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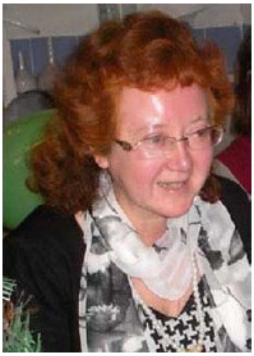

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MEIOBENTHOS OF THE OXIC/ANOXIC INTERFACE IN THE SOUTHWESTERN REGION OF THE BLACK SEA: ABUNDANCE AND TAXONOMIC COMPOSITION

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1. Introduction

Among the seas of Mediterranean basin, the Black Sea exhibits a number of striking features. The combined effect of great depth, considerable desalination of surface waters caused by river discharges, and the influx of saline deep water from the Sea of Marmara, creates a distinct stratification of the water column into an upper, relatively thin (150–250 m deep) oxic zone with plentiful flora and fauna and a huge anoxic zone (from 150 to 250 m depth down to the deepest point) with high hydrogen sulfide concentrations.

The interactions between these oxic and anoxic water masses are of great interest to researchers in different scientific fields. Study of the boundary region between them has shown that the redox zone is a good indicator of oxygen concentrations and also corresponds to the distribution of other parameters, namely temperature, pH, ammonium, manganese, phosphates, and the transparency of the water (Stunzhas and Yakushev 2006). The anoxic Black Sea water mass is separated from the oxic zone by a layer, several tens of meters thick, where oxygen concentrations decrease to 0.1–0.3 ml·L^{-1} (= 4.5–13.5 µmol L^{-1}) and hydrogen sulfide levels increase correspondingly (Vinogradov and Flint 1987). Long-term monitoring of the distribution of oxygen and sulfide across this boundary indicates that it is situated at a depth of 80–100 m in the center and 160–250 m at the periphery (Eremeev and Konovalov 2006).

Where the oxic/anoxic interface in the water column impinges on the seafloor, it creates a strong benthic gradient in oxygen and hydrogen sulfide concentrations. This O_2/H_2S-transition zone is highly dynamic, characterized by varying concentrations of oxygen and hydrogen sulfide in the bottom water, and oscillates above and below its average depth. The taxonomic composition and distribution of benthic fauna inhabiting the depth zone where the oxic/anoxic interface zone meets the sea floor is of special interest.

Specific communities of benthic organisms adapted to reduced oxygen concentrations occur within this zone in the NW Black Sea (Kiseleva 1998; Sergeeva and Zaika 2000; Zaika and Sergeeva 2008). This benthic region is termed the "periazoic zone" (Bacesco 1963). It has been studied in parts of the Black Sea off the coast of Romania (Gomoiu et al. 2008; Surugiu 2005), Bulgaria (Marinov 1978) and Ukraine (Sergeeva and Zaika 2000; Zaika and Sergeeva 2008). In recent years, attention has focused on the meio and microbenthos living in the deeper, sulfidic part of the Black Sea; there have been several reports of live and active eukaryotes from this hostile environment (Zaika 2008; Zaika and Sergeeva 2009).

Faunal studies in hypoxic/anoxic and sulfidic environments involve certain problems, particularly when Rose-Bengal staining is used to identify "live" specimens. Although easy to use, this protein stain has the disadvantage that it can color dead as well as live cytoplasm (Bernhard 2000), giving rise to "false positives" (Bernhard et al. 2006). Organic matter decomposes at a slower rate in hypoxic than in fully oxic sediments (van der Weijden et al. 1999; Cowie 2005). Under hypoxic conditions, the decomposition of animal tissues and protozoan cytoplasm may be retarded (Jorissen et al. 1994), while in anoxic sediments, the carcasses of animals and protozoans are likely to be preserved (Danovaro et al. 2010). Thus, unless they are seen alive, the unequivocal recognition of living organisms can only be achieved by observing tracer uptake, intact ultrastructural features, or by using a vital fluorogenic probe such as CellTracker Green, which fluoresces inside live cells after the original molecule has been modified by enzymatic activity (Bernhard et al. 2006; Danovaro et al. 2010).

Here, we review information on the composition and structure of Rose-Bengal-stained meiobenthic communities (protozoans and metazoans) along depth gradients that span the oxic/anoxic transition in the NW part of the Black Sea. Our review is based on a combination of published data and results obtained from new samples collected in 2007 during RV *Meteor* cruise 72/2. We also provide arguments to support our contention that the faunal patterns observed are real rather than artifacts of preservation under hypoxic/anoxic and sulfidic conditions.

2. Previous Research

Since the discovery of the anoxic zone, which occupies 77% of the floor of the Black Sea, it has been assumed that, except for bacteria, this vast region is a lifeless desert (Nikitin 1938; Kiseleva 1979; Klenov 1948; Kriss 1959; Sorokin 1962; Zhizhchenko 1974). Kiseleva (1979) recognized three zones in the Black Sea, reflecting the dominance of different size classes of organism. The region from the tide mark to 120–150 m depth is inhabited by macro (>1 mm), meio (0.1–1.0 mm), and microbenthic (<0.1 mm) organisms. The second zone, between 120–150 and 250–300 m depth, is characterized by meio and microbenthos, while the third, from 250 to 300 m to the deepest point, is occupied only by bacteria (Kiseleva 1979). According to this scheme, the lower border of eukaryotic life in the Black

Sea is located at a depth of ~250–300 m. In the second half of the twentieth century, an additional "periazoic" zone was recognized at 120–200 m depth in the lower part of the *Modiolula phaseolina* community off the Romanian coast (Bacesco 1963; Gomoiu et al. 2008)

Because the deeper part of the Black Sea basin is anoxic, it was long assumed that the aerobic zoobenthos did not penetrate into this region (Zaika et al. 1999). As a result, relatively little research has been conducted on the biota in the anoxic layers, limiting our understanding of the faunal changes across the oxic/anoxic interface and the occurrence of organisms at depths where conditions are permanently sulfidic (Luth and Luth 1997, 1998; Revkov and Sergeeva 2004). Moreover, although the occurrence, spatial distribution, and environmental role of methane seeps in the Black Sea are well studied, less is known about the bottom fauna associated with these features (Sergeeva and Gulin 2007, 2009), particularly those located across the oxic/anoxic interface.

Comparative studies of the structure of Black Sea benthic communities in areas with and without methane seepages were conducted for the first time in 1993–1994. The biomass and biological activity of bottom communities was similar at all the sites studied. Areas of seepage were characterized by larger body sizes among the macrobenthos (Luth and Luth 1998). The diversity and abundance of the meiobenthos were both relatively high within the oxic/anoxic transition zone across the same field of methane seeps (Sergeeva 2003a, b, 2004a; Sergeeva and Gulin 2007). Analyses of benthic eukaryotes (protozoa and metazoa), based on the collections of six cruises over the period 1993–2007 across the oxic/anoxic interface in the region of the Dnieper paleo-delta, revealed the presence of 23 higher taxa (Sergeeva and Gulin 2009). The species identified included both stenobiont and eurybiont forms adapted to hypoxia and the presence of hydrogen sulfide and methane (Sergeeva and Zaika 2000; Zaika et al. 1999; Zaika and Sergeeva 2008). The density of the meiobenthos varied from 2,400 to 53,000 ind.$\cdot$m^{-2} at depths of 182–252 m in the submarine Dnieper Canyon, where CH_4 concentrations in bottom sediments ranged from 2.40 to 5.75 nmol$\cdot$m^{-3}. The meiobenthos was represented by Ciliata, Foraminifera, Nematoda, Polychaeta, Bivalvia, Gastropoda, Amphipoda, and Acarina. Nematoda and Foraminifera were the dominant groups (Sergeeva and Gulin 2007). Over a slightly shallower depth range (70–235 m), Revkov and Sergeeva (2004) reported 12 higher meiobenthic taxa in areas with methane seepage in the Dnieper Canyon region; Nematoda, Turbellaria, Ostracoda, and Acarina occurred at the deepest sites (230–235 m).

3. Methods and Materials

New samples were collected during RV *Meteor* cruise 72/2 (February–March 2007) on the open slope northwest of the Crimea Peninsula (Boetius 2007). Ten stations were chosen along a transect from the oxic into the anoxic zone (Fig. 1, Table 1), crossing the shelf and the NW Crimea slope in an area characterized

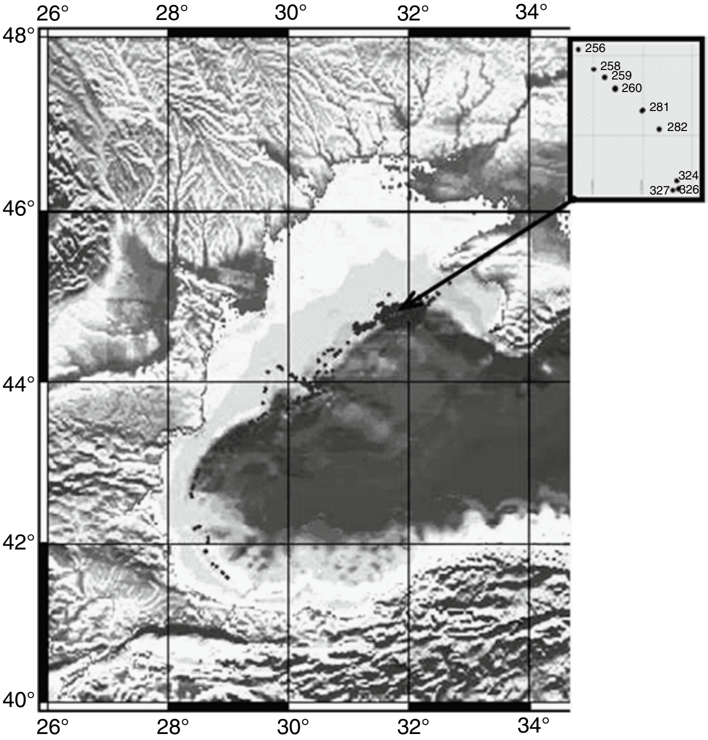

Figure 1. Stations were chosen to span the lower boundary oxygen layer, and the upper anoxic zone, crossing the shelf and the NW Crimean slope (based on Egorov et al. 2003; Boetius 2007; Sergeeva et al. 2010).

Table 1. Change of concentration of O_2 and sulfide with water depth in the NW part of the Black Sea.

Year	**2007**	**2007**	**1994**[a]	**1994**[a]
Depth (m)	**O_2 mmol• L^{-1}**	**H_2S µmol• L^{-1}**	**O_2 mmol• L^{-1}**	**H_2S µmol• L^{-1}**
120	0.14	0	–	–
123	–	–	0.006	–
130	–	–	0.006	0
132	0.12	0	–	–
140	0.09	0	–	–
150	0.07	0	0.004	6.3
160	0.06	<1	0.004	6.8
170	0.07	<1	–	–
188	–	–	0	14

Oxygen and sulfide concentrations in 2007 (M72/2) were measured in the overlying water of retrieved MUC cores. Oxygen was measured according to the Winkler method (Winkler 1888) and samples for sulfide were immediately fixed in ZnAc and measured with the photometric methylene blue method (Cline 1969) in the home laboratory. Pangaea event label: M72/2_256, M72/2_258 to 262 (www. pangaea.de)

[a] Data from Pimenov et al. (1998), – No data

by methane seeps (Egorov et al. 2003). The main field of methane seeps in the northwestern part of the Black Sea is located near the submarine Dnieper Canyon (Egorov et al. 1998), where they occupy an area 105 km in length and 43 km in width, covering 1,623 km^2 of seafloor and a depth range of 35–785 m. Bottom-water oxygen concentrations range from 0.14 mmol L^{-1} at 120 m water depth to 0.06–0.07 mmol L^{-1} at 160–170 m and zero at 188 m (Table 1) (Pimenov et al. 1998). There is a corresponding rise in sulfide concentrations from zero at 130 m to 14 μmol L^{-1} at 188 m. Bottom sediments are sandy silt with large quantities of bivalve, ostracod, and foraminiferan shells at 120–140 m depth, and silt with molluscan shell debris and bacterial aggregations at 150–240 m depth. The sediment surface is covered by various kinds of organic detritus, including the remains of macroalgae and microalgae, as well as bacterial mats of different sizes.

Samples for biological studies were obtained at eight sites located at 10 m intervals between 120 and 190 m, and from two additional sites located at 210 and 240 m water depth. They were collected using a modified version of the Barnett multiple corer (MUC), a device that takes virtually undisturbed sediment samples (Barnett et al. 1984). At each station, three replicate sediment cores (from a single multicorer deployment) were sectioned into the following horizontal layers: 0–1, 1–2, 2–3, and 3–5 cm. All sediment sections were preserved in 75% alcohol, which we know from previous experience, preserves morphological structures without distortion. We avoided prior fixation in formalin in order not to damage calcareous taxa. The sediments were washed through sieves with a mesh size of 1 mm and 63 μm and stained with Rose Bengal solution before being sorted in water under a microscope for "live" (stained) organisms. We extracted only those specimens that stained intensely with Rose Bengal and showed no sign of morphological damage. All of the organisms isolated were counted and identified to higher taxa, or in the case of nematodes and harpacticoids to species level. Protists were identified as gromiids based on test characteristics, e.g., test shape and the presence of an oral capsule (Rothe et al. 2010). However, because gromiids can be confused with allogromiid foraminiferans, confirmation of these identifications must await molecular analyses and an examination of the test-wall ultrastructure. Details of methods for estimating bacterioplankton production and bacterial chemosynthesis (Sect. 4.1.2) are given by Sorokin and Sorokina (2008) and Gulin (1991), respectively.

4. Meiobenthos of the Oxic/Anoxic Interface

We focus here on the meiobenthos, regarded as protozoans and metazoans retained on the 63 μm mesh (i.e., the 63 μm to 1 mm size fraction). We also included individuals of meiobenthic taxa retained on the 1 mm mesh, mainly large nematodes. The meiobenthos comprises the permanent meiofauna (eumeiobenthos) and the temporary meiofauna (pseudomeiobenthos), the latter represented by the juvenile stages of macrobenthos (Bougis 1950; Chislenko 1961).

The eumeiobenthos constitutes 81% to almost 100% of the bottom community (Table 2), while the pseudomeiobenthos constitutes only 0.3–19% (Table 3).

Table 2. Abundance (indiv m^{-2}) of eumeiobenthos and constituent taxa along the depth gradient near the Dnieper Canyon.

	Depth				
Taxon	**120 m**	**130 m**	**140 m**	**150 m**	**160 m**
Gromia	21,945 ± 5,315	20,461 ± 4,975	1,409 ± 178	856 ± 375	352 ± 100
Ciliophora	8,154 ± 1,967	1,510 ± 396	705 ± 125	7,097 ± 3,110	12,231 ± 3,830
Foraminifera	15,352 ± 3,042	11,929 ± 2,368	5,335 ± 1,224	35,586 ± 10,059	66,893 ± 22,210
Nematoda	1,347,675 ± 251,752	245,073 ± 21,690	202,289 ± 41,461	422,548 ± 95,913	727,719 ± 171,078
Kinorhyncha	302 ± 52	0	201 ± 53	0	0
Harpacticoida	91,758 ± 8,427	54,381 ± 7,570	28,514 ± 5,504	36,441 ± 6,487	10,268 ± 2,097
Ostracoda	705 ± 170	4,681 ± 761	201 ± 52	252 ± 39	0
Acarina	2,215 ± 443	755 ± 173	176 ± 27	0	151 ± 66
Tardigrada	34,227 ± 7,237	14,798 ± 3,531	604 ± 158	151 ± 39	101 ± 44
other	0	0	2,215 ± 580	0	201 ± 88
Total	**1,511,158 ± 263,978**	**345,358 ± 37,428**	**236,391 ± 49,178**	**492,461 ± 113,451**	**814,293 ± 192,525**
	170 m	**180 m**	**190 m**	**210 m**	**240 m**
Gromia	289 ± 61	828 ± 419	221 ± 153	265 ± 129	276 ± 170
Ciliophora	5,965 ± 3,018	10,754 ± 5,442	11,144 ± 7,722	1,324 ± 648	7,172 ± 4,444
Foraminifera	64,439 ± 21,599	717 ± 362	607 ± 420	66 ± 33	441 ± 273
Nematoda	0	0	0	0	0
Kinorhyncha	0	0	0	0	0
Harpacticoida	3,196 ± 710	0	276 ± 115	0	0
Ostracoda	0	0	0	0	0
Acarina	0	0	0	0	0
Tardigrada	0	0	0	0	717 ± 297
other	55,266 ± 27,967	0	110 ± 58	0	0
Total	191,556 ± 60,055	17,516 ± 5,468	21,074 ± 10,000	11,651 ± 5,708	10,758 ± 3,795

Table 3. Abundance (indiv m^{-2}) of pseudomeiobenthos and constituent taxa along the depth gradient near the Dnieper Canyon.

	Depth				
Taxon	**120 m**	**130 m**	**140 m**	**150 m**	**160 m**
Coelenterata	5,536 ± 1201	32,616 ± 8,291		10,973 ± 2,874	14,194 ± 4,643
Oligochaeta	302 ± 82	0	0	2,919 ± 765	101 ± 44
Polychaeta	2,970 ± 488	2,190 ± 626	9,261 ± 2,425	6,896 ± 1,579	21,341 ± 5,605
Turbellaria	151 ± 41	453 ± 124	0	0	0
Nemertini	0	0	0	151 ± 39	0
Bivalvia	5,285 ± 1,210	8,154 ± 1,531	1,233 ± 246	0	0
Gastropoda	0	0	0	50 ± 13	0
other	0	151 ± 66	201 ± 52	0	0
Total	14,244 ± 2,825	43,564 ± 9,484	56,172 ± 14,395	20,989 ± 5,269	35,636 ± 9,594
	170 m	**180 m**	**190 m**	**210 m**	**240 m**
Coelenterata	4,492 ± 2,273	0	0	0	0
Oligochaeta	302 ± 51	0	0	0	0
Polychaeta	2,076 ± 741	55 ± 28	55 ± 29	0	0
Turbellaria	38 ± 19	110 ± 56	0	0	0
Nemertini	76 ± 38	0	0	0	0
Bivalvia	76 ± 38	0	0	0	0
Gastropoda	0	0	0	0	0
other	151 ± 76	110 ± 55	0	0	0
Total	**7210 ± 2705**	**276 ± 139**	**55 ± 29**	**0**	**0**

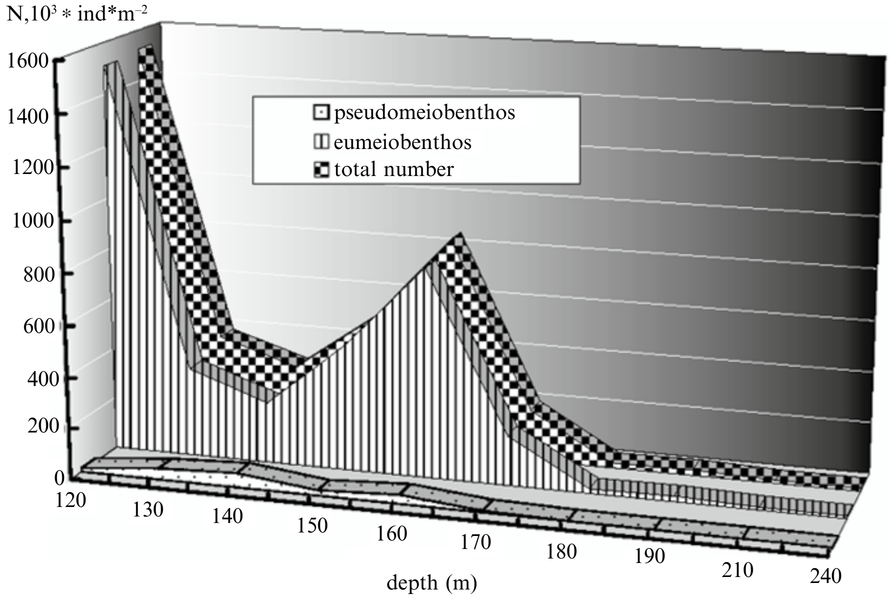

Figure 2. Distribution of meiobenthos abundance (N) along depth gradient.

Eumeiobenthos was found at all studied depths with two well-defined peaks of abundance at 120 m ($O_2 = 0.14$ mmol L^{-1}, sulfide = zero) and 160 m ($O_2 = 0.06$ mmol L^{-1}, sulfide = <1 µmol L^{-1}) (Table 1). The maximum abundance of eumeiobenthos corresponds to the 120 m peak; the minimum abundance is recorded at 240 m depth. Pseudomeiobenthos was most abundant at 140 m depth ($O_2 = 0.09$ mmol L^{-1}, sulfide = zero) and disappeared at 190 m (Fig. 2, Tables 2 and 3). These two categories are combined hereafter and referred to as the meiobenthos.

The meiobenthos present between 120 and 240 m included the following 16 taxa: Ciliophora, Gromia, Foraminifera (soft-shell and hard- shell forms), Nematoda, Kinorhyncha, Harpacticoida, Acarina, Ostracoda, and Tardigrada, and among the pseudomeiobenthos, Coelenterata, Oligochaeta, Polychaeta, Turbellaria, Nemertini, Bivalvia, and Gastropoda. Among these, the Nematoda were dominant and the Foraminifera and Ciliophora subdominant.

Biodiversity at the major taxon level declines with increasing water depth, although the decrease is not linear and there are minor peaks at 170 and 190 m (Fig. 3). Many of the species recognized along this transect are either completely new to science or new records for the Black Sea.

Maximum concentrations of meiofauna are usually found in the surface layers of bottom sediments. The vertical distribution of meiobenthos in the upper 5 cm of sediment has been analyzed at different water depths in the study area (Fig. 4).

Overall, the 0–1 cm layer contained 70% of total meiobenthos abundance, compared to 16% in the 1–2 cm layer, 8% in the 2–3 cm layer, and 6% in the

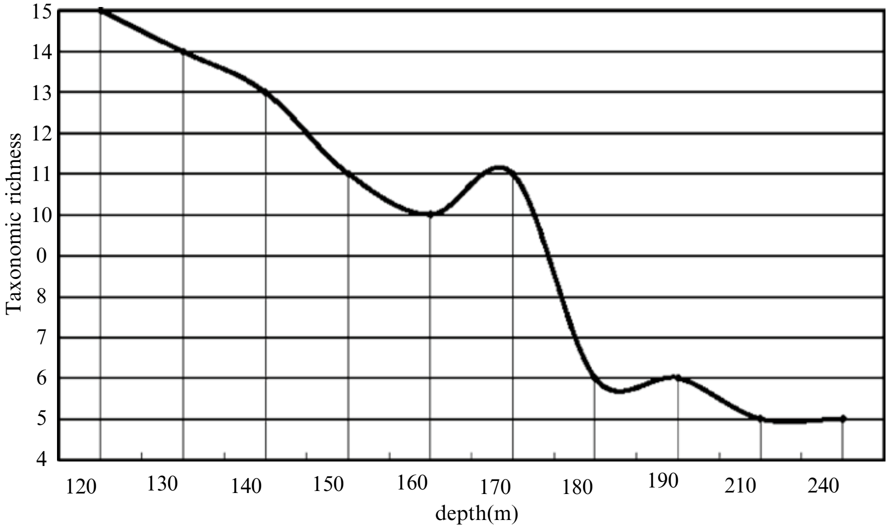

Figure 3. Higher taxon richness of meiobenthos along depth gradient near Dnieper Canyon.

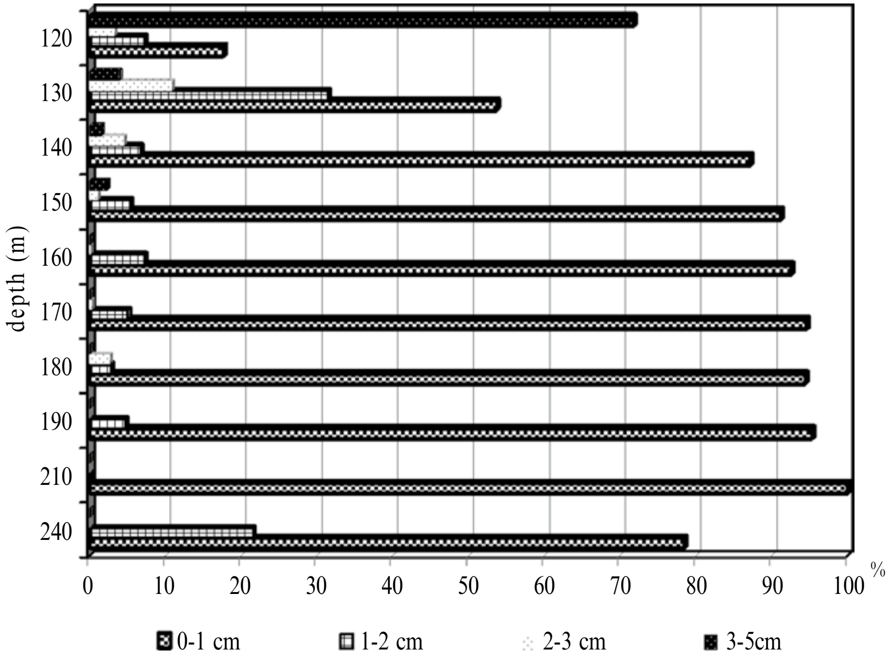

Figure 4. Proportion of meiobenthos (including protozoans) inhabiting different sediment layers along depth transect near Dnieper Canyon.

3–5 cm layer. The 0–1 cm layer yielded the largest number of specimens at all points along the transect, except at 120 m depth, where the meiobenthos was concentrated in the deepest (3–5 cm) sediment layer. The highest concentration of meiobenthos in the 1–2 cm layer was at 210–240 m in the anoxia zone.

4.1. PROTOZOA

Protozoans from the deep-water Dnieper Canyon area comprised Gromiida, Ciliophora, and Foraminifera, notably soft-shelled, single-chambered (monothalamous) taxa. Foraminifera were most abundant at depths of 150–170 m, gromiids at depths of 120–130 m, while ciliates were fairly evenly distributed across the transect (Fig. 5). We did not find any testate amoebae of the kind reported by Golemansky (2007 and papers cited therein) from supralittoral sediments on the Bulgarian Black Sea coast.

4.1.1. Gromiida

Our knowledge of gromiids from sublittoral sediments across the oxic/anoxic interface is limited (Sergeeva and Gulin 2009). Although organisms resembling gromiids were found at all studied depths, they were rare except at 120 and 130 m (Figs. 6 and 7). Preliminary examination of this material revealed three species, all of which are believed to be new to science. Specimens were concentrated in the 3–5 cm layer at the 120 m site and, to a lesser extend, at 140 m. At other depths, they were more or less confined to the top 1 cm layer.

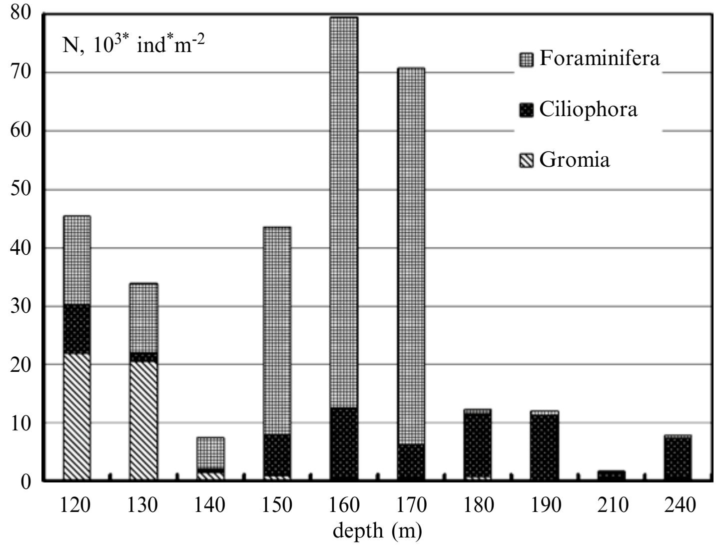

Figure 5. Abundance of the main protozoan taxa along the depth transect near the Dnieper Canyon.

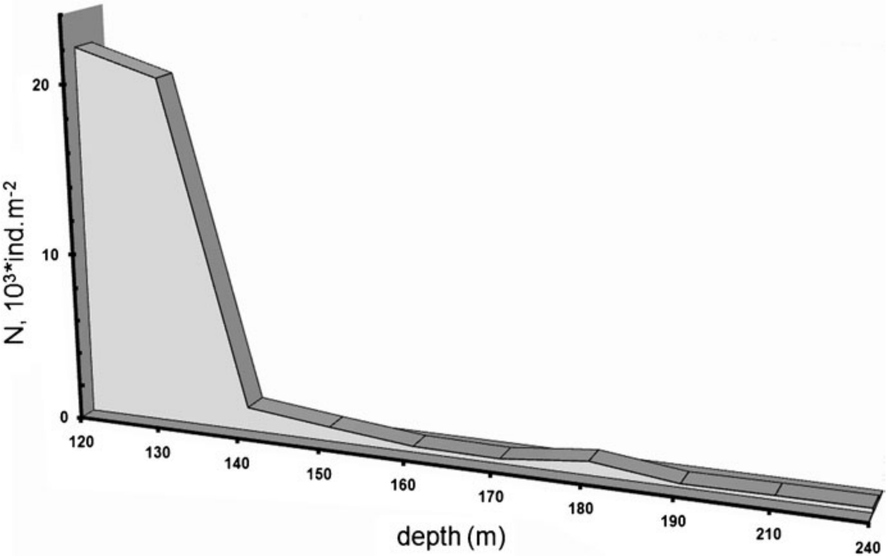

Figure 6. Trends in the abundance of gromiids along the depth transect near Dnieper Canyon.

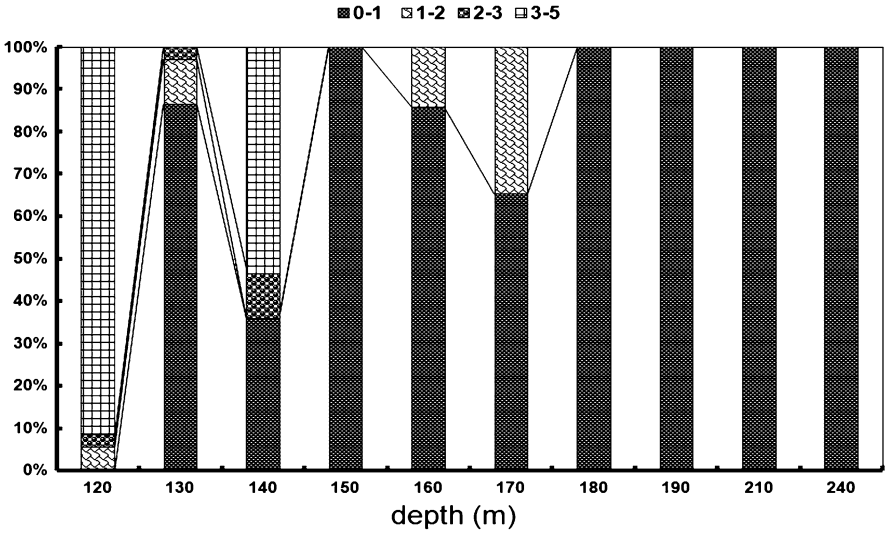

Figure 7. Proportion of gromiids inhabiting different sediment layers along depth transect.

4.1.2. Ciliophora

The following account is based on Zaika and Sergeeva (2008, 2009), who described the bathymetric distribution of the benthic ciliates at depths from 120 to 2,075 m near the Dnieper Canyon and the Sorokin Trough (eastern part of the Black Sea)

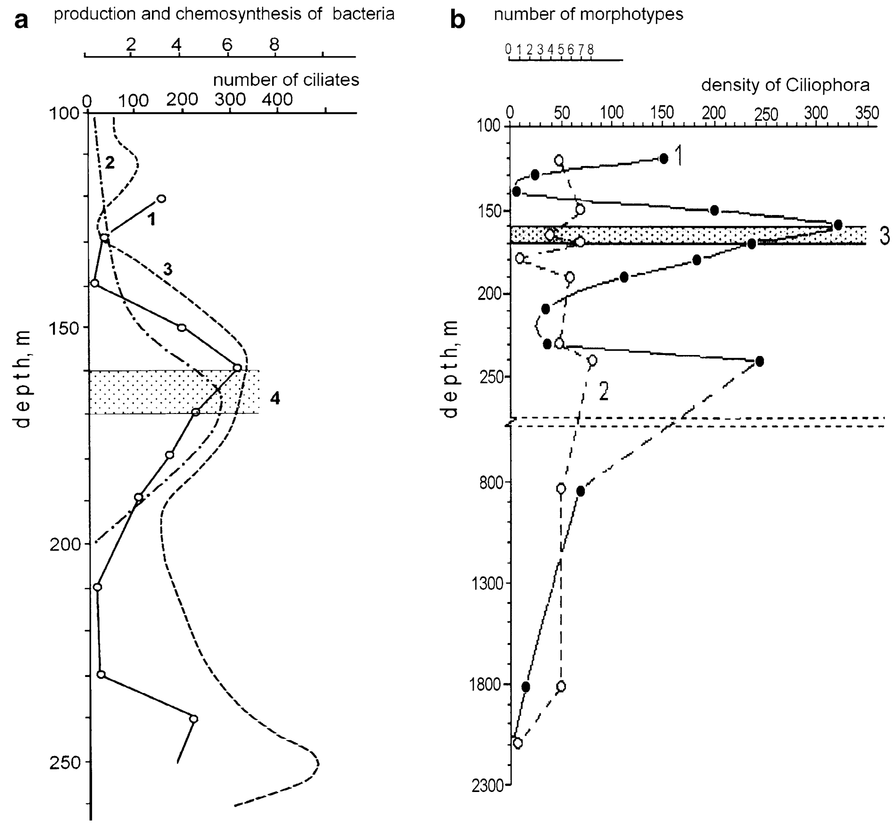

Figure 8. (**a**) Changes in the abundance (indiv. 100 cm^2) of ciliates with depth near the Dnieper Canyon. *1* number of ciliates, *2* production of bacteria, *3* intensity of bacterial chemosynthesis, and *4* border of hydrogen sulfide. (**b**) Vertical profiles of total abundance and number of ciliate morphotypes. *1* total abundance, *2* numbers of morphotypes, and *3* upper boundary of hydrogen sulfide. After Zaika and Sergeeva (2009).

(Fig. 8). They occurred in all studied samples of near bottom water, sediment surface detritus, and in the upper layer (0–1 cm) of sediment (Fig. 9). Different forms were present, including free living and attached forms, among which more than 30 morphospecies were recognized. Ciliates exhibited abundance peaks at 120, 160–190, and 240 m (Fig. 8).

4.1.3. *Foraminifera*

Previous studies. A total of 104 species of foraminifera has been recognized in the Black Sea (Yanko and Troitskaya 1987; Yanko and Vorobjeva 1990, 1991; Temelkov et al. 2006), in addition to the monothalamous supralittoral species reviewed by Golemansky (2007). The “hard-shelled” species are fairly well studied, but information about the monothalamous, soft-shelled taxa (“allogromiids”

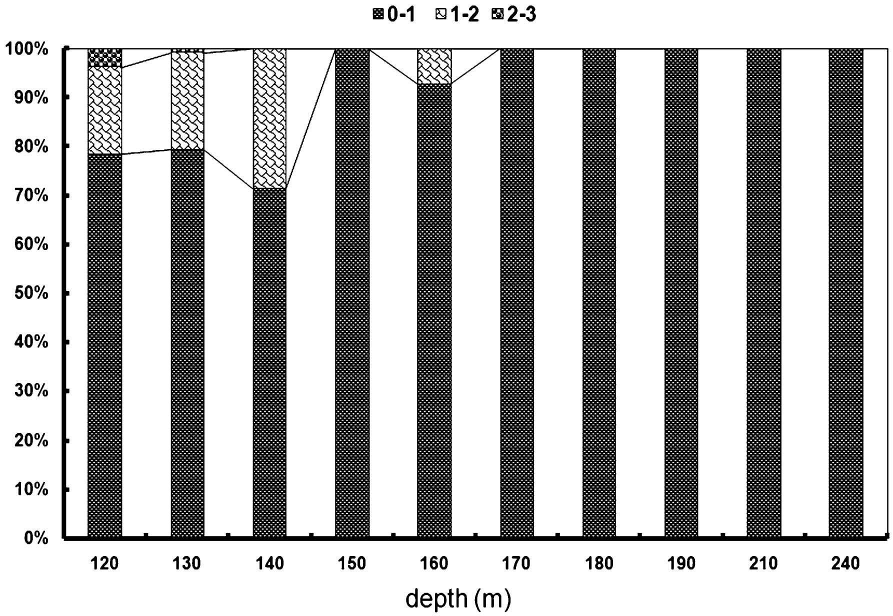

Figure 9. Proportion of ciliates inhabiting different sediment layers along the depth gradient near the Dnieper Canyon.

and "saccamminids") is rather limited. These protists were first reported in the Black Sea towards the end of the twentieth century (Golemansky 1974, 1999; Sergeeva and Kolesnikova 1996). It is now clear that they are a conspicuous and diverse element of the Black Sea coastal and deep-water benthic communities (Anikeeva 2003; Anikeeva and Sergeeva 2001; Golemansky 2007; Gooday et al. 2006; Revkov and Sergeeva 2004; Sergeeva and Anikeeva 2004).

The abundance of allogromiids and saccamminids reaches 116,000 indiv.m^{-2} at 260 m depth west of the Crimea (Sergeeva 2003b). Sergeeva et al. (2010) recognized a total of 40 informal groupings (morphospecies or morphotypes), and one described species, of monothalamous foraminifera, either organic-walled allogromiids or agglutinated saccamminids at sites along the 2007 *Meteor* transect in the region of the submarine Dnieper Canyon. Within the lower oxygen to upper hydrogen sulfide border zone, monothalamous foraminifera were more numerous than multichambered calcareous taxa. Both groups reached their highest abundance between 150 and 170 m, with a sharp peak at 160 m.

New data. In addition to the information reported by Sergeeva et al. (2010), new data about the vertical distribution of deep-water soft-shelled foraminiferans within the sediment column have been obtained across the oxic/anoxic interface in the Dnieper Canyon study area (Fig. 10). Most specimens were found in the top layer (0–1 cm) or in the overlying surface detritus. *Tinogullmia* sp., which occurred between 120 and 180 m, inhabited the 0–1 and 1–2 cm sediment layers.

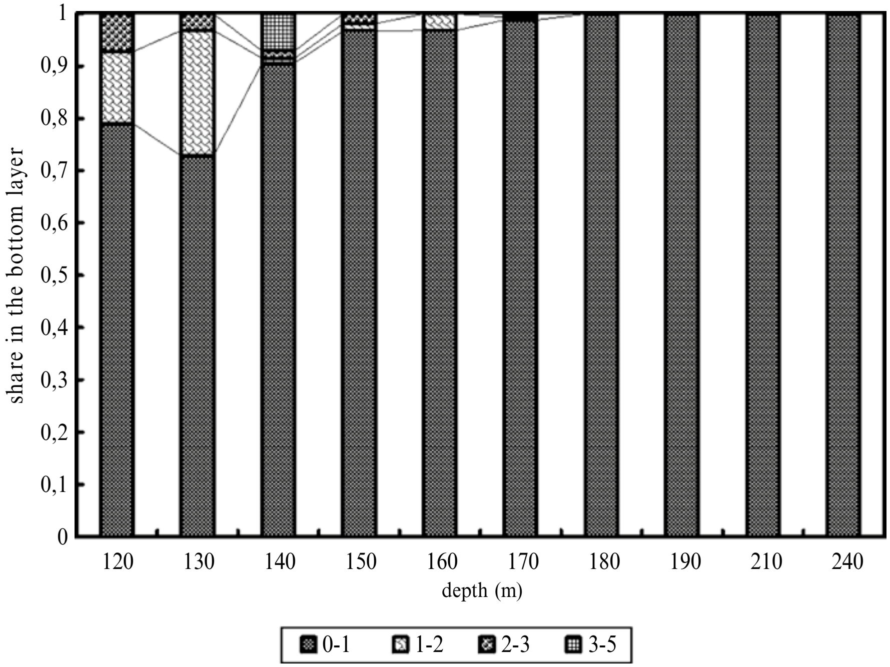

Figure 10. Proportion of foraminifera (hard-shelled and soft-shelled taxa) inhabiting different sediment layers along the depth gradient near the Dnieper Canyon.

Tinogullmia cf. *riemanni* and *Goodayia rostellatum* was also found in these upper two horizons, although they were concentrated in the 0–1 cm layer. *Bathyallogromia* sp. 2 was the only species that occurred in all three studied horizons and increased in abundance with depth into the sediment. Allogromiid sp. J was found only at 120 m water depth, where it was confined to the 1–2 and 2–3 cm layers, being equally distributed between these horizons. Saccamminid sp. 4 occurred only in the 2–3 cm horizon at 120 m. Thus, our new data suggest that ~70–75% of the studied soft-walled foraminiferal species are confined to the top layer (0–1 cm) of the sediments, presumably in order to gain access to the limited oxygen available in the bottom water, as well as to food.

4.2. METAZOA

A distinctive metazoan meiobenthic community is associated with the oxic/anoxic interface of the NW of the Black Sea (Sergeeva 2003b; Sergeeva and Zaika 2000; Sergeeva et al. 2008; Zaika 1999). In the area that we studied, it included Hydrozoa (two unknown species), Nematoda (including some unusual species), Polychaeta (two species), several species of Harpacticoida, and two undescribed species of Tardigrada. Here, we focus on the three most abundant groups, the nematodes, polychaetes, and harpacticoids. Of these, the nematodes were always the dominant (70–100%) metazoan meiobenthic organisms and the only taxon present at all investigated depths (Fig. 11).

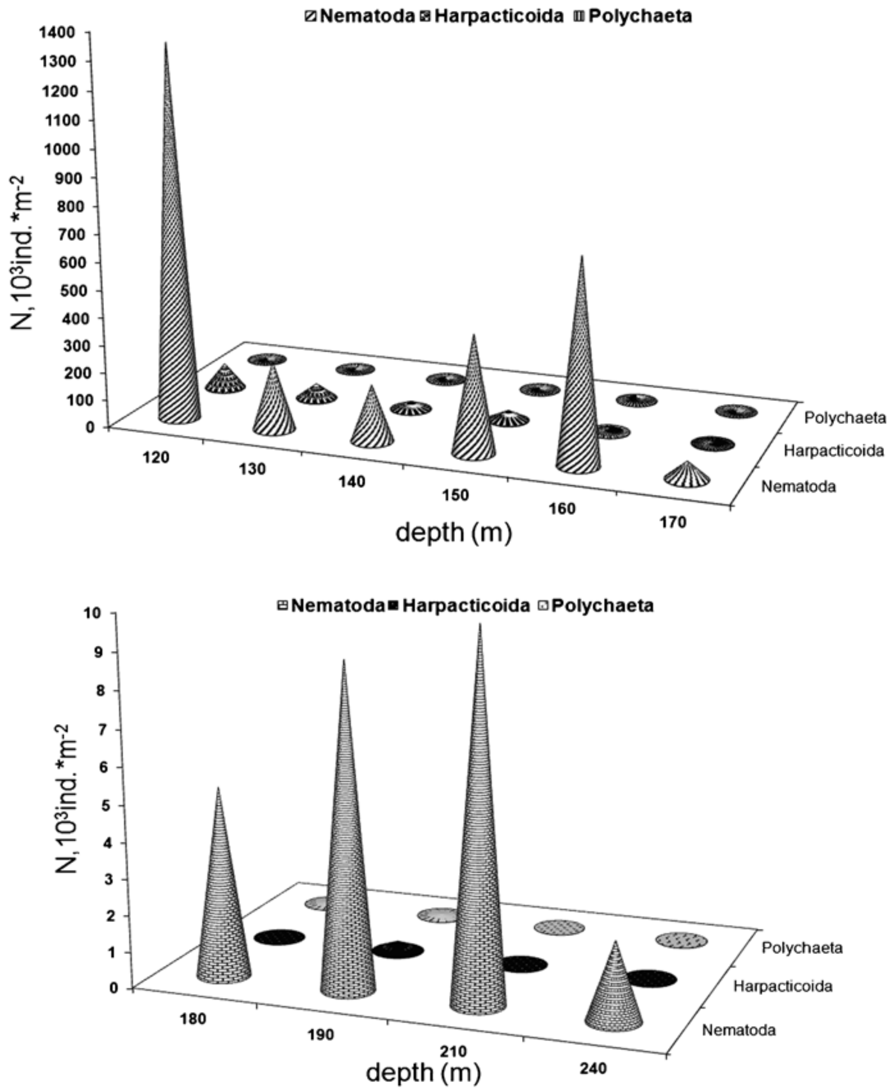

Figure 11. Abundance (10^3 indiv. m^{-2}) of the three main metazoan meiofaunal taxa along the depth transect near the Dnieper Canyon.

4.2.1. Free-Living Nematoda

Previous studies. In samples collected during 1994 in the NW Black Sea, the maximum abundance of nematodes was 490,000 ind. m^{-2} at a depth of 134 m and 478,800 indiv.m^{-2} at 77 m. Densities declined to 271,000, 185,600, and 10,200 indiv. m^{-2} at depths of 146, 151, and 172 m, respectively (Revkov and Sergeeva 2004), and a small number (1,000 indiv.m^{-2}) were recorded at the 232 m site. Nematodes were represented by 143 species at sites along this transect, with 69 species being recognized at 150 m, and 33–63 at depths between 120 and 140 m. The taxonomic composition was similar to that found on the Black Sea shelf, suggesting that some nematode species are eurybiotic. However, 38 species and 6 genera have been found only in the study area, where oxygen is either absent or present in minimal concentrations, and are previously unreported from the Black Sea.

New data. In samples collected during 2007, nematode densities reached 1,348,000 indiv.m^{-2} at 120 m depth and 727,700 indiv.m^{-2} at 160 m (Table 2, Fig. 12). They persisted to depths of 210 and 240 m at densities of 10,030 and 1,520 indiv.m^{-2}, respectively. Preliminary and ongoing analyses of species diversity at depths between 120 and 240 m includes 23 families and 6 orders. Our data show that some nematodes can live in permanently anoxic environments due to a high tolerance to hydrogen sulfide conditions.

The nematode fauna is unique at the studied depths. It includes 90 species and 9 genera unknown from the Black Sea, and 19 species, 9 genera, and 1 family recognized for the first time in this basin. The fauna includes stenobiontic and eurybiontic forms adapted to living in the redox zone. The species richness of

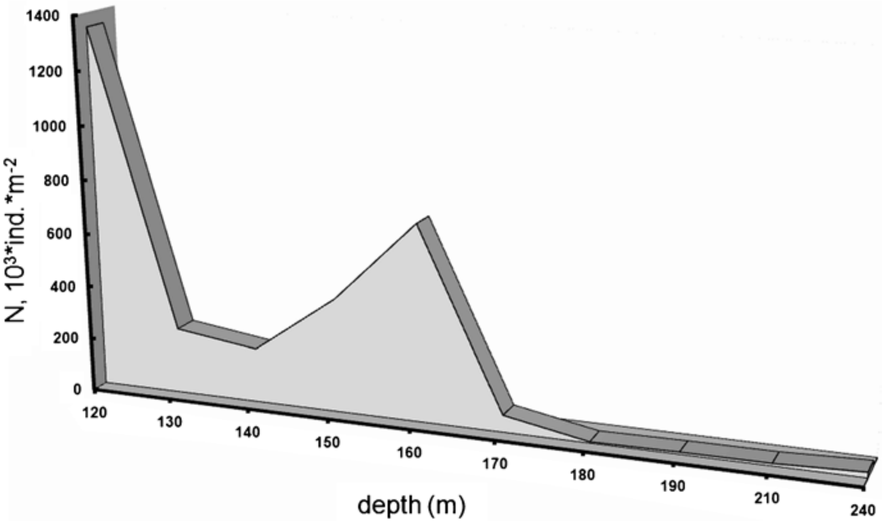

Figure 12. Abundance (10^3 indiv. m^{-2}) of nematodes along the depth transect near the Dnieper Canyon.

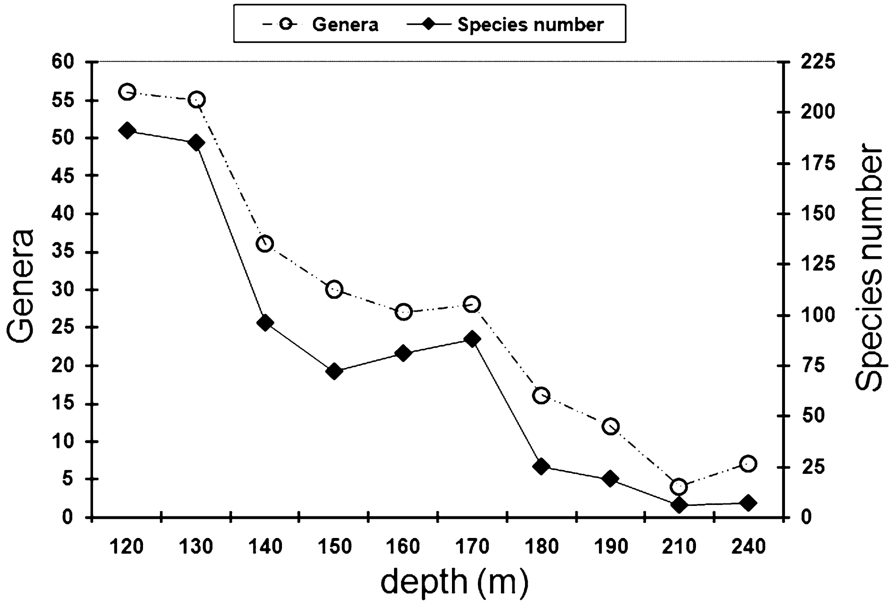

Figure 13. Distribution of nematode species and genera along the depth gradient near the Dnieper Canyon.

free-living nematodes decreased with increasing depth, highest values being found at depths of 120 and 130 m with a second peak in number of species and genera located at a depth of 170 m ($O_2 = 0.07$ mmol L^{-1}, sulfide = <1 µmol L^{-1}) (Fig. 13). Species adapted to anaerobic conditions occurred at depths ranging from 190 to 240 m. They included species (e.g., *Sabatieria pulchra*) usually found at shallower depths in the Black Sea. Among the nematodes at 150–240 m were species confined to these depths; these included *Quadricoma* sp. *U, Cobbionema* sp.*, Sabatieria* sp. 1*, Linhomoeus* sp. *X, Paralinhomoeus* sp 1*, Theristus* sp. 1*, Theristus sp. A, Theristus* sp. 4*, Monhystera* sp. *A, Campylaimus* sp. *4, Spirinia* sp 1*, Metalinhomoeus* sp. *O, Linhomoeus* sp. 1*, Aponema* sp. 1*, Microlaimus* sp. 2, and *Campylaimus* sp. 8.

The vertical distribution of nematodes in the sediment varied with water depth (Fig. 14). The 0–1 cm layer was occupied at all depths, and the 1–2 cm layer was also consistently inhabited, except at 210 m where the nematodes were confined to the upper layer. In most samples, nematodes were concentrated (81–96%) in the 0–1 cm layer. At 120 m, however, 77% were found in the 3–5 cm layer and at 240 m, where densities were much lower, 77% occurred in the 1–2 cm horizon. The 2–3 cm layer yielded a small proportion (0–16%) of nematodes at all water depths (Fig. 14). Studies are presently ongoing to determine the vertical distribution of individual species within the sediments.

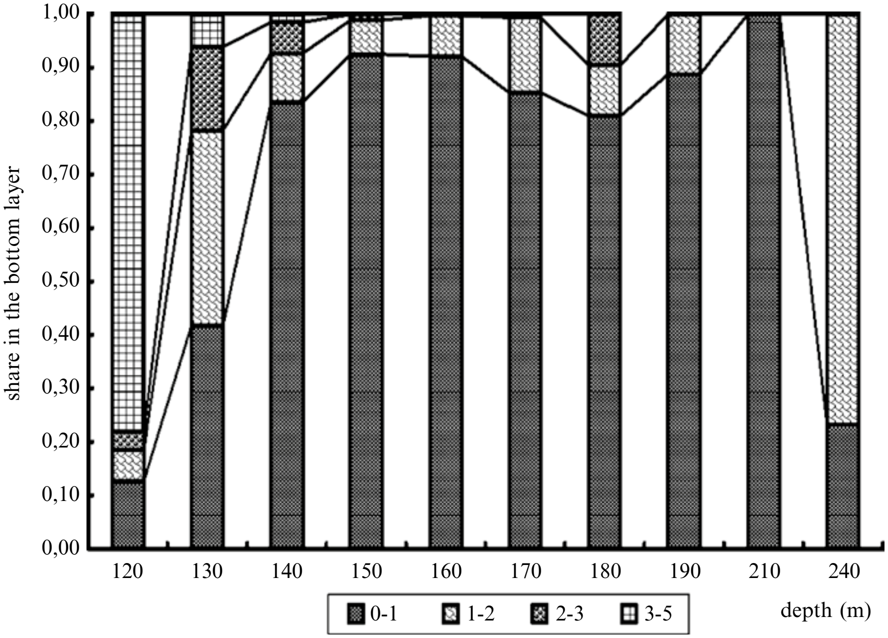

Figure 14. Proportion of nematodes inhabiting different sediment layers along the depth gradient near the Dnieper Canyon.

4.2.2. Polychaeta

Previous studies. Larval polychaetes belonging to two species are abundant in the deepest oxygenated waters across the basin throughout the year. One of them, which occurs in relatively low numbers, has been identified as *Protodrilus* sp. The second larval species is much more common. The growth of these larvae to the adult stage in the laboratory at IBSS led to their description as *Vigtorniella zaikai*, the type species of a new genus (Kiseleva 1992). Detailed information on the vertical distribution of zooplankton showed that they are pioneer metazoans inhabiting the narrow transition layer between oxic and anoxic water (Kiseleva 1959, 1990, 1998). These polychaetes have been found in all parts of the Black Sea (Zaika 1999; Sergeeva and Zaika 2000; Murina et al. 2006). This reflects the specific habitat requirements of the larvae, which are associated with a water layer characterized by constant low temperatures (8°C) and low oxygen concentrations (0.2–0.3 mL L^{-1} = 9–13.5 μmol L^{-1}). They are representatives of the metazoan plankton living in severely hypoxic water near the boundary of the hydrogen sulfide zone (Sergeeva and Zaika 2000). Where this layer impinges on the seafloor dwelling specimens of *Protodrilus* sp. and *Vigtorniella zaikai* were discovered in 1994 in the Black Sea around the shelf break to the west of the Crimean peninsula (Sergeeva et al. 1996). They dominated the meiobenthic community on at depths

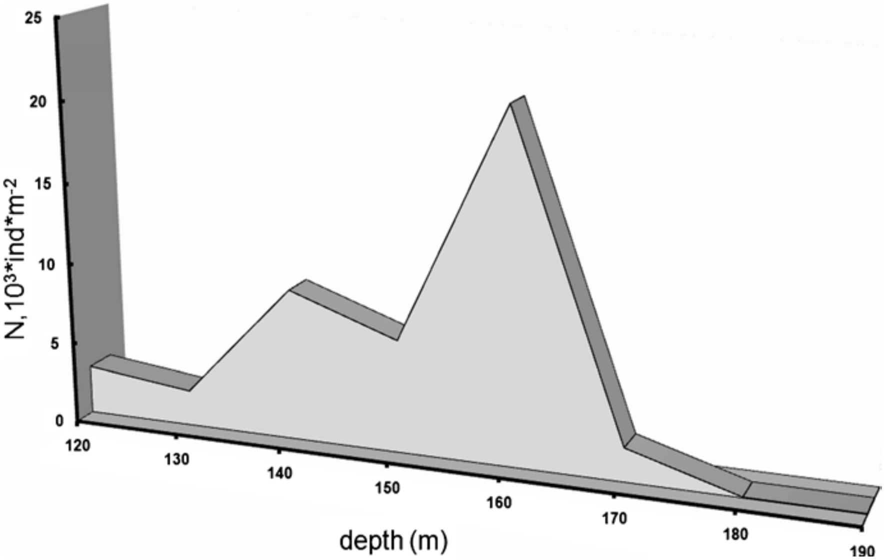

Figure 15. Abundance (10^3 indiv. m^{-2}) of polychaetes along the depth transect near the Dnieper Canyon.

of ~100–150 m, the larvae settle and adopt a benthic mode of life. Bottom the seafloor immediately above the hydrogen sulfide zone (Sergeeva and Zaika 2000; Zaika et al. 1999).

New data. In our new core samples, *Protodrilus* sp. and *Vigtorniella zaikai* were the only species present at depths between 140 and 160 m, where they were responsible for peaks in polychaete abundance (Fig. 15). At shallower sites (120–130 m), polychaetes were represented by species that are common in the middle part of the sublittoral zone. The polychaetes were concentrated (85–100%) in the upper layer of sediment across the transect, except at 120 m, where specimens were more evenly distributed through the sediment column (50% in the 0–1 cm layer, 31% in the 1–2 cm layer, and 9.5% in each of the two deeper layers) (Fig. 16).

4.2.3. Harpacticoida

Harpacticoid copepods (including nauplia) are a consistent component of benthic communities at depths of 120–190 m in the study area, with peaks in abundance at 120 m and 150 m (Fig. 17).

Harpacticoids were distributed unevenly in different sediment layers (Fig. 18). The upper layer (0–1 cm) was inhabited at all sites, except for the 180 m sample, which was devoid of harpacticoids. These crustaceans penetrated deeper into the sediment at the two shallowest sites. At 120 m, 51% were found in the 0–1 cm, 19% in the 1–2 cm, 5% in the 2–3 cm, and 25% in the 3–5 cm layer.

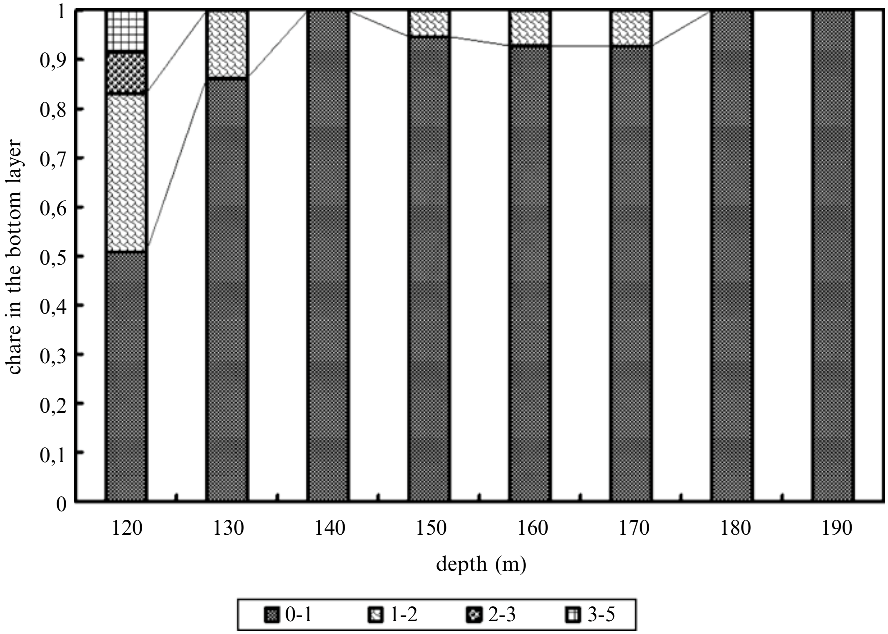

Figure 16. Proportion of polychaetes inhabiting different sediment layers along the depth gradient near the Dnieper Canyon.

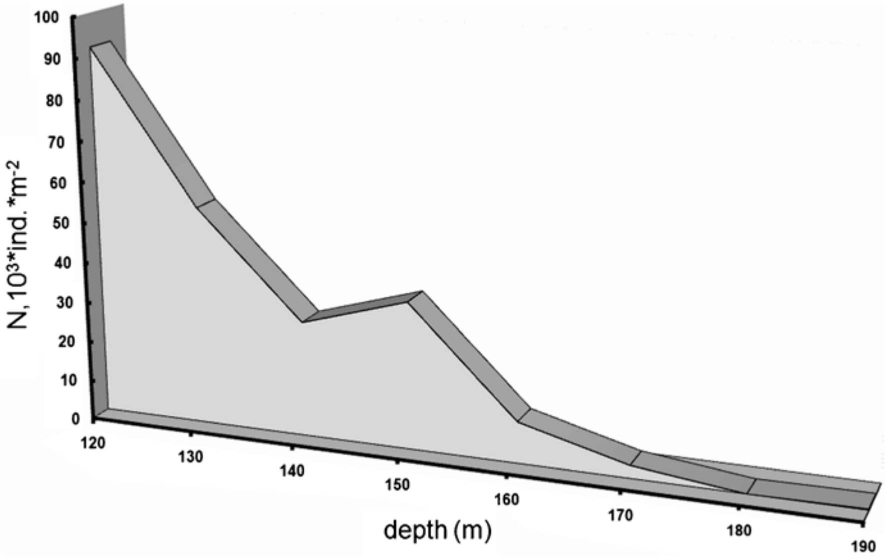

Figure 17. Abundance (10^3 indiv.m^{-2}) of harpacticoids (including nauplii) along the depth transect near the Dnieper Canyon.

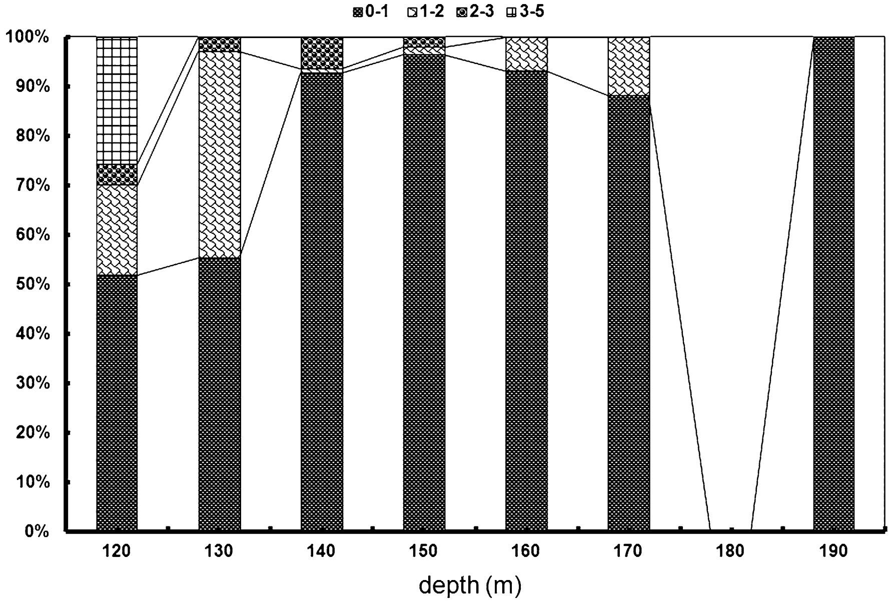

Figure 18. Proportion of harpacticoids inhabiting different sediment layers along the depth transect near the Dnieper Canyon.

Table 4. Harpacticoid species abundance (ind.m^{-2}) without nauplii along the depth transect near the Dnieper Canyon.

	Depth					
Species	**120 m**	**130 m**	**140 m**	**150 m**	**160 m**	**170 m**
Paramphiascopsis longirostris	38,175	2,068	8,638	9,690	1,510	361
Haloshizopera pontarchis	0	0	0	0	252	0
Amphascella subdebilis	10,411	0	0	0	0	0
Ameira parvula	7,982	0	0	0	252	0
Ameira sp.	0	414	0	0	0	0
Mesochra sp.	3,470	414	9,357	4,845	1,007	180
Enhydrosoma sp.	0	0	0	0	0	180
Laophonte sp.	0	0	0	0	0	0
Laophonte setosa	0	0	0	0	0	180
Normanella serrata	3470	0	0	0	0	0
Archesola typhlops	13882	827	0	969	0	180
Total without Nauplii	**77,392**	**3,723**	**17,995**	**15,504**	**3,021**	**1,081**

At 130 m, 55% were found in the 0–1 cm, 41% in the 1–2 cm, and 4% in the 2–3 cm layer. In contrast, between 87% and 95% of harpacticoids were concentrated in the top 1 cm at 140–170 m, while at the deepest site 190 m they present only in the upper layer. The harpacticoids unevenly on including only 11 species at 120–170 m (Table 4).

5. Are the Faunal Patterns Real or Artifacts of Preservation?

In this study, we identified "live" protists and other meiofaunal organisms based on Rose-Bengal staining. Because of the known limitations of this method (Bernhard 2000; Bernhard et al. 2006; Danovaro et al. 2010), particularly in hypoxic/anoxic and sulfidic settings, it is possible that some of the stained organisms found in Black Sea sediments were dead when collected. On the other hand, certain ciliate taxa have long been known to occur in anoxic sediments (e.g., Fenchel and Finlay 1995), while foraminifera possess various morphological and physiological adaptations to hypoxia (Bernhard and Sen Gupta 1999) and apparently can survive without oxygen by accumulating and respiring nitrate (Risgaard-Petersen et al. 2006; Piña-Ochoa et al. 2010). Recently, the existence of metazoans (loriciferans) that can live permanently in anoxic habitats (hypersaline basins in the deep Mediterranean) has been convincingly demonstrated (Danovaro et al. 2010).

Such unequivocal evidence is not yet available for the benthos from the deeper parts of the Black Sea. Nevertheless, a number of considerations suggest that at least some of the organisms were alive, rather than having been transported from adjacent oxygenated areas.

1. Specimens collected within the oxic/anoxic transition zone (120–240 m water depth) stained intensely with Rose Bengal and showed no sign of morphological damage (Fig. 19). Danovaro et al. (2010) also observed that the live loriciferans they studied were very strongly stained and morphologically intact, in contrast to other meiofaunal organisms that stained weakly and were therefore assumed to be transported carcasses.
2. Meiobenthic densities within the transition zone are similar to, and even exceed, those in sublittoral areas.
3. Our samples yielded a characteristic fauna of benthic organisms, adapted to limited oxygen concentrations. Among the main components were soft-shelled foraminiferans, large numbers of undescribed nematode species, the polychaetes *Vigtorniella zaikai* and *Protodrilus* sp., and two unknown tardigrade species, all of which appear to be confined to the transition zone.
4. The nematode and harpacticoid populations included specimens of all sizes (life stages), as well as gravid females containing eggs.
5. High ciliate densities appear to be associated with concentrations of bacteria, suggesting that these may be live populations.

Additional evidence that eukaryotes can live in the anoxic Black Sea comes from observations of live organisms. During a study of bottom sediments associated with methane gas hydrates in the Sorokin Trough (NE Black Sea), an endemic species of Cladocera was discovered in the hydrogen sulfide zone at depths of 1990 and 2,140 m (Sergeeva 2004b, c). This was described as *Pseudopenilia bathyalis,* the type species of a new genus (Sergeeva 2004b, c) and family Pseudopenilidae (Korovchinsky and Sergeeva 2008). One specimen of the new cladoceran was observed alive in a sample from the deeper site. In April–May

2010, during a cruise on the RV *Maria S. Merian,* we studied bottom sediments from 250 to 300 m depth in the Bosporus Strait region in order to search for live fauna in the permanent hydrogen sulfide zone of the Black Sea. Using light microscope, we observed actively moving protozoans (large ciliates) and metazoans (free-living nematodes). These observations were recorded on video. Assuming that they were indigenous, then these organisms provide good evidence that eukaryotes can live under anoxic/sulfidic conditions in the Black Sea. However, this question requires further investigation.

6. Discussion

The Black Sea is the largest and best-studied permanently anoxic body of deep water in the world. Since the discovery of sulfidic conditions in the 1880s, it has been widely assumed that the deeper parts are inhabited only by prokaryotes. However, the IBSS NAS of Ukraine (Sevastopol) has studied the possible occurrence of benthic protozoans and metazoans in the oxic/anoxic transition and permanently anoxic zones of the Black Sea for more than 30 years (Sergeeva 2000a, b; Sergeeva 2001; Zaika 1999; Zaika et al. 1999). The previous and new observations on meiobenthos summarized in the present paper were made at depths (120–240 m) corresponding to the transition between increasingly hypoxic but non-sulfidic bottom water and the anoxic/sulfidic zone. The poorly defined boundary between these two domains is located at approximately 150–180 m.

Our new data suggest that the oxic/anoxic transition zone supports a rich protozoan and metazoan biota. Although organisms are found in samples from deeper, anoxic/sulfidic areas, high faunal densities are typically located in depths where oxygen disappears. Both calcareous and monothalamous (soft-shelled) foraminifera exhibit a sharp peak at ~160 m (Sergeeva et al. 2010). Among the ciliates, abundances maxima are located at 120, 160–190, and at 240 m, where they are possibly associated with concentrations of bacterial cells in the area of transition between oxic and anoxic/sulfidic conditions. These observations echo those of Zubkov et al. (1992) who described a unique community of ciliates from the oxic/anoxic interface in the central Black Sea and off the coasts of Bulgaria and Georgia. *Pleuronema marinum* and members of the ciliate families Tracheliidae, Holophryidae, and Amphileptidae were concentrated in hypoxic waters ($O_2 = 15$ μmol L^{-1}). *Askenasia* sp. (family Mesodiniidae), many individuals of which were covered in epizoic bacteria, inhabited the lower part of the hypoxic layer and the upper part of the sulfidic zone ($H_2S = 6$ μmol L^{-1}). Zubkov et al. (1992) suggested that the ciliates were feeding on large sulfur bacteria. The distribution of ciliates in the Black Sea has parallels in other meromictic water bodies. In particular, molecular analyses have revealed the presence of protists, including ciliates, around and below the oxic/anoxic boundary in the Cariaco Basin (Caribbean Sea) (Stoeck et al. 2003) and in anoxic waters in the Framvaren Fjord (Norway), where bottom-water sulfide levels are 25 times higher than in the Black

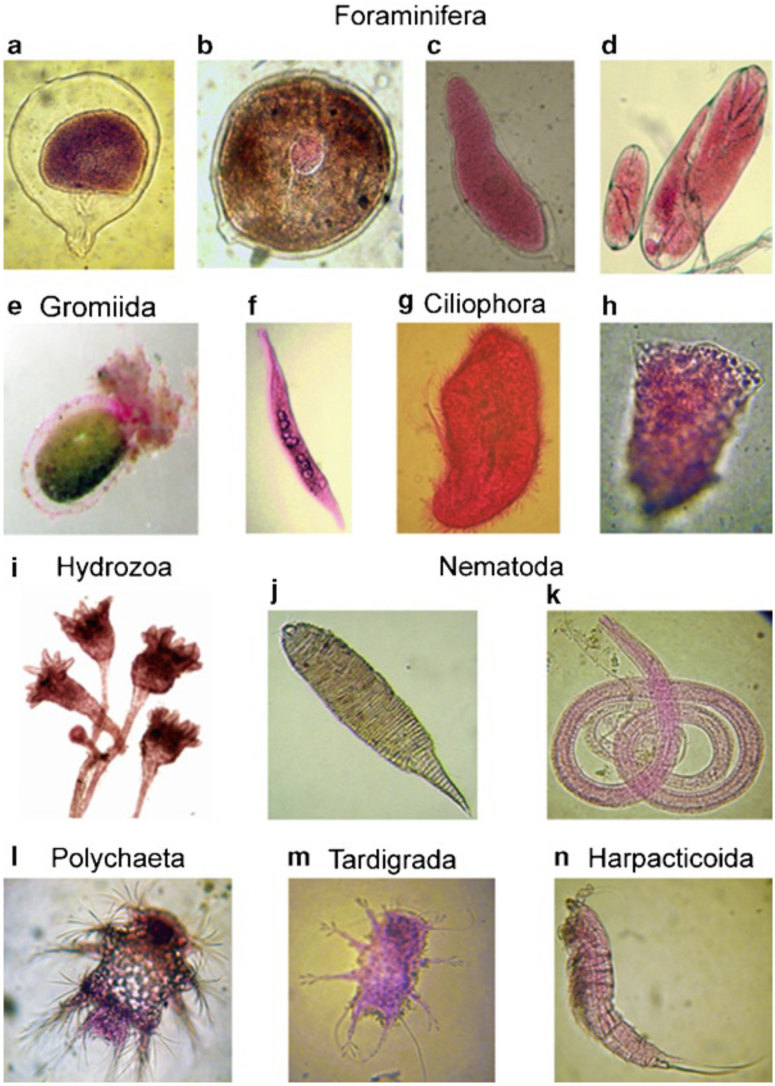

Figure 19. Examples of meiobenthos found in hypoxic/anoxic sediments at 120–2,075 m depth in the Black Sea. (**a–d**) Foraminifera, 140–170 m. (**e**) Gromida, 120–150 m. (**f–h**) Ciliophora, 190–240 m. (**f**) 2,075 m. (**g**) 170 m. (**h**) (**j–k**) Nematoda, 120–240 m. (**l**) Polychaeta, 120–150 m. (**m**) Tardigrada, 120–160 m. (**n**) Harpacticoida, 120–170 m.

Sea (Behnke et al. 2006). Earlier, distinct peaks of ciliates around oxic/anoxic boundaries were revealed using classical microscopic techniques in Danish fjords (Fenchel et al. 1990) and in Lake Cisó (Spain) (Massana and Pedros-Alio 1994).

Very large numbers of ciliated protozoa, contained symbiotic algae (*Chlorella* spp.), were reported to live beneath the oxic/anoxic boundary in a stratified freshwater pond (Finlay et al. 1996). The three most abundant metazoan taxa in our samples (nematodes, harpacticoids, and polychaetes) likewise display abundance maxima around the level where oxygen disappears. In particular, the polychaetes *Protodrilus* sp. and *Vigtorniella zaikai* are concentrated in this narrow zone in our new material, as well as elsewhere on the Black Sea margin (Bacesco 1963), suggesting that they can be considered as indicators of severe hypoxia in this basin.

The high abundance of different meiobenthos taxa at the depths with a low concentration of dissolved bottom-water oxygen is undoubtedly not accidental. These concentrations are reminiscent of the "edge effects" observed at the upper and/or lower boundaries of many continental margin oxygen minimum zones (Levin 2003; Gooday et al. 2009). OMZ edge effects generally coincide with rising oxygen levels across the upper or lower boundaries, whereas in the Black Sea, and perhaps other anoxic basins, abundance maxima appear where oxygen has almost disappeared. In both cases, however, the abundance of benthic organisms appears to be a response to an enhanced food supply.

7. Future Perspectives

Our data suggest that some benthic eukaryotes can tolerate anoxic and sulfidic conditions. Further comparative studies of shallow- and deep-water meiobenthic communities in the Black Sea are necessary in order to establish which species are characteristic and indicative of hypoxic/anoxic conditions as well as the proportion of Rose-Bengal-stained specimens that were alive when captured. The recent paper of Danovaro et al. (2010) provides a model for the kinds of analyses that could be conducted. The application of CellTracker Green to freshly collected samples is one obvious way forward. In the case of ciliates, a taxonomic study would reveal whether they include genera typical of anoxic sediments.

Further studies of the Black Sea seep fauna will yield more information about the taxonomic composition of benthos in the transitional oxic/anoxic water masses. They should reveal, among other things, the relationship between the diversity and abundance of meiofauna and concentrations of hydrogen sulfide and methane. The specific physiological and biochemical processes that facilitate the survival of eukaryotes in such "extreme" environments are important questions for future studies too.

8. Acknowledgements

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