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Vertical structure of the interstitial ciliate community in the Chernaya River estuary (the White Sea)

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Summary

Vertical structure of the interstitial ciliate community in the Chernaya River estuary (the White Sea) was investigated. Distinct change of the species structure of the ciliate community in the sediment column is observed at all stations in the estuary along the salinity gradient. There are three species groups, which prefer certain horizons of the sediment: 1) eurytopic species, not specific for the interstitial, occupying top horizons of the sediment; 2) basic structure-forming species represented by specific interstitial ciliates in the marine part of the estuary. They occupy subsurface layers and develop down to the border of the H_2S zone; 3) microaerophilous and anaerobic organisms, occupying the deepest layers of the sediment. A decrease in biomass, abundance, species richness and diversity of ciliate community with depth is detected. A sharp vertical Eh-gradient in the freshened zone of the estuary results in concentration of different ciliate species within the limits of small layers and, as a result, in sharp vertical differentiation of the community. Moreover, in the freshened zone most of abundance and biomass of ciliates (more than 70 %) is concentrated in the top 0.5 cm layer of the sediment. More gradual changes of the Eh-gradient and its higher absolute value in the marine zone determine deeper penetration of many species into the sediment and, as a consequence, a smaller differentiation of the community.

Key words: interstitial ciliates, vertical distribution, community structure

Introduction

In all benthic habitats the concentration gradients of free oxygen, hydrogen sulphide and Eh are distinctly expressed, which is reflected in organization of benthic communities (Fenchel and Riedl, 1970; Finlay, 1980; Fenchel and Finlay, 1990a, 1995).

Many ciliates develop in limited ranges of Eh level and concentration of free oxygen. Some species are obligate anaerobes (Fenchel et al., 1977; Finlay et al., 1986; Fenchel and Finlay, 1990b, 1991, 1995; Guhl et al., 1994). A greater number of species are micro-aerophiles, living at low O_2 concentration (Fenchel and Finlay, 1989; Fenchel et al., 1989; Guhl et al., 1994; Fenchel and Bernard, 1996). Finally, an overwhelming majority of species requires high O_2 levels (Fenchel and Bernard, 1996). These exacting requirements to an oxygen mode are expressed in concentration of species in certain vertical layers according to the content of free oxygen (Fenchel et al., 1990, 1995; Setala, 1991; Zubkov et al., 1992). This is provided for by appropriate behavioral features (Finlay, 1981, 1982; Fenchel and Finlay, 1986; Bernard and Fenchel, 1994; Fenchel and Bernard, 1996).

Three vertical zones in marine benthic sediments can be distinguished: oxidizing, reduced and sulfide (Fenchel and Jansson, 1966; Fenchel, 1971). Aerobes live in superficial layers, microaerophiles, a little deeper, anaerobes are found in the lowest horizons of deposits (Fenchel and Jansson, 1966; Burkovsky, 1968, 1987; Fenchel, 1969, 1971; Santangelo and Lucchesi, 1995; Berninger and Epstein, 1995). However, this vertical differentiation can be expressed more clearly or less clearly. Vertical spatial niches of aerobes, microaerofiles and anaerobes often overlap considerably. Furthermore, there are species, which are poorly limited in the vertical distribution (Hartwig et al., 1977). Moreover, the patterns observed are further complicated by trophic interactions (Fenchel, 1969; Burkovsky, 1992; Guhl and Finlay, 1993; Berninger and Epstein, 1995), daily changes in temperature and competitive interactions (Burkovsky et al., 1983), daily changes in light exposure (Agamaliev and Bagirov, 1975), the number of oxygenated micro-niches formed by burrowing animals (Fenchel, 1996a, 1996b), and competition with metazoans (Patterson et al., 1989).

The analysis of the main patterns of vertical community structure in different biotopes is a very important issue. Communities developing along a gradient of the environmental factors can serve as convenient models, allowing the comparison of structures under conditions of trended change of a limited number of factors. The change of species, trophic and temporal community structure along the salinity gradient in the Chernaya River estuary has been shown earlier (Burkovsky and Mazei, 2001; Mazei et al., 2001; Mazei and Burkovsky, 2002). The aim of the present study is to reveal patterns of vertical community structure of interstitial ciliates in the estuary.

Material and methods

Investigations were conducted in the summer of 2000 in the Chernaya River estuary (the Kandalaksha Bay, the White Sea). Material was collected at 5 permanent stations. The stations were located on the middle horizon of the intertidal zone along the estuary (Fig. 1). A detailed hydrological and hydrochemical characteristic of the stations was given in the previous article (Burkovsky and Mazei, 2001).

Each station was a strictly fixed sampling area 50 x 50 cm, where recordings of the ciliate abundance were performed. Extraction and quantitative counting of ciliates were performed on live individuals (Carey, 1991). With the purpose of the analysis of ciliates' vertical distribution, sediment columns (1 cm^2 in square, 3 cm high) were divided into 4 layers (sub-samples): 0-0.5 cm, 0.5-1 cm, 1-2 cm, 2-3 cm. Altogether 5 columns of sediments were taken at the each station. A random sampling corresponding to 1/15 of the total sample (i.e., 1/3 statistically average square centimeter) was examined. The ciliates were

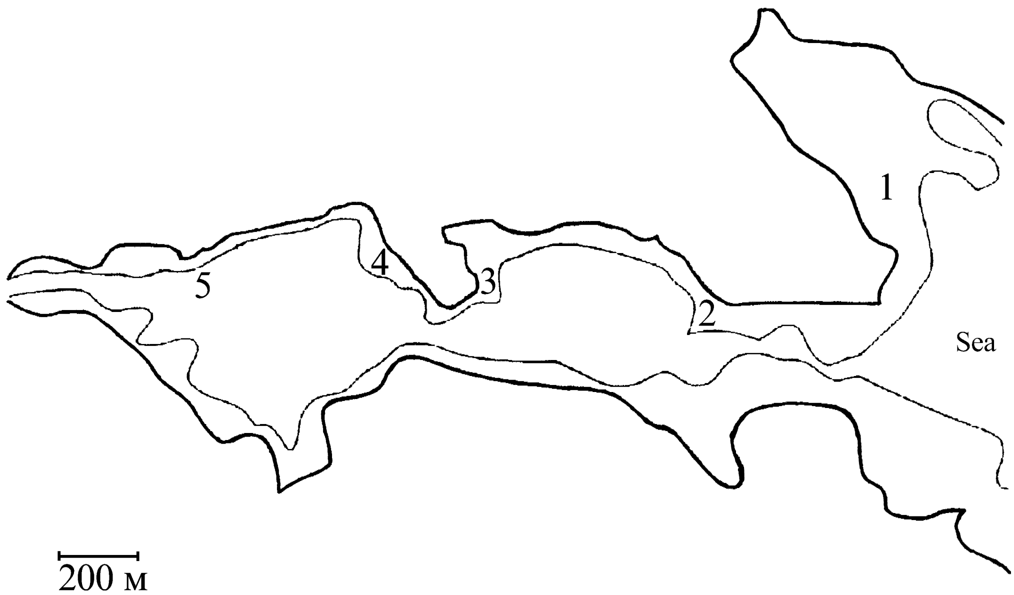

Fig. 1. A scheme of location of stations 1-5 in the estuary. Thick line - coastline, thin line - zero of depth.

identified on the Shatton-Lwoff silver-impregnated preparations (Foissner, 1991), according to Carey (1991).

To characterize the structural features of the ciliate communities at different stations, total abundance, biomass, average size of the organisms, species richness, Shannon diversity index and Shannon evenness index according to the biomass were calculated. For a generalized characterization of the vertical structure of ciliate community, Czekanovsky similarity index between all pairs of subsamples was measured. In addition, Czekanovsky similarity index between all species pairs according to their vertical distribution was calculated. To distinguish species groups with similar vertical distribution cluster analysis by complete linkage method on the basis of a matrix of Czekanovsky similarity indexes was performed. For estimation of patterns of vertical structure the successive cluster analysis by complete linkage method on the basis of Pianka similarity indexes was executed.

Calculations were performed with the help of ECOS and STATISTICA software packages.

Results

Vertical changes in species composition of the ciliate community

The patterns of vertical distribution of the ciliates' relative abundance in the sediments at different stations

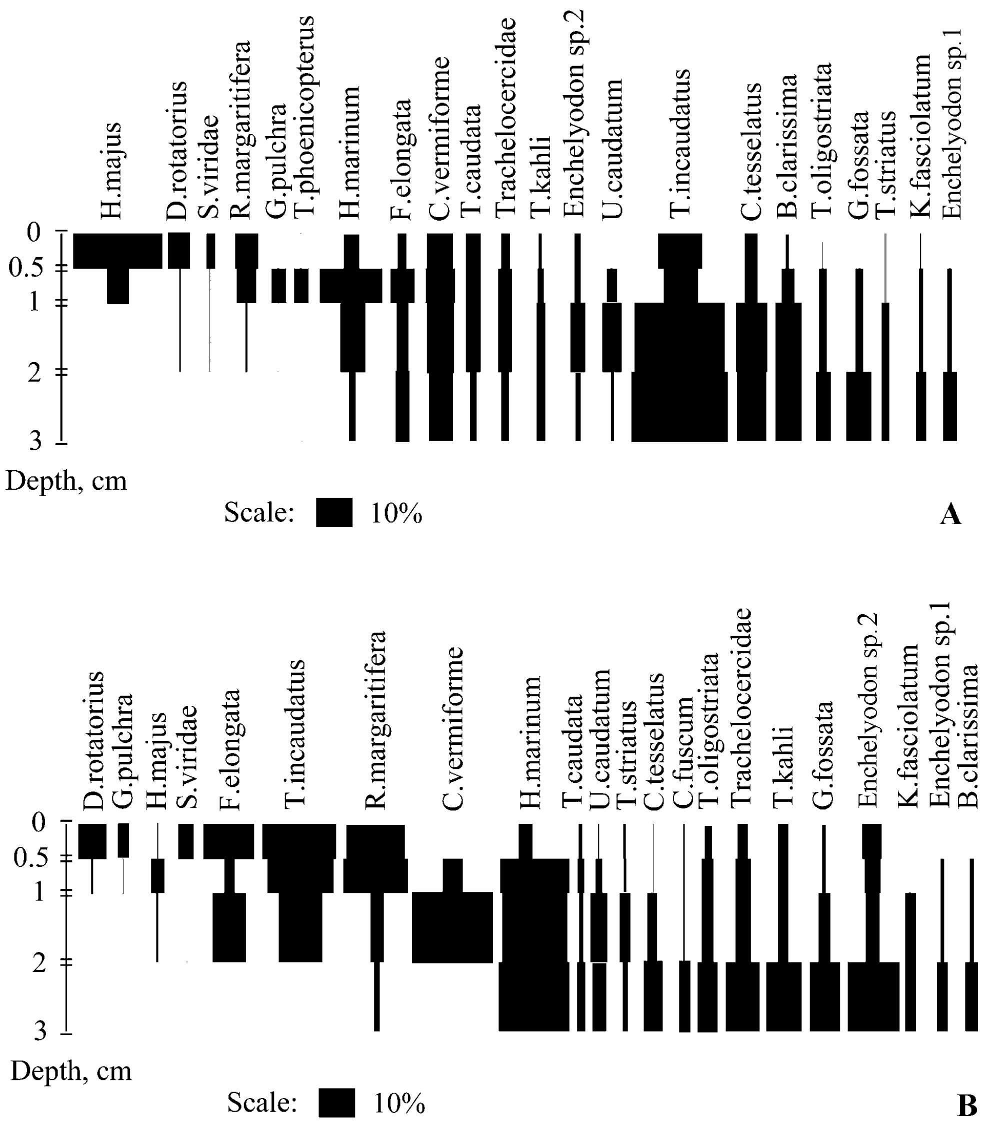

Fig. 2. Vertical distribution of the dominant ciliate species. A - station 1, B - station 2.

are shown in Fig. 2. In addition, vertical Eh-profiles in the sediments at each station are presented in Fig. 3. A clear zonality of species community structure affected by reduction-oxidation properties of the environment is marked. The results of the cluster analysis (Fig. 4) indicate the presence of species groups, which prefer certain horizons of the sediment.

There are 5 species groups distinguished at station 1. The first and the second groups include oxyphilic species inhabiting the superficial 0-1 cm layer of the sediment (*Histiobalantium majus*, *Strombidium viridae*, *Discocephalus rotatorius* - in the 0-0.5 cm layer; *Remanella margaritifera*, *Tracheloraphis phoenicopterus*, *Gastrostyla pulchra* - in the 0.5-1 cm layer). The third group comprises species, developing within the whole sediment column. (*Histiobalantium marinum*, *Frontonia elongata*, *Urostrongylum caudatum*, *Tracheloraphis kahli*, *Enchelyodon* sp.2, *Trachelostyla caudata*, *Cardiostomatella vermiforme*, as well as small trachelocercids). The forth and the fifth groups include species from the deepest horizons of the sediment (*Tracheloraphis incaudatus*, *T. striatus*, *Coleps tesselatus*, *Blepharisma clarissima* - in the 1-3 cm layer; *Geleia fossata*, *Kentrophoros fasciolatum*, *Trachelonema oligostriata*, *Enchelyodon* sp.1, different oxytrichids - in the 2-3 cm layer).

At station 2 five groups are also distinguished. The first and the second groups consist of organisms of the top layers of the sediment (*S. viridae*, *D. rotatorius*, *G. pulchra*, *F. elongata* - in the layer 0-0.5 cm; *R. margaritifera*, *T. incaudatus*, *H. majus* - in the layer 0-1 cm). The third group includes species with broad

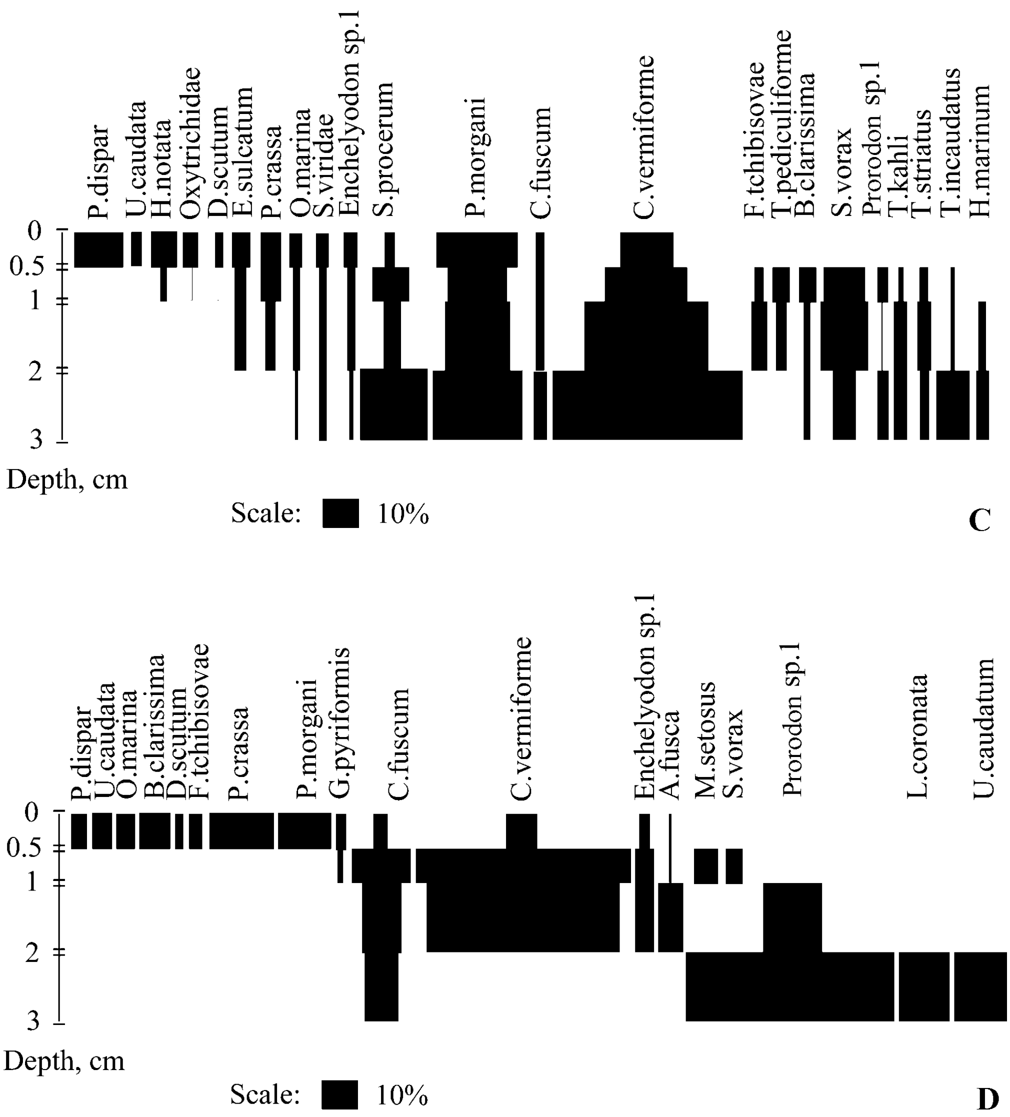

Fig. 2. Vertical distribution of the dominant ciliate species. C - station 3, D - station 4.

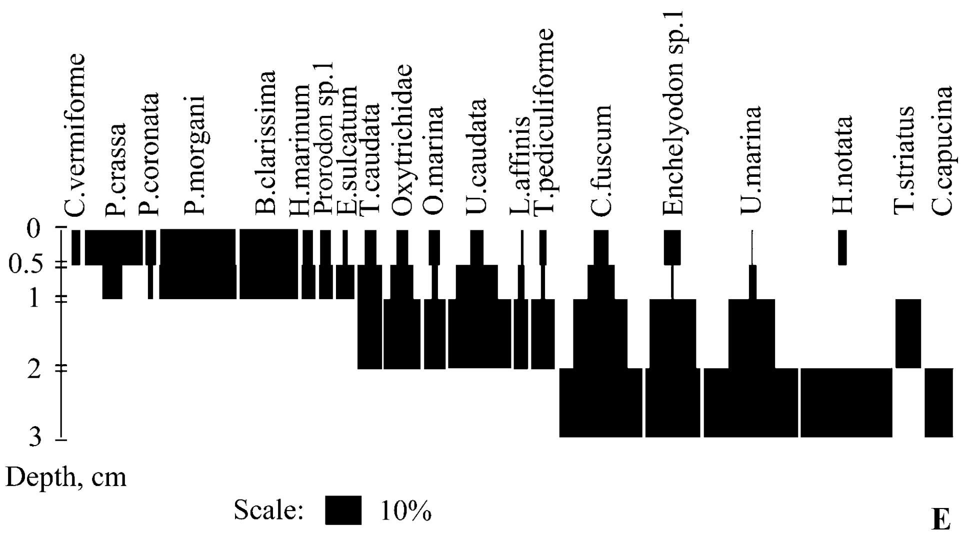

Fig. 2. Vertical distribution of the dominant ciliate species. E - station 5.

distribution within the sediment (*T. caudata*, *H. marinum*, *T. oligostriata*, *T. kahli*, *C. tesselatus*, Trachelocercidae). The two last groups comprise organisms from the deepest layers (*T. striatus*, *U. caudatum*, *K. fasciolatum*, *C. vermiforme* - in the layer 1-3 cm; *Enchelyodon* sp.1, *Enchelyodon* sp.2, *G. fossata*, *Cyclidium fuscum*, *B. clarissima* - in the layer 2-3 cm).

The community at station 3 is differentiated into four groups. The first and the second ones consist of organisms inhabiting the top layer (*Urosoma caudata*, *Paraurostyla dispar*, *Helicostoma notata*, *Diophrys scutum*, small oxytrichids - in the layer 0-0.5 cm; *Pleuronema crassa*, *Enchelyodon sulcatum*, *S. viridae*, *Enchelyodon* sp.1 - in the layer 0-1 cm). The third group is composed of ciliates living in the middle and deep layers of the sediment (0.5-3 cm) (*Trachelostyla pediculiforme*, *Sonderia vorax*, *Frontonia tchibisovae*, *Prorodon* sp., *B. clarissima*). The fourth group comprises

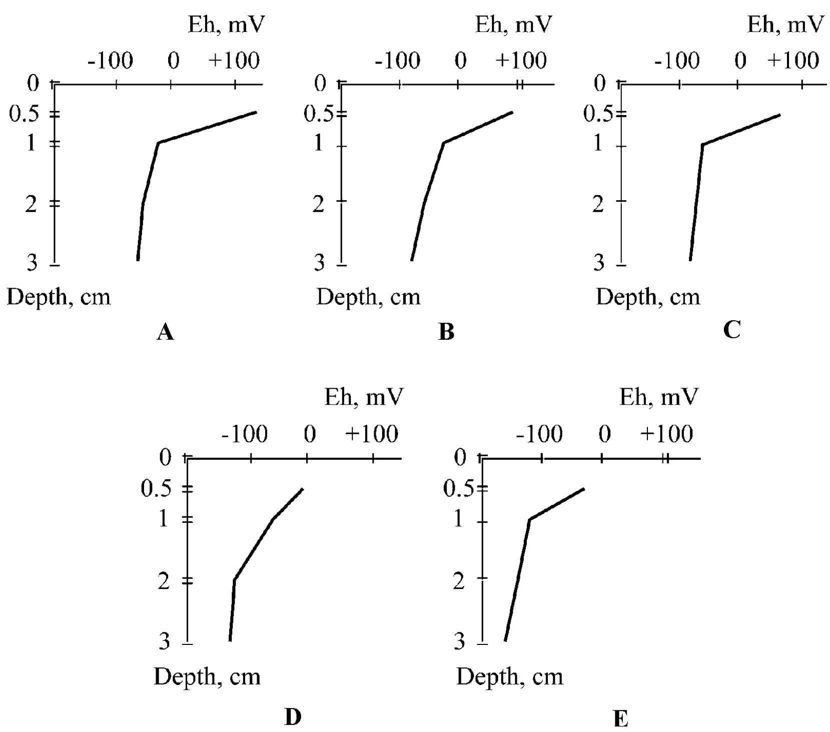

Fig. 3. Vertical Eh-profile in the sediment. A - station 1, B - station 2, C - station 3, D - station 4, E - station 5.

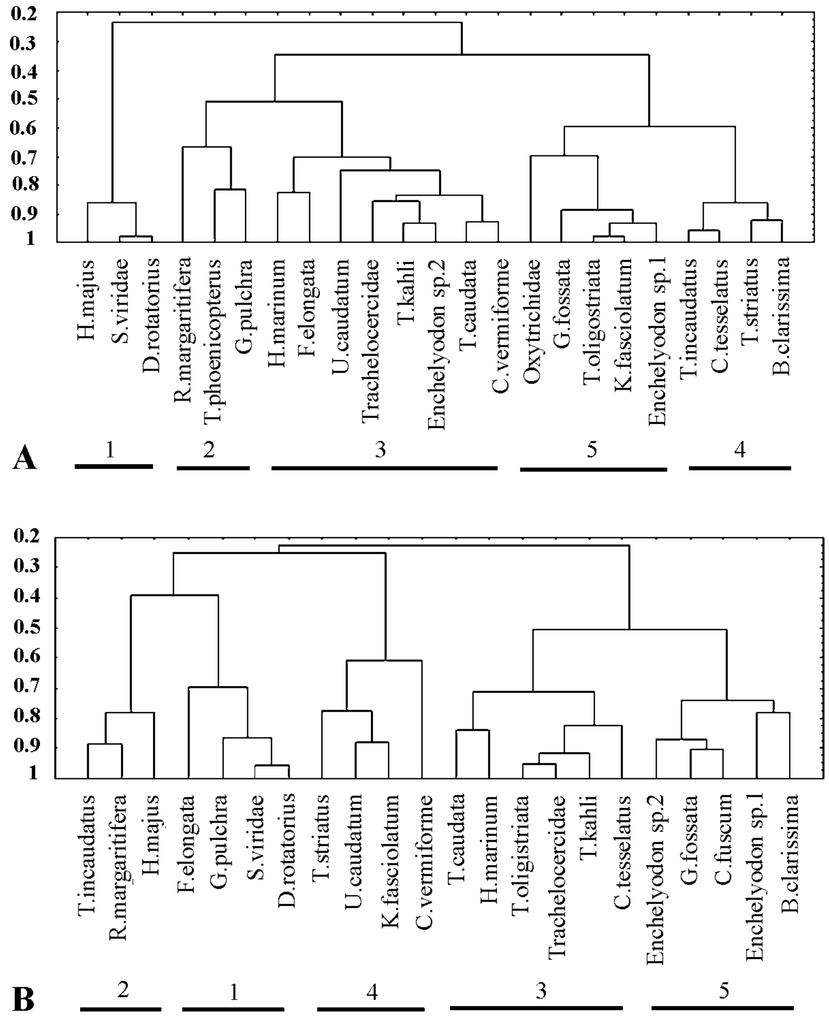

Fig. 4. Results of cluster-analysis of the species based on vertical species distribution similarity. A - station 1, B - station 2.

species living only in the lowermost horizon (1-3 cm) (*C. tesselatus*, *T. incaudatus*, *T. striatus*, *T. kahli*, *H. marinum*, various trachelocercids) or species that occur within the whole column but are the most abundant in the deepest layers (*Prorodon morgani*, *C. vermiforme*, *Spathidium procerum*, *C. fuscum*).

There are five groups developing at station 4. The first group includes ciliates of the top layer (*P. morgani*, *P. dispar*, *Oxytricha marina*, *P. crassa*, *F. tchibisovae*, *D. scutum*, *U. caudata*, *B. clarissima* - in the layer 0-0.5 cm; *Glaucoma pyriformis* - in the layer 0-1 cm). The second group consists of two species (*S. vorax*, *Metopus setosus*), occurring in the layer 0.5-1 cm. The third group (*C. vermiforme*, *C. fuscum*, *Enchelyodon* sp.1) comprises organisms, which are widely distributed in the whole column (0-2 cm), but are most abundant in the middle layers (1-2 cm). The fourth and the fifth groups include ciliates from the lowest layers (*Aspidisca fusca* - 1-2 cm; *Lacrymaria coronata*, *U. caudatum*, *Prorodon* sp. - 2-3 cm).

There are five groups occurring at station 5. The first and the second groups consist of species occupying the top horizon (*C. vermiforme* - 0-0.5 cm; *P. crassa*, *P. coronata*, *E. sulcatum*, *Prorodon* sp., *H. marinum*, *P. morgani*, *B. clarissima* - 0-1 cm). The third group (*T. caudata*, *U. caudata*, Oxytrichidae, *T. pediculiforme*, *O. marina*, *L. affinis*) is widely represented in the 0-2 cm layer. The fourth and the fifth groups consist of ciliates, which live in the bottom horizons (*T. striatus* - 1-2 cm; *H. notata*, *Caenomorpha capucina* - 2-3 cm; *C. fuscum*, *Uronema marina*, *Enchelyodon* sp.1 - species occurring within the whole column but the most abundant in the 1-3 cm layer).

Thus, a distinct change of the species structure of the ciliate community in the sediment column is observed at all stations. The distribution of some species

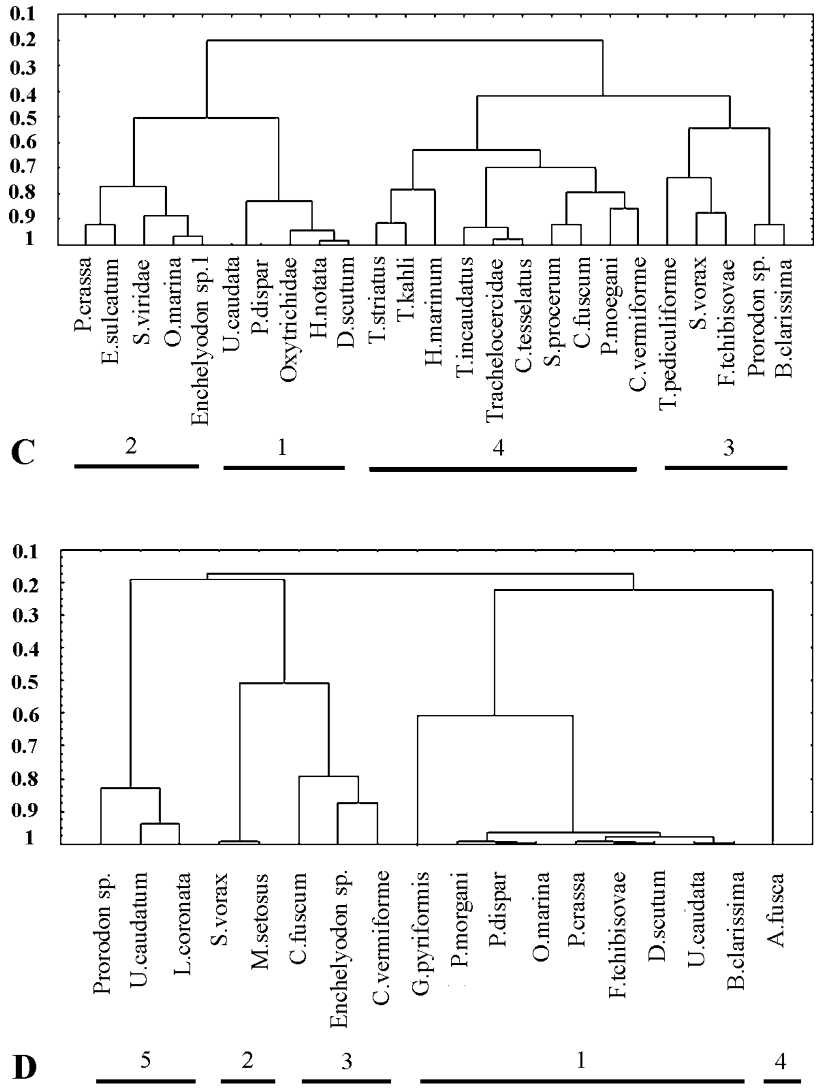

Fig. 4. Results of cluster-analysis of the species based on vertical species distribution similarity. C - station 3, D - station 4.

is limited to the top 1 cm layer of the sediment. They are *D. rotatorius*, *G. pulchra*, *H. majus*, *D. scutum*, *S. viridae*, *R. margaritifera* in the marine part of the estuary and *G. pyriformis*, *P. crassa*, *U. caudata* in the desalinated zone. Other species live predominantly in the deepest horizons in anaerobic conditions. They are *K. fasciolatum*, *G. fossata*, *T. striatus*, *C. tesselatus* in the marine part of the estuary and *S. vorax*, *M. setosus*, *C. capucina* in desalinated zone. Moreover, there are ciliates that are abundant in the whole column of the sediment, though they may exhibit preferences to some horizons. They are *F. elongata*, *T. incaudatus*, *T. kahli*, *T. oligostriata*, and small trachelocercids in the marine part of the estuary, and *C. vermiforme*, *H. marinum*, *U. marina*, *C. fuscum*, *T. caudata*, *T. pediculiforme* living all along the estuary. The latter ciliates seem to be the most tolerant to the changes in both reduction-oxidation and salinity conditions (Burkovsky and Mazei, 2001; Mazei et al., 2002).

However, preferences to certain horizons of the sediment can considerably change in some species at different stations. For example, *B. clarissima* prefers to occupy the bottom layers of the sediment in the marine zone of the estuary (stations 1-3), but inhabits top horizons in the desalinated zone (stations 4-5). Some other ciliate species (*E. sulcatum*, *F. tchibisovae*, *Prorodon* sp., *P. morgani*) penetrate less deep into the sediment in the desalinated zone. In marine stations (station 1 for *E. sulcatum* and *F. tchibisovae*, station 3 for *Prorodon* sp. and *P. morgani*) these ciliates are found

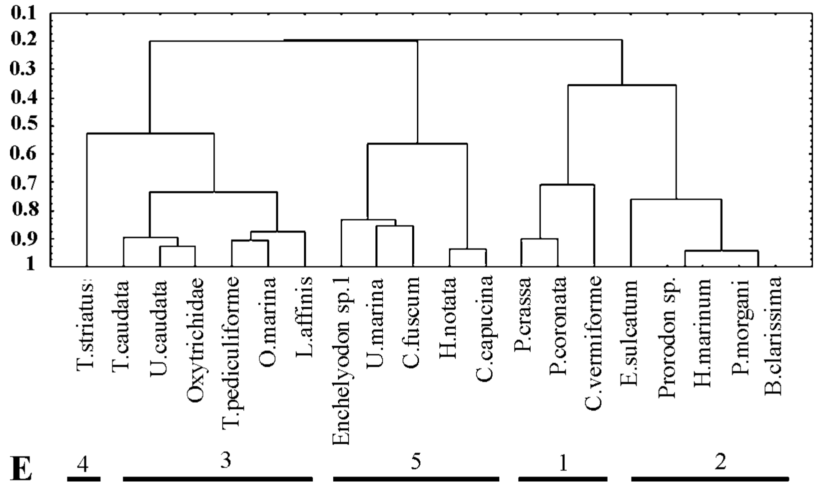

Fig. 4. Results of cluster-analysis of the species based on vertical species distribution similarity. E - station 5.

in the whole column of the sediment. On the contrary, they are distributed only within the top 1 cm layer at the brackish water stations. The cause of such distinctions may be a sharper gradient of redox-potential at stations 4 and 5, which considerably limits the opportunity of ciliates' penetration in the deeper layers of the sediment.

Vertical changes in the integral community characteristics

The vertical changes of the ciliate community structure are expressed not only in a change in the species composition, but also in modification of the integral community characteristics (Fig. 5). Biomass and abundance of ciliates decrease with depth. Moreover, the penetration of ciliates into the sediment at stations 4 and 5 is insignificant. The abundance and biomass are mostly (more than 70 %) concentrated in the top 0.5 cm layer of the sediment. A decrease in species richness is also observed. It is due to the fact that in each local community (at one station) the number of species that can survive strongly reduced conditions (facultative and obligate anaerobes) is always much less than that of oxyphilic forms. Shannon's diversity and evenness indices of species structure, demonstrating rather high absolute values, poorly depend on the horizon where the community is formed. However, a considerable decrease of species diversity with the depth is detected at stations 4 and 5. It indicates that the community at any depth is formed by several dominants, less numerous species also showing some level of abundance. Only in the freshened part of the estuary (stations 4 and 5), with the sharpest gradient and low absolute Eh levels (see Fig. 3), a very small number of species resistant to lack of oxygen develops in deep layers.

Vertical changes of the size structure of the ciliate community are also observed. In the marine zone of the estuary (stations 1-3) the upper 1 cm layer is inhabited by minute organisms, components of both the psammon and the bottom plankton. In the deeper layers specific interstitial species (predominantly, Trachelocercidae) develop. On the contrary, the mean size of ciliates does not change with the depth at station 4. It is due to the fact that large species are concentrated in different layers (*P. morgani* in the upper layer, *C. vermiforme* in the middle layer, and *Prorodon* sp. in the deepest layer). Finally, very small species inhabit the deepest layer at station 5 (*C. fuscum*, *U. marina*, *Enchelyodon* sp.1). They appear to be are the most tolerant species to reduced conditions.

Vertical structure of the ciliate community

As shown above, vertical changes of the community species structure are characteristic of all stations in the estuary. However, the degree of changes and the integral characteristics of the vertical structure differ within the estuary.

In Table 1 the average value of the Czekanovskii similarity indices between all the pairs of structural

Table 1. Mean Czekanovsky similarity indexes between structural variants of ciliate community in different horizons of the deposit (A) and between all species pairs in terms of their vertical distribution (B).

Indexes of similarity:	Stations 1	2	3	4	5
A	0,56	0,46	0,57	0,25	0,32
Standard deviation	0,12	0,14	0,14	0,25	0,23
B	0,43	0,37	0,40	0,54	0,61
Standard deviation	0,27	0,30	0,28	0,41	0,34

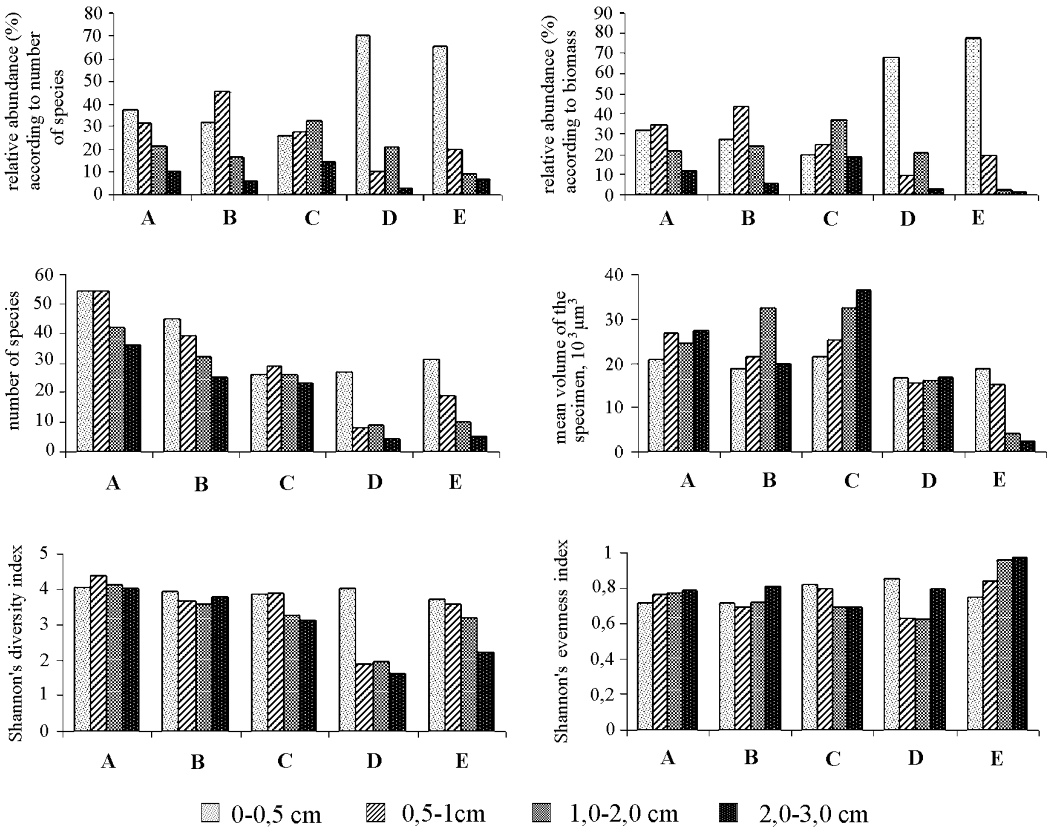

Fig. 5. Vertical changes of the integral community characteristics. Abbreviations: A - station 1, B - station 2, C - station 3, D - station 4, E - station 5.

variants of community at different depths in the sediment are presented. The minimal values of parameters in the freshened part of the estuary (stations 4 and 5) show that there are significant differences in species structure between the horizons. These differences appear to be caused by a sharper gradient and low Eh values, resulting in more significant vertical divergence of the species. The result of this vertical differentiation is the presence of groups of species with rather similar distribution within the sediment. The data in Table 1 testify to a greater species connectivity in the freshened part of the estuary. A sharp gradient of Eh at stations 4 and 5 results in concentration of different ciliate species within the limits of small layers (which is reflected in high values of similarity indices between species) and, thus, in sharp vertical differentiation of the community. More gradual changes of the Eh-gradient and its higher absolute value at stations 1-3 promote deeper penetration of many species into the sediment, and, as a consequence, lesser differentiation of community.

Dendrograms of the successive cluster analysis reflecting features of vertical differentiation of the community at different stations are given in Fig. 6. From the comparison of Fig. 2 and Fig. 6 it is clear that in each case the intensity of changes between layers is caused by the change in abundance of concrete species or species complexes and is associated both with the features of the Eh gradient and with the specificity of the species structure at different stations. The maximal changes in community structure at stations 1 and 3 occur in the top layers of the sediment (between the layers 0-0.5 and 0.5-1 cm), the changes in deeper layers being not so significant. This is associated with the replace-ment of the complex of non-specific eurytope species, formed in the top layer, by a complex of specific interstitial ciliates. On the contrary, at station 2 the changes are maximal in the deepest layer, the top layers differing from each other not so considerably, which is associated with the occurrence in deep layers of a complex of microaerophile and anaerobe ciliates. At station 4 the most constant structure is observed at a depth of 0.5-2cm, inhabited by large ciliates contributing most to the biomass and abundance of the community. In the superficial layer occupied by eurytopic species, and in the deepest horizon, where

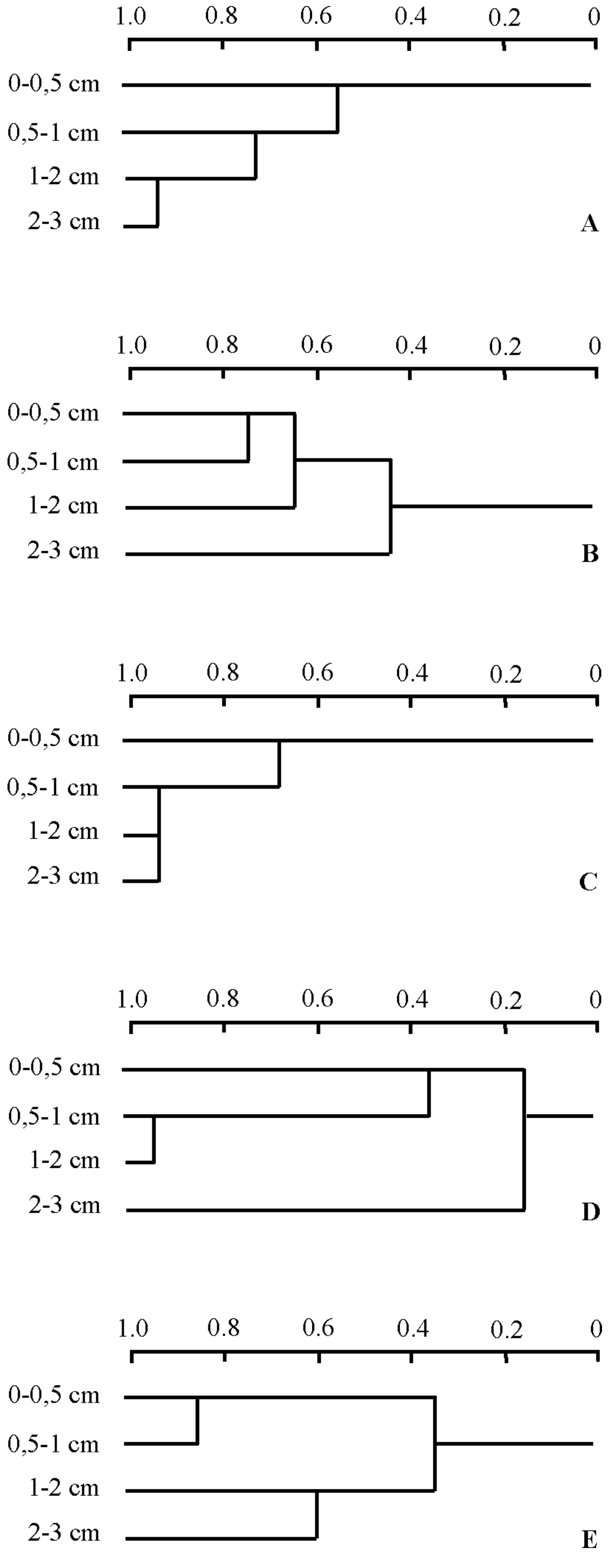

Fig. 6. Results of the successive cluster-analysis of the community structure at different horizons. A - station 1, B - station 2, C - station 3, D - station 4, E - station 5.

anaerobes develop, the structure differs considerably. At station 5, the «superficial» (0-1 cm) variant of community represented by oxyphilic ciliates sharply differs from the «bottom» (1-3 cm) one consisting exclusively of anaerobes.

The data obtained indicate that the ciliate community at each station in the estuary is a vertically differentiated structure consisting of three species complexes: 1) eurytope species, non-specific for the interstitial, occupying top horizons of the sediment; 2) basic structure-forming species represented by specific interstitial ciliates in the marine part of the estuary. They occupy subsurface layers and develop down to the border of the H_2S zone; 3) microaerophilic and anaerobe organisms, occupying the deepest layers of the sediment.

Species structure of these complexes, the degree of differences between them and the depth of penetration in the sediment depend both on the features of vertical changes in reduction-oxidation conditions and on the salinity regime at different stations.

Discussion

The results of our research show that:

1. At all stations in the estuary vertical zonality of the ciliate community in the sediment is noted. It is expressed in the change of species composition and structure and the community structure. The groups of species inhabiting the top, the bottom and the intermediate layers of the sediment are distinguished. Towards the deepest layers of the sediment total biomass, abundance, species richness and diversity decrease.

2. A significant proportion of the ciliates living in all horizons of the sediment is also found along the whole estuary; these species appear to be the most resistant both to reduction-oxidation conditions and to salinity.

3. Species composition of ciliates and intensity of distinctions between the layers of the sediment, as well as the depth of penetration of ciliates into the sediment, depend both on salinity and on reduction-oxidation conditions formed at different stations in the estuary.

4. In the freshened part of the estuary the sharpest vertical Eh gradient is observed. As a result, abundance, biomass and species richness are mostly concentrated in the top 0.5 cm layer of the sediment. Besides, under such conditions a sharp vertical differentiation of the community is observed, expressed in the concentration of different ciliate species within the limits of small layers. In the marine part of the estuary gradual changes in the Eh-profile and the low values of reduction-oxidation potential promote deeper penetration of

many species into the deposit and gradual changes of the vertical structure of the community.

5. In each community it is possible to distinguish three species groups, more or less differentiated vertically: complexes of eurytopic, structure forming (specific interstitial) and anaerobic ciliates.

The changes in ciliate species composition, as well as a sharp decrease in abundance and species diversity with depth in the sediments is noted practically for all psammophilous ciliate communities investigated in the White Sea (Burkovsky, 1968, 1984, 1987, 1992), the Caspian Sea (Agamaliev, 1970, 1983), the Baltic Sea (Fenchel and Jansson, 1966; Fenchel, 1969), the Black Sea (Petran, 1968; Djurtubaev, 1977) and the Northern Sea (Hartwig, 1973; Berninger and Epstein, 1995).

Vertical distribution of the dominant ciliates differs in different seas. For instance, the data of the present and earlier investigations (Burkovsky, 1984, 1987, 1992) carried out in the Chernaya River estuary indicate that the maximal depth of ciliate penetration into fine and medium-grained sand is 6 cm. Maximum abundance of *Diophrys scutum*, *Discocephalus rotatorius*, *Strombidium sulcatum*, *S. viridae, Gastrostyla pulchra*, *Mesodinium pulex* is registered in the uppermost layer (0-0.5 cm). Ciliates from the genera *Tracheloraphis*, *Remanella*, *Histiobalantium*, *Trachelostyla*, *Pleuronema* are abundant in the layer 0-3 cm, whereas *Kentrophoros*, *Sonderia*, *Urostrongilum*, *Geleia*, *Metopus*, *Caenomorpha*, in the layer 1-4 cm. Besides, there are species distributed throughout the sediment column: *Uronema marina*, *Cyclidium fuscum*, *Coleps tesselatus*, *Cardiostomatella vermiforme*.

In the Caspian Sea the same species penetrate deeper into the sediment. In some areas maximal development of the ciliates is observed in the layers 0-6 cm, the ciliates penetrating into the sediment down to 18-20 cm (Agamaliev, 1983). *Diophrys scutum* and *Remanella rugosa* are most numerous in the top layers of sand, but even in medium-grained sand they can penetrate down to a depth of 3 cm. Moreover, *Tracheloraphis incau-datus*, *Trachelonema oligostriata*, *Pleuronema coronata* are found down to a depth of 8-12 cm in medium- and coarse-grained sands.

In fine sand of the Black Sea ciliates penetrate into the sediment down to a depth of 6-8 cm (Petran, 1968; Dzhurtubaev, 1977). The distribution of many species in the sediment is similar to that in the White Sea. For example, *Diophrys* scutum is maximally abundant in the top 1 cm. At the same time, *Pleuronema coronata* and *Mesodinium pulex* dominate at a depth of 5-6 cm, i.e., much deeper than in the White and Caspian seas.

In the tidal flat of the Northern Sea vertical zonality of psammophilous ciliate community (Berninger and Epstein, 1995) has also been noted. In superficial layers of the sediment the fauna of epibenthic ciliates develops. The richest population represented by specific interstitial species is formed at 1 cm depth in reduction conditions. Most species forming the community are microaerophilic forms, a little number of true anaerobes being present.

In brackish-water biotopes of the Baltic Sea (Fenchel and Jansson, 1966) the maximal depth of ciliate penetration into the sediment is 8 cm. The species common with the White Sea dominate in the same layers of the sediment: *Diophrys scutum* dominates in the top 2 cm layer, *Sonderia vorax* is found down to a depth of 8 cm, *Coleps tesselatus* is found throughout the sediment column. Comparison of vertical structure of different community variants formed within the area of about 1 m^2 shows that species diversity, depth of penetration into the sediment and vertical differentiation of the community depend on sharpness of the vertical gradient and the absolute value of Eh-potential. In micro-biotopes with negative value of Eh-potential in superficial layers the minimal depth of ciliate penetration and the most expressed zonality of the community are noted. Aerophiles *Anigsteinia*, *Condylostoma*, *Spirostomum* inhabit the top layers, whereas ciliates with endosymbiothic bacteria (*Sonderia*, *Metopus*, *Mesodinium pupulain*) are found in the deep layers.

A somewhat different pattern of vertical zonality of the ciliate community is observed in sublittoral biotopes of the Baltic Sea (Fenchel, 1969) under the influence of gales and currents. Under these conditions a very poor (qualitatively and quantitatively) ciliate fauna develops in the top 6 cm layer of the sediment. It is mostly represented by non-specific algophages. In reduction layers (6-15 cm) a rich bacteriotrophic fauna develops, represented by *Remanella margaritifera*, *Kentrophoros* sp., *Geleia* sp., etc.

The vertical structure of benthic sublittoral ciliate community in the Baltic Sea depends on the depth of the biotope (Fenchel, 1969). At a depth of 10 m a distinct vertical zonality was observed. In the top layer (0-4 cm) a very poor fauna, represented by diatome-feeders, developed. The reduction zone of the sediment (4-12 cm) was occupied by the greatest number of species. The H_2S zone (14-16 cm) was inhabited by a small number of species containing endosymbiotic bacteria (*Metopus contortus*, *Caenomorpha laevandri*). No distinct zonality in the vertical structure of ciliate community at a depth of 15 m was observed. The species usually occupying only the top layers of the sediment, in this biotope are distributed throughout the sediment column (down to a depth of 16 cm). This is due to the fact that the sand is only weakly silted and oxygen can therefore penetrate down to significant depth in the sediment. On the contrary, at depths of 20 and 25 m, the sediment is strongly silted. As a result, the ciliate abundance and the degree of their penetration in the sediment decrease. For instance, in the biotope at a depth of 25 m only 4 individuals of ciliates were found in the superficial 1 cm.

Thus, the features of vertical structure of psammophilous ciliate community in the sublittoral zone are determined first of all by the characteristics of the sediment (granularity and silting), that determine the formation of different reduction-oxidation profiles and, consequently, the development of certain species complexes.

The penetration of ciliates into the sediment column in the Baltic Sea estuaries (Fenchel, 1969) is much less than in the sublittoral because of a sharper vertical Eh gradient in the sediment. In some estuarine biotopes ciliates are not found below the depth of 3 cm. In general, the highest species diversity, abundance and biomass are recorded in the top layers (0-2 cm).

The vertical structure of psammophilous ciliate community differs in sand of different granularity (Agamaliev, 1970, 1983). In the Caspian Sea the following patterns were observed. The coarser the sand, the greater the depth down to which ciliates can penetrate into the sediment and the depth where most species demonstrate their greatest abundance. For very fine sand (Mo=0.05-0.08 mm) these figures usually are, correspondingly, 5-6 and 0-1 cm, for fine sand (Mo=0.1-0.4 mm), they are 8-9 and 1-2 cm, for medium-grained sand (Mo=0.5-0.7 mm), 9-11 and 1-2 cm, for coarse sand (Mo=0.8-1.3 mm), 12-13 and 0-4 cm. Obligate psammophilous microporal and euryporal species (Trachelocercidae, *Remanella*, etc.) penetrate into the sediment column deeper than facultative psammophilous (non-specific) ciliates. This distinction is especially clearly expressed in fine and medium-grained sand and more poorly, in coarse sand.

Thus, the vertical structure of ciliate community in sediments is determined first of all by reduction-oxidation properties of the sediment. In the top layers of the sediment diffusion of oxygen from near-bottom layers of water and air occurs, oxygen also forming in the course of life activity of photosynthetic organisms. This results in formation of the oxidizing conditions favorable for development of aerophile organisms, represented, as a rule, by forms non-specific for the interstitial biotope. In deeper horizons the processes of accumulation of organic substance and its oxidation promote formation of anaerobic conditions. However, in the «anaerobic field» in the middle horizons of the sediment there are «aerobic pockets» occupied by microaerophile organisms (Fenchel and Bernard, 1996). The majority of specific interstitial forms develop under these conditions (Berninger and Epstein, 1995). The deepest H_2S-containing horizons, where there are no aerobic microniches (Fenchel and Bernard, 1996), are inhabited by ciliates, containing endosimbiothic chemotrophic bacteria.

To sum up, depth of penetration of ciliates into the sediment, the intensity and characteristics of vertical community zonation depend on the properties of the sediment and the specific location of a biotope, promoting the formation of certain reduction-oxidation regimes. Apparently, the most important of these properties are those controlling the processes of silt accumulation (resulting in development of reduction conditions), development of microphytobenthos and oxygen diffusion (resulting in formation of an oxidizing zone). It is possible to distinguish the main spatial gradients, which determine the features of organic matter accumulation in the sediment, the possibility of its decomposition and that of microphytobenthos development. Taken together, the presense of these gradients forms a diversity of reduction-oxidation conditions and determines significant polymorphism of the vertical structure of marine psammophilous ciliate community.

Sand granularity. As granularity decreases, the total volume of capillary spaces also decreases, whereas the processes of debris accumulation become more intensive. This brings about, firstly, lesser penetration of photosynthetic organisms and lesser oxygen diffusion deep into the sediment, and, secondly, a significant consumption of oxygen in process of oxidation of dead organic matter. As a result, with decreasing sand granularity the depth of ciliate penetration into the sediment decreases, and vertical zonality of the community becomes more clearly expressed.

Salinity. With decreasing salinity in estuaries processes of sediment accumulation are intensified, which considerably increases sediment silting and brings about development of H2S conditions at the surface of the sediment (Safianov, 1987). As a result, with decreasing salinity the depth of ciliate penetration into the sediment decreases and vertical zonality becomes more clearly expressed.

Depth of the biotope in the sublittoral. Silt accumulation is also more intensive at greater depths, whereas microphytobenthos development decreases with depth. As a result, at depths of 5-10 m the zone of maximal development of specific interstitial fauna is situated not at the surface of sediment, as in the littoral, but in the layer 8-9 cm. At greater depths (20-25 m) significant debris concentration prevents the development of specific interstitial community.

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