Freshwater Biology (2002) **47**, 53–64

Direct and indirect impact of two common rotifer species (*Keratella* spp.) on two abundant ciliate species (*Urotricha furcata, Balanion planctonicum*)

THOMAS WEISSE and ANGELA FRAHM
Max-Planck-Institute for Limnology, Plön, Germany

SUMMARY

1. We investigated the potential competition and feeding impact of the common rotifer species, *Keratella cochlearis* and *K. quadrata*, on the abundant prostomatid ciliates, *Urotricha furcata* and *Balanion planctonicum*, in laboratory batch culture experiments. All four species have similar feeding preferences, co-occur in many freshwater environments, and are thus potential competitors for the same algal food.
2. Two small *Cryptomonas* species served as food for the ciliates and the rotifers in the experiments. Growth rates of each ciliate species were measured when they grew alone and when they were paired with one of the rotifer species.
3. Both rotifer species reduced the growth rate of *U. furcata*, probably primarily by direct feeding on the ciliates. Growth rate of *B. planctonicum* was unaffected by *K. cochlearis*, but was drastically reduced by grazing and/or mechanical interference of *K. quadrata*.
4. These results suggest niche partitioning of the sympatric ciliates with respect to their rotifer competitors/predators.

Keywords: ciliates, competition, feeding, plankton, rotifers

Introduction

The small prostomatid ciliates *Urotricha furcata* Schewiakoff and *Balanion planctonicum* (Foissner, Oleksiv & Müller), renamed by Foissner, Berger & Kohmann, belong to the dominant planktonic ciliates in many stratifying temperate lakes (summarized by Weisse & Müller, 1998; Foissner, Berger & Schaumburg, 1999). Because of their short generation times, both genera are among the first zooplankton species that respond to developing phytoplankton blooms in spring (Müller *et al*., 1991; Weisse & Müller, 1998) when they may become the most important herbivores (Weisse *et al*., 1990). Among herbivorous metazooplankton, rotifers have the shortest generation times and peak shortly after ciliates (Sommer *et al*., 1986; Pauli, 1990; Sommaruga & Psenner, 1993). Most rotifers feed most efficiently on autotrophic and heterotrophic protists in the 4–17 μm size range (Gilbert, 1988a; Arndt, 1993). The small prostomatid ciliates seem to have very similar food requirements (Foissner *et al*., 1990; Müller, 1991; Müller *et al*., 1991; Sommaruga & Psenner, 1993). Competition between these ciliates and rotifers for the same food is therefore highly possible.

Direct and indirect interactions between zooplankton taxa significantly impact their seasonal succession. Competitive interactions between cladocerans and rotifers and the mechanisms by which, in particular, large (≥ 1.2 mm) *Daphnia* suppress rotifer populations have been studied in great detail (reviewed by Gilbert, 1988a; Walz, 1995). *Daphnia* are thought to be superior competitors for algae because their feeding size spectra are broader than those of rotifers and completely include the feeding range of the latter. Rotifers are thus not able to avoid exploitative competition with co-occurring *Daphnia* when algal food becomes limiting (Gilbert, 1988b).

Correspondence and Present address: Thomas Weisse, Institute for Limnology of the Austrian Academy of Sciences, Mondseestr. 9, A-5310 Mondsee, Austria.
E-mail: thomas.weisse@oeaw.ac.at

In contrast to interactions between daphnids and rotifers, the potential feeding relationships between rotifers and ciliates have been studied only slightly. Arndt (1993), Gilbert & Jack (1993), and Stenson & Svensson (1995) investigated feeding of predatory rotifers on some ciliates. Gilbert (1994) demonstrated that some oligotrich ciliates use a jumping behaviour to escape ingestion by rotifers. Indirect interactions such as exploitative competition between rotifers and ciliates have not yet been studied. It was thus our goal to investigate the potential direct and indirect feeding impact of the common rotifer species, *K. cochlearis* Gosse (*typica* form) and *K. quadrata* O. F. Müller on two dominant freshwater ciliates, *U. furcata* and *B. planctonicum*. As these ciliates are closely related to each other, have similar feeding modes and are of comparable size, we expected that the rotifer impact would be similar on both species (null hypothesis, H_0 = no species-specific difference).

Methods

Study organisms

The prostomatid ciliates *B. planctonicum* and *U. furcata* had been isolated by H. Müller (Limnological Institute Konstanz) from near-surface waters of mesoeutrophic Lake Constance (Müller, 1991; Müller & Geller, 1993). Both ciliate species range in length from about 10–25 μm (summarized by Foissner *et al.*, 1999). The volume of these ciliates is highly variable, depending on the particular isolate and temperature (Weisse & Montagnes, 1998; Montagnes & Weisse, 2000), and their nutritional status (Müller, 1991). For the experiments reported here, we assumed an average live volume of 2000 μm^3 for *Urotricha*, 1820 μm^3 for *Balanion*, which are typical for the respective species under the experimental conditions. We converted the ciliate biovolume to carbon assuming a conversion factor of 110 fg C μm^{-3} (Turley *et al.*, 1986). The ciliates have been kept in our laboratory as non-clonal cultures in Erlenmeyer bottles of 50–500 mL volume on a diet of several small cryptophyte species at 16 ± 1 °C and a 12 : 12 h light : dark cycle for over 2 years.

We isolated the rotifers *K. cochlearis* f. *typica* and *K. quadrata* repeatedly from mesotrophic Lake Schöhsee and eutrophic Lake Plußsee in the vicinity of the laboratory in spring and summer, 1996. Stock rotifer cultures were kept in Erlenmeyer bottles or volumetric flasks with the same algal species under identical light (30–40 μmol photons m^{-2} s^{-1}, L : D 12 : 12 h) and temperature (16 °C) conditions as the ciliates. With its body length ranging from 90 to 140 μm, *K. cochlearis* is smaller than *K. quadrata* (180–220 μm).

Growth experiments were conducted with non-axenic, exponentially growing cultures of the cryptophytes *Cryptomonas* sp., strain no. 26.80 obtained from the Culture Collection of Algae in Göttingen, Germany, and another unidentified *Cryptomonas* sp., isolated from Lake Constance by A. Giani (Limnological Institute Konstanz). For clarity, the latter, unidentified species is referred here as *Cryptomonas* 'A'. Both species are similar in size with an average biovolume of 270–290 μm^3 (Weisse & Kirchhoff, 1997).

Their equivalent spherical diameter measured by the electronic particle counter used in this study (see below) ranged from 7 to 12 μm. For conversion to carbon units, we assumed an average algal volume of 285 μm^3 and the carbon to volume conversion equation given by Strathmann (1967), resulting in a cellular carbon content of 46 pg. Algal cultures were grown in modified Woods Hole Medium (MWC) (Guillard & Lorenzen, 1972). This medium was also used for ciliate and rotifer stock cultures and for all experiments reported below. We maintained *Cryptomonas* sp. strain no. 26.80 in a chemostat culture at ~280 μmol photons m^{-2} s^{-1}, L : D 12 : 12 h, and 16 °C. *Cryptomonas* 'A' was maintained in semicontinuous batch cultures under continuous light at 20 °C.

Experimental design

All experiments were run in sterilized six-well (10 mL vol.) tissue-culture plates. Experimental volume in each well was 8 mL. The ciliates and rotifers were taken from their respective stock cultures and adapted to the experimental food and temperature conditions for at least 48 h prior to the beginning of the experiments. Bacterial contamination was periodically examined using epifluorescense microscopy and DAPI staining (Porter & Feig, 1980). Bacteria were not considered in growth experiments because the bacterial biovolume was small (< 0.2) relative to that of algae, and all ciliate and rotifer species used do not feed upon bacteria when cryptophytes are present (Weisse & Frahm, unpublished data). Rotifers were transferred individually by pipette to the tissue plates.

We used females with and without eggs as inoculum. While the percentage of egg-carrying females varied from experiment to experiment, care was taken to use an identical fraction in each replicate and parallel experiment. Algal abundance in each container was repeatedly measured by means of an electronic particle counter (CASY 1-Model TTC, Schärfe System) during the acclimatization period and adjusted to the experimental concentration by adding algae from stock cultures or diluting with MWC medium. Ciliates were usually counted from 1-mL subsamples fixed with neutral Lugol's solution using settling chambers and inverted microscopy at 250× magnification.

Routine experiments were conducted as pairwise treatments, each experiment performed in triplicate. Three tissue wells received one ciliate species (*U. furcata* or *B. planctonicum*) plus algae; a second set of three wells received one rotifer species (*K. cochlearis* or *K. quadrata*) plus the same amount of algae; a third set contained both the respective ciliate and rotifer species plus algae. In this paper we present results of the impact of rotifers on the ciliates only. Rotifer growth rates and potential effects of the ciliates on the rotifers will be presented elsewhere (Weisse & Frahm, 2001). The initial density of rotifers was 2 mL^{-1}, while the initial concentration of ciliates was approximately 100 cells mL^{-1}. The algal concentration was measured daily during the experiments in 200-μL subsamples with the electronic particle counter. Between 4 and 6 mL of each well were transferred each day to fresh algal suspensions in new wells. The volume in the new containers was filled up to 8 mL and re-adjusted to the initial experimental algal concentration. Ciliate cell numbers reported are corrected for this dilution effect. Rotifers were counted during transfer via pipette. Dead rotifers were counted separately. Ciliates were counted in subsamples from the remaining 2–4 mL of the old wells that were used during the previous day. All routine experiments were conducted under dim light at 12.5 ± 1 °C and lasted for 5–8 days. Our experimental design was similar to the one used by Stemberger & Gilbert (1985a,b).

Two additional short-term (26–33 h) experiments were conducted in order to test if the rotifers feed directly upon the ciliates. We combined relatively low *Cryptomonas* 'A' concentrations ($< 1 \times 10^7$ cells L^{-1}) with high ciliate ($1.3–3.8 \times 10^7$ cells L^{-1}) and rotifer (65–180 individuals per well) levels in these experiments. Each experiment was run in triplicate. Both the ciliates and the rotifers were adapted to the experimental conditions by feeding them at low algal concentrations over 4 days prior to the beginning of the experiments. To ensure that *K. cochlearis* was starved in these experiments, we transferred the rotifers to pure MWC medium 16 h before the start of the experiments. Six to seven subsamples of 0.5 mL each for ciliate cell counts were taken from each well over a period of 33 h (first experiment) or 26 h (second experiment). The number of live and dead rotifers was assessed at each subsampling interval.

Calculation of growth and grazing rates

Growth rate (μ) is defined as the change in population size assuming exponential growth according to

$$\mu = \frac{\ln N_t - \ln N_0}{t_1 - t_0} \quad (1)$$

where N_t and N_0 are final and initial population sizes, and t is time in days. Growth rates were calculated from least squares linear regressions of ln-transformed population sizes versus experimental time.

Rotifer ingestion rates of ciliates (I, in ciliates rotifer^{-1} h^{-1}) were calculated according to Frost (1972) and Heinbokel (1978):

$$I = \frac{C_m \times g}{R_m} \quad (2)$$

where g is the grazing rate ($g = \mu_{control} - \mu_{experiment}$ h^{-1}), R_m is the rotifer abundance and C_m is the mean ciliate abundance (mL^{-1}) in the experimental containers. For the short-term experiments, the latter was calculated as:

$$C_m = \frac{C_0 \times [\exp\{(k-g) \times \Delta t\} - 1]}{\Delta t \times (k-g)} \quad (3)$$

where C_0 is the initial ciliate abundance and k denotes ciliate population growth rate in the controls without rotifers. For the routine experiments, C_m was averaged over several sampling days. The grazing coefficient for routine experiments was derived from the slope of the regression line of ln-transformed cell numbers of ciliates versus time in controls minus the respective slope in the experimental bottles. In the few cases in which feeding rates were measured over periods of only 1 or 2 days (*K. quadrata* feeding on

B. planctonicum and the two short-term experiments), g was calculated as:

$$g = \frac{[\ln(Cc_t/Cc_0) - \ln(C_t/C_0)]}{\Delta t} \quad (4)$$

where Cc_0 and Cc_t are the initial and final ciliate numbers in the controls and C_0 and C_t are the initial and final ciliate concentrations in the containers with rotifers. The clearance rate CR (in μL individual^{-1} h^{-1}) was calculated as:

$$CR = \frac{I}{C_m} \times 10^3 \quad (5)$$

The factor 10^3 results from converting ciliate abundance reported per mL to units of μL.

Statistical analysis

Least squares linear regressions were calculated for the pooled data from each experiment triplicate. The regression equations of ln-transformed ciliate cell numbers versus time were tested for significant differences between treatments using a multiple linear regression model (Neter *et al.*, 1990) using the software package STATISTICA (version 5.1). The regression equation in controls was calculated as:

$$y_1 = \beta_0 + \beta_1 x_1 \quad (6)$$

where β_0 represents the y-intercept and β_1 the slope of the regression. The regression equation in the experimental bottles was calculated as:

$$y_1 = (\beta_0 + \beta_2) + (\beta_1 + \beta_3)x_2 \quad (7)$$

The regression equations differ with respect to their slope and y-intercept if β_2 and β_3 are significantly different from zero. We tested the null hypothesis (H_0: $\beta_2 = 0 = \beta_3$) against the alternative hypothesis (H_A: $\beta_2 \neq 0 \neq \beta_3$).

Results

Rotifer impact on Urotricha furcata

We investigated the growth of *U. furcata* in experiments with and without the rotifer *K. cochlearis* at a high and a moderate algal concentration (Fig. 1). Note

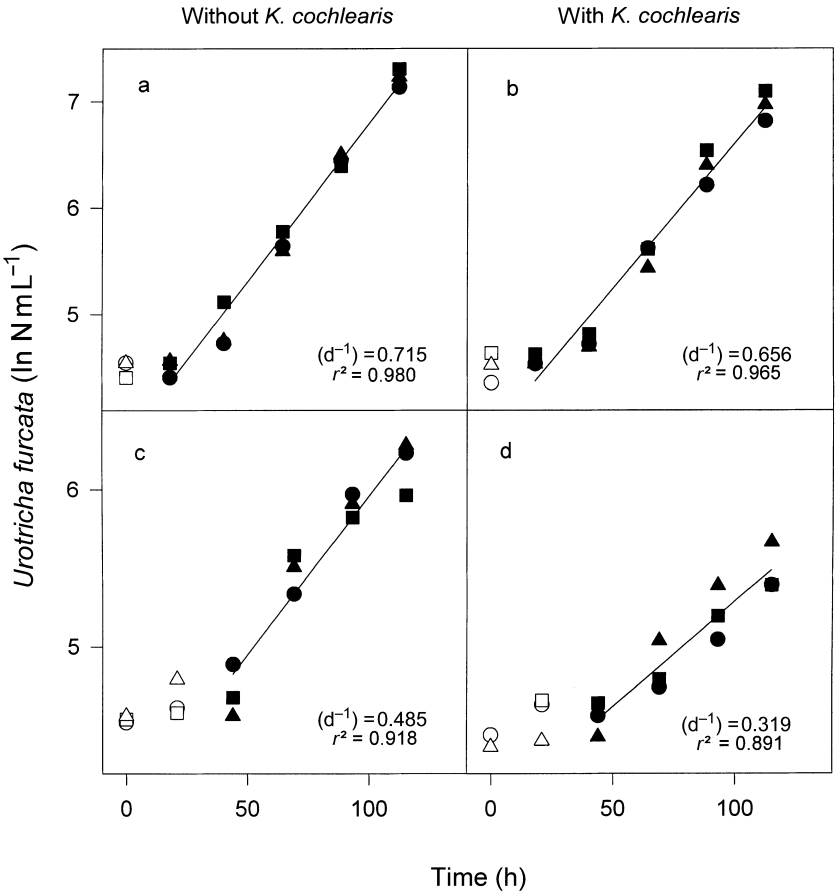

Fig. 1 Projected (i.e. corrected for dilution during the experiments) population development of *Urotricha furcata* without (a & c) and with (b & d) *Keratella cochlearis*. Algal food concentration was 1×10^8 *Cryptomonas* sp. L^{-1} (a & b) and 3×10^7 *Cryptomonas* sp. L^{-1} (c & d). The slope (μ) and the coefficient of determination of the least squares linear regression are given in each panel. Data shown by open symbols indicate the lag phase and were not considered in the regression analyses.

that ciliate cell numbers reported in Fig. 1 were corrected for the dilution by algal suspensions and medium during the experiments (see Methods). Because the daily dilution approximately compensated the ciliate growth rate, the actual cell numbers in the experimental containers remained relatively constant during the experimental period. The development of the *U. furcata* population followed the same general pattern in all treatments. The ciliates started growing exponentially after an initial lag phase of 1 or 2 days. Ciliate growth in the containers with *K. cochlearis* (Fig. 1b,d) was lower than when *U. furcata* grew alone (Fig. 1a,c) at both algal concentrations. The slopes of the respective regression equations with and without rotifers were not significantly different at the high algal concentration ($P = 0.198$), but were clearly different ($P < 0.0001$) at the lower algal density. We repeated the second experiment with an algal concentration of 3.0×10^7 cells L^{-1}. Compared with the previous experiment, the resulting growth rates of *U. furcata* in the third experiment (not shown) were somewhat lower, 0.300 day^{-1} in the containers without and 0.172 day^{-1} in the containers with rotifers. Again, growth of *U. furcata* was significantly ($P = 0.009$) reduced when *K. cochlearis* was present.

To test whether the observed reduction in the population growth rate of *U. furcata* in the presence of *K. cochlearis* was caused by exploitative competition or direct effects such as feeding or mechanical interference, we exposed the ciliates in two short-term (26–33 h) experiments in high numbers to increased rotifer concentrations of 10–20 *K. cochlearis* mL^{-1} (Fig. 2). These experiments were run at limiting algal cell numbers ($3–8 \times 10^6$ *Cryptomonas* sp. L^{-1}) and with rotifers that had been starved for 16 h prior to the beginning of the experiments. In terms of biomass, values for ciliates were similar (0.3–0.4 mg C L^{-1}, first experiment) or twofold higher (0.6–0.7 mg C L^{-1}, second experiment) than those for *Cryptomonas*. We conducted each short-term experiment in triplicate. Because, probably due to pipetting errors, the initial ciliate abundance differed somewhat in the parallel experiments, we refer to them as 'treatments' in Fig. 2.

It is obvious that cell numbers of *U. furcata* did not change or increase slightly in the wells without *K. cochlearis* (Fig. 2, left panels). The ciliate population in these controls increased on average at a low rate of $\mu = 0.095$ day^{-1} in the first, and $\mu = 0.049$ day^{-1} in the second experiment. The rotifers reduced the ciliate

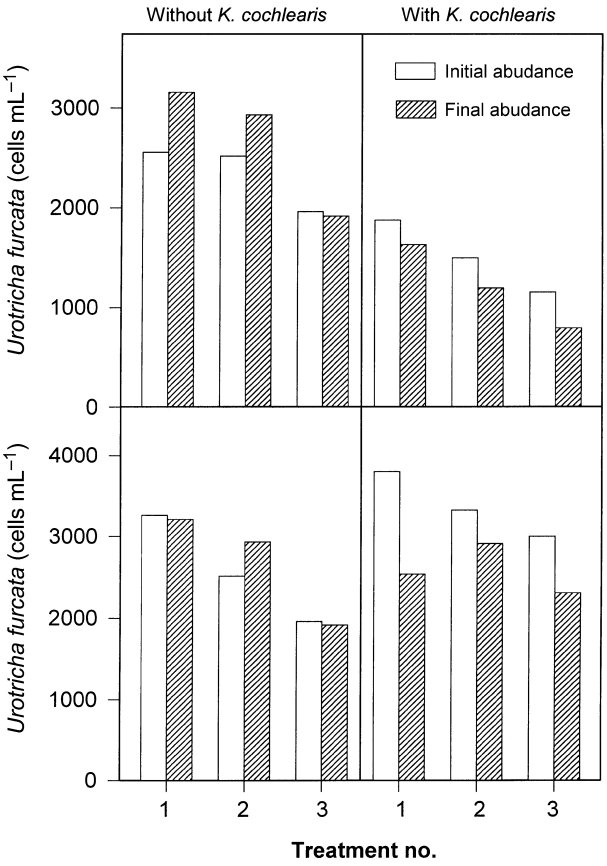

Fig. 2 Population dynamics of *Urotricha furcata* at low concentrations of *Cryptomonas* sp. ($< 1 \times 10^7$ cells L^{-1}) without (left) and with (right) high rotifer concentrations of 10 *Keratella cochlearis* mL^{-1} (top) and 20 *K. cochlearis* mL^{-1} (bottom).

concentration in every treatment (Fig. 2, right panels), and this effect was more obvious at the higher rotifer abundance in the second experiment (Fig. 2, lower right panel). We calculated rotifer ingestion rate from the mean experimental abundances of ciliates and rotifers, considering the slow ciliate growth rate measured in the controls without rotifers. The resulting ingestion rate was 1.3 *U. Keratella*$^{-1}$ h^{-1} in the first, and 2.2 *U. Keratella*$^{-1}$ h^{-1} in the second, experiment. Corresponding clearance rates were 0.9 and 0.8 μL *Keratella*$^{-1}$ h^{-1}. Total feeding rate of *K. cochlearis* should have been higher because *Keratella* probably also ingested some algae during these experiments.

The larger rotifer species, *K. quadrata*, had a similar impact on growth rate of *U. furcata*. Presence of *K. quadrata* reduced the growth rate of *U. furcata* in every experiment, irrespective of the algal abundance and algal species (Table 1). This effect was significant

Table 1 Growth rate (μ) of *Urotricha furcata* in experiments without and with *Keratella quadrata*. With the exception of the experiment at the lowest algal concentration, growth rates were calculated from changes in ciliate cell numbers over four consecutive days. At the lowest algal abundance, μ was calculated from changes in cell numbers occurring during the first 2 days of the experiment only (value given in parentheses; n.s. = μ not significantly different from zero; n.d. = not determined)

Algal species	Algal conc. (cells L^{-1})	Biomass (mg C L^{-1})	μ (day^{-1})		Level of significance
			Without *K. quadrata*	With *K. quadrata*	
Cryptomonas sp.	9.7×10^7	4.46	0.595 ± 0.222	0.555 ± 0.031	n.s.
Cryptomonas sp.	3.0×10^7	1.38	0.655 ± 0.034	0.480 ± 0.060	$P = 0.021$
Cryptomonas sp.	1.0×10^7	0.46	(0.525 ± 0.070)	n.s.	n.d.
Cryptomonas sp.	Mean value		0.631 ± 0.045	0.509 ± 0.100	$P = 0.034$
Cryptomonas 'A'	3.0×10^7	1.38	0.895 ± 0.065	0.852 ± 0.053	n.s.

at 3.0×10^7 cells L^{-1} of *Cryptomonas* sp., and when all three experiments with this algal strain were pooled. The lowest algal concentration tested, 1.0×10^7 cells L^{-1} of *Cryptomonas* sp. strain 26.80, was in the range of limiting algal abundance where growth rates of *U. furcata* approached zero (Weisse *et al.*, 2001). Ciliates grew in these experiments until 96 h after the beginning of the experiments. Growth rates were exponential only during the first 48 h. In the treatments with *K. quadrata*, ciliate cell numbers did not change significantly at the low algal concentration during the experimental period of 6 days. Because regression equations for all other experiments were calculated over four consecutive sampling periods, we did not test for significant differences between growth rates of *U. furcata* in the containers with and without rotifers in this experiment. The differences in the ciliate growth rates with and without rotifers were insignificant in the experiment with *Cryptomonas* 'A' as food.

We calculated ingestion rates from the routine experiments with both rotifer species. When pooling results from all experiments, including the two short-term experiments, it is obvious that feeding by *Keratella* spp. on *Urotricha* was positively and linearly related to the ciliate to algal ratio (Fig. 3).

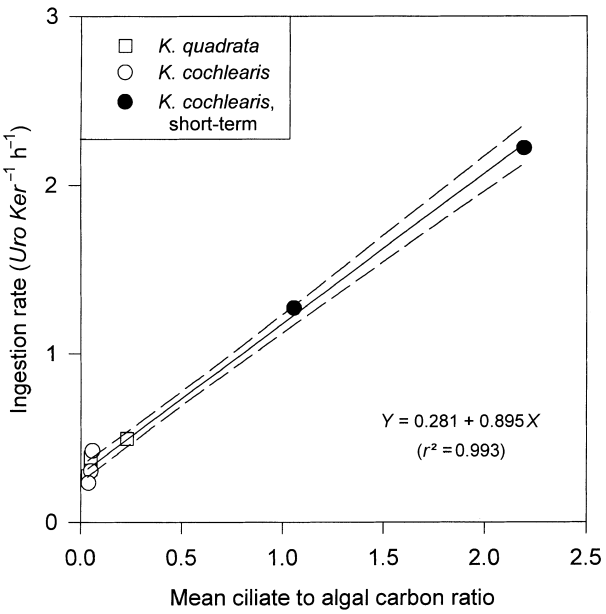

Fig. 3 Ingestion rate of *Keratella* spp. versus the mean ciliate to algal carbon ratio (C_{Uro}/C_{Crypt}) in routine (open symbols) and short-term (filled circles) experiments. Least squares linear regression (solid line) and 95% confidence interval (broken line).

Rotifer impact on Balanion planctonicum

The effects of the two rotifer species on *B. planctonicum* were species-specific. Two experiments conducted at an algal concentration of 9.0×10^7 *Cryptomonas* sp. cells L^{-1} revealed no significant impact of *K. cochlearis* on growth rates of *Balanion* (Table 2).

In contrast to *K. cochlearis*, *K. quadrata* exerted detrimental effects on *B. planctonicum*. Both at 6.0×10^7 *Cryptomonas* 'A' cells L^{-1} and at 2.6×10^7 *Cryptomonas* 'A' cells L^{-1}, cell numbers of *Balanion* declined in the presence of *K. quadrata* (Fig. 4b,d) while the ciliates grew well in the parallel experiments without rotifers (Fig. 4a,c). A third experiment at 2.8×10^7 *Cryptomonas* 'A' cells L^{-1} (data not shown) yielded even more negative growth rates of $\mu = -2.20$ day^{-1} in the containers with *K. quadrata* compared with positive *Balanion* growth rates of $\mu = 0.504$ day^{-1} in the wells without rotifers.

We calculated ingestion and clearance rates of *K. quadrata* from these three experiments during the periods when *Balanion* declined in the containers with

Table 2 Growth rate (μ ± 1 SD) of *Balanion planctonicum* in experiments without and with *Keratella cochlearis*. (n.s. = not significant)

Algal species	Algal conc. (cells L^{-1})	Biomass (mg C L^{-1})	μ ± SD (day^{-1}) without *K. cochlearis*	μ ± SD (day^{-1}) with *K. cochlearis*	Level of significance
Cryptomonas sp.	9.0×10^7	4.14	0.959 ± 0.091	1.031 ± 0.082	n.s.
Cryptomonas sp.	9.0×10^7	4.14	0.601 ± 0.047	0.658 ± 0.024	n.s.

rotifers, i.e. during the last two or three days of each experiment (Fig. 5). Results were up to one order of magnitude higher than the respective parameters for rotifer feeding on *Urotricha*. Ingestion and clearance rates of *K. quadrata* were inversely related and levelled off at the high ciliate concentrations. The different algal concentrations in these three experiments apparently did not affect feeding of *K. quadrata* on *B. planctonicum*.

Discussion

We have demonstrated species-specific effects of two common rotifer species on two of the most abundant planktonic ciliate species. Because our experiments were conducted in small containers, we will first discuss the possible constraints inherent in this approach before elaborating on our major findings.

The experimental design and the natural situation

The experimental design used in this study was similar to the approach taken by Stemberger & Gilbert (1985a,b) who investigated growth rates of common planktonic rotifer species. In additional experiments conducted in parallel to this study using the same experimental approach (Weisse & Frahm, 2001) we measured specific rotifer growth rates close to

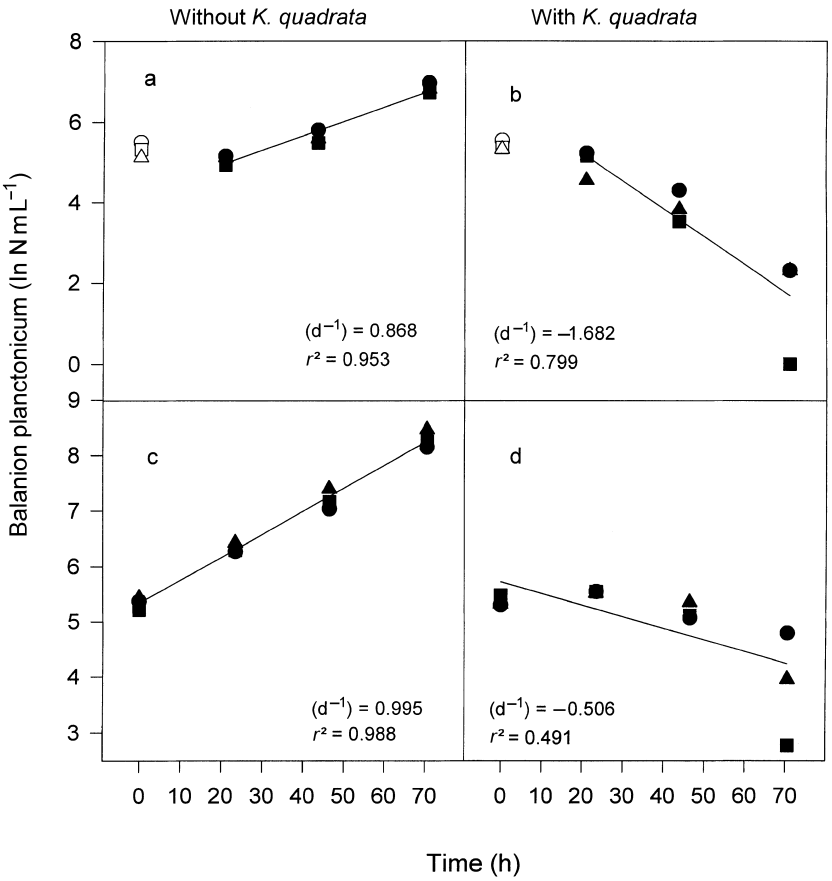

Fig. 4 Projected (i.e. corrected for dilution during the experiments) population dynamics of *Balanion planctonicum* without (a & c) and with (b & d) *Keratella cochlearis*. Algal food concentration was 6.0×10^7 *Cryptomonas* 'A' L^{-1} in the first (a & b) and 2.6×10^7 *Cryptomonas* 'A' L^{-1} in the second (c & d) experiment. The slope (μ) and the coefficient of determination of the least squares linear regression are given in each panel. Data shown by open symbols indicate the lag phase and were not considered in the regression analyses.

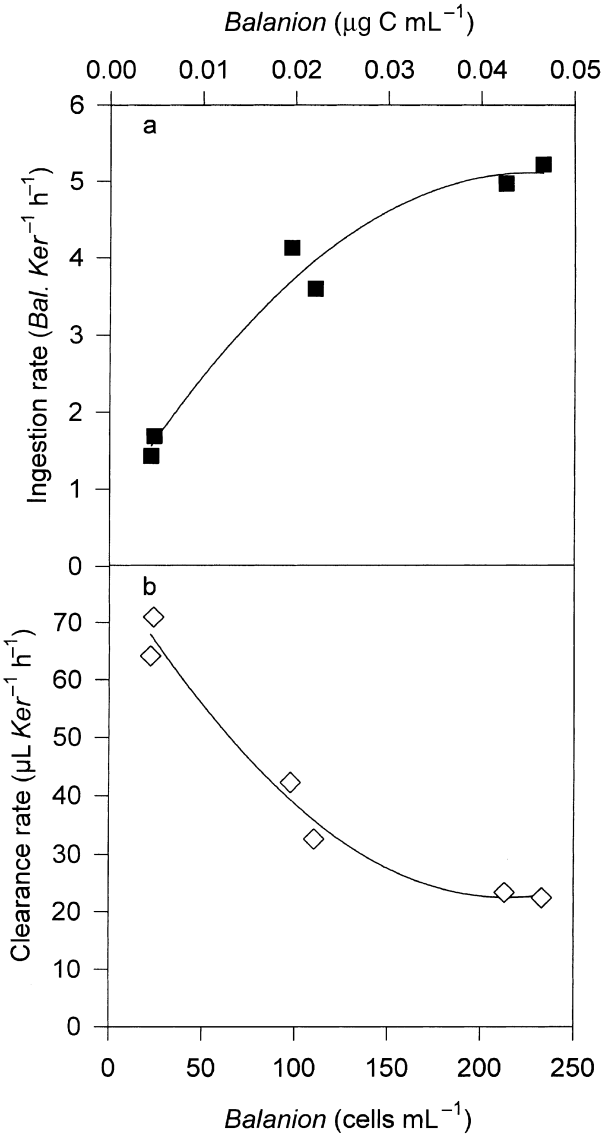

Fig. 5 Ingestion and clearance rates of *Keratella quadrata* calculated from feeding on *Balanion planctonicum*. Data were fit to a least squares second order regression.

maximum growth rates reported in the literature for the respective species (Stemberger & Gilbert, 1985a,b; Walz, 1995). We conclude that our experimental design provided an adequate environment for the rotifers. Similarly, tissue-culture plates have been used successfully to obtain maximum growth rates of the ciliates used in this study and other small planktonic ciliates (e.g. Madoni *et al.*, 1990; Montagnes, 1996; Weisse & Montagnes, 1998). For the two ciliate species, Müller & Geller (1993), when using the same algal food but larger experimental containers, reported r_{max} values of 0.70 day^{-1} for *U. furcata* and 1.01 day^{-1} for *B. planctonicum* at an experimental temperature of 12 °C. We measured even higher r_{max} values at the same or slightly higher temperature: 0.90 for *U. furcata* and 1.31 day^{-1} for *B. planctonicum*. Müller & Schlegel (1999) reported a maximum growth rate of 1.87 day^{-1} for *B. planctonicum* at 15 °C. We thus conclude that the small tissue wells offered optimum growth conditions for the ciliates and that both species were insensitive to the repeated transferring in the course of the experiments.

The abundance of our study organisms was towards the upper end of their natural range. Prostomatid ciliates may reach cell numbers up to 100 mL^{-1} in meso-eutrophic lakes (Müller *et al.*, 1991; Sommaruga & Psenner, 1993). Peak population sizes of *K. cochlearis* and *K. quadrata* exceeding several individuals mL^{-1} have been reported from highly eutrophic and hypertrophic waters (Hewitt & George, 1987; Fussmann, 1993; Haberman, 1995). We tried to minimize experimental artefacts that may result from crowding, such as, for instance, the enrichment of metabolic waste products, by transferring the organisms to new wells each day. The daily addition of 2–4 mL fresh algal suspension and/or MWC medium to the experimental containers allowed us to keep the algal and ciliate levels relatively constant during the experiments. We therefore presume that the experimental conditions did not significantly alter the biological interactions between the organisms under study.

Rotifer impact on ciliates – evidence for direct feeding

Both rotifer species had a similar impact on the slightly larger of the two prostomatid ciliate species, *U. furcata*. Their population growth rates were always lower in the presence of *Keratella* spp. With *K. cochlearis*, the relative effect of rotifers on *U. furcata* tended to be more pronounced at moderate algal concentrations (3×10^7 cell L^{-1}) below the satiating food level. Both growth and ingestion rates of *U. furcata* level off at *Cryptomonas* concentrations of approximately 4×10^7 cell L^{-1} (Weisse *et al.*, 2001). The rotifer impact was, however, also obvious at growth-satiating food concentrations (9×10^7 cell L^{-1}). We thus conclude that exploitative competition by rotifers alone cannot explain the observed decline in growth rates of *Urotricha* when they were paired with

Keratella. Results from the two additional experiments run at high ciliate and rotifer abundances (Fig. 2) suggest that *K. cochlearis* fed directly upon *U. furcata*. Direct rotifer feeding on *Urotricha* has been repeatedly observed in the course of this study (Weisse & Frahm, unpublished data). It should be noted that both *Cryptomonas* and both ciliate species used in this study fall into the size range of 4–17 μm, where the majority of rotifer species feed most efficiently (Gilbert, 1988a). Although some selectivity is known from *K. cochlearis* (Pourriot, 1977; Gilbert & Bogdan, 1981), a generalist feeding mode is attributed to *Keratella* (reviewed by Sterner, 1989 and Walz, 1995). In accordance with this notion, the linear increase of the rotifer feeding on *Urotricha* with increasing ciliate to algal ratio (Fig. 3) points to unselective feeding. The combined *Cryptomonas* abundance of $3–10 \times 10^7$ cells L^{-1} and the ciliate level of 10^5 cells L^{-1} was equivalent to a total carbon concentration of approximately 1.4–4.6 mg C L^{-1}, which is close to or above the 'incipient limiting level' (ILL, Rigler, 1961) of *K. cochlearis* and other small rotifers (Walz, 1993, 1995). We thus assume that the filtering rates of *Keratella* spp. varied little at the different algal concentrations.

The ingestion and clearance rates calculated from the two additional experiments at high ciliate concentrations are similar to rates previously reported for *K. cochlearis* (Gilbert & Bogdan, 1981; Bogdan & Gilbert, 1987) and other small rotifer species when feeding upon algae and protozoa including ciliates (Gilbert & Jack, 1993; reviewed by Arndt, 1993). Clearance rates calculated from feeding on *Urotricha* were 1.1 and 0.8 μL *Keratella*$^{-1}$ h^{-1}. Recently, Jürgens *et al*. (1996) measured maximum average clearance rates of 1.8 and 2.2 μL for *K. cochlearis*$^{-1}$ h^{-1} when they were feeding upon two heterotrophic flagellate species. Although we cannot rule out the possibility that some of the ciliates died from mechanical interference by the rotifers, the decreased mortality rate of *K. cochlearis* measured in our routine experiments (Weisse & Frahm, 2001) is another indication that the rotifers grazed upon, and digested, *U. furcata*.

Feeding of *K. cochlearis* on *B. planctonicum* was not obvious. Growth rate of *Balanion* appeared to be unaffected by the presence of *K. cochlearis*. It is not surprising that we found no evidence for exploitative competition because these experiments were run at high algal concentrations above the ILL of *Balanion*, where their ingestion rates are maximal (Müller & Schlegel, 1999). The fact that *Balanion* was not susceptible to grazing by *K. cochlearis*, while the closely related and similar sized *Urotricha* was, might be explained by behavioural differences. Like many rotifer and ciliate species, both prostomatids interrupt their swimming with small 'jumps' (Foissner *et al*., 1990), which is interpreted as an avoidance reaction against predators (Tamar, 1979; Wickham & Gilbert, 1991). Müller (1991) described differences in the swimming behaviour of *B. planctonicum* and small *Urotricha* species. A 'sudden speeding in a straight line' (Müller, 1991) is characteristic for *Balanion*. The length, speed and frequency of the jumps, as well as the general swimming speed of *B. planctonicum* and *U. furcata*, have not yet been measured.

If *Balanion* escaped from being grazed by *K. cochlearis* by a behavioural adaptation, this grazer-avoidance mechanism was apparently ineffective against the larger, faster swimming of the two rotifer species. *Keratella quadrata* evidently ingested and/or damaged *B. planctonicum* at much higher rates than *U. furcata*. We found no obvious evidence indicating that *K. quadrata* damaged *Balanion* mechanically by interference competition, analogous to *Daphnia*–*Keratella* interactions (Gilbert & Stemberger, 1985; reviewed by Gilbert, 1988a and Walz, 1995), such as remnants from ciliate cells. The ingestion (1.4–5.2 cells ind^{-1} h^{-1}) and clearance (22–71 μL ind^{-1} h^{-1}) rates calculated for *K. quadrata* feeding on *B. planctonicum*, under the assumption that mechanical damage was negligible, were up to one order of magnitude higher than for both rotifer species when feeding on *U. furcata*. This does not necessarily imply that *K. quadrata* was actively selected for *B. planctonicum*, because we did not measure clearance rates on *Cryptomonas* which might have been similarly high in these experiments.

Compared with *K. cochlearis*, little is known about the feeding ecology of *K. quadrata*. Lair & Ali (1990) measured filtering rates ranging from 3 to 53 μL ind^{-1} h^{-1} for *K. quadrata* in a eutrophic lake. A high ingestion rate of 4.8 cells ind^{-1} h^{-1} was obtained by Arndt *et al*. (unpublished, quoted by Arndt, 1993) for the rotifer *Brachionus rubens* Ehrenberg feeding on the ciliate *Cyclidium* sp. The *B. rubens* strain used by Arndt *et al*. was similar in size (200–260 μm, Rothhaupt, 1990a) to our *K. quadrata* while the 20-μm sized

Cyclidium sp. O. F. Müller was slightly larger than the average *B. planctonicum*.

For the same *B. rubens* strain, and a closely related, slightly larger (220–285 μm, Rothhaupt, 1990a) *B. calyciflorus* strain, Rothhaupt (1990b) found that their functional response changes with food particle size. For small particles, below the optimal size range of *Brachionus*, feeding was best described by the rectilinear model with constant maximal clearance rates below, and constant maximal ingestion rates above, the ILL. The rectilinear model corresponds to Holling's (1959) Type 1 functional response and represents a feeding mode in which numerous small particles can be processed simultaneously. In Rothhaupt's (1990b) experiments, ingestion and clearance rates followed the curvilinear model, i.e. Holling's (1959) Type 2 functional response, for particles larger than the optimal size. The curvilinear model can be expressed by the Michaelis–Menten equation. This feeding strategy indicates a handling time that is necessary to process individual, large food items. The optimal feeding size was below 10 μm for both *Brachionus* species, and the algae tested by Rothhaupt (1990b) larger than the optimal size ranged from 12 to 18 μm. This perfectly matches the size range of *B. planctonicum* used in this study, while both *Cryptomonas* species were below 10 μm in their equivalent spherical diameter. The ingestion and clearance curves presented in Fig. 5 resemble the curvilinear model. With only six data pairs each we could, however, not apply the Michaelis–Menten equation to fit the curves.

In conclusion, although we cannot rule out that exploitative competition played some role at the low to moderate algal concentrations ($\leq 3 \times 10^7$ cells L^{-1}), our experimental results suggest that direct feeding of rotifers on the small ciliates is the more important type of interaction.

The extent to which rotifers ingest ciliates is apparently species-specific and may vary both among closely related ciliates of similar cell size as well as among different species of the same rotifer genus. This species-specific rotifer impact may thus contribute to the niche partitioning within closely related and competing ciliate species. As all four species used in this study are common and abundant in many temperate lakes (e.g. Pauli, 1990; Weisse & Müller, 1998), we expect that our findings obtained in the laboratory are ecologically relevant.

Acknowledgments

We thank L. Janke for her excellent technical assistance and H. Müller for providing ciliate cultures. Comments by H. Müller, N. Crosbie, and two anonymous reviewers on the manuscript are gratefully acknowledged.

References

Arndt H. (1993) Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. *Hydrobiologia*, **255/256**, 231–246.

Bogdan K.G. & Gilbert J.J. (1987) Quantitative comparison of food niches in some freshwater zooplankton. A multi-tracer-cell approach. *Oecologia*, **72**, 331–340.

Foissner W., Berger H. & Schaumburg J. (1999) Identification and ecology of limnetic plankton ciliates. *Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft*, Heft 3/99, München.

Foissner W., Oleksiv I. & Müller H. (1990) Morphologie und Infraciliatur einiger Ciliaten (Protozoa: *Ciliophora*) aus stagnierenden Gewässern (Morphology and infraciliature of some ciliates (Protozoa: *Ciliophora*) from stagnant waters). *Archiv für Protistenkunde*, **138**, 191–206.

Frost B.W. (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnology and Oceanography*, **17**, 805–815.

Fussmann G. (1993) Abundance, succession and morphological variation of planktonic rotifers during autumnal circulation in a hypereutrophic lake (Heiligensee, Berlin). *Hydrobiologia*, **255/256**, 353–360.

Gilbert J.J. (1988a) Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. *Limnology and Oceanography*, **33**, 1286–1303.

Gilbert J.J. (1988b) Susceptibilities of ten rotifer species to interference from *Daphnia pulex*. *Ecology*, **69**, 1826–1838.

Gilbert J.J. (1994) Jumping behavior in the oligotrich ciliates *Strobilidium velox* and *Halteria grandinella* and its significance as a defense against rotifers. *Microbial Ecology*, **27**, 189–200.

Gilbert J.J. & Bogdan K.G. (1981) Selectivity of *Polyarthra* and *Keratella* for flagellate and aflagellate cells. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **21**, 1515–1521.

Gilbert J.J. & Jack J.D. (1993) Rotifers as predators on small ciliates. *Hydrobiologia*, **255/256**, 247–253.

Gilbert J.J. & Stemberger R.S. (1985) Control of *Keratella* populations by interference competition from *Daphnia*. *Limnology and Oceanography*, **30**, 180–188.

Guillard R.R.L. & Lorenzen C.J. (1972) Yellow-green algae with chlorophyllide c. *Journal of Phycology*, **8**, 10–14.

Haberman J. (1995) Dominant rotifers of Vortsjärv (Estonia). *Hydrobiologia*, **313/314**, 313–317.

Heinbokel J.F. (1978) Studies on the functional role of tintinnids in the Southern California Bight. I. Grazing and growth rates in laboratory cultures. *Marine Biology*, **47**, 177–189.

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.

Holling C.S. (1959) The components of predation as revealed by a study of small-mammal predation of the European sawfly. *Canadian Entomologist*, **91**, 293–320.

Jürgens K., Wickham S.A., Rothhaupt K.O. & Santer B. (1996) Feeding rates of macro- and microzooplankton on heterotrophic nanoflagellates. *Limnology and Oceanography*, **41**, 1833–1839.

Lair N. & Ali H.O. (1990) Grazing and assimilation rates of natural populations of planktonic rotifers *Keratella cochlearis*, *Keratella quadrata* and *Kellicottia longispina* in a eutrophic lake (Aydat, France). *Hydrobiologia*, **194**, 119–131.

Madoni P., Berman T., Hadas O. & Pinkas R. (1990) Food selection and growth of the planktonic ciliate *Coleps hirtus* isolated from a monomictic subtropical lake. *Journal of Plankton Research*, **12**, 735–741.

Montagnes D.J.S. (1996) Growth response of planktonic ciliates in the genera *Strobilidium* and *Strombidium*. *Marine Ecology Progress Series*, **130**, 241–254.

Montagnes D.J.S. & Weisse T. (2000) Fluctuating temperatures affect growth and production rates of planktonic ciliates. *Aquatic Microbial Ecology*, **21**, 97–102.

Müller H. (1991) *Pseudobalanion planctonicum* (Ciliophora, Prostomatida): ecological significance of an algivorous nanociliate in a deep meso-eutrophic lake. *Journal of Plankton Research*, **13**, 247–262.

Müller H. & Geller W. (1993) Maximum growth rates of aquatic ciliated protozoa: the dependence on body size and temperature reconsidered. *Archiv für Hydrobiologie*, **126**, 315–327.

Müller H. & Schlegel A. (1999) Responses of three freshwater planktonic ciliates with different feeding modes to cryptophyte and diatom prey. *Aquatic Microbial Ecology*, **17**, 49–60.

Müller H., Schöne A., Pinto-Coelho R.M., Schweizer A. & Weisse T. (1991) Seasonal succession of ciliates in Lake Constance. *Microbial Ecology*, **21**, 119–138.

Neter J.W., Wasserman W. & Kutner M.H. (1990) *Applied Linear Statistical Models*, 3rd edn. Irwin, Toronto, Canada.

Pauli H.-R. (1990) Seasonal succession of rotifers in large lakes. In: *Large Lakes* (Eds M.M. Tilzer & C. Serruya), 459–474. Springer, Berlin.

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*, **8**, 242–260.

Rigler F.H. (1961) The relation between concentration of food and feeding rate of *Daphnia magna* Straus. *Canadian Journal of Zoology*, **39**, 857–868.

Rothhaupt K.O. (1990a) Differences in particle size-dependent feeding efficiencies of closely related rotifer species. *Limnology and Oceanography*, **35**, 16–23.

Rothhaupt K.O. (1990b) Changes of the functional responses of the rotifers *Brachionus rubens* and *Brachionus calyciflorus* with particle size. *Limnology and Oceanography*, **35**, 24–32.

Sommaruga R. & Psenner R. (1993) Nanociliates of the order Prostomatida: Their relevance in the microbial food web of a mesotrophic lake. *Aquatic Sciences*, **55**, 179–187.

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.

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

Stemberger R.S. & Gilbert J.J. (1985b) Assessment of threshold food levels and population growth in planktonic rotifers. *Archiv für Hydrobiologie Beihefte Ergebnisse der Limnologie*, **21**, 269–275.

Stenson J.A.E. & Svensson J.-E. (1995) Food quality and population densities in *Asplancha priodonta*. *Limnologica*, **25**, 43–47.

Sterner R.W. (1989) The role of grazers in phytoplankton succession. In: *Plankton Ecology* (Ed. U. Sommer), 337–364. Springer, Berlin.

Strathmann R.R. (1967) Estimating the organic carbon content of phytoplankton from cell Volume or plasma Volume. *Limnology and Oceanography*, **12**, 411–418.

Tamar H. (1979) The movements of jumping ciliates. *Archiv für Protistenkunde*, **122**, 290–327.

Turley C.M., Newell R.C. & Robins D.B. (1986) Survival strategies of two small marine ciliates and their role in regulating bacterial community structure under experimental conditions. *Marine Ecology Progress Series*, **33**, 59–70.

Walz N. (1993) Carbon metabolism and population dynamics of *Brachionus angularis* and *Keratella cochlearis*. In: *Plankton Regulation Dynamics. Experiments and Models in Rotifer Continuous Cultures* (Ed. N. Walz), 89–105. Springer, Berlin.

Walz N. (1995) Rotifer populations in plankton communities: Energetics and life history strategies. *Experientia*, **51**, 437–453.

Weisse T. & Frahm A. (2001) Species specific interactions between small planktonic ciliates (*Urotricha* spp.) and rotifers (*Keratella* spp.). *Journal of Plankton Research*, **23** (in press).

Weisse T., Karstens N., Meyer V.C.M., Janke L., Lettnor S. & Teichgräber K. (2001) Niche separation in common prostome freshwater ciliates: the effect of food and temperature. *Aquatic Microbial Ecology* (in press).

Weisse T. & Kirchhoff B. (1997) Feeding of the heterotrophic freshwater dinoflagellate *Peridiniopsis berolinense* on cryptophytes: analysis by flow cytometry and electronic particle counting. *Aquatic Microbial Ecology*, **12**, 153–164.

Weisse T. & Montagnes D.J.S. (1998) Effect of temperature on inter- and intraspecific isolates of *Urotricha* (Prostomatida, Ciliophora). *Aquatic Microbial Ecology*, **21**, 97–102.

Weisse T. & Müller H. (1998) Planktonic protozoa and the microbial food web in Lake Constance. *Archiv für Hydrobiologie Special Issues Advances in Limnology*, **53**, 223–254.

Weisse T., Müller H., Pinto-Coelho R.M., Schweizer A., Springmann D. & Baldringer G. (1990) Response of the microbial loop to the phytoplankton spring bloom in a prealpine lake. *Limnology and Oceanography*, **35**, 781–794.

Wickham S.A. & Gilbert J.J. (1991) Relative vulnerabilities of natural rotifer and ciliate communities in cladocerans: laboratory and field experiments. *Freshwater Biology*, **26**, 77–86.

(Manuscript accepted 3 April 2001)