

## The components of feeding behavior in rotifers

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### Abstract

Feeding behavior of a rotifer can be broken into two classes of activities: the rate of successful search and the handling process. The former consists of the following components: Perceptual field (in planktonic rotifers the area of the corona), swimming rate, and attack rate. The second class consists of capture rate, handling time, rejection rate, ingestion, digestion, and assimilation. All evidence indicates that the perceptual field cannot be varied by the rotifer. Swimming rate is variable and under rotifer control, but does not appear to vary with degree of starvation. Attack rate is also under control of the rotifer, at least in the genus *Asplanchna*. Capture rates vary with the species of food item from zero to 100%. Handling times are longer than one would expect, as are rejection times. Digestion and assimilation appear to vary inversely with rate of ingestion. There is some suggestion in the literature that feeding behavior on very small particles differs from that on larger ones.

### Introduction

A study of the feeding of rotifers may be approached from several points of view. A proportional catalogue of the foods consumed tells us the rotifer's place in the aquatic food web. Measurements of clearance rates provide estimates of the impact of the rotifer on the dynamics of the food populations. Studies of the rate of population increase and the degree of mixis relative to food quality and quantity provide insights into rotifer populations in the wild.

However, the fundamental purpose of food consumption is to provide assimilable energy and nutrients for the rotifer's maintenance, growth, and reproduction. It is this aspect of feeding which will be emphasized in this review. More specifically an attempt will be made to identify the environmental and physiological factors which control feeding rate in rotifers. Most of the information available is derived from studies on *Brachionus* sp. or *Asplanchna* sp.

### Encountering the food items

Current models which consider collisions between an organism and its food items [e.g., Stanley, 1932; Gerritsen & Strickler, 1977; Cox, 1983] contain five major variables: (1) the size of the perceptual field of the organism, (2) the organism's speed of movement, (3) the size of the food items, (4) the density of the food items, and (5) the rate of movement of the food.

An organism's perceptual field is determined by the distance at which its sensory organs can detect a food item. *Asplanchna brightwelli* was found by Wurdak *et al.* [1983] to have seven receptors in its anterior end. These workers suggested functions of chemoreception for the ciliated pit located between the corona and the lateral horns, tactile recognition for the ventrolateral sensory bristles and the pseudotrochus, and mechanoreception for the ventrolateral sensory bristles. Gilbert [1977] demonstrated chemoreception in campanulate morphs of *Asplanchna intermedia* and *A. sieboldi* and conclud-

ed that prey recognition and the initiation of feeding behavior is mediated via chemoreception in these species. Gilbert (1976, 1980a: Table 2) found that campanulate females of *A. intermedia* can distinguish individuals of their own species from that of another, *A. sieboldi*, presumably via chemoreception. Male *Brachionus* are also known to possess chemoreceptors for females [Gilbert, 1963].

After extended electronmicroscopic studies of the sensory organs related to feeding in *Notommatia copeus*, *Philodina roseola*, *Brachionus calyciflorus*, *Asplanchna brightwelli*, *Trichocera rattus*, and *Rhinoglena frontalis*, Clément *et al.* [1983] concluded that tactile bristles are the most widespread rotifer sensory receptors and that some are developed to the point of showing tactile coordination at the level of perception itself. To the chemoreceptors, which they tentatively identified, these workers assigned functions of distance perception and contact recognition.

The question of distance perception is an important one, for were such an ability present, it would enlarge the perceptual field of the rotifer and hence its food gathering efficiency. On behavioral grounds, Dumont [1972] suggested that *Asplanchna priodonta* possessed the ability to detect vibrations in the water, but no evidence has been produced to support this speculation.

The sessile predatory rotifer, *Cupelopagis vorax*, is able to detect prey by vibrations and orientate its corona on the potential prey, but the item must come close to *Cupelopagis* before an attack may be attempted [Dr. R. L. Wallace, pers. commun.]. The majority position is exemplified by Gilbert & Stemberger's [1985a] statement, '*A. girodi* responded to prey only when prey contacted their coronae.' The perceptual field regulating the encounter rate of a rotifer with food items then, is not body size but the size of the corona.

Rotifers have the ability to withdraw the corona into the body cavity. In theory then, they should be able to vary the diameter of the corona and hence the perceptual field. If such a capability exists and is used, no one has reported it. *Brachionus calyciflorus* has pseudotrochal cirri which close over the mouth opening to form a screen which prevents the ingestion of food particles while still per-

mitting the animal to swim [Gilbert & Starkweather, 1977, 1978]. The pseudotrochal screen is formed when the food items are large (*Euglena*) but not when they are small (*Rhodotorula*). The screen serves the same purpose as a reduction in the size of the corona. This mechanism is the only observation of variation in the perceptual field or its analogue reported to this time.

Swimming speed is the second component of the encounter process. Recorded values for mobile forms range up to a maximum of slightly less than  $3 \text{ mm s}^{-1}$ , recorded in larval *Ptygura beauchampi* [Wallace, 1975, 1980]. Epp & Lewis [1984] measured maximum speeds in *A. sieboldi* of about  $1.3 \text{ mm s}^{-1}$  and in *Brachionus plicatilis* at  $0.8 \text{ mm s}^{-1}$ , a value nearly the same as that of  $0.75 \text{ mm s}^{-1}$  reported by Luciani *et al.* [1983] for mature individuals in a medium with calcium. Swimming speed varies with age and size [Epp & Lewis, loc. cit.], larger individuals swimming faster. A large campanulate *A. sieboldi* swims about  $1.5$  to  $2.3 \text{ mm s}^{-1}$ , while a saccate form about half as long swims at about  $0.6$  to  $1.3 \text{ mm s}^{-1}$  (Salt pers. obs.). Epp & Lewis (loc. cit.) concluded from their measurements on the swimming speeds of different sized *A. sieboldi* that although larger individuals swam faster, the increase with increase in body length was not linear. '... absolute speed increases with increasing body size, but at a rate less than the rate of increase in size. Relative speed therefore decreases with increasing size within clone 10C6 of *Asplanchna*.' They report a similar relationship in *B. plicatilis*.

However, there are some other considerations worth noting in this context. Suppose one assumes that the shape of a rotifer closely resembles that of a cylinder or a cone in which diameter is one-third the length. Then, a doubling of the length results in an eight-fold increase in volume, a better measure of size than length. The circumference of the base doubles with a two-fold increase in length. More importantly, the area of the base per unit volume decreases by one-half with a two-fold increase in length. In other words, if the body proportions remain the same, an individual which is twice as long as another, has only half the food finding area per

unit body volume of the smaller individual. This general morphological relationship may underlie the fact that larger campanulate morphs of trimorphic species of *Asplanchna* have proportionately larger coronae and are thought to be restricted to food-rich habitats [Stemberger & Gilbert, 1984a].

Luciani *et al.* [1983] found that swimming speed in *B. plicatilis* varied with age and presence or absence of calcium in the medium. Young and old individuals swam slower than mature adults. If the medium lacked calcium, swimming speeds were slower. Swimming speed is also temperature dependent. There is a regular increase in swimming rate from 14°C to 26°C after which the rate becomes somewhat less [Epp & Lewis loc. cit.]. The authors point out that mean absolute speeds in the range 20°C to 32°C are statistically indistinguishable.

This lack of statistical significance results from the high degree of variation in measurements at a given set of conditions, a characteristic of swimming speeds with which anyone who has measured them is familiar. This variability was dramatically documented by Coulon *et al.* [1983]. During 40 minutes of continuous recording under constant conditions, the swimming speed of a single female *A. brightwelli* varied from a low value of 0.81 mm s<sup>-1</sup> to a high value of 1.04 mm s<sup>-1</sup>, 28% higher than the low speed. If this kind of variation is a general one, then convincing conclusions about variation in swimming speed in response to changes in either internal or external conditions will require a very large number of replications.

For sessile rotifers, the rate at which ciliary action sweeps water past the buccal field is the functional equivalent of swimming speed. This is difficult to measure. Clearance rate can be substituted for it only if one assumes that the collection of food items is complete or if one has some independent estimate of the percentage of food items collected of those passing the corona.

Swimming speed in *A. brightwelli* and *B. calyciflorus* increases with light intensity and wave length [Clément, 1977; Clément *et al.*, 1983; Cornillac, 1982, cit. Clément *et al.*, 1983]. These findings agree with field observations that, in highly turbid water, *Asplanchna* sp. densities are highest in the

water near the surface where their swimming, and hence food gathering, would be the fastest.

All other things being equal, the probability of a rotifer encountering a large food item is greater than that of colliding with a small one. If food items are assumed to be spherical, each doubling of the diameter increases the cross-sectional area with which the rotifers collide by four times. Consequently, if large and small food items were present in the water in equal densities, the rotifer would encounter a higher proportion of large particles than of small. Such an equal density is not common in natural situations, so a verification of this hypothesis will have to take place in the laboratory.

Density of food particles is one of the major factors determining the rate at which rotifers encounter prey. The various models mentioned earlier describe encounter rate as a direct function of food density. In theory, if the density of the food items is high enough, the rotifer would be in continuous contact with a food particle. Food intake does not show this undiminished rate of increase with food density in most cases, but the phenomenon is apparently approached at the densities used in Starkweather *et al.*'s [1970] measurements of *B. calyciflorus* feeding on *Enterobacter* (= *Aerobacter*) *aerogenes*. Reasons for this lack of direct response to food density at higher concentrations will be considered later.

Movement by prey is the fifth component usually included in encounter models. If movements of the rotifer and its target organism are random with respect to one another, then the principal effect of movement by the food item is to cancel the loss in efficiency which the seeker generates by re-crossing its previous path. If, on the other hand, the food item (generally animals) actively avoid the rotifer, then the rate of encounter is reduced.

C. I. Haydock (pers. comm.) observed that individuals of *Paramecium aurelia* derived from laboratory cultures showed no response to the presence of *A. sieboldi* and remained dispersed randomly throughout the medium. When individuals of *P. aurelia*, *P. bursaria*, or *P. multimicronucleatum*, taken from a pond in which *A. sieboldi* was abundant, were placed alone in a drop of medium, they too remained dispersed randomly. When, how-

ever, an *A. sieboldi* was placed in the drop of fluid, the *Paramecium* immediately swam to the periphery of the drop of fluid and remained there. Similar behavior was observed in large test tubes where *Asplanchna* swam in the upper levels and *Paramecium* remained in the bottom of the tube. This kind of avoidance behavior may be more common than is suspected, as investigators rarely use stocks of food species derived from the same environment as the rotifers. Obviously such a response would appear only in food species which possess directional swimming abilities.

Inasmuch as most rotifers have no sensory organs which detect distant objects, every particle with which they collide must be identified by touch or by chemoreception. If the object is a conspecific or an organism that may represent a threat, or even an inert particle of debris, the corona is withdrawn into the body and the rotifer stops swimming momentarily. This halt has the effect of decreasing the swimming rate and hence the rate at which food particles are encountered. There is, to my knowledge, no data to support the idea, but it seems likely that the feeding rate of a rotifer could be significantly depressed in natural habitats by the occurrence of bits of decaying vegetation (e.g., in marshes where emergent vegetation provides a dense suspension of decaying leaf particles). One would expect to see the same effect in waters where cladocera and copepods were present in high numbers. It is possible that to some degree the inverse correlation of rotifer densities with cladoceran numbers may be due to this form of interference competition rather than to competition for food items [see also Gilbert & Stemberger, 1985b].

### The decision to attack

Having encountered a food item, the rotifer must either respond or not. This choice can be considered a decision in a mechanistic sense, although not in a cerebral one. By far the most important factor determining the decision is the species of food item encountered. This subject has been extensively reviewed [Pourriot, 1965, 1977; Dumont, 1977; Starkweather, 1980; Wallace, 1980] and will

not be considered here. However, factors other than species identity of the food item also play a part in this decision.

Rotifers show definite size preferences in their choice of food items. By analogy, one would expect to find intraspecific size differences between food items too. There are, however, few data on this subject in which other factors such as different encounter probabilities, different morphologies, or clonal differences are not confounded with size differences. Gilbert [1980b] recorded the feeding of *A. girodi* on large and small forms of *Keratella cochlearis*. One must assume that these two size forms do not differ in the chemical stimuli they emit in order to regard his data as reflecting size selectivity. *A. girodi* which were starved 2–5 h showed a higher percentage of attacks after an encounter with the large form than with the small one – 61.3% versus 43.1%. In *B. plicatilis*, feeding on sludge particles, the maximum size ingested is correlated with lorica length, but the smallest size ingested is correlated with the size of the trophi [Hino & Hirano, 1980].

Degree of satiation or starvation may also affect attack rate. Most investigators studying feeding performance of rotifers assume this to be true and starve the rotifers used in their experiments before testing them. There is, however, little data to support this general idea. Gilbert [1980a] stated that satiated *A. sieboldi* and *A. intermedia* do not exhibit feeding behavior. *Asplanchna girodi* offered small *K. cochlearis* after 2–5 h starvation initiated an attack in 43% of the encounters and 92.3% of the encounters when starved only 1.5–2.5 h [Gilbert, 1980a]. The subject of hunger will be considered further in a later section.

### Capture rate

The degree of success of an attack depends first of all on the species of food attacked. Most of our information is derived from studies on *A. girodi* [Gilbert 1980b; Gilbert & Williamson, 1978]. *Paramecium aurelia*, which are small and without defensive structures, are captured in 100% of the attacks on them, as are *Peridinium*. By contrast, *Kellicottia*

*bostoniensis*, which has long spines, is only successfully captured in 5.6% of the attacks on it, while *Keratella c. cochlearis* is intermediate with a capture success of 24% to 52%. *Brachionus calyciflorus* is captured in 18% to 26% of the attacks made on them.

In part, the differences in the success of attacks by *A. girodi* are explained by the method of capture described by Gilbert & Stemberger [1985a]. Prey are captured by aspiration resulting from a sudden dilation of the mastax brought about by changes in the shape of the peripharynx. Food items are swept into the mastax by the water current thus generated. The time required is about 50 ms. Trophi play no part in the capture of food items, at least of small prey such as *Polyarthra vulgaris* or *Synchaeta oblongata*.

Given that the capture mechanism is a short rush of fluid into the mastax, it is apparent that any obstacle to the free movement of the food item will hinder its passage into the mastax. This may account for the low capture percentage of *Kellicottia* for example. Gilbert & Williamson [1978] report that it is difficult for *A. girodi* to ingest *Keratella* if the posterior spine is oriented toward the esophagus. Similar obstruction may take place in the capture process. Presumably this protection from capture is the selective force behind the evolution of spines in *Brachionus* and *Keratella* [Gilbert, 1980a; Stemberger & Gilbert, 1984b].

Structural features of the food item may enhance capture. *Polyarthra vulgaris* and *P. dolichoptera* both ingest twice as many flagellated *Chlamydomonas reinhartii* as they do non-flagellated ones [Gilbert & Bogdan, 1981]. In some of the tests the flagella were removed by sonification, so there could have been no difference in the chemosensory character of the cells, nor could their nutritive qualities have been different. One must conclude that the flagella aided in the capture of the algal cells.

A problem arises in classifying avoidance by the food item after an encounter and before an attack can be initiated. Gilbert & Williamson [1978] scored 346 encounters between *A. girodi* and *P. vulgaris* as resulting in no attacks. Yet Gilbert & Stemberger [1985a] report on the feeding behavior of *A.*

*girodi* on *P. vulgaris*. The implication of zero attacks in 346 encounters is that *A. girodi* is unresponsive to *P. vulgaris*, which is obviously not the case. Rather, it would appear that the escape response of *P. vulgaris* is so fast that a true attack cannot usually take place. These incidents should more properly be considered escapes by the prey item.

### Ingestion and rejection

Considering the time and energy spent in affecting a capture, one would expect that all captured food items would be ingested. However, except for the small and morphologically simple food items, this is not the case. Some food items may actively escape, although there are no observations to verify this statement, and some may be rejected. Gosse (1856) provides one of the earliest descriptions. A *Brachionus* had captured an algal cell too large to be manipulated by the unci. It was rejected by the seemingly 'indignant' *Brachionus* by the use of the trophi. By contrast, Chotiyaputta & Hirama [1978] report that *B. plicatilis* rejected cells of *Olisthodiscus* sp. from the oral tube by ciliary action.

*Asplanchna* rarely capture *Bosmina* and frequently reject them from the mastax. Both *A. girodi* and *A. brightwelli* reject *Cephalodella* from the mastax, and *A. girodi* rejects *Proalides tentaculus* [De Beauchamp, 1951].

In most instances, however, rejection is not inevitable for a given species of food item. In one set of observations, *A. girodi* ingested all the *P. vulgaris* which could be captured whereas they ingested only 73% of the *K. cochlearis* captured [Williamson & Gilbert, 1980]. Short-spined *B. calyciflorus* and *P. aurelia* are nearly always ingested after capture by *A. girodi*, while the proportion of captures of *K. cochlearis* that result in ingestions is highly variable, ranging from 100% to a low of 17% [Gilbert, 1980b; Gilbert & Williamson, 1978]. *Kellicottia bostoniensis*, the ciliate peritrich *Rhabdostyla*, and *Peridinium* were never ingested after capture in Gilbert's [1980b] study. It seems likely, from the information above, that a large proportion of rejections result from mechanical difficul-

ties in transferring the food item into the stomach rather than because the food item is inherently unsuitable.

Gilbert & Starkweather [1977] observed that *B. calyciflorus* exhibited two methods for rejection of *Euglena gracilis*. (1) Some *Euglena* which had been transported through the buccal field and down the oral canal were expelled through the ventral cleft. (2) *Euglena* accepted into the distensible portion of the oral canal could be forced back into the buccal funnel by the trophi and rejected. Masses of *Rhodotorula glutinosus* might be rejected in this same fashion.

The times required for ingestion or rejection of *K. cochlearis* by *A. girodi* are surprisingly long. Gilbert & Williamson [1978] report mean values, from similar but not identical tests, of 40.4 to 95.0 s for ingestion times and even longer ones for rejection – 52.3 to 151.7 s.

### Assimilation rate

Once in the digestive system of the rotifer, all, or more commonly, a portion of the food items may be hydrolyzed and assimilated by extra- and intracellular processes [Wurdack, 1986]. In nearly all organisms the fraction of the food that is assimilated is a function of the food supply. When food is abundant and the ingestion rate is high, the fraction of food assimilated is low or moderate. As food supplies become scarce, the fraction assimilated increases. Assimilation rates in rotifers are measured either directly through the use of radio-tracers or indirectly. In the latter case, the sum of the energy used in respiration and that which appears as production is considered to be assimilation. The results of indirect calculations have been compared with values resulting from the use of tracers and been found to be in substantial agreement with them [Doohan, 1973; Pilarska, 1977].

An inverse relationship between the density of food and the assimilation efficiency in *Brachionus rubens* ranges from 60% when food concentration (*Chlorella vulgaris*) is low to 15% at high food densities [Pilarska, 1977]. *Brachionus calyciflorus* shows a similar response. Its assimilation efficien-

cy, calories assimilated per calories consumed, when feeding on *Kirchneriella lunaris* at a concentration of  $5 \times 10^6$  cell  $\text{ml}^{-1}$  is 20%. The efficiency increases as food concentration decreases to a value of 49% at a food concentration of  $4 \times 10^5$  cells  $\text{ml}^{-1}$  [Liemerth, 1980]. Galkovskaya [1963] found a similar relationship in this species.

By contrast, Borass [1983] studied *B. calyciflorus* feeding on *Chlorella pyrenoidosa* and concluded that assimilation did not decrease with increasing food concentration. His data do show, however, that ingestion rate does not decline in parallel with yield, which suggests that some process in the system is declining in efficiency as food density increases. Doohan [1973] concluded that the variability in assimilation efficiency in *B. plicatilis* feeding on different densities of *Dunaliella salina* was so high that one could not support the inverse efficiency hypothesis with these two species. She does point out, however, that the densities of food were at the high end of the scale for *Brachionus*, so that the degree of variation in food density may not have been great enough to show a response. This suggestion is supported somewhat by the low efficiency she reports, 19.4%.

Decrease in assimilation efficiency is apparently the result of rapid passage of food through the gut and a resulting failure in the digestion of a proportion of the food items. Both King [1967] in his studies on *Euchlanis dilatata* and Doohan [1973] in her investigations on *B. plicatilis* observed undigested cells in the feces of rotifers feeding at high food concentrations.

Droop & Scott [1978] concluded from their studies on *B. plicatilis* that assimilation efficiency did not show any obvious dependence on population growth rate.

Assimilation efficiency varies with age in *B. rubens* [Pilarska, 1977]. Young individuals are less efficient than mature ones, especially females with eggs. Overall, young individuals are about 70 to 80% as efficient as females with eggs.

There is evidence that the amount of assimilation of ingested food varies from one clone to another. Snell [1979] recorded the rates of increase of two strains of *A. brightwelli* when individuals of each clone were allowed a fixed number of *Paramecium*

*tetraurelia* per day. The ration at which the rate of increase was zero is a valid comparison point between the two clones. For one clone (RBH) this point was at a ration of about 67 *Paramecium* per rotifer per 24 h. For the other clone (9A1), zero rate of increase was at a ration of 44 *Paramecium* per rotifer per 24 h. These figures suggest that the second clone more efficiently digested the prey than the first, assuming that the body sizes of individuals in both clones were the same.

Using this same argument, the data of Stemberger & Gilbert [1984a] can be used to infer relative assimilation efficiencies in species of *Asplanchna*. The ration to maintain population growth at zero, the threshold ration, varies with body size for species in this genus. Calculations of the threshold ration per  $\mu\text{g}$  body weight normalizes for body size. On this latter basis, the most efficient form is the campanulate morph of *A. silvestrii*. The other species investigated, in declining order of efficiency, were: *A. girodi*, saccate *A. silvestrii*, *A. priodonta*, *A. brightwelli*.

The digestive tract of a rotifer is a finite space. No new food items can be ingested until there is room for them. Therefore, the time that food items remain in the digestive tract affects the feeding rate and the assimilation efficiency. Further, different foods have different residence times in the digestive tracts of a given species. Starkweather & Gilbert [1977], using radio-tracer techniques, determined that the gut passage time for *E. gracilis* eaten by *B. calyciflorus* is 15 minutes. Wallace and Starkweather [1983] found the gut passage time of the yeast *Rhodotorula glutinis* eaten by either *Ptygura cristallina* or *P. pilula* to be greater than 30 minutes. When *A. priodonta* feeds on *Ceratium hirundinella*, the mean time the food items remain in the stomach is about 14 minutes [Ejsmont-Karabin, 1974]. By contrast, Sawada & Enesco [1984] found that *A. brightwelli* required 12 hours to completely digest and assimilate a stomach full of *Paramecium caudatum*.

### Feeding and clearance rates

In many studies, no attention is paid to the steps

between the availability of food items and their appearance in the stomach of the rotifer. The number of food items ingested per unit time is compared to the density of the food items in the surrounding medium and the results are presented as the feeding rate. Frequently the converse of feeding rate is calculated, i.e., the clearance rate – the volume of water which, at the prevailing food density, would contain the number of food items consumed per unit time.

Most animals respond to an increase in food density by increasing the rate of food intake asymptotically until a food density is reached beyond which no increase in feeding rate takes place. The model most commonly fitted to these data is Holling's [1959] 'disc equation', so called because it was derived from observations of a blind-folded technician searching for and picking up discs of sandpaper. The numerator contains two terms, food density and the rate of successful search, which includes all the components considered above up to and including the attack. The denominator contains both those terms plus handling time, which includes the capture, rejection, ingestion, and egestion times. The value of the handling time sets the position of the asymptote or the density of food items at which the plateau in feeding rate occurs.

With two notable exceptions, the model appears to fit the feeding behavior of rotifers fairly well. Some examples are: *B. plicatilis* [Chotiyaputta & Hirama, 1978], *B. calyciflorus* [Erman, 1962; Starkweather, 1981; Starkweather & Gilbert, 1977] and *B. rubens* [Pilarska, 1977]. Despite many studies made on feeding rates in rotifers, it is difficult to find clear cut tests of the fit of the model because investigators frequently do not include measurements of feeding rate over a wide enough range of food densities.

Halbach & Halbach-Keup [1974] found that *B. calyciflorus* feeding on *Chlorella pyrenoidosa* followed the expected pattern of a hyperbolic increase in ingestion with increasing density of food, up to a point. As food density increased beyond that point, ingestion declined. This kind of performance can only be considered maladaptive, and it is difficult to see how it could evolve. The explanation for the phenomenon must lie in the perfor-

mance of the food organism, as suggested by the authors. Starkweather [1980] considered a number of other explanations for this behavior, some of which would require a failure in the performance of the regulatory mechanisms associated with feeding.

Another lack of fit with the model is displayed by *B. calyciflorus* feeding on small food items – *E. aerogenes* or *R. glutinis* [Starkweather & Gilbert, 1977; Starkweather *et al.*, 1979]. In both these circumstances, no critical food concentration was recorded. That is, no plateau in ingestion occurred even at high food densities. The only explanation for this lack of response consistent with the ideas presented here, is that the handling time for these small particles is very short and its role in regulating the feeding rate was not involved.

One can use morphological information, swimming speed, and clearance rate to derive an estimate of the efficiency of all facets of the feeding behavior combined. For example, Doohan [1973] gives the clearance rate of *B. calyciflorus* as  $1 \mu\text{l individual}^{-1} \text{h}^{-1}$  when the food concentration is greater than  $0.5 \times 10^6 \text{ cell ml}^{-1}$ . An individual *Brachionus* with a corona diameter of 0.19 mm, swimming at a speed of  $0.75 \text{ mm s}^{-1}$ , will search a volume of  $77 \mu\text{l h}^{-1}$ . Consequently, one can conclude that the rotifer ingested only one out of every 77 food items it encountered, a collection efficiency of 1.3%.

### The role of hunger

The phenomenon of hunger is not well understood in higher vertebrates, much less in rotifers. Nonetheless, it plays a role in regulating feeding. It appears to determine the attack rate when food is abundant. Two direct series of observation by C. I. Haydock (pers. comm.) illustrate this response. The first records the cumulative consumption of *P. tetraurelia* by *A. sieboldi* and *A. brightwelli* through time. (Figs. 1, 2). It will be noted that in the presence of abundant food, *Paramecium* were consumed at a regular rate which increased as the *Asplanchna* increased in age and hence size. Given the density of prey, the rate of consumption was far lower than the encounter rate. Consequently, one

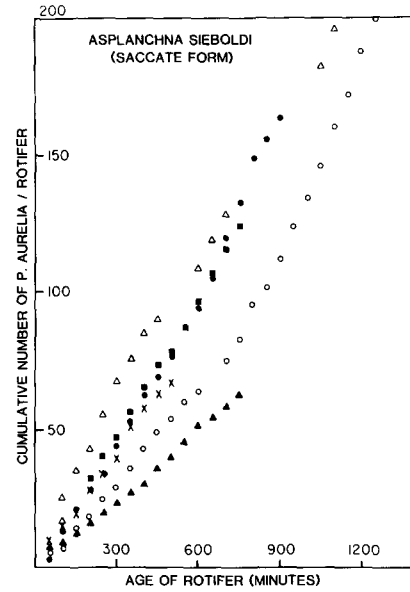


Fig. 1. Cumulative consumption of *Paramecium tetraurelia* from time of birth by six different females of the saccate form of *Asplanchna sieboldi*.

can infer that only at periodic intervals did the *Asplanchna* respond to contact with the *Paramecium*, presumably when its hunger level had built up to a critical level.

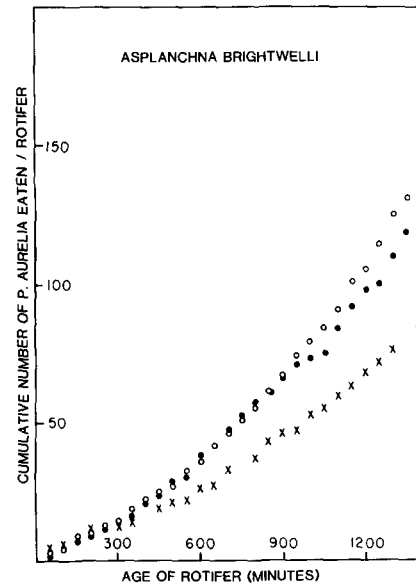


Fig. 2. Cumulative consumption of *Paramecium tetraurelia* from time of birth by three females of *Asplanchna brightwelli*.



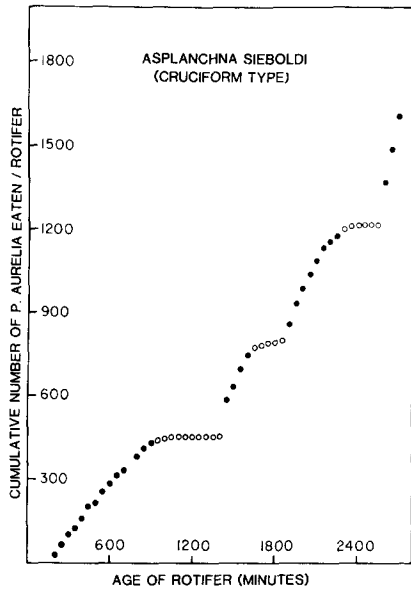


Fig. 3. Cumulative consumption of *Paramecium tetraurelia* by a female *Asplanchna sieboldi* with intermittent periods of starvation. Period without food are shown by open circles.

This interpretation is strengthened by a second series of observations on the same system. Following a period of starvation, the rate at which *Asplanchna* consumed *Paramecium* increased dramatically until it had returned to the previous well fed state, whereupon it resumed its original rate of food consumption (Fig. 3). Despite this evidence, there are no data to demonstrate that varying degrees of hunger produce proportional changes in swimming rate (Salt pers. obs.) or in any other facet of feeding behavior. Until more studies are completed, we shall have to conclude provisionally that hunger acts in an all or nothing fashion to turn feeding behavior on and off. Further, although we can be fairly sure that hunger plays a role in feeding, we have no information of how this condition is sensed by the rotifer nor how it is integrated by the neural system.

### Conclusion

One can conclude from this review that, to a large degree, the feeding rate is set by conditions external to the rotifer. Temperature (May 1980), prey densi-

ty, chemical composition of the water and other factors all have a strong influence on the rate of capture of food items. Among components of capture rate, only swimming and attack rate are potentially variable by the rotifer. Swimming rate certainly varies, but it does not seem to change in response to success or lack of it in capturing food. The rate of attack does change, at least in *Asplanchna*. It does not seem to in *Brachionus* where the screening of the mouth by the pseudotrochal cirri performs that function.

Within the handling process, there is little direct evidence that any of the components are varied by the rotifer in response to feeding success. Assimilation rate varies with ingestion rate, but as this response is an inverse one, it does little more than compensate for the lack of control in the ingestion rate.

In general, one can conclude that rotifers have relatively little control over their feeding rate to use to counteract variations in food availability. Maybe they have evolved the ability to manipulate their reproductive activities with variations in the food supply to compensate for their lack of regulatory ability in their feeding [King, 1967; Pourriot, 1983; Pourriot & Rougier, 1979; Robertson & Salt, 1981; Walz, 1983].

There are also hints throughout the literature that the processing of very small particles is not the same as that for large ones. Perhaps the trophi play no part in the handling of small particles. Maybe there is reduced control over the ingestion rate of small particles. Only further investigation aimed directly at this problem will answer these questions.

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