JOURNAL OF PLANKTON RESEARCH | VOLUME 26 | NUMBER 1 | PAGES 67–80 | 2004

Annual variability in ciliate community structure, potential prey and predators in the open northern Baltic Sea proper

MONA JOHANSSON*, ELENA GOROKHOVA AND ULF LARSSON
DEPARTMENT OF SYSTEMS ECOLOGY, STOCKHOLM UNIVERSITY, SE-106 91 STOCKHOLM, SWEDEN

*CORRESPONDING AUTHOR: mojo@system.ecology.su.se

Biomass of ciliates, bacteria and mesozooplankton, as well as biomass estimates of phytoplankton from chlorophyll a values, were studied in the mixed layer of the northern Baltic Sea proper, between February and December 1998. Production of phytoplankton and bacteria was measured, and production of ciliates and mesozooplankton was estimated. The phytoplankton spring bloom in late March was dominated by diatoms and dinoflagellates. Ciliates had a biomass peak shortly after the spring bloom, while mesozooplankton peaked in July. Thus, the predation pressure on ciliates was low in spring, and ciliates were major predators, potentially consuming up to 15% of the primary production. In summer, there was a shift from larger to smaller ciliates coinciding with a shift from larger to smaller primary producers, an increase in bacterial production, and also an increase in mesozooplankton abundance, mainly copepods. Elevated mesozooplankton predation and selective removal of larger ciliate species and/or a shift to smaller prey size presumably caused these changes. The potential carbon consumption from ciliates and mesozooplankton was highest in summer and autumn, reaching 55 and 40% of the primary production in summer and autumn, respectively. Ciliates consumed twice as much as mesozooplankton, thus acting as important regenerators.

INTRODUCTION

In pelagic environments, energy is supplied to higher trophic levels through two main pathways. The traditional grazing food chain transfers energy directly from larger phytoplankton to mesozooplankton (Cushing, 1989), in contrast to the microbial food chain, which transfers little energy to higher trophic levels (Azam *et al.*, 1983; Legendre and Rassoulzadegan, 1995). Numerous studies have reported ciliates feeding on picoplankton and nanoplankton (Stoecker and Evans, 1985; Bernard and Rassoulzadegan, 1990), making them a likely link in the transfer of energy from the microbial components in the food web to higher trophic levels (Azam *et al.*, 1983; Sherr and Sherr, 1986). Although most ciliates are heterotrophic, numerous species are mixotrophic (Jonsson, 1987; Stoecker and Michaels, 1991), which complicates the proper assignment of a trophic position. Ciliates are mainly preyed on by copepods, larger ciliates and heterotrophic dinoflagellates, and occasionally by rotifers, bivalve larvae and larval fish (Stoecker and Capuzzo, 1990; Verity and Paffenhöfer, 1996).

Protists are recognized as trophic intermediaries in Baltic Sea pelagic food webs. However, their occurrence and distribution are poorly studied, except for the mainly autotrophic ciliate *Mesodinium rubrum* Lohmann 1908 (=*Myrionecta rubra* Jankowski 1976) (Lindholm, 1985; Leppänen and Bruun, 1986). Ciliates are usually not included in regular Baltic Sea sampling programmes, though exceptions exist. Most of these studies were performed in coastal areas, some with seasonal coverage [e.g. (Smetacek, 1981; Witek, 1998)], and a few were conducted at offshore stations [e.g. (Mamaeva, 1988; Reckermann, 1996)]; none of the latter give seasonal coverage.

Ciliates are fragile, and thus problematic to sample and preserve (Stoecker *et al.*, 1994), which may explain the scarcity of data. To understand pelagic food webs better, there is a need for simultaneous estimates of the density and distribution patterns of all planktonic components, including ciliates. Here we report on the seasonal variability of the plankton community, in particular ciliates, in the mixed layer of the offshore Baltic Sea proper. We examined the ciliate community structure

doi: 10.1093/plankt/fbg115, available online at www.plankt.oupjournals.org

in relation to production of phytoplankton and bacteria, as well as the mesozooplankton community structure.

METHOD

Study area and sampling

The study was carried out at the Landsort Deep (the deepest point in the Baltic Sea, 458 m deep), in the northern Baltic Sea proper (58°35′N, 18°14′E) (Figure 1). The salinity in the Baltic Sea proper is 6–8 in the surface water, the average depth is ~60 m and tides are negligible. Surface currents in the Baltic Sea proper are typically anticlockwise, transporting surface water north along the eastern Baltic coast, then turning west to join surface water from the Bothnian Sea and continuing south along the Swedish coast. There is a permanent halocline between 60 and 80 m. The temperature generally ranges between 0 and 20°C in the surface waters, with a summer thermocline between 10 and 20 m depth. An ice cover can develop occasionally during winter, although it frequently breaks up. The photic zone is restricted to the upper 20 m, and the average Secchi depth is ~6–8 m during spring and summer (data from the Swedish Marine Monitoring Programme).

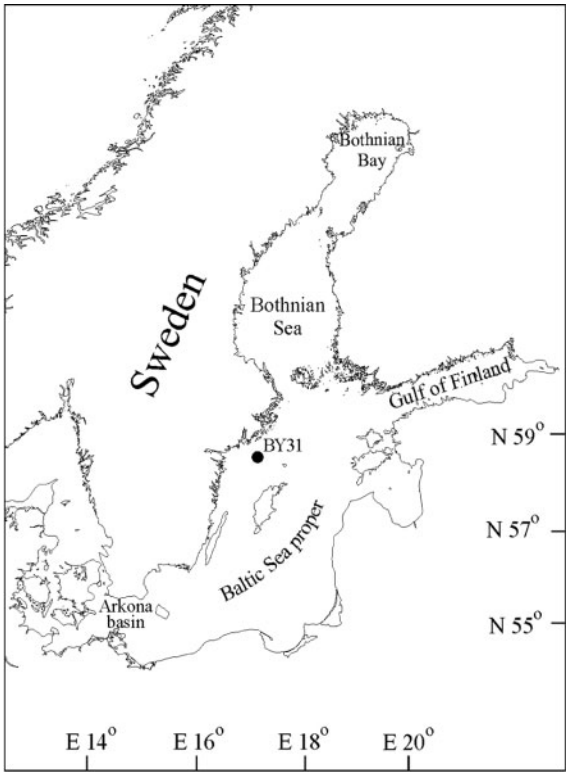

Fig. 1. Sampling station BY31 (58°35′N, 18°14′E) located in the Landsort Deep, the deepest part of the Baltic Sea.

We sampled the Landsort Deep station from 17 February to 8 December 1998, monthly during winter, weekly during the spring bloom (24 March–5 May) and every second week in summer and autumn (Figure 3; Table I). On each sampling occasion, water temperature and conductivity were measured in depth profiles with a CTD (Meerestechnik Elektronik GmbH, Germany). Water samples for chlorophyll *a*, primary production and bacteria were collected with serial 5 L Ruttner-type water samplers (Hydrobios, Germany).

Phytoplankton primary production

Rates of ^{14}C uptake were measured in duplicate 80 mL transparent polycarbonate bottles at 11 depths (0, 1, 2, 4, 6, 8, 10, 12.5, 15, 20 and 25 m, dark bottles at 0, 4 and 25 m). After 4 h of incubation, the water was filtered through 90, 40, 20, 10, 3, 1 and 0.2 μm filters, and the filtrate was also collected (Larsson and Hagström, 1982). Filters ≥20 μm were custom-made from nylon net sheets, while finer filters were Poretics polycarbonate filters, all mounted in Swinlock filter holders (Millipore Inc.).

A few drops of 1 N HCl were added to the filters before drying overnight at 60°C in plastic scintillation vials. After drying, 7 mL of scintillation cocktail (Filter count; Perkin-Elmer) were added to the scintillation vials with the filters, and thereafter they were counted in a Packard scintillator (Tri-Carb 1600 TR; Packard Corp) for 20 min. Rates of ^{14}C uptake in unfiltered sea water and in 0.2 μm filtrate were determined in 10 mL subsamples in glass scintillation vials after adding 2 drops of 1 M HCl, bubbling with air for at least 30 min and adding 10 mL of Lumagel Safe (Lumac LSC B.V.).

Carbon uptake was calculated according to Parsons (Parsons *et al.*, 1984). Dark uptake at incubation depths without dark bottles was calculated by linear interpolation and subtracted from the light uptake. Daily primary production was calculated by dividing the measured primary production by the fraction of total daily insolation at Visby on the island of Gotland (100 km south of the sampling station) received during the incubation. Integrated ^{14}C uptake rates were linearly interpolated over depth. Since post-fractionation leads to underestimation of phytoplankton growth compared to unfiltered samples (Larsson and Hagström, 1982), we proportionally recalculated the summed uptake rates in size fractions to equal the estimate from the unfiltered samples.

Bacteria

The abundance and production of bacteria were estimated at five depths: 0, 4, 10, 15 and 20 m. At each depth, two 20-mL water samples were immediately fixed with formaldehyde (2% final concentration) and kept in darkness at 4°C until processed further (storage time

<1 week). The water samples were filtered (0.2 μm), stained (acridine orange, 5 min), counted and measured (length and width) under an epifluorescence microscope (at least 10 fields or >300 bacteria, magnification ×1000) (Hobbie *et al.*, 1977). The volume was estimated from length and width measurements using standard geometric formulae (Blackburn *et al.*, 1998).

Bacterial production was estimated with the [^{3}H]thymidine method (Fuhrman and Azam, 1982). Triplicate 1 mL samples and controls from each depth were incubated in darkness with 20 nM [^{3}H]thymidine, for ~1 h, in a thermos flask with water from the sample depth. Bacterial activity in controls was stopped by addition of 200 μL of 50% trichloroacetic acid (TCA) prior to incubation, and in samples following incubation. Thereafter, all samples were centrifuged (<4°C, 13 000 r.p.m., ~19 000 *g*, 10 min) and the supernatant was removed by gentle suction (<20 kPa). The remaining pellet was washed with 1 mL of ice-cold 5% TCA. Prior to counting in a Tri-Carb 1600 TR scintillator (Packard Corp.), 1 mL of Lumagel Safe was added. The uptake of thymidine was calculated according to Fuhrman and Azam (Fuhrman and Azam, 1982) using formulae in Kemp *et al.* (Kemp *et al.*, 1993). In order to convert thymidine uptake to growth, we used 1.0×10^{18} cells mol^{-1} thymidine incorporated (Heinänen and Kuparinen, 1991). The carbon content was estimated after Simon and Azam (Simon and Azam, 1989) and Kemp *et al.* (Kemp *et al.*, 1993):

$$\text{pg C cell}^{-1} = 0.12 \times V^{0.7} \quad (1)$$

where V is volume (μm^3). Production (μg C L^{-1} h^{-1}) was calculated by multiplying the number of cells produced in 1 h by the average carbon content. The rate of bacterial production was assumed to be constant over a 24-h period.

Ciliates

To obtain an integrated water sample from the surface layer, a plastic tube (inner diameter 25 mm) equipped with a weight at the lower end was slowly lowered by hand at a constant rate to 20 m depth and stoppered at the upper end before being retrieved. The total volume of the tube was emptied into a bottle and carefully mixed. Thereafter a subsample of 3 L was fixed with acid Lugol solution (1–2% final concentration) and kept cold (4°C) when transported to the laboratory. The samples were concentrated in PVC plastic settling chambers (diameter 0.11 m, height 0.5 m) in darkness at 4°C. After 2 weeks, 75% of the sample was siphoned off from the top, and 50–100 mL of the remaining sample were settled for an additional 24–48 h in an Utermöhl chamber (Utermöhl, 1958).

At least 100 *M. rubrum* and 400 of the remaining ciliates were counted and identified to the lowest possible taxonomic level, using an inverted microscope (Leitz DM IRB; Leica; magnification ×200). The morphospecies were given scientific names after the ciliate species they most resembled. Note that identification of ciliates in Lugol-preserved samples is uncertain below genus. Cell volumes were estimated from length and width measurements (at ×400, minimum 10 individuals for each taxon), using standard geometric formulae (Edler, 1979; Olrik *et al.*, 1998). Mixotrophy of the ciliates was not measured, and consequently all ciliates were considered heterotrophic, except *M. rubrum*, which was considered autotrophic. To convert cell volume into biomass, the carbon:volume relationships of pg C cell^{-1} = 0.216 × volume$^{0.939}$ for protists were used (Menden-Deuer and Lessard, 2000). The potential maximum production of ciliates (*M. rubrum* excluded) was estimated for each sampling occasion by multiplying the biomass (μg C L^{-1}) by the maximum growth rate (day^{-1}) that was estimated from the empirical formula proposed by Müller and Geller (Müller and Geller, 1993):

$$\ln \mu = 1.52 \ln T - 0.27 \ln V - 1.44 \quad (2)$$

where μ is the maximal growth rate (day^{-1}), T is the average temperature (°C) at 0–20 m and V is the mean cell volume (μm^3).

Mesozooplankton

Zooplankton were sampled from three depth layers (0–30, 30–60 and 60–100 m) by vertical 90 μm WP-2 net hauls (0.5 m s^{-1}). The filtering efficiency was assumed to be 80% (Møhlenberg, 1987). All samples were immediately preserved in 4% buffered (di-sodium tetraborate) formaldehyde. Replicate subsamples (Kott, 1953) were counted with an inverted microscope (Leitz fluovert FS; Leica) until at least 500 specimens were identified. Copepods were classified according to copepodite stage and sex. Naupliar stages were not separated. Cladocerans were classified according to sex, and females as ovigerous or non-ovigerous. Biomass was estimated from individual wet weight and an assumed carbon content of 5% of the wet weight (Omori and Ikeda, 1984).

Production of rotifers, cladocerans and copepods was calculated from data on abundance and the temperature measured on each sampling occasion. Production rates of rotifers, i.e. *Synchaeta* spp. and *Keratella* spp., were estimated using equations established for *Synchaeta pectinata* and *Keratella quadrata* (Pourriot and Deluzarches, 1971). Production of cladocerans was estimated using temperature-dependent *P/B* (production/biomass) coefficients for *Bosmina* spp. (Kankaala *et al.*, 1984) and

physiological methods for podonids (Andronikova, 1976). When calculating the production for podonids, assimilation efficiency values and respiration rates were obtained from Petipa *et al.* (Petipa *et al.*, 1966) and Sushchenya (Sushchenya, 1972), respectively. Production of copepods was calculated as the sum of somatic, exuvial and generative production. The somatic production of copepods was determined by the instantaneous growth rate method (Chisholm and Roff, 1990). Temperature-dependent specific growth rates, and/or development time, and development stages were obtained from the literature (Mullin and Brooks, 1967; Zaika, 1972; Ivanova, 1973; Heinle and Flemer, 1975; Landry, 1975; Harris and Paffenhöffer, 1976; Paffenhöffer and Harris, 1976; Vidal, 1980). As we found no data for *Acartia bifilosa*, *Acartia longiremis* and *Centropages hamatus*, we used values for *Acartia clausi* (Landry, 1975) and *Centropages kroyeri* (Zaika, 1972).

Exuvial production, which is a part of the copepodite somatic production, was estimated as 8.4% of copepodite plus naupliar production (Chrisholm and Roff, 1990) for copepods of similar size. Somatic production of adults was assumed to be negligible (McLaren and Corkett, 1981). Generative production was estimated as egg production of females, based on the assumption that egg production rates in adult females are similar to growth rates in the oldest copepodites (Kiørboe *et al.*, 1985). Temperature-dependent rates of egg production were determined experimentally for *A. bifilosa* (Gorokhova, unpublished) and applied to *Acartia* spp. To obtain total mesozooplankton production on each sampling date, rotifer, cladoceran and copepod production were summed. Thus, the production of meroplankton and appendicularians was disregarded.

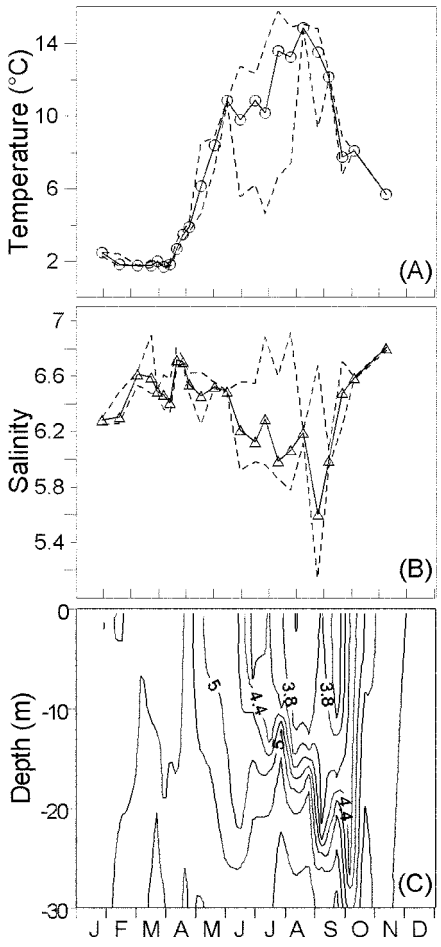

Fig. 2. Water temperature (°C) (**A**), salinity (**B**) and density (ρ) (**C**) at the Landsort Deep (BY31) in the open northern Baltic Sea proper during 1998. In (A) and (B), solid lines show mean values from the upper 20 m, and dotted lines show minimum and maximum values.

Seasonal standing stocks and production

Seasonal average biomasses (μg C L^{-1}) of autotrophic and heterotrophic components of the plankton community were obtained by linear interpolation between sampling dates. Seasons were determined from temperature and density profiles (Figure 2) as follows: spring = March 24–June 2; summer = June 2–September 24; autumn = September 24–November 3; winter = November 3–December 8. The autotrophic biomass in the size classes 0.2–3, 3–10, 10–20, 20–40 and >40 μm was estimated from chlorophyll *a* values measured on the same sampling occasions as this study, using a carbon:chlorophyll *a* factor of 40, the average value for the area (Kuosa, 1990; Kononen *et al.*, 1998; Walve, 2002). *Mesodinium rubrum* was considered an obligate autotroph, and its seasonal standing stock was calculated from measured biomasses, with seasons as described above. For the remaining ciliates, the taxonomic groups Choreotrichida, Oligotrichida, Prostomatea and Haptorida were treated separately, as were Rotatoria, Cladocera and Copepoda for the mesozooplankton. Seasonal averages of the net production (μg C L^{-1} day^{-1}) of bacteria and primary producers were calculated, as well as seasonal averages of the potential maximal production of the heterotrophic groups defined above. The seasonal maximum carbon demand, i.e. maximum carbon consumption, was calculated from the net production using a growth efficiency of 50% for bacteria (Williams, 1981) and 30% for ciliates and mesozooplankton (Downing and Rigler, 1984).

RESULTS

Temperature and salinity

The water temperature in the upper 20 m was below 2°C in spring, with little variation in salinity until mid-June, resulting in a homogeneous density profile in

spring (Figure 2A–C). At the beginning of May, the temperature rose rapidly and stable vertical gradients were present from July to mid-September (Figure 2A and C). Surface salinity decreased almost 0.5 in late June and remained low throughout the summer (Figure 2B). The low-salinity water extended down to the top of the summer thermocline, usually at 10–15 m depth. From October, the water temperature decreased rapidly. An exceptionally low salinity was recorded at the surface on one occasion in late September, and thereafter increased to levels close to spring values. There was little vertical variation from the end of September, resulting in a homogeneous density profile in autumn (Figure 2C). Throughout the year, the mixed layer was usually <20 m deep, except in early September when it was a few metres deeper.

Primary production, bacterial biomass and production

The distribution of ^{14}C uptake between size fractions varied greatly between spring and summer/autumn (Figure 3A). In spring, diatoms and dinoflagellates dominated the phytoplankton community (S. Hajdu, personal communication), and ~80% of the phytoplankton ^{14}C uptake was retained on a 10 μm filter. In contrast, in summer and autumn, 60–80% of the ^{14}C uptake was found in cells passing a 3 μm filter.

Bacterial biomass and production were low prior to the spring bloom peak (Figure 3B), then increased quickly until mid-May, and more slowly during summer to the annual peak on September 8, then decreased rapidly. Overall, both biomass and production of bacteria were positively correlated with the water temperature (r^2 = 0.78, P <0.0001 and r^2 = 0.48, P = 0.001, respectively, Pearson correlation).

Ciliate community structure, biomass and production

The 31 ciliate morpho-species found during the study are listed in Table I, together with their average length, width and cell numbers. Some of the species were found year round, but most were seasonal and some were rare. The highest number of species was found in autumn with a higher diversity within both Oligotrichida and Choreotrichida, mostly tintinnid species. Autumn and the beginning of winter were also the only time when Sessilida species were found (attached to phytoplankton and cyanobacteria). Most of the rare species were tintinnids, which were found mainly during autumn when the total diversity was highest.

Total biomass of ciliates (*M. rubrum* excluded) was low in early spring, peaked on May 5, then decreased and remained fairly stable through summer and autumn, then decreased further to the lowest values in winter

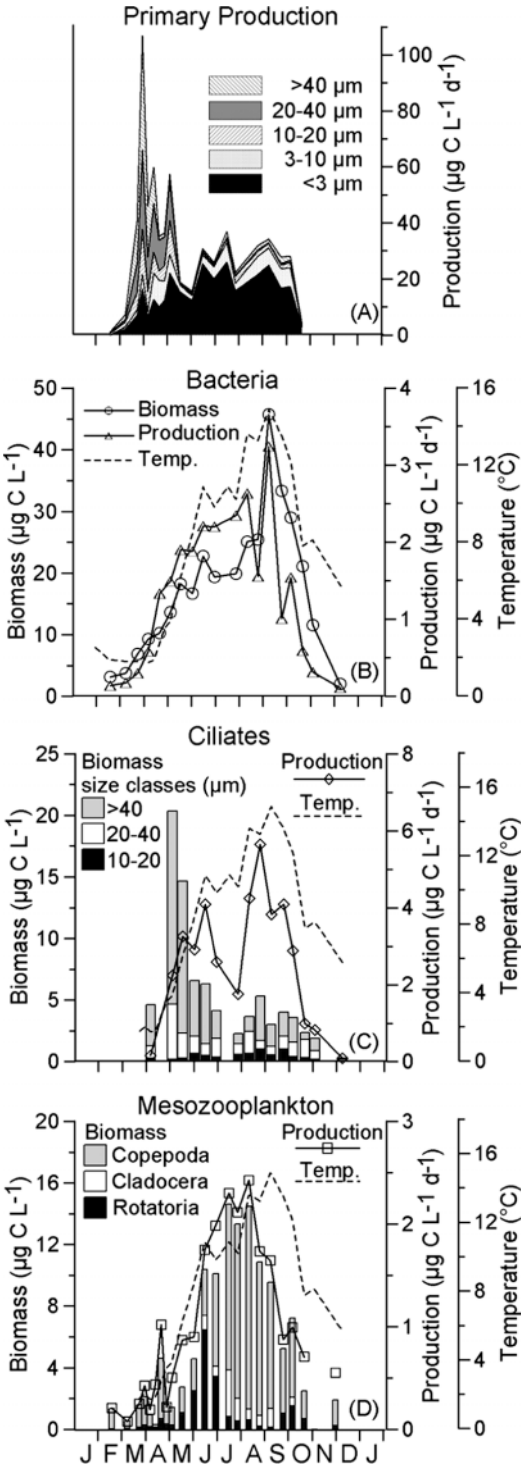

Fig. 3. Development of the plankton community in the upper 20 m at the Landsort Deep, northern Baltic Sea proper, during 1998. (**A**) Phytoplankton primary production (μg C L^{-1} day^{-1}) in size fractions. (**B**) Biomass (μg C L^{-1}) and production (μg C L^{-1} day^{-1}) of bacteria. (**C**) Biomass of ciliates (μg C L^{-1}) in size classes and their calculated production (μg C L^{-1} day^{-1}). (**D**) Biomass (μg C L^{-1}) and calculated production (μg C L^{-1} day^{-1}) of mesozooplankton in the upper 30 m. The biomass is divided into Copepoda, Cladocera and Rotatoria.

Table I: Abundance of ciliates (cells L^{-1}) in the upper 20 m of the Landsort Deep in the open northern Baltic Sea proper during 1998

Taxon	Length (μm)	Width (μm)	Abundance (cells L^{-1})														
			Spring			Summer						Autumn			Winter		
			Apr 7	May 5	May 15	Jun 2	Jun 16	Jun 30	Jul 28	Aug 11	Aug 25	Sep 8	Sep 24	Oct 6	Oct 21	Nov 3	Dec 8
Autotrophic spp.																	
Mesodinium rubrum large	33 (2)	28 (3)	962	5050	6868	8794	4848	5909	3055	1730	2326	1498	1274	1387	1771	863	402
Mesodinium rubrum small	17 (2)	14 (1)	3398	6060	7003	7575	5509	3496	1960	3231	1257	5181	4407	5675	5424	9487	2420
Heterotrophic spp.																	
Choreotrichida																	
Helicostomella subulata	70 (8)	18 (0.7)	–	–	–	–	–	–	–	–	1383	291	46	36	–	5	–
Lohmanniella cf *elegans*	28 (19)	25 (14)	–	63	–	21	534	1763	–	–	–	–	–	372	–	–	70
Lohmanniella oviformis	30 (2)	27 (2)	–	–	–	–	–	–	–	–	–	–	–	–	155	384	73
Strobilidium sp. 1	56 (11)	53 (11)	37	16	152	86	110	326	163	203	–	125	–	91	49	132	4
Strobilidium sp. 2	43*	35*	–	–	–	–	–	–	–	–	–	10	–	–	7	11	–
Strobilidium spiralis	28 (5.9)	27 (7)	–	–	–	–	–	–	576	1582	503	–	491	299	–	–	–
Tintinnidium mucicola	39 (10)	28 (7)	–	–	–	–	–	–	–	–	–	–	–	45	56	–	–
Tintinnopsis acuminata	32 (2)	20 (2)	46	266	413	43	–	–	–	–	42	–	–	–	–	–	–
Tintinnopsis baltica	43 (0.01)	27 (4)	–	–	–	–	–	–	–	–	–	–	–	45	–	–	–
Tintinnopsis brandti	66 (4)	34 (2)	–	–	–	–	–	–	10	–	–	–	–	–	14	–	–
Tintinnopsis labiancoi	60 (17)	34 (7)	212	78	344	192	55	26	–	–	–	–	15	–	–	–	
Tintinnopsis pistillum	101 (44)	39 (16)	–	–	–	–	–	–	–	–	–	–	–	9	–	–	–
Oligotrichida																	
Strombidium sp. 1	45 (5)	27 (2)	–	–	–	–	–	–	–	–	–	–	–	–	148	–	–
Strombidium cf *acuminatum*	48 (2)	34 (5)	–	–	–	–	–	–	–	–	–	–	292	127	7	–	–
Strombidium cf *conicum*	18 (1)	14 (1)	55	268	510	1112	123	–	355	1487	2305	1280	660	399	49	626	104
Strombidium cf *crassulum*	57 (6)	32 (3)	277	1943	399	791	1424	183	221	284	335	801	169	426	77	47	31

(continued)

Table I: continued

Taxon	Length (μm)	Width (μm)	Abundance (cells L^{-1})														
			Spring			Summer						Autumn			Winter		
			Apr 7	May 5	May 15	Jun 2	Jun 16	Jun 30	Jul 28	Aug 11	Aug 25	Sep 8	Sep 24	Oct 6	Oct 21	Nov 3	Dec 8
Strombidium cf *delicatissimum*	17 (0.4)	14 (0.2)	1567	611	–	–	–	–	–	–	–	–	–	–	423	–	–
Strombidium cf *elegans*	55 (16)	44 (12)	230	737	–	–	–	–	–	108	713	–	–	–	–	137	43
Strombidium cf *minutum*	29 (2)	23 (1)	516	1254	386	1198	1287	535	365	716	566	270	292	489	303	174	15
Strombidium cf *vestitum*	22 (2)	19 (0.3)	37	–	–	–	–	–	–	–	–	–	–	–	176	174	73
Prostomatea																	
Balanion comatum	17 (0.8)	14 (0.7)	304	423	523	5197	2041	1449	1969	1568	2515	1311	3946	1441	894	305	166
Holophrya sp. 1	31 (7)	24 (5)	295	235	647	235	14	–	–	81	42	104	123	–	–	21	–
Holophrya sp. 2	36 (3)	35 (3)	46	–	–	–	–	–	38	81	–	21	–	9	–	–	4
Haptorida																	
Askenasia stellaris	35 (6)	34 (7)	166	878	1639	64	27	287	288	284	42	281	154	190	472	84	8
Didinium gargantua	58 (0)	55 (0)	–	–	–	–	–	–	–	–	–	–	31	–	–	–	–
Euplotida																	
Euplotes cf *affinis*	44 (4)	29 (3)	–	–	96	–	–	770	67	–	21	–	–	–	–	–	–
Sessilida																	
Vaginicolidae sp.	33 (4)	25 (0.1)	–	–	–	–	–	–	–	–	–	–	77	9	7	21	–
Vorticella sp. 1	42 (7)	42 (6)	–	–	–	–	–	–	–	–	–	–	77	9	–	–	–
Vorticella sp. 2	49 (1)	40 (4)	–	–	–	–	–	–	–	–	–	–	31	9	–	11	–
Vorticella sp. 3	17 (1)	16 (1)	–	–	–	–	–	–	–	–	–	–	–	–	77	–	–

Length and width measurements are averages for all sampling occasions with the standard deviation in parentheses. –, species not found; cf, uncertain species name; *, single measurement.

(Figure 3B; Table II). Larger ciliates (>20 μm) generally contributed most to ciliate biomass during spring and early summer, while smaller ciliates (<20 μm) increased their proportion of total biomass in late summer and early autumn (Figure 3C). On most occasions, 50% or more of the biomass was Oligotrichida and Choreotrichida, mainly different species of *Strombidium* and *Strobilidium* (Figure 4; Table II). Only once, on May 18, was the biomass of Haptorida species (i.e. *Didinium* cf *gargantua*, *Askenasia* cf *stellaris*) higher than the summed biomass of Choreotrichida and Oligotrichida. The biomass of Prostomatea (including *Holophrya* spp. 1 and 2 and *Balanion comatum*) mostly contributed ~10% of the total biomass.

The estimated potential maximum production of ciliates (Figure 3C; *M. rubrum* excluded) was low on April 7, increased until May 5 and remained high until mid-June. At the end of June, ciliate biomass fell, resulting in a drastically decreased production of ciliates. A combination of increasing water temperature and a slight increase in ciliate biomass resulted in growth estimates in August and September similar to the spring maximum.

Mesozooplankton community structure, biomass and production

The biomass of mesozooplankton was generally dominated by copepods (69–99%; Figure 3D), except in the second half of June when rotifers (*Synchaeta* spp., mostly *S. baltica*) contributed up to 61% of the biomass. Cladocerans (mainly *Bosmina longirostris maritima*, *Evadne nordmanni* and *Pleopsis polyphemoides*) were present in most of the samples, but contributed little (maximum 13%) to the total mesozooplankton biomass (Figure 3D). During winter, up to 27% of the total mesozooplankton biomass was larvaceans (*Fritillaria borealis*).

Table II: Seasonal averages of biomass (μg C L^{-1}), net production (μg C L^{-1} day^{-1}) and carbon consumption (μg C L^{-1} day^{-1}) of autotrophs and heterotrophs in the upper 20 m of the Landsort Deep in the open northern Baltic Sea proper during 1998

	Biomass (μg C L^{-1})				Net production (μg C L^{-1} day^{-1})				Carbon consumption (μg C L^{-1} day^{-1})			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Autotrophs												
40–90					8.6	1.3	1.4					
20–40					11	0.37	0.47					
10–20 μm					6.1	1.5	1.4					
3–10 μm					5.0	4.8	5.1					
<3					14	21	13					
Total autotrophic	**141**	**66**	**69**	**45**	**45**	**29**	**21**					
Mesodinium rubrum	16	13	7.3	4.5								
Heterotrophs												
Bacteria	**13**	**26**	**28**	**9.4**	**1.3**	**2.2**	**1.2**	**0.28**	**2.6**	**4.5**	**2.3**	**0.55**
Ciliates												
Choreotrichida	2.1	1.2	1.0	0.59	0.35	0.83	0.58	0.21	1.2	2.8	1.9	0.71
Oligotrichida	5.1	1.7	0.86	0.30	0.75	1.4	0.66	0.16	2.5	4.7	2.2	0.52
Prostomatea	2.1	0.63	0.32	0.07	0.39	0.76	0.41	0.04	1.3	2.5	1.4	0.14
Haptorida	3.9	0.39	0.59	0.11	0.58	0.27	0.29	0.04	1.9	0.91	1.0	0.13
Others	0	0.27	0.17	0.01	0	0.21	0.13	0.01	0	0.71	0.43	0.02
Sum ciliates	**13**	**4.1**	**2.9**	**1.1**	**2.1**	**3.5**	**2.1**	**0.46**	**6.9**	**12**	**6.9**	**1.5**
Mesozooplankton												
Rotatoria	0.69	1.8	1.2	0.44	0.10	0.32	0.11	0.05	0.34	1.1	0.36	0.16
Cladocera	0.003	1.1	0.28	0.02	0	0.10	0.01	0.003	0.001	0.35	0.03	0.01
Copepoda	1.6	8.1	4.0	1.7	0.48	1.4	0.77	0.58	1.6	4.7	2.6	1.9
Sum mesozooplankton	**2.3**	**11**	**5.5**	**2.2**	**0.58**	**1.8**	**0.89**	**0.63**	**1.9**	**6.1**	**3.0**	**2.1**
Sum heterotrophs	**28**	**41**	**36**	**13**	**4.0**	**7.5**	**4.1**	**1.4**	**11**	**23**	**12**	**4.2**

Total autotrophic biomass was estimated from chlorophyll *a* values. Net production values of ciliate were estimated from maximum growth rates for the temperature on each sampling occasion, and are therefore maximum estimates of production. Carbon consumption was calculated from the net production using a growth efficiency of 50% for bacteria, and 30% for ciliates and mesozooplankton. All values are integrated over the seasons. Spring = March 24–June 2; summer = June 2–September 24; autumn = September 24–November 3; winter = November 3–December 8.

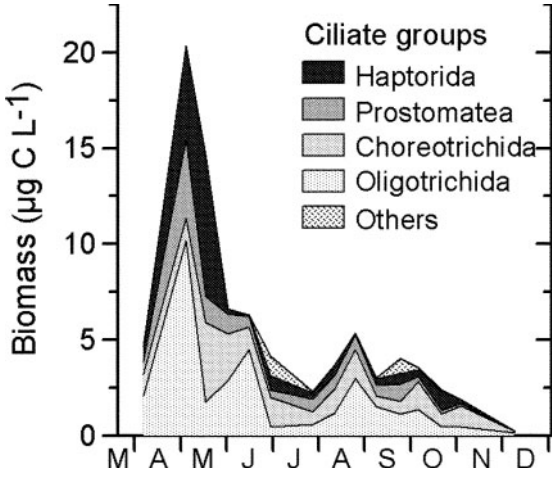

Fig. 4. Changes in biomass of heterotrophic ciliate taxa (µg C L^{-1}) (*M. rubrum* excluded) in the upper 20 m at the Landsort Deep (BY31) during 1998. Oligotrichida includes *Strombidium* spp. Choreotrichida includes *Lohmanniella* spp., *Strobilidium* spp. and Tintinnina spp. Haptorida includes *Didinium gargantua* and *Askenasia stellaris*. Prostomatea includes *Holophrya* sp. 1, *Holophrya* sp. 2 and *B. comatum*. 'Others' includes the remaining ciliate species.

In the surface layer (0–30 m), *Acartia* spp. constituted 20–80% of the mesozooplankton biomass/abundance over the year. A sharp increase in *Eurytemora affinis* abundance during July resulted in co-dominance of these two species in July–August. All copepod species had broad and overlapping biomass maxima in late summer, following a rapid increase in biomass in mid-July (Figure 3D). During this period (July–September), juvenile stages of *Acartia* spp. and *Temora longicornis* were most abundant. From January to May, 18–72% of the total biomass, mainly older copepodites and adults of *Pseudocalanus* and *Limnocalanus*, resided below 60 m. When the total zooplankton abundance and biomass increased in summer, the proportion of biomass concentrated in the upper 30 m also increased, contributing 50–67% of the total zooplankton biomass in July–August.

The integrated annual mesozooplankton production was 7.9 g C m^{-2} $year^{-1}$ for the upper 30 m (11.9 g C m^{-2} $year^{-1}$ for the 100 m water column), with copepods and rotifers contributing 5.7 (73%) and 1.8 (23%) g C m^{-2} $year^{-1}$, respectively. In February–June, *Acartia* spp. and *Pseudocalanus* contributed most to the production of copepods, while *Temora* and *Eurytemora* dominated in July–September. The production of nauplii and younger copepodite stages contributed 43% to copepod annual production and 38% to total mesozooplankton annual potential maximum production.

Seasonal standing stocks and production

The estimated biomass and the production of primary producers were highest during spring, with the size classes <3 and 20–40 µm contributing most to the production (Table II). Both biomasses and production of primary producers decreased during summer and autumn, and the smallest size classes dominated the production (Table II). The autotrophic ciliate *M. rubrum* contributed ~15% of the biomass of primary producers during spring and summer, 7% during autumn and 5% during winter. Biomass and production of bacteria were rather low in spring, doubled in summer, then the production decreased in autumn to values similar to the spring, while the biomass remained fairly constant (Table II).

The biomasses of the studied secondary consumers (ciliates and mesozooplankton) were highest in spring and summer, with ciliates dominating in spring (85%), and mesozooplankton in summer (73%) (Table II). In autumn, biomasses decreased by ~50% and were dominated by mesozooplankton (65%). The estimated potential maximum production and consumption of ciliates and mesozooplankton were highest during summer, and about half of that during spring and autumn (Table II). Ciliates had the highest production and consumption of the studied secondary consumers during all seasons, except during winter when total values were low, then mesozooplankton had slightly higher production and consumption (Table II).

DISCUSSION

This field study attempted to elucidate the role of ciliates both as predators and prey in the open Baltic Sea and is one of the most complete studies so far with respect to the temporal resolution and simultaneous measurements of the different species/groups of species of the plankton community. In spring, 85% of the heterotrophic biomass (ciliates and mesozooplankton) was ciliates. Thus, the predation pressure from mesozooplankton on ciliates was presumably low, and ciliates were major predators. The seasonal succession of phytoplankton in 1998 was similar to previous years, with a spring bloom initially dominated by diatoms, which were already largely replaced by dinoflagellates before the peak of the bloom (Larsson and Hagström, 1982; Kankaala *et al.*, 1984; Heiskanen and Leppänen, 1995). Shortly after the spring bloom, the ciliate biomass peaked, dominated by large ciliates (average length 40 µm; Oligotrichida and Haptorida). It appears that the large heterotrophic ciliates benefited from the late spring-bloom conditions, when nano-sized food was readily available and predation by copepods negligible.

During summer, the shift from larger to smaller ciliates coincided with an increase in mesozooplankton biomass, and a shift towards small phytoplankton. Thus,

smaller ciliates during summer were probably affected by predation from both mesozooplankton and remaining larger ciliates, and by prey size spectra. Ciliates were potentially important as regenerators of nutrients during summer and autumn, especially during summer when their estimated production was at its highest.

Seasonal patterns

Our estimates of carbon consumption indicate that during spring, summer and autumn ciliates potentially could consume considerably more food (a factor of ~2.5) than mesozooplankton. Ciliates were especially important consumers during spring, when there was hardly any mesozooplankton. The ciliates have a faster production rate then mesozooplankton, which is probably why they could respond quickly to the increasing food availability during the spring phytoplankton bloom, and thereby retain primary produced material in the water column. According to our carbon consumption estimates, up to 15% of the net primary production in spring was potentially consumed by ciliates and 4% by mesozooplankton. Ciliates are considered to be main consumers on spring phytoplankton in other areas of the Baltic Sea (Smetacek, 1981; Leppänen and Bruun, 1986). Since ciliates and their excreta settle slowly (Stoecker, 1984), their dominance in spring will probably increase the retention time for newly produced material.

In summer, we found the largest potential carbon consumption by both ciliates and mesozooplankton. The carbon demand from these consumers reached 55% of the summed production of phytoplankton and ciliates. The ciliates alone could potentially consume up to 40% of the total net primary production, almost three times more than in spring. However, during summer, most of the primary production was by cells <3 μm, and for ciliates to sustain their growth they had either to feed directly on these small prey or, more likely, on heterotrophic nanoflagellates (HNF) that fed on this fraction. Uitto examined a coastal planktonic food web in the northern Baltic Sea and found that, during summer, on average 40% (up to 80%) of the total nutritional requirements of ciliates came from HNF (Uitto *et al.*, 1997). The same authors found that on average ~20% of the carbon demand of larger zooplankton came from ciliates. This means that, potentially, mesozooplankton in this study could have consumed 40% of the ciliate production during summer. It is also possible that some of the larger ciliates could have preyed on the smaller sized ciliates, but the extent of this predation remains unclear.

In autumn, primary production decreased to half of that in spring. On the other hand, the estimated potential carbon consumption was almost equal to that in spring. Thus, ciliates and mesozooplankton could potentially consume twice as much of the primary production as in spring (maximum 43%). Since compared to summer there was slightly higher primary production in the prey sizes that the ciliates preferred (3–10 μm), and since there was a lower carbon demand from the ciliates, they could sustain their growth on primary produced material during autumn. Mesozooplankton could potentially obtain up to 70% of their carbon demand by consuming ciliates. It is more likely though that they fed on both primary producers and ciliates. Ciliates are a better quality food (Michels and De Meester, 1998) and can be actively selected by copepods (Jonsson and Tiselius, 1990). However, some ciliate species within the Choreotrichida and Oligotrichida are known to escape their predators (Gilbert and Jack, 1993; Broglio *et al.*, 2001). Therefore, it is probably not reasonable to assume that the predation pressure is equally high on similar sized phytoplankton and ciliates.

It is important though to be aware of the fact that these production and consumption values are estimates that were calculated to obtain seasonal trends and the maximum production and consumption of these predators. Naturally, maximum growth rates are not attainable at all times since food is not always saturating. Our estimates indicate that ciliates may be resource limited in summer, and this may decrease their production. It would thus be most interesting to validate these calculations with real production estimates during the different seasons in the future. It would also be interesting to study how much cannibalism there is among the ciliates and how much of their consumption comes from HNF.

Ciliates as predators: seasonal variations

Montagnes proposed a seasonal pattern for ciliates in the Gulf of Maine, with a 'spring assemblage' and a 'summer assemblage' (Montagnes *et al.*, 1988). The spring assemblage was mostly large ciliates feeding on diatoms, other large phytoplankton and small ciliates. The summer assemblage was mainly small ciliates consuming small flagellates and bacterioplankton. Our results resemble this pattern, with the largest ciliates in spring, mainly choreotrich ciliates (Choreotrichida and Oligotrichida) and Haptorida ciliates. The choreotrichs are selective feeders (Christaki *et al.*, 1998), and most species have an optimum prey size approximately equal to 15% of their length, and a minimum and maximum size range of ~5 and 30% of their length, respectively (Jonsson, 1986; Rassoulzadegan *et al.*, 1988; Kivi and Setälä, 1995).

The choreotrich species in spring were ~45 μm in length and were thus presumably feeding on prey in the size range 2–15 μm. The Haptorida species in spring were ~40 μm in length; these ciliates are raptorial

feeders that can consume large prey, some even similar sized prey (Smetacek, 1981; Jakobsen and Hansen, 1997). The remaining ciliate community during spring comprised somewhat smaller Prostomatea species (*B. comatum* and *Holophrya* spp., average length 30 μm). Jakobsen and Hansen found that *B. comatum* had an optimum prey size that was 47% of its length, and a prey size range of 24–59% of its length (Jakobsen and Hansen, 1997). A similar prey size optimum was found by Stoecker *et al.*, studying a *Balanion* species (Stoecker *et al.*, 1986). Thus, the Prostomatea presumably preferred prey 15 μm in length, and consumed prey in the size range 7–18 μm. This indicates that in spring we had a ciliate community that could consume prey in a very wide spectrum of sizes (2–40 μm). Thus, ciliates could potentially act on several levels in the food web, mainly as top predators, but the smaller ones also as consumers on smaller fractions. According to our estimates of consumption for the different ciliate taxonomic groups, and the prey sizes preferred by these ciliates, it seems likely that there was no food limitation for any of the ciliate groups during spring.

Directly after the biomass peak of ciliates in spring, an increase in abundance of *B. comatum* (Prostomatea) was observed. This species has been shown to prefer dinoflagellates (Stoecker *et al.*, 1986). It is therefore likely that it was favoured by the dinoflagellate predominance at the spring phytoplankton peak. *Balanion comatum* was also numerically important throughout the summer (25–58% of ciliate abundance; Table I). The rest of the ciliate community, and also the largest part of its biomass during summer, were species within Oligotrichida and Choreotrichida, with average sizes of 32 and 39 μm, respectively. Following the calculations above, ciliates during summer would mostly consume prey in the size range 2–11 μm, with an optimum around 5 μm. Thus, during summer, ciliates presumably consumed smaller prey and, due to their fast growth rate, were important as regenerators. This is supported by results from correlations between the potential ciliate production and their potential prey. The potential ciliate production correlates with bacterial production ($P < 0.01$, $r^2 = 0.42$, Pearson correlation), primary production in the <3 μm fraction ($P < 0.01$, $r^2 = 0.52$) and primary production in the 3–10 μm fraction ($P = 0.05$, $r^2 = 0.34$, Pearson correlation). According to our estimates of carbon consumption, and considering the preferred prey sizes, the ciliates during summer were food limited or preyed in the <3 μm size fraction or preyed on HNF. Bacteria are in the lower range of the size spectra of ciliates, where the retention efficiency is low (Kivi and Setälä, 1995). Normally, HNF are assumed to be the main consumers of bacteria, and ciliates are thought to prey mostly on autotrophic nanoplankton and on HNF (Azam *et al.*, 1983). HNF are common in coastal areas of the Baltic Sea, especially during summer, and are known to be major consumers of picoplankton (Kuuppo-Leinikki *et al.*, 1994; Kivi *et al.*, 1996; Uitto *et al.*, 1997), and may have been a food source for ciliates. Since there was a strong correlation between ciliate production and both bacterial production and primary production of <3 μm size, it would thus be most interesting to investigate these pathways further.

In late autumn and early winter, ciliate size structure remained similar to that of the summer period, but total diversity increased. This was mostly due to an increased diversity of tintinnids and the appearance of sessile ciliates. At this time, the water column was mixed, and it is likely that the tintinnids were transported upwards from deeper waters, where they were usually present in higher numbers, as indicated from the mesozooplankton samples from below 30 m (data not shown). The increase in sessilid ciliate species occurred directly after the peak of large filamentous cyanobacteria in early September (personal observation), and was possibly the result of feeding on the bacteria and flagellates associated with the degradation processes (Hoppe, 1981). However, in total, we found a lower abundance of sessilid ciliate species compared to other studies in the Baltic Sea (Leppänen and Bruun, 1986; Mamaeva, 1988; Witek, 1998). This may be due to the greater depth and more offshore location of our study site, which probably provides fewer particles for the sessilid species to grow on, and a comparably low abundance of cyanobacteria in 1998 (Larsson *et al.*, 2001).

Witek reported a similar seasonal pattern from the Gdańsk Basin in the Baltic Sea proper (Witek, 1998). However, contrary to our results, Witek found a second peak of large ciliates in the autumn, following a second peak of phytoplankton, where we only found a peak of small-sized ciliates. The higher proportion of small ciliates found in this study during summer and autumn is typical for a regenerating system driven by the microbial food web, which is normally found in offshore environments (Legendre and Rassoulzadegan, 1995). Also, the more coastal Gdańsk Basin had a different species composition of ciliates with more large and benthic species (i.e. genera of *Didinium*, *Euplotes*, *Lacrymaria* and *Tintinnopsis*). This is also true for other coastal studies of ciliates in the Baltic Sea (Smetacek, 1981). In conclusion, our offshore study differed from other more coastal studies in the Baltic Sea with respect to the species composition of ciliates and the lack of an autumn biomass peak of ciliates. However, the magnitude of the spring peak of ciliates and the number of ciliate species found were in the range of previous reports from the Baltic Sea.

Potential predation from mesozooplankton

Studies in the Baltic Sea have shown an inverse relationship between ciliates and mesozooplankton (Smetacek, 1981; Kivi *et al.*, 1993, 1996). The structure and seasonal dynamics of the mesozooplankton community at the Landsort Deep in 1998 were similar to those observed before (Johansson, 1983; Viitasalo, 1992; Johansson *et al.*, 1993) for other coastal and open areas of the Baltic Sea proper.

Mesozooplankton were generally dominated by copepods, with summer biomass peaks attributed to *Acartia* spp., *Eurytemora* and *Temora*. These, or closely related copepod species, are known to have high predation rates on ciliates (Wiackowski *et al.*, 1994; Merrell and Stoecker, 1998). Indeed, the decline of larger ciliates coincided with the increase in copepod biomass and production, suggesting possible copepod predation control of ciliate biomass and effective utilization of ciliates for copepod growth. Also, the decrease in total ciliate biomass in summer, in spite of an increase in their potential production from spring to summer, suggests predation losses.

The abundances and biomasses of Rotatoria observed in this study are relatively high compared to those reported by Viitasalo (Viitasalo, 1992) for open Baltic Sea areas, and more similar to the values obtained by Johansson (Johansson, 1983) for coastal areas of the Baltic Sea proper. In particular, in the second half of June, rotifer biomass, mostly *Synchaeta* spp., increased rapidly and dominated the mesozooplankton. Field and laboratory studies have shown that *Synchaeta* in fresh water can prey extensively on ciliates up to 60 μm in length (Gilbert and Jack, 1993). Inverse relationships between rotifers and herbivorous ciliates have been found in estuarine plankton communities (Dolan and Gallegos, 1992). Thus, increased abundance of *Synchaeta* spp. might be at least partially responsible for an increased predation pressure on ciliates. The potential role of cladocerans in regulating ciliate abundance is not clear. They occurred abundantly only from the end of June to the end of September, coinciding with a low biomass of larger ciliates. Moreover, species known as predators (podonids) and herbivores (bosminids) were present simultaneously, making it difficult to evaluate the overall effect of cladocerans on the ciliate abundance.

Concluding remarks

In conclusion, this study indicates that ciliates are major predators during all seasons, with a potential to consume considerably more food (a factor of ~2.5) than mesozooplankton. They also act on several levels in the food web, which vary seasonally. During spring, when there was hardly any mesozooplankton, they were major consumers on the primary production, and are thereby a key factor in retaining new production in the water column. During summer and autumn, ciliates act as important regenerators, especially during summer when they had their highest estimated production.

ACKNOWLEDGEMENTS

We are grateful to our technicians, and the crew on board the ships of the Swedish Maritime Administration, for valuable field assistance. Staff at the Umeå Marine Research Centre, Umeå University, kindly counted and measured bacteria. Earlier versions of the manuscript were greatly improved by constructive criticism from Professor Per Jonsson, Göteborg University, Dr Christoph Humborg, Stockholm University, and three anonymous reviewers. This study was supported by grants from the European Union through BASYS MAST III program (MAS3-CT96-0058), the Swedish EPA's Marine Monitoring Programme and grants to M.J. from Stockholm Marine Research Centre.

REFERENCES

Andronikova, I. N. (1976) Estimation of two methods for calculating fresh-water zooplankton production. *Gidrobiol. Zh.*, **12**, 71–75.

Azam, F., Fenchel, T., Field, F. G., Grey, J. S., Meyer-Reil, L. A. and Thingstad, F. (1983) The ecological role of water column microbes in the sea. *Mar. Ecol. Prog. Ser.*, **10**, 257–263.

Bernard, C. and Rassoulzadegan, F. (1990) Bacteria or microflagellates as a major food source for ciliates: possible implications for the microzooplankton. *Mar. Ecol. Prog. Ser.*, **64**, 147–155.

Blackburn, N., Hagström, Å., Wikner, J., Cuadros-Hansson, R. and Bjørnsen, P. (1998) Rapid determination of bacterial abundance, biovolume, morphology, and growth by neural network-based image analysis. *Appl. Environ. Microbiol.*, **64**, 3246–3255.

Broglio, E., Johansson, M. and Jonsson, P. R. (2001) Trophic interaction between copepods and ciliates: effects of prey swimming behavior on predation risk. *Mar. Ecol. Prog. Ser.*, **220**, 179–186.

Chisholm, L. A. and Roff, J. C. (1990) Abundance, growth rates, and production of tropical neritic copepods off Kingston, Jamaica. *Mar. Biol.*, **106**, 79–89.

Christaki, U., Dolan, J. R., Pelegri, S. and Rassoulzadegan, F. (1998) Consumption of picoplankton-size particles by marine ciliates: effects of physiological state of the ciliate and particle quality. *Limnol. Oceanogr.*, **43**, 458–464.

Cushing, D. H. (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. *J. Plankton Res.*, **11**, 113–181.

Dolan, J. R. and Gallegos, C. C. (1992) Trophic role of planktonic rotifers in the Rhode River estuary, spring–summer. *Mar. Ecol. Prog. Ser.*, **85**, 187–199.

Downing, J. A. and Rigler, F. H. (eds) (1984) *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters*. Blackwell Scientific, Oxford.

Edler, L. (ed.) (1979) *Recommendation on Methods for Marine Biological Studies in the Baltic Sea. Phytoplankton and Chlorophyll*, Vol. 5. The Baltic Marine Biologists, Lund.

Fuhrman, J. A. and Azam, F. (1982) Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. *Mar. Biol.*, **66**, 109–120.

Gilbert, J. J. and Jack, J. D. (1993) Rotifers as predators on small ciliates. *Hydrobiologia*, **255/256**, 247–253.

Harris, R. P. and Paffenhöfer, G.-A. (1976) Feeding, growth and reproduction of the marine planktonic copepod *Temora longicornis* Müller. *J. Mar. Biol. Assoc. UK*, **56**, 675–690.

Heinänen, A. and Kuparinen, J. (1991) Horizontal variation of bacterioplankton in the Baltic Sea. *Appl. Environ. Microbiol.*, **57**, 3150–3155.

Heinle, D. R. and Flemer, D. A. (1975) Carbon requirements of a population of the estuarine copepod *Eurytemora affinis*. *Mar. Biol.*, **31**, 235–247.

Heiskanen, A.-S. and Leppänen, J.-M. (1995) Estimation of export production in the coastal Baltic Sea: effect of resuspension and microbial decomposition on sedimentation measurements. *Hydrobiologia*, **316**, 211–224.

Hobbie, J. E., Daley, R. J. and Jasper, S. (1977) Use of nuclepore filters for counting bacteria by epifluorescence microscopy. *Appl. Environ. Microbiol.*, **33**, 1225–1228.

Hoppe, H.-G. (1981) Blue-green algae agglomeration in surface water: a microbiotope of high bacterial activity. *Kiel. Meeresforsch. Sonderh.*, **5**, 291–303.

Ivanova, M. V. (1973) Growth patterns of copepod crustaceans. *Gidrobiol. Zh.*, **9**, 15–21.

Jakobsen, H.-H. and Hansen, P.-J. (1997) Prey size selection, grazing and growth response of the small heterotrophic dinoflagellate *Gymnodinium* sp. and the ciliate *Balanion comatum*—a comparative study. *Mar. Ecol. Prog. Ser.*, **158**, 75–86.

Johansson, S. (1983) Annual dynamics and production of rotifers in an eutrophication gradient in the Baltic Sea. *Hydrobiologia*, **104**, 335–340.

Johansson, S., Hansson, S. and Araya-Nunez, O. (1993) Temporal and spatial variation of coastal zooplankton in the Baltic Sea. *Ecography*, **16**, 167–173.

Jonsson, P. R. (1986) Particle size selection, feeding rate and growth dynamics of marine planktonic oligotrichous ciliates (Ciliophora: Oligotrichina). *Mar. Ecol. Prog. Ser.*, **33**, 265–277.

Jonsson, P. R. (1987) Photosynthetic assimilation of inorganic carbon in marine oligotrich ciliates (Ciliophora, Oligotrichida). *Mar. Microb. Food Webs*, **2**, 55–68.

Jonsson, P. R. and Tiselius, P. (1990) Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. *Mar. Ecol. Prog. Ser.*, **60**, 35–44.

Kankaala, P., Alasaarela, E. and Sundberg, A. (1984) Phytoplankton and zooplankton production in the north eastern and central Bothnian Bay—a review of studies carried out in 1968–1978. *Ophelia*, **3(Suppl.)**, 69–88.

Kemp, P. F., Sherr, B. F., Sherr, E. B. and Cole, J. J. (eds) (1993) *Handbook of Methods in Aquatic Microbial Ecology*. Lewis Publishers, Boca Raton, FL.

Kiørboe, T., Møhlenberg, F. and Hamburger, K. (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar. Ecol. Prog. Ser.*, **26**, 85–97.

Kivi, K. and Setälä, O. (1995) Simultaneous measurement of food particle selection and clearance rates of planktonic oligotrich ciliates (Ciliophora: Oligotrichina). *Mar. Ecol. Prog. Ser.*, **119**, 125–137.

Kivi, K., Kaitala, S., Kuosa, H., Kuparinen, J., Leskinen, E., Lignell, R., Marcussen, B. and Tamminen, T. (1993) Nutrient limitation and grazing control of the Baltic plankton community during annual succession. *Limnol. Oceanogr.*, **38**, 893–905.

Kivi, K., Kuosa, H. and Tanskanen, S. (1996) An experimental study on the role of crustacean and microprotozoan grazers in the planktonic food web. *Mar. Ecol. Prog. Ser.*, **136**, 59–68.

Kononen, K., Hällfors, S., Kokkonen, M., Kuosa, H., Laanemets, J., Pavelson, J. and Autio, R. (1998) Development of a subsurface chlorophyll maximum at the entrance to the Gulf of Finland, Baltic Sea. *Limnol. Oceanogr.*, **43**, 1089–1106.

Kott, P. (1953) Modified whirling apparatus for the subsampling of plankton. *Aust. J. Mar. Freshwater Res.*, **4**, 387–393.

Kuosa, H. (1990) Subsurface chlorophyll maximum in the northern Baltic Sea. *Arch. Hydrobiol.*, **118**, 437–447.

Kuuppo-Leinikki, P., Autio, R., Hällfors, S., Kuosa, H., Kuparinen, J. and Pajuniemi, R. (1994) Trophic interactions and carbon flow between picoplankton and protozoa in pelagic enclosures manipulated with nutrients and a top predator. *Mar. Ecol. Prog. Ser.*, **107**, 89–102.

Landry, M. R. (1975) The relationship between temperature and the development of life stages of the marine copepod *Acartia clausi* Giesbr. *Limnol. Oceanogr.*, **20**, 854–857.

Larsson, U. and Hagström, Å. (1982) Fractionated phytoplankton primary production, exudate release and bacterial production in a Baltic eutrophication gradient. *Mar. Biol.*, **67**, 57–70.

Larsson, U., Hajdu, S., Walve, J. and Elmgren, R. (2001) Baltic Sea nitrogen fixation estimated from the summer increase in upper mixed layer total nitrogen. *Limnol. Oceanogr.*, **46**, 811–820.

Legendre, L. and Rassoulzadegan, F. (1995) Plankton and nutrient dynamics in marine waters. *Ophelia*, **41**, 153–172.

Leppänen, J.-M. and Bruun, J. E. (1986) The role of pelagic ciliates including the autotrophic *Mesodinium rubrum* during the spring bloom of 1982 in the open northern Baltic proper. *Ophelia*, **4(Suppl.)**, 147–157.

Lindholm, T. (1985) *Mesodinium rubrum*—a unique photosynthetic ciliate. *Adv. Aquat. Microbiol.*, **3**, 1–48.

Mamaeva, N. V. (1988) Ciliates as a component of planktonic communities in the open regions of the Baltic Sea. *Biol. Morya*, **4**, 24–28.

McLaren, I. and Corkett, C. J. (1981) Temperature dependent growth and reproduction by a marine copepod. *J. Fish. Res. Can.*, **38**, 77–83.

Menden-Deuer, S. and Lessard, E. J. (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol. Oceanogr.*, **45**, 569–579.

Merrell, J. R. and Stoecker, D. K. (1998) Differential grazing on protozoan microplankton by developmental stages of the calanoid copepod *Eurytemora affinis* Poppe. *J. Plankton Res.*, **30**, 289–304.

Michels, E. and De Meester, L. (1998) The influence of food quality on the phototactic behaviour of *Daphnia magna* Straus. *Hydrobiologia*, **379**, 199–206.

Møhlenberg, F. (1987) A submersible net-pump for quantitative zooplankton sampling; comparison with conventional net sampling. *Ophelia*, **27**, 101–110.

Montagnes, D. J. S., Lynn, D. H., Roff, J. C. and Tayler, W. D. (1988) The annual cycle of heterotrophic planktonic ciliates surrounding the Isles of Shoals, Gulf of Maine: an assessment of their trophic role. *Mar. Biol.*, **99**, 21–30.

Müller, H. and Geller, W. (1993) Maximum growth rates of aquatic ciliated protozoa: the dependence of body size and temperature reconsidered. *Arch. Hydrobiol.*, **126**, 315–327.

Mullin, M. M. and Brooks, E. R. (1967) Laboratory culture, growth rate and feeding behaviour of a planktonic marine copepod. *Limnol. Oceanogr.*, **12**, 657–666.

Olrik, K., Blomqvist, P., Brettum, P., Cronberg, G. and Eloranta, P. (eds) (1998) *Methods for Quantitative Assessment of Phytoplankton in Freshwater*, Vol. 1, No. 4860. Naturvårdsverket, Stockholm.

Omori, M. and Ikeda, T. (eds) (1984) *Methods in Marine Zooplankton Ecology*. Wiley-Interscience, New York.

Paffenhöfer, G.-A. and Harris, R. P. (1976) Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanus elongatus* Boeck. *J. Mar. Biol. Assoc. UK*, **56**, 327–344.

Parsons, T. R., Maita, Y. and Lalli, C. M. (eds) (1984) *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford.

Petipa, T. S., Pavlova, E. V. and Mironov, G. N. (1966) Energeticheskii balans planktonnykh organismov iz razlichnykh ekosistem Chernogo Morya. In *International Oceanography Congress, Moscow, 284* [The energy balances of planktonic organisms from different ecosystems of the Black Sea. Trans. Abstracts AEC-TR-6940 (NLL 179.7F).]

Pourriot, R. and Deluzarches, M. (1971) Recherches sur la biologie des rotiféres. II. Influence de la température sur la durée du développement embryonnaire et post-embryonnaire. *Ann. Limnol.*, **7**, 25–52.

Rassoulzadegan, F., Laval-Peuto, M. and Sheldon, R. W. (1988) Partitioning of the food ratio of marine ciliates between pico- and nanoplankton. *Hydrobiologia*, **159**, 75–88.

Reckermann, M. (1996) Ultraphytoplankton and protozoan communities and their interactions in different marine pelagic ecosystems (Arabian Sea and Baltic Sea). Doctoral dissertation thesis, University of Rostock, Rostock.

Sherr, E. B. and Sherr, B. F. (1986) Phagotrophic protozoa as food for metazoans: a missing link in marine pelagic food webs? *Mar. Microb. Food Webs*, **1**, 61–80.

Simon, M. and Azam, F. (1989) Protein content and protein synthesis rates of planktonic marine bacteria. *Mar. Ecol. Prog. Ser.*, **51**, 201–213.

Smetacek, V. (1981) The annual cycle of protozooplankton in the Kiel Bright. *Mar. Biol.*, **63**, 1–11.

Stoecker, D. K. (1984) Particle production by planktonic ciliates. *Limnol. Oceanogr.*, **29**, 930–940.

Stoecker, D. K. and Capuzzo, J. M. (1990) Predation on Protozoa: its importance to zooplankton. *J. Plankton Res.*, **12**, 891–908.

Stoecker, D. K. and Evans, G. T. (1985) Effects of protozoan herbivory and carnivory in a microzooplankton food web. *Mar. Ecol. Prog. Ser.*, **25**, 159–167.

Stoecker, D. K. and Michaels, A. E. (1991) Respiration, photosynthesis and carbon metabolism in planktonic ciliates. *Mar. Biol.*, **108**, 441–447.

Stoecker, D. K., Cucci, T. L., Hulburt, E. M. and Yentsch, C. M. (1986) Selective feeding by *Balanion* sp. (Ciliata: Balanionidae) on phytoplankton that best support its growth. *J. Exp. Mar. Biol. Ecol.*, **95**, 113–130.

Stoecker, D. K., Gifford, D. J. and Putt, M. (1994) Preservation of marine planktonic ciliates: losses and cell shrinkage during fixation. *Mar. Ecol. Prog. Ser.*, **110**, 293–299.

Sushchenya, L. M. (ed.) (1972) *Intensivnost' dykhaniya rakoobraznykh.* (*Respiration Intensity in Crustaceans.*) Naukova Dumka, Kiev.

Uitto, A., Heiskanen, A.-S., Lignell, R., Autio, R. and Pajuniemi, R. (1997) Summer dynamics of the coastal planktonic food web in the northern Baltic Sea. *Mar. Ecol. Prog. Ser.*, **151**, 27–41.

Utermöhl, H. (1958) Zur vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitt. Int. Ver. Theor. Angew. Limnol.*, **29**, 117–126.

Verity, P. G. and Paffenhöfer, G.-A. (1996) On assessment of prey ingestion by copepods. *J. Plankton Res.*, **18**, 1767–1779.

Vidal, J. (1980) Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. *Mar. Biol.*, **56**, 111–134.

Viitasalo, M. (1992) Mesozooplankton in the Gulf of Finland and northern Baltic proper—a review of monitory data. *Ophelia*, **35**, 147–168.

Walve, J. (2002) Nutrient limitation and elemental ratios in Baltic Sea plankton. Doctoral dissertation thesis, DocuSys Service Centre, Stockholm.

Wiackowski, K., Brett, M. T. and Goldman, C. R. (1994) Differential effects of zooplankton species on ciliate community structure. *Limnol. Oceanogr.*, **39**, 486–492.

Williams, P. J. (1981) Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. *Kiel. Meeresforsch.*, **5**, 1–28.

Witek, M. (1998) Annual changes of abundance and biomass of planktonic ciliates in the Gdansk Basin, southern Baltic. *Int. Rev. Hydrobiol.*, **83**, 163–182.

Zaika, V. E. (ed.) (1972) *Specific Production of Aquatic Invertebrates*. Naukova Dumka, Kiev.

Received on December 9, 2002; accepted on September 19, 2003