ASPECTS OF THE FEEDING BEHAVIOR AND TROPHIC ECOLOGY OF SUSPENSION-FEEDING ROTIFERS

Peter L. STARKWEATHER

Department of Biological Sciences, University of Nevada, Las Vegas, Las Vegas, Nevada 89154 U.S.A.

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Introduction

While the evidence is not yet adequate to provide a general assessment of rotifer feeding in the dynamics of planktonic communities, there can be no question but that the feeding biology of this group is a rich and exciting field for freshwater ecologists and natural historians. Two recent reviews, those of Dumont (1977) and Pourriot (1977), provide ample evidence for this assertion, together summarizing some 70 years of research on rotifer feeding behavior. This paper is a further discussion of certain aspects of the feeding behavior and feeding ecology of free-swimming, suspension-feeding rotifers. I will deliberately omit consideration of sessile or predacious genera since the feeding biology of these forms has been reviewed very recently; sessile rotifers are examined by Wallace (1980) and the predacious genus *Asplanchna* by Gilbert (1979).

The comments below relate to four areas of rotifer trophic ecology in which significant contributions have been recently made. The mechanisms by which members of the phylum regulate the quantity and quality of their diets are not fully understood. Accordingly, I review below the substantial literature describing the patterns of rotifer feeding rates relative to changes in food cell density. In addition, there is new work quantitatively examining the degree of food selectivity demonstrated by brachionids. The second section summarizes this work. As a third category, I have reviewed the literature on *in situ* determinations of rotifer feeding rates. This material is largely the result of experimentation between 1978 and the present. The final section of the current review considers the integration of chemostats with rotifer feeding biology. Experimental study with this technique appears likely to foster rapid progress in rotifer feeding, energetics and population dynamics.

Quantitative regulation of feeding rates

Perhaps the most obvious aspect of dietary regulation in rotifers is the modification of feeding rates with respect to food cell density. Since food consumption is the initial step in grazer productivity, the patterns of change of clearance and ingestion rates are of central importance in the trophic and population ecology of these animals. In addition, quantifying the potential grazing of a rotifer species or population permits evaluation of the impact that the rotifers may have on the food assemblage, both as a discrete taxonomic group and as a component of the larger suspension-feeding community.

Two terms that are conventionally used to describe the quantitative feeding activities of rotifers, and other grazing zooplankton, are clearance (or filtering) rate and ingestion rate. Ingestion rate is a straightforward unit, referring to the biomass or number of cells consumed by an animal (or per unit weight of an animal) in an interval of time. Clearance rate is ideally an estimate of the volume of water processed by an animal (or unit weight, as above) in a time interval during which it is engaged in feeding. In practice, the measured clearance rate conforms more exactly to Erman's (1956) usage, i.e. the volume of water which contains the biomass or number of cells actually ingested by the animal per unit time. This departure from the ideal is due to the fact that suspension-feeders are seldom 100% efficient in the removal of particles from water which they have processed, and is especially striking

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in the case of rotifers which readily reject particles already collected or behaviorally exclude particles before processing by the principal feeding structures.

Erman (1956) determined the clearance and ingestion rates of *Philodina roseola* and *Brachionus urceolaris* var. *rubens (B. rubens)* fed either *Scenedesmus acuminatus* or *Chlorella vulgaris.* For both foods, *P. roseola* clearance rates were constant (abour 1 μl animal^{-1}h^{-1}) over a cell density range between 10^3 and $> 10^7$ cells ml^{-1}. For the brachionid, on the other hand, clearance rates varied from less than 1 μl animal^{-1}h^{-1} to over 7 μl animal^{-1}h^{-1}, with the lowest rates obtained at the two extremes of food density used and the maximal rate at about 10^4 cells ml^{-1}. Pilarska (1977) found a similar pattern for *B. rubens* feeding on *C. vulgaris,* with a maximal clearance rate of 11.3 μl animal^{-1}h^{-1} near 10^4 cells ml^{-1}. The rotifers in Pilarska's study achieved ingestion rates which approximated 700 cells animal^{-1}h^{-1} (somewhat lower than those in Erman's work) and which became density-independent at greater than 3×10^6 cells ml^{-1}.

Comparable clearance and ingestion rates have been reported for *Brachionus plicatilis.* Ito (1955) reported a clearance rate of slightly greater than 3 μl animal^{-1}h^{-1} (from Doohan, 1973) based on *Synechococcus* consumption; this rate is within the range of other estimates but is certainly quite high considering the elevated cell density (ca. 8×10^6 cells ml^{-1}) under which it was obtained. Hirayama and Ogawa (1972) found *B. plicatilis* clearance rates between 0.18 and ca. 6.0 μl animal^{-1}h^{-1} inversely proportional to cell density *(Chlorella).* In later work with the same rotifer species but with two different foods *(Chlamydomonas* and *Olisthodiscus),* Chotiyaputta & Hirayama (1978) found clearance rate values higher and lower respectively than those obtained with *Chlorella.* Interestingly, the critical concentrations (critical concentration is defined as the maximal food density at which ingestion rate is directly proportional to food density) differed for the three food types, ranging between ca. 10^5 cells ml^{-1} for *Olisthodiscus* to 2×10^6 cells ml^{-1} for *Chlorella.* Doohan's (1973) clearance rates for *B. plicatilis* varied unsystematically over the tested range of *Dunaliella* densities, averaging close to 1.0 μl animal^{-1}h^{-1}. This fairly low rate might be due to high food density (near 10^6 cells ml^{-1}), inappropriateness of the food alga or a methodological error in the rate determinations (see Starkweather & Gilbert, 1977a). Like Hirayama and his colleagues, Dewey (1976) made feeding rate estimates for *B. plicatilis* feeding on three separate food types. Unlike the earlier work, the different cell suspensions (two species of *Dunaliella* plus *Isochrysis galbana*) produced only slight variation in clearance and ingestion rates. Dewey's (1976) clearance rate estimates fell between 1.0 and 9.0 μl animal^{-1}h^{-1} (20°C); the accompanying ingestion rate curves showed critical concentrations near 2×10^5 cells ml^{-1} for the *Dunaliella* spp. but no region of density-independence for consumption of the smaller *I. galbana.*

Feeding rates for *Brachionus calyciflorus* appear to fall in the same general range as those reported for the other brachionid species. Pennington (1941) found clearance rates approximately 0.3-0.5 μl animal^{-1}h^{-1} at food densities (of *Diogenes rotunda*) near 5×10^6 cells ml^{-1}. Erman (1962b) fed *B. caliciflorus* suspensions of *Lagerheimia ciliata* at densities between 2 and 140 μg dry weight ml^{-1}. With densities lower than 60 μg ml^{-1}, clearance rate was constant (2-5.6 μl animal^{-1}h^{-1} for different experiments) resulting in ingestion rate changes in direct proportion to food density. At a higher concentration (140 μg ml^{-1}), clearance rate dropped and ingestion rate became density-independent. Galkovskaja (1953) found *B. calyciflorus* clearance rates which were constant (ca. 1.0 μl animal^{-1}h^{-1}) at cell densities below 5×10^5 cells ml^{-1}, but which declined, as in Erdman's study, at higher food concentrations. Ingestion of the *Scenedesmus* cells increased with algal density until $0.5 - 1.0 \times 10^6$ cells ml^{-1}, above which ingestion rate was constant. Using *Chlorella pyrenoidosa* as the food cell, Halbach and Halbach-Keup (1974) tested *B. calyciflorus* feeding at densities between 0.05 and 5.0×10^6 cells ml^{-1}. Their data show a peak in clearance rate at 5×10^5 cells ml^{-1} (rate: 3.4 ± 0.12 μl animal^{-1}h^{-1}) and a minimal value (rate: 0.59 ± 0.01 μl animal^{-1}h^{-1}) at the highest tested cell concentration. In contrast to other results for brachionids, Halbach & Halbach-Keup (1974) report a decline, rather than a plateau, in ingestion rates found in the most dense cell suspensions.

More recent results for *B. calyciflorus* feeding regulation have been obtained for the rotifers exposed to microfungi and bacteria as well as algae. Starkweather & Gilbert (1976b) compared clearance and ingestion rates based on experiments run with *Euglena gracilis* and *Rhodotorula glutinis* at densities between 0.01 and 1000 μg dry wt ml^{-1}. For both foods, clearance rates varied between 45-50 μl animal^{-1}h^{-1} and < 0.5 μl animal^{-1}h^{-1} at low and high cell concentrations, respectively. Ingestion rates, on the other hand, differed substantially comparing the two foods, with yeast consumption far exceeding that of the alga except at the lowest food densities. The bacterium *Aerobacter (Enterobacter) aerogenese* elicited very low clearance rates (mean values always < 1.0 μl animal^{-1}h^{-1})

which did not vary systematically with cell density (Starkweather *et al.*, 1979). Accordingly, ingestion rates for *B. calyciflorus* feeding on *A. (E.) aerogenese* are distinctly density-dependent, with no obvious plateau in rate within the tested range. The differences among the feeding vs. food density relationships for the three foods equate with similar results of Hirayama & Ogawa (1972) and Chotiyaputta & Hirayama (1978) using *B. plicatilis*. For both species, different feeding rates and different critical concentrations were found using a variety of food cell types. A summary of the effects of food type on critical concentration for 3 species of *Brachionus* is provided in Table 1.

King (1967) measured the feeding rates of the sublittoral brachionid species *Euchlanis dilitata* based on three algal species, *Euglena gracilis, E. geniculata* and *Chlamydomonas reinhardti*. In each case, clearance rates declined with increased food density from ca. 10-16 μl animal^{-1}h^{-1} at 1.6 μg dry wt. ml^{-1} to 3-4 μl animal^{-1}h^{-1} at 49 μg ml^{-1}. The two *Euglena* species elicited identical feeding rates while both clearance and ingestion rates differed somewhat from those obtained with *C. reinhardti*.

A number of patterns arise from the results described above. It should be kept in mind, of course, that these patterns may be appropriate only for brachionid rotifers under laboratory conditions. A greater degree of generality must await study of additional families of rotifers.

1. Clearance rates may vary between less than 0.1 μl animal^{-1}h^{-1} to at least 50 μl anumal^{-1}h^{-1} depending upon food type and food density. By far the greatest number of published clearance rates fall between 1 and 10 μl animal^{-1}h^{-1} in the 20-25°C temperature range.

2. Clearance rates generally decrease with increasing food density, either in a progressive and continuous manner or abruptly at a high cell concentration. Some authors report a unimodal pattern of clearance rate vs. cell density with slight reduction in feeding activity at very low food levels. These declines are probably the result of malnutrition of animals maintained on a low food regime for long periods, and are not indicative of an active behavioral response to food shortage (see Starkweather & Gilbert, 1977b).

3. Ingestion rates are extremely variable, with published values from tens to many thousands of cells consumed animal^{-1}h^{-1}. The lowest ingestion rates (on a biomass basis) are found with the largest and smallest tested food types; high food consumption is associated with intermediate cell sizes (*n.b.*: this generalization may fail in particular instances involving selective behavior – see appropriate statements, below).

4. Ingestion rate increases with increased food cell density at low to moderate suspension concentrations. In dense food preparations, rotifer ingestion rates reach a maximal value and remain constant (the 'critical concentration', see Table 1). In some experiments, an ingestion rate plateau was not reached at normal cell densities, reflecting the continuous acceptance of food in proportion to its availability, even if such superfluous consumption is deleterious.

A variety of mechanisms have been proposed to explain the progressive (or occasionally abrupt) reduction in clearance rates with increased food density. The immediate effectors of such changes may be particulate interference with the feeding apparatus (Halbach & Halbach-Keup, 1974), inhibition of ciliary activity as reflected in reduced swimming speeds (Erman, 1956; J. V. Jackson, pers. comm.), increased food rejection frequency or intermittency of feeding effort (Starkweather & Gilbert, 1977b). In addition, Gilbert & Starkweather (1977, 1978) have proposed that the formation of 'screens' by the pseudotrochal cirri of *Brachionus* may dramatically reduce clearance rates in that genus, especially in dense suspensions of large food types.

The above regulatory mechanisms may be ultimately induced by nutritional causes such as reduced assimilation efficiency due to rapid gut passage of food (hence malnutrition) (Halbach & Halbach-Keup, 1974), or direct inhibition by algal, fungal or bacterial toxins or metabolites (Halbach & Halbach-Keup,1974; Pilarska, 1977). It is also conceivable that rotifers may directly sense cell density, through contact frequency, for instance, and modulate feeding in response to such stimuli. Work on *B. calyciflorus*, examining pseudotrochal screening behavior resulting from starvation or rapid transfers between food types, supports at least a partial role of nutrition in determining feeding activities (Gilbert & Starkweather, 1978).

Selective feeding

As discussed in another section, rotifers exposed to natural assemblages of particulate foods consume a diverse collection of phytoplankton, detritus and bacteria. It is also true, however, that while diets may vary among species, or within a species found in waters of differing character (or at different seasons), many rotifers collect

Table 1. Summary of the influence of food type on the feeding dynamics of 3 species of Brachionus. Critical concentration is the maximal food density at which ingestion rate is directly proportional to cell concentration.

Species	Food type	Critical concentration dry weight ($\mu g\ ml^{-1}$)	Critical concentration cell density (cells ml^{-1})	Temperature (°C)	Author
Brachionus calyciflorus	Lagerheimia	100		18.5 - 20.0	Erman (1962b)
	Scenedesmus		1.5×10^6	19.0 - 20.0	Galkovskaja (1963)
	Chlorella		5×10^5	19.0 - 21.0	Halbach and Halbach-Keup (1974)
	Euglena	5-10	$1\text{-}2 \times 10^4$	22.0 - 28.0	Starkweather and Gilbert (1977b)
	Rhodotorula	∿100	$\sim 5 \times 10^6$	"	"
	Aerobacter	>100	$> 10^{12}$	20.0 - 24.0	Starkweather et al. (1979)
B. plicatilis	Chlorella		2.1×10^6	24.0 - 26.0	Hirayama and Ogawa (1972)
	Dunaliella		2×10^5	20.0	Dewey (1976)
	Isochrysis		$>1.2 \times 10^6$	"	"
	Chlamydomonas		1.5×10^5	23.0	Chotiyaputta and Hirayama (1977)
	Olisthodiscus		$\sim 10^5$	23.0	"
B. rubens	Scenedesmus		$> 10^5$		Erman (1956)
	Chlorella		3×10^6	19.6 - 20.4	Pilarska (1977)

and ingest food items in proportions which may substantially depart from their relative availabilities in the surrounding water. Such dietary specialization has made it possible to classify several species groups based on their apparent feeding preferences (Erman, 1962a; Pourriot, 1965).

There are relatively few laboratory studies available which have directly investigated the selective feeding capabilities of suspension feeding rotifers, and those which have are all based on the genus *Brachionus*. Erman (1962b) demonstrated that *Brachionus calyciflorus* feeding rates determined with 20 cell types showed great variability (up to 10-fold differences) even though many of the food cells were of similar size. Other workers have found comparable degrees of difference among *Brachionus* feeding rates based on different foods, but cell sizes or cell shapes were always quite different in those cases (Dewey, 1976; Pilarska, 1977; Chotiyaputta & Hirayama, 1978; Starkweather & Gilbert, 1977b, 1978; Starkweather, 1979). Erman (1962b) was the first to report experiments specifically designed to quantitatively determine the degree of food selection which may occur in simple mixtures of cell types. Each of his mixtures was composed of 100 $\mu g\ ml^{-1}$ of *Lagerhemia ciliata* combined with 100 $\mu g\ ml^{-1}$ of one of 13 other algal varieties. Relative to *L. ciliata,* 2 algae were selectively removed, 4 algae were differentially avoided, and the remaining 7 were ingested at the same rate. The electivity indices for the 13 algae corresponded roughly to the rates at which each cell type was consumed compared to *L. ciliata,* when each was available in pure

suspension. In both sets of comparisons, no clear relationship was found between electivity and cell size or electivity and cell shape.

Erman (1962b) made the additional exciting observation that *B. calyciflorus* could distinguish (as demonstrated by different electivities relative to *L. ciliata*) between conspecific strains of food algae; the results show 4-fold differences between the electivities of paired strains of both *Chlorella vulgaris* and *C. terricola.*

Chotiyaputta & Hirayama (1978) measured the feeding rates of *Brachionus plicatilis* feeding on mixtures of *Chlamydomonas* and *Olisthodiscus.* They found differences in apparent filtering rates comparing the two cell types, with *Chlamydomonas* the preferred food in all cases. In general, the degree of 'selection' of *Chlamydomonas* was inversely proportional to *Chlamydomonas* density but was directly proportional to *Olisthodiscus'* relative concentration. *Olisthodiscus* ingestion was largely unaffected by the presence of the alternative cell type in the feeding mixtures, except with regard to differences in absolute feeding rate compared to values obtained with pure suspensions.

In addition to showing that *B. plicatilis* are able to distinguish between food cells of different species, Chotiyaputta & Hirayama (1978) found that the rotifers had feeding rates on *Chlamydomonas* which differed depending upon the age of the algal culture. Rates obtained with algae growing in exponential culture phase were at least twice those determined with senescent food. Unfortunately, the authors did not test exponential and senescent phase cells in a mixture to determine if the *Brachionus* could selectively consume one type of cell when both were were available simultaneously.

Additional direct tests of food selection have been performed using *Brachionus calyciflorus* (Starkweather & Gilbert, 1978, in prep; Starkweather, 1979; Starkweather *et al.,* 1979). In these studies, the rotifers were presented with mixtures of *Euglena gracilis* and *Rhototorula glutinis* or of *R. glutinis* and *Aerobacter (Enterobacter) aerogenese.* In one set of experiments, *E. gracilis* and *R. glutinis* were mixed in equal quantities (by dry weight) but with total biomass varying from 0.1 to 200 $\mu g\ ml^{-1}$. In these and other experiments using mixed food suspensions, the constituent cell types were labeled with different radioisotopes, permitting the measurement of feeding rates of the two foods simultaneously. The relationships between ingestion rate and food density differed for the yeast and the alga; the former food was always ingested in proportion to its absolute availability while *Euglena* ingestion varied in a complex pattern relative to total cell concentration (Starkweather, 1979; Starkweather & Gilbert, in prep.). As was true in Chotiyaputta & Hirayama's (1978) study using *B. plicatilis,* electivity values obtained from mixture experiments with *B. calyciflorus* reflected the relative feeding rates obtained for the different foods in pure suspensions.

In other experiments (Starkweather, 1979; Starkweather & Gilbert, in prep.), Starkweather and colleagues mixed two cell types in differing proportions; either keeping the combined density constant, or shifting total density by adding variable quantities of one cell type to fixed amounts of another. Three classes of results were found, also similar to those of Chotiyaputta & Hirayama (1978): 1) selection of a particular food type is usually inversely proportional to the relative abundance of that food in a two-species mixture, 2) total food ingestion may change depending upon the relative abundance of foods in simple mixtures even if the overall availability of food remains the same, and 3) the ingestion of some foods is more affected by the presence of alternative cell types than is the ingestion of other foods. By way of example for this last result, *E. gracilis* consumption by *B. calyciflorus* is dramatically affected by the presence of even small quantities of *R. glutinis* in a mixture, but *R. glutinis* ingestion rates are independent of the quantity of the alga present (Starkweather, 1979).

Field determinations of rotifer feeding

Ecologists concerned with trophic relations of rotifers, while often relying on laboratory observations for fundamental data on feeding behavior, are justifiably uncomfortable when called upon to generalize these results in terms of the activities of natural populations. To reduce this discomfort, and to provide a link between laboratory studies and animal feeding activities *in situ,* three approches have been taken: gut content analysis, correlation of rotifer and phytoplankton (as well as detritus and bacteria) dynamics, and direct measurement of feeding rates using radioisotope techniques.

Examinations of field-collected rotifers, with special attention to gut contents, have been accumulating for many years. Naumann's (1923) work characterized the diets of seven genera (eight species) including consideration of both the size and qualitative nature of food consumed. Erman (1962a) studied several additional species, stressing the high degree of feeding specialization apparent in many of the forms. Similar studies are available by

Table 2. Field determinations of clearance rates for various suspension-feeding rotifers.

Species	Method	Clearance rates ($\mu l\ animal^{-1} h^{-1}$)	Author(s)
Mixed species*	^{14}C-labeled natural seston	0.13 - 1.18	Nauwerck (1959)
Polyarthra dolichoptera	^{32}P(or ^{33}P)-labeled tracer cells	0.02 - 1.69	Bogden, *et al.* (1980; *in prep.*)
Polyarthra euryptera	"	0 - 0.36	"
Keratella cochlearis cochlearis (small morph)	"	0.45 - 2.53	"
K. cochlearis cochlearis (large morph)	"	0.29 - 8.12	"
Kellicottia bostoniensis	"	0.97 - 1.31	"
Conochilus dossuarius	"	3.01 - 4.73	Starkweather and Bogden (1980)
Brachionus calyciflorus	^{35}S-labeled tracer cells	1.45	T.M. Frost (pers. commun.)
B. havanaënsis	"	1.15 - 1.56	"
Keratella americana	"	0.50 - 2.09	"
Polyarthra sp.	Labeled tracer cells	0.5 - 1.0	J.F. Haney *et al.* (pers. commun.)

*species combinations varied during experiment but included: *Polyarthra dolichoptera*, *Synchaeta tremula*, *S. oblonga*, *Keratella hiemalis*, *K. cochlearis*, *Filinia terminalis* and *Kellicottia longispina*.

Nauwerck (1963), Pejler (1957), Hillbricht-Ilkowska (1972), Infante (1978), and especially by Pourriot (1965), who confirmed the nutritional value of many foods found in guts by performing subsequent laboratory culture experiments. These studies, and many others (see reviews of Pourriot, 1977 and Dumont, 1977) provide a clear indication that rotifers as a group may consume a wide range of natural sestonic foods, but that individual species may show extreme forms of diet specialization even in the presence of heterogeneous particle assemblages.

A variation of gut content analysis has been used by Gliwicz (1969) to determine the food size specificity of

Keratella and *Conochilus*. Gliwicz added finely ground sand to natural seston and examined the animals' guts after a 3 h. feeding interval. The results indicate that *Keratella cochlearis, K. quadrata* and *Conochilus unicornis* all have a degree of differential feeding based primarily on food size, but it is not clear how the ingestion of these inert tracers relates to consumption of natural organic particles.

Despite the value of gut content analysis in describing the qualitative aspects of rotifer diet, the technique suffers from its failure to provide information on the rate of food collection or ingestion, and from its inappropriateness for detection of soft-bodied or otherwise easily disrupted food cell types. Such foods are common in rotifer diets (Erman 1962a) and, as pointed out by Pourriot (1977), they are easily broken by the mastax or in the stomach. As a result, many important foods may be missed by such analysis unless identifiable fragments or distinctive cell pigments persist in the digestive tract. This disadvantage is amplified since the assimilation of a food type may be related to the degree to which it is physically disrupted during feeding (Infante, 1973). Thus, it is possible that in some cases the most nutritionally important foods are the least likely to be reliably observed or identified.

The second methodology used to assess the feeding activities of natural rotifer populations has been the statistical correlation of rotifer population parameters with the abundance of particular phytoplankton species on species groups (Nauwerck, 1963; Edmondson, 1965; Zimmerman, 1974; Halbach & Halbach-Keup, 1974; review of Dumont, 1977; reanalysis of Nauwerck's data by Cushing, 1976). This approach rests on the assumption that high birthrates and population sizes of rotifers occur during periods of peak biomass of readily consumed and utilized food types. A high correlation coefficient would logically imply, therefore, that the rotifers eat the particular food or foods in question.

This technique may be misleading in at least two respects. First, algal biomass is a static measure and may not necessarily reflect the actual rate of supply of various food types to the rotifers. The importance of less abundant but more quickly reproducing phytoplankton will be underestimated or missed altogether, especially if the phytoplankton are grazed rapidly (see critique of Lewis, 1977). Secondly, rotifers may not necessarily select the most abundant potential foods; many species of rotifers, as noted in the gut content studies, may preferentially consume rare particles or at least consume foods in proportions not reflecting their relative abundance in the water column.

Correlation techniques, like gut content studies, provide only qualitative indications of what natural rotifer populations are feeding on. To determine the rates at which the animals are removing particles from the surrounding medium requires a more direct quantitative analysis.

Until very recently, the only available *in situ* estimations of feeding rates for suspension-feeding rotifers were those of Nauwerck (1959). He determined clearance rates of mixed species populations feeding on ^{14}C-labeled natural foods from Lake Erken. Values ranged from 0.13 μl animal^{-1}h^{-1} for *Polyarthra dolichoptera* and *Synchaeta tremula* to 1.8 μl animal^{-1}h^{-1} for two *Synchaeta* species plus *Keratella hiemalis*. These rates are of the same order as those found in laboratory studies (Pourriot, 1977 and see Quantitative Regulation, above), but direct comparisons are difficult because of methodological and species differences.

Nauwerck's (1959, 1963) technique has the advantage of quantifying feeding rates on natural particles. However, the procedure estimated feeding activity only on photosynthetically-active plankton and ignores the contribution of detrital particles and heterotrophic cells, which are known to be important dietary constituents for many rotifers (Edmondson, 1957; Erman, 1962a; Pourriot, 1965). Furthermore, the photosynthetic assemblage is unlikely to be labeled uniformly (Rigler, 1971), allowing additional uncertainty about which autotrophic particles constitute the main fractions of the animals' diets. Thus, unless some particle types can be differentially labeled in multiple treatments (as in Saunder's (1963) use of ^{14}C-starch as a heterotroph tracer), or unless a particle fractionation is done before labeling (Bogdan & McNaught, 1975), Nauwerck's technique is of limited value in determining either overall feeding rates or the degree of differential feeding on various food types in the natural seston assemblage.

More recently, Bogdan, Gilbert & Starkweater (1980, in prep.) and Starkweather & Bogdan (1980) have used a modification of Haney's (1971, 1973) method to determine clearance rates of field populations of *Keratella cochlearis* (2 morphs), *Polyarthra dolichoptera, P. euryptera, Conochilus dossuarius* and *Kellicottia bostoniensis*. This technique requires the introduction of radioactively-labeled tracer particles into an enclosed sample of the rotifer community, a step accomplished with the use of a combination sampling/incubation chamber (see Haney, 1971). Using either one or two tracer particle types for each feeding estimate, Bogdan *et al.* (in prep.) have examined seasonal, diel and vertical variation in the feeding activity

of the dominant rotifers in their system. In addition, they have quantitatively documented differential feeding on bacteria, algae, yeast and detritus tracer particles by sympatric rotifer species, suggesting a food-based niche separation operating within the rotifer community (Bogdan *et al.*, 1980; Starkweather & Bogdan, 1980). J. F. Haney *et al.* (pers. comm.) have also used this method for determining clearance rates of *Polyarthra* sp. feeding on *Stichococcus* tracer cells. Their results, while preliminary, are consistant with those of Bogdan *et al.* in terms of the absolute values of the feeding parameters measured. These results, together with those of Nauwerck (1959), Bogdan *et al.* (1980, in prep.), Starkweather & Bogdan (1980) and T. M. Frost (pers. comm.) are summarized in Table 2.

Working in tropical Lake Valencia (Venezuela), Frost (pers. comm.) has measured *in situ* community cleartance rates using a sampling/incubation chamber identical to that used by Bogdan *et al.* (1980). Frost measured the grazing activity of both rotifers (principally *Brachionus* spp.) and microcrustaceans at 6 depths, comparing the calculated clearance rates based on 2 tracers, the bacterium *Aerobacter (Enterobacter) aerogenes* and the yeast *Rhodotorula glutinis*. Regression analysis of clearance rates versus animal population sizes indicated that rotifer density was a better predictor of bacterial consumption than was microcrustacean density, while the reverse was true for grazing rates based on yeast tracers. This suggests that bacteria may be relatively more important food sources for rotifers than for the co-occurring cladocerans and copepods, possibly reflecting a feeding niche separation between the major taxonomic groupings within the Lake Valencia zooplankton.

The use of laboratory-grown tracer cells to estimate *in situ* grazing activities suffers from at least three limitations. First, the technique measures differential clearance rate on only a limited number of sizes or types of radioactive particles, and does not estimate the ingestion of other materials represented in the pool of available foods. Secondly, as noted previously (Starkweather & Gilbert, 1978), the rotifers under study may selectively consume or reject the tracer cells relative to natural seston. Lastly, the addition of substantial quantities of tracers to the enclosed plankton community shifts both the size-frequency distribution and the absolute amount of food available to the rotifers. These changes are very likely to influence the feeding behavior of the suspension-feeders, producing results which may differ from those which occur with unmodified food spectra (see Starkweather, 1979; Starkweather & Gilbert, 1977b).

Chemostats and rotifer feeding

All the laboratory experiments described above, except those of Erman (1962a), were performed under static 'batch' conditions; that is, the rotifers and their foods were combined in systems where neither food cells nor cell nutrients were replenished during the course of the experiment. This may allow at least three important changes to occur in experimental vessels during a feeding determination: a) food cell condition (physiological state, growth rate, average cell size) may change as nutrients are depleted and cells are cropped, b) food cell numbers may change, through ingestion losses, settling or cell division, and c) rotifer condition may change via growth, reproduction, mortality or accumulation of metabolities. All of these factors are capable of inducing modifications in rotifer feeding behavior and performance, and all will be accentuated if the feeding determination requires a long period of time.

Chemostats are continuous-flow systems in which flow rates are held constant and biological populations are allowed to achieve steady-state levels controlled by the rate of supply of limiting nutrients. Chemostat techniques permit the culturing of foods appropriate for rotifers and provide supplies of cells of uniform size, shape, physiological state and suspension density. Thus, two of the three difficulties listed above are eliminated in experimental feeding systems which incorporate chemostat food culture and supply. In addition, the direct coupling of rotifer culture vessels to chemostats can produce conditions, after equilibration, which maintain animal populations with essentially constant age structure, physiological state and, presumably, feeding activity.

The use of chemostats in rotifer culture was first described in preliminary terms by M. R. Droop (in Conover, 1970). The system used by Droop combined a chemostat of *Brachiomonas submarina* which was coupled, through a metering dose switch, to a separate vessel containing *Brachionus plicatilis*. The design and construction of the equipment is detailed in a later paper (Droop, 1975).

Several variables relative to rotifer feeding, population dynamics and energetics are affected by the rate at which foods cells are supplied to *B. plicatilis*. Droop (1975) reports substantial differences in absolute food consumption, rate of food consumption and rotifer production with 2-or 3-fold differences in culture dilution rate. Lesser differences in steady-state population size and ecological growth efficiency were detected in the same experimental comparisons. More recently, Droop & Scott (1978) have

reported an extensive set of measurements confirming the effects of rate of food supply on *B. plicatilis*. Drawing their results from some 30 steady-state cultures and including systematic measurement of carbon, NO_3-nitrogen and vitamin B_{12} levels from all components of the culture system, the authors were able to describe the population dynamics, energetics and nutrient relation of the algae-rotifer system. Among the principal findings were that culture dilution rate (equivalent to rotifer specific growth rate in this system) has striking impact on rotifer respiration, excretion, and ecological growth efficiency, but has only minor effects on ingestion and assimilation efficiencies.

Relative to the population and reproductive structure of *B. plicatilis* populations in the above chemostat system, Scott (1977) has reported dilution rate influences on the mean numbers of amictic and egg-bearing amictic females per ml. It should be noted, however, that this result was somewhat inconsistent, and that the ratio of amictic to egg-bearing amictic females ml^{-1} changed only very slightly despite increased growth rate and decrease in mean age accompanying higher dilution values.

The only other report of chemostat use in providing food for rotifers is that of Boraas (1979). Boraas fed *Chlorella pyrenoidosa* to *B. calyciflorus* with chemostats of two designs, one similar to Droop's (Droop, 1975; Droop & Scott, 1978) with a two-stage operation segregating algal and rotifer growth vessels, and one where algae and rotifers were mixed in a single vessel. In two stage systems, both rotifers and algae entered steady-state relatively quickly with any population periodicity resembling a critically-damped oscillation. The maximal *B. calyciflorus* population doubling time Boraas measured with this technique was 12.5 h, indicative of the favorable nutritional conditions produced by the chemostat.

With mixed algae-rotifer chemostats, populations were either critically damped or showed 5-6 cycles of population oscillation before steady-state. The initial conditions of the innocula appeared to effect those differences, with low *C. pyrenoidosa* and high *B. calyciflorus* introductions producing rapid, critically damped dynamics and the reverse condition leading to delayed steady-states.

An additional aspect of this work is the incorporation of competing rotifers into one- or two-stage chemostat systems. Boraas (pers. comm.) is currently examining the affects of dilution rate on the outcome of food-based competition between congeneric brachionids. This approach, coupled with indications of size-selective feeding by chemostat-fed rotifers (Boraas, 1979), may lead to useful observations concerning the influence of rate of supply and cell quality in determining rotifer population interactions.

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