual scleractinian coral observation, we generated a predictive model to interpolate Ω_{arag} at the depth of each coral observation based on temperature, dissolved oxygen, and salinity (for methodology see Georgian et al., 2016a).

2.3.3 ROV video analysis

Colonial and solitary coral occurrences were documented using high-definition video transects during each of the ROV dives. Video segments where collections occurred, where the vehicle was too high off the bottom, moving backwards, or of generally poor quality, were removed from analysis. For the purpose of this analysis, we defined structure-forming corals as colonial members of the Scleractinia and hydrozoan family Stylasteridae. Consistent morphospecies identifications were used throughout the analyses. Voucher specimens for morphological identification were obtained using the

ROV platform. If necessary, further identifications of coral species were made using taxonomic keys and assistance from taxonomic specialists. Colony height was measured, where possible, by referencing scaling lasers. Individuals or colonies above a 5-cm height threshold were typically identifiable based on laser scalers. If occurrences could not be readily identified below the 5-cm threshold, they were omitted from analysis. Each observation was paired with an associated time-stamp for reference to *in situ* environmental data (temperature, depth, dissolved oxygen concentration, and salinity) collected by ROV CTD and oxygen optode sensors.

2.3.4 Community analyses

Sampling effort was evaluated for seamounts individually and for all seamounts combined by sample-based species accumulation curves. In order to assess community relationships among hard-coral assemblages, species abundance values (number of colonies or individuals for each species) were binned into 100 m depth segments for each seamount transect resulting in 28 total samples. Community-level analyses were conducted using standardized and 4th root transformed species abundance data in PRIMER v7 with PERMANOVA add-on (Clarke & Gorley, 2006; Anderson, Gorley & Clarke, 2008). Transformed and standardized species abundances were compiled into a Bray-Curtis resemblance matrix for further analyses. In order to test for significant differences among hard coral assemblages on different seamounts, a one-way analysis of similarity (ANOSIM) was conducted between features as well as between local water masses. Non-metric multidimensional scaling ordinations (nMDS) were conducted across all 28 samples. nMDS plots were overlaid with similarity profile (SIMPROF) analysis to show significant groupings of samples at the 95% level or greater (Clarke, Somerfield &

Gorley, 2008). Similarity percentage (SIMPER) tests were used to identify taxa that contributed disproportionately to assemblage similarities within and between seamounts and water masses.

Multivariate analyses were also used to explore the abiotic variables relevant to the variation observed in the coral assemblages. Environmental data for temperature, salinity, dissolved oxygen, and Ω_{arag} were obtained from the calculated mean in each 100 m depth segment within every transect. The mean was then 4th-root transformed and normalized within each variable. The BEST (BIO-ENV) routine (Clarke, Somerfield & Gorley, 2008) was applied to the dataset to determine which environmental variables would be useful predictor variables. A distance-based linear model (DistLM) with Akaike information criterion (AIC) was applied using the PERMANOVA add-on in PRIMER v7 (Anderson, Gorley & Clarke, 2008). Visualizations of the resemblance matrix with predictor variables were observed using a dbRDA (distance-based redundancy analysis) ordination with DistLM overlay.

2.4 Results

2.4.1 Survey summaries

A total of 106 hours of bottom time was assessed across 7 dives (Table 2.1). Video records were annotated between the depth range of 162-2157 m. In all, 264 observations of solitary and framework-forming scleractinian corals and stylasterid hydrocorals were made across all three seamounts (Table 2.2). Three dives at Dog Seamount yielded 64 records from 284-849 m. From Conrad Seamount, 182 records were made from 166m to 1230 m across 2 dives. The deepest two dives at Noroît Seamount had 18 records reported from 1014-1626 m. Stylasterids made up the majority (53%) of coral observations, however most were observed at depths shallower than 400 m (Table 2.2). The majority of scleractinians observed were colonial, framework-forming species (100 colonies observed) while only 22 observations were made of solitary coral species, as they were often on or below the threshold for identification. For this reason, abundances of solitary scleractinians represent a minimum value. No scleractinians or stylasterids above the 5 cm size threshold were observed deeper than 1626 m on any seamount.

Table 2.2 Summary of records and environmental variables for each taxon. Ranges of values for number of observations, depth, temperature, salinity, dissolved oxygen, model predicted Ω_{Arag} , and colony height are reported for each species by taxonomic grouping.

Class	Family	Species	Number of observations	Depth (m)	Temperature (°C)	Salinity (psu)	Dissolved oxygen (mg/L)	Model Predicted Ω_{arag}	Height (cm)
Hydrozoa	Stylasteridae	*Stylaster* sp. 1	65	166-174	22.1-22.5	37.00-37.05	7-7.12	3.38-3.45	-
		Crypthelia sp. 1	49	304-1096	4.9-18.0	34.53-36.55	2.41-7.22	0.99-2.83	1-12
		Stylaster cf. *duchassaingi*	30	181-408	13.8-22.1	35.82-37.01	5.39-6.99	2.07-3.39	12-37
		Stylasteridae spp.	2	525-838	6.7-10.9	34.89-35.39	4.96-5.28	1.08-1.62	3-5
Anthozoa	Caryophylliidae	*Solenosmilia variabilis*	44	490-569	10.9-13.3	35.37-35.75	4.88-5.15	1.61-1.98	12-18
		Caryophyllia sp. 1	3	665-677	8.2-8.7	35.03-35.07	4.78-4.86	1.24-1.29	-
	Oculinidae	*Madrepora oculata*	22	784-1540	4.3-6.9	34.53-34.97	5.22-8.23	1.00-1.10	10-125
	Pocilloporidae	*Madracis myriaster*	22	253-311	17.6-18.7	36.49-36.65	6.83-7.01	2.78-2.92	6-35
	Incertae familiae	Scleractinia spp. (solitary)	11	311-849	6.5-17.8	34.83-36.51	4.76-6.98	1.07-2.8	4-5
	Dendrophylliidae	*Dendrophyllia alternata*	5	490-598	10.7-13	35.33-35.71	4.84-5.13	1.57-1.95	16
		Enallopsammia rostrata	2	785	7.0	34.921	5.2	1.11	20-75
		Dendrophylliidae spp.	1	437	13.6	35.794	5.29	2.03	5
	Flabellidae	*Javania cailleti*	8	518-1626	4.2-12.0	34.557-35.54	4.96-8.34	1.02-1.77	4-7

2.4.2 Water mass structure

Downcast CTD profiles from the ROV sensors were plotted and assessed at each seamount using Ocean Data View v5 (Schlitzer, 2019). Profiles for each seamount were combined to create one consensus profile for the Anegada Passage (Fig. 2.2). Water masses were identified following published records of temperature, salinity, and dissolved oxygen profiles for the northeast Caribbean and Anegada Passage; these include Subtropical Underwater (SUW) 100-200 m, Sargasso Sea Water (SSW) 200-400 m, Tropical Atlantic Central Water (TACW) 400-700 m, Antarctic Intermediate Water (AAIW) 700-1200 m, and North Atlantic Deep Water (NADW) (>1200 m) (Morrison & Nowlin, 1982; Liu & Tanhua, 2019).

2.4.3 Carbonate chemistry analysis

Water samples for carbonate chemistry analyses were collected at depth from 50 m to 2170 m. Total alkalinity ranged from 2291.4 to 2405.9 $\mu\text{mol}\cdot\text{kg}^{-1}$, and pH ranged from 7.83 to 8.11, with minimum pH observed at 795 m depth. Measured Ω_{arag} values from Niskin bottle collections ranged from 4.13 at 50 m depth to 0.99 at 2170 m depth. The aragonite saturation state of the water column was modelled according to the following equation: $\Omega_{arag} = (T \times 0.11407018) + (O \times 0.00302922) + (S \times 0.18168448) - 6.5216044$ (stepwise backward regression, $R^2 = 0.9857$, $p < 0.001$) where T = temperature in °C, O = oxygen concentration in $\mu\text{mol}\cdot\text{L}^{-1}$, and S = salinity in parts per thousand (ppt). From this, predicted Ω_{arag} values ranged from 4.11 to 1.05, with highest value at 51 m at Dog Seamount and lowest value at 2195 m at Noroît Seamount.

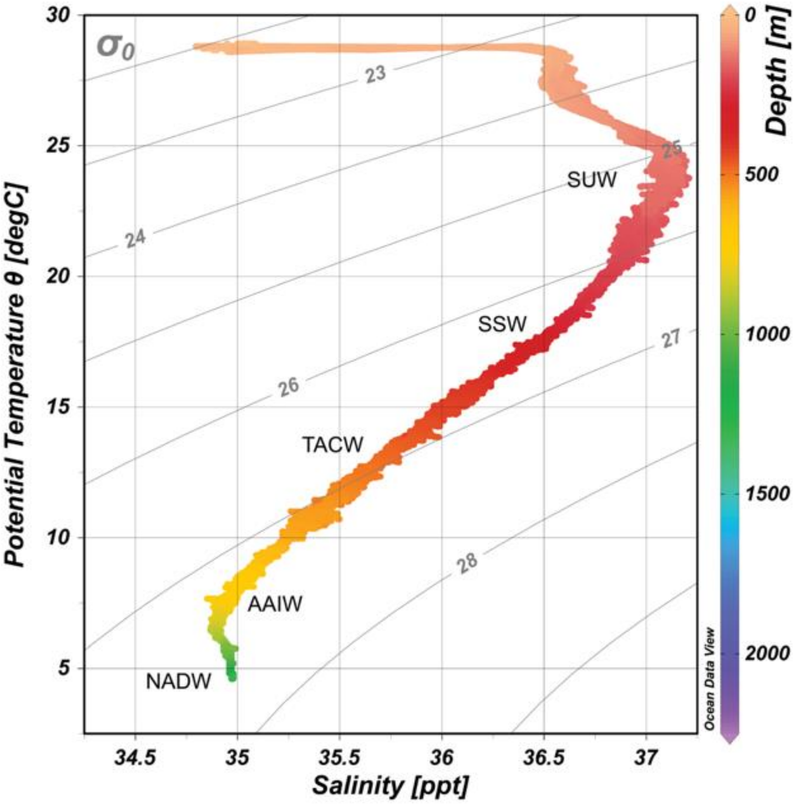


Figure 2.2 Temperature-salinity plot for the Anegada Passage based on CTD water column profiles. Water masses are overlaid and abbreviated by the following: SUW=Subtropical underwater, SSW=Sargasso Sea Water, TACW= Tropical Atlantic Central Water, AAIW=Antarctic Intermediate Water, and NADW=North Atlantic Deep Water. Isopycnal surfaces (σ_θ) are indicated in gray.

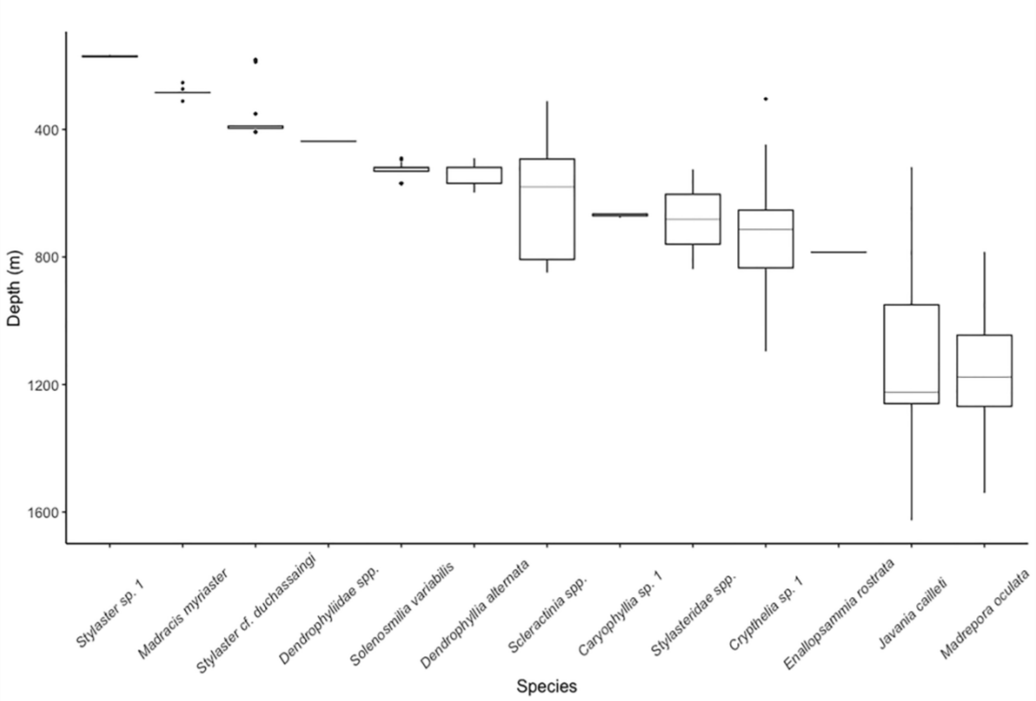


Figure 2.3 Depth distribution for scleractinian and stylasterid corals occurring on Dog, Conrad, and Noroît Seamounts. Box plots represent the interquartile range with whiskers extending from the upper and lower quartiles to the minimum and maximum values. Horizontal lines represent the median depth. Individual points represent outliers. Species are arranged on the x-axis from shallowest to deepest by median depth of occurrence.

2.4.4 Coral species distribution patterns

The single most abundant scleractinian coral species was *Solenosmilia variabilis* (44 colonies), but it was only observed on Conrad Seamount in a relatively narrow depth range, 409-569 m. Many structure-forming colonies were found to be associated with boulder and low, outcropping, hard rock substrate. This was followed by the more widespread *Madrepora oculata* (22 colonies), which occurred between 784 and 1540 m on all seamounts (Fig. 2.3). *Madrepora oculata*, which displayed two different growth forms from thin and sparsely branching to thick, robust colonies, possessed the widest depth distribution range for any colonial scleractinian coral. The deepest solitary scleractinian coral, *Javania cailleti,* was observed at 1626 m; this occurrence corresponds with one of the lowest measured Ω_{arag} values of 1.01.

The upper bathyal depths, shallower than 700 m, contained species with narrower depth distributions than those at lower bathyal depths (>800 m) (Fig. 2.3). The sub-700 m assemblage was composed of three species of scleractinians (*E. rostrata*, *M. oculata*, and *J. cailleti*) and one stylasterid (*Crypthelia* sp. 1). The shallowest depths, usually coinciding with the seamount summit, were dominated by two species of stylasterids, *Stylaster* sp. 1 and *Stylaster* cf. *duchassaingi*, as well as one azooxanthellate scleractinian, *Madracis myriaster*. On Conrad Seamount, pink and purple coralline algal crusts were observed as deep as 256 m depth and continued to be observed through shallower depths dominated by sponges, stylasterids, and black corals.

The majority of stylasterid species were restricted to depths less than 400 m with only *Crypthelia* exhibiting a wider depth distribution (Fig. 2.3). Only three morphospecies of stylasterids were large enough to be consistently identified during video annotation. Other unidentifiable stylasterids were combined into a fourth group, Stylasteridae spp. and shown for reference. The most abundant species, *Stylaster* sp. 1, was found in a narrow depth range between 166-174 m on the summit of Conrad Seamount.

2.4.5 Patterns of coral occurrences with aragonite saturation state

Measured Ω_{arag} values from water collected adjacent to corals were not significantly different (t-test, N=9, t=-0.23341, p=0.818) compared to what was calculated using the modelled aragonite saturation state data (Supplementary Fig. A1). All paired water samplings adjacent to coral observations occurred at or above the aragonite saturation horizon ($\Omega_{arag} > 1$) (Table 2.3). Multiple water samples for a single species were collected for only *M. oculata*.

Using predicted values derived from CTD and sensor data on temperature, oxygen concentration, and salinity, all scleractinian and stylasterid corals were observed at Ω_{arag} values of 0.99 to 3.45 (Fig. 2.4). For scleractinians, *Javania cailleti* occurred across the largest aragonite saturation state range, between 1.01 and 1.77. Among the Stylasteridae, *Crypthelia* sp. 1 occurred across the greatest range of saturation states from as low as 0.99 up to 2.83. Only three species were observed at or around the aragonite saturation horizon based on predicted saturation state values, *Crypthelia* sp. 1 ($\Omega_{arag} = 0.99$), *M. oculata* ($\Omega_{arag} = 1.00$) and *J. cailleti* ($\Omega_{arag} = 1.01$).

Table 2.3 Summary of measured values of Ω_{Arag} from water samples taken directly adjacent to corals. Sampling events are reported for each species arranged by taxonomic grouping.

Class	**Family**	**Species**	**Number of adjacent water samples**	**Ω_{arag} measured**
Hydrozoa	Stylasteridae	*Stylaster* sp. 1	0	-
		Crypthelia sp. 1	0	-
		Stylaster cf. *duchassaingi*	0	-
		Stylasteridae spp.	0	-
Anthozoa	Caryophylliidae	*Solenosmilia variabilis*	1	1.63
		Caryophyllia sp. 1	1	1.24
	Oculinidae	*Madrepora oculata*	2	1.13-1.16
	Pocilloporidae	*Madracis myriaster*	1	2.7
	Incertae familiae	Scleractinia spp. (solitary)	0	-
	Dendrophylliidae	*Dendrophyllia alternata*	1	1.35
		Enallopsammia rostrata	1	1.21
		Dendrophylliidae spp.	1	1.82
	Flabellidae	*Javania cailleti*	1	1.16

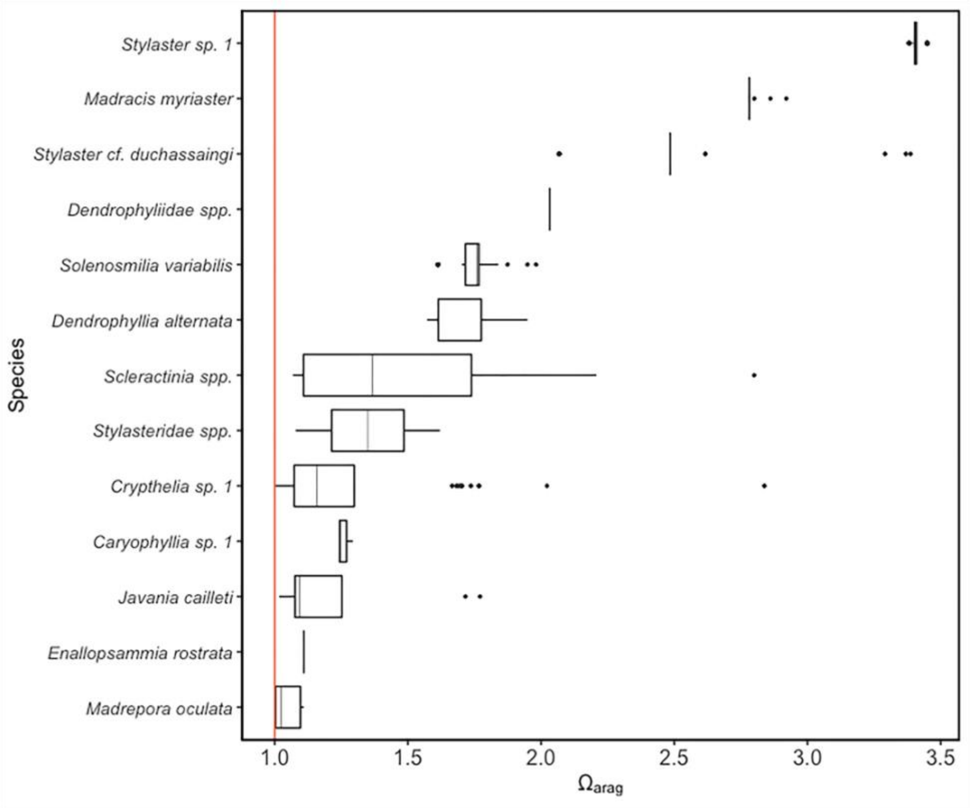


Figure 2.4 Distribution of scleractinian and stylasterid species against model predicted Ω_{Arag} values on the Anegada Passage seamounts. Box plots represent the interquartile range with whiskers extending from the upper and lower quartiles to the minimum and maximum values. Vertical lines represent the median aragonite saturation state. Individual points represent outliers. Species are arranged on the y-axis from highest to lowest median aragonite saturation occurrence. A solid red vertical line indicates the aragonite saturation horizon, where $\Omega_{\text{Arag}} = 1$.

2.4.6 Community structure patterns

Species-accumulation curves were evaluated for seamounts individually and in aggregate for all seamounts. Combined, all seamounts (100-1700 m) revealed a more complete sampling effort than among single seamount coral assemblages (Fig. 2.5).

Individually, species accumulation curves for Dog, Conrad, and Noroît seamounts were not asymptotic, and therefore are likely to accumulate additional coral species with increased sampling effort.

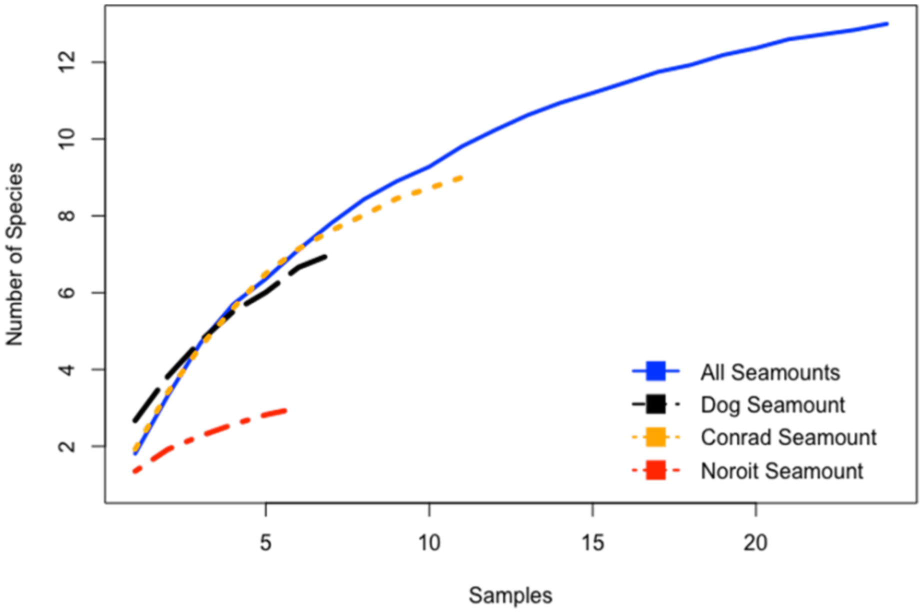


Figure 2.5 Species accumulation curves for the Anegada Passage seamounts. Curves are plotted for all transects on Dog Seamount, Conrad Seamount, Noroit Seamount, as well as for all three seamounts combined.

Analysis of similarity (two-way nested, depth within seamount, Global R=0.122, p=0.05) conducted among seamounts revealed significant differences in coral assemblages between Dog and Noroît Seamounts (R=0.544, p=0.006), but not Conrad and Dog seamounts (R=-0.001, p=0.379) or Conrad and Noroît seamounts (R=0.029, p=0.292) (Supplementary Table A1). A one-way ANOSIM (Global R=0.464, p=0.001) between water masses revealed significant differences in coral assemblages between SSW and TACW (R=0.46, p=0.003), AAIW (R=0.53, p=0.002), and NADW (R=0.60, p=0.008) as well as between TACW and NADW (R= 0.93, p=0.001) and AAIW and NADW (R=0.361, p=0.01) (Supplementary Table A2).

Non-metric multi-dimensional ordination with SIMPROF groupings revealed five statistically significant groupings; two shallow assemblages composed of 100 m depth-binned samples from between 100-600 m and 200-400 m, two mid-depth assemblages (500-700 m and 700-1100 m), and one deep assemblage (1100-1600 m) (Fig. 2.6). Outliers from these groupings occurred in the 600-700 m and 1100-1200 m depth bins on Conrad Seamount and between 1300-1400 m on Noroît Seamount. Within SIMPROF groupings, the shallowest depth grouping showed the greatest amount of dissimilarity among samples (a metric of beta diversity) among the three seamounts while the lowest occurred in the deepest group.

Dog Seamount exhibited the lowest beta diversity of coral assemblages among all three seamounts and the highest average similarity at 61% (one-way SIMPER analysis), with the average similarity between 100 m depth bins being most strongly influenced by *Crypthelia* sp. 1, which contributed to 96.6% of the relative abundance. Noroît Seamount had the second highest similarity (38.2%), with *M. oculata* accounting for 84.7% of the similarity. Conrad Seamount had the lowest average similarity (15%), with stylasterids *Crypthelia* sp. 1 and *Stylaster* cf. *duchassaingi* being the greatest contributors to average similarity with 48.4% and 21.5%, respectively. Between seamounts, Noroît differed from Dog and Conrad, primarily due to the higher abundance of *M. oculata* at Noroît Seamount. Noroît Seamount had nearly triple the average abundance of *M. oculata* compared to Conrad Seamount. Conrad and Dog Seamounts differed primarily due to the contribution of *Crypthelia* sp. 1 and *M. myriaster*, which were present on Conrad at 2 to 3 times higher average abundance than at Dog Seamount.

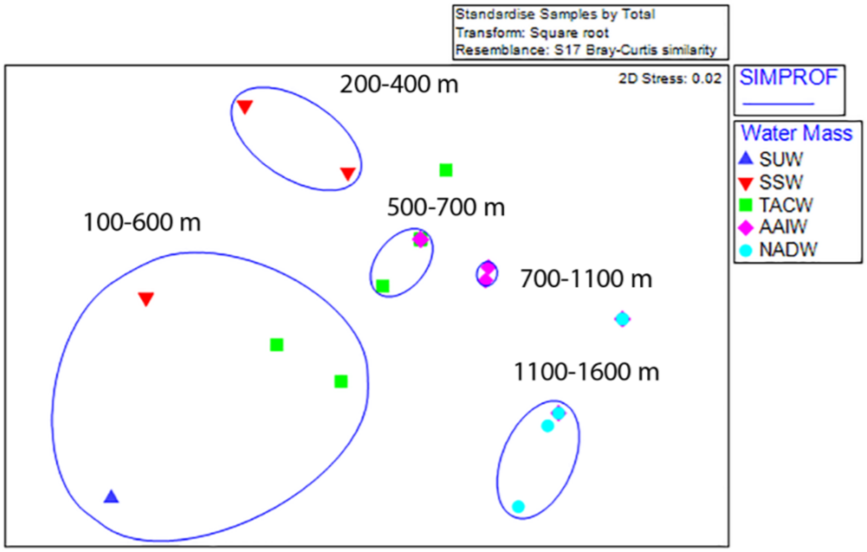


Figure 2.6 Non-metric multidimensional scaling analysis of standardized, fourth-root transformed coral assemblages on Dog, Conrad, and Noroît Seamounts. SIMPROF groups are overlaid around significant groupings at the 95% level or above. Depth ranges displayed within each statistical grouping are indicated in black text.

Within water masses, the greatest average similarity of coral assemblages occurred within NADW (54%) followed by TACW (51%) and finally SSW at (32 %). The abundance of scleractinians was responsible for greater similarities within deep water masses (*M. oculata* and *Javania cailleti* in NADW) while stylasterids were more commonly associated with driving patterns of similarity within intermediate and shallower water masses (*Crypthelia* sp. 1 in TACW, AAIW and *Stylaster* cf. *duchassaingi* in SSW). Between immediately adjacent water masses, the greatest average dissimilarity was observed between SUW and SSW (92.3%) and the lowest between TACW and AAIW (56.7%), indicating higher rates of turnover (beta diversity) for shallower water masses than deeper ones.

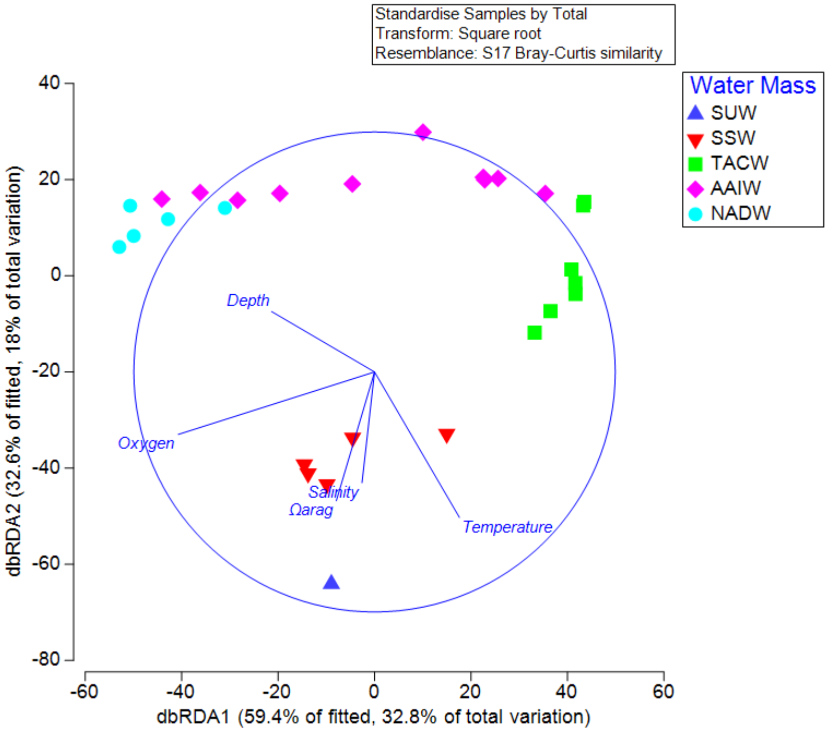


Figure 2.7 Distance-based linear model and redundancy analysis of coral assemblages and oceanographic variables. Sample points represent one 100 m depth assemblage. Axes shown are the results of a distance-based redundancy analysis with percent variation explained by the first and second axes.

Results from the BEST analysis indicated that the largest percentage of biological variation was correlated with depth (r=0.536). The BEST routine also indicated that the greatest correlation occurred with the four combined factors of depth, Ω_{arag}, temperature, and dissolved oxygen (r=0.614). Sequential tests in the DistLM analysis indicated that depth (AIC=223.88, p=0.001) and Ω_{arag} (AIC= 215.87, p=0.001) were the greatest explanatory variables influencing coral assemblages on seamounts in the Anegada Passage. Temperature, salinity, and oxygen did not explain a significant portion of the biological variation in this test. Redundancy analyses resulted in 59.4% of the DistLM model variation explained by the primary axis (dbRDA1) and 32.6% explained by the second (dbRDA2) (Fig. 2.7). Likewise, the first axis explained 32.8% of the total biological variation observed and the second axis explained 18%. The primary axis was most closely correlated with oxygen (r = -0.82), while the second was most closely related to temperature (r= -0.61).

2.5 Discussion

Seamounts in the Anegada Passage were found to harbor communities of stony and lace corals throughout the bathyal depth range from summit depths as shallow as 166 m to a maximum of 1626 m. Both stylasterid and scleractinian coral species with aragonitic skeletons were largely present above the aragonite saturation horizon in this region of the western Atlantic Ocean, with the understanding that sampling effort below the ASH was limited to one transect at Noroît Seamount (Table 2.1). Nevertheless, we were able to identify the depth of the ASH as occurring between 2000-2200 m in the Anegada Passage (Supplementary Fig. A1), which is consistent with previous reports from the North Atlantic Ocean (Jiang et al., 2015). Only stylasterids in the genus *Crypthelia* were observed to occur below the aragonite saturation horizon (Ω_{arag} =0.99), but others, including the framework-forming species *Madrepora oculata*, occurred at saturation states as low as Ω_{arag} =1.0. However, it is likely that aragonitic corals live below the aragonite saturation horizon within our study region, as our sampling effort was lower at these depths. Also noteworthy was the observation of live crustose coralline algae at a depth of 256 m, which is comparable to the deepest known record from San Salvador Island (268 m) in The Bahamas (Littler et al., 1986).

Overlying water masses were a significant indicator of community assembly differences between SSW (Sargasso Sea Water) and deeper water masses, but not the shallowest water mass, Subtropical Underwater (SUW) and deeper strata of the water column. Oceanographic variables that most strongly influenced the presence of aragonitic corals and their contribution to changes in community similarity were depth and aragonite saturation state, with temperature, salinity, and dissolved oxygen making less significant contributions. The tropical western Atlantic is a known diversity center for azooxanthellate scleractinian corals and stylasterid hydrocorals (Cairns, 2007, 2011). This study provides new distribution records for deep-water coral species in the northeastern Caribbean and builds on existing efforts to characterize the azooxanthellate coral fauna of the tropical western Atlantic (Cairns, 1979; Cairns & Chapman, 2001; Lutz & Ginsburg, 2007). Specifically, 7 species or morphospecies of stony corals within the genera *Javania*, *Madrepora*, *Madracis*, *Enallopsammia*, *Dendrophyllia*, and *Caryophyllia* have been added to local species inventories in the Anegada Passage (Fig. 2.8). New records from photographic and physical specimens aid in resolving the complex biogeography of the Greater-Lesser Antilles Transition zone seamounts with respect to the western North Atlantic. The paucity of records paired with environmental parameters from global biogeographic databases makes these observations critical to understanding the species distribution dynamics of marginal Atlantic seas and how coral distribution may be affected by future ocean climatic changes.

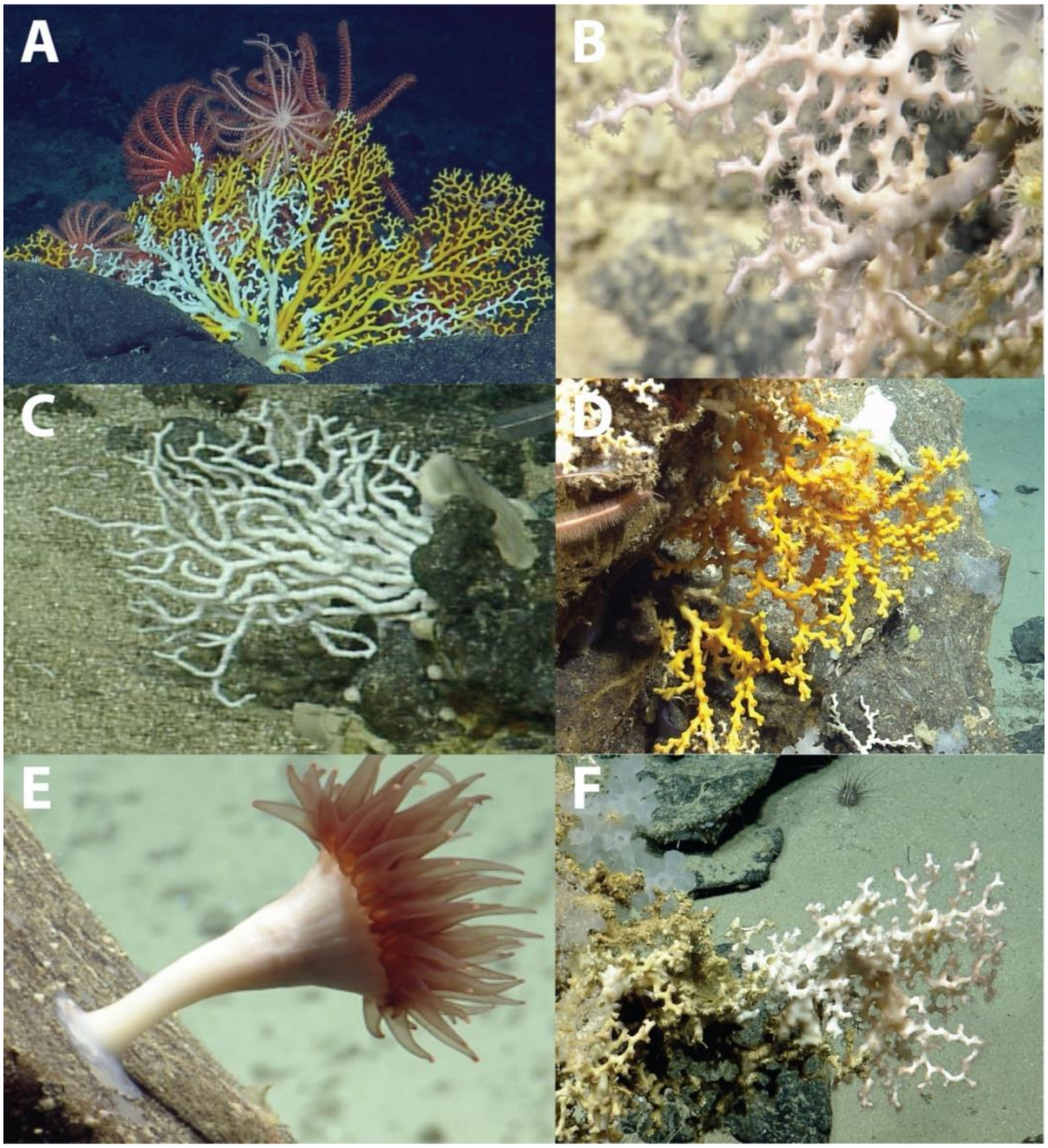


Figure 2.8 Deep-water scleractinians from the Anegada Passage seamounts. (A) *Enallopsammia rostrata*, (B) *Madrepora oculata*, (C) *Madracis myriaster*, (D) *Dendrophyllia alternata*, (E) *Javania cailleti, (F) Solenosmilia variabilis*.

Stony coral assemblages in the Anegada Passage were similar to those observed in other parts of the western Atlantic Ocean with a few noteworthy absences. Absent from our records from the Anegada Passage seamounts include reef-forming species like *L. pertusa* and *E. profunda*, as well as cosmopolitan cup coral species like *Desmophyllum dianthus*, which are reportedly more common throughout the U.S. southeast continental shelf and Gulf of Mexico (Schroeder et al., 2005; Reed, Weaver & Pomponi, 2006; Brooke & Schroeder, 2007; Lunden, Georgian & Cordes, 2013; Georgian et al., 2016a). While fossilized *Lophelia* rubble have been reported in the Colombian Caribbean (Santodomingo et al., 2007) and live *Lophelia* has been observed on the Brazilian continental margin (Arantes et al., 2009), the southern Caribbean (Hernández-Ávila, 2014), and off Roatan, Honduras (Henry, 2011), members of this genus have not been extensively reported in the insular Caribbean (OBIS, 2019).

We were also able to identify some variability in local distribution patterns among seamounts for three colonial scleractinian species. *Enallopsammia rostrata*, *Dendrophyllia alternata*, and *Solenosmilia variabilis* appear to have patchy distributions on the Anegada Passage seamounts. For example, only two colonies of *E. rostrata* were observed, both on Dog Seamount at 785m, and only five colonies of *D. alternata* were observed on Conrad Seamount between 490-598 m (Fig. 2.3). Similarly, *S. variabilis* was only observed in patches on Conrad Seamount from 490-569 m (Fig. 2.3). S*olenosmilia* has not been widely reported from the greater Caribbean basin based on records from the Ocean Biogeographic Information System (OBIS, 2019), but is known to be a contributor to coral mound formation off Brazil (Raddatz et al., 2020). *Solenosmilia* has been more commonly reported to asexually reproduce, and thus has a relatively short dispersal ability (Miller & Gunasekera, 2017), potentially explaining its patchy distribution.

Several coral taxa encountered in the Anegada Passage are important species for understanding biogeographic patterns of the Caribbean bathyal zone. *Madracis myriaster* was observed both on Dog and Conrad Seamounts, but only between 253 - 311 m. More recently, *M. myriaster* has been observed at similar depths and in high densities during surveys by the ROV *Deep Discoverer* on the NOAA Ship *Okeanos Explorer* east of Vieques Island and in the Mona Passage at similar depths (Wagner et al., 2019). Northern and eastern Caribbean coral communities at continental shelf depths have been found to be dissimilar from the southern Caribbean, such that they may constitute distinct ecoregions (Hernández-Ávila, 2014). These differences were found to be driven by differences in the abundance of *M. myriaster* (Fig. 2.8C), which is more common at mesophotic and upper bathyal depths (Reyes et al., 2005; Santodomingo et al., 2007; Hernández-Ávila, 2014).

At lower bathyal depths, regional biogeographic differences have also been attributed to variation in the frequency of solitary scleractinian species (e.g. *Stephanocyathus* spp., *Fungiacyathus* sp.) that may be difficult to detect during video transects (Hernández-Ávila, 2014). A greater diversity of solitary scleractinian corals and smaller stylasterids may have been present in the video but could not be documented due to limitations of ROV surveys (discussed in Everett & Park, 2018). The lack of easily identifiable diagnostic features from video, rugose terrain (e.g. overhangs and ledges), and rarity make most smaller species difficult to identify from ROV surveys without voucher specimens. A more thorough analysis incorporating modern (e.g. higher-resolution ROV video surveys with *in situ* collections) and historical datasets (e.g. museum-archived specimens) would be helpful in elucidating biogeographic patterns more broadly across the basin.

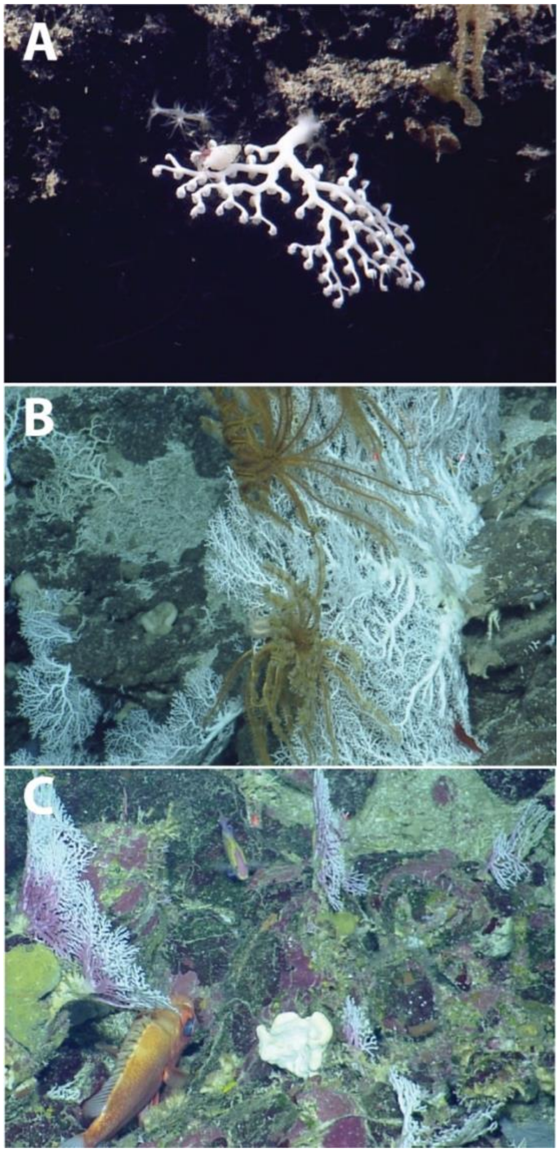


Figure 2.9 Deep-water stylasterids from the Anegada Passage seamounts. (A) *Crypthelia* sp. 1, (B) *Stylaster cf. duchassaingi*, (C) *Stylaster* sp. 1.

Several species in the genus *Crypthelia* occur in the eastern Caribbean at bathyal depths (Cairns, 1986). The difficulty of identifying stylasterids from ROV video remains a challenge in establishing species occurrences, necessitating a voucher collection to confirm morphospecies identity. Nevertheless, the depth distribution, colony morphology, and coloration of *Stylaster* sp. 1, is consistent with *Stylaster roseus* (Pallas, 1766), a tropically-distributed western Atlantic stylasterid from depths typically less than 500 m (OBIS, 2019). *Crypthelia* sp. and other stylasterid species are more likely to be underreported due to their small size (2-5 cm), on the threshold of being able to be accurately recorded from ROV video. These stylasterids were also observed under overhangs which made obtaining an accurate account of their abundance difficult. In this case, the reported occurrences of these corals represent a minimum value.

The ecological contribution of stylasterid corals is often understated, despite the ability of some species to produce significant three-dimensional structures that can act as habitat for other organisms. Larger structure-forming stylasterids are functionally analogous to some colonial scleractinian corals in that they can provide habitat for larger organisms such as deep-water fishes and invertebrates (Love, Lenarz & Snook, 2010; Braga-Henriques et al., 2011). *Crypthelia* spp., while relatively abundant in places and occurring over a wide range, were never observed above 12 cm in overall height and were observed to be extremely brittle when attempting collection (Fig. 2.9A). However, two species in the genus *Stylaster*, *S*. cf. *duchassaingi* (Fig. 2.9B) and *Stylaster* sp. 1 (Fig. 2.9C), can be classified as potentially important three-dimensional structure-forming species, primarily occurring between 150- 400 m depth.

The carbonate mineralogy of most stylasterids is similar to scleractinians in that a majority of known species, including those observed in this study, produce a skeleton composed primarily of the mineral aragonite (Cairns, 2011), although some are calcitic in composition (Cairns & Macintyre, 1992). Stylasterids do share distribution characteristics and overlapping depth ranges with many upper bathyal solitary and colonial scleractinian corals (Cairns, 1986, 2011). Like scleractinians, stylasterid hydrocorals also exhibit a vulnerability to changing aragonite saturation conditions over their depth distribution (Guinotte et al., 2006).

Knowledge of the chemical environment of deep-sea scleractinians has grown significantly in recent years as empirical measurements of the carbonate system at deep-sea coral habitats have been reported from different regions across the global ocean. On seamounts in the Indian Ocean off the coast of SW Australia, the majority of framework-forming scleractinians – including *E. rostrata* and *S. variabilis* – were found at Ω_{arag} values at or just below saturation, suggesting a control on the lower limit of these species' distributions (Thresher et al., 2011). However, live scleractinian reefs were recently discovered on seamounts in the North Pacific at Ω_{arag} values as low as 0.71 (Baco et al., 2017) and as low as 0.81 off Southern California (Gómez et al., 2018). Additionally, scleractinians have been observed below the ASH in the Indian Ocean (Trotter et al., 2019) and South Atlantic Ocean (Barbosa, Davies & Sumida, 2020). These revelations indicate that, under the right conditions, scleractinian corals can persist in undersaturated waters (Baco et al., 2017). Additionally, the presence of live tissue may buffer against the effects of low pH (Venn et al., 2011), but the underlying dead coral framework may be less resilient to undersaturated waters. Expanded surveys below 2000 m in northern

Caribbean, in tandem with additional effort in sampling of coral-adjacent deep-waters for carbonate chemistry analysis will aid in better determining the controls on aragonitic coral species distribution at lower bathyal depths in the tropical western Atlantic.

Productivity of the surface waters and export to the deep-sea benthos may contribute to differences in species distribution and abundance of deep-sea corals. In a 2016 laboratory experiment and field study comparing two spatially distinct and genetically isolated populations of the framework-forming scleractinian *Lophelia pertusa*, colonies from Norway exhibited enhanced respiration and prey capture rates under acidified conditions compared to individuals from the Gulf of Mexico (Georgian et al., 2016b). This study lends support to the hypothesis that species are locally adapted to environmental conditions, including food supply, which may allow individuals to better tolerate reduced carbonate saturation states.

2.6 Conclusions

Our results offer some insights to the distribution, diversity, and drivers of community assembly of scleractinian and stylasterid deep-water corals in a data-deficient region of the tropical western Atlantic Ocean. These findings lend support for the efficacy of targeted exploration surveys to understand coral distribution with respect to environmental gradients in the deep-sea environment. The presence of aragonitic corals, largely occurring above the aragonite saturation horizon, was not unexpected, but more surprising was the presence of known framework-forming scleractinians, like *Madrepora oculata*, living at or just above $\Omega_{arag} = 1$ in this locality. Future work should seek to expand upon coral community inventories for this area to include members of the Octocorallia and Antipatharia, particularly to refine the relationship between community assembly and water mass structure. Increased taxonomic effort is needed to better identify cryptic coral morphospecies from the deep-sea benthos, and particularly for those size classes below the identification threshold for ROV video surveys. In the Atlantic Ocean, deep-water coral ecosystem health is likely to be negatively impacted by environmental change by the end of the current century. Warming deep-waters (Gleckler et al., 2016), thermohaline driven deep-water acidification (Pérez et al., 2018), and low latitude deoxygenation in the Atlantic (Montes et al., 2016) are among the greatest threats facing deep-water framework-forming corals. The relationship between coral occurrences and environmental variables reported here establish a critical baseline for the detection of the effects of deep ocean change to seafloor communities, which is crucial to effective conservation.

CHAPTER 3

OCEANOGRAPHIC DRIVERS OF DEEP-SEA CORAL SPECIES DISTRIBUTION AND COMMUNITYASSEMBLY ON SEAMOUNTS, ISLANDS, ATOLLS, AND REEFS WITHIN THE PHOENIX ISLANDS PROTECTED AREA

3.1 Abstract

The Phoenix Islands Protected Area, in the central Pacific waters of the Republic of Kiribati, is a model for large marine protected area (MPA) development and maintenance, but baseline records of the protected biodiversity in its largest environment, the deep sea (>200m), have not yet been determined. In general, the equatorial central Pacific lacks biogeographic perspective on deep-sea benthic communities compared to more well-studied regions of the North and South Pacific Ocean. In 2017, explorations by the NOAA ship *Okeanos Explorer* and R/V *Falkor* were among the first to document the diversity and distribution of deep-water benthic megafauna on numerous seamounts, islands, shallow coral reef banks, and atolls in the region. Here, we present baseline deep-sea coral species distribution and community assembly patterns within the Scleractinia, Octocorallia, Antipatharia, and Zoantharia with respect to different seafloor features and abiotic environmental variables across bathyal depths (200-2500m). Remotely operated vehicle transects were performed on 17 features throughout the Phoenix Islands and Tokelau Ridge Seamounts resulting in the observation of 12,828 deep-water corals and 167 identifiable morphospecies. Anthozoan assemblages were largely octocoral-dominated consisting of 78% of all observations with seamounts having a greater number

of observed morphospecies compared to other feature types. Overlying water masses were observed to have significant effects on community assembly across bathyal depths. Revised species inventories further suggest that the protected area it is an area of biogeographic overlap for Pacific deep-water corals, containing species observed across bathyal provinces in the North Pacific, Southwest Pacific and Western Pacific. These results underscore significant geographic and environmental complexity associated with deep-sea coral communities that remain in under-characterized in the equatorial central Pacific, but also highlight the additional efforts that need to be brought forth to effectively establish baseline ecological metrics in data deficient bathyal provinces.

3.2 Introduction

Established in 2008, and later closed to commercial fishing in 2015, the Phoenix Islands Protected Area (PIPA) is among the largest (408,250 km_2) closed marine protected areas (MPA) and the deepest UNESCO world heritage site on Earth (Claudino-Sales, 2019). Despite these designations, the deep-sea benthos below 200m in this marine protected area remained vastly unexplored hindering the full understanding of what habitats the protected area encompasses. In 2017, several deep-sea exploration expeditions passed through PIPA on the NOAA ship Okeanos *Explorer*, as a part of the CAPSTONE (Campaign to Address Pacific monument Science, Technology, and Ocean Needs) program (Demopoulos et al., 2018), and on the R/V *Falkor* with the goal of enhancing understanding of deep-sea ecosystems in the MPA via international partnerships (Mangubhai et al., 2019; McKinnie et al., 2018).

Deep-sea exploration has been an on-going priority for PIPA, starting with the first formal research plan (Rotjan and Obura, 2010), and continuing in the first and second PIPA management plans. The earliest deep-sea surveys consisted of baited drop cameras deployed to observed fish communities below 1000m depth (Obura et al., 2011). Recent expeditions contributed high-definition multibeam mapping and seafloor exploration (Kennedy et al., 2019), which also helps to better define and manage the features that lie within protected boundaries. A United Nations voluntary commitment stemming from the Oceans Sustainable Development Goals (SDG14) was recently written by the PIPA Scientific Advisory Committee, with the specific goal to increase scientific knowledge and research capacity to improve ocean health in Kiribati. Deep-sea exploration in PIPA directly helps to fulfill these goals of increased knowledge and research capacity, as well as advancing the biodiversity inventory within PIPA boundaries.

The deep slopes of islands, atolls, reef-capped shallow banks (herein referred to as reefs), and seamounts comprise the majority of high-profile seafloor relief in PIPA with at least two major geographic seamount or island clusters, the Tokelau Seamount Chain and Phoenix Island cluster, occurring entirely within or passing through its boundaries (Fig. 3.1). Globally, seamounts are among the most extensive biomes in the Pacific Ocean with only a small percentage having been explored worldwide (Etnoyer et al., 2010). While seamounts are abundant deep-sea features, particularly in the western and central Pacific Ocean, exploration of these features and characterization of seafloor communities at bathyal depths are lacking in the region (Bohnenstiehl et al., 2018; Cantwell et al., 2018; Demopoulos et al., 2018; Herrera et al., 2018; Kelley et al., 2018;

Watling et al., 2013). Deep-sea corals, primarily from the Octocorallia (soft corals), Scleractinia (stony corals), and Antipatharia (black corals), represent some of the most common groups observed on seamounts studied worldwide (Rogers et al., 2007), making them a useful group of taxa for understanding how the oceanographic and physical environment influences benthic communities across a range of spatial scales. Structures produced by deep-water corals provide important vertical relief for associated species in deep-sea ecosystems (Buhl-Mortensen et al., 2010), in addition to supporting unique symbioses with invertebrate fauna (Mosher and Watling, 2009). Benthic invertebrate and demersal fish communities on seamounts have been reported to be strongly influenced by variables including local water column productivity, overlying water masses, depth, substrate type, and topographic variability (Auster et al., 2005; Clark et al., 2010; Genin et al., 1986; Quattrini et al., 2017; Rogers, 2018; Shank, 2010).

The exploration and exploitation of mineral resources from seafloor crusts and the impact to benthic fauna have become an increasing regional concern given the poor state of knowledge of deep-sea biodiversity (Miller et al., 2018). World-wide, seamounts have been found to harbor benthic communities that are vulnerable to a range of disturbances and are often slow to recover to their pre-disturbed state (Watling and Auster, 2017; Watling and Norse, 1998; Williams et al., 2010). In the central Pacific, cobalt-rich mineral crusts occur on seamounts at depths that coincide with those of deep-water coral and sponge communities (Morgan et al., 2015). Such species, which are characteristically slow-growing and long-lived, stand to be disrupted should such activities occur and result in physical disturbance and increased sedimentation rates within and around affected areas (Gollner et al., 2017). Identifying and quantifying species diversity within deep-water coral communities on features throughout the Pacific that exhibit a range of geomorphological characteristics (e.g., guyots, sharp-peaked seamounts, as well as on the flanks of atolls and islands) is essential to properly manage these species and communities.

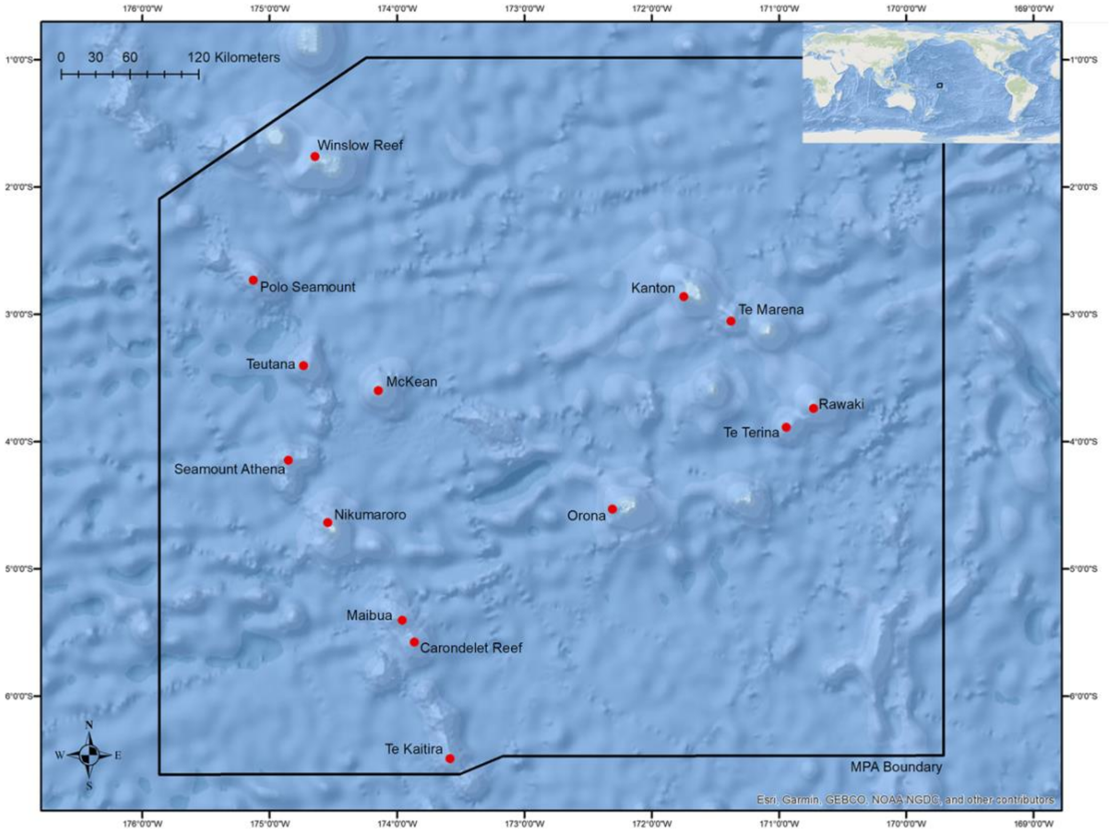


Figure 3.1 Overview of the boundaries of the Phoenix Islands Protected Area with locations of sites where dives were conducted in this study.

This study provides insight into the composition, diversity, and patterns among coral communities at bathyal depths in the Phoenix Islands Protected Area. Using ROV-collected high-resolution video and collections-based approaches, we provide the first deep-sea coral species inventory within PIPA boundaries. Additionally, we test two exploratory hypotheses designed to identify broader differences in community similarity between geographic features and across depth. The first being, do different feature types like islands, atolls, reefs, or seamounts harbor distinct deep-water assemblages within the protected area? Second, does vertical structure of the water column (i.e. water masses) result in differences in assemblages across depth? If so, which species might contribute most to the observed differences? And finally, which oceanographic environmental variables most strongly influence the observed variation in community structure at bathyal depths?

Due to the geographic remoteness of these features and the protected status of the area, we suggest that deep-water communities within PIPA are likely to rank among the least human-impacted environments in the deep Pacific Ocean and act as a foundation for comparison to other unprotected deep-sea features in the greater Central Pacific. The results of this work will help to set a much-needed baseline understanding of large remote marine reserves, specifically with respect to identifying abundant and diverse deep-sea communities and ensuring their future conservation.

Table 3.1 Summary of dives conducted at seamounts, islands, atolls, and reefs during EX1703 and FK171005.

Cruise	Dive	Location	Feature type	On bottom (Lat, Long Dec. Degrees)	Off bottom (Lat, Lon Dec. Degrees)	Depth range (m)	Bottom duration (hh:mm)	Seafloor distance covered (m)
EX1703	Dive03	Carondelet Reef	Reef	-5.62715, -173.835083	-5.6280833, -173.8394167	1603-1844	6:01	490
EX1703	Dive04	Seamount Athena	Seamount	-4.1469167,-174.8521	-4.150267, -174.854333	1030-1223	6:43	447
EX1703	Dive05	Polo Seamount	Seamount	-2.7300667,-175.12615	-2.72805, -175.1310667	1834-2134	5:44	590
EX1703	Dive14	Winslow Reef	Seamount	-1.70345,-175.2022667	-1.70431667, -175.205667	1303-1527	6:03	390
EX1703	DIve15	Teutana	Seamount	-3.40145,-174.73211667	-3.399516, -174.735766	976-1325	4:57	453
EX1703	Dive17	Maibua	Seamount	-5.403283,-173.958233	-5.40135, -173.9615	463-746	7:10	420
EX1703	Dive18	Te Kaitira	Seamount	-6.490766,-173.58045	-6.4918833, -173.58345	1778-2105	5:43	354
FK171005	SB0067	Kanton	Atoll	-2.859174,-171.744569	-2.826730,-171.714738	247-2135	19:06	4895
FK171005	SB0068	Te Marena	Seamount	-3.0539191,-171.374616	-3.036057,-171.357612	804-1856	9:50	2739
FK171005	SB0069	Rawaki	Island	-3.7819294,-170.731466	-3.759379,-170.718154	1550-2313	9:04	2908
FK171005	SB0070	Rawaki	Island	-3.738242,-170.725524	-3.732776,-170.716769	367-1198	7:40	1145
FK171005	SB0071	Te Terina	Seamount	-3.887563,-170.939562	-3.890913,-170.935158	1489-1724	3:44	614
FK171005	SB0072	Te Terina	Seamount	-3.891529,-170.933927	-3.891579,-170.930155	1127-1426	1:47	418
FK171005	SB0073	Orona	Atoll	-4.528743,-172.306548	-4.5205168,-172.307271	2050-2439	11:02	918
FK171005	SB0074	Orona	Atoll	-4.5121363,-172.272042	-4.51443033,-172.261741	600-1361	6:25	1169
FK171005	SB0075	Orona	Atoll	-4.498947,-172.25421	-4.5102886, -172.2421938	484-613	22:41	1833
FK171005	SB0076	Winslow Reef	Reef	-1.655299,-174.980157	-1.6391061,-174.973467	229-1502	9:19	1947
FK171005	SB0077	Winslow Reef	Reef	-1.660755,-174.952322	-1.6530499, -174.943519	561-1424	9:14	1300
FK171005	SB0078	Winslow Reef	Reef	-1.759119,-174.641697	-1.7685911,-174.64309	723-1365	9:52	1064
FK171005	SB0079	Winslow Reef	Seamount	-1.929302,-174.736812	-1.9221619, -174.732316	1375-1957	9:15	937
FK171005	SB0080	McKean	Island	-3.597142,-174.145254	-3.5947105,-174.136795	363-1206	9:37	976
FK171005	SB0081	Nikumaroro	Atoll	-4.634481,-174.543162	-4.6574490,-174.556903	829-1028	10:37	2972
FK171005	SB0082	Carondelet Reef	Reef	-5.5760301,-173.862591	-5.575719,-173.8616971	152-275	1:59	105
FK171005	SB0083	Carondelet Reef	Reef	-5.604389,-173.844220	-5.595109,-173.856552	429-1342	19:09	1710

3.3 Methods

Data for this study were collected from two expeditions to the Phoenix Islands Protected Area in March and October 2017 (Table 3.1). In March, the NOAA Ship *Okeanos Explorer* (ROV *Deep Discoverer*) surveyed and explored the western portion of PIPA along the Tokelau Ridge seamounts; in October, the R/V *Falkor* (ROV *Subastian*) focused on islands, atolls, and seamounts in the eastern Phoenix Islands, as well as additional dives along the Tokelau seamount chain. Both expeditions utilized remotely operated vehicle (ROV) systems to survey and characterize deep-water coral communities in the area. ROV *Deep Discoverer* completed 7 transects along 7 features on the Tokelau Seamount Chain and the ROV *Subastian* completed 17 transects across 10 features throughout the Phoenix Islands, Phoenix Seamounts, and Tokelau Seamounts (Supplementary Fig. B1).

Seafloor transects were conducted upslope from deeper to shallower depths across each feature. In each case, vehicles moved upslope, perpendicular to the contours of the slope, with only occasional short zooms to confirm identifications. Motion across the seafloor occurred at an average of 0.25 kt. Video segments on the seafloor spent sampling, during long duration zooming, not in forward motion, or otherwise not in visual contact with the seabed was not included in analyses. Collection opportunities were utilized to obtain voucher specimens for further identification of coral morphospecies.

3.3.1 ROV video analysis

Video segments where collections were made, where the vehicle was more than 3 m off bottom, moving backwards, during sampling events, or of generally poor quality, were not assessed. Individuals or colonies were identifiable above a 5cm height threshold, with measurements based on 10cm wide parallel lasers in the ROV field of view. If colonies or individuals were below this size threshold, they could not be consistently identified and were omitted from analysis. Each occurrence was associated with a UTC time-stamp, and this was used to associate each observation with *in situ* environmental data including latitude-longitude coordinates, temperature, depth, dissolved oxygen concentration, and salinity.

Video was analyzed for coral occurences from four major anthozoan taxonomic groups: the Scleractinia, Octocorallia, Zoantharia, and Antipatharia. Individuals or colonies were identified to the lowest taxonomic level possible or assigned morphospecies (msp.) identifiers. Only visibly live colonies were counted. If particular colonies could not be identified reliably to such a level, they were placed in family or genus-level groupings (i.e. family spp. or genus spp.). Observations with any uncertainty were flagged and underwent quality control by examining and omitting the potentially erroneous identifications. Final identification of coral species, using both photographic and voucher specimens, were made using published taxonomic keys, and assistance from taxonomic specialists.

3.3.2 Community analyses

Deep-water coral patterns were assessed by dividing each of the 24 dive transects into 100 m depth bins. Each bin provided a sampling that consisted of all coral morphospecies observations occurring within that 100m depth interval. Community-level analyses were conducted using standardized and 4th root transformed species abundance data in a resemblance matrix in PRIMER v7 with PERMANOVA add-on (Anderson et al., 2008; Clarke and Gorley, 2006). In all, 153 samples were identified across 24 dives. Samples were compiled into a Bray-Curtis similarity resemblance matrix for further analyses. Cluster analysis and non-metric multidimensional scaling ordinations (nMDS) were initially conducted to identify associations between groups of samples. For these analyses only, in order to reduce the effect of noise in the dataset, species abundances were averaged across samples in 100m depth bins resulting in one data point for each depth stratum. The significance of associations between sample clusters were evaluated using the similarity profile (SIMPROF) routine (Clarke et al., 2008).

Before conducting assessments of similarity in communities, adequacy of sampling effort and species richness comparisons were evaluated using permuted sample-based species accumulation and individual-based rarefaction for feature types and water masses in Vegan 2.5-3 in R (Oksanen et al., 2015). In order to test for similarities among coral assemblages between factors, analysis of similarity (ANOSIM) tests were employed. The first comparison tested differences between feature types while controlling for the effect of depth differences using a two-way nested ANOSIM. A one-way ANOSIM test was also used to determine if differences could be identified between assemblages bathed by different water masses. All ANOSIM tests were conducted using 999 random permutations.

In order to incorporate environmental data for each sample, an average of depth, temperature, salinity, dissolved oxygen was calculated in each 100m sample. The mean was then normalised within each variable to reduce the effects of differences in unit scales. The BEST routine (BIO-ENV) was employed to explore correlations between biological observations and environmental predictors. A distance-based linear model (distLM) was applied using the PERMANOVA package and utilized the Akaike Information Criterion (AIC) to identify environmental variables with strong explanatory power for observed variation within samples (Anderson et al., 2008). Visualizations of the resemblance matrix with predictor variables were paired with a dbRDA (distance-based redundancy analysis) ordination with distLM overlay.

3.4 Results

3.4.1 ROV video analysis summary

Across both cruises, 212 hours and 42 minutes of video were assessed from 24 dives, 7 dives from EX1703 and 17 dives from FK171005 (Table 3.1). A preliminary comparison revealed no significant difference between cruises due to methodology and thus both datasets were treated as one (two-way ANOSIM between cruises (depth within cruise), Global R=0.018, p=0.292). Dives spanned the depths of 152 – 2439m with deep-water corals being recorded across the depths of 192-2438m (Fig. 3.2). In total, 12,828 observations of deep-water corals were identified with 10,995 of those being assigned a morphospecies (msp.) or species-level identifier. The remaining 1833 records fell into coarser identification groupings at the genus or family level. All corals were identified and categorized using consistent morphospecies identifications from the Octocorallia, Antipatharia, Scleractinia, and Zoantharia. From these groups, 167 unique morphospecies identifiers were assigned based on visual identification, morphological identification from voucher collections, or a combination of those methods.

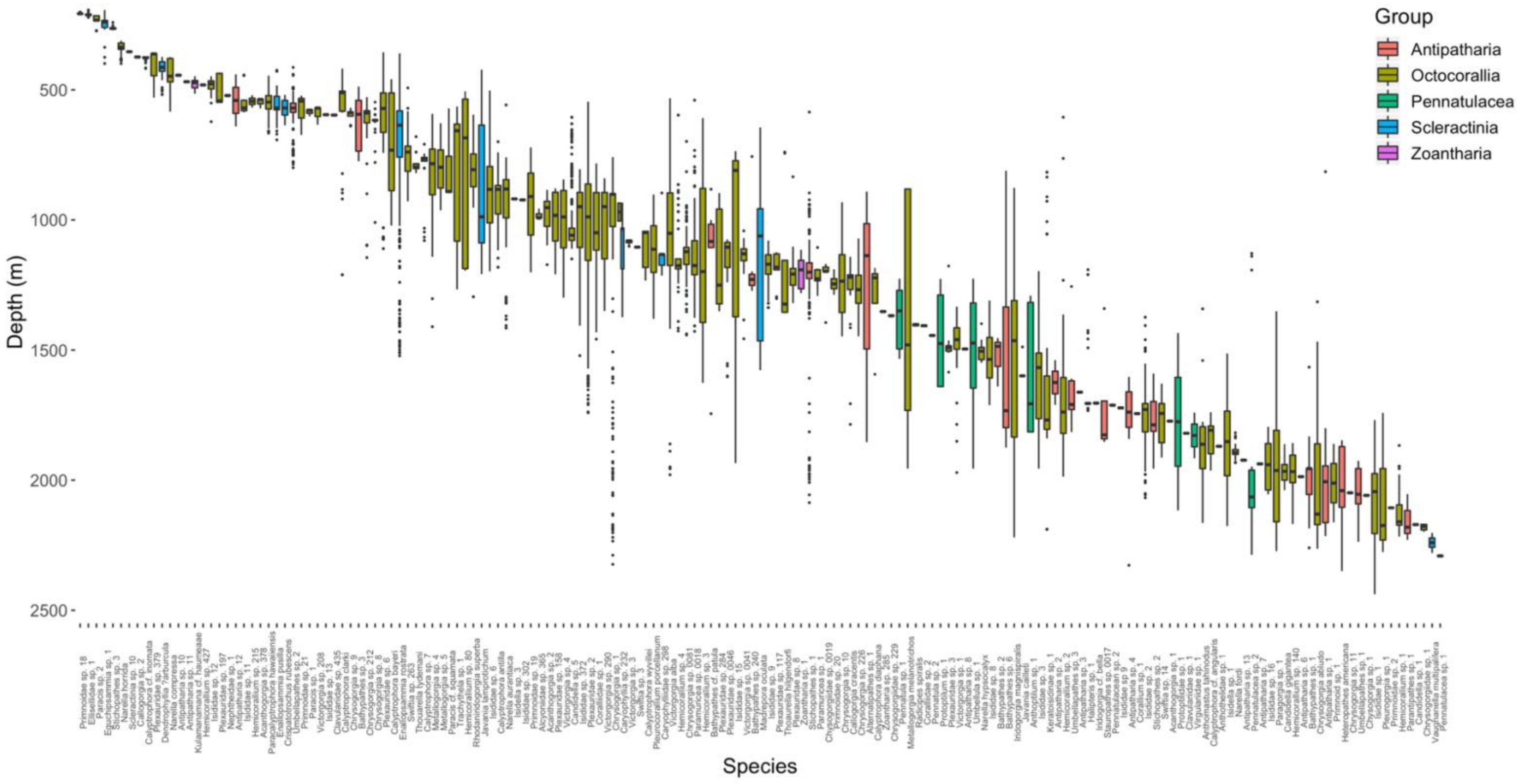


Figure 3.2 Depth distribution of 167 morphospecies observed from video analyses within PIPA. Boxes are colored according to taxonomic groupings and are arranged by increasing median depth of occurrence.

3.4.2 Oceanographic summary

In order to determine water mass structure in the area, downcast shipboard CTD profiles of the upper 3000m of the water column were examined for temperature and salinity changes across depth (Fig. 3.3). Using these characteristics, major deep-ocean water masses present in this area were generally defined as Pacific Equatorial Water (PEW) between 200-500m, Equatorial Pacific Intermediate Water (EqPIW) between 500-1500m, and Pacific Deep Water (PDW) below 1500m (Table 3.2). Temperature, salinity, and dissolved oxygen ranges for each water mass were consistent with accepted ranges from published records in the equatorial Pacific (Bostock et al., 2010).

Environmental variables from ROV-mounted CTD units were in agreement with downcast CTD profiles and provided *in situ* records at each coral observation (Fig. 3.4). Bottom temperatures overlying coral observations ranged from 1.91 – 21.34 °C. Salinity and dissolved oxygen across those same intervals ranged from 34.52 – 35.92 psu and 79.85 – 201.70 μmol/kg, respectively. Below the thermocline at 200-300m depth, temperature decreased to a minimum of 1.91°C at 2438m (Fig. 3.4A). Salinity decreased rapidly with depth to a minimum of 34.52 at 800m, gradually increasing at deeper depths (Fig. 3.4B). A persistent mid-water oxygen minimum of 110-120 µmol/kg was observed between 1000-1100m, but oxygen values in the viscinity of Winslow Reef were reported substantially lower at shallower depths (Fig. 3.4C). The lowest values concurrent with coral observations occurred at Winslow Reef where dissolved oxygen was measured at 79 µmol/kg at 608m. Low oxygen values (91 µmol/kg) were also identified at Rawaki Island at between 483-540m.

Table 3.2 Water masses and environmental characteristics observed in the Phoenix Islands Protected Area during cruises FK171005 and EX1703.

Water Mass	**Temperature (°C)**	**Salinity (psu)**	***Dissolved Oxygen (μmol/kg)***	**Characteristics**	**Observed Depth Range (m)**
Pacific Equatorial Water (PEW)	7.80 - 21.30	34.6-35.9	89-201	Decreasing oxygen concentration, decreasing temperature with increasing depth	197-500
Equatorial Pacific Intermediate Water (EqPIW)	3.08 - 7.80	34.5-34.6	79-150	Oxygen and salinity minima	500-1500
Pacific Deep Water (PDW)	1.90 -3.05	>34.6	132-163	Increasing oxygen concentration, decreasing temperature with increasing depth	1500-2197

3.4.3 Coral distribution patterns

The dominant taxonomic group across all depths were the octocorals, followed by antipatharians, scleractinians, and finally zoantharians (Table 3.3). Pennatulaceans were only observed deeper than 1191m and thus one of the only groups restricted to lower-bathyal depths (Fig. 3.2). Rapid coral morphospecies turnover was observed in the upper 600m of the water column with most morphospecies in this range occurring across a relatively narrow ranges of depth. The single most abundant coral morphospecies was

Pleurogorgia sp. 1, with 1046 colonies observed between 1741-2276m, primarily encountered at high densities on vertical walls or steep inclines.

Table 3.3 Summary of deep-water coral observations from ROV video by taxonomic groupings.

	Octocorallia		Hexacorallia		
	Alcyonacea	Pennatulacea	Scleractinia	Antipatharia	Zoantharia
Number of observations	9910	145	1095	1645	33
Number of families	13	6	4	3	1
Number of morphospecies	113	10	12	29	3
Observed depth range (m)	193-2439	1129-2291	Colonial: 193-1578 All: 193-2280	241-2349	448-1352

Octocorals, inclusive of the Pennatulacea, accounted for 78% of all deep-water coral observations. Primnoids were the most speciose as well as the most abundant family in the Octocorallia. With 672 records *Candidella* sp. 5 (605-1150m), and *Narella aurantiaca* with 738 records (558-1416m) were the dominant primnoid taxa. Chrysogorgiids followed with the two most abundant taxa being *Pleurogorgia* sp. 1 and *Chrysogorgia* sp. 1. Plexaurids were widespread, both geographically and across depth (213-2055m) but 38% of observations fell into coarser identifications as Plexauridae spp. due to difficulty in identifying distinguishing characters between morphospecies. Plexauridae sp. 2, Plexauridae sp. 6, and *Paramuricea* sp. 0018 were the most abundant taxa in this family. Among the 605 bamboo coral colonies observed, Isididae sp. 9

(n=271), a branched colony, was locally abundant at Te Marena and Orona between the depths of 1079-1336m. The broadly distributed unbranched Isididae sp. 2 (n=91) was observed at 7 sites throughout PIPA but only deeper than 1373m. Precious corals representation was dominated by *Pleurocorallium porcellanum* Pasternak, 1981, by abundance (n=179), and *Hemicorallium* spp. by morphospecies richness, with 8 morphospecies present. Victorgorgiids were also bathymetrically widespread with 202 observations among 8 morphospecies between the depths of 532-1979m.

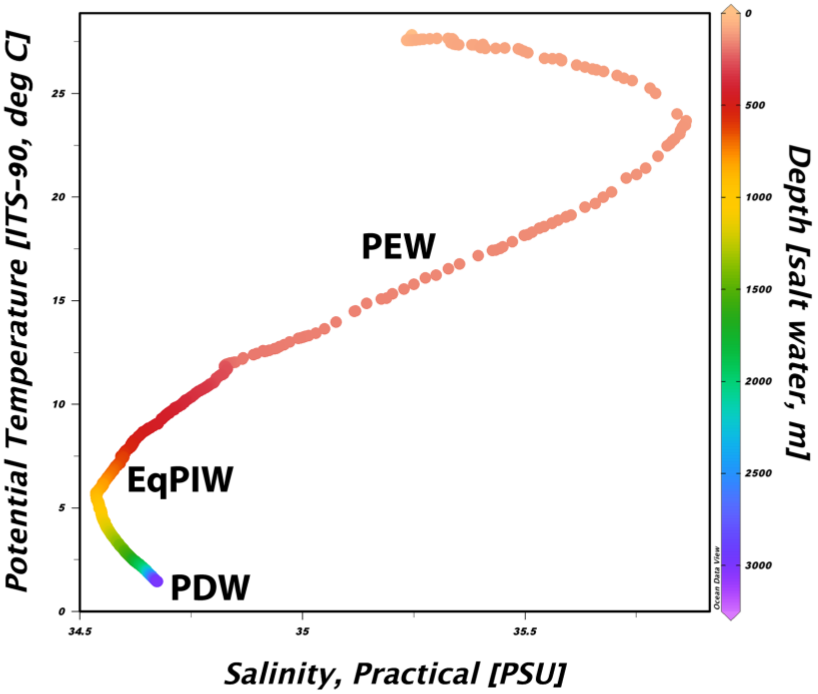


Figure 3.3 Temperature-salinity diagram from the sea surface to 3000 m collected via CTD rosette downcast North of Kanton Atoll. The approximate depth of each water mass identified below 200 m is overlaid in bold. Plot was constructed using Ocean Data View v5.1 (Schlitzer, 2019).

Black corals were the second most abundant taxon by number of observed colonies with 1645 records, or 12% of all records. The most abundant morphotype was *Stichopathes* sp. 1 with 981 records between 585-2086m followed by *Umbellapathes* sp. 2 with 413 colonies between 414-799m. *Bathypathes* was the most speciose genus but individual taxa were not very abundant with most morphospecies having 30 or fewer observations. At least 88 black coral colonies could not be identified to the family level due to low resolution singleton observations, or lack of voucher specimens for reference.

Scleractinians were most commonly distributed between 600 and 1500m depth, with only one solitary coral species (*Vaughanella multipalifera*) present below 2000m depth (Fig. 3.2). The deepest occurrences of framework-forming colonial scleractinians were *Madrepora oculata* (n=45) colonies found between the depths of 644-1577m. The most abundant colonial scleractinian species, *Enallopsammia rostrata* (n=462) was found to have a slightly shallower distribution between 359-1521m. A second species in the genus, *Enallopsammia pusilla*, was found to have a distribution that partially overlapped the shallower range of its congener, between 425-692m. Solitary coral species were the deepest scleractinians observed but most individuals occurred shallower than 650m. The single most abundant species, *Crispatotrochus rubesecens*, occurred across a depth range of 519-635m with other solitary species, *Javania cailleti* and *Javania lamprotichum* occurring deeper up to 1599 and 1208m, respectively (Fig. 3.2).

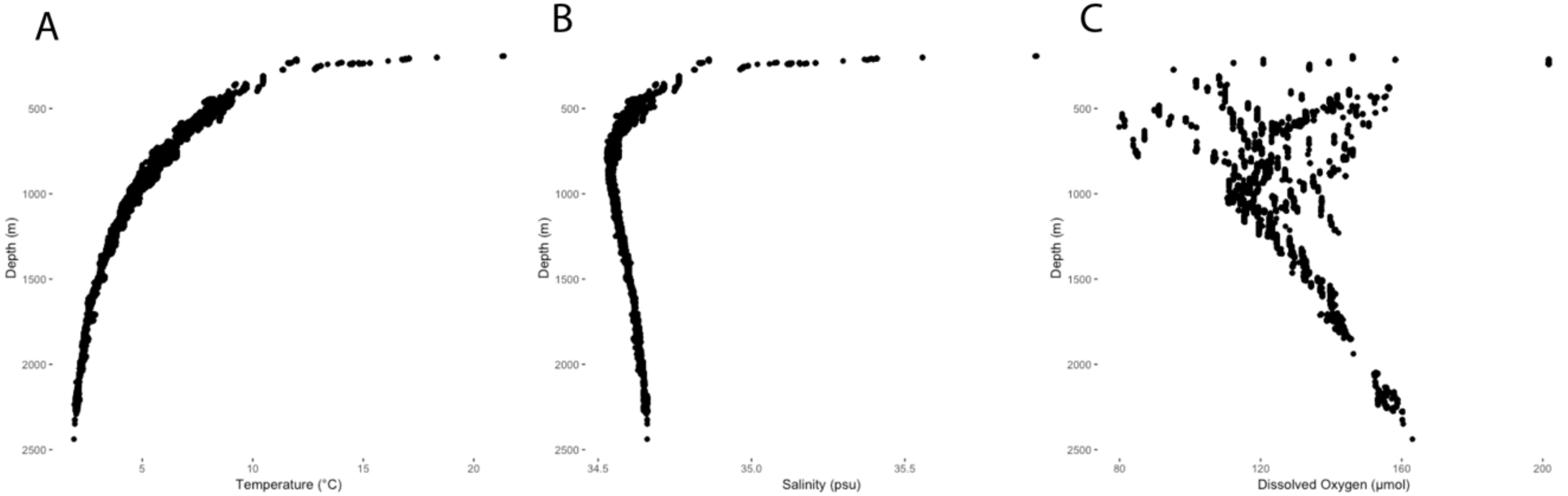


Figure 3.4 Temperature (A), salinity (B), and dissolved oxygen (C) profiles from ROV CTD unit records co-occurring with deep-water coral observations between 193 and 2439 m.

3.4.4 Patterns in coral community structure

In order to evaluate sampling effort, sample-based species accumulation analyses were conducted by feature type and water mass to evaluate the completeness of species inventories. Among feature types species accumulated at similar rates on seamounts, atolls, reefs, and islands. Overall, seamounts had the largest morphospecies inventory compared to reefs which exhibited the lowest despite similar sample sizes (Fig. 3.5A). Among all feature types, morphospecies accumulation approached asymptotic values signifying a potential to accumulate additional species with increased effort (Fig. 3.5A). Between water masses, morphospecies accumulation rates and numbers of morphospecies observed were highest across the depths bathed by EqPIW (Fig. 3.5B). Lower rates of accumulation and numbers of morphospecies were observed in PDW (76 mspp.) and PEW (30 mspp.). As sample sizes were smaller in PEW and PDW compared to EqPIW, accumulation curves did not approach asymptomatic values and suggest increased morphospecies richness with additional sampling effort in those water masses (Fig. 3.5B).

Individual-based rarefaction analyses indicated that the total number of species observed was higher at seamounts (86 mspp.) and atolls (82 mspp.) compared to reefs (77 mspp.) and islands (67 mspp). Greater morphospecies evenness, demonstrated by a rapid increase in morphospecies with increasing number of individuals was also higher on seamounts and atolls compared to reefs and islands (Fig. 3.5C). Overall, shallow-water reef banks accounted for the greatest number of coral observations (Fig. 3.5C). Between water masses, EqPIW was found to have both greater morphospecies richness (118 mspp.) and greater evenness than both PDW and PEW at comparable numbers of individuals (Fig. 3.5D).

Cluster analysis and non-metric multidimensional scaling analyses identified patterns in assemblage structure with depth. Similarities were highest in EqPIW samples and lowest among those in PEW (Fig. 3.6). SIMPROF analysis indicated that the significance of the 8 identified clusters were driven by a close proximity in depth between samples (Fig. 3.6). More SIMPROF groupings were identified encompassing samples covering the depths of EqPIW versus the above or underlying water masses (Fig. 3.7). The most dissimilar samples occurred on both the extreme upper and lower ends of the survey range. Similarities between samples were also found to occur along a clear gradient with increasing sampling depth, except those between 2300-2500m (Fig. 3.7) These two samples were the two deepest depth bins and contained only 4 combined coral observations.

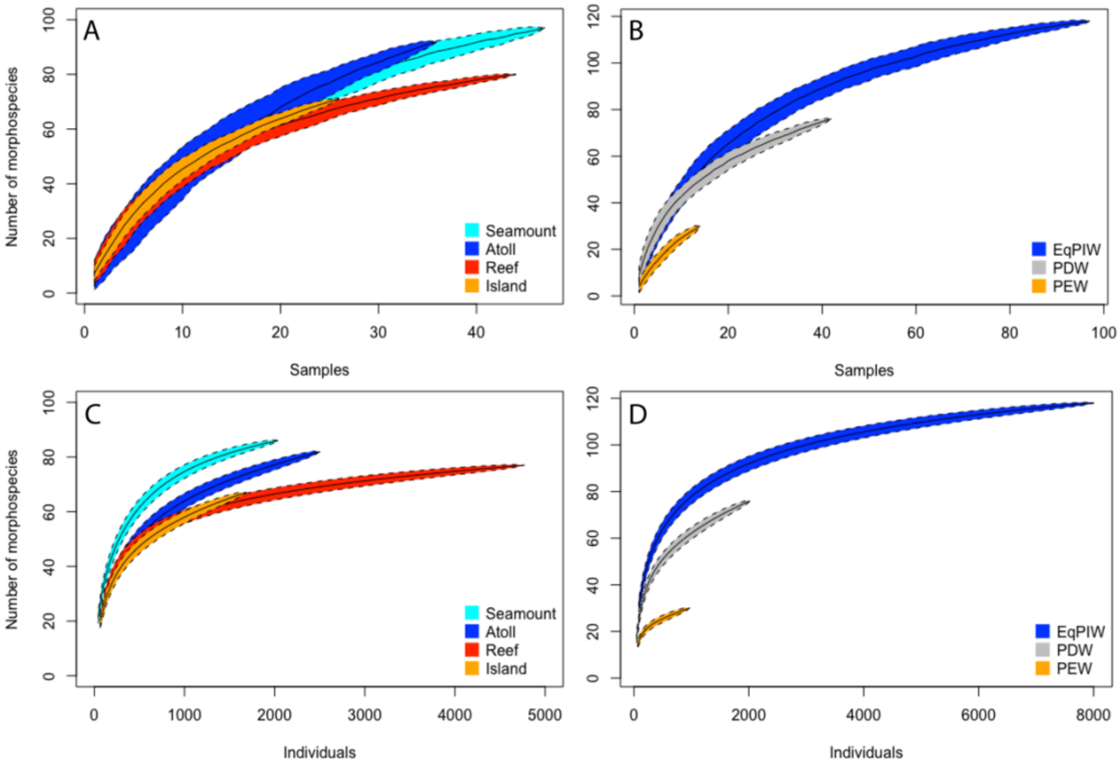


Figure 3.5 Species accumulation and individual-based rarefaction analyses by feature type and water mass. Sample-based species accumulation curves are presented for feature types (A) and water mass (B). All depths were included for each feature type with N = 26 samples for islands, N = 36 for atolls, N = 47 for seamounts, N = 44 for reefs. For water masses, N = 14 samples were used for the PEW (197–500 m), N = 97 for EqPIW (500–1500 m), and N = 42 for PDW (1500–2197 m). Rarefaction curves are indicated for feature types (C) and water masses (D). Curves are plotted with 95% confidence interval indicated by the colored polygons.

A two-way nested ANOSIM between feature types (depth within feature type) failed to identify differences in assemblages between most comparisons with the exception of reef-type features (Global R=0.036, p=0.096). For reefs, significant differences in assemblages were observed between each other feature, but R-statistic values remained very low indicating a high degree of similarity between samples in those comparisons (Supplementary Table B1). A one-way ANOSIM between water mass factors identified significant and highly dissimilar coral assemblages (Global R=0.302, p=0.001) between all 3 bathyal water masses (Supplementary Table B2). The highest dissimilarity was observed between PEW and PDW (R-statistic=0.619, p=0.001) and the lowest between EqPIW and PEW (R-statistic=0.177, p=0.006).

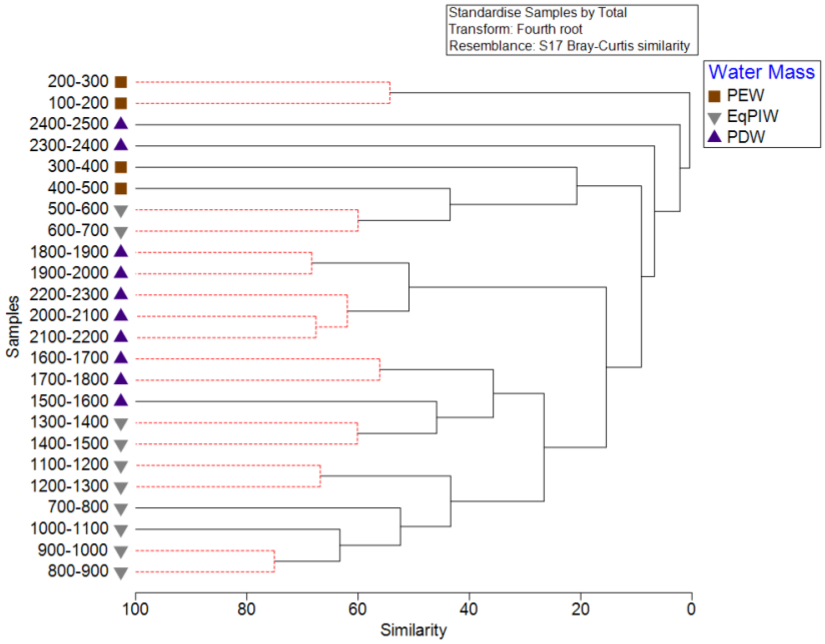


Figure 3.6 Cluster analysis of 100 m depth-averaged samples. Significant clusters are identified using SIMPROF analysis and are indicated by solid black lines. Symbols indicate the water masses in which those samples occurred.

The similarity percentage (SIMPER) routine identified particular species that contributed a disproportionate influence among significantly different water mass assemblages (Fig. 3.8). Average community similarity increased with increasing water mass depth from PEW (9.68 %), to EqPIW (9.8 %), to PDW (14.7 %). Similarities between samples within the PEW assemblage (200-500 m) were driven by 3 species, *Enallopsammia rostrata,* Plexauridae sp. 6, and *Paracalyptrophora hawaiiensis* contributed 58% of the within-group similarity (Fig. 3.8). In EqPIW (500-1500 m), *Enallopsammia rostrata*, Plexauridae sp. 2, and *Iridogorgia magnispiralis* contributed to 45% of the similarity in the group (Fig. 8). Within PDW (1000-2500m), the top 3 species *Iridogorgia magnispiralis, Chrysogorgia* sp. 1, *and Pleurocorallium porcellanum* contributed to 40 % of the observed similarity (Fig. 3.8). Between water masses, the greatest dissimilarity was found between the shallowest and deepest water masses PDW and PEW (99.4 % dissimilar). Present in each water mass, differences in the abundance of *Enallopsammia rostrata* alone was the dominant, single-species contributor (between 4.5-7%) of the dissimilarity observed between water masses.

Results from the BEST (BIO-ENV, Spearman Rank correlation) routine examined which environmental variable or combination of variables provided the best match for the observed variation in community among all samples. Depth and salinity together were found to be the best combination of variables describing resemblances between samples (Global test, 999 permutations, Rho=0.445, p=0.001). Yet, together, depth, temperature, salinity, and dissolved oxygen resulted in only a slightly lower correlation (Rho=0.415). In the distLM and dbRDA analyses, depth, temperature, salinity, and dissolved oxygen were found to explain 7.2% (dbRDA axis 1) and 3.6% (dbRDA axis 2) of the community variation for a total of 10.8% (Fig. 3.9). From the fitted model, 49.2% of the biological variation was correlated with dbRDA axis 1 and 24.9% with axis 2. DbRDA Axis 1 was most strongly correlated with depth (r=-0.773) and dbRDA axis 2 with temperature (r=0.800) (Supplementary Table B3).

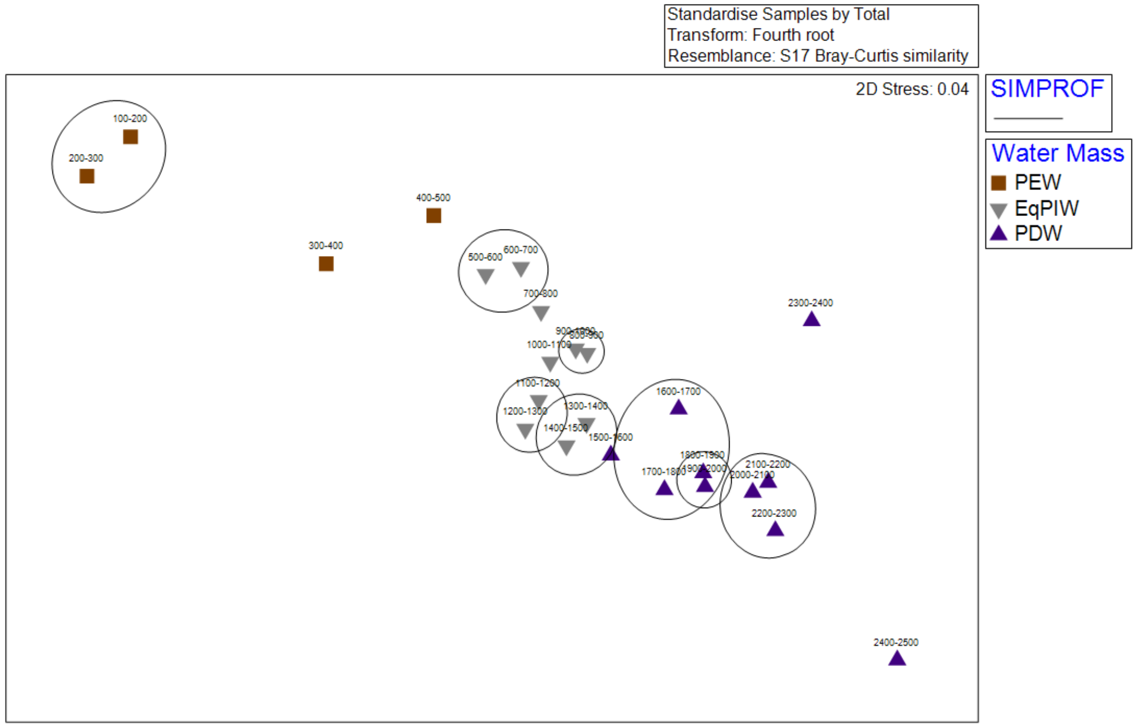


Figure 3.7 Non-metric multidimensional scaling ordination (nMDS) of 100 m depth-averaged samples. Abundances within samples were 4th root transformed, standardized, and analyses were conducted using a Bray-Curtis Similarity matrix. Symbols indicate the water masses in which those samples occurred. Significant SIMPROF groupings from cluster analysis are overlaid in black.

3.5 Discussion

This study provides a significant number of new deep-sea coral species records for a largely unexplored area of the equatorial central Pacific as well as within the boundaries of one of the largest marine protected areas in the world. Prior to these expeditions in 2017, no published records of any deep-water coral species were available from the Phoenix Islands below 200m (OBIS, 2019). Over 2 cruises, this study has identified 12,828 deep-sea coral observations and 167 morphospecies at bathyal depths within the boundaries of PIPA from ROV video. From these observations we sought to test two exploratory hypotheses of community assembly in the protected area based on differences in feature type and overlying water masses.

There was no clear evidence of different assemblages across most feature types. While reefs did have some statistically significance differences among assemblages compared to each other feature type, the assemblages themselves were still identified as having high degree of similarity based on low R-statistic (R= 0.01 to 0.12) values (Supplementary Table B1). In comparison, the three bathyal water masses in the area, Pacific Equatorial Water, Equatorial Pacific Intermediate Water, and Pacific Deep Water were identified as having distinctly different deep-water coral assemblages (Supplementary Table B2), largely dominated by widely distributed cosmopolitan deep-water coral species (Fig. 3.8). Furthermore, intermediate waters were found to have a greater number of morphospecies and greater evenness than shallower and deeper water masses suggesting that they are important pools of biodiversity at bathyal depths (Fig. 3.5D).

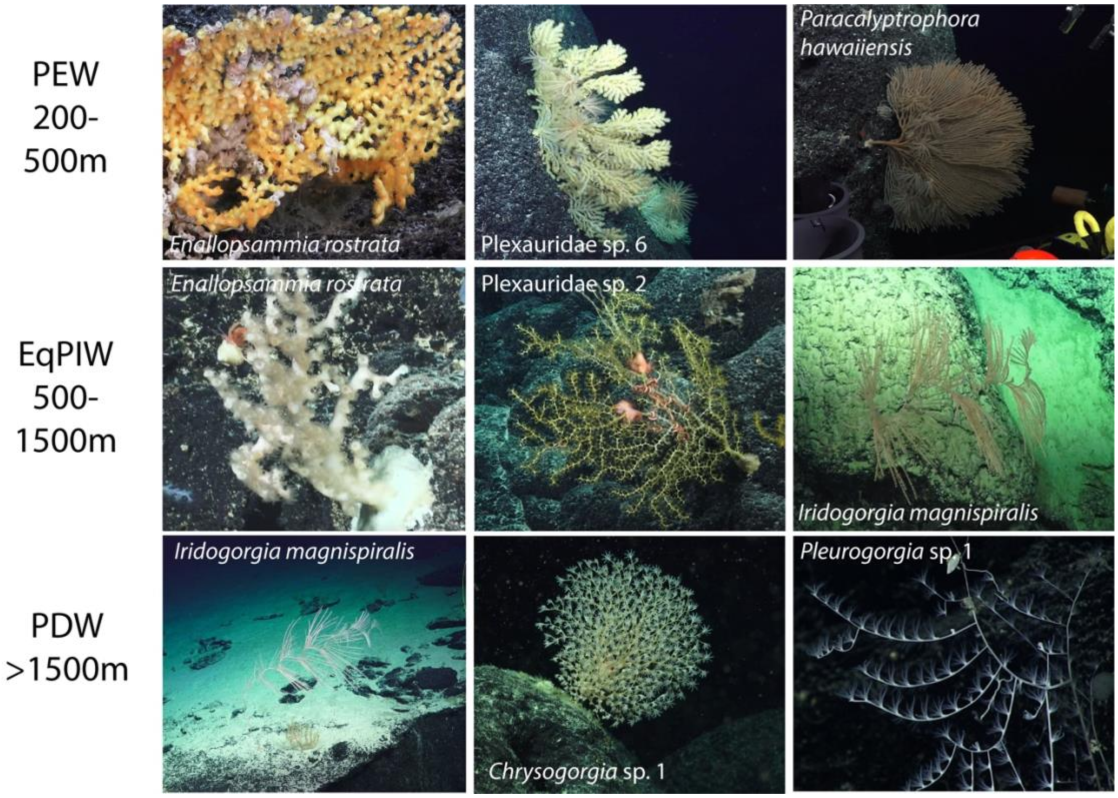


Figure 3.8 Top 3 morphospecies with disproportionate influence on coral assemblage similarity within each water mass as a result of the SIMPER analysis. Morphospecies on the far left are the largest contributors to within-water mass similarity with influence rank decreasing toward the right.

Finally, we sought to identify which environmental variables were most important for explaining variation in coral assemblages. Community models and redundancy analyses indicated that depth and temperature were the most important oceanographic variables for explaining biological variation (Fig. 3.9). However, dissolved oxygen and salinity also contributed significantly to the explanation of biological variation in the model (Supplementary Table B3). As a relatively low percentage (10.8%) of the total community variation was explained by oceanographic variables, it is likely that other environmental factors such as seafloor substrate and terrain variables would be useful to include in subsequent models (Supplementary Table B3). From a methodological perspective, both temperature and depth exhibited the greatest correlation between any two input variables ($|r|= 0.84$). However, it was not deemed necessary to remove either of these two variables due to concerns of collinearity prior to the analysis as they contained sufficiently different predictive information that would permit their inclusion to the model (Anderson et al., 2008). As temperature, salinity, and oxygen are the primary defining characteristics of major water masses (Fig. 3.3), water masses themselves can be useful units for predicting deep-water species occurences and community structure.

The role that water masses play in structuring biological communities in the deep-sea have been suggested as a major factor influencing species biogeography (Carney, 2005). In this study, differences were found to occur between coral assemblages bathed by PEW, EqPIW, and PDW indicating that oceanographic structure has a significant role in structuring communities. The pattern of within water mass similarities in species occurrence and community composition has been observed across multiple taxa including deep-water corals (Arantes et al., 2009; Miller et al., 2011; Radice et al., 2016), ostrocods (Ayress et al., 2004), and fishes (Quattrini et al., 2017). Furthermore, the boundaries of such water mass boundaries have been identified as important contributors to regional biodiversity in the deep ocean (Victorero et al., 2018). However, the mechanisms of why communities bear strong similarities within water masses are less clear but may include physical retention of planktotrophic larvae within water mass strata or relatively narrow physiological tolerances of species co-occurring within a water mass (Carney, 2005). The relationship between community similarities and water column structure requires further investigation to identify potential mechanisms driving such patterns.

Seamounts comprised the majority of features explored in this study and contained the greatest diversity of coral morphospecies of all feature types examined. Despite accounting for only 24% of all coral observations, seamounts hosted more than half of all morphospecies observed in this study. Diversity patterns on remote seamounts have been found to be strongly driven by species replacement along depth and temperature gradients, as well as topographic variability and along water mass interfaces (Victorero et al., 2018). From a population biogeographic perspective, seamounts may act as critical stepping stones for species distribution and population connectivity in the Pacific Ocean (Bors et al., 2012; Miller et al., 2011; Miller and Gunasekera, 2017). These baseline records of deep-sea coral abundance and diversity on seamounts in PIPA, as well as environmental factors driving community variation, will help generate new hypotheses for understanding benthic biodiversity on remote Pacific seamounts.

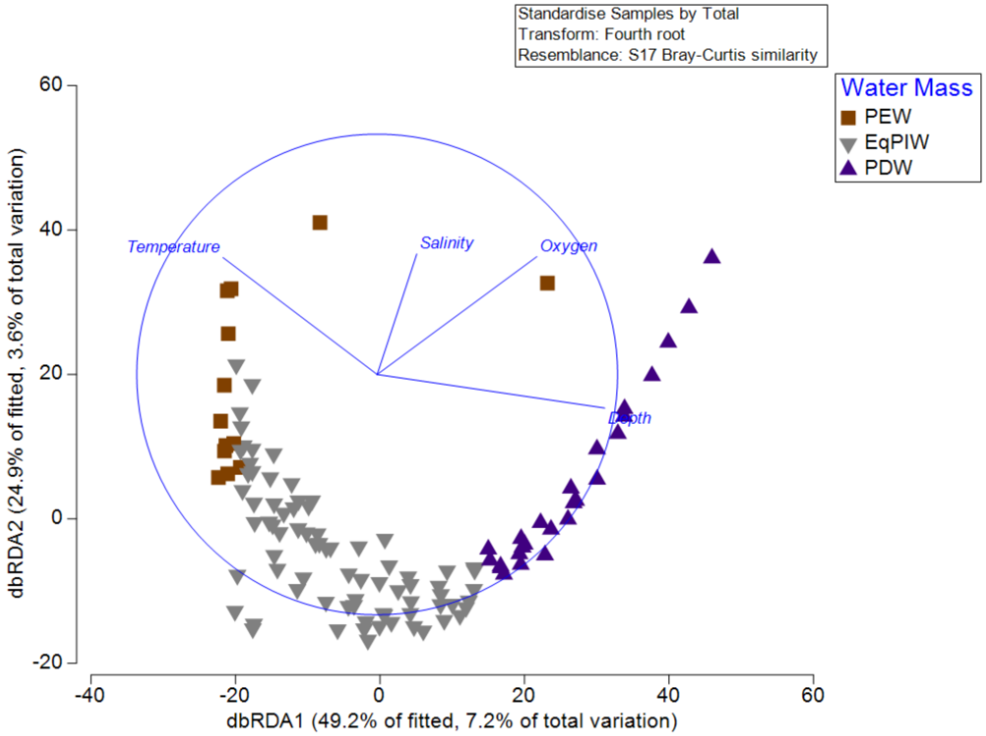


Figure 3.9 Distance-based redundancy analysis (dbRDA) from standardized and 4th root-transformed species abundances and normalized depth, temperature, salinity, and dissolved oxygen variables. DistLM circle is superimposed in blue with depth, temperature, salinity, and dissolved oxygen vectors. Symbol color and shape denote overlying water mass for each sample.

3.5.1 Insights to bathyal Pacific biogeography

The Phoenix Islands Protected Area lies in an area of the equatorial central Pacific that has been identified as a biodiversity and abundance hotspot for shallow-water marine organisms (Rotjan et al., 2014). At bathyal depths, benthic biodiversity is largely unknown and species inventories of deep-sea corals and sponges are lacking. One recently proposed biogeography of the bathyal regions of the Pacific suggests that the majority of seafloor features in PIPA lay in the BY14 (North Pacific Bathyal) biogeographic province (Watling et al., 2013). The PIPA boundaries also border the BY5 (Southeast Pacific Ridges), BY6 (New Zealand – Kermadec), and BY12 (West Pacific Bathyal) provinces suggesting that this area represents an area of biogeographic overlap, transition, or convergence. Still, further specimen collections and seafloor observations are necessary in refining proposed province boundaries and expanding species inventories within those provinces at bathyal depths.

Several deep-water coral species were found to have widespread geographic distributions in Pacific Ocean, but mechanisms for those observed distribution patterns remain poorly understood. Cosmopolitan deep-water coral taxa including *Enallopsammia rostrata*, *Metallogorgia melanotrichos*, *Paragorgia* spp., *Hemicorallium* spp. and *Pleurocorallium* sp., *Iridogorgia* spp., and several members of the Primnoidae were present throughout multiple sites in the Phoenix Islands at depths below 1000m providing a biogeographic continuity for species widely reported on seamounts in both the north and south Pacific Ocean. Some of these same species, like *Enallopsammia rostrata* and *Iridogorgia magnispiralis*, and were also found to exhibit a disproportionate effect on assemblage differences between water masses (Fig. 3.8). As a major source of hard substrate, seamounts and seamount chains likely provide pathways for species distribution across equatorial latitudes.

The large geographic extent of Pacific bathyal water masses may also help explain the prevalence of cosmopolitan species in PIPA. In the central and north Pacific below 1500m, PDW dominates much of the bathyal depth range but across tropical latitudes PDW contributes to the composition of EqPIW south of 20° N (Bostock et al., 2010). Environmental homogeneity and large geographic extent of PDW may provide a mechanism for species to become widely distributed within that water mass throughout the north Pacific Ocean while also extending their range southward via EqPIW. At the same time, mid-bathyal species in the southern hemisphere occurring in Antarctic Intermediate Water (AAIW) may be encountered in equatorial intermediate waters as this water mass contributes to EqPIW north of 20° S (Bostock et al., 2010). At upper bathyal depths, PEW (200-500m) has been identified as having a well-developed circulation along the equator (Emery, 2001) which could provide a potential distribution mechanism for species among low-latitude seafloor features.

3.5.2 Noteworthy observations

During both EX1703 and FK171005 expeditions, several collected specimens have been identified as new species and many others represent significant range extensions. Voucher samples were examined alongside records of visual observations to better understand the distribution of these species in their known localities. Recently, octocorals in the family Primnoidae have been relatively well-studied in the Pacific compared to other octocoral taxa, thus the majority of the new species encountered occur in that group (Cairns, 2018). In the genus *Narella*, two new species were described with material from sites within the Phoenix Islands. The type specimen of *Narella fordi* Cairns, 2018 was identified from Te Kaitira Seamount at 1899m. This species was only been observed at Te Kaitira Seamount between the depths of 1817-1932m. *Narella aurantiaca* Cairns, 2018 was identified off Nikumaroro at 1112m but also observed at McKean Island and Winslow Reef between 558 and 1105m. This species was also encountered in the Musicians Seamounts and off Wake Island at similar depths (Cairns, 2018). *Narella compressa* Kinoshita 1908, was identified off Carondelet Reef at 497m and is likely the first record since its encounter in 1906 off Japan (S. Cairns, pers. comm.). *N. compressa* was observed and collected within PIPA at Carondelet Reef and Maibua Seamount between 373-583m. One colony of *Thouarella tydemani* Versluys, 1906, a relatively rare species in that genus originally reported from Indonesia at 520m, was only observed 33 times and sampled at Winslow Reef at 801m. The sea fan, *Paracalyptrophora hawaiiensis* Cairns, 2009, was reported from the Phoenix Islands Protected Area between 445-666m. Along with new records from Tokelau (Pao Pao Seamount), American Samoa, and Rawaki Island, this suggests *P. hawaiiensis* has a wider distribution throughout the southwest Pacific and north to Hawaii at upper bathyal depths (Cairns, 2018). *Calyptrophora clarki* Bayer, 1951 was observed 48 times and sampled 3 times between 418-1211m in PIPA. Originally described from Hawaii, it has since been found in the Northern Mariana Islands and Phoenix Islands, representing a significant southward range extension. In the same genus, *Calyptrophora diaphana* Cairns, 2012 initially described off the North Island of New Zealand in 2012 was collected at a recorded depth of 1225m at Orona Atoll but also was recently found around Wake Island in the western Pacific (Cairns, 2018). Only 4 colonies of *C. diaphana* were observed in total, all occurring at Orona Atoll.

Despite efforts to identify many deep-water coral species from physical specimens in PIPA, a significant number morphospecies as well as voucher collections from the 2017 expeditions remain unidentified to the species level. From the 167 morphospecies identified, only 39 species were identifiable to the species level from voucher collections. Nevertheless, some similarities were seen among morphotypes observed in imagery to those encountered elsewhere in the region as a part of the CAPSTONE expeditions (Kennedy et al., 2019). In this study, the abundant *Pleurogorgia* sp. 1 strongly resembles *Pleurogorgia militaris*, a widely distributed Pacific deep-water coral, but cannot yet be confirmed because specimens were not taken of this morphotype within PIPA. In addition, 8 morphospecies were identified as distinct in both the precious coral genus *Hemicorallium* as well as the genus *Victorgorgia* with none being identified to species yet. A significant number of collections were also made in the enigmatic octocoral families Plexauridae and Isididae but detailed morphological taxonomic keys for these families in the central and south Pacific are incomplete and require further attention. Recent efforts to revise the taxonomy of families and genera within the Octocorallia have provided significant contributions to our knowledge of deep-water coral diversity in the Pacific Ocean (Cairns, 2018; Moore et al., 2017; Tu et al., 2016). It is likely that as these specimens are more widely scrutinized using both molecular and morphological taxonomic tools, more species identifications can be determined.

3.5.3 Conservation considerations

The Phoenix Islands Protected Area was designated as an ecologically and biologically significant area (EBSA) by the Convention on Biological Diversity (See https://www.cbd.int/ebsa/) and, upon further examination, it is becoming increasingly clear that its biological significance extends well into the deep-sea. Still, deep-sea biodiversity on remote features is still threatened by several factors including the effects of climate-driven ocean change (Sweetman et al., 2017; Tittensor et al., 2010) as well as physical disturbance from fishing gear (Clark et al., 2016; Clark and Koslow, 2007), and marine debris. Since PIPA has been closed to most fishing since 2015, with the exception of a small subsistence fishery around Kanton, it has been largely isolated from these negative impacts (Rotjan et al., 2014). Still, seamounts in the western and central Pacific have been found to be aggregators for commercially-important large pelagic fishes (Morato et al., 2011). Debris from derelict longline fishing gear, which remain prevalent in the region (McDermott et al., 2018), have the potential to have far-reaching effects deep-water benthic communities.

Other more significant risks to deep-sea coral conservation in the region include direct disturbance to the seafloor in the form of deep-sea mineral crust mining. Recently, commercial mining of ferromanganese crusts accumulating on seamounts have been proposed as a way to extract mineral resources (Hein et al., 2013; Miller et al., 2018). Detailed biological characterizations and species inventories for much of the adjacent Pacific Prime Crust Zone and south Pacific seamounts with cobalt-rich mineral crusts are critically lacking (Schlacher et al., 2014). As crust attributes are difficult to estimate from

ROV video transects, it remains a question where deep-water coral communities lie with respect to areas that harbor economically viable mineral crusts in the Phoenix Islands, but crust habitats in the South Pacific have been found to be important indicators of sensitive deep-sea communities (Delavenne et al., 2019). The precautionary approach should be applied to these resources to conserve seamount benthic communities for their biodiversity, unique evolutionary histories, and ecosystem services.

CHAPTER 4

THE INFLUENCE OF THE OXYGEN MINIMUM ZONE ON DEEP-SEA CORAL SPECIES DISTRIBUTION, DIVERSITY, AND COMMUNITY STRUCTURE ON PACIFIC COSTA RICA SEAMOUNTS

4.1 Abstract

Oxygen minimum zones (OMZs) are among the most significant abiotic environmental gradients found in the deep ocean. Yet, fine-scale species distribution patterns of organisms inhabiting OMZs are still spatially limited, hindering our understanding of how these oceanographic features influence species diversity and community structure. Deep-water corals are ecologically important habitat-forming species that are often considered to be sensitive to low seawater dissolved oxygen concentration and thus likely to be useful indicators for exploring change in megafaunal abundance and biodiversity across the OMZ. In the eastern tropical Pacific Ocean, the widespread oxygen minimum zone encompasses several thousand square kilometers of area and spans several hundred meters of the water column but is typically strongest between 300-700 m depth. A January 2019 cruise aboard the R/V *Falkor* using the ROV *SuBastian*, conducted video transects on 7 seamounts off Costa Rica and on the north side of Isla del Coco. In this study, we analyzed survey data for patterns in deep-water coral species distribution, diversity, and coral community structure relative to abiotic oceanographic variables in order to gain biogeographic insights to this area. Across all sites, we identified 3675 coral occurrences and 75 unique morphospecies between 177-

1565 m. Rapid species turnover with increasing depth occurred primarily across the upper (300 m) and lower OMZ boundaries (700 m). Coral communities within the OMZ depths were observed to contain distinct assemblages of species compared to those below at deeper bathyal depths. Stylasterid hydrocorals were disproportionally abundant above and within the OMZ, while octocoral and black coral species dominated in the more well-oxygenated waters below. Coral assemblage diversity and abundance was depressed within the OMZ and bathyal diversity peaked at intermediate water depths between 1200-1500 m. In addition to assessing the impact of OMZs on coral communities, these results provide unique insights to the abundance, diversity, and environmental drivers of deep-water coral community assembly in a data-deficient locality, thus improving biodiversity metrics leading to better data to inform marine conservation efforts off Costa Rica. These baseline data are particularly salient in the light of projected expansion and shoaling of tropical eastern Pacific oxygen minimum zones as a result of decreasing ocean oxygen concentrations driven by ocean warming and other climate variables.

4.2 Introduction

Oxygen minimum zones (OMZs) are geographically widespread water column strata where dissolved oxygen concentrations decline to hypoxic or anoxic levels (herein defined as dissolved oxygen concentrations < 22 µmol/L as described by Levin, 2003) resulting in significant effects on deep-sea biota (Levin, Huggett & Wishner, 1991; Levin, 2003; Stramma et al., 2010b; Guilini, Levin & Vanreusel, 2012; Neira et al., 2018). In the eastern tropical Pacific, the OMZ is widespread offshore and along the margins of North, Central, and South America (Levin, 2003). Regional variations in the intensity and thickness of the OMZ may result from differences in oceanographic currents, productivity, and aerobic respiration by marine organisms in the water column (Karstensen, Stramma & Visbeck, 2008). Specific to the tropical eastern Pacific off Costa Rica, reduced deep-water ventilation in the area of the Costa Rica Dome results in a relatively thick, widespread, and persistent layer of low oxygen between 300-900 m (Karstensen, Stramma & Visbeck, 2008). Environmental heterogeneity resulting from oxygen gradients in the OMZ have been identified as enhancing regional biodiversity in the deep ocean as well as a source of endemic species (Gooday et al., 2010). Persistent OMZs are likely to be important boundaries to species distribution and are hypothesized to be barriers to gene flow within populations of deep-water organisms (Rogers, 2000; Gooday et al., 2010). Looking into the future, the negative effects of OMZ expansion due to climate change drivers are expected to be strongest within tropical and low-latitude environments (Stramma et al., 2010b; Schmidtko, Stramma & Visbeck, 2017; Sweetman et al., 2017).

Global modelling and experimental efforts have indicated that many benthic megafaunal groups, and particularly cold-water corals, are highly sensitive to seawater dissolved oxygen concentration (Dodds et al., 2007; Tittensor et al., 2009; Fink et al., 2012; Lunden et al., 2014). For stony corals (Scleractinia) specifically, dissolved oxygen concentrations are predicted to exclude most species from seamount OMZs worldwide (Tittensor et al., 2009). Nevertheless, some examples, like the cosmopolitan reef-building coral *Lophelia pertusa* have been recently found persisting under hypoxic conditions along the Angola margin in the South Atlantic (Hebbeln et al., 2020). Other macrofaunal and megafaunal groups, like benthic foraminifera (Xenophyophores), sponges, and bryozoans (Hanz et al., 2019), are also more likely to be tolerant of dysoxic or hypoxic conditions (Gooday et al., 2010). In these cases, environmental drivers, like tidal mixing, internal waves, and enhanced surface-derived food supply, may ameliorate the negative impacts of living at low oxygen concentrations (Hanz et al., 2019; Puerta et al., 2020).

4.2.1 Seamount oxygen minimum zones

Seamounts are large, high-profile (extending > 2000 m above the surrounding abyssal plain) seafloor features that are widely known to contain unique habitat mosaics and diverse biological communities (Rogers, 2018). Compared to the more widely-studied continental margins (Levin et al., 2000, 2002; Helly & Levin, 2004; Jeffreys et al., 2012; Neira et al., 2018; Hanz et al., 2019), the effect of OMZs impinging on both pelagic and benthic environments of seamounts are limited to a few case studies, as estimates place the area of OMZs impacting seamounts at < 1% of the total area of OMZs worldwide (Helly & Levin, 2004). At one relatively well-studied seamount in the eastern North Pacific Ocean off Mexico, Volcano 7 (Wishner et al., 1990, 1995; Saltzman & Wishner, 1997a), the effect of the oxygen minimum zone has resulted in significant zonation effects on both pelagic and benthic communities (Levin, Huggett & Wishner, 1991; Levin, 2002). Macro- and megabenthic organisms were largely absent from the seamount summit (730-750 m) where oxygen concentrations were lowest (0.08-0.09 ml/l), followed by a rapid increase in abundance with increasing depth across trophic levels from fishes to corals and sponges. (Wishner et al., 1990). Further south, in the

Pacific off central Chile, deep-water coral communities identified by trawl bycatch on one seamount summit were identified as being both dense and diverse, composed of black coral and soft coral species in the comparatively well-oxygenated intermediate waters underlying the OMZ (Cañete & Haussermann, 2012).

In the pelagic environment above and near seamounts, mid-water planktonic species abundances and diversity are also strongly influenced by OMZs (Saltzman & Wishner, 1997a). For example, the zooplanktonic species, like the copepod *Rhincalanus nasutus*, have been observed above and below but absent within OMZs in the vicinity of Volcano 7 in the eastern Pacific (Saltzman & Wishner, 1997b). The role that OMZs have in structuring deep-water zooplanktonic communities is important both as a driver of species diversity and abundance (Wishner et al., 2018; Wishner, Seibel & Outram, 2020), but also potentially as a driver of change in food supply for deep-water suspension-feeding organisms, including corals (Gage & Tyler, 1992).

4.2.2 Deep-sea biodiversity conservation in Costa Rica

In the eastern Pacific, cold-water corals are important sources of biodiversity in the deep ocean. Structures formed by coral colonies have been found to provide habitats for invertebrate (Cairns, 1991, 2007, 2018a) and fish fauna alike (Auster et al., 2016). Cocos Island (Spanish: *Isla del Coco*), a national marine park and UNESCO World Heritage Site (Claudino-Sales, 2019), is already known as an important pool of shallow-water marine biodiversity (Cortés, 2012). Recent deep-sea coral species discoveries have given new motivation to understanding benthic biodiversity within Costa Rican waters

(Opresko & Breedy, 2010; Breedy, van Ofwegen & Vargas, 2012; Cortés, 2012; Breedy et al., 2019). Furthermore, mesophotic and shallow-water seamounts, like Las Gemelas, are suspected to host deep-water fish and invertebrate species that remain undescribed as well as communities that are uncharacterized (Breedy & Cortes, 2008; Starr et al., 2012; Starr, Green & Sala, 2012).While several protected areas exist off the continental margin of Costa Rica (Alvarado et al., 2012) as well as around Isla del Coco (Cortés, 2012; Arias et al., 2016), many of the Pacific Costa Rica seamounts remain external to protected boundaries. Further exploration of these seamounts and characterization of benthic communities and substrate types will aid in better informing conservation strategies for these deep-sea environments.

The presence of well-developed oxygen minimum zones can also be related to the deposition of commercially valuable metal-rich mineral crusts on seamounts (Halbach & Puteanus, 1984; Halbach et al., 1989). Low oxygen concentrations in the water column may enhance precipitation of mineral crusts onto the seafloor, which typically occurs on the order of 1-5 mm per million years (Halbach et al., 1989; Hein et al., 2013). Seamounts and other submarine features along the Cocos Ridge have been highlighted as potential areas containing Co-rich mineral crusts (Miller et al., 2018). With growing trends towards exploration and exploitation of deep-sea mineral resources (Miller et al., 2018), it is important to understand the abundance and diversity of species inhabiting these depths in order to better manage these activities (Niner et al., 2018).

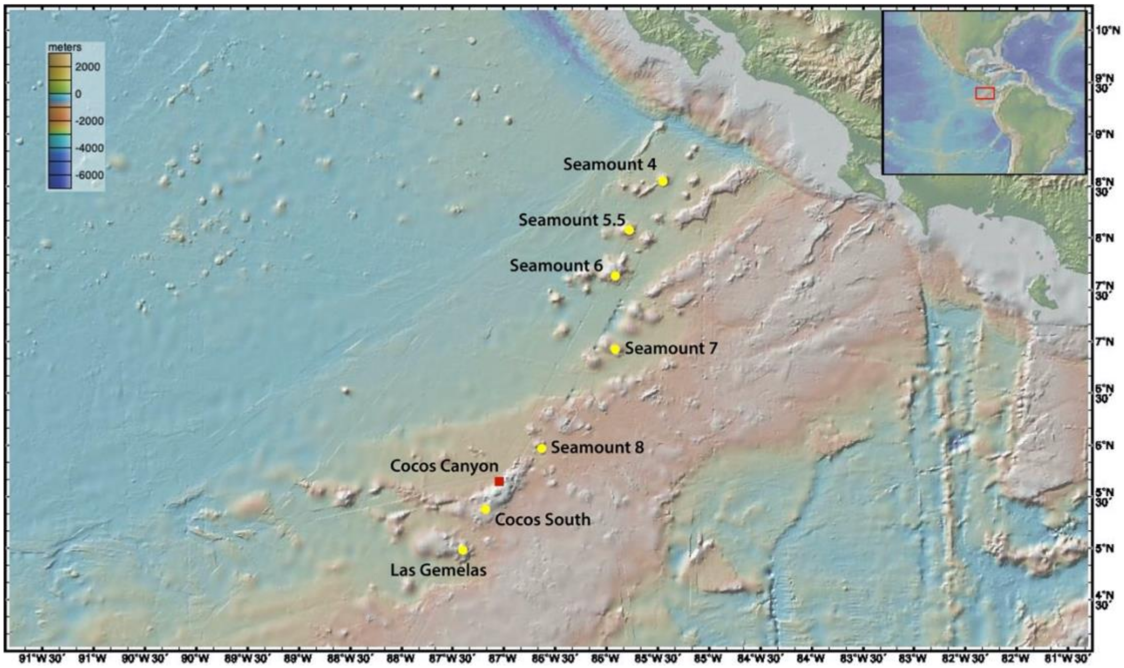


Figure 4.1 Overview of the study area with locations of the Cocos Ridge Seamounts and Cocos Island. Yellow circles represent seamount sites and red squares represent canyons surrounding Cocos Island. Gridded bathymetry is GMRT v3.7 (Ryan et al., 2009) obtained through GeoMapApp v3.6.10.

4.2.3 Objectives and hypotheses

In this study, we aim to characterize the distribution, diversity, and community structure of deep-water corals along abiotic gradients off the Pacific Costa Rica margin and in the vicinity of Isla del Coco. The effect of a strong, persistent OMZ in this area is likely to result in significant zonation patterns in coral communities across the bathyal depth range. Specifically, we aim to test the hypothesis that deep-sea coral assemblages within the OMZ are distinct from those in the above and below-lying waters. Additionally, as water mass boundaries are also important drivers of change in coral communities across depth, we will test for differences in coral community structure between eastern Pacific water masses. As deep-sea communities are expected to be subject to significant changes resulting from global climate drivers (Brito-Morales et al., 2020), establishing baseline datasets for understanding how benthic communities might respond to OMZ expansion and intensification (Stramma et al., 2010b) is a critical step to effective conservation.

4.3 Materials & Methods

4.3.1 Study area and ROV surveys

Surveys were conducted in January 2019 on the R/V *Falkor* using the ROV *SuBastian* on Pacific Costa Rica seamounts as well as off Isla del Coco proper (Fig. 4.1). In total, 8 sites were surveyed, 7 seamounts (including Las Gemelas) and one “canyon” site, Cocos Canyon, off Isla del Coco. Transects spanned a total depth range of 179-1614 m (Table 4.1). A total of 80 hours of seafloor video were assessed among all the locations encompassing 10.5 linear km seafloor. All surveys were conducted upslope along each feature, perpendicular to the bathymetric contours, typically at an over-ground velocity of 0.25-0.5 kt (0.1-0.25 m/s), stopping only for sampling events or brief detailed imagery. Onboard conductivity, temperature, and depth sensors (SeaBird FastCAT SBE49 CTD) and oxygen optode (Aandera O2 optode 4831) logged continuously in UTC time along the length of each dive profile. Seafloor position was logged using an ultrashort baseline (USBL) navigation sensor (Sonardyne WMT 6G).

Table 4.1 Summary statistics for dives conducted during FK190106 on Pacific Costa Rica seamounts and near Isla del Coco.

Dive	Site	Start Latitude (Deg.)	Start Longitude (Deg.)	End Latitude (Deg.)	End Longitude (Deg.)	Bottom Time (hh:mm)	Depth Range (m)	Linear Distance (m)
S0221	Seamount 5.5	8.04954	-85.75857	8.05072	-85.77417	10:19	777-1614	1721
S0222	Seamount 7	6.93338	-85.88089	6.91501	-85.88507	10:20	866-1265	2092
S0223	Cocos Canyon	5.58535	-87.06810	5.58114	-87.06264	10:28	546-976	764
S0224	Coco South	5.46551	-87.13686	5.46622	-87.12633	10:44	179-593	1167
S0225	Las Gemelas	4.97850	-87.45997	4.98710	-87.44329	10:45	243-670	2079
S0226	Seamount 8	5.99908	-86.64332	6.00781	-86.64915	7:35	1302-1451	1164
S0227	Seamount 6	7.67786	-85.90642	7.68012	-85.91151	9:52	525-662	614
S0228	Seamount 4	8.54279	-85.43900	8.55068	-85.43904	10:09	888-1260	878

4.3.2 Video analyses

Video was annotated from on bottom to off bottom times for coral occurrences along the length of each dive where the vehicle was in visual contact with the seafloor (< 2 m altitude above the seafloor, except during vertically sloped segments). Periods of time where the vehicle was not moving forward at a constant velocity or not in visual contact with the seafloor were not assessed. Corals occurrences were tagged with a UTC timestamp and identified to the finest taxonomic level possible based on imagery and associated specimen collections. For the purposes of this study, coral taxa refer to deep-water species in the Antipatharia (black corals), Scleractinia (stony corals), Octocorallia (sea fans and other soft corals), and Stylasteridae (lace corals). All corals were typically identifiable to a morphospecies above a roughly 5 cm size threshold gauged by on-screen scaling lasers, where visible. Additional taxonomic literature and taxonomist expertise were consulted for specimen collection identification. Where a species name could not be readily assigned, corals were given a unique morphospecies identifier based on the corresponding collected sample (e.g. Plexauridae sp. S0227-Q9) or another distinguishing identifier. Consistent morphospecies identifications were carried across all dives.

4.3.3 Coral community analyses

In order to evaluate changes in community assembly, all dive transects were binned into segments of 100 m depth samples. Each bin contained only consistent morphospecies observations thereby excluding those observations where a morphospecies could not be identified (e.g. Scleractinia spp.). Each sample reflected both the morphospecies abundance as well as diversity. For analysis, all samples were standardized by the total abundance and 4th root transformed to down-weight the influence of extremely abundant taxa. Environmental variables for each sample were calculated as the average of depth, temperature, salinity, and dissolved oxygen. Variables were normalized to the mean in order to reduce the effect of differences in unit scales among them.

Sampling effectiveness was evaluated among sites and across depths by sample-based species accumulation and individual-based rarefaction analyses using the R package Vegan 2.5-6 (Oksanen et al., 2015). Patterns of deep-water coral abundance and diversity across depth were evaluated for each sample using several diversity indices. To evaluate change in species richness we calculated exact species richness (S) and rarefied species richness, Es(100), at 100 individuals (Sanders, 1968; Hurlbert, 1971). Diversity patterns were evaluated using two commonly used indices, Shannon diversity (H’ $\log_e$), a metric sensitive to species diversity, and Pielou’s evenness index (J’), a metric of species equitability.

Multivariate community analyses were performed in PRIMER7 with PERMANOVA add-on (Anderson, Gorley & Clarke, 2008). Samples were initially compared in a Bray-Curtis similarity resemblance matrix. One-way analysis of similarity (ANOSIM) tests were used to assess for differences in *a priori* groupings related to the OMZ (above, within, or below the OMZ) and overlying water masses (Table 4.2). In order to evaluate relationships between *a priori* groupings, both CLUSTER with non-metric multidimensional scaling (nMDS) analyses were employed. Similarity profile (SIMPROF) analysis was used to evaluate the significance level of clusters (Clarke, Somerfield & Gorley, 2008). Bootstrap pseudo-replicates and averages for groups above, below, and within the OMZ were also calculated using nMDS ordination for further investigation of differences among sample means (Clarke & Gorley, 2015). Similarity percentage (SIMPER) analysis was used to identify patterns of dissimilarity among factors as well as indicating the relative importance of species abundances to community assembly. Principal coordinates analysis (PCO) was also conducted to further assess relationships among coral assemblages, in addition to identifying coral species that are highly correlated with groups of samples.

For establishing relationships between patterns in environmental variability and community structure, the BEST (BIO-ENV) routine was used to identify the strength of correlations between any single one or groups of environmental variables and coral assemblage variation (Clarke, Somerfield & Gorley, 2008). In order to model the role of environmental variables in structuring deep-sea coral communities, a distance-based linear model (DistLM) was constructed using biological and environmental data (i.e. depth, temperature, salinity, and dissolved oxygen) and evaluated with a distance-based redundancy analysis (dbRDA) (Anderson, Gorley & Clarke, 2008). An Akaike Information Criterion (AIC) was utilized to evaluate model selections (Akaike, 1998).

4.4 Results

4.4.1 Identification of the OMZ and local water masses

The oxygen minimum zone was defined as depths of the water column where the dissolved oxygen concentration was less than 22 µmol/L (Levin, 2003). Using this parameter, the core of the OMZ was identified between 300-700m (Fig. 4.2). The lowest seafloor oxygen values were measured with the *SuBastian* CTD and oxygen optode at both Isla del Coco and Las Gemelas around 450-500 m. The core depth of the OMZ was found to be slightly thicker and deeper at ship-based CTD rosette casts closer to the Costa Rica Margin and decreased with distance offshore (Las Gemelas, 300-700 m) (Fig. 4.2). In some instances, dissolved oxygen values observed on the seafloor *in situ* with the ROV CTD unit (as low as 0 µmol/L) were lower than those observed with the downcast CTD profiles (Fig. 4.2), which were all conducted in deeper waters off of the seamounts.

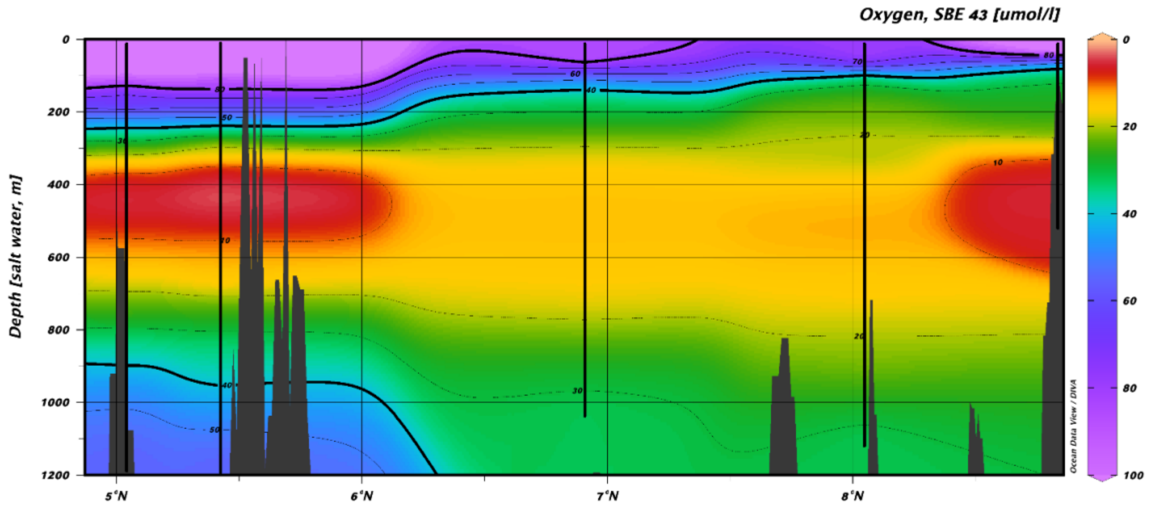
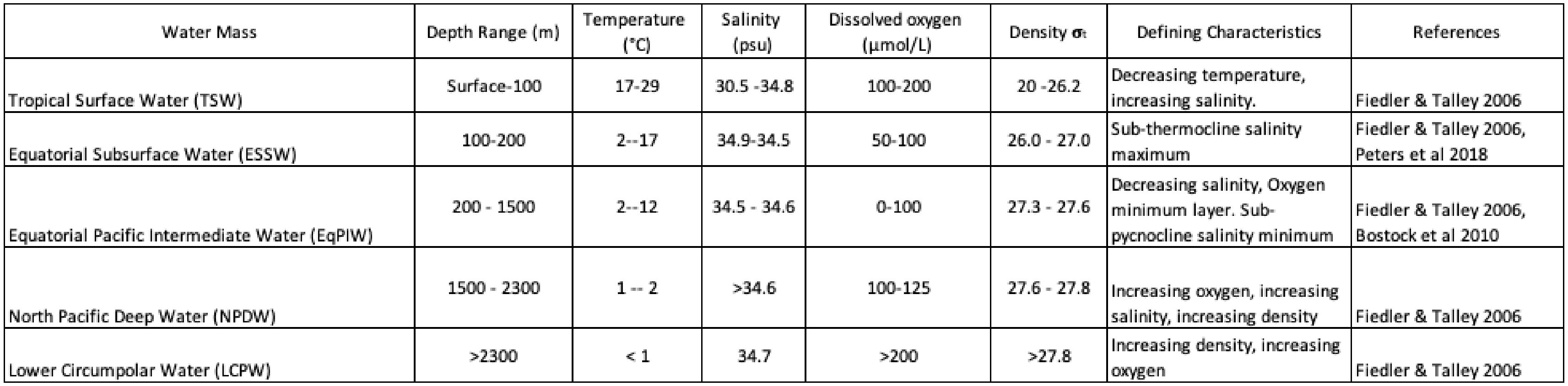


Figure 4.2 Oxygen profiles along the Cocos Ridge section from the continental margin (far right) to Las Gemelas (far left) between 0-1200 m. Color ramp on the right indicates measured values of dissolved oxygen (µmol/l) with cooler colors indicating more oxygen rich waters. Downcast CTD cast locations are represented by bold vertical lines. Bathymetry (GEBCO 2014 2x2 min resolution) is presented as dark grey polygons. Plot was constructed using Data-Interpolating Variational Analysis (DIVA) gridding in Ocean Data View v 5.2 (Schlitzer, 2019).

Water masses were characterized for the study area of the equatorial eastern Pacific from oceanographic literature that utilized both standard methods (e.g. potential temperature and salinity) as well as geochemical tracers (Fiedler & Talley, 2006; Bostock, Opdyke & Williams, 2010; Peters et al., 2018). Shipboard CTD downcasts indicated the presence of three water masses between 179-1614 m (Table 4.2). The shallowest, Equatorial Subsurface Water (ESSW) (sometimes referred to as 13°C Water (Evans et al., 2020)), was characterized by a sub-thermocline salinity maximum and rapidly decreasing oxygen concentration between 100 to 200 m. Underlying this was the largest water mass by thickness, Equatorial Pacific Intermediate Water (EqPIW), between the depths of 200-1500 m, which also contained the OMZ. Equatorial Pacific Intermediate Water in the eastern tropical Pacific can be differentiated into North and South EqPIW by dissolved oxygen concentration where North EqPIW is oxygen-poor compared to South EqPIW (Bostock, Opdyke & Williams, 2010). The deepest, North Pacific Deep Water (NPDW), occurred between 1500-2300 m and was defined by increasing dissolved oxygen concentration and salinity with increasing depth. It was also indicated that Lower Circumpolar Water (LCPW) underlies NPDW (Fiedler & Talley, 2006), but CTD casts for depths >2300 m were not conducted for the 8 sites in this study (Fig. 4.2).

Table 4.2 Water masses and associated environmental variables in the region of the Cocos Ridge and Isla del Coco at bathyal depths.



Water Mass	Depth Range (m)	Temperature (°C)	Salinity (psu)	Dissolved oxygen (µmol/L)	Density σ_t	Defining Characteristics	References
Tropical Surface Water (TSW)	Surface-100	17-29	30.5 -34.8	100-200	20 -26.2	Decreasing temperature, increasing salinity.	Fiedler & Talley 2006
Equatorial Subsurface Water (ESSW)	100-200	2--17	34.9-34.5	50-100	26.0 - 27.0	Sub-thermocline salinity maximum	Fiedler & Talley 2006, Peters et al 2018
Equatorial Pacific Intermediate Water (EqPIW)	200 - 1500	2--12	34.5 - 34.6	0-100	27.3 - 27.6	Decreasing salinity, Oxygen minimum layer. Sub-pycnocline salinity minimum	Fiedler & Talley 2006, Bostock et al 2010
North Pacific Deep Water (NPDW)	1500 - 2300	1 -- 2	>34.6	100-125	27.6 - 27.8	Increasing oxygen, increasing salinity, increasing density	Fiedler & Talley 2006
Lower Circumpolar Water (LCPW)	>2300	< 1	34.7	>200	>27.8	Increasing density, increasing oxygen	Fiedler & Talley 2006

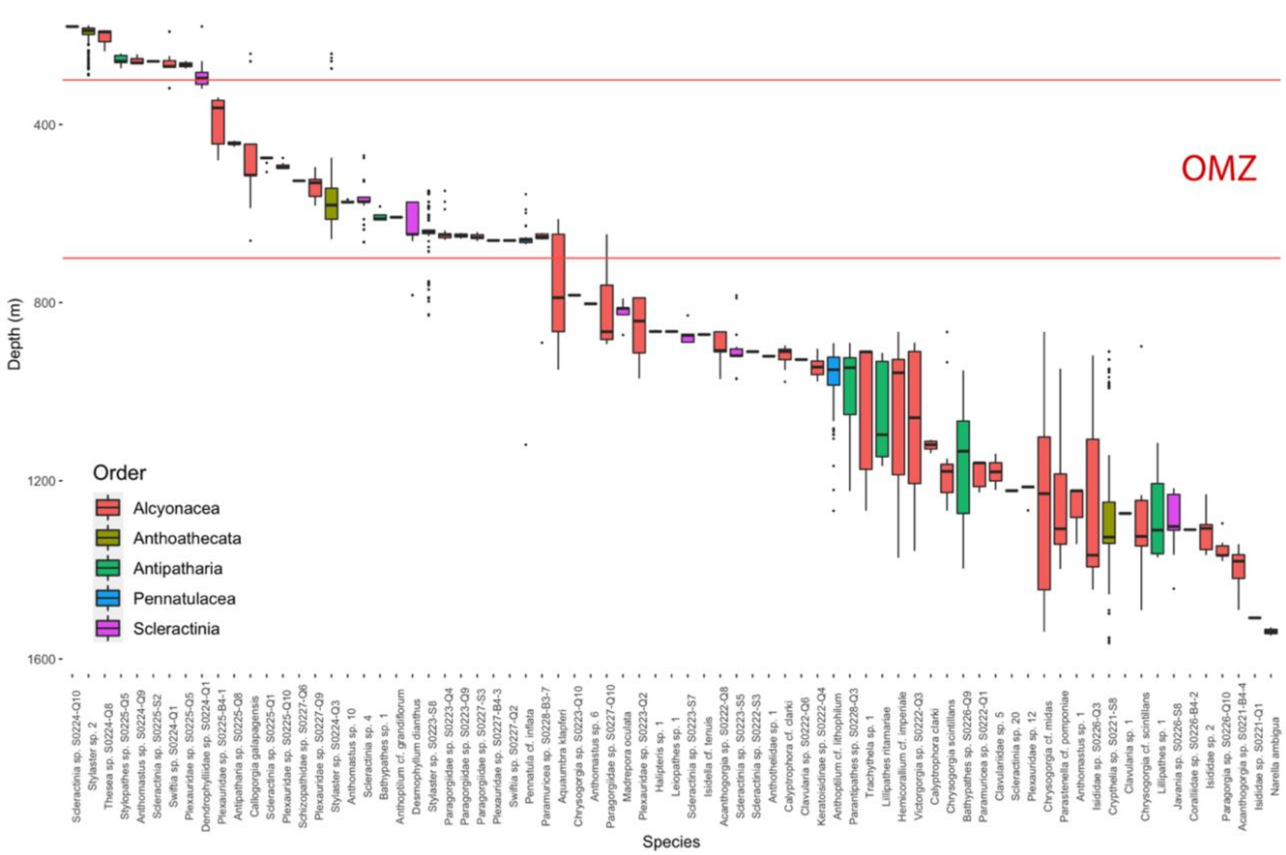


Figure 4.3 Boxplot of species distribution across depth. Species are arranged left to right by increasing median depth of distribution. Boxes are colored by taxonomic order for each species. OMZ depths (300-700 m) are indicated by solid red lines and bold red text.

4.4.2 Video survey summary

In all, 3675 coral occurrences were recorded between 177 – 1565 m depth across all 8 sites. Of these occurrences, 3386 observations were assigned to 75 identifiable coral morphospecies. (Fig. 4.3). The remaining 289 observations were assigned to coarser taxonomic groupings based on the observable traits in video imagery. Of the 75 morphospecies identified, 23% (17 species) were identified as a currently described species based on morphological examination of the associated collection(s) and taxonomic expert consultation.

Across all depths, the Alcyonacea dominated deep-sea coral assemblages by abundance (39%) as well as species richness (46 spp.). Together with pennatulaceans, the Octocorallia (50 species in total) comprised 55% of all corals observed. Stylasterid hydrocorals followed with 1185 records across 4 species, all within the genera *Stylaster* or *Crypthelia*. In nearly all cases, representatives of each order were observed across the full range of depths explored (177-1565 m) (Fig. 4.3). Scleractinians (294 records, 12 spp.) and Antipatharians (101 records, 9 spp.) were present from 179- 1508 m but these groups were not as abundant as the Octocorallia and Stylasteridae. Among the Scleractinia, solitary species (cup corals) were more abundant and occurred across a greater depth range than colonial species. As some smaller taxa like stylasterids and solitary cup corals often have few distinguishing characteristics to always place them into consistent morphospecies, it should be noted that these abundances represent a minimum value and the likelihood of identifying more individuals and more species increases with additional survey and collection effort.

4.4.3 Species accumulation and rarefaction analyses

Species accumulation analyses suggest incomplete species inventories at nearly all sites, with the exception of Seamount 5.5 (Fig. 4.4A). As the site with the largest depth range surveyed, species richness at Seamount 5.5 was found to approach asymptotic values (~ 12 species) suggesting a relatively well-sampled community (Fig. 4.4A). The remaining sites continued to accumulate species at similar rates. Seamount 7 was found to have more rapid species accumulation at lower levels of sampling effort, indicating high species richness at that particular site (Fig. 4.4A). Individual-based rarefaction analyses indicated the highest species richness at depths below the oxygen minimum zone (Fig. 4.4B). The OMZ layer was found to have roughly half the number of coral species as that lying immediately under (> 700 m). The shallowest layer immediately above the OMZ was the narrowest layer by depth (100-300 m) and coincided with the fewest number of coral species and half of the number of individual corals as the two lower depth strata (Fig. 4.4B).

4.4.4 Patterns in coral abundance and diversity

Across the entire depth range surveyed, the highest coral abundances were observed within the shallowest depth bin, 100-200 m (Fig. 4.5A). Within the oxygen minimum zone, mean abundances were lowest at the upper boundary (300-400 m) and peaked along the lower boundary (600-700 m) (Fig. 4.5A). Mean abundance was generally low (< 30 indiv.) at lower bathyal depths except within the 900-1000 m and

1300-1400 m ranges which were slightly higher. A localized regression model of coral abundances indicated two distinct peaks in abundance, one at the shallowest depth bin and one at the lower boundary of the OMZ (Fig. 4.5B).

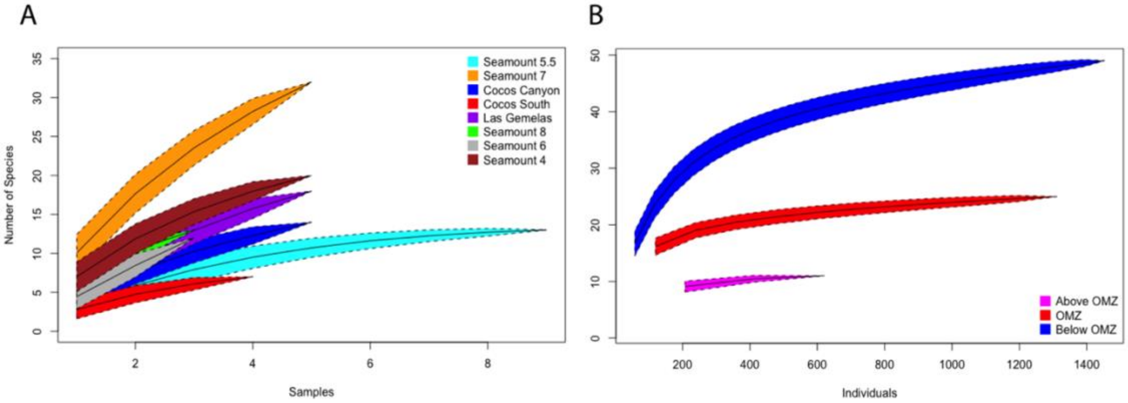


Figure 4.4 Species accumulation and rarefaction analyses. Permuted (1000 permutations) species accumulation (Coleman et al., 1982) curves are assessed between sites (A). Sample-based rarefaction curves (B) are indicated for each layer of the water column corresponding to depths above (100-300 m), below (700-1600 m), and within (300-700 m) the oxygen minimum zone. For both plots, confidence intervals (95%) are indicated by polygons around curve bounded by dashed lines.

Mean species richness (S) was observed to decline within the OMZ and then with increasing depth reaching an initial minimum in the upper oxygen minimum zone and increasing to a maximum around 1200 m (Fig. 6A). The patterns in coral species richness were also reflected in both Shannon diversity (H') and ES(100) rarefaction indices (Fig. 4.6B, C). Conversely, mean species evenness (J') was lowest at shallower depths above the OMZ and increased to maxima at depths just below the OMZ lower boundary (700-900 m) and between 1200-1300 m (Fig. 4.6D). As an indicator of beta diversity, changes in species evenness across shallower depths (Fig. 4.6D) is consistent with high rates of species turnover across depths above and within the OMZ (Fig. 4.3). Higher evenness at mid- and lower bathyal depths is indicative of more equitable representation of coral species with increasing depth.

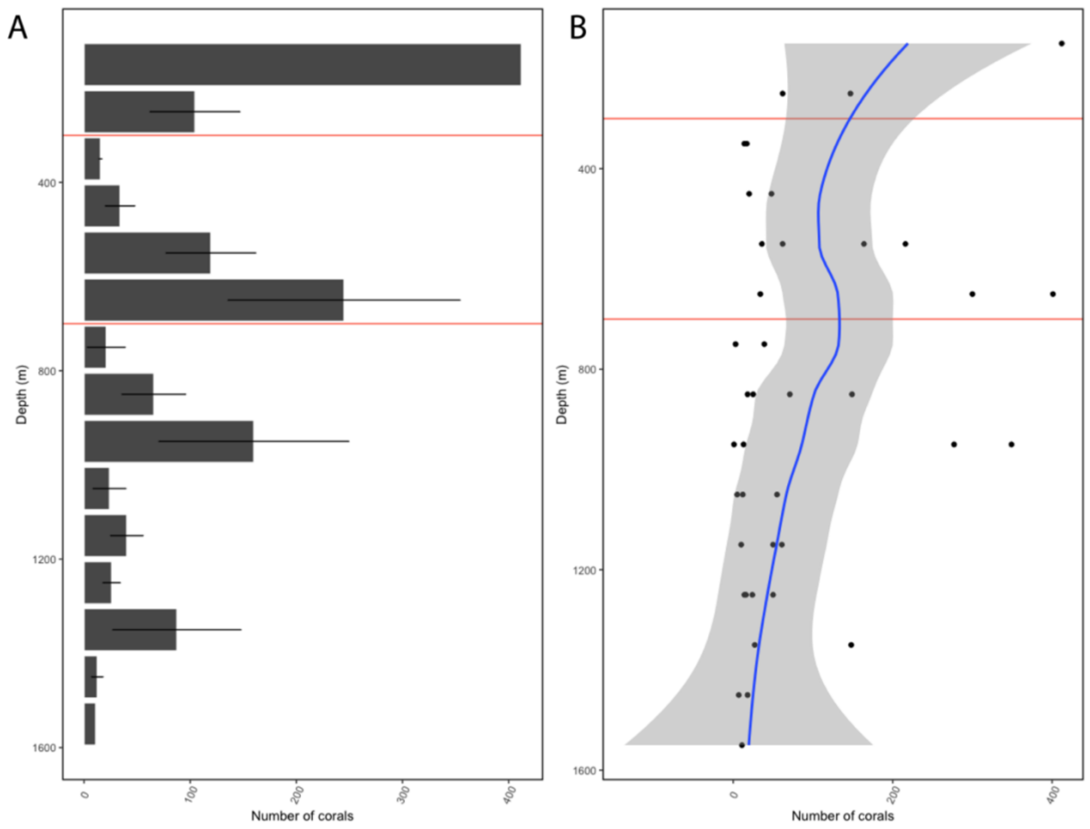


Figure 4.5 Patterns of coral abundance across depth along the Cocos Ridge. The depth of the oxygen minimum zone is plotted as solid red horizontal lines (300-700 m). A. Mean coral abundance (+/- 1 Standard Error) is indicated for each 100 m depth bin from 100-1600 m. B. Scatterplot showing the number of coral records in each sample with a fitted localized regression (loess) model represented by a solid blue line. The shaded region represents the 95% confidence interval for the regression model.

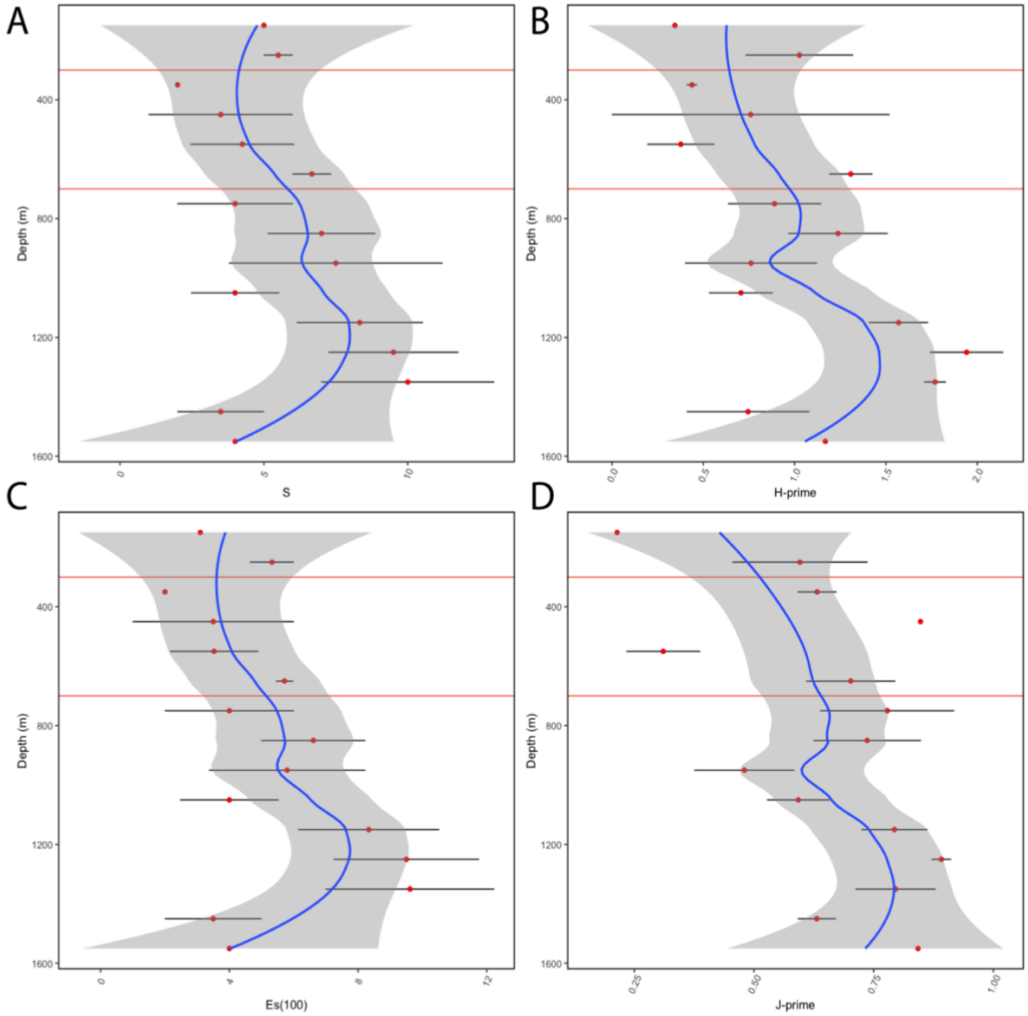


Figure 4.6 Patterns of coral diversity across depth along the Cocos Ridge. Four diversity indices are indicated: A. Species richness, S. B. Shannon Diversity Index (H’ log$_e$) C. Es(100) species rarefaction, and D. Pielou’s Evenness Index (J’). Points represent mean index values (+/- 1 Standard Error) In each panel the depth of the OMZ is indicated by solid red horizontal lines (300-700 m). For each index, a fitted local regression (Loess) model is represented by a solid blue line. The shaded region represents the 95% confidence interval for the regression model.

4.4.5 Patterns in coral community structure

An analysis of similarity test (ANOSIM, Global R=0.578, p=0.001) between depth strata above, below, and within the OMZ indicated significant differences between assemblages within the OMZ and below the OMZ (R-statistic=0.587, p=0.001) as well as between those above and below the OMZ (R-statistic=0.683, p=0.002) (Supplementary Table C1). The same test did not detect differences between the community above and within the OMZ (R=0.144, p=0.132). A one-way ANOSIM test between assemblages factored by water mass (EqSSW, EqPIW, and NPDW) failed to identify significant differences between any pairwise comparisons (Global R=0.152, p=0.16) (Supplementary Table C2).

Permuted SIMPROF tests (999 permutations) of the coral assemblage CLUSTER analysis (Fig. 4.7) identified 6 distinct groupings at or below the 5% significance level (illustrated by ellipses, Fig. 4.8A). Two significant clusters of assemblages were also identified with areas above and within OMZ depths (Fig. 4.7). Deeper assemblages occurring below the OMZ were largely clustered into four distinct significant groupings (Fig. 4.8A). Bootstrap resampling of samples by OMZ factors revealed fairly well constrained distribution of pseudo-replicates around the mean for coral assemblages within and below OMZ, but less so for those above the OMZ (Fig. 4.8B).

Principal coordinates ordination revealed about 33% of the total coral assemblage variation explained by the first two PCO axes (Fig. 4.9). Two distinct clouds of samples were evident, one grouping above and within the OMZ along PCO axis 2, and a second grouping for samples primarily occurring below the OMZ along PCO axis 1. Vector analysis identified 14 species that were most strongly correlated (cutoff R > 0.40) with the sample ordination (Fig. 4.9).

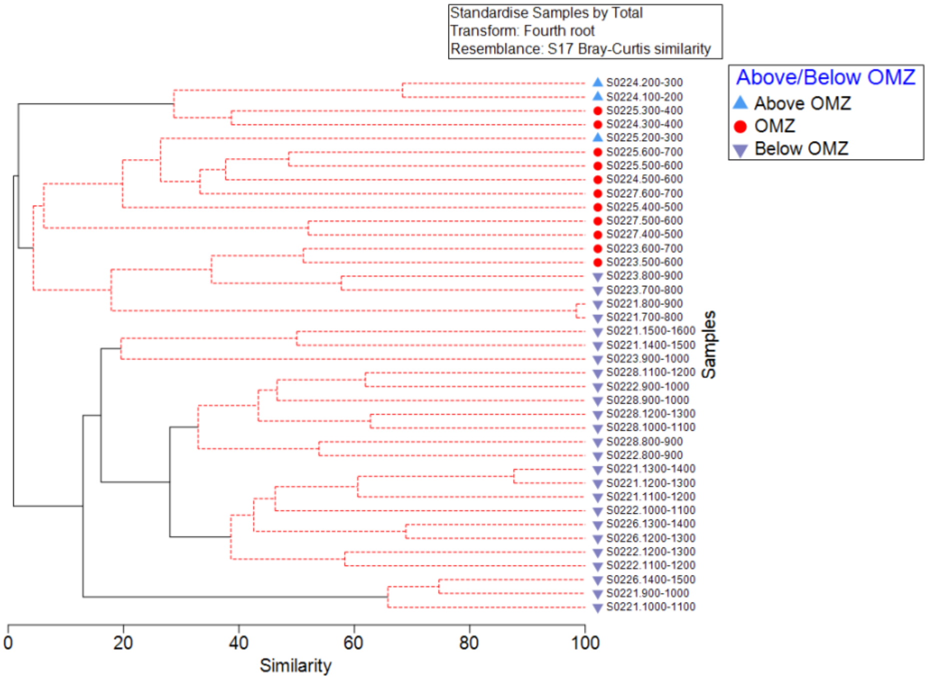


Figure 4.7 CLUSTER analysis performed on 39 coral assemblage samples from sites along the Cocos Ridge. Samples are identified by the dive number and depth range (e.g. S0226.1200-1300) and symbols indicate within, above, or below the depth of the OMZ. Similarity profile analysis (SIMPROF) is indicated by solid black lines for statistically significant clusters ($p < 0.05$) and dashed red for insignificant clusters.

Similarity percentage (SIMPER) analysis revealed within-group assemblage similarity was highest at depths above the OMZ (31.7%). This was followed by assemblages occurring below the OMZ where the average similarity was found to be 19.7%. Within the OMZ, the average similarity between samples was the lowest at 12%

of all three depth strata. As these group similarity values are also indicators of beta diversity, or change in species composition across a gradient, the greatest change in beta diversity occurred across the OMZ (300-700 m). Stylasterid corals were identified as having the highest average abundance and being the most representative taxon of the upper two depth strata, above the OMZ and within the OMZ (Fig. 4.10). Between-group dissimilarity was high (>90-100%) for all pairwise comparisons.

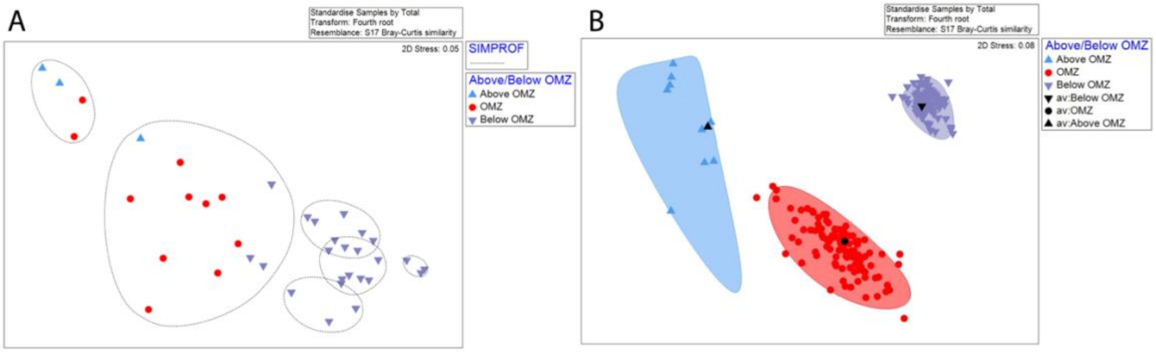


Figure 4.8 Non-metric multidimensional scaling analyses of 100 m depth sampling units. A. Samples are identified by above, below, and within OMZ. Circles represent statistically significant groupings according to the SIMPROF analysis results indicated in Fig. 4.7. B. Bootstrap averages analysis for sample pseudo-replicates and groupings. Groupings were resampled 100 times. Ellipses represent bootstrap regions where 95% of the bootstrap averages fall for each group.

SIMPER analysis also indicated that the shallowest depth layer was characterized by assemblages dominated with stylasterid (*Stylaster* sp. 2), scleractinian (Dendrophylliidae sp. S0224-Q1), and black corals (*Stylopathes* sp. S0225-Q5). The

OMZ was composed of a mixed assemblage dominated by a second *Stylaster* sp. (S0224-Q3) as well as soft coral fans (Paragorgiidae sp. S0223-Q4, Plexauridae sp. S0227-Q9) and one solitary coral species, Scleractinia sp. 4 (Fig. 4.10). At depths below the OMZ, octocorals (*Hemicorallium* cf. *imperiale*, Isididae sp. S0226-Q3, and *Aquaumba klapferi*), followed by black corals (*Bathypathes* sp. S0226-Q9) and one stylasterid, *Crypthelia* sp. S0221-S8, composed at least 70% of the cumulative abundance (Fig. 4.10).

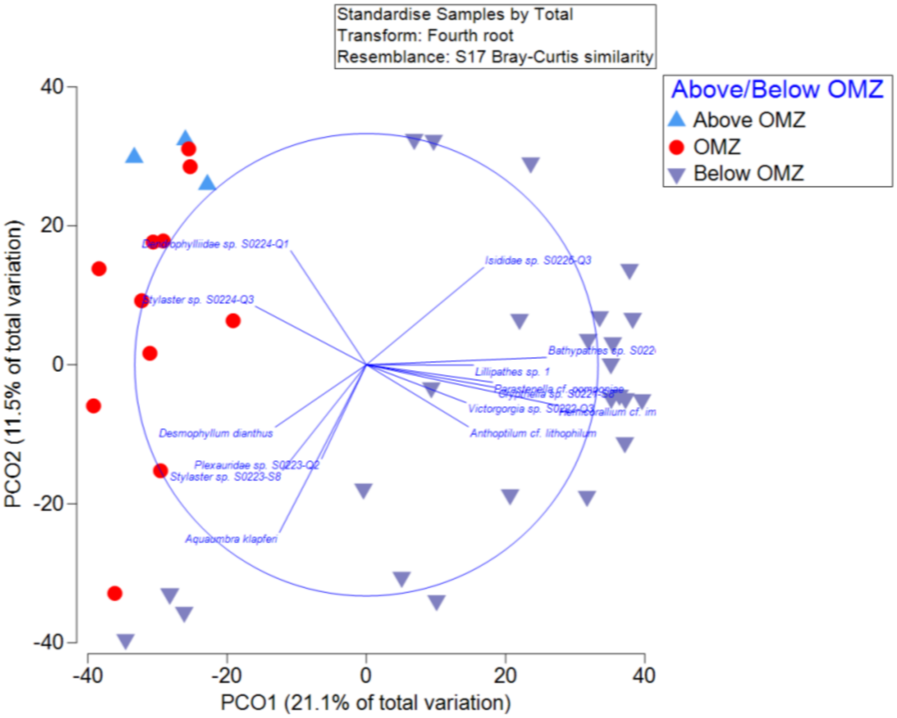


Figure 4.9 Principle coordinates analysis of 39 samples designated as above, below or within the OMZ. A circle with vector lines indicates any correlations (R= >0.40 cutoff) of species with samples in the PCO space.

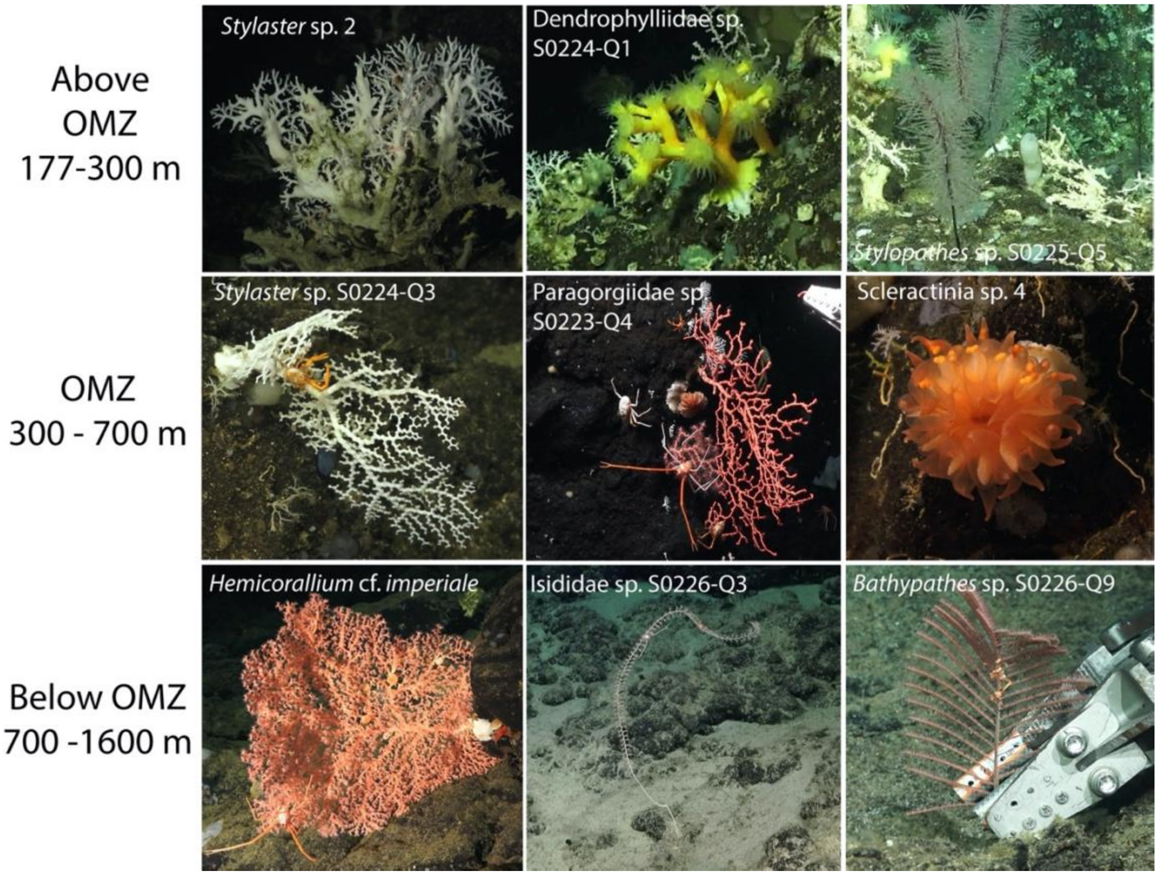


Figure 4.10 Characteristic species observed within, above, and below the depth of the OMZ along the Cocos Ridge seamounts and Cocos Island. The top three species by relative abundance were determined by SIMPER analysis and are arranged left to right in order of decreasing contribution to the total cumulative abundance.

The BEST (BIO-ENV, Spearman rank correlation based on a Euclidean distance resemblance matrix) analysis conducted with depth, temperature, salinity, and dissolved oxygen indicated that temperature alone had the highest correlation (Rho=0.692) with community dissimilarity among any combination of environmental variables. Additional inclusion of variables in any combination resulted in slightly lower predictive capability (e.g. depth, temperature, Rho = 0.670).

Patterns in coral community structure as explained by oceanographic environmental variables were examined in a distance-based linear model and distance-based redundancy analysis using depth, temperature, salinity, and dissolved oxygen variables (Fig. 4.11). The DistLM marginal and sequential tests reported explanatory significance in each of the variables, but in both tests, depth was identified as the strongest explanatory variable (AIC=321.41, p=0.001) Redundancy analyses indicated that the first two dbRDA axes combined explained 79.7% of the model-fitted variation and 26.6% of the total variation in coral communities (Fig. 4.11). Multiple partial correlations revealed that dbRDA axis 1 was most highly correlated with temperature (0.67), while dbRDA axis 2 was strongly correlated with salinity (0.94). Individual vector analysis indicated that salinity and temperature had the largest correlations with the shallowest assemblages (within and above the OMZ) (Fig 4.11). The vectors for dissolved oxygen and depth were most strongly associated with assemblages below the depth of the OMZ (Fig. 4.11).

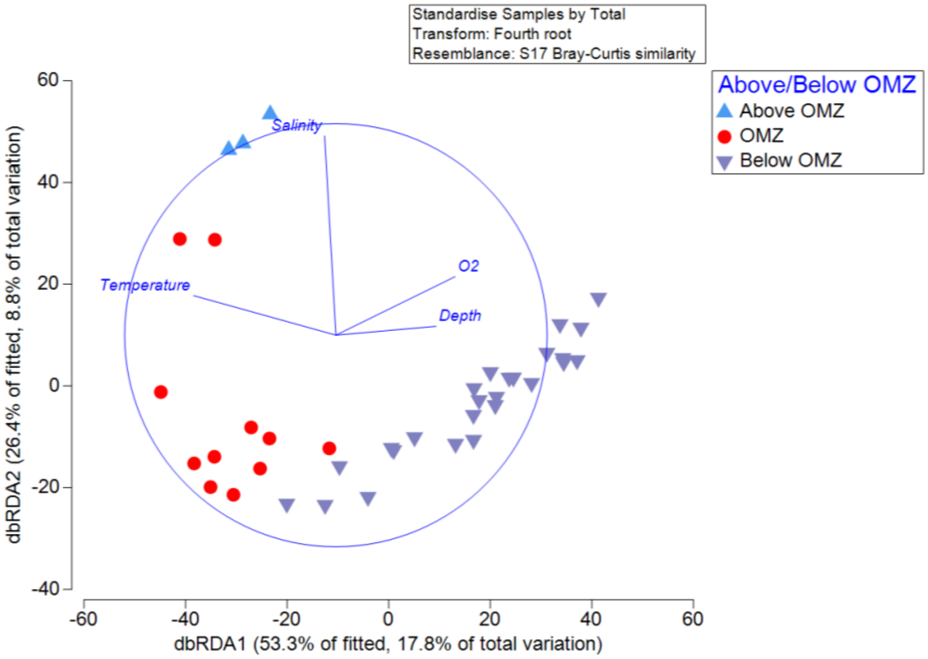


Figure 4.11 Distance-based linear model (distLM) and redundancy analysis (dbRDA) of coral assemblages and oceanographic variables. Points represent one 100 m depth assemblage. Axes titles are the results of a distance-based redundancy analysis with percent variation explained by the best fitted model and total variation. The dbRDA circle vectors identify the degree of correlation of each environmental variable with samples in the distLM space. The length of each vector is indicative of the strength of the correlation with the circle perimeter denoting a correlation of R=1.

4.5 Discussion

In this study we sought to characterize the distribution, diversity, and community structure of deep-water corals across environmental gradients off Pacific Costa Rica. More broadly, the results of this work provide critical baseline knowledge of deep-water coral species and the communities they compose in the eastern tropical Pacific. In all, 3386 observations of corals were identified among 75 morphospecies between 177 – 1565 m, adding important volume to local and regional species inventories in the eastern tropical Pacific. Octocorals dominated the coral fauna by abundance and species richness at bathyal depths with 55% of all coral observations and 67% of all identified morphospecies. However, stylasterids were disproportionately abundant within the depths of the OMZ and shallower, leading to greater similarities in the benthic coral fauna at upper bathyal depths. Most notably was the identification of a distinct OMZ community compared to deeper depths and marked species turnover across the OMZ upper and lower boundaries. In addition, no coral morphospecies were observed to occur both above and below the OMZ (Fig. 4.3), suggesting that dissolved oxygen concentration is a critical control of coral distribution on features in the eastern tropical Pacific Ocean, potentially forming a barrier to gene-flow between populations of deep-water corals that would reinforce allopatric speciation mechanisms (Rogers, 2000).

We failed to identify any significant differences in deep-water coral assemblages between oceanic water masses in this region but acknowledge that additional surveying effort in the shallowest (Equatorial Subsurface Water) and deeper water masses (North Pacific Deep Water and Circumpolar Deep Water) may provide addition useful data and may require a reevaluation of this hypothesis. In other basins, oceanographic water masses have been found to significantly influence community structure changes across bathyal depths (Ayress, De Deckker & Coles, 2004; Arantes et al., 2009; Quattrini et al., 2015; Radice et al., 2016; Auscavitch & Waller, 2017; Victorero et al., 2018; Auscavitch et al., 2020), leading to increased local (e.g. within-feature) and regional deep-water coral diversity. However, as discussed further below, the water mass structure of the upper bathyal eastern tropical Pacific is complex and strongly influenced by equatorial ocean current structure in the area (Firing, Wijffels & Hacker, 1998; Fiedler & Talley, 2006; Evans et al., 2020), which may make it difficult to assign characteristic assemblages to water masses at the present sampling resolution.

4.5.1 The effects of the OMZ on deep-water coral communities off Costa Rica

Deep-water coral assemblages were observed to change mostly as a function of dissolved oxygen changes in the water column and depth (Fig. 4.11). Coral abundances were slightly depressed across the upper boundary and within the OMZ and peaked along the lower boundary (Fig. 4.5), a pattern which has been observed in other taxa across both benthic and pelagic OMZ habitats (Gooday et al., 2010; Wishner et al., 2013). However, this is among the first instances where it has been explicitly identified in deep-water corals in the eastern tropical Pacific. Likewise, species richness (S) and Shannon’s diversity index (H’) were observed to decline through the upper boundary of the OMZ and increased along the lower boundary (Fig. 4.6A, B), peaking at intermediate bathyal depths. These observed patterns in faunal abundance and diversity peaks along the lower OMZ boundary are thought to be a result of three potential mechanisms: 1) the selective pressures that might exclude deep-water coral species from hypoxic or dysoxic conditions (Gooday et al., 2010; McClain & Hardy, 2010), 2) the potential for low oxygen tolerance provided by a metabolic offset associated with enhanced food supply along the lower OMZ (Rogers, 2000), and 3) the adaptation of sessile benthic organisms to natural variability in bottom oxygen concentration (Levin, 2003) changes along the lower OMZ boundary as a result of oceanographic processes (e.g. internal waves and tidal dynamics) (Hanz et al., 2019).

Several octocoral species were found to occur in the greatest abundances within 100 m of the lower boundary of the OMZ. For one sea pen, *Pennatula* cf. *inflata*, 96% of all records for this species occurred at Seamount 6 between a narrow depth range of 653-669 m. Additionally, 4 of the 5 large, branching paragorgiid (bubblegum coral) morphospecies identified here, consisting of both red and white color morphs, were all narrowly distributed along the lower boundary of the OMZ (549-893 m). In total, 21% (778) of all coral occurrences were observed within +/- 100 m of the lower boundary (700 m) of the OMZ, in contrast to the only 254 records +/-100 m of the upper OMZ boundary (300 m). In the eastern Pacific, the existence of a peak in suspended particulate organic carbon (POC) around the lower boundary of the OMZ near Volcano 7, off Mexico, has been identified as a potential driver of higher benthic megafauna abundance (Wishner et al., 1995).

This study also gives us insights to coral taxa which are low-oxygen tolerant and are able to colonize OMZ depths. In general, stylasterids as a group, and *Stylaster* spp. specifically, were among the most broadly distributed taxa across the bathyal oxygen gradient and the most likely to be disproportionally abundant within the OMZ. This observation is particularly noteworthy since they can be an important habitat and structure-forming group in the deep sea (Häussermann & Försterra, 2007; Buhl-Mortensen et al., 2010). We also observed 304 coral occurrences across 10 species within the OMZ at oxygen concentrations under 5 µmol/L (371-582 m depth) at Las Gemelas and Seamount 6. At the most extreme oxygen values <1 µmol/L, only one species was identified Plexauridae sp. S0227-Q9, with 40 colonies between 495-512 m only occurring at Seamount 6. However, it is important to note that ambient anoxic conditions measured on the seafloor are not static and may be temporally variable, influenced by tidal dynamics, seasonal current variability, and internal waves (Hanz et al., 2019).

4.5.2 Insights to Pacific deep-water coral biogeography

Deep-sea coral species inventories in the eastern tropical Pacific are further improved by the results of this study and, consequently, these data provide important context in which to evaluate proposed biogeographic provinces in the deep ocean. Bathyal depths across the area encompassing eastern Pacific latitudes from the Gulf of California to the continental margin off Peru, including the Cocos Ridge and Galapagos Islands, have previously been identified as a single biogeographic unit (BY7: Cocos Plate) (Watling et al., 2013). This province has been characterized as having a moderately high particulate organic carbon (POC) flux (4-6 g/m$_{-2}$/y$_{-1}$) to the seabed and relatively low dissolved oxygen concentration (1 mL L$_{-1}$). It is our finding that the bathyal depths of the Pacific Costa Rica seamounts and Isla del Coco host primarily cosmopolitan and pan-Pacific species, with only a few species possibly endemic to this region.

Within the Primnoidae, *Calyptrophora clarki* Bayer, 1951, observed between 896 -1138 m, is known to be distributed across the Pacific basin at similar depths (Cairns, 2018b). This same species has been found off Hawaii (Cairns & Bayer, 2009) and was identified during explorations of the Phoenix Islands Protected Area and Northern Mariana Islands (Cairns, 2018b; Auscavitch et al., 2020). At the same time, two species of *Callogorgia* are also present in this area, one of which, *Callogorgia kinoshitai* Kükenthal, 1913, appears to be restricted to the deeper Costa Rica margin (specimens from R/V *Atlantis* cruise AT- 37-13; unpublished data) and was not encountered at the sites examined in this study, despite having been collected in the Galápagos archipelago (Cairns, 2018a). The other, *Callogorgia galapagensis* Cairns, 2018, initially described from the Galápagos was present throughout the study area (Las Gemelas, Seamount 6, 241-661 m) and has also been previously identified at Isla del Coco between 628-656 m (Cairns, 2018a). In the genus *Narella*, one species encountered two times in this study and collected once (S0221-Q3), *Narella ambigua* Studer, 1894, has only ever been identified in this region of the tropical eastern Pacific in the Galapagos (Cairns, 2018a) and now at Seamount 5.5 between 1529-1548 m. Finally, in this study we extend the depth distribution and range of *Parastenella pomponiae* Cairns, 2018. Initially described from material collected in the Galápagos between 475-578 m (Cairns, 2018a), *Parastenella* cf. *pomponiae* was observed 19 times between 949-1398 m at Seamounts 5.5, 7, and 8. Additional collections from earlier Costa Rica margin cruises using the DSV *Alvin* (AT-37 and AT-42) also indicate its presence along the Costa Rica margin at Seamounts 1 (CR4925-1), 3 (CR4982-A1), and on the Quepos Plateau (CR4981-A2) down to 1752 m suggesting a truly wide depth distribution for this species in the region.

Other octocoral taxa from the Pacific Costa Rica seamounts that provide additional biogeographic insight come from the Chrysogorgiidae and Pennatulacea. Of the three *Chrysogorgia* species observed, two, *Chrysogorgia scintillans* Bayer and Stefani, 1988 and *Chrysogorgia midas* Cairns, 2018, were previously identified in the eastern Pacific from collections in the Galápagos (Cairns, 2018a). The most widespread, *C. scintillans*, has a broad equatorial and North Pacific distribution (Cairns, 2018a). In contrast, *C.* cf. *midas* (this study), was identified at Seamounts 4, 5.5, and 7 between 866-1539 m, which represents a depth range extension since its description from material in the Galápagos (560-816 m) (Cairns, 2018a). Lacking from sites studied in this area were the chrysogorgiid genera *Metallogorgia* and *Iridogorgia*, often observed in seamount environments throughout Pacific Ocean (Watling et al., 2011; Pante & Watling, 2012; Pante et al., 2012; Auscavitch et al., 2020).

Pennatulaceans, despite being represented by only 4 species, were locally abundant on some seamounts (Seamounts 4, 6, and 7) and were largely represented by two species, *Pennatula* cf. *inflata*, and *Anthoptilum* cf. *lithophilum*. The most abundant sea pen, *Anthoptilum* cf. *lithophilum*, noted for its ability to attach onto rocky hard substrate, appears to be widely distributed along the northeastern Pacific margin and further south to the Galápagos archipelago (Williams & Alderslade, 2011; Buglass et al., 2019). *Pennatula* cf. *inflata* has been reported globally (López-González, Gili & Williams, 2001; Schejter et al., 2018) as well as nearby in the Galápagos (Buglass et al., 2019). Both species were found to occur at similar depths but primarily in the lower OMZ and deeper (Fig. 4.3).

Stony corals were more well-represented by solitary species than colonial ones in this region. Of the 12 scleractinian species identified, 10 were solitary cup corals. The two colonial forms were *Madrepora oculata* (790-873 m), a cosmopolitan framework-forming species, and one yet shallower (180-320 m) dendrophylliid (Dendrophylliidae sp. S0224-Q1). Solitary species included *Desmophyllum dianthus* (574-783 m) and *Javania* sp. S0226-S8 (1217-1442 m) and several others of uncertain families. These early records indicate that stony coral fauna at bathyal depths in this region are likely to be composed of widespread species, but further examination of the many unidentified solitary individuals is required.

Finally, within the Antipatharia (black corals), one species observed in this area, *Lillipathes ritamariae* (913-1167 m), initially described from collections off Costa Rica (Opresko & Breedy, 2010), has since been observed to occur across the South Pacific and Southern Ocean with more recent records off Chile (Araya, Aliaga & Araya, 2018), and as far west as New Zealand (Opresko, Tracey & Mackay, 2014). Further examination of black coral collections from this and other recent expeditions along the Costa Rica margin are needed to obtain better species-level identifications in support of biogeographic analyses.

The complex water mass and equatorial current structure of the equatorial eastern Pacific provides a potential mechanism for the observation of widely distributed Pacific species in the region of the Costa Rica Dome and along the Cocos Ridge. At upper mid-bathyal depths (200-1500 m), Equatorial Pacific Intermediate Water (EqPIW), the largest water mass explored in this study, is sourced from Antarctic Intermediate Water (AAIW) extending northward from the South Pacific and North Pacific Intermediate Water (NPIW) and North Pacific Deep Water (NPDW) from the north (Bostock, Opdyke &

Williams, 2010). The mixing of these geographically extensive water masses into EqPIW provides a potential corridor for distribution of bathyal coral species from the northern and southern hemispheres in the eastern equatorial Pacific. Furthermore, observed peaks in coral diversity at intermediate depths (1200-1500 m) (Fig. 4.6), suggest that elevated diversity at intermediate depths may be a result of the mixing of multiple deep water masses and overlapping depth ranges of upper and mid-bathyal taxa. Below 900 m, the presence of widely distributed species with increasing depth appears to be characteristic of deeper ocean water masses, in this case NPDW.

On larger scales, the role that shallower currents have in species distributions across the Pacific Ocean, and particularly laterally along the equator, should not be overlooked as a means of biogeographic connectivity at upper bathyal depths. The flow of the Equatorial Undercurrent (EUC) provides rapid transport eastward along the equator eastward from the Western and Central Pacific directly to the equatorial eastern Pacific at depths between 150-300 m (Taft et al., 1974; Tsuchiya, 1981; Evans et al., 2020). In addition to being a potential vector for conveying rapid (0.9-1.0 m s_{-1}) transport of planktonic coral larvae at depth, the EUC supplies oxygen to upper bathyal depths of the eastern tropical Pacific (Tsuchiya et al., 1989; Fiedler & Talley, 2006; Stramma et al., 2010a). Below this (~500 m), a return current, the Equatorial Intermediate Current (EIC), carries a comparatively oxygen-poor water westward (Stramma et al., 2010a). As an important transport mechanism for dissolved oxygen, as well as seamount coral larvae, these currents represent potentially important dispersal vectors along vast expanses of the equatorial Pacific. The volume of oxygen that the EUC delivers to the equatorial eastern Pacific bathyal depths may even offset the effects of projected OMZ expansion in the region (Stramma et al., 2010a). As additional deep-water species distribution data continues to emerge from across the Pacific (Friedlander et al., 2019; Giddens et al., 2019; Kennedy et al., 2019; Auscavitch et al., 2020; López-Garrido et al., 2020), future biogeographic studies should continue to take into account physical oceanographic features, like water masses and major ocean currents, for identifying potential dispersal and connectivity pathways across the vast expanse of the Pacific Ocean Basin.

4.5.3 Deep-water corals and ocean deoxygenation

This work provides baseline metrics of deep-water coral biodiversity of the seamounts off Pacific Costa Rica, which are vital to understanding the effects that expansion of OMZs and ocean deoxygenation (Stramma et al., 2008; Gilly et al., 2013) will have on benthic communities. Measurements for the eastern tropical Pacific indicate expansion and intensification over the past half century with oxygen loss between 300-700 m as 0.09-0.34 μmol kg$_{-1}$ y$_{-1}$ (Stramma et al., 2008). With tropical oxygen minimum zones expanding horizontally and vertically (Stramma et al., 2010b), the strongest effects of ocean deoxygenation are likely to occur at upper bathyal and bathypelagic environments (Stramma et al., 2010b; Wishner et al., 2018; Wishner, Seibel & Outram, 2020). Effects on deep-sea coral distributions may result in compression of upper bathyal species distributions, particularly those with narrow depth ranges along the upper boundary of the OMZ and shallower (Fig. 4.3). However, those species with broader depth distributions, such as those inhabiting depths below the OMZ, may be more resilient to such expansions (McClain & Hardy, 2010).

The physiological tolerances of framework-forming stony coral species specifically may limit their distribution to more well-oxygenated waters (Dodds et al., 2007; Lunden et al., 2014), but in some cases they have been observed within hypoxic conditions (Hebbeln et al., 2020). Across all sites we noted a poor representation of framework-forming scleractinian species. One cosmopolitan deep-water species, *Madrepora oculata*, was observed 8 times between 790-873 m and only at Seamount 5.5. A second colonial species, Dendrophylliidae sp. S0224-Q1, was also found to be restricted largely above the depth of the OMZ (180-320 m) and only at the sites furthest from the continental margin (Las Gemelas, Cocos South). As with many other coral taxa, colonial scleractinian species are important for their function as ecosystem engineers, producing hard structures that can lead to increased biodiversity in the deep ocean (Roberts et al., 2009; Buhl-Mortensen et al., 2010). As a result of deoxygenation, the displacement or loss of coral fauna and the structures they produce, combined with other climate change-driven stressors (e.g. deep-ocean warming (Brito-Morales et al., 2020), changes in surface productivity (Ovsepyan, Ivanova & Murdmaa, 2018), and ocean acidification (Pérez et al., 2018)), will likely have manifold effects on the diversity of life supported within the deep benthic communities.

CHAPTER 5

CONCLUDING REMARKS

This work serves to establish baseline characterizations of deep-water coral communities on seamounts and similar deep-sea topographic features in both the tropical Atlantic and Pacific Oceans. The current state of knowledge of patterns and processes driving deep-water coral diversity and biogeography on seamounts, as well as potential explanatory mechanisms, has expanded greatly in recent years, but more still remains to be understood. Prior to this research, large knowledge gaps persisted within the completedness of species inventories and spatial distribution of deep-sea coral species in the equatorial central and eastern Pacfic, as well as the northeastern Caribbean Sea. For each locality studied in this work, the specific objectives were to: 1) characterize deep-sea coral communities on seamounts and other rugged submarine features by identifying corals to species from video survey transects and associated collections, 2) identify major oceanographic and environmental drivers of change in patterns of diversity and community structure across the bathyal depths, and 3) add biogeographic context to the distribution of deep-sea coral species to better understand the biogeography of bathyal depths in data-deficient localities. In accomplishing each of these objectives, I provide significant advances to the knowledge of deep-sea coral ecology, oceanographic influences on the deep-sea benthos, and bathyal biogeography in previously unexplored areas. Specifically, this work highlights the strong evidence for the role of oceanographic processes (e.g. water mass stratification) and variables (e.g. aragonite saturation state, temperature, dissolved oxygen) that are important for deep-sea corals from individual species to communities.

In Chapter 2, I discuss how abiotic environmental variables influence distribution of aragonitic coral taxa, scleractinians and stylasterids on 3 remote seamounts in the Anegada Passage. Deep Caribbean seamounts are often poorly explored leading to large knowledge gaps in the species that occur on them and environmental variables that might be useful predictors to identify species drivers. As a hotspot for deep-water stony coral diversity, exploring deep seamounts in the tropical western Atlantic, and Caribbean Basin specifically, can lead to significant advances (Cairns, 2007). This chapter is the first to provide direct measurements on the distribution of aragonitic scleractinian and stylasterid coral species across an aragonite saturation state gradient in the northeastern Caribbean. Aragonitic coral species were observed to occur down to 1626 m, but colonial species were often restricted to depths less than 1540 m. Solitary scleractinians and stylasterids were observed deeper but still primarily above $\Omega_{arag} = 1$. This work provides important baseline biodiversity records for effective management and conservation of deep-water coral ecosystems in the tropical western Atlantic Ocean. Understanding patterns in coral community structure across the aragonite saturation gradient in this region can also help identify impacts of ocean acidification on the tropical seafloor benthos.

In studying seamounts, it is clear that the greatest opportunity for understanding patterns of biological diversity and community patterns across depth occurs in the Pacific Ocean. Over 60% of the world’s seamounts are found in the Pacific within which the greatest concentration of unexplored features occurs in the equatorial and tropical central and western Pacific Ocean (Kitchingman et al., 2007). In Chapter 3, I analyzed deep-water surveys in the Phoenix Islands Protected Area for patterns in deep-water coral species distribution and community assembly on seamounts, islands, atolls, and submerged reefs. Two hypotheses were tested to assess community variation based on feature type and among deep-sea water masses. Feature type was not identified as an important variable in deep-sea coral community structure, but water masses were observed to have distinctly different assemblages. Equatorial Pacific Intermediate Water was also identified as having the greatest diversity of morphospecies highlighting another case of intermediate water masses as important pools of biodiversity in the bathyal zone. Among the most important findings was the identification as PIPA as an area of biogeographic overlap with bathyal species present from the North, Southwest, and Western Pacific Ocean. While these findings are significant advances in biogeography of deep-sea corals and ecology of seamounts, much still remains to be understood about the variation in community assembly and species distribution patterns between seamount environments, which are often composed of heterogeneous habitats (McClain, 2007), and whose total diversity may not be fully captured by a single survey.

Among the greatest advances in knowledge about deep-sea coral diversity was garnered from our studies of deep-sea coral diversity in the equatorial central Pacific (Chapter 3). Where prior to 2017 no records of any deep-sea corals existed in the Phoenix Islands Protected Area, now exist a dataset of 12,828 records among 167 morphospecies. The central and western Pacific provide the greatest potential for knowledge gain as the density of large, unexplored seamounts is greatest compared to all other ocean basins. In order to better understand the intra- and inter-feature variability of seamounts, the western and central Pacific basins are fertile ground for future exploration and hypothesis testing concerning the factors that control distribution, diversity, and community assembly patterns of deep-sea benthic communities.

In Chapter 4, I discuss the drivers of deep-sea coral distribution, diversity, and community structure in the eastern tropical Pacific off Costa Rica. This region differs oceanographically from the Caribbean and central Pacific owing to the presence of a strong oxygen minimum zone between 300-700 m. OMZs have been identified as important water masses for structuring pelagic and benthic communities more broadly (Levin, 2003), but rarely studied in their impact on seamount deep-sea coral diversity and community structure. I hypothesized that the OMZ off Costa Rica out to Cocos Island would result in significant changes in community structure across bathyal depths and that OMZ communities are distinct from those in above or below-lying depth ranges. This finding was strongly supported for coral assemblages observed within the OMZ and those below, but not between the OMZ community and those shallower. These differences were partially explained by a disproportionate abundance of Stylasterid hydrocorals within the OMZ and shallower and a transition to octocoral-dominated communities below the OMZ. While species diversity was found to be depressed with the depths of the OMZ and higher at mid-bathyal depths, it is noteworthy that OMZ communities represent distinct pools of biodiversity in the tropical eastern Pacific and that they are worthy of further exploration and study.

One important thread that has emerged in this work has been the importance of deep ocean water masses in structuring deep-sea coral communities and potentially contraining deep-sea coral species distributions. In Chapters 2 and 3 it was observed that water masses contained significantly dissimilar deep-water coral assemblages which provides additional geographical evidence that water mases are important factors in structuring biodiversity patterns in the deep sea. The hypothesis that deep-sea water mass stratification is a factor for species distribution and community assembly patterns has become more widely tested in recent decades (Gooday, 2003; Watling et al., 2013; Quattrini et al., 2015, 2017; Radice et al., 2016; Auscavitch & Waller, 2017; Victorero et al., 2018), but still more occurrence records are needed in data-deficient areas, and across a wider range of depths, to test this more broadly. In the context of seamounts, water mass distribution and associated currents can be hypothesized as potentially important connectivity pathways between isolated seamount environments. This hypothesis is particularly interesting in the case of intermediate waters which occur at mid-bathyal depths, are globally distributed (e.g. Antarctic Intermediate Water), and are often observed to have relatively high coral species diversities compared to upper-bathyal or abyssal depths. Water masses may provide an elegant distillation for biogeographic patterns in the deep sea compared to explaining species distributions with patterns of individual environmental variables (e.g. depth, temperature, salinity, dissolved oxygen, carbonate chemistry), many of which are themselves highly correlated.

All chapters presented herein highlight the significance of collections-based research and developing taxonomic expertise in deep-sea ecosystems. In each locality examined in this work only 23-25% of morphospecies identified from video could be readily assigned to an accepted species using available collections or other taxonomist-verified reference material. If it is the goal of conservationists to establish critical baseline metrics for conserving biodiversity and identifying change in seafloor communities with climate change, then attention must be paid to identifying voucher collections to species and establishing species inventories now. This goal is confounded by the fact that taxonomic expertise in the world is aging or retiring and opportunities for training the next generation are few and becoming more limited (Higgs & Attrill, 2015; Bik, 2017). In the short term, the loss of the ability to readily identify biodiversity in the deep sea is far more insidious and harmful to effective conservation efforts than any anthropogenic driver of biodiversity decline. For some coral taxa, once novel techniques like DNA barcoding are providing inconclusive or less insightful results for identifying coral biodiversity (France & Hoover, 2002; McFadden et al., 2011; Pinheiro et al., 2019). Nevertheless, newer and progressively cheaper technologies, including genomic and machine learning tools, can be useful and should be used to address taxonomic and systematic questions for deep-sea corals (Pante et al., 2015; Quattrini et al., 2018; Erikson et al., 2020). For each chapter presented in this work, there remain dozens of un- or under-identified specimens awaiting further examination by taxon specialists. In the coming years, I hope these specimens will yield additional insights to local biodiversity, seamount connectivity, and biogeographic patterns in the deep sea.

Looking more broadly, it is important to remember that it is difficult or impossible to identify priority protection areas and conservation or recovery goals for deep-sea environments if we do not understand what it is exactly that we are protecting (Cordes & Levin, 2018). As in the case of the Phoenix Islands Protected Area (Chapter 3) and Pacific Costa Rica seamounts (Chapter 4), these efforts are some first steps at addressing those questions and providing hard data into the hands of local conservation organizations and managers. The existential threats facing deep-sea benthic ecosystems on seamounts are manifold. Long-known direct impacts include bottom-contact fishing (e.g. trawling) (Althaus et al., 2009; Williams et al., 2010; Clark et al., 2016; Baco, Roark & Morgan, 2019) and derelict fishing gear resulting from long-line fishing for large pelagic fishes over seamounts (Morato et al., 2011; Amon et al., 2020). Technologies in developed for cobalt-rich mineral crust exploration and extraction have the potential to cause some of the greated disturbances unique to benthic and pelagic seamount environments, particularly in the Pacific Ocean (Gollner et al., 2017; Miller et al., 2018).

As a backdrop to all of these direct impacts are the more insidious climate-driven threats to deep-sea biodiversity which include deep-water warming (Brito-Morales et al., 2020), ocean acidification (Guinotte & Fabry, 2008; Pérez et al., 2018), and ocean deoxygenation (Stramma et al., 2010) whose effects constitute multiple stressors for deep-water ecosystems (Gruber, 2011). While protected areas may buffer the effects of some of these threats (Davies, Roberts & Hall-Spencer, 2007; Levin & Bris, 2015), their proper design, implementation, and enforcement are key to their success (Clark et al., 2011). With the results of this work, I hope that preliminary assessments using exploratory datasets can foster new exploration and conservation goals that can be acted upon for existing and future protected areas.

5.1 Future Directions

While the findings presented in this work provide significant biogeographic insights about deep-sea coral distribution and communities in offshore seamount environments, they have often been more important at generating hypotheses for future investigation. The past decades have seen the evaluation of a number of putative paradigms in seamount ecology (see Rowden et al., 2010). This work provides some additional evidence in support of a few of these supported or plausible hypotheses, namely, 1) that seamounts are hotspots of coral species richness (Chapter 3, Chapter 4), 2) that seamount communities are distinct from deep-sea habitats at comparable water depths (Chapter 3), and 3) that seamounts can be refugia for corals from ocean-scale catastrophic events (Chapter 2). Additionally, I provide additional evidence that confirms a lack of support for two other hypotheses: 1) that seamounts are just submarine islands and thus subject to the tenets of island biogeography (MacArthur & Wilson, 1967), and 2) that seamounts are environments where endemic species commonly occur. The seamounts studied herein are not considered to be isolated similar to islands based on the similarity of species composition and distribution observed inferring that there is some degree of connectivity. In fact, my work indicates that there are striking similarities among seamount coral communities across large geographic areas, largely due to the occurrence of cosmopolitan coral species, and that the differences that occur in coral communities are largely a function of depth and depth-related covariables. Further evaluation of these hypotheses provided by Rowden et al. (2010), particularly in data-poor regions where no or few studies have been conducted (e.g. central and western tropical Pacific), are still needed to advance paradigms in seamount research.

If deep-sea coral and seamount research is to continue to make significant advances as it has over the past two decades, it will be vital to make further strides in seafloor imagery survey effort and deep-sea coral specimen collection. Long duration cruises and limited berthing space aboard sea-going research expeditions can result in fewer opportunities for scientists, particularly at student and early career stages. One opportunity for enhancing collaborative efforts in deep-sea research is telepresence technology. All of the data used herein has resulted from telepresence-enabled exploration platforms, a potentially transformative way of collecting data and expanding scientific collaboration in deep-sea research (Marlow et al., 2017). Furthermore, it has the capacity of expanding broader impacts opportunities of the associated research through events like live-streams and virtual interactions (Fundis et al., 2018). The application of telepresence-enabled science in the Pacific also engages developing countries and small island nations to help identify requirements for better knowledge and management of marine resources (McKinnie, Rotjan & Peau, 2018). Having only had to directly participate at sea in two of the four cruises where data for this dissertation was collected, it has been an critical tool in allowing me to accomplish this research.

In closing, I hope that this work will serve as a contribution to the study of deep-sea biodiversity and provide building blocks for future biogeographic studies. It is clear that the deep ocean contains vast multitudes of coral life which appear to have exhibited tremendous evolutionary success (as in the case of the Octocorallia) compared to shallow-water environments. This unique diversity, combined with the increasingly common discoveries of large coral reefs and gardens on deep seamounts and continental margins, makes the deep-sea environment fertile for discovery and understanding about the places where life can exist. While the ocean is vast, incremental gains through exploration and subsequent ecological analyses are critical for the advancement of knowledge about the largest environment on Earth and effective conservation of the resources therein.

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NOTES

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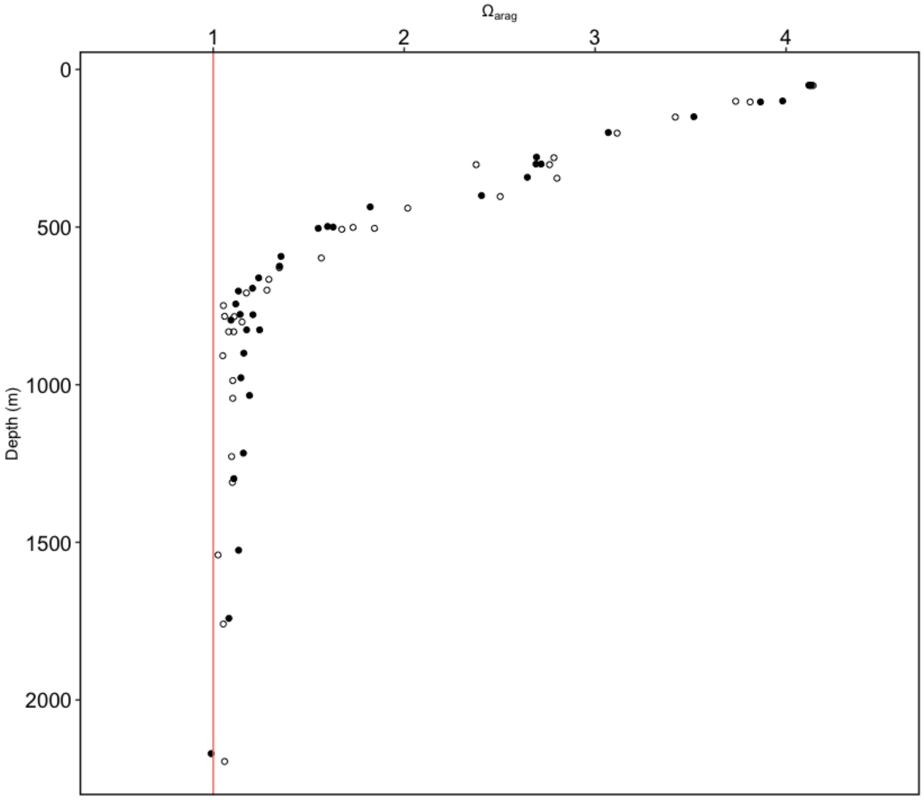
For all published or submitted manuscripts which resulted from Chapters 2 and 3, co-authorship was determined by those who proposed the initial ideas to obtain funding or who participated in field work and subsequent data analysis. In each case, I was responsible for the final writing, figure construction, editing, and organization of each chapter and manuscript.

APPENDIX A

ANEGADA PASSAGE SUPPLEMENTARY MATERIAL



Supplementary Figure A1. Aragonite saturation state profiles for the Anegada Passage using measured (closed circle) and model predicted (open circle) Ω_{arag} values. A solid red vertical line at $\Omega_{arag} = 1$ represents the aragonite saturation horizon.

Supplementary Table A1. Results of the two-way nested ANOSIM (depth within seamount) comparing coral assemblages between seamounts. Indicated values are R-statistics with p-values indicated in parentheses. Values in bold were observed to be significant at or below p=0.05.

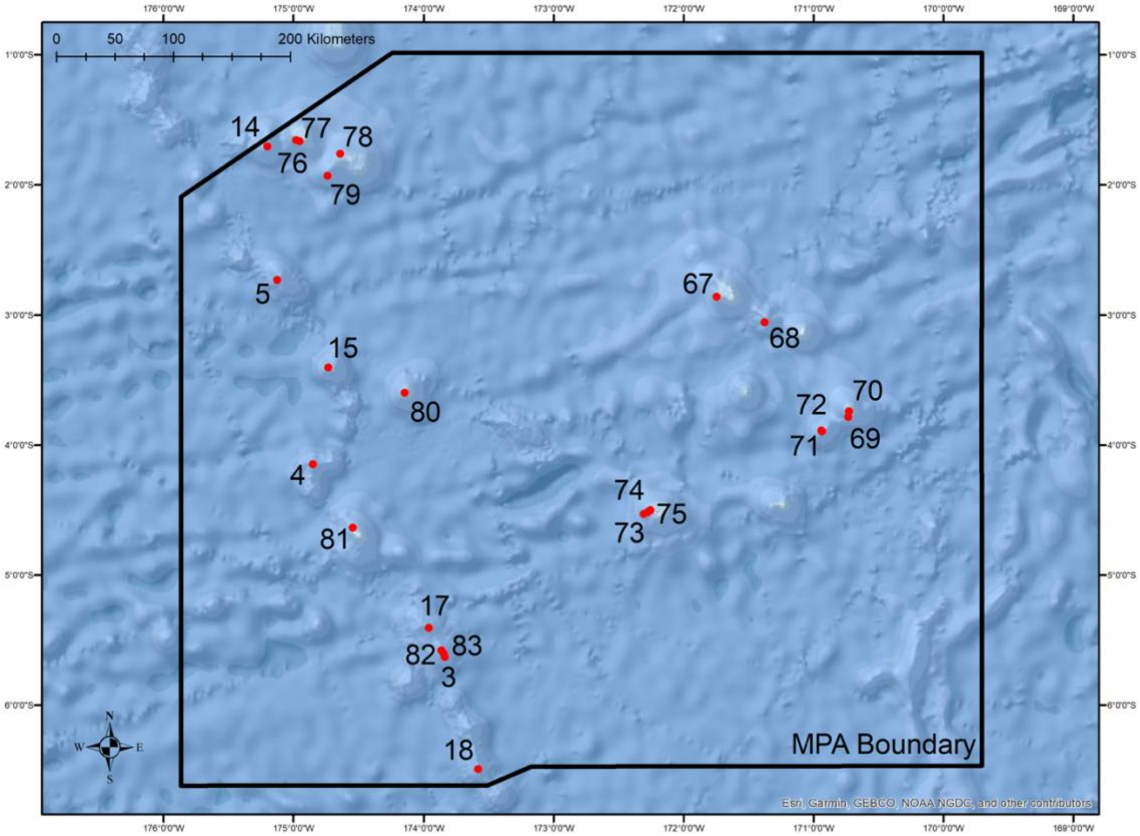
Seamount	Conrad Seamount	Dog Seamount	Noroît Seamount
Conrad Seamount			
Dog Seamount	-0.001 (0.379)		
Noroît Seamount	0.029 (0.292)	**0.544** **(0.006)**	

Supplementary Table A2. Results of a one-way ANOSIM comparing coral assemblages between water mass factors. Indicated values are R-statistics with p-values indicated in parentheses. Values in bold were observed to be significant at or below p=0.05. Water masses are abbreviated by the following: SUW=Subtropical underwater, SSW=Sargasso Sea Water, TACW= Tropical Atlantic Central Water, AAIW=Antarctic Intermediate Water, and NADW=North Atlantic Deep Water.

Water Mass	SUW	SSW	TACW	AAIW	NADW
SUW					
SSW	0.16 (0.167)				
TACW	1.0 (0.125)	**0.611** **(0.003)**			
AAIW	0.667 (0.091)	**0.530** **(0.002)**	0.089 (0.134)		
NADW	0.8 (0.167)	**0.6** **(0.008)**	**0.93** **(0.001)**	**0.361** **(0.01)**	

APPENDIX B

PHOENIX ISLANDS SUPPLEMENTARY MATERIAL



Supplementary Figure B1. Detailed map of dive locations assessed across expeditions EX1703 and FK171005. Boundaries of the Phoenix Islands Protected Area are outlined in black.

Supplementary Table B1. Two-way nested ANOSIM comparisons (depth within feature type). Values indicated are R-statistics with p-values indicated in parentheses. Values in bold were observed to be significant at or below the p=0.05 level.

Feature Type	Reef	Seamount	Atoll	Island
Reef				
Seamount	**0.116759** (0.03)			
Atoll	**0.099098** (0.029)	0.029601 (0.224)		
Island	**0.098934** (0.047)	-0.00904 (0.513)	-0.01412 (0.58)	

Supplementary Table B2. One-way ANOSIM comparisons between water mass factors. Values indicated are R-statistics with p-values of the test in parentheses. R-statistic values in bold were observed to be significant at or below the p=0.05 level. Abbreviations are as follows: PDW= Pacific Deep Water, EqPIW=Equatorial Pacific Intermediate Water, and PEW= Pacific Equatorial Water.

Water Mass	PDW	EqPIW	PEW
PDW			
EqPIW	**0.302** (0.001)		
PEW	**0.619** (0.001)	**0.177** (0.006)	

Supplementary Table B3. Output of distLM and dbRDA analysis.

Marginal Tests

Variable	SS(Trace)	Psuedo-F	P	Prop.
Depth	33526	8.1618	0.001	0.066812
Temperature	22395	5.3253	0.001	0.044628
Salinity	12128	2.8236	0.001	0.02417
Oxygen	23481	5.5962	0.001	0.046792

Sequential Tests

Variable	AIC	SS (trace)	Psuedo-F	P	Prop.	Cumul.	res.df
Depth	967.17	33526	8.1618	0.001	0.066812	0.066812	114
Temperature	965.22	15698	3.9195	0.001	0.031283	0.098094	113
Salinity	963.96	12534	3.1901	0.001	0.024978	0.12307	112
Oxygen	962.85	11652	3.019	0.001	0.02322	0.14629	111

Percentage of variation explained by individual axes

Axis	% explained variation out of fitted model		% explained variation out of total variation	
	Individual	Cumulative	Individual	Cumulative
1	49.25	49.25	7.2	7.2
2	24.87	74.12	3.64	10.84
3	13.51	87.63	1.98	12.82
4	12.37	100	1.81	14.63

	Depth	Temperature	Salinity	Oxygen
dbRDA1	-0.773	0.425	-0.308	-0.356
dbRDA2	0.136	0.800	0.100	0.576
dbRDA3	0.599	0.403	-0.170	-0.671
dbRDA4	-0.162	0.129	0.931	-0.302

APPENDIX C

COSTA RICA SUPPLEMENTARY MATERIAL

Supplementary Table C1. One-way pairwise ANOSIM comparisons between coral assemblages above, within, and below the OMZ along the Cocos Ridge. Values indicated are R-statistics with p-values indicated in parentheses. Values in bold were observed to be significant at or below the p=0.05 level.

Factor	Above OMZ	Within OMZ	Below OMZ
Above OMZ			
Within OMZ	0.144 (0.132)		
Below OMZ	**0.683** **(0.002)**	**0.587** **(0.001)**	

Supplementary Table C2. One-way ANOSIM pairwise comparisons among water mass factors. Values indicated are R-statistics with p-values indicated in parentheses. Water masses are indicated by the following abbreviations: Equatorial Subsurface Water (EqSSW), Equatorial Pacific Intermediate Water (EqPIW), North Pacific Deep Water (NPDW).

Water Mass	EqSSW	EqPIW	NPDW
EqSSW			
EqPIW	0.27 (0.053)		
NPDW		0.028 (0.50)	