



Epibenthic Community Variability on the Alaskan Beaufort Sea Continental Shelf

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Final Report

May 2013

OCS Study BOEM 2013-01148

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This study was funded in part by the U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM) through Cooperative Agreement M11AC00002 between BOEM, Alaska Outer Continental Shelf Region, and the University of Alaska Fairbanks. This report, OCS Study BOEM 2013-01148, is available through the Coastal Marine Institute, select federal depository libraries and <http://www.boem.gov/Environmental-Stewardship/Environmental-Studies/Alaska-Region/Index.aspx>.

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Abstract

The Arctic marine epibenthos contributes significantly to benthic biomass, remineralization and redistribution of organic carbon, and is a key element of the local food web. In 2011, epibenthic species composition, abundance and biomass were collected at 71 stations on the Alaskan Beaufort Sea shelf using epibenthic trawls. Additionally, environmental data (depth, position, bottom water temperature, salinity, pH, chlorophyll and phaeopigments, sediment grain size, sediment chlorophyll *a* and sediment organic matter, total organic carbon, total organic nitrogen and carbon/nitrogen ratios) were collected at each station. Significant spatial variability was observed in the community composition and dominant taxa with a total of 154 taxa identified. The shallow stations (<25 m) were dominated by mobile crustaceans and had the lowest diversity. The mid-depth stations (26-100 m) had the highest diversity indices. The deep stations (101-220 m) were mostly represented by echinoderms with intermediate diversity values. Biomass was highest at the western stations along the shelf break from longitude 155 to 150°W. While abundance mimicked the biomass stations, there was also an area of higher abundance on the far eastern mid-depth side of the study area from longitude 149 to 145°W. The most influential environmental drivers (bottom water temperature, salinity, pH, phaeopigments, sediment grain size, sediment organic matter, and carbon/nitrogen ratios) had a moderate to low correlation with abundance and biomass (≥ 0.5 at 0.1% significance level). However, the differences in taxonomic dominance, abundance and biomass among stations were linked to gradients in the physical environment throughout the study area. Environmental changes associated with variable climate could alter the epibenthic community with implications to higher trophic levels.

Introduction

Existing data of Alaskan Beaufort Sea shelf benthic communities date from the 1970's, when the nation's interest in off-shore oil exploration focused on this area (Carey et al. 1974; Carey 1976; Frost and Lowry 1983; Carey et al. 1984; Dunton 1984). The nearshore environment on the shore-side of the barrier islands has received particular attention, with ongoing long term studies focused on the community composition and the effect of disturbance on organisms associated with shallow water nearshore boulders (Dunton 1984; Dunton and Schonberg 2000; Konar and Iken 2005; Konar 2007). Outside the barrier islands, the shelf is a soft sediment habitat (Barnes et al. 1984). Surveys across the shelf have revealed shallow waters (5 to 25 meters) to support a rich bivalve fauna averaging 300 individuals per m^{-2} , which contrast with the shallow waters along the American Pacific coast that support less than 240 individuals per m^{-2} (Carey et al. 1984). This high density and species richness of bivalves in the Beaufort Sea has been proposed to be associated with finer and more heterogeneous sediments and also the reduced wave action along the inner continental shelf (Carey et al. 1984). As in other Arctic regions, epibenthic biomass in the Beaufort Sea is highly dominated by invertebrate species compared to fishes (Piepenburg 2005). West of Point Barrow, shrimp biomass alone surpassed the biomass of all fish groups combined in the same demersal trawl hauls (Frost and Lowry 1983). In a benthic survey performed on the western Alaskan Beaufort shelf, invertebrates made up to 94% of the total weight (Rand and Logerwell 2011). Considerably more effort has been dedicated to benthic communities in the Canadian Beaufort Sea in recent years, with particular focus on eastern Arctic infaunal communities (Cusson et al. 2007; Conlan et al. 2008; Link et al. 2011). In this area, epibenthic communities can be responsible for up to 41% of the carbon demand and are dominated by echinoderms with peaks in abundance and biomass in the 60–90 m depth range (Renaud et al. 2007a). Photographic surveys of these Canadian shelf communities showed highest ophiuroid abundance of 60 individuals m^{-2} , with important contributions of the amphipod *Anonyx* spp. to the total abundance (Renaud et al. 2007b). In other Arctic regions, such as the Chukchi and Greenland Seas, epibenthic communities have a patchy distribution with variable biomass and taxonomic diversity, but again, often dominated by echinoderms (Starmans et al. 1999; Piepenburg 2005; Bluhm et al. 2009; Ravelo et al. submitted). From an ecosystem perspective, they are important in recycling and redistributing organic matter deposited from the pelagic zone and are important bioturbators through their feeding activities (Ambrose 1993). Many epibenthic species are key elements of the local food web (Bluhm et al. 2005).

The Alaskan Beaufort Sea consists of a narrow shallow shelf with an extent of 50-100 km off the coast line and slopes down to the Canadian Abyssal Plain to depths exceeding 3,000 m (Norton and Weller 1984). Sea ice dominates the entire Beaufort Sea, covering the region completely for nine to ten months of the year. Landfast ice forms gradually in the fall and by winter, its

extent can reach up to 50 km offshore (Norton and Weller 1984). Water from the Bering Sea is advected through Barrow Canyon, forming a “jet” or “shelfbreak current.” The flow velocity, extent and direction of this water is highly affected by seasonality and wind (Aagaard 1984; Pickart et al. 2005). The shelfbreak current flows along the slope west of Barrow Canyon in three seasonal forms, warm summer Bering water flowing along the shelfbreak ranging from 50 to 100 m (with temperatures of 3°C and up to 5°C), cold winter-transformed Bering water located against the upper continental slope at > 100 m (-1.4°C), and warm Atlantic water against the slope at approximately 150 m depth (0°C) (Pickart et al. 2005). Wind has a profound effect on the direction and intensity of these water masses. During the fall and winter, easterly winds weaken and can reverse the direction of the shelf current, while promoting upwelling along the Alaskan north slope (Aagaard 1984; Weingartner et al. 1998; Pickart et al. 2005). Further along the eastern Beaufort shelf, the fate of this jet current is still unclear (Nikolopoulos et al. 2009). Evidence from drifters and the direction of ice scouring on the shelf seafloor indicate that divergence in water movement may occur around Barter Island (Barnes et al. 1987; Reimnitz et al. 1988). Off the shelf, the clockwise movement of the Beaufort Gyre, driven by the dominant northeasterly winds, creates westward currents, which flow along the shelf margin and on the inner shelf from Mackenzie Bay to Point Barrow (Aagaard 1984). In the winter, the Beaufort Gyre moves the ice pack westward and breaks against the fixed landfast ice, forming a large pressure-ridge system that runs aground along the inshore edge (Barnes et al. 1984). In this area, known as the Stamuki zone, the seafloor is scoured by dragging ice keels that form deep gouges. Some gouges are more than 4 m deep (Barnes et al. 1984), with the highest density found between water depths of 20 to 40 m (Barnes et al. 1984).

The Beaufort continental shelf is also highly influenced by the seasonal discharge of many large rivers, such as the Mackenzie and Colville rivers, which affect large areas with terrigenous sediments and reduced salinity (Macdonald et al. 1998; Carmack and Macdonald 2002). In general, low sediment organic carbon content has been attributed to low water column primary production, with a total annual estimate for the Canadian Beaufort shelf ranging from 12 to 16 g C m⁻² (Naidu 1974; Carmack et al. 2004). Sediments on the shelf and outer shelf are poorly sorted muds or sandy-muds, with distinct differences in the overall mean size of the sediments on the shelf, slope and basin (Naidu 1974). These depth zonation differences are attributed to the presence of well size sorted gravel or coarse sand in well sorted mud on the shelf, along with the absence of gravel and like fractions of silt and clay on the extra-shelf zone (Naidu 1974). The eastern Alaskan Beaufort is influenced by the Mackenzie River, resulting in finer sediment grain sizes and better sorting in that region (Naidu 1974). Sediment transport by ice rafting can be significant on the shelf, carrying gravel and sand particles from the coast onto the shelf (Naidu 1974; Barnes et al. 1982).

One of the most effective and standardized methods to obtain quantitative epibenthic community data is by trawling. Past demersal sampling efforts in the Beaufort Sea were performed using photography, dredges and otter trawls (Carey et al. 1974; Frost and Lowry 1983; Rand and Logerwell 2011). In temperate and subpolar regions, otter trawls have been used extensively for commercial demersal fisheries and stock assessment of commercially important species. Otter trawls depend on doors to maintain the net opening. The consistency of the horizontal opening of the net can vary with vessel speed, rigging features and bottom conditions (Wathne 1977; Gunderson and Ellis 1986). However, variability in the net opening may be minor when using large commercial sized gear (Gunderson and Ellis 1986). The past three systematic epibenthic surveys that took place on the Beaufort Sea shelf were performed using different types of otter trawls (Carey and Ruff 1977; Frost and Lowry 1983; Rand and Logerwell 2011). The 2008 Beaufort trawl survey used demersal trawl gear and standard survey methods as conducted by National Marine Fisheries Service. This gear type ensured comparability of results with surveys performed in the Bering and Chukchi Seas (Rand and Logerwell 2011). However, for Arctic regions where the catch per unit effort and the overall size of epibenthic invertebrates and fish is much smaller than in subpolar regions, other gear types have been utilized, such as the plumb staff beam trawl (PSBT) (Bluhm et al. 2009; Norcross et al. 2010; Ravelo et al. submitted). The PSBT has been proven very effective for systematic sampling of demersal and epibenthic organisms in Alaskan waters (Gunderson and Ellis 1986). This type of gear provides a constant net opening because of a rigid bar at the mouth of the net, which is necessary for consistent quantitative samples. In addition to the effectiveness of the PSBT, they can be deployed from smaller vessels using only one winch as opposed to the large otter trawls (Gunderson and Ellis 1986). In uneven and complex habitats, the trawl gear deployment can be challenging and the performance questionable, limiting the PSBT to smooth and even substrates. The modification of additional ground gear to the bottom of the PSBT reduces the likelihood of damage to the net in the presence of boulders or vertical biotic structures (Abookire and Rose 2005). However, the difference in performance of the PSBT with and without the modifications has yet to be tested. Without this knowledge it is impossible to merge data sets or make true quantitative comparisons among the different surveys occurring in other Arctic regions or as a time series analysis.

Global climate change and ocean acidification have the potential to create acute changes in the habitat for Arctic benthic organisms (Loeng et al. 2005; Fabry et al. 2008; Bluhm et al. 2009; Wassmann et al. 2011; Grebmeier 2012). Higher sedimentation rates associated with increased river runoff, could negatively affect benthic shelf filter feeders (Moore 1977; McClelland et al. 2006). In the northern Bering Sea, the close match of the peak in phytoplankton growth with the spring ice breakup suggests that earlier sea ice retreat would affect the intensity and timing of the spring bloom (Clement et al. 2004; Grebmeier 2012). Recent studies have shown an

increase in zooplankton grazing rates and growth and a reduction in the sizes of some amphipods in the Northern Bering and Chukchi Seas (Coyle et al. 2007; Matsuno et al. 2011). The prolonged ice free season and higher summer water temperature could cause similar changes in other regions, such as the Beaufort Sea. With the increase in pelagic grazing rates, less export production would be available for the benthos (Grebmeier et al. 2006a). Changes in the benthic coupling with the pelagic system will have a direct influence on benthic organisms, with implications for higher trophic levels (Grebmeier et al. 2006b; Bluhm and Gradinger 2008; Renaud et al. 2008). With the increase of atmospheric CO₂, the world's oceans are experiencing a reduction in pH, which is amplified by almost 20% in Arctic waters (Steinacher et al. 2009). Under-saturated aragonite surface waters have been detected off the Beaufort Sea shelf as a consequence of storm induced upwelling events. These outgassing events are predicted to increase in frequency as the ice covered season decreases (Mathis et al. 2012). In addition to the acute environmental changes the Arctic shelves are experiencing, rising economic interest in the region may increase pollutants and maritime traffic related disturbances. Many long term studies in the Chukchi Sea are focusing on how these changes are impacting the ecosystem, with particular focus on the benthic species distribution, biomass and respiration (Bluhm et al. 2009; Grebmeier 2012). The Beaufort Sea shelf is subject to many unique environmental forces, and the findings from the Chukchi Sea may not be directly transferred to this region.

There is a growing need to increase our understanding of the species composition, abundance, and biomass across the Alaskan Beaufort Sea shelf. This stems from a severe lack of existing knowledge of epibenthic communities in this area, the biological importance of the epibenthos to Arctic shelf systems, the rapid environmental changes that are occurring across the Arctic, and the increase in economic interest in this region (Loeng et al. 2005; Dunton et al. 2009; Grebmeier 2012; Dunton et al. 2012; Mathis et al. 2012). There is also a critical need for consensus in sampling gear utilized for epibenthic studies to enable quantitative comparisons between different research efforts. This project was designed to help address information needs regarding the epibenthic community of the Alaskan Beaufort Sea shelf and offer a benchmark for future studies in this region. Hypotheses tested were: 1) Alaskan Beaufort Sea shelf epibenthic communities are distributed across a depth gradient and are dominated by distinct taxonomic groups, 2) a select group of environmental parameters and their variability influences the epibenthic community distribution, 3) there are no significant differences between the samples collected using the PSBT and a modified version of this (PSBT-A) at the same site, and 4) there are no significant differences between replicate samples collected using the PSBT-A at the same site a few days apart.

Project Objectives

- 1) Characterize the epibenthic communities in the central Beaufort Sea (between 147° and 150° west longitude)
- 2) Compare these communities to ones found in the adjacent Chukchi Sea.
- 3) Compare these communities to ones found in other areas around the Beaufort Sea study area

Methods

For objectives 1 and 3, epibenthic samples were collected at 71 stations in an area extending from 70.45° N and 145.09° W to 71.66°N and 155.25°W in August 2011 (Figure 1). Stations ranged in water depth from 10 to 220 m. The study area was divided into three regions (Eastern, Central and Western Beaufort). Two gear types were used, a plum staff beam trawl (PSBT) designed after Gunderson and Ellis (1986) and a modified version of the former (PSBT-A) similar to the one developed by Abookire and Rose (2005). Both gear types were 3.05 m plumb-staff beam trawls with a 7 mm mesh and a 4 mm codend liner. A rigid 3 m pipe forward of the net held the mouth open for an effective swath of 2.26 m. The vertical opening of the net was approximately 1.2 m. The modification of the PSBT-A gear consisted of the addition of rubber rollers on the bottom of the net following the design of Abookire and Rose (2005). The PSBT-A was used at stations with very soft bottoms where the rubber rollers allowed for a more surficial swath of the gear over the seafloor. The trawl time varied from approximately 1 to 5 minutes on the seafloor at a vessel speed that ranged approximately from 2 to 5 knots. The trawl time varied depending on the sediment characteristics, determined by sediment retrieved from a van Veen grab at each station. The distance covered ranged from 63 m to 383 m.

A comparison was done at five opportunistically chosen stations (WB13, WB14, WB18, WB21 and CB33) to determine the variability in the performance of the two gear types (from here on called “gear comparison”). In contrast to many other gear types, trawl hauls typically do not get replicated (Rand and Logerwell 2011) due to the considerable time commitment. In addition to the gear comparison, we opportunistically resampled six stations (WB07, WB31, WB32, CB33, CB34 and CB35) no more than five days apart using the PSBT-A to determine the variability in samples collected at the same site (from here on called “site variability comparison”).

Figure 2 shows illustrations of the sampling procedures. After each trawl was brought on board, catches were cleaned of sediments and organisms were sorted to the varying taxonomic levels, in some cases to the species level but in most cases to genus (Appendix). All taxa were individually counted and their damp biomass determined. Voucher specimens were fixed in 10% buffered formalin for further taxonomic identification. Gastropod identifications were

supported by taxonomist Nora Foster, from NRF Taxonomic Services. Amphipod identifications were performed by Kenneth Coyle, from the University of Alaska Fairbanks. Caridea (shrimp) were identified using the taxonomic key by Vassilenko and Petryashov (2009). The Caridea taxa that were separated to lower taxonomic levels are specified in the species list, as opposed to the functional group “other Caridae” (other shrimp) (Appendix). For this analysis, taxa within the phyla Bryozoa and class Hydrozoa were grouped at the phylum and class level respectively.

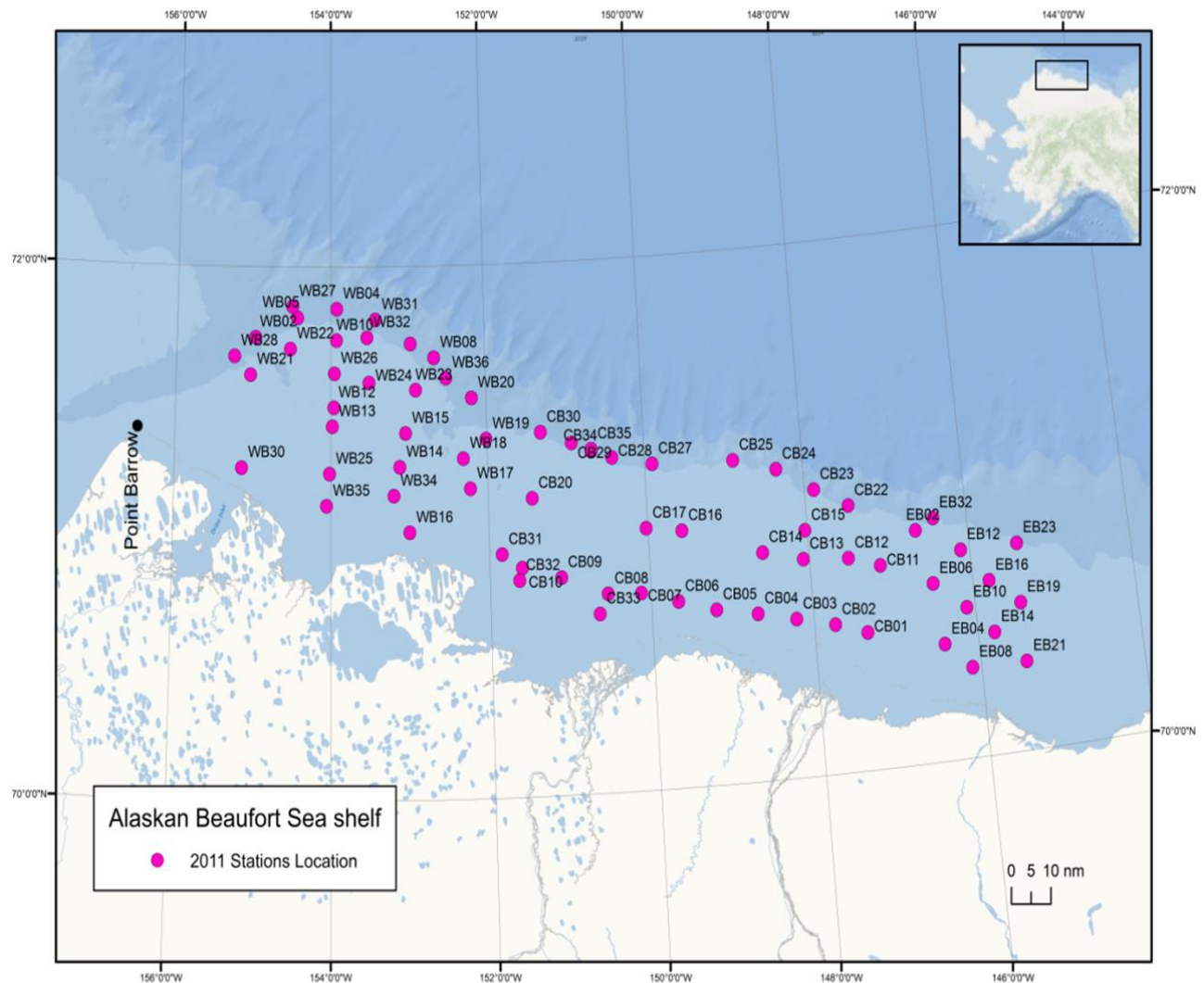


Figure 1. Map of stations sampled for epibenthos. Labels defined *a priori* for cruise logistics.

At each station, surface sediment characteristics were noted from a van Veen grab (presence of sand, silt and gravel) and from the trawl (presence of cobbles and boulders). Seafloor characteristics were categorized based on the presence/absence of cobbles, boulders or a combination of the two, resulting in four categories that were included as a variable for the environmental analysis. Also from grab sample observations, the presence of “sticky anoxic clay” and/or larger cobbles in grab samples was used to determine gear type and trawl duration

for each station. Sediment samples collected from a van Veen grab were immediately frozen for later chlorophyll *a*, percent organic matter content, percent total organic carbon (TOC), percent total organic nitrogen (TON), percent carbon to nitrogen ratios (C/N) and sediment grain size analysis. All sediment samples were processed at the University of Alaska Fairbanks (UAF). Environmental Protection Agency protocols were followed for chlorophyll *a* sediment samples (Arar and Collins 1997), percent sediment organic matter measures (Schumacher 2002), and sediment grain size samples (Strobel et al. 1995). Isotope analysis for sediment TOC, TON and C/N samples were processed following the same procedure as Iken et al. (2010). In addition, bottom water characteristics (temperature, salinity and pH) and water samples for chlorophyll *a* analysis were collected using a SeaBird 25 CTD. Water samples were filtered and processed for chlorophyll *a* content following the protocol in the manual of chemical and biological methods for seawater analysis (Parsons 1984).

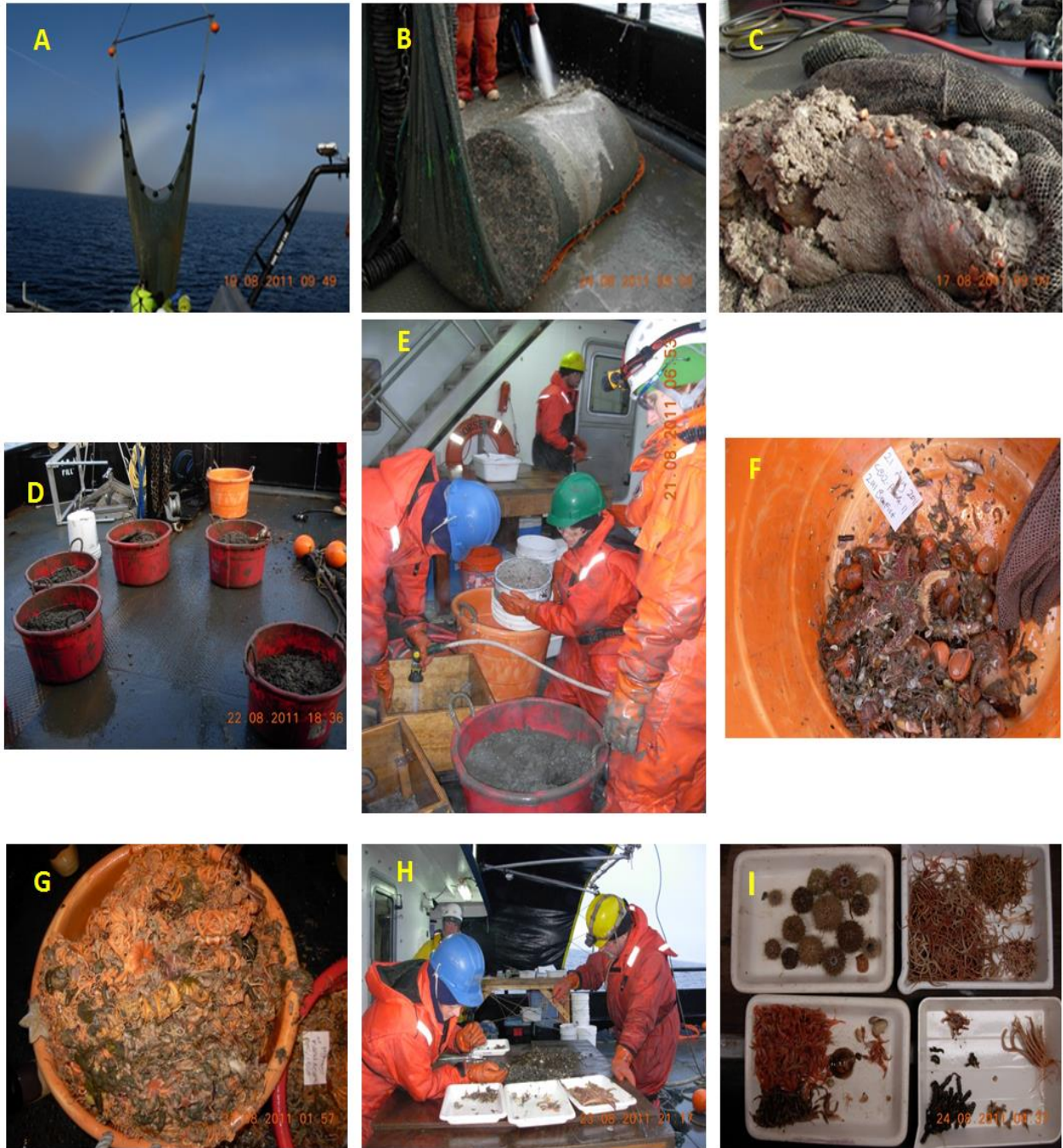


Figure 2. Illustrative images of the sampling process for epibenthic community analysis. (A) plumb staff beam trawl being pulled onto the ship, (B) codend with a large catch being rinsed, (C) and (D) unwashed catch, (E) washing the unsorted catch with sieves, (F) and (G) examples of two very different communities in washed unsorted catches, (H) sorting the catch with help of a crew member, (I) sorted catch. Clockwise from top left; sea urchins, three species of brittle stars, three taxa of shrimp with amphipods and a nudibranch, a sea star, a crinoid, tube worms and bryozoans.

For objective 2, biomass data from 53 stations sampled during the 2009 and 2010 COMIDA-CAB cruises in the NE Chukchi Sea were merged with the 71 stations sampled along the Beaufort Sea shelf (Figure 3). Organisms included in the analysis were classified to the lowest practical taxonomic level (genus and family in most cases). Damp biomass data were standardized to relative percentage of the total catch.

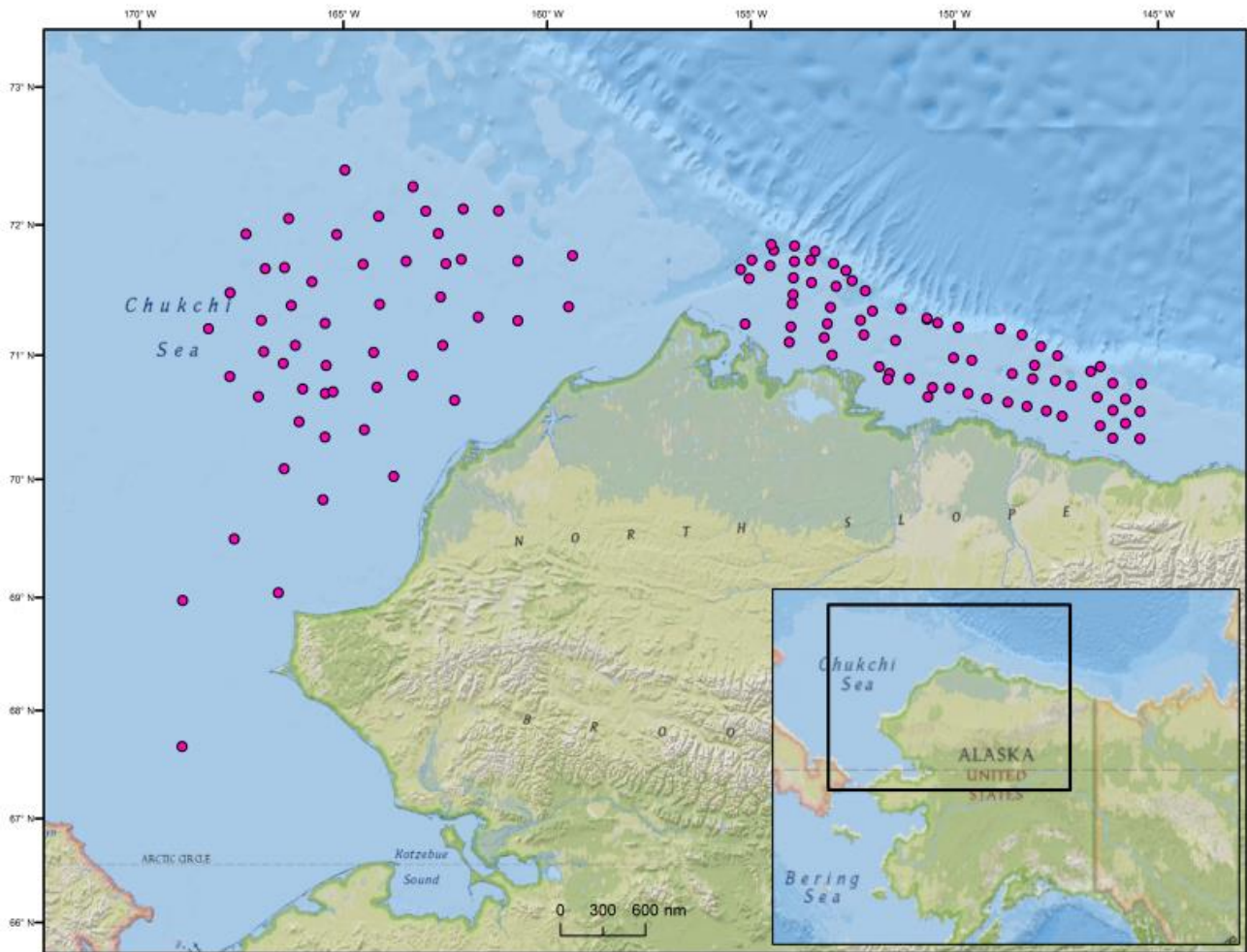


Figure 3. Map showing the study area. Sampled stations are represented by pink dots and inset shows the study location in Alaska.

Data Analysis: Objectives 1 and 3

For objectives 1 and 3, the following analyses were performed:

Epibenthic abundance and biomass data were standardized to 100 m² for the community description summary and diversity indices analysis. Maps were generated using ArcMap from ESRI software. Circle size ranges in the total abundance and biomass maps were determined by natural jerks. For non-parametric multivariate statistical analysis, the software package PRIMER v. 6 was used (Clarke and Gorley 2006). For that purpose, all taxa abundance and biomass were

standardized to relative percentage per trawl and square root transformed. Compositional data are commonly used in multivariate analysis when the size of the samples is not fixed, such as the area trawled. To determine the taxa that best explain the pattern of the epifaunal community across all stations, BVSTEP (Biological Variables Stepwise Procedure) was used separately on the abundance and biomass data, using a Bray-Curtis resemblance matrix and Spearman rank correlation. The BVSTEP procedure carries a step wise approach, searching for high rank correlations between a faunal data matrix and a fixed sample Bray-Curtis similarity matrix. Cluster analysis for abundance was used to analyze station similarity using group averaging from a Bray-Curtis resemblance matrix. The SIMPROF test (Similarity Profile) detects the statistical significance of the internal structure at each node of the dendrogram. To further investigate potential assemblages across the shelf, stations were divided into three depth categories, shallow (≤ 25 m), mid-depth (26-100 m) and deep stations (101-220 m). Shallow stations depth range was determined by the extent of the ice scouring that occurs on the sea floor, up to 20-25 m in depth (Mahoney et al. 2007; Barnes et al., 1984). The deeper limit for the mid-depth stations was determined by the shelf break. The deep station category corresponded to the portion of the shelf slope sampled. Also, to investigate the potential difference in communities longitudinally along the shelf, stations were divided in two regional categories (east and west) determined by the cluster analysis and a spatial gap between stations. An ANOSIM (Analysis of Similarity) was performed on depth-region station groups to determine statistical significance of groupings. To determine the taxa representing each of these groups of stations, a BVSTEP analysis was performed separately with the abundance and biomass data. As a visual representation of the longitudinal distribution of selected taxa throughout the study area, a plot of BVSTEP selected taxa vs. longitude was constructed. For this graph, only stations with $\geq 2\%$ of the taxon's total biomass were included for each taxon selected. Shannon's diversity ($H' = -\sum P_i \log_2(P_i)$), Pielou's evenness ($J' = H'/\log_e S$) and Margalef's richness ($d = (S-1)/\log_e N$) indices were calculated from biomass for all stations standardized to area trawled and fourth-root transformed, using the DIVERSE routine in PRIMER. For these indices, analysis of variance between spatial and depth defined groups were calculated at a 95% confidence level and pairwise comparisons of means were calculated at 0.05 significance level using R and R-Commander (public access statistical software).

The BIOENV (Biological-Environmental Interactions) routine in PRIMER was used to identify environmental variables with the highest correlation with epibenthic community (Clarke and Gorley 2006). The normalized environmental variables included in these analyses in a Euclidean Distance resemblance matrix were:

- Sediment chlorophyll a and phaeopigment concentration, percent organic matter in surface sediments, surface sediments percent total organic carbon content (TOC), and

carbon to nitrogen ratio (C/N) as indicators of food supply and quality. Note: Sediment total organic nitrogen content (TON) was not included in the analysis as it correlates to TOC at a 95% confidence level.

- Bottom water chlorophyll *a* and phaeopigment concentrations were included as indirect indicators of food supply and quality.
- Sediment grain size including percent gravel, percent sand, percent mud (silt and clay), and percent sediment water content were included as habitat descriptors. Coarser substrates were grouped in four categories; 1: only fine sediments (including sticky anoxic clay), 2: cobbles, 3: boulders, 4: cobbles and boulders based on the Wentworth scale (1922). These were included as a proxy for habitat complexity and availability of hard substrate for taxa that require it for attachment.
- Bottom water salinity, temperature and pH were included as hydrographic descriptors.

For gear and site variability comparisons, the relative abundance data were analyzed using a one-way design with “gear type” or “trawl” as the factor levels using PERMANOVA+ from the PRIMER v.6 package (Clarke and Gorley 2006). The PERMANOVA analysis tests the simultaneous response of the variables to the factor in an analysis of variance type experimental design on the basis of the resemblance measure, using a permutation method (Anderson et al. 2008). In this analysis, the null hypothesis of no difference between the factor levels is determined by a pseudo-F ratio and permutation p-value (P(perm)) (Clarke and Gorley 2006).

Data Analysis: Objective 2

For objective 2, the following analyses were performed:

1. Cluster analysis using PRIMER v.6 was performed on the biomass data to determine if, and how, the Chukchi Sea sites compared to the Beaufort Sea sites,
2. The BEST procedure in PRIMER v.6 was used to determine which taxa were driving trends seen between the Chukchi and Beaufort Sea sites,
3. ANOSIM analysis in PRIMER v.6, using depth categories as factor levels, was used to examine statistical differences between the Chukchi and Beaufort Sea communities.

Results

Objectives 1 and 3

Across all stations, 154 taxa in nine phyla were identified including 55 mollusca, 30 echinodermata, 24 arthropoda, 14 cnidaria, 14 bryozoa, nine chordata, six porifera, one platyhelminthes, and one brachiopoda. The mean total abundance per station was 2,527 individuals/100 m² (s.d. 5,337), ranging from a total abundance of four individuals/100 m² at station WB30 to 27,433 individuals/100 m² at station WB04 (Figure 4a). The mean total biomass amounted to 3,656.54 gr/100 m² (s.d. 7,854), ranging from a total biomass of 5.75 gr/100 m² at station CB07 to 50,103.1 gr/100 m² at station WB04 (Figure 4b). The average number of taxa across all stations was 22 (s.d. 10) with the total number of taxa ranging from three at station

WB30 to 44 at station WB15. Of the total abundance across all stations, *Ophiura sarsii* represented 73.5% of all taxa, followed by *Ophiocten sericeum* with 6.4%, *Ophiacantha bidentata* with 4.2% and other Caridea with 1.1%. The individual abundance for all other taxa amounted to $\leq 1\%$ of the total abundance. For the total biomass across all stations, *Ophiura sarsii* represented 39.1% of all taxa, *Gorgonocephalus* spp. 15.4%, *Ctenodiscus crispatus* 11.1%, *Psolus fabricii* 4.4%, *Ophiacantha bidentata* 3.2% and *Strongylocentrotus pallidus* with 2.3%. The individual biomass of all other taxa amounted to $\leq 2\%$ of the total biomass.

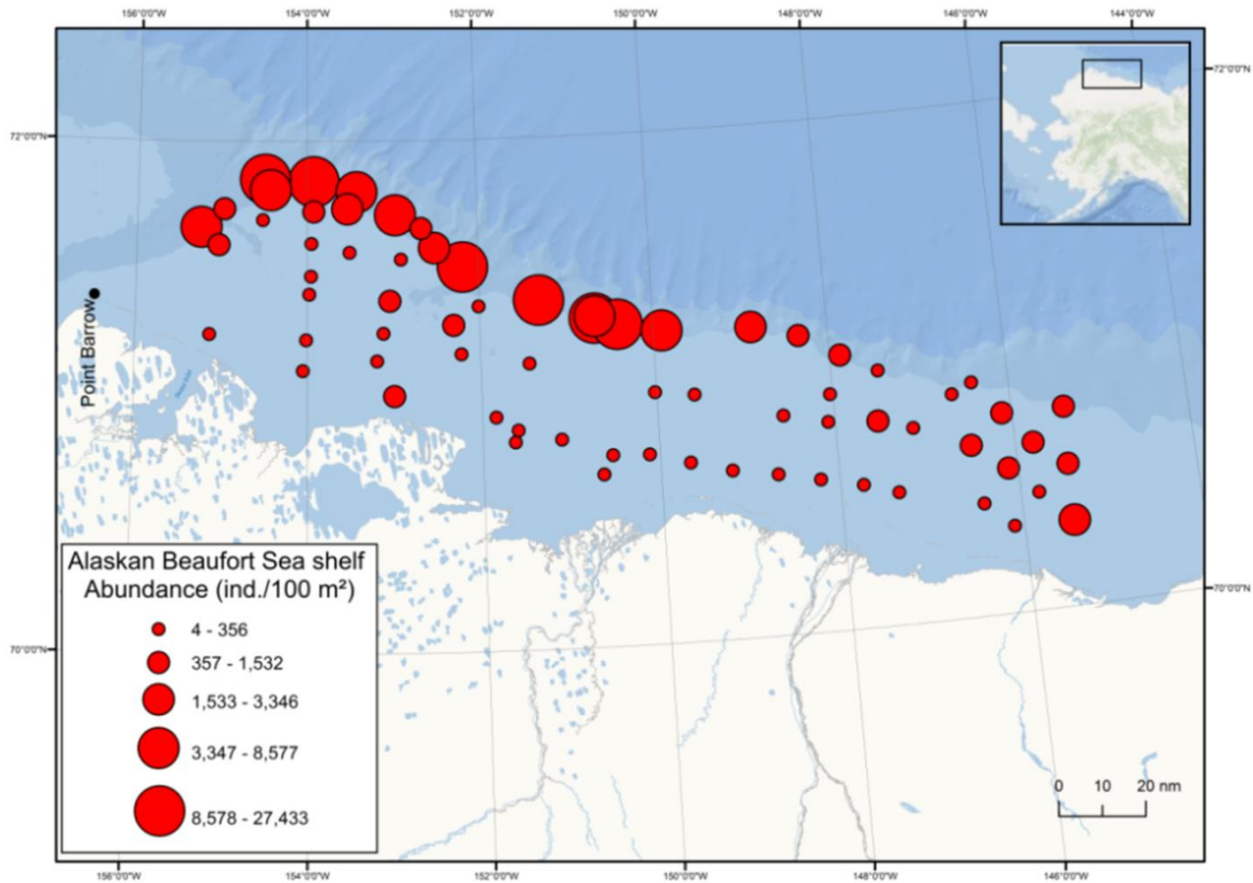


Figure 4a. Abundance of epibenthos. Stations are represented by scaled circles of total abundance (individuals/100m²) by station.

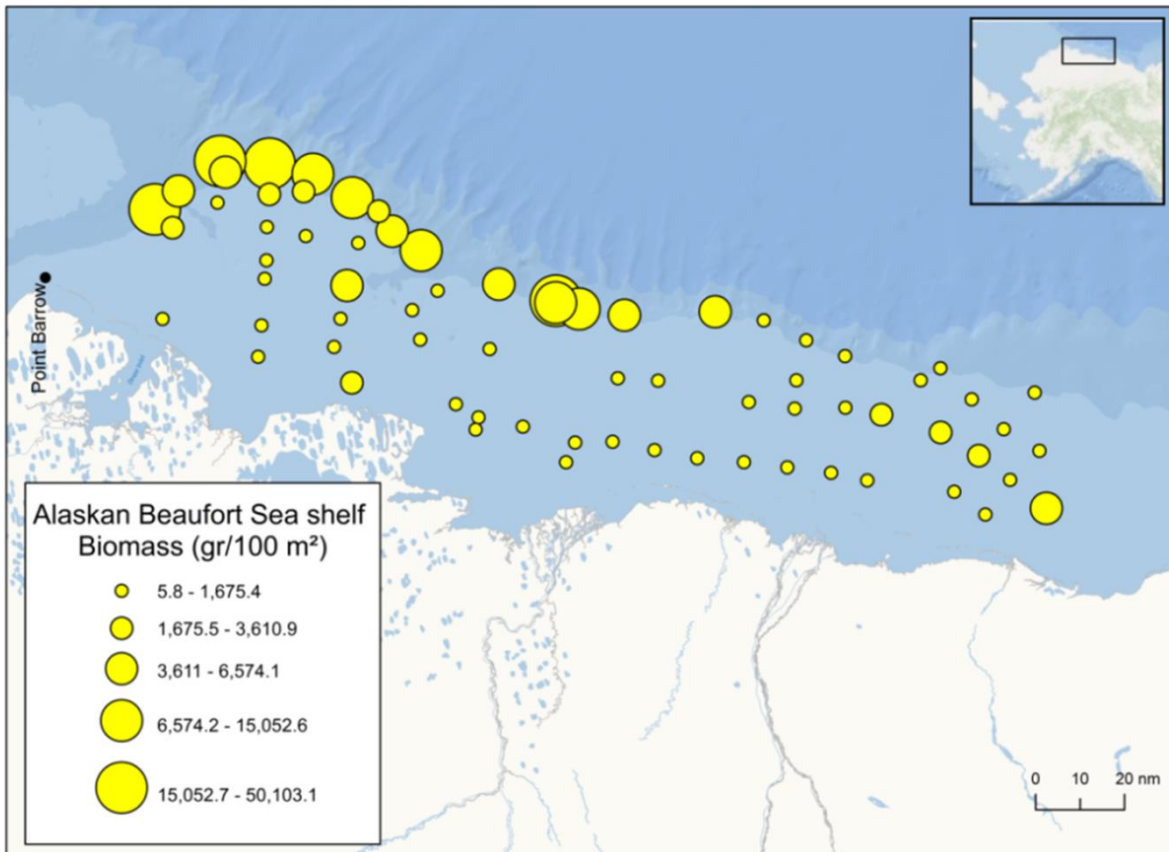


Figure 4b. Biomass of epibenthos. Stations are represented by scaled circles of total biomass (gram/100m²) by station.

Nine taxa best represented the epibenthic abundance across all stations, including the snail *Boreotrophon* spp., Amphipoda, the hermit crab *Pagurus* spp., the shrimp *Sabinea septemcarinata*, the isopod *Saduria entomon*, the shrimp category other Caridea, and the brittle stars *Ophiacantha bidentata*, *Ophiura sarsii*, and *Ophiocten sericeum* (BVSTEP Primer-e, Spearman correlation coefficient: 0.953 with 0.1% significance level; Figure 5a). Using biomass data, 11 taxa best represented the epibenthos in the study area. These taxa included the snail *Buccinum elatior*, Amphipoda, the hermit crab *Pagurus* spp., the shrimp *Sabinea septemcarinata*, the isopod *Saduria entomon*, the shrimp category other Caridea, the sea star *Ctenodiscus crispatus*, the brittle stars *Ophiacantha bidentata*, *Ophiura sarsii*, *Ophiocten sericeum*, and the sea urchin *Strongylocentrotus pallidus* (BVSTEP Primer-e, Spearman correlation coefficient: 0.910 with 0.1% significance level; Figure 5b).

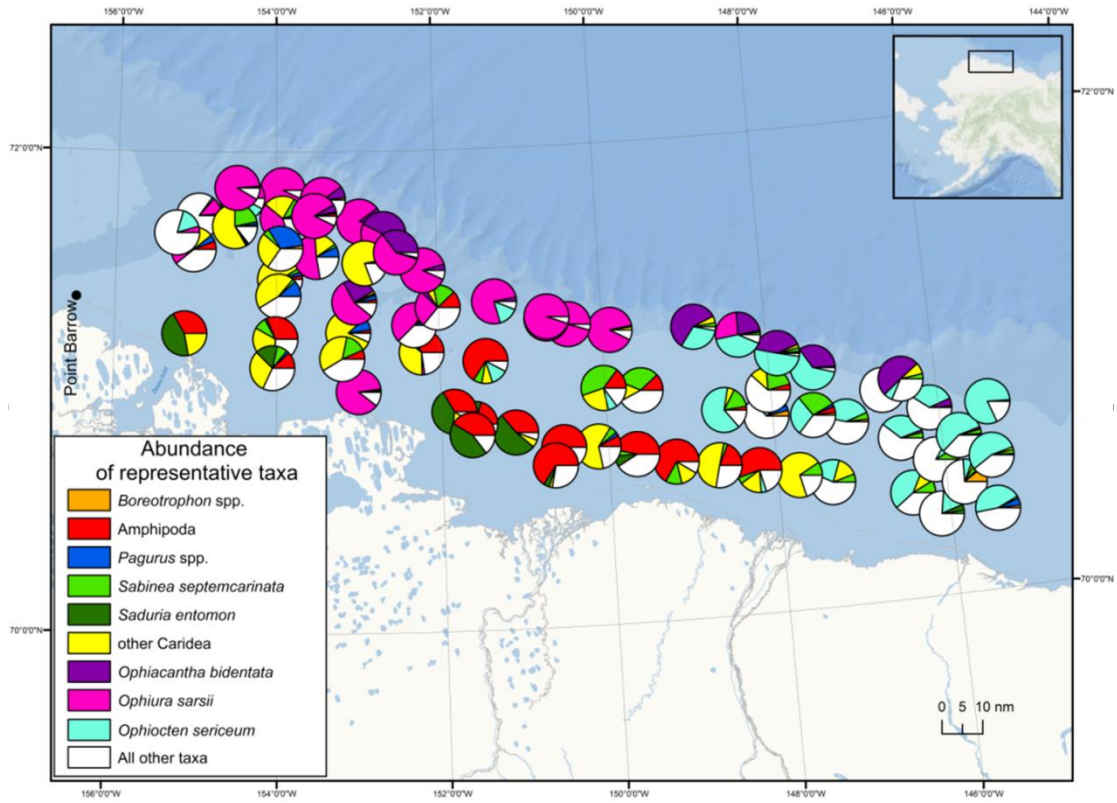


Figure 5a. Relative abundance of representative taxa. Taxa were selected by BVSTEP procedure.

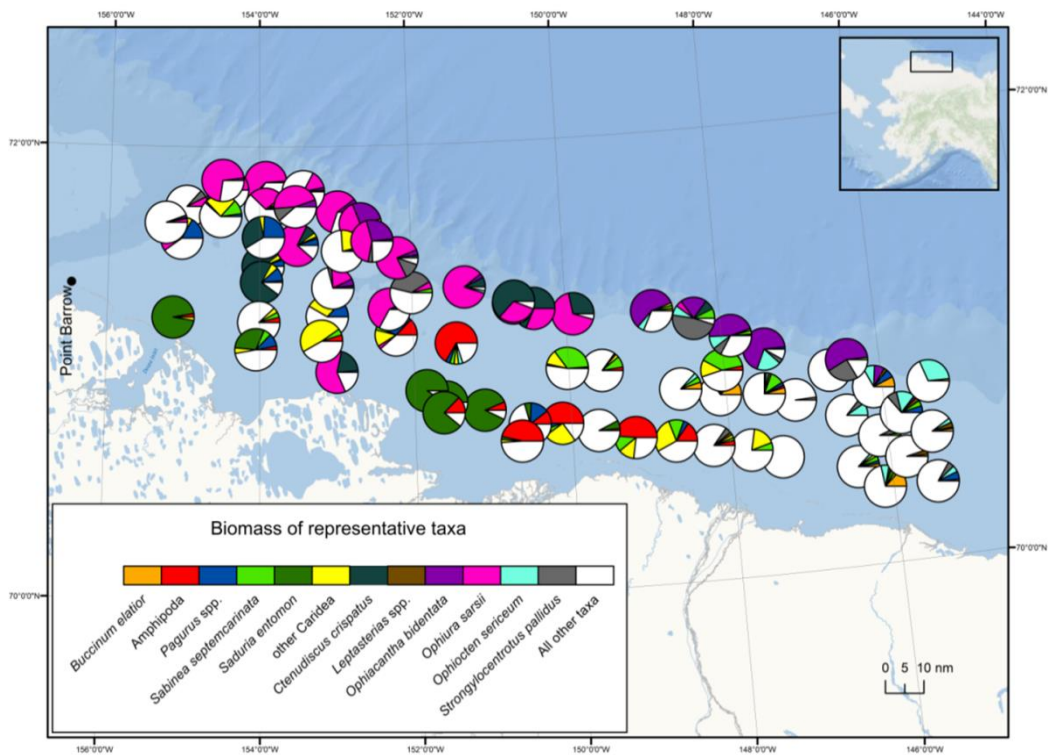


Figure 5b. Relative biomass of representative taxa. Taxa were selected by BVSTEP procedure.

Cluster analysis for abundance of all stations resulted in 12 statistically significant clusters and three independent stations determined by the SIMPROF test (Figure 6). The average similarity within clusters amounted to 63% (s.d. 11). Stations grouped by the cluster analysis had similar water depths and/or were located in close proximity of each other, indicating that depth and location are important in determining assemblages throughout the study area. To investigate the assemblages across the shelf, stations were grouped by depth categories (shallow, mid-depth and deep) in each region (east and west) (Figure 7). For details on grouping criteria, see the methods section.

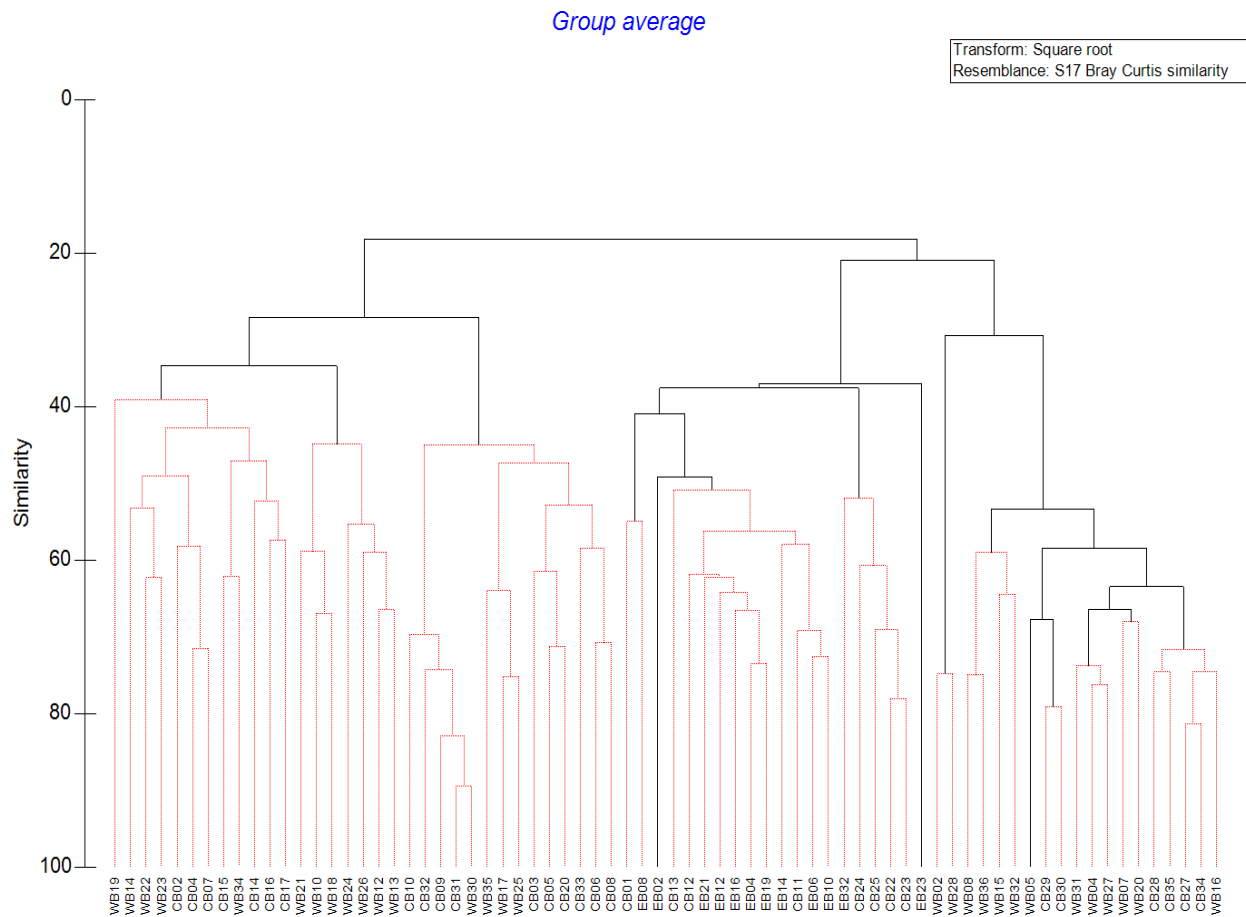


Figure 6. Dendrogram of the relative abundance of all stations. Cluster analysis of all stations based on a Bray-Curtis species resemblance matrix of relative abundance per trawl and square root transformed data. Red lines represent groupings with no statistical significance determined by SIMPROF test.

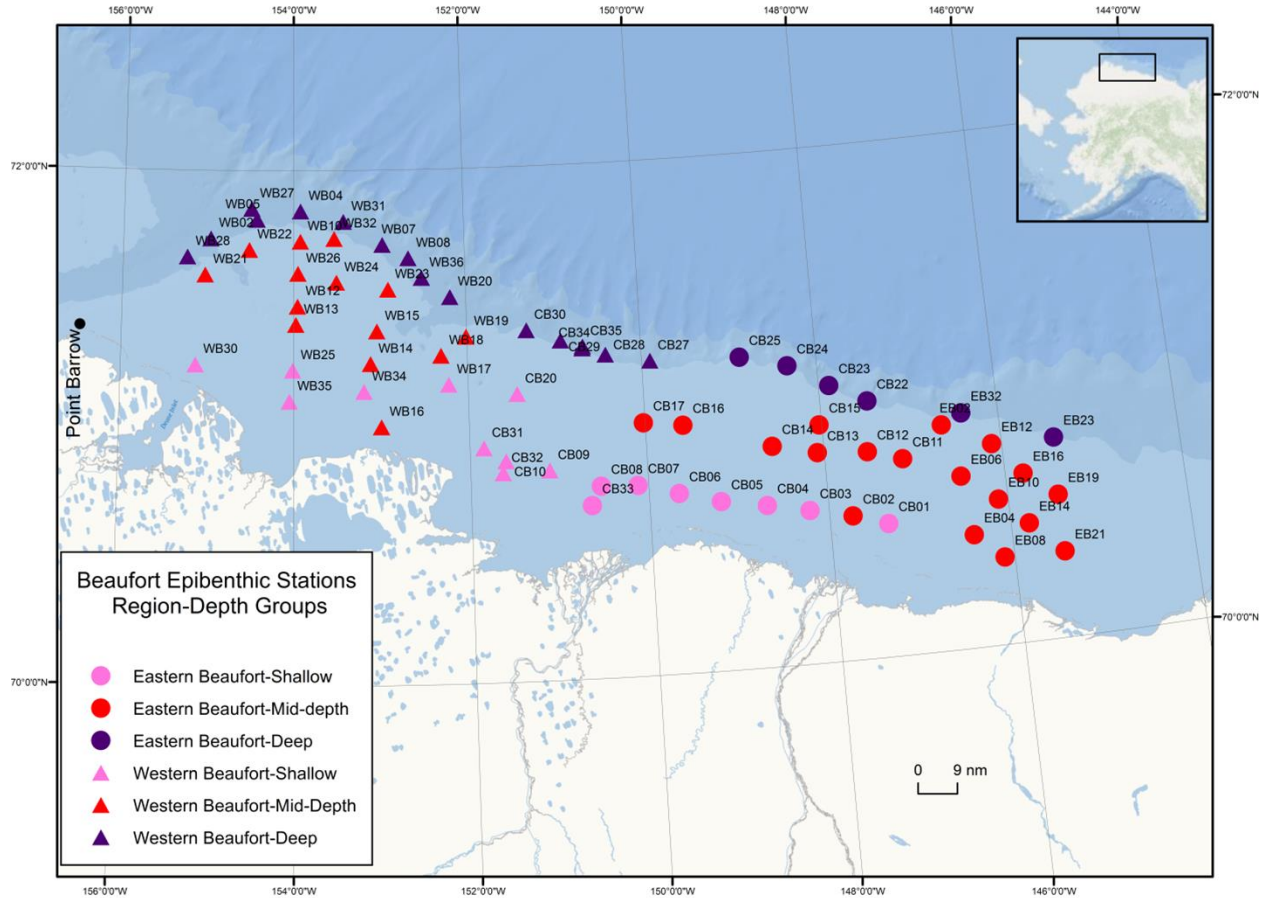


Figure 7. Region-depth groups of stations. Eastern stations symbolized by circles and western stations symbolized by triangles, depth category stations symbolized by colors.

A two-way crossed ANOSIM using depth category and region as factor levels revealed a moderately high difference between the two regions within each depth category (global R 0.687 with a significance level of 0.1%) and also a similar difference between depth categories within the same region (global R 0.694 at 0.1% significance level). A pairwise comparison between the three depth categories showed the overall largest difference between shallow and deep stations (Table 1).

Table 1. Depth categories pairwise comparison of means. Values derived from a two way crossed ANOSIM test using Primer 6.

Groups	R Statistic	Significance Level %
Shallow - Mid-depth	0.661	0.1
Shallow - Deep	0.975	0.1
Mid-depth - Deep	0.522	0.1

Diversity indices were calculated for all stations and then grouped by depth-region groups for analysis of variance (Table 2). Overall, Pielou’s index had high values for all station groups; this index indicates the evenness in abundance of each species present in the community. However, the one-way ANOVA was marginally significantly different among groups (p value: 0.046), with no significant difference among groups in the comparison of means test. It was, therefore, not possible to make inferences among station groups for this index. Shannon index of diversity ranges from 5.0 to 0.0, with values above 3.0 indicating that the habitat structure is stable and balanced. Values under 1.0 indicate degradation of habitat structure. The Margalef index has no limit value and its variation depends upon the number of species. One-way ANOVAs for Margalef and Shannon diversity indices showed high significant differences among groups (p values: 2.26e-6 and 1.14e-11 respectively). Pairwise comparison of means for these indices showed significant differences among depth groups within the same region and among different depths between regions; however, no significant difference was found in richness or diversity among longitudinal regions within the same depth category (Table 3). Overall, the shallow stations had the lowest mean values for Shannon index, Margalef index, and number of taxa (Table 2). Mid-depth stations in east and west Alaskan Beaufort had the highest means for Margalef index, diversity and number of taxa (Table 2). The deep stations had an intermediate mean Margalef index value in the eastern stations and a low mean in the westerns stations. The Shannon diversity index and the mean number of taxa were intermediate for east and west Alaskan Beaufort (Table 2).

Table 2. Diversity indices by region-depth group. Values presented are the means for the diversity indices and number of taxa by region-depth category group. Standard deviation is shown in parenthesis.

Group	<i>Index</i>			Number of taxa
	Margalef	Shannon	Pielou	
Western Shallow	7.64 (2.38)	1.92 (0.59)	0.94 (0.03)	9 (4)
Western Mid-depth	11.13 (1.16)	3.29 (0.14)	0.96 (0.01)	31 (5)
Western Deep	7.85 (1.85)	3.01 (0.35)	0.94 (0.02)	25 (7)
Eastern Shallow	7.98 (1.73)	2.33 (0.54)	0.96 (0.02)	13 (8)
Eastern Mid-depth	9.94 (1.24)	3.04 (0.32)	0.96 (0.02)	25 (8)
Eastern Deep	8.41 (1.41)	2.87 (0.13)	0.95 (0.01)	21 (3)

Table 3. Tukey test for the diversity indices of region-depth groups. The values presented are the significance level for the Tukey test between region-depth groups for Margalef's richness and Shannon's diversity index. Empty spaces indicate there is no significant difference between the two groups for that index.

Group	Index	
	Margalef	Shannon
Western Shallow - Western Mid-depth	<0.001	<0.001
Western Shallow - Western Deep		<0.001
Western Mid-depth - Western Deep	<0.001	
Eastern Shallow - Eastern Mid-depth		<0.001
Western Shallow - Eastern Mid-depth	0.01	<0.001
Western Shallow - Eastern Deep		<0.001
Western Mid-depth - Eastern Shallow	0.001	<0.001
Western Mid-depth - Eastern Deep	0.021	
Western Deep - Eastern Shallow		0.002
Western Deep - Eastern Mid-depth	0.01	

The correlation coefficients from the BVSTEP analysis by region-depth group using abundance and biomass data ranged from 0.928 to 0.982, with the significance level for most analyses at 0.1% (Table 4). The weak significance level in the eastern deep station group containing only six stations reduces the meaningfulness of the correlation value and the list of taxa selected. These taxa will therefore not be considered in the discussion as important representatives of the eastern-deep stations group. For abundance data in the western deep stations, the five taxa selected as best representatives were exclusively echinoderms. The mid-depth stations had the highest number of best representative taxa, representing three phyla. The shrimp *Spirontocaris* spp. and taxonomic group other Caridea were the only taxon in common among the regions for abundance. Shallow stations were best represented mostly by crustaceans and gastropods. Abundance data at these stations resulted in the most number of representative taxa shared by the east and west, including the isopods *Saduria sabinii* and *Saduria entomon* and Amphipoda (Table 4). For biomass deep stations in the west, five echinoderms resulted as the best representatives of the community. Mid-depth stations had the sea cucumber *Psolus* spp., the whelk *Neptunea* spp. and hermit crab *Pagurus* spp. and the taxonomic group other Caridea in common among regions. Similar to the abundance analysis, this depth category resulted in the highest number of taxa selected as representatives of the community in terms of biomass. Representatives from three phyla were selected for the biomass of shallow stations, with Amphipoda and Hydrozoa selected across regions (Table 4).

Table 4. Representative taxa for abundance and biomass of each region-depth group. Taxa were selected by BVSTEP (Biological Variables Stepwise Procedure) using Primer v6. Taxa in common in the same depth category across regions are in bold.

Group	Number of taxa selected	Correlation Value	Significance level (%)	Taxa
ABUNDANCE				
Eastern Shallow	6	0.959	0.1	<i>Boreotrophon</i> spp., Amphipoda , <i>Anonyx</i> spp., <i>Saduria entomon</i> , <i>Saduria sabini</i> , <i>Psolus</i> spp.
Eastern Mid-depth	11	0.958	0.1	<i>Boreotrophon</i> spp., <i>Buccinum elatior</i> , <i>Similipecten greenlandicus</i> , <i>Tachyrrhynchus</i> spp., <i>Sabinea septemcarinata</i> , other Caridea , <i>Spirontocaris</i> spp. , <i>Ophiacantha bidentata</i> , <i>Ophiocten sericeum</i> , <i>Psolus</i> spp. , <i>Stomphia</i> spp.
Eastern Deep	2	0.982	1.3	<i>Ophiacantha bidentata</i> , <i>Ophiocten sericeum</i>
Western Shallow	4	0.955	0.1	Amphipoda , other Caridea, <i>Saduria entomon</i> , <i>Saduria sabini</i>
Western Mid-depth	8	0.952	0.1	<i>Argis</i> spp., <i>Pagurus</i> spp. , other Caridea , <i>Spirontocaris</i> spp. , <i>Ctenodiscus crispatus</i> , Ophuroid 2, <i>Ophiura sarsii</i> , <i>Strongylocentrotus pallidus</i>
Western Deep	5	0.957	0.1	<i>Ctenodiscus crispatus</i> , <i>Ocnus</i> spp., <i>Ophioscolex glacialis</i> , <i>Ophiura sarsii</i> , Ophiuroid 1
BIOMASS				
Eastern Shallow	4	0.957	0.1	<i>Neptunea</i> spp., Amphipoda , <i>Sabinea septemcarinata</i> , Hydrozoa
Eastern Mid-depth	7	0.951	0.1	<i>Neptunea</i> spp. , <i>Similipecten greenlandicus</i> , <i>Sabinea septemcarinata</i> , other Caridea , <i>Pagurus</i> spp. , <i>Psolus</i> spp. , <i>Urasterias linckii</i>
Eastern Deep	5	0.957	7.4	<i>Chionoecetes opilio</i> , <i>Ophiacantha bidentata</i> , <i>Ophiocten sericeum</i> , <i>Strongylocentrotus pallidus</i> , <i>Stomphia</i> spp.
Western Shallow	7	0.947	0.1	<i>Margarites</i> spp./ <i>Solariella</i> spp., Amphipoda , <i>Hyas coarctatus</i> , <i>Saduria entomon</i> , <i>Pagurus</i> spp., <i>Spirontocaris</i> spp., Hydrozoa
Western Mid-depth	12	0.951	0.1	<i>Neptunea</i> spp. , <i>Hyas coarctatus</i> , <i>Pagurus</i> spp. , <i>Labidochirus splendescens</i> , other Caridea , <i>Ctenodiscus crispatus</i> , <i>Ophiura sarsii</i> , <i>Psolus</i> spp. , <i>Gersemia</i> spp., <i>Stomphia</i> spp. , Bryozoa, <i>Strongylocentrotus pallidus</i>
Western Deep	5	0.928	0.1	<i>Ctenodiscus crispatus</i> , Crionidea, <i>Gorgonocephalus</i> spp., <i>Ophiura sarsii</i> , <i>Strongylocentrotus pallidus</i> , <i>Stomphia</i> spp.

The distribution of the characteristic taxa varied across the shelf (Figure 8). Taxa that were present in the same depth category in the east and west Alaskan Beaufort for either abundance or biomass (i.e. *Saduria entomon*, *Saduria sabinii*, other Caridea, and other taxa in bold on Table 4) were not included in this graph, since the depth range at which they were selected seemed to be the strongest determinant of their distribution. The top nine taxa correspond to taxa characteristics of eastern stations and the following 15 correspond to taxa characteristic of western stations. Only three taxa selected as representatives of the community in the western stations were absent from all eastern study area stations. All other taxa were at least present in some small proportion at the eastern and western stations (western exclusive taxa are marked with an asterisk in Figure 8).

Environmental variables varied among regions and depths categories (Table 5). Overall, there was an increase from east to west in sediment organic matter, sediment chlorophyll *a*, sediment phaeopigments, percent gravel, percent mud, sediment water content, sediment TOC, TON and C/N, and bottom water salinity. There was a decrease in mean values from east to west in mean sediment categories and percent sand. There was an increase with depth in the east and the west for the mean values of sediment organic matter, sediment phaeopigments, percent gravel, percent mud, sediment water content, sediment TOC and TON, and bottom water salinity. There was an overall decrease with depth in the mean values of percent sand, sediment C/N and bottom water pH.

The BIOENV analysis was completed on data from 55 stations. Sixteen stations had missing environmental measures and were excluded from analysis. The BIOENV analysis resulted in a moderate to low correlation of the environmental variables examined with the relative abundance and biomass of all taxa in the trawls. For abundance, the combination of five variables had the highest correlation coefficient of 0.46 and a significance level of 0.1%. These variables were (in order of importance), bottom water salinity, sediment phaeopigments, bottom water temperature, percent organic matter, and sediment C/N; with the option of bottom water pH as an alternative for the last variable at the same correlation value. For biomass, the variables selected were (in order of importance) sediment phaeopigments, sediment C/N, percent sand, bottom water salinity and bottom water temperature at a correlation value of 0.43 and 0.1% significance level.

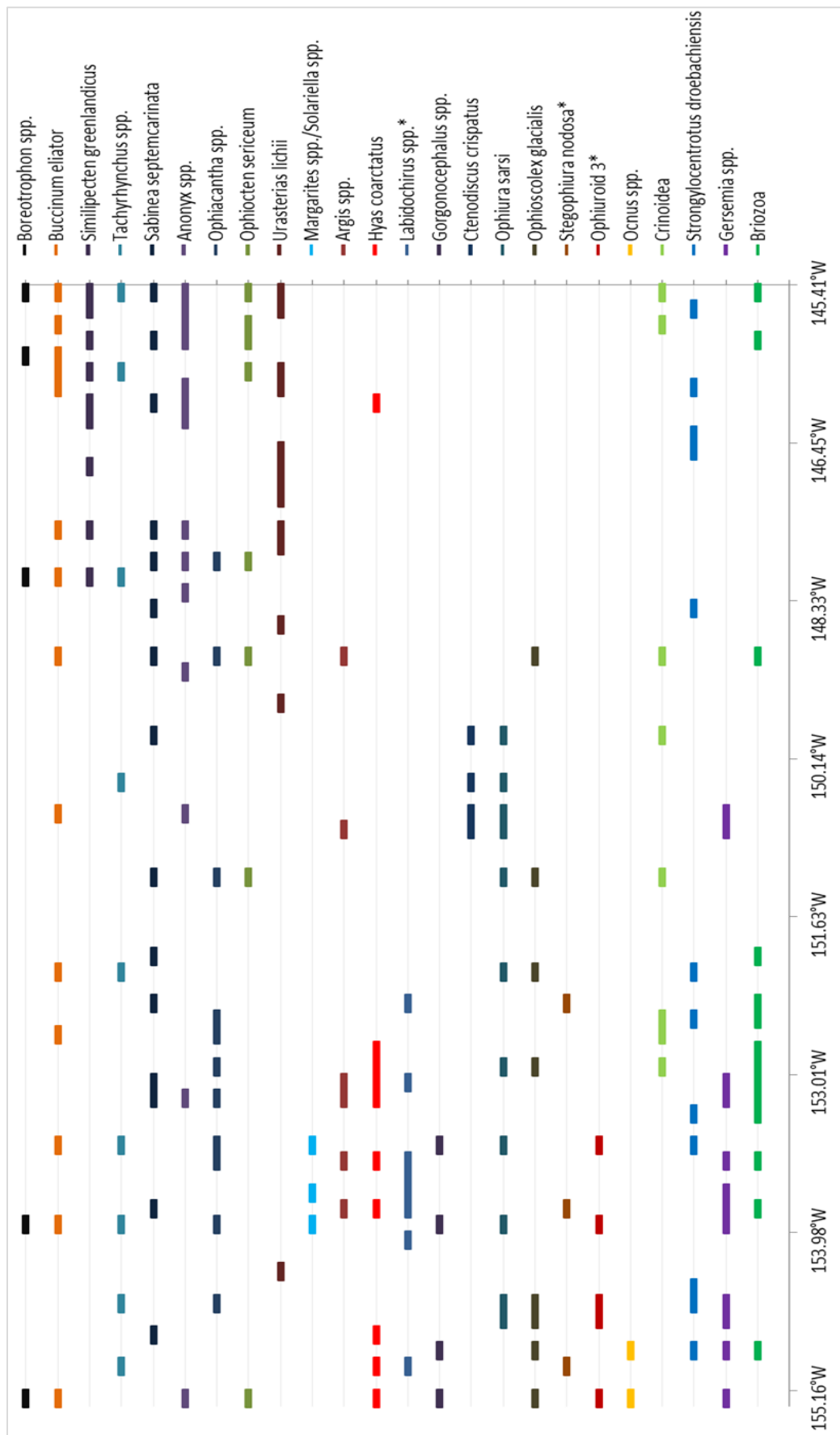


Figure 8. Longitudinal distribution of selected taxa. Range of distribution along the longitudinal extent of the study area for taxa selected in the BVSTEP analysis by region-depth groups. Only stations with $\geq 2\%$ of the taxa's total biomass were included. Taxa symbolized with an asterisk were only present on the western side of the study area.

Table 5. Mean value of environmental parameters for each region-depth group. All parameters were included in the BioEnv (Biological-Environmental Interactions) analysis using Primer v6. SD: Standard deviation.

Environmental Variables	Western Beaufort						Eastern Beaufort					
	Shallow		Mid-Depth		Deep		Shallow		Mid-Depth		Deep	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Number of Types Sediment	1.20	0.4	1.64	0.8	1.44	0.5	2.38	1.3	2.22	1.0	2.33	0.7
Sediment organic matter (% dry weight)	3.34	1.5	4.35	0.9	6.30	2.4	3.70	2.4	3.06	0.7	4.36	0.9
sediment chlorophyll <i>a</i> ($\mu\text{g}/\text{cm}^2$)	2.18	2.4	2.31	1.2	4.25	1.5	2.27	2.0	2.56	1.2	1.81	1.1
sediment phaeopigments ($\mu\text{g}/\text{cm}^2$),	1.64	0.8	4.99	1.8	7.62	3.1	1.76	2.1	4.16	2.1	5.32	2.5
gravel (%)	0.62	1.7	6.46	13.5	8.55	17.4	2.74	5.3	16.14	22.1	23.96	26.5
sand (%)	35.50	31.5	23.65	12.4	17.53	7.6	38.99	26.9	33.67	13.9	20.94	12.6
mud (%)	63.67	31.1	69.65	17.8	73.63	21.2	58.09	29.4	48.47	21.4	48.32	26.1
sediment water content (%)	31.74	7.3	41.30	9.1	47.72	11.1	25.99	7.3	34.75	13.2	36.64	5.5
sediment total organic carbon (%)	0.14	0.1	0.16	0.0	0.17	0.1	0.09	0.1	0.12	0.1	0.15	0.0
sediment total organic nitrogen (%)	1.47	0.7	1.44	0.4	1.54	0.4	0.91	0.8	0.93	0.4	1.24	0.1
carbon to nitrogen ratio	10.15	1.9	9.34	0.7	8.97	0.6	10.31	2.5	8.39	1.4	8.42	0.5
bottom water temperature ($^{\circ}\text{C}$)	3.17	0.9	2.95	1.4	-0.34	0.6	1.13	0.8	-0.39	1.1	0.03	0.7
bottom water pH	8.20	0.0	8.19	0.0	8.01	0.1	8.21	0.1	8.12	0.1	8.08	0.0
bottom water salinity	31.34	0.2	31.65	0.3	33.82	0.8	31.60	0.1	31.84	0.3	34.24	0.9
bottom water chlorophyll <i>a</i> ($\mu\text{l/l}$)	0.29	0.2	0.22	0.2	0.11	0.1	0.59	0.7	0.66	0.7	0.11	0.1
bottom water phaeopigments ($\mu\text{l/l}$)	0.16	0.1	0.10	0.1	0.12	0.1	0.36	0.4	0.34	0.3	0.07	0.1

The PERMANOVA analysis for the five stations trawled using both gear types (PSBT and PSBT-A) showed no significant difference in gear performance for the abundance and biomass data (Tables 6a and 6b). This result allowed for the inclusion of all stations in the community analysis, regardless of the gear type used. It should be noted that only the first sample of each station was included in the general data analysis. Epifaunal abundance and biomass at the six revisited stations was not significantly different between the repeat trawl hauls (Tables 7a and 7b).

Table 6a. PERMANOVA analysis of the epibenthic abundance collected for gear comparisons. The term P(perm) reflects significant evidence to not reject the null hypothesis of no difference between samples collected using the plum staff beam trawl and the modified version. df: degrees of freedom, SS: sum of squares, MS: mean squares, Pseudo-F P(perm): permutation p value

Source	df	SS	MS	Pseudo-F	P(perm)
Gear Comparison	1	394.33	394.33	0.16294	0.9922
Residuals	8	19360	2420.1		

Table 6b. PERMANOVA analysis of the epibenthic biomass collected for gear comparisons. The term P(perm) is showing significant evidence to not reject the null hypothesis of no difference between samples collected using the plum staff beam trawl and the modified version. df: degrees of freedom, SS: sum of squares, MS: mean squares, Pseudo-F P(perm): permutation p value.

Source	df	SS	MS	Pseudo-F	P(perm)
Gear Comparison	1	723.25	723.25	0.24642	0.9908
Residuals	8	23480	2935		

Table 7a. PERMANOVA analysis of the epibenthic abundance collected at revisited stations. The term P(perm) is showing significant evidence to not reject the null hypothesis of no difference between samples collected using the same gear types at the same site. df: degrees of freedom, SS: sum of squares, MS: mean squares, Pseudo-F P(perm): permutation p value.

Source	df	SS	MS	Pseudo-F	P(perm)
Site variability	1	434.02	434.02	0.21073	0.8679
Residuals	10	20596	2059.6		

Table 7b. PERMANOVA analysis of the epibenthic biomass collected at revisited stations. The term P(perm) is showing significant evidence to not reject the null hypothesis of no difference between samples collected using the same gear types at the same site. df: degrees of freedom, SS: sum of squares, MS: mean squares, Pseudo-F P(perm): permutation p value.

Source	df	SS	MS	Pseudo-F	P(perm)
Site variability	1	645.03	645.03	0.23959	0.9856
Residuals	10	26922	2692.2		

Objective 2

The Chukchi Sea had 17 times higher average biomass ($62.7 \text{ kg/m}^2 \pm 99.4$) than the Beaufort Sea ($3.6 \text{ kg/m}^2 \pm 7.8$). Stations with highest biomass were located on both sides of Barrow Canyon and along the slope of the Beaufort shelf (Figures 9). Similar high catch per unit effort values were recorded for fish, snow crab and brittle stars in the same area during the NOAA 2008 trawl survey (Logerwell et al. 2011).

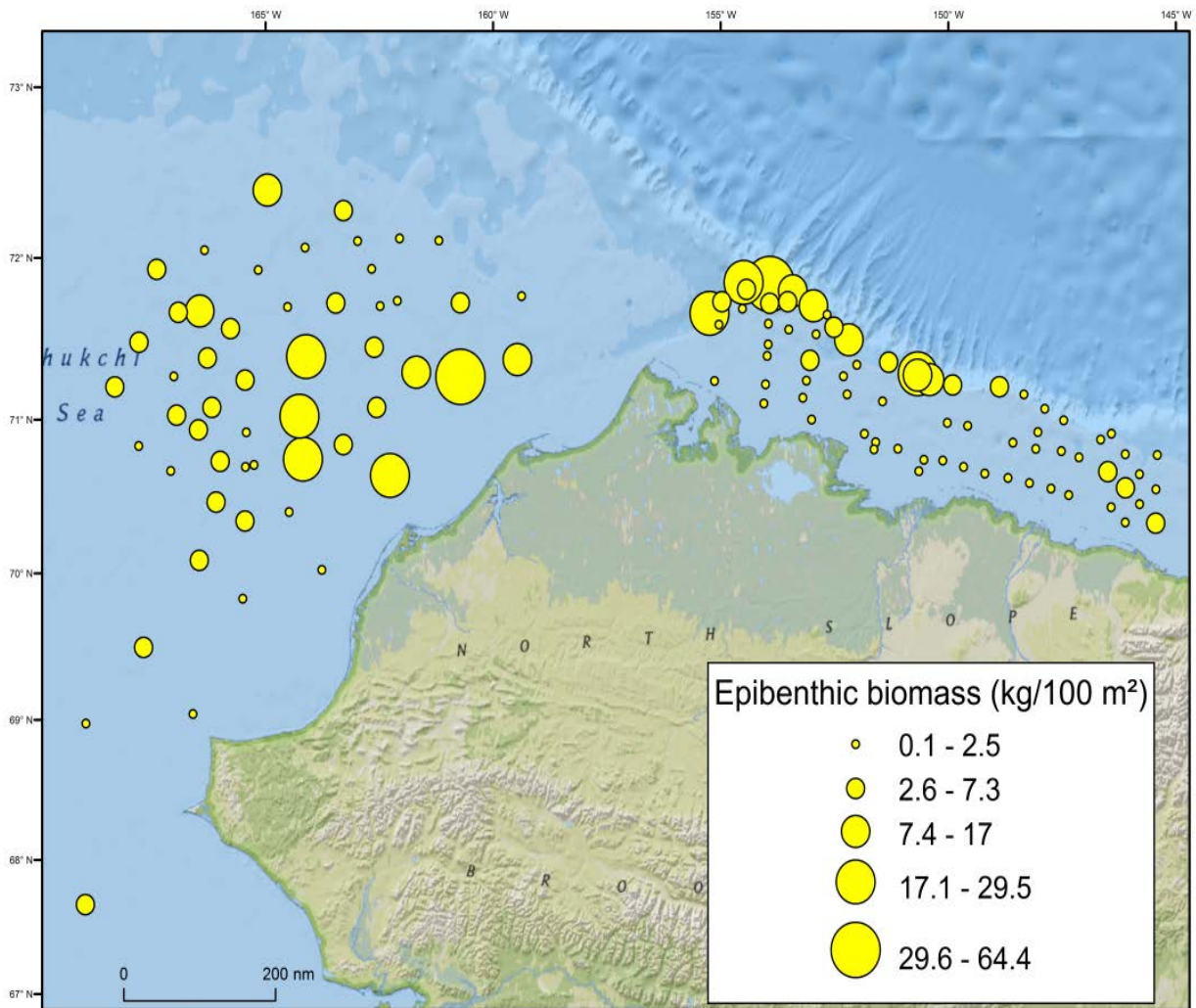


Figure 9. Total epibenthic biomass by station. The size of the circles represents total kilograms of organisms, in 100 m^2 .

Across regions, stations were dominated by either ophiuroids or crustaceans (Caridea, *Chionoecetes opilio* and Paguridae). The ten taxa selected as important representatives of the community in the BEST analysis were (in order of importance) the snow crab *Chionoecetes opilio*, the brittle star category Ophiuroidea, the hermit crab family Paguridae, the isopod genus *Saduria* spp., the shrimp Caridea, the gastropod family Buccinidae and genus *Neptunea* spp.,

the sea stars *Urasterias lincki* and *Ctenodiscus* spp. and the sea cucumber *Psolus* spp. Also, *Urasterias lincki* was encountered exclusively in the Beaufort region (Figure 10). Despite these taxonomic differences there was a low difference between regions in the ANOSIM test (R value 0.23 at a significance level of 0.1%).

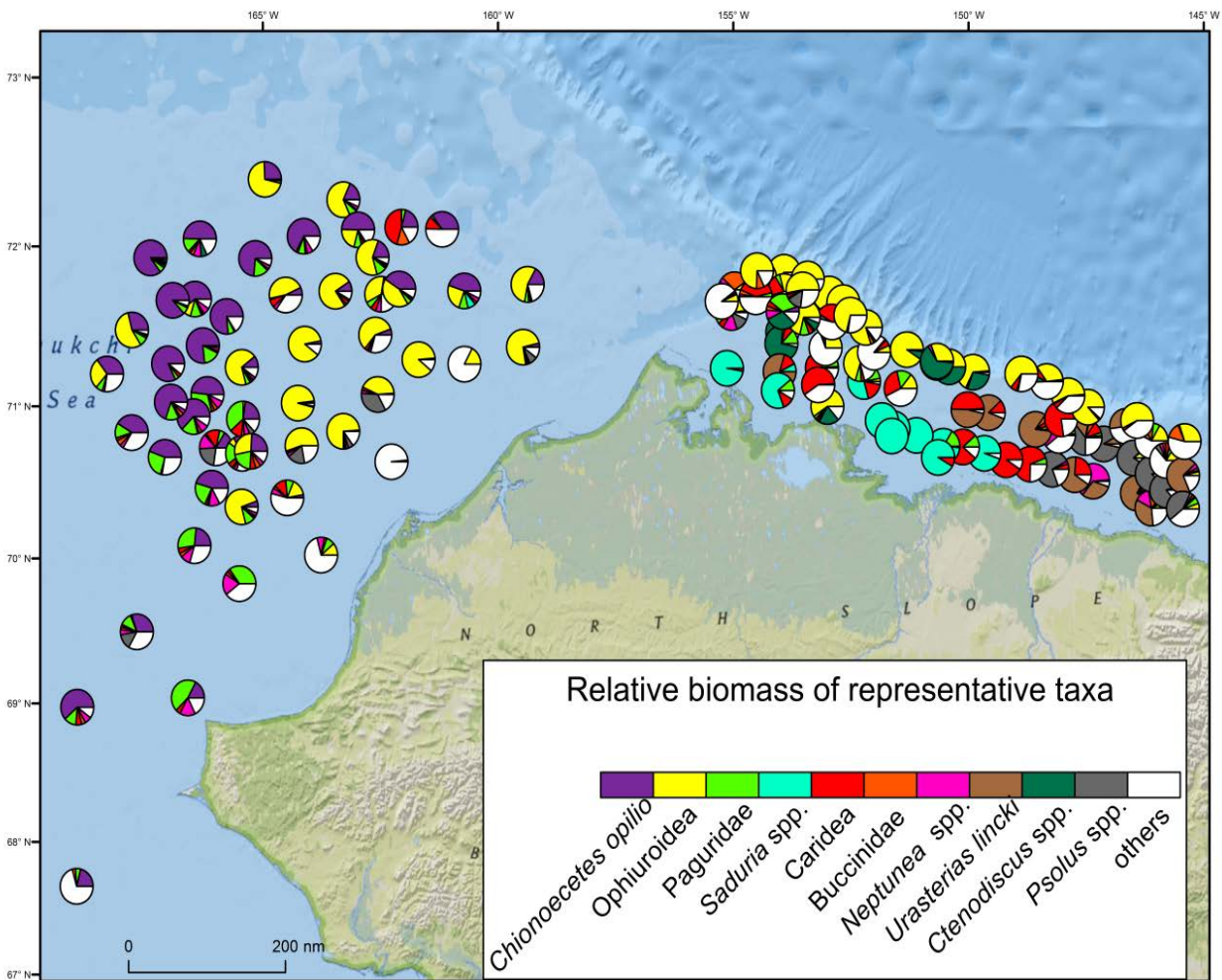


Figure 10. Distribution and relative biomass of representative taxa. The portion of the pie chart represents the relative biomass of each taxa for that station.

In the cluster analysis, stations were segregated by depth category (Figure 11). However, there was an overall low similarity among stations of the same depth category and stations from the same depth category of the two regions did not cluster together (Figure 11). This low similarity was also reflected in the moderate values obtained when using depth category as a factor level (R values for biomass from the ANOSIM test 0.51, at a significance level of 0.1%). While the Beaufort slope stations were dominated by ophiuroids, crustacean dominated at shallower stations. Segregation among ophiuroid and crustacean dominated stations in the Chukchi Sea was not associated to changes in depth (Figure10).

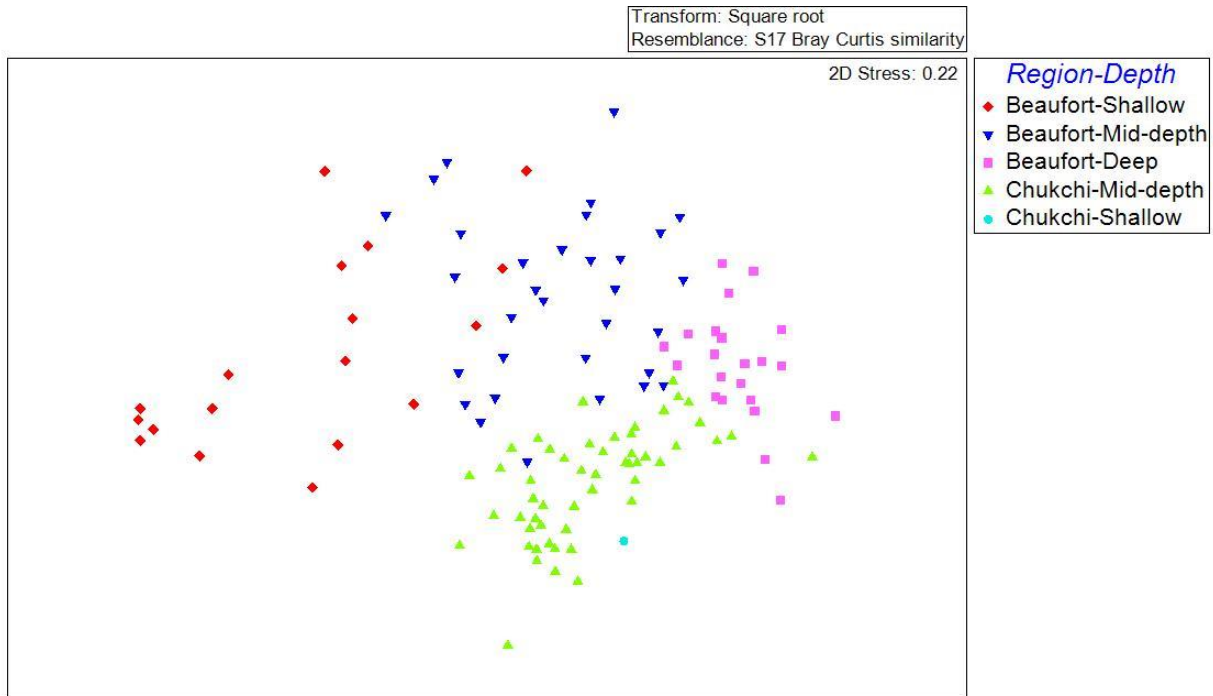


Figure 11. Multi-dimensional scaling plot (MDS) for epibenthic biomass. The proximity of the symbols in the plot reflects the level of similarity in the biomass of the taxa present at each station. The different symbols represent the region and depth category to which the station corresponds.

Discussion

Region-Depth Groups

Prior to the data collection, for logistic purposes and based on previous research efforts, the Beaufort shelf study area was divided longitudinally into three regions (east, central and west). The central area, ranging from 147.06° W to 151.84° W, was set as the first priority and possibly the only area to be sampled during the research cruise. It was based on these coordinates that the original project proposal and objectives were designed. Since we were able to extend the sampled area to the western and eastern Alaskan Beaufort (priority regions 2 and 3, respectively) during the cruise, all of the stations were included in the analysis (now 145.09° W to 155.25°W). This range extension showed a unique regional division in the epibenthic communities along the Alaskan Beaufort shelf, segregating station to eastern and western, at approximately 150° W.

Most taxa had a wide longitudinal distribution throughout the study area; however, the dominance of taxa changed greatly from east to west. The dominant ophiuroid species changed along the shelf, going from eastern stations dominated by *Ophiocten sericeum* and *Ophiura sarsii* being absent, to the western stations with *Ophiura sarsii* being dominant and *Ophiocten sericeum* being largely absent. In the Chukchi Sea, many studies have reported that the single most abundant brittle star was *Ophiura sarsii* (Ambrose et al. 2001; Feder et al. 2005; Bluhm et

al. 2009; Ravelo et al. submitted). In this study, the dominance of *Ophiura sarsii* over all other ophiuroids, and in many stations over all other taxa, was observed only at the western slope of the Beaufort Sea.

In the eastern end of the study area, the dominance of *Ophiecten sericeum* at the mid-depth stations and *Ophiacantha bidentata* at the deep stations coincided with the pattern described in the Northern Barents Sea. In that region, *Ophiecten sericeum* dominated in shallower waters (<150 m) and *Ophiacantha bidentata* was dominant at the deeper stations (150-360 m) (Piepenburg and Schmid 1996). These three dominant ophiuroids differ greatly in size (*Ophiura sarsii* is larger than *Ophiacantha bidentata*, which is larger than *Ophiecten sericeum*) and the change in their dominance throughout the shelf could be a reflection of the changes in food quantity and quality. The change in dominant taxa along the shelf was evident for other taxa such as the small translucent scallop *Similipected greenlandicus*, which dominated in abundance in the eastern stations but beyond longitude 150°W, had an accumulative biomass of 0.3% of the total biomass. This concurs with the 1976-77 survey that reported this species as absent beyond 150° W longitude (Frost and Lowry 1983). The brittle stars *Stegophiura nodosa*, ophiuroid 1 and the hermit crab *Labidochirus splendescens* were the only taxa selected as important that did not occur east of 150°W.

In the 2008 western Beaufort survey, the snow crab *Chionoecetes opilio* was the second most abundant benthic invertebrate after ophiuroids, with the highest CPUE (catch per unit effort) found at the 100 to 500 m depth range (Rand and Logerwell 2011). In our study, snow crabs were encountered at deeper stations along the shelf, but not consistently throughout the slope and never in high abundance. The shallowness of Beaufort's continental shelf ends with a steep slope that goes from 50 m in depth at the shelfbreak to 2500 m in less than 100 km. Considering that this study did not sample deeper than 220 m, it is likely that only the edge of their distribution was sampled and thus the high abundances reported previously were not found. In concordance with the 2008 survey in the western Beaufort, ophiuroids were the most abundant taxa followed by the "other Caridea" (shrimp unidentified).

Across the shelf and depth gradients, epifaunal communities showed significant differences in taxonomic composition, abundance and biomass. These findings support our first hypothesis that Alaskan Beaufort Sea shelf epibenthic communities are distributed across a depth gradient and are dominated by distinct taxonomic groups. Epibenthic communities in the Arctic are dominated by certain taxa over large spatial scales until changes in key environmental drivers interrupt their distribution (Piepenburg 2005; Ravelo et al. submitted). The patchiness in the communities was also reflected in the changes in average diversity values for each region group. Changes in diversity along an environmental gradient are termed beta diversity, as

opposed to gamma diversity, which denotes the different kinds of communities within larger geographic regions. In our analysis, changes in beta diversity were observed along a depth gradient (shallow, mid-depth and deep stations) and gamma diversity was observed longitudinally along the shelf (eastern and western Alaskan Beaufort); however no clear tendency of increased diversity was observed in either case. The trawl survey performed in the 1970s also found that species were limited in their distribution within depth zones (Carey et al. 1974). From the ANOSIM test among regions and depth categories, the largest correlation value was among depth categories; however, when analyzing the selected taxa by region-depth groups, there were only a few representative taxa in common among the same depth categories across regions. This stresses the importance of the variability in representative taxa across the shelf. From the taxa selected for each region-depth group, a few noticeable characteristics were that the shallow stations were mostly represented by the class Malacostraca, the mid-depth stations had the highest number of taxa and taxonomic groups selected, and the deeper stations were almost exclusively represented by echinoderms.

Environmental Drivers

The second hypothesis of this study, that a set of environmental parameters would explain the epibenthic community variability, was partially supported by our analysis. Correlation values of the included parameters to the abundance and biomass data resulted in moderate-low values (correlation value ≤ 0.5 with 0.1% significance level). Of the sediment parameters selected as important (phaeopigments, percent organic matter, C/N ratios and percent sand), sediment phaeopigment measurements were included as a proxy for the quality or “freshness” of the surface sediment chlorophyll content. There was an increase of these values in the east and western stations with water depth, indicating an increase in deposited phytodetritus, thus an increase of offshore phytoplankton production in the overlaying waters. However, this trend was not observed for the sediment chlorophyll *a* content. Sediment phaeopigment values were expected to be higher than the sediment chlorophyll *a* values. This held true for mid-depth and deep stations but not for the shallow stations to the east and west. The sediment C/N ratios have been used as a reflection of food quality advected to the benthos (Iken et al. 2010). The mean values presented (Table 5) were within the range of values published for this region and show the expected trend of lower values at the deeper stations and increasing towards the shallow stations (Naidu et al. 1975; Naidu et al. 2000). Along with an increase of organic matter in the sediments with depth, the C/N ratios indicate an increase in food quality as well, reflecting the higher carbon originated from riverine input close to shore and the higher oceanic nitrogen export to the benthos offshore.

Although percent of sand in the sediments was the only grain size parameter selected as important, there was a higher percentage of mud on the western side of the study area than on

the eastern side at all depth categories. These high percent mud values were also noted by earlier studies in the western Beaufort shelf and were attributed to the many low gradient rivers exporting high mud content to the shelf (Naidu et al. 1975). Also, the prevalent currents over the shallow shelf have an east to west direction, carrying finer size sediment particles imputed from the Colville River further to the west (Dunton et al. 2006). A higher percent gravel composition was found at the deeper stations. This could be a result of ice-rafting and the reworking of the sediments through long periods of time (Naidu et al. 1975). The percent sand composition was higher at the nearshore locations where the river has a direct influence over the region, depositing medium size entrained particles (Naidu et al. 1975). In other Arctic regions, studies have highlighted the importance of sediment grain size as a factor influencing species distribution and taxonomic richness (Feder et al. 1994; Mayer and Piepenburg 1996; Bluhm et al. 2009). In this study, the area with the highest percent sand values were also the most impoverished in terms of taxonomic diversity, abundance and biomass. These stations were dominated by isopods and amphipods, highly mobile scavengers that can take advantage of the high sediment deposition and re-suspension in this area (Macdonald et al. 2010; Dunton et al. 2012). The mid-depth stations had intermediate sediment percent values for mud, sand and gravel. These stations also had the highest diversity values and the highest number of taxa selected from the BVSTEP analysis.

The substrate categories included in the BIOENV analysis as a proxy of habitat complexity did not result in an important descriptor of the epibenthic communities. Large boulders and clusters of rocks offer an attachment surface for sponges and colonial sessile organisms, which in time offer refuge to smaller organisms and new recruits. In other regions, indicators of habitat complexity have been correlated to epibenthic community variability and directly correlated to higher diversity. For example, changes in community structure were visually correlated with increase rock counts in photographic surveys off the east of Greenland, despite the lack of statistically significant values resulting from the BIOENV analysis (Mayer and Piepenburg 1996). This lack of correlation was also true for this study, where we found no correlation among the habitat complexity indicators. However, at the mid-depth stations we observed an increase in the average diversity index values that coincided with the intermediate values for mud, sand and gravel. This repeated lack of correlation between community structure and the measurements of habitat complexity highlights the need to review our classification method and perhaps include video surveys along with the trawl samples to obtain more comprehensive information about epibenthic communities and the specific environments they inhabit.

The area around Barrow Canyon has been highlighted in other research as a hotspot for benthic fauna (Grebmeier, personal communication). The highest biomass and abundance stations

were concentrated close to Barrow Canyon and followed the shelf slope but then diminished towards the east. Also, there was a small group of stations with relatively higher abundance at the eastern end of the study area. The high abundance and biomass on the slope (> 100 m depth) on the western portion of this study area coincides with the higher CPUE for a number of benthic fish species encountered in a previous 2008 western Beaufort survey (Rand and Logerwell 2011). In that survey, high benthic abundance was associated with cold, nutrient rich water that traveled through the Chukchi shelf and then was advected through Barrow Canyon onto the Beaufort slope (Logerwell et al. 2011). Along with the enhanced nutrients flowing over the slope, upwelling can bring nutrients from deeper waters, stimulating higher local benthic abundance and biomass along the slope. However, there was a reduction in abundance and biomass along the slope moving east. This highlights the prevailing influence of the water advected through Barrow Canyon onto the slope, rather than the impact that the upwelling events may have along the slope (Weingartner, personal communication). In concordance with the 2008 survey, the western deep stations of this study were among the highest average salinity and lowest temperature of the six region-depth station groups. Moving eastward along the slope, the mid-depth eastern stations showed the same signature of cold water that the western deep stations had, with a mean salinity still within the range of the cold halocline. The deep eastern stations had the highest mean salinity, which is characteristic of the deep Atlantic waters that move eastwards along the deeper slope. Evidence from early drifter data from the eastern Alaskan Beaufort shelf suggested a divergence in water movement (Barnes et al. 1987; Reimnitz et al. 1988). This theory was also supported by the direction of the ice scouring over the shelf's sediments, which show gouges in a northeast to southwest direction semi-parallel to the coast on the Alaskan side. In contrast, sediment gouges on the Canadian side show a northwest to southeast direction, suggesting a divergence in the water circulation (Reimnitz et al. 1988). Divergence could explain the presence of colder saline water over the shelf that is characteristic of the 150 meter halocline. Also, the higher abundance observed at the mid-depth eastern stations could be a reflection of the changes in water movement adjacent to this area, due to the upwelling of colder nutrient rich waters. Incorporating biological and environmental data from further east along the shelf and slope would aid in explaining the cause of the increased epibenthic abundance but not the higher biomass of this area. It would also clarify how far east this very abundant epibenthic community extends.

The stations with the lowest abundance and biomass in the study area corresponded to the shallow stations of the east and west. The nearshore area of the Beaufort shelf is highly influenced by the drainage of many rivers, affecting benthic communities by increasing turbidity in the water column, increasing terrigenous nutrients, smothering, etc. (Carmack and Macdonald 2002; Dunton et al. 2006). In the shallow areas of the Beaufort shelf, the seafloor is affected every winter by ice scouring, particularly where land fast ice meets with pack ice

creating pressure ridges and forming deep draft-ice keels that scour the seafloor. The largest density of gouging was reported at 17 meters of water depth (Reimnitz and Kempema 1984). In addition to gouging, the ice keels create a barrier for water movement, trapping the nearshore environment and making the riverine influence even greater. Considering the environmental stress characteristics of shallow regions in the Beaufort shelf (± 25 m), it becomes apparent that many organisms that are slow growing, sessile or of limited mobility, might find it too challenging to prosper in large abundances. With this in mind, it is reasonable that at shallow depths, mobile crustaceans, such as the isopods *Saduria entomon*, *Saduria sabini*, and many species within the order Amphipoda and infraorder Caridea, dominated the community in terms of abundance.

Gear Comparison

Seldom do researchers have the time and resources to use two gear types and compare the difference in their performance *in situ* on one sea voyage, especially when these comparisons are not the primary objective of the cruise. In this research, the performance of a trawl (Figure 3) used in many other Arctic epibenthic studies was compared with a trawl that was modified for very soft sediment stations. This comparison showed no significant differences in the epibenthic abundance or biomass data from these trawls. The importance of this comparison resides not only in the ability to utilize all samples collected with these two types of trawls, but also as it allows for the comparison of this study to similar future and past studies using either of these gear types (Bluhm et al. 2009; Ravelo et al. submitted). These comparisons are necessary for quantitative assessments and contrasts across regions, making possible the construction of a much needed benchmark and time series data set for the Arctic regions. In contrast, without the knowledge of the difference in performance between the many gear types used for epibenthic studies, we are limited to qualitative comparisons of presence/absence data and taxa dominance. Some stations in the western portion of this study were similar to a 2008 western Beaufort survey, which was performed using the 83-112 Eastern otter trawl (Rand and Logerwell 2011). A quantitative comparison is not possible between these studies due to a lack of knowledge regarding the performance of the gear types used. However, some qualitative comparisons were made between these two studies and differences were found. The reason for these discrepancies can only be left to speculation.

Across Regions Comparison

The Chukchi Sea shelf has a higher average epibenthic standing stock and abundance than the Beaufort Sea shelf. High epibenthic abundance and biomass in the vicinity of Barrow Canyon are indicators of the oceanographic processes occurring in the area, which may be promoting this hotspot for epibenthic life. Transit of Bering Sea nutrient rich waters through Barrow Canyon, combined with upwelling events, could be a key factor in the existence of these

hotspots for marine life and explain the similarity between the communities of the two regions (Logerwell et al. 2011). In the Beaufort Sea, community composition changed along the depth gradient. In the Chukchi Sea, the changes in taxonomic dominance were not associated with the bathymetry, highlighting the different environmental drivers that take place in the two seas.

Summary

The dominance of taxa throughout the Beaufort Sea shelf varies longitudinally and throughout the depth gradients. Shallow stations were impoverished in abundance, biomass and diversity and were dominated by highly mobile scavenger crustaceans. This reflects environmental stressors that affect this area such as ice scouring, high terrigenous sedimentation rates and predation by marine birds and mammals. Mid-depth stations had the highest diversity indices and were dominated by echinoderms, crustaceans, molluscs and cnidarians. These stations also had intermediate percentages of mud sand and gravel. This heterogeneous substrate could be responsible in part for this higher diversity. Deep stations had intermediate diversity values and were populated primarily by echinoderms. Reflecting the importance of the water advected through Barrow Canyon and along the shelf slope, there was a decrease in abundance and biomass moving away from Barrow Canyon. However, an area of high abundance comparable to that of the western mid- and deep stations, exists at the far eastern mid-depth stations; possibly due to different oceanographic processes occurring in this area. Also, it is possible that different physiological tolerances allow the small ophiuroid, *Ophiocten sericeum*, and scallop, *Similipecten greenlandicus*, to dominate the eastern stations, while limiting their presence in the western area.

In general, the quality (type) of food and sediment grain size proved to be important variables in determining taxonomic distribution and richness, and the variability in abundance and biomass throughout the shelf. However, processes such as ice scouring, sedimentation rates and predation by marine birds and mammals also impact the epibenthic structure, and may be directly affected by global warming.

Our knowledge of the Beaufort Sea benthos is scarce and discontinuous in time and space. Considering the imminent changes this area is undergoing, and an increasing economic interest in the region, there is a grave need for scientific collaboration and consensus in the sampling tools utilized. In this way, we can better our chances of understanding the Alaskan Beaufort Sea shelf and how the organisms that inhabit this region will be affected.

Comparisons across large regions, such as the Chukchi and Beaufort shelves are important to gain a more comprehensive understanding of the influence of the environment on epibenthic organisms. The changes in taxonomic dominance in each region were driven by different

environmental factors. In the Chukchi shelf, the communities followed the trajectory of important water masses. In the Beaufort shelf, depth is an important proxy for the environmental changes occurring along the shelf. Also in both regions (Chukchi and Beaufort shelves), the stations close to the Barrow Canyon had the highest abundance and biomass, highlighting the importance of this pathway for nutrients and organisms across regions.

Acknowledgments

Funding for this project was provided by the Bureau of Ocean Energy Management (with special thanks to Kate Wedemeyer), the Prince William Sound Oil Spill Recovery Institute (with special thanks to Scott Pegau), and the Coastal Marine Institute. Many thanks go to Brenda Norcross from the University of Alaska Fairbanks for her role as lead scientist. Brenda Holladay, Lorena Edenfield, and the rest of the team provided outstanding deck support and logistics for the cruise. The captain and crew of the *Norsman II* were invaluable for their dedication and effort at sea. Special thanks to Martin Schuster, Katrin Iken and Bodil Bluhm for sampling assistance. Also, thanks to Bodil Bluhm, Lee Cooper, Ken Dunton, Rolf Gradinger, Andy Mahoney, Sathy Naidu, Tom Weingartner, and Peter Winsor for intellectual input into this research. Mette Kaufman helped process the sediment chlorophyll samples, Cheryl Hopcroft processed the bottom water chlorophyll samples, Lauren Divine shared the sediment isotope data, the Norcross lab processed the sediment grain size samples, Seth Danielson proofed the CTD data, Lara Horstmann loaned a muffle furnace to process the sediment organic matter samples, Dave Verbila gave technical support with ArcMap, and Bob Clarke gave technical support for PRIMER analysis.

Study Products (does not include reports)

- Ravelo AM and B Konar. 2012. Epifaunal communities in the central Beaufort Sea. Oral Presentation at the Alaska Marine Science Symposium, Anchorage Alaska, January 2012.
- Ravelo AM and B Konar. 2013. Alaskan Arctic shelf epibenthic communities: A tale of two seas. Poster Presentation at the Alaska Marine Science Symposium, Anchorage Alaska, January 2013.
- Oral Presentation at the Western Alaska Interdisciplinary Science Conference, Nome Alaska, March 2013.
- Ravelo AM and B Konar. In prep for Polar Biology. Epibenthic community variability on the Alaskan Beaufort Sea continental shelf.

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Appendix: Species List

Phylum	Taxa	Authority
Arthropoda	<i>Arctolembos arcticus</i>	(Hansen, 1887)
	<i>Argis</i> spp.	(Krøyer, 1843)
	<i>Chionoecetes opilio</i>	(Fabricius, 1788)
	Cirripedia	(Burmeister, 1834)
	<i>Hyas coarctatus</i>	(Leach, 1816)
	Idoteidae	(Samouelle, 1819)
	<i>Labidochirus splendescens</i>	(Owen, 1839)
	<i>Lebbeus groenlandicus</i>	(Fabricius, 1775)
	<i>Nototropis smitti</i>	(Goës, 1866)
	Other Caridea	(Dana, 1852)
	<i>Pagurus</i> spp.	(Fabricius, 1775)
	<i>Paralithodes platypus</i>	(Brandt, 1850)
	Pycnogonida 1	(Latreille, 1810)
	Pycnogonida 2	(Latreille, 1810)
	<i>Sabinea septemcarinata</i>	(Sabine, 1824)
	<i>Saduria entomon</i>	(Linnaeus, 1758)
	<i>Saduria sabini</i>	(Krøyer, 1849)
	<i>Sclerocrangon boreas</i>	(Phipps, 1774)
	<i>Spirontocaris arcuata</i>	(Rathbun, 1902)
	<i>Spirontocaris phippisii</i>	(Krøyer, 1841)
	<i>Spirontocaris spinus</i>	(Sowerby, 1805)
	Stegocephalidae	(Dana, 1855)
	<i>Synidotea bicuspada</i>	(Owen, 1839)
	<i>Weyprechtia heuglini</i>	(Buchholz, 1874)
Brachipoda	Brachiopoda	(Duméril, 1806)
Bryozoa	<i>Alcyonidium disciforme</i>	(Smitt, 1872)
	<i>Alcyonidium</i> sp. 1	(Lamouroux, 1813)
	<i>Alcyonidium</i> sp. 1	(Lamouroux, 1813)
	<i>Alcyonidium</i> sp. 2	(Lamouroux, 1813)
	<i>Alcyonidium vermiculare</i>	(Okada, 1925)
	Bryozoa 1	
	Bryozoa 2	
	Bryozoa 3	
	Bryozoa 4	
	Bryozoa 5	
	Bryozoa 6	
	Bryozoa 7	
	<i>Flustra</i> sp.	(Linnaeus, 1761)

Phylum	Taxa	Authority	
Cnidarian	<i>Flustra</i> sp.	(Linnaeus, 1761)	
	<i>Actinauge</i> sp.1	(Verrill, 1883)	
Chordata	<i>Actinauge</i> sp.2	(Verrill, 1883)	
	Anemone 1		
	Anemone 2		
	Anemone translucent		
	<i>Gersemia</i> sp.	(Marenzeller, 1877)	
	Hydrozoa 1	(Owen, 1843)	
	Hydrozoa 2	(Owen, 1843)	
	Hydrozoa 3	(Owen, 1843)	
	Red Striated Anemone		
	Soft Pink Coral		
	Staurozoa	(Marques & Collins, 2004)	
	<i>Stomphia</i> sp.	(Gosse, 1859)	
	<i>Urticina</i> sp.	(Ehrenberg, 1834)	
	<i>Trididemnum</i> sp.	(Della Valle, 1881)	
	Echinodermata	<i>Styela rustica</i>	(Linnaeus, 1767)
		<i>Halocynthia</i> spp.	(Verrill, 1879)
<i>Chelyosoma</i> spp.		(Broderip & Sowerby, 1830)	
Asciacea 5		(Nielsen, 1995)	
Asciacea 4		(Nielsen, 1995)	
Asciacea 3		(Nielsen, 1995)	
Asciacea 2		(Nielsen, 1995)	
Asciacea 1		(Nielsen, 1995)	
Echinodermata	Antedonidae	(Norman, 1865)	
	<i>Crossaster papposus</i>	(Linnaeus, 1767)	
	<i>Ctenodiscus crispatus</i>	(Retzius, 1805)	
	Cucumber UnID		
	Cucumber UnID 2		
	<i>Gorgonocephalus arcticus</i>	(Leach, 1819)	
	<i>Gorgonocephalus eucnemis</i>	(Müller & Troschel, 1842)	
	<i>Henricia sanguinolenta</i>	(Müller, 1776)	
	<i>Leptasterias arctica</i>	(Murdoch, 1885)	
	<i>Leptasterias groenlandica</i>	(Steenstrup, 1857)	
	<i>Lophaster verrilli</i>	(Clark, 1938)	
	<i>Ocnus</i> sp.	(Forbes & Goodsir, 1841)	
	<i>Ophiacantha bidentata</i>	(Bruzelius, 1805)	
	<i>Ophiocten sericeum</i>	(Forbes, 1852)	
	<i>Ophiopholis aculeata</i>	(Linnaeus, 1767)	

Phylum	Taxa	Authority
Echinodermata	<i>Ophioscolex glacialis</i>	(Müller & Troschel, 1842)
	<i>Ophiura sarsii</i>	(Lütken, 1855)
	Ophiuroid 1	(Gray, 1840)
	Ophiuroid 2	(Gray, 1840)
	Ophiuroid 3	(Gray, 1840)
	<i>Pontaster tenuispinus</i>	(Düben & Koren, 1846)
	<i>Poraniomorpha tumida</i>	(Stuxberg, 1878)
	<i>Psolus fabricii</i>	(Düben & Koren, 1846)
Mollusca	<i>Pteraster militaris</i>	(Müller, 1776)
	<i>Pteraster obscurus</i>	(Perrier, 1891)
	Sea star 1	(de Blainville, 1830)
	<i>Solaster stimpsoni</i>	(Verrill, 1880)
	<i>Stegophiura nodosa</i>	(Lütken, 1855)
	<i>Strongylocentrotus pallidus</i>	(Sars, 1871)
	<i>Urasterias lincki</i>	(Müller & Troschel, 1842)
Mollusca	<i>Admete</i> sp.	(Krøyer, 1842)
	<i>Admete viridula</i>	(Fabricius, 1780)
	<i>Amicula vestita</i>	(Broderip & Sowerby I, 1829)
	<i>Beringius</i> sp. 1	(Dall, 1887)
	<i>Beringius</i> sp. 2	(Gould, 1860)
	<i>Boreotrophon</i> sp. 1	(Fischer, 1884)
	<i>Boreotrophon</i> sp. 2	(Fischer, 1884)
	<i>Boreotrophon</i> sp. 3	(Fischer, 1884)
	<i>Buccinum angulosum</i>	(Gray, 1839)
	<i>Buccinum elatior</i>	(Tryon, 1880)
	<i>Buccinum glaciale</i>	(Linnaeus, 1761)
	<i>Buccinum morchianum</i>	(Dunker, 1858)
	<i>Buccinum polare</i>	(Gray, 1839)
	<i>Buccinum scalariforme</i>	(Møller, 1842)
	<i>Chlamys behringiana</i>	(Middendorff, 1849)
	<i>Clinopegma magnum</i>	(Dall, 1895)
	<i>Colus sabini</i>	(Gray, 1824)
	<i>Cryptonatica affinis</i>	(Gmelin, 1791)
	<i>Curtitoma conoidea</i>	(Sars, 1878)
	<i>Curtitoma decussata</i>	(Couthouy, 1839)
	<i>Curtitoma novajasemljensis</i>	(Leche, 1878)
	<i>Cylichna alba</i>	(Brown, 1827)
	<i>Cylichna occulta</i>	(Mighels & Adams, 1842)
	<i>Dendronotus</i> sp.	(Alder & Hancock, 1845)

Phylum	Taxa	Authority
Mollusca	<i>Habevolutopsius attenuatus</i>	(Dall, 1874)
	<i>Hermisenda crassicornis</i>	(Eschscholtz, 1831)
	<i>Iphione</i> sp.	(Kinberg, 1856)
	<i>Lacuna turneri</i>	(Dall, 1886)
	<i>Lepeta caeca</i>	(Müller, 1776)
	<i>Limneria undata</i>	(T. Brown, 1839)
	<i>Lunatia pallida</i>	(Broderip & Sowerby I, 1829)
	<i>Margarites costalis</i>	(Gould, 1841)
	<i>Margarites giganteus</i>	(Leche, 1878)
	<i>Neptunea communis</i>	(Middendorff, 1848)
	<i>Neptunea</i> sp.	(Röding, 1798)
Mollusca	<i>Neptunea ventricosa</i>	(Gmelin, 1791)
	<i>Nodulotrophon coronatus</i>	(Adams & Adams, 1864)
	<i>Oenopota elegans</i>	(Møller, 1842)
	<i>Onchidiopsis</i> sp.	(Bergh, 1853)
	Onchidorididae	(Gray, 1827)
	<i>Pandora glacialis</i>	(Leach, 1819)
	<i>Plicifusus kroeyeri</i>	(Möller, 1842)
	<i>Pyrulofusus deformis</i>	(Reeve, 1847)
	<i>Retifusus roseus</i>	(Dall, 1877)
	<i>Rossia pacifica</i>	(Berry, 1911)
	<i>Similipecten greenlandicus</i>	(Sowerby II, 1842)
	<i>Solariella varicosa</i>	(Mighels & Adams, 1842)
	<i>Stenosemus albus</i>	(Linnaeus, 1767)
	<i>Tachyrhynchus</i> sp.	(Mörch, 1875)
	<i>Tritonia</i> sp.	(Cuvier, 1797)
	<i>Velutina coriacea</i>	(Pallas, 1788)
	<i>Velutina velutina</i>	(Müller, 1776)
	<i>Volutopsius fragilis</i>	(Dall, 1891)
	<i>Volutopsius norwegicus</i>	(Gmelin, 1791)
	<i>Volutopsius</i> sp.	Mörch, 1857
Platyhelminthes	Platyhelminthes	
Porifera	<i>Halichondria sitiens</i>	(Schmidt, 1870)
	<i>Myxilla lacunosa</i>	(Lambe, 1893)
	<i>Polymastia</i> spp.	(Bowerbank, 1864)
	Porifera 1	(Grant, 1836)
	<i>Semisuberites cribrosa</i>	(Micklucho-Maclay, 1870)
	<i>Thenea muricata</i>	(Bowerbank, 1858)



The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the sound use of our land and water resources, protecting our fish, wildlife and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island communities.



The Bureau of Ocean Energy Management

The Bureau of Ocean Energy Management (BOEM) works to manage the exploration and development of the nation's offshore resources in a way that appropriately balances economic development, energy independence, and environmental protection through oil and gas leases, renewable energy development and environmental reviews and studies.