

Bacterial Feeding by the Rotifer *Brachionus calyciflorus*: Clearance and Ingestion Rates, Behavior and Population Dynamics

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Summary. The rotifer *Brachionus calyciflorus* is capable of collecting and ingesting cells or short chains of a laboratory-grown bacterium *Aerobacter aerogenes*. Clearance rate, the volume of water effectively processed animal⁻¹h⁻¹, does not vary systematically with bacterial density between 0.01 and 100 µg dry weight ml⁻¹. Consequently, ingestion rates are strongly density-dependent, reaching maximal values at the highest food densities tested. Bacterial feeding rates are consistently lower than those determined with larger food types, except in very dense cell suspensions. *A. aerogenes* in high concentration (100 µg ml⁻¹) induces *Brachionus* to orient their pseudotrochal cirri to form screens over the buccal funnel; this behavior is at least four times less frequently observed at low (10 µg ml⁻¹) food density. Despite its occurrence, pseudotrochal screening appears ineffective in regulating bacterial ingestion rate. *B. calyciflorus* can be cultured xenically for greater than 40 generations fed *A. aerogenes* alone, with no diminution in net reproductive rate or intrinsic rate of natural increase, and no lengthening in cohort generation time.

Introduction

There is considerable uncertainty concerning the importance of bacteria in the diets of suspension-feeding rotifers. It has been assumed for many years that small planktonic species are capable of feeding on particles in the bacterial size range (Edmondson, 1957; Gliwicz, 1969; Resvoi, 1924; Spittler, 1969), but the extent to which bacteria quantitatively contribute to rotiferan diets has never been assessed. The conventional view among zooplankton ecologists has been that free-living bacteria are seldom the primary constituents in rotifer nutrition, while they may serve as supplementary or diversifying food sources in the total diet (Dougherty et al., 1960; Edmondson, 1957; Kryuchkova, 1974; Nauwerck, 1963; Pourriot, 1965).

Evidence for the inadequacy of bacteria as the sole nutritional source for brachionid rotifers has come primarily from culturing studies. Pourriot (1965) was unable to sustain long-term cultures of *B. calyciflorus* or *B. rubens* on *Aerobacter aerogenes* alone, concluding that the bacteria were of practically no nutritional value to the animals (p. 177). Likewise, Pilarska (1972) found population growth and reproduction reduced for *B. rubens* fed pure *A. aerogenes*, relative to conspecifics fed *Chlorella*. She suggested that the poor growth results might be due to the low "physiological utility" of the bacteria or to the negative effects

of bacterial metabolites. In addition, Pilarska (1977) showed that the feeding rates of *B. rubens* on the bacteria were less than half those found with *Chlorella*, which suggests that differences in feeding behaviors might contribute to the observed inferiority of bacterial-fed cultures.

In this paper we report a series of studies performed to more fully evaluate the capacities of a brachionid rotifer to collect and utilize bacterial food, comparing both feeding and population dynamics using bacteria as food with similar measures based on alternative food types.

Methods and Materials

We maintained *Brachionus calyciflorus* in xenic culture using *Rhodotorula glutinis*, *Aerobacter aerogenes* or *Euglena gracilis* as monospecific food sources (see Gilbert, 1975; Gilbert and Starkweather, 1978 for culture techniques). All animals were members of subclones started more than 100 generations prior to these experiments.

We determined the dry weights of the three foods using replicate cell samples dried (100° C, 16–24 h) onto desiccated, pre-weighed aluminum pans and included samples for corrections due to residual salts from the suspending medium. We weighed all samples on a Cahn 4100 Electrobalance (sens. = 0.1 µg) and calculated dry weights per cell for each food as (in µg cell⁻¹): *A. aerogenes*, 9.45×10^{-8} ; *R. glutinis*, 1.97×10^{-5} ; *E. gracilis*, 5.01×10^{-4} . Ranges of estimates were less than 5% of the mean values in all cases.

We counted *Euglena* and *Rhodotorula* samples using an electronic particle counter (Particle Data, Inc.) and *Aerobacter* with a Petroff-Hausser counting cell. For some later experiments (life table experiments only) we prepared food suspensions using turbidity (absorbance at 750 nm) to assess stock suspension density relative to previously-prepared standard curves.

We determined feeding rates using radioactively-labeled cells of *A. aerogenes* and *R. glutinis*. Detailed descriptions of the labeling procedure for the yeast and of the feeding experiment protocol are found elsewhere (Starkweather and Gilbert, 1977a, b, 1978). We labeled the bacteria in 25 or 50 ml batches of nutritional medium (Frost, 1978) with either ³²P or ³³P added as H₃PO₄. The inoculated preparations were shaken at 28° C for 8–12 h and the cells harvested and washed twice by centrifugation and resuspension in rotifer medium. We compared feeding rate estimates using one-way ANOVA calculations among food treatments with probabilities drawn from the F-distribution (Rohlf and Sokal, 1969).

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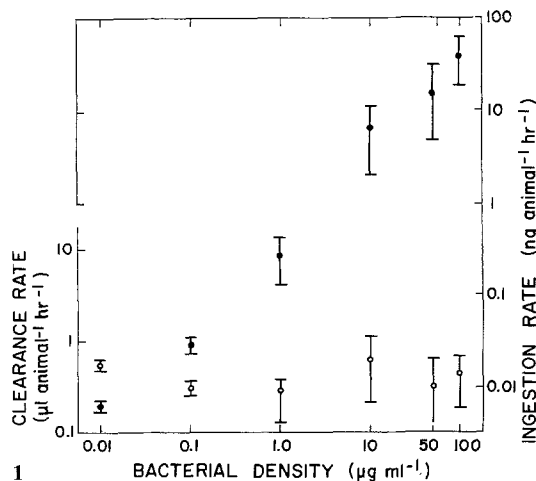


Fig. 1. Clearance rates (open circles) and ingestion rates (closed circles) of *Brachionus calyciflorus* feeding on various densities of *Aerobacter aerogenes*. All points are mean values \pm 1 s.d., $n=3-6$

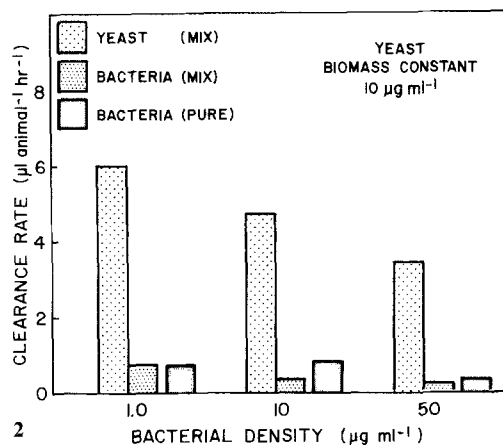


Fig. 2. Clearance rates of *Brachionus calyciflorus* feeding on mixtures of the yeast *Rhodotorula glutinis* and the bacterium *Aerobacter aerogenes*, as well as on pure suspensions of *A. aerogenes*. In the mixtures, clearance rates for both food types were obtained simultaneously using double-label radioisotope technique

We carried out direct observations of *B. calyciflorus* feeding on bacteria and yeast as before (Gilbert and Starkweather, 1977, 1978), noting the orientation of the pseudotrochal cirri of animals feeding in suspensions of various densities of the two foods. Comparison between food suspensions of the proportions of rotifers observed with the pseudotrochal cirri forming "screens" over the buccal funnel were made with the G-statistic (Gilbert and Starkweather, 1978).

For the life table experiments we isolated gravid adult *B. calyciflorus*, collecting neonates for up to 4 h before the start of an experiment. We cultured each neonate of the cohort individually in a cavity of a glass depression dish containing 0.5 ml of food suspension. We observed each rotifer twice each day removing any young produced and transferred all animals to fresh cell suspensions every 24 h. For daily observations we noted the survivorship (l_x) and the fecundity (m_x) of each cohort during the previous day (or age interval, x).

We calculated the life table parameters of net reproductive rate (R_0), intrinsic rate of natural increase (r) and the mean generation time (T_0) using methods of Birch (1948), such that $R_0 = \sum l_x m_x$, r is determined iteratively from $\sum e^{-rx} l_x m_x = 1$ and $T_0 = \log_e R_0 / r$. For the calculations, x was defined as the age interval, l_x as the proportion surviving at the beginning of the age interval and m_x as the number of offspring produced per female alive at the start of the age interval by the end of that interval.

Experimental Results and Discussion

Clearance and Ingestion Rates

The clearance rates and ingestion rates of *B. calyciflorus* feeding on six densities of *A. aerogenes* are shown in Fig. 1. With the exception of one group of animals at 10 µg dry weight bacteria ml⁻¹, all clearance rate estimates fall between 0.1 and 1.0 µl animal⁻¹ h⁻¹, with no consistent relationship between clearance rate and biomass. This result differs from clearance rate estimates obtained using two larger food types (Starkweather and Gilbert,

1977a) where we found strong density-dependence of clearance rate values over the same biomass range. Feeding on pure suspensions of *R. glutinis*, *B. calyciflorus* shows mean clearance rate values which are consistently greater than those found with *A. aerogenes*, with bacterial rates approximately one-tenth those for the yeast between 0.01 and 0.1 µg ml⁻¹ and one-half at 100 µg ml⁻¹. Comparing the current results with those for *E. gracilis* (Starkweather and Gilbert, 1977a), we find the bacterial clearance rates 10-times lower at low food densities (<1.0 µg ml⁻¹) but up to 5-times higher between 50 and 100 µg ml⁻¹.

The bacterial clearance rate results agree with the single estimate published by Pilarska (1977) for *B. rubens* feeding on *A. aerogenes* (26 µg ml⁻¹) which we have calculated to be between 0.2 and 0.3 µl animal⁻¹ h⁻¹.

Reflecting the clearance rate pattern of Fig. 1, ingestion rates (the product of clearance rate and available food density) for *B. calyciflorus* feeding on *A. aerogenes* are strongly density-dependent, with an 10-fold gain in biomass ingested per unit time for every order of magnitude increase in available food. By analogy with the clearance rate results, the ingestion rate vs. food density pattern for bacteria differs from both those of *R. glutinis* and *E. gracilis*.

At least three explanations are possible for the uniformly low clearance rates shown by the rotifers when in bacterial suspensions. First, the bacteria may be too small, or lacking some appropriate physical or chemical cue (or cues) to elicit normal, active feeding. Secondly, the bacterial food may induce rejection or a behavioral exclusion of particles from the oral region, by pseudotrochal screening (Gilbert and Starkweather, 1977) for instance, and thereby reduce the calculated feeding rates. The third, and perhaps most obvious possibility, is that the ciliary feeding structures of *B. calyciflorus* are inadequate to efficiently collect particles in the 0.5–1.0 µm size range, irrespective of feeding efforts made by the animals.

To test the first possibility, we added a food known to be actively consumed by *B. calyciflorus* (*R. glutinis*) to bacterial suspensions and compared bacterial consumption in these mixtures with that in pure bacteria of the same density. In each case

10 $\mu\text{g ml}^{-1}$ of yeast was added to a bacterial suspension and we monitored the clearance rates of both food types simultaneously. The results are compiled in Fig. 2. At all bacterial densities (1.0, 10.0 and 50 $\mu\text{g ml}^{-1}$) the mean clearance rates for yeast were significantly higher ($F=56.11$; $P<0.001$) than those for the bacteria, by a factor of between 8 and 15 times. Comparing the consumption of bacteria when mixed with yeast to that when bacteria was in suspension alone reveals no significant differences ($F=1.04$; $P>0.25$), indicating that the presence of yeast in the suspensions did not improve the animals' performance in collecting and consuming the bacterial cells. Since active feeding behavior is indicated by the relatively high clearance rates shown for yeast, we conclude that the low values for bacterial feeding are due to differential rejection of bacteria, a behavioral exclusion or reduced clearance efficiency, and not a diminished feeding effort.

It is interesting to note that the clearance rates for *R. glutinis* decline slightly with increased bacterial density, even though the yeast is present at 10 $\mu\text{g ml}^{-1}$ in all three treatments. While the estimates are not significantly different ($F=3.74$; $0.05 < P < 0.10$), the trend suggests that the presence of bacteria in a heterogeneous food suspension may influence the rotifers' consumption of alternative foods.

Incidence of Pseudotrochal Screening

We have previously described the behavior of *B. calyciflorus* when feeding on a variety of particulate foods, especially relative to the appearance of pseudotrochal screens which may restrict entrance of particles into the buccal region of the corona (Gilbert and Starkweather, 1977, 1978). The occurrence of these screens, which are formed by medially-bent pseudotrochal cirri, is dependent upon both the density and variety of food in suspension. Dense suspensions of large foods tend to induce the largest proportion of rotifers observed with screens, dilute suspensions of small cells the smallest proportions (Gilbert and Starkweather, 1978). Low or density-independent clearance rates appear to be correlated with the highest incidence of screening (Gilbert and Starkweather, 1977; Starkweather and Gilbert, 1977a).

Table 1 shows the results of direct observations made on *B. calyciflorus* while feeding in suspensions of *A. aerogenes* and *R. glutinis*. The latter food seldom induces a high frequency of pseudotrochal screening, irrespective of its density (Gilbert and Starkweather, 1978), and that result is confirmed here. *A. aerogenes* at 10 $\mu\text{g ml}^{-1}$ causes *B. calyciflorus* to form screens about 10% of the time, but at 100 $\mu\text{g ml}^{-1}$ this proportion increases to between 0.36 and 0.45 in experiments performed with animals from bacteria or yeast-fed cultures respectively. These two proportions are not significantly different ($G=14.12$; $P=0.94$), however, indicating that culturing history likely did not influence the outcome of these comparisons (\bar{x} of all estimates = 0.41 ± 0.13). Density-dependence of the bacterial screening behavior is clear; the pooled results at 100 $\mu\text{g ml}^{-1}$ are significantly different from those obtained at 10 $\mu\text{g ml}^{-1}$ ($G=38.76$; $P < 1 \times 10^{-9}$). Despite this relationship, pseudotrochal screens appear ineffective in restricting *Aerobacter* consumption, as evidenced by an apparently unregulated ingestion rate (Fig. 1) coincident with a 3- to 5-fold change in observed screening. It remains conceivable, however, that behavioral exclusion of particles may contribute somewhat to the reduced clearance rates shown by *B. calyciflorus* when feeding on *A. aerogenes* relative to yeast, at least at higher bacterial densities where pseudotrochal screening is frequent. The low feeding values obtained when the bacterial density is at or below

Table 1. Proportions of *Brachionus calyciflorus* observed with pseudotrochal screens when feeding in suspensions of the yeast *Rhodotorula glutinis*, the bacterium *Aerobacter aerogenes* or a mixture of both

Food type(s)	Food density ($\mu\text{g ml}^{-1}$)	Culturing conditions of <i>Brachionus</i>	Proportion <i>Brachionus</i> with pseudotrochal screens	
			$\bar{x} \pm \text{s.d}$	<i>n</i>
<i>Rhodotorula</i>	100	<i>Rhodotorula</i>	0.07 ± 0.04	3
<i>Aerobacter</i>	10	<i>Aerobacter</i>	0.09 ± 0.03	4
<i>Aerobacter</i>	100	<i>Aerobacter</i>	0.36 ± 0.14	5
<i>Aerobacter</i>	100	<i>Rhodotorula</i>	0.45 ± 0.04	4
<i>Aerobacter</i> and <i>Rhodotorula</i>	100/10	<i>Rhodotorula</i>	0.32 ± 0.04	4

10 $\mu\text{g ml}^{-1}$ (see again Figs. 1 and 2) must be due to poor collection efficiency or differential rejection as suggested earlier, since feeding activity is high (Fig. 2) and pseudotrochal screening rare (Table 1). We have not observed the rotifers to use obvious rejection behavior (Gilbert and Starkweather, 1977) when feeding on *Aerobacter*, and therefore suspect that collection inefficiency is the most important factor regulating bacterial consumption at low food density.

The increasing incidence of pseudotrochal screening with bacterial density may explain the reduction in yeast clearance rates as bacterial biomass increased from 1 to 50 $\mu\text{g ml}^{-1}$ in experiments shown in Fig. 2. The presence of yeast in the bacterial suspension does not significantly alter the incidence of pseudotrochal screening relative to bacteria alone (Tab. 1) ($G=2.59$; $P=0.11$), and the bacteria-induced behavior may thus reduce the collection and ingestion of yeast cells.

Life Table Experiments

As mentioned earlier, previous authors have reported little success in culturing *Brachionus* (Pourriot, 1965; Pilarska, 1972) and other monogonont rotifers (King, 1967) on *A. aerogenes*. Table 2 shows the results of three experiments where we collected life table data on *B. calyciflorus* cultured on *A. aerogenes* and two other foods, *R. glutinis* and *E. gracilis*. In experiment 1, all animals in each cohort were taken from cultures maintained on yeast for many generations. Comparing net reproductive rates (R_0), intrinsic rates of natural increase (r) or generation times (T_0) determined at two food densities, we detect no striking differences between animals fed *A. aerogenes* or *R. glutinis*. After 35 days of culture on bacterial food alone (experiment 2), the *B. calyciflorus* tested on *Aerobacter* show no loss of reproductive capacity or decrease in survivorship. After 92 days of bacterial feeding (experiment 3), the rotifers fed bacteria had demographic data which were equivalent or slightly superior to cohorts fed either *R. glutinis* or *E. gracilis*, and which indicated no decline in reproductive fitness after 3 months of culture on bacteria.

These results differ from those of Pourriot (1965) who found that both *B. calyciflorus* and *B. rubens* fed bacteria (including pure *A. aerogenes*) had low reproductive rates and persisted in culture for at most 4-6 weeks, and that *B. urceolaris sericus*, while

Table 2. Life table data for *Brachionus calyciflorus* cultured on the bacterium *Aerobacter aerogenes*, the yeast *Rhodotorula glutinis*, and the alga *Euglena gracilis* at food levels of 10 and 100 $\mu\text{g ml}^{-1}$ at 19–23° C. The symbols l_x , m_x , R_0 , r , and T_0 refer to survivorship and fecundity at a given age interval (x), net reproductive rate, intrinsic rate of natural increase, and generation time, respectively

Experi- ment	Food type	Food level ($\mu\text{g ml}^{-1}$)	No. in Para- cohort meter		Age interval (x) in days								R_0	r	T_0		
					0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8				8–9	
1 ^a	<i>Aerobacter</i>	10	17	l_x	1.00	1.00	1.00	0.76	0.71	0.59	0.29	0	4.24	0.55	2.64		
				m_x	0	0.12	1.71	1.62	1.33	0.40	0						
		100	19		l_x	1.00	1.00	1.00	0.79	0.47	0.42	0	4.84	0.74	2.13		
					m_x	0	0.68	2.16	1.87	1.00	0.13	0					
	<i>Rhodotorula</i>	10	11		l_x	1.00	1.00	1.00	0.82	0.64	0.64	0.45	0	4.82	0.60	2.60	
					m_x	0	0.45	1.55	1.44	1.00	1.00	0.80	0				
		100	21		l_x	1.00	1.00	1.00	0.76	0.52	0.29	0.19	0	3.99	0.70	1.99	
					m_x	0	0.95	1.57	1.06	1.00	0.33	0.25	0				
2 ^b	<i>Aerobacter</i>	100	24	l_x	1.00	1.00	1.00	1.00	1.00	0.88	0.71	0.29	0	6.30	0.84	2.18	
				m_x	0	1.17	1.75	1.54	1.21	0.57	0.18	0					
3 ^c	<i>Aerobacter</i>	100	21	l_x	1.00	1.00	1.00	0.76	0.48	0.33	0.19	0	5.48	0.83	2.04		
				m_x	0	1.24	1.62	2.00	1.50	0.57	1.00	0					
	<i>Rhodotorula</i>	100	14		l_x	1.00	1.00	1.00	0.93	0.57	0.43	0.29	0.14	0	2.29	0.25	3.27
					m_x	0	0.14	0.50	0.62	0.75	0.83	0.75	0.50	0			
	<i>Euglena</i>	100	18		l_x	1.00	1.00	1.00	0.94	0.78	0.56	0.28	0.17	0	5.90	0.72	2.47
					m_x	0	0.89	1.28	1.59	1.50	1.10	1.40	0.33	0			

^a *Brachionus* cultured on *Rhodotorula* prior to experiment; experiment at 19–21 C

^b *Brachionus* cultured on *Aerobacter* for 35 days prior to experiment; experiment at 19–21 C

^c *Brachionus* cultured on *Aerobacter* for 92 days prior to experiment; experiment at ~23 C

surviving in culture for 2.5 months, had very low reproduction. Pilarska (1972) cultured *B. rubens* on *A. aerogenes* for almost 8 weeks but her populations showed reduced fecundities after only 25–40 days.

Clearly, the present results show that *B. calyciflorus* can be cultured xenically for extended periods (>40 generations) when fed *A. aerogenes* alone, and that the population parameters are comparable to those obtained with other suitable foods. This appears to be in contradiction with the earlier results, but one must consider the possibility, as suggested by Pourriot (1965), that identical food sources may not have equivalent nutritional values for different ecological races of the same species. Additionally, in the case of Pourriot's (1965) work, bacterial densities may have been too low to support extended population growth.

Conclusions

The degree to which naturally free-living bacteria are directly utilized by freshwater zooplankton is still largely unknown. Successful collection and ingestion of bacteria have been previously confirmed for species representing the major planktonic suspension-feeding groups, including the calanoid copepods (Friedman, 1977), cladocerans (Peterson et al., 1978) and rotifers (Pilarska, 1977).

The work of Gliwicz (1969) suggested that crustacean and rotifer feeding efficiencies based on collection of bacteria-sized particles are, with some exceptions, lower than those for larger

foods in the nannoplankton size range. Pilarska (1977) found that *B. rubens* feeds on *A. aerogenes* at rates lower than those for some algal species, but higher than those for others. Our observations confirm these results but indicate that the relative efficiency of bacterial versus algal (or yeast) feeding by *B. calyciflorus* depends upon the types of food being compared as well as on their available densities.

Brachionus calyciflorus, while generally considered an active algal feeder (Erman, 1962a), does have an extremely varied potential diet depending upon habitat (Halbach and Halbach-Keup, 1974; de Infante, 1978). It seems likely that bacteria are frequently included in the rations of these rotifers and that bacteria may be readily utilized by them when available in large numbers. In addition, *Brachionus* may ingest larger detrital particles supporting bacterial aggregations, deriving nutritional benefit from those cells as well. This appreciation, coupled with the life table results indicating that bacteria are suitable as primary as well as secondary (supplementary) nutritional sources for *B. calyciflorus*, strongly suggests that bacterial feeding be considered in both laboratory and field evaluations as an important influence in the species' trophic ecology.

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