Megabenthic assemblages at the Hudson Canyon head (NW Atlantic margin): habitat-faunal relationships

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Abstract

The distribution of megabenthic communities at the head of Hudson Canyon and adjacent continental shelf was studied by means of underwater video transects and still photo imagery collected using a towed camera system. The goal was to explore the relationships between faunal distribution and physical seafloor conditions and to test the hypothesis that increased seafloor heterogeneity in the Hudson Canyon supports a larger diversity of benthic communities, compared with the adjacent continental shelf. Hierarchical cluster analysis was performed to identify benthic assemblages as defined in imagery. The BIO-ENV procedure and the Canonical Correspondence Analysis were carried out to elucidate species groupings in relation to terrain variables extracted from bathymetric data. Species accumulation curves were generated to evaluate species turn over in and out of Hudson Canyon. The results indicate that seafloor morphology is the main physical factor related to benthic community composition and distribution. Assemblages dominated by sponges, zoanthids and cup corals colonized the canyon margins and flanks, and were associated with coarse-grained sediments, while sea pen assemblages were observed along muddy seafloor within the thalweg. An assemblage dominated by sea stars occurred on the shelf, associated with a sandy seafloor. Some assemblages were exclusively observed in the canyon area, suggesting that the increased variability of seafloor composition, together with the oceanographic processes specific to the canyon area, enhance beta diversity. The colonization by benthic suspension feeders within the canyon, in contrast to shelf assemblages, mainly composed of carnivores and detritus feeders could be favored the intense hydrodynamics at the canyon head that increase the availability of suspended organic matter.

From the perspective of management and conservation of marine resources, the results obtained support the relevance of Hudson Canyon as a biodiversity hotspot. Such results are of particular significance in light of the recent action promoted by the Mid-Atlantic Fisheries Management Council, that restricts bottom trawling in most of the submarine canyons of the US Atlantic margin, including the Hudson Canyon, to protect cold-water corals from damage by fishing gear.

Keywords: Submarine canyons; Hudson Canyon; megabenthic communities; physical-benthos relationships; multivariate statistics.

1. Introduction

Submarine canyons are complex and common erosive features of continental margins (Harris & Whiteway, 2011) acting as main conduits for the transport of sediment, organic matter and water masses to bathyal and abyssal depths (Shepard and Dill, 1966; Puig et al., 2014).

The complex topography, the irregular hydrodynamic patterns and the enhanced and diverse sediment transport processes along submarine canyons can create a wide range of environmental conditions that differ from adjacent continental shelf and slope sectors, contributing to increased habitat heterogeneity both at regional (De Leo et al., 2010) and local scales (Huvenne et al., 2011). Heterogeneous environments are predicted to support more complex and diverse biological assemblages, as they provide a high number of niches and diverse ways to exploiting the environmental resources (Tews et al., 2004). Indeed, submarine canyons are generally portrayed as biodiversity hotspots, harboring a significantly higher benthic biodiversity and biomass as compared with the open slope (Rowe et al., 1982; Vetter et al., 2010; De Leo et al., 2010). The upwelling and mixing of water masses along submarine canyons can drive nutrient delivery from deep areas into the euphotic zone, resulting in an enrichment of the water column and pelagic systems (Allen et al., 2001). Increased food availability, along with the heterogeneity of substrates represent favorable conditions for the benthic fauna (Vetter & Dayton, 1998, 1999; De Leo et al., 2010). Canyon heads and walls can present rocky outcrops suitable for fragile sessile filter feeders such as cold water corals, gorgonians and sponges (Orejas et al., 2009; Huvenne et al., 2011; Bo et al., 2012; Johnson et al., 2013; Gori et al., 2013; Pierdomenico et al., 2016), while soft sediment areas typically host fauna dominated by deposit feeders, scavengers and predators, that may benefit from an enhanced food supply (Vetter & Dayton 1998; Okey, 2003).

Biodiversity within submarine canyons is regulated by a complex interplay of multiple factors. Seafloor heterogeneity, food supply, and physical disturbance are often cited as the most important environmental drivers affecting faunal distribution in these environments (Okey, 2003; McClain and Barry, 2010; De Leo et al., 2014). Such parameters depend on a large number of physical factors such as shelf morphology, proximity to river systems, substrate lithology, prevailing oceanographic conditions, sediment transport processes, sedimentation rates, nutrient input and depth (Harris & Whiteway, 2011). Therefore, differing canyons or diverse sections of a single canyon may vary substantially in their topography, hydrodynamic and sedimentary regimes (Puig et al., 2014). These differences result into a high degree of physical and biological variability on both the intra- and inter-canyon level (McClain and Barry, 2010; Würtz, 2012), so that understanding the various controlling factors that determine the complexity of the community structure of submarine canyons can be very challenging.

Submarine canyons are recognized to play important roles in various life stages of a large number of species, as they provide favorable habitats for spawning, recruitment and/or feeding for a broad range of benthic and demersal fishes and invertebrates, including commercially exploited species (i.e. shrimps, lobsters, crabs) (Sardà et al., 2004; Cartes et al., 2004; Danovaro et al., 2010). Furthermore, these topographic features can form natural refuges for faunal communities sensitive to anthropogenic disturbance (Huvenne et al., 2011; Fabri et al., 2014; Gori et al., 2013) and are recognized to be crucial in maintaining some fishery exploited species stocks at a sustainable exploitation level (Farrugio, 2012). On the other hand, the integrity of canyon ecosystems can be seriously threatened by anthropogenic activities. Not only do the heads and the margins of submarine canyons often represent preferential targets for fishing vessels (Puig et al., 2012), but these topographic features may also act as main vectors for litter and pollutant transport from the continental shelf to the deep sea (Mordecai et al., 2011; Tubau et al., 2015). Due to their ecological relevance and the adverse impacts resulting from anthropogenic activities, submarine canyons are often cited as priority areas for conservation (Marin and Aguilar, 2012). However, our understanding of physical and biological interactions in submarine canyons and their role in driving ocean biodiversity is still relatively limited (Bosley et al., 2004; De Leo et al., 2010; McClain and Barry, 2010; Harris and Whiteway, 2011). Due to the difficulty of surveying such complex environments, detailed studies of submarine canyons have only started in the last two decades, in parallel with advances in marine technology such as swath bathymetry, remote sensing, long term time-series observations through submarine observatories and Remotely Operated Vehicles (Ramirez-Llodra et al., 2010; Huvenne et al., 2011). Different investigations carried out in the last decades to promote knowledge of submarine canyons have culminated in recent years in the establishment of protection measures (Marin and Aguilar, 2012). A number of individual canyon systems around the world are currently designated as marine protected areas, such as the Gully Canyon (Canada) (Mortensen and Buhl-Mortensen, 2005), the Murray Canyon Group (Australia) (Williams et al., 2009) and the Soquel Canyon (a side-branch of the Monterey Canyon, USA) (Greene et al., 2002). Furthermore, in June 2015 the US Mid-Atlantic Fisheries Management Council has agreed upon a scheme for protection of cold-water corals, under the re-authorisation of the Magnuson-Stevens Fishery Conservation and Management Act of 2006 (*http://www.mafmc.org/actions/msb/am16*), which was subsequently approved by the U.S. Secretary of Commerce in November 2016. The protection scheme restricts bottom fishing activities over a large area of the US Atlantic continental margin, including 15 submarine canyons where the presence of cold-water coral was documented or deduced by habitat suitability models (Brooke and Ross, 2014; MAFMC and NMFS, 2014; Pierdomenico et al., 2015).

Hudson Canyon, about 200 km off New York City, represents a productive ecosystem that supports commercial and recreational fisheries (NEFMC, 2014) and has been included within the scheme of deep-sea coral protection. However, it has not been as extensively explored as other submarine canyons along the US continental margins (Hecker et al., 1983; Brooke and Ross, 2014), especially for the biological benthic communities. Recent studies (Pierdomenico et al., 2015; Rona et al., 2015) show that the upper reach of the Hudson Canyon is characterized by complex oceanographic patterns and by a great variability of sedimentary and topographic features that may contribute to create favorable conditions for the development of varied physical habitats, enhancing the local productivity and promoting biodiversity.

In order to investigate the effect of increased seafloor heterogeneity in the Hudson Canyon on the variability of benthic communities, a quantitative analysis of megafauna distribution along the canyon and surrounding shelf areas was performed using video transects and still photographs. The aim of this study is therefore to identify and describe the megabenthic assemblages of the canyon and surrounding shelf and to explore and evaluate the relationship between physical seafloor conditions and benthic faunal distribution in a highly productive environment recognized as an important commercial and recreational fishing “hotspot”.

2. Study area

Hudson Canyon (Fig. 1) is the largest shelf-sourced canyon system off the east coast of the United States and one of the largest of the world (Ericson et al., 1951; Pratt 1967). It extends for over 400 km, from the outer shelf at ~80 m depth down to the upper continental rise at ~3500 m depth (Heezen et al.,1959; Pratt,1968). The canyon head is composed of two branches NW-SE and N-S oriented, that merge at ~120 m depth (Fig. 2) (Stanley and Freeland, 1978). The canyon continues seaward cutting through the continental shelf and slope for ~ 50 km, with walls attaining a maximum relief of ~1200 m and rim-to-rim width of 5-10 km (Butman et al., 2006). The canyon walls display an intricate network of gullies indicating mass wasting (Twichell and Roberts, 1982).

The Hudson Shelf Valley, a shallow trough extending across the continental shelf, connected the Hudson River to the canyon head during glacial lowstands (Knebel et al., 1979). Current, sediment distribution, and direct observations along the Hudson Canyon indicate that during the present high-stand of sea level the canyon is relatively inactive in relation to the fluvial-sourced coarse-grained sediment transport processes; however it still functions as a conduit for the suspension and transport of fine-grained material to the continental rise and the abyssal plain (Cacchione et al., 1978; Keller & Shepard 1978; Stanley & Freeland 1978; Able et al., 1982; Hotchkiss and Wunsch, 1982). The main forces responsible for sediment transport within the canyon include tidal currents, internal waves and storms (Cacchione et al., 1978; Keller & Shepard 1978; Hotchkiss and Wunsch, 1982). Previous measurements of bottom current velocities within the Hudson Canyon revealed energetic along-canyon axis currents (> 20 cm/s) with semidiurnal flow reversal closely approximating the tidal cycles (Keller et al., 1973; Keller and Shepard, 1978). At the head of the canyon, breaking and dissipation of internal waves promotes sediment resuspension, mixing and water mass exchanges (Hotchkiss and Wunsch, 1982).

Holocene gravel and coarse-sand deposits of fluvial origin are present at the canyon head, showing evidence of reworking by currents and bioturbation (Schlee and Pratt, 1970). These coarse relict sediments occur down to 130-150 m depth, where a sharp boundary separates from muddy deposits starting to predominate at greater depths. This appears to record a long-term separation of different energy zones, i.e. below that boundary zone strong bottom currents are not frequent nor strong enough to erode fine-grained muddy sediments (Stanley and Freeland, 1978).

The head of Hudson Canyon represents a highly productive area recognized as a commercial and recreational fishing “hotspot” area (NEFMC, 2014). It also has been under evaluation for the assignment of a Habitat Area of Particular Concern (HAPC) status before being included in the aforementioned cold-water corals protection scheme.

As observed for other shelf-indenting canyons along the north-west Atlantic margin (Hecker et al. 1983; Brooke and Ross, 2014), the Hudson Canyon is suitable to host a richer and more varied fauna compared to the surrounding shelf and slope areas. Rowe et al. (1982) found that macrofaunal composition inside the canyon did not differ substantially from the adjacent slope (except for high densities within the canyon's head). Nevertheless, more recent climatological Coastal Zone Color Scanner (CZCS) satellite observations of surface chlorophyll values indicate enhanced surface primary productivity near the head of Hudson Canyon (Ryan et al., 1999). Catch data from the Northeast Fisheries Science Center (NEFSC) suggest a strong and persistent role of the canyon in enhancing fisheries on the surrounding shelf (NEFMC, 2014). Furthermore, commercial and recreational catches in the shelf areas surrounding Hudson Canyon indicate the occurrence of a great variety of demersal fishes and invertebrates (Jacobson et al., 2009; Mayo et al., 2009). Stevenson et al. (2004) reported intense bottom trawl fishing activity for the period between 1995 and 2001 in the shelf areas around the canyon. Limited observations of biological productivity in the pelagic environment suggest that krill aggregations within Hudson and other US Atlantic canyons attract a large number of marine mammals (Waring et al., 2001). Evidence of the occurrence of cold-water corals within Hudson Canyon are reported by Hecker and Blechschmidt (1980), who found abundant populations of the soft coral *Eunephthya fruticosa*, in its deeper portion (about 3000 m depth). Solitary stony cold-water corals were also observed at the canyon margins at about 120 m depth and on the shelf adjacent to the canyon (Packer et al., 2007; Pierdomenico et al., 2015).

3. Data and methods

The dataset used in this study includes video imagery and still photographs collected within the Hudson Canyon and surrounding shelf areas by the USGS Sea Bottom Observation and Sampling System (SEABOSS), a towed video vehicle. The use of bathymetric data collected by USGS (Butman et al., 2003) enabled the extraction of seafloor physical habitat variables (i.e. depth, slope and aspect) used to explore the relationships between faunal distribution and seafloor characteristics. In addition, demersal fishes and benthic megafaunal catches drawn from database records of 57 otter trawls (NEFSC Yankee 36, Politis et al., 2014) and 116 beam trawls made in or near Hudson Canyon, aboard 12 NEFSC benthic habitat cruises between years 2001 and 2011, provided voucher organisms for the taxonomical identification of the benthic fauna observed on videos and photos. All data stations used in this study are shown on the map in Fig. 2.

3.1 SEABOSS imagery data

Imagery data were acquired in 2004 during a benthic habitat characterization cruise conducted in the Hudson Canyon area aboard the NOAA Ship *Delaware II*, using the USGS SEABOSS drift transect camera vehicle that has no built-in propulsion. Transect deployments were made by positioning the vessel up-current of a selected center position for a transect, dropping SEABOSS, tethered on a conducting cable, to within 1-2 m of the bottom, then allowing it to drift with the ship for approximately 20-30 min. at speeds ranging up to 1 m/sec before retrieval. Live video feeds were used to continuously monitor vehicle altitude from the bottom and avoid obstructions, allowing the vehicle to be “flown” over the seafloor by a shipboard operator while the support vessel was drifting, using a dedicated winch to maintain its height off the bottom.

SEABOSS has two video cameras (forward and downward looking, Kongsberg Simrad Osprey), a downward looking 35 mm camera (Photosea), and a modified Van Veen grab sampler, used to take a single sediment sample per transect for grain size analysis. Quartz halogen lights provide illumination for the video, and an electronic flash unit provides lighting for still photography. Dual lasers provide accurate photographic range and scale information. Images from both video cameras are recorded on tape, but also viewed in real time, allowing collection of representative still photographic images, taken at an average rate of one photo per minute. As SEABOSS hangs nearly vertically from the ship during deployment, ship-mounted GPS provides georeferencing for these photos.

The image dataset used includes approximately 12 hours of low-resolution videos from the two video cameras (forward and downward looking), and 1134 high-resolution still photos from the downward looking camera, collected by the vehicle at 28 stations along the Hudson Canyon and the surrounding shelf areas, at depths ranging from 75 to 200 m (Fig. 2 and Tab. 1). SEABOSS transect stations were chosen based on pre-existing backscatter data (Butman et al., 2003) in order to include canyon margins and walls, the thalweg, and the adjacent shelf, characterized by different acoustic response of the seafloor and likely to represent different habitats.

Video sequences from the downward looking video camera were edited using the software Final Cut Pro (Apple® Inc.). All megafaunal organisms were enumerated and identified to the lowest possible taxon, which corresponded to species, genus, family or even higher taxonomic levels in some cases. When specific taxa could not be assigned, a general distinction in morphotypes was applied. Seafloor type was reported along with the identification of the organisms. Six classes of seafloor types were defined: Cobbles and pebbles, Mudstone outcrops, Gravelly sand, Sand, Muddy sand/Mud, Sub-outcropping/Outcropping rock.

All video sequences were then split into transect fragments of equal distances, based on the vessel position and the timecode of the edited videos, which are hereafter designated as sampling units (SU). Starting from the beginning of each transect, sampling units of 5 m^2 (0.5 m width and 10 m long) and 25 m^2 (0.5 m width and 50 m long) were defined and used for the statistical analyses.

Counts of epifauna were converted to individuals/m^2. Seafloor type, along with depth, slope and aspect extracted from multibeam data (see 3.2) were assigned to each of the 5 m^2-SUs. Sequences where silt clouds obscured the image or where the altitude of the towed vehicle above the seabed was too high to properly identify megabenthic organism (>2m) were considered of poor quality and removed for subsequent analyses. Highly mobile species such as fish were also removed from the dataset prior to statistical analyses.

The low resolution of the videos implied that the presence of some taxa (mainly small size organisms that could be observed on the photos) could not be detected reliably if at all on the video footage and had to be excluded from the subsequent statistical analyses. Among them, zoanthids and solitary corals, whose presence on the videos was distinguishable even though they could not be easily enumerated, were observed to be very abundant components of the epifauna at specific stations. Information about the abundance of these two groups along the video transects was therefore obtained from the analysis of simultaneous still photos and extrapolated to the videos. The density estimates of zoanthids and solitary corals extracted from the still photos included into a specific SU was used as a proxy for the entire 5 m^2 or 25 m^2 SU. In the case more than one photo was included in a single SU the mean density was calculated.

3.2 Terrain variables

The environmental descriptors used for the statistical analyses were extracted from multibeam bathymetric data provided by Dr. Bradford Butman (USGS). The acoustic dataset was collected by the USGS along the Hudson Shelf Valley down to the Hudson Canyon head (Butman et al., 2003), using a shipboard Simrad Subsea EM1000 Multibeam Echo Sounder (95 kHz). A 12 m resolution bathymetric grid from the study area was used to derive additional environmental layers (12 m resolution) such as slope and aspect (Fig. 2).

3.3 Statistical analyses

To identify the megafaunal assemblages, a hierarchical cluster analysis with group-averaged linkage was performed on the 25 m^2 SUs, using a Bray–Curtis similarity matrix derived from the square root transformation of the data. The similarity percentages (SIMPER) routine of the PRIMER v6 software (Clarke and Warwick, 1994) was used to identify the key species that characterized those clusters. Characterizing species were defined as those species that contributed >10% to cluster similarity.

Following initial analyses, the use of 50-m distance transect segments (25 m^2) was observed to provide the most appropriate level of data resolution to depict consistent groups, since the use of smaller sampling units would produce inconsistent results. This is similar to the strategy suggested by Orpin and Kostylev (2006), who suggest that data should be collected at the highest practical resolution, but be reduced to a resolution meaningful for statistical analysis, in accordance with the total sample population. Conversely, the relationships between patterns in multivariate community structure and the examined seafloor terrain variables (seafloor type, depth, slope and aspect) were examined at a finer spatial scale using the 5m^2 SUs. The choice of a sampling unit area of 5 m^2 was motivated by the sampling resolution of the still photos. The still photos were used to estimate the abundance of zoanthids and cold-water corals within SUs, therefore the average distance between consecutive photos (about 10 m) determined the finest resolution that could be obtained without losing information. Furthermore, the resolution of these SUs matched the resolution of the geophysical data used to extract the seafloor terrain variables.

The Biota Environment Matching (BIO-ENV) procedure in PRIMER v6 software (Clarke and Ainsworth, 1993) was used. This consists in a comparison between the similarity matrix of the biota and a parallel matrix of abiotic environmental variables to determine which variable best explains the distribution of taxa, using the Spearman’s correlation coefficient (ρ).

A Canonical Correspondence Analysis (CCA) was then carried out selecting the environmental variables most closely related to the megafaunal distribution, that resulted from the BIO-ENV procedure (seafloor type, depth and slope). The CCA is a multivariate constrained ordination technique that can be used to elucidate the relationships between biological assemblages of species and their environment (Ter Braak et al, 1995). This method operates on species abundances and corresponding environmental variables and extracts synthetic gradients from combinations of the measured environmental variables (ordination axes) that maximize the niche separation among species. In order to avoid distortions that can be produced by rare data, the sampling units containing taxa that were only sporadically observed on videos (less than three times) were removed prior to the analysis. In this manner, CCA was conducted on a revised dataset of 1241 10-m long ($5m^2$) sampling units containing 16 benthic taxa, using the statistical software R (R Development Core Team 2014) and the 'vegan' package for the permutation tests for the significance of constraints. The resulting ordination diagrams are used to identify and visualize species groupings in relation to environmental features.

To compare species richness among communities and to investigate the influence of habitat heterogeneity on species turn over (beta-diversity) in and out of Hudson Canyon, species accumulation curves were calculated. Using the statistical software R and the 'vegan' package, randomized species accumulation curves were generated for each community and for each seafloor type. Species accumulation curves were also calculated for canyon and continental shelf by pooling all SUs from all transects within canyon and shelf sites. The method used finds the mean species accumulation curves and their standard deviation from random permutations of the data, which avoids distortions in the curves due to variations in species abundance and sampling effort (Gotelli and Colwell, 2001).

4. Results

4.1 Megafaunal assemblages

The video sequences covered a linear distance of more than 13 km across a wide range of slopes, substrates and depths. A total of 20 invertebrate and 14 fish taxa (including all taxonomic and morphotype levels) were identified in all the analyzed video footage (Appendix A). In addition, 9 invertebrate taxa that were not visible on the low resolution videos, were identified from the still photos (Appendix A).

A total of 267 50-m-long SU were used for the cluster analysis, which recognized five significantly different benthic assemblages at 40% similarity level (Fig. 3) whose spatial distributions are illustrated in the map of Figure 4. These five groups are well defined in terms of species composition, with a mean within-assemblage similarity (based on Bray-Curtis distances of square root transformed data) between 60% and 77%.

Assemblage A (*Astropecten* assemblage) was largely dominated by the margined sea stars *Astropecten americanus* (Fig. 5) and by Maldanidae polychaetes. Other common species included the burrowing anemone *Edwardsia* sp, cancrid crabs (*Cancer* sp., Fig. 5) and several sea star species that could not be identified to species level. Less frequent species observed on the still photos comprised the top shell snail *Calliostoma bairdii* and the sidegill sea slug *Pleurobranchea tarda*. This assemblage was mainly distributed along the continental shelf between 80 and 100 m depth and at the canyon margins, especially on the western side close to the canyon head (Fig. 4). It occurred preferentially on flat (0-3° slope) sandy seafloor (Fig. 6), although along the canyon margin and walls it was sporadically present on gravelly sediment or muddy sand.

Assemblage B (*Placopecten* assemblage) featured the sea scallop *Placopecten magellanicus* (Fig. 5), *A. americanus* and Maldanidae polychaetes as the most common species. Less frequent taxa observed on videos included other sea stars and porifera. Still photos within this assemblage also showed significant occurrences of crangonid shrimps (*Crangon septemspinosa* and *Pontophilus brevirostris*). This assemblage was only observed at two stations on the continental shelf in the westernmost sector of the study area (70 m depth, Fig. 4), where the seafloor was mainly composed of gravelly sands (Fig. 6).

Assemblage C (zoanthids assemblage) was mainly composed of zoanthids (possibly *Epizoanthus* sp.) and porifera (Fig. 5). The low resolution of the video footage, and the lack of samples prevented the identification of porifera species to a lower taxonomic level. However, from the still photos at least five morphospecies of poriferans (including two encrusting and three erect morphospecies, all demosponges) were recognized. Other common species included different morphospecies of anemones, the sea stars *A. americanus*, *Leptasterias tenera* (Fig. 5) and other sea star species that could not be identified to species level. The sea star *Stephanasterias albula* and galatheid crabs (*Munida iris iris*) were also commonly observed on the still photos. Assemblage C occurred on a wide range of depths, slopes and substrates (Fig. 6), but its spatial distribution was mainly restricted to the canyon area, especially along the eastern margin and upper part of the wall (Fig. 4). Although the cluster analysis revealed a unique group for the Assemblage C, quantitative variation in the relative density of zoanthids and porifera along the video transects (Figs. 7 and 8) allowed recognition of two different "facies" within this assemblage: the zoanthids facies and the porifera facies (Fig. 5). Porifera were mainly distributed along the canyon margins, whereas zoanthids reached their highest density along the steeper sectors of the canyon walls (Fig. 8).

Assemblage D (*Dasmosmilia* assemblage) exhibited a similar composition as the previous one, from which it was distinguished by the lower abundance of porifera and the great abundance of the solitary splitting cup coral *Dasmosmilia lymani* (Fig. 5), which was the most abundant and frequent species of this assemblage, locally reaching very high densities of more than 300 individuals/m^2. This assemblage was only observed at the canyon margins between 100 and 120 m depth (Fig. 4), both on sandy and gravelly substrates (Fig. 6).

Assemblage E (*Stylatula* assemblage) was almost entirely represented by sea pen *Stylatula elegans* (Fig. 5). Some individuals of *A. americanus* are also observed on videos, while the still photos showed the arms of numerous partially buried brittle stars (Ophiuroidea) protruding from the seafloor. This assemblage was observed on muddy sands within the thalweg of the canyon and the tributary channel between 160 and 200 m depth (Figs. 4 and 6).

Regarding the fish fauna, the most abundant species overall were spotted and red hakes (*Urophycis chuss* and *U. regius*, Fig. 5) and Gulf Stream and four spot flounders (*Citharichthys arctifrons* and *Paralichthys oblongus*). Snake eels (Ophichthidae) and clearnose skates (*Raja eglanteria*) were also commonly observed on videos. The most frequent species at the canyon stations were the black belly rosefish (*Helicolenus dactylopterus*) and the chain dogfish (*Scyliorhinus retifer*). Other species identified in the video transects were monkfish (*Lophius americanus),* butterfish (*Peprilus triacanthus*) and the fawn cusk-eel *Lepophidium profundorum.*

4.2 Megafaunal distribution and relationships with the terrain variables: BIO-ENV and CCA results

The spatial distribution of the main taxa that characterize the observed assemblages (Fig. 7) showed that some of the species such as *Astropecten americanus*, were present with relative high density through the entire study area, whereas the presence of organisms like zoanthids and the splitting cup corals *Dasmosmilia lymani* were restricted to the immediate vicinity of Hudson Canyon (i.e. within <1 km of the canyon rim). Other taxa such as poriferans and white sea pens *Stylatula elegans*, although observed both on the continental shelf and the canyon, showed the highest frequency of occurrence and the highest densities in the canyon vicinity (Fig. 7).

Table 2 illustrates the rank correlation (ρ) obtained with the BIO-ENV procedure between the environmental parameters analyzed and the faunal distribution. Results show that the suite of environmental variables most closely correlated to the distribution of the different taxa ($\rho = 0.558$) includes seafloor type, slope and depth. Seafloor type is the single factor that reaches the maximum matching coefficient ($\rho = 0.523$) and when further explanatory variables are added ρ slightly increases. However, ρ decreases if aspect is included, probably due to its minor effects on community structure (Clarke and Gorley, 2006).

The CCA biplot (Fig. 9) shows that the first canonical axis (eigenvalue 0.61) mainly splits the data along a gradient between loose and cohesive substratum, while the second canonical axis (eigenvalue 0.42) splits across the grain size classes. The permutation tests on canonical axes show that all axes are significant ($p<0.01$) as well as the species-environment correlations ($p<0.01$ for all variables). The three environmental variables explain the 33.3% of the total inertia.

Most of the groups derived from the cluster analysis can be recognized on the CCA biplot (Fig. 9). Sampling units from the thalweg of the canyon and from the continental shelf form clearly distinct groups based on faunal composition, sediment type and depth. The group associated with muddy sediment and greater depths coincides with the *Stylatula* assemblage, while the two groups related to sandy and gravelly sands correspond respectively to the *Astropecten* and *Placopecten* assemblages, distributed along the continental shelf. Sampling units from the canyon margins (zoanthids and *Dasmosmilia* assemblages) do not form such distinct groups, although their position on the CCA biplot separates them from the other assemblages (Fig. 9). The distribution of these sampling units relates to increases in grain size (from gravelly sands to pebbles and cobbles to mudstone-outcrops) slope and depth.

4.3 Patterns of species richness and habitat heterogeneity

Analyses of species accumulation curves indicated an increased species turnover in the Hudson Canyon compared to shelf sectors. The rate at which new species accumulate after pooling multiple SUs within all canyon and shelf transects revealed higher canyon beta-diversity with respect to the continental shelf (Fig. 10a). Both curves nearly reach an asymptote, suggesting that both canyon and shelf sites were well sampled.

The enhancement of regional diversity resulting from the presence of increased seafloor heterogeneity in the Hudson Canyon is indicated by comparing species accumulation curves for different seafloor types. Analyzing these curves (Fig. 10b), higher species richness was observed for SUs located on gravelly sands, whereas SUs associated with muddy sands had the lowest species richness. The curve for samples associated with mudstone outcrop didn't reach an asymptote, likely due to the reduced number of SUs from this seafloor type. However, the slope of the curve still indicates higher species richness for this habitat as compared to sandy seafloor.

The species accumulation curves for the different assemblages (Fig. 8c) showed that Assemblage C (zoanthids assemblage) and Assemblage D (*Dasmosmilia* assemblage), whose presence was restricted to the canyon margins and walls, had higher species richness, while the lowest species richness was observed for the Assemblage E (*Stylatula* assemblage), distributed on muddy seafloor within the thalweg. Assemblages A (*Astropecten* assemblage) and B (*Placopecten* assemblage) showed intermediate species turnover.

5. Discussion

5.1 Physical factors affecting megafaunal distribution

Results from this study indicate that the variability of the megabenthic assemblages across the study area is largely determined by spatial differences in environmental conditions and evidence a marked difference between shelf and canyon benthic assemblages. The most important factor correlated with the faunal grouping was seafloor type, although depth and slope also contribute to explain the observed patterns.

A close relationship between faunal assemblages and seafloor composition was particularly evident for the *Astropecten* assemblage, associated with sandy seafloor, and for the *Stylatula* assemblage, exclusively distributed on muddy sands. These two groups clearly separated on the CCA biplot not only according to the different seafloor type, but also with respect to a depth increase, confirming the relevance of these environmental variables in discriminating benthic communities (Pires-Vanin, 2001; Kostylev et al., 2001; Sánchez et al., 2009; Beaman and Harris, 2007; Buhl-Mortensen et al., 2009). The zoanthids and cold-water coral assemblages clearly separated from the others being mainly associated with coarse-grained sediments. However, it was not possible to distinguish these two assemblages in the CCA biplot, as they are associated to a wide range of depths, slopes and different gravelly substrates. The spatial distribution of sponges, zoanthids and splitting cup coral communities suggests an influence of physical processes specific of the canyon area, since their presence was limited to the canyon margins and walls. Sponges and corals were mainly distributed at the canyon margins (the former along the eastern margin close to the canyon head, and the latter at both margins about 10 km downcanyon) and their abundance dramatically decreased beyond the canyon rims (Figs. 7 and 8). Conversely, zoanthids were always present, but reached maximum abundances along the steeper sectors of the canyon walls (Figs. 7 and 8). It is therefore possible that the distribution of these assemblages is driven by other environmental factors in addition to seafloor characteristics that were not measured in this study, probably related to the hydrodynamic regime of the canyon. Strong currents along the canyon axis (Keller et al., 1973) and intense mixing due to breaking and dissipation of internal waves at the canyon head (Hotchkiss and Wunsch, 1982) may increase the availability of suspended organic matter favoring active and passive benthic suspension feeders. The communities of the canyon are in fact dominated by sponges, zoanthids and splitting cup corals, whereas the shelf assemblage is mainly composed of carnivores and detritus feeders.

The asymmetric distribution of coarse-grained deposits between the two sides of the canyon highlighted by Pierdomenico et al. (2015), has been related to the present-day hydrodynamic conditions by Rona et al. (2015). These authors observed asymmetrical geostrophic along-canyon currents, with stronger flows on the eastern side, where the coarse-grained deposits form an almost continuous belt down to ~140 m depth, as opposed to the western side where the coarse-grained sediments are partially draped by a cover of fine sediment as result of less intense hydrodynamics. Such asymmetry was clearly reflected also in the distribution of benthic communities. In fact, along the first 10 km of its upper reach, the western side of the Hudson Canyon is characterized by a prevalent sandy seafloor (Pierdomenico et al., 2015) and is colonized by the same assemblage observed along the shelf. This assemblage is dominated by *A. americanus*, a common middle- to outer-shelf species of the middle Atlantic continental shelf (Franz et al., 1981), which co-occurs along with other common species of the Mid Atlantic Bight (Wigley and Theroux, 1981; Mahon et al., 1998). Conversely, the presence of zoanthids, sponges and coral communities was mainly restricted to the sectors where gravelly deposits are present.

Depth is another variable that resulted to affect megafaunal distribution within the Hudson Canyon, although its influence could still be related to changes in sediment distribution. A sharp change in faunistic composition can be found between the assemblages distributed at the canyon margins and walls and the assemblage colonizing the deep muddy substrates within the canyon thalweg. The latter consisted almost exclusively of the sea pen *S. elegans*, which is a common and fairly widespread species of the outer continental shelf and upper slope of the Atlantic margin. It has also been observed in other Mid-Atlantic canyons (Hecker et al., 1983; Theroux and Wigley, 1998). Such changes in faunal composition could be related to the presence of the "mud line", which is the sharp boundary separating the coarse-relict sediment along the canyon margins and walls from the present muddy cover along the thalweg (Stanley and Freeland, 1978). The mud line typically occurs at the shelf break and is recognized as a boundary separating deep-sea from shelf organisms (Gage and Tyler, 1991). Although the depth range covered by SEABOSS observations (80-200 m) was too narrow to properly assess the degree of faunal replacement with depth in the canyon, photo images acquired by the NIUST "Mola Mola" AUV within the Hudson Canyon thalweg at 500 m depth revealed the presence of a substantially different epifauna, with high abundances of the anemone *Bolocera tuediae* and the deep-sea red crab *Chaceon quinquedens* (Pierdomenico et al., 2015). Trawl catches in this area (around 700 m depth) also indicated the occurrence of demersal species typical of the upper slope environment, such as witch flounders (*Glyptocephalus cynoglossus*), marlin spike grenadiers (*Nezumia bairdii*), offshore hakes (*Merluccius albidus*) and thorny skates (*Amblyraja radiata*) (Pierdomenico et al., 2015). Overall, the morphological complexity, the complicated patterns of sediment distribution and the complex oceanographic condition of the Hudson Canyon lead to a rich habitat diversity, which in turn supports a higher variability of faunal assemblages, as also shown by the enhancement of species richness when canyon and shelf are compared (Fig. 10a). The increased species richness of the assemblages associated with coarse-grained sediments (Fig.10 b and c), that were exclusively distributed along the canyon, supports the hypothesis that enhanced habitat heterogeneity along submarine canyons promote beta diversity (Vetter et al., 2010; Mc Clain and Barry, 2010; De Leo et al., 2010). Furthermore, the canyon assemblages are mainly composed by species of high conservation values, such as cold-water corals and sponges. These benthic suspension feeders are habitat-structuring organisms which have been shown to play a relevant role in increasing biodiversity of marine communities (Buhl-Mortensen et al., 2010), and to be responsible for a major share of the biomass and energy transport in marine ecosystems (Gili and Coma, 1998).

5.2 Considerations about the video-analyses

While 14 fish and 29 megabenthic invertebrate taxa were recognized from visual imagery, 19 fish and 36 invertebrate taxa were obtained from beam trawls taken from the same stations during the same cruise. This discrepancy was undoubtedly due to a combination of avoidance of SEABOSS by some mobile organisms, the presence of some cryptic organisms, and the limits of visual resolution in video images in particular.

The most common species observed along the transects and those utilized for the analyses were large organisms, which were easy to identify despite the low quality of the videos. Taxonomic identification for these organisms, to species or genus level, was also supported by comparison with trawl catch data. However, the presence of smaller organisms (~1 to 3 cm) was difficult to distinguish on low-resolution videos and several taxa had to be excluded from the statistical analyses. The only exceptions were represented by the zoanthids and the solitary cold-water coral *Dasmosmilia lymani*, whose abundance was locally very high (>50 colonies/m^2 and >300 individuals/m^2, respectively). The exclusion of these taxa from the video analysis would have greatly affected the statistical results, as it was clear that zoanthids and corals constitute important components of the epibenthic community at specific locations. The strategy adopted was thus to infer their abundance along the video track based on density estimates extracted from the still photos.

Broad categories including different morphospecies were adopted for all the morphospecies of sea stars that could not be identified to species level (grouped into the category *"Asteroidea"*) and for the sponges (separated into the two broad categories of *"Erect Porifera"* and *"Encrusting Porifera"*).

Despite the restriction imposed by the quality of the data described above, it seems reasonable to consider the groups resulting from the cluster analysis as representative of the megafaunal assemblages in the study area. In fact, due to the general high degree of redundancy in marine benthic community data, it is suggested that the analysis of a small subset of the total number of species may give similar results to that of the full species analysis (Clarke and Warwick, 1998). After all, several studies have shown that both higher taxonomic levels (lower taxonomic resolution) or indicator groups (subsets of data) can be of use as proxies or surrogates for species distributions, and that the main faunal patterns identified by using the full species list can also be identified using such reduced data (Noss, 1990; Somerfield and Clarke, 1995; Olsgard and Somerfield, 2000; Magierowski and Johnson, 2006; Bevilacqua et al., 2012).

6. Conclusions

From the quantitative analysis of megafauna along the upper reach of Hudson Canyon and surrounding shelf areas five benthic assemblages were distinguished, whose distribution seems to be strongly influenced by the seafloor composition and by physical processes specific of the canyon area. The complicated patterns of sediment distribution along the Hudson Canyon, characterized by the occurrence of coarse-grained relict deposits, lead to a richer habitat diversity compared to the adjacent shelf sectors, which in turn supports a higher variability of megabenthic communities. Some of the assemblages identified in the study area are exclusively distributed along the canyon, supporting the hypothesis that the increased habitat heterogeneity at the Hudson Canyon can promote beta diversity. Specifically, the presence of gravelly sediment along the canyon rims and flanks, and intense hydrodynamic conditions at the canyon head create very specific environmental conditions that allow the presence of benthic species of high conservation values, such as cold-water corals and sponges. The mixing of water masses promoted by intense hydrodynamics along the upper reach of the canyon may contribute to further increase the availability of suspended organic matter, favoring the presence of these benthic suspension feeders. Sponges, zoanthids and cold-water coral communities are in fact present along the canyon rims and flanks, and communities dominated by sea pens colonize the thalweg areas, whereas the shelf assemblages are mainly composed of carnivores and detritus feeders like sea stars.

Under the perspective of management and conservation of marine resources, the results obtained in this study support the relevance of the Hudson Canyon as a biodiversity hotspot. Such results are of particular significance if framed in the recent action promoted by the Mid-Atlantic Fisheries Management Council that restricts bottom fishing activity from the head of the canyon out to the 200-mile U.S. territorial limit on the continental rise to protect cold-water coral communities from fishing gear damage. The Hudson Canyon has been included among the protected areas mostly because of its high suitability for various types of cold-water corals, resulting from broad-scale predictive models. The results shown here provide a much more detailed account of biological communities of the canyon and their distribution on much finer spatial scales, which can be useful to inform conservation planning. The limited biological observations in the deepest sectors of the Hudson Canyon require further explorations to improve our knowledge of this system to fully address management concerns.

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References

Able, K. W., Grimes, C. B., Cooper, R. A., & Uzmann, J. R. (1982). Burrow construction and behavior of tilefish, *Lopholatilus chamaeleonticeps*, in Hudson Submarine Canyon. *Environmental Biology of Fishes*, *7(3)*, 199-205.

Allen, S. E., Vindeirinho, C., Thomson, R. E., Foreman, M. G., & Mackas, D. L. (2001). Physical and biological processes over a submarine canyon during an upwelling event. *Canadian Journal of Fisheries and Aquatic Sciences*, *58(4),* 671-684.

Beaman, R. J., & Harris, P. J. (2007). Geophysical variables as predictors of megabenthos assemblages from the northern Great Barrier Reef, Australia. Geological Association of Canada.

Bevilacqua, S., Terlizzi, A., Claudet, J., Fraschetti, S., & Boero, F. (2012). Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers. *Journal of Applied Ecology*, *49*(2), 357-366.

Bo, M., Bertolino, M., Bavestrello, G., Canese, S., Giusti, M., Angiolillo, M., ... Taviani, M. (2012). Role of deep sponge grounds in the Mediterranean Sea: a case study in southern Italy. *Hydrobiologia*, *687*(1), 163-177.

Bosley, K. L., Lavelle, J. W., Brodeur, R. D., Wakefield, W. W., Emmett, R. L., Baker, E. T., & Rehmke, K. M. (2004). Biological and physical processes in and around Astoria submarine Canyon, Oregon, USA. *Journal of Marine Systems*, *50*(1), 21-37.

Brooke, S., & Ross, S. W. (2014). First observations of the cold-water coral Lophelia pertusa in mid-Atlantic canyons of the USA. *Deep Sea Research Part II: Topical Studies in Oceanography*, *104*, 245-251.

Buhl-Mortensen, P., Dolan, M., & Buhl-Mortensen, L. (2009). Prediction of benthic biotopes on a Norwegian offshore bank using a combination of multivariate analysis and GIS classification. *ICES Journal of Marine Science: Journal du Conseil*, *66*(9), 2026-2032.

Buhl-Mortensen, L., Vanreusel, A., Gooday, A. J., Levin, L. A., Priede, I. G., Buhl-Mortensen, P., ... & Raes, M. (2010). Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Marine Ecology*, *31*(1), 21-50.

Butman, B., Middleton, T. J., Thieler, E. R., Schwab, W. C. (2003). Topography, shaded relief and backscatter intensity of the Hudson Shelf Valley, offshore of New York. *US Geological Survey Open-File Report*, *3*(372), URL: http://pubs.usgs.gov/of/2003/of03-372/.

Butman, B., Twichell, D.C., Rona, P.A, Tucholke, B.E, Middleton, T.J., Robb, J.R. (2006). Sea floor topography and backscatter intensity of the Hudson Canyon region offshore of New York. *U.S. Geological Survey Open-File Report, 2004(1441),* URL: http://pubs.usgs.gov/of/2004/1441/.

Cacchione, D. A., Rowe, G. T., & Malahoff, A. (1978). Submersible investigation of outer Hudson submarine canyon. In D. J. Stanley and G. Kelling (Eds.): *Sedimentation in submarine canyons, fans and trenches.* Dowden, Hutchinson and Ross. 42-50.

Cartes, J.E., Maynou, F., Sardà, F., Company, J.B., Lloris D., Tudela, S. (2004). The Mediterranean deep-sea ecosystems: an overview of their diversity, structure, functioning and anthropogenic impacts. In: *The Mediterranean deep-sea ecosystems: an overview of their diversity, structure, functioning and anthropogenic impacts, with a proposal for conservation*. IUCN, Málaga and WWF, Rome. pp. 9-38.

Clarke, K. R., & Ainsworth, M. (1993). A method of linking multivariate community. *Marine ecology progress series*, *92*, 205-219.

Clarke, K. R., & Warwick, R. M. (1994). Similarity-based testing for community pattern: the two-way layout with no replication. *Marine Biology*, *118*(1), 167-176.

Clarke, K. R., & Warwick, R. M. (1998). Quantifying structural redundancy in ecological communities. *Oecologia*, *113*(2), 278-289.

Danovaro, R., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A. J., ... & Tselepides, A. (2010). Deep-sea biodiversity in the Mediterranean Sea: The known, the unknown, and the unknowable. *PloS one*, *5*(8), e11832.

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. *Proceedings of the Royal Society B: Biological Sciences, 277*, 2783-2792.

De Leo, F. C., Vetter, E. W., Smith, C. R., Rowden, A. A., McGranaghan, M. (2014). Spatial scale-dependent habitat heterogeneity influences submarine canyon macrofaunal abundance and diversity off the Main and Northwest Hawaiian Islands. *Deep Sea Research Part II: Topical Studies in Oceanography*, *104*, 267-290.

Ericson, D. B., Ewing, M., Heezen, B. C. (1951). Deep-sea sands and submarine canyons. *Geological Society of America Bulletin*, *62*(8), 961-966.

Fabri, M. C., Pedel, L., Beuck, L., Galgani, F., Hebbeln, D., Freiwald, A. (2014). Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: Spatial distribution and anthropogenic impacts. *Deep Sea Research Part II: Topical Studies in Oceanography*.

Farrugio, H. (2012). A refugium for the spawners of exploited Mediterranean marine species: the canyons of the continental slope of the Gulf of Lion. In: Würtz, M. (Ed.). *Mediterranean submarine canyons: Ecology and governance*. IUCN. 45-49.

Franz, D. R., Worley, E. K., & Merrill, A. S. (1981). Distribution patterns of common seastars of the middle Atlantic continental shelf of the northwest Atlantic (Gulf of Maine to Cape Hatteras). *The Biological Bulletin*, *160*(3), 394-418.

Gage, J. D., & Tyler, P. A. (1991). *Deep-sea biology: a natural history of organisms at the deep-sea floor*. Cambridge University Press.

Gili, J. M., & Coma, R. (1998). Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in ecology & evolution*, *13*(8), 316-321.

Gori, A., Orejas, C., Madurell, T., Bramanti, L., Martins, M., Quintanilla, E., ... Gili, J. M. (2013). Bathymetrical distribution and size structure of cold-water coral populations in the Cap de Creus and Lacaze-Duthiers canyons (northwestern Mediterranean). *Biogeosciences, 10*(3), 2049-2060.

Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters, 4,* 379-391.

Greene, H. G., Maher, N. M., & Paull, C. K. (2002). Physiography of the Monterey Bay National Marine Sanctuary and implications about continental margin development. *Marine Geology*, *181*(1), 55-82.

Harris, P. T., Whiteway, T. (2011). Global distribution of large submarine canyons: Geomorphic differences between active and passive continental margins. *Marine Geology*, *285*(1), 69-86.

Hecker, B., & Blechschmidt, G. (1980). Final historical coral report for the canyon assessment study in the Mid- and North Atlantic areas of the U.S. outer continental shelf: epifauna of the northeastern U.S. continental margin. Appendix A. In: *Canyon Assessment Study.* U.S. Department of Interior Bureau of Land Management, Washington, DC, USA, No. BLM-AA551-CT8-49.

Hecker, B., Logan, D. T., Gandarillas, F. E., & Gibson, P. R. (1983). Megafaunal assemblages in Lydonia Canyon, Baltimore Canyon, and selected slope areas. *Canyon and slope processes study*, *3*, 1-140.

Heezen, B. C., Tharp, M., Ewing, M. (1959). The Floors of the Oceans I. The North Atlantic. *Geological Society of America Special Papers*, *65*, 1-126.

Hotchkiss, F. S., & Wunsch, C. (1982). Internal waves in Hudson Canyon with possible geological implications. *Deep Sea Research Part A. Oceanographic Research Papers*, *29*(4), 415-442.

Huvenne, V. A., Tyler, P. A., Masson, D. G., Fisher, E. H., Hauton, C., Hühnerbach, V., ... & Wolff, G. A. (2011). A picture on the wall: innovative mapping reveals cold-water coral refuge in submarine canyon. *PLoS One*, *6*(12), e28755.

Jacobson, L., Hart, D., Hendrickson, L., Idoine, J., & Chute T. (2009). Northeast Invertebrate Fisheries. In: NMFS *Our living oceans. Report on the status of U.S. living marine resources, 6th edition* U.S. Deparment of Commerce. October 2009. 103-111.

Johnson, M. P., White, M., Wilson, A., Würzberg, L., Schwabe, E., Folch, H., & Allcock, A. L. (2013). A vertical wall dominated by Acesta excavata and Neopycnodonte zibrowii, part of an undersampled group of deep-sea habitats. *PloS one*, *8*(11), e79917-e79917.

Keller, G. H., Lambert, D., Rowe, G., & Staresinic, N. (1973). Bottom currents in the Hudson Canyon. *Science*, *180*(4082), 181-183.

Keller, G. H., & Shepard, F. P. (1978). Currents and sedimentary processes in submarine canyons off the northeast United States. In D. J. Stanley and G. Kelling [eds.]: *Sedimentation in Submarine Canyons, Fans and Trenches: Stroudsburg, Pennsylvania, Dowden, Hutchinson & Ross Inc.*, 15-32.

Knebel, H. J., Wood, S. A., & Spiker, E. C. (1979). Hudson River: evidence for extensive migration on the exposed continental shelf during Pleistocene time.*Geology*, *7*(5), 254-258.

Kostylev, V. E., Todd, B. J., Fader, G. B., Courtney, R. C., Cameron, G. D., & Pickrill, R. A. (2001). Benthic habitat mapping on the Scotian Shelf based on multibeam bathymetry, surficial geology and sea floor photographs. *Marine Ecology Progress Series*, *219*, 121-137.

MAFMC & NMFS (2014). Amendment 16 to the Atlantic mackerel, squid, and butterfish (MSB) Fishery Management Plan (FMP). Measures to protect deep sea corals from impacts of fishing gear: Public Information Document draft for Council Review, August 2014. Mid Atlantic Fisheries Management Council (MAFMC) and NOAA National Marine Fisheries Service (NMFS). Dover, DE, USA. 60 p.

Magierowski, R. H., & Johnson, C. R. (2006). Robustness of surrogates of biodiversity in marine benthic communities. *Ecological Applications*, *16*(6), 2264-2275.

Mahon, R., Brown, S. K., Zwanenburg, K. C., Atkinson, D. B., Buja, K. R., Claflin, L., ... & Sinclair, M. (1998). Assemblages and biogeography of demersal fishes of the east coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(7), 1704-1738.

Marin, P., & Aguilar, R. (2012). 5.1 Mediterranean Submarine Canyons 2012: Pending Protection. In: Würtz, M. (Ed.). *Mediterranean submarine canyons: Ecology and governance*. IUCN. 191-206.

Mayo, R.K., Brooks, L., Col, L., Hendrickson, L.C., Keith, C., Legault, C., ... & Wigley, S.E. (2009). Northeast Demersal Fisheries. In: NMFS *Our living oceans. Report on the status of U.S .living marine resources, 6th edition* (103-111). U.S. Dep. Commer. October 2009

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.

Mordecai, G., Tyler, P. A., Masson, D. G., & Huvenne, V. A. (2011). Litter in submarine canyons off the west coast of Portugal. *Deep Sea Research Part II: Topical Studies in Oceanography*, *58*(23), 2489-2496.

Mortensen, P. B., & Buhl-Mortensen, L. (2005). Deep-water corals and their habitats in The Gully, a submarine canyon off Atlantic Canada. In *Cold-water corals and ecosystems* (pp. 247-277). Springer Berlin Heidelberg.

NEFMC (2014). Omnibus Essential Fish Habitat Amendment 2. Volume 1: Executive summary, Background and purpose, and Description of the affected environment. May 19, 2014 draft. New England Fisheries Management Council document. Newburyport, MA 426 pp. http://www.nefmc.org/habitat/index.html

Noss, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conservation biology*, 355-364.

Okey, T. A. (2003). Macrobenthic colonist guilds and renegades in Monterey Canyon (USA) drift algae: partitioning multidimensions. *Ecological monographs*,*73*(3), 415-440.

Olsgard, F., & Somerfield, P. J. (2000). Surrogates in marine benthic investigations-which taxonomic unit to target?. *Journal of Aquatic Ecosystem Stress and Recovery*, *7*(1), 25-42.

Orejas, C., Gori, A., Lo Iacono, C., Puig, P., and Gili, J. M. (2009). Cold- water corals in the Cap de Creus canyon, northwestern Mediterranean: spatial distribution, density and anthropogenic impact. *Marine Ecology Progress Series, 397*, 37–51.

Orpin, A. R., & Kostylev, V. E. (2006). Towards a statistically valid method of textural sea floor characterization of benthic habitats. *Marine Geology*, *225*(1), 209-222.

Packer, D.B., Boelke, D., Guida, G., & McGee, L.A. (2007). State of deep coral ecosystems in the Northeastern US region: Maine to Cape Hatteras. In: S.E. Lumsden, Hourigan, T.F., Bruckner, A.W., & Dorr, G. (eds.). *The State of Deep Coral Ecosystems of the United States*. NOAA Technical Memorandum, CRCP-3. Silver Spring MD, 195-232.

Pierdomenico, M., Guida, V. G., Macelloni, L., Chiocci, F. L., Rona, P. A., Scranton, M. I., ... & Diercks, A. (2015). Sedimentary facies, geomorphic features and habitat distribution at the Hudson Canyon head from AUV multibeam data. *Deep Sea Research Part II: Topical Studies in Oceanography*, *121*, 112-125.

Pierdomenico, M., Martorelli, E., Dominguez-Carrió, C., Gili, J. M., & Chiocci, F. L. (2016). Seafloor characterization and benthic megafaunal distribution of an active submarine canyon and surrounding sectors: The case of Gioia Canyon (Southern Tyrrhenian Sea). *Journal of Marine Systems*, *157*, 101-117.

Pires-Vanin, A. M. S. (2001). Identifying the components of ecological variation in a marine benthic megafauna. *Revista Brasileira de Oceanografia*, *49*(1-2), 29-38.

Politis, P. J., Galbraith, J. K., Kostovick, P., & Brown, R. W. (2014). Northeast Fisheries Science Center bottom trawl survey protocols for the NOAA Ship Henry B. *Bigelow. US Department of Commerce, Northeast Fisheries Science Center Ref Doc*, 14-06.

Pratt, R. M. (1967). The seaward extension of submarine canyons off the northeast coast of the United States. In *Deep Sea Research and Oceanographic Abstracts* (Vol. 14, No. 4, pp. 409-420). Elsevier.

Pratt, R. M. (1968). *Atlantic continental shelf and slope of the United States-physiography and sediments of the deep-sea basin*. USGS Survey Professional Paper, 529-B.

Puig, P., Canals, M., Company, J. B., Martín, J., Amblas, D., Lastras, G., ... & Calafat, A. M. (2012). Ploughing the deep sea floor. *Nature*, *489*(7415), 286-289.

Puig, P., Palanques, A., Martín, J. (2014). Contemporary sediment-transport processes in submarine canyons. *Annual review of marine science*, *6*, 53-77.

R Development Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org.Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C. R., ... Vecchione, M. (2010). Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences*, 7, 2851–2899.

Rona, P., Guida, V., Scranton, M., Gong, D., Macelloni, L., Pierdomenico, M., ... & Haag, S. (2015). Hudson submarine canyon head offshore new york and new Jersey: A physical and geochemical investigation. *Deep Sea Research Part II* doi.org/10.1016/j.dsr2.2015.07.019.

Rowe, G. T., Polloni, P. T., & Haedrich, R. L. (1982). The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. *Deep Sea Research Part A. Oceanographic Research Papers*, *29*(2), 257-278.

Ryan, J. P., Yoder, J. A., & Cornillon, P. C. (1999). Enhanced chlorophyll at the shelfbreak of the Mid-Atlantic Bight and Georges Bank during the spring transition. *Limnology and Oceanography*, *44*(1), 1-11.

Sánchez, F., Serrano, A., & Ballesteros, M. G. (2009). Photogrammetric quantitative study of habitat and benthic communities of deep Cantabrian Sea hard grounds. *Continental Shelf Research*, *29*(8), 1174-1188.

Sardà, F., Calafat, A., Flexas, M., Tselepides, A., Canals, M., Espino, M., Tursi, A. (2004). An introduction to Mediterranean deep-sea biology. *Scientia Marina*, *68*(S3), 7-38.

Schlee, J., Pratt, R. M. (1970). Atlantic continental shelf and slope of the United States - Gravels of the northeastern part. US Department of the Interior, Geological Survey, Prof. paper, 529-H: 39 pp.

Shepard, F.P., Dill, R.F. (1966). *Submarine Canyons and Other Sea Valleys*. USA: Rand McNally.

Somerfield, P. J., Clarke, K. R. (1995). Taxonomic levels, in marine community studies, revisited. *Marine ecology progress series. Oldendorf*,*127*(1), 113-119.

Stanley, D. J., Freeland, G. L. (1978). The erosion-deposition boundary in the head of Hudson Submarine Canyon defined on the basis of submarine observations. *Marine Geology*, *26*(3), M37-M46.

Stevenson, D., Chiarella, L., Stephan, D., Reid, R., Wilhelm, K., McCarthy J., & Pentony M. (2004). *Characterization of the Fishing Practices and Marine Benthic Ecosystems of the Northeast U.S. Shelf, and an Evaluation of the Potential Effects of Fishing on Essential Fish Habitat*. NOAA Technical Memorandum NMFS-NE-181.

Ter Braak, C. J., & Verdonschot, P. F. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic sciences*, *57*(3), 255-289.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of biogeography*, *31*(1), 79-92.

Theroux, R. B., & Wigley, R. L. (1998). *Quantitative composition and distribution of the macrobenthic invertebrate fauna of the continental shelf ecosystems of the northeastern United States* (Vol. 140). US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Scientific Publications Office.

Tubau, X., Canals, M., Lastras, G., Rayo, X., Rivera, J., & Amblas, D. (2015). Marine litter on the floor of deep submarine canyons of the Northwestern Mediterranean Sea: The role of hydrodynamic processes. *Progress in Oceanography*, *134*, 379-403.

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*(8), 408-412.

Vetter, E. W., Dayton, P. K. (1998). Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep-Sea Research Part II*, *45*(1-3), 25-54.

Vetter, E. W., Dayton, P. K. (1999). Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. *Marine ecology. Progress series*, *186*, 137-148.

Vetter, E. W., Smith, C. R., De Leo, F. C. (2010). Hawaiian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. *Marine Ecology*, *31*(1), 183-199.

Waring, G. T., Hamazaki, T., Sheehan, D., Wood, G., & Baker, S. (2001). Characterization of beaked whale (Ziphiidae) and sperm whale (Physeter macrocephalus) summer habitat in shelf-edge and deeper waters off the northeast US. *Marine Mammal Science*, *17*(4), 703-717.

Wigley, R., & Theroux, T.N. (1981). *Atlantic Continental Shelf and Slope of the United States - Macrobenthic Invertebrate Fauna of the Middle Atlantic Bight Region - Faunal Composition and Quantitative Distribution*. Geological Survey professional Paper 529-N. US Government Printing Office, Washington DC. 198 pp.

Williams, A., Bax, N. J., Kloser, R. J., Althaus, F., Barker, B., & Keith, G. (2009). Australia’s deep-water reserve network: implications of false homogeneity for classifying abiotic surrogates of biodiversity. *ICES Journal of Marine Science: Journal du Conseil*, *66*(1), 214-224.

Würtz, M. (2012). *Mediterranean submarine canyons: Ecology and governance*. IUCN. Switzerland and Spain, 11–26, 2012.

Tables

Table 1. Seaboss video transect location, duration, lenght and water depth

Transect location	**Station**	**Start**		**End**		**Depth**	**Lenght**	**Time**
		Lat	**Long**	**Lat**	**Long**	**(m, start-end)**	**(m)**	**(min:sec)**
Continental Shelf	PR31	39°40'7.9" N,	72°19'53.1" W	39°40'11.9" N,	72°19'59.9" W	113-113	207	21:49
Continental Shelf	PR4	39° 42' 4.9" N,	72° 23' 7.5" W	39° 42' 2.9" N,	72° 22' 56.6" W	95-95	272	21:43
Continental Shelf	PR41	39° 42' 25.7" N,	72° 26' 22.3" W	39° 42' 45.1" N,	72° 26' 28" W	90-88	614	21:25
Continental Shelf	PR5	39° 42' 56.1" N,	72° 27' 52.9" W	39° 43' 3.3" N,	72° 28' 6.4" W	84-83	395	20:55
Continental Shelf	Z1	39° 35' 53.2" N,	72° 39' 29.8" W	39° 35' 45.9" N,	72° 39' 30.8" W	75-74	289	21:52
Continental Shelf	Z2	39° 36' 11.2" N,	72° 37' 20.1" W	39° 36' 2.2" N,	72° 37' 20.8" W	78-77	320	22:00
Continental Shelf	Z3	39° 35' 48.8" N,	72° 36' 9.2" W	39° 35' 40.4" N,	72° 36' 3.1" W	77-77	302	21:32
Hudson Canyon	Y1	39° 39' 51.5" N,	72° 28' 16.8" W	39° 39' 53.2" N,	72° 28' 16.1" W	199-199	57	11:35
Hudson Canyon	Y2	39° 40' 6.7" N,	72° 28' 34.1" W	39° 40' 47.8" N,	72° 28' 11.5" W	182-91	1386	44:24
Hudson Canyon	Y3	39° 40' 39.9" N,	72° 28' 40.6" W	39° 40' 59.3" N,	72° 28' 38.5" W	125-94	600	20:25
Continental Shelf	Y4	39° 43' 10.4" N,	72° 33' 36.8" W	39° 42' 57.8" N,	72° 33' 27.9" W	76-76	448	20:35
Continental Shelf	Y5	39° 41' 14.5" N,	72° 35' 32.6" W	39° 41' 17" N,	72° 35' 4.4" W	73-73	679	21:05
Continental Shelf	Y6	39° 38' 45.4" N,	72° 34' 17" W	39° 38' 55" N,	72° 33' 54.8" W	75-76	611	21:29
Continental Shelf	Y7	39° 37' 34.9" N,	72° 30' 53.9" W	39° 37' 48.2" N,	72° 30' 36.6" W	88-89	586	20:44
Hudson Canyon	WX1	39° 40' 47" N,	72° 29' 36.1" W	39° 40' 32.5" N,	72° 29' 31.3" W	95-106	466	21:28
Hudson Canyon	WX11	39° 39' 35.1" N,	72° 29' 3.6" W	39° 39' 37.4" N,	72° 28' 51.2" W	116-138	307	21:48
Hudson Canyon	WX2	39° 38' 49.7" N,	72° 28' 20.8" W	39° 38' 41.2" N,	72° 28' 16.8" W	116-105	283	21:02
Hudson Canyon	WX23	39° 37' 32.4" N,	72° 27' 8.4" W	39° 37' 39.3" N,	72° 27' 4.2" W	102-104	280	18:17
Hudson Canyon	WX31	39° 35' 50.2" N,	72° 26' 52.7" W	39° 35' 39.9" N,	72° 26' 56.2" W	108-107	327	21:14
Hudson Canyon	WX4	39° 34' 55.1" N,	72° 26' 22.4" W	39° 34' 59.5" N,	72° 26' 34.5" W	123-106	325	21:07
Hudson Canyon	WX5	39° 33' 34.3" N,	72° 26' 51.2" W	39° 33' 38.7" N,	72° 27' 14.3" W	117-105	573	23:39
Continental Shelf	UV00	39° 41' 22.3" N,	72° 27' 59" W	39° 41' 0.3" N,	72° 27' 59.5" W	87-87	682	25:13
Hudson Canyon	UV01	39° 39' 46.3" N,	72° 26' 38.2" W	39° 39' 32.9" N,	72° 27' 11.6" W	95-186	903	40:21
Hudson Canyon	UV02	39° 39' 18.6" N,	72° 24' 52.8" W	39° 38' 57.8" N,	72° 25' 27.4" W	104-190	1065	55:43
Hudson Canyon	UV2	39° 38' 48.4" N,	72° 24' 45.9" W	39° 38' 40.7" N,	72° 25' 19.6" W	110-177	844	39:37
Hudson Canyon	UV22	39° 39' 21.2" N,	72° 23' 42.8" W	39° 39' 23.3" N,	72° 23' 38.6" W	136-137	128	20:07
Hudson Canyon	UV3	39° 37' 57.2" N,	72° 23' 4.1" W	39° 37' 49.2" N,	72° 23' 42.9" W	105-148	962	35:19
Hudson Canyon	UV4	39° 36' 20.9" N,	72° 22' 37.3" W	39° 36' 18.3" N,	72° 22' 53.7" W	104-104	402	16:46

Table 2. Results of BIO-ENV analysis showing the combinations of the terrain variables, taken *k* at time, and the corresponding Spearman coefficient (ρ).

BIO-ENV Comparison		
k	Terrain Variables	(ρ)
3	Seafloor type, Depth, Slope	0.558
2	Seafloor type, Slope	0.544
2	Seafloor type, Depth	0.535
1	Seafloor type	0.523
4	Seafloor type, Depth, Slope, Aspect	0.487
3	Seafloor type, Depth, Slope	0.451
3	Seafloor type, Slope, Aspect	0.444
2	Depth, Slope	0.442
2	Seafloor type,Aspect	0.397
1	Slope	0.378

Figure Caption

Figure 1. Bathymetric map of northwestern Atlantic margin with the study area denoted by the black polygon. HSV – Hudson Shelf Valley. Bathymetry data: NOAA National Geophysical Data Center (*http://www. ngdc.noaa.gov*).

Figure 2. Bathymetric (A), slope (B) and aspect (C) map showing the location of the video tracks collected by the SEABOSS vehicle along and around the upper reach of the Hudson Canyon. Full contour lines every 50 m. Dashed contour lines every 10 m.

Figure 3. Dendrogram of hierarchical cluster analysis of species data and corresponding characteristic species from SIMPER analysis. The colored box indicate the megafaunal assemblages and colors refer to the legend in Figure 4.

Figure 4. Map of distribution of the assemblages from the cluster analysis. Striped contour lines every 50 m. Dashed contour lines every 10 m.

Figure 5. Selected still photos from SEABOSS vehicle showing the main megabenthic assemblages observed in the study area. Scale bar 20 cm.

Figure 6. Pie charts, box plots and rose diagrams illustrating the variability of environmental factors associated with each of the megabenthic assemblages identified from the cluster analysis.

Figure 7. Spatial distribution and abundance of the main characterizing species identifies from the video analysis.

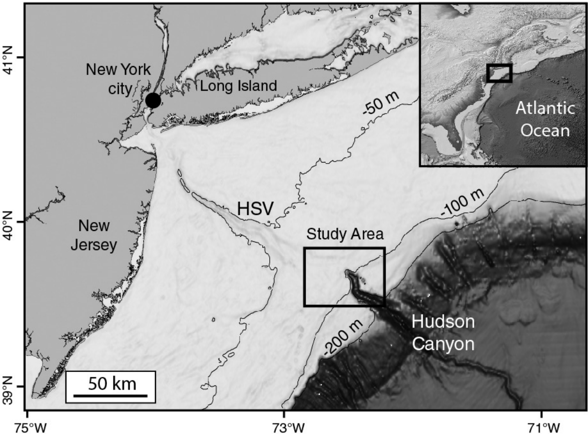
Figure 8. Density plots showing variation of the abundance of different faunal groups along selected video transects. The X axis indicates the distance along the track, expressed in meter from the origin of the transect while the Y axis indicate the density of the organisms, expressed in individual (or colony)/m2. Changes in seafloor composition and slope along the track are also illustrated. Sloping sectors refer to slopes >10°.

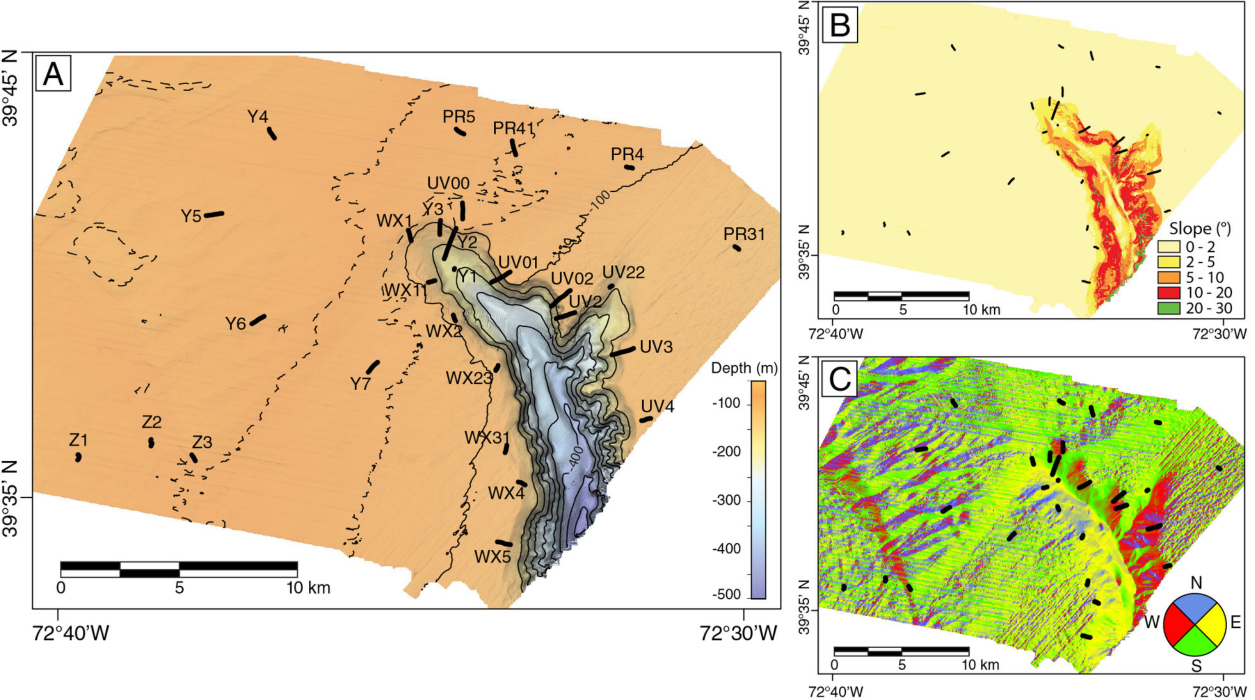
Figure 9. Canonical Correspondence Analysis (CCA). The biplot shows the main groups formed by the ordination of the sampling units and the role of significant environmental variables. The inset on the bottom right shows the contribution of the different species to faunal grouping. Sampling units are colored according to the corresponding seafloor type: Muddy sand-blue; Sand-Yellow; Gravelly Sand-Light green; Cobbles and pebbles-Dark green; Mudstone Outcrops-Red. The blue labels indicate the megafaunal assemblages (numbered as in Cluster analysis) and the black labels indicate the physical predictors: MS-Muddy sand; Sa-Sand; GS-Gravelly Sand; PC-Pebbles & Cobbles; MO-Mudstone Outcrops.

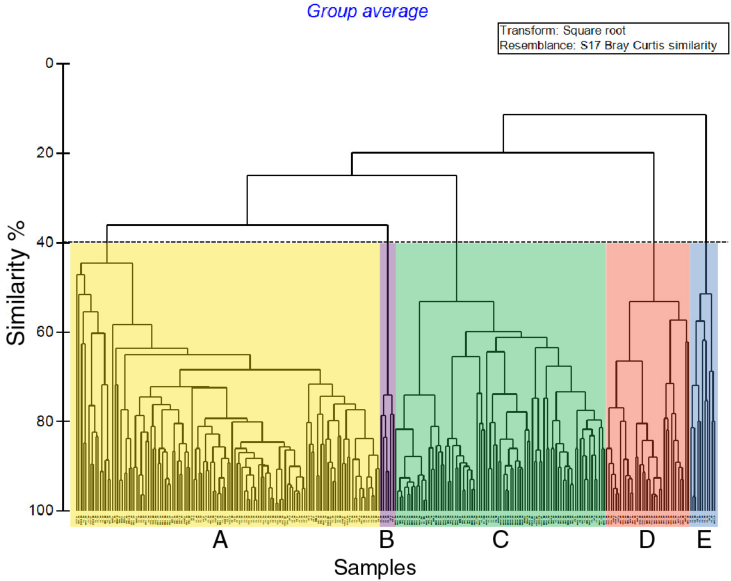
Figure 10. (a) Mean species accumulation curves calculated for Hudson Canyon and shelf sectors after pooling all the SUs from all canyon and shelf transects. (b) Mean species

accumulation curves calculates after pooling SUs associated to different seafloor types. (c) Mean species accumulation curves for the different assemblages derived from the cluster analysis.

The colored areas around the curves indicate the confidence intervals from standard deviation.


New York city
Long Island
New Jersey
HSV
Study Area
Hudson Canyon
Atlantic Ocean
-50 m
-100 m
-200 m
50 km
41°N
40°N
39°N
75°W
73°W
71°W


A
39°45' N
39°35' N
72°40'W
72°30'W
Y4
PR5
PR41
PR4
UV00
Y5
WX1
Y3
Y2
-100
UV01
Y1
UV02
UV22
WX11
UV2
Y6
WX2
UV3
Y7
WX23
PR31
Z1
Z2
Z3
WX31
UV4
-400
WX4
WX5
Depth (m)
-100
-200
-300
-400
-500
0
5
10 km
B
Slope (°)
0 - 2
2 - 5
5 - 10
10 - 20
20 - 30
C
N
W
E
S



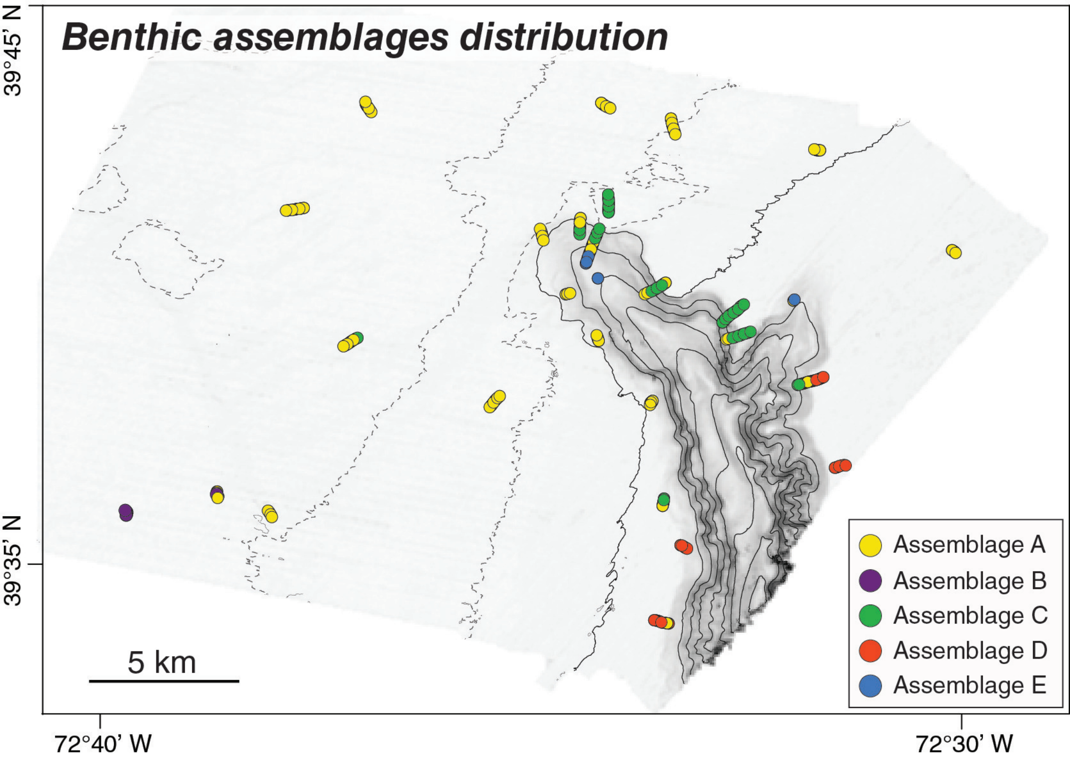
Assemblage A
Astropecten americanus
Maldanidae polychaetes
Unidentified Asteroidea

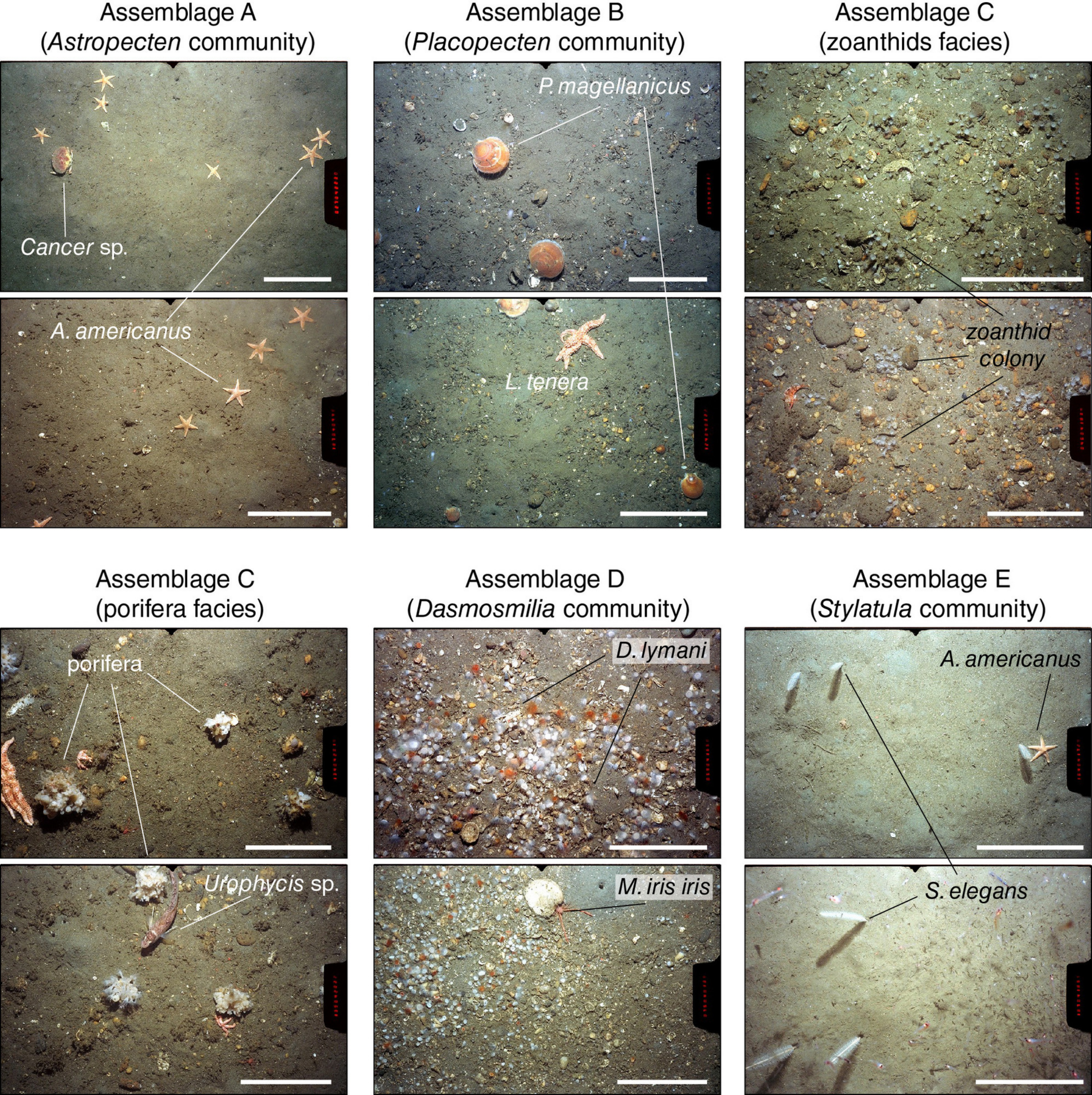
Assemblage B
Placopecten Magellanicus
Maldanidae polychaetes
Unidentified Asteroidea
Astropecten americanus
Porifera erect

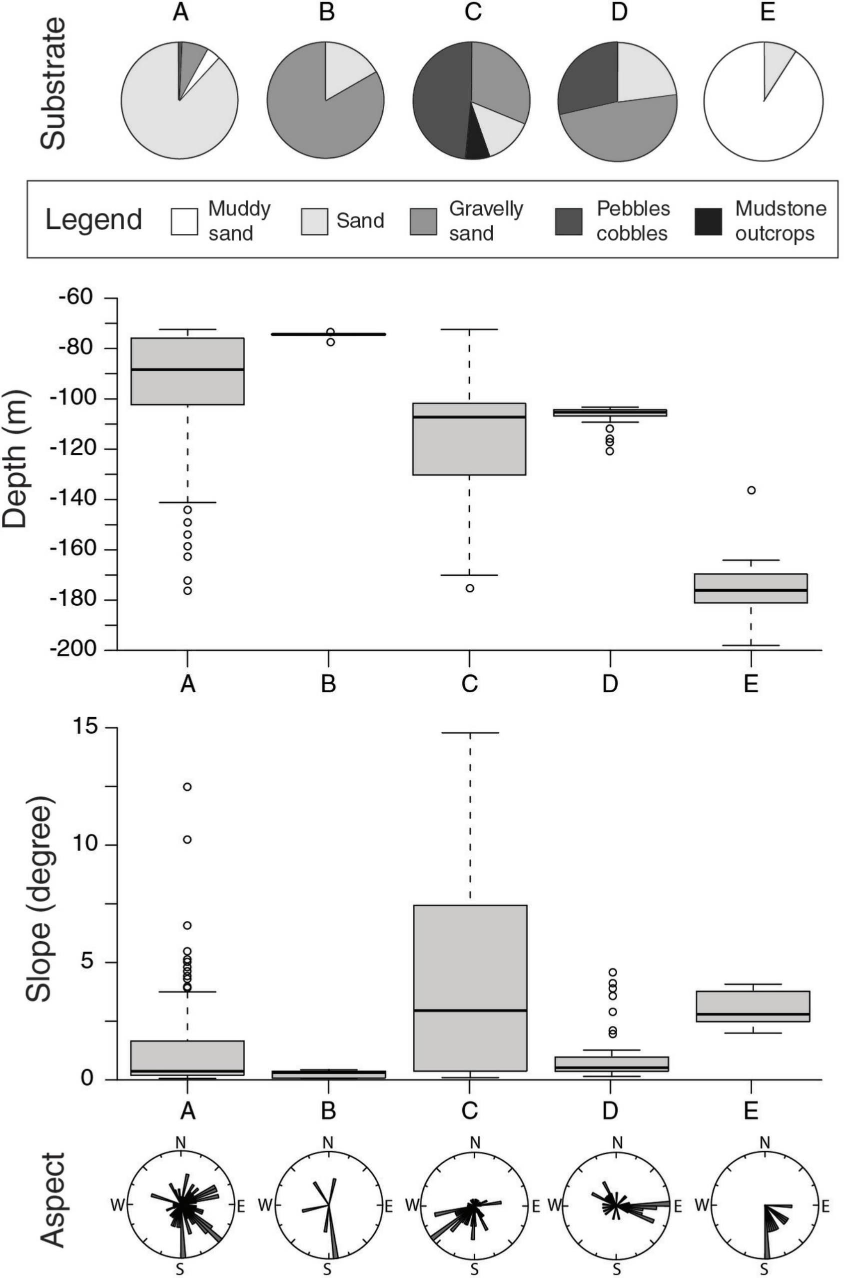
Assemblage C
Zoanthids
Porifera erect
Unidentified Asteroidea
Leptasterias Tenera
Astropecten americanus

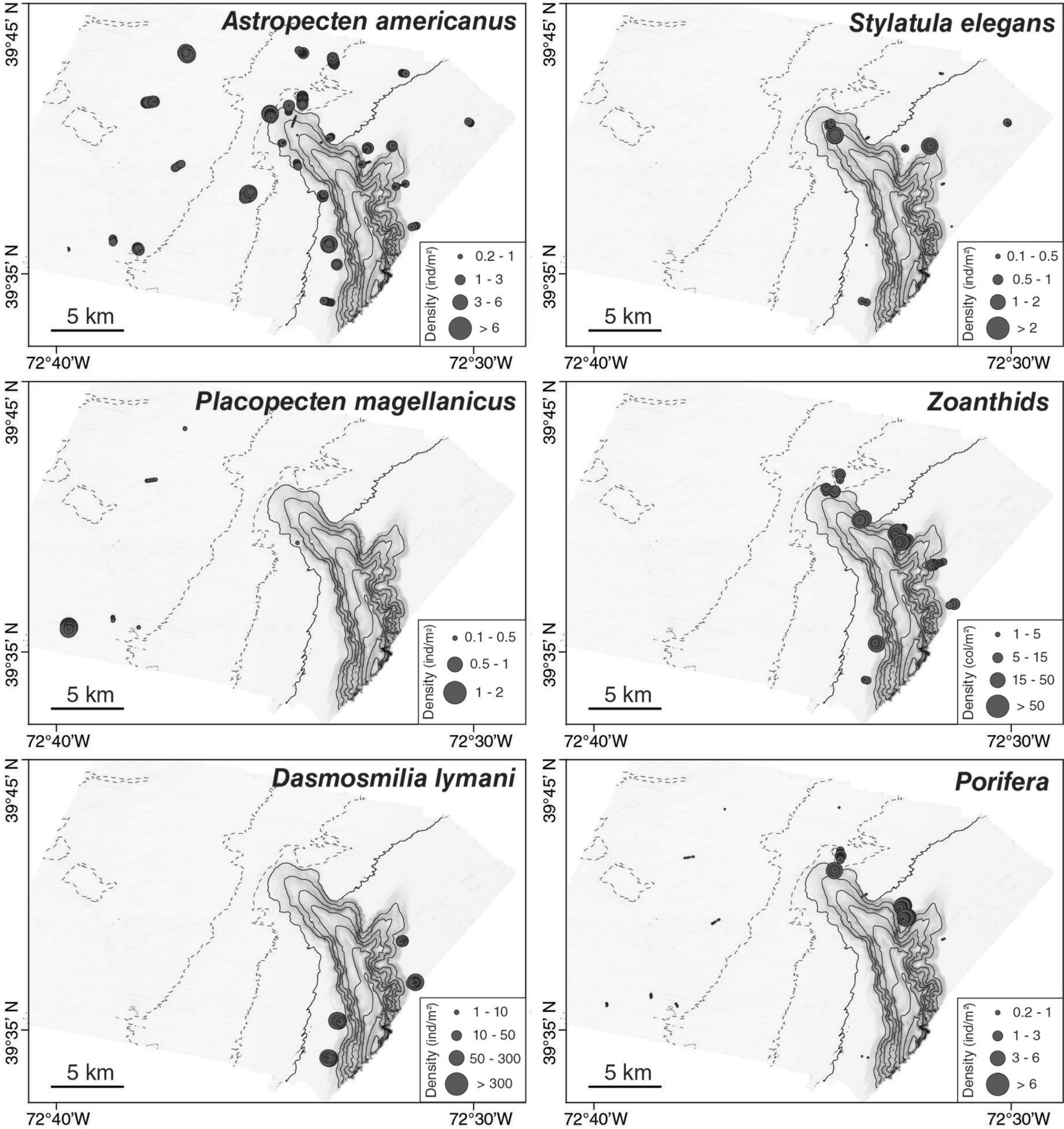
Assemblage D
Dasmosmilia lymani
Zoanthids
Astropecten americanus

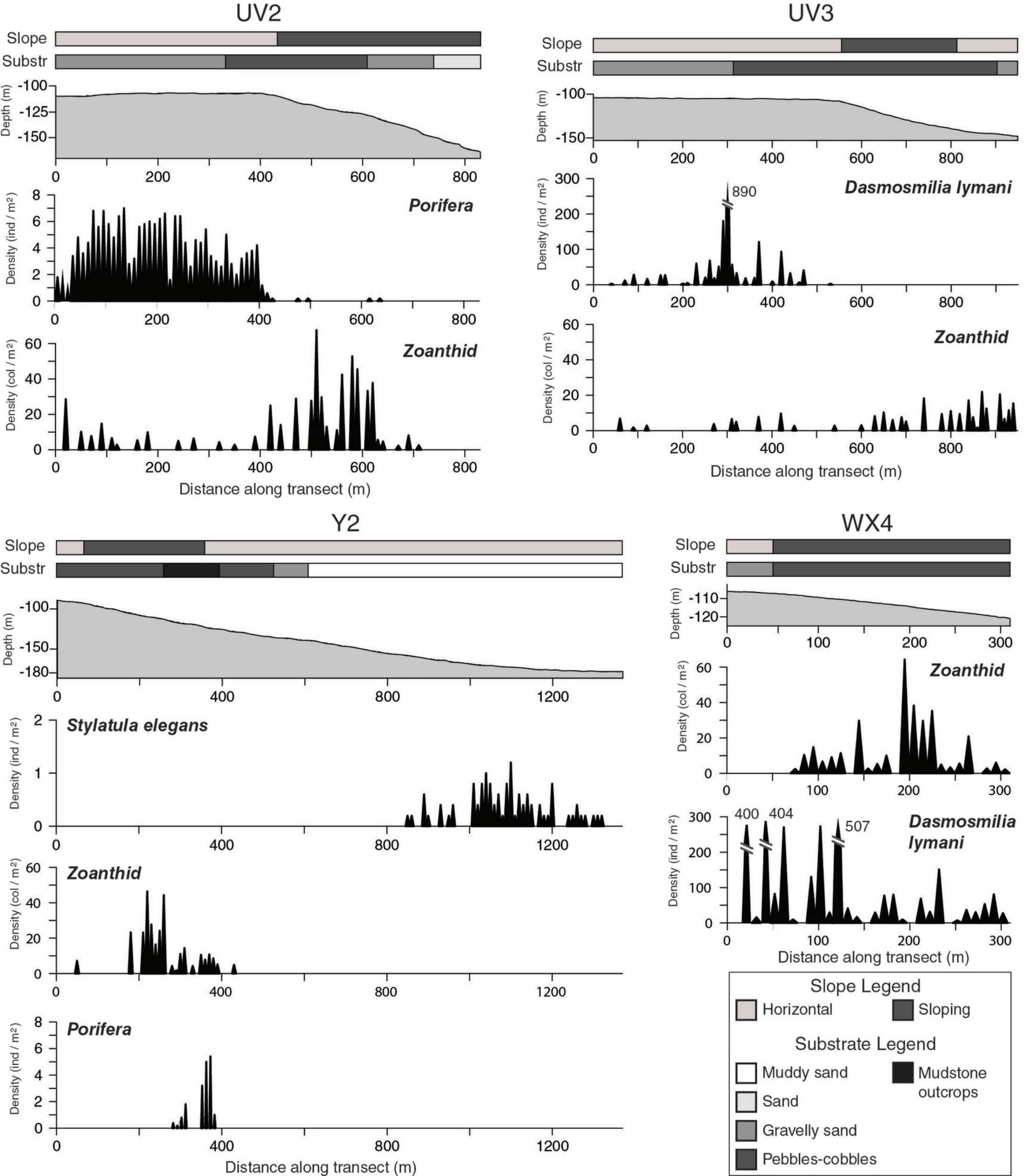
Assemblage E
Stylatula Elegans
Astropecten americanus

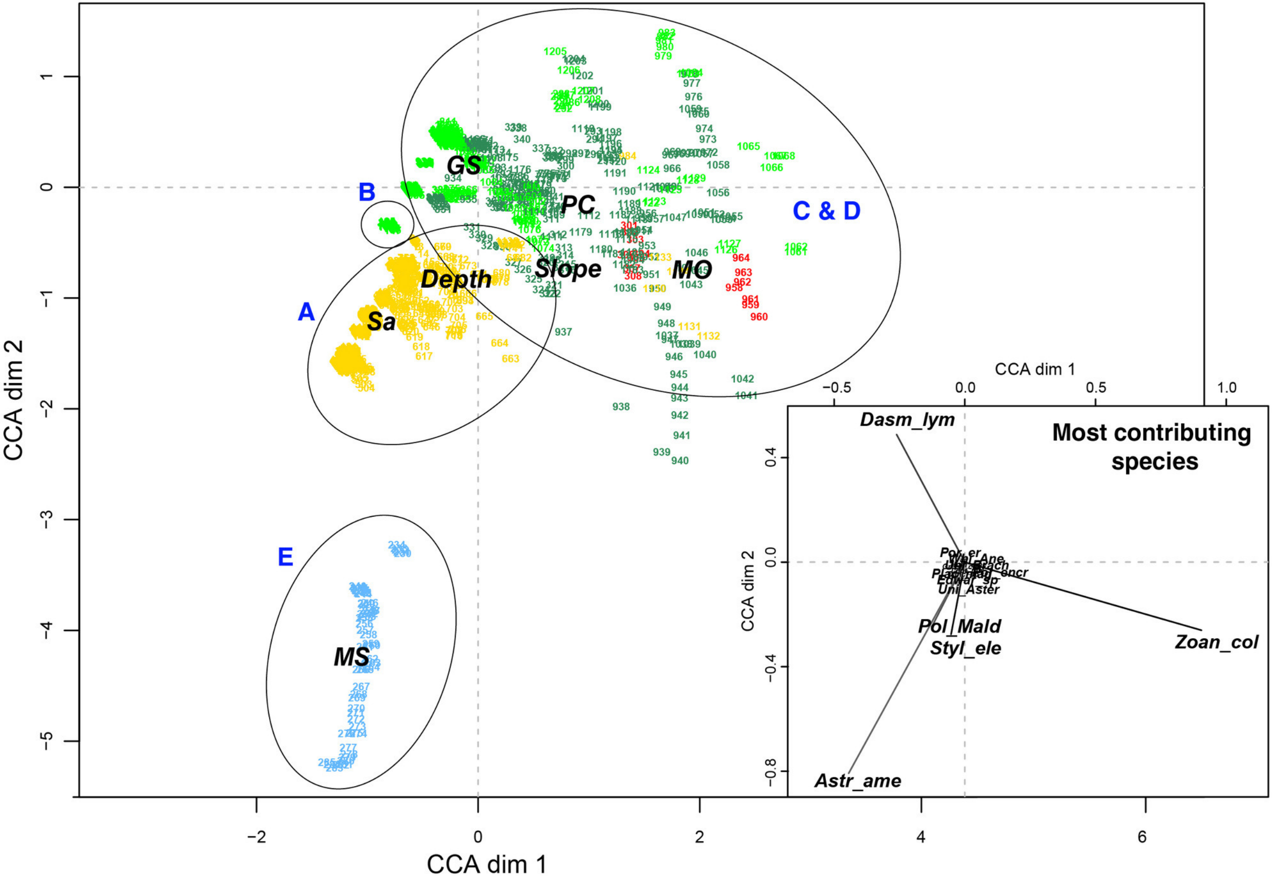

Benthic assemblages distribution
Assemblage A
Assemblage B
Assemblage C
Assemblage D
Assemblage E
5 km
39°45' N
39°35' N
72°40' W
72°30' W

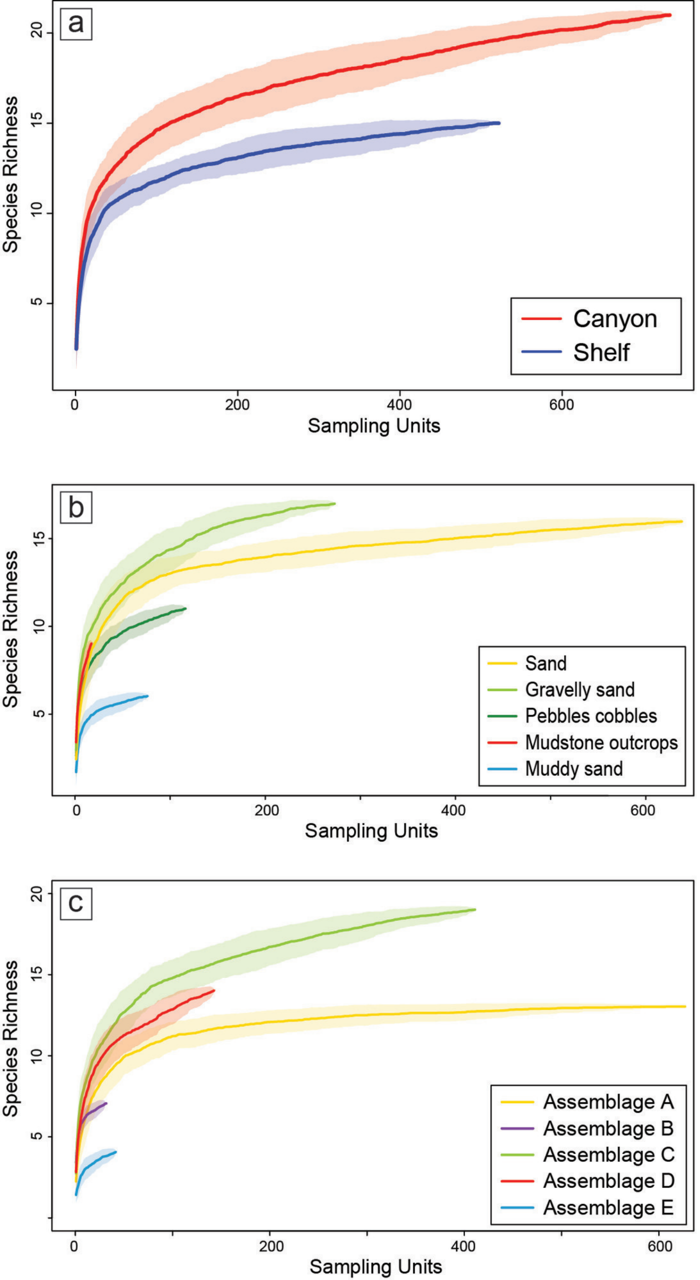

Assemblage A
(*Astropecten* community)
Cancer sp.
A. americanus
Assemblage B
(*Placopecten* community)
P. magellanicus
L. tenera
Assemblage C
(zoanthids facies)
zoanthid
colony
Assemblage C
(porifera facies)
porifera
Urophycis sp.
Assemblage D
(*Dasmosmilia* community)
D. lymani
M. iris iris
Assemblage E
(*Stylatula* community)
A. americanus
S. elegans


Substrate
A
B
C
D
E
Legend
Muddy sand
Sand
Gravelly sand
Pebbles cobbles
Mudstone outcrops
Depth (m)
-60
-80
-100
-120
-140
-160
-180
-200
A
B
C
D
E
Slope (degree)
15
10
5
0
A
B
C
D
E
Aspect
N
W
E
S


Astropecten americanus
Stylatula elegans
Placopecten magellanicus
Zoanthids
Dasmosmilia lymani
Porifera
39°45' N
39°35' N
72°40'W
72°30'W
5 km
Density (ind/m²)
0.2 - 1
1 - 3
3 - 6
> 6
0.1 - 0.5
0.5 - 1
1 - 2
> 2
Density (col/m²)
1 - 5
5 - 15
15 - 50
> 50
1 - 10
10 - 50
50 - 300
> 300


UV2
Slope
Substr
Depth (m)
-100
-125
-150
0
200
400
600
800
Density (ind / m²)
8
6
4
2
0
Porifera
Density (col / m²)
60
40
20
0
Zoanthid
Distance along transect (m)
UV3
Slope
Substr
Depth (m)
-100
-150
Density (ind / m²)
300
200
100
0
890
Dasmosmilia lymani
Density (col / m²)
60
40
20
0
Zoanthid
Distance along transect (m)
Y2
Slope
Substr
Depth (m)
-100
-150
-180
0
400
800
1200
Density (ind / m²)
2
1
0
Stylatula elegans
Density (col / m²)
60
40
20
0
Zoanthid
Density (ind / m²)
8
6
4
2
0
Porifera
Distance along transect (m)
WX4
Slope
Substr
Depth (m)
-110
-120
0
100
200
300
Density (col / m²)
60
40
20
0
Zoanthid
Density (ind / m²)
300
200
100
0
400
404
507
Dasmosmilia lymani
Distance along transect (m)
Slope Legend
Horizontal
Sloping
Substrate Legend
Muddy sand
Sand
Gravelly sand
Pebbles-cobbles
Mudstone outcrops


CCA dim 1
CCA dim 2
A
B
C & D
E
GS
PC
Depth
Slope
MO
Sa
MS
−2
0
2
4
6
1
0
−1
−2
−3
−4
−5
Most contributing species
Dasm_lym
Zoan_col
Astr_ame
Pol_Mald
Styl_ele
Uni_Aster
Edwar_sp
Pol_er
−0.5
0.0
0.5
1.0
0.4
0.0
−0.4
−0.8


a
Species Richness
5
10
15
20
0
200
400
600
Sampling Units
Canyon
Shelf
b
Species Richness
5
10
15
0
200
400
600
Sampling Units
Sand
Gravelly sand
Pebbles cobbles
Mudstone outcrops
Muddy sand
c
Species Richness
5
10
15
20
0
200
400
600
Sampling Units
Assemblage A
Assemblage B
Assemblage C
Assemblage D
Assemblage E