Microzooplankton Assemblages: Their Distribution, Trophic Role and Relationship to the Environmental Variables

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The distribution of microzooplankton and hydrographic variables were measured in the Virginia portion of Chesapeake Bay and its major rivers. Samples were collected at 14 locations at monthly interval from September 1993 through December 1995. Ciliates were numerically dominated (>90%) and copepod nauplii comprised highest proportion of the total microzooplankton biomass (>77%). Copepod nauplii and ciliates were the most abundant at oligohaline water and rotifers at freshwater. Total microzooplankton density and biomass were usually higher at oligohaline stations than fresh water and polyhaline stations. Despite high nutrient concentration and phytoplankton density at eutrophic water, micro- and mesozooplankton biomass were low. Mesozooplankton were relatively abundant at polyhaline stations. The comparison between annual mean biomass of ciliates (12.7 µgC/l) and that of autotrophic picoplankton (13.5 µgC/l) revealed that ciliates were a major consumer of picoplankton production. The secondary production by ciliates was 12.7 µgC/l/day, representing 5% of the annual mean primary production in Chesapeake Bay. Total microzooplankton comprised 84% of the total zooplankton carbon content, representing five times higher than mesozooplankton biomass.

INTRODUCTION

Zooplankton play an important role in the aquatic ecosystem by as links between primary producers and higher trophic levels in the nekton and benthos. These zooplankton components usually include micro-(20~200 µm) and mesozooplankton (200~2,000 µm). In the Chesapeake Bay and its rivers, they consist primarily of ciliates, copepods and rotifers (Birdsong et al., 1987, 1988, 1989; Brownlee and Jacobs, 1987; Park and Marshall, 1993; Park, 1997).

In 1960's and 1970's most plankton researches were focused on the phytoplankton and mesozooplankton in various aquatic systems.

Since Pomeroy (1974) proposed a new paradigm in which the microzooplankton played an important role in a microbial loop, many aquatic ecologists have recently studied the ecology and trophic role of microzooplankton mainly focused on ciliates (Beers et al., 1980; Smetacek, 1981; James and Hall, 1995). However, the microzooplankton have generally received less study than the mesozooplankton and rarely have both groups been studied concurrently. A few recent studies compared the microzooplankton proportion in a whole zoo-

plankton community and revealed that microzooplankton comprised over 50% of the total zooplankton biomass (Beaver and Crisman, 1982; Pace, 1986; Buskey, 1995).

Williams (1981) reported that as much as 50% of primary production may pass to the microheterotrophs. Although the ecology of microzooplankton has been widely studied since the 1980's, the field is somewhat lagging the studies of phytoplankton and mesozooplankton.

The first distributional survey of microzooplankton in Chesapeake Bay was conducted by Wolfe et al. in 1926. Except for the reference to their presence and abundance in the study by Park and Marshall (1993), the microzooplankton of the lower bay is unknown despite some 70 years of plankton records and a considerable number of published works on the phytoplankton (Marshall, 1966, 1980, 1982; Marshall and Lacouture, 1986; Marshall and Cohn, 1987; Marshall and Alden, 1990; Ray et al., 1989; Birdsong et al., 1987, 1988, 1989) and mesozooplankton (Jacobs et al., 1985; Birdsong et al., 1987, 1988, 1989). In the upper bay, the ciliates and rotifers have been investigated by Brownlee and Jacobs (1987), Dolan and Coats (1990, 1991), Dolan (1991), and Dolan and

Gallegos (1992). Even from these studies, they have partially shown the zooplankton community, and overall distribution patterns and trophic roles of microzooplankton are still unknown.

Accordingly, this study presents the relative contribution of microzooplankton to the total zooplankton components and relationships to the environmental variables, and also compares the secondary production by microzooplankton over the primary production.

METHODS

The study was conducted at 14 stations in the southern portion of the Chesapeake Bay and its major rivers from September 1993 through December 1995. Locations of each station are shown in Fig. 1. The station locations were designed to sample along with salinity gradients from the polyhaline bay mouth to tidal freshwater regions. Whole water samples were taken to collect a more accurate representation of the microzooplankton (Beers and Stewart, 1967; Brownlee and Jacobs, 1987). Two 15 liter carboys were filled at the station with a battery powered bilge pump, taken from a vertical series of 5 depths above the

Fig. 1. Location of sampling stations in the Chesapeake Bay and tributaries.

pycnocline. A 1 liter sub-sample was taken from each carboy and immediately preserved with Lugol' s solution (10 ml).

Most counts were performed with an inverted microscope at 100X-200X. Ciliate cell volumes were calculated using an appropriate geometric formula based on their sizes and shapes, and tintinnid cell volumes were considered as 1/2 the lorica volume (Beers and Stewart, 1969). Biomass estimations employed conversion of cell volumes to dry weight and to carbon using a conversion factor of 0.279 pg dry wt/μm^3 (Gates et al. 1982) and 0.19 pgC/μm^3 (Putt and Stoecker, 1989) respectively.

To estimate dry weight of copepod nauplii, body lengths were converted to dry weights using published length-dry weight regressions (McCauley, 1984) and then the dry weight to carbon content with 32.00% of dry weight for marine copepod (Wiebe et al., 1975) and 30.33% of freshwater copepods (Schram and Schmitz, 1983).

In the case of rotifers, biovolumes were calculated from the approximate geometric dimension, converted to dry weight (Ruttner-Kolisko, 1977; Pace, 1982) and to carbon with 50% of dry weight (Salonen et al., 1976).

To identify ciliates and picoplankton relationship at the eight stations in the Bay and Elizabeth River, carbon content of autotrophic picoplankton was estimated with a conversion factor of 210 fgC/cell (Waterbury et al., 1986) in 1994. Mesozooplankton biomass (as dry weight) values were also converted to carbon content, using the same approximations for copepod (Wiebe et al., 1975).

The secondary production of ciliates was estimated from biomass values, assuming an average generation time of one day (Lynn and Montagnes, 1991).

Physical and chemical factors were measured for analysis of species-to-environmental factor associations. Salinity, water temperature, dissolved oxygen, and pH were measured at one meter interval over the whole depths with Hydro-Lab (Model H20, Hydro-Lab Corporation). Transparency was also measured with Secchi disk. Chlorophyll, primary productivity and nutrient data were provided by the Applied Marine Research Laboratory at Old Dominion University. The phytoplankton and zooplankton data were provided from the Chesapeake Bay Plankton Monitoring Program.

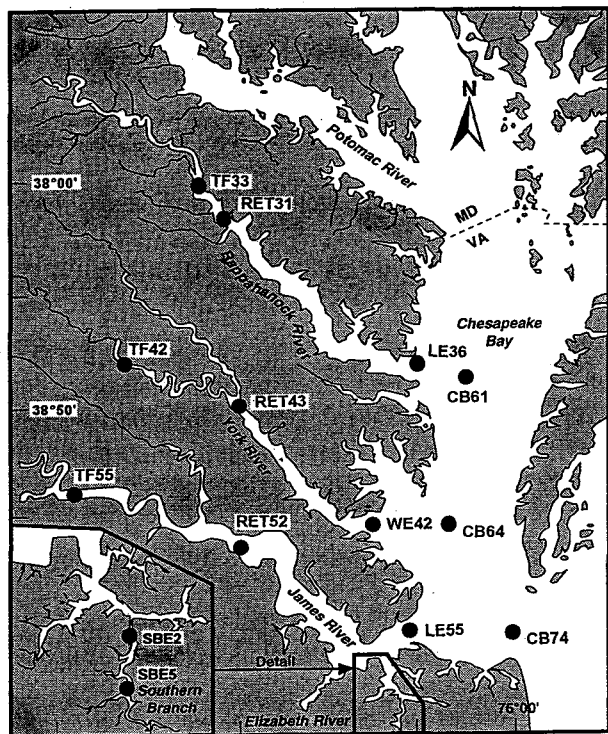Spearman's correlation analysis was performed to

identify relationships between the environmental variables and zooplankton biomass at the eight stations in the Bay and Elizabeth River. SAS (SAS Institute, 1983) programs were used for the statistical analysis.

RESULTS

Physical and chemical properties

Descriptive statistics of water qualities are given in Table 1. Annual mean salinities ranged from zero to 26.6‰, with lowest in the two tidal freshwater stations (TF42, TF55) and highest in the Bay entrance (CB74). Usually, river estuary transition sites (RET31, RET43, RET52) were oligohaline, river mouth (LE36, WE42, LE55) and mid bay (CB 61, CB64) mesohaline, and bay mouth (CB74)

polyhaline water. TF33 was sporadically experienced to salt water intrusion, reaching up to 10.1‰. Water temperatures showed typical patterns of temperate zones. Higher temperature at SBE5 was due to the cooling water input from the power plant near the station. DO values between stations were not different except hypereutrophic Elizabeth River (SBE2, SBE5). pH was higher at bay stations than at the freshwater and Elizabeth River stations. Secchi depths were approximately half meter at the tributary stations, and 1~2 meters at the bay stations.

Abundance and distribution of microzooplankton

The geographical heterogeneity of microzooplankton abundance and biomass is described and discussed using the data from September 1993 through December 1995 for the density, and from January 1994 through December 1995 for biomass.

Total microzooplankton: Ciliates were the major component of microzooplankton, comprising over 90% of the total microzooplankton density. The highest annual mean concentration of total microzooplankton was at station RET31, with 7,145 ± 854 cells/l, and the lowest concentration was 3,254 ± 475 cells/l at station TF42 (Table 2). Annual mean microzooplankton biomass ranged from 196.4 ± 51.7 at station RET31 to 48.3 ± 8.9 μg dry wt/l at station TF42 (Table 3). The spatial variation pattern of microzooplankton biomass coincided with that of copepod nauplii density since copepod nauplii contributed over 77% of the total microzooplankton biomass. Low biomass values were at station TF42 and TF55, which had low concentrations of copepod nauplii. In general, microzooplankton were

Table 1. Descriptive statistics of environmental variables in Chesapeake Bay and tribuataries from May 1993 through April 1995. Values are mean ± one standard error of the mean

Sites	Salinity (‰)	Temperature (°C)	DO (mg/l)	pH	Secchi Depth (m)
TF42	0.0±0.0	16.8±1.9	9.1±0.6	7.1±0.1	0.6±0.0
TF55	0.1±0.0	17.4±1.8	10.1±0.4	7.4±0.1	0.5±0.0
TF33	1.6±0.5	16.1±1.9	10.2±0.5	7.1±0.1	0.5±0.0
RET52	2.5±0.8	17.0±1.7	10.2±0.4	7.6±0.1	0.6±0.1
RET31	4.6±0.8	16.0±1.8	10.4±0.5	7.1±0.1	0.5±0.1
RET43	9.2±1.0	16.8±1.8	9.6±0.5	7.1±0.1	0.5±0.0
LE36	15.6±0.7	15.1±1.8	9.7±0.4	8.0±0.1	2.0±0.2
CB61	16.3±0.8	14.9±1.8	10.0±0.5	8.0±0.1	2.0±0.2
SBE5	16.8±1.0	19.8±1.7	7.1±0.5	7.2±0.1	1.2±0.1
SBE2	17.5±1.1	17.9±1.7	7.5±0.5	7.3±0.1	1.4±0.2
WE42	19.0±0.7	16.0±1.7	9.8±0.5	8.0±0.1	1.6±0.1
CB64	19.7±0.7	15.1±1.7	9.4±0.4	8.1±0.0	1.8±0.1
LE55	20.3±0.8	15.4±1.6	9.3±0.4	8.0±0.0	1.3±0.1
CB74	26.6±0.8	14.5±1.5	9.3±0.3	8.0±0.1	1.9±0.1

Table 2. Annual mean values of microzooplankton density (cells/l) at each station from September 1993 through December 1995. Values are mean ± one standard error of the mean

Sites	Copepod nauplii	Rotifers	Loricated ciliates	Aloricated ciliates	Total microzooplankton
CB61	119±31	97± 32	1,954± 425	3,149±598	5,318± 766
CB64	109±23	47± 18	1,898± 419	3,359±604	5,414± 804
DB74	112±19	34± 11	2,128± 652	3,263±644	5,540±1,081
LE36	83±19	92± 32	1,805± 266	3,375±586	5,355± 643
WE42	119±21	88± 28	1,953± 309	2,867±470	5,027± 643
LE55	106±18	81± 24	2,113± 293	3,098±504	5,398± 675
RET31	180±57	633±284	3,255± 567	3,077±621	7,145± 854
RET43	121±19	187± 51	2,639± 566	3,925±772	6,873± 995
RET52	135±25	438±103	2,952± 810	2,095±306	5,619± 936
SBE2	89±24	128± 37	949± 278	3,167±511	4,333± 646
SBE5	120±28	171± 68	997± 170	3,117±481	4,404± 528
TF33	158±33	401±139	3,018±1,047	2,850±852	6,427±1,387
TF42	55±12	261± 83	968± 340	1,969±305	3,254± 475
TF55	49±11	703±141	1,544± 255	3,107±558	5,403± 726

Table 3. Annual mean values of microzooplankton biomass (μg dry wt/l) at each station from January 1994 through December 1995. Values are mean±one standard error of the mean

Sites	Copepod nauplii	Rotifers	Loricated ciliates	Aloricated ciliates	Total microzooplankton
CB61	92.5±24.7	3.1±1.1	6.7±2.6	15.1±2.7	117.4±25.2
CB64	82.6±19.0	1.7±0.7	7.1±1.9	15.3±4.0	106.7±19.0
CB74	81.6±15.5	1.1±0.4	8.2±2.1	10.5±2.1	101.4±15.4
LE36	67.4±15.6	2.8±0.9	7.2±2.3	14.0±2.5	91.4±15.7
WE42	90.8±17.8	3.1±1.0	6.3±0.9	14.5±2.8	114.7±17.8
LE55	80.2±14.6	2.2±0.6	7.6±1.0	16.6±3.6	106.6±15.0
RET31	156.6±50.9	12.9±6.2	13.2±2.8	13.7±3.8	196.4±51.7
RET43	90.9±14.7	3.6±1.1	9.2±2.2	19.1±3.8	122.8±15.9
RET52	111.6±22.5	9.7±2.1	10.1±2.2	12.1±3.6	143.5±25.1
SBE2	77.0±21.8	2.7±0.8	3.6±1.3	12.0±3.6	95.3±22.1
SBE5	90.9±23.1	2.5±1.0	3.1±0.6	13.5±3.5	110.0±22.7
TF33	127.9±29.5	8.7±3.1	9.1±2.7	6.3±1.3	152.0±30.4
TF42	36.1± 7.6	4.4±1.6	2.4±0.9	5.3±0.8	48.3± 8.9
TF55	42.6±10.1	16.1±3.9	5.7±1.2	15.7±3.7	80.1±13.8

abundant at oligohaline water, with low at station TF42 and the Elizabeth River stations.

Copepod nauplii: Copepod nauplii were the most abundant at the oligohaline stations, with an annual mean density between 120 and 180 inds/l. The highest annual mean density was at station RET31, with 180±57 inds/l. The low concentrations were at the two tidal freshwater stations (TF55, TF42), with 49±11 inds/l and 55±12 inds/l, respectively. High monthly variations at station RET31 were due to the exceptional increase of copepod nauplii, reaching up to 1,400 inds/l in May 1994. Copepod nauplii biomass was also high at the oligohaline stations and low at the freshwater stations, and ranged from 36.1±7.6 at station TF42 to 156.6±50. 9 μg dry wt/l at station RET31. Most meso- and polyhaline stations had 80 to 90 μg dry wt/l in copepod nauplii biomass (Table 3). Copepod nauplii biomass was a major component of the total microzooplankton biomass throughout the stations (77% of the total biomass as an annual average), but their relative contribution to the total microzooplankton biomass was low at freshwater stations during summer and fall. At station TF55, their contribution was significantly lower (<50%) due to the relatively high contribution by rotifers and aloricated ciliates (Fig. 2). At meso- and polyhaline stations, the contribution of copepod nauplii was relatively higher than that at freshwater stations, but during winter their contribution was less than 50% of the total biomass due to the high density of rotifers (mainly *Syncheata* spp.).

Rotifers: Rotifers showed the greatest spatial variations among the microzooplankton components. They were abundant at tidal freshwater and oligo-
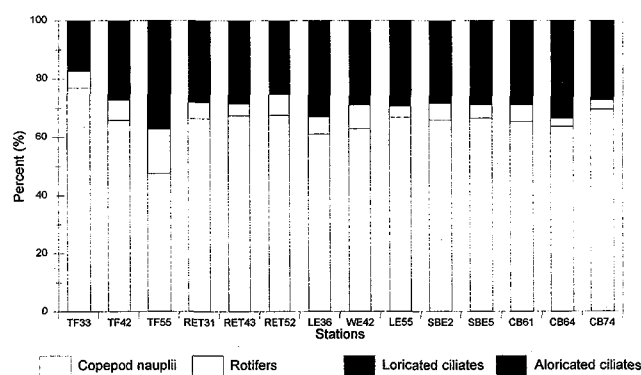

Fig. 2. Microzooplankton biomass composition using the annual means from January 1994 through December 1995. The percentages are based on the biomass of each microzooplankton component as a μg dry wt/l.

haline water. The highest annual mean concentration was 703±141 inds/l at station TF55. The bay mouth and mid bay stations showed very low density, with annual mean ranges between 34 and 100 inds/l (Table 2). The highest concentration occurred in August 1995 at station RET31, reaching up to 7,000 inds/l. The annual mean biomass ranged from 1.1±0.4 μg dry wt/l at the bay entrance (CB 74) to 16.1±3.9 μg dry wt/l at the tidal freshwater station (TF55). Most meso-and polyhaline stations had less than 3.0 μg dry wt/l in rotifer biomass (Table 3). During summer, rotifer biomass at tidal freshwater stations was comparable to the total ciliate biomass, comprising 10 to 20% of the total microzooplankton biomass, but their contribution at the meso- and polyhaline stations was less than 3%. On the other hand, rotifers were a major component of the microzooplankton biomass during winter at the mesohaline bay stations, occupying 10 to 15%

of the total microzooplankton biomass. However, their relative contribution was less than 5% at the tidal freshwater stations. During spring and fall, rotifers comprised the smallest proportion of the total microzooplankton biomass, although some stations (TF55, WE42) had relatively higher values. In general, annual mean biomass of rotifers was high at the tidal freshwater stations (Fig. 2).

Loricated ciliates: Oligohaline stations (TF33, RET31, RET52) indicated high concentrations of loricated ciliates, with an annual average of about 3,000 cells/l. However, station TF42 (York River) and the two stations in the Elizabeth River were consistently low in the density of loricated ciliates, less than 1,000 cells/l (Table 2). High biomass also occurred at the oligohaline stations and lower values in the Elizabeth River and at station TF42 (Table 3). The highest biomass was observed at station RET31 (13.2 μg dry wt/l), and the lowest at station TF42 (2.4 μg dry wt/l). The lowest contribution was during summer, due to the high abundance of rotifers and copepod nauplii, comprising less than 5% of the total microzooplankton biomass at meso- and polyhaline stations. However, at freshwater stations, their contribution increased to over 10%. The highest values occurred during winter throughout the stations, representing approximately 20% of the total biomass, due to the relatively low biomass of copepod nauplii. Throughout the seasons, loricated ciliate comprised the

lowest proportion of the total biomass at the hypereutrophic Elizabeth River (Fig. 2).

Aloricated ciliates: Aloricated ciliates represented a major microzooplankton component, comprising 60% of the total density. The high abundances occurred at stations RET43, LE36 and CB64 (3,400~3,900 cells/l). The low values were observed at stations RET52 and TF42, where there was an annual mean of 2,095 and 1,969 cells/l, respectively (Table 2). Biomass ranged from 5.3 to 19.1 μg dry wt/l (Table 3). The highest contribution was during winter at the Elizabeth River stations, where they represented approximately 50% of the total microzooplankton biomass, and the smallest contribution during summer. This was due to the high abundance of copepod nauplii at bay stations and high density of rotifers at freshwater and oligohaline stations. During spring and fall, their mean contribution was approximately 20%, with some exceptions.

Statistical analysis

Spearman's correlation analysis was performed to identify relationships between zooplankton biomass and the environmental variables at the eight stations in the bay and Elizabeth River. Six tributary stations were excluded from the analysis due to the absence of reliable nutrient and chlorophyll data. There was a significant negative correlation between copepod

Table 4. Spearman's correlation coefficients between biomass of zooplankton components and environmental variables. Annual mean values for each station were used from 8 stations in the Bay and Elizabeth River in 1994. Top numbers are correlation coefficients and bottom numbers are the calculated probabilities. Significant correlations are indicated by bold numbers

	Copepod nauplii	Rotifers	Loricated ciliates	Aloricated ciliates	Total microzoo plankton	Total mesozoo plankton
Chlorophyll a (μg/l)	-0.6429 0.0856	0.2928 0.4816	-0.4286 0.2894	0.5000 0.2070	-0.5714 0.1390	-0.6191 0.1017
Primary productivity (μgC/l/hr)	-0.4762 0.2329	0.2196 0.6013	-0.6905 0.0580	**0.9762 0.0001**	-0.3810 0.3518	-0.3095 0.4556
Salinity (‰)	0.6231 0.1017	-0.5124 0.1942	0.5476 0.1600	0.0714 0.8665	0.5476 0.1600	**0.7143 0.0465**
Dissolved oxygen (mg/l)	0.4762 0.2329	0.3660 0.3726	0.4048 0.3199	-0.3571 0.3851	0.5714 0.1390	0.3095 0.4556
pH	0.6467 0.0831	-0.0982 0.8171	0.6347 0.0909	-0.2755 0.5091	0.6827 0.0621	**0.7665 0.0265**
Water temperature (°C)	-0.571 0.1390	0.4636 0.2473	**-0.9762 0.0001**	**0.7619 0.0280**	-0.4524 0.2604	-0.6191 0.1017
Total dissolved nitrogen (μg/l)	**-0.7381 0.0366**	0.4880 0.2199	**-0.7857 0.0208**	0.1905 0.6514	-0.6667 0.0710	**-0.8810 0.0039**
Total dissolved phosphorus (μg/l)	-0.4762 0.2329	0.6343 0.0912	**-0.8810 0.0039**	0.3810 0.3518	-0.3810 0.3518	**-0.8810 0.0039**

nauplii and mesozooplankton biomass, and nutrient concentration (Table 4). Aloricated ciliates positively related to primary productivity (r=0.98, p< 0.0001) and water temperature (r=0.76, p=0.03). This was due to the high aloricated ciliate biomass in the Elizabeth River, where water temperature and primary productivity were relatively high. Total mes-

ozooplankton biomass were significantly correlated with pH (r=0.77, p=0.03) and salinity (r=0.71, p< 0.05) because of the high biomass at polyhaline stations. On the other hand, there was no significant correlation between chlorophyll a and dissolved oxygen, and zooplankton biomass. In general, phy-sicochemical variables had more persistent cor-
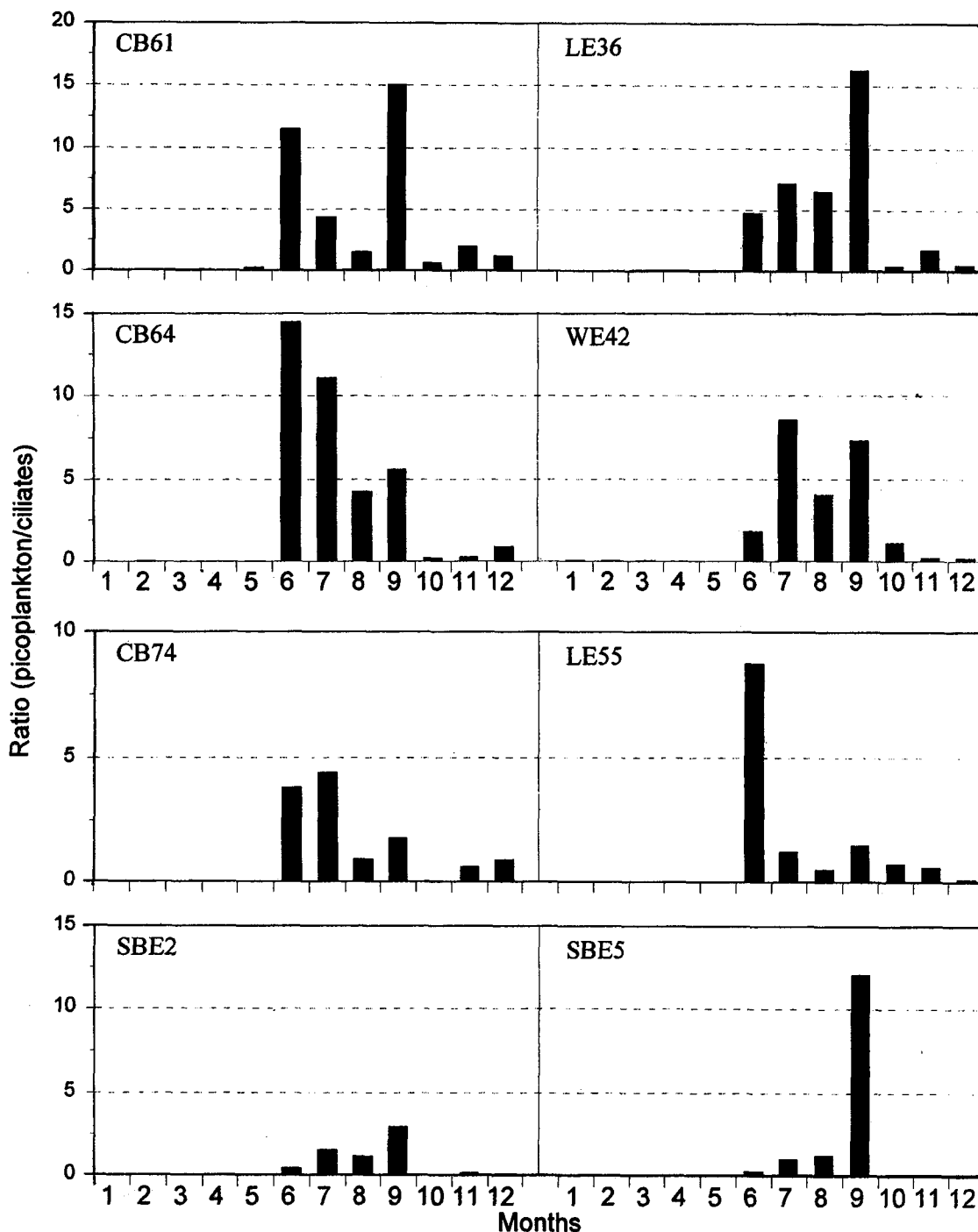

Fig. 3. Monthly variation of autotrophic picoplankton : ciliates biomass ratios (carbon) in Chesapeake Bay and the Elizabeth River from January through December 1994.

relation than biological parameters.

Contribution of microzooplankton to the total plankton components

Total microzooplankton represented 84% of the total zooplankton biomass, with a grand mean of 37.74 μgC/l during 1994 at the bay and Elizabeth River stations. Copepod nauplii comprised the highest biomass of the total zooplankton throughout seasons, with the annual mean of 23.82 ± 2.19 μgC/ l and annual mean percent of $47.5 \pm 2.7\%$. Rotifers had the smallest biomass (1.26 μgC/l) and proportion (4.5%) of the total zooplankton biomass. Ciliates contributed 33.5% of the total biomass, with annual average biomass of 12.66 ± 1.28 μgC/l. Microzooplankton were major components of total zooplankton (85.5%), representing six times higher than mesozooplankton biomass (14.5%). The ratios of autotrophic picoplankton and ciliate biomass by stations are plotted to identify the relative abundance of prey and predator through seasons (Fig. 3). The ratios ranged from zero to fifteen. During winter and spring, the ratios were near zero at most stations. During fall (October-December), autotrophic picoplankton biomass was at similar ranges with the ciliate biomass at most stations. Summer (June-September) was the only season during which picoplankton biomass exceeded ciliate biomass at all the stations. Picoplankton biomass exceeded the ciliate up to 15 times, but at some stations (CB74, SBE2) the ratios were less than 5 times. In general, ciliate biomass exceeded picoplankton biomass except summer months (June-September). The annual mean biomass of picoplankton (13.45 μgC/l) was comparable to the total ciliates biomass (12.66 μgC/l). The secondary productivity by ciliates was about 13 μgC/l/day, representing 5% of total primary production.

DISCUSSION

Heterotrophic ciliates and copepod nauplii were a major component of microzooplankton. Microzooplankton represented over 85% of the total zooplankton carbon contents. Copepod nauplii contributed the highest portion of the total zooplankton biomass (47.5%). Ciliates and rotifers represented 33.5% and 4.5% respectively. Mesozooplankton (mainly copepods and barnacle nauplii) constituted only 14.5% of the total zooplankton biomass (annual

mean). From the literature and the present study, microzooplankton are a major component of the total zooplankton biomass, comprising over 50% in the various aquatic ecosystems (Buskey, 1993; James and Hall, 1995; Bays and Crisman, 1983; Pace, 1986). However, it is difficult to compare zooplankton composition from study to study due to the different sampling methods, or conversion factors to estimate zooplankton biomass.

Dominant genera were Tintinnopsis for the loricated ciliates, with Strombidium and Strobilidium for the aloricated ciliates, and Trichocerca, Polyarthra, and Synchaeta for the rotifers.

The high abundance and biomass of total microzooplankton occurred usually at oligohaline sites. Copepod nauplii were abundant at the oligohaline and mesohaline stations but low at the freshwater stations (TF55, TF42). The density differences in copepod nauplii between freshwater and salt water systems are due to the different mesozooplankton species composition between two systems. Although cladocerans such as Bosmina longirostris and Diaphanosoma brachyurum are the dominant taxa in the freshwater zone of Chesapeake Bay tributaries (Birdsong et al, 1989), they have no nauplius stage during their development. The parthenogenetic eggs of cladocerans are developed in the brood chamber and hatched into young similar in form to the adults (Pennak, 1989). Accordingly, metazoan nauplii were not abundant at the freshwater stations. In contrast, copepods were a major component of the mesozooplankton in Chesapeake Bay and these were mainly composed of Acartia spp. (Birdsong et al., 1989).

Some physicochemical variables were significantly correlated with zooplankton biomass. The relationships, however, were not persistent. No consistency in the correlation coefficients may be due to narrow environmental gradients in some parameters. In the case of salinity, the gradient across the meso- and polyhaline stations was much smaller than when it was expanded to the freshwater stations. When considering all the stations from freshwater to polyhaline water, salinity was the most critical factor found to explain the spatial variations of rotifer density. Using annual mean values of salinity, rotifer biomass, and density from 14 stations, salinity had a significant negative correlation with both rotifer biomass ($r=-0.79$, $p< 0.001$) and density ($r=-0.92$, $p<0.0001$).

Loricated ciliate density was consistently asso-

ciated with nutrient concentration. There was a significant negative correlation between loricated ciliate density and nutrient concentration (TP, TN). Their abundance and biomass were significantly lower in the hypereutrophic Elizabeth River than that at meso- or eutrophic stations, and the relative contribution of loricated ciliate biomass to the total microzooplankton biomass in the River was also lower than at other stations ($\approx 5\%$). However, aloricated ciliates showed a weak positive correlation with nutrient concentrations. This difference in the correlation of two different ciliate categories indicated that they may have different ecological requirements in this system. During winter, the relative contribution of aloricated ciliate biomass to the total biomass exceeded 50% in the hypereutrophic Elizabeth River stations, but less than 30% at the meso- or eutrophic bay stations.

A few studies reported community shift toward ciliates with trophy increase. Bays and Crisman (1983, 1989) found in 35 Florida lakes an increase in the percentage of microzooplankton relative to total zooplankton biomass and abundance with lake trophic states. Pace (1986) also reported a significant correlation between microzooplankton biomass and total phosphorus from 12 lakes in Canada, but he didn't find a community shift toward microzooplankton with lake trophy increase. Mathes and Arndt (1994) also found the contribution of protozoans (mainly oligotrich ciliates) to

the total zooplankton (including metazoans) biomass increased from 20% in meso- or eutrophic lakes to about 50~60% in hypereutrophic lakes in 9 German lakes. Schoenberger (1994) in Neusiedler See (Austria and Hungary) found the planktonic ciliate community was dominated by tintinnids (*Tintinnopsis cylindrata*) in the open lake, whereas in a brown-water pond, small oligotrichs (*Strobilidium* spp.) prevailed. However, Laybourn-Parry and Rogerson (1993) reported an oligotrich-dominated ciliate community in an oligotrophic basin and a tintinnid-dominated community in the eutrophic basin of Lake Windermere, England.

Based on this study and among others, the aloricated ciliates seem to be more opportunistic and abundant within the eutrophic systems than the loricated ciliates. Mass occurrence events of oligotrichs can support this assumption. Dale and Dahl (1987) found a mass development of oligotrichs that exceeded two million oligotrichs per liter. Moreover, aloricated ciliates outnumbered loricated ciliates during most sampling months in this study.

Some significant correlations from the literature between microzooplankton and the environmental variables are given in Table 5. However, it must be noted that with a correlation analysis, some significant correlations could occur by chance alone (Rice, 1989), and may depend on the environmental gradients and number of observations. Sampling

Table 5. Results of correlation analysis between microzooplankton and environmental variables. ns: not significant, +: significant positive correlation, -: significant negative correlation

Sites	Variable I	Variable II	Pattern	Reference
Upper Chesapeake Bay	ciliates	heterotrophic flagellates	+	Dolan & Coats (1990)
Maine estuary	tintinnids	water temperature DO	+ -	Sanders (1987)
Kiel Bight, Germany	heterotrophic dinofl. & ciliate biomass	phytoplankton biomass metazooplankton biomass	+ -	Smetacek (1981)
West coast of South Is. New Zealand	ciliates	sigma-*t* chlorophyll particulate nitrogen	- + +	James & Hall (1995)
Nueces estuary	microzooplankton	water temperature, salinity and chlorophyll *a*	ns	Buskey (1993)
Lake Esthwaite, UK	ciliates	flagellates chlorophyll *a*	+ ns	Laybourn-Parry *et al.* (1990)
12 lakes in Canada	ciliates rotifers nauplii microzooplankton (biomass)	chlorophyll *a* chlorophyll *a* chlorophyll *a* total phosphorus	+ + + +	Pace (1986)
Lake Windermere, UK	ciliates	chlorophyll *a* flagellates	ns ns	Laybourn-Parry & Rogerson (1993)

periods, sampling intervals and geographical scales are also major factors for obtaining reliable results since the small ciliate densities are highly variable in time and space, due to their high specific growth rates, short generation time (Laybourn-Parry, 1992) and formation of micro-scale patches (Fenchel, 1987).

In an estuarine system, tidal effects also reduce the consistency in statistical analysis because plankton abundances and their composition are highly variable in regard to the tidal stages at a given space. Due to these difficulties, no persistent relationships between microzooplankton abundances (or biomass) and the environmental variables have been found in other studies (Table 5).

The trophic role of microzooplankton seems to be very important in Chesapeake Bay. The low autotrophic picoplankton/ciliate biomass ratios suggest that ciliates be able to fully utilize most of the picoplankton production. The ratios were near zero during winter and spring, and approached approximately 1 during fall. However, the ratios during summer reached about 5 to 15. Based on these results, autotrophic picoplankton may not be enough to support ciliate biomass except in summer, when heterotrophic nanoflagellates also consume autotrophic picoplankton (Kuuppo-Leinikki, 1990). The annual mean biomass of ciliates (12.66 μgC/l) was comparable to the autotrophic picoplankton biomass (13.45 μgC/l). On the other hand, total phytoplankton biomass, excluding autotrophic picoplankton, was 331.15 μgC/l for an annual mean from the eight stations in the bay and Elizabeth River, and 7 times higher than the total zooplankton biomass. Based on this comparison, autotrophic picoplankton may not be a major component for primary production in Chesapeake Bay. Accordingly, ciliates could not satisfy their carbon demand from autotrophic picoplankton. This deficiency in food demand for ciliates can be explained by partitioning the food ration. Rassoulzadegan et al. (1988) reported food partitioning based on the various body sizes of ciliates; tintinnids mainly consume nanoplankton (2~20 μm), the small ciliates (<30 μm) take 72% picoplankton and 28% nanoplankton, and the ciliates (30~50 μm) consume 30% pico- and 70% nanoplankton, while the larger ciliates (>50 μm) take nanoplankton exclusively (95% nano- and 5% picoplankton). As a comparison of relative proportion of microzooplankton to phytoplankton, Chang (1990) reported ciliate biomass was up to

49% of the phytoplankton biomass (3.8% in this study), and Hall and Vincent (1990) found autotrophic picoplankton contributed up to 65% of the total phytoplankton biomass (3.9% in this study). The secondary production by total ciliates represented 5% of the annual mean primary production in the Chesapeake Bay. When considering the short generation time and high growth rates of microzooplankton, the microzooplankton should have a great effect on the trophic dynamics in Chesapeake Bay.

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