Fine-scale mapping of deep-sea habitat-forming species densities reveals taxonomic specific environmental drivers

Short running title: Species-specific abiotic drivers of deep-sea habitat formers

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Biosketch: We are a group of researchers interested in mapping the seafloor, and the spatial and temporal distribution of species and benthic communities.

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ABSTRACT

Aim: Environmental variables are strongly tied to species occurrence and population growth, but approaches to predicting the location of deep sea species or their ability to withstand a changing environment stems primarily from presence data. We coupled environmental data with observed densities of deep-sea habitat-forming corals and sponges to determine environmental variables and geomorphology that best contributed to their occurrence.

Location: Northwest Atlantic

Time period: 2013 and 2014

Major taxa studied: Deep-sea coral and sponge communities

Methods: Multivariate and univariate analyses were used to determine significant environmental contributors to densities of genera and families of coral and sponges. We then assessed the relationship of densities of genera and families of corals and sponges with environmental variables found to be significant contributors to their occurrence and to geomorphology.

Results: Sponge and coral genera and families were influenced by different environment variables. Temperature, salinity, and dissolved oxygen contributed to the occurrence of sponges while seafloor properties of slope and substrate contributed to the occurrence of corals. While

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individuals of corals and sponges were observed across a range of a contributed environmental variable, high densities were only observed in very narrow ranges.

Main conclusions: Geomorphic setting is an effective approach for discerning coral associations with seabed features. High densities of coral and sponge genera and families restricted to narrow environmental ranges may be at greater risk of local extinction resulting in a loss of biodiversity. Differences in the occurrence of coral and sponge genera and families with environmental conditions suggest they will differentially respond to predicted environmental changes. As conditions in the deep-sea change with ongoing changes in climate, population expansion may be limited due to sub-optimal conditions and established populations may persist, but may have fewer individuals or species which may lead to reduced biodiversity.

Keywords: climate change, biodiversity, global warming, geomorphology, coral, sponge, deep-sea canyons, seamounts, Northwestern Atlantic

INTRODUCTION

Habitat-forming or foundation species are important members of benthic communities as they attract a diverse assemblage of upper trophic level species that use them as both refuge and sources of food (e.g., Ross, Rhode, & Quattrini 2015, Maldanado et al., 2017, Dijkstra, Boudreau, & Dionne 2012, Dijkstra et al. 2017). They can co-occur in communities as multiple foundation species or can form one-way nested facilitation cascades in which one foundation species facilitates establishment of other foundation species (Altieri, Silliman, & Bertness 2007, Gribben et al. 2009). In benthic systems that have strong trophic connections, foundation species are a driving force for the network of feeding interactions (e.g., Shurin, Borer & Seabloom 2002, O'Brien, Mello, Litterer & Dijkstra 2018, Ware et al. 2019). This may be particularly apparent in the deep-sea, an ecosystem of high species richness, but generally low densities in which the loss of foundational species, which add a third vertical dimension to an otherwise desolate seascape, may impact food webs. Indeed, this added structure has been shown to enhance the diversity of fishes and contribute to a fish assemblage that is different from those observed in the surrounding environment free of corals or sponges (Ross and Quattrini 2007, Ross et al. 2015). Further, they serve as nursery habitats for juvenile fishes, substrata for their eggs (Etnoyer & Warrenchuk 2007, Henry et al. 2013, Ross et al. 2015), and provide food for echinoderms (Mah

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2015). These studies, combined with the patchy distribution of individuals that is characteristic of communities in the deep-sea, suggest that loss of foundation species could have sustained damaging effects on its ecology and the ecosystem services they provide.

Recent studies indicate that water column properties of the deep-sea are changing in response to a changing climate (Purkey and Johnson, 2010, Bindoff et al. 2019, Brito-Morales 2020). Temperatures are predicted to increase with concurrent reductions in dissolved oxygen and elevated carbon dioxide levels (Joos et al., 2003; Schmidtko et al., 2017, Thomsen et al. 2017), factors that affect growth and reproduction of deep-sea species and, ultimately, their population size and structure (Sweetman et al. 2017). Particulate organic carbon is predicted to decline under climate-change scenarios (Bindoff et al. 2019), which may result in an 18% reduction in benthic biomass and changes to the composition of species particularly Holothuroidea and sponges (Kuhnz, Ruhl, Huffard, & Smith 2020). Yet, not all species will respond equally to these changes due to the particular environmental tolerances of each species. Some species may experience reduced growth and reproduction in an unfavorable environment, while other species may be relatively unaffected. These effects may be pronounced in deep-sea ecosystems in which inhabitant organisms have evolved in very stable environmental conditions in which minute environmental changes may have severe physiological and population growth consequences. Determining factors that contribute to not only their occurrence, but to their densities is critical to predicting the response of deep-sea corals and sponges to environmental change.

Globally, benthic communities observed in canyons and seamounts are exposed to rapid climate driven effects of warmer waters (Levin 2018), hypoxia (Breitburg et al. 2018) and lower salinity (Dickson et al. 2002). Canyons and seamounts of the Northwestern Atlantic are no exception as environmental conditions are expected to surpass current ambient water temperatures and oxygen concentrations (Bindoff et al. 2019). These seafloor features are important as they are topographically complex and support high organismal density and biomass (Kelly, Shea, Metaxas, Haedrich, & Auster 2010). High nutrient concentrations, along with fast currents that re-suspend sediments and expose hard bottom, contribute to a high secondary production and biomass of benthic fauna, particularly of suspension feeding organisms such as corals and sponges. The topography in canyons facilitates a downward transport of sediment and particulate organic matter (Harrold, Light, & Lisin 1998, Quattrini et al. 2015), and link the

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upper continental shelf to the abyssal plain and adjacent seamounts (Rowden, Dower, Schlacher, Consalvey, & Clarke 2010). Both canyons and seamounts are thought to be important hotspots of biodiversity and biomass and serve as stepping stones for larval dispersal (Rowden et al. 2010). Understanding the linkages between environmental variables and habitat forming corals and sponges will aid our ability to predict the effects of climate warming on these Vulnerable Marine Ecosystems (VME). Therefore, we analyzed variables that contribute to the occurrence of coral and sponge genera and families in the Northwestern Atlantic canyons and seamounts. We then examined the relationship of their densities with environmental variables found to be significant to their occurrence.

METHODS

Data Collection and Annotation of Underwater Video Footage

Corals and sponges were identified in 50 m x 0.5 m segments of a ROV underwater video track of the seafloor. High resolution video footage was collected by NOAA's Office of Ocean Exploration and Research's 6,000-meter rated remotely-operated vehicle (ROV) Deep Discoverer (see Appendix S1). Video was collected at five canyons and five seamounts along the Northeast Canyons and the New England Seamount Chain (Fig. 1). The approximate area of visual sampling in individual video frames was 0.25 m^2. Additional environmental parameters of slope, depth, temperature, dissolved oxygen, salinity, and primary substrate were also determined for each 50 m segment. Depth, temperature, dissolved oxygen and salinity were averaged over each segment. Slope for each segment was generated from the Slope tool in the Spatial Analyst toolbox in ArcMap 10.1 using available multibeam bathymetry data from the U.S. Atlantic Margin. Primary substrate was classified as the substrate that occupied at least 50% of the segment. These substrates were identified according to the definition provided by the Coastal Marine Ecological Classification Standard (CMECS) and further delineated using event logs from the associated expedition. Ten primary substrate classes were identified: bedrock (BEDROC), silty bedrock (SLTBRK), boulder (BOULD), pebble (PEBBLE), cobble (COBBLE), coarse sand (CRSSND), muddy sand (MUDSND), silty sand (SLTSND), clay sand (CLYSND), coral rubble (CORRUB).

High resolution underwater video footage was collected using the Deep Discover (D2) ROV. In addition to six HD cameras, D2 carries a Sea Bird 9/11+CTD with light scattering,

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dissolved oxygen (DO), temperature, salinity, and depth sensors. An ultra-short baseline (USBL) system with an accuracy of 0.25° (= ~8.8 m diameter circle at a depth of 2000 m) was used to obtain vehicle position relative to the ship during deployment. The ROV was also equipped with lights aimed at the seafloor for illumination. Two lasers that were 10 cm apart were projected onto the video image providing a scale to enable calculation of total area analyzed along each ROV track.

To minimize observer effects, identification and densities of taxa and substrata in the ROV video footage was manually analyzed by a single person. First, a customized MATLAB script divided the ROV track into 50 m segments by calculating the length of the track and then dividing it into successive segments using the speed of the ROV in combination with its georeferenced position. Second, playback and annotation of ROV video integrated with navigation and CTD data files (dissolved oxygen, depth, salinity, and temperature) were facilitated by using a customized Python script.

To obtain abundance of individuals within segments, the width plus 2x the width (total width: 0.5 m) on either side of the laser dots was analyzed for each 50 m segment. For segments in which the lasers were off, organisms were divided into bins of 1, 2-4, 5-9, 10-14, and 15-19 with corresponding values of 1, 3, 7, 12 and 17 used for further analysis. Segments with organismal densities higher than 20 were binned by groups of 10 (e.g., 20-30, 31-40 etc.) and were assigned the average. For example, if the abundance of an organism was between 20 and 29, then a value of 25 was assigned as the abundance of that organism for that segment.

Corals and sponges were taxonomically classified to the lowest possible level with the aid of the recorded (auditory and written) events log captured for each dive and verified using identification guides (NOAA Benthic Deepwater Animal Identification Guide 2020). While corals in the New England Seamount Chain have been extensively identified based on physical samples (reviewed in Watling, France, Pante, & Simpson 2011, Lapointe and Watling 2020), identification of corals and sponges was made based on video imagery without the collection of voucher specimens as the ROV was not equipped to collect specimens. Identifications ranged from species to family level, with individuals that could not be identified to this level identified at the class or phylum level. Higher identification level occurred when there was insufficient morphological detail of an individual for genera or family level identification.

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Annotations

Corals, sponges, and substrate were annotated in the full underwater video footage and then integrated with the navigation and CTD data files. Seafloor slope for the location of each observation was derived from multibeam sonar bathymetry gridded to 50 m resolution. These slope values may not reflect those directly at the site of the organism observation, but they reflect that of the 50 m seascape. Annotations and slope were integrated with navigation and CTD data files and were used to determine variables that contributed to their occurrence. Integrating navigation, CTD data files and slope with species occurrence along a track provided the most direct comparison of organism occurrence with abiotic variables, and allowed for further examination of densities along the range of the environmental variable that best explained their distribution.

Correlations between Taxa and Environmental Variables

Multivariate correlations between environmental variables and segment densities of coral and sponge genera and families were calculated using the software package PRIMER 6.0 (Clark and Gorley 2006). Individuals identified at USGS Hazards 2 were not included in this analysis as the CTD and DO sensors were not functioning properly. This site was a sandy substrate dominated by ophuroids and few individual coral or sponges.

To determine which environmental and seafloor variables influenced the distribution of individual taxa, a Bray-Curtis similarity index was first calculated on ROV segment densities (#/25 m^2) of a single coral or sponge identified at the family and, when possible, genus level. Bray-Curtis similarity was used as it has the flexibility to register differences in similarity when abundances are nearly identical. Individuals that were identified as coral or sponge only (i.e., not identified to a lower taxonomic level) were excluded from the analysis. Second, the BEST/BIO-ENV procedure (Clark and Ainsworth 1993) was used to find the best match between environmental variables and the segment resemblance matrix of single family/genus of sponge or coral using Spearman rank correlation coefficients in PRIMER 6.0. This procedure was used as few assumptions are made to the data and no assumption of linearity between environmental variables and taxa. Spearman rank correlation coefficients were used to match ranks between ROV segment biotic similarity matrix and ranks between segment, log+1 transformed and normalized, environmental variables for each family/genus. Final correlations were made with

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all environmental variables as removing highly correlated variables did not change the results (see Appendix S2). Randomization tests set to 1000 permutations were used to test the significance of the correlations. A significance level of 0.01 was used as the critical level due to potential spatial autocorrelation in the environmental variables among segments of an ROV track. This procedure does not indicate the amount of variance explained by each significant contributor. These statistics were performed using the PRIMER 6.0 software package.

When family/genera densities appeared to be linearly related to a continuous contributing variable (see Figure 3-5), standard linear regressions were used to determine the amount of variation that explained coral and sponge genera and family densities. Where the abiotic factor was not continuous, a Pearson chi-square test was used to determine equal likelihood of observed densities among substrata or geoforms. These statistics were generated using the JMP 10.1 software package.

Geomorphic Setting

Geomorphic classification of the seafloor provides insights into the spatial relationships among marine habitats and has been used in numerous studies to describe and predict marine ecological communities (e.g. Harris & Baker 2011 and references therein). This study utilized existing published geomorphological classifications for the study area (Sowers et al. 2020) to determine whether the frequency of coral occurrences appeared to be related to specific morphologies (referred to henceforth as "geoforms"). Within the study area, the following geoform classes were present: Continental Slope - Slope (CSS), Continental Slope - Valley (CSV), Seamount Ridge (SR), and Seamount Slope (SS). ROV tracks were overlain with geoform polygons in ArcGIS to classify each ROV segment with the underlying geoform. Frequency histograms of coral families plotted against geoforms were then generated to determine if densities varied with geomorphology feature class.

RESULTS

Twenty-six genera of corals, five genera of sponges and one genus of foraminifera were identified in transects from the continental slope submarine canyons and on the seamounts.

Statistical analysis of environmental drivers for habitat-forming corals and sponges were limited to families and genera that occurred across at least three separate ROV tracks (see Fig. 2

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for example). Results of the BEST analysis indicated there are significant relationships between genera- and family occurrences and environmental variables (Table 1). Substrate was a significant variable for unidentified bamboo coral and the cup coral Desmophyllum dianthus. Slope and substrate were significant explanatory variables for the families Isididae and the genus Farrea sp. Temperature and slope most strongly correlated to the family Caryophylliidae, Plexauridae and the genus Paramuricea sp. Temperature and dissolved oxygen correlated with the occurrence of the coral Solenosmilia sp. and the Porifera sp. 1, while temperature alone was correlated with the occurrence of the sponge Hertwigia sp. Depth was the only significant correlate of the genus Corallium. Dissolved oxygen most strongly correlated with the family Actinaria. Temperature and salinity were highly correlated with the family Euplectellidae.

Overall, high densities of coral genera and families were found to occur within a narrow environmental range along a significant environmental contributor (Fig. 3, see Table 1 for significant environmental variables). There was an unequal distribution of Isididae with substrates (X^2 (4) = 69.4, $p < 0.0001$), and slope explained 16% of the variation in densities (adj. $R^2 = 0.16$, $F(1,61) = 12.9$ $p < 0.001$). The majority of individuals in the family Isididae occurred on boulders and slopes less than 30°, while those of unidentified bamboo coral mainly occurred on boulders or rock outcrops. Temperature and slope explained 58% and 39%, respectively, of the variation in Paramuricea sp. densities (adj. $R^2 = 0.58$, $F(1,18) = 26.9$ $p < 0.001$, adj. $R^2 = 0.39$, $F(1,18) = 12.6$, $p = 0.002$, respectively). High densities were observed in areas with limited slope and at temperatures below 3.5°C. There was an unequal distribution of Caryophylliidae with substrate (X^2 (3) = 4364.4, $p < 0.0001$) with high densities primarily observed on bedrock. Temperature explained 15% of the variation in Caryophylliidae densities (adj. $R^2 = 0.15$, $F(1,114) = 20.5$, $p < 0.001$), with highest densities occurring above temperatures of 3.8°C. There was an unequal distribution of Desmophyllum dianthus densities among substrata (X^2 (3) = 4746.0, $p < 0.0001$), with densities almost exclusively observed on bedrock. Solenosmilia sp. occurred in a narrow temperature range (4.1-4.2°C), with temperature explaining 49% of their variation (adj. $R^2 = 0.49$, $F(1,32) = 33.0$, $p < 0.001$). Depth explained 25% of the variation in Corallium sp. (adj. $R^2 = 0.25$, $F(1,131) = 44.8$, $p < 0.001$), with densities more common at depths below 2200m. Correlations between significance levels of 0.01 and 0.5 between genera and families can be found in Appendix S3.

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Similar to corals, high densities of sponges were found to occur within narrow environmental ranges (Fig. 4). Greater densities of Euplectellidae were found at a narrow salinity range between 34.94 psu and 34.96 psu and at temperatures above 3.7°C. High densities of Hertwigia sp. were also observed at temperatures above 3.7°C, with temperature explaining 14% of the variation (adj. $R^2 = 0.14$, $F(1,48) = 8.71$, $p = .005$). Farrea sp. was almost exclusively observed on silt/bedrock substrate (SLTBRK, (X^2 (4) = 5612.0, $p < .0001$) and slopes above 20°, with 21% of density variance explained by slope (adj. $R^2 = 0.21$, $F(1,121) = 33.2$, $p < .001$). Dissolved oxygen concentrations and temperature explained 53% and 47% of the variation in Porifera sp. 1 densities, (adj. $R^2 = 0.53$, $F(1,38) = 44.9$, $p < .001$, adj. $R^2 = 0.47$, $F(1,38) = 35.7$, $p < .001$, respectively). High densities were mainly found between 5.6 and 5.7 ml/L dissolved oxygen concentrations and between 3.0°C and 3.2°C.

Geomorphic Setting

All but two coral families, Caryophylliidae (X^2 (3) = 2475.7, $p < .001$) and Acanthogorgiidae (X^2 (2) = 24.2, $p < .001$), preferred slope or ridge geoforms to valley geoforms (Fig. 5). Plexauridae, Paragorgiidae, and Coralliidae occurred more frequently on ridges (X^2 (3) = 66.0, $p < .001$, (X^2 (2) = 12.5, $p < .002$, (X^2 (1) = 106.6, $p < .001$), while Chrysogorgiidae, Anthothelidae, Actiniidae, and Pennatulacea had greater occurrence on slope geoforms (X^2 (2) = 150.6, $p < .0001$, X^2 (3) = 105.0, $p < .0001$, X^2 (3) = 10.0, $p < .019$, X^2 (3) = 47.3, $p < .0001$, respectively). There are striking coral family-specific disparities in the densities of individuals observed between continental slope and seamount geoforms. For instance, Schizopathidae had higher densities on seamount slopes but low densities on Continental Slope – Slope geoforms. Conversely, Actiniidae densities were high on Continental Slope – Slope geoforms and relatively low on Seamount Slope areas.

DISCUSSION

Overall, individuals of families and genera occurred over a broad range of environmental conditions. However, high densities were observed under much more restricted ranges of conditions. For example, the genus Paramuricea sp. occurred between water temperatures of 3.3°C and 4.3°C, yet the vast majority (72%) of individuals were observed between 3.4°C and 3.5°C. Using modeled distribution patterns, Howell et al. (2011) found individuals of Lophelia

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pertusa were distributed over broader environmental conditions than their reefs. Restricted high density ranges observed here suggest that only a narrow set of environmental conditions are favorable for population growth. It has long been known that species can physiologically persist in unfavorable environmental conditions (Potts 1975, Edwards 2000, Dijkstra, Westerman & Harris 2017), yet population growth is compromised in these sub-optimal conditions as individual metabolic processes will be directed towards survival rather than growth and reproduction (Bouchet & Taviani 1992). Previous studies on deep sea corals indicate that some species of corals may continually or periodically develop gametes (Waller, Tyler & Gage 2005, Waller & Tyler 2011), and that in the Northwest Atlantic broadcast spawning of gametes is triggered by primary production (Witte 1996). For broadcast spawning to bring about successful fertilization, Waller et al. (2005) suggest that sufficiently high local densities of individuals and gametes must be present for reproduction (i.e., planktonic larvae) to succeed. Since many of the taxa occurred either singly, in clumps, or in larger numbers along single ROV tracks, it may be that they are not contributing to the successful reproductive efforts of the species. As bathyal and abyssal environmental conditions (e.g., water temperature, oxygen concentrations) change with ongoing changes in climate and go beyond the relatively narrow thresholds that maintain higher densities of individuals, there may be a greater risk of local extinction due to the Allee effect in which individuals in smaller populations are unable to replace themselves.

Coral genera and family distribution and density varied substantially with geomorphic settings. Overall, corals were more abundant on seamount geoforms than Continental Slope geoforms. While high densities of coral families were mainly observed on slopes and seamount ridges, densities of the families Actiniidae, Pennatulacea, Caryophylliidae and Acanthogorgiidae were observed on the Continental Slope – Valley geoform. This family-specific association to geoforms may reflect the preference for oceanographic conditions or substrate surrounding these features. Previous studies have found that the strength of water flow surrounding seamounts is dependent on its topography with greater flow observed at the crest or base (Roden & Taft 1985, Genin, Dayton, Lonsdale, & Speiss 1986). These accelerated flow rates may favor large (highly branched or in height) suspension feeders as they bring greater concentrations of food particles and dissolved oxygen, variables that enhance their growth, reproduction and recruitment.

Depth, slope, bathymetric position indices, and other terrain derivatives are widely utilized as input variables in correlation analyses for benthic presence/absence studies and

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predictive marine habitat models. However, this study additionally used classified geomorphology units to examine statistical correlations between geoforms and the densities of deep sea corals. Differences in coral family density as a function of geomorphic setting suggests this approach can more effectively reveal coral affinities for specific types of seabed features, which provides additional relevant information for predictive spatial habitat modeling beyond simply depth and slope. Identification of the relationships between specific coral communities and geomorphic features also has immediate implications for effective conservation and management of vulnerable marine ecosystems. Continued systematic exploration of these deep sea habitats and evaluation of the variation of abundance with geomorphic settings will help discern relationships between geoforms and each coral family.

Sponges and corals were influenced by disparate environmental factors. Temperature, salinity, and dissolved oxygen influenced the occurrence of sponges while seafloor properties of slope and substrate, in combination with water column properties (e.g. Caryophylliidae), contributed to the occurrence of some genera and families of corals. Differences in the environmental contributions to taxonomic distributions may reflect their underlying biological and ecological traits. While both corals and sponges have sessile adult stages, their planktonic larvae may have varying development modes that dictate their level of dispersal (Gary, Fox, Biastoch, Roberts, & Cunningham 2020). For example, most sponges produce larvae that rely on yolk reserves which greatly limits their swimming ability and shortens their time in the plankton; these are life-history traits that facilitate local settlement (Maldonado 2006). Indeed, sponge larvae sampled above sponge beds revealed high larval retention (Mariani, Uriz, & Turon 2005, Mariani, Uriz, Turon, & Alcoverro 2006). These traits may be reflected in the spatial distribution of sponges observed in our study as densities of sponges often occurred in discrete sections of the ROV track. Previous studies indicate that many deep sea corals broadcast spawn and have planktotrophic larvae that can spend a few minutes to months in the plankton prior to settlement (Waller & Baco 2007, Waller & Tyler 2011, Watling et al. 2011, Larsson et al. 2014, Stromberg & Larsson 2017). Other studies reported that certain corals have large lecithotrophic larvae that spend 2-4 months in the plankton (Cordes, Arthur, Shea, Arvidson & Fisher 2001, Sun, Hamel, & Mercier 2010). Combined, these studies indicate the potential of coral for long distance dispersal. Differences in life-history traits between sponges and corals may therefore lead to contrasting sensitivities to climate induced changes in environmental conditions. In particular,

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sponges whose occurrences strongly correlate to ocean temperature or dissolved oxygen concentrations, as shown in this study, may be more susceptible to local extinctions due their limited dispersal potential while corals may be able to disperse to more favorable habitats. However, studies evaluating larval dispersal and mode of larval development in the deep sea are needed.

Continental slopes and seamounts are projected to experience significant warming, oxygen loss, and reductions in pH, with increasing temperatures projected to be more pronounced for the Northwestern Atlantic (Bindoff et al. 2019). These changes will undoubtedly affect the distribution of species in the deep sea as those species are evolutionarily adapted to relatively stable environmental conditions and thus are sensitive to environmental change (Portner & Farrell 2008). For example, a recent study that modeled suitable habitat for six species of corals under projected ocean warming scenarios found far less suitable habitat for the corals Lophelia pertusa, Paragorgia arborea, Acanella arbuscula, and Acanthogorgia armata (Morato et al. 2020). A laboratory study designed to culture Acanthogorgia armata and Acanella arbuscula, two species commonly observed in the Northwestern Atlantic (Watling et al. 2011), noted tissue contraction and loss of sclerites followed by polyp bailout with corresponding temperature increases of 1-2°C (Rakka et al. 2019). A previous study examining growth rates of encrusting Antarctic spirorbids on plates warmed by 1-2°C found increased growth of spirorbids (Ashton, Morley, Clarke, & Peck 2017), yet a further study revealed this increase in water temperature weakened the ability of the spirorbids to maintain cellular homeostasis (Clark et al. 2019). Additional studies relating hypoxic stress to physiology in young and old filter feeding clams found that older clams have greater levels of cell death and oxidative stress than younger clams, suggesting responses vary with ontogeny (Clarke et al. 2013). Levin et al. (2013) demonstrated that low oxygen levels lead to reductions in faunal body size which may reduce colonization potential as smaller sized animals will have fewer gametes or may require more time to attain reproductive maturity. Observed restrictive population densities of corals and sponges associated with narrow environmental conditions in this study, along with the above mechanistic and modeled studies, suggest that established individuals will likely experience sub-lethal and perhaps lethal stress under projected climate scenarios. This will be particularly true for individuals that currently exist at their upper or lower environmental tolerance range.

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The occurrence of foundation species in the deep-sea and their ability to withstand changes in local environmental conditions will depend on many factors such as temperature, food availability and life-cycle (Watling, Rowley, & Guinotte 1978, Morato et al. 2020). While habitat requirements for corals, and less so sponges, have received much attention in recent years (Quattrini et al. 2015, Auscavitch et al. 2020, Winship et al. 2020), predicting their occurrence remains a challenge as these communities are not always present even when conditions appear favorable (Georgian, Shedd, & Cordes 2014). High coral and sponge densities in local areas suggests these areas may be optimal for growth and reproduction. Small changes that exceed the stable ambient environmental conditions observed in the deep sea may create a sub-optimal local habitat that will lead to reduced survivorship and reproduction and ultimately limit population expansion. This is exemplified in a study that examined thermal sensitivities of invertebrates and found that populations exposed to temperature above their annual mean experience increased mortality and limited reproduction (Hughes et al. 2019). More biological (e.g., densities) and oceanographic (e.g., current velocities) variables are needed to improve our knowledge and predictions of the linkages between environmental drivers and spatial distribution of habitat-forming species. This is particularly true from a conservation or marine management perspective as it will enhance the capacity to not only predict the distribution of dense areas of corals and sponges, but also expand knowledge of their vulnerability to environmental change.

Many ecosystems often have multiple habitat-forming species that co-occur or are adjacent to one another. In the event that a species experiences mortality, there is often other species that will take over that space. For example, individuals in coastal tropical coral reefs are often adjacent to one another. In the event that an individual dies, neighboring corals can overgrow the dead individual or in more severe cases, macroalgae will take over the space (e.g., Chornesky 1989, Ferrari, Gonzalez-Rivero, Mumby 2012). In kelp forests, there are often neighboring species that can occupy the space or an understory composed of other macroalgae species that continue to be present when kelp senesce (e.g., Wernberg et al. 2016, Dijkstra et al. 2019). Compared to these benthic ecosystems, occurrence of individuals in the canyons and seamounts studied here are patchy, little to no understory with much of the substrate that is suitable for colonization unoccupied. Consequently, as deep-sea habitat-forming individuals experience climate induced stress and individuals that are currently observed in suboptimal conditions experience mortality, the communities observed in deep-sea canyons and seamounts

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become patchier and overall less biodiverse. Reduced biodiversity can have negative consequences for the function and sustainability of these ecosystems. Since high levels of biodiversity (i.e., abundance and species richness) enhance resistance to disturbance, reduced biodiversity will result, in the long-term, in a less resilient foundational system. Such losses of foundation species will likely propagate throughout the food web to species that directly feed on coral and sponges (e.g., hippasterid asteroids, pycnogonids), use them as leverage to obtain particles in the water column (e.g., crinoids), or utilize them for refuge (e.g., pycnogonids). Knowledge of environmental variables that contribute not only to the occurrence of a single individual, but multiple individuals as has occurred in this study, will enhance predictions of the occurrence of deep sea coral and sponge communities and help to forecast their response under changing ocean conditions.

Data accessibility: Raw data used in this study from NOAA expeditions (EX1304L1: Northeast U.S. Canyons Exploration; EX1404L2: Our Deepwater Backyard: Exploring the Atlantic Canyons and Seamounts and EX1404L3: Northeast Seamounts and Canyons) are publicly available and can be accessed via the OER Digital Atlas (https://www.ncei.noaa.gov/maps/oer-digital-atlas/mapsOE.htm, last accessed December 2020). To search, preview, and download the dive video for Okeanos Explorer, go to the OER Video Portal (https://www.nodc.noaa.gov/oer/video/). Data generated for this study can be found in the OBIS database at https://doi.org/10.15468/3u8vf7.

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Table 1: Rank Spearman correlations between the top ranking environmental variable to coral and sponge genera and families. Numbers in bold represent significant correlations.

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Taxa	Factor	R	P value
Cnidaria			
Isididae	**Slope and Substrate**	**0.34**	**0.001**
Acanella		0.27	0.083
Keratoisis			
Unidentified bamboo coral	**Substrate**	**0.26**	**0.006**
Lepidisis			
"Tanyostea"		0.41	0.12
Schizopathidae		0.07	0.587
Bathypathes		0.45	0.38
Stauropathes		0.23	0.5
Parantipathes			
Telopathes			
Plexauridae	**Slope and Temperature**	**0.50**	**0.001**
Paramuricea	**Slope and Temperature**	**0.61**	**0.002**
Swiftia			
Primnoidea		0.49	0.05
Candidella		0.59	0.74
Calyptotrophora			
Thouarella			
Caryophylliidae	**Substrate and Temperature**	**0.27**	**0.001**
Solenosmilia	**Temperature and Dissolved Oxgen**	**0.47**	**0.001**
Desmophyllum	**Substrate**	**0.32**	**0.001**
Pennatulacea		0.11	0.225
Chrysogorgiidae		0.09	0.231
Iridogorgia			
Metallogorgia		0.04	0.467
Radicipes			
Chrysogorgia		0.19	0.291
Paragorgiidae			
Paragorgia		0.20	0.004
Acanthogorgiidae			
Acanthogorgia		0.19	0.41
Alcyoniidae			
Anthomastus		-0.02	0.94
Anthothelidae			
Anthothela			
Clavulariidae			
Clavularia		0.46	0.478
Coralliidae			
Corallium	**Depth**	**0.32**	**0.001**
Actiniidae			
Anemone	**Dissolved Oxygen**	**0.32**	**0.001**
Porifera			
Euplectellidae	**Temperature and Salinity**	**0.18**	**0.007**
Euplectella		-0.08	0.929
Hertwigia	**Temperature**	**0.22**	**0.005**
Farreidae			
Farrea	**Slope and Substrate**	**0.25**	**0.001**
Grapefruit Sponge	**Temperature and Dissolved Oxgen**	**0.72**	**0.001**
Foraminifera			
Xenophyophore		0.14	0.026

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Figure 1: Locations of Northwestern Atlantic canyons and seamounts used in this study.

Figure 2: Example of 4 genera whose individuals occurred across at least 3 or more ROV dive tracks. Colored legend represents depth with each color in the figures (whole and inserted

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figures) correspond to depths in the legend. The larger inserted images show the bathymetry, ROV track in white with black dots along the track indicating location of an individual taxa. Black lines are contour lines of 50 m, and the range of depth for each site is given in the inserted location plots. The sub-image shows the ROV track (in red) relative to the local topography.

Figure 3: Frequency histograms of coral densities plotted against statistically significant explanatory environmental relationships determined in BEST (Table 1). There were genus and family specific predictors of environmental variables. While individuals occurred over a range of environmental conditions, greatest densities occurred over narrow ranges.

Figure 4: Frequency histograms of sponges along statistically significant explanatory environmental relationships determined in BEST (Table 1). Similar to corals, there were genus and family specific environmental predictors. Individuals of genera and families were observed over a range of environmental variables, but high densities were observed in narrow environmental ranges.

Fig. 5: Frequency histograms of corals as a function of geomorphic setting. Family specific associations to geomorphic settings were found. Geoform abbreviations: Continental Slope - Slope (CSS), Continental Slope - Valley (CSV), Seamount Ridge (SR), Seamount Slope (SS).

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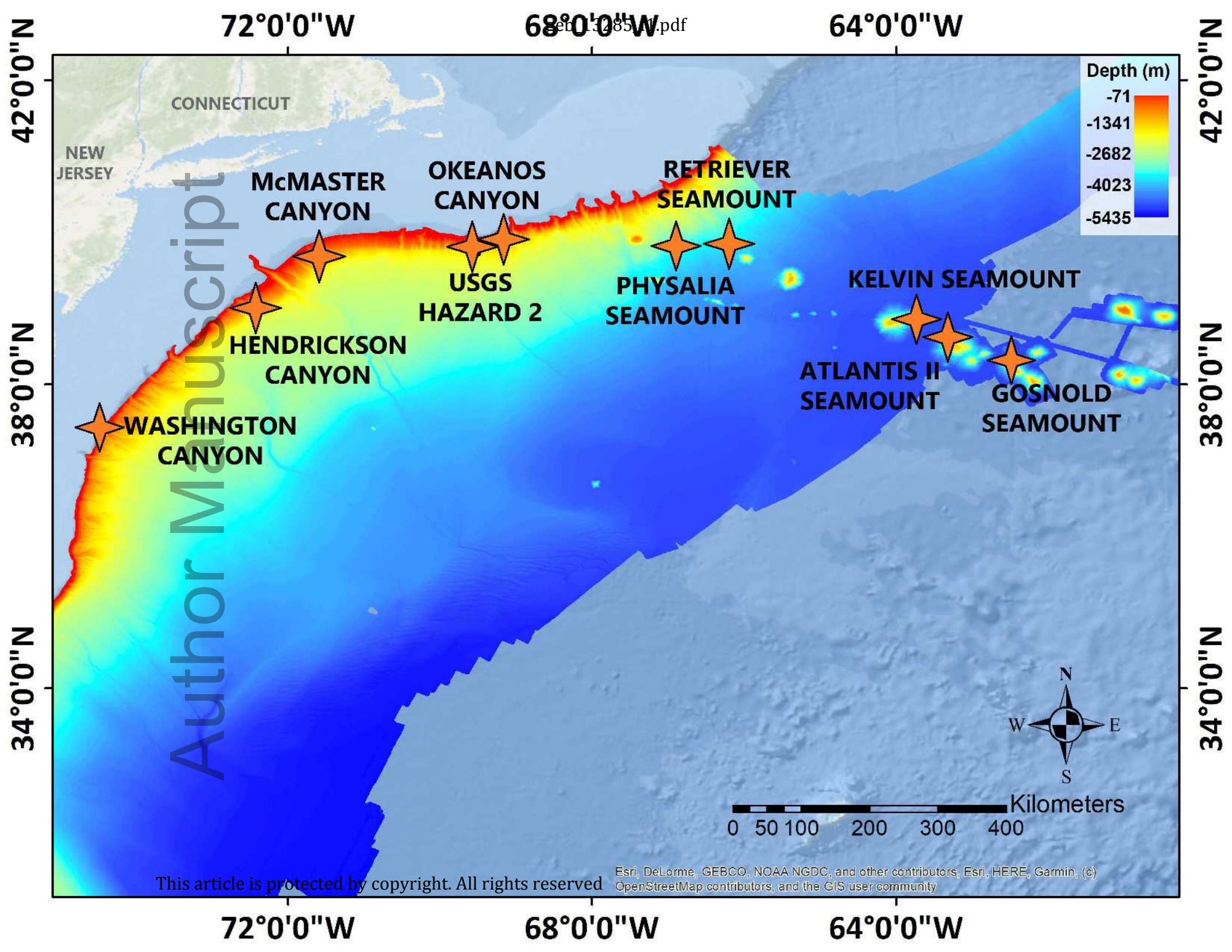

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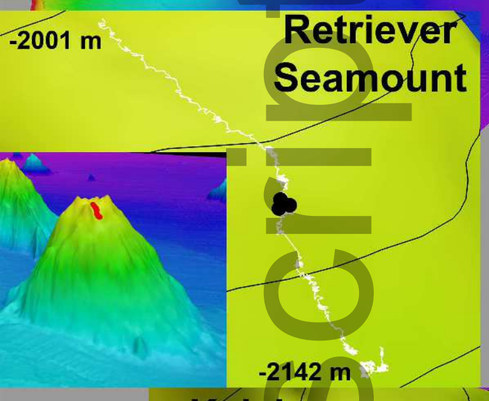
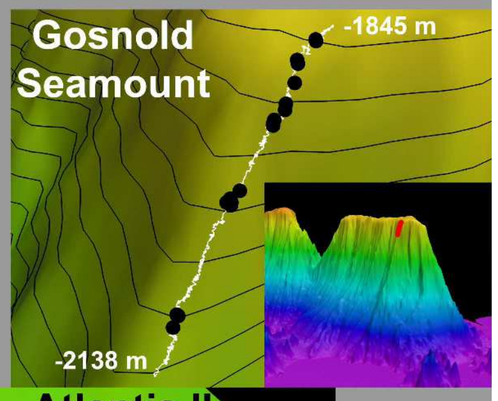
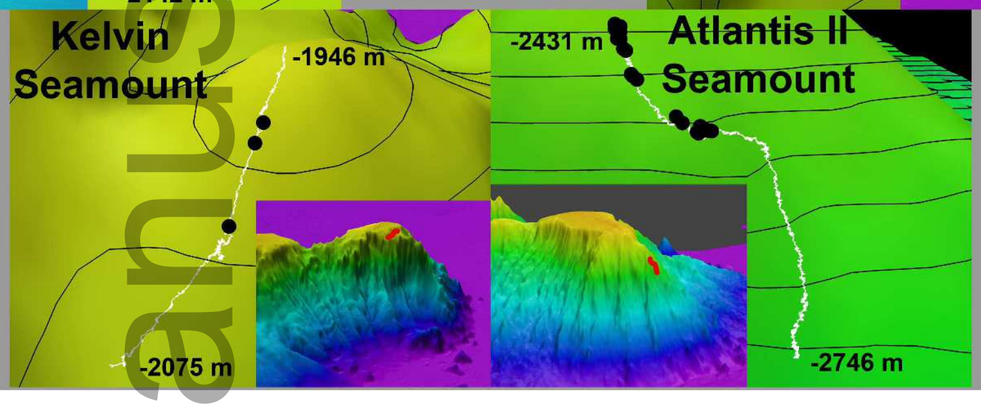
Porifera sp. 1

-750
-3000
-5250

Retriever Seamount
Kelvin Seamount
Gosnold Seamount
Atlantis II Seamount



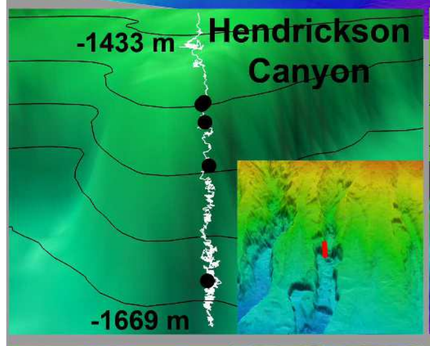


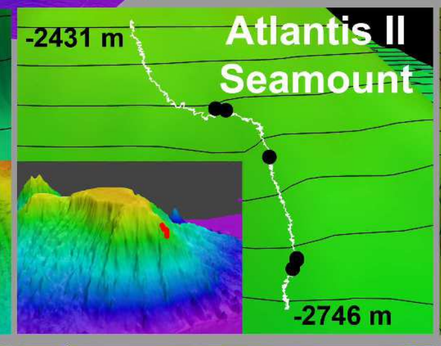


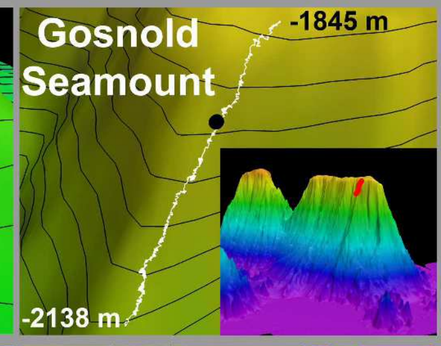
Unidentified bamboo coral

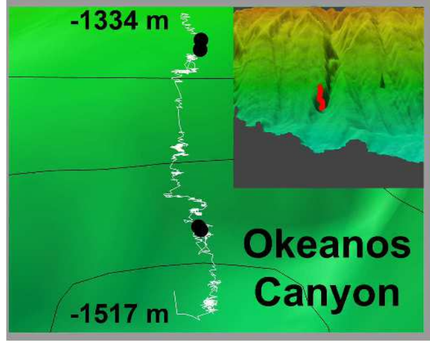
-750
-3000
-5250

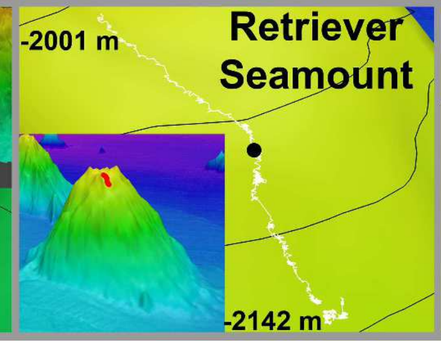
Retriever Seamount
Okeanos Canyon
Hendrickson Canyon
Kelvin Seamount
Gosnold Seamount
Atlantis II Seamount

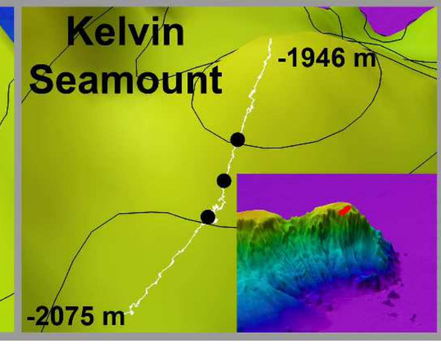








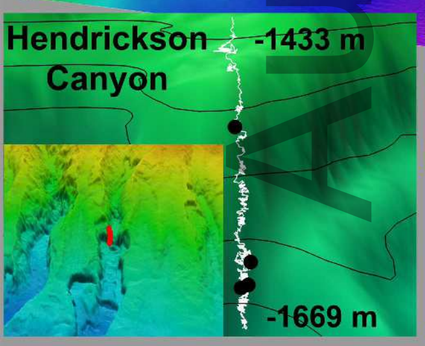


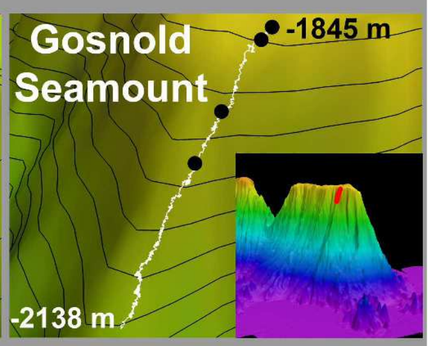


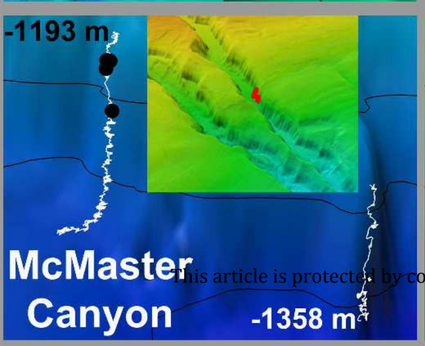
Paramuricea sp.

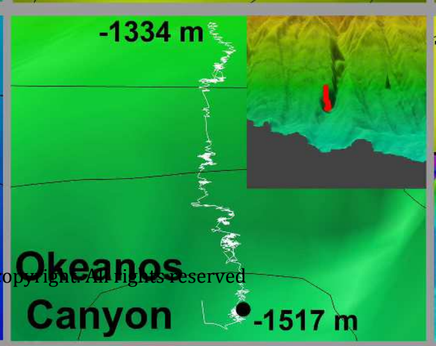
-750
-3000
-5250

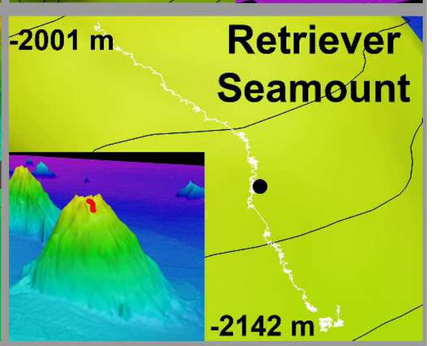
McMaster Canyon
Okeanos Canyon
Retriever Seamount
Kelvin Seamount
Hendrickson Canyon
Gosnold Seamount



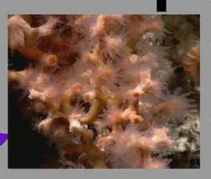






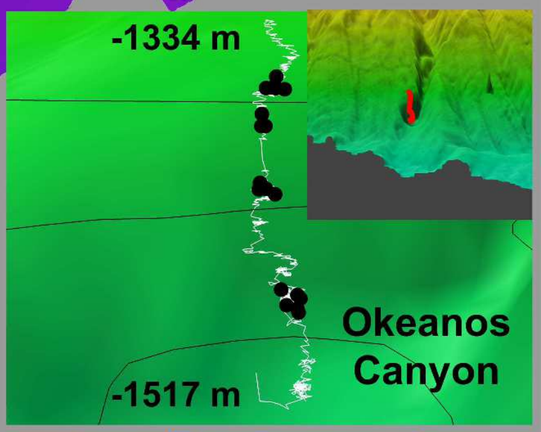


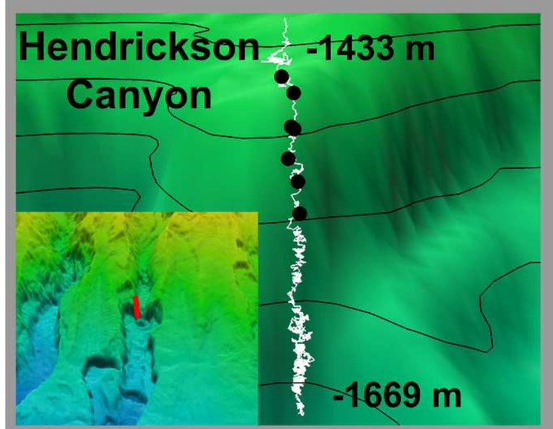
Solenosmilia sp.

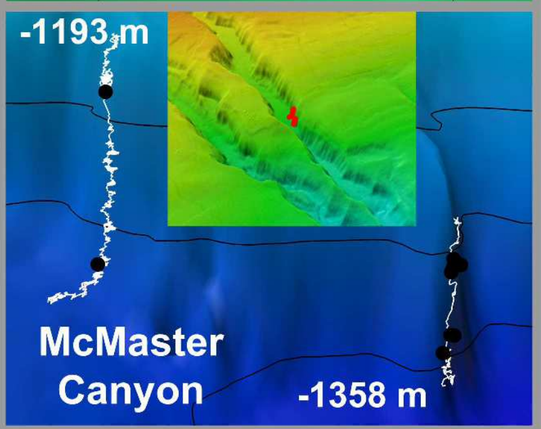


-750
-3000
-5250

McMaster Canyon
Okeanos Canyon
Hendrickson Canyon







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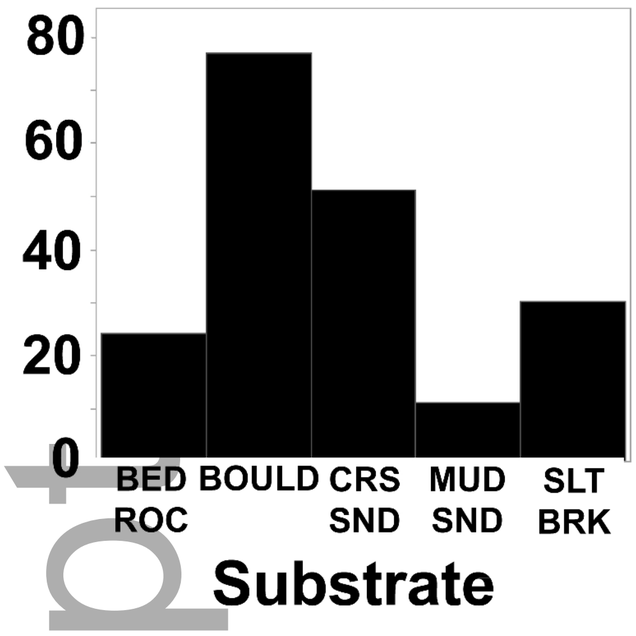
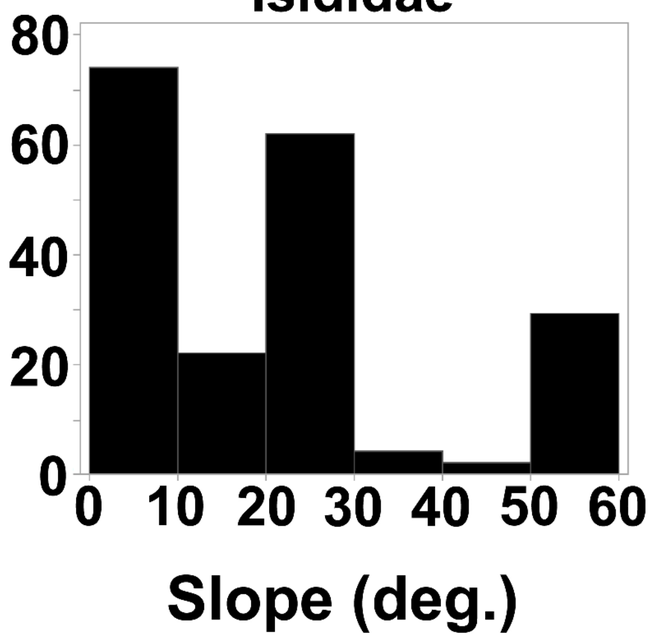
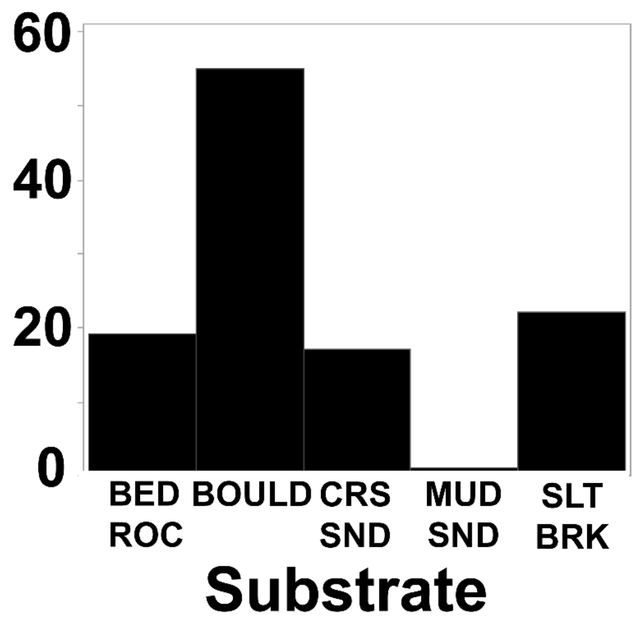
Isididae



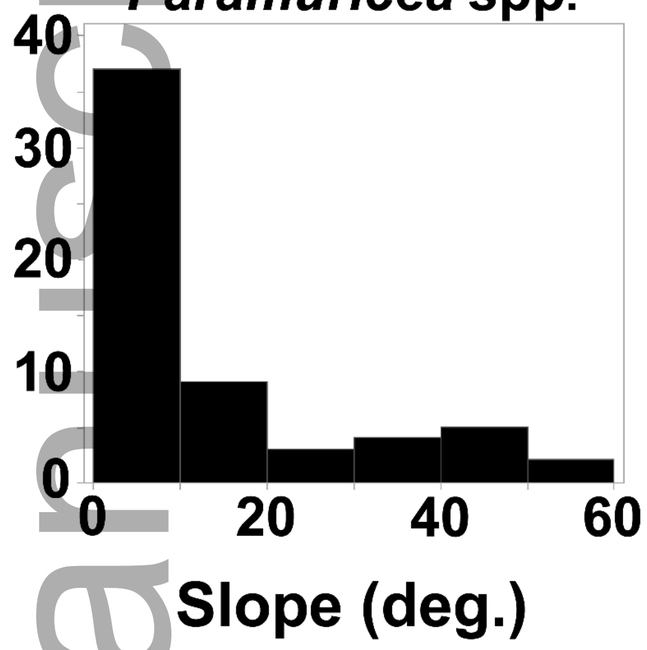
Isididae



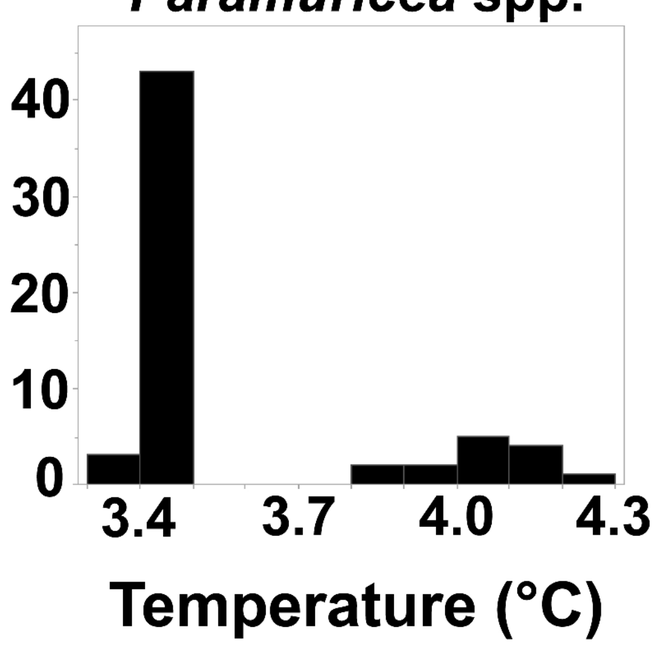
Unidentified Bamboo



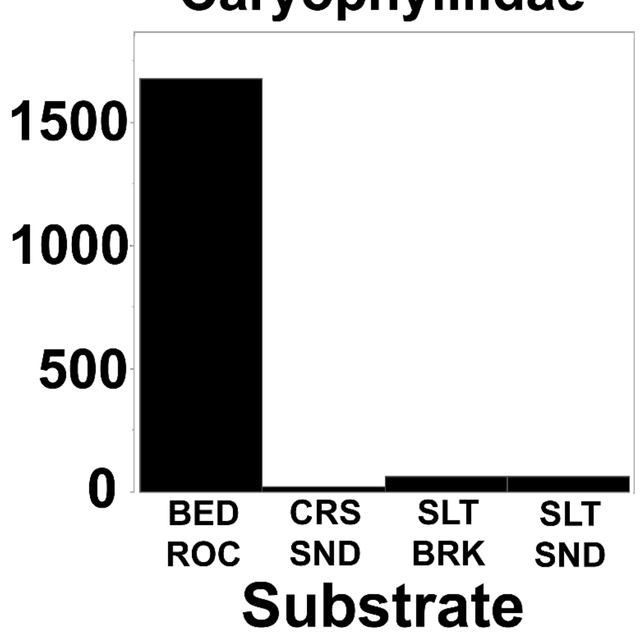
Paramuricea spp.



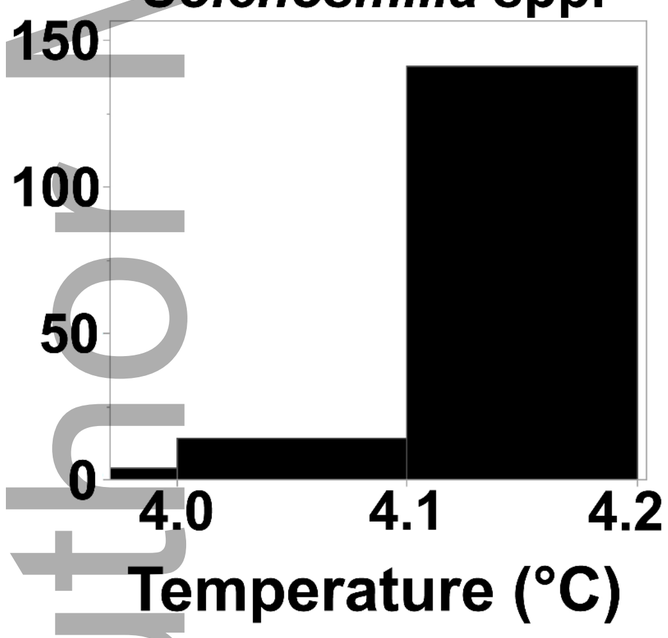
Paramuricea spp.



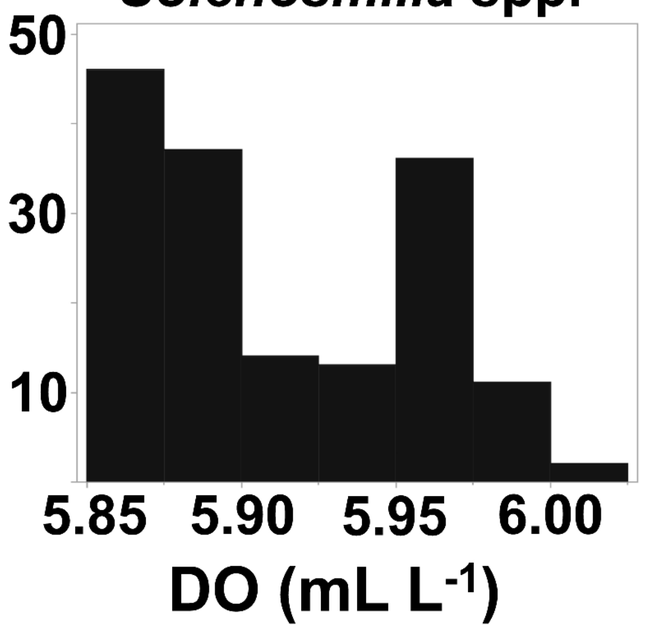
Caryophylliidae



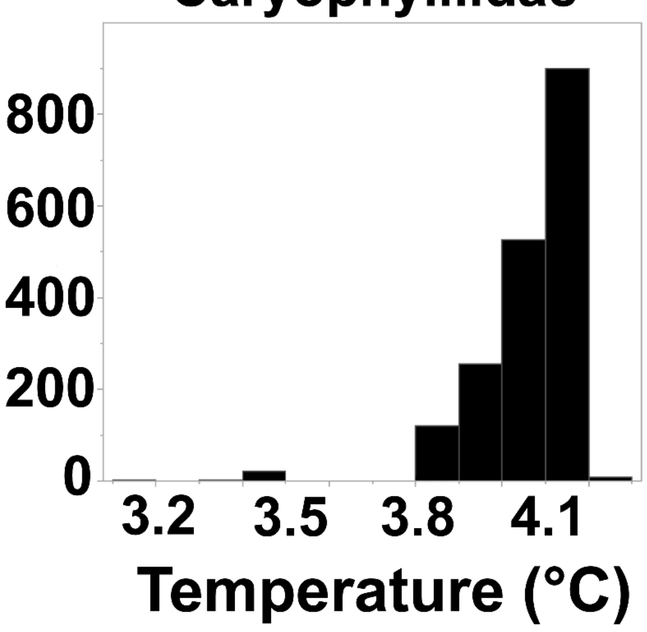
Solenosmilia spp.



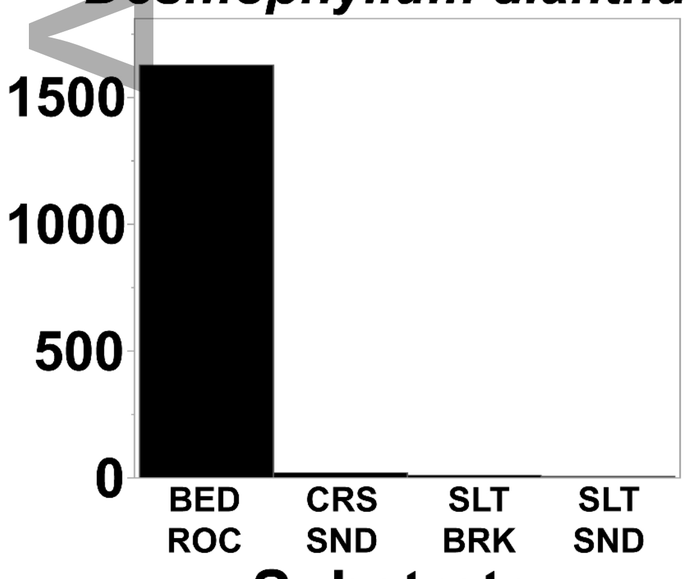
Solenosmilia spp.



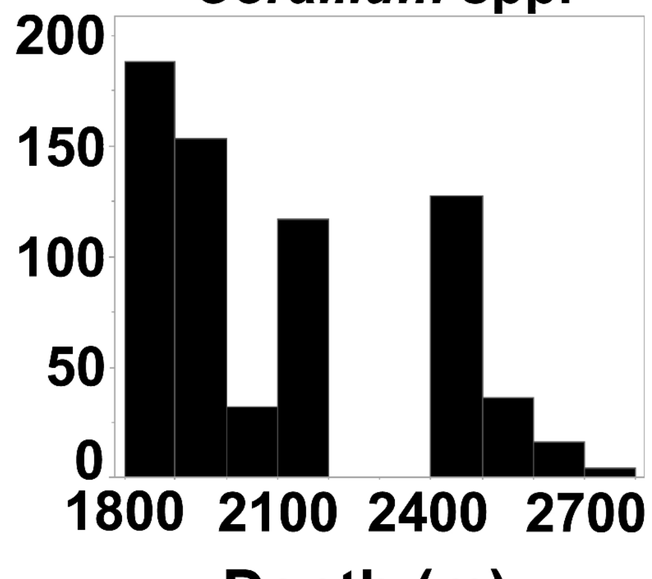
Caryophylliidae



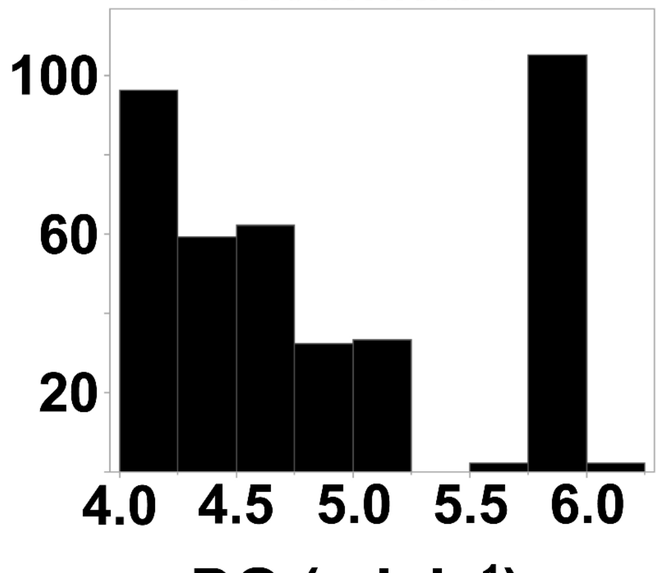
Desmophyllum dianthus



Corallium spp.



Actiniidae



Number of Individuals

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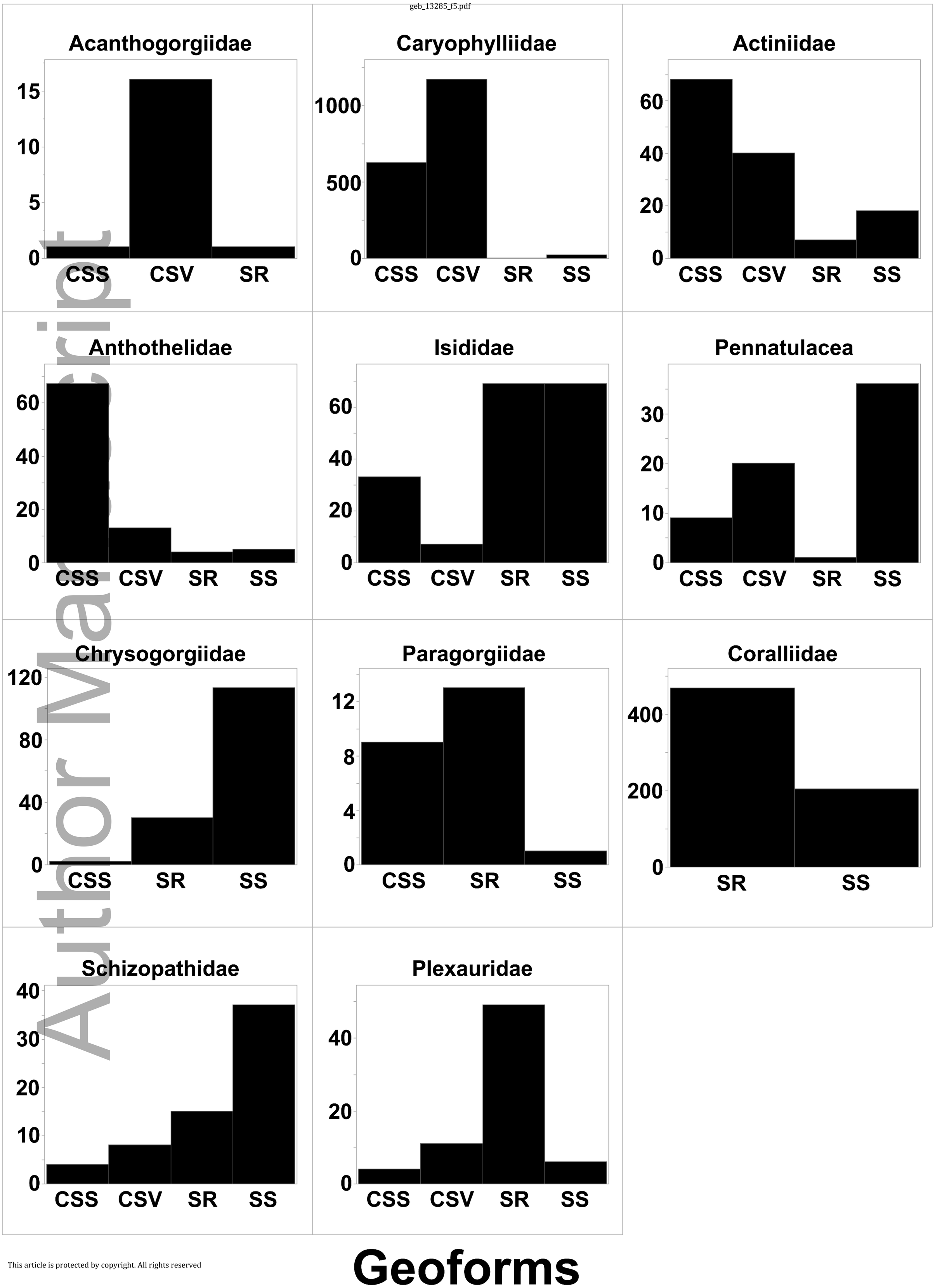

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