Vol. 85: 187–199, 1992 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published August 27

Trophic role of planktonic rotifers in the Rhode River Estuary, spring – summer 1991

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ABSTRACT: Rotifers were abundant (average ca 1000 ind. l^{-1}) from March through September 1991 in a shallow, eutrophic subestuary of the Chesapeake Bay (USA). The rotifer community was usually dominated by *Synchaeta cecilia* with *Brachionus plicatilis* as the second most common species. Rotifer concentrations were negatively related to microflagellate abundances. However, reproductive output of *S. cecilia*, as measured by eggs female^{-1} or egg ratio (ER) followed temporal trends in microflagellate numbers. An inverse relationship between rotifers and herbivorous ciliates, which were dominated by a heterotrophic *Strombidium* sp., was apparent late spring through mid-summer, corresponding to a period of parallel abundance trends of auto- and heterotrophic microflagellates. Field experiments with natural plankton populations examining the removal of rotifers by copepods and sea nettles yielded clearance rate estimates of ca 50 ml copepod^{-1} d^{-1} and 20 l sea nettle^{-1} d^{-1}. Calculations of predator removal rates and observations of shifts in ER with microflagellate concentration suggest that rotifer production is more likely food- than predator-limited in the Rhode River. Rotifer production figures, based on growth rates from ER data and grazing experiments, averaged ca 18 μg C l^{-1} d^{-1}, exceeding previous estimates of copepod production by an order of magnitude.

INTRODUCTION

Planktonic rotifers are thought to feed largely on algae of ≤ 20 μm in size (Allan 1976, Pourriot 1977). While considered characteristic of freshwaters (Pennak 1978), they are known to occur in estuarine and marine waters and are apparently restricted to coastal areas due to high nutritional requirements (Heinbokel et al. 1988). However, beyond these generalities little is known of the importance of their ecological role in estuarine and marine systems, due largely to a lack of reliable quantitative data. Reports of rotifer population densities are almost exclusively based on plankton samples collected with nets of mesh size ≥ 44 μm and often include little information on species composition (see Table 4, 'Discussion'). Based on the experiences of freshwater investigators, use of nets with mesh sizes ≥ 35 μm can greatly underestimate rotifer abundance (Likens & Gilbert 1970, Orcutt & Pace 1984) and the underestimation is probably most serious with common, highly contractile, soft-bodied forms such as *Synchaeta* spp. Very few studies have employed sampling methods appropriate to these small metazoans. Furthermore, even when sampled adequately, forms such as *Synchaeta* spp. are easily overlooked in preserved samples if the rotifers were not anaesthetized prior to fixation to prevent their contraction into small, nondescript, ovoid masses. Despite these problems, rotifers have been found to be an important component of estuarine plankton communities. In Baltic systems they can rival ciliates in terms of biomass (Eriksson et al. 1977) and in some locales, exceed total protozoan biomass by a factor of 4 (Kivi 1986). Rotifer production can represent a significant portion of zooplankton production. For example, Johansson (1983) estimated that *Synchaeta* spp. represented about 20 % of annual zooplankton production in a Swedish fjord and Allan et al. (1976) speculated that rotifer production might exceed copepod production by an order of magnitude in the Rhode River, a shallow eutrophic estuary. We have recently reported that rotifers, rather than ciliates or copepods, appear to be the dominant herbivores in a relatively simple planktonic food web during the fall in the Rhode River, Maryland, USA (Dolan & Gallegos 1991).

In this paper we report on the abundance and composition of the rotifer fauna in the Rhode River for the

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0171-8630/92/0085/0187/$ 03.00

spring and summer, a period in which trophic relationships appear more complex than during fall months (Dolan & Gallegos 1991). We present evidence suggesting a close relationship between rotifers and herbivorous ciliates. We calculate production rates of *Synchaeta cecilia*, the dominant rotifer species, based on egg ratios and field experiments and also estimate removal rates due to grazing by copepods and sea nettles.

METHODS AND MATERIALS

Study site. The Rhode River estuary (30° 52′ N, 76° 32′ W) is a shallow (mean depth ca 2 m), well-mixed subestuary of the Chesapeake Bay with a tidal amplitude of ca 30 cm and has been the subject of a large number of studies (see Jordan et al. 1991, Gallegos et al. 1992 and ref. therein). It is eutrophic, exhibiting high chl *a* (ca 50 $\mu g\ l^{-1}$) and nutrient concentrations (ammonium averages ca 4 μM) (Gallegos 1989).

Field sample collection and processing. Samples were collected from March 26 to September 13 at 1 to 7 d intervals (average interval = 2 d, SD = 1.5, n = 85) during daylight hours at slack tide off the Smithsonian dock on the Rhode River. Sampling protocols followed the methods outlined in Dolan & Gallegos (1991). Briefly, a 10 l jug was immersed ca 10 cm below the surface; 20 ml aliquots were preserved with glutaraldehyde for microflagellate and ciliate enumerations. For rotifers, 2 l to 250 ml aliquots, depending on density, were slowly concentrated over 20 μm Nitex screen to 20 ml, carbonated water (soda water, carbonation method and salinity unknown) was added to inhibit contraction and after a few minutes the sample was fixed with glutaraldehyde. Microflagellates were enumerated following Haas (1982); 2 ml subsamples were stained and 50 fields examined using a 100× objective. Ciliates were counted in whole water, rotifers in the 20 μm concentrate, in settled samples using an inverted microscope.

Rotifers were identified following descriptions and figures of standard monographic works and keys (Remane 1929, Berzins 1952, Björklund 1972, Ruttner-Kolisko 1974, Voigt & Koste 1978) as well as original species descriptions (Rousselet 1902, 1909, Smith 1904, Beauchamp 1907). Features of gross morphology, i.e. sizes and shapes of relaxed and contracted specimens, toe morphology and lorica morphology, were used in making taxonomic designations.

Eggs of *Synchaeta cecilia* populations were counted during 2 time periods when other rotifers, whose eggs could possibly be confused with *S. cecilia*, were not abundant (April 9 to May 11 and August 19 to September 12). This strategy was followed because *S. cecilia* eggs often disassociate with fixation in necessitating counting both attached and detached eggs, and the eggs of some other rotifer species could not be rapidly distinguished with confidence (e.g. *S. fennica*, whose eggs are apparently undescribed).

Ciliates were placed into guilds or trophic groups following the species and morphotype classifications outlined in Dolan (1991). An additional ciliate guild was distinguished, mixotrophic oligotrichs, consisting of species observed to contain chloroplasts based on the examination of glutaraldehyde-preserved material with epifluorescence at ca 500× total magnification. Only the abundances of aplastidic herbivorous ciliates [macrophagous in Dolan (1991)] are reported here. Data on bacteriovorous, carnivorous, mixotrophic and autotrophic ciliates will appear elsewhere.

Temperature and salinity data were gathered from an automated sampling station, previously described (Cory & Dressler 1981). Samples for chlorophyll were taken at approximately weekly intervals, as part of a separate study, and were processed following the protocol outlined in Gallegos (1989).

Predation experiments. Small-scale experiments were run to yield order of magnitude estimates of *in situ* predation rates. We employed the design of Frost (1972) in which clearance rates of grazers are calculated as prey disappearance rates in chambers with grazers, corrected for prey growth rates in chambers without grazers. Prey disappearance is assumed to equal grazer ingestion. The general approach in the copepod experiments was to monitor changes in rotifer concentrations in: (a) water gently passed through 280 μm mesh Nitex to remove late stage copepods; and (b) the remaining water, effectively reverse filtered, with high copepod density.

A single 20 l sample of whole water was taken from the dock station. After mixing, water was slowly siphoned through a 25 mm diameter hose held inside a cylinder (75 mm diameter) fitted with a 280 μm mesh Nitex bottom. The immersed end of the hose was kept 10 cm from the screen. The first 4 l of siphoned water (free of late-stage copepods) was retained, gently mixed, and used to completely fill three 1 l clear polycarbonate bottles. Siphoning was then continued until the 20 l volume was reduced to 5 l. This water, now containing 4 times the original concentration of late-stage copepods, was gently mixed and used to fill completely 3 clear polycarbonate bottles. Two each of the screened (copepod-free) water bottles and the reverse filtered (copepod-concentrated) water bottles were placed *in situ* (about 20 cm below the surface) for incubation, in a clear bucket, filled with water suspended from a floating portion of the dock. The 2 remaining samples were processed for time zero (t_0) determinations of rotifer concentrations. The incubated

bottles were retrieved and processed for rotifer and copepod enumerations after ca 20 h. All experimental parameters were calculated employing the system of equations devised by Frost (1972). Copepod grazing parameters were calculated based on the abundance of late-stage (size ≥ 750 µm long) copepods, all of which were *Acartia* sp. An average prey growth rate, from the 2 copepod-free bottles, was used to calculate individual grazing parameters for the 2 grazer (concentrated copepod) bottles. Experiments were run on July 25, 31 and August 8, 1991; all incubations began at ca 10:00 h local time.

Grazing experiments with sea nettles employed a slightly different design. Five clear polycarbonate buckets (20 l) were filled with water and suspended from a floating dock. A single sea nettle *Chrysaora quinquecirrha*, ca 75 mm bell diameter, was placed into each of 2 to 3 buckets. For each of the buckets 1 l samples were removed at t_0 and after 20 h incubation. Rates of prey growth were calculated separately for each control (i.e. buckets without sea nettle added). The average prey growth rate in the controls was used in calculating clearance and ingestion rates for the individual sea nettles. Water in the control containers was not screened to remove copepods but none were found in samples examined for rotifer enumerations.

Sea nettle egestion experiments. To determine if natural populations of sea nettles had consumed rotifers, an experiment, similar to that of Purcell et al. (1991), was run to monitor the egestion of recognizable rotifer remains. Rotifer-free water (20 l) was prepared by slowly siphoning water through a 20 µm screen. The water was then dispensed into 2 l containers (10 total). A single sea nettle (ca 75 mm bell diameter), scooped out of the surface water at the dock using a cylinder fitted with a 280 µm mesh bottom, was put into each container. The containers were placed in an incubator at 26 °C (ambient water temperature was 27 °C). Two or 3 containers were processed at hourly intervals for 4 h. The sea nettle was removed by pouring the water through the 280 µm screen and the water was then filtered through a 20 µm mesh Nitex screen and the concentrate settled and then examined using an inverted microscope. Only empty lorica of *Brachionus plicatilis* were enumerated, no other rotifer remains were recognizable.

Rotifer production. Production of *Synchaeta cecilia* was estimated using abundance figures from field samples, a biomass conversion factor (0.0168 µg C *S. cecilia*$^{-1}$) from the literature (Heinbokel et al. 1988), and growth rates derived from 2 different methods. For the 5 dates on which grazing experiments were run, growth rates from the control chambers were used. For the 2 extended periods in spring and summer when egg numbers for *S. cecilia* were determined (see above), the egg ratio method was used.

The egg ratio method, originally developed for rotifers by Edmondson (1960, 1965) allows calculation of birth rates given knowledge of the egg development time (EDT) and the average number of eggs per female, the egg ratio (ER). ER was determined by microscopic examination and EDT was calculated using the equation of Heinbokel et al. (1988) relating incubation temperature (*in situ* water temperature, T in °C) to EDT for *Synchaeta cecilia*:

$$\log \mathrm{EDT} = 1.77 + 0.557(\log T) - 0.902(\log T)^2 \quad (1)$$

Birth-specific reproductive rate, b (h^{-1}), was calculated following Paloheimo (1974):

$$b = \ln(1 + \mathrm{ER})/\mathrm{EDT} \quad (2)$$

Calculating production from birth rates and biomass assumes that all eggs reach adult size.

The accuracy of estimating production rates using ER was assessed by comparing changes in *Synchaeta cecilia* concentrations in water samples incubated for 24 h with a calculated birth rate based on ER. On August 12 a single 20 l sample of whole water was obtained from the dock at a typical sampling time (10:00 h). After thorough gentle mixing, a time zero sample of 2 l was withdrawn and processed for abundance and ER estimates. Replicate 1.5 l samples (5) were incubated at 24 °C for 24 h and processed for estimates of rotifer concentration and ER.

RESULTS

Field sample data

Nine rotifer species were encountered with *Synchaeta cecilia* and *Brachionus plicatilis* generally dominating in abundance (Fig. 1A, B). In descending order of numerical abundance, the other species were: *S. baltica, Proalides tentaculatus, S. fennica, S. baltica, Brachionus* sp., *S. vorax, Notholca acuminata* and *Trichocerca marina*. Generally, neither the gradual increases in temperature (from 11 to 30 °C) and salinity (from 7.5 to 12 ppt) nor marked variations in chl *a* concentrations (18 to 85 µg chl *a* l^{-1}), corresponded with obvious changes in rotifer abundance or the species assemblage (Fig. 1C). A singular exception was the occurrence of *P. tentaculatus* which appeared to coincide with dinoflagellate blooms (based on casual observations), although dinoflagellate remains were not detectable in any of the specimens examined.

Temporal changes in total rotifer concentrations (Fig. 2) did not parallel shifts in microflagellate numbers nor did the 2 groups show an inverse relationship. However, an inverse relationship between total rotifers

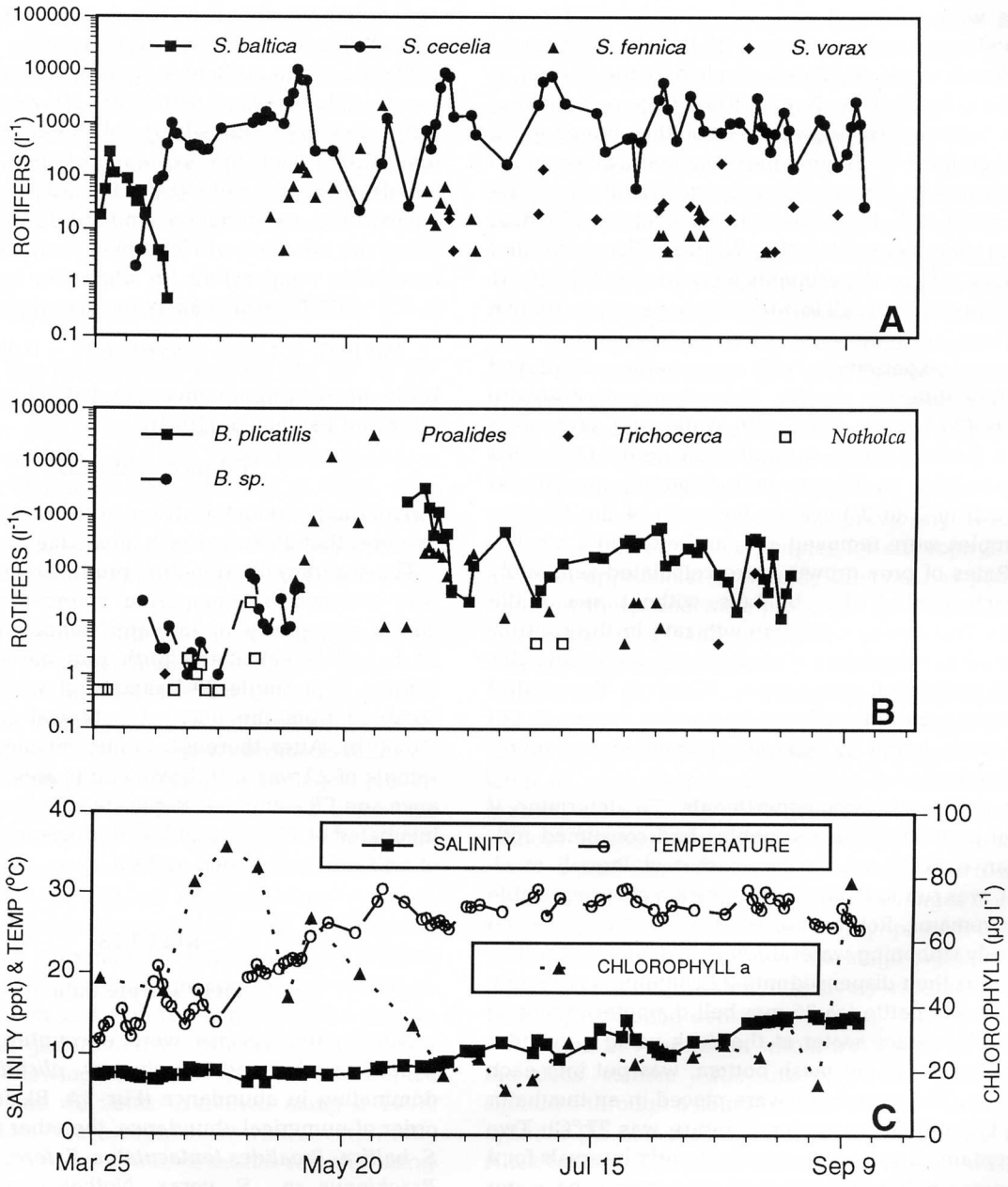

Fig. 1. Temporal abundances of (A) *Synchaeta* spp., (B) *Brachionus* spp. and other rotifers, and (C) temporal changes in salinity, temperature, and chl *a* concentrations in the Rhode River estuary

and herbivorous ciliates was apparent (Fig. 2A). Herbivorous ciliates were usually dominated numerically by a medium-sized (40 µm diameter) *Strombidium* sp. Occasionally tintinids were abundant, *Tintinnopsis* spp. and *Eutintinnus* spp., especially when oligotrich concentrations were low.

The inverse rotifer-herbivorous ciliate relationship was most obvious from early May through August when abundance trends of autotrophic and heterotrophic microflagellates closely paralleled each other. The parallel abundance pattern of the 2 microflagellate groups (Fig. 2B), which are ostensibly distinct trophically, suggests common regulation – presumably via predation.

Considerable variation was seen in the *Synchaeta cecilia* ER during both spring and summer. Changes in ER appeared to track changes in microflagellate concentration (Fig. 3).

Results of linear correlation analysis are given in Table 1. *Synchaeta cecilia* ER was positively correlated

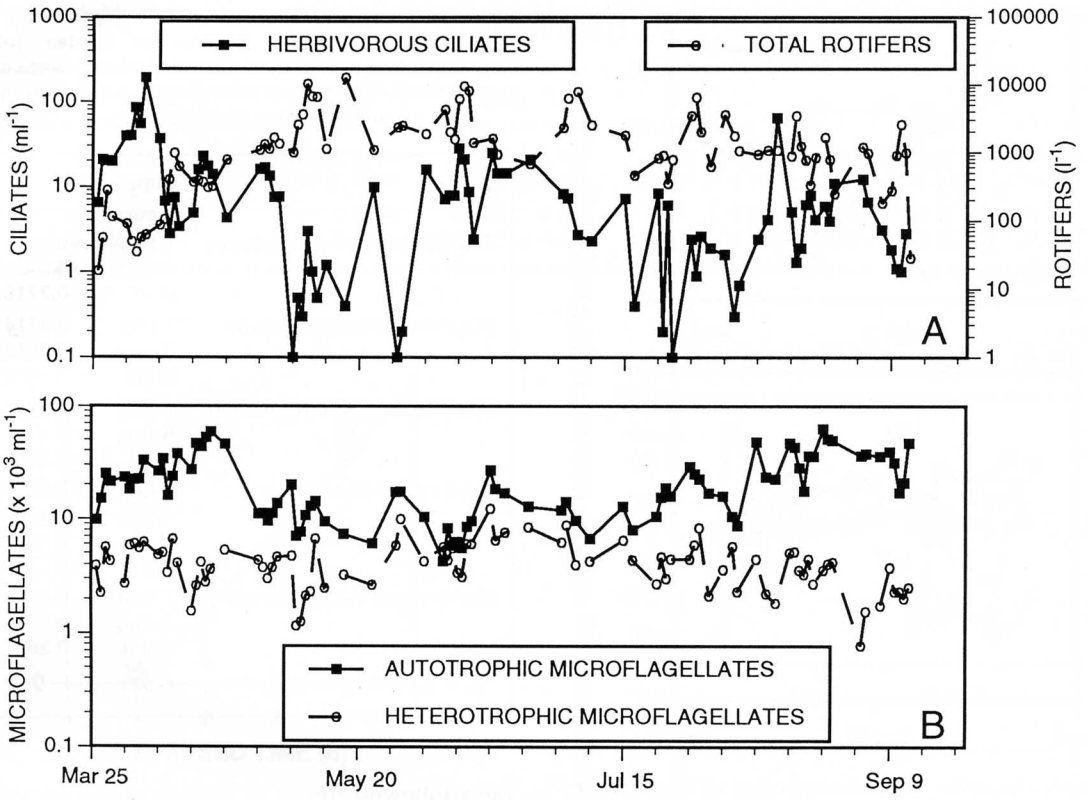

Fig. 2. (A) Concentrations of herbivorous ciliates and total rotifers. (B) Abundances of autotrophic (chloroplast-containing) and heterotrophic (aplastidic) microflagellates

with flagellate concentration. In contrast, the abundance of *S. cecilia* was negatively correlated with flagellate and herbivorous ciliate concentrations. Total rotifer abundance was also negatively related to microflagellate as well as herbivorous ciliate abundance.

Predation experiments

Copepods appeared to clear water of *Synchaeta cecilia* at higher rates (44 and 57 ml copepod^{-1} d^{-1}) than of *Brachionus plicatilis* (29 and 20 ml copepod^{-1} d^{-1}), although the rates were only significantly different in the August experiment (Table 2). Growth rates of the 2 rotifer species were of similar magnitude in the experiments but with *B. plicatilis* showing higher rates (0.042 to 0.060 h^{-1}) than *S. cecilia* (0.021 to 0.048 h^{-1}).

Experiments with sea nettles, in contrast to the copepod experiments, showed higher clearance rates on *Brachionus plicatilis* than on *Synchaeta cecilia* (Table 2). But few replicates and high variances precluded demonstration of significant difference. For the 2 experiments, mean clearance rates on *S. cecilia* were 13.8 and 6.4 l sea nettle^{-1} d^{-1} compared to 28.3 and 41.2 l sea nettle^{-1} d^{-1} for clearance of *B. plicatilis* (Table 3).

Sea nettle egestion experiment

Egested *Brachionus plicatilis* were easily distinguished from recently or long dead animals. Loricas were either completely empty and perforated with many small holes or contained only a small (30 μm diameter) brown bolus of material near the center of the lorica. *B. plicatilis* loricas were egested at ca 10 h^{-1} (Fig. 4). Assuming steady-state conditions by equating egestion to ingestion, and given a prey concentration of 36 *B. plicatilis* l^{-1} (based on a sample from the experimental date), yields a clearance rate estimate of 6.6 l sea nettle^{-1} d^{-1}. This rate, while not significantly different, is lower than the rates of 28.3 and 41.2 estimated from the grazing experiments which monitored rotifer disappearance rates.

Production estimates

The egg ratio method gave a similar but slightly higher estimate of population growth than that calculated from increases in rotifer concentrations in incubated water samples. The mean ER at t_0 (0.221) was statistically indistinguishable from the 24 h ER, 0.192 (SD = 0.0366). Based on the time zero ER, the predicted

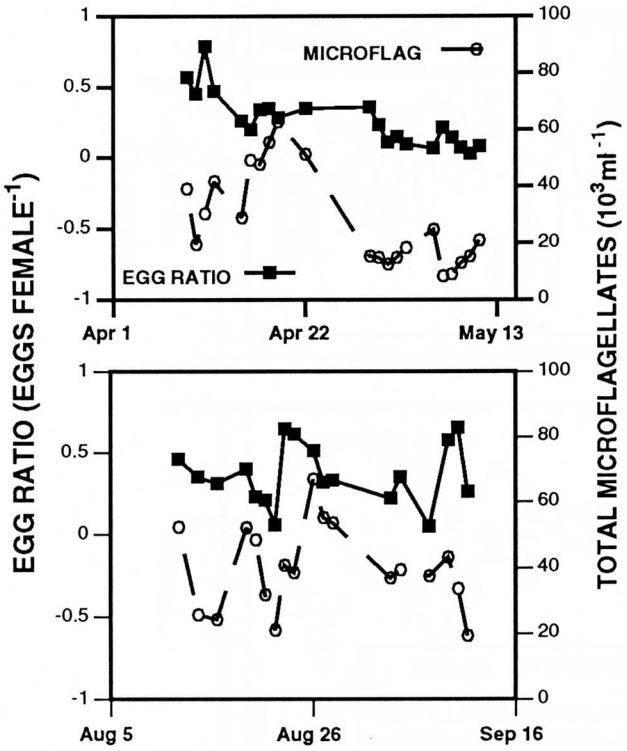

Fig. 3. *Synchaeta cecilia*. Reproductive effort as measured by eggs female^{-1} and food supply considered as microflagellate concentration

Table 1. Results of correlation analysis (Y_1 with Y_2). Organism concentrations (rotifers, herbivorous ciliates, total microflagellates and autotrophic microflagellates) were square root transformed. T flag: total microflagellates; A flag: autotrophic microflagellates; H cil: herbivorous ciliates

Y_1	Y_2	r	n
Synchaeta cecilia abundance	T flag	−0.4623***	75
	A flag	−0.3325**	75
	H cil	−0.27166*	75
Synchaeta cecilia egg ratio	T flag	0.3714*	39
	A flag	0.4478**	39
	H cil	0.0928	39
Synchaeta cecilia production	T flag	−0.0491	39
	A flag	−0.0215	39
	H cil	−0.2885	39
Total rotifer abundance	T flag	−0.4370***	85
	A flag	−0.4562***	85
	H cil	−0.3661***	85
	Chl *a*	−0.328	16
Herbivorous ciliate abundance	T flag	0.1883	85
	A flag	0.131	85
	Chl *a*	0.288	17

* p = 0.05; ** p = 0.01, *** p = 0.001

mean abundance in the incubated samples after 24 h, assuming no death, was 2360 ind. l^{-1} compared to an actual value of 2079 ind. l^{-1} (SD = 29.7).

Production estimates using the egg ratio method ranged from 1.9 to 48.2 µg C l^{-1} d^{-1} during the spring and 0.5 to 57.4 µg C l^{-1} d^{-1} during the summer. Estimates based on growth rates obtained in the control treatments of grazing experiments (late summer) ranged from 11.1 to 96.2 µg C l^{-1} d^{-1}. The mean production rate was 18.3 µg C l^{-1} d^{-1} (SD = 19.7) based on both ER and grazing experiment data. Production rates followed trends in flagellate concentration qualitatively, but not quantitatively (Fig. 5, Table 1).

DISCUSSION

Rotifer community composition

Rotifers in the Rhode River during the spring and summer were dominated by *Synchaeta* and *Brachionus* species and averaged ca 1000 ind. l^{-1}. Most brackish water systems are dominated by *Synchaeta* spp. but abundances seem to range widely among systems (Table 4). However, it should be noted that low concentrations have been reported based on large (≥ 50 µm)

Table 2. *Synchaeta cecilia, Brachionus plicatilis*. Summary of copepod grazing experiment results. t_0: time zero prey concentration in ind. ml^{-1}; K = prey growth constant in the absence of grazers; [C] = time-averaged prey concentration (ml^{-1}) to which the grazers were exposed; F = filtration or clearance rate, apparent volume swept clear of prey in ml grazer^{-1} d^{-1}; I = calculated grazer ingestion rate in organisms consumed d^{-1}; ND: no copepods present during the July 31 experiment. Parameters are given ± SD of the replicates

Date	Prey	t_0 conc	K (h^{-1})	[C]	F	I
July 25	*S. cecilia*	0.46	0.021 ± 0.016	0.16 ± 0.13	44 ± 11.2	6.9 ± 1.3
	B. plicatilis	0.34	0.055 ± 0.006	0.19 ± 0.02	29 ± 4.8	5.6 ± 1.0
July 31	*S. cecilia*	1.14	0.048 ± 0.000	ND	ND	ND
	B. plicatilis	0.29	0.060 ± 0.008	ND	ND	ND
August 8	*S. cecilia*	0.61	0.041 ± 0.033	0.33 ± 62.7	57 ± 11.9	18.5 ± 0.4
	B. plicatilis	0.21	0.042 ± 0.007	0.12 ± 14.7	20 ± 3.9	4.2 ± 0.5

Table 3. *Synchaeta cecilia, Brachionus plicatilis.* Summary of sea nettle grazing experiments results. Parameter abbreviations and units as in Table 1

Date	Prey	t_0 conc	K (h^{-1})	[C]	F	I
August 5	*S. cecilia*	2.14 ± 1.10	0.041 ± 0.004	2.449 ± 0.57	13 842 ± 11 801	30 426 ± 20 950
	B. plicatilis	0.30 ± 0.09	0.059 ± 0.006	0.237 ± 0.03	41 167 ± 11 347	9 910 ± 3 735
August 12	*S. cecilia*	0.40 ± 0.09	0.021 ± 0.002	0.49 ± 0.08	6 354 ± 5 951	2 887 ± 2 415
	B. plicatilis	0.06 ± 0.01	0.051 ± 0.009	0.06 ± 0.07	28 279 ± 2 904	1 564 ± 345

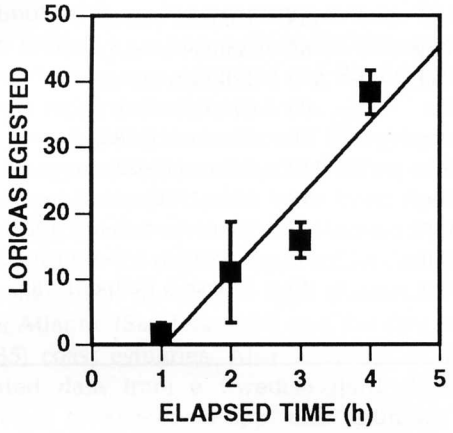

Fig. 4. *Brachionus plicatilis.* Egestion of rotifer remains in a wild population of *Chrysaora quinquecirrha.* Estimates of average numbers (± SE) of *B. plicatilis* loricas egested vs time, based on the appearance of loricas in containers of 20 μm screened water with single sea nettles

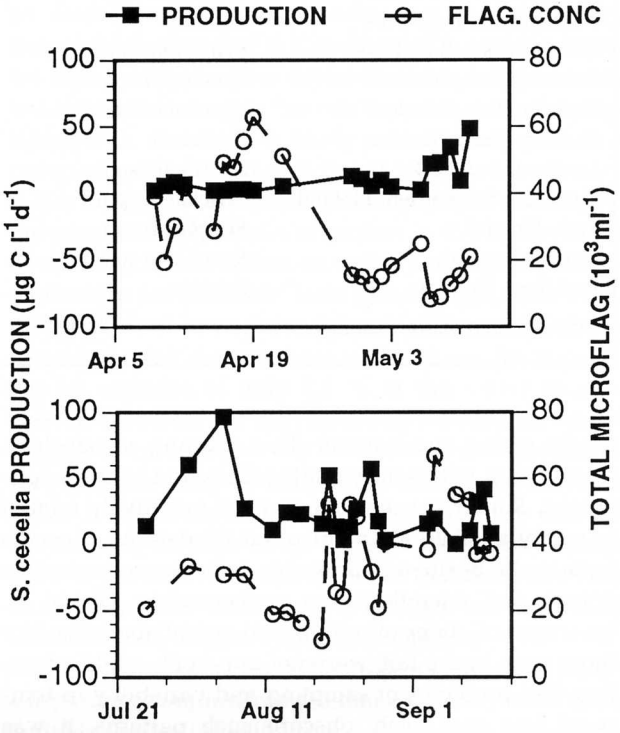

Fig. 5. *Synchaeta cecilia.* Production in the Rhode River estuary based on population growth rates estimated from egg ratio data and grazing experiments

mesh net samples (Fig. 6), resulting in likely underestimation of small or soft-bodied rotifer concentrations.

We do not know if the rotifer community we found is typical for the spring – summer season. However, 1991 data conform in certain respects to previous work in this system. Based on samples taken over a year with an 80 μm mesh net, Allan et al. (1976) described rotifers as abundant, ranging from 1 to 2500 ind. l^{-1} from late October to late May and appearing again briefly in July; *Brachionus plicatilis* was the most common species. The differences between the data of Allan et al. (1976) and ours could represent the results of a long-term trend toward eutrophication in the Rhode River (Correll 1981), inter-annual differences, or simply sampling methods. As noted above, *Synchaeta* spp. were probably underestimated in the 80 μm net samples of Allan et al. (1976). Recently, we reported that during fall months a *Synchaeta* sp. (now identified as *S. cecilia*), present at an average concentration of about 700 ind. l^{-1}, dominated the rotifer community (Dolan & Gallegos 1991).

Regulation of rotifers

The dominant rotifers (*Synchaeta* and *Brachionus*) found in the Rhode River are commonly considered as exploiters of small prey, as the same or similar species have been either cultured or found to feed readily on microflagellate prey (*Synchaeta*: Pourriot 1965, Blackbourn 1974, Stemberger & Gilbert 1985, Egloff 1988; *Brachionus:* Doohan 1973, Dewey 1976, Pilarska 1977, Pourriot & Rougier 1979, Walker 1981, Yúfera & Pascual 1985, Scmid-Araya 1991). In work conducted in the fall in the Rhode River, rotifers and microflagellates showed inverse oscillations; rotifer abundance was successfully modeled as a function of microflagellate density (Dolan & Gallegos 1991). Data presented here

Table 4. Comparison of maximum reported rotifer densities in estuarine systems. Studies employed a wide variety of sampling strategies, and generally reported concentrations integrated over the water column or through the surface layer

Study site	Taxa	Conc. (l^{-1})	Month	Net size (μm)	Source
Potomac River, USA	*Synchaeta cecilia*	4000	Mar	35	Hienbokel et al. (1988)
Chesapeake Bay, USA	Rotifers	500	Nov	44	Brownlee & Jacobs (1987)
Rhode River, USA	*Brachionus*	2500	Apr	80	Allen et al. (1976)
Rhode River, USA	*Synchaeta* sp.	6000	Nov	20	Dolan & Gallegos (1991)
Patuxent River, USA	*S. baltica*	1000	Dec	50	Sellner et al. (1991)
Damariscota River, USA	*Synchaeta* spp.	50–100	May	WW[a]	Sanders (1987)
Narragansett Bay, USA	Rotifers	22	Apr	153	Hulsizer (1976)
San Francisco Bay, USA	*Synchaeta* spp.	10	May	64	Ambler et al. (1985)
Bothnian Sea, Sweden	*Synchaeta* spp.	0.5	Aug	160	Eriksson (1973)
Bothnian Sea, Sweden	*Synchaeta* spp.	15	Jun	90	Eriksson et al. (1977)
Gullmar Fjord, Sweden	*S. vorax*	85	May	90	Hernroth (1983)
Limfjord, Denmark	*Synchaeta* spp.	100	Jul	110	Blanner (1982)
Tvarmine Storfjorden, Finland	*Synchaeta* spp.	1200	May	10	Kivi (1986)
Seili, Finland	*Synchaeta* spp.	100	May	150	Vuorinen & Ranta (1987)
Comacchio, Italy	*Synchaeta* spp.	10	Mar	71	Ceccerelli & Ferrari (1982)
Rosefjord, Norway	Rotifers	300	Mar	40	Krause & Kattner (1989)

[a] WW: whole water examined

for the spring and summer show a strong, yet unclear, relationship between microflagellate and rotifer populations. Rotifer concentrations were negatively related to microflagellate abundance but ER data for *S. cecilia* indicated a positive relationship between reproductive output and microflagellate concentration (Table 1). Inverse oscillations of rotifers and microflagellates, like those seen in the fall, were not apparent; while admitting that problems of sampling and variability in temporal lags can easily obscure such patterns, it was nonetheless surprising.

There are many possible explanations for a change in the abundance patterns of rotifers and microflagellates,

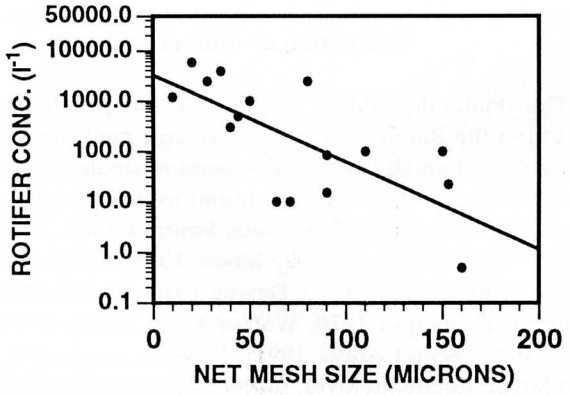

Fig. 6. Relationship between maximum rotifer concentration and sample concentration method from reports on estuarine waters. Data from Table 4, r = 0.716, n = 16, $p \leq 0.01$

ranging from parasitism to changes in the composition of the microflagellate community, most of which can not be addressed with our data. However, we considered 2 obvious possibilities: a competitive relationship with herbivorous ciliates and control of rotifers by predation.

The rotifer-ciliate relationship

Planktonic rotifers and ciliates have been described as having food niches which overlap considerably (Wickham & Gilbert 1991). Resource competition between the 2 groups could have complicated a rotifer-microflagellate relationship. Because ciliates can sustain growth at much lower food concentrations than rotifers (Heinbokel et al. 1988), ciliate numbers should increase and rotifers decrease when food levels are low. While field patterns are rarely unambiguous, no such relationship was obvious (Fig. 2). This observation, combined with the negative relationship between rotifers and ciliate concentrations (Fig. 2, Table 1), could tenuously support a hypothesis of interference competition. We have no data to directly evaluate this hypothesis but a review of the literature suggests that it is not an unreasonable possibility.

While rotifers are generally considered as grazers of small algal prey (Heinbokel et al. 1988), they are likely omnivorous to some extent as are most heterotrophic plankters. For example, one of the species encountered, *Synchaeta vorax*, has been reported to feed vora-

ciously both on other rotifers (Rousselet 1904) and the bloom-forming alga *Phaeocystis pouchetti* (Hollowday 1949). Freshwater *Synchaeta* and *Brachionus* species can ingest relatively large (≥ 20 µm) prey items (Gilbert & Starkweather 1977, Gilbert & Bogdan 1984) and feed on ciliates at high (0.2 to 5.4 ml cleared rotifer^{-1} d^{-1}) rates (Gilbert & Jack 1992). Furthermore, instances of brackish water *Synchaeta* spp. feeding on ciliates have been reported (Lindholm 1981, Arndt et al. 1990). Even the smallest *Synchaeta* species, *S. cecilia* (120 µm long), which dominated the Rhode River community, can feed on a dinoflagellate, *Prorocentrum micans*, 13 × 47 µm, (Egloff 1988) which approaches the size of the most common herbivorous ciliate in the Rhode River (a 40 µm diameter *Strombidium* sp.).

Other workers have mentioned intriguing relationships between estuarine or marine rotifers and ciliates. Rotifers and tintinnid ciliates have been described as dominating 'in turn' in an Adriatic lagoon (Ceccherelli & Ferrari 1982). Co-occurrence of rotifers and tintinnid ciliates has been noted in a fjord (Hernroth 1983) as well as Atlantic (Sanders 1987) and Pacific (Ambler et al. 1985) coast estuaries. Also, Eriksson et al. (1977) presented data from a Swedish fjord showing co-occurrence of *Synchaeta* spp. and tintinnids and an inverse relationship between aloricate ciliates and *Synchaeta* spp. While some workers have hypothesized that rotifers compete with tintinnids in estuaries (Hernroth 1983, Sanders 1987, Heinbokel et al. 1988), it has been suggested that rotifers are the primary consumers of ciliates in a Baltic fjord (Gast 1985). The relationship between rotifers and ciliates in eutrophic estuaries and coastal waters needs further study, especially considering the implications of carnivory in low trophic levels for food chain efficiency (Stoecker & Evans 1985).

Predation by copepods and sea nettles

Experiments were conducted with common co-occurring plankters to evaluate the possibility that predation may have had a significant impact on rotifers in the Rhode River. To our knowledge, these are the first estimates of grazing rates based on field experiments for either *Acartia* or *Chrysaora quinquecirrha* feeding on rotifers.

Estimates of clearance rates obtained in the copepod experiments correspond closely with previous laboratory studies with *Acartia tonsa*, the dominant copepod in the Rhode River during summer months (Allan et al. 1976). *Synchaeta cecilia* was cleared at ca 50 ml copepod^{-1} d^{-1} (Table 2) in natural Rhode River plankton assemblages compared to 37 to 124 ml copepod^{-1} d^{-1} determined over a range of rotifer, ciliate and phytoplankton concentrations in experiments with cultured organisms (Stoecker & Egloff 1987, Egloff 1988). Comparative data for the consumption of *Brachionus plicatilis* is lacking. However, laboratory studies of freshwater calanoid and cyclopoid copepods feeding on *Brachionus* and *Synchaeta* species at prey densities similar to those found in our field experiments (ca 500 ind. l^{-1}) have given clearance estimates of 35 to 85 ml copepod^{-1} d^{-1}, with the higher rates associated with grazing on *Synchaeta* (Williamson 1983, Williamson & Butler 1986), similar to the data for Rhode River organisms. Clearance rates for copepods determined on rotifer prey, like those estimated on ciliate prey (reviewed in Stoecker & Capuzzo 1990, Gifford 1991), are high relative to rates determined on phytoplankton, indicating that despite the relative abundance of phytoplankton, carnivory is likely an important part of a copepod's diet (Stoecker & Egloff 1987).

It is difficult to assess the role of copepod grazing on the population dynamics of rotifers in the Rhode River as contemporaneous data on rotifer and copepod abundances are not available. Data presented in Allan et al. (1976) showed low (about 0.5 ind. l^{-1}) average abundances of adult *Acartia tonsa* in the Rhode River yielding an estimate of only 2.5 % of the water column cleared of rotifers per day, assuming a clearance rate of roughly 50 ml copepod^{-1} d^{-1}. However, concentrations vary over an order of magnitude from week to week (Allan et al. 1976) so that predation pressure may be sporadically as high as ca 15 % of the water column cleared per day. It should be noted that these are only rough estimates since they are based on calculated instantaneous rates of copepod predation.

The clearance rates estimated for the sea nettle *Chrysaora quinquecirrha* (75 mm diameter) were quite variable, reflecting differences in estimates for individual animals. Averaging the rates for both *Synchaeta* and *Brachionus* as prey, over all the experiments (both grazing and egestion) yields an estimate of about 20 l ind.$^{-1}$ h^{-1}. Other clearance rate data for the sea nettle are apparently unavailable. However, our estimate is within the wide range of data reported for other scyphomedusa species of roughly similar size, feeding on a comparably sized prey, at temperatures ranging from 20 to 30 °C. For example, Stoecker et al. (1987) working with 110 mm diameter *Aurelia aurita* determined clearance rates of 17 to 52 l ind.$^{-1}$ d^{-1} on prey ranging in size from euglenoid flagellates to copepod nauplii at temperatures of 19 to 20 °C. Larson (1991) estimated clearance rates for 55 mm bell height specimens of *Stomolophus meleagris* at 28 to 30 °C to range from 4.8 to 172 l ind.$^{-1}$ d^{-1} on a variety of planktonic crustaceans. Larson (1991) also found a large amount of individual variability in clearance rates (i.e. SD ≥ 50 % of mean), aside from that expected due to differences in size and reproductive state.

Based on our clearance rate estimate, sea nettle abundances would have to be quite high, relative to reported average concentrations of 5 to 10 ind. m^{-3} (Purcell et al. 1991), to have a substantial impact on the rotifer community. At an average abundance of 7 sea nettles m^{-3}, sea nettles would clear only 15 % of the water column of rotifers per day, using our average clearance rate of 20 l sea $nettle^{-1}$ d^{-1}. However, sea nettle distribution is extremely patchy and concentrations of 50 to 100 ind. m^{-2} were visible at the surface from the dock in August (pers. obs.).

The grazing experiments provided evidence that one possible fate of rotifers in the Rhode River is consumption by other metazoan plankters. However, the magnitude of the feeding rates estimated, combined with reasonable approximations of predator abundance, indicate that rotifers, although periodically subjected to large removal rates, probably are not usually predator-controlled. Similar conclusions regarding rotifer population dynamics in a Baltic inlet were reached by Arndt (1989).

Production of *Synchaeta cecilia*

Estimates of production were based on population growth rates from ER data for most of the dates. While the ER method compared favorably to rates based on measured increases in numbers, the estimates should be considered with certain caveats in mind. The ER method contains the assumption that all eggs reach adult size; if any egg or juvenile mortality occurs production will be overestimated. This is a potential source of error for which we have no data. On many dates, ER was low (Fig. 3) and very large sample sizes are needed for estimates of even modest precision under such circumstances (Demott 1980). Calculations were based on the assumptions that there was no diel cycle of reproduction or significant spatial heterogeneity in ER; violations of these assumptions can lead to serious errors in estimating population dynamics (Magnien & Gilbert 1983). There are few data on diel periodicities in estuarine rotifers aside from a recent report of a diel rhythm of feeding in an estuarine population of *Brachionus plicatilis* (Arndt & Heerkloss 1989). On the other hand, limited data (not shown) from transect samples indicated that spatial differences appeared to be minor. Unless these possible sources of error led to consistent overestimation, the production of *Synchaeta cecilia* in the Rhode River is large, and of a magnitude similar to copepods and ciliates in the Chesapeake Bay and its tributaries (Table 5). The average calculated production for the Rhode River is an order of magnitude greater than that of copepods, as Allan et al. (1976) had speculated it might be.

The estimates for rotifer production in other brackish waters suggests that the magnitude of rotifer production in the Rhode River is probably not unusual. Heinbokel et al. (1988), based on ER data, calculated *Synchaeta cecilia* production during March in the Potomac River estuary to range from 0.97 to 8.27 μg C l^{-1} d^{-1} compared to 18.3 μg C l^{-1} d^{-1} in the Rhode River (Table 5). Hernroth (1983) estimated peak *Synchaeta* spp. production for the Gullmar Fjord to be about 1.5 μg C l^{-1} d^{-1} during the spring phytoplankton bloom, based on abundance data from samples collected with a large mesh (90 μm) plankton net which he noted likely missed small rotifers.

The pattern of rotifer production in the Rhode River, characterized by large temporal variability and a weak relation to microflagellate concentration, is difficult to relate to other estuarine systems as very few comparative data exist. However, a short-term study (≤2 wk) of rotifer reproduction in the Potomac River estuary, Maryland, USA (Tyler & Heinbokel 1985) noted the lack of a simple correlation between rotifer ER and apparent food levels, whether considered as separate phytoplankton taxa or as chl *a*. Later, Heinbokel et al. (1988) described a saturating relationship beween ER and chl *a* over a medium temporal and spatial scale, i.e. using data averaged over the water column from several Potomac River stations along a salinity gradient

Table 5. Estimates of average production rates (μg C l^{-1} d^{-1}) of various zooplankton groups in the Cheasapeake Bay and its subestuaries. Primary production is high in these systems: e.g. production in the Rhode River on an annual basis averages 1250 μg C l^{-1} d^{-1} (Correll 1978); in the Patuxent River during the summer, ca 600 μg C l^{-1} d^{-1} (Heinle 1966); and euphotic zone primary production in the mesohaline Chesapeake Bay ranges from ca 200 to 1000 μg C l^{-1} d^{-1} during spring and summer (Sellner 1987)

Organism	Location	Season	Production	Source
S. cecilia	Rhode River	Spring – summer	18.3	This study
S. cecilia	Potomac River	Spring	3.5	Heinbokel (1988)
Acartia tonsa	Rhode River	Summer	1.4	Allan et al. (1976)
Acartia tonsa	Patuxent River	Summer	27.8	Heinle (1966)
Copepods	Chesapeake Bay	Annual	33	Storms (1975)
Ciliates	Chesapeake Bay	Spring – summer	13.5	Dolan (1988)

sampled over several days. A similar relationship between rotifer production and microflagellate concentrations in the Rhode River may have been apparent had we integrated values over various time periods.

Rotifers have received little attention in studies of estuarine and marine plankton, and while this can be understood as due to their limited distribution and under-representation in net samples (Heinbokel et al. 1988), it is nonetheless a possibly serious omission. In the Rhode River at least, rotifers are numerous, with production rates comparable to copepods and ciliates. Although it is not clear what factors, if any, consistently regulate rotifer populations in the Rhode River, they appear to interact competitively with herbivorous ciliates and serve as food for other planktonic metazoans. It is quite possible that rotifers are equally important in other estuarine systems but have not been adequately sampled.

Acknowledgements. This work was supported by the Smithsonian Office of Fellowships and Grants. Paul Turner of the National Museum of Natural History provided a valuable and enthusiastic introduction to rotifer taxonomy. The manuscript was greatly improved by comments from D. W. Coats, J. J. Gilbert, R. S. Stemberger, D. K. Stoecker and 2 anonymous reviewers.

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This article was presented by D. K. Stoeker, Cambridge, Maryland, USA

Manuscript first received: January, 7, 1992
Revised version accepted: June 23, 1992