

Long-term dynamics of marine interstitial ciliate community

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Summary

We observed changes in the composition, structure and seasonal succession patterns in the community of interstitial ciliates in the White Sea over a period of 18 years. Considerable inter-year fluctuations of species abundances as well as species richness, diversity, trophic and size structure were recorded. During the first 12 years, the changes appeared to be multi-vectorial. However, in the last 6 years the community modification became direct, with an increasing number of specific interstitial ciliate species, and *Trachelocerca sagitta* as the leader. These changes were caused by the increase in the silt content and the amount of dead organic matter, as well as by the decrease in the concentration of oxygen and the size of interstitial spaces in the sediments. All the changes took place on the background of the same set of ciliate species and the same niche structure. The changes in the community structure during the period equivalent to thousands of generations of ciliate populations are realized through two major mechanisms. The first one acts through inter-annual fluctuations, and manifests itself in recombinations of species composition in response to local environmental factors. The second one acts through long-term directional changes in the community composition, in accordance with the trended transformations of the littoral ecosystem. Inter-year changes (e.g., the degree of seasonal fluctuations of abundance, species diversity and community structure) were also manifested at all the stages of seasonal succession. During the last 6 years, within-year variability of abundances clearly increased, and so did stability and direction of seasonal succession. Yearly renewed seasonal successions do not lead to the increase in the community complexity and order, but are rather stages on the way of the community's adaptation to the changing environment. Inter-year variability of the patterns of seasonal succession reflects the evolutionary potential of the community's resilience in a fluctuating environment.

Key words: ciliates, community, long-term dynamics, White Sea, marine littoral

Introduction

Studies of long-term processes, embracing the replacement of thousands of generations, could provide important information on temporal organization and stability of natural communities in a fluctuating environment. Obviously, the most appropriate objects for such studies are tiny, quickly reproducing organisms that form complex multispecies associations. Among such communities, those of marine littoral interstitial ciliates are distinguished by having a very high biodiversity and abundance, and also by the possibility of regular and long-term observations. Yet long-term changes in protozoan communities during time periods measuring thousands of generations have never been a subject of special investigations.

Long-term community studies are impossible without taking into the account the multi-scale spatial heterogeneity of organisms in the environment. It was shown that within one biotope there are many local structural variants of interstitial ciliate community that differ not only in species composition and dominance structure but also in the rates of succession processes (Burkovsky, 1992, 1992a, 2006; Burkovsky and Aksoenov, 1996; Burkovsky et al., 2003, 2004). Such structural diversity is the requirement of steady existence of complex systems in a fluctuating environment. The sizes of local communities, as a rule, do not exceed several square meters. Thus, the community as an entity appears as a blurred patchwork composed of a bulk of transient local structural formations. For the purposes of long-term studies it is very important that the object is as homogeneous and self-sustaining as possible within the original limits throughout the study period. Only in this case one can be sure that the data obtained reflect temporal changes of the system but not its spatial heterogeneity.

Marine interstitial ciliate communities are characterized by prominent annual cycles that are caused by dynamics of temperature, illumination, available food resources and interspecific interactions (Burkovsky, 1992a; Burkovsky et al., 2003, 2004). Psammophilous ciliate community is radically changed in the course of the year. The main tendency is heterospeed (irregular) movement from a reduced, simple and weakly structured community in the end of the hydrological winter (April) towards a complex, multispecies, highly spatially heterogeneous system in the end of the

summer season (August–September). At the same time, in different years in different locations the initial states of community (in early spring) can be quite different, whereas the final stages have similar composition and structure (Burkovsky, 1992b). Moreover, over the years, in accordance with the climate fluctuations, there emerge differences in duration and prominence of the seasonal succession stages, the relative speed of succession and the time of reaching and the degree of complexity of final succession stage (Burkovsky, 1992b, 2006; Burkovsky and Aksoenov, 1996).

During long-term studies of marine meiobenthos, directional changes depending on the temperature were detected (Harris, 1972). However, nobody observed the ecological succession that is characterized by progressive development of the community towards complexity and order. The cause of the lack of such studies, most likely, lies in the longer life duration and also less frequent changes of generations in the multicellular organisms as compared with unicellular ones. As a result, in this temporal scale multicellular organisms tend to react to the environment on the individual and population levels, and not on the community level, as unicellular organisms do (Burkovsky, 1992a, 2006).

At the same time, when the study period is longer, quite significant changes in meiobenthic community structure appear, particularly in relation of the dominant groups, nematodes and harpacticoid copepods, which is associated with the change in the sediment siltation (Coull, 1985a, 1985b). However, such directional processes, which are realized at the scale of several years, are not connected with the progressive community development (growing of complexity and order), and are exclusively adaptive. Most likely, only rapidly reproducing organisms with a short individual life and a short generation time can realize during one season the developmental trajectory that corresponds well to ecological succession.

The aim of the present research was to study, for the first time in scientific practice, a natural community of unicellular organisms during the period embracing the change of thousands of generations. Our task was to reveal the amplitude and periodicity of community structure fluctuations, as well as the major tendencies of the community changes over a long period of biological time. In addition, we aimed to investigate long-term changes in the patterns of seasonal succession.

Material and methods

Investigations were conducted on a small area (1 square meter) of sandy beach located on the borer between the low and the middle littoral in the Gryaznaya Bay (the Kandalaksha Gulf, the White Sea) from 1991 to 2008. Sampling was performed every week from May to September (in 2001 also in January, February and April) during low water. Fifteen samples were taken with the aid of a glass tube (with a diameter of 1 cm) submerged into the sand down to the depth of 3 cm, which resulted in a 45 cm³ total sample. In the laboratory, the ciliates were washed from the sand according to the Uhlig method (Uhlig, 1964, 1965, 1968) one hour after sampling. The ciliates were counted in a living state under the stereomicroscope BIOMED-9 (Russia) at a magnification of $\times 32$ –56. As a result, 1/15 of the total sample was microscopically analyzed. Fifteen simultaneously taken subsamples allowed one to grade possible spatial heterogeneity and to receive as much information as possible about the species composition of the community.

Several abiotic factors were measured at the sampling site weekly: Eh, pH, salinity and temperature of air and water. In May and September, the granulometrical composition of the sediment, the depth of the oxic zone, as well as the organic matter content were also measured.

For integral community characterization, the following parameters were used: abundance (ind. per cm²), biomass (mkg per cm²), average size of the organism in a community, Margalef index of species richness, Pielou indices of evenness and Shannon diversity index. Variation coefficient was applied in order to estimate the variability of these integral community characteristics in time. The existence of possible periodicity was tested with the aid of spectral analysis. A connection between some integral characteristics was estimated by linear regression analysis and Spearman correlation coefficients. Dependence between the number of species recorded and the sampling effort was approximated with power function, where power coefficient reflected beta-diversity.

For the classification of community variants, successive cluster analysis on the base of Pianka similarity index was performed. Principal component analysis was used in order to connect community changes with species composition of dominants.

All calculations were made with the use of MS Excel, ECOS 1.3, PAST 1.89, PRIMER 5.5.2 packages.

Results

BIOTOPE CHARACTERISTICS

Studies of different components of the littoral ecosystem conducted in the Gryaznaya Bay for 35 years allow describing the general principles of its organization and modification. The ciliate community is represented by 145 species (Mazei and Burkovsky, 2005), 30–40 of which are the most abundant in concrete years. Others occur in small numbers and cannot be identified every year. Besides the ciliates, the littoral sand is inhabited by more than 300 species from other groups of unicellular (bacteria, diatoms, dinoflagellates, heterotrophic nanoflagellates, rhizopods, fungi) and multicellular (nematods, turbellarians, harpacticoid copepods) organisms. Together they form a rather complex and autonomous system with a branching net of trophic and metabolic interactions, which are incorporated into the pathways of the whole littoral ecosystem (Burkovsky, 1992a, 2006).

Long-term observations on the situation in the Gryaznaya Bay allowed us to make a conclusion about the existence of progressive changes. The main tendency is the decrease of the space covered with pure sand and the replacement of sandy sites by silty sediments. In the period from 1991 to 2008, an increasing amount of silt and suspended organic matter within the sediments was noted (from 4 to 20–35% and from 0.3 to 2–5%, correspondingly).

The process of eutrophication was the most intensive during the last years. Thus, in 1978–1990 (before the collection of material for the present research began) the amount of silt was less than 4%, in 1993, it was 5–10%, and in 2008, 20–30%. The increasing amount of aleuropelite and suspended organic matter results in the decrease of oxygen concentration within sediments as well as reduction-oxidation potential (Eh). The level of Eh in the upper 0.5 cm layer was within the limits +200...+250 mV before 1993, and +50...+150 mV (usually +50...+80 mV) in 2006–2008. The depth of the oxygenized layer, where most of the microbenthic organisms dwell, decreased in the same direction. In 1991 the depth of the oxygenized layer reached 3–4 cm, while in 2006–2008 it did not exceed 0.5–1.0 cm. As a result, the living space for oxyphilic organisms (to note, more than 95% of psammophilous ciliates are oxyphilic) decreased several times during the last 20 years. Moreover, in the last years a thin layer of silt covering the sediments developed, decreasing the penetrability of sediments for light and hampering water-exchange. The photic zone decreased from

2.0–2.5 mm in 1991–1993 to 0–1 mm in 2006–2008, which immediately affected the composition and productivity of microphytobenthos (dinoflagellates and diatoms), the main food for ciliates. Since 2003, the abundance of unicellular algae decreased several times.

Changes of temperature during this period were not so directed. The years with maximal temperatures within the summer season (1993, 1997, 2005: 12.1–12.7 °C) alternated with colder years (1996, 1998, 1999: 10.1–10.8 °C). The average summer temperature during the last 18 years was 11.4 °C. Daily temperature variations (averaged for the season) were 8.1 °C: the minimal fluctuations were recorded in 1993 (5.6 °C), the maximal ones, in 2000 (9.1 °C). The lowest minimal (night) temperatures (averaged for the season) were recorded in 1996, 1999 and 2000 (6.1–6.6 °C), and the highest maximal (midday) temperatures, in 2005 (17.2 °C), 1997 and 2003 (16.0–16.2 °C). The most favourable temperature conditions were observed in 1993 and 2005, with the lowest daily fluctuations and the highest night temperatures. The worst conditions were observed in 1998 (the lowest average and midday temperatures).

The general aspect of the ecosystem has also changed distinctly. The space covered with macro-vegetation (graminoids with a powerful tussock on saline marsh on the upper littoral, *Zostera marina* on the lower littoral) has increased, which resulted in siltation and compression of the sediments (Burkovsky and Stolyarov, 2000).

SPECIES COMPOSITION AND DIVERSITY OF THE CILIATE COMMUNITY

In 1991–2008, on the area of 1 square meter 125 ciliate species were identified (85% from the total checklist of ciliates discovered in the Gryaznaya Bay during the last 30 years). Each year on the average 78 species occurred in the community (52–92 species in different years). In a single sample (15×15×3 cm in size), the average of 46 species were recorded in different months and under certain conditions (15–70 species in different years).

The dependence of species richness on the investigation effort is shown in Fig. 1. The beta-diversity (power coefficient) was rather low, indicating a rather homogeneous species structure of the community. It means that every year one could find many species from the previous year and only a few new species.

The set of dominant species is represented by 12 species in terms of biomass (Table 1). Usually

Trachelocerca incaudata was the leading organism. However, in some years it was replaced by the larger but not numerous *Cardiostomatella vermiformis* or by the medium-sized *Histiobalantium marinum* and *Histiobalantium majus*, and, in the last years, by the smaller *Trachelocerca sagitta*.

In terms of abundance, the number of dominants increased two-fold during the whole study period (Table 2). Relative abundances varied more than relative biomass (compare Tables 1 and 2). The leading species were *Remanella margaritifera*, *Trachelocerca incaudata*, *Coleps tessellatus*, *Histiobalantium marinum*, *Uronema marina*, but in the last years *Trachelocerca sagitta* was the most characteristic dominant. The community showed a clear trend from polymixic to oligomixic state: while in 1991–2003 more than 50% of the total abundance was formed by 5–7 species, in 2004–2005 the corresponding number of species was 3–4, and in 2006–2008, 1–2.

Dynamics of the relative abundances of dominants is shown in Fig. 2. The order of dominance changed from year to year (Table 2). The most constant component of the dominants was represented by *Remanella margaritifera* and *Trachelocerca incaudata*. Basing on the differences in the dominant composition, it was possible to distinguish several stages of community transformation: 1991–1995; 1998–2000; 2001–2002; 2003–2004; 2005–2006; 2007–2008. The rate of community transformation grew continuously from year to year, the growth being more evident after 2003.

The results of community ordination show that more than 70% of the total community variance (along the first principal component) is associated with the differences between the 2005–2008 assemblages and the other ones (Fig. 3). These differences correspond to the changes in the composition of the dominants (Tables 1 and 2; Fig. 3). Thus, since 2005 dominants *Remanella margaritifera* and *Trachelocerca incaudata* as well as subdominants *Coleps tessellatus* and *Uronema marina* cede their place to *Trachelocerca sagitta*. The rest of the variance (along the second principal component) is associated with the inter-annual fluctuations in the period from 1991 to 2004. Two community variants are the most prominent during this period: i) with dominants *Trachelocerca incaudata* and *Coleps tessellatus* in 1992, 1994, 1995 and 2001, and ii) with dominants *Remanella margaritifera* and *Uronema marina* in 1991, 1993, 2003 and 2004.

More clearly trended changes in the community structure were revealed via community ordination based on the averaged relative abundances norma-

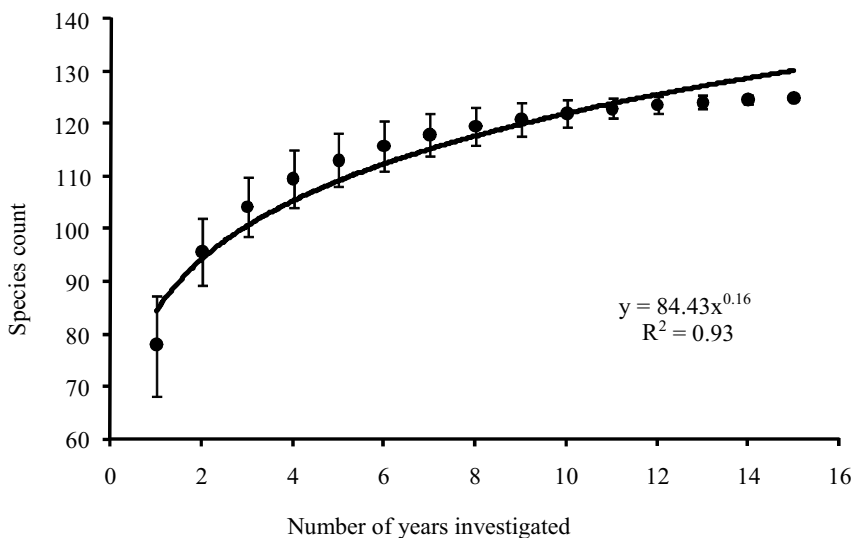


Fig. 1. Dependence between the number of species recorded and the number of years of study.

lized on the long-term (Fig. 4). It allowed us to consider trends in the changes of the abundances, but not the absolute values of relative abundances of species. More than 58% of the total community structure variance (along 1 and 2 PC) reflected trended (but not accidental!) changes of species abundances. This, from 1991 to 2002 the abundances of the following species decreased as compared with 2004–2007: *Histiobalantium majus*, *Pleuronema coronata*, *Coleps tessellatus*, *Discocephalus rotatorius*, *Kentrophoros fasciolatus*, *Geleia fossata*, *Diophrys histrix*. On the other hand, the abundances of trachelocercids (*Trachelocerca sagitta*, *Tracheloraphis kahli*, *Trachelocerca incaudata*) increased in 2004–2008, whereas the abundances of *Didinium balbiani*, *Uronema marina* and *Histiobalantium*

marinum increased in 1998–2004, in comparison with the previous period. So, during 18 years there were three major community states (stages of community transformation). The first one (1991–1995) was characterized (despite the dominants named above) by the species *Pleuronema marina*, *Gastrostyla pulchra*, *Mesodinium pulex*. The second stage (1998–2004) was distinguished by another combination of dominants: *Didinium balbiani*, *Strombidium viridae* (ecological doubles of the previously dominating *Mesodinium pulex* and *Diophrys histrix*, correspondingly), as well as some species common at the first (*Kentrophoros fasciolatus*, *Geleia fossata*, *Diophrys histrix*), and the third (*Histiobalantium marinum*, *Uronema marina*) stage of community transformation. The third stage (2005–2008) was

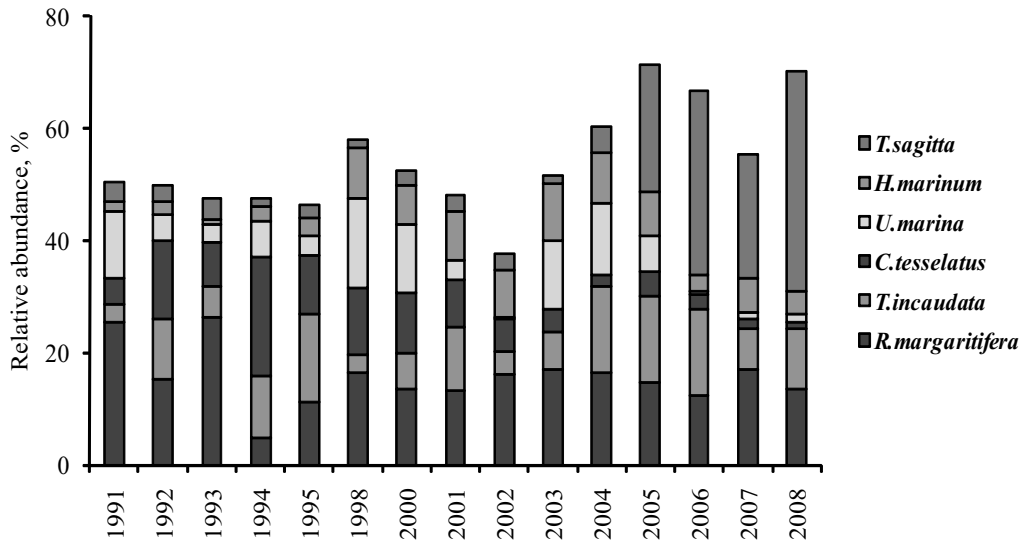


Fig. 2. Dynamics of relative abundances of the dominants.

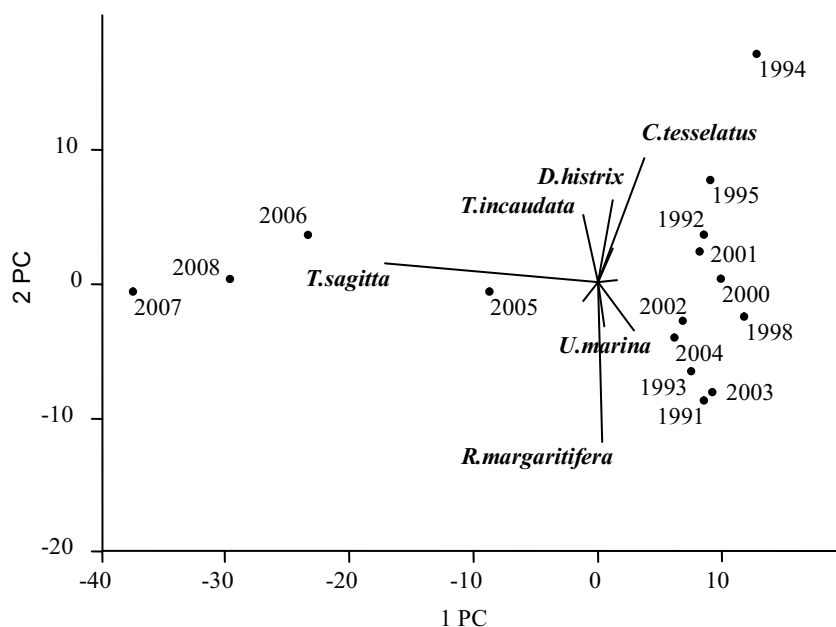


Fig. 3. Results of community ordination by principal component analysis based on relative abundances of dominant species. 1 PC – the first principal component (explained 71.1% of the total community variance), 2 PC – the second principal component (11.1%).

represented by *Trachelocerca sagitta* (dominant) and *Tracheloraphis kahli*, *Trachelocerca incaudata*, *Tracheloraphis oligostriatus*, *Tracheloraphis phoenicopterus*, *Histiobalanium marinum*, *Uronema marina*. So, clearly trended tendencies began in 2003, whereas alternate structural fluctuations occurred before that time (Fig. 4). It is very important that all the recombinations within the set of dominants existed on the background of the rather stable

existence of the most abundant species, *Remanella margaritifera* (Table 2).

A further insight into the pattern of long-term community dynamics is provided by the constrained cluster analysis (Fig. 5). The dendrogram confirmed and refined the patterning of community states obtained in the previous analyses. Three stages were distinguished, too: i) 1991–1994, with *Remanella margaritifera* as the dominant; ii) 1995–2003,

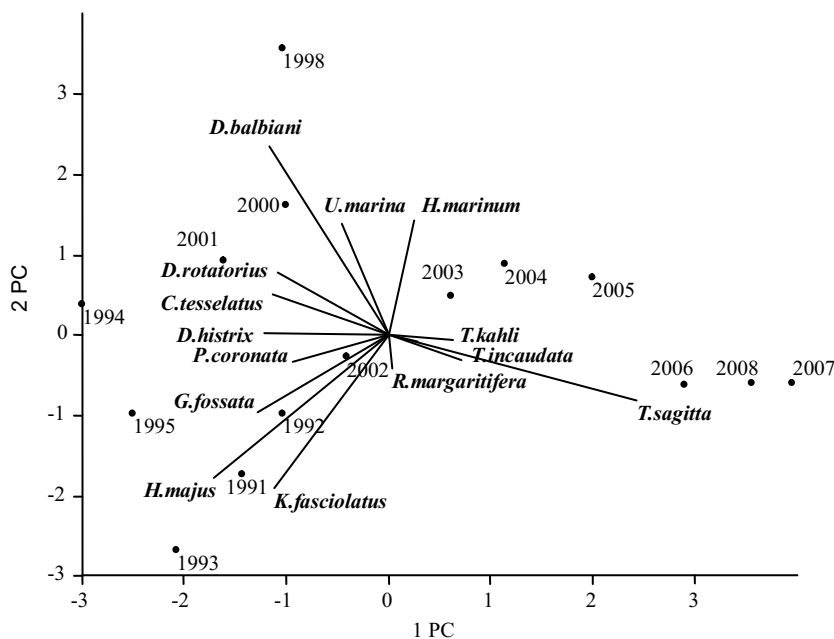


Fig. 4. Results of community ordination by principal component analysis based on averaged relative abundances of dominant species normalized on the long-term. 1 PC – 40.3%, 2 PC – 18.0%..

Table 1. Relative biomass (%) of the dominant species (more than 1% during the whole study period) in the community.

Species	Years														
	1991	1992	1993	1994	1995	1998	2000	2001	2002	2003	2004	2005	2006	2007	2008
<i>Trachelocerca incaudata</i>	12.4*	32.5	18.8	35.4	39.6	12.5	20.9	30.4	11.2	20.6	38.7	39.1	28.0	22.0	28.3
<i>Histiobalantium majus</i>	19.4	4.7	16.0	9.4	14.2	2.8	4.8	4.1	1.9	1.4	0.1	0.1	0.0	0.0	0.0
<i>Cardiostomatella vermiformis</i>	10.2	4.0	6.9	4.5	4.1	10.0	8.9	8.7	13.2	13.7	11.4	8.8	4.0	5.9	6.9
<i>Histiobalantium marinum</i>	5.1	5.3	2.4	5.7	5.7	28.5	16.8	17.5	17.8	22.8	17.3	15.3	8.0	15.0	8.2
<i>Trachelocerca sagitta</i>	2.9	1.9	2.4	1.0	1.2	1.4	1.8	1.7	1.8	0.8	2.5	12.0	30.3	31.3	27.0
<i>Remanella margaritifera</i>	10.2	4.6	8.7	1.5	2.9	6.9	4.3	3.6	4.6	5.0	4.2	3.8	3.1	3.5	3.8
<i>Geleia fossata</i>	2.0	11.6	7.1	7.4	4.0	1.1	2.4	5.8	3.3	2.0	0.9	0.3	0.0	0.0	0.2
<i>Coleps tessellatus</i>	2.6	6.0	3.6	9.4	3.7	7.1	4.9	3.3	2.4	1.6	0.7	1.5	1.1	0.8	0.5
Trachelocercidae gen.sp.	2.0	6.5	2.9	2.1	2.0	1.3	1.8	3.3	3.8	5.7	5.0	2.9	2.6	5.5	9.6
<i>Gastrostyla pulchra</i>	3.7	3.2	1.1	2.8	3.0	2.0	2.1	0.6	3.5	0.9	0.5	0.2	0.0	0.0	0.7
<i>Tracheloraphis kahli</i>	2.7	0.0	3.3	1.0	0.9	0.7	1.7	2.3	4.0	3.8	3.6	4.6	1.9	5.4	1.2
<i>Tracheloraphis phoenicopterus</i>	1.6	2.0	2.2	1.1	1.4	0.4	1.1	0.9	1.5	0.8	1.8	1.6	1.6	1.3	4.7

* Relative biomasses exceeding 10% are shown in bold.

with *Trachelocerca incaudata*, *Coleps tessellatus* and *Histiobalantium marinum* as dominants; and iii) in 2004–2008, with the mass development of *Trachelocerca sagitta*, *Trachelocerca incaudata* and *Remanella margaritifera*.

Summing up, long-term changes in the community structure are put into effect by two mechanisms. The first one acts through inter-annual fluctuations, and manifests itself in recombinations of species composition in response to local environmental factors. The second one acts through long-term directional changes in the community composition, in accordance with the trended transformations of the littoral ecosystem. In terms of species composition, the changes were reflected in the decreasing abundance of *Histiobalantium majus*, *Pleuronema marina*, *Coleps tessellatus*, *Gastrostyla pulchra*, *Discocephalus rotatorius*, *Pleuronema coronata*, *Mesodinium pulex*, *Kentrophoros fasciolatus*, *Geleia fossata*, *Diophrys hystrix* and the increasing abundance of *Trachelocerca sagitta*, *Tracheloraphis kahli*, *Trachelocerca incaudata*, *Tracheloraphis oligostriatus*, *Tracheloraphis phoenicopteris*, *Histiobalantium marinum*, *Uronema marina*. Importantly, all the recombinations took place within the same set of species, reflecting the possibility of the self-sustenance of a concrete biological unit (in our case, the ciliate community) in the broad range of environmental changes.

CHANGES OF INTEGRAL COMMUNITY CHARACTERISTICS

Data on the changes of integral community characteristics over 18 years are shown in Figs 6–10. The most stable characteristics of the community were species diversity and evenness (Figs 6, 10). These integral characteristics reflect general organization of the community, including the patterns of niche partitioning. We can conclude that the principal pattern of community structure was sustained during the long-term period of studies ($P > 0.05$; Mann-Whitney test with Bonferroni correction).

The most variable characteristics were the ciliate abundance and biomass (Figs 7, 10). Average abundance in the most productive year (1993) was 9.5 times greater than that in the least productive one (2006) (Fig. 7).

Important community characteristics are trophic and size structure. In a marine interstitial community, the most abundant trophic group are raptorial feeders, which feed on diatoms, dinoflagellates, heterotrophic nanoflagellates, and small ciliates. The second trophic group comprises filter-feeders, which feed on bacteria

Table 2. Relative abundance (%) of the dominant species (more than 1% during the whole study period) in the community.

Species	Years														
	1991	1992	1993	1994	1995	1998	2000	2001	2002	2003	2004	2005	2006	2007	2008
<i>Histiobalantium majus</i>	6.5	2.1	6.5	4.0	7.5	0.9	2.0	2.0	0.9	0.6	0.0	0.0	0.0	0.0	0.0
<i>Geleia fossata</i>	1.0	7.7	4.3	4.7	3.2	0.5	1.5	4.3	2.3	1.3	0.7	0.2	0.8	0.2	0.1
<i>Coleps tessellatus</i>	4.6	14.0	7.8	21.2	10.4	12.1	10.8	8.5	5.9	3.8	2.0	4.2	2.7	1.6	1.2
<i>Kentrophoros fasciolatus</i>	2.5	2.4	7.2	0.9	2.6	0.7	0.7	1.7	2.8	1.5	0.7	0.5	0.5	0.1	0.1
<i>Diophrys histrix</i>	0.0	0.4	1.9	8.9	5.0	0.1	1.8	1.1	2.2	3.7	1.4	1.7	0.6	1.1	0.4
<i>Uronema marina</i>	11.9	4.6	3.1	6.5	3.6	15.9	12.0	3.5	0.1	12.4	12.9	6.3	0.6	1.1	1.4
<i>Remanella margaritifera</i>	25.6	15.2	26.2	4.7	11.3	16.6	13.5	13.4	16.2	16.9	16.6	14.8	12.3	17.1	13.4
<i>Trachelocerca incaudata</i>	3.1	10.7	5.7	11.3	15.7	3.0	6.5	11.2	4.0	6.9	15.2	15.4	15.4	7.3	10.9
<i>Histiobalantium marinum</i>	1.7	2.3	1.0	2.4	3.0	9.0	7.0	8.6	8.4	10.2	9.1	8.0	2.9	6.3	4.1
<i>Trachelocercidae</i> gen.sp.	1.6	7.0	2.8	2.1	2.5	1.0	1.8	4.0	4.4	6.2	6.4	3.8	3.1	6.1	10.0
<i>Trachelocerca sagitta</i>	3.6	3.0	3.6	1.5	2.3	1.5	2.7	3.0	3.0	1.3	4.7	22.7	33.0	51.9	39.3
<i>Gastrostyla pulchra</i>	2.0	2.3	0.7	1.9	2.5	1.0	1.4	0.5	2.7	0.6	0.4	0.2	0.0	0.1	0.5
<i>Diophrys scutum</i>	1.4	0.6	1.5	0.6	1.3	0.9	0.6	0.5	2.0	1.3	1.0	0.5	0.2	0.1	2.4
<i>Mesodinium pulex</i>	2.2	0.5	0.4	3.5	0.3	0.4	1.5	2.6	2.1	0.8	0.5	0.3	0.1	0.4	0.3
<i>Pleuronema marina</i>	1.5	1.4	1.6	1.0	1.5	1.2	1.6	0.7	0.4	0.5	0.5	0.4	0.0	0.1	0.2
<i>Pleuronema coronata</i>	3.0	1.3	2.2	1.6	2.0	1.2	2.1	3.7	3.4	1.8	0.6	0.4	0.3	0.4	0.6
<i>Tracheloraphis oligostriatus</i>	1.2	1.4	1.6	0.9	1.2	0.2	0.9	1.0	1.4	0.9	0.7	1.2	3.8	1.1	0.4
<i>Strombidium viridae</i>	1.2	2.1	0.5	0.0	0.2	6.0	2.5	0.2	0.2	0.6	0.4	0.2	0.0	0.0	0.1
<i>Tracheloraphis phoenicopterus</i>	0.8	1.3	1.3	0.7	1.1	0.2	0.7	0.7	1.0	0.5	1.4	1.3	1.3	0.7	3.7
<i>Urostrongylum caudatum</i>	1.2	1.1	2.7	1.1	1.7	0.9	2.5	2.2	0.0	1.3	1.2	0.8	0.8	0.2	0.5
<i>Didinium balbiani</i>	0.3	1.2	1.3	2.2	1.9	7.5	3.5	2.8	1.3	0.7	0.3	0.8	0.0	0.1	0.0
<i>Discocephalus rotatorius</i>	1.7	1.3	1.3	2.8	3.4	2.4	3.3	3.4	2.2	1.1	1.3	0.2	0.3	0.2	0.4
<i>Cardiostomatella vermiformis</i>	1.1	0.6	0.9	0.6	0.7	1.1	1.2	1.4	2.1	2.0	2.0	1.5	0.5	0.7	1.2
<i>Tracheloraphis kahli</i>	1.3	0.0	2.0	0.6	0.7	0.3	1.1	1.7	2.8	2.5	2.8	3.6	1.4	3.0	0.8

* Relative abundances exceeding 4% are shown in bold.

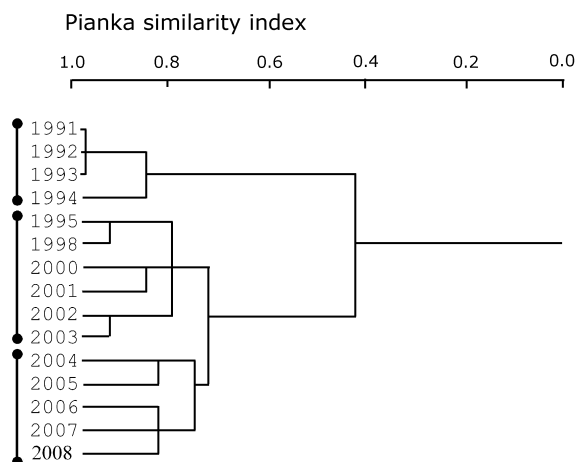


Fig. 5. Results of constrained cluster analysis of the community based on the Pianka similarity index with the use of average linkage method..

(Fig. 8). During 18 years, significant fluctuations in the trophic composition occurred. The general trend was towards the increase in the number of raptorial feeders and the decrease in the number of filter-feeders in the last 4 years. The former group

comprised mainly microaerophilic interstitial species from the family Trachelocercidae, and the latter, eurytopic oxyphilic ciliates *Uronema* spp., *Pleuronema* spp., *Euplotes* spp., *Aspidisca* spp.

The size of the ciliates varies in a very broad range (length, from 15 to 800 μm ; volume, from 0.8 to 170 thsd. μm^3). Any change in the community species composition affected the community size spectrum and the average size of the specimens in it (Fig. 9). Medium-sized ciliates (10-40 thsd. μm^3) predominated in the community studied. This size class was the most stable in time. There were no significant trends of size-structure modification during the long-term period, though some insignificant periodicity was visible.

The data on the long-term variability of different community characteristics are shown in Fig. 10. The most variable characteristics were abundance, biomass, abundance of large-sized ciliates, raptorial-feeders and downstream filter-feeders. The most stable characteristics were Shannon diversity and Pielou evenness indices, the average size of specimens in the community, the ratio of medium-sized ciliates and the total number of species identified per year.

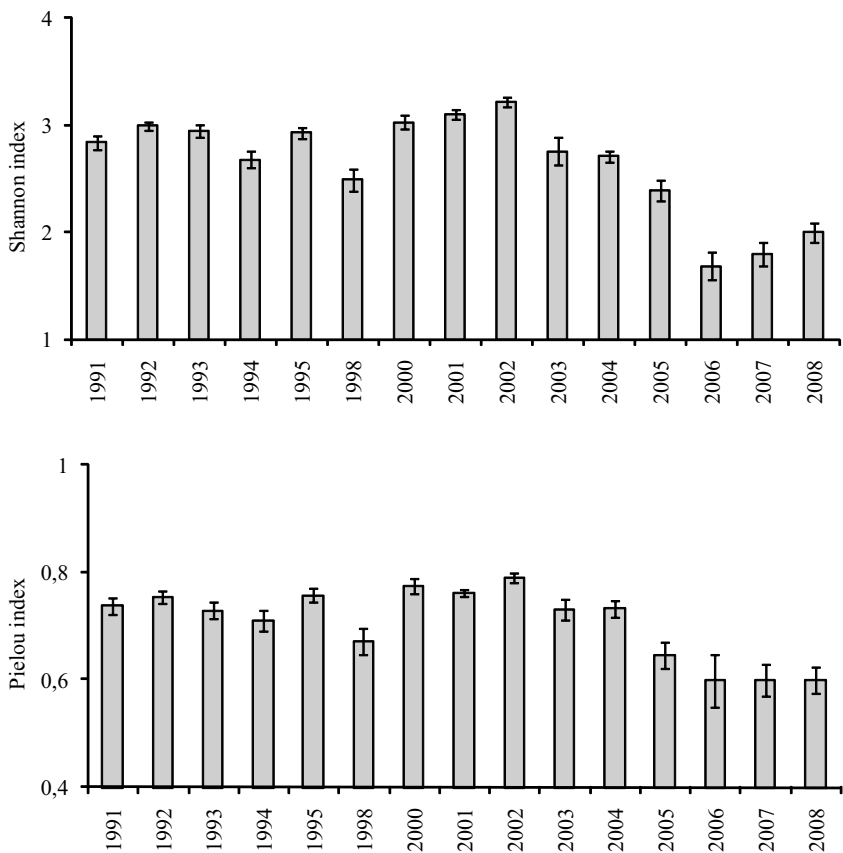


Fig. 6. Changes in species diversity of the ciliate community in 1991–2008. Whiskers — standard error of the arithmetic mean.

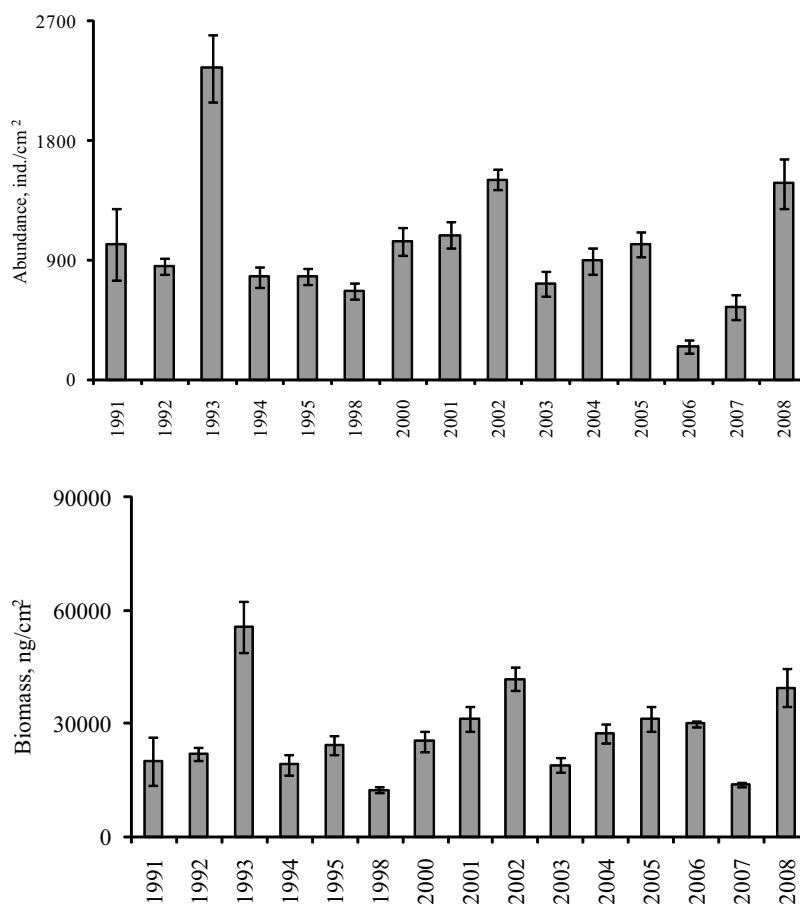


Fig. 7. Changes in abundance and biomass of the ciliate community in 1991–2008.
Whiskers — standard error of the arithmetic mean.

LONG-TERM DYNAMICS OF THE CILIATE POPULATIONS

The analysis of primary data-tables showed that the dynamics of the total abundance reflected the changes in the abundance of species groups associated with the most stable and abundant species, *Remanella margaritifera*. This group included trachelocercids (excluding *Trachelocerca incaudata* and *Trachelocerca sagitta*), as well as *Histiobalantium majus*, *Pleuronema marina*, *Urostrongilum caudatum*, *Frontonia* spp., *Trachelostyla* spp. and *Kentrophoros* spp. Changes in the abundances of most other species had alternate trends with a stochastic component in the community transformation. These species are *Trachelocerca incaudata*, *Uronema marina*, *Cardiostomatella vermiformis*, *Diophrys* spp., *Uronychia transfuga*, *Mesodinium pulex*, *Diophrys histrix* and small hypotrichs). On this background, general tendencies towards the decrease in the abundance in the last years were visible (*Coleps tessellatus*, *Diophrys histrix*, *Histiobalantium majus*, *Urostrongilum caudatum*, *Discocephalus rotatorius*,

Mesodinium pulex, *Strombidium* spp., *Pleuronema* spp., *Frontonia* spp., *Geleia* spp., *Kentrophoros* spp.), as well as a trend towards the increasing abundance (*Trachelocerca sagitta*, *Prorodon* spp., *Enchelyodon* spp., *Lacrymaria* spp., *Cyclidium fuscum*, *Caenomorpha capucina*, *Spirostomum teres*). The latter three species had considerable abundance only in the last years (2003–2008).

Some taxonomically and ecologically close species showed antagonistic inter-annual dynamics. This was the most evident in the case of *Histiobalantium majus* and *Histiobalantium marinum* (Tables 1, 2; Fig. 11). In the last years, the former species disappeared from the community, whereas the latter became dominant. The same tendency was revealed for the species from the genera *Pleuronema*, *Prorodon*, *Tracheloraphis* and *Remanella*, as well as for the pairs of ecologically close species *Strombidium sulcatum* — *Diophrys histrix* and *Mesodinium pulex* — *Didinium balbiani*. However, most potential competitors demonstrated antagonistic trends that manifested themselves not during inter-year

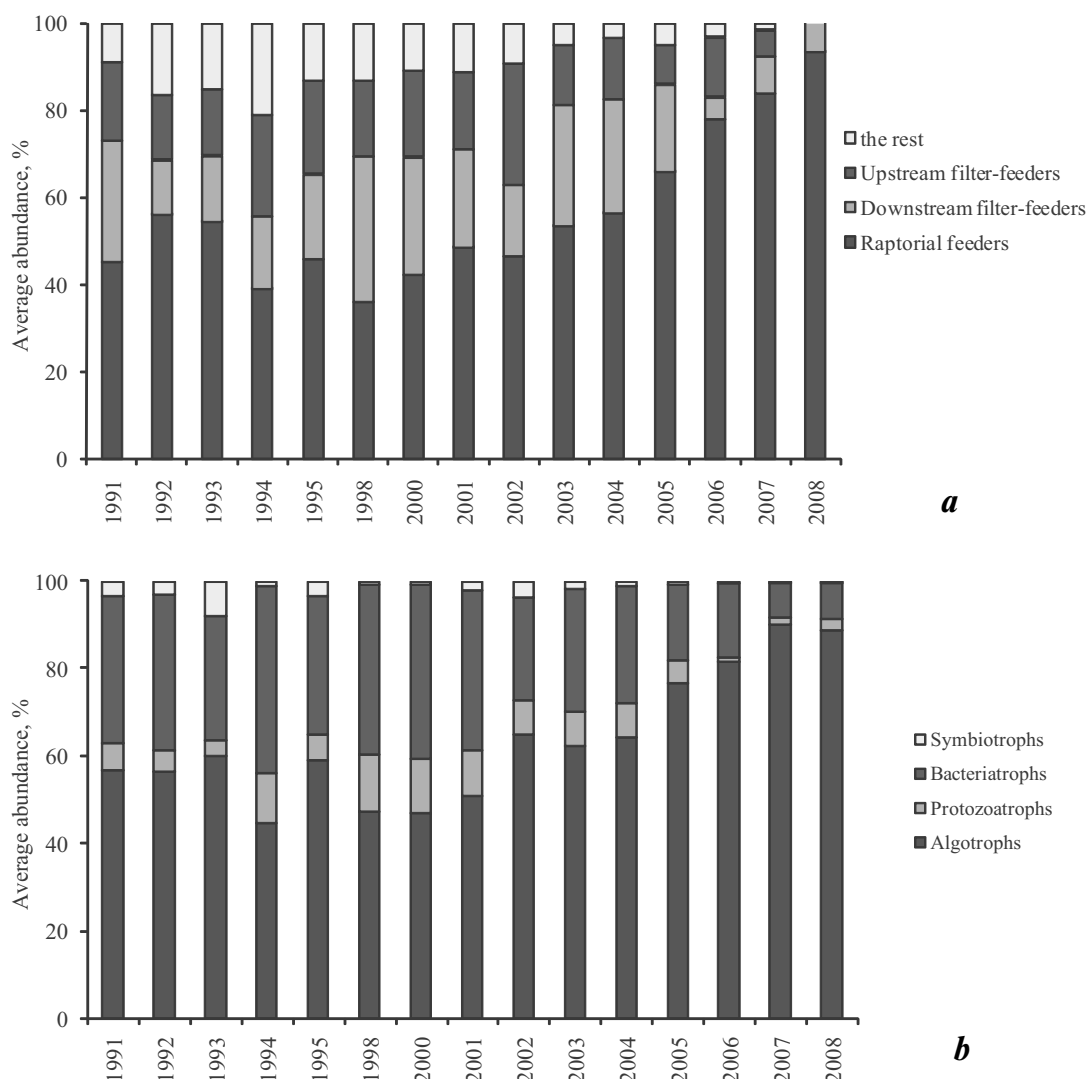


Fig. 8. Changes in trophic structure of the ciliate community in 1991–2008.
a and b – Different ways of distinguishing trophic groups.

community modifications but during within-year community modifications, which allowed them to coexist from year to year in a local area.

CYCLIC SEASONAL SUCCESSION IN THE MARINE CILIATE COMMUNITY

Long-term studies of the different components of the littoral ecosystem in the Gryaznaya Bay allow the description of the reiterative seasonal succession. In the course of the year, the ciliate community passes through a complex cycle of structural and functional modifications (Burkovsky et al., 2003). From late winter to early autumn, the community undergoes modification towards growing complexity and order. The starter of these processes is the fast increase in the energy (light

and heat) input in the beginning of spring, when the littoral is exposed after ice thawing (Table 3). The increase in the light flux and the heating of sediments up to 6–8 °C leads to a rapid increase in bacterial abundances (3–4 orders of magnitude), as well as in the increase in the abundance of the tiniest diatoms, dinoflagellates and heterotrophic flagellates (2–3 times), which are the main food for interstitial ciliates. These changes lead to a very fast growth of the abundance of some ciliate species: up to 2–3 times during 3–4 days. This is the beginning of the first stage of seasonal succession (Fig. 12).

Species composition and structure could differ considerably in different areas of the littoral. The basis of the community was formed by *Uronema marina* (or *Cyclidium fuscum*, *Pleuronema coronata*), *Diophrys histrix* (or *Strombidium sulcatum*, *Strombi-*

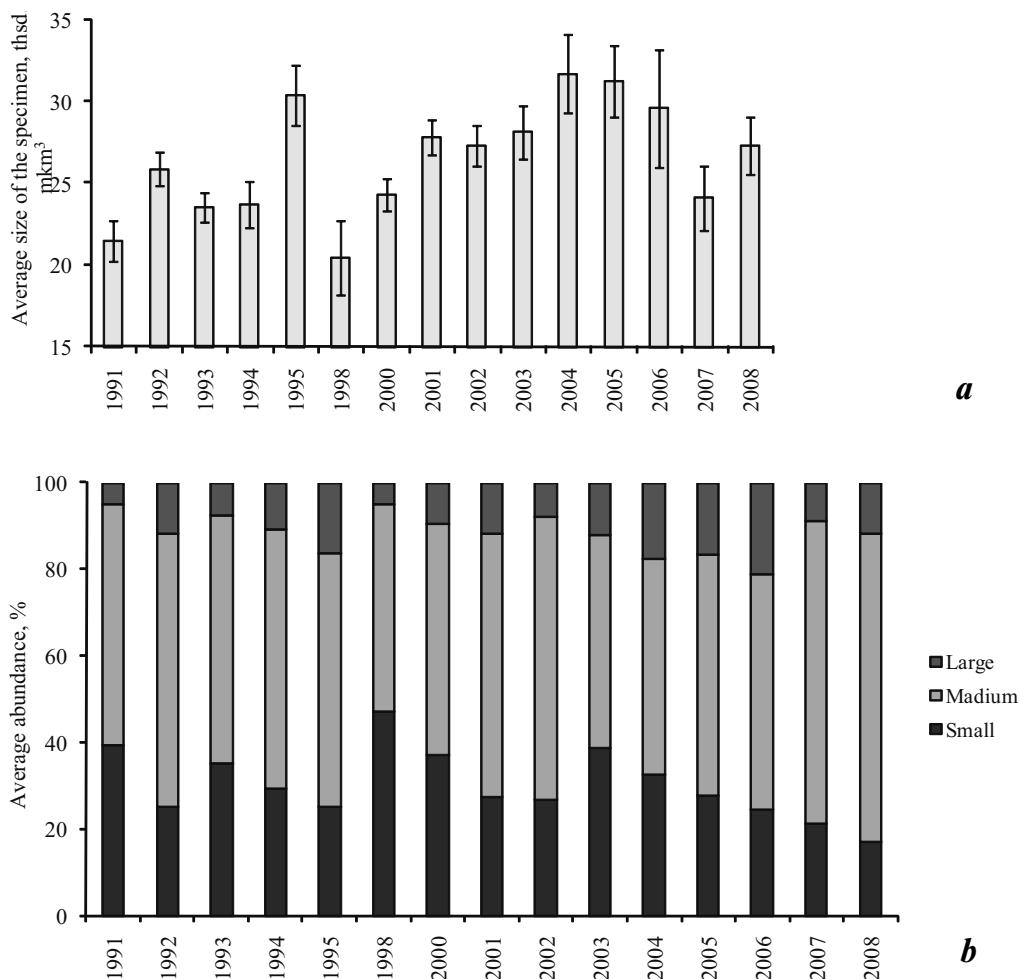


Fig. 9. Changes in size structure of the ciliate community in 1991–2008. *a* – Average size of specimens, *b* – ratio of different size classes. Whiskers – standard error of the arithmetic mean.

dium viridae), *Didinium balbiani* (or *Mesodinium pulex*, *Mesodinium pupula*) and *Coleps tessellatus* (or *Coleps pulcher*, *Coleps hirtus*, *Coleps similis*, *Plagiopogon loricatus*). These ciliates formed up to 90% of the total abundance and 60% of the biomass. Trophic preferences of the dominant species were very different. Overlapping of trophic spectra was low, varying in a range of 10–35%. To illustrate, *Uronema marina* fed on bacteria, *Diophrys histrix* was the consumer of dinoflagellates, *Mesodinium pulex* fed on heterotrophic nanoflagellates, while *Coleps tessellatus* consumed living and dead cells of unicellular organisms as well as particles of detritus.

The first stage of the seasonal succession was characterized by the maximal rates of community changes (up to 12% per day), which is 6–30 times more than in the other stages of annual community transformation (Table 3). The evident cause of this is the high rate of generation of small ciliates,

stimulated by the rapidly increasing temperature (from 0 to 10–12 °C), abundant food and minimal competition for resources from the ecological close but larger ciliates that do not reach maximal summer abundances.

The second stage of seasonal succession lasted 4–6 weeks and was characterized by a marked increase in complexity due to a more even species distribution in the community and a more intensive development of ciliates in deeper sediment layers (down to 0.5–2.0 cm). Species diversity, abundance and biomass increased considerably. The composition of dominants also changed. Species with high abundances were not only small-sized, but also to the medium-sized (20–60 thsd. μm^3 : *Lacrymaria* spp., *Diophrys scutum*, *Gastrostyla pulchra*, *Remanella* spp., *Histiobalantium* spp., Trachelocercidae gnn., spp.) and even rather large (80–170 thsd. μm^3 : *Trachelocerca incaudata*, *Cardiostomatella vermiformis*, *Geleia fossata*).

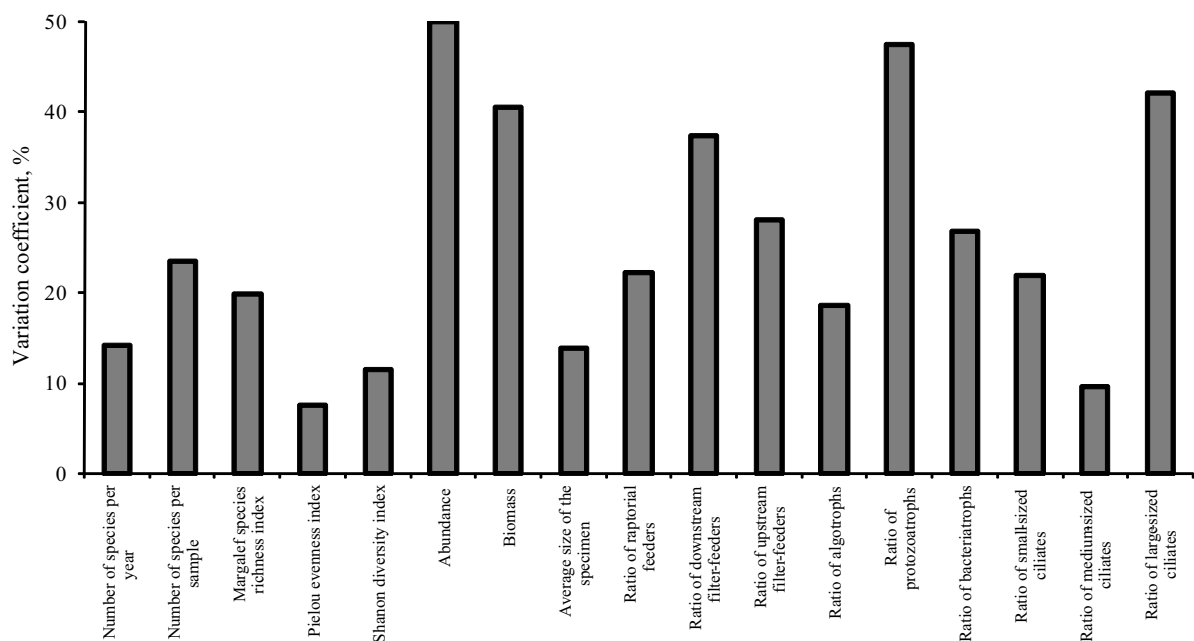


Fig. 10. Intensity value of variability of integral community characteristics in 1991–2008.

The food spectra of the new species overlapped considerably with those of the species from the first succession stage (up to 60-90%). At the same time, some of the new species could consume small ciliates that had been dominant during the first stage. As a result of predation and competition for food and space (Burkovsky, 1992a), the community structure continuously changed. The number of large ciliates with broad food spectra was increasing.

The trend towards increasing community complexity, outlined during the second stage, became more evident during the third stage (Table 3: summer period). The composition of dominants remained the same, but ratio of species was modified. In general, under the influence of population factors (reproduction), coenotic factors (predator-prey interactions, competition) and abiotic factors (light intensity, temperature, salinity, pH, Eh, etc.),

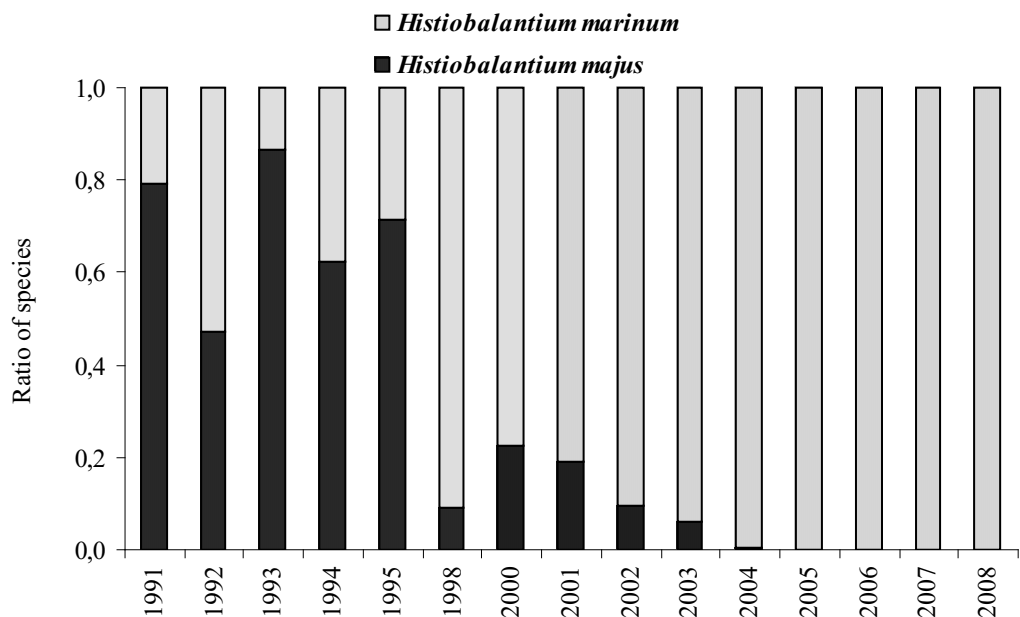


Fig. 11. Long-term dynamics of closely related species *Histiobalantium majus* and *Histiobalantium marinum*.

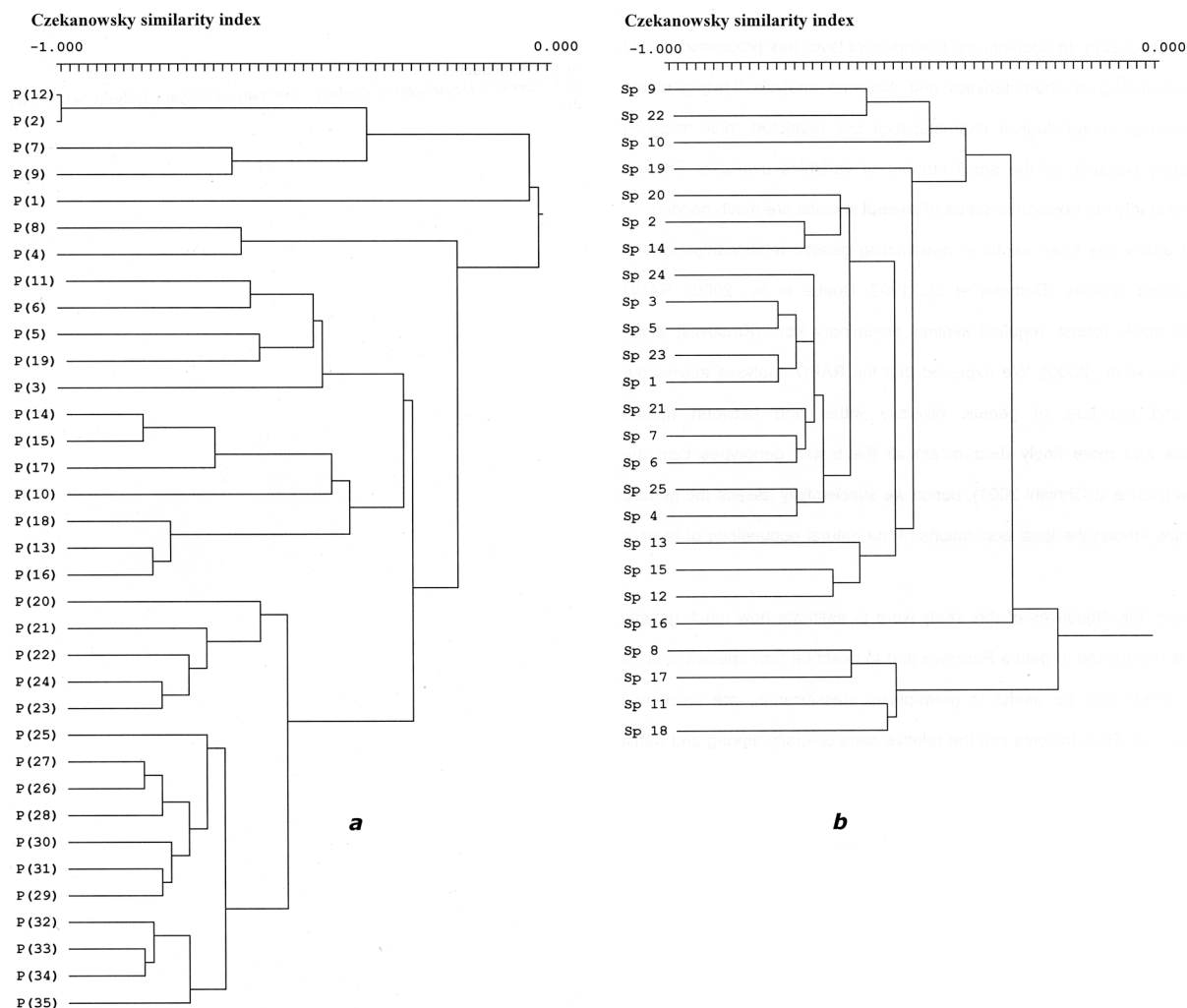


Fig. 12. Results of the cluster analysis basing on the data from April to September 2001. *a* – P(1)-P(35) – samples in different dates: 1-12 – April (end of the hydrological winter, fourth stage of seasonal succession), 13-18 – beginning of May (beginning of hydrological spring, first stage), 19-24 – middle of May – middle of June (continuation of hydrological spring, second stage), 25-35 – middle of June – beginning of September (hydrological summer, third stage). *b* – Sp1-Sp25 – species: 8, 11, 17, 18 – set of species from the first stage of seasonal succession; 2, 12-15, 19, 20 – set of species from the second stage, 1, 3-7, 21, 23-25 – set of species from the third stage. 1 – *Histiobalanthium marinum*, 2 – *Histiobalanthium majus*, 3 – *Trachelocerca incaudata*, 4 – *Trachelocerca sagitta*, 5 – *Tracheloraphis kahli*, 6 – *Trachelocercidae* gen. spp., 7 – *Remanella margaritifera*, 8 – *Didinium balbiani*, 9 – *Mesodinium pulex*, 10 – *Cyclidium fuscum*, 11 – *Uronema marina*, 12 – *Pleuronema coronata*, 13 – *Prorodon lemaneii*, 14 – *Coleps tessellatus*, 15 – *Diophrys appendiculata*, 16 – *Diophrys scutum*, 17 – *Diophrys histrix*, 18 – *Discocephalus rotatorius*, 19 – *Gastrostyla pulchra*, 20 – *Trachelostyla pediculiformis* + *T. caudata*, 21 – *Urostrongylum caudatum*, 22 – *Oxytricha discocephala* + *Holosticha discocephala*, 23 – *Cardiostomatella vermiformis*, 24 – *Geleia fossata*, 25 – *Kentrophoros fasciolatus*.

the community structure became more complex and stable. Species diversity and correlations between species grew, and the variability of abundances decreased. During this period the community was characterized by the maximal values of total abundance, biomass and species diversity. The set of dominant species included all size ranges and all trophic groups with a prominent

leader: *Trachelocerca incaudata*, one of the largest interstitial ciliates, which formed in different years from 30 to 60% of the total community biomass. This is the most mature state of the community, with the greatest integral community characteristics, the complementary trophic structure, the maximal assimilation of resources and the highest stability in space and time (Burkovsky et al., 2003).

Table 3. Changes in environmental variables and the ciliate community during cyclic seasonal succession in 2000–2001.

Characteristics	Seasons 2000-2001						
	spring 15.V–15.VI	summer 16.VI–6.IX	mid of winter 5.I–10.II	end of winter 25.IV –29.IV	beginning of spring 3.V –5.V	spring 13.V–15.VI	summer 16.VI–5.IX
Maximal light intensity,	18000	16000	400	800	17000	19000	17000
Temperature, °C	11.2	15.7	-0.5	-0.5	6.0	8.7	17.3
Salinity, ‰	10.3	19.7	22.1	22.6	8.1	10.4	19.2
Eh, mB	121	134	107	101	112	116	128
pH	7.6	7.7	7.2	7.2	7.5	7.7	7.7
Number of ciliate species	86	116	58	29	47	91	118
Number of species per	46.3	49.7	42.3	8.2	32.0	48.1	63.2
Shannon diversity index	4.31	4.49	3.43	1.92	3.12	4.4	4.65
Abundance, ind./cm ²	813.8	1163.3	294.4	20.8	585.5	778.3	1240.1
Biomass, mg/m ²	148.9	268.7	75.4	4.8	76.5	186.7	365.8
Average size of the	18.3	23.1	25.6	23.0	9.8	24.3	29.5
Main food of ciliates	A,B,P*	A,B,P	B,P,D	DOM,D,B	A,B	A,B,P	A,B,P
Average Czekanowsky							
– between species	0.639	0.725	0.448	0.207	0.604	0.675	0.735
– between samples	0.623	0.710	0.410	0.179	0.554	0.656	0.725
Average Spearman							
– between species	0.65	0.7	0.45	0.21	0.6	0.68	0.74
– between samples	0.64	0.73	0.48	0.2	0.58	0.66	0.77
CV** of the species, %	112.0	84.8	138.4	222.0	116.1	107.4	74.7
CV of the samples, %	13.4	5.8	7.1	41.5	15.9	12.6	5.0
Similarity between a	0.68	1.0	0.62	0.42	0.61	0.72	0.94
Average rate of community structure changes per day, %	–	0.72	0.19	0.38	12.0	2.0	0.65

* A – algae, B – bacteria, P – protozoa, D – detritus, DOM – dissolved organic matter.

** CV – variation coefficient

In autumn (September), the first signs of community simplification appeared; in winter (December–April, the fourth stage of seasonal succession) they became more evident. The process of simplification proceeded rather slowly. In the middle of the winter (January–February), the community still maintained a moderate level of species diversity, abundance and biomass (Table 3); in general, the community maintained traits from the beginning of autumn (community similarity between September and January was 55–65%). More than 60 species, from all size and trophic groups, constantly lived in this period under the ice. Small and medium-sized ciliates (*Histiobalantium marinum*, *Remanella margaritifera*, *Tracheloraphis kahli*, *Pleuronema coronata*, *Didinium balbiani*, *Uronema marina*) had the highest abundance, medium to large organisms (*Histiobalantium marinum*, *Tracheloraphis kahli*, *Trachelocerca incaudata*, *Spirostomum* sp.) had the highest biomass. The number of species that feed on dinoflagellates and large diatoms decreased, but the number of ciliates feeding on bacteria, debris, small diatoms and heterotrophic nanoflagellates increased. During this stage the species were not arranged into

stable associations. On the contrary, the community seemed to be more uniform and simple.

At the end of the hydrological winter (March–April), the community was characterized by the simplest organization. It included solitary specimens of the most eurybiotic species that consume dissolved or particular organic matter: *Uronema marina*, *Cyclidium fuscum*, *Aspidisca steini*, *Pleuronema coronata*, *Coleps tessellatus*, *Ciliofaurea* sp., *Histiobalantium marinum*. The total abundance in the community was 3–4 orders of magnitude higher than in summer. This was the end of the annual cycle of the community transformation (seasonal succession) that included two opposite trends: increasing of complexity and stability from May to September and gradual regression from October to April.

INTER-YEAR MODIFICATIONS OF SEASONAL SUCCESSION PATTERNS

Ecological factors peculiar for different years could considerably modify the above-described seasonal development of the ciliate community.

The renewal of the community after the winter simplification occurred in different years in different times from the end of April to the middle of May, lasting from 20 (1991, 1992, 2005) to 70–80 days (1994, 2003, 2007). The intensity of the first succession stage depended on the climatic regime in early spring. Sometimes this stage was completely or partly combined with the second one (in 2004 and 2006). The longevity of the second stage was 20–45 days in different years, while the third stage lasted 60–120 days, and the fourth, 180–220 days.

The results of the multivariate analysis provide the general view on the inter-year modifications of seasonal development patterns (Figs 13, 14). Here we present seasonal patterns in 1992 and in 2007 that represent extreme variants of patterning. In other years intermediate scenarios of seasonal succession were realized.

In 1992 the community changes were not trended. The first stage was mixed with the second one due to the fast development caused by early and intensive spring. As a result, a lot of species combinations replaced each other during the season without any prominent direction (Fig. 13a). The second and the third stages were rather separate (Fig. 13b). During the second stage the dominants were *Remanella margaritifera*, *Trachelocerca incaudata* and *Coleps tessellatus*, while during the third stage *Geleia fossata* and small trachelocercids in addition to the previous three species had the highest abundances.

In 2007 a different scenario was realized (Fig. 14). The first stage was the most peculiar one; it was characterized by the dominance of small- and medium-sized ciliates *Remanella margaritifera*, *Diophrys hystrix*, *Uronema marina*. Transition to the second stage took place very fast, in several days. Then, as a result of several continuous transformations (Fig. 14b), the community reached the most complex state in the second part of August and retained it until the middle of September. The most abundant species were *Remanella margaritifera*, *Trachelocerca sagitta*, *Trachelocerca incaudata*, small trachelocercids and *Histiobalantium marinum*. Thus, in 2007 (as well as in 2005, 2006, and 2008) the changes in the community structure were more directional. In other words, the strategy of community succession was considerably modified from the beginning towards the end of a long-term period. Modest, but frequent and alternate changes, common for the first years (1991–1995), in later years (2005–2008) gave place to more directional modifications during the season. Both stochastic and trended changes led to the emergence in the end

of the third succession stage of the most complex community, including *Trachelocerca incaudata*, *Remanella margaritifera*, *Histiobalantium majus* (or *Histiobalantium marinum*), *Geleia fossata* (or *Trachelocerca sagitta*) as dominants.

INTER-YEAR VARIABILITY OF THE INTEGRAL CHARACTERISTICS OF SEASONAL SUCCESSION

The values of abundance, biomass, species richness and diversity were characterized by a considerable seasonal and inter-year variability. The patterns of abundance and biomass modifications were similar (Fig. 15). There were two types of the dynamics of these characteristics. The first one was a rhythmic growth during the spring-summer period (Fig. 15 – 2001 as an example). The second one, a rhythmic decrease, was observed in two years only (2003 and 2006). The amplitude and periodicity could vary in a broad range (compare 2001, 2004 and 2007 on Fig. 15).

Species richness, as a rule, increased during the first and the second succession stages. After that, it could change in different ways (Fig. 16). For example, in 1991–1998 species richness increased gradually during the whole summer (Fig. 16, 1992). In 2000–2002 and in 2004–2006, fluctuations of this characteristic were observed (Fig. 16 – 2001). In 2003 a rhythmic decrease was noted, whereas in 2007 a rhythmic growth was observed.

Species diversity during seasonal succession could change in different ways. Usually, it fluctuated around a rather constant level (Fig. 17; 1991–2002 and 2004–2005) with a weak tendency to increase towards August. However, in 2003 a rhythmic decrease was observed, while in 2007 an increase was noted.

The analysis of the trends of changes of integral community characteristics during the seasonal succession allows distinguishing several periods within the 18-year-long study. Each period is characterized by a peculiar pattern of seasonal trend (Table 4). In 1991–1998, on the background of a rhythmic increase in abundance and the gradual growth of species richness, fluctuations around the stable level of species diversity (that was different in different years) were observed. In 2000–2002 and in 2004–2006, a rhythmic growth of the ciliate abundance coincided with fluctuations of species richness and diversity. The most peculiar years were 2003 on the one hand and 2007–2008 on the other hand. The former was distinguished by the fall of all the integral community characteristics during the summer period. The latter, on the contrary,

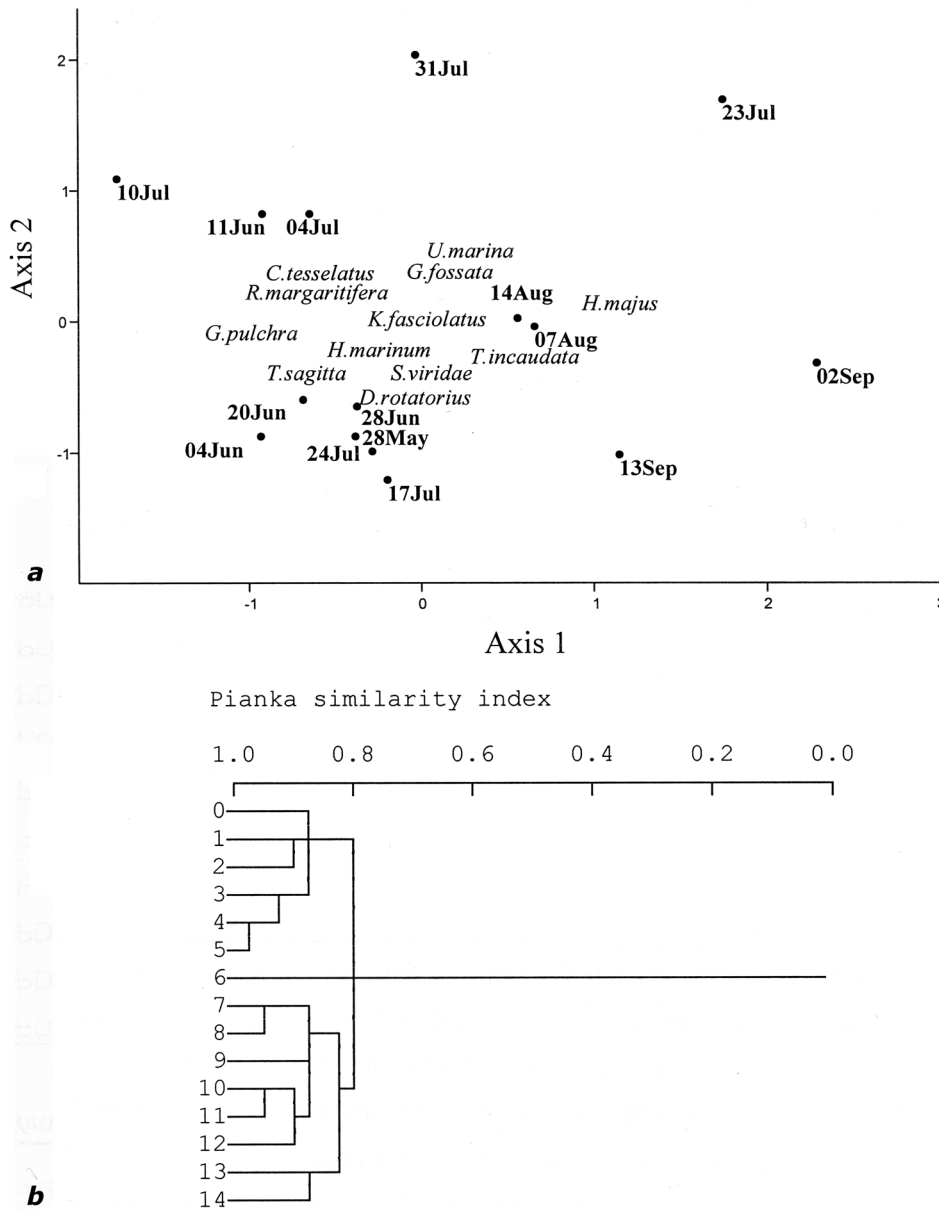


Fig. 13. Results of the community ordination (a) by detrended correspondence analysis (axis 1 explained 69% of the total community variance, axis 2, 19%) and constrained cluster analysis (b) (0-14 – successive dates of sampling) with the use of data on 1992.

was characterized by the growth of all indexes. Most likely, these peculiarities were caused by the negative reaction of the majority of the ciliates to sediment siltation and by the decreasing of the reduction-oxidation properties in 2003. In 2007, after the 4-year-long period of adaptation to the new conditions, the community demonstrated an increase in all the characteristics again.

Changes in the size and trophic structure of the community reflect the corresponding changes in the species composition and relative abundances

during the seasonal succession, which depend on the environmental conditions and the interspecies interactions (Burkovsky, 1992a). Changes in the size structure of the ciliate community could be characterized as fluctuations around a certain level. The ratio of small, medium and large ciliates varied in certain intervals (Fig. 18 – 2003 as an example). Moreover, in some years a more or less prominent tendency towards the increase in the number of large ciliates towards the end of the summer was evident.

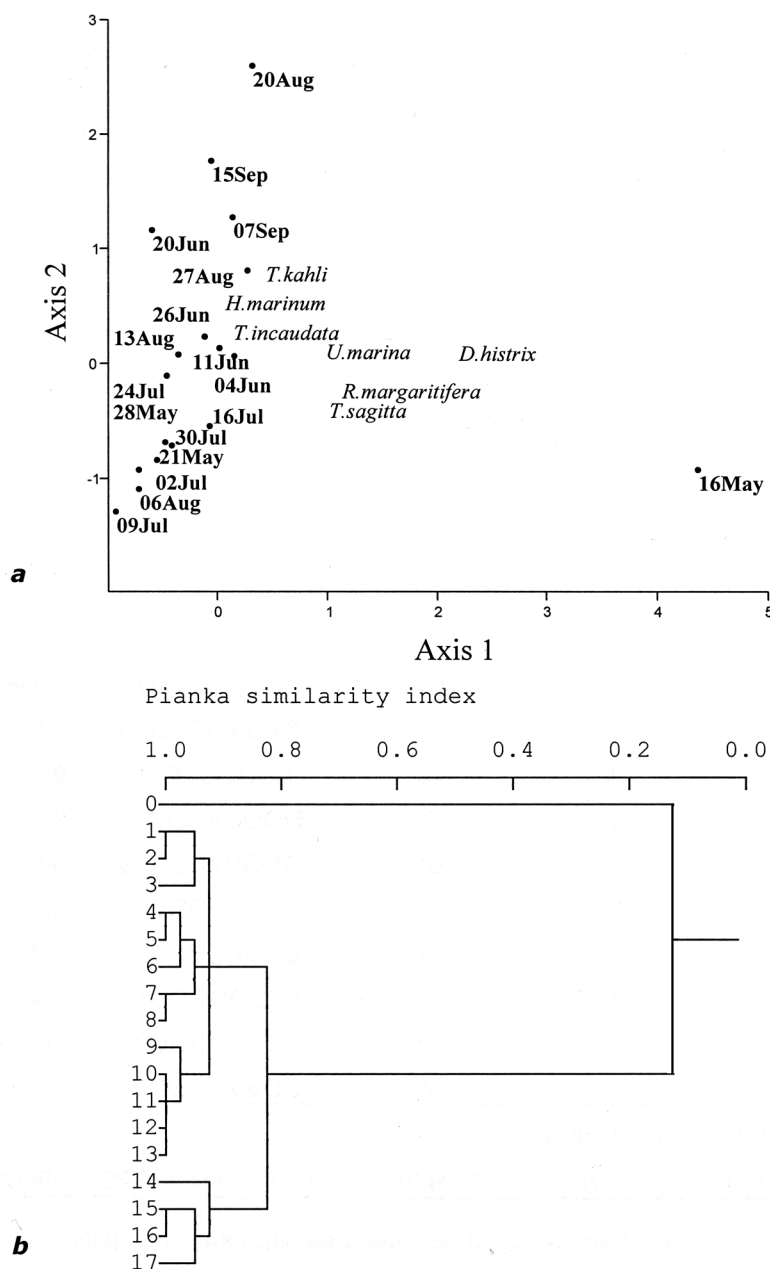


Fig. 14. Results of the community ordination (a) by detrended correspondence analysis (axis 1 explain 74% of the total community variance, axis 2 – 14%) and constrained cluster analysis (b) (0–14 – successive dates of sampling) using data on 2007.

Changes in the trophic structure of the community were distinctly untrended (Fig. 19 – 1998 as an example). During the 18-year-long period, in the course of the seasonal development of the community, a clear increase in the number of algal feeders was observed (compare Fig. 19 – 1993 and 2007). The ratio of raptorial feeders had different tendencies in different years, depending on the availability of prey (small ciliates and

nanoflagellates) and the environmental conditions. Thus, in 1993, 1995–2001 and 2003–2005 the abundance of protozoatrophs decreased, whereas in 1991–1992, 1994, 2002, 2006–2008 fluctuations of their abundances were registered. The number of symbiotrophs (*Kentrophoros* spp.) in some years (1991–2002) showed a tendency towards weak growth during the season, whereas in some other years (2003–2008) it was rather stable.

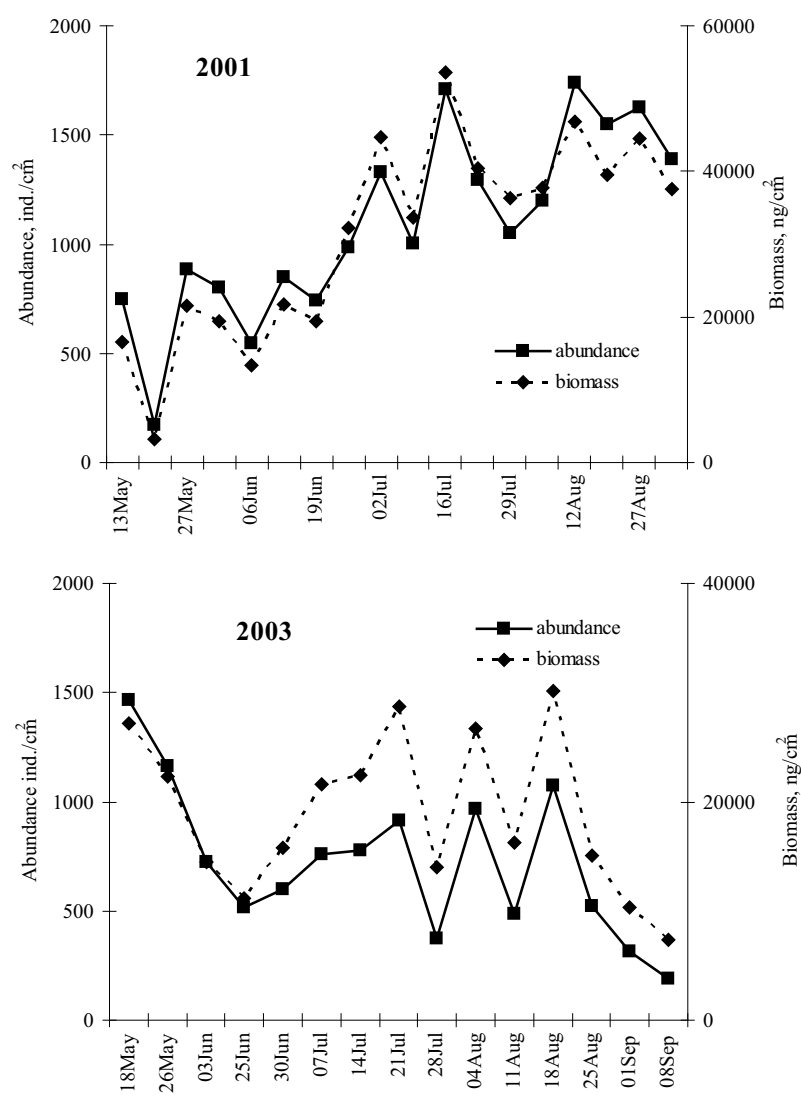


Fig. 15. Typical patterns of changes in abundance and biomass during seasonal succession in different years.

Discussion

High fluctuations of abundances of the majority of ciliate species in the interstitial localities in the marine littoral can result in rather accidental combinations of species in local communities

corresponding to one sample. Thus, 125 ciliate species that were identified in a local area during 18 years can form a huge number of structural variants. Multi-variance is a major trait of the ciliate community, as well of the communities of other organisms in the corresponding scale of space

Table 4. Types of trends of changes in the integral community characteristics during seasonal succession in 1991–2008.

Characteristics	Time				
	1991–1998	2000–2002	2003	2004–2006	2007–2008
Abundance	Rhythmic growth	Rhythmic growth	Rhythmic fall	Rhythmic growth	Rhythmic growth
Species richness	Gradual growth	Fluctuations around stable level	Rhythmic fall	Fluctuations around stable level	Rhythmic growth
Species diversity	Fluctuations around stable level	Fluctuations around stable level	Rhythmic fall	Fluctuations around stable level	Rhythmic growth

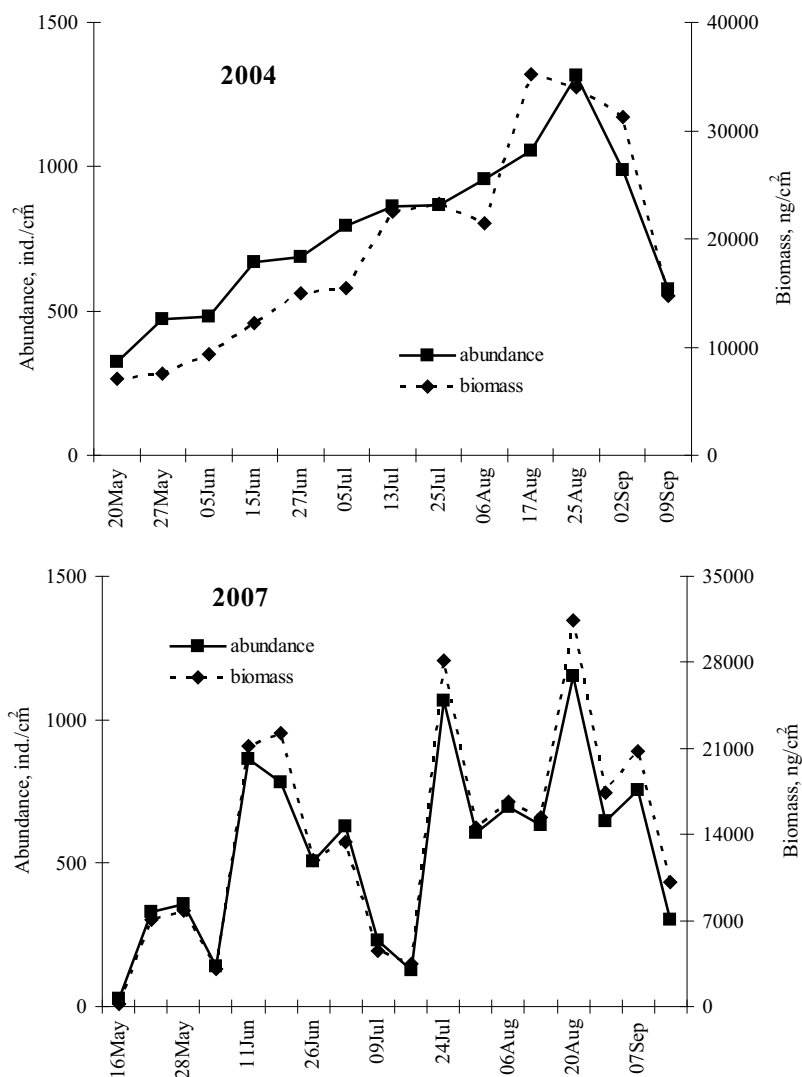


Fig. 15. (Continuation).

and time (Burkovsky, 2006). In different years and in different periods within the year, different combinations of dominant, subdominant and rare species are formed, which reflects the correspondence between the physiological characteristics of organisms and the environmental and biotic factors. The species that can find favourable conditions become dominants faster. Taking into the account the high generation rate of the ciliates (the doubling time varies from several hours to one or two days), the major factor of community organization was time. Under conditions optimal for certain species, the community could change beyond recognition in several days. This is the reason why in different time periods and in different localities in the marine littoral one can reveal many community variants, which are derivative from the overall community and are distinguished by combinations and ranking of dominant, subdominant and rare species (Burkovsky, 1992a, 2006).

There is only one possible cause of the substantial changes in community structure, and this is a significant change in the environmental characteristics. This is observed every year in the beginning of spring (Burkovsky et al., 2003). In other periods of the year, the major ecological factors (such as the availability of food, temperature, oxygen content, Eh, etc.) in the littoral sites never change that fast. On the other hand, the ciliate communities are well adapted to the gradual changes in the ecological factors, which results in the maintenance of the principal characteristics of the community (for instance, the patterns of niche partitioning, or the general set of species in the concrete littoral site) during a long-term period (Burkovsky, 1984).

However, since 1997, and particularly in 2003–2008 the siltation of the sediments grew considerably, decreasing the spaces of clean sand within the littoral. Siltation always leads to the decrease in the volume of interstitial spaces, the narrowing

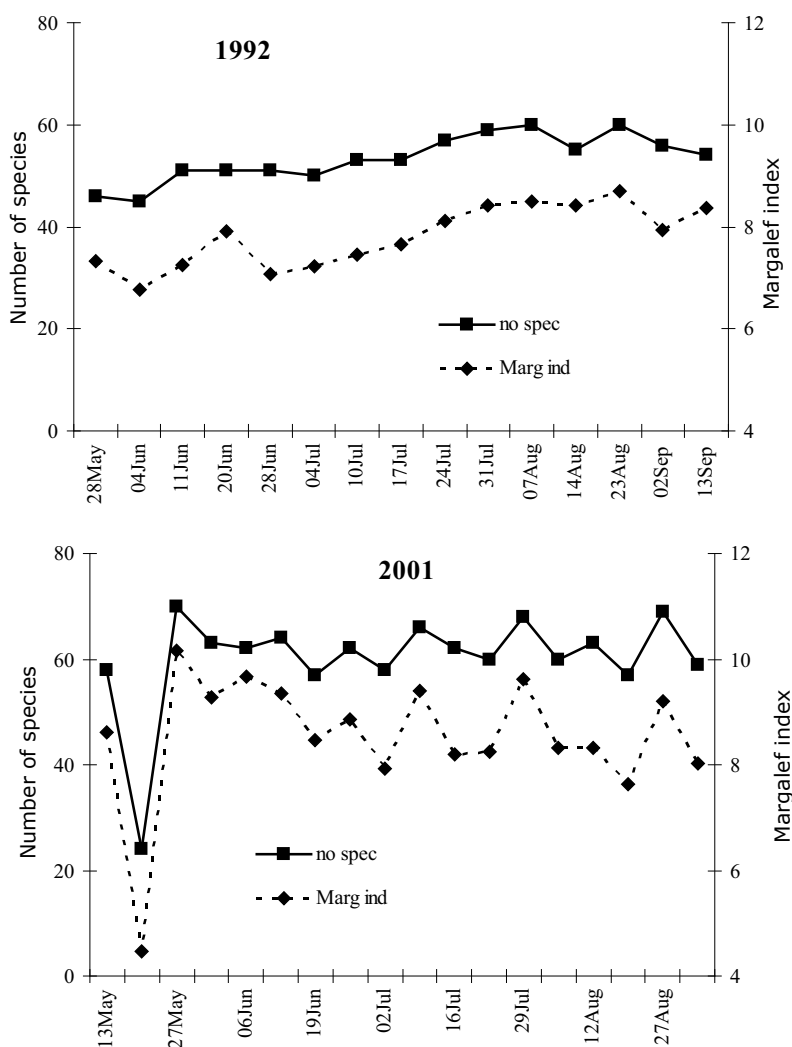


Fig. 16. Typical patterns of changes in species richness during seasonal succession in different years.

of the photic layer, the changes in the composition of the algal communities (the trend being from dinoflagellates to diatoms), the increasing amount of dead organic matter and the decrease in the oxygen content with the proportional increase in the concentration of carbon dioxide and hydrogen sulfide. As a result, the living space for oxyphilic organisms is reduced by several times. On the background of these interrelated changes, the abundance of eurytopic oxyphilic ciliate species (that are usually small-sized and feed on bacteria) decreased considerably during the last years, while the ratio of specific interstitial microaerophilic ciliates (that are predominantly medium to large-sized and feed on diatoms) correspondingly increased. Thus, both trophic and size structure were modified. The community of interstitial ciliates that in the first period of our investigation (1991–2002) was characterized by a multi-vectorial variation (within the indivisible pattern of community

organization), starting from a concrete moment (2003) became canalized in terms of community structure changes (in accordance with the trends of modifications of the major properties at the ecosystem level).

It is very important to emphasize that the changes in the community affect all the species but are more clearly visible in dominants. Thus, in the first years one of the common species, *Histiobalantium majus*, was replaced by an ecologically close but a more eurybiotic species *Histiobalantium marinum*. Another substantial modification was the appearance of a new dominant *Trachelocerca sagitta*, which had never been abundant previously. Moreover, in the beginning of the 18-year-long studies the most abundant set of species included *Remanella margaritifera*, *Trachelocerca incaudata*, *Coleps tessellatus*, *Histiobalantium majus*, *Uronema marina*, while at the end *Trachelocerca sagitta*, *Remanella margaritifera*, *Trachelocerca incaudata*

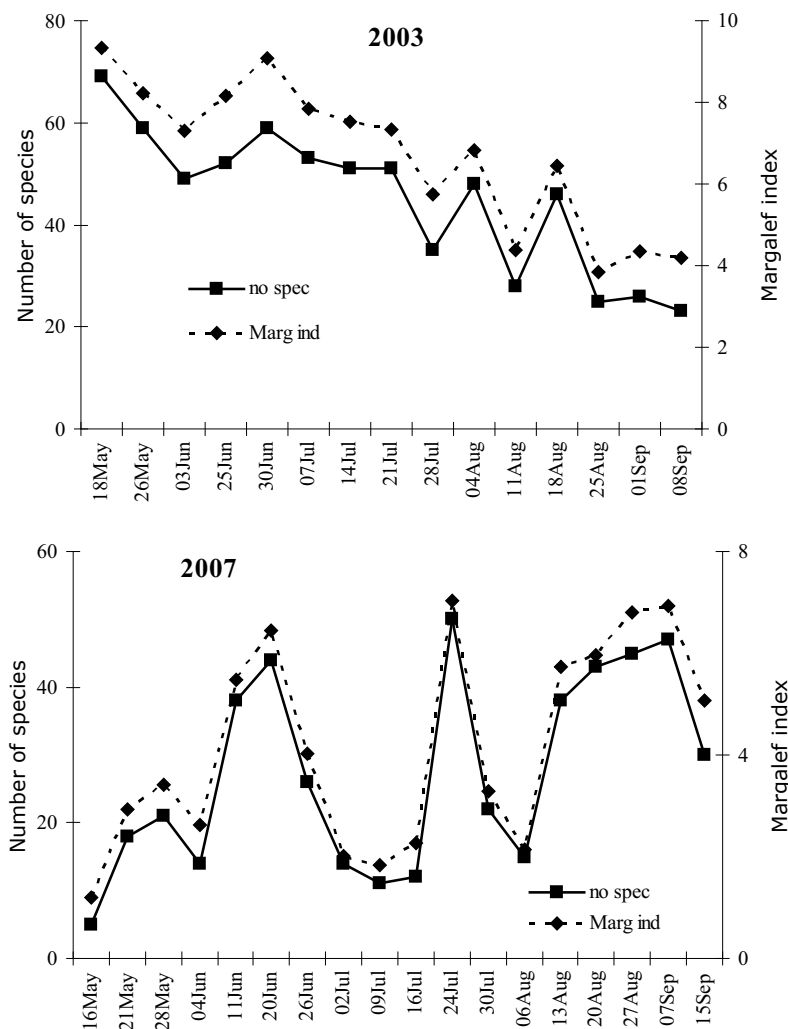


Fig. 16. (Continuation).

were abundant. In addition, some polysaprobic forms, such as *Cyclidium fuscum*, *Caenomorpha capucina*, *Tracheloraphis dogieli*, which can live in low oxygen concentrations, appeared in the community.

The periodicity observed in the community structure changes cannot be explained at present (one can distinguish the following stages: 1991-1995; 1998-2004; 2005-2008). This periodicity does not correspond either to the periods of solar activity or to the electromagnetic field perturbations. However, in two cases the beginning of the new stage was associated with the lowest (1998) or with the highest (2005) air temperature averaged for the season. Probably, this factor can change the strategy of the community development by affecting differentially the generation rates of different species. Moreover, since 2003 the ciliate community has been affected by a rather rapid siltation of

the sediment (this process has the periodicity of 11-12-years; Burkovsky, 2006), that modified the rhythm of modifications. The periodicity pattern observed is unlikely to be associated with other factors (salinity, amount of organic matter, Eh, pH). It is probable that it reflects the self-organization processes in the community and, therefore, is associated predominately with internal rather than external causes (Burkovsky et al., 2003).

It is interesting that similar rhythms were revealed in the 35-year-long changes in the macrobenthos community structure in the same littoral ecosystem (Burkovsky, 2006). During this period, on the background of stable species composition, fluctuations of the community structure were observed. They were realized as the replacement of dominant groups: either small-sized (gastropod *Hydrobia ulvae*, oligochaetes, polychaetes from the family Spionidae, large nematodes 1973-1984 and

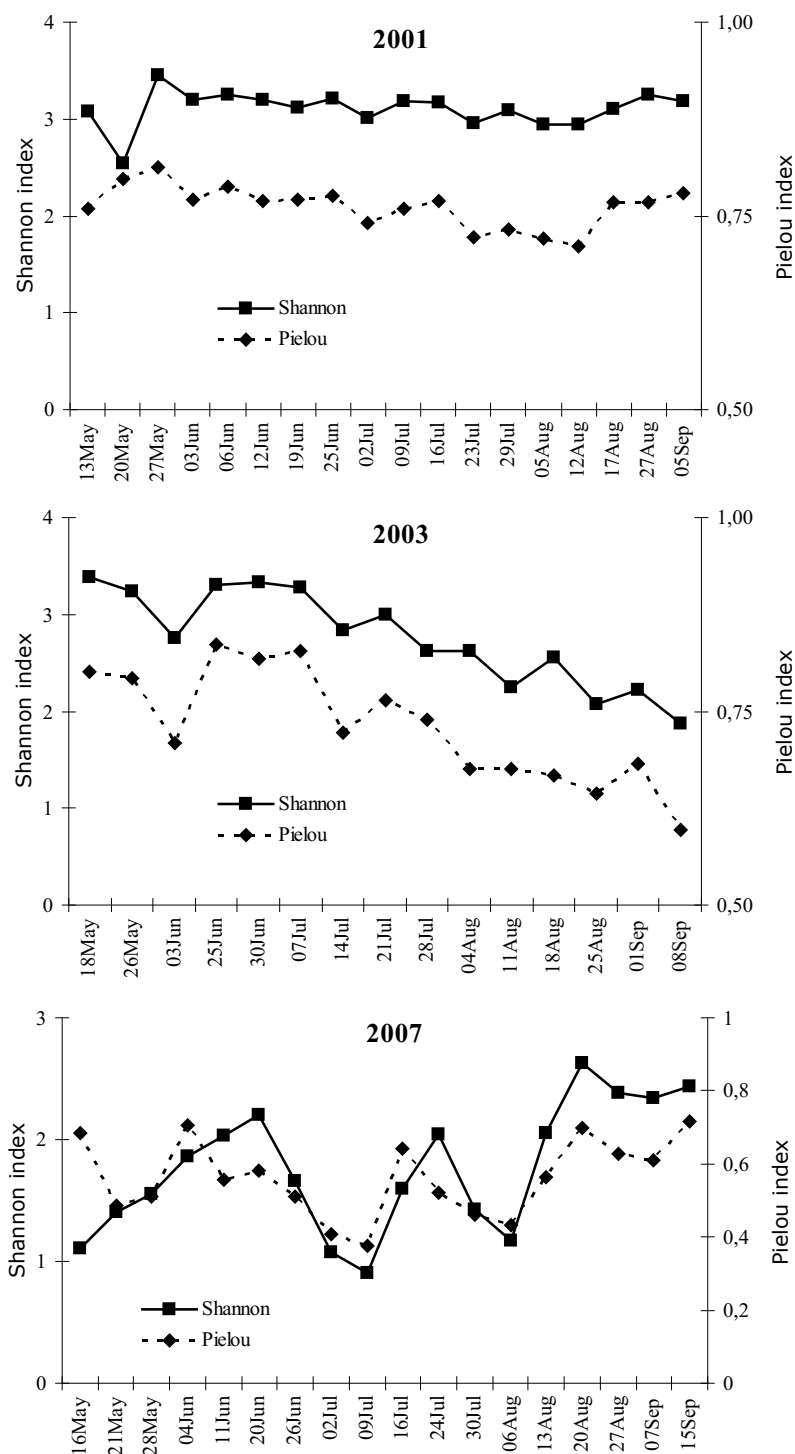


Fig. 17. Typical patterns of changes in species diversity during seasonal succession in different years.

1997-2007), or large-sized (bivalve mollusc *Mya arenaria* and polychaete *Arenicola marina* 1985-1996) organisms. This replacement corresponded to the changes of silt content in the sediment as well as with the development of halophytic vegetation.

Thus, despite the substantial differences in the perception of environment between tiny

protists (microbenthos) and large invertebrates (macrobenthos), long-term factors operating on the ecosystem level lead to the synchronization of community processes and maintenance of the unity of the whole ecosystem (Burkovsky, 1992a, 2006).

Unfortunately, there are no other investigations of the long-term dynamics of recent protozoan

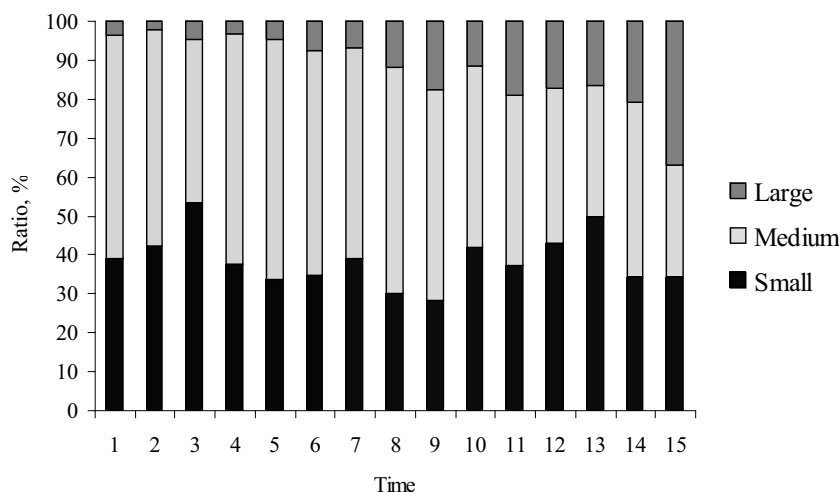


Fig. 18. Changes in size structure during seasonal succession in 2003. 1-15 — subsequent dates of sampling from May to September.

communities, and so possibilities for comparison are scarce. There were, however, some attempts to describe long-term variability of the communities of estuarine meiobenthos and marine macrobenthos. Coull (1985a, 1985b) studied the dynamics of total abundance and taxonomic composition of meiobenthic community on silty and sandy sediments in an estuary for 11 years. Similarly to our case, he revealed substantial inter year-fluctuations and a weak rhythm, which were in some cases correlated with salinity, temperature, Eh and granulometric structure of the sediment. The changes took place on the background of a rather stable taxonomic composition. No trends with an 11-year-long period were observed in our study.

Studies of the long-term changes in marine macrobenthic communities demonstrated prominent modifications caused by long-term anthropogenic influence: oil contamination in the Caspian Sea (Gasarov, 1972; Tarasov, 1988), eutrophication in the Black Sea (Zaika, 1992), and rapid fall of the water level in the Aral Sea (Andreev, 1999). All these changes have a destructive character. Substantial transformations are usually not observed in naturally developing communities. Changes caused by hydrological factors are rather smooth, and do not affect the basics of the community organization (Burkovsky, 2006; Galkin, 1991; Oshurkov, 1985; Yablonskaya, 1971). To note, in some cases the community structure can be substantially affected by predators (Oshurkov et al., 1989). For example, mass migrations of sea-ape towards the sea-urchins concentrations lead to the decrease in the abundances of the latter, as well as of bivalve molluscs and crustaceans, and affect considerably the whole benthic community. However, the peculiarity of

this situation is that once the predator is absent the community turns to the initial state.

Acknowledgements

We would like to thank Natalia Lentsman for considerably improving the English text. The work was supported by the Russian Foundation for Basic Research (grant No. 10-4-00511).

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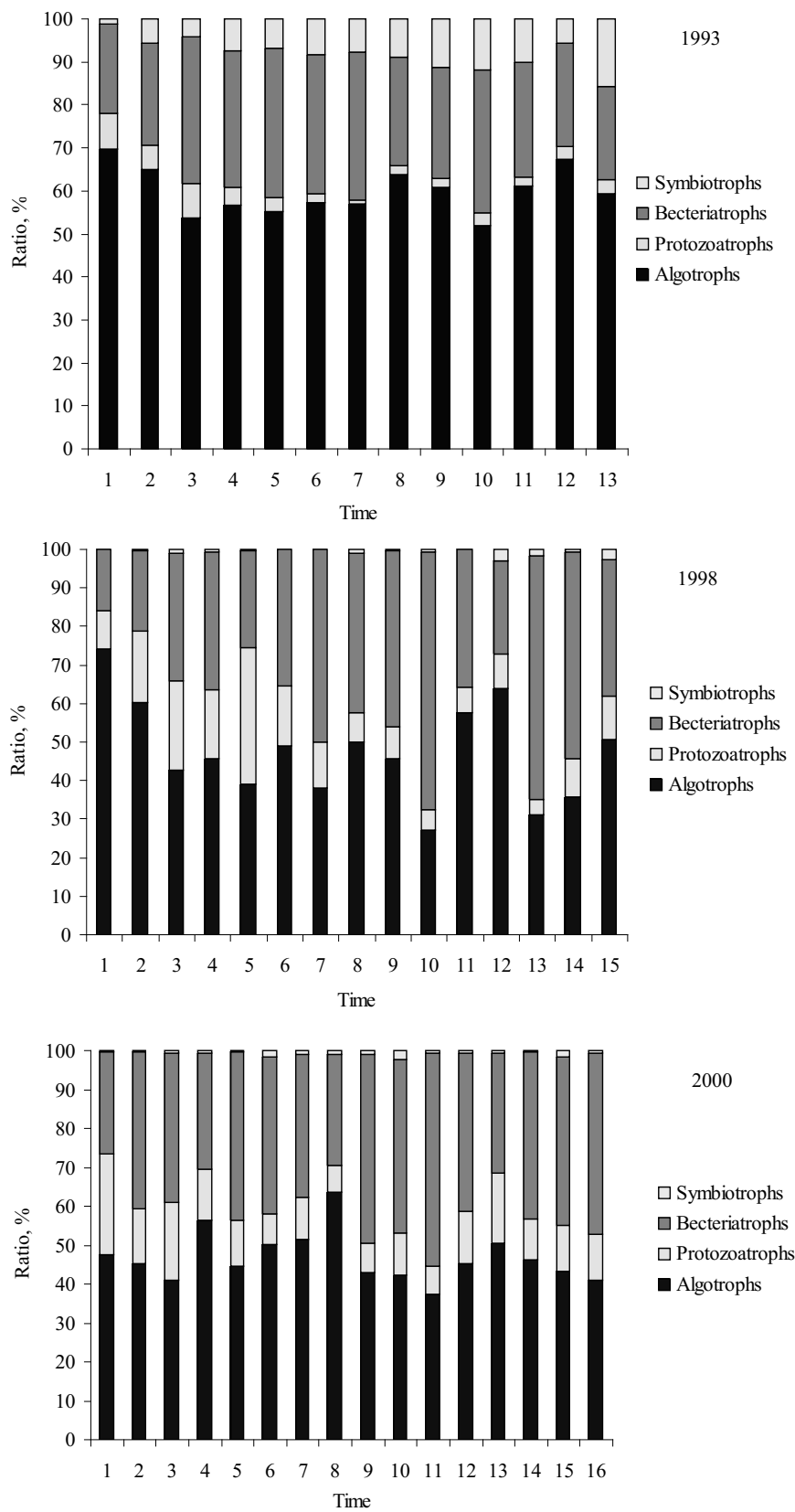


Fig. 19. Typical patterns of changes in size structure during seasonal succession in different years. 1-18 – subsequent dates of sampling from May to September.

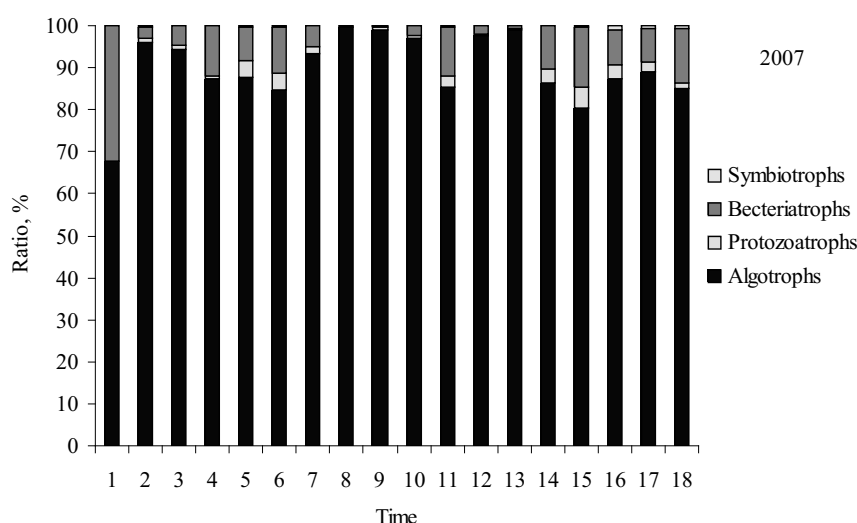


Fig. 19. (Continuation).

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