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Particle grazing efficiency and specific growth efficiency of the rotifer *Brachionus plicatilis* (Muller)

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Abstract

A complete particle retention spectrum for the grazing of *Brachionus plicatilis* on phytoplankton of different cell size revealed optimal grazing on an algae (*Tetraselmis suecica*) with an equivalent spherical diameter (ESD) of 8.3 μm. Furthermore, although grazing sub-optimally, the rotifer grazed with an equal efficiency (60%) on two different algae *Rhodomonas baltica* (*R.b.*) and *Thalassiosira fluviatilis* (*T.f.*) with equivalent spherical diameters of 6.5 μm and 12.9 μm, respectively, when they were offered one algae at a time. These two algal species were in size positioned symmetrically in the bell shaped curve around the optimal prey size for the rotifers. In mixtures of these two algal species the total grazing on the two algae remained equal regardless of the ratio between the two species in the mixtures. The functional responses to the two algal species offered separately resulted in similar maximum ingestion (I_{max}) but different half saturation constants (K_m).

In order to describe the growth efficiency for the rotifer, a 7 day growth experiment with the haptophyte *Rhodomonas baltica* was conducted at 15°C with 7 different food concentrations. The specific growth rate vs. food availability followed Monod kinetics with a maximum specific growth rate (G_{max}) = 0.49 day^{-1} and a K_m = 2.25 ppm (*R.b.* 12 150 ml^{-1}). The mean carbon content of the individual rotifers vs. algal concentration also followed a Monod curve. Body length could be related to carbon by $C_{(ngC)} = 1.06 \times 10^{-4} L_{(\mu m)}^{2.74}$. The carbon density of the rotifers were 0.11 pgC μm^{-3}. The carbon yield (specific growth rate vs. specific ingestion rate) was 0.29. The maintenance food concentration was 1.02 ppm (*R.b.* 5000 ml^{-1}). The rotifer lost 0.22 day^{-1} when starved. The high specific growth rate and the high saturation food concentrations as well as the high energy requirement during starvation supports the idea that the rotifer follows a life strategy with a fast growth response. © 1997 Elsevier Science B.V.

Keywords: Particle retention; Functional response; Particle selection; Growth; Yield; Starvation

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1. Introduction

Marine rotifers occur frequently in mass abundances in neritic waters during spring when they are thought to perform a significant grazing impact on phytoplankton (e.g. Hernroth, 1983; Dolan and Gallegos, 1992). The scientific focus concerning studies of grazing and growth has been focused on a few rotifer species which are possible to cultivate, e.g. the suspension feeding rotifers *Brachionus* spp. (e.g. Schlüter et al., 1987). The species *B. plicatilis* is used for first feeding of fish larvae in aquaculture (Lubzens, 1987; Sarma, 1991) and great effort has been put into rearing rotifers and maintaining them in large scale cultures with a high growth and a tolerable mortality (e.g. James and Rezeq, 1989; Lubzens et al., 1990).

The limited number of published studies of particle retention by pelagic suspension feeders all indicate food selectivity based on prey size. Generally, grazing efficiency plotted against prey size results in a bell shaped curve—the particle retention spectrum (Hansen et al., 1994). To our knowledge there has only been one reported study with relatively complete retention spectra for *Brachionus angularis*, *B. rubens* and *B. calyciflorus* (Rothhaupt, 1990a). In that study the optimal prey size and the width of the retention spectrum were related to body sizes between the different rotifer strains, but apparently not within a single strain. The study by Rothhaupt showed that the optimal particle size for the rotifers was about 8 μm ESD and that the lower size for retention was 1 μm. Several other studies emphasize generalist rotifers as being able to catch particles as small as bacteria (e.g. Starkweather et al., 1979). The upper particle size for retention, however, was not given by Rothhaupt (1990a) but indicated as >15 μm ESD with a $50\pm20\%$ retention efficiency. In contrast to Rothhaupt (1990a), Hino and Hirano (1980) found a clear relation between lorica length and maximum size of particles ingested within a single strain of *B. plicatilis*.

The particle grazing by suspension feeding rotifers has been reported to be governed by additional factors than particle size and is suggested to be behavioural influenced, i.e. capability to select or reject particles according to their quality. This is related to the possibility of pseudotrochal screening and particle rejection in the grazing process. The behaviour is due to the presence of chemo- and mechanoreceptors in connection to the corona (Gilbert and Starkweather, 1977; Clement et al., 1980) and the ability to perform backward ciliary movements for downstream collectors (Strathmann et al., 1972). Selectivity has among other things been linked to particle characteristics such as algal cell surface (Dumont, 1977; Pourriot, 1977), physiological conditions of algal cells (Chotiyaputta and Hirayama, 1978) and algal motility (Gilbert and Bogdan, 1984). In contrast, Rothhaupt (1990a) suggested that apart from particle size, feeding was unselective.

Generalist rotifers are characterized by their capability of attaining high growth rates as a response to high concentrations of food (Doohan, 1973; Booras and Bennett, 1988) while presumably having high maintenance requirements (Stemberger and Gilbert, 1985). Growth efficiency is described in a few chemostat studies, but a thorough analysis of yield and of starvation tolerance for *B. plicatilis* is still lacking. This basic physiological information can help elucidate generalist rotifers' natural adaptability to fluctuating in situ concentrations of food resources. The present study is a comprehen-

sive laboratory study revealing a complete particle retention spectrum for *B. plicatilis* for algal food particles. Additionally, it illustrates whether *B. plicatilis* is a mechanical (i.e. does not differentiate between particles besides from prey sizes) or a behavioural grazer. Data on the individual carbon content and carbon density of the rotifer as well as fundamental growth physiology, growth yield, maintenance energy requirement and starvation tolerance are discussed in the context of adaptation to natural fluctuating food availabilities.

2. Materials and methods

2.1. Grazing

The following grazing experiments were conducted at 18±1°C in a walk-in incubation room under dim light conditions (approximately 50 $\mu Em^{-2}s^{-1}$) using animals which were pre-adapted to their respective food concentrations and food types for 24 h. The animals were incubated in 70 ml screw-cap bottles mounted on a plankton wheel (0.5–1 r.p.m).

The experiments were conducted with cultures of algae and rotifers in 29 ppt natural sea water during a period of two years. The phytoplankters were grown in B1 media (Hansen, 1989) with silica added for the diatom species and kept for use in logarithmic growth phase. The rotifer culture originated from Marine Biological Laboratory, Copenhagen University. They were cultivated at 16°C as a batch culture with high densities (10–20 ind. ml^{-1}) and kept on a mixture of several phytoplankton species (*Nannochloris maculata, Pavlova lutherii, Isochrysis galbana* and *Rhodomonas baltica*) applied in excess. The culture medium (0.2 μm filtered natural sea water) was renewed once a week. In each experiment either particle counter measurements or linear dimensions of algal cells, measured in microscope by a magnification of 400 ($n = 10$–25), were obtained and $ESD = (vol./0.523)^{0.33}$ given. The ESD calculations converts particles with a nonspherical shape to a geometry equivalent to a sphere making it more easy to compare algae with different shapes. The initial rotifer lorica length and width were measured by microscope at a magnification of 80 in each experiment ($n = 25$–80).

2.2. Functional response

The effect of algal concentration of *Rhodomonas baltica* or *Thalassiosira fluviatilis* on rotifer grazing rates (individually pipetted rotifers with a mean±SD lorica length of 225±32 μm ($n = 52$) and 238±29 μm ($n = 80$) for *R.b.* and *T.f.*, respectively, were studied by incubating 100–200 individuals in triplicate grazing bottles. Two control bottles without animals were also used for each algal concentration. The algal concentrations used were within the range of 2–70 ppm (*R.b.* 10 000–315 000 ml^{-1}, *T.f.* 1300–25 000 ml^{-1}). The particle concentrations were measured at the start and at the end of the incubation period (24 h) with an electronic particle counter (Sysmex F-800 modified by Merck, Denmark) and the number of grazers were counted and measured in a stereomicroscope. Ingestion was calculated according to Frost (1972). Only experi-

ments with $< 30\%$ particle reduction during grazing were used to avoid difficulties with calculating the mean available food concentrations during the incubations. Very few data were discarded. The relationships between ingestion and algal concentration were fitted to a Holling type II (Monod) functional response by iterative nonlinear regression.

2.3. Particle retention

The range of algal sizes captured by *B. plicatilis* (individually pipetted rotifers with a lorica length 248 ± 23 μm, $n = 57$) was recorded from incubation experiments with 100 individuals in each grazing bottle. The algal size ranged from 1.4 to 21 μm ESD (Table 1). The experiments were performed with unialgal suspensions (one algae offered at a time in each experiment) with an equal initial algal volume fraction (number of a certain algae $ml^{-1} \times$ individual algal biovolume = initially constant). The algal volume fraction corresponded to an algal concentration (12 ppm *R.b.* 58 000 ml^{-1}; Hansen et al., 1991) where the particle uptake had not reached saturation levels to insure a reasonably high clearance rate. All experiments with each algal species were performed with duplicate grazing bottles with duplicate controls without animals. Algal suspensions were measured by an electronic particle counter (Coulter Counter Multisizer). Relative clearance, where 100% equals clearance for the optimal algal size for retention, were calculated for each algal species.

2.4. Grazing on mixed algal species

The effects of selective grazing were tested using the same two algal species as used to measure the functional responses. The rotifers (individually pipetted rotifers with a lorica length 226 ± 28 μm, $n = 25$), 100–200 individuals per bottle, were exposed to 7 different algal mixtures. All suspensions contained an equal total algal volume fraction of 6.2 ppm with a mutual biovolume percentage of *R. baltica*: *T. fluviatilis* in the

Table 1
Brachionus plicatilis. Experimental algal species, their dimensions and their carbon content. Equivalent spherical diameter (ESD) was measured by the electronic particle counter except for *Thalassiosira fluviatilis* and *Scripsiella faröense* where it was calculated from linear dimensions measured by microscope and simple geometrical formulas (see text)

Algal species	ESD (μm)	Volume (μm^3)	Carbon (pg $cell^{-1}$)
Synecococcus sp.	1.4	1.4	n.d.
Nannochloris maculata	1.8	3.6	1.80
Pavlova lutherii	4.3	41	10.1
Isochrysis galbana	4.5	49	13.1
Rhodomonas baltica	6.5	206	36.7[a]
Tetraselmis suecica	8.3	298	n.d.
Thalassiosira fluviatilis	12.9	1499	267
Scripsiella faröense	21.0	4838	801

[a]Carbon measured in this study; n.d. no available carbon content. The carbon content of other algae was measured by Berggreen et al. (1988).

following relationships: 100:0, 81:19, 67:33, 57:53, 43:57, 28:72 and 0:100 (see Verity, 1991). Three grazing bottles and two controls without animals were used for each algal mixture. The algal concentrations were determined by electronic particle counter (Sysmex F-800). The ingestion was given as mean with standard error for each mixture combination of the two algae.

2.5. Growth experiment

A 7 day growth experiment with 7 different algal concentrations was performed in gently aerated 500 ml round bottom Pyrex glass bottles (Table 2). The rotifers were acclimated to 15°C and to their respective algal concentration for 2 days before the experiment was started as suggested by Korstad et al. (1989). Each day 80% of the algal suspensions was renewed by inverse filtration through 45 μm mesh size (a 20 mm hose of the full length of the glass bottles equipped with a plankton sieve and inside that a 10 mm hose to transport the algal suspension by siphoning) and algal concentrations were recorded by electronic particle counter (Sysmex F-800) (Fig. 1). Starvation experiments were treated similarly using instead 0.2 μm filtered salt water. The starvation experiments were performed with animals pre-adapted to 56 500 cells ml^{-1} and 249 740 cells ml^{-1} (Table 2) exposed to zero food in order to determine whether the past history of the rotifers influenced their starvation tolerance. Each day rotifers from each bottle were subsampled to determine mortality, individual rotifer body size (length and width) and carbon content, and to determine growth in the rotifer culture. Subsamples of 3 times 5 ml were taken while gently shaking the suspension. A minimum of 80 individuals were obtained in total. The rotifers' lorica length and width were measured after fixating by acid Lugols solution (Serra and Miracle, 1987) and body volume and egg volume calculated from formulae given by Ruttner–Kollisko (1977) and Sarma and Ramakrishna (1988), respectively. The rotifers were rinsed by an insect needle for adhering algae and mucus, washed in 0.2 μm filtered sea water and pipetted under the stereo microscope. The rotifers were divided into batches of 25 individuals and pipetted into pre-ashed small aluminium bowls (2 h at 550°C) and then dried for 2 h at 50°C. The rotifers were stored in a dessicator for a month before they were analyzed for carbon

Table 2
Brachionus plicatilis. Incubation conditions for the growth experiment with rotifers offered *Rhodomonas baltica* as food. Rotifer abundance refers to the initial abundance at the time of the acclimation period

Experimental bottle no.	Rotifer abundance individuals ml^{-1}	Algal concentration (cells ml^{-1})	Algal concentration (ppm)
1	1.3	0	0.0
2	0.7	9210	1.9
3	1.2	15 941	3.3
4	2.9	30 790	6.3
5[a]	2.1	56 700	11.7
6	1.3	128 362	26.4
7[a]	2.0	249 740	51.5

[a] = rotifers continued in the starvation experiment after the growth experiment was finished with a rotifer abundance of approximately 5.6 individuals ml^{-1} (see text).

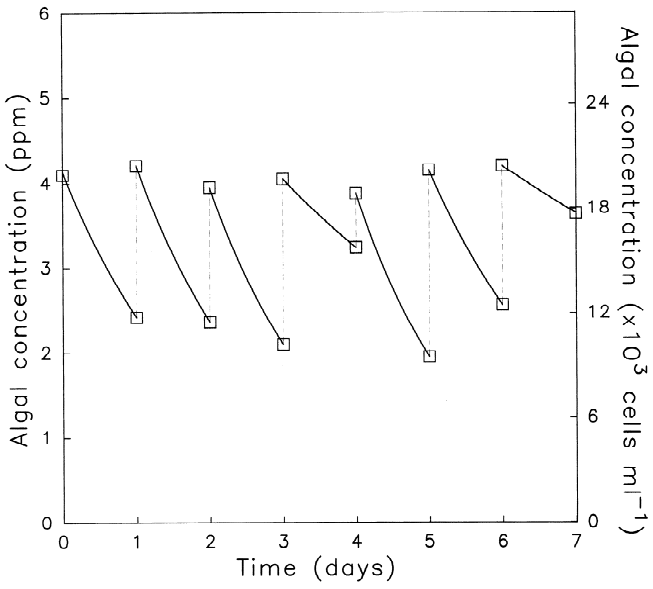

Fig. 1. *Brachionus plicatilis*. Example of development in algal concentration over time during the 7 day growth experiment. Notice the exponential decline of food concentration between the daily renewal of algal suspension.

content. The carbon content was determined with an infrared gas analyzer (ADC 225 MK 3) provided with a tube furnace. The machinery was calibrated with ascorbic acid (Hansen and Ockelmann, 1991; Hansen, 1993).

3. Results

3.1. Grazing experiments

The functional responses showed grazing saturation resembling Monod curves. The curves could be described for *R. baltica* with a $I_{max} = 130.7 \pm 8.3 \times 10^3$ μm^3 ind.$^{-1}$ h^{-1} (634 ± 40 cells ind.$^{-1}$ h^{-1}) and a $K_m = 2.95 \pm 0.71$ ppm ($14\,300 \pm 3500$ cells ml^{-1}) $r^2 = 0.59$ (Fig. 2) and for *T. fluviatilis* with a $I_{max} = 127.4 \pm 7.77 \times 10^3$ μm^3 ind.$^{-1}$ h^{-1} (85 ± 5 cells ind.$^{-1}$ h^{-1}) and a $K_m = 7.48 \pm 1.40$ ppm (4990 ± 994 cells ml^{-1}) $r^2 = 0.82$ (Fig. 3).

B. plicatilis was able to graze on algae ranging in size from 1.4 μm to 21 μm ESD with a retention efficiency $> 20\%$. The maximum retention (optimal prey size) was approximately 8 μm ESD with reduced retention for smaller and larger algae but still with a measurable retention of the largest offered particle (Fig. 4). The retention efficiencies for *R. baltica* and *T. fluviatilis* were exactly equal (60%) and distributed symmetrically around the optimal prey size for the rotifer (Fig. 4). Because the retention

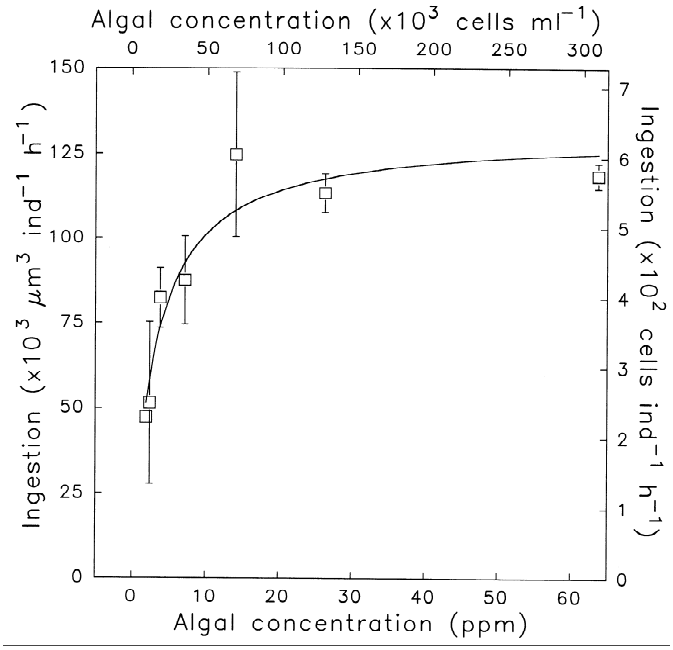

Fig. 2. *Brachionus plicatilis*. Influence of algal concentration, *Rhodomonas baltica*, on ingestion rates. Each point represents mean±s.e. of triplicate experiments.

efficiencies of the two algal species were equal an experiment with equal algal volume fraction but different mutual algal concentrations was conducted to test potential algal selectivity among the two algae offered during grazing. The rotifer ingested *R. baltica* in exact proportion to its volume fraction ($I = 0.991 \times$ Volume added $- 3.33$; $r^2 = 0.99$) (Fig. 5).

3.2. Growth experiment

The relationship between mean rotifer body (lorica) length and mean individual carbon content at all food concentrations can be expressed by a power function $C_{(\mathrm{ngC})} = 1.06 \times 10^{-4} \pm 0.11 \times 10^{-4}\ L_{(\mu\mathrm{m})}^{2.74 \pm 1.94}$ ($r^2 = 0.68$) (Fig. 6). Rotifer carbon:body volume ratio was 0.11 pgC $\mu\mathrm{m}^{-3}$ (Fig. 7).

The mean individual rotifer carbon content (calculated as individual rotifer biovolume multiplied by the carbon density, 0.11 pgC $\mu\mathrm{m}^{-3}$) varied with food concentration a factor of 1.6 and resulted in a curve which levelled off at a maximum level of 227 ngC ind.$^{-1}$ (Fig. 8) (the maximum carbon content of a rotifer was equal to the sum of the Monod variable $C_{\max}$ which was 82.92 ng plus $C_{\text{carbon content at 0 food}}$ which was equal to 143.90 ng = 227 ngC).

The rotifer growth rate depended on the food concentration offered. Rotifers showed exponential and constant growth responses during the 7 days of the experiment. The

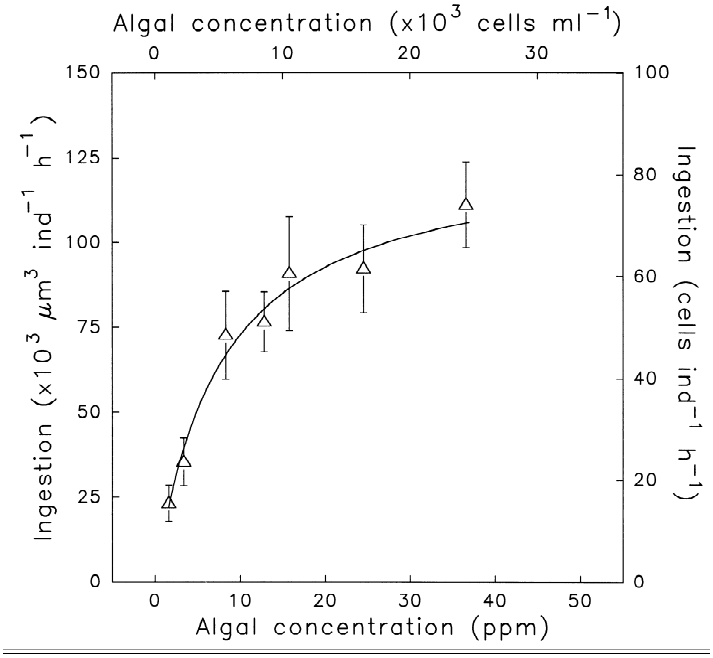

Fig. 3. *Brachionus plicatilis*. Influence of algal concentration, *Thalassiosira fluviatilis*, on ingestion rates. Each point represents mean±s.e. of triplicate experiments.

slopes of the exponential regressions express the specific growth rates G (Fig. 9). Growth in the 3 starvation experiments were not significantly different and the data therefore lumped together. Growth was negative in the starvation experiment due to maintenance requirements, $G = -0.22 \pm 0.05$ day^{-1}. The specific growth approached a plateau of 0.49 ± 0.08 day^{-1} with increasing food concentration available. The saturation curve gave a $K_m = 3.27 \pm 1.60$ ppm (*R.b.* 15 850±7750 cells ml^{-1}). The maintenance food concentration, where ingestion balances basic energy requirements, is indicated by the curve intercept with the *x*-axis in Fig. 9 (Stemberger and Gilbert, 1985; Hansen, 1993), and calculated to 1.02 ± 0.45 ppm (*R.b.* 5000±2200 cells ml^{-1}).

The maximum specific carbon ingestion rate for *Brachionus plicatilis* was close to 2.3 day^{-1} [Calculated as $I_{max} = 130.7 \times 10^3$ μm^3 ind.$^{-1}$ h^{-1} (Fig. 2) × carbon density of *R. baltica* (cell carbon 36.7 pgC; cell volume 206 μm^3 = 0.17 pgC μm^{-3}; Table 1). The body size of the rotifer (Fig. 7) × carbon density of rotifers (0.11 pgC μm^{-3}, Fig. 7)]. The carbon specific yield (specific growth rate vs. specific ingestion rate) was calculated to be 0.29 (Fig. 10).

4. Discussion

The prey size spectrum for our strain of *Brachionus plicatilis* confirmed the potential for bacterivory (able to retain *Synecococcus* sp.) although with a very reduced retention

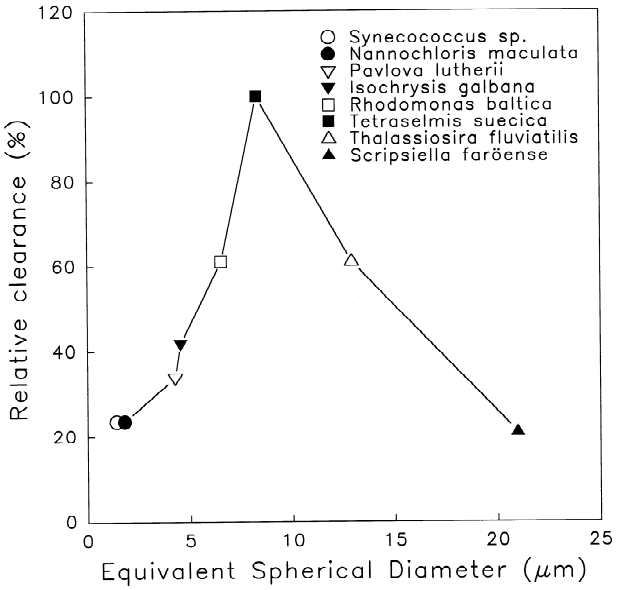

Fig. 4. *Brachionus plicatilis.* Retention spectrum; relative clearance versus equivalent spherical diameter (ESD) of algal food. The measured points represents mean of the duplicate experiments and are connected by linear interpolation.

efficiency at prey items of that size. It has been demonstrated that the smallest particle size captured by downstream collecting ciliary feeders is invariant with size of the filtrator due to the morphology of the ciliar structures (Hansen, 1991). The rotifer had an optimal prey size of approximately 8 μm EDS resembling what Rothhaupt (1990a) described for other rotifer species with the same body size and belonging to the same genus. The upper size limit for retention was 20–25 μm ESD in the present study and it has been observed that the dinoflagellate *Heterocapta triquetra* (27×17 μm) consequently was lost at the ciliated food uptake apparatus during grazing (B. Hansen, unpublished). The upper particle size catchable for a given rotifer is dependent on its body size (Hino and Hirano, 1980). This is presumably due to the fact that the ciliated food groove, as part of the downstream based food apparatus, is responsible for transporting the particles to the mouth and it increases with body size as demonstrated for gastropod larvae (Hansen, 1991). The particle retention spectrum we measured indicates that the rotifers preferentially graze on nanoplankton within the same size range as other ciliary downstream collectors (Strathmann et al., 1972; Sprung, 1984, 1989; Riisgaard, 1988; Hansen and Ockelmann, 1991; Hansen, 1993). The prey size range for *B. plicatilis* is similar to the qualitative description given by Halbach and Halbach Keup (1974).

It was clear that the rotifer grazed nonselectively when offered the two algal species with different cell sizes, apart from selection based on prey size. Gilbert and Bogdan (1984) state that generalist suspension feeding rotifers exhibit no significant selectivity on particles for sizes within their retention spectrum and therefore can be described as

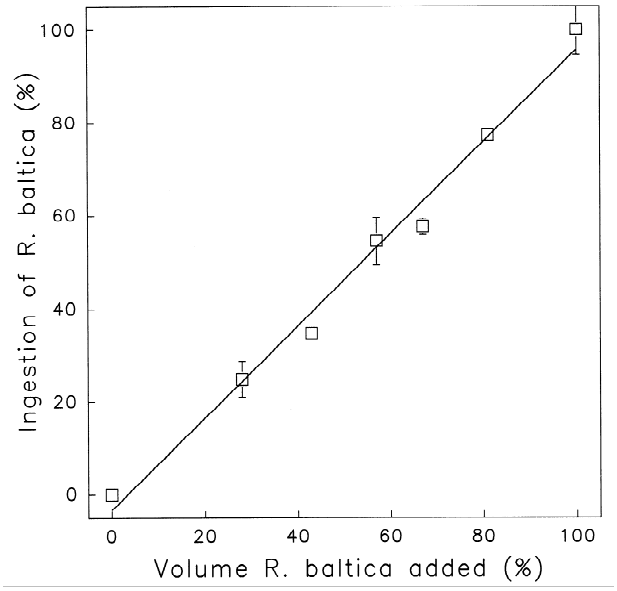

Fig. 5. *Brachionus plicatilis*. Ingestion of *Rhodomonas baltica* during a grazing experiment where two algal species were offered (*Rhodomonas baltica* and *Thalassiosira fluviatilis*) with different mutual concentrations. Each point represents mean±s.e. of triplicate experiments. Where no s.e. is visible it is because it is smaller than the symbol on the graph. The line represents the regression line which is not significantly different from 1.

mechanical grazers. Another downstream collector, the gastropod larvae *Philine aperta*, exhibits similar mechanical particle capture when given 2 or 3 different prey items simultaneously (Hansen, 1991).

The functional responses, which are useful relationships for evaluating the grazing strategy for a given suspension feeding species, showed identical I_{max} but different K_m as a function of prey size. This result is the same as described by Rothhaupt (1990b) for other *Brachionus* spp. and also for muscle-based suspension feeding zooplankton such as copepods (Frost, 1972). Generally, K_m, in contrast to I_{max}, is a difficult parameter to determine precisely due to experimental variability, especially at low food concentrations. The I_{max} for *B. plicatilis* is high allowing fast growth at high food concentrations, a strategy well adapted for a quick response to phytoplankton bloom situations. Maximum specific carbon ingestion in the present growth experiment was calculated to be 2.3 day^{-1}. It has been reported to be 2 day^{-1} for the same species grazing on the smaller algae *Isochrysis galbana* (Korstad et al., 1989) and to be 0.75 day^{-1} grazing on *Dunaliella* sp. which is approximately similar in size to *R. baltica* (Schlosser and Anger, 1982). However, *Dunaliella* sp. has been verified to be an insufficient food source for copepod zooplankton when offered as the only food item. This is suggested to be resulting from a mismatching lipid content (Støttrup and Jensen, 1990; Jonasdóttir et al., 1995). For *B. rubens*, maximum specific ingestion was reported to be 3.6 day^{-1} in a situation where the algal food experienced no limitations of micronutrients and was assumed to be biochemically sufficient food (Pilarska, 1977).

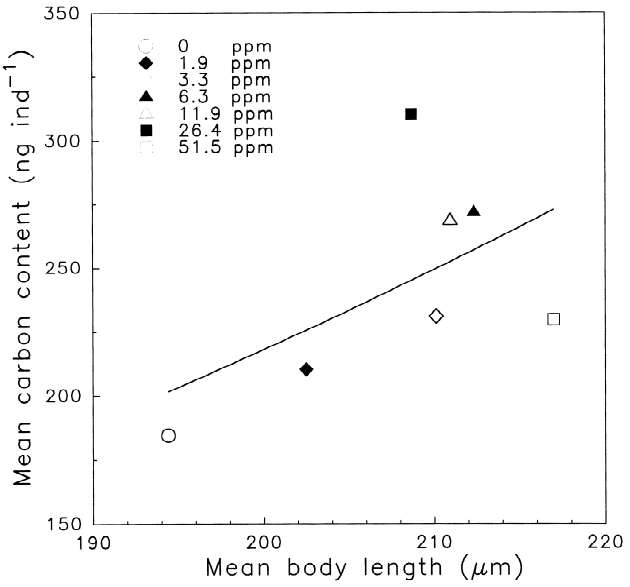

Fig. 6. *Brachionus plicatilis*. Length/carbon content of individual rotifers from the growth experiment; see Table 2 for conversion of ppm to cells ml^{-1}. Each data point represents mean values of all measured rotifers in each experiment (n = several hundreds).

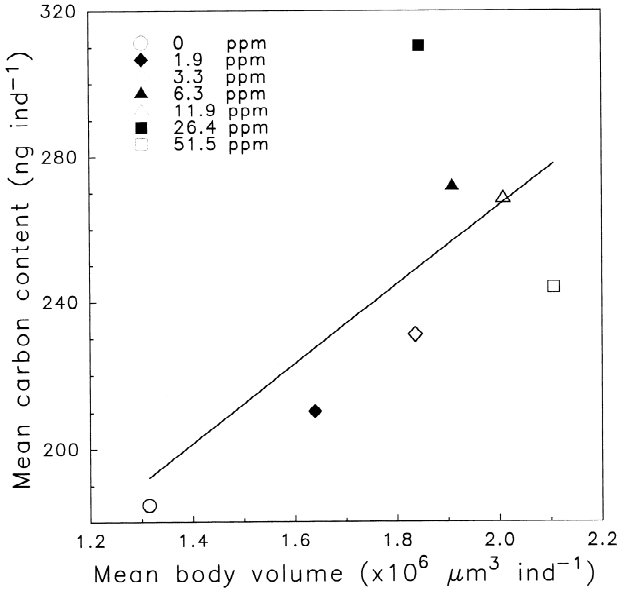

Fig. 7. *Brachionus plicatilis*. Carbon density of rotifers, inclusive attached eggs, from the growth experiment; see Table 2 for conversion of ppm to cells ml^{-1}. Each data point represents mean values of all measured rotifers in each experiment (n = several hundreds). $C_{(\mathrm{ngC})} = 108.5 \times 10^6\ V_{(\mu\mathrm{m3})} + 49.6$ ($r^2 = 0.68$).

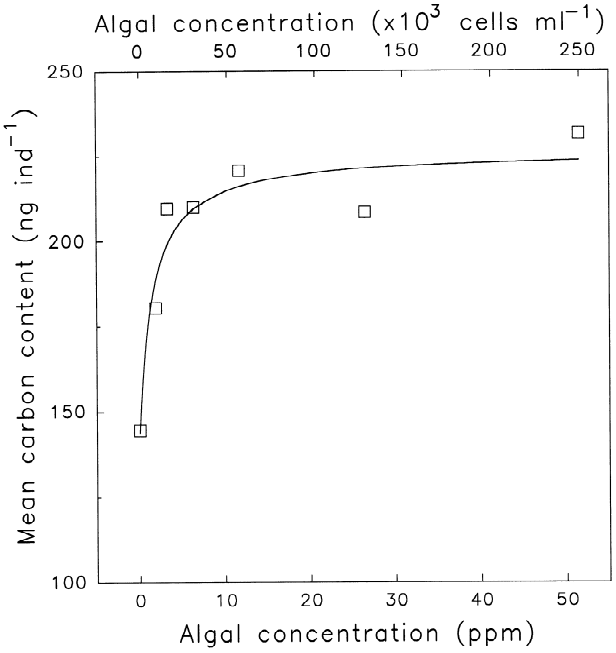

Fig. 8. *Brachionus plicatilis*. Mean carbon content of rotifers grown on different algal concentrations. Each data point represents mean values of all measured rotifers in each experiment (n = several hundreds). $C_{(\mathrm{ngC})} = [(82.92 \pm 12.58 \times C)/(1.60 \pm 0.86 + C)] + 143.90 \pm 10.33$.

The basic parameter, mean carbon content as a function of lorica length of the rotifer, is a useful tool in e.g. carbon budget studies to predict biomass, growth, etc. from abundance and linear measurements of individuals. The regression analysis of our results (Fig. 6) showed a slope (exponent b in the allometric equation) of 2.74, which is higher than that found for *B. calyciflorus* ($b = 1.44$; Dumont et al., 1975). The carbon density, however, was not significantly different from values given by Boraas (Booras, 1983; $b = 0.12$–0.21 depending on gut fullness) from a rotifer culture. This could indicate that the rotifer culture used in the present study, acclimated to food ad libitum, was in a better physiological condition in comparison to the organisms used by Dumont et al. (1975), which were sampled from coastal waters. An overall value for carbon density in cultivated zooplankton (ciliates, rotifers, copepods, cladocerans, meroplankton larvae) ranging 2–2000 μm in body size was 0.12 pgC μm^{-3} (Hansen et al., in press).

Body size of the rotifer increased with food availability following a Monod curve in a similar fashion as reported for *B. ratula* (Sarma and Ramakrishna, 1988). In the present study, rotifers from starvation situations appeared very slim and the lorica were bending inwards resembling an ‘‘hourglass’’. These rotifers were still swimming and foraging after 48 h, after losing significant body mass which strongly indicates a potential for the rotifer to tolerate extreme variations in in situ food availabilities.

The $G_{\max}$ was 0.49 day^{-1} at 15°C. Temperature corrected to 18°C with a $Q_{10} = 2.5$ (Nielsen and Kiørboe, 1994) it equals 0.51 ± 0.13 day^{-1}, which equals that found by

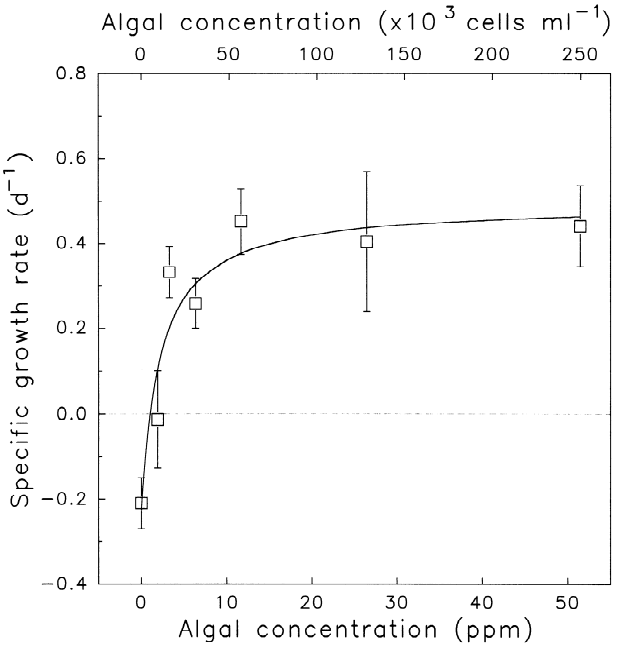

Fig. 9. *Brachionus plicatilis*. Mean±s.e. specific growth rate of rotifers grown on different algal concentrations. $G_{(\mathrm{day}^{-1})}=[((0.49\pm0.08\times(C-1.022\pm0.45\ \ \mathrm{ppm}))/((3.27\pm1.60+(C-1.022\pm0.45\ \ \mathrm{ppm}))]$ ($r^2=0.85$).

Stemberger and Gilbert (1985) for *B. calyciflorus* and for *B. rubens* (Rothhaupt and Lambert, 1992), but is somewhat lower than that reported for *B. plicatilis* in other studies (Doohan, 1973; Starkweather, 1988). The inconsistency in $G_{\max}$ among the studies presumably reflects different cultivation techniques and food algal qualities, different body sizes of rotifers (which is unfortunately seldom given in the literature) and presumably inherited genetic differences between strains (e.g. Carlotti and Nival, 1991).

The dynamic food concentration range for quick-growth response by the rotifer, defined here as the algal concentration range between maintenance food concentration and half saturation concentration, was between 1.02 and 2.25 ppm (5000–11 000 cells ml^{-1}) for *Rhodomonas baltica*. The half saturation constant for grazing on the same algal species was 2.95 ppm (14 300 cells ml^{-1}), not significantly different from K_{m} found in the food concentration dependent growth experiment. Hansen et al. (1991) found a $K_{\mathrm{m}}=2.5$ ppm (*R.b.* 12 000 cells ml^{-1}) grazing on the same algal species and with the same rotifer strain grown under similar conditions. In a recent review K_{m} was described to be 2±2 ppm (*R.b.* 9700 cells ml^{-1}) for pelagic suspension feeders ranging in body size from 2 to 2000 μm and covering cultivated zooplankton from nanoflagellates to neritic copepods (Hansen et al., in press). However, in the data compiled by Hansen et al., the generalist suspension-feeding rotifers showed a clear tendency to be in the very high end of this range of mean K_{m}. In the present study $G_{\max}$ was first achieved at >20 ppm (*R.b.* $>97\,000$ cells ml^{-1}) for rotifers growing on *R. baltica*. This food

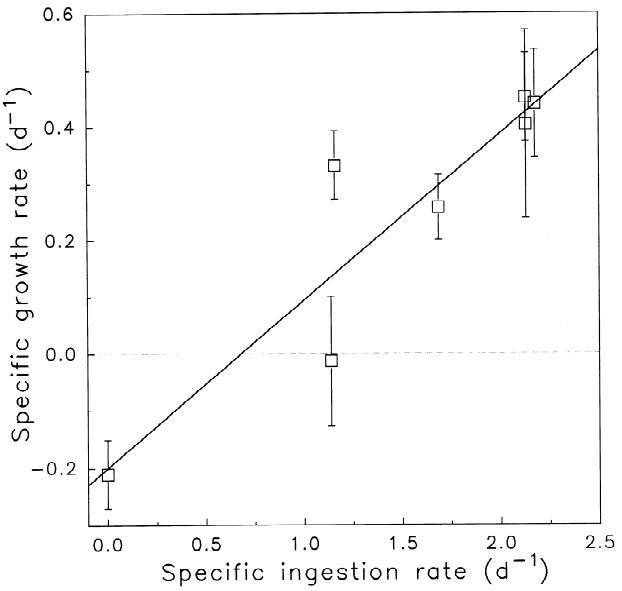

Fig. 10. *Brachionus plicatilis*. Carbon yield, specific growth rate (G, day^{-1}) vs. specific ingestion rate (I, day^{-1}). G integrated over entire experimental period and I from Fig. 2. Regression is: $Y=0.29\times I-0.20$ ($r^2=0.92$).

particle size is obviously not optimal with regard to particle capture (Fig. 4) so, in accordance with Rothhaupt (1990b), we expect K_m to be somewhat lower for the optimal food particle size, represented by *Tetraselmis suecica*. The food concentration necessary for sustaining the basic energy requirements is 1.02 ppm (*R.b.* 5000 cells ml^{-1}) for the rotifer in the present study. This is close to the reported 1.7 ppm (equivalent to 8250 *R. baltica* cells ml^{-1}) for *B. calyciflorus* feeding on algal culture (Stemberger and Gilbert, 1985) and to what Rothhaupt (1990c) have found for *B. calyciflorus* feeding on a 10 μm ESD particle (0.19 mgC l^{-1} equivalent to *R.b.* 5200 ml^{-1}) and *B. rubens* feeding on a 5 μm ESD particle (0.07–0.09 mgC l^{-1} equivalent to 5350–8900 *Isochrysis galbana* cells ml^{-1}). Our starvation experiments showed a specific loss rate of 0.22 day^{-1} which is similar to the 0.28 day^{-1} reported for *B. calyciflorus* (Stemberger and Gilbert, 1985) and lower than a reported threshold for mictic *B. plicatilis* production (15.3×10^3 *Dunaliella tertiolecta* ml^{-1} equal to 2.5 ppm assuming a cell volume of 163 μm^3; Støttrup and Jensen, 1990). The yield was 0.29 which is close to literature values (Droop and Scott, 1978; Scott, 1980; Booras, 1983; Schlüter et al., 1987; Hansen et al., in press).

4.1. Ecological significance of the rotifers' physiological adaptations

The rotifer *Brachionus plicatilis* is adapted to graze nonselectively upon nanoplankton, with a capacity to still process food particles at very high bloom concentrations and to allocate the gained energy into fast developing eggs. In addition, the high K_m for

growth and the fast starvation rate suggest that *B. plicatilis*, as is the case with other species of large-bodied rotifers, needs a high food concentration to survive. Additionally, the rotifer can allocate its sparse storage compounds during starvation and that it is able to catch up if food is again available within a few days. Based on the observed steep initial growth response vs. food concentration (Fig. 9) the rotifer reacts rapidly to increasing food availability (Stemberger and Gilbert, 1985). This growth physiology suggests a potential for a high maximum populational growth which enables *B. plicatilis* to build up a large population quickly (Johansson, 1983; Hernroth, 1983). This is considered an adaptive strategy for phytoplankton biomass tracking in situ and thereby an opportunistic life strategy tightly coupled to fluctuating food resources.

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References

Berggreen, U., B. Hansen and T. Kiørboe, 1988. Food size spectra, ingestion and growth of the copopod *Acartia Tonsa* during development: Implications for determination of copopod production. *Mar. Biol*., Vol. 99, 341–352.

Booras, M.E., 1983. Population dynamics of food-limited rotifers in two-stage chemostat culture. *Limnol. Oceanogr*., Vol. 28, pp. 546–563.

Booras, M.E. and W.N. Bennett, 1988. Steady-state rotifer growth in a two-stage, computer-controlled turpidostat. *J. Plankton Res*., Vol. 10, pp. 1023–1038.

Carlotti, F. and S. Nival, 1991. Individual variability of the development in laboratory reared *Temora stylifera* copepodites: consequences for the population dynamics and interpretation in the scope of growth and development rules. *J. Plankton Res*., Vol. 13, pp. 801–813.

Chotiyaputta, C. and K. Hirayama, 1978. Food selectivity of the rotifer *Brachionus plicatilis* feeding on phytoplankton. *Mar. Biol*., Vol. 45, pp. 105–111.

Clement, P., J. Amsellem, A.-M. Cornillac, A. Luciani and C. Ricci, 1980. An ultrastructural approach to feeding behaviour in *Philodina roseola* and *Brachionus calyciflorus* (Rotifers). *Hydrobiologia*, Vol. 73, pp. 127–131.

Dolan, J.R. and C.C. Gallegos, 1992. Trophic role of planktonic rotifers in the Rhode River Estuary, spring–summer 1991. *Mar. Ecol. Prog. Ser*., Vol. 85, pp. 187–199.

Doohan, M., 1973. An energy budget for adult *Brachionus plicatilis* Muller (Rotatoria). *Oecologia*, Vol. 13, pp. 351–362.

Droop, M.R. and J.M. Scott, 1978. Steady-state energetics of a planktonic herbivore. *J. Mar. Biol. Ass. U.K*., Vol. 58, pp. 749–772.

Dumont, H.J., 1977. Biotic factors in the population dynamics of rotifers. *Arch. Hydrobiol. Beih*., Vol. 8, pp. 98–112.

Dumont, H.J., I. Van de Velde and S. Dumont, 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda and rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, Vol. 19, pp. 75–97.

Frost, B.W., 1972. Effects of size and concentration of food particles of the feeding behaviour of the marine planktonic copepod *Calanus pacificus*. *Limnol. Oceanogr*., Vol. 17, pp. 805–815.

Gilbert, J.J. and K.G. Bogdan, 1984. Rotifer grazing: *in situ* studies on selectivity and rates. In, *Trophic interactions within aquatic ecosystems*., edited by D.G. Meyer and J.R. Strickler, AAAS Symposium 85, Westview Press, Boulder, pp. 97–133.

Gilbert, J.J. and P.L. Starkweather, 1977. Feeding in the rotifer *Brachionus calyciflorus* I. Regulatory mechanisms. *Oecologia*, Vol. 28, pp. 125–131.

Halbach, U. and G. Halbach Keup, 1974. Quantitative relations between phytoplankton and the population dynamics of the rotifer *Brachionus calyciflorus* Pallas. Results of laboratory experiments and field studies. *Arch. Hydrobiol*., Vol. 73, pp. 273–309.

Hansen, B., 1991. Feeding behaviour in larvae of the opisthobranch *Philine aperta* II. Food size spectra and particle selectivity in relation to larval behaviour and morphology of the velar structures. *Mar. Biol*., Vol. 111, pp. 263–270.

Hansen, B., 1993. Aspects of feeding, growth and stage development by trochophora larvae of the boreal polychaete *Mediomastus fragile* (Rasmussen) (Capitellidae). *J. Exp. Mar. Biol. Ecol*., Vol. 166, pp. 273–288.

Hansen, B. and K. Ockelmann, 1991. Feeding behaviour in larvae of the opisthobranch *Philine aperta* I. Growth and functional response at different developmental stages. *Mar. Biol*., Vol. 111, pp. 255–261.

Hansen, B., P.J. Hansen and T.G. Nielsen, 1991. Effects of large nongrazable particles on clearance and swimming behaviour of zooplankton. *J. Exp. Mar. Biol. Ecol*., Vol. 152, pp. 257–269.

Hansen, B., P.J. Hansen and P.K. Bjørnsen, 1994. The size ratio between planktonic predators and their prey. *Limnol. Oceanogr*., Vol. 39, pp. 395–403.

Hansen, P.J., 1989. The red tide dinoflagellate *Alexandrium tamarense*: effects on behaviour and growth of a tintinnid ciliate. *Mar. Ecol. Prog. Ser*., Vol. 53, pp. 105–116.

Hansen, P.J., P.K. Bjørnsen and B. Hansen, Zooplankton grazing and growth: scaling within the 2 μm–2000 μm body size range. *Limnol. Oceanogr*., In Press

Hernroth, L., 1983. Marine pelagic rotifers and tintinnids—important trophic links in the spring plankton community of the Gullmar Fjord, Sweden. *J. Plankton Res*., Vol. 5, pp. 835–846.

Hino, A. and R. Hirano, 1980. Relationship between body size of rotifer *Brachionus plicatilis* and the maximum size of particle ingested. *Bull. Jap. Soc. Sci. Fish*., Vol. 46, pp. 1217–1222.

James, C.M. and T.A. Rezeq, 1989. Intensive rotifer cultures using chemostats. *Hydrobiologia*, Vol. 186/187, pp. 423–430.

Johansson, S., 1983. Annual fluctuations and production of rotifers in an eutrophication gradient in the Baltic Sea. *Hydrobiologia*, Vol. 104, pp. 335–340.

Jonasdóttir, S.H., D. Fields and S. Pantoja, 1995. Copepod egg production in Long Island Sound, USA, as a function of the chemical composition of seston. *Mar. Ecol. Prog. Ser*., Vol. 119, pp. 87–98.

Korstad, J., O. Vadstein, O. and Y. Olsen, 1989. Feeding kinetics of *Brachionus plicatilis* fed *Isochrysis galbana*. *Hydrobiologia*, Vol. 186, pp. 51–57.

Lubzens, E., 1987. Raising rotifers for use in aquaculture (a review). IV. Rotifer Symposium, Edinburg, Scotland. *Hydrobiologia*, Vol. 147, pp. 245–255.

Lubzens, E., G. Kolodny, B. Perry, N. Galai, R. Sheshinski and Y. Wax, 1990. Factors affecting survival of rotifers (*Brachionus plicatilis* O.F. Müller) at 4°C. *Aquaculture*, Vol. 91, pp. 23–47.

Nielsen, T.G. and T. Kiørboe, 1994. Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. *Limnol. Oceanogr*., Vol. 39, pp. 508–519.

Pilarska, J., 1977. Eco-physiological studies on *Brachionus rubens* Ehrbg (Rotatoria) I. Food selectivity and feeding rate. *Pol. Arch. Hydrobiol*., Vol. 24, pp. 319–328.

Pourriot, R., 1977. Food and feeding habits of rotifera. *Arch. Hydrobiol. Beih*., Vol. 8, pp. 243–260.

Riisgaard, H.U., 1988. Feeding rates in hard clam (*Mercenaria mercenaria*) veliger larvae as a function of algal (*Isochrysis galbana*) concentration. *J. Shellfish Res*., Vol. 7, pp. 377–380.

Rothhaupt, K.O., 1990a. Differences in particle size-dependent feeding efficiencies of closely related rotifer species. *Limnol. Oceanogr*., Vol. 35, pp. 16–23.

Rothhaupt, K.O., 1990b. Changes in the functional responses of the rotifers *Brachionus rubens* and *Brachionus calyciflorus* with particle sizes. *Limnol. Oceanogr.*, Vol. 35, pp. 24–32.

Rothhaupt, K.O., 1990c. Population growth rates of two closely related rotifer species: effects of food quantity, particle size, and nutritional quality. *Freshw. Biol.*, Vol. 23, pp. 561–570.

Rothhaupt, K.O. and W. Lambert, 1992. Growth-rate dependent feeding rates in *Daphnia pulicaria* and *Brachionus rubens*: adaptation to intermediate time-scale variations in food abundance. *J. Plankton Res.*, Vol. 14, pp. 737–751.

Ruttner–Kollisko, A., 1977. Suggestions for biomass calculations of planktonic rotifers. *Arch. Hydrobiol. Beih. Ergebn. Limnol.*, Vol. 8, pp. 71–76.

Sarma, S.S.S., 1991. Rotifers and aquaculture. *Environment and Ecology*, Vol. 9, pp. 414–428.

Sarma, S.S.S. and T. Ramakrishna Rao, 1988. Effect of food level on body size and egg size in a growing population of the rotifer *Brachionus patulus* Muller. *Arch. Hydrobiol.*, Vol. 111, pp. 245–253.

Schlosser, H.J. and K. Anger, 1982. The significance of some methodological effects on filtration and ingestion rates of the rotifer *Brachionus plicatilis*. *Helgoländer Meeresunters.*, Vol. 35, pp. 215–225.

Schlüter, M., C.J. Soeder and J. Groeneweg, 1987. Growth and conversion of *Brachionus rubens* in continuous culture. *J. Plankton Res.*, Vol. 9, pp. 761–783.

Scott, J.M., 1980. Effect of growth rate of the food alga on the growth/ingestion efficiency of a marine herbivore. *J. mar. biol. Ass. U.K.*, Vol. 60, pp. 681–702.

Serra, M. and M.R. Miracle, 1987. Biometric variation in three strains of *Brachionus plicatilis* as a direct response to abiotic variables. *Hydrobiologia*, Vol. 147, pp. 83–89.

Sprung, M., 1984. Physiological energetics of mussel larvae (*Mytilus edulis*). II. Food uptake. *Mar. Ecol. Prog. Ser.*, Vol. 17, pp. 295–305.

Sprung, M., 1989. Field and laboratory observations of *Dreissena polymorpha* larvae: abundance, growth, mortality and food demands. *Arch. Hydrobiol.*, Vol. 115, pp. 537–561.

Starkweather, P.L., 1988. Reproductive and functional responses of the rotifer *Brachionus plicatilis* to changing food density. *Verh. Internat. Verein. Limnol.*, Vol. 23, pp. 2001–2005.

Starkweather, P.L., J.J. Gilbert and T.M. Frost, 1979. Bacterial feeding by the rotifer *Brachionus calyciflorus*: Clearance and ingestion rates, behaviour and population dynamics. *Oecologia*, Vol. 44, pp. 26–30.

Stemberger, R.S. and J.J. Gilbert, 1985. Assessment of threshold food levels and population growth in planktonic rotifers. *Arch. Hydrobiol. Beih.*, Vol. 21, pp. 269–275.

Strathmann, R.R., T.L. Jahn and J.R.C. Fonseca, 1972. Suspension feeding by marine invertebrate larvae: clearance of particles by ciliated bands of a rotifer, pluteus and trochophore. *Biol. Bull.*, Vol. 142, pp. 505–519.

Støttrup, J.G. and J. Jensen, 1990. Influence of algal diet on feeding and egg production of the calanoid copepod *Acartia tonsa*, Dana. *J. Exp. Mar. Biol. Ecol.*, Vol. 141, pp. 87–105.

Verity, P.G., 1991. Measurement and simulation of prey uptake by marine planktonic ciliates fed plastidic and aplastidic nanoplankton. *Limnol. Oceanogr.*, Vol. 36, pp. 729–750.