1871
ИнБЮМ – IBSS

ISSN 2499-9768 print

МОРСКОЙ БИОЛОГИЧЕСКИЙ ЖУРНАЛ

MARINE BIOLOGICAL JOURNAL

Vol. 7 No. 2
2022

A. O. KOVALEVSKY INSTITUTE OF BIOLOGY OF THE SOUTHERN SEAS OF RAS
ZOOLOGICAL INSTITUTE OF RAS

МОРСКОЙ БИОЛОГИЧЕСКИЙ ЖУРНАЛ

MARINE BIOLOGICAL JOURNAL

2022 Vol. 7 no. 2

Established in February 2016 SCIENTIFIC JOURNAL *4 issues per year*

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1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 3–22
https://doi.org/10.21072/mbj.2022.07.2.01

SCIENTIFIC COMMUNICATIONS

UDC 574.587(262.54)

BENTHIC FAUNA OF THE SOUTHWESTERN SEA OF AZOV. MACROZOOBENTHOS TAXONOMIC COMPOSITION AND ITS BIOCOENOTIC STRUCTURE IN 2016–2017

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Received by the Editor 18.01.2020; after reviewing 16.07.2020;
accepted for publication 03.03.2022; published online 07.06.2022.

The Sea of Azov is a semi-enclosed and relatively shallow water basin, with lower salinity than in the Black Sea. Salinity values vary within 9–14 ‰ and depend mainly on the volume of river flow. Increasing salinity is a favorable factor for penetration and development in the Sea of Azov of some Black Sea species; this was noted in the 1970s, with a mean rise in salinity up to 13–14 ‰. After a period of decline down to 9–10 ‰, a steady salinization of the water basin is recorded since 2007; salinity averaged 13.37 ‰ in 2015. The aim of the work was to assess taxonomic composition and biocoenotic organization of the bottom macrofauna in the southwestern Sea of Azov based on the results of benthic surveys carried out in 2016–2017 in 84th, 86th, 90th, 96th, and 100th cruises of the RV “Professor Vodyanitsky”. Sediments were sampled with an “Ocean-50” bottom grab with a capture area of 0.25 m^2. Bottom sediments were washed through sieves with the minimum diameter of 1 mm. In total, 46 macrozoobenthos species were recorded; out of them, 15 Polychaeta species, 12 Mollusca, and 13 Crustacea. Four species well known for the Black Sea were found in the Sea of Azov for the first time – *Molgula euprocta*, *Phoronis psammophila*, *Gouldia minima*, and *Iphinoe elisae*. Out of species recorded, 14 % were alien to the Sea of Azov–Black Sea basin. These were bivalves *Anadara kagoshimensis* and *Mya arenaria* and polychaetes *Polydora cornuta*, *Streblospio gynobranchiata*, and *Marenzelleria neglecta*. In the area studied, *A. kagoshimensis* biocoenotic complex was registered in all the seasons, with mean abundance and biomass values (4,818 ± 1,019) ind.·m^{-2} and (878.4 ± 129.5) g·m^{-2}, respectively. Three biocoenotic complexes were identified which could be the variants in the manifestation of the dynamic state of *Anadara* community. Seasonal dynamics in macrozoobenthos biomass mainly depended on fluctuations of its dominant species – *A. kagoshimensis* and *Cerastoderma glaucum* – and was determined by their different physiological and biochemical adaptations to hypoxia which is frequent for the Sea of Azov in summer. Maximum macrozoobenthos abundance was recorded in October 2016 (~ 6,600 ind.·m^{-2}) and was associated with reproduction of several species (including alien ones) in summer and autumn and enrichment of the benthic complex by their juveniles. In this period, at individual stations, abundance of *A. kagoshimensis* reached ~ 14,000 ind.·m^{-2}, and abundance of an alien polychaete *S. gynobranchiata* reached 2,300 ind.·m^{-2}. *A. kagoshimensis* juveniles were recorded in the Sea of Azov June to October, peaking in October. The maximum length of *A. kagoshimensis* registered was 52.7 mm. The ratio of mature molluscs (shell size > 10 mm) in the studied *A. kagoshimensis* population varied from 6 % (October 2016, the period of mass replenishment with juveniles) to 85 % (December 2017). Well-developed *C. glaucum* settlements were registered at the inshore stations, peaking in July. The ratio of mature molluscs (shell size > 6 mm) in the studied *C. glaucum* population varied from 7 % (July 2017, the period of mass replenishment with juveniles) to 100 % (December 2017). Under lack of solid substrate, *A. kagoshimensis* – an alien species for the Sea of Azov – formed a new consort community of biofiltrators which supplemented a benthic biofilter zone in the Sea of Azov previously based on bivalve *C. glaucum*.

Keywords: macrozoobenthos, alien species, taxonomic structure, species richness, *Anadara kagoshimensis* biocoenotic complex, Sea of Azov

The benthic fauna of the Sea of Azov has been studied quite fully (Vorob'ev, 1949 ; Mordukhai-Boltovskoi, 1960 ; Stark, 1960). In comparison with the fauna of the Mediterranean and Black seas, it is characterized by a relative poverty of species composition, the main reason for which is considered to be the very low salinity of the Sea of Azov waters (Zaika, 2000). However, already in the late 1960s, data began to appear in the literature on changes occurring in the structure and distribution of biocoenoses in the benthos of the Sea of Azov, which were associated primarily with the regulation of the flow of the Don and Kuban rivers (Zakutskii et al., 1978 ; Nekrasova, 1972).

The subsequent studies revealed that the taxonomic composition and distribution of the benthos of the Sea of Azov, its quantitative characteristics, are variable and depend on many factors. These are, first of all, fluctuations in river runoff (cause changes in the degree of salinization of water and changes in the surface layer of sediments) and regimes of temperature (determines the amount of winter death of benthos), of gas (determines mass mortality of benthic fauna due to the summer near-bottom hypoxia and suffocation phenomena), and of wind (Matishov et al., 1999, 2010 ; Nekrasova, 1972 ; Stark, 1960). In addition to changes in the hydrochemical regime, an important feature of the Sea of Azov ecosystem is a tendency to increase the production of primary organic matter and, in accordance with this, to increase the content of organic matter in bottom sediments (Aleksandrova et al., 2014). The water salinity factor is considered by many researchers to be one of the most strongly influencing the state and dynamics of the Sea of Azov benthos (Matishov et al., 1999 ; Nekrasova, 1977 ; Frolenko, 2000). Thus, during periods of a temporary increase in salinity up to 13–14 ‰, over 30 species of benthic fauna new to the Sea of Azov – invaders from the Black Sea – were found in the area of the Kazantip and Arabat bays (Zakutskii et al., 1978 ; Litvinenko & Evchenko, 2016).

Since the 1960s, after a change in the water balance and intensification of the anthropogenic pressure, the fauna of the Sea of Azov was enriched by far-sea invaders (Anistratenko et al., 2011 ; Boltachova & Lisitskaya, 2019). In the benthos, these are primarily the molluscs *Mya arenaria* Linnaeus, 1758, *Rapana venosa* (Valenciennes, 1846), and *Anadara kagoshimensis* (Tokunaga, 1906) (Anistratenko et al., 2011 ; Savchuk, 1980 ; Chikhachev et al., 1994).

After the salinity minimum observed in 2005, since 2007, there has been a steady increase in the salinity of the Sea of Azov waters; in 2015, it averaged 13.37 ‰ (Dyakov et al., 2016 ; Frolenko & Maltseva, 2017). In 2016, the salinity of the surface layer of most of the Sea of Azov proper reached 13.5 ‰, and the salinity of its southern area reached 14 ‰ (Kochergin et al., 2018). It is known that earlier in the southern sea area, especially in the area close to the Kerch Strait, the centers of the highest salinity were observed. Thus, in 1976, the salinity here reached 15 ‰ (Kuropatkin et al., 2013 ; Litvinenko & Evchenko, 2016).

An increase in salinity in the current period contributed to the further expansion of previously naturalized alien species (Anistratenko et al., 2011 ; Frolenko & Maltseva, 2017) and the emergence of new, both Black Sea and alien species in the Sea of Azov–Black Sea basin from the "distant" seas – the polychaetes *Marenzelleria* sp., *Streblospio gynobranchiata* Rice & Levin, 1998, and *Laonome calida* Capa, 2007 (Lisitskaya & Boltacheva, 2016 ; Boltachova et al., 2017 ; Syomin et al., 2017). The noted changes in the composition and quantitative development of some benthic species, especially of alien ones, determine changes in general biocoenotic structure. In this regard, the aim of this work was to assess the modern taxonomic composition and biocoenotic structure of the benthic macrofauna of the Sea of Azov in its southwestern area, adjacent to more saline waters of the Kerch Strait and the Black Sea.

MATERIAL AND METHODS

Sampling of macrozoobenthos in the Sea of Azov was carried out at 4 permanent stations during the 84th, 86th, 90th, 96th, and 100th cruises aboard the RV "Professor Vodyanitsky" (April, June, and October 2016, July and December 2017, respectively; quantitative samples), as well as during the 93rd and 108th cruises (April 2017 and July 2019, respectively; qualitative samples) in the depth range 9–12 m (Fig. 1, Table 1). The sampling of bottom sediments at each station was carried out in duplicate using an "Okean-50" bottom grab (capture area of 0.25 m^2). The sediments were washed through sieves with the smallest filtration mesh diameter of 1 mm. The material was fixed with 4 % neutralized formalin solution. A total of 38 quantitative and 2 qualitative samples were processed at 21 benthic stations.

Fig. 1. Location of benthos sampling stations (1–4) in the southwestern Sea of Azov

The occurrence rate of species was calculated relative to the total number of stations (19 in total) performed in the southwestern Sea of Azov in different seasons of 2016–2017. Species of macrozoobenthos with an occurrence rate of more than 50 % are referred to leading ones; those with an occurrence rate of 25–50 % are characteristic; and those with less than 25 % are rare. The Czekanowski–Sørensen index (similarity of faunas) was calculated by the formula $2a / (b + c)$, where a is the number of common species, and b and c are the numbers of species in the compared lists.

Table 1. Characteristics of benthic stations performed in the southwestern Sea of Azov (* denotes qualitative samples)

Date (No. of the RV "Professor Vodyanitsky" cruise, station numbers)	St. No.	Coordinates	Depth, m	Sediment
24.04.2016 (84th cruise, st. 1, 3, 4) 15.06.2016 (86th cruise, st. 1–4) 29.10.2016 (90th cruise, st. 1–4) 22.07.2017 (96th cruise, st. 1–4) 08.12.2017 (100th cruise, st. 1–4) *02.04.2017 (93rd cruise, st. 2) *25.07.2019 (108th cruise, st. 4)	1	45°50.095′N, 36°00.555′E	12	Soft bottom sediments with shells debris. On the surface of the sediments, there is a thin red silt; deeper, black silt with the smell of hydrogen sulfide
	2	45°30.031′N, 35°30.432′E	9	Soft bottom sediments with shells debris and smell of hydrogen sulfide
	3	45°29.976′N, 36°00.115′E	10	Silted shells debris
	4	45°29.989′N, 36°30.472′E	11	Silted shells debris

The shell size composition in populations of massive bivalves – *Anadara kagoshimensis* and *Cerastoderma glaucum* (Bruguière, 1789) – was determined by summing stations of each survey within a relatively homogeneous group of zoobenthos at the level of biocoenosis.

When describing the quantitative development of benthic fauna, the parameters of abundance, wet weight, and index of functional abundance (IFA) (Maltsev, 1990) were used in the following form:

$$IFA = N_i^{0.25} \times B_i^{0.75} ,$$

where N_i and B_i are abundance (ind.·m^{-2}) and wet weight (g·m^{-2}) of taxon *i*, respectively.

The wet weight of bivalves was determined without removing the mantle cavity fluid.

Identification of spatial groupings of benthos was carried out both by the biomass-dominated species (Vorob'ev, 1949) and using multivariate statistics algorithms (the PRIMER v5 software package; Cluster, MDS, and SIMPER analyzes) (Clarke, 1993 ; Clarke & Gorley, 2001). In the multivariate analysis, a transformed (presence/absence) data matrix for stations was used, with the exclusion of rare species (with an occurrence of less than 11 %). This recommended procedure (Clarke & Gorley, 2001) provided an acceptable stress factor value (less than 0.2) with the ability to reliably interpret the results of cluster and 2D ordination analyzes. The Bray–Curtis statistics was used as a measure of station similarity. The determination of the coenosis-forming benthic species was carried out using untransformed IFA values based on their contribution to intracomplex similarity (SIMPER analysis).

The water salinity in the bottom layer during surveys in 2016 varied from 13.49 ‰ (16.06.2016, st. 2) to 14.39 ‰ (29.10.2016, st. 1); in 2017, from 14.18 ‰ (22.07.2017, st. 2) to 15.22 ‰ (08.12.2017, st. 1). In the surface water layers, salinity varied within 12.53–14.39 ‰ in 2016 and 14.19–15.21 ‰ in 2017. In general, in all seasons and at all horizons in the surveyed southwestern Sea of Azov, water salinity in 2017 was higher than in 2016. Temperature range of the bottom water layer in 2016 was from +7.45 °C (29.10.2016, st. 4) to +21.95 °C (16.06.2016, st. 2); in 2017, it was from +6.07 °C (09.12.2016, st. 2) to +24.83 °C (23.07.2016, st. 3). In all seasons and different years of observations at the same station, the sediments had similar characteristics. In general for the site, those are represented by silty deposits, with an admixture of varying amounts of shells debris. At 2 of 4 stations, the smell of hydrogen sulfide was present (see Table 1).

RESULTS AND DISCUSSION

Taxonomic composition of macrozoobenthos. During benthic surveys, 46 species of macrozoobenthos were found, including Polychaeta (15 species), Mollusca (12), Crustacea (13), Cnidaria (3), Phoronida (1), and Ascidiacea (1), as well as not identified down to species level representatives of Porifera, Platyhelminthes, Oligochaeta, Nemertea, and Bryozoa, each of which was taken as one species in calculations (Table 2). Of these, two species – the polychaeta *Marenzelleria neglecta* Sikorski & Bick, 2004 and the ascidian *Molgula euprocta* (Drasche, 1884) – were recorded in qualitative samples. In spring, 22 species were noted in the biocoenosis; in summer, 40; in autumn, 21; and in winter, 18.

Table 2. Taxonomic composition and quantitative indicators of macrozoobenthos in the southwestern Sea of Azov for different seasons of 2016–2017 (mean abundance, ind.·m^{-2} / mean wet biomass, g·m^{-2})

Taxon	2016			2017	
	April	June	October	July	December
Porifera					
Porifera g. sp.		1 / 0.002			
Cnidaria					
Actinia equina (Linnaeus, 1758)			24 / 1.54		
Edwardsiidae g. sp.	4 / 0.04			1 / 0.005	37 / 0.06
Sagartiogeton undatus (Müller, 1778)		1 / 0.15	5 / 0.005	2 / 0.01	20 / 0.44
Platyhelminthes					
Platyhelminthes g. sp.		17 / 0.02	2 / 0.003	9 / 0.01	4 / 0.005
Nemertea					
Nemertea g. sp.	41 / 0.16	8 / 0.04	4 / 0.06	0	4 / 0.02
Annelida					
Alitta succinea (Leuckart, 1847)	24 / 6.88	12 / 0.87	52 / 2.17	70 / 2.93	37 / 5.38
Harmothoe imbricata (Linnaeus, 1767)	21 / 0.26	4 / 0.07	4 / 0.04	13 / 0.18	
Hediste diversicolor (O. F. Müller, 1776)					4 / 0.014
Heteromastus filiformis (Claparède, 1864)	37 / 0.08	9 / 0.02	14 / 0.11	6 / 0.01	22 / 0.04
**Marenzelleria neglecta* Sikorski & Bick, 2004					
Melinna palmata Grube, 1870	1 / 0.03	18 / 0.21			2 / 0.05
Mysta picta (Quatrefages, 1866)	1 / 0.28	3 / 0.05			
Nephtys hombergii Savigny in Lamarck, 1818	175 / 5.36	163 / 3.21	180 / 10.43	348 / 4.84	314 / 4.61
Pholoe inornata Johnston, 1839					8 / 0.001
Phyllodoce mucosa Örsted, 1843				2 / 0.01	
Polydora cornuta Bosc, 1802	4 / 0.01	29 / 0.04	267 / 0.39	53 / 0.05	379 / 0.45
Prionospio cirrifera Wirén, 1883	4 / 0.01				
Spio decorata Bobretzky, 1870					1 / 0.002
Streblospio gynobranchiata Rice & Levin, 1998		2 / 0.002	579 / 0.1		

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Taxon	2016			2017	
	April	June	October	July	December
Spionidae g. sp.			2 / 0.002		
Oligochaeta g. sp.	1,963 / 0.39	443 / 0.1	636 / 0.11	191 / 0.02	2,442 / 0.47
Crustacea					
Ampithoe ramondi Audouin, 1826			2 / 0.001		
Amphibalanus improvisus (Darwin, 1854)	891 / 22.9	959 / 12.17	233 / 4.87	173 / 1.43	144 / 9.03
Cardiophilus baeri G. O. Sars, 1896	3 / 0.006				
Gastrosaccus sanctus (Van Beneden, 1861)					1 / 0.002
Iphinoe elisae Băcescu, 1950	168 / 0.15	75 / 0.03		36 / 0.004	144 / 0.02
Iphinoe maeotica Sowinskyi, 1893				10 / 0.001	
Mesopodopsis slabberi (Van Beneden, 1861)					21 / 0.1
Microdeutopus gryllotalpa Costa, 1853		2 / 0.001			
Microdeutopus sp.				2 / < 0.001	
Mysidacea g. sp.		16 / 0.02			2 / 0.01
Perioculodes longimanus (Spence Bate & Westwood, 1868)		2 / < 0.001			
Rhithropanopeus harrisii (Gould, 1841)				3 / 0.05	
Upogebia pusilla (Petagna, 1792)				4 / 1.0	
Mollusca					
Bittium reticulatum (da Costa, 1778)		2 / 0.01			
Hydrobia acuta (Draparnaud, 1805)	79 / 0.21	1,645 / 4.42	51 / 0.1	43 / 0.1	201 / 0.4
Retusa umbilicata (Montagu, 1803)	61 / 0.12	66 / 0.12		2 / 0.002	1 / < 0.001
Abra nitida (O. F. Müller, 1776)		10 / 0.02			
Abra segmentum (Récluz, 1843)	203 / 13.8	170 / 18.3	32 / 0.15	51 / 8.65	34 / 1.69
Anadara kagoshimensis (Tokunaga, 1906)	497 / 406	267 / 545.3	4,458 / 661	2,619 / 755	915 / 1,445
Cerastoderma glaucum (Bruguière, 1789)	391 / 154	345 / 149	7 / 4.4	173 / 16.9	29 / 32.6
Gouldia minima (Montagu, 1803)					1 / 0.007
Lentidium mediterraneum (O. G. Costa, 1830)					1 / 0.001
Mya arenaria Linnaeus, 1758	41 / 3.74	6 / 0.14			
Mytilus galloprovincialis Lamarck, 1819		1 / < 0.001			
Mytilaster lineatus (Gmelin, 1791)	3 / 0.25	1 / 0.03	22 / 0.68	15 / 0.12	6 / 0.47
Bryozoa					
Bryozoa g. sp.		1 / 0.004			
Conopeum seurati (Canu, 1928)		2 / 0.004	3 / 0.007		1 / < 0.001
Phoronida					
Phoronis psammophila Cori, 1889		5 / 0.007	1 / 0.002		
Chordata (Ascidiacea)					
***Molgula euprocta* (Drasche, 1884)					

Note: * denotes qualitative sample, 02.04.2017, st. 2; ** denotes qualitative sample, 25.07.2019, st. 4.

In the taxonomic structure of the fauna, the contribution of the main groups of macrozoobenthos (Mollusca, Crustacea, and Annelida) is approximately the same (25, 24, and 31 %, respectively). Similar data on the ratio of different groups of organisms in the macrozoobenthos are given in the results of studies of the Sea of Azov proper both in the 1990s and in the first decade of the XXI century (Litvinenko & Evchenko, 2016 ; Frolenko, 2000 ; Frolenko & Maltseva, 2017).

Alien species in the Sea of Azov. The extreme poverty of the species composition of the Sea of Azov fauna V. Vorob'ev (1949) explained as follows: a species that invades the Sea of Azov must be simultaneously eurythermal, euryhaline, stenobathic-shallow, and euryoxygenic. To date, due to construction of water channels, development of mariculture and aquarism, intensification of shipping, and associated transportation of organisms as part of the fouling of ship hulls and with ballast water, the possibility of such "eurytopic" species entering the Sea of Azov has significantly increased.

A total of 14 % of the species found are far-sea invaders. These include 3 polychaete species out of 15 registered by us: *Polydora cornuta*, *Streblospio gynobranchiata*, and *Marenzelleria neglecta*. *Polydora cornuta* was the first of them to be found in the Sea of Azov. In samplings of 1983, it was identified as *Polydora ciliata limicola* (Kiseleva, 1987). It was assumed that this is the only autochthonous Black Sea species of the genus *Polydora* which entered the Sea of Azov from the Black Sea. However, in recent years it was established (Boltachova, 2013 ; Radashevsky & Selifonova, 2013) that the species that spread in the Sea of Azov is *P. cornuta* – a distant invader, first recorded in the Black Sea in 1962 (Losovskaya & Nesterova, 1964). Taking into account the morphological similarity between *P. ciliata* and *P. cornuta*, it was suggested that *Polydora* representatives, which were found in the Sea of Azov from the 1980s to the present (Kiseleva, 1987 ; Litvinenko & Evchenko, 2016 ; Frolenko, 2000), also belonged to the species *P. cornuta* (Boltachova, 2013). At present, this species is widely distributed in the Sea of Azov; in our samplings in the southwestern area, its occurrence rate in general was 84 %. The maximum abundance of *P. cornuta* (1,014 ind.·m^{-2}) was recorded on 29.10.2016 (st. 4) which is due to the reproduction of this species in the Sea of Azov in late summer and early autumn (Boltachova & Lisitskaya, 2019).

Streblospio gynobranchiata was first noted in the Black Sea in 2007 (Boltacheva, 2008); in the Sea of Azov, it was registered in September 2015 in macrozoobenthos samples from the Temryuk Bay (Lisitskaya & Boltacheva, 2016). In our material, this species was recorded in the summer–autumn samples of 2016 at st. 4 with a maximum abundance of 2,316 ind.·m^{-2}.

Marenzelleria neglecta is known for the Atlantic and Pacific coasts of North America, the Canadian Arctic, and the North and Baltic seas (Sikorski & Bick, 2004). It entered the Sea of Azov, possibly, with the ballast water of ships coming from the North Atlantic and the Baltic Sea through the Volga–Baltic Waterway and Volga–Don Canal. It was first found here in the Taganrog Bay in 2014 (Syomin et al., 2017); later, it spread to other sea areas (Frolenko & Maltseva, 2017). We noted this species in qualitative samples at st. 4 in 2017.

The crab *Rhithropanopeus harrisii* was first recorded in the Taganrog Bay in 1948, and in the Sea of Azov proper, it was registered in 1952 (Reznichenko, 1967). To date, it has spread widely throughout the sea; in 1997, its occurrence rate was 20 % (Litvinenko & Evchenko, 2016). In our samples, single specimens of this species were noted, with an occurrence rate of 10 %.

The bivalve *Mya arenaria* was first recorded in the Black Sea in 1966 and brought into the Sea of Azov in 1975 (Savchuk, 1980). In the latter, the species is widely distributed and forms especially dense aggregations near the northern coasts (Frolenko, 2000). We found this mollusc at 21 % of the stations; however, its abundance and biomass were low, and juveniles predominated.

The expansion in the Sea of Azov of the bivalve *Anadara kagoshimensis* classified as one of 100 the most dangerous alien species in Russia (Soldatov et al., 2018), has a 30-year history. After the first registration of this far-sea alien species off the coast of the Caucasus in 1968 (Kiseleva, 1992) and further successful development of its population in the Black Sea in the 1980s (Revkov, 2016), *A. kagoshimensis* was first detected in the Sea of Azov in the northern Kazantip Bay in 1989 (Chikhachev et al., 1994). To date, *A. kagoshimensis* has successfully spread throughout the Sea of Azov, up to the most desalinated spots in the Taganrog Bay area (Frolenko & Maltseva, 2017), which corresponds to the final stage of colonization of the whole Sea of Azov–Black Sea basin by this species. In our surveys, the species had an occurrence rate of 100 % and high abundance rates; it dominated among all macrozoobenthos species.

In 2015, in the southern Sea of Azov, sea anemones of the family Edwardsiidae were first recorded (Frolenko et al., 2017). It is known that some representatives of this family at the larval stage are endoparasites of ctenophores. For example, the larva of *Edwardsiella lineata* (Verrill in Baird, 1873) parasitizes *Mnemiopsis leidyi* A. Agassiz, 1865, and *Edwardsiella carnea* (Gosse, 1856) parasitizes *Bolinopsis infundibulum* (O. F. Müller, 1776), while adult sea anemones are free-living organisms (Daly, 2002). Anemones of this family are common within the native range of *M. leidyi* (Atlantic coast of North America), and sometimes more than 50 % of ctenophores are infested with *E. lineata* larvae (Reitzel et al., 2007). However, in the Black Sea and the Sea of Azov, where *M. leidyi* was introduced in the 1980s, and then in other European seas, where this species naturalized, no infested individuals were noted for a long time. In European waters, parasitic larvae of the genus *Edwardsiella* were first detected in alien ctenophores *M. leidyi* in 2008 off the coast of Sweden (Selander et al., 2010). It was suggested that the duration of development of *Edwardsiella* larvae is sufficient for them to be able to cross the ocean with currents or be transported with the ballast water of ships (Selander et al., 2010). It is possible that representatives of this genus ended up in the Sea of Azov following the ctenophore *M. leidyi*. In 2015, a very high abundance of sea anemones Edwardsiidae g. sp. was noted in the Kerch pre-strait area (up to 17,400 ind.·m^{-2}) (Frolenko & Maltseva, 2017). In our surveys, this species was recorded at 32 % of the stations, but in relatively small abundance.

Based on the results of our research, four representatives of the Black Sea fauna were recorded in the Sea of Azov for the first time – the bivalve *Gouldia minima*, the ascidian *Molgula euprocta*, the phoronid *Phoronis psammophila*, and the crustacean *Iphinoe elisae*. *G. minima* was noted singly in December 2017 (st. 1); *M. euprocta* was registered in a qualitative sample in July 2019 (st. 4). *Ph. psammophila* was found at 16 % of the stations (with abundance up to 20 ind.·m^{-2}); *I. elisae* was recorded at 42 % of the stations (up to 568 ind.·m^{-2}). In the Black Sea, *I. elisae* inhabits soft bottoms (especially in the zone of phaseolina silts) at a depth of 30–125 m (Bechesku, 1969 ; Revkov et al., 2015). In recent decades, this species has been recorded at shallow depths (0.5–16 m) in Sevastopol bays, as well as in shallow (down to 6 m) lagoons of the Kerch Strait under conditions of water salinity varying from 13 to 19 ‰ (Boltacheva et al., 2018 ; Revkov et al., 2008 ; Spiridonov et al., 2016). It can be assumed that the penetration of these Black Sea species into the Sea of Azov is associated with an increase in water salinity, which in 2016 and especially in 2017 at the studied site exceeded its maximum values noted in the 1970s for the Sea of Azov (Kuropatkin et al., 2013).

It should be noted that in the southern Sea of Azov in 2015, 36 taxa of macrozoobenthos were recorded in the *Anadara* biocoenosis (Frolenko & Maltseva, 2017). The Czekanowski–Sørensen index value for these data and for those obtained by us is 0.64, which indicates a great similarity in the taxonomic composition of the *Anadara* biocoenosis in different areas of the sea.

Biocoenotic structure of macrozoobenthos. The results of cluster and ordination analyzes (Fig. 2) indicate the existence of a relatively homogeneous group in the benthos of the southwestern Sea of Azov with a total species similarity of stations (the Bray–Curtis similarity) of about 65 %. The total contribution to the intracomplex similarity of the first five most significant species of grouping is estimated at 99.27 %. *A. kagoshimensis* has the highest value of the quantitative development according to IFA (763.76), with a relative contribution to intracomplex similarity, $\overline{\alpha_i}$%, of 89.6 %. The following positions are occupied by *Cerastoderma glaucum* (IFA = 79.48; $\overline{\alpha_i}$% = 4.47 %); *Amphibalanus improvisus* (22.17; 2.37), *Nephtys hombergii* (13.52; 1.70); and *Abra segmentum* (14.63; 1.12). The obtained results give us reasons to name the identified relatively homogeneous group of benthos in the southwestern Sea of Azov as the *A. kagoshimensis* biocoenosis.

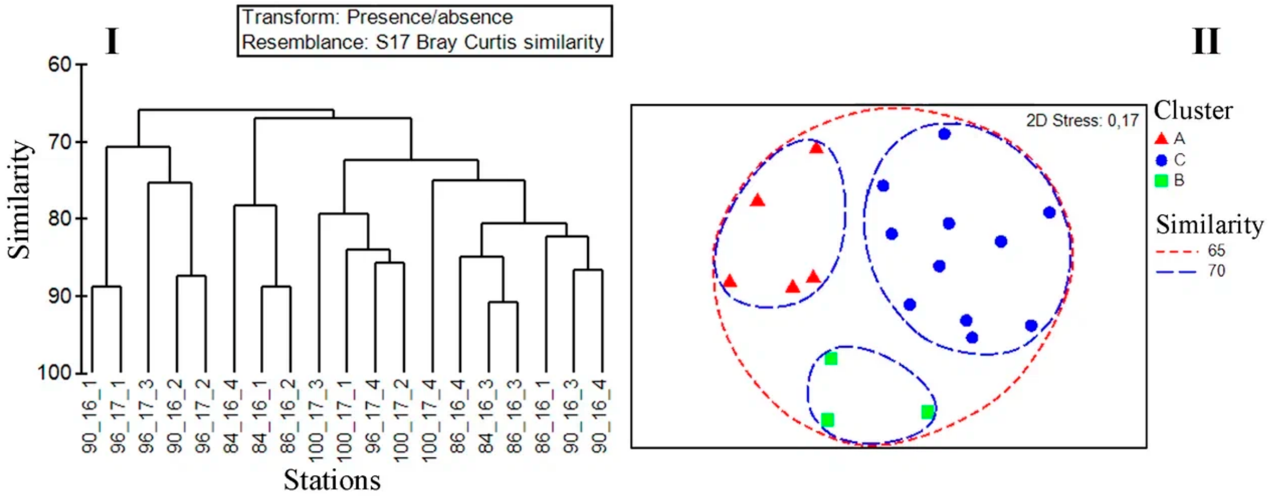

Fig. 2. Hierarchical clustering (I) and MDS ordination (II) of sampling stations in the southwestern Sea of Azov in 2016–2017. On I, the designation is "cruise_year_station"

Within the framework of the identified *Anadara* biocoenosis, all stations are grouped into three biocoenotic complexes (A, B, and C; see Fig. 2), represented by the set of main complex-forming species indicated above. Among them, the main complex-forming species is still *A. kagoshimensis*, which has the highest values of integral indicators of quantitative development according to IFA and contributions to intracomplex similarity (Table 3). According to the results of the analysis, despite the slightly different station characteristics of the bottom sediments (see Table 1), we did not mark marginal stations (see Fig. 2) that fall out of the general scheme of a single biocoenotic structure represented at the site by labile biocoenotic complexes. Each of these complexes does not have a strict reference to a specific season and study area (stations). Thus, complex A can manifest itself in autumn and summer within st. 1, 2, and 3; complex B, in spring and summer within st. 1, 2, and 4; and complex C, in all seasons at all stations of the site. Together, from our point of view, these biocoenotic complexes can be characteristics / variants of the manifestation for the dynamic state of the *Anadara* biocoenosis itself.

Table 3. Ranked list (by contribution to the intracomplex similarity) of main species in biocoenotic complexes of bottom macrofauna in the southwestern Sea of Azov

Taxon	Average IFA	$\overline{\alpha_i}$	$\overline{\alpha_i}$/SD($\overline{\alpha_i}$)	$\overline{\alpha_i}$%	Cum. $\overline{\alpha_i}$%
Complex A. Average similarity: 36.29					
Anadara kagoshimensis	829.35	34.58	1.37	95.29	95.29
Nephtys hombergii	9.62	0.70	2.29	1.92	97.21
Amphibalanus improvisus	9.70	0.57	0.58	1.57	98.78
Cerastoderma glaucum	19.63	0.30	0.58	0.83	99.61
Complex C. Average similarity: 62.72					
Anadara kagoshimensis	871.81	57.09	3.22	91.03	91.03
Cerastoderma glaucum	110.40	2.59	0.40	4.12	95.15
Amphibalanus improvisus	28.72	1.17	0.89	1.86	97.01
Nephtys hombergii	16.68	0.94	1.33	1.49	98.50
Abra segmentum	14.17	0.32	0.40	0.51	99.02
Complex B. Average similarity: 46.84					
Anadara kagoshimensis	258.29	35.74	1.34	76.30	76.30
Cerastoderma glaucum	65.84	5.20	5.47	11.10	87.40
Abra segmentum	22.64	2.53	0.61	5.41	92.81
Amphibalanus improvisus	18.93	1.92	1.00	4.10	96.91
Nephtys hombergii	8.44	1.05	4.80	2.24	99.15

Note: IFA is mean value of the index of functional abundance; $\overline{\alpha}$ and $\overline{\alpha_i}$% are absolute and relative contributions of species *i* to the mean Bray–Curtis similarity within the complex; SD is standard deviation; and Cum. is cumulative.

In terms of biomass, *A. kagoshimensis* dominated throughout the entire site in all the studied seasons of 2016–2017, which, according to the concept of V. Vorob'ev (1949), also testifies in favor of the existence of a single *Anadara* biocoenosis. There was only one exception: in the westernmost site (st. 2), in June 2016, *C. glaucum* dominated in biomass, but *A. kagoshimensis* was the codominant (its biomass was only 23 % lower than that of *C. glaucum*).

Based on frequency of occurrence rate, 9 species are assigned to the leading ones for the highlighted *Anadara* biocoenosis: molluscs *A. kagoshimensis*, *C. glaucum*, *A. segmentum* and *H. acuta*; polychaetes *N. hombergii*, *A. succinea*, *P. cornuta*, and *H. filiformis*; and crustacean *A. improvisus*. The characteristic group includes 7 species: molluscs *M. lineatus* and *R. umbilicata*; crustacean *I. elisae*; polychaeta *H. imbricata*; bryozoan *C. seurati*; sea anemones *S. undatus* and Edwardsiidae g. sp. Among the rare species (29 ones), the above-mentioned aliens should be noted – *M. arenaria*, *S. gynobranchiata*, and *R. harrisii*.

Bottom sediments at the stations in the Sea of Azov were represented by silty deposits, which hinders the development of populations of species that require (at least at the initial stage of bottom settlements) the presence of a hard substrate. Under these conditions, the shells of large *A. kagoshimensis* are a convenient substrate for larvae settling. In the samples studied by us, *A. kagoshimensis* was only partially immersed in the sediment, which determined the formation of multitiered druses of *A. improvisus* on the shell in the area of siphon holes. Herewith, the weight share of balanus in the *Anadara* consortium in some cases reached 76 % (October 2016, st. 1). On average, one mollusc in the size range of 6–9 mm can account for about two balanuses. It is due to this that *A. improvisus* has rather high, noted above, average indicators of quantitative development at the studied site; maximum values of abundance and biomass at separate stations were up to 2,056 ind.·m^{-2} (April 2016, st. 1) and 56.1 g·m^{-2} (April 2016, st. 3), respectively. In addition to balanuses, the *Anadara* consortium contains juveniles of mytilids and *A. kagoshimensis*, the sea anemones, and bryozoans.

Abundance and biomass values of macrozoobenthos in the *Anadara* biocoenosis. The total biomass of the *Anadara* biocoenosis at the site varies from 36.4 to 1,825.6 g·m^{-2} and averages (878.4 ± 129.5) g·m^{-2}. The abundance varies from 1,082 to 19,335 ind.·m^{-2}; average value is (4,818 ± 1,019) ind.·m^{-2}. The biomass and abundance of *A. kagoshimensis* itself are (781.2 ± 132.3) g·m^{-2} (89 % of the total macrozoobenthos biomass) and (1,817 ± 770) ind.·m^{-2} (38 % of the total macrozoobenthos abundance), respectively. The subdominant is *C. glaucum*, whose biomass and abundance were (67 ± 27.7) g·m^{-2} (8 % of the total macrozoobenthos biomass) and (178 ± 60) ind.·m^{-2} (4 % of the total macrozoobenthos abundance), respectively. Relatively high values of biomass were also noted for the barnacle *A. improvisus* [(9.4 ± 3.0) g·m^{-2}], the bivalve *A. segmentum* [(8.2 ± 2.9) g·m^{-2}], and polychaetes *N. hombergii* [(5.7 ± 1.7) g·m^{-2}] and *A. succinea* [(3.5 ± 1.2) g·m^{-2}]. The relatively high values of abundance were recorded for Oligochaeta [(1,091 ± 422) ind.·m^{-2}], the gastropod *H. acuta* [(420 ± 224) ind.·m^{-2}], the barnacle *A. improvisus* [(458 ± 144) ind.·m^{-2}], and polychaetes *N. hombergii* [(238 ± 42) ind.·m^{-2}], *P. cornuta* [(154 ± 68) ind.·m^{-2}], and *S. gynobranchiata* [122 ind.·m^{-2}].

During the spring–summer–autumn seasons of 2016–2017, the average biomass of the *Anadara* biocoenosis varied within 600–700 g·m^{-2}; in December 2017, it was two times higher – 1,501 g·m^{-2} (Fig. 3). At the same time, the maximum abundance of macrozoobenthos was noted in October 2016 (6,574 ind.·m^{-2}). In other seasons, the values varied within 3,815–4,761 ind.·m^{-2}. This abundance peak is associated with the reproduction in the summer–autumn period of a number of macrozoobenthos species, including recent aliens, and the replenishment of their populations with juveniles (Boltachova & Lisitskaya, 2019 ; Revkov & Scherban, 2017). In October 2016, the highest abundance values of the leading biocoenosis species – *A. kagoshimensis* – were noted (average (4,458 ± 3,174) ind.·m^{-2}; maximum 13,896 ind.·m^{-2}). At st. 4, there was a very high abundance of the invasive polychaete *S. gynobranchiata* – 2,316 ind.·m^{-2}. For another invasive polychaete, *P. cornuta*, abundance values in October 2016 [(267 ± 249) ind.·m^{-2}; 1,014 ind.·m^{-2}] were close to those in December 2017 [(379 ± 180) ind.·m^{-2}; 888 ind.·m^{-2}].

The changes in biomass we observed are mainly related to its fluctuations in the dominant species – *A. kagoshimensis* and *C. glaucum* (Fig. 4). At the same time, against the backdrop of an increase in the absolute values of *A. kagoshimensis* biomass from (405.9 ± 112.7) g·m^{-2} in April 2016 to (1,444.8 ± 154.5) g·m^{-2} in December 2017, there is a sharp decrease in biomass values of *C. glaucum* – from (153.6 ± 134.8) g·m^{-2} in April 2016 and (149.3 ± 65.6) g·m^{-2} in June 2016 to (4.4 ± 3.7) g·m^{-2} in October 2016 and (32.6 ± 31.7) g·m^{-2} in December 2017.

These multidirectional changes in the beds of the two species are presumably related to their different ability to survive oxygen-deficient conditions typical for summer in the benthal of the Sea of Azov. The currently available data on the biology of *A. kagoshimensis* clearly indicate high physiological and biochemical adaptive capabilities of the recent invader to survive adverse environmental conditions (Revkov & Scherban, 2017), which gives it certain advantages in competing with local species when expanding into new water areas. *C. glaucum* reaction to periodic oxygen-deficient conditions is well known (Vorob'ev, 1949) and is reduced to partial or complete elimination of its aggregations in certain spots of the water area.

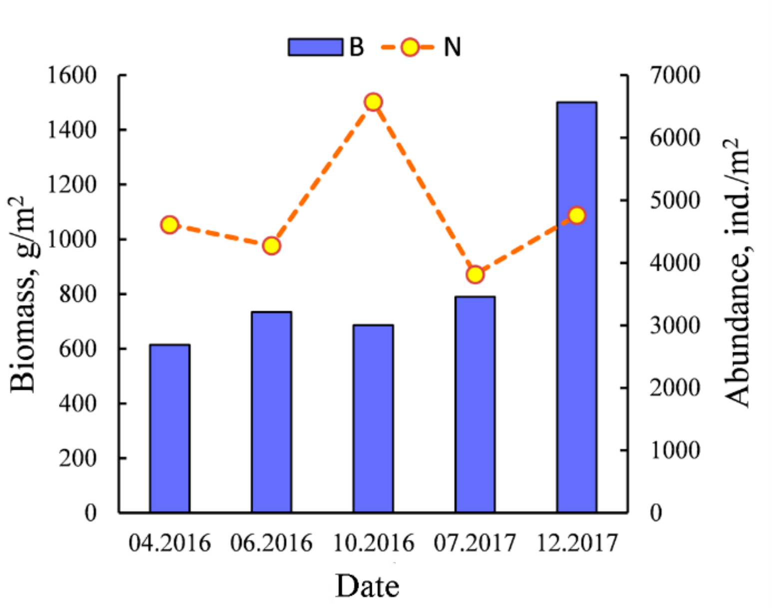

Fig. 3. Changes in abundance (N) and biomass (B) of macrozoobenthos in *Anadara* biocoenosis in the southwestern Sea of Azov in 2016–2017

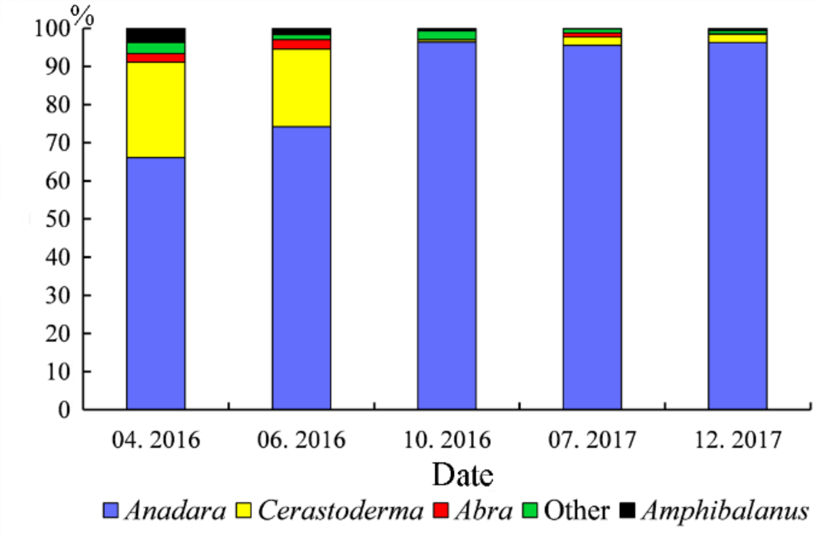

Fig. 4. Changes in the structure of *Anadara* biocoenosis in 2016–2017 in the southwestern Sea of Azov

The results obtained by us in 2016–2017 are comparable with similar data for the periods of 1997 (the Kazantip Bay area) and 2015 (the eastern and southern Sea of Azov). For these years, the average values of the biomass of the *Anadara* biocoenosis and weight shares of *A. kagoshimensis* are given; those are 722 g·m^{-2} and 80 % (Frolenko & Dvinyaninova, 1998) and 379.5–1,187.8 g·m^{-2} and 75.9–83 % (Frolenko & Maltseva, 2017), respectively.

Size structure of *A. kagoshimensis* and *C. glaucum* populations. In our studies, *A. kagoshimensis* population is represented by different-sized molluscs with a maximum shell length of 52.7 mm (age 5+, October 2016, st. 3) (Fig. 5). The share of molluscs of reproductive size (with a shell length of more than 10 mm) ranges from 6 % (October 2016, the period of mass replenishment of the population with juveniles) to 85 % (December 2017) in the total population structure. The largest percentage of early juveniles (76 %) was recorded in October, which coincides with the known period of autumn replenishment of *A. kagoshimensis* population with juveniles described for the Black Sea (Revkov & Scherban, 2017). Apparently, the earlier warming of the Sea of Azov waters creates conditions for earlier reproduction of *A. kagoshimensis*, which determines the replenishment of its population already in summer (June–July). On the histograms presented for this period, early juveniles (up to 2 mm) make up 2–10 % in the population structure (see Fig. 5). The extended period of replenishment of the Sea of Azov population of *A. kagoshimensis* (from June to October) is possibly associated with both the own larvae pool in the Sea of Azov and the pool of larvae penetrating from the Black Sea.

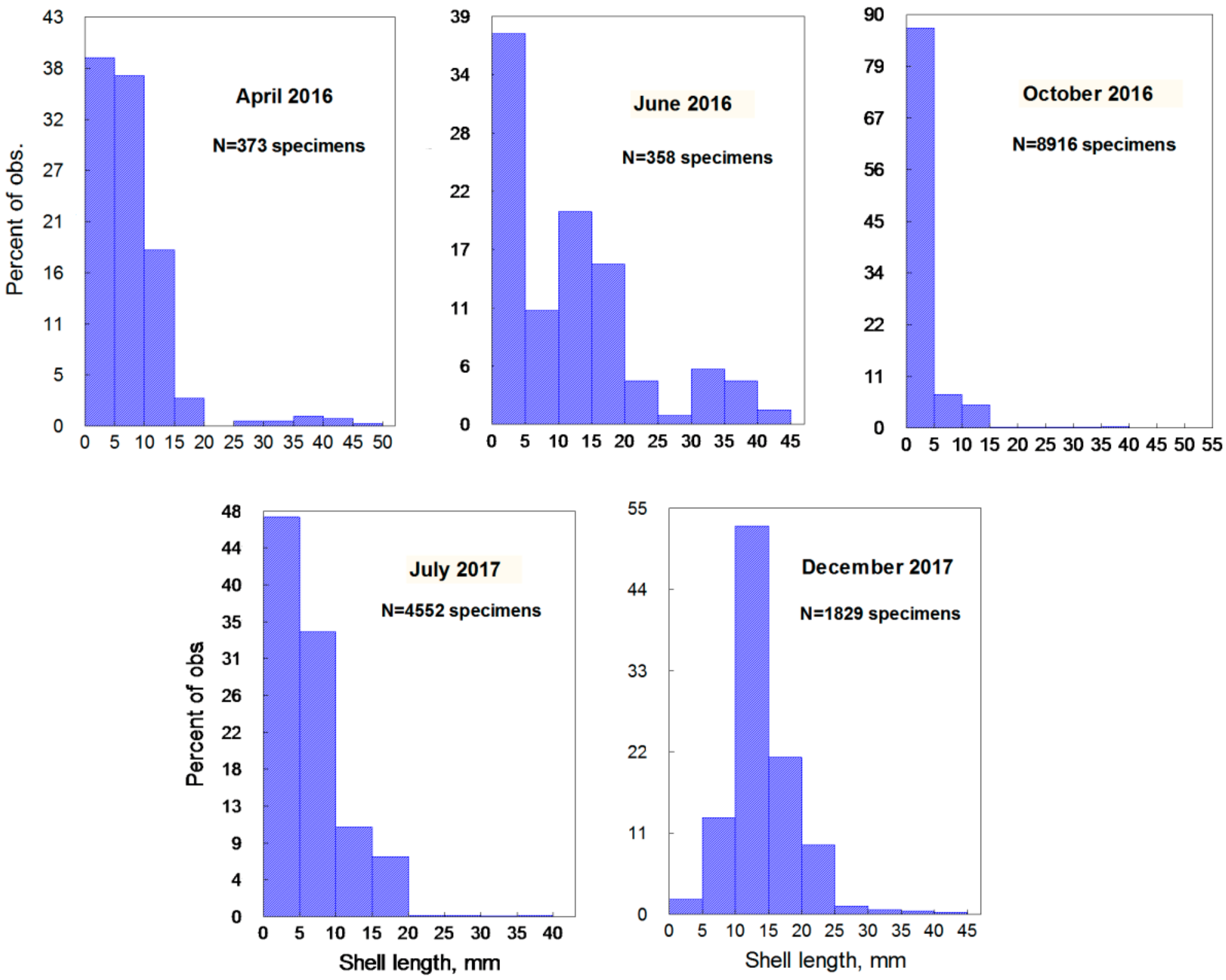

Fig. 5. Histograms of the shell-size composition of *Anadara kagoshimensis* population in the southwestern Sea of Azov in different seasons of 2016–2017

The presence of early juveniles in spring in the population of *A. kagoshimensis*, apparently, is not directly related to the reproduction of molluscs, but is determined by the natural growth retardation of the autumn spat in winter. The presence of such “reserve” juveniles was described for other Black Sea molluscs (Kiseleva, 1978 ; Revkov et al., 2015).

C. glaucum population in the benthos of the studied area is less abundant (in comparison with that of *A. kagoshimensis*) and is represented by molluscs of different sizes (Fig. 6). A comparison of the material obtained with the available literature data on the age structure of the Sea of Azov population of *C. glaucum* (Vorob’ev, 1949) shows that all age groups, including four-year-olds, are present in the studied Sea of Azov area. The mollusc we noted, with a maximum size of 25.6 mm (December 2017, st. 2), according to the Table presented in that work, had an age of 5+.

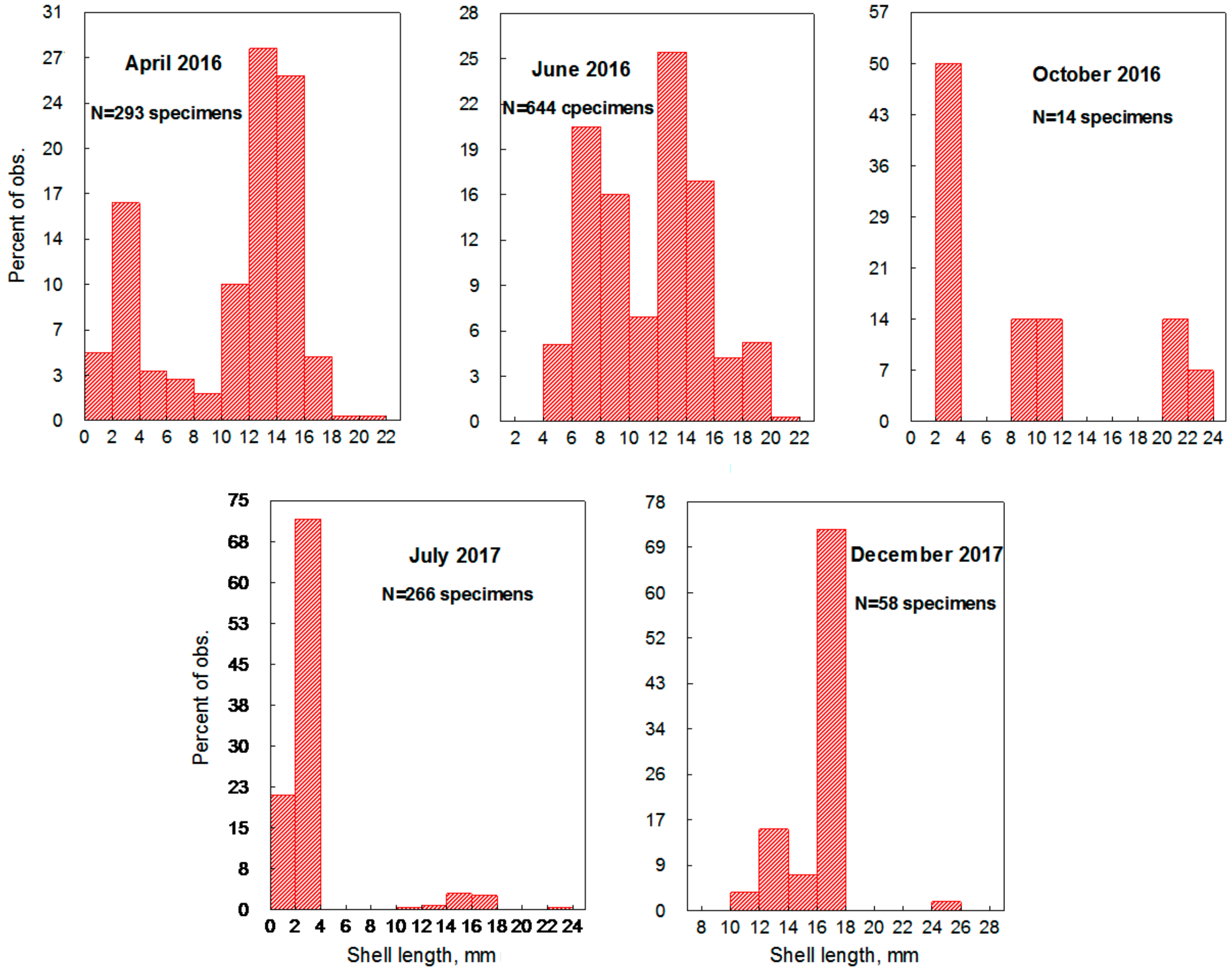

Fig. 6. Histograms of the shell-size composition of *Cerastoderma glaucum* population in the southwestern Sea of Azov in different seasons of 2016–2017

It is known that *C. glaucum* spawning in the Black Sea extends from May to December, with two peaks – in May–June and August–September (Mikhailova, 1986). In the Sea of Azov, the spawning period of *C. glaucum* is more prolonged, presumably with three peaks – in spring, summer, and autumn (Vorob'ev, 1949). Apparently, due to the peculiarity of the thermal regime and the earlier spring warming of the Sea of Azov waters (in comparison with the Black Sea), *C. glaucum* reproduction can be shifted in time to earlier spring period. In our studies, recently settled juveniles (0–2 mm) were recorded in April 2016 (4 %) and July 2017 (20 %). Molluscs of reproductive size (with a shell length of more than 6 mm) ranged from 7 % (July 2017, the period of mass replenishment of the population with juveniles) to 100 % (December 2017) in the general structure of *C. glaucum* population.

Defined as stenooxygenic form (Vorob'ev, 1949), *C. glaucum* is sensitive to the presence of hydrogen sulfide. Therefore, it is no coincidence that under conditions of summer near-bottom hypoxia and suffocation phenomena, which are more typical for the central Sea of Azov, regular elimination of its population occurs. According to the results of our studies, at st. 1, which belongs to the central area, either *C. glaucum* beds were not numerous (April and June 2016), or molluscs were not recorded at all (October 2016, July and December 2017).

Conclusion. In 2016–2019, a total of 46 species of macrozoobenthos were recorded in the southwestern Sea of Azov, of which 7 are invaders. Under conditions of the current increase in salinity, the process of pontization of the Sea of Azov fauna continues: 4 new representatives of the Black Sea fauna were found here – the bivalve *Gouldia minima*, the ascidian *Molgula euprocta*, the phoronid *Phoronis psammophila*, and the crustacean *Iphinoe elisae*.

The obtained results testify to the high convergence of two used methods for assessing the structure of the benthos in the southwestern Sea of Azov – the method of Vorob'ev (based on the dominant biomass species) and the method of multivariate data analysis according to IFA.

In all seasons of 2016–2017, despite the existence of relative spatial heterogeneity of the sediment composition, a single biocoenosis of the bivalve *A. kagoshimensis* was identified in the benthos of the area, with average values of abundance and biomass being (4,818 ± 1,019) ind.·m^{-2} and (878.4 ± 129.5) g·m^{-2}, respectively. *Anadara* biocoenosis in the framework of the study is represented by three biocoenotic complexes, which may be variants of the manifestation of its dynamic state. The share of the leading species of the biocoenosis, *A. kagoshimensis*, was 66–96 % of the total biomass of macrozoobenthos; the share of subdominant *C. glaucum*, which was the main coenosis-forming species in the benthos of the Sea of Azov in the 1930s, was 1–25 %. Seasonal changes in the biomass of the biocoenosis are mainly due to its fluctuations in the dominant species – *A. kagoshimensis* and *C. glaucum*.

The composition of *A. kagoshimensis* beds in the southwestern Sea of Azov during 2016–2017 corresponded to the structure of a full-fledged population of different ages. An extended period of replenishment of *A. kagoshimensis* beds with juveniles (from June to October) with a peak in October was noted. Molluscs of reproductive size (with a shell length of more than 10 mm) made up from 6 % (October 2016) to 85 % (December 2017) in the total population structure. The most massive aggregations of *C. glaucum* were recorded at the alongshore stations of the studied area. The main period of replenishment of *C. glaucum* population was registered in July. Molluscs of reproductive size (with a shell length of more than 6 mm) made up from 7 % (July 2017) to 100 % (December 2017) in the total structure of *C. glaucum* population.

Under lack of hard substrate, *A. kagoshimensis* – an alien species for the Sea of Azov – formed a new consort community of biofiltrators which supplemented a benthic biofilter zone in the Sea of Azov.

This work was carried out within the framework of IBSS state research assignment "Regularities of formation and anthropogenic transformation of biodiversity and biological resources of the Sea of Azov–Black Sea basin and other areas of the World Ocean" (No. 121030100028-0).

Acknowledgement. The authors express their gratitude to V. Timofeev, M. Makarov, and V. Kopiy for their participation in material sampling. The authors are grateful to the reviewers of the article for valuable comments.

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ДОННАЯ ФАУНА ЮГО-ЗАПАДНОЙ ЧАСТИ АЗОВСКОГО МОРЯ. ТАКСОНОМИЧЕСКИЙ СОСТАВ И БИОЦЕНОТИЧЕСКАЯ ОРГАНИЗАЦИЯ МАКРОЗООБЕНТОСА В 2016–2017 ГГ.

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Азовское море является полузамкнутым, относительно мелководным водоёмом, имеющим, в сравнении с Чёрным морем, более низкую солёность. Последняя не стабильна (изменяется в пределах 9–14 ‰) и в основном связана с изменением речного стока. Повышение солёности оказывается благоприятным фактором для проникновения и развития в Азовском море некоторых черноморских видов, что было отмечено в 1970-е гг. при возрастании его солёности в среднем до 13–14 ‰. Вслед за периодом спада до 9–10 ‰, с 2007 г. зарегистрировано устойчивое осолонение бассейна, достигшее в 2015 г. в среднем 13,37 ‰. Целью работы стала оценка таксономического состава и биоценотической организации донной макрофауны юго-западной части Азовского моря по результатам бентосных съёмок, выполненных в 2016–2017 гг. в 84, 86, 90, 96 и 100-м рейсах НИС «Профессор Водяницкий». Отбор донных осадков осуществляли с помощью дночерпателя «Океан-50» (площадь захвата — 0,25 м^2). Грунт промывали через сита с наименьшим диаметром ячеи фильтрации 1 мм. Зарегистрировано 46 видов макрозообентоса, в том числе 15 видов Polychaeta, 12 Mollusca и 13 Crustacea. Четыре представителя черноморской фауны отмечены в фауне Азовского моря впервые: асцидия *Molgula euprocta*, форонида *Phoronis psammophila*, двустворчатый моллюск *Gouldia minima* и кумовый рак *Iphinoe elisae*. Из обнаруженных видов 14 % являются дальнеморскими вселенцами в Азово-Черноморский бассейн. Это двустворчатые моллюски *Anadara kagoshimensis* и *Mya arenaria*, полихеты *Polydora cornuta*, *Streblospio gynobranchiata* и *Marenzelleria neglecta*. Во все сезоны года в бентосе региона отмечен биоценоз двустворчатого моллюска *A. kagoshimensis*, средние значения численности и биомассы — (4818 ± 1019) экз.·м$^{-2}$ и (878,4 ± 129,5) г·м$^{-2}$ соответственно. Выделены 3 биоценотических комплекса, которые могут быть вариантами проявления динамического состояния биоценоза анадары. Сезонные изменения биомассы макрозообентоса в основном обусловлены её колебаниями у доминирующих видов — *A. kagoshimensis* и *Cerastoderma glaucum* — и связаны с их различной способностью к переживанию кислороддефицитных условий, характерных для Азовского моря в летний сезон. Максимум численности макрозообентоса отмечен в октябре 2016 г. (~ 6600 экз.·м$^{-2}$) и обусловлен размножением в летне-осенний период ряда видов, включая недавних вселенцев, и пополнением их донных поселений молодью. В это время на отдельных станциях численность *A. kagoshimensis* достигала ~ 14000 экз.·м$^{-2}$, полихеты-вселенца *S. gynobranchiata* — ~ 2300 экз.·м$^{-2}$. Зарегистрирован растянутый период пополнения азовоморской популяции *A. kagoshimensis* молодью (с июня по октябрь) с пиком в октябре. Максимальный размер их раковины — 52,7 мм. Моллюски репродуктивного размера (с длиной раковины более 10 мм) составляли от 6 % (октябрь 2016 г., период массового пополнения популяции молодью) до 85 % (декабрь 2017 г.). Наиболее развитые поселения *C. glaucum* зарегистрированы на вдольбереговых станциях исследованного полигона. Основной период их пополнения молодью — в июле. Моллюски репродуктивного размера (с длиной раковины более 6 мм) составляли от 7 % (июль 2017 г., период массового пополнения популяции молодью) до 100 % (декабрь 2017 г.) в общей структуре популяции церастодермы. В условиях дефицита твёрдого субстрата недавний вселенец в Азовское море *A. kagoshimensis* сформировал новую консорцию биофильтраторов (собственный ресурс плюс ресурс фильтраторов-обрастателей), дополняющую биофильтрационный пояс бентали на основе *C. glaucum*.

Ключевые слова: макрозообентос, виды-вселенцы, таксономический состав, видовое богатство, биоценоз *Anadara kagoshimensis*, Азовское море

1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 23–31
https://doi.org/10.21072/mbj.2022.07.2.02

UDC 574.3(268.45)

SPECIES COMPOSITION AND BIOGEOGRAPHIC STRUCTURE OF THE POLYCHAETE FAUNA OF THE PECHORA SEA DURING WARMING IN THE ARCTIC

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Received by the Editor 06.10.2021; after reviewing 12.01.2022;
accepted for publication 03.03.2022;

A comprehensive study of benthos allows not only to see the current changes in benthic communities and better understand what happened to them in the past, but also to predict their future with a certain degree of reliability. Polychaete worms are one of the most numerous and significant groups of benthos, and those can serve as bioindicators of the state of the environment. This article attempts to analyze changes in the biogeographic groups of polychaetes in the Pechora Sea over a relatively long time period (~ 50 years) in order to understand whether the climate change affects the ratio of these groups and, consequently, whether polychaetes can serve as bioindicators to a certain degree. Based on the analysis of new data and material obtained earlier, a general list of polychaete worms of the Pechora Sea was formed. The list includes 198 taxa (out of them, 186 are identified down to a species level) belonging to 127 genera, 37 families, and 15 orders. The ratio of biogeographic groups of polychaetes in the Pechora Sea indicates the consistency of their biogeographic structure over the past 50 years and confirms the cyclicity of processes occurring in the Arctic.

Keywords: biogeography, bioindicators, Pechora Sea, polychaete worms

For understanding natural processes occurring in the Arctic, hydrobiological indicators are of key significance. Those allow to reconstruct the past and record the present; moreover, those help to predict changes in ecosystems. No wonder that A. I. Vilkitsky wrote in the early XX century that "plant and animal life are closely related to physical properties of water, and therefore, when studying biological conditions, information significant for hydrography is found at the same time" (Evgenov & Kupetskiy, 1985).

The interest of researchers in the groups of polychaete worms is due to a noticeable role those play in benthic communities – both in the entire World Ocean and in the Arctic seas. Polychaetes prevail in macrozoobenthos of shelf and continental slope: they usually make up 45–50 % of the total species number and up to 80 % of the total number of multicellular consumers (Blake, 1997 ; Zhirkov, 2001). Several works were focused on studying the species diversity and quantitative development of polychaetes in the southeastern Barents Sea, specifically in the Pechora Sea; the taxonomic composition and distribution of these worms in the 1950s and 1990s were characterized (Frolova, 1996 ; Petrovskaya, 1963 ; Sikorski, 1989 ; Streltzov, 1966). Based on new material, the modern taxonomic and biogeographic composition of polychaete worms of the Pechora Sea was examined.

In the Pechora Sea, 107 species were recorded in 1959; 113 species in 1993; and 163 species in 2004, 2006, and 2016. The ratio of biogeographic groups of polychaete worms in the Pechora Sea indicates the consistency of their biogeographic structure over the past 50 years and can be considered as another argument in favor of the idea of cyclical climatic processes in the Arctic.

The aim of the study is to establish the possibility of using polychaete worms as bioindicators of the ongoing climate change in the Arctic.

MATERIAL AND METHODS

Sampling. To study the fauna and analyze the quantitative distribution of polychaetes within the Pechora Sea, material was used from 214 quantitative zoobenthic samples collected by PINRO staff at 44 stations onboard the RV "Smolensk" (2004 and 2006), as well as material sampled at 26 stations by ZIN RAS staff onboard the RV "Professor Vladimir Kuznetsov" (August 2014 and September 2016).

The sampling was carried out at depths from 6 down to 120 m with a Van Veen grab sampler (0.1 m^2), 5 samples at each station; those were washed through a sieve with a mesh of 0.5 mm. The material was fixed with buffered 4–5 % formaldehyde; in 3–4 months, samples were transferred to 75 % ethanol and identified down to the lowest taxonomic level possible.

The biogeographic nature of each species was determined in accordance with generally accepted schemes for biogeographic zoning of the northern seas (Buzhinskaja, 2001 ; Frolova, 1996 ; Sirenko et al., 2009):

a) Arctic species (a) which are exclusively restricted to the Arctic Ocean north of the Iceland–Faroe Ridge;
b) widespread boreal–Arctic species (wb-a) inhabiting mainly temperate waters of the Atlantic, Pacific, and Arctic;
c) high-boreal–Arctic species (hb-a) which occur mainly in the high latitudes, northern boreal waters of the Atlantic and Pacific, and the Arctic Ocean;
d) subtropical boreal–Arctic species (sb-a) which are distributed from the subtropic Pacific and Atlantic oceans up to the Arctic Ocean;
e) Atlantic high-boreal–Arctic species (atlhb-a) whose distribution is similar to that of the high boreal–Arctic species (hb-a), except in Pacific waters;
f) Pacific boreal–Arctic species (pwb-a) which, in contrast, are found in all the areas except for the Atlantic Ocean;
g) cosmopolitan and bipolar species (c&bip) which occur throughout the World Ocean and/or in temperate and polar latitudes of the Northern and Southern hemispheres.

RESULTS

Based on taxonomic identification of the samples and considering the material collected during expeditions in the XX century, a general list of polychaete worms from the Pechora Sea was formed. The list includes 198 taxa (with 186 out of them identified down to a species level) belonging to 127 genera, 37 families, and 15 orders (Table 1).

Table 1. List of polychaetes of the Pechora Sea: a, Arctic; atlb-a, Atlantic boreal–Arctic; atlhb, Atlantic high-boreal; atlhb-a, Atlantic high-boreal–Arctic; atlwb, Atlantic widespread boreal; atlwb-a, widespread Atlantic boreal–Arctic; amph, amphiboreal; b-a, boreal–Arctic; c, cosmopolitans; hb-a, high-boreal–Arctic; phb-a, Pacific high-boreal–Arctic; psb-a, Pacific subtropical boreal–Arctic; pwb-a, Pacific widespread boreal–Arctic; sb-a, subtropical boreal–Arctic; wb-a, widespread boreal–Arctic; and whb-a, widespread high-boreal–Arctic. ? denotes species with unclear distribution. Finding of each species in the corresponding period is marked with +; absence is marked with –. See text for other explanations

Order	Family	Genus	Species	1959	1996	2000s	Biogeographic group
Phyllodocida	Phyllodocidae Örsted, 1843	*Eteone* Savigny, 1882	*E. flava* (Fabricius, 1780)	+	+	+	wb-a
			E. longa (Fabricius, 1780)	+	+	+	sb-a
			E. spetsbergensis Malmgren, 1865	+	+	+	psb-a
		Eulalia Savigny, 1882	*E. bilineata* (Johnston, 1840)	–	+	+	sb-a
		Eumida Malmgren, 1865	*E. arctica* (Annenkova, 1946)	–	–	+	atlhb-a
		Mysta Malmgren, 1865	*M. barbata* Malmgren, 1865	+	+	+	sb-a
		Mystides Théel, 1879	*M. borealis* Théel, 1879	–	–	+	amph
		Phyllodoce Lamarck, 1818	*P. citrina* Malmgren, 1865	–	–	+	wb-a
			P. groenlandica Örsted, 1842	+	+	+	wb-a
			P. maculata (L., 1767)	–	+	+	sb-a
	Polynoidae Kinberg, 1856	*Bylgides* Chamberlin, 1919	*B. elegans* (Théel, 1879)	+	+	+	hb-a
			B. groenlandicus (Malmgren, 1867)	–	–	+	hb-a
			B. promamme (Malmgren, 1867)	+	–	+	a
		Enipo Malmgren, 1865	*E. torelli* (Malmgren, 1865)	+	+	+	wb-a
		Eucranta Malmgren, 1865	*E. villosa* Malmgren, 1867	–	–	+	a
		Gattyana McIntosh, 1900	*G. amondseni* (Malmgren, 1867)	–	–	+	wb-a
			G. cirrhosa (Pallas, 1866)	+	+	+	wb-a
		Eunoe Malmgren, 1865	*E. nodosa* (M. Sars, 1861)	–	+	–	wb-a
		Harmothoe Kinberg, 1855	*H. aspera* (Hansen, 1878)	–	–	+	wb-a
			H. imbricata (L., 1767)	+	+	+	sb-a
			H. impar (Johnston, 1839)	+	–	+	wb-a
			H. rarispina (M. Sars, 1861)	+	–	–	wb-a
		Melaenis Malmgren, 1865	*M. loveni* Malmgren, 1865	–	–	+	a
	Pholoidae Kinberg, 1858	*Pholoe* Johnston, 1839	*P. assimilis* Örsted, 1845	–	–	+	wb-a
			P. longa (O. F. Müller, 1776)	+	+	+	wb-a
	Chrysopetalidae Ehlers, 1864	*Dysponetus* Levinsen, 1879	*D. pygmaeus* Levinsen, 1879	–	–	+	sb-a
	Glyceridae Grube, 1850	*Glycera* Lamarck, 1818	*G. capitata* Örsted, 1842	+	+	+	wb-a
			G. lapidum Quatrefages, 1866	–	–	+	atlwb-a
	Goniadidae Kinberg, 1866	*Goniada* Audouin et Milne-Edwards, 1833	*G. maculata* Örsted, 1843	–	+	–	amph
	Syllidae Grube, 1850	*Myrianida* Milne-Edwards, 1845	*M.* sp.	–	–	+	?
		Erinaceusyllis San Martin, 2003	*E. erinaceus* (Claparède, 1863)	+	–	–	wb-a
		Eusyllis Malmgren, 1867	*E. blomstrandi* Malmgren, 1867	–	–	+	sb-a
		Pionosyllis Malmgren, 1867	*P.* sp.	–	–	+	?
		Proceraea Ehlers, 1864	*P. cornuta* (Agassiz, 1862)	–	–	+	hb-a
			P. prismatica (Fabricius, 1780)	+	–	–	wb-a
		Syllis Lamarck, 1818	*S. oerstedi* nom. dub. (Malmgren, 1867)	+	–	–	sb-a
	Hesionidae Grube, 1850	*Gyptis* Marion et Bobretzky, 1875	*G. vittata* Webster et Benedict, 1887	–	–	+	sb-a
		Nereimyra Blainville, 1828	*N. aphroditoides* (Fabricius, 1780)	–	–	+	phb-a
	Nereididae Savigny in Lamarck, 1818	*Nereis* Linnaeus, 1758	*N. pelagica* L., 1758	–	–	+	amph
			N. zonata Malmgren, 1867	+	+	+	sb-a
	Nephtyidae Grube, 1850	*Aglaophamus* Kinberg, 1866	*A. malmgreni* (Théel, 1879)	+	–	+	wb-a
		Micronephthys Friedrich, 1937	*M. minuta* (Théel, 1879)	+	+	+	a
			M. neotena (Noyes, 1980)	–	–	+	atlwb-a
		Nephtys Cuvier in Audouin et Milne-Edwards, 1833	*N. ciliata* (O. F. Müller, 1776)	+	+	+	wb-a
			N. longosetosa Örsted, 1841	+	+	+	wb-a
			N. paradoxa Malmgren, 1874	+	+	+	sb-a
			N. pente Rainer, 1984	–	+	+	wb-a

Continue on the next page…

Order	Family	Genus	Species	1959	1996	2000s	Biogeographic group
Phyllodocida	Sphaerodoridae Malmgren, 1867	*Sphaerodoropsis* Hartman et Fauchald, 1971	*S. philippi* (Fauvel, 1911)	+	–	+	wb-a
		Sphaerodorum Örsted, 1843	*S. gracilis* (Rathke, 1843)	+	+	+	wb-a
Eunicida	Onuphidae Kinberg, 1865	*Nothria* Malmgren, 1867	*N. hyperborea* (Hansen, 1878)	+	+	+	phb-a
	Lumbrineridae Schmarda, 1861	*Abyssoninoe* Orensanz, 1990	*A. hibernica* (McIntosh, 1903)	–	–	+	atlhb-a
		Lumbrineris Blainville, 1828	*L. mixochaeta* Oug, 1998	–	–	+	atlhb-a
		Paraninoe Levenstein, 1977	*P. minuta* (Théel, 1879)	+	+	+	wb-a
		Scoletoma Blainville, 1828	*S. fragilis* (O. F. Müller, 1776)	+	+	+	wb-a
	Dorvilleidae Chamberlin, 1919	*Ophryotrocha* Claparède et Mecznikow, 1869	*O.* sp.	–	–	+	?
		Protodorvillea Pettibone, 1961	*P. kefersteini* (McIntosh, 1869)	–	–	+	sb-a
		Parougia Wolf, 1986	*P. caeca* (Webster et Benedict, 1884)	–	–	+	atlhb-a
Amphinomida	Amphinomidae Lamarck, 1818	*Paramphinome* Sars, 1869	*P. jeffreysii* (McIntosh, 1868)	+	–	–	atlwb
Orbinida nomen dubium	Orbiniidae Hartman, 1942	*Orbinia* Quaterfages, 1865	*O. glebushki* Averincev, 1990	–	–	+	a
		Leitoscoloplos Day, 1977	*L. acutus* (Verrill, 1873)	–	–	+	sb-a
		Scoloplos Blainville, 1828	*S. armiger* (O. F. Müller, 1776)	+	+	+	c
Spionida	Spionidae Grube, 1850	*Dipolydora* Verrill, 1881	*D. coeca* (Örsted, 1843)	–	+	+	wb-a
			D. caulleryi (Mesnil, 1897)	–	–	+	sb-a
			D. quadrilobata (Jacobi, 1883)	+	+	+	wb-a
			D. socialis (Schmarda, 1861)	–	–	+	atlwb
		Laonice Malmgren, 1867	*L. cirrata* (M. Sars, 1851)	+	+	+	sb-a
		Marenzelleria Mesnil, 1896	*M. arctia* (Chamberlin, 1920)	–	+	+	phb-a
			M. wireni Augener, 1913	–	+	+	a
		Prionospio Malmgren, 1867	*P. cirrifera* Wirén, 1883	+	+	+	wb-a
		Pygospio Claparède, 1863	*P. elegans* Claparède, 1863	+	+	+	wb-a
		Scolelepis Blainville, 1828	*S. burkovskii* Sikorski, 1994	–	+	+	a
			S. laonicola (Tzetlin, 1985)	–	–	+	a
		Spio Fabricius, 1785	*S. armata* (Thulin, 1957)	–	–	+	wb-a
			S. arctica (Söderström, 1920)	–	+	+	wb-a
			S. filicornis (Müller, 1776)	+	–	+	wb-a
			S. theeli (Söderström, 1920)	–	+	+	wb-a
		Spiophanes Grube, 1860	*S. kroyeri* Grube, 1860	+	+	–	amph
	Trochochaetidae Pettibone, 1961	*Trochochaeta* Levinsen, 1884	*T. multisetosa* (Örsted, 1844)	–	+	+	amph
	Apistobranchidae Mesnil et Caullery, 1898	*Apistobranchus* Levinsen, 1883	*A. tenuis* Orrhage, 1962	–	–	+	atlwb
			A. tullbergi (Théel, 1879)	–	+	+	wb-a
Chaetopterida nomen dubium	Chaetopteridae Audouin et Milne-Edwards, 1833	*Spiochaetopterus* M. Sars, 1853	*S. typicus* M. Sars, 1856	+	+	+	wb-a
Cirratulida nomen dubium	Paraonidae Cerruti, 1909	*Aricidea* Webster, 1879	*A. (Acmira) catherinae* Laubier, 1967	–	+	+	atlwb
			A. hartmanae (Strelzov, 1968)	–	–	+	atlwb-a
			A. (Acmira) laubieri Hartley, 1981	–	–	+	atlb-a
			A. nolani taxon inquirendum Webster et Benedict, 1887	+	+	+	wb-a
			A. (Strelzovia) quadrilobata Webster et Benedict, 1887	–	–	+	wb-a
		Cirrophorus Ehlers, 1908	*C. branchiatus* Ehlers, 1908	–	–	+	c
			C. lyra (Southern, 1914)	+	+	+	atlwb
		Levinsenia Mesnil, 1897	*L. gracilis* (Tauber, 1879)	+	+	+	c
		Paraonides Cerruti, 1909	*P. nordica* (Strelzov, 1968)	–	–	+	hb-a
	Cirratulidae Ryckholt, 1851	*Aphelochaeta* Blake, 1991	*A.* cf. *marioni* (Saint-Joseph, 1894)	–	–	+	?
		Chaetozone Malmgren, 1867	*C. setosa* Malmgren, 1867	+	+	+	?
		Cirratulus Lamarck, 1801	*C. cirratus* (O. F. Müller, 1776)	+	+	+	sb-a
		Tharyx Webster et Benedict, 1887	*T. killariensis* (Southern, 1914)	–	–	+	atlwb

Continue on the next page…

Order	Family	Genus	Species	1959	1996	2000s	Biogeographic group
Ctenodrilida nomen dubium	Ctenodrilidae Kennel, 1882 taxon inquirendum	*Raricirrus* Hartman, 1961	*R.* sp.	–	–	+	?
Cossurida nomen dubium	Cossuridae Day, 1963	*Cossura* Webster et Benedict, 1887	*C. longocirrata* Webster et Benedict, 1887	+	+	+	wb-a
Flabelligerida nomen dubium	Flabelligeridae Saint-Joseph, 1894	*Brada* Stimpson, 1854	*B. granulosa* Hansen, 1880	–	+	+	wb-a
			B. inhabilis (Rathke, 1843)	+	+	+	wb-a
			B. nuda Annenkova, 1922	–	–	+	phb-a
		Bradabyssa Hartman, 1967	*B. villosa* (Rathke, 1843)	+	+	+	wb-a
		Diplocirrus Haase, 1915	*D. glaucus* (Malmgren, 1867)	–	+	–	atlhb
		Saphobranchia Chamberli, 1919	*S. hirsuta* (Hansen, 1879)	+	+	–	atlhb-a
			S. longisetosa (Marenzeller, 1890)	–	+	+	a
		Flabelligera M. Sars, 1829	*F. affinis* M. Sars, 1829	–	–	+	sb-a
		Pherusa Oken, 1807	*P. plumosa* (O. F. Müller, 1776)	+	+	–	sb-a
Opheliida nomen dubium	Scalibregmatidae Malmgren, 1867	*Polyphysia* Quatrefages, 1865	*P. baffinensis* (Blake, 1972)	+	–	+	a
		Scalibregma Rathke, 1843	*S. inflatum* Rathke, 1843	+	+	+	wb-a
	Opheliidae Grube, 1850	*Ophelia* Savigny, 1818	*O. limacina* (Rathke, 1843)	+	+	+	c
		Ophelina Örsted, 1843	*O. acuminata* Örsted, 1843	+	+	+	a
			O. cylindricaudata (Hansen, 1878)	–	+	+	wb-a
	Travisiidae Hartmann-Schröder, 1971	*Travisia* Johnson, 1840	*T. forbesii* Johnson, 1840	+	+	+	wb-a
Capitellida nomen dubium	Capitellidae Grube, 1862	*Capitella* Blainville, 1828	*C. capitata* (Fabricius, 1870)	+	+	+	sb-a
		Heteromastus Eisig, 1887	*H. filiformis* (Claparède, 1864)	+	+	+	sb-a
		Notomastus M. Sars, 1850	*N. latericeus* M. Sars, 1851	+	+	+	c
	Maldanidae Savigny in Lamarck, 1818	*Axiothella* Verrill, 1900	*A. catenata* (Malmgren, 1865)	+	+	–	wb-a
		Clymenura Verrill, 1900	*C. polaris* (Théel, 1879)	+	+	+	atlwb-a
		Euclymene Verrill, 1900	*E. droebachiensis* (M. Sars in G. O. Sars, 1872)	–	–	+	atlwb-a
		Lumbriclymene Sars, 1872	*L. cylindricauda* M. Sars in G. O. Sars, 1872	–	–	+	atlhb-a
			L. minor Arwidsson, 1906	–	–	+	atlhb-a
		Maldane Grube, 1860	*M. arctica* Detinova, 1985	–	–	+	hb-a
			M. sarsi Malmgren, 1865	+	+	+	wb-a
		Microclymene Arwidsson, 1906	*M. acirrata* Arwidsson, 1906	–	–	+	a
		Nicomache Malmgren, 1865	*N. lumbricalis* (Fabricius, 1780)	+	–	+	wb-a
			N. (Nicomache) minor Arwidsson, 1906	–	–	+	wb-a
		Notoproctus Arwidsson, 1906	*N. oculatus arcticus* Arwidsson, 1906	–	–	+	wb-a
		Petaloproctus Quatrefages, 1865	*P. tenuis* (Théel, 1879)	+	+	+	wb-a
		Praxillella Verrill, 1881	*P. gracilis* (M. Sars, 1861)	+	+	+	wb-a
			P. praetermissa (Malmgren, 1865)	+	+	+	sb-a
		Praxillura Verrill, 1880	*P. longissima* Arwidsson, 1906	+	+	+	hb-a
		Asychis Kinberg, 1867	*A. biceps* (M. Sars, 1861)	+	–	–	atlhb
		Rhodine Malmgren, 1866	*R. gracilior* Tauber, 1879	+	+	+	wb-a
			R. loveni Malmgren, 1865	–	+	+	amph
Oweniida nomen dubium	Oweniidae Rioja, 1917	*Galathowenia* Kirkegaad, 1956	*G. oculata* (Zachs, 1923)	+	+	+	sb-a
		Myriochele Malmgren, 1867	*M. heeri* Malmgren, 1867	+	+	+	wb-a
		Owenia Delle Chiaje, 1844	*O. polaris* Koh, Bhaud & Jirkov, 2003	–	–	+	a
Terebellida	Pectinariidae Quatrefages, 1865	*Cistenides* Malmgren, 1866	*C. hyperborea* Malmgren, 1866	+	+	+	hb-a
		Lagis Malmgren, 1866	*L. koreni* Malmgren, 1866	–	+	–	atlhb
	Ampharetidae Malmgren, 1865	*Amage* Malmgren, 1866	*A. auricula* Malmgren, 1866	+	–	–	atlwb
		Ampharete Malmgren, 1865	*A. acutifrons* (Grube, 1860)	+	+	+	wb-a
			A. borealis (M. Sars, 1856)	+	+	+	hb-a
			A. finmarchica (M. Sars, 1865)	–	+	+	wb-a
			A. goesi Malmgren, 1865	+	+	+	phb-a
			A. lindstroemi Malmgren, 1867	–	+	+	wb-a
			A. octocirrata (M. Sars, 1835)	–	–	+	atlwb
			A. vega (Wirén, 1883)	–	+	+	a

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Order	Family	Genus	Species	1959	1996	2000s	Biogeographic group
Terebellida	Ampharetidae Malmgren, 1865	*Amphicteis* Grube, 1850	*A. gunneri* (M. Sars, 1835)	+	+	+	wb-a
			A. sundevalli (Malmgren, 1866)	+	+	−	a
		Anobothrus Levinsen, 1884	*A. gracilis* (Malmgren, 1865)	+	+	+	wb-a
		Glyphanostomum Levinsen, 1884	*G. pallescens* (Théel, 1879)	+	−	−	wb-a
		Lysippe Malmgren, 1866	*L. labiata* Malmgren, 1866	+	+	+	pwb-a
		Melinna Malmgren, 1866	*M. cristata* (Sars, 1851)	+	−	−	wb-a
			M. elisabethae McIntosh, 1914	+	+	+	wb-a
	Trichobranchidae Malmgren, 1866	*Terebellides* M. Sars, 1835	*T. gracilis* Malm, 1874	−	−	+	wb-a
			T. stroemii M. Sars, 1835	+	+	+	c
		Trichobranchus Malmgren, 1866	*T. glacialis* Malmgren, 1866	−	+	+	wb-a
	Terebellidae Grube, 1850	*Amphitrite* O. F. Müller, 1771	*A. birulai* Ssolowiew, 1899	+	+	+	sb-a
			A. cirrata Müller, 1776	+	+	−	atlwb-a
			A. groenlandica Malmgren, 1866	+	+	−	wb-a
		Artacama Malmgren, 1866	*A. proboscidea* Malmgren, 1866	+	+	+	wb-a
		Axionice Malmgren, 1866	*A. flexuosa* (Grube, 1860)	−	+	+	pwb-a
			A. maculata (Dalyell, 1853)	+	+	+	sb-a
		Lanassa Malmgren, 1866	*L. nordenskioldi* Malmgren, 1866	−	−	+	whb-a
			L. venusta (Malm, 1874)	−	+	+	wb-a
		Laphania Malmgren, 1866	*L. boecki* Malmgren, 1866	+	+	+	wb-a
		Leaena Malmgren, 1866	*L. ebranchiata* (M. Sars, 1865)	+	+	−	wb-a
		Lysilla Malmgren, 1866	*L. loveni* Malmgren, 1866	+	−	−	wb-a
		Nicolea Malmgren, 1865	*N. zostericola* (Örsted, 1844)	+	+	+	wb-a
		Pista Malmgren, 1866	*P. bansei* Saphronova, 1988	−	+	+	hb-a
		Polycirrus Grube, 1850	*P. medusa* Grube, 1850	+	+	+	sb-a
			P. norvegicus (Wollebaek, 1912)	−	−	+	atlhb-a
		Proclea Saint-Joseph, 1894	*P. graffii* (Langerhans, 1884)	+	+	+	wb-a
			P. malmgreni (Ssolowiew, 1899)	−	+	−	b-a
		Thelepus Leuckart, 1849	*T. marthae* Jirkov, 2018	+	+	+	a
Sabellida	Sabellidae Latreille, 1825	*Bispira* Krøyer, 1856	*B. crassicornis* (M. Sars, 1851)	−	−	+	wb-a
			B. fabricii (Krøyer, 1856) Knight-Jones, 1990	+	−	−	wb-a
		Branchiomma Kölliker, 1858	*B. arcticum* (Ditlevsen, 1937)	+	−	−	atlhb-a
		Chone Krøyer, 1856	*C. duneri* Malmgren, 1867	+	+	+	sb-a
			C. infundibuliformis Krøyer, 1856	+	+	+	sb-a
			C. oculata Annenkova, 1952	+	+	+	a
		Euchone Malmgren, 1866	*E. analis* (Kröyer, 1856)	+	+	+	sb-a
			E. papillosa (M. Sars, 1851)	+	+	+	wb-a
			E. perseyi (Zenkevitch, 1925)	−	−	+	hb-a
		Laonome Malmgren, 1866	*L. kroyeri* Malmgren, 1866	+	+	+	sb-a
		Myxicola Koch in Renier, 1847	*M. infundibulum* (Montagu, 1808)	+	−	−	amph
	Serpulidae Rafinesque, 1815	*Chitinopoma* Levinsen, 1884	*C. serrula* (Stimpson, 1853)	−	−	+	atlhb
	Spirorbidae Pillai, 1970	*Bushiella* Knight-Jones, 1973	*B. (Jugaria) granulata* (L., 1767)	+	−	+	atlwb-a
			B. (J.) quadrangularis (Stimpson, 1854)	−	−	+	sb-a
		Circeis Saint-Joseph, 1894	*C. spirillum* (L., 1758)	+	+	+	wb-a
		Paradexiospira Caullery et Mesnil, 1897	*P. (Paradexiospira) violacea* (Levinsen, 1883)	+	−	+	hb-a
			P. (Spirorbides) vitrea (Fabricius, 1780)	−	+	+	hb-a

Out of the entire list, 81 % of species are classified as boreal–Arctic, with boreal, Arctic, and cosmopolitan species amounting to approximately 6.3 %.

Based on the analysis of all the taxonomic levels, a formula was used (Fig. 1) which shows the dependence of each taxon on its rank for the water area studied. A conclusion was made on insufficient investigation of the polychaete population (Golikov, 1976).

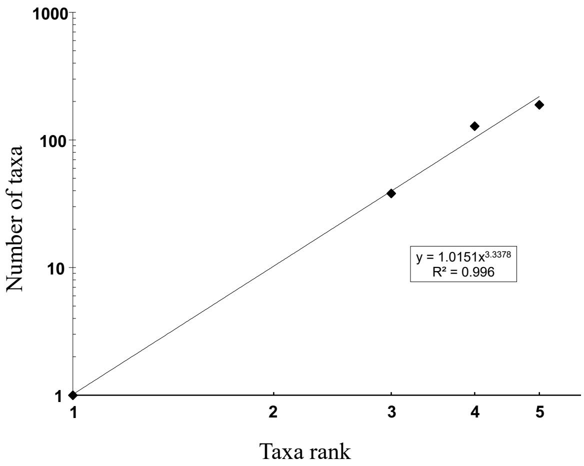

Fig. 1. Relationship between number of taxa and their ranks. X-axis: 1, class; 2, order (this taxon is not used on the graph since the issue of belonging to a particular order causes disagreement among specialists); 3, family; 4, genus; and 5, species

DISCUSSION

As indicated in the last review most fully characterizing the state of knowledge of the Pechora Sea (Denisenko, 2013), there are 176 polychaete taxa, and out of them, 129 are identified down to a species level. Based on our own data collected since the early XXI century, we came to a conclusion that the diversity of polychaetes in the studied area is even higher. To a greater extent, the data include taxa of the lowest ranks – species and genera. The rise in figures does not result from increasing warming of the Arctic alone: it is also a consequence of the progress in polychaete taxonomy and the improvement of methods for collecting worms, *inter alia* higher intensity of sampling and use of fine mesh for sediment flushing. Definitely, the latter contributes to discovery of new Polychaeta species (not recorded in the Pechora Sea earlier) and will expand the total list by several dozen.

At the same time, despite the increasing number of polychaete species recorded in the studied fauna, the ratio of the main biogeographic groups remains approximately the same since the 1950s (Fig. 2). In the sea fauna, boreal–Arctic species of polychaete worms prevail, and their ratio has changed insignificantly from the late 1950s to the early XXI century – from 82 to 77 %. The ratio of Arctic species increased from 6 to 10 %. The ratio of pan-oceanic and bipolar species (those are designated as cosmopolitan ones) decreased over the same period; importantly, the main reason was the progress in polychaete taxonomy, not the effect of abiotic factors. The ratio of boreal species remained approximately at the same level – 5–7 %.

Conclusion. The number of polychaete species constantly increases, to a greater or lesser extent due to environmental warming since the 1950s. Despite this, the ratio of the main biogeographic groups of species remains relatively stable, and this indicates a balanced mechanism for the regulation of internal processes in taxocenes of the Pechora Sea polychaetes. In other words, the ongoing climate change is neither unexpected nor extraordinary for the populations of polychaete worms. Those are genetically expected, are not new in the general history of the development of polychaetes, and are easily compensated by their innate tolerance abilities.

Apparently, the remarks given in the article on the stability of the biogeographic structure of the fauna and some other characteristics of polychaete worms, as well as other groups playing a noticeable role in benthic invertebrate communities, show that those can serve as a kind of a status indicator of natural processes in various areas of the World Ocean.

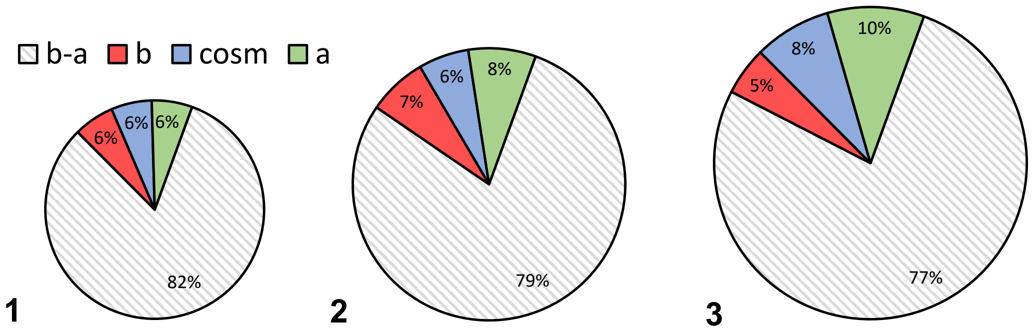

Fig. 2. Ratio of various biogeographic groups in the polychaete fauna in different periods: 1, 1959; 2, 1993; and 3, 2004, 2006, and 2016 (107, 113, and 163 species, respectively, with the circle diameter proportional to the species number)

This work was carried out within the framework of ZIN RAS state research assignment (No. AAAA-A17-117030310207-3) and with RFBR sponsorship (No. 18-05-60157). Financial support was provided by the Research Council of Norway (projects NFR 233635/H30 "Environmental management of petroleum activities in the Barents Sea: Norwegian–Russian collaboration" and NFR 280724 "Environmental monitoring of Arctic coastal ecosystems: Sensitivity to petroleum pollution (Arctic EcoSens)") and the Norwegian Taxonomy Initiative ("Cryptic polychaete species in Norwegian waters", knr 49-13, pnr 70184228).

Acknowledgement. The authors express their deepest gratitude to V. V. Potin – chief custodian of the annelids collection, ZIN RAS – for his technical support.

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ВИДОВОЙ СОСТАВ И БИОГЕОГРАФИЧЕСКАЯ СТРУКТУРА ФАУНЫ POLYCHAETA ПЕЧОРСКОГО МОРЯ В ПЕРИОД ПОТЕПЛЕНИЯ АРКТИКИ

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Всестороннее изучение бентоса позволяет не только видеть текущие изменения донных сообществ и лучше понимать, что́ происходило с ними в прошлом, но и с некоторой степенью достоверности прогнозировать их будущее. Многощетинковые черви являются одной из самых многочисленных и значимых групп бентоса, способных выступать своеобразными биоиндикаторами состояния среды. В настоящей статье предпринята попытка проанализировать изменения биогеографических групп полихет Печорского моря в сравнительно длительный период времени (около 50 лет), чтобы понять, ка́к влияют изменения климата на соотношение биогеографических групп многощетинковых червей и, как следствие, могут ли полихеты в той или иной степени выступать в качестве биоиндикаторов. На основе анализа новых и прежних данных составлен список многощетинковых червей Печорского моря. Он насчитывает 198 таксонов (из них 186 определены до вида), относящихся к 127 родам, 37 семействам и 15 отрядам. Соотношение биогеографических групп полихет Печорского моря указывает на постоянство их биогеографического состава в течение последних 50 лет и является ещё одним подтверждением цикличности процессов, происходящих в Арктике.

Ключевые слова: биогеография, биоиндикаторы, Печорское море, многощетинковые черви

Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 32–40
https://doi.org/10.21072/mbj.2022.07.2.03

UDC 582.261.1-15:556.114.5

HALOTOLERANCE LIMITS OF THE BLACK SEA REPRESENTATIVE OF THE GENUS *ENTOMONEIS* EHRENBERG, 1845 (BACILLARIOPHYTA)

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Received by the Editor 03.06.2020; after reviewing 10.08.2020;
accepted for publication 03.03.2022;

The genus *Entomoneis* Ehrenberg, 1845 is quite rich in species. Underestimated diversity of this genus requires its deeper morphological and molecular study, as well as an investigation of ecological and physiological characteristics of its species – specifically, their tolerance limits to environmental factors. Considering the distribution of *Entomoneis* species in water bodies with various salinity, we aimed at studying the tolerance limits and determining optimal salinity for vegetative growth and sexual reproduction of the diatom *Entomoneis* sp. from the Black Sea. We used reproductively compatible clonal cultures isolated from samples taken on the Crimean and Turkish Black Sea coasts. For *Entomoneis* sp. clone 7.0906-D, the nucleotide sequence of the *rbc*L gene was obtained; it is presented in the GenBank database under the number MT424817. Morphologically, the studied species resembles *E. paludosa*; according to molecular data, it is far from it. In accordance with its ecological and physiological characteristics, this species is a marine one. According to published material available, *E. paludosa*, unlike *Entomoneis* sp., inhabits brackish, slightly saline, and even fresh water bodies. Experiments on halotolerance show the following: the Black Sea clones of *Entomoneis* sp. are viable in a range of at least 40 ‰ (8 to 48 ‰). A salinity range of the medium within which *Entomoneis* sp. revealed sexual reproduction is much narrower – 18 to 36 ‰. Optimal salinity values for vegetative growth and sexual reproduction were determined (27.4 and 26.4 ‰, respectively); those turned out to be higher in both cases than the values in the natural habitat of this species. As salinity of the medium increased, *Entomoneis* sp. initial cells resulting from sexual reproduction tended to decrease in size.

Keywords: diatoms, sexual reproduction, vegetative growth, salinity, *Entomoneis* sp.

Limits of salinity tolerance (halotolerance) are one of the key ecological and physiological characteristics of species. Those determine the possibility of species existence in a particular water area (Brand, 1984). High halotolerance is one of the indispensable conditions for the species to spread everywhere and become cosmopolitan. On the contrary, stenohalines are much less likely to be widely distributed. The results obtained in the previous studies show that clones from populations of several Black Sea species have much higher salinity optima than salinity of their habitats (Davidovich & Davidovich, 2020).

The diatom genus *Entomoneis* Ehrenberg, 1845 includes species with unique morphology: those have a two-lobed keel elevated above the valve surface, a sigmoid curvature of the raphe, and numerous perforated copulae. The genus is quite rich in species. To date, AlgaeBase (2020) contains 36 species and 21 intraspecific names of its representatives. Out of all the species names, 28 are considered as taxonomically accepted. In some cases, opinions on the validity of species names differ among authors.

As established, most of the species belonging to this genus are brackish or marine; only a few of them have been recorded in fresh or highly desalinated water bodies (Liu et al., 2018 ; Round et al., 1990). The Black Sea representative of the genus *Entomoneis* chosen by us for the study is morphologically similar to *Entomoneis paludosa* W. Smith, 1853 (Fig. 1).

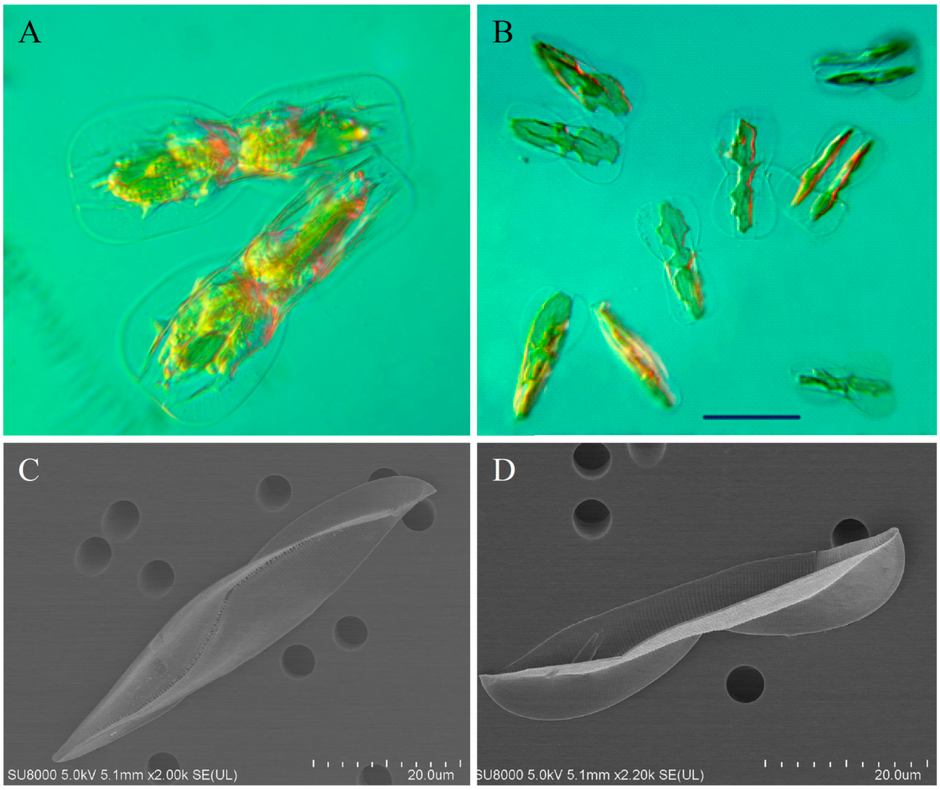

Fig. 1. *Entomoneis* sp. A, B, alive dividing cells, light microscopy (differential interference contrast), scale bar 50 μm; C, D, valves of the frustule, scanning electron micrographs

The latter inhabiting benthos and plankton of seas and brackish waters was recorded in the Black Sea as well (Ryabushko, 2006). Morphologically, the species studied in our experiments resembles *E. paludosa*; according to preliminary molecular data, it is far from it in the phylogenetic tree constructed. Undoubtedly, we should agree with the opinion of Mejdandžić *et al.* (2018): underestimated diversity of *Entomoneis* requires a deeper morphological and molecular study of this genus, as well as an investigation of ecological and physiological characteristics of its species – specifically, their tolerance limits to environmental factors. Given the wide distribution of *Entomoneis* species in water bodies with various salinity, we aimed at studying the tolerance limits and determining optimal salinity for vegetative growth and sexual reproduction of *Entomoneis* sp. from the Black Sea.

MATERIAL AND METHODS

Clones used in the experiments were isolated by micropipette from samples taken on the Crimean and Turkish coasts of the Black Sea. The clone 7.0906-D was derived from the population near Akçakoca (Düzce-Akçakoca, Turkey, 41°05′25″N, 31°07′26″E); clones 8.0727-A, 8.0727-B, 8.0727-D, and 8.0727-E were derived off the Tarkhankut Peninsula (45°19′50″N, 32°34′36″E). At the time of the experiments, mean length of vegetative cells in the clones was as follows: 8.0727-A, 31 μm; 8.0727-B, 31 μm; 8.0727-D, 42 μm; 8.0727-E, 42 μm; and 7.0906-D, 21 μm. For *Entomoneis* sp. clone 7.0906-D, the nucleotide sequence of the *rbc*L gene was obtained which is presented in the GenBank database (https://blast.ncbi.nlm.nih.gov/Blast.cgi) under the number MT424817.

A reproductively active pair of the Black Sea clones 7.0906-D + 8.0727-D was used in the experiment aimed at studying salinity effect on the sexual reproduction of the diatom *Entomoneis* sp. A culture in the exponential growth stage was used as the inoculum. *Prior* to the experiment, the cultures were kept in glass Petri dishes at a temperature of (20 ± 2) °C under natural light from a northern window in the ESAW medium (Andersen et al., 2005) with modifications (Polyakova et al., 2018) adjusted to salinity of 18 ‰. The experiments were carried out under similar light and temperature conditions. Each Petri dish (5 cm in diameter) was filled with 10 mL of the medium with different salinity: 4.5; 8; 12; 18; 24; 30; 36; 42; 48; and 54 ‰. Reduced salinity was obtained by diluting the ESAW medium (36 ‰) with distilled water – similarly to that described by other authors (Karaeva & Dzhafarova, 1993 ; Bagmet et al., 2017). A medium with salinity above 36 ‰ was prepared by adding the required amount of sodium chloride to the ESAW medium. The salinity level was measured with a handheld refractometer (model RHS-10ATC, China). Then, the mixture of reproductively compatible clones (30 μL) was added to each Petri dish. In the experiments on salinity effect on vegetative growth, 20 μL of each clonal culture were inoculated into Petri dishes with media with different salinity. The results of sexual reproduction were evaluated on the third, fourth, and fifth days after mating. The number of vegetative and generative cells was counted in 20 microscope fields of view. The number of cells that entered the sexual process was estimated as the ratio of the number of generative cells to the total number of cells on average over three days of the experiment. Gametes, zygotes, auxospores, and developing initial cells were considered generative cells.

Five clones were involved in the experiments on environmental salinity effect on vegetative growth to obtain biological replicates and process statistical data. Salinity effect on alga vegetative reproduction was assessed by the rate of change in the number of cells. Specifically, the number of cells in 15 microscope fields of view was counted on the third, fourth, and fifth days after the inoculation. Then, the rate of cell division (r, day^{-1}) was determined based on the equation of exponential population growth:

$$N_t = N_0 \exp(r\Delta t) ,$$

where N_t and N_0 denote mean number of cells in the field of view at time t and at initial time t_0, respectively;

Δt denotes a time interval between t and t_0.

The values of the coefficient r were calculated using a least squares method, with the capabilities of Microsoft Excel. In order to switch to a unit of measurement “$\text{divisions}\cdot\text{day}^{-1}$”, obtained r values were divided by ln2. Salinity values optimal for the growth were determined from the position of the maximum of the parabolic function used to fit the data. The position of the approximating function maximum was found from the value of the first derivative equal to zero.

Cell sizes were determined under a Biolar PI microscope (PZO, Poland) equipped with an eyepiece ruler calibrated with an object micrometer that has a unit value of 1.60 µm – with an eyepiece magnification of 12× and a water immersion objective magnification of 40×. The photographs were obtained with a Canon PowerShot A640 digital camera.

For examination under a scanning electron microscope, diatom cells were purified from organic material by boiling in 35 % hydrogen peroxide (H_2O_2) in a sand bath for two days for three hours; then, cell suspension was centrifuged and washed with distilled water; the operation was repeated 7–8 times. A few drops of the resulting suspension were placed on aluminum stub, dried in air, and covered with gold. The electron micrographs were obtained on a Hitachi SU8020 scanning electron microscope.

RESULTS

The experiments showed that the investigated diatom of the genus *Entomoneis* is not viable in the medium with salinity of 4.5 and 54 ‰: cells died on the second day after the inoculation. Obviously, the sharper the change in salinity, the stronger the stress experienced by the alga. To avoid hypoosmotic shock, we carried out an experiment with a gradual decrease in salinity. Within a week, *Entomoneis* sp. clones were adapted to the medium with 8 ‰ salinity; then, those were transferred to the medium with 4.5 ‰ salinity. The results of the experiment showed that the cells remained alive for two days after inoculation in the medium with 4.5 ‰ salinity; on the third day, chloroplasts began to break down, and the alga lost its ability to divide and finally died.

In the medium with salinity of 8 and 12 ‰, the cells reproduced vegetatively, and the division rate for five clones averaged 0.48 and 0.96 $\text{divisions}\cdot\text{day}^{-1}$, respectively. With an increase in medium salinity up to 42 ‰, the rate of cell division remained high (0.90 $\text{divisions}\cdot\text{day}^{-1}$); however, at this salinity level, there was no auxospore formation. In the medium with 48 ‰ salinity, a positive dynamics of population growth was recorded, but with a low division rate – as few as 0.28 $\text{divisions}\cdot\text{day}^{-1}$. The maximum vegetative growth was observed at 27.4 ‰ (Fig. 2A).

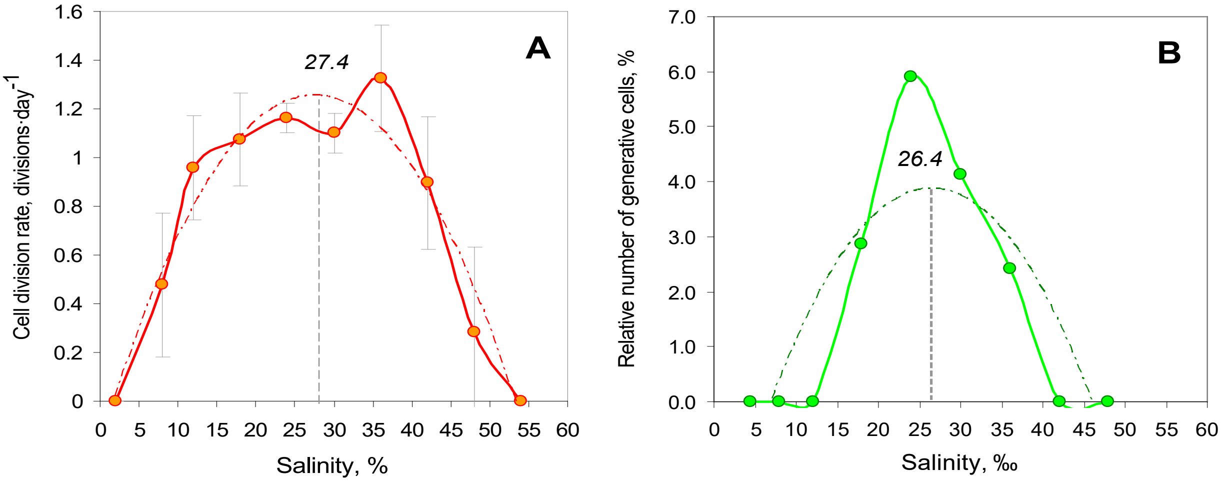

Fig. 2. A, dependence of the cell division rate of *Entomoneis* sp. on salinity of the medium; B, relative number of generative cells in mixed cultures of reproductively compatible *Entomoneis* sp. clones depending on the salinity level of the medium. The approximation was performed by a second-order polynomial (dashed-dotted line). The dashed line indicates the optimum position

Sexual reproduction with formation of initial cells occurred with the salinity level gradations of 18, 24, 30, and 36 ‰. An increase in salinity favorably affected the sexual reproduction of the alga. When transferred – after preliminary acclimation to 18 ‰ – to the medium with higher salinity, the ratio of cells participating in the sexual process increased significantly. Specifically, in the medium with salinity of 18 ‰, the relative number of *Entomoneis* sp. cells that entered the sexual process was two times less than in the medium with salinity of 24 ‰. For the Black Sea clones studied, optimal salinity for auxospore formation turned out to be 26.4 ‰ (Fig. 2B).

We studied the dependence of the length of initial cells on the salinity level of the medium as well (Fig. 3). The size range of the initial cells obtained in the experiment varied from 106 to 139 µm.

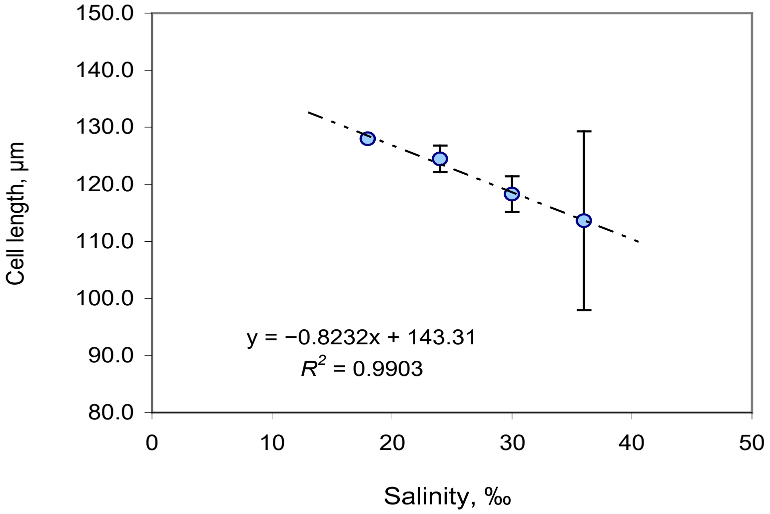

Fig. 3. Dependence of the length of initial cells on the salinity of the medium at which mixtures of *Entomoneis* sp. clones were maintained in mating experiments

DISCUSSION

The data on environmental salinity effect on *Entomoneis* representatives are quite contradictory. Specifically, in the literature, one can find information that *E. paludosa* is relatively abundant in the environment with salinity lower than 1 ‰ (Dalu et al., 2015). Considering this, the species could be assigned to inhabitants of fresh and slightly brackish waters. Other authors describe the species as widespread in brackish-water bodies (Kulikovskiy et al., 2016 ; Weckstrom & Juggins, 2006). At the same time, many publications report *E. paludosa* presence in a typical marine environment (Morant-Manceau et al., 2007 ; Rech et al., 2005 ; Ryabushko et al., 2019). The results of our experimental studies indicate that the investigated representative of the genus *Entomoneis* is viable in quite a wide salinity range – 8 to 48 ‰, but it cannot be assigned to freshwater or brackish-water inhabitants. When placed in a medium with salinity of lower than 8 ‰, the cells died soon, even if it was preceded by gradual acclimation. Salinity of the Black Sea water off the Crimean coast is 17–18 ‰. Under conditions of lower salinity, existence of the studied *Entomoneis* representative is hardly possible: according to the results of our experiments, auxospore formation is limited to a salinity range 18 to 36 ‰ (perhaps, the range is somewhat wider, taking into account the gradations adopted in the experiments). Sexual reproduction in this species, as well as in other diatoms studied, turned out to be more sensitive to environmental conditions (Davidovich & Davidovich, 2020). According to references in the literature (an extensive list is presented in AlgaeBase), *E. paludosa* should be considered as a cosmopolitan inhabiting water bodies with different salinity – from freshwater to typical marine ones. However, the question arises whether all those diatoms, that are found under completely different salinity conditions and are assigned to *E. paludosa*, in fact belong to this species. As is often in diatomology, the problem of species identification comes to the fore. Assuming that in all cases the species was identified correctly, another question arises whether it is possible to relate such a wide range of halotolerance to one species. Indeed, there are some species with a very high salinity tolerance. Specifically, *Nitzschia palea* (Kützing) W. Smith can develop at salinity 0 to 22 ‰ (Bagmet et al., 2017 ; Trobajo et al., 2011). *Tabularia tabulata* (C. A. Agardh) Snoeijs is capable of developing in a wider salinity range – 0.5 to 49 ‰ (possibly, even wider), with sexual reproduction occurring within a very wide range – 8 to 49 ‰ (Davidovich, 2017). As noted above, halotolerance range of the *Entomoneis* representative studied by us is relatively narrower. With regard to *E. paludosa* salinity tolerance, it is premature to draw any conclusions until reliable data on this species are obtained.

Of interest is the question of salinity effect on the size of initial cells resulting from sexual reproduction. The life cycle duration of clones of the new generation depends on the initial cell size. As established in experiments with the centric diatom *Coscinodiscus wailesii* Gran, smaller initial cells formed under conditions of higher salinity (Nagai & Imai, 1999). In *T. tabulata*, the size of initial cells did not depend on medium salinity (Davidovich, 2017). These examples show that the response of organisms to environmental salinity is species-specific. According to the data obtained, size of *Entomoneis* sp. initial cells tended to decrease with salinity increase. However, since the resulting initial cells differed slightly in size (by about 10–15 %), the potential duration of the existence of new generation clones will not differ noticeably.

Summarizing, *Entomoneis* sp. inhabiting the Black Sea can be assigned to euryhaline organisms with environmental salinity tolerance ranging from 8 to 48 ‰ for vegetative growth and from 18 to 36 ‰ (perhaps, a little wider) for sexual reproduction. Optimal salinity for vegetative growth is 27.4 ‰, and for sexual reproduction, it is 26.4 ‰, which significantly exceeds salinity of the Black Sea water in its habitats. A more detailed study of the Black Sea representative of the genus *Entomoneis* might provide grounds for describing a new species.

This work was carried out within the framework of the KSS – NS RAS – Branch of IBSS state research assignment "Study of fundamental physical, physiological, biochemical, reproductive, population, and behavioral characteristics of marine hydrobionts" (No. 121032300019-0). Sampling on the Turkish coast was supported by the program TR-YÖK-Proje Tabanlı Değişim Programı (grant No. MEV-2016-46).

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ПРЕДЕЛЫ ГАЛОТОЛЕРАНТНОСТИ ЧЕРНОМОРСКОГО ПРЕДСТАВИТЕЛЯ РОДА *ENTOMONEIS* EHRENBERG, 1845 (BACILLARIOPHYTA)

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Род *Entomoneis* Ehrenberg, 1845 достаточно богат видами. Недооценённое разнообразие *Entomoneis* требует более глубокого морфологического и молекулярного исследования этого рода, а также изучения эколого-физиологических характеристик видов, в частности пределов толерантности к факторам среды. Учитывая распространение видов *Entomoneis* в водоёмах с различной солёностью, мы поставили задачу исследовать пределы толерантности и установить оптимальную солёность для вегетативного размножения и полового воспроизведения диатомовой водоросли *Entomoneis* sp. из Чёрного моря. В работе использованы оказавшиеся репродуктивно совместимыми клоновые культуры, которые были выделены из проб, отобранных у крымского и турецкого побережий Чёрного моря. Для клона *Entomoneis* sp. 7.0906-D получена нуклеотидная последовательность гена *rbc*L, которая представлена в базе данных GenBank под номером MT424817. Использованный в экспериментах вид хотя и напоминает по морфологическим критериям *E. paludosa*, но, по молекулярным данным, далеко отстоит от такового и по эколого-физиологическим характеристикам является морским видом. Согласно литературным материалам, *E. paludosa*, в отличие от изученного нами *Entomoneis* sp., обитает в солоноватых, слабосолёных и даже пресных водоёмах. Эксперименты по изучению пределов галотолерантности показали, что черноморские клоны *Entomoneis* sp. жизнеспособны в диапазоне, охватывающем как минимум 40 ‰ (от 8 до 48 ‰). Диапазон солёности среды, в котором *Entomoneis* sp. способен к половому воспроизведению, значительно у́же и находится в пределах от 18 до 36 ‰. Определены оптимальные значения солёности для вегетативного роста и для полового воспроизведения (27,4 и 26,4 ‰ соответственно), оказавшиеся в обоих случаях выше тех значений, при которых вид обитает в природе. У *Entomoneis* sp. по мере увеличения солёности среды отмечена тенденция к уменьшению размеров инициальных клеток, образующихся в результате полового воспроизведения.

Ключевые слова: диатомовые водоросли, половое воспроизведение, вегетативное размножение, солёность, *Entomoneis* sp.

1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 41–62
https://doi.org/10.21072/mbj.2022.07.2.04

UDC 574.5:504

ECOSYSTEM HEALTH: A CONCEPT, METHODOLOGICAL APPROACHES, AND ASSESSMENT CRITERIA

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Received by the Editor 24.03.2021; after reviewing 13.06.2021;
accepted for publication 03.03.2022; published online 07.06.2022.

Increasing anthropogenic load on aquatic ecosystems threatens environmental safety. In this regard, it is important to apply the ecosystem approach to the exploitation of natural resources in order to develop integrated regulatory environmental measures. The term "ecosystem health" is commonly used in assessment of the ecological state of water areas by representatives of foreign scientific communities (HELCOM, ICES, OSPAR, and MEDPOL), but it is not widespread among domestic researchers. The concept of "ecosystem health" is not a new paradigm. Specifically, it is the subject of discussion in the scientific literature since the early 2000s and the issue enshrined in long-term documents of the European Union and the EU Water Framework Directive on environmental preservation strategy. Based on a review of existing literature data, this article presents the principal concepts, approaches, and criteria for assessing the ecological state (health) of aquatic ecosystems. As emphasized, the assessment of the ecosystem health depends on goals and objectives of environmental research, and those are related to applied methodology and, accordingly, to selection of methods and indicators of the ecosystem state. The paper discusses the concept of "organism's health" and several its attributes: homeostasis maintenance, cause-and-effect relationships in the *health–disease* continuum, and functional adaptations. Several approaches for assessing the health of rivers and marine areas are compared. Various indicators, complex indices, and biomarkers of exposure and effects are considered which reflect the susceptibility of aquatic ecosystems to changes resulting from natural and anthropogenic load. Attention is drawn to the need for applying the integrated ecosystem approach in the analysis of the aquatic ecosystem state: this will contribute to holistic assessment of the consequences of human activity on the ecosystem integrity. Based on the experience of the BONUS+/BEAST project, a comprehensive biomarker approach is presented to determining the health of bioindicators with subsequent interpretation of data on the health status of the ecosystems these organisms inhabit. The authors hope that the review will be of interest to both specialists in ecology of aquatic ecosystems and representatives of environmental organizations steeped in ecological expertise.

Keywords: ecosystem health, assessment of the aquatic ecosystem state, reference ecosystem states, physiological state, functional adaptations, macrobenthic invertebrates

A rapid deterioration of the state of the ecosystems has exacerbated the need for introducing an integrated management of human activities based on accumulated knowledge on ecosystems and specifics of their functioning. The United Nations proclaimed 2021–2030 the Decade on Ecosystem Restoration. The ecosystem approach to exploitation of natural resources is significant for the analysis and taking actions to establish relationship between human activities and environmental issues, as well as for development of integrated regulatory environmental measures. In this regard, it is important to define some concepts and clarify methodological approaches (Directive 2000/60/EC, 2000); those are often used in foreign scientific communities and expert groups (The Helsinki Commission, HELCOM; Institute for Clinical Evaluative Sciences, ICES WKIMON; Working Group on Ecosystem Effects of Fishing Activities, WGECO; and Study Group for the Development of Integrated Monitoring and Assessment of Ecosystem Health in the Baltic Sea, SGEH) and are not widespread either in domestic biomonitoring studies or in publications on the environmental risk assessment.

Since the early 1990s, the issue of the "ecosystem health" definition and approaches to its assessment has been actively discussed in foreign literature. To a greater extent, this concerns approaches to assessing the aquatic ecosystem state. In the monograph *Ecosystem Health*, Robert Costanza and co-authors (1992) emphasized that this issue is complex: it includes economic, social, and environmental aspects. The concept of "ecosystem health" unites several meanings, even philosophical one – to the same extent as biological and medical ones. This implies the use of different indicators (biological, physical, and chemical) for assessing the ecological state and requires taking into account social and economic consequences of the shifts in "health". Thus, the multiambiguity of the "ecosystem health" definition is embedded in the methods of its cognition and in initial setting of the goal/goals achieved during the research.

When considering the concept of "ecosystem health", we have to start with defining what we mean by the ecosystem.

The ecosystem is a "localized in space and dynamic in time set of various organisms living together and forming communities and conditions of their existence which are in a regular relationship with each other and form a system of interdependent biotic and abiotic processes" (Alimov, 2000). The ecosystem can be characterized by structural and functional indicators that are in certain relationships with each other but can alter the vector of such relationships and the relationship between the flows of matter, energy, and information (Beyers & Odum, 1993). The ecosystem boundaries are mobile; those can vary depending on the research task.

The concept of "health" is primarily an attribute of living organisms.

Health as **homeostasis** is the maintenance of the internal stability of an organism aimed at its further survival and prosperity. Homeostasis can be considered as a non-equilibrium system which, however, does not go beyond the "swing". In the late XIX century, Claude Bernard – a French physiologist – introduced the concept of the "stability of the internal environment as the condition for a free life." According to C. Bernard, maintaining the stability of the conditions of the internal environment is the only goal of the organism.

Later, Academician A. Ugolev gave a definition of homeostasis as follows (1987): "In a broad sense, homeostating is maintaining the stability of basic biological, physical, and chemical constants. This concept is the main one in modern interpretations of such various phenomena and conditions as health, disease, and preservation of the environment and the biosphere."

Health as the **absence of disease**. A disease means a significant alteration in an organism, in its functional systems, organs, and tissues, as well as a failure in the regulation of physiological and biochemical processes due to homeostasis-disrupting effects or external and internal changes. The transition from health to disease can be considered as a process of gradual decrease in the organism's ability to adapt to environmental changes which results in a decline in functions.

The assessment of changes in the organism's state is **time-dependent** (in the *organism–ecosystem* structure, it should be time-scaled), and this allows to understand the cause of an alteration in the health of animals (Chernysheva, 2007) or plants and indirectly assess a shift in the habitat quality that could lead to the changes. The "time component" is a continuum, a change in the health of an organism associated with some kind of stressor event (a disturbance, *e. g.* environmental pollution) allowing to link the moment of onset of a stressful effect resulting in deterioration in ecosystem health since sometimes the process has a considerable time lag. However, the time factor has its own "relativity" there: even after industrial accidents or terrorist acts (both heavily affect the biotic component of the ecosystem), the onset of consequences does not begin immediately (it takes time). Sensitive biota components are the first to react. Serious disturbance or even degradation of the affected aquatic ecosystem occurs much later (sometimes in several years) due to ongoing compensatory processes at each structural level of the ecosystem; moreover, it occurs only under imbalance in repair processes (Alimov, 2000 ; Aleksandrov, 2010 ; Ostroumov, 2005). ' Importantly, a chemical or other stressful effect does not always result in deterioration in the health of an organism and its disease. The organism is capable of changing its functioning parameters within certain limits: there is a **functional (physiological) adaptation**.

In the middle of the XX century, a new approach was formed defining health as **organism's ability to adapt** to environmental conditions. I. Davydovsky (1950s–1960s) developed the foundations of the medicine of the future, where health is considered as adaptive capabilities of an organism. He defined the disease as the result of a decline in reserves and depletion of the organism's defenses (Davydovskii, 1962).

Later, this direction was developed in space medicine, where the **measure of a person's (operator's) health is defined as the functional capacity** of an organism, the ability to adapt quickly and painlessly to new conditions (challenges) (Baevskii & Berseneva, 1997). In fact, identification and quantitative assessment of this functional capacity is carried out by scientists involved, for example, in pre-flight training of pilots – to minimize possible stressful effects and to detect "defects" in their health at an early stage.

Hans Selye, based on his own long-term experience in neurophysiology and psychoanalysis, created the doctrine of **stress** for isolating a non-specific component in organism's reactions to various effects resulting from the **mobilization of functional reserves** (Selye, 1982). He was the first to note that the stressful effect depends on modality, strength, and duration of the disturbance, as well as on the adaptive capabilities of the organism.

Adaptation is considered as a functional property of biological objects, along with homeostasis. In organisms, the existence of certain cycles of activity which repeat in different time ranges (circadian, ultradian, minute, decasecond, and other rhythms) can be considered as an adaptation as well (Ashoff, 1984 ; Bursian, 2012). A decline in the ability of an organism to change its functional parameters under rhythmic daily shifts in environmental conditions is one of the earliest indicators of deterioration in its adaptive capabilities and, consequently, health.

The lower the adaptive capabilities, the more uniform the reactions of an organism and the smaller the arsenal of its probable responses to shifts in the environment. After "heavy" effects, the organism loses lability (in terms of adaptability) due to a shutdown of some functions supporting the plasticity of the transition from one level of regulation of the functional system to another.

The issue of **assessing the ecological state (health) of aquatic ecosystems** is complex and ambiguous (Report of Working Group 28, 2019). In most cases, the criteria are developed for small river ecosystems with a limited set of components and with simple trophic chains and relationships. The term “ecosystem health” was first proposed by David Rapport (1989).

As previously believed, one of the indispensable signs of the ecosystem health is its stability (Costanza et al., 1992). The easiest way to assess it is to analyze the constancy of the population size of key species. Specifically, stable populations determine the favorable ecological status of the system.

This statement also meant that such systems are capable of maintaining a stable biocoenosis determining the stability of their structure, coherence of the functioning of ecosystem components, and sufficient completeness of biodiversity. Healthy ecosystems can maintain their self-purification capacity (Ostroumov, 2005) and, as a result, stability of the water quality acceptable for local biota species.

However, it turned out that the statement about the stability (as a kind of immutability or constancy) of the ecosystem is debatable since the ecosystem might have some lability and be capable of rebuilding its functioning under sudden external effects (The Ecosystem and How It Relates to Sustainability, 2017). “The slight instability is the necessary condition for the true stability of the organism,” are the words attributed to Walter Cannon, a famous American psychophysiologist.

Assessing the stability of a system is not an easy task: it implies the ability to predict the dynamics of the system under stress. Michael Mageau and co-authors (1995) identified two components of resilience that can be measured using simulation models – recovery time (R_T) and maximum magnitude of stress (MS). R_T can be estimated by measuring the time it takes for a system to recover from a wide range of stressors and to reach previous steady state. MS can be measured by increasing the simulated stress gradually until the system returns to its new steady state (with the strength of the stress causing the shift taken into account). The total resilience score can be derived from MS/R_T ratio. With constant MS value, the system with the shortest R_T is more stable. With equal R_T, the system with the highest MS value is more stable.

Importantly, in the early XX century, V. Vernadsky in his doctrine of the biosphere strived to connect the biological component with the geochemical structure of the biosphere, productivity and diversity of living organisms, and energetics. The scientist claimed that complexes of biogeochemical interactions in ecosystems have the property of homeostasis and, therefore, have natural mechanisms for regulating the resistance to affecting factors (Vernadskii, 1989).

In modern reference books, the term “homeostasis” refers to self-regulation, ability of an open system to maintain the internal stability through coordinated reactions aimed at keeping dynamic equilibrium. In biological systems, it can be implemented through adaptive modes associated with the adaptation of the organism’s structure and functions, restructuring, or shift in metabolic or energy characteristics of ecosystems (Egorov, 2019). From the perspective of control theory, the ecosystem homeostasis is realized by negative feedbacks between their components according to the Le Chatelier–Braun principle.

In the monograph by G. Polikarpov and V. Egorov (1986), new mechanisms for the formation of ecosystem homeostasis according to a marine environmental pollution factor were identified and mathematically developed, biogeochemical criteria for normalizing anthropogenic load were substantiated, and theoretical basis for studying anthropogenic ecology and biogeochemical cycles of marine ecosystems was formed. Based on the results of long-term research, Academician of RAS V. Egorov (2019) proposed methods for implementing the concept of sustainable development of critical and recreational zones in the Black Sea by regulating the balance between the consumption of water quality resources and their reproduction resulting from natural biogeochemical processes.

The assessment of the sustainability of marine ecosystems to anthropogenic load was developed by several domestic researchers. The issue was generalized in the concept of assimilation capacity, and it served as the scientific basis for the ecological regulation of anthropogenic load on the World Ocean aimed at maintaining the ecosystem integrity (Izrael & Tsyban, 1989).

In assessing the ecosystem health, **biodiversity** of plant and animal species forming the ecosystem is a key component. The quantitative stability of inhabiting species is of great importance for long-term monitoring of water areas. Obviously, water basins inhabited for a long period by stable populations of key species can be classified as environmentally safe. However, there are regions, *e. g.* the Baltic Sea areas, where biodiversity is extremely limited by a set of physical and chemical factors. Those are hypoxia spots, natural sources of sulfur gases emission, critical salinity of some water areas creating boundary conditions for existence (or even survival) of animal and plant species, and thermo- and haloclines as natural environmental factors limiting the ranges of various organisms (Drozdov & Smirnov, 2008). Consequently, in nature, species diversity can be affected by both natural and anthropogenic factors. To analyze the water quality in the ecosystems, various methods for assessing biodiversity are applied, for example, the Shannon, or Shannon–Wiener, index (Strong, 2016). At the same time, there is an opinion that the Shannon diversity index provides a slightly overestimated assessment of water quality under conditions of eutrophication of water basins (Barinova, 2000).

A widely used criterion is O/E ratio. It is the ratio between the observed (O) and expected (E) number of taxa based namely on a taxon richness, not on abundance data.

Importantly, among the approaches to assessing the pollutant effect on the ecosystem state, one of the most significant ones is applying of methods based on determining the physiological response of native organisms (Fig. 1).

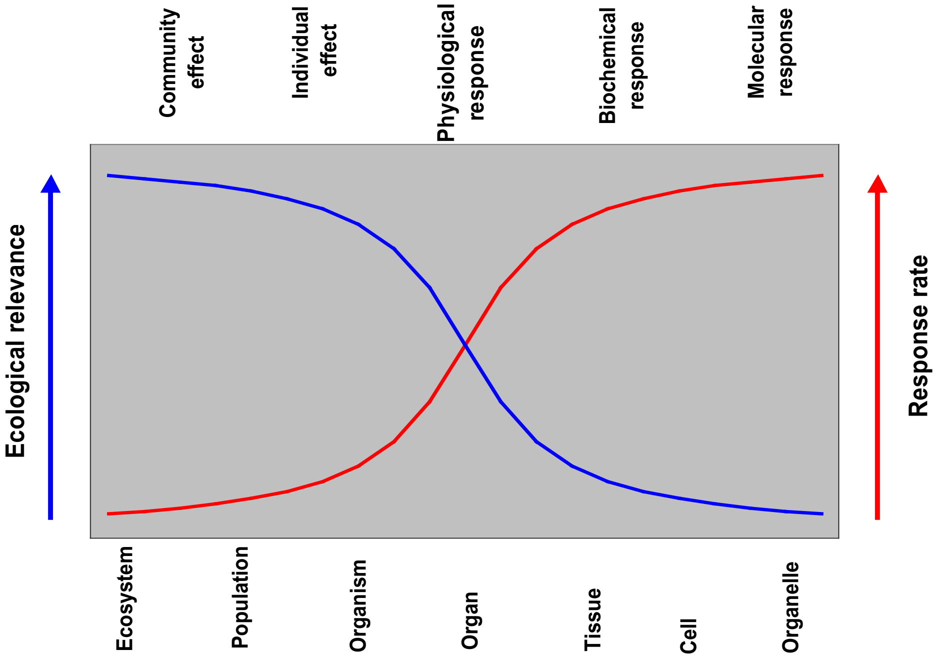

Fig. 1. Scheme of the relationship between the response rate at different levels of biological organization and the ecological relevance [from: (ICES, 2010)]

The scheme given (see Fig. 1) shows how limited the approach is when based on the biodiversity index alone. For biodiversity, it takes time to change (from the moment of a polluting factor effect to the onset of clear consequences for the ecosystem). In this regard, there is a problem of timely adoption of cost-effective management decisions aimed at protecting and eliminating the processes of ecosystem health disturbance.

Functional diversity is a component of biodiversity describing the diversity of functions that organisms in a community or ecosystem have evolved while interacting. David Tilman (2001) analyzed it in detail.

Usually, studies of the functional diversity assess how organisms affect properties/processes of the ecosystem (Gagic et al., 2015) and what environmental factors and disturbances form the diversity and distribution of functional traits in space and time.

Ecosystem health as a **harmonious unity of the organism and the environment** involves the study of a balanced interaction of environmental components with living organisms. Even V. Vernadsky wrote (1978), "Living matter covers and restructures all chemical processes of the biosphere, and its effective energy is enormous compared to the energy of inert matter. Living matter is the most powerful geological force growing over time." He put forward the hypothesis that "living matter creates for itself an area of life."

Researchers continue to develop this direction. Clive Jones and co-authors (1994) noted that many living organisms act as constructors of environmental elements. The following definition is given: ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials. Among "ecosystem engineers", there are autogeneic ones (those change the environment with their own living and dead tissues) and allogeneic ones (those transform other's living and dead materials from one physical state to another by mechanical or other effects thus changing the environment). In this case, the vital activity of organisms themselves results in creating a new ecosystem or its components. If the health of an "ecosystem engineer" deteriorates, the ecosystem health is threatened. Specifically, a marine worm *Sabellaria alveolata* (Linnaeus, 1767) is capable of creating extensive bioconstructions that currently form the largest reefs in Europe (Curd et al., 2019). This sedentary colonial polychaete widely distributed in both intertidal and shallow subtidal zones all over the world builds tubes out of sand and shell fragments gluing them together with its mucus (Holt et al., 1998). Such tubes can be inhabited by other animal species. Out of complex relationships between the non-biological and biological components, the most studied are those of a reef community – a multicomponent and structurally and functionally complex "association", with organisms or their communities capable of acting as "engineers" of ecosystem components (Abelson et al., 2016).

In classical domestic publications, **for an integral assessment** of the ecosystem state, it is customary to consider the ratio of production and destruction in the environment (Alimov, 2000). Ecosystem production is the difference between its primary production and total expenditure on metabolic processes for all hydrobionts in the ecosystem. There, the balance of metabolic processes is of key importance. As A. Alimov specified (2000), "if the energy spent on them exceeds the energy contained in primary production, a negative balance of energy in the ecosystem is registered." Usually, the balance in ecosystems is considered as energy flows from accumulator organisms to consumer organisms. It is generally accepted to estimate phosphorus and nitrogen fluxes. "Thus, in a water basin, the key part of the biotic cycle of matter is phosphorus assimilation by autotrophic organisms when creating primary production in aquatic ecosystem," A. Alimov noted (2000).

Due to accelerated dynamics of anthropogenic load on aquatic ecosystems, priority in ecological research should be given to the study of the ecological state (health) and ecosystem functioning under modern challenges.

In 2015, in order to create measures mitigating the effects of climate change and allowing to achieve the sustainable use of marine resources, the United Nations adopted the Sustainable Development Goals. Adapting to current and expected changes in marine ecosystems is essential for human society in the context of successful and sustainable use of ecosystem services. Therefore, decision makers need information on the state of regional marine ecosystems, as well as forecasts of their changes based on a comprehensive understanding of the limits of ecosystem variability.

So, the discrepancy between environmental conservation goals and economic development has been and remains the main problem for achieving healthy ecosystem quality (Margules & Pressey, 2000). This has created and continues to create a serious gap in environmental management (Griggs et al., 2013).

To bridge this gap, the **ecosystem approach concept** was developed. Its core is integrated management of human activities based on the best available knowledge on ecosystems, their dynamics, and stress resilience in order to identify and eliminate the main causes of ecosystem degradation (Decisions Adopted by the Conference, 2000 ; The Convention on Biological Diversity, 1993). Such an approach should ensure the use of elements of the ecosystem without loss of its integrity. To a greater extent, this refers to the state of coastal water areas as recipients of insufficiently treated or untreated wastewaters.

Management based on the ecosystem approach should ensure that implementation of economic activities does not interfere with providing ecosystem services. At the same time, its ultimate goal is to preserve and increase the ability of ecosystems to produce services in the long run (Directive 2000/60/EC, 2000 ; HELCOM, 2010, 2014). Moreover, it is important to establish a relationship between an assessment of the ecosystem health and assessment of environmental risks.

Methodological approaches to assessing the health status of aquatic ecosystems. To date, several methods have been developed and tested that are in complementarity relations (field research, observation, description, classification, modeling, forecast, *etc.*). Since methods and approaches to assessing the ecosystem ecological state (health) are numerous, we will dwell on only a few.

When implementing the EU directives and the Water Framework Directive (Directive 2000/60/EC, 2000 ; Directive 2006/44/EC, 2006), several assessment criteria were developed – Environmental Quality Standards (EQS) required for water areas to achieve a good ecological status.

These recommended standards should be based on the Background Assessment Criteria and Ecological Assessment Criteria (BAC and EAC, respectively). BAC characterize the variability of the estimated indicators normal for natural systems (variability ranges); EAC are based on the series of values obtained during toxicological experiments (10–100–1000 × LC_{50}, LOEC, NOEC, PNEC, *etc.*) which indicate a deterioration in the environmental quality. As a rule, EAC quantitative indicators are obtained in experiments on laboratory animals – test organisms when determining the effect of various toxicants or their mixtures. Nevertheless, the question arises on the environmental relevance of these values for natural conditions.

From an environmental perspective, the environmental quality is defined as a stable state and functioning of all the ecosystem components, “with fluctuations in the values of parameters not going beyond the natural limits registered over a considerable period of time” (Moiseenko, 2009). Thus, the ability of the biocoenosis to maintain physicochemical and other characteristics of the environment (Odum, 1986) and to recover quickly from any effects which are negative in terms of their direction (final result) can serve as a criterion for the good quality of natural waters.

In recent decades, more and more attention has been paid to biological research methods in monitoring of the environmental state.

When beginning assessment, an essential task is the selection of a bioindicator – an animal or plant taken as a key species. This requires a good knowledge of the hydrobiological state of a water basin (in particular, species diversity of its fauna and flora) and a clear understanding of trophic relationships between its inhabitants (Ekosistema estuariya reki Nevy, 2008). Various taxonomic groups – fish, algae, birds, *etc.* – are used as bioindicators characterizing the health of both river and marine ecosystems, but macrobenthic invertebrates are preferred (Dale & Beyeler, 2001 ; Heink & Kowarik, 2010 ; Rosenberg & Resh, 1993 ; *etc.*). The reasons are as follows: those are present in most aquatic habitats; are relatively easy to sample (compared to other biota); are a diverse group; and are long-lived and sedentary organisms (serve as a site sample). Bioindicator species should be well studied biologically. Such animals should respond to stress in a predictable manner and have low variability in their responses (Attrill & Depledge, 1997 ; Depledge & Galloway, 2005). They are known to integrally respond to chronic anthropogenic environmental pollution (Rosenberg et al., 2004). Sampling and analysis of the composition of aquatic invertebrates can be used to monitor continuous or intermittent disturbances, as well as to study the effects of single or multiple stressors and pollutants in their aquatic environment.

However, when selecting bioindicators for biomonitoring, human economic use of certain species comes to the fore in some cases. It is important to apply relevant (acceptable) physiological or behavioral indicators (biomarkers) and their reference limits, as well as to have a possibility of their non-invasive registration.

In the last century, methods and criteria for assessing the ecological state of **freshwater (river) ecosystems** were actively developed due to their relative simplicity, fixed set of components of such ecosystems, and the fact that trophic and functional relationships are properly studied.

In biomonitoring, there are several approaches to assessing the ecosystem health. The main ones are outlined in the publications (Mageau et al., 1995 ; O'Brien et al., 2016 ; Savić et al., 2017) and are reflected in the recommended criteria developed in the course of international environmental projects – Index of Biological Integrity and River Invertebrate Prediction and Classification System (hereinafter IBI and RIVPACS, respectively).

IBI emphasizes the possibility of biota to serve as an integrator of human effects on nature (ecosystem). This indicator allows analyzing the degradation of river ecosystems taking into account the assessment of biological diversity, complexity and rearrangement of trophic relationships, and ecological organization of ecosystem components (Karr, 1999).

RIVPACS aims at determining the composition of animal and plant species for their protection and reproduction. To do this, locations with "fairly good quality" or "free of serious pollution" have to be found – spots free from severe chemical contamination (Wright et al., 1984).

These two approaches differ both in biological data collected and analyzed and in aims of the assessment. River and estuary monitoring and projects based on the proposed indicators have been successfully implemented in Australia according to IBI (AUSRIVAS) and in the UK for 30 years (RIVPACS I, II, and III).

What do IBI and RIVPACS have in common:

- focuses on biological implications in determining river health;
- using the concept of reference states (as fundamental ones);
- subdivision of locations by classes, with a selected set of environmental characteristics;
- assessment of changes and degradation resulting from anthropogenic load;
- requirements for standardization of sampling methods, as well as requirements for technical equipment of a laboratory, used methodology, *etc.*;
- finding of reference environmental standards (EQS).

Moreover, in earlier works involving similarity indices in community studies, *e. g.* Bray–Curtis index, and multivariate analysis techniques [see in particular (Chiu et al., 2011)], it was noted as follows: these indices and techniques are an integral part of predictive modeling approaches that should become the next step in the development of evaluative biological methods. Multivariate techniques compare test sites with reference ones, and this requires an initial model building by means of computer software.

The concept of reference status, or reference condition, was introduced by John Wright (Wright et al., 1984). Reference is fundamental to multivariate bioassessment approaches used throughout the world: it provides a benchmark for comparison for the water basin studied. A commonly used definition of reference condition was given by Trefor Reynoldson and co-authors (1997), "…a condition representing a group of minimally disturbed areas organized according to individual physical, chemical, and biological characteristics." The advantage of the reference condition approach in multivariate techniques is the following: once the reference sites are grouped (based on indicators of biota status), the independent data, *e. g.* physical and chemical indicators, are used to compare the test sites with the reference ones.

In 1999, a special issue of the journal *Freshwater Biology* included detailed analysis of the river health concept [see in particular (Karr, 1999)] which offers assessments based on the state of the biological components of aquatic ecosystems. Changes in species composition of fish communities are often used as an indicator of the consequences of chemical pollution for the environment.

The environmental values associated with the river health are based on preservation of ecological integrity (ecosystem functioning) and sustainability. In some cases, ecological values and human needs are in conflict when determining the river health. As noted (Karr, 1999), one of the reasons for the river bloom was the inability of the river system to regulate the quantity and qualitative composition of the nutrients required – the loss of ecological function; this led to death of several animal species. Accordingly, the ecological "attractiveness" for human recreational use was reduced.

Recent ecological assessments of the health of forest ecosystems and fish communities within the river basin of the Inland Columbia showed a strong relationship between them (Pausas & Parr, 2018): the degradation of fish communities is often associated with significant changes in surrounding forests. Thus, the need for sustainable existence of various natural habitats / spawning grounds of valuable (for humans) fish species for their natural reproduction and protection usually conflicts with the goals of timber or gold mining enterprises. The core is that the loss of forest areas or changes in the quality of natural waters are obligatory consequences of human activity.

Some disorders result from natural processes. Specifically, a fire can be caused by lightning in a prairie or forest. The effect of fires on the change of animal and plant populations can be analyzed from the perspective that those affect the ecosystem state by changing the gene pool of the species included (Pausas & Parr, 2018). Among ecosystem disturbances resulting from anthropogenic load, there are acid rains, deforestation, algal blooms, and introduction of invasive animal and plant species.

In the last ten years, the **Functional Feeding Groups** (hereinafter FFG) approach is actively used. Developed over 30 years ago, it has been modified in some detail [see in particular (Cummins et al., 2005)], but the core of FFG relationship remains fairly simple. FFG are based on a direct correspondence between the categories of food resources in the environment (ecosystem) and populations of freshwater invertebrates adapted to harvest a particular food resource efficiently. Analysis of the trophic structure of benthic macroinvertebrate communities can be carried out for biological assessments of the river ecosystem state. With trophic, or functional, approach applied, the Index of Trophic Completeness was developed (Pavluk et al., 2000). Moreover, FFG coefficients can be used as surrogates when attributing aquatic ecosystems – also based on the reference standards. This approach can be useful in describing the ecological state of freshwater ecosystems. For the Nišava River in southeastern Serbia, Ana Savić and co-authors (2017) showed that surrogate FFG coefficients are consistent with material on observations of ecosystem properties at sampling sites. So, trophic relationships, the nature of the *predator–prey* relationship, the assessment of the physiological state of macrobenthic organisms, and physicochemical data can serve as a measure for attributing a water area in terms of water quality.

The reference condition approach is considered relevant for the environmental assessment of both river and marine ecosystems.

To assess the ecological state of **marine areas**, a number of international communities have been created and are actively working and interacting, *inter alia* HELCOM, OSPAR, and MEDPOL.

HELCOM is aimed at providing up-to-date information for target users of the Baltic Sea region, both at national and international levels, as well as submitting material for pan-European and global forums (European Union; United Nations Environment Programme, UNEP; and International Maritime Organization, IMO). For the Baltic Sea, the main problem is water eutrophication. The comprehensive assessment of eutrophication carried out by HELCOM includes a section on technical/scientific aspects (science for management) and a section on general political actions of the Baltic Rim countries to achieve good ecological status of its water areas. This is necessary to make informed decisions on restoration of the Baltic Sea ecosystem and on achievement and maintenance of the good ecological status of its subregions. Moreover, it is important for achieving HELCOM goals. The quality of the studies is confirmed by the requirements of strict adherence to HELCOM COMBINE recommendations (Manual for Marine Monitoring, 2017). Besides that, indicators of the status of phytoplankton, aquatic vegetation, and benthic invertebrate fauna, as well as physical and chemical characteristics and various types of loads (usually, phosphorus and nitrogen loads) are presented in national, regional, and European reports on the Baltic Sea status assessment (ICES, HELCOM Reports, and PICES Scientific Groups Reports).

However, in most reports, it is customary not to use specific numerical data, but to apply generalized coefficients. Thus, the Ecological Quality Ratio (EQR) is actively used in assessing the ecological status of water areas. The EQR is recommended in the Water Framework Directive aimed at achieving or maintaining a good ecological status of surface waters by 2021. Therefore, the values of biological quality elements should be taken into account when attributing water basins to any class of ecological status or ecological potential. The EQR scale was adopted as a generalized criterion for comparative regular monitoring of the status of different ecosystems, especially in assessments based on indicators of phyto- and zooplankton state. In this case, for each category of surface water quality (from high down to poor ecological status), it is proposed to calculate boundaries by assigning a numerical value for each category and establishing borders between quality classes. In practice, high EQR values (close to one) indicate a status with no deviation, with unsignificant or little deviation from the reference values; therefore, such values are a sign of an acceptable status corresponding to "areas not affected by eutrophication." Low EQR values indicate moderate, significant, or severe deviations from baseline and unacceptable status corresponding to "eutrophicated areas," with moderate or poor ecological status. As a rule, EQR values are comparable with those of other complex indices. But in the case of the Benthic Quality Index (Blomqvist et al., 2006 ; Rosenberg et al., 2004), significant deviations of indicators (up to 86 %) were allowed; therefore, even extremely low EQR values can sometimes be considered as exceeding the boundary of the good/moderate water class.

To date, the status of benthic invertebrates is assessed for the high sea alone. It can vary significantly between Baltic subregions due to wide distribution of hypoxic and anoxic zones in the Baltic Sea and the Gulf of Finland. Currently, the Baltic Proper – from the Bornholm Deep to the basin northern area and the Gulf of Finland – is in a disturbed state.

The assessment of water quality by various indicators can differ significantly. These discrepancies highlight the issue of using different indices in different countries (regional specifics) and the obvious need for careful intercalibration of methods. Moreover, integral methodological approaches should be developed. Only the use of several indicators will reduce the risk of erroneous assessment of the ecosystem state and increase the reliability of the final conclusions on its health.

To assess environmental quality and health status of marine organisms more accurately, European researchers proposed several approaches and developed complex indices based on biomarkers. Those are the Integrated Biomarker Response, IBR (Beliaeff & Burgeot, 2002); Metal Pollution Index, MPI (Usero et al., 1997); Biomarker Response Index, BRI (Hagger et al., 2008); and Bioconcentration Factor, BCF. The latter one assesses the bioavailability of heavy metals for tissues of living organisms (Mendoza-Carranza et al., 2016). These approaches involving integrated indices (for effect and exposure biomarkers) have been successfully applied for assessing ecological state in many marine areas throughout the world, especially in European coastal zones [see in particular (Biomarkers, 1992 ; Turja et al., 2014 ; Yeats et al., 2008)].

To assess the ecological state of several locations in the eastern Gulf of Finland (the coastal Baltic Sea), N. Berezina and co-authors (2017) proposed a set of well-known biotic indices and methods, including a Saprobity System (based on phytoplankton), Raffaelli and Mason index (meiobenthos), and two macrobenthic derived indices (Goodnight–Whitley index and Benthic Quality Index). As a non-widely implemented index, the authors of this work used the embryo malformation frequency in benthic amphipods (Sundelin & Eriksson, 1998).

In the development of modern methods for analyzing biological effects of anthropogenic load on aquatic ecosystems, one of the key aims is to determine the criteria for assessing their health based on certain biological indication methods. One of the benefits of their applying is that the indicators recorded (biomarkers) reveal themselves at the organism level when the aquatic environment is exposed to sublethal concentrations of pollutants. This allows detecting shifts in the functional state of individual animal species long before the onset of serious changes, degradation of populations and communities, and disturbances of ecosystems they inhabit (Kholodkevich et al., 2018 ; Depledge & Galloway, 2005 ; Kuznetsova & Kholodkevich, 2015). Based on the data obtained, it is possible to develop scientifically grounded methods for assessing the environmental risk for ecosystems. This approach is based on the classical works of the representatives of the British scientific school analyzing the biological effects of environmental pollution and methods for assessing the aquatic ecosystem health. The approach is postulated on the statements substantiated in a number of publications [see in particular (Depledge & Galloway, 2005)]:

- healthy ecosystems are inhabited mainly by healthy animals;
- by measuring the health status of key animal species in the ecosystem, it is possible to assess the environmental consequences of pollution of their habitat.

In most developed countries, this approach is currently a priority for analyzing pollution and its effects on the ecosystem health. The approach allows to carry out an objective assessment of the functional parameters (health) of animals and the ecological state (health) of the aquatic ecosystems these animals inhabit.

Integrative index approaches to monitoring and assessing marine pollution are still under development and improvement. This allows to create a holistic approach to understanding the marine ecosystem health.

The most commonly used biochemical markers of exposure are:

- detoxification enzymes activity – EROD and GST;
- effects of the antioxidant defense system – expression level of mRNA for SOD and SOD activity;
- biomolecular damage levels – DNA breaks (F value);
- lipid peroxidation (LPO) and protein carbonyl (PC) content;
- assessment of the microbiome state of bioindicators.

In this review, it is not possible to list all the indicators used or recommended.

When assessing the ecosystem ecological state (health), an approach involving multi-integrated biomarker indices is actively used: this lays a solid foundation for multiple assessment of marine pollution. The data obtained in the course of integrated studies can serve as a reliable base for a timely and adequate assessment of the state of marine ecosystems, *inter alia* estuarine ones, allowing to predict their changes and to plan environmental measures.

Experience of participating in the pan-Baltic BONUS+/BEAST project. The strategic HELCOM Baltic Sea Action Plan (BSAP) defines the main long-term objectives and the need for appropriate management decisions to achieve "good ecological status" and "healthy wildlife." Hazardous substances were marked as one of the main threats to the Baltic Sea ecosystem and its biota. Accordingly, the BSAP pointed out the need for developing monitoring of the biological effects of pollutants and their mixtures on biota aimed at reliable assessment of ecosystem health. The BEAST (Biological Effects of Anthropogenic Chemical Stress) project contributed to achievement of these goals and solution of several problems (Lehtonen et al., 2014).

The BONUS+/BEAST project involved 16 partners – European institutions – from all the Baltic Rim countries, including the St. Petersburg Research Centre for Ecological Safety of the Russian Academy of Sciences (RFBR grant No. 08-04-92424-BONUS_a). In 2008–2011, within the framework of this project, biomonitoring studies were carried out in several subregions of the Baltic Sea which differ significantly in water salinity, biodiversity, oxygen conditions, *etc.* Field and experimental studies were carried out, with both long-settled and new methods applied in selected water areas of five Baltic Sea subregions; so far, information on the biological effects of hazardous substances there was limited. To establish a relation between the organism's reactions associated with anthropogenic chemical pollution of the environment and the effects observed at higher biological levels, the participants of the BEAST project formed integrated multi-box tools, with biomarkers as sensitive diagnostic tools included. To date, the biomarker approach in assessing the ecosystem state is widely used: this can provide valuable data on suitable methods for effect assessment (Rudneva & Roshchina, 2008 ; Handy & Depledge, 1999 ; Soldatov et al., 2014) and thereby reduce uncertainties related to extrapolation of biological effects to studied species, endpoints, and chemicals.

The BEAST project uses biochemical markers of oxidative stress, lipid metabolism, acetylcholinesterase content, disruption of lysosome membrane integrity, cardiac activity (heart rate recovery time after a standardized load), presence of genetic disorders (occurrence of micronuclei in cells of various tissues), violations of the early stages of ontogenetic development, presence of parasites in the organisms of bioindicator species of hydrobionts, *etc.* In detail, the issue is discussed in the monograph *Biomarkers: Biochemical, Physiological, and Histological Markers of Anthropogenic Stress* (1992). The peculiarities were taken into account of changes in physical and chemical characteristics of the environment, *inter alia* involving passive samples, for different study areas. Historically established conditions were considered for the exploitation of certain water areas in connection with economic activity, *e. g.* use of water areas as ports. The results of the BEAST project were published in several papers and articles, with the main ones being (ICES, 2010 ; Lehtonen et al., 2014 ; Turja et al., 2014).

The project was focused on detecting deterioration in health parameters of bioindicator species (fish, molluscs, and crustaceans) applying biomarkers to compare the ecological state of the areas studied with conditionally reference water areas with similar hydrological and temperature regimes, as well as with similar natural populations of local bioindicator animals. As a result, Integrated Biomarker Response was determined for different study stations.

In the course of the project, a principal component analysis was carried out as well. This allowed to link some indicators of the organism's susceptibility to environmental pollution (Turja et al., 2014).

Experience in developing a methodological approach to assessing the health of key species of aquatic ecosystems. Extremely high dynamism of anthropogenic processes imposes special requirements on the speed of detection of ecosystem disturbances and on the speed of taking adequate environmental measures. This necessitates creation and implementation of express methods for diagnosing the current ecological state of surface waters in order to promptly identify the areas of "environmental trouble". In the BEAST project, there was a "novelty": non-invasive recording of the heart rate (hereinafter HR) and analysis of the peculiarities of cardiac activity of local mollusc species from water areas with different anthropogenic load in order to determine possible differences in their functional state were proposed. As shown earlier [see in particular (Depledge & Galloway, 2005 ; Kholodkevich et al., 2017 ; Kuznetsova & Kholodkevich, 2015)], an effective assessment of the ecosystem state (health) can be based on the long-term monitoring of any vital function of the bioindicator – motor, cardiac activity, respiration, *etc.* Specifically, the reaction of the cardiovascular system can be considered as an integral response of the organism to shifts in environmental factors. At the same time, we can apply HR as an ecotoxicological biomarker since it reflects the intensity of physiological processes; moreover, in many cases, it allows to draw a conclusion on the organism's functional state (Kuznetsova & Kholodkevich, 2015).

The pulse is one of the key indicators of the cardiovascular system functioning. The rate may change under various factors (physical activity, stress, and nutrition), but in the absence of pathologies, heart contractions should quickly return to normal. This well-known and verified statement served as the basis of our methodology for testing the functional state of bioindicators taking into account HR recovery time in molluscs and crustaceans after removing the functional load (Kuznetsova, 2013).

As a functional test, it is proposed to consider **reflex actions** under standardized test loads:

- change in water salinity;
- change in water temperature;
- change in lighting;
- effect of vibration.

According to these test stimuli causing test reactions, we propose to assess the adaptive capabilities of the organism – its measure of health.

As mentioned above, we proposed to use a rapid **change in water salinity** in the range of physiological tolerance for a certain animal species as one of the test stimuli (Kuznetsova, 2013).

In a number of our studies on bivalves, it was shown as follows: molluscs responded to a rapid **change in water salinity** (freshwater influx) with a **characteristic behavioral reaction** – valve closure; this resulted in isolation of mussels (their mantle cavities) from the unfavorable environment (Kholodkevich et al., 2009). The process was accompanied by an initial sharp increase in HR, and this can be considered as the primary non-specific response of the mollusc cardiovascular system to stress. Thus, a generalized response to a change in salinity (as a non-damaging osmotic stress effect, within the tolerance range of the species studied) can be used as a standardized stimulus. For freshwater molluscs, we recommend increasing salinity for 1 or 2 hours (up to 10–12 ‰, according to the results of T. Kuznetsova's personal experiments in 2012–2019). For marine molluscs, we recommend halving salinity of their natural habitat.

A **change in temperature** can also serve as a test and can be used to analyze changes in HR in populations of littoral *Patella caerulea* Linnaeus, 1758 differing in the settlement horizon (Santini et al., 1999). Importantly, a change in temperature of the environment necessarily affects the level of metabolism. As known, with a change (increase) in temperature of the environment by 10 °C, the level of metabolism of hydrobionts rises by 2–3 times. The Q10 coefficient has been experimentally determined for different molluscs and crustaceans, and it varies slightly between species due to peculiarities of their biology (Braby & Somero, 2006).

Previously, it was found that molluscs sampled in environmentally safe water areas differ from animals sampled in polluted water areas: those show a higher adaptive ability expressed in a significantly shorter HR recovery time (T_{rec}) after removing the functional load (Kholodkevich et al., 2009 ; Kuznetsova & Kholodkevich, 2015). Moreover, animals from environmentally safe water areas, compared with those from polluted water areas, show higher uniformity of reactions expressed in a low coefficient of variation of individual HR values ($CV_{HR} \leq 0.1$) for this group of animals after the test exposure and recovery of initial water salinity. After a raw of investigations, a methodological approach was proposed (Kholodkevich et al., 2018, 2009 ; Kuznetsova et al., 2010, 2018) to a comparative assessment of the ecological status of water area based on the analysis of adaptive capabilities of bioindicators. It was successfully applied not only in laboratory studies, but also in several field ones (Kholodkevich et al., 2015 ; Kuznetsova et al., 2018 ; Turja et al., 2014); those revealed a relationship between anthropogenic pollution of the aquatic environment and the proposed physiological indicators (biomarkers). A peculiarity of this method for assessing the organism's functional state is the absence of subregional limits. This makes the method more accessible during intercalibration.

The scheme of this methodological approach is shown in Fig. 2.

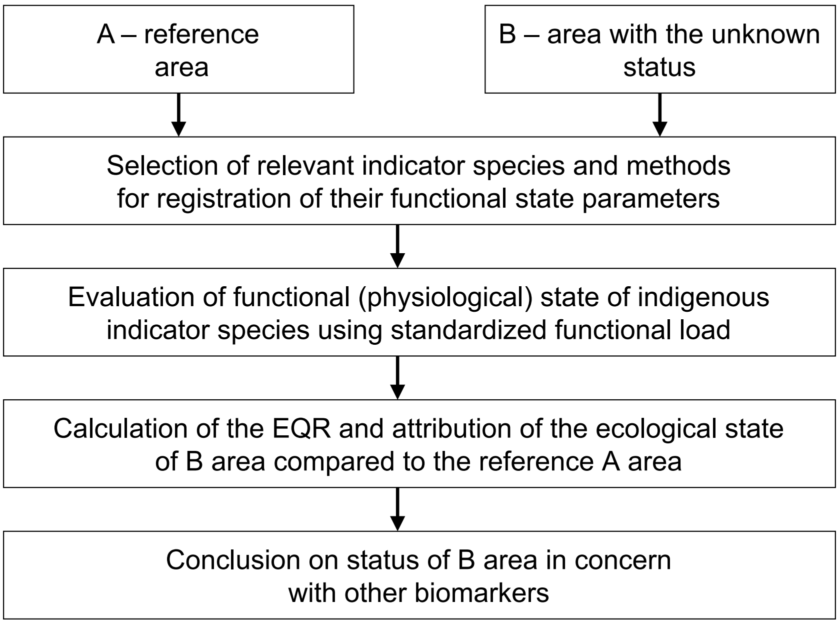

Fig. 2. Scheme of the proposed methodological approach to the comparative assessment of the ecological status of water areas

Thus, an experimental possibility was shown to study the adaptive capabilities of various organisms from various ecosystems and, therefore, according to I. Davydovsky, to draw a conclusion on their physiological health (Kholodkevich et al., 2017 ; Kuznetsova & Kholodkevich, 2015 ; Kuznetsova et al., 2018). This is necessary both for practical purposes (the use of animals with stable biomarkers to analyze the quality of natural waters as a habitat for aquatic organisms) and for assessing the state of natural populations in which, due to natural variability, there are individuals of different health. Molecular genetics, biochemical, and behavioral biomarkers of selected key population species (prevailing in abundance and biomass), the degree of animal infestation with parasites, *etc.* will help to establish a grounded conclusion on the population health and, possibly, to represent the health of the studied ecosystem with certain degree of reliability.

All the data obtained on the assessment of the state of local invertebrates can be supplemented with material on the bioaccumulation of heavy metals in the tissues of local animal species (for example, bivalve molluscs, gastropods, and crustaceans). This integrated information allows us to extrapolate the results of studying several indicators of individual animals on the assessment of the population health and the ecosystem state in various water areas where water, sediments, and animals were sampled. The analysis helps in ranking water areas by the level of their pollution taking into account the peculiarities of the operation of vital functional systems in biological objects studied – living “biomonitors” of the habitat quality. It can be concluded that in locations with signs of shifts in the functional state of the bioindicator (with significant changes in the operation of its main functional systems), we should expect changes in the ecosystem state. This can also be identified and proved by applying various approaches and assessment criteria for the environmental safety of natural waters.

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ЗДОРОВЬЕ ЭКОСИСТЕМ: ПОНЯТИЕ, МЕТОДОЛОГИЧЕСКИЕ ПОДХОДЫ, КРИТЕРИИ ОЦЕНКИ

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Всё возрастающая антропогенная нагрузка на водные экосистемы создаёт угрозы экологической безопасности, и в этой связи важным является экосистемный подход к эксплуатации природных ресурсов с целью разработки комплексных регулирующих мер в природоохранной сфере. Термин «здоровье экосистемы» широко используют в оценке экологического состояния акваторий представители зарубежных научных сообществ (HELCOM, ICES, OSPAR, MEDPOL), однако нечасто применяют отечественные исследователи. Концепция «здоровье экосистемы» не является новой парадигмой: она не только активно обсуждается с начала 2000-х гг. в научной литературе, но и закреплена в долговременных документах Евросоюза и в Водной рамочной директиве ЕС по стратегии сохранения окружающей среды. В статье на основе обзора существующих литературных данных представлены основные понятия, подходы и критерии оценки экологического состояния (здоровья) водных экосистем. Подчёркнуто, что оценка здоровья экосистем зависит от целей и задач экологических исследований, с чем связана применяемая методология и, соответственно, выбор методов и показателей, характеризующих состояние экосистемы. В обзоре рассмотрены понятие «здоровье организмов» и некоторые его атрибуты: поддержание гомеостаза, причинно-следственные связи в континууме здоровье — болезнь, функциональные адаптации. Представлен сравнительный анализ ряда подходов к оценке здоровья рек и морских акваторий. Рассмотрены различные показатели, комплексные индексы, биомаркеры экспозиции и эффектов, указывающие на подверженность водных экосистем изменениям в результате природных и антропогенных воздействий. Отдельное внимание обращено на необходимость применения комплексного экосистемного подхода в анализе состояния водных экосистем, что будет способствовать интегральной оценке последствий деятельности человека для целостности экосистем. На основе опыта выполнения международного проекта BONUS+/BEAST представлен комплексный биомаркерный подход к определению здоровья биоиндикаторов с последующей интерпретацией данных о состоянии здоровья экосистем, в которых эти организмы обитают. Авторы надеются, что обзор будет интересен как специалистам в области экологии водных экосистем, так и представителям природоохранных организаций, ответственным за проведение экологических экспертиз.

Ключевые слова: здоровье экосистемы, оценка состояния водных экосистем, референтные состояния экосистем, физиологическое состояние, функциональные адаптации, макробентосные беспозвоночные

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Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 63–71
https://doi.org/10.21072/mbj.2022.07.2.05

UDC 639.64:582.276

GROWTH OF THE CRYPTOPHYTE MICROALGA *RHODOMONAS SALINA* (WISLOUCH) D. R. A. HILL & R. WETHERBEE, 1989 UNDER DIFFERENT CULTIVATION CONDITIONS

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Received by the Editor 10.06.2020; after reviewing 04.12.2020;
accepted for publication 03.03.2022; published online 07.06.2022.

Temperature and irradiance effect was studied on the specific growth rate and biomass accumulation of the cryptophyte alga *Rhodomonas salina*. Optimal conditions for its cultivation were determined allowing to obtain the maximum biomass. *R. salina* was cultivated on the Conway medium (in our own modification) at a temperature of (20 ± 1), (24 ± 1), and (28 ± 1) °C and irradiance of 13, 67, 135, and 202 μmol photons$\cdot$m$^{-2}\cdot$s^{-1}. As shown, an increase in temperature up to above-optimal values resulted in a decrease of the microalga growth rate and biomass. For *R. salina*, there were no significant differences in growth rates at irradiance of 135 and 202 μmol photons$\cdot$m$^{-2}\cdot$s^{-1} (μ values were of (0.69 ± 0.04) and (0.64 ± 0.02) day^{-1}, respectively). The microalga growth slowed down at low irradiance (13 μmol photons$\cdot$m$^{-2}\cdot$s^{-1}) (μ value was of (0.33 ± 0.03) day^{-1}). The maximum biomass [(3.74 ± 0.28) g$\cdot$L^{-1}] was obtained at the optimal temperature [(24 ± 1) °C] and irradiance of 135 μmol photons$\cdot$m$^{-2}\cdot$s^{-1}. Under optimal cultivation conditions, maximum accumulation of proteins was registered at the exponential growth phase (29 %), and maximum accumulation of lipids was recorded at the stationary phase (41 %).

Keywords: microalga *Rhodomonas salina*, cultivation, temperature, irradiance, growth rate, biomass

The cryptophyte alga *Rhodomonas salina* (Wislouch) D. R. A. Hill & R. Wetherbee, 1989 is widely used in aquaculture, as well as in food and cosmetic industries. It is the main food object when culturing larvae and juveniles of commercial molluscs (oysters, scallops, and mussels) and has high nutritional value (Kholodov et al., 2017 ; Zhang et al., 2013). The microalga provides zooplankton with vitamins, fatty acids, and pigments that are transmitted through food chains (Vu et al., 2016). Larvae and juveniles of bivalve molluscs reared in a nursery are most vulnerable during the metamorphosis period (this is the time when their mortality can be maximum). *R. salina* inclusion in mollusc diet contributes to a significant increase in the growth rate of larvae and spat due to their accumulation of a sufficient amount of total lipids (Tremblay et al., 2007 ; Videla et al., 1998 ; Whyte et al., 1989).

Moreover, the microalga *R. salina* is a promising object for phycoerythrin production, and phycoerythrin can be used as a natural dye for food and cosmetics (Chaloub et al., 2015).

When cultivating *R. salina*, irradiance and temperature are the main factors affecting its growth rate (Ladygina, 2010), biomass accumulation, and biochemical composition – protein, carbohydrate, lipid, and phycoerythrin content. With temperature increasing +20 to +32 °C, *R. salina* maximum growth rate is known to decrease; with irradiance rising 15 to 150 μmol photons·m^{-2}·s^{-1}, it increases (Chaloub et al., 2015). An optimal irradiance range for photosynthesis and alga growth is 60–100 μmol photons·m^{-2}·s^{-1} (Vu et al., 2016). Irradiance of 200 μmol photons·m^{-2}·s^{-1}, as well as high concentrations of nitrates (3.529 mM) and phosphates (0.144 mM) – regardless of temperature – contributed to an increase in *R. salina* growth rate. Moreover, high concentrations of nitrates and phosphates – regardless of irradiance and temperature – resulted in maximum accumulation of protein in algal cells (Guevara et al., 2016 ; Silva et al., 2009). Analysis of the results of several studied shows that *R. salina* biomass accumulation and biochemical composition are sensitive to changes in cultivation conditions.

The aim of the work is to determine optimal conditions for *R. salina* cultivation for its use as a food object in aquaculture.

MATERIAL AND METHODS

The studied microalga was *Rhodomonas salina* – strain CCAP 978127 obtained in 2011 from the collection of IFREMER (Institut Français de Recherche pour l'Exploitation de la Mer) (France).

Experiments on the effect of cultivation conditions on the microalga production parameters were carried out in two stages:

1. Determining optimal temperature. *R. salina* was batch-cultivated on the Conway medium in our own modification (Kholodov et al., 2017), at a temperature of (20 ± 1), (24 ± 1), and (28 ± 1) °C, 24-hour irradiance with Philips TL-D 36W/965 lamps, and continuous air bubbling with a microcompressor. The microalga was cultivated in 2-L flasks, and irradiance was the same – 67 μmol photons·m^{-2}·s^{-1}.
2. Determining optimal irradiance. The microalga was cultivated at optimal temperature of (24 ± 1) °C (this value was obtained during the first stage of the experiment), 24-hour irradiance of the flask surface of 13, 67, 135, and 202 μmol photons·m^{-2}·s^{-1}, and continuous air bubbling.

The experiments were carried out in triplicate. The concentration of algal cells was counted daily in a Goryaev chamber in four fields of view under an MBI-6 microscope. The microalga growth rate was determined according to the formula (Vonshak, 1986):

$$\mu = \frac{\ln N_1 - \ln N_0}{T_1 - T_0} ,$$

where N_0 is the concentration of algal cells at the beginning of cultivation;

N_1 is the concentration of algal cells at the end of the selected cultivation interval;

$T_1 - T_0$ is the cultivation interval (days).

Biochemical analysis of the alga (protein, carbohydrate, and lipid content) was carried out at each growth phase at a temperature of (24 ± 1) °C and irradiance of 135 μmol photons·m^{-2}·s^{-1}. To obtain *R. salina* dry biomass, a certain volume of the culture with a known cell concentration was centrifuged for 3 minutes on an OPN-3 centrifuge at 3000 rpm; then, it was washed twice with isotonic NaCl solution (9 g·L^{-1}). Later, raw biomass was dried to constant weight at +105 °C for 24 hours. The mass fraction of total protein, lipids, and carbohydrates in dry matter (%) was determined by photocolorimetric methods. Total protein content was analyzed according to Lowry *et al.* (1951); lipid content, using a phospho-vanillin reagent; and carbohydrate content, by a color reaction with L-tryptophan reagent (Metody gidrokhimicheskikh issledovanii, 1988). The data were statistically processed using standard Microsoft Excel software packages. All the calculations were performed for a significance level $\alpha = 0.05$. In the text and on the graphs, mean values are given, and the boundaries of a confidence interval are indicated (Lakin, 1990).

RESULTS AND DISCUSSION

R. salina cells are motile, with two flagella and one chloroplast. Mean cell size is as follows: width, (7 ± 0.35) μm; length, (12 ± 0.58) μm; and volume, (527 ± 0.43) μm^3 (Fig. 1).

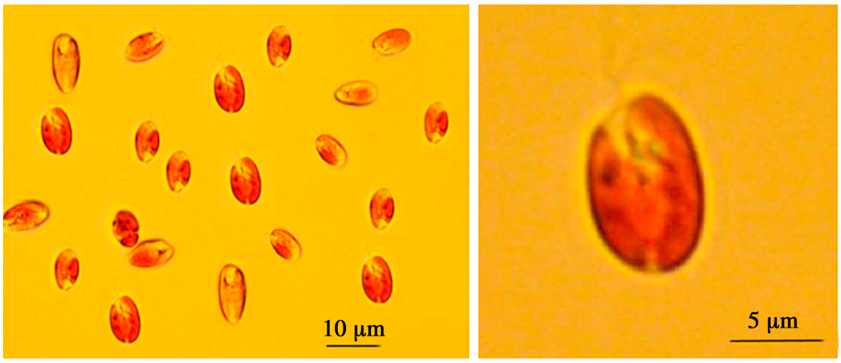

Fig. 1. Microalga *Rhodomonas salina*

Optimal temperature value affecting the growth rate, nutrient uptake, and cell chemistry is species-specific. When cultivating the microalga *R. salina* under different temperatures, the highest rate of cell division was recorded at (24 ± 1) °C; at a temperature of (28 ± 1) °C, it sharply decreased. The maximum culture density (5.43×10^6 cells·mL^{-1}) was obtained at (24 ± 1) °C on the 9th day of cultivation (Fig. 2). At (20 ± 1) and (28 ± 1) °C, maximum cell concentrations were significantly lower – 3.28×10^6 and 3.72×10^6 cells·mL^{-1}, respectively. At (20 ± 1) °C, *R. salina* exponential growth lasted for 8 days; at (24 ± 1) °C, for 6 days; and at (28 ± 1) °C, for 4 days. The period of alga cultivation was the longest at low temperatures – when the culture entered the stationary phase on the 11th–12th day. The cultures kept at (28 ± 1) °C entered the stationary phase on the 7th day; at (24 ± 1) °C, on the 9th day. Under such cultivation conditions, *R. salina* linear growth was observed for 4–7 days; then, a decrease in the cell concentration was recorded, and the culture entered the stationary phase (after 7–11 days of cultivation). A linear dependence of cell concentration on temperature was obtained, with the coefficient R^2 at (20 ± 1), (24 ± 1), and (28 ± 1) °C being 0.85, 0.94, and 0.77, respectively.

The maximum mean daily growth – 0.79×10^6 cells·mL^{-1}·day^{-1} – was recorded at a temperature of (24 ± 1) °C. The values were significantly lower at (20 ± 1) and (28 ± 1) °C – 0.27×10^6 and 0.39×10^6 cells·mL^{-1}·day^{-1}, respectively. The growth rate at a temperature of (24 ± 1) °C is more than 2 times higher than the value at (28 ± 1) °C (Table 1). The obtained results are comparable with the data of other researchers (Brown et al., 1997); according to them, an increase in temperature +26 to +32 °C during *R. salina* cultivation on the F/2 medium results in a decrease in its maximum growth rate.

The dynamics of *R. salina* biomass accumulation under different temperatures was similar to the change in cell density in the culture. Maximum algal biomass – 2.87 g·L^{-1} – was obtained at (24 ± 1) °C. At (20 ± 1) and (28 ± 1) °C, the values differed slightly and amounted to 1.73 and 1.99 g·L^{-1}, respectively (see Table 1). Therefore, a temperature of (24 ± 1) °C was optimal for *R. salina* cultivation under conditions of our experiment.

Table 1. Indicators of the microalga *Rhodomonas salina* growth at different temperatures

Growth indicator	Temperature, °C		
	20 ± 1	24 ± 1	28 ± 1
Mean daily growth, $\times 10^6$ cells·mL^{-1}·day^{-1}	0.27 ± 0.04	0.79 ± 0.06	0.39 ± 0.05
Growth rate, day^{-1}	0.19 ± 0.05	0.53 ± 0.07	0.24 ± 0.03
Maximum biomass (raw), g·L^{-1}	1.73 ± 0.15	2.87 ± 0.24	1.99 ± 0.11

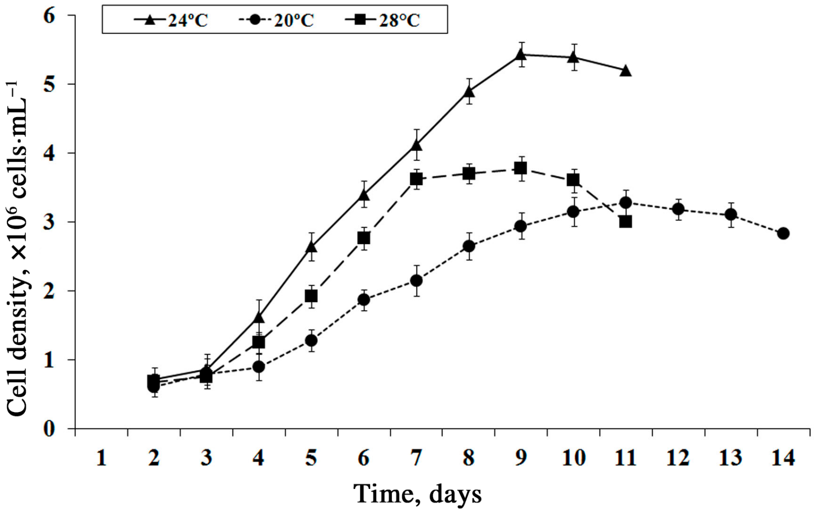

Fig. 2. Dynamics of the microalga *Rhodomonas salina* growth at different temperatures

Irradiance significantly affected *R. salina* growth. This dependence is shown in Fig. 3. At optimal cultivation temperature [(24 ± 1) °C] and different irradiance [13, 67, 135, and 202 µmol photons·m^{-2}·s^{-1}], the growth rate was maximum [(0.69 ± 0.04) day^{-1}] at 135 µmol photons·m^{-2}·s^{-1}.

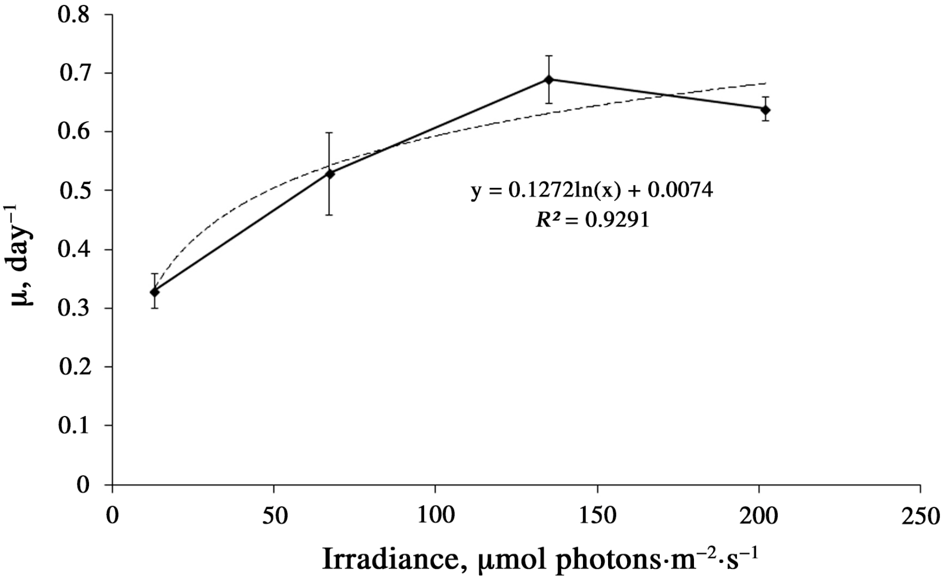

Fig. 3. Dynamics of the microalga *Rhodomonas salina* specific growth rate depending on irradiance

The maximum values of algal biomass were obtained on the 8th and 9th days of cultivation at irradiance of 135 and 202 μmol photons·m^{-2}·s^{-1} – 3.74 and 3.52 g·L^{-1}, respectively (Table 2).

Table 2. Indicators of the microalga *Rhodomonas salina* growth at different irradiance

Growth indicator	Irradiance, μmol photons·m^{-2}·s^{-1}			
	13	67	135	202
Maximum cell concentration, ×10^{6} cells·mL^{-1}	2.53 ± 0.20	5.45 ± 0.38	7.10 ± 0.45	6.55 ± 0.40
Maximum biomass (raw), g·L^{-1}	1.41 ± 0.25	2.87 ± 0.24	3.74 ± 0.28	3.52 ± 0.21

There were no significant differences in *R. salina* growth rates under irradiance of 135 and 202 μmol photons·m^{-2}·s^{-1} (μ values were of (0.69 ± 0.04) and (0.64 ± 0.02) day^{-1}, respectively). The lowest growth rates were registered at 13 μmol photons·m^{-2}·s^{-1} (μ value was of (0.33 ± 0.03) day^{-1}); maximum biomass at such irradiance accounted for 1.41 g·L^{-1}.

With a rise in irradiance of the flask surface 13 to 67 μmol photons·m^{-2}·s^{-1}, the concentration of algal cells and biomass increased by 2 times (see Table 2), but the values were significantly lower than those at 135 and 202 μmol photons·m^{-2}·s^{-1} (7.10×10^{6} and 6.55×10^{6} cells·mL^{-1}, respectively). The maximum values of the specific growth rate and biomass were obtained at 135 μmol photons·m^{-2}·s^{-1}. Therefore, an irradiance of 135 μmol photons·m^{-2}·s^{-1} is optimal for *R. salina* batch cultivation.

During the alga growth, the color of the culture medium changed. At a temperature of (24 ± 1) °C and the lowest irradiance (13 μmol photons·m^{-2}·s^{-1}) on the 7th–8th day (exponential growth phase), the suspension in the flasks became red, and this color differed significantly from the color at 135 and 202 μmol photons·m^{-2}·s^{-1} (Fig. 4).

Fig. 4. Phycoerythrin accumulation in the microalga *Rhodomonas salina* cells at the exponential growth phase at irradiance of 13 μmol photons·m^{-2}·s^{-1}

As the biomass was accumulated and the culture entered the stationary phase, the suspension turned greenish which probably resulted from a change in pigment content in algal cells.

R. salina pigments are phycoerythrin, chlorophyll *a* and *b*, and carotenoids (Chaloub et al., 2015 ; Rowan, 1989). Maximum phycoerythrin accumulation in algal cells is possible at low irradiance levels on the 4th–8th days of cultivation (Bartua et al., 2002). As established (Chaloub et al., 2015), phycoerythrin content in the alga cultivated at +20 and +26 °C was approximately 2–4 and 6–13 times higher when irradiance decreased 150 to 15 μmol photons·m^{-2}·s^{-1}, respectively. The maximum phycoerythrin concentration was obtained on the 8th day of *R. salina* cultivation at +26 °C and 15 μmol photons·m^{-2}·s^{-1}. According to the data of other researchers (Bartua et al., 2002 ; Chaloub et al., 2015), when the culture enters the stationary growth phase, phycoerythrin concentration in microalgal cells decreases, while chlorophyll concentration increases. Apparently, this contributed to the change in the color of the culture medium. Therefore, phycoerythrin biosynthesis in *R. salina* cells occurs at the exponential growth phase and under low irradiance.

A study of the biochemical composition of *R. salina* cultivated at the temperature of +24 °C and irradiance of 135 μmol photons·m^{-2}·s^{-1} showed as follows: accumulation of protein, carbohydrates, and lipids depends on the microalga growth phase. The maximum protein content [(42.8 ± 3.34) %] was recorded at the exponential phase; lipid content [(39.9 ± 4.12) %], at the stationary one. Carbohydrate concentration in algal cells is significantly lower than protein and lipid content; it peaks [(30.0 ± 1.75) %] at the end of the stationary growth phase (Fig. 5).

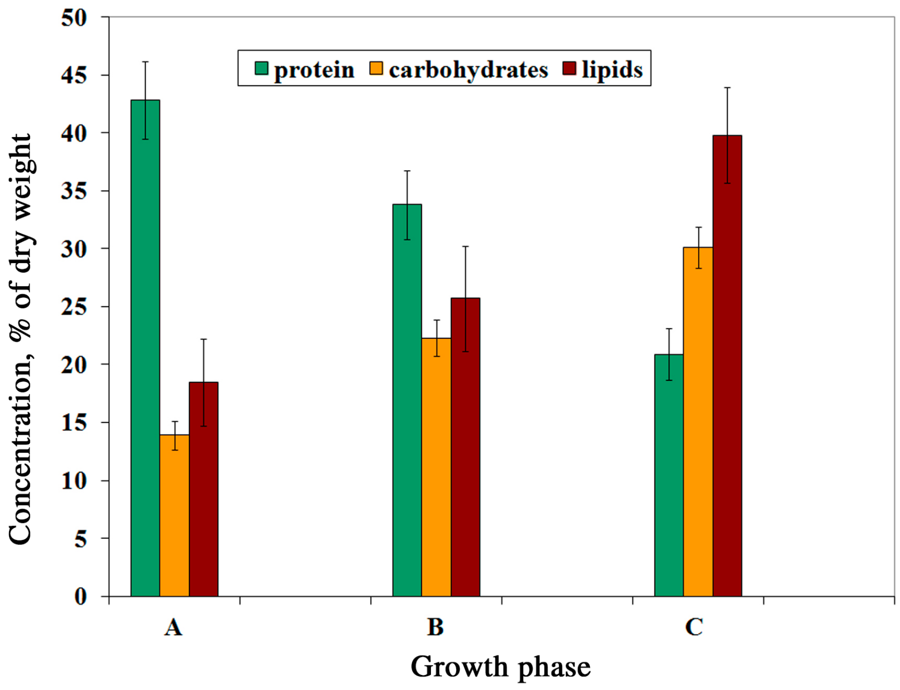

Fig. 5. Biochemical composition of the microalga *Rhodomonas salina* at different growth phases: A, exponential; B, growth retardation; and C, stationary

The content of total lipids, as well as arachidonic, eicosapentaenoic, and docosahexaenoic acids, depends on the alga cultivation conditions – temperature, irradiance, and nutrient availability (Guevara et al., 2016 ; Vu et al., 2016). It was previously established that total content of fatty acids in *R. salina* is maximum at irradiance of 60–100 μmol photons·m^{-2}·s^{-1} and nutrient deficiency. Maximum concentrations of polyunsaturated fatty acids were recorded at 10–40 μmol photons·m^{-2}·s^{-1} and an excess of nutrients in the medium (Vu et al., 2016). The content of polyunsaturated fatty acids – eicosapentaenoic (C20:5ω-3) and eicosahexaenoic (C20:6ω-3) ones – is 12 and 17 %, respectively (Fernández-Reiriz et al., 1989).

Therefore, high concentrations of protein and total lipids in *R. salina* cells allow using this alga as a food object in aquaculture. Specifically, when culturing larvae of a Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in the nursery, the microalga inclusion in the diet contributed to an increase in their survival and growth rate (Kholodov et al., 2017).

Conclusion. Cell density and biomass of the microalga *Rhodomonas salina* varied depending on cultivation conditions. The maximum biomass of *R. salina* (3.74 $g{\cdot}L^{-1}$) was obtained with a batch cultivation on the Conway medium at the temperature of (24 ± 1) °C, 24-hour irradiance of 135 μmol photons$\cdot m^{-2}\cdot s^{-1}$, and continuous air bubbling. The maximum amount of protein [(42.8 ± 3.34) %] was accumulated at the exponential growth phase; the maximum amount of lipids [(39.9 ± 4.12) %], at the stationary one.

This work was carried out within the framework of IBSS state research assignment "Investigation of mechanisms of controlling production processes in biotechnological complexes with the aim of developing scientific foundations for production of biologically active substances and technical products of marine genesis" (No. 121030300149-0).

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РОСТ КРИПТОФИТОВОЙ МИКРОВОДОРОСЛИ *RHODOMONAS SALINA* (WISLOUCH) D. R. A. HILL & R. WETHERBEE, 1989 ПРИ РАЗНЫХ УСЛОВИЯХ КУЛЬТИВИРОВАНИЯ

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Исследовано влияние температуры и освещённости на удельную скорость роста и на накопление биомассы криптофитовой микроводоросли *Rhodomonas salina*; определены оптимальные условия её культивирования для получения максимальной биомассы. *R. salina* культивировали на питательной среде Конвея (в собственной модификации) при температуре (20 ± 1), (24 ± 1) и (28 ± 1) °C и освещённости 13, 67, 135 и 202 μмоль квантов·м$^{-2}$·с$^{-1}$. Показано, что увеличение температуры до значений выше оптимальных приводит к снижению скорости роста и биомассы микроводоросли. Существенных различий в показателях роста *R. salina* при освещённости 135 и 202 μмоль квантов·м$^{-2}$·с$^{-1}$ (значения μ — (0,69 ± 0,04) и (0,64 ± 0,02) сут$^{-1}$ соответственно) не зарегистрировано. Рост микроводоросли замедлялся при низкой освещённости (13 μмоль квантов·м$^{-2}$·с$^{-1}$) (значение μ — (0,33 ± 0,03) сут$^{-1}$). Максимальная биомасса [(3,74 ± 0,28) г·л$^{-1}$] получена при оптимальной температуре [(24 ± 1) °C] и освещённости 135 μмоль квантов·м$^{-2}$·с$^{-1}$. При оптимальных условиях культивирования максимальное накопление белка отмечено в экспоненциальной фазе роста (29 %), а липидов — в стационарной фазе (41 %).

Ключевые слова: микроводоросль *Rhodomonas salina*, культивирование, температура, освещённость, скорость роста, биомасса

Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 72–87
https://doi.org/10.21072/mbj.2022.07.2.06

UDC 581.526.323(292.471-751.2)

REVISION OF MACROPHYTOBENTHOS OF THE PROTECTED TERRITORIAL-AQUATIC COMPLEX OF THE BAKALSKAYA SPIT (THE BLACK SEA)

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Received by the Editor 27.04.2020; after reviewing 30.08.2020;
accepted for publication 03.03.2022;

The territorial-aquatic complex of the Bakalskaya Spit located in the northwestern Crimean Peninsula is a unique natural object, with a high variety of biota and landscapes. Despite the fact that it has the conservation status of a landscape park, its components undergo significant anthropogenic transformation. In this complex, structural and functional basis of the most coastal-marine and lagoonal biotopes is formed by microphytobenthos. However, the information on flora species composition and systematic structure was incomplete, and the latest changes in nomenclature and taxonomy adopted in phycology were not taken into account. In this regard, based on the data of our own research, we revised the macrophyte flora of marine and lagoonal water areas within the boundaries of the protected territorial-aquatic complex. As established, the flora includes 64 species: Chlorophyta, 23; Ochrophyta, 5; Rhodophyta, 31; and Tracheophyta, 5. The taxonomic structure includes 5 classes, 16 orders, 26 families, and 37 genera. According to the analysis of the ratio of ecological and floristic groups, 51.6 % are oligosaprobes. Short-vegetation species prevail (68.7 %). Among halobity groups, prevalence of marine and brackish-marine species was registered (in total, 90.7 %). A warm-water complex prevailed (45.3 %), but the contribution of cosmopolitan species characterized by eurybiontity was quite large (15.6 %). The rare fraction of the marine macrophyte flora includes 21 genera (32.8 %); habitats formed by macrophyte communities are listed in the EU Habitats Directive – Council Directive 92/43/EEC of 21 May, 1992 (codes 1110, 1150, and 1160). Considering high sozological significance of the territorial-aquatic complex analyzed, industrial sand mining must be stopped, since this is the main threat and a transforming factor. Moreover, the area of the complex has to be expanded, and the conservation status has to be risen (either as an independent object or as part of a large national park). It is also advisable to include the complex in the Emerald Network to provide additional opportunities for its protection and preservation. The presented results are the basis for additional hydrobotanical studies aimed at revealing the scale and vector of alterations in the composition and structure of macrophytobenthos and the entire ecosystem.

Keywords: Black Sea, Crimean Peninsula, Bakalskaya Spit, macrophytobenthos, species composition, revision

Due to specific physical and chemical properties of water in natural water bodies, dissolved substances and suspended matter are transferred to different distances altering hydrochemical parameters of the habitat of organisms and causing a direct physical transformation of the coastal zone.

In areas with accumulative shores, anthropogenic interference affects direction and thickness of loose sediment flows and rapidly changes configuration and size of coastal macroforms. Protected objects undergo transformation as well, though those seem to be located quite far from sources of negative effect. The same happened to the Bakalskaya Spit in the northwestern Crimean Peninsula. In recent years, due to sand mining at the Bakalskaya Bank, the situation has become so complicated that it even drew attention of representatives of the central media. For the scientific community, the Bakalskaya Spit – a unique natural phenomenon – is of great interest for a long time. So, it was reasonable and relevant to publish a special issue of the journal *Ecological Safety of Coastal and Shelf Zones of Sea* (2018, iss. 4), with the available data summarized and new material given by leading experts in various fields. Structural and functional basis of coastal-marine biotopes is formed by macrophytes; their thicket communities (first of all, seagrasses) slow down bottom and coastal abrasion, and this is extremely significant for the area. Importantly, the alterations affected the vegetation cover as well, but hydrobotanical information – neither compiled nor original – was not reflected in the special issue mentioned. Previously, NBG-NSC and IBSS staff carried out investigation on macrophytobenthos of the coastal-marine and lagoonal water areas of the protected territorial-aquatic complex of the Bakalskaya Spit (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010). Their results were not summarized, and data on the species composition were not published in full. At the same time, floristic lists are the basis of all further research for identification and preservation of biodiversity of the area and require regular revision (Yena, 2012). Taking into account the circumstances above and significant latest changes in nomenclature and taxonomy adopted in phycology, we aimed at summarizing the available data and revising the macrophyte flora of the coastal-marine and lagoonal water areas within the boundaries of the protected territorial-aquatic complex of the Bakalskaya Spit.

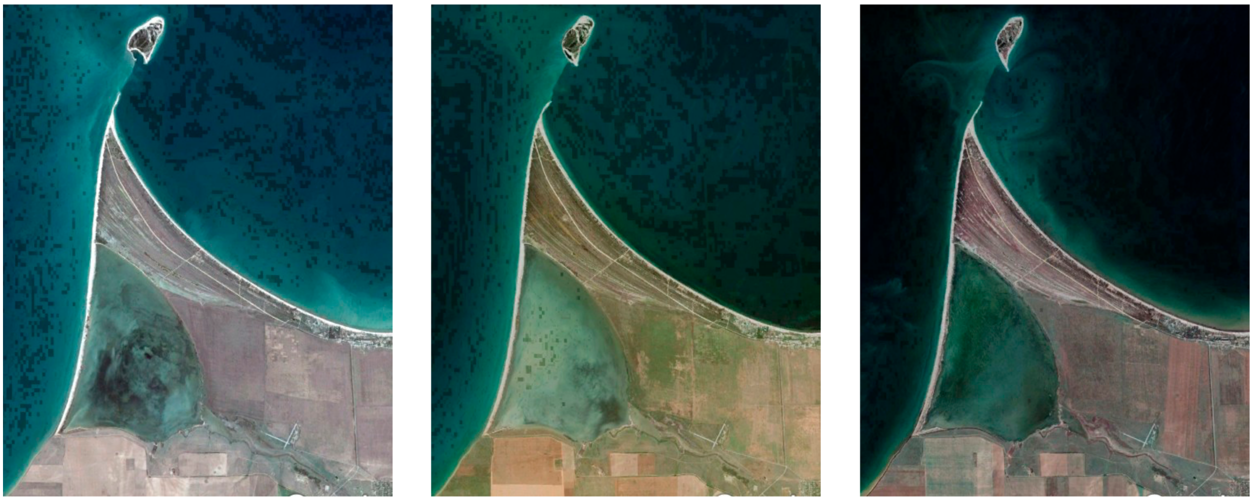
MATERIAL AND METHODS

Study area. A description of environmental conditions of the study area, along with data on localization of hydrobotanical sections and stations, is important for understanding composition and distribution of phytobiota, as well as for carrying out repeated investigations.

The accumulative Bakalskaya Spit is located in the northwestern Crimean Peninsula, in the Karkinitsky Bay of the Black Sea. It is formed by narrow western and wide eastern branches, with the lagoonal Bakalskoye Lake (Bakal) enclosed between them (Fig. 1). During our observations, its length from the base to the distal end (Peschany Cape) was about 8 km, but the macroform has an underwater continuation – in the form of a bank of the same name (Goryachkin & Kosyan, 2018 ; Zenkovich, 1960). The seabed is deep. The western branch of the spit and the seabed are composed of unsorted sediments with no signs of siltation (Zenkovich, 1960). An intense alongshore current and sediment flow (directed from the Tarkhankut Peninsula to the northeast) split near the Bakalskaya Spit. Previously, one branch leaving to the north formed a bank, and the second bending around Peschany Cape again deviated to the bedrock bank and increased both the spit tip and the wide eastern branch. At the same time, its steep underwater slope gradually flattened and silted up with depth and in the direction of the bedrock bank. In the study area, there are no natural solid soils. During the observation period, temperature of seawater surface layer reached +23…+25 °C, and mineralization reached 17.2 $g \cdot L^{-1}$ (Sadogurskiy, 2010); to date, the latter has slightly increased due to cessation of water discharge from rice fields (Goryachkin & Kosyan, 2018). On the eastern branch of the spit, in depressions between coastal ridges, swampy areas and small shallow isolated water bodies are localized. During the observation period, those had a depth up to 0.5 m, temperature +30…+34 °C, and mineralization 31–58 g·L^{-1}. Both branches adjoin an intensively abraded cliff (0.5–3 m *per* year) which is composed of clays and forms southern and eastern shores of the Bakalskoye Lake.

During the observation period, the lake, with a silty lakebed (silty-shelly near the sand embankment), had a depth 0.6–0.8 m, temperature +28…+34 °C, and mineralization 100 g·L^{-1} (salt deposits were observed), although the values of the latter vary widely over the years (Kurnakov et al., 1936 ; Shadrin et al., 2004). On the distal, extended spit part, a complex network of semi-isolated lagoonal water bodies was recorded, with a shell-sandy bottom (silty sometimes), depths up to 0.5 m, temperature +26…+29 °C, and mineralization 18–22 g·L^{-1} (Sadogurskiy, 2010).

a) configuration of 2003 **b) configuration of 2007** **c) chart of 2003–2007**



d) configuration of 2013 **e) configuration of 2016** **f) configuration of 2018**

Fig. 1. Dynamics of the Bakalskaya Spit configuration in 2003–2018 (a, b, and d–f) according to https://earth.google.com/web/ and a map of sampling points location in 2003–2007 (c) in accordance with (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010). On the map: ○ denotes stations where bottom vegetation was recorded and sampling was carried out in 2003; ● denotes stations where bottom vegetation was not registered in 2003; ★ denotes stations where bottom vegetation was recorded and sampling was carried out in 2007

The macroform was relatively stable (see Fig. 1a, b) during the observation period. However, against the backdrop of sea level rise and alongshore sediment flow weakening, researchers have already recorded an acceleration of abrasion, with the distal spit part tending to shift and separate (Klyukin, 2005). Sand mining which became industrial in 2015 exacerbated the sediment deficit and catastrophically accelerated the process (see Fig. 1d–f). To date, a 1-km wide channel separates the newly formed Peschany Island from the spit body which has decreased down to 5.7 km; this resulted in a complete change in litho- and hydrodynamic conditions in the area, and its consequences have not been studied (Goryachkin & Kosyan, 2018).

Back in 1972, coastal waters near the Bakalskaya Spit, with an area of 410 hectares, received the status of a natural monument (coastal aquatic complex). In 2000, with adding 300 hectares of the spit itself and 810 hectares of the lake (in total, 1,520 hectares), the object was turned into a territorial-aquatic one. Its status was changed, and it is known as the regional landscape park "Bakalskaya Spit" (since 2018, in fact, it is in the status of a landscape and recreational park). The territorial-aquatic complex is part of both IBA (Important Bird and Biodiversity Area) by BirdLife International and Ramsar wetlands of international importance "Karkinitsky and Dzharylgachsky bays" (Ramsar List, 2020).

Material was sampled in summer according to the generally accepted hydrobotanical method (Kalugina, 1969). In 2003, dives were carried out with surface-supplied equipment at 19 stations in marine and lagoonal areas (*inter alia* the Bakalskoye Lake), and 95 hydrobotanical samples were taken. In 2007, 25 samples were taken manually at 5 stations (see Fig. 1c). A visual survey (with no sampling) of the seabed was carried out down to a depth of 12 m. Thus, stations and visual surveys span all the benthal zones and most of a depth spectrum where macroscopic vegetation cover is recorded in the study area.

The object of the study is benthic macrophytes. Their nomenclature for the divisions Chlorophyta, Ochrophyta, Rhodophyta, and Tracheophyta is given according to AlgaeBase (2020); the names of taxa authors are abbreviated as standard, in accordance with IPNI recommendations (The International Plant Names Index, 2020). When needed, we added nomenclatural combinations from biological keys used as basic guidelines for identification of macroalgae (Zinova, 1967 ; Opredelitel' vysshikh rastenii Ukrainy, 1987). The vegetation period duration and phytogeographic characteristics of algae are given according to A. Kalugina-Gutnik (1975), and saprobiological and halobic characteristics are presented in accordance with A. Kalugina-Gutnik and T. Eremenko (unpublished data) – with clarifications concerning seagrasses (Sadogurskiy, 2013 ; Sadogurskiy & Belich, 2003). Given the small size of the Black Sea, as well as interconnection and interdependence of some of its coastal areas, identification of a rare fraction was carried out taking into account all published national and international phytosozological lists on macrophytobiota.

RESULTS AND DISCUSSION

Within the boundaries of the protected territorial-aquatic complex of the Bakalskaya Spit, macroscopic benthic vegetation with a biomass 0.1–2.7 $kg \cdot m^{-2}$ developed on soft soils during the observation period. In the sea, the most mobile sandy and shell-sandy sediments (especially near convex sections of the coast along the western branch and on the steepest underwater slopes of the eastern branch) had no permanent vegetation cover. From a depth 4–5 m, a community of unattached form of *Phyllophora crispa* (Hudson) P. S. Dixon, 1964 was recorded there. With a local decrease in hydrodynamics, small accumulations are found much closer to the coast as well (up to the pseudolittoral zone).

Inactive silty soils in the bay, near the eastern branch, were covered with *Zostera marina* Linnaeus, 1753 communities, but with increasing depth and decreasing light intensity, seagrasses contributed less to the composition of the vegetation cover, and the unattached *Ph. crispa* contributed more. In inland hyperhaline water bodies of the eastern branch of the spit and in the Bakalskoye Lake, communities of *Cladophora siwaschensis* K. I. Meyer, 1922 and *Ruppia maritima* Linnaeus, 1753 prevailed. In the pseudolittoral and the shallowest areas of the sublittoral of water bodies in the distal spit part, semi-isolated from the sea by accumulative macroforms, *Ulva maeotica* (Proshkina-Lavrenko) P. M. Tsarenko, 2011 communities prevailed. With growing connection with the sea, increasing depth, and decreasing amplitude and duration of surge oscillations (with water redistribution through the channel system), the pseudolittoral was less and less pronounced in these lagoons, while in the sublittoral, various macroalgal communities were replaced by thickets of *Zannichellia palustris* subsp. *major* (Hartm.) Van Ooststroom & Reichgelt and *Zostera noltei* Hornemann, 1832. In total, 13 communities were registered within the boundaries of the object; out of them, 10 were attributed to inland water bodies, including 6 to the distal spit part. There, on a small area in the system of lagoons, due to their different isolation from the sea, a spatial complex gradient of the environment was formed; along it, mineralization, temperature, water level, and granulometric composition of the substrate changed concomitantly. Importantly, in the marine area, a small fragment of an anthropogenic solid substrate covered with macrophytes was examined in 2007. Among other things, this contributed to expansion of the species list given below but did not significantly affect either general characteristics of the flora or vegetation of the studied object.

When specifying the conservation status of taxa in the species list, the following designations are used: ◆ – European Red List of Vascular Plants (Bilz et al., 2011); ● – Convention on the Conservation of European Wildlife and Natural Habitats (Appendix I) (1979); ○ – Convention for the Protection of the Mediterranean Sea Against Pollution – Barcelona Convention, 1976 (Proposal for a Council Decision, 2009); ✱ – Red Data Book of Ukraine (2009); ✚ – Red Book of the Russian Federation (2008); ◻ – Red Data Book of the Republic of Bulgaria (2015); ★ – Black Sea Red Data Book (1999); ✪ – Black Sea Red Data List (1997); ▲ – Red Book of the Republic of Crimea (2015); ❖ – Red Data Book of Priazovsky Region (2012). The following abbreviations are used: LP, lagoonal pseudolittoral; LS, lagoonal sublittoral; MP, marine pseudolittoral; and MS, marine sublittoral.

CHLOROPHYTA Rchb.

Ulvophyceae Mattox et K. D. Stewart

Bryopsidales J. H. Schaffn.

Bryopsidaceae Bory

Bryopsis J. V. Lamour.

***Bryopsis hypnoides* J. V. Lamour.** ◻: MS (Sadogurskiy, 2010).

Cladophorales Haeckel

Cladophoraceae Wille

Chaetomorpha Kütz.

***Chaetomorpha aërea* (Dillwyn) Kütz.** [*Chaetomorpha chlorotica* (Mont.) Kütz.; *Chaetomorpha crassa* (C. Agardh) Kütz.]: LS (Sadogurskiy, 2010).

***Chaetomorpha gracilis* Kütz.**: LS (Sadogurskiy, 2010).

***Chaetomorpha linum* (O. F. Müll.) Kütz.**: LS, MS (Sadogurskiy, 2010).

Cladophora Kütz.

***Cladophora albida* (Nees) Kütz.** [*Cladophora albida* (Huds.) Kütz.]: LS, MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Cladophora laetevirens* (Dillwyn) Kütz.**: LS, MP (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Cladophora liniformis* Kütz.**: MP (Evstigneeva & Tankovskaya, 2011).

***Cladophora sericea* (Huds.) Kütz.**: LS, MS (Sadogurskiy, 2010).

***Cladophora siwaschensis* K. I. Mey. ▲**: LP, LS predominantly in the Bakalskoye Lake (Sadogurskiy, 2010). Note: the author of this nomenclature combination incorrectly indicated C. J. Meyer (AlgaeBase, 2020), while the standard abbreviation for K. I. Meyer (1881–1965) is K. I. Mey. (The International Plant Names Index, 2020).

***Cladophora vadorum* (Aresch.) Kütz. ✱**: MP (Evstigneeva & Tankovskaya, 2011).

Rhizoclonium Kütz.

***Rhizoclonium riparium* (Roth) Harv.** [*Rhizoclonium implexum* (Dillwyn) Kütz.]: LS (Sadogurskiy, 2010).

Ulotrichales Borzi

Ulotrichaceae Kütz.

Ulothrix Kütz.

***Ulothrix flacca* (Dillwyn) Thur.**: LP, LS (Sadogurskiy, 2010).

Ulvales F. F. Blackman et Tansley

Phaeophilaceae D. F. Chappell, C. J. O'Kelly, L. W. Wilcox et G. L. Floyd

Phaeophila Hauck

***Phaeophila dendroides* (P. Crouan et H. Crouan) Batters**: LS (Sadogurskiy, 2010).

Ulvaceae J. V. Lamour. ex Dumort.

Ulva L.

***Ulva clathrata* (Roth) C. Agardh** [*Enteromorpha clathrata* (Roth) Grev.]: LS (Sadogurskiy, 2010).

***Ulva intestinalis* L.** [*Enteromorpha intestinalis* (L.) Link, nom. illeg.?]: LP, LS, MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Ulva linza* L.** [*Enteromorpha linza* (L.) J. Agardh; *Enteromorpha ahlneriana* Bliding, nom. illeg.]: MP (Evstigneeva & Tankovskaya, 2011).

***Ulva maeotica* (Proshk.-Lavr.) P. M. Tsarenko** [*Enteromorpha maeotica* Proshk.-Lavr.]. **✱▲**: LP, MP (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Ulva prolifera* O. F. Müll.** [*Enteromorpha prolifera* (O. F. Müll.) J. Agardh]: LS (Sadogurskiy, 2010).

Ulvellaceae Schmidle

Epicladia Reinke

***Epicladia perforans* (Huber) R. Nielsen** [*Entocladia perforans* (Huber) Levring]: MP (Evstigneeva & Tankovskaya, 2011).

Ulvella P. Crouan et H. Crouan

***Ulvella lens* P. Crouan et H. Crouan**: LS (Sadogurskiy, 2010).

***Ulvella leptochaete* (Huber) R. Nielsen, C. J. O'Kelly et B. Wysor** [*Ectochaete leptochaete* (Huber) Wille]: LS, MS (Sadogurskiy, 2010).

***Ulvella scutata* (Reinke) R. Nielsen, C. J. O'Kelly et B. Wysor** [*Pringsheimiella scutata* (Reinke) Marchew.]: LS, MS (Sadogurskiy, 2010).

***Ulvella viridis* (Reinke) R. Nielsen, C. J. O'Kelly et B. Wysor** [*Entocladia viridis* Reinke]. ✪: LS, MS (Sadogurskiy, 2010).

OCHROPHYTA Caval.-Sm.

Phaeophyceae Kjellm.

Ectocarpales Bessey

Acinetosporaceae G. Hamel ex J. Feldmann

Feldmannia Hamel

***Feldmannia lebelii* (Aresch. ex P. Crouan et H. Crouan) Hamel**: MP (Evstigneeva & Tankovskaya, 2011).

Chordariaceae Grev.

Stilophora J. Agardh

***Stilophora tenella* (Esper) P. C. Silva** [*Stilophora rhizodes* (Ehrh.) J. Agardh, nom. illeg.?]. ✱✚▲: MS (Sadogurskiy, 2010).

Fucales Bory

Sargassaceae Kütz.

Treptacantha Kütz.

***Treptacantha barbata* (Stackh.) S. Orellana et M. Sansón** [*Cystoseira barbata* (Stackh.) C. Agardh; *Cystoseira barbata* (Gooden. et Woodw.) C. Agardh, nom. illeg.]. ★✪○▲: MP (Evstigneeva & Tankovskaya, 2011). Note: is not a typical inhabitant of the Bakalskaya Spit; was recorded in small quantity on a solid substrate of anthropogenic origin.

Sphacelariales Mig.

Cladostephaceae Oltm.

Cladostephus C. Agardh

***Cladostephus spongiosum* f. *verticillatum* (Lightf.) Prud'homme** [*Cladostephus verticillatus* (Lightf.) C. Agardh, nom. illeg.]. ✱: MP (Evstigneeva & Tankovskaya, 2011).

Sphacelariaceae Decne.

Sphacelaria Lyngb.

***Sphacelaria cirrosa* (Roth) C. Agardh**: MS (Sadogurskiy, 2010).

RHODOPHYTA Wettst.

Florideophyceae Cronquist

Acrochaetiales Feldmann

Acrochaetiaceae Fritsch ex W. R. Taylor

Acrochaetium Nägeli

***Acrochaetium parvulum* (Kylin) Hoyt** [*Kylinia parvula* (Kylin) Kylin]: MS (Sadogurskiy, 2010).

***Acrochaetium secundatum* (Lyngb.) Nägeli** [*Kylinia virgatula* (Harv.) Papenf.; *Kylinia secundata* (Lyngb.) Papenf.]: MP (Evstigneeva & Tankovskaya, 2011).

Colaconematales J. T. Harper et G. W. Saunders

Colaconemataceae J. T. Harper et G. W. Saunders

Colaconema Batters

***Colaconema savianum* (Menegh.) R. Nielsen** [*Acrochaetium savianum* (Menegh.) Nägeli]: MS (Sadogurskiy, 2010).

Corallinales P. C. Silva et H. W. Johans.

Corallinaceae J. V. Lamour.

Hydrolithon (Foslie) Foslie

***Hydrolithon farinosum* (J. V. Lamour.) Penrose et Y. M. Chamb.** [*Melobesia farinosa* J. V. Lamour.]: MP (Evstigneeva & Tankovskaya, 2011).

Pneophyllum Kütz.

***Pneophyllum confervicola* (Kütz.) Y. M. Chamb.** [*Melobesia minutula* Foslie]: LS, MS (Sadogurskiy, 2010).

***Pneophyllum fragile* Kütz.** [*Melobesia lejolisii* Rosan.]: LS, MS (Sadogurskiy, 2010).

Gigartinales F. Schmitz

Phyllophoraceae Willk.

Phyllophora Grev.

***Phyllophora crispa* (Huds.) P. S. Dixon** [*Phyllophora nervosa* (DC.) Grev.]. ✚★✪▲: MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

Hapalidiales W. A. Nelson, J. E. Sutherland, T. J. Farr et H. S. Yoon

Hapalidiaceae J. E. Gray

Phymatolithon Foslie

***Phymatolithon lenormandii* (Aresch.) W. H. Adey** [*Lithothamnion lenormandii* (Aresch.) Foslie]: LS, MS (Sadogurskiy, 2010).

Peyssonneliales D. M. Krayesky, S. Fredericq et J. N. Norris

Peyssonneliaceae Denizot

Peyssonnelia Decn.

***Peyssonnelia dubyi* P. Crouan et H. Crouan**: MS (Sadogurskiy, 2010).

Ceramiales Nägeli

Callithamniaceae Kütz.

Callithamnion Lyngb.

***Callithamnion granulatum* (Ducluz.) C. Agardh. ✱**: LS (Sadogurskiy, 2010).

Ceramiaceae Dumort.

Ceramium Roth

***Ceramium arborescens* J. Agardh**: LS, MS (Sadogurskiy, 2010). Note: earlier, *C. arborescens* was considered a synonym for *C. rubrum* and, accordingly, was not indicated for water areas within the boundaries of the protected object; however, there was a corresponding remark on its registration (Sadogurskiy, 2010).

***Ceramium deslongchampsii* Chauv. ex Duby**: MP (Evstigneeva & Tankovskaya, 2011).

***Ceramium diaphanum* (Lightf.) Roth** [*Ceramium tenuissimum* (Lyngb.) J. Agardh]: LS, MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Ceramium siliquosum* var. *elegans* (Roth) G. Furnari** [*Ceramium diaphanum* var. *elegans* (Roth) Roth; *Ceramium elegans* Ducl.]: LS, MS (Sadogurskiy, 2010).

***Ceramium virgatum* Roth** [*Ceramium pedicellatum* (Duby) J. Agardh, nom. illeg.; *Ceramium rubrum* (Huds.) C. Agardh, nom. illeg.]: LS, MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

Dasyaceae Kütz.

Dasya C. Agardh

***Dasya apiculata* (C. Agardh) J. Agardh** [*Dasyopsis apiculata* (C. Agardh) Zinova; *Eupogodon apiculatus* (C. Agardh) P. C. Silva]. ✱▲: MS (Sadogurskiy, 2010).

***Dasya baillouviana* (S. G. Gmel.) Mont.** [*Dasya pedicellata* (C. Agardh) C. Agardh]. ✪: LS, MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

Rhodomelaceae Horan.

Chondria C. Agardh

***Chondria capillaris* (Huds.) M. J. Wynne** [*Chondria tenuissima* (Gooden. et Woodw.) C. Agardh]: LS, MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Chondria dasyphylla* (Woodw.) C. Agardh**: MP (Evstigneeva & Tankovskaya, 2011).

Laurencia J. V. Lamour.

***Laurencia coronopus* J. Agardh.** ✱▲: MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Laurencia obtusa* (Huds.) J. V. Lamour.** ✪: MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

Lophosiphonia Falkenb.

***Lophosiphonia obscura* (C. Agardh) Falkenb.**: LS (Sadogurskiy, 2010).

Osmundea Stackh., nom. rejic.

***Osmundea hybrida* (DC.) K. W. Nam** [*Laurencia hybrida* (DC.) Lenorm., nom. illeg.?]. ✱▲: LS (Sadogurskiy, 2010).

Palisada K. W. Nam

***Palisada thuyoides* (Kütz.) Cassano, Sentíes, Gil-Rodríguez et M. T. Fujii** [*Laurencia paniculata* J. Agardh]: LS (Sadogurskiy, 2010).

Polysiphonia Grev.

***Polysiphonia denudata* (Dillwyn) Grev. ex Harv.** [*Polysiphonia denudata* (Dillwyn) Kütz., nom. illeg.?]: LS, MS (Sadogurskiy, 2010).

***Polysiphonia elongata* (Huds.) Spreng.** [*Polysiphonia elongata* (Huds.) Harv., nom. illeg.?]: MS (Sadogurskiy, 2010).

***Polysiphonia opaca* (C. Agardh) Moris et De Not.** [*Polysiphonia opaca* (C. Agardh) Zanardini, nom. illeg.?]: LS, MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

Vertebrata Gray

***Vertebrata fucoides* (Huds.) Kuntze** [*Polysiphonia fucoides* (Huds.) Grev.; *Polysiphonia nigrescens* (Dillwyn) Grev., nom. illeg.?]: LS, MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Vertebrata subulifera* (C. Agardh) Kuntze** [*Polysiphonia subulifera* (C. Agardh) Harv.]: MP, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

Wrangeliaceae J. Agardh

Spermothamnion Aresch.

***Spermothamnion strictum* (C. Agardh) Ardiss.** ✪: MP (Evstigneeva & Tankovskaya, 2011).

Stylonematophyceae H. S. Yoon, K. M. Müller, R. G. Sheath, F. D. Ott et D. Bhattacharya

Stylonematales K. M. Drew

Stylonemataceae K. M. Drew

Chroodactylon Hansg.

***Chroodactylon ornatum* (C. Agardh) Basson** [*Asterocytis ramosa* (Thwaites) Gobi ex F. Schmitz]. ✱: LP, LS, MS (Sadogurskiy, 2010).

TRACHEOPHYTA Sinnott ex Cavalier-Smith.

Monocots

Alismatales R. Br. ex Bercht. et J. Presl

Ruppiaceae Horan., nom. cons.

Ruppia L.

***Ruppia maritima* L.** ◆▲❖: LS, *inter alia* in the Bakalskoye Lake (Sadogurskiy, 2010).

Potamogetonaceae Bercht. et J. Presl

Stuckenia Börner

***Stuckenia pectinata* (L.) Börner** [*Potamogeton pectinatus* L.]: LS (Sadogurskiy, 2010).

Zannichellia L.

***Zannichellia palustris* subsp. *major* (Hartm.) Ooststr. et Reichg.** [*Z. major* Boenn.]. ▲❖: LS (Sadogurskiy, 2010).

Zosteraceae Dumort., nom. cons.

Zostera L.

***Zostera marina* L.** ●★✪▲❖: MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

***Zostera noltei* Hornem.** [*Z. minor* (Cavol.) Nolte ex Rchb.; *Z. nana* Roth., nom. illeg.]. ★✪▲❖: LS, MS (Evstigneeva & Tankovskaya, 2011 ; Sadogurskiy, 2010).

Thus, the macroflora of marine and lagoonal water areas within the boundaries of the territorial-aquatic complex of the Bakalskaya Spit includes 64 species (hereinafter, intraspecific taxa are taken into account as well): Chlorophyta, 23 (35.94 %); Ochrophyta, 5 (7.81 %); Rhodophyta, 31 (48.44 %); and Tracheophyta, 5 (7.81 %). The smallest number of species was recorded for inland water bodies with the highest mineralization and water temperature; the minimum number (*Cladophora siwaschensis* and *Ruppia maritima* alone) was registered in the Bakalskoye Lake and in shallow water bodies between relatively young swells of the eastern branch of the spit. In the water bodies of the older part of this branch (closer to the lake), with greater depth and lower temperature and mineralization, the species composition was more diverse (6 species). In the lagoons of the distal spit part – with a rise in the sea effect and a decline in temperature and mineralization – the number of species from the western, most isolated water basin to the eastern increased 14 to 34. In total, in the network of semi-isolated lagoonal water bodies, the level of species diversity of macrophytes was lower (37 species) but comparable with that in adjacent marine areas (45 species).

In coastal-marine biotopes, macroalgae develop mainly epiphytically. The richest species composition of epiphytes (and some endophytes) was noted for *Phyllophora crispa* thalli; together with animal population, the total weight of fouling could exceed the weight of the phorophyte. In this regard, the role of mollusc shells and seagrass shoots is lower here. In lagoons, on the contrary, this is the main substrate for macroalgae development. *Cladophora siwaschensis* should be mentioned as well: in the central Bakalskoye Lake, it forms free-floating accumulations which along the periphery are attached to bottom sediments of self-depositing salt.

The taxonomic structure of the macrophyte flora includes 4 divisions, 5 classes, 16 orders, 26 families, and 37 genera (Table 1). If compared with similar structures of Crimean territorial-aquatic nature reserves (being a fairly large object, the landscape park approaches them in terms of its area), then, quite expectedly, the greatest similarity can be traced to indicators established for the Lebyazhye Islands (Sadogurskiy et al., 2019). Interestingly, it can be traced despite the difference in the total number of species (which is due to a lesser degree of study as well) and the absence of charophytes. This is explained not so much by geographical proximity, but by an almost identical set of coastal-marine biotopes, including a series of lagoons isolated from the sea to varying degrees.

Table 1. Taxonomic structure of the macrophyte flora in the coastal-marine and lagoonal water areas of the territorial-aquatic complex of the Bakalskaya Spit

Division	Taxa number by divisions, units / %				
	Classes	Orders	Families	Genera	Species
Chlorophyta	1 / 20.0	4 / 25.0	6 / 23.1	9 / 24.3	23 / 35.9
Ochrophyta	1 / 20.0	3 / 18.8	5 / 19.2	5 / 13.5	5 / 7.8
Rhodophyta	2 / 40.0	8 / 50.0	12 / 46.2	19 / 51.4	31 / 48.4
Tracheophyta	1 / 20.0	1 / 6.3	3 / 11.5	4 / 10.8	5 / 7.8
In total	**5 / 100.0**	**16 / 100.0**	**26 / 100.0**	**37 / 100.0**	**64 / 100.0**

Analysis of the ecological and floristic groups shows that oligosaprobes make up more than half of the species list (Fig. 2).

By the vegetation period duration, short-vegetative (annual and summer seasonal) species prevail. Out of halobity groups, prevalence of marine and brackish-marine species is registered. Among phytogeographic groups united in two complexes, the warm-water one prevails. At the same time, the contribution of cosmopolitan species characterized by eurybiontity was quite large there, the same as near the Lebyazhye Islands. In terms of a set of ecological and floristic characteristics, the flora of the studied object is also very similar to that of the Lebyazhye Islands (Sadogurskiy et al., 2019). Of the obvious differences, we should note the absence of winter seasonal species (which are not uncommon even in summer) and freshwater ones. The latter, together with the absence of charophytes, is due to the following fact: during the observation periods, there were no desalinated coastal-marine and lagoonal water areas on the spit (importantly, to date, those are no longer present near the Lebyazhye Islands as well).

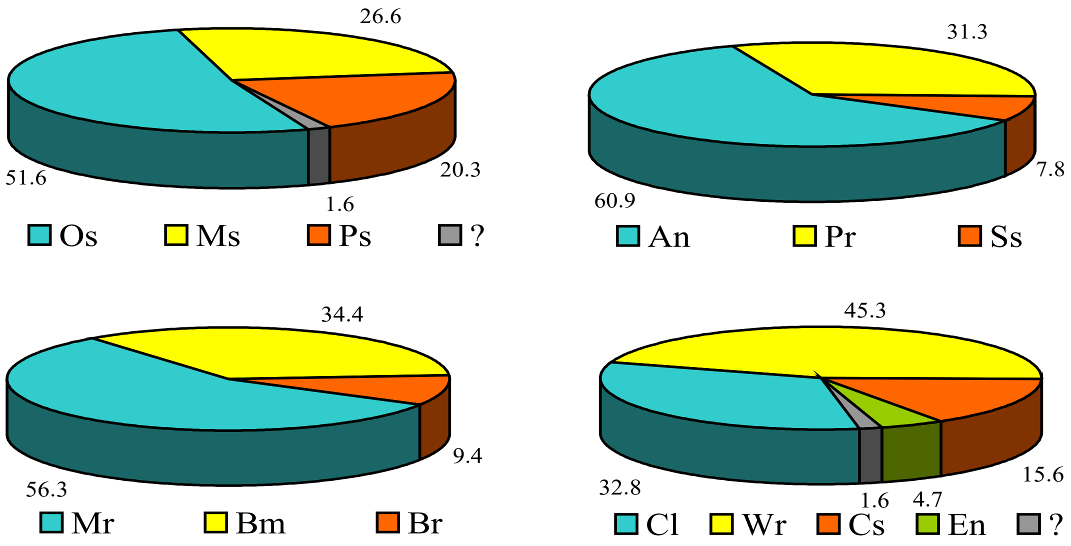


Fig. 2. Ecological and floristic characteristics of the macrophyte flora in the coastal-marine and lagoonal water areas of the territorial-aquatic complex of the Bakalskaya Spit (ratios of groups are shown in %). Saprobiological groups: Os, oligosaprobes; Ms, mesosaprobes; and Ps, polysaprobes. Groups in terms of vegetation period duration: An, annual; Pr, perennial, and Ss, summer seasonal. Halobity: Mr, marine; Bm, brackish-marine; and Br, brackish. Phytogeographic groups: Cl, cold-water; Wr, warm-water; Cs, cosmopolitans; and En, endemics. ? denotes lack of data

The rare fraction of the macrophyte flora in the territorial-aquatic complex of the Bakalskaya Spit includes 21 species (32.81 %). Within its boundaries, there are coastal-marine biotopes which are subject to special protection in accordance with the EU Habitats Directive – Council Directive 92/43/EEC of 21 May, 1992 (biotope codes: 1110, sandbanks which are slightly covered by sea water all the time; 1150, coastal lagoons; and 1160, large shallow inlets and bays) (Interpretation Manual of European Union Habitats, 2007).

Considering high regional and international conservation status of the spot and significant diversity and rarity of its phytobiota, ten years ago we already recommended to include it in the national natural park as an integral territorial-aquatic core, along with the "Lebyazhye Islands" reserve and "Karkinitsky" nature reserve (Sadogurskiy, 2009, 2010 ; Sadogurskiy et al., 2009). The national natural park was expected to be one of the key objects of ecological networks of various ranks in the Northern Black Sea Region: it was supposed to increase the area of absolutely protected territories and ensure the continuity of the international Sea of Azov–Black Sea eco-corridor. Unfortunately, these recommendations have not been implemented, but it is gratifying that those were updated (Milchakova & Alexandrov, 2018). Considering the anthropogenic disturbance of the lithodynamic balance which, apparently, resulted in the transformation of all the components of the protected territorial-aquatic complex, it is necessary to carry out a new comprehensive survey, *inter alia* a large-scale hydrobotanical study, with re-sampling at previously investigated points (at least, at those preserved on the map). But even in its current state, with the available level of information, the object meets the criteria and deserves to be included in the Emerald Network – as part of the Pan-European Ecological Network. It is aimed at uniting and effective management of the spots that are of particular value for the conservation of biota species and natural biotopes (Area of Special Conservation Interest, ASCI) in Eastern Europe.

Conclusion. After the nomenclatural and taxonomic revision, 64 macrophyte species were recorded in the marine and lagoonal water areas of the protected territorial-aquatic complex of the Bakalskaya Spit: Chlorophyta, 23; Ochrophyta, 5; Rhodophyta, 31; and Tracheophyta, 5. The taxonomic structure of the macrophyte flora includes 5 classes, 16 orders, 26 families, and 37 genera. Almost one third of the floristic list belongs to the rare fraction, and biotopes formed by macroalgae and seagrasses are subject to special protection in accordance with international environmental documents. Considering high sozological significance of the territorial-aquatic complex and accelerating degradation of the spit, urgent measures are required. First of all, it is necessary to eliminate one of the key threats – to stop sand mining. It would be relevant to expand the area of the territorial-aquatic complex and to raise its conservation status – either as an independent object or as part of a larger object in the rank of a national park or reserve, since those have real management and security structures. Moreover, it is advisable to include the area in the Emerald Network, since this will provide new opportunities and additional arguments for its protection and preservation. The results of this publication are the basis for further hydrobotanical studies with re-sampling: this will help in revealing the scale and vector of alterations in the composition and structure of macrophytobenthos and the entire ecosystem.

The work was carried out within the framework of state research assignment of NBG-NSC (No. AAAA-A19-119091190049-6) and IBSS (No. 121030300149-0).

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РЕВИЗИЯ МАКРОФИТОБЕНТОСА ЗАПОВЕДНОГО ТЕРРИТОРИАЛЬНО-АКВАЛЬНОГО КОМПЛЕКСА БАКАЛЬСКОЙ КОСЫ (ЧЁРНОЕ МОРЕ)

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Территориально-аквальный комплекс Бакальской косы, расположенной на северо-западе Крымского полуострова, представляет собой уникальный природный объект, который отличается высоким разнообразием биоты и ландшафтов. Несмотря на то, что он имеет статус ландшафтного парка, его компоненты претерпевают существенную антропогенную трансформацию. Структурный и функциональный фундамент большинства прибрежно-морских и лагунных биотопов комплекса формирует макрофитобентос. Однако информация о видовом составе и систематической структуре их флоры была неполной и не учитывала номенклатурно-таксономические изменения, принятые в фикологии в последние годы. В связи с этим по результатам собственных исследований выполнена ревизия флоры макрофитов морских и лагунных акваторий в границах заповедного территориально-аквального комплекса. Установлено, что она включает 64 вида: Chlorophyta — 23, Ochrophyta — 5, Rhodophyta — 31, Tracheophyta — 5. Таксономическая структура включает 5 классов, 16 порядков, 26 семейств, 37 родов. Анализ соотношения эколого-флористических группировок показал, что 51,6 % составляют олигосапробы. Преобладают коротковегетирующие виды (68,7 %). Среди галобных группировок доминируют морские и солоноватоводно-морские виды (суммарно 90,7 %). Преобладает тепловодный комплекс (45,3 %), но достаточно велик вклад видов-космополитов, отличающихся эврибионтностью (15,6 %). Раритетная фракция насчитывает 21 вид (32,8 %); макрофиты формируют основу биотопов, подлежащих особой охране согласно Директиве ЕС о местообитаниях (Council Directive 92/43/EEC; коды 1110, 1150 и 1160). С учётом высокого созологического значения территориально-аквального комплекса необходимо прекратить промышленную добычу песка (она представляет основную угрозу и является трансформирующим фактором), а также увеличить площадь комплекса и повысить заповедный статус (либо как самостоятельного объекта, либо в составе крупного национального парка). Целесообразно включение территориально-аквального комплекса в структуру экологической сети Emerald для получения дополнительных возможностей для его защиты и сохранения. Представленные результаты являются основой для повторных гидроботанических исследований, которые позволят выявить масштаб и вектор изменений в составе и структуре макрофитобентоса и экосистемы в целом.

Ключевые слова: Чёрное море, Крымский полуостров, Бакальская коса, макрофитобентос, видовой состав, ревизия

1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 88–97
https://doi.org/10.21072/mbj.2022.07.2.07

UDC [574.587:591.54](262.54.04)

MEROPLANKTON TAXONOMIC COMPOSITION AND SEASONAL DYNAMICS IN THE SEAPORT KAVKAZ AREA, KERCH STRAIT

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Received by the Editor 12.10.2020; after reviewing 22.10.2020;
accepted for publication 03.03.2022; published online 07.06.2022.

Meroplankton taxonomic composition, distribution of abundance, and seasonal population dynamics were studied in the northern Kerch Strait (the seaport Kavkaz area). For the study, zooplankton material was sampled in different seasons in 2017–2019 in the seaport area and outside it. Zooplankton was sampled totally throughout the water column at depths 5 to 8 m with a large Juday net (opening diameter of 37 cm and mesh size of 120 μm). The samples were fixed in 2–4 % neutral formaldehyde and processed in the laboratory by the conventional method. In total, 32 meroplankton taxa were found. As noted, meroplankton density in the polluted area is not inferior to that of the relatively clean area and provides sufficient reproductive potential there. In the seaport area, barnacle (cirripedian) and mollusc larvae were widespread; outside, barnacle and bivalve larvae were common. The basis of meroplankton pool was formed by species tolerant to water eutrophication and bottom sediment sulfide contamination – larvae of gastropod *Bittium reticulatum*, larvae of bivalves *Abra segmentum*, *Cerastoderma glaucum* (in summer), and *Mytilaster lineatus* (in early autumn), and larvae of barnacle *Amphibalanus improvisus* (in spring). The seasonal dynamics of meroplankton in the study area revealed a summer–autumn increase in abundance which is common for the Black Sea water. The period of the greatest zoobenthos spawning and larvae release into the pelagial lasted April to October. Three density peaks were recorded (April, June, and September), and those were most pronounced in the seaport area in spring and in the open area in early autumn.

Keywords: meroplankton, abundance, seasonal dynamics, Kerch Strait

The Kerch Strait with the adjacent waters of the Sea of Azov–Black Sea basin is the most significant transport artery, a zone of intensive navigation, a spot of port complexes functioning, and a fishing area (Budnichenko & Firulina, 1998 ; Fashchuk & Petrenko, 2008). Location of large terminals and ports, construction of the Tuzla dam, soil dumping, transshipment of liquid and dry cargo, and oil pollution resulted in a disruption of natural sedimentation process, changes in water dynamics, and contamination of bottom sediments; moreover, those became key factors of the alteration in the structure of macrozoobenthos– the basis of the food supply for commercial fish in the strait area (Eremeev et al., 2008 ; Fashchuk et al., 2012). In the northern Kerch Strait (the Chushka Spit), the seaport Kavkaz is located – the second port in terms of cargo turnover in the Sea of Azov–Black Sea basin. Until 2018–2020, passenger and car ferry services to the seaport of Crimea were carried out there, and freight trains were transported. In November 2007, during a severe storm in the Kerch Strait, merchant ships were damaged, about a thousand tons of oil products spilled into the water, and a bulker with sulfur sank near the seaport Kavkaz. Significant water pollution negatively affected the development of psammophilic bottom communities near the western coast of the Chushka Spit (Golovkina & Nabozhenko, 2012). Based on the analysis of current and retrospective distribution of macrozoobenthos in the Kerch Strait, its species structure, and indicators of the development of bottom communities, researchers assessed alterations in bottom communities under the anthropogenic load (Golovkina & Nabozhenko, 2012 ; Samyshev, 2004 ; Fashchuk et al., 2012). However, for the seaport Kavkaz area, with its chronic technogenic pollution, there are no such data.

It is well known that the state of larvae of benthic invertebrates (meroplankton) is one of the key indicators of benthos state, taxonomic composition, and density (Kulikova et al., 2017). At the same time, there was no full-season monitoring of the dynamics of meroplankton structure and its current state in this water area.

The aim of our work is to study meroplankton species composition and abundance distribution for the seaport Kavkaz and to analyze seasonal dynamics of meroplankton abundance.

MATERIAL AND METHODS

The material for the study was zooplankton sampled in different seasons of 2017–2019 in the seaport Kavkaz and outside it (Fig. 1). Zooplankton was sampled totally with a large Juday net (opening diameter of 37 cm; mesh size of 120 μm) at depths 5 to 8 m. The samples were fixed in 2–4 % neutral formaldehyde and processed under laboratory conditions by the conventional method. Mollusc larvae were preliminarily isolated from total zooplankton samples and fixed in 70 % ethanol. A total of 56 plankton samples were analyzed.

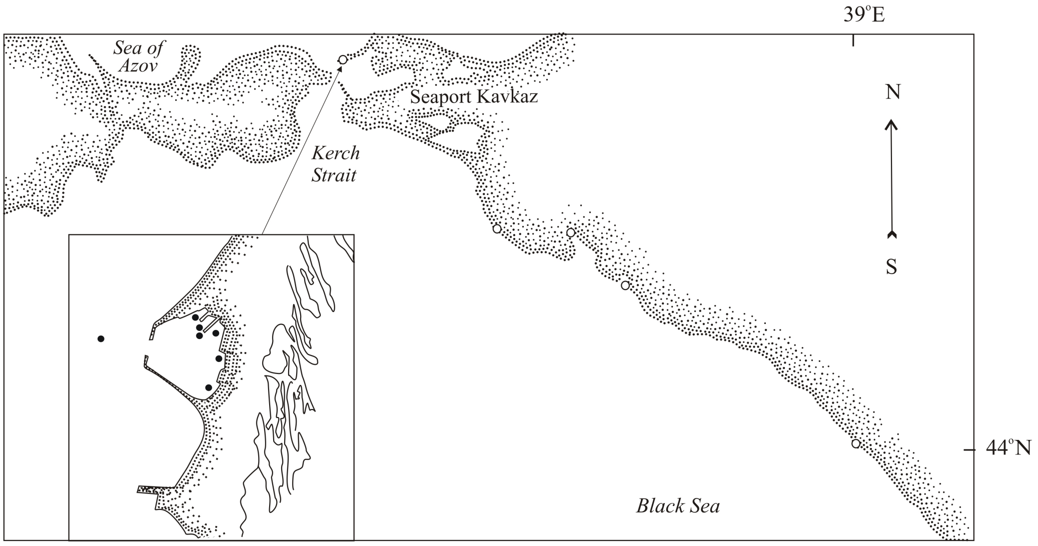

Fig. 1. Map of sampling in the Kerch Strait (the seaport Kavkaz is shown in the inset)

The seaport Kavkaz is located on the Taman Peninsula (the Chushka Spit) in the northern Kerch Strait (see Fig. 1). The Kerch Strait – shallow and relatively narrow one – belongs to the Sea of Azov water area and connects it with the Black Sea. Its length is 43 km, and width varies 4 to 42 km. From the Sea of Azov side, the greatest depths at the strait mouth are ≤ 10.5 m; from the Black Sea side, those are 18 m. As moving towards the mid-strait, the depths gradually decrease; for a large area, those are about 5.5 m. The Kerch Strait currents are mainly caused by wind (Eremeev et al., 2003). Water circulation in the strait depends both on wind and difference in sea levels at two strait sides (the latter one results from surge fluctuations in the level and different freshwater balances of two seas). In the strait, according to the authors' data, the water transfer from the Sea of Azov to the Black Sea is the prevailing one. In the Kerch Strait, water temperature in autumn–winter is usually 2–4 °C higher than in the open sea. In summer, resulting from water exchange between the Sea of Azov and the Black Sea, water temperature in the strait is lower than off the coast. In this area, at the junction of the waters of two seas, there is a frontal zone with large salinity gradients (from 11 ‰ in the north of the strait to 17 ‰ in the south), and this is of key importance for the distribution of bottom communities.

RESULTS

In the community of benthic invertebrate larvae in the seaport Kavkaz, 32 taxa were recorded for the entire study period: Bivalvia, 7; Gastropoda, 6; Polychaeta, 13; Cirripedia, 1; and Decapoda, 5. Out of them, 1 was identified down to a family level; 4, down to a genus level; and 27, down to a species level (Table 1).

Table 1. Meroplankton taxonomic composition in the seaport Kavkaz area (+, the taxon was found; ++, common; and +++, mass)

POLYCHAETA	
Nephtyidae Grube, 1850	
Nephtys hombergii Savigny in Lamarck, 1818	+
Nephtys sp.	+
Polynoidae Kinberg, 1856	
Harmothoe imbricata (Linnaeus, 1767)	+
Nereididae Blainville, 1818	
Alitta succinea (Leuckart, 1847)	+
Hediste diversicolor (O. F. Müller, 1776)	+
Nereididae gen. sp.	+
Spionidae Grube, 1850	
Prionospio cirrifera Wirén, 1883	+
Pygospio elegans Claparède, 1863	+
Microspio mecznikowianus (Claparède, 1869)	+
Polydora cornuta Bosc, 1802	+
Marenzelleria neglecta Sikorski & Bick, 2004	+
Capitellidae Grube, 1862	
Heteromastus filiformis (Claparède, 1864)	+
Capitella capitata (Fabricius, 1780)	+
DECAPODA	
Diogenidae Ortmann, 1892	
Diogenes pugilator (P. Roux, 1829)	+
Upogebiidae Borradaile, 1903	
Upogebia pusilla (Petagna, 1792)	+
Alpheidae Rafinesque, 1815	
Alpheus dentipes Guérin, 1832	+
Palaemonidae Rafinesque, 1815	
Palaemon elegans Rathke, 1836	+
Panopeidae Ortmann, 1893	
Rhithropanopeus harrisii (Gould, 1841)	+

CIRRIPEDIA	
Balaninae Leach, 1817	
Amphibalanus improvisus (Darwin, 1854)	+++
BIVALVIA	
Mytilidae Rafinesque, 1815	
Mytilus galloprovincialis Lamarck, 1819	++
Mytilaster lineatus (Gmelin, 1791)	+++
Myidae Lamarck, 1809	
Mya arenaria Linnaeus, 1758	+
Arcidae Lamarck, 1809	
Anadara kagoshimensis (Tokunaga, 1906)	+
Cardiidae Lamarck, 1809	
Cerastoderma glaucum (Bruguière, 1789)	++
Moerellinae M. Huber, Langleit & Kreipl, 2015	
Moerella sp.	+
Semelidae Stoliczka, 1870 (1825)	
Abra segmentum (Récluz, 1843)	++
GASTROPODA	
Muricidae Rafinesque, 1815	
Rapana venosa (Valenciennes, 1846)	+
Cerithiidae J. Fleming, 1822	
Bittium reticulatum (da Costa, 1778)	+++
Hydrobiidae Stimpson, 1865	
Hydrobia acuta (Draparnaud, 1805)	+
Pyramidellidae Gray, 1840	
Chrysallida sp.	+
Nassariidae Iredale, 1916 (1835)	
Tritia reticulata (Linnaeus, 1758)	+
Rissoidae Gray, 1847	
Rissoa sp.	+

The largest number of taxa (23–26) was registered in June and September, and the smallest one (2–4) was recorded in cold season. Long-term mean quantitative indicators of meroplankton density in the seaport area [(0.77 ± 0.32) thousand ind.·m^{-3}] differed slightly from those at the background station [(0.93 ± 0.31) thousand ind.·m^{-3}] (Table 2).

Table 2. Mean meroplankton abundance in different areas of the seaport Kavkaz in 2017–2019

Area	Abundance, thousand ind.·m^{-3}					
	N_{total}	N_{cir}	N_{biv}	N_{gast}	N_{pol}	N_{dec}
Seaport	0.77 ± 0.32	0.42 ± 0.33	0.15 ± 0.07	0.12 ± 0.1	0.06 ± 0.02	0.02 ± 0.03
Background station	0.93 ± 0.31	0.33 ± 0.2	0.54 ± 0.6	0.013 ± 0.01	0.027 ± 0.02	0.02 ± 0.02

Note: N_{total} denotes total abundance; N_{cir}, N_{biv}, N_{gast}, N_{pol}, and N_{dec} denote abundance of Cirripedia, Bivalvia, Gastropoda, Polychaeta, and Decapoda, respectively.

In the seaport, larvae of cirripedians were abundant (54.5 % of total meroplankton abundance), as well as larvae of molluscs (34.9 %; out of them, 19.4 % were Bivalvia representatives, and 15.5 % were Gastropoda ones). Outside the seaport, larvae of cirripedians (35.4 %) and bivalves (58.0 %) prevailed. Meroplankton ratio in zooplankton composition averaged 30.4 % in the seaport and 19.9 % at the background station. In the study area, surface water layer temperature varied from +6.2 °C in February to +24.7 °C in July (Fig. 2).

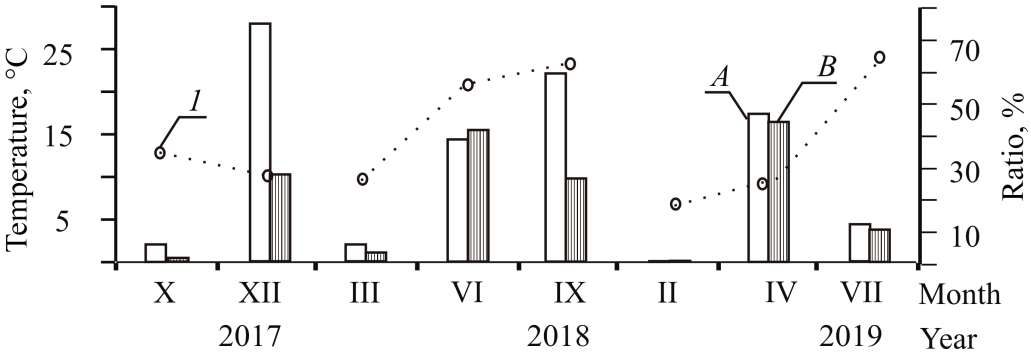

Fig. 2. Seasonal changes in surface water temperature (1) and ratio of meroplankton in zooplankton (% of total zooplankton abundance) in the seaport Kavkaz area in 2017–2019 (A, the seaport; B, the background station)

Meroplankton ratio in zooplankton during the study period varied from 0.003–0.0015 % in February to 74.8 % in December (see Fig. 2).

A significant increase in meroplankton ratio in zooplankton was observed at low temperatures (+6…+10 °C) – during a seasonal decline in holoplankton reproduction. The value was high in December and April when larvae of cirripedians formed the basis of meroplankton pool. In summer and early autumn – with the water warming up to +21…+24.5 °C – abundance of benthic invertebrate larvae in zooplankton naturally increased. In the dynamics of meroplankton abundance, three density peaks were noted (April, June, and September); those were most pronounced in the seaport area in spring (2.9 thousand ind.·m^{-3}) and in the open area in early autumn (2.6 thousand ind.·m^{-3}) (Fig. 3).

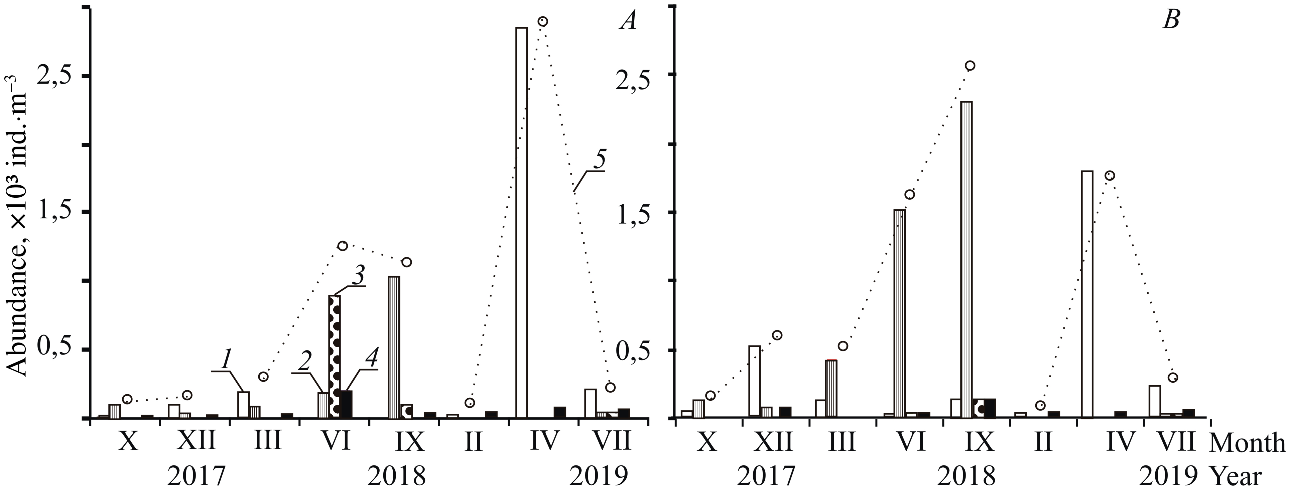

Fig. 3. Seasonal dynamics of meroplankton abundance (thousand ind.·m^{-3}) in the seaport Kavkaz area in 2017–2019: A, the seaport; B, the background station (1, cirripedians; 2, bivalves; 3, gastropods; 4, polychaetes; and 5, total meroplankton)

Phenology of benthic invertebrate larvae. In October–December 2017, at a temperature of +10…+13 °C, meroplankton was poorly represented (2–4 taxa) due to a seasonal decline in the reproduction of benthic invertebrates. In October, meroplankton ratio in zooplankton composition did not exceed 0.5–4.5 %. Everywhere, total abundance of benthic invertebrate larvae was lower than 0.12 thousand ind.·m^{-3}. An autumn generation of benthic invertebrate larvae was represented mainly by those of bivalve *Mytilus galloprovincialis* (93.6 %) and cirripedian *Amphibalanus improvisus* (6.4 %). In December, total meroplankton abundance varied from (0.3 ± 0.07) thousand ind.·m^{-3} in the seaport to 0.61 thousand ind.·m^{-3} in the open area. Meroplankton contribution to total zooplankton abundance increased on average up to 30 and 74.8 %, respectively. In the seaport area, larvae of cirripedian *A. improvisus* prevailed – (0.29 ± 0.06) thousand ind.·m^{-3} (96.2 % of total meroplankton abundance). In the open area, along with them, larvae of bivalve *M. galloprovincialis* were recorded.

By the end of March 2018, the water warmed up to +10 °C, and meroplankton ratio in zooplankton composition increased up to 4–5.6 %. In plankton, larvae of polychaete *Polydora cornuta*, cirripedian *A. improvisus*, and bivalve *M. galloprovincialis* were found. Total meroplankton abundance was of (0.34 ± 0.05) thousand ind.·m^{-3} (the seaport) and 0.57 thousand ind.·m^{-3} (the background station). In June, with a rise in water temperature up to +21 °C, the number of taxa increased up to 23–26; meroplankton abundance varied from (1.4 ± 0.09) thousand ind.·m^{-3} in the seaport area to 1.6 thousand ind.·m^{-3} outside it. Meroplankton ratio in zooplankton composition reached 38.6–44.9 %. In the seaport area, larvae of gastropod *B. reticulatum* were abundant [(0.9 ± 0.05) thousand ind.·m^{-3}]; outside the seaport, larvae of bivalve *Mytilaster lineatus* (0.8 thousand ind.·m^{-3}), *Abra segmentum* (0.33 thousand ind.·m^{-3}), and *Cerastoderma glaucum* (0.3 thousand ind.·m^{-3}) prevailed. Along with larvae of these species, larvae of decapods *Diogenes pugilator*, *Upogebia pusilla*, *Palaemon elegans*, and *Rhithropanopeus harrisii* were registered in small abundance, as well as larvae of polychaetes *Nephtys hombergii*, *Harmothoe imbricata*, *Alitta succinea*, *Hediste diversicolor*, Nereididae gen. sp., *Pygospio elegans*, *Microspio mecznikowianus*, and *P. cornuta*; trochophores *Heteromastus filiformis* and *Capitella capitata*; bivalves *Mya arenaria* and *Moerella* sp.; gastropods *Tritia reticulata*, *Hydrobia acuta*, *Rissoa* sp., and *Chrysallida* sp.; and cirripedian *A. improvisus*. In September, 12 meroplankton taxa were identified.

Meroplankton ratio in zooplankton composition reached 27.4–59.9 %. Meroplankton abundance ranged from (1.2 ± 0.07) thousand ind.·m^{-3} (the seaport) to 2.6 thousand ind.·m^{-3} (the background station). An autumn rise in meroplankton abundance in September can be associated with a ctenophore *Beroe ovata* Bruguière, 1789 presence in plankton (0.001 thousand ind.·m^{-3}) – a species which feeds on a ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865. A decrease in density of a zooplankton feeder *M. leidyi* results in an increase in density of holo- and meroplankton (Ctenophore *Mnemiopsis leidyi*, 2000). In early autumn, the complex of prevailing meroplankton species included mainly larvae of bivalve *M. lineatus*; its density in the open area reached a maximum of 2.3 thousand ind.·m^{-3} (84.8–86 % of total meroplankton abundance). The contribution of gastropod *B. reticulatum* was not more than 7–8.6 %. At that time, larvae of the following species were recorded sporadically: bivalve *Anadara kagoshimensis*; gastropod *Rapana venosa*; decapods *D. pugilator*, *U. pusilla*, and *Alpheus dentipes*; polychaetes *Prionospio cirrifera*, *P. cornuta*, Nereididae gen. sp., and *Nephtys* sp.; and cirripedian *A. improvisus*.

In late February 2019, meroplankton was poorly represented due to low water temperature (+6 °C) and a seasonal decline in breeding of benthic invertebrates. Meroplankton ratio in zooplankton composition was negligible – 0.015–0.03 %. In this period, larvae of cirripedian *A. improvisus* were noted, as well as larvae of cold-loving polychaetes *H. imbricata* and *Marenzelleria neglecta*. Total meroplankton abundance varied from (0.008 ± 0.0007) thousand ind.·m^{-3} in the seaport area to 0.003 thousand ind.·m^{-3} outside it. Abundance of *M. neglecta* – a species new for the area – averaged (0.003 ± 0.0008) thousand ind.·m^{-3} (Selifonova, 2019). In April, with a rise in temperature up to +10.5 °C, meroplankton contribution to total zooplankton abundance increased up to 44–47 %. Total meroplankton abundance ranged from (2.9 ± 0.08) thousand ind.·m^{-3} (the seaport) to 1.8 thousand ind.·m^{-3} (the background station). Three taxa of benthic larvae were identified – *H. imbricata*, *P. cornuta* (Polychaeta), and *A. improvisus* (Cirripedia). At the same time, *A. improvisus* larvae made a significant contribution to a larval pool in April 2019 (99.9–100 % of total zooplankton abundance). In July, during a seasonal maximum of a planktonic predator *M. leidyi*, density of benthic invertebrate larvae was low everywhere [(0.2 ± 0.07) thousand ind.·m^{-3}], and meroplankton contribution to total zooplankton abundance was ≤ 12 %. In meroplankton, benthic invertebrate larvae were found – *A. succinea*, *Nephtys* sp., *P. cornuta* (Polychaeta), *A. improvisus* (Cirripedia), *M. lineatus* (Bivalvia), and *H. acuta* (Gastropoda). In total meroplankton abundance, cirripedian larvae prevailed accounting for 95.2–98.2 %.

DISCUSSION

Meroplankton taxonomic composition and peculiarities of its seasonal cycle registered by us in the seaport Kavkaz area (the northern Kerch Strait) correspond to those previously recorded for the Sea of Azov and the coastal zone of the northeastern Black Sea (Selifonova, 2008, 2014). Differences in structure and dynamics of meroplankton quantitative indicators result from zoobenthos distribution, hydrochemical water regime, direction of prevailing currents in the strait, and other factors (Kazankova & Nemirovsky, 2003 ; Kulikova et al., 2017 ; Lisitskaya, 2017 ; *etc.*). As known, the nature of meroplankton seasonal distribution in the Sea of Azov depends primarily on the pressure of a predatory ctenophore *M. leidyi* feeding on a significant part of meroplankton at a peak of its development (Matishov et al., 2015). Therefore, in dynamics of zooplankton density in the Sea of Azov, there is no summer–autumn peak, while in the Black Sea, such a peak is observed annually (Lisitskaya, 2017 ; Selifonova, 2014). For *M. leidyi*, the only natural enemy in the Black Sea waters is *B. ovata* – not a permanent inhabitant, but a species forming a pseudo-population in late summer and early autumn (Volovik et al., 2008). At this season, an outbreak of *B. ovata* abundance leads to constructive changes in the Black Sea zooplankton community. In the Kerch Strait, with salinity closer to that of the Black Sea, we recorded a similar autumn increase in meroplankton abundance. The lower salinity of the Sea of Azov waters hinders *B. ovata* development, and similar processes in this water area occur in the Kerch pre-strait alone (the southern Sea of Azov) (Ctenophore *Mnemiopsis leidyi*, 2000).

Meroplankton of the Kerch Strait in the seaport Kavkaz area and the Sea of Azov – in contrast to meroplankton of bays of the northeastern shelf and Crimea – is characterized by low taxonomic richness (Lisitskaya, 2017 ; Selifonova, 2008, 2014). However, sufficient reproductive potential of both the Sea of Azov and Black Sea species of benthic invertebrates is concentrated in this area (Golovkina & Nabozhenko, 2012 ; Fashchuk et al., 2012). Mass spawning of benthic invertebrates occurs April to September. In the dynamics of meroplankton abundance in the seaport Kavkaz area, three density peaks were registered (in April, June, and September); those werev most pronounced in the seaport area in spring and in the open area in early autumn (up to 3 thousand ind.·m^{-3}). In June, at water temperature of +21 °C, meroplankton was diverse and constituted a significant ratio of zooplankton. In its structure, mollusc larvae prevailed (85.3–93.7 % of total meroplankton abundance); out of them, the most noticeable ones were larvae of gastropod *B. reticulatum* and bivalves *A. segmentum* and *C. glaucum*. Mass spawning of these bivalve species is usually observed in the Sea of Azov (Selifonova, 2008). In winter, larvae of polychaete *M. neglecta* – a species new for the area – were recorded sporadically in the study area. In the Sea of Azov, at low water temperature (0…+1.2 °C), this species gives an outbreak of abundance – up to a hundred thousand ind. *per* m^3; it is most pronounced in the Taganrog Bay (Selifonova, 2019).

Long-term mean quantitative indicators of meroplankton density in the seaport area differed insignificantly from those at the background station. In the seaport area, larvae of cirripedians, bivalves, and gastropods were abundant; outside the seaport, larvae of cirripedians and bivalves prevailed. Meroplankton ratio in zooplankton composition in the seaport Kavkaz area was on average 1.5 times higher than at the background station. As known, communities of detritus-rich port waters include mainly organisms resistant to high content of organic matter, *inter alia* meroplankton (Selifonova, 2014). In the seaport Kavkaz area, the basis of meroplankton pool was formed by species tolerant to water eutrophication and bottom sediment sulfide contamination (Sorokin & Burkatskii, 2007) – larvae of gastropod *B. reticulatum*, larvae of bivalves *A. segmentum*, *C. glaucum* (in summer), and *M. lineatus* (in early autumn), and larvae of cirripedian *A. improvisus* (in spring).

Conclusion. For the first time, meroplankton state under conditions of pollution in the seaport Kavkaz area (the northern Kerch Strait) was analyzed. As noted, meroplankton density in the polluted area is not inferior to that of the relatively clean area and provides sufficient reproductive potential there. In the seaport area, larvae of cirripedians and molluscs were abundant, while outside the seaport, larvae of cirripedians and bivalves prevailed. The basis of meroplankton pool was formed by species tolerant to water eutrophication and bottom sediment sulfide contamination. Those were larvae of gastropod *B. reticulatum*, larvae of bivalves *A. segmentum*, *C. glaucum* (in summer), and *M. lineatus* (in early autumn), and larvae of cirripedian *A. improvisus* (in spring).

In the seasonal dynamics of meroplankton in the study area, a summer–autumn increase in abundance was revealed which is characteristic for the Black Sea waters. The period of the greatest zoobenthos spawning and larvae release into the pelagial lasted April to October. Three density peaks were registered (April, June, and September), and those were most pronounced in the seaport area in spring and in the open area in early autumn.

The obtained data give an idea of the current state of both pelagic and benthic communities and may be useful for further monitoring in this area.

This work was carried out within the framework of IBSS state research assignment "Functional, metabolic, and toxicological aspects of hydrobionts and their populations existence in biotopes with different physical and chemical regimes" (No. 121041400077-1).

Acknowledgement. The authors are grateful to the Sea of Azov–Black Sea Directorate for the Technical Support of Maritime Supervision for organizing the research.

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ТАКСОНОМИЧЕСКИЙ СОСТАВ И СЕЗОННАЯ ДИНАМИКА МЕРОПЛАНКТОНА В РАЙОНЕ МОРСКОГО ПОРТА КАВКАЗ, КЕРЧЕНСКИЙ ПРОЛИВ

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В северной части Керченского пролива (район морского порта Кавказ) был проведён мониторинг видового состава меропланктона, распределения его обилия и сезонной динамики численности. Материалом для исследования послужили сборы зоопланктона в разные сезоны 2017–2019 гг. в портовом районе и за его пределами. Тотальные ловы зоопланктона производили большой сетью Джеди (диаметр входного отверстия — 37 см, размер ячеи — 120 мкм) на глубинах от 5 до 8 м. Пробы фиксировали 2–4%-ным раствором нейтрального формальдегида и обрабатывали в лабораторных условиях по стандартной методике. Обнаружено 32 таксона меропланктона. Отмечено, что по плотности меропланктон загрязнённого района не уступает меропланктону относительно чистого участка и обеспечивает в них достаточный репродуктивный потенциал. В портовом районе массовыми были личинки усоногих раков и моллюсков, за пределами порта — личинки усоногих раков и двустворчатых моллюсков. Основу пула меропланктона составляли виды, толерантные к эвтрофикации вод и сульфидному заражению донных осадков, — личинки брюхоногих моллюсков *Bittium reticulatum*, личинки двустворчатых моллюсков *Abra segmentum*, *Cerastoderma glaucum* (летом) и *Mytilaster lineatus* (в начале осени), личинки усоногих раков *Amphibalanus improvisus* (весной). В сезонной динамике меропланктона исследуемого района выявлено летне-осеннее увеличение обилия, характерное для черноморских вод. Период наибольшего нереста донных животных и выхода в пелагиаль личинок продолжался с апреля по октябрь. Отмечено три пика плотности (апрель, июнь и сентябрь), которые были наиболее выражены в районе порта весной, а в открытой части — в начале осени.

Ключевые слова: меропланктон, численность, сезонная динамика, Керченский пролив

1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 98–112
https://doi.org/10.21072/mbj.2022.07.2.08

UDC [582.261.1:551.326.7](265.54.04)

QUANTITATIVE STRUCTURE OF THE SEA ICE MICROALGAE COMMUNITY (RUSSKY ISLAND, PETER THE GREAT BAY, SEA OF JAPAN)

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Received by the Editor 15.07.2021; after reviewing 21.09.2021;
accepted for publication 03.03.2022; published online 07.06.2022.

For the Russian coast of the Sea of Japan, a study of the quantitative structure of sea ice microalgae was carried out for the first time. The investigation covered biotopes of ice core and under-ice phytoplankton of two Russky Island bays during winter season of 2020 and 2021. In total, 88 microalgae species from 50 genera and 7 divisions were identified. As found, the ice microalgae flora was characterized by a greater species richness than the phytoplankton biotope. Out of prevailing species, the most abundant ones were planktonic diatoms *Chaetoceros socialis* f. *radians*, *Nitzschia frigida*, *Thalassiosira nordenskioeldii*, and *Nitzschia* sp. Diatoms formed the basis of the community. Specifically, in 2020, their abundance was 1,861.2 cells·mL^{-1} in the Voevoda Bay and 751.2 cells·mL^{-1} in the Novik Bay; in 2021, the values reached 6,846.3 and 17,143.1 cells·mL^{-1}, respectively. In 2020 in the Voevoda Bay, cell abundance was maximum in the upper layer of the ice core and gradually decreased closer to a border with under-ice water; in the Novik Bay, it was distributed approximately evenly throughout the core. In 2021 in the Voevoda Bay, the opposite pattern was observed: microalgae abundance was minimal in the upper layers of the ice core and gradually increased as moving down, to a border with under-ice water. In the Novik Bay, maximum microalgae abundance was recorded in the upper layer of the ice core, with a relatively uniform distribution over all layers. Thus, the differences are shown in the quantitative structure of ice microalgae depending on a layer of the ice core, year, and study area.

Keywords: quantitative structure, microalgae, phytoplankton, Peter the Great Bay, Russky Island, Sea of Japan

Microalgae (hereinafter MA) are the main biological component of a sea ice cover. There are branched pores and channels in ice, and cells of planktonic and benthic MA get there from under-ice water. Some species prove to be adapted to such extreme habitat conditions and begin to develop rapidly (Buinitskii, 1973 ; Mel'nikov, 1989). This is more pronounced for multi-year ice, but even in an ice cover which is formed in the bays in winter alone, significant differences are sometimes recorded from phytoplankton in terms of MA qualitative and quantitative composition.

In winter, MA production in ice samples can make up to 7.5 % of the total primary production of a water area (Dupont, 2012). During ice cover melting, MA are the main food source for organisms of higher trophic levels. This alone determines the importance of analyzing the structure of ice communities in water areas with a seasonally formed ice cover. In terms of sea ice MA studies, Peter the Great Bay is of significant scientific interest: it is the only water area at this geographical latitude where a stable ice cover can be formed.

Investigations of MA communities in ice of the Sea of Japan are mainly focused on ice physicochemical and production characteristics and the analysis of patterns of ice formation conditions. The first description of ice conditions was made by L. Schrenk in 1869 and covered the Tatar Strait alone. The closest publication in terms of the study object in Peter the Great Bay area is the work on chlorophyll and primary production of ice-related MA for the Amur Bay (Kuznetsov, 1980). In this article, the author both analyzed composition of photosynthetic pigments and provided some data on MA species composition and abundance. In the joint work of the staff of the Pacific Oceanological Institute (POI FEB RAS) and National Scientific Center of Marine Biology (NSCMB FEB RAS) aimed at studying ice production peculiarities in the Razdolnaya River estuary during a freeze-up, it was specified as follows: ice was characterized by a significantly lower species richness than phytoplankton (Zvalinsky et al., 2010).

When studying ice-related MA communities, Russian and foreign researchers mainly focused on polar regions (Ryabushko, 2016 ; Arrigo et al., 2014 ; Kauko et al., 2018 ; Werner et al., 2007). Investigations of the water areas of Peter the Great Bay, as well as other water areas of the Russian coast of the Sea of Japan, are mostly concentrated either on water floristic composition or on ice physicochemical parameters and its production characteristics. To date, scientific data are very scarce on quantitative characteristics of ice-related MA communities for the Russian coast of the Sea of Japan, especially for various ice horizons. Such information is relevant for ice of considerable thickness. Both Voevoda and Novik bays are of great scientific interest due to certain environmental problems. Specifically, there are mariculture farms in the Voevoda Bay that affect the seagrass *Zostera marina* Linnaeus, 1753 growing there, while it is one of the plants contributing to formation of local environmental conditions (Barabanshchikov et al., 2018). The Novik Bay is under certain anthropogenic stress because of domestic wastewater from the Far Eastern Federal University campus. There were several hydrological, hydrochemical, and ecological studies focused on these problems; those, with the data obtained by us, could be expanded in the context of investigating the dynamics of these two water areas under anthropogenic load. So, a fundamental interest arose in the analysis of the quantitative structure of sea ice MA in two Russky Island bays during two winter seasons.

The aim of this work was to study the quantitative structure of MA community in sea ice in two Russky Island bays (the Sea of Japan) during the winter periods of 2020 and 2021.

MATERIAL AND METHODS

The material for the study was ice cores and samples of under-ice water. Sampling was carried out on 18.02.2020 in the Voevoda Bay (43°00′05.6″N, 131°79′30.8″E), 19.02.2020 in the Novik Bay (43°01′38.9″N, 131°88′16.3″E), and 25.02.2021 in both bays at the same coordinate points (Fig. 1).

The meteorological conditions during sampling were as follows: cloudless weather and air temperature about −0.3 °C. In 2020 in the Voevoda Bay water area, there was a snow cover with a depth about 10 cm; in 2021, a depth was about 3 cm. In the Novik Bay water area, there was no snow cover. In the Voevoda Bay in 2020, depth down to the bottom was 3 m; in 2021, a depth was about 2.5 m. In the Novik Bay in 2020, depth down to the bottom was 7 m; in 2021, it was 7.5 m.

Ice cores were sampled using a circular drill with a diameter 15 cm. After sampling, the ice cores were divided into 10-cm-long layers and placed into sterile plastic containers. The length of the ice cores in 2020 in the Voevoda Bay was 44 cm, and in the Novik Bay, 38 cm. The length in 2021 in the Voevoda Bay was 62 cm; in the Novik Bay, it was 64 cm (Fig. 2).

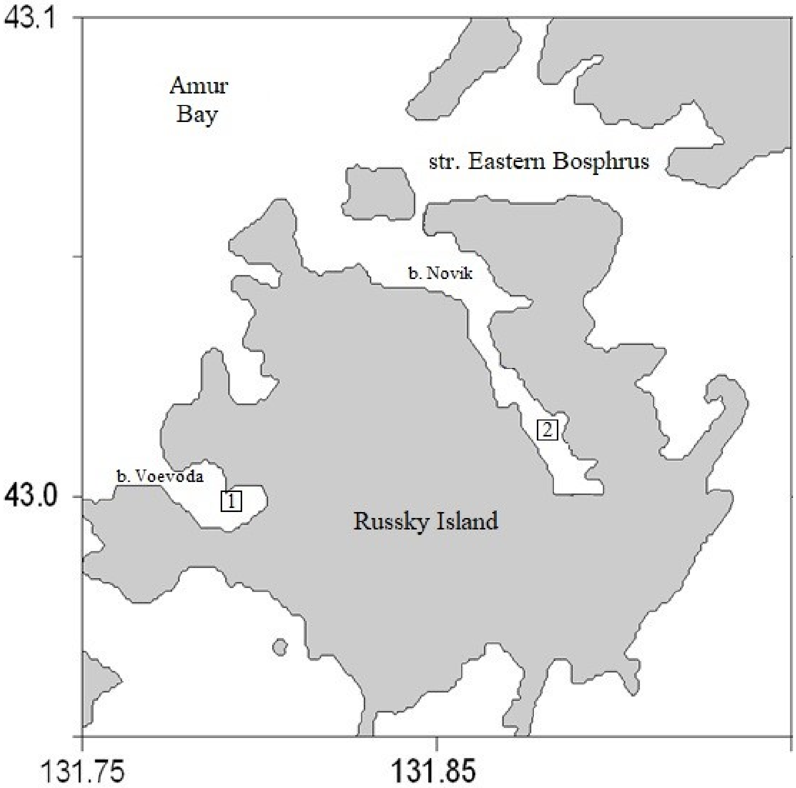

Fig. 1. Ice core and under-ice water sampling stations: 1, the Voevoda Bay; 2, the Novik Bay

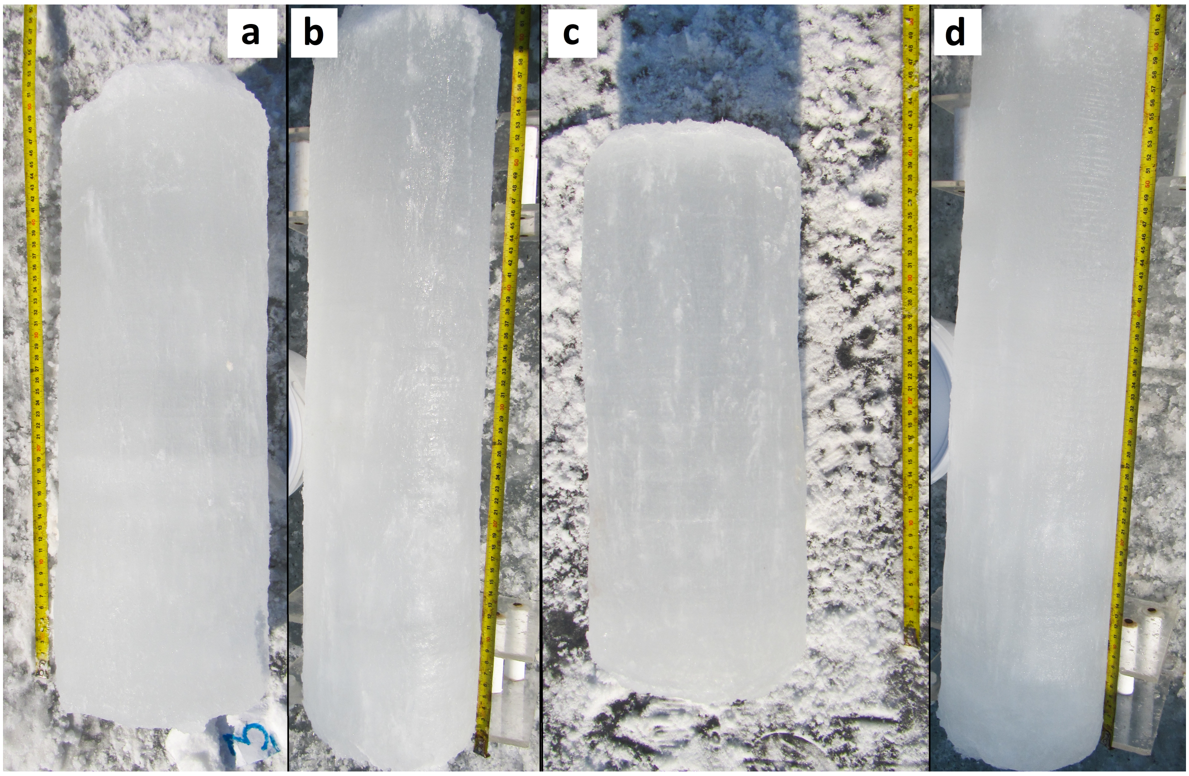

Fig. 2. Ice cores from the Voevoda Bay (a, 2020; b, 2021) and the Novik Bay (c, 2020; d, 2021)

In addition to ice core sampling, under-ice water sampling was carried out using a 5-L Niskin bottle. Hydrochemical composition of the samples was analyzed at POI FEB RAS. Species identification and calculation of MA quantitative characteristics were carried out in the laboratory of marine microbiota of the NSCMB FEB RAS.

The cores were melted at a temperature of +24 °C; melt water was poured into sterile containers. The samples were fixed with 5 % potassium iodide solution in the ratio as follows: 2.5 mL of iodine *per* 1 L of melt water. In accordance with the method of Radchenko (Radchenko et al., 2010), after 12 days, excess water was drained to 100–200 mL of the residue from each layer.

MA species were identified under an Olympus BX41 transmitted light microscope with an UPLanF1 100×/1.30 objective (Japan). To verify the species composition, the material was examined under a scanning electron microscope Sigma 300 VP (the UK). Diatom shells were cleaned from organic substances by “cold” and “hot” methods of treatment with concentrated sulfuric acid, followed by washing in distilled water (Ryabushko & Begun, 2015).

Cells were counted in a 1-mL Sedgewick–Rafter counting cells. MA biomass was estimated by a volumetric method using original and published data on measurements of cell volume for each species (Biovolumes and Size-Classes, 2006 ; Sun & Liu, 2003). MA divisions are given according to the system adopted in the work of G. Konovalova *et al.* (1989). Species with a density of at least 20 % of the total density were considered prevailing ones (Konovalova, 1984).

For statistical data analysis, Shannon and Pielou indices were applied. The Shannon–Wiener index (H) was calculated as follows:

$$H = -\sum p_i \ln p_i \ ,$$

where p_i is the ratio of the i-th species in the total density.

The Pielou evenness index (e) was calculated by the formula:

$$e = H / \ln S \ ,$$

where H is the Shannon index;

S is the total species number (Megarran, 1992).

RESULTS

MA of Russky Island bays were represented by 88 species from 7 divisions. In the ice biotope, a greater species richness was recorded than in the phytoplankton biotope: in ice, 80 species from 7 divisions were found; in phytoplankton, 40 species from 5 divisions were identified. In terms of species number, diatom genera *Navicula* Bory, 1822, *Nitzschia* Hassall, 1845, and *Protoperidinium* Bergh, 1881 prevailed, as well as a dinoflagellate genus *Gyrodinium* Kofoid & Swezy, 1921.

Analysis of the quantitative structure of sea ice MA showed that the ratio of diatoms was the highest in terms of abundance and biomass (Table 1). This was evidenced by increased content of silicates in water and ice samples as well: the value reached 3.05 $\mu\text{mol}\cdot\text{L}^{-1}$ in 2020 and 5.53 $\mu\text{mol}\cdot\text{L}^{-1}$ in 2021.

In the ice flora, prevailing diatom species were *Chaetoceros socialis* f. *radians* (F. Schütt) Proshkina-Lavrenko, 1963, *Nitzschia frigida* Grunow in Cleve & Grunow, 1880, *Thalassiosira nordenskioeldii* Cleve, 1873, and an unidentified small-cell *Nitzschia* species. Dinoflagellates were represented less significantly; out of them in 2020, *Amphidinium sphenoides* Wulff, 1919 and *Protoperidinium depressum* (Bailey) Balech, 1974 stood out; in 2021, representatives of green algae (unidentified prasinophytes).

The least contribution was made by a golden alga *Octactis speculum* (Ehrenberg) F. H. Chang, J. M. Grieve & J. E. Sutherland, 2017 and euglena alga *Eutreptiella braarudii* Throndsen, 1969. In phytoplankton of both bays in 2021, the prevalence of cryptophytic algae of the genus *Plagioselmis* Butcher, 1994 was registered. Haptophytes with relatively low quantitative values were found only in the upper ice layers in the Novik Bay in 2021.

Table 1. Quantitative characteristics of algal divisions representatives (N, abundance, cells·mL^{-1}; B, biomass, mg·m^{-3})

Division	The Voevoda Bay				The Novik Bay			
	2020		2021		2020		2021	
	N	B	N	B	N	B	N	B
Chrysophyta	15.5	52.6	76.2	243.4	0.3	1.1	0.2	1.7
Bacillariophyta	1,861.2	9,327.5	6,846.3	53,457.8	751.2	9,851.4	17,143.1	165,143.0
Cryptophyta	0.0	0.0	4,500.0	121.5	0.0	0.0	1,714.3	46.3
Dinophyta	11.8	1,490.3	1.7	15.1	40.5	438.9	2.6	36.3
Chlorophyta	0.0	0.0	578.0	83.0	0.0	0.0	493.6	71.0
Euglenophyta	0.0	0.0	20.4	211.2	3.8	39.3	1.9	20.0
Haptophyta	0.0	0.0	0.0	0.0	0.0	0.0	47.9	4.2
In total	1,888.5	10,870.4	12,022.6	54,132.0	795.8	10,330.7	19,403.6	165,322.5

Analysis of MA quantitative distribution over ice layers showed the following: in 2020 in the Voevoda Bay, cell abundance was maximum in the upper layer of the ice core and gradually decreased closer to a border with under-ice water (Fig. 3a). In the Novik Bay, abundance was distributed approximately evenly throughout the core (Fig. 3b).

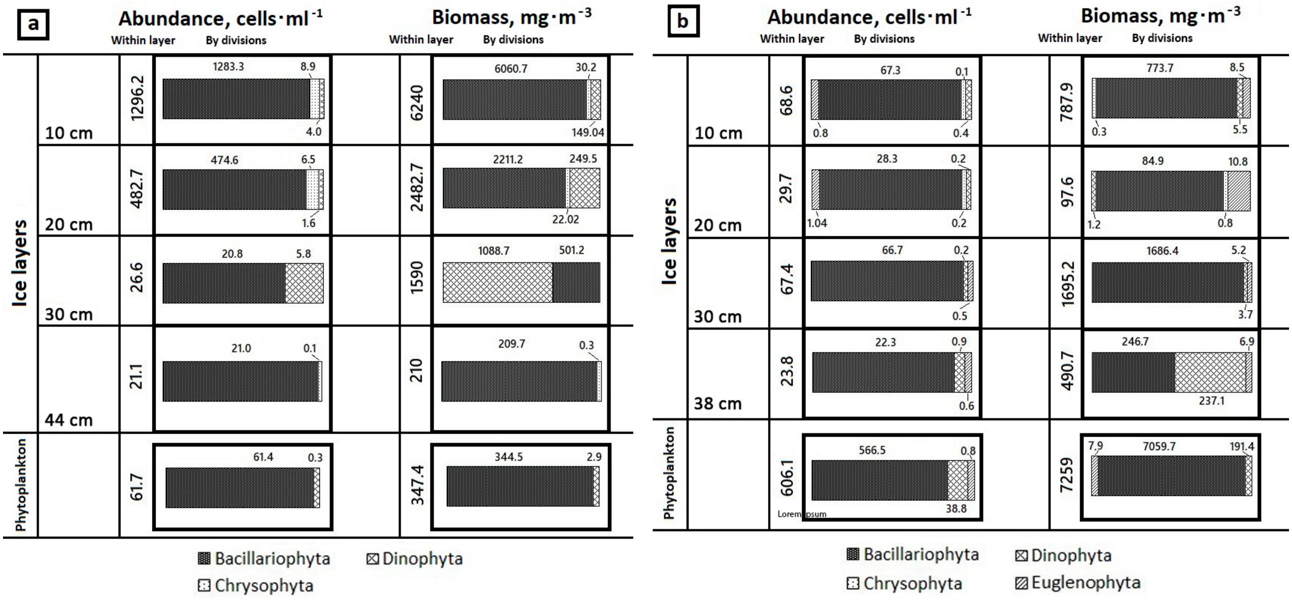

Fig. 3. Diagrams of the distribution of microalgal divisions abundance and biomass by ice layers and in phytoplankton in the Voevoda Bay (a) and the Novik Bay (b) in 2020

At the same time, abundance of sea ice MA in the Novik Bay was almost an order of magnitude lower than in the Voevoda Bay, whereas in phytoplankton, abundance was an order of magnitude higher.

In the Voevoda Bay in 2021, the pattern was in general opposite to that of the previous year: cell abundance was minimal in the upper layers of the ice core and gradually increased as moving down, to a border with under-ice water (Fig. 4a). MA abundance in ice exceeded the value of the previous year by almost three times; in phytoplankton, by three orders of magnitude.

In the Novik Bay, MA abundance was maximum in the upper layer of the core; at the same time, it was relatively evenly distributed over the ice layers (Fig. 4b). Compared to the values of 2020, MA abundance in ice and phytoplankton was an order of magnitude higher. At the same time, cell abundance in ice was an order of magnitude higher than the values for the Voevoda Bay, while cell abundance in phytoplankton was comparable.

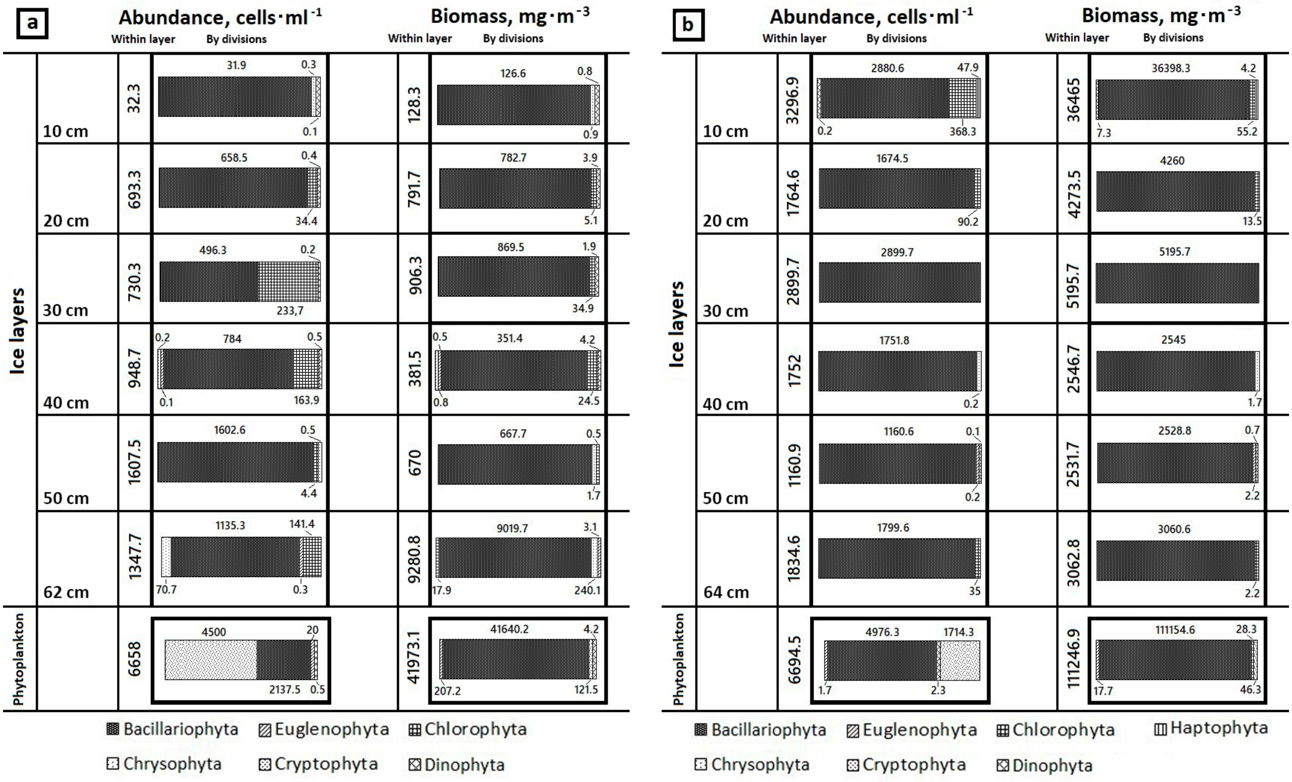

Fig. 4. Diagrams of the distribution of microalgal divisions abundance and biomass by ice layers and in phytoplankton in the Voevoda Bay (a) and the Novik Bay (b) in 2021

Analysis of the quantitative structure of sea ice MA in two Russky Island bays in 2020 and 2021 showed more or less significant differences in the values of the total abundance and biomass for the main prevailing species (Figs 5–8).

MA abundance in ice samples from the Voevoda Bay in 2020 was 1,826 cells·mL^{-1}, with a diatom *N. frigida* prevailing (93.12 % of the total abundance). In phytoplankton, the value was 62 cells·mL^{-1}, with the prevalence of diatoms *Nitzschia* sp. (40.91 %) and *Cylindrotheca closterium* (Ehrenberg) Reimann & J. C. Lewin, 1964 (31.25 %) and the sub-prevalence of *N. frigida* (10.80 %). The biomass in the ice core was 10,522.8 mg·m^{-3}; in phytoplankton, 347.5 mg·m^{-3}.

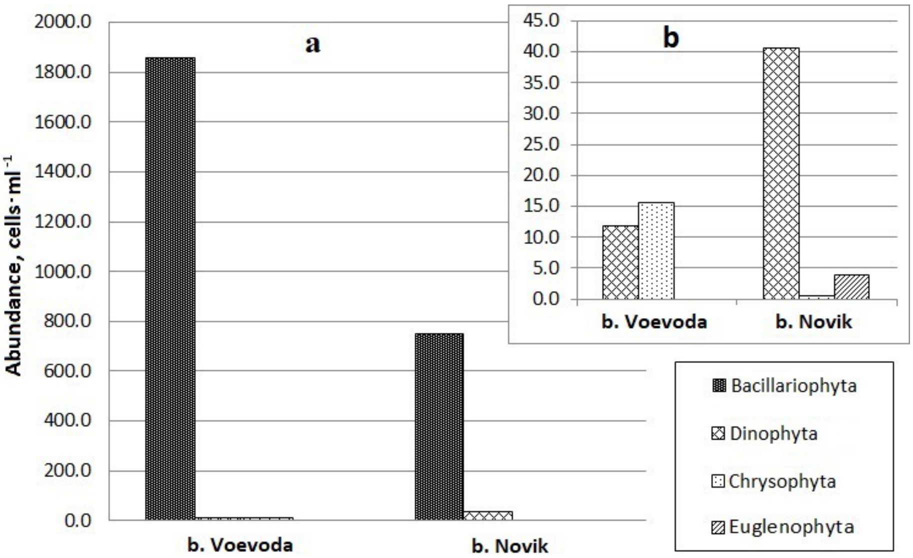

Fig. 5. Diagrams of microalgal divisions abundance in 2020: a, for representatives of prevailing divisions; b, for representatives of small divisions

Low species richness and structural evenness of the MA community in both biotopes are evidenced by the values of species diversity index (1.7 and 1.6 for ice and phytoplankton, respectively) and evenness index (0.4 and 0.5, respectively).

In ice of the Novik Bay in 2020, an order of magnitude lower MA abundance was recorded than in the Voevoda Bay (189 cells·mL^{-1}). A diatom *T. nordenskioeldii* prevailed, with a ratio of 22.63 % of the total abundance – higher than the ratio in the Voevoda Bay (5 %). The sub-prevailing species were *Pseudo-nitzschia pungens* (Grunow ex Cleve) Hasle, 1993 (19.12 %), *N. frigida* (16.32 %), and *C. closterium* (12.90 %). In phytoplankton, cell abundance was 606 cells·mL^{-1} – an order of magnitude higher than the value in the Voevoda Bay; a diatom *Thalassiosira gravida* Cleve, 1896 prevailed (88.83 % of the total abundance).

In the Novik Bay in 2020, the total MA biomass in the ice core and phytoplankton was similar to the value in the Voevoda Bay. In the ice core, the biomass was 3,071.7 mg·m^{-3}, and this was much lower than that in the Voevoda Bay. The biomass in the bay phytoplankton was 7,259.1 mg·m^{-3} – an order of magnitude higher than the values obtained for the Voevoda Bay.

MA species richness in the Novik Bay turned out to be significantly higher in ice than in phytoplankton; this is confirmed by the Shannon–Wiener index values (2.6 and 0.6 for ice and phytoplankton, respectively). Moreover, a considerable difference was observed in the Pielou index values (0.8 and 0.2, respectively) indicating a higher level of structural evenness in ice than in phytoplankton.

In the Voevoda Bay in 2021, the total cell abundance was an order of magnitude higher than in 2020. Specifically, it was 5,360 cells·mL^{-1} in the ice core – an order of magnitude higher than the values obtained for ice of this bay in the previous year. A diatom *Chaetoceros socialis* f. *radians* prevailed (46.22 % of the total abundance). *Navicula granii* (Jørgensen) Gran, 1908 (12.29 %), *Nitzschia* sp. (11.34 %), and unidentified prasinophytes (9.93 %) were the sub-prevailing species. Cell abundance in phytoplankton was 6,658 cells·mL^{-1} which was two orders of magnitude higher than the value for this biotope in 2020. The prevailing species was a cryptophyte *Plagioselmis* sp. (67.59 %); significant contribution was made by diatoms *T. nordenskioeldii* (11.26 %) and *Nitzschia* sp. (7.5 %).

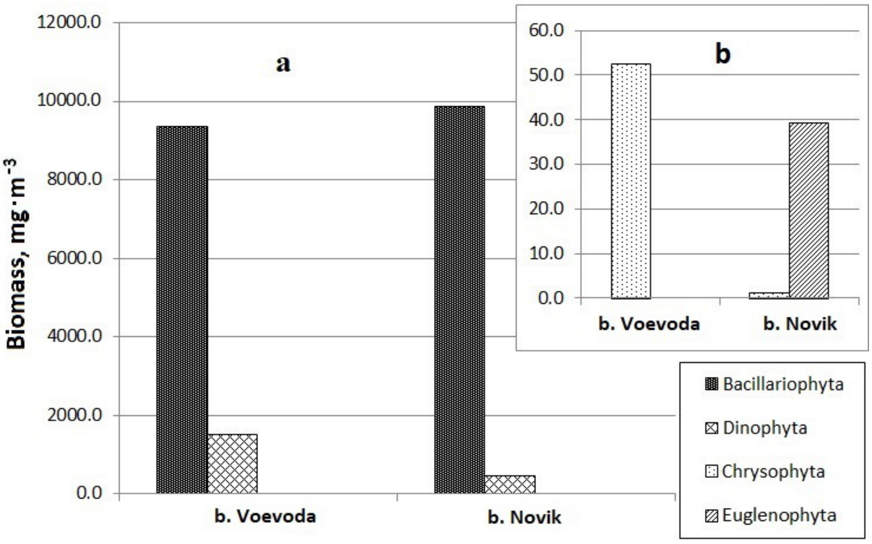

Fig. 6. Diagrams of microalgal divisions biomass in 2020: a, for representatives of prevailing divisions; b, for representatives of small divisions

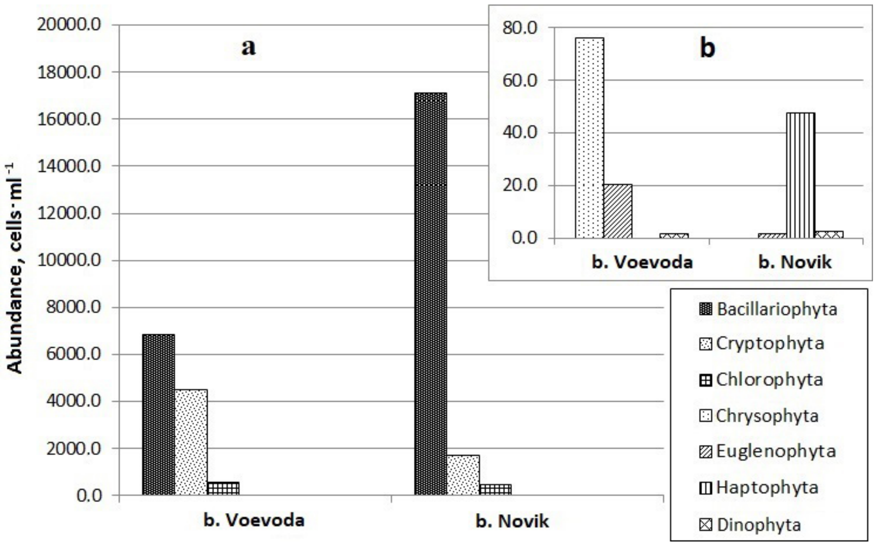

Fig. 7. Diagrams of microalgal divisions abundance in 2021: a, for representatives of prevailing divisions; b, for representatives of small divisions

In ice samples, MA biomass was 12,158.8 mg·m^{-3}; in phytoplankton, it was 41,973.1 mg·m^{-3}. Compared to phytoplankton, ice was characterized by higher species richness (the Shannon–Wiener index values were 2.8 and 1.2, respectively) and evenness (the Pielou index values were 0.7 and 0.4, respectively).

In the Novik Bay in 2021, the total cell abundance in ice and phytoplankton was an order of magnitude higher than in 2020. Abundance in the ice core was 12,709 cells·mL^{-1}; algae *Nitzschia* sp. and *N. frigida* prevailed (51.90 and 28.43 %, respectively). Less significant contribution was made by the species *Entomoneis gigantea* var. *decussata* (Grunow) Nizamuddin, 1982 (5.96 %), *Navicula septentrionalis* Cleve, 1896 (4.59 %), and unidentified prasinophytes (3.61 %). In phytoplankton, abundance was 6,694 cells·mL^{-1}. *T. nordenskioeldii* (34.14 %) and *Plagioselmis* sp. (25.61 %) were the prevailing species, while *N. septentrionalis* (11.95 %), *N. granii* (7.34 %), and *N. frigida* (5.12 %) were the sub-prevailing ones.

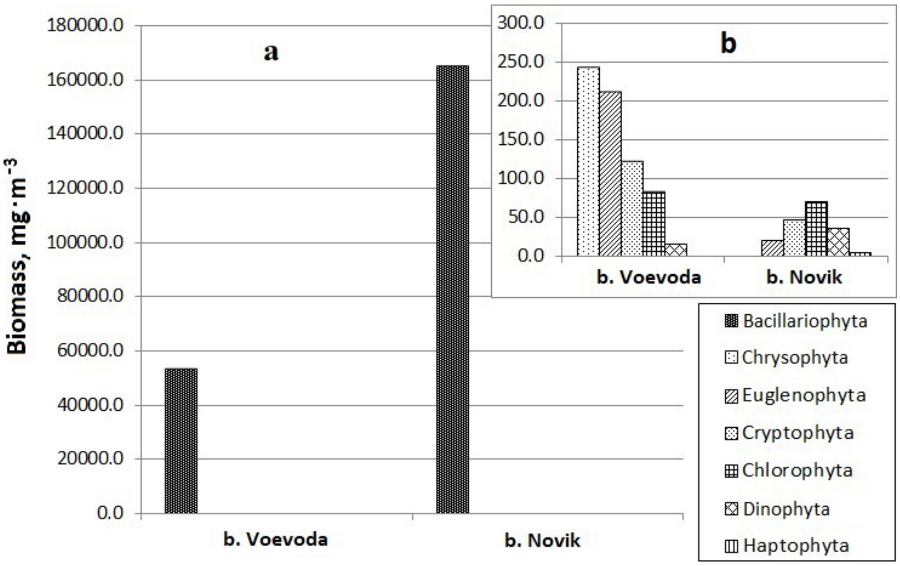

Fig. 8. Diagrams of microalgal divisions biomass in 2021: a, for representatives of prevailing divisions; b, for representatives of small divisions

MA biomass in ice was 54,075.6 mg·m^{-3}; the value in phytoplankton was 111,247 mg·m^{-3}. As in 2020, species richness and its evenness in 2021 in the ice biotope were higher (the values of the indices were 2.8 and 0.8, respectively) than in the phytoplankton biotope (the values were 1.8 and 0.6, respectively).

DISCUSSION

Study of sea ice and under-ice phytoplankton in Russky Island bays was carried out during two winter periods and showed more or less significant differences in the quantitative structure of the MA community. The most considerable differences in the quantitative structure were revealed by the years of the investigation: in 2020, MA communities were generally characterized by low species richness. A difference was recorded in terms of quantitative characteristics of the ice and phytoplankton biotopes between the studied bays as well. Specifically, in the Voevoda Bay, MA abundance and biomass in ice significantly exceeded the values for phytoplankton; in the Novik Bay, the opposite pattern was recorded. The total cell abundance in the Novik Bay was two times lower than the value in the Voevoda Bay, while the total biomass was comparable.

In 2021, species richness and evenness, as well as the quantitative structure, were characterized by higher values in both bays. Differences in MA abundance in the Voevoda Bay were insignificant between the ice biotope and the phytoplankton one, while the value of biomass in under-ice water was three times higher than that in ice. A slightly different pattern was observed in the Novik Bay: cell abundance in ice was two times higher than in phytoplankton, and the value of biomass in phytoplankton was two times higher than that in ice. In total, MA flora in the Novik Bay was characterized by higher values of the quantitative indicators in both biotopes than in the Voevoda Bay. Phytoplankton was the exception: its abundance was comparable for two bays.

Importantly, during sampling (in February), the ice cores had no visual coloration indicating MA mass development. However, according to V. Buinitskii (1973) who carried out similar studies in the Antarctic in 1962, MA abundance is not always reflected in ice color intensity. In our case, the lack of coloration can be explained by significant thickness of the ice cover over which algae are distributed during its formation. In 2020 and 2021, considerable thickness of the ice cover in Russky Island bays was recorded (38 to 64 cm), and these values are not typical for most studies of young ice in polar regions. Specifically, according to the recent investigation of young Arctic ice by Norwegian researchers (Kauko et al., 2018), the ice cover was about 27 cm thick.

The results obtained are consistent with the literature data on the quantitative structure of MA communities in Peter the Great Bay in winter. According to the material published, the basis of the ice and under-ice algae community is formed by the diatoms – in terms of both species composition and quantitative structure. In various works, due to differences in meteorological, hydrochemical, and other conditions for specific water areas, different data are given on their quantitative ratio in a community (50 to 100 % of the total abundance). In the ice biotope, flagellate algae – mainly dinoflagellates – are usually less abundant; in 2020, their quantitative contribution was similar to that from the literature (Kauko et al., 2018). In 2021, representatives of green algae were the second in terms of abundance (following diatoms). The ratios of golden and euglena algae were the lowest, and this is also consistent with the results of the original study.

Many MA species prevailing and sub-prevailing in ice of Russky Island bays were registered in other works focused on phytoplankton in winter. Specifically, high abundance of a planktonic diatom *Chaetoceros socialis* f. *radians* was repeatedly noted in February in the southeastern Sea of Japan (Konovalova et al., 1989), *inter alia* in the Amur Bay (Orlova et al., 2009). A benthic–planktonic diatom *Cylindrotheca closterium* was previously reported for phytoplankton (Konovalova et al., 1989) and for microphytobenthos of Peter the Great Bay (Ryabushko, 1990 ; Ryabushko et al., 2019). Another prevailing species of the ice flora – a planktonic diatom *Nitzschia frigida* – was recorded among the prevailing representatives of the Arctic ice biotope as well (Kauko et al., 2018). Its mass development was observed in Peter the Great Bay water areas (Begun et al., 2011 ; Ponomareva, 2017). Moreover, representative of this genus – *Nitzschia* sp. – was also reported among prevailing ice-related MA species in the Amur Bay of the Sea of Japan (Kuznetsov, 1980).

Out of prevailing MA of the sea ice in Russky Island water areas, a planktonic diatom *Thalassiosira nordenskioeldii* should be noted. This species prevailed in under-ice phytoplankton in winter and spring and reached its maximum blooming force at low and negative water temperatures in some Peter the Great Bay water areas (Begun et al., 2011 ; Konovalova et al., 1989 ; Shevchenko et al., 2020), *inter alia* in the Paris Bay (Ponomareva, 2017). In winter, a diatom *Thalassiosira gravida* and the species of the genus *Pseudo-nitzschia* were recorded as prevailing ones in Peter the Great Bay coastal areas (Konovalova et al., 1989 ; Orlova et al., 2009 ; Ponomareva, 2017) and in young Arctic ice (Kauko et al., 2018). Less abundant species of the ice and plankton biotopes of Russky Island – a dinoflagellate *Protoperidinium depressum* and a diatom *Coscinodiscus oculus-iridis* Ehrenberg, 1840 – were noted in Peter the Great Bay water areas in late winter and in spring (Konovalova et al., 1989).

For the first time for phytoplankton of Peter the Great Bay, the prevalence of representatives of the division Cryptophyta – *Plagioselmis* species – was registered. According to the literature data, cryptophytic algae of this genus prevailed in the Golden Horn Bay in September (Stonik, 2018). Moreover, *Plagioselmis* species were recorded among MA of the Amur Bay plankton, but those were not the prevailing ones (Orlova et al., 2009).

Other MA registered in ice during our study were mentioned in the composition of the prevailing MA in the work of L. Kuznetsov on ice MA of the Amur Bay (1980). Among them, there were a golden alga *Octactis speculum* and a diatom *Entomoneis paludosa* (W. Smith) Reimer, 1975 representing the same genus as *Entomoneis gigantea* var. *decussata* which was found by us in small abundance.

According to the literature data (Kauko et al., 2018), during the sea ice formation, MA cells present in the water column become incorporated into ice composition due to complex processes of turbulent mixing. However, several researchers showed that not only phytoplankton, but also benthos is a source of replenishment for the ice biotope (Olsen et al., 2017 ; Ratkova & Wassmann, 2005). According to some authors (Okolodkov, 1992 ; Niemi et al., 2011), as young ice develops, centric diatoms become more abundant than pennate ones. In accordance with other data (Campbell et al., 2018 ; Galindo et al., 2017), during the sea ice formation, centric diatoms begin to quantitatively prevail over pennate ones or dinoflagellates. There are also investigations indicating the following: in general, the prevalence of pennate diatoms is the main stage of succession during the blooming of the representatives of ice flora communities (Leeuwe et al., 2018 ; Leu et al., 2015).

In the Vostok Bay (the Sea of Japan) in January 1980 at a depth of 0.5 m and a water temperature of −1.2 °C during the ice cover formation on rocky soils, maximum biomass of diatoms reached 2,576 $\text{mg}\cdot\text{m}^{-2}$ due to benthic–planktonic species *Odontella aurita* (Lyngbye) C. Agardh, 1832 and *Melosira moniliformis* (O. F. Müller) C. Agardh, 1824. Those – along with pennate diatoms *Tabularia tabulata* (C. Agardh) Snoeijs, 1992 and *Licmophora abbreviata* C. Agardh, 1831 and a small-cell species *Diatomella salina* var. *septata* (Nikolaev) I. V. Makarova, 1968 – formed a massive accumulation at the very ice edge (Ryabushko, 1990). The listed species were also found by us in MA communities of the studied bays, but in contrast to the above-mentioned investigations, our study showed that the basis of ice MA in Russky Island bays was formed by planktonic diatoms from the classes Coscinodiscophyceae and Bacillariophyceae. Apparently, this is due to climatic peculiarities of different years manifesting during ice formation and due to specific abiotic environmental characteristics of local habitats in each water area studied.

The data obtained by us do not allow drawing conclusions on succession processes of sea ice, since the material was sampled once – in February. At the same time, in the ice flora in Russky Island water areas, one can observe a mixed composition of MA life forms which are the basis of the quantitative structure of ice studied.

As a result of the study carried out during the ice period of 2020 and 2021, differences were registered in the quantitative structure of sea ice MA and under-ice water MA in the Voevoda and Novik bays (sometimes, by more than an order of magnitude). The differences in the total MA abundance and biomass in the ice biotope depended on the year of the study, water area, and ice layer. Those could be related to the peculiarities of the hydrometeorological regime formed in Peter the Great Bay water areas in different years, as well as to specifics of hydrological and hydrochemical parameters of the aquatic environment in each water area studied.

Conclusion. For the first time for the latitude of Peter the Great Bay (the Sea of Japan), the quantitative structure of sea ice microalgae communities in the Voevoda and Novik bays of Russky Island was studied. In total, 88 species from 50 genera and 7 divisions were identified. The ice biotope was characterized by a higher species richness compared to the phytoplankton biotope: in ice, 80 species from 7 divisions were recorded; in phytoplankton, 40 species from 5 divisions were registered.

In the MA communities in ice, diatoms *Chaetoceros socialis* f. *radians*, *N. frigida*, *T. nordenskioeldii*, and *Nitzschia* sp. prevailed. For the first time for Peter the Great Bay, the prevalence of a cryptophytic algae *Plagioselmis* was registered in the under-ice phytoplankton.

The study covered the main quantitative characteristics of MA of two biotopes and ice core horizons in two Russky Island bays. A sufficiently high level of quantitative abundance in the ice cover of the Voevoda and Novik bays was established. In the first year of the study, the MA communities were characterized by considerably lower MA abundance and biomass compared to those of the second year. Diatoms formed the basis of the quantitative structure of the community, with abundance values reaching 1,861.2 cells·mL^{-1} for the Voevoda Bay and 751.2 cells·mL^{-1} for the Novik Bay in 2020. In 2021, the values were 6,846.3 and 17,143.1 cells·mL^{-1}, respectively.

In the Voevoda Bay in 2020, cell abundance was maximum in the upper layer of the ice core and gradually decreased closer to a border with under-ice water, while in the Novik Bay, it was distributed approximately evenly throughout the core. In the Voevoda Bay in 2021, the opposite pattern was recorded: microalgae abundance was minimal in the upper layers of the ice core and gradually increased as moving down, to a border with under-ice water. In the Novik Bay, maximum MA abundance was registered in the upper layer of the ice core, with a relatively uniform distribution over all layers.

Thus, the differences are shown in MA quantitative structure in ice samples of two bays depending on a layer of the ice core, year, and study area. Further investigation of sea ice in Peter the Great Bay is required – first of all, in the seasonal aspect: at this geographical latitude, a stable ice cover can be formed only in this water area.

Acknowledgment. The authors are grateful to the colleagues from POI FEB RAS – P. Tishchenko, P. Semkin, Yu. Barabanshchikov, and S. Sagalaev – for their assistance in organizing and carrying out field work. The authors also thank T. Orlova and A. Lazaryuk for scientific advice. The work was carried out on the basis of the resource collection “Marine Biobank” at NSCMB FEB RAS.

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КОЛИЧЕСТВЕННАЯ СТРУКТУРА СООБЩЕСТВА МИКРОВОДОРОСЛЕЙ МОРСКОГО ЛЬДА (ОСТРОВ РУССКИЙ, ЗАЛИВ ПЕТРА ВЕЛИКОГО, ЯПОНСКОЕ МОРЕ)

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Впервые для российского прибрежья Японского моря изучена количественная структура сообщества микроводорослей морского льда. Исследованием охвачены биотопы льда и подлёдного фитопланктона двух бухт острова Русский в зимний период 2020 и 2021 гг. Идентифицировано 88 видов микроводорослей из 50 родов и 7 отделов. Установлено, что сообщество микроводорослей льда характеризовалось бо́льшим видовым богатством, чем подлёдный фитопланктон. Среди доминирующих видов наиболее многочисленными были планктонные диатомовые водоросли *Chaetoceros socialis* f. *radians*, *Nitzschia frigida*, *Thalassiosira nordenskioeldii* и *Nitzschia* sp. Диатомеи составляли основу сообщества, достигая в 2020 г. численности 1861,2 кл.·мл$^{-1}$ в бух. Воевода и 751,2 кл.·мл$^{-1}$ в бух. Новик, а в 2021 г. — 6846,3 и 17143,1 кл.·мл$^{-1}$ соответственно. В 2020 г. в бух. Воевода численность клеток была максимальной в верхнем слое ледового керна и постепенно снижалась ближе к границе с подлёдной водой; в бух. Новик она была распределена почти равномерно по всему керну. В 2021 г. в бух. Воевода отмечена противоположная закономерность: в верхних слоях керна численность микроводорослей была минимальной, а по ходу продвижения вниз, к границе с подлёдной водой, она постепенно возрастала. В бух. Новик максимум численности зарегистрирован в верхнем слое керна, притом что распределение по всем слоям было относительно равномерным. Таким образом, показаны различия в количественной структуре микроводорослей льда в зависимости от слоя ледового керна, года и места исследования.

Keywords: quantitative structure, microalgae, phytoplankton, Peter the Great Bay, Russky Island, Sea of Japan

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Морской биологический журнал
Marine Biological Journal
2022, vol. 7, no. 2, pp. 113–114
https://marine-biology.ru

CHRONICLE AND INFORMATION

IN MEMORIAM: OLEG MIRONOV
(09.03.1933 – 16.03.2022)

On 16 March, 2022, at the age of 89, Prof., D. Sc. Oleg Mironov passed away. He organized the first marine sanitary hydrobiology laboratory in the USSR (1964) which was transformed in 1971 into the department.

Almost all his scientific activities were connected with the Sevastopol Biological Station and IBSS. He worked here as a librarian even *prior* to going to university. In 1952, he entered Kirov Military Medical Academy in Leningrad and began specializing in marine sanitary ecology. In 1963, after defending his PhD thesis in medical science, he started working at IBSS of the Academy of Sciences of the Ukrainian SSR as a junior researcher. In 1964, IBSS scientific council decided to develop research on marine sanitary biology at the institute, and O. Mironov was instructed to organize the laboratory. In 1971 on the base of this laboratory, the marine sanitary hydrobiology department was formed. In 1970, he defended D. Sc. dissertation in biology and launched experimental and field research which is still of great scientific and practical interest.

He was the first to study on a large scale the effect of oil and oil products in various concentration ranges on mass hydrobiont species. The investigation carried out allowed to make recommendations on biotesting of polluted seawater and to provide material for the establishment of maximum permissible concentrations for seafloor sediments. Oleg Mironov obtained new data on the patterns of distribution, abundance, biochemical peculiarities, and species composition of oil-oxidizing microorganisms in the Black, Red, and Mediterranean seas, as well as in some areas of the Pacific, Indian, and Atlantic oceans. He was the first to carry out such studies, and those reflected a new stage in the development of marine and oceanic microbiology. Based on the investigation of destructive activity of hydrocarbon-oxidizing microorganisms, he calculated the potential ability of the Black Sea to self-purify from oil pollution.

By the mid-1970s, he substantiated the fundamental concept of interaction of hydrobionts and their communities with pollution as a part of the general natural process of matter transformation and energy transfer in the marine environment. This concept both determined the main directions of the department's research for decades and became the basis of the international program on oil pollution biomonitoring in the Mediterranean basin. O. Mironov developed the scientific directions of great relevance.

O. Mironov and V. Tyninika, captain of the RV "Professor Vodyanitsky"

This was confirmed by the fact that the staff of the marine sanitary hydrobiology department was involved in the key state programs and projects – "World Ocean", "GIZM", "Environment", GESAMP (Joint group of experts on the scientific aspects of marine environmental protection), *etc.* The research covered waters of the Black, Caspian, and Barents seas, *inter alia* several areas of the Pacific coast.

Oleg Mironov created the basic concept of the purposeful use of hydrobionts and their communities for purification and sanitation of polluted (oil-containing) seawater in coastal areas. The concept was implemented: technical hydrobiological systems were located in several anthropogenically stressed coastal water areas of Sevastopol. This repeatedly confirmed the applied significance of fundamental research of the marine sanitary hydrobiology department.

His contribution to the formation of a system of long-term monitoring studies in Sevastopol coastal and marine areas is invaluable. In 1973, he was the first to organize complex chemical and biological surveys of practically all the city bays, and the investigations are carried out till now.

O. Mironov published more than 400 scientific papers. The results of the studies are summarized in several monographs edited by him: "Interaction between sea organisms and oil hydrocarbons" (1985), "Sanitary-biological aspects of the Sevastopol bays ecology in XX century" (2003), "Sanitary-biological investigations in coastal area of Sevastopol region" (2009), *etc.* Those present a unique and scientifically based "anthropogenic history" of the area.

A talented scientist and an excellent organizer, Oleg Mironov created a school of marine sanitary hydrobiologists–ecologists. Under his supervision, more than 20 PhD theses were defended, as well as 1 D. Sc. dissertation. He was an active science communicator – he repeatedly appeared on television and gave comments in other media on actual environmental problems of the city and the country.

O. Mironov was born by the sea, truly loved it, and devoted his whole life to it. The bright memory of an outstanding scientist and amazing person will forever remain in our hearts.

Students, colleagues, and friends

ПАМЯТИ ОЛЕГА ГЛЕБОВИЧА МИРОНОВА
(09.03.1933 – 16.03.2022)

16 марта 2022 г. ушёл из жизни Олег Глебович Миронов — профессор, доктор биологических и кандидат медицинских наук, организатор первой в СССР лаборатории морской санитарной гидробиологии. Олег Глебович внёс огромный вклад в становление системы долгосрочных мониторинговых исследований прибрежно-морских зон Севастополя и стал автором более чем 400 научных работ.

Учредитель и издатель журнала:
Федеральное государственное бюджетное учреждение науки
Федеральный исследовательский центр
«Институт биологии южных морей
имени А. О. Ковалевского РАН»
(ОГРН 1159204018478)

Соиздатель журнала:
Федеральное государственное бюджетное учреждение науки
Зоологический институт РАН

Рекомендовано к печати решением учёного совета
Федерального государственного бюджетного учреждения науки
Федерального исследовательского центра
«Институт биологии южных морей
имени А. О. Ковалевского РАН»
(протокол № 4 от 03.03.2022).

Журнал зарегистрирован в Федеральной службе по надзору в сфере связи,
информационных технологий и массовых коммуникаций
(свидетельство о регистрации средства массовой информации
ПИ № ФС 77 - 76872 от 24.09.2019).

Выпускающий редактор номера:
д. б. н., проф. Довгаль И. В.

Корректор:
Копытова О. Ю.

Перевод:
Тренкеншу Т. А., Надточенко И. А.

Компьютерная вёрстка:
Баяндин А. С.

Оригинал-макет подготовлен в пакете XeLaTeX (TeX Live 2015 / Debian Linux)
с использованием свободных шрифтов FreeSerif и FreeSans.

Подп. к печати 03.03.2022 Дата выхода в свет 07.06.2022 Заказ № 49993 Тираж 100 экз.
Формат 60 × 84/8 Уч.-изд. листов 9,3 Усл. печ. листов 13,25 Печать цифровая

Отпечатано в типографии: ИП Ермолов М. П., ОГРНИП 314920436710081 от 26.12.2014;
ул. Кулакова, д. 59, г. Севастополь, 299011;
тел.: +7 978 70-45-111; e-mail: print-e@yandex.ru.

ISSN 2499-9768
9 772499 976005 22002 >

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Институт биологии южных морей
имени А. О. Ковалевского РАН,
Зоологический институт РАН

издают
научный журнал

Морской биологический журнал
Marine Biological Journal

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- Периодичность — четыре раза в год.
- Подписной индекс в каталоге «Пресса России» — Е38872. Цена свободная.

Заказать журнал

можно в научно-информационном отделе ИнБЮМ.
Адрес: ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН», пр. Нахимова, 2, г. Севастополь, 299011, Российская Федерация.
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ISSN 2499-9768 *Морской биологический журнал Marine Biological Journal* 2022 Том 7 № 2