

**Distributions and habitat associations of deep-water corals in Norfolk and Baltimore Canyons, Mid-Atlantic Bight, USA**

Brooke, S.D.; Watts, M.W.; Heil, A.D.; Rhode, M.; Mienis, F.; Duineveld, G.C.A.; Davies, Andrew; Ross, S.W.

**Deep Sea Research Part II: Topical Studies in Oceanography**

DOI:

[10.1016/j.dsr2.2016.05.008](https://doi.org/10.1016/j.dsr2.2016.05.008)

Published: 01/03/2017

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*

Brooke, S. D., Watts, M. W., Heil, A. D., Rhode, M., Mienis, F., Duineveld, G. C. A., Davies, A., & Ross, S. W. (2017). Distributions and habitat associations of deep-water corals in Norfolk and Baltimore Canyons, Mid-Atlantic Bight, USA. *Deep Sea Research Part II: Topical Studies in Oceanography*, 137, 131-147. <https://doi.org/10.1016/j.dsr2.2016.05.008>

**Hawliau Cyffredinol / General rights**

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

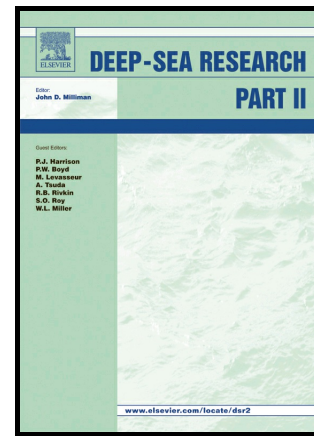
**Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

# Author's Accepted Manuscript

Distributions and habitat associations of deep-water corals in Norfolk and Baltimore canyons, Mid-Atlantic Bight, USA

S.D. Brooke, M.W. Watts, A.D. Heil, M. Rhode, F. Mienis, G.C.A. Duineveld, A.J. Davies, S.W. Ross



www.elsevier.com/locate/dsr2

PII: S0967-0645(16)30122-9  
DOI: <http://dx.doi.org/10.1016/j.dsr2.2016.05.008>  
Reference: DSRII4055

To appear in: *Deep-Sea Research Part II*

Received date: 5 February 2016  
Revised date: 9 May 2016  
Accepted date: 10 May 2016

Cite this article as: S.D. Brooke, M.W. Watts, A.D. Heil, M. Rhode, F. Mienis, G.C.A. Duineveld, A.J. Davies and S.W. Ross, Distributions and habitat associations of deep-water corals in Norfolk and Baltimore canyons, Mid Atlantic Bight, USA, *Deep-Sea Research Part II* <http://dx.doi.org/10.1016/j.dsr2.2016.05.008>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and a review of the resulting galley proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain

**Distributions and habitat associations of deep-water corals in Norfolk and Baltimore canyons, Mid-Atlantic Bight, USA**

Brooke SD<sup>a\*</sup>, Watts MW<sup>b</sup>, Heil AD<sup>a</sup>, Rhode M<sup>c</sup>, Mienis F<sup>d</sup>, Duineveld GCA<sup>d</sup>, Davies AJ<sup>e</sup>, Ross SW<sup>c</sup>

<sup>a</sup> Florida State University Coastal and Marine Lab, St Teresa, FL, USA.

<sup>b</sup> Oregon Institute of Marine Biology, Charleston, OR, USA.

<sup>c</sup> University of North Carolina-Wilmington, Wilmington, USA.

<sup>d</sup> NIOZ, Royal Netherlands Institute for Sea Research, Den Burg, The Netherlands

<sup>e</sup> Bangor University, School of Ocean Sciences, Bangor, UK

\* **Correspondence:** sbrooke@fsu.edu

**Abstract**

A multi-disciplinary study of two major submarine canyons, Baltimore Canyon and Norfolk Canyon, off the US mid-Atlantic coast focused on the ecology and biology of canyon habitats, particularly those supporting deep-sea corals. Historical data on deep-sea corals from these canyons were sparse with less than 750 records for the mid-Atlantic region, with most being soft sediment species. This study substantially increased the number of deep-sea coral records for the target canyons and the region. Large gorgonians were the dominant structure-forming coral taxa on exposed hard substrates, but several species of scleractinians were also documented, including first observations of *Lophelia pertusa* in the mid-Atlantic Bight region. Coral distribution varied

within and between the two canyons, with greater abundance of the octocoral *P. arborea* in Baltimore Canyon, and higher occurrence of stony corals in Norfolk Canyon; these observations reflect the differences in environmental conditions, particularly turbidity, between the canyons. Some species have a wide distribution (e.g., *Paragorgia arborea*, *Primnoa resediformis*, *Anthothela grandiflora*), while others are limited to certain habitat types and/or depth zones (e.g., *Paramuricea placomus*, *L. pertusa*, *Solenosmilia variabilis*). The distribution of a species is driven by a combination of factors, which include availability of appropriate physical structure and environmental conditions. Although the diversity of the structure-forming corals (gorgonians, branching scleractinians and large anemones) was low, many areas of both canyons supported high coral abundance and a diverse coral-associated community. The canyons provide suitable habitat for the development of deep-sea coral communities that is not readily available elsewhere on the sedimented shelf and slope of the Mid-Atlantic Bight.

Keywords: Deep-sea corals, canyons, Mid-Atlantic Bight, stony corals, gorgonians, environmental conditions

## 1. Introduction

Submarine canyons are widespread features that (Harris and Whiteway, 2011) connect continental shelves to deep ocean basins via transport of sediments and nutrients (Bennett et al., 1985) and channel deep ocean water onto the shelf via upwelling. There is also evidence that canyon topography can concentrate migrating zooplankton, providing a rich food source for higher trophic levels (Green et al., 1988). With a few exceptions (Hudson and Haedrich 1984; King et al., 2008), canyon communities differ in species composition from those in similar depths outside canyons, and many canyons are biomass hotspots (de Leo et al., 2010). Megafauna are often more abundant in canyons at all depths than on the adjacent slopes (Griggs et al., 1969; Rowe 1972; Vetter and Dayton 1998; Carne 2005; de Leo et al., 2010). This phenomenon may be driven by entrainment of terrestrial and marine sediments, and organic material into canyons (Heezen et al., 1955; Keller and Shepard 1978), enhancing food availability in a normally food-poor area. Canyons represent areas of high diversity and biomass (including commercial fisheries) in the deep sea (Stefanescu et al., 1994; Gartner et al., 2008; de Leo et al., 2010), likely due to high levels of environmental heterogeneity, e.g., in physical structure, hydrography, and geological structure, which creates spatial and temporal heterogeneity in sedimentation rates, substrates, food and environmental factors (Vetter and Dayton 1999; Allen et al., 2001; Kuhnze et al., 2002; Buhl-Mortensen et al., 2010). This complex interplay of factors contributes to the observed patchiness in faunal assemblages (McClain and Barry 2010). Exposed hard substrates are common in canyons and are generally found where currents are strong around outcrops or relict shorelines along canyon walls, and sometimes along the canyon thalweg, around boulders deposited by turbidity flows (Stanley and Fenner 1973; Hecker et al., 1980; Malahoff et al., 1982). Hard substrates often support dense

communities of sessile suspension and filter feeders, such as cnidarians and sponges, which provide habitat for diverse and abundant faunal assemblages. Submarine canyons may also provide refuge for demersal fish species (Ross et al., 2015), as bottom-tending fishing gear is not easily operated on the rugged topography common in submarine canyons (Huvenne et al., 2011). Their large size, complex topography and fast currents make canyons some of the most challenging of deep-sea environments to explore. Underwater vehicles are the most effective tools for surveying and sampling canyon habitats and communities, and their use in recent years has greatly increased our understanding of canyon ecology and processes.

The Mid-Atlantic Bight (MAB) region of the U.S. Atlantic margin extends from Cape Hatteras to Cape Cod and contains between 30 and 40 submarine canyons; at least 13 of these are considered major canyons (Andrews et al., 2013). The canyons vary in size, shape, and topographic complexity; some are the product of ancient riverine systems (e.g., Wilmington, Hudson), but most formed via other erosional processes, such as slides, debris flows, and turbidity currents (Uchupi 1968; Malahoff et al., 1980; Tucholke 1987; Obelcz et al 2014).

Early work in the MAB canyons carried out via submersibles and towed cameras included anthropogenic impact studies (Cooper et al 1992; Able 2002), fisheries surveys (Grimes et al., 1987) and studies of benthic epifauna (Hecker et al., 1980, 1983), and revealed a wide range of habitat types including soft sediments, cobbles, rocky outcroppings and extensive excavations by fish and invertebrates (Grimes et al., 1987; Tucholke 1987). Visual surveys revealed deep-sea coral communities, dominated by octocorals, solitary scleractinians, and anemones (Cairns 1981; Watling and Auster 2005; Packer et al., 2007) rather than the reef-forming stony corals (*Lophelia pertusa*, *Enallopsammia profunda*) that are the foundation of deep-sea coral communities in the southeastern U.S. and Gulf of Mexico (Brooke and Schroeder 2007; Ross and Nizinski 2007). A

comprehensive compilation of deep-sea octocoral (Alcyonaria) observations in the northeastern US (Cape Hatteras to the Canadian border) fall into two distinct time periods: 1874-1920 and 1950-2001 and contains 761 records (Watling et al., 2003). . The earlier records were primarily incidental catches in dredge hauls taken by US vessels as part of mapping and geological studies (summarized by Deichmann, 1936). The later time period included visual surveys for fisheries, energy industry surveys and ocean dumping projects (Hecker et al., 1980 1983; Malahoff et al., 1982; Grimes et al., 1987; Cooper et al., 1992; Able 2002). This database includes 10 families and 25 species (Watling and Auster, 2005), all of which, with the exception of the *Acanella* sp., were hard-substrate taxa. The NOAA Deep Sea Coral Research and Technology Program (DSCRTP) deep-sea coral data portal lists 166 records of gorgonians, 98 soft corals and 455 sea pens for the MAB alone. For Scleractinia, the data portal has 334 records for the MAB, of which ~200 are taxa such as *Flabellum* and *Dasmosmilia* that live in unconsolidated sediments. In soft sediments of the western Atlantic slope, additional sessile cnidarians include pennatulids and burrowing cerianthid anemones, all of which are also found in sandy sediments within the canyons (Shepard et al., 1986; Packer et al., 2007).

The use of submersibles, ROVs, AUVs and towed cameras has facilitated exploration of topographically complex features such as canyons, and several U. S. federal agencies (NOAA, BOEM, USGS) have recently supported geological and biological surveys of the MAB and New England canyons (Quattrini et al., 2015; Obelcz et al., 2014; Skarke et al., 2014; Pierdomenico et al., 2012). These studies resulted in range extensions for octocoral and fish species (Quattrini et al., 2015) and new observations of *L. pertusa* for the MAB region (Brooke and Ross 2014). Although the importance of deep-sea corals to other macrofauna has not been fully established (Auster 2005; Purser et al., 2013; Ross et al., 2015), deep-sea corals nevertheless contribute

substantial structure and complexity to MAB canyon benthic habitats (Hecker et al., 1980; Brooke and Ross 2014; Ross et al., 2015).

Data reported in this manuscript were generated by a large multi-disciplinary study of two MAB canyons: Baltimore Canyon and Norfolk Canyon. One of the objectives was to explore and characterize the little known hard-substrate habitats and their associated communities within these canyons, and relate the distribution of structure-forming corals with geological and environmental variables to identify potential drivers of species distributions and community structure both within and between canyons.

## **2. Materials and methods**

### **2.1 Study area**

This study concentrated on Baltimore and Norfolk canyons and the immediate surrounding slope areas (Fig. 1). These large, shelf-incised canyons have rugged terrain mostly on the north and south walls and near the canyon heads, including a series of terraces that stepped down many of the canyon walls (Obelcz et al., 2014). Hard substrates mostly consisted of ridges and walls of consolidated mud, rocks, and talus fields (Tucholke 1987; authors pers. obs.). The MAB slope is impinged by several different water masses at different depths that provide diagnostic signatures in temperature and salinity; those pertinent to this study are the North Atlantic Central Water (< 500 m depth, 7-20°C, 35-36 salinity) and the Western Atlantic Subarctic Intermediate Water (500-1500 m depth, 3-9°C, 33-35 salinity) (Csanady and Hamilton 1988; Csanady et al., 1988). The cyclonic Slope Sea Gyre dominates larger scale surface water movement in the MAB (Brooks 1996), with periodic meanders of the Gulf Stream that cause upwelling and shoreward



movement of nutrient-rich waters (Fitzgerald and Chamberlin 1981). However, tidal currents and internal waves are the major forcing functions for upwelling and down-welling flows along canyon axes (Keller and Shepard 1978; Allen and Durrieux de Madron 2009). Turbidity within canyons is higher than on the adjacent slopes and an upper slope nepheloid layer occurs in both canyons, but particularly Baltimore Canyon (Gardner 1989, authors' unpubl. data).

Prior to the current study, images of deep-sea corals taken within Baltimore and Norfolk canyons came primarily from studies by Hecker and colleagues (Hecker et al., 1980, 1983). They documented abundant gorgonians (*P. arborea*, *P. resedaeformis*, *A. armata*), soft corals and dense assemblages of anemones, particularly on the northern and western walls of Baltimore Canyon and the north and south walls of Norfolk Canyon at depths of ~160-600m. Analysis of these and other historical visual materials, in combination with multibeam maps of the canyons (generated during the current study), were used to guide ROV dives.

## 2.2 Field methods

The 2012 research cruise (17 Aug - 14 Sept) used the NOAA Ship *Nancy Foster* and the ROV *Kraken II* (Univ. of Connecticut), a Max Rover science-configured ROV with an operating depth of 1000 m. The ROV was equipped with a Kongsberg OE14-502 high definition (HD) video camera mounted on a pan and tilt and with parallel lasers (10 cm apart) for scaling, Kongsberg OE13-408 digital still camera (10 MP), five-function manipulator arm and a hydraulic collection platform with a suite of collecting containers. The vehicle also had a rotating carousel of 8 buckets connected to a suction sampler for collecting small mobile or delicate samples. The ROVs position was continuously tracked using an ORE Trackpoint II Ultrashort Baseline

system; position data was relayed through a Winfrog integrated navigation system that provided near real-time view of the ROV location as well as logging the data for post-dive analysis.

The 2013 research cruise (2-18 May 2013) used the NOAA Ship *Ronald H. Brown* and the ROV *Jason II* (Woods Hole Oceanographic Inst.), which can operate to 6500 m. The science camera on the ROV was an Insite Pacific Mini-Zeus HD video camera with parallel lasers (10 cm apart) for scaling. There were two digital still cameras: a Nikon CoolPix (3 MP) and an Insite Pacific Super Scorpio (3.34 MP). Two seven-function hydraulic manipulator arms were used to collect samples. A retractable sled on the front of the ROV was equipped with sampling devices, as well as a carousel of 6 buckets with a suction sampler. The ROV navigation system was a Sonardyne Ranger Ultra Short Baseline (USBL) and integrated navigation system, allowing a near real-time view of the ROV position.

Color-shaded bathymetric GeoTiff maps (products of the 2011 *Nancy Foster* multibeam mapping cruise) of each dive site were uploaded into the ROV navigation systems and provided background maps for the ROV tracks. This approach greatly increased the efficiency of ROV dives as the pilots and scientists could continuously visualize the ROV position relative to the site topography. The ROVs conducted standardized video transects of variable distances across multiple habitat types while moving at slow speeds (< 0.5 kts). During transects, the color video cameras with scaling lasers were set on wide angle and positioned to record in front of the ROV. Digital still images were taken frequently to augment the digital video and to assist in species identifications. Specimens were collected using the manipulator arm, which transferred samples to a variety of containers attached to the ROV sampling platform. Every sample was documented with video, and collection data were recorded. Data for physical variables were collected around the habitats of interest using a Seabird SBE 19+ data logger attached to the ROVs, which

recorded conductivity ( $\mu\text{S}/\text{cm}$ ), temperature ( $^{\circ}\text{C}$ ), depth (m), density ( $\sigma_{\theta}$ ,  $\text{kg m}^{-3}$ ), dissolved oxygen (DO, ml/L), pH and turbidity (formazin turbidity units) at a frequency of once per second during each dive. Two Niskin bottles were mounted on the ROVs to make near-bottom water collections that were subsequently analyzed for carbonate chemistry. ROV position (ultra-short baseline tracking) data were time-synchronized with all imagery, collections and environmental data.

A small (5 m) otter trawl was used to make off-canyon collections of benthic fauna. The net was deployed at depths between 150-1700 m for 30-minute intervals over soft sediment habitats on the slopes adjacent to the target canyons. Both vessels had a CTD carousel with an array of 12 Niskin bottles (5 L on the *Nancy Foster*; 10 L on the *Ronald H. Brown*). Water samples were collected (during the upcast) from near surface, mid-water and near bottom over a depth range of 97-1032 m in Baltimore Canyon and 100-1387 m in Norfolk canyons. These samples were used for analysis of carbonate chemistry.

### 2.3 Habitat and community analysis

The ROV navigation files (including latitude, longitude and depth) and the dive videos were synchronized via their time codes so that position and depth data could be assigned to observations on the video. Video from the ROV dives was only analyzed when the vehicle was in transect configuration (Section 2.2) with lasers on and with adequate visibility to enable habitat and faunal descriptions. All poor quality video and sections where the ROV was stationary (usually for sampling) were removed. The remainder of the video was categorized into one of six geological habitat types, which encompassed the dominant combinations of soft and hard substrates found in the canyons (Table 1; Fig. 2). In addition to these structural

categories, the video data were further classified according to percentage cover (<25%, 25-75%, >75%) and type of structure-forming cnidarians (SFC) (Table 1). The habitat analysis generated georeferenced habitat types and percent cover of SFC, which were used to create maps of dive tracks with habitat and SFC superimposed on bathymetry collected with multibeam sonar during previous cruises.

To generate high-resolution information with uniform-sized replicates, video of each habitat category was split into one-minute intervals; segments of habitat type that were less than one minute were discarded. For each time interval, all corals and large anemones were counted. Coral distributions were analyzed using multivariate statistics (Primer-E V6 software; Clarke and Gorley 2006) to identify any significant differences among factors (canyon, ROV dive, and habitat type). Prior to analysis, a fourth root transform was applied to the frequency count data to reduce the dominance of very abundant species. Bray-Curtis similarity matrices were created and multi-dimensional scaling (MDS) plots were generated for corals by each factor. Records of *Keratoisis cf. grayi* and Antipathidae were removed from the analysis due to their absence or rarity (< 10 records) in one or both canyons, and/or their taxonomic uncertainty. A two-way analysis of similarity (ANOSIM) was used to analyze differences in coral abundance by dive, nested within canyon. A one-way ANOSIM was used to determine the effect of habitat type.

#### 2.4 Physical environment

Data from the Seabird (SBE 19+) instrument attached to the ROVs were incorporated into the habitat and community analysis data sheets by cross referencing the time stamps on the data from the instrument with the ROV navigation files. This process created geo-referenced coral location data with environmental conditions. These data were used in statistical analyses to

identify potential environmental drivers for the observed coral distributions. A Spearman Rank correlation analysis was performed on the environmental data from all coral records to identify redundant variables (i.e. those with  $\rho > 0.95$  or  $< -0.95$ ). Environmental data were square root transformed and normalized. The BEST routine (Primer-E V6) was used to generate correlations between environmental data and coral abundance. Principal Component Analysis (PCA) was used to determine which environmental variables had the greatest contribution to coral abundances. To determine whether the relationship between environmental variables and coral abundance was statistically significant, the RELATE routine (Primer-E V6) was applied to the matched resemblance matrices for coral abundance (Bray-Curtis) and environmental data (Euclidean) using a Spearman Rank correlation.

Water samples were taken from Niskin bottles attached to the ROV and from near-bottom collections made during the CTD casts. Dissolved organic carbon (DIC,  $\mu\text{mol/kg}$ ) and total alkalinity (TA,  $\mu\text{mol/kg}$ ) were measured by the NOAA Pacific Marine Environmental Laboratory, using standard analytical techniques (Dickson et al., 2007). Levels of other parameters of interest were calculated using DIC and TA measurements, including  $\text{CO}_2$  ( $\mu\text{mol/kg}$ ),  $\text{HCO}_3^-$  ( $\mu\text{mol/kg}$ ),  $\text{CO}_3^{2-}$  ( $\mu\text{mol/kg}$ ), and saturation states of Aragonite ( $\Omega_{\text{Arag.}}$ ) and Calcite ( $\Omega_{\text{Calcite}}$ ). Since carbonate chemistry may influence the distribution of both octocorals and stony corals, these data are presented and discussed.

### 3. Results

#### 3.1 Habitat and community analysis

During the 2012 cruise, the ROV *Kraken II* made 17 dives that targeted coral/hard-bottom habitats over a depth range of 234-1001 m; 15 dives were made in Baltimore Canyon and two in Norfolk Canyon. In 2013, the ROV *Jason II* made 10 dives on coral/hard-bottom habitats, one in Baltimore Canyon (288-388 m), and the remaining nine in Norfolk Canyon (320-1390 m). The ROV dives from both years combined generated 2,542 minutes (~42.4 hours) of video for habitat/community analysis of Baltimore Canyon, and 2,198 minutes (~36.6 hours) for Norfolk Canyon. Table 2 summarizes the total number of observations of each coral taxon by canyon, together with its depth range, habitat types and environmental conditions. To visualize the habitat and coral distribution data, two maps were constructed for each ROV dive; habitat maps comprised habitat data (extracted during video analysis) that was superimposed along the ROV dive track. Coral distribution maps were generated by overlaying coral locations along each ROV dive track. Both tracklines were overlaid on local bathymetry to provide topographic context for the data. These maps are presented as supplementary material (SM Fig. 1).

Species richness of corals was low in both canyons with some species locally abundant (Table 2); however, richness of other sessile hard substrate fauna was higher, particularly for anemones and sponges. In addition to the large anemones counted as SFC, numerous smaller anemones often occurred in large patches of single morphotype (as defined by size and color variations but most of these were not sampled and identified) on exposed hard substrates. Sponges were more diverse, with > 30 different morphotypes of hexactinellid and demosponges recorded during video analysis.

Octocoral species that were observed in both canyons included the gorgonians (Order Alcyonacea) *Paragorgia arborea* (Fig. 3A) *Primnoa resedaeformis* (Fig. 3B) *Anthothela grandiflora* (Fig. 3C), *Paramuricea placomus* (Fig. 3D), as well as the soft corals (Order

Alcyonacea) *Duva florida* (Fig. 3E) and *Anthomastus* sp. (Fig. 3F). Colonies attributed to *A. grandiflora* may include a cryptic species and possibly a cryptic genus (Lawler et al., 2016); however, since it is not possible to distinguish between these taxa visually, *A. grandiflora* will be used to represent this taxonomic complex. The small, yellow gorgonian *Acanthogorgia aspera* (Fig. 3G) was common in Norfolk Canyon, but was not observed in Baltimore Canyon. Bamboo corals (Gorgonacea, Isididae) (Fig. 3H) were observed infrequently in the canyon habitats, but large numbers of the soft-sediment bamboo coral *Acanella arbuscula* (Fig. 3I) plus some sea pens (Order Pennatulacea) were collected in five deep trawls (1576-1694 m) conducted in Norfolk Canyon.

Hexacoral taxa that were observed in both canyons included stony corals such as *Lophelia pertusa* (Fig. 4A) and the cup corals, *Javania* sp. and *Desmophyllum dianthus* (Order Scleractinia) (Fig. 4B, C), a yellow zoanthid (Order Zoantharia) (Fig. 4D), and large anemones (Order Actinaria) (Fig. 4E-G). The scleractinians *Solenosmilia variabilis* and *Flabellum alabastrum* (Fig. 4H, I), and black corals (Order Antipatharia), such as *Telopathes magna* (Fig. 4J), were only found in the deeper areas of Norfolk Canyon (> 956 m) and were not observed in Baltimore Canyon, possibly because of the limited number of deep dives (three > 800 m) conducted there. The distribution of coral species collected with the ROV within Baltimore Canyon is presented in Figure 5A, B and within Norfolk Canyon in Figure 6A, B. Soft-sediment cup corals were also collected using otter trawls from near the head of Baltimore Canyon at ~270 m depth (*Dasmosmilia lymani*) and from Norfolk Canyon at 1500 m depth (*Flabellum alabastrum*).

Both octocorals and hexacorals were observed predominantly on walls and steep slopes and on large boulders of rock or consolidated sediment. Colonies of the gorgonian *Paramuricea*

*placomus* however, were observed in one location in each canyon on flat pavement with sediment cover (Table 2). On occasion, large amounts of apparently suitable habitat such as steep rocky walls were observed, but with very few corals (ROV-2012-NF-17; SM Fig. 1). Some of the habitat maps indicate high SFC cover, but had no octocorals or stony corals; these areas were dominated by large anemones (Order Actinaria) such as *Bolocera tunediae*, *Actinoscyphia* sp. or tube-dwelling anemones (order Ceriantharia). Areas dominated by large anemones occurred frequently in both Baltimore Canyon (SM Fig. 1, ROV-2012-NF-02, 13, 15, 16) and Norfolk Canyon (SM Fig. 1, ROV-2013-RB-686, 688, 691). The common gorgonians *P. arborea*, *P. resedaeformis*, *A. grandiflora*, *A. aspera*, (Table 2), and Parazoanthidae (which grows over gorgonian colonies) were all found in a wide range of hard substrate habitats (Table 2), whereas other species were found under more restricted conditions; for example *L. pertusa* was observed only on steep walls within a depth range of 374-424 m (Table 2), and *S. variabilis* was only observed deeper than 1250 m.

The number of observations per hour of ROV transect time was calculated for each octocoral and hexacoral taxa documented during video analysis of each canyon (Fig. 7 and 8). The most common species overall was *Desmophyllum dianthus*, with > 34,000 records; however, most (> 30,000) of these were from one long (~2.5 km) wall in Norfolk Canyon between 1190 m and 1390 m depth (SM Fig 1. ROV-2013-RB-685). A steep wall on the western flank of Baltimore Canyon also had several clusters of this cup coral (SM Fig. 1, ROV-2012-NF-17, 18), but *D. dianthus* was generally observed in groups of 1-3 individuals. Of the gorgonians, *P. arborea* was the most common in both canyons, although more were observed in Baltimore than in Norfolk Canyon. These colonies were also by far the largest of the corals observed, often reaching over 2 m in height and width. The soft coral, *Duva florida* was locally very abundant in



both canyons, but was not observed frequently, although the habitats where they were found were similar to those for the other gorgonians (Table 2).

Octocorals included in the statistical analyses were *Paragorgia arborea*, *Primnoa resedaeformis*, *Paramuricea placomus*, *Anthothela grandiflora*, *Acanthogorgia aspera* and *D. florida*, and hexacorals included *Lophelia pertusa*, *Desmophyllum dianthus*, *Solenosmilia variabilis*, and Parazoanthidae. A two-way analysis of similarity (ANOSIM) for ROV dives nested within canyons showed significant differences in distribution by canyon ( $R=0.123$ ,  $p < 0.05$ ) and by dive ( $R=0.500$ ,  $p < 0.001$ ). Multi-dimensional scaling (MDS) plots are shown for coral abundance by canyon (Fig. 9A) and by ROV dive number (Fig. 9B); in the latter figure, all the coral records from the deepest dive (ROV-2013-RB-685, 1257-1398 m) are clustered together with little overlap with other dives. The corals observed on this long steep wall included the only observations of *S. variabilis* and the black coral *T. magna* as well as extremely high numbers of *D. dianthus*. The ANOSIM was re-run excluding this atypical dive but the statistical outcome did not change; therefore these observations are not driving the statistical differences between canyons and among dives.

A one-way ANOSIM showed significant differences in coral abundance by habitat type ( $R=0.125$ ,  $p < 0.001$ ), with the greatest differences between the habitat extremes such as soft sediment and walls ( $R = 0.511$ ,  $p < 0.001$ ) and no significant differences ( $R = -0.031$ ,  $p = 0.88$ ) between habitat categories that were relatively similar such as sediment-rubble (SR) with  $< 50\%$  hard substrate and rubble (R) with  $> 50\%$  hard substrate. Figure 9C shows an MDS plot for coral abundance by habitat type.

A Spearman Rank Correlation test showed significant correlations between temperature and salinity ( $\rho = 0.95$ ) and between temperature and density ( $\rho = 0.99$ ), so salinity and density were

removed from further analysis (correlations among all variables are shown in Table 3). The BEST routine (Primer-E V6) applied to the environmental data and coral abundance similarity matrix (Bray-Curtis) showed that depth had the greatest correlation with coral distribution ( $\rho = 0.395$ ), followed by depth and temperature combined ( $\rho = 0.378$ ). Turbidity ( $\rho = 0.356$ ), pH ( $\rho = 0.332$ ), or oxygen ( $\rho = 0.317$ ) in addition to temperature and depth showed decreasing correlations with coral abundance.

Principal Component Analysis (PCA) on coral environmental data (Fig. 10) resulted in the highest coefficients for temperature and depth in PC1 (0.636, 0.515), followed by oxygen (0.492), pH (0.270) and turbidity (0.122). In PC2, the ranks of these variables were exactly reversed. Together, PC1 and PC2 accounted for 79.7% of the variation. The RELATE analysis showed a statistically significant relationship between environmental variables and coral abundance ( $\rho = 0.291$ ,  $p = 0.001$ ).

### 3.2 Physical environment

The average ( $\pm$ SD) and range of environmental data collected during all the ROV dives (SM Table 1) reflected only near-bottom conditions during the dives, and depth data are provided for reference. Each variable showed depth related trends; temperature and salinity decreased and density increased with depth similarly for both canyons (Fig. 11A, B, C). The relationship between depth and each of these variables was non-linear; beyond approximately 600 m depth, the curves flattened and there was less change with increasing depth. Oxygen and pH generally increased with depth (Fig. 11D, E), but oxygen levels were generally lower in Norfolk Canyon than Baltimore at comparable depths. Turbidity was variable for both canyons with highest turbidity at mid-depths (600-800 m), and consistently lower at depths  $>1000$  m (Fig. 11F).

Carbonate chemistry of water samples also reflected primarily near-bottom conditions; however midwater and near surface samples were collected with the CTD in both canyons (SM Table 2). Aragonite saturation state ( $\Omega_{\text{Arag}}$ ) values ranged from 2.27 near the surface (~100 m) to 1.2 at the deepest point measured (1387 m). Between 100 and 250 m depth, the  $\Omega_{\text{Arag}}$  declined rapidly from ~2.3 to 1.6, then declined more slowly with depth to a minimum of ~1.2 (Fig. 12).

#### 4. Discussion

The data from our study substantially increased the number of deep coral observations for the MAB region; these included new observations of *Lophelia pertusa* for Norfolk and Baltimore canyons (Brooke and Ross 2014) and new records of *Solenosmilia variabilis* and the black coral *Telopathes magna* for Norfolk Canyon. In addition to the deep coral communities, two methane seeps were documented in Baltimore Canyon (410-430 m) and Norfolk Canyon (1500-1600 m). Recent surveys have revealed an additional ~ 570 gas seepage sites along the western Atlantic margin, although few have been ground-truthed to date (Skarke et al., 2014; Quattrini et al., 2015). Several colonies of *P. arborea* were observed on authigenic carbonate (a byproduct of bacterial metabolism of methane) at the Baltimore Canyon seep. These carbonates, while somewhat limited in area, can provide habitat for sessile benthic fauna in otherwise soft-sediment environments.

Surveys of steep canyon walls in the NE Atlantic revealed previously unknown aggregations of *L. pertusa* (Huvenne et al., 2011), and exploration of canyons in the northeastern US documented new deep coral communities and methane seeps (Quattrini et al., 2015). Such data illustrate that a modest number of visual surveys can yield large amounts of new information from poorly studied habitats. Although several range extensions have been reported, no new

coral species (with the exception of the cryptic *Anthothela*) were identified during our study, indicating that the canyons, at least for these taxa, provide habitat for a regional fauna, rather than providing unique niches for endemic species.

*Paragorgia arborea* was the most abundant, widely distributed and largest of the gorgonians and exhibited several phenotypes (white, pink and red color morphs, robust and delicate branches). Morphological differences were not genetically defined, as all *Paragorgia* phenotypes collected were verified as *P. arborea* using mitochondrial gene sequencing (Clostio and France, unpubl. data). Color and branching structure variation also occurs in other species of deep corals; *L. pertusa* colonies may have heavily calcified or fragile branching patterns (Brooke and Schroeder 2007), and colonies from the eastern Atlantic often have orange pigmentation in their tissues. Coral pigments are created by different forms of carotenoids derived from diet (Elde et al., 2012), and can also be vertically transmitted through the eggs of pigmented colonies (Larsson et al., 2014). The purpose of these pigments has not been resolved, but possibilities include anti-oxidant and antibiotic properties (Shnit-Orland et al., 2008; Elde et al., 2012) or they may confer a nutritional advantage (Neulinger et al., 2008). In the MAB canyons, all of the different *P. arborea* phenotypes were observed together with no clear distribution pattern; therefore, the selective benefits/costs (if any) of the different phenotypes are unclear and warrant further study. Other common octocoral species that usually co-occurred with *P. arborea* were *P. resedaeformis* and *A. grandiflora*, which had similar habitat associations and ranges of depth and environmental conditions.

Some species of octocorals (e.g., *P. placomus* and *D. florida*) were observed infrequently, but were locally highly abundant. Most coral species were found on steep terrain with little or no sediment accumulation; however, a single patch of ~250 colonies of *P. placomus* was observed

once in each canyon along the top of a flat rocky ledge with a sediment layer sufficiently thick in some places that the underlying hard substrate was invisible. Most corals cannot tolerate chronic high sediment environments, as particles can clog feeding and respiration apparatus (Reigl 1995; Kelmo et al., 2003). Corals produce mucus in order to remove particles, and this energetically-expensive process cannot be sustained over long periods (Dallmeyer et al., 1982). Some species, such as *L. pertusa*, appear to have a moderately high tolerance to sediment (Brooke et al., 2009) and reduced oxygen levels (Dodds et al., 2007). Colonies of *P. placomus* can also evidently tolerate chronic suspended sediment and/or episodic high sediment deposition, which may allow them to exploit habitats that other species cannot. This species is also found in areas with significant sediment cover in the deep Gulf of Maine (Watling and Auster 2005), and congeners *P. biscaya* are found in similar habitats in the deep Gulf of Mexico (Fisher et al., 2014). Flat sandy/rocky terraces were observed frequently in both canyons, but the very limited number of *P. placomus* observations implies the presence of a limiting factor (e.g., current speed, food, larval delivery) beyond habitat availability. The soft coral *D. florida* occurred in few locations but in extremely high numbers; they were observed in similar habitats to other octocorals, i.e., rocky boulders or walls, so (as with *P. placomus*) it seems the distribution of *D. florida*, was also driven by factors other than habitat.

Hexacorals (excluding anemones) were generally less abundant in both canyons than the octocorals, with two exceptions; a yellow *Parazoanthus* sp. that grows over dead (and possibly live) octocorals, and the cup coral *D. diathus*. The zoanthid was observed on *A. grandiflora*, *P. placomus* and *P. resedaeformis* (but not *P. arborea*). The yellow zoanthids overgrowing *P. placomus* were identified as *Corallizoanthus* sp using gene sequence data. (Clostio and France, unpubl. data), but zoanthids collected from other octocorals were identified morphologically by

J. Reimer as *Parazoanthus* sp. This taxon is currently being revised so Reimer's identification will be used here, with the understanding that future revisions may classify this genus as *Corallizoanthus*. The *Parazoanthus* sp. had often completely overgrown the 'host' octocoral skeleton, but it was also observed growing on partially-live colonies. It is not clear whether the zoanthids are parasitic on live colonies or merely take advantage of dead skeleton as opportunistic substrate. These zoanthids were considerably more abundant in Norfolk Canyon than Baltimore Canyon. The abundance of *P. placomus* and *P. resedaeformis* was comparable between the two canyons, but there were more than twice as many *A. grandiflora* in Norfolk Canyon; therefore, the distribution of *Parazoanthus* sp. may be determined to some extent by the distribution of the 'host' species as well as the environmental tolerances of the zoanthid. The extremely high numbers of *D. dianthus* in Norfolk Canyon are driven by observations made during a single ROV dive (J2-685). A series of deep (~1200 m) vertical walls were heavily colonized by thousands of small *D. dianthus*, as well as *S. variabilis* and a new species of fileshell (*Acesta cryptadelphe* sp.nov., Gagnon et al., 2015). This extreme *D. dianthus* abundance was only observed on these deep walls of Norfolk Canyon where the individuals were small with fragile skeletons; however a moderately high abundance (~170 individuals) was also observed on a steep wall in Baltimore Canyon at ~670 m, but calices were much more robust. In shallower habitats (< 500 m), this species occurred on different types of rocky habitat, as large heavily calcified single specimens or in small clusters and was generally uncommon.

Environmental data used for correlations with coral distributions were collected during the ROV dives, and therefore do not necessarily reflect long term conditions; however, since the dives occurred over a two-week to one-month period, in two consecutive years and over a wide depth range, the data were considered useful for distributional analysis. These correlative

statistics are useful, but must be interpreted with caution, and more work is needed to understand the causal relationships between environment and species distributions.

Coral abundances are most highly correlated with temperature and/or depth followed by pH, turbidity and oxygen. Depth and temperature have both been recognized as primary drivers of deep-sea coral distributions (Roberts et al., 2009; Baker et al., 2012) so this is not a surprising outcome. Some species however, have a wide tolerance to temperature, which could reduce the influence of temperature on their distribution. For example, *L. pertusa* can survive highly variable environments (Brooke et al., 2013) and has been observed in unusually warm conditions (up to 14°C) in the Mediterranean (Freiwald et al., 2009). Other research has indicated the importance of water mass density to *L. pertusa* (Dullo et al., 2008); in the northeastern Atlantic, living reefs were found between densities of 27.35 and 27.65  $\sigma_\theta$ , but *L. pertusa* colonies were observed in more dense waters (27.74-27.84  $\sigma_\theta$ ) in Whittard Canyon, NE Atlantic (Huvenne et al., 2011) and over a wider density range (27.32-28.23) in Baltimore and Norfolk canyons.

After depth and temperature, turbidity showed the highest correlation with coral abundance. Both of the canyons have chronically high turbidity levels, but Baltimore Canyon has a persistent dense nepheloid layer along the thalweg between 300-800 m depth (Davies et al., unpubl. data). This phenomenon was observed during ROV dives and was also reported by Gardner (1989), which adds support for a consistent pattern of mid-canyon turbidity maxima. In contrast, Norfolk Canyon has smaller, separate turbidity layers between 400-1100 m depth and a more uniform sediment deposition pattern (Davies et al., unpubl. data). Ample evidence exists that high sediment loads have detrimental effects on stony corals, including reduced skeletal growth, reproductive capacity and lipid content as they shed sediment through the energetically costly processes of ciliary action and mucus production and, in extreme cases, corals can

suffocate under sediment load (Dallmeyer et al., 1982; Wesseling et al., 1999; Kelmo et al., 2003). Stony corals in the canyons were most frequently observed on steep walls or other areas with little or no sediment accumulation, and there were many more stony corals observed in Norfolk Canyon than Baltimore Canyon, especially *D. dianthus* and *S. variabilis* at the deeper sites where turbidity is low (Fig. 11F). This distribution could reflect low stony coral tolerance to sediment; however *L. pertusa* has shown high survival under chronic moderate sediment loads and even short term burial (Brooke et al., 2009), so turbidity alone may not explain the observed differences in stony coral abundance between the canyons, at least for *L. pertusa*.

Another notable difference in coral distribution between the canyons is the very high abundance of *P. arborea*, in Baltimore Canyon (more than double the number observed in Norfolk Canyon), which has a depth range that coincides with the nepheloid layer. *Paramuricea placomus* was also found living in potentially high sediment environments on flat pavements in both canyons. Some species can therefore tolerate high turbidity, and may even benefit from it nutritionally. Stable isotope studies have shown that deep corals living in high sediment environments are consuming re-worked material such as older POM, whereas those living in current-swept conditions have access to fresher material and have a higher trophic level (Sherwood et al., 2008; Demopoulos et al., unpubl. data). Generally in the deep sea, deposition of organic material decreases with depth (Levin and Gooday 2003; Rex and Etter 2010); however, increased organic material and high turbidity are characteristic of submarine canyons globally (Durrieu de Madron 1994; de Stigter et al., 2007; Huvenne et al., 2011), and are important drivers of benthic communities (Ingels et al., 2009; De Leo et al., 2010; Rex and Etter 2010).



As depth increases,  $\Omega_{\text{Arag}}$  decreases (Feely et al., 2004), potentially making production of calcified skeletons more energetically costly (Fabry 2008). Most of the corals in the current study were found in  $\Omega_{\text{Arag}} > 1.35$ , which is within the currently known limits for deep-sea corals such as *L. pertusa* (Lunden et al., 2012). The deepest dive off Norfolk Canyon (1257-1398) was dominated by a steep wall, densely covered in thousands of small fragile *D. dianthus*. At this depth the  $\Omega_{\text{Arag}}$  was  $\sim 1.2$  and in shallower areas, where *D. dianthus* was heavily calcified ( $\sim 400$ - $700$  m), the  $\Omega_{\text{Arag}}$  was  $\sim 1.5$ ; however, it seems unlikely that this difference would explain the great differences in skeletal structure (particularly when both locations have  $\Omega_{\text{Arag}} > 1$ ). Extreme high abundances ( $\sim 1500$  individuals/m<sup>2</sup> in the Chilean fjords; Forsterra and Haussermann 2003) have been observed elsewhere for this species under low  $\Omega_{\text{Arag}}$  (Fillinger and Richter 2013). It seems therefore, that under certain circumstances *D. dianthus* shifts from small robust calices to very large numbers of fragile individuals. The reasons for this are not clear, but it is possible that the availability of large areas of good habitat (steep wall with little sedimentation) in the deep part of Norfolk Canyon allowed for high recruitment, but growth rates were reduced by other factors such as low temperatures, reduced food and competition for space. Differences in habitat availability and conditions between deep and shallower areas potentially create the different observed distributions and size structure in this species.

The deep coral reefs in the South Atlantic Bight (SAB) and Gulf of Mexico (GOM) are constructed by the stony corals *Lophelia pertusa* and *Enallopsammia profunda*, which can create large bioherms of consolidated coral rubble with live coral on the flanks and peaks. These deep reefs (and other abundant hard-substrates in the region) have a high diversity of gorgonians, antipatharians, sponges and other mobile and sessile invertebrates (Brooke and Schroeder 2007, Ross and Nizinski 2007). The deep corals that colonize the numerous seamounts and canyons of

the northeastern US are primarily octocorals with some species of black corals and stony corals, but the overall coral species diversity is low (Packer et al., 2007). The western Atlantic can be divided into two biogeographic provinces: the Warm Temperate Carolinian Province south of Cape Hatteras, NC and the Western Atlantic Boreal Region that extends from Cape Hatteras north to Labrador, Canada (Briggs 1974). There has, however, been disagreement over the geographic extent of the boreal region, as many of the fauna from the MAB belong to the southern Carolinian province. A recent realignment of marine biogeographic provinces based on fishes (Briggs and Bowen 2012) clearly places the MAB in the northern boreal region. The deep coral fauna from the canyons also more closely resembles those of the northeastern US, than the SAB. The three most frequently observed species of octocorals in the MAB are also common in the northeastern US but are either absent (*P. resedaeformis*, *A. grandiflora*) or very rare (*P. arborea*) in the SAB and GOM (Brooke and Schroeder 2007; Ross and Nizinski 2007). Other species such as *L. pertusa*, *S. variabilis* and *D. dianthus* have broad distributions and are found throughout the North Atlantic. One exception is the gorgonian *Acanthogorgia aspera*, which was frequently observed in Norfolk Canyon. This species had not been documented north of Cape Hatteras prior to this study (Watling and Auster 2005) so it is more allied to the Carolinian province; its congener *A. armata* occurs in the northern boreal province.

Various forms of debris were observed on almost every ROV dive, primarily plastic bags and lost fishing gear (traps, lines, nets). Although the canyon axes and walls are not targeted by regional fisheries due to their rugged topography and unpredictable currents, derelict fishing gear was often observed tangled in rocky outcrops, particularly near the canyon heads. In June 2015, the Mid-Atlantic Fisheries Management Council (MAFMC) proposed to create Deep-Sea Coral Zones to protect ~98,420 km<sup>2</sup> of canyon and slope habitats to bottom-tending fishing gear. This

proposal is currently under consideration at the U.S. Department of Commerce, and if approved, will provide legislation to preserve these fragile and valuable resources. Data from this study and others (funded by NOAA) will assist U.S. Federal agencies in the management and conservation of canyon ecosystems.

## **5. Conclusions**

This multi-disciplinary study greatly increased our understanding of the complex physical conditions in submarine canyons of the MAB, and their influence on biological communities. Observations of different coral species correlated with specific habitat types and environmental conditions, although these correlations do not fully explain the patchy or limited distributions of some species. Future studies that integrate physical and ecological approaches are needed to understand the complex interactions that drive the distribution and population structure of different species. Such information is needed to refine deep-sea coral predictive habitat models, which are useful management tools for data-poor ecosystems. Exploration and research of deep-sea ecosystems are challenging and expensive; however these efforts not only advance scientific knowledge, but also inform management and generate public empathy to protect these valuable resources.

## **Acknowledgements**

Funding for this project was supplied by the Bureau of Ocean Energy Management (BOEM), under contract to CSA Ocean Sciences, Inc. (contract M10PC00100), in partnership with the National Oceanographic Partnership Program. We thank Greg Boland (BOEM) and Steve Viada (CSA) for support during the development of these cruises and the overall project. NOAA ships

*Nancy Foster* and *Ronald H. Brown*, and *Kraken II* and *Jason II* ROVs were provided by the NOAA Office of Ocean Exploration and Research. The US Geological Survey contributed equipment and personnel to this project. We thank the ship and shore-based personnel who operated the ships and ROVs, and all the science and outreach personnel for their hard work during the cruises. Special thanks to Kelly Kingon for helping with some of the video analysis before taking a faculty position at the University of Trinidad and Tobago and to Kirstin Meyer for long hours on the ship helping to process samples.

Accepted manuscript

## References

- Able, K.W., 2002. An evaluation of the impact of mobile fishing gear on tilefish habitat: review of archived video images from submersible. Prog. Rept. to the Mid-Atlantic Fishery Management Council, pp. 6.
- Allen, S.E., Vindeirinho, C. Thomson, R.E., Foreman, M.G.G., Mackas, D.L., 2001. Physical and biological processes over a submarine canyon during an upwelling event. *Canadian J. Fish. Aquat. Sci.* 58, 671–684.
- Andrews, B.D., Chaytor, J.D., ten Brink, U.S., Brothers, D.S., Gardner, J.V., 2013. Bathymetric terrain model of the Atlantic Margin for marine geological investigations. U.S. Geological Survey Open-File Report 2012-1266.
- Auster, P.J., 2005. Are deep-water corals important habitats for fishes? In: Freiwald, A., Roberts, J.M. (Eds.). *Cold-Water Corals and Ecosystems*. Springer-Verlag. Berlin Heidelberg, pp.1243.
- Baker, K.D., Wareham, V.E., Snelgrove, P.V., Haedrich, R.L., Fifield, D.A., Edinger, E.N., Wilkinson, K.D., 2012. Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada. *Mar. Ecol. Prog. Ser.* 445, 235–249.
- Bennett, R.H., Lehman, L., Hulbert, M.H., Harvey, G.R., Bush, S.A., Forde, E.B., Crews, P., Sawyer, W.B., 1985. Interrelationships of organic carbon and submarine sediment geotechnical properties. *Mar. Georesources Geotech.* 6, 61-98.
- Briggs, J.C., 1974. *Marine zoogeography*. McGraw-Hill, New York.
- Briggs, J.C., Bowen, B.W., 2012. A realignment of marine biogeographic provinces with particular reference to fish distributions. *J. Biogeogr.* 39, 12-30.

- Brooke, S., Schroeder, W.W., 2007. Chapter 7: State of deep coral ecosystems in the Gulf of Mexico region: Texas to the Florida Straits In: Lumsden, S.E. Hourigan, T.F. Bruckner, A.W. (Eds.). The State of Deep Coral Ecosystems of the United States NOAA Technical Memorandum NOS-CRCP-3, Silver Spring MD, pp 271-306.
- Brooke, S., Ross, S. W., 2014. First observations of the cold-water coral *Lophelia pertusa* off the mid-Atlantic coast of the United States. *Deep Sea Res. II* 104, 241-251.
- Brooke, S., Holmes, M., Young, C.M., 2009. Effects of sediment on two morphotypes of *Lophelia pertusa* from the Gulf of Mexico. *Mar. Ecol. Prog. Ser.* 390, 137–144.
- Brooke S., Ross, S.W., Bane, J.M., Seim, H.E., Young, C.M., 2013. Temperature tolerance of the deep-sea coral *Lophelia pertusa* from the southeastern United States. *Deep Sea Res. II.* 92, 240-248
- Brooks, D.A., 1996. Physical oceanography of the shelf and slope seas from Cape Hatteras to Georges Bank: a brief overview. In: Sherman, K., Jaworski, N.A., Smayda, T.J. (Eds.). The Northeast Shelf Ecosystem: Assessment, Sustainability, and Management. Cambridge, MA, USA. Blackwell Science, pp 47-75.
- 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. *Mar. Ecol.* 31, 21-50.
- Cairns, S.D. 1981. Marine flora and fauna of the northeastern United States: Scleractinia. NOAA Tech. Rep. NMFS Circ. 438, 1-14.
- Carne, R.S., 2005. Zonation of deep biota on continental margins. *Oceanogr. Mar. Biol. Annu. Rev.* 43, 211-278.

- Cooper, R.A., Stewart, L., Baker, J., Babb, I., 1992. Assessment of impact of sewage sludge dumping (106 mile dump site) on ocean habitats and megabenthic fauna, progress report. NOAA National Undersea Research Center, U. of Connecticut, Avery Point, pp. 41.
- Csanady, G.T., Churchill, J.H., Butman, B., 1988. Near-bottom currents over the continental slope in the Mid-Atlantic Bight. *Cont. Shelf Res.* 8, 653-671
- Csanady, G.T., Hamilton, P., 1988. Circulation of slope water. *Cont. Shelf Res.* 8, 565-624
- Dallmeyer, D.G., Porter, J.W., Smith, G. J., 1982. Effects of particulate peat on the behavior and physiology of the Jamaican reef-building coral *Montastrea annularis*. *Mar. Biol.* 68, 229–233
- Deichmann, E., 1936. The Alcyonaria of the western part of the Atlantic Ocean. Harvard Univ. Mus. Comp. Zool. Mem. 53, 1-317
- de Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A., Clark, M.R., 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. *Proc. Royal Soc. B.* 277, 1-10. doi:10.1098 /rspb.2010.0462.
- de Stigter H.C., Boer, W., de Jesus Mendes, P.A., Jesus, C.C., Thomsen, L., van den Bergh, G.D. van Weering, T.C.E., 2007. Recent sediment transport and deposition in the Nazaré Canyon, Portuguese continental margin. *Marine Geology* 246, 144–164.
- Dickson, A.G., Sabine, C.L., Christian, J.R., (Eds.), 2007. Guide to best practices for ocean CO<sub>2</sub> measurements. PICES Special Publication 3, pp. 191.
- Dodds, L, Roberts, J. M., Taylor, A. C., Marubini, F., 2007. Metabolic tolerance of the cold-water coral *Lophelia pertusa* (Scleractinia) to temperature and dissolved oxygen change. *J. Exp. Mar. Biol. Ecol.* 349(2), 205-214

- Dullo, W.-C., Flögel, S., Rüggeberg, A., 2008. Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin. *Mar. Ecol. Prog. Ser.* 371, 165–176.
- Durrieu de Madron, X.D., 1994. Hydrography and nepheloid structures in the Grand-Rhône Canyon. *Continental Shelf Research* 14, 457-477.
- Elde, A.C., Pettersen, R., Bruheim, P., Järnegren, J., Johnsen, G., 2012. Pigmentation and spectral absorbance signatures in deep-water corals from the Trondheimsfjord, Norway. *Mar. Drugs*. 10, 1400-1411
- Fabry, V.J., 2008. Ocean science – Marine calcifiers in a high-CO<sub>2</sub> ocean. *Science* 320, 1020–1022.
- Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J., Millero F.J., 2004. Impact of anthropogenic CO<sub>2</sub> on the CaCO<sub>3</sub> system in the oceans. *Science* 305, 362–366
- Fillinger, L., Richter, C., 2013. Vertical and horizontal distribution of *Desmophyllum dianthus* on Comau Fjord, Chile: a cold water coral thriving at low pH. *PeerJ* DOI 10.7717/peerj.194
- Fitzgerald, J., Chamberlin, J.L., 1981. Anti-cyclonic warm core Gulf Stream eddies off the northeastern United States during 1979. *Ann. Biol. Copenh.* 36:44-51.
- Forsterra, G., Haussermann, V., 2003. First report on large scleractinian (Cnidaria: Anthozoa) accumulations in cold-temperate shallow water of south Chilean fjords. *Zoologische Verhandelingen Leiden* 345:117–128.
- Freiwald, A., Beuck, L., Rüggeberg, A., Taviani, M., Hebbeln, D., 2009. The white coral community in the central Mediterranean Sea revealed by ROV surveys. *Oceanography* 22, 58–74.



- Gagnon, J.M., Kenchington, E., Port, A., Anstey, L. J., Murillo, F.J., 2015. Morphological and genetic variation in North Atlantic giant file clams, *Acesta* spp. (Bivalvia: Limidae), with description of a new cryptic species in the northwest Atlantic. *Zootaxa* 4007(2), 151-180
- Gardner, W.D., 1989. Periodic Resuspension in Baltimore Canyon by Focusing of Internal Waves. *Journal of Geophysical Research-Oceans*. 94, 18185-18194.
- Gartner, J.V., Jr., Sulak, K.J., Ross, S.W., Necaie, A.M., 2008. Persistent near-bottom aggregations of mesopelagic animals along the North Carolina and Virginia continental slopes. *Mar. Biol.* 153, 825-841.
- Gilkinson, K.D., Edinger, E.N., 2009. The ecology of deep-sea corals in Newfoundland and Labrador waters: Biogeography, life history, biogeochemistry, and role as critical habitat. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2830.
- Griggs, G.B., Carey, A.G., Kulm, L.G., 1969. Deep-sea sedimentation and sediment-fauna interaction in Cascadia Channel and on Cascadia Abyssal Plain. *Deep-Sea Res.* 16, 157-170.
- Greene, C.H., Wiebe, P.L., Burczynski, J., Youngbluth, M.J., 1988. Acoustical detection of high-density krill demersal layers in the submarine canyons off Georges Bank. *Science* 241, 4863.
- Grimes, C.B., Able, K.W., Jones, R.S., 1986. Tilefish, *Lopholatilus chamaeleonticeps*, habitat, behavior and community structure in Mid-Atlantic and southern New England waters. *Env. Biol. Fishes* 15, 273-292.
- Harris, P.T., Whiteway, T., 2011. Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins *Marine Geology* 285, 69-86
- Hecker, B., Blechschmidt, G., Gibson, P., 1980. Epifaunal zonation and community structure in three mid- and north Atlantic canyons. Final Rept. for the Canyon Assessment Study in the

- Mid-and North Atlantic Areas of the U.S. Outer Continental Shelf. Prepared for Bureau of Land Management, Dept. of the Interior. Contract BLM AA5 51-CT8-49. 139 pp + app
- Hecker, B., Logan, D.T., Gandarillas, F.E., Gibson, P.R., 1983. Canyon and Slope Processes Study Vol. III Biological Processes. Minerals Management Service Rept. Pp. 212.
- Heezen, B.C., Ewing, M. Menzies, R.J., 1955. The influence of submarine turbidity currents on abyssal productivity. *Oikos* 6, 170-182.
- Hudson, K.A., Haedrich, R.L., 1984. Abundance and biomass of macrobenthos in the vicinity of Carson Submarine Canyon, northwest Atlantic Ocean. *Mar. Biol.* 82, 301-305.
- Huvenne, V.A.I., Tyler, P.A., Masson, D.G., Fisher, E.H., Hauton, C., Huhnerbach, V., Le Bas, T.P., Wolff, G.A., 2011. A picture on the wall: Innovative mapping reveals cold-water coral refuge in submarine canyon. *PLoS ONE* 6(12), e28755. doi:10.1371/journal.pone.0028755
- Ingels J., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A., 2009. Nematode diversity and its relation to the quantity and quality of sedimentary organic matter in the deep Nazare Canyon, Western Iberian Margin. *Deep-Sea Res. Part I.* 56, 1521-1539.
- Keller, G.H., Shepard, F.P., 1978. Currents and sedimentary processes in submarine canyons off the northeast United States. In: Stanley, D.J., Kelling G. (Eds.). *Sedimentation in submarine canyons, fans, and trenches*. Dowdon, Hutchings and Ross, Inc. Stroudsburg, PA. pp. 15-32.
- Kelmo, F., Attrill, M.J., Jones, M.B., 2003. Effects of the 1997–1998 El Niño on the cnidarian community of a high turbidity coral reef system (northern Bahia, Brazil). *Coral Reefs* 22, 541–550.
- Kenchington, E. L., Cogswell, A. T., Macisaac, K. G., Beazley, L., Law, B. A., Kenchington, T. J., 2014. Limited depth zonation among bathyal epibenthic megafauna of the Gully submarine canyon, northwest Atlantic. *Deep-Sea Res. II.* 104, 67-82.

- King, N.J., Jamieson, A.J., Bagley, P.M., Priede, I.G., 2008. Deep-sea scavenging demersal fish fauna of the Nazare Canyon system, Iberian coast, north-east Atlantic Ocean. *J. Fish Biol.* 72, 1804-1814.
- Kuhnze, E., Rosenfeld, L.K., Carter, G.S., Gregg, M.C., 2002. Internal waves in Monterey Submarine Canyon. *J. Phys. Oceanogr.* 32, 1890–1913.
- Lawler S.N., Kellogg, C.A., France S.C., Clostio, R.W., Brooke, S.D., Ross, S.W., 2016. Coral-associated bacterial diversity is conserved across two deep-sea *Anthothela* species. *Front. Microbiol.* 7, 458.
- Larsson, A.I., Järnegren, J., Strömberg, S.M., Dahl, M.P., Lundälv, T., Brooke, S., 2014. Embryogenesis and larval biology of the cold-water coral *Lophelia pertusa*. *Plos ONE* 9(7): e102222
- Levin, L, Gooday, A.J., 2003. The deep Atlantic Ocean. In: Tyler, P.A. (Ed.) *Ecosystems of the World Volume 28: Ecosystems of the Deep Ocean*. Elsevier, Amsterdam, pp. 111-178
- Malahoff, A., Embley, R.W., Fornari, D.J., 1982. Geomorphology of Norfolk and Washington canyons and the surrounding continental slope and upper rise as observed from DSRV *Alvin*. In: Scrutton, R. A., Talwani M. (Eds.). *The Ocean Floor*, John Wiley Sons, pp. 97-111.
- Mann, K.H., 1982. *Ecology of coastal waters*. Univ. of California Press. Berkeley, CA, USA.
- McClain, C. R., Barry, J. P., 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91(4), 964-976.
- Mid-Atlantic Fishery Management Council, 2015. Deep sea corals amendment to the Atlantic mackerel, squid and butterfish fishery management plan. Public Information Document, January 2015. Pp. 95.

- Mortensen, P.B., Buhl-Mortensen, L., 2004. Distribution of deep water gorgonian corals in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). *Mar. Biol.* 144, 1223-1238.
- Neulinger, S.C., Jarnegren, J., Ludvigsen, M., Lochte, K., Dullo, W.-C., 2008. Phenotype-specific bacterial communities in the cold-water coral *Lophelia pertusa* (Scleractinia) and their implications for the coral's nutrition, health, and distribution. *App. and Env. Microbiol.* 74(23), 7272–7285.
- Obelcz, J., Brothers, D., Chaytor, J., ten Brink, U., Ross, S.W., Brooke, S., 2014. High-resolution geophysical and ROV surveys of four major submarine canyons of the US mid-Atlantic margin. *Deep Sea Res. II* 104,106-119.
- Packer, D.B., Boelke, D., Guida, V., McGee, L.A., 2007. Chapter 5: State of deep coral ecosystems in the northeastern region: Maine to Cape Hatteras In: *The State of Deep Coral Ecosystems of the United States* (Eds. S.E. Lumsden, T.F. Hourigan, and A.W. Bruckner), NOAA Technical Memorandum NOS-CRCP-3, Silver Spring MD, pp 195-232.
- Pierdomenico, M., Guida, V.G. Macelloni, L., Chiocci, F.L., Rona, P.A., Scranton, M.I., Asper, V., Diercks, A., 2012. Sedimentary facies, geomorphic features and habitat distribution at the Hudson Canyon head from AUV multibeam data. *Deep-Sea Res. II* 121, 112-125.
- Purser, A., Orejas, C., Gori, A., Tong, R., Unnitahn, V., Thomsen, L., 2013. Local variation in the distribution of benthic megafaunal species associated with cold-water coral reefs on the Norwegian margin. *Cont. Shelf. Res.* 54, 37-51.
- 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.C., 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. doi:10.1371/journal.pone.0139904

Rex M.A., Etter R.J., 2010. Deep-sea biodiversity: pattern and scale. Harvard University Press

Riegl, B. 1995. Effects of sand deposition on scleractinian and alcyonacean corals. Mar. Biol.

121, 517–526.

Roberts J.M., Wheeler, A.W. Freiwald, A., Cairns S., (Eds.), 2009. Cold-water corals: the

biology and geology of deep-sea habitats. Cambridge University Press pp 334

Ross, S.W., Nizinski, M.S., 2007. Chapter 6: State of deep coral ecosystems in the US southeast

region: Cape Hatteras to southeastern Florida In: The State of Deep Coral Ecosystems of the

United States. Lumsden, S.E., Hourigan, T.F., Bruckner A.W. (Eds.), NOAA Technical

Memorandum NOS-CRCP-3, Silver Spring MD: pp 233-270.

Ross, S.W., Rhode, M., Quattrini, A.M., 2015. Demersal fish distribution and habitat use within

and near Baltimore and Norfolk canyons, US Middle Atlantic Slope. Deep Sea Res. I 103,

137-154

Rowe, G.T., 1972. The exploration of submarine canyons and their benthic faunal assemblages.

Proc. Roy. Soc. Edinburgh (B), 73 (17), 159-169.

Schlee, J.S., Robb, J.M., (1991) Submarine processes of the middle Atlantic continental rise

based on GLORIA imagery. Geol. Soc. Am. Bull. 103, 1090–1103.

Shepard, A.N., Theroux, R.B., Cooper, R.A., Uzman, J.R., 1986. Ecology of *Ceriantharia*

(Coelenterata, Anthozoa) of the northwest Atlantic from Cape Hatteras to Nova Scotia. Fish.

Bull. 84, 625-646

- Shnit-Orland, M., Kushmaro, A., 2008. Coral mucus bacteria as a source for antibacterial activity. In: Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, FL, USA, 7–11 July 2008
- Skarke, A., Ruppel, C., Kodis, M., Brothers, D., Lobecker, E., 2014. Widespread methane leakage from the sea floor on the northern US Atlantic margin. *Nat. Geosci.* 7(9), 657-661
- Stanley, D.J., Fenner, P., 1973. Underwater television survey of the Atlantic outer continental margin near Wilmington Canyon. *Smithsonian Cont. Earth Sci.* No. 11.
- Stefanescu, C., Nin-Morales, B. Massuti, E., 1994. Fish assemblages on the slope in the Catalan Sea (western Mediterranean): influence of a submarine canyon. *J. Mar. Biol. Assoc. UK* 74, 499-512
- Theroux, R.B., Wigley, R.L., 1998. Quantitative composition and distribution of the microbenthic invertebrate fauna of the continental shelf ecosystems of the northeastern United States. NOAA Tech. Rept. NMFS 140, pp. 240.
- Tucholke, B.E., 1987. Submarine geology. In: Milliman, J.D., Wright W.R. (Eds.), *The Marine Environment of the US Atlantic Continental Slope and Rise*. Jones and Bartlett Publ., Inc. Boston, MA, pp. 56-113.
- Twichell, D.C., Roberts D. G., 1982. Morphology, distribution, and development of submarine canyons on the United-States Atlantic continental-slope between Hudson and Baltimore canyons. *Geology* 10, 408-412.
- Uchupi, E., 1968. Seismic profiling survey of the east coast submarine canyons Part 1. Wilmington, Baltimore, Washington and Norfolk Canyons. *Deep-sea Res. Ocea. Abstr.* 15
- Vetter, E.W., Dayton P.K., 1998. Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep-Sea Res. II* 45, 25–54.

- Watling, L., Auster, P. J., 2005. Distribution of deep-water Alcyonacea off the northeast coast of the United States. In: Freiwald, A., Roberts J.M. (Eds.) Cold-water corals and ecosystems. Springer-Verlag, Berlin Heidelberg. pp. 259-276.
- Wesseling I, Uychiaoco, A.J., Aliño, P.M., Aurin, T., Vermaat, J.E., 1999. Damage and recovery of four Philippine corals from short-term sediment burial. *Mar. Ecol. Prog. Ser.* 176, 11–15
- Wilson, W.H.J., 1991. Competition and predation in marine soft-sediment communities. *Ann. Rev. Ecol. Syst.* 21, 221–241.

**Figure 1.** Map of four of the major submarine canyons off the mid-Atlantic including Baltimore and Norfolk canyons which were the focus of this study. Shaded area represents coverage by multibeam sonar.

**Figure 2.** A-F Examples of different canyon habitat types A) S: Soft sediment with no hard substrate visible (goosefish *Lophius americanus* is visible in the image), B) SR: Soft sediment with small pieces of rock or emergent hard substrate (note cerianthid anemones and sponges) C) R: Isolated rock, rubble > 50% cover of hard substrate D) PB: Large areas of hard substrate >50% cover with attached sponges and anemones, E) B: Large boulder of rock or consolidated sediment with attached octocorals and anemones, F) W: Walls and steep slopes. Red squat lobsters *Eumunida picta* (Eumunidae) are visible in B and D.

**Figure 3.** Images of octocorals observed in Baltimore and Norfolk canyons. A) *Paragorgia arborea*, B) *Primnoa resedaeformis*, C) *Anthothela grandiflora*, D) *Paramuricea placomus*, E) Soft coral *Duva florida*, F) *Anthomastus* sp., G) *Acanthogorgia armata*, H) Bamboo coral *Keratoisis* cf *grayi*, I) *Acanella arbuscula* and sea pen *Funiculina quadrangularis*



**Figure 4.** Images of hexacorals observed in Baltimore and Norfolk canyons: A) *Lophelia pertusa*, B) *Javania cf cailleti*, C) *Desmophyllum dianthus* with Brisingsid asteroid, *Acesta* sp. bivalve and octopus, D) Zoanthids (*Parazoanthus* sp.) overgrowing dead octocoral skeleton, E) *Actinoscyphia* sp., F) *Bolocera tunediae*, G) Cerianthid anemones, H) *Solenosmilia variabilis* with *D. dianthus* in top right corner, I) *Flabellum alabastrum*, J) *Telopathes magna* with a Ghost Catshark (*Apristurus manis*) swimming next to the colony.

**Figure 5.** Distribution of A) Baltimore Canyon octacorals, B) Baltimore Canyon hexacorals observed during ROV dives

**Figure 6.** Distribution of A) Norfolk Canyon octacorals, B) Norfolk Canyon hexacorals observed during ROV dives

**Figure 7.** Number of octocoral observations per hour of ROV transects in Baltimore and Norfolk canyons

**Figure 8.** Number of hexacoral observations per hour of ROV transects in Baltimore and Norfolk canyons

**Figure 9.** Multi-dimensional scaling plots on fourth root transformed coral abundance data using a Bray-Curtis similarity matrix. A) by canyon B) by dive and C) by habitat type

**Figure 10.** PCA plot of environmental variables for all corals combined

**Figure 11.** Environmental data taken during ROV dives A) Temperature ( $^{\circ}\text{C}$ ), B) Salinity, Density ( $\sigma_{\theta}$ ,  $\text{kg m}^{-3}$ ), D) Dissolved oxygen (ml/L), E) pH, F) Turbidity (formazin turbidity units).  
Water column data has been removed

**Figure 12.** Aragonite saturation state data ( $\Omega_{\text{Arag.}}$ ) for Baltimore and Norfolk canyons, compiled from water samples taken during ROV dives and CTD casts

**Table 1.** Codes used in habitat characterization for ROV dives conducted in Norfolk and Baltimore canyons

**Table 2.** Number of observations (extracted from ROV video transects), depth range, habitat type and environmental conditions associated with corals in A) Baltimore and B) Norfolk canyons. See Table 1 for habitat type descriptions

**Table 3.** Correlations between environmental variables observed during ROV dives in both canyons (Spearman rank correlation coefficients,  $\rho$ ). Significant correlations \* occurred between temperature and both salinity and density.

Table 1.

<b>Habitat Type</b>	
<b>S</b>	Sediment with no hard substrate visible.
<b>SR</b>	Sediment with pieces of rock or emergent hard substrate (EHS); < 50% hard substrate.
<b>R</b>	Isolated rock, rubble, EHS; > 50% cover of hard substrate.
<b>PB</b>	Large areas of EHS, consolidated sediment or hard pavement; >50% hard substrate.
<b>B</b>	Large boulder of rock or consolidated sediment.
<b>W</b>	Walls and steep slopes (rock or consolidated sediment).
<b>Percentage cover categories</b>	
<b>1</b>	0
<b>2</b>	<25% cover
<b>3</b>	25-75% cover
<b>4</b>	>75% cover
<b>Type of Structure-Forming Cnidarians (SFC)</b>	
<b>LC</b>	Large corals: <i>Paragorgia</i> , <i>Primnoa</i> , <i>Anthothela</i> , <i>Paramuricea</i> , <i>Lophelia</i> , <i>Solenosmilia</i>
<b>LA</b>	Large anemones and small corals: Cerianthids, <i>Actinoscyphia</i> , <i>Bolocera</i> , cup corals
<b>M</b>	Mix of TC and LA

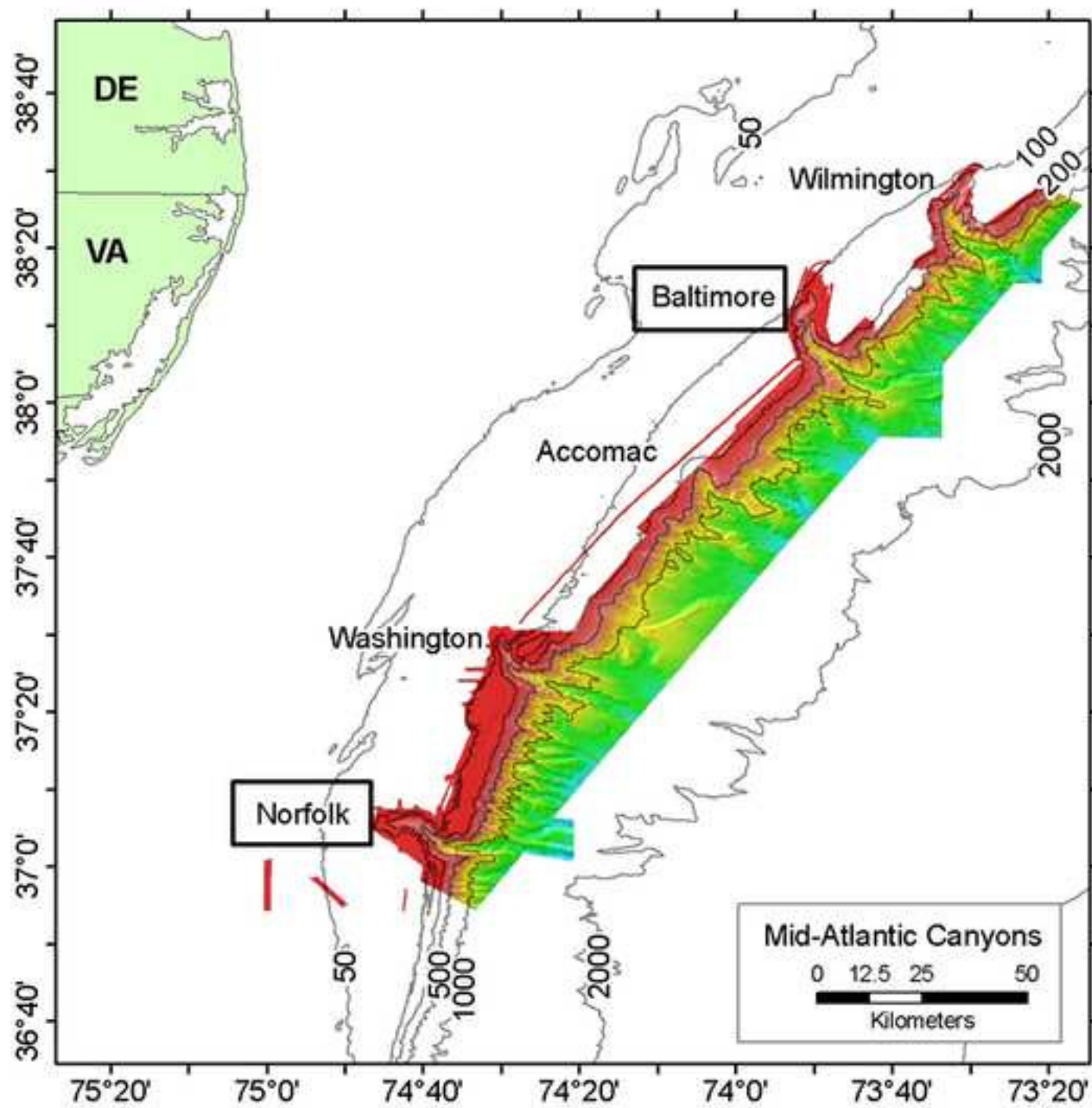
Table 2.

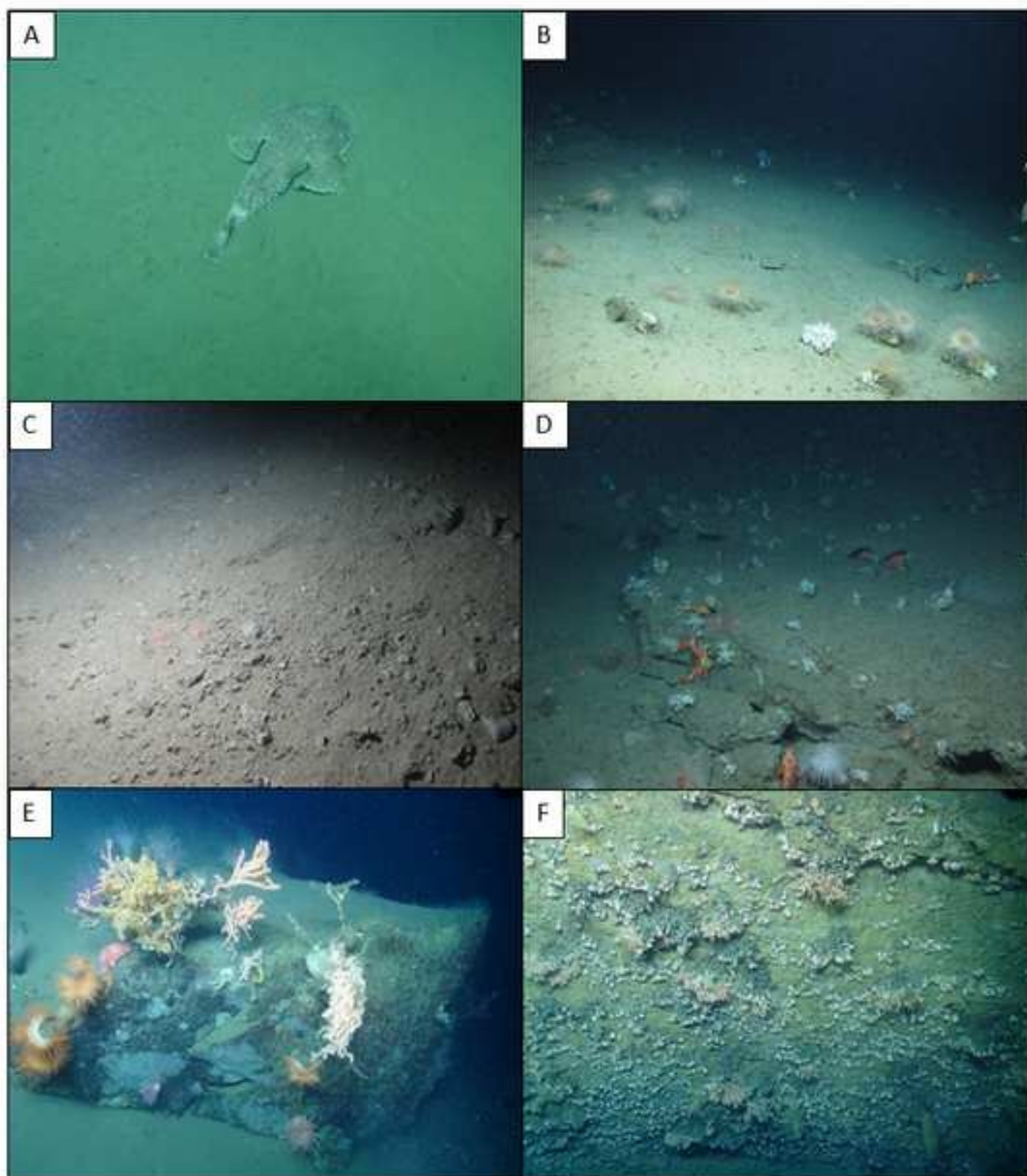
A) Baltimore Canyon							
Species/Taxa	# Obs.	Depth (m)	Habitat types	Temp. (°C)	DO (ml/l)	pH	Turbidity
<i>Desmophyllum dianthus</i>	174	660-672	B, W	4.96-5.17	5.19-5.27	8.07-8.09	52.57-62.56
<i>Lophelia pertusa</i>	5	374-381	W	6.88-7.78	2.86-2.95	8.04-8.05	55.37-55.62
<i>Solenosmilia variabilis</i>	0						
<i>Antipathidae</i>	0						
<i>Parazoanthidae</i>	169	334-448	R, PB, B, W	5.69-9.88	2.46-4.90	8.00-8.07	22.51-90.14
<i>Acanthogorgia aspera</i>	0						
<i>Anthothela grandiflora</i>	571	320-672	PB, B, W	5.02-9.91	1.76-5.30	7.94-8.09	22.51-110.90
<i>Duva florida</i>	1,078	288-396	R, PB, B, W	5.80-11.16	2.24-4.84	8.00-8.10	14.57-90.67
<i>Keratoisis cf grayi</i>	3	428-447	W	6.73-7.27	4.11-4.43	7.96-8.03	27.47
<i>Paragorgia arborea</i>	5,697	331-793	R, PB, B, W	4.86-10.26	1.99-5.08	7.96-8.10	22.51-227.97
<i>Paramuricea placomus</i>	281	306-559	SR, R, W	6.37-9.51	3.73-4.91	8.03-8.08	52.87-144.81
B) Norfolk Canyon							
Species/Taxa	# Obs.	Depth (m)	Habitat types	Temp. (°C)	DO (ml/l)	pH	Turbidity
<i>Desmophyllum dianthus</i>	34,314	417-1390	R, PB, B, W	4.10-8.63	2.95-5.32	8.06-8.15	3.85-192.15
<i>Lophelia pertusa</i>	19	386-424	W	6.39-8.49	2.60-2.83	7.97-8.11	14.42-65.39
<i>Solenosmilia variabilis</i>	306	1264-1388	B, W	4.10-4.29	2.13-4.41	8.11-8.12	3.85-11.10
<i>Antipathidae</i>	9	956-1339	SR, B, W	4.15	4.11	8.11	174.14
<i>Parazoanthidae</i>	531	384-1326	SR, R, PB, B, W	4.12-10.51	2.10-4.45	8.05-8.13	9.08-291.56
<i>Acanthogorgia aspera</i>	1,340	422-1341	SR, R, PB, B, W	4.10-6.67	2.55-5.30	8.05-8.12	3.85-192.15
<i>Anthothela grandiflora</i>	1,709	385-714	R, B, W	4.96-9.09	2.07-5.09	8.04-8.15	11.14-192.15
<i>Duva florida</i>	3,370	416-522	R, B, W	5.22-8.65	2.11-5.09	8.06-8.11	18.92-291.56
<i>Keratoisis cf grayi</i>	9	421-1223	SR, R, B, W	4.10-7.51	No data	No data	No data
<i>Paragorgia arborea</i>	2,166	383-716	SR, R, PB, B, W	4.94-11.41	2.07-5.32	8.04-8.15	10.38-219.23
<i>Paramuricea placomus</i>	256	421-460	PB, W	6.65-6.87	2.38-3.54	8.09-8.11	16.18-45.47
<i>Primnoa resedaeformis</i>	1,641	387-683	R, B, W	4.94-10.91	2.06-4.66	8.04-8.15	12.7-192.15

Table 3.

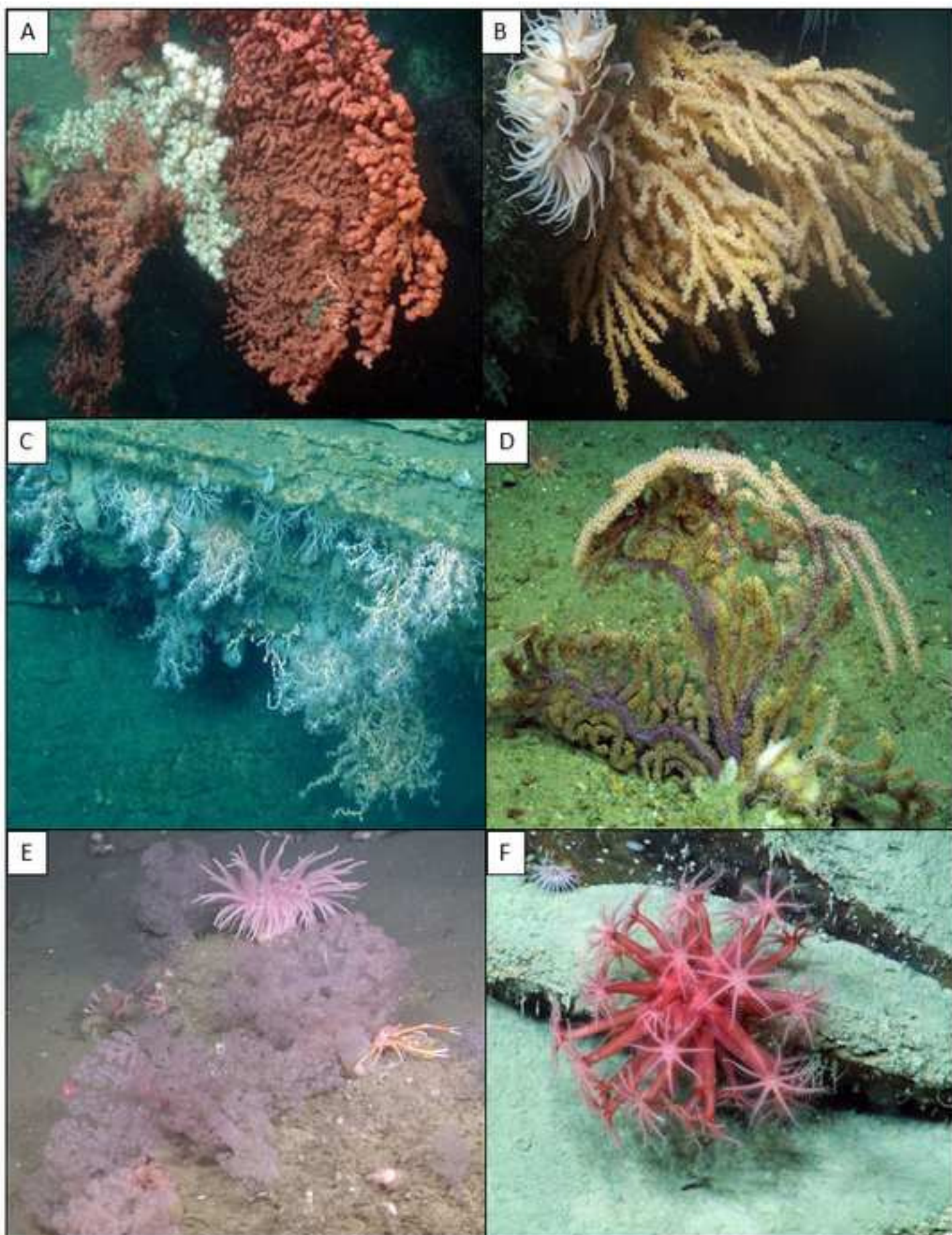
	Depth (m)	Temp. (°C)	Salinity	O <sub>2</sub> (ml/L)	pH	Density $\sigma_\theta$ , kg m <sup>-3</sup>
Temp. (°C)	-0.6628					
Salinity	-0.5526	0.9494*				
O <sub>2</sub> (ml/L)	0.2835	-0.6960	-0.6484			
pH	0.4331	-0.3346	-0.2684	-0.1284		
Density ( $\sigma_\theta$ kg/m <sup>3</sup> )	0.6467	-0.9889*	-0.9011	0.6795	0.3390	
Turbidity (FTU)	-0.2740	-0.1876	-0.2059	0.5106	-0.2830	0.1895

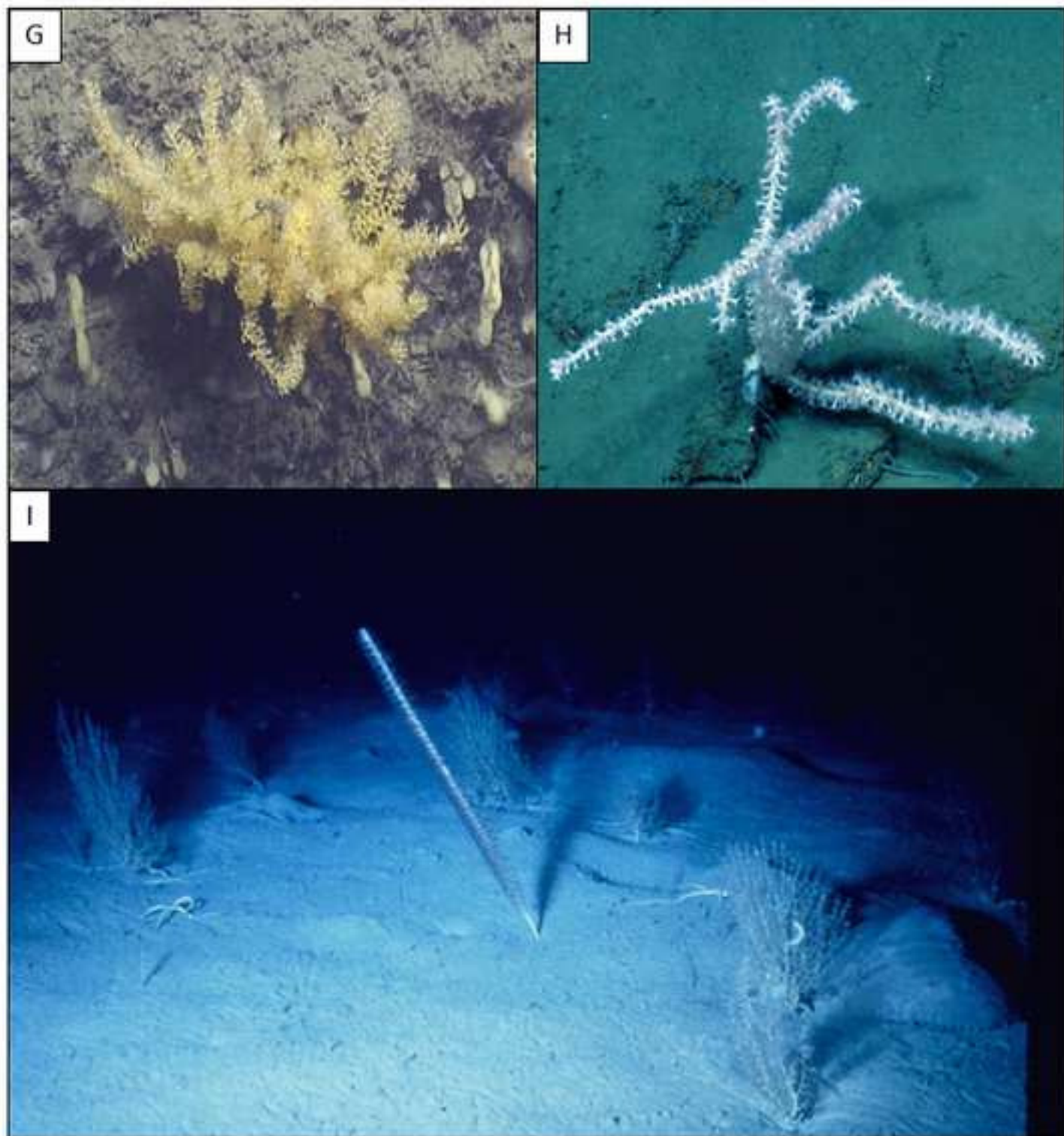
Accepted manuscript

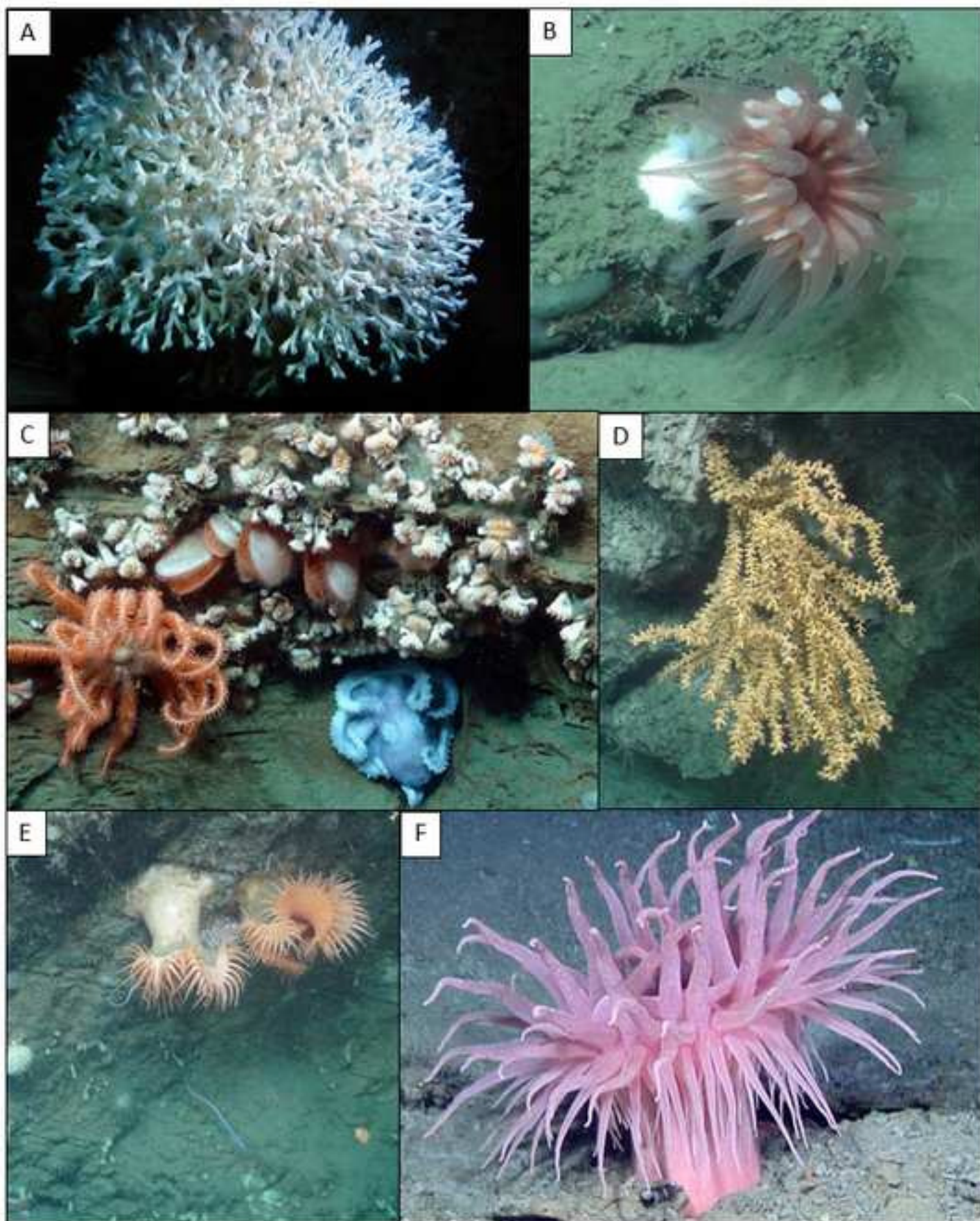


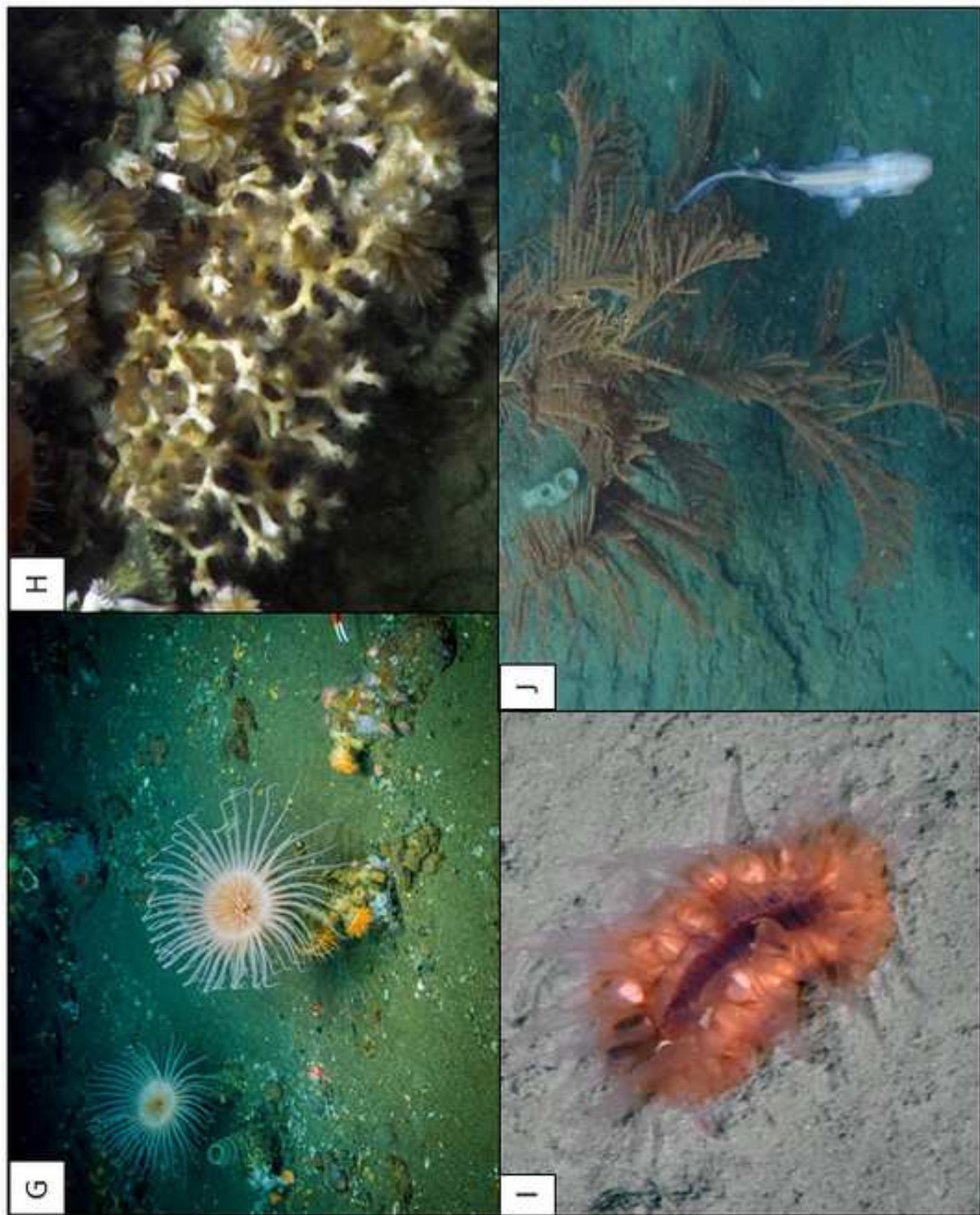




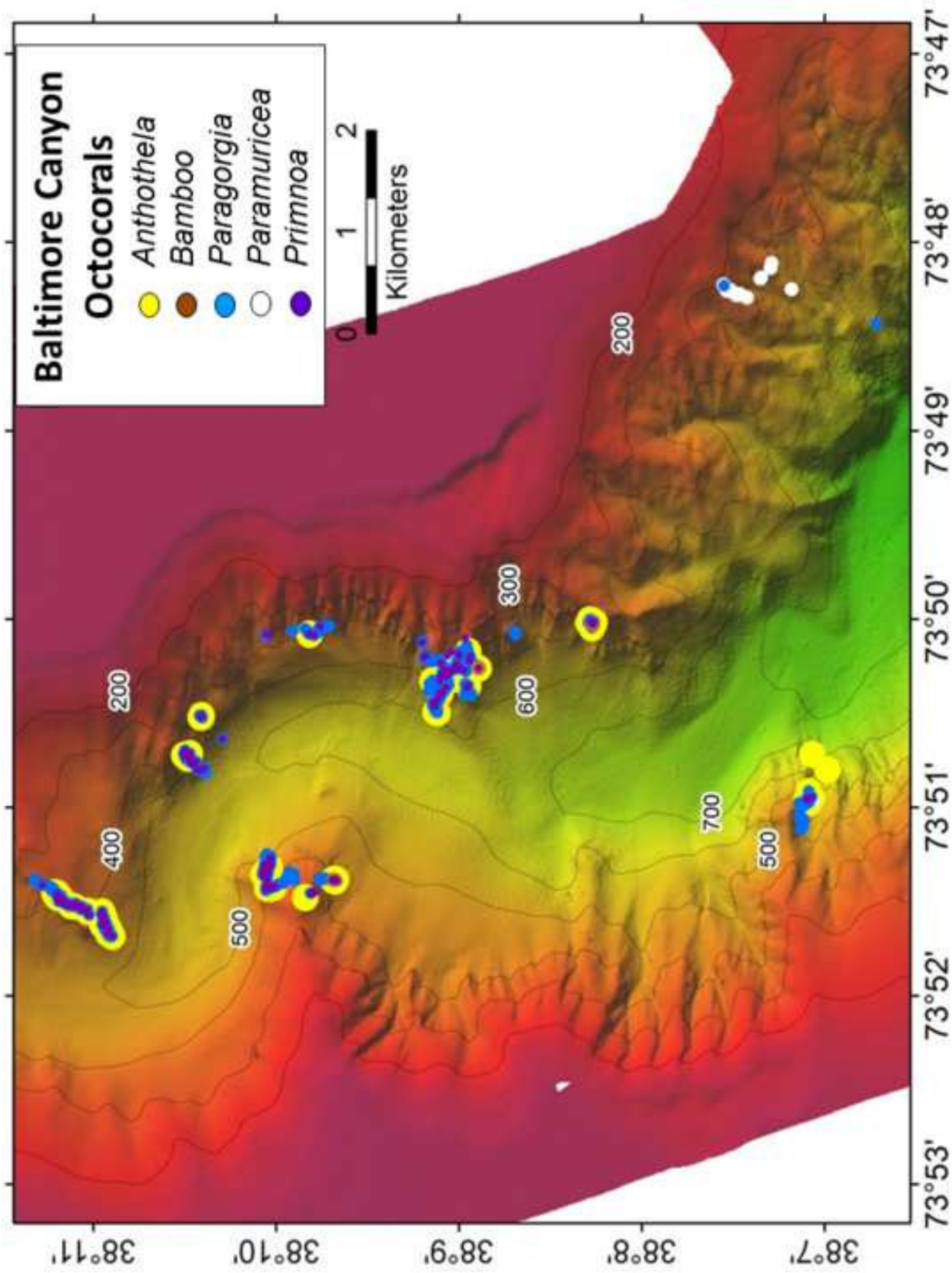


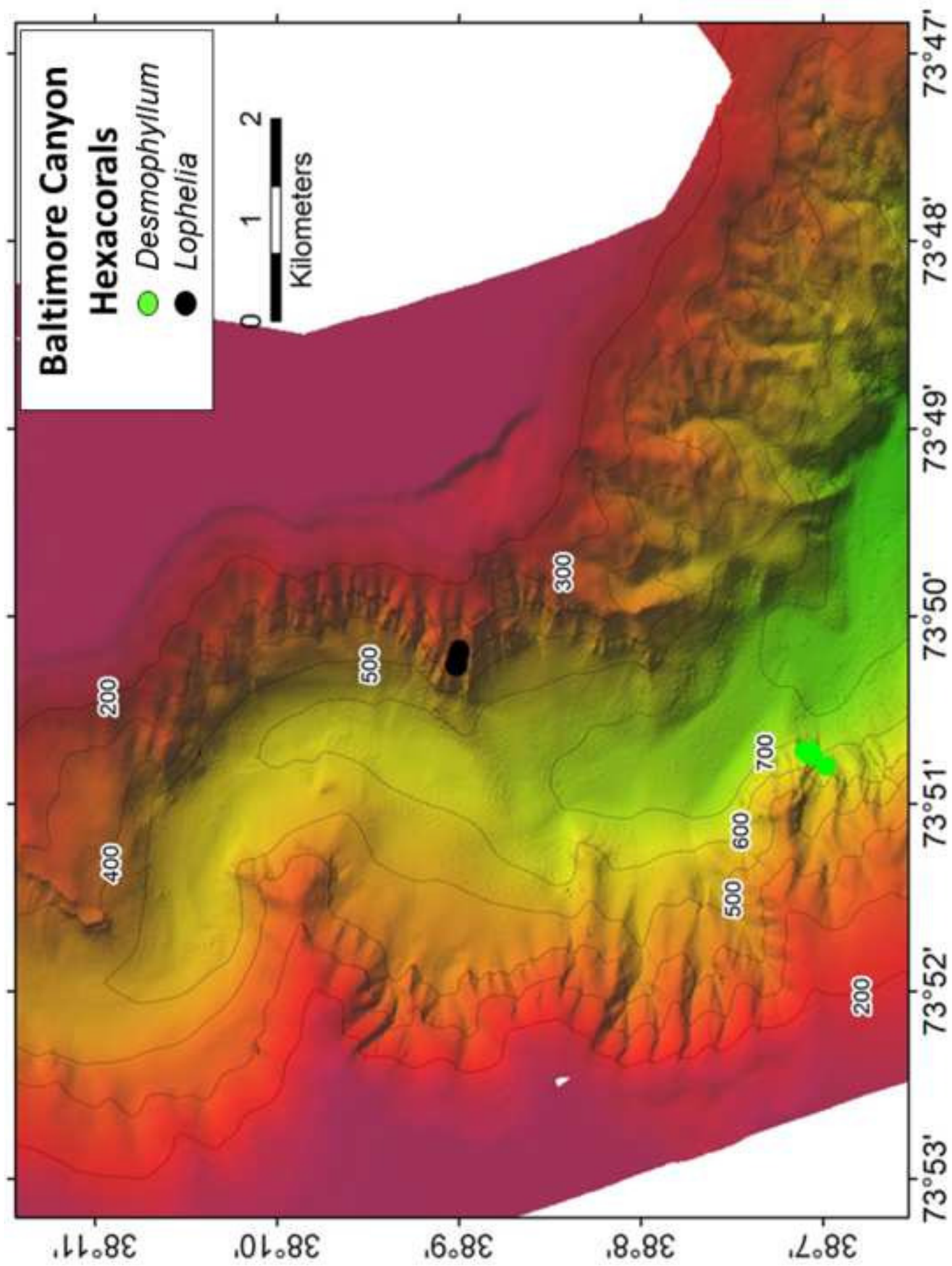




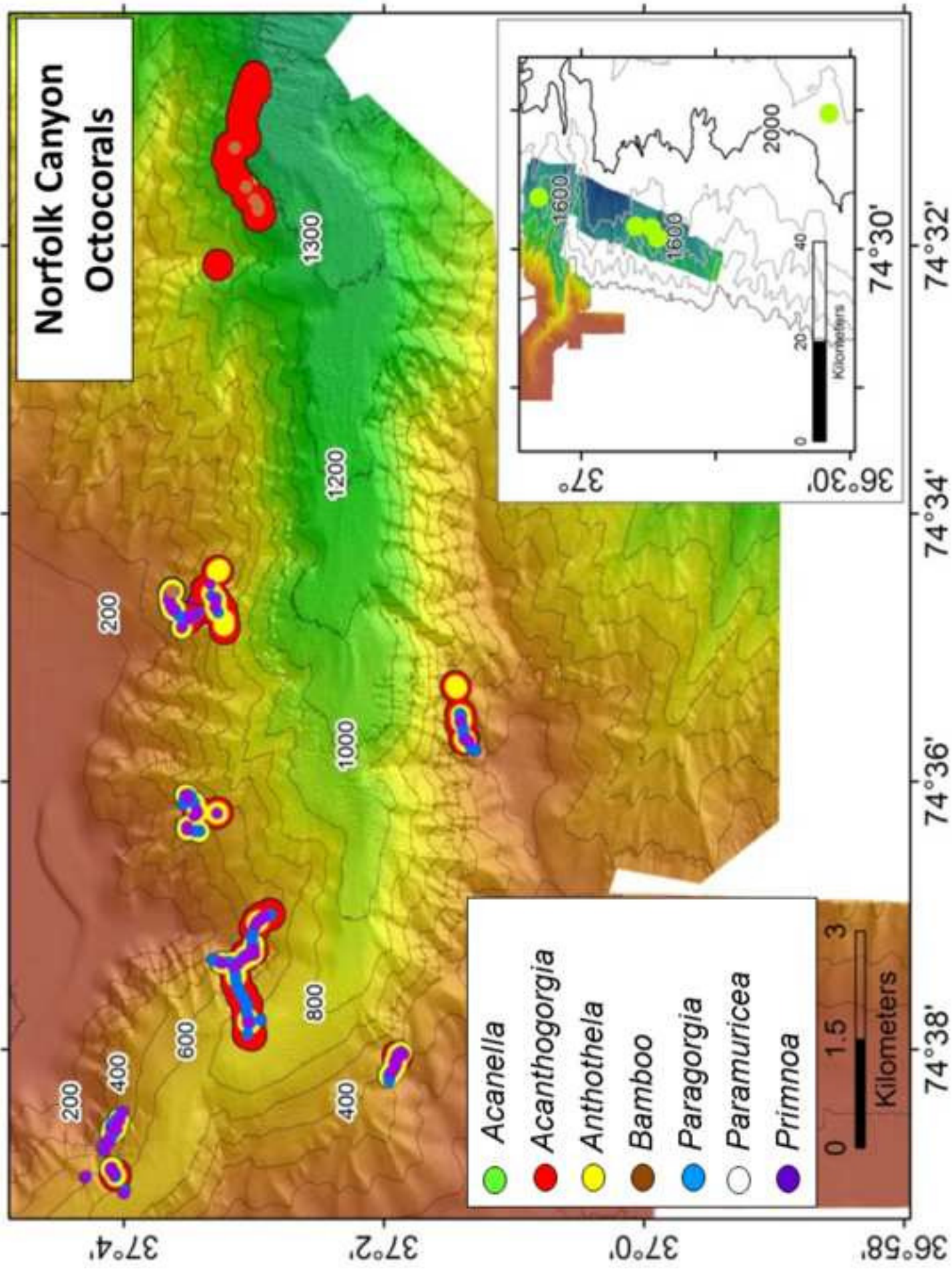


Figure

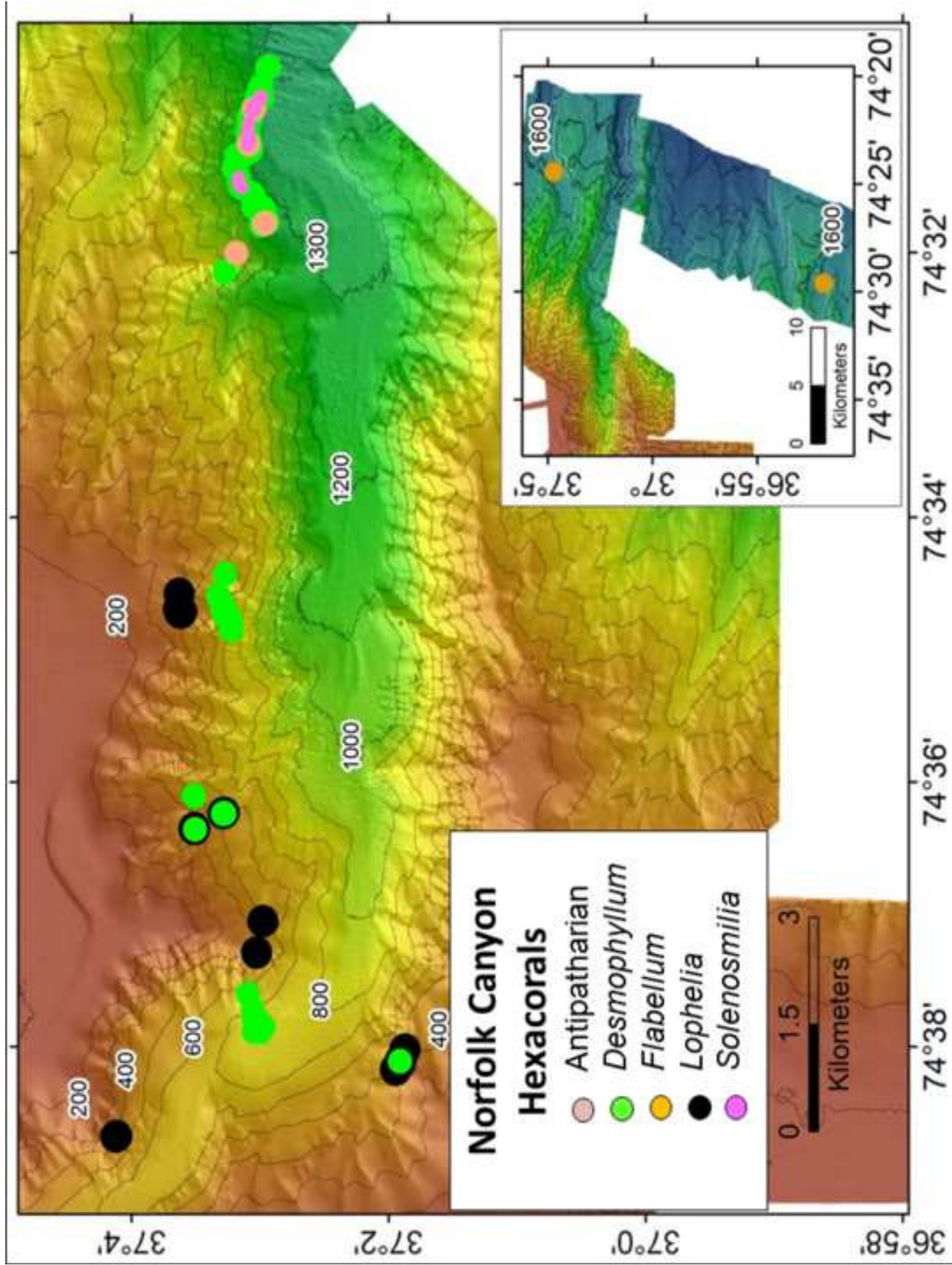




Figure

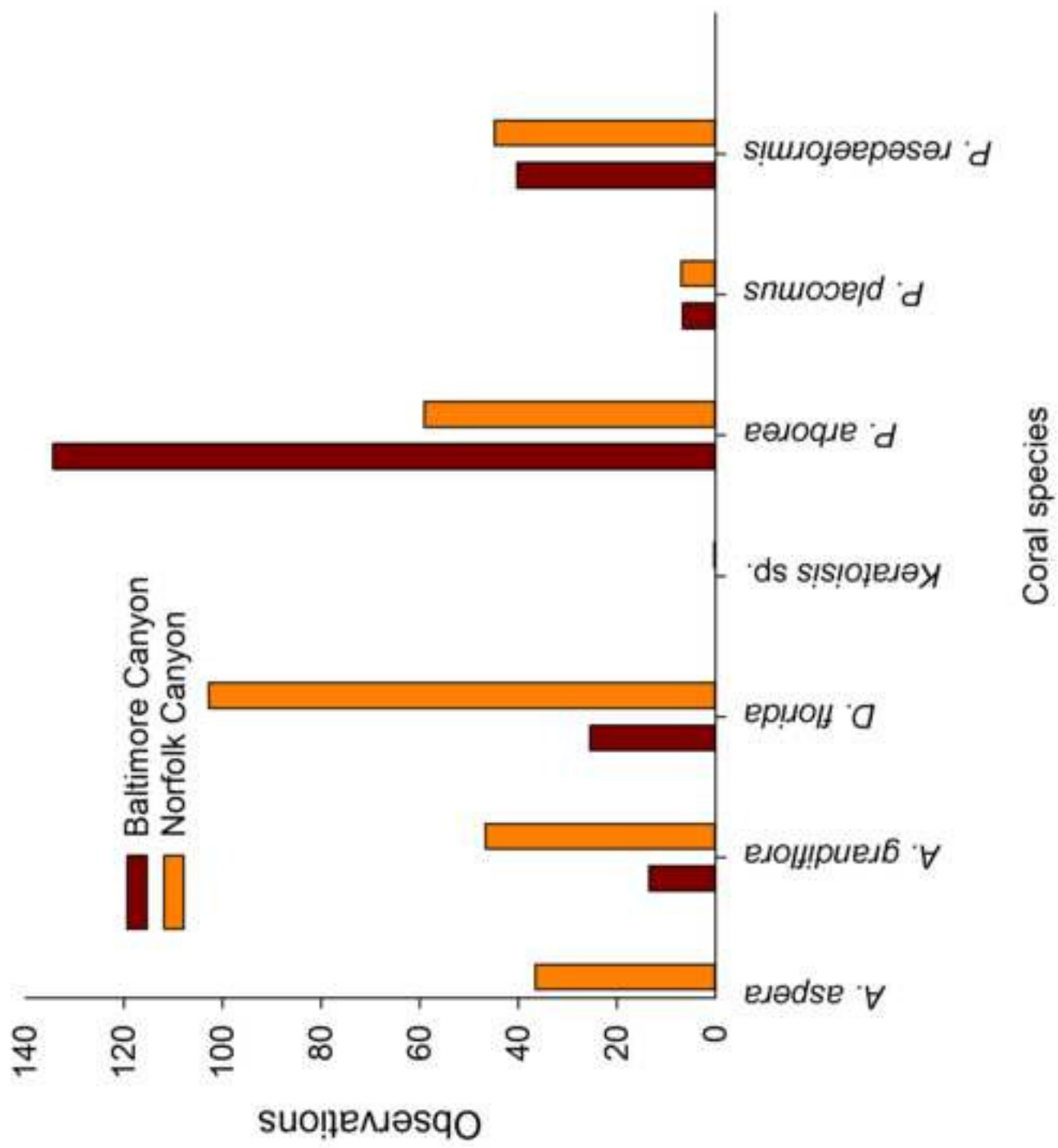


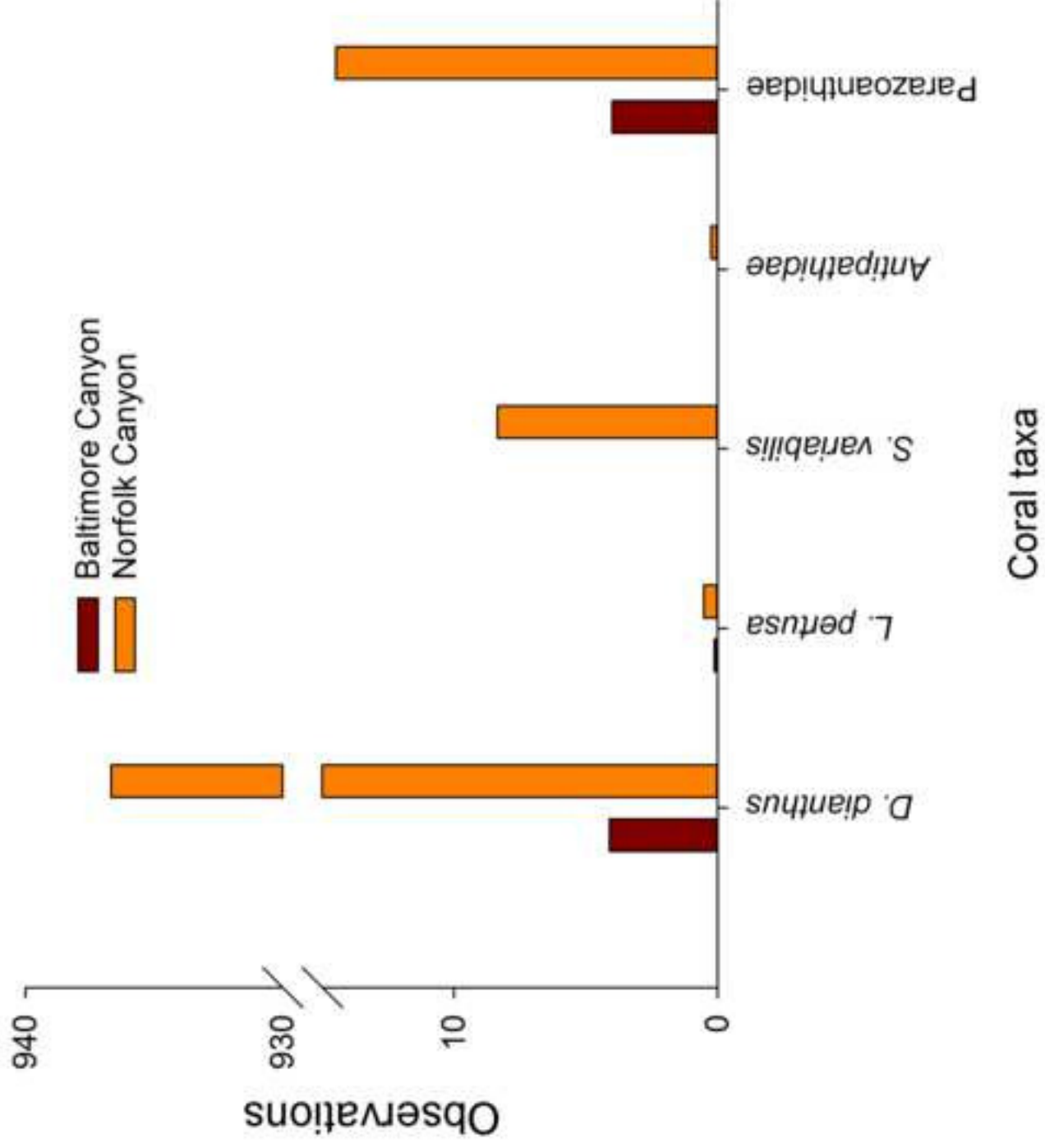
Figure



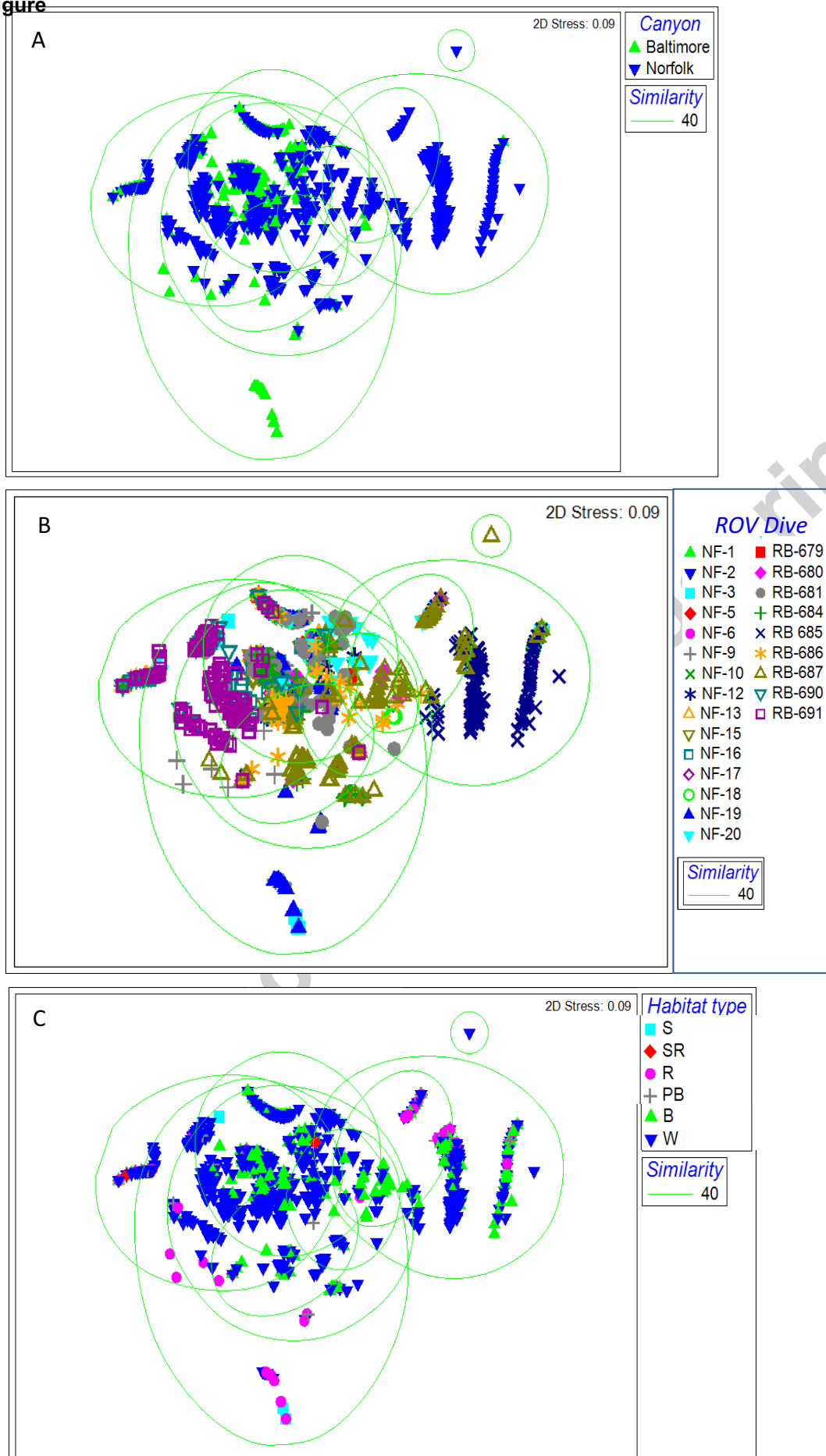
Figure

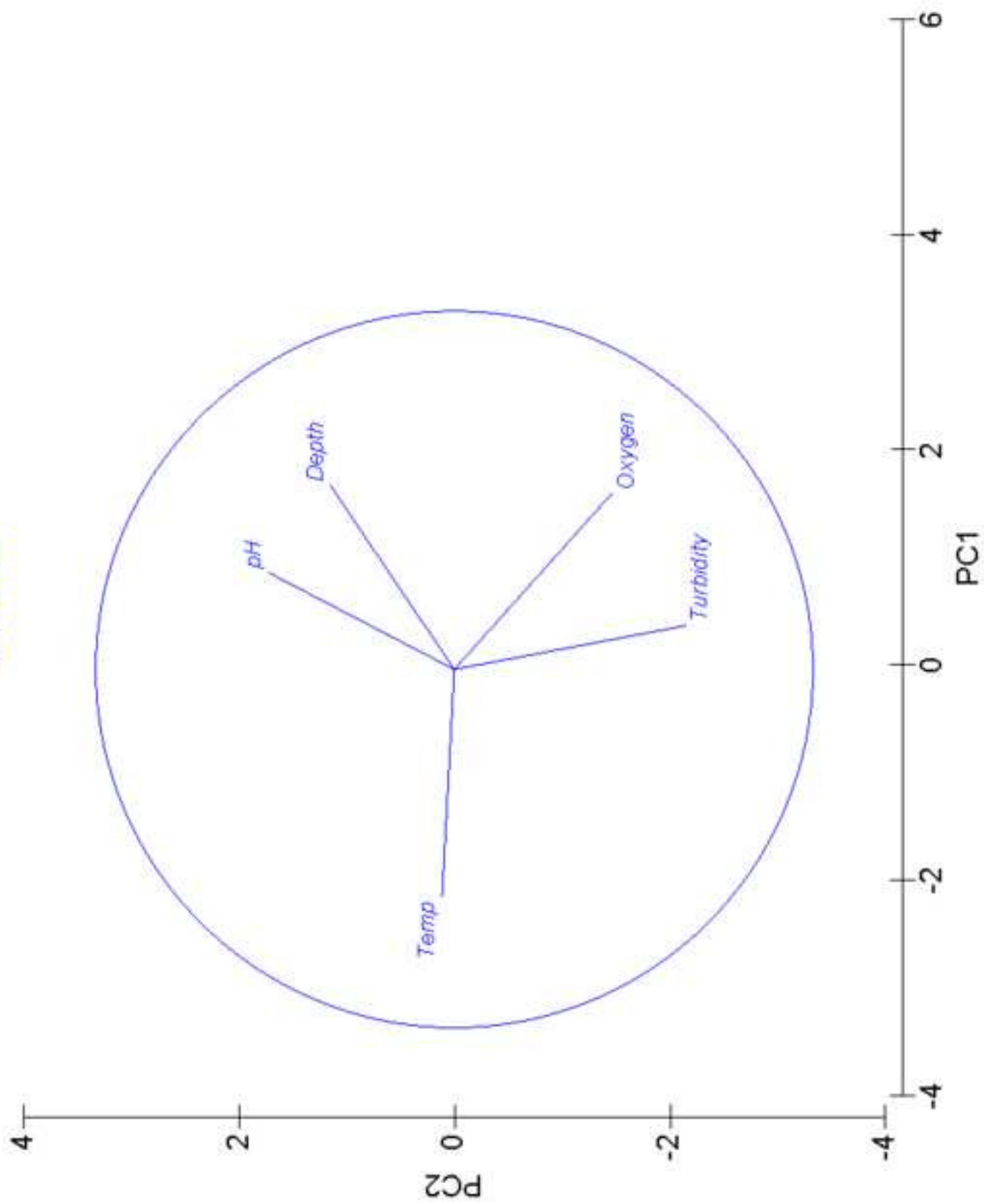


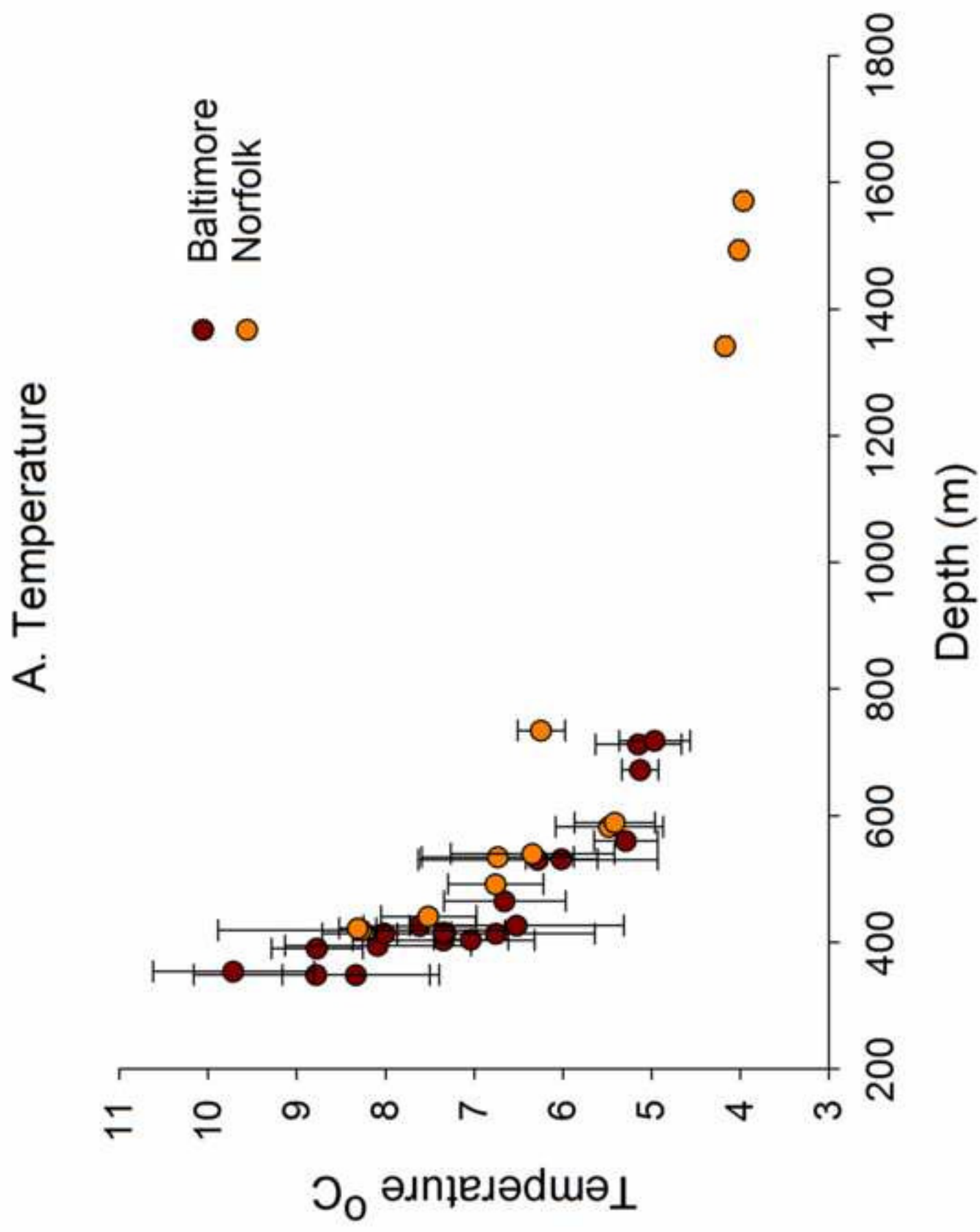




Figure



*Env A11*



## B. Salinity

