Estuarine, Coastal and Shelf Science (1998) **47,** 261–273
Article No.ec980364

Temporal and Spatial Dynamics of Planktonic Rotifers in the Elbe Estuary during Spring

H. Holst[a,c], H. Zimmermann[a], H. Kausch[a] and W. Koste[b]

[a]*Institut für Hydrobiologie und Fischereiwissenschaft, Hydrobiologische Abteilung, Universität Hamburg,*
D-22765 Hamburg, Zeiseweg 9, Germany
[b]*Ludwig-Brill-Strasse 5, D-49410 Quakenbrück, Germany*

Received 11 August 1997 and accepted on 8 April 1998

The spatial and temporal distribution of planktonic rotifers in the Elbe Estuary, Germany, was investigated at weekly intervals from March to July, 1995. Samples were taken at a fixed site in the Hahnöfer Nebenelbe, and the main channel was surveyed four times at eight stations from Hamburg to the upstream limits of the brackish-water zone. Abiotic and biotic parameters were determined and correlated with rotifer abundance to gain information about the forces that structure the rotifer community in this dynamic environment. A maximum density of 2048 ind. l^{-1} was observed at the beginning of June. More than 70 rotifer species were identified during the whole period, but only a few of them appeared at significant densities. The predominant species were *Keratella cochlearis*, which accounted for over 32% of the total abundance, *Keratella quadrata*, *Brachionus calyciflorus* and species of the genera *Synchaeta* and *Polyarthra*. At the end of July *Synchaeta bicornis* appeared at the low density of 23 ind. l^{-1} at the station farthest downstream. Except for this typical brackish-water species, all rotifers encountered belonged to freshwater taxa, which decreased in abundance rather rapidly toward the river mouth. From March to the middle of June, rotifers grazed predominantly on heterotrophic components of the microbial food-web, such as planktonic and aggregate-associated bacteria, detritus and heterotrophic flagellates. Toward the end of June, the chlorophyll *a* concentration increased sharply, and a new rotifer community established itself, feeding mainly on autotrophic organisms in the Elbe Estuary.

Keywords: rotifers; mesoplankton; microplankton; seasonal variation; spatial distribution; Elbe Estuary

Introduction

The seasonal dynamics of planktonic populations in lacustrine environments of the northern hemisphere have been well studied and generally conform to the PEG model of seasonal succession of planktonic events in fresh waters (Sommer *et al.*, 1986). Rotifers are important components of planktonic communities seasonally. In early spring, because of their rapid heterogonetic reproduction, they are the first metazooplankters to cause an impact by grazing on the phytoplankton. Furthermore, rotifers influence various interactions within the microbial food-web which occur at several trophic levels (Arndt, 1993).

While many studies have dealt with rotifers in lentic systems, considerably fewer have provided data about them in lotic environments, especially estuaries. Only about 4% of all publications on flowing waters concern large rivers (Hynes, 1989), and in these, little attention has been paid to the ‘potamoplankton’ (Thorp *et al.*, 1994) which, in any case have often focused on crustaceans. Rotifer abundance was either not mentioned, or the samples were taken in nets with mesh sizes larger than 35 µm which underestimate their abundance (Green, 1977; Orcutt & Pace, 1984). Nevertheless, rotifers are well adapted to river ecosystems, where zooplankton abundance is often regulated by advective losses (Ketchum, 1954), and population densities are maintained by rapid heterogonetic reproduction with short generation times (Stemberger & Gilbert, 1985). Estuarine zooplankton studies which took rotifers into consideration were conducted in the Rhine (Admiraal *et al.*, 1994; Van Dijk & Van Zanten, 1995), Hudson (Pace *et al.*, 1992; Vaque *et al.*, 1992), Westerschelde (Bakker & Pauw, 1975; Soetaert & Van Rijswijk, 1993), Guaraú (Lopes, 1994), Vistula (Adamkiewicz-Chojnacka & Rózanska, 1990), and Sacramento Rivers (Orsi & Mecum, 1986), and in San Francisco Bay (Ambler *et al.*, 1985).

Detailed studies dealing only with rotifers in estuarine environments are rare (Egborge & Tawari, 1987; Heinbokel *et al.*, 1988; Guisande & Toja, 1988; Papinska, 1990; Dolan & Gallegos, 1991, 1992; Neumann-Leitâo *et al.*, 1992; Egborge, 1994; Green,

---

[c]Corresponding author.

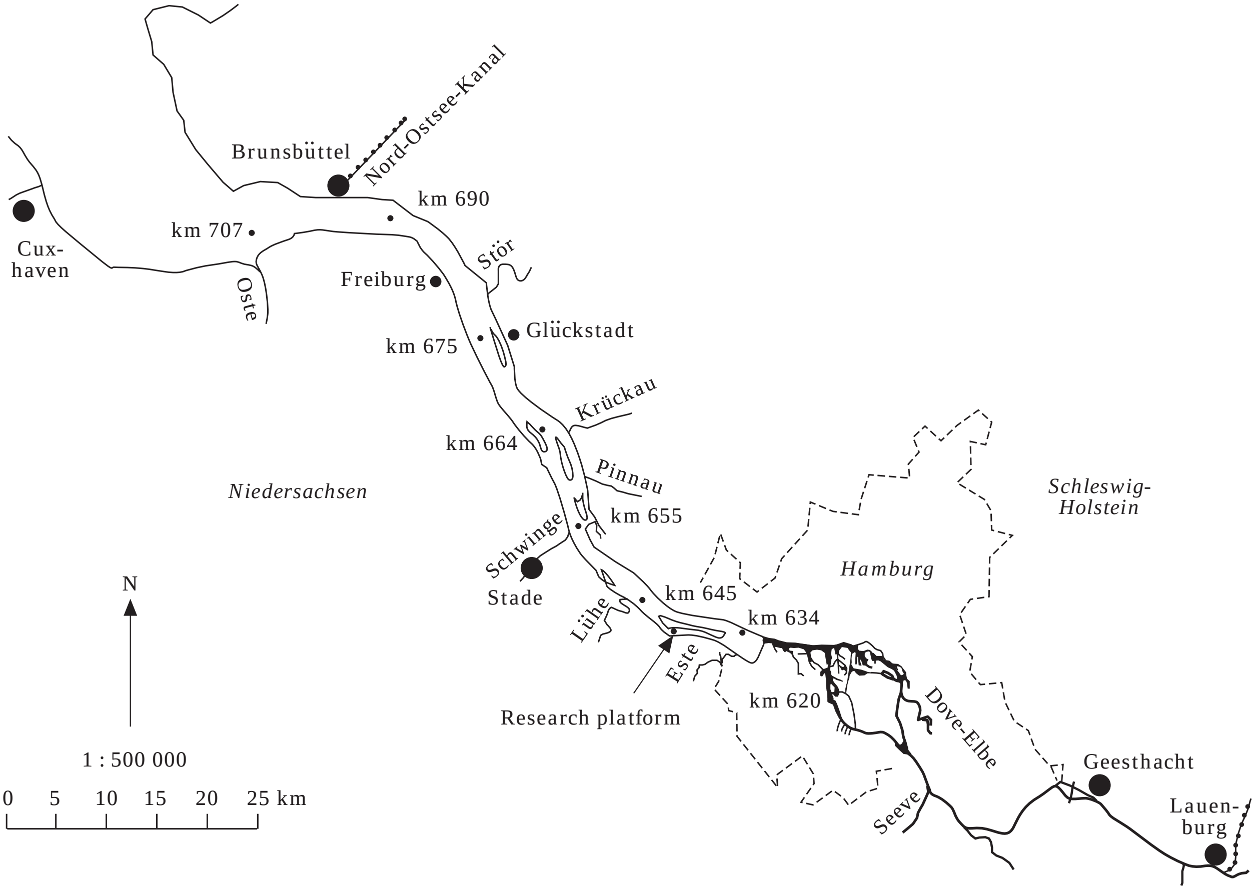

FIGURE 1. Map of the Elbe Estuary, Germany, showing the sampling stations in the main channel from km 620 to km 707 and in the Hahnöfer Nebenelbe where the platform lab was anchored.

1995; Telesh, 1995). Information about seasonal changes in various abiotic and biotic parameters in the Elbe Estuary are available, but the most recent information about the abundance and dynamics of rotifer populations was provided by Schulz (1961) and Nöthlich (1972), who conducted comprehensive studies.

In the spring of 1995, a survey was carried out to characterize the rotifer fauna and their temporal and spatial dynamics in relation to abiotic and biotic parameters at different locations in the Elbe Estuary.

Materials and methods

Study site

The Elbe Estuary is a coastal-plain estuary, classified as ‘ partially mixed ’ (Day, 1981) and characterized by salinity gradients and a large amount of suspended particulate matter (Kausch, 1990). It extends about 140 km between the funnel-shaped river mouth at Brunsbüttel and Cuxhaven, where it flows into the North Sea, and a weir at Geesthacht, 45 km upstream from Hamburg, which forms the upper tidal boundary (Figure 1).

The mean river discharge is about 700 $m^3 s^{-1}$, and the current velocity reaches 1–2 $m\ s^{-1}$. Although the pollution of the Elbe River has been reduced since 1990, it is still one of the most polluted European rivers and carries high loads of sewage and wastes (Adams *et al.*, 1996).

Sampling

Samples were collected weekly from March to July 1995 from a research platform anchored in the Hahnöfer Nebenelbe (km 640), a shallow backwater 15 km downstream from Hamburg (Figure 1) and in the main channel between Hamburg (km 620) and the mouth of the estuary at km 707. Samples were taken from the research platform 1 and 2 h before low tide, at low tide and 1 and 2 h after low tide. Water was collected at a depth of 1 m using a 2·25 l horizontal tube constructed by HYDROBIOS in Kiel, Germany. Samples were taken from the main channel at low tide from a research vessel, which sailed from km 707 to km 620. Data were collected from eight stations approximately 10 km apart (Figure 1). At each station, one sample was taken from the surface using a horizontal sampler.

Rotifers

The sample volume of 2·25 l was filtered through a 30 µm sieve, and the organisms were fixed in 200 ml of 5% formaldehyde (Koste, 1978). The specimens were counted in sedimentation chambers at 60–100 × magnification using an inverted OLYMPUS microscope. Three samples taken at each date were counted completely to detect taxa represented by very few individuals and two samples were separated into subsamples containing at least 100 individuals of the dominant species. In addition, live rotifers were examined to obtain qualitative information about the soft-bodied (illoricate) species which are difficult to identify and easily overlooked in preserved samples. In some cases, reliable species identification requires examination of the trophi, after the animals were macerated in 5% NaOH (Koste, 1978).

Additional parameters

For chlorophyll *a* determinations, 150–500 ml samples were concentrated on a WHATMAN GF/F glass-fibre filter and analysed spectrophotometrically after hot ethanol extraction following Nusch (1980). For determining bacterial, flagellate and ciliate abundance, the number of aggregate associated organisms (Zimmermann & Kausch, 1996; Zimmermann, 1997) and planktonic organisms per litre were added together.

For determination of aggregate associated organisms, aggregates were selected from the horizontal sampling tube with a pipette and were counted under a dissecting microscope in five bottles with openings 5 cm in diameter. Several aggregates were always examined under a microscope at 10 × magnification and their size was measured using an ocular micrometer. The mean area of at least 20 particles per sample was calculated from the number of particles and the longest dimensions multiplied by the mean width of each particle. Ciliates and flagellates were counted using the live counting technique at 20 × and 40 × magnification. Bacteria were dislodged by ultrasonic vibration, stained and counted on filters (Porter & Feig, 1980).

Samples for determinations of planktonic flagellate abundance were fixed in 1·5% formalin and stained with fluorochrome, 4′,6-diamidino-2-phenylindole (DAPI), by the method of Porter and Feig (1980) and counted on black membrane filters. In 0·2 l samples, the planktonic ciliates were fixed in 0·06% HgCl and counted at 200 × magnification under the Uthermöhl inverted microscope (Utermöhl, 1958).

From the research platform, pH, dissolved oxygen [%], conductivity [$\mu S\ cm^{-1}$], water temperature [°C] and current veloctiy [$m\ s^{-1}$] were determined using a multiprobe exposed at a depth of 2 m (G. Schymura, GKSS in Geesthacht, pers. comm.). In the main channel, conductivity [$\mu S\ cm^{-1}$] was recorded using a transportable WTW LF-96 Conductometer from the research vessel. In addition temperature [°C] and dissolved oxygen [%] were determined using a transportable WTW OXI-96 Oximeter. Water discharge rates were measured by the ARGE ELBE (T. Gaumert in Hamburg, pers. comm). Spearman rank correlation coefficients (*r*) were computed using SPSS for the following parameters: rotifer abundance with temperature, river discharge, chlorophyll *a* concentration and bacteria, flagellate and ciliate abundance at an alpha level between 0·01 and 0·05.

Results

Hahnöfer Nebenelbe (Stationary sampling)

From March to the middle of April, water temperature showed a slow increase from 4·7 to 8·9 °C, rising 17·6 °C in June and 21·8 °C in July (Figure 2).

During March the river discharge decreased then rose to a maximum of 1863 $m^3\ s^{-1}$ at the end of April. In May, the discharge dropped rapidly to 841 $m^3\ s^{-1}$ followed by a small peak at the end of the month, caused by heavy rainfall. During June, the discharge rose again to a second maximum of 1732 $m^3\ s^{-1}$ (T. Gaumert, pers. comm.; Figure 2).

During March and April, chlorophyll *a* concentration was low (12 $\mu g\ l^{-1}$). In early May, a slow increase in the amount of phytoplankton was observed, and by the middle of June, the chlorophyll *a* concentration had reached 78·6 $\mu g\ l^{-1}$ (Figure 2). In July, the chlorophyll *a* concentration reached a value of 495·5 $\mu g\ l^{-1}$, which resulted from a bloom of centric diatoms, mainly *Actinocyclus normanii*.

The number of planktonic and aggregate-associated bacteria was low at the beginning of the investigation, but a maximum abundance of $20{\cdot}8 \times 10^9$ cells l^{-1} was quickly reached in the middle of April, followed by a graduate decline throughout the next few weeks. A small peak of $17{\cdot}2 \times 10^9$ cells l^{-1} was reached in the middle of June (Figure 2).

Flagellate abundance also reached a maximum of $6{\cdot}0 \times 10^6$ cells l^{-1} in the middle of April. There was

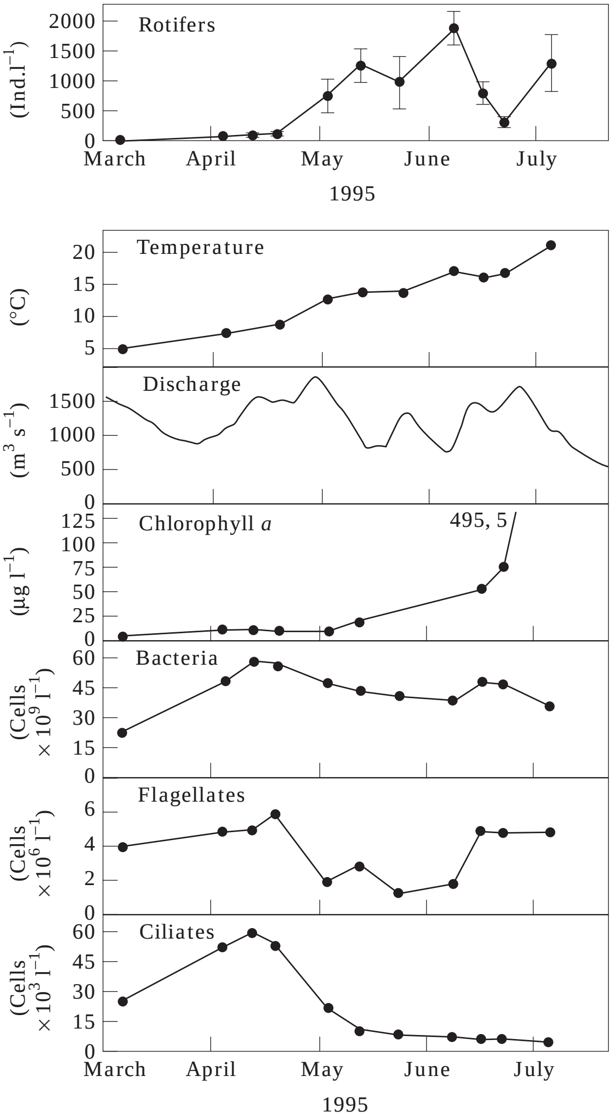

FIGURE 2. Changes in rotifer abundance (ind. l^{-1}), water temperature (°C), river discharge (m^3 s^{-1}), chlorophyll *a* concentration (µg l^{-1}), bacteria (cells × 10^9 l^{-1}), flagellates (cells × 10^6 l^{-1}) and ciliates (cells × 10^3 l^{-1}) in the Hahnöfer Nebenelbe between March and July 1995.

then a sharp decrease in the numbers and abundance remained low throughout May. In June, flagellate abundance increased again to 5·0 × 10^6 cells l^{-1} at the end of the month. Planktonic and aggregate-associated ciliates reached maximum abundances of 60·8 × 10^3 cells l^{-1} in April and were low throughout the rest of the investigation (Figure 2).

During March and early April the rotifer density was below 200 ind. l^{-1} . In the middle of May, the numbers had reached 1389 ind. l^{-1}. A maximum density of 2048 ind. l^{-1} was reached at the beginning of June, followed by a decrease to 895 ind. l^{-1} at the end of the month. At the beginning of July, the rotifer density had risen again to 1439 ind. l^{-1} (Figure 2). A significant negative correlation between the total rotifer abundance and river discharge was observed ($r_s = -0{\cdot}618$, $\alpha = 0{\cdot}05$), and there was a positive correlation between rotifer abundance and water temperature ($r_s = 0{\cdot}830$, $\alpha = 0{\cdot}01$). Samples from different depths and during different tidal phases indicated that the distribution of rotifers was random. During the period of the investigation, 77 rotifer species were encountered in the Hahnöfer Nebenelbe (Table 1). The numerically dominant rotifer was *Keratella cochlearis*, which, including the variety *K. cochlearis* var. *tecta*, accounted for over 32·4% of the total rotifer community. Other very common species included *Keratella quadrata*, *Brachionus calyciflorus*, species of the genus *Synchaeta* such as *Synchaeta pectinata*, *Synchaeta stylata* and *Synchaeta tremula* and members of the *Polyarthra vulgaris-dolichoptera* group. These accounted for 17·5, 16·7, 9·8 and 8·7% of the total number of individuals, respectively (Figure 3).

At the beginning of the investigation in early March, *K. quadrata* and *Polyarthra* sp. were the dominant rotifers but the abundance of each taxon remained below 10 ind. l^{-1} (Figure 4). *Brachionus calyciflorus*, mainly *B. c.* f. *anuraeformis* and *K. quadrata* were the most common rotifers in early April at densities between 30 and 50 ind. l^{-1}. At the beginning of May, species of the genus *Notholca*, predominantly *Notholca squamula* and *Notholca acuminata*, reached their peak abundances of 32 and 11 ind. l^{-1}, respectively. *Filinia* spp., mainly *Filinia longiseta*, also reached a maximum of 25 ind. l^{-1} (Figure 4).

In mid-May, *Asplanchna priodonta* attained a short-term peak of 67 ind. l^{-1}, and *Polyarthra* sp. had also reached a maximum abundance of 125 ind. l^{-1}. The slight decrease in total rotifer abundance observed on 22 May affected almost every taxon (Figure 4). The peak at the beginning of June coincided with the maximum abundance of *K. cochlearis*, including *K. cochlearis* var. *tecta*, and of *K. quadrata* and *Brachionus angularis*. The density of *K. cochlearis* exceeded 1300 ind. l^{-1} and it accounted for over 60% of the total rotifer community. After the sharp decline in total abundance observed during June, a new rotifer community developed, including predominantly *Brachionus calyciflorus* with a peak density of 601 ind. l^{-1}. Other species, such as *Trichocerca pusilla*, *Asplanchna brightwelli*, *S. pectinata*, *S. stylata* and *S. tremula*, also increased in abundance.

Main channel from Hamburg to Brunsbüttel

A conductivity gradient on 25 April and 27 June was not well developed due to the great river discharge.

Conductivities between 670 and 800 µS cm^{-2} were recorded at km 620, while 940–1167 µS cm^{-2} were determined at km 707. The highest conductivity of 6440 µS cm^{-2} was determined at the river mouth during a period of extremely slow outflow at the end of July.

The chlorophyll *a* concentration decreased sharply toward the river mouth, and the highest values were recorded in July at the upper reaches of the estuary (Figure 5). The numbers of bacteria did not change significantly during downstream transport and ranged between 4 and 20 × 10^{9} cells l^{-1}. In May and June, flagellates displayed a relatively homogeneous spatial distribution. In April and July, flagellate abundance was greatest the the upstream end of the estuary, decreased sharply toward the river mouth, but rose again at the station farthest downstream at km 707. Ciliates exhibited almost the same pattern of spatial distribution from April to June.

The species composition of the rotifers in the main channel did not differ significantly from that in the Hahnöfer Nebenelbe. All rotifers encountered, except *Synchaeta bicornis*, are freshwater species and decreased in abundance toward the most seaward station at km 707. When the river discharge was low the section of the estuary in which the rotifer abundance sharply decreased shifted upstream.

In April, when the river discharge was high, a relatively homogeneous spatial distribution of the total rotifer abundance was observed (Figure 6). *Keratella quadrata* was the predominant rotifer species in the lower parts, and its maximum density was observed at station 675. At the station farthest upstream, km 620, *K. cochlearis*, at a density of 63 ind. l^{-1}, was slightly more abundant than *K. quadrata*. *Brachionus calyciflorus* and *B. angularis* reached maxima between km 655 and km 675. Species of the genus *Synchaeta*, mainly *S. pectinata* and *S. tremula* at that time, were found predominantly in upstream sections of the estuary.

At the end of May, the discharge from the river had dropped below 1000 m^{3} s^{-1}. The dominant species from km 690 to km 620 was *K. cochlearis* which attained densities up to 740 ind. l^{-1} (Figure 7). The most numerous species at km 707 was still *K. quadrata*, the density of which was 129 ind. l^{-1}. *Brachionus calyciflorus* reached a maximum density of 130 ind. l^{-1} between km 675 and km 664 and then declined in abundance toward the sea. At the stations farthest upstream, km 634 and km 620, high densities of *S. pectinata, S. stylata,* and *S. tremula* were observed. In this area, *Synchaeta* spp. reached a density up to 388 ind. l^{-1}, but this decreased sharply toward the lower section of the estuary.

At the end of June the discharge from the river had again risen to 1508 m^{3} s^{-1}, and low conductivities were recorded at the river mouth, where *K. cochlearis* had become the most abundant rotifer with a density of 130 ind. l^{-1} (Figure 8). At km 690, over 50% of the rotifers belonged to the genus *Trichocerca*, predominantly *Trichocerca pusilla*. This dominance of *Trichocerca* was restricted only to this station. *Brachionus calyciflorus* reached a maximum density of 137 ind. l^{-1} at km 675 and showed a sharp decline toward the sea. The upper reaches of the estuary were dominated by the genus *Synchaeta*, mainly *S. pectinata*, *S. tremula* and *S. stylata*. At km 645 *Synchaeta* reached a maximum density of 528 ind. l^{-1} accounting for over 60% of the total number of rotifers.

A very low rate of discharge from the river and the highest conductivity at the river mouth were recorded at the end of July (Figure 9). At the station farthest upstream, km 620, the total rotifer density reached 2560 ind. l^{-1} but it decreased rapidly toward the sea. The total rotifer density at km 707 was 26 ind. l^{-1}, and one species, *Synchaeta bicornis,* a typical brackish-water form was dominant. *Keratella cochlearis* and *T. pusilla* were the dominant rotifers at km 620, where the density of each species was over 700 ind. l^{-1}. *Brachionus calyciflorus* and *B. angularis* also reached maximum densities at km 620, but they decreased sharply in abundance toward the lower part of the estuary. At km 675, no individuals belonging to these species were detected. The same pattern was observed for the freshwater species of the genus *Synchaeta* (see above).

Discussion

Planktonic rotifer communities in the freshwater parts of estuaries are often dominated numerically by members of the genera *Keratella* and *Brachionus* (Guisande & Toja, 1988; Ferrari *et al*., 1989; Saunders & Lewis, 1989; Telesh, 1995; van Dijk & van Zanten, 1995; Crump & Baross, 1996), whereas species of the genus *Synchaeta* are often dominant in the brackish-water regions (Bakker & de Pauw, 1975; Ceccherelli & Ferrari, 1982; Ambler *et al*., 1985; Orsi & Mecum, 1986; Dolan & Gallegos, 1991, 1992; Lopes, 1994; Gaughan & Potter, 1995). Throughout the investigation *K. cochlearis* (32·4%), *K. quadrata* (17·5%) and *B. calyciflorus* (16·7%) were the dominant freshwater rotifers in the Elbe Estuary and, in early summer, *S. bicornis* was the most numerous species in the brackish-water region. Judging from the results of previous studies (Schulz, 1961; Nöthlich, 1972), there have been no appreciable change in species composition and abundance in the past decades.

TABLE 1. Rotifer taxa found in the Hahnöfer Nebenelbe from March to July 1995

	March	April			May			June			July
Rotifer taxon	6	3	11	18	2	11	22	6	14	20	3
Rotaria neptunia (Ehrenberg, 1832)		1									
Rotaria rotatoria (Pallas, 1766)											X
Philodina sp. (Ehrenberg, 1830)			X					X			
Adineta vaga (Davis, 1873)			X								
Bdelloidea n. ident.		1	1								
Brachionus leydigi (Cohn, 1862)			2	2	3	1	1	1	1		
Br. quadridentatus f. *brevispinus* (Ehrenberg, 1832)								1		1	1
Br. quadr. var. *cluniorbicularis* (Skorikov, 1894)										X	X
Brachionus urceolaris (Müller, 1773)		3	3	4	3	1	1	1	1	1	
Brachionus diversicornis (Daday, 1883)								X	1		1
Brachionus calyciflorus (Pallas, 1766)	4	5	5	5	2	3	3	1	1	1	
Br. calyciflorus f. *amphiceros* (Ehrenberg, 1838) & *Br. cal.* f. *anuraeiformis* (Brehm, 1909)	2	4	5	5	4	2	4	4	3	5	
Brachionus budapestinensis (Daday, 1885)									X		1
Brachionus angularis (Gosse, 1851)	2	4	4	3	4	3	3	3	3	2	1
Keratella quadrata quadrata (Müller, 1786)	5	5	5	5	5	5	5	5	3	3	3
K. quadrata var. *frenzeli* (Eckstein, 1895)						X	X				X
Keratella valga (Ehrenberg, 1834)											X
Keratella testudo (Ehrenberg, 1832)											X
Keratella ticinensis (Callerio, 1920)					X				X		
Keratella tropica reducta (Fadeew, 1927)								X			
Keratella cochlearis cochlearis (Gosse, 1851)	5	4	5	5	5	5	5	5	5	5	5
K. c. var. *tecta* f. *micracantha* (Lauterborn, 1900)	1	1	1	1	1	2	3	5	5	5	4
K. cochlearis var. *robusta* (Lauterborn, 1900)											X
Notholca acuminata (Ehrenberg, 1832)		3	2	2	2	1	1	1	1		
Notholca labis (Gosse, 1887)		1	1	1	1						
Notholca squamula (Müller, 1786)	1	1	2	3	3	1	1	1	1	1	
Notholca foliacea (Ehrenberg, 1838)	1	1	1	1	1	1	1	1			
Kellicottia longispina (Kellicott, 1879)	1	1	2	1	1	1	1	1	1	1	1
Anuraeopsis fissa (Gosse, 1851)	1							1	1		1
Anuraeopsis navicula (Rousselet, 1910)											X
Euchlanis sp. (Ehrenberg, 1832)									1		
Euchlanis dilatata (Ehrenberg, 1832)								X			
Trichotria pocillum (Müller, 1776)						1	1				
Trichotria tetractis (Ehrenberg, 1830)					X	X					
Colurella sp. (Bory de St. Vincent, 1824)					1		1	X	1	1	
Colurella colurus (Ehrenberg, 1830)					X						
Colurella uncinata (Müller, 1773)								X		X	
Lepadella sp. (Bory de St. Vincent, 1826)	X									1	
Lepadella ovalis (Müller, 1786)										X	
Lecane sp. (Nitsch, 1827)						1		1	1	1	1
Lecane hamata (Stokes, 1896)					X						
Lecane stokesi (Pell, 1890)		X									
Lecane copeis (Harring & Myers, 1926)										X	
Lecane luna luna (Müller, 1776)								X			
Cephalodella sp. (Bory de St. Vincent, 1826)						X	1				
Cephalodella gibba (Ehrenberg, 1838)								X	X		
Trichocerca sp. (Lamarck, 1801)		1	1				1	1	2	3	5
Trichocerca relicta (Donner, 1950)											X
Trichocerca pusilla (Lauterborn, 1898)							X			X	X
Trichocerca cylindrica (Imhof, 1891)											X
Synchaeta sp. (Ehrenberg, 1832)	4	1	2	1	5	3	5	3	5	5	5
Synchaeta tremula tremula (Müller, 1786)					X				X		
Synchaeta stylata (Wierzejski, 1893)					X		X			X	
Synchaeta pectinata (Ehrenberg, 1832)					X		X		X		
Polyarthra sp. (Ehrenberg, 1834)	5	5	4	4	4	4	4	3	3	3	3

Table 1 continued on next page

TABLE 1. *Continued from previous page*

	March	April			May			June			July
Rotifer taxon	6	3	11	18	2	11	22	6	14	20	3
Polyarthra vulgaris (Carlin, 1943)				X		X	X				X
Polyarthra dolichoptera (Idelson, 1925)						X					
Asplanchna sp. (Gosse, 1850)		1	1	1	2	3	1	1	1	1	3
Asplanchna priodonta (Gosse, 1850)		X	X		X	X		X	X		X
Asplanchna girodi (de Guerne, 1888)									X		
Asplanchna brightwelli (Gosse, 1850)											X
Dicranophorus uncinatus (Milne, 1886)											X
Dicranophorus epicharis (Harring & Myers, 1928)											X
Pompholyx sulcata (Hudson, 1885)									1	1	1
Pompholyx triloba (Pejler, 1957)									X		
Conochilus sp. (Ehrenberg, 1834)							1			1	
Conochilus natans (Seligo, 1900)											X
Conochilus unicornis (Rousselet, 1892)											X
Conochilus dossuaris (Hudson, 1875)											X
Filinia sp. (Bory de St. Vincent, 1824)	2	1	2	2	3	2	2	1	2	2	1
Filinia cornuta (Weisse, 1847)						X		X	X	X	
Filinia longiseta longiseta (Ehrenberg, 1834)				X		X					X
Filinia longiseta var. *passa* (Müller, 1786)									X		
Filinia longiseta var. *limnetica* (Zacharias, 1893)						X					
Collotheca sp. (Harring, 1913)										1	
Collotheca pelagica pelagica (Rousselet, 1893)											X

Rotifers from quantitative samples are listed according to their dominance grades, using the methods of Schwerdtfeger (1975): 5, ≥10%; 4, 10–5%; 3, 5–2%; 2, 2–1%; 1, ≤1%. X, rotifer taxa found in qualitative samples.

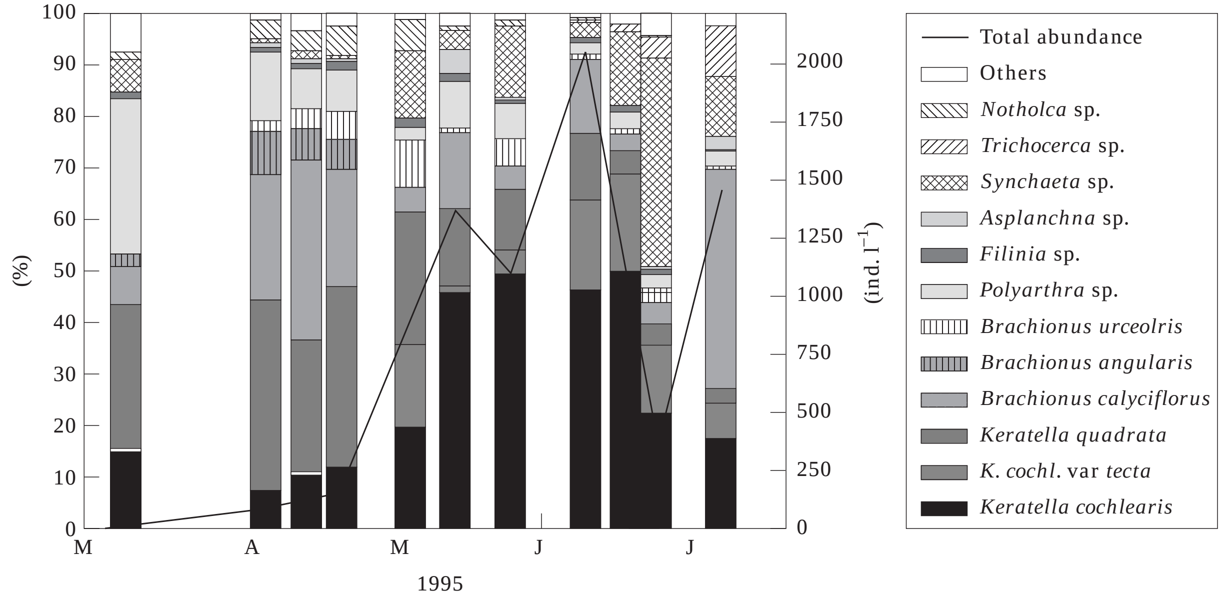

FIGURE 3. Variation in species composition shown as a percentage of total numerical abundance of the most important rotifer taxa in the Hahnöfer Nebenelbe between March and July 1995.

In the Hahnöfer Nebenelbe, the current velocity is lower and the biological production higher than in the comparable station in the main channel at km 634. Rotifer community structure and abundance in the main channel were very similar to those in the Hahnöfer Nebenelbe. All dominant species detected in the main channel were eurytopic freshwater forms that became less abundant toward the river mouth.

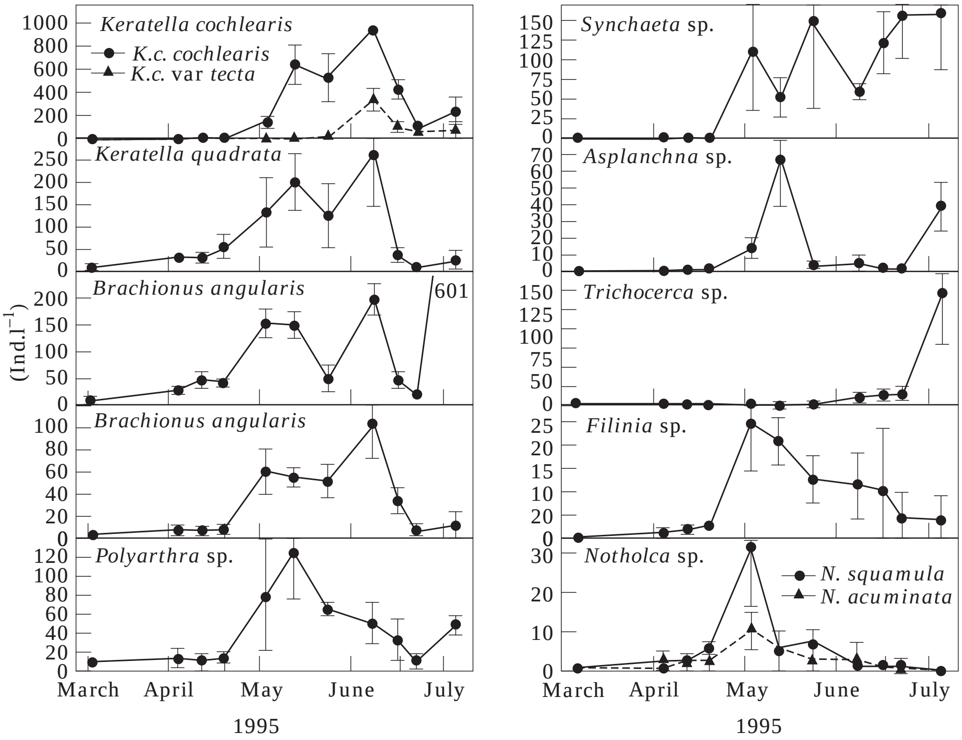

FIGURE 4. Variation in the abundance (ind. l^{-1}) of the most important rotifer taxa in the Hahnöfer Nebenelbe between March and July 1995.

The salinity gradient alone could not have been responsible for this reduced abundance because the density of the rotifers always decreased before the conductivity started to rise. Many conditions reduce rotifer abundance in areas of maximal turbidity, such as a low chlorophyll *a* concentration (Figure 5) and high densities of small aggregates containing little organic material (Zimmermann, 1997). The transition from an autotrophic system upstream to a heterotrophic one downstream is reflected by the dominance of generalists such as *K. quadrata* (up to 58% of total abundance) and *K. cochlearis* (up to 74%) in the lower parts of the estuary. These ubiquitous rotifers feed on bacteria, detritus and flagellates (Pourriot, 1977; Arndt, 1993). *Synchaeta bicornis*, which started to increase in abundance at the end of July in the downstream section of the estuary (Figure 9), has often been found to inhabit brackish-waters (Koste, 1978; Orsi & Mecum, 1986; Lopes, 1994). Previous studies showed that this rotifer is typical of the oligohaline zone of the Elbe Estuary (Schulz, 1961; Nöthlich, 1972) and attains maximum densities in late summer. The massive locally limited appearance of *T. pusilla* at station 690 in June (Figure 8) is probably attributed to a discharge of water rich in this species from a tributary, the Oste (Figure 1).

At the beginning of March, the high rate of river discharge and a low water temperature were presumably the main factors limiting the growth of planktonic rotifer populations in the Elbe Estuary. High rates of river discharge are known to be main factors limiting the development of planktonic populations in advective environments (Ketchum, 1954; Barlow 1955; Miller 1983; Pace *et al.*, 1992). Several publications on potamoplankton dynamics in rivers (Saunders & Lewis, 1988, 1989; Ferrari *et al.*, 1989; Thorp *et al.*, 1994) and estuaries (Onwudinjo & Egborge, 1994; Telesh, 1995; Van Dijk & Van Zanten, 1995) mentioned river discharge as a controlling parameter for rotifer abundance. Periods of intensive flow increased the density of freshwater rotifers at the station closest to the sea at km 707 (Figures 6 and 8) as has also been observed in other estuaries (Egborge, 1994).

Water temperature is known to be another important abiotic parameter that controls the population growth of rotifers (Radwan, 1984; Galkovskaja, 1987; Berzins & Pejler, 1989). During April, the water temperature exceeded 10 °C, correlated with a pronounced increase in rotifer abundance from 162 to 1388 ind. l^{-1} in 30 days (Figure 2).

Throughout April and May, when the phytoplankton density was low, the majority of rotifers fed predominantly on heterotrophic components of the microbial food-web, such as bacteria, heterotrophic flagellates and ciliates, which declined in abundance toward the end of April (Figure 2), although real

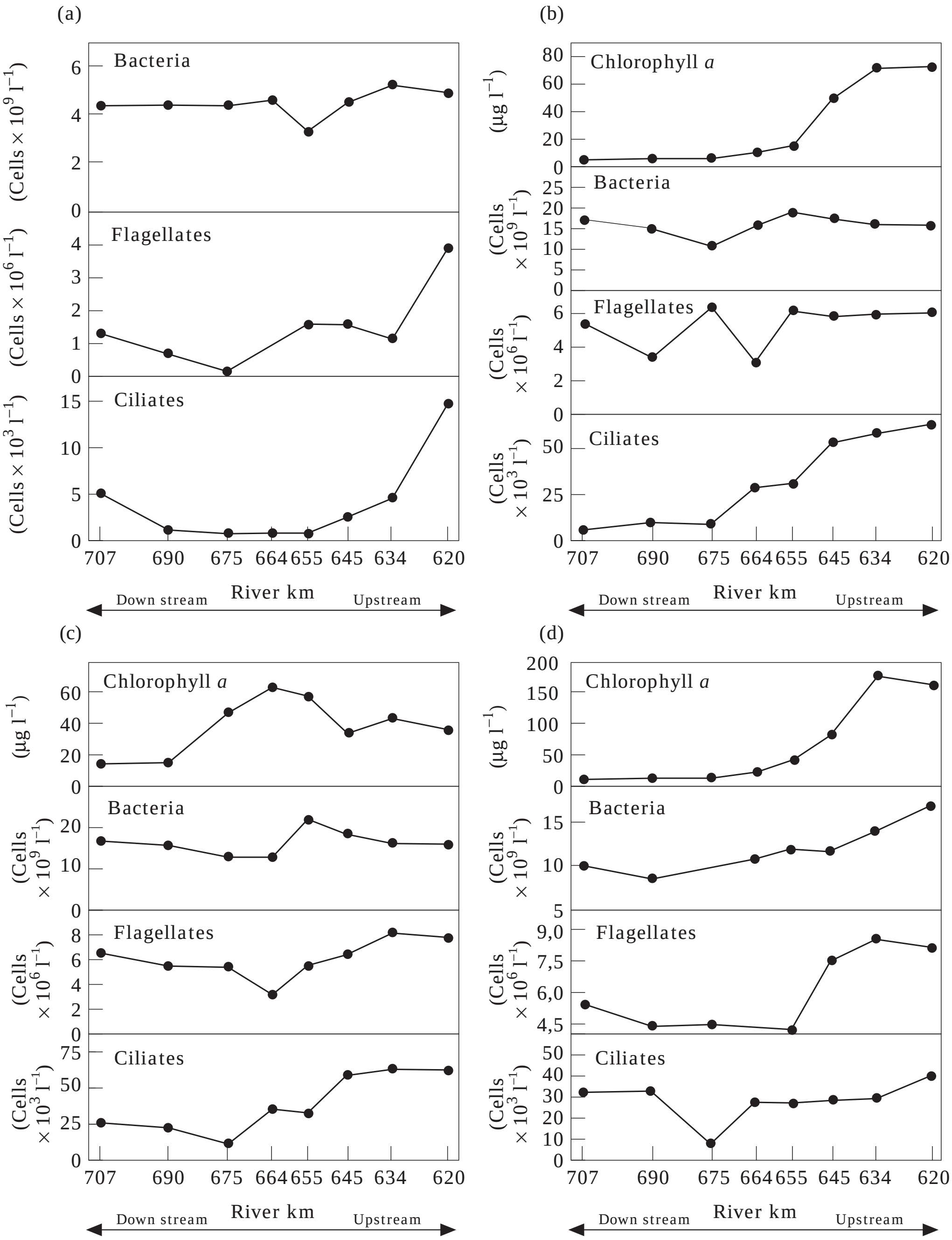

FIGURE 5. Longitudinal changes in the chlorophyll *a* concentration (μg l^{-1}) and the numbers of bacteria (cells × 10^{9} l^{-1}), flagellates (cells × 10^{6} l^{-1}) and ciliates (cells × 10^{3} l^{-1}) in the main channel between km 620 and km 707 during spring, 1995. (a) April, (b) May, (c) June, (d) July.

bottom-up control of rotifer abundance at this time is unlikely because of the eutrophic condition of the environment. *Keratella cochlearis*, the dominant species from the middle of May to early June, is a filter-feeding rotifer with a preference for particles within the size range of approximately 1 to 12 μm, such as bacteria and small flagellates (Dumont, 1977; Pourriot, 1977, Bogdan & Gilbert, 1982, 1987). Additional size fractionation experiments, feeding experiments with fluorescent microspheres and direct observation of living individuals indicated that *K. cochlearis* fed mainly on bacteria that were planktonic or attached to particles, and also on detritus (Holst, 1996). Recent publications described *K. cochlearis* as an important consumer of bacteria (Sanders *et al.*, 1989; Arndt, 1993; Ooms-Wilms *et al.*, 1995).

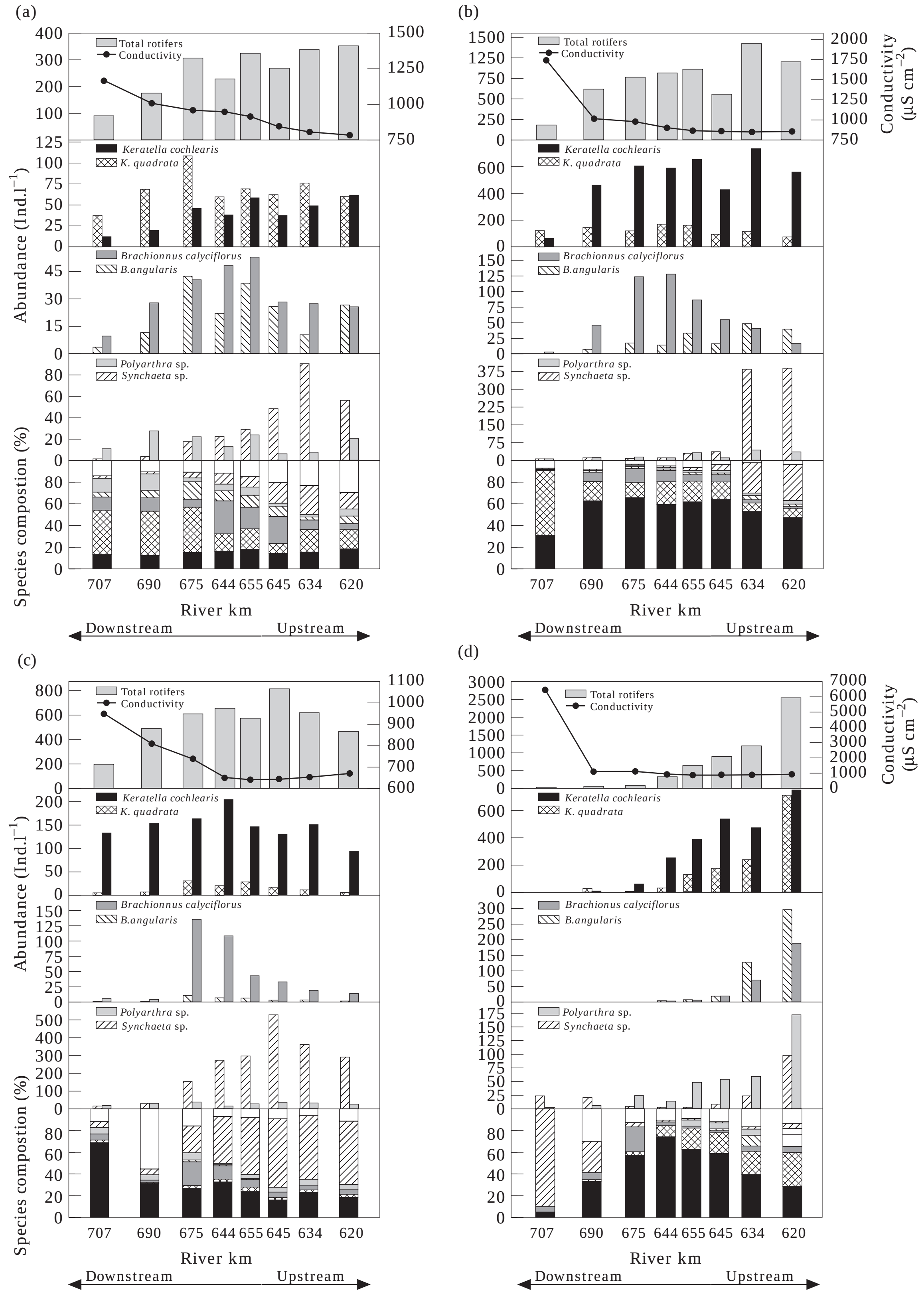

FIGURE 6. Longitudinal changes in total rotifer abundance (ind. l^{-1}), conductivity (µS cm^{-2}), rotifer species composition as percentages of total numerical abundance and abundances of the most important rotifer taxa in the main channel between km 620 and km 707 during spring, 1995. The river discharge (m^3 s^{-1}), is shown above. (a) 25 April, discharge 1734 m^3 s^{-1}; (b) 29 May, discharge 983 m^3 s^{-1}; (c) 27 June, discharge 1508 m^3 s^{-1}; (d) 27 June, 465 m^3 s^{-1}.

Starkweather and Bogdan (1980) observed that this species preferred to consume detrital material. *Keratella quadrata* and *Polyarthra* ssp., the dominant rotifers during March to early April, grazed mainly on heterotrophic flagellates (Dumont, 1977; Pourriot, 1977; Gilbert & Bogdan, 1981; Bogdan & Gilbert, 1982). Observations of living individuals and stomach content analyses revealed that *Asplanchna priodonta*, which attained maximum abundance in May (Figure 4), was mainly phytophagous, feeding on centric diatoms and other algae and sometimes capturing larvae of the mussel, *Dreissena polymorpha*. Observations showed, however, that *A. priodonta* was not capable of digesting the mussel larvae which continued swimming after being regurgitated (Holst, 1996). There is no evidence that the peak density of *A. priodonta* in the middle of May was responsible for the sudden decline of *Synchaeta* sp. (Figure 4). These small soft-bodied rotifers have no effective defense against being ingested by *Asplanchna* (Gilbert, 1980; Williamson, 1983; Gilbert & Stemberger, 1985; Stemberger & Gilbert, 1987) and the absence of a lorica would make them difficult to detect in the stomach contents of the predator. However, *A. priodonta* is thought not to prey significantly on other rotifers (Guiset, 1977; Stemberger & Gilbert, 1984; Bielañska-Grajner, 1995; Stenson & Svensson, 1995). A significant top-down control of rotifer populations was not observed during spring. Cyclopoid copepods and other invertebrate predators were rare at this time, and predation by fish larvae on planktonic rotifers occurs only for a short time and is usually not a limiting factor, due to the rapid growth rates of rotifers (Hewitt & George, 1987; Thiel, 1996).

At the end of June a high rate of river discharge caused a pronounced decrease in rotifer abundance, reflected by almost every taxon. Only *Synchaeta* spp. increased in numbers and dominated the rotifer community for a short period, probably due to a good food supply and its high reproduction rate. The reason for the decrease in the number of *B. calyciflorus* at this time may be the water temperature, which was still too low to promote rapid reproduction of this species (Galkovskaja, 1987) to compensate for the losses due to the drift. This species is known to be one of the fastest growing metazoans (Bennett & Boraas, 1989), often described as a pioneer species (Ferrari *et al.*, 1989). Along with the increase in total rotifer abundance in early July, which was caused by a decrease in the river discharge and a phytoplankton bloom, the rotifer community developed a new structure (Figure 3). The dominant species became *B. calyciflorus*, which was promoted by water temperatures above 20 °C and high densities of flagellates. The chlorophyll *a* concentration at that time was extremely high in comparison with that of other estuaries (Heinbokel *et al.*, 1988; Pace *et al.*, 1992; Van Dijk & van Zanten, 1995) and the Elbe Estuary during previous years, according to the literature (Schuchardt & Schirmer, 1991). This maximum was caused mainly by a bloom of the centric diatom, *A. normanii*, which is too large to serve as food for most rotifers. Observations of the stomach contents of *Asplanchna girodi* and *Asplamchna brightwelli*, which were increasing in abundance, confirmed previous reports (Gilbert & Williamson, 1978; Gilbert, 1980; Garreau *et al.*, 1988; Sarma, 1993) and showed that these rotifers are predominantly carnivorous and preyed on *K. cochlearis* var. *tecta* and other small rotifers, including *Anuraepsis fissa* and *Pompholyx sulcata*. Furthermore, cyclopoid copepods, apparently present at low densities at this time, preyed upon rotifers.

Rotifers seem to be more important in estuarine environments than previously believed. In the context of the seasonal succession of the entire planktonic community, rotifers play a dual role. They are efficient grazers of bacteria, flagellates and algae and thus compete with ciliates, flagellates and crustaceans. However, most of them fall into the food size range of larger zooplankters.

Through the present investigation, the authors have only begun to demonstrate that rotifers have the ability to structure and regulate the population dynamics of planktonic communities in the Elbe Estuary during the first part of the year. Based on the data in this paper, the following sequence was determined:

1. In early spring, the abundance of bacteria, flagellates and ciliates increased, but low water temperature and high river-discharge rates inhibited rotifer population growth.
2. At the end of April, a decreasing discharge rate and water temperatures above 10 °C promoted a rapid growth of rotifers, which grazed mainly on detritus and heterotrophic organisms such as bacteria and heterotrophic flagellates. The dominant species were *K. cochlearis* and *K. quadrata*. A significant top-down control of rotifer populations was not apparent.
3. In the middle of June, rotifer abundance decreased due to the great amount of river discharge. Thereafter, the river discharge rate was low, and a high chlorophyll *a* concentration developed. Rotifer abundance rose again, and a new rotifer community established itself, feeding mainly on planktonic algae and flagellates. *Brachionus calyciflorus*, *Synchaeta* sp. and *T. pusilla* became dominant in the rotifer community. *Asplanchna brightwelli*, *Asplanchna girodi* and cyclopoid copepods preyed upon the rotifers but could not reduce the total rotifer abundance.

Acknowledgements

This study was supported by the Deutsche Forschungsgemeinschaft Sonderforschungsbereich 327 and the ‘ Aktion seeklar ’ in Hamburg. The authors thank their colleagues for their help, especially G. Schymura from Geesthacht for chemical and physical data, S. Müller from Hamburg for the chlorophyll determinations, T. Gaumert from Hamburg for water discharge data and the team of the *Tromper Wiek*, H. Neumann and J. Lingner. The authors are also indebted to C. W. Heckman for correcting the English.

References

Adamkiewicz-Chojnacka, B. & Rozanska, Z. 1990 Seasonal Variations of the Biomass of Copepoda and Rotatoria: Permanent Components of the Zooplankton in the Vistula Lagoon. *Limnologica* **20,** 71–73.

Adams, M. S., Kausch, H., Gaumert, T., Krüger, K.-E. 1996 The effect of the reunification of Germany on the water chemistry and ecology of selected rivers. *Environmental Conservation* **23,** 35–43.

Admiraal, W., Breebaart, L., Tubbing, G. M. J., van Zanten, B., de Ruyter van Steveninck, E. D. & Bijkerk, R. 1994 Seasonal variation in composition and production of planktonic communities in the lower River Rhine. *Freshwater Biology* **32,** 519–531.

Ambler, J. W. & Cloern, J. E. & Hutchinson, A. 1985 Seasonal cycles of zooplankton from San Francisco Bay. *Hydrobiologia* **129,** 177–197.

Arndt, H. 1993 Rotifers as Predators on Components of the Microbial web (bacteria, heterotrophic flagellates, ciliates)—a review. *Hydrobiologia* **255/256,** 231–246.

Bakker, C. & de Pauw, N. 1975 Comparison of plankton assemblages of identical salinity ranges in estuarine tidal, and stagnant environments II. Zooplankton. *Netherlands Journal of Sea Research* **9,** 145–165.

Barlow, J. P. 1955 Physical and biological processes determining the distribution of zooplankton in a tidal estuary. *Biological Bulletin* **109,** 211–225.

Bennett, W. N. & Boraas, M. E. 1989 A demographic profile of the fastest growing metazoan: a strain of Brachionus calyciflorus (Rotifera). *Oikos* **55,** 356–369.

Berzins, B. & Pejler, B. 1989 Rotifer occurence in relation to temperature. *Hydrobiologia* **175,** 223–231.

Bielañska-Graijner, I. 1995 Influence of temperature on morphological variation in populations of *Keratella cochlearis* (Gosse) in Rybnik Reservoir. *Hydrobiologia* **313/314,** 139–146.

Bogdan, K. G. & Gilbert, J. J. 1982 Seasonal patterns of feeding by natural populations of *Keratella*, *Polyarthra*, and *Bosmina*: Clearance rates, selectivities, and contributions to community grazing. *Limnology and Oceanography* **27,** 918–934.

Bogdan, K. G. & Gilbert, J. J. 1987 Quantitative comparison of food niches in some freshwater zooplankton. *Oceologia* **72,** 331–340.

Ceccherelli, V. H. & Ferrari, I. 1982 Annual and Seasonal Variations of Zooplankton in a Shallow-water Lagoon System, the Valli of Comachio. *Estuarine, Coastal and Shelf Science* **14,** 337–350.

Crump, B. C. & Baross, J. A. 1996 Particle attached bacteria and heterotrophic plankton associated with the Columbia estuarine turbidity maxima. *Marine Ecology Progress Series* **138,** 265–273.

Day, J. H. 1981 The nature, origin and classification of estuaries. In: *Estuarine Ecology with Particular Reference to Southern Africa* (Day, J. H., ed.). Rotterdam, Balkema, pp. 1–6.

Dolan, J. R. & Gallegos, C. L. 1991 Trophic coupling of rotifers, microflagellates, and bacteria during fall months in the Rhode River Estuary. *Marine Ecology Progress Series* **77,** 147–156.

Dolan, J. R. & Gallegos, C. L. 1992 Trophic role of planctonic rotifers in the Rhode River Estuary, spring–summer 1991. *Marine Ecology Progress Series* **85,** 187–199.

Dumont, H. J. 1977 Biotic factors in the population dynamics of rotifers. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie* **8,** 98–122.

Egborge, A. B. M. 1994 Salinity and the distribution of rotifers in the Lagos Harbour–Badagry Creek system, Nigeria. *Hydrobiologia* **272,** 95–104.

Egborge, A. B. M. & Tawari, P. 1987 The rotifers of Warri River, Nigeria. *Journal of Plankton Research* **9,** 1–13.

Ferrari, I., Farabegoli, A. & Mazzoni, R. 1989 Abundance and diversity of planktonic rotifers in the Po River. *Hydrobiologia* **186/187,** 201–208.

Galkovskaja, G. A. 1987 Planktonic rotifers and temperature. Hydrobiologia **147,** 307–317.

Garreau, P. F., Rougier, C. & Pourriot, R. 1988 Exploitation des ressources alimentaires par le prédateur planctonique *Asplanchna girodi* De Guerne 1888 (Rotifères) dans un lac de sablière. *Archiv für Hydrobiologie* **112,** 91–106.

Gaughan, D. J. & Potter, I. C. 1995 Composition, distribution and seasonal abundance of zooplankton in a shallow, seasonally closed estuary in temperate Australia. *Estuarine, Coastal and Shelf Science* **41,** 117–135.

Gilbert, J. J. 1980 Observations on the susceptibility of some protists and rotifers to predation by *Asplanchna girodi*. *Hydrobiologia* **73,** 87–91.

Gilbert, J. J. & Bogdan, K. G. 1981 Selectivity of *Polyarthra* and *Keratella* for flagellate and aflagellate cells. *Verhandlungen. Internationale Vereinigung für theoretische und angewandte Limnologie* **21,** 1515–1521.

Gilbert, J. J. & Stemberger, R. S. 1985 Prey capture in the rotifer *Asplanchna girodi*. *Verhandlungen. Internationale Vereinigung für theoretische und angewandte Limnologie* **22,** 2997–3000.

Gilbert, J. J. & Williamson, C. F. 1978 Predator-Prey Behavior and Its Effect on Rotifer Survival in Associations of *Mesocyclops edax*, *Asplanchna girodi*, *Polyarthra vulgaris*, and *Keratella cochlearis*. *Oceologia* **37,** 13–22.

Green, J. 1977 Sampling rotifers. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie* **8,** 9–12.

Green, J. 1995 Associations of planktonic and periphytic rotifers in a Malaysian estuary and two nearby ponds. *Hydrobiologia* **313/314,** 47–56.

Guisande, C. & Toja, J. 1988 The dynamics of various species of the genus Brachionus in the Gualdalquivir River. *Archiv für Hydrobiologie* **112,** 579–595.

Guiset, A. 1977 Stomach contents in *Asplanchna* and *Ploesoma*. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie* **8,** 126–129.

Heinbokel, J. F., Coats, D. W., Henderson, K. W. & Tyler, M. A. 1988 Reproduction rates and secondary production of three species of the rotifer genus *Synchaeta* in the estuarine Potomac River. *Journal of Plankton Research* **10,** 639–674.

Hewitt, D. P. & George, D. G., 1987 The population dynamics of *Keratella cochlearis* in a hypereutrophic tarn and the possible impact of predation by young roach. *Hydrobiologia* **147,** 221–227.

Holst, H. 1996 *Untersuchungen zur Ökologie der Rotatorien auf den Schwebstoffflocken und im Freiwasser der Elbe während der Frühjahrs.* Mthesis Univ. Göttingen.

Hynes, H. B. N. 1989 Keynote address. In *Proceedings of the International Large River Symposium (LARS)* (Dodge, D. P., ed.). Canadian special publication of fisheries and aquatic sciences, Volume 106, pp. 5–10.

Kausch, H. 1990 Biological processes in the estuarine environment. In *Estuarine Water Quality Management* (Michaelis, W. ed.). Ser. Coastal and Estuarine Studies, Volume 36, Springer Verlag, Berlin, Heidelberg, New York, 353–361.

Ketchum, B. H. 1954 Relation between circulation and planktonic populations in estuaries. Ecology **35,** 191–200.

Koste, W. 1978 *Rotatoria. Die Rädertiere Mitteleuropas*. Gebrüder Bornträger Berlin, Stuttgart. Bd. I & II.

Lopes, R. M. 1994 Zooplankton Distribution in the Guarau River Estuary (South-eastern Brazil). *Estuarine, Coastal and Shelf Science* **39,** 287–302.

Miller, C. B. 1983 The Zooplankton of Estuaries. In *Ecosystems of the World*, No. 26. *Estuaries and Enclosed Seas* (Ketchum, B. H., ed.), Elsevier, Amsterdam, Oxford, New York, pp. 103–149.

Neumann-Leitâo, S., Paranaguá, M. N. & Valentin, J. L. 1992 The planktonic rotifers in the estuarine lagunar complex of Suape (Pernambuco, Brasil). *Hydrobiologia* **232,** 133–143.

Nöthlich, I. 1972 Trophische Struktur und Bioaktivität der Planktongesellschaft im unteren limnischen Bereich des Elbe-Ästuars. *Archiv für Hydrobiologie. Supplement* **43,** 33–117.

Nusch, E. A. 1980 Comparison of different methods for Chlorophyll and Phaeopigment determination. *Archiv für Hydrobiologie. Beiheft Ergebnisse der Limnologie* **14,** 14–36.

Onwudinjo, C. C. & Egborge, A. B. M. 1994 Rotifers of Benign River, Nigeria. *Hydrobiologia* **272,** 87–94.

Ooms-Wilms, A. L., Postema, G. & Gulati, R. D. 1995 Evaluation of bacterivory of Rotifera based on measurements of *in situ* ingestion of fluorescent particles, including some comparisons with Cladocera. *Journal of Plankton Research* **17,** 1057–1077.

Orcutt, J. D. & Pace, M. L. 1984 Seasonal dynamics of rotifer and crustacean zooplankton populations in a eutrophic, monomictic lake with a note on rotifer sampling techniques. *Hydrobiologia* **119,** 73–80.

Orsi, J. J. & Mecum, W. L. 1986 Plankton Distribution and Abundance in Sacramento-San Joaquin Delta. *Estuaries* **9,** 226–239.

Papinska, K. 1990 Abundance and composition of rotifers in Vistula river. *Polskie archiwum hydrobiologii* **37,** 449–459.

Pace, M. L., Finlay, S. E. G. & Lints, D. 1992 Zooplankton in Advective Environments: The Hudson River Community Comparative Analysis. *Canadian Journal of Fisheries and Aquatic Sciences*. **49,** 1060–1069.

Porter, K. G. & Feig, Y. S. 1980 The use of DAPi for identifying and counting aquatic microflora. *Limnology and Oceanography* **25,** 943–948.

Pourriot, R. 1977 Food and feeding habits of rotifera. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie* **8,** 243–260.

Radwan, S. 1984 The influence of some abiotic factors on the occurence of rotifers of Leczna and Wlodawa Lake District. *Hydrobiologia* **112,** 117–124.

Sanders, R. W. & Porter, K. G., Bennet, S. J. & Debiase, A. E. 1989 Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. *Limnology and Oceanography* **34,** 673–687.

Sarma, S. S. S. 1993 Feeding responses of *Asplanchna brightwelli* (rotifera): laboratory and field studies. *Hydrobiologia* **255/256,** 275–282.

Saunders, J. F. & Lewis, W. M. 1988 Zooplankton abundance and transport in a tropical white-water river. *Hydrobiologia* **162,** 147–155.

Saunders, J. F. & Lewis, W. M 1989 Zooplankton abundance in the lower Orinoco River, Venezuela. *Limnology and Oceanography* **34,** 397–409.

Schuchardt, B. & Schirmer, M. 1991 Phytoplankton Maxima in the Tidal Freshwater Reaches of two Coastal Plain Estuaries. *Estuarine, Coastal and Shelf Science* **32,** 187–206.

Schulz, H. 1961 Qualitative und quantitative Planktonuntersuchungen im Elbe-Aestuar. *Archiv für Hydrobiologie. Supplement* **26,** 5–105.

Schwerdtfeger, F. 1975 *Ökologie der Tiere, Bd. III: Synökologie*. Paul Parey, Hamburg, Berlin.

Soetart, K. & van Rijswijk, P. 1993 Spatial and temporal patterns of the zooplankton in the Westerschelde estuary. *Marine Ecology Progress Series* **97,** 47–59.

Sommer, U., Gliwicz, Z. M., Lampert, W. & Duncan, A. 1986 The PEG-model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie* **106,** 433–471.

Starkweather, P. L. & Bogdan, K. G. 1980 Detrical feeding in natural zooplankton communities: discrimination between live and dead algal foods. *Hydrobiologia* **73,** 83–85.

Stemberger, R. S. & Gilbert, J. J. 1984 Spine development in the rotifer *Keratella cochlearis*: induction by cyclopoid copepods and *Asplanchna*. *Freshwater Biology* **14,** 639–647.

Stemberger, R. S. & Gilbert, J. J. 1985 Body size, food concentration, and population growth in planktonic rotifers. *Ecology* **66,** 1151–1159.

Stemberger, R. S. & Gilbert, J. J. 1987 Defenses of Planktonic Rotifers Against Predators. In *Predation: Direct and Indirect Impacts on Aquatic Communities* (Kerfoot, W. C. and Sih, A., eds). University Press of New England, Hanover, NH, pp. 227–240.

Stenson, J. A. E. & Svensson, J. E. 1995 Food Quality and Population Density in *Asplanchna priodonta*. *Limnologica* **25,** 43–47.

Telesh, I. V. 1995 Rotifer assemblages in the Neva Bay, Russia: principles of formation, present state and perspectives. *Hydrobiologia* **313/314,** 57–62.

Thiel, R. 1996 The impact of fish predation on the zooplankton community in a southern Baltic bay. *Limnologica* **26,** 123–137.

Thorp, J. H., Black, A. R. & Haag, K. H. 1994 Zooplankton Assemblages in the Ohio River: Seasonal, Tributary, and Navigation Dam Effects. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 1634–1643.

Utermöhl, H. 1958 Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Verhandlungen der Internationalen Vereinigung für Theorethische und Angewandte Limnologie* **9,** 1–39.

Van Dijk, G. M. & Van Zanten, B. 1995 Seasonal changes in zooplankton abundance in the lower Rhine during 1987–1991. *Hydrobiologia* **304,** 29–38.

Vaque, D., Pace, M. L., Finlay, S. & Lints, D. 1992 Fate of bacterial production in a heterotrophic ecosystem: grazing by protists and metazoans in the Hudson Estuary. *Marine Ecology Progress Series* **89,** 155–163.

Williamson, C. E. 1983 Invertebrate predation on planktonic rotifers. *Hydrobiologia* **104,** 385–396.

Zimmermann, H. 1997 The microbial community on aggregates in the Elbe Estuary. *Aquatic Microbial Ecology* **13,** 37–46.

Zimmermann, H. & Kausch, H. 1996 Microaggregates in the Elbe-Estuary: structure and colonization during spring. *Archiv für Hydrobiologie Special Issues Advances Limnology* **48,** 85–92.