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Diversity and seasonality in structure of ciliate communities in the Neva Estuary (Baltic Sea)

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Diversity and structure of ciliate communities in the Neva Estuary (Baltic Sea) were studied at two near-shore stations from October 2007 to January 2009. Ciliates from 111 taxa were detected, including new records of 24 species for the Baltic Sea. The ciliate taxa were grouped into size-categories and trophic guilds and their species composition, abundance and biomass were monitored in different seasons. Two distinct associations replaced each other during seasonal succession at water temperatures 5–12°C. During the warm season (late April–October) ciliate communities were composed essentially of pico- and nano-filterers (mostly algivorous) that became less important in the cold season (October–early April). The predator, *Monodinium balbiani*, and bactivorous peritrichs were characteristic of the warm season, while in the cold season, other predatory (*Lacrymaria coronata* group) and bactivorous (*Cyclidium* spp., *Aspidisca* sp., *Chilodonella* sp.) ciliates occurred. The most abundant size groups were small ciliates (20–30 μm) and nanociliates (<20 μm). A proportion of large ciliates (>60 μm) increased in the cold season due to the appearance of benthic species in the plankton. Total ciliate abundance and biomass ranged $0.12–10.3 \times 10^3$ ind L^{-1} and 0.3–53.3 μg C L^{-1}, respectively. An unusual winter peak of the ciliate *Trithigmostoma* sp. was observed (32.8 μg C L^{-1}) although generally the overall ciliate numbers decreased in the cold season.

KEYWORDS: ciliates; species diversity; community structure; Neva Estuary; Baltic Sea

INTRODUCTION

Ciliates play an important role in various aquatic environments. When abundant, small planktonic ciliates make a major contribution to the recycling of matter and energy through the 'microbial loop' (Azam *et al.*, 1983; Pomeroy *et al.*, 2007; Fenchel, 2008; Sherr and Sherr, 2008) and consume a large portion of bacterial (Sherr and Sherr, 1987; Simek *et al.*, 1998) and phytoplankton production (Gismervik *et al.*, 1996; Löder *et al.*, 2011). Ciliates constitute a significant part of the diet of mesozooplankton (Stoecker and Capuzzo, 1990) and fish larvae (Fukami *et al.*, 1999; Dickmann *et al.*, 2007). Therefore, they act as the trophic link in the transformation of organic matter from picoplankton to higher trophic levels. Rare species may be an important

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reservoir of ecological redundancies (Dolan *et al.*, 2009) that can buffer the effects of dramatic environmental shifts, such as those caused by accidental oil spills (e.g. act as colonizers) and thus ensure the maintenance of basic biogeochemical processes in natural ecosystems (Caron and Countway, 2009; Sime-Ngando and Niquil, 2011).

The existing knowledge of ciliate diversity in the Baltic Sea was recently reviewed (Mironova *et al.*, 2009). The latest annotated checklist comprises 814 currently known species of ciliates from the Baltic Sea (Telesh *et al.*, 2009). However, even the most recent investigations in the Neva Estuary (the Gulf of Finland, eastern Baltic Sea) led to the discovery of a considerable number of species that are new records for the Baltic Sea (Mironova *et al.*, 2009). This indicates that current knowledge of the diversity of Baltic ciliates is still incomplete.

In spite of the variety of investigations into different aspects of ciliate ecology in the Baltic Sea, there are only a few reports illustrating seasonal changes in community structure of planktonic ciliates (Smetacek, 1981; Kivi, 1986; Witek, 1998; Johansson *et al.*, 2004). The majority of these studies provide information only for dominant species, whereas the rare as well as the common, though not numerous, species are often ignored. Therefore, the complete ciliate community structure and its seasonal dynamics are seldom analysed. Several assemblages of ciliate species have been detected in various regions of the open Baltic Sea in midsummer (Setälä and Kivi, 2003). Meanwhile, it is still unknown whether similar associations exist during seasonal succession of ciliate communities in other regions.

During the recent decades, there has been increasing interest in the smallest ciliates (nanociliates, <20 μm in size) due to their high abundance in various pelagic ecosystems that had remained underestimated for a long time (Sherr *et al.*, 1986; Müller, 1989; Pitta and Giannakourou, 2000). It was found that nanociliates constituted a significant part of the ciliate communities in the various benthic and offshore pelagic ecosystems of the Baltic Sea (Dietrich and Arndt, 2000; Setälä and Kivi, 2003). However, information about nanociliate taxonomic diversity and abundance in major Baltic coastal ecosystems is still lacking.

In this study, we examined the taxonomic, size and trophic structure of communities of planktonic ciliates in the coastal zone of the Neva Estuary which is located in the eastern part of the Baltic Sea. Special attention was paid to nanociliates and to the seasonal dynamics of the community's characteristics, to shed light on the problem of whether or not certain species associations exist during seasonal succession.

METHOD

Investigation area

The inner Neva Estuary consists of the freshwater Neva Bay (the upper inner estuary) and brackish-water lower inner estuary (salinity 1–5 PSU) separated from each other by the storm-surge barrier (Fig. 1). Like most of the Baltic estuaries, the Neva Estuary is (i) shallow (mean depth of the Neva Bay is 4 m, in the eastern Gulf of Finland—20 m), (ii) meso-eutrophic, (iii) characterized by intensive benthic-pelagic coupling, (iiii) dominated by eurytopic species (Telesh *et al.*, 2008a).

A high external load of organic matter favours bacteria; their density varies within the range of $2.5–10 \times 10^6$ cells mL^{-1} (Telesh *et al.*, 2008a). Cyanobacteria and cryptophytes dominate among the phytoplankton (especially in summer and autumn), whereas diatoms and green algae are less abundant. Phytoplankton blooms occur in spring (14.7–19.7 μg Chl *a* L^{-1}, biomass $1.54–1.815 \times 10^3$ μg C L^{-1}) and autumn (15.3–16.0 μg Chl *a* L^{-1}, biomass $0.891–1.22 \times 10^3$ μg C L^{-1}) (Nikulina, 2003; Telesh *et al.*, 2008a and references therein). Primary production in the Neva Bay is limited by light (annual production 348 g Cm^{-2} a^{-1}), whereas in the eastern Gulf of Finland, the limiting factor is phosphorous (annual production 100 g Cm^{-2} a^{-1}). Zooplankton is characterized by the substantial contribution of microzooplankters (ciliates, rotifers, nauplii of copepods; total biomass 1.6–132 μg C L^{-1}) and young copepodite stages, particularly in the Neva Bay; adult copepods and cladocerans dominate in the lower inner estuary, with a total biomass of 14.5–81.5 μg C L^{-1} (Telesh *et al.*, 1999, 2008a). For detailed information on hydrology, salinity regime, sediments and structure of pelagic communities of the study area, see Telesh *et al.* (Telesh *et al.*, 2008a) and references therein.

Study sites and sampling procedure

Samples were collected in the inner Neva Estuary at two near-shore stations located ~40 km distance from each other (Fig. 1). Station 1 was in the lower inner estuary, close to Zelenogorsk city, in the resort district of the eastern Gulf of Finland, station 2 was in the upper inner estuary (the Neva Bay), in the vicinity of Lahta (Fig. 1). Both sampling stations were at shallow (depth 0.8 m), open-water, wind-exposed sites characterized by intensive water mixing.

Sampling was carried out once a month (except for the winter period when the intervals were longer); from October 2007 to January 2009. In addition, five samples were collected every three days at the

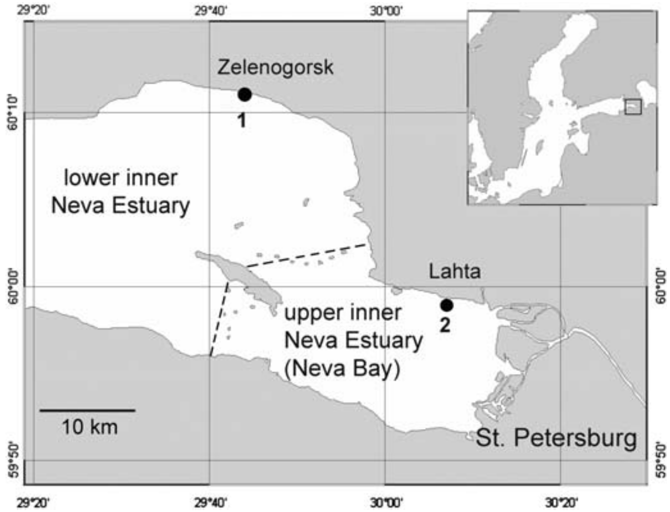

Fig. 1. Scheme of the Neva Estuary and location of sampling stations: Station 1, near the town of Zelenogorsk (the resort district); Station 2, near Lahta; modified from Telesh *et al.* (2008a). Broken line indicates the storm-surge barrier.

beginning of July 2008 to evaluate the short-term dynamics of ciliates. All samples were obtained from below the surface water layer during the day time using 1–2-L plastic bottles, and the water temperature was measured simultaneously with the sampling.

Counts, measurement techniques and species identification

Immediately after sampling, 50–100 mL subsamples were preserved with 25% glutaraldehyde solution to reach a final 2% concentration before being taken to the laboratory and kept at 4°C.

Enumeration of ciliates was carried out on black 2 μm Nuclepore filters by epifluorescence microscopy after primulin staining (Caron, 1983). Filtered water volume varied from 30 to 85 mL to obtain enough material for reliable cell counts (usually >200 cells were counted). In cases where detritus and numerous colonies of cyanobacteria were present in a sample, two parallel counts were performed. Data on abundance and biomass of large ciliates were obtained from the same slides. Filters were mounted and examined with a Zeiss Axiophot microscope at magnification ×200 to ×400. Plastidic ciliates were counted as a separate group. Cell sizes were measured using an eyepiece micrometer. Biovolume and wet weight of ciliates were calculated from measurements of their cell dimensions by comparing the organisms with geometrical figures. For the calculation of carbon biomass, the relationship $\text{pg C cell}^{-1} = 0.216 \times \text{cell volume}^{0.939}$ was used (Menden-Deuer and Lessard, 2000).

Species of ciliates were identified in live samples and qualitative enrichment cultures (rice/wheat grain cultures or Føyns–Erdschreiber medium, Page, 1983). Some of these mixed cultures were incubated under illumination from cool-white fluorescent lamps. Species identification was carried out under a Leica DM 2500 microscope (×600 to ×1350 magnification) and was supported by images taken with a Leica DFC 420 photo camera. Fine diagnostic features of ciliates were recognized after silver nitrate impregnation (Corliss, 1953) and preparation for scanning electron microscopy (Leadbeater, 1993) using a Hitachi S570 microscope. Species identification was made using the keys of Maeda and Carey (Maeda and Carey, 1985); Maeda (Maeda, 1986); Foissner *et al.* (Foissner *et al.*, 1991, 1992, 1994, 1995); Carey (Carey, 1992); Foissner and Berger (Foissner and Berger, 1996).

The following size groups of ciliates were recognized: nanociliates (<20 μm), small (20–30 μm), medium-sized (30–60 μm) and large (for plankton) ciliates (>60 μm), differing in taxonomic composition, food preferences, generation rates and grazing by predators.

Nanociliates were separated from next size category (20–30 μm) because (i) most nanociliates are known to be pico-filterers, while the share of nano-sized organisms in the diet of <30 μm ciliates increased (Rassoulzadegan *et al.*, 1988; Tadonleke *et al.*, 2005; Bojanic *et al.*, 2006); (ii) nanociliates have higher generation rates (Perez *et al.*, 1997); (iii) differences in top-down control, e.g. copepod clearance rates of nanociliates, are lower than those of larger ciliates (20–30 μm) (Perez *et al.*, 1997; Zöllner *et al.*, 2003).

However, large inter- and intra-specific differences in ciliate feeding, swimming behaviour and growth rates could remove the boundary between these size classes. The group of medium-sized (30–60 μm) ciliates mainly consisted of strombidiids, therefore, taxonomically and ecologically distinguished from other size groups. Large ciliates (>60 μm) is a complex of groups with a loose upper size limit. It includes ciliates, which are relatively large for the plankton: mostly predators, benthic and periphytic ciliates, which just occasionally occurred in the plankton.

Information about the ecology of ciliates (e.g. salinity tolerance, habitat preferences and feeding modes) was taken from the literature (Chorik, 1968; Maeda and Carey, 1985; Maeda, 1986; Foissner and Berger, 1996; Montagnes, 1996; Gaedke and Wickham, 2004) and internet sources (Struder-Kypke *et al.*, 2003; Xu, 2007; Appeltans *et al.*, 2010).

Ciliate species were grouped in several trophic guilds according to their mode of grazing (interceptors/filterers) and food preferences (type/size of prey). In particular, pico-filterers (bactivorous ciliates), nano-filterers (algivorous ciliates + consumers of heterotrophic flagellates + mixotrophs), pico-/nano-filterers (bacterio/algivorous ciliates), nano-/micro-interceptors (predatory ciliates + omnivorous ciliates that feed on algae, heterotrophic flagellates and ciliates) and *Myrionecta rubra* have been distinguished.

Data on phyto- and zooplankton wet weight, reported for the Neva Estuary (Telesh *et al.*, 2008a and references therein) were recalculated in carbon units, using conversion factors from the literature (Mullin, 1969; Edler, 1979; Gradinger *et al.*, 1999).

Statistical analyses

The program PRIMER 5 (PRIMER-E Ltd, Plymouth) was used for the statistical analysis of the data sets. Non-metric multi-dimensional scaling using a Bray–Curtis dissimilarity matrix based on the relative abundance of ciliates according to taxonomic classes and size fractions was used to compare ciliate community structure in different samples to analyse their spatial and temporal trends. Square root transformation of data was used to weigh the contributions of common and rare species. The similarity/dissimilarity between groups of samples was tested using ANOSIM analysis (analysis of similarities). The SIMPER (similarity percentage) procedure was used to examine the contribution of each species to the average dissimilarity between groups of samples in this study.

RESULTS

Taxonomic composition and structure of ciliate communities

During a 16-month study of the ciliates in the coastal waters of the inner Neva Estuary (Fig. 1), a list of altogether 111 taxa was compiled, 94 of which were identified to the species level (among them 24 new records for the Baltic Sea) and 17 to the genus level.

The new records in the Baltic Sea are: *Anteholosticha brevis, Amphisiella oblonga, Aspidisca lynceus, Chilodontopsis depressa, Cinetochilum margaritaceum, Coleps elongatus, Colpidium kleini, Cyrtolophosis mucicola, Dexiostoma campylum, Histriculus vorax, Holosticha pullaster, Lembadion lucens, Litonotus alpestris, Litonotus varsaviensis, Loxodes rostrum, Metacineta mystacina, Oxytricha setigera, Placus luciae, Sphaerophrya stentori, Sterkiella histriomuscorum, Stichotricha secunda, Tintinnidium semiciliatum, Trithigmostoma srameki, Trochilia minuta*.

The most species-rich groups of planktonic ciliates comprised different oligotrichs (e.g. genera *Strombidium*, *Strobilidium, Tintinnidium*), litostomatids (e.g. genera *Mesodinium, Monodinium*) and small hymenostomatids (e.g. genera *Cyclidium, Cristigera*). Most species of ciliates were rare during the period of investigation; very few were observed in the majority of samples (e.g. *Rimostrombidium humile, Lohmaniella elegans, Monodinium balbiani*). These most common species made a considerable contribution to the total abundance of ciliates and

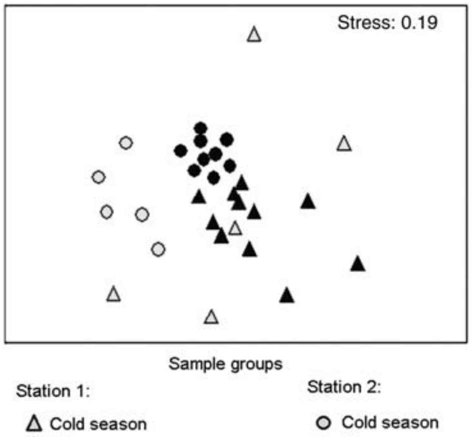

Fig. 2. Four groups of samples, distinguished by ordination (MDS) on the basis of similarity of the ciliate community structure (significance level 0.1–0.8). Seasonal differences in community structure (grey and black symbols; *R* range 0.5–0.86) were larger, than differences between stations (circles and triangles; *R* range 0.37–0.39). For detailed information about seasonal changes in the community structure see Table II.

often were the dominants; for example, *R. humile* was responsible for up to 87% of total numbers.

Ordination of all samples by similarity of their community structure revealed four groups of samples in the data array (Fig. 2). These groups were distinguished from each other by season ('cold': October through early April, and 'warm': late April through September) and by station. The global *R* statistics from ANOSIM of these groups ($R = 0.545$, $P < 0.01$) demonstrated that the overall differences between them were statistically significant (Table I). The seasonal differences in community structure were significantly larger (*R* values between 0.506 and 0.862, $P < 0.01$) than the differences between stations (*R* values between 0.366 and 0.399, $P < 0.01$). Community structure at station 2 was more homogeneous ($R = 0.862$, $P < 0.01$) over the period of investigation if compared with station 1 ($R = 0.506$, $P < 0.01$). At both stations, significant seasonal changes in ciliate community structure occurred in April and during the interval between 26 September and 23 October at water temperatures 5−12°C, which allowed discrimination between the two groups of samples.

Table I: Analysis of similarity (ANOSIM) of the four groups of samples

Group comparison	*R* statistic	Significance level (%)
Station 1/Cold season, Station 1/Warm season	0.506	0.4
Station 1/Cold season, Station 2/Cold season	0.366	0.8
Station 1/Cold season, Station 2/Warm season	0.687	0.2
Station 1/Warm season, Station 2/Cold season	0.658	0.1
Station 1/Warm season, Station 2/Warm season	0.399	0.1
Station 2/Cold season, Station 2/Warm season	0.862	0.2

Similarity was calculated on the basis of data on relative ciliates abundance.

During the warm season (late April−October) when phytoplankton bloomed, mostly algivorous pico- and nano-filterers (oligotrichids *Strobilidium caudatum, L. elegans, Strombidium sulcatum, R. humile, Strombidium vestitum* and prostomes *Balanion comatum*) formed the core of the ciliate community. Bactivorous peritrichs (*Vorticella anabaena, V. convallaria* complex) were also characteristic species for this season. During the cold period (October − early April), when phytoplankton numbers and diversity decreased (Nikulina, 2003), pico- and nano-filterers became less important and the composition of the characteristic bactivorous ciliates (*Cyclidium* species, *Aspidisc*a sp. and *Chilodonella* sp. arose) changed; meanwhile, the abundance of common omnivorous ciliates (*Mesodinium* species) increased. Seasonal changes were observed also among predators: *Lacrymaria coronata* group, typical for the cold period, replaced *M. balbiani*, which was characteristic for the warm period. The species composition of associations typical for 'cold' and 'warm' seasons is given in Table II.

Table II: Members of the ciliate species associations typical for warm and cold seasons

Cold season (October–early April)		Warm season (late April–October)	
Taxa	Feeding type	Taxa	Feeding type
Characteristic species[a]			
Cyclidium sp.	Pico-filterer (Ba)	*Pelagostrobilidium spirale*	Nano-filterer (Al, HFl)
Aspidisca sp.	Pico-filterer (Ba)	*Strombidium sulcatum*	Pico/nano-filterer (Ba, Al)
Chilodonella sp.	Pico-filterer (Ba)	*Strombidium vestitum*	Nano-filterer (Al)
Strobilidium sp.	NN	*Strobilidium* spp.	NN
Lacrymaria coronata group	Nano/micro-interceptor (P)	*Vorticella convallaria* complex	Pico-filterer (Ba)
		Vorticella anabaena	Pico-filterer (Ba)
		Monodinium balbiani	Nano/micro-interceptor (P)
Common species[b]			
Mesodinium pulex (4)	Nano/micro-interceptor (O)	*Rimostrombidium humile* (15)	Nano-filterer (Al)
Mesodinium sp. (2)	Nano/micro-interceptor (O)	*Lohmaniella elegans* (10)	Pico/nano-filterer (Ba, Al)
Chilodonella sp. (5)	Pico-filterer (Ba)	*Strobilidium* sp. (*diversum)* (7)	NN
Frontonia sp. (2)	NN	*Strombidium conicoides* (10)	NN

Ba, bactivorous; Al, algivorous; HFl, feeding on heterotrophic flagellates; P, predator (feeding on ciliates); O, omnivorous (feeding on algae, heterotrophic flagellates and ciliates); NN, no data on food preferences.

Feeding types are classified by mode of grazing (filterer or interceptor) and by prey size-class (pico-, nano- or microplanktonic), based on reference publications (see "Methods"). Data about prey type are presented in brackets.

Numbers in brackets indicate the ratio of average abundance of each species in one season to its average abundance in another season.

[a] Characteristic species: occurred only in one season.

[b] Common species: found in both seasons but more abundant in a certain one.

Ecology (salinity tolerance, habitat preferences)

A small proportion of the ciliate species observed were 'truely planktonic' (15%), whereas the majority belonged to hypotrichs (e.g. genera *Aspidisca, Euplotes, Holosticha*), which are typical for the benthos, and periphytic sessilids (e.g. genera *Vorticella, Carchesium, Cothurnia, Epistylis*).

According to the literature (Chorik, 1968; Maeda and Carey, 1985; Maeda, 1986; Foissner and Berger, 1996; Montagnes, 1996), most of the ciliate species observed are able to exist in fresh and brackish waters with salinity <5 PSU, which is a characteristic feature of the Neva Estuary. A small proportion of these species are freshwater (12%), whereas the majority of the others occur in a broad spectrum of habitats at salinities from 1 to 30 PSU. However, 14% of the detected ciliate species previously have been found only in marine and brackish waters with salinities >10 PSU (Agamaliev, 1983; Maeda and Carey, 1985; Maeda, 1986; Jee *et al.*, 2001; Struder-Kypke *et al.*, 2003; Xu, 2007; Berger, 2008; Appeltans *et al.*, 2010).

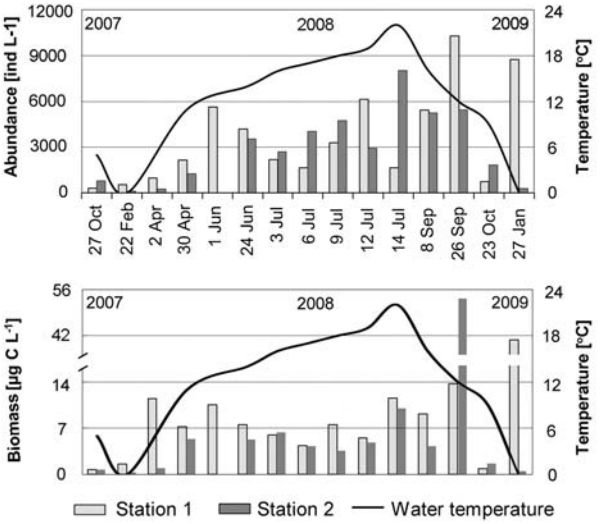

Fig. 3. Seasonal dynamics of total abundance (ind L^{-1}, bars), biomass (µg C L^{-1}, bars) of ciliates and water temperature (°C, line) at two stations in the Neva Estuary. *Top panel:* abundance; *bottom panel*: biomass.

Abundance and biomass

At both stations, total abundance and biomass of ciliates during the period of investigation were of the same order of magnitude and varied within the ranges $0.12-10.3 \times 10^3$ ind L^{-1} and 0.3–53.3 µg C L^{-1}, respectively (Fig. 3). Changes in ciliate abundance and biomass were rather irregular at both stations. At station 1, two maxima of abundance were registered: the greatest peak was reached on 26 September (10.3×10^3 ind L^{-1}) and the second peak on 27 January (8.7×10^3 ind L^{-1}), while at station 2, the peak in autumn was not as obvious ($<5.5 \times 10^3$ ind L^{-1}) as the mid-summer peak in July (8×10^3 ind L^{-1}).

For a short period of time at the beginning of July, abundance of ciliates fluctuated significantly (more than 2-fold) every 3 days (Fig. 3). These short-term fluctuations were comparable with the seasonal changes in the ciliate abundance.

Biomass of ciliates also changed substantially during the period of investigation. Two different pronounced maxima were observed: on 26 September (53.3 µg C L^{-1}) at station 2 and on 27 January (40.7 µg C L^{-1}) at station 1. On a short-term time scale, the biomass variation exceeded 2-fold every third day (Fig. 3). These biomass fluctuations were of an amplitude similar to the short-term changes of ciliate abundance.

At both stations, there was no correlation between water temperature and abundance or biomass of ciliates (Fig. 3).

Table III: Numerical characteristics of ciliate communities reported from the annual studies of various regions of the Baltic Sea

Region	Abundance ($\times 10^3$ ind L^{-1})	Biomass (µg C L^{-1})	Source
Neva Estuary	0.12–10.3	1–53	this study
Neva Bay	0.1–8	0.9–63.3[a]	Khlebovich (1987)
Shallow inlets of the Southern Baltic	0.17–88	0–220	Garstecki *et al.* (2000)
Gdańsk Basin	0–28	0–23[b]	Witek (1998)
Kiel Bight	2–92	0–56[b]	Smetacek (1981)
Various regions of the open Baltic Sea (western Gulf of Finland; Gotland, Bornholm and Arkona Basins)[d]	0–20	0–6.7[b,c]	Setälä and Kivi (2003)
Landsort Deep (the northern Baltic Proper)	0–9	0–20[b]	Johansson *et al.* (2004)

[a] Carbon weight recalculated from the data on wet weight.

[b] *Myrionecta rubra* Jankowski 1976 [syn. *Mesodinium rubrum* Lohmann 1908] excluded.

[c] Found above the thermocline. At the deep oxic/anoxic water interface, maximum of ciliate carbon (28.8 µg C L^{-1}) was detected.

[d] Data for July–August.

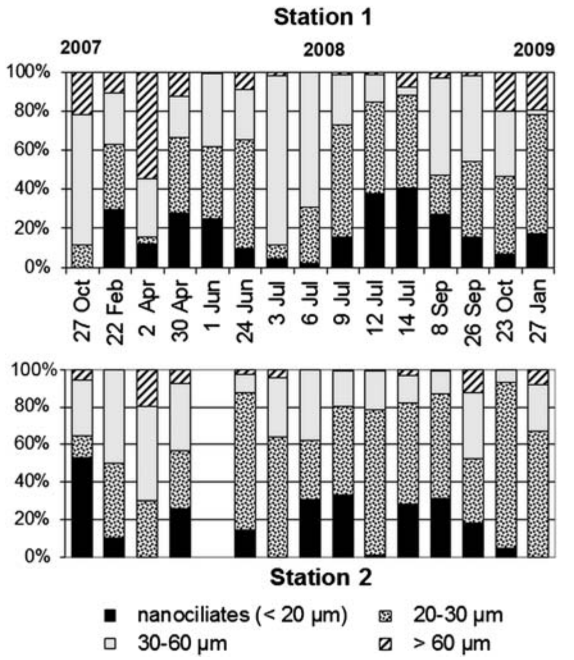

Fig. 4. Seasonal dynamics of abundance (percentage) of ciliates from different size classes. The share of large ciliates (>60 μm) increased in the cold season and reached their maximum in early spring (April, 2). *Top panel*: Station 1; *bottom panel*: Station 2.

Abundance and biomass of ciliates recorded during the present study fit within the same range as reported for other regions of the Baltic Sea (Table III).

Size structure of ciliate communities

Small ciliates (20–30 μm) were the most abundant size group in the community which formed 7–87% of total abundance and dominated in 58% of samples (Fig. 4). The second most abundant size class, the nanociliates (<20 μm), reached 53% of overall ciliates numbers.

Nanociliates were represented essentially by different oligotrichids (*L. elegans, R. humile, Strombidium compressum, Halteria grandinella*), scuticociliates (*Uronema marinum, Cyclidium glaucoma, C. citrullus, C. candens*), litostomatids (*Mesodinium pulex, M. acarus*) and prostomes (*B. comatum, Holophrya* sp.), although other taxa were also observed in the samples (*Aspidisca turrita, T. minuta, Chilodonella* sp., *C. margaritaceum, C. mucicola, Microthorax* sp.). The most part of nanociliates were identified only to the genus level, although the details of their morphology were studied by means of electron microscopy and photographed (Fig. 5). According to our observations, nanociliates included algivorous (*B. comatum*), bactivorous (*C. glaucoma*), omnivorous (*M. pulex*) and parasitic species (*S. stentori*), thus being a functionally diverse group.

Medium-sized ciliates (30–60 μm) were less abundant than smaller ciliates and dominated in 34% of samples. The proportion of large ciliates (>60 μm) was low, but increased in cold seasons (late October, February and early April) and reached a maximum in early spring (up to 55% of the total abundance) (Fig. 4). Large ciliates were primarily haptorids (planktonic *Monodinium* and benthic *Lacrymaria, Loxophyllum, Litonotus*), hypotrichs (e.g. *Euplotes*), hymenostomatids (e.g. *Frontonia*) and cyrtophorids. It is noticeable that the size structure of the ciliate community changed irregularly. Short-term fluctuations in size composition were comparable in amplitude with long-term changes (Fig. 4). At station 1, the average individual carbon mass of the cells was higher (3.2×10^{-3} μg C) than at station 2 (2.3×10^{-3} μg C), and the dynamics of the average cell mass at both stations differed significantly (Fig. 6).

Trophic structure of ciliate communities

Pico- and nano-filterers were the most numerous in the majority of samples (up to 80 and 90% of total abundance, respectively). Predatory and omnivorous ciliates were present in the community almost throughout the whole year, but their contribution to the total abundance did not exceed 35% (Fig. 7). The share of *M. rubra* was negligible (<3.5% of total abundance). On the whole, the trophic structure of the community changed irregularly, while the abundance of nano-filterers decreased in winter (January, February) and also in the beginning of July at both stations (Fig. 7).

Mixotrophic ciliates occurred almost all year round, but were not numerous; their average contribution was 9% of total abundance, and it was only in September and July that they reached 34% of total abundance. Hence, our results on mixotrophic ciliates may be overestimated because not only true mixotrophic organisms with kleptoplastids fluoresced, but also algivorous ciliates, which have recently ingested their algal prey (Sherr *et al.*, 1986).

DISCUSSION

Taxonomic diversity

Planktonic ciliates in the Baltic Sea have long been little studied and knowledge of the structure of their communities in different regions of this water body has been limited or totally lacking. Our own results and the meta-analysis of the available published data on the ciliate species composition in the Baltic Sea revealed an

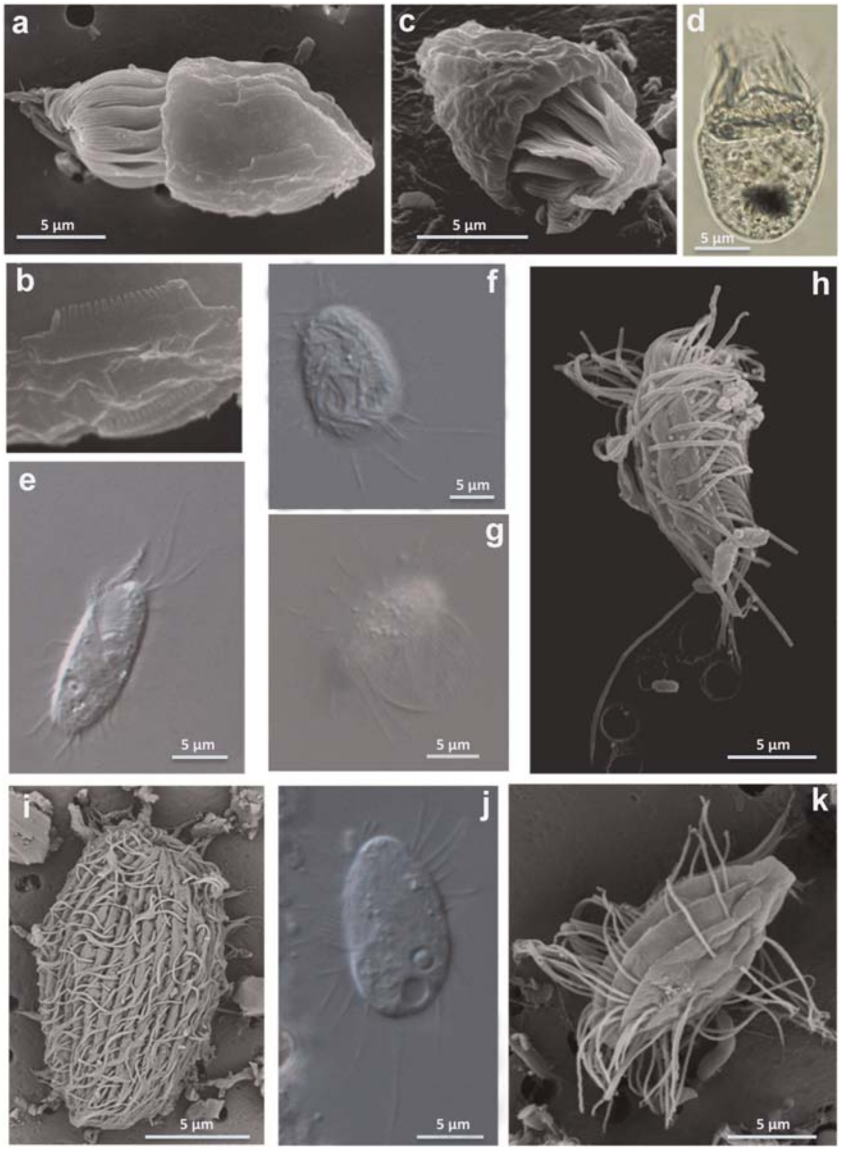

Fig. 5. Some species of nanociliates detected in this study. (**a**–**c**) *Strobilidium* sp. with distinct somatic kinety rows (**b**) SEM, ×7000, ×12 000 and ×14 000, respectively. (**d**) *Rimostrombidium humile*, BF, ×1350. (**e**) *Cyrtolophosis mucicola*, DIC, ×1350. (**f**) *Cinetochilum margaritaceum*, DIC, ×1350. (**g**) *Cyclidium candens*, DIC, ×1350. (**h**) *Cyclidium* sp., SEM, ×5000. (**i**) Unidentified prostome ciliate, SEM, ×5000. (**j**) *Cyclidium glaucoma*, DIC, ×1350. (**k**) *Cyclidium* sp., SEM, ×5000. *Bar* represents 5 µm.

unexpectedly high overall diversity of ciliates (814 taxa) in this brackish water body (Telesh *et al*., 2008b, 2009; Mironova *et al*., 2009). This new knowledge of the remarkable biodiversity at the micro-scale dismisses the view that the Baltic Sea is generally poor in species and supports the novel 'protistan species-maximum concept' (Telesh *et al*., 2011a, b).

Diversity of ciliates in estuaries and many other near-shore Baltic pelagic communities is enhanced by numerous bentho-pelagic and periphytic species. Such a situation is generally typical for the plankton of vast coastal areas of the Baltic Sea due to intensive wind-induced water mixing in these regions (Telesh, 1995, 2004; Gerlach, 2000; Telesh *et al*., 2008a, b, 2009).

An important finding of this study is the identification of 24 ciliate species in the Neva Estuary, which are new records for the Baltic Sea. The discovery of marine ciliates in the brackish waters of the Neva Estuary (including its freshwater part, the Neva Bay) during this study also indicates the limited nature of our knowledge about the diversity and ecology of planktonic ciliates in this region.

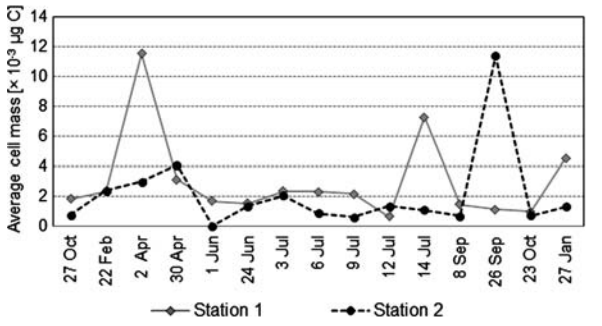

Fig. 6. Seasonal dynamics of the average cell mass (µg C) in the ciliate communities.

Nanociliates are the most under-studied group, and their taxonomic diversity is poorly investigated, especially in comparison to the knowledge about their abundance and biomass (Sherr *et al*., 1986; Dietrich and Arndt, 2000; Setälä and Kivi, 2003). Our study indicates that nanociliates are a functionally diverse group; therefore, accurate species identification is necessary to evaluate their role in aquatic ecosystems, which has been underestimated so far. Several investigations into this problem have been performed (Sommaruga and Psenner, 1993; Perez *et al*., 1997), although in the majority of such studies nanociliates were considered as a single group. Perhaps, environmental rDNA surveys may enhance taxonomic identification of nanociliates, as in the case of other small protists (Caron *et al*., 1999; Countway *et al*., 2005; Katz *et al*., 2005; Sime-Ngando *et al*., 2011).

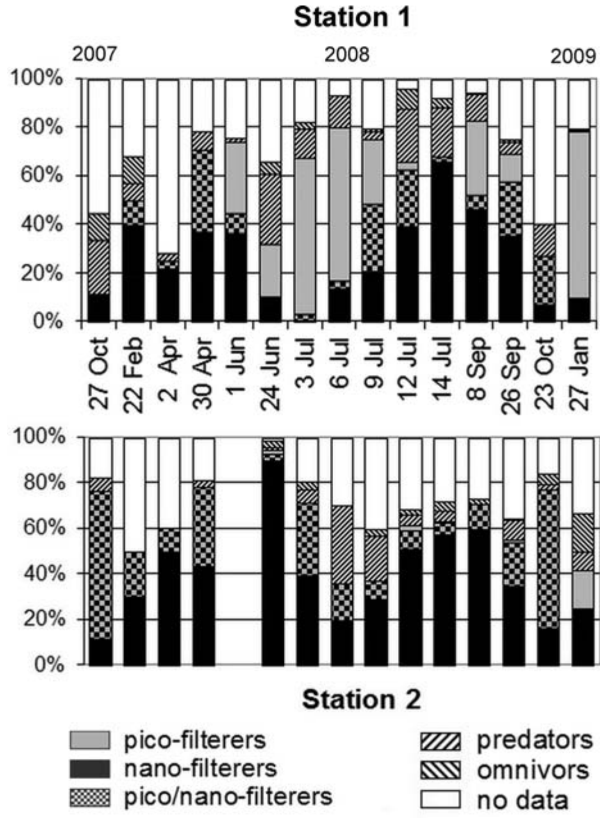

Fig. 7. Seasonal dynamics of abundance (percentage) of ciliates from different trophic groups; pico-filterers (bactivorous), nano-filterers (algivorous + consumers of heterotrophic flagellates + mixotrophic), pico-/nano-filterers (bacterio/algivorous), predators (feeding on ciliates), omnivors (feeding on algae, heterotrophic flagellates and ciliates). *Myrionecta rubra* excluded (<3.5% of total abundance). *Top panel*: Station 1; *bottom panel*: Station 2.

Species composition

Our study showed that the basis of the ciliate community in the Neva Estuary was formed by different species of oligotrichids, scuticociliates and gymnostomes, which are typical in the plankton of many aquatic ecosystems, including the open Baltic Sea (Mironova *et al*., 2009). Although the basic structure of the ciliate community at the group level in our study was similar to that in the northern and western Baltic Sea, the dominants differed considerably (Smetacek, 1981; Johansson *et al*., 2004), with the exception of *R. humile*, which also dominated in the Tvärminne Storfjärden (Kivi, 1986). Furthermore, the composition of the dominant ciliates in this study differed considerably from that in the previous investigation of the Neva Estuary which was carried out >20 years ago (Khlebovich, 1987).

The characteristic feature of the region examined is the significant contribution of benthic and periphytic ciliates to the plankton species richness in the Neva Estuary, which is possibly due to the shallowness of the sampling sites and the intensive wind-induced water mixing which intensifies bentho-pelagic coupling (Telesh, 2004; Telesh *et al*., 2008a), as in the case of other near-shore ecosystems (Garstecki *et al*., 2000).

Abundance and biomass

Our results indicate strong variability of abundance and biomass of ciliates on both short- and long-time scales. This might be a consequence of their generally recognized ability to reproduce rapidly (one or two times per day) in response to changes in environmental conditions (Müller and Geller, 1993; Montagnes and Lessard, 1999; Becks *et al*., 2005). Instability of the hydrological regime contributes significantly to the extremely high variability of the numerical data on these tiny pelagic protists. Similar to the results of the present study, it has been shown earlier that spatial variation in abundance and biomass of planktonic ciliates and rotifers in the Neva Bay was comparable with the annual variation of the hydrological parameters (Telesh, 1995).

Interestingly, ciliate abundance observed during our and the previous studies (Khlebovich, 1987) in the Neva Estuary was low, which is atypical for the other Baltic coastal ecosystems (Smetacek, 1981; Garstecki *et al.*, 2000; Johansson *et al.*, 2004). Such low values of ciliate abundance is a characteristic feature of nutrient-limited open waters (van Beusekom *et al.*, 2007), but it is an unexpected result for the shallow and eutrophicated Neva Estuary.

Since the abundance and biomass of ciliates changed irregularly at both stations during the period of our investigation, it is difficult to establish any general trends in seasonal succession of these parameters. For example, the first biomass peak, which usually occurs in late spring (Smetacek, 1981; Johansson *et al.*, 2004) and is typical for seasonal dynamics of Baltic ciliates, was not observed during our study; whereas, the second (autumn) peak was seen at only one of the two stations. It is possible, however, that some peaks of ciliate abundance could have been missed in our study due to the relatively long sampling intervals. In addition, ciliates demonstrated a peculiar, unexpected biomass peak in winter, although in general there was a tendency for a decrease in ciliate biomass and abundance in the cold season, as it is usually reported (e.g. Smetacek, 1981; Dietrich and Arndt, 2000). The winter maximum of biomass caused by a bloom of large cyrtophorids *Trithigmostoma* sp. was only observed at one station.

Seasonal changes in community structure

According to our data, the community structure of planktonic ciliates undergoes strong changes at water temperatures 5–12°C, when two different species associations replace each other. It is established that the species composition of ciliates is strongly affected by water temperature (Montagnes and Weisse, 2000; Aberle *et al.*, 2007). However, bacteria and phytoplankton also exert considerable bottom-up influence on the structure of ciliate communities, along with the top-down effects of mesozooplankton grazing (Johansson *et al.*, 2004; Samuelsson *et al.*, 2006; Löder *et al.*, 2011).

It is noticeable that the presence of species associations in the inner Neva Estuary revealed during our study was timed to the phytoplankton growth period, as known from published data (Nikulina, 2003; Telesh *et al.*, 2008a). While seasonality of algivorous ciliates obviously depends on phytoplankton development, in the case of predatory ciliates, such seasonality in composition is difficult to explain so far. No published data is available to support specialization of the predators *M. balbiani* and *L. coronata* group and their feeding on strictly defined food objects, and certain predatory ciliates reported to feed on various prey (Lynn, 2008). Therefore, the composition of predatory ciliates was most likely determined by temperature and/or top-down control. The size of the predatory ciliates *M. balbiani* and *L. coronata* group differed strongly (average size 32 and 66 μm, respectively), so they could be consumed by different mesozooplankton grazers; however, this assumption requires further verification. Development of the epiphytic bactivorous ciliates (e.g. *Vorticella anabaena*) in the plankton strongly depends on the presence of colonies of cyanobacteria, used as food and substrate (Herdendorf and Monaco, 1983; Stabell, 1996). This specific factor apparently determined the occurrence of *V. anabaena* in our samples only during the warm period, when cyanobacteria bloomed. Thus, due to the complexity and variety of relationships within natural assemblages, it is an important, though elusive task for future research to reveal mechanisms structuring the estuarine ciliate communities.

Size structure of ciliate communities

Dominance of the small ciliates (20–30 μm), as observed in the Neva Estuary during the present study, is commonly reported from various pelagic ecosystems (Beaver and Crisman, 1989; Setälä and Kivi, 2003). Nanociliates (<20 μm) form the second most important size class, as in the case of studies in the open Baltic (Setälä and Kivi, 2003), whose role in plankton communities, however, is largely under-evaluated so far.

In the earlier investigations in the western Baltic Sea, the prevalence of large cilates (50–100 μm) was observed (Smetacek, 1981). Our results show that the share of large ciliates (>60 μm, mainly predators) in the Neva Estuary was generally negligible and reached a maximum in early spring (up to 55% of total abundance). Perhaps, the abundance of their prey (bactivorous and algivorous ciliates) and low mesozooplankton predation was the reasons for this finding. Such a situation is typical for initiation of the clear water phase in spring and commonly observed in the diverse Baltic habitats (Smetacek, 1981; Setälä and Kivi, 2003; Johansson *et al.*, 2004) and other marine pelagic ecosystems (Montagnes *et al.*, 1988). However, our findings of the increase in proportions of large ciliates in late autumn and winter do not support the conventional view on the seasonal succession of ciliates (Montagnes *et al.*, 1988). Most probably, such occurrence of large benthic ciliates (generally, bactivorous cyrtophorids and predatory haptorids) in the plankton is caused by the intensive water mixing and by an absence of metazooplankton grazers in the shallow Neva Estuary during the cold season (Telesh *et al.*, 2008a, b, 2009).

Overall, a variety of size classes within the wide range of cell sizes (12–190 μm) can be distinguished among the planktonic ciliates of the Neva Estuary almost all-year round. The smallest fraction of the ciliate community was mainly composed of different strobilidiids (>15 μm in size), which can consume prey as large as 5–30% of their own length, with an optimum equal to 15% of a ciliate's length (Jonsson, 1986; Kivi and Setälä, 1995); thus, the calculated size of their potential prey is equal to 0.8–6.0 μm. Meanwhile, large raptorial ciliates are capable of feeding on the prey of similar or even larger sizes (Lynn, 2008). So, they could consume food objects from 60 μm in size (small predators *M. balbiani*, *Loxophyllum* species, generally in summer) to nearly 200 μm (large predators *Lacrymaria* spp, generally during cold season), along with smaller prey. Thus, considering the presence of both size groups during the period of our investigations, ciliates in the Neva Estuary were able to feed on the very wide spectrum of food objects, from bacteria to small metazoans (e.g. rotifers). All the detected size groups of ciliates could be effectively consumed by various mesozooplankton (Stoecker and Capuzzo, 1990; Schnetzer and Caron, 2005).

In conclusion, this study indicates that abundance, biomass and size structure of the ciliate community varied greatly at both short- and long-time scales, and changed irregularly in different parts of the inner Neva Estuary. Spatial variation of community structure was not as significant as its temporal changes. Our study indicates replacement of two distinct associations of ciliate species, most probably timed to the growth period of phytoplankton and its dynamics.

The results also demonstrate that the inner Neva Estuary differs from other Baltic coastal ecosystems in the relatively low ciliate abundance and distinctive composition of the dominant species. Moreover, large ciliates displayed a pronounced increase in abundance during the cold months, which is unusual for seasonal dynamics of ciliates in other pelagic ecosystems. Further investigations of ciliate diversity and dynamics during cold seasons and the environmental factors which structure ciliate communities are necessary for better understanding the reasons for and the mechanisms of establishment of certain species associations.

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