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The Trophic Contributions of Rotifers in Tidal Freshwater and Estuarine Habitats

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Distribution patterns and trophic contributions of rotifers from freshwater through polyhaline estuarine waters were examined in the southern Chesapeake Bay and its major tributaries for a two-year period. *Trichocerca marina* and *Synchaeta* spp. were the major taxa in abundance, followed by *Polyarthra vulgaris*, *Keratella cochlearis* and *Brachionus* spp. There was a significant negative correlation between salinity and rotifer density, biomass, and number of species. Rotifers were a component of the microzooplankton biomass during specific periods and at particular sites, dominating summer assemblages in tidal freshwater and river–estuary transition sites, plus the winter communities in estuarine waters. This observation indicates that rotifers may play an important trophic role by seasonally replacing metazoan nauplii as a biomass source in both tidal freshwater and estuarine ecosystems. The annual contribution of rotifers to the total microzooplankton biomass exclusive of heterotrophic dinoflagellates was brief but intensive, achieving over 50% of annual biomass during a 2–3 month period. Despite the small annual mean contribution of rotifers to the total microzooplankton biomass, rotifers may have a limited, but significant impact on the trophic dynamics of the zooplankton community in Chesapeake Bay and its major tidal tributaries.

Keywords: rotifers; microzooplankton; community structure; trophic contribution; estuaries; Chesapeake Bay

Introduction

The phylum Rotifera (rotifers) are important in aquatic environments because their reproductive rates are among the fastest of the metazoans due to their parthenogenetic production and short developmental periods (Herzig, 1983). Consequently, they can populate vacant niches with extreme rapidity, and convert primary production into a form usable for secondary consumers, producing up to 30% of the total plankton biomass (Nogrady *et al.*, 1993).

Rotifers are not as diverse or abundant in marine environments as microcrustaceans, but they are common in many nearshore (Heinbokel *et al.*, 1988) and interstitial marine communities (Egloff, 1988; Turner, 1993) where they occasionally constitute the dominant portion of the biomass (Schnese, 1973; Johansson, 1983). Limited data from Chesapeake Bay have suggested the rotifers in this estuary may represent a significant link in the various food webs. For instance, Loftus *et al.* (1972) observed the rapid development of rotifers near the Severn River in response to a temporally and spatially limited bloom of phytoplankton. In a study of the predator–prey interactions during dinoflagellate blooms in Chesapeake Bay, Heinbokel *et al.* (1988) noted rotifers associated with the blooms, often constituting the dominant grazer on the dinoflagellates. Allan *et al.* (1976) reported rotifers were similar in abundance to copepods over a course of a year in the Rhode River, a tributary of Chesapeake Bay. Based on production data from the literature, Allan *et al.* (1976) and Dolan and Gallegos (1992) estimated rotifer production in the Rhode River exceeded that of the copepods. Polgar and Souza (1981), and Setzler-Hamilton *et al.* (1981) have shown rotifers constitute a large portion of the diet of larval fish that spawn in the Chesapeake Bay.

Rotifer studies in Chesapeake Bay have been limited to the northern Bay regions (Loftus *et al.*, 1972; Allan *et al.*, 1976; Brownlee & Jacobs, 1987; Heinbokel *et al.*, 1988; Dolan & Gallegos, 1992). Although these studies provide information on species composition and abundances, the overall distribution patterns and trophic status of rotifers within this microzooplankton community are still unknown.

The objective of this study is to provide the first comprehensive survey of rotifers in the southern portion of Chesapeake Bay and its major tributaries.

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The study will provide distribution patterns, species composition, and the trophic role of rotifers within the microzooplankton community exclusive of heterotrophic dinoflagellates from tidal freshwater through to polyhaline waters.

Methods

The study was conducted at 14 stations in the southern portion of Chesapeake Bay and its major tributaries from January 1994 through December 1995 (Figure 1). Station locations were selected by salinity regimes at these sites. Three tidal freshwater (TF33, TF42, TF55), three river–estuary transitional sites (RET31, RET43, RET52) and three river mouth stations (LE36, WE42, LE55) are located in the Rappahannock, York, and James Rivers. Two stations are in the mid-channel of Chesapeake Bay (CB61, CB64) and one at the Bay mouth (CB74). Two other stations (SBE2, SBE5) are located in the southern branch of the Elizabeth River, which has a history of industrial and domestic waste contamination.

Two 15 l carboys were filled with water between the pycnocline and surface with a battery powered bilge pump. The water in the carboys was thoroughly mixed when filled, and two 1 l subsamples were taken from each. Bottle A was immediately preserved with 10 ml Lugol's solution and bottle B was initially treated with 200 ml of carbonated water for 20–30 min to allow for less body contraction of the rotifers than by direct contact with the fixative (Dolan & Gallegos, 1992; Nogrady *et al.*, 1993). This was followed by adding 10 ml of Lugol's solution for final preservation.

The samples were settled for 72 h in the laboratory before a series of three siphoning and settling steps were taken to obtain a 100 ml concentrate from each water sample. The first step involved separating relatively large detritus and specimens, by passing each 100 ml concentrate through a 73 μm mesh screen. The rotifers trapped on the screen were stored in two 50 ml vials before transfer to an Utermohl settling chamber for examination with an inverted plankton microscope. The two 100 ml concentrates were then combined to form a 200 ml mixture. To obtain a second subset, the 200 ml were gently swirled and thoroughly mixed in a graded cylinder. Based on the amount of detritus and plankton remaining, a 5 or 10 ml aliquot from the 200 ml mixture was taken and placed in a second settling chamber, with buffered 5% formalin solution added to total 25 ml volume. All the chambers were allowed to settle for 24 h before examination with an inverted plankton microscope at 100–200 × magnification.

Rotifer identification followed Berzins (1960), Edmondson (1959) and Pennak (1989). Biovolumes of rotifers were calculated from the approximate geometric dimensions, converted to dry weight (Ruttner-Kolisko, 1977; Pace, 1982), and finally to carbon weight assuming it to be 50% of dry weight (Salonen *et al.*, 1976).

The same carboys were the source of water used for the microzooplankton analysis of the ciliates and copepod nauplii. Ciliates were classified into two groups; aloricated and loricated ciliates. Ciliate cell volumes were calculated using a geometric formula based on their size and shape, and tintinnid cell volumes were considered as half the lorica volume (Beers & Stewart, 1969). Biomass estimations employed conversion of cell volumes to dry weight using 0·279 pg dry wt μm^{-3} (Gates *et al.*, 1982) and to carbon content using a conversion factor of 0·19 pg C μm^{-3} (Putt & Stoecker, 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).

Salinity, water temperature, dissolved oxygen (DO) and pH were measured at surface from January 1994 through December 1995 with Hydro-Lab (H20, Hydro-Lab Corporation).

Principal component analysis was performed to identify similarities in species composition at different salinity ranges and correlation analysis to clarify the relationship between rotifer species and salinity in the study area using SAS programming (SAS, 1983).

Results

Hydrology of the study area

Descriptive statistics of hydrological data are given in Table 1. Salinities ranged from 0·00 at tidal freshwater river stations to 31·90 at the Bay mouth. Depending on the tidal cycle and freshwater runoff, salinities varied at all the stations, with a maximum of 23·13 annual variation at station SBE2. Monthly variations of salinity at each station are given in Figure 2. Tidal freshwater stations had typically low salinity ranges (<0·5), except station TF33 in the Rappahannock River, which had a maximum of 10·10 with an annual average of 1·52 ± 0·47. Even though all the tidal freshwater stations had bidirectional tidal flow, salt water intrusions were only observed at the tidal freshwater station TF33. Salinity at the river–estuary transitional sites (RET31, RET43, RET52) ranged from 0·00 to 18·65, with high coefficient of

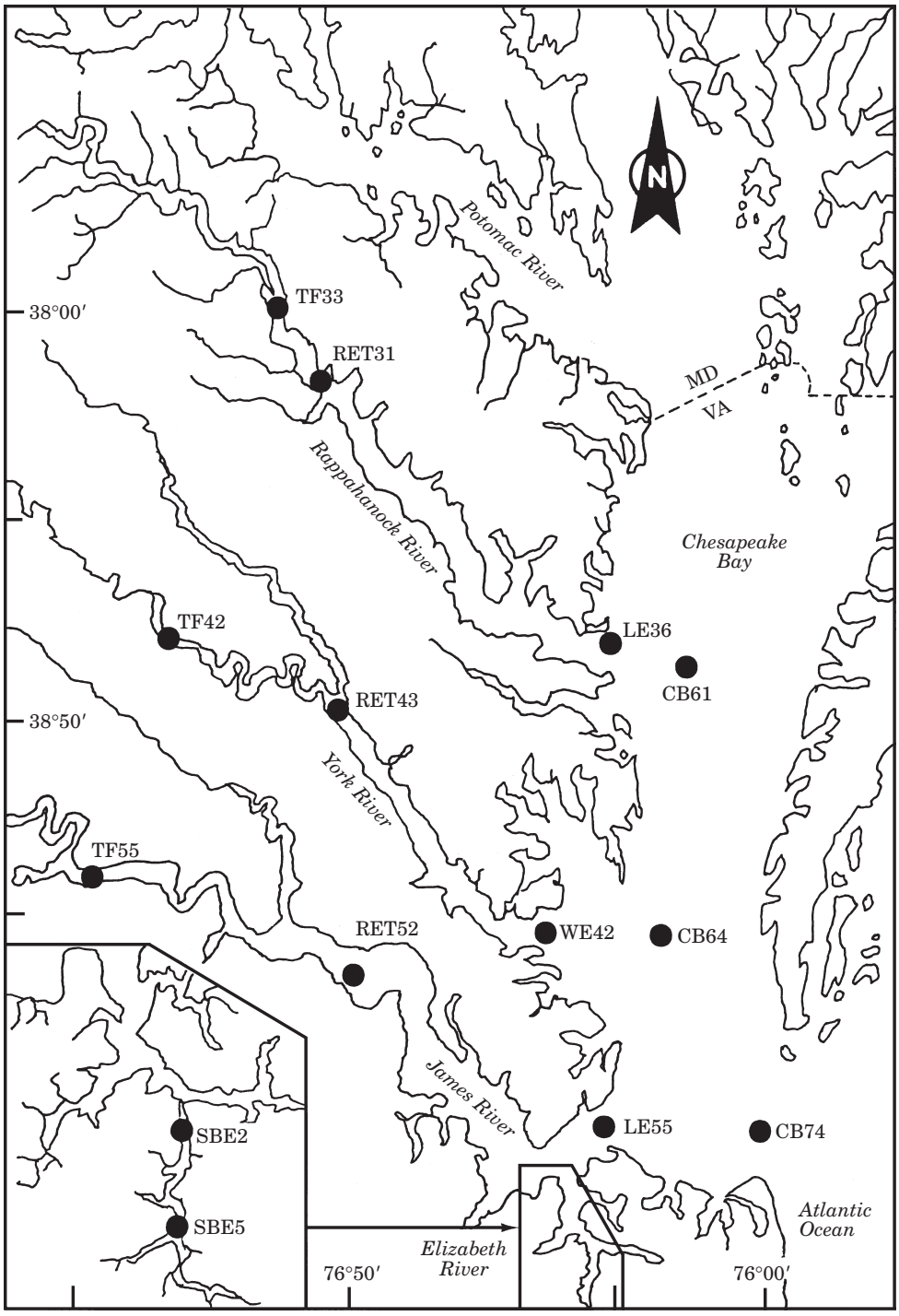

FIGURE 1. Location of sampling stations in the southern Chesapeake Bay and its major tributaries.

variation (CV) values, indicating high monthly variations of salinity at these stations. In general, these sites were in oligohaline water, with an annual mean of 4·73 ± 0·78 (RET31) and 2·31 ± 0·82 (RET52). The York River station RET43 was however continuously exposed to a higher salinity range than the other two transitional sites, including oligohaline and mesohaline waters, with an annual average of 8·96 ± 0·91. The two sites in the southern branch of Elizabeth River (SBE2, SBE5) also had wide ranges of salinity (from freshwater to mesohaline water), with an annual average of 17·97 ± 1·09 for SBE2 and 17·38 ± 0·99

TABLE 1. Descriptive statistics of water quality parameters from January 1994 through December 1995 at each station

Stations	Depth (m)	Salinity		Water temperature (°C)		DO ($mg l^{-1}$)		pH		Secchi depth (m)	
		mean ± SE	range	mean ± SE	range	mean ± SE	range	mean ± SE	range	mean ± SE	range
TF42	10	0·05 ± 0·02	0·00–0·40	17·4 ± 1·9	1·2–30·4	8·6 ± 0·7	3·6–14·8	7·2 ± 0·1	6·0–8·5	0·7 ± 0·1	0·3–1·8
TF55	9	0·07 ± 0·01	0·00–0·10	17·5 ± 1·8	3·9–30·4	9·7 ± 0·5	5·6–13·9	7·4 ± 0·1	6·6–8·1	0·5 ± 0·0	0·2–0·7
TF33	7	1·52 ± 0·47	0·00–10·10	16·2 ± 1·8	1·9–28·7	9·5 ± 0·6	5·8–14·7	7·1 ± 0·1	6·4–7·5	0·5 ± 0·0	0·1–0·8
RET52	8	2·31 ± 0·82	0·00–18·65	17·2 ± 1·7	4·0–29·2	9·7 ± 0·5	6·0–13·8	7·6 ± 0·1	6·8–8·3	0·5 ± 0·1	0·2–1·4
RET31	6	4·73 ± 0·78	0·00–16·80	16·0 ± 1·8	1·9–28·7	9·7 ± 0·6	5·5–15·2	7·1 ± 0·1	6·4–7·9	0·5 ± 0·1	0·1–1·7
RET43	6	8·96 ± 0·91	0·80–17·40	17·2 ± 1·8	2·3–29·7	9·1 ± 0·6	5·9–14·4	7·1 ± 0·1	6·1–7·8	0·5 ± 0·0	0·3–1·2
LE36	9	16·03 ± 0·60	8·70–20·41	15·5 ± 1·8	2·3–28·3	10·0 ± 0·6	6·5–19·2	8·1 ± 0·1	7·6–8·6	1·9 ± 0·1	1·3–3·3
SBE5	11	17·38 ± 0·99	0·03–22·30	19·9 ± 1·7	3·1–31·6	7·1 ± 0·5	3·5–12·8	7·4 ± 0·1	6·7–8·2	1·2 ± 0·1	0·5–2·7
CB61	13	17·51 ± 0·78	8·70–23·50	14·7 ± 1·8	1·4–27·9	9·6 ± 0·4	6·7–14·0	8·0 ± 0·1	7·0–8·4	2·2 ± 0·2	0·9–4·5
SBE2	12	17·97 ± 1·09	0·07–23·20	18·0 ± 1·7	3·5–28·3	7·6 ± 0·6	4·0–13·1	7·5 ± 0·1	6·9–8·3	1·4 ± 0·2	0·6–4·3
WE42	12	19·77 ± 0·63	12·70–24·26	16·3 ± 1·7	2·9–28·3	9·4 ± 0·5	6·1–14·9	8·0 ± 0·1	7·7–8·5	1·8 ± 0·1	0·9–2·6
CB64	11	20·44 ± 0·67	12·00–26·70	15·0 ± 1·8	2·0–28·2	9·5 ± 0·4	5·2–13·3	8·1 ± 0·0	7·6–8·3	1·9 ± 0·1	1·1–2·9
LE55	21	20·60 ± 0·68	11·20–24·30	15·0 ± 1·6	2·9–26·8	9·1 ± 0·5	6·0–14·8	7·9 ± 0·1	7·2–8·3	1·4 ± 0·1	0·8–2·3
CB74	14	27·26 ± 0·57	20·60–31·90	14·3 ± 1·6	3·3–25·5	9·2 ± 0·3	7·1–12·3	7·9 ± 0·1	7·3–8·2	2·1 ± 0·1	1·2–3·4

SE: standard error of the mean.

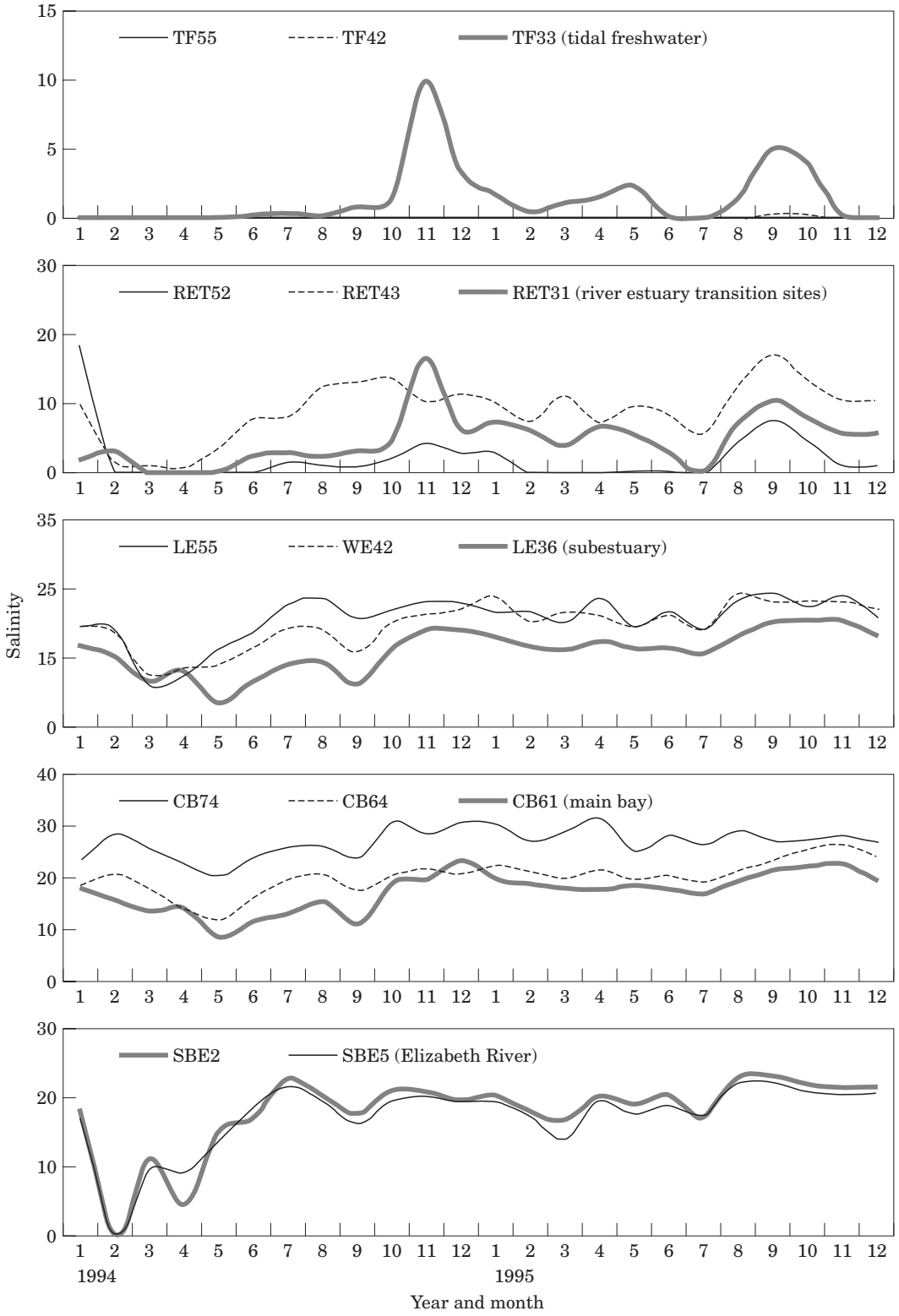

FIGURE 2. Monthly variation of salinity at each station from January 1994 through December 1995.

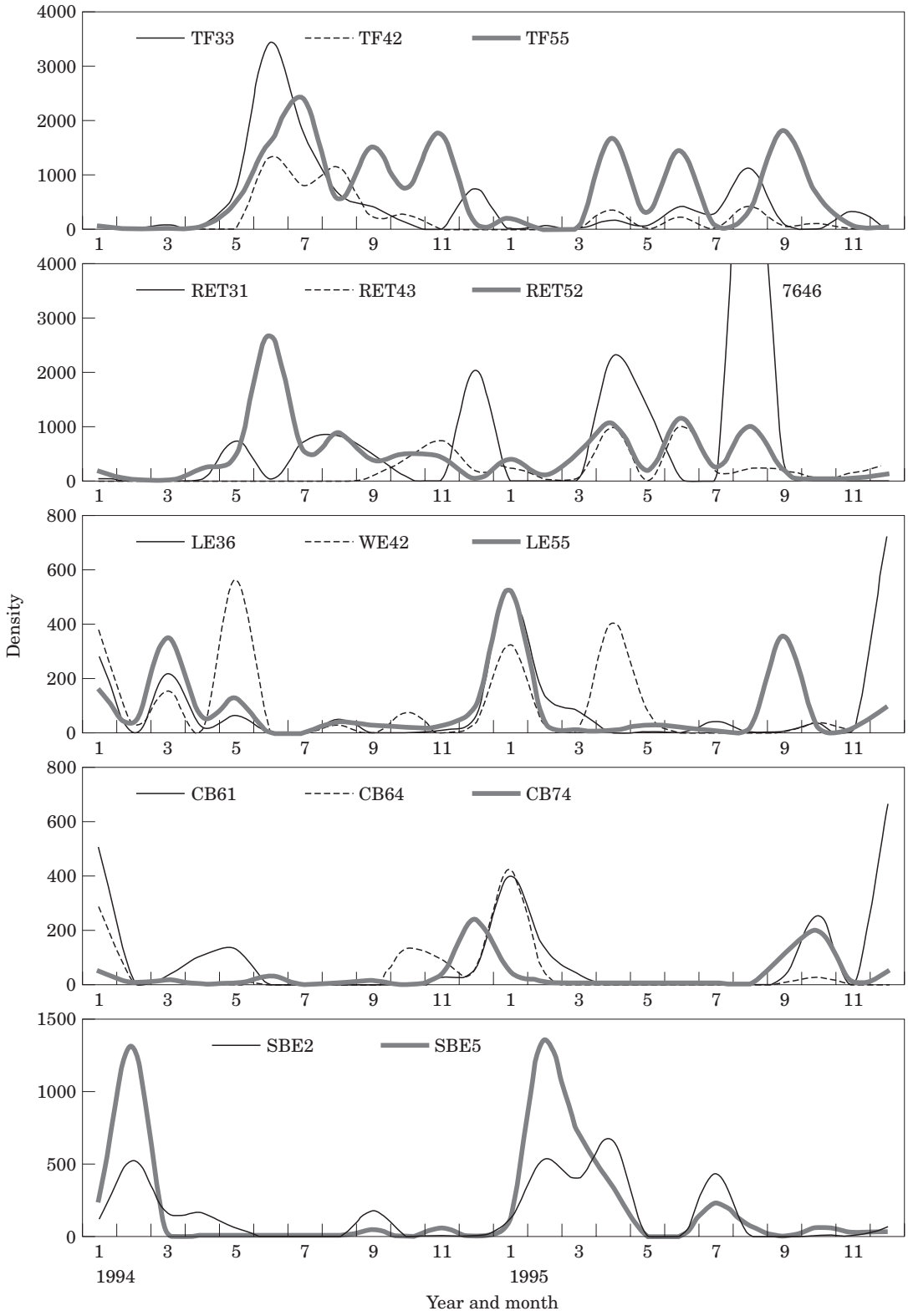

FIGURE 3. Monthly variation of rotifer density (no. l^{-1}) in the lower Chesapeake Bay and its major tributaries from January 1994 through December 1995.

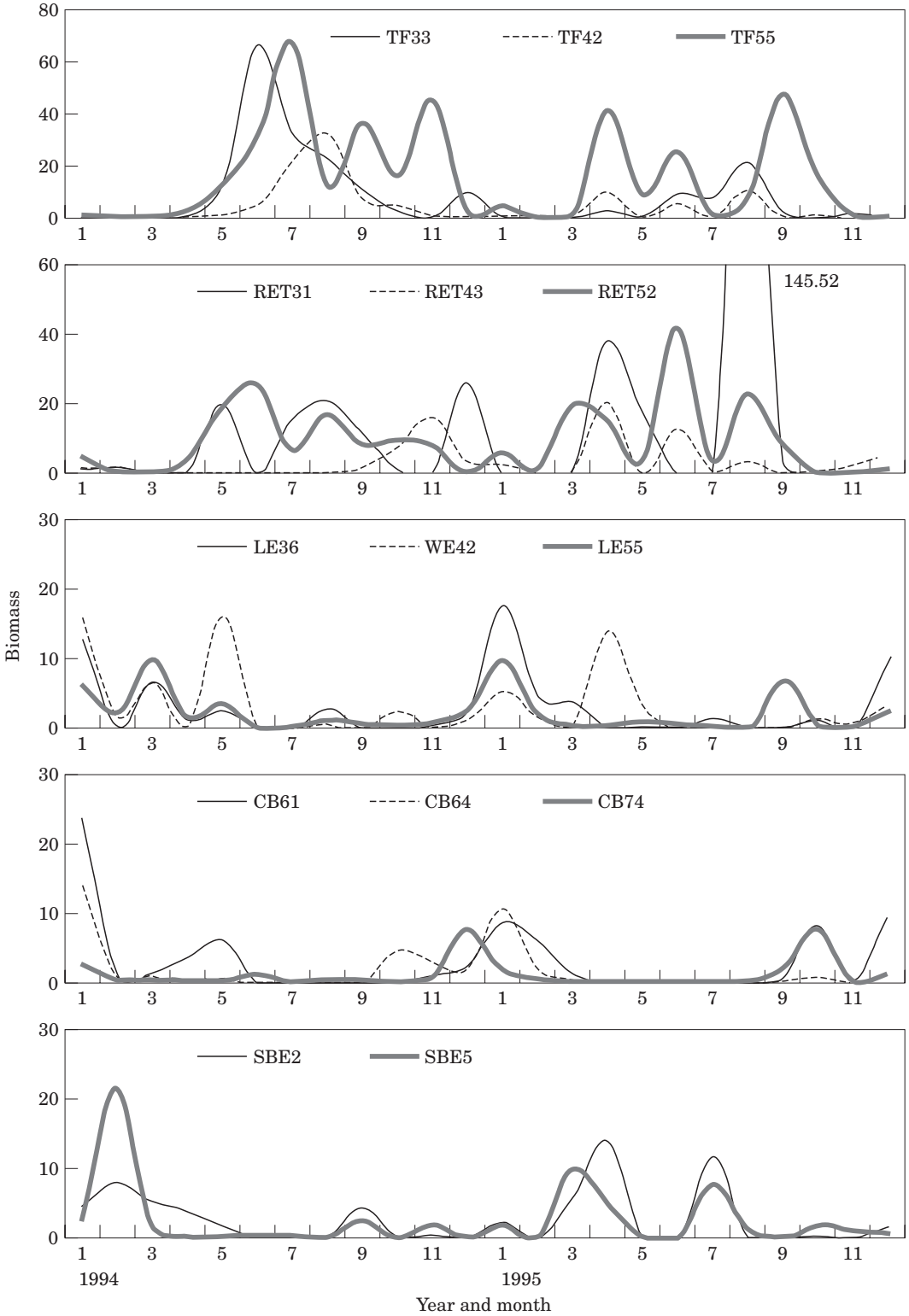

FIGURE 4. Monthly variation of rotifer biomass (μg dry wt l^{-1}) in the lower Chesapeake Bay and its major tributaries from January 1994 through December 1995.

TABLE 2. Descriptive statistics of rotifer density and biomass from January 1994 through December 1995

Stations	Density (no. l^{-1})			Biomass (μg dry wt l^{-1})		
	mean ± SE	range	CV (%)	mean ± SE	range	CV (%)
TF42	225·0 ± 76·3	0–1349	166·1	4·39 ± 1·57	0·00–32·25	175·72
TF55	675·4 ± 156·6	5–2443	113·6	16·12 ± 3·90	0·09–67·75	118·63
TF33	458·7 ± 159·3	5–3491	170·1	8·74 ± 3·06	0·11–66·36	171·43
RET52	481·1 ± 123·2	9–2682	122·8	9·69 ± 2·12	0·21–42·13	106·93
RET31	692·7 ± 330·2	0–7646	233·5	12·87 ± 6·16	0·00–145·52	234·56
RET43	197·3 ± 59·2	1–986	146·6	3·61 ± 1·12	0·01–20·69	152·51
LE36	95·1 ± 36·8	0–716	189·3	2·80 ± 0·94	0·00–17·58	163·91
SBE5	196·3 ± 78·7	0–1342	196·5	2·53 ± 0·97	0·00–21·52	189·06
CB61	101·3 ± 36·2	0–660	175·1	3·11 ± 1·10	0·00–23·76	172·63
SBE2	146·0 ± 42·1	0–668	141·4	2·70 ± 0·79	0·00–13·92	144·20
WE42	97·5 ± 31·9	0–567	160·0	3·09 ± 1·01	0·00–16·03	159·94
CB64	47·9 ± 20·6	0–420	211·1	1·67 ± 0·71	0·00–13·75	207·35
LE55	88·6 ± 27·5	0–528	152·1	2·17 ± 0·60	0·00–9·82	135·59
CB74	34·5 ± 12·5	0–237	176·5	1·13 ± 0·43	0·00–7·66	188·19

SE: standard error of the mean, CV (%) : coefficient of variation.

for SBE5. River mouth and mid bay sites (LE36, WE42, LE55, CB61, CB64) had salinity within meso- and polyhaline ranges (16·03–20·60), with relatively small seasonal variations (<25% in CV). The highest salinity (31·90) was observed at the Bay mouth (CB74), with an annual average of 27·26 ± 0·57. Temporal variation of salinity was smallest at station CB74 (13·88% in CV), having small monthly fluctuations of salinity. In terms of the annual mean salinity, the Bay mouth was polyhaline, the river mouth, upper bay and Elizabeth River were mesohaline, with the river–estuary transition sites and TF33 oligohaline, and TF42 and TF55 freshwater (Table 1). A seasonal pattern of salinity for the study period was not apparent (Figure 2).

Transparency (as measured by Secchi depth) was lowest at the tidal freshwater and oligohaline stations, ranging from 0·5 to 0·7 m, and from 1·2 to 2·2 m at the meso- and polyhaline stations as an annual average. Low transparency in the study area was due to the large input of plant debris from the drainage basin of the tributaries.

The other water quality parameters were in the typical ranges of temperate aquatic systems. Higher annual water temperature and lower DO at the Elizabeth River stations were due to the cooling water from the adjacent power plants. Lower pH at the freshwater stations reflects the different buffering capacity between salt and freshwater.

Distribution patterns and species composition of rotifers

Rotifers were most abundant at freshwater and river–estuary transition sites during summer, and at the Bay and Elizabeth River stations during late fall through to winter (Figure 3). Rotifers were absent in the samples from the meso- and polyhaline stations during summer and from the freshwater stations during winter. Their concentrations ranged from zero to a maximum of 7646 individuals l^{-1} at station RET31 in August 1995. All the tidal freshwater (TF33, TF42, TF55) and two river–estuary transition sites (RET31, RET52) had mid-summer peaks (July or August). Station RET43 showed a fall peak (October) due to the high abundance of *Synchaeta* and *Trichocerca* species. In the meso- and polyhaline stations rotifers had a maximum density and biomass from late fall through to winter (Figures 3, 4).

R-strategy principal component analysis using annual mean values of major species composition (Table 3) revealed clear species and station groups (Figure 5). The station coordinates was used to identify community similarities between stations. Principal components I, II, and III accounted for 52, 23, and 12% of the total variation, respectively. Bay and river mouth stations were clearly separated from the river–estuary transition sites and freshwater stations. This separation of station groups was mainly due to the dominance of cold water assemblages, *Synchaeta baltica* and *S. curvata*, in the meso- and polyhaline stations, and summer assemblages in the freshwater stations. Station RET43 was located close to the Bay and river mouth station group on the hypospace owing to the low abundance of freshwater species such as *Keratella cochlearis*, *Brachionus anguralis*, *B. calyciflorus* and *Filinia longiseta*. The highest species diversity of rotifers was found at the oligohaline stations (RET31, TF33, RET52)

TABLE 3. Spatial composition of major rotifer species. Values are annual mean (no. l^{-1}) of each station ordered by annual mean salinity

Species name	Stations													
	TF42	TF55	TF33	RET52	RET31	RET43	LE36	SBE5	CB61	SBE2	WE42	CB64	LE55	CB74
Brachionus angularis (BA)	0·9	15·8	24·8	21·0	16·6	0·4	0·0	0·0	0·0	0·8	0·0	0·0	0·0	0·0
B. calyciflorus (BC1)	0·3	63·8	3·8	4·3	1·2	0·4	0·0	0·4	0·4	0·0	0·0	0·0	0·0	0·0
B. caudatus (BC2)	0·2	48·3	0·8	4·3	0·3	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
B. pterodinoides (BP)	0·3	2·8	2·6	0·3	12·4	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
Filinia longiseta (FL)	17·3	45·5	21·0	12·5	18·3	0·3	0·0	0·4	0·0	0·0	0·0	0·0	0·0	0·4
Hexarthra fennica fennica (HF)	1·8	3·2	5·4	1·5	5·8	0·4	0·0	0·0	0·0	0·4	0·0	0·0	0·0	0·0
H. rousseleti (HR)	0·1	2·5	2·3	2·9	5·3	0·0	0·0	0·0	0·0	0·1	0·0	0·0	0·0	0·0
Keratella cochlearis (KC)	67·6	78·4	39·3	119·4	8·8	1·7	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·4
Notholca acuminata (NA)	15·1	11·8	2·8	14·5	0·4	0·4	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
Poleosoma trunctatum (PT)	0·4	21·9	6·0	6·3	0·6	0·4	0·0	0·0	0·0	0·0	0·4	0·0	0·0	0·0
Polyarthra vulgaris (PV)	68·8	18·3	49·8	74·3	14·5	1·6	0·0	0·0	0·0	0·4	0·0	0·0	0·8	0·0
Synchaeta baltica (SB)	1·9	5·6	0·1	17·5	3·7	1·9	24·9	71·8	22·3	41·8	2·8	14·0	16·6	12·8
S. curvata (SC)	8·1	12·0	3·8	8·3	12·1	1·4	19·3	24·8	2·1	29·5	38·9	19·8	7·5	12·6
S. fennica (SF)	0·4	38·5	4·3	24·9	189·9	69·1	46·6	75·8	53·8	5·5	18·4	8·5	25·8	0·2
Trichocerca marina (TM)	45·0	134·3	254·3	137·4	397·6	19·7	4·4	17·8	6·0	24·2	19·8	5·8	38·8	8·8

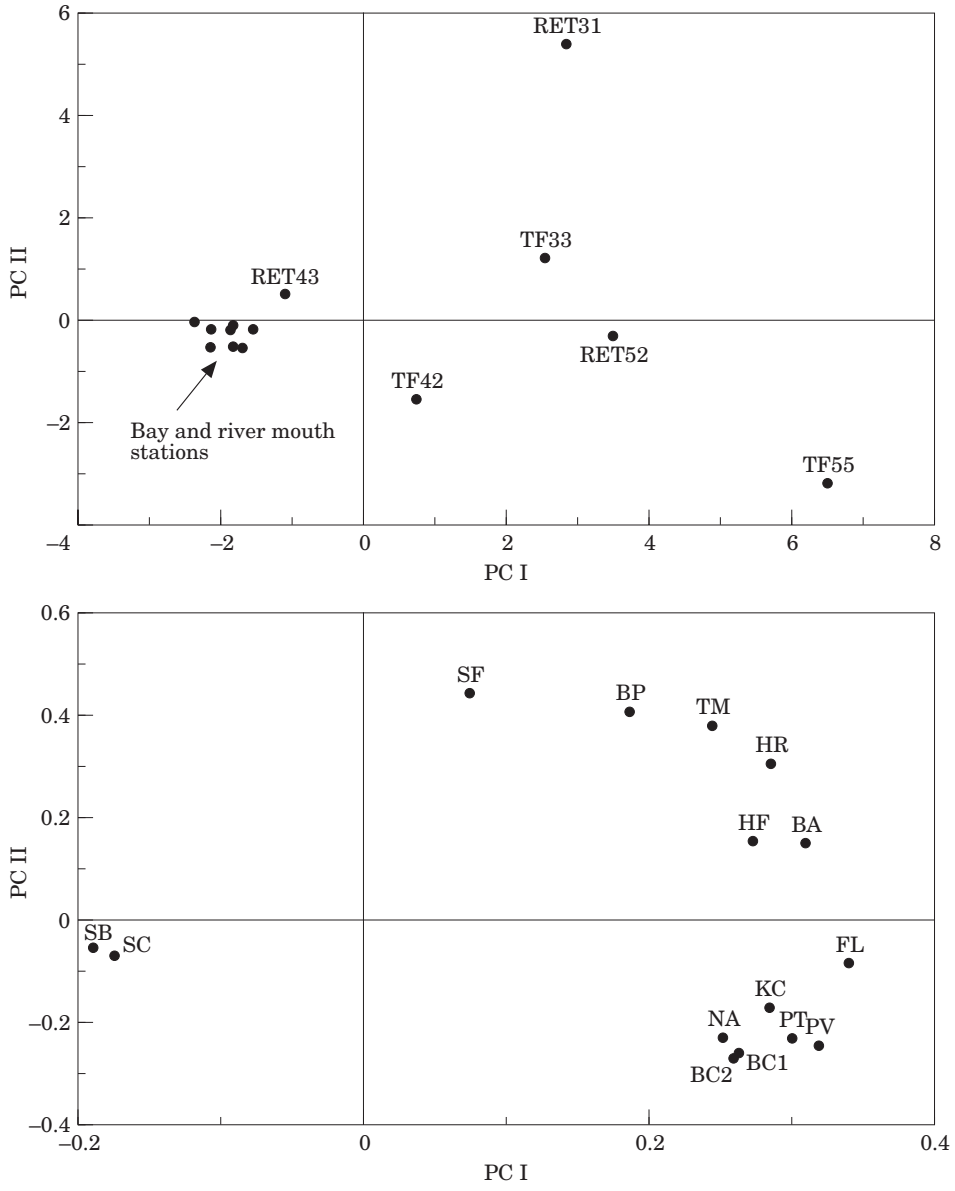

FIGURE 5. Principal component ordination of sampling stations (top) and rotifer species (bottom) using the annual mean density from January 1994 through December 1995. Abbreviations refer to Table 3.

dominated by freshwater and brackish water species depending on the salinity changes. High density of *S. fennica* made the positive movement of station RET31 on principal component axis II. Even though the tidal freshwater stations (TF42, TF55) showed very similar species compositions, station TF55 moved positively on principal component axis I due to the higher density of rotifers. *Synchaeta baltica* and *S. curvata* exclusively dominated the mesohaline stations from late fall through early winter, and *Trichocerca marina* and *Polyarthra vulgaris* were ubiquitous throughout the stations and seasons.

Contribution of rotifers to the total zooplankton biomass

The relative contribution of rotifers to the total microzooplankton biomass exclusive of heterotrophic dinoflagellates was highly variable depending on station locations and seasons (Table 4, Figure 6). 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% (Figure 6). During winter, rotifers were a major component of the

TABLE 4. Microzooplankton biomass compositions (μg C l^{-1}) with salinity gradients. Stations are ordered by annual mean salinity

Sites	Rotifers		Copepod nauplii		Ciliates		Total biomass
	biomass	percent	biomass	percent	biomass	percent	
TF42	2·2 ± 0·8	8·9 ± 1·9	11·2 ± 2·4	51·4 ± 4·6	5·3 ± 0·9	39·7 ± 5·0	18·7 ± 3·2
TF55	8·1 ± 2·0	16·6 ± 2·8	13·2 ± 3·1	36·1 ± 4·3	14·5 ± 2·6	47·3 ± 4·4	35·8 ± 5·8
TF33	4·4 ± 1·5	8·1 ± 2·0	39·6 ± 9·1	65·0 ± 4·8	10·4 ± 1·9	26·9 ± 4·1	54·5 ± 10·0
RET52	4·9 ± 1·1	9·1 ± 1·5	34·6 ± 7·0	55·9 ± 5·0	15·1 ± 2·7	35·0 ± 5·2	54·5 ± 8·8
RET31	6·4 ± 3·1	7·3 ± 2·5	48·6 ± 15·8	53·1 ± 5·8	18·3 ± 3·1	39·6 ± 6·1	73·3 ± 16·4
RET43	1·8 ± 0·6	4·4 ± 1·0	28·2 ± 4·5	53·1 ± 5·2	19·3 ± 3·5	42·6 ± 4·9	49·2 ± 6·0
LE36	1·4 ± 0·5	5·6 ± 2·0	20·9 ± 4·8	48·9 ± 5·9	14·4 ± 2·2	45·5 ± 5·1	36·7 ± 5·3
SBE5	1·3 ± 0·5	4·2 ± 1·4	28·2 ± 7·2	57·8 ± 6·9	11·3 ± 2·4	38·0 ± 6·1	40·7 ± 7·1
CB61	1·6 ± 0·6	5·3 ± 1·8	28·7 ± 7·7	55·1 ± 6·5	14·8 ± 2·6	39·7 ± 5·6	45·1 ± 8·3
SBE2	1·4 ± 0·4	5·0 ± 1·3	23·9 ± 6·8	58·7 ± 7·1	10·6 ± 2·0	36·2 ± 6·2	35·8 ± 7·1
WE42	1·5 ± 0·5	6·7 ± 2·5	28·2 ± 5·5	54·6 ± 5·8	14·1 ± 2·3	38·7 ± 4·7	43·8 ± 5·9
CB64	0·8 ± 0·4	2·8 ± 1·2	25·6 ± 5·9	55·0 ± 6·5	15·2 ± 2·9	42·3 ± 5·9	41·7 ± 6·3
LE55	1·1 ± 0·3	3·7 ± 1·3	24·9 ± 4·5	54·9 ± 5·2	16·4 ± 2·7	41·4 ± 4·7	42·4 ± 5·2
CB74	0·6 ± 0·2	3·5 ± 2·5	25·3 ± 4·8	59·8 ± 5·6	12·7 ± 2·6	36·7 ± 5·3	38·6 ± 5·1

microzooplankton biomass at the Bay stations, occupying 10–20% of the total microzooplankton biomass, even exceeding the biomass of copepod nauplii, whereas their relative contribution was less than 5% at the tidal freshwater stations. During spring and fall, rotifers generally comprised the smallest proportion of the total microzooplankton biomass, although some sites (TF55, WE42) had relatively higher values.

Copepod nauplii and ciliates contributed the major proportion of the total microzooplankton biomass, representing 44% as an annual mean carbon content (Figure 6). Copepod nauplii were abundant in the estuarine waters, and comprised the highest proportion of the annual total microzooplankton biomass throughout the stations. Their density and biomass at the freshwater stations (TF55, TF42) were however relatively lower due to increased rotifer biomass. In contrast, station TF33 had higher concentrations of copepod nauplii compared to the other tidal freshwater stations. This difference in copepod nauplii density may be due to the higher salinity ranges at station TF33 than the other tidal freshwater stations.

Discussion

Rotifers were the dominant microzooplankton component at freshwater and oligohaline sites during summer, and at meso- and polyhaline stations during winter. Their contribution to the total microzooplankton biomass during the seasons at these stations was comparable to the copepod nauplii and ciliate biomass. The annual mean contribution of rotifers to the total microzooplankton biomass was however low compared to the ciliates and copepod nauplii. At freshwater stations the annual contribution of rotifers in carbon content was about 13%, and that of copepod nauplii and ciliates about 44%. Similarly, Pace (1986) reported biomass distribution as 52% ciliates, 18% rotifers, and 30% nauplii from lakes in Quebec.

When considering the high specific growth rates and short generation time of rotifers, their trophic contribution in both freshwater and estuarine systems may be significant as a major grazer of algae and small ciliates (Havens, 1991; Arndt, 1993; Gilbert & Jack, 1993), and a prey for large crustaceans, copepods, and larval fish (Polgar & Souza, 1981; Setzler-Hamilton *et al.*, 1981; Williamson, 1983; Stoecker & Egloff, 1987; Telesh, 1993; Conde-Porcuna & Declerck, 1998). Virro and Haberman (1993) estimate that the contribution of rotifers to the total zooplankton production ranged from 13·6 to 89·8%. Heinbokel *et al.* (1988) reported a significant contribution of *Synchaeta* to the trophic flow of carbon in the Potomac River, a tidal tributary of Chesapeake Bay.

Salinity is considered here to be an important variable to explain the spatial variations of rotifer density. Using annual mean values of salinity, rotifer biomass, and density from the 14 stations, salinity had a significant negative correlation with density and biomass (Figure 7). PCA using the species composition data at each station also revealed clear site groups depending on the annual salinity ranges. Negative movement of station RET43 reflects changes of rotifer community structure similar to the Bay and river mouth assemblages (Figure 5),

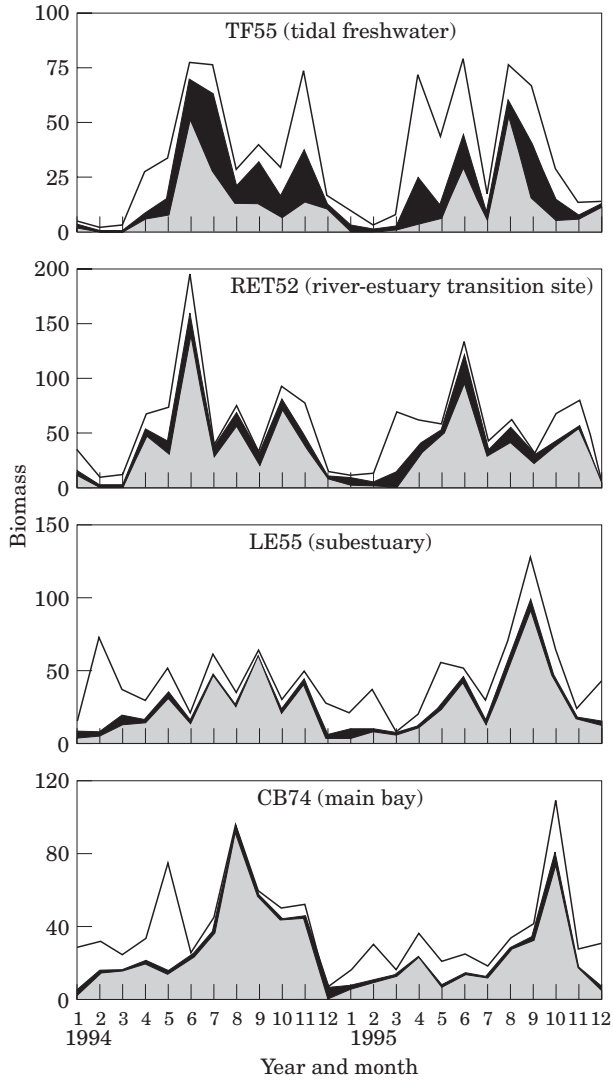

FIGURE 6. Temporal and spatial changes of rotifer (black), copepod nauplii (shaded), and ciliate (white) contribution to the total microzooplankton biomass (μg C l^{-1}) in the lower Chesapeake Bay and James River.

associated with higher salinity ranges than the other transition sites (Table 1). Separation of station TF33 from the other tidal freshwater stations was also associated with a higher salinity at this station (Table 1, Figure 2). With the increase of salinity the rotifer diversity decreased significantly (Table 3).

In terms of size ranges, rotifers and copepod nauplii may play similar trophic roles in freshwater and estuarine systems, respectively. Rotifers may provide an additional major food resource in place of metazoan nauplii during specific seasons and sites; e.g. in winter in meso- and polyhaline waters when the copepod nauplii density was low. The contributions of rotifers to the total microzooplankton biomass was about twice as high in the freshwater stations as in the meso- and polyhaline stations (Table 4). Rotifers may also partially replace the trophic role of metazoan nauplii in freshwater systems when the density of metazoan nauplii decrease.

In addition to the copepod nauplii, planktonic ciliates were also major constituents of the microzooplankton representing 35–47% of total microzooplankton carbon content (Park & Choi, 1997). They may compete with rotifers for bacterioplankton (Buikema *et al.*, 1978), and reach their maximum density in spring and fall when rotifer density was low in the Chesapeake Bay (Park & Marshall, 1998). Dolan and Gallegos (1992) also reported a negative relationship between rotifers and herbivorous ciliates in the Rhode River estuary of Chesapeake Bay.

Rotifer contributions to the zooplankton community may also increase with eutrophication (Zankai, 1989; Park & Marshall, 2000). In hypereutrophic Elizabeth River stations (SBE2 and SBE5), representing annual mean DIN and DIP values of 981 μg l^{-1} and 45 μg l^{-1} in 1994, respectively, rotifer contribution (%) to the total zooplankton

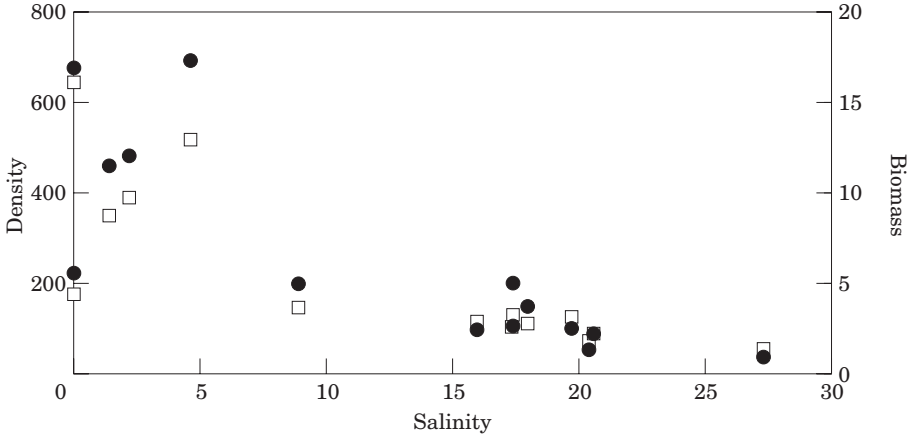

FIGURE 7. Relationship between salinity and rotifer density (no. l^{-1}) and biomass (μg dry wt l^{-1}). Closed circles: density, r=0·82, P<0·01; open squares: biomass, r=0·79, P<0·01.

biomass (as carbon) including meso- and microzooplankton positively correlated with DIN (N=8, r=0·89, P=0·005) and DIP (N=8, r=0·85, P=0·008). However, there was no significant correlation between rotifer biomass and eutrophication (Park & Marshall, 2000).

Trophic contributions by rotifers have been reported by Hernroth (1983) and Andrew and Fitzsimons (1992) to occur during a short time period (2–3 months per year), but dominated only by a few species. Cajander (1983) noted 49% of the total annual production in a Finnish lake was achieved during one month (July) and 88% during 3 months of summer. In the present study, more than 50% of the annual rotifer biomass was in summer at the freshwater stations and during winter in estuarine waters. These results support findings of earlier studies that rotifers have seasonal periods of significant biomass contributions in tidal freshwater and estuarine waters.

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