



Benthic macrofauna and megafauna assemblages in the Arctic deep-sea Canada Basin

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ABSTRACT

The benthic component of an interdisciplinary expedition on icebreaker USCG *HEALY* analyzed box core samples and seafloor photographs to quantify deep-sea assemblages in the Canada Basin and Chukchi Borderland area. Soft bottom metazoan macrofauna ($> 250 \mu\text{m}$) were collected with 33 box cores at 11 stations ranging from 817 to 3961 m water depth in the high-Arctic Canada Basin from 28 June to 25 July 2005. Megabenthic epifauna was quantified with a digital camera platform suspended < 5 m above the bottom at six stations (940–3800 m water depth), of which the shallowest and northernmost one targeted a pockmark ~ 40 m deep by 800 m wide. A total of 99 macrofauna taxa were identified, including at least three previously undescribed species of polychaetes. Total macrofauna abundance ranged from 0.6 to 50 individuals 0.06 m^{-2} ($89\text{--}2722 \text{ ind m}^{-2}$) and total biomass ranged from 0.2 to 1.6 g wet weight 0.06 m^{-2} ($< 0.1\text{--}26.1 \text{ g wet weight m}^{-2}$). Macrofauna diversity numbered between 8 and 55 taxa per station. Abundance, biomass, number of taxa, and diversity indices of macrofauna declined significantly with water depth. Polychaetes, crustaceans and bivalves dominated the macrofaunal densities, biomass and species numbers. The megafauna visible in the seabed photographs was assigned to a total of 67 provisional taxa; the lowest taxon count per station was 11, and the highest was 51 at the pockmark station. Epifauna abundance was also highest in this pockmark (mean 5.8 ind m^{-2}) and generally lower at deepest stations ($0.1\text{--}0.9 \text{ ind m}^{-2}$), but was skewed by large numbers of the holothuroid *Kolga hyalina*. Epifauna observed in the center of the pockmark was significantly different from all other station groups, but did not include known chemosynthetic fauna or bacterial mats. Multivariate analysis indicated that station groupings “Chukchi slope”, “Canada Basin abyss” and the “Chukchi Cap” were significantly different in community composition in the macrofauna box corer samples, but could not be similarly distinguished as such in the epifauna photographs.

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1. Introduction

Potential impacts of climate change on the marine environment may be acute, but will be difficult to verify where baseline data are lacking. In the Arctic, major changes are already underway and are projected to continue in response to sea ice shrinkage, warming water, coastal erosion, and species range shifts, among other processes (ACIA, 2004). Access to the Arctic marine environment is challenging, particularly for its deep-sea regions. The Canada Basin, the largest of the four Arctic deep-sea basins, is isolated from exchange with surrounding deep-sea areas

of the North Atlantic by the Mendeleev and Lomonosov Ridges and the Canadian Archipelago (Jakobsson et al., 2008). On the Pacific side, the shallow Bering and Chukchi Sea shelves that connect the Amerasian Arctic to the North Pacific via Bering Strait provide a barrier for exchange of deep-sea species. The western Canada Basin abyssal plain reaches depths of > 4000 m. Adjacent to it lies the shallower Chukchi Borderland area, including the Chukchi Cap, Northwind Ridge and Northwind Plain (Edwards and Coakley, 2003), where Arctic, Atlantic and Pacific water masses interact over complex bottom topography and create intricate currents and sea ice drifts (Perovich et al., 2003; Woodgate and Aagaard, 2005).

The proximity to the Chukchi shelf, along with the unique water mass and topographic characteristics of the Canada Basin and the Chukchi Borderland area, provide the environmental context for the benthic deep-sea ecosystem in this area. Results from a pilot study in 2002 (Bluhm et al., 2005; Gradinger and

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Bluhm 2005) and from the Arctic Ocean Transect project (Clough et al., 1997; Vanreusel et al., 2000) showed a trend of decreasing macrofaunal abundance and biomass with water depth, which is well established for other oceanic deep-sea regions (e.g. Thistle, 2003). Both vertical and advective fluxes appear to be important food sources explaining faunal patterns in the area (Vanreusel et al., 2000; Iken et al., 2005). Our initial findings in 2002 also agree with other macro-macrofauna studies documenting the dominance of polychaetes, crustaceans and bivalves in marine soft sediments (Thistle, 2003). Benthic epifauna consisted of echinoderms, cnidarians, polychaetes, molluscs and fishes, although epifaunal data were few (Bluhm et al., 2005). Cosmopolitan Arctic boreal and Atlantic boreal species dominated the fauna in our 2002 box core samples, but new species records and range extensions suggested that more sampling would reveal more undescribed and unrecorded species.

A particularly interesting feature of the study area, possible pockmarks, can be found on the Chukchi Cap, and are therefore included in this baseline study. Pockmarks are seabed craters of < 1 to > 100 m in diameter, usually formed through seepage of gases (methane or CO₂), pore fluids in soft-sediment areas (Hovland and Judd, 1988; Vogt et al., 1994), and/or destabilizing gas hydrates (Wood et al., 2002). On the Chukchi Cap, sub-circular pockmark-like depressions ranging from approximately 250 m to over 1000 m in diameter with depth of up to 50 m below the surrounding seabed were mapped near the eastern edge of the Chukchi Plateau at approximately 76.6°N, 163.9°W; (Fig. 1; Mayer, 2004; Gardner et al., 2007). The origin and faunistic characteristics of these intriguing craters (hereafter referred to as pockmarks) on the Chukchi Cap are as yet unknown. Other active pockmark fields in the Arctic and subarctic are known from Fram Strait (Vogt et al., 1994), the Norwegian Sea (Hovland and Svensen, 2006), and the central Barents Sea (Solheim and Elverhoi, 1985).

This article reports on the second interdisciplinary expedition to the Canada Basin that was undertaken in the summer of 2005 to expand the sparse collections made in 2002. This effort contributes to the Census of Marine Life (CoML, Yarincik and O'Dor, 2005) and its Arctic component, the Arctic Ocean Diversity project (ArcOD) (Iken and Konar, 2003; Bluhm et al., 2008). There is a conspicuous geographic gap in our knowledge of biodiversity in the Canada Basin (Iken and Konar, 2003), particularly for the benthos. Thus, the goals of our research included the following: (1) increased geographic coverage and replication of macro-macrofaunal sampling, (2) baseline quantitative study of visible megafauna using a camera system, and (3) the first faunistic investigation of one of the pockmark-like features on the Chukchi Cap. Our hypotheses were as follows: (1) abundance, biomass and diversity of in- and epifauna would decrease substantially with depth from the Chukchi slope to the abyss, and (2) species assemblages would be characteristic for specific ecosystem features within the Canada Basin and Chukchi Borderland area. The specific objectives of this study, consequently, were to characterize the species inventory of benthic invertebrates for the Canada Basin and Chukchi Borderland area, quantify benthic macrofauna and megafauna abundance and biomass (for macrofauna) in the study area, and describe and quantify the benthic fauna in a pockmark-like feature on the Chukchi Plateau. We hope these results can serve as benchmarks against which to measure future change.

2. Materials and methods

All materials were collected between 28 June and 25 July 2005 during the expedition HLY05-02 of the US Coastguard icebreaker HEALY from Barrow to Barrow, Alaska (Fig. 1, Table 1).

2.1. Box cores

Thirty-three quantitative box core samples (all collected with a spade-corer with a surface area of 0.06 m⁻²) were collected in three replicates at 11 locations at water depths ranging from 817 to 3961 m in both the Canada Basin and the Chukchi Borderland area (Fig. 1, Table 1). At each station, for two replicates, the whole surface area of the cores was used for faunal investigations; for the third replicate, only half the surface area was used because the remainder was required to measure sediment variables described below. The upper 10 cm of the sediment and the water overlaying the sediment were sieved through 250 μm mesh, and the remaining fauna preserved in buffered 4% formaldehyde-seawater solution (final concentration). Macrofauna was later sorted to the lowest taxonomic level possible and transferred to 50% isopropanol. Blotted wet weight of preserved samples (including shells) was determined by taxonomic group since individual specimens were sensitive to desiccation; no correction factor was applied for preservation effects. The dominant taxa: molluscs, crustaceans (except for ostracods and harpacticoids), polychaetes and echinoderms, were identified to species level.²

Sediment samples of the upper 1 cm were collected from the remaining surface layer of the box core sample and maintained frozen until further analysis. Water samples at these same stations were collected from Niskin bottles on a CTD-rosette, filtered onto GF/F filters and stored frozen until further analysis (Lee et al., pers. com.). Organic carbon and nitrogen content of the sediment as well as C/N ratios of sediment and pelagic particulate organic matter (POM) were determined on a Costech elemental analyzer interfaced with a Thermo Finnigan Delta plus isotope mass spectrometer at the Alaska Stable Isotope Facility after washing sediments with 10% HCl and fuming pelagic POM filters with 6 N HCl to remove inorganic carbon. Calcium carbonate content of the sediment was determined using loss on ignition correcting for the organic matter lost through the process (Dean, 1974). Grain size analysis was conducted according to Folk and Ward (1957). The statistical parameters were calculated according to Folk and Ward (1957).

2.2. Digital Camera system

Photographic sampling was used to investigate the benthic megafauna at six stations along the cruise route (Fig. 1). Five of the stations (6, 9, 11, 13 and 15) were chosen to be representative of the benthic environment of the Canada Basin and Chukchi Borderlands. Station 12, in addition, targeted a pockmark thought to be formed by fluid expulsion through the seafloor (Mayer, 2004; Gardner et al., 2007). At this station, the photographic sampling targeted the center and margin of the pockmark feature.

The digital camera system (DCS) comprised a vertically mounted 3.3 megapixel (Nikon CP990) digital camera, a pair of 300 W s strobes, and a CTD with altimeter. These devices were mounted on a pipe frame and were powered by deep-sea batteries. The CTD and altimeter transmitted real-time information regarding the DCS depth and altitude above bottom so that a distance of between 2 and 3 m above the bottom (Table 4) could be maintained with a drift speed of < 0.5 m s⁻¹. The altimeter malfunctioned at station 6 and a 5-m target altitude was

² Taxonomic analyses of macrofauna were kindly assisted by the following specialists: N. Foster, Univ. of Alaska Fairbanks (Mollusca), Dr. K Coyle, Univ. of Alaska Fairbanks (Amphipoda), Dr. S. Gerken, Univ. of Alaska Anchorage (Cumacea), Dr. R. Heard, USM Dept. of Coastal Sciences, Ocean Springs (Tanaidacea), Dr. G. Wilson, Australian Museum Sydney (Isopoda), Dr. I. Smirnov, Zoological Institute St. Petersburg (Ophiuroidea), A. Rogacheva, Shirshov Institute Moscow (Holothuroidea).

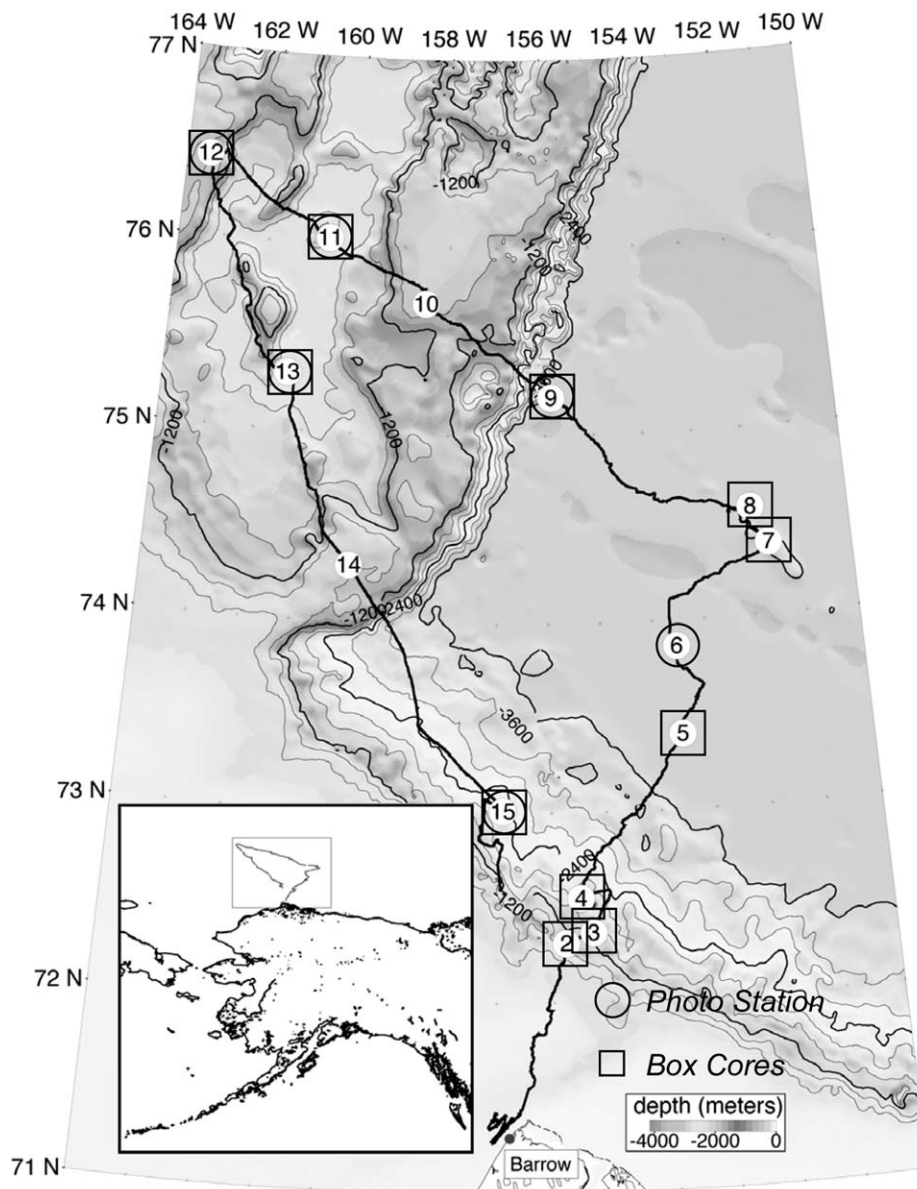


Fig. 1. Map of cruise track and sampling stations for USCGS HEALY 28 June to 25 July 2005. Station numbers refer to descriptions throughout this paper. Symbols indicate box core sampling (square) and/or photo-survey stations (circle).

maintained using an acoustic release pinger mounted on the cable above the DCS. The camera and strobes were triggered autonomously at 12 s intervals.

Benthic images were recorded while the ship drifted lodged to sea ice for a sampling period of 4 h. Distance transited during this time was a function of the ice drift speed, and for the drift speeds experienced, the tow angle and the offset between the ship and the position of the camera platform were relatively constant.

The exposure time for each bottom picture was extracted from the data (EXIF) header recorded with each image file. This time was then used as an index to merge the CTD records, including altitude, and the ship's GPS position as variables associated with each image. The position of each image was estimated from the ship's position. This estimate was therefore biased by the lateral offset of the DCS at the end of the cable. In practice, with the ship held fast against the ice edge and the DCS fully lowered, the wire angle remained constant during each DCS deployment, so the relative distance transited by ship between images accurately reflected the distance over the seafloor. The area of each image

was calculated based on altitude above bottom the vertical and horizontal acceptance angles of the camera lens ($48^\circ \times 36^\circ$).

For analysis, the images were displayed on a computer monitor and the visible fauna was identified to nearest practical taxon, and counted. Intensity stretch and image sharpening routines were routinely applied to the total image to enhance discrimination of subjects. Taxonomic resolution was inexact due to the lack of voucher specimens (in most cases) and because animals were often small and photographed from a distance. Sample images and some individuals collected with a beam trawl and an ROV (see below) were sent to appropriate specialists for expert opinion³. The priorities were internal consistency and optimum taxonomic

³ Taxonomic analyses of megafauna were kindly assisted by the following specialists: Dr. O. Tendal, Zoological Museum Copenhagen, Dr. D. Fautin, University of Kansas (Anthozoa), K. Mecklenburg, Pt. Stephens Research (Pisces) Dr. K. Raskoff, Monterey Peninsula College, California (Cnidaria), Dr. T. Shirley (Crustacea), Dr. I. Smirnov, Zoological Institute St. Petersburg (Ophiuroidea), A. Rogacheva, Shirshov Institute Moscow (Holothuroidea).

Table 1
Stations sampled for benthic macrofauna in the Canada Basin in the summer of 2005.

Station-Cast	Day-Month 2005	Depth (m)	Latitude °N	Longitude °W
2-1	28 June	817	72°18.0750'	155°47.3291'
2-2	28 June	906	72°19.3192'	155°45.3950'
2-3	28 June	972	72°19.2902'	155°44.9833'
2-4	28 June	1004	72°19.1860'	155°44.5010'
3-1	30 June	1852	72°21.4850'	155°19.1212'
3-2	1 July	1836	72°21.3592'	155°19.4875'
3-3	1 July	1836	72°21.3043'	155°19.7357'
3-4	1 July	1825	72°21.2323'	155°19.7323'
4-1	2 July	1945	72°33.1603'	155°27.5750'
4-2	3 July	1830	72°32.9466'	155°28.8470'
4-3	3 July	1747	72°32.8880'	155°32.9588'
4-4	3 July	1672	72°33.9054'	155°30.6649'
5-1	6 July	3847	73°21.8396'	153°30.9406'
5-2	6 July	3961	73°21.8677'	153°39.8422'
5-3	6 July	3880	73°22.2617'	153°25.1511'
7-1	10 July	3842	74°24.9021'	151°41.0552'
7-2	10 July	3840	74°25.2588'	151°41.4391'
7-3	10 July	3841	74°25.5173'	151°42.8291'
8-1	11 July	3845	74°35.1910'	151°58.6385'
8-2	11 July	3845	74°35.1048'	151°57.7543'
8-3	12 July	3843	74°34.9671'	151°57.5044'
9-1	13 July	3854	75°10.8472'	155°55.6142'
9-2	13 July	3848	75°10.4357'	155°54.3757'
9-3	13 July	3848	75°10.1906'	155°54.2355'
11-1	16 July	1458	76°01.3097'	160°40.2567'
11-2	16 July	1365	76°01.2874'	160°41.2122'
11-3	16 July	1298	76°01.3101'	160°40.2598'
12-1	17 July	937	76°25.6797'	163°28.9008'
12-2	17 July	938	76°25.6391'	163°29.0525'
12-3	17 July	936	76°25.6131'	163°29.1345'
13-1	21 July	2090	75°16.0824'	161°13.5014'
13-2	21 July	2090	75°15.9477'	161°13.0337'
13-3	21 July	2090	75°15.8609'	161°12.3781'
15-1	24 July	2570	73°04.1370'	157°10.0059'
15-2	24 July	2670	73°04.4598'	157°11.3736'
15-3	24 July	2678	73°04.4985'	157°11.9315'

accuracy. Each group of photographs included an “unknown” category, which comprised various specimens that lacked clear distinguishing characteristics.

To improve taxonomic resolution, benthic DCS observations were occasionally supplemented by non-quantitative collections and seafloor video collected by ROV (*Global Explorer*, Deep-Sea Systems Inc.). The ROV, capable to 2800 m depth, was equipped with a suction hose, as well as a manipulator arm, to collect benthic organisms. A beam trawl with 7 mm mesh size was deployed at two stations to collect additional voucher specimens.

2.3. Data analysis

2.3.1. Macrofauna

Community analysis was performed using multivariate statistics in the software package PRIMER™ version 6 (Clarke and Gorley, 2006). Bray–Curtis similarity was calculated on the dispersion-weighted abundance matrix. Dispersion weighting corrects for abundant, spatially clustered groups by dividing group counts by the variance to mean ratio and averaging across all groups (Clarke and Gorley, 2006). Non-metric multi-dimensional scaling (nMDS) was used to visualize the similarity patterns. Similarities between station groups based on MDS patterns were tested using analysis of similarities (ANOSIM) in which global $R=1$ indicates complete separation of groups and global $R=0$ indicates no separation (Clarke and Warwick, 2001). Species contributing most to the similarities of stations within the three groups were identified using SIMPER analysis. Diversity indices (Pielou's evenness, Shannon diversity (\log_2))

were calculated using the DIVERSE routine in PRIMER. Depth-related trends of total abundance, biomass, Shannon diversity and Pielou's evenness indices were tested with a Spearman rank correlation using StatView software.

Normalized environmental variables suspected to drive benthic macrofaunal communities were depicted based on their Bray–Curtis similarity in an nMDS ordination. They were then correlated with the macrofauna species matrix using the BIO-ENV procedure (Clarke and Gorley, 2006). The following variables were included in the analysis: Water depth (m), % CaCO_3 in sediment, % organic C in sediment, % organic N in sediment, temperature and salinity of bottom water (Stockwell et al., unpubl.), C/N ratios of sediment and pelagic particulate organic matter, pelagic primary production (Lee et al., unpubl.), integrated pelagic chlorophyll concentration (Chl m^{-2}) (Stockwell et al., unpubl.), integrated zooplankton biomass (Kosobokova and Hopcroft, 2010), sand and clay fractions of the sediment, mean grain size (ϕ) and sorting index of the sediment.

2.3.2. Megafauna

Specimen counts in the photographs were normalized to density based on the area covered in each image. On many occasions, subsequent images overlapped in area. Two strategies were employed to avoid double-counting of specimens while still accurately compiling the total areas sampled. On most stations, alternate images were skipped to reduce overlap. Additionally, as each new image was examined, it was overlain with the previously analyzed image so that only the newly imaged region was accrued for specimen counts or area calculation.

The underlying assumption was that each photograph (or portion of a photograph) was a replicate sample within the relatively uniform benthic habitat. The results of taxa counts and density calculations were analyzed with routines in the PRIMER software suite. The six DCS stations were compared on the basis of log-transformed densities for the taxa enumerated at each station. Because two of the stations (6 and 11) were far less populated than the others, a dummy variable was added to the densities to mitigate the effect of the many zero observations. Stations were compared with use of Shannon (\log_{10}) and Simpson (\log_e) diversity indices and nMDS. At station 12, the photographs were sorted by depth and distance along the transect to compare the center, slope, and exterior of the pockmark feature. Megafaunal community similarities were compared with the same environmental variables using BIO-ENV procedure as explained above.

3. Results

3.1. Macrofauna assemblages

3.1.1. Community characteristics

Metazoan abundances in box cores ranged from 5 (± 0.6 standard deviation) to 163 (± 50) individuals (hereafter abbreviated ind) 0.06 m^{-2} , which corresponds to 89 (± 10) to 2722 (± 865) ind m^{-2} (Fig. 2A). Values were lowest at the northern stations of the deep central Canada Basin (stations 7–9) and highest at some of the Chukchi Sea slope stations (stations 2 and 15) (Fig. 2A). In general, abundances decreased significantly with water depth (Spearman's $\rho = -0.495$, $p = 0.0051$, $n = 33$; Fig. 3A). Polychaetes, crustaceans and molluscs contributed the majority of all individuals collected (Fig. 2B). The group ‘other’ included nematodes, sipunculids, nemertean, pogonophorans, turbellarians, sponges, bryozoans, cnidarians, ascidians, holothurians and ophiuroids; the first two taxa were most frequent within this group.

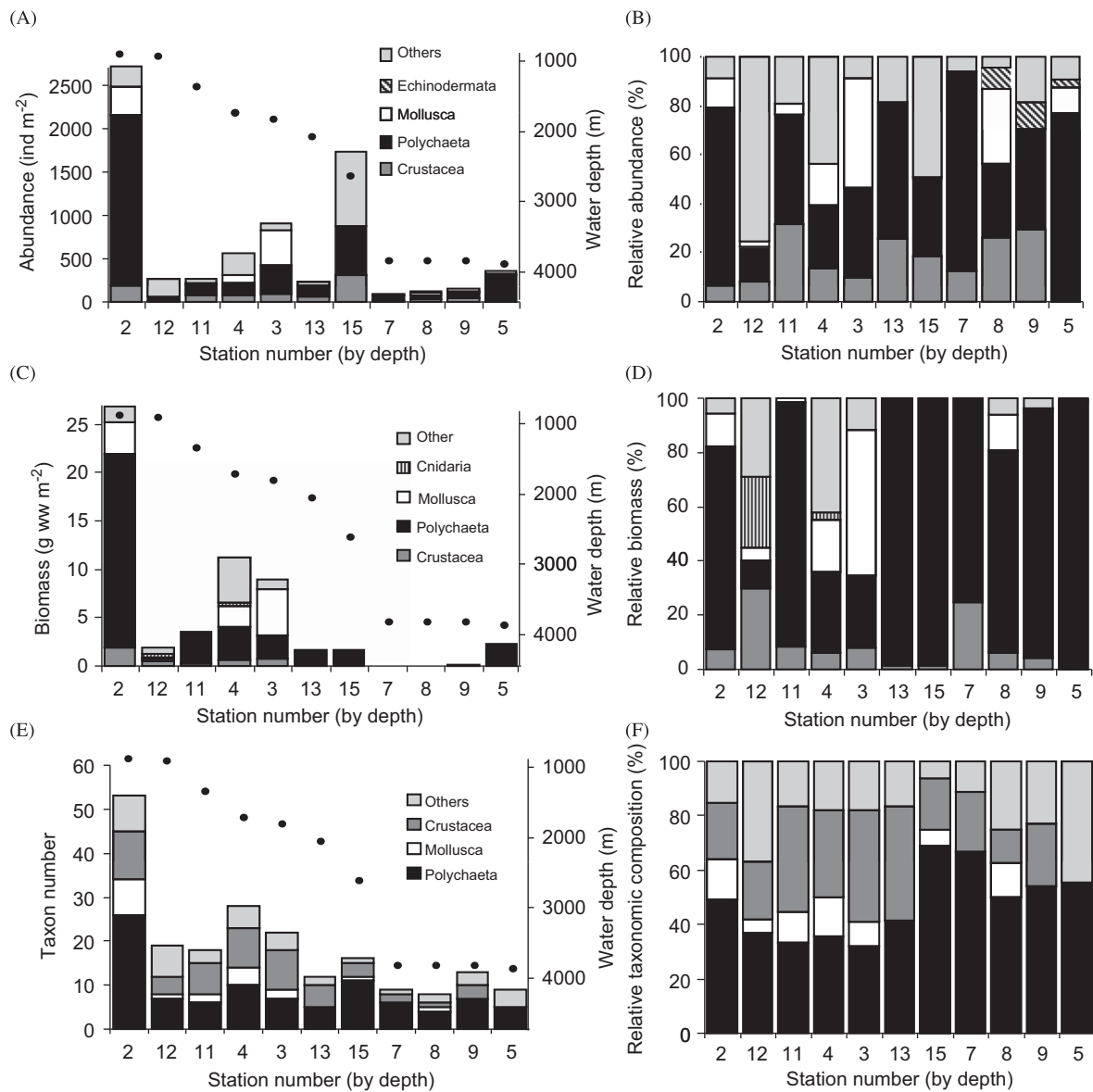


Fig. 2. Benthic metazoan infaunal abundance (A, B), wet weight biomass (C, D) and taxonomic richness (E, F) at eleven stations (sorted by water depth) in the Canada Basin. Values are averages of three replicates per station. Black line in a, c and e represents mean water depth at each station, which ranged from 909 to 3896 m.

Mean biomass ranged from 0.2 to 1568 (± 169) mg wet weight 0.06 m^{-2} ($< 0.1\text{--}26.1$ (± 2.8) g wet weight m^{-2}) (Fig. 2C) and also decreased significantly with depth (Spearman's $\rho = -0.647$, $p = 0.0002$, $n = 33$; Fig. 3B). Biomass was highest at three of the Chukchi Sea slope stations (stations 2–4), and lowest at three of the central basin (stations 7–9). At most stations, polychaetes dominated the biomass (Fig. 2D). Molluscs, in particular bivalves, dominated at station 3; crustaceans and others mostly ranked third. Cnidarians (mostly polyps of Coronata) were important in relative biomass contribution at station 12 (Fig. 2D).

The number of macrobenthic taxa per station ranged from 8 to 55 with highest numbers at some of the Chukchi Sea slope locations (stations 2–4) and lowest numbers at some of the central Canada Basin sites (stations 5–9, Fig. 2E). Taxon number significantly decreased with water depth (Spearman's $\rho = -0.627$, $p = 0.0473$, $n = 11$; Fig. 3C). Polychaetes were the most speciose taxon of those identified to family or lower level (50 species total; Fig. 2F); particularly abundant (albeit only occurring at few stations) species were *Minuspio cirrifera* (9.7% of all specimens of

all taxa collected), *Aricidea nolani* (3.4%), *Anobothrus laubieri* (2.3%) and *Augeneria albidentata sadko* (2.0%). In addition, three species of previously undescribed polychaetes were found (Gagaev, 2008; Gagaev, 2009). Crustaceans (19 taxa total) were comprised of harpacticoid copepods, tanaids, isopods, cumaceans, amphipods, and ostracods with the first two taxa by far dominating densities among the crustaceans (Table 2). The single-most common species of molluscs (11 species total) was the bivalve *Axinopsida serricata* (6.1% of all specimens of all taxa collected). A complete list of taxa found in the box cores will be provided to the Ocean Biogeographic Information System upon publication of this article.

Pielou's evenness index (J') ranged from 0.56 ± 0.10 at station 2 to 0.96 ± 0.04 at station 7 and was not significantly related to water depth (Spearman's $\rho = 0.116$, $p = 0.367$, $n = 11$) (Fig. 4A). In contrast, Shannon's diversity index H' ranging from 1.04 ± 0.12 at station 5 to 2.37 ± 0.31 at station 4 (Fig. 4B), decreased significantly with water depth (Spearman's $\rho = -0.673$, $p = 0.0334$, $n = 11$), although H' was highest at intermediated depths around 1800 m.

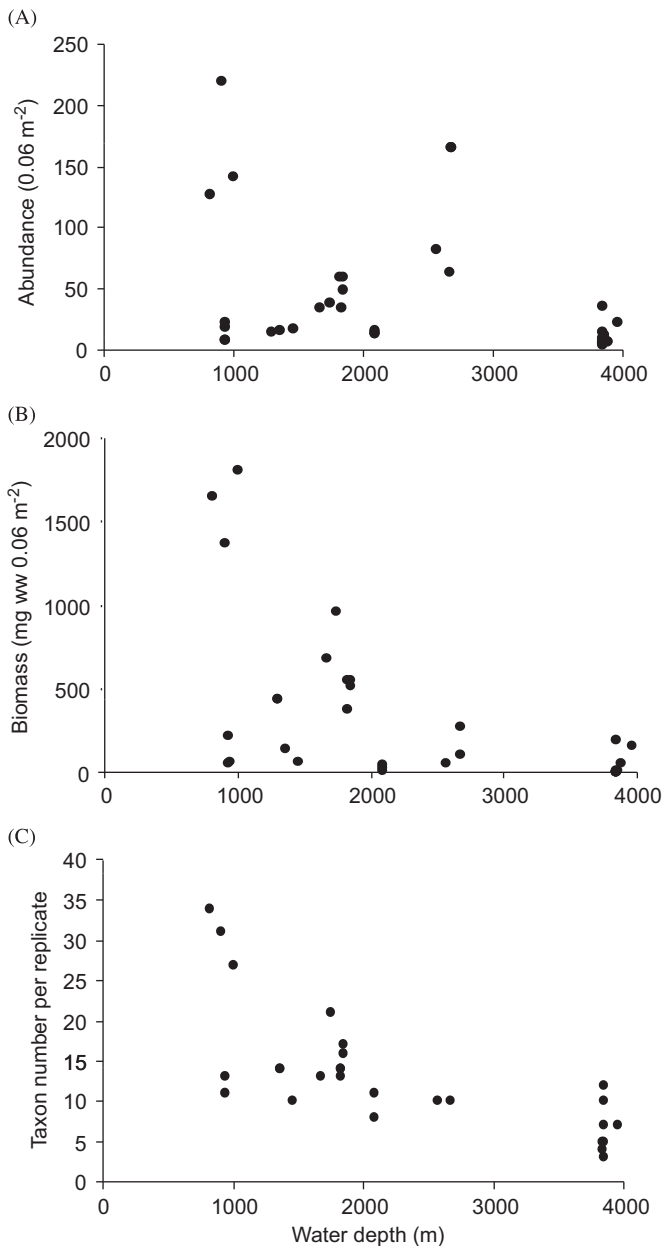


Fig. 3. Depth trends of infaunal benthos in the Canada Basin with regard to abundance (A), biomass (B), and taxonomic richness (C). Values are from individual box cores. All three variables decreased significantly with depth based on Spearman rank correlation (for details see text).

Analysis of similarities of macrofauna communities based on abundance indicated that three groups, 'Canada Basin abyss' (stations 5–9), 'Chukchi slope' (stations 2–4 and 15) and 'Chukchi Cap' (stations 11–13), were significantly different in taxonomic composition (global $R=0.494$; $p=0.001$, Fig. 5A). The pairwise, *post hoc* comparison between the groups showed a greater difference between the 'Chukchi slope' and 'Chukchi Cap' communities ($R=0.606$) than between the 'Chukchi slope' and the 'Canada Basin abyss' groups ($R=0.552$) and between the 'Canada Basin abyss' and the 'Chukchi Cap' groups ($R=0.349$, significance level 0.1% for all). The analysis gave similar results when including station 13 in 'Canada Basin abyss' instead of 'Chukchi Cap'.

Four taxa in each of the three station groups contributed > 60% to the similarity within each group. Species contributing most to the similarity within 'Chukchi slope' were the bivalve *Axinopsida serricata*, Tanaidacea, and the polychaetes *Augeneria*

albidentata sadko and *Aricidea nolani* (68% cumulative contribution). Within 'Canada Basin abyss', Harpacticioidea, the holothurian *Elpidia heckeri* and the polychaetes *Aricidea nolani* and *Chaetozone* sp. contributed 67% to the similarity within this group. Within 'Chukchi Cap' benthic coronate cnidarians, Tanaidacea, the polychaete *Potamethus malmgreni* and Nemertini contributed 82% to the group similarity. Taxa contributing most to the dissimilarity between 'Chukchi slope' and 'Canada Basin abyss' included *Axinopsida serricata*, *Aricidea nolani*, *Augeneria albidentata sadko*, *Minuspio cirrifera*, Tanaidacea, Nematoda and Harpacticioidea (52% cumulative dissimilarity). The same taxa plus Coronata contributed 53% to the dissimilarity between 'Chukchi slope' and 'Chukchi Cap'. The 52% dissimilarity between 'Canada Basin abyss' and 'Chukchi Cap' were contributed by Coronata, Tanaidacea, *Potamethus malmgreni*, Bryozoa, *Chaetozone setosa*, *Aricidea nolani*, Nemertini and *E. heckeri*.

3.1.2. Macrofauna characteristics of pockmark station

Station 12 had the lowest or second lowest values for C/N ratios of sediment and pelagic POM, sediment mud content, and organic-carbon content. The box cores were collected in the base of the pockmark near the start of the DCS photographs. Values for sand content, sediment sorting, sediment CaCO₃ content, and mean grain size were highest or second highest. Three polychaete species only occurred at station 12 (*Progoniada* sp., *Proclea graffi*, *Protula (Apomatus) globifera*). From all box core samples, cnidarians (*Nausithoe* sp. and unidentified anthozoans) were most abundant at this station. macrofaunal abundance, biomass and taxon number were low compared to the other site of similar depth (station 2), but comparable to the geographically closest stations (stations 11 and 13).

3.1.3. Environmental variables and Macrofauna

In the nMDS, environmental variables grouped in a similar fashion as the macrofaunal community (Fig. 5B). Sediments at the sampling stations were poorly to extremely poorly sorted, sandy-clayey silts with a nearly symmetrical size distribution (Table 2). The mean phi size ranged from 6.9 to 10.3 with highest phi sizes (smallest grain size) at the abyssal stations where the mud fraction was almost 100%. Sediment organic content was highest at the slope stations and lowest at the two shallow Chukchi Cap stations. C/N ratios of the sediment POM ranged from 8.2 to 13.0 with lowest values (=highest N content, indicating least degraded material) at the two shallow Chukchi Cap stations. C/N ratios of pelagic POM were variable, with highest values at most abyssal sites and lowest values at the shallow Chukchi Cap stations, but also a low value at the northern abyssal site (station 9).

The best match between benthic macrofaunal biota and environmental variables in the BIOENV procedure was achieved by the combination of water depth, organic N content of the sediment, C/N ratio of pelagic POM, pelagic primary production, zooplankton biomass, and %CaCO₃ in the sediment (Table 3). The single variable with the best match was water depth (52.3% variability), the best 2-variable combination involved water depth and pelagic primary production (Table 3). Despite the large set of variables, no more than 60% of the variability was explained by any combination of the measured variables.

3.2. Megafauna assemblages

The summarized results, including numbers of photographs analyzed, area covered and total taxa observed for the six DCS stations are given in Table 4. Taxon counts for the individual stations ranged from 11 (station 6) to 51 (station 12), with provisional taxa used in all stations. A total of 67 distinct taxa

Table 2
Characteristics of sediments from the Canada Basin and C/N ratio of pelagic POM. Bold italic print marks the lowest values among all stations; bold underlined print marks the highest values among all stations.

Station	% Organic carbon	% Organic nitrogen	Mean grain size (phi)	% Gravel & sand	% Mud (silt+clay)	Sorting	%CaCO ₃	C/N sediment POM	C/N pelagic POM
2	1.82	0.16	8.8	8.9	91.1	3.55	7.5	<u>13.0</u>	12.1
3	<u>2.35</u>	<u>0.21</u>	9.2	5.5	94.5	2.79	10.9	12.9	8.9
4	2.00	0.19	8.9	5.3	94.7	2.63	9.7	12.7	12.6
5	1.34	0.13	8.9	1.4	98.6	2.66	8.4	12.0	10.4
6a	1.43	<u>0.11</u>	10.0	0.5	99.5	<u>1.77</u>	<u>5.4</u>	12.5	15.6
7	1.32	0.13	9.1	<u>0.4</u>	<u>99.6</u>	2.77	9.7	11.8	15.6
8	1.19	0.13	10.1	0.7	99.3	1.89	7.7	10.8	<u>18.3</u>
9a	1.08	0.13	<u>10.3</u>	1.8	98.2	1.96	10.0	9.9	<u>8.5</u>
11a	0.98	0.12	7.5	23.0	77.0	<u>4.51</u>	13.2	9.3	8.8
12a	<u>0.96</u>	0.14	<u>6.9</u>	<u>23.7</u>	<u>76.3</u>	4.08	<u>13.8</u>	<u>8.2</u>	8.6
13a	1.24	0.14	9.0	8.0	92.0	3.57	11.4	10.2	10.0
15a	1.65	0.20	8.5	6.0	94.0	2.56	9.0	9.9	10.8

^a Photographic station.

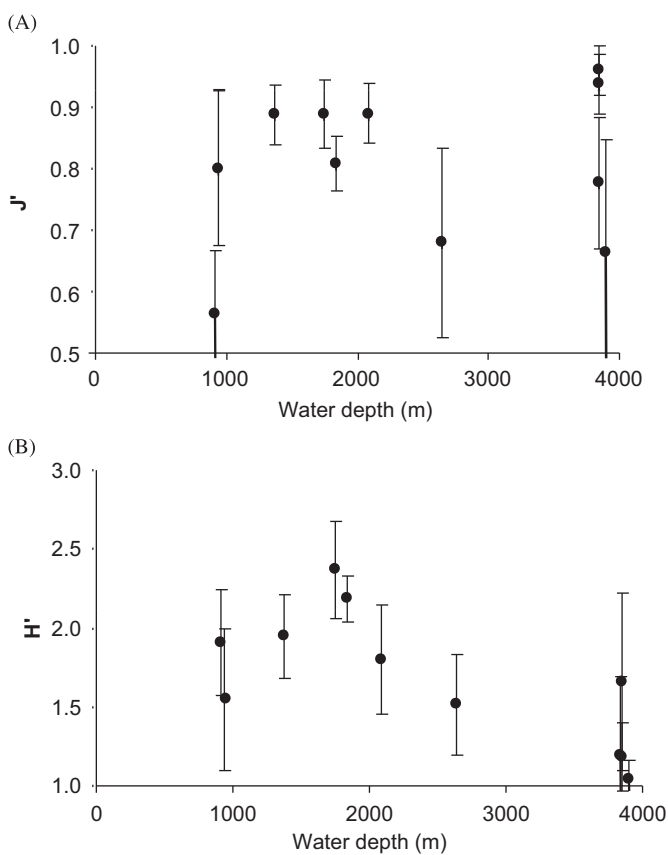


Fig. 4. Pielou's evenness index (A) and Shannon's diversity index (B) of benthic infauna in the Canada Basin. Values are means \pm standard deviations.

were identified among the six stations; echinoderms, which were predominantly holothuroids, were the numerical dominant at three of the six stations (stations 9, 12, and 15). Benthic cnidarians were the second-most prevalent group (Fig. 6). Abundance ranged from 0.08 (station 6) to 5.83 (station 12) ind m^{-2} . Shannon diversity indices for each station ranged from 0.26 (station 12) to 0.80 (station 11). Benthic communities and seafloor characteristics differed among the stations (Figs. 6 and 7, Table 2). An ANOSIM test of megafauna abundance indicated significant differences among the stations compared to random iterations of sample groupings ($R=0.82$, $p < 0.01$). A brief description of each of the stations is given below.

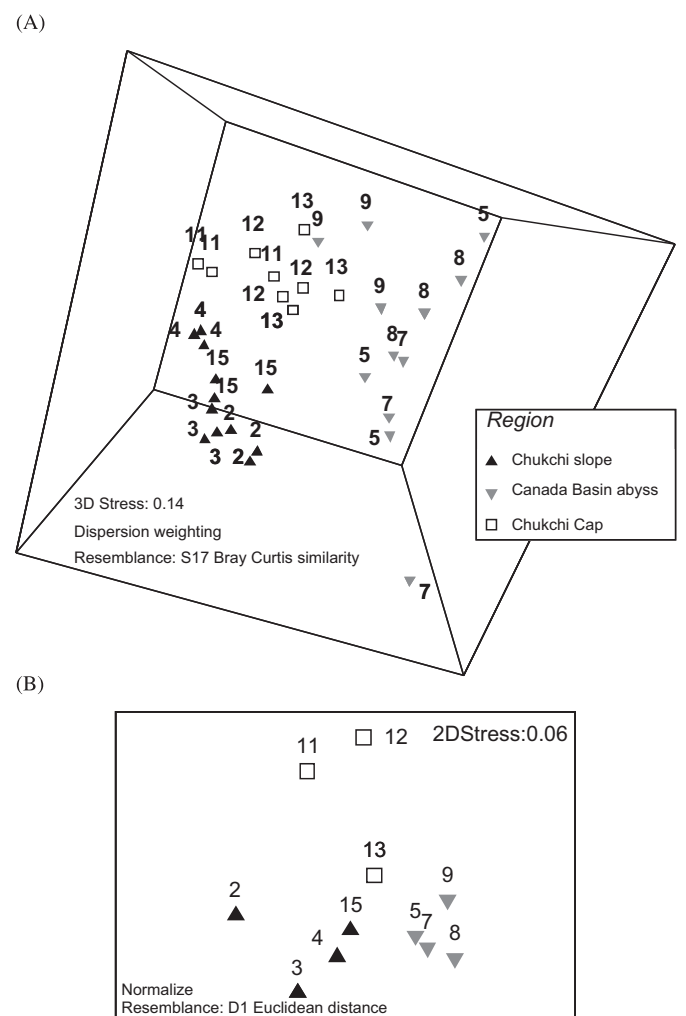


Fig. 5. Similarity of the macrofaunal community (A: values are for individual replicates) and environmental variables (B: values are for single measurements) from eleven Canada Basin stations depicted in multi-dimensional-scaling plots.

3.2.1. Station 6

This was one of two deep stations in the Canada Basin abyss (3843 m). This station was characterized by the lowest densities and fewest taxa, but the evenness of the taxa was relatively high. Sediments in the photographs were uniformly fine-grained silts or clays (also see Table 2), light in color with frequent light patches.

This deepest station supported the fewest visible organisms although lebensspuren consisting of meter-long curving trails and frequent solitary burrows were visible throughout. The most abundant taxa were a white Actiniaria and a holothuroid, neither of which could be identified to the family level.

3.2.2. Station 9

This was the second Canada Basin abyss station (3816 m), but was situated at the base of the Chukchi Borderland area rather than in the abyssal plain as was station 6. Sediment color and characteristics, and lebensspuren closely resembled those at station 6. However, abundance of animals was much greater, dominated by the holothuroid *K. hyalina* (765 observations) and by the white Actiniaria observed at station 6. The evenness was low ($J' = 1.00$) due to locally dense occurrences of *K. hyalina*. Simpson's and Shannon diversity indices ($1 - \lambda = 0.51$, $H' = 0.37$) also indicate an uneven distribution of the 15 taxa that were observed at the site.

Table 3

Results of the BIO-ENV procedure providing the combinations of environmental variables best matching the macrofauna community similarity matrix.

Number of variables	Best variable combination	2 nd best variable combination
1	Water depth (0.523)	Pelagic primary production (0.494)
2	Water depth, pelagic primary production (0.545)	Zooplankton biomass (0.529)
3	Water depth, %CaCO ₃ , pelagic primary production (0.556)	Water depth, C/N ratio of pelagic POM, pelagic primary production (0.550)
4	Water depth, org. N sediment, C/N ratio of pelagic POM, zooplankton biomass (0.579)	Water depth, org. N sediment, C/N ratio of pelagic POM, pelagic primary production (0.571)
5	Water depth, org. N sediment, C/N ratio of pelagic POM, pelagic primary production, zooplankton biomass (0.592)	Water depth, org. N sediment, C/N ratio of pelagic POM, %CaCO ₃ , pelagic primary production (0.580)
6	Water depth, org. N sediment, C/N ratio of pelagic POM, pelagic primary production, zooplankton biomass, %CaCO ₃ (0.594)	Water depth, org. N sediment, C/N ratio of pelagic POM, C/N of sediment POM, pelagic primary production, zooplankton biomass (0.564)

Correlation coefficients are given in parentheses. The following variables were included in the analysis: Water depth (m), %CaCO₃ in sediment, % organic C in sediment, % organic N in sediment, temperatures and salinity of bottom water (Stockwell et al., unpubl.), C/N ratios of sediment particulate organic matter (POM), C/N of pelagic POM, pelagic primary production (Lee et al., unpubl.), integrated pelagic Chlorophyll concentration (Chl m⁻²) (Stockwell et al., unpubl.), integrated zooplankton biomass (Kosobokova and Hopcroft, 2010), sand and clay fractions of the sediment, mean grain size (phi) and sorting index of the sediment.

Table 4

Summary of results for photographic stations.

Station	Latitude N	Longitude W	Mean depth	Photos analyzed	Survey Results				Diversity Indices		
					Total area (m ²)	Total individuals	Mean density (ind m ⁻²)	Total taxa	H'	J	1-λ
6	73° 53.8'	153° 37.6'	3843	107	2045	155	0.08	11	0.764	1.831	0.802
9	75° 11.2'	155° 57.3'	3816	153	1348	1198	0.91	15	0.370	1.001	0.509
11	76° 1.6'	160° 38.1'	1582	283	2128	182	0.09	18	0.802	2.317	0.871
12	76° 25.7'	163° 28.8'	911	736	2313	15674	5.83	51	0.263	1.034	0.356
13	75° 16.3'	161° 14.3'	2087	313	691	2536	1.84	21	0.498	1.518	0.668
15	73° 22.5'	158° 7.8'	2298	542	2001	7646	4.01	26	0.531	1.728	0.782

(See text for station coordinates.) The camera aperture was set to $f/5.6$ and the lens was zoomed to its maximum wide-angle, whereby the acceptance angles of the lens were 48° (horizontal) by 36° (vertical) for a 2048 × 1536 pixel image. Overlapping areas between photographs are not included in totals. Mean densities are number of individuals per m². The following diversity indices were calculated from summed results for each station: Shannon (H'), Pielou evenness (J), and Simpson ($1 - \lambda$).

3.2.3. Station 11

At ~1580 m, this station on the Chukchi Cap (mound in Northwind Abyssal Plain) was the second shallowest of the six DCS stations. Sediment texture and color appeared visually similar to stations 6 and 9, but lebensspuren were less frequent and were dominated by short, irregular impressions rather than long trails. Faunal abundances were similarly depauperate to station 6. The dominant taxon was the polychaete *Bathypolaria carinata* (46 observations). Sediments were coarse (23% gravel and sand, Table 2). Occasional dropstones were noted and were invariably associated with a distinct cluster of mobile and attached animals. These highly localized aggregations contributed to the high Shannon diversity value for the station ($H' = 0.80$).

3.2.4. Station 13

This station on the Chukchi Cap slope (2087 m) had an intermediate taxon number (21 taxa observed) with a relatively high evenness ($J' = 1.52$) and moderate diversity ($H' = 0.50$). Sediments at this station were a silty clay without dropstones or patches of coarse material. Lebensspuren were dominated by small, solitary holes, which were observed in almost every image. Larger, burrow-like depressions were also seen. A long, narrow trail with distinct edges was also common and was tentatively attributed to a gastropod. The numerical dominant was an unidentified aplacophoran (654 specimens) followed by the scaphopod *Siphonodentalium lobatum* (307 specimens).

3.2.5. Station 15

Epifauna at this 2298 m station on the Chukchi slope had a relatively high taxon number (26 taxa observed) and mean densities were almost twice as high as at the Chukchi Cap slope station (station 13). The taxa were evenly distributed among the photographic samples as evidenced by moderately high diversity ($H' = 0.53$) and high evenness indices ($J' = 1.73$, $1 - \lambda = 0.78$). Sediments were silty clay and heavily imprinted with lebensspuren including trails marked by parallel rows of indentations suggesting crustacean tracks. The isopod *Saduria sabini* was observed with 33 specimens; the numerical dominants were two holothuroids *E. heckeri* (2551 specimens) and an unidentified species (1379 specimens).

3.2.6. Station 12

This pockmark station was distinct from the other stations in every respect. It was the shallowest of the six DCS stations (940 m), had the highest percent gravel and sand (23.7%, Table 2), and was the only site with distinct habitat zonation along the photo-transect (Fig. 8). Depths difference of 50 m between the center and the exterior changed with a prominent slope in the transition. Sediments appeared darker and were coarser than other stations (Table 2). The bottom was blanketed with

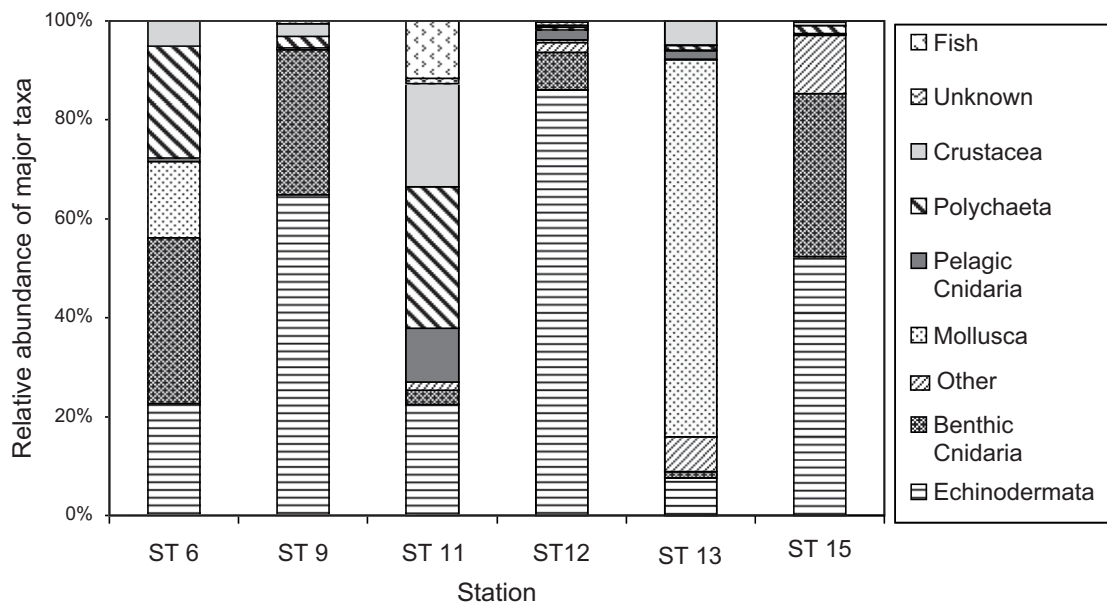


Fig. 6. Relative abundances of major fauna groups at the six photographic stations.

scaphopod shells, generally partly fragmented, and featured numerous dropstones colonized by actinians, barnacles, and crinoids. Lebensspuren were abundant and included several distinct varieties of lengthy trails. The taxon number was the highest among the DCS stations (51 taxa observed); diversity of the fauna was the lowest observed ($H' = 0.26$), and the evenness ($J' = 1.03$) and proportional abundance of species was also low ($1 - \lambda = 0.78$), suggesting that the mix of taxa was relatively consistent. The numerically dominant taxon was the holothuroid *K. hyalina*, mobile on the bottom or swimming above the interface. Assemblies of *K. hyalina* were observed at maximum densities of over 34 ind m^{-2} (mean $4.6 \text{ ind m}^{-2} \pm 4.94$). They were common along the entire 600 m sampling transect, but were significantly (t -test of means, $p < 0.01$) more abundant in the center and slope of the transect (Fig. 8). Midwater cnidarians (jellyfish) were frequently observed on or just above the interface. Unidentified tubes, possibly from polychaetes, were an abundant biogenic feature observed at the station. An unidentified actinian, the urchin *Pourtalesia* sp. and the ophiuroid *Ophiolimna bairdi* were other taxa commonly contributing to the differences between the pockmark center, the slope and the exterior regions (Table 5). No clear examples of fauna commonly associated with cold-seep chemosynthetic communities, such as pogonophoran tubes or bacterial mats (Levin, 2005; Levin and Mendoza, 2007) were observed at the pockmark station.

3.3. Megafauna station similarities

Species-accumulation results for the combined stations based on counts and taxa from the individual photographs at each station suggest that the photographic sampling was reasonably able to define the diversity of the stations within the limits posed by the taxonomic resolution (Fig. 9). The within-station similarities for the photographic samples are given in Table 6. Stations 6 and 11, which had the lowest faunal densities overall, displayed the highest similarity among their respective photographic samples (Fig. 10). These results were probably due to a substantial proportion of samples in which there were no visible fauna. The remaining stations showed less respective similarity among photographic samples.

Environmental data did not explain more than 20% of the variation in the megafauna observed in the DCS stations. The best match of the megafauna with environmental data was achieved by a combination of organic N content of the sediment and C/N ratio of pelagic POM.

4. Discussion

This study addressed the gap in our knowledge of macro-infaunal and mega-epibenthic assemblages, the latter of which had not been described in a quantitative fashion previously for the Canada Basin and the Chukchi Borderland area. In addition to abundance, community composition and biomass (for infauna) this study documents the diversity of deep-sea benthic habitats in the study region.

4.1. Macrofauna

The most recent list of Arctic invertebrate fauna included 837 free-living invertebrate species in the central basins (Sirenko, 2001). Since then, species have been added to the overall inventory (4784 Arctic species total for the Eurasian Arctic, Sirenko, 2001), for example from the Laptev and Chukchi Seas, but a current update has not been published yet (Sirenko, pers. com.). Compared to Sirenko (2001), our study added at least 21 species that were not previously included in the list for the Eurasian Arctic. We found an additional 19 species (for a total of 40 new records) that were listed for some area of the Arctic but not for the central basins (Table 7). It is likely that these species occurred in the Canada Basin previously but were not sampled or identified due to the low sampling effort in the region. It is unlikely, although not inconceivable, that species range changes occurred because of climate changes, dispersal of organisms through ballast water or other mechanisms.

This expedition yielded at least six putative new species (three polychaetes, two isopods, plus a new species of Komokiacea not listed in results; Kamenskaya, pers. comm.) in 33 box cores covering a total area of 1.65 m^2 . An additional putative new isopod species (Wilson, pers. comm.) was collected with the ROV. This amounts to 6% of all polychaete species and 20% of all isopod species being new species in this study. In addition, our previous

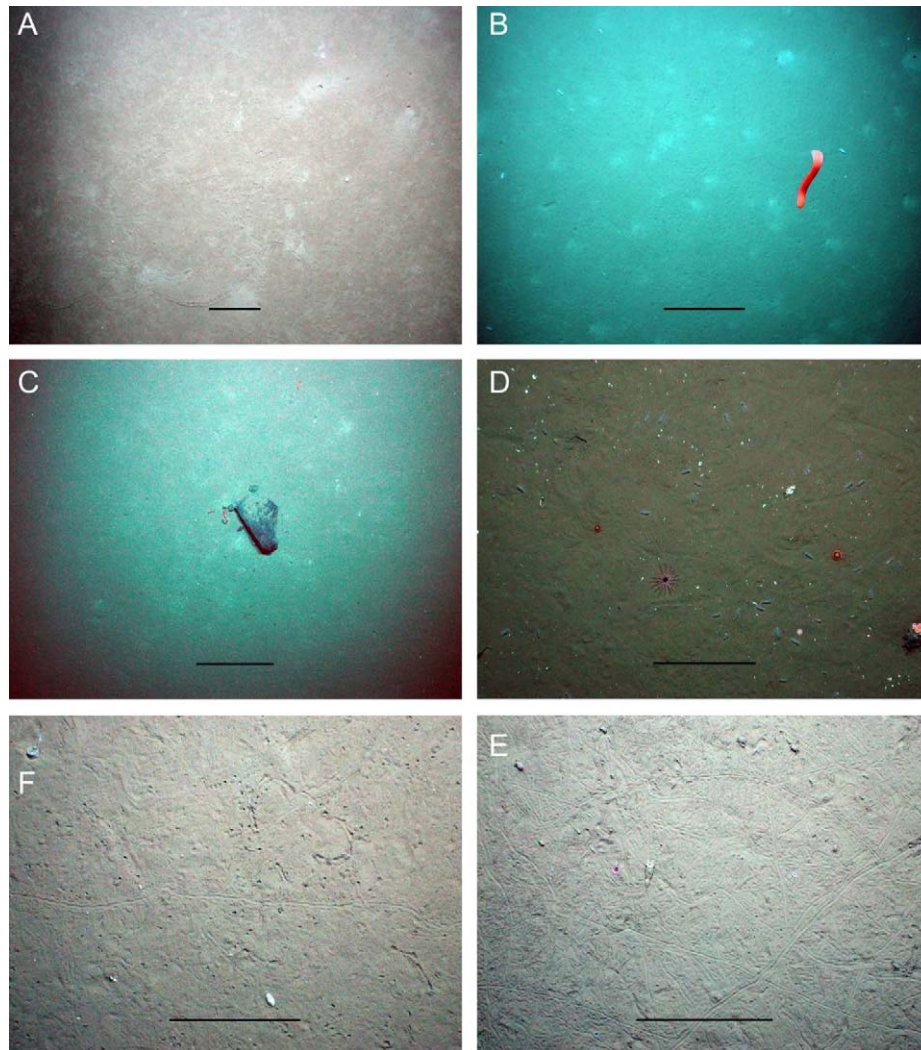


Fig. 7. Plate shows example photographs from each photo-survey station. Scale bars are 50 cm. (A) Station 6 (Canada Basin Abyss, 3843 m): two specimens of *Actiniaria 1*, a white anemone seen at several stations. (B) Station 9 (Canada Basin Abyss 3816 m): the holothuroid *Kolga hyalina* and a swimming nemertine worm. (C) Station 11 (Chukchi Cap, 1582 m): fauna associated with a drop stone. (D) Station 12 (Pockmark, 911 m): at least five taxa including the holothuroid *Kolga hyalina* and pelagic cnidarians resting on the bottom. (E) Station 13 (Chukchi Cap Slope, 2087 m): Aplacophora (upper left) and distinctive lebensspuren (tracks and holes). (F) Station 15 (Chukchi Slope, 2298 m): the isopod *S. sabini* and its characteristic lebensspuren as well as two taxa of holothuroids.

work in the Canada Basin in 2002 yielded three (possibly four) new isopod species (Wilson, pers. comm.), representing 66% of all isopod species found in 2002, in 11 box core samples of a total area of 0.44 m² (Bluhm et al., 2005). Discovering a total of nine or ten putative new species in only about 2 m² of sea floor suggests that potentially hundreds of more new species can be found in future inventories in the Arctic basins or even in the Canada Basin alone. The species discovery rate is clearly higher than that on the Arctic shelves from where, to our knowledge, few new macrofaunal species have been published in recent years (e.g. Shirley and Storch, 1999) despite much higher sampling effort (e.g. Grebmeier et al., 2006). The fraction of putative new species is much lower, however, compared to ongoing work in other deep-sea areas such as the Southern Ocean where putative new species discoveries in three expeditions were 40% (81 species) for polychaetes and 86% (579 species) for isopods (Brandt et al., 2007). However, it should be noted in the comparison that overall macrofauna collection effort was substantially higher in these Antarctic studies (epibenthic sled tow lengths of 711–6464 m per station) and that, consequently, epibenthic sled catches generally yield much more taxonomic material (i.e., number of specimens) than box corer samples (Brandt et al.,

2007). Future Arctic deep-sea studies focusing on taxonomic inventories should thus consider the addition of an epibenthic sled for macrofaunal collections.

In the last decade, topics of particular interest in deep-sea (e.g. Glover et al., 2002: polychaetes, Gage et al., 2004: cumaceans) and polar (Renaud et al., 2006: macrofauna and nematodes; Brandt et al., 2007: various taxa) biodiversity studies have been to identify biodiversity trends with water depth, latitude and ocean productivity. Results are controversial and range from increases in species richness with depth (e.g. Levin et al., 2001) to decreases (this study); decreases of diversity with increasing latitude in the northern hemisphere (e.g. Rex et al., 2000) to no latitudinal trend (e.g. Gray, 2002; Renaud et al., 2006); and unimodal relationships between diversity and productivity (e.g. Rosenzweig and Abramsky, 1993) to weak increases of diversity with productivity (e.g. Glover et al., 2002). In our – admittedly limited – data set, macrofaunal species richness (species number) and Shannon diversity decreased with water depth from 817 to 3380 m and had no obvious pattern over the ~4° latitude covered. Direct comparisons with other Arctic deep-sea studies (e.g., Kröncke, 1994, 1998; Schnack 1998) are limited by differences in methodology, but it is suggested the present data will be a valuable contribution if all data holders of

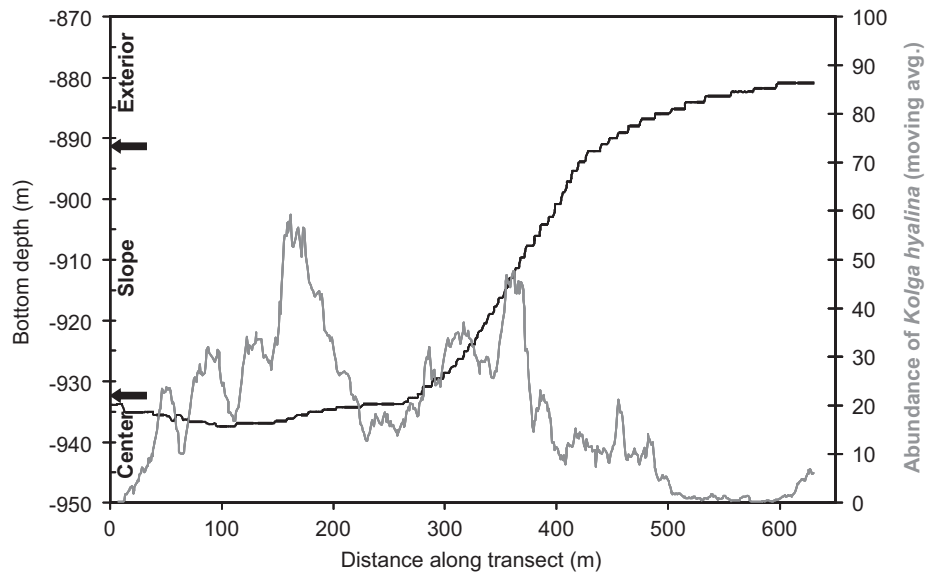


Fig. 8. Transect through pockmark at Station 12, showing bottom depth profile and abundance of the dominant holothuroid *Kolga hyalina*.

Table 5

Comparison of dissimilarity in benthic fauna from photographic survey of pockmark at Station 12.

Comparison Taxa	Avg. Density	Avg. Density	Avg. Diss	Diss/SD	Contrib. %	Cum. %
Pockmark Center vs Slope						
Average dissimilarity=50.54	Center	Slope				
<i>Kolga hyalina</i>	2.82	2.98	11.42	0.72	22.60	22.60
<i>Actinaria_unident_1</i>	0.66	0.45	6.23	1.05	12.32	34.92
<i>Pourtalesia</i>	0.24	0.58	5.10	1.01	10.09	45.01
<i>Crossota millsae</i>	0.46	0.04	3.88	0.89	7.67	52.68
<i>Ophiolimna bairdi</i>	0.33	0.22	3.54	0.82	7.01	59.69
<i>Actinaria_unident_2</i>	0.29	0.10	2.72	0.77	5.38	65.07
<i>Ceriantharia cf actinoscyphiidae</i>	0.24	0.04	2.20	0.52	4.36	69.43
<i>Trichostemma sol</i>	0.15	0.16	2.20	0.62	4.34	73.77
Unknown	0.10	0.13	1.75	0.53	3.47	77.24
Pockmark Slope vs Exterior						
Average dissimilarity=64.88	Slope	Exterior				
<i>Kolga hyalina</i>	2.98	1.12	26.98	1.55	41.59	41.59
<i>Pourtalesia</i>	0.58	0.33	6.98	1.04	10.75	52.34
<i>Actinaria_unident_1</i>	0.45	0.36	6.86	0.93	10.57	62.91
<i>Ophiolimna bairdi</i>	0.22	0.22	4.28	0.72	6.59	69.50
<i>Trichostemma sol</i>	0.16	0.07	2.51	0.54	3.87	73.37
Unknown	0.13	0.06	2.12	0.51	3.27	76.64
Pockmark Center vs Exterior						
Average dissimilarity=70.94	Center	Exterior				
<i>Kolga hyalina</i>	2.82	1.12	24.74	1.48	34.88	34.88
<i>Actinaria_unident_1</i>	0.66	0.36	8.08	0.94	11.38	46.26
<i>Pourtalesia</i>	0.24	0.33	5.09	0.70	7.18	53.44
<i>Crossota millsae</i>	0.46	0.00	5.06	0.82	7.13	60.56
<i>Ophiolimna bairdi</i>	0.33	0.22	4.89	0.68	6.89	67.45
<i>Actinaria_unident_2</i>	0.29	0.03	3.21	0.70	4.52	71.97
<i>Ceriantharia cf actinoscyphiidae</i>	0.24	0.01	2.62	0.48	3.69	75.66

The photo-transect extended ~700 m from the center of pockmark to its slope and to the area exterior from the pockmark. Comparisons were made by distinguishing the three regions based on depth (see Fig. 8). Faunal densities (ind m^{-2}) in the center and slope were significantly different from the exterior (ANOSIM, $p < 0.01$). Relative density of a few taxa (mainly the holothuroid *Kolga hyalina*) explained most of the differences. Avg-average, diss-dissimilarity, contrib-contribution, cum-cumulative.

Arctic deep-sea data attempt a joint comparative diversity analysis for multiple taxa and size groups.

4.2. Environmental control of macrofaunal assemblages

Infaunal abundance and biomass in this study was generally in the same order of magnitude as in previous Arctic deep-sea

studies (Kröncke, 1994, 1998; Clough et al., 1997; Schnack, 1998; Seiler, 1999; Deubel, 2000; also see table in Bluhm et al., 2005). Abundances in these studies were mostly below 1000 ind m^{-2} at depths greater than 3000 m, while those between 800 and 3000 m were up to three-fold higher. Direct comparisons between investigations are flawed to some degree because of different sieve mesh sizes and taxa included. For example, the lower values for the Eurasian basins (Fig. 11) are likely due to the larger mesh

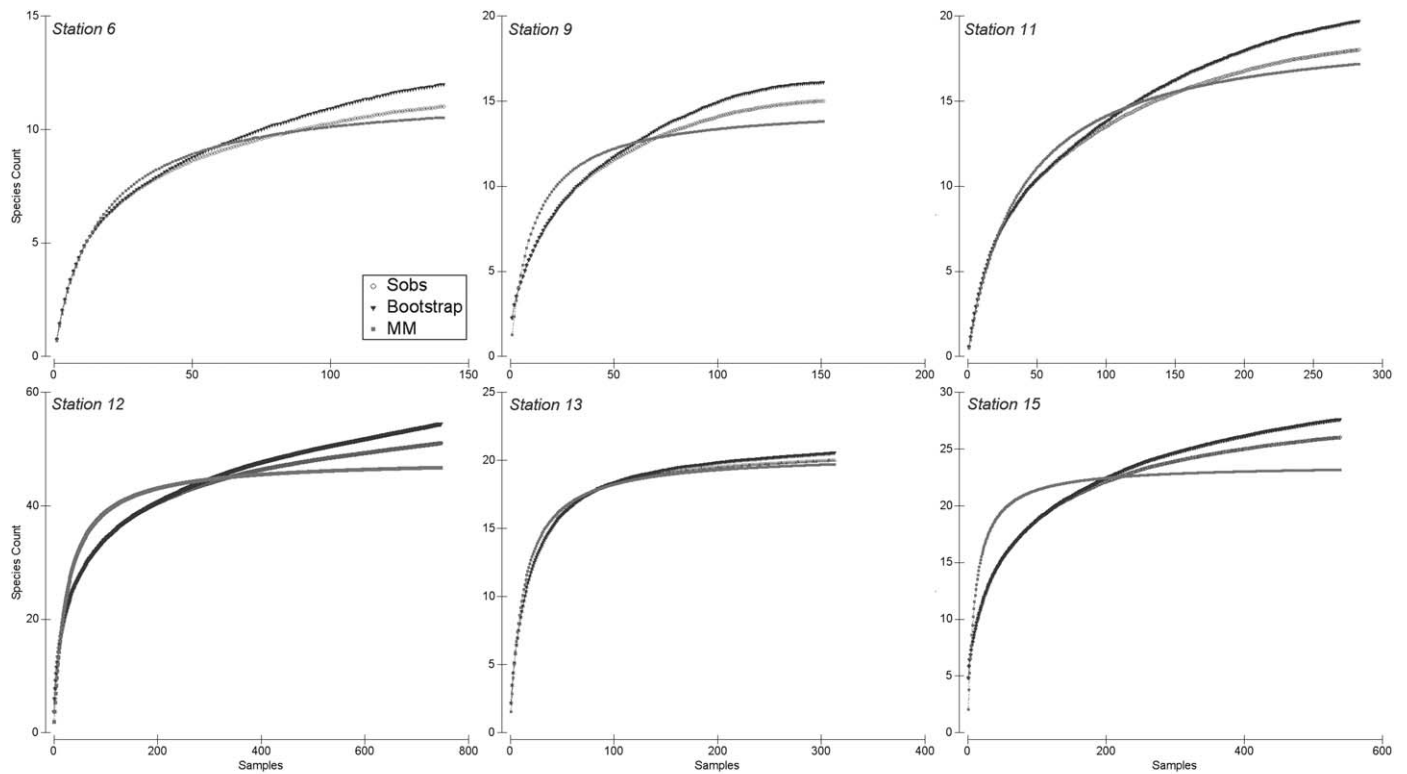


Fig. 9. Species-area curves for taxa identified in the six photo-survey stations, generated by the species-accumulation functions in PRIMER. Three indices are shown: taxon counts (Sobs), Bootstrap estimator based on proportion of photos containing each species, and a Michaelis-Menton (MM) fit of the Sobs curve.

size used relative to the other studies mentioned above. Despite these difficulties, relative gradients or trends should be valid.

In the majority of Arctic macrofaunal deep-sea studies, macrofaunal abundance and biomass decrease with water depth (Kröncke, 1994, 1998; Clough et al., 1997; Schnack, 1998; Seiler, 1999; Deubel, 2000; Bluhm et al., 2005; our Fig. 11) and the same is true for deep-sea areas around the world (Rowe, 1983). Also, depth often is the single-best variable explaining a significant fraction of the variability in faunistic distribution patterns (this study, Clough et al., 1997; Schnack, 1998). In the present study, depth differed greatly between the stations groups “slope” (mean 1700 m) and “abyss” (mean 3850 m). Water depth has often been considered a proxy for food availability in the deep sea (Rex et al., 2000; Thistle, 2003). Such a conclusion is corroborated by our finding that variables related to food availability [e.g., primary production (Lee et al., unpubl.), zooplankton biomass (Kosobokova and Hopcroft, 2010)] and freshness (e.g., C/N ratios) are better correlated with the macrofaunal assemblages than ambient physical properties such as temperature, salinity or sediment grain size characteristics. C/N ratios in sediments tend to decrease from shallow Arctic coastal river deltas to the deep sea because of the seaward dilution of less labile, terrigenous organic material by marine residues (Naidu, 1985). Several of our slope stations may receive terrigenous material especially from the Yukon River, while others (stations 11–15), due to their location further west, presumably receive less terrigenous, but fresher material from the Chukchi Sea shelf (Iken et al., 2010). These relationships to food availability and quality are in agreement with some (e.g. Schnack, 1998), but not all (e.g. Clough et al., 1997), other Arctic deep-sea studies. Integrated annual food availability is difficult to assess during a typically single month-long expedition in the summer. Some deep-sea areas such as the deep Antarctic shelf can act as foodbanks integrating the annual phytoplankton bloom signal with the result that food may not be as seasonally limiting as

previously believed (Mincks et al., 2005). In other deep-sea regions, however, peaks in primary production settle fast and mobile fauna such as holothurians exploit the material quickly (Billett et al., 2001; Iken et al., 2001), so that the time of sampling may affect the inferences made.

Steep gradients in temperature and salinity critically influence benthic community structure in the nearshore Arctic and in the large estuaries of the Russian and North American shelves where these variables have steep gradients (e.g., Deubel et al., 2003). However, these key environmental factors tend to vary little in the deep sea (Thistle, 2003) and in the Canada Basin in particular (< 0.1 in salinity, < 0.7 °C in temperature; also see McLaughlin et al., 2002; Shimada et al., 2004). Therefore, these variables had little influence on the macrofaunal community structure. Likewise, sediment grain size varied only little in the study area (Darby et al., 1989) and, consequently, is also not among the most influential environmental control variables. Dropstones observed on the photographs, however, were responsible for a pronounced small-scale patchiness in megafauna abundance and composition (see below).

4.3. Megafaunal assemblages

This study represents, to our knowledge, the first quantitative assessment of megafauna (epifauna) visible in photographs in the Canada Basin. It may be the first such study for any Arctic deep-sea basin except for AWI Hausgarten (Soltwedel et al., 2009). Individual specimens were previously collected by trawl during the Arctic drifting stations (Mohr and Geiger, 1968) and non-quantitative photographs were published by Hunkins et al. (1970). Echinoderms, in particular holothurians, dominated the megafaunal benthos at several stations in this study. Echinoderms typically also prevail on Arctic shelves, where the dominant group

Table 6
Comparison of similarity of benthic fauna (provisional taxa) observed among the individual photographic samples from each station.

Station (Avg. similarity) Taxa	Avg. Sim.	Sim/SD	Contrib. %	Cum. %
Station 6 (7.47)				
Actinaria_unident_1	4.71	0.28	63.06	63.06
Tube_unident	1.15	0.15	15.36	78.43
<i>Siphonodentalium lobatum</i>	0.70	0.12	9.39	87.81
<i>Elpidia heckeri</i>	0.51	0.10	6.79	94.61
Holothuroidea_2	0.33	0.08	4.36	98.97
Station 9 (54.82)				
<i>Kolga hyalina</i>	37.57	1.76	68.54	68.54
Actinaria_unident_1	16.77	1.10	30.58	99.12
Station 11 (3.57)				
<i>Bathypolaria carinata</i>	1.82	0.17	50.91	50.91
Caridea_unident	0.71	0.10	19.94	70.84
Holothuroidea_1	0.35	0.07	9.88	80.72
<i>Lycodes cf. frigidus</i>	0.27	0.06	7.63	88.35
Medusa	0.20	0.06	5.67	94.01
Holothuroidea_3	0.14	0.05	3.98	98.00
Station 12 (38.60)				
<i>Kolga hyalina</i>	31.46	1.33	81.49	81.49
Actinaria_unident_1	2.53	0.42	6.54	88.03
<i>Pourtalesia</i>	2.09	0.41	5.42	93.45
<i>Ophiolimna bairdi</i>	1.02	0.28	2.65	96.11
Station 13 (36.27)				
Aplacophora_1	24.36	0.97	67.16	67.16
Scaphopoda	10.08	0.64	27.79	94.95
Crustacean_unident	0.57	0.15	1.57	96.52
Station 15 (64.34)				
<i>Elpidia heckeri</i>	23.34	2.61	36.28	36.28
Actinaria_unident_1	16.10	1.94	25.02	61.30
Holothuroidea_4	11.49	1.37	17.85	79.15
Ceriantharia_unident_1	6.59	1.02	10.24	89.39
Sipunculida_burrowed	6.43	0.99	9.99	99.38

Similarity is expressed in scale of 0 (no similarity) to 100 (no difference). The assembly of taxa that contributed to ~95% of the characteristic abundances in each station is listed in ranked order. Comparisons (ANOSIM) between paired stations are significant at $p=0.01$. Avg-average, diss-dissimilarity, contrib-contribution, cum-cumulative.

is ophiuroids, which can reach peak densities of several hundred ind m^{-2} (Piepenburg, 2000; Sejr et al., 2000; Ambrose et al., 2001). Similar to our results, holothurians also are dominant megafauna in some other deep-sea areas of the world oceans, for example the Hausgarten in Fram Strait (Soltwedel et al., 2009) and the well-studied Porcupine Seabight in the North Atlantic where *K. hyalina*, the same sea cucumber species as was found in our study, reached densities of up to 50 ind m^{-2} at 3700 m (Billett and Hansen, 1982). One of the possible reasons for the success of echinoderms in polar and deep-sea environments is that many species are highly mobile (Thistle, 2003), which allows them to respond quickly to spatially and seasonally patchy food input (Iken et al., 2001). Based on our observations from the ROV and abundant individuals photographed off-bottom, *K. hyalina* is a very active swimmer. In the Porcupine Seabight and Abyssal Plain, holothurian (e.g., *K. hyalina*) abundance was found to correlate well with organic-carbon flow (Billett and Hansen, 1982; Iken et al., 2001), which also could be the case in our study where high holothurian abundances occurred at stations 9, 12 and 15. These stations were characterized by relatively low sediment and pelagic POM C/N ratios, indicating high-quality food. The relatively patchy holothuroid distribution at station 9 may be driven by non-uniform down-slope particle transport in canyons in the Northwind Ridge, which the holothurians are able to exploit

(Bett et al., 2001; Iken et al., 2001). Similar considerations may apply to another highly mobile, dominant Arctic deep-sea megafauna species, the swimming polychaete *Bathypolaria carinata* (this study; Bluhm et al., 2005).

The six DCS stations were characterized by several relatively distinct assemblages of megafauna (Fig. 6), indicating that the regions of the Canada Basin and Chukchi Borderland areas investigated support a variety of benthic communities. Differences in megafaunal communities may arise from the influence of depth, sediment characteristics, and possibly food transfer from slopes or other geologic features.

Stations 6 and 9 were relatively similar in depth (> 3800 m) and faunal composition. As typical for deep-sea settings, small-scale variability in hydrographical factors could contribute to an uneven distribution of fauna (Jumars and Eckman, 1983). But while station 6 had a depauperate fauna, with little or no clustering, station 9 was characterized by clusters of holothuroids. As explained above, this difference is likely due to differences in food abundance. Station 11 on the Chukchi Cap (mound in Northwind Abyssal Plain), though much shallower (1582 m), was similarly depauperate in megafauna as station 6, although occasional, highly local concentrations of diversity occurred around dropstones. Such dropstones are known to generate nodes of diversity in an otherwise species-poor setting (Wienberg et al., 2008) and are reflected in an inflected species-accumulation curve and elevated H' diversity and J' evenness values. It is well-known that small, isolated hard substratum such as manganese nodules (Mullinaux, 1987; Veillette et al., 2007), whale bones (Baco and Smith, 2003), rocks (Hargrave et al., 2004; Felley et al., 2008) etc., can significantly increase local biodiversity in deep-sea systems. Stations 13 and 15 were similar in depth, but had distinct species assemblages and rather different taxon numbers, primarily as a result of the relative dominance of patches of holothuroids at station 15, which in turn are possibly related to high carbon and nitrogen content in the sediment.

Station 12 was the pockmark on the Chukchi Cap. Pockmarks are typically thought to form due to fluid or gas expulsion (Hovland and Judd, 1988), although ice rafting has also been suggested as a formation mechanism (Paull et al., 1999). They may include gas hydrates or active gas venting (Hovland and Svensen, 2006) and often support dense chemoautotrophic fauna (MacDonald et al., 1990). However, there were no indicators of chemically enriched benthos, e.g. chemosynthetic bacterial mats (such as *Beggiatoa*) or chemoautotrophic host tube worms or bivalves, in the DCS photos or ROV video footage recorded at the site. Moreover, stable isotope samples were not indicative of a chemosynthesis-based food web (Iken et al., unpubl.). As such, our observations provide little evidence on the possible formation mechanism of the pockmark. Our results do agree, however, with the occasional observations that non-seep specific species, in particular holothurians, have elevated abundances near deep-water seeps or pockmarks (Sibuet et al., 1988; MacDonald et al., 2003; Wildish et al., 2008). The pockmark appeared to be rather old based on the undefined edge contours and heavy sediment fill in the central region. Increasing patch age or ceased seep activity can lead to a decline in chemosynthetic primary producers and increasing importance of phytoplankton-based food webs and higher trophic level consumers as well as non-seep-endemic species (Levin, 2005). Also, the shallow water depth and the bowl-shape of the pockmark can act as an enhanced collection area for fresh, settling phytodetritus, increasing food availability for organisms especially within the center of the pockmark. This is further indicated by the high amount of authigenic carbonates, which can be a sign of high past or present food availability, and also have been attributed to chemoautotrophic productivity in pockmarks formed by gas venting elsewhere (Kasten et al., 2003).

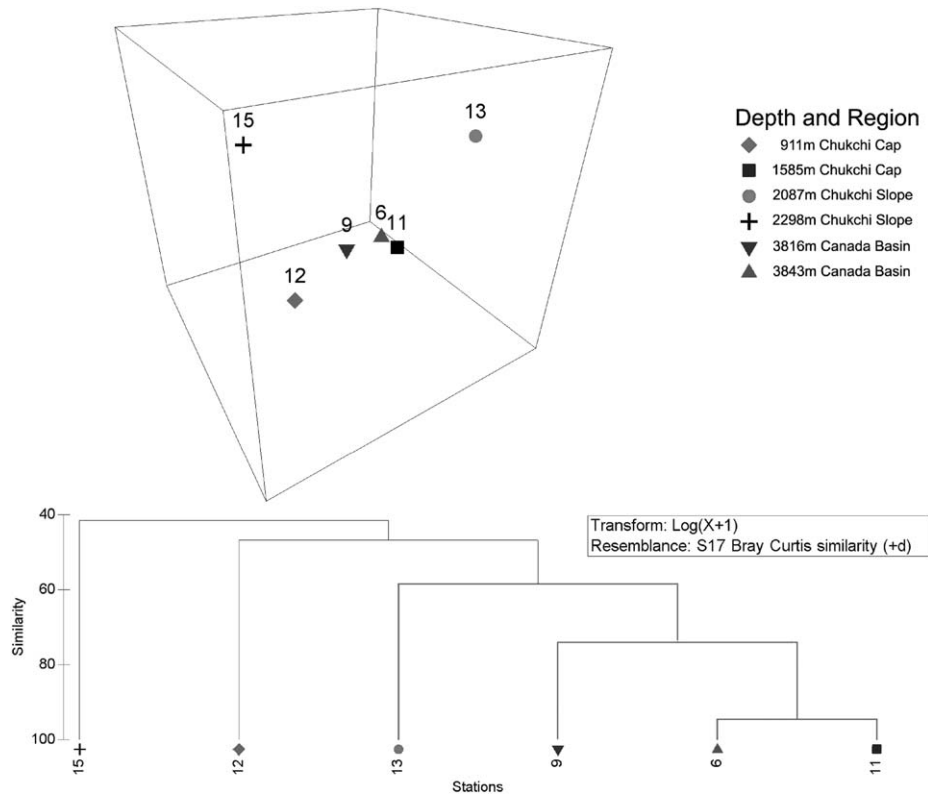


Fig. 10. Multi-dimensional scaling of photo-stations based on taxa observed. Upper panel shows MDS plot of six photo-stations qualified by depth and region. Lower panel shows cluster dendrogram of Bray—Curtis similarity.

Table 7

Additions of Arctic and Arctic deep-sea basin species recovered in box core samples to previous species inventory (Sirenko, 2001).

Arctic species additions (not recorded in Sirenko, 2001)	Additional central Arctic basin species (not recorded in Sirenko, 2001)
Polychaeta <i>Leitoscoloplos pugettensis</i> <i>Pholoe assimilis</i> <i>Sphaerodoridium</i> sp. <i>Sigambra healy</i> sp. nov. <i>Sosane bathyalis</i> <i>Terebellides</i> sp. nov. <i>Anobothrus laubieri</i> <i>Ymerana pteropoda</i> <i>Laonice blakei</i> <i>Macrochaeta</i> sp. <i>Progoniada</i> sp. <i>Protula globifera</i> <i>Ophelina</i> aff. <i>modesta</i> <i>Polycirrus fedorovi</i> Parergodrilidae	Polychaeta <i>Ampharete</i> gr. <i>lindstroemi</i> <i>Aricidea nolani</i> <i>Laonice cirrata</i> <i>Notoproctus oculatus</i> <i>Pseudoscalibregma parvum</i> <i>Ophelina abranchiata</i> <i>Chaetozone</i> sp. <i>Nereimyra</i> sp. <i>Notomastus latericerus</i> <i>Proclea graffi</i> <i>Aricidea</i> aff. <i>hartmanae</i> <i>Nicomache (Loxochona) quadrispinata</i> <i>Praxillella affinis</i> <i>Apistobranthus</i> sp.
Bivalvia <i>Axinopsida serricata</i> <i>Ledella tamara</i>	Bivalvia <i>Boreacola maltzani</i> <i>Portlandia intermedia</i>
Tanaidacea <i>Collettea</i> sp. <i>Leptognathia</i> cf. <i>acanthifer</i>	Gastropoda <i>Oenopota novajaseiliensis</i> <i>Diaphana minuta</i>
Isopoda <i>Eurycope</i> n. sp.	Amphipoda <i>Aceroides latipes</i>
Cnidaria <i>Nausithoe</i> sp.	

Unique among the DCS stations, the pockmark station had clearly defined sub-habitats (Fig. 8), harboring distinctly different megafaunal communities. This feature is one of a large number of similar pockmarks distributed northward of station 12 on the Chukchi Cap. Pockmarks may, therefore, represent a common source of biodiversity and high benthic biomass in this region.

5. Conclusions

The box core and DCS stations occupied during this study covered a large and varied extent of the Arctic benthos, although the generality of our results should be interpreted cautiously because of both relatively limited numbers of stations and replication. Our analyses suggest that mega- and macrofaunal community trends may differ within the benthic systems sampled here. Stations grouped as “Chukchi slope”, “Canada Basin abyss” and “Chukchi Cap” for the macrofaunal communities but not for the megafaunal communities. Infaunal abundance was, overall, inversely related to depth, while megafauna patterns were inconsistent although densities were highest at the shallowest station and lowest at the deepest station. Diversity (Shannon) index was inversely related to water depth (slight peak close to 2000 m) for macrofauna but was mostly increasing with water depth for megafauna. However, it seems that both size fractions of the benthic fauna are strongly influenced by the general food availability. Epifaunal communities were dominated by very mobile species that are able to exploit patchy food sources, while macrofaunal communities appeared to respond to variable food availability with changing community composition, especially in

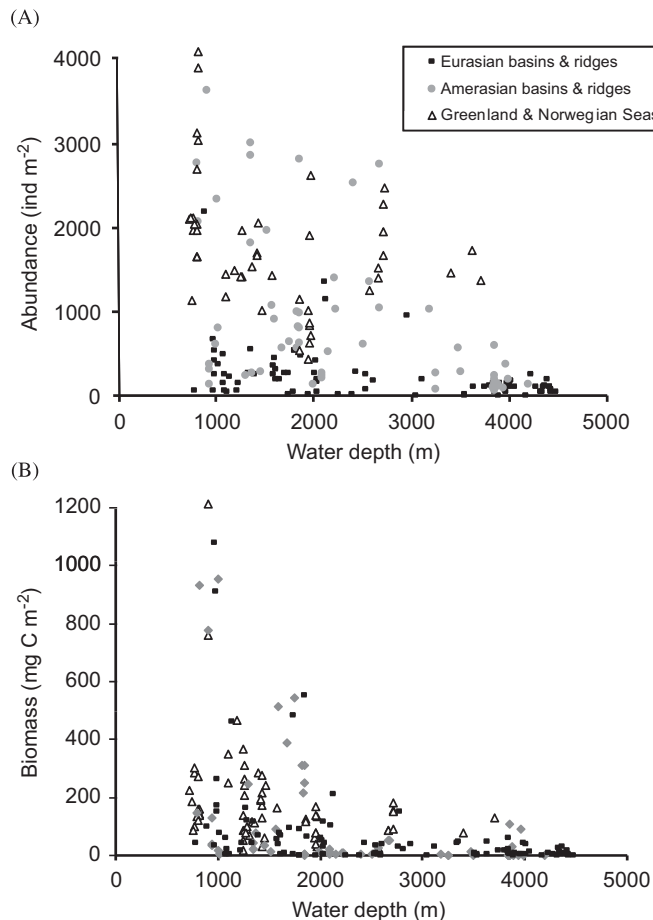


Fig. 11. Pan-Arctic trends in macrofaunal (A) abundance and (B) biomass in the Arctic deep-sea. Data sources are listed in text. Wet weight data from Romero-Wetzel and Gerlach (1991), Kröncke (1994, 1998), Bluhm et al. (2005) and this study were converted using organic carbon = $0.034 \times$ wet weight (Rowe, 1983). Ash free dry weight data from Deubel (2000) were converted using organic carbon = $0.5 \times$ ash free dry weight (Brey et al., 1988).

polychaetes that dominate the macrofauna at most high-Arctic deep-sea locations in abundance, biomass and species numbers (this study; Kröncke, 1994, 1998; Clough et al., 1997; Schnack, 1998; Deubel, 2000; Bluhm et al., 2005). Within the widely variable feeding strategies of polychaetes (Fauchald and Jumars, 1979), many deep-sea species are deposit feeders, able to exploit deposited organic matter long-term (Iken et al., 2001, 2005; Thistle, 2003). Differences in mega- and macrofaunal community responses to food availability were most clearly seen at the pockmark station (station 12 in this study), where polychaetes and other macrofauna were not particularly abundant or rich in biomass but where megafaunal abundances were extremely high.

The study area of the Canada Basin and Chukchi Borderland has been experiencing strong environmental changes in the past years (Stroeve et al., 2007). In 2005, the ice edge had retreated beyond its median extent during the study time and the retreat has even accelerated significantly in 2006 and 2007 (Maslanik et al., 2007). A wide range of oceanographic processes are very likely to be impacted by this rapid change, and this impact will eventually also have a strong effect on the deep-sea benthos (Glover and Smith, 2003). The results presented here are descriptive snapshots in a variety of areas that may be subject to rapid change. These descriptions are sufficiently distinctive that major change may be detectable if the stations are re-occupied in future efforts.

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