



Epifaunal communities across marine landscapes of the deep Chukchi Borderland (Pacific Arctic)



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ABSTRACT

Epifaunal communities from the poorly studied Arctic deep sea of the Chukchi Borderland region were investigated to: (1) determine differences in community structure among ridges, plateau with pockmarks, and much deeper basins as three main habitat types, (2) analyse the environmental factors that might shape these communities, and (3) investigate biogeographic affinities dominating the epifaunal communities. Epifaunal samples were collected in summer 2016 with a beam trawl (6 stations) and ROV (10 stations) from 486 to 2610 m depth. Seventy-eight and eighty-six taxa were registered from ROV images and trawl samples, respectively, with Echinodermata and Arthropoda dominating overall taxon richness. Epifaunal densities were estimated at 2273 to 14,346 ind/1000 m² based on ROV images but only 342 to 2029 ind/1000 m² based on trawl samples. Epifaunal biomass based on trawl catches ranged from 173 to 906 g wet weight/1000 m². There was no significant difference in density, biomass and community composition between plateau and ridge communities, though the western and eastern parts of the study area differed in plateau/ridge community properties. Abundance in the eastern part of the study area was dominated by annelids (Ampharetidae and Sabellidae), and the western part by an unknown cnidarian (likely polyps of *Atolla*). Trawl samples from both western and eastern regions were dominated by the echinoderms *Ophiopleura borealis* and *Pontaster tenuispinus*. Deep basin communities differed from shallower plateau/ridge stations by significantly lower number of taxa and densities based on the images, and by lower biomass based on trawl catches. Polynoid annelids and sponges were characteristic taxa of the basin stations. Water depth and number of stones providing hard substrate significantly influenced epifaunal community structure, with sediment pigments and grain size also being influential. Arcto-boreal-Atlantic species dominated communities in the Chukchi Borderland, presumably mediated by Atlantic water dominance in the deep water layers of the Pacific Arctic. This study adds to the limited knowledge of ecology of the Arctic deep sea and improves existing baseline data that can be used to assess future effects of climate change on the system.

1. Introduction

Deep-sea regions occupy roughly half of the Arctic Ocean area (Jakobsson, 2002), yet the understanding of Arctic deep-sea biodiversity still remains extremely limited. Recent scientific programs such as the International Polar Year 2007–2009, Census of Marine Life (e.g. Bluhm et al., 2011), and studies at the HAUSGARTEN, a biological long-term deep-sea observatory located in Fram Strait (Soltwedel et al., 2005, 2009; Bergmann et al., 2011; Meyer et al., 2013), have helped increase current knowledge of the Arctic deep-sea biodiversity. Results

have shown benthic communities within the Arctic Ocean basins exhibit higher biodiversity – including numerous species new to science described in the last decades (e.g. Gagaev, 2009; Rodríguez et al., 2009) – than previously expected. A recent count estimated 1125 invertebrate taxa inhabit the central Arctic Ocean deeper than 500 m (Bluhm et al., 2011). The most abundant taxa reported were nematodes among the meiofauna, crustaceans, polychaetes, and bivalves among the macrofauna, and sponges, cnidarians, and echinoderms among the epifaunal megafauna (Bluhm et al., 2011). Despite these efforts much of the Arctic deep-sea region remains poorly known and virtually unsampled.

Abbreviation: CBL, Chukchi Borderland

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Epifaunal organisms, those animals living attached to or on the sediment surface (Nichols and Williams, 2009), are currently among the least studied in the Arctic deep sea (except at HAUSGARTEN; Bergmann et al., 2011; Meyer et al., 2013), which is partly related to the difficulty of deploying trawls or photographic gear at great depths in often ice-covered waters. It is known from studies of Arctic shelf systems that epifaunal organisms contribute considerably to total benthic biomass in Arctic ecosystems and play key roles in trophic interactions, bioturbation, and remineralization (Feder et al., 2005; Piepenburg, 2005). In addition, epifaunal sensitivity to natural disturbance and human impacts (Teixidó et al., 2007; Jørgensen et al., 2011) necessitate basic knowledge of their biodiversity patterns given the ongoing sea-ice loss and the potential for enhanced deep-sea fisheries, shipping, and petroleum/mineral exploitation in Arctic deep-sea areas (Thiel, 2003). As benthic communities integrate the effects of physical, chemical and biological factors, they can be used as indicators of ecosystem status.

Globally, epifaunal community structure differs among different regions of the deep-sea floor (e.g. Levin et al., 2001) which is now recognized as a system of great complexity with diverse habitats at different spatial scales (Danovaro et al., 2014). These differences arise from environmental factors such as sediment characteristics, sea floor morphology, current flow regimes, chemical conditions, depth, and food availability (Levin et al., 2010; Bluhm et al., 2011; Pierdomenico et al., 2015). Deep-sea sediments consist mainly of silt and clay, while ridges and plateaus can have a higher sand fraction (Stein et al., 1994; Bluhm et al., 2011). Hard substrate (e.g., drop stones from ice-transport processes, carbonate outcrops at methane seeps, whale bones) and other forms of increased complexity of sea floor morphology (e.g., elevations, canyons, depressions in the sea floor) occasionally occur in the deep sea and may enhance benthic biodiversity and biomass compared to abyssal plain deep-sea environments (McClain and Barry, 2010; Pierdomenico et al., 2015; Åström et al., 2016; Meyer et al., 2016). Seafloor morphology also affects direction and strength of bottom currents transporting food particles, eggs and larvae (Buhl-Mortensen et al., 2015), even though currents are usually very slow in Arctic deep-sea systems (Macdonald and Carmack, 1991). Food availability is often the major depth-related factor driving benthic community structure and limiting biomass (Soltwedel et al., 2009; Bluhm et al., 2011; Kröncke et al., 2013). Arctic deep-sea ecosystems are usually described as oligotrophic with highly seasonal food supply to the benthos (Iken et al., 2005) resulting in decreasing benthic biomass with depth (Bluhm et al., 2011). Despite the low food availability in the deep sea benthic biodiversity can be comparatively high which has previously been discussed in light of (1) comparatively stable, 'stress-free' environmental conditions (time-stability hypothesis, Sanders, 1969) or alternatively (2) as a result of patchy food deposition enriching habitat heterogeneity (patch dynamics theory, Grassle, 1989).

This study investigates epifaunal benthic communities in the poorly studied Chukchi Borderland area (CBL) which is currently impacted by dramatic decreases in sea-ice thickness (Stroeve et al., 2005; Perovich, 2011), warming Atlantic water below the surface and halocline waters (Shimada et al., 2004), and increased Pacific water inflow through Bering Strait in surface waters (Woodgate et al., 2007). Consequently, biological change may be expected in the future. Changes in biological communities, however, would be impossible to detect given that only few benthic studies have been conducted here (Cromie, 1961; Mohr and Geiger, 1968; Hunkins et al., 1970; Bluhm et al., 2005; MacDonald et al., 2010) with only one of the epifaunal studies being quantitative (MacDonald et al., 2010). Thus, there is a need to characterize the biodiversity in the complex landscape of that area that hold the potential for high biodiversity and heterogeneity, and to gain insights into mechanisms structuring benthic habitats in the Arctic deep sea.

The CBL is bathymetrically complex (Mayer et al., 2010) in that it comprises comparatively shallow ridges, plateaus, and much deeper, isolated basins (Jakobsson et al., 2008). In addition, the Chukchi Plateau is characterized by the presence of pockmarks, i.e., rounded or

elliptical depressions of <1 to >100 m in diameter and depth that were formed as a result of explosion of gas or fluids from decomposing organic material or leaking gas reservoirs in underlying sediment layers (Hovland and Judd, 1988; Astakhov et al., 2014). Though little is known about patterns of life within pockmarks worldwide and especially in the Arctic, endemic chemosynthetic communities and/or high density of epibenthic fauna have been documented for both active and inactive seeps (Gibson et al., 2005; Webb et al., 2009a; MacDonald et al., 2010; Åström et al., 2016). Finally, the CBL region also is hydrographically complex in that Pacific surface and deeper Atlantic water meet here (Woodgate et al., 2007). This layering of these water masses results in cosmopolitan Arctic boreal and Atlantic boreal species dominating over Pacific affinities in the macro-infauna of the Canada Basin and CBL (Bluhm et al., 2005). However, biogeographic patterns and transitions in epifaunal communities of the CBL have not yet been mapped.

The aim of the present study is to investigate epifaunal communities in the heterogeneous CBL area using bottom trawl samples and remotely operated vehicle (ROV) imagery. The specific objectives are: (1) to compare epifaunal community structure, taxonomic diversity, and distribution patterns across ridge, plateau and basin locations of the CBL; (2) to identify environmental parameters that may influence epifaunal community characteristics; and (3) to evaluate biogeographic affinities of epifauna in the study area. Given the large difference in depth between basin and plateau/ridges, and the presence of pockmarks on the Chukchi Plateau, we specifically tested the hypothesis that (1) epifaunal community structure differs among plateau, basin and ridge locations, with the highest diversity and density at pockmarks plateau locations and the lowest at deep basin locations. Considering the hydrological complexity of the study area with increasing importance of Atlantic origin water with increasing depth, the second hypothesis tested was that (2) the CBL epifaunal species inventory represents a gradient of declining Pacific-affinity proportion with increasing depth.

2. Material and methods

2.1. Study area

The study was conducted in the CBL, north of Alaska between 74 and 78°N and 158 - 165°W during the Hidden Ocean III expedition (HLY1601) on the USCGC *Healy* in July–August 2016 (Fig. 1, see <http://oceanexplorer.noaa.gov/explorations/16arctic/welcome.html>). The CBL occupies a roughly rectangular area of 600 × 700 km, ranging in depth between ~300 and 3000 m, and extends into the Amerasian Basin north of the Chukchi Sea (Hall, 1990). Dynamic geological formation processes have led to the present-day CBL that consists of north-trending topographic highs, including the Northwind Ridge and Chukchi Plateau that surround the isolated Northwind Basin, which also contains several small ridges (Fig. 1) (Hall, 1990; Jakobsson et al., 2008; Mayer et al., 2010). On the Chukchi Plateau, pockmarks were first discovered in 2003 (Gardner et al., 2007) with later surveys revealing many more, typically of 300–400 m in diameter and 30–50 m deep (Mayer et al., 2010). It was suggested that these pockmarks were formed under the effect of pulsed fluid flows with the last modification occurring about 30–15,000 years ago (Astakhov et al., 2014).

Waters of Arctic, Atlantic and Pacific origin interact over the complex CBL bottom topography (Perovich et al., 2003; Woodgate and Aagaard, 2005). The Pacific-origin water comprises the Polar Mixed Layer and upper halocline originating from Bering Sea and Alaska Coastal water entering the Chukchi Sea via the shallow and narrow Bering Strait (McLaughlin et al., 2004; Steele et al., 2004; Woodgate, 2013). The influence of Pacific water decreases with depth and increasing latitude, being virtually absent north of the 2000 m isobath at ~79°N (Woodgate and Aagaard, 2005). The lower halocline is of Atlantic origin and enters the area from the Eurasian Basin via Fram

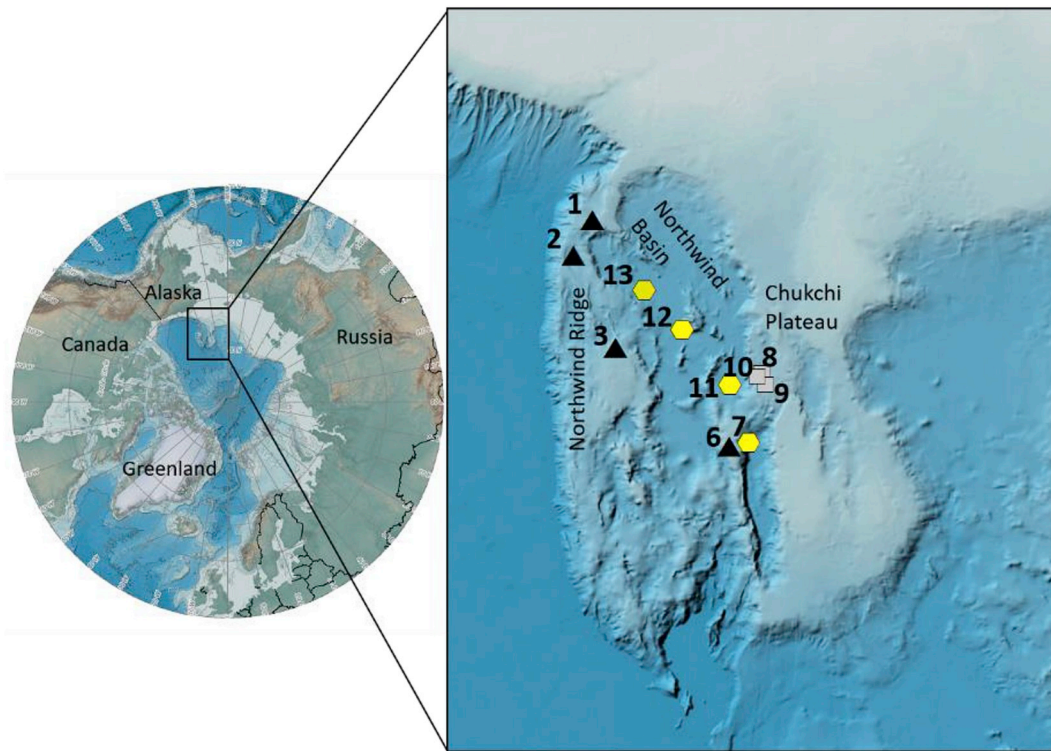


Fig. 1. Study area and stations sampled for epifauna during Hidden Ocean: Chukchi Borderland expedition in 2016; stations symbols indicate different type of topography (triangular – ridge, square – plateau, diamond – basin).

Strait and the Barents Sea (Woodgate and Aagaard, 2005). Underneath it, the Atlantic layer water consists of Fram Strait Branch water and Barents Sea Branch water (McLaughlin et al., 2004; Woodgate et al., 2007). The Arctic Ocean deep-water layer originates from the Greenland Sea; it enters from the Fram Strait and spreads across the Eurasian Basin, finally reaching the Canada Basin (Bluhm et al., 2015).

Sampling stations were chosen to represent the three main habitat types: ridges, basins, and plateau with pockmarks (Fig. 1, Table 1). Ridge stations located on the Northwind Ridge (stations 1, 2) and on one of the ridges in the Northwind Abyssal Plain (station 6), ranged in depth from 486 to 1059 m. Three plateau stations (stations 8, 9, 10)

were sampled relatively close to each other, and their depth ranged from 508 to 873 m. For stations 9 and 10, it was possible to investigate epifaunal communities on the plateau surrounding a pockmark and within the pockmark. Station 8 was in a large groove that was linked to a pockmark. The basin stations were located within the Northwind Basin (stations 11, 12, 13) and isolated from station 7 by a ridge. The depth of the basin stations ranged from 1882 to 2610 m (Fig. 1, Table 1).

Table 1

Information on stations where ROV images and the beam trawl samples were collected. Note the low number of images used for the analysis of the station 8 was due to limited time for the bottom ROV dive at this particular station. The high number of images used for the analysis for station 9 is due to two stations (9a and 9b) being combined. Bottom temperature, salinity and fluorescence values are given; O – no samples are taken, X – samples are taken.

Station	1	2	3	6	7	8	9	10	11	12	13
Latitude, °N	74.32	74.71	75.64	77.06	77.07	76.63	76.59	76.43	76.4	75.93	75.4
Longitude, °W	-159.42	-158.48	-158.82	-161.82	-162.53	-164.06	-163.98	-163.47	-162.26	-161.45	-160.73
Temperature, deg C	0.07	-0.05	0.28	0.70	-0.30	0.41	0.48	0.06	-0.29	-0.28	-0.29
Bottom salinity, PSU	34.87	34.88	34.86	34.84	34.93	34.86	34.85	34.84	34.92	34.92	34.92
Fluorescence, mg/m ³	0.40	0.39	0.39	0.40	0.38	0.39	0.40	0.39	0.38	0.37	0.38
Depth, m	853	1059	746	486	2610	557	508	873	1882	2107	2091
Mean sediment Phaeo, µg pigment/g dry sediment	0.773	0.298	0.088	0.145	0.117	0.192	0.197	0.240	0.192	0.185	0.266
Mean sediment Chl, µg pigment/g dry sediment	0.098	0.039	0.010	0.016	0.012	0.023	0.021	0.026	0.020	0.020	0.027
Sediment organic carbon, %	1.26	1.14	0.81	0.63	0.77	0.98	0.78	0.88	1.09	1.13	1.25
Mud, %	93	96	96	97	98	99	99	95	98	99	100
Sand, %	7	4	4	3	2	1	1	5	2	1	0
Topography	Ridge	Ridge	Ridge	Ridge	Basin	Plateau	Plateau	Plateau	Basin	Basin	Basin
ROV	X	X	O	X	X	X	X	X	X	X	X
Trawl	X	X	X	O	O	O	X	X	O	O	X
Number of pictures analyzed	100	80	0	98	99	39	180	69	79	80	80
Mean area per image, ROV	0.8 ± 0.4			0.8 ± 0.6	0.3 ± 0.1	0.3 ± 0.2					
Average amount of stones per picture	0.3	0.0		1.0	0.0	0.6	0.8	0.1	0.0	0.0	0.1
Trawl transect length, m	1577	1589	2280				713	1246			1689

2.2. Biological sampling

Epifaunal communities (including invertebrates and demersal fishes) were investigated with two main tools, the ROV Global Explorer (www.deepseasystems.com/) and a plumb-staff beam trawl. The ROV was used to perform a photographic survey of the seafloor at each of ten stations, with two dives each at stations 1 and 9 for a total of 12 ROV dives (Table 1). Analyses were performed on 24-megapixel images collected with a downward-looking DSSI DPC-8800 digital camera. The ROV was equipped with DSSI Ocean Light Underwater LED lights. Forward looking 10x and 3.8x zoom 4K video cameras were used to guide the photographic surveys, control distance from the sea floor, and collect taxonomic vouchers with the suction sampler and manipulator arm. We kept the ROV to a linear transect as much as possible but deviations from straight lines occurred at some stations due to variable drift speeds and bottom currents, irregular topography and occasional inspection and collection of taxa of interest, which might have led to a slight bias in estimation of taxonomic abundance and diversity. Still images were taken every 5–8 s, depending on drift speed. Four digital laser pointers, one located at each corner of a fixed distance of a 10 - cm square, were used to estimate the photographed area at four stations, after which they stopped functioning. The average bottom time of the ROV dives was 3:29 h, and the average distance between start and end point during bottom time was about 3800 m (distance measured with ArcMap from ESRI software).

Trawl samples were collected at six stations with one haul per station to compare abundance estimates to those from ROV images and to verify taxonomic identification inferred from ROV images (Table 1). The 3.05 m modified plumb-staff beam trawl was equipped with rubber rollers on the footrope (Abookire and Rose, 2005), a 7 mm mesh net with 4 mm in the cod end, and had an effective mouth opening of 2.26×1.20 m. Trawling at all stations was performed for a target duration of about 30 min at a target speed of 1.5 knots speed over ground. Actual trawl duration and speed varied due to challenges of trawling under the local environmental conditions, resulting in actual distance swept ranged from 713 to 2280 m. Trawl bottom time was estimated from a time depth recorder (TDR, Star Oddi) affixed to the net. The TDR also showed whether the trawl stayed at seafloor. Trawl hauls were rinsed of sediments over a 2 mm mesh on deck. Organisms were sorted and identified to the lowest possible taxonomic level. All organisms were counted and weighed by taxon to 1 g accuracy. Vouchers of taxa that were difficult to identify on board were preserved in 10% formalin or 190 proof ethanol. The vouchers were later sent to expert taxonomists for further detailed identification (see acknowledgments). Taxon names were verified using WoRMS (<http://www.marinespecies.org/>, on 30.10.2018).

2.3. Environmental sampling and processing

At each station, a range of environmental variables was collected with a SBE9/11 + CTD and an Ocean Instruments BX 650 0.25 m² box corer (Table 1). Water temperature, salinity and fluorescence of the water were measured with the CTD package as close to the bottom as possible, on average around 20 m from the bottom. Sediment samples were collected from box core samples. The upper surface (0–1 cm) of the sediments was subsampled and frozen at -20°C for later determination of grain size composition, organic carbon content, and concentration of sediment chlorophyll *a* and phaeopigments. Only cores with intact surface layers were used for sediment analyses. Sediment grain size was analyzed on a Beckman Coulter Particle Size Analyzer LS 13320 at the Geology Laboratory of UiT The Arctic University of Norway in Tromsø. The samples were pre-treated with HCl and H₂O₂ to remove calcium carbonate and organic material, respectively. Each sample was analyzed three times and mean grain-size values were calculated. Sediment organic carbon (%) was determined on a Costech ESC 4010 elemental analyzer at the stable isotope facility at the

University of Alaska Fairbanks, USA. Concentration of sediment chlorophyll *a* and phaeopigments ($\mu\text{g pigment/g dry sediment}$) was measured at the University of Alaska Fairbanks. Pigments were extracted with 5 ml of 100% acetone for 24 h in the dark at -20°C . A Turner Designs TD-700 fluorometer was used to measure pigment concentration. The fluorescence of the sample was read before and after acidification with HCl (final concentration of HCl was 0.003N) for determination of phaeopigments (Arar and Collins, 1997; Jeffrey and Welschmeyer, 1997).

2.4. Image analysis

A subset of the useable images of the sea floor was chosen from each station for the image analysis. Images that were overlapping, blurred, had suspended sediment, were poorly illuminated, or that were far off the seafloor were classified as unusable. In total, 940 images were manually analyzed for faunal densities and proportional organism abundances. Faunal densities were determined at the four stations (stations 1a, 6, 7, 8) where laser pointers were still functioning so that total image area could be determined. The mean area per image varied from 0.2 to 0.8 m² (Table 1). For remaining stations proportional organism abundances were determined. Typically, 70–100 pictures per station were analyzed (Table 1). Image processing and analyses were performed with ImageJ (<https://imagej.nih.gov/ij/>, (Rasband, 2009)).

All putative taxa present in the study area were used to create a taxonomic image library. Taxa were identified to the lowest possible level based on a combination of the ROV imagery, the voucher collection, and additional identifications by experts (see acknowledgments). Where identification was difficult, taxa were named morphotypes (taxa that are distinguishable on the basis of their gross morphology (Oliver and Beattie, 1996)). The image library allowed for standardization of taxonomic identification and nomenclature, in particular in case of morphotypes.

All taxa and morphotypes present on the images were counted per image. In addition, lebensspuren, burrows, colour of the sediments, and presence of stones were noted. Stones larger than a few cm were counted, and their approximate size and associated fauna were recorded. The average number of stones per picture was calculated and included in the statistical analyses.

2.5. Biogeographic affinity

Invertebrates and fishes collected in the trawl hauls were assigned to one of the following biogeographic groups: (1) Arctic – occurring only in the Arctic, (2) Arcto-boreal-Pacific – found in Arctic and boreal Pacific waters, (3) Arcto-boreal-Atlantic – found in Arctic and boreal Atlantic waters, (4) Arcto-boreal – found in Arctic and in both Atlantic and Pacific boreal waters, and (5) other – occurring also outside of boreal and Arctic zones. Biogeographic affinities were assigned based on the best current distribution information available in the published literature (Zhirkov, 2001; Vassilenko and Petryashov, 2009; Stepanjants et al., 2012), internet sources (OBIS: <http://www.iobis.org/>, Encyclopedia of Life: <http://eol.org/>, WoRMS: <http://www.marinespecies.org/>), and expert knowledge by collaborating taxonomists (all sources listed in Table S2). The list of taxa analyzed for biogeographic affinities included 44 taxa identified to species level; all taxa not identified to species level were excluded from this analysis. Percent of species from different biogeographic regions was presented based on densities and number of taxa by station. Data collected by the ROV were not used in this analysis due to considerably fewer taxa identified to species and given weighting by density was not possible for all ROV stations.

2.6. Statistical analysis

For the six trawl stations, biomass and density were estimated from

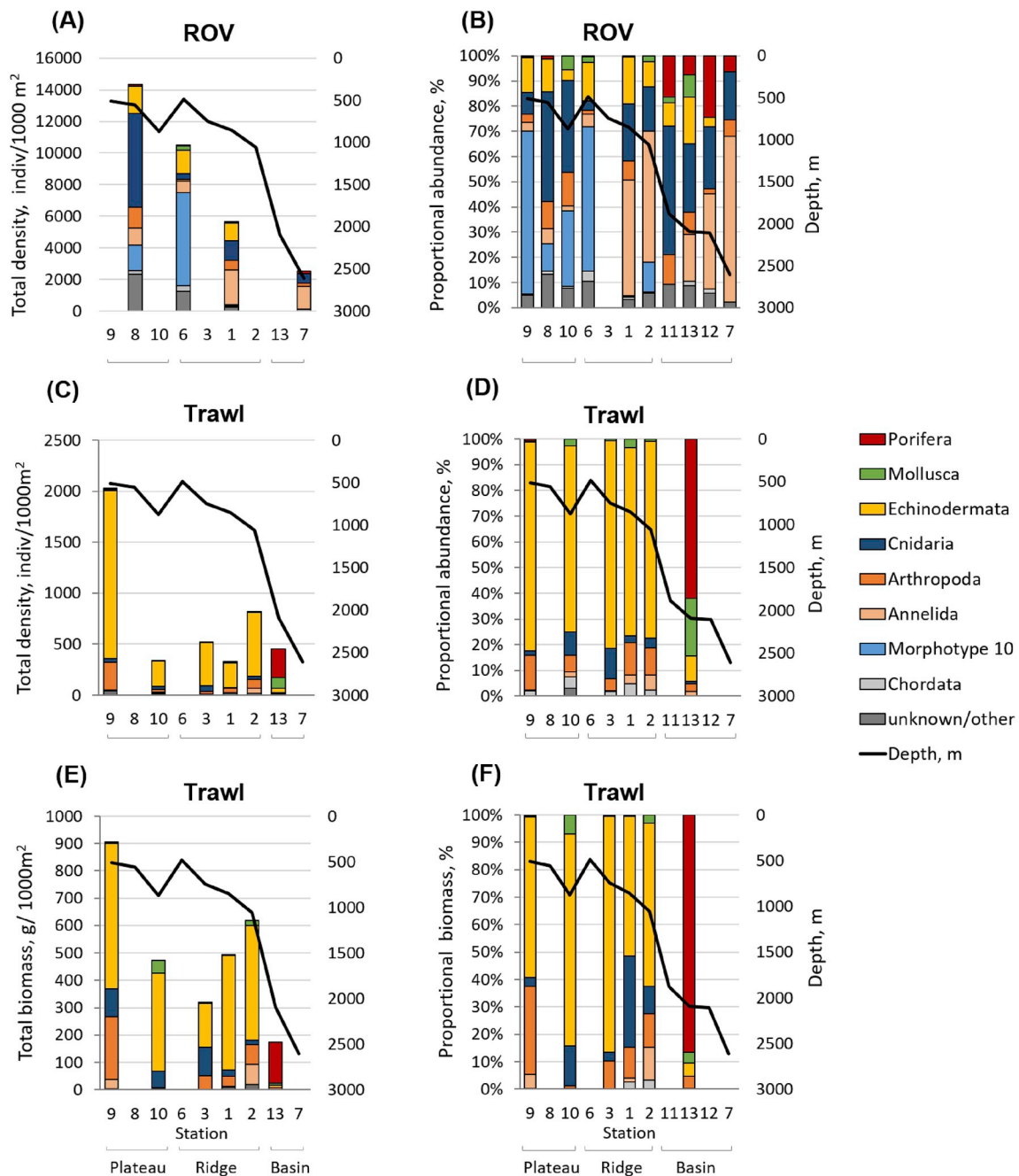


Fig. 2. Total density and biomass and proportional abundance and biomass of epifauna at different stations based on trawl and ROV samples; total density (A) and proportional abundance (B) based on ROV samples, total density (C) and proportional abundance (D) based on trawl samples, total and proportional biomass based on trawl samples (E, F, respectively); note the scale is different in A, C and E, (A) has less bars than (B) due to laser pointers problem that did not allow us to calculate density and biomass.

area swept as follows: distance towed × net opening; then estimates were normalized to individuals 1000 m⁻². For the four ROV stations where laser pointers were functioning, taxa counts were also converted to density as individuals 1000 m⁻². In addition, counts were converted to proportional abundance for all ROV stations. The Simpson diversity index (D) was calculated since it is less sensitive to variation in densities than other commonly used diversity indices (e.g., Shannon-Wiener index) (Magurran, 2013). The Simpson index was calculated based on the formula:

$$D = 1 - \left(\sum n_i(n_i - 1) / N(N - 1) \right)$$

where n_i = the number of individuals in ith species; and N = the total

number of individuals. Thus, D ranges from 0 to 1, and lower values indicate lower diversity. Morphotypes were treated as species in diversity estimates (Magurran, 2013). The diversity measures were not scaled to transect length, which might have caused a slight bias in comparisons.

Factorial analyses of variance (ANOVAs) were used to compare ROV-based number of taxa and Simpson index values among three habitat types (ridge, plateau and basin). For trawl stations, comparison of number of taxa, Simpson index, density and biomass for ridge and plateau stations was conducted with the Student's *t*-test. This test was also used to compare Simpson index values of ridge and plateau stations between trawl and ROV samples. Prior to analyses, data were tested for normality (Shapiro–Wilk test) and for homogeneity of variances

Table 2

ANOVA results comparing number of taxa and Simpson index for ridge, plateau and basin stations based on ROV samples; and *t*-test results comparing: (1) number of taxa, Simpson index, density, and biomass for ridge and plateau stations, (2) Simpson index of plateau and ridge stations for trawl and ROV samples; statistically significant results are indicated with asterisks.

Variable	df	F-value/t-value	P-value
ROV			
F-value			
Number of taxa	2	6.4	0.03*
Simpson index	2	0.2	0.8
Trawl			
t-value			
Number of taxa	3	0.5	0.6
Simpson index	3	0.5	0.6
Density	3	0.8	0.5
Biomass	3	1.0	0.4
Simpson index (ROV vs trawl)			
Plateau stations	2	0.9	0.5
Ridge stations	2	1	0.4

(Bartlett test) (Crawley, 2007). The analyses were performed in the statistical computing software R (RDevelopment, 2012).

The epifaunal community composition was analyzed by means of multivariate statistics including hierarchical cluster analysis using the PRIMER v 6.0 software package (Clarke and Gorley, 2001). Density data collected with the trawl were used for the analyses. Proportional abundance data were used for all ROV stations since density could not be determined for all stations. Square-root data transformation, which down-weighs the influence of dominant taxa, was applied prior to calculating similarities. The abundance data were grouped *a priori* as ridge, basin, and plateau with pockmark. A similarity matrix was calculated based on the Bray-Curtis coefficient (Bray and Curtis, 1957). A similarity profile test (SIMPROF) was used to explore statistical significance of difference among cluster branches. The magnitude of differences among ridge, plateau and basin categories and the significance of potential differences were tested with the analysis of similarities (ANOSIM). Statistical significance of the ANOSIM global R statistic was assessed by a permutation (999 times) test. When ANOSIM detected a significant grouping (at $\alpha = 0.05$ level), a SIMPER (a similarity percentage procedure) analysis was carried out to establish taxa contributing most to the dissimilarities between epifaunal communities.

The potential influence of environmental factors on epifaunal community structure was tested with canonical correspondence analysis (CCA) using the package 'vegan' (Oksanen et al., 2013) in the statistical computing software R (RDevelopment, 2012). In the CCA ordination biplot, the environmental variables are presented as arrows that are roughly oriented in the direction of maximum variation in value of the corresponding variable (Ter Braak, 1986). Water depth, bottom temperature, sediment grain size (clay and silt fraction combined), number of stones per picture, sediment pigments, and sediment organic carbon were included in the analysis, and correlated with the square root transformed proportional abundance of the taxa. Environmental variables included in the model were obtained with a forward selection procedure. Monte Carlo permutation tests were used to determine the statistical significance of the model and the individual terms.

In addition, correlations between univariate epifaunal characteristics from trawl surveys (total density, total biomass, and number of taxa), ROV surveys (number of taxa) and physical-chemical characteristics of water and sediments (water depth, bottom temperature, sediment grain size, number of stones per picture) were evaluated using parametric Pearson's correlation analysis (when data were normally distributed) and non-parametric Spearman's rank correlation analysis (when data were not normally distributed). Maps presented in the paper were generated using ArcMap 10.5 software (ESRI).

3. Results

3.1. Epifaunal community structure, taxonomic diversity and distribution patterns

3.1.1. Epifaunal density and biomass

A total of 2721 individuals were recorded across all stations from ROV images, of which 1584 individuals were classified into eight phyla (Cnidaria, Annelida, Echinodermata, Arthropoda, Porifera, Mollusca, Chordata, Nemertea; phyla are listed from most to least abundant, Fig. 2, Tables S1) and 1137 individuals were classified into 10 morphotypes of uncertain phyla (Table S1). At the four ROV stations where laser pointers were present, densities showed a clear increasing trend with decreasing depth from 2273 ind/1000 m² at the basin station 7 at 2610 m depth to 14,346 ind/1000 m² at the plateau station 8 at 557 m depth (Fig. 2A). Relative composition of the number of individuals per phylum obtained from all ROV stations showed different phyla dominated across the study area. Annelida were most numerous at two ridge stations (stations 1 and 2) as well as at three basin stations (stations 12, 13, and 7), where they comprised 18–66% of the total abundance (Fig. 2B). Cnidaria were numerous at all stations, but dominated at the plateau stations 8 and 10 and basin station 11, where they comprised 37–51% of the total abundance. Epifaunal communities at ridge station 6 and plateau station 9 were dominated by morphotype 10, possibly *Atolla* polyps, which was also a co-dominant community member at plateau station 10 (Fig. 2B).

A total of 2505 individuals were registered in six trawl samples and represented nine phyla: Echinodermata, Arthropoda, Porifera, Cnidaria, Mollusca, Chordata, Annelida, Sipuncula and Nemertea (phyla are listed from most to least abundant; Fig. 2 Table S1). Total density and biomass were variable across stations with no significant difference indicated by the Student's *t*-test for biomass and densities between ridge and plateau stations (Table 2). Densities calculated from the trawl samples were 6–7 times lower than those calculated from the ROV images (Fig. 2 A, C). The highest and lowest total densities were found at the two plateau stations and varied from 342 ind/1000 m² at station 10 to 2029 ind/1000 m² at station 9 (Fig. 2 C). The biomass ranged from 173 g/1000 m² at the basin station 13–906 g/1000 m² at the shallow plateau station 9 (Fig. 2 E).

Results of the relative composition of phyla from trawls suggested certain taxa were missed by the trawl compared to ROV samples taken at the same stations. For example, the relative abundance of Annelida and Cnidaria was generally much lower in trawls than in ROV images. Also, in contrast to the ROV samples, morphotype 10 was encountered only once in trawl catches at station 9. The by far dominating phylum, in terms of relative abundance and biomass, at the plateau and ridge stations was Echinodermata with 72–80% of relative abundance and 51–86% of relative biomass, followed by Arthropoda and Cnidaria (Fig. 2D, F). The only basin station 13 sampled by trawl was markedly different from the rest of the stations in that it was dominated by Porifera with 62% and 87% of relative abundance and biomass, respectively, and Mollusca with 23% of relative abundance (Fig. 2 D, F).

3.1.2. Epifaunal diversity

In total, 152 taxa and morphotypes were identified from the trawl and ROV samples, with at least 34 taxa common to both sampling tools. From the ten ROV stations combined, 78 taxa including morphotypes were registered, mostly within Echinodermata (16 taxa), Cnidaria (15), Arthropoda (12), and Chordata (10, 8 of which were fishes) (Fig. 3 A, S1 Table). In general, the total number of taxa was significantly higher at the plateau and ridge stations than at the basin stations (Table 2). The number of taxa ranged from 41 to 40 taxa at ridge station 1 and plateau station 10, respectively, to 9 taxa at basin station 7. The relatively low number of taxa at station 8 might be a result of fewer images available for the analysis at this station (Fig. 3 B, Table 1). The high number of images analyzed at station 9 (where two stations (9a, 9b)

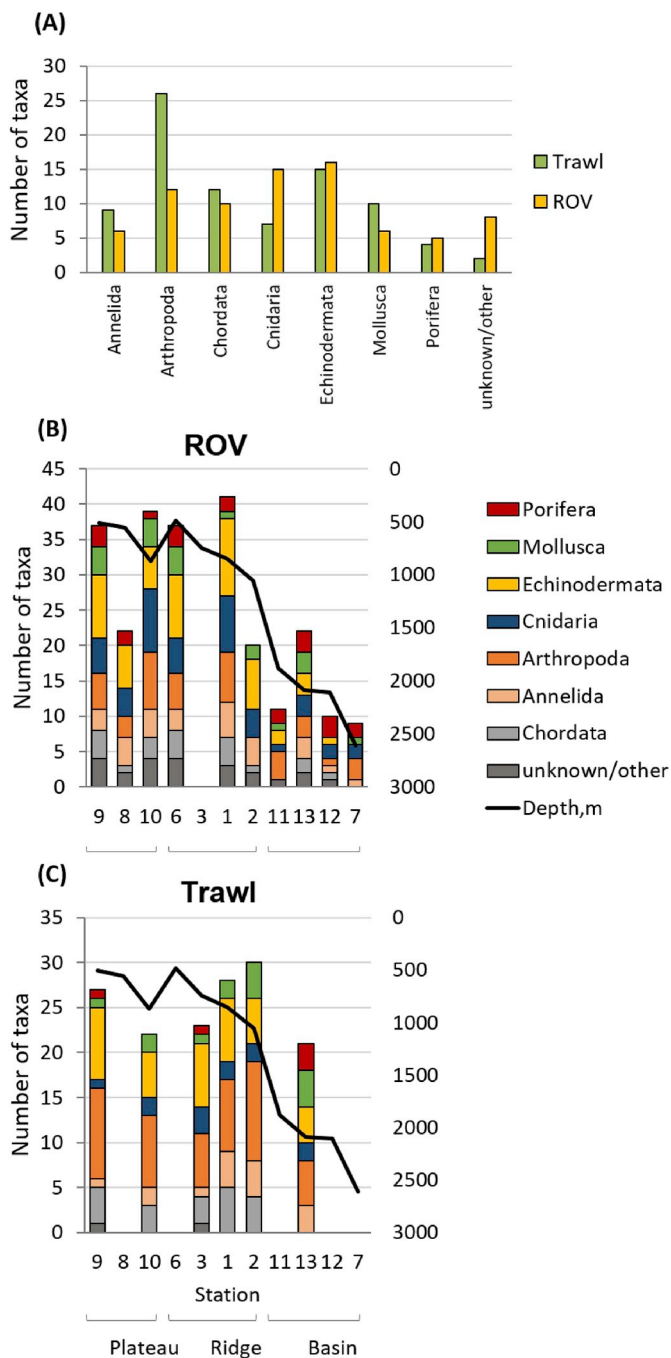


Fig. 3. Number of taxa per phylum based on ROV and trawl samples across all stations (A) and at different stations based on ROV (B) and trawl (C) samples.

combined), however, did not appear to affect diversity estimates at this station. Echinoderms together with Arthropoda and Cnidaria were most diverse at the plateau and ridge stations. The number of taxa per phylum was relatively evenly distributed at the basin stations (Fig. 3B).

Eighty-six taxa were recorded from the six trawl stations. Patterns of diversity for taxa per phylum were relatively similar to those observed from ROV images (Fig. 3A). The most diverse phyla in the trawl samples were Arthropoda (24 taxa), Echinodermata (15 taxa), Chordata (12, 9 of which were fish taxa), and Mollusca (10) (Fig. 3A). The total number of taxa varied from 21 at basin station 13 to 30 taxa at ridge station 2, with no significant difference between ridge and plateau stations (Table 2). The majority of taxa across all trawl stations were Arthropoda and Echinodermata (Fig. 3C). Particularly low diversity was

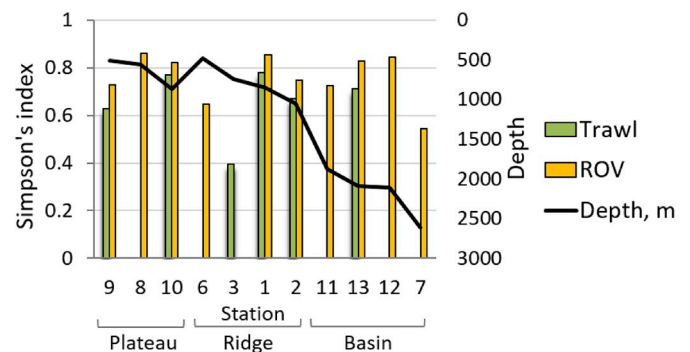


Fig. 4. Simpson's index for epibenthic community from ROV and trawl samples.

found in the trawl catch at ridge station 3 based on the Simpson's diversity index though there were no statistically significant differences among different stations for either trawl and ROV samples (Table 2). The Simpson's diversity index was slightly lower in trawl catches than ROV images at all stations where both gears were employed (Fig. 4), but these differences were not statistically significant either (Table 2).

Several species found in the CBL represented geographic and depth range extensions compared to literature values. The bivalve *Yoldiella intermedia* (M. Sars, 1865) extended its depth range from a previous maximum of 1150 m (Sirenko et al., 2004) to 2037 m depth at station 13 in our study. Geographic range extension was registered for four mollusks, and five sponges: *Rhinochlama filatovae* F. R. Bernard, 1979, *Tindaria compressa* Dall, 1908, *Hyalopecten c.f. frigidus* (Jensen, 1904), *Bathyarca c.f. imitata* (E. A. Smith, 1885), (all Mollusca), and *Radiella sol* Schmidt, 1870, *Grantia phillipsi* Lambe, 1900, *Scyphidium septentrionale* Schulze, 1900, *Stylocordyla borealis* (Lovén, 1866), and *Hyalonema (Cyliconema) apertum simplex* Koltun, 1967 (all Porifera). *Hyalopecten c.f. frigidus* and *Bathyarca c.f. imitata* might prove to be new species.

3.1.3. Community structure

Results of the hierarchical cluster analysis on relative abundances obtained from ROV images revealed two main clusters of 74% dissimilarity (SIMPROF, $p = 0.05$, Fig. 5). The first cluster included all basin stations, while the second cluster included both plateau and ridge stations (Fig. 5). Similarly, ANOSIM showed a significant difference between basin stations and combined plateau and ridge stations, though no significant difference was found between ridge and plateau stations (Table 3). SIMPER analysis for the two main clusters (basin and ridge/plateau) determined that the difference between ROV communities was mainly due to morphotype 10, and polychaetes belonging to the

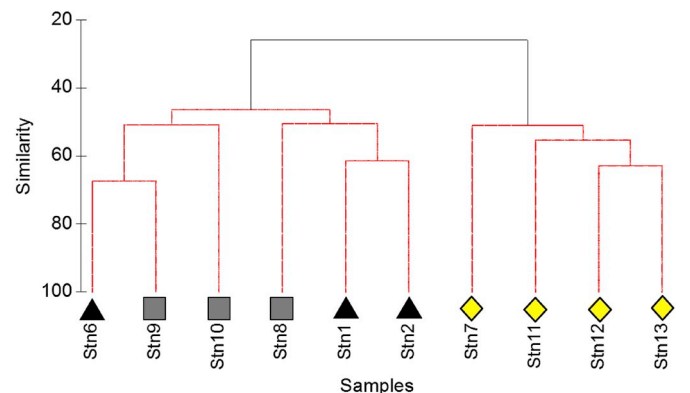


Fig. 5. Hierarchical cluster analysis based on Bray-Curtis dissimilarity of epifauna relative abundance at different stations based on the ROV samples. Black lines indicate statistically significant differences (SIMPROF, P = 0.05); red lines indicate intervals where clusters are not significantly different; triangular – ridges, square – plateau, diamond – basins.

Table 3

Results of ANOSIM test of epifauna community, based on square root transformed relative abundance obtained from the ROV images, at the ridge (R), plateau (P), and basin (B) stations.

	Withing group comparison	Pairwise test		
		R/B	P/B	R/P
R global	0.80	0.99	0.99	<0.10
P-value	0.005	0.029	0.029	0.1

Table 4

Results of SIMPER analysis showing the five taxa contributing most to dissimilarities among combined ridge/plateau and basin communities.

Taxa	Contribution %
ROV	
Morphotype 10 (c.f. <i>Atolla</i> sp.)	9
Polynoidae	8
Ampharetidae	5
Polymastiidae	4
<i>Bathypheilia</i> cf. <i>margaritacea</i>	4
TRAWL	
<i>Radiella</i> sol	11
<i>Ophiopleura borealis</i>	9
<i>Pontaster tenuispinus</i>	8
<i>Bathycaris nucleator</i>	5
<i>Elpidia</i> sp.	4

Polynoidae and Ampharetidae families (Table 4).

Cluster analysis performed for the trawl samples (not shown) indicated similar differences as for ROV samples, with the one basin station sampled clustering separately from the ridge and plateau stations (SIMPROF, $p = 0.05$). The average dissimilarity between the two main clusters was 93%. Species contributing most to dissimilarities between the two clusters were the sponge *Radiella sol*, the brittle star *Ophiopleura borealis*, and the sea star *Pontaster tenuispinus* (Table 4).

Based on the ROV images, relative abundance of dominant taxa changed across the study area indicating marked difference between ridge/plateau and basin communities. In addition, ridge/plateau communities differed between the eastern and the western side of the study area (Fig. 6 A). The geographically close ridge communities at stations 1 and 2 (east) were dominated by polychaetes of the families Ampharetidae and Sabellidae, which comprised more than 40% of relative abundance at each station (Fig. 6 A, C, D). The subsequent most common taxa were the anthozoan *Bathypheilia* cf. *margaritacea* (14–16%) and ophiuroids, especially *Ophiopleura borealis* (5–9%) (Fig. 6 A, E, F). Ridge station 6 and plateau stations 8, 9 and 10 in the western study region were characterized by high proportions of morphotype 10 (possibly, *Atolla* polyps) particularly at stations 9 and 6 (57–64%, Fig. 6 A, G1). In addition, morphotype 6 (possibly a sponge) was regularly found, and was attached to stones at these stations (up to 10%) (Fig. 6 A, G2). At stations 6, 8, and 9 ophiuroids, especially *Ophiostriatus striatus* (4–7%) were also regularly occurring (Fig. 6 A, H). Similar to the geographically distant ridge stations 1 and 2, the anthozoan *B. cf. margaritacea* was common at plateau stations 8, 9, and 10 (5–35%) and dominated at station 8 (34%, Fig. 6 A, E). Characteristic for only ridge station 6 were an ascidian *Ciona* sp. (3%) (Fig. 6 I) and morphotype 5 (5%), resembling “holes” in the seafloor (Fig. 6 J). Characteristic of plateau station 10 (within a pockmark) were small unidentified pycnogonids as well as the large pycnogonid *Colossendeis proboscidea* (10%) (Fig. 6 A, K). The latter was not observed in other parts of the study area and was particularly numerous at this station based on the video records (personal observations). In addition, video recordings from the ROV indicated a considerable increase in number of anemones on the slope towards the center of pockmark and inside of the pockmark at the plateau station 9 (personal observation).

Basin stations, for the most part, differed in dominant taxa from ridge/plateau stations (Fig. 6 B), with the exception of *B. cf. margaritacea*, which was common almost everywhere and contributed 17–51% to relative abundance at basin stations (Fig. 6 B, E). A polychaete of the family Polynoidae (possibly genus *Pelagomacellicephala*) was the second most common taxon at all basin stations except station 11 (17–51%) (Fig. 6 B, L). Porifera were recorded at all basin stations with Polymastiidae contributing most to total abundance at stations 11 and 12 (16–13%) and an unknown white sponge (11%) at station 12 (Fig. 6 B, M, N). At stations 11, 12 and 13, the sea cucumber *Elpidia* sp. occurred regularly (4–17%) as did morphotype 1, resembling a gastropod with an oval, laterally compressed shell (6–9%) (Fig. 6 B, O, P). In addition, the shrimps *Bythocaris* spp. were recorded at all basin and ridge/plateau stations, but contributed most at station 13 (8%, Fig. 6 B, R). Proportional abundance of fish taxa never exceeded 2% at any station, with *Lycodes* spp. being most common and recorded at most stations (Fig. 6 S).

Based on the trawl samples, the most abundant species of the plateau/ridge stations were the brittle star *Ophiopleura borealis* and the sea star *Pontaster tenuispinus*. *O. borealis* dominated at the shallower stations 9, 3 and 1 (43–56% relative abundance), while *P. tenuispinus* was dominant at the deeper stations 10 and 2 (43–56%). Other abundant taxa at the plateau/ridge stations were other ophiuroids (e.g., *Ophiacantha bidentata*, *Ophioscolex glacialis*) and the shrimp *Bythocaris* spp. Porifera of the family Polymastiidae (*Radiella sol* and *Polymastia* sp.) contributed 62% to total abundance at the basin station 13, followed by the bivalve *Bathycaris* c.f. *imitata* and the sea cucumber *Elpidia* sp. (11% and 8%, respectively). As with the ROV images, *Lycodes* spp. were found at all trawl stations (except station 13), with highest relative abundance at the pockmark station 10, though it never exceeded 3%.

3.2. Environmental parameters and epifaunal communities

Bottom temperatures gradually decreased with increasing water depth from 0.7 °C at station 6 to -0.3 °C at station 7. Salinity ranged between 34.84 and 34.93 PSU at stations 10 and 7, respectively. Concentration of chlorophyll (0.010–0.098 µg pigment/g dry sediment), phaeopigments (0.088–0.773 µg pigment/g dry sediment) and percent carbon content (0.81–1.26%) in sediments were similarly low across all stations but station 1, where concentrations of phaeopigments and chlorophyll was higher (Table 1).

The sediments at all stations were almost entirely composed of mud (95–100% of silt and clay combined) (Table 1). This was generally in agreement with the images, which showed most of the stations were characterized by fine, usually light-colored sediments (Fig. 7), but images also showed interspersed hard substrate. Station 6 was covered by numerous, dark-colored pebbles a few mm size on top of fine-grained sediments (Fig. 7 B, Table 1). Stones (larger than a few cm) were present at most plateau/ridge stations except station 2 (Fig. 7 C). In contrast, there were no stones registered at the basin stations except station 13. The number of stones was highest at station 6 and 9 (Table 1).

Lebensspuren of different shapes and sizes were observed at all stations. They were particularly numerous inside the pockmark at station 10 and the isolated basin station 7 (Fig. 7D and E). In general, the most recognizable traces were those left by gastropods (relatively wide, long and straight lines, Fig. S1A), fish (two lines with “dots” occurring in two parallel rows with undisturbed sediments in between, Fig. S1B), and an unidentified animal leaving narrow, non-linear tracks more or less concentrated in one spot (Fig. S1C). At the plateau/ridge stations, many tracks from sea stars or ophiuroids were present (Fig. S1D). Abundant lebensspuren at basin station 11 were small near-circular holes with a tail, which were also present but less numerous at some other stations (Fig. 7F). There was no sign of chemosynthetic activity at any of the pockmark plateau stations such as gas bubbling or obvious

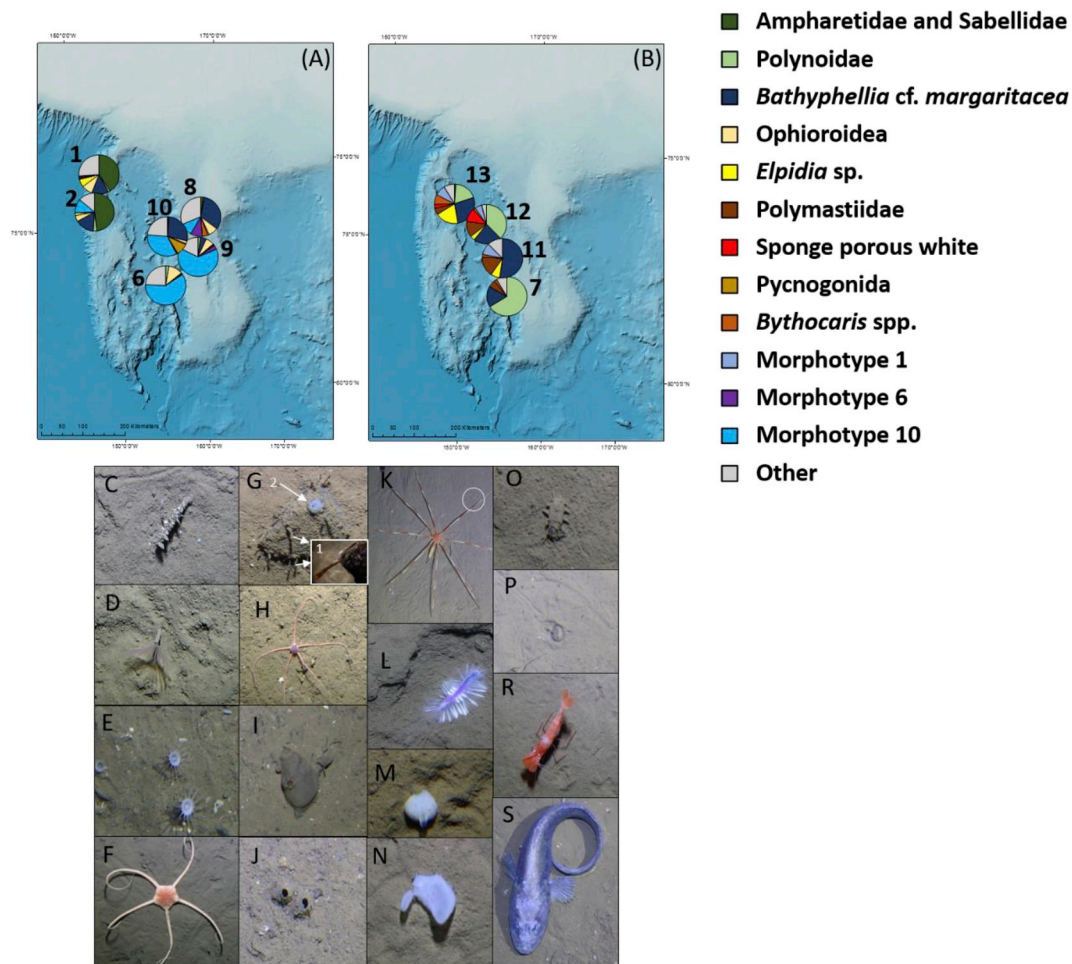


Fig. 6. Proportions of dominant taxa at the ridge and plateau (A) and basin (B) stations based on ROV images (upper panels), and images of the dominant taxa (lower panel), C- Ampharetidae, D – Sabellidae, E– *Bathypheilia cf. margaritacea*, F – *Ophiopleura borealis*, G (1) - morphotype 10, G (2) - morphotype 6, H – *Ophiostriatus striatus*, I – *Ciona* sp., J – morphotype 5, K – Pycnogonida (*Colossendeis proboscidea* and a small unidentified pycnogonid, circled), L – Polynoidae (possibly genus *Pelagomacellicephalo*), M – Polymastiidae, N - white sponge, O – *Elpidia* sp., P – morphotype 1, R – *Bythocaris* sp., S - *Lycodes frigidus*.

bacterial deposits. In addition, burrows of unknown origin and patches of sediment of different coloration indicating recent sediment disturbance/movement, were registered at the stations 1, 2, 9 and 11 (Fig. S2).

There was no significant correlation between abundance, biomass or number of taxa obtained and any of the environmental variables at the six trawl stations. For the ten ROV stations, the number of taxa was negatively correlated with depth ($r^2 = -0.75$, $p = 0.012$) and positively correlated with the number of stones per picture ($r^2 = 0.73$, $p = 0.017$) (Table 5). The main taxa associated with the stones on the images were morphotype 10, tubeworms in a white calcareous tube (possibly Serpulidae), morphotype 6, and various anemones (Figs. 8 and 9). At the ridge/plateau stations, brittle stars were often observed by arms sticking out from beneath the stones.

The CCA biplot showed the position of benthic taxa in relation to the environmental variables at different stations (Fig. 10). The environmental variables water depth, percent mud, amount of stones per picture, and sediment chlorophyll *a* showed significant relationships with epifaunal community composition ($p = 0.001$) and explained 65% of variance, with the first ordination axis explaining 32% and the second ordination axis explaining 18% of the variance in epifaunal community composition at the sampling stations. Among these, depth and amount of stones were the strongest predictors (Table 6). Stations and associated taxa separated into two main groups: basin stations on the right side of the plot and ridge/plateau stations on the left (Fig. 10). Basin stations were characterized by greater depth and finer sediments. The

ridge and plateau stations were spread along the second axis on the ordination plot, mostly reflecting the west-east gradient of stations. Ridge station 6 and plateau stations 8 and 9 grouped together and were characterized by a high number of stones. Ridge stations 1 and 2 and plateau station 10 were associated with high sediment chlorophyll *a* concentrations and had coarser sediments (Fig. 10). Polynoidae and Porifera were closely associated with greater depth. Ampharetidae, Sabellidae and *Ophiopleura borealis* were associated with high sediment chlorophyll *a* concentration. Morphotype 10 was positively associated with the amount of stones.

3.3. Biogeographic affinities

The majority of species identified to species level across all trawl stations were of Arcto-boreal-Atlantic affinity (Table S2). They represented 50–59% of the total number of taxa per station. Species occurring only in the Arctic region were represented with 14–28% of the number of taxa. Arcto – boreal taxa comprised 11–29% of all taxa and were not observed at basin station 13. Pacific-boreal taxa were present only at the two shallower ridge/plateau stations 3 and 9, and with only 6% of total number of species. Taxa occurring with “other” biogeographic affinity were present at the deepest station 13 (25%) and at the relatively shallow ridge station 1 (6%), (Fig. 11A).

In terms of relative abundance, trawl communities were by far dominated by Arcto-boreal-Atlantic species. They represented > 90% of total abundance at the deeper stations (basin station 13 and ridge

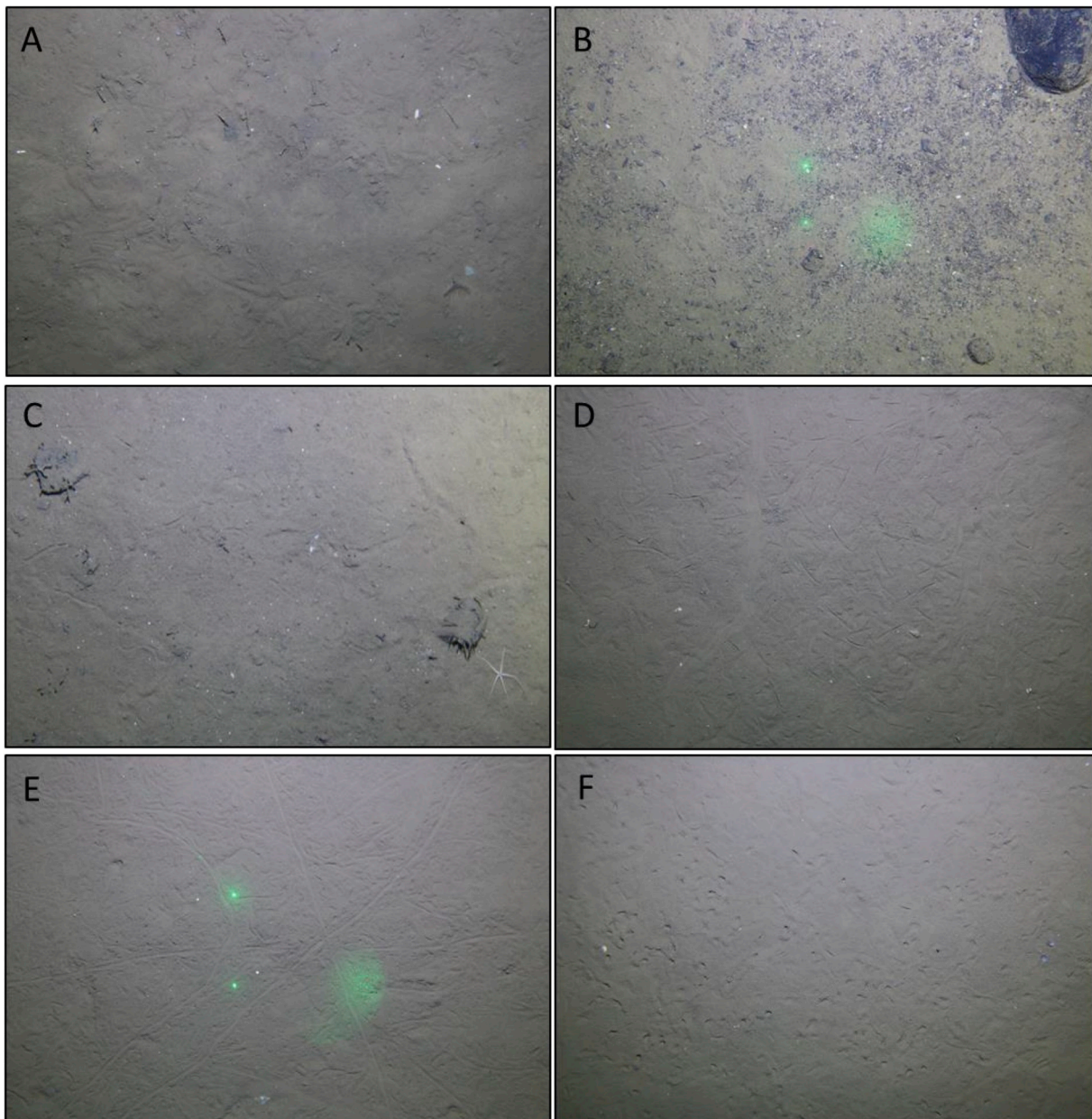


Fig. 7. Examples of the images taken in the CHB. Ridge stations: (A) Station 1 showing dense polychaete tubes, (B) Station 6 showing coarse sediment; Plateau stations: (C) Station 9 showing stones on the seafloor, (D) Station 10 showing numerous lebensspuren; Basin stations: (E) Station 7 showing very dense lebensspuren, (F) Station 11 showing near-circular lebensspuren.

station 2) and 77–87% at the remaining stations. The contribution of Arcto-boreal species increased with decreasing depth from 2 to 15%. The contribution of Arctic species to total abundance was low at the deeper stations (2–4%), and did not exceed 9% at the shallower

stations. The contribution of Arcto-boreal-Pacific taxa was less than 1%, and contribution of species occurring outside of boreal and Arctic areas (“other”) did not exceed 2% of total abundance (Fig. 11B).

Table 5

Pearson's and Spearman's correlation coefficients between biological variables (density, biomass for trawl and number of taxa for both trawl and ROV samples) and environmental variables. Significant relationships are shown in bold; * $p < 0.05$, ** $p < 0.01$

	Depth	Bottom Temperature	%Mud	%Carbon	Phaeopigments	Chlorophyll	Number of stones
TRAWL							
Total density	-0.31	0.31	0.64	-0.71	-0.49	-0.49	
Total biomass	-0.71	0.69	-0.01	-0.42	0.14	0.14	
Number of taxa	-0.44	0.20	-0.37	-0.20	0.54	0.54	
ROV							
Number of taxa	-0.75**	0.63	-0.63	-0.15	0.55	0.54	0.73*

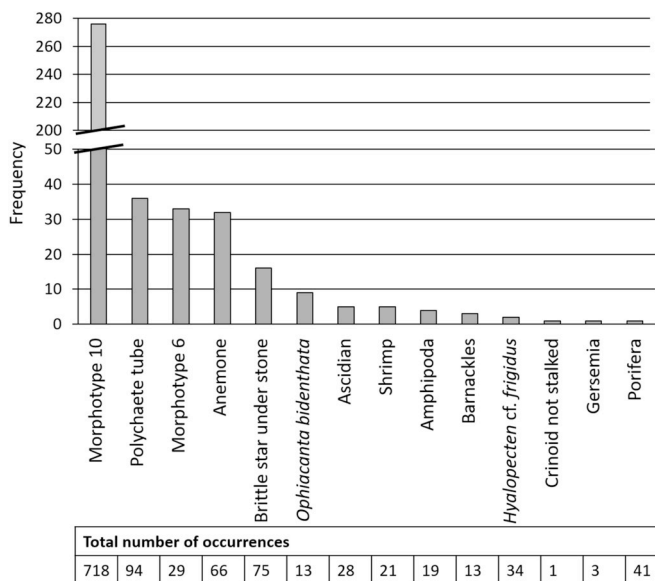


Fig. 8. Frequency of occurrence of different taxa on stones from all stations combined. The total number of occurrence of these taxa is shown in the table below the figure. Note that the y-axis is broken between 50 and 200.

4. Discussion

Our study in one of the least known parts of the Pacific Arctic deep sea revealed marked epifaunal community differences among habitat types, partly supporting the first hypothesis tested. We found lower density, diversity (in ROV observations but not in trawl samples) and biomass (in trawl samples), as well as different taxon composition in the deep basin compared to the shallower ridge and plateau fauna. However, there was no significant difference between ridge and plateau epifaunal communities, although western and eastern parts of the CBL

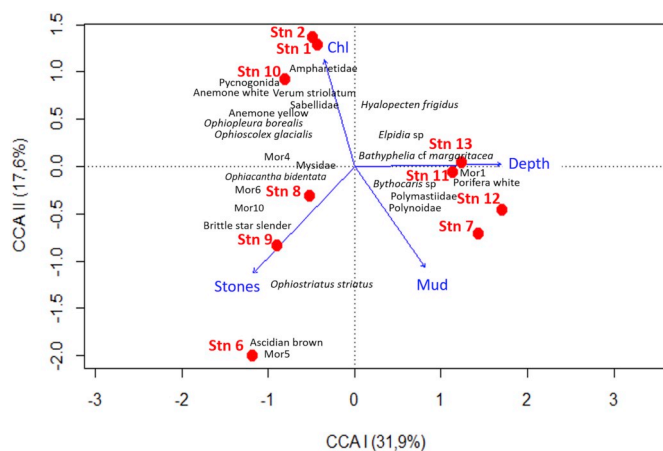


Fig. 10. Canonical correspondence analysis (CCA) based on relative abundance of taxa obtained from the ROV images ordinated with normalized environmental variables (depth, temperature, amount of stones per picture, chlorophyll concentration in the sediments, and percent of mud (clay and silt sediment fractions combined)); chl – chlorophyll, Mor – morphotype.

Table 6

Results of the CCA on square root transformed proportional abundance obtained from the ROV images, at ridge, plateau, and basin stations.

Explanatory variables/model	Df	F-ratio	P-value
Full model	4	1.9	0.001***
Depth	1	0.5	0.001***
Amount of stones per picture	1	0.2	0.048*
Mud	1	0.1	0.51
Chlorophyll α	1	0.7	0.17

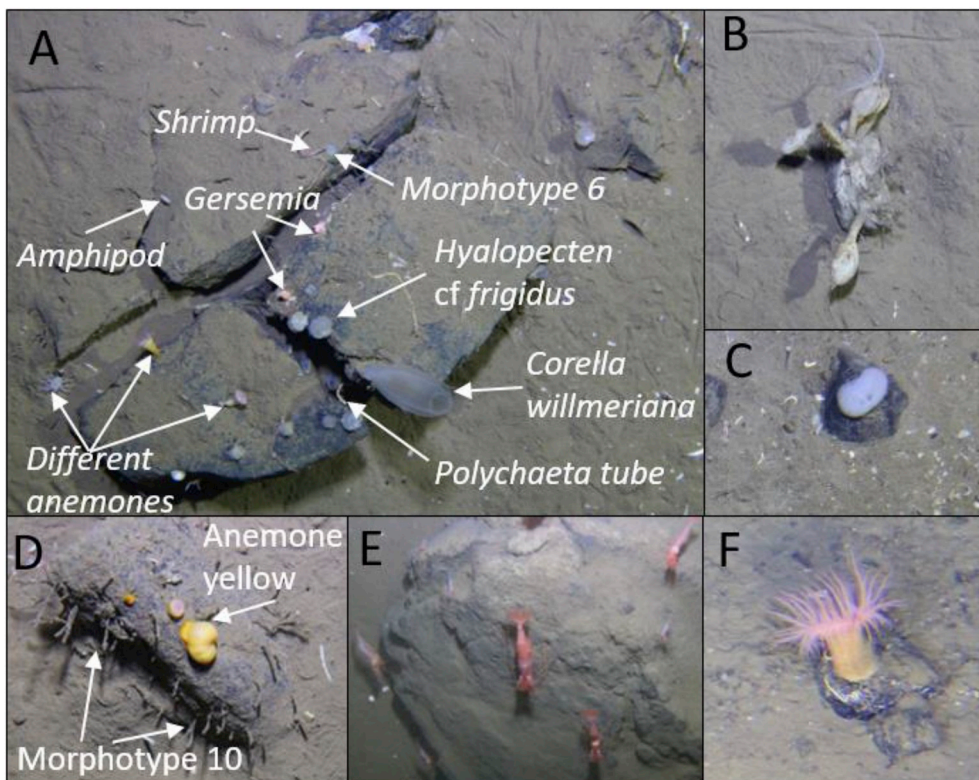


Fig. 9. Examples of fauna associated with the stones, A: Shrimp, *Gersemia* sp., Amphipoda, *Hyalopecten* c.f. *frigidus*, *Corella willmeriana*, Polychaete tubes, and various anemones on the stone, station 10; B: *Verum striolatum*, station 10; C: Morphotype 6, station 10; D Morphotype 10 and a yellow anemone, station 10; E: *Bythocaris* sp., station 13; F: pink anemone, station 6. In color in both print and online version.

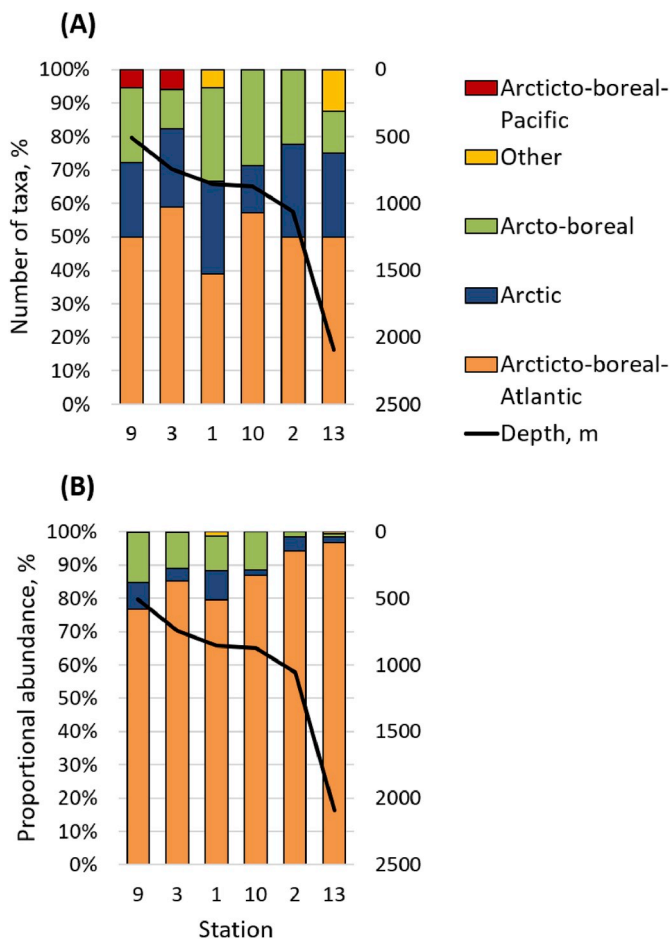


Fig. 11. Proportion of different biogeographic groups of the epifauna taxa collected by trawl in the Chukchi Borderland area based on number of taxa (A) and proportional abundance (B).

differed in plateau/ridge community properties. As is typical with deep-sea studies, water depth and availability of hard substrate in the form of stones were the strongest predictors of benthic community structure, along with sediment grain size and indicators of food availability. Results of the study supported our second hypothesis as Arcto-boreal-Atlantic taxa dominated species richness and biomass; the latter increased with increasing water depth while taxa with Pacific affiliations were essentially absent.

4.1. Epifaunal community structure, taxonomic diversity, distributional pattern

4.1.1. General characteristics of the epifaunal communities

The total number of taxa/morphotypes found across the CBL in the present study was 78 (ROV) and 86 (trawl) with a grand total of 134. This is higher compared to the previous records from the same area, where 15 (with only 4 stations analyzed from video, Bluhm et al., 2005) and 67 (MacDonald et al., 2010) epifaunal taxa were documented. Most of the taxa from the CBL are found throughout the Arctic deep sea and shelf (Bergmann et al., 2011; Taylor et al., 2016). The most speciose phyla across the study area were Echinodermata, Arthropoda and Cnidaria, which is typical of Arctic deep-water epifaunal communities (e.g. Mayer and Piepenburg, 1996; Soltwedel et al., 2009).

In general, knowledge on Arctic deep-sea epifaunal biomass is extremely sparse and mostly restricted to continental slopes (Piepenburg and Schmid, 1996; Ravelo et al., 2015; Ravelo, Bluhm, Foster, Iken, unpubl. data). Our study adds to this limited knowledge with epifaunal biomass measured from trawl catches ranging from 173 to 906 g ww/

1000 m². The values obtained are generally within those registered from the Alaska Beaufort Sea slope, where biomass varied from 37 to 5250 g ww/1000 m² between 500 and 1000 m with values mostly below 700 g ww/1000 m² at stations at 1000 m (Ravelo, Bluhm, Foster, Iken, unpubl. data). Our epifaunal biomass estimates from the CBL tended to be one to two orders of magnitude lower than the highest values recorded on Arctic shelves (Bluhm et al., 2009; Anisimova et al., 2010; Ravelo et al., 2015). At least in part, these differences are related to gear bias as was obvious from the density estimates. Total epifaunal densities from trawl samples (329 - 2029 ind/1000 m²) were much lower than those recorded from ROV images (2743 - 14,457 ind/1000 m²). The difference in estimates of densities obtained by trawl and ROV have previously been reported for some fish species and decapods (McIntyre et al., 2015; Ayma et al., 2016), again with higher values obtained from imagery. Trawl efficiency in the deep sea can be reduced based on difficulty of maintaining consistent bottom contact. In contrast, ROV images may provide more accurate quantitative estimates of community properties, at least for fauna easily seen on images (Rice et al., 1982). Densities reported from the single previous quantitative study of the CBL area and adjacent Canada Basin varied from 90 to 5830 ind/1000 m² (MacDonald et al., 2010). The total epifaunal densities reported from images at the HAUSGARTEN observatory in Fram Strait were generally higher and ranged from 120 to 54,800 ind/1000 m² (Soltwedel et al., 2009; Meyer et al., 2013; Taylor et al., 2017). Like biomass, densities tend to be much higher on Arctic shelves (Bluhm et al., 2009; Degen et al., 2016).

4.1.2. Habitat and regional differences

In general, epifaunal diversity, density and biomass varied across the ridge and plateau stations, but with no significant difference found between these two habitat types. The ridge stations were flat rather than steep and the pockmarks associated with the plateau stations did not indicate signs of chemosynthetic activity (see below), perhaps making the sites in these habitats quite similar. Based on the ROV images, however, the pattern of numerical taxon dominance differed across the eastern and western groups of ridge and plateau stations. Eastern communities at the Northwind Ridge were dominated in abundance by annelids of the Ampharetidae and Sabellidae have been previously observed in relatively high numbers in the deep sea of the Southern Ocean (particularly Ampharetidae, Schüller and Ebbe, 2007), and in hydrodynamically active areas with strong deep sea currents (Thistle et al., 1985) such as in Fram Strait (Sabellidae, Meyer et al., 2013). These polychaetes are sessile surface deposit feeders (Ampharetidae) and suspension feeders (Sabellidae), though they are capable of also using other feeding strategies, a plasticity that might allow them to be common in the deep sea (Fauchald and Jumars, 1979). In addition, the higher abundance of these polychaetes on the Northwind Ridge might be due to higher input of organic matter here compared to other stations (see discussion in section 4.2), which can be efficiently taken up by these families (Gambi and Bussotti, 1999; Gontikaki et al., 2011).

In the western CBL, ridge and plateau stations were characterized by high numbers of unidentified coronate tubes, (morphotype 10), a common deep sea taxon (Jarms et al., 2002). The medusa phase of the coronates *Atolla* sp. and *Nausithoe* sp. was previously reported from the pelagic realm in this area, where the abundance of *Atolla* was significantly higher (Raskoff et al., 2010). Polyp stages of coronates are morphologically very similar (Jarms, 1991), but given that *Atolla* medusae were also recorded in pelagic ROV dives (R. Hopcroft, pers. communication), we suggest that morphotype 10 might be *Atolla* polyps. These polyps need hard substrate for attachment (Jarms et al., 2002), and the higher availability of stones on the western side of the study area may explain the dominance of coronate polyps here.

Unlike at pockmarks with active gas venting, we did not find characteristic seep organisms that are known to rely on chemosynthetic energy (Hovland and Svendsen, 2006; Olu-Le Roy et al., 2007; Sahling et al., 2008). A single pockmark previously investigated in the CBL also

did not indicate active seepage or typical seep-associated biota (MacDonald et al., 2010). Active fluid flux is actually rarely observed in pockmarks (Webb, 2009), since many of them are relicts formed several thousand years ago (Buhl-Mortensen et al., 2015). Instead of chemosynthetic biota, increased biological abundance and taxonomic richness were previously observed in inactive pockmarks elsewhere (Webb et al., 2009b; Zeppilli et al., 2012), including the pockmark of the CBL, where abundance of epifauna, and holothurians in particular, was high (MacDonald et al., 2010). Such enhanced values have been linked to morphology of pockmarks altering hydrodynamic conditions, causing turbulent re-suspension of material and enhanced settling of organic matter, resulting in higher food supplies and increased larval settlement (Webb et al., 2009b; MacDonald et al., 2010). While densities could not be calculated in the present study, dense population of anemones were observed in the shallower pockmark (station 9, 508 m depth), possibly indicating increased water movement over the pockmark. The deeper pockmark (station 10, 973 m) was instead characterized by higher number of pycnogonids, again a taxon previously recorded in pockmarks with active seepage of gases, cold seeps, mud volcanos and under-water pingos, though these studies did not offer explanations of these observations (Hovland et al., 2005; Krylova et al., 2011; Rybakova et al., 2013; Sen et al., 2018).

4.1.3. Basin stations

Deeper locations of the CBL were characterized by lower biomass (trawl samples), density and species richness (ROV but not trawl samples), as well as different benthic community composition from the shallower ridge and plateau stations. Such changes with depth are in agreement with other studies (e.g. Southern Ocean: Linse et al., 2007; Arctic: Soltwedel et al., 2009; Sswat et al., 2015) and knowledge on bathymetric trends in global deep-sea faunal communities (Rex et al., 2006).

High proportional abundance of mobile swimming polynoid annelids and the sea cucumber *Elpidia* sp. was characteristic for the basin stations. The identified subfamily Pelagomacellicephalia is characteristic of deeper waters (Levenstein, 1978; Uschakov, 1982) including the Arctic Basin (Bluhm et al., 2005; MacDonald et al., 2010). High abundance of holothurians is also typical for deep-sea communities both elsewhere (Billett et al., 2001; Brandt et al., 2007) and in the Arctic (e.g. MacDonald et al., 2010). Both taxa are mobile, a useful trait allowing these taxa to respond fast to seasonally and spatially changing food input in polar deep seas (Iken et al., 2005; MacDonald et al., 2010).

Sponges were also prominent at basin stations in terms of densities and biomass (trawl samples), as well as proportional abundance (ROV samples). Indeed, sponges often occur in abyssal benthos (Barthel and Tendal, 1993) and as well as submarine canyons (Schlacher et al., 2007), the east Greenland slope (Mayer and Piepenburg, 1996), and the Angola Basin in the SE Atlantic (Kröncke et al., 2013). Sponges found in basins of the CBL were mainly the polymastiids *Radiella sol* and *Polymastia* sp. growing in a mud-dominated environment. Though Polymastiidae have previously been found to colonize hard substrate (Mayer and Piepenburg, 1996; Buhl-Mortensen et al., 2015), some develop root like structures, cement small particles of sediments to create their own hard substrate or use small sized hard substrate (Barthel and Tendal, 1993). The variable feeding strategies of deep-sea sponges such as suspension feeding (e.g. Witte et al., 1997), taking up dissolved organic matter (de Goeij et al., 2008), and carnivory (Vacelet, 2006; Ereskovsky and Willenz, 2007) might allow them to survive in oligotrophic conditions of the Arctic deep sea.

Among the most abundant taxa of the basin stations also was the common Arctic deep-sea anthozoa *Bathypheilia cf. margaritacea*, which was found almost everywhere in the study area. The species' flexible choice of substrata (Sanamyan et al., 2009; Schulz et al., 2010) might be a reason for its wide distribution across the study area.

4.2. Environmental factors

In the CBL, depth was among the main environmental factors significantly affecting epifaunal community structure, species richness, numerically important taxa, density and biomass. This is in accordance with other studies reporting depth zonation in epifaunal community composition (Mayer and Piepenburg, 1996; Piepenburg et al., 1996; Piepenburg and Schmid, 1996; Sswat et al., 2015), and decreases in density, diversity and biomass with depth (e.g. synthesized by Bluhm et al., 2011). These changes are likely indicative of changes in environmental factors co-varying with depth (e.g., food availability, sediment composition, temperature and salinity change) (Soltwedel et al., 2009; Sswat et al., 2015).

Food availability and presence of hard substrate (stones) were the factors affecting epifauna across habitats and also contributing most to the difference between eastern and western parts of the CBL. Quality and quantity of food was previously described as the most important factor structuring deep-sea benthic communities (Soltwedel et al., 2009; Wei et al., 2010; Kröncke et al., 2013). The main source of organic matter for benthic deep-sea organisms is derived from the upper water layers (e.g. Smith et al., 2009), and benthic availability of food is strongly linked to depth, seasonality and presence of sea ice in the Arctic (e.g. Bluhm et al., 2015). Indicators of organic matter availability within sediments (benthic pigments) measured in this study suggested very low organic matter content across the study area and low-quality food for benthic organisms (Table 1). The higher benthic pigment concentrations at Northwind Ridge was probably due to organic matter transported here from the productive Chukchi shelf, which is located closest to the Northwind Ridge station. This transport is mediated through the nutrient-rich Pacific-origin water abundant in the eastern part of the Northwind Ridge in the upper ~225 m (McLaughlin et al., 2004). While pigment concentration is a point-in-time measurement largely depending on the time of sampling, long-term trends in organic carbon supply are often more closely reflected in community characteristics of macrobenthos such as density (Renaud et al., 2008) that correlates well with production regimes in upper water masses and vertical carbon flux due to their limited mobility (Grebmeier et al., 2006). Indeed, order of magnitude higher densities of macrobenthos were observed at the Northwind Ridge station compared to other stations (S. Hardy, Univ. of Alaska Fairbanks, unpublished data), along with the higher abundance of sessile Ampharetidae and Sabellidae worms in our study. The majority of epifaunal taxa, however, did not respond to the potentially higher food supply by elevated abundance or biomass at that station. This is consistent with previous epifaunal studies on the Chukchi shelf and Greenland Sea slope (Mayer and Piepenburg, 1996; Bluhm et al., 2009; Ravelo et al., 2014), where total organic content and pigment concentration were less correlated with epifauna than other environmental factors. Detectability of pelagic-benthic coupling is lower for epifaunal than sessile/less mobile macrofaunal organisms because the higher mobility of epifaunal organisms allows them to move to food patches diluting the spatial coupling (Bluhm et al., 2009).

(Drop)stones are known to support complex epifaunal communities and enhanced faunal diversity compared to the surrounding soft bottom deep-sea environment (Soltwedel et al., 2009; Meyer et al., 2016; Ziegler et al., 2017). They are often colonized by encrusting and sessile fauna like cnidarians, crinoids, barnacles, sponges (Brandt et al., 2007; MacDonald et al., 2010; Schulz et al., 2010; Meyer et al., 2016). This habitat enhancement was also indicated in our study, where species richness was positively correlated with the number of stones. The most abundant taxon associated with stones in our study was a sessile coronate polyp (morphotype 10; section 4.1.1). Mobile fauna (e.g., arthropods and brittle stars in our study) in the vicinity of stones are likely feeding on organic matter produced by the dropstone community (MacDonald et al., 2010; Schulz et al., 2010).

Finally, grain size composition also affected epifaunal community

composition in the CBL, which is in accordance with, for example, studies from the Chukchi Sea where the importance of sediment grain size for epibenthic distribution and taxon richness has been shown (Feder et al., 1994; Bluhm et al., 2009). Although sediments grain size composition of the CBL actually varied little the highest mud content was observed in basins and the highest sand fraction on the Northwind Ridge. This pattern indicates higher current velocities at Northwind Ridge than in the basin, which was also evident by more abundant lebensspuren in the basins and higher abundance of the suspension feeding sabellid polychaetes and stalked crinoids (the latter seen in video records).

4.3. Biogeographic affinities

The biogeographic pattern of the CBL fauna was characterized by strong (over 50% of total number of species and over 70% of total abundance) dominance of species with Atlantic affinity across the entire study area. The share of species of only Pacific affinity was small at shallow stations (6% of total number of species and 1% of total abundance), and zero deeper than 850 m. Prevalence of species of Atlantic affinity in deep Arctic areas is consistent with earlier studies from the Beaufort Sea (Ravelo, Bluhm, Foster, Iken, unpubl. data), Arctic Basins and Norwegian and Greenland Seas (bivalves, though in the Canada basin, endemic species were more important; Krylova et al., 2013). This pattern reflects the current geomorphology, bathymetry and oceanography, as well as the evolutionary history of the Arctic Ocean, including changes in geological settings and glaciation events over time (e.g. reviewed in papers of Bluhm et al., 2011; Jirkov, 2013; Petryashov et al., 2013; Renaud et al., 2015).

The near absence of Pacific taxa might be explained by a limited connection to the Pacific Ocean. The deep-water connection between the Arctic and Pacific oceans closed 80–100 million years ago (Dunton, 1992). Currently, the Arctic Ocean connects to the Pacific via the shallow Bering Strait (around 50 m deep), which partly acts as a barrier for dispersal of benthic organisms adapted to deep water. On the contrary, the more saline, denser Atlantic water dominates in the Arctic deep sea with the only deep-water connection to the Arctic via Fram Strait (about 2500 m deep). The water mass distribution and circulation pattern strongly contribute to dominance of Atlantic affinity species over Pacific affinity in the study area.

Additional possible underlying reasons for the observed biogeographic pattern are the multiple glaciation events during the Pleistocene, an asymmetry in glacial ice cover, and the consequent re-invasion of fauna in the Atlantic and Pacific parts of the Arctic (Nesis, 1984; Vermeij, 1991; Briggs, 2003; Nesis, 2003; Maggs et al., 2008; also reviewed by Dilman, 2009). The Pacific Arctic shelves were only partly glaciated, providing refugia and allowing fauna to survive and maintain their presence on the shelf (Nesis, 1984, 2003; Maggs et al., 2008). After the glaciations, the Pacific Arctic was reinvaded by the fauna from the shallow refugia and through the shallow Bering Strait, which explains why most of the current Pacific species are stenobathic and therefore almost absent from the CBL. On the Atlantic side of the Arctic, shelves were covered by ice down to the deep ocean (Nesis, 1984, 2003; Maggs et al., 2008). Thus, shallow water fauna on the Atlantic side of the Arctic could not survive glaciation and had to find refugia in deeper unfrozen areas or be extirpated. After the glaciation, species adapted to depth reinvaded from the Atlantic, which is a reason why we find more eurybathic fauna on the Atlantic side of the Arctic (Nesis, 1984, 2003; Fedyakov and Naumov, 1987; Maggs et al., 2008; Piepenburg et al., 2011). CBL fauna was in fact also eurybathic indicated by the fact that around 80% of the fauna used for the biogeographical analysis in our study (Table S2) is shared with Arctic shelves (Piepenburg et al., 2011; Sirenko, 2013).

5. Summary and conclusions

Our results suggest taxon richness, biomass and density of epifauna decrease with depth in the CBL leading to marked differences between basin and plateau/ridge communities. These changes were mainly driven by depth. No statistically significant differences in community metrics were observed between ridge and plateau stations. Regional differences in numerically dominant taxa, however, were recorded between western and eastern ridge/plateau stations, which were attributed to differences in food supply and hard substrate availability. The majority of epifaunal species of the CBL were of Atlantic-boreal affinity documenting stronger biogeographic influence of Atlantic than Pacific waters on CBL communities. In addition, the study contributes to the yet incomplete biodiversity inventory of the Arctic deep sea with at least nine species showing new distribution records and more than 16 taxa added to the previously documented species list from this area.

This documentation of the current biodiversity and community structure of Arctic deep sea fauna and its interaction with the environment is urgently needed given that the Arctic is changing due to climate change. The environmental changes most prominent in the study area include: decrease in sea ice cover with most pronounced changes in the Pacific sector of the Arctic (Perovich, 2011); decrease in sea ice thickness, much of which occurred in the CBL region (Perovich et al., 2003; Stroeve et al., 2005); increased inflow of warming Atlantic water into the Pacific Arctic (Shimada et al., 2004; McLaughlin et al., 2011); and the rising volume of fresher and warmer Pacific water inflow reaching the Chukchi shelf (Woodgate and Aagaard, 2005; Woodgate et al., 2010). It is anticipated that these changes, along with effects such as acidification, atmospheric changes, and potentially increased human impact, might significantly affect community composition, diversity and functioning of the Arctic ecosystems in the future. For example, a shift in benthic species composition (Grebmeier et al., 2006); decrease in diversity of ice-associated taxa (Melnikov et al., 2001); northward faunal range expansion of fishes (Mueter and Litzow, 2008), decrease in phytoplankton cell size in the Canada Basin (Li et al., 2009) and increased primary production across much of the Arctic Ocean (Arrigo et al., 2008) have been documented. These observations are based on time series and are therefore mostly restricted to shallow areas. The lack of Arctic deep-sea data restrict the evaluation of biological responses to large-scale change in the Arctic environment. In order to provide adequate answers concerning how Arctic deep-sea ecosystems will change, long-term observations are needed. Currently, the HAUSGARTEN observatory in Fram Strait is the only Arctic deep-sea research observatory, where biological and physical parameters are being documented. Response to environmental change may vary between Atlantic and Pacific parts of the Arctic deep sea. Thus, placement of a long-term observatory in the Pacific sector of the Arctic deep sea that includes measurement of environmental and biological parameters at different trophic levels is advisable. We suggest the CBL is an ideal location for this purpose because of the prominent climate-related alterations in that region which could act as a Pacific counterpart to the Atlantic HAUSGARTEN long-term observatory.

Contribution of authors

KI and BB conceived the study idea, KI obtained the funding for field work, KI and IZ conducted the field work. IZ conducted the image analysis with input by BB, PR and KI, IZ conducted the data analysis and most writing with all authors participating in data interpretation and article preparation., All authors have approved the final article.

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Appendix A. Supplementary data

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