The Black Sea Meiobenthos in Permanently Hypoxic Habitat

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Abstract: Usually the redox potential at the sediment surface changes rapidly, making it difficult to assess the degree of hypoxia which meiofauna can tolerate. In the Black Sea, in the anoxic zone, there is a layer of permanent hypoxia and a sprawling redoxcline along the bottom surface. This facilitates the study of the distribution of meiobenthos in a gradient of hypoxia. The article describes the structure of a layer of permanent hypoxia in the Black Sea. The data on the distribution of meiofauna (Harpacticoida, Polychaeta, and in less detail, Nematoda) within a layer of constant hypoxia are presented.

Key words: Meiofauna, distribution, abundance, gradient of hypoxia, Black Sea

Introduction

In water ecology, the term hypoxia means low oxygen content. This ecological term was introduced when low level of tolerance of many coastal benthic forms was observed at oxygen concentrations of less than 2 ml• L^{-1} (Rosenberg 1980). It was later found that the deep-sea benthic animals can tolerate oxygen concentrations of about 1 ml• L^{-1} (Rosenberg *et al.* 1991), and hypoxia was defined as oxygen concentrations of about 1-2 ml• L^{-1}. As a result, the following gradation of oxygen content was proposed (Middelburg, Levin 2009): normoxic (> 63 μM O$_2$• L^{-1} ; > 2mg O$_2$• L^{-1} ; > 1.4ml O$_2$• L^{-1}); hypoxic (<63 μM O$_2$• L^{-1} ; <2mg O$_2$• L^{-1} ; <1. .4ml O$_2$• L^{-1}); anoxic (0 μM O$_2$• L^{-1}); and sulfide (0 oxygen and the presence of free sulfide).

We adopt this classification bearing in mind that in the Black Sea, the hydrogen sulfide zone is also called euxinic, and that the layer above this zone (in which by modern methods of measuring oxygen and hydrogen sulfide are not found), is named suboxic (Murray *et al.* 2007).

A known reaction of zoobenthos to hypoxia is to reduce the number of species and total abundance, as repeatedly shown in different waters. The increasing oxygen deficiency changes the behavior of animals, then gradually reduces species richness, abundance and biomass of the benthic community. At a certain stage of development of hypoxia, the soil becomes sulfide and black. Degeneration of benthic communities continues as long as normoxia is not restored (Rosenberg *et al.* 1991). Described signs were traced primarily on macrofauna. Reaction of meiofauna is less studied, but there is a generalization (Wetzel *et al.* 2001), according to which all meiofauna is sensitive to prolonged hypoxia. Thus there is a wide range of tolerance. Some representatives tolerate oxygen deficiency a short time, others-weeks or even months. Usually some foraminifera and nematodes are most tolerant to hypoxia/anoxia, while crustacean meiofauna is less stable (Wetzel *et al.* 2001). At the same time it was demonstrated that the crustacean *Cletocamptus confluens* (Schmell)

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(Harpacticoida) tolerates complete anoxia and the presence of sulfides (VOPEL *et al.* 1996). Therefore, the tolerance to hypoxia is a property not of the whole taxonomic group, but of each species separately.

In the Black Sea, the distribution and abundance of meiobenthos were studied in various types of hypoxic habitats: (1) seasonal hypoxia in the bottom area of the coastal zone associated with stagnation and a high content of organic matter (ZAIKA *et al.* 2011), (2) detrital-microbial mat formed around a shallow active methane seep (IVANOVA, SERGEEVA 2006, SERGEEVA, GULIN 2007, SERGEEVA *et al.* 2011), (3) the deep water bottom in contact with the layer of permanent hypoxia (SERGEEVA *et al.* 2011, 2012, 2013, ZAIKA, SERGEEVA 2012). The last type of habitat has a large spatial scale (covering the entire sea) and is permanent.

Much of the experimental research on hypoxia was conducted to find out how long the species can survive the lack of oxygen. The study of meiobenthos in the Black Sea from the layer of permanent hypoxia, revealed species, constantly living (and performing full life cycles) in hypoxic conditions to varying degrees, depending on the depth and distance from the boundary of the hydrogen sulfide zone.

This review focuses on the layer of constant hypoxia underlain by anoxic waters. First, we define the limits of permanent hypoxic layer and describe its structure, particularly for the area of contact with the bottom (ZAIKA in press). Features of the distribution of meiobenthos by depth within the layer of hypoxia are described for two areas: the northwestern part of the sea and the Bosporus area.

The main features of the oxygen distribution in the Black Sea.

The total volume of the Black Sea is estimated at 534 000 km^3, but only 13% of it contains dissolved oxygen (KUCUKSEZUGIN 2003, MURRAY *et al.* 2007). The surface layer of the water is supplied with oxygen from the atmosphere, in addition to the oxygen from algae released during photosynthesis. But in the area of the oxicline, oxygen content decreases rapidly, and below 200 m the water column is entirely anoxic and saturated with hydrogen sulfide. The water in the Black Sea is heavily stratified, especially in summer. The cyclonic major Black Sea Rim current (RC) defines the dome-shaped form of all isosurface. Thus, the dome pycnocline in the centers of two cycles, eastern and western, can rise above the peripheral portion of 25-30 m (OVCHINNIKOV *et al.*

1966). One reason for this is that RC generates anticyclonic eddies near the shore (NAE), which have important effects on the dynamics of the coastal zone (OVCHINNIKOV *et al.* 1966, YAKUBENKO *et al.* 2003).

Water inside the ring of the RC has a tendency to upwelling, while the NAE cause downwelling (STUNZHAS, YAKUSHEV 2006), which accumulates any suspension, including plankton and pollution, and sinking into the depths. The NAE are transient in nature, formed mainly along the coasts with a minimum width of the shelf. In recent years, the NAE in the Black Sea have been tracked by satellite. If the research ship registers 19-46 NAE per year, then on the pictures from space the number estimated for the northern half of the sea is 51-105. Along the Anatolian coast more than 230 NAE per year are produced. According to the statistical estimate of the dimensions of the NAE, modal diameter is slightly less than 50 km (KARIMOVA 2011).

Described phenomena lead to the fact that oxygenated water penetrates most deeply around the border of the shelf, where the sinking water is in contact with the bottom. This usually occurs at depths of 150–170 m. In the Bosporus area, due to the influence of the Marmara water flow, oxygen and animals are recorded at depths up to 250 m (SERGEEVA *et al.* 2011, ZAIKA, GULIN 2011, HOLTAPPELS 2011). For example, a brief description of the situation was made at the coast of the Caucasus, where a study along the same transect was conducted for 5 years (OVCHINNIKOV *et al.* 1996). Coastal anticyclonic eddies were formed along the coast, their chain creating the coastal zone of convergence. In these vortices suspension, pollution and oxygen were lowered causing the hydrogen sulfide zone boundary to deepen. At 5 miles from the coast the depth was 550 m, the average oxygen content was: 4.39 ml • L^{-1} at a depth of 100 m, 0.97 ml • L^{-1} at a depth of 150 m, and 0.26 ml • L^{-1} at 200 m.

The oxygen concentration in the upper mixed layer and in the CIL, according to recent data, comes to 250-350 μM O$_2$ • L^{-1}, and at the lower boundary of the oxicline is reduced to 10-20 μM O$_2$ • L^{-1} (EREMEEV, KONOVALOV 2006). This is confirmed in both the northern and southern part of the sea (KUCUKSEZUGIN *et al.* 2003, STUNZHAS, YAKUSHEV 2006). In the Black Sea vertical profiles are often compared with the values of the water density (σ_θ). Thus, when σ_θ = 15.7 oxygen concentration is less than 10 μM O$_2$ • L^{-1} (MURRAY *et al.* 2007). This may occur at depths from 45 m to 197 m, even in the anticyclonic eddies at the

edge of the shelf depths (EREMEEV *et al.* 1997).

The appearance of sulfides occurs at depths from 110 to 170 m, at density of $\sigma_\theta = 16.15 – 16.2$ (EREMEEV, KONOVALOV 2006; MURRAY *et al.* 2007). In the cyclonic areas the density of $\sigma_\theta = 16.2$ is reached at a depth of 105-123 m, and in the anticyclonic-at a depth of 160-193 m (YUNEVA *et al.* 1999). Thus, the depth of the NAE often reaches 150 m, but in some cases the downwelling traces with presence of oxygen, can register up to 200 m. This involves internal waves that are "pump" oxygen to depths of 150-200 m (OVCHINNIKOV *et al.* 1996).

It is often believed that the depth of occurrence of sulfides is at the lowest end of the aerobic layer. But over the hydrogen sulphide zone there is another discovered layer, which lacks both O_2 and H_2S (or rather, their concentration is less than $10\ \mu M \cdot L^{-1}$). This layer is called "suboxic" (MURRAY *et al.* 2007; EREMEEV, KONOVALOV 2006, STUZHAS, YAKUSHEV 2006).

So, the water masses of the Black Sea are normoxic throughout the upper mixed (quasi-homogeneous) layer. In oxicline, the top of which is held by $\sigma_\theta = 14.6$, and the lower by $\sigma_\theta = 15.6$ (EREMEEV *et al.* 1997), normoxic water is replaced by hypoxic. At the 5-year transect in the Caucasus such density, on average, was observed at a depth of 150 m (OVCHINNIKOV *et al.* 1996). The vertical distribution of oxygen at the edge of the shelf is extremely unstable. Along the coast at a depth of 75 m, there are normoxic conditions (EREMEEV, KONOVALOV 2006). But hypoxia may be observed at a depth of 60-70 m; in addition, at these depths, the oxygen concentration may be $20\ \mu M\ O_2 \cdot L^{-1}$ only. Hypoxia can begin at $\sigma_\theta = 5.25–15.5$, at the bottom of the oxicline: at a given conditional density of the oxygen concentration in the range of $80–35\ \mu M\ O_2 \cdot L^{-1}$ (average 60 $\mu M\ O_2 \cdot L^{-1}$) (OGUZ 2002, KUCUKSEZUGIN *et al.* 2003, GLAZER 2006).

Oxygen concentration of $50\ \mu M\ O_2 \cdot L^{-1}$ can be detected at depths from 60 to 160 meters. Recently, it was shown that the value $\sigma_\theta = 16.2$, appropriate depth occurrence of sulfides, are at quasi-periodic variations in the depth range from 130 to 165 m (GULIN, STOKOZOV 2010). Similar oscillations in the upper limit hydrogen sulfide zone (offset its depth from 146 to 168 m) were reported in other studies (ZAIKA, GULIN 2011). For these reasons, it is impossible to give exact boundary depths occupied by hypoxic waters, especially since within the layer of hypoxic water with every meter increase in depth, the oxygen content is reduced from $63\ \mu M\ O_2 \cdot L^{-1}$ to zero. We will focus on the depth of 150 m, at which, in a narrow shelf (as in the Caucasus), the average $\sigma_\theta = 15.6$ is at the lower end of the oxicline, under which is a suboxic layer («no oxygen, no hydrogen sulfide»).

The contact area of the bottom and water with different oxygen contents are graphically presented in the figure (Fig. 1), which shows a vertical section that covers the depth of 100 to 175 m in the area of the shelf edge. The scheme shows the area of contact with the bottom of the normoxic, hypoxic (to varying degrees), suboxic and, finally, with sulfide waters. This scheme corresponds with the available data, but it is static and does not reflect the great instability of the layers with different oxygen content. This instability is shown in recent works (ZAIKA, BONDAREV 2010, GULIN, STOKOZOV 2010, ZAIKA, GULIN 2011, ZAIKA, SERGEEVA 2012, HOLTAPPELS *et al.* 2012). Without going into the less known physical causes of the border fluctuations, we will only mention the most likely-short existence and movement of the NAE in the space, the difference in their power and vertical proliferation, as well as "internal waves". In the Bosporus, an additional cause of fluctuations is the pulsation of the Marmara water flow in the Black Sea.

The presence of such fluctuations affects all boundaries shown in Fig. 1. The smaller the angle of the bottom, the greater the distance that can be shifted to the boundary. There is evidence (ZAIKA, GULIN 2011) for the movement of the boundary layer

Fig. 1. Chart showing the contact area of the bottom and water layers with different oxygen content (from normoxic to sulfide).

between the depths of the sulfide-146 and 168 m. For these reasons the "permanent" zone of hypoxia is, in effect, quasi-permanent.

Material and Methods

We used the "operational" definition, according to which meiobenthos are animals that pass through a sieve of 1 mm and retain on 63 micron sieve. In this case we consider all animals, including protozoan meiobenthos and metazoan meiobenthos with two components-the permanent meiofauna (eumeiobenthos) and the temporary meiofauna (pseudomeiobenthos), representing juvenile stages of macrobenthos.

Sea bottom sediments for meiobenthos studies along oxic/anoxic interface were collected in the northwestern part of the Black Sea during cruises on board of the research vessel (RV) *'Professor Vodyanitsky'* (Ukraine) and RVs *'Meteor'*, *'Poseidon'*, *'M. S. Merian'* (Germany), and in the Bosporus region on board of the RVs *'Arar'* (Turkey) and *'M. S. Merian'* (Table 1).

Samples of bottom sediments were collected using a modified version of the Barnett multiple corer (MUC), a gravity corer and push corer from SL "Jago". These devices provided sample collecting without disturbing the stratification of the sediment. For the analysis of the distribution of the meiobenthic fauna along a bottom column at each station, from 1 to 3 sediment cores were sectioned into the following horizontal layers: 0–1, 1–2, 2–3, 3-4, 4–5, 5-7, 7-9 cm.

Results and Discussion

In the Black Sea at a depth of 40-50 m, species composition and abundance of the total macrobenthos gradually decrease. In the layer of the oxicline, the reduced concentration of oxygen accelerates this process, and at a depth of 100 m, the biomass of macrobenthos is typically less than 4-8 g m^{-2} (Zaika 2011).

Comparable values of biomass of meiobenthos (4.6 g m^{-2}) were registered in the northwestern part of the sea at a depth of 142 m (Revkov, Sergeeva 2004), but this value is specified as the maximum.

The closer to the anoxic water, the less adult macrofauna, and as a result, the early stages of macrobenthos disappear. For this reason, the percent of pseudomeiobenthos in total meiobenthos is decreased (Fig. 2). At the depth of 130 -140 m pseudomeiobenthos is 10-20% (by number), and at 150 m, it is reduced to 4%. These data were obtained in the northwestern part of the Black Sea in February-March 2007 (Sergeeva *et al.* 2012).

For comparison, we use data for shallow waters in the northwestern shelf of the Black Sea, where the percentage of pseudomeiobenthos reaches 37-58% (biomass). More than half of the temporary meiobenthos falls on polychaetes, especially in the aftermath of mass reproduction of the latter (Vorob'eva, Bondarenko 2007).

As shown in the shallow waters of the Black Sea (Zaika *et al.* 2011a,b), oxygen is detected only in the upper layer of sediment. In the case of hypoxia in the bottom water anoxic zone, the boundary is approaching from the depths of the sediment to the surface. Therefore, the vertical distribution of animals is indirect evidence of the oxygen conditions in the ground. In this connection it is interesting to com-

Fig. 2. Pseudomeiobenthos percentage of the total meiobenthos (NW Black Sea, RV 'Maria S. Merian').

Table 1. List of cruises with vessels used, cruise dates, depths and region of research

Research Vessel, Cruise No	Cruise dates	Depth, m	Region of the Black Sea
Professor Vodyanitsky, 45	June 1994	77-260	NW, methane seeps
Meteor, 72/2	February-March 2007	120-240	NW, methane seeps
Poseidon, 317/3	October 2004	182-252	NW, methane seeps
Arar	November 2009	75-300	Near Bosporus area
M. S. Merian, 15	April-May 2010	80-300	Near Bosporus area, NW

Table 2. Changes in vertical distribution of temporary and permanent meiobenthos with depth (1- meiobenthos is present; 0-none).

Temporary meiofauna (pseudomeiobenthos)											
Horizon	Depth, m										
	120	130	140	150	160	170	180	190	210	221	240
0-1 cm	1	1	1	1	1	1	1	0	0	0	0
1-2 cm	1	1	1	0	1	1	0	0	0	0	0
2-3 cm	1	1	1	0	0	0	0	0	0	0	0
3-4 cm	0	1	1	0	0	0	0	0	0	0	0
Permanent meiofauna (eumeiobenthos)											
0-1 cm	1	1	1	1	1	1	1	1	1	0	1
1-2 cm	1	1	1	1	1	1	1	1	0	1	1
2-3 cm	1	1	1	1	1	1	1	0	0	0	0
3-4 cm	1	1	1	1	1	0	0	0	0	0	0

pare the vertical distribution of the different groups of meiobenthos with the increasing total depth in the northwestern part of the sea (Table 2) (SERGEEVA *et al.* 2012).

The upper part of Table 2 confirms the results illustrated in Fig. 2 showing the decrease of share of temporary meiobenthos with depth, which is due to the proximity of the anoxic zone. It is seen that pseudomeiobenthos inhabits the layers 0-5 cm at depths up to 150 m, it occurs no deeper than layers 0-2 cm at higher depths, and is found only in the layer 0-1 cm at depth of 180 m. This is consistent with the likely increase in the near-bottom hypoxia, which is accompanied by an approximation of anoxia in the sediment to the surface. Table 2 shows that a decisive change in the distribution of pseudomeiobenthos occurs at depths of 150-180 m.

The lower part of Table 2 shows that eumeiobentos is generally much more tolerant to increased hypoxia. In the same samples permanent meiobenthos occurs over the entire layer 0-5 cm at a depth of 160 m, and later gradually leaves all horizons, except the layer 0-1 cm. This occurs only at a depth of 210 meters! We will not discuss the depth of over 200 m, and will only mention two circumstances: (1) the "right" pattern of the change in depth habitat permanent meiobenthos shows evidence that it was in a sample from that depth (2) the distribution of meiobenthos in layers at depths of 221 and 240 m suggest that we have not seen species from the previous depths here and that they have other respiratory features. However, one can not exclude the effect of random mechanical causes for features of the distribution of meiobenthos in layers at depths of 210 and 221 m.

In the Black Sea with depth increase, there is a shortage of oxygen, and the eumeiofauna changes the ratio of individual taxonomic groups. According to reports (REVKOV, SERGEEVA 2004, SERGEEVA *et al.* 2012, 2013), in metazoan meiobenthos at depths of 70 -120 m, Nematoda dominated in number, and the next most abundant group was Harpacticoida.

At depths of 130-150 m the proportion of Coelenterata and Polychaeta increases, so that at a depth of about 150 m a peculiar meiobenthos community is recorded, named for the mass species of the small polychaete community-*Vigtorniella zaikai* KISSELEVA. Almost all settlements of *V. zaikai* represented the early stages of development, and the size is related to the meiobenthos. Adults of the species are also referred to the meiobenthos, although their length is little more than 1 mm (REVKOV, SERGEEVA 2004; ZAIKA, SERGEEVA 2012).

In the northwestern part of the sea, an abundance of Nematoda at a depth of 150 -160 m forms a significant peak (SERGEEVA *et al.* 2012), then the number is reduced; Harpacticoida also shows a peak at a depth of 150 m. As indicated below, the peak abundance of Foraminifera, in this case mainly with soft shells (Allogromiids), was near this depth. This raises questions about the reasons for the accumulation of different groups of meiobenthos in the depths and the sources of food for the animals.

In different parts of the sea, at oxygen-depleted depths, there are differences in the composition of meiobenthos (REVKOV, SERGEEVA 2004). It is not known whether this is due to the differences in the region or because of the usual patchiness. So, in the Karadag area (southeastern part of the Crimea), at a depth of 160 m, Acarina had 57.5% of the biomass of

meiobenthos, while Foraminifera-22.5%. In contrast, in the northwestern part of the sea, at a depth of 142 m, 65% of the biomass of meiobenthos were hydroid polyps, and 24%-foraminifera with soft shells.

It must be remembered that among the Foraminifera, starting from a depth of 70 m, the species of the Allogromiida begin to dominate. This trend continues to a depth of 175-240 m (Revkov, Sergeeva, 2004, Sergeeva *et al.* 2010). Foraminifera with soft shells and hard shells have a maximum number at depths of 150-170 m (Fig. 3) (Sergeeva *et al.* 2010). Other Protozoa possessing protein shells (*Gromia* sp.), are in the northwestern part of the sea in higher numbers in depths up to 130 m, and further *Gromia* abundance is significantly reduced (Sergeeva *et al.* 2012).

In the area of the Bosporus, their maximum number is marked at a depth of 196 m (unpublished data). Ciliophora is found in the Black Sea (Sergeeva *et al.* 2012) at all studied depths from 120 to 2075 m. Thus, changes in the composition of groups of meiobenthos with depth and increased hypoxia, are, above all, responsible for the disappearance of the temporary metazoan meiobenthos, in parallel decline to the number of groups of permanent metazoan meiobenthos, until only Nematoda, Harpacticoida and Annelida remain.

In this section we mention finding metazoans at a depth of 240 m (in the northwestern part of the sea it means – in a true hydrogen sulfide zone), and the presence of ciliates at all depths of the Black Sea. We also mention the endemic Cladocera discovered in the hydrogen sulfide zone at depths of about 2 km, which has been described as a representative of a special family (Sergeeva 2004, Korovchinsky, Sergeeva 2008). This information is given for the completion of the overall picture of the occurrence

of eukaryotes. But other researchers have not found the representatives of the eukaryotes in the anoxic zone of the Black Sea. They also did not even find polychaetes at a depth of 150 m. Therefore, these findings raise some distrust. For further discussion new data is necessary, preferably obtained by independent researchers. In this paper we restrict ourselves to the data obtained mainly in the layers of hypoxic waters.

In April-May 2010, during a cruise on the RV '*Maria S. Merian'*, we studied bottom sediments from 250 to 300 m depths in the Bosporus Strait region in order to search for live fauna in the permanent hydrogen sulfide zone of the Black Sea. Using a light microscope, we observed actively moving protozoans (large ciliates) and metazoans (free-living nematodes). These observations were recorded on video. Since we have already referred to the data on the presence of oxygen in the Bosporus at depths greater than 200 m (Holtappels 2011), the described observation needs further confirmation, specifying the presence of oxygen.

Changes in permanent metazoan meiobenthos with the increasing hypoxia.

Our review will focus on these groups of metazoan permanent meiobenthos, which are abundant in the area of hypoxia and for which data are available for the analysis of changes in the composition and abundance with depth. These are the Nematoda, Harpacticoida and Polychaeta. Of these groups of meiobenthos, nematodes always dominate in numbers, having no less than 70% and this is the only group represented in all the samples.

As will be discussed, in depths near the border of the sulfide zone, the increase of depth indirectly reflects increasing hypoxia. Recall that the sulfide zone is preceded by the suboxic layer, which contains no oxygen or hydrogen sulfide, so that with every meter of depth, the degree of hypoxia is increasing rapidly. Unfortunately, each taken sample of meiobenthos was not accompanied by measurements of oxygen concentration on the surface of the ground, so you have to refer to the rare scraps of hydrochemical data measurements.

Nematoda. In 1994, the maximum number of nematodes in the northwestern part of the Black Sea was at a depth of 134 m (490 000 ind.m^{-2}). Deeper than that, the number decreased and at a depth of 150 m, it was 185600 ind.m^{-2}, at a depth of 172 m, it was equal to 10 200 ind.m^{-2}. In 2007, the nematodes

Fig. 3. Protozoan meiobenthos distribution with depth.

showed a clear peak at a depth of 150–160 m (at 160 m their number was 727 700 ind.m^{-2}). At a depth of 170 m, O_2 and H_2S content was measured, which was $O_2 = 0.07\mu$ M $\cdot$ L^{-1}, and $H_2S = <1\mu$M $\cdot$ L^{-1}.

As for the number of species of nematodes, in 1994, at a depth of 150 m there were 69 species. Some forms were close to inhabiting the shallows. But 38 species and 6 genera were found only in the area of permanent hypoxia. Processing of samples and identification of species is not over yet. According to the data of 2007, the largest number of species was confined to the depths of 120-130 m, but a large enough species richness was recorded at depths of 140-170 m (SERGEEVA *et al*. 2012). Some of the species found at depths of 150 m or more, for example, *Sabatieria pulchra* (SCHNEIDER), also occurred at shallow depths in the hypoxic habitat.

Among the genera, whose species affiliation will be specified are: *Quadricoma* sp., *Cobbionema* sp., *Sabatieria* sp., *Linhomoeus* sp., *Paralinhomoeus* sp., *Theristus* sp., *Theristus* spp., *Monhystera* sp., *Metalinhomoeus* sp., *Aponema* sp., *Microlaimus* sp. and *Campylaimus* sp.

Everything stated in the previous section on the vertical distribution of permanent meiobenthos in the upper centimeters of the sediment holds true for the nematodes. According to SERGEEVA *et al*. (2012), in samples from a depth of 120 m a high percentage of nematodes penetrated into the 3-5 cm layer, but with a further increase in the depth, the nematodes were increasingly confined to the 0-1 cm layer. At depths of 150-160 m nematodes were found only in a layer of 0-1 cm, and at depths of 170-180 m the trend was broken.

Harpacticoida. In a study of meiobenthic crustaceans in shallow habitats where there was a seasonal hypoxia, the differences in the response of different species of Harpacticoida to enhanced hypoxia were shown. Although the abundance of most species declined at acute hypoxia, the number of *Darcythompsonia fairliensis* (T. SCOTT) increased (KOLESNIKOVA *et al*. in press). There was an inverse dependence of the number of *D. fairliensis* on the concentration of oxygen at the surface of the sediments. This species of Harpacticoida was found in different areas of the Crimea, every time-in acute hypoxia (KOLESNIKOVA, SERGEEVA 2011, SERGEEVA *et al*. 2011).

In the deep, permanently hypoxic waters of the Bosporus area, differences in the tolerance of

Harpacticoida to the lack of oxygen were also observed (KOLESNKOVA *et al*. in press). Changes in total number of meiobenthos related to depth in the Bosporus area (according to RV 'Arar') are shown in Fig. 4. The number was gradually reduced until a depth of 200 m, but at a depth of 250 m, it increased markedly. This occurred at the boundary between the hypoxic and anoxic zones, where the largest numbers belonged to Nematoda, and the next most abundant group-Harpacticoida. *Gromia* sp., Ostracoda and the polychaete *V. zaikai* were presented among others.

After a brief presentation of data on the distribution of meiobenthos in the depths, we turn directly to the Harpacticoida, combining data from the two cruises (RV '*Arar'*, in November 2009, and RV '*Maria S. Merian'*, April 2010). This allows us to describe the distribution of Harpacticoida in the depth interval from 75 to 300 m (Fig. 5). The total number of Harpacticoida species found in the surveyed depths in the Bosporus area of the Black Sea was 40.

When we compare the distribution of Harpacticoida with depth from the two cruises,

Fig. 4. The distribution of meiobenthos on a depth transect in the Bosporus area.

Fig. 5. Numbers of Harpacticoida related to depth in the Bosporus area during the two cruises (RV 'Arar', November 2009 - white squares and RV 'Maria S. Merian', April 2010 – black squares; the data without nauplial stages).

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we see that according to the data from the cruise RV 'Arar', the numbers of Harpacticoida quickly dropped from 200 000 ind. m^{-2} at a depth of 75 m to 25 000 ind.m^{-2}, forming a small peak at a depth of 160 m and there were only 520 ind.m^{-2} at a depth of 190 m, but then increased slightly at 250 m according to data from the cruise RV 'Maria S. Merian ', Harpacticoida numbers were much lower at shallow depths (80-117 m) than in the previous cruise. The maximum abundance was observed at a depth of 150-160 m, and a slight increase was observed at a depth of 200 m. Note that in both cruises, at depths of 150-160 m, Harpacticoida numbers showed a marked increase, and at a depth of 250 m, they were about 1000 ind.m^{-2} in November and in April.

The total number of species of Harpacticoida decreased with increasing depth. At depths of 75-100 m we observed from 4 to 27 (usually 7-10) species, at depths of 150-170 m there were 6-12 species, and in the range of 200-250 m-only 1-3 species in the sample. During the cruise RV 'Arar' the greatest number of Harpacticoida (27 species) was recorded at a depth of 82 m, and during the cruise RV 'Maria S. Merian ' the maximum number of species (12) was found at a depth of 152 m.

In April 2009 (RV 'Arar'), at a depth of 75 m, the total numbers of Harpacticoida were 213 700 ind.m^{-2}, dominated by *Ectinosoma melaniceps* BOECK (116 600 ind.m^{-2}). At a depth of 100 m, 11 species were found. Relatively abundant (4000-18 000 ind.m^{-2}) were *Enhydrosoma caeni* RAIBAUT, *E. sarsi* (SCOTT T.) and *Normanella mucronata* SARS G.O., while the numbers of the others were <500 ind.m^{-2}. The species mentioned above were found at depths of 75-82 m. The maximum number of Harpacticoida (27 400 ind.m^{-2}) during the cruise RV 'Maria S. Merian ' was found at a depth of 152 m (it was 8 times lower than the maximum found by RV ' Arar '). The depth of 152 m was dominated by three species: *Haloschizopera pontarchis* POR (10 400 ind.m^{-2}), *Amphiascoides subdebilis* (WILLEY) (5 350 ind.m^{-2}), *Enhydrosoma longifurcatum* SARS (4 930 ind.m^{-2}). For comparison, during the cruise RV 'Merian', *E. longicaudum, Bulbamphiascus imus* (BRADY) and *Mesochra* sp dominated at a depth of 200 m with the total abundance of 34 440 ind.m^{-2}.

Thus, the species composition during the two cruises at similar depths varied considerably. The focus was on species that were found in a large number of samples, and in greater abundance. During both cruises, *Cletodes tenuipes* SCOTT T. was found at almost all the stations in a large range of depths (80 to 250 m), at a density of 1600-1700 ind.m^{-2}. The abundance of species was the highest at 152 m, then it decreased with depth up to 250 m, where *C. tenuipes* had 240 ind.m^{-2}. The discussed species is tolerant to hypoxia, as it occurs at depths greater than 150 m (Fig. 6). However, it is not known what the oxygen conditions were at the stations with less depth. Hypoxia can occur at small and large depths. Therefore, Fig. 6 makes it impossible to characterize the peculiarities of the reaction of *C. tenuipes* to hypoxic and normoxic conditions.

The maximum numbers of the following species were as follows: *H. pontarchis* (10 400 ind.m^{-2}) was recorded at a depth of 152 m, *E. longifurcatum* had a peak population at 159 m (19 000 ind.m^{-2}), and the peak of *B. imus* (24 400 ind.m^{-2}) was at 200 m. At a depth of 172 m all three compared species had a similar abundance (4000-5000 ind.m^{-2}), but at a depth of 250 m, only the first two species were presented with low abundance (400-700 ind.m^{-2}). Fig. 7 shows the data of the cruise RV 'Maria S. Merian'. During the cruise RV 'Arar', *B. imus* species was found only at depths of 75 and 80 m and had a number of 11 000-13 000 ind.m^{-2}. At a depth of 172 m, 8 species of Harpacticoida were found. In addition to the above, there were *Halectinosoma herdmani* (SCOTT T. & A.)*, C. tenuipes*, *Typhlamphiascus confusus* (SCOTT T.)*, Laophonte brevifurca* SARS G.O. and *Amphiascus* sp. These species were previously recorded in the Black Sea only at depths of 50–150 m off the southern coast of the Crimea.

So, Harpacticoida have a low number of species at depths of acute hypoxia, and their number decreases with increasing depth. Species composition changes with increasing hypoxia. At a depth of 250 m, 4 species of Harpacticoida were found, two

Fig. 6. The distribution of *Cletodes tenuipes* with depth.

Fig. 7. The abundance of *H. pontarchis, E. longifurcatum* and B. imus at various depths.

of which had the numbers of 700-1000 ind.m^{-2}. The finding of two species at a depth of 300 m was not considered, because their numbers were low, and they can be considered random. However, it will be interesting to continue the studies at a depth of 300 m. The presence of two species of *Enhydrosoma* at a depth of 250 m and very large numbers of *B. imus* at a depth of 200 m, leads to the conclusion that the conditions at this depth are well suited for certain Harpacticoida, adapted to acute hypoxia and the presence of hydrogen sulfide in the environment.

According to data collected with RV '*Arar*', the concentration of oxygen at even lower depths (90-120 m) was 0.12-0.17 µM O$_2$ • L^{-1} (SERGEEVA *et al.* 2013). During the cruise RV '*Maria S. Merian* ' vertical distribution of oxygen in the study area was different. The anoxic boundary zone was at a depth of about 140-160 m, and normoxic conditions were detected at a depth of 116 m.

Recall that there are significant variations of conditions in the Bosporus area caused by the fluctuation of the lower flow of the Bosporus. This is reflected in the distribution of benthos, as shown, for example, in the shift of the peak position in the settlement of the polychaete *V. zaikai* (ZAIKA, SERGEEVA 2012).

Polychaeta. In the northern part of the sea, at a depth of 150 m, there is the community of meiobenthos, which is called the border community because of its proximity to the anoxic zone. This is the community of polychaete *Vigtorniella zaikai*. This species is always present in the border community of benthos in almost every sample, and forms a peak of abundance (2000-8000 ind. m^{-2}) at a depth of about 150 m (ZAIKA *et al.* 1999, 2008, 2009). Obviously, the species is adapted to the conditions at these depths. The second polychaete species *Protodrilus* sp., apparently, has somewhat different requirements

for environmental conditions, but in general, is distributed in the same transition zone.

In NW Black Sea, the samples of *V. zaikai* have been collected three times already, which makes it possible to compare. The peak numbers found in 2010 were similar to these observed in February and March 2007 (2600 ind.m^{-2}) (ZAIKA *et al.* 2009). Perhaps this value is typical for the seasonal minimum abundance of *V. zaikai*, which in 2010 lasted until May. Furthermore, this low level of maximum numbers of species in other areas was not observed. But, according to available data, with the onset of summer the maximum abundance of the species in the area rises to 7900-8000 ind. m^{-2} which is observed in July 1994 and in May-June 2007.

The minimum number of *V. zaikai* observed at a depth of 120 m, rises to a maximum at a depth of 130 and 144 m (4060 and 4500 ind.m^{-2}, respectively). Values of this species in the depth range 148-163 m are also quite high. In general, the greatest development of *V. zaikai* in Ukrainian waters in April-May is observed at depths of 130-163 m, although the number may be small at some stations of this depth interval, which may be due to differences in micro-habitats.

The distribution of *Protodrilus* sp. is evident of its affinity to the specified depth range, but the numbers of species are much lower than *V. zaikai*. The peak of the quantitative development of *Protodrilus* sp. is found at depth of 148 m, and at this depth, its population exceeds that of *V. zaikai*. A comparison of the quantitative parameters of both species suggests a difference in their environmental requirements. However, there may be local or temporal features of the structure of the border zone. The distribution of these species in the depth range of acute oxygen deficiency, points to the possibility of using them to indicate the boundaries of the hydrogen sulfide zone.

Comparison of the data in the northern half of the sea showed that the numbers of *V. zaikai* were: 2500-8000 ind.m^{-2} at the site in the northwestern part of the sea, 4500 ind.m^{-2} at the Crimean site, and 11400-17100 ind.m^{-2} at the Kerch site. Therefore, the maximum numbers of *V. zaikai* were recorded in May and June 2007 in the Kerch area (ZAIKA *et al.* 2009).

In the southern part of the sea, the distribution of *V. zaikai* was twice investigated in the Bosporus area. During the cruise of the RV '*Arar*' (November 2009) the species was first discovered at a depth of 250 m. In the other investigated depths (75-122, 160 and 190 m) this polychaete species was absent.

Perhaps this was due to the small amount of material studied. At a depth of 250 m, a live gastropod was also found, so that depth is accepted as a local boundary between the hypoxic and anoxic waters and the macrobenthos border (Sergeeva et al. 2011). The total numbers of *V. zaikai* at a depth of 250 m were 7280 ind.m^{-2}, and the polychaete penetrated into the sediment deeper than in the northern part of the sea. 25% of the individuals were found in the layers of 1-2 cm, while a small number of the polychaetes was even found in the layers of 5-7 cm.

During the cruise of the '*Maria S. Merian*' in May 2010, the two border polychaete species were found in a wide range of depths (*V. zaikai*-at depths of 134-250 m, *Protodrilus* sp. at 116-159 m) (Fig.8).

We draw attention to three aspects in the results from 2010: 1-the large width of the belt where *V. zaikai* was registered; 2 – confirmation of the presence of this species at a depth of 250 m; 3 – identification of "core populations" with the highest abundance of V. *zaikai* at depths of 150-159 m, and of *Protodrilus* sp. at a depth of 134 m. The term "core population", in relation to the bottom belt populations of the Black Sea, was introduced by Zaika et al. (2008), similar to the "core community" (Kiseleva 1981).

The broad band habitat of *V. zaikai* in 2010, compared with that in 2009, when the species was found only at a depth of 250 m, indicates the unstable conditions in the Bosporus area. In 2009, the number of *V. zaikai* at a depth of 250 m was 7300 ind.m^{-2}, which was close to the maximum observed in the same area in 2010 (7200-7800 ind.m^{-2}). In the northwestern part of the sea in 1994 and 2007, the maximum numbers (averaged) were also equal to 7900-8000 ind.m^{-2}. Note that the population in 2009 consisted primarily of individuals with 3-4 segments,

and the largest polychaetes were with only 5-6 segments. In 2010, the population was also dominated by individuals with 3-5 segments, and the polychaetes rarely had 7-8 segments. Consequently, the population was represented mainly by newly settled juveniles, which, according to our laboratory observations periodically popped up above the ground. Polychaete juveniles even penetrated the upper centimeters of sediment, and apparently were able to migrate, if necessary. Changing the position of the bottom flows of the Marmara seawater enriched with oxygen, made the structure of the hypoxic benthic habitat variable.

Comparing the data obtained on the two species of polychaetes, *V. zaikai* and *Protodrilus* sp., in the northern and southern parts of the Black Sea, we can conclude that the upper limit of occurrence of both species was always kept at a depth of 116-134, usually 120-130 m (with one exception). The lower boundary of each species was sometimes recorded in a narrow depth interval of 151-163 m, and sometimes at a depth of 170-190 m, and in the Bosporus area-even at 250 m. In the graphs, the maximum numbers of the two species during different surveys rarely coincide, but in general, the peaks of the numbers are in the same range of depths. During one of the cruises in the Bosporus area, the peaks of the numbers were at the same depth as those at the northern coast, while during the other cruise the peak was at the lower limit of occurrence of the species *V. zaikai*, at a depth of 250 m, and *Protodrilus* sp. was not detected. Of the two polychaete species, *V. zaikai* was

Fig. 8. The distribution of the polychaete species related to depth in the Bosporus area: 1 - *V. zaikai*, 2 - *Protodrilus* sp. (in Zaika, Sergeeva 2012).

Fig. 9. Position of the boundary zone occupied by the meiobenthos community and dominated by *V. zaikai* (in Zaika, Sergeeva 2012)

usually more abundant and was found close to water containing hydrogen sulfide.

The obtained data on border polychaete species allows us to offer an indicative map of a position of the border zone occupied by the meiobenthos community and dominated by *V. zaikai* (Fig. 9). In the scale of the map, the hydrogen sulfide zone starts just behind the border zone of the meiobenthos community.

Conclusion

When comparing the information on the distribution of metazoan meiobenthos, we drew attention to the relatively poorly presented materials on nematodes compared to Harpacticoida and some polychaetes. This is explained by the fact that the list of species of nematodes from different depths collected during the past cruises is not yet complete. The Harpacticoida example shows that species differences in the meiobenthos and their response to hypoxia are the most important. Therefore, the completion of the work on the nematodes, the most abundant group of metazoan meiobenthos, will reveal interesting details of their distribution in the gradient of hypoxia observed with the increase in depth in the Black Sea.

Currently, more than 40 forms of nematodes belonging to one order Desmoscolecida were detected at depths of 120-240 m. The maximum size of the group of nematodes was at a depth of 120-130 m (Kosheleva 2012). The permanent hypoxic zone of the Black Sea is an interesting research polygon. We can compare the spatial gradients of hypoxia when moving from the water column into the sediments and when moving on the sediment surface in the area of permanent hypoxia in the Black Sea. Usually the redox potential at the sediment surface changes rapidly, making it difficult to assess the degree of hypoxia which meiofauna can tolerate.

In the Black Sea, in the area of permanent hypoxia, at depth changes we detect much distended redoxcline along the bottom surface. Therefore, it is crucial to measure the oxygen content at each point of the sampling, in order to establish the conditions of hypoxia characteristic for each species.

Data received on polychaetes and Harpacticoida show that to only define tolerance of species to varying degrees of hypoxia-is a one-sided approach. There are species of meiobenthos, which not only can tolerate hypoxia, but also prefer the conditions of acute hypoxia.

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