



UDC 591.524.11:543.272.1(262.5)(1-16)  
DOI 10.47143/1684-1557/2026.1.5

## INFLUENCE OF OXYGEN REGIME ON MEIOBENTHOS OF UKRAINIAN SHELF OF THE BLACK SEA

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The hydrochemical characteristics of the Northwestern Part (NWBS) of the Black Sea offer a unique opportunity to study the development of meiofauna ecological features in hypoxic zones under field conditions. A comprehensive array of factual data allowed us to identify specific features of meiofauna structure development and its quantitative indicators, obtained through long-term, ongoing research. A total of 520 quantitative samples collected during regular annual scientific expeditions over more than 30 years were analyzed. Data analysis allowed us to determine the dynamics of quantitative indicators for both the general meiobenthos and its major large taxa (Foraminifera, Nematoda, Harpacticoida, Ostracoda, and Bivalvia), which are sensitive to changes in oxygen levels in the bottom layers of the northwestern shelf of the Black Sea. The quantitative indices of the aforementioned taxa were examined over a wide range of dissolved oxygen levels near the bottom in this marine region (from 0 to 12 mg·L<sup>-1</sup> O<sub>2</sub>). The studies showed that only foraminifera maintain very high abundances even at very low dissolved oxygen levels. Crustaceans (harpacticoids and ostracods) and juvenile bivalves cannot survive under hypoxic conditions. The obtained data allowed us to determine two oxygen thresholds that determine both the biodiversity and abundance of the main representatives of the permanent and temporary components of the meiofauna. Long-term observations and analysis of the obtained data allow us to assess the environmental quality in the northwestern Black Sea using the meiobenthos. The nematode to harpacticoid abundance ratios presented in the paper reflect the structure, abundance, and biomass of the meiofauna under different oxygen conditions. The higher the values of this ratio, the worse the ecological state of the environment in the bottom layers of water.

**Key words:** Black Sea, Northwestern Shelf, meiofauna, oxygen regime.

### Introduction

Extreme marine environments cover more than 50% of the Earth's surface and provide numerous opportunities to study biological responses and adaptations of organisms to stressful living conditions. Extreme marine environments are sometimes associated with ephemeral and unstable ecosystems, but can host abundant, often endemic and well-adapted meiofauna species (Zeppilli et al. 2018). Oxygen is the main driver among the abiotic parameters determining habitat conditions and the presence of meiofauna (Coull 1985). Meiobenthic organisms have relatively large surface areas and mostly high oxygen demands: only a few specialized organisms will prefer hypoxic conditions (Geer 2009).

Vertical distribution patterns showed that areas with severe oxygen deficiency in the surface sediments contained lower meiofauna than deeper areas. Because of their small size, high abundances, short life cycles, meiobenthic organisms are good test objects to determine the effects of perturbations in aquatic ecosystems. There are species of meiobenthos, which not only can

tolerate hypoxia, but also prefer the conditions of acute hypoxia (Sergeeva and Zaika 2013).

The water area of the NWBS, in terms of its hydrochemical characteristics, represents a unique opportunity to study the formation of ecological characteristics of the meiofauna at hypoxic zones in field conditions. Analysis of data for 40 years of continuous research in this part of the sea made it possible to determine the dynamics of quantitative indicators of the whole meiobenthos, as well as its main large taxa under different oxygen conditions (0–13 mg·L<sup>-1</sup> O<sub>2</sub>) in the bottom layers of water.

The NWBS is an area of particularly high risk of anthropogenic damage to ecosystems. There are many reasons for this, but the fundamental one is apparently the unprecedented size of the specific area of the catchment basin. The total area of the basins of rivers, entering the northwestern part of the Black Sea is 1,456,000 km<sup>2</sup>, while the water area is equal to 278,000 km<sup>2</sup>. Consequently, each square kilometer of shelf water area is subject to a load from 52 square kilometers of highly urbanized

territory of the basin. Initially this ratio of areas was a positive factor mobilizing great volumes of entry of nutrients from the hinterland of the basin. Thus, the high productivity of the shelf ecosystem was guaranteed. In conditions of highly elevated technogenic chemical stress on the watershed, it has become one of the main prerequisites for anthropogenic degradation (Bogatova et al. 1990).

Since the mid-1980s, the main problem of the NWBS has been associated with a constant deficiency of dissolved oxygen in the bottom layers of water. This was first described in publications in 1977 (Zaitsev 1977 a, b). Many researchers have noted that hypoxia and anoxia on the NW shelf are associated with significantly increased anthropogenic eutrophication (Garkavaya, Bulanaia and Bogatova 1982). Large-scale bottom hypoxia over several decades covered 1/3 or more of the entire NWBS water area in the summer and partly in the autumn. This phenomenon was especially acute in the 1980s and 1990s.

The need to oxidize large additional masses of autochthonous organic matter in conditions of restrained vertical water exchange usual for the warm period of the year has determined the active formation of wide zones of hypoxia/anoxia near bottom waters on the shelf. This has been observed previously, but it has been episodic-temporally and local-spatiality. Since 1972, when hypoxia was first recorded at a large scale the oxygen deficiency in the near bottom layers has been observed almost annually, occupying the area from depths of 4 to 20 m between the Dnieper-Bug Estuaries. Towards autumn this process spreads to a depth of 40 m in the open sea. Recently, a tendency has been noted for a decrease in the amount of oxygen in the near bottom layer in summer and spreading on the hypoxia zone. On average, in the summer period of 1988-1989, the amount of dissolved oxygen in the near bottom layer made up 1/9 mg·l<sup>-1</sup>, degree of saturation 22%.

The localization of the benthos biomass is generally determined by the distribution of the plankton biomass in the upper layers of the pelagic zone. As it is known (Zenkevich et al. 1971), the main source of food resources for bottom animals is the population of the surface layers of the ocean. The abundance of organisms of various meiobenthos taxa in a given biotope is determined by the presence of a sufficient amount of food available to them and, accordingly, by a more active colonization of various types of substrates.

The development and functioning of meiobenthic animals are closely dependent on biological processes occurring in the surface layers of the pelagic zone (Coull 1999). Therefore, shifts in the structure of pelagic communities subject to eutrophication have a mirror image in the benthos. The concentrations of various compounds in the upper sediment layer, the oxygen regime, and the rate of chemical exchange between sediments and bottom water change (Zaika 1992).

The aim of this work is to demonstrate the main patterns of formation of the numbers of the main taxa of meiofauna under different oxygen conditions based on long-term research in the northwestern part of the Black Sea.

### Materials and Methods

The results obtained are an analysis of long-term observations (1983–2018) of the formation of quantitative meiobenthos parameters on the Ukrainian shelf of the Black Sea under varying oxygen conditions. Methods for collecting and processing samples are described in numerous publications by the author (Vorobyova 2000).

A total of 520 quantitative samples collected in the northwestern part of Black Sea were included in present analysis. Dissolved oxygen values in the bottom water layers during the study period ranged from 0–1 to 11 mg·L<sup>-1</sup> O<sub>2</sub>.

### Results and discussion

Numerous studies have shown that the oxygen regime is of key importance in the formation of biological diversity and quantitative indicators of meiobenthos representatives (Coull 1985; Zeppilli et al. 2018 et al.).

As noted above, analyses of data for 40 years of continuous research in NWBS made it possible to determine the dynamics of quantitative indicators of both the general meiobenthos and its main large taxa under different oxygen conditions (0–13 mg·L<sup>-1</sup> O<sub>2</sub>) in the bottom layers of water.

In the NWBS, in the zones of formation of periodic large-scale hypoxia zones, meiobenthos is characterized by very low biodiversity, but the highest possible abundance due to the mass development of small-sized forms with short-cycle development. Scientific publications indicate that the lower level of tolerance of benthic forms in the coastal zone is observed at an oxygen concentration of less than 2 mg·L<sup>-1</sup> O<sub>2</sub>, and this value was taken as the boundary between normal conditions and hypoxia (Zaika, Konovalov and Sergeeva 2011; Rosenberg 1980). Sometimes the dissolved oxygen content of 2.8–3 mg·L<sup>-1</sup> O<sub>2</sub> is also considered as the boundary (Modig and Olafsson 1998).

Our studies in the NWBS have established that when the hydrochemical regime deteriorates, the dominance of individual species or groups of meiobenthos increases (Vorobyova 2000). Under current conditions, the dominant nematode-harpacticoid complex of organisms has been replaced by a Foraminifera-nematode complex on the entire northwestern shelf. At the same time, Foraminifera often accounted for 79.7–80% of the total population density in the NWBS (1982–1995). With dissolved oxygen content in the bottom layers of up to 6–9 mg·L<sup>-1</sup> O<sub>2</sub>, the quantitative indicators of meiobenthos are formed by almost all groups characteristic of a given community (Fig. 1, 2).

The high biomass of meiobenthos under favorable oxygen conditions is an indicator that it is mainly formed by crustaceans and representatives of the temporary component (pseudomeiobenthos).

With low oxygen content in the meiobenthos, small-sized individuals with a short development cycle develop. With oxygen levels from 3.5 to 5 mg·L<sup>-1</sup> O<sub>2</sub>, representatives of five to seven groups are usually present in the meiobenthos. In the meiobenthos of water areas where the benthic ecosystem experiences significant pressure from various types of pollution, quantitative indicators are 87–100% formed by one or two groups. This is especially typical for estuary areas, bays, estuaries, and gulfs.

There are species of meiobenthos, which not only can withstand hypoxia, but prefer the conditions of acute hypoxia. Our long-term research in the NWBS allowed us to obtain extensive factual material on the ecological characteristics of meiobenthos at various oxygen regime indicators in the bottom layers of water. From

1982 to 1998, systematic annual collection of material (in spring, summer and autumn) was carried out to study the meiobenthos of the Ukrainian shelf of the NWBS in complex marine expeditions on research scientific vessels (standard grid – 50 stations). From 1994 to 2017, the reaction of the meiobenthos to the dissolved oxygen content was studied using materials collected in the OMR (Odesa Marine Region).

*Foraminifera*. Studies in the NWBS (Vorobyova 2000) showed that with repeated extensive zones of hypoxia and anoxia, the species diversity of Foraminifera sharply decreases, but their population density can reach up to 1-2 million. ind.·m<sup>-2</sup>. Scientists have known for a long time that many bottom Foraminifera can live in anoxic conditions (Risgaard-Petersen et al. 2006).

Research in the North Sea has shown (Moodley and Hess 1992) that *Ammonia beccarii* is irregularly distributed in the subtidal sediment of the southern North Sea, with substantial numbers occurring as deep as 35 cm below the water-sediment interface. Deep infaun-

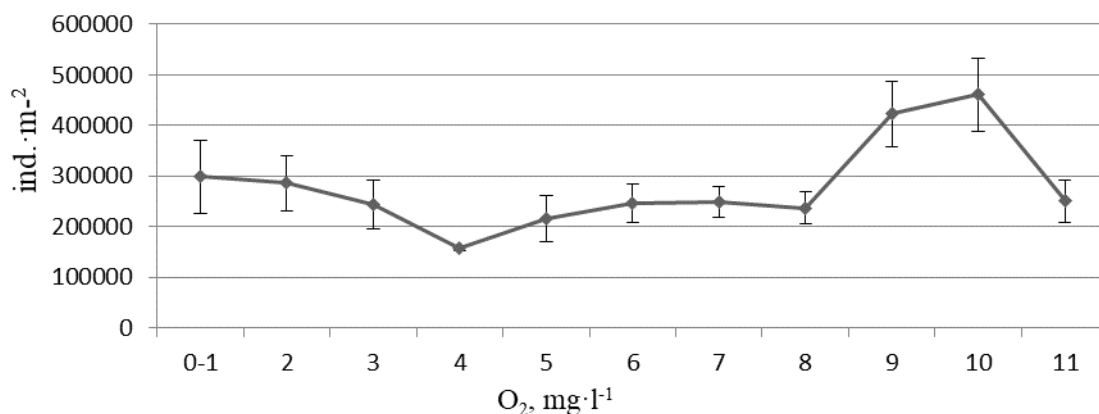


Fig. 1. Average total abundance of meiobenthos at different oxygen levels at the bottom

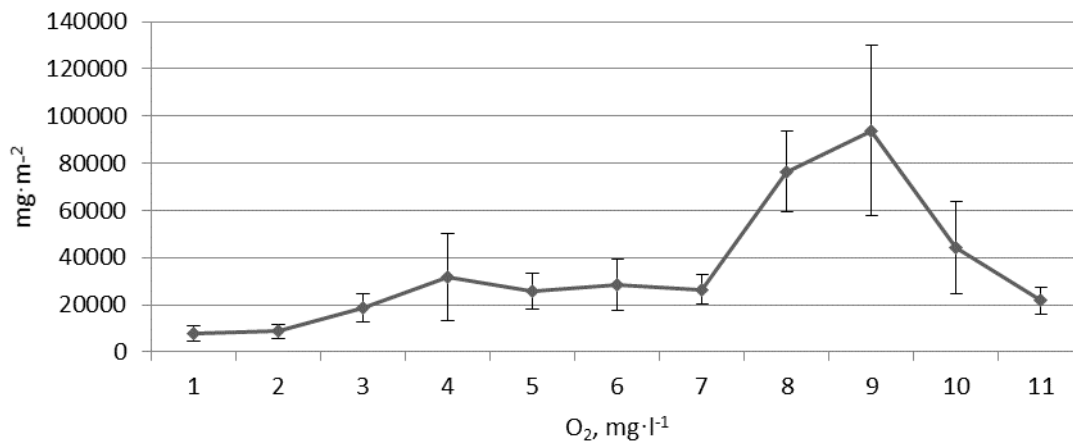


Fig. 2. Average total biomass of meiobenthos at different oxygen levels at the bottom

nae specimens are insensitive to oxygen concentrations, and all specimens isolated from different depth intervals continued their normal activities (feeding and growth) when exposed to dysaerobic oxygen content. Specimens of *E. excavatum*, *Q. seminulum*, and *E. scabra*, when subjected to the same conditions, behave similarly to *A. beccarii*. These benthic foraminifera have very low oxygen requirements. The chambers of *A. beccarii* that are formed in situ at different depth intervals in the sediment have a wide range in the porosity (i.e., % of area occupied by pores) which is adequate for gas exchange under both high and low oxygen conditions. Foraminifera live at the oxic-anoxic boundary throughout the sediment and therefore must occasionally be subjected to completely anoxic conditions. *A. beccarii*, *E. excavatum*, and *Q. seminulum* actively survived at least 24 h without oxygen, indicating that they are capable of facultative anaerobic metabolism (Moodley et al. 1997).

Many benthic Foraminifera associated with oppressed oxygen environments retain chloroplasts. They provide a metabolic advantage that allows foraminifers to inhabit these habitats. Thus, it has been suggested that many benthic foraminifers are facultative anaerobes. It has now been established that foraminifers can dwell in soil to a depth of 12–15 cm and periodically transfer oxygen-free conditions (Basov and Chusid 1983; Moodley and Hess 1992). When studying meiobenthos in the northwestern part of the Black Sea, we recorded live Foraminifera in the thickness of the soil up to 10 cm in water areas at depths of 25–90 m (Vorobyova and Kulakova 2009). The analysis of long-term data allowed us to show the dynamics of the formation of average abundance of Foraminifera at various levels of dissolved oxygen in the bottom layers of water (Fig. 3). An analysis of the quantitative indicators of the main taxa of meiobenthos, which form its total abundance

and biomass, showed the regularity of this process with different parameters of dissolved oxygen in the bottom layers of water.

To form the ecological characteristics of Foraminifera (abundance, biomass, share in the total number of meiobenthos, etc.), there are two indicator values of dissolved oxygen in the bottom layers of the sea, which determine both the species diversity and the total number of protozoa. The first, which is characteristic of hypoxia ( $1\text{--}4\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$ ), in which foraminifera are present in the meiobenthos, capable of living at low  $\text{O}_2$  levels. The second –  $8\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$  and above, at which oxyphilic species develop.

As can be seen, a significant concentration of Foraminifera is confined to both very low and high levels of dissolved oxygen. Based on the results obtained, it can be assumed that the first peak is formed by species that continue to develop during hypoxia. The second peak should relate to oxyphilic species. A similar picture is given for the Sea of Okhotsk (Saidova 1960), where the author describes two groups of Foraminifera, one of which forms the maximum abundance at a dissolved oxygen content of  $4\text{--}5\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$  or more, and the second, forming the southern maximum, lives with less dissolved oxygen (about  $2\text{--}4\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$ ).

To determine the significance of foraminifers in the formation of quantitative indicators of small bottom invertebrate animals (meiobenthos) of the OMR ecosystem, we calculated the average indices of portion of Foraminifera in the total number of meiobenthos under different oxygen conditions (Fig. 4).

As can be seen, from the presented figure, foraminifers are constantly an essential component of the meiobenthic community of eutrophic water areas of the Black Sea. To some extent they can reflect the quality of the marine environment in the benthal

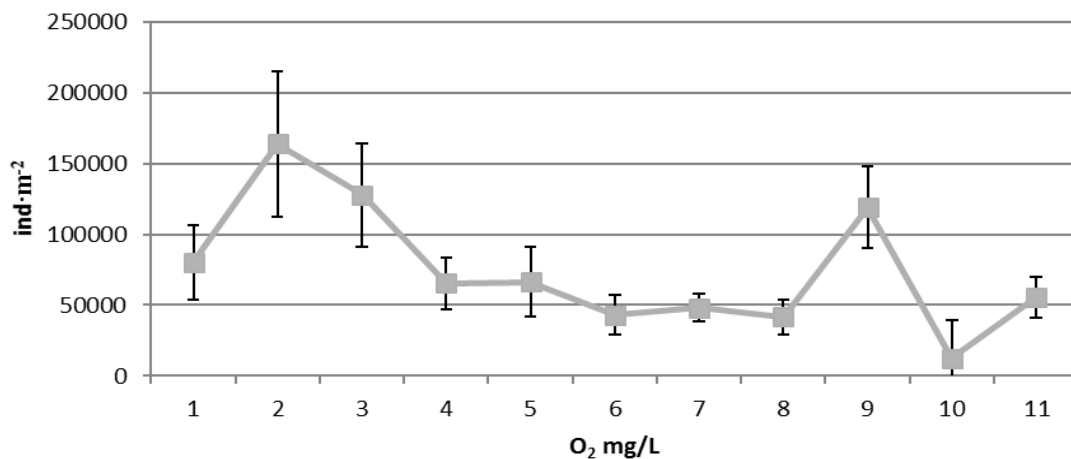


Fig. 3. Average indices of the density of foraminiferal settlements (ind.·m<sup>-2</sup>) under different oxygen conditions (Vorobyova 2021)

and the formation of quantitative indicators of the rest of the meiobenthic community, which is valuable as a food for young fish and some species of macrozoobenthos.

*Nematoda.* In order to clarify the distribution boundaries of life on the shelf and beyond, in 1984–1986 we collected samples at depths from 75 to 600 m, covering the lower shelf area and the upper part of the adjacent continental slope of the western Black Sea (Zaitsev et al. 1987). Representatives of various hydrobionts typical of the Black Sea meiobenthos were found in the samples. However, while most of them were found at depths of 100 m, nematodes of the orders Desmoscolecida and Chromadorida were discovered by I.I. Kulakova at the maximum depth studied – 600 m (Data from Kulakova I.I. (Zaitsev et al. 1987). It is evident from the data presented (Table 1) that traces of oxygen are still present at a depth of 203 m, and the oxy-

gen-free zone begins deeper. At present, it can be stated that the lower boundary of the meiobenthos distribution is 600–645 m.

We have proposed several hypotheses. One of them is based on the following conclusions. At all deep-sea stations, increased amounts of carotenoid pigments were found in the surface sediment layer up to 1 cm thick data. The main source of these pigments is phytoplankton cells that have settled to the bottom. However, at depths of less than 100 m, carotenoids are destroyed faster than at 200–600 m; they accumulate, are preserved, and in some cases form concentrations an order of magnitude higher than in shallow, oxygen-rich shelf area.

Another reason for the introduction of free-living marine nematodes into the anaerobic zone is their assimilation of new food sources, such as, for example, sulfur bacteria and newly synthesized organic substances (Galtsova 1976, 1991). Living in a new envi-

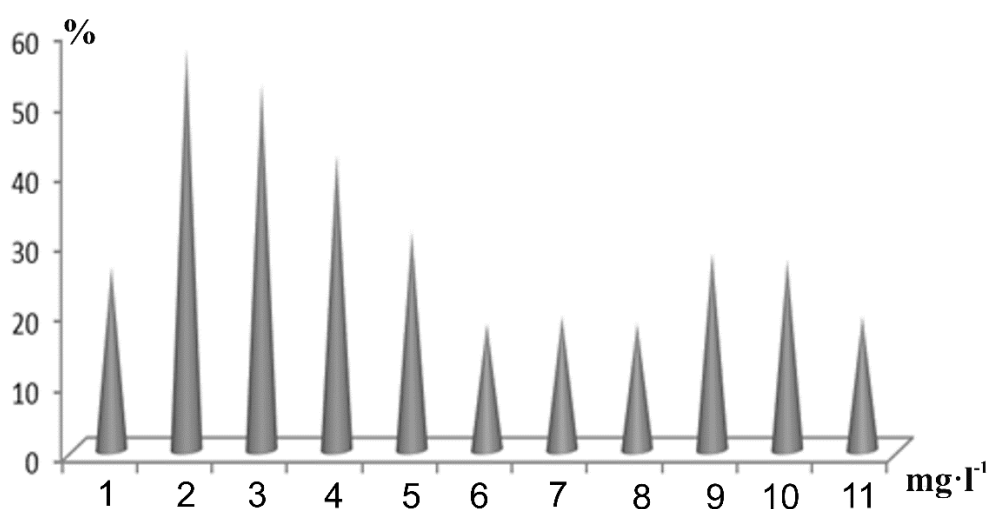


Fig. 4. Proportion (%) of Foraminifera in the total abundance (ind.·m<sup>-2</sup>) of meiobenthos under different oxygen conditions (Vorobyova 2021)

Table 1

Vertical distribution of some deep-sea bottom animals in the Black Sea and the conditions of their existence (Zaitsev et al. 1987)

Depth, m	t, °C	S, ‰	pH	O <sub>2</sub> , mg L <sup>-1</sup>	H <sub>2</sub> S, ml·l <sup>-1</sup>	Pigments in the surface layer of sediments, mg·g <sup>-2</sup>	Nematoda	
							Number of species	Number ind.·m <sup>-2</sup>
76	7.68	17.86	8.15	4.90	–	0.6	10	12 500
100	7.90	18.02	8.08	4.13	–	0.5–0.9	12	2 400
145	8.55	19.08	7.80	0.27	0.02	0.2–0.3	10	1 900
203	8.73	20.57	7.80	0.10	0.20	7.0	2	1 500
250	9.24	20.89	7.72	0	0.30	2.1	2	500
307	8.83	21.01	7.80	0	0.66	5.9	3	1 500
400	8.90	21.22	7.82	0	2.50	2.1–3.5	2	400
500	8.91	21.30	7.75	0	3.20	2.3	3	500
600	8.90	21.30	7.75	0	3.60	4.1–5.1	2	400

ronment led to adaptations. As V.V. Galtsova points out, they developed a new type of “oxygen-free respiration”, and at the same time, thiobiont forms are capable of switching to the usual aerobic type of respiration in an oxygen environment.

In relation to oxygen, four groups of nematodes have been identified (Keegan, Boaden and Ceidigh 1977): 1st – oxybionts, 2nd – inhabitants of the transition layer with a reduced content of free oxygen, 3rd – anoxybionts and 4th – facultative anoxybionts. Representatives of the Chromadorida and Desmoscolicida orders, which we found at a depth of 250–600 m, belong to the 3rd group.

For more than a century, the world of science has considered the anoxic zone of the Black Sea to be azoic, or lifeless. But data (Sergeeva 1988; Sergeeva et al. 2011) indicate that the deep-water bottom sediments of the Black Sea, which possesses permanent hydrogen sulfide pollution, are the natural habitats for some species of eukaryotic fauna (Protozoa and Metazoa).

Therefore, the completion of the work on the nematodes, the most abundant group metazoan meiobenthos will reveal interesting details of their distribution in the gradient of hypoxia observed with increasing depth of the Black Sea. Now it was detected at depths of 120–240 m more than 40 forms of nematodes belonging to one order Desmoscolicida. The maximum size of the group of nematodes honored at a depth of 120–130 m. Permanent hypoxic zone of the Black Sea is an interesting research polygon. Later, in 1987, representatives of meiobenthos (9 species) were discovered at a depth of 300–645 m (Mikhailova and Sergeeva 1987; Sergeeva 1988).

There is information (Sergeeva and Kolesnikova 1996) about the findings of nematodes, harpacticoids and other representatives of the meiobenthos at a depth of more than 600 m, up to 2000 m. The authors cannot state whether these organisms were alive at the time

of their discovery or whether they had not yet undergone the process of decomposition.

Our studies have shown that for nematodes, as well as Foraminifera, there are two maximum oxygen levels (4 and 8 mg·L<sup>-1</sup> O<sub>2</sub>), which determine the formation of the density of nematode taxocene settlements. The maximum average number of nematodes was noted at 1 mg·L<sup>-1</sup> O<sub>2</sub>, 207,056.3 ± 51,388.2 ind.·m<sup>-2</sup>, the minimum – at 4 mg·L<sup>-1</sup> O<sub>2</sub> – 47,854.5 ± 7,255.7 ind.·m<sup>-2</sup> (Fig. 5).

Their share in the total number of organisms at oxygen concentration below 4 mg·L<sup>-1</sup> O<sub>2</sub> varied from 31 to 68% and averaged 47.3%. The number of nematodes increases due to the inhabitants of the transition layer with a reduced content of free oxygen (the second group). The maximum indicator is 157,108.1 ± 24,745.0 ind.·m<sup>-2</sup>.

The minimum density of nematodes was characteristic for 8 mg·L<sup>-1</sup> O<sub>2</sub> (101,572.1 ± 14,527.3 ind.·m<sup>-2</sup>). The proportion of worms in the total number of meiobenthos varied from 54 to 64.5%. At high oxygen content, the density of nematodes increases due to the development of oxybiont species. Their proportion in the total number of meiobenthos remains high – on average 53.5%.

*Harpacticoida*. All meiofauna appear to have some sensitivity to extended periods of hypoxia, but a wide range in tolerance (from hours to days, weeks or months of exposure) have been observed. Within a given habitat certain species of Foraminifera and Nematoda are typically most tolerant to hypoxia/anoxia while crustacean meiofauna often are the least tolerant. More specifically, the present study harpacticoid copepods as they represent, after nematodes, the second-most-abundant meiofauna group (Giere 2009) and are known to respond rapidly to hypoxic/anoxic conditions (Modig and Olafsson 1998). Moreover, harpacticoid copepods form an essential link between primary producers and higher trophic levels (Giere 2009).

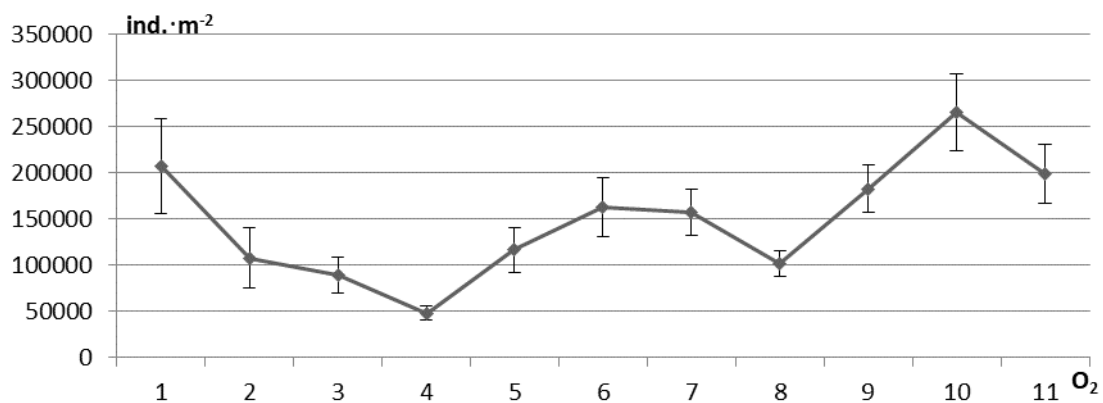


Fig. 5. Average indices of the density of Nematoda settlements (ind.·m<sup>-2</sup>) under different oxygen conditions

With a low content of dissolved oxygen in the bottom layers of water ( $1\text{--}3\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$ ), the average density of crustacean settlements was  $11,689\text{ ind}\cdot\text{m}^{-2}$ . It increased sharply at  $4\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$  to  $31,637.9\text{ ind}\cdot\text{m}^{-2}$ . The average value of the copepod abundance at oxygen of  $4\text{--}7\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$  was  $28,005.1\text{ ind}\cdot\text{m}^{-2}$ . The highest average density of crustacean settlements (Fig. 6) was associated with oxygen values of  $8\text{--}9\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$  ( $76,399.6 \pm 10,961.0\text{ ind}\cdot\text{m}^{-2}$  and  $93,890.7 \pm 36,112\text{ ind}\cdot\text{m}^{-2}$ , respectively). On average, for the  $\text{O}_2$  range of  $8\text{--}12\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$ , the abundance of harpacticoids reached an average of  $50,934.0\text{ ind}\cdot\text{m}^{-2}$ .

When considering the significance of harpacticoids in the formation of the total number of meiobenthos, it was shown that their share in it differs significantly and is highest at  $4$  and  $8\text{ mg}\cdot\text{L}^{-1}\text{ O}_2$  of dissolved oxygen (Fig. 7). This confirms our conclusion that for harpacticoids, as well as foraminifera and nematodes, these two indicators are borderline, determining the formation of the main ecological characteristics

of these taxa. Most harpacticoid species are very sensitive to the conditions of the surrounding marine environment. In areas experiencing high anthropogenic load, their species diversity and quantitative indicators are extremely poor. Thus, in the Sukhoi Estuary, which is in a critical ecological state, Harpacticoida representatives are very rare throughout the entire water area of the estuary. Their numbers do not exceed  $2,000\text{ ind}\cdot\text{m}^{-2}$ . In the Grigorievsky Estuary, the ecosystem of which experiences significant anthropogenic loads, the density of harpacticoid settlements differed sharply and averaged  $1,600\text{--}24,470\text{ ind}\cdot\text{m}^{-2}$ . Analysis of long-term data on the formation of the number of representatives of the Harpacticoid taxocene showed the following.

*Ostracoda.* The populations of the Ostracoda taxocene are mostly inhabitants of the upper sublittoral and prefer rocky substrates with an abundant amount of macrophytes on them. They develop well in high-quality environments (Fig. 8).

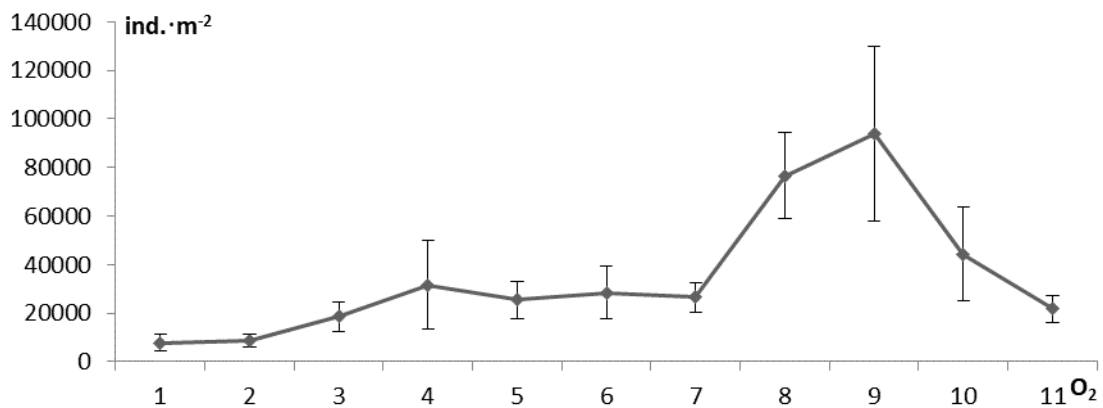


Fig. 6. Average indices of the density of Harpacticoida settlements ( $\text{ind}\cdot\text{m}^{-2}$ ) under different oxygen conditions

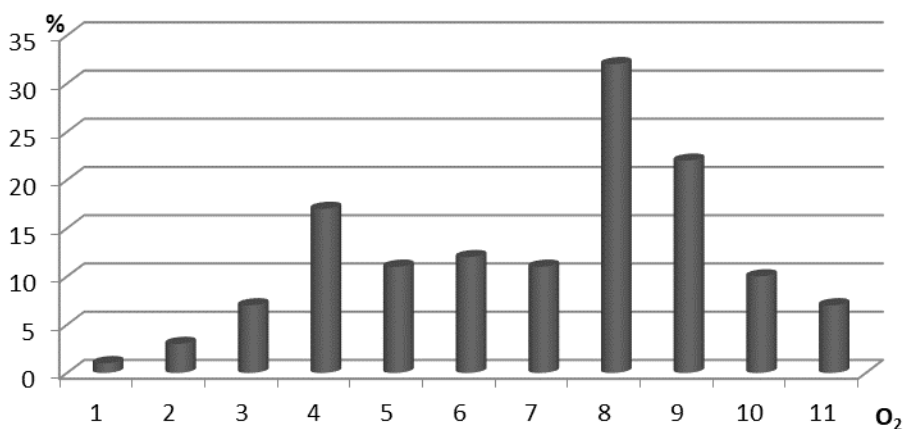


Fig. 7. Share (%) of Harpacticoida different dissolved oxygen content in the bottom layers of water

The overall abundance and biomass of meiobenthos under varying oxygen conditions in the sea's bottom layers depend not only on the population density of the permanent (eumeiobenthos). This is particularly true for the larvae and juveniles of mollusks and meiobenthic polychaetes (temporary meiobenthos).

Under favorable conditions for metamorphosis, the abundance and biomass of juvenile mollusks and polychaetes can play a significant role in shaping the overall density and biomass indicators for the entire meiobenthic community. In critical situations for the marine benthos (high anthropogenic load, oxygen deficiency in the bottom water layers, low salinity, etc.), their share in the overall indicators decreases sharply, even during favorable seasonal periods for the mass settling of benthic invertebrate larvae from the pelagic zone to the benthal.

The settling of mollusk larvae from the pelagic zone to the benthal zone and the successful completion of their metamorphosis occurs at depths of up to 50 meters. This is typically characteristic of most of the Black Sea shelf. In areas of increased eutrophication, characterized by the periodic formation of extensive hypoxic

zones, the potential for successful larval development from the velikoncha stage to a size category that allows them to transition into macrozoobenthos is sharply reduced. Even under favorable temperature conditions and substrate quality, larvae that settle to the bottom die massively due to oxygen deficiency. An analysis of their population density distribution in various areas of the Black Sea (mid-1990s) revealed that the highest abundance of larval and juvenile mollusks, as well as polychaetes, is on the Caucasian shelf, somewhat lower on the Crimean shelf, and lowest on the northwestern shelf. Their shares in the total meiobenthos abundance are distributed accordingly: on the Caucasian shelf, they averaged 29.7 %, on the Crimean shelf 7.5%, and on the NWBS 2.1% (Vorobyova 2009).

A large database has made it possible to demonstrate the formation of quantitative indicators of meiobenthos in the NWBS (Table 2).

Thus, regular annual sampling on the NWBS for 40 years allowed us to establish the main patterns of formation of the number and biomass of not only the total meiobenthos, but also its main large taxa, which play the main role in the formation of the biodiversity

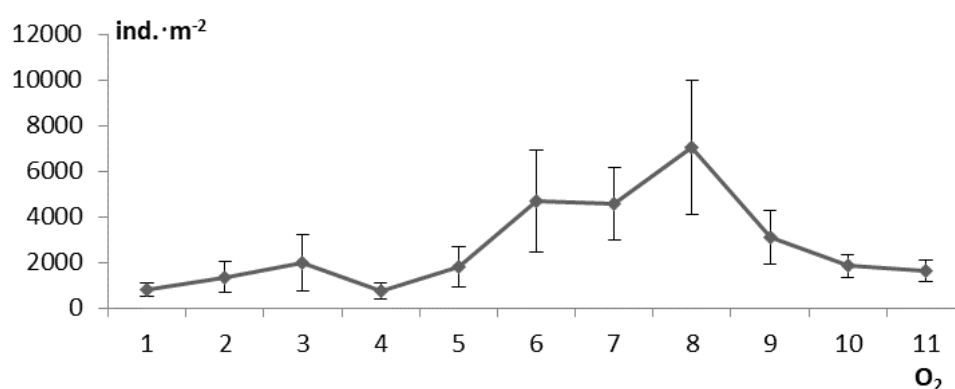


Fig. 8. Average indices of the density of Ostracoda settlements (ind.·m<sup>-2</sup>) under different oxygen conditions

Table 2

Indices (ind. m<sup>-2</sup>) of the main taxa of the temporary component of meiofauna under different oxygen conditions

O <sub>2</sub> , mg·L <sup>-1</sup>	Number, ind.·m <sup>-2</sup> Oligochaeta	Number, ind.·m <sup>-2</sup> Polychaeta	Number, ind.·m <sup>-2</sup> Bivalvia	Number, ind.·m <sup>-2</sup> Temporary meiofauna, total
0-1	262.5 ± 171.5	1362.5 ± 555.5	300 ± 248.1	2706 ± 874.6
2	1589.2 ± 1064.4	2050.1 ± 1274.9	828.6 ± 533.2	4467.8 ± 1984.6
3	982.8 ± 537.7	1518.5 ± 443.6	960.2 ± 533.3	4524.0 ± 1097.6
4	2237.5 ± 1463.5	3387.5 ± 1002.3	529.0 ± 248.4	9300.1 ± 5278.3
5	727.0 ± 582.5	202.0 ± 703.4	835.4 ± 3145	4675.3 ± 1379.1
6	2361.4 ± 633.4	2326.1 ± 658.5	940.9 ± 359.5	5798.9 ± 1223.8
7	3435.6 ± 984.7	4646.3 ± 244.0	1975.5 ± 683.9	10407.2 ± 2558.0
8	2794.1 ± 694.6	3828.4 ± 957.2	3296.4 ± 819.2	9529.3 ± 1768.4
9	4322.55 ± 1031.1	6397.0 ± 2591.6	9721.0 ± 4781.6	21164.6 ± 6179.7
10	1366.1 ± 301.7	8668.3 ± 2196.1	10317.1 ± 4180.2	5798.4 ± 2087.4
11	1734.5 ± 452.2	6003.2 ± 1601.0	5708.5 ± 2196.3	13670.6 ± 3446.2

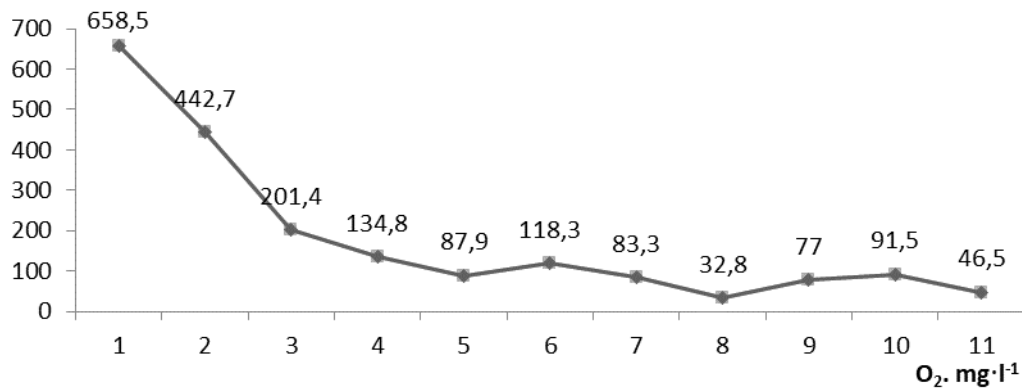


Fig. 9. Indices of the ratio of nematodes and harpacticoids at different oxygen indices of the ratio of nematodes and harpacticoids at different oxygen

of the meiobenthos and its quantitative indicators. In addition, a large amount of factual material allows us to assess the quality of the marine environment in the benthos. For this, we used the indices of the ratio of nematodes and harpacticoids at different oxygen regimes in the bottom layers of water. As we can see (Fig. 9) on the presented graph, they are highest at a dissolved oxygen content of 1–3 mg·L<sup>-1</sup> O<sub>2</sub>.

Thus, the data presented demonstrate that we are examining the formation of meiofauna abundance at the following dissolved oxygen levels: 1) 0–3 to 4 mg·L<sup>-1</sup> O<sub>2</sub>; 2) 5–7 mg·L<sup>-1</sup> O<sub>2</sub>; 3) 7 or more to 12 mg·L<sup>-1</sup> O<sub>2</sub>. In the first case, the meiobenthos contains a few species, primarily from two large taxa (foraminifera and nematodes, with minimal numbers of polychaetes and oligochaetes). Thus, our long-term research has shown that under hypoxia and even anoxia, the structure of the meiobenthic community of the NWBS changes dramatically. At oxygen levels up to 3 mg·L<sup>-1</sup> O<sub>2</sub>, foraminifera and nematodes usually dominate, i.e., the total abundance of meiobenthos is formed by a foraminifera-nematode or nematode-foraminifera complex of organisms (Vorobyova 2009). In the second case, meiobenthic biodiversity increases sharply with the development of euryoxybiont forms. However, the total biomass increases only slightly due to the high density of nematodes and Foraminifera. Harpacticoida account for 10–12% of the total meiobenthic

abundance. In the third case, the meiobenthos is typically represented by stenooxybiont species, and this is where the highest total biomass of the meiobenthic community of organisms occurs.

#### Conclusions

In the vast waters of the northwestern shelf, which has been negatively impacted by various types of anthropogenic influences for many decades, large areas of hypoxia in the bottom water layers are constantly forming.

Analysis of long-term observations has revealed the main patterns of formation of the structure and quantitative indicators of meiofauna across a wide range of oxygen levels in the bottom water layers. It has been established that the maximum indicators of the total meiobenthos are formed at oxygen levels of 7 mg·L<sup>-1</sup> O<sub>2</sub> and above. Of the major large taxa, only foraminifera are very abundant, even under severe hypoxia. Moreover, their share of the total meiobenthos could be over 50%.

The abundance of crustaceans increases only in good environmental conditions, with oxygen levels above 6 mg·L<sup>-1</sup> O<sub>2</sub>.

The ratio of total nematode abundance to total harpacticoid abundance indicates that small-sized forms with short life cycles develop in the meiobenthos under hypoxic conditions. At high oxygen levels, the total biomass of the meiobenthos is formed by crustaceans and juvenile mollusks.

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## ВПЛИВ КИСНЕВОГО РЕЖИМУ НА МЕЙОБЕНТОС УКРАЇНСЬКОГО ШЕЛЬФУ ЧОРНОГО МОРЯ

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Гідрохімічні характеристики північно-західного шельфу Чорного моря надають унікальну можливість для вивчення розвитку екологічних особливостей мейофауни в гіпоксичних зонах у польових умовах. Комплексний набір фактичних даних дав змогу виявити специфічні особливості розвитку структури мейофауни та її кількісні показники, отримані під час тривалих неперервних досліджень. Було проаналізовано загалом 520 кількісних проб, зібраних під час регулярних щорічних наукових експедицій протягом понад 30 років. Аналіз даних дав можливість визначити динаміку кількісних показників як для мейобентоса в цілому, так і для його основних великих таксонів (форамініфери, нематоди, гарпактикоїди, остракоди та бівальвії), чутливих до змін рівня кисню в придонних шарах північно-західного шельфу Чорного моря. Кількісні показники вказаних таксонів були вивчені в широкому діапазоні рівнів розчиненого кисню в цьому морському регіоні (від 0 до 12 мг л<sup>-1</sup> O<sub>2</sub>). Дослідження показали, що тільки форамініфери зберігають дуже високу чисельність навіть за дуже низького рівня розчиненого кисню. Ракоподібні (гарпактикоїди та остракоди) та молоді двостулкові молюски не можуть вижити в умовах гіпоксії. За отриманими даними визначено два кисневі пороги, що визначають як біорізноманіття, так і чисельність основних представників постійних та тимчасових компонентів мейофауни. Довгострокові спостереження й аналіз отриманих даних дають змогу оцінити якість довкілля в північно-західній частині Чорного моря з використанням мейобентосу. Представлені у статті співвідношення чисельності нематод і гарпактикоїд відображають структуру, чисельність та біомасу мейофауни в різних кисневих умовах. Чим вище значення цього співвідношення, тим гірший екологічний стан середовища в придонних шарах води.

**Ключові слова:** Чорне море, північно-західний шельф, мейофауна, кисневий режим.

Дата першого надходження статті до видання: 25.03.2026

Дата прийняття статті до друку після рецензування: 27.04.2026

Дата публікації (оприлюднення) статті: 29.05.2026



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