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Planktonic ciliates in the Baltic Sea in summer: distribution, species association and estimated grazing impact

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ABSTRACT: Samples for studying the ciliate communities of the open Baltic Sea were taken on 2 transects from the Kattegat to the entrance of the Gulf of Finland during 1988 and 1990. The abundance of HCIL (heterotrophic ciliates) was highest close to the surface, the maximum values ranging from ca. 7000 (entrance of the Gulf of Finland in 1988) to ca. 20 000 cells l^{-1} (Arkona Basin in 1990). The dominating HCIL groups were small strobilidiids, strombidiids, or prostomatiids. The photoautotrophic ciliate *Mesodinium rubrum* was most abundant in the surface water of Arkona Basin in 1990 (ca. 26 000 cells l^{-1}) but was also found at a high concentration in deeper layers during both cruises in daytime (down to 80 m in 1988). Large ciliates dwelling in the oxic/anoxic boundary layer at ca. 100 m depth were found in both years, the highest numbers being ca. 1000 cells l^{-1} (1988). HCIL community grazing was estimated by using a biovolume-dependent, mostly experimentally derived exponential function. We estimated that in 1988 the ciliate community cleared close to 50% of the water volume per day, whereas in 1990 the highest values reached up to 125% cleared d^{-1}. In both years, small (≤30 µm ESD) ciliates dominated the communities and were also responsible for most of the estimated grazing. Three distinct ciliate associations were revealed from the data of both years by correlation analysis. A deep-water association characterized by large ciliates was found at the oxic/anoxic water interface at the 2 deepest stations, Bornholm and Gotland Basins, in both years, whereas the other associations found were found closer to the surface. Some of these groups may represent true feeding guilds bound together by utilization of same resources, while others could be united by abiotic factors or internal dynamics (e.g. predator-prey relationships) of the association.

KEY WORDS: Heterotrophic ciliates · Distribution · Clearance · Species associations

INTRODUCTION

Planktonic protists in the size range of approximately 20 to 200 µm, i.e. the microprotozoans, are acknowledged as a major functional component in pelagic food webs (e.g. Azam et al. 1983). In the Baltic Sea, as in most marine and brackish water environments, the planktonic microprotist community is dominated by ciliates and heterotrophic dinoflagellates (Beers et al. 1980, Smetacek 1981, Andersen & Sørensen 1986, Kivi 1986, Sherr et al. 1986, Hansen 1991, Pierce & Turner 1992, Bralewska & Witek 1995, Tiselius & Kuylenstierna 1996, Witek 1998). For the Baltic Sea, the basic outline of the annual cycle of the microprotist community with a biomass peak in spring and another in autumn has been described (Kivi 1986), and it involves changes in the species composition during the succession. An increase in ciliate biomass is connected with the onset of phytoplankton spring bloom in the northern Baltic Sea, and relatively large species such as some haptorids, and certain choreotrichs, are most abundant at this time of the year. During early- and mid-summer, the ciliate community consists mostly of naked oligotrich species (e.g. strobilidiids and strombidiids), often described as grazers on pico- and nano-size plankton (e.g. Verity

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1986, Rassoulzadegan et al. 1988, Kuosa 1990, Dolan 1991b, Kivi & Setälä 1995).

In reality, studies on ciliate abundance and species distribution in the Baltic Sea have been sporadic and have mostly been concentrated on coastal areas (Smetacek 1981, Boikova 1984, Gast 1985, Kivi 1986, Mamaeva 1988, Witek 1998) with only a few studies from the open sea areas (Leppänen & Bruun 1986, 1988, Detmer et al. 1993). Interestingly though, the functional role of ciliates in the microbial food web has been the subject of several experimental studies in the northern Baltic Sea region (e.g. Jonsson 1986, Kuuppo-Leinikki 1990, Kivi et al. 1993, 1996, Kivi & Setälä 1995, Jonsson & Johansson 1997, Kuuppo et al. 1998, Broglio et al. 2001).

Planktonic ciliates are known to be important micrograzers of different organisms in various aquatic environments (e.g. Heinbokel & Beers 1979, Gast 1985, Lessard & Swift 1985, Sherr et al. 1986, Verity 1986, Paranjape 1987, 1990, Sherr & Sherr 1987, Hall et al. 1993, Kivi & Setälä 1995, Verity & Smetacek 1996, Stoecker et al. 2000, Johansson & Coats 2002). Nevertheless, estimates on the grazing impact or clearance capacity of a ciliate community are often based on average clearance values, regardless of average ciliate cell size, which may give biased estimates of the actual grazing capacity of the ciliate community. In this study we present data based on samples from the open Baltic on ciliate species distribution and abundance combined with values of size-specific clearance rates from grazing studies made with natural communities.

The aim of this study was to examine the structure of various ciliate communities, search for possible species associations, give reasonable estimates of the grazing capacity of the communities, and finally to assess the role of planktonic ciliates in the Baltic summer pelagial food web.

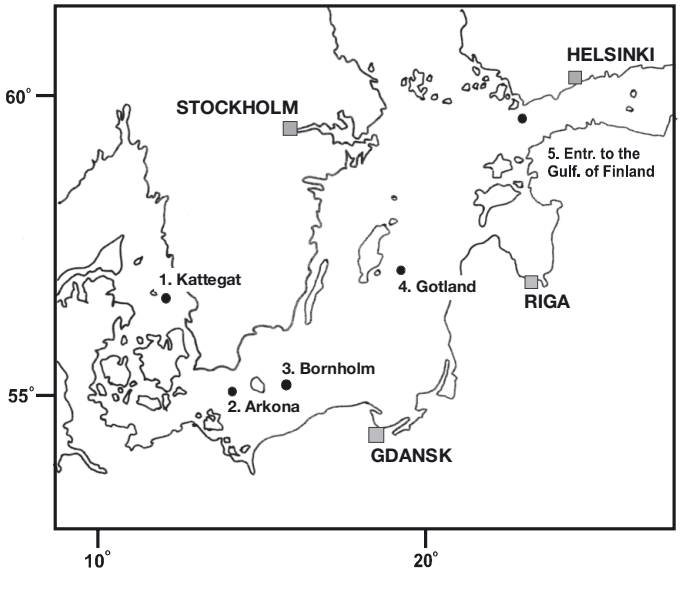


Fig. 1. Locations of the sampling stations along the Baltic Sea transects

MATERIALS AND METHODS

Material for this study was collected during 2 periods in the years 1988 and 1990. Samples were taken at 5 stations between the Kattegat and the entrance to the Gulf of Finland (Fig. 1) during 2 research cruises (RV 'Poseidon', 14 to 21 July 1988; RV 'Aranda', 27 July to 1 August 1990). Salinity and temperature were measured with a CTD probe; inorganic nutrients, oxygen, and chlorophyll *a* (chl *a*) concentrations were analysed according to standard methods (Grasshoff 1976).

Sampling depths varied between stations and years. Water was collected in the morning with rosette-type samplers equipped with 5 l Niskin bottles. Samples for microprotist counts (500 ml) were fixed with 0.5 to 1% acid Lugol's solution (Hällfors et al. 1979), routinely used at that time, concentrated to a smaller volume through a 10 µm plankton net (Kivi 1986), and subsequently settled in 50 ml tubes for 24 h (Utermöhl 1958). This concentration method was used because the number of ciliates is often rather low in unconcentrated water samples from open-sea areas. The disadvantage of this method is the probable loss of small cells that may escape through the 10 µm filter. However, the loss of cells >10 µm due to the concentration method in earlier studies has proved to be negligible when the cells have been preserved with Lugol's solution and the concentration is done carefully (Kivi 1986). Ciliates were counted with a Leitz Labovert inverted light microscope with 140× and 280× magnifications. Different geometric formulae were used to estimate the mean volume for each species or unidentified cell. The ciliate cell measurements were based on Lugol's-solution-fixed specimens only.

Acid Lugol's solution is known to cause shrinkage of cells. The change in the shape and size of the cells is, among many factors, related to the concentration of the fixative used (Choi & Stoecker 1989, Putt & Stoecker 1989, Stoecker et al. 1994). In general, the higher the Lugol's-solution concentration, the more the cells tend to shrink (Stoecker et al. 1994, O. Setälä unpubl.). The biovolume:carbon conversion (0.19 pg μm^{-3}) factor recommended by Stoecker for cells fixed with 2% Lugol's solution may give a slight overestimate of the carbon content of ciliates preserved in this study with a low concentration of Lugol's solution. Although the conversion factor (0.11 pg μm^{-3}) adopted by Edler (1979) may in contrast give underestimates of ciliate carbon content, it was chosen for 2 reasons: (1) this study is in

accordance and comparable with other 'older' studies from the Baltic, and (2) the fixative concentration used in this study was rather low (final conc. 0.5 to 1%), and does not cause severe shrinkage of the cells (O. Setälä unpubl.).

Since ciliate species are often difficult or impossible to identify to species level from Lugol's-solution-fixed samples, unidentified cells were frequently encountered and classified to the most accurate taxonomic level possible. All ciliate species were treated as heterotrophic (HCIL), with the exception of *Mesodinium rubrum*, which was considered as a photoautotroph. Recent studies have revealed the capability of *M. rubrum* to ingest cryptophyte algae in laboratory conditions (Gustafson et al. 2000) in order to renew its endosymbionts and to enhance the photosynthetic rate. However, since no observations of *M. rubrum* truly feeding on any other group of organisms for any other purpose exist, photoautotrophy was considered to be the mode of nutrition for *M. rubrum*.

Certain Baltic strombidiids (e.g. *Strombidium conicum*, *Laboea strobila*) are capable of mixotrophy (Stoecker et al. 1987, 1988, Stoecker & Michaels 1991). However, identification of symbiotic algae or kleptochloroplasts from Lugol's-solution-fixed samples could not be done.

Ciliate clearance-rate calculations were based on an exponential biovolume-dependent equation (Fig. 2):

$$y = 0.1493x^{0.906} \ (r^2 = 0.790;\ F\text{-test } p < 0.05)$$

where x is the estimated spherical diameter of the ciliate (ESD, µm) and y is the clearance rate (µl cell^{-1} h^{-1}). This function was mostly derived from experimental data published in Kivi & Setälä (1995), where ciliate clearance rates and food selection were studied with 'food' particles (wheat starch) added at tracer level to natural communities of planktonic ciliates. Some literature values were added to the data for the final function (Heinbokel 1978, Scott 1985, Taniguchi & Kawakami 1985, Verity 1985, Andersen & Sørensen 1986, Jonsson 1986). Clearance rates (expressed as volume swept clear of suitable food particles per cell per hour), and not ingestion rates were used, because clearance rates are not very dependent on the food-particle density over a large range of concentrations. The rates used here should thus be applicable to the food-item concentrations indicated by the chl *a* data in this study (for a detailed treatise, see Chow-Frazer & Sprules 1992).

The clearance rates were calculated for the whole ciliate data divided into size groups with 10 µm intervals; also, the size distribution of the ciliates at different sampling sites was calculated with the same intervals, as depth-weighted averages for the whole water column. These hourly values were then multiplied by 24 to obtain the daily clearance percentages, meaning the percentage of the water volume cleared in 24 h. No temperature correction was applied, as the results in Kivi & Setälä (1995) did not show any clear temperature dependence of the clearance rates in the range of 10 to 18°C.

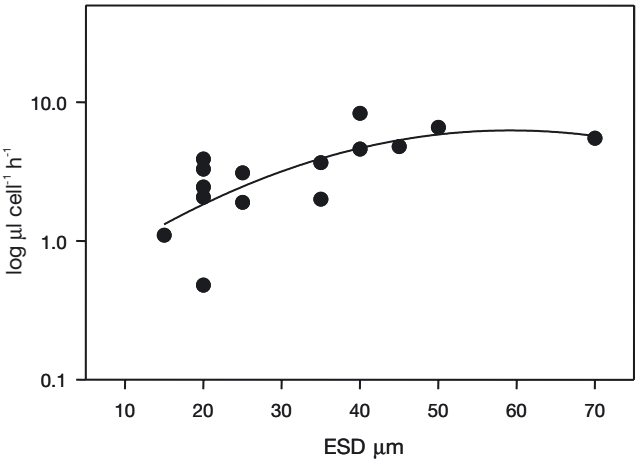


Fig. 2. Experimentally obtained ciliate clearance rates (log µl cell^{-1} h^{-1}) vs ciliate ESD (estimated spherical diameter)

To study possible interspecific associations of the ciliates, and their connections with abiotic and biotic factors, Pearson's correlation coefficients were calculated between all ciliate species, temperature, and chl *a* concentrations. Correlation coefficients were also calculated between daily clearance of ciliate communities and chl *a* concentrations as well as daily clearance and HCIL cell numbers. The sampling depths for different parameters varied occasionally, which caused some limitations in the correlation analysis.

Associations between ciliate species were determined by the significance of the correlation factors between cell numbers of the different species from the whole data. The associations are based on 'head' species, defined as that species which had the highest numbers of significant correlations with other species. Cell-number averages weighted by both depth and the cell numbers of the 'head' species were then plotted to graphically present the location of the associations on depth versus 'head' species cell-number scales.

RESULTS

Hydrography

The surface water temperature varied somewhat between stations (17 to 19°C), and the thermocline was situated between 10 and 25 m (Fig. 3). Stn 1, Kattegat,

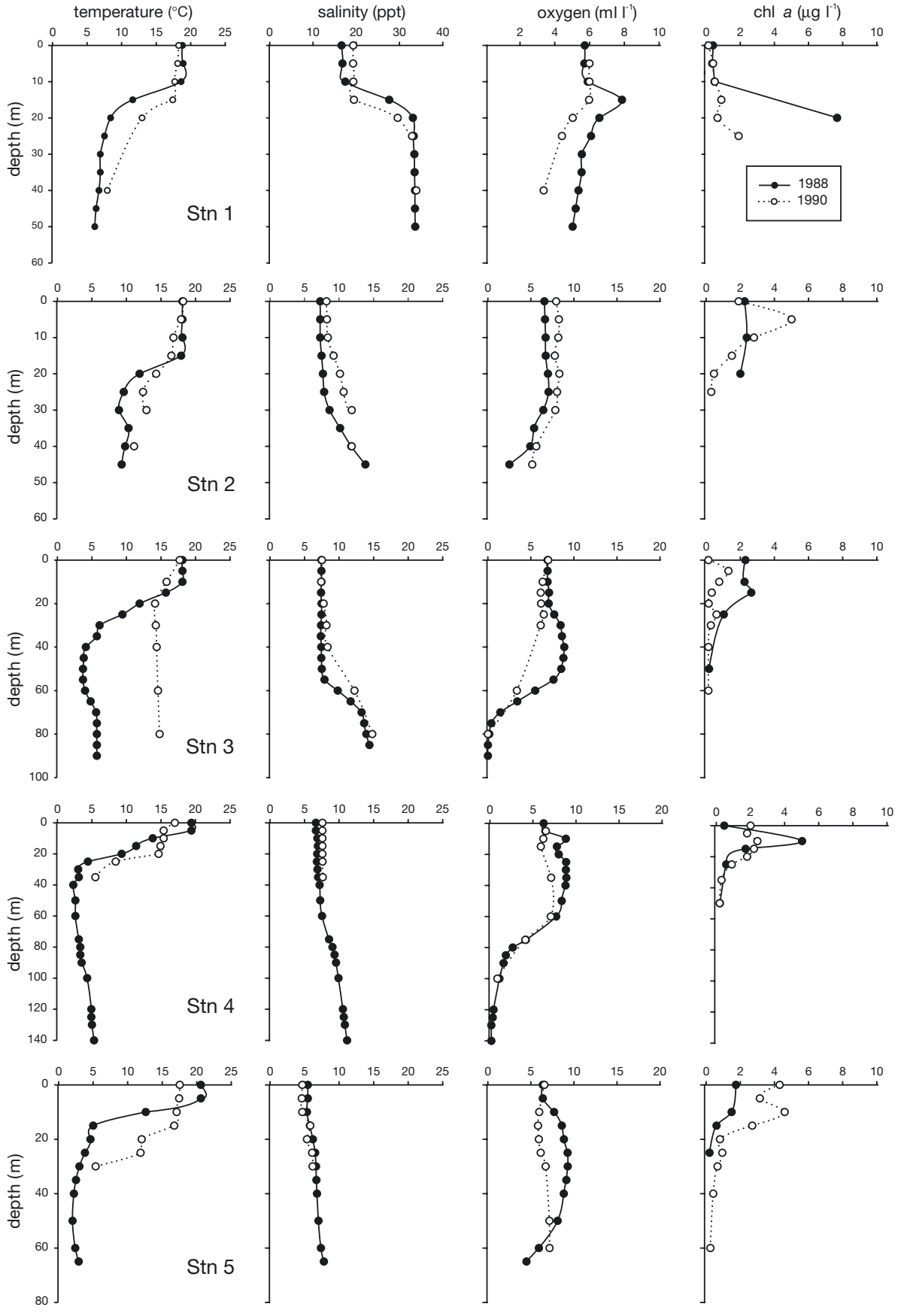


Fig. 3. Temperature, salinity, oxygen, and chl *a* profiles at the different sampling stations in 1988 and 1990

which is in contact with North Sea water through the Danish Straits, had higher-salinity water compared to the other stations. Surface-water salinity between Stn 1 and Stn 5, the northernmost station at the entrance to the Gulf of Finland, decreased from 17 to 5 ppt, and below the thermocline from 34 to 7 ppt. A distinct pycnocline was observed only at Stn 1 (10 to 20 m). The water column at all stations was well oxygenated from the surface to the thermocline and below. At the 2 'deep stations', Stns 3 and 4 (Bornholm and Gotland Basins), the deep layers were poorly oxygenated or anoxic, with detectable concentrations of H_2S (Fig. 3; Gast & Gocke 1988, Setälä 1991, Detmer et al. 1993).

During both cruises, and at all stations, the main inorganic nutrients (NH_4-N, NO_3-N, and PO_4-P) were practically depleted from the uppermost 0 to 40 m (both years on average <1 µmol l^{-1} at all stations). In deeper water, somewhat higher concentrations (average <1 to 5 µmol l^{-1}) of these nutrients were occasionally found. As a whole, the situation was typical for the summer season, with low ambient concentrations of nutrients, but probably high regeneration rates in the water column above the thermocline.

The chl *a* concentrations varied between <1 and 4 µg chl *a* l^{-1}. The maximum chl *a* values were measured near the surface, except the subsurface maximum value measured at 20 m depth at Stn 1 in 1988 (Fig. 3).

Abundance and distribution patterns of ciliate communities

1988

The bulk of the ciliate cell numbers was, with few exceptions, found above the thermocline (Fig. 4A). The total densities of HCIL were rather low throughout the study area (<100 to approx. 6000 cells l^{-1}). The dominance of relatively small (≤30 µm) species was reflected as moderate or low organic carbon content of the communities (max. 6.7 µg C l^{-1}) in the waters above the thermocline. Due to the occurrence of very large ciliates at the deep oxic/anoxic water interface, the highest total HCIL carbon values were found at Stn 3 close to 90 m depth (max. 28.8 µg C l^{-1}). Also, at Stn 4 deep high maxima of ciliate carbon (up to 13.9 µg C l^{-1}) were detected. However, the total cell numbers of HCIL were positively correlated with temperature ($r = 0.687$; $p < 0.01$), but not with chl *a* ($r = 0.417$, ns).

The ciliate communities at different stations were in most cases dominated by strobilidiids, small species of the genera *Balanion* (*Balanion* cf. *comatum*) and small unidentified prostomatiids, such as *Urotricha* spp. The proportion of strombidiids was large only at Stn 5. A marine mixotrophic species, *Laboea strobila*, was found at Stn 1, where also a dense population of *Strobilidium spiralis* was found at 50 m depth (1780 cells l^{-1}: 12.8 µg C l^{-1}). Low numbers of large unidentified ciliates, unusual for plantonic ciliate communities in the Baltic were found at the oxic/anoxic deep water boundary layers of Stns 3 and 4. These species were either elongated and narrow, or ovoid in shape and with rather uniform ciliation. The cells were preserved in very strong Lugol's solution, which effectively masked all possible details for species identification. The occurrence of these species in the oxic/anoxic boundary layer and their origin has been discussed in Setälä (1991).

Mesodinium rubrum was encountered at all stations. The maximum densities were found above the thermocline, although *M. rubrum* cells were frequently found in deeper samples as well. Since classification of *M. rubrum* into size groups was not done, the carbon content estimates were based on the 'average' *M. rubrum* cell (0.24 ng C $cell^{-1}$), which has been used in other studies on the southwest coast of Finland (e.g. Kivi 1986, Kivi et al. 1996, Kuuppo et al. 1998).

1990

As in 1988, the bulk of the ciliates was concentrated in the water column above the thermocline, but generally at higher densities (ca. 1000 to 20 000 cells l^{-1}; Fig. 4B). Again, at Stn 4 a deep-water maximum of ciliate carbon (10.3 µg C l^{-1}), which was produced by only a few cells, at the depth of 120 m was noted. In general, small prostomatiids (*Balanion* cf. *comatum* and *Urotricha* spp.) were equally as important as in 1988, whereas the number of strobilidiids was small, and strombidiid species were the most important choreotrichs. *Mesodinium rubrum* occurred throughout the whole study area. The maximum density of *M. rubrum* was 26 600 cells l^{-1} (6.4 µg C l^{-1}; Fig. 4B). There was a significant correlation between HCIL numbers and temperature ($r = 0.585$; $p < 0.01$) as well as between HCIL and chl *a* ($r = 0.685$; $p < 0.01$).

Size distribution of the ciliates

The size distribution of the ciliates in 1988 was found to differ from our previous observations. Although small cells tend to dominate summer ciliate communities, there still typically exists a continuum of different size groups, the cell numbers decreasing with increas-

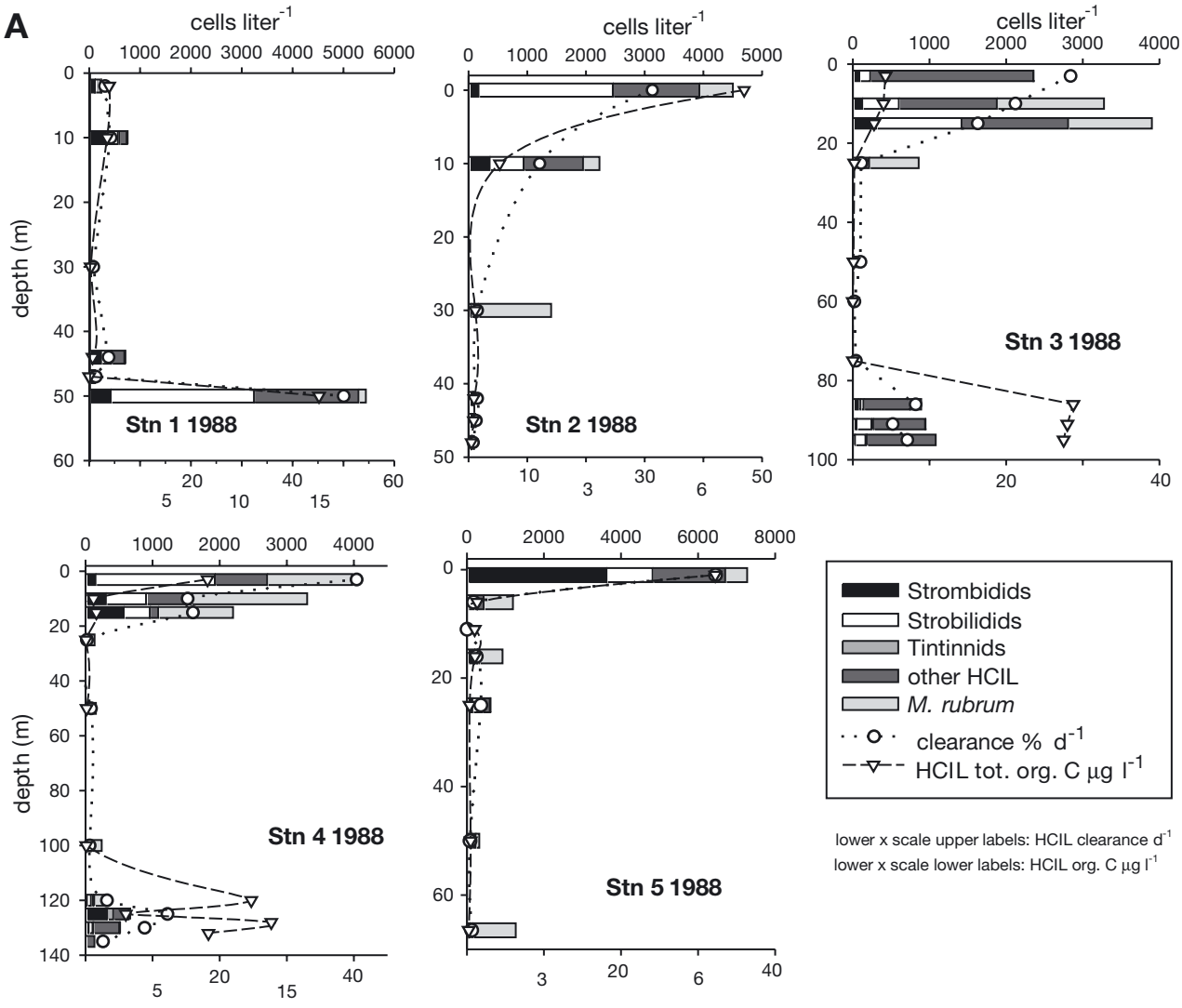


Fig. 4. (Above and facing page.) Numbers and depth profiles of different ciliate groups, daily clearance percentages, and total organic carbon content of heterotrophic ciliates at different stations in (A) 1988 and (B) 1990

ing size (Kivi 1986). In the data for both years, the 2 smallest size groups (<10 to 20 µm) were well represented, but the number of cells in the next size group (>20 to 30 µm) were negligible at Stns 1 to 4 in 1988. However, in the >30 to 40 µm size group, ciliate numbers were considerably higher in 1988 (Fig. 5). The overall χ^2-test value (21.44; $p < 0.01$) between the 2 years (calculated with the between-station average proportions of each size group) indicated that the HCIL size distributions were significantly different.

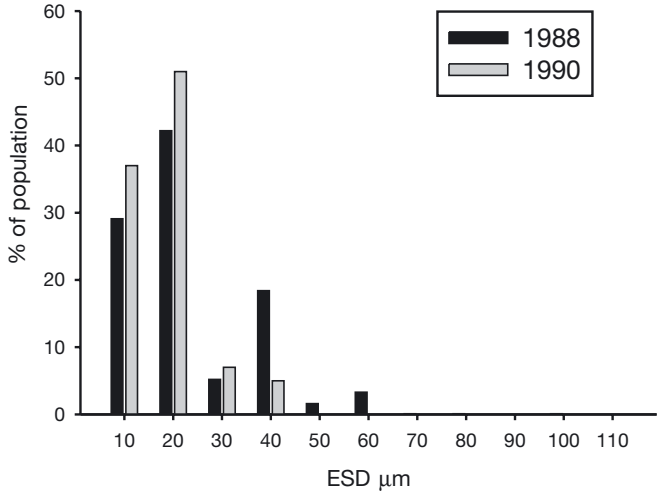
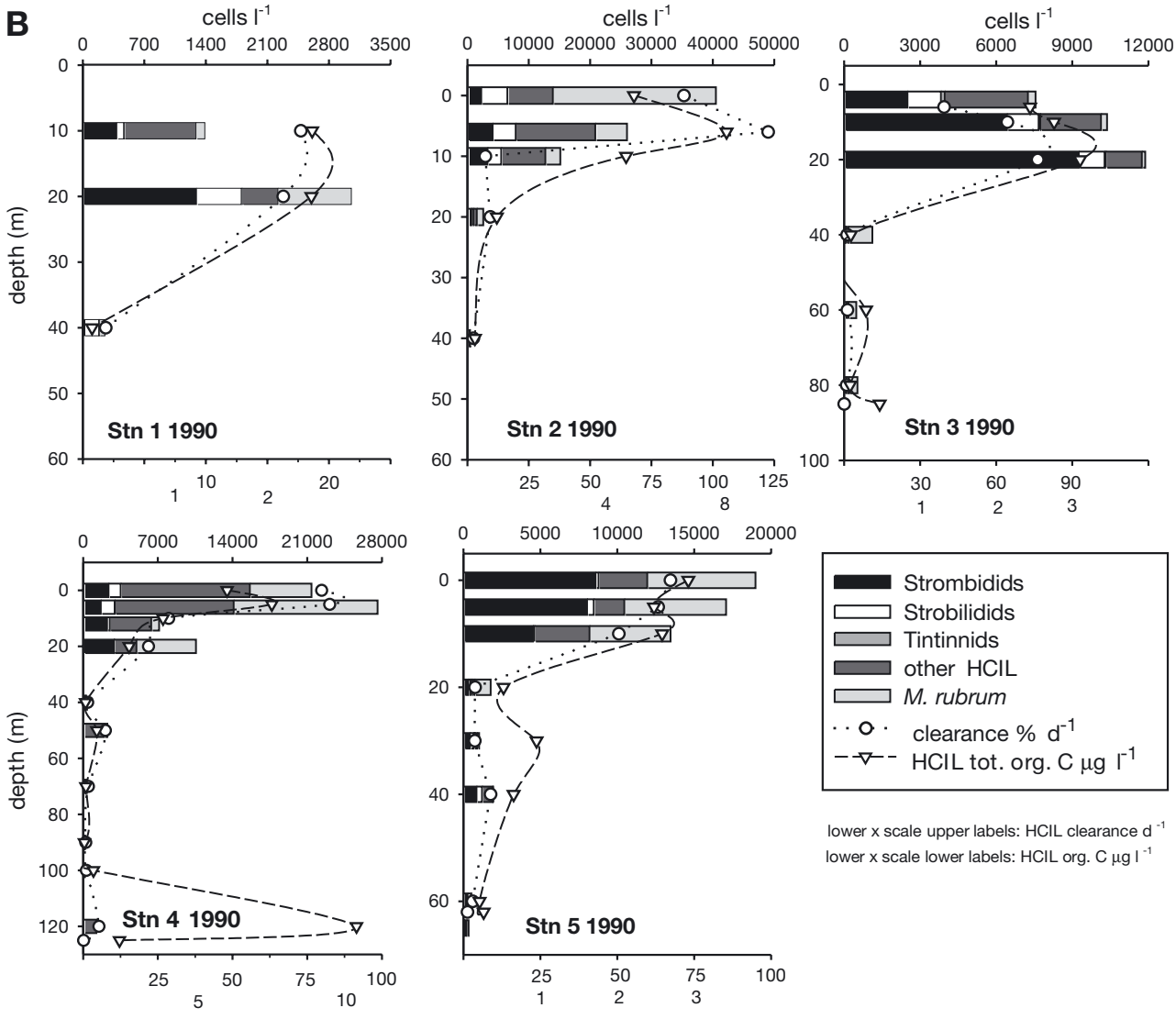


Fig. 5. Average size distributions (ESD, µm) of HCIL in 1988 and 1990. For example, the size group '30 µm' includes cells with the largest measured diameter (D) larger than 30 µm and up to 40 µm (30 µm < $D \leq$ 40 µm)



Ciliate grazing estimates

The estimates of community clearance rates (% of water volume cleared per day), although based both on size and numbers of the ciliates, were highly dependent on the total cell numbers (Fig. 4). Significant positive correlations were found in both years between ciliate numbers and the daily clearance percentage (1988: $r = 0.906$, $p < 0.01$; 1990: $r = 0.988$; $p < 0.01$). The daily clearance was in general rather low in 1988 (at best up to ca. 50%), but usually higher in 1990, mainly because of higher numbers of ciliates present. However, the clearance rate relative to cell numbers was actually higher in 1988, because the cells were generally larger than those in 1990. In some cases (for instance, at Stns 1 and 2 in 1990) the daily clearance rate exceeded the values expected from cell numbers alone. Usually, more than 50% of all grazing took place in size groups ≤ 30 µm ESD, but in the cases with elevated clearance rate, there were also larger ciliates present. The daily clearance percentage varied largely (approx. 0 to 125%) between the stations and different depths. In 1990, a significant positive correlation was found between the daily clearance and chl *a* ($r = 0.684$; $p < 0.01$). In 1988, the clearance rate:chl *a* correlation was non-significant ($r = 0.332$).

Ciliate associations

For both 1988 and 1990 data, 3 distinct ciliate associations were revealed by correlation analysis (Fig. 6, Table 1). The tightest bond between species was that of the ciliates *Coleps* spp., large unidentified ciliates,

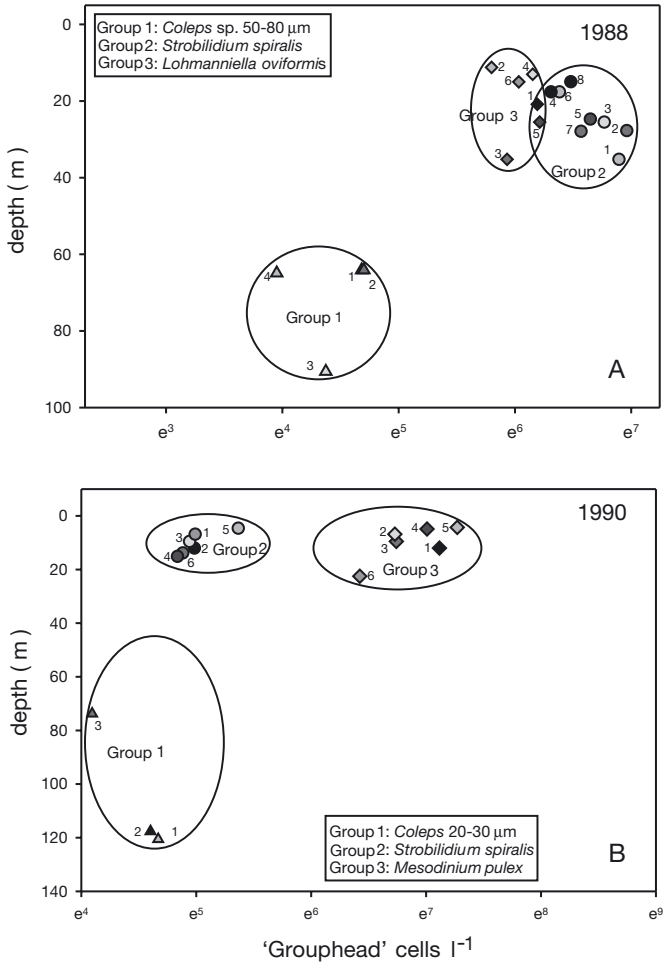


Fig. 6. Three different associations of ciliates distinguished by correlation analysis in (A) 1988, (B) 1990. For details, see Table 1

and *Metopus* sp., restricted to deep, cold, saline, and poorly oxygenated water layers (Group 1 in both Fig. 6A and B). All the other associations consisted of rather diverse collection of species. The members of the different groups are presented in Table 1, and the characteristics of these associations are described in detail below.

DISCUSSION

During the 2 cruises, the environmental factors were quite similar. Some differences in environmental parameters were recorded, but in general both transects represented a typical late summer situation, with high surface temperatures, mostly a well-defined thermocline, and very low ambient nutrient concentrations in the euphotic layer. This combination of circumstances gives rise to planktonic communities where standing stocks of primary producers are low, and nutrients are regenerated rapidly (e.g. Dugdale & Goering 1967). The differences in species composition and biomass between the years and sampling sites emphasize the dynamic and rapidly changing nature of HCIL populations.

The basic structure of the ciliate communities at the group level (Fig. 4) was rather similar in the 2 years. The communities were dominated by aloricate choreotrichs (strombidiids and strobilidiids) or by small prostomatiids. Only a few tintinnids were found; however, they may occasionally be quite numerous in Baltic plankton (Kivi 1986). The numbers of large (ESD > 60 µm) choreotrichs or predatory haptorids (e.g. *Didinium gargantua*), usually abundant in springtime, were negligible.

The unique and ubiquitous phototrophic ciliate *Mesodinium rubrum* was abundant on many occasions. While the highest numbers were always found in the euphotic layer, there were several samples in the material where *M. rubrum* was virtually the only ciliate present in deeper layers, down to 80 m (Fig. 4). Considerable densities of *M. rubrum* in the deep-water layers of the Baltic have been observed previously (O. Setälä unpubl.), when a maximum of *M. rubrum* densities was found at 90 m depth (Bornholm Basin: 9050 cells l^{-1}, 2.2 µg C l^{-1}). *M. rubrum* cells are extremely motile and thus able to perform large diel vertical migrations, perhaps to take up nutrients from deeper layers at night (e.g. Lindholm 1985, Villarino et al. 1995). The increasing concentration of nutrients towards deeper layers at Stn 4 (1990: NO_3-N from 0 µmol l^{-1} at 0–25 m depth to 7.3 µmol l^{-1} at 80 m; PO_4-P from 0.12 to 1.76 µmol l^{-1}, respectively) in otherwise nutrient-depleted conditions might well be one reason for the occurrence of *M. rubrum* in deep-water layers. It may also be that part of the *M. rubrum* population does not migrate according to a diel cycle over such a large depth range, but follows a 48 h, or longer, migration pattern, which would account for the daytime deep maxima.

In both years, a distinct community of deep-dwelling ciliates was found to exist at depths close to the oxic/anoxic boundary. As these ciliates were generally very large, they may have a significant effect on the ciliate carbon estimates calculated for the whole water column. However, this kind of community is apparently separated from the pelagic carbon cycle by '1-way transport' (connected to the rest of the pelagic system only by receiving settling matter from surface layers), and it should probably be considered as a part of an ecosystem living mainly on resources not available to other pelagic organisms.

In spite of the many similarities between the ciliate communities of the 2 years, some major differences

Table 1. Members of the 3 main ciliate associations found in 1988 and 1990. The correlation coefficients between them and the guild 'head' species are shown. df: 1988, 35; 1990, 39. **Bold**: $p < 0.01$; normal: $p < 0.05$

Group	1988 Taxon	r	Group	1990 Taxon	r
1	***Coleps* sp. ≤ 80 µm**		1	***Coleps* sp. 20–30 µm**	
	Coleps spp. ≤50 µm	**0.708**		*Metopus* sp.	**0.991**
	Ciliata spp. ≥50 µm	**0.689**		*Coleps* sp. ≤80 µm	**0.990**
	Ciliata spp. ≥100 µm	0.469		*Ciliata* spp. = 100 µm	**0.497**
	Ciliata spp. ≤50 µm	0.449			
2	***Strobilidium spiralis***		2	***Strobilidium spiralis***	
	Strombidium sp. 60–70 µm	**0.787**		*Balanion/Urotricha* spp. ≤20 µm	**0.826**
	Strombidium conicum	**0.708**		*Ciliata* spp. ≤20 µm	**0.713**
	Strobilidium spp. ≤20 µm	**0.678**		*Lohmanniella oviformis*	**0.688**
	Lohmanniella oviformis	**0.663**		*Strombidium conicum*	**0.579**
	Balanion/Urotricha spp. ≤20 mm	**0.625**		*Strombidium* spp. ≤50 µm	**0.557**
	Mesodinium pulex	**0.530**		*Ciliata* spp. ≤30 µm	0.411
	Ciliata spp. ≤30 mm	**0.512**			
	Halteria grandinella	0.403			
3	***Lohmanniella oviformis***		3	***Mesodinium pulex***	
	Strobilidium spiralis	**0.663**		*Ciliata* spp. ≤20 µm	**0.905**
	Balanion/Urotricha spp. <20 µm	**0.602**		*Balanion/Urotricha* spp. ≤20 µm	**0.610**
	Strombidium conicum	**0.547**		*Lohmanniella oviformis*	**0.557**
	Mesodinium pulex	**0.515**		*Strombidium* sp. 25–30 µm	**0.540**
	Strobilidium spp. ≤20 µm	**0.514**		*Strombidium* spp. ≤50 µm	**0.552**
	Halteria grandinella	0.334		*Askenasia stellaris*	0.343

were observed. The most conspicuous was the marked dissimilarity of HCIL cell numbers (except at Stn 1), which were roughly an order of a magnitude higher in 1990 than in 1988. If we take into account the differences in the population size structure between the years as well, it is obvious that the potential grazing impact of the ciliates on pico- and nanoplankton was quite different in 1988 than in 1990.

Planktonic ciliates, with high metabolic rates, often hold a key position in the planktonic food web as major grazers of pico- and nanoplankton, and as intermediaries in the transfer of otherwise unavailable production of these organisms to metazoan plankton (e.g. Stoecker & Capuzzo 1990, Dolan 1991b, Kivi et al. 1996, Merrel & Stoecker 1998). The daily community clearance rates in the euphotic layer in 1988 were probably not high enough to have a substantial regulatory effect on pico- and nanoplankton growth (on average 21% of water cleared per day in the 0 to 10 m layer). However, as the grazing impact of the ciliates in 1990 was significantly higher (average 52% of water cleared d^{-1} in the 1 to 10 m layer), we conclude that ciliates could, at least to some extent, control the populations of their food items near the surface, especially in daytime, when practically all crustacean plankton and most of the rotifers stay below 10 m depth (K. Kivi unpubl.).

The correlations between cell numbers and chl *a* give some additional information on the coupling of ciliates and phototrophic pico- and nanoplankton. This correlation was non-significant in 1988, but highly significant in 1990. Similarly, the daily clearance was not significantly correlated with chl *a* in 1988, but in 1990 the positive correlation was highly significant. These results (together with cell numbers and size distributions) may indicate that the pico/nanoplankton-ciliate-crustacean chain could have been different in 1988, whereas in 1990, the smallest ciliates were more tightly coupled with the production of pico- and nanoorganisms. The ciliates could have been, in turn, heavily grazed on by metazoan plankton, with the smallest size groups being capable of escaping predation by rapid growth.

The search for species assemblages, associations, or 'guilds' is common in terrestrial ecology (e.g. Brown & Davidson 1968), but virtually unheard of in plankton research (but see Dolan 1991a). However, when this kind of approach was tested with our material, 3 different groups from the data of both years could be distinguished (Fig. 6).

Group 1 in both years represents the usually large, deep-dwelling ciliates. These species may be bound together mainly by the abiotic environmental factors the cold, saline and hypoxic water offers them. However, there are also other factors typical of the environment of these species. Detmer et al. (1993) observed that in the oxic/anoxic boundary layer of the Gotland Deep the numbers of coccoid cyanobacteria were very

high. In earlier studies (Gast & Gocke 1988, Setälä 1991), high numbers of large bacterial cells were also found at these depths. Thus, the deep-water pico-organisms may form a common food resource for these ciliates, thus also playing a role in the formation of the associations.

The ciliate diversity in the other groups was higher than in the 2 deep-water groups (Group 1 in the 2 years). The members of these associations may be bound together by utilisation of the same food resources, or just by preference for a similar environment, or by the inner dynamics of the association (e.g. predator-prey relationships). In addition, some of these groups may be true 'feeding guilds', since many of the members are known to be able to utilise at least partly the same food size spectrum (e.g. Kivi & Setälä 1995). But inner predator-prey dynamics of a group may well be involved here, as the largest members of the group can probably ingest particles of the size of the smallest members (for instance, Group 2 in 1988: the large 60 to 70 µm *Strombidium* sp. might readily utilise the tiny *Balanion* cf. *comatum* and *Urotricha* spp. as food). In this light, Groups 2 and 3 in 1990 may be the closest representatives of real feeding guilds, since the size differences of the members are not great, and, for instance, the 'head' species of Group 2 (*Strobilidium spiralis* ≤60 µm) prefers food particles similar in size (5 to 6 µm) to those utilised by some smaller members of the group (Kivi & Setälä 1995).

There are probably several factors working simultaneously together to keep the group members together: environmental factors (e.g. temperature), food, and the inner dynamics of the association. The strong correlations between the spatial co-occurrence of these species, however, point towards a true connection between the members of a group, whatever the ultimate bond might be.

The results of this study demonstrate that there are diverse ciliate communities in the Baltic Sea summer pelagial ecosystem, even in the abyssal hypoxic regions, and that, at least in 1990, these ciliates were functioning vigorously as grazers of pico- and nanoplankton, and also may have fulfilled an important task by mediating the otherwise unavailable primary production to higher trophic levels. There also appears to be distinct associations of ciliates, the inner dynamics of which are well worth further detailed studies.

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