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Assessing Bioresources and Standing Stock of Zoobenthos (Key Species, High Taxa, Trophic Groups) in the Chukchi Sea

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ABSTRACT. We describe total standing stock and spatial biomass distribution of the key macrofaunal species, as well as the main taxonomic and trophic groups of zoobenthos, in the Chukchi Sea based on data collected over the period 1986–2012. The dominant species, ranked by biomass, are the bivalves *Macoma calcarea*, *Ennucula tenuis*, *Astarte borealis*, *Nuculana radiata*, *and Yoldia hyperborea*; the sipunculid, *Golfingia margaritacea*; the polychaete *Maldane sarsi*; and the sea cucumber *Psolus peroni*. We discuss the influence of bottom sediments and water masses on zoobenthos bioresources and standing stock and present a hypothesis for the mechanism that facilitates the phenomenon of very high benthic biomass in the southern Chukchi Sea. The relationship between biomass of filter feeders and deposit feeders indicates that the Chukchi Sea should be classified as a eutrophic marine system.

INTRODUCTION

With increasing depletion of commercial fisheries, the number of newly harvested marine species is on the rise. Thus, there is an immediate need to estimate all available biological resources (termed bioresources in this paper) used by humans, including food for consumption, forage feed for domestic animals, and industrial raw materials. These new resources and their potential economic importance require a quantitative assessment of the total biomass (abundance) and the spatial distribution of the resource base.

In order to monitor and study the long-term dynamics of zoobenthic populations, it is necessary to analyze the spatial distributions of those species or higher-level taxa that contribute most to the total biomass in an area of interest. As a rule, the number of such species in each Arctic sea does not exceed 20 (Denisenko, 2004), with 50% of the zoobenthos biomass being formed by fewer than 10 species. These few can be considered the "key species" influencing the structure and function of the associated ecosystems and they have key roles in controlling the structure, development, and distribution of ecological communities, including energy flows (Piraino et al., 2002). Biological metrics include faunal biomass, abundance, productivity, and function in the ecosystem.

The Chukchi Sea's marine resources (Figure 1a) are not harvested commercially, although local people fish, hunt marine mammals, and harvest benthic invertebrates for their own use. Locally potential harvested benthic species in the Chukchi Sea include the bivalves *Mya, Serripes, Mytilus, Chlamys*, and *Macoma*; several carnivorous gastropods from the genera *Buccinum* and *Neptunea*; the snow crab *Chionoecetes opilio*; and sea urchins from the genus *Strongylocentrotus*. However, the exact quantity of this bioresource available for harvesting is not known.

Other bioresources include plants and animals consumed by marine mammals, fishes, and birds. The Chukchi Sea attracts large numbers of walruses, seals, bowhead and gray whales, and eiders that are either resident to the area or migrate to specific regions every year to feed, some on benthic prey. Some of these benthic species are listed in the Red Data Book of the Russian Federation (Illiashenko and Illiashenko, 2000) and/or are protected under the Endangered Species Act of the United States.

Among the marine mammals, the main consumers of benthos in the Pacific Arctic region are Pacific walruses and gray whales (Moore et al., 2014). Walruses feed on bivalves and gastropods, crustaceans, worms, and ascidians (Krylov, 1971; Sheffield and Grebmeier, 2009), while gray whales prefer crustaceans, especially amphipods, and other high biomass benthic species (Blokhin and Pavluchkov, 1996; Highsmith et al., 2006).

Benthic biomass in the northern Pacific Ocean increases northward from the Sea of Japan to the Bering Sea (Zenkevich, 1951; Shuntov, 2001), increasing to high values in the southern Chukchi Sea (Makarov, 1937; Sirenko and Koltun, 1992; Grebmeier et al. 2006). A considerable proportion of this benthic fauna is represented by mollusks, crustaceans, polychaetes, sipunculid worms, echinoderms, and ascidians, and known regions of high benthic prey abundance attracts walruses, seals, whales, and birds to these areas to feed.

In order to identify and quantify the bioresources of the Chukchi Sea, we present a general assessment of the key species of benthic invertebrates, based on quantitative grab samples of macrobenthic fauna. This study also evaluates the bioresource potential of the major higher taxa components (at the level of class or phylum) and associated trophic groups. We present (1) key species identified by their contributions to the total zoobenthos biomass, and (2) spatial distribution of

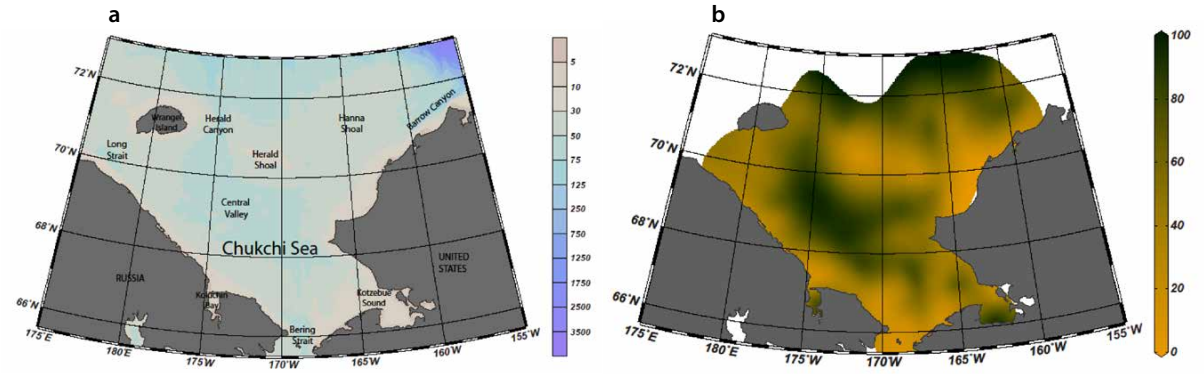

FIGURE 1. (a) Bathymetry of the Chukchi Sea, and (b) proportion of silt + mud content (%) in the bottom sediments. *Modified after Kosheleva and Yashin (1999); Grebmeier (2012)*

these species using geographical imagery, together with an evaluation of the quantitative distribution of the dominant benthic taxa and their trophic levels in the food web. A companion paper by Grebmeier et al. (2015b) in this special issue discusses total benthic community composition of benthic macro- and megafauna in the context of environmental factors.

MATERIALS AND METHODS

This study was based on quantitative zoobenthos samples collected at 640 stations in the Chukchi Sea by specialists from the Zoological Institute of the Russian Academy of Sciences and scientists from the University of Alaska Fairbanks and the University of Maryland Center for Environmental Science over the period 1976–2012 (Figure 2). Macrofauna were collected during multiple cruises in both Russian and US waters through programs that included the Russian-American Long-term Census of the Arctic (RUSALCA). Three to five replicates (with a few two-replicate stations) were collected using either a 0.25 m^2 Okean grab or a 0.1 m^2 van Veen grab, with sediment sieved over primarily 1 mm screens (a few over 0.8 mm screens). The remaining macrofauna were preserved in 4–10% seawater formalin buffered with borax or hexamethylenetetramine. Macrofauna were later identified to genus or species levels (or to the lowest taxon possible), with the taxa subsequently counted and weighed after three to four months in formalin.

Station-wise species lists of abundance and biomass for all data were pooled into a common data set. Based on these files, maps of the spatial distributions of species, taxonomic groups, and trophic groups were constructed using Ocean Data View 4.7.3 (Schlitzer, 2015). The total benthic biomasses of components were displayed spatially using geostatistical interpolations performed with Surfer 8 and MapViewer 7.2 (http://www.goldensoftware.com). Kriging, with a spherical variogram and search ellipse with a radius of –5° longitude and –1.8° latitude (Software Surfer, v8), was used as a universal interpolator. These parameters were experimentally found to be optimal with respect to the deviation of calculated values from the actual data. On average, the calculated deviation made up not more than 10% of the actual benthic faunal biomass found at the study sites. The map surface areas were based on the northern border of the Chukchi Sea being located along 72°30'N°, with a total area of ca. 335,000 km^2. The western border was located to the north of Wrangel Island along 180°W and further to the south from Cape Blossom to Cape Yakan. The eastern border was located along 158°W (Figure 1).

In order to assess the similarity of spatial distributions of individual species, taxonomic groups, and trophic groups, the Spearman rank coefficient rather than the Pearson correlation was used. This was necessary in order to compare different biomass values in the same local maxima or minima. A significant difference between these values can considerably decrease Pearson correlation even when the spatial distributions under comparison are visually very similar.

Organism feeding types were also used in the analysis and are based on previously published categorizations (Kuznetsov, 1980, 1986).

RESULTS

Comparison of benthic faunal biomass, statistically weighted by area at each station, revealed eight macrofaunal species contributing up to 50% of the total zoobenthos bioresources of the Chukchi Sea (Table 1). Five of these species were bivalve mollusks: *Macoma calcarea*, *Ennucula tenuis*, *Astarte borealis*, *Nuculana radiata*, and *Yoldia hyperborea*. Of these, *M. calcarea* was the most important and abundant, with a total biomass (i.e., bioresources) several times greater than those of any other bivalve species evaluated separately.

The zoobenthos biomass and the five key bivalve species were unevenly distributed. The highest values of total macrofaunal biomass were observed in the southern and northwestern areas of the sea (Figure 3a), and *M. calcarea* had the highest biomass of all species in the southern and the southwestern areas (Figure 3b). The highest biomass values of a second bivalve, *E. tenuis*, also occurred in the southwestern portion of the Chukchi Sea (Figure 3c). The highest biomass of *A. borealis* was recorded in the northern part of the sea as well as in the south, in Koluchin Bay and Kotzebue Sound (Figure 3d). The major settlements of *N. radiata* extended toward the western part of the Chukchi Sea (Figure 3e). High biomass values of the sipunculid *Golfingia margaritaceum* were mostly recorded in northern and the northeastern areas (Figure 3f).

Significant Spearman correlations indicated some degree of spatial distribution similarity, by biomass, of *M. calcarea* and

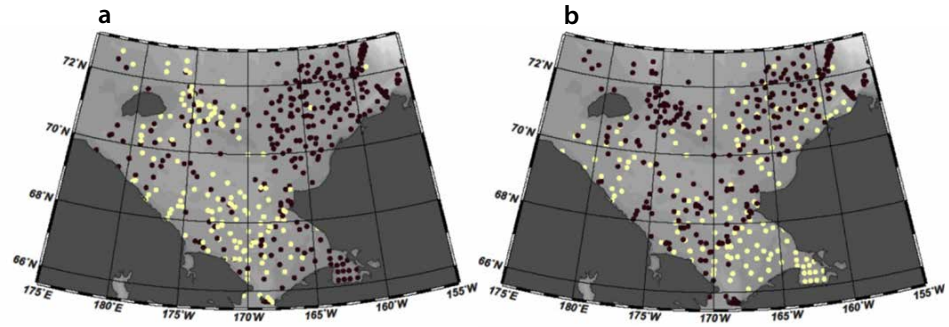

FIGURE 2. Locations of 640 sample stations in the Chukchi Sea collected on (a) Russian (light circles) and American expeditions (dark circles) from 1986 to 2012, and (b) locations of the stations collected before the year 2000 (light circles) and after 2000 (dark circles). Note that by convention, the northern border of the Chukchi Sea in the west extends to 75°N, with an areal extent of the sea of 595,000 km^2 (Anonymous, 1985).

E. tenuis (S = 0.51), and of *A. borealis* and *G. margaritacea* (S = 0.52). Bivalves clearly dominate in biomass compared with the other large macrofaunal taxa in the Chukchi Sea (Table 2). They made up more than 50% of the zoobenthos bioresources by both wet and dry weight biomass. Even considering that the calcium carbonate shell accounts for about 30–50% of the molluskan wet biomass (Alexey V. Golikov, Kazan Federal University, *pers. comm.*, 2015; Stoker, 1978; Brey, 2001; Denisenko, 2013), bivalves are still the dominant taxa by biomass. This finding was also supported by recalculating the wet biomass on an organic carbon basis (Stoker, 1978; Grebmeier, 2012). The contribution of other taxonomic groups was an order of magnitude lower than that of bivalves (see Table 2). Polychaetes accounted for ~11% of total zoobenthos bioresources, as did echinoderms (holothurians and sea urchins).

The distribution of bivalve biomass (Figure 4a) resembled that of the total zoobenthos biomass (see Figure 3a). However, the biomass values for Bivalvia were much lower in the northwestern and, especially, in the northeastern part of the sea relative to the high southern Chukchi Sea biomass values, although they can be regionally important. Polychaetes dominated locally in Herald Canyon in the north (Figure 4b), while significant communities of holothurians were observed near Wrangel Island (Figure 4c). In the eastern part of the Chukchi Sea as well as in Bering Strait, dense settlements of sea urchins were found alongside those of holothurians (Figure 4d).

Ascidians (Figure 5a), barnacles (Figure 5b), amphipods (Figure 5c), along with sea urchins, mostly formed biomass aggregations in the southern and northern parts of the Chukchi Sea, where water dynamics were the greatest. Judging from the location of the local biomass maxima of these groups, these varying taxon

TABLE 1. Contribution of different species into total bioresources (by mass, tons) and total specific biomass (g wet weight m^{-2}) of zoobenthos over the whole Chukchi Sea. *R%* = Proportion of the total bioresources. *R,t* = Bioresources (tons). *B* = Average specific total biomass (g wet weight m^{-2}) within regions. B_{Err} = Statistical error of the average specific total biomass.

Species	Feeding mode	*R%*	*R,t* (tons)	*B* (gww m^{-2})	B_{Err} (gww m^{-2})
*Macoma calcarea**	Filter/Surface Deposit Feeder	9.4	8,269,498	92.8	16.3
Ennucula tenuis	Surface Deposit Feeder	7.4	6,492,153	33.2	5.8
Astarte borealis	Filter Feeder	4.6	4,087,168	89.0	10.4
Golfingia margaritacea	Subsurface Deposit Feeder	2.7	2,384,643	62.3	5.7
Nuculana radiata	Surface/Subsurface Deposit Feeder	7.6	6,740,267	35.8	5.6
Yoldia hyperborea	Surface/Subsurface Deposit Feeder	5.9	5,215,108	18.1	2.7
Maldane sarsi	Subsurface Deposit Feeder	8.2	7,269,498	25.9	2.4
Psolus peroni	Filter Feeder	6.2	5,492,154	143.7	7.8
Others		48.0	42,373,638		
Total		**100**	**88,324,127**	**592.5**	**39.7**

*All mollusks from the family Tellinidae were considered to be an intermediate group between filter feeders and surface deposit feeders (Kuznetsov, 1986).

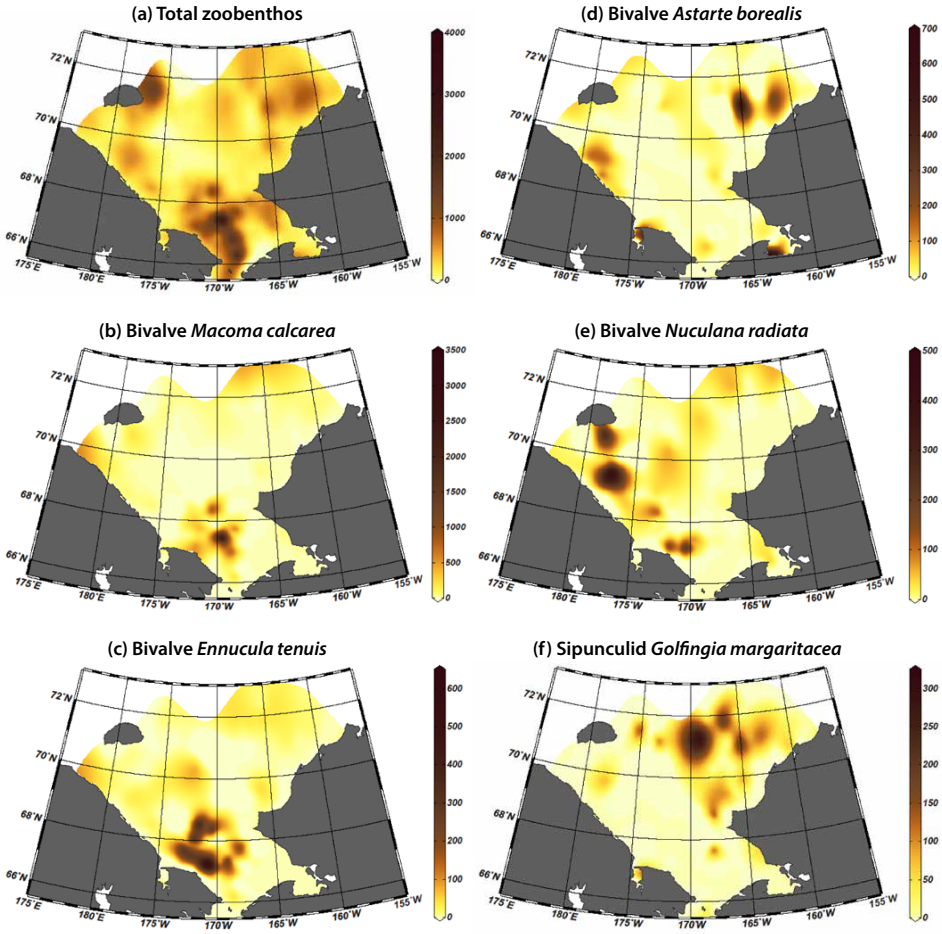

FIGURE 3. Biomass (g wet weight m^{-2}) distribution of (a) total zoobenthos; the bivalves (b) *Macoma calcarea*, (c) *Ennucula tenuis*, (d) *Astarte borealis*, and (e) *Nuculana radiata*; and the (f) sipunculid *Golfingia margaritacea* in the Chukchi Sea from 1986–2012. Note the higher vertical scale of *Macoma calcarea* biomass compared with the biomass of other species in the Chukchi Sea that are shown in subsequent maps.

TABLE 2. Contribution of higher taxa into total bioresources (by mass, tons) and total specific weight (g wet weight m^{-2}) of zoobenthos in the Chukchi Sea. *R%* = Proportion of the total bioresources. *R,t* = Bioresources (tons). *B* = Average specific total biomass (g wet weight m^{-2}) within regions. B_{Err} = Statistical error of the average specific total biomass.

Higher taxa	*R%*	*R,t* (tons)	*B* (gww m^{-2})	B_{Err} (gww m^{-2})
Bivalvia	54.1	47,777,578	169	32.4
Polychaeta	11.0	9,722,948	36.9	4.2
Holothuroidea	6.8	5,966,515	47.7	15.6
Echinoidea	4.2	3,687,117	127	41.7
Ascidiacea	3.8	3,363,200	34.1	8.4
Sipunculida	3.1	2,697,232	25.2	3.1
Cirripedia	2.6	2,311,321	31.1	9.7
Amphipoda	2.4	2,100,767	8.1	1.7
Anthozoa	2.4	2,090,435	20.1	3.9
Others	9.7	8,607,014		
Total	**100**	**88,324,127**	**592.5**	**39.7**

Note: All mollusks from the family Tellinidae were considered to be an intermediate group between filter feeders and surface deposit feeders (Kuznetsov, 1986).

TABLE 3. Contribution of different trophic groups into total bioresources and total biomass of zoobenthos in the Chukchi Sea. *R%* = Proportion of the total bioresources. *R,t* = Bioresources (tons). *B* = Average biomass in settlements, g m^{-2} of wet conserved biomass; B_{Err} = Statistical error of the average biomass.

Trophic mode	*R%*	*R,t* (tons)	*B* (gww m^{-2})	B_{Err} (gww m^{-2})
Filter feeders	44.2	39,035,073	153	21.3
Surface deposit feeders	26.2	23,176,154	202	10.1
Subsurface deposit feeders	19.0	16,819,154	59.2	4.5
Carnivorous	6.2	5,448,669	39.7	5.3
Omnivorous	2.5	2,248,628	37.0	4.9
Scavengers	0.1	80,468.4	0.48	0.12
Unclear	1.7	1,515,981		
Total	**100**	**88,324,127**	**592.5**	**39.7**

Note: All mollusks from the family Tellinidae were considered to be an intermediate group between filter feeders and surface deposit feeders (Kuznetsov, 1986).

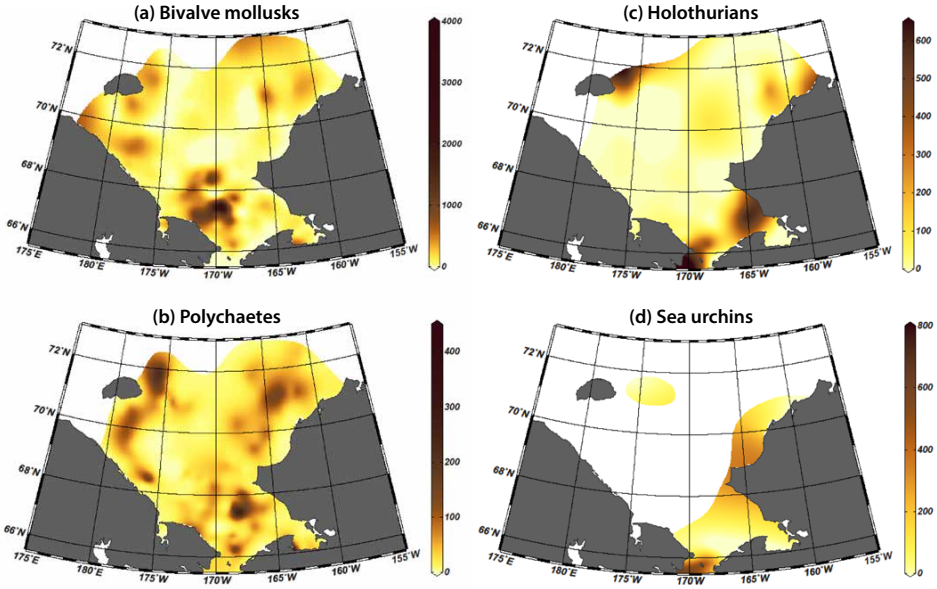

FIGURE 4. Biomass distribution (g wet weight m^{-2}) of (a) bivalve mollusks, (b) polychaetes, (c) holothurians, and (d) sea urchins in the Chukchi Sea from 1986–2012.

settlements did not overlap each other. Due to this separation of groups, the significant Spearman correlation coefficients, which indicate similarity of the spatial distribution of fauna by biomass, were only obtained for Ascidiacea and Echinoidea (S = 0.77).

Filter feeders (suspension feeders) predominate overall for much of the spatial extent of the Chukchi Sea. Their proportion exceeded 44% of the total biomass, making up approximately 40 million tons, with an average wet biomass of 141 g m^{-2} (Table 3). The proportion of deposit feeders (including both surface and subsurface deposit feeders) is about equal to the filter feeders, making up 45.2% of the overall biomass or approximately 40 million tons. The bioresources proportion of surface deposit feeders to subsurface deposit feeders was 3:2. Omnivorous and predatory species contributed less than 10%, and made up 7.5 million tons. On the whole, the average biomass value of each trophic group was better correlated with its individual bioresource value than biomass of the large taxa or the key species groups with their individual bioresource values (see Tables 1, 2, and 3).

The spatial distribution of trophic groups shows a tendency toward replacement of communities where filter feeders dominate (mostly in the southernmost and northwesternmost parts; Figure 6a) with communities in which surface deposit feeders dominate (in the northeastern and southwestern parts; Figure 6b). Slow-moving subsurface deposit feeders dominate in the northeastern Alaska Chukchi coastal waters, around Hanna Shoal, and to the east and south of Wrangel Island (Figure 6c) within silty-clay sediments (Figure 1b). The highest biomass of predators coincides partly with the total zoobenthos biomass.

DISCUSSION

Benthic Communities Defined by Biomass Spatial Patterns

Visual or computerized demarcation of benthic communities based on the results of clustering or ordination is the most

common method used for local zonation of marine benthic biota and for comparing qualitative and quantitative characteristics of zoobenthos in various regions and over temporal periods (Denisenko, 2007). Most researchers define a "biological community" as the combination of populations of organisms interacting with each other and with the environment in space and time (Möbius, 1877; Whittaker, 1975; Bigon et al., 2006). However, this definition is somewhat vague because the communities usually have no distinct borders but rather transition into each other imperceptibly (Pianka, 1994). Besides, the use of different approaches and software yields different, and often not comparable, results describing the dominance of a given group in a given area.

Certain methods can be limiting in their demarcation of benthic communities because of assumptions that species always have the same quantitative representation in communities (Vorobyev, 1949; Clarke and Warwick, 2001). The possibility of detecting changes in the abundance and biomass of populations can be obscured, although long-term fluctuations and quantitative indices of many benthic invertebrates (Pearson and Rosenberg, 1978; Gerasimova and Maksimovich, 2000; Kortsch et al. 2012; Denisenko, 2013), plankton (Krause-Jensen et al., 2012), and fish (Klyashtorin and Lubushin, 2005) are well known. As a result, comparing the distributions of the so-called communities in different marine areas and for different research periods might be reduced to a comparison of the degree of dominance of a few key species, such as indicated in our present study. A cyclic decrease or increase in the abundance or biomass of these species, caused by any environmental changes, may result in a misclassification of communities on the basis of species dominance (Denisenko, 2013).

Our research indicates that the most abundant species can also dominate by biomass in benthic communities (Table 1; Denisenko, 2004, 2007; Sirenko et al., 2009; Grebmeier et al., 2015a). These species often serve as the major food source for numerous benthic-feeding mammals and birds. Therefore, the assessment of macrobenthos biomass should be based on direct calculations of the quantitative spatial distributions of those key species, higher taxa, and trophic groups that dominate the biomass (i.e., bioresources) in a study area. The importance of these species as future human resources may better be assessed by a simple interpolation of biomass on a map. In contrast to various methods of "community" classification, including visual recognition of dominant species, our simplified approach will more directly facilitate comparative analysis in the future. In addition, using interpolation approaches, the outliers on the maps are to some degree smoothed, which compensates for possible sampling errors and the mosaic nature of organismal distributions on the seafloor.

Using this approach of statistically

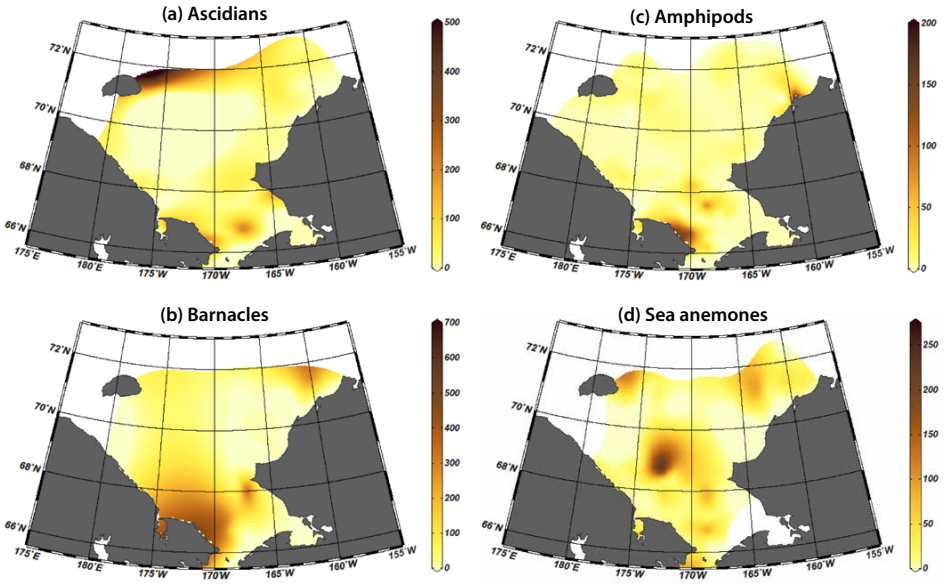

FIGURE 5. Biomass distribution (g wet weight m^{-2}) of (a) ascidians, (b) barnacles, (c) amphipods, and (d) sea anemones in the Chukchi Sea from 1986–2012.

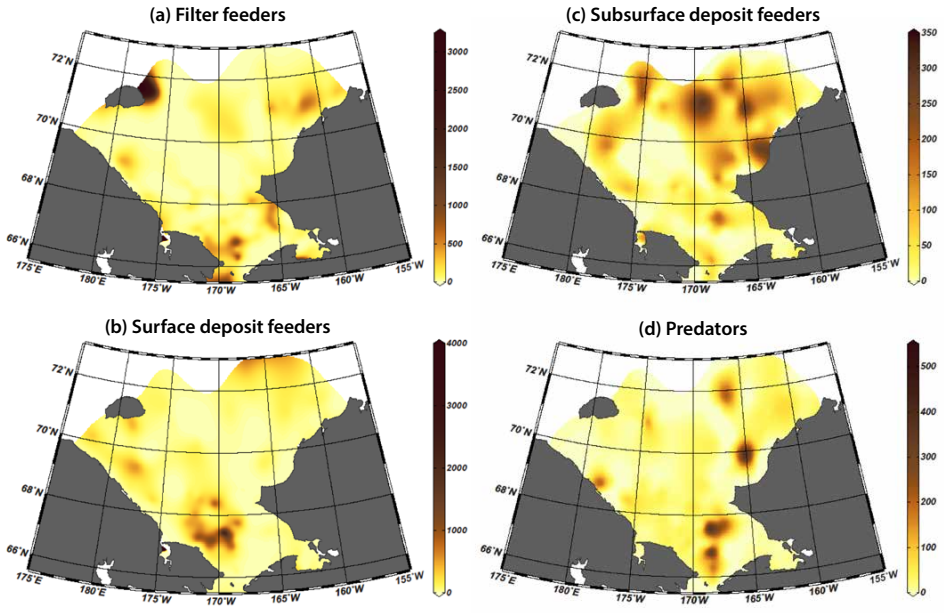

FIGURE 6. Biomass distribution (g wet weight m^{-2}) of (a) filter feeders, (b) surface deposit feeders, (c) subsurface deposit feeders, and (d) predators in the Chukchi Sea from 1986–2012.

weighted spatial benthic data analysis, it was determined that 75–80% of the total macrofaunal biomass of the Barents Sea during a defined study period was made up of 15–20 taxa, with 7–10 species making up 40–50% of the total benthic biomass (Denisenko, 2004; Wassmann et al., 2006). By comparison, using the same statistical methods with a large suite of data in the Chukchi Sea, we found fewer taxa were dominant, with eight species making up nearly 50% of the total benthic biomass (or bioresources).

Environmental Factors Influencing Benthic Community Structure

The composition and biomass of macrobenthos in the Chukchi Sea are determined by the locations of water masses and associated frontal zones, currents, seawater temperature and salinity, and the content of organic carbon in the sediments and in the water column (Grebmeier et al., 1989; Feder et al., 2005, 2007). Seafloor topography, combined with the current regime, is the critical factor influencing the characteristics of bottom sediments and ultimately the associated concentration of organic carbon in them (Gorshkova, 1975; also see Pisareva et al., 2015, in this issue).

Comparison of the distributions of bottom sediment grain size, total benthic biomass, and the biomass of the dominant taxa in the Chukchi Sea shows that sediments with similar contents of sand, silt, and clay fractions are the most favorable for the development of zoobenthos settlements, and they are also characterized by a large amount of bioresources (see Figures 1b and 3a). Faunal abundance and availability of food have major influences on the quantitative development of the zoobenthos. Average annual primary production in the Chukchi Sea varies from 20 to 200 gC m^{-2} (Sakshaug, 2004; Codispoti et al., 2013). Regions with increased concentrations of suspended and freshly deposited organic matter depend on the intensity of the nutrients supplied via currents from the Bering Sea as well as locations of frontal water masses (Grebmeier, 1993, 2012) and of the ice edge (Denisenko, 2002).

The Chukchi Sea is three to four times shallower (average depth of 50 m) than the western seas of the Russian Arctic, and the amount of detritus deposited on the bottom from the surface layers of the water is thus higher. The shallow depths of the Chukchi Sea ensure abundant food is supplied to benthic invertebrates (Grebmeier et al., 1989; Grebmeier, 1993; Iken et al., 2010). As a result, very high zoobenthos biomass, exceeding 1 kg m^{-2}, is formed even in the open sea areas (see Figure 3a). The bottom of the Chukchi Sea is a flattened plain that dips slightly toward the center and has an average depth of less than 80 m. Contrary to other Arctic seas, there is a distinct dependence of zoobenthos distribution on phytoplankton biomass (Grebmeier, 1993, 2012). The bottoms of other Arctic seas (e.g., the Barents Sea) are highly uneven and characterized by a considerable (hundreds of meters) depth range between shallow banks and deep channels (average depth of 250 m). Thus, different areas of the seafloor receive different amounts of biologically degraded organic matter produced by phytoplankton. In the Chukchi Sea, where depth variations are much less pronounced, there is tighter pelagic-benthic coupling of upper water column production to the underlying benthos. However, a recent synthesis by Grebmeier et al. (2015a) found a definite latitudinal decline in export production and benthic biomass overall from the southern to the northern Chukchi Sea due to reduced levels of primary production and water mass variability. The complex water mass structure and current flow in the northern Chukchi Sea, with its shoals and canyons, adds to the heterogeneity of ecosystem dynamics and underlying benthic populations in that region.

Potential Mechanisms for Maintenance of High Benthic Biomass Zones

The biomass maxima of benthic invertebrates recorded in the southern part of the Chukchi Sea (Grebmeier et al., 2006; Sirenko and Gagaev, 2007) coincide with the locations of known particle depositions sites to the north of Bering Strait (Sirenko and Koltun, 1992; Cooper et al., 2005; Grebmeier et al. 2006; Pisareva et al., 2015, in this issue). This high benthic biomass zone may result from slowing current speeds (Ratmanov, 1937) and possible cyclonic features that are present in the autumn (Pickart et al., 2013; Figure 7). A nearly continuous input of nutrients through Bering Strait allows the phytoplankton community to function actively throughout the period of sufficient light and to provide the underlying sediments with a continuous supply of fresh phytodetritus, the major source of food for benthic invertebrates. In contrast, in other Arctic regions, spring development of phytoplankton blooms is subsequently inhibited by depletion of nutrients in the surface layers of stratified water columns (Sakshaug 2004). Thus, during most of the season when light is available, the sinking of phytodetritus to the bottom in these other regions is weak, thus limiting the production and biomass of underlying zoobenthic communities.

The exact mechanism for this strong pelagic-benthic coupling is uncertain, but its role in the annual formation of a zone of high benthic biomass in the southern Chukchi Sea is critical. The existence of periodic cyclonic type circulation is supported by hydrographic section data. However, we disagree with Ratmanov's (1937) interpretation that the cyclonic gyre arises from the interaction of northward-flowing Pacific water and a southwest-flowing East Siberian Current. More recent data indicate a variable, more ephemeral flow from the East Siberian Sea along the Chukchi Sea coast to the southern Chukchi Sea (Münchow et al., 1999; Weingartner et al., 2005). It is more likely that the greater depth to the northwest helps facilitate a cyclonic-type circulation in the upper portion of Central Valley. This alternative mechanism would result in enrichment of the photosynthetic water layer by nutrients and enhanced carbon export to the

underlying sediments that support the high bivalve biomass in this region. This southern Chukchi Sea gyre may exist as a persistent feature, regardless of the presence or absence of an opposed current, with only the size of the cyclonic gyre varying with variable current flows of the different water masses in the region.

Functional Feeding Groups

Our schematic maps indicate that the Chukchi Sea can be separated into two regions of almost equal size: (1) southern and northwestern with an active current regime, and (2) northern with slower, but more variable, near-bottom hydrodynamics (Figure 1). This hydrodynamic separation is reflected in the distribution of suspension feeders vs. deposit feeders, whose nearly equal bioresources are divided in distribution and follow the hydrodynamic regimes (also see Pisareva et al., 2015, in this issue).

Hydrodynamics are most intense in the southern area just north of Bering Strait, along the Alaska and Chukotka coastlines, and within Herald Canyon to the east of Wrangel Island. Coarse sandy deposits (Figure 1b) on the seafloor in this region are better suited for attached organisms such as ascidians, barnacles, and several filter-feeding amphipods (Figure 5a–c). These areas are characterized by moderately high values of zoobenthos biomass (Figure 3a). The presence of suspension feeders indicates high organic matter content in the near-bottom water layer. The suspended particulate matter may originate both autochthonously, resulting from the development of local phytoplankton, and allochthonously, as organic matter transported into the Chukchi Sea via the Bering Strait inflow. Surface deposit feeders generally dominate in the upper Herald Valley and in the south central Chukchi Sea, with decreasing biomass to the northwest (Figure 6b).

The prevalence of subsurface deposit feeders in the northeastern and northern Chukchi Sea areas indicates a horizontal input of fresh organic matter. This functional group is especially characteristic of eastern areas (Feder et al., 2005; Blanchard et al., 2013a,b; Blanchard and Feder, 2014) and depends on the transfer of the fresh organic matter from southern areas (Grebmeier et al., 2015a). A second region of organic matter accumulation is observed to the northwest in Herald Canyon (Kosheleva and Yashin, 1999). Increased concentrations of organic matter in the near-bottom water layer along the canyon slopes ensure ample development of filter-feeding organisms, while the accumulation and burial of organic matter in the bottom sediments provide food for subsurface deposit feeders.

Finally, the highest biomass of predators (Figure 6d) coincides with areas of highest zoobenthos biomass (i.e., southeast Chukchi Sea and in Herald Canyon; Figure 3a). The distributions of Chukchi Sea trophic groups identified in this study, and the fact that they are determined by environmental factors, agree well with the results of earlier studies carried out in the eastern part of the sea (Feder et al., 2005, 2007). In the southern Chukchi Sea, as in the Pechora Sea, the shallow part of the Barents Sea, the distribution of filter feeders was not just confined to the coastal areas, as occurs in the Barents Sea (Denisenko, 2007), but they were often most abundant in the offshore regions.

Observations of almost equal proportions of suspension and deposit feeders are consistent with the findings of Neiman (1961), who concluded that such a distribution of trophic zones is characteristic of seas with a broad and gently sloping continental shelf. According to Neiman (1988), the trophic structure of zoobenthos in the Chukchi Sea, on the whole, may be considered eutrophic. Such a structure usually develops due to a weakly balanced trophic cycle in the pelagic community where zooplankton are insufficient to consume the available organic carbon (Grebmeier et al., 2006).

Indeed, all the key zoobenthos species of the Chukchi Sea have a broad or a cosmopolitan boreal-Arctic distribution. *Astarte borealis* may reach an age of 26 years (Denisenko, 1997), *Macoma calcarea* 15–17 years (Petersen, 1978; Denisenko, 1997), *Yoldia hyperborea* 13 years (Rusanova, 1963), *Golfingia margaritacea* at least six years (Denisenko, 2006), and *Maldane sarsi* at least four years (Denisenko, 2006). A limited, but detailed, study of the growth rate of *Y. hyperborea* (Box 1) indicates that bivalve growth rate is tied to climate forcing parameters, such as the Arctic Oscillation; thus, the future stability of bivalve populations may change. Since bivalves are a major bioresource in the Chukchi Sea for upper

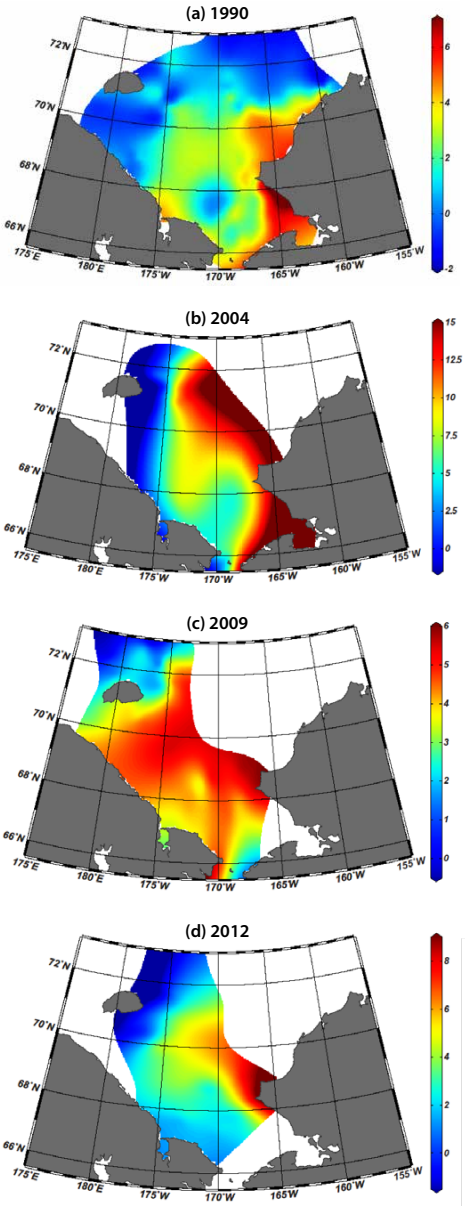

FIGURE 7. Distribution of surface seawater temperatures in August/September of (a) 1990, (b) 2004, (c) 2009, and (d) 2012 in the Chukchi Sea.

Box 1. Relationship of Growth Patterns in a Chukchi Sea Bivalve Population to the Arctic Oscillation

By Stanislav G. Denisenko and Vladimir V. Skvortsov

Figure B1. The bivalve *Yoldia hyperborea*, showing annual growth lines.

Forty live specimens of *Yoldia hyperborea* (Figure B1), one of the dominant bivalve taxa in the Chukchi Sea, were collected at one station (CS12) on the Chukchi South line in the southern Chukchi Sea during the RUSALCA September 2012 expedition. These specimens were used to estimate individual growth rates by measuring annual increments of carbonate added to their shells. To test the hypothesis that climatic factors have a significant impact on the growth of mollusks, the following climatic parameters were examined in relation to measured growth rates: a 10-year time series of bottom water temperatures observed from moorings in Bering Strait (Temp), the annual flux of incoming water flowing through Bering Strait (FW), the Arctic Oscillation (AO), and the Pacific/North American (PNA) pattern (Wallace and Gutzler, 1981; Woodgate et al., 2012).

We plotted individual mollusk growth increment curves (Figure B2) and calculated a theoretical growth curve using the Gompertz formula (Bowers et al., 1997). The Gompertz equation was used to describe the growth rates of the 40 individuals collected. This equation is based on growth rates (L), the growth coefficient (k), and the inflection point when growth rates change (i) (Table B1). We also calculated the standardized growth rates of these mollusks, that is, the ratio of difference and derivative (RDD) (Denisenko, 2013). We determined that these standardized rates of growth for the mollusks collected (RDD) show long-term oscillations (Figure B3).

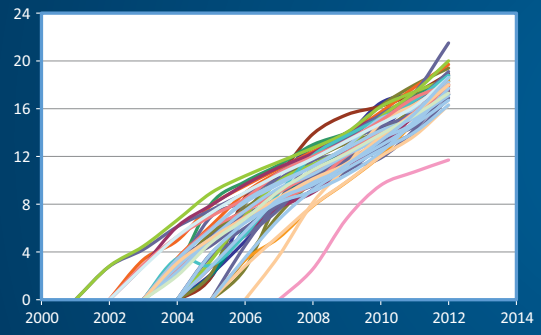

FIGURE B2. Linear growth curves over time for 40 individual *Yoldia hyperborea* shells collected at one station (CS12) during the RUSALCA 2012 expedition in the Chukchi Sea.

TABLE B1. Gompertz equation parameters used to approximate the growth of *Yoldia hyperborea*. L_x = maximum width of clams of this population, based upon model (theoretical), in mm). k = coefficient that describes growth rate (mm^{-1}). I = inflection point where growth rates changed.

R^2	L_∞	±95%	k	±95%	i	±95%
0.991	21.662	0.589	0.337	0.017	3.198	0.167

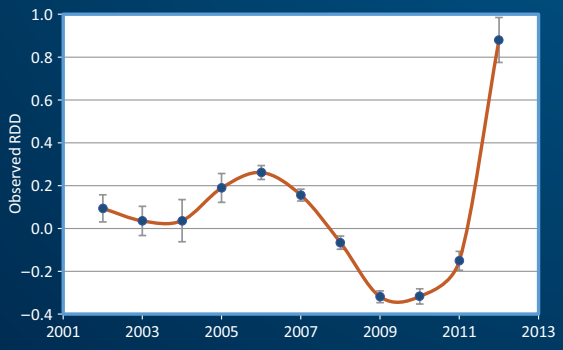

FIGURE B3. Time-series observations of the collected mollusks' growth rates (RDD) showing a long-term oscillation of this parameter.

Correlation of Growth Rates with Climatic Parameters

The statistical analysis of the relationship between the growth rates of the 40 *Y. hyperborea* and climatic factors was carried out using correlation analysis, multiple regression analysis, and time series analysis. Multiple regression analysis was performed in two ways: stepwise multiple regressions and ridge multiple regressions (using Statistica 6). We used both raw data (untransformed) and transformed data (ln (x+2)) to determine the best approximation for the dependence of the growth rate on climatic variables. Significant correlations ($p < 0.05$) were found between the transformed values of the RDD and water temperature and the AO (partial correlations are 0.680 and 0.674, respectively, for the transformed data).

As a result of multiple regression analysis undertaken in the model analysis, only one predictor—water temperature (Table B2)—provided satisfactory results with good agreement between predicted and observed values (Figure B4). The initial data were treated as a time series and analyzed based on cross correlation between the RDD index and the climatic parameters. Figure B5 shows good coherence between the variability of the RDD and the AO indices. However, shifting the relationship of the standardized growth rate of *Y. hyperborea* (RDD) relative to the AO index provides a better match if a two-year delay ($R^2 = 0.782$) is assumed (Table B3, Figure B6). The relationship between observed RDD and modeled RDD also improves when a two-year lag is assumed between the AO and the RDD (Figure B7). The AO index is a measure of climatic influence, including water temperature (lag = one year, $R^2 = 0.903$) and water flow (lag = two years, $R^2 = 0.964$), as evidenced by the high values of the coefficient of determination. Therefore, we conclude that the AO index is the most reliable predictor of standardized rate of growth for clams in this population (Figures B6 and B7).

TABLE B2. Summary of the ridge regression for the dependent variable standardized mollusk growth rates (RDD) using transformed data.

Adjusted $R^2 = 0.651$, $p < 0.025$

	Beta	Std. Err.	B	Std. Err.	p-level
Intercept			**2.447**	**0.973**	**0.040**
Temp	**0.618**	**0.213**	**0.412**	**0.142**	**0.023**
FW	–0.464	0.213	–0.280	0.128	0.066

TABLE B3. Summary of distributed lags regression model.

Lag: 2 years, $R^2 = 0.782$

Lag	B	Std. Err.	p-level
0	–0.0287	0.1592	0.8630
1	0.2298	0.1550	0.1888
2	**–0.7001**	**0.1721**	***0.0066**

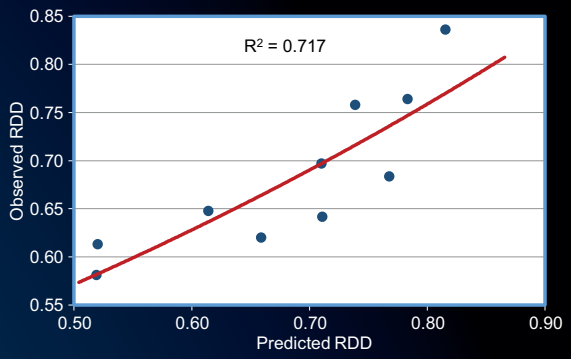

FIGURE B4. Observed mollusk growth rates (RDD) vs. predicted RDD.

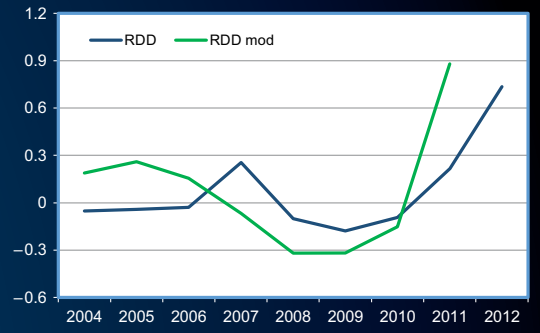

FIGURE B5. Comparison of long-term dynamics of the mollusks' growth rates (RDD) to the Arctic Oscillation (AO).

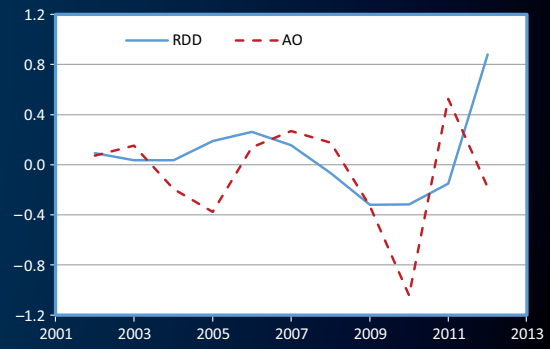

FIGURE B6. Long-term dynamics of observed and predicted values of the mollusks' growth rates (RDD) showing a two-year lag, which provides the best model agreement between the Arctic Oscillation and RDD.

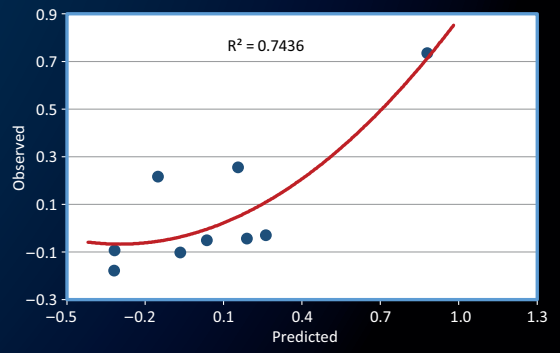

FIGURE B7. Observed vs. predicted values of the mollusks' growth rates (RDD) according to the distributed two-year lag model.

trophic-feeding marine mammals such as walrus, time-series studies on specific benthic animals, or at select sites (Grebmeier et al., 2015b, in this issue), are needed. Finally, there are no data on the maximum life span or the average age of *Nuculana radiata*, *Ennucula tenuis*, and *Psolus peroni*, but, judging from their sizes in the Chukchi Sea, it is likely they also live for at least several years. The implication of these findings is that, on the large spatial scale, benthic populations are stable, with slowly changing generations (Neiman, 1988). Our studies, reported here, support previous classifications of trophic characteristics and taxonomic structures of the benthic fauna of the Chukchi Sea. However, we see impacts of changing environmental conditions on bivalve growth rates (Box 1) and declining bivalve biomass in the rich southern Chukchi Sea region (Grebmeier et al., 2015b, in this issue). These two results suggest that although the overall benthic population structure may be stable on the large scale, small-scale studies are needed at specific sites to track the status of and changes in bivalve populations that are a critical component of the food web in the Chukchi Sea.

CONCLUSIONS

Chukchi Sea benthic ecosystems are among the most productive in the seas of the Russian and US sectors of the Arctic. The average biomass of zoobenthos in the Chukchi Sea is two times greater than in the Barents Sea. Because the Chukchi Sea is relatively shallow, pelagic-benthic coupling of upper water column production is stronger than in the Barents Sea. Maximum values of zoobenthos biomass in the Chukchi Sea were found in the southern region due to a possible cyclonic gyre where seasonal changes in hydrodynamics can result in high primary production, with phytodetritus being subsequently and efficiently exported to the underlying benthic communities. The persistence of this hydrographic feature is likely influenced by the northward flow of cold, nutrient-rich Pacific water, across-shelf differences in current speed, and variable bathymetric steering of these waters. Due to the resulting deposition of large amounts of fresh phytodetritus to the benthos, the proportion of surface deposit feeders in the zoobenthos is rather high, while that of filter feeders is smaller than in the Barents Sea. Analysis of the spatial distribution of the key species may be useful not only for assessment of bioresources but also for studies of long-term fluctuations of zoobenthos under the influence of various natural and anthropogenic factors.

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