THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY
# Oceanography

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Denisenko, N.V., and J.M. Grebmeier. 2015. Spatial patterns of bryozoan fauna biodiversity and issues of biogeographic regionalization of the Chukchi Sea. *Oceanography* 28(3):134–145, http://dx.doi.org/10.5670/oceanog.2015.62.

DOI

http://dx.doi.org/10.5670/oceanog.2015.62

# Spatial Patterns of Bryozoan Fauna Biodiversity and Issues of Biogeographic Regionalization of the Chukchi Sea

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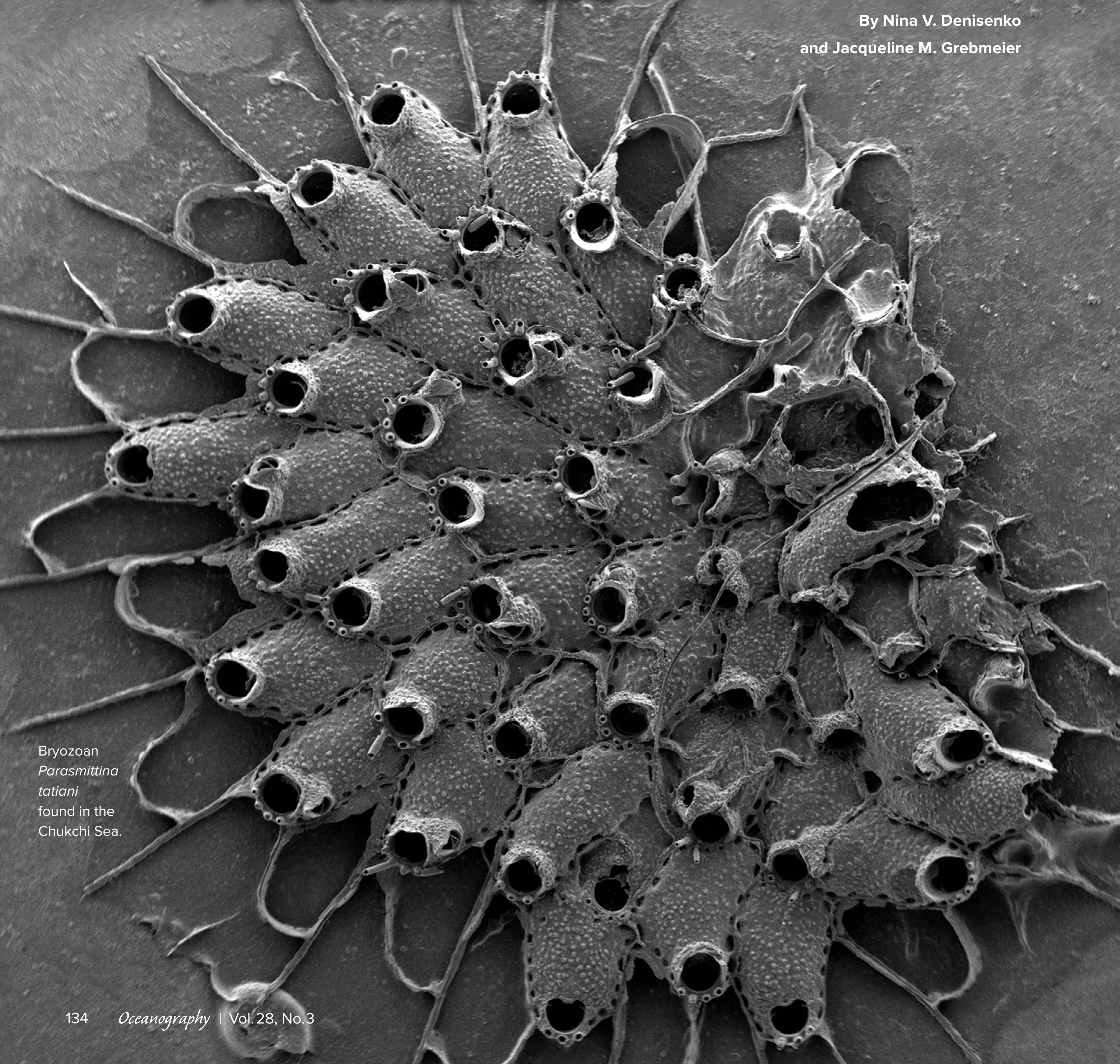

Bryozoan *Parasmittina tatiani* found in the Chukchi Sea.

**ABSTRACT.** Based on extensive data from a variety of sources, including Russian-American Long-term Census of the Arctic expeditions in 2009 and 2012, this paper provides an update on the richness of bryozoans in the Chukchi Sea and evaluates the variation in bryozoan biodiversity along environmental gradients (e.g., depth, bottom water temperature, and bottom sediment composition). Though bryozoans have been studied in only about 77% of the Chukchi Sea, temperature gradients across geographical zones appear to control fauna richness. The inflow of Pacific water through the Bering Strait into the Chukchi Sea strongly influences the distribution of the 204 registered bryozoan species, about 30% of which have a Pacific origin. The greatest similarities between bryozoan fauna in the Chukchi Sea and those occurring further south in the Bering Sea are found in the southern and eastern parts of the Chukchi Sea. The transitional zone between Arctic and Pacific high-boreal biogeographic regions occurs in the western and northern areas of the Chukchi Sea. The dominance of boreal bryozoan species over Arctic species in the southeastern and southern areas of the Chukchi Sea identifies this area as part of a Pacific high-boreal region. The boundary between boreal and northern transitional zones corresponds to a 50:50 ratio of boreal to Arctic species, with the transition extending from Cape Serdtse-Kamen' in the western Chukchi Sea northward to Point Franklin (68°30'N) in the eastern Chukchi Sea.

## INTRODUCTION

The study of Earth's faunal biodiversity remains a pressing challenge within the field of biology. The number of publications devoted to this problem has increased, although most studies are devoted to terrestrial ecosystems; only about 10% represent biodiversity studies in the marine environment (Hendriks et al., 2006), and most of these have been conducted in the temperate seas of the world ocean.

Biodiversity studies of fauna in Arctic seas are steadily increasing, although the number of publications on this issue remains limited. In recent years, a number of reviews (e.g., Bluhm at al., 2011; Kosobokova et al., 2011; Piepenburg et al., 2011; Josefson et al., 2013) have been based on an increasing number of field expeditions over the past two decades. However, the biodiversity and spatial distribution of bryozoans, in particular, still have not been estimated, although this group is one of the most diverse fauna in the Arctic (Gontar and Denisenko, 1989; Josefson et al., 2013). Chukchi Sea bryozoans were one of the poorest known Arctic faunal types (around 140 species; Kluge, 1962; Gontar and Denisenko, 1989; Gontar, 2001) until recent compilations by N. Denisenko (2008) and N. Denisenko and Kuklinski (2008) increased the number of known bryozoan species (see online supplementary materials). Notably, most publications concerning bryozoans have been mainly descriptive, with listings of species and their synonymy, and less focused on their ecological importance.

Understanding of Chukchi Sea bryozoan fauna has been enhanced by a synthesis using modern nomenclature of all bryozoan faunal data based on both the collection of animals at the Zoological Institute of the Russian Academy of Sciences and early data collected in the framework of the Russian-American Long-term Census of the Arctic (RUSALCA) program that began in 2004 (N. Denisenko, 2008; N. Denisenko and Kuklinski, 2008). Additional collection of benthic samples during the RUSALCA 2009 and 2012 expeditions further increased records of bryozoans and species counts beyond the 2008 publications. We describe these findings here.

Magurran (2004) argued that species richness is the simplest way to estimate assemblage species diversity. However, estimation of species richness is quite difficult if information about species composition is lacking, especially for large regions. Although biodiversity is often estimated using quantitative characteristics of abundance and biomass, estimating biomass for a majority of bryozoan species is difficult due to the colonial and often encrusting nature of the organism (N. Denisenko, 1983). Moreover, old archived data do not contain information about bryozoan abundance. This fact may be one additional reason why there has been no statistical estimation of bryozoan biodiversity for the Arctic. As a result, there has been no generalized report on bryozoan biodiversity or the relationship between faunal richness and environmental factors such as depth, bottom water temperature, and bottom sediment composition. Taking into account the intensity of zoobenthos sampling in the Chukchi Sea (about 500 stations made by Russian expeditions and over a 1,000 stations by US expeditions alone), it could be assumed that the bryozoan records are sufficient to evaluate the biodiversity of this faunal group; however, the quality of the available data varies greatly and assumptions must be made to utilize the different data sets.

The Chukchi Sea is one of the world ocean's transitional areas, and there are contrasting opinions regarding its biogeographic status. Some scientists consider the whole sea to be completely in the Arctic zone (Golikov, 1980; Andriyashev and Shaposhnikova, 1985; Briggs, 1995), while others regard it as a transitional zone between the Arctic and boreo-Arctic zones, depending on spatial location (Grebmeier et al., 2006). Yet other scientists offer an intermediate interpretation, where the southern part of the Chukchi Sea is a transitional zone, with the remainder belonging to the Arctic zone (Mironov, 2013). Still others regard the southern part of the Chukchi Sea as part of the Pacific boreal zone (Filatova, 1957; Scarlato, 1981; Petryashov at al., 2013).

Based on our data compilations, first, we hypothesize that bryozoan diversity is higher in the Chukchi Sea than previously recognized. Bryozoan species there are distributed unequally and, in fact, form local assemblages. The level of our understanding of bryozoan diversity depends on the intensity of bryozoan sampling in different regions of the Chukchi Sea, coincident with the known relationship between the variability of environmental factors (e.g., seawater temperature, sediment grain size) and the different water masses in the region. Second, we hypothesize that bryozoans, as sessile animals, are suitable organisms to use to determine biogeographic zonations within the sea. Our current analysis of spatial changes in the biogeographic composition of bryozoans within the Chukchi Sea should help reduce the disparity in interpretations of their biogeographic status in this region.

## MATERIALS AND METHODS

This work is based on an analysis of archived data and data available in the literature, faunal collections held at the Zoological Institute of the Russian Academy of Sciences that were evaluated previously (N. Denisenko, 2008), and new material collected in the Chukchi Sea in the framework of the RUSALCA program in 2009 and 2012, resulting in bryozoans being identified in 170 samples collected at 128 stations (Figure 1). Equipment used to collect the recent bryozoan samples included dredges, trawls, and grabs; all samples collected at the same stations were combined for the analysis. Animals were preserved in 4% formalin in seawater, buffered by hexamine. Within two to three months, animals were sorted, identified as to species, counted, and weighed, and subsequently archived in 70% ethanol. The results from these new bryozoan samples were combined with published data, including information from American waters in the eastern section of the Chukchi Sea. Both physical samples and electronic data are archived at the Zoological Institute of the Russian Academy of Sciences.

In preparing the list of species, we used the most recent information about species taxonomy (Dick and Ross, 1988; Grischenko, 2002; Dick et al., 2005; Kuklinski and Taylor, 2006; Kuklinski et al., 2007; N. Denisenko, 2008; Bock, 2015). The determination of biogeographic groups was based on a literature review of species habitats and thermal tolerances (Golikov and Scarlato, 1972; Golikov, 1982).

### Data Analysis

Variation in bryozoan diversity was estimated at station (α-diversity) and regional (γ-diversity) levels, where species richness is seen in large areas of embayments and seas. Beta (β) diversity (the ratio between local and regional diversity) was used to show similarity or dissimilarity of species composition of regional faunas (Magurran, 2004). The data on species numbers were processed statistically using Microsoft Excel and StatSoft Statistica. Station-based rarefication curves were used to compare species numbers from the whole Chukchi Sea and at different depth ranges. The nonparametric Chao2 estimator was calculated by means using the statistical PRIMER software (v.4) in order to predict the expected number of species that would be observed in the Chukchi Sea (Clarke and Warwick, 1994). Similarity of the bryozoan fauna within the Chukchi Sea and in comparison with nearby areas (Bering Sea, Canadian Arctic Archipelago, East Siberian Sea) was estimated using presence-absence information of species with the Czekanowski-Sørensen index (Czekanowski, 1909; Sørensen, 1948), based on the formula: $Is = 2\ c/(D_i + D_{i+1}) * 100\%$, where c is the number of species in common to both stations, $D_i$ is the number of species found at the first station, and $D_i + D_{i+1}$ is the number of species at the second station. Similarity values were used for cluster analysis using a moving average routine (Pesenko, 1982; Pielou, 1984). Fauna heterogeneity was evaluated using the multidimensional scaling (MDS) method in PRIMER (v.4). In order to evaluate the reliability of the MDS analysis, the ANOSIM (analysis of similarity) statistical program was used in Primer (Clarke and Warwick, 1994).

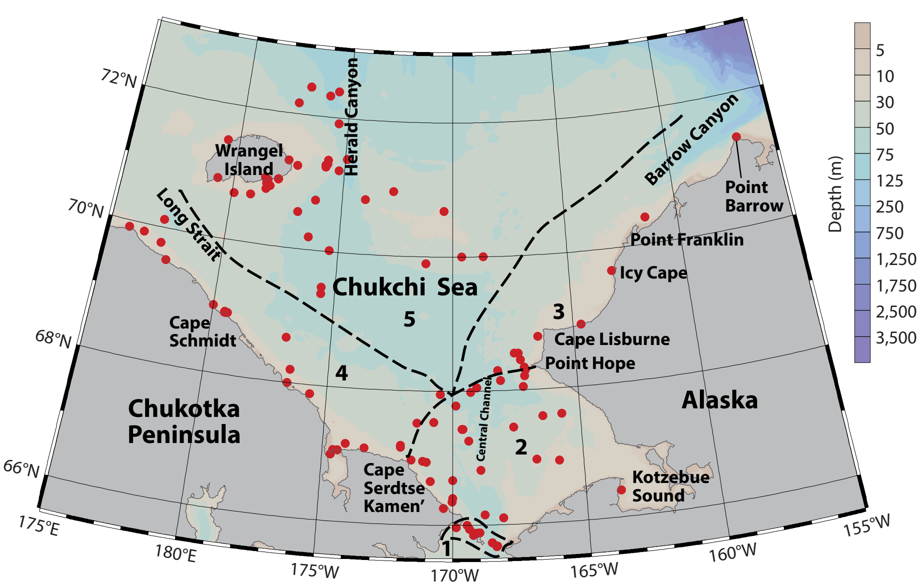


**FIGURE 1.** Station locations in five separate areas of the Chukchi Sea where bryozoan species were collected in RUSALCA 2009 and 2012 and prior cruises. 1 = Bering Strait region. 2 = Southern region. 3 = Northeastern region. 4 = Northwestern region. 5 = Northern region. Further details on the characteristics of each area are provided in the text.

## STUDY AREA

About 50% of the Chukchi Sea is shallower than 50 m (Hunt et al., 2013), and the seafloor slopes gently northward to the edge of the Arctic basin (Figure 1). Irregular seafloor relief in the Chukchi Sea is more pronounced in the northern region. In the central part of the sea, there is a small depression with depths up to 55 m that extends to the north (Weingartner et al., 1999; Pisareva et al., 2015, in this issue), and two canyons—Herald and Barrow, with depths of up to 120 m—are located in the northern portions of the western and eastern areas, respectively, at the edge of the continental slope (Dobrovolsky and Zalogin, 1982; Weingartner et al., 1999).

The Chukchi Sea is characterized by intense hydrodynamics, with current speeds ranging from 15–75 cm $s^{-1}$, depending on location (Woodgate et al., 2005; Weingartner et al., 2005, 2013). There are two main currents. The Alaska Coastal Current (ACC) generally flows northward along the Alaskan coast toward Barrow Canyon (Aagaard and Carmack, 1989; Walsh et al., 1989), and it advects Alaska Coastal Water (ACW) into the region. ACW is present from May to about the end of December (Woodgate and Aagaard, 2005). Bottom water temperatures can reach 10°C over the shallow southeastern portions of the Chukchi Sea. By comparison, the bulk of the water transiting the Chukchi Sea (>80%) is a combination of Anadyr Water and Bering Shelf Water that mixes through the Bering Strait to form Bering Sea Water (BSW; Coachman et al. 1975; Weingartner et al., 2005; Woodgate et al., 2005). BSW during summer is colder (about 2°–4°C) and saltier (>31.8) than ACW ($T > 4$°C and $S < 31.8$) (Weingartner et al., 2005). Topographic shoals in the northern Chukchi Sea split the northward flow of BSW into three branches. One branch flows east toward Barrow Canyon, one flows west through Herald Canyon, and the other flows between the shoals via the Central Channel (Woodgate et al., 2010; Weingartner et al., 2013; Danielson et al., 2014).

In the extreme southwestern Chukchi Sea, the seasonal Siberian Coastal Current (SCC) flows southward along the coast in some years (Weingartner et al., 1999, 2013). This cold, fresh SCC (bottom water temperature 0°–1.5°C) may occasionally reach the Bering Strait, but it is usually deflected into the central Chukchi Sea. There are two opinions about outflow from the East Siberian Sea in the SCC. One is that the flow is present permanently, forming a cyclonic water flow circulation in the southern part of the Chukchi Sea (Sirenko and Gagaev, 2007). The second is that there is a variable current that reverses periodically between the East Siberian and Chukchi Seas (Münchow et al., 1999; Weingartner et al., 2005).

The current flowing northward through Bering Strait is well mixed and has high nutrient content. As the current moves northward, it slows down and spreads out north and northwest of the strait, resulting in enhanced production in the southern Chukchi Sea (Weingartner et al., 2005). Bering Strait and southern Chukchi Sea waters are rich in organic matter, driven by both the high nutrient inflow water supporting high seasonal in situ production as well as advected organic carbon from the south (Feder et al. 2005, 2007; Grebmeier et al., 2006, 2015; Hirawake et al., 2012). Although soft sediments dominate the seafloor in this region, coarse-grained sediments are found in some areas of the Chukchi Sea. Their distribution is related to variable current flow and transport within ice, with subsequent deposition of heavier particles when the currents slow down and the ice melts. The most favorable habitats for bryozoans are coarse bottom sediments, which mainly occur near capes, in Bering Strait, in nearshore coastal areas, and with patchy distribution in the Chukchi Sea (Kosheleva and Yashin, 1999).

To evaluate the similarity of local bryozoan fauna among different sites and to identify the biogeographic status of the species within the Chukchi Sea as part of an MDS analysis, we assigned each station to one of five areas (Figure 1) based on habitat descriptions. These areas, summarized below, differ in environmental conditions that include thermal regime, duration of ice cover, hydrodynamic activity, and grain size of bottom sediments.

**AREA 1:** The most distinctive area is the Bering Strait region, where the influence of Pacific waters and current flow are the highest in our study area. Bering Strait is characterized by relatively high bottom water temperatures in summer (~4°C), with fast near-bottom currents coincident with coarse-grained bottom sediments.

**AREA 2:** The southern part of the Chukchi Sea is relatively shallow (<50 m deep). The influence of Pacific waters is highest here, with above 0°C bottom water temperatures during the ice-free season. Current speeds are lower at this site than in Bering Strait further south, resulting in a mixture of mud and sand fractions, with some intermixing of coarser sediments (S. Denisenko et al., 2015, and Pisareva et al., 2015, both in this issue).

**AREA 3:** This region is influenced by ACW in the coastal areas to the east, with depths of less than 20 m. It has large concentrations of coarse-grained sediments mixed with boulders and rocks near the capes (e.g., Cape Lisburne).

**AREA 4:** This region in the southwestern part of the Chukchi Sea includes Long Strait, the coastal waters of Russia, and the offshore waters of the Chukchi Sea north to 70°N. This shallow area is characterized by predominantly below 0°C bottom water temperatures, and coastal erosion that is the source of the fine-grained sediment that dominates the seafloor in this region and that is not suitable for bryozoan settlements.

**AREA 5:** This region is located in the northern Chukchi Sea. It covers the coastal waters around Wrangel Island and the offshore regions of the Chukchi Sea extending to 73°N and eastward to Barrow Canyon. Compared to the other sites, Area 5 as a whole is characterized by a significant variation in depths that reach 100–150 m in the canyons. Bottom water temperatures in both shallow and deep waters in this region are low, often dropping to negative values (Weingartner et al., 2013). Although soft sediments exist in this area, rocks and mixed sediments that include pebble and gravel fractions form local subregions (Kosheleva and Yashin, 1999; Grebmeier et al., 2006).

**TABLE 1.** Taxonomic structure of bryozoan fauna of the Chukchi Sea.

| FAMILY | TOTAL GENERA FOR EACH FAMILY WITH ASSOCIATED NUMBER OF SPECIES IDENTIFIED IN PARENTHESES |
|---|---|
| Adeonidae | *Adeonella* (1) |
| Alcyonidiidae | *Alcyonidium* (9), *Alcynioides* (1) |
| Annectocymidae | *Entalophoroecia* (2) |
| Aspidostomatidae | *Reussinella* (1) |
| Bitectiporidae | *Schizomavella* (2), *Hippomonavella* (1), *Hippoporina* (6) |
| Bugulidae | *Bugula* (1), *Crisularia* (1), *Dendrobeania* (9), *Semibugula* (1), *Bugulopsis* (2) |
| Calloporidae | *Callopora* (5), *Cauloramphus* (3), *Tegella* (8), *Bidenkapia* (2), *Septentriopora* (1), *Doryporella* (1), *Amphiblestrum* (2) |
| Candidae | *Caberea* (1), *Notoplites* (1), *Scrupocellaria* (2), *Aquiloniella* (2), *Tricellaria* (5) |
| Celleporidae | *Celleporina* (3), *Buffonellaria* (1) |
| Cerioporidae | *Borgella* (2), *Fungella* (1) |
| Cheiloporinidae | *Cheiloporina* (3) |
| Cribrilinidae | *Membraniporella* (1),*Cribrilina* (2) |
| Crisiidae | *Crisiella* (1), *Crisia* (5), *Diplosolen* (2) |
| Cryptosulidae | *Harmeria* (1) |
| Electridae | *Einhornia* (2) |
| Escharellidae | *Escharella* (5), *Hincksipora* (1), *Hemicyclopora* (1) |
| Eucrateidae | *Eucratea* (4) |
| Exochellidae | *Escharoides* (1) |
| Fascigeridae | *Fasciculiporoides* (1) |
| Flustrellidridae | *Flustrellidra* (3) |
| Flustridae | *Carbasea* (2), *Serratiflustra* (1), *Securiflustra* (1), *Hincksina* (1), *Terminoflustra* (1) |
| Gigantoporidae | *Cylindroporella* (1) |
| Hippothoidae | *Hippothoa* (1), *Plesiothoa* (1), *Celleporella* (2) |
| Lepraliellidae | *Lepraliella* (1), *Hippoporella* (2), *Rhamphostomella* (10) |
| Lichenoporidae | *Lichenopora* (1), *Patinella* (2), *Disporella* (2) |
| Microporellidae | *Microporella* (3) |
| Microporidae | *Microporina* (1) |
| Myriaporidae | *Myriapora* (2), *Myriozoella* (2) |
| Oncousoeciidae | *Oncousoecia* (3), *Proboscina* (1) |
| Plagioeciidae | *Plagioecia* (2) |
| Porellidae | *Porella* (13), *Cystisella* (3) |
| Romancheinidae | *Arctonula* (1) |
| Schizoporellidae | *Schizobrachiella* (2) |
| Smittiniidae | *Smittina* (6), *Smittoidea* (1), *Parasmittina* (4) |
| Stomachetosellidae | *Stomachetosella* (6), *Pachyegis* (2), *Lepralioides* (1) |
| Teuchoporidae | *Phylactella* (1) |
| Tretocycloeciidae | *Tetrocycloecia* (1) |
| Tubuliporidae | *Tubulipora* (3), *Diaperoecia* (1), *Bathysoecia* (3) |
| Umbonulidae | *Umbonula* (1), *Ragionula* (1), *Posterula* (1) |
| Vesiculariidae | *Amathia* (2), *Vesicularia* (1) |

**TABLE 2.** Correlation analysis of bryozoan diversity at individual stations (α-diversity) with environmental and geographic parameters.

| PARAMETER | PEARSON CORRELATION VALUE | *p*-LEVEL |
|---|---|---|
| Depth | 0.11 | 0.156 |
| Bottom water temperature | 0.33 | **0.016** |
| Latitude | 0.02 | 0.850 |
| Longitude | 0.37 | **0.000** |

## RESULTS

### General Characteristic of Bryozoan Fauna

The present study increased the number of bryozoan species identified in the Chukchi Sea from 187 (N. Denisenko, 2008; N. Denisenko and Kuklinski, 2008) to 204. These species belong to 87 genera, 40 families, three orders, and two classes (Table 1). Five families (Calloporidae, Bugulidae, Candidae, Lepraliellidae and Smittinae) were the richest in species composition (Table 1). The most diverse fauna were found within four genera: *Alcyonidium*, *Tegella*, *Dendrobeania*, and *Rhamphostomella* (Table 1).

### Local or α-Diversity and Its Relation to Environmental Parameters

Bryozoan species richness varied from one to 89 species per station. Higher diversity (from 30 to 89 species) was found at stations located near capes, regardless of sampling gear, but in most samples, the number of species varied from one to five. Changes in bryozoan species richness at the local level were not significantly related to changes of depth, but there was a trend of increasing species richness with bottom water temperature (Table 2). There was also no significant relationship of α-diversity of bryozoan richness with a latitudinal gradient (Table 2), but there was some trend toward increasing bryozoan richness longitudinally, from west to east in the Chukchi Sea (Table 2).

### Regional or γ-Diversity and Its Relation to Environments

As noted above, analysis of material collected during RUSALCA cruises in 2009 and 2012 increased the number of identified bryozoan species to 204 (Table 1). However, applying the Chao2 index for estimating the number of expected species within this group indicates that the Chukchi Sea bryozoan fauna could contain 264 ± 20 species. Assessment of species richness by the rarefication method (Clarke and Warwick, 1994) indicates that the curve of changes in the number

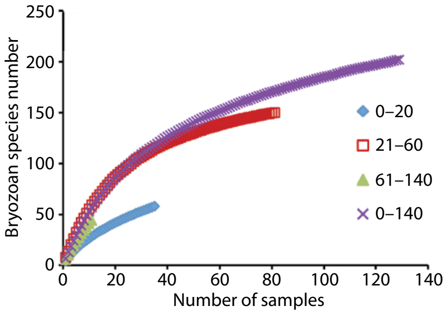


**FIGURE 2.** Station-based rarefication curves of bryozoan species richness in the Chukchi Sea (average curves from 900 permutations). Depth range (m) is shown by different symbols and colors.

of species, even including all the collections from stations in the Chukchi Sea, has not approached the asymptote, suggesting that there are still bryozoan species to be found (Figure 2). Examination of bryozoan species richness at different water depths indicates that most bryozoan species occur at 20–60 m depth, a range that covers most of the Chukchi Sea (Figure 2). However, species richness is low at depths less than 20 m (particularly in the eastern Chukchi Sea along the Alaska coast) as well as in deeper areas within the canyons and troughs with depths >60 m (Figure 2) and the upper slope regions likely due to the small number of stations that were sampled at these depths. It is possible that since most of the samples were collected at depths from 20 m to 60 m, a region supporting the maximum diversity of bryozoans, our data are biased by the inequity of sampling at shallower depths (Figure 3a), as could also be the case with α-diversity that focused on depths of 30 m to 50 m.

Most bryozoan species were found in the temperature range from 1°C to 2°C and on mixed muddy-sand and pebble-gravel bottom sediments, although they were not significantly correlated with those parameters (Figure 3b and 3c, respectively). However, bryozoan species richness increased significantly with longitude from west to east ($R^2$ = 0.25; $p$ < 0.01; Figure 3e).

## Differential or β-Diversity

The level of similarity of species composition at different depths indicated that at a similarity level of 13%, calculated as the average value for the matrix, there are two different bathymetric complexes of bryozoan species in the Chukchi Sea (Figure 4): (1) the shallow complex, covering almost all the waters of the sea (depth <100 m), and (2) the deeper sublittoral faunal complex found deeper than 100 m in canyons and at the edge of the continental shelf. The 45% level of similarity separates nearshore (0–20 m) from offshore (>20 m), and shelf (20–50 m) from canyons and upper slope (50–100 m) (upper branches of Figure 4).

The level of similarity of bryozoan species composition among selected areas of the Chukchi Sea (see Figure 1) was also evaluated by MDS, coincident with results from the similarity cluster analysis. The calculations indicate the presence of two faunistic complexes at a 45% dissimilarity level (Figure 5). One complex is composed of stations in the southern and eastern parts of the sea, including Bering Strait (Areas 1–3), and the second complex is composed of stations in the remainder of the sea and extending to the shelf edge (Areas 4 and 5). Subsequently, using ANOSIM to test differences between predetermined regional groups indicated that the level of their difference is high, although barely significant (R = 0.875; $p$ = 0.06).

In order to evaluate biodiversity on a regional level, we compared the five Chukchi Sea areas in our study with neighboring seas (East Siberian and Bering Seas) and the Canadian Arctic Archipelago. Using the MDS method, the results indicate that the southern part of the Chukchi Sea (Area 2), the Bering Strait (Area 1), and the eastern part of the

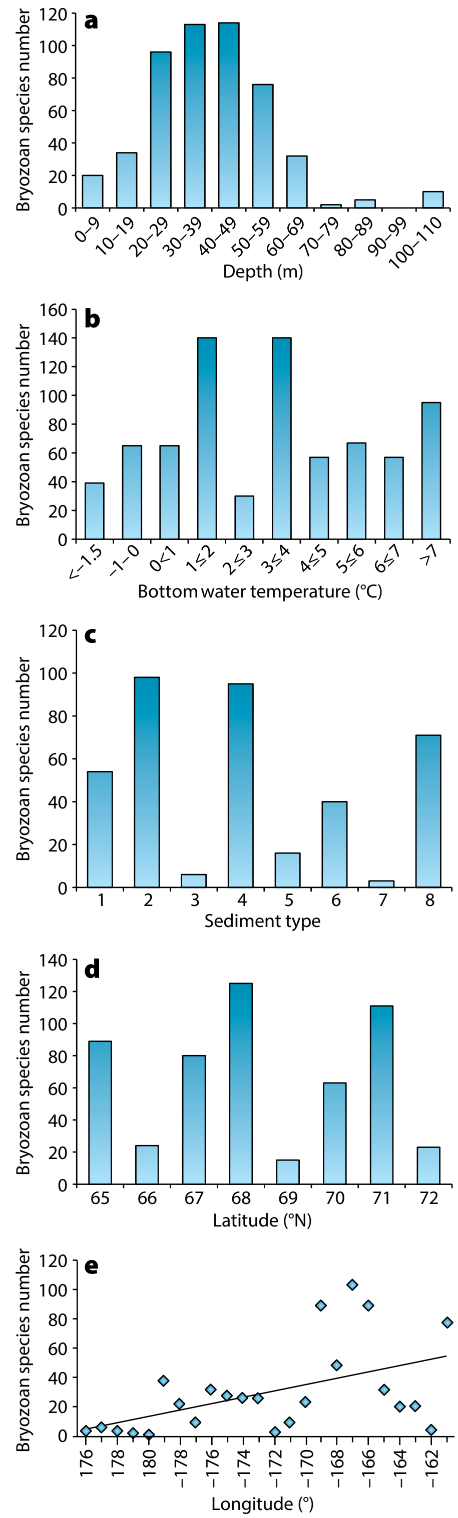


**FIGURE 3.** Variation of regional diversity of bryozoans within the Chukchi Sea along the general environmental gradients of (a) depth, (b) bottom water temperature, and (c) sediment types, and along the geographical gradients of (d) latitude and (e) longitude (R = 0.51; p <0.01) in the Chukchi Sea. The line in (e) is the trend in variation of the bryozoan fauna. Types of sediments in (c): 1 = Mud with clay (0.005–0.1 mm). 2 = Muddy or fine sand (0.1–1.0 mm). 3 = Coarse sand (2–3 mm). 4 = Sand with small pebbles and gravel (1–5 mm). 5 = Pebbles, gravel (5–20 cm). 6 = Shells with gravel and sand (1–5 cm). 7 = Stones, boulders, rocks (>20 cm). 8 = Rocks with pebbles. Sediment data were obtained from Kosheleva and Yashin (1999) and ZIN RAS data sets.

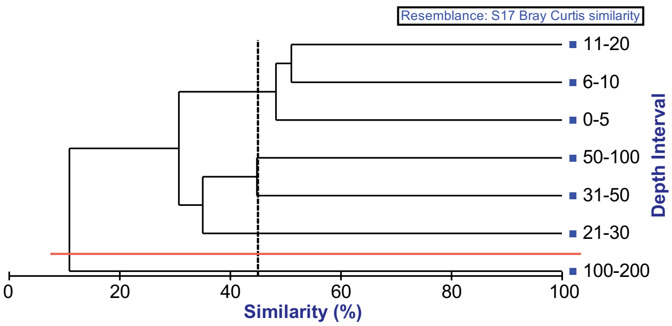


**FIGURE 4.** Bathymetric complexes of bryozoan species of the Chukchi Sea. The red line divides the shallow shelf complex from the deeper sublittoral faunal complex.

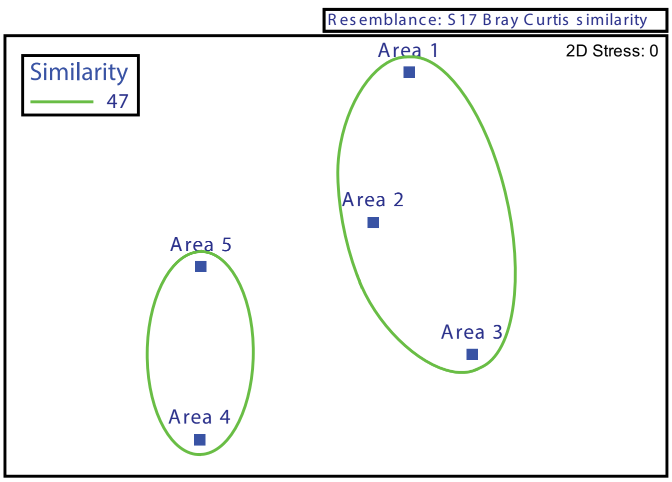


**FIGURE 5.** Bryozoan complexes inhabiting the Chukchi Sea. Area 1 = Bering Strait region. Area 2 = Southern region. Area 3 = Northeastern region. Area 4 = Northwestern region. Area 5 = Northern region. The text contains further details on the characteristics of each area.

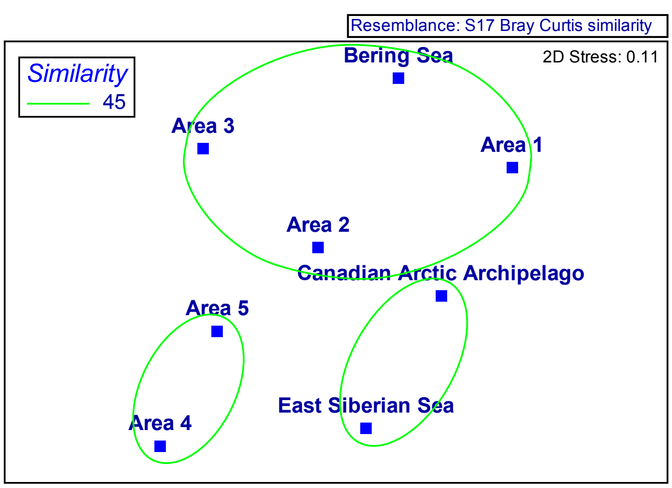


**FIGURE 6.** Species composition similarities in subareas of the Chukchi Sea compared with neighboring Arctic seas. Area 1 = Bering Strait region. Area 2 = Southern region. Area 3 = Northeastern region. Area 4 = Northwestern region. Area 5 = Northern region. The text contains further details on the characteristics of each area.

Chukchi Sea (Area 3) form a common cluster with the Bering Sea bryozoan fauna at a 45% similarity level (Figure 6). The western (Area 4) and northern (Area 5) parts of the Chukchi Sea form a separate cluster that shows low similarity with the Bering Sea bryozoan fauna as well as with the bryozoan fauna of neighboring Arctic regions, specifically the East Siberian Sea and the Canadian Arctic Archipelago (Figure 6). Testing the differences between station clusters using ANOSIM indicates a high level of difference between these groupings ($R = 0.675$; $p = 0.005$)

## Biogeographic Composition of the Bryozoan Fauna of the Chukchi Sea and Its Change Along Environmental Gradients

Biogeographic characteristics of bryozoan species in the Chukchi Sea were evaluated by analyzing geographical distribution data in the world ocean (see Materials and Methods section). We determined that 204 species found in the Chukchi Sea can be attributed to 12 biogeographic categories (Table 3). Boreo-Arctic species that have a wide range dominated all other bryozoan species in the study. No boreo-Arctic bryozoan species of Atlantic origin were found in the Chukchi Sea, whereas boreo-Arctic bryozoans of Pacific origin made up about 17% of the whole faunal group. By comparison, the majority of boreal species (60%) was of Pacific origin. Arctic bryozoans were mainly represented by circumpolar species (>50%). The numbers of Arctic and boreal species in the Chukchi Sea were roughly equal (31 and 30 species, respectively; Table 3).

Rather than providing a detailed analysis of the formation of modern bryozoan fauna in the Chukchi Sea here, we combined categories in Table 3 into three main groups for further analysis: Arctic, boreal, and boreo-Arctic. The latter two categories mainly describe the biogeographic status of the Chukchi

**TABLE 3.** Biogeographic composition of bryozoan fauna of the Chukchi Sea.

| BIOGEOGRAPHIC CATEGORY ACCORDING TO GOLIKOV (1982) | SPECIES NUMBER OF EACH CATEGORY | PORTION WITHIN CATEGORY |
|---|---|---|
| Arctic, Circumpolar | 17 | 53.1% |
| Arctic, Amerasian | 6 | 18.8% |
| Arctic, Eurasian | 9 | 28.1% |
| Boreal, Pacific | 8 | 25.0% |
| High Boreal, Pacific | 20 | 62.5% |
| Amphiboreal | 4 | 12.5% |
| Subtropic-Arctic | 3 | 2.1% |
| Boreo-Arctic, Widespread | 72 | 51.4% |
| High Boreo-Arctic, Circumpolar | 31 | 22.2% |
| Boreo-Arctic, Pacific, Circumpolar | 3 | 2.1% |
| High Boreo-Arctic, Pacific | 31 | 22.2% |

Sea. We found that proportions were not constant in the five different Chukchi areas of our study (Figure 7), and regression analysis (Figure 8) indicated that the most significant relationship was for boreal species that occur where bottom water temperatures vary.

Changes in the ratio of boreal to Arctic species indicated the dominance of boreal species in the southern part of the Chukchi Sea (Areas 1 and 2) and in the coastal zone of the Alaskan Arctic (Area 3; Figures 1 and 7). In addition, two small regions dominated by boreal bryozoans were found in the northern and western areas of the Chukchi Sea (Areas 4 and 5; Figure 7). The biogeographic boundary between the boreal and the Arctic regions is located where the ratio of boreal and Arctic species is 50:50 (N. Denisenko, 1990). Mapping of the proportions of boreal to Arctic species in the Chukchi Sea indicates a boundary that divides the southern and eastern areas from the western and northern areas of the Chukchi Sea (Figure 7).

## DISCUSSION

### Bryozoan Fauna Diversity

Because bryozoan fauna of the Chukchi Sea remains understudied, knowledge of their distribution patterns is limited. The present study is the most comprehensive investigation of bryozoan ecological diversity in the Chukchi Sea ever undertaken: Sampling during the RUSALCA 2004 to 2012 cruises increased our documentation of bryozoan species richness by 14%, resulting in a total of 204 species identified overall. Despite the high number of bryozoan samples collected to date, expected species richness is still low (Chao2 = 264 species). As indicated by bryozoan species accumulation curves, the most poorly studied regions are at depths less than 20 m and deeper than 60 m. Our work found the maximum diversity of bryozoans in the Chukchi Sea at 20–60 m depth; however, because most of the benthic samples were collected at depths of 30–50 m, our findings may be biased relative to the less sampled shallower depths.

Also, a comparison of our bryozoan data with published information on other faunal groups (Piepenburg et al., 2011) indicates that despite fewer stations with bryozoan records (136 stations), the current level of bryozoan diversity in the Chukchi Sea is comparable to the level of polychaete diversity (77.4%). However, both groups are still less studied than other fauna, such as mollusks, arthropods, and echinoderms, where nearly 90% of the species are known.

Higher bryozoan diversity may be expected in the eastern part of the Chukchi Sea (Area 3) where, despite a larger number of samples, bryozoans were not identified as to their species (Feder et al., 2005, 2007; Grebmeier et al., 2006). It is expected that bryozoan species richness is higher in the eastern Chukchi Sea and that it will be comparable to bryozoan richness of the southern part of the sea (Figure 7). This southern area is most influenced by bryozoan larvae carried into the region by Pacific waters (Bering Sea Water, Alaska Coastal Current) through Bering Strait (Aagaard and Carmack, 1989; Walsh et al., 1989; Woodgate and Aagaard, 2005).

Comparison of the total number of bryozoan species identified in the Chukchi Sea with those found in other Arctic seas indicates that they are nearly equal in taxonomic richness (Gontar and Denisenko, 1989; Gontar 2001, 2004; N. Denisenko, 2008, 2010). The most diverse families in the Chukchi Sea are also common in the Arctic Ocean (Table 1); however, the bryozoan fauna in the Chukchi Sea differs from Arctic Ocean fauna in the higher

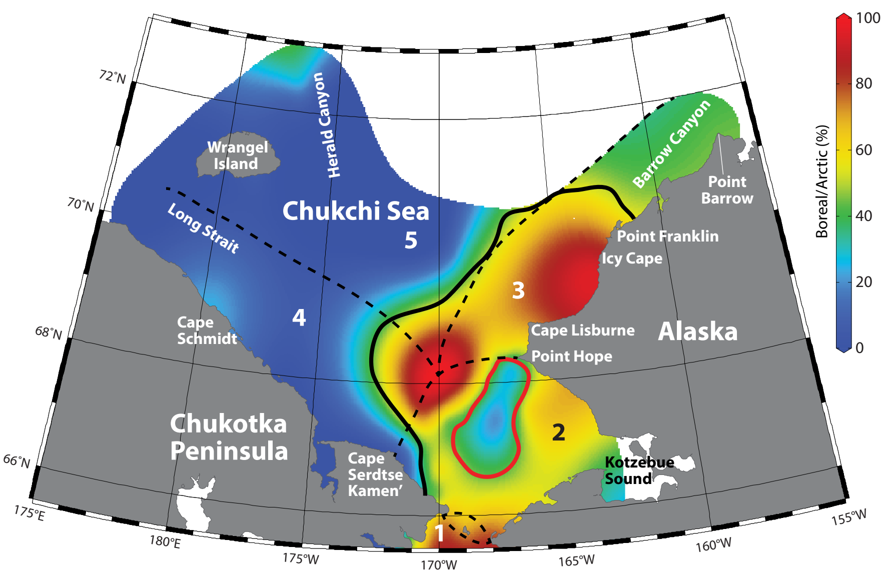


**FIGURE 7.** Predicted proportion of boreal and Arctic species of bryozoans and biogeographic boundary (solid black line) between the Arctic and the North Boreal Pacific biogeographic zones corresponding to the 50:50 ratio of boreal to Arctic species. Subareas 1–5 are separated by dashed black lines; the subarea dominated by Arctic species within the area of stable, on average, cyclonic water circulation is indicated by the solid red line.

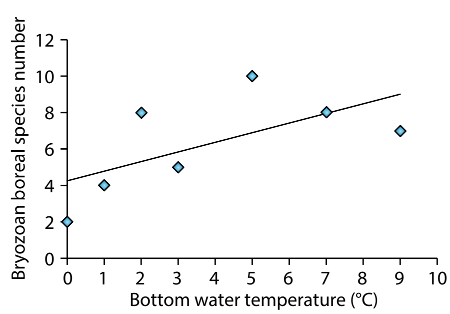


**FIGURE 8.** Number of boreal bryozoan species in relationship to bottom water temperatures (°C) in the Chukchi Sea ($R$ = 0.63; $p$ <0.09).

portion of boreal and boreo-Arctic species with Pacific origin that occur due to the strong influence of Pacific waters. The Chukchi Sea bryozoan fauna is characterized by a larger number of species in the families Flustrellidridae, Electridae, Hippothoidae, and Microporellidae that inhabit mainly the boreal regions of the shelf seas of the world ocean (Osburn, 1950, 1952, 1955; Dick and Ross, 1988; Grischenko, 2002). The Chukchi Sea is a transitional area between the Pacific boreal and the Arctic biogeographic regions, just as the Barents Sea is a transitional area between the Atlantic boreal and the Arctic biogeographic regions. But there are considerably fewer bryozoan species in the Chukchi than in the Barents Sea (N. Denisenko, 1990). The difference is due not only to the geographic positions of the seas and the origins of their associated water masses but also to a much greater variety of biotopes in the Barents Sea, its greater depth and width, and its deeper straits through which warm Atlantic Water enters the sea.

The ecological importance of spatial diversity is related to the determination of key factors that influence the biological diversity over different spatial scales. One of the most important findings of terrestrial and aquatic biodiversity studies of the temperate latitudes was the determination that many animal and plant taxonomic groups decrease in species richness from the tropics to the poles, as well as with increasing depth in the ocean (Buzas and Culver, 1991; Kendall and Aschan, 1993; Kendall, 1996; Gray, 1997; Gray et al., 1997; Clarke and Lidgard, 2000; Crame, 2000; Culver and Buzas, 2000; Roy et al., 2000; Włodarska-Kowalczuk et al., 2004; Clarke and Crame, 2010; Josefson et al., 2013). A similar latitudinal trend has been observed in the Chukchi Sea for megabenthos richness (Bluhm et al., 2009). Moreover, depth and sediment type are two important factors that influence small-scale species composition (α-diversity; Grebmeier et al., 1989; Kostylev et al., 2001). Bryozoans form epibenthic attached faunal assemblages, and their composition should be sensitive to multiple environmental factors. However, our analysis of variations in bryozoan species richness at small localities (α-diversity) in the Chukchi Sea indicated significant positive trends only with longitude and bottom water temperatures (Table 2).

Latitude has also been suggested as a moderator for epifaunal megazoobenthos, and it is considered an indirect indicator of some environmental features characteristic of the Chukchi Sea (e.g., water mass type, primary production) impacting bottom fauna (Bluhm et al., 2009; Nelson et al., 2014). Bryozoan species variation was spatially high, and our study indicates that latitude as well as longitude are important indicators of environmental variation (e.g., bottom water temperatures). Although a direct relationship between bryozoan diversity and most environmental parameters was not observed, the presence of five bathymetric bryozoan complexes, determined at a 45% similarity level, can reflect the influence of variable environmental factors. This finding may be explained by the high variability of environmental characteristics over small spatial scales (Aagaard and Carmack, 1989; Walsh et al., 1989; Weingartner et al., 1999; Woodgate et al., 2010). Comparison of our results with macrozoobenthic studies in different parts of the Arctic shelf systems supports the presence of variable relationships of bottom fauna with environmental gradients (Feder et al., 1994; Grebmeier et al., 2006; Conlan et al., 2008). Variation in the Sørensen similarity coefficients (β-diversity) also results from the complex effect of environmental heterogeneity. The presence of two major bryozoan assemblages located in both the southern and the northern parts of the Chukchi Sea is a result of large-scale physical factors, specifically in our case the Pacific water masses that have reduced influence and more complexity in the northern portions of the Chukchi Sea. The remainder of the northern bryozoan assemblage in our study is self-maintained, with low similarity to bryozoans in the southern Chukchi Sea areas, the Bering Sea further south, and the coastal waters of the East Siberian Sea and Canadian Arctic Archipelago.

## Biogeographic Aspects

Traditionally, the description of the biogeographic regionalization of the Chukchi Sea is based on comparative studies of regional fauna of different areas (species or biotic regionalization) and their evolutionary adaptation to their specific environments (Filatova, 1957; Golikov et al., 1989; Briggs, 1995). Another approach to analyzing the spatial-geographic distribution of zoobenthos is community-level or biocenotic regionalization, where the importance of species differs with respect to quantitative characteristics of the zoobenthos (e.g., biomass and/or abundance; Feder, 2005, 2007; Grebmeier et al., 2006; Blumn, 2009; Day et al., 2013) and the lower trophic taxa (e.g., microbes and plankton, Nelson et al., 2014). Population changes due to natural and anthropogenic impacts primarily take place at the species level, which can be regarded as the most sensitive. To understand how fauna will respond to an impact, we should know what changes can be expected and we should understand the state of an ecosystem prior to any impact, so knowledge about biogeographic regionalization (zonation) will be very useful for mapping ecosystem status and trends. There is no unique opinion about biogeographic regionalization of the Chukchi Sea even in the most recent faunal reviews (Mironov, 2013; Petryashov et al., 2013).

Bryozoans are sessile animals that have limited dispersal ability because the planktonic larvae of a majority of species are lecithotrophic (lipid-rich), a characteristic that can be used as a reasonable parameter for determining biogeographic zonation in Arctic seas. The bryozoan fauna of the Chukchi Sea are mainly characterized as allochthonous (originating outside of the local area). The majority of bryozoan species are widely distributed (boreo-Arctic elements) and include a large number of species with Pacific origin (boreo-Arctic and boreal elements) that most likely penetrated into the Chukchi Sea in the late Pleistocene after the opening of Bering Strait. During the thermal maxima in the Holocene, heat output of water temperatures was lower than at present, which caused penetration of Pacific waters, and Pacific boreal and boreo-Arctic species with them, far into the northwest up to the Laptev Sea. Also, Arctic fauna occupied the Chukchi Sea after the glaciers receded and with increasing sea level resulting from melting periods before thermal maxima (Golikov and Scarlato, 1989; Dunton, 1992; Petryashov, 2002, 2009). At present, atmosphere-ocean interactions and current flow directly influence the spreading of Arctic species south and boreal species north into the Chukchi Sea.

The transition in benthic community composition or ecotone is discrete in the Chukchi Sea due to changes in water masses and sediment types. The result is that dramatic ecological differences are found in closely spaced communities over a scale of a few tens of kilometers (Day et al., 2013). The transitional zone(s) of epibenthic communities occurs around 71°N, 166°W, an area in the northeastern part of the Chukchi Sea where bottom water temperatures range from 2°C to 4°C (Blanchard et al., 2013a,b). Analyses carried out using either the biotic or the species approach indicate a wider transitional zone, although its exact location has not yet been established. Mironov (2013) suggests that the boundary between the Arctic and boreal Pacific biogeographic regions is not a discrete line, but instead it corresponds to a wide transitional zone that occupies half of the Chukchi Sea, from Cape Schmidt on the Chukotka Peninsula coast of Russia to Point Barrow on the Alaskan coast of the United States, with the remainder of the Chukchi Sea belonging to the Arctic zone. Petryashov et al. (2013), by comparison, regard the southern part of the Chukchi Sea from Cape Serdtse-Kamen' on the Chukotka Peninsula, Russia, to Point Hope, Alaska, United States, as part of the boreal Pacific zone and the remainder of the Chukchi Sea toward the north as a transitional zone between the boreal and Arctic biogeographic regions. A similar region is characterized by an epibenthic community dominated by Pacific species (Bluhm et al., 2009). Our results support the studies that suggest the southern part of the Chukchi Sea is part of the boreal zone and, in addition, we propose an extension of the boundary toward the northeast near Point Franklin, Alaska. This proposed extension is supported by results of biocenotic research on macrozoobenthos that reflect a sharp change in community structure not far from Point Franklin at Icy Cape (Blanchard et al., 2013a,b). The location of a boundary in the US sector of the central Chukchi Sea also corresponds to a known hydrographic front located just north of Icy Cape (Feder et al., 1994). Therefore, according to bryozoan distributions, the biogeographic boundary in the Chukchi Sea begins just south of Cape Serdtse-Kamen' and extends north to 69°00'N and then northeast to just above Point Franklin (Figure 7). The features of our proposed revised Chukchi Sea biogeographic boundary are similar to those of the Barents Sea, the other boreal to Arctic transitional sea, where the boundary also reflects a 50:50 ratio of Arctic to boreal species (N. Denisenko, 1990) that corresponds to the largest bottom water temperature range observed in that sea (S. Denisenko, 2013). Again, our results indicate that where great variability in bottom water temperatures are observed seasonally, a variety of the bryozoan fauna are adapted to these oscillations (Figure 7). The bryozoan biodiversity variations observed in the Chukchi Sea are also likely due to the relative youth of the fauna and the variable environmental conditions in this region.

The remainder of the Chukchi Sea located north of the boundary delineated in Figure 7 is dominated by Arctic bryozoan species that are distinct from other neighboring Arctic regions, but it should nevertheless be regarded as a transitional zone. This hypothesis is supported by our study's MDS analysis, which indicates low similarity between the northern part of the Chukchi Sea and the East Siberian Sea and Canadian Arctic Archipelago. In general, our view that the northern part of the Chukchi Sea is transitional between Arctic and boreal zones does not contradict the research on mollusks, crustaceans, and echinoderms (Petryashov et al., 2013). However, station-by-station analysis of species composition revealed several small localities in the northern Chukchi Sea where boreal bryozoan species were dominant, likely the result of interannual variability and intense inflow of Pacific waters into the Chukchi Sea.

The distribution of zoobenthos is closely related to changes in environmental characteristics (e.g., Feder et al., 2005; Grebmeier et al., 2006; Hirawake et al., 2012). When unsuitable environmental conditions occur, some bryozoan species either become sterile or their reproductive functions are depressed. Thus, boreal as well as Arctic species can survive in areas where bottom water temperatures vary greatly and may warm above 4°C. However, the temperature range for reproduction is more limited, (Golikov and Scarlato, 1972) although reproduction will occasionally occur when water masses warm to optimal values, even for brief periods (Kaufman, 1977). A similar situation can occur for Arctic species in areas where temperatures are higher than optimal for them. Earlier reviews of Arctic phylogeography (Weider and Hobæk, 2000; Hardy et al., 2011) described observations of a glacial refuge in the southern Chukchi Sea. The occurrence of low bottom water temperatures just north of Bering Strait (the area indicated by the red line in Figure 7) within the southern portion of the Pacific boreal biogeographic zone (area bounded by the solid line in Figure 7) supports the finding that Arctic bryozoans are dominant in this area. In comparison, the high bryozoan species richness in the Pacific boreal biogeographic zone surrounding this Arctic patch is also characterized by higher bryozoan diversity within soft bottom sediments not suitable for most species of bryozoans.

In conclusion, bryozoan biogeography is driven by advective regimes in the Chukchi Sea and associated seasonal seawater temperatures that impact the habitat and the reproductive potential of bryozoan fauna.

## SUPPLEMENTARY MATERIALS

Supplemental information on bryozoans in the Chukchi Sea is available online at http://dx.doi.org/10.5670/oceanog.2015.62.

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## ACKNOWLEDGMENTS


We appreciate the efforts of colleagues from the Zoological Institute of the Russian Academy of Sciences, specifically S. Denisenko, S. Gagaev, V. Petriashov, and B. Sirenko for bryozoan sample collections during cruises carried out in the RUSALCA project. Research was supported by the Russian Academy of Sciences (Project N 01201351181, "Fauna and ecology of invertebrates of the Russian eastern Arctic seas and neighbouring areas"). Financial support was provided by the US National Oceanic and Atmospheric Administration Arctic Office to J. Grebmeier for RUSALCA synthesis activities via NOAA Cooperative Agreement #NA09OAR4320129: WHOI CINAR #19930.00 UMCES. We are very thankful to the two anonymous reviewers who made constructive comments and suggestions that improved the manuscript.


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## ARTICLE CITATION


Denisenko, N.V., and J.M. Grebmeier. 2015. Spatial patterns of bryozoan fauna biodiversity and issues of biogeographic regionalization of the Chukchi Sea. *Oceanography* 28(3):134–145, http://dx.doi.org/10.5670/oceanog.2015.62.