1871
ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2025, vol. 10, no. 2, pp. 34–60
https://marine-biology.ru

UDC 594-155.3(262.5)

TAXOCENE OF MOLLUSCS OF COASTAL SOFT SEDIMENTS IN THE NORTHEASTERN SECTOR OF THE BLACK SEA AT THE BEGINNING OF THE XXI CENTURY

© 2025 **G. Kolyuchkina[1], I. Lyubimov[1], and N. Danilova[1,2]**

[1]Shirshov Institute of Oceanology of Russian Academy of Sciences, Moscow, Russian Federation
[2]Russian State Agrarian University – Moscow Timiryazev Agricultural Academy, Moscow, Russian Federation
E-mail: *galka.sio@gmail.com*

Received by the Editor 13.11.2023; after reviewing 19.04.2024;
accepted for publication 20.03.2025.

The key question of modern ecology is to understand the relationship between changes in marine ecosystems and the environment under ongoing climate change and increasing anthropogenic load. However, not all changes occurring in marine shelf ecosystems can be explained by the action of external factors, since the dynamics of ecosystems associated with internal processes, such as natural succession, is poorly understood. Benthic communities play a crucial role in ecosystem functioning by modifying habitats and affecting nutrient cycling and primary productivity. Bottom ecosystems are associated with the potential for carbon immobilization and sequestration the assessment of which remains a fundamental scientific challenge. Coastal communities of the Black Sea are a convenient model for such studies. Carbonate-producing organisms – molluscs – dominate in benthic ecosystems of this basin. The aim of the present work was to investigate the dynamics of abundance and population structure of molluscs in soft sediments of the coastal zone of the Black Sea at the North Caucasus in 2015–2022. Annual sampling was carried out at depths of 10 and 25 m. The structure of the mollusc taxocene and the dynamics of the size structure of populations of its main dominants were analyzed: at 10-m depth, *Chamelea gallina* and *Lucinella divaricata*; at 25-m depth, *Gouldia minima* and *Pitar rudis*. Fluctuations in their abundance reached orders of magnitude. The highest taxocene biomass was recorded in 2020 which coincided with the maximum surface water temperature and salinity (a drought period). Successful annual recruitment and multimodal appearance of size–frequency diagrams of these species were observed, except for *G. minima*, as its juvenile stages were almost absent in the samples. Based on the analysis of size–frequency diagrams, an attempt was made to estimate the mean limiting age of individuals in the population of these species. No linear relationships were revealed between values of abiotic factors and the taxocene structure. Trends of parallel changes in abundance of juveniles in a population and total biomass of each of the studied species were characterized.

Keywords: Black Sea, bivalves, macrozoobenthos, population dynamics

Benthic communities play a key role in functioning of marine ecosystems by modifying habitats and affecting nutrient cycling and primary productivity. Benthic ecosystems are associated with the possibility of carbon immobilization and sequestration, and their assessment remains a fundamental scientific problem [Romankevich, Vetrov, 2001]. In the context of more and more active climate and anthropogenic changes, the main issue of modern ecology is to study the formation of the response of marine ecosystems: structural rearrangements of communities, alterations in trophic interactions, and species adaptation to fluctuating environmental conditions. Interestingly, not all changes occurring in benthos of the marine shelf can be explained by the effect of external factors alone. The dynamics of ecosystems driven by the effect of internal processes, such as natural successions, has been studied fragmentary [Zhirkov, 2010]. Macrozoobenthic communities of soft bottom sediments of the Black Sea are a convenient model for this kind of research. There are no papers on the dynamics of Black Sea macrozoobenthos analyzing a unified series of long-term data (4–5 years and more). However, the Black Sea benthic ecosystems are known to have undergone dramatic changes in the late XX–early XXI century. The reasons for these transformations are rooted in uncontrolled overfishing, regulation of large watercourses flowing into the Black Sea, anthropogenic hypereutrophication of the basin, and its increased pollution in the early XX century [Bologa et al., 1995]. Invasion of alien species has governed the transformation of communities as well. As a result, in the 1970s, there was a shift in biodiversity indices and macrozoobenthos abundance, with the northwestern Black Sea being most affected [Exotic Species in the Aegean, 2001; Marinov, Stoykov, 1990; Mitilidy, 1990; Revkov, 2003; Tiganus, 1997]. Hypereutrophication resulted in outbreaks in plankton proliferation followed by a gain in organic carbon content in the water column, an increase in sedimentation, and a drop in oxygen concentration in the bottom layer [Bologa et al., 1995]. In the northwestern Black Sea, annual hypoxia areas were formed, suffocation of the benthic community occurred, and the structure of bivalve population changed: juveniles became the predominant class [Bologa et al., 1995]. Subsequently, in the 1980s, there were an almost twofold decrease in the number of macrozoobenthos species, mainly due to crustaceans, a drop in the role of psammophiles, and a rise in pelophiles, *inter alia* far invaders [*Anadara kagoshimensis* (Tokunaga, 1906), Bivalvia] [Alekseev, Sinegub, 1992; Bologa et al., 1995]. Importantly, by the beginning of the XXI century, after disastrous transformations, a trend towards recovery of species diversity and community structure was observed in the northwestern Black Sea [Dumitrache, Abaza, 2004; Revkov et al., 2018].

Conversely, on the northeastern coast of the Black Sea, a decrease in species diversity of macrozoobenthos was recorded in 1999–2005 against the backdrop of significant annual fluctuations in abundance and biomass in *Chamelea gallina* (Linnaeus, 1758) biocenosis [Chikina, Kucheruk, 2005; Kucheruk et al., 2002]. This biocenosis was registered in the early XX century at depths of 10–30 m [Kiseleva, 1981, 1992]. By 1999, due to double pressure by predatory invaders [the warty comb jelly *Mnemiopsis leidyi* A. Agassiz, 1865 affected planktonic larval stages; a gastropod *Rapana venosa* (Valenciennes, 1846) affected adult bottom stages], bivalves were not found at 10–30 m [Kucheruk et al., 2002]. In the autumn of 1999, *Beroe ovata* Bruguière, 1789 – a new invasive obligate ctenophore – became highly abundant. The pressure on larval stages was weakened, and mass settling of bivalves was recorded along the entire coast of the North Caucasus from Gelendzhik to Adler [Chikina, Kucheruk, 2005; Kucheruk et al., 2002]. In 2001, biomass of the main dominants was more than 1 $kg\cdot m^{-2}$, and abundance was about 2.5 thousand $ind.\cdot m^{-2}$ [Chikina, Kucheruk, 2005]; by 2005, these indicators dropped to almost zero values [Kucheruk et al., 2012]. At a depth of 10–15 m, *Ch. gallina* remained the dominant, the same as in the XX century. However, at 20–30 m, the key species was *A. kagoshimensis*, an invader. By 2005, due to a re-gain in *R. venosa* pressure on bivalves, macrozoobenthos abundance and biomass decreased by an order of magnitude: down to 340–554 $ind.\cdot m^{-2}$ and 12–146 $g\cdot m^{-2}$, respectively [Chikina, 2009]. In 2005–2007, at depth of 10–15 m, *Ch. gallina* prevailed; at 20–30 m, *Pitar rudis* (Poli, 1795) dominated, the former minor species of its biocenosis [Chikina, 2009; Kucheruk et al., 2012]. The belt community was clearly divided into two zones in the 2010s as well [Kolyuchkina et al., 2020]. At the same time, in 2014–2017, an increasing role of a bivalve *Gouldia minima* (Montagu, 1803) was noted. Not registered in the early 2000s, this mollusc was one of the key species of *Ch. gallina* community in the XX century [Kiseleva, 1981]. Lately, there have been reports on stabilization of macrozoobenthos abundance and species diversity off the North Caucasus [Frolenko, Zhivoglyadova, 2020; Frolenko et al., 2019; Kolyuchkina et al., 2020; Selifonova, Chasovnikov, 2017], but none of the papers has analyzed long-term series of macrobenthos abundance and populations dynamics of the chief community dominants, bivalves. Researchers of the Shirshov Institute of Oceanology of RAS carried out annual monitoring of macrozoobenthos state in a narrow shelf area (the Inal Bay). The aim of this work was to study the structure and dynamics of Mollusca taxocene, as well as the dynamics of the population structure of dominant bivalves, and to reveal factors causing changes of mollusc taxocene in the Inal Bay at depths of 10 and 25 m in 2015–2022.

MATERIAL AND METHODS

The studies were carried out in 2015–2022 in late June–early July on the narrow shelf of the northeastern Black Sea near the Inal Bay (Tuapsinsky District, Krasnodar Krai, Russian Federation) during annual expeditions of the Shirshov Institute of Oceanology on the small research vessel "Ashamba." Sampling was carried out with an Ocean grab, with a capture area of 0.1 m^2, at depths of 10 m (N44.3276°, E38.6146°) and 25 m (N44.3212°, E38.6024°) in three replicates *per* station, except for samples from a depth of 25 m in 2021–2022 (there were two replicates). In total, 46 samples from 16 stations were analyzed. Upper 5 cm of bottom sediments were sampled from an additional grab with a plastic cylinder to determine the grain size. The mean surface water temperature in February–March at the Tuapse weather station area was derived from the website http://portal.esimo.ru/portal. Water temperature at the survey time was measured by a portable data logger Star-Oddi DST centi-TD (±0.1 °C).

Right after sampling, macrozoobenthic samples were thoroughly washed through a sieve with a mesh diameter of 0.5 mm and then fixed in 4% buffered formalin diluted by seawater. In a laboratory, all molluscs were picked from each sample, transferred to 75% ethanol, and taxonomically identified. Abundance and wet biomass of species in the samples were determined (on scales with a resolution up to 0.001 g), and the mean weight of individuals was established (the quotient of biomass and abundance). For each sample, the obtained data on abundance and biomass were recalculated *per* 1 m^2. Identification keys of the Black Sea fauna guide [1972] and lists of alien species [Shalovenkov, 2020] were used. The validity of species names (as of December 2023) was checked in the WoRMS taxonomic database [2023].

The grain size of sediments was analyzed by the staff of the analytical laboratory at the Shirshov Institute of Oceanology by the water–sieve method. The content of key fractions was determined: from < 0.01 to > 10 mm.

The main statistical data on the taxocene structure were processed in PRIMER v6.1.16 with PERMANOVA+ v1.0.6 add-on. The species diversity was assessed using the cumulative curve of accumulation of species abundance with an increase in the number of samples. The expected total number of species was established with the Chao2 estimator for the occurrence rate of rare species [Chao, 1987]. To identify sample groupings, cluster analysis was carried out. Similarity matrices were calculated using the Bray–Curtis index for $\log(x + 1)$-transformed biomass. *R. venosa*, a migratory predator feeding on other molluscs, was preliminarily excluded from the species list for the analysis of taxocene structure. In the present study, the rapa whelk abundance was considered as a factor. The SIMPROF method was used to determine the significance of differences between clusters (significance level of 0.01). The significance of differences between data sets was tested by non-parametric Permutational ANOVA (PERMANOVA). To confirm the adequacy of the methods applied (to assess the contribution of spatial and temporal factors to the variability of community structure), an additional two-factor PERMANOVA was performed on data on the log-transformed biomass of species in the samples for depths of 10 and 25 m (factor 1, depth; factor 2 nested in depth, year).

To identify the taxocene dynamics, we averaged similarity matrices of biomass data ('distance among centroids' procedure, PERMANOVA+); the year of the study served as a grouping factor [Anderson, 2001]. To reveal species with the greatest contribution to similarities and differences in clusters, we used the SIMPER procedure for the $\log(x+1)$-transformed biomass in the samples. Species contributing most to the taxocene biomass were considered dominant ones. Based on data on species occurrence rate in the samples within each cluster (sample grouping), we distinguished [Vorob'ev, 1949]: leading species ('constants'), with the occurrence rate of 50–100%; characteristic ones, 25–50%; and rare ones, less than 25%.

To analyze correlations between the macrozoobenthos structure and environmental factors, we applied the non-parametric regression analysis DistLM [Clarke, Gorley, 2006]; the Bray–Curtis index for $\log(x+1)$-transformed biomass of species in the samples was used as a measure of similarity. As predictors, we applied year from the beginning of the study, geographic coordinates reflecting spatial location of stations, grain size of sediments (10 fractions), the mean surface water temperature in February–March at the Tuapse weather station area, and abundance of a predatory gastropod *R. venosa*. Before the analysis, predictor data were normalized. The predictors were grouped by type (using 'group variables'); the selection criterion was Adjusted R^2, and the selection procedure was Stepwise. In all cases, $p < 0.001$ was considered a reliable value. For unified data (the number of species *per* station, as well as taxocene abundance and biomass), non-parametric Spearman correlation analysis was performed (the rank correlation coefficient R_{Sp}) with the same predictors; correlation was considered significant at $p < 0.001$. Pairwise differences between independent samples were assessed by the non-parametric Mann–Whitney test; differences were considered significant at $p < 0.001$.

For dominant species, we investigated the dynamics of the size structure of their populations analyzing totally all specimens of each species in two samples *per* station. If the total sample volume was less than 100 ind., material from three samples was united. If the number of individuals *per* sample exceeded 300, material from one sample was used. The number of studied samples could differ from the species number in a sample, since some molluscs were lost during repeated measurements, or their shells were damaged. We did nor re-measure damaged specimens. In total, 89.4–97.9% of individuals in the samples were measured. Shell length was determined for all specimens: totally, molluscs of each species from every investigated sample were separately placed on a flat surface and photographed with a scale ruler (division value of 0.1 mm), with a camera oriented parallel to the surface. The images obtained (300 dpi) were analyzed using ImageJ 1.53a (Wayne Rasband, National Institutes of Health, the USA). The accuracy of the software determination exceeded the division value of the scale ruler; so, values were rounded to 0.1 mm. The deviation of shell lengths obtained using the program and a caliper (division value of 0.02 mm) was 2.4%, or 0.3 mm (threefold measurement of shell lengths in the program; results of measurements with a caliper were taken as 100%). Thus, the accuracy of digital measurements was 0.3 mm. The size–frequency distributions were formed and analyzed in PAST 4.03 ('mixture analysis'). The procedure was based on the EM algorithm [Dempster et al., 1997] allowing to reveal local optima. The procedure automatically runs 20 times, each time with new random starting positions for a data array. The stability of the solution was checked by re-running the algorithm three times. The optimal solution (number of groupings) was chosen with simultaneous minimum value of the Akaike information criterion [Akaike, 1974] and maximum value of the logarithmic likelihood.

RESULTS

Habitat characteristics. The study area features sandy sediments (at a depth of 10 m) and sandy-gravel ones (at a depth of 25 m). At 10 m, there was practically no gravel fraction in sediments, (0.4 ± 0.8) %, in contrast to a depth of 25 m, where the gravel fraction reached (15.2 ± 8.9) % (Fig. 1). Siltation degree between 10 and 25 m differed insignificantly. In 2015–2022, a weakly noticeable trend of increasing pelite content was observed at a depth of 25 m ($R_{Sp} = 0.69$; $p = 0.06$).

Fig. 1. Grain-size distribution of bottom sediments (A); mean water surface temperatures in February–March (T_{FM}) according to the Tuapse weather station data and water temperatures at observation sites in different seasons (B) at depths of 10 and 25 m in the Inal Bay in 2015–2022

The temperature regime at 10 and 25 m differed only during summer. For both 2021 and 2022, a noticeably higher water temperature was recorded: in 2021, (+17.4 ± 2.9) °C *vs.* (+14.1 ± 2.9) °C; in 2022, (+19.7 ± 3.1) °C *vs.* (+13.9 ± 2.6) °C (Fig. 1B). No significant trends in the mean temperature in February–March were observed during the study. The minimum values were registered in 2017 (+8.1 °C). Also, a lower value, compared to the mean for the period, was recorded in 2022 (+9.1 °C).

Structure and dynamics of Mollusca taxocene. In 2015–2022, 29 mollusc species were found at depths of 10 and 25 m. At 10 m, 20 species were noted in 27 samples, 3–12 *per* sample [(7 ± 2) on average; hereinafter mean ± standard deviation] (Fig. 2A). The expected number of species with the Chao2 correction was (21 ± 1) evidencing for a fairly high representativeness of our sample. No trends in the species number over time were revealed; differences were reliable for 2019 and 2020 only, when the species number increased almost twofold. At a depth of 25 m, 24 species were recorded in 25 samples [(30 ± 8) with the Chao2 estimator], 3–14 *per* sample [(8 ± 3) on average] (Fig. 2A). The species number fluctuated, with a minimum in 2016–2017 and a maximum in 2020 (differences were significant, $p < 0.05$).

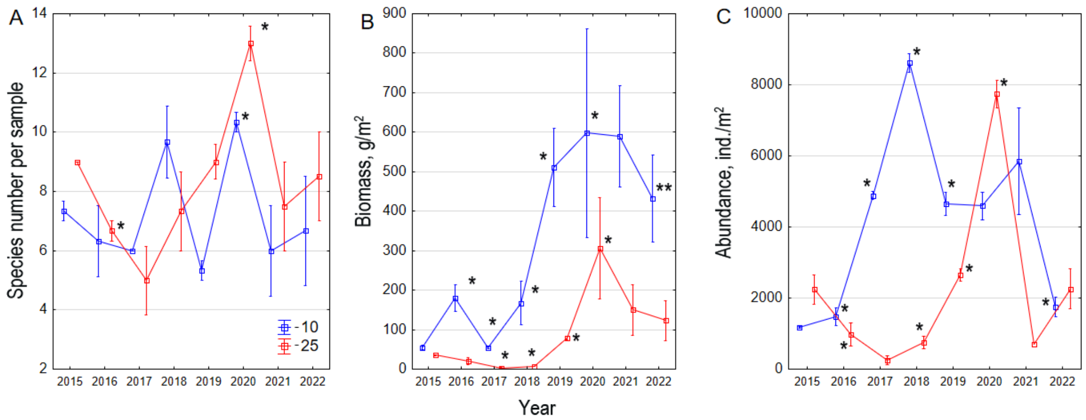

Fig. 2. Dynamics of the species number *per* sample (A), total biomass (B), and abundance (C) of Mollusca taxocene at depths of 10 and 25 m. * marks values of the parameter that significantly differ from those of the previous year; ** mark values that significantly differ from those of 2020. Error bars are standard error of the mean; points are the mean

Within 2015–2022, the total biomass in the Mollusca taxocene varied widely: 45.8–869.1 g·m^{-2} at 10 m and 0.3–513.8 g·m^{-2} at 25 m (Fig. 2B). In 2015–2018, the biomass at a depth of 10 m changed annually (interannual differences were significant, $p < 0.05$) reaching minimum values in 2015 and 2017 and maximum ones in 2016 and 2018. In 2019, the taxocene biomass at this depth rose more than 2 times compared to that of 2018 (Fig. 2B). The biomass growth trend continued in 2020. In 2021–2022, there was a downward trend in biomass, and differences between the values of 2020 and 2022 were significant (Fig. 2B). At 25-m depth, biomass dropped from (35.1 ± 3.5) g·m^{-2} in 2015 to (3.4 ± 2.7) g·m^{-2} in 2017. Within 2018–2020, the taxocene biomass increased (interannual differences were significant, $p < 0.05$) by two orders of magnitude. Already in 2021, the value decreased threefold (differences from 2020 were unreliable due to a small number of samples). In 2022, biomass remained at approximately the same level (differences from 2020 were unreliable). When uniting samples from 2021 and 2022, their differences in biomass from the values of 2020 became significant. Thus, both at 10-m and 25-m depths, a rise in biomass in the Mollusca taxocene was observed in 2018–2020, and a decrease was recorded in 2021 (it was reliably determined in 2022).

The abundance in Mollusca taxocene fluctuated widely during these years: from 60 to 10,050 ind.·m^{-2} (Fig. 2C). At a depth of 10 m, abundance was low in 2015–2016; it reliably increased by 3.3 times in 2017 and almost doubled in 2018. In 2019, a noticeable drop in abundance to the values of 2017 was revealed. In 2020 and 2021, no significant interannual differences were found; in 2022, abundance in the taxocene decreased by half. At a depth of 25 m, within 2015–2017, a decline in abundance by an order of magnitude was registered. In 2018–2020, a rise in abundance by an order of magnitude was noted. In 2021 and 2022, the values were similar and noticeably differed from those of 2020 by 4.5 times.

R. venosa was found only in six samples in 2017, 2018, 2021, and 2022 (Fig. 3). No significant trends in abundance of this predatory gastropod were revealed.

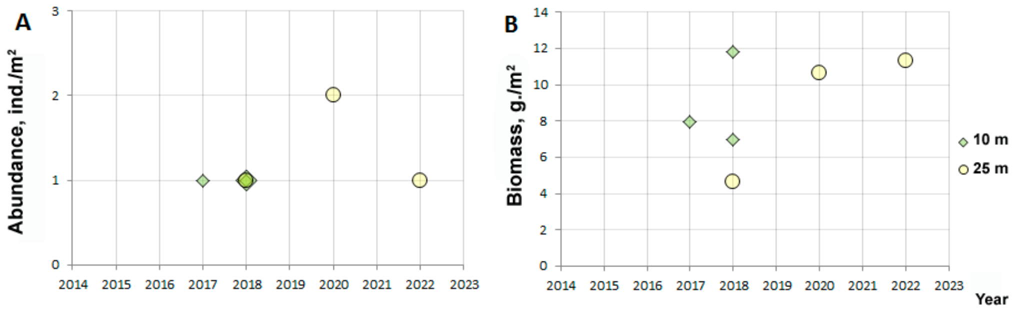

Fig. 3. *Rapana venosa* abundance (A) and biomass (B) in samples of 2015–2022 at depths of 10 and 25 m in the Inal Bay

A two-factor analysis (PERMANOVA) showed as follows: the contribution of depth to the overall biomass data variability was greater than that between years within each depth range (Table 1). Accordingly, we reject the null hypothesis that there are no statistically significant differences between the taxocene structure at 10 and 25 m and that there are no interannual differences.

Table 1. Results of two-way analysis of variance (PERMANOVA) for log(x + 1)-transformed biomass of species of Mollusca taxocene at depths of 10 and 25 m in the Inal Bay in 2015–2022

Factor	Degree of freedom	Sum of squares	Mean sum	Pseudo-*F*	*P* (permutational)	Number of permutations	Proportion of explained variation (SS/SS_{total}), %
Depth, m	1	38,827	38,827	94,303	0.001	999	48
Year (depth, m)	14	28,849	2,060.7	5,005	0.001	999	36
Residual variation	31	12,763	411.7				
Total variation	46	80,636					

Cluster analysis of biomass data allowed us to identify four main groupings of samples (Fig. 4). Species composition and occurrence rates are provided in Table 2.

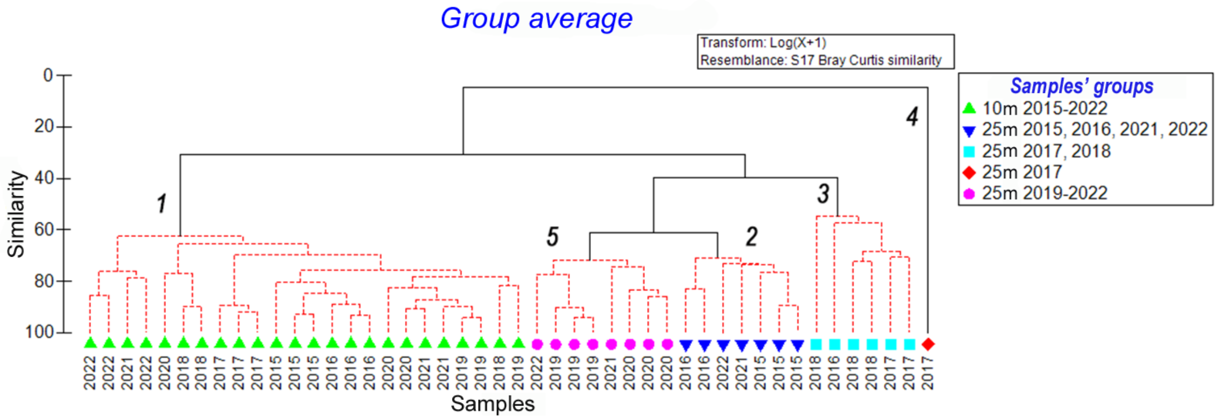

Fig. 4. Results of cluster analysis of Mollusca taxocene structure based on values of the Bray–Curtis similarity index calculated from the log(x + 1)-transformed biomass for samples of 2015–2022 in the Inal Bay. Red dotted lines show the groupings identified by SIMPROF procedure (confidence level of 1%). Digits indicate numbers of the groupings

Table 2. Mollusca occurrence in 2015–2022 in the Inal Bay (%). The groupings: 1, a depth of 10 m, 2015–2022; 2, a depth of 25 m, 2015, 2016, 2021, and 2022; 3, a depth of 25 m, 2016–2018; 4, a depth of 25 m, 2017; 5, a depth of 25 m, 2019–2022

Class	Species	Grouping				
		1	2	3	4	5
Bivalvia	*Abra alba* (W. Wood, 1802)	4	29	17	38	0
	Abra nitida (O. F. Müller, 1776)	0	0	0	13	0
	Acanthocardia paucicostata (G. B. Sowerby II, 1834)	0	0	17	25	0
	Anadara kagoshimensis (Tokunaga, 1906)	50	86	67	100	0
	Parvicardium simile (Milaschewitsch, 1909)	0	14	17	0	0
	Chamelea gallina (Linnaeus, 1758)	100	100	100	100	0
	Donax semistriatus Poli, 1795	88	0	33	63	0
	Gouldia minima (Montagu, 1803)	46	100	100	100	100
	Lentidium mediterraneum (O. G. Costa, 1830)	42	0	0	0	0
	Lucinella divaricata (Linnaeus, 1758)	100	100	100	100	0
	Mytilaster lineatus (Gmelin, 1791)	17	0	33	38	0
	Mytilus galloprovincialis Lamarck, 1819	4	14	17	38	0
	Pitar rudis (Poli, 1795)	25	100	100	100	100
	Spisula subtruncata (da Costa, 1778)	92	100	83	100	100
	Fabulina fabula (Gmelin, 1791)	83	43	0	63	0
	Bela nebula (Montagu, 1803)	4	0	0	0	0
Gastropoda	*Bittium reticulatum* (da Costa, 1778)	4	0	0	0	0
	Brachystomia scalaris (MacGillivray, 1843)	25	0	0	13	0
	Calyptraea chinensis (Linnaeus, 1758)	0	14	0	63	0
	Epitonium clathrus (Linnaeus, 1758)	0	0	0	13	0
	Hydrobia acuta (Draparnaud, 1805)	0	14	0	0	0
	Parthenina interstincta (J. Adams, 1797)	8	0	0	0	0
	Parthenina terebellum (R. A. Philippi, 1844)	0	14	0	0	0
	Retusa truncatula (Bruguière, 1792)	0	14	0	25	0
	Retusa variabilis (Milaschewitsch, 1912)	0	14	0	0	0
	Rissoa splendida Eichwald, 1830	4	14	0	25	0
	Tragula fenestrata (Jeffreys, 1848)	13	29	0	0	0
	Tritia neritea (Linnaeus, 1758)	4	0	0	0	0
	Tritia reticulata (Linnaeus, 1758)	8	0	0	13	0
	Rapana venosa (Valenciennes, 1846)	13	14	17	13	0
Number of samples *per* a grouping		24	7	6	1	8

The grouping 1 included all 24 samples from a depth of 10 m in 2015–2022. The average sample similarity (SIMPER) in this grouping accounted for 71%. The main contributors to the sample similarity (96%) were three species: *Ch. gallina*, *Donax semistriatus* Poli, 1795, and *Lucinella divaricata* (Linnaeus, 1758). Two main dominants of the taxocene had an occurrence rate of 100%: *Ch. gallina* and *L. divaricata* (Table 2). These two species, along with *D. semistriatus* (occurrence rate of 88%) and *A. kagoshimensis* (occurrence rate of 50%), ensured the major contribution to the intra-complex similarity by log-transformed biomass (up to 96–100% in total). In this grouping, the leading species were *Spisula subtruncata* (da Costa, 1778) and *Fabulina fabula* (Gmelin, 1791), but their contribution to the intra-complex similarity in the taxocene biomass did not exceed 3%. Gastropods were characterized by a lower occurrence rate than bivalves (up to 25%) and low biomass. Only 3 ind. of a predatory gastropod *R. venosa* were noted: in 2017 (a weight of a specimen was 7.9 g) and in 2018 (11.7 and 6.9 g).

All the other groupings included samples from 25-m depth. The grouping 2 united 7 samples from 2015, 2016, 2021, and 2022. The species number *per* sample ranged 6–11, (8 ± 2) on average, and biomass was (45.0 ± 24.5) g·m^{-2}. This grouping included samples with low biomass. Abundance varied 700 to 3,040 ind.·m^{-2}. The average sample similarity (SIMPER) accounted for 74%. The chief contributors to the sample similarity (96%) were three species: *G. minima*, *P. rudis*, and *Ch. gallina*. These ones, as well as *S. subtruncata* and *L. divaricata*, had an occurrence rate of 100%. The main contribution to the intra-complex similarity in biomass in this grouping was made by *G. minima* (35–83%) and *P. rudis* (4–49%) providing a total of 56–93% of biomass. *Ch. gallina* contributed 3–17%, *S. subtruncata*, 1–7%, and *L. divaricata*, 2–10%. The characteristic species of the taxocene in this grouping was an invader *A. kagoshimensis* recorded at 86% of the stations. Its contribution to biomass ranged 1–3%; only in one sample, where one large specimen (shell length of 36.2 mm) with a weight of 10.8 g was found, the contribution of this species accounted for 32%. The occurrence rate of Gastropoda representatives did not exceed 29%. The only *R. venosa* individual was registered in 2022 (its weight was 11.3 g).

The grouping 3 included 6 samples of 2016–2018. The average sample similarity (SIMPER) accounted for 54%. The number of species was 5–10, (7 ± 2) *per* sample. The taxocene biomass was (6.2 ± 1.3) g·m^{-2} there, and abundance was (560 ± 293) ind.·m^{-2}. Thus, this grouping united the samples with minimum values of biomass and abundance during the study period. The key contributors to the sample similarity (96%) were four species: *G. minima*, *P. rudis*, *Ch. gallina*, and *L. divaricata*. They were found in all samples of the grouping and provided 63–92% of the taxocene biomass. The characteristic species were also *A. kagoshimensis* (occurrence rate of 67%) and *S. subtruncata* (occurrence rate of 83%); in one sample, their biomass reached 12 and 16%, respectively. Gastropoda were not found there, except for *R. venosa*: 1 ind. was noted in one of the samples in 2017 (its weight was 4.7 g).

One sample – that from a depth of 25 m in 2017 – was not included in any other grouping (marked with number 4). There, only three species were recorded: *S. subtruncata* (79% of biomass), *P. rudis* (18%), and *G. minima* (3%). The total biomass was 0.33 g·m^{-2}. *R. venosa* was not registered.

The grouping 5 united 8 samples of 2019–2022. The average sample similarity (SIMPER) accounted for 49%. The species number *per* sample ranged 7–14, (11 ± 3) on average. Taxocene biomass was (250.5 ± 182.6) g·m^{-2}, and abundance was (4,444 ± 2,799) ind.·m^{-2}. This grouping united the samples with high abundance, biomass, and species diversity. The major contributors to the sample similarity (96%) were four species: *G. minima*, *P. rudis*, *Ch. gallina*, and *A. kagoshimensis*. They accounted for 88–98% of the biomass, with the highest values for *G. minima* (27% on average) and *P. rudis* (33% on average). *Ch. gallina* biomass accounted for a mean of 18% (3–28%), and *A. kagoshimensis* biomass, 15% (3–42%). In each of two samples with a high contribution of *A. kagoshimensis* to biomass, 1 ind. of this species was found: with a shell length of 31.2 mm and a weight of 7.1 g and with a shell length of 19.8 mm and a weight of 2.4 g. Characteristic Bivalvia species were *S. subtruncata* and *L. divaricata* recorded in 100% of the samples (total contribution to biomass was < 5%), as well as *F. fabula* and *D. semistriatus* identified in 63% of the samples (2–9% of biomass in total). The only characteristic Gastropoda species was *Calyptraea chinensis* (Linnaeus, 1758) also registered in 63% of the samples (< 1% of biomass). Two *R. venosa* individuals were noted in one sample in 2020 (a weight of 4.7 and 5.9 g).

So, at a depth of 25 m, a change in the taxocene structure was determined during the study period. The trend is well illustrated by a non-metric multidimensional scaling (MDS) diagram constructed on the matrix of distances between centroids of samples with a grouping factor of year (Fig. 5). Two states of the system were identified: 1) 2015 and 2019–2022; 2) 2016–2018. Differences between them are significant (PERMANOVA pseudo-$F = 9.1$; $p = 0.02$). SIMPER analysis showed that it was mediated by the difference in biomass of three leading species. Their biomass was high in 2015 and 2019–2022 (on average, 126.2 g·m^{-2} for *P. rudis*, 86.6 g·m^{-2} for *G. minima*, and 66.6 g·m^{-2} for *Ch. gallina*) and low in 2016–2018 (on average, 8.1 g·m^{-2} for *P. rudis*, 9.9 g·m^{-2} for *G. minima*, and 4.6 g·m^{-2} for *Ch. gallina*).

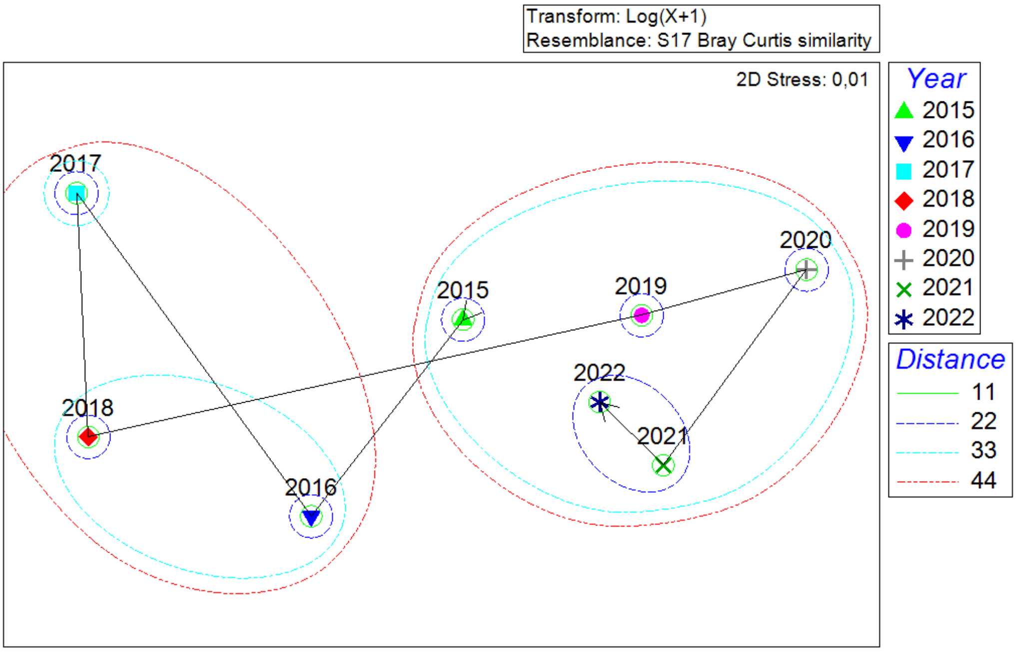

Fig. 5. MDS diagram constructed on the basis of a matrix of distances between centroids of samples from a depth of 25 m with a grouping factor of year

Dynamics of abundance and size structure of dominant species. The major contribution to biomass and its interannual variability was made by dominants of the communities: at 10 m, *Ch. gallina* and *L. divaricata*; at 25 m, *P. rudis* and *G. minima*, and also *Ch. gallina* in 2019–2022 (Fig. 6). Biomass of *Ch. gallina*, *P. rudis*, and *G. minima* underwent the greatest changes during the study period. At a depth of 10 m, the basis of abundance was ensured by *L. divaricata* and *Ch. gallina*; at 25 m, by *G. minima* and *P. rudis*, and also *Ch. gallina* in 2019–2020.

Chamelea gallina. Quantitative characteristics of *Ch. gallina* samples in 2015–2022 are provided in Table 3. Abundance of the key dominant at 10-m depth fluctuated during the study period (Fig. 6A). The highest biomass was recorded in 2020–2021: the species formed 82 to 96% of the total taxocene biomass. The period of the highest abundance (2018) preceded the period of the maximum biomass (Fig. 6C). In 2018, the minimum mean weight of *Ch. gallina* individuals in the samples was registered; also, their low weight was noted in 2017 (Fig. 6E). Analysis of the size–frequency distributions showed as follows: in 2017–2018, the population consisted of 81–95% individuals with a shell length < 3 mm. Within 2017–2019, only two maximums were revealed in histograms (Fig. 7). However, in 2019, molluscs with a shell length < 3 mm (juveniles) accounted for only 20% of the studied ones, while most of them had a shell length of 7–12 mm. A similar distribution pattern was established for 2015 and 2016, but with an intermediate peak of 4–7-mm individuals. In 2020–2021, a gap between the first and second population peaks widened. There were two main population peaks: juveniles and 10–18-mm adults;

between these groups, single individuals of medium sizes were found (4–6 and 7–10 mm). In 2022, the number of population peaks increased. We have identified five maximums, but conditionally, as the sample was insufficient. The first two peaks seem to refer to juveniles, and the last one is an aggregate one, since the sample of 2022 included individuals of the maximum size for this population (in 2015–2022) – 19.7 mm.

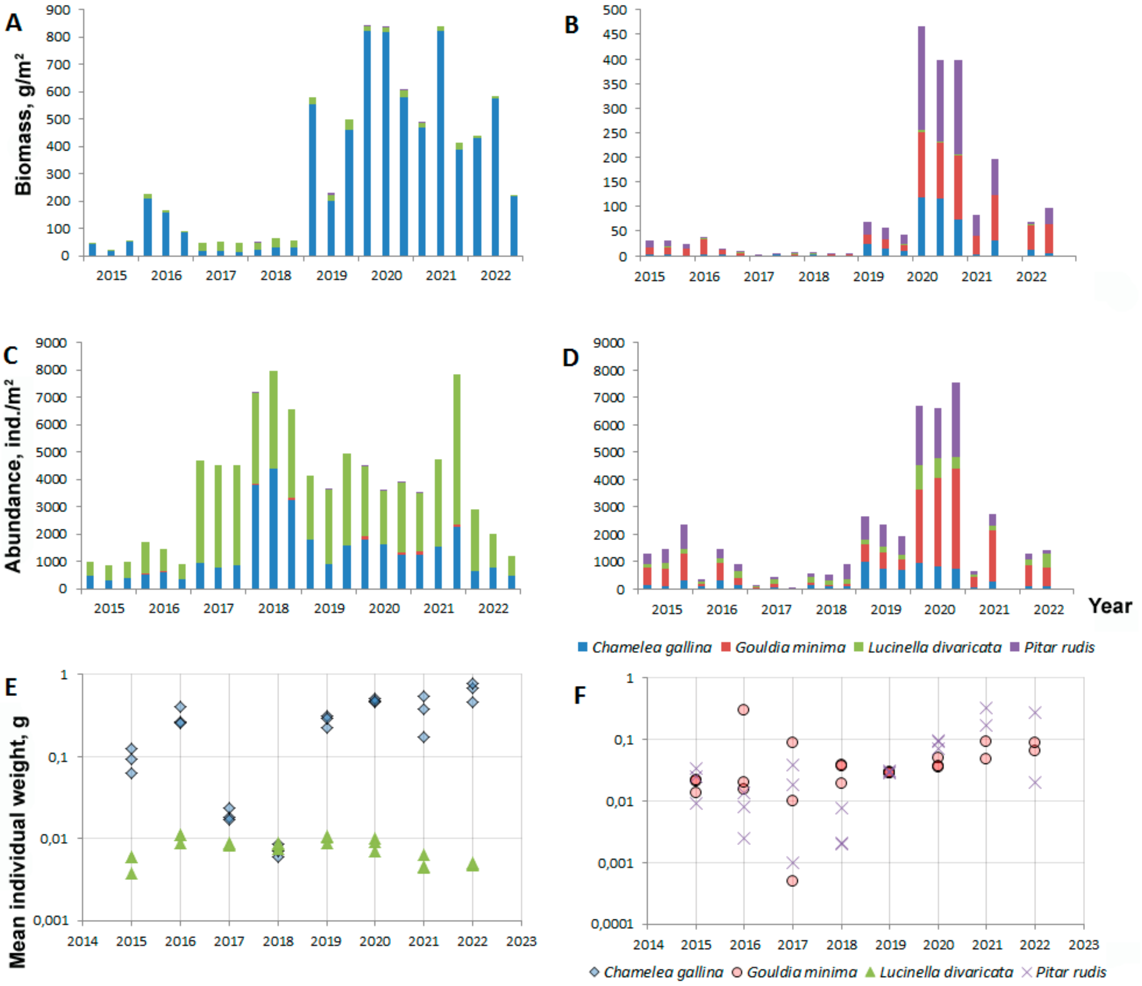

Fig. 6. Dynamics of biomass (A, B), abundance (C, D), and mean weight of individuals (E, F) of the main dominants at depths of 10 m (A, C, E) and 25 m (B, D, F) in the Inal Bay in 2015–2022

Table 3. Quantitative characteristics of *Chamelea gallina* samples in 2015–2022

Characteristics of the samples	Year							
	2015	2016	2017	2018	2019	2020	2021	2022
Total number of samples	2	3	3	1	2	2	2	3
Total number of studied individuals	84	137	228	366	249	327	329	184
Minimum shell length, mm	0.8	0.7	0.5	0.5	0.9	0.6	0.5	1.0
Mean shell length, mm	5.6	8.1	2.3	1.8	7.6	9.7	6.7	10.4
Maximum shell length, mm	12.2	17.1	13.0	8.9	13.8	17.3	19.7	19.0

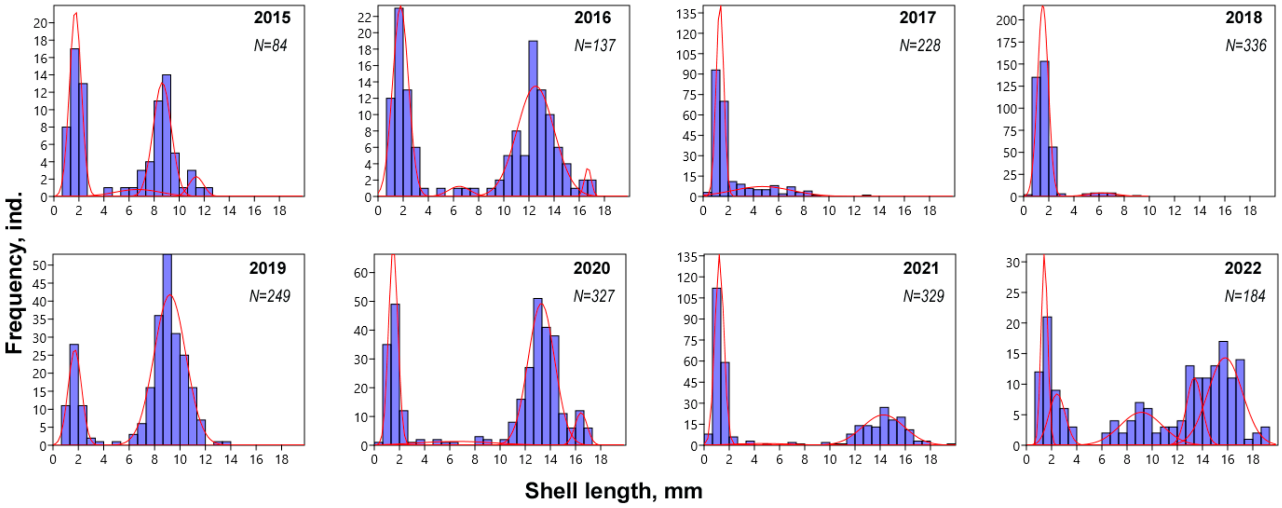

Fig. 7. Size structure of *Chamelea gallina* population in different years in the Inal Bay at a depth of 10 m. Red curves are approximation curves of normal distribution for abundance peaks (hereinafter); *N* is sample size

Pitar rudis. Quantitative characteristics of *P. rudis* samples in 2015–2022 are provided in Table 4. In 2015–2016, its abundance and biomass were similar, and a mean weight of molluscs was 0.02–0.03 g. The population was represented by different-sized individuals of three size groups: 0–4, 4–6, and 6–10 mm (Fig. 8). In 2017–2018, biomass dropped by an order of magnitude, down to 1.6 g·m^{-2}. In 2017, abundance was minimum and valued to 20–60 ind.·m^{-2}. In 2017–2018, the population consisted chiefly of juveniles, and the mean weight of individuals was the lowest for the entire study period. In 2018–2020, a trend of increasing *P. rudis* biomass, abundance, and mean weight was revealed. In 2019, the population included three size groups: juveniles up to 4 mm and adults of 4–8 and 9–10 mm. In 2020, after settling of molluscs of the previous year, the population was replenished, and the proportion of juveniles reached 48%. Groups of adults identified for 2019 were indistinguishable from each other, and the histogram had only two maximums. In 2021, there were a decline in biomass and abundance and a rise in the mean size of individuals. At the same time, the proportion of juveniles accounted for only 27% of the total abundance, and this evidenced for the lack of mass settling in 2020. The view of the histogram for 2022 was similar to that for 2021, but low abundance did not allow us to reveal four peaks. Only two ones were reliably identified: those of juveniles and adults. The largest size of specimens in the samples was 15.6 mm.

Table 4. Quantitative characteristics of *Pitar rudis* samples in 2015–2022

Characteristics of the samples	Year							
	2015	2016	2017	2018	2019	2020	2021	2022
Total number of samples	3	3	3	3	3	2	2	2
Total number of studied individuals	180	64	13	76	221	427	56	37
Minimum shell length, mm	0.7	0.7	1.5	0.9	0.8	0.4	0.7	0.6
Mean shell length, mm	3.1	2.5	2.7	2.2	3.7	4.9	7.5	6.1
Maximum shell length, mm	9.5	6.8	7.8	5.5	10.2	13.2	15.6	12.9

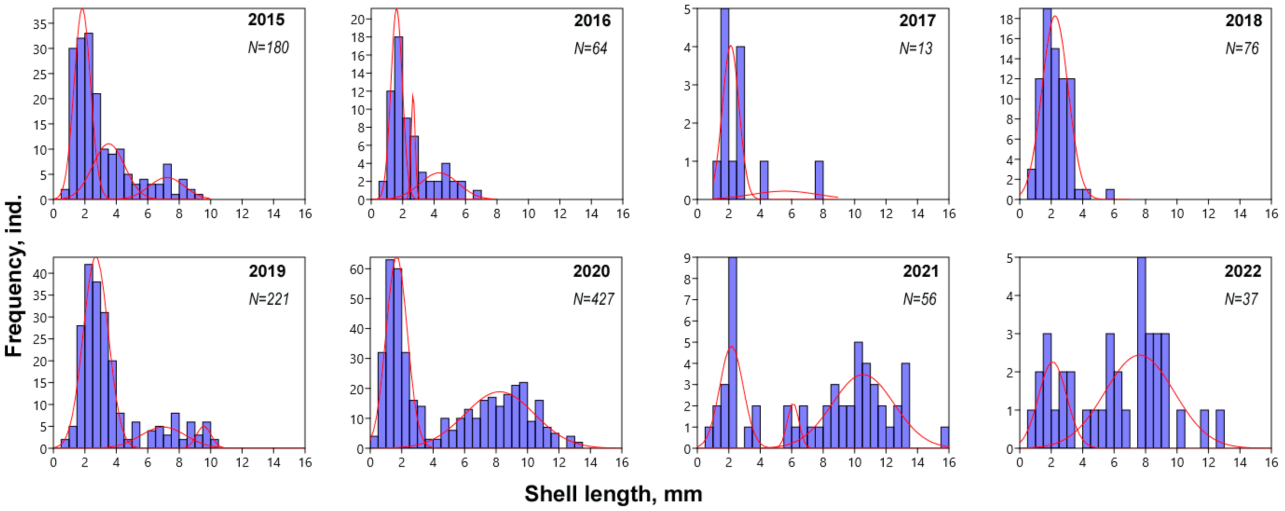

Fig. 8. Size structure of *Pitar rudis* population in different years in the Inal Bay at a depth of 25 m

Gouldia minima. Quantitative characteristics of *G. minima* samples in 2015–2022 are provided in Table 5. The pattern of changes in abundance of its population over time was generally similar to that for *P. rudis* population (these two species co-inhabit one biotope). In most cases, *G. minima* exceeded *P. rudis* in abundance, but had lower biomass. The mean weight of *G. minima* and *P. rudis* was similar. In 2016, the mean weight of *G. minima* was the highest, 0.3 g; in 2017, it had a wide range, 0.001 to 0.04 g. There were no reliable differences in the mean weight of individuals of this species in the population. Within the study period, similar to *P. rudis*, *G. minima* had the lowest biomass in 2017–2018. In 2019, biomass and abundance increased, and in 2020, they reached their maximums. In 2021–2022, a gradual decrease in these parameters was observed, but the only statistically significant difference was that between 2020 and 2022.

Table 5. Quantitative characteristics of *Gouldia minima* samples in 2015–2022

Characteristics of the samples	Year							
	2015	2016	2017	2018	2019	2020	2021	2022
Total number of samples	3	3	3	3	3	2	2	2
Total number of studied individuals	211	102	14	20	156	626	224	140
Minimum shell length, mm	0.9	1.1	2.1	2.2	1.5	0.6	0.6	1.1
Mean shell length, mm	3.9	5.0	3.3	4.2	4.6	4.6	4.7	5.9
Maximum shell length, mm	6.6	8.2	7.0	8.5	8.2	10.1	11.7	9.6

G. minima differs from the two species described above in its smaller size. The maximum shell length recorded in our survey was 11.7 mm (in 2021). Up to three peaks were observed in the histograms (Fig. 9). The first one was formed by individuals with a shell length up to 3 mm; the second, 3–6 mm; and the third, more than 6 mm. The proportion of juveniles did not exceed 29%, and this is in sharp contrast to the pattern recorded for the two previous species. Molluscs of 1.0–2.5 mm were abundant only in the samples of 2015 and 2021. The highest abundance in almost all years was provided by specimens with a shell length of 4–9 mm. There were no shifts in peaks between years. The pattern for *G. minima* differed from that for the first two species: for this hydrobiont, in most cases, no clear separation of peaks was revealed (with no intermediate-sized individuals). The exceptions were the size histograms of 2015, 2021, and 2022.

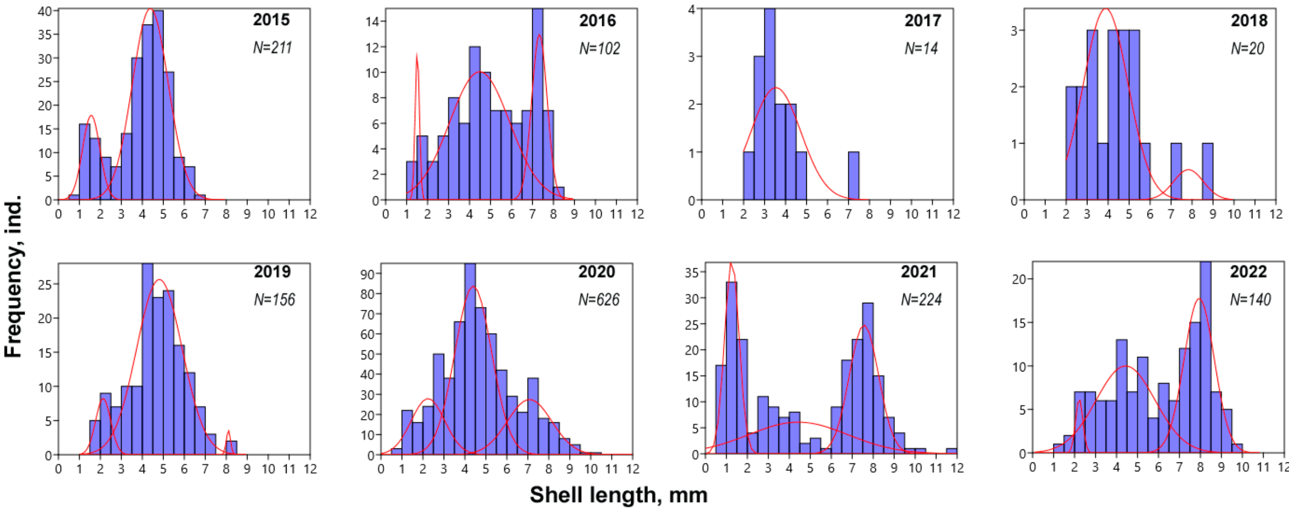

Fig. 9. Size structure of *Gouldia minima* population in different years in the Inal Bay at a depth of 10 m

Lucinella divaricata. Quantitative characteristics of *L. divaricata* samples in 2015–2022 are provided in Table 6. It is the smallest species inhabiting a depth of 10 m. This mollusc was characterized by the lowest amplitude of fluctuations in abundance, biomass, and mean weight of individuals (see Fig. 6). In 2015–2016, its abundance was low and comparable to that of the main dominant, *Ch. gallina*. Already in 2017, *L. divaricata* abundance increased fourfold compared to that for previous years and *Ch. gallina* abundance. Biomass of *L. divaricata* population rose as well. Both parameters remained stable during 2017–2021, and their values decreased slightly in 2022. *L. divaricata* population in the Inal Bay in 2015–2022 was characterized by the presence of two or three peaks in the size–frequency histograms (Fig. 10). The first one – peak of the smallest individuals with a shell length of about 0.5–2 mm (juveniles) – was registered in all years, except for 2019. The second peak, extremely abundant, included *L. divaricata* with a shell length of 2–4 mm and was also recorded in all years of the study. The third peak – that of 4–5.3-mm individuals – was the least abundant and formed by single molluscs. No shifts in peaks were noted between years, and the general view of the histograms was relatively stable.

Table 6. Quantitative characteristics of *Lucinella divaricata* samples in 2015–2022

Characteristics of the samples	Year							
	2015	2016	2017	2018	2019	2020	2021	2022
Total number of samples	3	3	1	3	2	2	2	2
Total number of studied individuals	146	256	370	570	404	373	297	353
Minimum shell length, mm	0.9	0.7	0.9	0.9	0.5	0.7	0.5	0.6
Mean shell length, mm	2.2	2.7	2.2	2.6	2.7	2.5	1.8	1.9
Maximum shell length, mm	4.5	5.1	4.9	5.3	5.3	4.6	4.7	4.9

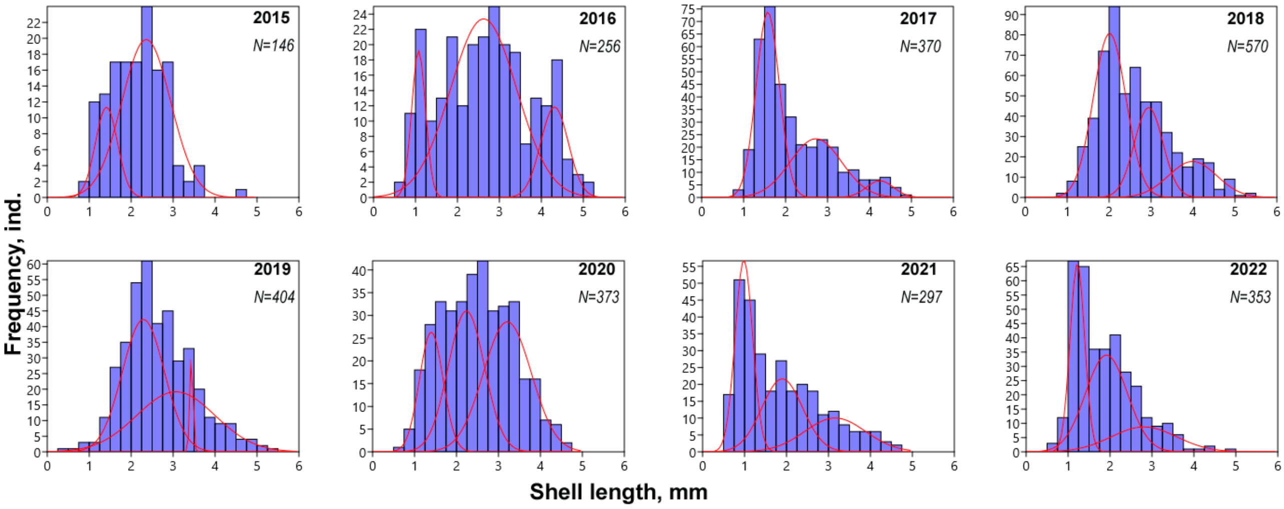

Fig. 10. Size structure of *Lucinella divaricata* population in different years in the Inal Bay at a depth of 10 m

Factors driving the taxocene structure and dynamics. We carried out a non-parametric analysis of correlations between available data on abiotic factors (mean surface water temperature in February–March at the Tuapse weather station area and grain size of sediments), *R. venosa* abundance in the samples, information on complex characteristics (abundance, biomass, and species number in the samples), and the taxocene structure (based on log-transformed biomass of species in the samples). No reliable correlations between complex characteristics and aforementioned factors were established. Habitats at 10-m and 25-m depths differed significantly in the rate of the sediment gravel fraction and summer temperature.

DistLM analysis (sequential tests) showed as follows: for a depth of 10 m, the selected predictors accounted for 45.9% of the variability. The grain size of sediments and the mean surface water temperature in February–March had a reliable linear correlation with the biotic data (Table 7, Fig. 11). The only reliable factor turned out to be the aleurite content (Table 8). It was significantly lower in the samples of the last two years (2021 and 2022). However, contribution of this factor to the explained variation of biotic data was small (21.8% only), since the population structure in 2021–2022 did not differ noticeably from that of previous years (see Fig. 4). For the taxocene at a depth of 25 m, no reliable correlations were revealed with any of the predictors available.

When comparing biomass dynamics of studied species and the proportion of juveniles in their populations, we identified no reliable relationships because of the fact that time series were too short. However, certain trends can be recorded. An outbreak of abundance of *Ch. gallina* juveniles was registered against the backdrop of low population biomass (in 2017–2018), and with a subsequent rise in biomass, there was a parallel drop in abundance of juveniles (in 2019) (Fig. 12A). A similar pattern was revealed for *G. minima* and *P. rudis* (Fig. 12C, D). It was the period of minimum mean temperatures for February–March.

In 2019–2020, there was a parallel increase in biomass and abundance of juveniles for *Ch. gallina* and *G. minima*, and in 2021, a parallel decline in these parameters. For *P. rudis*, the same as for the other two venerids, a peak in biomass was observed in 2020, but it occurred against the backdrop of a steady decrease in abundance of juveniles in the samples since 2017.

Table 7. Results of DistLM analysis of the effect of abiotic factors on Mollusca taxocene structure (optimal combinations obtained in sequential tests)

Predictor	Adjusted determination coefficient	Pseudo-*F*	*P*-value	Proportion of explained total variation
Depth of 10 m				
+Grain size	0.326	3.777	0.001	0.443
+Spatial position	0.449	3.116	0.006	0.149
+Temperature	0.649	10.710	0.001	0.163
Depth of 25 m				
+Spatial position	0.172	3.181	0.009	0.251
+Grain size	0.364	2.438	0.004	0.295
+Year	0.413	2.248	0.059	0.063
+Temperature	0.460	2.210	0.062	0.057

Table 8. Results of DistLM analysis of the effect of abiotic factors on Mollusca taxocene structure (optimal combinations obtained in sequential tests) at a depth of 10 m

Factor	Adjusted determination coefficient	Pseudo-*F*	*P*-value	Proportion of explained total variation
+Aleurite	0.183	6.137	0.001	0.218
+Temperature	0.253	3.066	0.016	0.100
+Pelite	0.329	3.387	0.017	0.099
+Sand	0.346	1.506	0.227	0.043
+Gravel	0.406	2.944	0.034	0.076

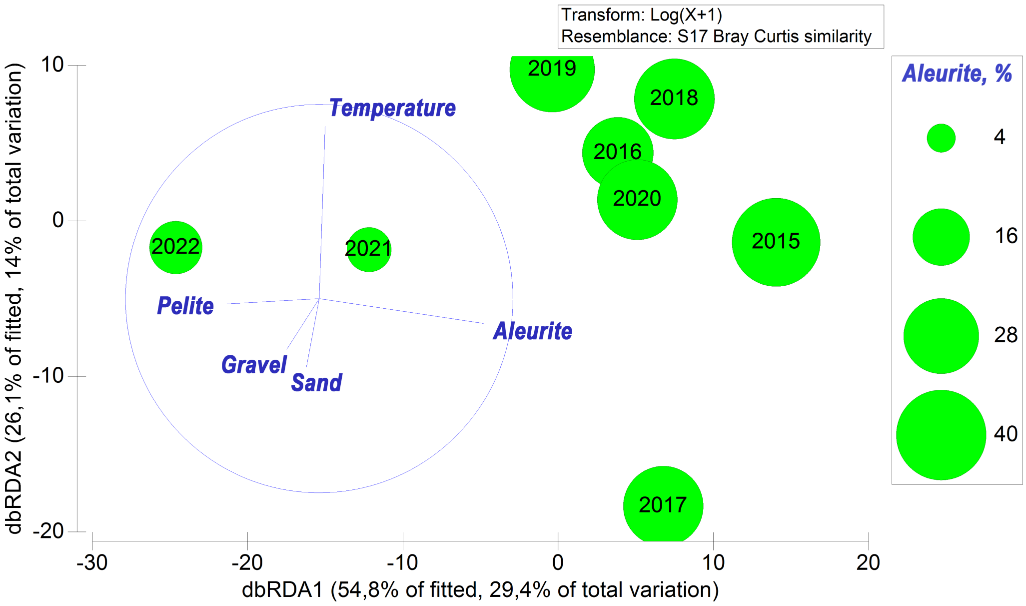

Fig. 11. Analysis of the effect of abiotic factors on Bivalvia taxocene structure by the dbRDA method within 2015–2022; similarity measure is Bray–Curtis index (based on log(x + 1)-transformed biomass); different-sized circles indicate the percentage of aleurite in bottom sediments

The dynamics of *L. divaricata* settlements was different: there were two periods with abundance of juveniles and total biomass changing in antiphase (2015–2017 and 2020–2022) and one period with parallel changes (2017–2019) (Fig. 12B). The period of the highest biomass coincided with that of the lowest temperature, when *Ch. gallina* abundance was minimal. Unlike *Ch. gallina* biomass, *L. divaricata* biomass decreased in 2017–2020.

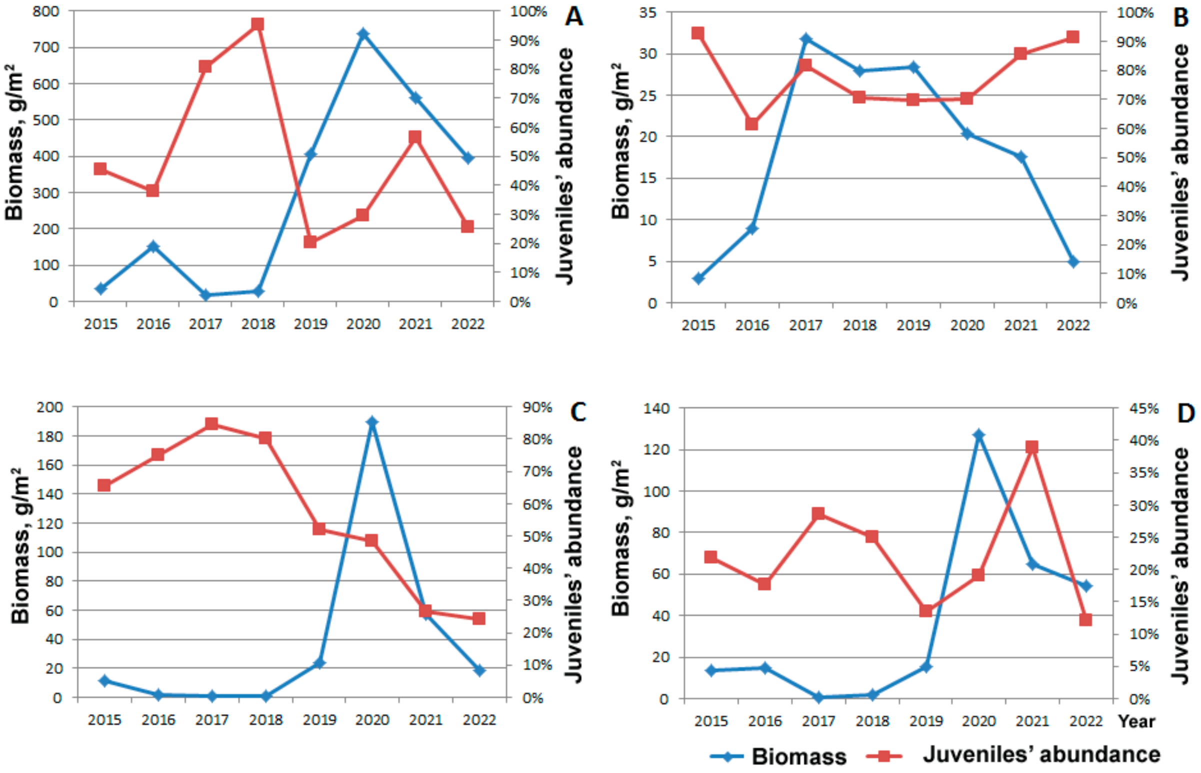

Fig. 12. Parallel changes in total biomass of population and abundance of juveniles of *Chamelea gallina* (A), *Lucinella divaricata* (B), *Pitar rudis* (C), and *Gouldia minima* (D) in the Inal Bay in 2015–2022

DISCUSSION

Dynamics of size structure and age of molluscs. In the Black Sea, all the four mollusc species studied in this work are known to have a single peak of reproduction *per* year, although extended in time [Kiseleva, 1981; Revkov et al., 2014]. *Ch. gallina* reproduces mostly in late summer, and just-settled individuals occur in samples in early autumn [Kiseleva, 1981]. Larvae are found in plankton until February [Vinogradova, 1950]. We carried out sampling in late June–early July, before new individuals of the current year appeared. In addition, the mesh size of the sieve we used (0.5 × 0.5 mm) does not allow taking into account the earliest stages, while settling *Ch. gallina* specimens have a size of 0.2 mm [Kiseleva, 1981; Zakhvatkina, 1959]. Therefore, the first peak of individuals with a shell length up to 3 mm in the size–frequency histograms for this species most likely includes molluscs that settled in autumn–winter of the previous year (a generation 0+). In winter, their growth seems to be extremely slow [Revkov et al., 2014]; according to our data, they grow only to 2.5 mm by July. A cohort 1+ covered specimens of 5–10 mm in different years, and this is consistent with the data of M. Kiseleva [1981] on growth rates of this species in the Black Sea. Adults – representatives of cohorts 1+ and more – mostly formed a continuous smoothed peak in the histograms.

In 2018, high abundance of small-sized *Ch. gallina* (0–3 mm) was recorded in benthic samples from a 10-m depth. This generation (molluscs that settled in the autumn of 2017) was found in the samples of the following year (2019) and boosted biomass in 2019. At the same time, there was no new mass settling in the autumn of 2018, and, accordingly, there was no corresponding high peak of juveniles in 2019. The mean size of individuals in the population and its total biomass increased. As a result, the next year (2020), a gap was formed between generations: either small-sized specimens of a cohort 0+, up to 3 mm, were registered or individuals larger than 10 mm were recorded, while the cohort 1+ was represented by single molluscs. This gap persisted in 2021. It allowed us to fully examine the generation of 2017 (in 2019, these individuals were aged 1+; in 2020, 2+; in 2021, 3+; and in 2022, 4+). Its abundance dropped over time, and by 2020, it became difficult to clearly distinguish it from later generations. In the autumn of 2020, there was a new abundant replenishment of *Ch. gallina* population evidenced by a peak of juveniles in the histograms of 2021. In 2022, after successful settling of molluscs of 2020, individuals of the cohort 1+ appeared again, and specimens that settled in 2017 still occurred forming a cohort 4+. In 2020, molluscs of this generation reached about 13 mm in length (2+), and in 2021, 15 mm (3+). Apparently, in 2022, size of these individuals ranged 17 to 20 mm (4+). Throughout the entire study period, there were no *Ch. gallina* with a shell length more than 20 mm, whereas in the middle of the XX century, the largest recorded size was 27 mm [Kiseleva, 1981]. Thus, according to our data, the maximum age of molluscs was at least 4.5 years. The extended period of the population replenishment during the year governs the fact that the histograms have a narrow peak of juveniles and a flatter total peak of adults which is wide due to the combination of generations with different time of settling [Chukhchin, 1965; Kiseleva, 1981; Revkov et al., 2014]. This is exactly the pattern for most cases in 2015–2022 (with the exception of 2017 and 2018). However, the population structure of this species still experiences annual fluctuations. After it was eliminated by the rapa whelk in 2003–2006, small-sized juveniles alone were noted in samples; gradual recovery began only in 2007, after a decrease in *R. venosa* abundance [Kucheruk et al., 2012]. In the early 2000s, due to massive simultaneous settling of bivalves, all individuals in the population were of similar sizes, but since the mid-2010s, the occurrence of several size groups is registered, with a dominance of juveniles.

For another species, *P. rudis*, inhabiting the Black Sea at a depth of 25 m, no published data on the lifespan were found. Our material may indirectly indicate the highest mean age of this mollusc in the study area. According to available literature information, larvae of this species are recorded in plankton in June–August [Kiseleva, 1978]. The same as *Ch. gallina*, *P. rudis* has one peak of reproduction, distributed over time, and settling occurs in autumn [Kiseleva, 1978]. Thus, the smallest individuals (1–4 mm) were apparently about 8–10 months old (0+). Such specimens formed a peak in all years of observation and, with the exception of 2021–2022, dominated in the population. We identified four size groups which seem to correspond to different mollusc generations: 0+ (up to 4 mm), 1+ (4–8 mm), 2+ (9–13 mm), and 3+ (more than 13 mm, singly registered in 2021). Individuals larger than 16 mm were not included in this sample. Importantly, hydrobionts with a shell length of 19 mm were noted in the Gelendzhik Bay in 2023 (own unpublished data); in the XX century, size of *P. rudis* reached 25 mm in the Black Sea [Kiseleva, 1981]. We found no information on the maximum age of this species in literature; based on the analysis carried out, we assume that it may be at least about 4 years. However, in most cases, we recorded simultaneously two or three size groups in the population evidently belonging to different generations. Thus, the maximum age seemed to be at least 3 years. The occurrence of younger age groups and their predominance evidence for a stable replenishment of the population, but since 2020, the intensity of replenishment declines.

G. minima was a codominant of *P. rudis* at 25 m in 2015–2022. In our samples, these species were comparable in size (up to 12 mm). Its maximum size in the Black Sea is known to be exactly 12 mm [Kiseleva, 1981]; accordingly, it is a smaller-sized species compared to the previous two. There is no material on exact reproduction period of *G. minima*; the only information covers the fact that it is observed in summer [Kiseleva, 1981]. According to our data, in the Inal Bay populations, there were fewer juveniles (up to 3 mm) in summer than medium-sized individuals in almost all years of the study. To clarify this issue, more detailed research on the maturation and spawning periods is required, along with a seasonal analysis of the population dynamics. Apparently, this species settles already in August and manages to grow by the beginning of winter, unlike *P. rudis* and *Ch. gallina*, or, settling at the same time as they do, it has a higher growth rate. Its high growth rate is confirmed by data of M. Kiseleva [1978]: June to November, *Gouldia* representatives grew by 3–4 mm, *i. e.*, in 5 months, 6-mm individuals became 9–10-mm ones. Interestingly, shell length increased from half the maximum size to almost the maximum size for this species in the Black Sea. The growth rate of *P. rudis* in the same biotope was only 2 mm in 5 months [Kiseleva, 1981]. Thus, the growth rate of *G. minima* seems to be higher than that of *P. rudis*. The maximum age of *G. minima* is also unknown [Kiseleva, 1981]. We assume that its age does not exceed three years in the study area. Firstly, we determined no more than three peaks in the histograms clearly separated from each other. Secondly, the view of the histograms was completely different from the standard form of size–frequency distributions of long-lived species [Revkov et al., 2014] characterized by a narrow and high peak of small-sized individuals and an extended and flat peak of older ones. In *G. minima*, there were no narrow and high peak of juveniles and extended peak of adults, and this may indicate a high growth rate of these molluscs because of their short lifespan. Thirdly, no clear correspondence of peaks was registered in different years. For example, in 2016, there was a peak of individuals with a shell length of about 4.5 mm; in 2017, such a peak was not observed, and the maximum was reached in specimens of about 3 mm.

Finally, *L. divaricata*, the smallest species, an inhabitant of a depth of 10 m, was characterized by the presence of two or three peaks in the histograms, the same as *G. minima*. Their intensity was much lower than even in *G. minima*. No clear separation of peaks was observed. *L. divaricata* was even smaller than *G. minima*: up to 5.3 mm. We failed to find data on the Black Sea *L. divaricata* reproduction, growth rate, and age. According to information for the western Mediterranean basin, this species reproduces in spring, and its juveniles settle in early summer [Sardá et al., 1999]. Assuming that the reproduction period is approximately the same, settling in the studied population could have occurred before we carried out the survey (late June–early July). This may explain the presence of a peak of juveniles in the histograms during the study period. The highest number of peaks we revealed is three. Therefore, we can cautiously assume as follows: off the North Caucasus, the maximum age of *L. divaricata* was no more than three years. However, according to N. Revkov *et al.* [2014], off the Crimea, such a pattern of peak distribution in size–frequency histograms of shell lengths for this species persists in other periods of the year. This contradiction necessitates further investigation on seasonal dynamics of *L. divaricata* size structure on the North Caucasus coast.

Patterns of change in the size structure of bivalves in soft sediments of the North Caucasus have been poorly studied. The latest data on the structure of Bivalvia populations were provided by M. Chikina *et al.* [2003], with a focus on an invader *A. kagoshimensis* prevailing at depths of 20–30 m. As shown, in the early 2000s, its population structure was extremely uniform: most molluscs were of similar size which resulted from mass settling in the autumn of 1999. Their growth rate was low due to high density of populations: in 2001, *A. kagoshimensis* abundance was 2,462 ind.·m^{-2}, and in 2002, 1,420 ind.·m^{-2} [Chikina et al., 2003]. At the age of two years, the mollusc had a mean size of about 15–16 mm [Chikina et al., 2003]. According to data for the Kerch Strait, the annual growth in the first and second years of life was 17 and 12 mm, respectively (unfortunately, the population density was not indicated by the author) [Zhavoronkova et al., 2022]. In the Black Sea off the Crimea, under conditions of cage culture, this species reached a size of (27.0 ± 1.2) mm in two years [Pirkova, 2012]. A similar decrease in growth rates against the backdrop of high abundance was recorded at a depth of 10 m in the early 2000s for *Ch. gallina* [Chikina, 2009; Kucheruk et al., 2002]. As shown, in the Black Sea, its individuals were of 6–10 mm at the age of one year [Kiseleva, 1981] and 17–25 mm at the age of two years [Boltachova, Mazlumyan, 2001]. In the early 2000s, one-year-old *Ch. gallina* had a shell length of about 2–3 mm, and two-year-old ones were no more than 5 mm [Chikina, 2009]. Currently, its growth rates have risen compared to those of the early 2000s. Apparently, one of the reasons is lower abundance in populations in recent years: the total abundance does not exceed 10 thousand ind.·m^{-2} in 2015–2022 *vs.* 36 thousand ind.·m^{-2} in 2001 [Kucheruk et al., 2002]. The maximum age recorded for this long-lived species has increased as well. In the early 2000s, *Ch. gallina* age did not exceed 3 years [Chikina, 2009; Kucheruk et al., 2012]: individuals settled in 1999 were completely eliminated by 2003 by the rapa whelk. Currently, there is another pattern. Thus, many *Ch. gallina* specimens that settled in 2017 were still alive in 2022 (their age was about 4.5 years).

Dynamics of Mollusca taxocene off the North Caucasus. In the 2000s, invaders (*R. venosa* and *A. kagoshimensis*) played an important role in benthic communities of soft sediments off the North Caucasus [Chikina, 2009; Kucheruk et al., 2012]. Already in the 2010s, according to our data, the former autochthonous dominants came to the forefront: *Ch. gallina*, *L. divaricata*, *P. rudis*, and *G. minima*. Besides, in a community of depths of 10–30 m, minor species began to be recorded again: *S. subtruncata* and *D. semistriatus* [Kolyuchkina et al., 2020; this study]; their abundance was extremely low in the early XXI century [Chikina, 2009; Kucheruk et al., 2002]. This evidences for a gradual recovery of the taxocene structure after disastrous transformations of the early XXI century. However, it is unreasonable to claim that the taxocene structure has returned to the pre-crisis state. Abundance and biomass of dominant species, along with the size structure of their populations, still experience annual fluctuations. Shifts in taxocene abundance and size structure of mollusc populations could be governed by both changes in abiotic factors and food abundance or interspecific/intraspecific interactions. No reliable correlations were established between biomass, abundance, and species number in the taxocene, as well as biomass and abundance of analyzed species, available environmental characteristics, and *R. venosa* abundance. However, the analysis of the taxocene structure by biomass showed that the proportion of explained variation in biotic data for a depth of 10 m due to the grain size of sediments was 44.3%. At the same time, the grain size differed for the last two years only. Thus, in 2021, a low content of silt fractions was determined. In 2021, the content of aleurite was still low, but that of pelite rose by 3.5 times compared to 2021 and was 2 times higher than within 2015–2020 (see Fig. 1A). The second factor that significantly contributed to the variation in biotic data was the mean temperature in February–March. Its variability accounted for 16.3% of the variation. Against the backdrop of relatively similar annual values, temperatures in February–March were lower in 2017 and 2022 (see Fig. 1B).

The study period covered years with different temperature conditions. The winter of 2016–2017 was severe [Podymov et al., 2021]. Back then, abundance and biomass of molluscs were relatively low both at 10 and 25 m, and large individuals occurred rarely. Apparently, it was directly and/or indirectly driven by temperature conditions. A prolonged cold period could have caused death of both adult molluscs and specimens that settled in autumn. Moreover, cold winters tend to mediate later spring bloom of phytoplankton – the main food source for bivalves. With a gain in water temperature and salinity in 2019–2020 [Chasovnikov, Borodulina, 2022; Podymov et al., 2021], there was a trend of restoring the taxocene abundance and biomass. After low abundance registered by 2020, the taxocene, on the contrary, was characterized by extremely high values of abundance and biomass of molluscs. In 2021, after two years of drought, there was an almost twofold rise in precipitation level, and river runoff increased [Korshenko et al., 2022]. This caused an outbreak of diatoms [Chasovnikov, Borodulina, 2022] which are the key food of the studied bivalves [Kiseleva, 1981]. The trend appeared to continue in 2022: that year, against the backdrop of heavy flood, an extreme outbreak of coccolithophore bloom was recorded in spring [Korshenko et al., 2022]. However, there was no further growth in biomass of molluscs. Quite a similar pattern was observed during the crisis in the northwestern Black Sea in the late XX century, when anthropogenic eutrophication governed a cascade of events that led to annual suffocation in the bottom layer [Bologa et al., 1995]. One of phenomena of that period was annual abundant phytoplankton bloom. Interestingly, despite high food availability, there was no increase in abundance, but rather suppression of benthic filter feeders. However, it is hard to assume that stable hypoxia zones, let alone suffocation zones, can be formed on the open shelf in the upper quasi-homogeneous layer, with its significant and constant wave action. Another explanation for a drop in biomass in 2021–2022 may be the pressure by adults on planktonic larvae: a phenomenon reported for coastal ecosystems [André et al., 1993]. According to our data, after the mass settling of *Ch. gallina* in 2017 which resulted in a peak of juveniles in July 2018, high abundance of large molluscs was noted in the next two years (2019 and 2020), and juveniles were approximately 2–3 times less abundant than large individuals (see Fig. 12). A new abundant replenishment occurred only in 2021 – against the backdrop of a decrease in abundance of large specimens parallel with a gain in their mean size.

We cannot rule out the role of interspecific interactions in regulating abundance of the surveyed bivalve populations. Thus, mass settling in 1999 was most likely caused by limitation of the pressure by a planktotrophic species *M. leidyi* on larval stages of bivalves and absence of adults due to predation by the rapa whelk [Kucheruk et al., 2002]. During the study period (2015–2022), cases of mass settling of bivalves were registered as well: in 2017, *Ch. gallina* and *L. divaricata*; in 2020, *P. rudis*; and in 2021, *G. minima*. The same as in 1999, this was preceded by a drop in abundance of adult individuals. However, in 2015–2022, a decline in abundance was not so dramatic: values of macrozoobenthos biomass roughly corresponded to those of the middle of the XX century [Kiseleva, 1981]. In the mid-2010s, no outbreaks of *R. venosa* abundance were recorded; within the study period, single medium-sized rapa whelks were occasionally found in samples. Thus, the pressure by this predator unlikely triggered mass settling. The pressure by jellyfish on planktonic mollusc larvae in the mid-2010s significantly decreased, and the planktonic community reached an equilibrium state by 2014 [Arashkevich et al., 2015]. Apparently, this largely governs the occurrence of annual replenishment by juveniles for all benthic species. During the study period, the species under the most pressure by jellyfish were those whose larvae appeared in plankton during late spring–early summer, *i. e.*, in the season of mass reproduction of *M. leidyi*, their main consumer [Louppova, 2017]. However, due to water warming off the northeastern Black Sea in recent years, *Beroe ovata*, an obligate ctenophore feeding on the warty comb jelly, appears already in June-July, not in August, as in the early 2000s [Martynyuk, 2017]. This reduces the probability of the fact that *M. leidyi* would eat away planktonic larvae of benthic animals during summer and autumn. *M. leidyi* could affect *L. divaricata* alone if its reproduction occurred in late spring–early summer. However, very high abundance was recorded for this species, and this may indirectly evidence for success of its population in the study area. Abundant settling of *L. divaricata* in 2017 may have resulted from the suppression of *Ch. gallina* populations inhabiting the same biotope during this period.

Conclusions:

1. In 2015–2022, *Chamelea gallina* and *Lucinella divaricata* dominated at a depth of 10 m, and *Pitar rudis* and *Gouldia minima* prevailed at 25 m. No stabilization of abundance of these species was revealed during the study period. In 2020, an outbreak of their biomass was recorded at depths of 10 and 25 m. In 2021–2022, a decline in biomass was observed.
2. The size structure of populations of the surveyed species was unstable in 2015–2021, but small-sized molluscs from the previous-year settling were registered in the populations almost every year. The only exception was *G. minima*: its small-sized individuals were noted in 2015 and 2021 alone. The most successful generation was that of *Ch. gallina* – the generation of 2017.
3. The highest age of molluscs determined by the cohort method in the investigated populations in 2015–2022 was 4.5 years for *Ch. gallina*, 3.5 years for *P. rudis*, and about 3 years for *G. minima*. To confirm an assumption that *L. divaricata* reproduction is confined to the late spring, additional research is required covering seasonal changes in the size structure of populations and the stage of gonad maturation.
4. The key factors driving the population dynamics of the analyzed species in the modern period seem to be abiotic ones (grain size of sediments and temperature). The period of low temperatures coincided with low abundance of the leading species of the taxocene: *Ch. gallina*, *P. rudis*, and *G. minima*. The period of their declining biomass coincided with a decrease in the content of aleurite in bottom sediments.

The work was supported by the Russian Science Foundation grant No. 23-27-00181

Acknowledgments. The authors are extremely grateful to all colleagues who participated in sampling in 2015–2022: U. Simakova, A. Basin, M. Simakov, V. Timofeev, V. Syomin, A. Vedenin, V. Kokarev, and V. Svasyan, as well as the crew of the small research vessel “Ashamba.”

REFERENCES

1. Alekseev R. P., Sinegub I. A. Macrozoobenthos and bottom biocenoses from the Black Sea shelves off the Caucasus, Crimea and Bulgaria. In: *Ecology of the Black Sea Coastal Areas* : collected papers / V. V. Sapozhnikov (Ed.). Moscow : VNIRO, 1992, pp. 218–234. (in Russ.)
2. Arashkevich E. G., Louppova N. E., Nikishina A. B., Pautova L. A., Chasovnikov V. K., Drits A. V., Podymov O. I., Romanova N. D., Stanichnaya R. R., Zatsepin A. G., Kuklev S. B., Flint M. V. Marine environmental monitoring in the shelf zone of the Black Sea: Assessment of the current state of the pelagic ecosystem. *Okeanologiya*, 2015, vol. 55, no. 6, pp. 964–970. (in Russ.). https://doi.org/10.7868/S0030157415060015
3. Boltachova N. A., Mazlumyan S. A. The linear growth and lifetime of *Chamelea gallina* (Bivalvia: Veneridae) in the Black Sea. *Ekologiya morya*, 2001, iss. 55, pp. 50–52. (in Russ.). https://repository.marine-research.ru/handle/299011/4385

4. Vinogradova Z. A. Materialy po biologii mollyuskov Chernogo morya. *Trudy Karadagskoi biologicheskoi stantsii*, 1950, iss. 9, pp. 100–159. (in Russ.). https://repository.marine-research.ru/handle/299011/6718
5. Vorob’ev V. P. *Bentos Azovskogo morya.* Simferopol : Krymizdat, 1949, 193 p. (Trudy AzCherNIRO ; iss. 13). (in Russ.)
6. Golikov A. N., Starobogatod Ya. I. Klass bryukhonogie molluski – Gastropoda. In: *Opredelitel’ fauny Chernogo i Azovskogo morei.* Vol. 3 : *Svobodnozhivushchie bespozvonochnye. Chlenistonogie (krome rakoobraznykh), mollyuski, iglokozhie, shchetinkochelyustnye, khordovye* / V. A. Vodyanitsky (Ed.). Kyiv : Naukova dumka, 1972, pp. 65–166. (in Russ.). https://repository.marine-research.ru/handle/299011/6078
7. Zhavoronkova A. M., Sytnik N. A., Zolotnitsky A. P. Age composition and linear growth of the invasive ark clam species (*Anadara kagoshimensis* (Tokunaga, 1906)) in the Kerch Strait. *Vodnye resursy i sreda obitaniya*, 2022, vol. 5, no. 1, pp. 45–55. (in Russ.). https://elibrary.ru/jgjqki
8. Zhirkov I. A. *Zhizn’ na dne. Bioekologiya i biogeografiya bentosa.* Moscow : KMK Scientific Press, 2010, 453 p. (in Russ.). https://elibrary.ru/qksrxf
9. Zakhvatkina K. A. Lichinki dvustvorchatykh mollyuskov Sevastopol’skogo raiona. *Trudy Sevastopol’skoi biologicheskoi stantsii*, 1959, vol. 11, pp. 108–152. (in Russ.). https://repository.marine-research.ru/handle/299011/5397
10. Kiseleva M. I. *Bentos rykhlykh gruntov Chernogo morya.* Kyiv : Naukova dumka, 1981, 165 p. (in Russ.). https://repository.marine-research.ru/handle/299011/8133
11. Kiseleva M. I. Peculiarities of size composition of bivalves populations inhabiting different zones of biotope. *Gidrobiologicheskii zhurnal*, 1978, vol. 14, no. 1, pp. 54–58. (in Russ.). https://repository.marine-research.ru/handle/299011/10110
12. Kiseleva M. I. Sravnitel’naya kharakteristika donnykh soobshchestv u poberezh’ya Kavkaza. In: *Mnogoletnie izmeneniya zoobentosa Chernogo morya* / V. E. Zaika (Ed.). Kyiv : Naukova dumka, 1992, pp. 84–99. (in Russ.). https://repository.marine-research.ru/handle/299011/5644
13. Kolyuchkina G. A., Syomin V. L., Grigorenko K. S., Basin A. B., Lyubimov I. V. The role of abiotic factors in the vertical distribution of macrozoobenthos on the northeastern Black Sea coast. *Zoologicheskii zhurnal*, 2020, vol. 99, iss. 7, pp. 784–800. (in Russ.). https://doi.org/10.31857/S0044513420070053
14. Korshenko E. A., Panasenkova I. I., Osadchiev A. A., Belyakova P. A. Synoptic and seasonal variability of small river plumes in the northeastern part of the Black Sea. In: *Marine Research and Education (MARESEDU) – 2022* : proceedings of the XI International conference, Moscow, 24–28 October, 2022. Tver : PoliPRESS, 2022, vol. 2 (4), pp. 236–240. (in Russ.). https://elibrary.ru/ehtque
15. Kucheruk N. V., Basin A. B., Kotov A. V., Chikina M. V. Macrobenthos of crumbly sediments of the Black Sea Caucasian coast: Long-term dynamics of the communities. In: *Multi-Disciplinary Investigations of the North-Eastern Part of the Black Sea* / A. G. Zatsepin, M. V. Flint (Eds). Moscow : Nauka, 2002, pp. 289–297. (in Russ.)

16. Kucheruk N. V., Flint M. V., Maksimova O. V., Chikina M. V., Simakova U. V. Sovremennaya dinamika bentosnykh soobshchestv severo-vostochnogo shel’fa Chernogo morya. In : *The Change of the Natural Environment of Russia in the XX Century* / V. M. Kotlyakov, D. I. Lyuri (Eds). Moscow : Molnet, 2012, pp. 274–287. (in Russ.)
17. Louppova N. E. Coadaptation of Black Sea cross-crops *Beroe ovata* Mayer and *Mnemiopsis leidyi* A. Agassiz. *Mezhdunarodnyi zhurnal gumanitarnykh i estestvennykh nauk*, 2017, no. 9, pp. 12–15. (in Russ.). https://elibrary.ru/zhzkxt
18. Martynyuk M. L. Features of development of invasive Ctenophora *Mnemiopsis leidyi* (A. Agassiz, 1865) and *Beroe ovata* Mayer, 1912 in the north-eastern Black Sea. In: *Proceedings of AzNIIRKh (rezul’taty rybokhozyaistvennykh issledovanii v Azovo-Chernomorskom basseine)* : sbornik nauchnykh trudov po rezul’tatam issledovanii za 2014–2015 gg. / V. N. Belousov (Eds). Rostov-on-Don : AzNIIRKh, 2017, vol. 1, pp. 97–103. (in Russ.). https://elibrary.ru/vlcolz
19. *Mitilidy Chernogo morya* / V. E. Zaika (Ed.) ; AN USSR, Institut biologii yuzhnykh morei imeni A. O. Kovalevskogo. Kyiv : Naukova dumka, 1990, 208 p. (in Russ.). https://repository.marine-research.ru/handle/299011/1459
20. Pirkova A. V. Growth of bivalve mollusk *Anadara inaequivalvis* (Bivalvia) in the Black Sea while growing in cages. In: *Current Fishery and Environmental Problems of the Azov–Black Sea Region* : materials of VII International conference, Kerch, 20–23 June, 2012. Kerch : YugNIRO Publishers, 2012, vol. 2, pp. 73–78. (in Russ.). https://elibrary.ru/yscpwo
21. Revkov N. K., Timofeev V. A., Lisitskaya E. V. Composition and seasonal dynamics of macrozoobenthos in local biotic complex *Chamelea gallina* (Western Crimea, the Black Sea). *Ekosistemy*, 2014, no. 11 (30), pp. 247–259. (in Russ.). https://elibrary.ru/vkczqp
22. Revkov N. K. Fluffy bottom bed zoobenthos longstanding changes in the southwest Crimea region. In: *Modern Condition of Biological Diversity in Near-shore Zone of Crimea (the Black Sea Sector)* / V. N. Eremeev, A. V. Gaevskaya (Eds) ; NAS of Ukraine, Institute of Biology of the Southern Seas. Sevastopol : EKOSI-Gidrofizika, 2003, pp. 222–229. (in Russ.). https://repository.marine-research.ru/handle/299011/1467
23. Romankevich E. A., Vetrov A. A. *Tsikl ugleroda v arkticheskikh moryakh Rossii.* Moscow : Nauka, 2001, 302 p. (in Russ.)
24. Selifonova Zh. P., Chasovnikov V. K. Ecological condition of zoobenthos on the Caucasus coast near Dzhubga – Khosta (the Black Sea). *Sistemy kontrolya okruzhayushchei sredy*, 2017, no. 10 (30), pp. 119–128. (in Russ.). https://elibrary.ru/qjgrpb
25. Frolenko L. N., Zhivoglyadova L. A. Status of the *Chamelea gallina* and *Pitar rudis* communities in the north-eastern Black Sea in the autumn of 2019. *Vodnye resursy i sreda obitaniya*, 2020, vol. 3, no. 3, pp. 45–55. (in Russ.). https://doi.org/10.47921/2619-1024_2020_3_3_45
26. Frolenko L. N., Zhivoglyadova L. A., Kovalev E. A. Results of the zoobenthos studies in the north-eastern Black Sea according to the data obtained in 2016–2017. *Vodnye resursy i sreda obitaniya*, 2019, vol. 2, no. 4, pp. 85–97.

(in Russ.). https://doi.org/10.47921/2619-1024_2019_2_4_85

27. Chasovnikov V. K., Borodulina P. A. Trends in the interannual variability of nutrients in the northeastern part of the Black Sea according to ship observations for 2017–2021. *Ekologiya gidrosfery*, 2022, no. 2 (8), pp. 37–46. (in Russ.). https://doi.org/10.33624/2587-9367-2022-2(8)-37-46
28. Chikina M. V. *Makrozoobentos rykhlykh gruntov severokavkazskogo poberezh'ya Chernogo morya: prostranstvennaya struktura i mnogoletnyaya dinamika.* [dissertation]. Moscow, 2009, 116 p. (in Russ.). https://elibrary.ru/nqjfxd
29. Chikina M. V., Koluchkina G. A., Kucheruck N. V. Some features of reproduction biology of *Scapharca inaequivalvis* (Bruguière) (Bivalvia, Arcidae) in the Black Sea. *Ekologiya morya*, 2003, iss. 64, pp. 72–77. (in Russ.). https://repository.marine-research.ru/handle/299011/4597
30. Chukhchin V. D. Biologiya razmnozheniya *Venus gallina* L. (Lamellibranchiata) v Chernom more. In: *Bentos* : sbornik statei. Kyiv : Naukova dumka, 1965, pp. 15–23. (in Russ.). https://repository.marine-research.ru/handle/299011/97
31. Shalovenkov N. N. Tendencies of invasion of alien zoobenthic species into the Black Sea. *Rossiiskii zhurnal biologicheskikh invazii*, 2020, vol. 13, no. 1, pp. 72–80. (in Russ.). https://elibrary.ru/bpcrvn
32. Akaike H. A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 1974, vol. 19, no. 6, pp. 716–723. https://doi.org/10.1109/TAC.1974.1100705
33. Anderson M. J. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 2001, vol. 26, iss. 1, pp. 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x
34. André C., Jonsson P. R., Lindegarth M. Predation on settling bivalve larvae by benthic suspension feeders: The role of hydrodynamics and larval behaviour. *Marine Ecology Progress Series*, 1993, vol. 97, no. 2, pp. 183–192.
35. Bologa A. S., Bodeanu N., Petranu A., Ţigănuş V., Zaitsev Yu. P. Major modifications of the Black Sea benthic and planktonic biota in the last three decades. In: *Les mers tributaires de Méditerranée* / F. Briand (Éd.). Monaco : Musée océanographique, 1995, pp. 85–110. (Bulletin de l'Institut oceanographique, Monaco, n° special 15 ; CIESM, Science Series no. 1).
36. Chao A. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, 1987, vol. 43, iss. 4, pp. 783–791. https://doi.org/10.2307/2531532
37. Chikina M. V., Kucheruk N. V. Long-term changes in the structure of coastal benthic communities in the northeastern part of the Black Sea: Influence of alien species. *Oceanology*, 2005, vol. 45, suppl. 1, pp. 176–182. https://elibrary.ru/ljkvgr
38. Clarke K. R., Gorley R. N. *PRIMER v6: User Manual. Tutorial.* Plymouth : PRIMER-E, 2006, 190 p.
39. Dempster A. P., Laird N. M., Rubin D. B. Maximum likelihood from incomplete data *via* the EM algorithm. *Journal of the Royal Statistical Society: Series B (Methodological)*, 1977, vol. 39, iss. 1, pp. 1–22. https://doi.org/10.1111/j.2517-6161.1977.tb01600.x
40. Dumitrache C., Abaza V. The present state

of benthic communities in the Romanian coastal waters. *Cercetări Marine – Recherches Marines*, 2004, no. 35, pp. 61–75.

41. *Exotic Species in the Aegean, Marmara, Black, Azov and Caspian Seas* / Yu. P. Zaitsev, B. Öztürk (Eds). Istanbul : Turkish Marine Research Foundation, 2001, 267 p.
42. Marinov T., Stoykov S. Seasonal investigations of macrozoobenthos in the Bulgarian shelf of Black Sea. *Oceanology [Bulgarian Academy of Sciences]*, 1990, vol. 19, pp. 49–62. (in Bulg.)
43. Podymov O. I., Zatsepin A. G., Ocherednik V. V. Increase of temperature and salinity in the active layer of the north-eastern Black Sea from 2010 to 2020. *Physical Oceanography*, 2021, vol. 28, no. 3, pp. 257–265. https://doi.org/10.22449/1573-160X-2021-3-257-265
44. Revkov N. K., Boltacheva N. A., Timofeev V. A., Bondarev I. P., Bondarenko L. V. Macrozoobenthos of the Zernov's *Phyllophora* field, northwestern Black Sea: Species richness, quantitative representation and long-term variations. *Nature Conservation Research. Zapovednaya nauka*, 2018, vol. 3, no. 4, pp. 32–43. https://doi.org/10.24189/ncr.2018.045
45. Sardá R., Pinedo S., Martin D. Seasonal dynamics of macroinfaunal key species inhabiting shallow soft-bottoms in the Bay of Blanes (NW Mediterranean). *Acta Oecologica*, 1999, vol. 20, iss. 4, pp. 315–326. https://doi.org/10.1016/S1146-609X(99)00135-6
46. Tiganus V. Present state of marine biodiversity in the Romanian Black Sea waters. In: *CIESM Workshop on Mediterranean Marine Biodiversity*, Nicosia (Cyprus), 1–3 May, 1997. [Monaco] : [Commission International pour l'Exploration Scientifique de la Mer Méditerranée], 1997, pp. 61–62. (CIESM Workshop Series ; n° 1).
47. *WoRMS. World Register of Marine Species* : [site]. URL: https://www.marinespecies.org/ [accessed: 10.10.2023].

ТАКСОЦЕН МОЛЛЮСКОВ РЫХЛЫХ ГРУНТОВ ПРИБРЕЖНОЙ ЗОНЫ СЕВЕРО-ВОСТОЧНОГО СЕКТОРА ЧЁРНОГО МОРЯ В НАЧАЛЕ XXI ВЕКА

Г. А. Колючкина[1], И. В. Любимов[1], Н. А. Данилова[1,2]

[1]Институт океанологии имени П. П. Ширшова РАН, Москва, Российская Федерация
[2]Российский государственный аграрный университет — МСХА имени К. А. Тимирязева, Москва, Российская Федерация
E-mail: *galka.sio@gmail.com*

В условиях нарастающих климатических и антропогенных изменений одной из наиболее актуальных задач современной экологии является понимание взаимосвязи динамики морских экосистем и окружающей среды. В то же время далеко не все происходящие в морских шельфовых экосистемах изменения можно объяснить влиянием внешних факторов, поскольку динамика экосистем, связанная с действием внутренних процессов, таких как естественные сукцессии, известна фрагментарно. Донные сообщества играют ведущую роль в функционировании экосистем, модифицируя среду обитания, влияя на круговорот питательных веществ и первичную продуктивность. С донными экосистемами связывают возможность иммобилизации и секвестра углерода, оценка которых остаётся фундаментальной научной задачей. Прибрежные сообщества Чёрного моря являются удобной моделью для такого рода исследований. Здесь доминирующие позиции в бентосе занимают карбонатпродуцирующие организмы — моллюски.

Целью настоящей работы было изучение динамики обилия и популяционной структуры моллюсков рыхлых грунтов прибрежной зоны северокавказского побережья Чёрного моря в 2015–2022 гг. Выполнены ежегодные сборы материала на глубинах 10 и 25 м. Проанализированы структура таксоцена моллюсков и динамика размерной структуры поселений его основных доминантов: на 10-м глубине — *Chamelea gallina* и *Lucinella divaricata*, а на 25-м глубине — *Gouldia minima* и *Pitar rudis*. Колебания обилия этих видов достигали порядка величин. Наибольшие биомассы таксоцена отмечены в 2020 г., что совпало с максимальными значениями температуры и солёности поверхностных вод (с засушливым периодом). Выявлено успешное ежегодное пополнение, установлен мультимодальный вид размерно-частотных диаграмм этих моллюсков, за исключением *G. minima*, ювенильные стадии которой в пробах практически не встречались. На основании анализа размерно-частотных диаграмм сделана попытка оценить средний предельный возраст особей в поселениях этих видов. Не выявлено линейных зависимостей между значениями абиотических факторов и структурой таксоцена. Охарактеризованы тенденции параллельного изменения обилия ювенильных особей в поселениях и общей биомассы каждого из исследованных видов.

Ключевые слова: Чёрное море, двустворчатые моллюски, макрозообентос, динамика поселений