

Bryozoans as Biological Indicators and Their Role in Arctic Research

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Received October 16, 2020; revised March 2, 2021; accepted March 3, 2021

Abstract—The Arctic Ocean ecosystems are the most recent on the globe, and knowledge of their structure and function provides information for understanding the results of large-scale changes in the biosphere. This study considers trends in the distribution of the bryozoan fauna of the Eurasian shelf of the Arctic seas in modern conditions. Bryozoa serve as precise biological indicators. Changes in the species composition of their regional fauna corresponded to changes of water masses with different hydrological characteristics. Comparison of the literature data and our own data allowed us to get general across of the stability of biocenoses in some areas of the Laptev Sea during more than a century of the research history.

Keywords: Bryozoa, biological indicators, Arctic seas, biocenoses

DOI: 10.1134/S0031030122070061

INTRODUCTION

The seas of the Arctic basin are not insufficiently studied, despite a long history of exploration, as they are mostly covered by ice throughout the year, which complicates research. Most of the data obtained before the second half of the 20th century concerned only the mid-continental shelf of areas with relatively less severe ice conditions. The vast majority of the data was of a qualitative nature and did not provide information about quantitative distribution of the Arctic marine flora and fauna. Shallow waters have been especially poorly investigated, as ice conditions are commonly severe, and the large ships cannot reach them due to their draft. At the same time, there is an apparent necessity to increase fishing in poorly studied Arctic areas with difficult access. Prospecting for mineral resources has increased on the Arctic Ocean shelf, thus making it critical to understand properties of the marine Arctic ecosystems to take measures to protect them. Numerous expeditions of the marine research laboratory of the Zoological Institute to the seas of the Russian Sector of the Arctic were carried out with the aim of identifying and describing biocenoses of the shelf zone and estimating quantitative distribution of different species and biocenoses of marine animals and plants included in their composition. Additionally, these studies also aimed to study the influences of the living conditions of the environment on the fauna formation in different Arctic areas. The species composition of the fauna of the Arctic seas is nonuniform, despite their latitudinal location along the Eurasian coast, which is largely determined by the history of

settlement of the seas' populations and differences in the living conditions. Bryozoans play a significant role in benthic biocenoses of the upper shelf of Spitsbergen and the Laptev Sea, often creating dominant total biomass with a high population density in biocenoses occupying large areas in the upper shelf.

MATERIALS AND METHODS

The history of exploration of the Laptev Sea, one of the most inaccessible regions of Russian seas, has continued intermittently for more than 120 years. The first data on qualitative composition of the Laptev Sea fauna were obtained by the *Vega* expedition in 1875–1879 led by Nordenskiöld and on the ship *Fram* by Nansen. Specimens from the Laptev Sea fauna were collected by the Russian Polar Expedition led by E. Toll on the schooner *Zarya* (1900–1903), L.M. Starokadomsky during the ocean hydrographic expedition led by B. Vilkitzky on the ships *Taimyr* and *Vaigach* in 1912–1915. Further collecting from the Laptev Sea was made by an expedition led by R. Amundsen on the ship *Maud* (1918–1920).

Data on qualitative composition of fauna became available owing to collection of A.M. Popov in south-eastern part of the sea and in the Lena River mouth (1927); V.L. Vagin, N.L. Kondakov, and L.O. Retovskii in 1932; on the vessel *Temp in 1934*; Z. Makarov on icebreaker *Sedov* (1937), G.P. Gorbunov on icebreaking steamship *Sadko* (1937–1938), A.P. Andriyashev on icebreaker *Malygin* (1937); V.L. Valgin and V.M. Koltun on the icebreaking

steamship *Litke* (1948), and an American expedition on the vessel *Northwind* (1963). The benthos of the Lena River estuary is summarized by Deryugin (1932) and the benthos of the New Siberian shoal is described by Gorbunov (1946).

Until recently, the quantitative distribution of benthos in the Laptev Sea has remained nearly unexplored. The first systematic quantitative studies were conducted in August–September 1973 by the Zoological Institute of the USSR Academy of Sciences. The upper regions of the shelf down to depths of 35–40-m were examined by diving, using the pyramid system of quantitative inventory of benthic algae and invertebrates. Of particular interest are the materials predominantly collected using quantitative diving technique in July–September 1973 in the southeastern part of the Laptev Sea, on the New Siberian Shoal, and north-eastward between Kotelny and Bennett islands. The work was done on board the schooner *Farvater* using a *Zenith* data logger owned by Tiksi Hydrobase. Additionally, quantitative samples were collected using a Petersen bottom grab (with grip area of 0.025 sq. m) and a Sigsby trawl in the coastal continental waters, where high turbidity of brown water with transparency less than 0.3 m due to a complete lack of visibility minimized the advantage from research diving. On hard substrates with zero visibility, samples were collected “in the blind” by a diver using a bottom grab with sampling area of 0.05 sq. m. The quantitative diving technique was used in sufficiently transparent waters, allowing for at least minimal visibility near the bottom. At the same time, measurements were made of areas of each biotope occupied by a homogeneous population. Large and rarely encountered organisms were collected from three differentiated areas of 5 sq. m each along a measuring halyard or from frames of 1 sq. m in area. Additionally, three samples of 0.1 sq. m in area were collected from each uniform site of the biotope using a frame or a diver’s bottom grab. Seven expeditions to the Laptev Sea and neighboring areas were organized over a short period from 1993 to 1998; namely, on the vessels *Ivan Kireev* (1993), *Polarstern* (1993, 1995, and 1998), and *Professor Multanovskiy*, *Yakov Smirnitky*, *Kapitan Dranitsyn*, and *Alpha-Helix* (1995). The richest material (more than 370 samples) was collected during these expeditions at more than 150 stations. The value of these materials is that the major part is represented by quantitative samples distributed evenly to a greater or lesser degree all over the shelf of the Laptev Sea. Works in the deep water parts of the underwater Lomonosov Ridge during the latest expeditions (Gontar, 2015a, 2015b) were unquestionably successful.

Material on benthic fauna from different areas of Kongsfjorden (Spitsbergen) was collected by diving expedition as a part of the BIODAF (Biodiversity and Fluxes in Glacial Arctic Fjords) project to describe biodiversity of phyto- and zoobenthos on hard grounds from different parts of Kongsfjorden at vari-

ous depths, in 1996 and 1998. The studies were conducted using the methods on quantitative inventory of benthic population developed in the Zoological Institute of the Russian Academy of Sciences along different transects from outer part (outlet) of the fjord to inner (inlet) ice front. The animals and substrate fragments were collected by the divers using 0.25 sq. m frames at depths of 0–2.5–5–10–15–20–25–30 m. Bryozoan colonies were collected together with fragments of substrate. A total of 65 quantitative samples were collected.

Any species colonizing a new territory or basin faces similar challenges; therefore, investigation of how species spread is important for understanding the mechanisms of invasive species spreading, whether these species were introduced by humans or spread independently of human activity.

This problem can be considered as one of the aspects of general biogeography (Piccoli et al., 1986, 1991; Gontar and Naumov, 1994; Piccoli, 2002a, 2002b; Naumov and Gontar, 2004). To solve this problem, it was necessary to study the spreading of fauna along the shelf of the Arctic seas. We conducted this research together with A.D. Naumov (Gontar and Naumov, 1994; Naumov and Gontar, 2004), and it was based both on the published data and materials from the collections of the Zoological Institute of the Russian Academy of Sciences. Data on distribution of bryozoans were provided by V.I. Gontar. The analysis was limited to Boreal and Boreal-Arctic forms, which could have begun to colonize the Arctic Ocean simultaneously with the retreat of the ice shelf. All considered cases are exclusively concerned with species of Atlantic origin, since the Pacific forms are represented in the Eurasian Arctic by the small number of species; therefore, their analysis is not yet possible. Only species with uninterrupted range were considered. Exceptions were made in cases, when discontinuity did not exceed more than one sea and could be attributed to a low level of knowledge of the water area. No circum-polar species were included.

RESULTS

The Spitsbergen fauna is significantly influenced by the warm Spitsbergen current, on the one hand, and the Arctic environment due to its position beyond the Polar Circle on the other. It undergoes seasonal and annual changes dependent on large-scale climate processes. Species diversity of bryozoans and the quantitative parameters, such as biomass and the number of colonies, total biomass, and sometimes size of the colonies, varied with a depth, a type of substratum used, and distance to glaciers in Kongsfjorden (Gontar et al., 2001; 2002; Gontar, 2006), as well as being dependent on water temperature and salinity variations. Kongsfjorden and shelf meet at the outlet of the fjord, which lacks threshold, but has a deep channel, shallowing toward the marine shelf. Exchange between

the shelf and fjord at this active boundary clearly influences the hydrophysical and biological changes in the fjord system. The intermediate and deep-water layers are replaced with relatively fresh Arctic coastal water and warmer and more saline Atlantic water of the West Spitsbergen current, respectively. As a glacial fjord, Kongsfjorden is characterized by an inflow of fresh water due to melting of glaciers, seasonal variations in water temperatures, and monsoon wind system, which affects stratification and circulation of waters seasonally. The considerable inflow of freshwaters makes the fjord vulnerable to climate change. Seasonal variations in freshwater input generate very stable water stratification in summer and very weak in winter. This effect is enhanced due to heat supply from the atmosphere in summer and cooling in winter. Consequentially, in summer, circulation in the surface water layer involves shallow layer with the brackish water current. In the inner part of the fjord, salinity of the surface layers drops below 28‰ and thickness of this water layer reaches several meters in depth. Salinity increases to 33‰ with depth. Down to 20 m depth, the fjord waters are represented by mixed water due to glacier-derived runoff during the summer and fall seasons. Based on our data, the bryozoan fauna of Kongsfjorden is currently represented by 147 species and 23 subspecies collected in 1996 and 1998, which accounts for more than half of all the species known from the Spitsbergen and Barents Sea waters.

In the fjord, distribution of bryozoans along the depths gradient depends on the distance to glaciers, since the latter are a source of input of the large volume of freshwater and sediments, and is additionally determined by the presence of suitable substrates and hydrologic characteristics of the water masses. The small number of species near the surface seems to be determined by estuarine waters with salinity <28–30‰, which appear in the fjord in summer time. Distribution of bryozoans varies depending on depth. The number of bryozoan species presumably increases with depth and distance from glaciers in the fjord apex. Relative decline in the number of species at 15–20-m depth was observed in the intermediate and mouth parts of the fjord. Decline in the number of species at these depths was accompanied by a decrease in values of the total biomasses of the discovered species. This appears to be related to a change of water masses or pycnocline, which is a transition from the surface estuarine waters to deeper marine waters. In the fjord apex, distribution of bryozoans through the depths is restricted by the existence of suitable substrate due to the presence of a thick silty layer below a definite depth.

For Kongsfjorden, a combined (joint) species distribution model has shown an increase in the mean number of species to a depth of 10 m. The number of species then decreases to 20-m depth and sequentially increases in 20 to 30 m depth interval. Inside the fjord, biogeographic composition and depth distribution of

groups primarily depends on hydrological characteristics, such as water temperature and salinity. Depth distribution of different biogeographic groups largely reflects distribution of the number of species along the depth gradient. Importantly, the number of species in locations more remote from glaciers at 15–20-m depth decreases on account of the eurybiont boreal-Arctic species, having occurred in shallower waters.

The maximum values of total bryozoan biomasses at depth of 5 m was recorded from relatively shallow-water areas exposed to glacial meltwater with a low salinity <28‰ in the surface layer in summer time, areas at a certain distance from glaciers in the apex, and areas in the fjord mouth. These biomasses in the more open areas were presumably contributed by species with upright (vertical) bush-like colonies; three to four species in general. These high biomasses appear to have been caused by a current flowing from the fjord apex at 5-m depth. It defines by low salinity level and carries a vast amount of organic suspended matter. Bryozoans are sestonophages and detritophages and prefer reophilic conditions. The effect of the current is additionally supported by a species distribution along depths, which suggests that the largest number of species do not have any relationship with these maximum values of total biomasses: for instance, it was recorded from different depth ranges at Hansneset Point. It should also be stressed that the change of estuarine fauna for deeper marine fauna is accompanied by an increase in the number of encrusting species with depth, as well as an increasing contribution of encrusting organisms to total biomasses in comparison to vertical colonies. Therefore, the values of total biomass, most likely, can also be used to determine the conditions of the existence of fauna. It would be interesting to estimate variations in values of the total biomasses in different fjord areas along the same depth level. An increase in value of the total biomasses was observed everywhere towards the open part of fjord down to the 10-m depths due to the vertical colonies, occurring under the lower salinity conditions. Deeper the total biomass values decrease everywhere in open parts of the fjord. In the latter, the maximum values of total biomass were not directly related to the number of species or a particular special association of species.

Distribution of temperatures and salinity along transects in the fjord down to 50 m depth significantly differed between 1996 and 1998 (Gontar et al., 2002). The total biomasses of the entire fauna were generally higher in 1998 with a reduced meltwater runoff. By contrast, in 1996 the total bryozoan biomasses were higher down to 10 m depth, when the level of salinity was lower, whereas temperatures were higher with accordingly higher meltwater runoff. These data may leave an impression that all of the above conclusions are wrong. However, if we compare in detail the distribution of total biomass in different years, we can trace the peak of total biomass at a depth of 5 m everywhere except for Kapp Guisnez, although here they were

Table 1. Similarity (left) and inclusion measure (right) in % of bryozoan fauna at Hansneset Point, Kapp Guiszez, and Kapp Mitra in Kongsfjorden between the 0–15 m and 20–30 m ranges of depths in 1996 and 1998: (D5) Hansneset, (D6) Kapp Guiszez, and (D7) Kapp Mitra.

1996	1998	Collection areas
44.61/63.04	47.52/78.68	D5
5.40/100	46.75/72	D6
38.09/55.17	41.83/61.19	D7

higher in 1996. It should also be emphasized that the total biomass was higher in 1998 at depths lower than 15 m, where salinity and temperature were more constant throughout the seasons. In our opinion, this suggests that despite bryozoans usually prefer marine conditions, some eurybiontic species can survive and adapt to the seasonal high nutrient estuarine environment. This conclusion is confirmed by depth distribution of the number of species during these two years. The number of species was universally higher in 1998, which was determined not only by the greater quantity of samples in 1998, but also by differences in environmental conditions and food resources. Differences in species composition between 1996 and 1998 in more open Kongsfjorden areas (Hansneset Point, Kapp Guiszez, and Kapp Mitra) between 0–15 m and 20–30 m depths ranges were analyzed using the Jaccard similarity index (Jaccard, 1901) and the inclusion measure (Semkin and Komarova, 1977). As shown in Table 1, fauna in the 0–15 m range in more open areas had more similarity with fauna in the 20–30 m range (below pycnocline) in 1998, despite the similarity between them being less than 50% in both years. This is an additional argument in favor of the estuarine fauna within the 0–15 m range having unique features; strictly speaking, this may be regarded as two water basins in Kongsfjorden with different species composition and dominant species.

Based on data obtained by the expedition of the Zoological Institute of the Russian Academy of Sciences in 1973 and collections available in the Zoological Institute, Gontar compiled a list of 114 species and subspecies from three orders of Bryozoa (Gontar and Denisenko, 1989; Gontar, 1990) for the Laptev Sea. Based on the materials obtained by expeditions on the

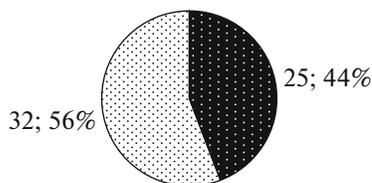


Fig. 1. Number of species of the Atlantic and Pacific origin in bryozoan fauna of the Laptev Sea: 25 Pacific and 32 Atlantic.

vessels *Ivan Kireev* (1993), *Polarstern* (1993, 1995, and 1998), and *Professor Multanovskiy*, *Yakov Smirnitky*, and *Kapitan Dranitsyn* (1995) identified by the author, the complete list numbers 147 bryozoan species and subspecies. To summarize, 195 species and subspecies from the orders Cyclostomatida, Ctenostomatida, and Cheilostomatida are presently known from the Laptev Sea according to the literature and our own data. In biogeographic terms, the bryozoan fauna of the Laptev Sea is represented by Arctic species (86 species and subspecies or 44% of the total) and boreal-Arctic species (98 species and subspecies or 50%), with a part of them being of the Atlantic and another part of the Pacific origin (Gontar, 1990, 2001, 2004, 2015a, 2015b, 2015c, 2016). Of 57 boreal-Arctic and Arctic and subtropical-boreal and subtropical-boreal-Arctic species, data on which origin is known, 25 species are of the Pacific (25.44%) and 32 species (32.56%) are of the Atlantic origin (Fig. 1). Eleven species or 6% represent a group of species heterogeneous in their origin; namely, widespread amphiboreal and Atlantic subtropical-boreal and subtropical-boreal-Arctic (Fig. 2).

Depths down to 50 m prevail in the Laptev Sea; 97 species and subspecies from known 195 ones (Fig. 3) from the Laptev Sea were found within this depth range. South of the 76th parallel, bottom areas are situated at a depth less than 25 m; thus, the number of encountered species is insignificant in this region due to brackish-water environment. The number of species increases with depth and salinity. Salinity of the marine water near the surface is 34‰ in the north-western part of the sea and up to 20–25‰ in the southern part in winter, declining to 30–32‰ and 5–10‰, respectively, in summer. Salinity rapidly increases with depth reaching 33‰. It is below 10‰ near the mouths of rivers. Ice melting and Siberian rivers discharge have a strong effect on surface water salinity.

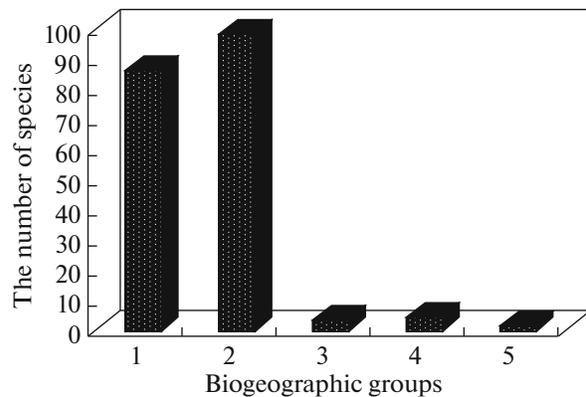


Fig. 2. Contribution of different biogeographic groups to bryozoan fauna in the Laptev Sea: (1) Arctic species; (2) boreal-Arctic; (3)–(5) other widespread group of species (non-uniform in their origin: amphiboreal and Atlantic subtropical-boreal, subtropical-boreal-Arctic).

First data on qualitative composition of the Laptev Sea fauna and, to a lesser degree, flora were obtained by expeditions on vessel *Vega* of 1875–1879 led by the Swedish researcher Nordenskiöld and Nansen’s *Fram* expedition. The qualitative studies were first systematically conducted in August–September 1973 by the Zoological Institute of the USSR Academy of Sciences. In accordance with the requirements, qualitative distribution was studied both in macro- and meio-benthos. Concurrently, the New Siberian Shoal and adjoining Laptev Sea waters were examined with respect to the plankton and general hydrological and landscape background in the upper shelf down to the depths of 35–40 m in diving equipment. Of special interest are the explorations in the southeastern part of the Laptev Sea and northeastward between the Kotelnny and Bennett islands. Alongside with the Zoological Institute expeditions, this area was explored by expeditions led by A.Yu. Gukov from the Lena Delta Wildlife Reserve. Bryozoans were recorded based on materials from all expeditions, which collected quantitative data, in 44 biocenoses. Some data on stability of the presence of some bryozoan species in a number of biocenoses of the Laptev Sea throughout the entire history of the sea exploration beginning the second half of the 19th century are of interest from the standpoint of history of the fauna formation and assumptions on hydrological conditions in the course of its formation (Gontar, 2016). They testify that with the availability of suitable substrates, it is precisely the hydrological regime of water masses that plays an important role in the occurrence of certain species associations. Published data on quantitative distribution of bryozoan species in the Laptev Sea in biocenoses, some of which were dominated by bryozoans were particularly interesting as they could be com-

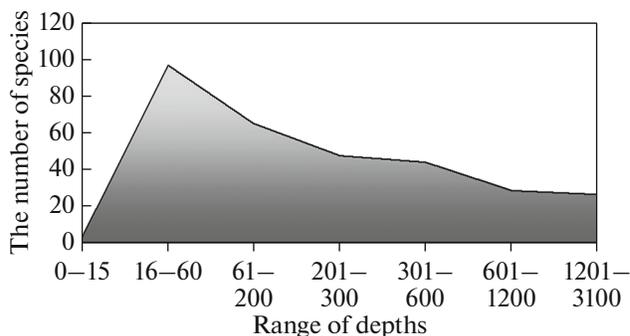


Fig. 3. Distribution of bryozoan species and subspecies encountered in the Laptev Sea along the depth gradient.

pared with our data that were based on the Zoological Institute collections.

Stuxberg (1883), who described the *Alcyonidium*–formation (generous amount of *Alcyonidium mammilatum* Alder, 1857), was the first to mention a biocenosis dominated by bryozoans. Most likely it has been the biocenosis reported by him from station 74, southwest of Olenek Bay with the depth of four to six feet (1.2–1.8 m) with a substrate represented by silt or coarse sand. According to his report, numerous species of Bryozoa occurred in that community. At 14.5 m depth, *A. mammilatum* was reported by Kluge (1929) from rocky bottom of western part of Olenek Bay (Table 2).

Gukov (1994b) who studied the bottom fauna of Lena Polynya in 1985–1990 north of Olenek Bay (apparently, close to the biocenosis location indicated by Stuxberg) at 22.5 m depth and of sandy silts in the *Tridonta borealis* + *Portlandia siliqua* biocenosis (Table 2) indicated the permanent presence of the

Table 2. Biocenosis *Alcyonidium* in the southwestern part of the Laptev Sea

Southwest of the Laptev Sea					
Kluge, 1929	In western part of Olenek Bay on rocky substrate <i>Alcyonidium mammilatum</i> at a depth of 14.5 m	In 1985–1990 Gukov, 1994a	While studying a bottom fauna of Lena Polynya north of Olenek Bay (apparently, close to the biocenosis location indicated by Kluge and Stuxberg) at a depth of 22.5 m and on sandy silt in the <i>Tridonta borealis</i> + <i>Portlandia siliqua</i> biocenosis, Gukov (1994b) noted a persistent occurrence of bryozoans <i>Eucratea loricata</i> , <i>Alcyonidium disciforme</i> in samples (six samples).	1878–1879	Stuxberg described <i>Alcyonidium</i> –formation (<i>Alcyonidium mammilatum</i> in extremely large quantities); this appears to have been the biocenosis reported by him from station 74, southwest of Olenek Bay with the depth of four to six feet (1.2–1.8 m) and seabed substrate represented by silt or coarse sand. Numerous species of Bryozoa occurred as well

Table 3. Biocenosis *Alcyonidium disciforme* in the southwest of the Laptev Sea

Southwest of the Laptev Sea					
Abrikosov, 1929	Toward in the direction of Bol'shoi Lyakhovskii Island and collected from the 16–24 m depth range on silty substrates, <i>Alcyonidium disciforme</i> encountered on silty substrates at lower salinity, ranging from 21.56 to 23.37‰.	In 1985–1990 Gukov (1994b)	Northeast of the Lena River delta 130 km away from the shore at a depth of 26 m and on sandy silt in the <i>Rhizomolgula globularis</i> + <i>Saduria sabini</i> biocenosis, <i>Alcyonidium disciforme</i> was a characteristic species for the biocenosis	Petryashev et al. (1994) based on the 1990s expeditions materials	Northeast of the Lena River delta at 17 m depth and on silty–sandy ground, biocenosis <i>Alcyonidium disciforme</i> (biomass 8 g/sq. m).

Table 4. Biocenosis with the dominant species *Eucratea loricata*

New Siberian Shoal			
Petryashev, 1990	<i>Eucratea loricata</i> was found in biocenosis of sponges <i>Suberites domuncula</i> at 12–35 m depth and on rocky bottoms. Its biomass reached 4.8 g/sq. m. Sessile (attached) organisms were dominant in this biocenosis.	Golikov et al., 1974	<i>Alcyonidium gelatinosum</i> was found in 1973 in the <i>Balanus crenatus</i> + <i>Suberites domuncula</i> + <i>Eucratea loricata</i> biocenosis at 12–18 m depth with the highest colony density of the latter of 1.16 ± 0.45 colony/sq. m. The highest biomass (10 ± 3.53 g/sq. m) was reached by the species in the <i>Musculus corrugatus</i> + <i>Suberites domuncula</i> biocenosis

bryozoans *Eucratea loricata* (L., 1758) and *A. disciforme* Smitt, 1872. All the collections in this area were made from the low-salinity seawater.

In a short paper, Abrikosov (1932) described ten bryozoan species of the order Cheilostomatida which were found at seven stations in the direction of Bol'shoi Lyakhovskii Island and collected from a 16–24 m depth range on silty ground from collections of Hydrobiological Team of the USSR Academy of Science Expedition to Yakutiya in 1927. He found *A. disciforme* on silty ground at lower salinity ranging between 21.56 and 23.37‰ (Table 3). Map of distribution of biocenoses, some of which with bryozoans, was compiled by Petryashev et al. (1994, 2004) based on materials of the 1990s expeditions (Fig. 4). Thus, a biocenosis with the dominant species *A. disciforme* ($B = 8 \text{ g/m}^2$, where B is biomass) was recorded northeast of the Lena River delta at 17 m depth and on silty-sandy ground. As recorded by Gukov (1994a), bryozoan *A. disciforme* was a characteristic species of the *Rhizomolgula globularis* + *Saduria sabini* biocenosis northeast of the Lena River delta 130 km away from the shore at a depth of 26 m and on sandy silt.

The materials presumably collected using the diving quantitative method in July–September 1973 in southeastern part of the Laptev Sea, New Siberian Shoal, and between the Kotelny and Bennett islands,

as well as literature data additionally present information about the relationships between some of the biocenosis and decreased salinity levels typical of this area due to the rivers' discharge. Salmon migrates to this area to feed. In 1973, *A. gelatinosum* (L., 1761) was also found in the *Balanus crenatus* + *Suberites domuncula* + *Eucratea loricata* biocenosis at 12–18 m depth with the highest colony density of the latter of 1.16 ± 0.45 colony/sq. m. The highest biomass (10 ± 3.53 g/sq. m) was reached by the species in the *Musculus corrugatus* + *Suberites domuncula* biocenosis (Table 4).

Based on the 1990s expedition materials, Petryashev et al. (1994) reported data on biocenoses, where bryozoans were found in this area (Fig. 4). *E. loricata* was encountered in biocenosis of sponges *Suberites domuncula* (Olivi, 1792) at 12–35 m depth and on rocky bottoms. Its biomass approached 4.8 g/sq. m. Sessile (attached) organisms were dominant in this biocenosis.

As indicated by Golikov et al. (1974) (Table 5), species *E. loricata* was met in the New Siberian Shoal in the *Eucratea loricata* + *Saduria entomon* biocenosis at a depth of 7–8 m with the highest colony density of 70 ± 24.7 colony/sq. m and the highest biomass of 44 ± 15.5 g/sq. m (Table 5). The *A. disciforme* was observed in the *Portlandia arctica* + *Alcyonidium disciforme* + *Rhizomolgula globularis* biocenosis at 4.8 m depth

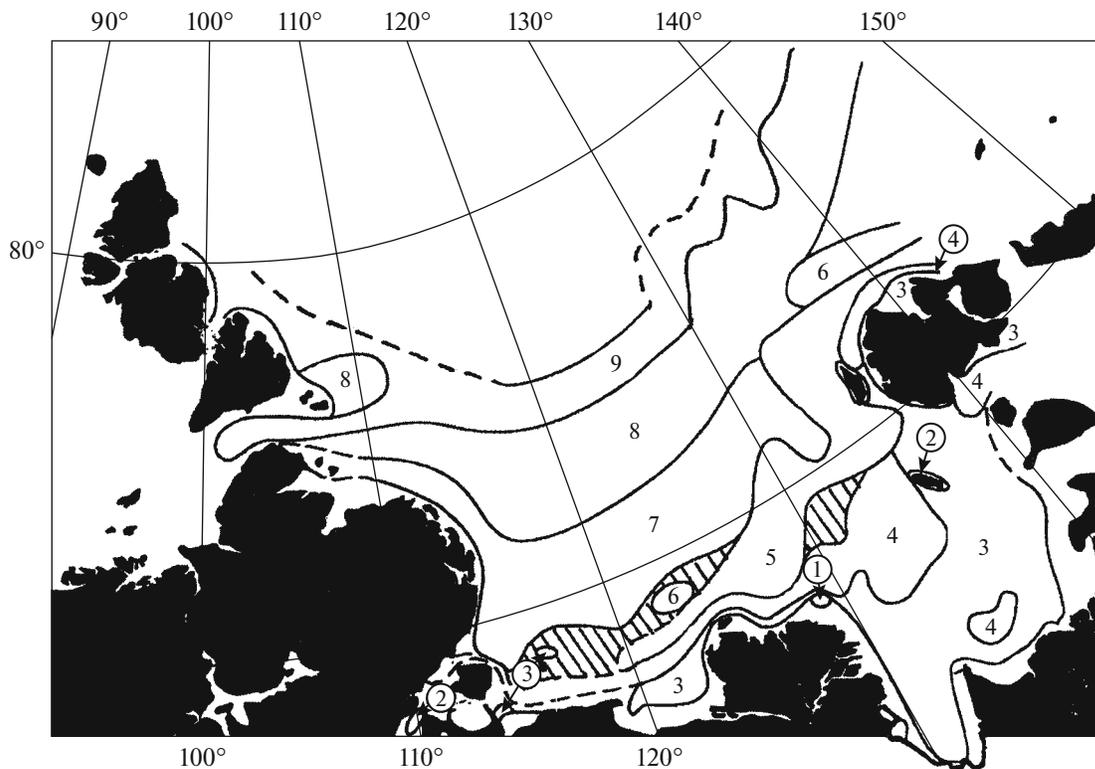


Fig. 4. Distribution of biocenoses below 10 m in southwestern part of the Laptev Sea (after Petryashev et al., 1994). (1) *Alcyonidium disciforme*; (2) *Suberites domuncula*; (3) *Portlandia arctica*; (4) *Astarte borealis* + *A. montagui* + *Portlandia arctica*; (5) *Leionucula tenuis*; (6) *Ocnus glacialis*; (7) *Astarte borealis* (*A. montagui* + *Maldane sarsi*); (8) *Ophiocten sericeum*; (9) *Ophioplreura borealis* + *Ophiocten sericeum* + *Ophiacantha bidentata* (areas with insufficient data are shaded).

with the highest colony density of 40.2 ± 1 colony/sq. m and the highest biomass of 14.5 ± 4.72 g/sq. m. Dominance of macrophytes and bryozoans was pointed out by Gukov (1994b) (Table 5) for benthic biocenoses in straits of the New Siberian Islands in coastal zone of the straits. In particular, the *Eucratea loricata* + *Saduria sabini* biocenosis was observed at the Kotelny Island in Guba (small bay) Nerpich'ya on silty ground at a

depth of 2–3 m. In the biocenosis the colony density of settlement of *E. loricata* reached 50 ± 16.6 colony/sq. m and biomass 11.6 ± 3.2 g/sq. m. As depth increased to 4–5 m, change of biocenosis was occurred, but *A. gelatinosum* was a notable species in the epifauna. The biocenosis *E. loricata* was found in Sannikov Strait at cape Medvezhii at a depth of 5–7 m on silted gravel with colony density of 80 ± 27 colony/sq. m and

Table 5. Biocenoses with dominant species *Eucratea loricata* at the New Siberian Islands

		New Siberian Islands	
Golikov et al., 1974	<i>Eucratea loricata</i> + <i>Saduria entomon</i> at a depth of 7–8 m with the highest colony density of 70 ± 24.7 colony/sq. m and the highest biomass of 44 ± 15.5 g/sq. m	Gukov, 1994b	the <i>Eucratea loricata</i> + <i>Saduria sabini</i> was observed in Guba (small bay) Nerpich'ya on silty ground at a depth of 2–3 m. Colony density of <i>E. loricata</i> at 50 ± 16.6 colony/sq. m and biomass at 11.6 ± 3.2 g/sq. m. The <i>Eucratea loricata</i> biocenosis was discovered in Sannikov Strait at Cape Medvezhii at a depth of 5–7 m on silted gravel with colony density of 80 ± 27 colony/sq. m and biomass 10.2 ± 3.6 g/sq. m. The <i>E. loricata</i> biocenosis was found at 32 m depth on silty ground 25 km southeast of Cape Medvezhii along the section line Cape Medvezhii–Cape Khvoivova. The bryozoan colony density in this biocenosis was 125.6 ± 3.95 colony/sq. m with biomass of 26.4 ± 6.7 g/sq. m.

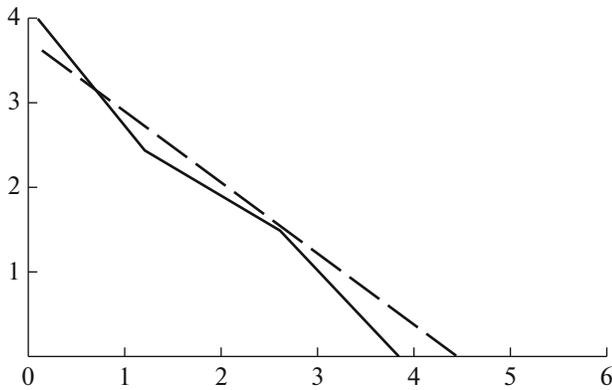


Fig. 5. Dispersal of Bryozoa across the Arctic seas. Continuous line represents empirical evidence; dashed line is theoretical function. Y-axis is the number of boreal and boreal-Arctic bryozoan species of the Atlantic origin along the main dispersal pathway on the shelf of the Arctic seas. X-axis is dispersal pathway, that is, the Barents, Kara, and Laptev seas.

biomass 10.2 ± 3.6 g/sq. m. The biocenosis *E. loricata* was found at 32 m depth on silty ground 25 km southeast of Medvezhii Cape along the section line Cape Medvezhii–Cape Khvoynova (northeasternmost point of Maly Lyakhovsky Island) at 32 m depth on silty ground. The bryozoan colony density in this biocenosis was 125.6 ± 3.95 colony/sq. m with a biomass of 26.4 ± 6.7 g/sq. m. The *A. disciforme* was also recorded.

Distribution of biocenoses based on Petryashev et al. (1994) data (Fig. 4) and at monitoring stations based on data by Gukov (1999) also showed some similarity: bryozoans with significant biomasses were found in biocenoses 1 and 2. No bryozoans are indicated by Petryashev in biocenosis 5; but its boundaries largely coincide with the same *Leionucula tenuis* (*L. beliotii*) biocenosis described by Gukov and found by him at stations 3 and 6 on sandy silt and at station 7 on silty ground at 22.5–24.5 m depth range, which (the biocenosis) featured the richest species composition. Epifauna was recorded to have in the composition the bryozoans *E. loricata* (colony density 20 colony/sq. m, biomass 1.2 g/sq. m), *A. disciforme* (colony density 40 colony/sq. m, biomass 0.7 g/sq. m), *Escharella ventricosa* (Hassall, 1842) (10 colony/sq. m, 0.08 g/sq. m), and *Myriapora subgracilis* (d’Orbigny, 1853) (20 colony/sq. m, 0.03 g/sq. m).

The combined (joint) mode of distribution of bryozoan species along the depth gradient in Kongsfjorden with two provisional basins of brackish waters to the depths of 20–30 m and the normal ocean salinity to 50 m depths allowed an analogy with a latitudinal gradient of bryozoan species distribution in the Laptev Sea, in which over approximately 50% of the sea area has water with decreased salinity to 50 m depth with the further increase of salinity with depths. Data

obtained on the dependence of distribution of biocenoses with dominant bryozoan species on hydrological regime and substrate allowed for the assumption that spreading of bryozoan species on the upper regions of shelf of the studied Arctic seas reveal certain patterns, which can be described using a mathematical model. A species, expanding its areal, should possess a definite set of features, making it possible to occupy new habitats. Obviously, this process is affected dependent on its eurybionty, reproduction mode, survivorship of the young, etc. Additionally, this species needs to be able to compete with the local fauna and flora of the region, which it colonizes; in other words, its competitive ability is of the major importance. Various species can be very much different from each other in these features; therefore, their spreading success will also vary. Overall, spreading can be considered a random process, which allows it to be approached in rather general terms and an attempt made to track colonization of great spaces by major taxonomic categories of species. The problem of occupation of new regions by different groups of living organisms is not well-understood. Piccoli et al. (1986, 1991) and Piccoli (2002a, 2002b) were the first to address the problem, investigating colonization of the Tethys by “Tertiary” bivalves and demonstrated that this process is subject to certain regularities. They proposed a mathematical model, that supposes that a relative decline in the number of spreading species is in proportion to the distance from the dispersal center.

$$S = S_0 e^{-D/L},$$

where S_0 is the number of species in source fauna; S is the number of species in the local fauna; positive coefficient L is a criterion of spreading capability of a group of organisms, showing the distance, at which the number of species declines by half; D is a distance from the dispersal start point; e is a base of the natural logarithms.

The life form and the presence in a life cycle of the pelagic stage may have an effect on spreading potential of species. Consequently, parameter L may serve as a criterion of the spreading capability of a group of organisms, therefore, in what follows, it will be referred to in the text using the term *spreading potential*. Decline in the number of species along the major pathway of distribution across the shelf of the Russian Sector of the Arctic seas is satisfactorily described by the Piccoli–Sartori function (Gontar and Naumov, 1994; Naumov and Gontar, 2004). Decline in the number of the Boreal and Boreal-Arctic bryozoan species of the Atlantic origin along the main route of spreading on the shelf of the Arctic seas, including the Barents, Kara, and Laptev seas, is shown in Fig. 5. The published and our own data were used on bryozoan fauna of these seas. The Laptev Sea represents an ecological barrier for spreading of some biogeographic groups of bryozoan species of both the Atlantic and Pacific origin due to the fauna brackish-water envi-

ronment over a significant area of relatively shallow depths to 50 m, occupying more than 50% of the total sea area. A dramatic drop in the species number, i.e., 75–90%, leads to a loss of a significant part of the species (genetic) diversity. Precisely this period of undergoing a “bottleneck” is considered the time of appearance of colonist species. In our study, the bottleneck is represented by the Pechora Sea and Yugorski Shar Strait, in which salinity levels sharply drop compared to other areas of the Barents Sea due to the considerable volume of the freshwater inflow. Only the eurybiontic Boreal and Boreal-Arctic taxa survived these conditions. As a consequence, the bryozoan fauna of the Kara Sea is greatly impoverished compared to bryozoan fauna of the Barents Sea. Due to the hydrological regime with a low salinity over significant area, the Laptev Sea is likewise inhabited by eurybiontic species; decline in the number of species is observed in sea fauna of these areas. The number of species only increases in the deep-water areas of the Laptev Sea due to the normal oceanic salinity.

DISCUSSION

Bryozoans play an important role in many marine shelf benthic biocenoses and may serve as indicators of the environmental conditions and their changes due to a wide distribution of bryozoans across the World Ocean waters and high species diversity. Bryozoans are encrusting organisms and prefer hard substrates, but there are species capable of inhabiting soft grounds, e.g., *A. disciforme*, as well as floating objects.

As noticed by Andriyashev (1939, 1954): “slow-mobile species of marine benthos, not going beyond the continental shelf and having a small amplitude of temperature fluctuations have the most value for biogeographers. Biogeographic conclusions should be based on these species”.

The bottom fauna of the Arctic Ocean and regional seas has a number of features the analysis of which leads to certain conclusions about its origin and history of formation. “This fauna is highly original and authentic and can be distinguished in a system of biogeographic subdivisions of the World Ocean as an independent Arctic subregion. The position of its boundaries is determined by bottom topography and a system of constant oceanic currents of the Northern Hemisphere. It is a common knowledge that a full exchange was observed between mid-latitude fauna of the Northern Hemisphere through the Arctic during the Pliocene and Arctic fauna was mixed (Guryanova, 1939, 1951; Dyakonov, 1945); in the opinion of many authors, the second invasion was observed during the Climate Optimum period (Guryanova, 1939, 1951; Dyakonov, 1945; Andriyashev, 1954). Thus, the origin of the recent fauna of the Arctic basin can be traced back to three roots. The recent Arctic fauna features there are three groups of species, which belong, first, to the autochthonous Arctic marine; second, Atlantic;

and third, Pacific genera. Distribution over the Arctic Ocean of the endemic species for the Arctic subregion suggests the existence of three centers of the shelf Arctic fauna formation during the Pleistocene. Namely, (1) the Kara located north of the Kara and Laptev seas; (2) Chukchi-American (north of the Chukchi Sea and Canadian Arctic Archipelago); and (3) Siberian, associated with shallow waters of southern parts of the Kara and Laptev seas, in which the brackish-water fauna of desalinated areas and estuarine waters was formed.” (Guryanova, 1970).

“The term *biological indicators* or *biological parameters* are commonly used by hydrobiologists in the literature. Biological indicators were considered by Gorbunov as definite organisms or associations of organisms, which characterize one or another hydrological element (Gorbunov, 1934) “... Benthic organisms are the indicators of the average hydrological regime of bottom water layers for the known more or less continuous time interval. Additionally, bottom organisms may serve as indicators of origin of the waters characteristic for this place during the period of one or several years, but not for this moment. ... Many deepwater forms rise to the shallow-water zone under the high Arctic conditions, where life is generally more impoverished. Despite a greater or lesser degree of significance of the depth, the latter should be taken into account first, since no hydrological inferences are possible based on hydrobiological data without this corrective. In essence, a ground composition can also be additional, but in many cases of primary importance. ... Another overwhelmingly important circumstance should be emphasized, that is, interaction of the organisms on each other. ... The most critical is also a question on the geologic past of each individual organism. ... To clarify the existing relationship of each of the organisms with the factors of depths, ground, temperature, and salinity, indicating, however, the center, if not the origin of this form, then at least its modern maximum development ... biological parameters are of especial value in hydrological investigations of the high Arctic, which is accessible during favorable years only ..., where benthic organisms are used as biological indicators. Biology can illuminate on origin of the waters, the average or prevailing hydrologic regime, and, probably, the direction of its long-term changes.” (Gorbunov, 1934).

In the west of the Arctic sub-region (Guryanova, 1970), due to large-scale invasion by the boreal North Atlantic fauna of the Barents Sea, the boundary between the Arctic and North Atlantic faunas is, first, very complex and, second, moves in a multi-year cycle sometimes to the northeast, sometimes to the west as a consequence of (shear) force changes of the warm Atlantic current and its branches, washing the southwestern area of the Arctic Ocean shelf and Spitsbergen. This boundary between the Arctic and North Atlantic faunas is not faunally important in itself, while being the intermediate ...; it has, however, a

great significance in biogeography of the Arctic Ocean seas. The influence of the Atlantic current waters, bending around Spitsbergen from the north, is noticeable even in sea trenches, in the Kara Sea (St. Anna Trench) and Laptev Sea (Sadko Trench) and even further eastward; while this current serves as a path of the eastward migration for North Atlantic and West Atlantic marine forms. This is all the more important for many marine forms because this is the only possible route, since the lower salinity of the Siberian seas prevents their penetration to the east via the sublittoral zone.

All our data on the Barents (Kongsfjorden) and Laptev seas obtained using the diving techniques of quantitative method collecting of bottom fauna of the upper shelf regions confirm the conclusion of Gorbunov following his investigation of the Kara Sea fauna using the qualitative samples. Bryozoans play one of the leading roles in the benthic fauna in the Arctic high latitudes. The quantitative samples in Kongsfjorden and Laptev Sea allowed us to define more accurately and identify spreading trends of different species of Atlantic origin in the upper regions of shelf which depend on the hydrological regime and its influence on qualitative and quantitative composition of the existing biocenoses in the upper shelf regions of the studied Arctic seas. The role of bryozoans as dominant species in these biocenoses allowed to be considered the bryozoans as biological indicators based on their thermopathy, halinopathy, and relation to depths. Additionally, bryozoans, being biological indicators, significantly influence the inferences on biogeographic regionalization of shelf zones of the Barents, Kara, and Laptev seas.

Skeletons of the recent marine bryozoans are of different chemical compositions. The chitinous skeletons of the order Ctenostomatida (class Gymnolaemata) contain almost no mineral substances, while skeletons of bryozoans from the order Cyclostomatida (class Stenolaemata) and order Cheilostomatida (class Gymnolaemata) are mineralized to varying degrees. Calcareous skeletons of extinct forms compose the major part of the marine seabed sediments. Bryozoans are the major carbonate producers in some ancient and recent benthic environments of marine water bodies, including parts of the Arctic Ocean (Kuklinsky and Taylor, 2009).

FUNDING

The study was conducted on the State Topic for 2022–2024, no. 122031100274-7.

CONFLICT OF INTEREST

The author declares no conflicts of interest.

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Translated by E. Kuznetsova