=== OCEANOLOGY ===

Portlandia-dominated Communities in the Arctic: Taxonomic Composition and Structure along the Geographical Gradient

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Abstract—The species composition and structure of bottom communities with a predominance of bivalve mollusks of the *Portlandia* genus, which are widespread on the shelf of the Russian Arctic, were analyzed. Molecular genetic analysis confirmed that *Portlandia aestuariorum* and *P. arctica* are valid species; it has been shown that all *P. arctica* from different regions belong to the same species regardless their morphological variations. Ten different variants of benthic communities from the White, Kara, Laptev, and East Siberian seas were described, in which *P. aestuariorum* and *P. arctica* play the dominant role. No associated species complexes have been identified for *Portlandia* spp. Communities practically do not have common species, and their composition and structure are determined by the selection of species with similar ecological preferences from the local fauna. The differences in communities are determined by both geographical and environmental factors.

The combination of descriptions (stations) by the dominant species [1] is one of the widespread and traditional approaches to distinguishing communities of organisms. All descriptions with the same dominant are considered to belong to the same community. In the case of species with a wide distribution, this approach may lead to the unification of associations of species that are different in species composition and origin. At the same time, analysis of the composition and structure of communities with the same dominant serves as a good object for studying the problem of the contiguity of species in the bottom communities and assessing the role of interspecific interactions in the organization of the benthos.

The prevailing species by biomass can act as an ecosystem engineers transforming the habitat for related species, but this does not always happen and certainly not in all communities. The question of the degree of contiguity of species and the regulatory role of the dominant species is poorly studied for infaunal communities [2]. The study of geographically distant communities with the same dominant allows us to evaluate its role as an edificator and to identify a set of associated species, if any such species exist.

Communities dominated by the bivalve mollusk *Portlandia arctica* can serve as a good object for quantifying geographical differences in similar communities and analyzing the relationship between the dominant and associated species.

P. arctica has a circum-arctic distribution; it is common in all seas of the Eurasian Arctic shelf and often acts as the dominant species in the communities of silt sediments [3–7, 11].

In this investigation we used the material for analysis provided by quantitative bottom grab sampler collections from expeditions on the research vessels of the Shirshov Institute of Oceanology, Russian Academy of Sciences (SIO RAS): *Academician Mstislav Keldysh* and *Professor Shtokman* in the Kara, Laptev, and East Siberian seas, and the collections of the White Sea coastal-marine expedition (SIO RAS) in cooperation with the White Sea Biological Station of Moscow State University from the White Sea (2007–2017). The analysis included data on the abundance of the macrobenthos at 61 stations where species of the genus

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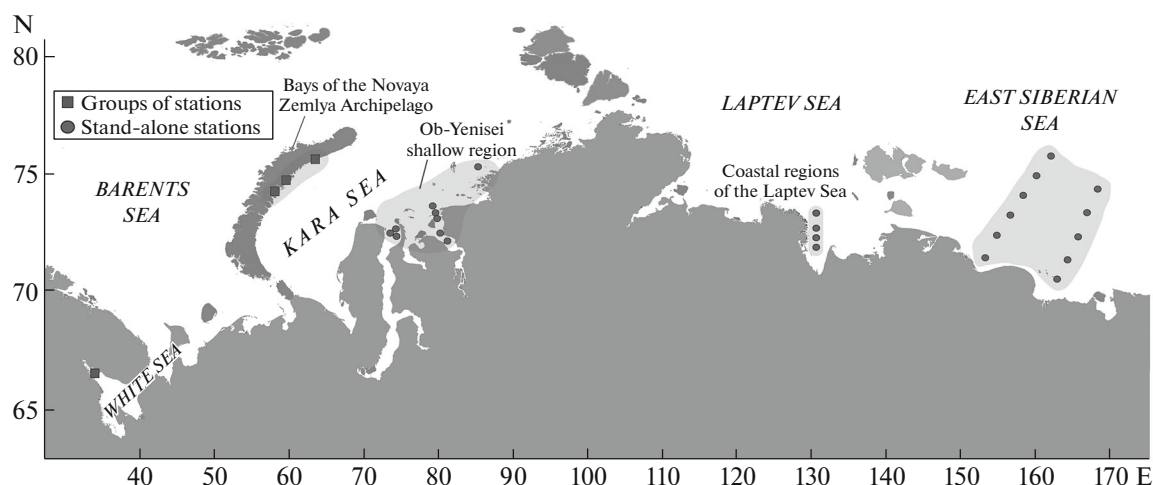
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Fig. 1. Chart of the stations and variants of *Portlandia* communities in the Arctic seas.

Portlandia were among the dominant or characteristic ones (Fig. 1).

The taxonomic composition of the genus *Portlandia* is still under discussion. The morphological variability of *Portlandia* shells in different parts of its habitat led to distinguishing a large number of morphological forms of various taxonomic ranks [4]. Before solving the problem of the composition and structure of similar communities on an extended geographical gradient, it was necessary to make sure that in all cases the dominant form refers to the same species.

We analyzed both *Portlandia* morphological species (*P. aestuariorum*, ten samples from the estuaries of the Ob, Yenisei, and Khatanga, and *P. arctica* related to three varieties: var. *typica*, var. *portlandica*, var. *siliqua* from 12 samples taken in the Kara, Laptev, White, and East Siberian seas). A sequence analysis of the mitochondrial COI gene has been performed. For comparison, we used the data published in the BOLD database [8] of mollusks from the Canadian Arctic (*P. arctica*, *Yoldia hyperborea*). The results of phylogenetic reconstruction (RAxML, 1000 bootstrap [9]) indicate the divergence of the two species regardless of the geographical location of the samples. The average evolutionary distances [10] between morphological species (0.089 ± 0.0160, M ± S.E.) notably exceeded the intragroup distances (*P. aestuariorum* −0.001 ± 0.0008, *P. arctica* −0.007 ± 0.002). On this basis we can conclude that *P. aestuariorum* Mosevich, 1924, which was originally distinguished as a subspecies and then transferred to the rank of species, is an independent species. All specimens of *P. arctica* from different regions, including the Canadian Arctic, belong to the same species, regardless of their morphological variations.

The analysis of the structure of community structure (similarity of the species composition, similarity of the structure of samples based on the species ratios,

composition of the dominant group) allows us to divide our entire sample into several independent complexes. All stations dominated by *Portlandia aestuariorum* are clearly distinguished. Communities with the dominance of this species are described based on our material from brakish regions of the estuaries of the Lena and Yenisei rivers, in which salinity is 18–26 psu. These communities are dominated by the species of the brackish-water complex, such as *Marenzelleria arctia* and *Mesidotea sabini* in the Yenisei estuary, *Prionospio cirrifera* in the estuary of the Lena (Table 1). The composition and structure of *P. aestuariorum* communities in the two regions studied are very different, although they are united by low species richness (Table 1). Among the leading species, only *Mesidotea sibirica* is present in both regions.

Communities dominated by *Portlandia arctica* are represented in our material by the collections from two regions of the White Sea, from two regions of the Kara Sea, from the Laptev Sea, and from the East Siberian Sea. All communities studied are formed in a wide range of temperature (from +5 to −1.5° C) and salinity (24–34 psu) on muddy sediments in the depth range from 10 to 140 m. Nevertheless, it should be noted that most of them live in conditions of low salinity and shallow depths, and only a few types are formed in deep (up to 150 m) basins of the bays along the eastern coast of Novaya Zemlya with high (34.5 psu) salinity. Based on our material we distinguished eight main groups which differ in structural characteristics and dominant species (Table 1). In the species composition, there are practically no common species. Among the 250 species we found, only a few (fewer than ten) (*Micronephthys minuta*, *Terebellides stroemii*, *Macoma calcarea*, Cirratulidae gen. sp., *Cossura* spp.) were found in all regions, but not always as part of the leading complex. The differences in the species composition of communities from different seas and sea regions are determined by both geographical and envi-

Table 1. Characteristics of *Portlandia arctica* communities in different regions

Region	Depth, m	*N*, specimens/m^2	*B*, g/m^2	Number of species:			Dominating species complex
				total	per sample 0.1 m^2	ES(100)	
Gulf of Yenisei, fresh-water part (Kara Sea)	13—14	2388	14	23	17	9	*Marenzelleria arctia*, ***Portlandia aestuariorum***, *Mesidotea sabini*
Region near the Lena delta, freshwater part (Laptev Sea)	10—12	872	30	27	17	9	***Portlandia aestuariorum***, *Prionospio cirrifera*
Velikaya Salma Strait, Kandalaksha Gulf (White Sea)	69—133	1949	106	75	29	15	***Portlandia arctica***, *Galathowenia oculata*, *Aricidea nolani*, *Scoloplos* sp., *Pectinaria hyperborea*, *Maldane sarsi*, *Nuculana pernula*
Semi-isolated depleted lagoon Bab'e Sea (White Sea)	11—31	1117	25	38	12	8	***Portlandia arctica***, *Prionospio cirrifera*, *Aricidea nolani*
Gulf of Ob, offshore part (Kara Sea)	15—21	1196	17	32	20	12	***Portlandia arctica***, *Trochochaeta carica*, *Micronephthys minuta*, *Terebellides stroemii*, *Cossura* spp.
Gulf of Yenisei and Yenisei shallow water region (Kara Sea)	30—53	1086	58	69	36	15	***Portlandia arctica***, *Mesidotea sabini*, Cirratulidae gen. sp., *Pectinaria hyperborea*, *Micronephthys minuta*, *Pandora glacialis*, *Macoma calcarea*
Inner part of the bays in the Novaya Zemlya Archipelago (Kara Sea)	56—138	1393	55	56	22	14	*Ennucula tenuis*, ***Portlandia arctica***, *Scoletoma fragilis*, *Mendicula ferruginosa*, Cirratulidae gen. sp.
Bays of the Novaya Zemlya Archipelago, terminal stations (Kara Sea)	21—109	402	22	13	8	7	*Portlandia arctica*
Coastal regions of the Laptev Sea and East Siberian Sea	17—32	2937	81	72	36	17	***Portlandia arctica***, *Mesidotea sabini*, *Artacama proboscidea*, Cirratulidae gen. sp., *Praxillella praetermissa*, *Aglaophamus malmgremi*, *Thyasira gouldi*, *Lyonsia arenosa*
East Siberian Sea, major part	13—50	1024	45	68	19	9	***Portlandia arctica***, *Mesidotea sabini*

N is the numbered specimens, *B* is biomass, ES(100) number of species per 100 specimens.

ronmental causes. A number of species (*Golfingia margaritacea*, *Ophiopleura borealis*, *Yoldiella lenticula*, *Mendicula ferruginosa*, *Yoldiella solidula*, *Bathyarca glacialis*) are typical only for deep-sea kinds of communities from the bays of the Novaya Zemlya archipelago, which were described. In the regions of low salinity, the *P. arctica* community includes a number of meso-haline species (*Trochochaeta carica*, *Aulodrilus pluriseta*, *Halicryptus spinulosus*, *Aulodrilus pigueti*, *Marenzelleria arctia*), some of which are also found in the *Portlandia aestuariorum* communities.

The geographic differences in the composition of communities are no less pronounced. In the White Sea communities, the composition is depleted due to the loss of a number of arctic forms that are widespread in other seas: *Bathyarca glacialis*, *Mendicula ferruginosa*, *Mesidotea sabini*, *Ophiocten sericeum*, and *Ophiopleura borealis*. Several species are typical only for the western kinds of the *Portlandia* community and are absent in the East Siberian Sea (*Maldane sarsi*, *Scoletoma fragilis*, *Pectinaria hyperborea*, and *Aricidea nolani*). Shallow-water boreal species (*Galathowenia oculata*, *Nuculana pernula*, *Yoldia hyperborea*) are numerous in the White Sea as part of the Portlandia communities.

The structural characteristics of communities involving *P. arctica* also differ from one region to another (Table 1). The average values of biomass and abundance differ in different types of communities by a factor of two or three, while the species richness differs three times. The lowest diversity (7−9 species per 100 specimens found) was noted in the marginal communities: in the semi-isolated basins and in the extreme inshore parts of the bays, as well as in the most geographically isolated eastern variant of the community: in the East Siberian Sea (Table 1).

We do not see characteristic species in the composition of the communities that would be closely related in their occurrence to these mollusks and are unique precisely to these communities. On the contrary, the composition of subdominant species differs in each sea and biotope, being formed from a number of widespread eurybiotic species distributed in the neighboring communities.

All *Portlandia* communities are confined to the biotopes that appeared in the Holocene at the peak of the last glaciation. The areas of modern distribution of the *Portlandia* communities were covered with ice (White Sea, bays of the Novaya Zemlya archipelago) or were located above sea level (Ob−Yenisei shallow water, shallow waters of the East Siberian and Laptev seas). In each case, the set of species during community formation was determined by the composition of the regional fauna and local biotope conditions.

Comparative analysis of *Portlandia arctica* communities from different regions of the Arctic and a wide range of biotopes showed that the presence of a constant characteristic or dominant species remains the only common feature that unites groups of species that differ in taxonomic composition and structure. Even the few species that are included in all *P. arctica* complexes studied (about ten species) turn out to be eurybiotic species of circum-arctic distribution, characteristic of a number of neighboring communities. The role of *Portlandia arctica* as an ecosystem engineer that determines the appearance of the community and the selection of species has not been confirmed by our data; the composition and structure of communities in all biotopes is formed by the selection of species with similar ecological preferences from of the local fauna.

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