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ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2025, vol. 10, no. 2, pp. 18–33
https://marine-biology.ru

UDC 574.587(265.54.04)

INTERANNUAL CHANGES IN THE STRUCTURE OF MEIOBENTHOS IN SANDY SHALLOWS OF THE TRIOZERYE BAY (SEA OF JAPAN)

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Received by the Editor 31.05.2024; after reviewing 07.07.2024;
accepted for publication 20.03.2025.

This paper is the first one to provide results of the study on the dynamics of biological parameters of the meiobenthos within the coastal strip of sandy sediments in the Triozerye Bay (Sea of Japan) in July–August 2021–2023. During the investigation, 20 taxa of the meiofauna were registered, with the basis formed by representatives of Harpacticoida, Nematoda, Copepoda, Turbellaria, Gastrotricha, Annelida, Halacaridae, and Ostracoda. The nematofauna mostly covered free-living nematodes *Daptonema normandicum*, *Enoplolaimus pectinatus*, *Metadesmolaimus innii*, and *Parascolaimus proprius*. In general, the structure of qualitative and quantitative indicators of meiobenthos and nematofauna changed annually due to fluctuations in the grain size distribution of bottom sediments.

Keywords: Sea of Japan, interannual changes, grain size distribution, organic matter, meiobenthos, nematofauna

Information on coastal ecosystems of the Sea of Japan shoreline is still scarce. While the taxonomic composition and distribution of meiobenthos in relation to environmental factors have been studied in several areas of Peter the Great Bay [Pavlyuk, 2004; Smirnova, Fadeeva, 2012; Trebukhova, Pavlyuk, 2006; *etc.*], the structural organization and spatial and temporal variability of interstitial communities in low-tidal beaches dominated by wave action have been poorly investigated [Fadeeva, 1991; Smirnova, Fadeeva, 2012].

In the upper subtidal zone, in open bays, bottom sediments are formed under active hydrodynamics (both wave action and current-related) and are characterized by intensive water exchange with the open sea. On sandy shores, an environment of high physical stress for marine fauna is formed; consequently, relatively few species inhabit this unique transitional ecosystem laying between terrestrial and marine habitats. At first sight, sandy beaches appear lifeless, resembling 'biological deserts'; however, rich meiobenthic communities are formed in interstitial areas.

The Triozerye Bay, an open and sandy one, is known for its three freshwater lakes bordering saline waters. It is a popular beach destination in summer. It is located in the southeastern Primorye, in the Partizansky District, along the western coast of the Sea of Japan (see Fig. 1). Several marine biological studies carried out in the Triozerye Bay were focused only on some macrobenthic species and abundant macrophytes [Kulepanov et al., 2023].

The aim of this work is to examine interannual variations in the density of meiobenthic and nematode communities in the upper subtidal zone (at depths down to 1 m) of open shallows in the Triozerye Bay in 2021–2023 in relation to environmental conditions.

MATERIAL AND METHODS

The study area was the Triozerye Bay: a shallow sandy open site in the western Sea of Japan. Its central part is dominated by the dome-shaped landscapes extending from the northeast. Those are bordered by extensive arenoid fields. To the northwest, those are bordered by the littoral zone; to the north, by concizium; and to the southwest, by landscapes adjacent to a group of rocks [Arzamastsev, Preobrazhensky, 1990; Preobrazhensky et al., 2000]. A sandy beach stretches for over 1.5 km. Three lakes near the bay are located 200 m from the shoreline; those do not affect directly water conditions. The mean salinity ranges 30 to 33‰.

The morphometric index determining the degree of a bay openness was established as the ratio of depth of the bay's incision into the land to the distance between the entrance capes [Manuilov, 1990]. This index was calculated using the 'ruler and planimeter' tool in a mapping service Yandex.Maps (https://yandex.ru/maps). A schematic map was built using Ocean Data View software package and Yandex.Maps.

The investigation was carried out in July–August 2021–2023 (at temperature of +18.5…+24 °C) in the Triozerye Bay (the Sea of Japan) (Fig. 1), within a depth range of 0.5–1.0 m.

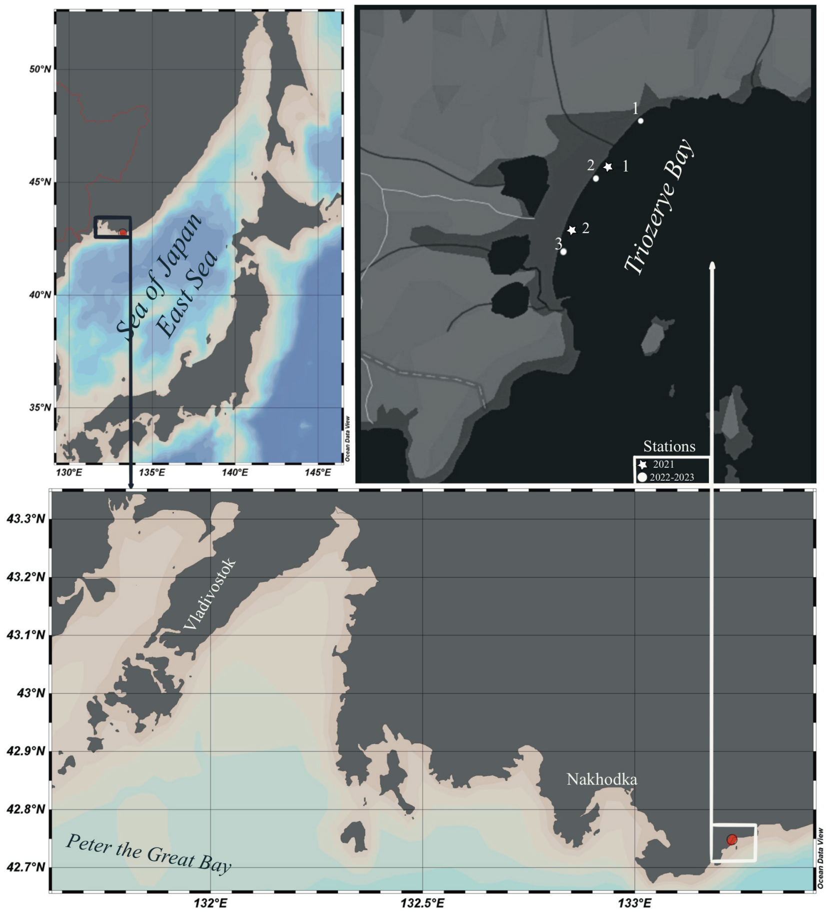

Fig. 1. Scheme map of the Triozerye Bay study area. White dots mark stations 1, 2, and 3 of 2022–2023 (st1_22, st2_22, and st3_22 in 2022; st1_23, st2_23, and st3_23 in 2023). White stars mark stations 1 and 2 of 2021 (st1_21 and st2_21). Sources: Ocean Data View and Yandex.Maps

Over the study period, 24 samples were collected in the Triozerye Bay: on 19 August, 2021, 6 samples at two stations; on 19 July, 2022, and 10 August, 2023, 9 samples at three equally spaced stations. Weather data for the sampling periods were obtained from an open-source archive [Arkhivy pogody, 2024]. Alongside the quantitative sampling, we sampled material to analyze organic matter content and grain size distribution of sediments.

Bottom sediments were sampled with a tubular corer with an inner diameter of 2.2 cm and a sediment column height of 5 cm. The core cross-sectional area was 3.8 cm^2. Grain size was analyzed by the standard sieve method [Petelin, 1967], and the obtained data were classified according to the dominant grain fraction [GOST 12536-2014, 2015]. Organic matter content was determined following the State Standard 26213-91: carbon content was assessed by wet combustion by the Tyurin method [GOST 26213-91, 1992]. Meiobenthic organisms were extracted from sediments by a standard method using sieves with mesh sizes of 32–40 µm and fixed in filtered seawater with buffered 4% formaldehyde.

All meiobenthos was counted and taxonomically classified. Species identification of nematodes and measurements of key morphological parameters (body length and maximum diameter) were carried out under a stereo microscope Axio Imager applying AxioVision software v4.8.

To characterize the taxocene structure of meiobenthos and nematodes, we calculated the Shannon index (H), the Margalef index (D_{Mg}), the Pielou index (E), and the Simpson index ($1 - D$). Estimations and similarity analysis between the sampling stations were carried out applying the Bray–Curtis dissimilarity (PRIMER v6), while correlation analysis involved Pearson coefficient (PAST 4.04). The trophic structure of the Nematoda community was preliminarily evaluated based on W. Wieser's classification [1953] categorizing nematodes according to their buccal cavity morphology.

Index of Trophic Diversity, *ITD*, was calculated by the formula:

$$ITD = g_1^2 + g_2^2 + ... + g_n^2 \,,$$

where g is the relative contribution of each trophic group to the total number of individuals;

n is the number of trophic groups [Heip et al., 1985].

In literature, the more common form is $1 - ITD$, where the value ranges 0 to 0.75.

The biomass (M) of nematodes was determined by the formula:

$$M = V \times p \times N \,,$$

where V is volume of organisms;

p is specific density (1.13 $mg \cdot m^{-3}$ for Nematoda);

N is the number of organisms *per* 1 m^2.

The volume (V) of organisms was calculated in accordance with the formula:

$$V = k \times L \times w \,,$$

where k is the conversion factor (530 for Nematoda);

w is the maximum body width;

L is the body length [Chislenko, 1968].

Qualitatively, the community was assessed applying the ABC method (Abundance–Biomass Comparison) based on plotting two cumulative curves – the abundance and biomass ones:

$$ABC_{index} = \sum_{i=1}^{N}(B_i - A_i) ,$$

where B_i and A_i are cumulative values of relative biomass and abundance of the i-th species, %;

N is the number of species.

If the index value is positive, communities are considered undisturbed; if it is negative, those are under stressful conditions; and if value is close to zero, those experience minor or negligible effects. To have more data and to compare ABC curves, we calculated Clarke's W statistics [Clarke, 1990]. It assesses the area between two cumulative curves – the biomass and abundance ones:

$$W = \frac{\sum(B_i - A_i)}{[50(S-1)]} ,$$

where B_i are accumulated biomass values for the i-th ranked species;

A_i are accumulated abundance values for the i-th ranked species;

S is the number of species.

W statistics defines the ABC effect and ranges −1 to +1. Its value approaches −1 in highly disturbed communities and +1 in undisturbed ones (PRIMER v6).

To fully characterize the grain size distribution of sediments, the percentage content of grain fractions of certain size was calculated. Then, the median (mean grain size, Md), sorting coefficient (S_0), and asymmetry coefficient (S_k) were established. These coefficients were determined by constructing cumulative curves from which quartile values were derived. The degree of sediment sorting S_0 was evaluated according to P. D. Trask [1932]: well sorted sediments (S_0 = 1.0…1.58), moderately sorted (S_0 = 1.58…2.12), and poorly sorted (S_0 > 2.12).

For multivariate assessment of communities, cluster analysis and non-metric multidimensional scaling were applied. Station clustering was performed using the Bray–Curtis dissimilarity (PRIMER v6). Univariate parametric correlation coefficients were calculated between numerical environmental parameters, meiofaunal density, biomass of nematodes, and various diversity indices. The relationship between the environmental variables and the structure of meiofaunal and Nematoda community was examined using the BEST procedure with Spearman's rank correlation coefficient (PRIMER v6).

Statistical analysis was carried out using MS Office Excel, PRIMER v6, and PAST 4.04 software packages.

RESULTS

The Triozerye Bay features active hydrodynamic regime and absence of silts, with a morphometric index of 0.2; this allows for classifying it as an open-type bay. According to [Arkhivy pogody, 2024] data for Nakhodka city district, during sampling in August 2021 and July 2022, weather conditions were similarly moderate. In both periods, the sea was calm; there was no precipitation; and air temperature ranged +25…+32 °C. During the first decade of August 2023, strong wind gusts, up to 13 $m \cdot s^{-1}$, occurred intermittently. From the beginning of the month until the sampling day, cloud cover prevailed, 10/10, with air temperature not exceeding +23 °C; precipitation was recorded daily. On 10 August, 2023, rainfall reached 27 mm *per* day (a heavy rain occurred). In August 2023 (during sampling), the water temperature in the Triozerye Bay was lower than +18 °C.

Over the three years, the composition of bottom sediments changed. Specifically, the proportion of coarse particles increased. The predominant fractions shifted from fine sand in 2021 to medium and coarse sand in 2022 and to medium gravel at st1_23 in 2023. Cumulative curves (Fig. 2) clearly illustrate the differences in composition in 2021 and 2023.

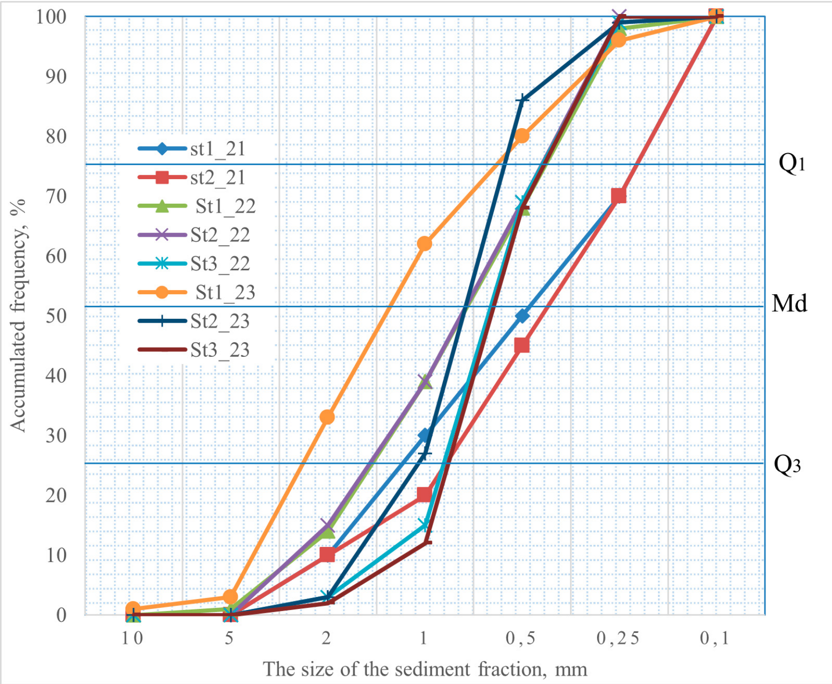

Fig. 2. Cumulative curves of the grain size distribution of bottom sediments in the Triozerye Bay in 2021–2023

Despite low organic matter content recorded in bottom sediments at all the stations in 2021–2023, there was a gain in its concentration from 0.03 to 0.08% within this period (Table 1).

Table 1. Characteristics of the stations: parameters of the grain size distribution of bottom sediments (S_0, sorting coefficient; S_k, asymmetry coefficient; Md, mean grain size of sediments) and organic matter content (C_{org}, %)

Station	S_0	S_k	Md	Sorting characteristics [Trask, 1932]	Predominant fraction, mm [Bezrukov, Licitzin, 1960]		C_{org}, %
st1_21	2.54	0.45	0.75	poorly sorted	0.25–0.01	fine sand	0.03
st2_21	2.12	0.9	0.45	moderately sorted	0.25–0.01	fine sand	0.03
st1_22	2.06	1.06	0.8	moderately sorted	0.5–0.25	medium sand	0.05
st2_22	2.06	1	0.8	moderately sorted	0.5–0.25	medium sand	0.05
st3_22	1.4	0.88	0.6	well sorted	1–0.5	coarse sand	0.05
st1_23	1.96	0.84	1.5	moderately sorted	5–2	medium gravel	0.05
st2_23	1.3	0.9	0.8	well sorted	1–0.5	coarse sand	0.08
st3_23	1.4	0.9	0.6	well sorted	1–0.5	coarse sand	0.05

During investigations in the Triozerye Bay in 2021–2023, a total of 20 meiofaunal taxa were identified. The interstitial community was primarily formed by Harpacticoida, Nematoda, Copepoda, Turbellaria, Gastrotricha, Annelida, Halacaridae, and Ostracoda (Fig. 3). The number of taxa *per* station ranged 9 to 12. In 2022 and 2023, 13 taxa were recorded in the bay, and in 2021, 14 taxa were noted.

The dominant taxa varied throughout the study period (Fig. 3). In 2021, the proportion of Nematoda was the largest in the meiobenthos, 71%. In 2022, it dropped to less than 5%, while crustaceans (Harpacticoida and Copepoda) became predominant accounting for more than 80%. In 2022, the mean meiofaunal density across three stations reached (2,196.8 ± 1,407) ind. *per* 10 cm^2 being the highest during the research. In 2023, taxa distribution was more uniform, with no clearly prevailing groups. Turbellaria, Annelida, and Harpacticoida occurred in almost equal proportions (see Fig. 3); Ostracoda accounted for 16%. This year also showed the lowest nematode abundance: 6% of total meiofauna in the bay. Moreover, in 2023, at all the three stations, the lowest meiofaunal density was revealed: (288.3 ± 212) ind. *per* 10 cm^2.

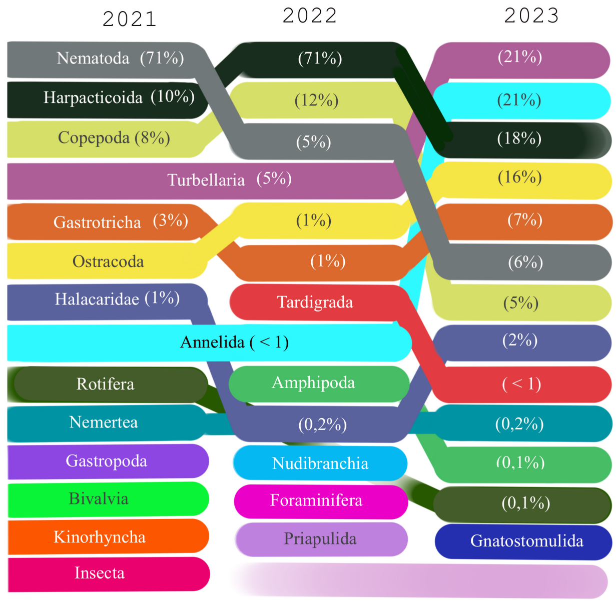

Fig. 3. Dynamics of changes in the share of main taxa in meiobenthos in the Triozerye Bay in 2021–2023

A total of 33 Nematoda species from 29 genera and 15 families were identified in the Triozerye Bay. The highest species diversity was recorded for Xyalidae (6 species), Axonolaimidae, and Chromadoridae (4 species each). All the registered species are listed in Table 2. The number of species varied 1 to 21 *per* station peaking at st2_21 in 2021 and reaching minimum at st3_23 in 2023. Notably, euryhaline free-living nematodes were observed in the bay: Linhomoeidae gen. sp. and *Leptolaimoides propinquus* at st3_23 in 2023 and *Anoplostoma cuticularia* at st1_21 in 2021.

Table 2. List of nematode species found in the Triozerye Bay in 2021–2023, their frequency of occurrence, and trophic affiliation

No.	Species	Family	Trophic index according to [Wieser, 1953]*	Frequency of occurrence, %	Ind. *per* 10 cm^2		
					2021	2022	2023
1	*Daptonema normandicum* (de Man, 1890) Lorenzen, 1977	Xyalidae	1B	71	34.2	57.5	2.2
2	*Parascolaimus proprius* Belogurov & Kartavseva, 1975	Axonolaimidae	1B	50	9	22.8	2.7
3	*Metadesmolaimus innii* Fadeeva & Karpova, 2024	Xyalidae	1B	42	35.6	0.9	4
4	*Enoplolaimus pectinatus* Fadeeva & Zograf, 2010	Thoracostomopsidae	2B	42	31.6	4.7	1.3

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No.	Species	Family	Trophic index according to [Wieser, 1953]*	Frequency of occurrence, %	Ind. *per* 10 cm²		
					2021	2022	2023
5	*Ascolaimus elongatus* (Bütschli, 1874) Shuurmans Stekhoven & de Coninck, 1932	Axonolaimidae	1B	38	1.8	2.9	0
6	*Neochromadora poecilosoma* (de Man, 1893) Micoletzky, 1924	Chromadoridae	2A	21	60.5	0	0
7	*Theristus macroflevensis* Gerlach, 1954	Xyalidae	1B	21	13.2	0	1.3
8	*Oncholaimus domesticus* (Chitwood & Chitwood, 1938) Rachor, 1969	Oncholaimidae	2B	21	11.1	0.9	2.2
9	*Oncholaimus* sp. Dujardin, 1845	Oncholaimidae	2B	21	3	8,1	0
10	*Parachromadorita* sp. nov. Blome, 1974	Chromadoridae	2A	21	10.4	0	0.7
11	*Bolbolaimus* sp. 1 Cobb, 1920	Microlaimidae	2A	21	8,4	0	0
12	*Bathylaimus anatolii* Smirnova & Fadeeva, 2011	Tripyloididae	1B	21	3.2	1.6	0
13	*Desmodora* sp. de Man, 1889	Desmodoridae	2A	17	8.2	0	0
14	*Trileptium* sp. Cobb, 1933	Thoracostomopsidae	2B	17	1.6	4.3	0.7
15	*Microlaimus* sp. de Man, 1880	Microlaimidae	2A	17	0.6	0	1.6
16	*Axonolaimus seticaudatus* Platonova, 1971	Axonolaimidae	1B	13	0.4	6.3	0
17	*Theristus* sp. Bastian, 1865	Xyalidae	1B	13	4	1.7	0
18	*Tripyloides* sp. de Man, 1886	Tripyloididae	1B	13	4.1	0	0
19	*Chromaspirina* sp. Filipjev, 1918	Desmodoridae	2A	13	0	2.5	0.9
20	*Chromadora heterostomata* Kito, 1978	Chromadoridae	1A	13	0	0	3
21	*Enoplus* sp. Dujardin, 1845	Enoplidae	1B	13	0	1.1	0
22	*Daptonema* sp. nov. Cobb, 1920	Xyalidae	1B	8	3	0	0
23	*Lauratonema juncta* Fadeeva, 1989	Lauratonematidae	1A	8	0	0.9	0.9
24	*Metachromadora itoi* Kito, 1978	Desmodoridae	2A	8	1	0	0.5
25	*Leptolaimoides propinquus* Fadeeva & Morduchovic, 2007	Leptolaimidae	1A	8	0	0	1.4
26	Linhomoeidae gen. sp. Filipjev, 1922	Linhomoeidae	1B	8	0	0	1.3
27	*Desmoscolex* sp. Claparède, 1863	Desmoscolecidae	2A	8	0.6	0	0
28	*Dichromadora* sp. Kreis, 1929	Chromadoridae	2A	4	4	0	0
29	*Viscosia epapillosa* Platonova, 1971	Oncholaimidae	2B	4	0	0	1
30	*Metadesmolaimus canicula* (Wieser & Hopper, 1967) Gerlach & Riemann, 1973	Xyalidae	1B	4	1	0	0
31	*Nudora* sp. nov. Cobb, 1920	Monoposthiidae	1A	4	1	0	0
32	*Parodontophora* sp. Timm, 1963	Axonolaimidae	2B	4	0.3	0	0.5
33	*Anoplostoma cuticularia* Belogurov & Alekseev, 1977	Anoplostomatidae	1B	4	0	0	0.5

Note: *, see Fig. 6 caption for explanation.

Over the three years, the Nematoda community showed shifts with changes in dominants. Five species forming the basis demonstrated both highest frequency of occurrence and density: *Daptonema normandicum*, *Parascolaimus proprius*, *Metadesmolaimus innii*, *Ascolaimus elongatus*, and *Enoplolaimus pectinatus*. *Oncholaimus domesticus* also had high frequency of occurrence in the bay, but lower values of density.

Certain interannual fluctuations in Nematoda density were observed in the Triozerye Bay. Specifically, within 2021–2023, total meiofaunal abundance has undergone some changes. The highest mean nematode density was recorded in 2021 at st2_21: (370 ± 296) ind. *per* 10 cm^2. The lowest value was noted in 2023 at st3_23: (5 ± 1.8) ind. *per* 10 cm^2 (Table 2). Within 2021–2022, the mean density across stations decreased by 2.2 times. In 2021–2023, it declined 10-fold evidencing for substantial interannual variability.

In 2021, the short-lived phytophagous species *Neochromadora poecilosoma* dominated: its proportion was 24% (Fig. 4). Interestingly, it was absent in subsequent years in the Triozerye Bay suggesting that its abundance is tightly associated with its feeding strategy depending on microphytobenthos dynamics. At the stations of 2021, half of the Nematoda community was formed by juveniles, and males accounted for only 12%. A shift in dominant species occurred in 2022, and *D. normandicum* proportion was 51%. This was reflected in the values of the Simpson index ($1 - D$) (Table 3): those were < 0.7 at st3_22. In 2023, the prevailing forms have changed, and there were no dominants among 18 Nematoda species recorded. The proportions were as follows (Fig. 4): *M. innii*, 14%; *Chromadora heterostomata*, 12%; and *A. elongatus*, *O. domesticus*, and *D. normandicum*, 9–10% each. Age and gender structures were similar in the samples of 2022–2023: females dominated at a level of 50%, and proportions of juveniles and males accounted for 30 and 20%, respectively.

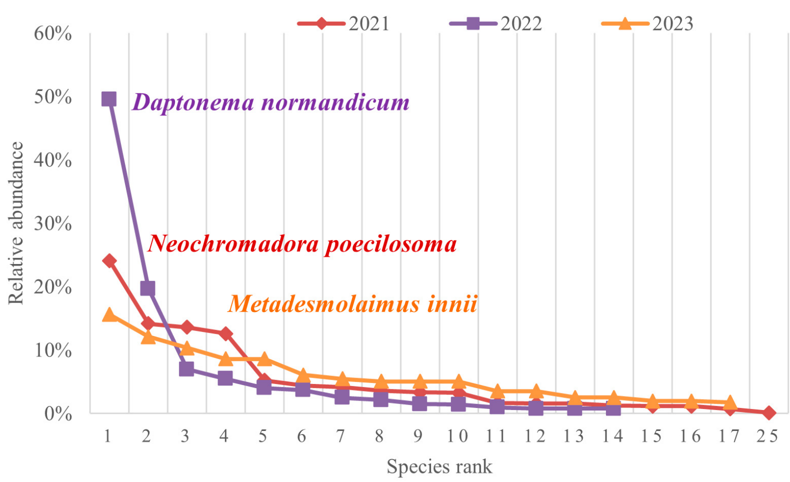

Fig. 4. Curves of the rank distribution of nematode relative abundance in 2021–2023 and dominant nematode species (the signature color corresponds to the dominance curve color)

Applying the ABC method, we revealed that in 2021–2023, the biomass curve was typically located above the abundance curve (Fig. 5) evidencing for the lack of physical stress.

In 2021 and 2022, the biomass of Nematoda remained relatively at the same level: 1,090 and 960 $\mu g \cdot m^{-2}$. In 2023, the value dropped 10-fold, to 90 $\mu g \cdot m^{-2}$. In 2021, 6 out of 25 registered species accounted for 80% of the total biomass, while in 2022, only 3 out of 14. The mean length of the found nematodes ranged 498 to 5,241 μm.

Table 3. Indices of biological diversity for the stations studied in 2021–2023

Index	2021		2022			2023		
	st1_21	st2_21	st1_22	st2_22	st3_22	st1_23	st2_23	st3_23
Shannon (H)	2.3	2.4	1.4	1.9	1.2	2.0		
Simpson ($1-D$)	0.9		0.7	0.8	0.6	0.9		
Margalef (D_{Mg})	3.7	3.4	1.1	2.2	1.4	2.5		
Pielou (E)	0.8		0.8	0.8	0.6	0.9	0.9	1.0
$1-ITD$	0.66		0.55			0.74		
ABC_{index}	1.6		0.97			3.6		

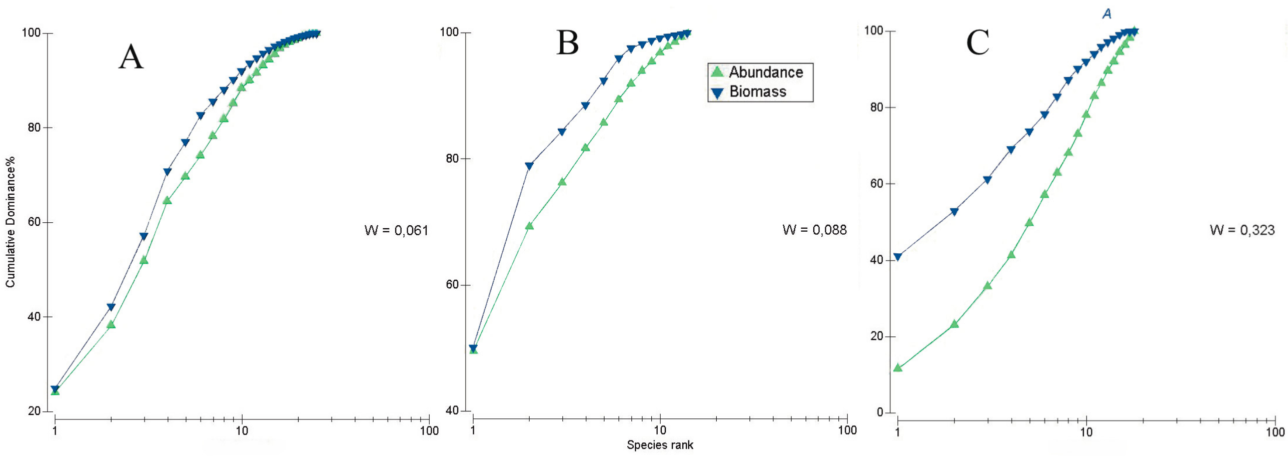

Fig. 5. Cumulative curves of abundance and biomass according to the data of 2021 (A), 2022 (B), and 2023 (C)

A large nematode *P. proprius* was the primary contributor to the nematocene biomass in the bay's community annually (Table 2). Some specimens reached a length of 6,500 µm. In 2021, the proportion of *P. proprius* in the total biomass was 17%, and in 2022, it increased to 50%. In 2023, the main contribution to the biomass was made by 7 out of 18 species of free-living nematodes, including *P. proprius* (up to 40%).

The maximum ABC_{index} values, at the level of 3.6, were recorded in 2023; those were 2.25-fold higher than in 2022 (Table 3). The values of three indices, ABC_{index}, $1-ITD$, and Pielou index (E), rose within 2021–2023 (see Table 3), and the values of the Pearson correlation coefficient between them were not lower than 0.8. However, at the stations of 2023, relatively high values of biological diversity indices were noted. Also, there were no dominant taxa in both meiobenthic and Nematoda communities. The maximums of the Shannon index (H) and Margalef index (D_{Mg}) were characteristic of the stations of 2021. Thus, st1_21 featured a high value of D_{Mg}, about 3.7, indicating significant species diversity in the Triozerye Bay in 2021 (Table 3).

The trophic structure of Nematoda communities is illustrated in the diagram (Fig. 6). Despite a sharp rise in the proportion of non-selective deposit feeders (1B) in 2022, omnivores/predators (2B) maintained a proportion of 20% of the total nematofauna in the trophic structure within 2021–2023 and were represented by 6 species (see Table 2). Three omnivores, *E. pectinatus*, *O. domesticus*, and *Trileptium* sp., were found in the bay every year.

In 2021, the prevailing trophic groups were non-selective deposit feeders (1B) and epistratum feeders (2A), with proportions of 44 and 36%, respectively (Fig. 6). Importantly, there were no selective deposit feeders (1A) in several samples of 2021 and 2022; this fact manifested itself in the index 1 − *ITD* (Table 3). Its minimum occurred at the stations of 2022, where non-selective deposit feeders (1B) dominated, 81% (Fig. 6). Out of the stations surveyed, st2_23 exhibited the highest trophic diversity (all four feeding types were equally represented) (Fig. 6, Table 3) and had the index value of 0.74. The year of 2023 was marked by a notable rise in the proportion of selective deposit feeders (1A). Those accounted for 22% (Fig. 6, Table 2), and this value was an order of magnitude higher than in previous years.

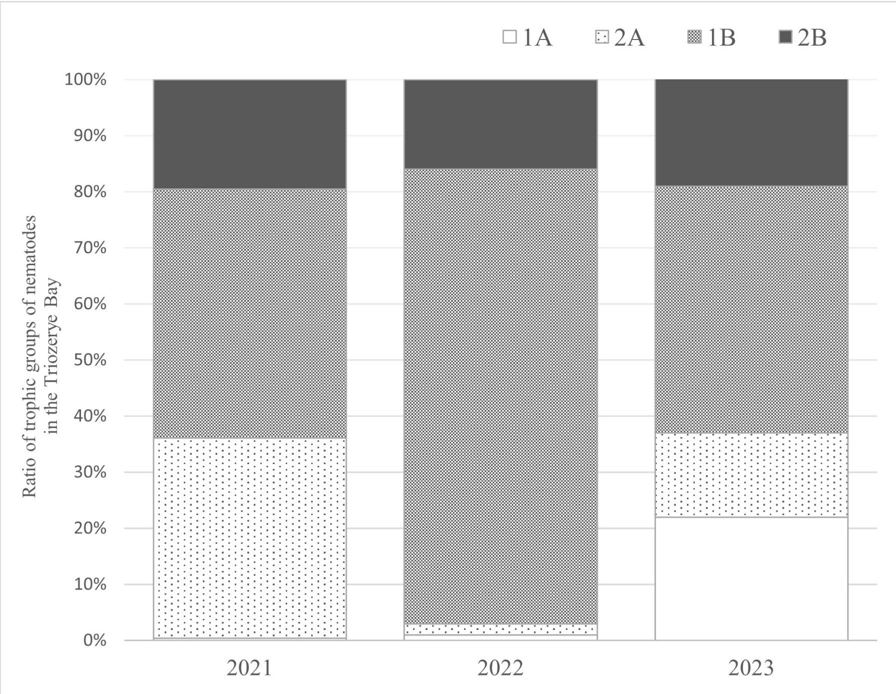

Fig. 6. Trophic structure of the nematofauna compiled according to W. Wieser classification based on the structure of the oral cavity of nematodes [1953]: 1A, deposit feeders, with no buccal armature; 1B, non-selective deposit feeders, oral cavity without weapons; 2A, epistratum feeders with a developed oral cavity surrounded by sclerotized teeth or plates; 2B, omnivores/predators with a large oral cavity armed with powerful teeth, jaws, and onchas

According to the results of the cluster analysis, nematocenes feature low levels of both interspecies and interstation similarity. The highest similarity (up to 60%) was found between two stations of 2022, st1_22 and st2_22, and between all the stations of 2021. Classification and ordination performed using non-metric multidimensional scaling (Fig. 7) revealed clear grouping of the stations by the sampling year (with a stress value of 0.02). These data combined with the values of diversity indices evidence for interannual variability in environmental conditions (Table 3).

The BIOENV procedure allowed for evaluating multiple combinations of abiotic variables to identify an optimal one explaining structural patterns of the Nematoda community [Clarke, Gorley, 2006].

Grain size distribution was the primary factor affecting the community structure. We revealed a weak positive effect (Spearman's rank correlation coefficient was about 0.31) (Table 4) between nematode distribution depending on predominant grain fraction that varied interannually from fine sand to medium gravel (see Table 1).

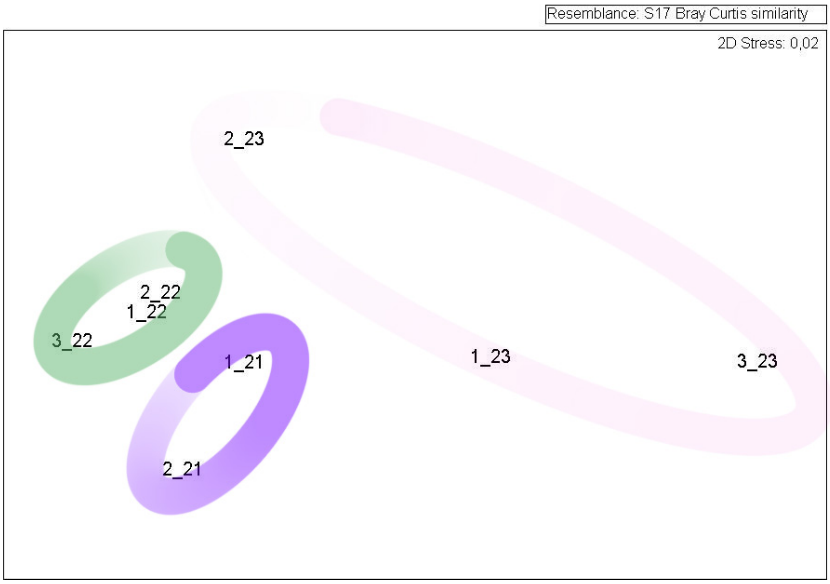

Fig. 7. Scheme of multidimensional scaling (MDS) by species composition of nematodes

Table 4. The best combination of abiotic variables according to results of the BEST analysis, with variables divided by station (year) using the LINKTREE procedure

Period	Spearman's rank correlation coefficient	Combination of variables
July 2021	0.31	fraction < 0.5 mm
August 2022	0.31	fraction ≥ 0.5 mm, C_{org} = 0.05%
August 2023	0.3	fraction ≥ 1 mm, C_{org} = 0.05%, $S_0 < 2$

Note: fraction, predominant fraction of bottom sediment (see Table 1); C_{org}, organic matter content; S_0, sorting coefficient.

DISCUSSION

In the Triozerye Bay, the species richness in the sandy zone of the upper sublittoral horizon was formed by 33 species. This bay featured active hydrodynamics. Its surface layer of bottom sediments experienced the strongest wave action at depths down to 1 m. Accordingly, the distribution of sediments was uneven.

Constant mixing of bottom sediments mediates a decrease in food availability and provides unfavorable conditions for meiofaunal organisms, as small ones struggle to stay attached to such a surface [Galtsova, 1991]. The taxonomic composition of meiobenthos and the species composition of nematodes are often poorer in shallow areas than in deeper ones [Pavlyuk et al., 2012].

Interannual changes in the meiobenthic community covered fluctuations in biomass and a rise in evenness of the species structure. Within 2021–2023, there were shifts in benthic biocenotic complexes governed by coarsening of sand particles and changes in dominant forms of meiobenthos and nematofauna. Cumulative curves of the grain size distribution (see Fig. 2) reflect significant differences between bottom sediment composition. The BIOENV procedure showed a direct effect of sediment indicators on Nematoda communities in the bay.

Meiobenthos is known to be unevenly distributed even in seemingly homogeneous bottom sediments, as small-scale changes in physical conditions occur in visually uniform sediments [Chesunov, 2006; Galtsova, 1991]. Environmental heterogeneity is primarily mediated by microtopography of the seabed and the type of food distribution [Galtsova, 1991]. Within the study period, Nematoda communities differed in terms of dynamics, and changes in sediment types govern a shift in dominant species.

Sampling in the Triozerye Bay in 2023 was carried out during prolonged rainfall and strong wave action that affected meiofaunal composition. Moreover, heavy rainfall in tidal shallows caused abrupt salinity changes triggering migration into deeper sediment layers and an increase in euryhaline nematode abundance. This is consistent with literature data [Steyaert et al., 2001].

The prevalence of Turbellaria at st1_23 and Annelida at st2_23 (see Fig. 3) was associated with bottom sediments dominated by grain fractions of 0.5–5 mm (coarse sand to medium gravel) in 2023 (see Table 1). According to regional studies, other groups become the key ones in meiofauna: oligochaetes, turbellarians, polychaetes, and nemerteans; the significance of macrobenthic larvae may rise as well [Giere, 2009; Gowing, Hulings, 1976; McLachlan, 1985; Mokievsky, 2009; Udalov, Burkovskii, 2002; Udalov et al., 2005]. In the Triozerye Bay, *D. normandicum* were consistently abundant across all the stations. *Ascolaimus*, *Axonolaimus*, and *Enoplolaimus* nematodes were significant in fine sands. On sandy beaches, Xyalidae often occur among the most common taxa. This family is typically represented by several genera (the most characteristic are *Daptonema*, *Theristus*, and *Metadesmolaimus*), and some genera are represented by several species [Fadeeva, Karpova, 2024; Gheskiere et al., 2005; Heip et al., 1985; Lee, Riveros, 2012; Nicholas, Hodda, 1999]. In literature, their prevalence is associated with high organic matter content, 0.5–2% [Gheskiere et al., 2005; Maria et al., 2012]. However, species we recorded inhabit the Triozerye Bay against the backdrop of much lower organic matter content, 0.03–0.05%.

Nematode density and biomass decreased 10-fold within 2021–2023. The ABC method showed as follows: in the Triozerye Bay, the biomass curves were located above the abundance ones, and *W* statistics rose 5-fold since 2021. A community is considered undisturbed when the biomass curve lies entirely above the abundance one (the ABC method). Under enhancing environmental stress, biomass and abundance curves converge and may cross. Sometimes, the abundance curve may surpass entirely the biomass one, and *W* statistics reaches its minimum [Shitikov, Golovatyuk, 2013; Warwick, Clarke, 1994]. As known, physically stressed communities are typically dominated by small and abundant organisms with high reproductive rates and short lifespan (r-strategists), while stable communities are inhabited by larger and less abundant ones with lower fecundity and longer lifespan (K-strategists) [Warwick, Clarke, 1994].

In the Triozerye Bay, the ABC method revealed prevalence of large species by biomass and small ones by abundance. The role of a nematode *P. proprius* is especially important: it is 4-fold larger in size than the most abundant species in the bay, *D. normandicum*. These data align with low values of diversity indices, including *ITD* (see Table 3), and the registration of pronounced dominants in the Nematoda community in 2022. The key reasons for restructuring of the community during the study period could be shifts in population density of some prevailing species and changes in their spatial distribution, as well as alterations in regional climatic and hydrological factors.

Conclusion. During short-term observations in the Triozerye Bay, we analyzed sandy shallow-water biotopes and registered a typical psammophilic fauna showing genus-level similarity with that in other areas. Within 2021–2023, structural shifts occurred in the meiobenthos: in composition and ratio of high-rank taxa and mass species affected by hydrodynamics and salinity. The Nematoda community exhibited both qualitative and quantitative changes, with notable alterations in dominant forms. Currently observed variability in meiobenthic community structure was also governed by life cycles of organisms and their migrations into deeper and more stable layers of bottom sediments.

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МЕЖГОДОВЫЕ ИЗМЕНЕНИЯ СТРУКТУРЫ МЕЙОБЕНТОСА ПЕСЧАНОГО МЕЛКОВОДЬЯ БУХТЫ ТРИОЗЕРЬЕ (ЯПОНСКОЕ МОРЕ)

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Впервые представлены результаты анализа динамики биологических параметров мейобентоса прибрежной полосы песчаных грунтов в бухте Триозерье (Японское море) в июле — августе 2021–2023 гг. За время исследования зарегистрировано 20 таксонов мейофауны, которую формировали представители Harpacticoida, Nematoda, Copepoda, Turbellaria, Gastrotricha, Annelida, Halacaridae и Ostracoda. Основой нематоцена являлись свободноживущие нематоды *Daptonema normandicum*, *Enoplolaimus pectinatus*, *Metadesmolaimus innii* и *Parascolaimus proprius*. В целом структура качественных и количественных показателей мейобентоса и нематофауны ежегодно менялась в связи с гранулометрическим составом грунтов.

Ключевые слова: Японское море, межгодовые изменения, гранулометрический состав, органическое вещество, мейобентос, нематофауна