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Composition, diversity and distribution of microbenthos across the intertidal zones of Ryazhkov Island (the White Sea)

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Abstract

The composition and distribution of the main unicellular eukaryotic groups (diatom algae, ciliates, dinoflagellates (DF), other phototrophic (PF) and heterotrophic flagellates (HF)) were investigated in sandy sediments at five stations allocated across the tidal sheltered beach of the White Sea. Overall, 75 diatoms, 98 ciliates, 16 DF, 3 PF and 34 HF species were identified; some are new records for the White Sea. Common species for each group are illustrated. Diatoms and ciliates showed high alpha-diversity (species richness per sample), whereas flagellates were characterized by high beta-diversity (species turnover across the intertidal flat). Each group demonstrated its own spatial pattern that was best matched with its own subset of abiotic variables, reflecting group-specific responses to environmental gradients. Species richness increased from the upper intertidal zone seaward for ciliates but decreased for HF, whereas autotrophs showed a relatively uniform pattern with a slight peak at the mid-intertidal zone. Across the littoral zone, all groups showed distinct compositional changes; however, the position of the boundary between “upper” and “lower” intertidal communities varied among groups. Most of the species found at Ryazhkov Island are known from many other regions worldwide, indicating a wide geographic distribution of microbial eukaryotic species. © 2013 Elsevier GmbH. All rights reserved.

Keywords: Ciliates; Diatoms; Diversity; Flagellates; Microbenthos; White Sea

Introduction

The microbenthos (unicellular eukaryotic organisms inhabiting marine sediments) includes various groups commonly presented in interstitial environments, with a

noticeable abundance and diversity. These groups are important for coastal ecosystem functioning, participating both as producers and consumers (e.g., Dietrich and Arndt 2000; Patterson et al. 1989). Whereas the role of meio- and macrofauna received considerable attention, the structure and function of microbenthic communities in intertidal sediments are largely unknown, and many aspects of their ecology are still poorly understood. There are very few studies simultaneously investigating all components of microbenthos, especially in the Arctic (Azovsky et al. 2004; Dietrich and Arndt 2000; Epstein 1995, 1997; Fernandez-Leborans

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2001). The lack of studies encompassing the main groups of microbiota along with their environmental characteristics impedes meaningful comparisons between various seas and/or regions.

Various groups of the White Sea microbenthos have been studied in various depths. While free-living ciliates in the region are relatively well studied, both in taxonomic and ecological aspects (e.g., [Burkovsky 1970](#); [Burkovsky and Mazei 2010](#); [Mazei and Burkovsky 2005, 2006](#); [Raikov 1962](#); and references therein), information regarding the diversity of benthic diatoms is rather scarce ([Bondarchuk 1980](#); [Saburova 1995](#); [Tchesunov et al. 2008](#)). Data on benthic flagellates of the White Sea intertidal flats are almost completely lacking (but see [Tikhonenkov and Mazei 2006](#); [Tikhonenkov et al. 2006](#)). The diversity of sand-dwelling dinoflagellates of the White Sea has not been examined, yet. The data on the relationship between microbenthic assemblages and environmental parameters are fragmentary.

The purpose of this study was to analyze the composition and distribution of different protist groups on the environmental background across the intertidal flat of the White Sea.

Material and Methods

Study area

Investigations were conducted from 28 to 30 July 2009 at the Yuzhnaya Bay of Ryazhkov Island, situated in the inner part of the Kandalaksha Gulf of the White Sea (67°02' N, 32°35' E, [Fig. 1a, b](#)). The area studied was a wide, flat and sheltered beach, 146 m across the intertidal zone, protected from wave action. The tides had a regular semi-diurnal cycle with a maximum tidal range of 2.5 m. Sediments were silty sands. The beach index was equal to 2.7, which corresponds to protected, highly dissipative beach conditions ([McLachlan and Dorvlo 2005](#)).

Sampling design

Five stations were selected along a transverse transect across the bay ([Fig. 1c](#)): station 1 – at the upper intertidal zone (23 m seawards from the shore defined as the astronomic high-tide line), st. 2 – at the upper part of the mid-intertidal zone, st. 3 – at the lower part of the mid-intertidal zone, st. 4 – at the upper part of the lower intertidal zone, and st. 5 – at the lower part of the lower intertidal zone near the low-tide mark. The top 3 cm of the sediment layer was sampled by plastic tube corer (sectional area 1 cm²). At each station, two series of 15 subsamples were collected from a 50 × 50 cm² area. The subsamples from each series were pooled to yield the composite samples, one to enumerate flagellates and ciliates, and another one for diatom analysis (see below). One extra sample for ciliates was collected from the mid-intertidal zone part of the main transect.

Measurement of environmental parameters

Salinity, pH and Eh of the pore water at the sampling sites were measured *in situ* simultaneously with the collection of samples from the surface (0–1 cm) layer of intact sediment, with a hand refractometer (Krüss S-10 salinometer, Germany), a pocket-sized pH-meter and a Redox-meter with automatic temperature compensation (Hanna Instruments, USA). Air-dry weight-based particle size distribution was determined by sieving method; then mean particle size, sorting (as logarithmic standard deviation) and silt content (as fraction < 0.1 mm) were calculated.

Methods of microbenthos extraction and treatment

Sand-dwelling dinoflagellates (DF), phototrophic flagellates (PF) and ciliates were extracted from the sediment using [Uhlig's \(1964\)](#) frozen seawater method and a 125 µm mesh filter. Cells were collected in a Petri dish beneath the filter and examined alive using a stereomicroscope. To enumerate the ciliates, a random set of microscopic fields corresponding to 1/15 of the total sample was examined (i.e., one mean statistical square centimeter). For detailed observations, cells were isolated by micropipette and examined and photographed using a Leica DM 2500 light microscope (Leica, Wetzlar, Germany) with a differential interference contrast (DIC) optics and a Leica DFC 420C digital camera at 400× and 1000× magnifications. Ciliates were identified using living observations as well as protargol impregnation ([Foissner 1991](#)). The thecal plate patterns of armored dinoflagellates were examined after staining with Calcofluor White (Sigma Chemical Co.) as described by [Fritz and Triemer \(1985\)](#). All presented observations are based on freshly collected living cells utilizing a light microscope.

Alternatively, one replicate from each sample was subjected to standard diatom analysis. Sediment samples were treated with ultrasound (5 min, 75 Hz) to detach adherent epipsammic diatoms from sediment particles. Diatoms were eluted by repeated washing and decantation, and the elutant was centrifuged (5 min, 3000 rpm). Diatom frustules were cleaned in a mixture of the concentrated nitric acid and K₂Cr₂O₇, and rinsed with 3–4 changes of distilled water. Identifications were made from cleaned material mounted in Hyrax ($n = 1.71$), and frustules were observed and photographed with an Axiovert 200M (Zeiss, München-Halbergmoos, Germany) microscope equipped with a phase contrast optic and digital camera. Cell dimensions were measured from images using AxioVision 3.0 (Carl Zeiss) software. A total of 200–300 diatom frustules per sample were identified and counted for qualitative analyses of species composition. All diatom species were classed according to their life-forms: epipellic (non-attached, highly motile benthic forms), epipsammic (virtually non-motile forms attached to sediment grains), epilithic (usually fixed on hard substrata) or

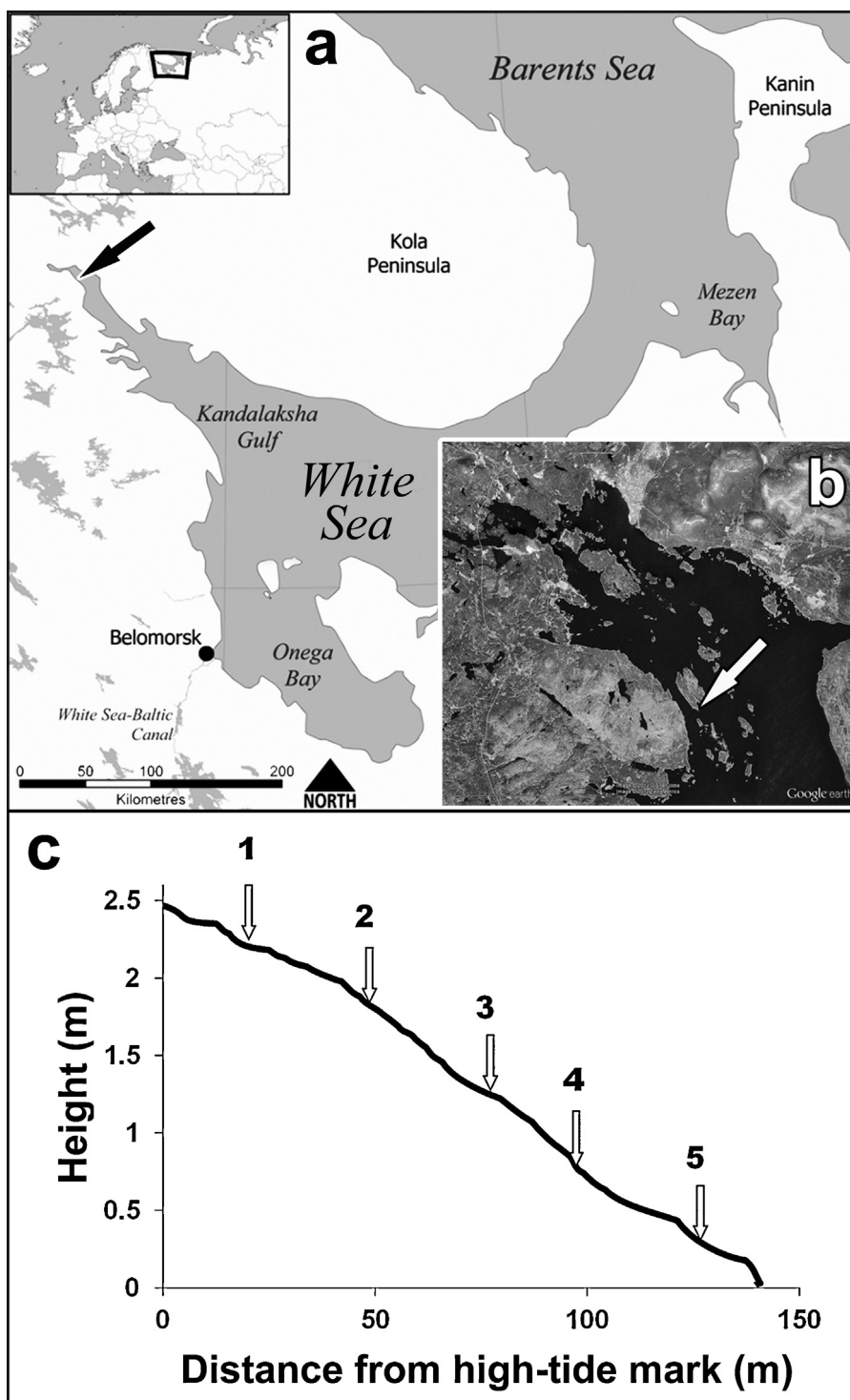


Fig. 1. Location of the studied area. A – map of the White Sea; B – satellite image of the Kandalaksha Gulf (Google Earth) where the sampling area was located; C – position of sampling stations 1–5 at the tidal flat profile (vertical axis – height above low-tide level, m). Arrows in A and B indicate the sampling area.

epiphytic (fixed on plants or macroalgae) using the literature and our personal observations.

To study heterotrophic flagellates (HF), the sediment samples with water were stored in 50-ml flasks and maintained at approximately 33 °C during transportation to the laboratory. Two replicates, each of 5 ml, were analyzed in Petri

dishes from each sample to study species composition. The light microscope observations were made using a Biolam-I microscope (Lomo, Russia), equipped with a phase contrast and water immersion objectives, giving a total magnification 770 \times , and using a Reichert (Austria) microscope with interference Nomarski contrast and glycerin immersion objectives

Table 1. Environmental features for stations sampled from the upper (station 1) to lower (station 5) intertidal zone.

	Station				
	1	2	3	4	5
Distance from shore, m	23	53	83	104	136
Salinity of pore water, psu	13	15	16	19	20
Eh in upper 1-cm sediment layer, mV	120	120	120	160	190
pH in upper 1-cm sediment layer	8.3	8.2	8.1	8.1	8.0
Mean particle size, mm	0.177	0.152	0.177	0.158	0.176
Sediment sorting (particle size SD, mm)	0.197	0.120	0.124	0.112	0.238
Silt content, %	14.9	29.1	9.7	22.3	22.3

(1000×). The microscopes were equipped with an analog video camera AVT HORN MC – 1009/S, which was connected to a Panasonic NV-HS 850 video recorder. Image acquisition was in VHS and S-VHS modes, followed by the digitalization of images and conversion of videofragments to AVI files, which were conducted in order to more precisely identify flagellates, in addition to direct observations on living cells.

To standardize our data, all identified taxa were assigned to groups according to the system of classifying eukaryotes and protists presented by Adl et al. (2005), whereas within groups, taxa were arranged according to particular taxonomic schemes. Diatoms were classified according to Round et al. (1990); DF according to Sournia (1986), with some later additions and modifications (Chrétiennot-Dinet et al. 1993; Hoppenrath 2000a); and PF and HF according to Adl et al. (2005) and Lee and Patterson (2000). The classification system by Lynn (2008) was applied to ciliates. Species names are listed in alphabetical order within genera.

Statistical analyses

Several diversity measures were used for each group (diatom algae, DF, PF, HF and ciliates). To evaluate species richness, the total number of species identified (S_{TOT}) and mean number of species per station (S_{ST}) were estimated. The non-parametric Chao2 method was applied to estimate the “full” number of expected species (S_{CHAO}) at the five stations, accounting for potentially overlooked rare species (Clarke and Warwick 2001). To standardize the values of diversity estimated using different number of cells, we applied the expected number of species $ES(n)$. Based on the minimal sample counts, the expected numbers of species for a theoretical sample of 100 specimens (for diatoms) or 250 specimens (for ciliates) were calculated at each station.

Two measures of beta-diversity (also known as ‘species turnover’) were used: Whittaker’s $\beta_W = S_{TOT}/S_{ST} - 1$ and a slope of the species accumulation curve estimated in double logarithmic coordinates, β_{SAC} (Azovsky et al. 2012).

Cluster analysis of stations (unweighted pair group average method) was conducted using the Sørensen similarity index for presence–absence data. Also, cluster analysis was

performed on the basis of quantitative data for diatoms and ciliates. These cluster analyses employed the Bray–Curtis similarity index; the data were standardized to give the percentage of the total abundance (overall species). The relationship between environmental variables and microbenthic community structure was explored by means of the BIOENV procedure (Clarke and Warwick 2001), correlating Euclidian distance similarity matrices of environmental variables with Sørensen among-stations similarity matrices for each group. In addition, Bray–Curtis similarity matrices based on quantitative data were examined for diatom algae and ciliates. All environmental variables were normalized before the analysis. On account of the low number of stations, the maximum number of trial variables per model was limited to two (out of the complete set of seven environmental variables, see above), to avoid over-fitting the models.

All statistical analyses were performed using the PRIMER 6 (Plymouth Routines In Multivariate Ecology, PRIMER-E Ltd., Plymouth, UK) software package.

Results

Environmental parameters

Hydro-chemical conditions gradually changed downward from upper to lower intertidal zone (Table 1). In particular, salinity increased from 13 to 20 psu, and pore water Eh increased from +120 up to +190 mV. Sediment composition was similar at all stations (fine silty sand with modal particle size 0.15–0.17 mm), whereas stations 1 and 3 were less silted than the others.

Taxonomic composition

The full taxonomic list of the species is presented as an electronic supplement (Table S1).

Diatoms

Seventy-five taxa were found, 64 of them were identified to the species/subspecies level (Table S1). The richest families were Naviculaceae (17 species), Fragilariaceae (7),

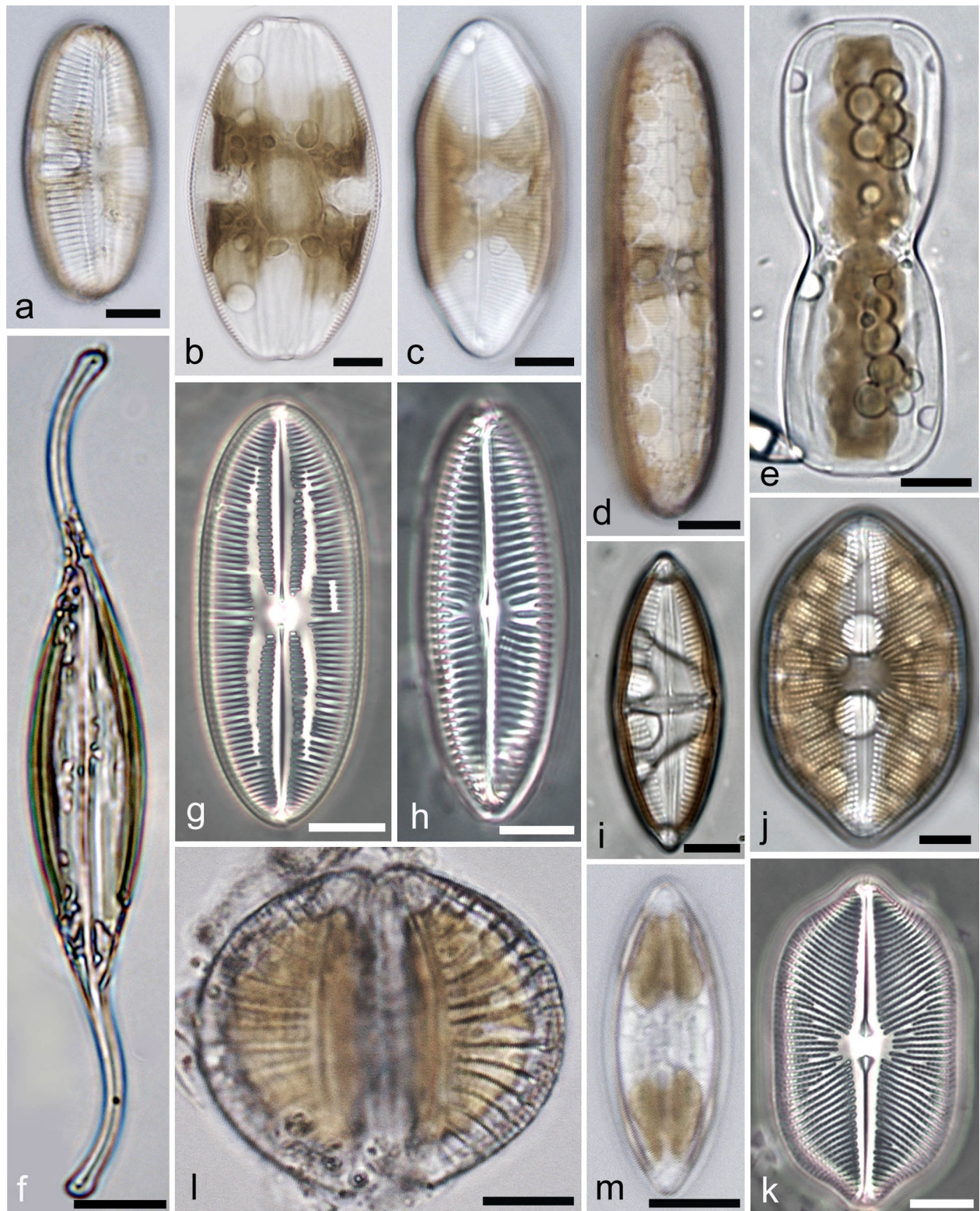


Fig. 2. Common diatoms of the Ryazhkov Island: a – *Diploneis smithii*; b – *Amphora proteus*; c – *Caloneis africana*; d – *Caloneis excentrica*; e – *Gyrosigma rectum* (girdle view); f – *Gyrosigma fasciola*; g – *Lyrella abrupta*; h – *Navicula digitoradiata*; i – *Navicula palpebralis* var. *angulosa*; j – *Petroneis latissima*; k – *Petroneis humerosa*; l – *Rhopalodia musculus*; m – *Mastogloia exigua*. a–f, i–m – bright field, living cells; g, h, k – phase contrast, permanent slide; scale bars = 10 µm.

Cocconeidaceae (7) and Lyrellaceae (4 species). Eight species (*Halamphora hybrida*, *Caloneis africana*, *C. excentrica*, *Dickieia subinflata*, *Ctenophora pulchella* var. *lanceolata*, *Navicula bipustulata*, *Opephora schwartzii* and *Rhopalodia pacifica*) can be considered as new records for the White Sea diatom flora. Common species are illustrated in Fig. 2.

In regard to their ecological properties, 26 species were epipsammic, 36 were epipelagic, and 10 were epilithic and epiphytic. In terms of relative abundance, the composition of diatom flora was rather similar on stations 2–5. The epipsammic forms predominated here (about 80% of the total abundance), whereas epipelagic forms composed 17–18%. The exception was the uppermost station 1, where epipsammic forms made up 53.4% of the total abundance, while epipelagic and epiphytic forms contributed 35.9% and 10.7%, respectively.

Only twenty-one species were present at all five stations, whereas twenty-five species were unique (each represented by a single cell). The most abundant species were *Martyana martyi*, *Planothidium lemmermannii*, *P. delicatulum*, *P. hauckianum* and *Opephora mutabilis*. These species constituted 31–54% of the total abundance of diatoms.

Dinoflagellates

Dinoflagellates were quite diverse and comprised mostly of unarmored phototrophic sand-dwelling forms. We identified a total of 16 DF species from 9 genera (Table S1); most are reported for the first time from the White Sea. The genus *Amphidinium* was the richest one, with seven identified species; followed by *Togula*, with two species; and *Prorocentrum*, *Gymnodinium*, *Durinskia*, *Herdmania*, *Katodinium*, *Oxyrrhis* and *Sabulodinium* all with a single species each. Some common species are illustrated in Fig. 3.

It is worth noting that *Durinskia* cf. *baltica* from our material was similar to that described by Carty and Cox (1986) with respect to general appearance and plate tabulation. However, it differed in having seven precingular plates (Fig. 3f–h) rather than six in precingular series as originally described for *D. baltica*. Similar species possessing seven precingular plates were described from Australian marine sediments by Murray (2003) (as *D. baltica*) and from the Wadden Sea sediments by Hoppenrath (2000b) (as *Durinskia* sp.). Affinity of the form, with the deviant plate pattern, from our material to the genus *Durinskia* is questionable due to the presence of one extra precingular plate.

The most abundant DF species was *Togula britannica* (syn. *Amphidinium britannicum*, Fig. 3e), which bloomed in the surface layer of the sand (more than 10^4 cells/cm²) at the middle intertidal level (station 3). *Amphidinium carterae* and *A. herdmanii* were also quite abundant, mainly at the middle intertidal level. Only one species, *Katodinium asymmetricum* (Fig. 3l), was widely distributed throughout the entire examined area. This ubiquitous small-sized

heterotrophic dinoflagellate was commonly observed at nearly every station from the upper down to the lower intertidal zone.

Phototrophic flagellates

Three species were identified (Table S1, Fig. 4). Maximum species diversity and abundance were associated with the upper and middle intertidal zones.

Heterotrophic flagellates

Thirty-four species were identified (Table S1, Fig. 5). Flagellates were dominated in terms of species richness from the following groups: Choanomonada, Kinetoplastea, Bicosoecida, and Apusozoa. The highest numbers of species were from the genera *Salpingoeca* (4 species), *Amastigomonas* (4) and *Cafeteria* (3). The most common species (observed in more than 60% of samples) were *Ancyromonas sigmoides* (Fig. 5n–p), *Cafeteria roenbergensis*, *Neobodo designis* (Fig. 5e–g), and *Goniomonas amphynema*; the first two were found at every station. Twenty-one species (62% of the total species richness) were detected in samples only once. Six HF species (*Amastigomonas muscula* (Fig. 5a–d), *Colpodella pugnax*, *Monosiga* aff. *micropelagica*, *Pendulomonas adriperis*, *Hemistasia amylophagus*, and *Rhynchobodo thaeniata*) are new records for the White Sea.

Ciliates

Altogether, 98 species and forms of ciliates from 49 genera were identified (Table S1). Some common species are illustrated in Fig. 6. Twenty-eight species occurred at a single station, and four of them were found only once (singletons). Eight species (*Loxodes penardi*, *Kentrophoros fistulosus*, *Geleia swedmarkii*, *Condylostoma patula*, *C. psammophila*, *Chlamydon minutus*, *Amphileptus lanceolatus* and *A. marina*) were recorded for the first time in the White Sea. *Remanella margaritifera* (Fig. 6a), *R. rugosa*, *Kentrophoros fasciolatus*, *Trachelocerca incaudata*, *T. sagitta*, *Coleps pulcher* and *Uronema marinum* (Fig. 6d) were the most abundant species (mean abundance > 30 cells cm⁻² each). These seven species constituted 13.4–74.0% (average 44.7%) of the total ciliate abundance.

Diversity

The estimated values for the diversity components are presented in Table 2. The most species-rich groups (ciliates and diatom algae) also had higher species richness per station (alpha-diversity), while dinoflagellates and heterotrophic flagellates demonstrated noticeably higher beta-diversity (i.e., these groups were more heterogeneously distributed between stations). The expected “full” species richness for ciliates (estimated by Chao2 method) was rather close to the observed value (119.8 vs. 98 species). In contrast, the expected richness for the other groups was 50–70% higher

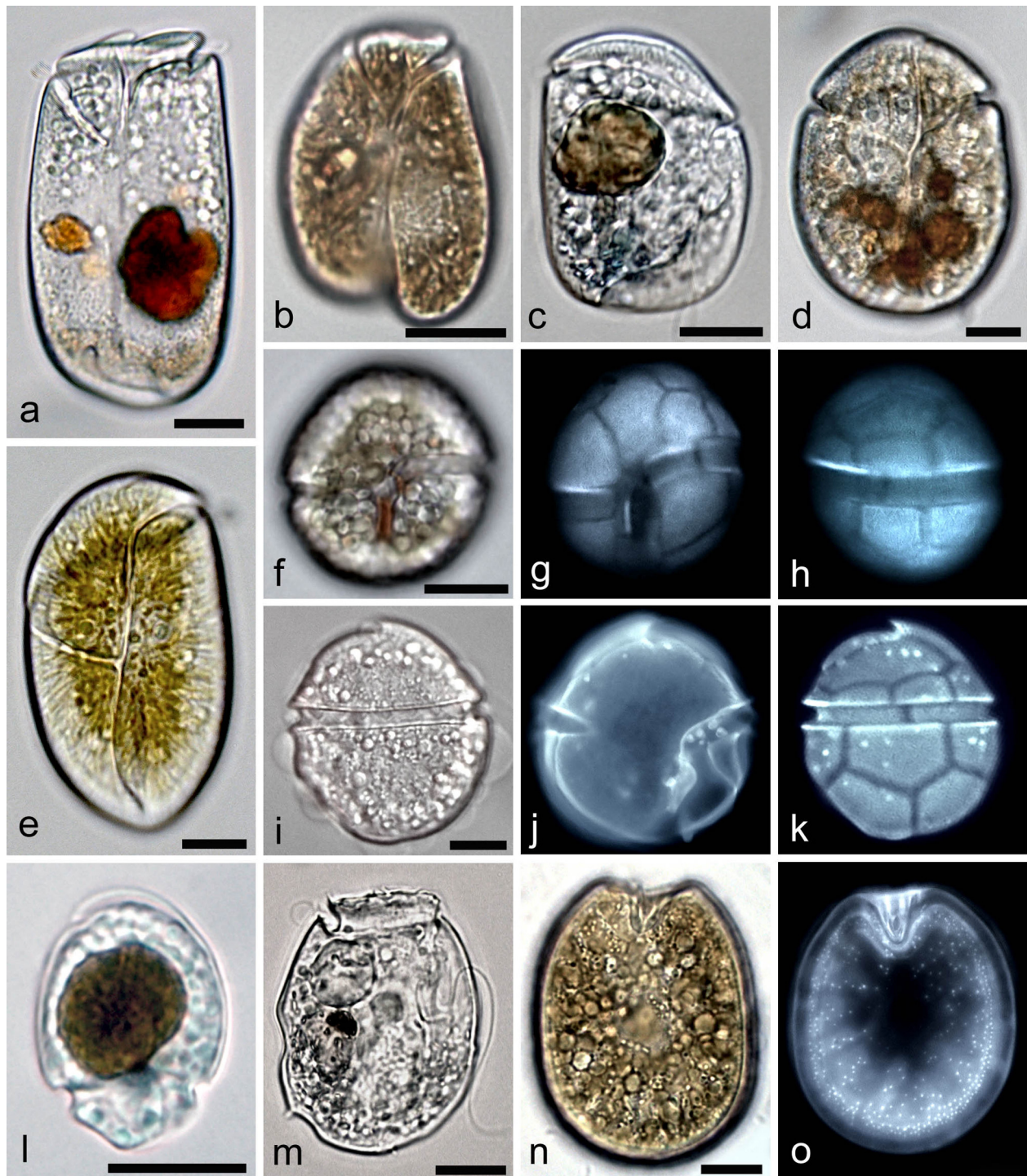


Fig. 3. Common dinoflagellates of the Ryazhkov Island: a – *Amphidinium glabrum*; b – *Amphidinium herdmanii*; c – *Amphidinium semilunatum*; d – *Gymnodinium venator*; e – *Togula britannica*; f–h – *Durinskia* cf. *baltica*; i–k – *Herdmania litoralis*; l – *Katodinium asymmetricum*; m – *Sabulodinium undulatum*; n, o – *Prorocentrum fukuyoi*. a–f, i, l–n – bright field, living cells; g, h, j, k, o – epifluorescent images after Calcofluor White staining; scale bars = 10 μ m.

than the observed values, due to their increased patchiness and larger number of unique species. No single group showed noticeable saturation of the species accumulation curve, indicating potentially higher diversity and/or under-sampling.

Across-beach distribution

Diatoms

No pronounced differences among stations could be observed for species richness (Fig. 7) or composition

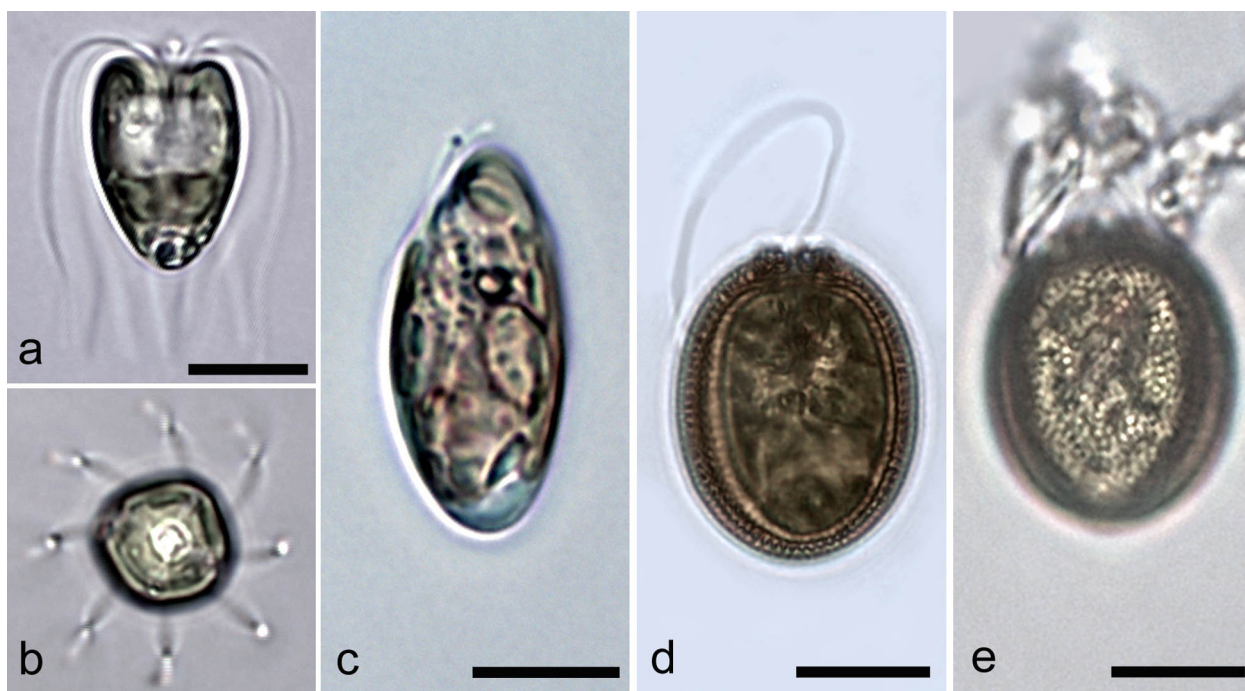


Fig. 4. Common phototrophic flagellates of the Ryazhkov Island: a, b – *Pyramimonas* cf. *octopus*; c – *Rhodomonas salina*; d, e – *Trachelomonas* sp. Bright field, living cells; scale bars = 10 μ m.

(Fig. 8a). Only a few species clearly preferred a certain horizon (e.g., *Mastogloia elliptica* and *Rhopalodia musculus* occurred at the upper intertidal zone, while *Rhabdonema minutum*, *Cocconeis placentula* var. *euglypta*, *Dimerogramma minor*, *Achnanthes brevipes* var. *intermedia* and *Halamphora hybrida* occurred at the middle and low intertidal zones). All these species were rare or unique. However, the uppermost station 1 differed significantly from all others in terms of relative abundances (Fig. 9a). Epipelagic (e.g., genera *Navicula*, *Parlibellus*, and *Fallacia*), epilithic and epiphytic forms (*Mastogloia*, *Synedra*) played a noticeable role at this station (almost 50% of the total abundance). By contrast, epipsammic diatoms (e.g., genera *Achnanthes*, *Amphora*, *Planothidium*, *Opephora*, and *Cocconeis*) were strongly predominant at the middle and low intertidal levels, constituting over 80% of the total abundance there. Surprisingly, this pattern was not consistent with the distribution of sediment properties. Station 1 had an even lower silt content compared to the others (Table 1). The BIOENV analysis indicated that salinity and sediment sorting best explained the commu-

nity variation in terms of the species presence–absence data (Spearman's $\rho = 0.681$, Table 3). This combination also best explained community variation in terms of species relative abundances.

Dinoflagellates

Most of the DF species were associated with the upper or mid-intertidal zones (Fig. 7a). Three assemblages could be distinguished, based on the cluster analysis (Fig. 8b). *Prorocentrum* spp., *Oxyrrhis marina*, *Herdmania litoralis*, *Amphidinium operculatum* and *A. steinii* were associated with the upper intertidal zone (stations 1 and 2), while a relatively rich assemblage with predominance of *Amphidinium* (5 species) and *Togula* (2 species) occupied the middle part (stations 3 and 4). *Gymnodinium venator* and *Sabulodinium undulatum* were recorded in low numbers only at the lower intertidal zone (station 5). The BIOENV analysis indicated the highest correlation between DF composition and hydrochemical parameters (redox potential and pH, Spearman's $\rho = 0.845$, Table 3).

Table 2. Diversity parameters for different groups of microbenthos (DF – dinoflagellates, PF – phototrophic flagellates, and HF – heterotrophic flagellates).

	Diatoms	DF + PF	HF	Ciliates
Total species number observed	75	19	34	98
Chao2-estimated species number	126.1	29.0	58.5	119.8
Mean species number per station	43.2	7	11.2	52.6
Whittaker' beta-diversity, β_w	0.71	1.71	2.04	0.81
Accumulation curve slope, β_{SAC}	0.350	0.624	0.694	0.366

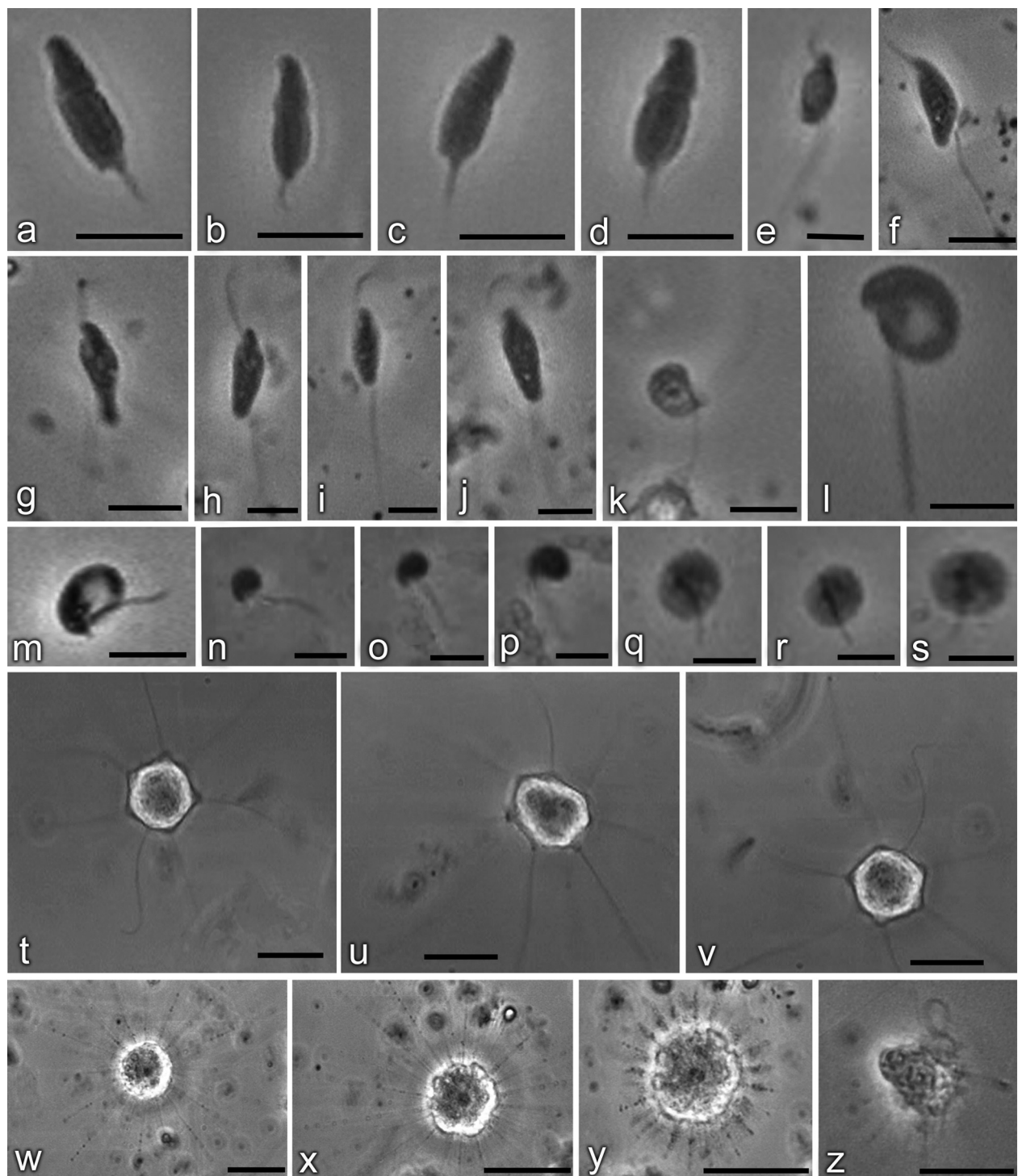


Fig. 5. Common heterotrophic flagellates of the Ryazhkov Island: a–d – *Amastigomonas muscula*; e–g – *Neoodo designis*; h–j – *N. saliens*; k – *Pseudobodo tremulans*; l, m – *Metopion fluens*; n–p – *Ancyromonas sigmoides*; q–s – *Discocelis saleuta*; t–v – *Multicilia marina*; w–z – *Ciliophrys infusionum*. Phase contrast, living cells; scale bars = 5 μm for a–s, 20 μm for t–v, 10 μm for w–z.

Heterotrophic flagellates

Species diversity was the highest at the upper intertidal zone (Fig. 7a). Out of 23 HF species presented at station 1, fourteen were only found here. This specificity determined the particular position of the station on the dendrogram

(Fig. 8c). Diversity at the lower intertidal zone (stations 4 and 5) was poorer and less specific (only 4 out of 13 species were restricted to this zone). Because both freshwater and marine forms occurred irregularly across the intertidal flat, differences were not related to the salinity gradient. Indeed,

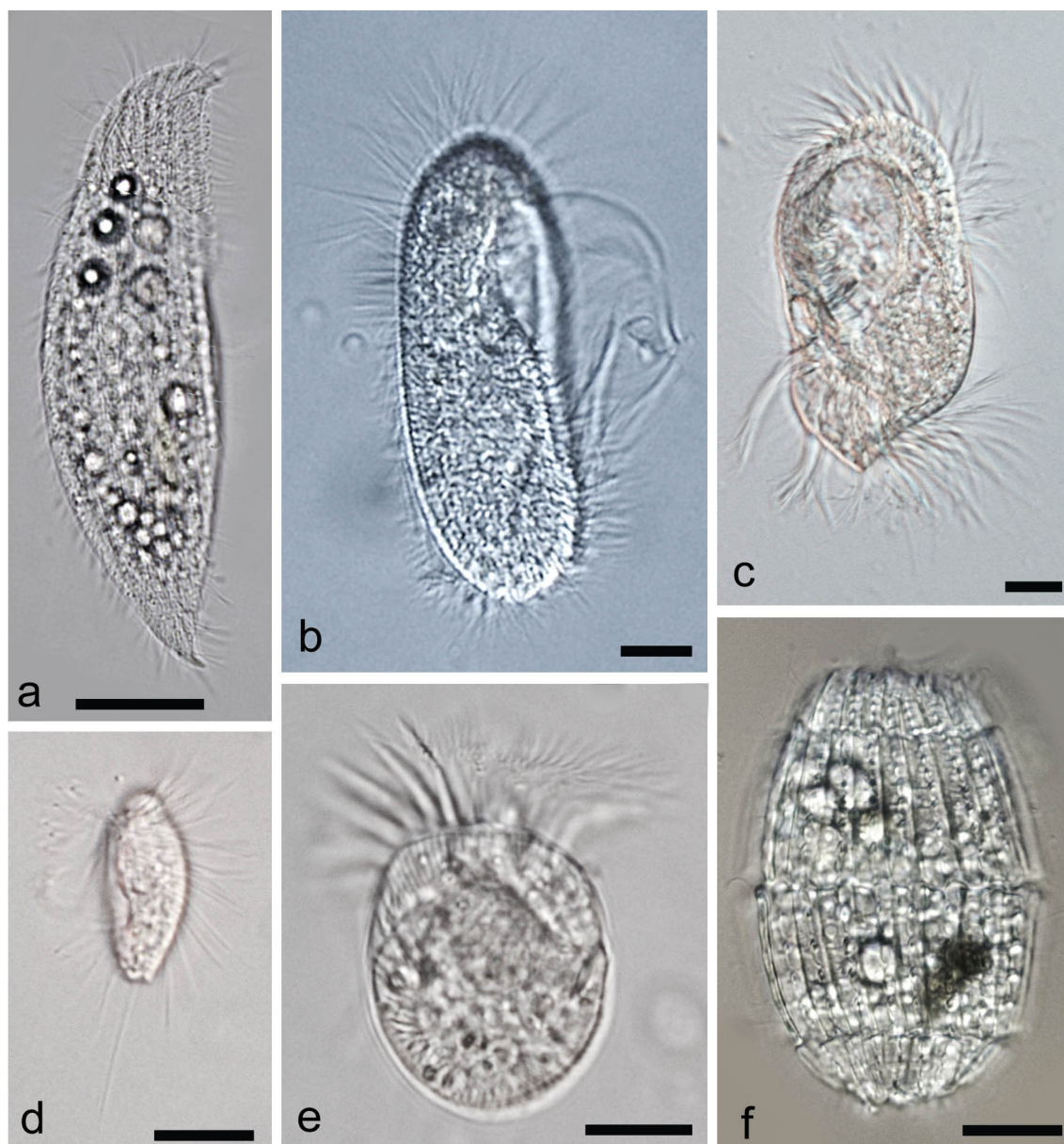


Fig. 6. Common ciliates of the Ryazhkov Island: a – *Remanella margaritifera*; b – *Pleuronema marina*; c – *Diophrys scutum*; d – *Uronema marinum*; e – *Strombidium sulcatum*, f – *Coleps tessellatus*. Bright field, living cells; scale bars = 10 μm .

Table 3. BIOENV results for different groups of microbenthos (DF – dinoflagellates, PF – phototrophic flagellates, and HF – heterotrophic flagellates, P/A – presence/absence data).

	“Best-fitting” subset of variables	Spearman’s ρ	Significance level
Diatoms (P/A data)	Salinity + sediment sorting	0.515	0.29
Diatoms (% abundance)	Salinity + sediment sorting	0.681	0.12
DF + PF (P/A data)	Eh + pH	0.845	0.06
HF (P/A data)	pH + silt content	0.709	0.12
Ciliates (P/A data)	pH + mean particle size	0.760	0.07
Ciliates (% abundance)	pH + mean particle size	0.626	0.23

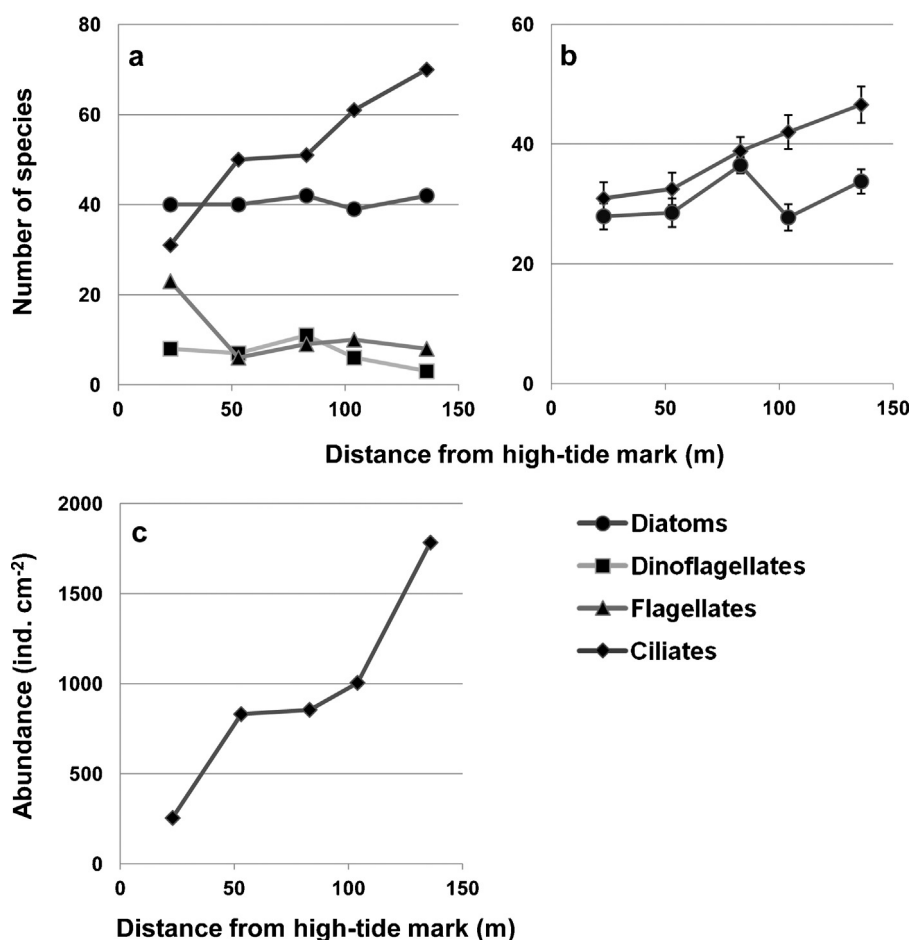


Fig. 7. Beach-wide distribution of the microbenthos species richness and abundance: A – species richness per station; B – expected number of species ($ES(100)$ for diatoms, $ES(250)$ for ciliates; bars are standard errors); C – distribution of ciliates' total abundance.

the BIOENV analysis indicated the strongest correlation between HF composition and combination of pH and silt content ($\rho=0.709$, Table 3).

Ciliates

Abundance and diversity increased from the upper intertidal zone toward the more saline lower horizons (Fig. 7). There were three local communities distinguished within the tidal flat that differed in structure and composition of dominants (Figs 8d, 9b). The low and mid-intertidal zones (stations 3–5) were inhabited by rich and abundant assemblages (50–70 species per station, mean abundance 1214 cells cm^{-2}), with a predominance of: *Trachelocerca incaudata*, *Remanella margaritifera*, *R. rugosa*, *Didinium balbiani*, and *Coleps pulcher*. In addition, *Pleuronema marina*, *P. coronata*, *P. crassa*, *Histiobalanthium marinum*, *H. majus*, *Kentrophoros fasciolatus*, *Gastrostyla pulchra*, *Oxytricha discifera*, *Diophrys appendiculata*, *D. histix*, and *Discocephalus rotatorius* were also abundant. All these species are typical inhabitants of marine sandy sediments and usually reach high abundances in the White Sea intertidal sands (Burkovsky 1984; Mazei and Burkovsky 2006). By contrast, a local community in the upper site with low salinity

(station 1) was relatively poor in richness and abundance (31 species, 254 cells cm^{-2}). The nonspecific, euryhaline ubiquitous ciliates *Anigsteinia salinaria*, *Cyclidium fuscum*, *Condylostoma curva*, *Caenomorpha capucina*, *Chilodontopsis* sp., *Chilodonella psammophila*, *Chlamydon minutus*, *Uronema marinum* and members of the *Lacrymaria* genus (*L. acuta*, *L. coronata*, *L. cohni*, and *L. conifera*) were the most abundant here. Station 2 was transitional in its composition, including representatives from both communities (*Remanella margaritifera*, *R. rugosa*, *Tracheloraphis oligostriata*, *Cyclidium fuscum*, and *Uronema marinum*). The combination of mean grain size and pH showed the best match with variations in ciliate community composition, both for presence–absence and abundance data (Table 3).

Discussion

Taxonomic composition

Diatoms

The composition of diatoms is rather typical at the White Sea sandy beaches, with the predominance of

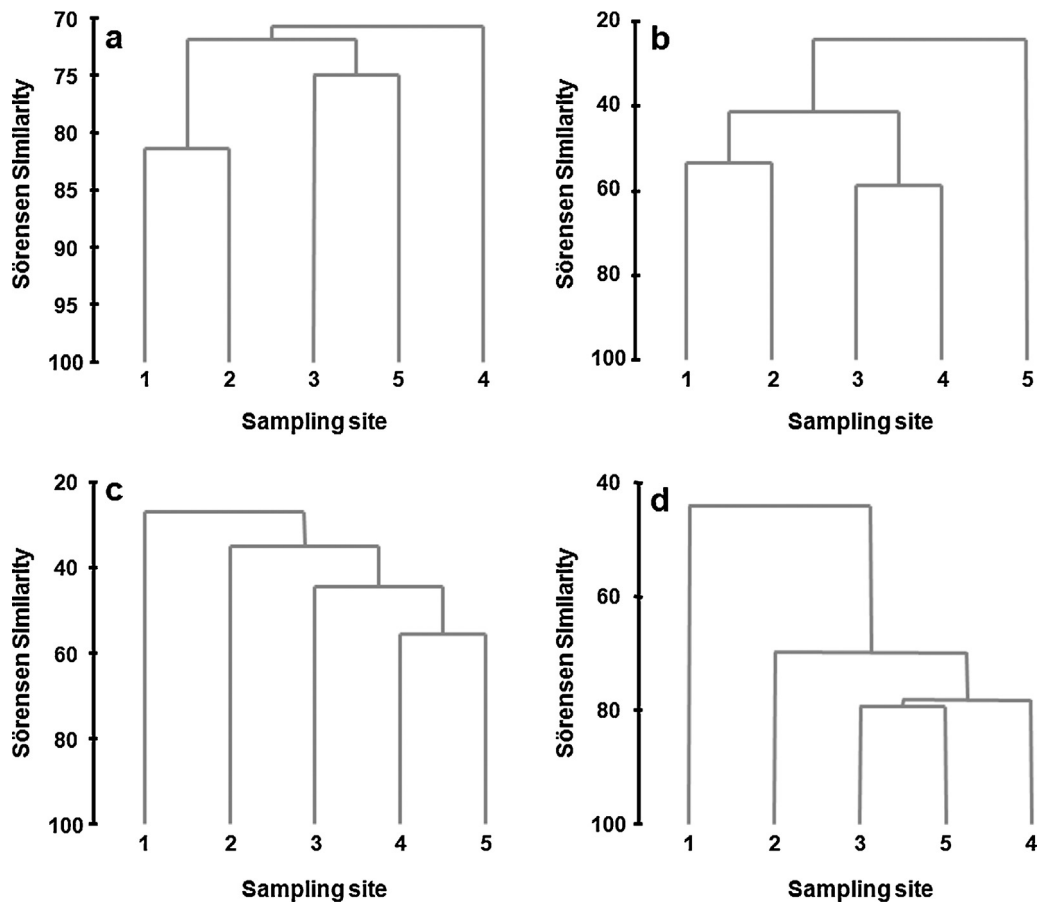


Fig. 8. Classification of stations based on the species presence–absence data: A – diatoms, B – dinoflagellates and phototrophic flagellates, C – heterotrophic flagellates, D – ciliates.

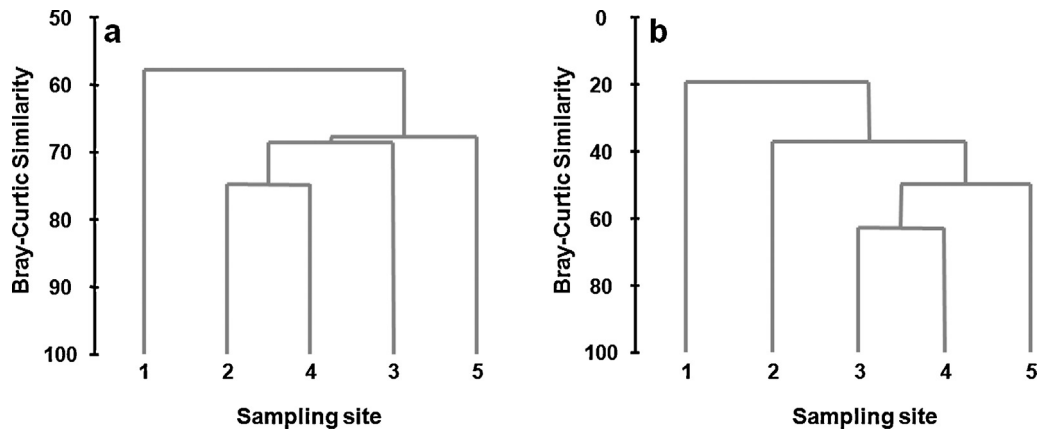


Fig. 9. Classification of stations based on the species abundance data: A – diatoms, B – ciliates.

small epipsammic forms, mainly from the families Naviculaceae, Fragilariaceae and Cocconeidaceae (Bondarchuk 1980; Saburova 1995; Ulanova 1999, 2001). The dominance of small *Navicula* species is a common feature of European intertidal mudflats (Scholz and Liebezeit 2012). Some peculiarities of the Ryazhkov diatom assemblage are relatively low diversity (only two species) and abundance of Bacillariaceae, which usually belong to the main components

of intertidal microphytobenthos (e.g., Bondarchuk 1980; Underwood 2001).

Dinoflagellates

Members of the genus *Amphidinium* commonly constitute a major part of sand-dwelling benthic dinoflagellates worldwide (e.g., Flø Jørgensen et al. 2004; Hoppenrath 2000b; Larsen and Patterson 1990). This is in agreement with our

results that *Amphidinium*, with 7 species, was among the most diverse sand-dwelling unarmored dinoflagellates in the Ryazhkov intertidal sediments. Another dominating species, *Togula britannica*, has been previously reported (as *A. britannicum*) from the White Sea intertidal sediments in large numbers, mainly at the middle littoral zone, where it often caused distinct sand discoloration (Azovsky et al. 2004; Saburova 1995; Saburova et al. 1995, 2001). A four-year survey of the White Sea benthic DF undertaken from 2008 to 2011 (72 samples from eight sites) yielded 33 species (Saburova, unpubl. data). Among the 16 species found in the present study, no one is specific to Ryazhkov Island.

Heterotrophic flagellates

The most species-rich groups of HF at Ryazhkov Island are choanoflagellates, euglenids, kinetoplastids, bicosoecids, chrysomonads, and thaumatomonads. The same groups dominated in terms of species richness in other intertidal communities of the White and Barents Seas (Mazei and Tikhonenkov 2006; Tikhonenkov and Mazei 2006). Among the 29 species identified in the present study, 18 have previously been revealed in the White Sea marine intertidal sites; another 5 species (*Anisonema trepidum*, *Goniomonas amphinema*, *G. pacifica*, *Petalomonas minuta*, and *Salpingoeca amphoridium*) were reported from brackish-water estuarine sediments with a salinity of 2–12 psu (Tikhonenkov et al. 2006). As a whole, most of the HF species from Ryazhkov Island are common (and often predominant) in marine sediments of polar, temperate and tropical regions (Al-Qassab et al., 2002; Larsen and Patterson 1990; Lee and Patterson 1998). Six species have been observed for the first time in this region and are new for the White Sea; three of them (*Colpodella pugnax*, *Hemistasia amylophagus* and *Rhynchobodo thaeniata*) have never been reported in the Arctic seas before. *C. pugnax* has been reported from Australia only (Simpson and Patterson 1996).

Choanoflagellates and bicosoecids are often considered to be mainly planktonic or periphytonic forms (Zhukov 1993), but they also dominate in marine sediments (Tikhonenkov et al. 2006). Many of the species found in our samples are known from both fresh and marine waters, as well as in soils (Ekelund and Patterson 1997; Foissner 1991; Lee et al. 2005; Mylnikov et al. 2006; Tikhonenkov 2007/2008; Tikhonenkov et al. 2010, 2012); only apusomonads are generally regarded as typical benthic inhabitants (Cavalier-Smith and Chao 2010). Our finding confirms the view that a great number of HF species are ubiquitous (Ekebom et al. 1995/1996).

Ciliates

Generally, the composition of the community is typical for the White Sea intertidal sediments, with a prevalence of the marine interstitial complex that includes mainly the karyorelictid genera (*Trachelocerca*, *Tracheloraphis*, *Remanella*, and *Kentrophoros*) and some others (*Histiobalanthium*, *Coleps*, *Uronema*). Six out of seven of the most abundant species have also been reported as dominating

forms from the Chernaya River estuary in the Kandalaksha Gulf of the White Sea (Burkovsky and Mazei 2010; Mazei and Burkovsky 2005, 2006). Two species (*Geleia swedmarkii* and *Chlamyodon minutus*) are the first records for the Arctic seas.

Earlier, benthic ciliates from Ryazhkov Island were comprehensively investigated by I. Raikov during the summer of 1961 (Raikov 1962). He also provided some ecological data comprising of distribution along tidal horizons and types of sediments. As in our study, he noted the decreasing species richness and abundances from the lower to upper intertidal zones. Raikov identified 59 species and 2 varieties, including 9 new taxa for science. This value is noticeably lower than the 98 species found in the present study, despite his rather extensive sampling (72 samples from 43 sites). Only 23 species have been presented in both our (2009) and Raikov's (1961) lists. The difference is possibly due to the methods of extraction: Raikov used rinsing of sediments by sea water, which was less effective than Uhlig's method in extracting live organisms from sandy sediments (Uhlig et al. 1973). The later yielded a higher diversity of haptorids, pleurostomatids and prorodontids, which are raptorial feeders and, probably, better attached to the sediment particles, and thus less effectively extracted by rinsing. In addition, some of the ciliates under-represented in Raikov's data are fast-swimming forms (genera *Histiobalanthium*, *Pleuronema*, *Cyclidium*, *Frontonia*, *Enchelyodon*, *Lacrymaria*, *Didinium*, *Mesodinium*). It is hard to judge, whether this difference is due to the methods applied or whether it reflects the actual changes in the community composition. By our experience, however, the Uhlig method is also rather suitable for other sand-dwelling inhabitants, including dinoflagellates. For example, dinoflagellate *Roscoffia capitata* Balech was not found for a long time since its original description, despite diligent searching at the type locality and at some other places, up to its rediscovery from the North Sea using the Uhlig method (Hoppenrath and Elbrächter 1998).

Combining Raikov's and our data, the total species list for Ryazhkov Island includes 136 species. Interestingly, the main dominant groups were the same in both surveys, but they were represented by different species. In 1961, the most abundant trachelocercids were *Tracheloraphis phoenicopterus*, *T. dogieli*, and *T. prenanti*; while in 2009, *Trachelocerca incaudata* and *Trachelocerca sagitta* occurred with highest cell numbers. The most abundant *Remanella* species were *R. granulosa* and *R. multinucleata* in 1961, but *R. margaritifera* and *R. rugosa* in 2009. *Diophrys scutum* was replaced by *D. appendiculata* and *D. histrix*, *Condyllostoma arenaria* by *C. curva*. Thus, the composition of the leading taxa shifted toward their smaller sized relatives.

Diversity and biogeographic notes

Observed values of the diversity from the Ryazhkov Island microbiota are within the range of values reported from other

sites in the White Sea. For example, benthic diatoms typically have 90–130 species at a site, and an average of 40–60 species per station (Azovsky et al. 2000, 2005; Petrov 1967; Saburova et al. 2001; Sazhin et al. 2011; Ulanova 1999, 2001). The relatively low total richness of diatoms obtained in this study is obviously the result of under-sampling and/or underestimating due to the low number of frustules counted. On the other hand, the preparation technique employed does not distinguish active from dead cells. Therefore, some of the diversity may represent dead or inactive cells. Regarding ciliates, a five year study (ca 300 samples) in the Chernaya River estuary yielded 123 ciliate species, with an average point diversity ranging from 36 to 56 species per sample (Azovsky 2011; Mazei and Burkovsky 2005, 2006). Intensive survey for heterotrophic flagellates in the same estuary yielded 7–38 (mean 17.8) species per sample (Tikhonenkov et al. 2006).

Both beta-diversity measures (estimated both as β_W and β_{SAC} , see Table 2) show a significant difference among groups with higher values for flagellates than for ciliates and diatom algae. A similar difference was found earlier for these groups in the polar seas. In the Chernaya River estuary (the White Sea), the mean β_{SAC} values were: 0.628 for heterotrophic flagellates, 0.302 for ciliates (Tikhonenkov et al. 2006), and 0.178 for diatoms (Azovsky 2011). On the Barents Sea sublittoral zone, the β_{SAC} value for HF communities was 0.64 (Mazei and Tikhonenkov 2006), while for ciliates and diatoms, it was 0.395 and 0.248, respectively (Azovsky 2011; Azovsky and Mazei 2007). These results are consistent with the values obtained in this study. Thus, flagellates commonly demonstrate higher spatial heterogeneity than ciliates or diatom algae.

Most of the species found at Ryazhkov Island are widely distributed forms known from many other localities. To illustrate this point, we compare our data with the species lists available for geographically remote, ecologically contrasting and relatively well-studied regions such as the Arabian (Persian) Gulf and Australia. Out of 64 diatom algae identified to species level, 33 species (51.6%) are known from the Arabian Gulf (Al-Mamoori 2011; Al-Yamani and Saburova 2011; M. Sanilkumar, unpubl. PhD dissertation, Kochin Univ., India, 2009) and 42 (65.6%) are known from the Australian coasts (Guiry and Guiry, 2012). All 16 dinoflagellate species have been found in Kuwait's marine sediments (Al-Yamani and Saburova, 2010), and 11 of them (68.8%) are also known from Australia (Murray, 2009). Among the 30 HF forms identified to species level in the present study, 23 have been reported from marine biotopes of Australia, the world's best studied region in terms of heterotrophic flagellate diversity (Al-Qassab et al. 2002; Lee and Patterson 1998, 2000), and 7 species were observed from Australian freshwater sites (Lee et al. 2005). Regarding ciliates, this group is insufficiently studied in the tropics and in the Southern hemisphere as a whole. Nevertheless, forty-six species in our list have been reported from the Arabian Gulf (55.4%), and 27 (32.5%) from the Australian waters (data from Azovsky and Mazei 2013). These figures do not claim to be an exhaustive biogeographic

analysis and must be treated with caution because of the incomparability of the species lists (single-site 'snapshot' vs. large geographic regions), their incompleteness and problems with species identification (Azovsky and Mazei 2013; Foissner 2006). These data could nevertheless be treated as additional evidence for a wide geographic distribution of most microbial morpho-species.

Distribution across the littoral zone

Each group of microbenthos demonstrates its own spatial pattern on the same environmental matrix. Species richness increases from the upper intertidal zone seaward for ciliates but decreases for heterotrophic flagellates, while both autotrophic groups show a relatively uniform pattern with a slight peak at the mid-intertidal. Across the littoral zone, all groups show distinct changes in their species composition. However, the position of the boundary between "upper" and lower" communities varies among the groups. For autotrophs, station 2 (upper part of the mid-intertidal zone) is closer to station 1 (the upper intertidal assemblage), whereas the assemblages of heterotrophs from these stations differ noticeably.

Unfortunately, the BIOENV analysis revealed no statistically significant relationships for any group due to the limited number of samples. However, the rather high Spearman's correlations (see Table 3) at least provide indications that some environmental parameters match closely with microbenthic distributional patterns. The analysis also reveals that each group has its own "best fitting" subset of explanatory variables. Although the analysis is strictly exploratory, and does not necessarily indicate a cause and effect relationship, these differences presumably reflect group-specific responses to environmental gradients.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ejop.2013.05.002>.

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