

Feeding behaviour of the rotifer *Ascomorpha ovalis*: functional response, handling time and exploitation of individual *Ceratium* cells

Claus-Peter Stelzer

Max-Planck-Institut für Limnologie, Postfach 165, 24302 Plön, Germany

Abstract. The planktonic rotifer *Ascomorpha ovalis* feeds on large dinoflagellates (e.g. *Ceratium* sp., *Peridinium* sp.) and is able to extract their cell contents by means of its virgate mastax. This paper presents the results of experiments on the feeding behaviour of laboratory-cultured *Ascomorpha* with *Ceratium furcoides* as food algae. *Ascomorpha* are three times larger than their prey *Ceratium* (by volume), but with regard to total length, their prey was even 20% larger. *Ascomorpha* showed a hyperbolic functional response curve with a plateau of the feeding rate at 8 *Ceratium* cells animal⁻¹ day⁻¹ when concentrations of *Ceratium* were >100 cells ml⁻¹. The mean handling time (time for capturing and extracting one *Ceratium* cell) was 3 min. The shape of the functional response was better described by a curvilinear model than by a rectilinear model. However, handling times cannot be responsible for this, since they were too short to set limits on ingestion rates. At low food concentrations, encounter rates with prey seemed to limit the feeding rates of *Ascomorpha*, whereas at medium to high food concentrations, satiation effects (lower attack rates) seemed to set limits on the feeding rates. *Ascomorpha* showed a significant decrease in the exploitation of single *Ceratium* cells at high prey concentrations. This decrease could be explained by a saturation effect in which the partly filled guts of *Ascomorpha* did not permit the total extraction of the contents of a *Ceratium* cell.

Introduction

The planktonic rotifer *Ascomorpha ovalis* has a very specialized diet, which consists exclusively of large dinoflagellate algae such as *Ceratium* sp. and *Peridinium* sp. (Kolisko, 1938). These algae are inedible for most other planktonic predators due to their large size and thick cell wall (Pollinger, 1987). *Ascomorpha* is not able to ingest these algae as a whole, since the rotifers are only 2–3 times bigger than their prey. They possess specialized mouthparts, a virgate mastax, which allows them to pierce holes through the thick cell wall of dinoflagellates and to extract the cell contents (Figure 1).

Many previous experimental studies on feeding in rotifers have been performed with microphages (e.g. Starkweather, 1980a; Rothhaupt, 1990) and macrophages (e.g. Gilbert, 1980), but detailed information on the feeding biology of rotifers with a very pronounced macrophagous feeding behaviour, such as *Ascomorpha*, is lacking. This is the first report on laboratory culturing and experimental studies on *A. ovalis*. Previous work on this species has been carried out with sampled field material and consisted solely of short-term observations (Lauterborn, 1893; Kolisko, 1938; Pourriot, 1965, 1977). Attempts to culture *Ascomorpha* were hindered by difficulties in culturing their food algae, e.g. *Ceratium* sp. (Pourriot, 1965). However, one culturable strain of *Ceratium furcoides* can now be obtained from the Culture Collection of Algae and Protozoa, Ambleside, UK.

In this study, two hypotheses concerning the feeding behaviour of *Ascomorpha* were tested.

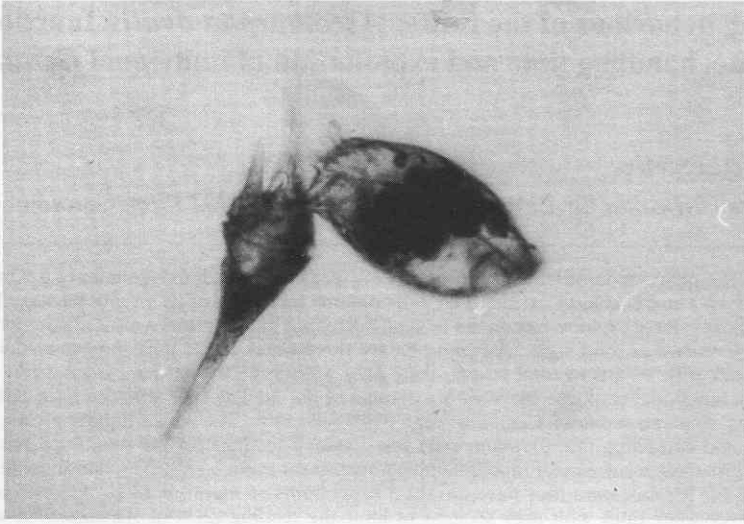


Fig. 1. *Ascomorpha ovalis* (right) feeding on *C. furcoides* (left).

(i) *Ascomorpha* can only feed on a single prey item at one time and this process requires a certain handling time. Thus, *Ascomorpha* should show a Type 2 functional response (Holling, 1959; curvilinear model), instead of a Type 1 functional response, where feeders do not spend time on handling prey items. In the Type 1 functional response, feeding rates below the incipient limiting level (ILL; Rigler, 1961) are proportional to the concentration of prey items.

Two models have been conceptualized for the case where the response is not linear. Holling's 'disc equation' [$f(P) = aP/(1 + ahP)$, where P is the prey concentration, h is the average handling time and a is the encounter rate] considers the components of feeding such as encounter rate, search time and handling time, whereas the Ivlev model [$f(P) = f_{\max}(1 - e^{-dP})$, where f_{\max} is the maximum rate of predation and d is the constant for the decrease in motivation to hunt] assumes that the attack rate decreases linearly with the satiation of the predator. Both describe a Type 2 functional response, but with different assumptions.

In this study, the following questions should be answered. Is the functional response of *Ascomorpha* Type 1 (rectilinear) or Type 2 (curvilinear)? Which of the assumptions of the two curvilinear models (e.g. handling time, changing motivation to hunt) apply for the *Ascomorpha*–*Ceratium* system and what is their relative importance? These problems were addressed by both fitting the different models to the experimental data on feeding rates and assessing the components of prey capture (probabilities of attack, capture and ingestion), including calculations of theoretical encounter rates using a modified mathematical model of Gerritsen and Strickler (1977).

(ii) When culturing *Ascomorpha*, it was frequently observed that the animals did not extract all of the cell contents of *Ceratium*, although they sometimes did. This led to the hypothesis that *Ascomorpha* is an optimal forager with a strategy

similar to that of the hemipteran *Ranatra dispar*, which is also a macrophagous predator with a sucking feeding mode (Bailey, 1986): at high food concentrations, *Ascomorpha* would exploit *Ceratium* cells incompletely and switch to the next food item more quickly. This should result in a maximization of energy input per unit time.

Thus, exploitation of single *Ceratium* cells should be negatively correlated to food density. Additionally, the time for opening a *Ceratium* cell should be shorter than the time needed for extracting the cell contents.

Method

Culturing and routine techniques

Ascomorpha ovalis was kindly provided by Dr B. Meyer (Max-Planck-Institut für Limnologie, Plön) and was originally isolated from a small lake in northern Germany in late summer 1994. The dinoflagellate alga *C. furcoides* was obtained from the Culture Collection of Algae and Protozoa (CCAP), Ambleside, UK (culture number 1110/4). All culturing and experimentation on these organisms was carried out in temperature-controlled chambers at $20 \pm 1^\circ\text{C}$. Both algae and rotifers were kept in WC (= MBL) medium (Guillard and Lorenzen, 1972).

Ceratium furcoides (47 μm equivalent spherical diameter, 150 μm longest linear dimension) was grown in 300 ml Erlenmeyer flasks in a light regime of 100 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ provided by cool-white fluorescent bulbs on a 16:8 h light–dark cycle. Owing to the slow growth rate of these algae (maximum $\sim 0.1 \text{ day}^{-1}$), the batch cultures had to be renewed only every 1.5 months. Initial densities of *Ceratium* were $\sim 100 \text{ cells ml}^{-1}$ and densities after 1.5 months growth were 1000–2000 cells ml^{-1} .

Algae fed to the animals were usually in the late exponential or stationary phase of growth. To provide different food concentrations for *Ascomorpha*, the concentration of a *Ceratium* culture was estimated by counting 1 ml aliquots, fixed by Lugol's solution, in a sedimentation chamber under an inverted microscope. Then, the *Ceratium* culture was diluted with WC medium to the desired concentration. Very low food concentrations were obtained by transferring individual *Ceratium* cells with a sterile micropipette into a defined volume of WC medium. The mean carbon content of a *Ceratium* cell was determined in three replicates with a carbon analyser (Na 1500 Carlo Erba) and was $7.24 \times 10^{-3} \mu\text{g}$.

Ascomorpha ovalis (125 μm , mean adult body length) were cultured in polystyrene Petri dishes; each contained 20 ml WC medium with *Ceratium* in concentrations of 100–300 cells ml^{-1} . The animals were kept under low light conditions (10 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) on a 16:8 h light–dark cycle. Batch cultures of *Ascomorpha* had initial densities of 15–20 individuals per dish. Food concentrations were checked every other day and, if necessary, *Ceratium* was added from dense cultures. New cultures were started after 10–14 days of growth in the same Petri dish. The highest *Ascomorpha* densities that were reached by this culturing method were around 150 individuals per dish. To prevent *Ascomorpha* getting caught in the surface film of the growth medium, small pieces of cetyl alcohol (Desmarais, 1997) were placed on the surface.

Experiment 1 (determination of feeding rates)

Single *Ceratium* cells, which have been sucked out by *Ascomorpha*, are easily recognizable as the cell contents are partly or completely missing. The hole pierced through the cell wall is very small ($\sim 1.5 \mu\text{m}$ diameter) and can only be recognized by using scanning electron microscopy. Per capita feeding rates were calculated by counting the numbers of empty and half-empty *Ceratium* cells after incubating a known number of *Ascomorpha* in defined *Ceratium* concentrations.

All animals were adults, taken from healthy stock cultures and pre-fed for 6 h with *Ceratium* in the respective concentrations, which ranged from 5 to 200 cells ml^{-1} . The concentrations 5–50 and 100 cells ml^{-1} were adjusted by transferring single *Ceratium* cells with a micropipette into the respective volumes of WC medium, whereas the concentrations 75, 150 and 200 cells ml^{-1} were obtained by dilution from dense cultures of *Ceratium*. In the feeding experiments, *Ceratium* was provided in different volumes of WC medium and in experimental vessels of different sizes (polystyrene Petri dishes with diameters of 86, 52 and 32 mm, 12-well tissue culture plates with a diameter of 22 mm) to ensure a constant filling height of 2.5 mm, so that differences in the vertical distribution of *Ceratium* due to the sinking of the cells were approximately the same in all treatments (Table I).

Ascomorpha was allowed to feed in the different *Ceratium* concentrations for 12 h. After the feeding period, the surviving animals were counted and it was assumed that any deaths had occurred in the middle of the feeding period. However, in most of the experiments, no mortality was observed. All replicates were fixed with a few drops of Lugol's solution and then transferred to 50 ml sedimentation chambers. After a sedimentation period of 12 h, the samples were examined under an inverted microscope at 50-fold magnification, and the *Ceratium* cells were counted in two categories: first, *Ceratium* cells that looked healthy and did not show any losses of the cell contents; second, obviously dead *Ceratium* (i.e. cells with losses of plasma), empty thecae or fragments. Clearance rates, CR ($\mu\text{l animal}^{-1} \text{ day}^{-1}$), were calculated using the formula:

$$CR = 24 (\ln D - \ln D_C) V / (nt)$$

Table I. Experimental design used for the determination of the functional response of *A. ovalis*

Food density (cells ml^{-1})	Diameter of Petri dish (mm)	Filling volume (ml)	<i>Ascomorpha</i> (no. per vessel)	Replicates
5	86	15	3	7
15	52	5.5	3–4	6
20	52	5.5	3	6
35	33	2.3	4–6	5
50	33	2.3	3–6	6
75	52	5.5	12–22	7
100	22	1	3	7
150	33	2.3	9–10	6
200	33	2.3	10	7

where D is the number of dead *Ceratium* in the experimental treatment, D_C is the average number of dead *Ceratium* in the controls, V is the volume of the experimental vessel (μl), n is the number of *Ascomorpha* and t is the incubation period (h). Food depletion was usually $<10\%$, hence corrections for average cell concentrations were not necessary.

Feeding rates, F (cells animal $^{-1}$ day $^{-1}$), were calculated from the clearance rates using the formula:

$$F = CR \cdot C$$

where C is the concentration of *Ceratium* (cells μl^{-1}).

To test whether the functional response of *Ascomorpha* is Holling Type 1 or Type 2, a rectilinear Blackman model (Condrey, 1982), a curvilinear Michaelis–Menten model (which is mathematically identical with Holling's 'disc equation') and a curvilinear model according to Ivlev (1961) were fitted to the data. For the curvilinear models, the fits were made directly to the untransformed data by iterative non-linear regression. The rectilinear Blackman model was fitted by linear regression on two straight lines, one below and one above the ILL (Rigler, 1961). To separate between these two regions, linear regressions for low food concentrations were calculated, successively adding data points for higher food concentrations until a reduced correlation coefficient indicated that the ILL was exceeded (Rothhaupt, 1990). To compare the quality of the model fits, the following criterion was applied: the best model should have the lowest sum of squares for error (SSE). The significance of differences in variances was tested by two-tailed F tests for dependent samples on the mean square errors (MSEs) comparing each Type 2 model ('disc equation', Ivlev) to the Type 1 model (Blackman).

Experiment 2 (components of prey capture and handling times)

All measurements were made by direct observations on 12 h pre-starved animals under a dissecting microscope at 6- to 20-fold magnification. Single *Ascomorpha* were exposed to a *Ceratium* concentration of ~ 200 cells ml^{-1} in a small polystyrene Petri dish. Since the animals were hungry and the high *Ceratium* concentration provided high encounter rates, it took only a few minutes until an algal cell was captured. Each animal was used only once.

When swimming *Ascomorpha* contacted *Ceratium* with their corona, it was considered as an encounter. A successful attack was recorded when the *Ceratium* cell was captured. Sometimes *Ascomorpha* showed a conspicuous swimming behaviour (rapid spiral movements) shortly after an encounter with *Ceratium*. Such events were recorded as unsuccessful attacks. However, in some rare cases, it was observed that this 'searching behaviour' led to the capture of the previously escaped *Ceratium* cell. Capture and ingestion (extraction of the cell contents) of *Ceratium* are easily visible and were also recorded. The handling time was considered to be the time from capture of a *Ceratium* cell to release after extraction of cell contents.

Experiment 3 (mathematical model for theoretical encounter rates and estimation of model parameters)

Theoretical encounter rates were calculated using the mathematical model of Gerritsen and Strickler (1977). The model was modified including an average prey radius R_p to the encounter radius of the predator R , since in the model of Gerritsen and Strickler (1977) prey is assumed to be dimensionless. This led to the equation:

$$Z = (\pi \cdot N_p (R + R_p)^2/3) \cdot ((u^2 + 3v^2)/v)$$

where Z is the encounter rate of *Ascomorpha* with *Ceratium* (cells s^{-1}), N_p is the prey concentration (cells μm^{-3}), u is the swimming speed of *Ceratium* ($\mu m s^{-1}$) and v the swimming speed of *Ascomorpha* ($\mu m s^{-1}$). R and R_p both have the dimensions μm .

The parameters R and R_p were estimated using an image analysis system (SIS = Soft Imaging Software), which was connected to an inverted microscope. For *Ascomorpha*, the breadth of the corona from dorsal view was considered as the diameter ($2 \cdot R$) of the encounter field. For *Ceratium*, total length L and maximum breadth B were measured, and the form of the cell was abstracted to a pyramid. Surface areas of this pyramid were averaged and R_p was calculated as the radius of a circle with the same area.

Swimming speeds of *Ascomorpha* and *Ceratium* were estimated using a 0.81 mm² square grid under a dissecting microscope. A bootstrap program (Krambeck, unpublished) allowed calculations from squares s^{-1} into $\mu m s^{-1}$: if A was the length of the square, the conversion factor F was $F = 0.866 \cdot A$. Hence, the average distance moved was 0.779 mm when *Ascomorpha* or *Ceratium* were crossing a square of the grid. This method gave rough estimates of the swimming speeds, although vertical movements of the organisms were neglected.

Experiment 4 (effect of food density on the exploitation of single food items)

In this experiment, the extent to which single *Ceratium* cells were extracted by *Ascomorpha* at different food densities was measured. All animals were 4 days old and were previously fed *ad libitum*. At the fifth day, 50 animals were placed in Petri dishes filled with 20 ml WC medium and *Ceratium* in concentrations of 20, 30, 60 and 100 cells ml^{-1} . After an incubation period of 24 h, 18 randomly selected animals from each treatment were placed in groups of three animals per well into 24-well tissue culture plates containing 1 ml WC medium and exactly 50 *Ceratium* cells. Each treatment had six replicates. The animals were then allowed to feed for 1.5 h and afterwards all samples were fixed with 4% formaldehyde.

Measurements on the size and contents of *Ceratium* cells were made with the image-analysis system as in experiment 3. Every *Ceratium* from which the cell contents were extracted was viewed at 250-fold magnification. The area covered by the remaining cell contents, F_R , and the area covered by the silhouette of the

theca, F_T , were measured. Only F_T was measured when the *Ceratium* cell was totally empty. To estimate the original contents of a *Ceratium* cell, 10 randomly selected undamaged cells were measured for the areas covered by the cell contents, F_F and for F_T . Thus, the proportion $Q = F_F/F_T$ could be calculated, which allows an estimate of the original content of an extracted *Ceratium* cell: $F_F = Q \cdot F_T$. For *C.furcoides*, grown under culture conditions as described above, the value for Q was 0.75. The difference between F_F and F_R is F_S , the amount of cell content that has been sucked out by *Ascomorpha*. Additionally, the percentage exploitation of a *Ceratium* cell I_E (%) could be calculated: $I_E = F_S/F_F \cdot 100$. To examine whether the exploitation of *Ceratium* cells was correlated to food concentration, the slope of the regression line of I_E versus food concentration was tested to see whether it was significantly different from zero.

Results

The feeding rates of *Ascomorpha* showed a hyperbolic increase with increasing concentrations of *Ceratium* (Figure 2a). A plateau was reached at 100 cells ml^{-1} at ~ 8 cells $\text{animal}^{-1} \text{ day}^{-1}$. The maximum clearance rate was $165 \mu\text{l ind.}^{-1} \text{ day}^{-1}$ (Figure 2b). The handling time ranged from 1 to 7 min (Figure 3), 66% of all interactions observed had a duration of 2.5–4.5 min and the mean handling time was 3 min.

The exploitation of single *Ceratium* cells was significantly negatively correlated to food density ($P < 0.01$). At high *Ceratium* concentrations, such as 100 cells ml^{-1} , exploitation was very variable and from several cells only very small amounts down to 5% were extracted, whereas at low *Ceratium* concentrations, such as 20 cells ml^{-1} , at least 40% of the contents were sucked out from nearly every cell (Figure 4). Also, the number of *Ceratium* consumed by the experimental animals varied at the different food concentrations. During the incubation period of 1.5 h, the 18 *Ascomorpha* pre-fed at 20 cells ml^{-1} together consumed 30 *Ceratium*, whereas the 18 *Ascomorpha* pre-fed at 30, 60 and 100 cells ml^{-1} consumed only 20–21 *Ceratium* together. These differences suggest that the animals pre-fed at 20 cells ml^{-1} were more hungry than the animals of the other treatments and showed a higher attack rate after an encounter with a *Ceratium* cell.

Combining the results of experiment 1 and experiment 4, feeding rates in terms of ingested carbon per animal and time were calculated (Figure 5). For food densities between 20 and 100 cells ml^{-1} , the regression line fitted through the values of Figure 4 was used ($y = -0.18x + 71.4$, $R^2 = 0.0753$). Above food densities of 100 cells ml^{-1} , exploitation was assumed to be constant at 53.4% as there was little difference between 60 and 100 cells ml^{-1} . Both curvilinear models had lower SSEs than the rectilinear Blackman model, but these differences were not significant (F test; Table II). However, the Blackman model would produce a significant positive y intercept ($P = 0.016$), which by definition is not possible since feeding rates cannot be positive if no food is present.

Another sign for the superiority of curvilinear Type 2 models was the marginally significantly negative slope of the regression line fitted through the measured clearance rates (Figure 2b) between 5 and 100 cells ml^{-1} ($P = 0.063$). In rectilinear

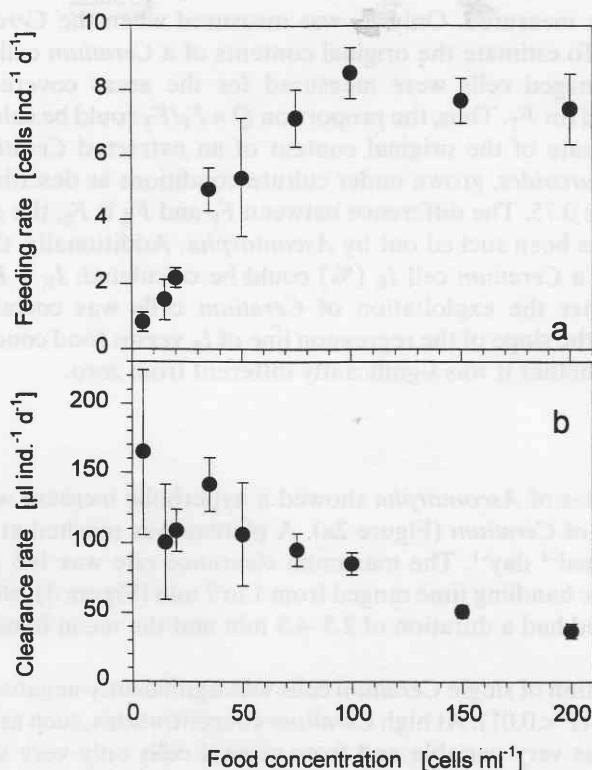


Fig. 2. Functional response of *A. ovalis* with *C. furcoides* as food algae. (a) Feeding rates of *A. ovalis* at different food concentrations. (b) Clearance rates of *A. ovalis* at different food concentrations (means \pm SE; $n = 5-7$).

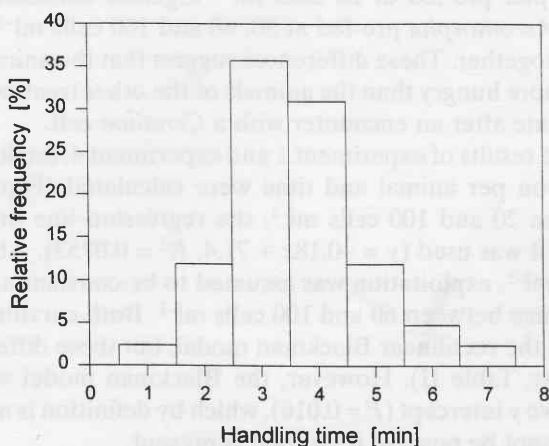


Fig. 3. Handling times in *A. ovalis* (i.e. time required for the capture of a *Ceratium* cell and for the extraction of the cell contents). The measured handling times were grouped into intervals of 1 min length. The mean handling time was 3 min ($n = 42$).

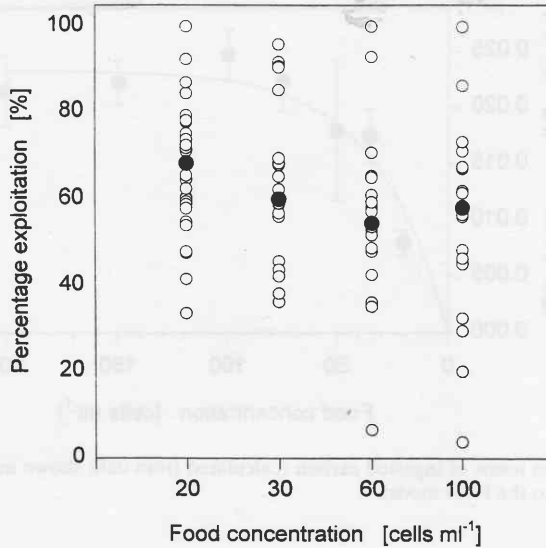


Fig. 4. Exploitation of single *Ceratium* cells by *A. ovalis* at different food concentrations. Open circles, measured values; closed circles, medians (20 cells ml⁻¹; $n = 34$; other concentrations; $n = 20, 21$).

Table II. Quality of the models fitted to the data in Figure 5. Three models were tested: Blackman model (rectilinear, Holling Type 1), 'disc equation' (curvilinear, Holling Type 2) and Ivlev model (curvilinear, Holling Type 2). For each model, the sum of squares for error (SSE) and the mean square error (MSE) are given. P is the P value of the F test for the MSEs of both curvilinear models compared with the MSE of the Blackman model (d.f. = 56)

	Blackman	'Disc equation'	Ivlev
SSE	8.66×10^{-4}	8.43×10^{-4}	7.98×10^{-4}
MSE	2.06×10^{-5}	2.01×10^{-5}	1.9×10^{-5}
P		0.463	0.382

Type 1 functional responses, the slope of this line is zero (Frost, 1980) because the clearance rates of Type 1 feeders are constantly maximal below the ILL, and decrease only after the ILL is exceeded. However, in Type 2 feeders, clearance rates have their highest values only at the lowest food concentrations, and decrease immediately as food concentration increases.

Theoretical encounter rates calculated from the estimated parameters of Table III increased linearly with food concentration (Figure 6, broken line) and were somewhat higher than the feeding rates at low food concentrations. However, not every *Ceratium* cell encountered was successfully captured and extracted by *Ascomorpha* (Table IV), although the rotifers used in this experiment were 12 h pre-starved and thus highly motivated to feed. The probability of ingestion following an encounter was $P_{IE} = 0.31$. Multiplication of the theoretical encounter rates by P_{IE} gave the 'maximal successful encounters' (Figure 6, straight line), which can be taken as a measure for the highest feeding rate that would be possible for a given food concentration. These maximal successful encounters for

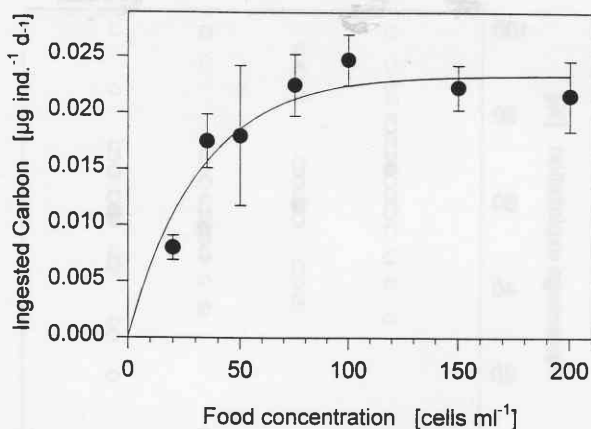


Fig. 5. Feeding rates in terms of ingested carbon (calculated from data shown in Figures 2a and 4). Line fitted according to the Ivlev model.

Table III. Parameter estimates for the calculation of theoretical encounter rates according to a mathematical model of Gerritsen and Strickler (1977). Means, standard deviations (SD) and number of observations (n) are given. R is the encounter radius of *Ascomorpha*, R_p is the encounter radius of *Ceratum*, v is the average swimming speed of *Ascomorpha* and u is the average swimming speed of *Ceratum*.

Parameter	Mean	SD	n
R (μm)	24.9	2.3	50
R_p (μm)	43	3.9	30
v ($\mu\text{m s}^{-1}$)	853	134	29
u ($\mu\text{m s}^{-1}$)	58	14	10

Table IV. Components of prey capture in *A. ovalis*. P_A is the probability of attack following encounter, P_C is the probability of capture following attack and P_I is the probability of ingestion following capture.

		n
P_A	0.603	58
P_C	0.685	35
P_I	0.75	24

food concentrations up to 35 cells ml^{-1} were very close to the actual feeding rates, suggesting that feeding rates at these low food concentrations were limited by low encounter rates.

Discussion

The planktonic rotifer *A. ovalis* feeds on the dinoflagellate *C. furcoides*, which are very large prey, their cell contents are probably almost as large as the gut capacity of their predator. In this respect, the maximum feeding rate of ~ 8 cells animal^{-1}

day⁻¹ seems to be quite high. Additionally, the material ingested is probably of high nutritional quality because poorly digestible substances, such as cell wall material, are avoided by the sucking feeding mode of *Ascomorpha*. However, most of the time, *Ceratium* cells are not completely sucked out, hence the actual amount of prey biomass ingested per day is lower than the summed cell contents of eight *C.furcoides*. The maximum clearance rate of 165 $\mu\text{l animal}^{-1} \text{ day}^{-1}$ is in accordance with reported clearance rates of other planktonic rotifers (Starkweather, 1980b).

There are some similarities in the foraging behaviour between *Ascomorpha* and other macrophagous rotifers. Similar to *Asplanchna* (Gilbert, 1980), the *Ascomorpha* were swimming randomly and only responded to prey when their corona physically contacted with them (personal observation). Additionally, they did not orient to prey at a distance and therefore appear to depend upon chance encounters for prey location. The handling time (time from the first contact with prey to ingestion) of *Ascomorpha* was much longer than that of *Asplanchna*. Gilbert and Stemberger (1985) reported 30 ms for the time between the first contact and the initiation of a feeding response (recognition of prey) and approximately another 50 ms for swallowing the prey through the mouth into the expanding mastax (ingestion of prey). The time for recognition of prey may be similar in *Ascomorpha*: during direct observations, no time lag between encounter and capture was recognizable. However, the time required for prey ingestion was much longer in *Ascomorpha* due to the need for piercing the hole first.

The shape of the functional response curve was better described by curvilinear Type 2 than rectilinear Type 1 models. In a Type 2 feeder, the handling time is commonly regarded as the main factor limiting ingestion rates. Compared to other rotifers, *Ascomorpha* spend a considerably longer time on the ingestion of one single prey item. Nevertheless, handling time cannot be the factor limiting ingestion rates since one individual consumes up to 8 cells day⁻¹ on average and the time necessary to do this amounts to only 24 min, which is ~1.6% of the total time.

Saturation effects, as implied in the Ivlev model, may be more important in shaping the functional response curve of *Ascomorpha* than handling times. In experiment 4, *Ascomorpha* attacked 50% more *Ceratium* cells when pre-fed at the concentration of 20 cells ml⁻¹ than when pre-fed at the higher concentrations. This suggests that the 'motivation to hunt' decreases with increasing food concentrations, but this decrease begins at food concentrations that are considerably lower than those permitting the highest ingestion rates. At very low food concentrations, feeding rates in *Ascomorpha* seem to be limited by low encounter rates, since the actual feeding rates were very close to the 'maximal successful encounters' (Figure 6).

Feeding at low food concentrations in *Ascomorpha* is a discontinuous process: *Ascomorpha* may starve for considerable time periods due to a lack of encounters with *Ceratium*. However, after having just one or two successful prey contacts the gut is full, not permitting any further ingestion for a now following 'satiated period'. 'Gut passage time' is probably the wrong term for this period, since the

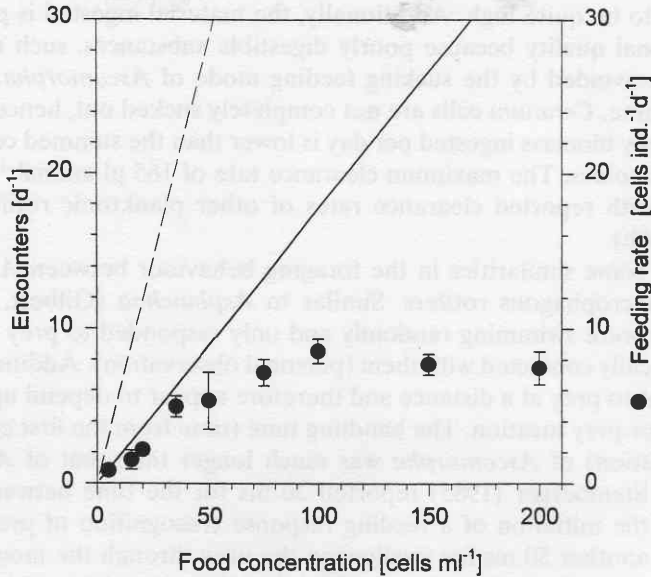


Fig. 6. Feeding rates (dots; same data as in Figure 2a), encounter rates (broken line) as calculated from the mathematical model of Gerritsen and Strickler (1977), and 'maximal successful encounters' (straight line) calculated as encounter rates multiplied by P_{IE} (probability of ingestion following an encounter).

extracted contents of *Ceratium* are digested intracellularly and indigestible substances are stored in specialized tissues (Remane, 1929). I do not have quantitative data on the length of this 'satiated period', but it seems plausible that after the gut of *Ascomorpha* has been filled totally, the attack rate is extremely low for subsequent encounters with *Ceratium* as there would be no gain of energy (no material can be ingested), but costs for piercing the hole into the cell wall of *Ceratium*.

One explanation for the decrease in exploitation of single prey units at high prey densities can be an optimal feeding strategy. Such behaviour was shown for the hemipteran *R. dispar* (Bailey, 1986), which is also a macrophage with an extracting feeding mode. At high prey densities, these predators also release their prey and restart searching before the prey is totally extracted, as it would take more time to extract the remaining contents than to find the next prey, from which cell contents can be extracted very rapidly at the beginning. Such behaviour can be interpreted as a maximizing of energy input per unit time. However, such a theory cannot apply to *Ascomorpha*, as the searching time, which depends on the prey concentration, and the time needed for piercing the hole through the cell wall of a *Ceratium* (~3 min), is usually much longer than the time required for sucking out the cell contents (~10–20 s). Hence, the amount of prey biomass consumed per unit time would be maximized if every *Ceratium* which was captured and opened were completely extracted. The decrease in the exploitation

of single prey items at high prey concentrations in *Ascomorpha* may be explained by a saturation effect, in which more encounters with *Ceratium* than necessary occur at high prey concentrations. At the time of a subsequent encounter, the gut of an *Ascomorpha* is still partly filled and so only a fraction of cell contents can be sucked from the captured *Ceratium*.

In conclusion, one basic feature of organisms with very pronounced macrophagous feeding, like *Ascomorpha*, may be that even at constantly low prey concentrations, the individual continuously goes through periods of starvation and satiation. In contrast, microphages are always at the same state of hunger at constantly low prey concentrations because they continuously ingest algae, but the gut is never completely filled below the ILL.

Acknowledgements

I thank S.E. Mitchell, M. Boersma, N. Weider and W. Lampert for constructive comments on the manuscript and linguistic help, B. Meyer for providing the *A. ovalis* stock, and K.-O. Rothhaupt, who gave helpful suggestions on the design of the 'exploitation' experiment.

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Received on July 30, 1997; accepted on January 26, 1998