

Functional responses of the rotifers *Brachionus calyciflorus* and *Brachionus rubens* feeding on armored and unarmored ciliates

Abstract—Density dependent grazing experiments were performed to investigate the feeding behaviour of the rotifers *B. calyciflorus* and *Brachionus rubens* on the ciliates *Coleps* sp. and *Tetrahymena pyriformis*. The ciliates are similar sized but differ in their body surface texture. The surface of *Coleps* sp. consists of calcareous plates while *T. pyriformis* is a soft bodied ciliate. The two rotifers, which differ in their body size, were allowed to feed for 4 h on the ciliates, and the clearance and ingestion rates were calculated to fit functional response models. For *B. calyciflorus* fed with *Coleps* sp., the curvilinear functional response Type 2 gave the best fit to the data (maximal clearance and ingestion rate of 30 $\mu\text{l rotifer}^{-1} \text{h}^{-1}$ and 5.7 ciliates $\text{rotifer}^{-1} \text{h}^{-1}$), whereas the functional response for the ciliate *T. pyriformis* changed to the rectilinear Type 1 model (maximal clearance and ingestion rate of 8.5 $\mu\text{l rotifer}^{-1} \text{h}^{-1}$ and 4.2 ciliates $\text{rotifer}^{-1} \text{h}^{-1}$). In contrast, *B. rubens* could not eat *Coleps* sp., but when fed with *T. pyriformis* a functional response Type 2 was observed (maximal clearance and ingestion rate of 8 $\mu\text{l rotifer}^{-1} \text{h}^{-1}$ and 3.3 ciliates $\text{rotifer}^{-1} \text{h}^{-1}$). There is evidence that the surface texture of prey organisms influences the type of functional response. The change from a Type 2 (*Coleps* sp.) to a Type 1 model (*T. pyriformis*) for *B. calyciflorus* suggests that the handling time for the armored *Coleps* sp. is longer than for the soft bodied *T. pyriformis*. The smaller rotifer *B. rubens*, which generally prefers smaller food items than *B. calyciflorus*, was able to ingest the soft bodied *T. pyriformis* but needed a longer handling time for this ciliate than did *B. calyciflorus*. The hard surface texture of *Coleps* sp. probably prevented its ingestion by *B. rubens*.

Rotifers as suspension-feeders are able to regulate their food uptake by modification of their feeding behaviour with respect to prey density and type of prey. The density-dependent feeding relationship (functional response), expressed by clearance or ingestion rates, can be described by three basic models (Holling's Type 1, 2, and 3) which represent different ecological feeding strategies (Holling 1959). The rectilinear Type 1 model describes a feeding process where the handling time of prey items is negligible. In contrast, the curvilinear functional response Type 2 according to Holling or the modified Ivlev Type 2 model (Ivlev 1961) is considered to be typical for larger prey items where the handling time is longer. The main difference between the different Type 2 models lies in the estimate of the maximal ingestion rate. The sigmoidal Type 3 model results from reduced encounter rates at low prey densities.

For rotifers, several feeding experiments with various prey items were summarised in the review of Starkweather (1980). Although there is disagreement about the magnitude of clearance and ingestion rates, a general pattern of feeding behaviour arises especially for brachionid rotifers. Studies by Rothhaupt (1990a) with *B. calyciflorus* and *B. rubens* have demonstrated that the type of functional response changes with increasing algal size. Above an optimal prey size the

feeding behaviour changes from a Type 1 functional response to a Type 2 model. This implies that the handling time increases with prey size. *Brachionus* species seem to interrupt the feeding process to screen their mouth with their pseudotrochal cirri when feeding on large prey, which leads to a longer handling time of prey (Gilbert and Starkweather 1978).

Many rotifer species are described as herbivores (Koste 1978), but there is evidence from laboratory and field studies that rotifers are capable to feed on small prey such as bacteria as well as on large prey such as ciliates (for review see Arndt 1993; Sanders and Wickham 1993). However, there are only a few laboratory studies which document the predatory effects of rotifers on ciliates (Maly 1975; Gilbert and Jack 1993), although many ciliates are within the food size range of rotifers (Pourriot 1977). So far, functional response relationships between rotifers and ciliates are unknown. However, the different shape and surface texture of ciliates and their complex mobility or escape responses make them very different prey items as compared to algae or bacteria.

In the experiments we now report, the type of functional response was studied for the rotifers *B. calyciflorus* and *B. rubens* feeding on the ciliates *Coleps* sp. and *T. pyriformis*. These closely related rotifer species differ in body length and prey size preferences. *B. calyciflorus* prefers algae with an equivalent spherical diameter (ESD) of 10 μm , while the smaller *B. rubens* feeds more efficiently on prey with an ESD of 5 μm (Rothhaupt 1990b). The two ciliates are of similar size but differ in their surface texture. *T. pyriformis* is a soft bodied ciliate while the surface of *Coleps* sp. consists of calcareous plates with short posterior spines. Furthermore, both ciliate species have a similar swimming behavior. We will address the question as to how *B. calyciflorus* and *B. rubens* differ in their functional response for ciliates of similar size, shape and mobility, but which differ in their surface texture. We chose the armored ciliate *Coleps* sp. as a prey organism since it is commonly found in lakes throughout the year (Pace 1982; Salbrechter and Arndt 1994). The counterpart *T. pyriformis* is not a typical pelagic species, but was chosen as a soft bodied species of similar size, shape, and mobility. Problems in choosing a type of functional response will be discussed in relation to plausibility.

B. calyciflorus (adult lorica length of 250–300 μm) and *B. rubens* (adult lorica length of 200–250 μm) were cultured in batch cultures with filtered water (<0.2 μm) from Lake Müggelsee (Berlin, Germany) and fed with the green algae *Monoraphidium minutum*. The rotifers were transferred into new food suspensions weekly. *M. minutum* was grown in Z/4 medium (Zehnder and Gorham 1960) in a frequently diluted batch culture. *Coleps* sp. (length: 40–45 μm , width 10–15 μm) was isolated from Lake Müggelsee, cultured in filtered lake water (<0.2 μm) and fed with *Cryptomonas phaseolus*. *C. phaseolus* was grown in WC medium (Guil-

lard and Lorenzen 1972) in a frequently diluted batch culture. The ciliate *T. pyriformis* (length: 40–45 μm , width 10–15 μm) was grown in a medium consisting of yeast and bacteria. A tablet of yeast (Fa. Tartex) and a small piece of banana skin (1 cm^2) was suspended in 300 ml sterilized tap water for 24 h. Both ciliates were transferred into fresh medium weekly. All cultures were incubated at $20^\circ\text{C} \pm 1^\circ\text{C}$ in a 16:8 h light:dark regime.

To evaluate the functional response of brachionids for ciliate uptake, we established a series of prey densities between 20–1,300 ciliates ml^{-1} . Ciliates were separated from their food suspension by centrifugation (1,000 rpm) for 10 min. After centrifugation a wad of cotton wool was bathed in the upper region of the centrifuged suspension. The ciliates in the pellet after centrifugation swam through the cotton wad into the oxygen-rich surface layer from which they were carefully taken to prepare the prey dilutions. The series of densities were set up by combining appropriate volumes of ciliate suspensions and filtered ($<0.2 \mu\text{m}$) Müggelsee water. Seven to 13 different dilutions were used in each predator/prey combination (*B. calyciflorus*/*Coleps* sp.; *B. calyciflorus*/*T. pyriformis*; *B. rubens*/*Coleps* sp.; *B. rubens*/*T. pyriformis*). Experiments were run in macrotiter plates (3×4 chambers with a volume of 6 cm^3 each) with four replicates per dilution. The rotifers were separated from their food suspension via filtration through a 70- μm mesh. Ten well-fed rotifers, mainly without eggs, were added to 1 ml of the respective ciliate prey suspension. The experiments were run for 4 h at 20°C and at constant light conditions. Experimental set ups without rotifers served as controls.

Samples were fixed with acid Lugol's solution (10%) and all rotifers and at least 20% of the ciliates were counted under a stereoscope (Nikon, PFX) in a Sedgewick-Rafter cell at $\times 20$ magnification. The prey densities at the end of the experiments were never less than 75% of the initial density. Clearance and ingestion rates were calculated according to Peters (1984).

Holling's (1959) rectilinear functional response Type 1 was fitted to the ingestion rate data by linear regression. To separate between the linear increase of ingestion rates and the constant rates above the incipient limiting level (ILL), data points were added successively for higher concentrations until a reduced correlation coefficient indicated that the ILL was exceeded. Functional response Type 2 and 3 models were fitted by iterative nonlinear regression procedures. For functional response Type 2 the model of Holling (1959) and the modified model of Ivlev (1961) were applied. Data analysis was performed using SPSS for Windows 6.1.

For each model type, the maximal ingestion rate (I_{max}), and the ciliate density at which half the maximal ingestion rate was reached, were calculated according to the fitted ingestion rate curves. To evaluate the type of functional response, the ingestion rates of each functional response curve were transformed to clearance rates by dividing by the respective ciliate density. We used several criteria to determine the quality of the model fits: the coefficient of determination (R^2), the residual sum-of-squares for error (SSE), and the mean-square error (MSE). In addition, residuals were tested for normal distribution with the Kolmogorov–Smirnov test (K–S test), the observed and predicted clearance rates were

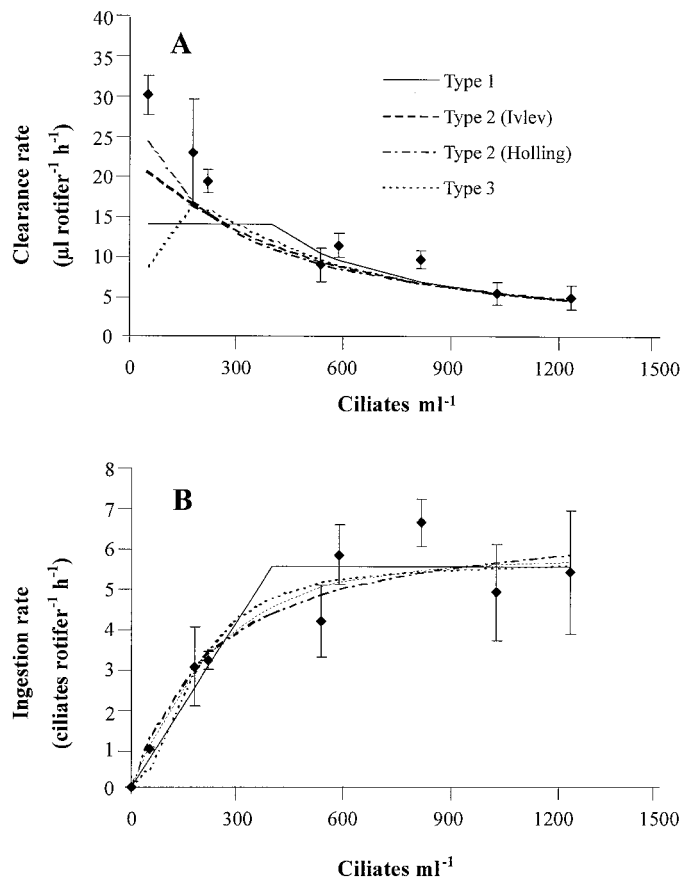


Fig. 1. (A) Clearance and (B) ingestion rates (\pm standard error) of *B. calyciflorus* feeding on *Coleps* sp., and the fitted model Types 1, 2, 3.

tested for significant differences via Mann–Whitney U test (M–W test), and the differences between the models were tested by a two-tailed F -test on the residuals. The K–S test and the M–W test revealed good fits for all model types and all predator/prey combinations ($P > 0.05$), whereas no differences were found between the models via F -test ($P > 0.05$) apart from two cases for the predator/prey combination *B. rubens*/*T. pyriformis*. Therefore, the determination of the appropriate model was based on the R^2 , the SSE, the MSE, and the plausibility of the results.

B. calyciflorus/*Coleps* sp.—Based on clearance rates, the Holling Type 2 model gave the best fit for *B. calyciflorus* feeding on *Coleps* sp. (Fig. 1A). The R^2 was highest, and the SSE and MSE values were lowest for this model type (Table 1). However, the F -test indicated no significant differences between the models ($P > 0.05$). A maximal clearance rate of $30.2 \mu\text{l rotifer}^{-1} \text{h}^{-1}$ was measured at a ciliate density of 50 ciliates ml^{-1} . *B. calyciflorus* showed a hyperbolic increase in ingestion rates with increasing *Coleps* sp. densities (Fig. 1B). Based on ingestion rates we found no differences between the four models (R^2 always approximated 0.91, Table 2). Predictions for maximal ingestion rates (I_{max}) and ciliate densities at $I_{\text{max}}/2$ differed between the two Type 2 models and were lower based on the Ivlev Type 2

Table 1. Quality of the fitted functional response curves based on clearance rates. R^2 is the coefficient of determination, SSE is the residual sums-of-squares for error, MSE is the mean-square-error. FR refers to functional response. Asterisks denote that the associated regression coefficients are significantly different from zero ($P < 0.05$). Bold numbers indicate the best model fit.

Predator	<i>B. calyciflorus</i>						<i>B. rubens</i>		
	<i>Coleps</i> sp.			<i>T. pyriformis</i>			<i>T. pyriformis</i>		
FR-Type	R^2	SSE	MSE	R^2	SSE	MSE	R^2	SSE	MSE
Type 1	0.77*	231.4	49.4	0.47*	47	3.6	0.47	11.35	2.9
Type 2									
Holling	0.97*	47.1	13.4	0.15	120	9.3	0.93*	4.36	0.8
Ivlev	0.97*	87.8	21.4	0.12	102	7.8	0.93*	3.07	1.2
Type 3	0.29	368.8	67.6	0.02	106	8.1	0.27	64.11	14.0

model. This was generally the case for all predator/prey combinations (Table 2). It is striking that the Holling's Type 2 model always provided higher maximal ingestion rates than the Ivlev model. However, regarding the ingestion rates at high ciliate densities (Fig. 1B, 2B, 3B) the predicted maximal ingestion rates of the Ivlev model seem to be more appropriate to describe the data (Table 2). Our findings agree with the results of Stelzer (1998), who found for *Ascomorpha ovalis* feeding on *Ceratium*, that the Ivlev Type 2 model best described the data. As a functional response Type 3 model was not observed in either predator/prey combination, it will not be discussed further.

B. calyciflorus/T. pyriformis—For *B. calyciflorus* feeding on *T. pyriformis*, the best fit was given by the rectilinear Type 1 model based on clearance rates (Table 1; Fig. 2A). However, the F -test was not significant in any case ($P > 0.05$). Given the high variation in the clearance rates between replicates, especially at low prey densities, a range of constant maximal clearance rates was hard to define (Fig. 2A). Calculated maximal clearance rates for functional response Types 1 and 2 varied between 8.4 and 13.6 $\mu\text{l rotifer}^{-1} \text{h}^{-1}$.

B. rubens/Coleps sp.—*B. rubens* was not able to feed on the armored *Coleps* sp. Ciliate densities from 50 to 850 ciliates ml^{-1} were tested and ingestion rates ranged from -0.8 to 1.9 ciliates $\text{rotifer}^{-1} \text{h}^{-1}$, but were mostly close to zero.

B. rubens/T. pyriformis—The functional response between *B. rubens* and *T. pyriformis* was best described by the curvilinear Type 2 models (Table 1; Fig. 3A). Significant differences were found between the Type 1 and the Type 3 model ($F = 25.71$, $P < 0.01$) and between the two Type 2 models and the Type 3 model (Holling: $F = 24.43$, $P < 0.01$; Ivlev: $F = 21.42$, $P < 0.01$). A maximal clearance rate of 9.3 $\mu\text{l rotifer}^{-1} \text{h}^{-1}$ was calculated at a density of 17 ciliates ml^{-1} .

Model fits—The determination of functional response types is of importance when predicting the competition between organisms, and the grazing impact under natural conditions, or when investigating aspects of food quality. The main differences between the models are manifested at very low prey densities where ingestion rates do not differ much between the different models. We therefore used clearance rates to determine the appropriate model, since clearance rates reflect the differences between the models at low densities.

As the width of the two ciliate species (10–15 μm) fell within the food size range of *B. calyciflorus* (about 10 μm ESD), but lay above the preferred size range of *B. rubens* (about 5 μm ESD) (Rothhaupt 1990b), the type of functional response was assumed to differ for the two brachionids. Given that both *Brachionus* species grasp the ciliates from the anterior or posterior end, a Type 1 model should be determined for *B. calyciflorus* while a Type 2 model would be plausible for *B. rubens* (Rothhaupt 1990a). Indeed, predation

Table 2. Maximal ingestion rates (I_{max} , ciliates $\text{rotifer}^{-1} \text{h}^{-1}$) and ciliate densities (ciliates ml^{-1}) where ingestion rates were half the maximal as predicted from the different functional response models. R^2 is the coefficient of determination. FR refers to functional response. Asterisks denote that the associated regression coefficients are significantly different from zero ($P < 0.05$). Bold numbers refer to the best model fit.

Predator	<i>B. calyciflorus</i>						<i>B. rubens</i>		
	<i>Coleps</i> sp.			<i>T. pyriformis</i>			<i>T. pyriformis</i>		
FR-Type	I_{max}	Ciliate density at $I_{\text{max}}/2$	R^2	I_{max}	Ciliate density at $I_{\text{max}}/2$	R^2	I_{max}	Ciliate density at $I_{\text{max}}/2$	R^2
Type 1	5.6	200	0.90*	4.2	245	0.87*	3.3	293	0.94*
Type 2									
Holling	7.0	236	0.92*	6.6	455	0.76*	6.6	876	0.98*
Ivlev	5.7	173	0.91*	4.6	240	0.78*	3.4	433	0.98*
Type 3	5.7	176	0.91*	6.0	245	0.82*	4.4	271	0.98*

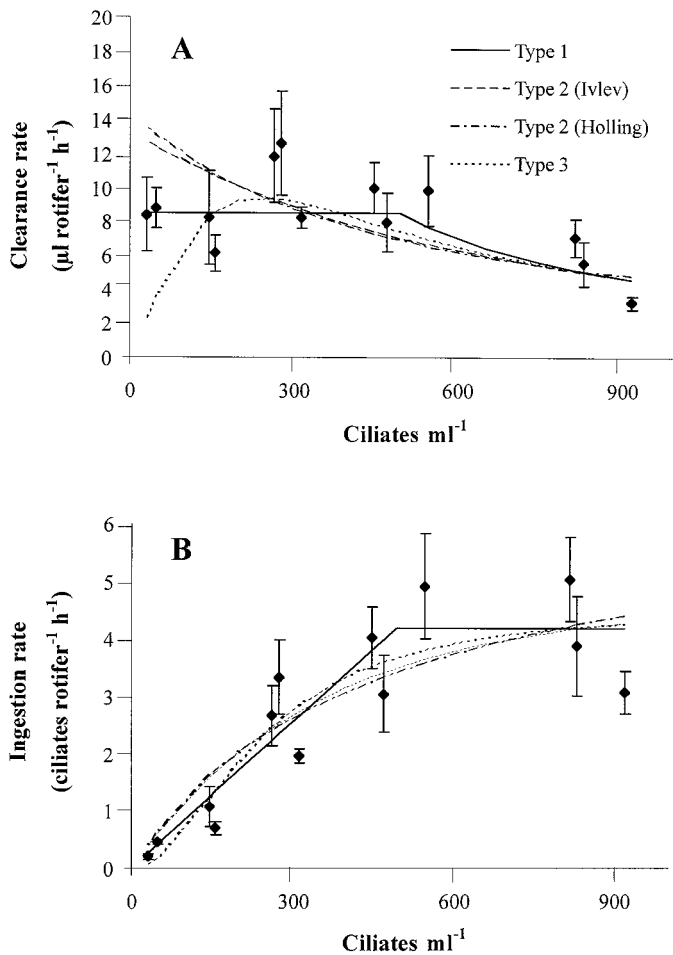


Fig. 2. (A) Clearance and (B) ingestion rates (\pm standard error) of *B. calyciflorus* feeding on *T. pyriformis*, and the fitted model Types 1, 2, 3.

of *B. calyciflorus* on *T. pyriformis* was best described by a Type 1 model (Table 1), while the statistical parameters clearly pointed to a Type 2 model for *B. rubens* feeding on *T. pyriformis*. Although no differences between Type 1 and Type 2 were found via *F*-test in any case, plausibility aspects go along with the above mentioned statistical evidence.

The change from a Type 1 (*T. pyriformis*) to a Type 2 (*Coleps* sp.) model for *B. calyciflorus*, as well as the rejection of *Coleps* sp. by *B. rubens*, suggests that the armored *Coleps* sp. is more difficult to handle than the soft bodied *T. pyriformis*. The hard inflexible body of *Coleps* sp. seems to be a successful defence mechanism against predation by *B. rubens*. Indeed, one can imagine that soft bodied prey organisms can easily be masticated by the malleate mastax, which may not be the case for armored prey organisms.

The differences in the predator/prey interactions for *B. rubens* feeding on *T. pyriformis* versus *Coleps* sp. suggest that the surface texture of the prey determines the upper prey size limit for brachionids. This is consistent with findings by Nadin-Hurley and Duncan (1976) and Rothhaupt (1990b). Rothhaupt (1990b) found that *B. angularis* with a prey size preference of $<5 \mu\text{m}$ ESD was not able to ingest hard plastic

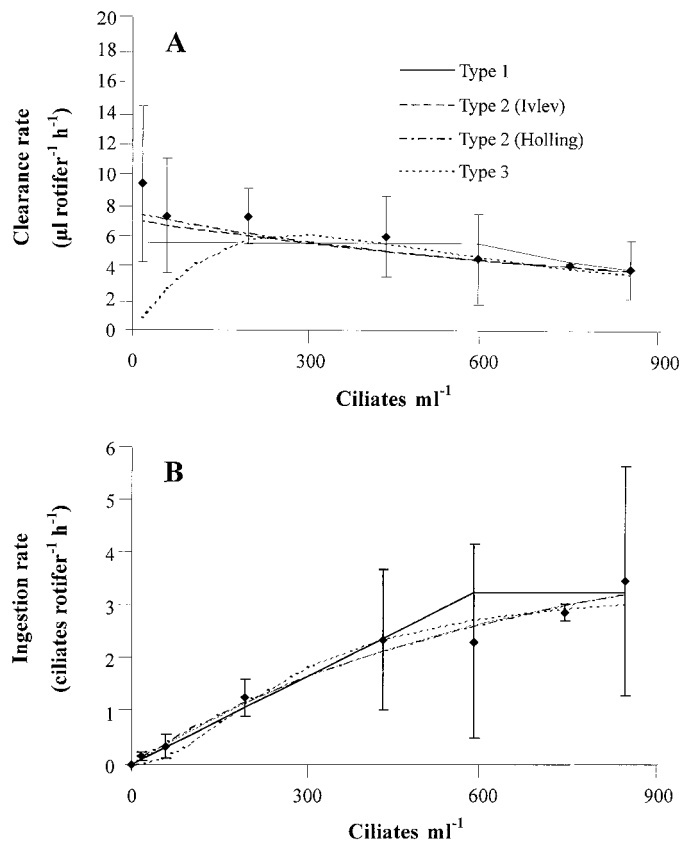


Fig. 3. (A) Clearance and (B) ingestion rates (\pm standard error) of *B. rubens* feeding on *T. pyriformis*, and the fitted model Types 1, 2, 3.

beads of $12 \mu\text{m}$ ESD, but could ingest algae of the same size, although with low efficiency.

Overall, *B. rubens* is a less efficient predator on large ciliates than is *B. calyciflorus*. This was also confirmed by lower clearance and ingestion rates of *B. rubens* for *T. pyriformis* (Fig. 3) as compared to *B. calyciflorus* (Fig. 2). Contrary to expectation, *B. calyciflorus* exhibited lower clearance rates for *T. pyriformis*, a prey organism with a short handling time (Type 1), as compared to *Coleps* sp., a prey organism with a longer handling time (Type 2). This may be related to prey selection. In situ experiments (Mohr and Adrian unpubl. data) demonstrated that *B. calyciflorus* strongly preferred *Coleps* sp. in a seminatural ciliate community. Since clearance rates of *Brachionus* species are highest for preferred food items (Rothhaupt 1990b) positive prey selection may explain why *B. calyciflorus* exhibited higher clearance rates for *Coleps* sp. than for *T. pyriformis* although the soft bodied ciliate was easier to handle. Furthermore, our results correspond with findings of Rothhaupt (1990a) who found lower clearance rates and a higher ILL for *B. calyciflorus* feeding on *M. minutum* with a functional response Type 1 as compared to higher clearance rates and a lower ILL when feeding on *Chlamydomonas sphaeroides* with a functional response Type 2. These findings indicate that a functional response Type 2 does not necessarily lead to lower clearance rates for rotifers.

Ecological relevance—In this study, maximal ingestion rates were reached at high ciliate densities (400–1,750 ciliates ml⁻¹), which are not commonly found in natural ciliate communities (Pace and Orcutt 1981). However, it is known that the ciliate density increases with increasing trophic (Pace 1986) and varies throughout the year (Laybourn-Parry et al. 1990; Müller et al. 1991). Moreover, ciliate communities associated with a deep chlorophyll maximum may exceed densities of 200 cells ml⁻¹ (Adrian, unpubl. data).

The results demonstrate that the closely related rotifers *B. calyciflorus* and *B. rubens* are both able to ingest large soft bodied ciliate prey, but the smaller *B. rubens* had lower maximal ingestion rates. Therefore *B. calyciflorus* should have a higher predatory impact on large ciliates in natural ciliate communities than *B. rubens*.

Another interesting ecological question is related to aspects of energy uptake through ciliates. In the study of Rothhaupt (1990a), *B. calyciflorus* and *B. rubens* had maximal ingestion rates of 18.5 and 13.3 ng C rotifer⁻¹ h⁻¹ when feeding on the green algae *M. minutum*. In our study, ingested carbon for *B. calyciflorus* and *B. rubens* feeding on *T. pyriformis* was somewhat lower, but the ratio of ingested carbon was about the same. *B. calyciflorus* ingested maximal 6.6 ng C rotifer⁻¹ h⁻¹, and *B. rubens* 4 ng C rotifer⁻¹ h⁻¹ (given a volume of 10,000 µm³ for *T. pyriformis* (Fenchel and Finley 1983), and a C: volume ratio of 0.132 pg C µm³ (Turley et al. 1986). The lower C uptake through ciliates may be related to the lower C: volume ratio for ciliates (0.132 pg C µm³; Turley et al. 1986) as compared to algae (0.24 pg C µm³; Reynolds 1984). To what extent population growth or survival of *Brachionus* is affected by that, is yet unanswered.

Our experiments document that for closely related species such as *B. calyciflorus* and *B. rubens*, the type of functional response is both species- and prey-specific. The upper prey size limit is likely to be larger for soft bodied prey as compared to inflexible armored forms of the same size range. As our results are in line with studies of Rothhaupt (1990a,b) for brachionids feeding on algae, it is most likely that besides prey size, the surface texture of the prey generally influences the type of functional response.

Silvia Mohr
Rita Adrian

Institute of Freshwater Ecology and Inland Fisheries
Müggelseedamm 301
12587 Berlin, Germany

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Mass transfer versus kinetic control of uptake across solid-water boundaries

Abstract—We present general nondimensional solutions for uptake across a solid-water boundary, considering the combined influences of mass transfer flux limitation and uptake reaction kinetics. Mass transfer processes are represented by a general mass transfer velocity. Reaction kinetics are represented by first-order and Monod models. Mathematical solutions are well approximated by standard mass transfer models for low values of the derived nondimensional mass transfer velocity and by standard kinetic models for high values. Approximate limiting values of the nondimensional mass transfer velocity are defined for mass transfer control and kinetic control. The intermediate region, where both mass transfer and kinetics influence the solution, is relatively broad for first-order kinetics and Monod kinetics in oligotrophic environments. Both limits decrease as concentration increases in the Monod solution, such that under increasingly eutrophic conditions mass transfer control becomes less important, the intermediate range shrinks, and kinetic control becomes an increasingly good approximation. Example calculations using data from experimental ecosystems indicate that boundary nutrient uptake was mass transfer controlled or intermediate under oligotrophic conditions. Nutrient pulses applied to the systems caused temporary eutrophication, which resulted in temporary kinetic control.

Uptake of nutrients and dissolved gases across solid-water boundaries is an important part of biogeochemical cycling in natural aquatic ecosystems (Pasciak and Gavis 1974; Boudreau and Guinasso 1982; Jorgensen and Revsbech 1985; Riber and Wetzel 1987; Santschi et al. 1990; Koch 1994). Uptake is affected both by mass transfer across the thin layer of fluid adjacent to the boundary and by reaction kinetics at or below the boundary. Uptake tends to be mass transfer controlled when reaction rates are faster than mass transfer rates (Boudreau and Guinasso 1982; Santschi et al. 1991; Thomas and Atkinson 1997). Conversely, uptake tends to be kinetically controlled when mass transfer rates are faster than reaction rates. The relative influences of these two factors have been studied for many different aquatic processes, including diagenesis and dissolution at the sea floor (Boudreau and Guinasso 1982; Santschi et al. 1990), uptake of nutrients by phytoplankton (Pasciak and Gavis 1974), uptake of phosphorus by periphyton (Riber and Wetzel 1987), fixation of carbon at leaf surfaces (Wheeler 1980; Koch 1994), and uptake of nutrients by coral reefs (Patterson et al. 1991; Atkinson and Bilger 1992).

Previous investigators have used several experimental methods for determining whether a reaction is taking place under mass transfer control or kinetic control. Frank-Kamenetskii (1969) advocated estimating the maximum possible mass transfer rate and comparing it to the observed uptake rate. If the observed uptake rate is lower than the maximum mass transfer rate, then uptake is either intermediate between the two extremes or kinetically controlled. If the observed uptake rate is equal to the maximum mass transfer rate, then uptake is mass transfer controlled. Another technique is to measure uptake rate under different flow conditions. If observed uptake rate increases with increased turbulence or mixing, then uptake is either mass transfer controlled or intermediate (Koch 1994; Thomas and Atkinson 1997). Riber and Wetzel (1987) used yet another method in which experiments were performed with the same flow but with varying amounts of biomass at the interface. Because no change in overall flux was observed, they concluded that the process was mass transfer controlled.

These experimental techniques are useful for estimating the influence of mass transfer processes on uptake, but they have two inherent problems. First, they require extensive experimentation to achieve even baseline characterizations. Second, none of these techniques can distinguish the relative degree of mass transfer control versus kinetic control. In particular, it is difficult to distinguish experimentally between the intermediate range, where both mass transfer and kinetics are important, and true mass transfer control or kinetic control.

Another technique that has been applied to the problem is mathematical modeling, assuming a steady state balance in which the uptake rate is equal to the mass transfer rate (Frank-Kamenetskii 1969). Mathematical models of this balance may be distinguished by both the physical configuration of the problem of interest and the choice of kinetic model. Frank-Kamenetskii (1969) and Boudreau and Guinasso (1982) equated expressions for mass transfer across flat boundaries to first-order reaction kinetics. Bilger and Atkinson (1995) equated expressions for mass transfer in coral reef communities to first-order kinetics. Pasciak and Gavis (1974) considered mass transfer to phytoplankton cells with Monod uptake kinetics. Boudreau and Scott (1978) formulated an expression for mass transfer to manganese nodules with Monod kinetics. Wheeler (1980) considered mass transfer to giant kelp leaves with Monod uptake kinetics. Ploug