

# The Impact of Geological Feature Shape on the Abundance and Diversity of Deep Sea Corals

Brian Kennedy<sup>1</sup> and Randi Rotjan<sup>1</sup>

<sup>1</sup>Boston University

December 22, 2022

## Abstract

The role of seamount gross geomorphology (shape) as an abiotic control governing the abundance and diversity of deep-sea corals has not been previously considered, but has the potential to provide easily-accessible and transformative insight into deep water coral community dynamics. 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 (shape) 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 shape category. Across the 50 most abundant deep water coral genera in the data set, all 50 showed a statically significant preference for at least one geomorphology. 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 and resulting conservation implications.

## 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 that they support is critical to understanding any ecosystem, and fundamental ecological literature from terrestrial (Chesson, 2000), freshwater (Matthews, 2012), and marine systems (Longhurst, 1985) has demonstrated a notable diversity of interactions. However, despite the large body of literature on this topic, the abiotic mechanisms that drive biological communities in the deep sea have been relatively less studied (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), but though 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 et al., 2015) seamounts (Clark et al., 2010; Morato et al., 2008; Shank, 2010), hydrothermal vents (Ramirez-Llodra et al., 2010; Van Dover, 2021) 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 (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 levels of accuracy (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 et al., 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 very common benthic macrofauna on all deep water 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 the best 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 (Lisa, 2003; Woulds et al., 2007), organic matter supply (Cathalot et al., 2015; 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 good 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 1000m 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 more abundant 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 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 otherwise geologically resemble 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 Administration's (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 every 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 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? Although seamounts are currently considered to be a single category of underwater mountain feature, we hypothesize that feature shape will influence biological communities of deep water corals.

## Materials and Methods

### 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.

### 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.

## 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 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).

## 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 an 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.

## Seamount classification

Pacific basin seamounts were defined as atolls, islands, banks, guyots, conical seamounts, and ridge seamounts (Figure 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 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, but the number of atolls was not recorded. The location of all islands and atolls was also viewed using Google Satellite ([earth.google.com/web/](http://earth.google.com/web/)) imagery to determine the shape of the terrestrial portion of the feature. Features that met the Yesson (2011) definition of a seamount (greater than a 1000m above the seafloor) that were not included in the original Yesson data set were added, and likewise, putative seamounts were removed if they did not meet the Yesson definition or if they were duplicates of the same feature. To assess the dispersion of different feature shapes, we utilized 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).

## Results

Of the 50 most abundant deep water coral genera 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 2, Supplemental Table 1). Some genera, such as *Chrysogorgia* 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 seen almost exclusively on banks, while *Thourella spp* displayed a strong preference for islands (Figure 2, Supplemental Table 1).

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 genera identified in the CAPSTONE dataset. All genera showed a statistically significant (Supplemental Table 2) impact of feature type on coral genera for all features except island when compared to atolls as the reference class (Supplemental Table 2). Depth and temperature also had significant impacts on coral distribution (Supplemental Table 2).

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 in Figure 3, instead of the total number of individuals per dive as shown in Figure 2. Figure 3 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.

The non-metric multidimensional scaling (nMDS) plot (2D stress = 0.18) with SIMPROF cluster analysis shows five distinct clusters, with some unassigned outliers (Figure 4). One cluster was made up of coral genera that showed the highest abundance on atolls or islands, 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.

When examining the biodiversity of coral genera (Figure 5), we determined 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 6). The conical features were by far the most abundant feature type examined (Supplemental Table 3). 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) (Supplemental Table 3).

## 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 identically. For example, there are only 238 ridges Pacific-wide, which is a relatively rare feature by comparison, 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 now-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, 2021). 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 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 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 more simple 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 very 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 a 1,000 meters from the sea floor, 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 sufficient for the remaining genera, suggesting that there are additional attributes of feature shape that are important drivers of deepwater coral communities. For example, *Acanthogorgia*, *Mettalogorgia*, *Trissopatheis* and *Hemicorallum* spp. (Figure 2) all 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, but they lack the euphotic and terrestrial conditions associated with atolls and islands. We found that banks showed the highest biodiversity, 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 biodiversity. 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 biodiversity.

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, and the presence of terrestrial communities 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 taxa. Because there is variation in deep water coral community dynamics influenced 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 (Fig 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 (Fig 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) containing deep-sea corals (Rowden et al., 2020; Watling & Auster, 2021), and our findings may help fill that gap in understanding by using 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 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 requires 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 have very 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 delicate deep water corals.

-----

Figures and Supplemental Tables


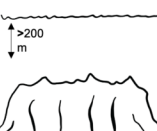
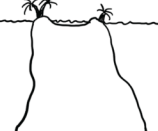
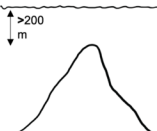
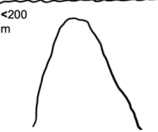
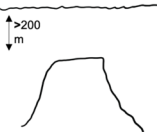
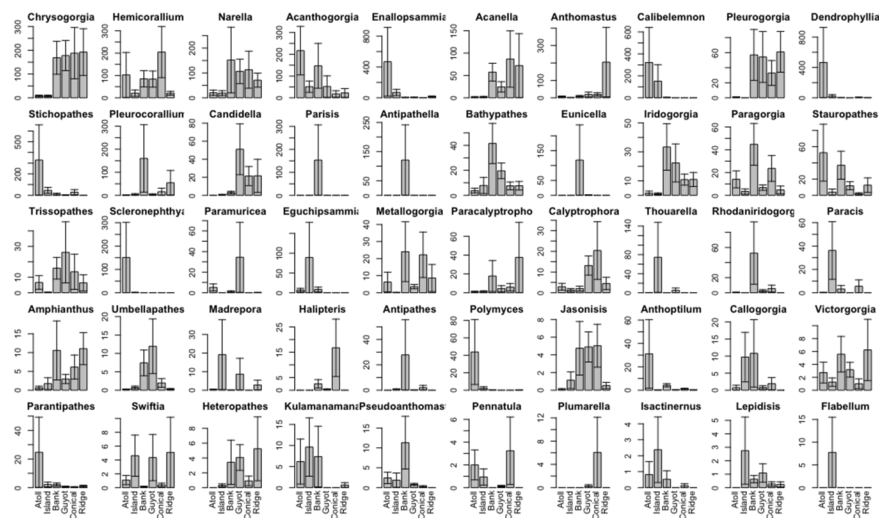
Geological feature type	Example	Geological feature type	Example
<b>Island:</b> Emergent land mass surrounded by water		<b>Ridge:</b> Rising from the seafloor with an elongated summit forming a ridge-like feature	
<b>Atoll:</b> Emergent land and a central lagoon either partially or fully enclosed by land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

Figure 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 from 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 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.

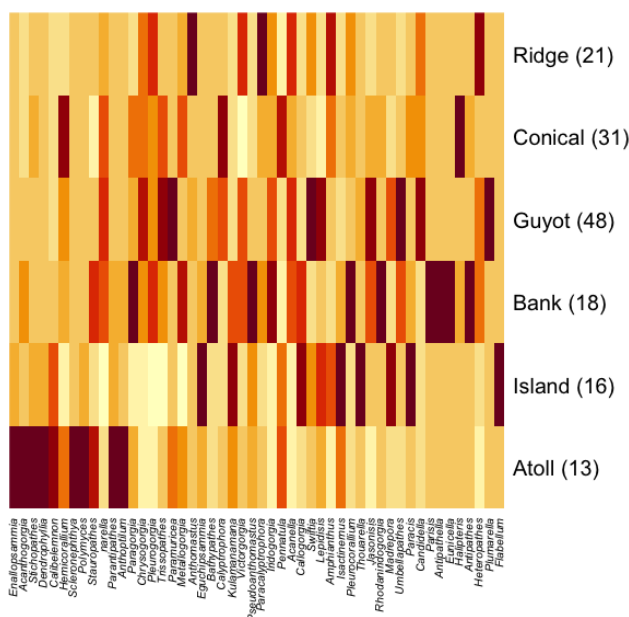


Figure 3: Heatmap showing the density (observations per square kilometer) of the 25 most abundant anthozoan genera. Genera are organized in descending abundance (left to right) for the Atoll feature shape. Number of dives per feature type are shown in parentheses next to feature shape.

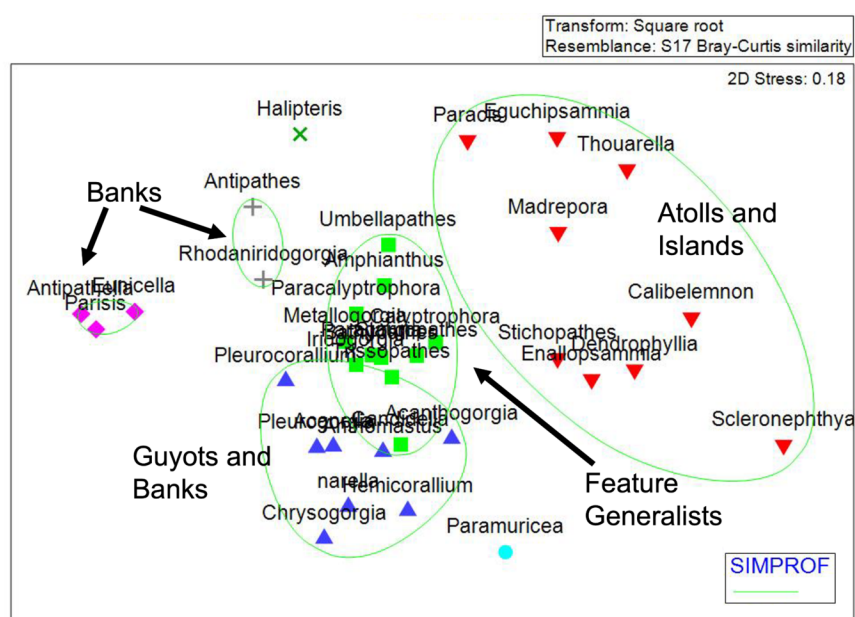


Figure 4: Non-metric multi-dimensional (nMDS) plot showing genera clustering. Green ovals are 95% confidence intervals from a SIMPROF (a similarity profile permutation test) cluster analysis. One group of genera that are associated with Atolls and Islands shows up. In the center of the figure there is a group of feature generalists that include most of the genera found on conical and ridge seamounts. Bank specific taxa appear to be broken up into 3 groups. Two that are specific to banks and one that is shared with Guyots.

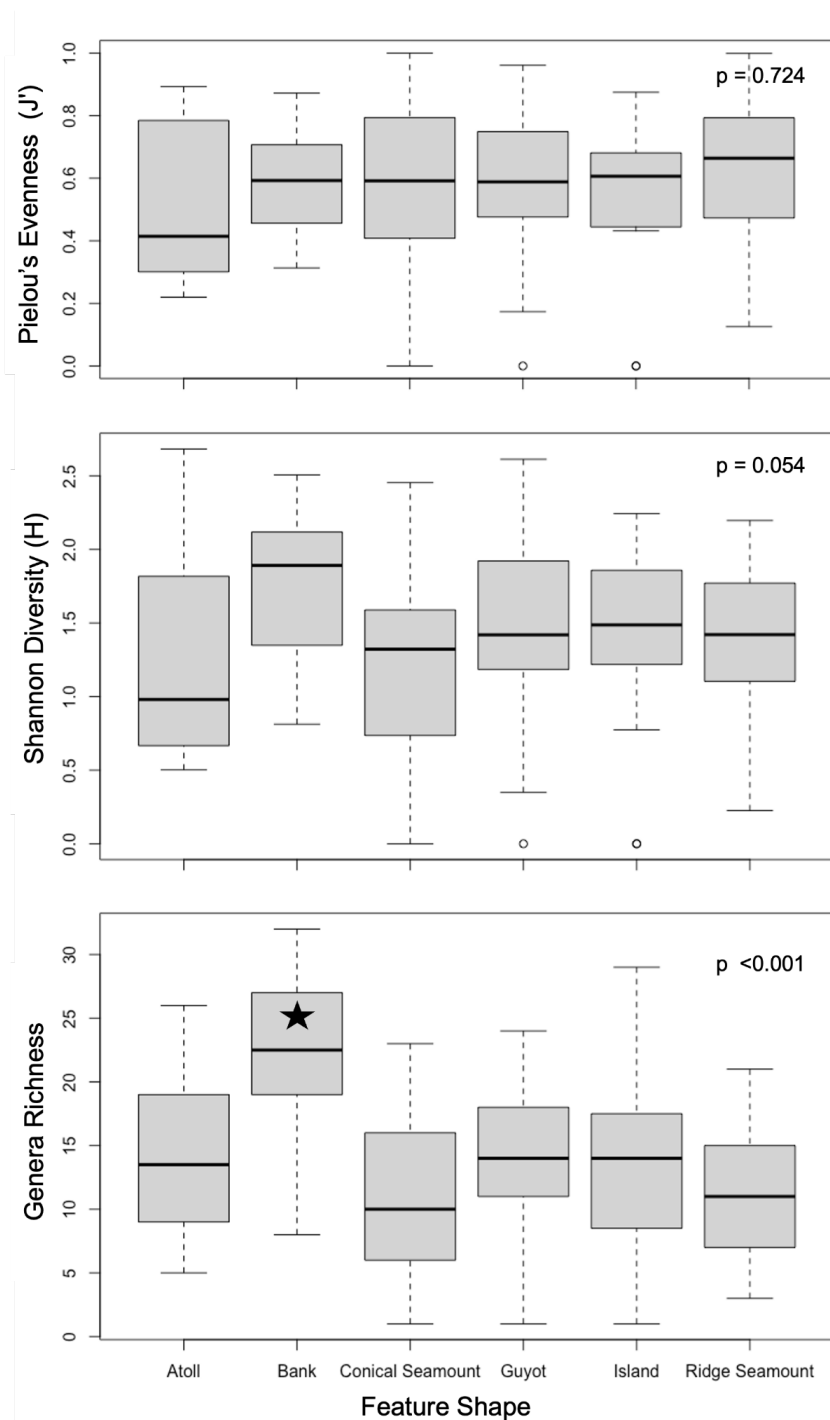


Figure 5: Top box and whisker plot is the Pielou's evenness index ( $J'$ ) for the anthozoan genera . All the feature shapes were very even with no statistically significant difference (ANOVA  $p = 0.724$ ,  $f = 0.568$ ). The middle boxplot is Shannon diversity index( $H$ ). Bottom inset means species 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  $p = 0.054$ ,  $f = 2.235$ ).

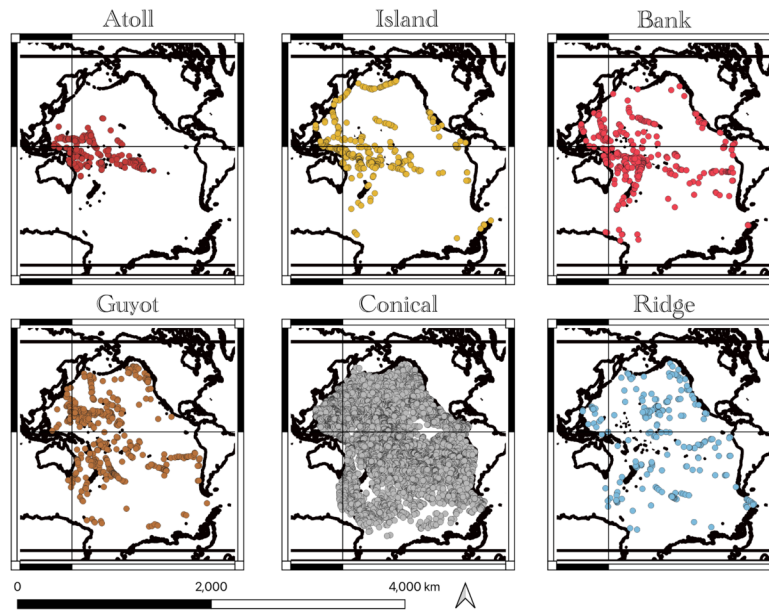


Figure 6: In total 12,597 features were identified in the Pacific basin. Of those features 267 were categorized as atolls, 477 as islands, 426 as banks, 494 as guyots, 238 as ridges and 10,695 as conical type features. All feature types showed a clustered distribution using a Clarke Evans Aggregation index (conical = 0.408, guyot = 0.300, island = 0.199, ridge = 0.346, bank = 0.265, atoll = 0.231)

Feature type	Chrysogorgia	Hemicorallium	Narella	Acanthogorgia	Enallipsammia	Acanella	Anthomastus	Calibelemon	Pleurogorgia	Dendrophyllia
Atoll	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005
Bank	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005
Guyot	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	none seen
Conical	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	none seen	0.0005	0.0005
Island	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	none seen	0.0005
Ridge	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.4003	0.0005	0.0005
Stichopathes	Pleurocorallium	Candidella	Paris	Antipathella	Bathypathes	Eunicella	Iridogorgia	Paragorgia	Stauroopathes	
Atoll	0.0005	0.0005	none seen	none seen	none seen	0.0005	none seen	0.0005	0.0005	0.0005
Bank	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005
Guyot	0.0005	0.0005	0.0005	none seen	none seen	0.0005	0.0005	0.0005	0.0005	0.0005
Conical	0.0005	0.0005	0.0005	none seen	none seen	0.0005	none seen	0.0005	0.0005	0.0005
Island	0.0005	0.0005	0.0025	0.0550	none seen	0.0005	none seen	0.0005	0.0005	0.0005
Ridge	0.1279	0.0005	0.0005	none seen	none seen	0.0005	none seen	0.0005	0.0005	0.0005
Trissopathes	Scleronephthya	Paramuricea	Eguchipsammia	Metallogorgia	Paracalyptophora	Calyptophora	Thouarella	Rhodaniridogorgia	Paracis	
Atoll	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0650	0.0205	0.0680	
Bank	0.0005	none seen	0.0005	0.0005	0.0005	0.0005	none seen	0.0005	0.0005	
Guyot	0.0005	none seen	0.0005	none seen	0.0005	0.0005	0.0005	0.0005	none seen	
Conical	0.0005	none seen	none seen	none seen	0.0005	0.0005	none seen	0.0005	0.0005	
Island	0.0225	0.0005	none seen	0.0005	0.0565	0.0005	0.0010	0.0005	none seen	0.0005
Ridge	0.0005	none seen	0.0005	none seen	0.0005	0.0005	0.0005	none seen	none seen	0.0005
Amphiphanthus	Umbellapathes	Madrepora	Hallipteris	Antipathes	Polymyces	Jasonia	Anthoplitum	Callogorgia	Victorgorgia	
Atoll	0.0625	1.0000	0.1349	none seen	none seen	0.0005	1.0000	0.0005	0.0080	0.0005
Bank	0.0005	0.0005	1.0000	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005	0.0005
Guyot	0.0005	0.0005	0.0005	0.0005	0.2324	1.0000	0.0005	0.2309	0.0005	0.0005
Conical	0.0005	0.0005	none seen	0.0005	0.0005	none seen	0.0005	0.0005	0.0005	0.6877
Island	0.0005	0.0420	0.0005	none seen	0.0005	0.0005	0.0005	none seen	0.0005	0.0070
Ridge	0.0005	0.2059	0.0005	none seen	none seen	1.0000	0.0055	0.0080	none seen	0.0005
Parantipathes	Swiftia	Heteropathes	Kulamanamana	Pseudoanthomastus	Pennone seentula	Plumarella	Isactinernus	Lepidisis	Flabellum	
Atoll	0.0005	0.0315	none seen	0.0005	0.0005	0.0005	0.0140	0.4223	none seen	
Bank	0.0005	0.8296	0.0005	0.0005	0.0005	none seen	0.0120	0.8916	none seen	
Guyot	0.0005	0.0005	0.0005	none seen	0.0260	0.9910	0.0005	0.0005	none seen	
Conical	1.0000	0.0055	0.0005	none seen	0.3483	0.0005	none seen	0.0855	1.0000	none seen
Island	0.0005	0.0005	0.4353	0.0005	0.0005	0.0025	none seen	0.0005	0.0005	0.0005
Ridge	0.0005	0.0005	0.0005	0.0005	none seen	none seen	none seen	0.9385	none seen	

Supplemental Table 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.

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	<b>0.044</b>
Conical Seamount	1.38	0.62	2.19	1766.70	<b>0.000</b>
Guyot	1.12	0.41	1.91	1779.50	<b>0.003</b>
Island	-0.33	-1.03	0.39	2083.40	0.3810
Ridge Seamount	1.40	0.55	2.32	1568.70	<b>0.000</b>
Scaled Depth	-1.58	-1.85	-1.31	236.70	<b>&lt; 2e-</b>
Temperature	-6.24E-04	-1.06E-03	-1.52E-04	979.90	<b>0.010</b>

Supplemental Table 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.

	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

Supplemental Table 3:

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

Literature Cited

Allee, W. C., Emerson, A. E., Park, O., Park, T., & Schmidt, K. P. (1949). *Principles of Animal Ecology* . W.B. Saunders Co.

Amon, D. J., Kennedy, B. R. C., Cantwell, K., Suhre, K., Glickson, D., Shank, T. M., & Rotjan, R. D. (2020). Deep-Sea Debris in the Central and Western Pacific Ocean. *Frontiers in Marine Science* , 7 . <https://doi.org/10.3389/fmars.2020.00369>

Amon, D. J., Rotjan, R. D., Kennedy, B. R., Alleng, G., Anta, R., Aram, E., Edwards, T., Creary-Ford, M., Gjerde, K. M., & Gobin, J. (2022). My Deep Sea, My Backyard: a pilot study to build capacity for global deep-ocean exploration and research. *Philosophical Transactions of the Royal Society B* , 377 (1854), 20210121.

Auscavitch, S. R., Deere, M. C., Keller, A. G., Rotjan, R. D., Shank, T. M., & Cordes, E. E. (2020). Oceanographic drivers of deep-sea coral species distribution and community assembly on seamounts, islands, atolls, and reefs within the Phoenix Islands protected area.*Frontiers in Marine Science* , 7 , 42.

Auscavitch, S. R., Lunden, J. J., Barkman, A., Quattrini, A. M., Demopoulos, A. W., & Cordes, E. E. (2020). Distribution of deep-water scleractinian and stylasterid corals across abiotic environmental gradients on three seamounts in the Anegada Passage. *PeerJ* ,8 , e9523.

Auster, P. J., Moore, J., Heinonen, K. B., & Watling, L. (2005). A habitat classification scheme for seamount landscapes: assessing the functional role of deep-water corals as fish habitat. In*Cold-water corals and*

*ecosystems* (pp. 761-769). Springer.

Baddeley, A., & Turner, R. (2005). Spatstat: an R package for analyzing spatial point patterns. *Journal of statistical software* ,12 , 1-42.

Beeston, M. A., Cragg, S. M., & Linse, K. (2018). Hydrological features above a Southern Ocean seamount inhibit larval dispersal and promote speciation: evidence from the bathyal mytilid *Dacrydium alleni* sp. nov.(Mytilidae: Bivalvia). *Polar Biology* , 41 (7), 1493-1504.

Bell, K. L., Mowitt, W., Zykov, V., Delgado, J. P., Tartt, M., Stout, M., Wagner, K., Marquis, S., Bell, K. L., & Phillips, B. (2017). New Frontiers in Ocean Exploration The E/V Nautilus, NOAA Ship Okeanos Explorer, and R/V Falkor 2016 Field Season. *Oceanography* ,30 (1), 1-+.

Blanchon, P., Medina-Valmaseda, A. E., Islas-Dominguez, E., Guerra-Castro, E., Blakeway, D., Garza Perez, J. R., Jordan-Garza, A. G., Marino-Tapia, I., & Zapata-Ramirez, P. A. (2022). Linear breakwater reefs of the greater Caribbean: Classification, distribution & morphology. *PLoS One* , 17 (11), e0270053. <https://doi.org/10.1371/journal.pone.0270053>

Brink, K. (1995). Tidal and lower frequency currents above Fieberling Guyot. *Journal of Geophysical Research: Oceans* , 100 (C6), 10817-10832.

Bryan, T. L., & Metaxas, A. (2006). Distribution of deep-water corals along the North American continental margins: Relationships with environmental factors. *Deep Sea Research Part I: Oceanographic Research Papers* , 53 (12), 1865-1879. <https://doi.org/10.1016/j.dsr.2006.09.006>

Buhl-Mortensen, L., Vanreusel, A., Gooday, A. J., Levin, L. A., Priede, I. G., Buhl-Mortensen, P., Gheerardyn, H., King, N. J., & Raes, M. (2010). Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology* ,31 (1), 21-50. <https://doi.org/10.1111/j.1439-0485.2010.00359.x>

Cantwell, K., Elliott, K., & Kennedy, B. R. (2018). Deepwater exploration of the pacific remote islands marine national monument and Central Pacific Basin. *Oceanography* , 31 (1), 74-75.

Cantwell, K., Kennedy, B. R. C., Malik, M., Suhre, K., Medley, R., Lobecker, E., Hoy, S., Adams, C., Dorndack, M., & Cromwell, M. (2020). 10 years of the Explorer Model: Lessons from 10 Years of Community-led Ocean Exploration and Open Data. *The Journal of Ocean Technology* ,15 , 77-86.

Cathalot, C., Van Oevelen, D., Cox, T. J. S., Kutti, T., Lavaleye, M., Duineveld, G., & Meysman, F. J. R. (2015). Cold-water coral reefs and adjacent sponge grounds: hotspots of benthic respiration and organic carbon cycling in the deep sea. *Frontiers in Marine Science* ,2 . <https://doi.org/10.3389/fmars.2015.00037>

Cavanaugh, C. M. (1983). Symbiotic chemoautotrophic bacteria in marine invertebrates from sulphide-rich habitats. *Nature* ,302 (5903), 58-61. <https://doi.org/10.1038/302058a0>

Chapman, D. C., & Haidvogel, D. B. (1992). Formation of Taylor caps over a tall isolated seamount in a stratified ocean. *Geophysical & Astrophysical Fluid Dynamics* , 64 (1-4), 31-65. <https://doi.org/10.1080/03091929208228084>

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics* , 31 , 343-366. <http://www.jstor.org/stable/221736>

Clark, M. R., Rowden, A. A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K. I., Rogers, A. D., O'Hara, T. D., White, M., Shank, T. M., & Hall-Spencer, J. M. (2010). The ecology of seamounts: structure, function, and human impacts. *Ann Rev Mar Sci* , 2 , 253-278. <https://doi.org/10.1146/annurev-marine-120308-081109>

Clark, M. R., Schlacher, T. A., Rowden, A. A., Stocks, K. I., & Consalvey, M. (2012). Science priorities for seamounts: research links to conservation and management. *PLoS One* , 7 (1), e29232. <https://doi.org/10.1371/journal.pone.0029232>



- Clark, P. J., & Evans, F. C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* ,35 (4), 445-453.
- Collart, T., Verreydt, W., Hernández-Molina, F. J., Llave, E., León, R., Gómez-Ballesteros, M., Pons-Branchu, E., Stewart, H., & Van Rooij, D. (2018). Sedimentary processes and cold-water coral mini-mounds at the Ferrol canyon head, NW Iberian margin. *Progress in Oceanography* ,169 , 48-65. <https://doi.org/10.1016/j.pocean.2018.02.027>
- Corliss, J. B., Dymond, J., Gordon, L. I., Edmond, J. M., von Herzen, R. P., Ballard, R. D., Green, K., Williams, D., Bainbridge, A., Crane, K., & van Andel, T. H. (1979). Submarine Thermal Springs on the Galapagos Rift. *Science* , 203 (4385), 1073-1083. <https://doi.org/doi:10.1126/science.203.4385.1073>
- Crawley, M. J. (2005). *Statistics: an introduction using R* . Wiley.
- Cunha, M. R., Hilário, A., & Santos, R. S. (2017). Advances in deep-sea biology: biodiversity, ecosystem functioning and conservation. An introduction and overview. *Deep Sea Research Part II: Topical Studies in Oceanography* , 137 , 1-5. <https://doi.org/10.1016/j.dsr2.2017.02.003>
- Danovaro, R., Company, J. B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A. J., Lampadariou, N., Luna, G. M., Morigi, C., Olu, K., Polymenakou, P., Ramirez-Llodra, E., Sabbatini, A., Sarda, F., Sibuet, M., & Tselepidis, A. (2010). Deep-sea biodiversity in the Mediterranean Sea: the known, the unknown, and the unknowable. *PLoS One* , 5 (8), e11832. <https://doi.org/10.1371/journal.pone.0011832>
- Danovaro, R., Snelgrove, P. V., & Tyler, P. (2014). Challenging the paradigms of deep-sea ecology. *Trends Ecol Evol* , 29 (8), 465-475. <https://doi.org/10.1016/j.tree.2014.06.002>
- Darwin, C. R. (1842). *The structure and distribution of coral reefs. Being the first part of the geology of the voyage of the Beagle, under the command of Capt. Fitzroy, R.N. during the years 1832 to 1836* . Smith Elder and Co.
- Demopoulos, A. W., Auscavitch, S., Sowers, D., Pawlenko, N., & Kennedy, B. R. (2018). Discovering the deep: exploring remote Pacific marine protected areas. *Oceanography* , 31 (1 Supplement), 76-77.
- Dijkstra, J. A., Mello, K., Sowers, D., Malik, M., Watling, L., Mayer, L. A., & Pandolfi, J. (2021). Fine-scale mapping of deep-sea habitat-forming species densities reveals taxonomic specific environmental drivers. *Global Ecology and Biogeography* ,30 (6), 1286-1298. <https://doi.org/10.1111/geb.13285>
- Dolan, M. F. J., Grehan, A. J., Guinan, J. C., & Brown, C. (2008). Modelling the local distribution of cold-water corals in relation to bathymetric variables: Adding spatial context to deep-sea video data. *Deep Sea Research Part I: Oceanographic Research Papers* ,55 (11), 1564-1579. <https://doi.org/10.1016/j.dsr.2008.06.010>
- Donnelly, K. (1978). Simulation to determine the variance and edge-effect of total nearest neighbour distance. *Simulation methods in archeology* .
- Fernandez-Arcaya, U., Ramirez-Llodra, E., Aguzzi, J., Allcock, A. L., Davies, J. S., Dissanayake, A., Harris, P., Howell, K., Huvenne, V. A. I., Macmillan-Lawler, M., Martin, J., Menot, L., Nizinski, M., Puig, P., Rowden, A. A., Sanchez, F., & Van den Beld, I. M. J. (2017). Ecological Role of Submarine Canyons and Need for Canyon Conservation: A Review. *Frontiers in Marine Science* , 4 . <https://doi.org/10.3389/fmars.2017.00005>
- GEBCO 2022 Grid . (2022). <https://doi.org/doi:10.5285/e0f0bb80-ab44-2739-e053-6c86abc0289c>
- Genin, A. (2004). Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems* , 50 (1-2), 3-20.
- Gregory, T., Lovalvo, D., Mohr, B., McLetchie, K., & Ryan, M. (2016). Advancing Undersea Technology. *Oceanography* , 29 , 52-55.
- Guinan, J., Brown, C., Dolan, M. F. J., & Grehan, A. J. (2009). Ecological niche modelling of the distribution of cold-water coral habitat using underwater remote sensing data. *Ecological Informatics* , 4 (2), 83-92.

<https://doi.org/10.1016/j.ecoinf.2009.01.004>

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of statistical software* , 33 , 1-22.

Hedges, J. I., Clark, W. A., & Come, G. L. (1988). Organic matter sources to the water column and surficial sediments of a marine bay. *Limnology and Oceanography* , 33 (5), 1116-1136.

Henry, L.-A., & Roberts, J. M. (2007). Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers* , 54 (4), 654-672. <https://doi.org/10.1016/j.dsr.2007.01.005>

Howell, K. L., Holt, R., Endrino, I. P., & Stewart, H. (2011). When the species is also a habitat: Comparing the predictively modelled distributions of *Lophelia pertusa* and the reef habitat it forms. *Biological Conservation* , 144 (11), 2656-2665. <https://doi.org/10.1016/j.biocon.2011.07.025>

Hu, A., Wang, J., Sun, H., Niu, B., Si, G., Wang, J., Yeh, C. F., Zhu, X., Lu, X., Zhou, J., Yang, Y., Ren, M., Hu, Y., Dong, H., & Zhang, G. (2020). Mountain biodiversity and ecosystem functions: interplay between geology and contemporary environments. *ISME J* , 14 (4), 931-944. <https://doi.org/10.1038/s41396-019-0574-x>

Jamieson, A. J., Fujii, T., Mayor, D. J., Solan, M., & Priede, I. G. (2010). Hadal trenches: the ecology of the deepest places on Earth. *Trends in Ecology & Evolution* , 25 (3), 190-197. <https://doi.org/https://doi.org/10.1016/j.tree.2009.09.009>

Kennedy, B. R. C., Cantwell, K., Malik, M., Kelley, C., Potter, J., Elliott, K., Lobecker, E., Gray, L. M., Sowers, D., White, M. P., France, S. C., Auscavitch, S., Mah, C., Moriwake, V., Bingo, S. R. D., Putts, M., & Rotjan, R. D. (2019). The Unknown and the Unexplored: Insights Into the Pacific Deep-Sea Following NOAA CAPSTONE Expeditions. *Frontiers in Marine Science* , 6 . <https://doi.org/10.3389/fmars.2019.00480>

Kennedy, B. R. C., Elliott, K. P., Cantwell, K., & Mesick, S. (2016). Telepresence-Enabled Exploration with NOAA Ship Okeanos Explorer. *Oceanography* , 29 , 50-51.

Kennedy, B. R. C., & Rotjan, R. D. (2020). Deep-sea ecosystem engineers. *Frontiers in Ecology and the Environment* , 18 (4), 180-180. <https://doi.org/10.1002/fee.2200>

Lavelle, W., & Mohn, C. (2010). Motion, Commotion, and Biophysical Connections at Deep Ocean Seamounts. *Oceanography* , 23 , 90-103.

Leitner, A. B., Neuheimer, A. B., & Drazen, J. C. (2020). Evidence for long-term seamount-induced chlorophyll enhancements. *Sci Rep* , 10 (1), 12729. <https://doi.org/10.1038/s41598-020-69564-0>

Leonardi, A., Armor, J., Montanio, P., & Werner, C. (2018). CAPSTONE NOAA's Campaign to Address Pacific monument Science, Technology, and Ocean Needs. *Oceanography* , 31 (1), 48-52.

Levin, L. A., Bett, B. J., Gates, A. R., Heimbach, P., Howe, B. M., Janssen, F., McCurdy, A., Ruhl, H. A., Snelgrove, P., Stocks, K. I., Bailey, D., Baumann-Pickering, S., Beaverson, C., Benfield, M. C., Booth, D. J., Carreiro-Silva, M., Colaco, A., Eble, M. C., Fowler, A. M., . . . Weller, R. A. (2019). Global Observing Needs in the Deep Ocean. *Frontiers in Marine Science* , 6 . <https://doi.org/10.3389/fmars.2019.00241>

Lisa, A. L. (2003). Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanography and Marine Biology: an Annual Review*, 41, 1-45.

Long, D. J., & Baco, A. R. (2014). Rapid change with depth in megabenthic structure-forming communities of the Makapu'u deep-sea coral bed. *Deep Sea Research Part II: Topical Studies in Oceanography* , 99 , 158-168. <https://doi.org/10.1016/j.dsr2.2013.05.032>

Longhurst, A. R. (1985). The structure and evolution of plankton communities. *Progress in Oceanography* , 15 (1), 1-35. [https://doi.org/https://doi.org/10.1016/0079-6611\(85\)90036-9](https://doi.org/https://doi.org/10.1016/0079-6611(85)90036-9)

- Matthews, W. J. (2012). *Patterns in freshwater fish ecology* . Springer Science & Business Media.
- McClain, C. R. (2007). Seamounts: identity crisis or split personality? *Journal of Biogeography* , 34 (12), 2001-2008. <https://doi.org/10.1111/j.1365-2699.2007.01783.x>
- McClain, C. R., & Hardy, S. M. (2010). The dynamics of biogeographic ranges in the deep sea. *Proc Biol Sci* , 277 (1700), 3533-3546. <https://doi.org/10.1098/rspb.2010.1057>
- Menard, H. W. (1964). *Marine geology of the Pacific* .
- Mienis, F., de Stigter, H. C., White, M., Duineveld, G., de Haas, H., & van Weering, T. C. E. (2007). Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall Trough Margin, NE Atlantic Ocean. *Deep Sea Research Part I: Oceanographic Research Papers* , 54 (9), 1655-1674. <https://doi.org/10.1016/j.dsr.2007.05.013>
- Mohn, C., White, M., Bashmachnikov, I., Jose, F., & Pelegri, J. L. (2009). Dynamics at an elongated, intermediate depth seamount in the North Atlantic (Sedlo Seamount, 40° 20' N, 26° 40' W). *Deep Sea Research Part II: Topical Studies in Oceanography* , 56 (25), 2582-2592.
- Morato, T., Varkey, D. A., Damaso, C., Machete, M., Santos, M., Prieto, R., Pitcher, T. J., & Santos, R. S. (2008). Evidence of a seamount effect on aggregating visitors. *Marine Ecology Progress Series* , 357 , 23-32. <https://doi.org/10.3354/meps07269>
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., & Oksanen, M. J. (2007). The vegan package. *Community ecology package* , 10 (631-637), 719.
- Quattrini, A. M., Nizinski, M. S., Chaytor, J. D., Demopoulos, A. W., Roark, E. B., France, S. C., Moore, J. A., Heyl, T., Auster, P. J., Kinlan, B., Ruppel, C., Elliott, K. P., Kennedy, B. R., Lobecker, E., Skarke, A., & Shank, T. M. (2015). Exploration of the Canyon-Incised Continental Margin of the Northeastern United States Reveals Dynamic Habitats and Diverse Communities. *PLoS One* , 10 (10), e0139904. <https://doi.org/10.1371/journal.pone.0139904>
- Radice, V. Z., Quattrini, A. M., Wareham, V. E., Edinger, E. N., & Cordes, E. E. (2016). Vertical water mass structure in the North Atlantic influences the bathymetric distribution of species in the deep-sea coral genus *Paramuricea*. *Deep Sea Research Part I: Oceanographic Research Papers* , 116 , 253-263. <https://doi.org/10.1016/j.dsr.2016.08.014>
- Raineault, N., & Flanders, J. (2019). New Frontiers in Ocean Exploration: The E/V Nautilus, NOAA Ship Okeanos Explorer, and R/V Falkor 2018 Field Season. *Oceanography* , 32 (1). <https://doi.org/10.5670/oceanog.2019.supplement.01>
- Raineault, N., & Flanders, J. (2020). New Frontiers in Ocean Exploration: The E/V Nautilus, NOAA Ship Okeanos Explorer, and R/V Falkor 2019 Field Season. *Oceanography* , 33 (1), 1-122. <https://doi.org/10.5670/oceanog.2020.supplement.01>
- Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R., Levin, L. A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B. E., Smith, C. R., Tittensor, D. P., Tyler, P. A., Vanreusel, A., & Vecchione, M. (2010). Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences* , 7 (9), 2851-2899. <https://doi.org/10.5194/bg-7-2851-2010>
- RFMO. (2019). *VME indicators, thresholds and encounter responses adopted by R(F)MOs in force during 2019*. FAO. <https://www.fao.org/in-action/vulnerable-marine-ecosystems/vme-indicators/ru/>
- Richer de Forges, B., Koslow, J. A., & Poore, G. (2000). Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* , 405 (6789), 944-947.
- Roark, E. B., Guilderson, T. P., Dunbar, R. B., Fallon, S. J., & Mucciarone, D. A. (2009). Extreme longevity in proteinaceous deep-sea corals. *Proc Natl Acad Sci U S A* , 106 (13), 5204-5208. <https://doi.org/10.1073/pnas.0810875106>

- Roberts, J. M., Wheeler, A., Freiwald, A., & Cairns, S. (2009). *Cold-water corals: the biology and geology of deep-sea coral habitats* . Cambridge University Press.
- Robison, B. H. (2009). Conservation of deep pelagic biodiversity. *Conserv Biol* , 23 (4), 847-858. <https://doi.org/10.1111/j.1523-1739.2009.01219.x>
- Rogers, A. (1994). The biology of seamounts. In *Advances in marine biology* (Vol. 30, pp. 305-350). Elsevier.
- Rogers, A. D. (2018). The Biology of Seamounts: 25 Years on. *Adv Mar Biol* , 79 , 137-224. <https://doi.org/10.1016/bs.amb.2018.06.001>
- Rowden, A. A., Pearman, T. R. R., Bowden, D. A., Anderson, O. F., & Clark, M. R. (2020). Determining Coral Density Thresholds for Identifying Structurally Complex Vulnerable Marine Ecosystems in the Deep Sea. *Frontiers in Marine Science* , 7 . <https://doi.org/10.3389/fmars.2020.00095>
- Samadi, S., Bottan, L., Macpherson, E., De Forges, B. R., & Boisselier, M.-C. (2006). Seamount endemism questioned by the geographic distribution and population genetic structure of marine invertebrates. *Marine Biology* , 149 (6), 1463-1475. <https://doi.org/10.1007/s00227-006-0306-4>
- Sanchez-Vidal, A., Canals, M., Calafat, A. M., Lastras, G., Pedrosa-Pamies, R., Menendez, M., Medina, R., Company, J. B., Hereu, B., Romero, J., & Alcoverro, T. (2012). Impacts on the deep-sea ecosystem by a severe coastal storm. *PLoS One* , 7 (1), e30395. <https://doi.org/10.1371/journal.pone.0030395>
- Sayre, R., Dangermond, J., Wright, D., Breyer, S., Butler, K., Van Graafeiland, K., Frye, C., Karagulle, D., Kopp, S., & Noble, S. (2019). A new map of global islands. *American Association of Geographers, Washington, DC*, 24p .
- Shank, T. M. (2010). Seamounts: Deep-ocean laboratories of faunal connectivity, evolution, and endemism. *Oceanography* , 23 , 108-122. <https://doi.org/https://doi.org/10.5670/oceanog.2010.65>
- Shank, T. M., Cordes, E. E., Auscavitch, S., Heyl, T. P., McCartin, L., McElwee, E., Kelley, C., & Rotjan, R. (2018). Biodiversity, Biogeography, and Relationships of Deep-Water Coral-Symbiotic Fauna of the Seamounts in the Phoenix Islands Protected Area (PIPA). 2018 Ocean Sciences Meeting,
- Smith, D. K., & Cann, J. R. (1990). Hundreds of small volcanoes on the median valley floor of the Mid-Atlantic Ridge at 24–30 N. *Nature* , 348 (6297), 152-155.
- Somoza, L., Ercilla, G., Urgorri, V., Leon, R., Medialdea, T., Paredes, M., Gonzalez, F. J., & Nombela, M. A. (2014). Detection and mapping of cold-water coral mounds and living Lophelia reefs in the Galicia Bank, Atlantic NW Iberia margin. *Marine Geology* , 349 , 73-90. <https://doi.org/10.1016/j.margeo.2013.12.017>
- Sullivan-Stack, J., Aburto-Oropeza, O., Brooks, C. M., Cabral, R. B., Caselle, J. E., Chan, F., Duffy, J. E., Dunn, D. C., Friedlander, A. M., Fulton-Bennett, H. K., Gaines, S. D., Gerber, L. R., Hines, E., Leslie, H. M., Lester, S. E., MacCarthy, J. M. C., Maxwell, S. M., Mayorga, J., McCauley, D. J., . . . Grorud-Colvert, K. (2022). A Scientific Synthesis of Marine Protected Areas in the United States: Status and Recommendations [Policy and Practice Reviews]. *Frontiers in Marine Science* , 9 . <https://doi.org/10.3389/fmars.2022.849927>
- Sutton, T. T., Clark, M. R., Dunn, D. C., Halpin, P. N., Rogers, A. D., Guinotte, J., Bograd, S. J., Angel, M. V., Perez, J. A. A., Wishner, K., Haedrich, R. L., Lindsay, D. J., Drazen, J. C., Vereshchaka, A., Piatkowski, U., Morato, T., Błachowiak-Samolyk, K., Robison, B. H., Gjerde, K. M., . . . Heino, M. (2017). A global biogeographic classification of the mesopelagic zone. *Deep Sea Research Part I: Oceanographic Research Papers* , 126 , 85-102. <https://doi.org/10.1016/j.dsr.2017.05.006>
- Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature* , 466 (7310), 1098-1101. <https://doi.org/10.1038/nature09329>

- Tong, R., Purser, A., Unnithan, V., & Guinan, J. (2012). Multivariate statistical analysis of distribution of deep-water gorgonian corals in relation to seabed topography on the Norwegian margin. *PLoS One* ,7 (8), e43534. <https://doi.org/10.1371/journal.pone.0043534>
- Turnewitsch, R., Falahat, S., Nycander, J., Dale, A., Scott, R. B., & Furnival, D. (2013). Deep-sea fluid and sediment dynamics—Influence of hill-to seamount-scale seafloor topography. *Earth-Science Reviews* , 127 , 203-241.
- Tyler, P. A., Baker, M., & Ramirez-Llodra, E. (2016). Deep-sea benthic habitats. *Biological sampling in the deep sea* , 1-15.
- Van Dover, C. L. (2021). The ecology of deep-sea hydrothermal vents. In *The Ecology of Deep-Sea Hydrothermal Vents* . Princeton University Press.
- van Haren, H., Mienis, F., Duineveld, G. C. A., & Lavaleye, M. S. S. (2014). High-resolution temperature observations of a trapped nonlinear diurnal tide influencing cold-water corals on the Logachev mounds. *Progress in Oceanography* , 125 , 16-25. <https://doi.org/10.1016/j.pocean.2014.04.021>
- Wagner, D., Friedlander, A. M., Pyle, R. L., Brooks, C. M., Gjerde, K. M., & Wilhelm, T. A. (2020). Coral Reefs of the High Seas: Hidden Biodiversity Hotspots in Need of Protection. *Frontiers in Marine Science* , 7 . <https://doi.org/10.3389/fmars.2020.567428>
- Watling, L., & Auster, P. J. (2021). Vulnerable Marine Ecosystems, Communities, and Indicator Species: Confusing Concepts for Conservation of Seamounts. *Frontiers in Marine Science* , 8 . <https://doi.org/10.3389/fmars.2021.622586>
- Watling, L., Guinotte, J., Clark, M. R., & Smith, C. R. (2013). A proposed biogeography of the deep ocean floor. *Progress in Oceanography* , 111 , 91-112. <https://doi.org/10.1016/j.pocean.2012.11.003>
- Watling, L., & Lapointe, A. (2022). Global biogeography of the lower bathyal (700–3000 m) as determined from the distributions of cnidarian anthozoans. *Deep Sea Research Part I: Oceanographic Research Papers* , 181 , 103703.
- Webb, T. J., Vanden Berghe, E., & O'Dor, R. (2010). Biodiversity's big wet secret: the global distribution of marine biological records reveals chronic under-exploration of the deep pelagic ocean. *PLoS One* ,5 (8), e10223. <https://doi.org/10.1371/journal.pone.0010223>
- Wessel, P., Watts, A. B., Kim, S.-S., & Sandwell, D. T. (2022). Models for the evolution of seamounts. *Geophysical Journal International* , 231 (3), 1898-1916.
- White, M., Bashmachnikov, I., Arístegui, J., & Martins, A. (2007). Physical processes and seamount productivity. *Seamounts: ecology, fisheries and conservation* , 65-84.
- White, M., Wolff, G. A., Lundälv, T., Guihen, D., Kiriakoulakis, K., Lavaleye, M., & Duineveld, G. (2012). Cold-water coral ecosystem (Tisler Reef, Norwegian Shelf) may be a hotspot for carbon cycling. *Marine Ecology Progress Series* , 465 , 11-23. <https://doi.org/10.3354/meps09888>
- Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale Terrain Analysis of Multibeam Bathymetry Data for Habitat Mapping on the Continental Slope. *Marine Geodesy* ,30 (1-2), 3-35. <https://doi.org/10.1080/01490410701295962>
- Woulds, C., Cowie, G. L., Levin, L. A., Andersson, J. H., Middelburg, J. J., Vandewiele, S., Lamont, P. A., Larkin, K. E., Gooday, A. J., & Schumacher, S. (2007). Oxygen as a control on sea floor biological communities and their roles in sedimentary carbon cycling. *Limnology and Oceanography* , 52 (4), 1698-1709.
- Wu, Y., Zhu, D., Chu, Z., Zhong, C., & Luo, C. (2016). Autonomous underwater vehicles navigation method based on ultra short base line and dead reckoning. 2016 IEEE International Conference on Underwater System Technology: Theory and Applications (USYS),

Yasuhara, M., & Danovaro, R. (2016). Temperature impacts on deep-sea biodiversity. *Biol Rev Camb Philos Soc* , 91 (2), 275-287. <https://doi.org/10.1111/brv.12169>

Yesson, C., Clark, M. R., Taylor, M. L., & Rogers, A. D. (2011). The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep Sea Research Part I: Oceanographic Research Papers* ,58 (4), 442-453. <https://doi.org/10.1016/j.dsr.2011.02.004>