Title: Community composition of epibenthic megafauna on the West Greenland Shelf

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Abstract

Epibenthic organisms are a critical component of the marine environment, functioning as ecosystem engineers, habitat, and food for other organisms. Our knowledge of the diversity, complexity and sensitivities of these habitats is limited, particularly at higher latitudes and greater depths. The West Coast of Greenland is the site of a commercially important shrimp trawl fishery, but there are few published records describing the benthic community structure of the region. Here we report results from benthic camera surveys conducted at 119 sites, over 3 years, spanning 1400km of the west Greenland continental shelf (61-725m depth). A total of 29 classes of epibenthic taxa were identified from the images. There are significant differences of composition and diversity in sites with hard and soft substrate. Hard substrate communities are relatively diverse with higher abundances, and are characterised by sessile, attached groups such as Hydrozoa, Anthozoa, Bryozoa and Porifera. Soft sediment sites are less diverse and dominated by Polychaeta and have specialist Malacostraca such as the commercially exploited shrimp, *Pandalus borealis*. Distribution patterns and variation in epibenthic megafauna are related to substrate and the environmental parameters depth, temperature and current speed. This study represents the first quantitative characterization of epibenthic megafaunal assemblages on the west Greenland continental shelf. These data constitute an important baseline, albeit in a region heavily impacted by trawl fisheries and demonstrate the utility of benthic photography for examining and monitoring seabed diversity and change.

Key words: West Greenland; epibenthic communities; continental shelf; hard substrate; soft substrate; benthic invertebrates

Introduction

The epibenthic organisms that constitute seafloor communities are critical components of the marine ecosystem. They provide three-dimensional habitat which can be protective or supportive to other organisms. They function as substrate upon which and within which other organisms settle or live (Levin and Dayton 2009; Buhl-Mortensen et al. 2010). Furthermore they are food for other organisms, and can play important roles as ecosystem engineers, functioning to redistribute and remineralise carbon (Renaud et al. 2007).

West Greenland study area

The West Greenland coastline extends from the Arctic (85°N) to subarctic (60°N) and is traversed by numerous fjords, many of them acting as direct links between the inland ice sheet and the ocean. Moreover, many islands are scattered directly off the coast resulting in an extremely long coastline and a variety of benthic habitats. The continental shelf often extends >100 km offshore. A mix of shallow banks (<50 m) and deep troughs (>300 m) results in a highly complex bathymetry in the shelf area. In Southwest Greenland two water masses dominate: 1) the cold low-saline polar/coastal water from the East Greenland Current and 2) the warmer, more saline Atlantic water entering the area via the Irminger Current (Myers et al. 2007). The continental shelf in this southwestern region is relatively narrow and rocky with a steep shelf edge, and the West Greenland current is relatively strong. Further north the current slows, the influence of the relatively warm Atlantic water is weaker, and the area is characterized by seasonal sea ice cover and a wide and less well defined shelf (Boertmann and Mosbech 2011).

There are few published records describing benthic community structure in Greenland, and all of them focus on coastal and shelf habitats, while the deep offshore basins are largely unstudied (Boertmann and Mosbech 2011). The available studies of benthic invertebrates in West Greenland reveal a considerable amount of local scale variation in individual abundances and taxon richness on both local and regional scales. This is caused primarily by differences in sediment composition, currents, food input and disturbance level (Boertmann and Mosbech 2011). Clear differences in growth rates (of bivalves and sea urchins) related to differences in temperature and food availability have also been measured in coastal Greenlandic waters (Blicher et al. 2007; Sejr et al. 2009).

Currently, little information is available to assess and describe benthic faunal composition and diversity on the larger geographic scale of the West Greenland Shelf area. Benthic diversity studies undertaken in Greenland have been largely confined to local scale, inshore areas (Schmid and Piepenburg 1993; Piepenburg and Schmid 1996; Sejr et al. 2000). However, one survey in the Godthaabsfjord system in southwest Greenland (Sejr et al. 2010) used Van Veen grabs to survey macrobenthic infauna community composition and diversity. This survey stretched from the inner fjord, across the shallow banks, and down the continental slope. They found high beta diversity, but this covers one transect and may not be representative of the wider region.

A recent compilation of data from across the Arctic suggested that West Greenland has a relatively high diversity of benthic species richness (Piepenburg et al. 2011). Impact assessments undertaken in Disko Bay and Eastern Baffin Bay (Boertmann and Mosbech 2011) document high richness, diversity and abundance of infaunal organisms (>100 infauna species in grab samples of $0.1m^2$) including several species believed to be new to science. However the variation within the West Greenland region remains poorly described and only a modest part of benthic biodiversity is quantified and described in the published literature at present (Boertmann and Mosbech 2011).

Substrate types (rock, mud and gravel, mixed substrate) in areas that are exploited by the shrimp fishery in West Greenland have been characterized and charted in the fishery management plan (Lassen et al. 2013). The distribution and abundance of corals and sponges has not been systematically studied. A review of coral and sponge bycatch collected during experimental trawls between 2010 and 2012 included notably few corals collected from depths less than 500m, and knowledge of shallower distributions remains sparse. Only one high diversity coral area was identified between 63°N and 64°N and at 1000-1500m (Jørgensen et al. 2013).

The aims of this study are to identify taxa from benthic images of West Greenland and quantify taxon richness and diversity of epibenthic megafauna (>1cm) at the taxonomic rank of class. Community composition will be examined in relation to environmental variables along a large range of the continental shelf.

Materials and Methods

Image collection

Three benthic invertebrate surveys were carried out in June and July 2011, 2012, and 2013 as part of the annual stock assessment of the West Greenland shrimp fishery. Fieldwork was conducted aboard the R/V Paamiut, a 1085 tonne shrimp trawling vessel operated by the Greenland Institute of Natural Resources (GINR). Sampling took place between the hours of 6pm and 6am. Images of the seabed were taken with a drop camera, deployed from a winch. The camera system consisted of a Nikon digital SLR camera, DSC-10000 Digital Ocean Imaging Systems (DOIS) deep sea camera housing, and 200W-S Remote Head Strobe flash unit (DOIS, Model3831), all mounted on a weighted steel frame. A weight suspended below the frame triggered the camera on contact with the seabed. Each image sampled an area of approximately $0.3m^2$.

Ten images were taken at each sampling station. The location, time, depth and length of winch wire extension were recorded for each image. In between pictures, the camera was raised 10-20m off the seabed for 1 minute to ensure subsequent pictures did not sample the same area. Typically, the ship and camera would drift 20-50m (based on ship GPS) during the 1 minute interval between pictures. Stations were selected to represent a spread of geography, depth, seabed and fishing impact within the geographic limitations imposed by daytime operations (sampling had to be relatively nearby the start/end locations of daytime operations).

Taxon identification

We identified, counted and recorded taxa from images with the aid of guides and collaborators. Colonial organisms (such as encrusting Bryozoa) were counted as 1 'individual' per continuous 'patch' or 'unit'. Images were compared with physical samples collected from grabs and bycatch. Twenty-nine taxonomic classes were observed for which identification could be regarded as reliable (Online Resource 1). The majority of fauna identified were epifauna, but some clams could be identified due to visible siphons, and others (polychaetes, holothuria) were also often identifiable. Images were processed with the aid of the software “Poseidon”, developed by computer scientists at University

College London, in collaboration with the authors of this study, specifically to aid identification of benthic taxa.

Two phyla were not examined at class-level due to difficulties with identifications. Porifera were subdivided into three categories based on their morphology. These were i) encrusting sponges, those forming a continuous mat over another object such as a stone; for example *Myxilla* spp. and *Halichondria* spp. ii) arborescent sponges, those with a branching structure; such as *Haliclona* spp. iii) massive sponges, large (unbranched) sponges such as *Geodia* or *Polymastia*. Bryozoa were also subdivided into three categories i) encrusting Bryozoa (as encrusting sponges – example *Escharina* spp.); ii) soft Bryozoa, such as *Securiflustra* spp. and *Alcyonidium* spp.; iii) stony Bryozoa, with rigid branching (for example *Hornera* spp.) or lattice structures (such as *Reptorella* spp.).

Analysis

Although 10 images were taken at each station, some stations did not produce 10 images suitable for analysis, due to sediment disturbance in soft-sediment areas, or a tilted camera in rocky areas. Five images per station were selected for analysis (representing the best balance between image quality and maximising the number of stations to analyse). Data from these images were aggregated into station-level data to be used for analysis.

Taxon richness, abundance, Evenness (Pielou's measure of evenness), and Shannon-Wiener's diversity index were determined for each camera station. Abundance was defined as the total number of individuals (or distinct individual colonies). Taxa were identified as generalist, or specialist to hard or soft seabed using the "clam" multinomial classification method (Chazdon et al. 2011). Sample-based taxon accumulation curves were used to test the degree to which all taxa were successfully observed using seabed images. The expected total number of taxa in hard and soft substrate communities was calculated using three different extrapolation methods: Bootstrap, 1st order jackknife, and Chao (Magurran and McGill 2010).

Prior to subsequent analysis, 'singleton' taxa that appeared as a single observation in just one site were removed from the data set. Taxon observation data were transformed using both the Wisconsin and square root transformation to reduce influence of very abundant taxa (Legendre and Gallagher 2001).

A multidimensional scaling analysis (MDS) was performed on the community composition data (Faith et al. 1987). Environmental data were fit to the MDS ordination to test for significant association of composition and environment. Environmental data for the sea bed was gathered at the location of each station using the TOPAZ4 Arctic Ocean Reanalysis oceanographic model (http://catalogue.myocean.eu.org/static/resources/myocean/pum/MYO2-ARC-PUM-002-ALL_V4.1.pdf). Mean values for salinity, temperature and current speed were calculated over the full time period of the oceanographic model (1991-2010).

Sites were clustered into groups using a bray-curtis distance matrix with a ward linkage method (Jørgensen et al. 2015). The top two hierarchical classifications were considered in subsequent analyses. The multi-response permutation procedure was used to test for differences between clusters. The simper method (Clarke 1993) was used to find taxa discriminating between clusters based on bray-curtis distances. An analysis of similarities (ANOSIM) was used to determine significance of taxon dissimilarity by cluster (Clarke 1993). All analysis was performed using the vegan library of the R statistical software program (Oksanen et al. 2013).

Results

Fauna surveyed

A total of 119 stations were photographically sampled between 2011-2013. A map showing the location of sites along the west Greenland continental shelf is presented in Figure 1. The stations span depths of 61-725m but are concentrated on the 100-500m depth zone around the areas of the shrimp fishery. The environmental conditions covered by these stations are broadly similar to the region covered by the 100-500m depth zone (Figure 2), although are over-represented in the warmer, more southerly areas. Fifty-five stations were classified as 'hard' substrata (i.e. rocky seabed), while 64 were classified as 'soft' (either sandy or muddy). A total of 29 taxonomic classes were identified from at least one station (Table 1).

A full list of taxa identified is provided in Online Resource 1. Polychaeta, Ophiuroidea and Ascidiacea are the most commonly encountered taxa, seen in the majority of sites and regarded as generalists for the area. There are many specialist taxa in hard-bottomed areas including sessile, attached fauna such as Porifera, Bryozoa, Hydrozoa and Anthozoa.. Distribution maps for all taxa are presented in Online

Resource 2. There was a large variation in abundance estimates between stations, and abundances were consistently higher in hard-bottomed communities (Table 1). Soft bottom communities were more likely to be dominated by Polychaeta, but soft-specialist taxa include Malacostraca, observations of which are predominantly composed of the commercially caught shrimp *Pandalus borealis*. Hard and soft substrate communities are significantly different (ANOSIM, $p<0.001$).

Community clusters

Sites were clustered based on taxonomic similarity. Example images from each cluster are presented in Online Resource 3. The primary partition of the cluster analysis (Figure 3 – Cluster 1+2 / Cluster 3+4) agrees broadly with substrata (Figure 3). The ANOSIM indicates these two clusters are significantly different ($p<0.001$). Furthermore, the second tier of clustering (clusters 1,2,3 & 4) are also significantly different (ANOSIM test, $p<0.001$). The hard-substrata clusters have the highest within-group similarities (Table 2).

Cluster similarities and their most discriminating taxa are presented in Table 2. Cluster one is most readily distinguished by the presence of Ascidiacea; cluster two is characterised by Anthozoa and encrusting Bryozoa; and cluster three is discriminated by the relative abundance of Gastropoda and Malacostraca; cluster four has the greatest abundance of Polychaeta.

Community clusters differ by environment, with the predominantly soft-bottom clusters 3 & 4 found in colder and deeper water with slower currents. Conversely, the (mostly) hard-bottom cluster 1 & 2 are found predominantly in warmer, shallower water with faster current speeds (Figure 4). There are geographic patterns evident (Figure 5) although there is strong geographic overlap between some clusters. Cluster 1 sites are focussed in the south (with 2 outliers), while cluster 3 sites are found predominantly in the north; clusters 2 and 4 exhibit a wider geographical range.

The MDS plot (Figure 6) summarises taxonomic similarities between sites. The tight grouping of clusters 1 and 2 indicates that stations in these groupings have more similar community composition than those in clusters 3 and 4. Latitude, depth, current speed and temperature all have significant directional associations with community composition, although these are all strongly correlated (as they are with substrate).

Discussion

This study presents a baseline survey and first description of epibenthic megafauna composition and distribution along the West Greenland shelf. The outer shelf from the latitude of Disko bay to Upernavik is defined by groups such as Malacostraca, Gastropoda and Bivalvia. Moving south we see a transition to rockier habitats with sessile, attached fauna more dominant (including Anthozoa and Porifera). Documenting the distributions of potentially habitat-forming taxa such as sponges and corals is an important first step to support their conservation.

The soft-substrate epibenthic megafaunal communities described here are notably less diverse than hard-substrate communities. This is consistent with the results of grab sample studies of infauna characterising soft-sediment habitats in other areas around the Northwest Atlantic (Kenchington et al. 2001, Sparks-McConkey and Watling 2001). Polychaeta are the most common taxa on both hard and soft substrate areas and account for more than half of all observations. Ophiuroidea are found in 107 of 119 stations and are the next most widespread taxon. The predominance of this group was observed in earlier studies in NE Greenland, where Echinodermata were the most common component of epibenthic communities, and Ophiuroidae the dominant taxa in each study area (Starmans et al. 1999). In NE Greenland sites this dominance was much more pronounced (63% of observations were Echinodermata). The substrata, depth range and latitude surveyed in these studies are not directly comparable. Echinoderms also dominated bycatch in Barents Sea surveys (Jørgensen et al. 2015) though photographic surveys and bycatch data are not directly comparable.

Measuring diversity

Although biodiversity indices are primarily designed for use in species-level analysis, higher taxon-based approaches are common for image-based marine studies given the difficulty of identifying organisms from *in-situ* photographs (Freese et al. 1999; Collie et al. 2000; Compton et al. 2013). Some biodiversity dynamics will not have been described by this analysis, due to the aggregation of species at higher taxonomic levels. For example, examining taxonomic classes such as Anthozoa ignores the differences between species with very different ecological requirements. Anthozoa includes the soft-sediment specialist sea pens (such as *Pennatula* and *Umbellula* spp. which are common in northern Greenland) with organisms requiring rock-attachment such as large gorgonians (i.e. *Paragorgia* *arborea* which is seen in some southern sites). The two phyla for which Class level identification proved difficult (Porifera, Bryozoa), were subdivided into functional groups to limit the aggregation of broad ecological differences. The implications of aggregation at such a coarse taxonomic resolution should be kept in mind when interpreting the results presented herein. However, the use of higher taxonomic levels as biodiversity indices is suited to investigating broader-scale patterns (Robert et al. 2014) and the wide geographic spread of this analysis is concordant with examining this broad scale.

This study is limited to epifaunal diversity. In the future, this should be supplemented with the infaunal component to complete biodiversity estimates. Grab sampling of undisturbed soft sediment has recorded high infaunal diversity, with >100 different invertebrate species per m^2, and several thousand individuals per m^2 (up to >10000 ind. m^2) in coastal and shelf areas of West Greenland (Sejr et al. 2010; Blicher et al. 2011).

Temporal variation

The variability and accuracy of some community indices have been shown to be highly dependent on the temporal variability of species abundances (Trebitz et al. 2003). This study does not attempt to account for temporal variation. Each of our stations were sampled once at a fixed point in time from June and August between 2011-2013. One of the most frequently observed taxon in this study is the motile Ophiuroidea, and several stations show what appears to be large feeding aggregations. Sampling dense feeding aggregations could reveal ephemeral patterns of high local diversity. However, local aggregations of Ophiuroidea are known to persist over time (at least in dynamic, shallow environments, Dauvin et al. 2013, see also Piepenburg 2000; Blicher and Sejr 2011). In this study all ophiuroids are grouped into a single taxon and the majority of the most populous taxa are positionally fixed and likely to endure for multiple years, which reduces the potential for large temporal variation.

Another type of temporal variation results from diurnal migration. For example, the commercially fished shrimp *Pandalus borealis* (the most commonly observed decapod seen in 41 stations) exhibits a diurnal migration pattern, inhabiting the seabed in the day and moving up into the water column during the night (Bergström 2000). The night time sampling of this survey will lead to under-represented of this species. It is not known if other diurnally migrating taxa are under-represented in these data.

Environment

We find evidence of environmental influence on community composition, with factors temperature, depth, slope and current speed showing significant association with community structure. Sejr et al. (2010) found strong infauna species turnover along sediment and depth gradients in the Godthaabsfjord system, but weak correlation of diversity and environment. Jørgensen et al. (2015) found temperature, salinity and ice cover to be significant determinants of epibenthic community structure in the Barents. It should be noted that our study area follows a north-south strip of shelf, with northern regions being notably colder, deeper, muddier, less saline and with weaker currents. It is unclear to what extent the environmental results of this study are obfuscated by co-variation along a latitudinal gradient.

Fishing impacts

A direct and current influence on the diversity and functioning of the benthic systems of West Greenland is the disturbance impact of bottom trawling, primarily for shrimp. Shrimp trawling has occurred across the western Greenland shelf since at least the mid 1950s with intense fishing (>50,000 tonnes/year) occurring from 1975 onwards (Buch et al. 2004; Hammeken Arboe 2014). However the impacts of otter trawling, and the biological implications of this disturbance, vary widely according to the environmental conditions, substrate types, natural variability and natural disturbance regime of the site in question. Major impacts of trawling on benthic biodiversity and functioning are known from other regions (Engel and Kvitek 1998; Watling and Norse 1998; Freese et al. 1999; Blanchard et al. 2004; Asch and Collie 2008; Bolam et al. 2014). An important (but not the sole) impact of trawling is the direct physical disturbance to the areas fished. Intense, repeated and widespread trawling reduces habitat complexity by removing habitat-forming species such as corals and sponges on hard-bottom habitats colonised by these communities. In contrast, experimental trawling on sandy bottoms of offshore fishing grounds have caused declines in some taxa, but not the associated large or long-term changes in benthic assemblages (Løkkeborg 2005) and mixed responses to trawling are reported for motile groups in these habitats (McConnaughey et al. 2000). This reduced impact observed in these soft bottom communities may indicate some natural resistance to trawling disturbance in areas with higher natural variability (Prena et al. 1999; Kenchington et al. 2001; Kutti et al. 2005). Furthermore, the negative impact of trawling is known to be diminished in areas exposed to high natural disturbance regimes, including wave action, fluctuations in salinity, and temperature (Auster and Langton 1999).

The Western shelf of Greenland is subject to significant seasonal ice flows, with observations of ice scouring at depths exceeding 1km (Kujpers et al. 2007). This 1000m scouring depth may be exceptional, but the target depth of the main fishery is 150-600m, which may be inside the keel depth of larger icebergs. The impacts of otter trawling and the biological implications of this disturbance vary widely, and results of existing impact studies are highly specific to each site. This study does not attempt to incorporate fishing effort into the analysis, but acknowledges that trawling is likely to be a significant driver of community composition. Proper consideration of this variable must begin with a sound understanding of the faunal assemblages as they currently exist, and of their spatial and temporal distributions. This study provides the first quantitative description of the epibenthic megafaunal assemblages as they currently exist on the west Greenland continental shelf.

In recent years international fishery management organizations have recommended the initiation of monitoring of benthic communities as part of a more ecosystem oriented approach to management (FAO 2003). For countries heavily dependent upon fishing industries, such as Greenland, it is now critically important to start documenting temporal and spatial changes in the benthos, parallel to trends in trawling intensity, in order to understand, measure and manage actual disturbance impacts.

Next steps

This study could be improved by further, carefully selected sampling, particularly focussing on countering: the southern over-representation; the restrictions imposed by night-time sampling; and spatial bias caused by fitting around existing surveys. Identifications could be improved by complementary physical sampling using methods such as grabs or beam trawl. The inclusion of fishing effort as an influencing factor will improve the analysis. These steps will increase the potential of detecting future changes and improve our ability to detect environmental drivers of composition. Such efforts are recommended by CAFF (Conservation of Arctic Flora and Fauna) and the Circumpolar Biodiversity Monitoring Programme (http://www.caff.is/monitoring). Indeed, ongoing initiatives sampling trawl by-catch in Norway and Russia are being expanded to other Arctic territories including Greenland, which will serve to enhance the results of the present study.

Conclusion

This study represents the first widespread characterization of epibenthic megafauna on the area of the West Greenland shrimp fishery. Although the region has been heavily impacted by trawl fisheries, these data constitute an important baseline. We conclude that benthic photography can be a useful tool for examining and monitoring seabed diversity.

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Table Captions

Table 1 – Summary of station data for hard and soft areas. Class pool estimates are based on taxon accumulation curves. Specialist/generalist taxa are defined by the clam test, which examines relative abundance across habitats.

	Hard	Soft	All
Number of Stations	55	64	119
Total Observations	40,714	23,205	63,919
Abundance Range	46-2,837	8-3,900	8-3,900
Total Classes	28	29	29
Class Richness (min-max)	10-21	2-18	2-21
Class Evenness (min-max)	0.1-0.9	0.0-0.9	0.0-0.9
Shannon Index (min-max)	0.2-2.4	0.1-2.5	0.1-2.5
Class pool estimates			
Chao	28 (+/- 1)	29 (+/- 0)	29 (+/- 0)
Jackknife	29 (+/- 1)	30 (+/- 1)	30 (+/- 1)
Bootstrap	29 (+/- 1)	30 (+/- 1)	29 (+/- 1)
Most abundant classes			
Rank 1	Polychaeta	Polychaeta	Polychaeta
Rank 2	Ophiuroidea	Ophiuroidea	Ophiuroidea
Rank 3	Ascidiacea	Ascidiacea	Ascidiacea
Rank 4	Bryozoa (stony)	Maxillopoda	Bryozoa (stony)
Class specialisation	**Hard specialists**	**Soft specialists**	**Generalists**
	Bryozoa (stony)	Polychaeta	Ophiuroidea
	Bryozoa (encrusting)	Bryozoa (soft)	Ascidiacea
	Porifera (encrusting)	Malacostraca	Maxillopoda
	Anthozoa		Bivalvia
	Hydrozoa		Holothuroidea
	Porifera (massive)		Gastropoda
	Porifera (arborescent)		Asteroidea
	Rhynchonellata		Crinoidea
	Polyplacophora		Echinoidea
			Pycnogonida
			Scaphopoda
			Nemertea

Table 2 – Summary of stations by cluster group. Discriminating taxa are defined by the simper analysis, where row headings identify the groups where this taxa predominates compared with the group identified by the column heading (e.g. cluster 3 is positively associated with Gastropoda and Malacostraca in comparison with all other clusters). The pairwise anosim section shows the anosim statistic R (upper triangle) and the p-value associated with this statistic (lower triangle).

	Cluster 1	**Cluster 2**	**Cluster 3**	**Cluster 4**
N	30	27	16	46
N (hard)	27	20	0	8
N (soft)	3	7	16	38
Depth Range	181-323	109-517	206-411	61-725
Latitude (min)	60º 13'N	60º 18'N	62º 33'N	60º 18'N
Latitude (max)	63º 10'N	70º 34'N	72º 16'N	71º 44'N
Class summary				
Total Classes	24	28	16	28
Total Observations	23,413	12,712	829	26,965
Most abundant classes				
Rank 1	Polychaeta	Polychaeta	Polychaeta	Polychaeta
Rank 2	Ascidiacea	Ophiuroidea	Malacostraca	Ophiuroidea
Rank 3	Ophiuroidea	Bryozoa (encr.)	Ophiuroidea	Ascidiacea
Rank 4	Bryozoa (stony)	Bryozoa (stony)	Bivalvia	Bryozoa (encr.)
Rank 5	Porifera (encr.)	Ascidiacea	Hydrozoa	Maxillopoda
Rank 6	Hydrozoa	Anthozoa	Bryozoa (soft)	Bryozoa (stony)
Discriminating Classes				
Cluster 1	-	Ascidiacea, Holothuroidea	Ascidiacea, Porifera (massive)	Ascidiacea, Hydrozoa
Cluster 2	Nemertea, Pycnogonida	-	Anthozoa, Porifera (massive)	Anthozoa, Bryozoa (encr.)
Cluster 3	Malacostraca, Gastropoda	Malacostraca, Gastropoda	-	Malacostraca, Gastropoda
Cluster 4	Polychaeta, Asteroidea	Polychaeta, Asteroidea	Polychaeta, Asteroidea	-
Pairwise Anosim (p\R)				
Cluster 1	-	0.432	0.889	0.201
Cluster 2	0.001	-	0.850	0.107
Cluster 3	0.001	0.001	-	0.183
Cluster 4	0.001	0.013	0.003	-

Figure captions

Figure 1: Location of sampling stations. Seabed images were taken on three cruises over three years between 2011 and 2013.(Map projection epsg:3411)

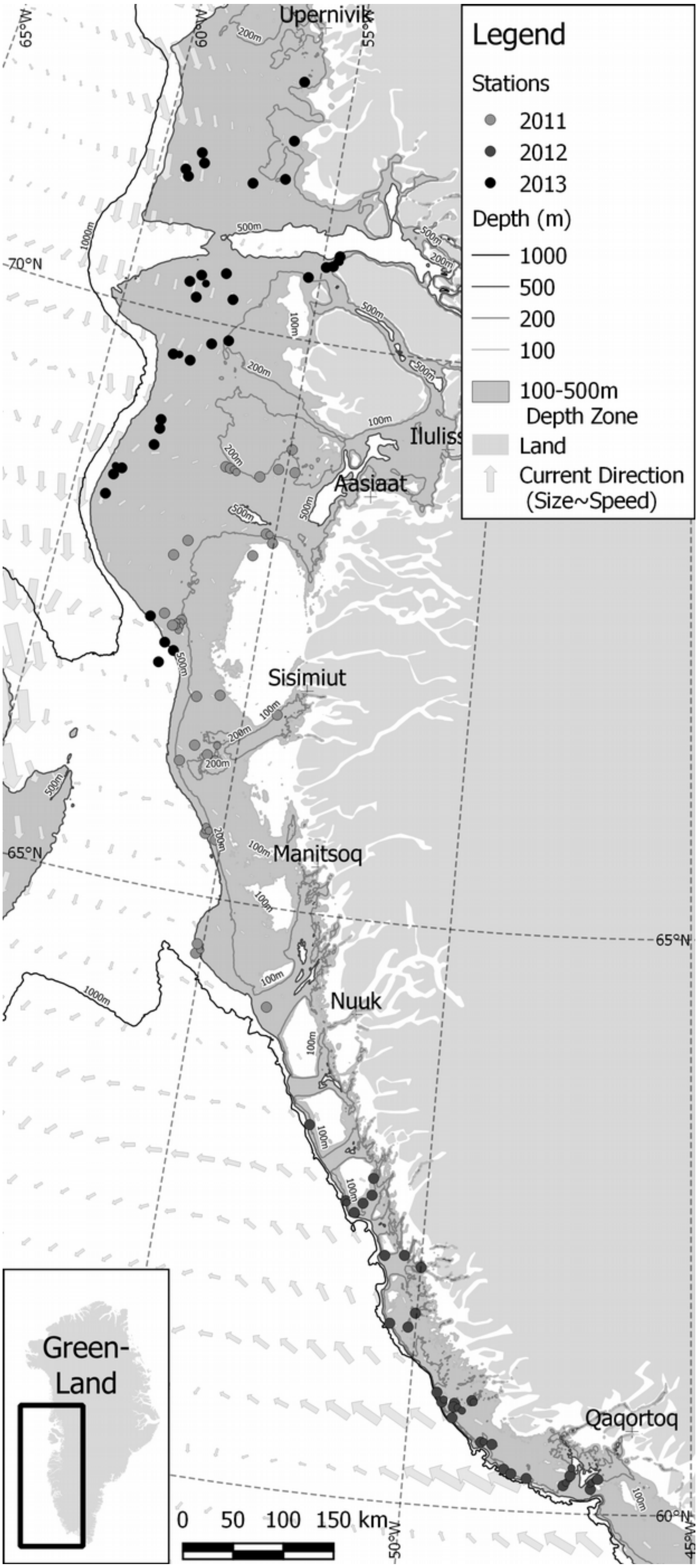


Figure 2: Environmental profile of sampling stations. Histograms represent the 119 stations sampled. The curves show the equivalent profile for the study area, based on 1000 random locations selected within the 100-500m depth zone of Figure 1.

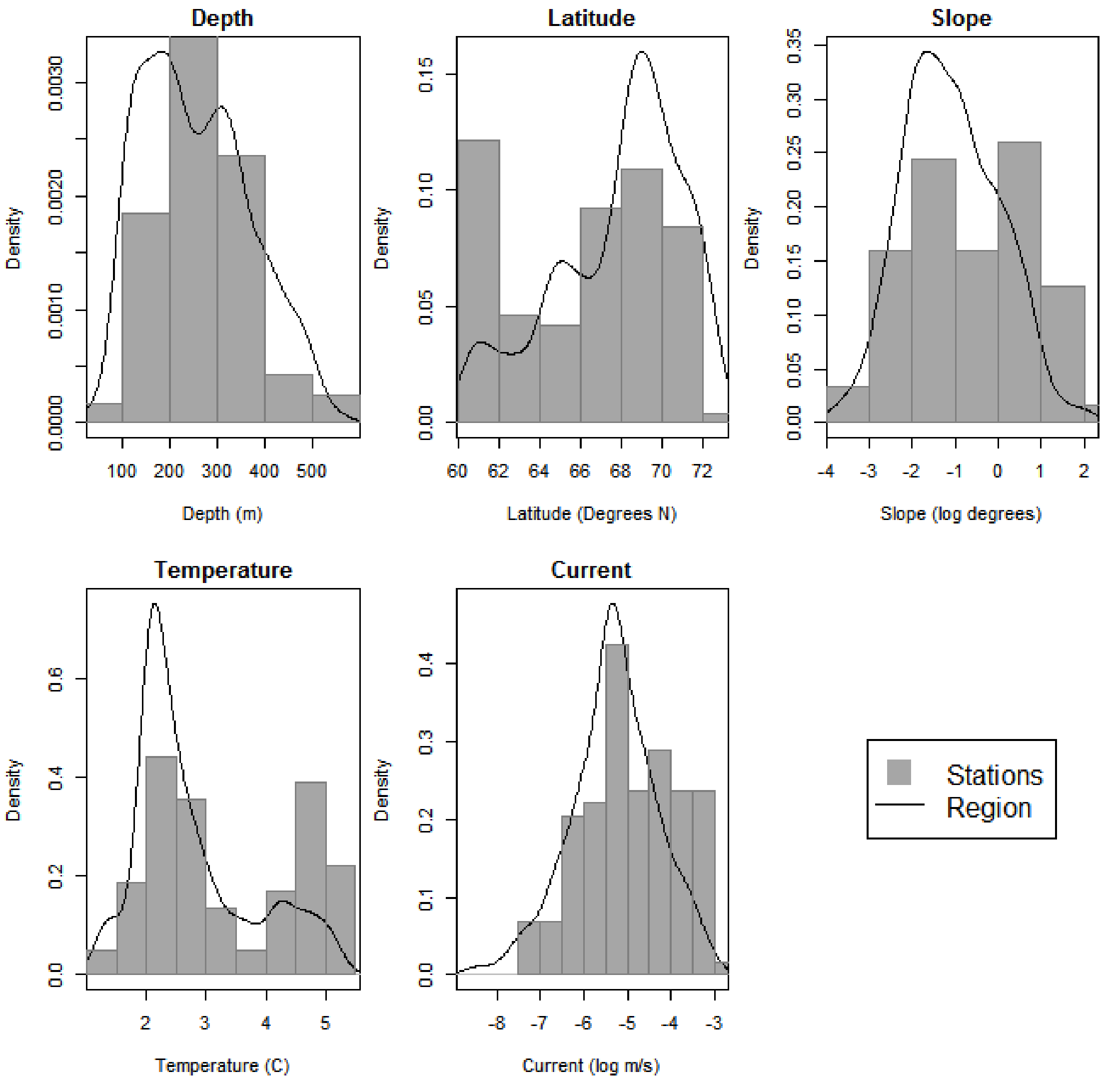


Figure 3: Dendrogram of hierarchical cluster analysis based on bray-curtis distances using the ward method. Numbers in parentheses represent mean within group taxonomic distances based on a Multiple Response Permutation Procedure. Labels preceded by * show stations classified with hard substrata.

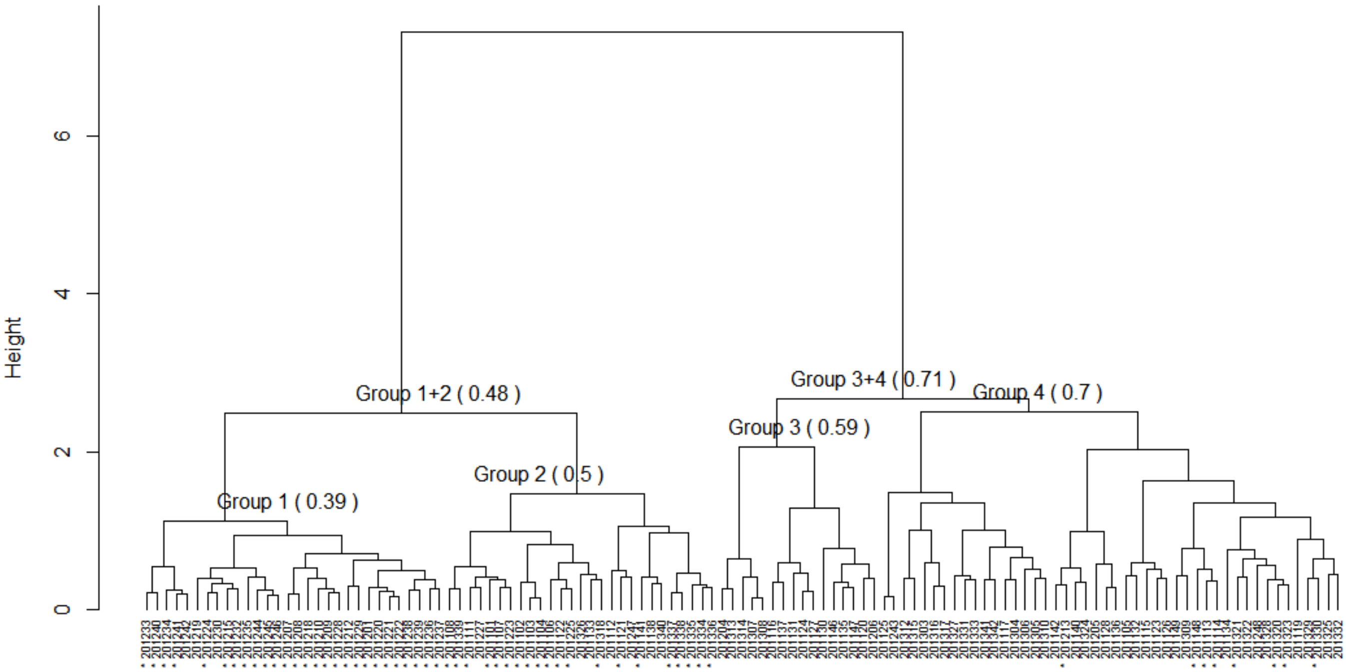


Figure 4: Box plot showing the range of selected environmental variables by cluster grouping.

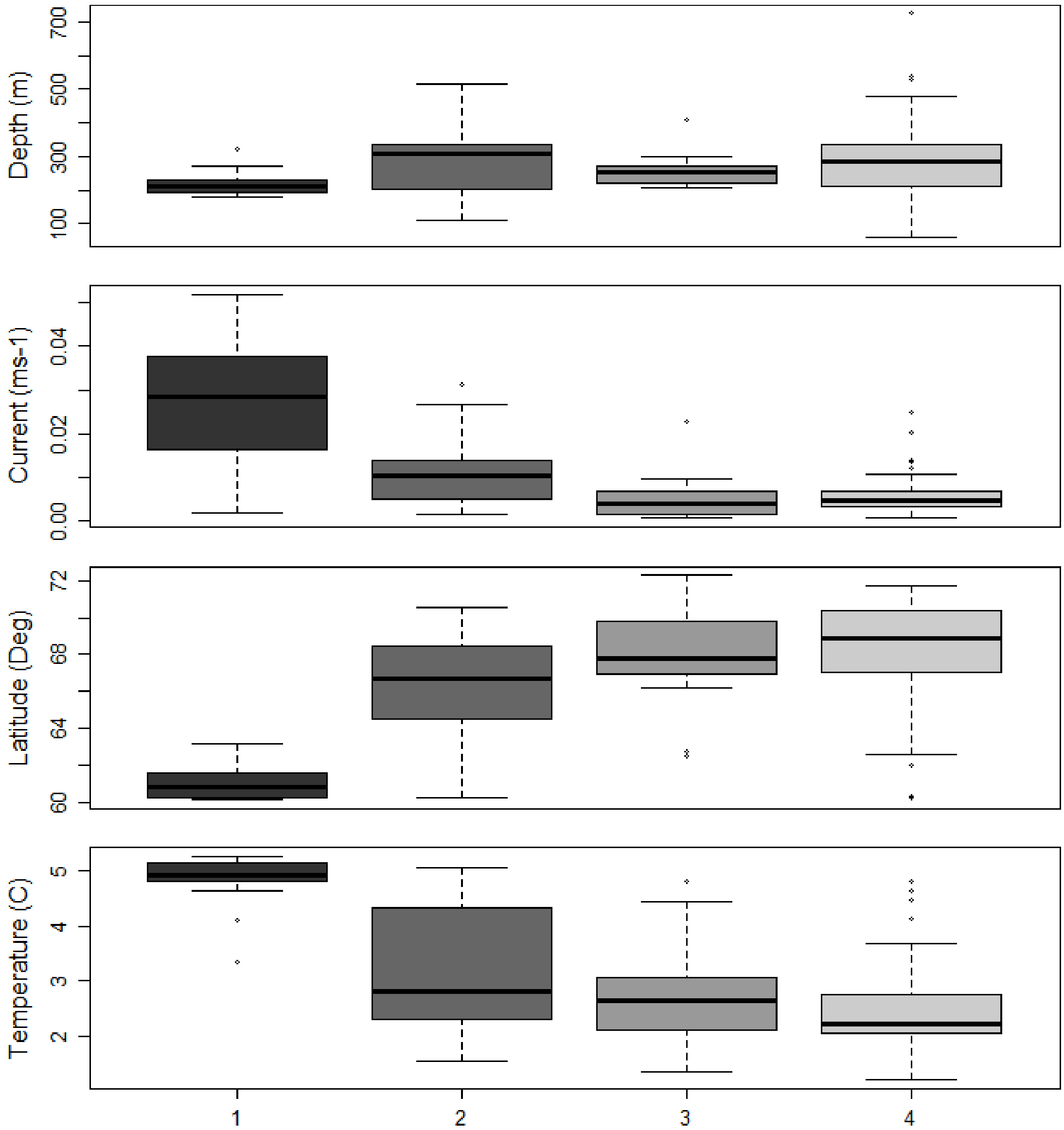


Figure 5: Map of stations by cluster groupings. Approximate seabed temperatures are shown for reference (Map projection epsg:3411).

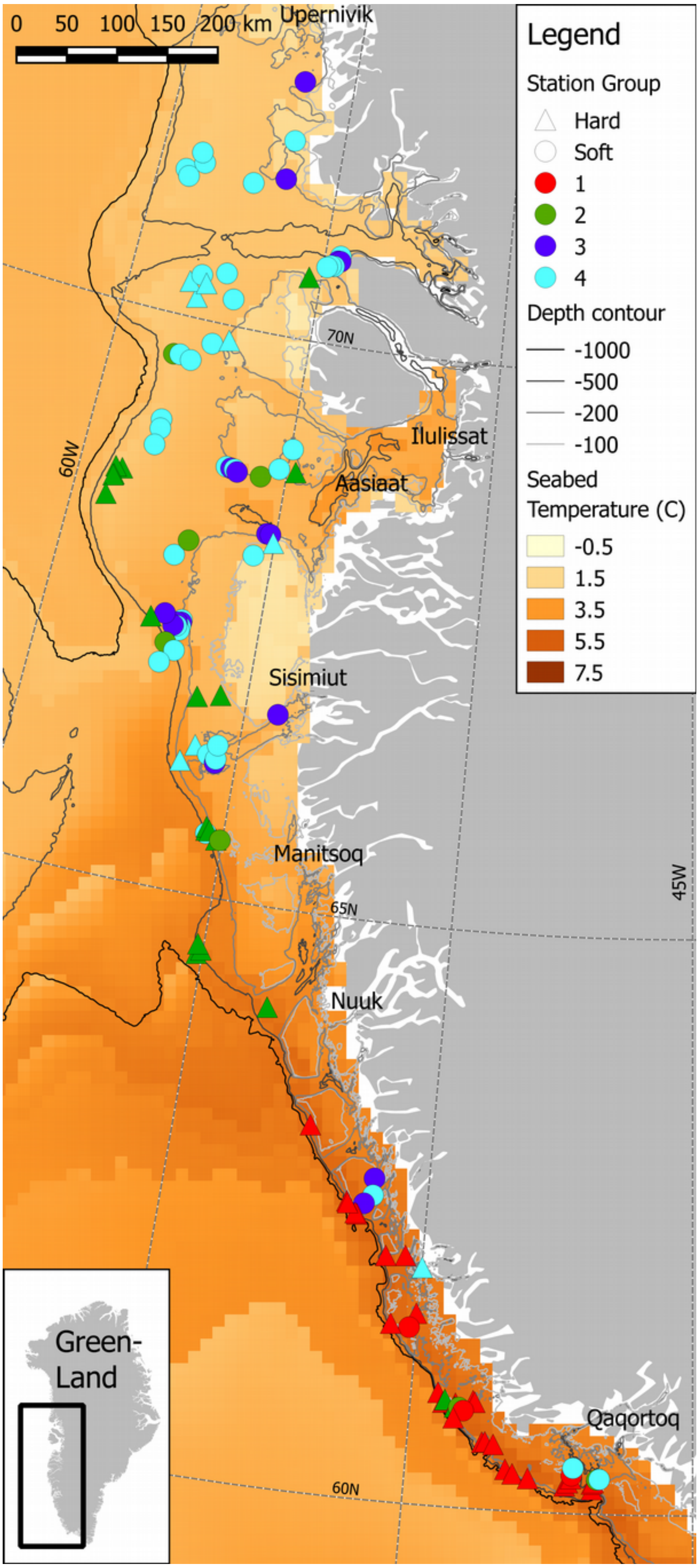
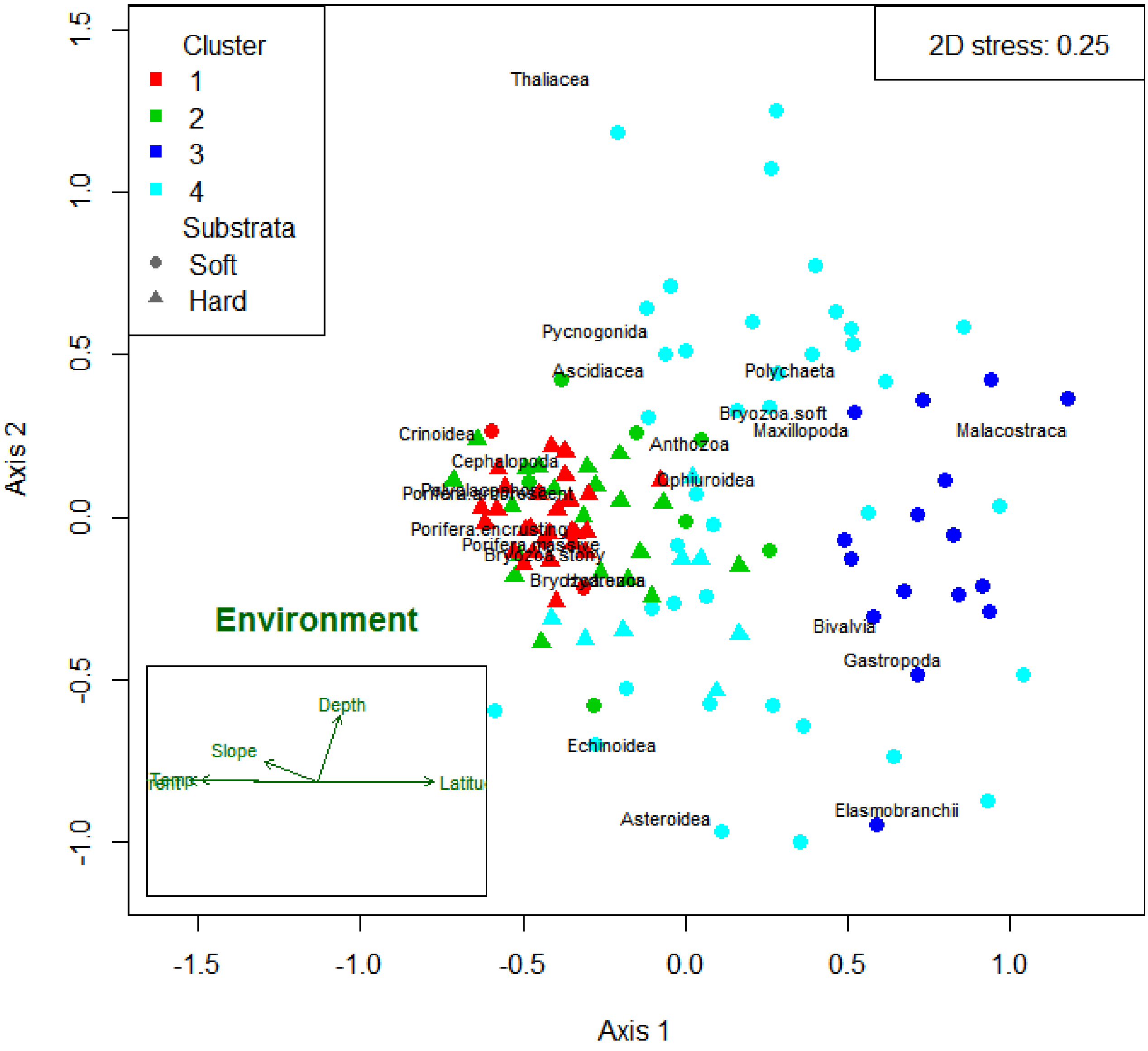


Figure 6: Plot of first two axes of multidimensional scaling (MDS) analysis, based on the community composition data. Points represent stations. Multiple taxa are excluded from the centre of Inset vectors show directional influence of significant environmental parameters ($p<0.05$).

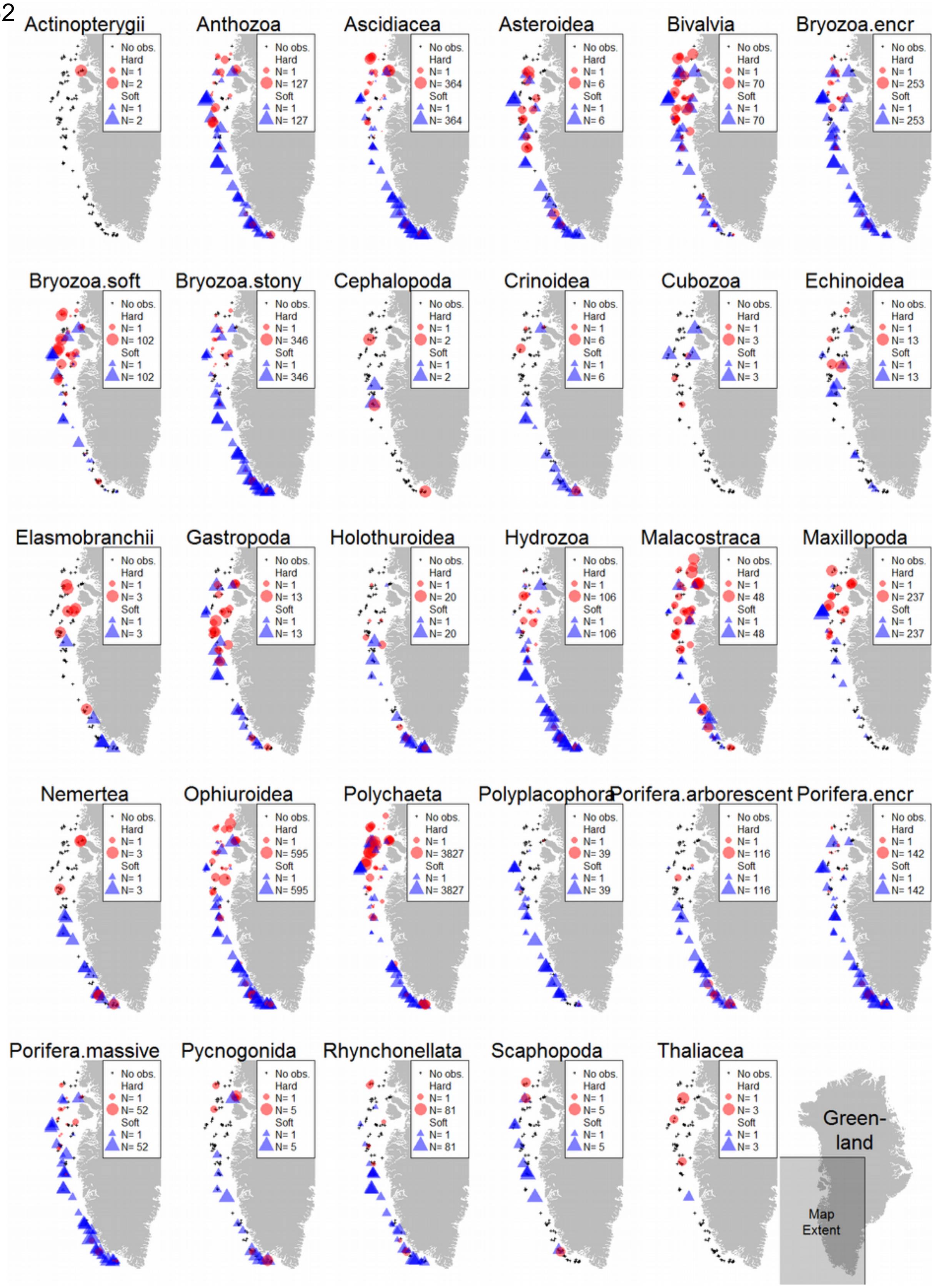


Electronic Supplementary Material

Online Resource 1: Table showing all taxa identified in the benthic imagery. Specialist hard/soft categories are based on a multinomial taxon classification method.

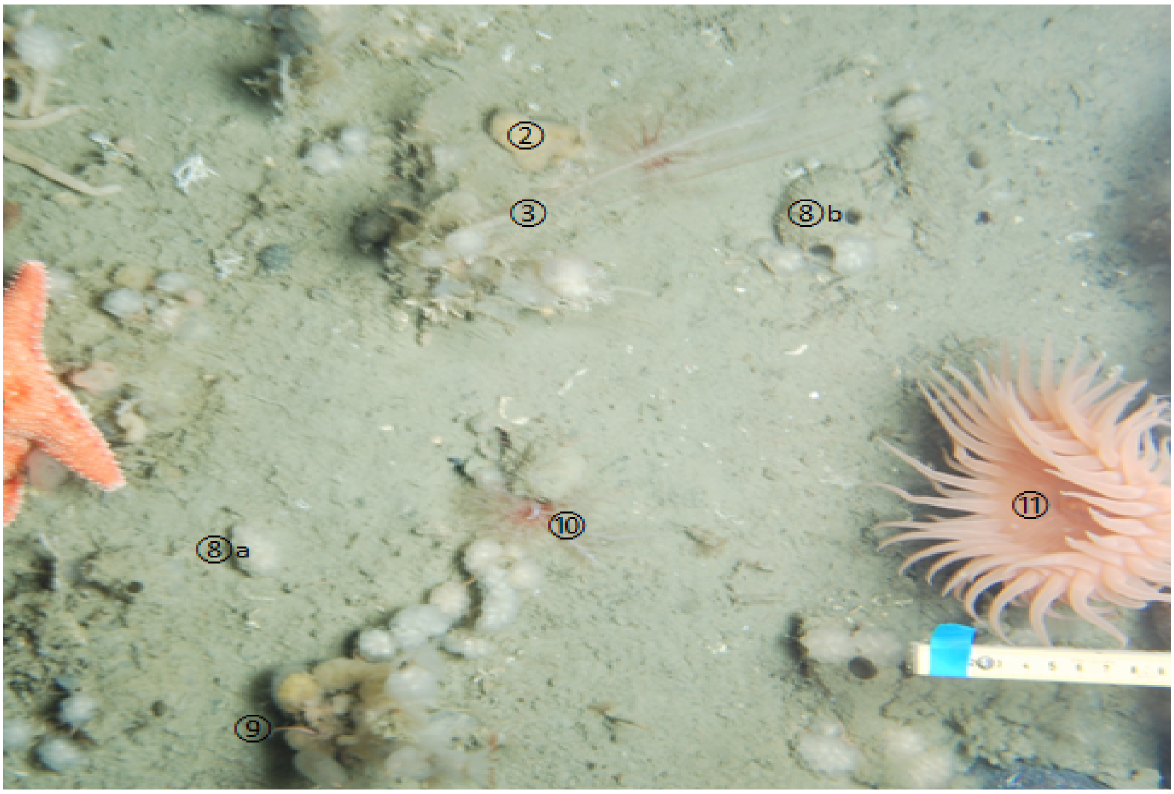
		Total		Soft ground		Hard ground		Generalist /
Phylum	Class	Obs.	Stations	Obs.	Stations	Obs.	Stations	Specialist
Annelida	Polychaeta	32,448	118	17,543	63	14,905	55	Specialist_soft
Echinodermata	Ophiuroidea	7,294	107	1,582	53	5,712	54	Generalist
Chordata	Ascidiacea	7,193	95	1,530	41	5,663	54	Generalist
Bryozoa	Bryozoa (stony)*	4,766	85	314	31	4,452	54	Specialist_hard
Bryozoa	Bryozoa (encrusting)*	3,023	85	182	31	2,841	54	Specialist_hard
Porifera	Porifera (encrusting)*	1,655	72	126	21	1,529	51	Specialist_hard
Cnidaria	Anthozoa	1,486	88	243	37	1,243	51	Specialist_hard
Cnidaria	Hydrozoa	1,414	81	189	31	1,225	50	Specialist_hard
Arthropoda	Maxillopoda	1,021	37	438	22	583	15	Generalist
Porifera	Porifera (massive)*	674	76	59	23	615	53	Specialist_hard
Bryozoa	Bryozoa (soft)*	560	52	351	28	209	24	Specialist_soft
Mollusca	Bivalvia	542	83	202	43	340	40	Generalist
Porifera	Porifera (arborescent)*	482	45	48	8	434	37	Specialist_hard
Arthropoda	Malacostraca	329	65	244	41	85	24	Specialist_soft
Brachiopoda	Rhynchonellata	317	37	16	8	301	29	Specialist_hard
Mollusca	Polyplacophora	239	40	3	3	236	37	Specialist_hard
Echinodermata	Holothuroidea	150	35	22	10	128	25	Generalist
Mollusca	Gastropoda	80	42	34	22	46	20	Generalist
Echinodermata	Asteroidea	61	41	19	14	42	27	Generalist
Echinodermata	Echinoidea	45	15	17	4	28	11	Generalist
Echinodermata	Crinoidea	35	18	6	4	29	14	Generalist
Arthropoda	Pycnogonida	30	20	9	7	21	13	Generalist
Nemertea	Nemertea*	21	19	7	6	14	13	Generalist
Mollusca	Scaphopoda	20	13	3	3	17	10	Generalist
Chordata	Elasmobranchii	14	13	7	7	7	6	-
Cnidaria	Cubozoa	9	6	3	3	6	3	-
Mollusca	Cephalopoda	5	5	3	3	2	2	-
Chordata	Thaliacea	5	4	4	3	1	1	-
Chordata	Actinopterygii	1	1	1	1	0	0	-

Online Resource 2: Distribution of each taxon observed in this study. Stations are coloured by substrate with symbols sized proportional to taxon abundance.



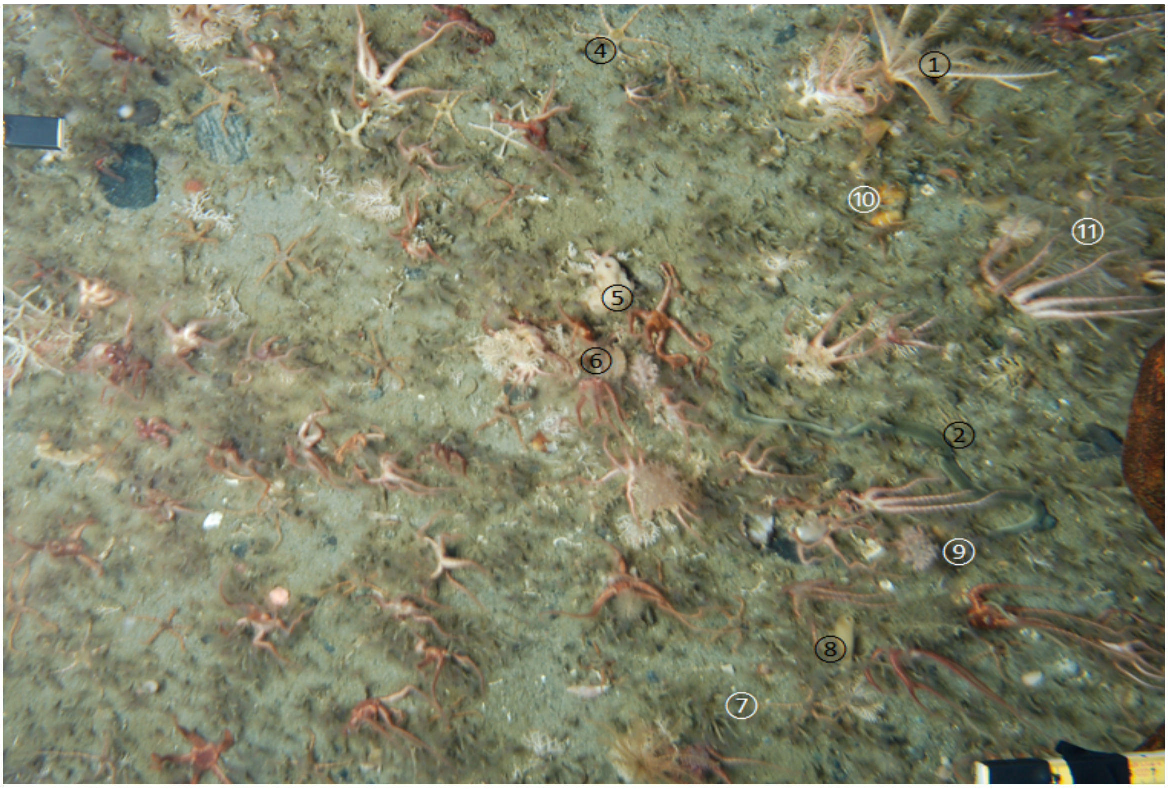
Online Resource 3: Benthic images representing each of the 4 cluster groups. Examples of each taxon group present within the images are numbered. Names of each taxon present and total number of observations within the image can be seen in the accompanying key.

Cluster 1.



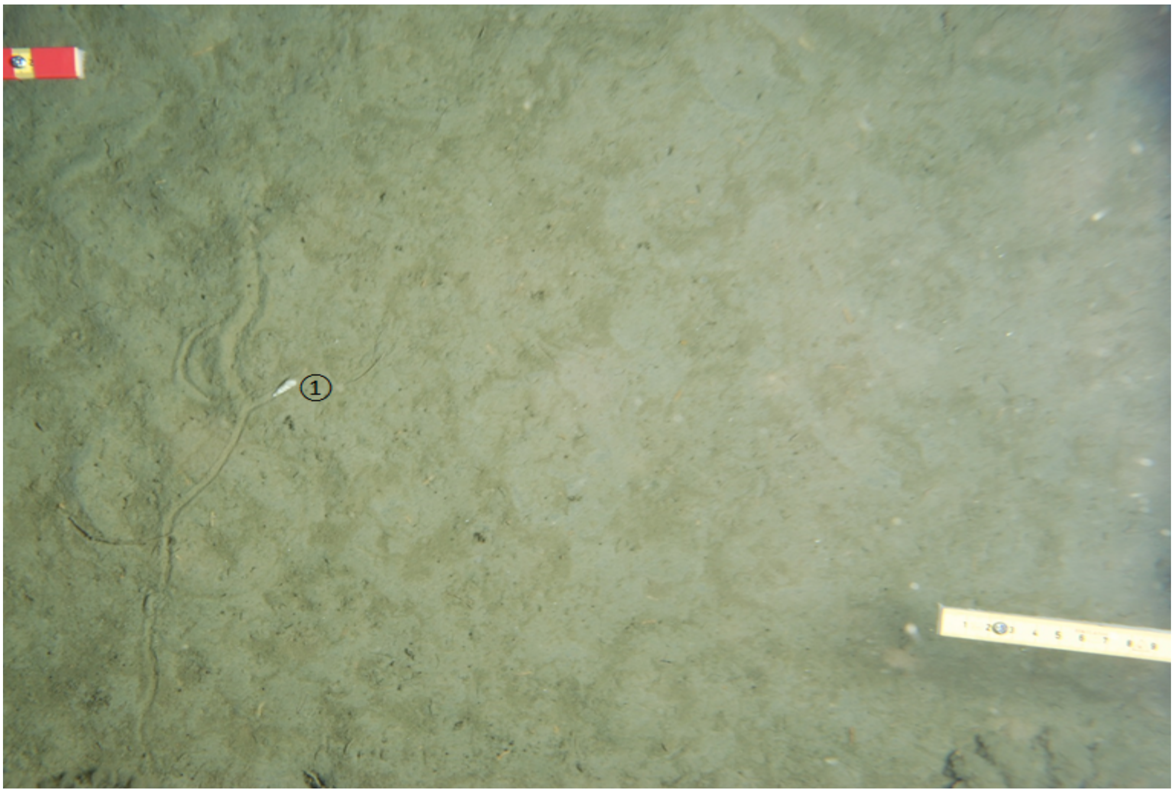
1. Asteroidea
2. Porifera encrusting *(Number of records in image: 2)*
3. Hydrozoa *(6)*
4. Porifera arborescent *(2)*
5. Polychaeta *(8)*
6. Bryozoa erect *(4)*
7. Porifera massive *(4)*
8. Ascidiacea (a) colonial b) individual) *(82)*
9. Ophiuroidea *(3)*
10. Holothuroidea *(3)*
11. Anthozoa

Cluster 2.



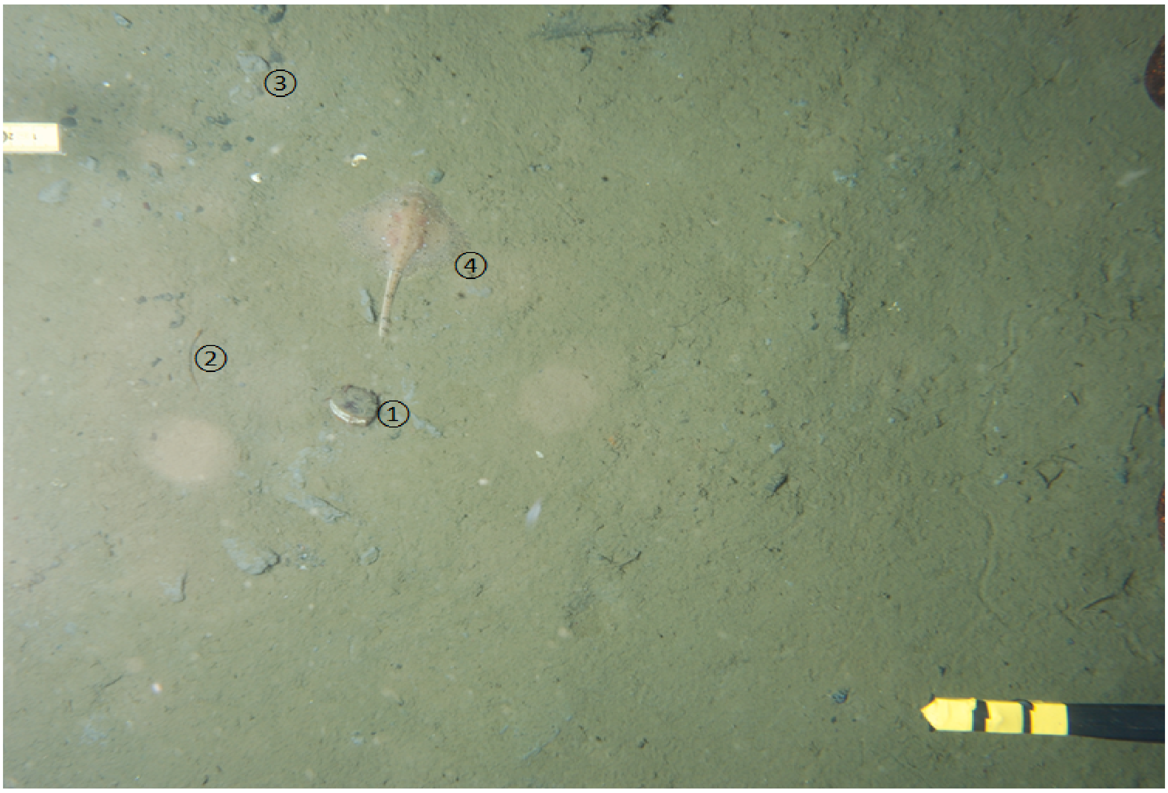
1. Crinoidea *(Number of records in image:2)*
2. Nemertea
3. Bryozoa erect *(17)*
4. Ophiuroidea *(84)*
5. Porifera massive
6. Bivalva
7. Polychaeta *(13)*
8. Ascidiacea *(15)*
9. Anthozoa *(6)*
10. Porifera encrusting
11. Hydrozoa *(3)*

Cluster 3.



1. Gastropoda
2. Polychaeta *(Number of records in image: 5)*

Cluster 4.



1. Bivalva
2. Polychaeta
3. Bryozoa encrusting *(Number of records in image: 2)*
4. Chondrichthyes