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

© 2022 **N. A. Boltachova, N. K. Revkov, A. A. Nadolny, and I. N. Anninskaya**

A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation
E-mail: *nrevkov@yandex.ru*

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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 84^{th}, 86^{th}, 90^{th}, 96^{th}, and 100^{th} 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.$\cdot$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.$\cdot$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.

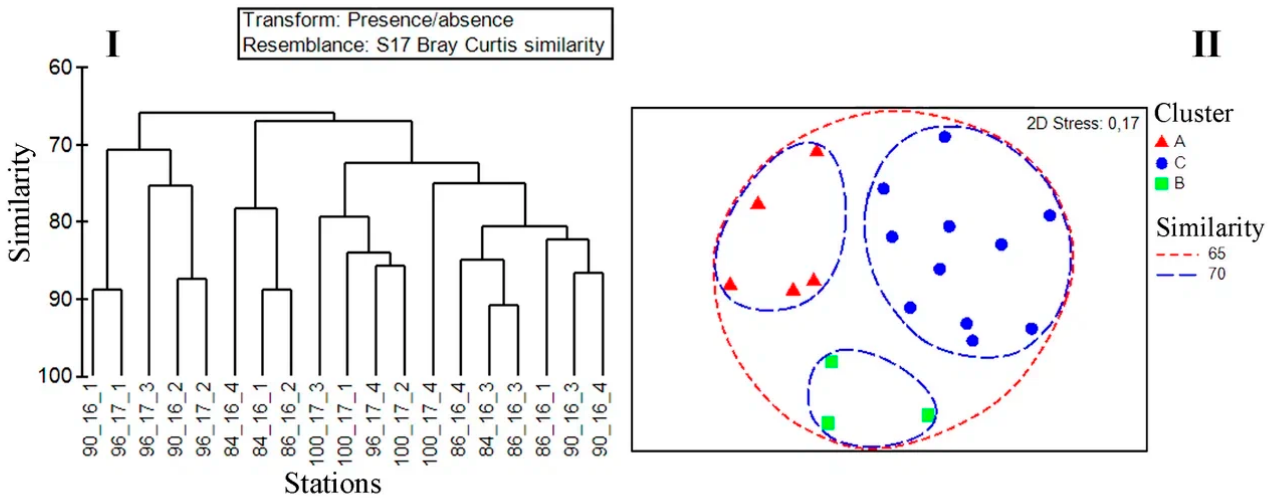

Fig. 2. Hierarchical clustering (I) and MDS ordination (II) of sampling stations in the southwestern Sea of Azov in 2016–2017. On I, the designation is "cruise_year_station"

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.

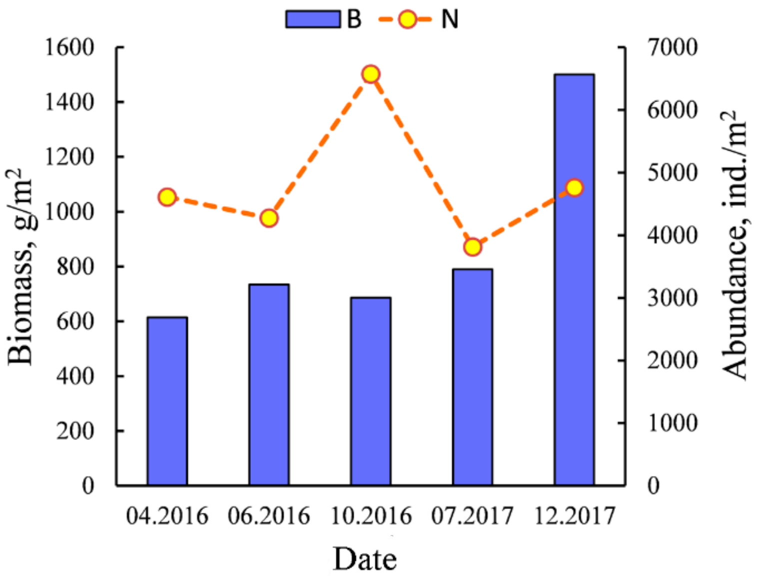

Fig. 3. Changes in abundance (N) and biomass (B) of macrozoobenthos in *Anadara* biocoenosis in the southwestern Sea of Azov in 2016–2017

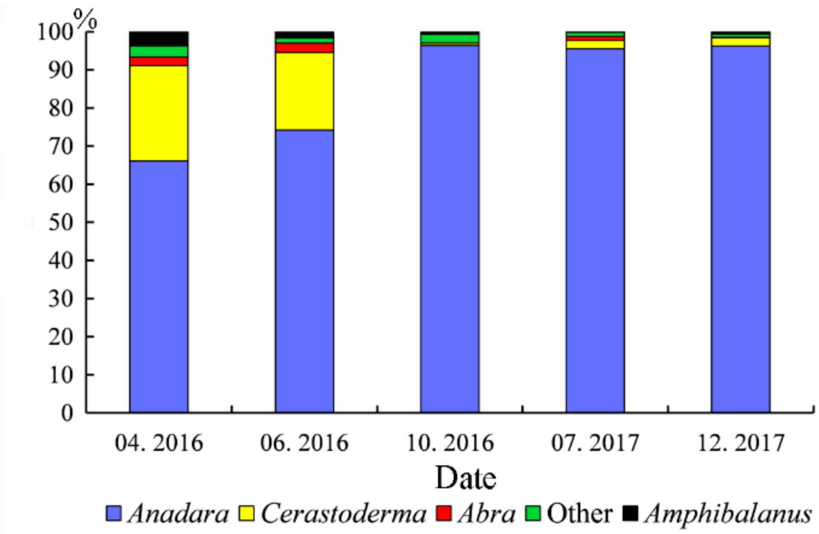

Fig. 4. Changes in the structure of *Anadara* biocoenosis in 2016–2017 in the southwestern Sea of Azov

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.

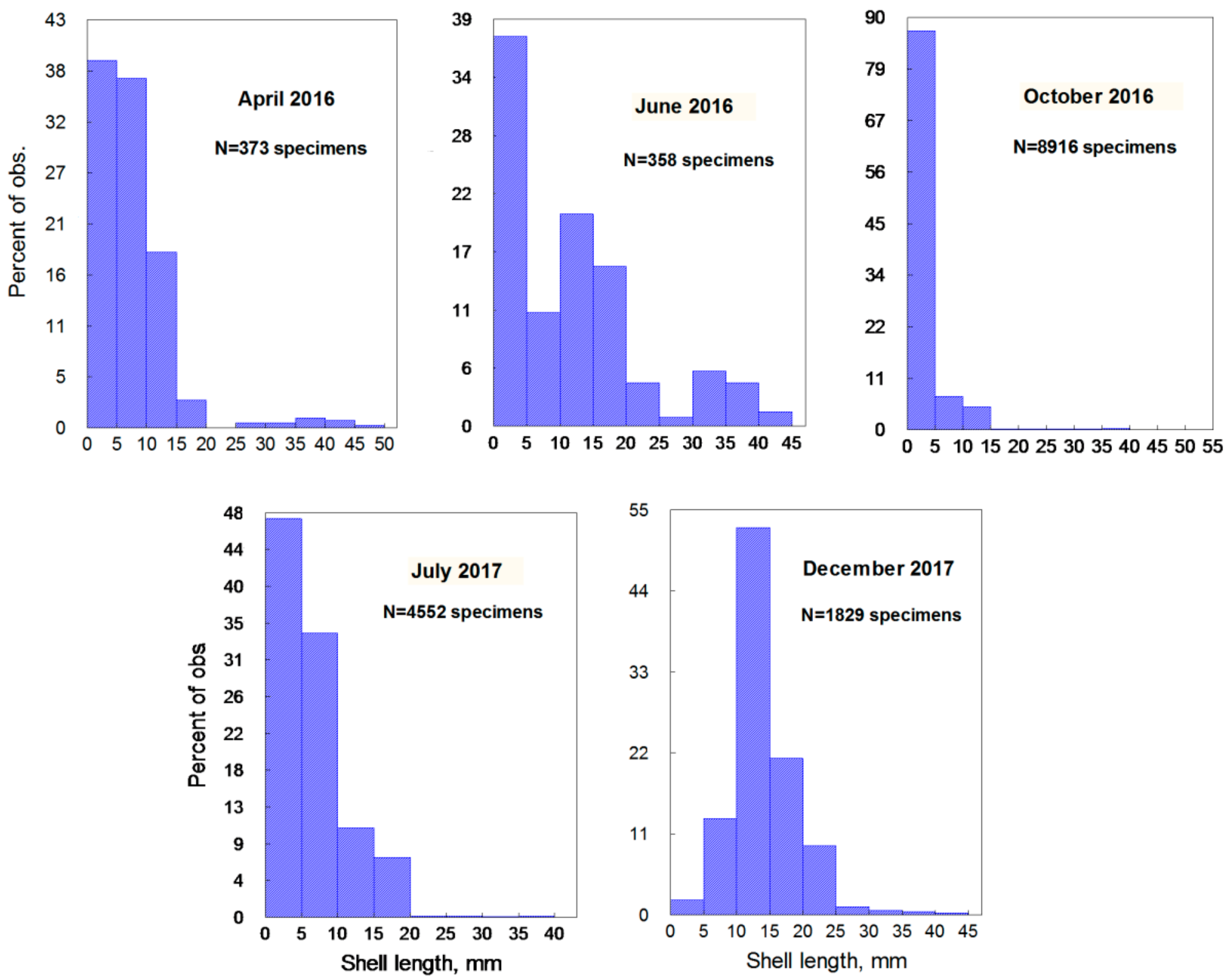

Fig. 5. Histograms of the shell-size composition of *Anadara kagoshimensis* population in the southwestern Sea of Azov in different seasons of 2016–2017

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+.

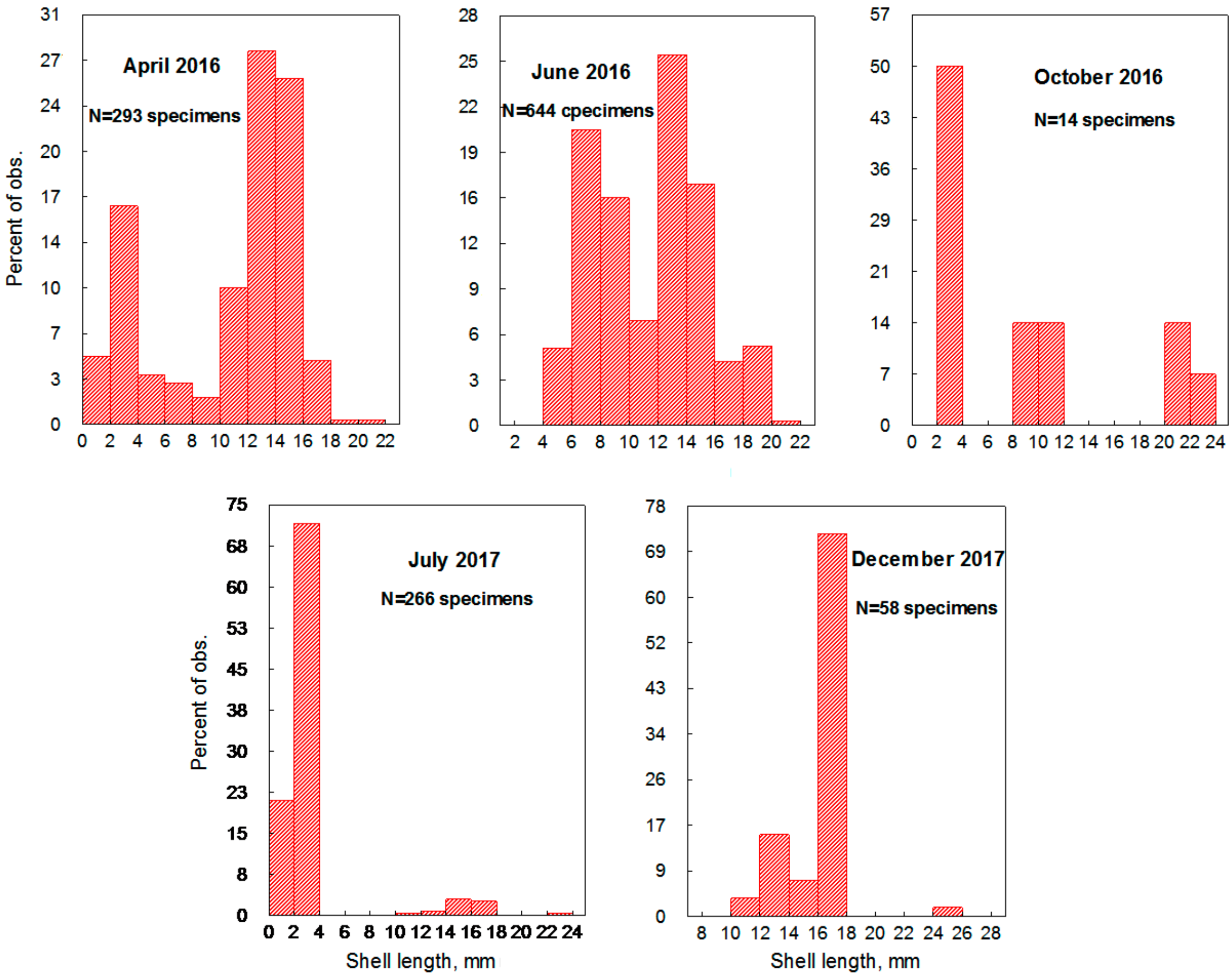

Fig. 6. Histograms of the shell-size composition of *Cerastoderma glaucum* population in the southwestern Sea of Azov in different seasons of 2016–2017

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.$\cdot$m^{-2} and (878.4 ± 129.5) g$\cdot$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.

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

Н. А. Болтачева, Н. К. Ревков, А. А. Надольный, И. Н. Аннинская

ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН»,
Севастополь, Российская Федерация
E-mail: *nrevkov@yandex.ru*

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