

Distribution and community structure of benthic ciliates in the North-Eastern part of the Black Sea

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Summary

Diversity and distribution of free-living benthic ciliates were studied at eight localities at the north-eastern (Caucasian) coast of the Black Sea, at the depths from 0 to 432 m. The highest diversity was revealed in the heterogeneous sublittoral sands at 3-10 m depths, the lowest one, at exposed littoral beaches with well-sorted coarse sands and in the silty sediments deeper than 25 m. No ciliates were found in the hydrosulphuric zone (below 100 m). With increasing depth, raptorial feeders became relatively more diverse, while the proportion of down-stream filter feeders decreased. On the basis of species composition, several communities were distinguished corresponding to depth range and sediment properties. Point diversity of ciliates (defined as number of species per sample) depends mainly on local habitat conditions (depth and sediment properties), under similar conditions its variations between regions are insignificant. Local diversity (total number of species found at a site) depends strongly on sampling effort and is potentially comparable with that of larger areas.

Key words: ciliata, benthos, Black Sea, diversity, distribution, community structure, depth, sediments

Introduction

Studies of ciliates at the Black Sea began in the end of the 19th century (Merezhkovsky, 1880; Andrussova, 1886; Perejaslawzewa, 1886). Despite a long history of protozoological research, the sea was investigated rather unequally. During the 20th century, the main

efforts were concentrated on Romanian and Bulgarian coasts, as well as the Crimea (Lepsi, 1926a, 1926b; Jeliaskova-Paspalewa, 1933; Valkanov, 1934, 1935, 1936, 1954; Tucolesco, 1961; Kovaleva and Golemansky, 1979; Djurtubaeva and Mohammed, 1995; Azovsky and Mazei, 2003b). North-eastern part of the sea has never been investigated until the beginning of the 21st

century. Recently we have published some data concerning the composition of ciliate fauna of this region (Azovsky, 2002; Azovsky and Mazei, 2003a, 2003b). In this article, we describe the distribution patterns of ciliate diversity and community structure in relation to depth, sediments and geographical location.

Material and Methods

The study was carried out in August-September, 2000-01 at the shelf zone on the north-eastern (Caucasian) coast of the Black Sea (three hundred kilometers along the coastline, Fig. 1). Totally, 45 samples were obtained at eight localities (Table 1), at the depths from 0 to 432 m. The sediment varied from coarse sands with gravel and shell debris at littoral and uppermost sublittoral zone to silts and mud from 20-25 m and deeper.

Down to 10-12 m the sediments were sampled by SCUBA diving, deeper, by box corer "Ocean-0.1" on low winch speed to prevent the washing out of the boundary layer. Samples were taken by handle piston corer (2 cm² in cross-section). Ciliates were extracted by modified Uhlig method (Burkovsky, 1978). Samples of silty and muddy sediments were additionally diluted with filtered sea water, decanted and visually examined, a small quantity at a time. For ciliate identification, we used vital staining by neutral red or fixation by OsO₄ or glutaric aldehyde and then staining by Chatton-Lwoff silver nitrate, methyl green-pyronin or Perc-Silva crystal-violet techniques (Foissner, 1991). For taxonomic details see Azovsky and Mazei, 2003a, 2003b. At six points from the Blue Bay, the abundance of ciliates

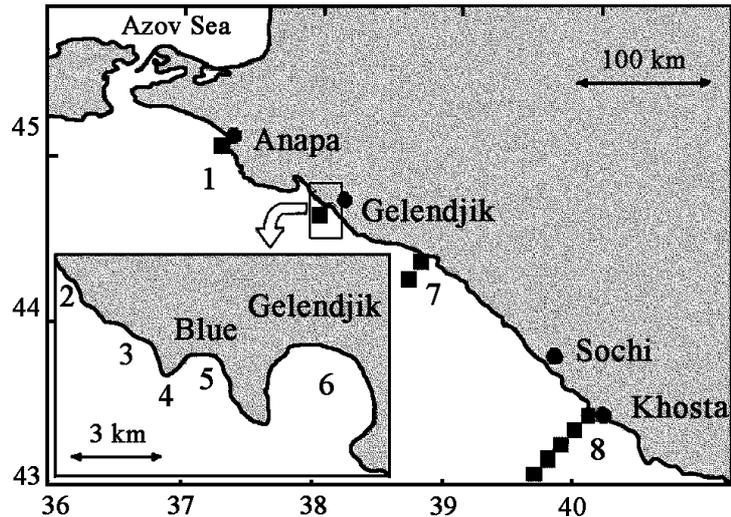


Fig. 1. Map of the area studied. Squares with numbers mark sampling sites (enumerated according to Table 1).

was assessed quantitatively by the vision fields method. In other samples, abundance of species was estimated qualitatively using three categories: rare (1-3 individuals per a sample part examined), common (4-8 individuals) or abundant (more than 8 individuals).

Trophic strategies were distinguished after Fenchel (1986) and Verni and Gualtieri (1997). The main strategies of phagocytosis characteristic of psammophilous ciliates are: "upstream filter feeding", "downstream filter feeding" and "raptorial feeding". Upstream filter feeders (orders Heterotrichida, Oligotrichida and some Hypotrichida, e.g. *Aspidisca*) cannot concentrate the finest food fraction (less than 1-2 µm); downstream filter feeders (order Scuticociliatida and most Hypotrichida) can consume relatively fine particles (on the

Table 1. Location, number of samples, water depths and ciliate diversity of sampling sites.

N	Locality / Site	Number of samples (2000/01 years)	Range of depths studied, m	Number of species found	
				Total	Per sample (mean ±SE)
1	Anapa	2 / 0	1-3	23	15.5 ± 2.5
2	Divnomorsk	0 / 4	7-20	44	16.5 ± 3.2
3	Pine Canyon	0 / 2	10	26	16.7 ± 2.9
4	Sunny Cape	3 / 0	3-4.5	37	15.3 ± 8.5
5	Blue Bay	8 / 8	0-9	105	18.2 ± 3.1
6	Gelendjik Bay	2 / 0	3-5	47	29.5 ± 3.5
7	Inal Bay	2 / 7	7-41	77	15.4 ± 4.4
8	Khosta	0 / 7	10-432	37	15.3 ± 5.0

average, 0.3 μm). "Raptorial feeders" (ord. Hymenostomatida and all Kinetofragminophora species except *Kentrophoros*) capture food with the help of various structures for active hunting (extrusomes, rhabdos apparatus). The main food objects of "raptorial feeders" are rather large (algae, flagellates, ciliates) and are captured individually.

Between samples similarity in species composition was estimated by Jaccard index of similarity: $S_j = a / (a + b + c)$, where a is the number of species found in both samples; b and c , the number of species found in one of the two samples only. To classify samples by species composition, hierarchical cluster-analysis was performed using Ward's linkage method (Wilkinson, 1996).

Results

DISTRIBUTION BETWEEN LOCALITIES

Altogether 168 species of ciliates were found, and 35 of them turned out to be new records for the sea (Azovsky and Mazei, 2003a, 2003b).

Various locations differed noticeably in respect of their total species richness (Table 1). The highest diversity (105 species, almost two thirds of the whole species list) was observed in the Blue Bay, where more samples (16) were taken than in any other region. Relatively diverse ciliofauna occurred also in the Inal and Gelendjik bays, while only 26 species were found at the Pine Canyon. The mean number of species per sample (point diversity), however, was much more constant for most of the regions studied (at average 15-18 species, Table 1). Only two samples from the Gelendjik Bay were characterized by higher richness (26 and 33 species).

The total species richness of a region is obviously correlated with the number of samples taken there. To take into account the effect of unequal sampling, we consider the relation between the number of species found, S_N , and number of samples (N). To do this, the mean species numbers were calculated for repeated draws of N samples chosen randomly from the total dataset of 42 nonempty samples using the rarefaction procedure. The cumulative species number as a function of sampling effort (Fig. 2) follows well the power relation $S_N = 23.66 N^{0.55}$ ($R^2 = 0.974$). In other words, the expected richness increases approximately as the square root of the number of samples. The curve does not flatten out, so the species list obtained should be

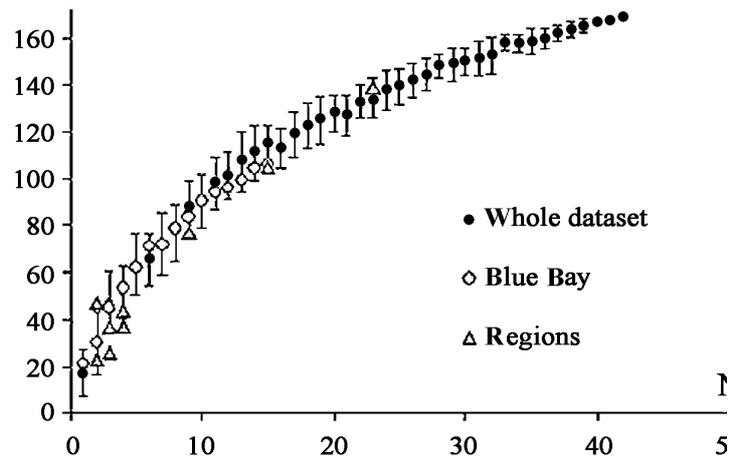


Fig. 2. Mean number of species (S) found at N samples. Filled circles: random draws from all 44 samples. Open circles: random draws from 16 Blue Bay samples. Triangles show the total richness for each site.

considered as far from complete, and each new sample should yield new species.

The local diversity data for various localities (shown as triangles in Fig. 2) fit well the rarefaction curve, and individual deviations do not exceed the confidence bounds. Thus, the between-site differences in local diversity observed are mainly determined by unequal sampling efforts. Moreover, the second curve is plotted separately for the samples taken from the Blue Bay. There is only a slight difference between the curves (the approximation for this dataset is $S_N = 21.95 N^{0.60}$ ($R^2 = 0.988$)), so potential richness of this small (kilometer-wide) bay seems to be comparable with the richness of the whole region.

To sum up, different localities did not differ significantly by their average point diversity, whereas their summarized local diversity was the function of sampling effort.

DISTRIBUTION ALONG THE DEPTH GRADIENT

Species diversity was related to depth and sediment properties (Fig. 3a). The lowest diversity and density was noted both at the inshore zone of exposed beaches with well-sorted coarse sands and in the silts deeper than 25 m. Ciliates from coarse sands were represented by meso- and eurytopic species. Sediments of this type are typical for surf zones of the littoral and upper sublittoral (down to the depth of wave breakdown, 2-3 meters), as well as zones with intensive hydrodynamics. Small eurytopic ciliates, covered with hard testae (*Coleps*, *Spathidiopsis*) or possessing pellicular skeletal structures (*Pleuronema*, *Uronema*, *Cyclidium*, *Euplotes*, *Aspidisca*)

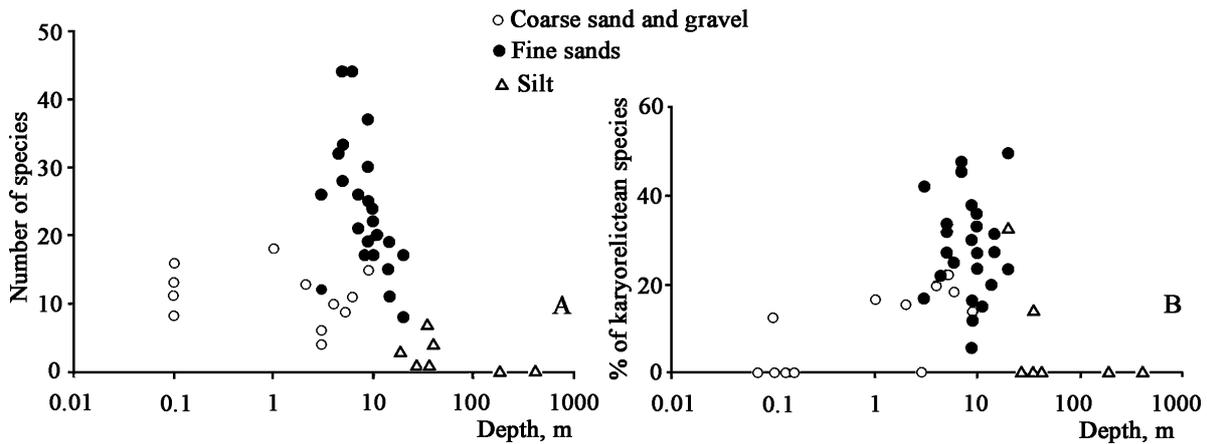


Fig. 3. Species number per sample (A) and percentage of Karyorelictida species (B) in relation to depth and type of sediments.

dominated in these biotopes. Such species as *Didinium nasutum*, *Euplotes trisulcatus* and *Frontonia leucas* were found almost exclusively in these shallow habitats.

The highest diversity (25-35 species per sample) and abundance (1.5-3.8 million ind/cm³) were revealed in heterogeneous sublittoral sands below the wave breakdown zone, at depths ranging from 3 to 9 meters. Micro- and euryportal ciliates predominated there, followed by mesoporal ones. Some typically psammophilous ciliates from the genera *Trachelocerca*, *Tracheloraphis*, *Remanella*, *Loxophyllum* are mainly restricted in their distribution by this range of depths. These specific forms constituted a significant part of communities there (Fig. 3b), together with the genera *Holosticha*, *Trachelostyla*, *Lacrymaria*, *Kentrophoros*, *Strombidium*, *Uronema* and *Enchelyodon*.

With increasing depth, both abundance and diversity of ciliates dropped drastically, in parallel with changes in sediment properties (increase in silt fraction). In the samples from 10-14 m, diversity decreased down to 15-20 species per sample. Nonspecific euryportal ciliates (*Holosticha*, *Trachelostyla*, *Lacrymaria*, *Enchelyodon*) predominated, whereas psammophilous ciliates became much less abundant.

Below 25 m, only a few individuals of non-specific eurytopic forms, such as *Enchelyodon* spp., *Lacrymaria coronata*, *L. acuta*, *Kentrophoros tubiformis* *Strombidium elegans*, *Euplotes* sp., *Condylostoma psammophila*, *Cyclidium veliferum*, *Chilodontopsis numerosus* occurred, with average diversity as low as 4-6 species per sample. No ciliates were found below the depth of 100 meters, at the hydrosulphuric zone.

The changes in diversity along the depth gradient are summarized in Fig. 4. The depth ranges were chosen so as to equalize the sampling efforts (5-7 samples each). Both total and local (per sample) species numbers reached their maximums at the depths between 4 and 7 m. The ratio between total and point richness was also

highest at these depths, indicating a high spatial variability in species composition from site to site.

Trophic structure of the community also changed distinctly with the depth. In the littoral zone, the species of all three feeding strategies were equally represented (Fig. 5), in sublittoral samples, the raptorial feeders became relatively more diverse while the proportion of down-stream filter feeders decreased with depth. Ciliates occurring deeper than 20 m were mainly raptorial feeding forms.

Analysis of 6 quantitative samples from the Blue Bay generally confirmed the results obtained from the presence/absence data. The highest species richness and abundance of ciliates were revealed there at a depth of 5 m, followed by a depth of 9 m. The littoral community is characterized by the lowest values of these parameters (Fig. 6a). The same pattern is also observed in the trophic structure of the community. Ciliates of all three feeding strategies were equally abundant in the littoral zone, while the raptorial feeders predominated deeper (Fig. 6b).

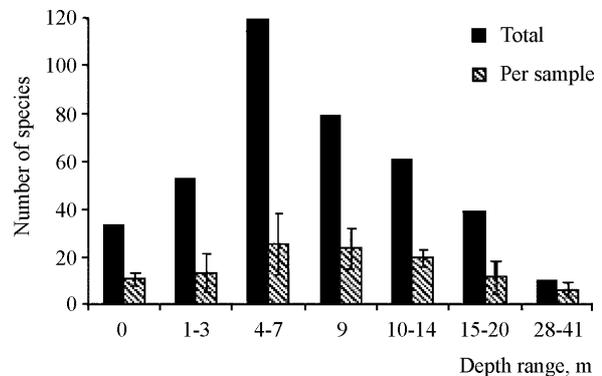


Fig. 4. Species diversity (total and mean per sample) at different depths.

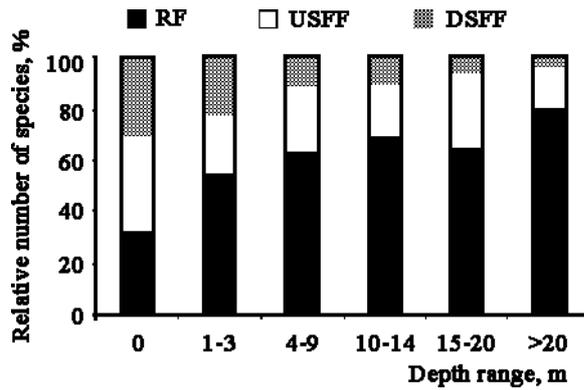


Fig. 5. Proportion of species with different feeding strategies at different depths. RF - raptorial feeders, USFF - upstream filter feeders, DSFF - downstream filter feeders.

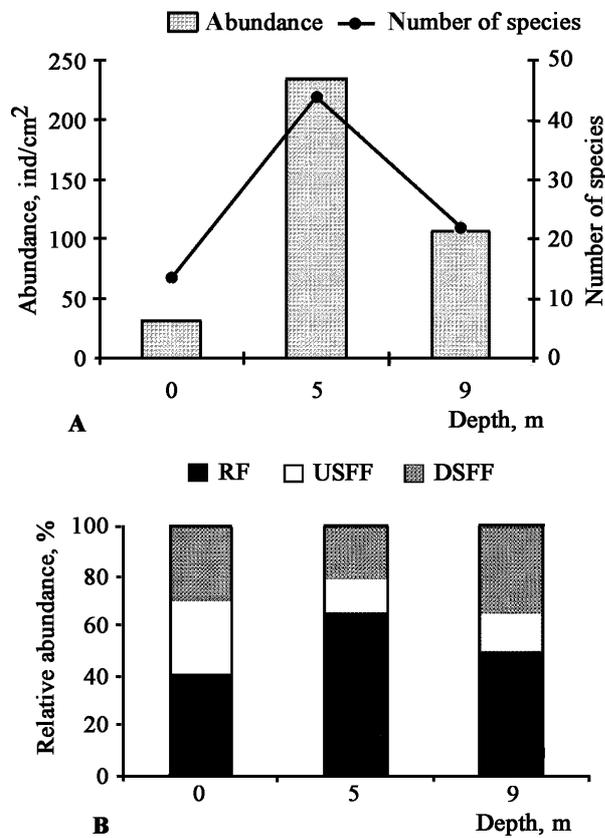


Fig. 6. Quantitative data from the Blue Bay. A - abundance and diversity; B - trophic structure at different depths.

CLASSIFICATION OF COMMUNITIES

Hierarchical cluster-analysis was performed to classify the samples by species composition. Since many species were rare (33% of species were found only once, and about half of species, in one or two samples), this bulk of rare species could blur the general picture.

Therefore, only 114 species that were marked as mass or common ones at least once were chosen for further comparison. Using this subset of species, the matrices of pair-wise similarities between samples were calculated and then used for the classification procedure. The resulting dendrogram is shown in Fig. 7. There was no obvious regularity in aggregation of samples, either according to their location or to the year of sampling. At the same time, samples from similar depth tended to combine together by their species composition.

Three large groups could be obviously distinguished at the dendrogram, designated as I, II and III. Group I mainly consists of shallow-water samples, while group III includes the deepest samples. Group II is broader and more heterogeneous, and could be further subdivided into four sub-groups also confined to definite depth ranges: IIc includes most of littoral and uppermost sublittoral samples, while IIa, the samples from 10-15 m. Subgroups IIb and II d include samples from 3-11 m and are similar in this respect with group I. However, they clearly diverge by sediment properties: all samples of gr. I were taken from habitats with poorly sorted, heterogeneous sands with shall fragments, while subgroups IIb and II d represent well-sorted fine sands.

Thus, samples of every group represent a separate type of community characteristic of a definite habitat. Dominant species and habitat properties of these communities are presented in Table 2. It can be seen that groups I, II a and II b+d have many species in common and represent in fact the variants of the same community, differing in the proportion of psammophilous and non-specific eurytopic forms, whereas the deep-water community (III) is an extremely depleted derivative of shallower fauna.

Discussion

Species diversity and composition of benthic ciliates were found to depend clearly on depth and sediment properties (mean particle size and degree of sorting), that were, in their turn, closely interrelated and characterized the hydrodynamic regime of the habitat. Several community types, with some local variations, could be distinguished according to compositional differences: community of littoral zone, sublittoral communities with fine sand and heterogeneous medium-grained sand, and deep-water community of silts and mud.

It should be noted that the beaches investigated are high-energy exposed, with unstable coarse sands at the surf zone (mean particle size 1-2 mm). Only rather poor fauna of eurybiotic forms survives in these habitats. It is only in the sublittoral below the wave breakdown zone (3-10 m), in better sheltered habitats with stable sediments that ciliates, especially specific interstitial

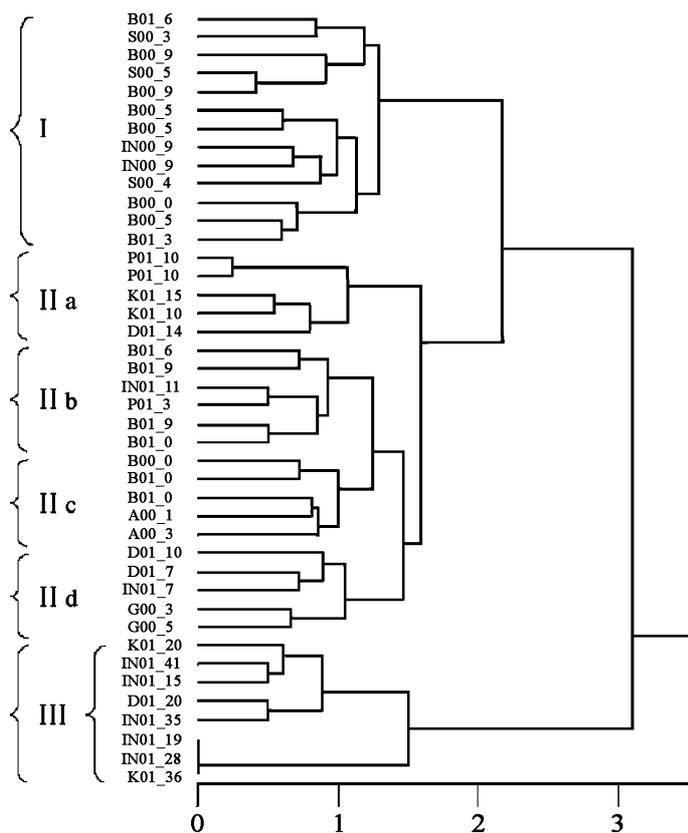


Fig. 7. Classification of samples by their species composition. Abbreviations: sites are designated by letters (A - Anapa, D - Divnomorsk, P - Pine Canyon, S - Sunny Cape, B - Blue Bay, G - Gelendjik Bay, IN - Inal Bay, K - Khosta), following letters indicate the year of sampling (00 or 01) and depth. Braces with Roman figures indicate groups of samples (community types).

forms, find the optimal conditions and reach their highest abundance and diversity. Still deeper, in compacted flocculent sediments, abundance and diversity of ciliates decrease again. The highest diversity of ciliofauna in fine heterogeneous sands in comparison with both coarse sands and silts was also reported earlier for the Black Sea (Kovaleva, 1966; Detcheva, 1983; Djurtubaeva and Mokhammed, 1995), as well as for the White Sea (Burkovsky, 1978, 1984) and the Caspian Sea (Agamaliyev, 1983). Such distribution agrees in general with other data on sediment preferences of ciliates (Burkovsky, 1984; Patterson et al., 1989).

The decrease in ciliate diversity with depth is also well-known, though it is much less investigated than distribution by sediments. As Fig. 4 shows, the fauna becomes not only generally poorer with depth, but also less spatially variable (the difference between total and point diversity smoothes out). According to Agamaliyev's (1983) data on the Caspian ciliates, the total number of species falls down twofold at 10 m, fourfold at 20 m, and tenfold at 40 m. Our results are in very good

agreement with these figures. At the same time, in some investigations ciliates were discovered down to a depth of several km, though at very low species numbers and abundances (Uhlig, 1973; Hausmann et al., 2002). In our study, however, no ciliates were found deeper than 100 meters, the border of the hydrosulphuric zone in the Black Sea. The absence of ciliates at these depths may be caused by anoxic conditions, although the small number of samples does not allow us to state this fact with certainty.

However, the pattern revealed is contrasting with the common opinion about the highest ciliate diversity of littoral beaches, usually considered as a typical biotope for the interstitial fauna (McLachlan, 1983; Fenchel, 1986; Patterson et al., 1989). Moreover, the sublittoral fauna is usually treated as a depleted derivative of the littoral one (Burkovsky, 1984). Our data show that this is only the case for sheltered, relatively stable sandy beaches, which have been most often studied at the Romanian and Bulgarian coasts of the Black Sea. We have earlier observed a similar picture at the Barents Sea, where the ciliofauna of exposed littoral zone was impoverished due to storms and ice action, and the peak of diversity shifted to the less disturbed habitats of the upper sublittoral zone (Azovsky, 1996). A similar pattern was observed in distribution of diatom algae of this region: the highest abundance and diversity of microphytobenthos also occurred at the depths between 4 and 8 m at the Black Sea north-eastern coast (Sapozhnikov, 2002) or even deeper, at 11-20 m, in the Crimea (Revkov and Nevrova, 2003).

Point diversity of ciliates (defined as number of species per sample) depends mainly on local habitat conditions (such as depth and sediment properties); under similar conditions, the diversity variations between regions are insignificant (Table 1). The local diversity (total number of species found at a site) is high and potentially comparable with that of larger areas (provided the sampling effort is sufficient, Fig. 2). Thus, geographic variations in local diversity are the function of sampling effort, so any suggestions about regional distribution of ciliates should be made with great care, at least before the data on species composition are incomplete (Patterson et al., 1989; Azovsky and Mazei, 2003 b).

ACKNOWLEDGEMENTS

This research was supported by the Russian Foundation for Basic Research (grant № 03-04-48018).

Table 2. Characteristics of communities (species assemblages) distinguished as a result of cluster-analysis.

Notation (see Fig. 7)	Depth range, m	Sediments	Diversity, species per sample	Dominating and common species
I	3-9	Heterogeneous, coarse and median-grained sands with shell debris	19.4	<i>Mesodinium pulex</i> , <i>Uronema marina</i> , <i>Remanella margaritifera</i> , <i>Trachelocerca incaudata</i> , <i>Tracheloraphis phoenicopterus</i> , <i>Strombidium sulcatum</i> , <i>Trachelostyla caudata</i> , <i>Prorodon marinus</i>
II a	10-15	Heterogeneous, silty sands with shell debris	18.6	<i>Enchelyodon</i> sp., <i>Holostycha diademata</i> , <i>Holostycha fasciola</i> , <i>Trachelostyla pediculiforme</i> , <i>Lacrymaria coronata</i> , <i>Lacrymaria versatilis</i> , <i>Trachelonema minima</i> , <i>Trachelocerca minuta</i> , <i>Trachelocerca incaudata</i> , <i>Trachelocerca</i> sp., <i>Prorodon morgani</i> , <i>Strombidium cinctum</i>
II b+d	3-11	Well-sorted fine and median-grained sands	24.0	<i>Enchelyodon</i> spp., <i>Remanella margaritifera</i> , <i>R. granulosa</i> , <i>Lacrymaria coronata</i> , <i>Cyclidium veliferum</i> , <i>Trachelocerca incaudata</i> , <i>Tracheloraphis phoenicopterus</i> , <i>Holostycha diademata</i> , <i>Trachelostyla pediculiforme</i> , <i>Chilodontopsis numerosus</i> , <i>Kentrophoros tubiformis</i>
II c	0-3	Unstable, well-sorted coarse sand	12.4	<i>Cyclidium veliferum</i> , <i>C. glaucoma</i> , <i>Mesodinium pulex</i> , <i>Didinium nasutum</i> , <i>Pleuronema coronata</i> , <i>Strombidium cinctum</i> , <i>Frontonia leucas</i> , <i>Uronema marina</i>
III	15-41	Silt, mud	6.5	<i>Enchelyodon</i> sp., <i>Lacrymaria coronata</i> , <i>Kentrophoros tubiformis</i>

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Editorial responsibility: Sergei Fokin