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Suspension feeding in *Bithynia tentaculata* (Prosobranchia, Bithyniidae), as affected by body size, food and temperature

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Abstract. The suspension feeding of *Bithynia tentaculata* was tested in laboratory experiments. The animals were fed in 1-l aerated glass beakers, and filtration rates were calculated from changes in cell concentrations during the 6-h experiment. Temperature influenced the filtering rate, with minimum values of 5 ml · ind^{-1} · h^{-1} at 5° C and maxima of 17.2 ml · ind^{-1} · h^{-1} at 18° C. Three food species of different size, motility and cell surface characteristics (*Chlamydomonas reinhardii, Chlorella vulgaris* and *Chlorogonium elongatum*) did not affect filtration rates. Suspension feeding increased with increasing food concentrations up to 12 nl · ml^{-1}, above which feeding rate was kept constant by lowering the filtering rates. Even the smallest animals tested (<4 mm body length) were found to be feeding on suspended food at a rate of 2.7 ml · ind^{-1} · h^{-1}, and increasing rates up to 8.4 ml were found in the 6–7 mm size class. All size classes of *Bithynia* showed a circannual fluctuation of their filtration rates. The ecological consequences of *Bithynia*'s ability to switch between two feeding modes, grazing and suspension feeding, are discussed.

Key words: *Bithynia tentaculata* – Gastropoda – Suspension feeding – Filtration rate – Functional response

Many freshwater habitats (e.g. lowland rivers, lakes and reservoir outlets) are characterized by a high content of suspended particles. Various groups of animals have developed mechanisms to use these particles as a food source. Among molluscs, suspension feeding is the dominant mode of food collection for bivalves. Gastropods, in contrast, are generally considered to be grazers. However, some species of freshwater snails are capable of feeding more or less efficiently on suspended food. The extent of this specialization ranges from species like *Littorina littorea*, which retain suspended particles very inefficiently, and includes species like *Crepidula fornicata*, which feed exclusively on suspended food (Werner 1952). *Bithynia tentaculata* (Prosobranchia, Bithyniidae) has a fairly efficient mechanism of suspension feeding, but is still capable of grazing food from firm substrates (Schäfer 1951; Starmühlner 1952). Such an ability to switch between two feeding modes should give *Bithynia tentaculata* an ecological advantage, manifested as faster growth, better reproductive success or competitive superiority. Harman (1968) presents evidence that this is in fact the case in the field: in North American waters the neozoon *Bithynia tentaculata* coexists with indigeneous pleurocerids in habitats where grazing is the only feeding mode, but it outcompetes the pleurocerids whenever suspended food is available.

Despite the importance that such an additional food source might have for *Bithynia*, very little is known about the fundamental features of this species' suspension feeding. We therefore tested the effects of temperature, food species, food concentration and body size on the suspension feeding of *Bithynia tentaculata* under controlled laboratory conditions.

Materials and methods

Animals

Adult *Bithynia tentaculata* (L.) were collected in springtime in a ditch on the floodplain of the lower Rhine. The animals were transferred to the laboratory and kept under constant conditions of light (L : D = 16 : 8) and temperature (18 ± 1° C) in aquaria filled with aerated tapwater. They were fed on lettuce (ad lib) and algae (*Chlamydomonas*, once per week). Soon after their transfer to the laboratory the animals began to lay eggs. The offspring from these eggs were reared in the laboratory under the same conditions and later used to investigate suspension feeding by different size classes (see below). Animals were transferred to aquaria with fresh water and no food 4 days before the feeding experiments, to allow for gut evacuation and a constant hunger level at the start of the experimental feeding.

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Algae

Three different green algae were used in feeding experiments: *Chlamydomonas reinhardii* (Volvocales), *Chlorella vulgaris* (Chlorococcales) and *Chlorogonium elongatum* (Volvocales). *Chlamydomonas* is considered to be a good food for suspension feeders because of its suitable shape (more or less spherical), size (6 µm diameter) and motility, provided by two flagella of equal length, which reduces sedimentation of food cells during a feeding experiment. The thin cell wall of *Chlamydomonas* contains no cellulose (van den Hoek 1984) which should make these cells easily digestible. *Chlorella* has exactly the same size and shape as *Chlamydomonas*, but is non-motile, and its cell wall contains cellulose. Therefore, *Chlorella* is considered to be less digestible than *Chlamydomonas*. *Chlorogonium*, the third food item, is much larger (10 × 20 µm) and of elongate shape. It is also very motile (two flagella) and its cell wall contains no cellulose. The choice of these three food species should allow a comparison of motile versus non-motile food particles of the same size (*Chlamydomonas* vs. *Chlorella*) and of the effect of cell size (*Chlamydomonas* vs. *Chlorogonium*) with the same motility and cell wall features.

The algae, provided by "Sammlung für Algenkulturen" (Göttingen, FRG), were grown in batch cultures in Kuhl medium (*Chlamydomonas* and *Chlorogonium*) or in *Euglena* medium 9a (*Chlorogonium*) (Schlösser 1982). They were harvested during the exponential growth phase by centrifugation (4000 rpm, 10 min) and resuspended in sterile-filtered (0.2 µm Nuclepore filter), aerated tap water.

Experimental setup

The animals were fed in tall (185 × 99 mm) glass beakers. These contained 1 l sterile-filtered, aerated tap water and algae adjusted to the desired concentration. Algal cell concentrations and experimental food concentrations were counted with an electronic particle counter (CASY-1, Schärfe-System, Reutlingen, FRG). Algal sedimentation during the experimental period was prevented by strong aeration of the beakers with a glass pipette.

A standard experiment consisted of three beakers containing 10 animals each and one control beaker, with the same food and aeration, but without animals. Experiments were performed at 18° C, with 20,000 *Chlamydomonas* cells per ml at the beginning, for 6 h and with adult (9–11 mm shell length) animals ("standard conditions"), if not stated otherwise. The effect of the snails' suspension feeding was followed continuously by taking aliquots (1–5 ml) of the food suspension every 30 min and measuring cell concentrations. The following details are critical to the experimental design:

1. Algal sedimentation during the experimental period must be prevented and algae must be distributed evenly throughout the beakers. This was tested by taking aliquots of the food suspension from both experimental beakers and the control. Cell concentrations were always identical at various depths and sides of the control beaker.
2. By following cell numbers in the control, any increase in cell density during the 6-h experimental period could be excluded.
3. Pseudofaeces did not influence particle counting because food concentrations were too low for pseudofaeces formation. This was checked by microscopical examination.
4. *Bithynia tentaculata* is capable of two different feeding modes: grazing and suspension-feeding (Schäfer 1953). In order to investigate the details of suspension feeding, grazing had to be excluded. This was done by (a) optical control: given the possibility of suspension-feeding *Bithynia* instantly stops grazing and does not move around any longer; and (b) experimental control: pipette tips were glued to the shells of a group of animals, and by means of these "suspenders" the animals were positioned hanging freely in the beaker. The only contact with a firm substrate was a foot-rest (foot-pole), which enabled the animals to assume a nearly natural position of head, foot and mantle cavity openings in relation to the (fixed) shell. By comparing the filtering rates of these fixed snails with the filtering rates of free-ranging snails under standard conditions any possible contribution of grazing to the decrease in algal cell numbers could be evaluated. A schematic view of the experimental setup is shown in Fig. 1.

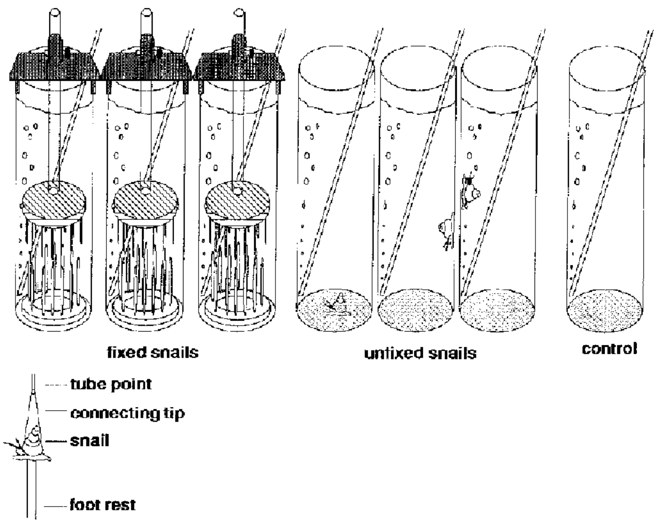

Fig. 1. Schematic view of experimental setup, with three beakers for fixed snails (*left*), three beakers for unfixed snails (*center*) and one control; *lower left*: detail of fixed snail

Calculations and statistics

Suspension feeding of *Bithynia tentaculata* was quantified indirectly by calculating the filtering rate, i.e. the difference in cell concentration between beginning and end of an experiment, taking into account the experimental time, experimental volume and number of animals per experiment. This calculation was done according to the formula given by Peters (1984).

All experiments were performed with at least three replicates and ten animals per replicate, unless otherwise stated. Additionally, one "standard experiment" was run parallel to all other experiments for direct comparison. Differences between experimental treatments were considered to be significant when t-statistics were positive at $P \leq 0.05$.

Experiments

Suspension feeding can be influenced by many factors. We examined the effect of

A). Temperature over the range 5–18° C, with adaptation of the animals to the experimental temperature for a minimum of 1 week.

B). Food species: three different algae (see above) were tested at concentrations of 20,000 and 40,000 (*Chlorogonium*: 44,000) cells · ml^{-1}.

C). Food concentration: *Chlamydomonas* was used at concentrations ranging from 20,000 to 100,000 cells · ml^{-1}.

D). Body size: we examined suspension feeding in young *Bithynia tentaculata* of < 4 mm, 4–5 mm, 5–6 mm and 6–7 mm shell length, and in adults (9–11 mm shell length).

Results

Whenever the freshwater snail *Bithynia tentaculata* encounters an environment containing suspended food particles, the animal's behaviour changes characteristically: it comes to rest almost immediately, the shell is

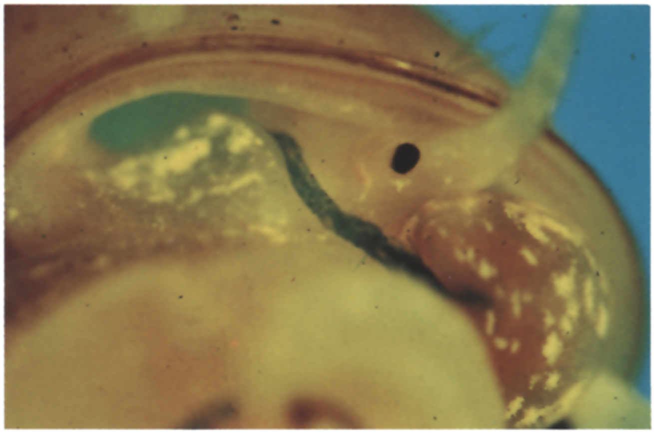

Fig. 2. Head of *Bithynia tentaculata*, with food string leaving mantle cavity

lifted and inhalant and exhalant opening of the mantle cavity are conspicuous. Soon after that a food string consisting of (formerly) suspended particles entrapped in mucus leaves the mantle cavity at the right side of the body. (Fig. 2). The animal's head also turns towards the right and the food string is taken up by the mouth. This process is repeated every 2–5 min (Schäfer 1951).

We observed such behaviour in all our experiments with unfixed snails, and we also saw production and uptake of the food string in our suspended (fixed) snails. Comparison of the filtering rates of suspended snails (9.7 ± 3.5 ml · ind^{-1} · h^{-1}; 44 animals) versus free snails (11.8 ± 2.2 ml · ind^{-1} · h^{-1}; 44 animals) showed no statistical difference (*t*-test; $P \leq 0.05$) between these two experimental treatments. Therefore, we concluded that grazing contributes only very little (if at all) to the removal of suspended food particles.

The body temperature and hence the ecological performance of gastropods is influenced by the temperature of the environment. Table 1 shows filtering rates for fixed snails at different temperatures from 5° C to 18° C. Intermediate temperatures – the ones most often experienced by the animals in their natural habitats – do not affect filtration rates: in this temperature range the filtration rates were around 12 ml · ind^{-1} · h^{-1}. A temperature decrease of only 3° C, however, from 8° C to 5° C, caused filtering rates to fall to 5 ml · ind^{-1} · h^{-1}, only 40% of the rate at 8° C. At temperatures above 15° C the uptake of suspended particles increased by about 40%, to 17.5 ml · ind^{-1} · h^{-1} at 18° C.

Table 1. Filtering rates (FR, ml · ind^{-1} · h^{-1}) of *Bithynia tentaculata* at different temperatures (T, °C)

T	FR ± SD	*n*
5	5.0 ± 2.4*	80
8	12.4 ± 2.4	60
12	12.6 ± 4.0	60
15	12.2 ± 2.0	60
18	17.5 ± 3.7*	100

mean ± SD; *n* = number of animals; * = differences from all other values significant at $P \leq 0.05$ (*t*-test)

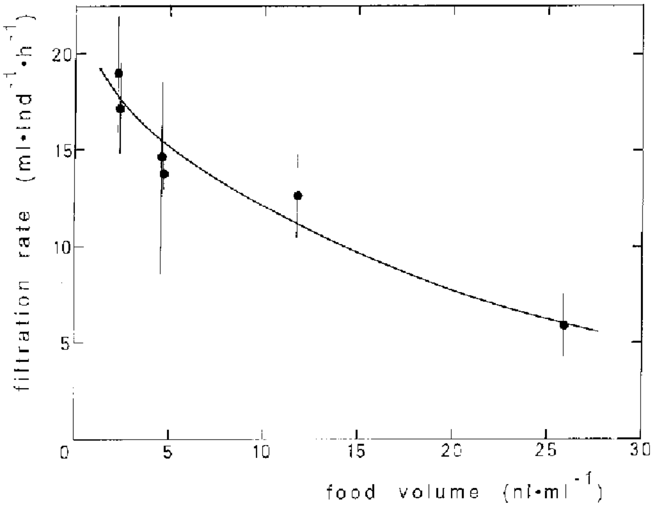

Fig. 3. Relationship between filtration rates (mean ± SE) and food volume offered (for numerical values see Table 2)

In the field suspended food is composed of a variety of different particle sizes, volumes and nutritional values. To test whether *Bithynia tentaculata* feeds selectively on this highly diverse assemblage of food particles, we offered three green algae differing in size, motility and cell wall characteristics at two different concentrations (Table 2). Filtering rates were between 12.7 and

Table 2. Results of feeding experiments (mean of 3 replicates with 10 animals each per concentration) with three different food species

Food			Filtering rate (ml · ind^{-1} · h^{-1}) ± SD	Feeding rate (cells · ind^{-1} · h^{-1} · 10^3)	Volume eaten (nl · ind^{-1} · h^{-1})
Species	Concentration (cells · ml^{-1})	Volume (nl · ml^{-1})			
Chlorella	20,000	2.31	19.0 ± 5.2	380	43.9
	40,000	4.61	14.7 ± 10.6	588	67.8
Chlamydomonas	20,000	2.31	17.2 ± 4.0	344	39.7
	40,000	4.61	13.8 ± 1.2	552	63.6
Chlorogonium	20,000	11.78	12.7 ± 3.7	254	149.6
	44,000	25.91	5.9 ± 2.8	260	152.8

Differences are significant between: *Chlorogonium* at 44,000 cells · ml^{-1} and *Chlorella* at 20,000, *Chlamydomonas* at 20,000 and *Chlamydomonas* at 40,000 cells · ml^{-1} (*t*-test, $P \leq 0.05$)

19.0 ml · ind^{-1} · h^{-1}. The only exception was *Chlorogonium* at a concentration of 44,000 cells · ml^{-1}, where filtration rates were significantly reduced. Comparison of *Chlorella* and *Chlamydomonas* shows that cell motility did not influence the results. At the standard concentration of 20,000 cells · ml^{-1}, neither cell shape nor size affected the filtration capacity, as can be seen comparing *Chlorogonium* (12.7 ml · ind^{-1} · h^{-1}) with *Chlorella* and *Chlamydomonas*. The cell volume of *Chlorogonium*, however, is about five times greater than that of *Chlorella* and *Chlamydomonas*. Taking this into consideration it can be shown that at higher food concentrations of 11.8 and 25.9 nl · ml^{-1} (see Table 2) filtering rates were reduced. Figure 3 shows this change of filtration rates with food concentration in *Bithynia tentaculata*. The experimental results can be described by a negative exponential function $\mathrm{FR} = 19.11 \cdot e^{(-0.044 \cdot 10^{-3} x)}$ (χ^2 goodness of fit, $P \leq 0.05$).

A detailed examination of the effect of food concentration was made with a series of *Chlamydomonas* concentrations. By using one species of alga only, the effects of cell shape, motility and taste could be excluded. The cell concentrations tested ranged from 20,000 to 100,000 cells · ml^{-1}, with the results for 20,000 and 40,000 cells · ml^{-1} taken from the previous experiment. As was found in the experiment with different algae, higher cell concentrations resulted in lower filtering rates (Fig. 4). Absolute values ranged from 4.9 ml · ind^{-1} · h^{-1} at the highest cell concentrations to 17.2 ml · ind^{-1} · h^{-1} at the lowest cell numbers. The correlation between cell number and filtration rate was not linear: when cell number was doubled from 20,000 to 40,000 cells · ml^{-1}, filtration rate decreased by about 20%. When cell numbers were doubled from 50,000 to 100,000 cells · ml^{-1}, however, filtration rates fell to 40% of their former value.

A better insight is gained by plotting feeding rate (filtration rate × cell number) against the food concentrations in the different trials. This (Fig. 5) shows that below 50,000 cells, feeding rate increases with the amount of food offered. Above 50,000 cells, in contrast, the rate of food uptake seems to be saturated and remains more or less constant. This is because the filtering rate drops considerably when food concentration increases from 50,000 to 100,000 cells · ml^{-1}.

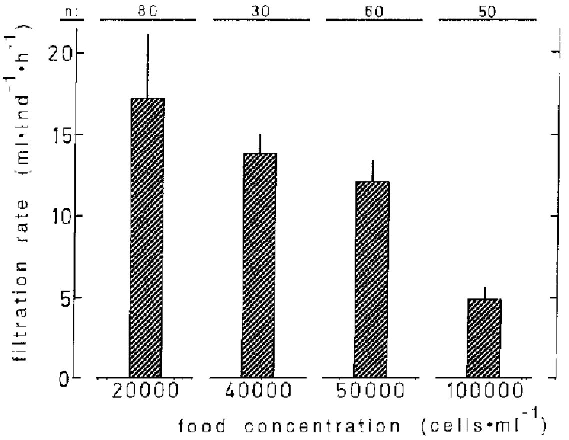

Fig. 4. Relationship between filtration rates (mean) and food concentration (cells · ml^{-1}); n = number of animals; *vertical bars*: standard deviation. Differences are statistically significant for the highest food concentration (t-test, $P \leq 0.05$)

Such a functional response to increasing food concentrations was also observed in the experiments with different algae. This can be seen from the last column of Table 2, where the food volume eaten per animal per hour did not exceed a maximum value of about 150 nl.

It is interesting to know the feeding performance of juveniles as well as that of adults. We therefore measured the filtration rates of four size-classes of immature *Bithynia tentaculata*, from below 4 mm up to 7 mm body size. A body size of 7 mm was the maximum reached by the animals reared in our laboratory during the first summer (*Bithynia* is biennial); therefore we had no animals between 7 and 9 mm available for these experiments.

Experiments were of the standard design. The "gross"results are shown in Table 3. Even the smallest size class of animals showed a filtration rate of 2.7 ml · ind^{-1} · h^{-1}, and these rates gradually increased to 8.4 ml in the 6–7 mm size class. We called these results "gross"results because they conceal a finding shown clearly in Fig. 6: when repeating these experiments eight times over a period of 5 months, we found that the filtering rates of all size classes of *Bithynia* changed seasonally. In August and September, we found high filtration rates of up to 15 ml · ind^{-1} · h^{-1} in the 6–7 mm size class, which is almost as high as the filtering rate of adults (cf. Fig. 4). In October and November, we found very low filtering rates in all size classes, and in December the rates increased again. Possible reasons for this are dis-

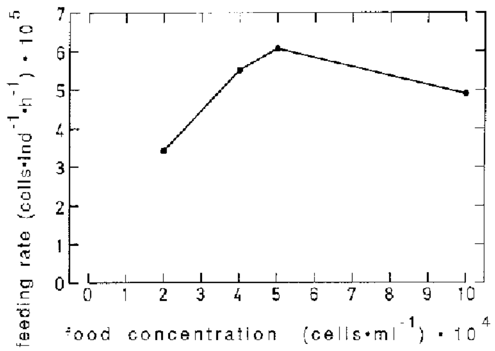

Fig. 5. Relationship between feeding rate (cells · ind^{-1} · h^{-1}) of *Bithynia tentaculata* and food concentration (*Chlamydomonas*, cells · ml^{-1})

Table 3. Mean of filtration rates (FR, ml · ind^{-1} · h^{-1}) of four size classes (SL = shell length, mm) of immature *Bithynia tentaculata*

SL	FR ± SD	CV	n
<4	2.7 ± 2.3	0.85	80
4–5	4.9 ± 2.8	0.75	80
5–6	7.7 ± 3.3	0.43	80
6–7	8.4 ± 5.3	0.63	70

SD = standard deviation; CV = coefficient of variation; n = number of animals per size class. Differences are statistically significant between the <4 mm and the 5–6 and 6–7 mm size class (t-test, $P \leq 0.05$)

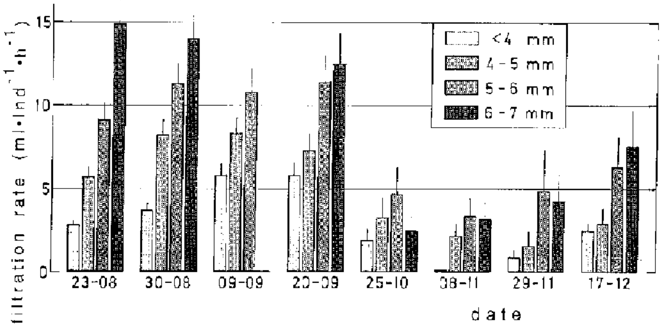

Fig. 6. Filtration rates (mean ± SD; ml · ind^{-1} · h^{-1}) of four different size classes (3–4 replicates with 10 animals each per size class) of *Bithynia tentaculata*, as observed in eight experiments from 23 Aug to 17 Dec 1991

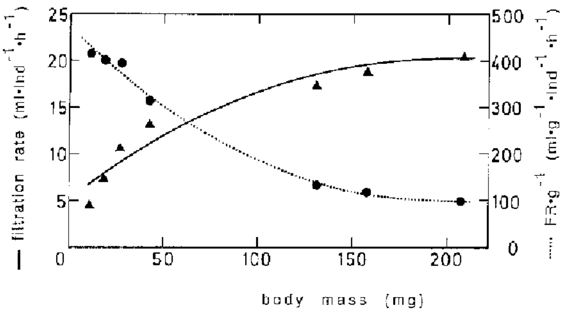

Fig. 7. Correlation between body mass (fresh body mass, mg) of *Bithynia tentaculata* and filtration rate (*triangles, full line*) as well as weight-specific filtering rate (*points, dotted line*) (χ^2-goodness of fit, $P \leq 0.05$)

cussed later. The seasonal differences are the reason for the high coefficients of variation in Table 3, where the mean and standard deviation were calculated over all dates.

Taking into consideration the different body weights of young and adult animals, it becomes clear that absolute filtration rates increase with body weight (Fig. 7). Weight-specific filtering rates, however, are up to four times higher in young *Bithynia tentaculata* than in adults, following the general physiological trend of higher metabolic rates per unit body weight in smaller organisms (Hemmingsen 1960).

Discussion

Unlike most other freshwater snails, *Bithynia tentaculata* has two modes of feeding: grazing and suspension feeding. Of these two, suspension feeding seems to be the preferred mechanism of food uptake. This can be inferred from the observation that *Bithynia* immediately comes to rest and changes from grazing to suspension feeding whenever suspended food is abundant. This behaviour is reasonable in terms of animal energetics as has been shown by Hunter (1975), Tashiro (1982) and Tashiro and Coleman (1982): the net energy gain for the animals is much higher when they are feeding on suspended food.

We examined some of the fundamental aspects of suspension feeding by *Bithynia* under well controlled laboratory conditions. By feeding 10 animals per beaker the individual variability of the experimental results was reduced. All experiments were run at least in triplicate, and a beaker without animals was used to control the homogeneous distribution and constancy of algal cell numbers over the experimental period of 6 h. Although filtration rates were calculated from cell concentrations at the beginning and end of an experiment ($C_t - C_0$), food concentrations were checked every 30 min to give a continuous experimental record. A control experiment with fixed snails hanging freely in the beaker with minimal contact of the soft body parts with firm substrate (see Fig. 1) showed that there was no grazing in these experiments. This minimal contact allowed the animals to obtain a natural position of foot, head and mantle cavity openings in relation to the fixed shell. In another experiment contact was absent and the animals showed no suspension feeding. This is the explanation for Lilly's failure (Lilly 1953) to observe suspension feeding by *Bithynia*. He glued his animals to cotton threads and hung them freely in an aquarium, without offering a foot rest, so they could not feed on suspended particles. His second trial, where the animals' shells were glued upside down on a pin fixed in the sediment, gave the same results.

Temperature was one of our experimental parameters. We tested the performance of adult (9–11 mm shell length) *Bithynia tentaculata* at 5–18° C and found that over a range of intermediate temperatures (8–15° C), temperature did not influence the average rate of 12.5 ml · ind^{-1} · h^{-1}. At 5° C, however, filtering rates were reduced considerably, to 5 ml · ind^{-1} · h^{-1} and at 18° C the suspension feeding increased to 17.2 ml · ind^{-1} · h^{-1}. These results are similar to those reported by Tashiro (1980) (18 ml · ind^{-1} · h^{-1}) and Schäfer (1953) (16.7 ml · ind^{-1} · h^{-1}) for *Bithynia tentaculata* and by Meier-Brook and Kim (1977) for *Bithynia manchourica* (12.6 ml · ind^{-1} · h^{-1}). There are no data in the literature on *Bithynia*'s filtration rate at lower temperatures, so we can only speculate on our results: as *B. tentaculata* lives in waters with temperatures between 8 and 15° C during most of the year, a high filtering rate in this temperature range seems very reasonable. This would even allow the colonization of deeper parts of lentic waters during summer, with better refuge from predatory waterfowl and increased sedimentation rates supplying more suspended food than near the surface. It also guarantees efficient filtration in surface waters early in spring and until late autumn. At 5° C the physiological performance of these animals is generally reduced. These low temperatures are encountered in the field during winter, when *Bithynia* is in a state of reduced activity. At higher temperatures like 18° C suspension feeding increases again. Probably this is a consequence of greater general activity of the animals at higher temperatures and higher respiration rates. The fact that respiration and suspension feeding are not independent of each other, because they both use the same water transport system, has to be taken into account whenever suspension feeding of *Bithynia tentaculata* is discussed. Two possible consequences are that suspension feeding can never go back to a value of zero (provided that there are suitable particles in the environment) and that the upper limit of the filtering rate is not set by the amount of water passing through the gills. The rate of mucus production, food string transport, food string uptake or the amount of gut fullness are possible limiting factors in this case.

Gazing *Bithynia tentaculata* prefer diatoms over other food (Schäfer 1953). By using three algal species differing in size, motility and cell surface characteristics we investigated whether suspension feeding is also selective. The results showed that under "standard" conditions there is no statistical difference between the experimental results. The only exception was *Chlorogonium* at a high concentration of 44,000 cells $\cdot$ ml^{-1}, when filtration rate decreased to about half of the usual value. The reason for this became evident when we compared the feeding rates in terms of cell volume eaten (Table 2): feeding rate increases up to a value of 150 nl $\cdot$ ind^{-1} $\cdot$ h^{-1} and is constant thereafter. In other words, the functional response of feeding rate versus food volume can be described by a saturation curve – up to a biovolume of 12 nl $\cdot$ ml^{-1} (= *Chlorogonium elongatum* at 20,000 cells per ml) feeding rate increases with food concentration, whereas above 12 nl $\cdot$ ml^{-1} (we tested: 25.9 nl $\cdot$ ml^{-1} = 44,000 *Chlorogonium* cells $\cdot$ ml^{-1}) feeding rate remains constant due to lowering of the filtering rate. As discussed in the previous paragraph, this does not necessarily mean that the rate of water passage through the mantle cavity is reduced.

These findings are, however, of limited practical value: comparing the cell numbers and biovolume of one place in the field (lower river Rhine near Cologne, August-December 1991) we found numbers of 5–7 µm particles of 4,000–25,000 cells $\cdot$ ml^{-1}, and maximum biovolumes of all suspended particles in the range of 1.6–80 µm were 8–9 nl $\cdot$ ml^{-1}. This means that the feeding rate of animals in the field most probably never reaches saturation, at least at this location where *Bithynia tentaculata* usually is very abundant.

In general these findings could be confirmed by the experiments with different concentrations of *Chlamydomonas* up to 100,000 cells $\cdot$ ml^{-1}. Here too, we had a decreasing filtering rate with increasing cell concentrations (Fig. 4) and saturation of the feeding rate at high biovolumes (Fig. 5). The absolute values, however, were slightly different from the previous experiment: saturation of the feeding rate was reached at 50,000 *Chlamydomonas* cells $\cdot$ ml^{-1}, which is equivalent to 5.75 nl $\cdot$ ml^{-1}, and not at 12 nl $\cdot$ ml^{-1} as in the former case. One reason for this may be the time of the year when the experiment was made (21 October): in autumn there was a strong reduction in the animals' performance (see time series below). Another explanation may be a slight difference in nutritive value between *Chlamydomonas* and *Chlorogonium*: we always found intact cells in the feces of animals which had been feeding on *Chlorogonium* whereas we never found any intact *Chlamydomonas* cells in our snails' feces. We conclude from this that *Chlamydomonas* cells are digested better and faster than *Chlorogonium* cells, and that gut fullness is reached earlier (at a lower amount of food eaten) when feeding on *Chlamydomonas* than when feeding on *Chlorogonium*.

The experiment with different size classes of *Bithynia tentaculata* showed that even the smallest animals tested (<4 mm body length) could feed on suspended food. This contradicts Mattice (1970), who found no suspension feeding for animals below 4.5 mm body size. But comparing the small absolute values in this size class (2.7 ml $\cdot$ ind^{-1} $\cdot$ h^{-1}) and the methods used by Mattice (1970), who fed single animals for 2 h only in 150-ml beakers it becomes clear that he simply had no chance of detecting such a small (3.6%) change in cell numbers during his experiments.

Filtration rate increases with body size, up to an average value of 8.4 ml $\cdot$ ind^{-1} $\cdot$ h^{-1} in 6–7 mm animals. But these results are again influenced by strong seasonal dynamics (Fig. 6). Maximum filtering rates of all size classes of juveniles were found until late summer, whereas in autumn the rates decreased to values of less than a third of the summer values. This was completely unexpected because all these juveniles were reared from eggs laid in the laboratory, and all these eggs and animals had been kept under constant conditions for their whole lifetime. From this we postulate the presence of an innate seasonal rhythm in *Bithynia tentaculata* influencing the animal's performance. Such a seasonal rhythm of activity in *Bithynia tentaculata* has also been reported by Lilly (1953) and Tashiro (1980). One can compare these observations to the circannual rhythms described in the mollusc *Limax flavus*, and also many examples from birds and mammals (Gwinner 1986).

Figure 7 shows that the weight-specific filtering rate decreases with increasing body size. Such a weight-specific reduction of metabolic processes with increasing body size is common in animals (Hemmingsen 1960).

The overall significance of *Bithynia*'s suspension feeding ability cannot be judged completely to date. Without a doubt, this additional feeding mode can provide extra food for *Bithynia*, as has been stated by Schäfer (1953) and Fretter and Graham (1962). It provides the animals with a higher net income of protein carbon and nitrogen per unit respiration than grazing (Hunter 1975; Tashiro and Colman, 1982), makes them less dependent on benthic structures (Schäfer 1953) and increases competitive ability, especially under eutrophic conditions, when suspended particles are abundant (Harman 1968).

The ecosystem, in turn, benefits from *Bithynia*, which can occur in numbers of up to several thousand per square meter, by a considerable increase in its self-purification properties.

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References

Fretter V, Graham A (1962) British prosobranch molluscs. Ray Society, London

Gwinner E (1986) Circannual rhythms. Springer, Berlin

Harman WN (1968) Interspecific competition between *Bithynia* and pleurocerids. Nautilus 82:72–73

Hemmingsen AM (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rep Steno Memorial Hosp Nord Insulinlab 9:1–110

Hoek C (1984) Algen. Einführung in die Phykologie. Thieme, Stuttgart

Hunter RD (1975) Growth, fecundity, and bioenergetics in three populations of *Lymnaea palustris* in Upstate New York. Ecology 56:50–63

Lilly MM (1953) The mode of life and the structure and functioning of the reproductive ducts of *Bithynia tentaculata* L. Proc Malacol Soc London 30:87–110

Mattice JS (1970) Trophic biology of a natural population of *Bithynia tentaculata* in terms of ecological energetics. PhD Dissertation, Syracuse University, Syracuse, New York

Meier-Brook C, Kim CH (1977) Notes on ciliary feeding in two Korean *Bithynia* species. Malacologia 16:159–163

Peters RH (1984) Methods for the study of feeding, grazing and assimilation by zooplankton. In: Downing JA, Rigler FH (eds) A manual on methods for the assessment of secondary productivity of fresh waters. Blackwell, Oxford, pp 336–395

Schäfer H (1951) Ein Beitrag zur Ernährungsbiologie von *Bithynia tentaculata* L. (Gastropoda, Prosobranchia). Zool Anz 148:299–303

Schäfer H (1953) Beiträge zur Ernährungsbiologie einheimischer Süßwasserprosobranchier. Z Morphol Ökol Tiere 41:265–277

Schlösser G (1982) Sammlung von Algenkulturen. Ber Dtsch Bot Ges 95:181–276

Starmühlner F (1952) Zur Anatomie, Histologie und Biologie einheimischer Prosobranchier. Österr Zool Z 3:546–590

Tashiro JS (1980) Bioenergetic background to reproductive partitioning in an iteroparous population of the freshwater prosobranch *Bithynia tentaculata*. PhD Dissertation, Syracuse University, Syracuse, New York

Tashiro JS (1982) Grazing in *Bithynia tentaculata*: age-specific bioenergetic patterns in reproductive partitioning of ingested carbon and nitrogen. Am Midland Nat 107:133–150

Tashiro JS, Colman SD (1982) Filterfeeding in the freshwater prosobranch snail *Bithynia tentaculata*: bioenergetic partitioning of ingested carbon and nitrogen. Am Midland Nat 107:114–132

Werner B (1952) Ausbildungsstufen der Filtrationsmechanismen bei filtrierenden Prosobranchiern. Verh Dtsch Zool Ges 34:529–546