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Seasonal Abundances of Planktonic Ciliates and Microflagellates in Mesohaline Chesapeake Bay Waters

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Ciliate, heterotrophic microflagellate (hflag) and autotrophic microflagellate (aflag) abundances are reported for mesohaline Chesapeake Bay waters based on samples gathered from April through October 1985–1987. Total water column averages for ciliate and microflagellate abundances were typical of eutrophic marine systems. Ciliate density ranged from 17·2 cells ml^{-1} in April to 1·8 cells ml^{-1} in September; hflag ranged from $3{\cdot}7 \times 10^3$ cells ml^{-1} in June to $1{\cdot}1 \times 10^3$ cells ml^{-1} in October. In spring the majority of ciliate and hflag standing stocks (70% and 64%, respectively) were located in bottom and transition waters; during summer months the majority (approximately 85% of both groups) were in surface and transition waters. During fall, ciliate stock was concentrated (72%) in surface waters and hflag were relatively evenly distributed in the three water column zones. Ciliate and microflagellate numbers were not directly related to chlorphyll *a* concentration except in the bottom layer, where simultaneous declines accompanied anoxia. Ciliate concentrations correlated with total numbers of microflagellates and hflag abundance, but not aflag density. We discuss the relative importance of predation and food availability in regulating ciliate and hflag concentrations in mesohaline Chesapeake Bay waters.

Introduction

Today with the wide acceptance of the ' microbial loop ' concept (Azam *et al.*, 1983), ciliates and heterotrophic microflagellates are viewed as occupying a pivotal role in the carbon flow of pelagic ecosystems (Sherr *et al.*, 1988). Thus, it is not surprising that protozooplankton have been the focus of many studies in recent years (Sherr & Sherr, 1988). However, few field studies have considered more than one protistan component of the microbial loop. Most investigations of the seasonal variability of ciliates or microflagellates have been fragmentary and: (i) dealt only with flagellates and bacteria (Andersson *et al.*, 1986; Caron, 1984; Coffin & Sharp, 1987; Davis *et al.*, 1985; Wright *et al.*, 1987), (ii) considered only ciliates and large flagellates (Smetacek, 1981; Montagnes *et al.*, 1988); (iii) were restricted to ciliates (Revelante & Gilmartin, 1983, 1987; Revelante *et al.*, 1985; Sanders, 1987) or to only a portion of the ciliate community, tintinnids (Capriulo & Carpenter, 1983;

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Hargraves, 1981; Kimor & Golandsky-Baras, 1981; Krsinic, 1987; Middlebrook *et al.*, 1987; Paranjape, 1987; Verity, 1985). With one exception (Andersen & Sorensen, 1986), no studies have quantified both ciliates and microflagellates using modern techniques of epifluorescenece microscopy to differentiate microflagellate types. Consequently, there is actually very little data on the seasonal variability of both ciliates and hflag within the same system. This is unfortunate because field data can, through the formulation of empirical relationships, shed light on the nature of microbial loop relationships.

This report deals with the seasonal abundance and vertical distribution of ciliates and flagellates in a highly productive coastal plain estuary seasonally subject to anoxic bottom water. Two questions are addressed: first, what are the relationships between ciliates and flagellates over medium term temporal (months) and spatial (the mesohaline zone of the Chesapeake Bay) scales; second, do these relationships change with the different regimes of chlorophyll and oxygen content found in different parts of the water column? Answers to these questions are used to examine the factors regulating ciliate and hflag abundances in the Chesapeake Bay.

Methods and materials

Study site and sampling

The Chesapeake Bay is a partially mixed coastal plain estuary. In the mesohaline zone, which extends from approximately 39°N latitude to the mouth of the Potomac River, water column gradients of salinity and oxygen are closely linked to the flow rate of the Susquehanna River (Schubel & Pritchard, 1986). Oxygen concentrations typically begin to decline by April and anoxic bottom waters are usually present from June through August; reoxygenation occurs with the early fall mixis (Seliger *et al.*, 1985). Mesohaline waters represent the zone of maximum phytoplankton biomass and productivity (Harding *et al.*, 1986); biomass peaks in the spring whereas primary production rates are highest in mid-summer (Malone *et al.*, 1988; Sellner, 1987). In contrast, bacterioplankton densities are maximal in early fall (Tabor & Neihof, 1984). The dominant metazoan zooplankter from early spring through late fall is the copepod, *Acartia tonsa* with peak concentrations occurring in late summer–early fall (Brownlee & Jacobs, 1987; Olson, 1987).

Station locations are given in Figure 1. Three stations were sampled: '858' (38°58′N Lat., 77°40′W Long.), '845' (38°45′N Lat., 77°32′W Long.), and '834' (38°34′N Lat., 77°31′W Long.). In 1985 one or two stations were sampled at approximately monthly intervals from May to October, in 1986 all three stations were visited biweekly from April to October, and in 1987 Station 858 was sampled monthly from April to September. Due to the time constraints involved with processing microflagellate samples (see later), samples were taken for microflagellate enumerations at monthly intervals in 1985, 1986 and 1987. Station protocol consisted of first obtaining depth profiles of physical parameters with a CTDFO$_2$-Niskin bottle cast. Following assessment of physical parameters, eight to ten Niskin bottles were tripped at selected depths to give two to three samples above the pycnocline, three to four samples through the transition zone, and two to three bottles in the bottom waters.

Water for Winkler dissolved oxygen (D.O.) determination (Carpenter, 1965) was immediately drawn from each Niskin bottle. Samples for chlorophyll *a* were filtered onto 25 mm A/E filters (Gelman Corp.), stored frozen and processed using standard methods (Strickland & Parsons, 1972). Samples for flagellate counts were fixed with glutaraldehyde

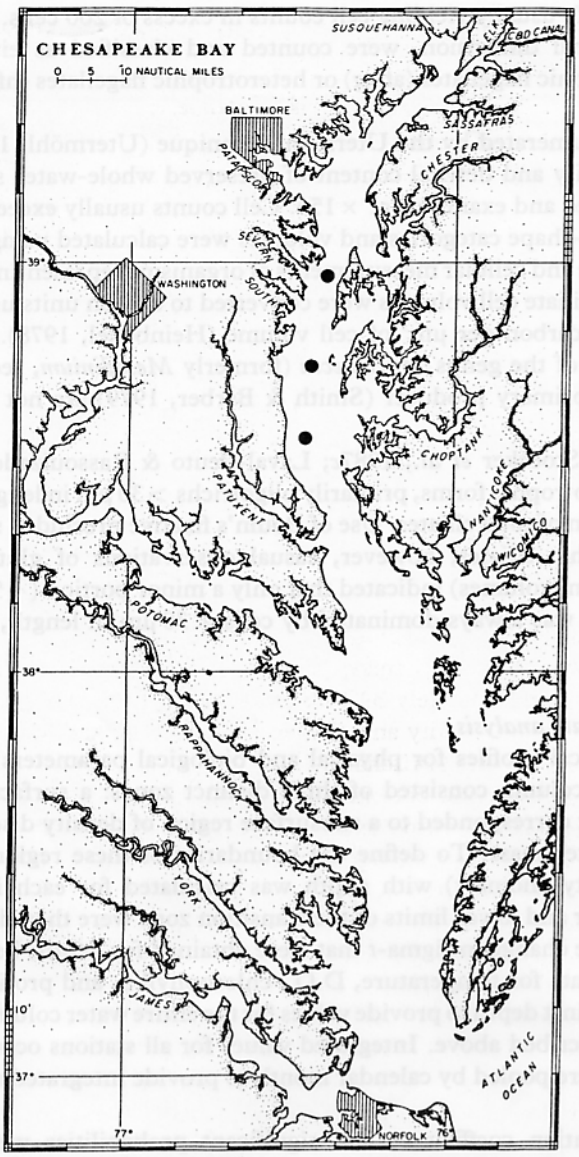

Figure 1. Study site: stations sampled in the mesohaline portion of the Chesapeake Bay. Station numbers from north to south are 858, 845, 834.

(final concentration 1%) and stored refrigerated in darkness. Aliquots taken for ciliate counts were preserved using a modified Bouin's solution (Coats & Heinbokel, 1982).

Microscopic methods

Flagellate counts were made from samples stained with primulin, and examined by epifluorescence microscopy following the procedure of Caron (1983). Optimum protocols of rapid processing (within 2–14 days) and gentle filtration (1–10 cm Hg) were followed (Bloem *et al.*, 1986). For each sample, 2–5 ml were filtered and 100–200 fields were

examined at × 1000, usually yielding cell counts in excess of 200 cells. Flagellated cells, 2–10 μm in maximal dimension, were counted and classified as either chloroplast-containing autotrophic flagellates (aflag) or heterotrophic flagellates (hflag) cells without chloroplasts.

Ciliates were enumerated by the Utermöhl technique (Utermöhl, 1958). Depending on the ciliate density and detrital content of preserved whole-water samples, 5–50 ml aliquots were settled and examined at × 156. Cell counts usually exceeded 100. Ciliates were placed in size-shape categories and volumes were calculated using the appropriate geometric formulae and cellular measurements of organisms representing the median size of each category. Ciliate cell volumes were converted to carbon units using a conversion factor of 0·088 pg carbon per μm^3 of cell volume (Heinbokel, 1978). Cell counts and biomass of ciliates of the genus *Myrionecta* (formerly *Mesodinium*, see Small & Lynn, 1986), which is a primary producer (Smith & Barber, 1979) are not included in data reported here.

Recent reports (Stoecker *et al.*, 1987*c*; Laval-Peuto & Rassoulzadegan, 1988) have suggested that mixotrophic forms, primarily oligotrichs > 30 μm in length, can represent a significant fraction of total ciliates. Use of Bouin's fixative precluded separate enumeration of mixotrophic ciliates; however, casual observations of gluteraldehyde-fixed water samples (10 ml volumes) indicated that only a minor portion (~5%) of the ciliate community, which was always dominated by cells < 30 μm in length, contained intact chloroplasts.

Data analysis

Inspection of vertical profiles for physical and biological parameters revealed that in general the water column consisted of three distinct zones: a surface mixed layer, a transition zone that corresponded to a subsurface region of density discontinuity, and a subpycnoclinal water mass. To define the boundaries of these regions the change in sigma-*t* (the density anomaly) with depth was calculated for each interval between samples. The upper and lower limits of the transition zone were then defined as the two largest values of the change in sigma-*t* that were obtained for depths below the first two surface samples. Data for temperature, D.O., chlorophyll *a*, and protistan abundances were integrated against depth to provide values for the entire water column and for each of the three zones described above. Integrated values for all stations occupied during the three year study were pooled by calendar month to provide integrated averages for each variable.

Pearson's correlation coefficients and significant probabilities were calculated to examine the relationships between protistan groups, and with chlorophyll *a* and oxygen concentrations. For these analyses integrated station data were not pooled and only dates with both ciliate and hflag abundance estimates were used ($n = 31$). Estimates of protistan abundances, as values based on count data, were log-transformed prior to conducting correlation analysis (Sokal & Rohlf, 1969).

Results

Water column zonation

In general, both physical (sigma-*t*, temperature, D.O.) and biological (ciliates, microflagellates, chlorophyll *a*) parameters displayed large surface-bottom gradients. Typical

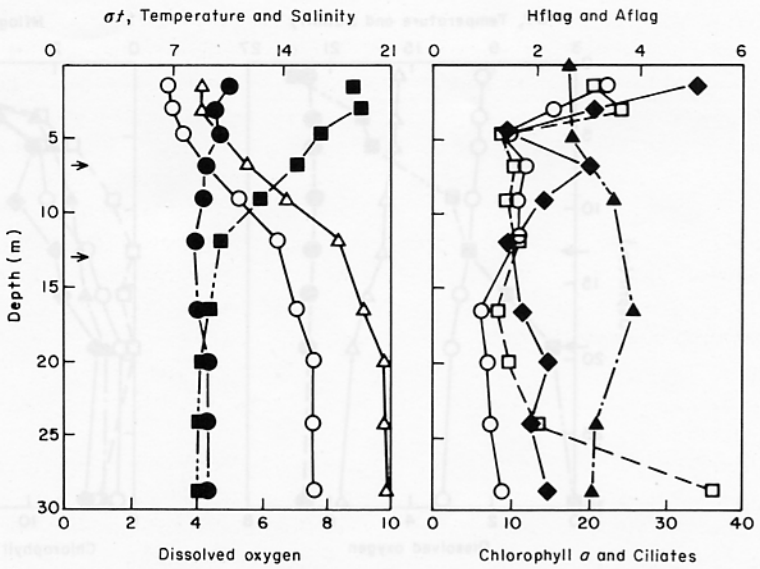

Figure 2. Early spring water column profiles (Station 845, 14 April 1986) of sigma-*t* (○), salinity (‰) (△), temperature (°C) (●), dissolved oxygen (ml l^{-1}) (■), hflag (10^3 cells ml^{-1}) (◆), aflag (10^3 cells ml^{-1}) (○), chlorophyll *a* (μg l^{-1}) (▲) and ciliates (cells ml^{-1}) (□). Arrows indicate the calculated limits of the transition layer.

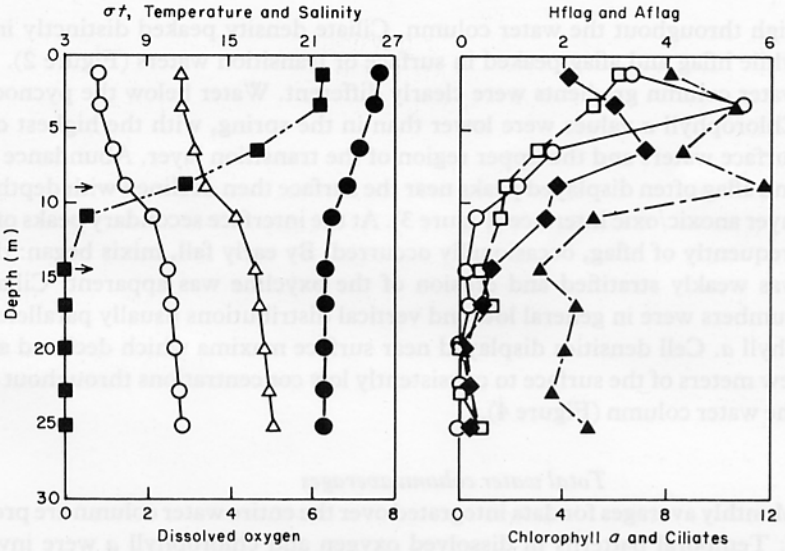

Figure 3. Mid-summer water column profiles (Station 845, 8 July 1986) of sigma-*t* (○), salinity (‰) (△), temperature (°C) (●), dissolved oxygen (ml l^{-1}) (■), hflag (10^3 cells ml^{-1}) (◆), aflag (10^3 cells ml^{-1}) (○), chlorophyll *a* (μg l^{-1}) (▲) and ciliates (cells ml^{-1}) (□). Arrows indicate the calculated limits of the transition layer.

water column profiles from spring, summer, and fall sampling dates are given in Figures 2, 3 and 4 and described below to illustrate this point.

In early spring the water column usually showed strong temperature-salinity stratification. Water below the pycnocline was well oxygenated and chlorophyll *a* values were

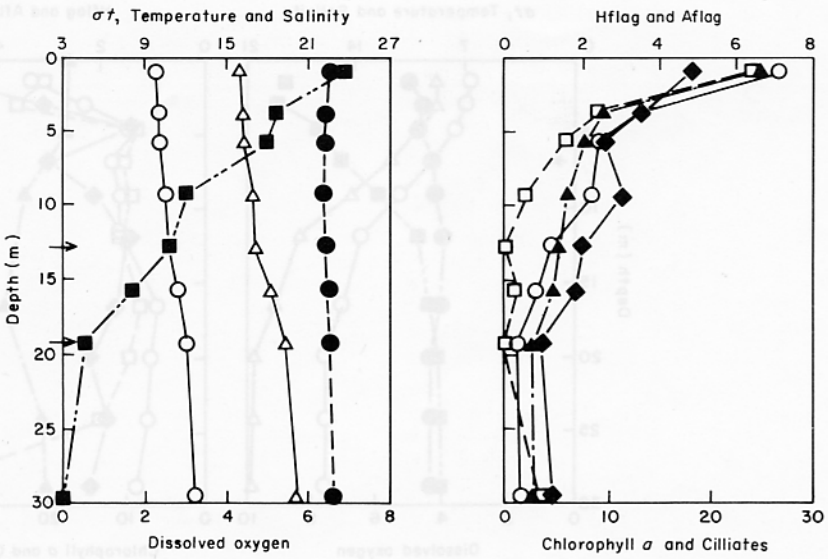

Figure 4. Early fall water column profiles (Station 845, 24 September 1986) of sigma-*t* (○), salinity (‰) (△), temperature (°C) (●), dissolved oxygen (ml l^{-1}) (■), hflag (10^3 cells ml^{-1}) (◆), aflag (10^3 cells ml^{-1}) (○), chlorophyll *a* (μg l^{-1}) (▲) and ciliates (× 10 cells ml^{-1}) (□). Arrows indicate the calculated limits of the transition layer.

high throughout the water column. Ciliate density peaked distinctly in bottom waters, while hflag and aflag peaked in surface or transition waters (Figure 2). By mid-summer water column gradients were clearly different. Water below the pycnocline was anoxic. Chlorophyll *a* values were lower than in the spring, with the highest concentrations in surface waters and the upper region of the transition layer. Abundance of ciliates, hflag, and aflag often displayed peaks near the surface then declined with depth to the transition layer anoxic/oxic interface (Figure 3). At the interface secondary peaks of ciliates, and less frequently of hflag, occasionally occurred. By early fall, mixis began: the water column was weakly stratified and erosion of the oxycline was apparent. Ciliate and flagellate numbers were in general low and vertical distributions usually paralleled that of chlorophyll *a*. Cell densities displayed near surface maxima which declined abruptly within a few meters of the surface to consistently low concentrations throughout the remainder of the water column (Figure 4).

Total water column averages

Monthly averages for data integrated over the entire water column are presented in Figure 5. Temporal patterns in dissolved oxygen and chlorophyll *a* were inversely related to temperature. D.O. was high in April, dropped sharply during early summer to a minimum during July and August, and then returned to ~60% of the April value by October. Chlorophyll *a* concentrations displayed a distinct April maximum followed by an abrupt decline to relatively low and invariant values from June through October.

Total ciliate numbers were highest in late spring and early summer, with peak concentrations in April and in June. Ciliate abundance declined steadily during mid-to late summer, reached a minimum in September, and showed a slight increase in October. Ciliate biomass generally followed the same seasonal trend as observed for cell density.

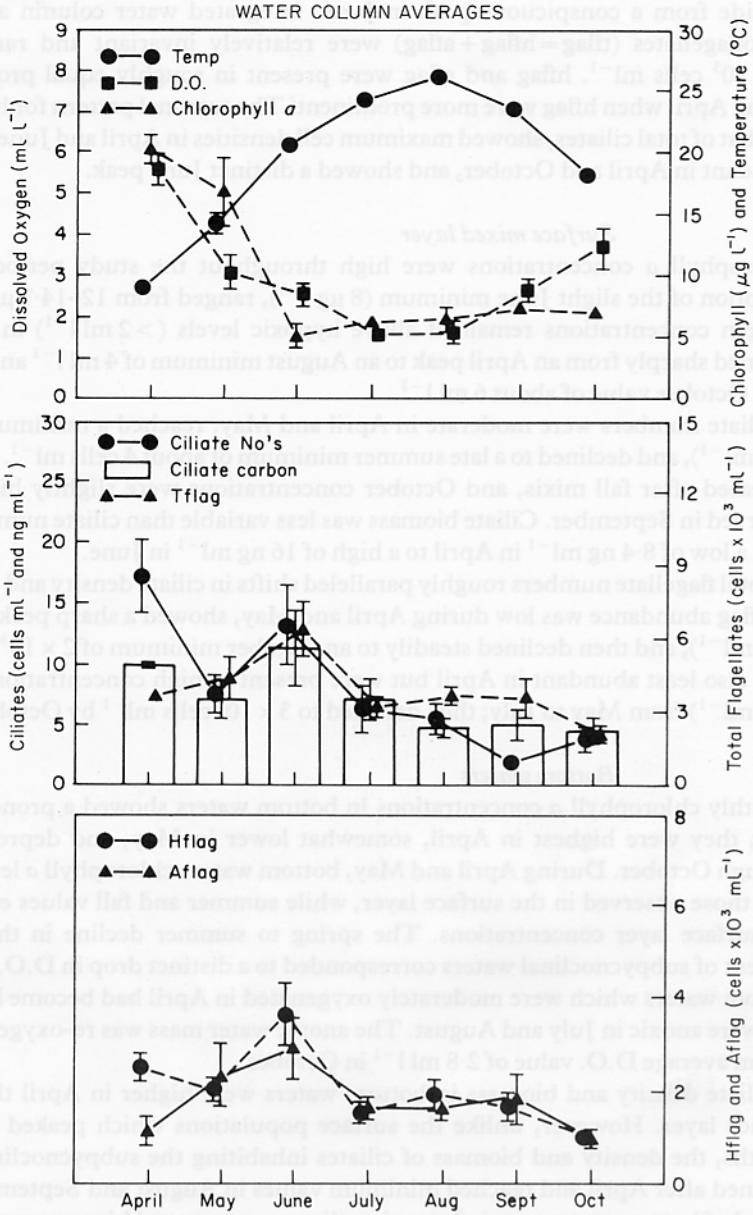

Figure 5. Average monthly water column characteristics and protistan concentrations. Sample sizes for each month (number of integrated average values for temperature, oxygen, chlorophyll *a*, and ciliates were: April, $n=4$, May, $n=8$; June, $n=9$; July, $n=9$; August, $n=8$; September, $n=4$; and, October, $n=4$. Sample sizes for flagellate abundances were: April, $n=4$; May, $n=4$; June, $n=6$; July, $n=4$; August, $n=5$; September, $n=4$; and, October, $n=4$. Error bars represent ± 1 SE.

However, differences in these patterns reflected the presence of large numbers of small ciliates in April, primarily scuticociliates, and the occurrence of relatively large species, mostly oligotrichs and tintinnids, in September.

Aside from a conspicuous peak in June, integrated water column averages of total microflagellates (tflag = hflag + aflag) were relatively invariant and ranged from 2·5–3·5 × 10^3 cells ml^{-1}. hflag and aflag were present in roughly equal proportions except during April when hflag were more prominent. The seasonal pattern for hflag abundance, like that of total ciliates, showed maximum cell densities in April and June. aflag were least abundant in April and October, and showed a distinct June peak.

Surface mixed layer

Chlorophyll *a* concentrations were high throughout the study period and, with the exception of the slight June minimum (8 μg l^{-1}), ranged from 12–14·7 μg l^{-1} (Figure 6). Oxygen concentrations remained above hypoxic levels (> 2 ml l^{-1}) in all months but declined sharply from an April peak to an August minimum of 4 ml l^{-1} and then increased to an October value of about 6 ml l^{-1}.

Ciliate numbers were moderate in April and May, reached a maximum in June (22·5 cells ml^{-1}), and declined to a late summer minimum of about 4 cells ml^{-1}. Ciliate numbers increased after fall mixis, and October concentrations were slightly higher than those observed in September. Ciliate biomass was less variable than ciliate numbers and ranged from a low of 8·4 ng ml^{-1} in April to a high of 16 ng ml^{-1} in June.

Total flagellate numbers roughly paralleled shifts in ciliate density and biomass (Figure 6). hflag abundance was low during April and May, showed a sharp peak in June (6 × 10^3 cells ml^{-1}), and then declined steadily to an October minimum of 2 × 10^3 cells ml^{-1}. aflag were also least abundant in April but were present in high concentrations (4·8–5·9 × 10^3 cells ml^{-1}) from May to July; they declined to 3 × 10^3 cells ml^{-1} by October (Figure 6).

Bottom waters

Monthly chlorophyll *a* concentrations in bottom waters showed a pronounced seasonal shift; they were highest in April, somewhat lower in May, and depressed from June through October. During April and May, bottom waters chlorophyll *a* levels were higher than those observed in the surface layer, while summer and fall values equalled a fourth the surface layer concentrations. The spring to summer decline in the chlorophyll *a* content of subpycnoclinal waters corresponded to a distinct drop in D.O. concentrations. Bottom waters which were moderately oxygenated in April had become hypoxic by June and were anoxic in July and August. The anoxic water mass was re-oxygenated in fall and had an average D.O. value of 2·8 ml l^{-1} in October.

Ciliate density and biomass in bottom waters were higher in April than those of the surface layer. However, unlike the surface populations which peaked during summer months, the density and biomass of ciliates inhabiting the subpycnocline layer steadily declined after April and reached minimum values in August and September. During the period of bottom water anoxia/hypoxia, ciliate numbers and biomass ranged from ~ 1–4 cells ml^{-1} and 0·5–3 ng ml^{-1}.

Monthly averages for tflag abundance in bottom waters were always much lower than those above the pycnocline. tflag densities were highest in April, declined to a July minimum (0·5 × 10^3 cells ml^{-1}), and ranged from 1–1·5 × 10^3 cells ml^{-1} in August, September and October. hflag numbers paralleled seasonal changes in tflag density. hflag were most abundant in April (2·3 × 10^3 cells ml^{-1}), declined to a minimum in July, (0·4 × 10^3 cells ml^{-1}) and ranged from 0·7–1·0 × 10^3 cells ml^{-1} from August to October. aflag were present in bottom waters but never occurred in substantial numbers; concentrations ranged from near 0 in July to 0·9 × 10^3 cells ml^{-1} in April and May.

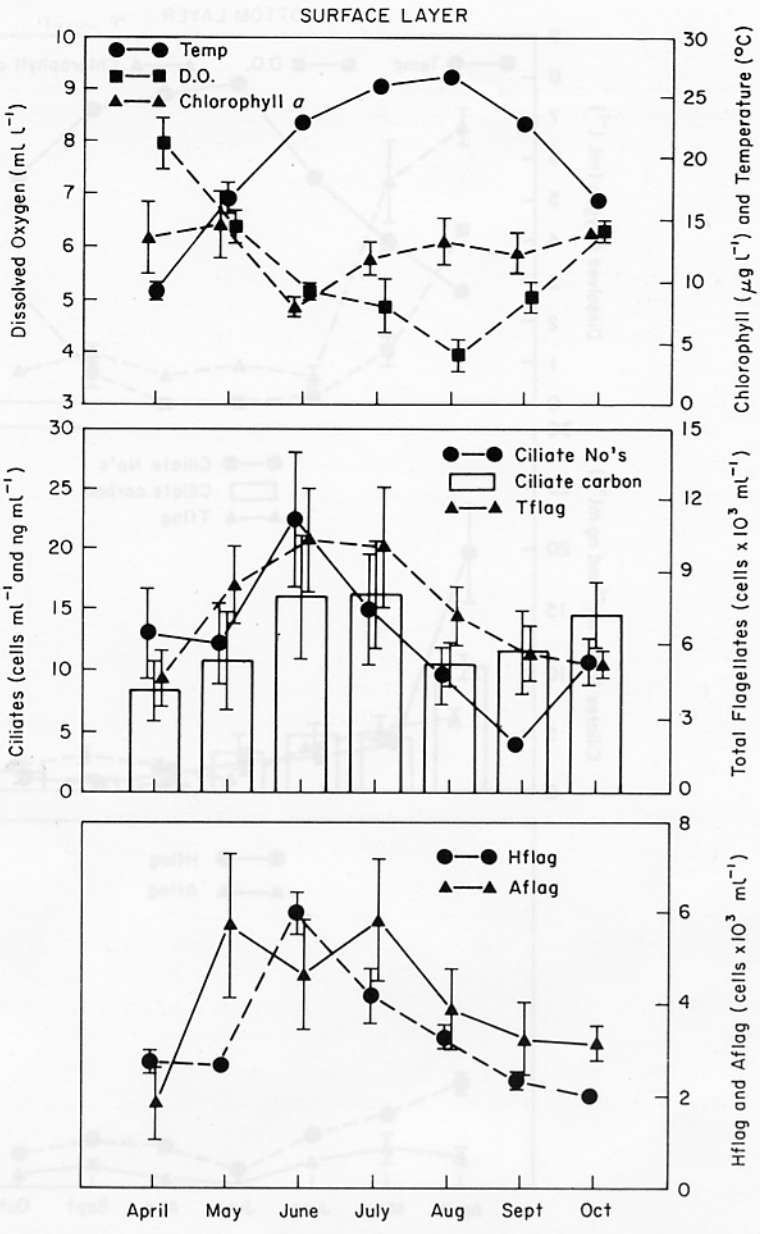

Figure 6. Surface layer characteristics and protistan concentrations. Sample sizes as in Figure 5.

Transition waters

The seasonal trend in chlorophyll *a* concentration in the transition zone paralleled that observed for bottom waters [compare Figures 7(a) and 8(a)]. During April and May, chlorophyll *a* levels were high and then declined to relatively low values during summer and fall. Monthly D.O. values for the transition zone [Figure 8(a)] were generally intermediate in value to those of surface and bottom waters and show a seasonal pattern similar

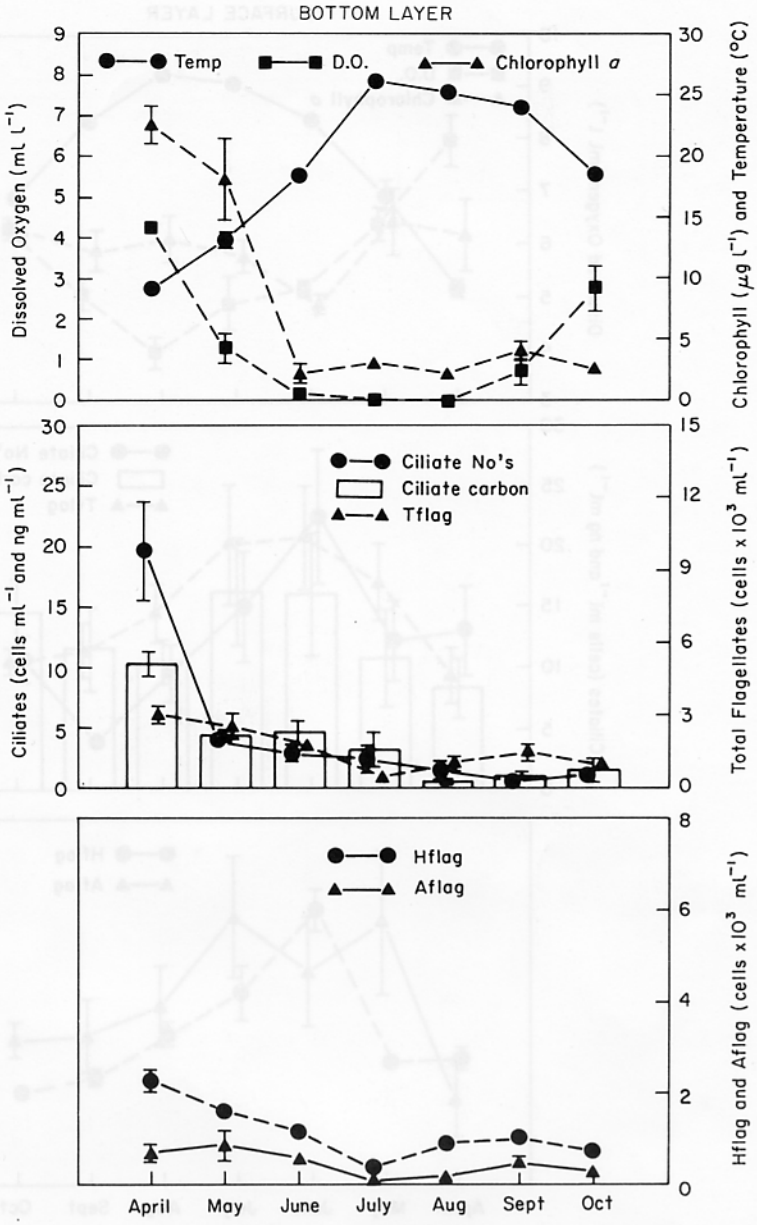

Figure 7. Bottom layer characteristics and protistan concentrations. Sample sizes as in Figure 5.

to that of the other two regions (i.e. highest concentrations in spring and fall, minimum levels in summer).

Ciliate number and biomass estimates for the transition layer were also generally intermediate to surface and bottom water values and exhibited seasonal patterns that appeared to combine features observed in the other two regions. Both transition and bottom samples had maximum cell densities and biomass in April. However, transition

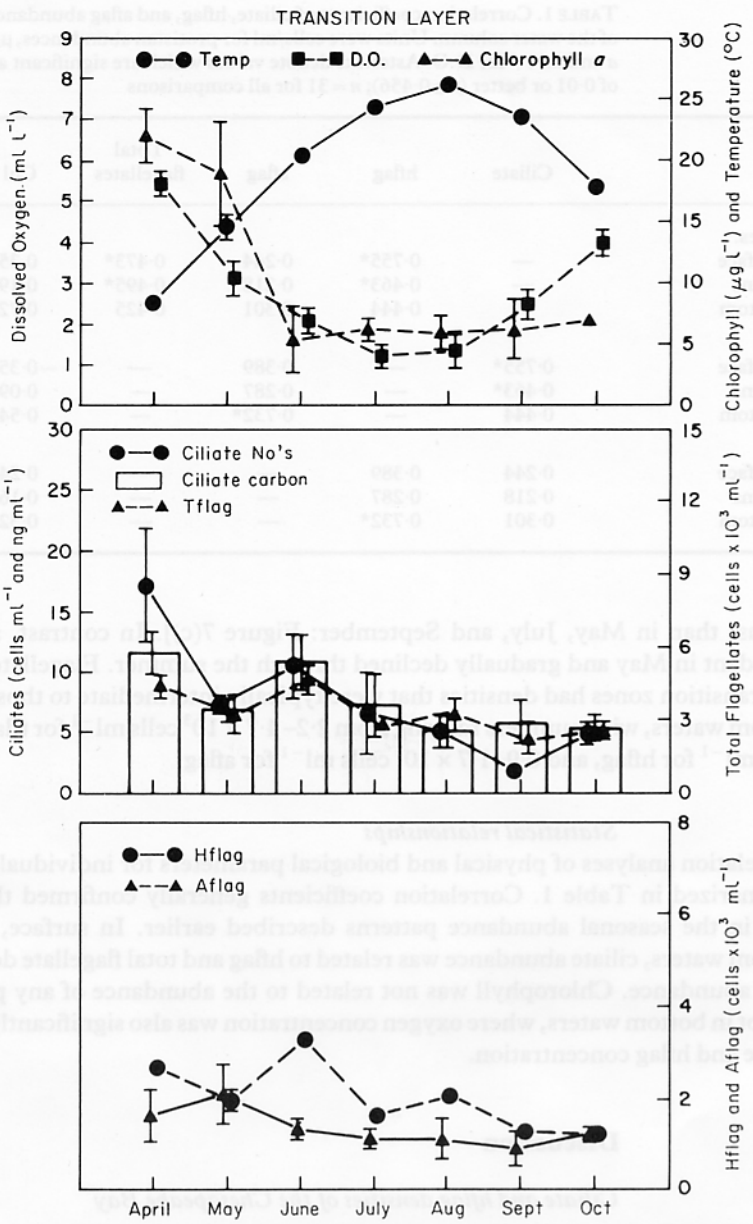

Figure 8. Transition layer characteristics and protistan concentrations. Sample sizes as in Figure 5.

waters also showed a second peak in June that coincided with elevated surface water values. Interestingly, all three regions had minimum ciliate densities in September, but biomass estimates for the surface and transition zone, unlike those for bottom waters remained relatively high. These data reflect the presence of large oligotrichs and tintinnids in the upper two regions during September.

Temporal patterns in tflag and hflag abundance paralleled that of ciliate populations and showed peak concentrations in alternating months [i.e., higher in April, June, and

TABLE 1. Correlation coefficients of ciliate, hflag, and aflag abundances in different parts of the water column. Units were cells/ml for protistan abundances, $\mu g\ l^{-1}$ for chlorophyll *a* and $ml\ l^{-1}$ for D.O. Asterisks denote values which are significant at a probability level of 0·01 or better ($r \geq 0{\cdot}456$); $n = 31$ for all comparisons

	Ciliate	hflag	aflag	Total flagellates	Chl *a*	D.O.
Ciliates:						
Surface	—	0·755*	0·244	0·473*	0·355	0·213
Trans	—	0·463*	0·218	0·495*	0·192	0·357
Bottom	—	0·444	0·301	0·425	0·726*	0·748*
hflag:						
Surface	0·755*	—	0·389	—	−0·358	0·107
Trans	0·463*	—	0·287	—	0·096	0·253
Bottom	0·444	—	0·732*	—	0·545*	0·564*
aflag:						
Surface	0·244	0·389	—	—	0·248	0·209
Trans	0·218	0·287	—	—	0·166	0·253
Bottom	0·301	0·732*	—	—	0·326	0·327

August than in May, July, and September: Figure 7(c)]. In contrast, aflag were most abundant in May and gradually declined through the summer. Flagellate populations of the transition zones had densities that were typically intermediate to those of surface and bottom waters, with numbers ranging from $2{\cdot}2–4{\cdot}7 \times 10^3$ cells ml^{-1} for tflag, $1{\cdot}3–3{\cdot}3 \times 10^3$ cells ml^{-1} for hflag, and $0{\cdot}9–1{\cdot}7 \times 10^3$ cells ml^{-1} for aflag.

Statistical relationships

Correlation analyses of physical and biological parameters for individual station data are summarized in Table 1. Correlation coefficients generally confirmed the relationships seen in the seasonal abundance patterns described earlier. In surface, transition, and bottom waters, ciliate abundance was related to hflag and total flagellate density but not to aflag abundance. Chlorophyll was not related to the abundance of any protistan group, except in bottom waters, where oxygen concentration was also significantly related to both ciliate and hflag concentration.

Discussion

Ciliate and hflag densities of the Chesapeake Bay

Comparison to other systems. Chesapeake Bay protist densities and seasonal abundance patterns appear to be typical for eutrophic waters (Tables 2 and 3). For examples, April–October values for ciliate biomass integrated over the entire water column ranged from 5–12 ng ml^{-1} in Chesapeake Bay, 3–16 ng ml^{-1} for Kiel Bight (Smetacek, 1981), and 0·4–20 ng ml^{-1} in the Damariscotta River estuary (Revelante & Gilmartin, 1987). Total ciliate biomass showed a late spring/early summer maximum and a late summer/early fall minimum in each of these estuaries (Table 2). hflag densities of the Chesapeake with a range of $2–6 \times 10^3$ cells ml^{-1} are close to the median of reported ranges, i.e. $1–37 \times 10^3$ cells ml^{-1} in Narragansett Bay (Davis *et al.*, 1985) to $1{\cdot}6–3{\cdot}3 \times 10^3$ cells ml^{-1} in the Duplin

TABLE 2. Seasonal variability of ciliate concentrations in eutrophic meso- and polyhaline waters. ND denotes no data given or data not given in a form allowing transformation (e.g. cells to carbon units)

System	Max (Month)	Min (Month)		Reference
(a) Surface Waters				
Damariscotta	6–12 (May)	1–2·5 (June)	cells ml^{-1}	Sanders, 1987
River	ND	ND	ng ml^{-1}	
Solent	ND	ND	cells ml^{-1}	
River	6·5 (May)	1·3 (July)	ng ml^{-1}	Burkill, 1982
Kiel	ND	ND	cells ml^{-1}	
Bight	10 (May, Sep.)	>1 (June, July)	ng ml^{-1}	Smetacek, 1981
Limfjorden	160 (June, July)	1 (Apr., Aug.)	cells ml^{-1}	Andersen & Sorensen, 1986
	ND	ND	ng ml^{-1}	
Northern	10·2 (May)	0·3 (Mar.)	cells ml^{-1}	Leppanen & Bruun, 1986
Baltic	4 (May)	0·3 (Mar.)	ng ml^{-1}	Leppanen & Bruun, 1986
Chesapeake	23 (June)	3 (Sep.)	cells ml^{-1}	This study
Bay	15 (June, July)	8 (Apr.)	ng ml^{-1}	This study
(b) Total water column				
Damariscotta	ND	ND	cells ml^{-1}	
River	20 (June)	3 (Aug.)	ng ml^{-1}	Revelante & Gilmartin, 1987
Kiel	ND	ND	cells ml^{-1}	
Bight	16 (Apr.)	3 (Aug.)	ng ml^{-1}	Smetacek, 1981
Chesapeake	17·5 (Apr.)	3 (Sep.)	cells ml^{-1}	This study
Bay	12 (June)	5 (Aug., Oct.)	ng ml^{-1}	This study

TABLE 3. Seasonal variability of hflag (10^3 cells ml^{-1}) in eutrophic meso- and polyhaline waters based on surface water sampling

System	Max (Month)	Min (Month)	Reference
Narragansett Bay	37 (May, Aug.)	1 (Sep., Oct.)	Davis *et al.*, 1985
Delaware Bay	7 (May)	2 (May)	Coffin & Sharp, 1987
Parker River	4–6 (July)	0–2 (Apr.)	Wright *et al.*, 1987
Duplin River	3·3 (Sep.)	1·6 (July)	Sherr *et al.*, 1984
Limsfjorden	15 (May, June)	0·5 (Apr., Aug.)	Andersen & Sorensen, 1986
Chesapeake Bay	6 (June)	2 (Oct.)	This study

River estuary (Sherr *et al.*, 1984). Maximum abundances of hflag commonly occur during summer months in eutrophic estuaries (Table 3).

Seasonal trends in different parts of the water column. In the mesohaline Chesapeake Bay the importance of different regions of the water column as a ciliate or hflag habitat changes with the seasons. In the spring the bulk of both the ciliate (approximately 70%) and the hflag (approximately 64%) standing stocks are in bottom and transition zone waters. During summer months the majority of ciliate (approximately 85%) and hflag (approximately 84%) stock are in surface and transition zone waters. In fall surface water populations alone account for most of the ciliates (approximately 72%) while hflag are evenly distributed between the three water column zones.

The bottom water peak of ciliates and hflag in spring, co-incident with high chlorophyll *a* values (Figure 6), is possibly related to the cycle of subsurface transport and ' seeding ' of the bloom dinoflagellate *Prorocentrum marie-lebouriae* (Tyler & Seliger, 1978). Late spring surface water blooms of *P. marie-lebouriae* in the northern Chesapeake Bay originate from populations transported from the southern end of the Bay in deep, north-flowing, saline waters. The deep central channel of the Bay shallows abruptly just north of station 858 and is the presumptive site of the vertical transport of the *P. marie-lebouriae* population which ' seeds ' the surface waters. Dense *P. marie-lebouriae* accumulations in deep water are perhaps associated with high bacterioplankton production which would in turn support the abundant ciliate and hflag populations. Unfortunately, at present there is little data available on bacterial production for the Chesapeake Bay.

In bottom waters, following the early spring peak, protistan densities decline rapidly with reductions in D.O. content. In contrast, transition zone cell densities showed secondary peaks during months of low D.O. content: peaks of ciliates and hflag in June and hflag alone in August (Figure 8). The secondary peaks were not all explicable as simple reflections of changes in surface population densities, since from July to August average hflag concentrations declined in surface waters but increased in the transition zone. The abundance shifts which occur in the transition layer may be associated with the anoxic/oxic interface which is often found from late June through August in transition zone waters (Seliger *et al.*, 1985).

Anoxic/oxic interfaces are characterized by high levels of labile dissolved organic matter (Carlucci *et al.*, 1987) and are considered zones of increased microbial activity (Caumette, 1988; Caumette *et al.*, 1983). Ciliates, in particular, have been found to accumulate at anoxic/oxic interfaces in freshwater lakes (Bark, 1985; Finlay, 1981; Pace, 1982; Psenner & Schlott-Idl, 1985). In the Chesapeake Bay, averaging protistan densities over the whole transition zone yielded values which indicate that the interface was not generally a zone of maximum protistan abundance. However, while individual water samples taken at the anoxic/oxic interface never contained dense populations of hflag, they did occasionally contain large numbers of ciliates. For an individual station the interface was occasionally the site maximum ciliate abundance. The importance of the interface zone is difficult to evaluate without knowledge of ciliate growth rates in interface *vs.* surface waters.

Factors affecting ciliate and hflag abundances in the Chesapeake Bay

Food availability. The seasonal changes in ciliate densities which occurred were not clearly relatable to shifts in chlorophyll *a* concentrations. Both laboratory and field studies have indicated that ciliates are likely to consume only a limited range of the phytoplankton available in natural systems (Burkill *et al.*, 1987; Gifford, 1985; Stoecker *et al.*, 1981, 1986; Verity & Stoecker, 1982; Verity & Villareal, 1986) thus chlorophyll *a* concentration is probably a poor indicator of potential ciliate food levels.

However, flagellate abundance may provide an indication of potential ciliate food levels. Abundance trends of ciliates paralleled those of tflag in both transition and surface waters (Figure 6 and 8) and data for the two groups were correlated (Table 2). Furthermore, laboratory studies have shown that, in general, high ciliate growth rates are achieved with microflagellate prey relative to the generally larger diatoms and dinoflagellates (Gifford, 1985; Verity & Stoecker, 1982; Verity & Villareal, 1986), and field studies of tintinnid ciliates in other systems have concluded that tintinnid abundance was mainly a function of the concentration of nanoplankton-size phytoplankton (Capriulo & Carpenter, 1983;

Verity, 1985). The abundance trends of ciliates in the Chesapeake Bay could then be a function of food, perhaps tflag, availability.

hflag abundance in the Chesapeake Bay, like ciliate numbers, also showed no obvious relationship with chlorophyll *a* levels (Table 2). According to the paradigm of the microbial loop (Azam *et al.*, 1983), hflag are assumed to subsist on bacteria which, in turn, are assumed to be closely linked with phytoplankton, usually the dominant source of labile dissoved organic matter. Therefore one might expect a correlation between hflag and chlorophyll *a* levels. However, the lack of such a correlation may be due to the consistent presence of relatively high concentrations of bacteria. While hflag abundances in the Chesapeake Bay are similar to those found in other estuaries (Table 3), bacterial abundances are elevated relative to other systems. The estimates of bacteria abundance for the mesohaline Chesapeake Bay, $3–15 \times 10^6$ cells ml^{-1} (Tabor & Niehof, 1984) and $3–20 \times 10^6$ cells ml^{-1} (Malone *et al.*, 1986), are among the highest reported for estuaries (Malone *et al.*, 1986). These values greatly exceed the minimum concentrations of bacteria ($0·5–1.5 \times 10^6$ cells ml^{-1}) allowing the logarithmic growth of moderate population densities of hflag (Fenchel, 1986). These considerations lead to the conclusion that hflag are probably not food-limited in the mesohaline Chesapeake Bay.

Studies of bacterial production and hflag grazing of bacteria in the Parker and Delaware estuaries have concluded that in those systems hflag abundance was not related to bacterial abundance, but to bacterial production, which was in turn linked not to chlorophyll *a* levels but to primary production (Wright *et al.*, 1987; Coffin & Sharp, 1987). However, estimates of minimum concentrations of bacteria are lower for the Parker ($0·9 \times 10^6$ cells ml^{-1}) and Delaware River ($1·0 \times 10^6$ cells ml^{-1}) estuaries (Wright *et al.*, 1987; Coffin & Sharp, 1987) than for the mesohaline zone of the Chesapeake Bay [$3–3·5 \times 10^6$ cells ml^{-1} (Tabor & Neihof, 1984; Malone *et al.*, 1986)]. hflag may be then occasionally food-limited in the Parker and Delaware River estuaries, and perhaps not in the Chesapeake Bay. A relationship between hflag abundance and bacterial production could exist in the Chesapeake Bay but at present there are no data available on seasonal shifts in bacterial production with which to evaluate this hypothesis.

Grazing. The similar seasonal abundance trends of ciliates and microflagellates could be the result of grazing pressure exerted on both populations by metazoan zooplankton. However, at least with regard to microflagellates, the hypothesis that metazoan grazing controls hflag density is not supported by existing estimates of the composition, feeding rates, and abundances of the Chesapeake Bay metazoan zooplankton community.

The dominant metazoan grazer from spring through fall is the estuarine copepod, *Acartia tonsa* (Brownlee & Jacobs, 1987; Olson, 1987). Capriulo and Ninivaggi (1982) examined the clearance rates of *A. tonsa* using natural plankton assemblages and concluded that for flagellate-sized (10 μm diameter) particles, copepod clearance rates are near zero. However, clearance rates of ~1–10 ml per copepod per day were found in laboratory studies in which *A. tonsa* was presented with only microflagellates for food (Berggreen *et al.*, 1988; Caron, 1984). Assuming clearance rates of ~5 ml per copepod per day, with abundances of copepods ranging from $4–20\,l^{-1}$ from April to October (Brownlee & Jacobs, 1987) copepods would clear hflag from only 2–10% of the water column every day. For copepod grazing to control hflag abundance, hflag would then have to be growing at considerably less than 1 generation per day. hflag are presumably capable of growing at 1–2 generations per day with minimal ($0·5–1 \times 10^6$ cells ml^{-1}) bacterial concentrations (Fenchel, 1986), well below those reported for the Chesapeake Bay.

The possibility that copepod grazing exerts a significant control on ciliate abundance is more difficult to judge, as a wide variety of clearance rates for copepods feeding on ciliates have been reported and range from ~8–249 ml per copepod per day (Ayukai, 1987; Berk *et al.*, 1977; Gifford & Dagg, 1988; Robertson, 1983; Stoecker & Egloff, 1987; Stoecker & Sanders, 1985; Turner & Anderson, 1983; Wiadnyana & Rassoulzadegan, 1989). Using the high estimates of copepod clearance rates [249 ml per copepod per day (Stoecker & Egloff, 1987)] and moderate copepod densities ($10\,l^{-1}$), ciliates would have to be growing at about 3 generations per day to maintain population density. This rate is close to the maximum estimate reported for *in situ* growth rates of ciliates (Brownlee, 1982; Verity, 1986). Whereas with the low clearance rate estimates [8 ml copepod per day (Turner & Anderson, 1983)], net accumulation of ciliates could occur with copepod densities of $20\,l^{-1}$ if ciliates were growing at over 0·2 generation day^{-1}.

Metazoan zooplankters other than postnaupliar copepods such as copepod nauplii, rotifers, ctenophores and jellyfish are present in the mesohaline Chesapeake Bay (Brownlee & Jacobs, 1987). However, unless present in high concentrations, they appear to be even poorer candidates for the control of ciliate and flagellate populations as they exhibit extremely low clearance rates, relative to copepods, when fed small flagellates or ciliates (Berggreen *et al.*, 1988; Egloff, 1988; Stoecker *et al.*, 1987*a*,*b*).

As hflag are probably not food-limited nor metazoan grazer-limited, it is tempting to conclude that grazing by ciliates (by default) regulates hflag abundance in the Chesapeake Bay. However, such a conclusion would at this time be premature. Preliminary reports giving estimates of *in situ* ciliate grazing rates on phytoplankton and bacterioplankton in Chesapeake Bay waters have emphasized findings of temporal and spatial variability (Lessard *et al.*, 1988; Sellner *et al.*, 1987). Further work clarifying the magnitude, and the factors regulating ciliate microzooplankton grazing is needed.

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References

Anderson, P. & Sorensen, H. M. 1986 Population dynamics and trophic coupling of pelagic microorganisms in eutrophic coastal waters. *Marine Ecology Progress Series* **33**, 99–109.

Andersson, A., Larsson, U. & Hågsström, Å. 1986 Size-selective grazing by a microflagellate on pelagic bacteria. *Marine Ecology Progress Series* **33**, 51–57.

Ayukai, T. 1987 Predation by *Acartia clausi* (Copepoda: Calanoida) on two species of tintinnids. *Marine Microbial Food Webs* **2**, 45–52.

Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L. A. & Thingstad, F. 1983 The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* **10**, 257–263.

Bark, A. W. 1985 Studies on ciliated protozoa in eutrophic lakes: 1. seasonal distribution in relation to thermal stratification and hypolimnetic anoxia. *Hydrobiologia* **124**, 167–176.

Berggreen, U., Hansen, B. & Kiorbe, T. 1988 Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. *Marine Biology* **99**, 341–352.

Berk, S. G., Brownlee, D. A., Heinle, D. R., Kling, H. J. & Colwell, R. R. 1977 Ciliates as a food source for marine planktonic copepods. *Microbial Ecology* **4**, 27–40.

Bloem, J., Bar-Gilissen, M-J.B. & Cappenberg, T. E. 1986 Fixation, counting, and manipulation of heterotrophic nanoflagellates. *Applied and Environmental Microbiology* **52,** 1266–1272.

Brownlee, D. C. 1982 *Measuring the secondary production of marine planktonic tintinne ciliates*. Ph.D. thesis, University of Maryland, College Park, MD.

Brownlee, D. A. & 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). Easton, PA: Pennsylvania Academic Science, pp. 217–269.

Burkill, P. H., Mantoura, R. F. C., Llelewellyn, C. A. & Owens, N. J. P. 1987 Microzooplankton grazing and selectivity of phytoplankton in coastal waters. *Marine Biology* **93,** 581–590.

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.

Capriulo, G. M. & Ninivaggi, D. A. 1982 A comparison of the feeding activities of field collected tintinnids and copepods fed identical natural particle assemblages. *Annales de l'Institut Oceanographie Paris* **58,** 325–334.

Carlucci, A. F., Shimp, S. L. & Craven, D. B. 1987 Bacterial response to labile dissolved organic matter increases associated with marine discontinuities. *FEMS Microbial Ecology* **45,** 211–220.

Caron, D. A. 1983 Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy, and comparison with other procedures. *Applied and Environmental Microbiology* **46,** 491–498.

Caron, D. A. 1984 *The role of heterotrophic microflagellates in plankton communities*. Ph.D. Thesis. Woods Hole Oceanographic Institution and Massachusetts Institute of Technology, MA.

Carpenter, J. H. 1965 The Chesapeake Bay Institute technique for the Winkler dissolved oxygen methods. *Limnology and Oceanography* **10,** 141–143.

Caumette, P. 1988 Les lagunes et les marais maritimes. In: *Micro-organismes dans les Ecosystems Oceaniques* (Bianchi, M., Marty, D., Bertrand, J.-C., Caumette, P. & Gauthier, M., eds). Paris: Masson, pp. 249–282.

Caumette, P., Pagano, M. & Saint-John, L. 1983 Répartion vertical du phytoplancton, des bactéries et du zooplancton dans un milieu stratifié en Baie de Biétri (lagune Ebrié, Cote d'Invoire). Relations trophic. *Hydrobiologia* **106,** 135–148.

Coats, D. W. & Heinbokel, J. F. 1982 A study of reproduction and other life cycle phenomena in planktonic protists using an acridine organe 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.

Davis, P. G., Caron, D. A., Johnson, P. W. & Sieburth J. McN. 1985 Phototrophic and apochlorotic components of picoplankton and nanaoplankton in the North Atlantic: geographic, vertical, seasonal and diel distributions. *Marine Ecology Progress Series* **21,** 15–26.

Egloff, D. A. 1988 Food and growth relations of the marine microzooplankter, *Synchaeta cecilia* (Rotifera). *Hydrobiologia* **157,** 129–141.

Fenchel, T. 1986 The ecology of heterotrophic microflagellates. *Advances in Microbial Ecology* **9,** 57–97.

Finlay, B. J. 1981 Oxygen availability and seasonal migrations of ciliated protozoa in a freshwater lake. *Journal of General Microbiology* **123,** 173–178.

Gifford, D. J. 1985 Laboratory culture of marine planktonic oligotrichs (Ciliophora, Oligotrichida). *Marine Ecology Progress Series* **23,** 257–267.

Gifford, D. J. & Dagg, M. J. 1988 Feeding of the estuarine copepod *Acartia tonsa* Dana: carnivory vs. herbivory in natural microplankton assemblages. *Bulletin of Marine Science* **43,** 458–468.

Harding, L. W., Meeson, B. W. & Fisher, T. R. 1986 Phytoplankton production in two east coast estuaries: photosynthesis-light functions and patterns of carbon assimilation in Chesapeake and Delaware Bays. *Estuarine Coastal and Shelf Science* **3,** 773–806.

Hargraves, P. E. 1981 Seasonal variations of tintinnids (Ciliophora: oligotrichida) in Narragansett Bay, Rhode Island, U.S.A. *Journal of Plankton Research* **3,** 81–91.

Heinbokel, J. F. 1978 Studies on the functional role of tintinnids in the Southern California Bight 1. Grazing and growth rates in laboratory cultures. *Marine Biology* **47,** 177–189.

Kimor, B. & Goldansky-Baras, B. 1981 Distribution and ecology of the tintinnids in the Gulf of Elat (Aqaba), Red Sea. *Journal of Plankton Research* **3,** 445–459.

Krsinic, F. 1987 On the ecology of tintinnines in the Bay of Mali Ston (Eastern Adriatic). *Estuarine Coastal and Shelf Science* **24,** 401–418.

Laval-Peuto, M. & Rassoulzadegan, F. 1988 Autofluorescence of marine planktonic Oligotrichina and other ciliates. *Hydrobiologia* **159,** 99–110.

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* **4(suppl.),** 147–157.

Lessard, E. I., Brownlee, D. C. & Caron, D. A. 1988 Role of microzooplankton biomass, growth and grazing in plankton dynamics in Chesapeake Bay (abstract). *Eos* **69,** 1103.

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.

Malone, T. C., Crocker, L. H., Pike, S. E. & Wendler, B. W. 1988 Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Marine Ecology Progress Series* **48,** 235–249.

Middlebrook, C. W., Emerson, C. W., Roff, J. C. & Lynn, D. H. 1987 Distribution and abundances of tintinnids in the Quoddy region of the Bay of Fundy. *Canadian Journal of Zoology* **65,** 594–601.

Montagnes, D. J. S., Lynn, D. H., Roff, J. C. & Taylor, W. D. 1988 The annual cycle of heterotrophic planktonic ciliates in the waters surrounding the Isles of Shoals, Gulf of Maine: an assessment of their trophic role. *Marine Biology* **99,** 21–30.

Olson, M. M. 1987 Zooplankton. In: *Ecological Studies in the Middle Reach of Chesapeake Bay* (Heck, K. L. Jr. ed.). New York: Springer-Verlag, pp. 38–81.

Pace, M. L. 1982 Planktonic ciliates: their distribution, abundance, and relationship to microbial resources in a monomictic lake. *Canadian Journal of Fisheries and Aquatic Science* **39,** 1106–1116.

Paranjape, M. A. 1987 The seasonal cycles and vertical distribution of tintinnines in Bedford Basin, Nova Scotia, Canada. *Canadian Journal of Zoology* **65,** 41–48.

Psenner, R. & Scholtt-Idl, K. 1985 Trophic relationships between bacteria and protozoa in the hypolimnion of a meromictic mesotrophic lake. *Hydrobiologia* **121,** 111–120.

Revelante, N. & Gilmartin, M. 1983 Microzooplankton distribution in the Northern Adriatic Sea with emphasis on the relative abundance of ciliated protozoans. *Oceanologica Acta* **6,** 407–415.

Revelante, N. & Gilmartin, M. 1987 Seasonal cycle of the ciliated protozoan and micrometazoan biomass in a gulf of Maine estuary. *Estuarine Coastal and Shelf Science* **25,** 581–598.

Revelante, N., Gilmartin, N. & Smodlaka, N. 1985 The effects of Po River induced eutrophication on the distribution and community structure of ciliated protozoa and micrometazoan populations in the northern Adriatic Sea. *Journal of Plankton Research* **7,** 461–471.

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

Sanders, R. W. 1987. Tintinnids and other microzooplankton-seasonal distributions and relationships to resources and hydrography in a Maine estuary. *Journal of Plankton Research* **9,** 65–67.

Schubel, J. R. & Pritchard, D. W. 1986 Responses of upper Chesapeake Bay to variations in discharge of the Susquehanna River. *Estuaries* **9,** 236–249.

Seliger, H. H., Boggs, J. A. & Biggley, W. H. 1985 Catastrophic anoxia in the Chesapeake Bay in 1984. *Science* **228,** 70–73.

Sellner, K. G. 1987. Phytoplankton in Chesapeake Bay: role in carbon, oxygen and nutrient dynamics. In: *Containment Problems and Management of Living Chesapeake Bay Resources* (Majumdar, S. K., Hall, L. W. Jr. & Austin, H. M. eds). Easton, PA: Pensylvania Academic Science, pp. 134–157.

Sellner, K. G., Brownlee, D. C. & Harding, L. W. Jr. 1987 Implications of microzooplankton grazing on carbon flux and anoxia in Chesapeake Bay. In: *Dissolved Oxygen in the Chesapeake Bay* (University Maryland Sea Grant) (publication no. UM-SG-TS-87-03). College Park, MD: Maryland Sea Grant College, pp. 86–90.

Sherr, E. & Sherr, B. 1988 Role of microbes in pelagic food webs: a revised concept. *Limnology and Oceanography* **33,** 1225–1227.

Sherr, B. F., Sherr, E. B. & Newell, S. Y. 1984 Abundance and productivity of heterotrophic nanoplankton in Georgia coastal waters. *Journal of Plankton Research* **6,** 195–202.

Sherr, B. F., Sherr, E. B. & Hopkinson, C. S. 1988 Trophic interactions within pelagic microbial communities: indications of feedback regulation of carbon flow. *Hydrobiologia* **159,** 19–26.

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

Smetacek, V. 1981 The annual cycle of protozooplankton in the Kiel Bight. *Marine Biology* **63,** 1–11.

Smith, W. O. & Barber, R. T. 1979 A carbon budget for the autotrophic ciliate *Mesodinium rubrum*. *Journal of Phycology* **15,** 27–33.

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

Stoecker, D. K. & Sanders, N. K. 1985 Differential grazing by *Acartia tonsa* on a dinoflagellate and a tintinnid. *Journal of Plankton Research* **7,** 85–100.

Stoecker, D. K. & Egloff, D. A. 1987 Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. *Journal of Experimental Marine Biology and Ecology* **110,** 53–68.

Stoecker, D. R., Guillard, R. L. & Kavee, R. M. 1981 Selective predation by *Favella ehernbergii* (Tintinnia) on and among dinoflagellates. *Biological Bulletin* **160,** 136–145.

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., Verity, P. G., Michaels, A. E. & Davis, L. H. 1987*a* Feeding by larval and post-larval ctenophores on microzooplankton. *Journal of Plankton Research* **9,** 667–683.

Stoecker, D. K., Michaels, A. E. & Davis, L. H. 1987*b* Grazing by the jellyfish, *Aurelia aurita*, on microzooplankton. *Journal of Plankton Research* **9,** 901–915.

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

Strickland, J. R. & Parsons, T. R. 1972 A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board of Canada*, No. 167.

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

Turner, J. T. & Anderson, D. M. 1983 Zooplankton grazing during dinoflagellate blooms in a Cape Cod embayment, with observations of predation upon tintinnids by copepods. *P. S. Z. N. I: Marine Ecology* **4,** 359–374.

Tyler, M. A. & Seliger, H. H. 1978 Annual subsurface transport of a red tide dinoflagellate to its bloom area: water circulation patterns and organism distributions in the Chesapeake Bay. *Limnology and Oceanography* **23,** 227–246.

Utermöhl, H. 1958 Zur Vervollkommnung der Qualititativen phtyoplankton-Methodik. *Mitteilungen der Internationalen Vereinigung fur Limnologie* **9,** 1–38.

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

Verity, P. G. 1986 Growth rates of natural tintinnid populations in Narragansett Bay. *Marine Ecology Progress Series* **29,** 117–126.

Verity, P. G. & Stoecker, D. R. 1982 Effects of *Olisthodiscus luteus* on the growth and abundance of tintinnids. *Marine Biology* **72,** 79–87.

Verity, P. G. & Villareal, T. A. 1986 The relative food value of diatoms, dinoflagellates, flagellates, and cyanobacteria for tintinnid ciliates. *Archive fur Protistenkunde* **131,** 71–84.

Wiadnyana, N. N. & Rassoulzadegan, F. 1989 Selective feeding of *Acartia clausi* and *Centropages typicus* on microzooplankton. *Marine Ecology Progress Series* **53,** 37–45.

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.