

Identification of Microzooplankton Seasonality Using Time Series Analysis

Gyung Soo Park* and Harold G. Marshall¹

National Fisheries Research and Development Institute,

West Sea Fisheries Research Institute, Incheon 400-201, Korea;

¹Department of Biological Sciences, Old Dominion University, Norfolk, Va 23529-0266, U.S.A.

Key Words:

Microzooplankton
Seasonality
Time series analysis
Chesapeake Bay

Seasonal changes in microzooplankton abundance were identified in the mesohaline Chesapeake Bay and several tributaries from July 1992 through December 1995. Ciliates numerically dominated, comprising over 90% of the total microzooplankton density and aloricate ciliates usually outnumbered loricate ciliates. Copepod nauplii accounted for the highest microzooplankton biomass (>75% in dry weight). Rotifers made small contributions to the total microzooplankton density and biomass (<5%). Time series analysis indicated a twelve month cycle in microzooplankton abundance, and mid-summer (August) peaks for copepod nauplii, and a spring through fall peaks (May-October) for ciliates. Rotifers showed two seasonal peaks; one in mid-summer (August) at the river stations and the other in mid-winter (February) at the mesohaline stations. Seasonal peaks of copepod nauplii and rotifers coincided with the mesozooplankton abundance peak. On the other hand, ciliate maximum usually occurred between the phytoplankton and mesozooplankton peaks. This pattern of microzooplankton seasonality suggests the intermediate trophic role of microzooplankton (especially ciliates) between the phytoplankton (especially picophytoplankton) and mesozooplankton in Chesapeake Bay and its tributaries.

The Chesapeake Bay is the largest estuary in the United States and is a plankton based ecosystem. The zooplankton act as the trophic intermediates between phytoplankton and bacteria, and higher trophic levels, including many of the economically important fish and shellfish (Brownlee and Jacobs, 1987; EPA, 1987). The Bay is approximately 320 km long and ranges in width from about 6 to 50 km. The water surface of the Bay proper encompasses approximately 5,700 km², with an average depth of 9 m (EPA, 1987).

In the Chesapeake Bay and its tributaries, microzooplankton consist primarily of ciliates, rotifers, and copepod nauplii (Brownlee and Jacobs, 1987; Park and Marshall, 1993; Park and Choi, 1997). Ciliates are the major component of the microbial loop (Pomeroy, 1974; Azam et al., 1983) as a consumer of the dissolved organic matter and picoplankton, and as prey of the metazoans. Williams (1981) reported that as much as 50% of primary production may pass to the microheterotrophs. Seasonal distribution in the abundance of ciliates has well documented from various aquatic systems (Beers and Stewart, 1969; Heinbokel, 1978; Hargraves, 1981; Smetacek, 1981; Sanders, 1987; Nothig and Gowing, 1991; Buskey, 1993; Edwards and

Burkill, 1995; James and Hall, 1995).

The first distributional survey of microzooplankton in Chesapeake Bay was conducted by Wolfe et al. (1926). Despite some 70 years of plankton records and a considerable number of published works on phytoplankton (Marshall and Lacouture, 1986; Marshall and Cohn, 1987; Marshall and Alden, 1990) and mesozooplankton (Jacobs et al., 1985; Birdsong et al., 1987, 1988, 1989), microzooplankton have been poorly studied except recent studies by Park and Marshall (1993) and Park and Choi (1997). In northern Chesapeake Bay, ciliates and rotifers have been discussed by Brownlee and Jacobs (1987), Dolan and Coats (1990, 1991), Dolan (1991), and Dolan and Gallegos (1992). However, they have only partially shown the species compositions and abundances of limited components of microzooplankton, the overall distribution patterns of the whole microzooplankton components are still unknown.

The purpose of this study is to provide the first comprehensive survey of microzooplankton in southern Chesapeake Bay and its major tributaries. The seasonal peaks and periodicity of the microzooplankton abundance are identified using time series analysis.

Materials and Methods

Microzooplankton were collected at 14 stations in the

* To whom correspondence should be addressed.
Tel: 82-32-764-6652, Fax: 82-32-761-0467

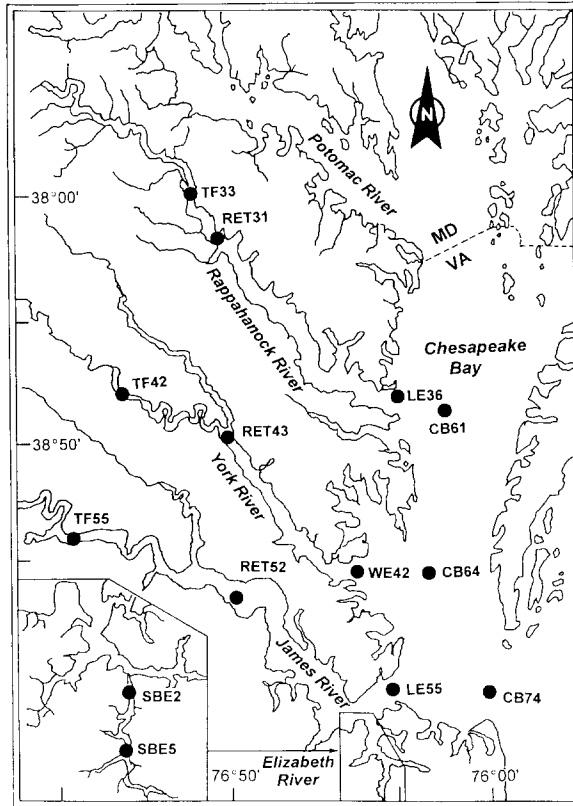


Fig. 1. Location of sampling stations in the Chesapeake Bay and major tributaries.

Virginian southern portion of the Chesapeake Bay and four tributaries. Samples were taken from September 1993 through December 1995 at four stations (TF33, RET31, LE36, CB64), and from July 1992 through December 1995 at the other 10 stations (Fig. 1). Station locations were based on the salinity regimes at these sites. Tidal freshwater (TF33, TF42, TF55), river-estuary transitional sites (RET31, RET43, RET52) and river mouth stations (LE36, WE42, LE55) are located in the Rappahannock, York, and James Rivers. Two stations are in the mid-channel of the Bay (CB61, CB64), with another located at the Bay entrance (CB74).

Two stations (SBE2, SBE5) are in the southern branch of Elizabeth River, which has a history of industrial and domestic waste contamination.

Two 15 L carboys were filled with water on station with a battery powered bilge pump (PAR Model 34600-0000, ITT Jabsco Products), taken from a vertical series of 5 depths above the pycnocline. After mixing, a 1 L sample was taken from each carboy and preserved with 10 ml Lugol's solution. The samples settled for 72 h before a series of two siphoning and settling steps were taken to obtain a 100 ml concentrate from each 1 L water sample. The analysis consists of three subsets from the 100 ml concentrate. The first step involved separating relatively large detritus and specimens such as rotifers and copepod nauplii by passing each 100 ml concentrate through a 73 µm mesh screen. The plankters trapped on the screen represent the Group I subset. The two remaining 100 ml concentrates (after sieving) were combined to form a 200 ml mixture. The 200 ml was gently swirled and thoroughly mixed in a graded cylinder. Based on the amount of detritus and plankters, a 5 or 10 ml aliquots from the 200 ml mixture was taken in three different depths from the cylinder and placed in a second settling chamber, with buffered 5% formalin solution added to total 25 ml volume. After 3-5 minutes, 15 ml water was removed from the top of the second settling chamber and placed in a third settling chamber. Both chambers were adjusted to 25 ml final volumes with buffered 5% formalin and represented Group II and Group III subsets, respectively. The size ranges of plankters for each group are as follows: Group I over 73 µm, Group II between 30 µm and 73 µm, and Group III less than 30 µm in size. Group I usually included copepod nauplii and rotifers, and Group II and III contained mostly ciliates. All the chambers were allowed to settle for 24 h before examination with the inverted plankton microscope. Most counts were performed at 100-200X and identifications at 200-400X, respectively.

Ciliate cell volumes were calculated using an appropriate geometric formula based on their size and shape, and tintinnid cell volumes were considered as

Table 1. Spatial mean of water quality parameters in the southern Chesapeake Bay and four tributaries from May 1993 through April 1995. Values are mean ± S.E. and coefficient of variation (%)

Sites	Salinity (‰)	Temperature (°C)	DO (mg/L)	pH	Secchi depth (m)
TF33	1.6 ± 0.5(152)	16.1 ± 1.9(57)	10.2 ± 0.5(23)	7.1 ± 0.1(5)	0.5 ± 0.0(38)
TF42	0.0 ± 0.0(237)	16.8 ± 1.9(55)	9.1 ± 0.6(20)	7.1 ± 0.1(7)	0.6 ± 0.0(29)
TF55	0.1 ± 0.0(97)	17.4 ± 1.8(52)	10.1 ± 0.4(21)	7.4 ± 0.1(5)	0.5 ± 0.0(20)
RET31	4.6 ± 0.8(89)	16.0 ± 1.8(56)	10.4 ± 0.5(21)	7.1 ± 0.1(6)	0.5 ± 0.1(61)
RET43	9.2 ± 1.0(51)	16.8 ± 1.8(52)	9.6 ± 0.5(25)	7.1 ± 0.1(6)	0.5 ± 0.0(38)
RET52	2.5 ± 0.8(166)	17.0 ± 1.7(50)	10.2 ± 0.4(20)	7.6 ± 0.1(6)	0.6 ± 0.1(53)
LE36	15.6 ± 0.7(22)	15.1 ± 1.8(58)	9.7 ± 0.4(21)	8.0 ± 0.1(3)	2.0 ± 0.2(54)
WE42	19.0 ± 0.7(18)	16.0 ± 1.7(53)	9.8 ± 0.5(25)	8.0 ± 0.1(3)	1.6 ± 0.1(34)
LE55	20.3 ± 0.8(19)	15.4 ± 1.6(51)	9.3 ± 0.4(23)	8.0 ± 0.0(2)	1.3 ± 0.1(40)
CB61	16.3 ± 0.8(24)	14.9 ± 1.8(60)	10.0 ± 0.5(24)	8.0 ± 0.1(4)	2.0 ± 0.2(44)
CB64	19.7 ± 0.7(18)	15.1 ± 1.7(55)	9.4 ± 0.4(22)	8.1 ± 0.0(2)	1.8 ± 0.1(30)
CB74	26.6 ± 0.8(14)	14.5 ± 1.5(50)	9.3 ± 0.3(17)	8.0 ± 0.1(3)	1.9 ± 0.1(29)
SBE2	17.5 ± 1.1(32)	17.9 ± 1.7(45)	7.5 ± 0.5(36)	7.3 ± 0.1(7)	1.4 ± 0.2(59)
SBE5	16.8 ± 1.0(30)	19.8 ± 1.7(42)	7.1 ± 0.5(33)	7.2 ± 0.1(7)	1.2 ± 0.1(50)

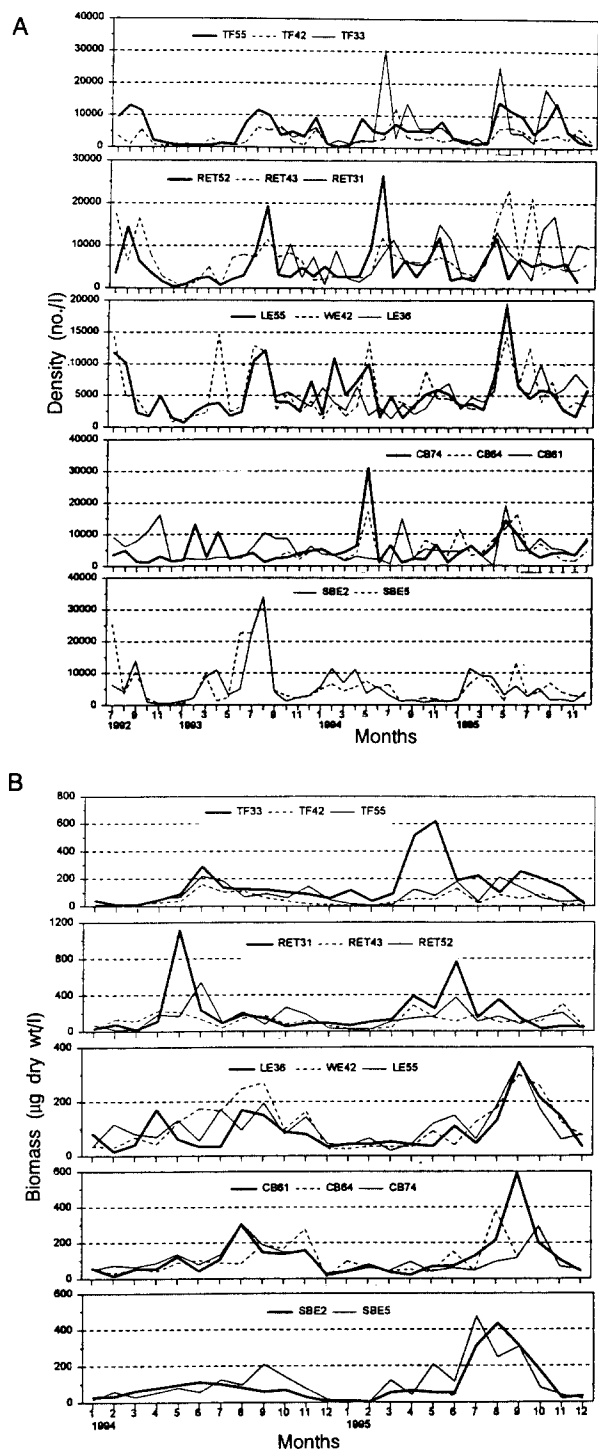


Fig. 2. Monthly variation of total microzooplankton density (A) and biomass (B).

$\frac{1}{2}$ the lorica volume (Beers and Stewart, 1969). Biomass estimations employed conversion of cell volumes to dry weight using $0.279 \text{ pg dry wt}/\mu\text{m}^3$ (Gates et al., 1982) and to carbon content using a conversion factor of $0.19 \text{ pgC}/\mu\text{m}^3$ (Putt and Stoeker, 1989). To estimate

biomass (dry weight) of copepod nauplii, lengths were converted to dry weights using published length-dry weight regressions (McCauley, 1984) and then the dry weight was converted to carbon as 32.0% of the dry weight (Wiebe et al., 1975). In the case of rotifers, biovolumes were calculated from the approximate geometric dimension, converted to dry weight (Ruttner-Kolisko, 1977; Pace, 1982) and finally to carbon as 50% of dry weight (Salonen et al., 1976).

Salinity, water temperature, dissolved oxygen and pH were measured at one meter intervals over the whole depth with Hydro-Lab (Model H20, Hydro-Lab Corporation). The other plankton data were provided by the Applied Marine Research Laboratory at Old Dominion University.

To identify seasonal cycles and the month of peak abundance for each microzooplankton component, time series analysis was performed using an ARIMA (Auto Regressive Integrated Moving Average) Model. Time series data were cross-correlated with a cosine wave in which the highest cosine value was given to July of each year for the identification of the month of peak abundance. Autocorrelation function coefficients (AFC) were used to identify seasonal cycles, and SAS software (SAS/ETS) (1993) was used to analyze the time series data.

Results

General hydrology

The descriptive statistics of water quality parameters 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 stations (CB61, CB64) mesohaline, and bay entrance (CB74) polyhaline water. TF33 sporadically had salt water intrusion, with a maximum of 10.1‰ and an annual mean of 1.6‰. Water temperatures showed typical ranges for temperate zones. DO values were not different between stations except Elizabeth River (SBE2, SBE5) which has been exposed to industrial and domestic contamination. pH values were higher in meso- and polyhaline water than freshwater due to the different weathering process. Tributary stations showed high turbidity due to the various sources of suspended matters from terrestrial area and resuspension of sediment.

Microzooplankton composition and seasonality

Total microzooplankton: Microzooplankton were identified to broad taxonomic groups (eg, aloricate ciliates, loricate ciliates, rotifers and copepod nauplii). The microzooplankton density over the sampling period in the Bay and major tributaries ranged from 68 to 33,949/L (Fig. 2), with a mean abundance of $5,494 \pm$

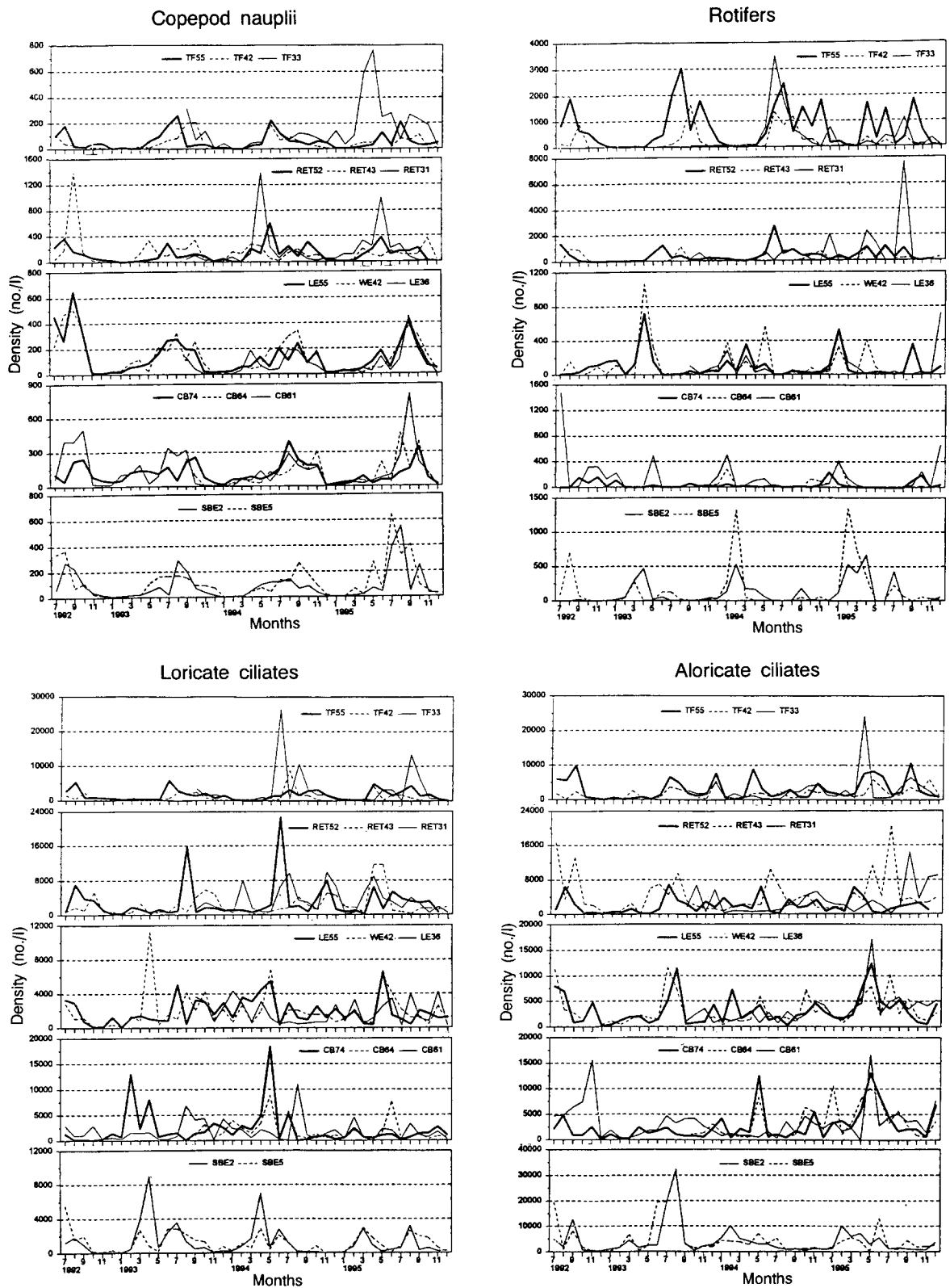


Fig. 3. Monthly concentration of each microzooplankton component.

18/L. Using monthly means from the 14 stations, spring (April and May) and summer (June, July and August) was a period of high abundance, with a sharp decrease in fall at most stations. Ciliates were the major component of microzooplankton, contributing 98% of total microzooplankton abundance. Aloricate ciliates comprised 59% of the total microzooplankton density, with loricate ciliates representing 39%. Rotifers and copepod nauplii contributed 4% and 2% of the total microzooplankton density, respectively. The average microzooplankton biomass (January 1994 - December 1995) from the 14 stations was $113.32 \pm 6.43 \mu\text{g}$ dry wt/L ($77 \mu\text{gC/L}$), having from a minimum of $2.90 \mu\text{g}$ dry wt/L (SBE2 in February, 1995) to a maximum of $1,114.7 \mu\text{g}$ dry wt/L (RET31 in May, 1994) (Fig. 2). Seasonal patterns of biomass followed copepod nauplii abundances, with the copepod nauplii having the highest microzooplankton biomass (77%). Peak biomass values occurred in mid-summer through early fall due to the high density of copepod nauplii, with an additional ciliate peak in late spring (May). Ciliates and rotifers represented 18% and 5% of the total microzooplankton biomass, respectively.

Copepod nauplii: A variety of copepod nauplii, representing different species and stages in development, were in the samples. Most of the copepod nauplii had size ranges of 80-200 μm (excluding appendages). The peak concentration occurred at RET43 (September 1992), with 1,418/L. The lowest concentration was one nauplius/L at station CB64 (December 1993) (Fig. 3). Autocorrelation plots for each station identified a strong 12-month cycle in copepod nauplii concentrations (Fig. 5). All correlation values from the 14 stations were significant ($P < 0.05$). A 12-month peak in the autocorrelations confirmed the presence of a year cycle in copepod nauplii density. The results of cross-correlation analysis for copepod nauplii are given in Fig. 6. Eight of 14 stations had the highest positive correlation at lag 1, which indicated an August peak in copepod nauplii density. Five stations had July peaks and one station (RET31) a June peak. In general, the seasonal pattern of copepod nauplii density had the highest concentration during mid summer (July, August), with a gradual decrease in fall. Across all stations and sampling months, average concentration of copepod nauplii was $115 \pm 7/L$ and represented the smallest portion of the total microzooplankton density (2%). The mean biomass of copepod nauplii comprised the highest proportion (77%) of the total microzooplankton biomass. Their biomass ranges were 0.78-1078.48 μg dry wt/L, with a grand mean of $87.77 \pm 6.20 \mu\text{g}$ dry wt/L throughout the sampling period. Time series analysis for copepod nauplii biomass was not applied due to the short time periods of observations (two years). In general, peak biomass values occurred in late summer and early fall (August-September) in the meso- and polyhaline stations, and in spring and early summer at

tidal freshwater and river-estuary transition sites (Fig. 4).

Rotifers: Rotifers were most abundant at tidal freshwater and river-estuary transition sites during summer, and at Bay and Elizabeth River stations during late fall and winter (Fig. 3). *Keratella cochlearis*, *Brachionus angurialis*, *Brachionus calyciflorus*, and *Filinia longiseta* were the dominant species at the tidal freshwater stations during summer. *Synchaeta* spp. dominated the mesohaline stations during late fall and early winter, and *Trichocerca marina* and *Polyarthra vulgaris* were ubiquitous throughout the stations. Rotifers were absent in samples from the meso- and polyhaline stations during summer and in tidal freshwater during winter. Their concentrations ranged from zero to a maximum of 7,646/L (August 1995 at station RET31). In general, the rotifers made small contributions to the total microzooplankton density and biomass. As a grand mean, the rotifer density and biomass were $232 \pm 4/L$ and $5.33 \pm 0.66 \mu\text{g}$ dry wt/L. They comprised 4% of the total microzooplankton density and 5% of the total biomass. However, when considered only at the tidal freshwater stations, rotifer proportions were doubled, constituting 9% (442/L) of the total density and 12% ($10 \mu\text{g}$ dry wt/L) of the total biomass. In 10 of 14 stations, time series data of rotifer density indicated significant autocorrelation. All the tidal freshwater and mid-Bay stations had strong autocorrelation (Fig. 5). A 11- or 12-month peak in the autocorrelation revealed a year cycle in rotifer density. Cross-correlation results indicated two different seasonal patterns in rotifer density from the sampling stations. All the tidal freshwater (TF33, TF42, TF55) and two river-estuary transition sites (RET31, RET52) showed mid-summer peaks (July, August). However, at the Bay and Elizabeth River stations (meso- or polyhaline) the highest positive correlations were at lag 5 or lag 6, which indicated high concentration of rotifers during winter (December-March) (Fig. 6). Freshwater taxa (*Brachionus*, *Keratella* and *Filinia*) were abundant during mid-summer, but meso- and polyhaline species (mainly *Synchaeta* spp.) dominated during winter in the Bay and Elizabeth River. However, RET43 had a different pattern from the other river-estuary transition sites. It showed a fall peak (October) due to the high abundance of *Synchaeta* and *Trichocerca* species. The difference in this seasonal pattern of rotifer density from the other river-estuary transition sites may be due to salinity; since station RET43 had higher salinity (5-7‰) than the other sites (Table 1).

Loricata ciliates: Loricate ciliates less than 30 μm in diameter dominated numerically at all the stations and included the small tintinnids, *Tintinnopsis minuta*, *T. acuminata* and *T. parva*. *Favella* spp., *Tintinnopsis fimbriata* and *Tintinnopsis radix* were abundant in size group I ($>73 \mu\text{m}$) with *Eutintinnus* spp. and *Helicos-tomella subulata* in size group II (30-73 μm). The

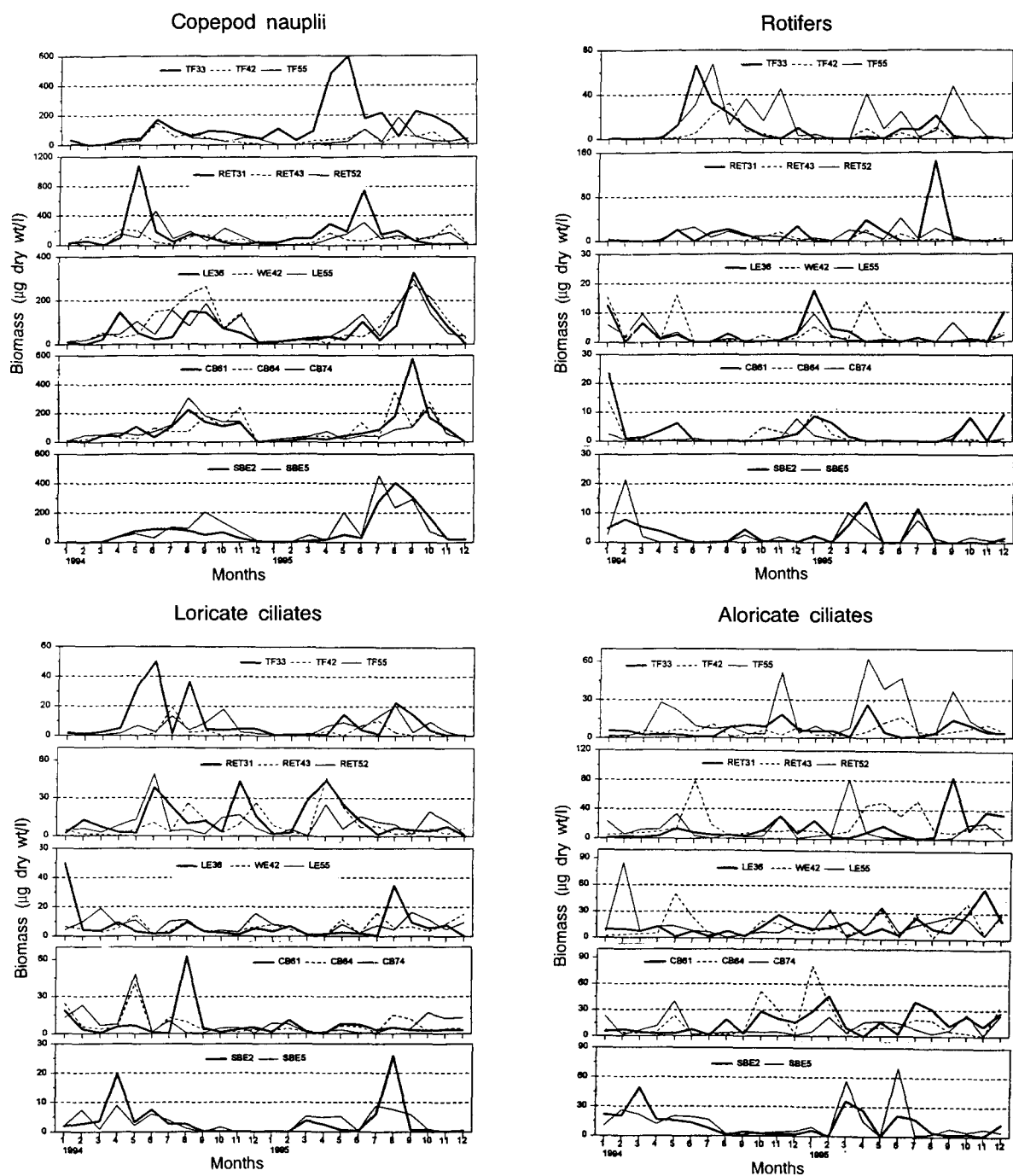


Fig. 4. Monthly biomass of each microzooplankton component.

seasonal variation of loricate ciliate density is shown in Fig. 3. Autocorrelation for loricate ciliates was not significant at most stations. Only three stations showed significant correlation (TF42, TF55, SBE2). Based on the results of time series analysis from the three stations, the autocorrelation plots identified a strong cycle in loricate ciliate density. A 11- or 12-month peak

in the autocorrelation indicated a year cycle (Fig. 5). Cross-correlation values showed significant differences in the seasonal density pattern between stations. Tidal freshwater and river-estuary transition sites had the highest positive correlation at lag 0 or lag 1, which indicated mid-summer peaks (July, August). However, meso- and polyhaline stations generally had a March

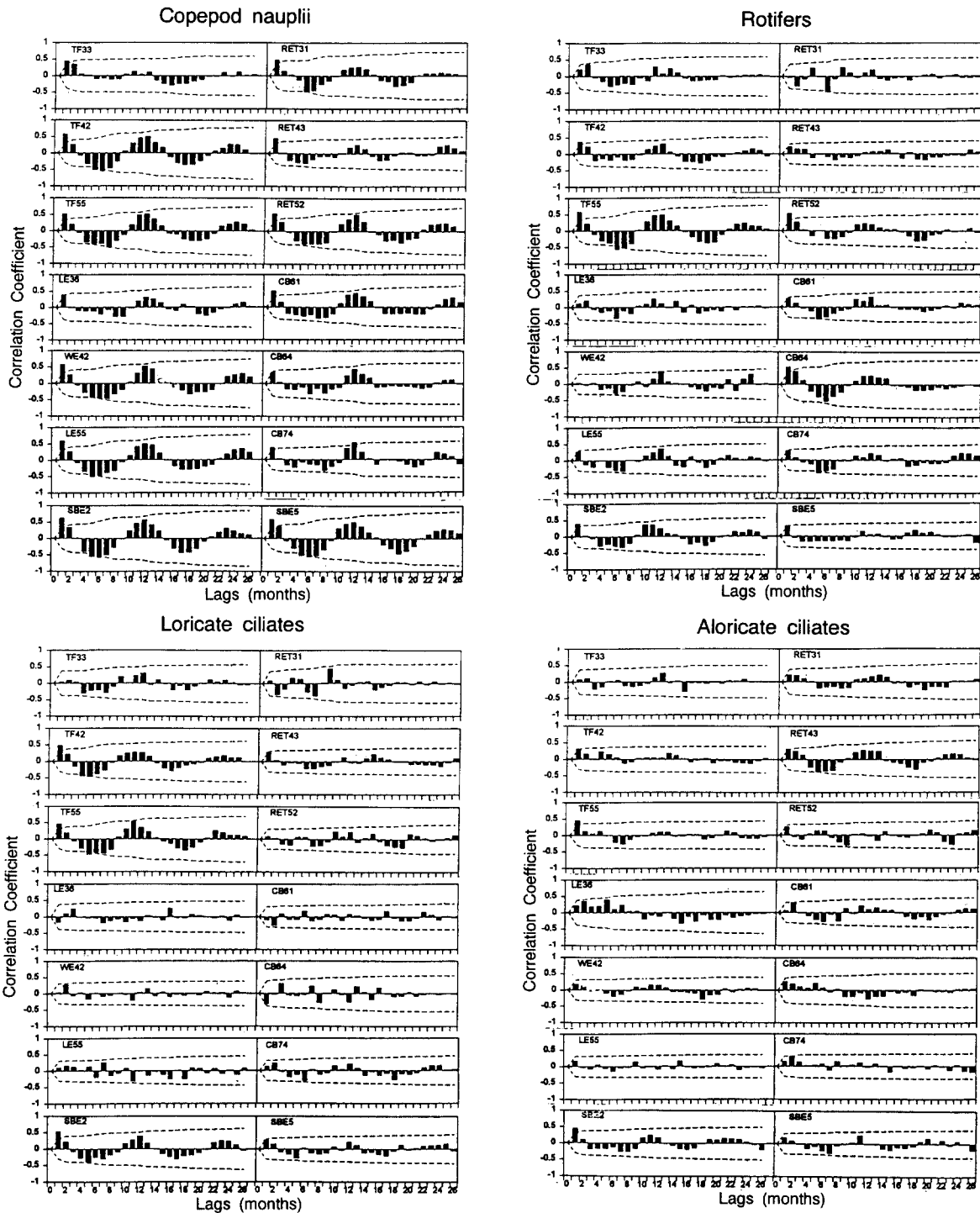


Fig. 5. Autocorrelation function of logged concentration of each microzooplankton component. Dashed lines indicate two standard errors.

through June peak. At stations RET43 and LE36 there was an indication of a fall peak (October), although the correlation coefficients were not statistically significant (Fig. 6). The mean density during the sampling period was $1,928 \pm 117/L$, with a minimum of zero

concentration at CB61 (April 1995) and a maximum of 26,365/L at TF33 (June 1994). Although these taxa were less abundant than aloricate ciliates, they contributed 35% of the total microzooplankton density. The biomass of loricate ciliates ranged from zero to

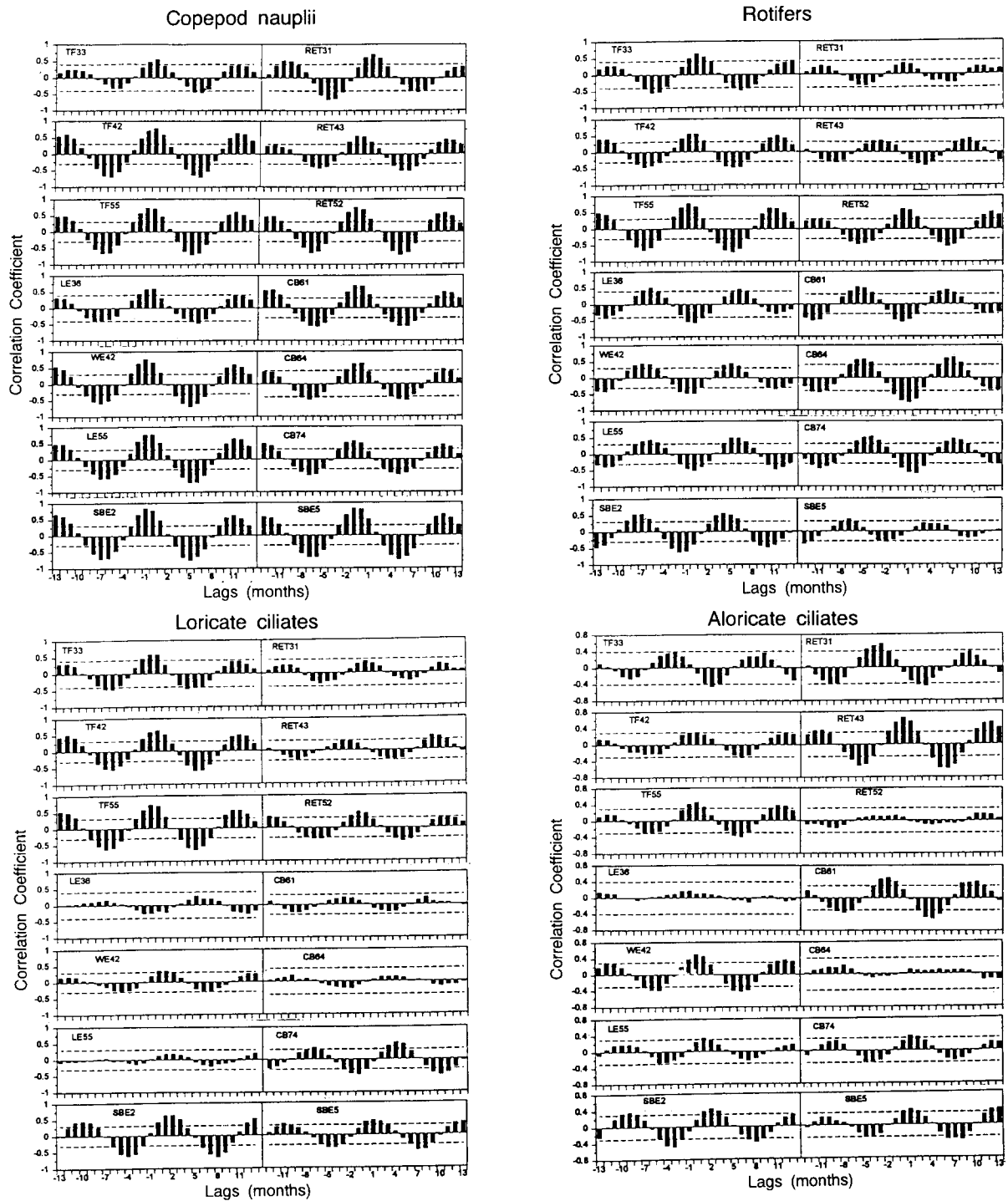


Fig. 6. Cross-correlation function of logged concentration of each microzooplankton component. Dashed lines indicate two standard errors.

62.13 μg dry wt/L, with an annual mean of 7.10 ± 0.52 μg dry wt/L comprising 6% of total microzooplankton biomass. Seasonal patterns for biomass were similar to density changes: being high during spring and summer, and low in late fall and winter (Fig. 4).

Aloricate ciliates: Aloricate ciliates were the most abundant microzooplankton component (59%). Common genera within this group were *Strombidium*, *Strobilidium*, *Didinium* and *Vorticella*. Seasonal density randomly fluctuated throughout the stations (Fig. 3). Only three

(LE36, RET43 and SBE2) of 14 stations had significant autocorrelations. From these stations, there was an indication of an annual cycle at their density levels (Fig. 5). Using cross-correlation analysis, the peak abundance for aloricate ciliates occurred from May through October (Fig. 6). Concentrations ranged from 20 to 32,287/L, with a mean of 3218 ± 167 /L. Their high occurrence was over 20,000/L at SBE2 and SBE5 (August 1993), and at TF33 (April 1995). The biomass of these ciliates ranged from near zero to 85.33 μ g dry wt/L, with a mean of 13.13 ± 0.82 μ g dry wt/L. The mean contribution of aloricate ciliates to the total microzooplankton biomass was 11.59%. The small ciliates (<30 μ m) had the highest portions of density, although their contribution to the total microzooplankton biomass was relatively small. Peak biomass for this group occurred in spring, along with a high density of small ciliates, plus an additional peak in fall (October-November) by the larger ones (*Didinium* spp.).

Other microzooplankton: Polychaete larvae were occasionally abundant (20-30/L) at meso- and polyhaline stations during late summer and fall, but were never observed at the tidal freshwater stations. Most polychaete larvae exceeded microzooplankton size ranges (20-200 μ m) and made a small contribution to the total density (<0.1%). Some metazoan eggs, tunicates and sarcodina were observed in samples, but they were generally observed in low numbers (<5/L).

Discussion

Protozoan ciliates were a major component of microzooplankton in southern Chesapeake Bay and major tributaries contributing over 90% of the total microzooplankton density. Another major component was copepod nauplii which accounted for 77% of the total microzooplankton biomass. Rotifers contributed 4% of the total density and 5% of the total microzooplankton biomass. Ciliates were predominantly oligotrichs, less than 30 μ m in diameter, and ranged from 20 to 32,287/L. Aloricate ciliates usually outnumbered loricate ciliates, which comprised 35% of the total density. The dominant loricate ciliate taxa were *Tintinnopsis*, with *Strombidium* and *Strobilidium* for aloricate ciliates, and *Trichocerca*, *Polyarthra*, *Synchaeta*, *Brachionus*, and *Keratella* for rotifers.

Autocorrelation analysis for each microzooplankton component revealed an annual cycle (11 or 12 month) in microzooplankton density. Autocorrelation coefficients for copepod nauplii and rotifers were significant throughout the stations, but not for ciliates. This non-consistency in the seasonal pattern of ciliates may be due to the great temporal and spatial heterogeneity of population density. Ciliates have high specific growth rates and short generation times when compared with other small animals such as nematodes and coelenterates (Stemberger, 1987, 1988; Pennak, 1989; Laybourn-Parry,

1992; Christou and Verriopoulos, 1993). With rapid division rates it is easy for a large population of a given species to develop over a short period of time when suitable conditions and abundant food prevail. Accordingly, one month of sampling interval may be too long to estimate a true monthly population density for ciliates, when considering their short generation time and rapid growth rates.

Encystment is also a well-known event for both loricate and aloricate ciliates (Reid and John, 1978; Reid, 1987). This event contributes to great fluctuation of their population density over a short time period (Reid, 1987). Spatial heterogeneity can also produce sampling errors. In the real habitat, patches of protozoa may be considerably smaller and defined protozoan communities are known to occur in niches as small as on the scale of millimeters (Fenchel, 1987). The spatial and temporal heterogeneity in ciliates may influence the estimation of population density if sampling frequency and spatial coverage are not enough to cover the heterogeneity.

The cross-correlation analysis identified seasonal peaks for each microzooplankton component. Copepod nauplii showed mid-summer peaks (July, August), but rotifers had two different patterns in seasonal density. From the tidal freshwater and river-estuary transition sites, rotifers had a mid-summer (July, August) peak in density, while meso- and polyhaline stations (Bay and Elizabeth River) showed a winter peak (December through March). These differences in rotifer density patterns were due to the differences in species development. Cold water species, *Synchaeta* spp., exclusively dominated at meso- and polyhaline stations during winter. However, freshwater species such as *Keratella*, *Brachionus*, and *Filinia* species were abundant during summer. In general, ciliates started to develop several months earlier than the copepod nauplii. This allows ciliates to be preyed upon by copepod nauplii in the Bay and tributaries following the density pattern of prey-predator relationship (Wilson and Bossert, 1971). It is not uncommon for copepods (adults) to prey on planktonic ciliates (Stoecker and Egloff, 1987; Gilbert, 1980; Robertson, 1983).

The microzooplankton density and biomass ranges in this study were comparable to other microzooplankton studies. In northern Chesapeake Bay, Dolan and Coat (1990) found 3,000 (September) to 23,000 ciliates/L (April), with the biomass ranging from 17.3 to 32.4 μ gC/L. Dolan (1991) reported ciliate density of 400 to 78,600/L, with high dominance of microphagous ciliates. Ciliate density and biomass in northern Chesapeake Bay were slightly higher than those in this study with an annual mean density of 5,146/L and a biomass of 13.7 μ gC/L. Species composition throughout the Bay was similar with small ciliates (<30 μ m) dominant and mainly composed of *Strombidium*, *Strobilidium* and *Balanion* for aloricate ciliates, and *Tintinnopsis minuta*, *T. acuminata* for loricate ciliates (Dolan, 1991; Park

and Marshall, 1993; Park and Choi, 1997).

In other estuarine systems, Hargraves (1981) reported tintinnid density ranging from 20 to 13,900/L in Narragansett Bay, Rhode Island. In a subtropical estuary, Buskey (1993) found high densities of microzooplankton which ranged from 32,300 to 50,800/L in Nueces and Corpus Christi Bay, Texas, and 17,000 tintinnids/L and 31,000 aloricate ciliates/L in San Antonio Bay. Smetacek (1981) reported ciliate densities from 2,000 to 28,000/L with 1.7 to 17.2 $\mu\text{gC/L}$ in Kiel Bight during spring. In coastal areas, ciliate abundances were much smaller than in estuarine systems: 200-630 ciliates/L in North Pacific near San Diego (Beer and Stewart, 1969), and 205-1,204 ciliates/L in the West Coast of New Zealand (James and Hall, 1995).

In freshwater, high abundances of ciliates have also been reported: 10,060-18,460 ciliates/L in Lake Constance (Muller et al., 1991) and 3,318-21,556 ciliates from 12 lakes in Quebec (Pace, 1986). These are higher than those in the tidal freshwater stations which ranged from 2,600 to 5,868/L.

Discoloration of water due to the mass occurrence of oligotrichs was reported by Dale and Dahl (1987) in southern Norway. They found over 2 million individuals/L of *S. reticulatum*. In the Chesapeake and tributaries discoloration by heterotrophic ciliates was not found during these collections. However, *Mesodinium rubrum* (autotrophic ciliate) caused an extensive reddish-brown discoloration of surface water at the Bay mouth in October 1995, having counts of over 350,000 cells/L (personal observation).

Rotifers primarily dominated the tidal freshwater stations, but their overall contribution to the total microzooplankton density and biomass was small. The rotifers were numerically abundant for limited periods of time; especially during summer at tidal freshwater and during late fall and winter at mesohaline water. Dolan and Gallegos (1992) reported an average density of rotifers, 1,000/L, in the Rhode River estuary (eutrophic subestuary of Chesapeake Bay) from March through September, with *Synchaeta* and *Brachionus* the dominant genera. In Potomac River (5.35-18.96%), Heinbokel et al. (1988) reported *Synchaeta* dominant in the rotifer population, ranging from 5 to 4,000/L. These results are comparable with this study in terms of species composition and density. Although rotifers contributed small portions to the total microzooplankton density and biomass, they are considered a major component of the microzooplankton because their reproductive rates are the greatest for any of metazoans (Nogrady, 1993). By Pennak (1989)'s broad survey on rotifer density, it is obvious that most plankton communities average between 40 to 500 rotifers/L, with populations in excess of 1,000/L being unusual. In this study, tidal freshwater stations during summer months had over 1,000 rotifers/L and as high as 7,000/L, which indicated the rotifer population could at times present a large portion of the total micro-

zooplankton density. Based on production data from the literature, Allan et al. (1976) and Dolan and Gallegos (1992) estimated that the production of rotifers in Rhode River exceeded that of the copepods. In northern Chesapeake Bay, Brownlee and Jacobs (1987) indicated copepod nauplii density ranging from 136 to 171/L in Choptank River and 75 to 109/L in Chester River, using 20 μm mesh nets. Nauplii studies in the literature are rare. In addition, comparison of microzooplankton density for Chesapeake Bay to those of other systems is difficult since collecting techniques and frequencies differ, and so as habitats.

Total microzooplankton compositions in terms of biomass and density have rarely been reported from estuaries. But in the freshwater systems, Pace (1986) reported compositions for 12 lakes in Quebec, Canada. Based on his results, the total microzooplankton biomass ranged from 23.9 to 147.7 $\mu\text{g dry wt/L}$, with a mean of 74.5 $\mu\text{g dry wt/L}$. Copepod nauplii contributed 43% of total biomass with ciliates 34% and rotifers 16%. His results were a little different in the relative contribution for each microzooplankton component to the total. Copepod nauplii contribution to the total biomass was little less than the one found here (77% in this study), and ciliates and rotifers were slightly higher (18% for ciliates and 5% for rotifers in this study). But the level of their relative contribution was similar with the highest proportion by copepod nauplii, and ciliates and rotifers followed. In freshwater, the relative proportion of rotifers increased, while copepod nauplii decreased. The contribution of ciliates was very similar in both systems. In summary, the copepod nauplii comprised the highest proportion of the total microzooplankton biomass. However, the ciliates and rotifers should also be considered as major components of the microzooplankton community because their rapid growth rates and short generation time result in significant contributions to the secondary production by microzooplankton.

Acknowledgements

This study was supported by the Virginia Department of Environmental Quality and the U.S. Environmental Protection Agency.

References

- Allan JD, Kinsey TG, and James MC (1976) Abundance and production of copepods in the Rhode River subestuary of Chesapeake Bay. *Chesapeake Sci* 17: 86-92.
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, and Thingstad F (1983) The ecological role of water column microbes in the sea. *Mar Ecol Prog Ser* 10: 257-263.
- Beers JR and Stewart GL (1969) Microzooplankton and its abundance relative to the larger zooplankton and other seston components. *Mar Biol* 4: 182-189.
- Birdsong RS, Marshall HG, Alden RW, and Ewing RM (1987) Lower Chesapeake Bay Mainstem Plankton Monitoring Program. Final Report. July 1985~June 1986. Old Dominion University Research Foundation, Norfolk, Virginia, pp 1-112.

- Birdsong RS, Marshall HG, Alden RW, and Ewing RM (1988) Lower Chesapeake Bay Mainstem Plankton Monitoring Program. Final Report. 1986-1987. Old Dominion University Research Foundation, Norfolk, Virginia, pp 1-137.
- Birdsong RS, Marshall HG, Alden RW, and Ewing RM (1989) Lower Chesapeake Bay Mainstem Plankton Monitoring Program. Final Report. 1987-1988. Old Dominion University Research Foundation, Norfolk, Virginia, pp 1-152.
- Brownlee DC and Jacobs F (1987) Mesozooplankton and microzooplankton in the Chesapeake Bay. In: Majumdar SK, Hall LW, and Austin HM (eds), Contaminant Problems and Management of Living Chesapeake Bay Resources. Pennsylvania Academy of Sciences, Easton, pp 217-269.
- Buskey EJ (1993) Annual pattern of micro- and mesozooplankton abundance and biomass in a subtropical estuary. *J Plankton Res* 15: 907-924.
- Christou ED and Verriopoulos GC (1993) Analysis of the biological cycle of *Acartia clausi* (Copepoda) in a meso-oligotrophic coastal area of the eastern Mediterranean Sea using time-series analysis. *Mar Biol* 115: 643-651.
- Dale T and Dahl E (1987) Mass occurrence of planktonic oligotrichous ciliates in a bay in southern Norway. *J Plankton Res* 9: 871-879.
- Dolan JR (1991) Guilds of ciliate microzooplankton in the Chesapeake Bay. *Estu Coast Shelf Sci* 33: 137-152.
- Dolan JR and Coats DW (1990) Seasonal abundance of planktonic ciliates microflagellates in mesohaline Chesapeake Bay waters. *Estu Coast Shelf Sci* 31: 157-175.
- Dolan JR and Coats DW (1991) Changes in fine-scale vertical distribution of ciliate microzooplankton related to anoxia in Chesapeake Bay water. *Mar Microb Food Webs* 5: 81-93.
- Dolan JR and Gallegos CC (1992) Trophic role of planktonic rotifers in the Rhode River Estuary, Spring-Summer 1991. *Mar Ecol Prog Ser* 85: 187-199.
- Edwards ES and Burkill PH (1995) Abundance, biomass and distribution of microzooplankton in the Irish Sea. *J Plankton Res* 17: 771-782.
- EPA, 1987. Chesapeake Bay; Introduction to an Ecosystem. United States Environmental Protection Agency, Annapolis, pp 1-33.
- Fenchel T (1987) Ecology of Protozoa. The Biology of Free-living Phagotrophic Protists. Science Technique Publishers. Madison, pp 1-197.
- Gates MA, Rogerson A, and Berger J (1982) Dry to wet weight biomass conversion constant for *Tetrahymena ellioti* (Ciliophora, Protozoa). *Oecologia* 55: 145-148.
- Gilbert JJ (1980) Observations on the susceptibility of some protists and rotifers to predation by *Asplanchna girodi*. *Hydrobiologia* 73: 87-91.
- Hargraves PE (1981) Seasonal variation of tintinnids (Ciliophora: Oligotrichida) in Narragansett Bay, Rhode Island, USA. *J Plankton Res* 3: 81-91.
- Heinbokel JF (1978) Studies on the functional role of tintinnids in the Southern California Bight. II. Grazing rates of field populations. *Mar Biol* 47: 191-197.
- Heinbokel JF, Coats DW, Henderson KW, and Tyler MA (1988) Reproduction rates and secondary production of three species of the rotifer genus *Synchaeta* in estuarine Potomac River. *J Plankton Res* 10: 659-674.
- Jacobs F, Burton W, and Moss I (1985) Pattern of zooplankton abundance, species composition, and biomass in upper Chesapeake Bay. *Estuaries* 8: 78A.
- James MR and Hall JA (1995) Planktonic ciliated protozoa: their distribution and relationship to environmental variables in a marine coastal ecosystem. *J Plankton Res* 17: 659-683.
- Laybourn-Parry J (1992) Protozoan Plankton Ecology. Chapman & Hall, New York, pp 231.
- Marshall HG and Alden RW (1990) A comparison of phytoplankton assemblages and environmental relationship in three estuarine rivers of the lower Chesapeake Bay. *Estuaries* 13: 287-300.
- Marshall HG and Cohn MS (1987) Phytoplankton distribution along the eastern coast of the USA. Part 4. Shelf waters between Cape Henry and Cape May. *J Plankton Res* 9: 139-149.
- Marshall HG and Lacouture R (1986) Seasonal patterns of growth and composition of phytoplankton in the lower Chesapeake Bay and vicinity. *Estu Coas Shelf Sci* 23: 115-130.
- McCauley E (1984) The estimation of the abundance and biomass of zooplankton in samples. In: Downing JA and Rigler FH (eds), Secondary Productivity in Fresh Waters, IBP Handbook 17, 2nd ed, Blackwell, pp 228-265.
- Muller H, Schone A, Pinto-Coelho RM, Schweizer A, and Weisse T (1991) Seasonal succession of ciliates in Lake Constance. *Microb Ecol* 21: 119-138.
- Nogrady T (1993) Rotifera. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World. SPB Academic Publishing, Hague, pp 1-142.
- Nothig EM and Gowing MM (1991) Late winter abundance and distribution of phaeodarian radiolarians, other large protozooplankton and copepod nauplii in the Weddell Sea, Antarctica. *Mar Biol* 11: 473-484.
- Pace ML (1982) Planktonic ciliates: their distribution, abundance and relationship to microbial resources in a monomictic lake. *Can J Fish Aquat Sci* 39: 1106-1116.
- Pace ML (1986) An empirical analysis of zooplankton community size structure across lake trophic gradients. *Limnol Oceanogr* 31: 45-55.
- Park GS and Marshall HG (1993) Microzooplankton in the lower Chesapeake Bay, and the tidal Elizabeth, James, and York River. *Virginia J Sci* 44: 329-340.
- Park GS and Choi JK (1997) Microzooplankton assemblages: their distribution, trophic role and relationship to the environmental variables. *J Korean Soc Oceanogr* 32: 145-155.
- Pennak RW (1989) Freshwater Invertebrates of the United States. The Ronald Press Company, New York, pp 59-213.
- Pomeroy LR (1974) The ocean's food web: a changing paradigm. *BioScience* 24: 499-504.
- Putt M and Stoecker DK (1989) An experimentally determined carbon: volume ratio for marine oligotrichous ciliates from estuarine and coastal waters. *Limnol Oceanogr* 34: 1087-1103.
- Reid PC (1987) Mass encystment of a planktonic oligotrich ciliate. *Mar Biol* 95: 221-230.
- Reid PC and John AWG (1978) Tintinnid cysts. *J Mar Biol Assoc UK* 58: 551-557.
- Robertson JR (1983) Predation by estuarine zooplankton on tintinnid ciliates. *Estu Coast Shelf Sci* 16: 27-36.
- Ruttner-Kolisko A (1977) Suggestions for biomass calculations of plankton rotifers. *Ergeb Limnol* 8: 71-76.
- Salonen K, Sarvala H, Hakala I, and Viljanen ML (1976) The relation of energy and organic carbon in aquatic invertebrates. *Limnol Oceanogr* 21: 724-730.
- Sanders RW (1987) Tintinnids and other microzooplankton seasonal distribution and relationships to resources and hydrography in a Maine estuary. *J Plankton Res* 9: 65-77.
- SAS (1993) SAS/ETS User's Guide, Version 6. SAS Institute, Cary, pp 102-107.
- Smetacek V (1981) The annual cycle of protozooplankton in the Kiel Bight. *Mar Biol* 63: 1-11.
- Stemberger RS (1987) The potential for population growth of *Ascomorpha ecaudis*. *Hydrobiologia* 147: 297-301.
- Stemberger RS (1988) Reproductive costs and hydrodynamic benefits of chemically induced defenses in *Keratella testudo*. *Limnol Oceanogr* 33: 593-606.
- Stoecker DK and Egloff DA (1987) Predation by *Acartia tonsa* on planktonic ciliates and rotifers. *J Exp Mar Biol Ecol* 110: 53-68.
- Wiebe PH, Boyd S, and Cox JL (1975) Relationships between zooplankton displacement volume, wet weight, dry weight,

Microzooplankton Seasonality Using Time Series Analysis

and carbon. *Fish Bull* 73: 777-786.

Williams PJL (1981) Incorporation of microheterotrophic processes into the classic paradigm of the food web. *Kiel Meeresforsch* 5: 11-28.

Wilson EO and Bossert WH (1971) A Primer of Population Biology. Sinauer Associates Inc, Sunderland, pp 127-138.

Wolfe JJ, Cunningham B, Wilkerson N, and Barnes J (1926) An investigation of the microzooplankton of Chesapeake Bay. *Elisha Mitchell Sci Soc* 42: 25-54.

[Received April 8, 1998; accepted May 4, 1998]