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Investigating patterns of deep sea coral and sponge diversity and abundance across multiple spatial scales in the Central Pacific

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Dissertation

**INVESTIGATING PATTERNS OF DEEP SEA CORAL AND
SPONGE DIVERSITY AND ABUNDANCE ACROSS MULTIPLE
SPATIAL SCALES IN THE CENTRAL PACIFIC**

by

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DEDICATION

To Elena my greatest supporter and Eva my research inhibitor

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I have to start with my parents who fostered my love of science and the natural world from the earliest age. They took me to new places to see new animals and put up with the television always set to the Discovery Channel. From my high school years, I need to call out Vicki Soutar who was the coach of our national ocean science bowl team. She made opportunities for us to learn about the ocean even though we were hours from the coast. In college, two professors had a huge impact in my development as a researcher Dr. Leslie “Doc” Sautter and Dr. Gorka Sancho they both opened new doors for me and were so generous with their time.

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ABSTRACT

The deep sea is the largest ecosystem on the planet, comprising more than 90% of the volume that life can inhabit, yet it is the least explored biome in the world. The deep sea includes the benthos, which makes up 91.5 % of all the seafloor globally, and the water column deeper than 200 meters. It hosts a wealth of ecosystems including deep-sea vents, seamount coral gardens, abyssal plains, high-productivity whale falls, and life even in the deepest trenches. We now understand that all of these ecosystems host a variety of habitats, each with their own ecology and unique species. These ecosystems and habitats- and their associated biodiversity- provide essential ecosystem services such as carbon sequestration, nutrient regeneration, microbial processes detoxification, fisheries provisioning, and many others. However, despite the uniqueness of these ecosystems and the importance of the services they provide, we still know far less about them than we do about their shallow water and terrestrial counterparts. In this dissertation, I contribute new insights about the patterns of biodiversity in the Pacific Ocean across a large geographic area, and across a wide range of depths. To that end, in Chapter 1, I have used one of the largest ocean exploration datasets to look for patterns of the abundance and diversity across the most

common benthic invertebrate families found on Pacific seamounts: Anthozoa, Porifera, and Echinodermata across the Central and Western Pacific. In addition to quantifying the diversity and abundance of known taxa, I also documented patterns of as-of-yet unidentified taxa by region, depth, and deepwater feature (seamount shape). Building on patterns associated with seamount shape that were described in Chapter 2, I focused on the effect of seamount shape on the diversity and abundance of deep-sea coral communities in Chapter 3. The analysis presented in Chapter 3 provides strong support for the novel hypothesis that gross seamount morphology is a significant driver of community composition. In Chapter 4, I focused on a single seamount to investigate biodiversity and abundance of coral and sponge taxa on a finer spatial scale, examining the role of direction (N, S, E, W) on different flanks of a single equatorial seamount. This analysis yielded interesting consistent patterns of zonation on all sides of the seamount in terms of depth, but with differences in abundance patterns on each flank for individual taxa. Finally, in Chapter 5, I took a global perspective to investigate gaps in deepwater data, with the goal of determining what regions need further exploration to conclusively determine patterns of deep-sea biodiversity, which will be critical for determining the health of deepwater ecosystems under climate change conditions with increased exploitation pressure and co-occurring with increased conservation efforts. Merging Ocean Biogeographic Information System (OBIS) records with the largest collection of deep submergence dive records ever collected, I used proposed biogeographic provinces schema to identify areas with the least supporting data. Additionally, I coupled records from OBIS with climate change projections to identify the areas with the fewest number of biodiversity records that are

likely to change the fastest under different IPCC projections. These areas of low number of records and high likelihood of change by the end of the century should become priority targets for future exploration. Taken together, this dissertation provides valuable insights and generates new hypotheses about patterns and drivers of deep-sea biodiversity, and puts forth recommendations for future research and exploration efforts.

TABLE OF CONTENTS

| | |
|---|-----|
| DEDICATION | iv |
| ACKNOWLEDGEMENTS | v |
| ABSTRACT..... | vii |
| LIST OF TABLES | xiv |
| LIST OF FIGURES | xv |
| CHAPTER ONE: INTRODUCTION..... | 1 |
| 1.1 Biological Study System..... | 2 |
| 1.2 Physical study system | 4 |
| 1.3 Goals and objectives | 7 |
| CHAPTER TWO: THE UNKNOWN AND UNEXPLORED: INSIGHTS INTO THE PACIFIC DEEP-SEA FOLLOWING THE NOAA CAPSTONE EXPEDITIONS..... | 9 |
| 2.1 Abstract | 9 |
| 2.2 Introduction..... | 11 |
| 2.3 Methods..... | 16 |
| 2.3.1 Expeditions | 16 |
| 2.3.2 Mapping | 17 |
| 2.3.3 Dive Site Selection..... | 18 |
| 2.3.4 ROV Dives..... | 18 |
| 2.3.5 Area Imaged..... | 20 |
| 2.3.6 Image Annotation..... | 22 |
| 2.3.7 Annotation Limitations | 23 |

| | | |
|--|--------------------------------------|----|
| 2.3.8 | Analysis..... | 23 |
| 2.3.9 | Data Management | 27 |
| 2.4 | Results..... | 28 |
| 2.4.1 | Mapping | 28 |
| 2.4.2 | Analysis of Unknown Diversity..... | 29 |
| 2.4.3 | Diversity of Identifiable Taxa | 30 |
| 2.4.4 | Anthazoa | 31 |
| 2.4.5 | Porifera..... | 33 |
| 2.4.5 | Echinodermata | 34 |
| 2.4.6 | Regional Comparisons | 36 |
| 2.5 | Discussion | 38 |
| 2.6 | Acknowledgements | 47 |
| 2.7 | Data availability | 49 |
| | | |
| CHAPTER THREE: THE IMPACT OF GEOLOGICAL FEATURE SHAPE ON THE ABUNDANCE AND DIVERSITY OF DEEP SEA CORALS | | 64 |
| 3.1 | Abstract | 64 |
| 3.2 | Introduction | 65 |
| 3.3 | Methods..... | 70 |
| 3.3.1 | Data collection | 70 |
| 3.3.2 | Data accessibility | 71 |
| 3.3.3 | Annotations | 71 |
| 3.3.4 | Statistical approach | 73 |

| | | |
|--|--------------------------------------|-----|
| 3.3.4 | Seamount classification | 74 |
| 3.4 | Results | 75 |
| 3.5 | Discussion | 78 |
| 3.6 | Acknowledgements | 88 |
| CHAPTER FOUR: UNMASKING THE MOUNTAIN: VISUALIZING DEEP-WATER | | |
| CORAL AND SPONGE COMMUNITIES ON FOUR SIDES OF AN EQUATORIAL | | |
| CENTRAL PACIFIC SEAMOUNT..... 99 | | |
| 4.1 | Abstract | 99 |
| 4.2 | Introduction | 99 |
| 4.3 | Methods..... | 104 |
| 4.3.1 | Site selection | 104 |
| 4.3.2 | Data collection and annotation..... | 105 |
| 4.3.3 | Statistical analysis | 107 |
| 4.4 | Results | 108 |
| 4.4.1 | Currents | 108 |
| 4.4.2 | Physical oceanographic findings..... | 109 |
| 4.4.3 | ROV observations | 109 |
| 4.5 | Discussion | 113 |
| 4.6 | Acknowledgements | 121 |

| | |
|--|-----|
| CHAPTER FIVE: MIND THE GAP: COMPARING EXPLORATION EFFORT WITH GLOBAL BIODIVERSITY PATTERNS AND CLIMATE PROJECTIONS TO DETERMINE OCEAN AREAS WITH GREATEST EXPLORATION NEEDS..... | 140 |
| 5.1 Abstract..... | 140 |
| 5.2 Introduction..... | 141 |
| 5.3 Methods..... | 143 |
| 5.4 Results..... | 147 |
| 5.5 Discussion..... | 149 |
| 5.6 Acknowledgements..... | 154 |
| CHAPTER SIX: CONCLUSIONS..... | 171 |
| BIBLIOGRAPHY..... | 175 |
| CURRICULUM VITAE..... | 204 |

LIST OF TABLES

| | |
|------------------|-----|
| Table 2.1. | 50 |
| Table 2.2. | 51 |
| Table 3.1. | 89 |
| Table 3.2. | 91 |
| Table 3.3. | 91 |
| Table 4.1. | 122 |
| Table 4.2. | 125 |
| Table 4.3. | 127 |
| Table 5.1. | 156 |
| Table 5.2. | 160 |
| Table 5.3: | 162 |
| Table 5.4. | 163 |

LIST OF FIGURES

| | |
|------------------|-----|
| Figure 2.1. | 52 |
| Figure 2.2. | 53 |
| Figure 2.3. | 54 |
| Figure 2.4. | 55 |
| Figure 2.5. | 57 |
| Figure 2.6. | 59 |
| Figure 2.7. | 62 |
| Figure 2.8. | 63 |
| Figure 3.1. | 92 |
| Figure 3.2. | 93 |
| Figure 3.3. | 94 |
| Figure 3.4. | 95 |
| Figure 3.5. | 97 |
| Figure 3.6. | 98 |
| Figure 4.1. | 128 |
| Figure 4.2. | 129 |
| Figure 4.3. | 131 |
| Figure 4.4. | 132 |
| Figure 4.5. | 133 |
| Figure 4.6. | 134 |
| Figure 4.7. | 135 |

| | |
|-------------------|-----|
| Figure 4.8. | 136 |
| Figure 4.9. | 138 |
| Figure 4.10. | 139 |
| Figure 5.1. | 164 |
| Figure 5.2. | 165 |
| Figure 5.3. | 166 |
| Figure 5.4. | 167 |
| Figure 5.5. | 168 |
| Figure 5.6. | 169 |
| Figure 5.7. | 170 |

CHAPTER ONE: INTRODUCTION

The deep sea is the largest ecosystem on the planet, comprising more than 90% of the volume available to macrofauna, yet it is the least explored ecosystem in the world (Ramirez-Llodra et al., 2010; Robison, 2009). Deep sea includes both the benthos which make up 91.5 % of all the seafloor globally (Watling et al., 2013) and the water column deeper than 200 meters. The deep ocean is a place of extremes with cold temperatures (2-4 deg C), low oxygen levels (0.08 – ~6 ml/l) and high pressure (295–9000 psi) leading to harsh conditions that influence the evolution of its inhabitants. These extreme conditions coupled with long term stability have led at least in part to the deep-sea being a host to numerous hot spots of biodiversity (Grassle & Maciolek, 1992; Hessler & Sanders, 1967; Rex, 1981), it is also an ark of ancient taxa that have remained little changed for hundreds of millions of years (Ameziane & Roux, 1997). In addition, deep sea biodiversity is thought to rival some of the most biodiverse ecosystems like shallow coral reefs and terrestrial rainforests despite comparably low levels of fixed carbon (Paulus, 2021). Importantly, the deep sea fills numerous critical planetary functions such as carbon sequestration, nutrient regeneration, microbial processes, detoxification, fisheries provisioning and many others (Thurber et al., 2014). Yet despite their depth and remoteness, deep-sea ecosystems are not immune to human impacts (Thurber et al., 2014). Climate change is projected to impact the deep ocean through ocean acidification, declining oxygen concentration as well as increasing temperature (Levin, 2003; Mora et al., 2013). These impacts will almost certainly disrupt or alter these supporting functions, including biodiversity, nutrient cycling, biomass, and primary production (Jones et al., 2014).

The biodiversity of the deep sea underpins all of the ecosystem services it provides, but deepwater biodiversity remains vastly underappreciated in terms of taxonomic identification, life history, and ecology (Thurber et al., 2014). The elusivity of deep-sea life is especially problematic in a time of rampant global climate change because species and systems are changing or disappearing before they are studied or known, potentially prohibiting a complete understanding of the mechanisms that contribute to deepwater ecosystem functioning (Paulus, 2021). Determining the drivers of biodiversity is therefore a priority for scientists, conservationists and resource managers. However, our relative lack of knowledge of the deep-sea compared to shallow water ecosystems means that the deep-sea still requires a lot of baseline characterization before we can truly address these fundamental questions of biodiversity to the same level of detail as terrestrial and shallow water.

Here, I will ask questions such as how does the frequency of unidentifiable organisms change over spatial regions and depths (Chapter 2)? How does coral abundance vary based on seamount shape (Chapter 3)? How does biodiversity change between one flank of a seamount versus another (Chapter 4)? and finally, what is the extent of exploration efforts globally, and what ecoregions are more or less explored compared to their relative levels of biodiversity (Chapter 5)? The answer to these questions will help to guide future research on investigating the patterns of biodiversity in the deep-sea.

1.1 Biological Study System

Anthozoans (corals) and poriferans (sponges) are the best documented of the deep-sea sessile macrofauna, but are still vastly understudied, with new discoveries and new

taxonomic descriptions occurring regularly. Unlike their shallow water relatives deep-sea corals do not have photosynthetic symbionts (Cairns, 2007). Deep-sea corals as a group are comprised of 6 major taxonomic groups: the Scleractinia (Kitahara et al., 2010), Antipatharia (Wagner et al., 2012), Alcyonacea and Pennatulacea (Williams, 2011) within the Octocorallia (Watling et al., 2011), and Zoantharia (Carreiro-Silva et al., 2017) within the Hexacorallia, and the calcified hydrozoan family Stylasteridae (Cairns, 2011). Deep-sea corals are noted for slow growth and long life spans with the oldest coral being aged to 4,265 years (Roark et al., 2009), and are generally thought to be key ecosystem engineers and biodiversity multipliers (Kennedy & Rotjan, 2020).

In contrast to shallow water corals, cold water corals are completely reliant on particulate organic matter (POM) and small zooplankton captured by suspension feeding for their supply of fixed carbon (Dodds et al., 2009; Goldberg, 2018; Orejas et al., 2016). As such, the distribution of deep water corals is considered to be heavily influenced by local hydrodynamics and physical oceanographic processes (Genin, 2004; Genin et al., 1986; Lavelle & Mohn, 2010; Morgan et al., 2019). Their distributions are to be strongly influenced by a several abiotic factors such as depth (Quattrini, Baums, et al., 2015; Thresher et al., 2014), dissolved oxygen (Hanz et al., 2021; Hebbeln et al., 2020), pH (Georgian et al., 2016) overlying water masses (Auscavitch, Deere, et al., 2020; Auscavitch & Waller, 2017; Buhl-Mortensen et al., 2015; Miller et al., 2011; Puerta et al., 2020; Radice et al., 2016), temperature (Brooke et al., 2013), and carbonate saturation state (Auscavitch, 2020; Georgian et al., 2016; Roberts et al., 2021). In deep-sea benthic environments like seamounts, additional variables such as seafloor topography, particulate organic material

export from the water column (Baco et al., 2017; Duineveld et al., 2004), and current flow also influences coral diversity and abundance (Genin, 2004; Genin et al., 1986). This body of literature provides basic insights into deep-sea coral distribution, and lays the groundwork for the questions proposed in this dissertation.

Corals provide a complex, rich, and varied habitat that promotes high biodiversity (Clark et al., 2010) and provides congregation points for juvenile and adult fish (Auster, 2005). As such, they have been widely recognized as an indicator species of vulnerable marine ecosystems (VMEs) (RFMO, 2019; Watling & Auster, 2021). This makes the study of deep-sea corals critical for understanding deep-sea benthic environments (Morato et al., 2020).

1.2 Physical study system

Seamounts are generally defined as any mountain-like feature rising more than 1000 meters above the surrounding seafloor (Menard, 1964; Staudigel et al., 2010; Yesson et al., 2011). In the Pacific, these are primarily created by hotspot volcanism (Pitcher et al., 2008), but can also be formed by tectonic uplift (Schmidt et al., 2000). Historically, seamounts are understudied (Rowden 2010), with the majority of existing work being conducted via human operated submersibles (HOVs), remotely operated vehicles (ROVs), autonomous underwater vehicles (AUVs), towed camera transects and/or stationary observation using drop cameras (e.g., Stocks, 2004; Rowden et al., 2010; Vetter et al., 2010; Clark et al., 2012, Auscavitch et al., 2020). The mobile approaches of ROVs, HOVs, and AUVs provide data on a much larger scale than stationary sampling methods, but still only cover a few kilometers or less on average per dive and each dive is often limited to

one side of a feature. Clark et al. (2010) estimated that less than 300 seamounts have been visited by a deep submergence vehicle and the seamounts that have been sampled have only been visited one or two times with a few notable exceptions like Davidson Seamount (McClain et al., 2010) and Axial Seamounts (Chadwick et al., 2010). While Rowden et al.'s estimate is now 12 years old and numerous additional studies have been conducted, still only a small percentage of the estimated 33,000 seamounts (Yesson et al., 2011) have been visited. Notably, in this dissertation I have taken a very broad definition of seamounts, expanding beyond the definition used by Yesson et al. (2011) and others. Here, I include atolls and islands as seamounts, since they are volcanically-derived features that provide bathymetric relief across the entire Pacific. Because they are mountain-like features that rise more than 1000 meters from the sea floor, and provide habitat for coral growth regardless of whether or not they break the surface.

Seamounts have steep flanks that help shed sediment and expose hard ground which almost all deep-sea corals require. Seamounts can also have a significant effect on the local hydrodynamic conditions by physically altering the water flow and hypothetically producing water column features such as Taylor columns (Chapman & Haidvogel, 1992), localized upwelling and downwelling (White et al., 2007), internal waves to break resuspending sediment (Turnewitsch et al., 2013), and tidal rectification (Brink, 1995; Mohn et al., 2009). This physical alteration has been documented to have an effect on the biological conditions as well. Seamounts have been associated with increased chlorophyll a concentrations (Leitner et al., 2020) and general increased biomass associated with islands and seamounts (Hasegawa, 2019), which also help provide fixed carbon to deep-

sea benthic communities.

Seamounts fauna are under threat, as the loss of biodiversity and changes to faunal assemblage structures are increasing due to anthropogenic disturbances such as deep sea trawl fishing and deep sea mining (Amon, Gollner, et al., 2022; Ramirez-Llodra et al., 2011). Open ocean deepwater trawlers often target seamounts (Clark & Koslow, 2007) which leads to removal of seafloor structures (Althaus et al., 2009; Clark & Rowden, 2009; Rossi, 2013). Work by Clark et al. (2007) documented almost 2.3 million tons of fish removed by trawling globally, with 900,000 tons (39%) of that coming from seamounts in the North Pacific, annually. Similarly, the Food and Agriculture Organization of the United Nations reports 14.4 million tons of fish caught by trawling globally with 2.07 million tons caught in the north Pacific (Victorero, Watling, et al., 2018). This level of trawling pressure means that large swaths of coral and sponge habitat are often disturbed repeatedly, with little/no opportunity for regrowth (Clark et al., 2012). Seamounts also face increased danger from the renewed push for mining of deep-sea polymetallic crusts (Cuvelier et al., 2020; Mengerink et al., 2014). Seamounts in the 800 to 2500 meters depth range can accrue polymetallic crusts (Hein et al., 2009; Hein et al., 2013; Mizell et al., 2020), which contain rare earth minerals such as molybdenum, manganese, platinum, tantalum, bismuth, tungsten, cobalt, sulfides, and titanium (Hein et al., 2009; Hein et al., 2013; Mizell et al., 2020) used in numerous modern technologies. These increased threats will devastate long-lived biodiversity on seamounts, and thus it is imperative that we improve our understanding of seamount communities (Amon, Gollner, et al., 2022).

It is often said that the ocean is more than 95% unexplored (Kennedy et al., 2019) and that only 20% has been mapped in high resolution (GEBCO 2020). However, we have over 150 years of biodiversity data and have mapped the entire ocean at 15 arc second resolution (NCEI 2023) and data densities have reached the point where high quality predictive models of ocean and deep-sea biodiversity are possible and are routinely published (Bryan & Metaxas, 2006; Davies et al., 2008; Etnoyer et al., 2018). Thus, the nexus of deepwater marine science is straddling two opposing narratives: one of lack of data and exploration, and one of 150 years of accumulated research, poised for major advance with the advent of new and emerging technologies (Bell, Chow, et al., 2022; Crosby et al., 2023; Kennedy et al., 2020; Shank et al., 2019; Van Dover et al., 2012). However, even with the modern tools and growing resources, a fully explored ocean is not tenable on a short timeline, and thus future exploration efforts need to be optimized towards priority biodiversity data needs, filling existing data gaps, and answering critical questions about ecosystem functioning with an eye towards ecosystem services and management.

1.3 Goals and objectives

In this dissertation, I combine several approaches to ask fundamental questions about drivers of deep-sea biodiversity at the ocean basin, ecosystem, and single-feature scale. Specifically, I combine hypothesis testing research with analysis and visualization of exploration and data visualization tools to investigate the patterns of diversity and abundance of deep-sea life at different spatial scales and take a novel approach to assessing the areas of highest priority for future exploration. The second chapter of this work focuses

on the Central and Western Pacific basin documenting the patterns of deep-sea life at both the genus and broader community levels and how it compares between regions within the basin. I also quantify the as-yet-unknown taxa by looking at the organisms that were unidentified and use that as a proxy for level of exploration between regions. The third chapter continues at the basin scale but focuses on one ecosystem type with an investigation of the influence of seamount shape on its associated biodiversity. The fourth chapter zooms into focus on a single seamount and examines how depth zonation along its' flanks are shifted by abiotic factors such as strong currents and water characteristics, evoking an Alexander von Humboldt-style infographic to help visualize biodiversity and abundance patterns of deepwater corals and sponges on seamounts. Finally, the fifth chapter compares overall global ocean exploration effort with several different proposed biogeographic classification schemes, biodiversity patterns and climate change projections to propose deep sea areas that are in highest need for further exploration.

CHAPTER TWO: THE UNKNOWN AND UNEXPLORED: INSIGHTS INTO THE PACIFIC DEEP-SEA FOLLOWING THE NOAA CAPSTONE EXPEDITIONS

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2.1 Abstract

Over a 3-year period, the National Oceanic and Atmospheric Administration (NOAA) organized and implemented a Pacific-wide field campaign entitled CAPSTONE: Campaign to Address Pacific monument Science, Technology, and Ocean NEeds. Under the auspices of CAPSTONE, NOAA mapped 597,230 km² of the Pacific seafloor (with ~61% of mapped area located within US waters), including 323 seamounts, conducted 187 ROV dives totaling 891.5 h of ROV benthic imaging time, and documented >347,000 individual organisms. This comprehensive effort yielded dramatic insight into differences in biodiversity across depths, regions, and features, at multiple taxonomic scales. For all deep-sea taxonomic groups large enough to be visualized with the ROV, we found that fewer than 20% of the species were able to be identified. The most abundant and highest diversity taxa across the dataset were from three phyla (Cnidaria, Porifera, and Echinodermata). We further examined these phyla for taxonomic assemblage patterns by depth, geographic region, and geologic feature. Within each taxon, there were multiple genera with specific distribution and abundance by depth, region, and feature. Additionally, we observed multiple genera with broad abundance and distribution, which may focus

future ecological research efforts. Novel taxa, records, and behaviors were observed, suggestive of many new types of species interactions, drivers of community composition, and overall diversity patterns. To date, only 13.8% of the Pacific has been mapped using modern methods. Despite the incredible amount of new known and unknown information about the Pacific deep-sea, CAPSTONE is far from the culminating experience the name suggests. Rather, it marks the beginning of a new era for exploration that will offer extensive opportunities via mapping, technology, analysis, and insights.

2.2 Introduction

The oceans contain 1,335 million km³ of water covering 361.9 million km² of seafloor across 71% of the planet (Eakins & Sharman, 2010). Abyssal plains cover ~70% of the seabed, while the oceanic ridge system extends for 80,000 km around the globe, and there are an estimated 100,000 seamounts throughout the world ocean (Wessel et al., 2010). In the past few decades, there has been substantial effort put into mapping and exploring these benthic seafloor habitats (Mayer et al., 2018) fueled by the advent of new technologies that more easily enable deep-water access (Tyler et al., 2016).

Modern day deep-sea exploration has experienced a renaissance in recent years as massive exploratory infrastructure, expeditions, and institutions have entered the landscape ((Tyler et al., 2016). Results from these growing efforts have demonstrated that the seafloor possesses a wealth of biodiversity often exceeding that of coastal systems, and rivaling that of coral reefs and tropical rainforests (McClain & Schlacher, 2015). These abundant and diverse ecosystems, and organisms within, play vital roles in carbon sequestration (Zachos et al., 2008), decomposition (Graf, 1989), nutrient cycling (Danovaro et al., 2001), and fisheries (De Leo et al., 2010). Mapping and exploration technology contribute to our understanding of deep-sea ecosystem dynamics, including tectonic spreading centers and subduction zones as well as a variety of seafloor features (Dunn et al., 2018; Watling & Auster, 2017). Benthic storms, down-slope transport, seamount- and canyon-influenced hydrodynamics, turbidity flows, temporal pulses of food, and even tidal dynamics point to an ever-changing deep sea (Levin et al., 2001). From the discovery of deep-sea vents, seamount coral gardens, high-productivity whale falls, and life even in the deepest

trenches, we now understand that the deep sea hosts a variety of habitats, each with their own ecology and unique species (McClain & Schlacher, 2015; Van Dover, 2000). Yet, we still have limited knowledge of these ecosystems, which is increasingly problematic as they may be influenced by drivers such as sea level rise, ocean warming, deoxygenation, acidification, commercial fishing, seabed mining, and other dynamic drivers with unknown potential for feedback to the climate system (Koslow et al., 2011; Mengerink et al., 2014; Ramirez-Llodra et al., 2011; Sarmiento et al., 2004).

The Pacific is the world's largest ocean, and hosts a large diversity of deep-sea habitat including the deepest troughs on the planet, trenches, ridges, hadal holes, seamounts, abyssal plains, and other benthic features (Jamieson, 2015). The Pacific Ocean covers a total area of 161.76 million km², and hosts a volume of 660 million km³ (Eakins & Sharman, 2010). The history of Pacific Ocean exploration dates back to 1521, when Ferdinand Magellan first attempted to measure the depth by deploying a 732 m weighted line but did not reach the bottom (Murray, 1895). The United States' first major foray into the Pacific was the Explorations Expedition (1838–1842); while this expedition mapped many of the Pacific Islands for the first time, it largely ignored the marine fauna and oceanographic conditions (Philbrick, 2004). The first systematic oceanographic exploration of the Pacific (as part of a circumglobal tour) was the Challenger Expedition in the mid-1870s, which discovered 715 new genera and 4,417 new species globally in 4 years, with 37% of the sampling effort focused on the Pacific (Murray, 1895). Despite this Herculean effort, the vast majority of the Pacific still remained (and remains) unexplored.

The United States has approximately 60% of its exclusive economic zone (EEZ) in

the Pacific, and characterizing these Pacific benthic habitats is important to (a) fundamentally understand and effectively manage US submerged resources, (b) enable novel insights into Pacific benthic ecosystems, and (c) to establish baselines of these habitats to better understand their vulnerability and resilience to change. To address the growing need for exploration in the Pacific US EEZ, the National Oceanic and Atmospheric Administration (NOAA) launched a 3-year exploration campaign entitled CAPSTONE: Campaign to Address Pacific monument Science, Technology, and Ocean NEeds. Led by NOAA's Office of Ocean Exploration and Research (OER), CAPSTONE was a multiyear initiative to collect deep- water mapping and seafloor characterization data — providing a baseline dataset. These data were primarily acquired via the NOAA Ship *Okeanos Explorer* in and around US EEZ, US marine protected areas (MPAs), and international sister sites in the central and western Pacific (Friedlander et al., 2016). CAPSTONE was initiated in July 2015 and concluded in September of 2017, and engaged nearly 270 scientists, student researchers, and managers, making it one of the largest dedicated ocean exploration efforts ever conducted by the US government (Leonardi et al., 2018).

Deep-water areas documented during CAPSTONE (Figure 2.1; track lines) included nearly every type of marine geological feature, including conical seamounts, guyots, banks, ridges, islands, atolls, vents, and abyssal habitat. Given the consistency in operations over a wide geographic and temporal scale, CAPSTONE may provide one of the largest systematically acquired, basin-wide data sets across the Pacific Ocean with 187 remotely operated vehicle (ROV) dives spanning numerous ecosystem types and 597,230

km² of seafloor mapped. These data have created an incredible opportunity to examine broad- scale geographic patterns of benthic deep-sea diversity, and also present the opportunity for discovery of new taxa and geologic features, as well as the quantification of the unknown.

It is a widely held assumption that most deep-sea biota are yet-to-be-discovered (Mora et al., 2011). As such, the process of exploration in the deep-sea goes hand-in-hand with the task of species collection and description, and pending that, grappling with the unknown. For most of the world's taxa, both extant and extinct, unknowns must be estimated because they cannot be directly measured. For example, with 527 genera of non-avian dinosaurs known from fossil and genetic evidence, there are an estimated ~1,850 genera total, but the true number may never be known (Wang & Dodson, 2006). Microbial diversity is another area that requires estimation, typically using a combination of genetics and statistics (e.g., (Hughes et al., 2001)). In the deep-sea, species diversity has also only been estimated to-date. For example in the Mediterranean, species diversity was estimated across taxa and depth with rarefaction curves, and it was found that each unique habitat or ecosystem contributed significantly to biodiversity (Danovaro et al., 2010). Across these (and other) studies, the challenge of adequately estimating species diversity is a major source of attention and debate. However, in the case of CAPSTONE, a unique opportunity is presented in that the unknowns are visually identified as unknown taxa. Each observed organism was assigned the highest confidence taxonomic identification, or characterized as unidentified, creating an inventory of what can (and cannot) be identified by video and images, noting that taxonomic evaluation remains pending for many organisms collected

during CAPSTONE.

Benthic exploration science is evolving, looking to answer more sophisticated questions regarding drivers of biodiversity, patterns of reproduction and recruitment, genetic and ecosystem connectivity, oceanographic influences on benthic diversity and abundance, and trophic connectivity (Baco et al., 2016; McClain & Rex, 2015; McClain & Schlacher, 2015). To begin to address these questions, one aim of this paper is to quantitatively assess the contributions of unknown taxa to deep-sea biodiversity. Another objective is to contextualize the known taxa by depth, geologic feature, and geographic region in terms of diversity and abundance patterns. Finally, this paper will describe, with broad strokes, the findings of CAPSTONE in terms of mapping and visual surveys, to become a resource for future investigations of Pacific patterns of diversity and abundance.

In this study, >347,000 individual organisms were recorded across a subset of 168 dives, coupled with over 597,230 km² of seafloor mapped, to look for emergent patterns of diversity and abundance by depth, benthic feature, and geographic region. We explored these patterns in more detail for a single class, Anthozoa, and two phyla, Porifera and Echinodermata, which together were the three most characterized biota by both diversity and abundance during CAPSTONE. Because CAPSTONE is the first modern-era exploration expedition of this scope, we describe, in great detail, the technology and methodology employed to obtain data used for analyses. The main goals of this paper are thus to generate a detailed methodological description and a high-level data overview of the CAPSTONE campaign. The specific scientific aims are to (a) describe what we now know about the Pacific deep-ocean, and (b) describe what we still don't know about the

Pacific deep-ocean, and how to contextualize these findings and challenges.

2.3 Methods

2.3.1 Expeditions

Mapping and exploration took place aboard the NOAA Ship *Okeanos Explorer*, a 68 m vessel equipped with a full suite of mapping sonars capable of telepresence-enabled operations (Cantwell et al., 2020). While CAPSTONE efforts were further augmented by Schmidt Ocean Institute's R/V *Falkor* and other partners, we exclusively worked with *Okeanos Explorer* data in this study. The *Okeanos Explorer* was also equipped with a dedicated two-body ROV system, *Deep Discoverer* (D2) and *Seirios*, with a 6,000 m depth rating. Using telepresence, the ship was able to sail with only two to three scientists onboard while simultaneously interfacing with dozens of scientists onshore to provide real-time, minute-to-minute feedback and scientific expertise (Kennedy et al., 2016). A suite of Internet-based tools connected the remote teams to enable a unique exploration model with global reach, input, and diverse feedback.

This community-driven science agenda was operationalized with a designated science lead or co-science leads, coupled with a NOAA OER expedition coordinator, who together were responsible for building a consensus among the full community of participants and scientists, regardless of their onboard vs. telepresence participation. In this manner, expertise was available organically or “on-call,” and interdisciplinary teams of scientists could collaborate on common interests, which were usually focused around organisms, depth range, region, or geological feature. To help guide at-sea operations throughout CAPSTONE, NOAA adopted a set of guiding exploration themes: support

priority US Monument and Sanctuary science and management needs; identify and map vulnerable marine habitats — particularly high-density deep-sea coral and sponge communities; characterize seamounts in and around the Prime Crust Zone (PCZ), a region with the highest concentration of commercially valuable deep-sea minerals in the Pacific (Hein et al., 2013; Mizell et al., 2020); investigate the geologic history of Pacific seamounts; and increase understanding of deep-sea biogeographic patterns across the central and western Pacific (Leonardi et al., 2018). Additional scientific objectives were also solicited in each operating area from local stakeholders, resource managers, and the science community to help address region-specific data gaps and management needs.

2.3.2 Mapping

Acoustic mapping during CAPSTONE was conducted with EM302, EK60, and Knudsen sub-bottom profilers (SBP). The EM302 is a multibeam sonar with nominal frequency of 30 kHz, capable of providing data to a water depth of ~7,000 m. The system is capable of producing three different types of data: bathymetry, seafloor backscatter, and water column backscatter. The data were collected using Kongsberg's Seafloor Information System (SIS version: 4.3.2). The bathymetric data were processed in near real-time and results made available to participating scientists. Acoustic data collected by EM 302, EK60, and Knudsen SBP data, along with preliminary processed products, are publicly available at National Centers for Environment Information (NCEI). To understand the structure of the seafloor, bathymetric data (summarized in Figure 2.1) was examined at a grid resolution of 25–50 m (depth dependent).

2.3.3 Dive Site Selection

All dive sites were chosen through the collaborative process between the ship- and shore-based science participants. Priority targets were submitted pre-cruise, and then refined over a series of dive planning meetings (pre-cruise, pre- and post- each ROV deployment). Throughout the expedition, operational planning meetings streamed data via high-definition video originating on-ship to provide situational awareness for the shore-based team, showing the latest bathymetry and other available data, previous exploration in the region, and current weather conditions. In selecting dive sites, lessons learned were implemented throughout each expedition, and dive targets were refined based on feedback from previous dives. Care was taken to focus dive and mapping effort on sites and depths that were unexplored by previous efforts. For example, in the Hawaiian Islands region, there had been numerous dives by the *Pisces* submersibles (1973–present), and thus CAPSTONE focused efforts below the *Pisces* maximum operating depth of 2,000 m.

2.3.4 ROV Dives

All ROV dives in CAPSTONE were conducted with NOAA’s dual body 6,000 m rated ROV system *Deep Discover* (D2) and *Seirios* that were operated by the Global Foundation for Ocean Exploration (GFOE) personnel. ROV dives typically last 8 h, but were occasionally extended to 10+ h based on science objectives, at-sea conditions, and operational limits. Dives were primarily conducted during the day for ease of operations for the crew (described in detail by Quatrini et. al. 2015) *Seirios* is negatively buoyant and therefore remains in the water column, directly below the stern of the ship. It is tethered to the *Okeanos Explorer* with a standard oceanographic armored, fiber-optic cable (1.73 cm

diameter), and operated 3–10 m above D2, providing additional lighting and allowing for wide landscape views of the seafloor. D2 was linked to *Seirios* with a neutrally buoyant tether, isolating the ROV from surface ship's motion and allowing precise maneuvering in steep bathymetry close to the seafloor (0–4 m). D2 typically traversed the seafloor at a speed of approximately between 0.1 and 0.3 knots ($1 \text{ knot} = 0.514 \text{ m s}^{-1}$) and normally operates between 0 and 1.5 m above the seafloor. Both ROVs were outfitted with a suite of high-definition video cameras, two of which were maneuverable and used principally for scientific observation; these data were recorded for archival and subsequent analysis. All HD video from *Seirios* and D2 were recorded in PRORES 1080i format. In addition, numerous fixed pilot cameras were used in real-time, but data were often not recorded or used for scientific operations. Lighting consisted of numerous LED lamps providing 272,000 lumens of light across both vehicles. D2 has eight LED lamps mounted on four hydraulically positioned booms to allow for precise adjustment to the light field. During every descent, the HD cameras on D2 are color- and white-balanced *in situ* to a known reference card to ensure accurate color on the video. During the dive, expert video engineers made minor color balance adjustments to compensate for changes in water clarity and location of the object of interest within D2 light field (Gregory et al., 2016).

To record physical oceanographic measurements, Sea-bird 911 + conductivity–temperature–depth (CTD) loggers with dissolved oxygen (DO) sensors were attached to both D2 and *Seirios* and recorded for the entire duration of the dive. In 2017, Oxidation and Reduction Potential (ORP) and light scattering sensors (LSSs) were added to the vehicles suite of sensors. In addition to the CTD to log ambient water conditions, D2 was equipped with a

high temperature probe to make targeted measurements of vents or brine flows. Paired lasers (10 cm apart) were mounted on the primary high-definition video camera to estimate the size of objects being imaged.

Deep Discover was also equipped with two manipulator arms that were used to collect physical samples. Throughout CAPSTONE, NOAA practiced a limited sampling protocol, only collecting a few voucher samples per dive. During 2015 and 2016, the only biological samples collected were those that were thought to be potential new species, or demonstrate a substantial range extension. In 2017, the sampling protocol was widened to include collection of dominant-morphotype taxa that could not be identified by video. In addition, geological samples were collected on the majority of dives to aid in isotopically dating features and to help characterize the overall geology of the dive site.

2.3.5 *Area Imaged*

To An Ultra Short BaseLine (USBL) navigation system was used on D2. The precision and accuracy of the system is heavily dependent on water depth, and to a lesser degree both sea state and local bathymetry (Wu et al., 2016). The accuracy of this system can range between ~5 and 50 m depending on these conditions. In addition to this wide range, there were additional operational decisions and technical limitations that made it difficult to quantify the total seafloor area captured on video. These challenges include: (1) distinguishing errors in the USBL navigation versus rapid changes in vehicle position, due to rapid and abrupt movement as D2 searched for new and novel organisms or maneuvered around geological features and (2) the continuous and constant tweaks and adjustments to the camera angle and zoom values that are required to precisely calculate view angle, but

were not recorded. To provide estimates of the seafloor area imaged during CAPSTONE, we quantified the minimum and maximum area of seafloor likely documented during a dive to provide a range of possible area visualized. The average of that range was used to estimate the area of seafloor imaged. To accomplish this, we measured the linear distance traveled by D2 by manually tracing a line of best fit based on the subsampled (1 Hertz) USBL navigation file provided by NOAA as part of the ROV data collection available via the OER Digital Atlas (see the section “Data Management”). When D2 is at an altitude of 1 m, and the camera angle of the primary HD camera is at a 45-degree angle, the field of view yields 2.7 m of seafloor horizontally across the video frame (assuming a steady ROV heading). Because the pilots were nearly continuously changing the heading of the vehicle while scanning the seafloor, as well as flying the vehicle at variable altitudes as the bathymetry dictated, we estimated a visual swath width of a minimum of 5 m (2.5 m on either side of the vehicle path over the bottom) and a maximum of 50 m (calculated as twice the effective length of the tether connecting D2 and *Seirios*). The minimum range value of 5 m corrects for the changes of altitude and heading changes. The maximum range value of 50 m estimates the effective length of the neutrally buoyant tether between D2 and *Seirios*. While the tether is on average 30 m in length, the effective tether length is more accurately estimated at 25 m given the placement of positively buoyant floats, and the difference in depth between the vehicles. Therefore, the maximum range assumes that D2 can never move >50 m quickly without having to move the ship, which controls the movement and placement of *Seirios*. Any move of >50 m would be slower and would be clear in the USBL navigation, and is easy to distinguish from erroneous readings in

navigation files. Based on these assumptions and estimates, we assume that the area surveyed during CAPSTONE dives included the seafloor between 2.5 and 25 m on both sides of the averaged dive track

2.3.6 Image Annotation

A detailed video analysis was carried out at the University of Hawai‘i, supported by NOAA’s Deep Sea Coral Research and Technology Program (DSCRTP). The annotation creation process was completed based on benthic video from *Okeanos Explorer* using Video Annotation and Reference System (VARS), created by the Monterey Bay Aquarium Research Institute (Schlining & Stout, 2006) and customized for the University of Hawai‘i. VARS was used to generate records of animals from ROV dive video captured while on the seafloor. This system was used to quantify the abundance of deep-sea fishes, corals, sponges, and associated animals observed during CAPSTONE. The records of deep-sea invertebrates and fishes were catalogued and characterized with their *in situ* environmental conditions including habitat, substrate, water chemistry, and geographic location. Animals were identified using a deep-water identification guide, with 1,700 reference images prepared with taxonomic assistance from experts around the world.

All records were subjected to a custom quality assurance/quality control (QA/QC) protocol, looking for inconsistencies in depth, substrate, and identifications. Any potentially problematic records were re-reviewed in triplicate for QC. In addition, each identification was double-checked against the WoRMs online taxonomic database (Ahyong et al., 2023). The annotations used in this study can be accessed through the DSCRTP web-based data portal. In total, there were 89,398 annotations describing the

presence of taxa in an area, yielding more than 347,000 individual organisms recorded (abundance) across 168 dives over the 3-year CAPSTONE campaign. While there were 187 ROV dives completed in total during CAPSTONE, we eliminated dives that were focused on marine archeology, midwater exploration, and ROV engineering trials for the purposes of this study, for a total of 168 dives used in this study.

2.3.7 *Annotation Limitations*

Many annotations made during CAPSTONE expeditions could not be identified to a specific taxon and thus were categorized as “unidentified” or unknown. This category includes several types of unknowns: (a) unclassified species that are new to science, (b) organisms that require microscopy for identification, and (c) bad imagery where the detail required to make an identification is not available. These limitations make it impossible to draw conclusions about the absolute number of unknowns. However, given that all the CAPSTONE annotations were based on video from the same platform, and analyzed by the same team at the University of Hawai‘i, data collection and analysis were consistent across the entire 3-year CAPSTONE campaign. Thus, comparisons between unknowns observed across feature, depth, and region are valid as a relative comparison.

2.3.8 *Analysis*

All dives were characterized by the predominant geological feature on which the dive took place, geographical region, and the depth of the vehicle when the annotation was made. The *geological feature* categories (Table 2.1) were as follows: (a) Island: emergent land mass at the summit but is not an atoll, (b) Atoll: emergent land mass at the seamount summit with a central lagoon, (c) Bank: a seamount where the summit depth is shallower

than 200 m but does not break the surface, (d) Guyot (table mount): a flat top seamount that is expected to have a carbonate cap and was thought to have once been emergent, (e) Conical Seamount: an underwater mount rising at least 1,000 m above the surrounding seafloor that has a cone shaped summit, (f) Ridge Seamount: an underwater mount rising at least 1,000 m above the surrounding seafloor that has a ridgeback summit feature that is connected continuously with several other feature to form a subsea ridge, (g) Inactive vent system: any area that was obviously previously hydrothermally altered or has had a recent volcanic activity creating new seafloor, (h) Active vent system: any site that has active warm or hot water venting caused by geological activity, (i) Abyssal: any area between 4,000 and 6,000 m.

The *geographic regions* (Figure 2.1) were as follows: (1) Hawaiian Islands Region, including the main inhabited Hawaiian Islands, the Northwest Hawaiian Islands, Johnston Atoll, Geologist and Musician Seamounts; (2) Marianas region, including all dives conducted within the US EEZ around Guam and the Commonwealth of the Northern Mariana Islands (CNMI); (3) Western Pacific Region, including the US EEZ surrounding Wake Island and the High Seas between Wake and Guam; (4) South Central Pacific Region, including all dives conducted in the Phoenix and Line Islands, as well as in the US EEZ around Jarvis Island and along the Manihiki Plateau; and (5) American Samoa, which includes all dives conducted in the US EEZ around American Samoa. The American Samoa region was broken out based on a hypothesized biogeographic break in the area (Herrera et al., 2018; Watling et al., 2013). Of note, the following features were not included in this paper, but do have some limited representation (20 dives) in the

CAPSTONE campaign: archeology dives, submerged cultural heritage sites, midwater dives and transects, engineering dives, and special purpose dives for equipment recovery. Archived data associated with these dives can be found via the OER Digital Atlas (see the section “Data Management”).

Annotations in the DSCRTP web-based data portal were recorded (1) each time an individual taxon was seen (presence), and (2) the number of individuals seen at the same time (abundance). We used presence data for nested pie-charts and for depth ranges within each taxonomic group. Abundance data were displayed and used for regional comparisons (Shannon– Weiner diversity indices and corresponding heat maps), and for groupings by feature. We chose a conservative cap of a maximum of 100 individuals seen in any one observation period to correct for inaccuracies when organisms were too abundant to count. Thus, our abundance calculations are likely very conservative in total number of organisms.

To visually examine relative taxonomic diversity at the family, genus, and species level within taxa, across region, and across feature, nested pie-charts were generated depicting all known annotated organisms vs. all unknown (represented by the largest black bar originating vertically at the 12 o’clock position, progressing counter-clockwise). In every nested pie- chart, diversity at the family level is represented by the inner circle, the genus level is represented by the middle ring, and species level is shown on the outer ring. Pearson’s chi-square statistics was calculated to compare known versus unknown annotations across taxa, or between taxonomic levels. Pearson’s chi-square tests were completed using R (version 3.5.1).

To ecologically compare taxonomic diversity between the five geographic regions (American Samoa, Hawaiian Islands, Southern Central Pacific, Western Pacific, and Marianas), video annotations were used to analyze community composition. Annotations were grouped by region and then assessed for abundance, evenness and diversity, using Shannon–Weiner’s index (Levin et al., 2012; Rex & Etter, 2010). Overall diversity, relative abundance (the proportion of focal organisms relative to the total observed), and evenness (a measure of organismal distribution across taxa) were assessed for each region at the family and genus levels. Separately, genus-level diversity, abundance, and evenness were assessed for Anthozoa, Echinodermata, and Porifera, the three taxonomic groups with the largest number of annotations. Annotations that could not be identified to a family or genus (categorized as “unknown”) were excluded from family and genus diversity analyses.

Measures of genus-level density were calculated using observation-based rarefaction curves (taxa accumulation curves, in this case, at the genus-level), with 95% confidence intervals. This analytical technique provides a means to standardize taxonomic counts to a given level of sampling-effort, in this case, number of ROV dives conducted. Rarefaction curves were computed using the community ecology Vegan package for R, version 3.5.1 (Oksanen et al., 2007). Results are reported for the number of genera observed for each ROV dive, tabulated separately for Anthozoa, Porifera, and Echinodermata. Rarefaction curves were tabulated by depth, broken down into bins of 0–1,000, 1,000–2,000, 2,000–3,000, 3,000–4,000, and 4,000–6,000 m depth, with the number of ROV dives corresponding to the number of dives per depth.

Non-metric multidimensional scaling (NMDS) plots were created using the 35 most abundant genera for Anthozoa, Porifera, and Echinodermata. Plots were created using Bray-Curtis dissimilarity in the metaNMDS function in the R vegan package (Oksanen et al., 2007). To plot major taxa by geographic region and geologic feature, the most abundant genera were selected; for Anthozoa, any genus represented by >1,500 sightings per km² by geologic feature ($N = 37$ genera), for Porifera and Echinodermata, any genus represented by >50 sightings per geologic feature ($N = 33$ and $N = 34$ genera, respectively).

2.3.9 Data Management

In order to facilitate effective collaborative teamwork between ship and shore through telepresence, *Okeanos Explorer* expeditions used real-time data management strategies. Data collected on the ship needed to be moved to shore as quickly as possible to help shore-based participants maintain situational awareness. To facilitate this, OER employed a shore-side repository server where data became immediately accessible through a secure File Transfer Protocol (FTP) site. Once the cruise was complete, data from this intermediate repository server were moved to the NOAA's NCEI long-term archives. This system provided real-time data access during the cruise, and also met the requirements for long-term archival data access and discoverability after the cruise (Mesick et al., 2016). Data were distributed across several different archives within NCEI by data type, and aggregated into a discoverability tool called the OER Digital Atlas³. The OER Digital Atlas provides search capability and links the user to the appropriate data archive to access both raw and processed data. All data collected during CAPSTONE were made publicly available through the NCEI data archives (Mesick et al., 2016).

Although not analyzed in detail as part of this paper, CAPSTONE expeditions collected biological and geological samples, many of which are thought to be new species, new records, or unusual morphotypes. These specimens were archived for public use and future analysis through the Smithsonian National Museum of Natural History Invertebrate Zoology collection and the Oregon State University Marine and Geology Repository. Additionally, genetic subsamples of most biological specimens are available through the Ocean Genome Legacy Center at Northeastern University (Cantwell, Elliott, Kelley, et al., 2018).

2.4 Results

2.4.1 Mapping

Campaign to Address Pacific monument Science, Technology, and Ocean NEeds contributed a substantial amount of mapping effort, totaling 597,230 km² (Table 2.2), with 323 total seamounts mapped. Specifically, *Okeanos Explorer* mapped 10 atolls, 7 banks, 148 conical seamounts, 114 guyots, 24 islands, and 61 ridge seamounts. Many of these features were located within MPAs, and in many cases, CAPSTONE made major contributions to the overall bathymetry available in these locales (Figure 2.1 Table 2.2). Of the 363,526 km² mapped during CAPSTONE, 60.86% was within the US EEZ, amounting to 2.99% of US EEZ total. This effort represents 0.37% of the total Pacific Ocean mapped. While CAPSTONE made a contribution to both domestic and international mapping initiatives, the Pacific Ocean is vast, with only 13.78% currently mapped using modern techniques (Figure 2.1 Table 2.2) — highlighting that there remains a substantial data gap in coverage of the Pacific Ocean.

2.4.2 Analysis of Unknown Diversity

Campaign to Address Pacific monument Science, Technology, and Ocean NEeds logged 891.5 h of ROV bottom time over 168 dives, making 89,398 annotations of biota over an estimated 29.3 km² of seafloor imaged (Table 2.2). At the family and genus level, 87.2 and 61.4% of taxa were known and identifiable, respectively. However, at the species level, only 21% of taxa were identifiable, with a corresponding 79% unknown (Table 2.1). This trend is consistent across features, depths, and regions (Table 2.1 and Figures 2.2, 2.3). Similarly, the highest percentage of identifiable taxa was always at the family level across regions, features, and depth, and within Anthozoa, Porifera, and Echinodermata (Figures 2.4 - 2.6 inner circle of nested pie-charts; family-level Pearson's chi-square $\chi^2 = 7,843.5$, $df = 2$, $p < 0.001$). For echinoderms, there were fewer knowns compared to unknowns at the genus level (Figures 2.4 - 2.6 middle ring of nested pie-charts; Echinodermata-specific comparison across family, genus, and species Pearson's chi-square $\chi^2 = 8.5642$, $df = 2$, $p < 0.001$). For all taxa at the species level, there were more unknowns than knowns (Figures 2.4 - 2.6 outer circle of nested pie-charts; species-level Pearson's chi-square $\chi^2 = 2,057.3$, $df = 2$, $p < 0.001$). Anthozoa was better categorized at the family and species levels compared to Porifera (Figures 2.4 - 2.5).

Across geologic features, inactive vents had the least well-characterized biological communities, with the highest unidentifiable taxa at the genus and species levels (Table 2.1). Islands, atolls, banks, guyots, conical seamounts, and ridges, which all share similar vertical relief from the seafloor, were similarly diverse at the genus and species level, with guyots and conical seamounts hosting the highest number of identifications at the family

level (Table 2.1). Despite disproportionate dive effort in the Hawaiian Islands Region, all regions showed similar diversity at the species level. However, the South-Central Pacific and Marianas regions are the least well known at the genus level (Figure 2.3). Of this unknown diversity, CAPSTONE expeditions collected 786 biological and 278 geological samples, many of which are thought to be new species, new records, or unusual morphotypes (Figure 2.7) and are currently available for taxonomic classification.

2.4.3 Diversity of Identifiable Taxa

Although there were many visual observations unable to be identified, there are data hotspots where more is known than unknown. For example, the best characterized depth is 2,000–2,500 m, where 90% of all taxa were identifiable at the family level (Figure 2.3). Similarly, at the family level, anthozoans are particularly well characterized. Across all regions, features, depths, and most taxa, there were more identifiable annotations at the genus level than the species level. Thus, for all analyses of diversity, we used genus-level taxonomic information unless otherwise noted. The three taxa with the largest number of observations were the class Anthozoa (221,264 individuals), phylum Porifera (46,128 individuals), and phylum Echinodermata (29,934 individuals). Thus, these three taxonomic groups were selected for further analysis by depth, geographic region, and geologic feature (Figures 2.4 – 2.6). It is important to note that the focus of the annotations was to document coral and sponge communities, and their associates. As such, not every free-living individual invertebrate may have been noted, which may bias the analysis toward corals and sponge symbionts.

The basin-wide scale approach of these data crossed 48 degrees of latitude and 61 degrees of longitude. While postulating biogeographic provinces is outside the scope of this paper, it should be noted that the South-Central Pacific region had highest family ($H = 3.23$) and genus ($H = 3.96$) diversity, estimated using the Shannon–Weiner diversity index. The South-Central Pacific region also had the most even distribution ($J = 0.68$) of genera among communities observed. Both family and genus diversity were lowest in the American Samoa region ($H = 2.10$ for family diversity; $H = 2.02$ for genus diversity). In both assessments, the American Samoa region had the lowest evenness with evidence of dominant taxa. The top three genera in the American Samoa region were all corals: *Enallopsammia* spp, *Stichopathes* spp, and *Scleronephthya* spp, which combined represented 79.5% of genera observed.

2.4.4 Anthazoa

There were 122 anthozoan genera observed during CAPSTONE. To assess whether anthozoan diversity saturates with effort, we conducted rarefaction analyses across depth ranges at the genus level, noting that coral genera can dramatically vary with depth (Figure 2.4A). Most dive efforts were focused at the 1,000–3,000 m depth range, which also showed generic diversity approaching saturation. Genera between 0 and 1,000 m deep accumulated rapidly with increased sampling effort, as did diversity between 3,000 and 4,000 m, with curves not reaching a clear asymptotic value therefore suggesting the need for further sampling effort at those depths (Figure 2.4B). There is a very distinct anthozoan community at shallower depths (Figure 2.4A), but deeper than ~800 m, coral genera appear more widely distributed across depths (Figure 2.4A).

The South-Central Pacific region had the highest diversity ($H = 3.01$), using the Shannon-Wiener Diversity Index, and most even distribution ($Jt = 0.73$) among Anthozoa (Figure 2.4C). The American Samoa region had the lowest anthozoan diversity ($H = 1.47$) and least even distribution ($Jt = 0.40$) of all regions, yet two of the three most abundant genera overall were found there; *Stichopathes* and *Enallopsammia* spp. (Figure 2.4C). Across geologic feature, the most abundant coral genera appear on atolls, with the exception of *Chrysogorgia* and *Narella* spp. (Figure 2.4D). There appears to be higher abundance on atolls compared to islands overall, and higher abundance on banks compared to guyots (Figure 2.4D). There are also some genera that appear to be highly feature-specific. For example, *Anthomastus* spp. are more abundant on ridge seamounts, *Scleronephthya* spp. and *Polymyces* spp. are found almost exclusively on atolls, and there are several genera found almost exclusively on banks, e.g., *Parisis*, *Antipathella*, *Antipathes*, and *Eunicella* spp. (Figure 2.4D). Very few corals are found at vents, but *Pennatula*, *Trissopathes*, *Bathypathes*, and *Enallopsammia* spp. all had representation near vent features.

Overall diversity of the Anthozoa is well characterized at the family level and genus level, though there are more unknowns than knowns at the species level (Figure 2.4E), Pearson's chi-square $\chi^2 = 55,664$, $df = 2$, $p < 0.001$). Anthozoans at vent communities were similar to those found on ridge seamounts, guyots, and conical seamounts (Figure 2.8). Islands and atolls shared similar assemblages (Figure 2.8), even though abundances differed dramatically by genus (Figure 2.4D). The top 35 coral genera were not represented in abyssal habitats, even when corrected for effort (Figures 2.4D

2.8). Across regions, the diversity assemblages in the Marianas region were the most distinct (Figure 2.8).

2.4.5 Porifera

There were 55 poriferan genera identified during CAPSTONE (Figure 2.5), which is dramatically lower than the diversity of anthozoans (Figure 2.4). We conducted rarefaction analyses across depth ranges to assess whether poriferan generic diversity saturated with effort, with depth. Genera in Porifera differed from Anthozoa, in that the shallowest sponge communities were not the most diverse (Figure 2.5B). Instead, the highest diversity (per effort) was observed 1,000–3,000 m. From 3,000 to 6,000 m, rarefaction curves suggest the potential for greater generic diversity than has previously been documented, given the rapid accumulation with no clear asymptote at those depths (Figure 2.5B). Unlike Anthozoa, poriferan genera appear to be more widely tolerant of depth changes, with few exceptions shallow (e.g., *Leiodermatium* and *Psilocalyx* spp.), and deep (e.g., Cladorhizidae cf. *Chondrocladia*), and some unusually depth-specific taxa in intermediate depths, e.g., cf. *Bolosoma*, *Asceptrulum*, *Bathydorus*, *Polymastia*, and *Corallistes* spp. (Figure 2.5A).

Across regions, the Hawaiian Islands had the highest diversity ($H = 2.69$) using the Shannon–Wiener Diversity Index, and most even distribution ($Jt = 0.72$) among 41 genera within Porifera (Figure 2.5C). The Hawaiian Islands also had the highest number of identifiable genera among the regions, with only 18% of annotations excluded due to a lack of taxonomic identification. The lowest diversity among Poriferan genera was observed in the Western Pacific Region (Figure 2.5C); $H = 1.95$); however, 42% of annotations

were excluded because they could not be identified reliably to genera. The Marianas Islands had the most unique sponge assemblage at the genus level (Figure 2.8). Across geologic feature, the most abundant sponge genus, *Poecillastra* spp., was most prevalent on islands, but that appears to be the exception among sponges (Figure 2.5D). Broadly across taxa, sponges appeared most abundant on banks, guyots, and ridges, with some taxa appearing almost exclusively on a single feature, e.g., *Asbestopluma* spp. on guyots, *Psilocalyx* and *Semperella* spp. on banks, and *Hertwiga* spp. on ridges (Figure 2.5D). Overall, very few poriferans were identifiable to species (Figure 2.5E). Although the percent identifiable was similar to Anthozoa at the genus level, there are more unknown taxa at the family level (Pearson's chi-square $\chi^2 = 16,956$, $df = 2$, $p < 0.001$). Guyots, conical seamounts, and ridge seamounts had relatively similar poriferan communities, whereas banks, island, and atolls had more unique assemblages (Figure 2.8).

2.4.5 Echinodermata

There were 29,934 echinoderm annotations, overall, representing 106 genera (Figure 2.6). Echinoderm genera appear to be highly specific at shallow depths (200–500 m), where each taxon was only observed in a very narrow depth range (Figure 2.6A). In contrast, deep-water genera (3,000–6,000 m) were observed across a much broader depth range, displaying a high degree of flexibility (Figure 2.6A). To examine whether and how diversity saturated with effort, we built rarefaction curves displayed by ROV dive effort, categorized by depth. The highest degree of under sampled diversity was noted in the 3,000–4,000 m depth range (Figure 2.8). Although there was more effort 1,000–2,000 m, shallower depths (0–1,000 m) achieved the same taxonomic saturation (Figure 2.8).

Among Echinodermata, the Western Pacific had the most even distribution ($Jt = 0.90$) among observed genera, though all communities were comparatively even with little evidence of a dominant genus (Figure 2.8). One exception was *Ophiocreas* in the Hawaiian Islands, which had 417.32 records (corrected for effort), which was the most abundant of any echinoderm taxon observed (Figure 2.8). Measured using the Shannon–Wiener Diversity Index, the highest diversity among Echinoderm genera was documented in the Southern Central Pacific ($H = 3.19$; Figure 2.6C), though generally all regions had similar diversities (H ranged from 2.65 to 3.11).

When examining the organization of echinoderms on various features, some trends were notable or consistent with their known life mode. For example, many filter-feeding echinoderms were observed on features where they or associated fauna could exploit desirable water currents. The brisingid *Novodinia* and two crinoids, *Glyptometra* spp., and *Thaumatoctrinus*, exploit water currents for food, and displayed high abundance on atolls. The feather star *Psathyrometra* as well as two stalked crinoids, *Bathycrinus* and *Proisocrinus*, which are filter-feeders, were observed on guyots and conical seamounts (Figure 2.6D). The deep-sea coral commensal ophiuroid *Ophiocreas* was also observed in high abundance on atolls, likely in association with optimal current habitat of its octocoral host.

The brisingid *Freyastera* was observed on several inactive vents with its arms extended into the water. In contrast, the sea cucumber, cf. *Hansenothuria* spp. was also observed on inactive vent settings but feeding mode was suggested deposit feeding (Figure 2.6D). Other trends included the sea cucumber *Psolus* spp. present only on islands, and

brisingid species in the genus *Freyella* were abundant in abyssal habitats (Figure 2.6D). Of all the taxa examined in this study, echinoderms were the least well characterized, showing a higher ratio of knowns to unknowns only at the family level (Pearson's chi-square $\chi^2 = 8,564.2$, $df = 2$, $p < 0.001$). In general, community assemblages are similar across ridge and conical seamounts, banks, guyots, atolls, and islands, and surprisingly, vents harbor similar assemblages as well (Figure 2.8). Abyssal and inactive vents have distinct echinoderm communities at the genus level (Figure 2.8). American Samoa displayed the most unique taxonomic assemblage (Figure 2.8). Several observations of undescribed echinoderm taxa, including nine new species and two new genera of asteroids, in the families Goniasteridae and Ganeriidae were made during CAPSTONE. Important ecological observations of rarely encountered species, known only from unique or damaged specimens, were also made throughout the campaign. The goniasterid, *Circeaster arandae*, described by Mah (2006), was originally described from two dried specimens collected in the early 20th Century and not seen since. CAPSTONE was the first to observe this species *in situ* and as a significant predator on deep-sea octocorals.

2.4.6 Regional Comparisons

Across anthozoans, poriferans, and echinoderms, the most abundant taxa are concentrated in the Western Pacific, Hawaiian Islands, and South-Central Pacific Regions (Figure 2.4-2.6). Marianas and American Samoa Regions have unique taxa (heatmaps, Figure 2.4-2.6). Despite this, all regions show similar patterns of known versus unknown diversity at the family, genus, and species level (Figure 2.2). The Western Pacific Region appears to have the most known diversity at the genus level (Figure 2.2), but note that the

majority of dives in this region were on guyots.

The family Chrysogorgiidae was the only family to be in the top five most abundant for all regions, with abundance ranging from 4.58% (American Samoa region) to 15.50% (Hawaiian region; Figure 2.4). Isididae was the most abundant family in Hawaiian region, fifth most abundant in Marianas, and was in the top 10 most abundant for all other regions. Primnoidae was the most abundant family in South- Central Pacific (17.59%) and Western Pacific (21.06%) and in the top five most abundant for the Hawaiian region (10%). Primnoidae represented only 3.82% of individuals observed in the Marianas and 0.39% of individuals in the Marianas.

While the family Coralliidae was common in the Hawaiian Region (11.77%), South-Central Pacific (2.76%), and Western Pacific (10.17%), it was completely absent from the American Samoa region and represented only 0.26% of individuals in the Marianas. Conversely, other families were common in the Marianas and absent elsewhere. For example, Stylasteridae only appeared in the top five most abundant families in the Marianas region (14.34%). Although geographically distant, there were some similarities between American Samoa and the Marianas, which generally grouped away from other regions (Figure 2.8). For example, the most abundant family in American Samoa was Dendrophylliidae (39.3%), which was the third most abundant family in the Marianas (10.33%), but not in the top five most abundant for any other region. Antipathidae was only in the top five most abundant families in the American Samoa region (26.08%). There was no overlap between the most abundant genus in each region.

2.5 Discussion

The Pacific Ocean, totaling 161,760,000 km², has hosted voyaging and discovery since the beginning of human history, and as such has become an icon of vastness and exploration. CAPSTONE was a systematic exploration effort aimed to increase the mapping and ROV image data available for the Pacific seafloor. In this, CAPSTONE greatly succeeded, and has generated new ideas and hypotheses as well as highlighted challenges and opportunities for future exploration. The main contributions of this paper are therefore (1) providing a high-level overview of the methods, datasets, and key findings of CAPSTONE; (2) conducting a high-level initial analysis of basin-scale patterns of biogeography and biodiversity across the Pacific; (3) generating new hypotheses about distribution of taxa across depth, geographic regions, and geologic features, and (4) highlighting the knowledge gaps in mapping, exploration, and biodiversity in the Pacific deep-ocean. Prior to CAPSTONE, the best bathymetry available in most of the areas was satellite-derived bathymetry (Amante & Eakins, 2009). The bathymetry acquired during CAPSTONE enabled detailed examination of 323 seamounts and seafloor features, which in turn enabled 168 ROV dives. This overall effort yielded 0.37% bathymetry mapping of the seafloor in the Pacific Ocean. However, because ~68% of the Pacific is abyssal plain (deeper than 3,000 m), and because CAPSTONE mapping data were disproportionately focused on features of interest (e.g., seamounts, atolls, and vents), the contribution of CAPSTONE to our understanding of Pacific Ocean geology and biology is much >0.37% and 3% of US EEZ. At the same time, these statistics reveal how much is still yet-to-be-explored.

One of the major findings of this paper is the extent of unidentified observations over the 3 years of CAPSTONE. It has long been known that the deep-sea is one of the largest and last earth wildernesses to be explored (Ramirez-Llodra et al., 2011) but the ability to quantify the extent to which we need to explore it has not previously been fully articulated. It is now clear that 86.22% of the Pacific has yet-to-be mapped (Table 2.2), and over 99% of it yet-to-be-imaged (Ramirez-Llodra et al., 2010). For all taxonomic groups examined in the deep sea, we found that fewer than 20% of the species were able to be identified, and this number is limited to the organisms large enough to be visualized in habitats accessible with the ROV. In the Mediterranean deep- sea, biodiversity among different taxa was estimated to the species level across depths, with meiofauna expected to be the most biodiverse (Danovaro et al., 2010). CAPSTONE did not assess any meiofauna, thus even with the incredible diversity measured on this campaign, quantitative unknowns are still likely to underestimate overall diversity. Clearly, more taxonomy and systematics work is needed, in addition to basic mapping and exploration.

Patterns of biodiversity across the Pacific are still unresolved, as there are very few extensive studies that occur over a basin- wide scale. A recent paper proposed biogeographic provinces for the bathyal, abyssal, and hadal faunal communities across the Pacific (Watling et al., 2013), but full tests of the proposed Pacific boundaries have been challenging due to lack of data. The basin-wide scale approach of CAPSTONE crossed 48 degrees of latitude and 61 degrees of longitude. While postulating biogeographic provinces is outside the scope of this paper, the South-Central Pacific region had highest family and genus diversity, which is consistent with previous evidence showing that the Central Pacific deep sea has relatively high

benthic diversity (Lambshead et al., 2002). Although geographically close, American Samoa is very distinct from the South-Central Pacific, likely due to ocean circulation passages in the region that may act as a barrier for larval dispersal, specifically the Samoan Passage (Herrera et al., 2018). In addition, American Samoa lies in close proximity to the intersection of bathyal provinces predicted by Watling et al. (2013), which may also contribute to the difference in community assemblage compared to the South-Central Pacific. In contrast, though geographically distant, American Samoa and Marianas had some unexpected similarities in community assemblages, especially within Anthozoa, that beg further investigation.

More broadly, species biodiversity has been thought to be unimodal with an equatorial peak and a corresponding decline in species richness from the lower to higher latitudes, generally demonstrated in terrestrial (Gaston, 2000; Kaufman, 1995), and shallow-water marine species distributions (Fautin et al., 2013; Hillebrand, 2004). However, Chaudhary et al. (2016) found a dip in shallow marine species richness just below the equator. Although taxonomic assemblages varied widely among regions and features across the Pacific, we found that all regions show similar patterns of known versus unknown diversity at the family, genus, and species level (Figure 2.2), which was relatively surprising. However, the current proposed biogeographic boundaries for bathyal species (Watling et al., 2013) were largely derived from ophiuroid fauna on the Austral plate (O'Hara et al., 2011) and from seamount data largely describing deep-sea sponge and coral communities. We thus similarly restricted our focused taxonomic examinations to the class Anthozoa, and phyla Porifera and Echinodermata, which were the top three most abundant and highest confidence identifications, though CAPSTONE annotation data captured all taxa identifiable by visual surveys on ROV dives.

There are many insights to be gleaned from CAPSTONE data, many of which will require substantial further investigation. For example, we found that Anthozoa, Porifera, and Echinodermata all have some genera that are highly specific to geologic features. This is surprising because, at depth (1,000–4,000 m), no major differences were expected between vertical slopes on islands, atolls, banks, guyots, or conical seamounts. Historically, seamounts have been proposed as deep-sea refugia and stepping stones for dispersal due to similarities among clusters of seamounts (reviewed by Clark et al. 2010, Shank 2010). Generally, these features are all manganese-encrusted, residing in similar oceanographic conditions (Hein et al., 2013; Mizell et al., 2020), and often in close geographic proximity. Therefore, we expected that dispersal and recruitment on available structures would be indiscriminate of seamount shape or height. Yet, the apparently preferential distribution and abundance of specific taxa to one feature over another in our data suggests otherwise. Recent work in shallow reef environments has shown that the terrestrial environment has been more important than previously appreciated, mostly mediated by bird guano and nutrient inputs via groundwater and lagoonal flow (Graham et al., 2018; McMahon & Santos, 2017); anthropogenic impacts via wastewater and manure have been shown to affect nutrient coastal fluxes on tropical Pacific islands via groundwater as well (Shuler et al., 2019). Submarine groundwater discharge has been shown to impact marine biota across all kingdoms of life, around the globe (reviewed by Lecher and Mackey, 2018), but the depths to which these impacts reach have thus far remained uninvestigated. Our study tantalizingly suggests that surface or shallow-water dynamics on islands versus atolls versus banks may influence deep-sea benthic communities; this requires further study.

Several new genera and new species were observed and collected during CAPSTONE, including a previously undescribed genus and species of sea star (family Goniasteridae, class Asteroidea) discovered in the Musicians Seamounts in 2017 (Figure 2.7). CAPSTONE data have already been instrumental in the description of 13 new species and two new genera of Primnoid corals (Cairns, 2018), as well as a new species of stylasterid coral, *Crypthelia kelleyi* from the Northwest Hawaiian Islands (Cairns, 2017). One new genus, *Macroprimnoa* spp., possesses some of the largest polyps in the family (Cairns, 2018). A likely novel species of *Neopilina* monoplacophoran was observed in American Samoa, which expands the known diversity of living monoplacophorans (Sigwart et al., 2018), which were previously known from the fossil record but only discovered to be extant in 1952 (Lemche, 1957). New species are still regularly being discovered, to some extent scaling with exploration effort (e.g., Ramirez-Llodra et al., 2010). As such, our rarefaction curves for each taxon, demarcated by depth, should help to focus exploration effort by depth and taxa for the future.

In addition to new taxa, there have been several new records of range, depth, size, or behavior. In the Hawaiian Islands Region, incirrate octopods were discovered deeper than had previously been reported, 4,120–4,197 m (Purser et al., 2016). One of the largest living sponges in existence, a hexactinellid sponge in the subfamily Lanuginellinae, was documented at 2,117 m in the Papahānaumokuākea Marine National Monument in the Hawaiian Islands region (Wagner & Kelley, 2017). The only other living sponges known to be comparable in size are *Monorhaphis chuni* sponges from the East and South China Sea, with spicules reaching up to 2.7 m in length (Jochum et al., 2017). Our study did not examine fish in any detail beyond inclusion in all-taxa diversity pie-charts; however, CAPSTONE has already yielded some

teleost discoveries. The first aphyonid- clade brotula fish was observed alive in its natural habitat in the Mariana Archipelago (2,504.2 m); this improbable fish, which is translucent with no swim bladder and diminished eyes, had never been imaged *in situ* prior to CAPSTONE (Mundy et al., 2018). Myriad other new records likely exist in the dataset. For example, in the deepwater areas around Kingman Reef, several gastropods were observed putatively grazing on bathyocrinid stalked crinoids, reminiscent of coprophagus snails (Platyceratidae) known from Paleozoic fossils but thought to be extinct (Figure 2.7). These, and other observations have yet to be fully described and require additional analysis.

Whole new features have also been discovered, for example three new sites of hydrothermal activity in the Marianas, including the first survey of a new black smoker vent field composed of multiple chimneys in the Mariana Back Arc (Figure 2.7). While not covered in this analysis, CAPSTONE also included some of the first-ever midwater ROV exploration dives in many of these areas (Netburn et al., 2018) and collected numerous geological samples that may provide new insights into seafloor history or ferromanganese crust dynamics. Additionally, on the benthos, many more features were discovered with high resolution multibeam mapping over areas that had previously only been mapped using satellite altimetry, often resolving great discrepancies in depth or form of features. For example, in the Jarvis Unit of the Pacific Remote Islands Marine National Monument (PRIMNM), multibeam data revealed an approximate 1,700 m height difference when compared to previous satellite altimetry (Figure 2.7). Yet, despite these massive leaps forward in mapping, exploration, taxonomic description, and functional insights, the context for our ocean understanding is still derived from a scant 5% of the seafloor explored, with <10% mapped with modern methods

(Mayer et al., 2018). Thus, the discovery of new features is expected to increase with additional mapping and exploration effort.

In addition to providing valuable information on the features, habitats, and species in the Pacific, CAPSTONE also contributed publicly accessible baseline data and critical information needed to respond to emerging regional issues such as deep-sea mining, sustainable deep-sea fisheries, and changes in ocean dynamics. During the 3 years of CAPSTONE expeditions, *Okeanos Explorer* visited every US National Marine Monument in the Pacific, including many that previously had no information about their deepwater communities, thus greatly expanding our deep-sea knowledge within these boundaries (Cantwell, Elliott, & Kennedy, 2018; Maxon et al., 2021; Wagner et al., 2016). These expeditions conducted the deepest surveys in every unit of PRIMNM, Papahānaumokuākea Marine National Monument, and Rose Atoll Marine National Monument/the National Marine Sanctuary of American Samoa. In several areas, CAPSTONE expeditions were the first to explore in deep-water, for example in the Phoenix Islands (in both the United States and Kiribati), Wake Island, Johnston Atoll, and the Musicians Seamounts (Bohnenstiehl et al., 2018; Demopoulos et al., 2018; Elliott et al., 2016; Smith et al., 2018).

Modern advances are broadening the opportunities for exploration with increased robotics, optics, and telepresence (Gregory et al., 2016; Kaiser et al., 2012; Kennedy et al., 2016; Kennedy et al., 2020; Vogt et al., 2018). While there are still more advances to be made, CAPSTONE represents the largest area of seafloor imaged in a single campaign. While using video data for taxonomic identification has limitations, such as instances of poor image quality

and the inability to conduct lab-based analyses, the key advantage is that video annotation affords an efficient and tractable method to study taxa. Given emerging deep-sea technologies and exploits, exploration is a global priority (Cordes & Levin, 2018). Exploration helps to describe species and habitats, understand the drivers of community structure, and generate testable hypotheses about deep-sea ecosystems that will better-serve all users and stakeholders. One major contribution of this paper is intended to be the initial consolidation and presentation of the CAPSTONE data suite, to showcase the opportunities for novel hypothesis-testing and seed novel ideas. Differences between islands vs. atolls, or conical seamounts vs. guyots, for example, were not previously thought to be important in structuring deep-sea communities. Our analyses suggest otherwise, and these observations (and others) in this paper would benefit from future, finer-scale analysis efforts. Additionally, as technology improves, new methods for maximizing the utility of deep-sea video data for biological research will allow the use of emergent technologies such as machine-learning and autonomous data collection platforms to increase the pace of exploration. The current video archive can be re-annotated and mined for new observations and patterns that were not originally intended. Thus, CAPSTONE data offer the opportunity to test how large-scale video analysis and annotation can be creatively used now, and into the future.

Now that data baselines have been set across 168 dive sites in the Pacific, it is important to leverage these visual observations to more thoroughly test mechanisms and drivers of community composition in the deep-sea. Many of the places visited during CAPSTONE are remote and infrequently visited, thus the ability to deploy expendable technology that would continue to record time series data after the ships have departed, without the need to return to

for retrieval, will be critical to turn single-visit observations into a much richer dataset. With forward planning, ROV visitation could optimize our ability to understand community distribution, long-term site conditions, and how deep-sea fauna interact with their environment and begin to inform connectivity patterns, basin- wide. Especially because most of the Pacific CAPSTONE sites reside within large-scale marine protected areas (LSMPAs), these locales will likely remain free from exploitation, thus serving as valuable benchmarks for deep-sea community response to larger-scale issues and changes in global and Pacific-wide ocean dynamics. Although historically LSMPAs lack sufficient deep-water information for government officials to effectively manage these areas and monitoring these LSMPAs has been shown to be particularly difficult (Friedlander et al., 2016), the baseline provided by CAPSTONE and the potential for future autonomous monitoring will enable managers to better assess LSMPA status.

Coordinated field efforts that result in consistent datasets are absolutely critical in order to reduce “unknowns” in the deep sea. Standardized efforts across large areas offer opportunities to better understand geographic patterning as well as the rare ability to make regional comparisons. CAPSTONE has made major inroads into the necessary data to generate these comparisons, though there are still major gaps in our understanding, due in part to the uneven distribution of effort across feature types and depth ranges that could be remedied with a gap analysis and a future targeted effort to fill exploration gaps by region, and also by depth and feature. Nonetheless, CAPSTONE represented a model of systematic exploration that is critical to understanding one of the earth’s largest ecosystems (Ramirez-Llodra et al., 2011). As we look to the future of ocean exploration, coordinated field campaigns should incorporate

multiple ships and additional technologies including towed arrays, ship mounted systems, and autonomous systems, in order to maximize data collected. Projects like Seabed 2030 (Mayer et al., 2018) have set ambitious goals that can only be accomplished through internationally coordinated efforts. If one ship can only map 0.37% of the Pacific in 3 years, additional assets with a diversity of systems will need to work together to map the whole ocean in just over a decade.

Ironically named, CAPSTONE is more of a beginning than a culminating experience. It is the launch of decades of data-mining, visual analyses, hypothesis-generation, and justification for future exploration. The trends highlighted in this paper offer a snapshot of what is known, and what remains unknown, in the Pacific Ocean. What we have learned from 3 years and 891.5 h on the seafloor is that the Pacific is not just a place of historical exploration and voyaging: it is a place that offers extensive opportunities for technology innovations, and insights. In other words, it is a place for future discovery.

2.6 Acknowledgements

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018; and Marshall Islands Ministry of Foreign Affairs permit #US/98-15. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

2.7 Data availability

The datasets generated by the NOAA Ship *Okeanos Explorer* that were analyzed for this study are archived in the NOAA archives and can be found through the OER Digital Atlas (https://www.ncddc.noaa.gov/website/google_maps/OE/mapsOE.htm). ROV video annotations can be found in the Deep Sea Coral Research and Technologies' Deep Sea Coral Data Portal at [https:// deepseacoraldata.noaa.gov/](https://deepseacoraldata.noaa.gov/).

Table 2.1.

Nested pie chart shows overall taxonomic diversity at the family level (inner circle), genus level (middle circle), and species level (outer circle), for all taxa annotated at each feature. Unidentified annotations are represented by the largest black bar originating at 12:00, progressing counter-clockwise. Bottom right-table indicates number of ROV dives per feature (defined in this table) in each geographic region (defined by [Figure 2](#)).


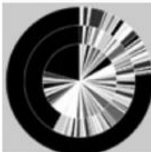
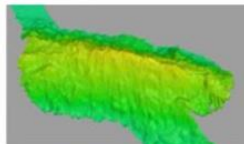
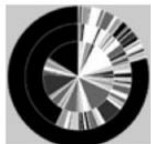

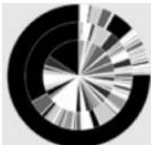

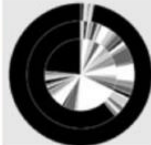
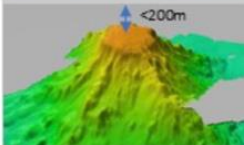
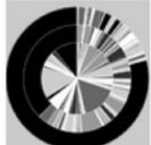

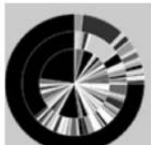
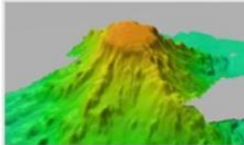
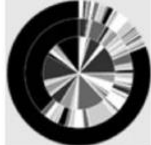

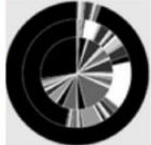
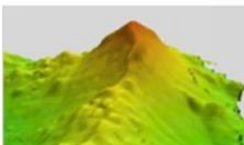
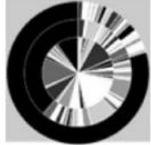
| Geological feature type | Example | Diversity chart | Geological feature type | Example | Diversity chart | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|--|---|---|--|---|---|----------------|---------------|-------|---------|-------|------------------|----------------|---------------|------|---------|--------|---|---|----|----|----|----|---|---|---|----------|---|---|---|---|---|---|---|---|---|-----------------|---|---|----|---|---|---|---|---|---|----------------|---|---|---|---|---|---|---|---|---|------------------------|---|---|---|---|---|---|---|---|---|
| Island: Emergent land mass surrounded by water |  |  | Ridge seamount: Rising from the seafloor with an elongated summit forming a ridge-like feature |  |  | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Atoll: Emergent land and a central lagoon either partially or fully enclosed by land |  |  | Inactive vent: recent hydrothermal or volcanic activity that is not currently active |  |  | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Bank: A guyot-shaped feature where the shallowest point is <200 m water depth |  |  | Vent: A dive site with active hydrothermal activity |  |  | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Guyot: undersea mountain rising from the seafloor with a flat top deeper than 200 m |  |  | Abyssal: Any dive site between 4,000 and 6,000 m |  |  | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Conical seamount: undersea mountain rising from the seafloor: pointed summit. |  |  | <table><tr><th></th><th>Island</th><th>Atoll</th><th>Bank</th><th>Guyot</th><th>Conical Seamount</th><th>Ridge Seamount</th><th>Inactive Vent</th><th>Vent</th><th>Abyssal</th></tr><tr><td>Hawaii</td><td>4</td><td>4</td><td>13</td><td>25</td><td>15</td><td>12</td><td>0</td><td>0</td><td>1</td></tr><tr><td>Marianas</td><td>3</td><td>1</td><td>4</td><td>4</td><td>6</td><td>3</td><td>4</td><td>7</td><td>8</td></tr><tr><td>Western Pacific</td><td>0</td><td>2</td><td>10</td><td>0</td><td>0</td><td>0</td><td>0</td><td>0</td><td>0</td></tr><tr><td>American Samoa</td><td>3</td><td>3</td><td>0</td><td>0</td><td>6</td><td>0</td><td>0</td><td>1</td><td>0</td></tr><tr><td>South Central Pacific.</td><td>6</td><td>3</td><td>1</td><td>9</td><td>3</td><td>6</td><td>0</td><td>0</td><td>1</td></tr></table> | | | | Island | Atoll | Bank | Guyot | Conical Seamount | Ridge Seamount | Inactive Vent | Vent | Abyssal | Hawaii | 4 | 4 | 13 | 25 | 15 | 12 | 0 | 0 | 1 | Marianas | 3 | 1 | 4 | 4 | 6 | 3 | 4 | 7 | 8 | Western Pacific | 0 | 2 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | American Samoa | 3 | 3 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | South Central Pacific. | 6 | 3 | 1 | 9 | 3 | 6 | 0 | 0 | 1 |
| | Island | Atoll | Bank | Guyot | Conical Seamount | Ridge Seamount | Inactive Vent | Vent | Abyssal | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Hawaii | 4 | 4 | 13 | 25 | 15 | 12 | 0 | 0 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Marianas | 3 | 1 | 4 | 4 | 6 | 3 | 4 | 7 | 8 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Western Pacific | 0 | 2 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| American Samoa | 3 | 3 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| South Central Pacific. | 6 | 3 | 1 | 9 | 3 | 6 | 0 | 0 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

Table 2.2.

CAPSTONE multibeam mapping accomplishments after 3 years of effort by the Okeanos Explorer.

| Location | Total area (km ²) | Total mapped after CAPSTONE (km ²) | % Area mapped after CAPSTONE | Area mapped by CAPSTONE (km ²) | % Area mapped by CAPSTONE |
|--|----------------------------------|---|---------------------------------|---|---------------------------------|
| Pacific Ocean | 161,760,000 | 22,299,018 | 13.78 | 597,230 | 0.37 |
| Papahānaumokuākea MNM | 1,508,874 | 578,008 | 38.31 | 94,157 | 6.24 |
| Johnston Atoll PRIMNM | 442,443 | 122,804 | 27.76 | 62,482.4 | 14.12 |
| Wake Island PRIMNM | 406,970 | 111,580 | 27.42 | 53,259 | 13.09 |
| Marianas Trench MNM | 204,543 | 167,129 | 81.71 | 21,611 | 10.57 |
| Phoenix Islands Protected Area | 406,801 | 68,020 | 16.72 | 19,196 | 4.72 |
| NMS of American Samoa (Muliava Sanctuary Unit/Rose Atoll MNM) | 34,934 | 16,216 | 46.42 | 1,195.4 | 34.22 |
| Jarvis Island PRIMNM | 315,339 | 58,889 | 18.67 | 11,911 | 3.78 |
| NZ Territory of Tokelau | 318,507 | 79,874 | 25.08 | 10,604.2 | 3.33 |
| Howland Island and Baker Island PRIMNM | 51,149 | 15,041 | 29.41 | 6,356.38 | 12.43 |
| Kingman Reef and Palmyra Atoll PRIMNM | 53,175 | 46,665 | 87.76 | 5,379.92 | 10.12 |
| Marae Moana (proposed) | 1,961,280 | 344,043 | 17.54 | 3,776.59 | 0.19 |
| Swains Island Sanctuary Unit | 135 | 135 | 99.61 | 112.645 | 83.22 |

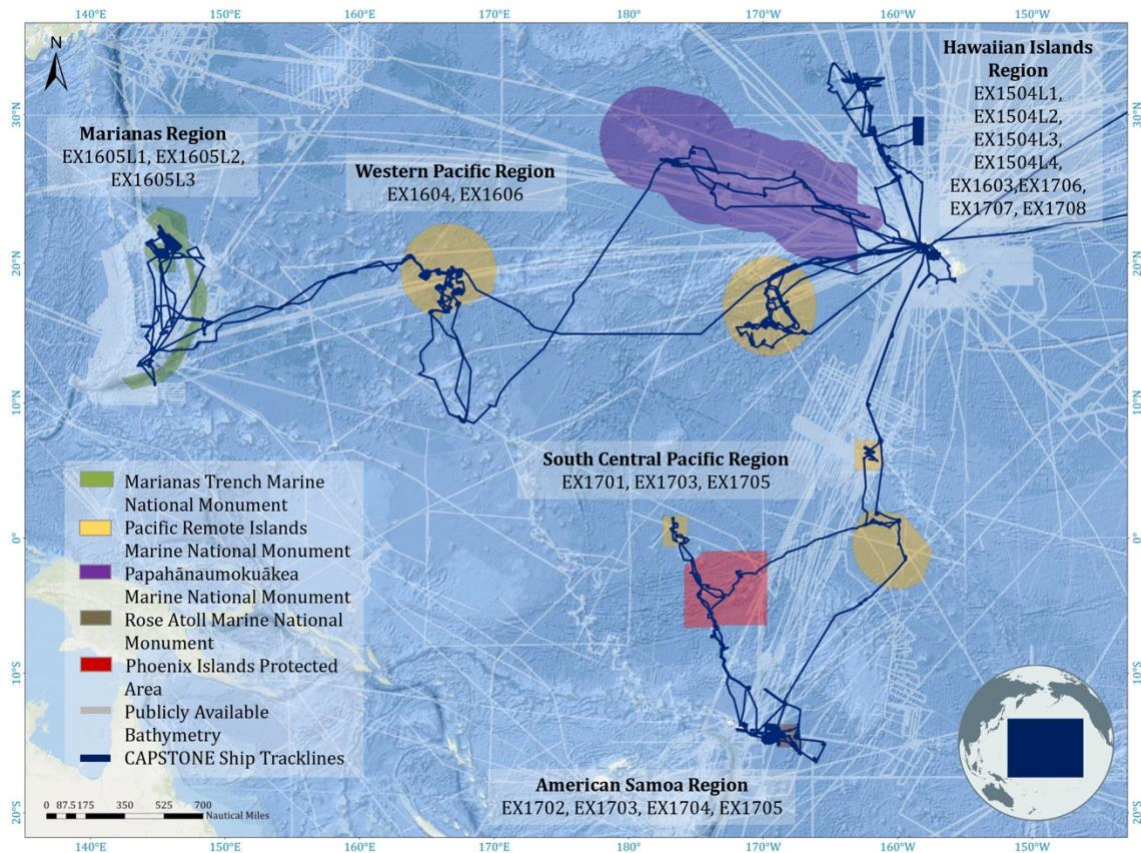


Figure 2.1. Multibeam EM302 operations conducted by NOAA Ship *Okeanos Explorer* (dark blue ship track lines) during CAPSTONE 2015–2017. Existing bathymetry background layer was obtained from National Centers for Environmental Information (NCEI), made available through a request to NCEI staff to provide multibeam footprint of data held at NCEI.

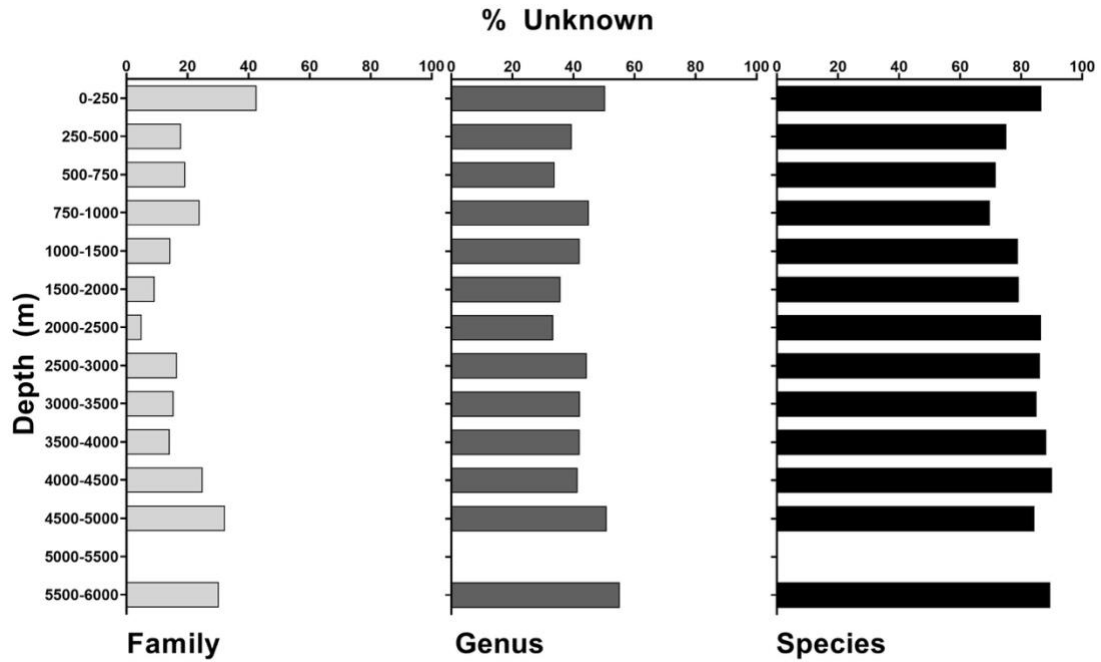


Figure 2.2. CAPSTONE ROV dive sites (black dots) organized by region (Marianas, Western Pacific, Hawaiian Islands, South-Central Pacific, American Samoa). Marine Protected Areas boundaries are indicated by polygons. Nested pie charts show overall taxonomic diversity at the family level (inner circle), genus level (middle circle), and species level (outer circle), for each region. Unidentified annotations are always represented by the largest black bar originating at 12:00, progressing counter-clockwise.

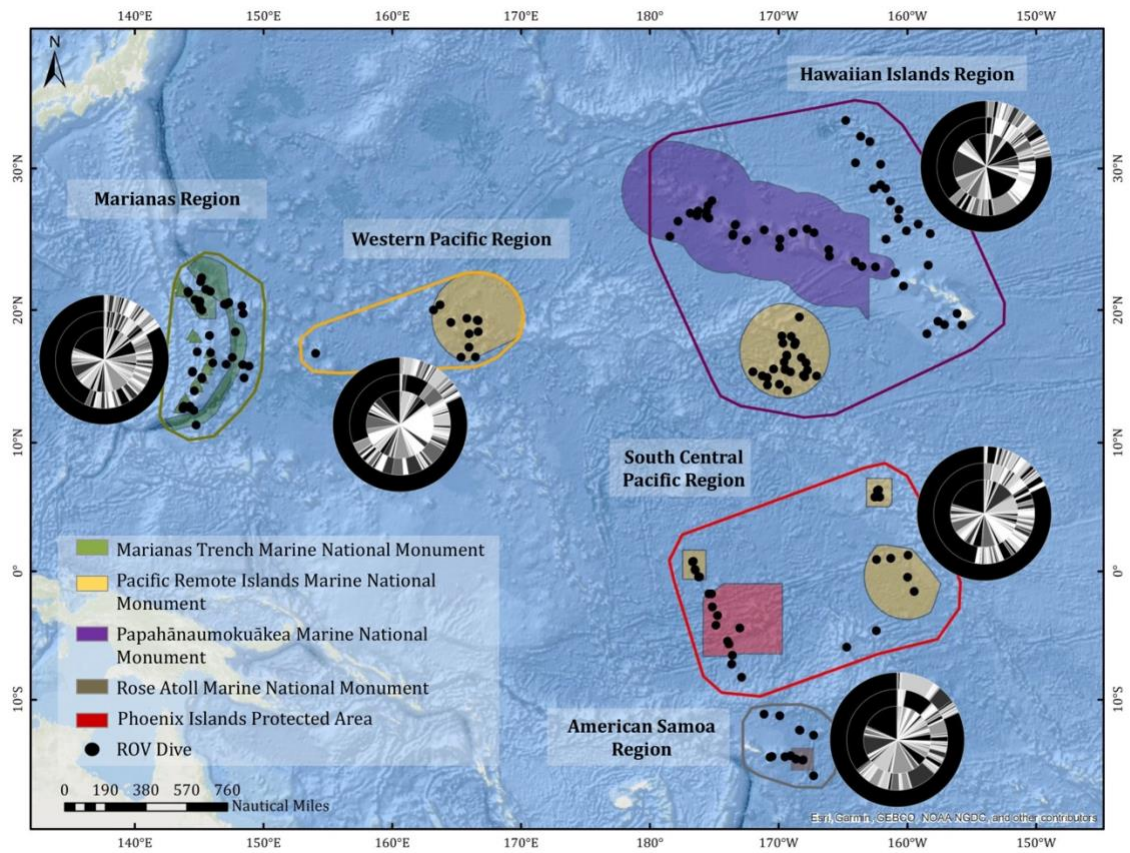


Figure 2.3. Unidentified annotations (%) across all taxa at the family, genus, and species levels for all of CAPSTONE, demarcated by depth ranges.

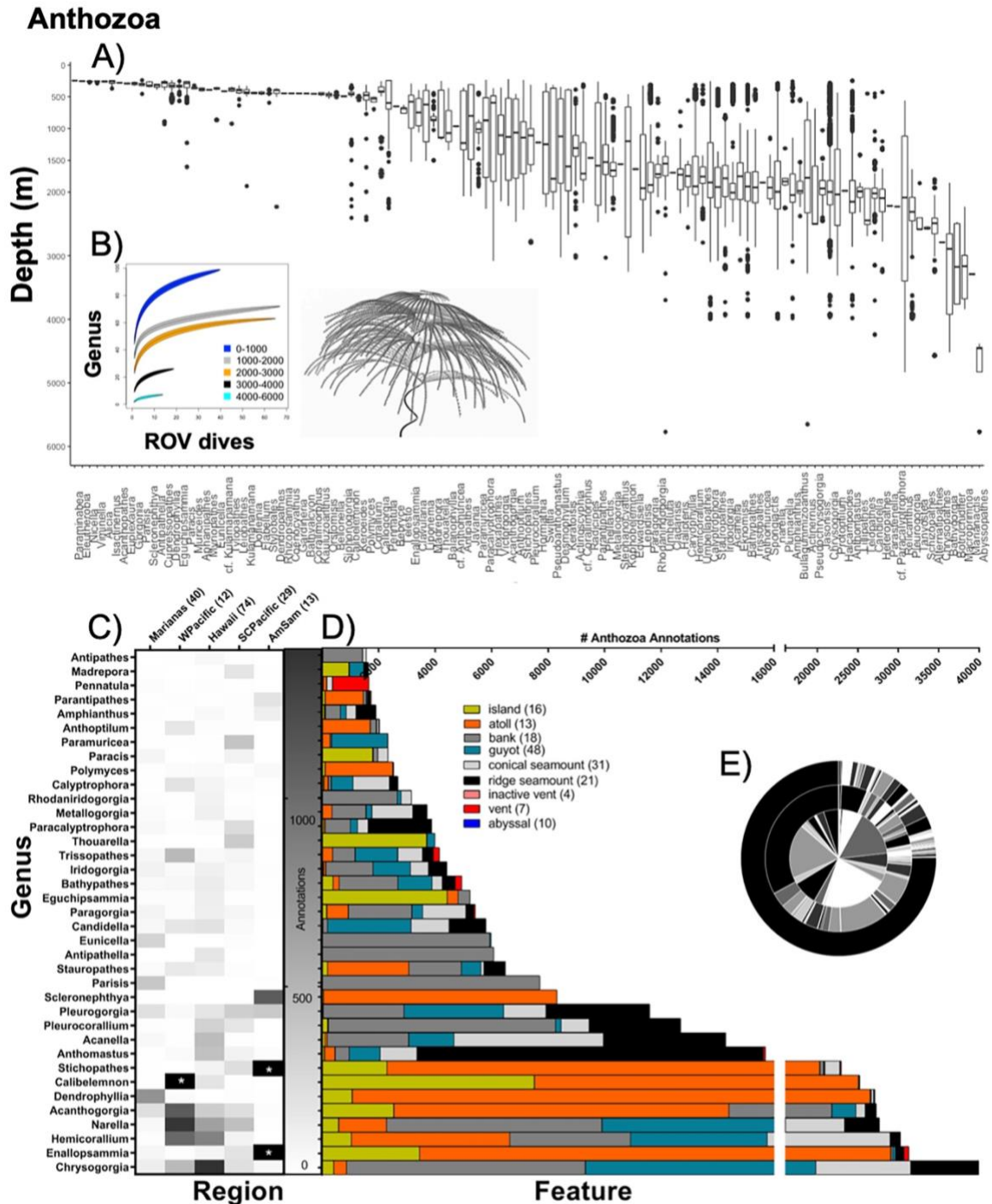


Figure 2.4. Top panel: **(A)** Anthozoa annotations at the genus-level demarcated by depth (m). A total of 221,264 anthozoan annotations were used to make box-and-whisker plots, organized from shallow to deep along the x-axis. A total of 122 anthozoan genera were observed over CAPSTONE. Rarefaction curves **(B)** are shown for all of Anthozoa (122 genera), color coded by depth 0–1,000 m (blue) 1,000–2,000 m (gray), 2,000–3,000 m

(orange), 3,000–4,000 m (black), and 4,000–6,000 m (cyan). Lines are drawn with a 95% confidence envelope. Bottom panel: Anthozoa annotations representing at the genus-level demarcated by **(C)** geographic region and **(D)** geologic feature; the number of dives for both are in associated parentheses. A total of 37 anthozoan taxa are shown, representing every genus where 1,500 observations or more were made during CAPSTONE. Starred boxes on heatmap represent abundances outside the range represented, specifically, 33,080.25 *Enallopsammia* spp. corals and 24,342.32 *Stichopathes* spp. were observed (corrected for effort) in American Samoa. Axis breaks by feature do not omit any data; breaks instead allocate annotation effort on different scales. **(E)** Nested pie chart shows overall taxonomic diversity at the family level (inner circle), genus level (middle circle), and species level (outer circle), for all anthozoans annotated. Unidentified annotations are represented by the largest black bar originating at 12:00, progressing counter-clockwise.

Porifera

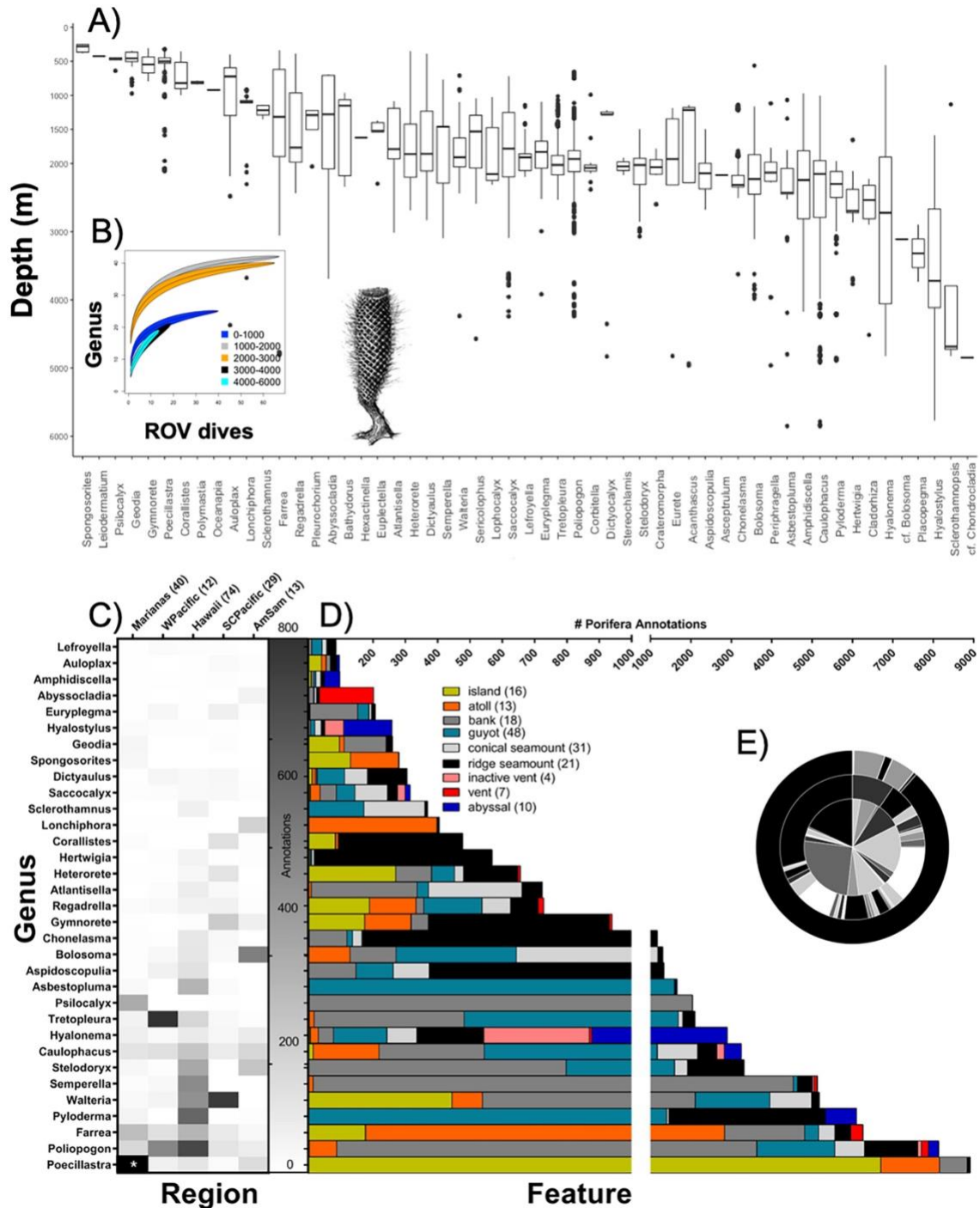


Figure 2.5. Top panel: (A) Poriferan annotations at the genus-level demarcated by depth (m). A total of 46,128 poriferan annotations were used to make box-and-whisker plots, organized from shallow to deep along the x-axis. A total of 55 poriferan genera were

observed over CAPSTONE. Rarefaction curves **(B)** are shown for all of Porifera (55 genera), color coded by depth 0–1,000 m (blue) 1,000–2,000 m (gray), 2,000–3,000 m (orange), 3,000–4,000 m (black), and 4,000–6,000 m (cyan). Lines are drawn with a 95% confidence envelope. Bottom panel: Porifera annotations representing at the genus-level demarcated by **(C)** geographic region and **(D)** geologic feature; the number of dives for both are in associated parentheses. A total of 33 poriferan taxa are shown, representing every genus where 50 observations or more were made during CAPSTONE. Starred boxes on heatmap represent abundances outside the range represented, specifically, 2,877.59 *Poecillastra* spp. were observed (corrected for effort) in the Marianas Region. Axis breaks by feature do not omit any data; breaks instead allocate annotation effort on different scales. **(E)** Nested pie chart shows overall taxonomic diversity at the family level (inner circle), genus level (middle circle), and species level (outer circle), for all poriferans annotated. Unidentified annotations are represented by the largest black bar originating at 12:00, progressing counter-clockwise.

Echinodermata

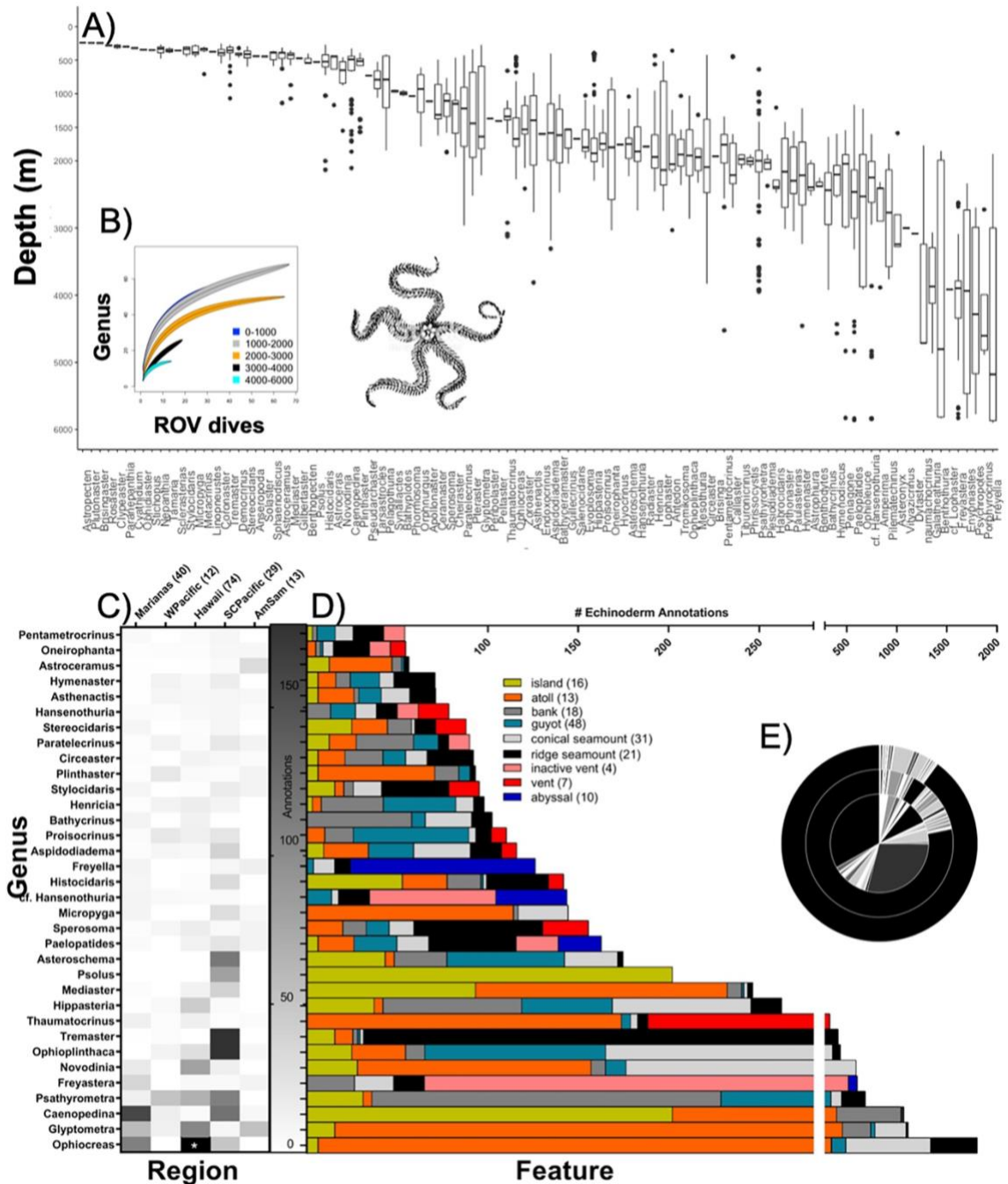


Figure 2.6. Top panel: Echinoderm annotations at the genus-level demarcated by depth (m). **(A)** A total of 29,934 echinoderm annotations were used to make box-and-whisker plots, organized from shallow to deep along the x-axis. A total of 106 echinoderm genera were observed over CAPSTONE. Rarefaction curves **(B)** are shown for all of Echinodermata (106 genera), color coded by depth 0–1,000 m (blue) 1,000–2,000 m (gray),

2,000–3,000 m (orange), 3,000–4,000 m (black), and 4,000–6,000 m (cyan). Lines are drawn with a 95% confidence envelope. Bottom panel: Echinoderm annotations representing at the genus-level demarcated by **(C)** geographic region and **(D)** geologic feature; the number of dives for both are in associated parentheses. A total of 34 echinoderm taxa are shown, representing every genus where 50 observations or more were made during CAPSTONE. Starred boxes on heatmap represent abundances outside the range represented, specifically, 417.32 *Ophiocreas* spp. were observed (corrected for effort) in the Hawaiian Islands Region. Axis breaks by feature do not omit any data; breaks instead allocate annotation effort on different scales. **(E)** Nested pie chart shows overall taxonomic diversity at the family level (inner circle), genus level (middle circle), and species level (outer circle), for all echinoderms annotated. Unidentified annotations are represented by the largest black bar originating at 12:00, progressing counter-clockwise.

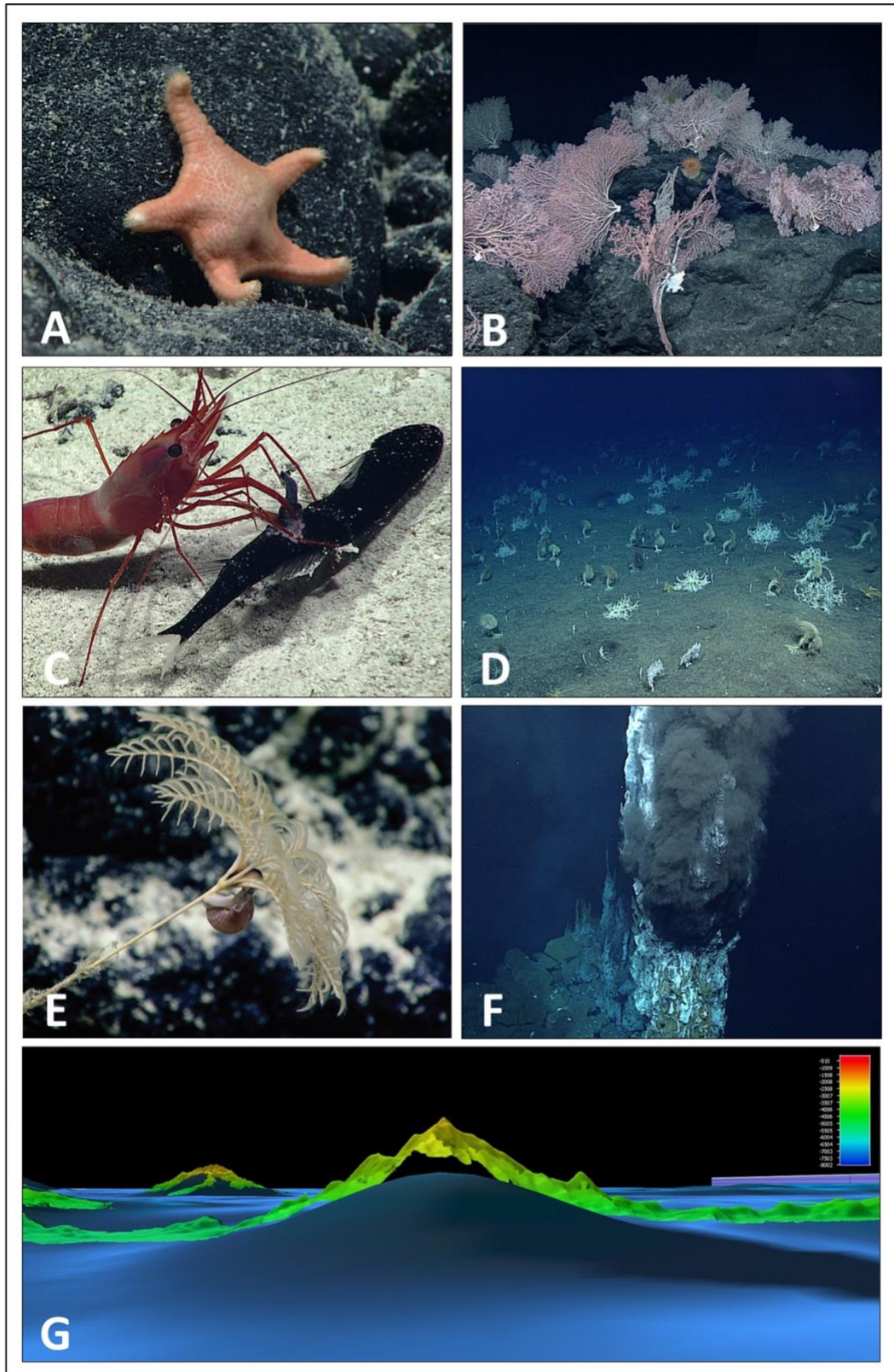


Figure 2.7. Plate of CAPSTONE curiosities: novel taxa, features, and interactions. Several new genera and new species were observed and collected during CAPSTONE, including (A) a previously undescribed genus and species of sea star (family Goniasteridae, class Asteroidea) (C. Mah, personal communication, description in preparation) discovered in the Musicians Seamounts in 2017 (EX1708). In several areas, CAPSTONE expeditions documented deep-sea corals for the first time, including (B) in the Musicians Seamounts (EX1708) where coral communities were observed on every dive not focused on water column exploration or archeology characterization. As the number of observations in the deep sea are limited when compared to the size of the biome, every predator–prey interaction observed contributes to our understanding of deep-sea life history. (C) A caridean shrimp, *Heterocarpus* sp., was observed capturing and feeding on a mid-water dragonfish, potentially *Astronesthes* sp., at Ufiata Seamount in Tokelau (EX1703), an unusual observation as *Heterocarpus* sp. are typically thought to be scavengers. Of particular interest to CAPSTONE were high density communities. Although most observed during CAPSTONE were composed of corals and sponges ([Demopoulos et al., 2018](#); [Smith et al., 2018](#)) (D) at Zealandia Bank in the Marianas (EX1603L1) we documented a rarely observed large aggregation of gorgonocephalid basket stars. (E) In the deepwater areas around Kingman Reef (EX1705) several gastropods were observed with mouth apparently placed on the anal vent of multiple bathyrcrinid stalked crinoids, reminiscent of coprophagus snails (Platyceratidae) known from Paleozoic fossils but thought to be extinct. CAPSTONE also included exploration of hydrothermal vents in the Marianas (EX1605L1 and L3) revealing three new site of hydrothermal activity, including (F) the first survey of a new black smoker vent field composed of multiple chimneys in the Mariana Back Arc. Multibeam data collected over areas that had previously only been mapped using satellite altimetry, often showed significant differences in depth or form of features. (G) In the Jarvis Unit of PRIMNM, multibeam data (EX1701) revealed an approximate 1,700 m height difference when compared to previous satellite altimetry.

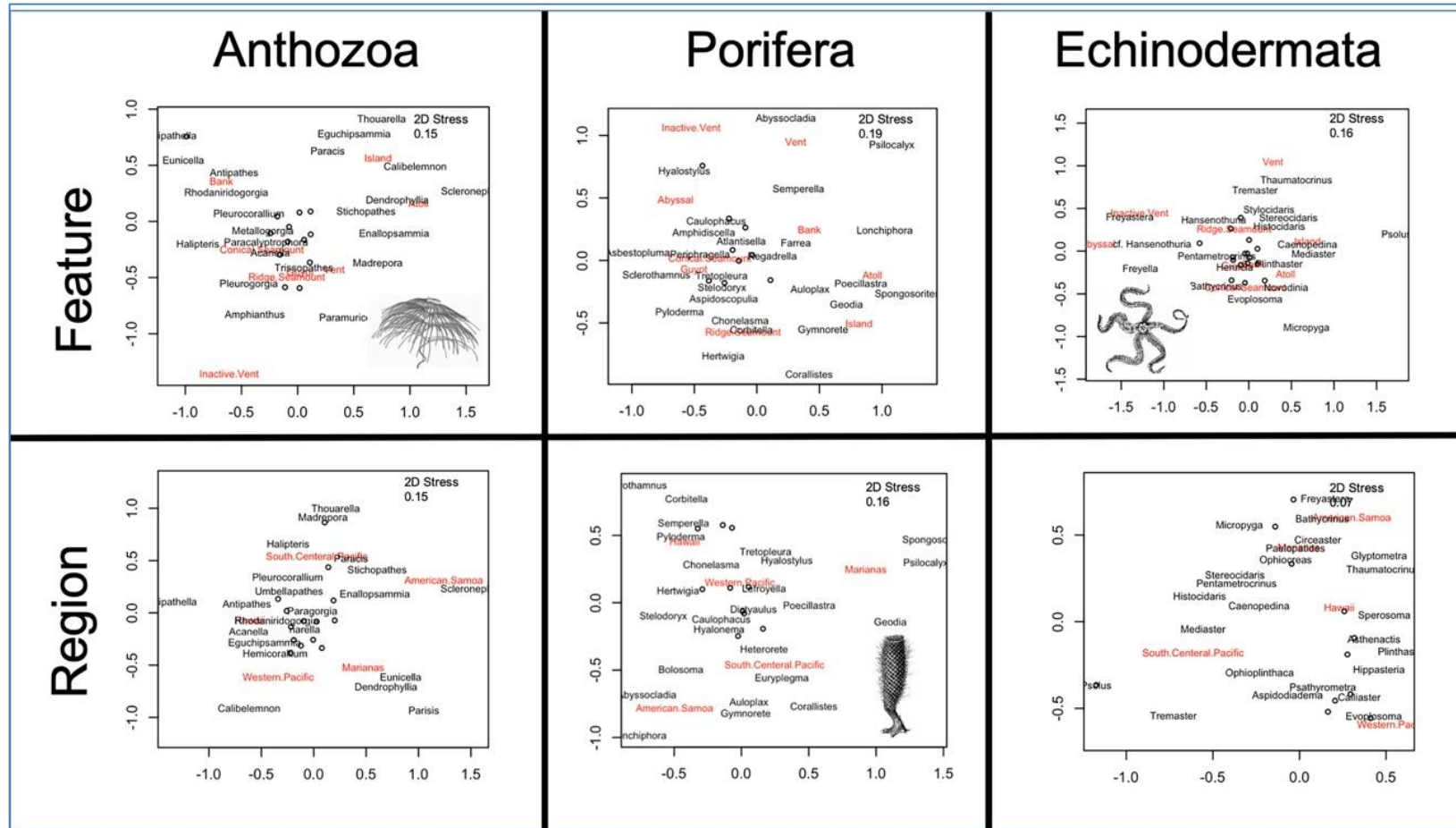


Figure 2.8. Non-metric multiple dimensional scaling ordination of the Bray-Curtis dissimilarity matrices are displayed, with geologic feature (**top panel**) and geographic region (**bottom panel**) groups noted. Taxonomic assemblages are abundances corrected for effort at the genus-level for the highest frequency genera observed ($N = 35$ for each).

CHAPTER THREE: THE IMPACT OF GEOLOGICAL FEATURE SHAPE ON THE ABUNDANCE AND DIVERSITY OF DEEP SEA CORALS

3.1 Abstract

The role of seamount gross geomorphology (i.e., shape) as an abiotic control governing the abundance and diversity of deep-sea corals has not been previously considered and has the potential to provide easily-accessible and transformative insights into deep-water coral biodiversity and its distribution in the global ocean. This study aims to investigate the influence of geological shape (e.g., atolls, islands, banks, guyots, conical, ridges) on deep-sea coral genera and habitats in the Pacific Ocean to determine whether seamount shape is an important predictor of deep-water biological communities. Multivariate analyses were used to test whether the gross geomorphology of seamounts influences the abundance and diversity of deep-water coral genera. Seamounts across the entire Pacific basin were categorized using a standard classification scheme to determine their categorical shape. Across the 50 most abundant deep water coral genera in the data set, all 50 showed a statically significant preference for at least one geomorphological shape. Additionally, the abundance of the different seamount shapes was not evenly distributed across the Pacific basin. Gross geomorphology influences the abundance and diversity of deep-sea corals across the central Pacific, which provides insight into deep water coral community structure the biodiversity coral ecosystems support, and resulting implications for conservation

3.2 Introduction

A fundamental goal of ecology is to disentangle the abiotic mechanisms that control the diversity, abundance and biomass of organisms (Hu et al., 2020). Understanding the interplay between the physical environment and the biological communities they support is critical to understanding any ecosystem. Foundational ecological literature from terrestrial (Chesson, 2000), freshwater (Matthews, 2012), and marine systems (Longhurst, 1985) has demonstrated a notable diversity of interactions. Despite the large body of literature on this topic (Longhurst, 2010), the abiotic mechanisms that drive biological communities in the deep sea are relatively less studied (e.g. Shank et al. 1998, but see Dijkstra et al 2021). Deep-sea ecosystems, which exist at greater than 200 meters of water depth (Levin et al., 2019), are among the least studied ecosystems on the planet, though they contain the majority of Earth's livable space (Robison, 2009). The deep sea has long been considered to be fairly homogeneous with broad distributions of deep-sea species across large areas (McClain & Hardy, 2010). Yet while the deep sea is large, it is not abiotically or biologically uniform (Ramirez-Llodra et al., 2010). The deep sea hosts distinct biological communities that have adapted to the abiotic conditions in each deep water habitat, including submarine canyons (Fernandez-Arcaya et al., 2017; Quattrini, Nizinski, et al., 2015) seamounts (Clark et al., 2010; Morato et al., 2008; Shank, 2010), hydrothermal vents (Ramirez-Llodra et al., 2010; Van Dover, 2000) and cold-water coral reefs (Roberts et al., 2009). However, the ability to fully interrogate the abiotic preferences of biological communities has only recently emerged, thanks to burgeoning technology that is only now becoming more accessible (Danovaro et al., 2010; Ramirez-Llodra et al.,

2010; Webb et al., 2010). Modern access to the deep sea has started to yield large basin-wide datasets (e.g., Kennedy et al. 2019), which can enable opportunities for insight into the drivers of deep-sea biodiversity and abundance at the mesoscale, which is relevant to community-level taxonomic diversity.

To date, deep-sea science has focused on biological organization either from the large ocean basin scale (e.g., North vs South Pacific Ocean) or at a microscale (e.g., one small patch of seafloor), leaving a major knowledge gap at the mesoscale that includes island chains, seamount clusters, or broad benthic habitat types. There has been major progress at the large ocean basin scale with remote sensing technologies that have helped to generate insight into biogeographic patterns that have yielded partitioning of biogeographic provinces (Sutton et al., 2017; Watling et al., 2013; Watling & Lapointe, 2022). However, data densities have historically been too low to empirically measure biotic-abiotic patterns, and instead have relied upon extrapolations from focused-area studies (McClain & Hardy, 2010). The development of predictive habitat models has progressed in terms of taxonomic presence and absence predictions in areas where high resolution bathymetric maps are available (Buhl-Mortensen et al., 2010; Henry & Roberts, 2007), but they still fall short of desired resolution (Rowden et al., 2020). As such, these approaches leave a significant gap in our understanding of the patterns of biological diversity across the ocean floor at the mesoscale. However, recent efforts in exploration-at-scale have greatly expanded available information (Bell et al., 2017; Cantwell, Elliott, & Kennedy, 2018; Demopoulos et al., 2018; Kennedy et al., 2019; Raineault & Flanders, 2019, 2020) making it possible to closely examine mesoscale biodiversity patterns for

highly abundant and common taxa for the first time.

Deep-sea corals are common benthic macrofauna on seamounts and are important deep water ecosystem engineers (Kennedy & Rotjan, 2020). It is increasingly understood that coral taxa provide the foundation for a highly specific suite of associated organisms (Shank et al., 2018), thus, understanding the drivers of coral habitat preference will also inform the accompanying biodiversity associated with those coral taxa (Shank et al., 2018). Corals are widely documented studied and documented of the deep sea sessile macrofauna and as such, the large data sets available on deep water coral taxa can enable investigation of their abiotic preferences at the mesoscale (Cunha et al., 2017; Danovaro et al., 2014; Tyler et al., 2016). Previous work has already provided important insights, and has demonstrated that deep-sea anthozoan abundance and diversity are influenced by localized, microscale seafloor characteristics such as bathymetry, slope, rugosity, aspect, terrain complexity (rugosity and terrain ruggedness index), bathymetric position index, and sedimentary process (Collart et al., 2018; Dolan et al., 2008; Tong et al., 2012; Wilson et al., 2007). There is also strong support in the literature for the role of basin-scale and meso-scale water mass characteristics to influence biomass and diversity of cold water corals; these characteristics include temperature (Auscavitch, Deere, et al., 2020; van Haren et al., 2014; Yasuhara & Danovaro, 2016), current conditions (Mienis et al., 2007; Somoza et al., 2014), oxygen concentration (Levin, 2003; Woulds et al., 2007), organic matter supply (Cathalot et al., 2015; D. P. Tittensor et al., 2010; White et al., 2012), and hydrodynamics (Radice et al., 2016) (Auscavitch, Lunden, et al., 2020; Bryan & Metaxas, 2006; Guinan et al., 2009; Howell et al., 2011). Broadly speaking, these studies have shown that deep-water

corals tend to be found in areas of moderate to high slopes with higher oxygen concentrations and substantial current flow, but this can vary widely based on individual taxa. Further, there are dramatic differences in coral biodiversity and abundance from seamount to seamount, even when depth and many other abiotic factors are similar (Kennedy et al., 2019; Richer de Forges et al., 2000; Shank, 2010).

Volcanic seamounts are distributed globally and are some of the most common landforms on Earth (Menard, 1964). Seamounts are submerged topographic rises greater than 1000 m above the surrounding seafloor (Smith & Cann, 1990) and can provide a range of hard ground habitat needed for deep-sea corals to settle (Shank, 2010). Seamounts have been hypothesized to act as oases in the deep-sea and support endemic and diverse communities than surrounding waters (Samadi et al., 2006), however, these assumptions have been challenged by others (McClain, 2007). Nonetheless, in contrast to the surrounding abyssal plain, all seamounts have abrupt bathymetry that offers sharp relief, which alters the local hydrodynamic environment by causing mixing in the surrounding water masses, resulting in varying currents at seafloor far above the abyssal plain (Wagner et al., 2020). Globally, though seamounts share many commonalities, there are also distinct styles of geomorphology that may influence surrounding water masses and currents. Seamount geomorphology (shape) can change over geological time scales as seamounts grow or erode (Wessel et al., 2022). Conical seamounts are fully submerged features that have never broken the surface, compared to flat-topped guyots that previously were emergent but have since subsided and become fully submerged. Ridge seamounts have extended summits of similar depth without a single pinnacle, and banks can be ridges,

guyots, or conical seamounts that rise to mesophotic depth but are fully submerged. Atolls and islands are not commonly thought of as seamounts because they are emergent features with terrestrial and shallow-water ecosystems, but islands and atolls functionally resemble seamount shapes at depth due to their submerged vertical flanks extending to the abyssal plain. Emergent atolls and islands alter the local hydrodynamic environment, provide hard substrate, and are otherwise geologically similar to other seamounts. These seamount categories are not static; for example, many deep water seamounts have previously been islands in a distant geologic past (e.g., guyots), and some conical seamounts may one day become islands over millennia (Rogers, 2018). However, considering the time scale of deep water coral growth and recruitment, ranging up to 4000 years for the oldest known colonies (Roark et al., 2009), seamount shape is stable. To date, there has been no investigation of the possible effects that these different shapes may have on the biomass and diversity of deep-sea corals that reside on their flanks.

In this study, we leveraged a large mesoscale data set to investigate whether and how deep-water corals discriminate across seamount shapes, using data from the National Oceanic and Atmospheric Administrations' (NOAA) Office of Ocean Exploration and Research Campaign to Address Pacific monument Science, Technology, and Ocean Needs (CAPSTONE) project. This project explored US deep water marine protected areas in the Pacific between 2015 and 2017 and was one of the largest dedicated ocean exploration efforts ever undertaken by the US Government (Leonardi et al., 2018), with 187 remotely operated vehicle (ROV) dives covering nearly 47 degrees of latitude and 64 degrees of longitude, resulting in 891 hours of annotated sea floor video (Kennedy et al., 2019). Deep-

water areas documented during CAPSTONE included nearly every type of seamount geomorphology found at shallower than 6,000 meters depth, including conical seamounts, guyots, banks, ridges, islands, and atolls (Figure 3.1). Given the consistency in operations over a wide geographic and temporal scale, CAPSTONE is one of the largest systematically acquired, basin-scale data sets across the Pacific Ocean (Kennedy et al., 2019). Thus, we can now use this large dataset with its broad geographic range to look for patterns in abundance and diversity of deep-sea corals to ask the question: does seamount shape influence deep-sea coral diversity and abundance? We hypothesize that feature shape will influence biological communities of deep-water corals.

3.3 Methods

3.3.1 Data collection

Mapping and exploration took place aboard the NOAA Ship *Okeanos Explorer*, a 68 m vessel equipped with a full suite of mapping sonars capable of telepresence-enabled operations (Cantwell et al., 2020). The *Okeanos Explorer* was also equipped with a telepresence-enabled, dedicated two-body ROV system, *Deep Discoverer* (D2) and *Seirios*, with a 6,000 m depth rating (Gregory et al., 2016; Kennedy et al., 2016). ROV dives typically lasted 8 hours, but were occasionally extended to 10+ hours based on science objectives, at-sea conditions, and operational limits. D2 was outfitted with a suite of high-definition video cameras, two of which were maneuverable and used principally for scientific observation. These data were recorded for archival and subsequent analysis. Video for 187 deep water dives was recorded in PRORES 1080i format. Lighting consisted of numerous LED lamps, providing 272,000 lumens of light across the entire ROV system.

The CAPSTONE campaign was conducted in the Central and Western Pacific, ranging from 33.3 N (Musician Seamounts) to 15.8 deg S (American Samoa) and 155.7 W (Main Hawaiian Islands) to 143.7E (Marianas Islands). Please see Kennedy et al (2019) for details on dive locations ranging in depth from 4,807 meters to 193 meters.

3.3.2 Data accessibility

Data were derived from public domain resources. The data that support the findings of this study are available from the NOAA Office of Ocean Exploration at <https://oceanexplorer.noaa.gov/data/access/access.html> and annotations were created by the Deep Sea Coral Research and Technology program (<https://deepseacoraldata.noaa.gov/>). These data were derived from the following resources available in the public domain: Video Portal <https://www.ncei.noaa.gov/access/ocean-exploration/video/>), NOAA Ship Explorer Data Landing Pages (<https://www.ncei.noaa.gov/waf/oceanos-rov-cruises/>) for the entire CAPSTONE campaign.

3.3.3 Annotations

The entire 891 hours of video collected during the CAPSTONE project was annotated by a team of experts from the University of Hawaii (UH) using the Video Annotation and Reference System (VARS) system created by the Monterey Bay Aquarium Research Institute (Schlining & Stout 2006). Every organism was identified to the lowest taxonomic level possible and was subjected to a rigorous custom quality assurance/quality control (QA/QC) protocol, looking for inconsistencies in depth, substrate, and identifications. Any potentially problematic records were re-reviewed in triplicate for QC. In addition, each identification was double-checked against the World Order of Marine Species (WoRMs) online taxonomic database. Using the classification scheme described

in Kennedy et. al. (2019), we used a subset of the CAPSTONE data for those dives occurring on atolls, islands, banks, guyots, conical seamounts, and ridge seamounts (Figure 3.1). We excluded all annotations where the genus could not be identified. This left 145 deepwater ROV dives (out of the total 187 in the CAPSTONE dataset) and yielded 219,315 coral individuals identified. As described by Kennedy et al. (2019) and Amon et al. (2020), the ROV was equipped with an Ultra Short BaseLine (USBL) navigation system. The precision and accuracy of the system was heavily dependent on water depth (Wu et al., 2016) and ambient noise, which can cause positional variation between pings to range between 5 and 50 meters. As outlined in Kennedy *et al.* (2019), by measuring the linear distance traveled by D2 via manually tracing a line of best fit based on the 1 Hertz averaged vehicle trackline. When D2 is at an altitude of 1 m, and the camera angle of the primary HD camera is at a 45-degree angle, the field of view yields 2.7 m of seafloor horizontally across the video frame (assuming a steady ROV heading). Because the pilots were nearly continuously changing the heading of the vehicle while scanning the seafloor, as well as flying the vehicle at variable altitudes as the bathymetry dictated, we estimated a visual swath width of a minimum of 5 m (2.5 m on either side of the vehicle path over the bottom) and a maximum of 50 m (calculated as twice the effective length of the tether connecting D2 and *Seirios*). For area imaged calculations in this study, we used the mean value of 25 meters imaged along the track. Detailed explanations for the implied assumptions and methodologies for this approach can be found in Kennedy et al. (2019).

3.3.4 *Statistical approach*

To test the effect of seamount shape on the abundance of deep sea coral genera, we utilized a mixed methods generalized linear model using R version 4.2.0 (R Core Team 2022) and the statistical package MCMCglmm (Hadfield, 2010), which is used to fit Generalized Linear Mixed Models (GLMM) using Markov chain Monte Carlo techniques (Hadfield, 2010). In order to correct for unequal sample size, the individual dive sites were included as a random effect in the model. Given that we were working with count data, a Poisson distribution was used as the distribution for the non-linear link function of the GLMM. The data were also checked for zero-inflation. The MCMC was run for 5000 cycles, and the first 50 iterations were discarded. Models with depth (scaled by dividing by 1000), feature type, temperature, and genus as covariates were tested with deviance information criterion (DIC) scores through a forwards model selection approach (Crawley, 2005). Starting with a null model and then adding each additional model term with each iteration, we considered the DIC score and change in the P-value as outlined by Crawley (2016) to choose the best model. The model with the lowest DIC score was the model that included feature type, genus, scaled depth and temperature. Other abiotic factors were considered for the model (dissolved oxygen and salinity) but did not improve the DIC or P values of the model output, so they were not included in the final model.

Nonmetric multidimensional scaling (nMDS) plots were created with PRIMER 7 version 7.0.17 (<https://www.primer-e.com/>). Coral abundance data were normalized using a square root transformation prior to generating a Bray-Curtis similarity matrix, which was used to parameterize the NMDS. This improved the confidence of the clustering analysis

SIMPROF (a similarity profile permutation test), run with a 95% confidence interval also using PRIMER 7. For individual comparison of the effect of feature shape on each coral genus, a Fisher's Exact test was run in R with the average number of coral individuals observed across the dataset compared to the average number seen per dive within each of the respective feature shapes. Heatmaps were generated in R, correcting based on density (number of coral individuals seen/ square meter) of each genus per feature. Species richness and Shannon diversity scores were calculated using R's Vegan package (Oksanen et al., 2007). Comparison between feature shapes was conducted with an ANOVA between individual feature classification and a perMANOVA across the entire data set.

3.3.4 *Seamount classification*

Pacific basin seamounts were defined as atolls, islands, banks, guyots, conical seamounts, and ridge seamounts (Figure 3.1). Each seamount was manually examined using the GEBCO 2022 grid (*GEBCO 2022 Grid*, 2022), which is a 15 arc-second interval global bathymetric data layer. Features were identified using the 2019 update to Yesson et al. (2011), and the locations of Pacific islands were derived from the United States Geological Survey (USGS) and ERSI's Global Islands Explorer dataset (Jamieson et al., 2010; Sayre et al., 2019). Only features on the continental slope or starting from the abyssal plain were examined; continental shelf associated features were not included. The locations of the seamounts and islands from these two datasets were manually assessed using two dimensional profiles and slope maps generated in Quantum Geographic Information System (QGIS) version 3.22 (QGIS development team 2022). Conical features were considered the default condition, so if the classification of a feature was in doubt or unclear,

it was classified as a conical feature. Features were classified by the summit feature only, so if there were multiple atolls on the top of the same feature, it was classified as an atoll. The location of all islands and atolls was also viewed using Google Satellite (earth.google.com/web/) imagery to determine the shape of the terrestrial portion of the feature. Features that met the Yesson et al. (2011) definition of a seamount (greater than a 1000 m above the seafloor) that were not included in the original Yesson et al. data set were added, and likewise, putative seamounts were removed if they did not meet the Yesson et al. definition or if they were duplicates of the same feature. To assess the dispersion of different feature shapes, we used a Clark and Evans Aggregation Index with a Donnelly edge effects correction (Clark & Evans, 1954; Donnelly, 1978) using the ‘spatstat’ package in R (Baddeley & Turner, 2005).

3.4 Results

Of the 50 most abundant deep water coral genera (out of the 122 coral genera total) identified found on seamounts from the CAPSTONE dataset, all genera had a statistically significant (Fisher’s exact test; Supplemental Table 1) increase in abundance on at least one feature type compared to the average number of coral individuals encountered per dive across the entire dataset (Figure 3.2). Some genera, such as *Chrysosorgia* and *Narella* spp., were encountered in high numbers across more similar features such as completely submerged features (banks, guyots, conical, and ridge type features) compared to *Enallopsammia*, *Calibellemnon*, and *Stichopathes* spp, which seem to have an affinity for features with an emergent component, such as atolls and islands that break the surface. Though this affinity for emergent features may be confounded by the shallower depth

ranges available, this affinity was not present for shallow banks, suggesting that the emergent properties of atolls and islands was influential in coral distribution. Other genera were encountered at the highest frequency per dive on a single feature type, for example, *Eunicella* and *Rhodaniridogorgia* spp were observed almost exclusively on banks, while *Thourella* spp displayed a strong preference for islands (Figure 3.2).

To further test whether coral genera showed discriminatory preference or avoidance for different seamount shapes, we used a generalized linear mixed methods model approach that included all of the 122 coral genera identified in the CAPSTONE dataset. All genera showed a statistically significant impact (Table 3.2) of feature type on coral genera for all features except island when compared to atolls as the reference class. Depth and temperature also had significant impacts on coral distribution.

Figure 3.2 is a heatmap organized by descending abundance of observations made on atolls and shows that each feature class has a unique banding pattern, indicating different “preferences” of each genera for different feature types. To visualize the data differently while taking a different effort correction approach, we displayed the number of encounters per genus per square kilometer of seafloor (Figure 3.3), instead of the total number of individuals per dive as shown in Figure 3.2.

In order to test if the different feature types hosted different coral communities we constructed nMDS plots. The resulting non-metric multidimensional scaling (NMDS) plot (2D stress = 0.18) with SIMPROF cluster analysis revealed five distinct clusters, with some unassigned outliers (Figure 3.4). One cluster consisted of coral genera with the highest abundance on atolls or island shapes, which were always grouped together. Additionally,

a central cluster of coral feature-generalists was apparent, which was distinct from the two separate clusters of genera with high abundances on shallow banks. Finally, a cluster of deep-water submerged seamounts showed taxa with their highest abundance found on guyots, ridges, and conical type features.

We examined the diversity of coral genera in the absence of depth or any other abiotic feature than shape (Figure 3.5), and revealed that banks had the highest average richness per dive with 28.9 coral genera, while atolls had the lowest richness at 13.9 genera per dive (ANOVA $p = <.001$, $f = 7.997$). A similar pattern was noted using Shannon diversity; however, the strength of the signal was reduced, falling below the traditionally assigned alpha of 0.95 (ANOVA $p = 0.054$, $f = 2.235$). We calculated Pielou's evenness index (J') across all features. All features types showed remarkable evenness with no statistically significant differences (ANOVA $p = 0.724$, $f = 0.568$).

In total, 12,597 seamount features were identified in the Pacific basin as rising more than 1,000 meters from the surrounding seafloor, resulting from features either previously identified in the existing dataset, or newly added by this effort (Figure 3.6). The conical features were by far the most abundant feature type examined. The other feature types did show some geographic specificity, with most of the atolls identified in the tropical and subtropical areas of the central and western Pacific likely originating from their volcanic origin and dependence on shallow-water coral growth, which is restricted to tropical waters. Banks, guyots, and islands were more evenly distributed but still showed some bias to the north and western edges of the Pacific basin. Ridges were found in clusters spread throughout the basin. All feature types showed a clustered distribution using a Clark Evans

Aggregation index (conical = 0.408, guyot = 0.300, island = 0.199, ridge = 0.346, bank = 0.265, atoll = 0.231). Sum total, 49.6% of the features were located within exclusive economic zones (EEZs), while 50.4% were located in the high seas, in areas beyond national jurisdiction (ABNJ).

3.5 Discussion

This study raises interesting potential for using seamount shape to predict the abundance and diversity of deep-sea coral communities, in lieu of or as a proxy for more effort intensive measurements of high-resolution mapping and *in-situ* oceanographic conditions. Here, we have shown that the shape of seamounts affects the abundance and biodiversity of coral communities, and have categorized seamounts by shape for the entire Pacific Ocean, building on previous work that has drawn attention to the connection between larger scale features and the diversity and abundance of deep-sea sessile fauna (Dijkstra et al., 2021; Kennedy et al., 2019). Kennedy et al (2019) was the first to propose the question of whether seamount shape may affect the coral communities they host, and found unexpected relationships between coral abundance and the type of feature they inhabited, using the CAPSTONE exploration dataset. Similarly, Dijkstra et al (2020) drew the connection between geological features and benthic coral communities by using geomorphic classification of the seafloor (continental slope, continental slope valley, seamount ridge [pinnacle], and seamount slope), and demonstrated that the frequency of coral occurrences was driven at least in part by specific seafloor types and shapes in the North Atlantic. The major contribution of our study is that seamount shape influences coral communities throughout the Pacific, suggesting that the 12,597 seamounts in the Pacific

basin should not be considered identical. For example, there are only 238 ridges Pacific-wide, which is a relatively rare feature by comparison to seamounts, that may host a distinct biological community compared to other features (e.g. dominated by coral taxa that prefer a ridge-feature shape). Understanding the underlying abiotic drivers of biodiversity of deep-sea corals is improved by efforts to classify and describe geological features in ways that affect fauna, and our study — along with limited previous work exploring seamount shape - is a logical extension of understanding faunal habitat preference. The classic work on deep-sea biology and geology has already fundamentally shown that fauna differ dramatically across a broad range of seafloor habitats, including seamounts, hydrothermal vents, methane seeps, whale falls, trenches, and submarine canyons (Cavanaugh, 1983; Corliss et al., 1979; Jamieson et al., 2010; Menard, 1964; Van Dover, 2000) Our work takes a closer look at seamounts specifically to test the hypothesis that mesoscale differences of seamount shape influence deep water coral communities. While seamount shape has not received extensive previous attention, numerous studies have described the role of seamounts in modifying physical oceanographic conditions (Clark et al., 2010; Clark et al., 2012; Lavelle & Mohn, 2010; Rogers, 1994; Rogers, 2018; Wagner et al., 2020; White et al., 2007) and different shape seamounts have been shown to produce different oceanographic effects (Lavelle & Mohn, 2010) that have the potential to drive biological communities. Seamounts can form hypothetical Taylor columns (Chapman & Haidvogel, 1992), localized upwelling and downwelling (White et al., 2007), internal waves to break resuspending sediment (Turnewitsch et al., 2013), tidal rectification (Brink, 1995; Mohn et al., 2009), and increased chlorophyll a concentrations (Leitner et al., 2020). Similarly,

in shallow water coral reefs, it has recently been shown that variation in wind, wave, and climate regime have influenced the geomorphic development of different reef types (Blanchon et al., 2022). However, few studies have directly drawn the connection between these physical oceanographic changes (that are caused in part by the shape of the seamount) with the variation of their benthic communities; though seamounts are known to be hotspots of biodiversity (Rogers, 2018). These areas of investigation are challenging because oceanographic current alteration caused by seamounts tends to be ephemeral and periodic (Genin, 2004; Lavelle & Mohn, 2010), making it difficult to characterize the relationship between benthic fauna and oceanography on a short-term timescale. Additional work is needed at a finer resolution to predict specific biological communities by feature shape, depth, latitude, and biogeographic province, but progress is understandably slow due to the technical and financial challenges associated with deep-sea research (Amon, Rotjan, et al., 2022). Nonetheless, there are studies that have effectively documented the connection between flow and fixed carbon input with coral abundance and diversity (Beeston et al., 2018), which lends further support to the hypothesis that seamount shape influences flow patterns, that in turn influences benthic life.

To date, there have been only a few attempts to subcategorize seamounts. For example, Clark et al (2010) approached seamount classification using both hierarchical and multivariate approaches incorporating organic matter flux, biogeographic patterns, dissolved oxygen, summit depth and proximity to other seamounts. The hierarchical method yielded 194 different types of seamounts across 14 provinces globally. This classification scheme, along with a proposed scheme by Auster et al. (2005), relied on

numerous different environmental factors to define different classes of seamount. However, the complexity of the variables resulted in so many different categories that it limited the effectiveness of the tool, preventing broad strokes insights into community-level biodiversity. Here, we found that the simpler metric of seamount shape, translating to only six categories, was sufficient to differentiate features in terms of their coral communities. Our re-categorization of seamounts is similar to a concurrent parallel effort in shallow, linear breakwater reefs, which recently parsed 1023 breakwater reefs in the Caribbean into 16 reef subtypes only 9 of which were common (Blanchon et al., 2022).

Using our six category classification scheme, several different deep water coral abundance patterns were noted. Some taxa showed a preference for features that are completely submerged. For example, *Chrysogorgia* spp. and *Narella* spp. display this pattern, with nearly all the recorded observations on either banks, conical seamounts, guyots or ridge features. In contrast, *Enallopsammia* and *Calibelemon* spp., are found in much higher numbers on emergent features (atolls and islands). There are multiple reasons that might explain the fidelity of corals to these shapes. For example, having terrestrial ecosystems on the same feature would cause an increase of organic matter in the water column from plant debris (Hedges et al., 1988), and terrestrial erosion processes would increase sedimentation flowing down from shallow waters (Sanchez-Vidal et al., 2012). Some taxa with a preference for living on atolls and islands may have evolved better ways to deal with increased sedimentation to take advantage of the increased organic matter flux associated with these features. Preferences for submerged-only features has not yet been fully explored in the literature but may relate to the reduction in sedimentation or changes

in current flow. Future research should consider the driver behind the preferences between features with and without terrestrial inputs.

It is important to note that we have taken a markedly broad definition of seamounts here as opposed to the more traditional definition used by Yesson et al (2011) and others. Here, we include atolls and islands as seamounts, since they are volcanically-derived features that provide bathymetric relief across the entire Pacific. Because they are mountain-like features that rise more than 1,000 meters from the seafloor, they provide habitat for coral growth regardless of whether or not they break the surface. However, while the emergent/submergent classification scheme was an apparent driver for 9 of the 50 most abundant genera, it was not sufficiently correlated with the remaining genera, suggesting that there are additional attributes of feature shape that are important drivers of deepwater coral communities. For example, *Acanthogorgia*, *Mettallogorgia*, *Trissopatheis* and *Hemicorallum* spp. (Figure 3.2) exhibit feature type preferences without demonstrating a preference for emerged vs submerged, suggesting that more work is required to understand the abiotic processes that are driving these patterns.

Banks are an interesting intermediate between emergent and submergent features because their summit reaches into the mesophotic zone, however, they lack the euphotic and terrestrial conditions associated with atolls and islands. We found that banks showed the highest coral diversity, defined as the mean generic richness compared to other feature types, which is consistent with previous work that has highlighted the shallowest areas of these features as biodiversity hotspots (Wagner et al., 2020). Our work extends this finding, showing that the deeper slopes of banks are also deep-water coral biodiversity hotspots

compared to other seamount shapes. One possible explanation for this pattern is that there is enhanced current flow over the top of banks (Lavelle & Mohn, 2010), which may play a role in stimulating coral diversity. Banks reach into shallower mixed waters while still enabling current flow directly over the seamount summit. This shallow but not emergent topography may maximize the positive effects of flow and turbulence without terrestrial consequences such as sedimentation, excess nutrients, and potential anthropogenic pollution. As such, seamount rugosity as well as feature height (depth) may play a previously underappreciated role in deep water coral diversity.

Depth is known to be a strong driver of zonation for deep-sea corals (Auscavitch, Deere, et al., 2020; Long & Baco, 2014) and as such, the impact of feature shape and depth on coral abundance and diversity is inherently intertwined. In addition, it is well-established that seamount height is highly variable (Yesson et al., 2011), though all 12,593 Pacific seamounts included in this study rise at least 1000m off the seafloor. These variable heights correspond to various depths, and not all seamounts have the same range of depth habitat available. Taxa that only live at shallow depths will obviously only be able to live on features with shallower depths. To disentangle the effects of depth and shape, we considered depth as a covariate in the generalized linear mixed methods model, which takes into account variation attributed solely to depth. Even with depth included, statistically significant differences were observed between atolls and all other feature classes except islands, which grouped with atolls by depth, thereby indicating that there are drivers beyond depth alone that influence the patterns of coral diversity presented here. Therefore, even though depth is a key factor in deep water benthic organization, depth alone does not

fully describe coral community differences between seamount shapes. Other compounding variables, such as seafloor rugosity, current flow, regional productivity, and the presence of terrestrial communities on the same feature may also drive benthic community structure, and all of these are likely to be influenced by seamount shape. Due to the simplicity of this six category scheme and the complexity of all the factors that influence the abundance and diversity of deep water corals, further research is required to understand the mechanisms underlying the influence of seamount shape, and how all of these factors influence each taxa.

One potential implication of classifying seamounts by shape is the idea that not all seamounts may equally contribute to the larval supply pool for each coral taxon. Because of the observed variation in deep-water coral community structure by seamount shape, the previously assumed relationship between seamounts based on distance alone would no longer be adequate. Previous studies have suggested that seamounts are important stepping stones for genetic connectivity and as refugia in the open ocean (Shank, 2010), but our results indicate that there is more heterogeneity between seamounts than previously thought. We found that seamount dispersion by shapes was not random or even, but rather clumped within feature type (Figure 3.6), suggesting that certain biogeographic regions may be rich in one shape and lacking in another. As such, the “seamounts as stepping stones” hypothesis needs additional revision in light of seamount shape to include biogeographic province, latitude, country-specific management structure and depth, now adding seamount shape as well. Put simply, rarer seamount shapes may be more likely to host rarer taxa, and future considerations of the stepping stone hypothesis should consider

the distance to the nearest seamount of the same type as opposed to just the closest seamount feature.

The dispersion of seamounts by seamount shape is a logical extension of their geological formation. For example, atolls were much more clumped together and were only found in the tropics and subtropical latitudes because their formation is dependent in large part on the biological activity of photosymbiotic reef building corals that are limited to the relatively warm waters of lower latitudes (Darwin, 1842). In addition, all atolls and islands are found within exclusive economic zones since all land masses are claimed by at least one country. In contrast, the vast majority of the seamounts in the Pacific Ocean are conical, which are the least clumped together. However, despite the clumped dispersion of most seamount shapes, there is surprisingly even distribution of biological communities on each seamount shape (Figure 3.5), suggesting that each shape makes a relatively equally important contribution to the overall biodiversity of deep-water seamounts.

There have been calls for new and better ways to estimate areas that may contain vulnerable marine ecosystems (VMEs)(Ardron et al., 2014) containing deep-sea corals (Rowden et al., 2020; Watling & Auster, 2021), and our findings may help fill that gap in understanding by utilizing gross geological feature shape as a predictor of abundance. Our six-feature type classification scheme provides a useful metric for future biodiversity studies as well as for conservation and management purposes. It is specific enough to show variations within the coral communities but simple enough to be broadly utilized. This scheme is certainly not comprehensive in explaining all the variation differences, and future work will undoubtedly refine the definitions of the various types of features and

provide a better understanding of the drivers behind the observed patterns of coral life documented here. However, even with this simple scheme, the comparative rarity of island, banks, guyots, and ridge type features suggests that they are relatively vulnerable and thus important to protect.

As countries and high sea management groups race to meet thirty by thirty conservation goals of protecting thirty percent of the world's oceans before the year 2030 (Sullivan-Stack et al., 2022), it is imperative to take a “Noah’s Ark” approach to include representatives of all different ecosystems, including depth, biogeographic province, latitude, and now seamount shape. However, at the same time, some rarer features or taxa may require more comprehensive conservation and shape alone is not sufficient to categorize rarity or importance. We are still at the beginning of understanding seamount ecosystems and how they interact in terms of nutrient provisioning, larval supply, and ecosystem services, so the precautionary principle is still warranted. In the interim, the comparative rarity of certain seamount shapes, and the political jurisdiction they are in, may justify more urgent disproportionate conservation of certain venerable marine ecosystems (VMEs). For example, there are only 55 Banks within Pacific high seas areas beyond national jurisdiction (ABNJ), which may call for protection of all of these features given both their rarity and their increased biodiversity. However, their protection and management require international cooperation that is currently still under development.

The conservation and management implications resulting from this seamount shape classification scheme intersect with current calls for action around VMEs and their encompassing vulnerable marine communities (VMCs). For example, current Regional

Fisheries Management Organization (RFMO) classifications of VME indicators for the North and South Pacific employ vague taxonomic indicators and extremely high thresholds for response (RFMO, 2019). Our data suggest that a more nuanced taxonomic approach is warranted, in addition to a lower threshold for action, given the likelihood of rarity of certain taxa per feature type. Further, it has long been argued that current classifications of VMEs are instead describing vulnerable marine communities, encompassed within VMEs (e.g. Allee et al., 1949). As such, seamount VMEs would include multiple seamounts of a similar type in a similar biogeographic region (Watling and Auster 2021). Our findings support the need for demarcating VMCs versus VMEs, and provide additional evidence that seamount ecosystems require further classification to adequately describe and protect biodiversity. In addition, the UN General Assembly Resolution 61/105 calls for enhanced protection of VMEs including associated and dependent species; our data provide further justification for this resolution, given that we found distinct biological communities associated with each seamount shape type. Because deep-water coral and sponge taxa are ecosystem engineers (Kennedy & Rotjan, 2020), providing habitat for high-fidelity associated organisms (Shank et al., 2018), it is clear that they provide the support structure for deep water seamount ecosystems, including deep-sea fisheries (Clark et al., 2010). At the same time, however, these corals are simultaneously threatened by these same deep water fisheries (Clark et al., 2012), as deep water trawling scours the seafloor removing larger and likely older corals. Given the long life spans and slow growing nature of deep-sea corals (Roark et al., 2009), even a single encounter with a trawl net could destroy a thousand-plus year old ecosystem, thus damaging the habitat for the next thousand-plus

years. Consideration of seamount shape in the larger landscape of marine conservation will enable more strategic protections of these ancient, important, and vulnerable deep water corals.

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Table 3.1. P values from Fisher’s Exact test comparing the average number of individuals per dive for each feature class compared to the average number of individuals per dive across the all the feature types.

| Genus | Atoll | Bank | Guyot | Conical Seamount | Island | Ridge Seamount |
|-------------------------|--------------|-------------|--------------|-------------------------|---------------|-----------------------|
| <i>Chrysogorgia</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Hemicorallium</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Narella</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Acanthogorgia</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Enallopsammia</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Acanella</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Anthomastus</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Calibelemnon</i> | 0.0005 | 0.0005 | 0.0005 | None Seen | 0.0005 | 0.4003 |
| <i>Pleurogorgia</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | None Seen | 0.0005 |
| <i>Dendrophyllia</i> | 0.0005 | 0.0005 | None Seen | 0.0005 | 0.0005 | 0.0005 |
| <i>Stichopathes</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.12794 |
| <i>Pleurocorallium</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Candidella</i> | None Seen | 0.0005 | 0.0005 | 0.0005 | 0.0025 | 0.0005 |
| <i>Parisis</i> | None Seen | 0.0005 | None Seen | None Seen | 0.05497 | None Seen |
| <i>Antipathella</i> | None Seen | 0.0005 | None Seen | None Seen | None Seen | None Seen |
| <i>Bathypathes</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Eunicella</i> | None Seen | 0.0005 | 0.0005 | None Seen | None Seen | None Seen |
| <i>Iridogorgia</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Paragorgia</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Stauropathes</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Trissopathes</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.02249 | 0.0005 |
| <i>Scleronephthya</i> | 0.0005 | None Seen | None Seen | None Seen | 0.0005 | None Seen |
| <i>Paramuricea</i> | 0.0005 | 0.0005 | 0.0005 | None Seen | None Seen | 0.0005 |
| <i>Eguchipsammia</i> | 0.0005 | 0.0005 | None Seen | None Seen | 0.0005 | None Seen |
| <i>Metallogorgia</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.05647 | 0.0005 |
| <i>Paracalyptophora</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |

| | | | | | | |
|--------------------------|-----------|-----------|-----------|-----------|-----------|-----------|
| <i>Calyptrophora</i> | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.001 | 0.0005 |
| <i>Thouarella</i> | 0.06497 | None Seen | 0.0005 | None Seen | 0.0005 | None Seen |
| <i>Rhodaniridogorgia</i> | 0.02049 | 0.0005 | 0.0005 | 0.0005 | None Seen | None Seen |
| <i>Paracis</i> | 0.06797 | 0.0005 | None Seen | 0.0005 | 0.0005 | None Seen |
| <i>Amphianthus</i> | 0.06247 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| <i>Umbellapathes</i> | 1 | 0.0005 | 0.0005 | 0.0005 | 0.04198 | 0.2059 |
| <i>Madrepora</i> | 0.13493 | 1 | 0.0005 | None Seen | 0.0005 | 0.0005 |
| <i>Halipteris</i> | None Seen | 0.0005 | 0.0005 | 0.0005 | None Seen | None Seen |
| <i>Antipathes</i> | None Seen | 0.0005 | 0.23238 | 0.0005 | 0.0005 | None Seen |
| <i>Polymyces</i> | 0.0005 | None Seen | 1 | None Seen | 0.0005 | 1 |
| <i>Jasonisis</i> | 1 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | 0.0055 |
| <i>Anthoptilum</i> | 0.0005 | 0.0005 | 0.23088 | 0.0005 | None Seen | 0.008 |
| <i>Callogorgia</i> | 0.008 | 0.0005 | 0.0005 | 0.0005 | 0.0005 | None Seen |
| <i>Victorgorgia</i> | 0.0005 | 0.0005 | 0.0005 | 0.68766 | 0.007 | 0.0005 |
| <i>Parantipathes</i> | 0.0005 | 0.0005 | 0.0005 | 1 | 0.0005 | 0.0005 |
| <i>Swiftia</i> | 0.03148 | 0.82959 | 0.0005 | 0.0055 | 0.0005 | 0.0005 |
| <i>Heteropathes</i> | None Seen | 0.0005 | 0.0005 | 0.0005 | 0.43528 | 0.0005 |
| <i>Kulamanamana</i> | 0.0005 | 0.0005 | None Seen | None Seen | 0.0005 | 0.0005 |
| <i>Pseudoanthomastus</i> | 0.0005 | 0.0005 | 0.02599 | 0.34833 | 0.0005 | None Seen |
| <i>Pennatula</i> | 0.0005 | None Seen | 0.991 | 0.0005 | 0.0025 | None Seen |
| <i>Plumarella</i> | None Seen | None Seen | 0.0005 | None Seen | None Seen | None Seen |
| <i>Isactinernus</i> | 0.01399 | 0.01199 | None Seen | 0.08546 | 0.0005 | None Seen |
| <i>Lepidisis</i> | 0.42229 | 0.89155 | 0.0005 | 1 | 0.0005 | 0.93853 |
| <i>Flabellum</i> | None Seen | None Seen | None Seen | None Seen | 0.0005 | None Seen |

Table 3.2. Results from the generalized linear mixed methods model. Number of individuals ~ Genus + feature class +scaled depth (depth in meters /1000) + temperature in Celsius. Data used here included all 121 genera present in the CAPSTONE dataset. Model selection was based on additive model selection and DIC scores.

| Feature type (Atoll reference class) | Posterior Mean | l-95% CI | u-95% CI | Effective Sample Size | pMCMC |
|---|-----------------------|-----------------|-----------------|------------------------------|-------------------|
| Bank | 0.83 | 0.01 | 1.65 | 1912.60 | 0.0444 |
| Conical Seamount | 1.38 | 0.62 | 2.19 | 1766.70 | 0.0004 |
| Guyot | 1.12 | 0.41 | 1.91 | 1779.50 | 0.0032 |
| Island | -0.33 | -1.03 | 0.39 | 2083.40 | 0.3810 |
| Ridge Seamount | 1.40 | 0.55 | 2.32 | 1568.70 | 0.0004 |
| Scaled Depth | -1.58 | -1.85 | -1.31 | 236.70 | < 2e-04 |
| Temperature | -6.24E-04 | -1.06E-03 | -1.52E-04 | 979.90 | 0.0101 |

Table 3.3. Number of seamounts by feature type separated out by the number occurring within Exclusive Economic Zones (EEZ) or Areas Beyond National Jurisdiction (ABNJ)

| | EEZ | ABNJ | Total |
|---------|------|------|-------|
| Atoll | 269 | 0 | 269 |
| Island | 475 | 0 | 475 |
| Bank | 371 | 55 | 426 |
| Conical | 4794 | 5901 | 10695 |
| Guyot | 230 | 264 | 494 |
| Ridge | 103 | 135 | 238 |


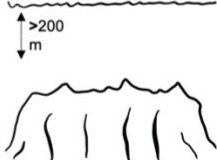
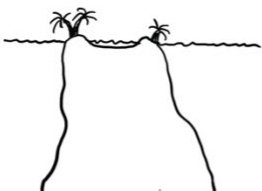
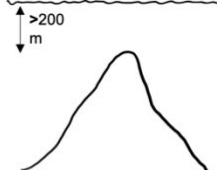
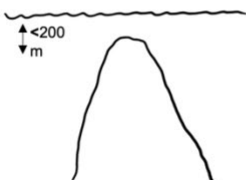
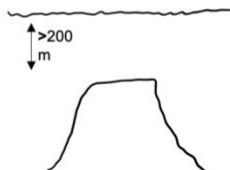
| Geological feature type | Example | Geological feature type | Example |
|--|--|--|--|
| Island: Emergent land mass surrounded by water |  | Ridge: Rising from the seafloor with an elongated summit forming a ridge-like feature |  |
| Atoll: Emergent land and a central lagoon either partially or fully enclosed by land |  | Conical: undersea mountain rising from the seafloor; pointed summit. |  |
| Bank: A guyot shaped feature where the shallowest point is less than 200 meters water depth |  | Guyot: undersea mountain rising from the seafloor with a flat top deeper than 200m |  |

Figure 3.1. Definitions and examples of each feature shape. Islands are defined as seamounts with an emergent terrestrial component. Atolls are also defined as seamounts with an emergent terrestrial component but only have low lying sandy land surrounding a central lagoon that has tidal water exchange with the surrounding ocean. Banks are seamounts that are fully submerged with a summit shallower than 200 meters and most likely have a mesophotic community at the summit given the clear pacific waters. Ridge is an elongated seamount with multiple peaks all about the same depth but all deeper than 200 meters. Conical features are the “classic” seamount with a single peak rising form the abyssal sea floor. Guyots are flat topped features that were at one point were emergent and have had their summits eroded and a carbonate cap over the volcanic substrata and then subsided back below the ocean surface. These features all have a summit depth greater than 2000 meters. All feature types rise more than 1000 meters from the surrounding seafloor.

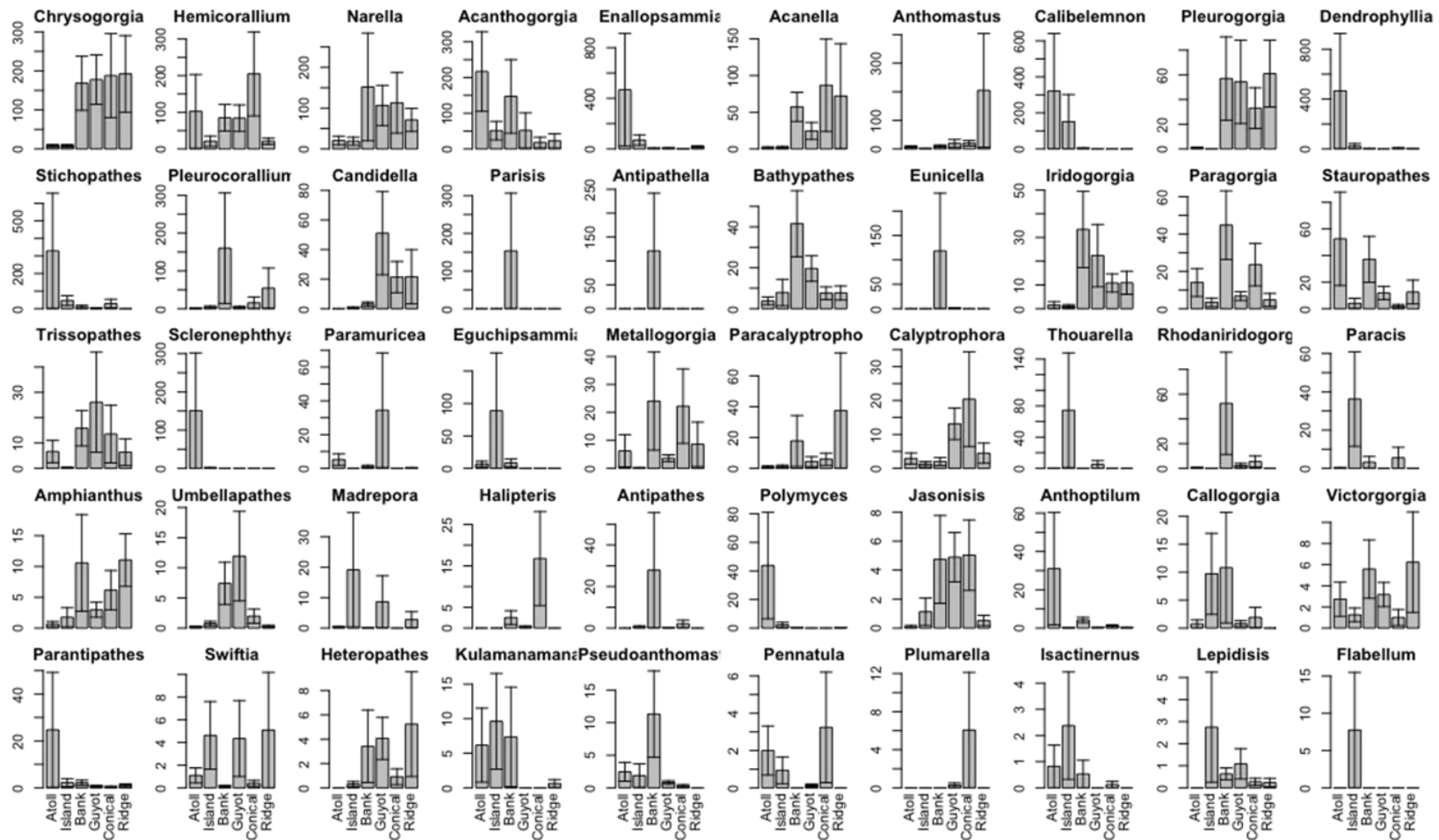


Figure 3.2. Count data of the 50 most abundant anthozoan genera from the CAPSTONE dataset. Organized in descending abundance from the top left moving right and down. X- axis labels are right to left atoll, island, bank, guyot, conical, and ridge. All 50 genera show at least one statistical significant difference in abundance across the different feature types (p values in Supplemental table 1). Error bars are standard error.

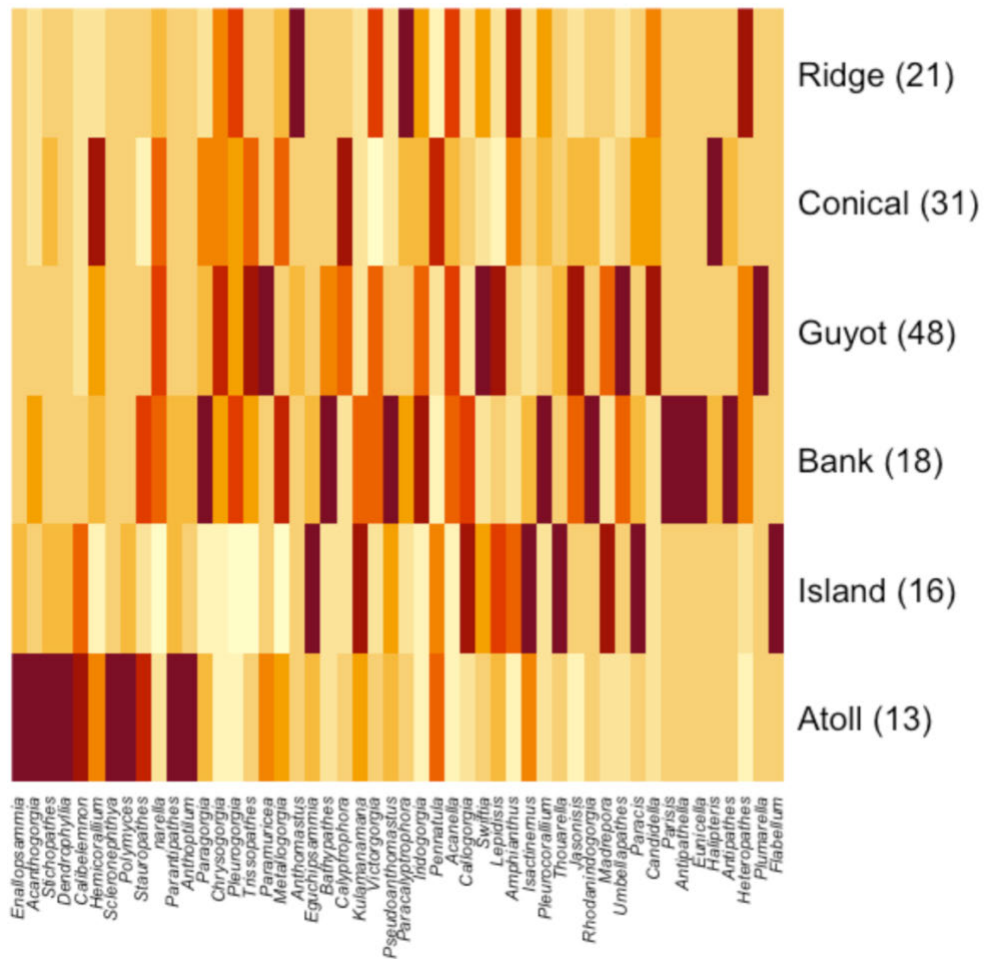


Figure 3.3. Heatmap showing the density (observations per square kilometer) of the 25 most abundant anthozoan genera. Genera are organized in descending abundance (left to right) for the Atoll feature shape. Number of dives per feature type are shown in parentheses next to feature shape.

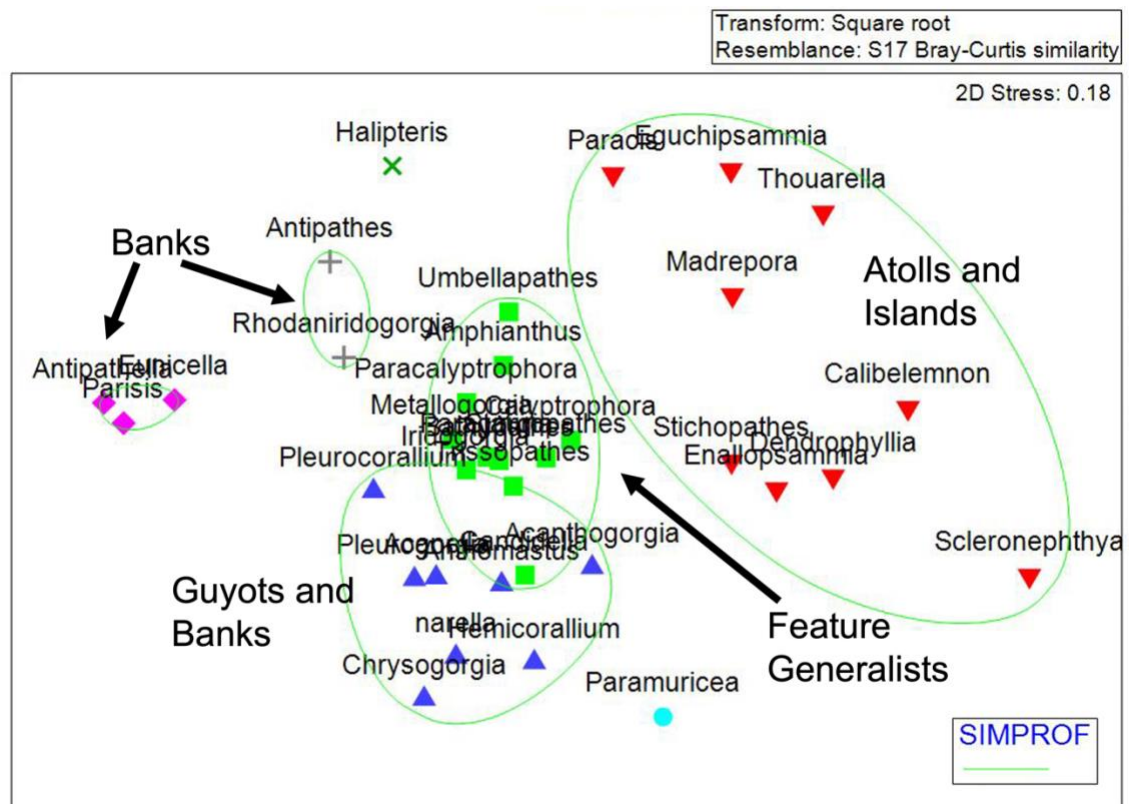


Figure 3.4. Non-metric multi-dimensional (NMDS) plot showing genera clustering. Green ovals are 95% confidence intervals from a SIMPROF (a similarity profile permutation test) cluster analysis. A distinct group of genera are associated with Atolls and Islands form a cluster, while Bank specific taxa appear to be broken up into 3 groups. Two that are specific to banks and one that is shared with Guyots. In the center of the figure there is a group of feature generalists that include most of the genera found on conical and ridge seamounts.

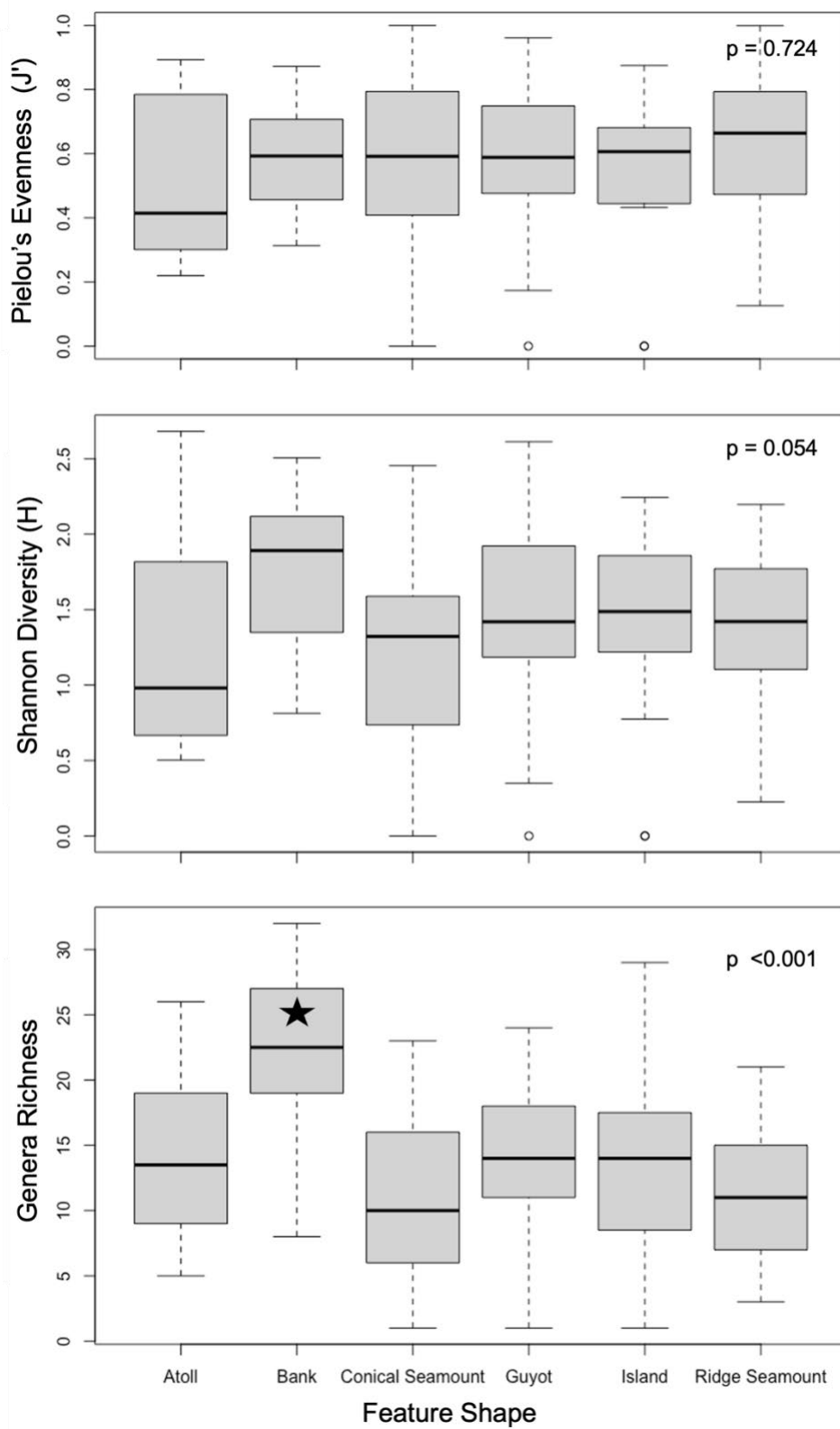


Figure 3.5. Top box and whisker plot is the Pielou's evenness index (J') for the anthozoan genera. All the feature shapes were very even with no statistically significant difference (ANOVA $p = 0.724$, $f = 0.568$). The middle boxplot is Shannon diversity index (H). Bottom inset means species richness per feature type). In terms of genus richness banks have the highest average per dive with 28.9 genera while atolls had the lowest at 13.9 genera per dive (ANOVA $p < .001$, $f = 7.997$). A similar pattern is noted using Shannon diversity, however, the strength of the signal is reduced falling just short of an alpha of .95 (ANOVA $p = 0.054$, $f = 2.235$)

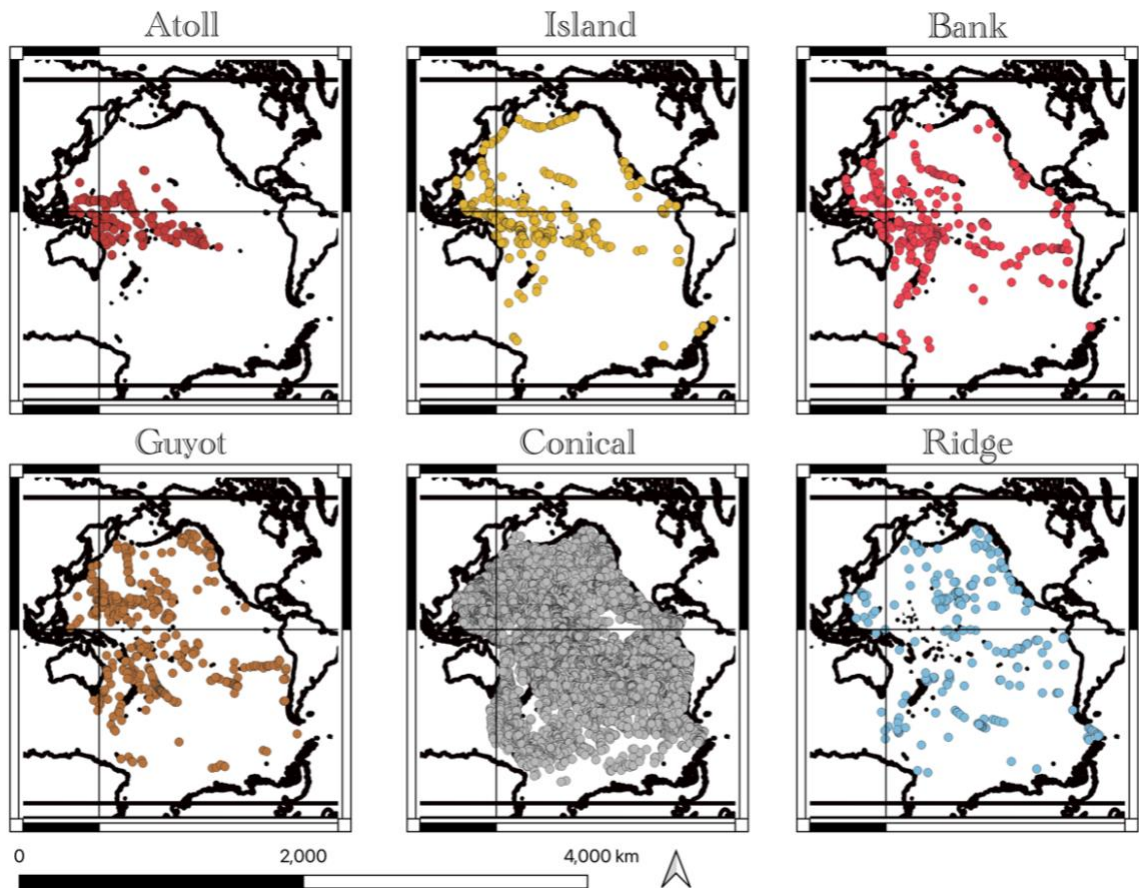


Figure 3.6. In total 12,597 features were identified in the Pacific basin. Of those features 267 were categorized as atolls, 477 as islands, 426 as banks, 494 as guyots, 238 as ridges and 10,695 as conical type features. All feature types showed a clustered distribution using a Clarke Evans Aggregation index (conical = 0.408, guyot = 0.300, island = 0.199, ridge = 0.346, bank = 0.265, atoll = .231).

CHAPTER FOUR: UNMASKING THE MOUNTAIN: VISUALIZING DEEP-WATER CORAL AND SPONGE COMMUNITIES ON FOUR SIDES OF AN EQUATORIAL CENTRAL PACIFIC SEAMOUNT

4.1 Abstract

Changes in benthic communities have been observed across abiotic natural gradients of environmental variables for many deep-sea ecosystems, but these patterns remain under sampled on seamounts. Differences in local-scale community changes have been hypothesized to vary on different flanks of seamounts depending on current flow and variations in water mass characteristics on different sides of a seamount, but this hypothesis has not yet been rigorously tested. Here, we identify depth zones and assess coral and sponge similarities within a single central Pacific equatorial seamount. This conical seamount rises from a depth of more than 5,000 meters (m) to mesophotic depths of 196 m and is directly influenced by the Equatorial Undercurrent. In 2021, we conducted four ROV transects from the R/V *Falkor*. Transects were completed on each flank of the seamount based on cardinal direction. Strong vertical zonation of corals and sponges was observed or documented or encountered on all flanks. Between ~500 m and 250 m, the glass sponge *Aphrocallistes cf beatrix* was the dominant sessile organism, with the chaetopterid worm *Phyllochaetopterus limicolus* interspersed. Shallower than ~250 m, the seafloor was composed of scoured carbonate pavement with sediment accumulation only found in rocky depressions. The majority of the organisms were scleractinians and small *Paracis* spp. octocorals. Differences in faunal abundance were noted between flanks including Euplectellidae, Plexauridae and *Chrysogorgia*, which each showed a preference for one or two flanks. The correlation between these zonation patterns and oxygen concentration

suggests a strong effect on the location of corals. For example, almost no scleractinian corals were found within the oxygen minimum zone (OMZ). As expected, waters below 500 m hosted communities predominantly composed of octocorals, however, several coral taxa showed flank preference. To investigate possible drivers of flank preference, we investigated the influence of current flow, oxygen, and substrate type. Statistically the coral community composition (or distribution) between the different flanks of the seamount did not differ, however, the local contribution to beta diversity varied by depth. To help visualize and inspire future work on the zonation of seamounts, we created an Alexander Von Humboldt-style infographic of the biodiversity patterns of our target seamount. Given the importance of seamounts to ocean biodiversity and productivity, this study is an early attempt at a holistic visualization of seamount biology that can advance new hypotheses about seamount ecology.

4.2 Introduction

Resolving patterns of biological communities on individual seamounts is a continued interest in the deep-sea (Clark et al., 2010). The increased number of ship and deep submergence assets, resulting in a notable increase in visual seafloor data now make it possible to study deep-sea biological communities at a previously unprecedented scale. To-date, it has been aggregately shown that community distribution with depth are consistently the most obvious patterns that emerge on any individual seamount, and many previous studies have demonstrated depth-ranges of deep-water benthic taxa at the species, genus, and family level (Long & Baco, 2014; Thresher et al., 2014). Further, interactions between depth and other oceanographic conditions have also been investigated, and it is

clear that depth — while a key driver of benthic species distribution — is not the only abiotic factor of importance (Auscavitch, Deere, et al., 2020; Auscavitch, Lunden, et al., 2020; Levin, 2003). While seamounts may be individually biological distinct (Samadi et al., 2006; Shank, 2010), and foster some degree of endemism (Richer de Forges et al., 2000), recent bursts of exploration expeditions have also shown wider geographic spread of many taxa within a region, thereby suggesting that there may be ecological organization of biological communities on seamounts that may share similarities across a regional scale (McClain, 2007). For example (Kennedy & Rotjan, 2022) showed that some benthic coral taxa in the Pacific have an affinity for specific seamount shapes. Similarly, Summers and Watling (2021) found that there are distinct biogeographic provinces that capture ranges of specific benthic taxa. Yet, these patterns have mostly been derived from single transect lines on a single seamount and there have been few attempts to characterize benthic communities across a seamount from multiple flanks.

To-date, only a few studies have investigated a single seamount holistically with multiple transects on different sides, and to our knowledge, no seamount has been comprehensively assessed (every square meter). One example of this type of holistic approach comes from Morgan et al. (2019), who described the assemblages on flanks of Mokumanamana Island in Hawaii and found that different sides of the feature hosted different species assemblages. Conversely, Du Preez et al. (2016) reported more similarity across the different sides of Cobb seamount (also a north Pacific seamount) with depth being a greater influence than seamount side (flank). However, both studies documented heterogeneity in the communities across flanks, and both studies assigned communities to

assemblages and started to demarcate biological zones.

These putative biological zones may be viewed as early tools to establish hypotheses of seamount community organization that can serve to test ecological drivers of benthic community patterns. However, so few seamounts have been investigated on multiple flanks that examining consistent patterns of zonation is not yet possible at or beyond the regional scale. Work such as Morgan (2019) and Du Preez et al. (2016) have created a viable path for looking more holistically at seamounts and as such, we are now poised for rapid advance. Essentially, we are at the same point in our understanding of seamount ecology as when Alexander von Humboldt, Alexander Keith Johnston, and Aimé Bonpland first boldly articulated hypothesized zones of plant life on terrestrial mountains in the early 1800s. This collaborative team together created some of the first scientific infographics of how ecosystems and communities changed as a function of elevation and wind direction on volcanic mountains in the Andes (Moret et al., 2019). Those early infographics provided a visually compelling and artful framework that propelled the biological community forward - daring the community to provide data to either support or refute their understanding of botanical organization on a mountain-by-mountain scale, which then led to the genesis of zone differentiation by elevation and other abiotic contributors. However, 200 years later, a similar effort has not yet been undertaken for underwater seamounts.

Seamounts are as diverse as mountains, but suffer from a lack of feature-specific data. One 2010 study estimated that less than 1% of seamounts had been imaged and the vast majority had been dove only once, along a single flank, covering only a limited depth

range (Rowden et al., 2010). This chronic under sampling is largely due to the cost of operating deep submergence vehicles and the remoteness of seamounts (Rowden et al., 2010). Given the challenges of working in the deep sea, a model seamount is needed to answer questions about community changes across a single feature. Ideally, the model seamount would be simple, relatively symmetric without strong, distinctive bathymetric features, and would cover a wide range of depths. Simplistic morphological features would be contrasted with strong environmental gradients such as strong surface current flow or changes in dissolved oxygen across the range of depths that would help test the hypotheses related to the drivers of community composition.

In this study, we tested whether benthic biodiversity patterns shifted by flank and depth on a relatively small, comparatively smoothly shaped seamount in the equatorial Pacific. Specifically, we investigated the local contribution of beta diversity for depth bins for deep-water corals and sponges. Our seamount is located in the equatorial undercurrent, which has strong surface currents running west-to-east, thus further contributing support for using this seamount as a model case study. As such, we measured physical oceanographic parameters at depth (temperature, salinity, and dissolved oxygen) as well as current flow from the surface to 600 m depth. We also estimated seafloor slope to determine its influence on benthic animal habitat preference. Using video data from four deep-water ROV dives, we described the vertical transitions between communities along transects on different sides and along the top of this conical seamount. Taken together, we used these data to construct a Von Humboldt-style infographic to illustrate putative bands of benthic communities around the seamount, with the aim of advancing seamount ecology towards

a deeper understanding of community organization at the seamount scale and beyond.

4.3 Methods

4.3.1 Site selection

All work presented here was conducted on the as of yet unnamed seamount in United States (US) waters near the border with Kiribati's exclusive economic zone (EEZ) (1.61 S, 175.20 W, Figure 1). This feature rises from a depth of more than 5,000 meters up to 196 meters and is roughly symmetrical at the 20-meter resolution of our bathymetry with even contour lines and similar depths and slopes on each side. The only major bathymetric variation is the remnants of a discrete mass wasting event on the North side of the feature. The water around the target feature is heavily influenced by a complex system of east- and west-flowing currents and countercurrents that include the Equatorial Undercurrent (EUC), North Equatorial Countercurrent (NECC), North and South Equatorial Currents (NEC, SEC, and respectively), and the North and South Deep Countercurrents (NDCC, SDCC, and respectively). This feature lies in close proximity to the Winslow Reef Complex, which has been noted for its high benthic invertebrate abundance (Auscavitch, 2020) and contains four other seamounts (within 30 NM) with one peak reaching as shallow as 20 meters, supporting a robust photic coral reef (Rotjan et al., 2014). The target seamount is in US waters only 3 kilometers North of the border of Kiribati's Phoenix Islands Protected Area and 120 km south east of the boundary of the Howland and Baker Unit of the Pacific Remote Island Marine National Monument. While this feature is not inside of a marine protected area, its proximity to two of the largest deep-water marine protected areas in the world makes it a particularly interesting study site because of potential spillover effect and

the implication of regional marine policy.

4.3.2 Data collection and annotation

In June 2021, we conducted four continuous transects during each of four dives (S0434, S0435, S0436, and S0437), using Schmidt Ocean Institute's SuBastian remotely operated vehicle (ROV) aboard the *R/V Falkor*. Each transect was conducted on a single flank of the seamount based on cardinal direction (N, S, E, W), all starting between 1200 and 1500 meters and terminating at the summit (196 m). The average transect bottom track length was 2250 m. All surveys were conducted from deep to shallow, perpendicular to the bathymetric contours, typically at an over-ground speed of 0.25–0.5 kt (0.1–0.25 m/s), stopping only to zoom into features of interest or to collect physical samples. SuBastian was equipped with an onboard CTD (SeaBird FastCAT SBE49) and oxygen optode (Aandera O2 optode 4831), which logged continuously in UTC time. Seafloor position was logged using an ultrashort baseline (USBL) navigation sensor (Sonardyne WMT 6G) and an inertial guidance system (Sonardyne Sprint). During the end of dive S0433, the CTD data was intermittent, and was unavailable for dives S0434, S0435, and S0436. To substitute for these gaps in CTD data, two shipboard CTD casts (SBE 911+) were conducted immediately following dives S0434 and S0435 in waters approximately 2,000 meters deep in close proximity to the start of the ROV dive. Data from shipboard CTDs was processed using Seabird Data Processing v7.26.7. ROV CTD data was processed by the crew of *R/V Falkor* using the NOAA created Scientific Computing System (SCS) (<https://scsshore.noaa.gov/>). Data from both sensors were combined and analyzed using Ocean Data View (Schlitzer, 2015).

The seafloor video was annotated from the time the ROV reached the sea floor until it left the bottom as long as the ROV was in visual contact with the bottom ($< \sim 2$ meters altitude). All corals, sponges, and other dominant sessile benthic fauna greater than 5 cm in size were recorded using Google spreadsheets. All annotated organisms were identified to the lowest taxonomic level possible from the video utilizing the physical specimens that were collected to aid the identification whenever possible. Organisms that could not be identified to the species level were instead assigned a morphospecies identifier. Additional taxonomic literature and taxonomic expertise was consulted for specimen collection identification. To determine if slope had an effect on habitat preference, we visually estimated the angle of the seafloor for each sessile organism observation. Seafloor slope was categorized for the location of the coral or sponge attachment location in one of four categories: flat (< 15 deg), slope (15-70 deg), vertical (70-90 deg), or overhang (> 90 deg).

Current data was collected by R/V *Falkor*'s Teledyne Ocean Surveyor 75 kHz Acoustic Doppler Current Profiler (ADCP) and the data were processed by the University of Hawaii Common Ocean Data Access System (www.currents.soest.hawaii.edu/uhdas_home/). The processed data yielded current data in 25-meter depth bins and 5-minute temporal ensembles. ADCP current data vector components were converted to cardinal direction and velocity using R (R core team 2023) then the data was visualized in QGIS (www.qgis.org).

Bathymetry was collected by R/V *Falkor*'s two multibeam sonar systems Kongsberg EM710 (Freq) and EM302 (30 kHz). Data were processed onboard using a

Fledermaus Qymera workflow (qps.com). A cube-processing algorithm was applied to clean the sonar data. No tidal corrections were performed given the water depth.

4.3.3 *Statistical analysis*

All statistical analyses were conducted using R (R Core Team 2022). In order to test for significant differences between the sides of the seamounts, Analysis of Similarities (ANOSIM) were conducted using morphospecies binned by 30-meter depth zones. Using the same depth zone binning, we also created rarefaction curves for each side of the feature. The ANOSIM and species accumulation curves were both made using the R package ‘vegan’ (Oksanen et al., 2007).

To investigate the role of slope on abundance of sessile organisms, we conducted a generalized linear mixed methods model with slope and genus as covariates using the ‘glmer.nb’ function from the ‘lm4’ package (Bates et al 2015). We employed an additive model selection process comparing Akaike information criterion (AIC) scores to choose the best model (Crawley 2015). We employed a negative binomial distribution for best fit; we could not use a Poisson distribution because it underestimated the number of zeros in our dataset.

Total beta diversity and Local contribution to beta diversity (LCBD) was calculated for 30 meter depth bins using the ‘beta.div’ function from the ‘adespatial’ package (Dray et al., 2018). For this analysis, we removed all the singletons from the dataset because they were not deemed to be common representatives of the biological community. The LCBD represents the ecological comparative uniqueness of each sample. The significance for each

bin was assessed through permutation analysis (999 iterations), testing the null hypothesis that genera distribution is random among the sampling depths. The methods behind this approach are outlined by Dray et al. (2018).

4.4 Results

4.4.1 Currents

The 75 kHz acoustic doppler current profiler data (ADCP) showed several distinct current regimes that changed with depth over our target seamount (Figure 4.2). Above the feature, the dominant current flow progressed from west to east in excess of 0.5 m/s, which is consistent with the Equatorial Undercurrent (Figure 4.2A; Bostock et al., 2010). The summit of the seamount at 196 meters is still in the flow of the Equatorial Undercurrent, however the velocity reduced noticeably from the shallower waters above the feature (Figure 4.2B). Below 250 meters, the current flow switched direction 180 degrees from East to West (see online supplemental video of ADCP data). By 300 meters depth, there was a noticeable difference between the current flow on the north and south seamount flanks compared to the east and west. The north and south flanks experienced a moderate flow ~0.2 m/s that was consistently east to west while the east and west flanks experienced lower flow and the direction of the flow changed as the distance increased from the sides of the seamount indicating greater turbulence on these two sides of the feature. By 600 meters — the maximum effective depth of the ADCP given the conditions during our survey — the overall velocity was greatly reduced and the general flow became south to north, but there were also localized variations depending on distance from the seamount.

4.4.2 *Physical oceanographic findings*

First, CTD data of the area showed minimal variation around the seamount for temperature and salinity (Figure 4.3). However, we noted significant variability in oxygen concentration throughout the water column. We identified two oxygen minima, one at approximately 450 meters and a second one at approximately 600 meters depth. However, when in contact with the seafloor, these oxygen minima merged to form one larger OMZ between 400 and 700 meters on all sides. These oxygen minima seem to have an impact on colonial scleractinians such as *Enallopsammia* and *Madrepora spp.*, which have been shown to be oxygen sensitive in previous work (Auscavitch, 2020; Lunden et al., 2014). There was a circumferential band between 500 and 800 meters around the seamount where almost no colonial scleractinians were documented (Figure 4.3); this gap clearly corresponded with the oxygen minimum seen in the CTD data.

4.4.3 *ROV observations*

In total, 18,123 individual organisms were identified from 52.5 hours of ROV bottom time across the 4 dives. There were differences in community composition and abundance noted on all sides of the features. In general, total abundance was higher near the top of the feature with lower abundance in deeper water (Figure 4.4). The North and West transects showed the greatest abundance across all taxa, but the depths at which the highest abundance was found varied between sides of the feature. The East transect overall had the lowest abundance and the majority of the organisms documented were found between 200 meters and 380 meters, which contrasts with the western face where the majority of the abundances were found in between the two shallowest depth bands of the

eastern side (Figure 4.4B). The north and south transects were more similar to each other with maximum abundance found between 200 and 300 meters.

While there were differences between the sides of the seamount in terms of abundance at different depths, the overall transition between communities was very similar (Figure 4.5). Below 500 meters, we found communities that were sparsely populated with octocorals and Hexactinellid sponges with few scleractinians making up the majority of the individuals (Figure 4.7C). Between 380 and 430 meters — depending on flank — this general deep sea coral community transitioned to a much higher biomass community dominated by *Aphrocallistes cf beatrix* sponges and *Phyllochaetopterus limicolus* worms with plexaurids and parchment worm (*Chaetopterus* spp.) tubes interspersed (Figure 4.7B). This high-density community abruptly ended between 235 and 245 meters. Of note, over 70% of the individuals observed had some level of dead tissue, though we did not investigate mortality drivers. For 2,435 (54%) individuals observed, the dead tissue was estimated at less than 25 % of the total colony. *Aphrocallistes cf beatrix* with dead tissue making up between 25 and 50% of the colony accounted for 9.8% of individuals, while the final two categories 50%-75% and 75%-100% tissue loss accounted for 5.5% and 0.8% respectively. *Aphrocallistes cf beatrix* sponge dominated community persisted for approximately 160 meters of depth before transitioning to a sparsely populated carbonate pavement with the majority of the sessile fauna being Dendrophylliidae cup corals that were found in sedimented pockets that had collected in pockmarks in the pavement (Figure 4.7A). The start of crustose coralline algae (CCA) was documented between 255 and 265 meters on all sides, and continued upwards to the summit.

While the general trend of depth zonation described in the previous paragraph held true for all sides of the seamount there were several differences between seamounts for specific taxa. Three distribution patterns were noted across several of the abundant genera. The first were the groups that were most prevalent on the north and south sides of the seamount. *Enallopsammia* and *Gymnorete* spp were the strongest examples of this pattern (Figure 4.8A,B). While these individuals were found on all sides they were far more abundant on the north and south sides (Table 1). The second distribution pattern of note were taxa that were found in much higher numbers on both the North and West sides of the seamount such as *Hemicorallium*, *Paracalyptrophora*, and *Narella* spp. (Figure 4.8 C,D,E). Thirdly, we noted one genus — *Swiftia* — that was only found on the east and west sides (Figure 4.7E). However, a one-way ANOSIM comparing the abundance between the different flanks of the seamount indicated that the communities on all sides of the seamount were not different ($p < 0.01$, $R = 0.069$).

The east side of the seamount had the lowest abundance and diversity of sessile fauna (Figure 4.4 and 4.8). The rarefaction curves for the east sides showed a notable reduction in the number of genera observed and the rarefaction curve had a shallower slope than the other sides indicating that our sampling effort had approached saturation. The curves for the north and south transect are very similar while the west side of the feature had the highest biodiversity and the curve of the slope indicated that there are still additional taxa that were not documented by our level of sampling effort.

The total beta diversity index for seamount was relatively high, with the value of 0.831 out of the maximum possible value of 1 and minimum of 0. When comparing the

local contribution to beta diversity (LCBD) across the sides, there was only one discernable pattern of side by depth. The north and south side depths between 750 and 900 meters had an outsized effect on the beta diversity, but otherwise, no single side or depth appeared to strongly contribute to beta diversity below 300 m. The shallows, however, had strong contributions to beta diversity regardless of side (Figure 4.10 and Table 4.2).

The role of seafloor slope was a significant predictor of abundance from the generalized mixed methods model (slope: $p < 0.01$, vertical: $p = < 0.01$, overhang: $p = < 0.01$) compared to flat areas with less than a 15 deg slope. The role of genus played a significant role in the model with many genera exhibiting a preference for steeper or shallow slopes (Table 4.3).

Opportunistic collections of deep-water benthic megafauna at this seamount provided additional species diversity and biogeographic insights of the site. Cosmopolitan coral species at this site included those well-represented throughout the US central Pacific (see Parrish et al 2017) such as *Metallogorgia melanotrichos*, and the colonial scleractinians *Madrepora oculata* and *Enallopsammia rostrata*. Central Pacific bathyal species, including *Paracalyptrophora hawaiiensis*, *Calyptraphora agassizii*, *Narella horrida*, *Narella alata*, *Bebryce brunnea*, *Rhodaniridogorgia superba*, and *Hemicorallium cf. imperiale*, were also represented at this site and are indicative of biogeographic affinities with the Hawaiian archipelago to the northeast at deeper depths (>1000 m). A shallower, morphologically-distinct congener of *Metallogorgia melanotrichos* was also observed at this site at 953 m. The observed distribution patterns of this species thus far throughout the Phoenix Archipelago suggests a narrow geographic distribution within the genus (see

Metallogorgia sp. 4 in Auscavitch et al 2020).

In addition to the cosmopolitan deep-water stony corals, *Madrepora oculata* and *Enallopsammia rostrata*, solitary scleractinians and smaller colonial species were also collected across the seamount depth gradient.

Among the sponges, the morphological identification of *Aphrocallistes* cf. *beatrice* at this site indicates a substantial expansion of its reported range into the central Pacific from western Indo-Pacific archipelagos and higher southern latitude regions around New Zealand (WoRMS, 2023). In summary, these collections support initial findings by Auscavitch, Deere, et al. (2020) that the Phoenix Archipelago is an area of biogeographic overlap or transition for southern hemisphere, equatorial Indo-Pacific, and north Pacific deep-water corals, but also other habitat-forming organisms like glass sponges (Figure 4.7B).

4.5 Discussion

This study is among the first to examine deep-sea benthic community assemblages on multiple sides of a single seamount in the equatorial central Pacific (but see Morgan et al., 2019 and Du Peerz et al., 2016). We identified a relatively small and symmetric “model” seamount in an oceanographically complex location and examined four transects (one in each cardinal direction) to determine whether benthic communities would be similar across all flanks or would vary correspondingly with oceanographic variables. We found that on all seamount flanks, similar communities were noted at similar depths within an approximate depth range of 50 m, however, on a finer scale of depth change (~30 m), we noted patchiness and relative heterogeneity between sides. Within the larger depth

bands, we posited four putative types of biological assemblages that were observed on all flanks of the feature, all starting and ending within 50 meters of depth on each transect. However, we also observed that abundance within assemblages shifted on a taxa-by-taxa basis across seamount flanks, suggesting flank-specific preferences that likely reflect oceanographic current dynamics. To illustrate this concept, we applied these assemblages to a Von Humboldt-style seamount infographic to lay the foundation for ecological zonation work on seamounts and pose new hypotheses for understanding benthic community ecology on seamounts. Our findings point to unanticipated nuance in terms of biological communities across a bathymetrically simple conical seamount feature that requires further attention.

While vertical zonation with depth has been well documented globally, it is typically treated as a continuous linear variable (Auscavitch, Lunden, et al., 2020; M. J. Costello & C. Chaudhary, 2017) and we have very little context for how that vertical zonation may or may not change circumferentially around a seamount (but see Morgan et al 2019 and Du Preez et al. 2016). We found that our four assemblages were roughly consistent with depth, and were found on all four sides of the seamount, suggesting that zonation might be relatively robust to variable oceanographic conditions — which include temperature, salinity, oxygen, and currents — on this morphologically simple seamount. However, we also noticed patchiness within a depth band, which is consistent with many previous observations of hyperlocal habitat preference, for example, on a single boulder or a single face of a vertical wall. Such patchiness has yet to be well-understood, but our results suggest an intermediate driver of habitat preference between depth and benthic

substrate. Though we certainly observed hyperlocal patchiness, we observed the same taxa throughout the depth band circumferentially, but not in the same abundance. For example, some taxa (e.g., *Narella* spp. *Paracalyptrophora* spp., and *Hemicorallium* spp. corals, Figure 4.8) were found in patchy abundance on all sides of the seamount, but were found in much higher abundances overall on the North and West flanks. While additional work will be required to attribute a causal relationship to this pattern, the ADCP data down to 600 meters indicated strong shifts in current velocities that vary by seamount flank (Figure 4.2). Thus, our data demonstrate that vertical zonation patterns are not strictly a function of depth; instead, they are a triangulation of depth, benthic substrate, and oceanography (Rengstorf et al., 2013). This triangulation is not surprising, as many predictive habitat models use these variables in concert (Etnoyer et al., 2018), however, this seamount is the first to empirically demonstrate the circumferential pattern of diversity, coupled with abundance patterns corresponding to oceanography, which includes temperature, salinity, oxygen, and currents.

The only two previous studies to our knowledge to examine benthic biodiversity circumferentially had findings that differed from ours in several key aspects. Du Preez et al. (2016) documented nine different types of communities on Cobb Seamount, a large guyot in the North Pacific, but five of those communities were located on the flat top structure of the guyot, and oceanographic variables were not measured and thus not cross-correlated. Similar to our study, however, Du Preez et al. (2016) did find evidence of taxonomic structuring by depth and substrate characteristics such as slope on multiple flanks of the feature. A recent study similarly found taxonomic structuring by depth, slope

and substrate type (bedrock, cobble, pebble, mixed vs soft sediment, or spicule mat) for sponges in the North Atlantic (Meyer et al., 2022), suggesting again that the empirical determination of benthic taxa is not determined by depth alone. Morgan et al. (2019) identified nine community assemblages from an extensive survey of Mokumanamana (Necker) Island, but found no evidence of circumferential zonation. However, it is important to note that Mokumanana Island is more than 10 times larger than our focal seamount, has a fundamentally different feature shape, and is far more morphologically variable. Seamount shape has recently been suggested as an important factor in driving benthic community structure (Kennedy & Rotjan, 2022), possibly due to how shape influences local hydrodynamics. Taken together, these findings demonstrate the importance of multiple surveys on different feature shapes, sizes, and regions in order to more broadly depict biological patterning.

Of all the taxa encountered, *Enallopsammia* spp. corals were the most influenced by oceanographic patterns within their habitable depth range, and displayed strong sensitivity to both current and dissolved oxygen concentrations (Figures 4.2, 4.3 and 4.4). This scleractinian coral was found on all flanks, however it was observed in much greater numbers on the north and south flanks that experienced the most persistent current flow across the depth range sampled (Figure 4.2). This is consistent with previous findings such as Tracey et al. (2011) and Hebbeln et al. (2014), which have demonstrated *Enallopsammia* spp. sensitivity to current flow. *Enallopsammia* spp. and the other colonial scleractinians appear to be strongly influenced by dissolved oxygen concentration: we observed a clear gap in coverage where DO levels dropped (Figure 4.4), consistent with numerous other

studies that have shown scleractinian coral sensitivity to oxygen concentrations (Auscavitch, 2020; Auscavitch, Lunden, et al., 2020; Davies et al., 2008). Numerous studies have detailed the importance of oxygen levels on coral communities (Levin, 2003; Stramma et al., 2008; Stramma et al., 2010). The oxygen minimum zones (OMZ) are a geographically widespread water column strata where dissolved oxygen (DO) concentrations decline (defined as DO concentrations $< 22 \mu\text{mol/L}$ as described by Levin, 2003). Regional differences in the OMZ may result from variation in oceanographic currents, productivity, and respiration by marine organisms (Karstensen et al., 2008). Understanding the effect of oxygen sensitivity will help to interpret the influence of the OMZ on benthic communities, which is predicted to dramatically expand due to climate change (Levin et al., 2003), in some cases by as much as eight million cubic kilometers by the end of this century (Busecke et al., 2022).

Organismal sensitivity and habitat preference contribute to community-level biodiversity, and previous studies have measured beta diversity to compare communities on different seamount sections. Victorero, Robert, et al. (2018) investigated the beta diversity of Annan Seamount in the north Atlantic and found a beta diversity of 0.92 over a depth range of 200-2700 m, which is similar to our value of 0.831 over a depth range of 196-1500 m, indicating that seamounts even in different ocean basins consistently have a high level of variation across depths. Victorero, Robert, et al. (2018) compared beta diversity of communities parsed along a single transect, whereas we calculated beta diversity on all flanks by depth, and did not find much variation across the seamount even though there were shifts in abundance distributions by taxa (Figure 4.10, Table 4.2). This

suggests that — with the exception of the shallowest depths — beta diversity is highly robust within depth ranges by flank. Given the very clear patterns of uneven distribution within a depth range, our observations of robust beta diversity are somewhat surprising, and may be an indication of previously unrecognized ecological competition among deep sea benthic megafauna. This observation raises the question as to whether or not sessile benthic organisms compete for ideal patches of seafloor, and therefore may adaptively partition themselves by seamount flank within a depth range to minimize competition. Competition in low biomass coral communities is a novel concept, but may be ecologically plausible given the qualitatively observed clumped dispersion pattern that commonly appears: high density communities are often observed in a small benthic footprint, surrounded by seemingly comparable but uninhabited substrate. As such, though the mechanisms contributing to ideal settlement location are not yet understood, they clearly exist. This concept thus leads to the novel hypothesis as follows:

Hyp 1: In high biodiversity seamounts, benthic taxa will partition by seamount flank to maximize available resources delivered by variable current flow

Hyp 2: In high biodiversity seamounts, benthic taxa will partition by seamount flank to maximize available high quality benthic substrate (geology, slope, etc.)

One factor that may contribute to idealized settlement substrate may be slope steepness, which has long been hypothesized as a factor contributing to successful prey capture via topographically-induced current flow (Lavelle & Mohn, 2010). As such, we

examined how slope steepness would impact the abundance of sessile fauna. Nearly half of our taxa (20 out of 45) showed a statistically significant preference for at least one of the four categories of slope we identified (flat, sloped, vertical, and overhung). Previous work has well established that seafloor steepness plays an important role in habitat preference for sessile filter/suspension feeding benthic organisms (Etnoyer et al., 2018; Rengstorf et al., 2013). However, we noted a novel biotope - a physical habitat associated with a particular ecological community (Connor et al., 2004). Specifically, the underside of rocky overhangs, or hardgrounds with slopes in excess of 90 degrees. We found nearly all of the *Poecillastra* and *Autoplax* spp sponges in these overhanging environments, while several other taxa like *Psilocalyx* and *Gymnorete* spp were found in high abundance on both vertical and overhang environments. One advantage of inhabiting the underside of overhangs may be changes in hyperlocal hydrodynamics, which may in turn modulate current speed, eddy dynamics, or sedimentation that may impact feeding success and/ or settlement probability.

Taken together, the high habitat heterogeneity of seamounts prevents easy extrapolation of biodiversity information from bathymetrically or geographically narrow surveys, thus justifying a more comprehensive approach to seamount characterization. Our results suggest that a single survey, surveys on a single side, or surveys that are limited to a narrow depth range on a seamount will not adequately describe the entire feature. This is not surprising, given that there are already numerous oceanographic demonstrations of seamount heterogeneity, for example large bathymetric gradients in temperature (Yasuhara & Danovaro, 2016) and dissolved oxygen concentrations (Levin, 2003). Though the

justification for increased survey effort on seamounts is apparent, very few seamounts have been sampled or visited more than once or twice, though there are a few notable exceptions such as Davidson and Axial seamounts (Chadwick et al., 2010; McClain et al., 2010). However, recent explorations efforts (e.g., NOAA Office of Ocean Exploration, the Ocean Exploration Trust, Schmidt Ocean Institute and others) are amassing publicly available seamount data and biological collections that may be approaching a data density useful for addressing these types of questions. Data collected across previous expeditions may become urgently necessary as regulations are being written for environmental impact statements that will be required for deep-sea mining and bottom trawling on seamounts, without comprehensive data available (Amon, Gollner, et al., 2022).

Starting with HMS Challenger, the efforts to explore and characterize the deep ocean have been steadily increasing for over a century and a half, but still have not kept pace with the rate of exploitation. Now, with eight plus billion people on the planet, we are simultaneously exploiting (fisheries, mining, etc.) and protecting (30x30) the deep ocean at unprecedented rates (Sullivan-Stack et al., 2022). Humanity is faced with the need to make policy decisions about how to manage our deep-sea resources with a very limited understanding of deep-sea biology when compared to the state of the science in terrestrial ecosystems. Seamounts are particularly important in the open ocean because they make up nearly all the benthic substrate shallower than 3000 meters away from the continental slopes and host a wide range of life, serving as both a way station for migrating species (Shank, 2010) and habitat for numerous endemic species (Richer de Forges et al., 2000). However, all seamounts are not the same, and deep-sea ecologists have only a limited

understanding of different biological communities on a single seamount. Infographics like the Von Humboldt terrestrial mountains have become iconic and have withstood the test of time because they created a compelling, simple visual to advance an important idea: that elevation and wind direction on terrestrial mountains could shape biological communities. Despite the intense interest in oceans writ large and the deep sea in particular, we have yet to rally around the nuance and biological complexity of seamounts because they remain dark, hidden, opaque. Our intent is to emulate the stylings of Von Humboldt at this pivotal moment in ocean history — both for conservation and exploitation — as a rallying point to showcase the beauty, nuance, and complexity of seamounts, and how much more we could know. There are a handful of papers that are starting to advance these ideas, this paper among them, and it is critical for future studies to continue to advance our understanding of biodiversity patterns on seamounts.

4.6 Acknowledgements

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Table 4.1.

Counts of individuals per depth bin for each flank of the seamount for each of the 25 most abundant taxa.

| Genus | Flank | 275 | 400 | 525 | 650 | 775 | 900 | 1025 | 1150 | 1275 | 1400 | 1525 |
|-----------------------|-------|------|------|-----|-----|-----|-----|------|------|------|------|------|
| <i>Anthomastus</i> | West | 0 | 0 | 0 | 0 | 0 | 2 | 8 | 1 | 0 | 0 | 0 |
| <i>Anthomastus</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Anthomastus</i> | North | 0 | 0 | 0 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 |
| <i>Anthomastus</i> | South | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Aphrocallistes</i> | West | 366 | 278 | 3 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Aphrocallistes</i> | East | 156 | 46 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Aphrocallistes</i> | North | 1406 | 1070 | 6 | 9 | 4 | 2 | 1 | 0 | 0 | 0 | 0 |
| <i>Aphrocallistes</i> | South | 613 | 504 | 10 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Auloplax</i> | West | 0 | 0 | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Auloplax</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Auloplax</i> | North | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Auloplax</i> | South | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bolosominae</i> | West | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bolosominae</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Bolosominae</i> | North | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 0 | 0 | 0 | 0 |
| <i>Bolosominae</i> | South | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Calyptrophora</i> | West | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 23 | 0 | 0 | 0 |
| <i>Calyptrophora</i> | East | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 2 | 0 | 0 |
| <i>Calyptrophora</i> | North | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Calyptrophora</i> | South | 0 | 0 | 0 | 0 | 0 | 10 | 1 | 0 | 0 | 0 | 0 |
| <i>Candidella</i> | West | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Candidella</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Candidella</i> | North | 0 | 0 | 3 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Candidella</i> | South | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Chrysogorgia</i> | West | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 7 | 2 | 5 |
| <i>Chrysogorgia</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| <i>Chrysogorgia</i> | North | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| <i>Chrysogorgia</i> | South | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dactylotrachus</i> | West | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dactylotrachus</i> | East | 29 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | | | | | |
|--------------------------|-------|-----|-----|-----|----|----|----|----|-----|---|---|---|
| <i>Dactylotrochus</i> | North | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dactylotrochus</i> | South | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Eguchipsammia</i> | West | 182 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Eguchipsammia</i> | East | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Eguchipsammia</i> | North | 24 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Eguchipsammia</i> | South | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Enallopsammia</i> | West | 0 | 1 | 12 | 5 | 1 | 16 | 22 | 6 | 0 | 1 | 1 |
| <i>Enallopsammia</i> | East | 0 | 0 | 8 | 2 | 0 | 5 | 2 | 1 | 0 | 0 | 0 |
| <i>Enallopsammia</i> | North | 0 | 2 | 70 | 4 | 0 | 3 | 3 | 4 | 0 | 0 | 0 |
| <i>Enallopsammia</i> | South | 0 | 7 | 49 | 1 | 0 | 41 | 11 | 0 | 0 | 0 | 0 |
| <i>Gymnorete</i> | West | 0 | 2 | 24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Gymnorete</i> | East | 0 | 1 | 13 | 4 | 9 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Gymnorete</i> | North | 0 | 112 | 167 | 66 | 19 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Gymnorete</i> | South | 0 | 153 | 52 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Hemicorallium</i> | West | 0 | 0 | 0 | 1 | 2 | 5 | 27 | 13 | 2 | 1 | 0 |
| <i>Hemicorallium</i> | East | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Hemicorallium</i> | North | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 10 | 4 | 0 | 0 |
| <i>Hemicorallium</i> | South | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 |
| <i>Madrepora</i> | West | 0 | 0 | 0 | 0 | 0 | 2 | 34 | 0 | 0 | 0 | 0 |
| <i>Madrepora</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Madrepora</i> | North | 0 | 0 | 0 | 6 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| <i>Madrepora</i> | South | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Metallogorgia</i> | West | 0 | 0 | 0 | 0 | 1 | 34 | 21 | 0 | 0 | 1 | 4 |
| <i>Metallogorgia</i> | East | 0 | 0 | 0 | 0 | 1 | 4 | 2 | 0 | 0 | 0 | 0 |
| <i>Metallogorgia</i> | North | 0 | 0 | 0 | 0 | 1 | 8 | 0 | 0 | 0 | 0 | 0 |
| <i>Metallogorgia</i> | South | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 0 |
| <i>Narella</i> | West | 0 | 10 | 4 | 1 | 4 | 1 | 36 | 171 | 0 | 4 | 0 |
| <i>Narella</i> | East | 0 | 0 | 0 | 0 | 12 | 8 | 3 | 0 | 1 | 0 | 0 |
| <i>Narella</i> | North | 22 | 39 | 42 | 7 | 3 | 9 | 1 | 0 | 0 | 0 | 0 |
| <i>Narella</i> | South | 0 | 6 | 5 | 0 | 1 | 13 | 21 | 0 | 0 | 0 | 0 |
| <i>Paracalyptrophora</i> | West | 0 | 0 | 0 | 29 | 0 | 0 | 1 | 26 | 0 | 0 | 0 |
| <i>Paracalyptrophora</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Paracalyptrophora</i> | North | 0 | 0 | 0 | 18 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Paracalyptrophora</i> | South | 0 | 0 | 4 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Paracis</i> | West | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | | | | | |
|---------------------------|-------|-----|-----|----|----|----|---|----|----|---|---|---|
| <i>Paracis</i> | East | 336 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Paracis</i> | North | 80 | 157 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Paracis</i> | South | 195 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Phyllochaetopterus</i> | West | 372 | 795 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Phyllochaetopterus</i> | East | 186 | 1 | 14 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Phyllochaetopterus</i> | North | 10 | 10 | 90 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Phyllochaetopterus</i> | South | 585 | 19 | 82 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Poecillastra</i> | West | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Poecillastra</i> | East | 12 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Poecillastra</i> | North | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Poecillastra</i> | South | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Psilocalyx</i> | West | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Psilocalyx</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Psilocalyx</i> | North | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Psilocalyx</i> | South | 0 | 0 | 0 | 41 | 13 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Regadrella</i> | West | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Regadrella</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Regadrella</i> | North | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| <i>Regadrella</i> | South | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Rhodaniridogorgia</i> | West | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Rhodaniridogorgia</i> | East | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Rhodaniridogorgia</i> | North | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Rhodaniridogorgia</i> | South | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sclerothamnus</i> | West | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sclerothamnus</i> | East | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Sclerothamnus</i> | North | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Sclerothamnus</i> | South | 0 | 0 | 0 | 0 | 0 | 2 | 5 | 2 | 0 | 0 | 0 |
| <i>Swiftia</i> | West | 0 | 0 | 0 | 0 | 0 | 1 | 14 | 12 | 0 | 2 | 0 |
| <i>Swiftia</i> | East | 0 | 0 | 0 | 0 | 3 | 7 | 0 | 0 | 0 | 0 | 0 |
| <i>Swiftia</i> | North | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Swiftia</i> | South | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Victorgorgia</i> | West | 0 | 0 | 0 | 0 | 3 | 1 | 11 | 22 | 2 | 1 | 3 |
| <i>Victorgorgia</i> | East | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Victorgorgia</i> | North | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 |
| <i>Victorgorgia</i> | South | 0 | 0 | 0 | 0 | 1 | 3 | 7 | 3 | 0 | 0 | 0 |

Table 4.2.

Local Contribution to Beta Diversity for each dive. The LCBD represents the ecological comparative uniqueness of each sample. The p = value for each bin was assessed through permutation analysis (999 iterations) testing if the null hypothesis that genera distribution is random among the sampling depths. Blank cells were not covered by the dives.

| Depth (m) | West | P value | East | P value | North | P value | South | P value |
|----------------------|-------------|--------------------|-------------|--------------------|--------------|----------------|--------------|--------------------|
| 240 | 0.01055821 | 0.054 | 0.01053052 | 0.057 | 0.00858532 | 0.298 | 0.01006325 | 0.121 |
| 270 | 0.00805435 | 0.448 | 0.01021841 | 0.091 | 0.00793561 | 0.468 | 0.00989966 | 0.119 |
| 300 | 0.0083673 | 0.342 | 0.00864487 | 0.295 | 0.00788643 | 0.464 | 0.0084734 | 0.339 |
| 330 | 0.0090314 | 0.212 | 0.00869924 | 0.263 | 0.0081948 | 0.409 | 0.00857671 | 0.303 |
| 360 | 0.00747817 | 0.605 | 0.0073957 | 0.651 | 0.00730431 | 0.668 | 0.00858532 | 0.298 |
| 390 | 0.00727077 | 0.699 | 0.00858532 | 0.31 | 0.00696166 | 0.767 | 0.00651281 | 0.854 |
| 420 | 0.00638528 | 0.868 | 0.00738118 | 0.645 | 0.00650819 | 0.872 | 0.00600253 | 0.926 |
| 450 | 0.00682924 | 0.804 | 0.00627381 | 0.897 | 0.00541583 | 0.966 | 0.00635738 | 0.887 |
| 480 | 0.00723586 | 0.717 | 0.00687236 | 0.78 | 0.00588666 | 0.939 | 0.00629876 | 0.881 |
| 510 | 0.00723586 | 0.695 | 0.00626187 | 0.886 | 0.00594171 | 0.95 | 0.00558561 | 0.961 |
| 540 | 0.00744296 | 0.659 | 0.00886612 | 0.249 | 0.00764536 | 0.572 | 0.00709199 | 0.729 |
| 570 | 0.00717039 | 0.717 | 0.00772243 | 0.565 | 0.00705541 | 0.748 | 0.00876228 | 0.3 |
| 600 | 0.01074697 | 0.028 | 0.00853901 | 0.301 | 0.00689112 | 0.783 | 0.00777145 | 0.529 |
| 750 | 0.00583402 | 0.95 | 0.00847706 | 0.326 | 0.01032445 | 0.088 | 0.01069218 | 0.066 |
| 780 | 0.00756151 | 0.595 | 0.00784163 | 0.529 | 0.00680404 | 0.8 | 0.01100839 | 0.025 |
| 810 | 0.00851202 | 0.33 | 0.00787259 | 0.483 | 0.00755021 | 0.631 | 0.0113664 | 0.009 |
| 840 | 0.00705522 | 0.765 | 0.00817198 | 0.403 | 0.00886612 | 0.256 | 0.01131041 | 0.009 |
| 870 | 0.00725551 | 0.702 | 0.00598095 | 0.938 | 0.0065599 | 0.848 | 0.00884393 | 0.265 |

| | | | | | | | | |
|-------------|------------|-------|------------|-------|------------|-------|------------|-------|
| 900 | 0.00720663 | 0.723 | 0.00793272 | 0.466 | 0.01148559 | 0.002 | 0.00952776 | 0.167 |
| 930 | 0.00735553 | 0.678 | 0.00570298 | 0.965 | 0.00848703 | 0.314 | 0.00723586 | 0.689 |
| 960 | 0.00536527 | 0.96 | 0.00675389 | 0.813 | 0.00713557 | 0.718 | 0.00598204 | 0.935 |
| 990 | 0.00560929 | 0.958 | 0.00740992 | 0.651 | 0.00752544 | 0.635 | 0.00588986 | 0.941 |
| 1020 | 0.00689243 | 0.78 | 0.00806319 | 0.414 | 0.00796048 | 0.468 | 0.00587606 | 0.942 |
| 1050 | 0.00682304 | 0.814 | 0.01015673 | 0.1 | 0.01039125 | 0.068 | 0.00459338 | 0.98 |
| 1080 | 0.00765272 | 0.562 | 0.0066572 | 0.835 | 0.00723586 | 0.699 | 0.00544941 | 0.96 |
| 1110 | 0.00649042 | 0.88 | 0.00764892 | 0.58 | 0.00701761 | 0.77 | 0.00642882 | 0.882 |
| 1140 | 0.00688821 | 0.784 | 0.00894451 | 0.248 | 0.00723586 | 0.726 | 0.00912712 | 0.22 |
| 1170 | 0.0070776 | 0.732 | 0.01177894 | 0.001 | 0.00809427 | 0.429 | 0.00982934 | 0.134 |
| 1260 | 0.00978394 | 0.125 | 0.01057369 | 0.05 | 0.00723586 | 0.711 | | |
| 1290 | 0.00981308 | 0.142 | | | 0.0101406 | 0.119 | | |
| 1320 | 0.00781336 | 0.5 | | | 0.0106294 | 0.067 | | |
| 1380 | 0.00654144 | 0.866 | | | 0.01019403 | 0.09 | | |
| 1410 | 0.00764892 | 0.579 | | | 0.00968751 | 0.153 | | |
| 1440 | 0.00975518 | 0.154 | | | | | | |
| 1470 | 0.00963813 | 0.16 | | | | | | |
| 1500 | 0.00974644 | 0.161 | | | | | | |

Table 4.3.

Percent of individuals observed via each slope category.

| Genus | flat (<15 deg) | slope (15-70deg) | vertical (70-90 deg) | Overhang (>90 deg) |
|---------------------------|----------------|------------------|----------------------|--------------------|
| <u>Aphrocallistes</u> | 54.04 | 40.92 | 3.35 | 1.70 |
| <u>Phyllochaetopterus</u> | 3.56 | 94.09 | 1.99 | 0.37 |
| <u>Paracis</u> | 28.77 | 69.71 | 0.00 | 1.52 |
| <u>Gymnorete</u> | 1.28 | 12.16 | 63.36 | 23.20 |
| <u>Narella</u> | 15.33 | 17.92 | 42.69 | 24.06 |
| <u>Enallopsammia</u> | 24.46 | 36.69 | 30.22 | 8.63 |
| <u>Eguchipsammia</u> | 14.55 | 83.18 | 1.82 | 0.45 |
| <u>Paracalyptrophora</u> | 11.63 | 20.93 | 37.21 | 30.23 |
| <u>Metallogorgia</u> | 26.83 | 69.51 | 3.66 | 0.00 |
| <u>Hemicorallium</u> | 1.30 | 18.18 | 42.86 | 37.66 |
| <u>Victorgorgia</u> | 7.94 | 22.22 | 33.33 | 36.51 |
| <u>Psilocalyx</u> | 0.00 | 0.00 | 59.26 | 40.74 |
| <u>Calyptrophora</u> | 2.22 | 31.11 | 15.56 | 51.11 |
| <u>Madrepora</u> | 2.22 | 35.56 | 20.00 | 42.22 |
| <u>Swiftia</u> | 6.98 | 25.58 | 34.88 | 32.56 |
| <u>Dactylotrachus</u> | 0.00 | 55.17 | 44.83 | 0.00 |
| <u>Poecillastra</u> | 0.00 | 7.41 | 0.00 | 92.59 |
| <u>Chrysogorgia</u> | 8.00 | 72.00 | 12.00 | 8.00 |
| <u>Anthomastus</u> | 0.00 | 0.00 | 58.33 | 41.67 |

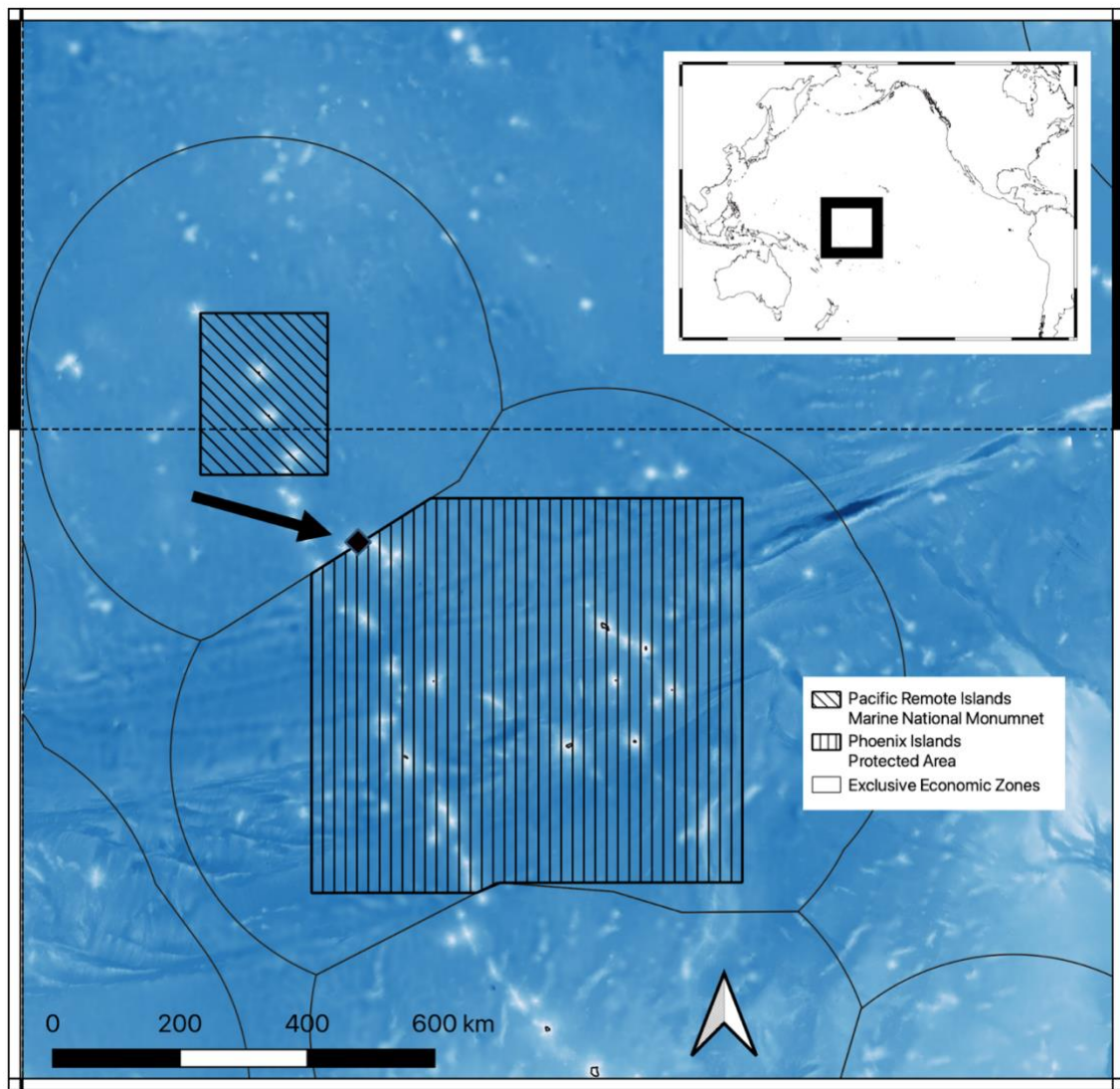


Figure 4.1. Map of study area. The focus of this project is a single seamount feature that is part of a cluster of seamounts that is being referred to as “The Winslow Complex” in the Phoenix Archipelago. This seamount is just south of the Equator (dashed line) in US territorial waters. The feature rises from 5,000 meters depth to just shallower than 200 meters. The features’ location on the equator makes for dynamic oceanographic conditions with high current velocities with the equatorial undercurrent hitting the top of the feature. Dots are ROV dive sites, crosses are ship-based CTD casts.

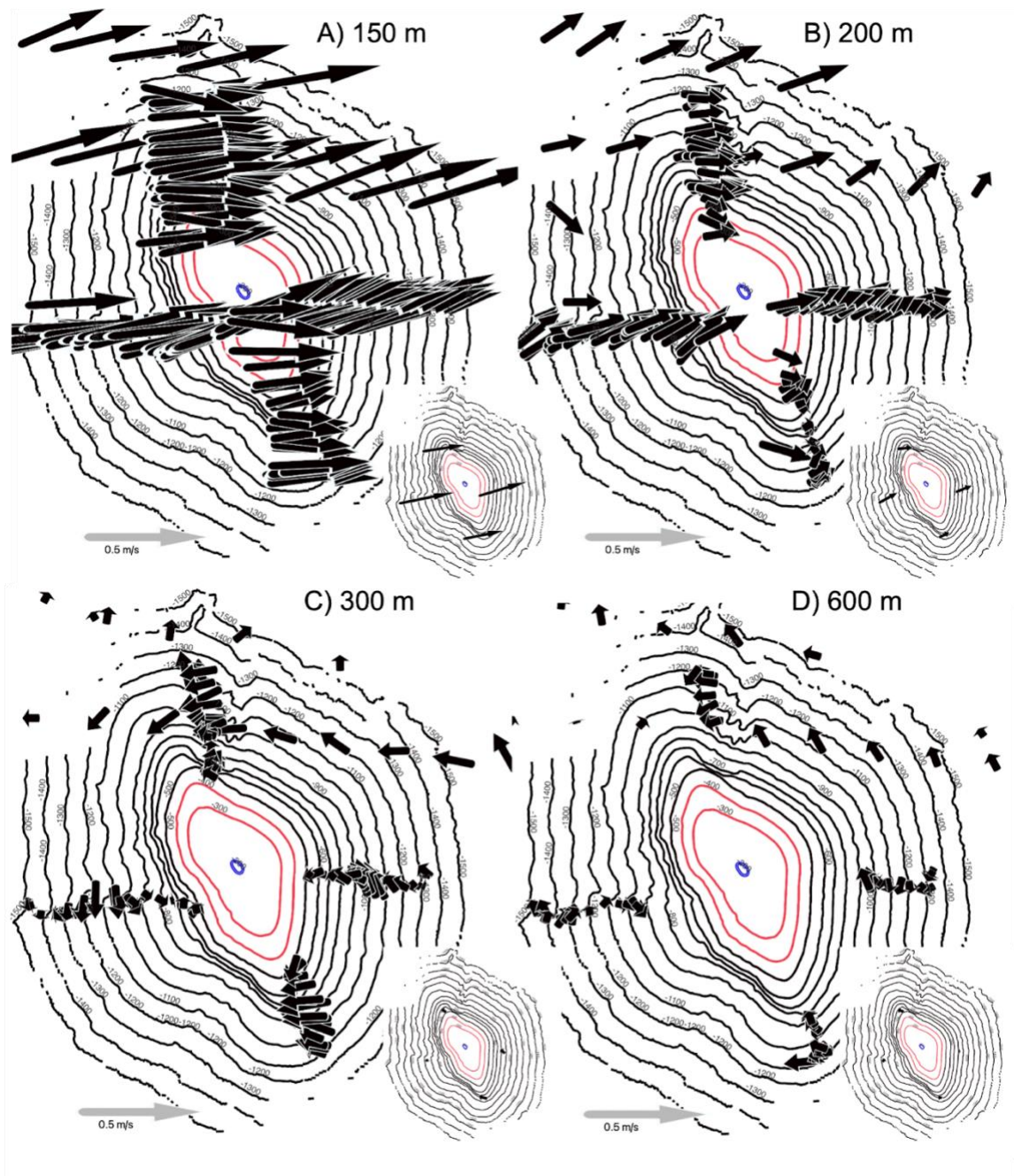


Figure 4.2. 75 kHz Acoustic current doppler current profiler (ADCP) data collected from the hull mounted transducer from the R/V *Falkor*. Arrow direction shows the direction of current flow. The length of the arrow indicated the relative velocity of the water mass at that location. (A) Water flows at 150 meters, which is above the shallowest point of the seamount. (B) 200 meters depth, which is the shallowest point of the seamount. (C) depth ~300 meters, there is a strong current reversal at this depth where the water switches from

predominantly flowing West to East to East to West. (D) Depth 600 meters. This is the deepest depth the ADCP data was reliable across most of the seamount and corresponds with the oxygen minimum zone. Note the turbulence in the lee of the seamount on the West side.

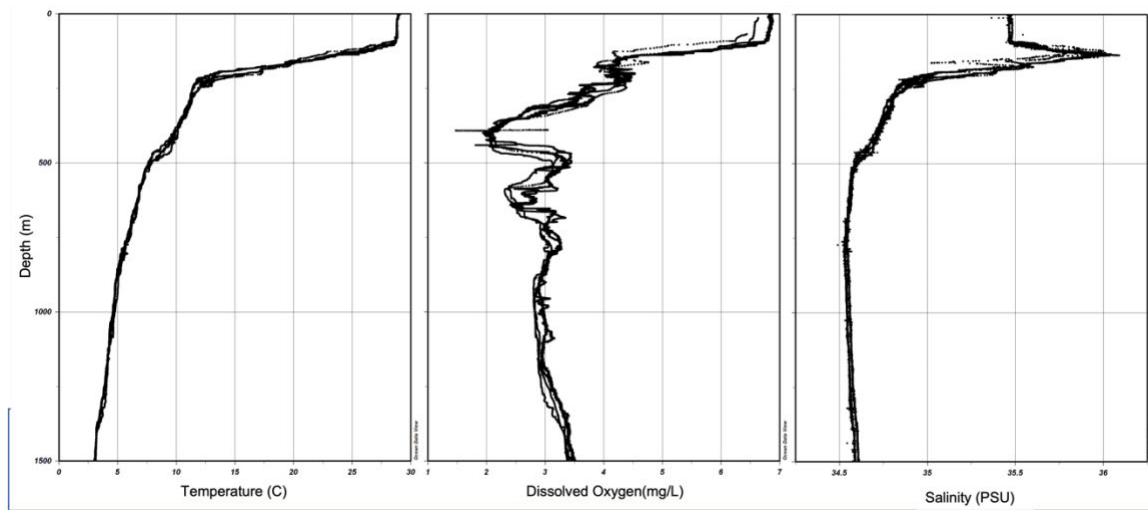


Figure 4.3. Temperature, oxygen, and salinity profiles. Data is merged from two SBE 49 casts conducted from the ships CTD along with SBE 32 that is mounted on the ROV. ROV CTD data were lost from part of S0433 and all of S0334 through S0336 due to a mechanical failure, which prompted the two SBE 49 casts to compensate. The left panel is temperature presented in degrees Celsius. The right is the salinity in practical salinity units (PSU). The middle is dissolved oxygen displayed in mg/L units. This data was collected over a five day window and may not represent longer term average conditions.

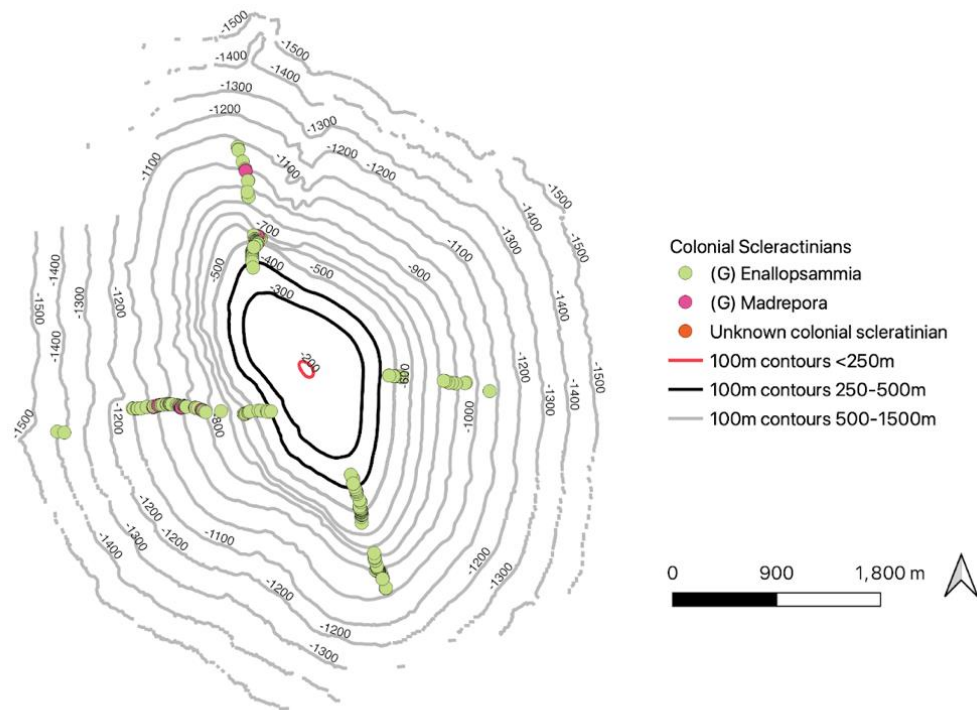


Figure 4.4. Distribution of colonial Scleractinians on all sides of the feature. There is a gap in their distribution between ~500 and ~800 meters depth which corresponds to the two oxygen minima that can be seen in figure 4.3.

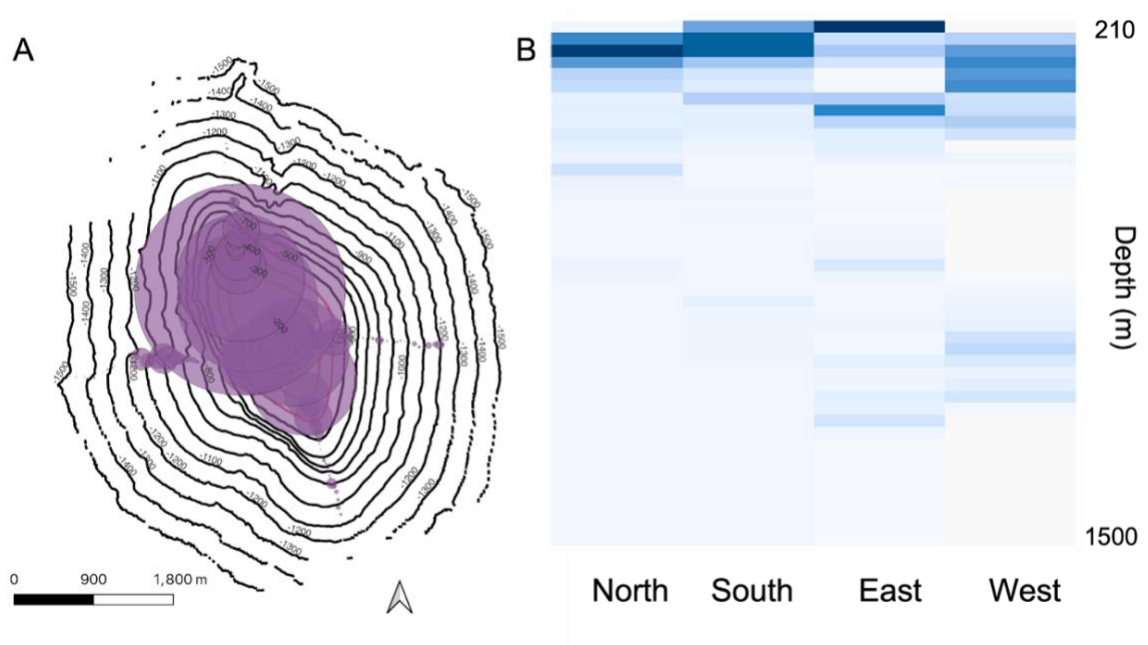


Figure 4.5. Total abundance of benthic taxa. A) Total number of individuals observed across all taxa based on 30-meter depth bins. B) Heatmaps of total number of individuals based on 30-meter depth bins.

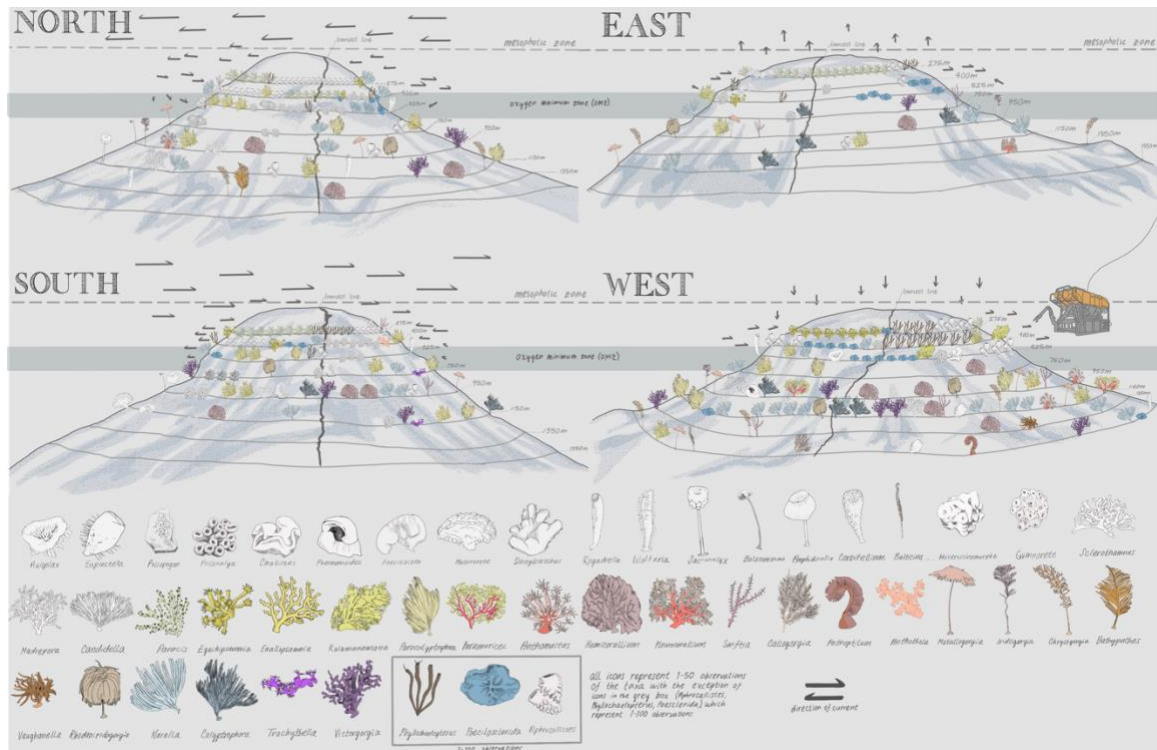


Figure 4.6. Artist rendition of the zonation of target seamount. In the style of Alexander Von Humboldt and Alexander Keith Johnston, the science party partnered with an artist to make this scientifically accurate artistic rendition of life along the flanks of the seamount. Each panel depicts a flank of the seamount. Each icon represents 50 individuals per 125 meters of depth except for the three genera with a black box. They represent 100 individuals. Artist: Constance Sartor, © 2023 CRS. Used by Permission.

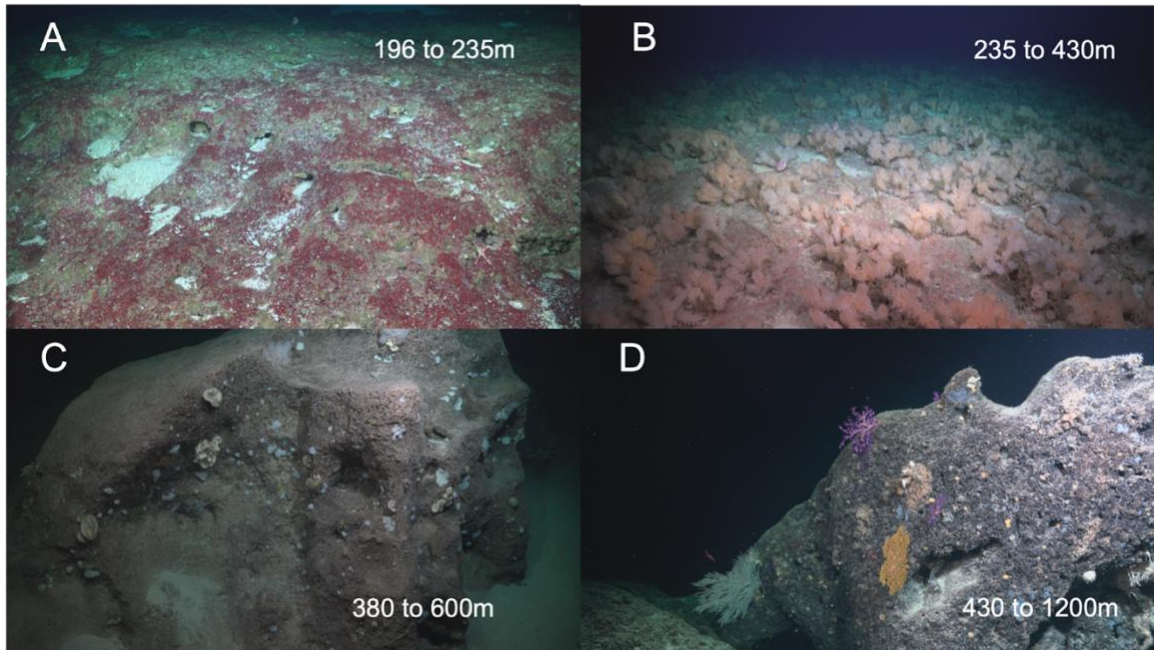


Figure 4.7. Image plate of example of vertical zonation along the flanks of the seamount. While there were numerous differences between the sides of the feature, three basic zones remained the same on all sides. A) The top of the seamount was predominantly carbonate pavement with sediment filled depressions that hosted *Vaughanella* sp. cup corals. The CCA encrusting the carbonate was also common. B) between 380- and 430-meters depth on all side there was a high density community of *Aphrocallistes cf beatrix* sponges with tufts of *Phyllochaetopterus limicolus* worms living amongst the sponges. C) Below the band of *Aphrocallistes cf beatrix* sponges smaller encrusting sponges that were predominantly found on vertical or overhung faces dominated the benthic community. D) the deeper depths were a mix of sponges and octocorals taxa made up the comparatively thinly populated patchy community.

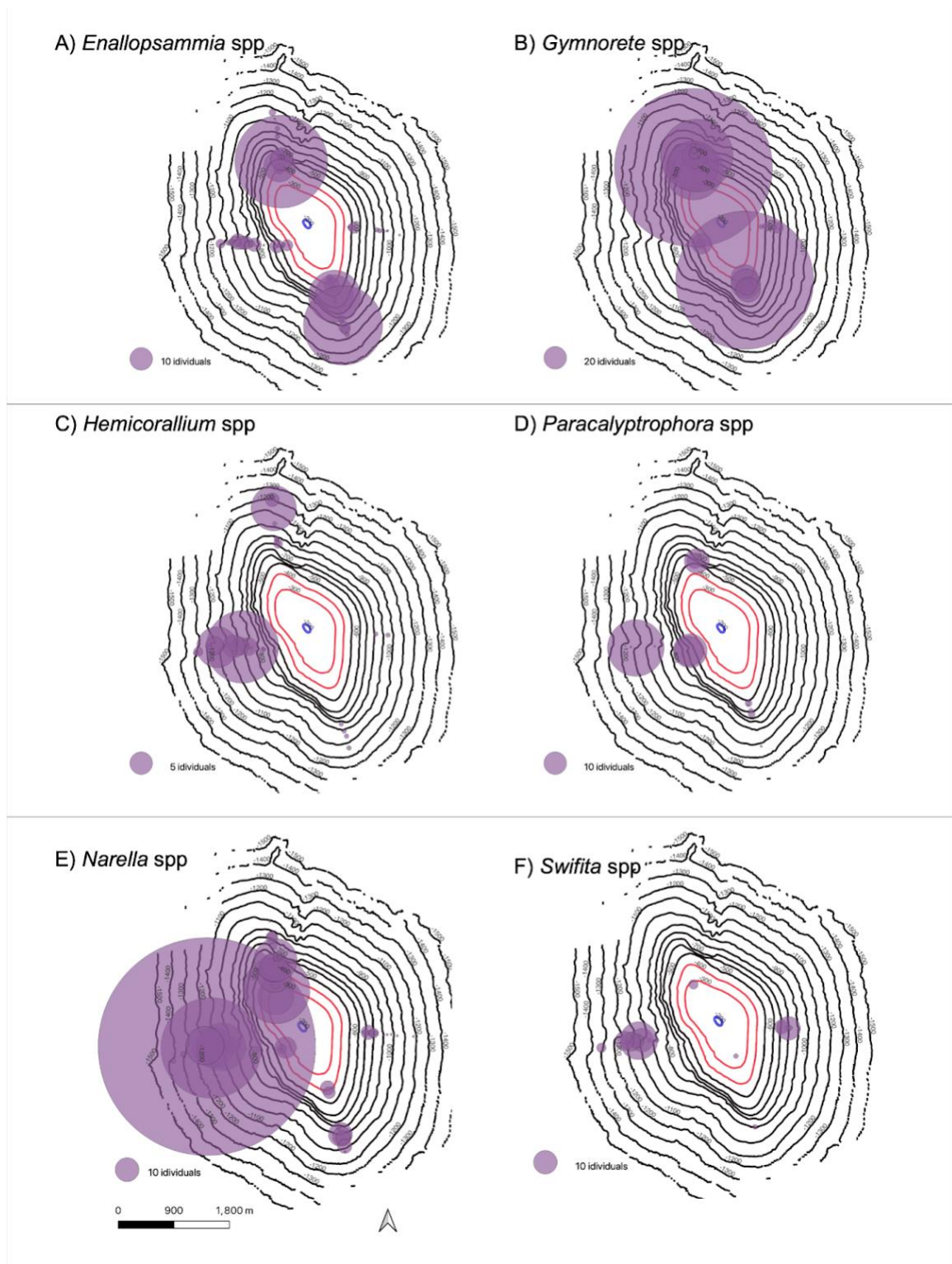


Figure 4.8. Density of observation of each deepwater taxon by 30-meter depth zones. Dots are scaled of the number of individuals seen within each depth bin. Each panel is internally

scaled so the dot size to count number is not consistent in all panels. (A) colonial scleractinians, note the reduction in observations between 600 and 900 meters that corresponds with the oxygen minimum zone. (B) Serpulid Worm tufts were one of the dominant organisms found between 200 and 470 meters. (C) *Aphrocallistes cf. beatrix* sponges make up the majority of biomass on one of the most noticeable zones on the seamount, forming a continuous ring of high density conization all the way around the feature between 240 and 500 meters. On the East face of the seamount, the high-density ring is shifted nearly hundred meters shallower than where it started on the other sides.

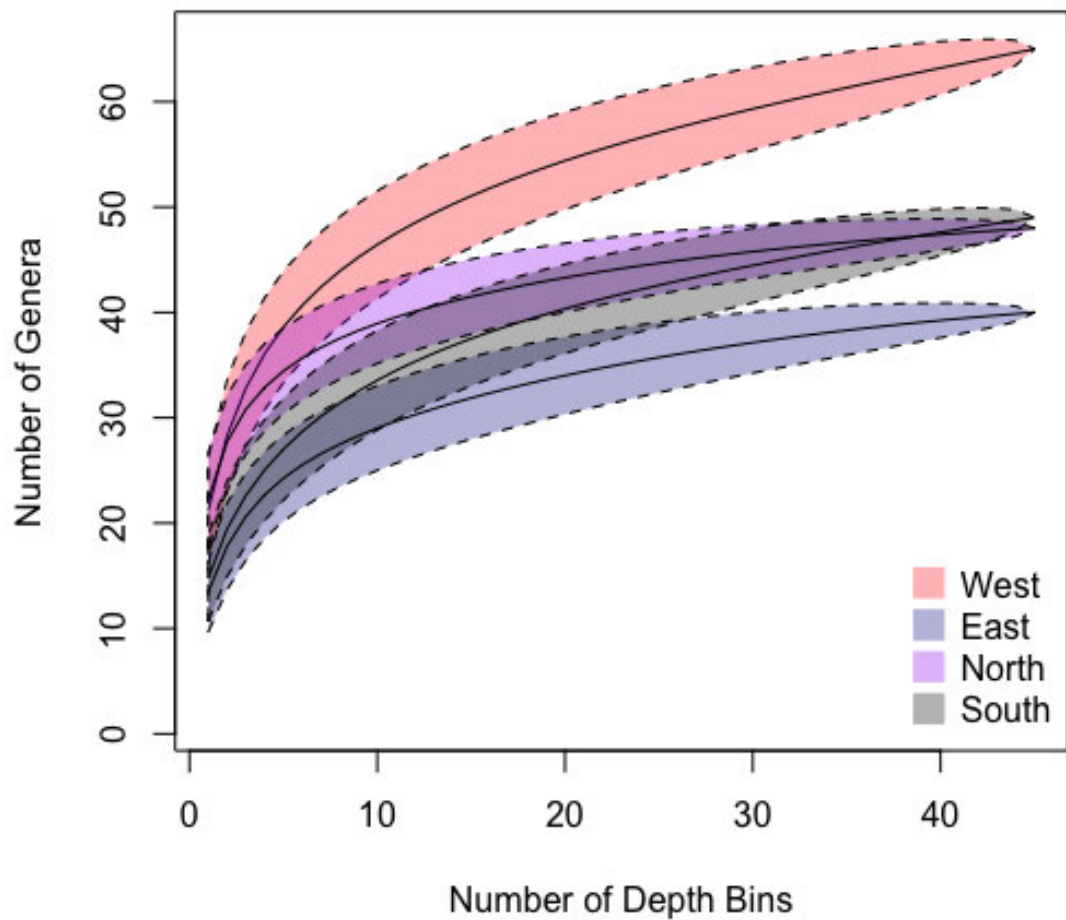


Figure 4.9. Rarefaction curves by 30-meter depth bin for each side of the seamount. The North and East dives are nearly identical. There is a noticeable difference between the East and West dives. The East side of the feature has a much lower number of unique taxa and approaches the asymptote much quicker than the north side which has a larger total number of taxa retains a steeper slope throughout the sampling range.

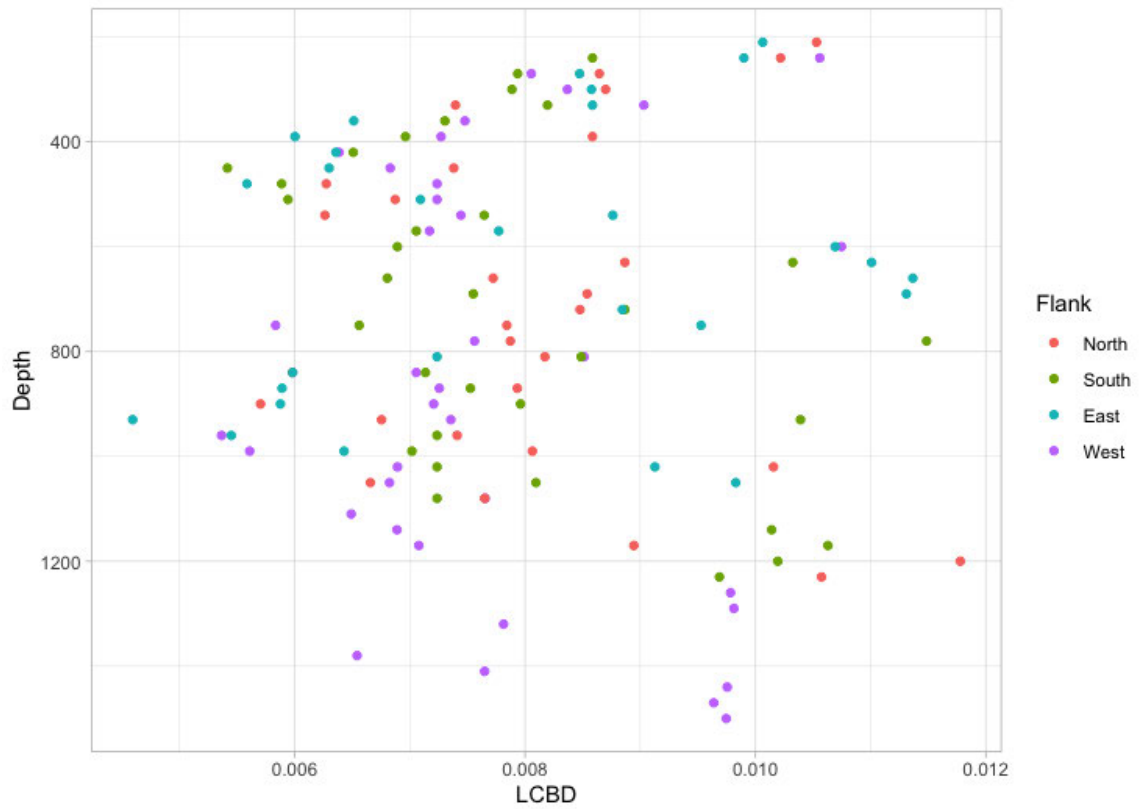


Figure 4.10. Local Contribution to Beta Diversity (LCBD) for each side of the seamount. The LCBD represents the ecological comparative uniqueness of each sample. The wide variation of values between each side of the feature at any given depth indicates that the communities in those depths contribute differently to the overall beta diversity of the feature and that each side is different. See table 2 for the statistical significance of each depth bin.

CHAPTER FIVE: MIND THE GAP: COMPARING EXPLORATION EFFORT WITH GLOBAL BIODIVERSITY PATTERNS AND CLIMATE PROJECTIONS TO DETERMINE OCEAN AREAS WITH GREATEST EXPLORATION NEEDS

5.1 Abstract

The oceans contain 1,335 million km³ of water covering 361.9 million km² of seafloor across 71% of the planet. In the past few decades, there has been substantial effort put into mapping and exploring the ocean fueled by the advent of new technologies that more easily enable deepwater access. However, we are still far from achieving our shared goals of a well characterized and documented ocean. In 2010, Webb et al. documented the paucity of deep-sea data in the Ocean Biogeographic Information System OBIS, which is the largest of the ocean biodiversity archives. While significant exploration progress has been made, the rate of change in the ocean is outstripping the rate of characterization and research. Given the limited resources available, future work needs to be prioritized to focus on areas of greatest need. Here, we investigate several lines of inquiry to determine priority areas for future exploration. We accumulated the largest database of global deep submergence dive records ever compiled and use OBIS biodiversity records to assess the level of exploration in different ocean regions. Then, we compared these measures of exploration effort with different biogeographic province schemas and estimates of climate change velocity projections to identify the largest remaining gaps in exploration and research sampling. Given that marine science has only explored between 5 and 20% of the ocean (depending on estimates) in the last hundred and fifty years, future exploration needs to be more targeted to attempt to keep pace with the rate and impact of environmental and biodiversity change in the ocean.

5.2 Introduction

We are facing a global crisis of biodiversity (Boyce et al., 2022; Ceballos et al., 2015). More than a million species are known to be at risk for extinction globally (IPBES, 2022), the majority of which reside in marine environments (Mora et al., 2011). Because the ocean is still so underexplored, the need to value and conserve taxa and habitats that we know so little about has been termed a ‘paradox of marine conservation’ (Webb, 2009). A 2006 *Science* editorial highlighted that biodiversity research was ‘grounded’ in terrestrial environments (Hendriks et al., 2006) with only about 10% of the research published or presented at international biodiversity conferences focused on marine biodiversity, with a similar terrestrial-focus found in related disciplines including conservation biology and macroecology (Raffaelli et al., 2005; Richardson & Poloczanska, 2008). This terrestrial focus logically extends from ease of access; however, it is not representative of our planet. The ocean covers 71% of the planet’s surface and represents nearly 90% of the habitable space (over a billion km³) for multicellular life (Angel, 1993; Kunzig, 2003; Robison, 2004; Robison, 2009). Several efforts have been made to address the knowledge gap in ocean biodiversity research. In the early 2000s, the Census of Marine Life (Ausubel et al., 2010) and other projects such as the Marine Biodiversity and Ecosystem Functioning EU Network of Excellence (Heip et al., 2009) made major strides in documenting new species in the ocean. More recently, projects such as the UN Ocean Decade (Ryabinin et al., 2019) and Challenger 150 (Baker et al., 2021) continue to cast a spotlight on gaps, with the goal of filling them. While this mismatch of effort (terrestrial) and habitable area (marine) is a well-known paradox, marine scientists still struggle to close the gap between ocean area

and terrestrial research because the ocean is disproportionately large, expensive to study, and historically under characterized.

As the planet faces a rapidly shifting climate (IPBES, 2022) and a biodiversity crisis (Boyce et al., 2022), the lack of knowledge about the biodiversity of our oceans is becoming a problem that is increasingly an issue of global relevance for food security, national security, and international peacekeeping (e.g. Grabarz 2009, Fedotova et al. 2021, Talukder et al. 2022). The ocean provides a range of globally important ecosystem services (Thurber et al., 2014) including support of fisheries, natural products for medical and industrial chemical processes, regulation of climate and ocean chemistry, providing approximately 50 percent of atmospheric oxygen (Riser & Johnson, 2008) and sequestering 37,000 Gigatonnes of carbon that includes the absorption of ~25% of the carbon aggregately released from the sum total of human activities (Canadell et al., 2007; Gruber et al., 2019; Sabine & Feely, 2007). The biological mechanisms that regulate these processes come from a diversity of organisms, many of which are as-of-yet undescribed or unknown (Mora et al., 2011). These new taxa are not just cryptic invertebrates, but also include large megafauna such as whales and sharks (Rosel et al., 2021; Weigmann et al., 2020).

The ocean is not a monolith. It hosts a wide variety of ecosystems and different habitats that are governed by a range of abiotic and biotic factors such as light input, ocean currents, depth, upwelling, migrations, etc. (Derek P Tittensor et al., 2010), all of which contribute to biodiversity. To account for the complexity, numerous attempts have been made to understand the structure of biodiversity of the ocean by defining eco-regions or

biogeographic provinces, which continues to be an area of active research (Longhurst, 1985; Longhurst, 2010; Sutton et al., 2017; Watling et al., 2013). The ocean community has not yet reached consensus on a single geodescriptive system, because each has different strengths in characterizing biodiversity patterns by specific depth range or taxa (Costello et al., 2017; Longhurst, 1985; Longhurst, 2010; Sutton et al., 2017; Watling et al., 2013). As such, it remains challenging to point to a specific ecoregion or biogeographic province and infer associated biodiversity estimates, which hinders ocean practitioners from being able to manage, conserve, restore, or predict biodiversity loss/gain at scale.

Webb et al. (2010) quantified the gaps in biodiversity information in the ocean using the Ocean Biodiversity System (OBIS) and found significant gaps in biodiversity records across distance from shore, and across depths. Here, we build upon that to document progress in the last decade and to identify remaining areas of priority exploration needs. To accomplish this, we have integrated biogeographic provinces of the ocean with OBIS data to identify the least characterized areas. Additionally, we compiled a global dataset of deep submergence dive records to build upon the OBIS records to identify the areas of the world's oceans that are least explored by deep submergence vehicles. Finally, we integrated this information with climate change projections to determine the areas of greatest expected change with lowest number of biodiversity records.

5.3 Methods

Deep submergence dive locations and depths were collected from 12 institutions globally including: The National Oceanic and Atmospheric Administration's Office of

Ocean Exploration (NOAA-OE), the Hawaii Undersea Research Laboratory (HURL), Ocean Exploration Trust (OET), Harbor Branch Oceanographic Institute (HBOI), Monterey Bay Aquarium Research Institute (MBARI), National Deep-Submergence Facility (NDSF) and the Schmidt Ocean Institute (SOI) form the United States. Outside the United States, records were collected from the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), the French National Institute for Ocean Science (IFREMER), the United Kingdom's Natural Environment Research Council (NERC), Russian Academy of Sciences, and GEOMAR Helmholtz Centre for Ocean Research Kiel. Attempts to gather additional records from other institutions were made but the authors were unable to obtain them. Records for human-occupied submersibles, remotely operated vehicles, autonomous underwater vehicles, and towed cameras were included in the dataset. Dive locations were accessed through publicly available data portals when possible (NOAA-OE, HURL, OET, NDSF, NERC) or through data requests made to the institutions (MBARI, HBOI, SOI, GEOMAR, IFREMER, JAMSTEC). Records without position data were eliminated from the dataset and records for sites that are not publicly available were rounded to the nearest 0.01 of a degree to protect sensitive site locations.

Biogeographic provinces for different depths were overlaid from the literature as follows: Longhurst provinces were used to describe the surface waters (Longhurst, 2010), accessed from <https://www.marineregions.org/> (Flanders Marine Institute, 2019); Sutton et al.'s (2017) proposed biogeographic provinces for the mesopelagic was accessed via the supplementary information; and Watling et al.'s (2013) proposal for the lower bathyal and abyssal pelagic was accessed through personal communications with the authors. Ocean

biodiversity records were downloaded from the Ocean Biodiversity Information System (OBIS.org database up to date as of 2022-10-22). Records that were flagged as terrestrial and those without depth information were excluded from the data set. The total number of OBIS records is 107,390,009. Reduced by nonsensical geographic positioning and negative depths left us with 94,053,712 records. We then removed all records with no depth information, which left us with a total of 58,442,819 records that were used in this study. OBIS records, as well as all four of the biogeographic province schemes noted above, were spatially joined with a global 100 x 100 km grid (Equal Earth Projection) for surface waters (0–200 m, mesopelagic (200–1,000), Bathypelagic (1,000–4,000m), Abyssopelagic (>4,000) using the R package ‘sf’ (Pebesma, 2018). OBIS records for each grid or province were tallied for total number of records, and the number of unique families, genera, and species found in each area. A quartile rank for the number of records was assigned for each 100 km x 100 km grid.

Following the methods outlined in (Webb et al., 2010), we used the ETOPO2 30 arcs-second relief model (NCEI, 2022) to get ocean depths for each occurrence record. Together, sample depth and bottom depth describe the position in the water column of each record. Prior to analysis, we removed any record with a negative depth. For any record with unreconciled depths (e.g., where the sample depth was greater than the reported depth from ETOPO2), we assumed the record was a benthic one, and thus replaced the bathymetry maximum depth with the sample depth assuming the sample depth is more accurate for that location. We then used global seafloor bathymetry to determine the proportional area of the oceans occurring in each zone, represented by cells (Figure 5.2).

We corrected the number of OBIS records based on the proportional volume of ocean meeting the appropriate criteria for sample depth and ocean depth. A more detailed description of this method can be found in (Webb et al., 2010).

Climate change velocity estimates were harvested from the supplementary information of Brito-Morales et al. (2020). They used data from Coupled Model Intercomparison Project Phase 5 (CMIP5) climate models averaged annually with a one-degree resolution to estimated climate velocity for different depths of the ocean based on three scenarios published by the Intergovernmental Panel on Climate Change (IPCC). Climate change velocity illustrate the distance north an organism would have to move north to find the same temperature conditions based on different warming scenarios. We took the average value of Brito-Morales et al change velocity estimates contained within each of the same 100km x 100km grid cells populated with OBIS data. We then assigned a rank-ordered value for the mean change velocity across all of the grid cells. To determine the areas of highest priority for exploration, we multiplied the climate change velocity rank (indicative of the likelihood of species movement under various IPCC scenarios) by the inverse OBIS rank (indicative of the areas with the fewest records available). This data manipulation yielded cells, translating to spatial coordinates, demonstrating areas with the lowest number of biodiversity records and the highest value for climate change velocity. Data for the IPCC RCP 8.5 are presented here; visualizations using IPCC RCP 2.6 and 4.5 are located in the Supplementary Information.

5.4 Results

In total, we were able to collect location information for 30,733 dives made by deep-submergence platforms (Figure 5.1B). While the majority of the ocean has no dives, there are three grid cells that dominate the dive records (Figure 2B): Monterey Canyon, California where MBARI focuses most of its work with 4237 dives, and offshore of Yokohama, Japan with two cells containing 1,715 dives combined where JAMSTEC has conducted much of their work. These three cells alone account for 19% of the dives recorded in this dataset, even though they only account for ~0.03% of the surface area of the ocean. Notably, 94.6% of the dives were conducted in the Northern Hemisphere, with only 1,664 dives (5.4%) conducted in the Southern Hemisphere.

The number of OBIS biodiversity records per cell varies by seven orders of magnitude across the globe (Figure 5.3). With highest numbers of records per cell topping out at 2,813,641 records, corresponding with 1,985 species, however the vast majority of cells have a significantly lower number of records. The median number of records per cell per 40,000 km² ranged between 5 in the abyss to 55 in the surface waters. All the depth zones examined had more cells without any OBIS records than cells with OBIS records. In surface waters, 49% of cells had at least one record, and in the abyss only 5% did.

The global distribution through the water column of recorded marine biodiversity is shown in Figure 5.3. Even on the logarithmic scale of number of records, the dominance of shallower and coastal waters within the OBIS database is clear. The deep pelagic ocean in particular reflects the paucity of records from this habitat with less than one OBIS record per 3,500,000 km³. When we consider that each cell of 200m depth over the abyssal plain

represents a volume of c. 3.5 million km³ and that the color scale of the fissure exceeds 7 orders of magnitude, the global mean number of OBIS records per cell is only 585 and the median is 11 records per 3.5 million km³ of ocean; in other words, over half the ocean has less than 11 records total.

Ocean biodiversity records for different proposed geodescriptive schema were examined for total number of records as well as number of unique species, genera and families. For surface waters, we used the Longhurst (1985) proposed provinces (Figure 5.4), which include 53 provinces across 4 ‘biomes’. The number of records per square kilometer of each zone varied widely. For example, there were 12.5 records/km² in the Coastal - NE Atlantic shelves province, compared to only 0.009 records/km² in the Trades - South Atlantic Gyral Province (Table 5.1). Across the Longhurst province, there was substantial variation in the proportion of records that were identified to the species level. The Guinea Current Coastal Province had over 95% of its records contain a species level identification, while the Subtropical Convergence province had less than 18% of records identified to the species level. The Sutton et al. (2017) provinces represented the mesopelagic, with 33 provinces for this depth range. The biodiversity records for this schema were much sparser than the surface waters, with the most records in the Tasman Sea (0.8 records/km²; Table 5.2). The highest species level identification for the mesophotic provinces was 86%, which is lower than surface waters. Watling et al. (2013) provinces for the lower bathyal and abyssal depth were likewise assessed (Table 5.3 and 5.4): the South East Pacific Ridges province had the lowest number of records (0.0004 records per km²). Consistent with global trends, abyssal depths displayed the fewest records

(0.00000204 records/km², only 14 total records) which were found in the Brazil Basin province. The Brazil Basin from Watling et al.'s abyssal province (>4000m) only had 6 different species recorded, while in the surface waters, the Longhurst Trades - Archipelagic Deep Basins province had 23,357 unique species records in surface waters (0–200m). In the abyssal South Pacific province, 34.7% of records contained a family level identification, but only 3.6% at the species level.

To help prioritize future research and exploration, we coupled climate change velocity estimates with OBIS biodiversity records to find the ocean areas with the fewest biological records coupled with the highest intensity climate change projections at the end of the century (2050–2100; Figure 5.7). In surface waters, the equatorial east Pacific was the largest tract of highest priority area for future exploration. There were also high priority bands located in the South Atlantic and central Indian Ocean. In mesopelagic waters, there were two high priority bands flanking the Equator. Additionally, mesopelagic waters near the Maldives, the Bay of Bengal, and the Coral Triangle all had some of the highest values. In the Bathypelagic, the highest priority waters are found in both the Atlantic and Indian oceans, flanking the mid-ocean ridges. In the abyssopelagic, there are so few OBIS records that the priority ranks are nearly completely driven by the climate velocity projections, and it is clear that there is a need for increased exploration at these depths on the whole.

5.5 Discussion

The ocean is chronically underexplored compared to terrestrial environments, especially corrected for the oceans size and depth (Kennedy et al., 2019; Rowden et al.,

2010; Webb et al., 2010). Though previous attempts have been made to assess the distribution of OBIS records globally (Kot et al., 2010; Webb et al., 2010), gaps still remain, creating the opportunity for the ocean exploration community to strategically assess these remaining gaps and prioritize targeted exploration efforts. There is a global need for accurate and comprehensive biodiversity data, given the increasing emphasis on ocean protection targets and exploitation limits that use biodiversity as their key indicator (Hughes et al., 2021). However, the current disparity of biodiversity data spans from no data available to areas with over 1M records. One of the key contributions of this paper is a comprehensive visualization of existing biodiversity data parsed by biogeographic provinces by depth, generating a biology-centered approach to prioritizing effort for the future.

There are areas in the ocean that are notably well-explored with repeated effort, and these areas provide some of the best insights into biodiversity dynamics. However, sites with high data density are extremely rare, and only target a small geographic area. We found that the three areas with the highest density of dives were in close proximity to some of the largest deep submergence research institutions (MBARI and JAMSTEC). Of all the deep submergence dives that we compiled globally, 19% of them were located in less than ~0.03% of the surface area of the ocean (Figure 5.2B). We also found a strong exploration effort in the Northern Hemisphere (94.6% of deep submergence dives), with only 5.4% of dives (1,644 deep submergence dives) in the Southern Hemisphere. This finding is consistent with a recent Global Capacity Survey that showed that the majority of deep submergence platforms are based in North America and Europe (Bell, Quinzin, et al.,

2022). Similarly, a recent study by Amon, Rotjan, et al. (2022) showed a strong bias toward the Northern Hemisphere in terms of the capacity to conduct deep-sea science and exploration. This northern bias in terms of research and effort is exacerbated in terms of understanding global patterns of biodiversity by the fact that the majority (81%) of oceanic waters are contained in the southern hemisphere (Webb, 2019). These spatial biases are likely driven by the practical constraints of fuel and time costs, but they must be considered when researchers use this spatially biased data in OBIS to extrapolate larger spatial scale patterns.

Disproportionate exploration effort, as noted above, is one of the contributors to uneven distribution of biodiversity data across the globe (Hughes et al., 2021). Even OBIS, which is a comprehensive, community driven, user-input marine biodiversity database (Klein et al., 2019) cannot adequately catalog or index every taxa on the planet because there is uneven distribution of records, and there is interest in database improvement (Klein et al., 2019). The uneven distribution of OBIS records makes the description of marine biogeographic provinces difficult, and prohibits comprehensive biodiversity hypothesis-testing in different regions. For example, in abyssal waters, Watling et al.'s Brazil Basin province is described using only 14 total records (0.00000204 records km^{-2}) in OBIS representing only six species, while in contrast, Longhursts' Coastal - Alaska Downwelling Coastal Province is represented by 2,175,924 records (3.32 records/ km^2). This issue is further exacerbated by the level of taxonomic identification provided within the OBIS records; while higher classification is typical, family, genus, and/or species classifications are not guaranteed. For example, in the abyssal South Pacific province, 34.7% of records

contained a family-level identification, but only 3.6% at the species level. Indeed, when examining across the entirety of OBIS records with depth information, only 53.8% are identified to species level (31,448,375 out of 58,442,819 records), and even at the family level, only 69.9% (40,872,702 records). Because biogeographic research most typically requires genus or species level identification (Mark J Costello & Chhaya Chaudhary, 2017), OBIS records with only order or higher level identifications are of limited utility.

In addition to geographic disparities in data density, we also found data density to be strongly influenced by depth, as evidenced by examining records by biogeographic province (surface, mesophotic, and deepwater). We found that — in places with records with known depths — there was a spread of records ranging from 0.00116 to 172,702 per 3.5M km³, with the fewest records per cell below 4,000 m (Figure 3.5). It should be noted that this disparity is not fully due to lack of deep submergence dives: even in places where deep submergence dives have been done, not all ROV image data gets annotated or incorporated into OBIS records. Annotating visual data from ROV video is particularly time intensive to process and has a large volume of observations, which makes it challenging to ingest into OBIS (Tippett et al., 2022). Several efforts have been launched to help streamline this process from improving annotation software (Gomes-Pereira et al., 2016) through metadata standardization (Tippett et al., 2022), but there is still significant work to be done in this regard.

Though deep-sea records in OBIS are sparse compared to surface records, there is additional bias within deepwater records towards benthically-associated species. We found that at all ocean depths, there are increased OBIS occurrence records near the seafloor when

compared to the water column below 200 meters. This finding is consistent with other works pointing out that the water column is particularly under sampled (Drazen et al., 2020; Netburn et al., 2018). However, the data paucity at depth and in certain regions provides a clear directive and justification to prioritize future exploration efforts in service of global marine biodiversity records. Such baseline records are urgently needed, especially in the Anthropocene where species migrations and other climate change impacts are expected to have dramatic impacts on biodiversity, globally (Burrows et al., 2011).

As the planet experiences an unprecedented rate of change (Pörtner et al., 2022), the oceans are changing faster than the pace of exploration (Halpern et al., 2019). To determine the priority areas for future exploration in different climate change scenarios, we determined the regions with the lowest data densities that were simultaneously the most likely to be impacted by climate change. In the mesopelagic, one of the priority areas includes the Coral Triangle, which is well known to be the center of marine biodiversity on the planet (Veron et al., 2009), suggesting that even well-studied areas require additional effort at certain depths in preparation for inevitable climate change consequences. The bathypelagic unsurprisingly has a need for additional data throughout, but one of the priority regions we identified are the areas flanking mid-ocean ridges, which should help to set targets for future exploration in a post-high seas treaty era (Gjerde et al., 2021). However, on the whole, predicting climate velocities is an area of active research and therefore these priorities should all be re-visited and updated as new IPCC projections are released in future years.

Future efforts for exploration need to be thoughtfully targeted given limited

resources (Bell, Quinzin, et al., 2022). Future prioritization will focus new fieldwork efforts and new data collection in areas with the fewest records and effort to-date. However, this is not the only path to addressing existing data gaps. Large quantities of biodiversity data remain hidden and unpublished within institutions, or linger behind when only subsets of the data (e.g., for specific taxa) get published (Chavan & Ingwersen, 2009). These non-public or underused data can be rescued to help fill some of these gaps comparatively inexpensively and on an accelerated timeline because no field work is required. Although these types of rescue efforts are labor intensive and require new injection of funding into old projects, they are a valuable source of baseline data and insight into the past. In short, data gaps can be filled via a) new effort, and/or via b) rescue efforts of hidden or forgotten raw data that can be revived, mined, or utilized for a new purpose. However, at the same time, existing data quality in explored regions is sufficient to start enabling ocean protection, management, and insight into biological processes even though these data sets are incomplete. Given this caveat, inference and the precautionary principle can be used in order to make progress. Achieving truly comprehensive data and a fully explored ocean is unattainable in a short time frame, but focused and prioritized efforts can make disproportionately large contributions to our understanding of the ocean if we take into account data scarcity and data need.

5.6 Acknowledgements

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Table 5.1.

Breakdown of OBIS data for each Longhurst province

| Province Name | # of Unique Species | % of records ID'd to Species | # of Unique Genera | % of records ID'd to Genus | # of Unique Family | % of records ID'd to Family | Total Number of Records | Number of Records per Km2 |
|---|---------------------|------------------------------|--------------------|----------------------------|--------------------|-----------------------------|-------------------------|---------------------------|
| Coastal - Alaska Downwelling Coastal Province | 3638 | 90.9 | 2,234 | 95.8 | 1,060 | 97 | 2,175,924 | 3.302 |
| Coastal - Australia-Indonesia Coastal Province | 17650 | 50.6 | 8,546 | 58.2 | 2,631 | 64 | 3,667,233 | 1.252 |
| Coastal - Benguela Current Coastal Province | 3198 | 89.6 | 2,298 | 97.2 | 1,104 | 98.1 | 468,545 | 0.404 |
| Coastal - Brazil Current Coastal Province | 6860 | 82.2 | 4,520 | 96.2 | 1,754 | 98 | 135,506 | 0.111 |
| Coastal - California Upwelling Coastal Province | 7701 | 77.7 | 5,070 | 86.5 | 2,131 | 90.3 | 4,694,396 | 1.756 |
| Coastal - Canary Coastal Province (EACB) | 5567 | 77.1 | 3,406 | 88.5 | 1,502 | 88.8 | 364,553 | 0.487 |
| Coastal - Central American Coastal Province | 5701 | 82.0 | 3,278 | 88.3 | 1,424 | 90.7 | 194,619 | 0.157 |
| Coastal - Chile-Peru Current Coastal Province | 4915 | 86.2 | 3,566 | 92 | 1,593 | 92.6 | 978,894 | 0.359 |
| Coastal - China Sea Coastal Province | 6277 | 74.4 | 3,442 | 92.5 | 1,299 | 96.8 | 136,136 | 0.12 |
| Coastal - E. Africa Coastal Province | 11615 | 75.4 | 5,846 | 93.1 | 1,890 | 94.3 | 1,175,406 | 0.331 |
| Coastal - E. India Coastal Province | 4130 | 39.4 | 2,705 | 59.8 | 1,207 | 65.4 | 51,688 | 0.054 |

| | | | | | | | | |
|--|-------|------|-------|------|-------|------|------------|--------|
| Coastal - East Australian Coastal Province | 20371 | 21.0 | 9,733 | 28.8 | 2,949 | 41.6 | 11,150,211 | 10.052 |
| Coastal - Guianas Coastal Province | 8405 | 65.1 | 4,951 | 77.3 | 1,946 | 81.1 | 358,640 | 0.3 |
| Coastal - Guinea Current Coastal Province | 3311 | 95.5 | 2,349 | 98.1 | 1,078 | 99 | 312,516 | 0.232 |
| Coastal - NE Atlantic Shelves Province | 11028 | 79.6 | 6,552 | 89.8 | 2,639 | 92 | 18,587,717 | 12.504 |
| Coastal - New Zealand Coastal Province | 6315 | 61.7 | 4,678 | 70.7 | 1,965 | 75.8 | 1,101,366 | 0.936 |
| Coastal - NW Arabian Upwelling Province | 6483 | 42.9 | 4,074 | 74.8 | 1,609 | 76.2 | 508,088 | 0.151 |
| Coastal - NW Atlantic Shelves Province | 12841 | 83.0 | 7,357 | 91.9 | 2,611 | 94 | 8,941,562 | 4.351 |
| Coastal - Red Sea, Persian Gulf Province | 3793 | 48.2 | 2,560 | 73.7 | 1,120 | 77.8 | 69,057 | 0.1 |
| Coastal - Sunda-Arafura Shelves Province | 18815 | 50.3 | 8,071 | 61.2 | 2,416 | 69.1 | 1,558,987 | 0.252 |
| Coastal - SW Atlantic Shelves Province | 3739 | 79.6 | 2,677 | 93.2 | 1,277 | 94.5 | 250,637 | 0.17 |
| Coastal - W. India Coastal Province | 8381 | 50.8 | 4,291 | 73.1 | 1,648 | 75.8 | 123,438 | 0.153 |
| Polar - Antarctic Province | 5525 | 62.5 | 3,384 | 71.5 | 1,508 | 75.1 | 1,445,441 | 0.062 |
| Polar - Atlantic Arctic Province | 3396 | 62.1 | 2,394 | 81 | 1,210 | 79.6 | 391,428 | 0.12 |
| Polar - Atlantic Subarctic Province | 6552 | 84.6 | 3,851 | 92.1 | 1,654 | 92.9 | 2,361,195 | 0.997 |
| Polar - Austral Polar Province | 6619 | 90.6 | 3,907 | 94.2 | 1,682 | 95.3 | 1,547,076 | 0.169 |
| Polar - Boreal Polar Province (POLR) | 4545 | 72.2 | 3,187 | 84.1 | 1,451 | 87.4 | 1,021,165 | 0.078 |

| | | | | | | | | |
|--|-------|------|-------|------|-------|------|-----------|-------|
| Polar - N. Pacific Epicontinental Province | 3422 | 58.9 | 2,131 | 75 | 1,064 | 83.6 | 578,636 | 0.127 |
| Trades - Archipelagic Deep Basins Province | 23357 | 77.8 | 8,987 | 90.5 | 2,633 | 95.4 | 595,456 | 0.068 |
| Trades - Caribbean Province | 18908 | 86.7 | 8,997 | 93 | 2,935 | 95.5 | 4,417,728 | 1.024 |
| Trades - Eastern Tropical Atlantic Province | 2583 | 85.3 | 2,102 | 90.2 | 1,001 | 92.5 | 161,752 | 0.03 |
| Trades - Indian Monsoon Gyres Province | 11779 | 62.9 | 5,928 | 77.4 | 2,150 | 82 | 612,153 | 0.039 |
| Trades - Indian S. Subtropical Gyre Province | 5984 | 41.0 | 3,526 | 61.1 | 1,472 | 65.4 | 333,589 | 0.02 |
| Trades - N. Atlantic Tropical Gyrals Province (TRPG) | 5099 | 82.1 | 3,435 | 89.9 | 1,437 | 91.9 | 172,339 | 0.021 |
| Trades - N. Pacific Equatorial Countercurrent Province | 3813 | 63.2 | 2,581 | 79 | 1,203 | 83.3 | 231,006 | 0.025 |
| Trades - N. Pacific Tropical Gyre Province | 5844 | 78.7 | 4,473 | 88.3 | 1,859 | 92.4 | 932,653 | 0.063 |
| Trades - Pacific Equatorial Divergence Province | 4730 | 21.5 | 3,153 | 31 | 1,440 | 40.1 | 722,971 | 0.05 |
| Trades - South Atlantic Gyrals Province (SATG) | 5270 | 82.7 | 3,338 | 91.9 | 1,439 | 94.5 | 159,454 | 0.009 |
| Trades - W. Pacific Warm Pool Province | 7388 | 80.2 | 3,773 | 90 | 1,411 | 95.1 | 356,522 | 0.028 |
| Trades - Western Tropical Atlantic Province | 3122 | 85.8 | 2,214 | 92.2 | 1,067 | 94 | 147,939 | 0.028 |
| Westerlies - Gulf Stream Province | 2285 | 72.8 | 1,635 | 85.5 | 822 | 88.3 | 141,359 | 0.129 |

| | | | | | | | | |
|---|-------|------|-------|------|-------|------|-----------|-------|
| Westerlies - Kuroshio Current Province | 9523 | 68.2 | 5,154 | 84.5 | 1,999 | 86.2 | 786,957 | 0.248 |
| Westerlies - Mediterranean Sea, Black Sea Province | 10951 | 71.5 | 5,741 | 83.8 | 2,184 | 87.5 | 1,421,300 | 0.474 |
| Westerlies - N. Atlantic Drift Province (WWDR) | 6702 | 63.7 | 3,895 | 81.3 | 1,671 | 80.7 | 771,833 | 0.219 |
| Westerlies - N. Atlantic Subtropical Gyral Province (East) (STGE) | 5972 | 63.0 | 3,994 | 85.3 | 1,764 | 85.5 | 664,014 | 0.15 |
| Westerlies - N. Atlantic Subtropical Gyral Province (West) (STGW) | 4641 | 75.7 | 3,189 | 88.9 | 1,486 | 90.1 | 225,422 | 0.039 |
| Westerlies - N. Pacific Polar Front Province | 1212 | 85.7 | 982 | 90 | 603 | 92.3 | 65,553 | 0.009 |
| Westerlies - N. Pacific Subtropical Gyre Province (West) | 6412 | 77.0 | 4,030 | 90.8 | 1,684 | 93.6 | 613,984 | 0.044 |
| Westerlies - Pacific Subarctic Gyres Province (East) | 1354 | 59.6 | 954 | 77 | 576 | 81.3 | 169,853 | 0.053 |
| Westerlies - Pacific Subarctic Gyres Province (West) | 1907 | 42.5 | 1,285 | 77.8 | 685 | 81.1 | 126,050 | 0.053 |
| Westerlies - S. Pacific Subtropical Gyre Province | 14401 | 21.9 | 7,514 | 32.4 | 2,536 | 40.4 | 2,620,915 | 0.074 |
| Westerlies - S. Subtropical Convergence Province | 8443 | 17.7 | 5,636 | 26.4 | 2,309 | 36.6 | 3,822,205 | 0.227 |
| Westerlies - Subantarctic Province | 7749 | 62.3 | 4,645 | 69.1 | 1,917 | 73.3 | 2,556,233 | 0.084 |
| Westerlies - Tasman Sea Province | 8475 | 45.2 | 5,347 | 51.4 | 2,120 | 64.4 | 703,733 | 0.424 |

Table 5.2.

Breakdown of OBIS data for each Sutton mesopelagic province

| Province Name | # of Unique Species | % of records ID'ed to Species | # of Unique Genera | % of records ID'ed to Genus | # of Unique Family | % of records ID'ed to Family | Total Number of Records | Number of Records per Km2 |
|--------------------------------|---------------------|-------------------------------|--------------------|-----------------------------|--------------------|------------------------------|-------------------------|---------------------------|
| Southern Central Pacific | 13,405 | 13.3 | 7,490 | 23.5 | 2,533 | 32.7 | 3,280,990 | 0.113 |
| Tasman Sea | 8,453 | 13.6 | 5,829 | 21 | 2,223 | 39.4 | 2,449,868 | 0.031 |
| Coral Sea | 12,468 | 21.2 | 6,211 | 31.2 | 2,143 | 44.5 | 911,414 | 0.392 |
| Equatorial Pacific | 3,133 | 31.3 | 2,029 | 41.4 | 990 | 49.4 | 324,099 | 0.112 |
| Bay of Bengal | 2,833 | 31.6 | 1,983 | 47.8 | 1,047 | 55.5 | 43,468 | 0.339 |
| Southern Indian Ocean | 4,772 | 37.8 | 3,296 | 55.9 | 1,492 | 60.6 | 357,650 | 0.281 |
| Somali Current | 1,903 | 39.9 | 1,330 | 77.8 | 647 | 78.1 | 256,777 | 0.027 |
| California Current | 3,883 | 40.8 | 3,070 | 62.9 | 1,546 | 69.6 | 897,650 | 0.294 |
| Mid-Indian Ocean | 5,460 | 42.0 | 3,546 | 60.1 | 1,471 | 65.5 | 233,667 | 0.168 |
| Arabian Sea | 2,417 | 44.5 | 1,790 | 69.9 | 948 | 72.1 | 173,926 | 0.141 |
| Subantarctic | 4,993 | 49.4 | 3,357 | 57.3 | 1,543 | 63.5 | 813,077 | 0.032 |
| Circumglobal Subtropical Front | 7,443 | 50.5 | 5,009 | 59.7 | 2,016 | 65.6 | 1,121,027 | 0.01 |
| Northern Indian Ocean | 12,184 | 59.4 | 5,880 | 74.7 | 2,039 | 79.2 | 543,067 | 0.061 |
| North Atlantic Drift | 6,474 | 64.3 | 4,058 | 81.8 | 1,757 | 81.5 | 751,340 | 1.147 |
| Mauritania/Cape Verde | 3,020 | 68.7 | 2,190 | 78.1 | 1,035 | 81.6 | 92,196 | 0.038 |
| Arctic | 4,917 | 69.1 | 3,279 | 82.4 | 1,433 | 84 | 682,112 | 0.06 |
| Mediterranean | 5,735 | 69.3 | 3,618 | 83.3 | 1,567 | 87.2 | 330,959 | 0.071 |

| | | | | | | | | |
|---|--------|------|-------|------|-------|------|-----------|-------|
| Northern Central Pacific | 11,148 | 69.6 | 6,180 | 82.1 | 2,209 | 87 | 1,026,974 | 0.008 |
| Sea of Japan | 1,005 | 71.0 | 834 | 82 | 515 | 82.5 | 43,069 | 1.287 |
| Eastern Tropical Pacific | 6,371 | 71.5 | 3,816 | 79.8 | 1,649 | 83.4 | 355,237 | 0.026 |
| Northwest Atlantic Subarctic | 8,443 | 71.7 | 4,631 | 87.7 | 1,820 | 89.4 | 2,896,174 | 0.199 |
| Agulhas Current | 6,111 | 75.1 | 3,572 | 87.5 | 1,371 | 91.8 | 222,233 | 0.017 |
| Central North Atlantic | 14,043 | 76.2 | 7,350 | 88.5 | 2,497 | 90.6 | 1,601,223 | 0.006 |
| Gulf of Mexico | 7,266 | 76.5 | 4,505 | 85.8 | 1,755 | 89.4 | 440,540 | 0.506 |
| Antarctic/Southern Ocean | 9,486 | 77.8 | 5,051 | 83.9 | 1,972 | 86 | 3,944,633 | 0.028 |
| Indo-Pacific ""Pocket"" Basins | 6,521 | 78.2 | 3,387 | 88.1 | 1,278 | 90.9 | 42,955 | 0.021 |
| Pacific Subarctic | 5,400 | 79.7 | 3,516 | 88.5 | 1,587 | 91 | 1,680,058 | 0.057 |
| South Atlantic | 4,800 | 85.2 | 3,220 | 95.1 | 1,378 | 96.1 | 86,337 | 0.012 |
| Guinea Basin and East Equatorial Atlantic | 2,319 | 85.2 | 1,855 | 90.8 | 895 | 92.4 | 109,150 | 0.726 |
| Benguela Upwelling | 2,825 | 85.3 | 1,913 | 96.9 | 967 | 96.1 | 135,921 | 0.326 |
| Tropical and West Equatorial Atlantic | 5,451 | 85.6 | 3,620 | 92.4 | 1,538 | 94.6 | 256,351 | 0.046 |
| Peru Upwelling/Humboldt Current | 2,269 | 86.0 | 1,738 | 93.4 | 981 | 92.4 | 225,974 | 0.013 |
| South China Sea | 3,837 | 86.0 | 2,153 | 94.1 | 880 | 96 | 76,216 | 0.035 |

Table 5.3:

Breakdown of OBIS data for each Watling lower bathyl province

| Province Name | # of Unique Species | % of records ID'ed to Species | # of Unique Genera | % of records ID'ed to Genus | # of Unique Family | % of records ID'ed to Family | Total Number of Records | Number of Records per Km ² |
|-------------------------|---------------------|-------------------------------|--------------------|-----------------------------|--------------------|------------------------------|-------------------------|---------------------------------------|
| Antarctic | 2,240 | 21.1 | 1,932 | 33.6 | 1,007 | 44.9 | 112,129 | 0.018 |
| Arctic | 1,162 | 63.6 | 941 | 79.7 | 509 | 83.7 | 36,405 | 0.008 |
| Cocos Plate | 920 | 49.1 | 741 | 79.5 | 446 | 85.8 | 13,556 | 0.003 |
| Indian | 2,627 | 73.7 | 1,891 | 87.8 | 931 | 93.3 | 34,442 | 0.002 |
| Nazca Plate | 519 | 48.4 | 568 | 78.5 | 360 | 83.9 | 2,233 | 0.002 |
| New Zealand Kermadec | 4,338 | 49.5 | 3,283 | 59.2 | 1,453 | 69.7 | 431,383 | 0.101 |
| North Atlantic | 6,123 | 58.7 | 3,607 | 80.1 | 1,388 | 86.5 | 220,764 | 0.026 |
| North Pacific | 563 | 18.6 | 615 | 61.2 | 381 | 86 | 99,350 | 0.072 |
| Northern North Atlantic | 1,691 | 69.6 | 1,185 | 79.4 | 630 | 88.6 | 81,284 | 0.024 |
| Northern North Pacific | 1,623 | 30.6 | 1,334 | 67.8 | 708 | 76 | 273,924 | 0.084 |
| SE Pacific Ridges | 278 | 46.2 | 257 | 84.9 | 176 | 91.3 | 2,689 | 0 |
| South Atlantic | 2,225 | 71.2 | 1,684 | 88.4 | 809 | 92.5 | 12,765 | 0.002 |
| Subantarctic | 2,161 | 67.1 | 1,805 | 80.8 | 939 | 85.8 | 49,917 | 0.007 |
| West Pacific | 2,848 | 51.8 | 1,862 | 73.9 | 917 | 85.2 | 34,225 | 0.003 |

Table 5.4.

Breakdown of OBIS data for each Watling abyssal provinces

| Province Name | # of Unique Species | % of records ID'ed to Species | # of Unique Genera | % of records ID'ed to Genus | # of Unique Family | % of records ID'ed to Family | Total Number of Records | Number of Records per Km2 |
|--------------------------------|---------------------|-------------------------------|--------------------|-----------------------------|--------------------|------------------------------|-------------------------|---------------------------|
| South Pacific | 771 | 3.6 | 841 | 16.3 | 512 | 34.7 | 132,256 | 0.0122 |
| East Antarctic Indian | 634 | 8.4 | 685 | 23.3 | 472 | 34.9 | 19,286 | 0.0458 |
| Indian | 810 | 5.3 | 946 | 12.1 | 591 | 36.1 | 90,857 | 0.0038 |
| Central Pacific | 412 | 13.2 | 870 | 34.6 | 525 | 50.9 | 61,141 | 0.0002 |
| West Antarctic | 444 | 43.0 | 465 | 60.2 | 326 | 65.8 | 2,568 | 0.0011 |
| North Central Pacific | 176 | 11.4 | 204 | 33 | 179 | 68.9 | 3,917 | 0.0001 |
| North Pacific | 348 | 23.4 | 526 | 59.2 | 382 | 68.9 | 6,259 | 0.00001 |
| Arctic | 114 | 71.1 | 114 | 80.6 | 94 | 84.2 | 609 | 0.00026 |
| East Pacific Basins | 609 | 46.0 | 493 | 75.6 | 314 | 84.9 | 9,998 | 0.00494 |
| Argentine Basin | 98 | 53.9 | 105 | 77.2 | 89 | 86.5 | 334 | 0.00012 |
| Angola and Sierra Leone Basins | 364 | 77.0 | 320 | 84.6 | 195 | 86.7 | 1,433 | 0.00004 |
| North Atlantic | 2,013 | 77.6 | 1,455 | 90 | 693 | 91.4 | 21,547 | 0.0002 |
| West Pacific Basins | 53 | 76.7 | 59 | 92.2 | 54 | 94.4 | 90 | 0.00003 |
| Brazil Basin | 6 | 57.1 | 8 | 78.6 | 9 | 100 | 14 | 0.00001 |

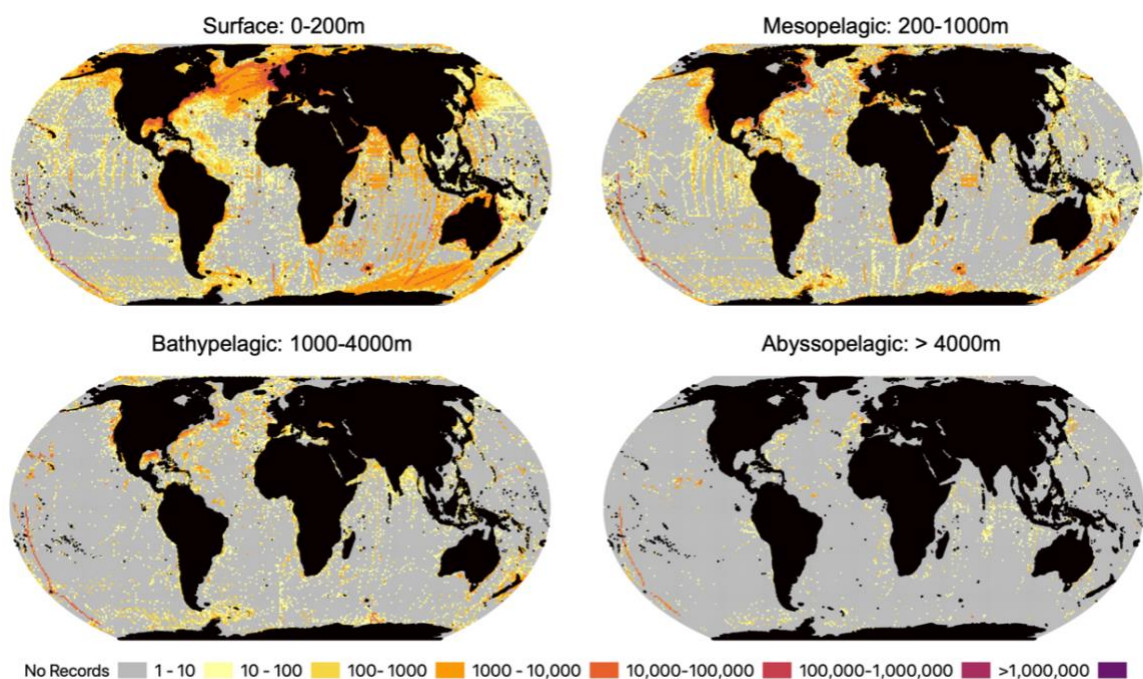


Figure 5.1. Number of OBIS records with depth information per 100 x 100 km grid for surface (0–200m), mesopelagic (200–1,000), bathypelagic (1,000–4,000m) and abyssopelagic (>4,000m) waters. Black cells denote areas with no OBIS records.

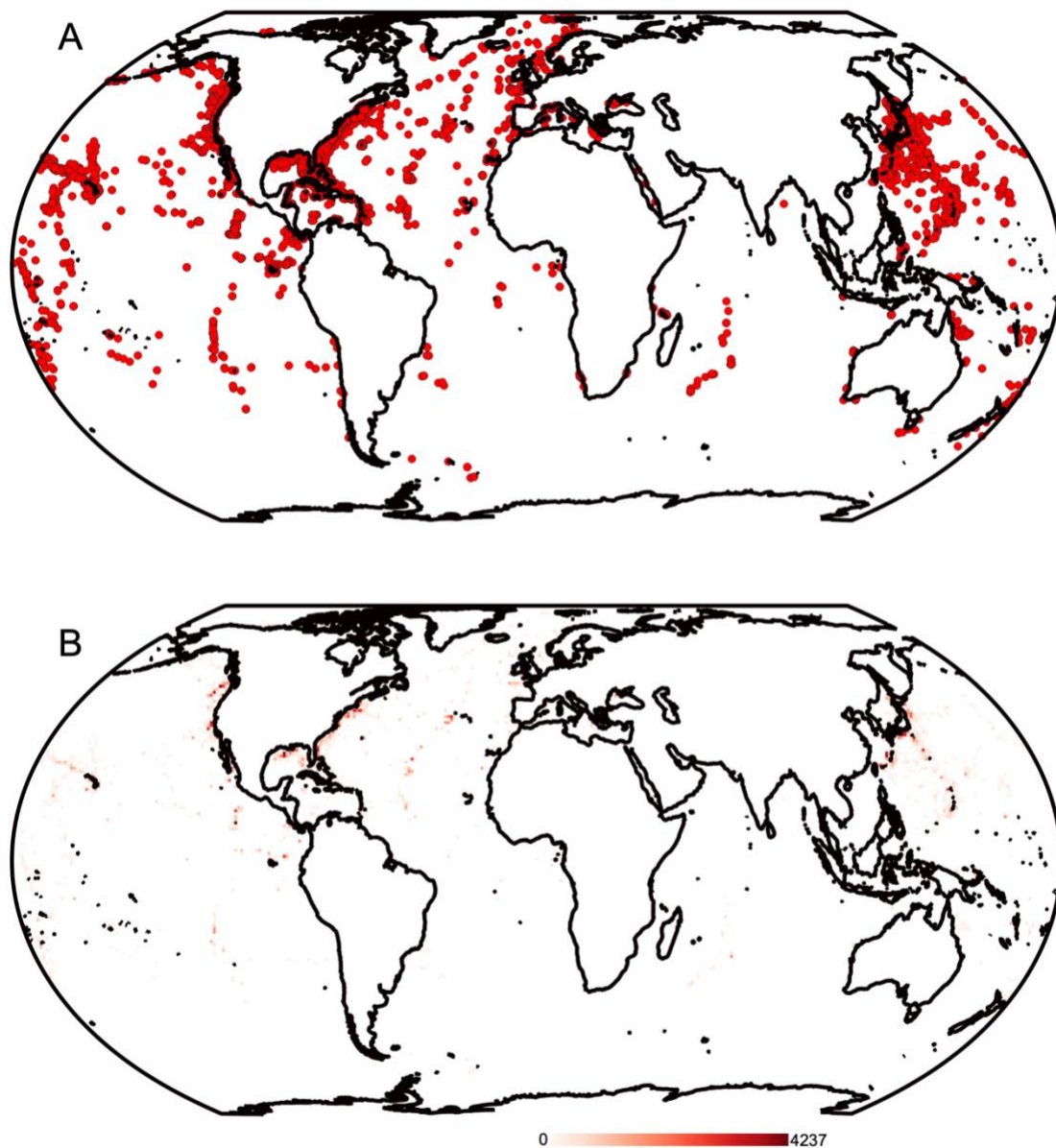


Figure 5.2.

(A) all 30,733 dive records collected including HOV, ROV, AUV, and towed imaging vehicle deployments from SOI, MBARI, NOAA, HURL, OET, SOI, GEOMAR, JAMSTEC, HBOI, IFREMER, and cruise locations from the Russian Academy of Sciences MIR 1 and 2 expedition. (B) Number of dives per 100x100 km grid

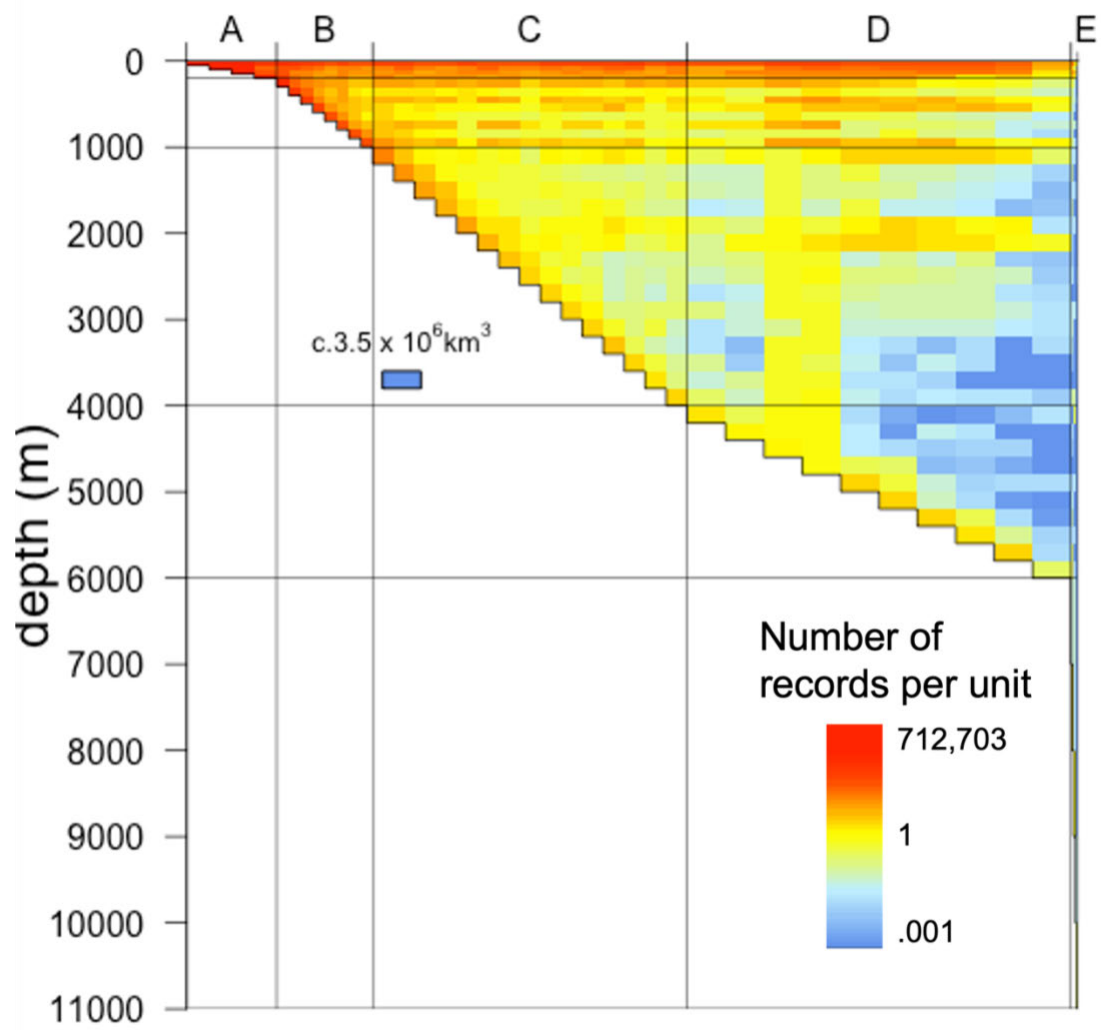


Figure 5.3. Global distribution within the water column of recorded marine biodiversity. The horizontal axis splits the oceans into five zones on the basis of depth, with the width of each zone on this axis proportional to its global surface area. The vertical axis is ocean depth, on a linear scale. This means that the area on the graph is proportional to the volume of the ocean. For instance, in the deep sea, each cell of 200 m depth represents c. 3.5M km³. The number of records in each cell is standardized to the volume of water represented by that cell, and then log10-transformed.

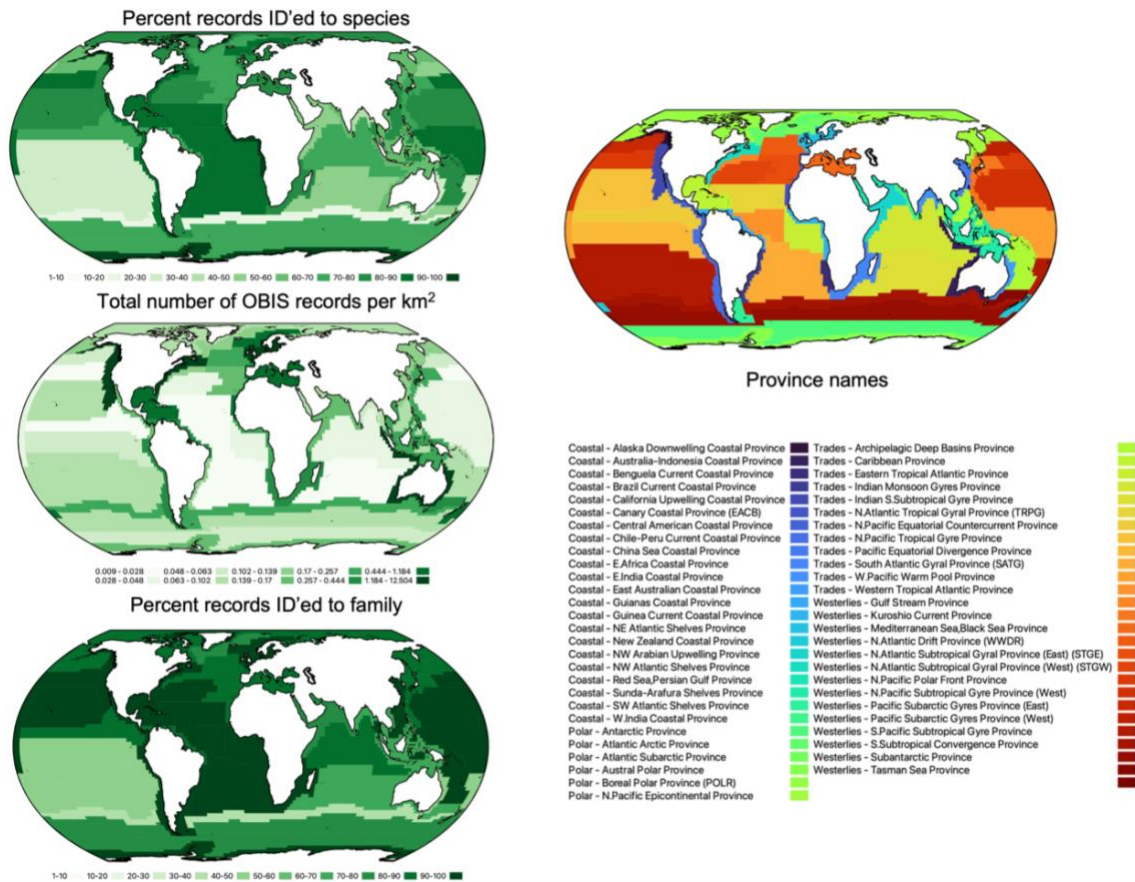


Figure 5.4. Longhurst (2010) proposed biogeographic provinces for surface waters. Top left is the percentage of records that were identified to the species level. Bottom left is the percentage of records that were identified to the family level. Middle left represents the total number of OBIS records per km² for each proposed province (range of records goes from 0.009 to 12.5). Right column is the names of each province.

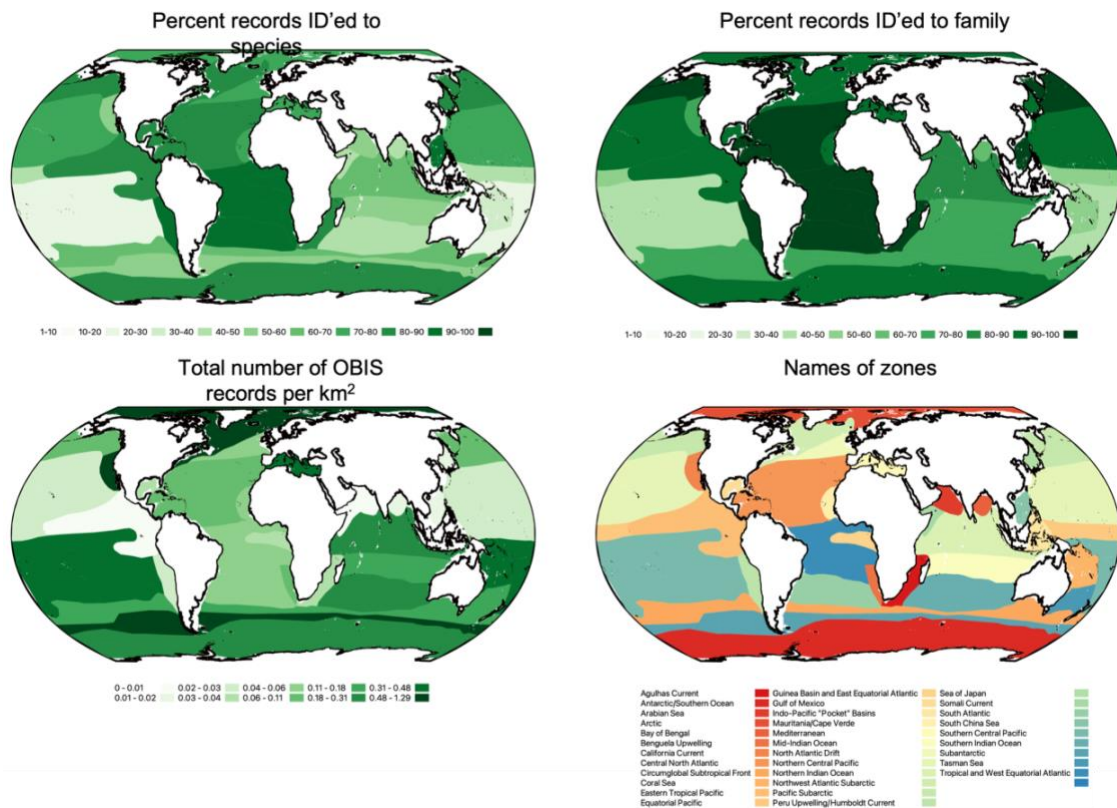


Figure 5.5. Sutton et al. (2017) proposed biogeographic provinces for mesopelagic waters (200-1,000 m). Top left is the percentage of records that were identified to the species level. Top right is the percentage of records that were identified to the family level. Bottom left represents the total number of OBIS records per km² for each proposed province (range of records goes from 0.006 to 1.287). Bottom right is the names of each province.

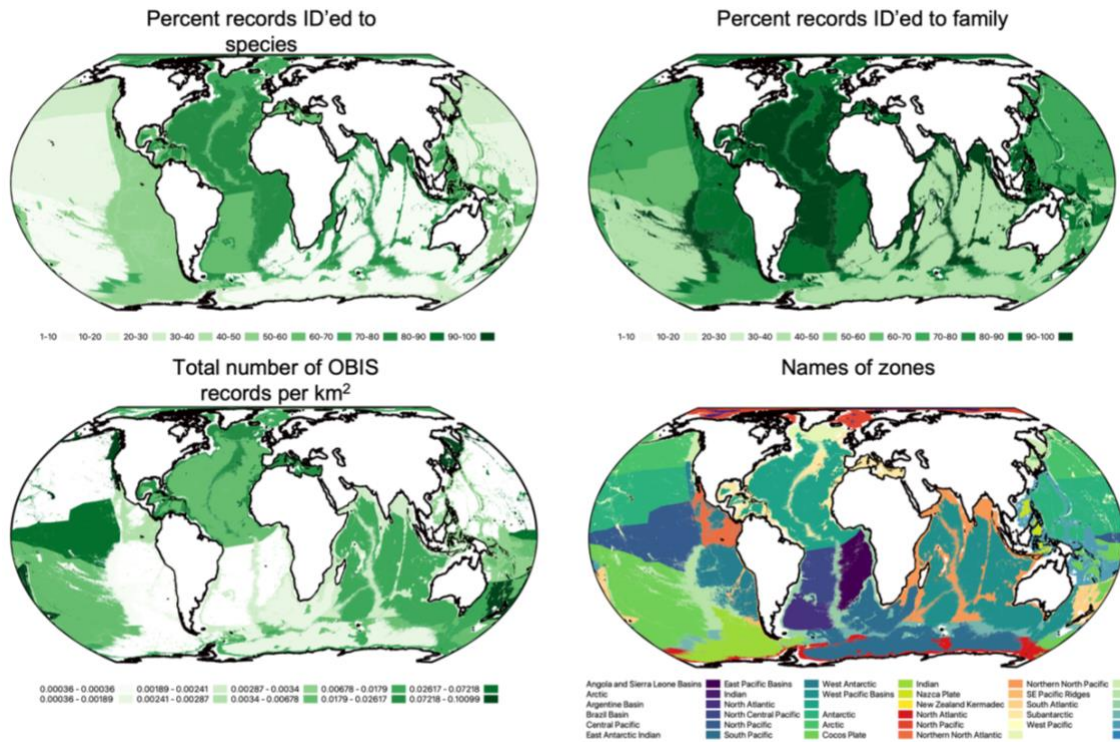


Figure 5.6. Watling et. al. (2013) proposed biogeographic provinces for the lower bathyal and abyssal seafloor. Top left is the percentage of records that were identified to the species level. Top right is the percentage of records that were identified to the family level. Bottom left represents the total number of OBIS records per km² for each proposed province (range of records goes from 0.00001 to .0458). Bottom right is the names of each province.

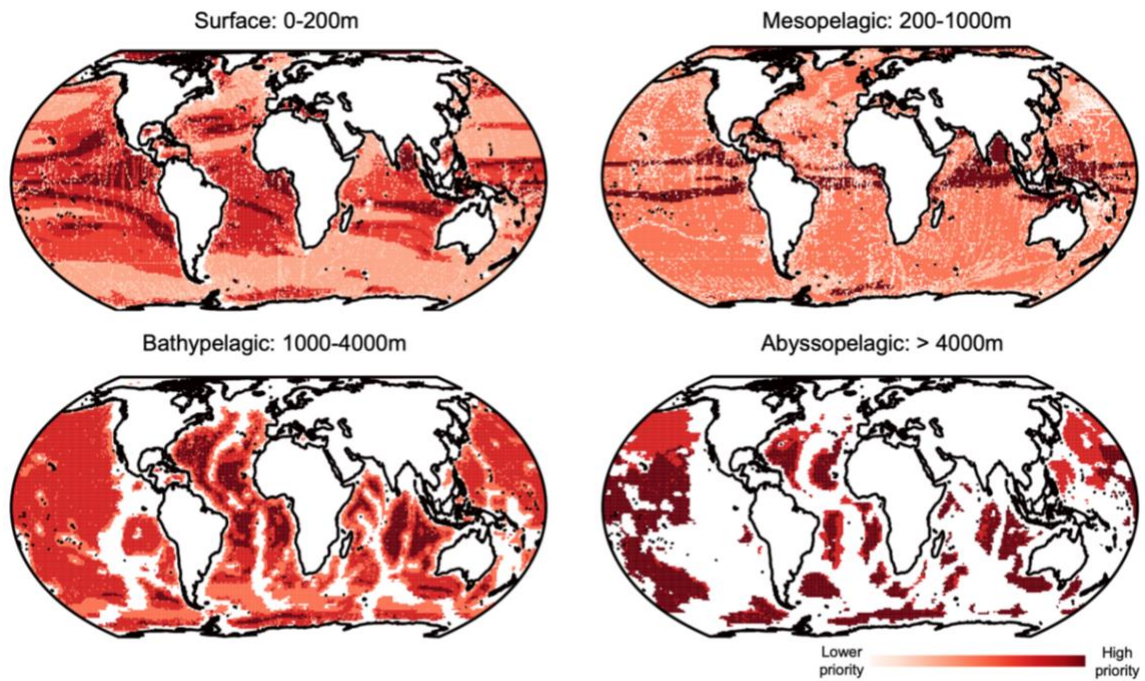


Figure 5.7.

Areas of highest priority for exploration in an era of global change. Combining climate velocity estimates from Brito-Morales et al (2020) with the lowest number of OBIS records for surface (0–200m), mesopelagic (200–1,000), bathypelagic (1,000–4,000m) and abyssopelagic (>4,000m) waters. Redder colors denote areas of lower number of biodiversity records and higher estimated climate change velocities.

CHAPTER SIX: CONCLUSIONS

The goal of this dissertation is to contribute new understanding about the drivers of distribution of deep-sea coral and sponge communities. These types of patterns and questions in the deep sea have historically been difficult to elucidate and answer (and remain so) due to access challenges and historic lack of data. However, this dissertation was written during a resurgence in ocean exploration where new technologies and new partners have produced data at a scale and pace that far exceeds what has been possible in the past. From systematic exploration efforts like NOAA's CAPSTONE campaign to new philanthropic efforts by the Schmidt Ocean Institute, we now have data over both a temporal and spatial scale that have enabled me to ask new questions in this dissertation.

Here, I have tested several hypotheses about the patterns of biodiversity on deep sea seamounts. Chapter two focused on the Central and Western Pacific basin and documented the variation in coral and sponge communities across different regions, depths, and features. This study contributed the novel observation that geomorphology of a seamount may play an unexpected role in influencing coral community composition. In chapter three, I explored this pattern in detail through the use of generalized mixed methods linear modeling indicating strong evidence that there is a previously undocumented relationship between the physical shape of a seamount and associated coral communities. I continued to build upon this relationship by classifying all the seamounts in the Pacific based on the feature shape classification scheme used in both Chapters two and three to show that there is significant variability in the distribution and abundance of seamount types across the Pacific. These findings have the potential to impact seamount management

and conservation: if seamount shape and type are among the key drivers of deepwater coral and sponge community composition, it provides justification for strategic management that takes seamount type into account.

In Chapter four, I focused on the drivers of deepwater coral and sponge community composition on one specific seamount, classifying the zonation of benthic life found on its flanks. There have been very few studies comparing the zonation patterns on different sides of a feature, and none of the previous studies have focused on an equatorial Pacific seamount. In the work presented here, I documented the same pattern of communities that change with depth on all four flanks examined, however I note that there was substantial variation in the abundance of individual taxa within the different depth zones. This investigation also yielded two new hypotheses about patterns of biodiversity on equatorial seamounts: (1) In high biodiversity seamounts, benthic taxa will partition by seamount flank to maximize available resources delivered by variable current flow; and (2) In high biodiversity seamounts, benthic taxa will partition by seamount flank to maximize available high quality benthic substrate (geology, slope, etc.). Future studies are needed to test these hypotheses, but the genesis of these ideas is a major contribution of this work.

This dissertation was written at the height of modern ocean exploration effort, and capitalized on the recent influx of deepwater data to note novel patterns and ask original questions. However, the deep sea is far from fully explored. To-date, only between 5–20% of the deep ocean has been visualized or mapped, which limits our ability to understand patterns of deepwater biodiversity. These data gaps exist despite 150 years of deep-sea science. New technology and renewed interest in deep-sea science have laid the

groundwork for urgently-needed ocean characterization in an era of climate change, but resources to enable these efforts remain lacking and unfocused. To that end, Chapter five explored the gaps in our biodiversity records and deep submergence dive locations. I gathered the largest data set of deep submergence dive locations (to my knowledge) and coupled those locations with all of the records from OBIS to document ocean areas with the least available data. In this chapter, I also combined the OBIS records with climate change projections to identify areas that have the lowest number of biodiversity records and the highest rate of expected climate change, which should be considered the highest priority areas for future exploration efforts.

The research presented in this dissertation highlights the need for several follow-up studies. The first is additional hypothesis testing on the effect of seamount shape on coral communities. The large exploratory dataset used in this work covered a wide spatial range and numerous seamounts. Additional work to confirm the findings here should be targeted on different feature types in close proximity to each other to see if their effect holds on smaller spatial scales. Here, I hypothesized that one of the possible drivers for the apparent variation in coral communities is due at least in part to the local hydrodynamic changes caused by the different seamount shapes. Additional work will be needed to test the mechanistic effects of the local hydrodynamics on coral communities. Remaining questions from chapter four include testing the two new hypotheses presented above as well as sampling more heavily on specific seamounts to test the intra feature variability. Finally, and perhaps most importantly, this work documents the continued need for more large-scale efforts in deep sea science. The deep ocean was once thought to be devoid of

all life, coined the “azoic hypothesis” by Forbes 182 years ago in 1841. When the Challenger expedition sailed 31 years later in 1872, it was clear that biological life was abundant on the deep seafloor, and we have been accelerating our understanding of deepwater taxonomy, evolution, and ecology ever since. However, there is still much to be discovered, and this dissertation contributes some essential novel findings that will catalyze our next steps in understanding our oceans.

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