Estuarine, Coastal and Shelf Science (1991) **33**, 137–152

Guilds of Ciliate Microzooplankton in the Chesapeake Bay

John R. Dolan

Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, U.S.A.

Received 21 November 1990 and in revised form 19 February 1991

Keywords: plankton composition; ciliata; microplankton; plankton distribution; Chesapeake Bay

The composition and abundance of three major guilds, or different trophic groups, of ciliates are reported for the Chesapeake Bay. Ciliates were classified either (a) macrophagous (consumers of nanoplankton-size or larger prey), (b) microphagous (consumers of picoplankton-size prey), or (c) predatory (consumers of other ciliates). The three guilds show seasonal changes in species composition and distinct abundance trends, based on samples taken from April to October, 1985–87. Macrophagous forms (mostly tintinnids and large oligotrichs) represent, on average, *c.* 73% of ciliate biomass. However, microphagous species (largely scuticociliates and small oligotrichs) are dominant in terms of cell numbers and often form a substantial portion of the ciliate biomass in deep waters; they probably account for *c.* 15% of total protozooplankton grazing pressure on bacteria in the Chesapeake Bay. Predatory ciliates, while numerically a minor component of total ciliate numbers, were correlated with microphagous ciliate biomass and may, at times, have had a major impact on the microphagous guild.

Introduction

Within the now widely accepted paradigm of the ' microbial loop ', ciliate microzooplankton are seen primarily as consumers of heterotrophic and autotrophic nanoplankton (Laval-Peuto *et al.*, 1986; Pomeroy & Wiebe, 1988). However, ciliate microzooplankton have long been recognized as an assemblage of morphologically and ecologically diverse organisms (Fauré-Fremiet, 1924) which exploit a variety of food resources, ranging in size from bacteria to animal tissue. While it should be recognized that most ciliates are not highly specialized or fastidious feeders, guilds, or sets of species which use similar foods, can be identified and there is reason to suspect that ciliates other than nanoplankton-consumers play significant roles. For example, bacteriovorous ciliates may be important in regulating bacterioplankton populations both quantitatively (Gast, 1985; Rivier *et al.*, 1986; Sherr *et al.*, 1986*a,b*, 1987; Albright *et al.*, 1987; Sherr & Sherr, 1987; Bernard & Rassoulzadegan, 1990), and qualitatively, through selective feeding (Gonzalez *et al.*, 1990; Turley *et al.*, 1986). The existence of ciliate predation on other ciliates, and its implications for food chain efficiency, have also received some attention (Robertson, 1983; Stoecker & Evans, 1985).

0272–7714/91/080137+16 $03.00/0

However, other than recent work on mixotrophic oligotrichs (Stoecker *et al.*, 1987, 1989), there are no data on the relative abundances of guilds of ciliates in estuarine or marine environments. Many basic questions remain: What proportion of the ciliate community is composed of nanoplankton-consuming, picoplankton-consuming, and ciliate-consuming forms? Are the species compositions of the guilds constant or do they show seasonal succession patterns? Do these different trophic groups co-exist in a consistent manner or do they show distinct seasonal patterns? Does the composition of the ciliate community differ in different parts of the water column?

The present study addresses these questions through an investigation of the composition and distribution of the ciliate microzooplankton community in the mesohaline zone of the Chesapeake Bay. Ciliate species were assigned to one of three categories: (a) macrophagous (functionally equivalent to ciliates that consume nanoplankton), (b) microphagous (functionally equivalent to species that feed on picoplankton), and (c) predacious (functionally equivalent to forms that prey on other ciliates). The species compositions, abundances, and vertical distributions of the different groups of ciliates were examined. This study is a companion paper to Dolan and Coats (1990) which reported seasonal trends in ciliate and microflagellate abundances in the Chesapeake Bay.

Methods and materials

Detailed descriptions of the study site, sampling protocol, and methods used for the enumeration, identification, and biomass estimations of ciliates appear elsewhere (Dolan & Coats, 1990). Briefly, a CTD-FO_2-Niskin bottle rosette sampler was used to gather water samples and physical data at biweekly to monthly intervals from three central channel locations in the mesohaline portion of the Chesapeake Bay (Figure 1) from April to October 1985–87. Ciliates were enumerated in settled whole water samples and identified using lorica morphology for tintinnids following Marshall (1969) and by examining protargol-stained specimens (Montagnes & Lynn, 1987) for non-tintinnid taxa following Small and Lynn (1986). Biomass estimations employed conversion of cell volumes to carbon units using a conversion factor of 0·088 pg carbon μm^{-3} cell volume (Heinbokel, 1978).

Trophic categorization of ciliates

Three methods were used to group the numerically dominant species into three categories: (a) macrophages, which subsist mainly on food particles of nanoplankton-size or greater, (b) microphages, i.e. ciliates capable of ingesting bacteria-size particles, and (c) predacious, i.e. forms which consume other ciliates. Ciliates were grouped using literature reports, examinations of food vacuole content, and microsphere ingestion experiments.

The microsphere ingestion experiments, based on the technique of Borshiem (1984), were carried out on-board ship at station 858 on 19 April, 22 May, and 23 June 1987. They were conducted with surface and bottom water (23 m) samples in April and with surface and anoxic transition zone (*c.* 13 m) waters in May and June. Surface water samples were gathered with a plastic bucket; bottom and transition zone water samples were gathered using a Niskin bottle. A 500-ml sample of whole water was placed in a dialysis sac (15 000 molecular weight cutoff, Spectrapor Corp.), and approximately 1 ml of a suspension of fluorescent latex microspheres, 1·06 μm diameter (Polyscience Co.) was quickly added. The final concentration of microspheres was *c.* 1×10^6 beads ml^{-1}, a tracer concentration for Chesapeake Bay waters where bacterial abundances of 2×10^7 cells ml^{-1} are common

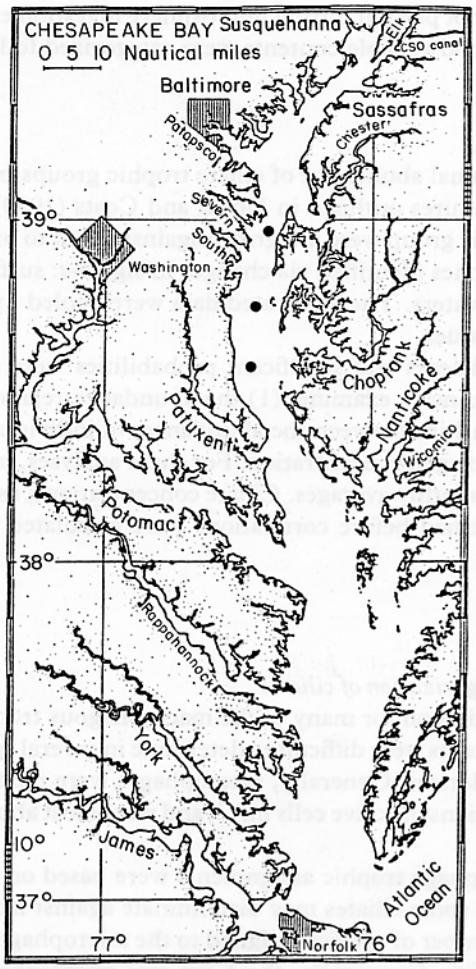

Figure 1. Study site: stations sampled in the mesohaline portion of the Chesapeake Bay. Station numbers from north to south are 858, 845, 834, denoted by ●.

(Tabor & Neihof, 1984; Malone *et al.*, 1986; Jonas & Tuttle, 1990). The dialysis sacs were immediately sealed and immersed in a water bath flushed with water pumped from the depth of the sample's origin. After 10 min, samples were taken from the dialysis sacs and preserved with a modified Bouin's fixative (Coats & Heinbokel, 1982). Aliquots (10 ml) of the Bouin's preserved material were settled and the entire surface of the chamber was examined with an inverted epifluorescent microscope at 480×. Ciliate species were categorized as microphagous when over 33% of the specimens contained at least two microspheres.

Food vacuole contents were determined using protargol-stained preparations. A minimum of 10 specimens of each of the numerically dominant ciliate species was examined. No bacterial or microflagellate remains were evident, but the remains of ciliates, diatoms, and dinoflagellates were identifiable and used to categorize species as either macrophagous (containing diatom and/or dinoflagellate remains) or predacious (containing ciliate

remains). Forms which were not present during microsphere ingestion experiments and/or did not have identifiable food vacuole contents were categorized following literature reports.

Data analysis

Analysis of trends in the seasonal abundance of ciliate trophic groups in different water column zones followed procedures outlined in Dolan and Coats (1990). Briefly, ciliate concentrations for each trophic group were integrated against depth to provide values for each of three water column zones identified via changes in sigma-*t*: surface mixed layer, transition zone, and bottom waters. The integrated data were pooled by month to yield monthly integrated average values.

Pearson's correlation coefficients and significant probabilities were calculated using data for each water column zone to examine: (1) the abundance relationships between ciliate groups; (2) the relationships between the abundances of individual ciliate trophic groups and chlorophyll and oxygen concentration. For these analyses, individual station data were used ($n = 47$), not monthly averages. Ciliate concentrations, as values based on count data, were log-transformed before correlations were calculated (Sokal & Rohlf, 1969).

Results

Trophic categorization of ciliates

Literature reports were relied upon for many of the macrophagous trophic assignments (Table 1) as food vacuole contents were difficult to determine in several species, especially tintinnids with agglutinated loricas. Generally, macrophages were relatively large cells, showed maximum concentrations of < five cells ml^{-1}, and were most abundant at shallow depths (Table 1).

The majority of the microphage trophic assignments were based on the microsphere ingestion experiments. Since some ciliates may discriminate against latex microspheres (Pace & Bailiff, 1987), the number of species assigned to the microphagous category may be a very conservative estimate. Conversely, the 1-μm size microsphere used, slightly larger than the maximal dimension of most estuarine bacterial cells, may have been more easily captured than natural cells. The microphagous ciliate group included representatives of tintinnid, oligotrich, scuticociliate, and peritrich taxa. None of the larger tintinnid and oligotrich taxa, nor the *Balanion* spp. present, ingested microspheres. Species classified as microphages were commonly smaller than the macrophages, and displayed much higher maximum concentrations that generally occurred in deep water (Table 2).

Three ciliate species were identified as predacious (Table 3). They were generally present in low numbers relative to macrophagous and microphagous species and reached maximum abundances in the middle of the water column.

When data were integrated over the whole water column and averaged by month, macrophagous ciliates appeared, overall, to be dominant in terms of biomass (72·7%) and the second most abundant in terms of cell numbers (49·3%). Microphagous forms were the most abundant group in cell numbers (49·7%) and the second most abundant in terms of biomass (24·6%). Predacious ciliates were a small portion of the community both in terms of numbers (0·6%) and biomass (3·5%). However, there were distinct seasonal differences in these dominance patterns which correspond with changes in water column

TABLE 1. Chesapeake Bay macrophagous ciliates: numerically dominant species April–October 1985–87. Categorization was based on observation of food vacuole contents or on literature reports. Ciliates which had identifiable food vacuole contents are denoted 'FVC(A)' for dinoflagellate remains, 'FVC(B)' for diatom remains, and 'FVC(A&B)' when both dinoflagellate and diatom remains were observed. For the species which had non-identifiable food vacuole contents: tintinnids were categorized as macrophagous following the general findings of Heinbokel (1978) and Kopylov and Tutmanseva (1987) and are denoted by 'LIT(1)'; *Balanion* spp. denoted 'LIT(2)' were categorized following the findings of Stoecker *et al.* (1986)

Ciliate species	Size L × W (μm)	No. ml^{-1}	Maximum concentration depth (m)	Date	Grouped via
Tintinnids					
Tintinnopsis acuminata	60 × 18	6·5	3	8/5/86	LIT(1)
T. dadayi	100 × 45	1·4	12	6/25/85	LIT(1)
T. levigata	95 × 20	3·1	1	5/5/86	LIT(1)
T. radix	300 × 40	0·9	2	8/19/86	LIT(1)
T. rapa	50 × 20	2·3	7	5/27/86	FVC(A)
T. subacuta	100 × 40	2·5	3	7/29/85	LIT(1)
T. turbo	55 × 40	6·4	10	10/29/86	LIT(1)
Tintinidium mucicola	100 × 40	1·6	1	4/14/86	LIT(1)
Tintinidium sp.	70 × 20	2·2	1	10/7/85	LIT(1)
Eutintinnus pectinus	120 × 20	3·8	1	8/4/86	FVC(A&B)
Eutintinnus sp.	70 × 20	3·6	3	5/27/86	LIT(1)
Helicostomella subulata	200 × 10	0·9	8	4/14/86	LIT(1)
Oligotrichs					
Laboea strobila	100 × 30	1·8	2	7/22/86	FVC(B)
Strobilidium velox	45 × 30	10·0	3	7/22/86	FVC(B)
Strobilidium sp. 1	65 × 20	2·4	9	5/19/87	FVC(A&B)
Strombidinopsis acuminatum	50 × 15	2·8	5	7/22/86	FVC(A)
Strombidium sp.	20 × 10	11·6	1	7/8/86	FVC(B)
Others					
Balanion sp. 1	35 × 20	16·6	4	6/9/86	LIT(2)
Balanion sp. 2	20 × 15	38·6	4	6/9/86	LIT(2)
Balanion sp. 3	12 × 16	8·0	3	6/9/86	LIT(2)
Urotrichia sp.	30 × 22	8·2	9	6/9/86	FVC(A)
Euplotes sp.	30 × 15	13·2	1	7/24/87	FVC(A)

gradients of chlorophyll and oxygen. Complete oxygen, chlorophyll, and temperature data have appeared elsewhere (Dolan & Coats, 1990). A synopsis is provided below to aid in interpreting the ciliate patterns.

Seasonal changes in water column conditions

In April and May water temperatures were minimal (10–15 °C) and dissolved oxygen values were maximal; chlorophyll *a* (chl *a*) concentrations were high throughout the water column and peaked (17–23 μg l^{-1}) in bottom waters. From May to June average concentrations of both chl *a* and oxygen declined abruptly in bottom and transition waters (2·5 μg l^{-1} chl *a* and 0·1 ml l^{-1} O_2 in bottom waters, and 5 μg l^{-1} chl *a* and 2 ml l^{-1} O_2 in transition waters) and remained low through October. The surface layer remained oxygenated (> 4 ml l^{-1}) and chlorophyll-rich (8–14 μg l^{-1}) from April through October.

Macrophagous ciliates

In April macrophagous ciliates made up the majority of the ciliate community in terms of biomass throughout the water column, and dominated cell densities in surface and

TABLE 2. Chesapeake Bay microphagous ciliates: numerically dominant species April–October 1985–87. Ciliates denoted 'MI' ingested bacteria-sized latex microspheres in experiments conducted with whole water samples in April, May and June 1987. Species denoted 'LIT' were categorized as representatives of ciliate forms generally considered bacteriovorous following Fenchel (1987)

Ciliate species	Size L × W (μm)	No. ml^{-1}	Maximum concentration depth (m)	Date	Grouped via
Tintinnids					
Tintinnopsis minuta	20 × 12	30	10	6/25/85	MI
Oligotrichs					
Strombidium sulcatum	35 × 30	26	1	7/22/86	MI
Strobilidium sp. 2	15 × 10	14·8	7	5/6/85	MI
Others					
Cyclidium sp. 1	20 × 12	20·6	20	4/14/86	MI
Cyclidium sp. 2	35 × 15	20	3	7/22/87	LIT
Pleuronema sp.	60 × 25	78·6	11	7/8/86	MI
Peritrich sp.	35 × 20	1·8	10	6/25/85	LIT

TABLE 3. Chesapeake Bay predacious ciliates: numerically dominant species April–October 1985–87. *Didinium* spp. denoted by 'LIT' were categorized as predacious as this genus is considered to consist of highly specialized predators on ciliates (Antipa *et al.*, 1983). *Euplotes woodruffi* were categorized as predacious after observing the remains of *Pleuronema* sp. in food vacuoles

Ciliate species	Size L × W (μm)	No. ml^{-1}	Maximum concentration depth (m)	Date	Grouped via
Didinium sp. 1	30 × 25	2·8	11	7/8/86	LIT
Didinium sp. 2	55 × 35	0·4	2	6/25/85	LIT
Euplotes woodruffi	150 × 50	2·1	11	8/5/86	FVC

transition waters (Figure 2). The spring assemblage typically included the tintinnids *Tintinnopsis acuminata, T. rapa, T. levigata*, the oligotrich *Strombidinopsis acuminata* and the prostome *Urotrichia* sp.

A shift from a spring to summer assemblage was evident by June. The summer community of macrophagous ciliates was diverse and showed a distinct June peak in cell numbers (16 cells ml^{-1}). It was dominated by the tintinnids *Eutintinnus pectinus, Eutintinnus* sp., *T. acuminata, T. sacculus*, the oligotrich *Strombidium velox*, other unidentified large (40–60 μm diameter) *Strombidium* spp. and the prostome *Balanion* spp. These species were virtually absent from bottom waters in July and August and present in low concentrations in transition waters relative to surface concentrations.

The change from a summer community to a fall fauna corresponded with minor shifts in cell densities but marked increases in biomass concentrations for all three water column zones, reflecting the larger average size of the fall macrophages. By October, common macrophages included *T. kofoidi, T. levigata, T. rapa, S. acuminata* and *Urotrichia* spp.

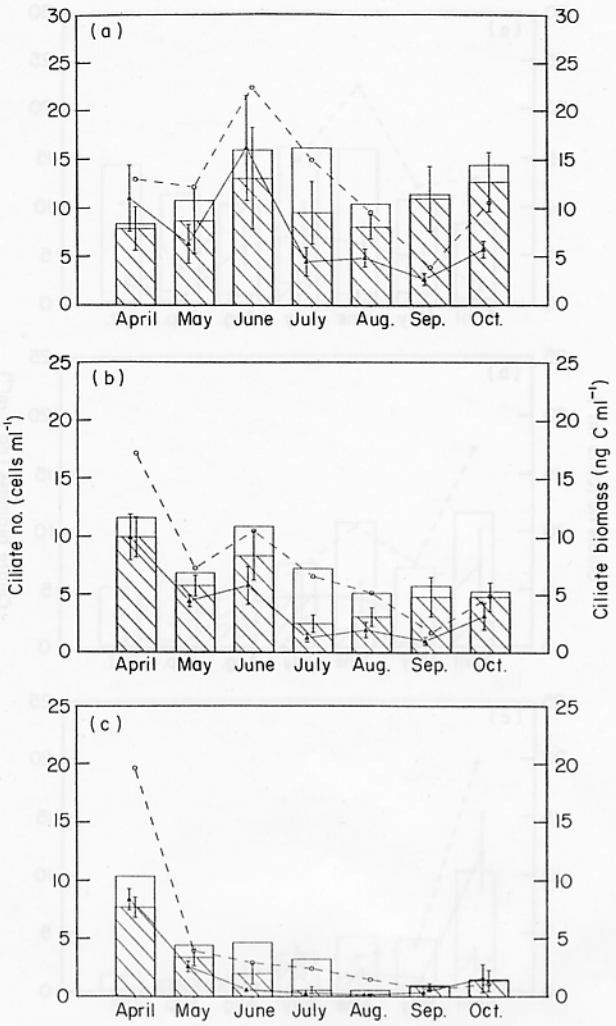

Figure 2. Macrophagous relative to total ciliate concentrations: average monthly values. Sample sizes for each month (number of integrated average values were: April = 4, May = 8, June = 9, July = 9, August = 8, September = 4, October = 4). Error bars represent ±1 SE. (a) Average surface layer concentrations, (b) average transition layer concentrations, and (c) average bottom layer concentrations. Symbols: ○ - - ○, total number of ciliates; □, total ciliate biomass; ▲ —— ▲, number of macrophagous ciliates; ▨, macrophagous ciliate biomass.

Microphagous ciliates

In surface waters, microphagous ciliates only formed a substantial portion of the total ciliate biomass in July and August, but in cell numbers they represented at least 20% of the ciliate community in all months (Figure 3). The numbers and biomass of microphages usually increased steadily from April to July. Densities of microphagous ciliates decreased in late summer and then declined abruptly to low values by early fall. In spring the dominant microphages were the small tintinnid, *T. minuta* and *Strobilidium* sp. By July,

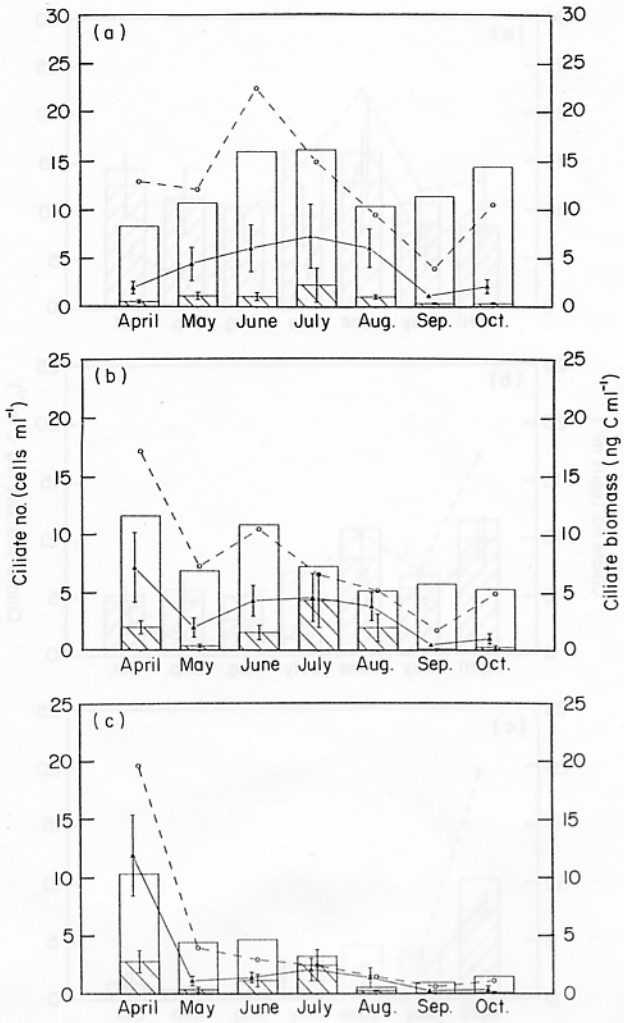

Figure 3. Microphagous relative to total ciliate concentrations: average monthly values. Sample sizes as in Figure 2. Error bars represent ±1 SE. (a) Average surface layer concentrations, (b) average transition layer concentrations, and (c) average bottom layer concentrations. Symbols: ○ - - ○, total number of ciliates; □, total ciliate biomass; ▲ —— ▲, number of microphagous ciliates; ▨, microphagous ciliate biomass.

Cyclidium spp. were found in surface waters. Microphages in September and October were usually low in number but high in diversity with all the species listed in Table 3 present.

In contrast to the surface layer, microphagous ciliates often constituted a large portion of the ciliate microzooplankton community in transition and bottom waters, accounting for up to 80% (in July) of total ciliate biomass and numbers (Figure 3). In both transition and bottom waters, the maximum population density for microphagous ciliates occurred in the bottom waters in April (2·5 ngC ml^{-1} and 12·5 cells ml^{-1}) and was composed almost entirely of *Cyclidium* sp. 1. Standing stocks declined from May through June and then

rose to a second peak in July, which was formed largely by a *Pleuronema* sp. or a small *Strobilidium* sp. Following the July peak, concentrations declined slightly in August and then to very low levels in September and October.

Predatory ciliates

Relative to total ciliates, predatory ciliates were not very abundant in the surface waters and were usually *Didinium* spp. However, they can form a considerable portion of the total ciliate biomass, as was seen in June and July (*c.* 10%). Seasonal trends in predacious ciliate density roughly followed shifts in total ciliate concentration in surface waters from May through October (Figure 4). Predatory forms were not observed in April samples; they increased in numbers and biomass from May to June then declined from July through August to barely detectable concentrations in September. In October, predators returned to levels similar to those in May.

In transition and bottom waters both *Didinium* spp. and *Euplotes woodruffi* were found, but generally in low numbers. However, they represented *c.* 20% of total May ciliate biomass in bottom waters (Figure 4) and *c.* 25% of total August ciliate biomass in transition waters. As in the surface waters, they were absent in April.

Statistical relationships

Correlation analysis of the different ciliate groups in different parts of the water column (Table 4) indicated that neither macrophagous nor microphagous ciliate abundance was related to chlorophyll levels except in bottom waters, where concentrations of macrophagous ciliates were also related to oxygen content. With two exceptions, ciliate trophic group abundances were not significantly related to one another: predatory ciliate biomass was associated with microphagous ciliate biomass in surface waters; and in bottom waters, concentrations of macrophages and microphages were related.

Discussion

Chesapeake Bay relative to other systems

Direct comparison of the macrophagous group identified here with reports from other systems is difficult as the group has not previously been enumerated as a distinct component of ciliate microzooplankton. However, if it is conceded that microphagous or bacteriovorous ciliate abundances have usually been underestimated due to problems of preservation and recognition (Sherr *et al.*, 1986*a*), then ' total ciliates ' reported by other authors in earlier studies may correspond roughly to the category ' macrophagous ciliates '. Total ciliate abundances in eutrophic meso- and polyhaline systems vary considerably spring through fall but surface layer concentrations commonly range from 1 to 10 cells ml^{-1} and from 1 to 10 ngC ml^{-1} (Dolan & Coats, 1990) compared to the ranges 3–16 ml^{-1} and 7·5–12·5 ngC ml^{-1} for concentrations of macrophages in the surface waters of the Chesapeake Bay. Macrophagous ciliates displayed a June peak in surface waters of the Chesapeake Bay while total ciliates in other systems peak in May or June (Dolan & Coats, 1990).

The microphagous ciliate group identified for the mesohaline Chesapeake was composed of scuticociliates, small oligotrichs, a peritrich ciliate and a small tintinnid. This assemblage corresponds closely to one found in the Duplin River, a Georgia saltmarsh embayment; ' bacteriovorous ciliates ' included small scuticociliates, small oligotrichs and a peritrich species, based on the ingestion of labelled bacterial cells (Albright *et al.*, 1987).

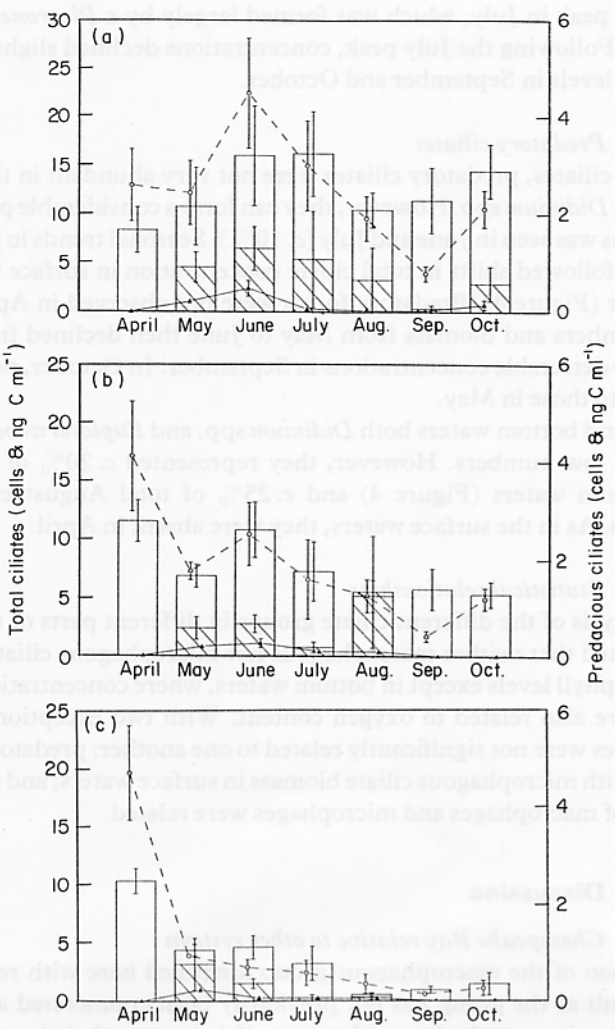

Figure 4. Predacious relative to total ciliate concentrations: average monthly values. Note change in scales for predacious ciliates. Sample sizes as in Figure 2. Error bars represent ±1 SE. (a) Average surface layer concentrations, (b) average transition layer concentrations, and (c) average bottom layer concentrations. Symbols: ○ - - ○, total number of ciliates; □, total ciliate biomass; ▲ —— ▲, number of predacious ciliates; ▨, predacious ciliate biomass.

As in the present study, ciliates capable of ingesting bacteria-sized particles were mostly ⩽20 μm in maximal dimension (Albright *et al.*, 1987).

The abundance of bacteriovorous ciliates, taken as the abundance of all ciliates ⩽20 μm in size, was investigated for several marine systems by some of the same authors; they reported that their eutrophic estuary site, the Duplin River, displayed the highest numbers of 'bacteriovorous ciliates' (Sherr *et al.*, 1986*a*). Based on samples taken at 1 m depth in August, estimates of Duplin River concentrations of 16 cells ml^{-1} and 1·8 ngC ml^{-1} were reported (Sherr *et al.*, 1986*a*). These values compare well with six cells ml^{-1} and 2 ngC ml^{-1}, the average integrated surface water density of microphagous

TABLE 4. Correlations between ciliate guilds, chlorophyll *a*, and D. O.

		Chl. *a.* concentration	D.O. concentration	Macrophagous cells no.	Macrophagous biomass	Microphagous cells no.	Microphagous biomass	Predacious cell no.	Predacious biomass
Macrophagous No. ml^{-1}	Surface	−0·056	0·091	—	—	0·315	0·132	0·234	0·106
	Trans	0·285	0·484*	—	—	0·332	0·104	0·051	0·035
	Bottom	0·666*	0·612*	—	—	0·579*	0·317	−0·233	−0·157
Microphagous No. ml^{-1}	Surface	0·071	−0·024	0·315	0·149	—	—	0·222	0·397*
	Trans	0·089	0·484*	0·332	0·332	—	—	0·137	0·083
	Bottom	0·429*	0·364	0·579*	0·504*	—	—	0·115	0·151
Predacious No. ml^{-1}	Surface	−0·249	0·038	0·234	0·150	0·222	0·222	—	—
	Trans	−0·117	0·209	0·051	0·137	0·137	0·176	—	—
	Bottom	0·096	−0·147	−0·223	−0·153	0·115	0·255	—	—

*$P \geqslant 0{\cdot}01$ ($r \geqslant 0{\cdot}372$); $n = 47$ for all comparisons.

ciliates in the mesohaline zone of the Chesapeake Bay in August. Unfortunately, comparison of the seasonal trends and vertical distributions of Chesapeake Bay microphages with those of other systems is difficult as these ciliates have never before been separately enumerated in seasonal or entire water column studies.

The occurrence of predacious ciliates such as *Didinium* has been noted previously in the Chesapeake Bay (Brownlee & Jacobs, 1987) and in a variety of marine systems: the arctic and subarctic Pacific (Taniguichi, 1983), the tropical Pacific (Beers & Stewart, 1971), the Antarctic and sub-Antarctic seas (Hada, 1970), the Black Sea (Zaika & Averina, 1969), and the northern Atlantic (Fauré-Fremiet, 1924), as well as associated with sedimenting material (Silver *et al.*, 1984; Taylor, 1989). However, there is very little quantitative data available on the abundances of predacious forms, as they are usually lumped with other non-tintinnid ciliates. However, Leppanen and Brunn (1986) reported that a *Didinium* species constituted 7–14% of the total ciliate biomass during a late spring phytoplankton bloom in the Baltic. In the Chesapeake Bay, predacious ciliates represented *c.* 3·5% of total ciliate biomass (averaging monthly whole water column values) and peaked at *c.* 25% of total ciliate biomass (in the transition waters in August, Figure 4), values similar to those found in the Baltic.

Factors regulating ciliate guilds

The abundance of macrophagous ciliates in the Chesapeake Bay is likely regulated, in oxygenated waters, by the abundance of nanophytoplankton as has been found for tintinnids in other systems (Capriulo & Carpenter, 1983; Verity, 1985). Microphagous ciliate abundance could be related to bacterial concentrations or productivity. For bacteriovorous microflagellates, density is apparently related more to bacterial production than to concentration (Wright *et al.*, 1987; Coffin & Sharp, 1987). Both of these measures independently correlate with chl *a*, but with a 1–2-week lag period, in the southern end of the mesohaline zone of the Chesapeake Bay (Jonas & Tuttle, 1990). Given the lag, it is perhaps not surprising that microphagous ciliates peak after macrophagous forms, a sequence which resembles the ' heterotrophic phase of succession ' described by Sorokin (1977) in which bacteriovore follows herbivore abundance in the Japan Sea.

The correlation analysis indicated that there is at least one physical factor, oxygen concentration, which may limit the habitat of one ciliate guild. In both transition and bottom waters, macrophage abundance is correlated with dissolved oxygen (Table 4). In contrast, microphagous ciliates appear to be tolerant of low oxygen conditions; their peak biomass concentration occurs in transition waters in July when the transition layer includes the anoxic/oxic interface zone (Figure 3).

Predatory ciliate concentration generally follows trends in total ciliate concentration in the three water column zones. However, in surface waters where predacious forms are most abundant, there is a significant correlation between microphage biomass and predacious ciliate biomass. Furthermore, in transition waters, the maximum predacious ciliate biomass that was recorded coincides with the secondary peak in microphage ciliate biomass (Figures 3 and 4). These facts suggest that the abundance of the generally small and aloricate microphagous ciliates may regulate predacious ciliate abundance. Macrophagous ciliates, mostly tintinnids and large oligotrichs, may not represent suitable prey items for predacious ciliates because of physical constraints of prey handling. There is at present, however, no data with which to judge this possibility.

A specialized guild of ciliates whose significance has only recently been recognized are mixotrophic oligotrichs (Stoecker *et al.*, 1987; Laval-Peuto & Rassoulzadegan, 1987). In

addition to feeding on algae, they use photosynthate produced by chloroplasts sequestered from ingested algae (Putt, 1990; Jonsson, 1987). Mixotrophic oligotrichs were not considered in this study because the fixative used precluded separate enumerations and casual observations indicated that they form a minor part of the oligotrich fauna in the Chesapeake Bay (Dolan & Coats, 1990). These forms are most common in mesotrophic estuarine and marine environments (D. K. Stoecker, pers. comm.). Competitive interactions may explain their low abundance in the relatively turbid and chlorophyll-rich waters of the mesohaline Chesapeake Bay.

Importance of non-herbivorous ciliates

Recent work has emphasized the idea that some ciliates may function as important bacteriovores (Albright *et al.*, 1987; Rivier *et al.*, 1986; Sherr & Sherr, 1987; Sherr *et al.*, 1986*a*,*b*, 1987). For the Chesapeake Bay, an estimate of how important microphagous ciliates are, relative to heterotrophic microflagellates (hflag), can be approached using established clearance rate estimates. Rates for typical bacteriovores, under *in situ* conditions, are *c.* 200 nl cell^{-1} h^{-1} and *c.* 3 nl cell^{-1} for ciliates and hflag, respectively (Sherr *et al.*, 1987). Using these clearance rates, with typical water column abundances of about five bacteriovorous ciliates (this study) and 2000 hflag ml^{-1} (Dolan & Coats, 1990), ciliates probably account for approximately 15% of the bacteriovory due to protozooplankton in the Chesapeake Bay. The relative activity of ciliates can, at times, be significantly greater, as in the bottom waters in early spring when ciliate densities are high (12 cells ml^{-1}) compared to hflag abundances (*c.* 2000 cells ml^{-1}, Dolan & Coats, 1990).

It is difficult to assess the importance of predacious ciliates in structuring or regulating the ciliate community based on this study because the sampling and enumeration procedures used were not well suited to quantify the relatively rare predacious forms. However, predacious ciliates may occasionally have a large impact on microphagous forms. Distributional data for *Pleuronema* sp. and the predacious *E. woodruffi* showed an increase in the *Euplotes* population shortly preceding a decrease in the *Pleuronema* population (Figure 5). The relationship between *Euplotes* and *Pleuronema* distributions, and the fact that remains of *Pleuronema* were found in *Euplotes* (Table 3), suggests that *Euplotes* may have been responsible for the decline of the *Pleuronema* population.

Laboratory studies of freshwater *Didinium* indicate that even in the low abundances reported here, *Didinium* could also have a large impact on the ciliate community. *Didinium* is known to feed on a variety of ciliate species (Antipa *et al.*, 1983), but most investigations have used *Paramecium* sp. as prey. Hewett (1980) calculated the half-saturation constant of prey density for *Didinium* as six cells ml^{-1} and reported maximum predation rates of approximately one cell h^{-1} which corresponded with a *Didinium* growth rate of about three divisions day^{-1}. Assuming that these feeding rates are representative of *in situ* rates at the peak densities found in surface waters (*c.* one *Didinium* and 24 total ciliates ml^{-1} in June) (Figure 4), and assuming that only ciliates are consumed, didinia would have been capable of clearing the surface waters of ciliates every 24 h.

Conclusion

In the mesohaline zone of the Chesapeake Bay, distinct groups of ciliates can be distinguished. These groups, macrophagous, microphagous, and predacious ciliates, to a large extent co-exist in the plankton. Overall, the nanoplankton-consuming macrophages constitute the majority of ciliate microzooplankton, but at certain times, and in certain

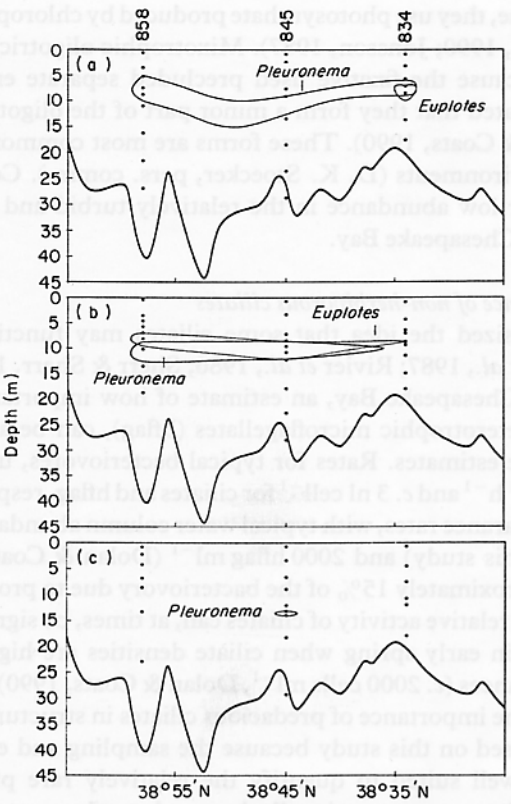

Figure 5. Vertical distributions of *Pleuronema* sp. and *Euplotes woodruffi* at stations 858, 845, and 834 22 July–19 August 1986. Enclosed areas represent species presence; dots represent depths sampled. (a) 22 July: *Pleuronema* were found in transition waters at all three stations (two–12 cells ml^{-1}), *E. woodruffi* present at 834 only (0·1 cells ml^{-1}). (b) 5 August: *E. woodruffi* present at all three stations (0·3–2·1 cells ml^{-1}) overlapping the *Pleuronema* population (0·1–17·8 cells ml^{-1}). (c) 19 August: *Pleuronema* present only at 845 (0·1 cells ml^{-1}); no *E. woodruffi* were detected.

parts of the water column, ciliates capable of ingesting bacteria, the microphages, can dominate the composition of the ciliate community. Predatory forms appear to be a common component of ciliate microzooplankton communities and may have a significant impact on microphagous ciliates.

Acknowledgements

This work was funded in part by the University of Maryland Sea Grant, and the Department of Zoology at the University of Maryland, College Park. The research reported here is based on a dissertation submitted to the University of Maryland in partial fulfillment of the requirements for a Ph.D. I gratefully acknowledge the aid provided by E. B. Small for ciliate identifications, D. W. Coats and J. J. Hiesler for gathering samples, and the captain and crew of the R/V *Ridgely Warfield* for ship operations.

References

Albright, L. J., Sherr, E. B., Sherr, B. F. & Fallon, R. D. 1987 Grazing of ciliated protozoa on free and particle-attached bacteria. *Marine Ecology Progress Series* **38,** 124–129.

Antipa, G. A., Martin, K. & Rintz, M. T. 1983 A note on the possible ecological significance of chemotaxis in certain ciliated protozoa. *Journal of Protozoology* **30,** 198–202.

Bernard, C. & Rassoulzadegan, F. 1990 Bacteria or microflagellates as a major food source for marine ciliates: possible implications for the microzooplankton. *Marine Ecology Progress Series* **64,** 147–155.

Beers, J. R. & Stewart, J. L. 1971 Micro-zooplankters in the plankton communities of the upper waters of the eastern tropical Pacific. *Deep Sea Research* **18,** 861–883.

Borshiem, K. Y. 1984 Clearance rates of bacteria-sized particles by freshwater ciliates measured with monodisperse fluorescent latex beads. *Oecologia* **63,** 286–288.

Brownlee, D. C. & Jacobs, F. 1987 Mesozooplankton and microzooplankton in the Chesapeake Bay. In *Containment Problems and Management of Living Chesapeake Bay Resources* (Majumdar, S. K., Hall, L. W. Jr & Austin, H. M., eds). Pennsylvania Academy of Science, Easton, PA, pp. 217–269.

Capriulo, G. M. & Carpenter, E. J. 1983 Abundance, species composition and feeding impact of tintinnid microzooplankton in central Long Island Sound. *Marine Ecology Progress Series* **10,** 277–288.

Coats, D. W. & Heinbokel, J. F. 1982 A study of reproduction and other life cycle phenomena in planktonic protists using an acridine orange fluorescence technique. *Marine Biology* **67,** 71–79.

Coffin, R. B. & Sharp, J. H. 1987 Microbial trophodynamics in the Delaware Estuary. *Marine Ecology Progress Series* **41,** 253–266.

Dolan, J. R. & Coats, D. W. 1990 Seasonal abundance of planktonic ciliates and microflagellates in mesohaline Chesapeake Bay waters. *Estuarine, Coastal and Shelf Science* **31,** 157–175.

Fauré-Fremiet, E. 1924 Contribution à la conaissance des infusoires planktonique. *Bulletin Biologique Française Belgique* **6,** 1–171.

Fenchel, T. 1987 *The Ecology of Protozoa.* Science Tech Publishers, Madison, WS, U.S.A.

Gast, V. 1985 Bacteria as a food source for microzooplankton in the Scheil Fjord and Baltic Sea. *Marine Ecology Progress Series* **22,** 107–120.

Gonzalez, J. M., Sherr, E. B. & Sherr, B. F. 1990 Size-selective grazing on bacteria by natural assemblages of estuarine flagellates and ciliates. *Applied and Environmental Microbiology* **56,** 583–589.

Hada, Y. 1970 Protozoan plankton of the Antarctic and subAntarctic Seas. *Japanese Antarctic Research Scientific Reports*, August 1970, E(31).

Heinbokel, J. F. 1978 Studies on the functional role of tintinnids in the southern California Bight. II. Grazing rates of field populations. *Marine Biology* **47,** 191–197.

Hewett, S. W. 1980 The effect of prey size on functional and numerical responses of a protozoan predator to its prey. *Ecology* **61,** 1075–1081.

Jonas, R. B. & Tuttle, J. H. 1990 Bacterioplankton and organic carbon dynamics in the lower mesohaline Chesapeake Bay. *Applied and Environmental Microbiology* **56,** 747–757.

Jonsson, P. 1987 Photosynthetic assimilation of inorganic carbon in marine oligotrich ciliates (Ciliophora, Oligotrichina). *Marine Microbial Food Webs* **2,** 55–68.

Kopylov, A. I. & Tutmanseva, N. I. 1987 Analysis of the content of tintinnid food vacuoles and evaluation of their contribution to the consumption of phytoplankton production off the Peru coast. *Oceanology* **27,** 343–347.

Laval-Peuto, M. & Rassoulzadegan, F. 1988 Autofluorescence of Marine Planktonic Oligotrichiua and other ciliates. *Hydrobiologia* **159,** 99–110.

Laval-Peuto, M., Heinbokel, J. F., Anderson, O. R., Rassoulzadegan, F. & Sherr, B. F. 1986 Role of micro- and nanoplankton in marine food webs. *Insect Science Applications* **7,** 387–395.

Leppanen, J. H. & Brunn, J. E. 1986 The role of pelagic ciliates including the autotrophic *Mesodinium rubrum* during the spring bloom of 1982 in the northern Baltic proper. *Ophelia* (suppl.) **4,** 147–157.

Malone, T. C., Kemp, W. M., Ducklow, H. W., Boynton, W. R., Tuttle, J. W. & Jonas, R. B. 1986 Lateral variation in the production and fate of phytoplankton in a partially stratified estuary. *Marine Ecology Progress Series* **32,** 149–160.

Marshall, S. M. 1969 Protozoa, order Tintinnia. *Conseil International pour L'Exploration de la Mer, Fiches d'Identification de Zooplancton*, 117–127.

Montagnes, D. W. S. & Lynn, D. H. 1987 A quantitative protargol stain (QPS) for ciliates: a description of the method and tests of its quantitative nature. *Marine Microbial Food Webs* **2,** 83–93.

Pomeroy, L. R. & Wiebe, W. J. 1988 Energetics of microbial food webs. *Hydrobiologia* **159,** 7–18.

Pace, M. & Bailiff, M. D. 1987 Evaluation of a fluorescent microsphere technique for measuring grazing rates of phagotrophic microorganisms. *Marine Ecology Progress Series* **40,** 185–193.

Putt, M. 1990 Metabolism of photosynthate in the chloroplast-retaining ciliate *Laboea strobila*. *Marine Ecology Progress Series* **60,** 271–282.

Rivier, A., Brownlee, D. C., Sheldon, R. W. & Rassoulzadegan, F. 1986 A comparative study of the growth responses to bacterial food concentration in two types of microzooplankters: flagellates and ciliates. *Marine Microbial Food Webs* **1,** 51–60.

Robertson, J. R. 1983 Predation by estuarine zooplankton on tintinnid ciliates. *Estuarine, Coastal and Shelf Science* **16,** 27–36.

Sherr, E. B. & Sherr, B. F. 1987 High rates of consumption of bacteria by pelagic ciliates. *Nature* **325,** 710–711.

Sherr, E. B., Sherr, B. F., Fallon, R. D. & Newell, S. Y. 1986*a* Small aloricate ciliates as a major component of the marine heterotrophic nanoplankton. *Limnology and Oceanography* **31,** 177–183.

Sherr, B. F., Sherr, E. B., Andrew, T. L. & Fallon, R. D. 1986*b* Trophic interactions between heterotrophic protozoa and bacterioplankton in estuarine water analysed with selective metabolic inhibitors. *Marine Ecology Progress Series* **32,** 169–179.

Sherr, B. F., Sherr, E. B. & Fallon, R. D. 1987 Use of monodispersed, fluorescently labeled bacteria to estimate *in situ* protozoan bacterivory. *Applied and Environmental Microbiology* **53,** 958–965.

Silver, M. W., Gowing, M. M., Brownlee, D. C. & Corliss, J. O. 1984 Ciliated protozoa associated with oceanic sinking detritus. *Nature* **309,** 246–248.

Small, E. B. & Lynn, D. H. 1986 Phylum Ciliophora. In *Illustrated Guide to the Protozoa* (Lee, J. J., Hunter, S. H. & Bovee, J. C., eds). Society of Protozoology, Lawrence, KS, pp. 393–575.

Sokal, R. R. & Rohlf, F. J. 1969 *Introduction to Biostatistics*. W. H. Freeman and Co., San Francisco.

Sorokin, Y. I. 1977 The heterotrophic phase of plankton succession in the Japan Sea. *Marine Biology* **41,** 107–117.

Stoecker, D. K. & Evans, G. T. 1985 Effects of herbivory and carnivory in a microplankton food web. *Marine Ecology Progress Series* **25,** 159–167.

Stoecker, D. K., Cucci, T. L., Hulbert, E. M. & Yentsch, C. M. 1986 Selective feeding by *Balanion* sp. (Ciliata: Balanionidae) on phyoplankton that best support its growth. *Journal of Experimental Marine Biology and Ecology* **95,** 113–130.

Stoecker, D. K., Michaels, A. E. & Davis, L. H. 1987 Large proportion of marine planktonic ciliates found to contain functional chloroplasts. *Nature* **326,** 790–792.

Stoecker, D. K., Taniguchi, A. & Michaels, A. E. 1989 Abundance of autotrophic, mixotrophic and heterotrophic planktonic ciliates in shelf and slope waters. *Marine Ecology Progress Series* **50,** 241–254.

Tabor, P. S. & Neihof, R. A. 1984 Direct determination of activities for microorganisms of Chesapeake Bay populations. *Applied and Environmental Microbiology* **48,** 1012–1019.

Taniguichi, A. 1983 Microzooplankton distribution along a transverse section crossing a marked oceanic front. *La Mer* **21,** 95–101.

Taylor, G. T. 1989 Variability in the vertical flux of microorganisms and biogenic material in the epipelagic zone of a North Pacific central gyre station. *Deep Sea Research* **36,** 1287–1308.

Turley, C. M., Newell, R. C. & Robbins, D. B. 1986 Survival strategies of two small marine ciliates and their role in regulating bacterial community structure under experimental conditions. *Marine Ecology Progress Series* **33,** 59–70.

Verity, P. G. 1985 Grazing, respiration, excretion and growth rates of tintinnids. *Limnology and Oceanography* **30,** 1268–1282.

Wright, R. T., Coffin, R. B. & Lebo, M. E. 1987 Dynamics of bacteria and heterotrophic microflagellates in the Parker Estuary, northern Massachusetts. *Continental Shelf Research* **7,** 1383–1393.

Zaika, V. Y. & Averina, T. Y. 1969 Proportions of infusoria in the plankton of Sevastopol Bay, Black Sea. *Oceanology* **9,** 843–845.