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# Influence of food size and food quantity on the feeding of the mussel *Dreissena polymorpha*

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**Summary.** In common with many other suspension feeders, the freshwater mussel *Dreissena polymorpha* has a maximum filtration rate at low food concentrations and a maximum ingestion rate at high food concentrations. These high rates, which reflect the potential maximum food uptake of the animal, are called the *filtration capacity* and the *ingestion capacity* respectively. The ingestion capacity was attained without forming pseudofaeces with *Chlamydomonas reinhardii* as food. The *incipient limiting level* could be calculated as the quotient of these two values. A decrease of the filtration rate at high food concentrations was correlated with changes in pumping activity, which showed more frequent interruptions, or a lower level of water transport. *Dreissena* can filter out particles of diameter greater than 0.7 μm from the water. Retention reaches a plateau at about 5 μm particle diameter. Scanning electron micrographs of the arrangement of the cilia on the gill filaments are given.

**Key words:** *Dreissena polymorpha* – Filtration capacity – Ingestion capacity – Incipient limiting concentration – Particle retention

The filtration process in suspension feeders depends on many environmental factors such as temperature, oxygen content of the water, salinity, and many others (see e.g. Bayne et al. 1976). It is, however, frequently overlooked that in addition to these factors (a) the quality and (b) the quantity of the food in the water may also have a pronounced effect on the filtration process:

a) The filtration rate, i.e. the volume of water swept clear of particles, depends on particle size. The filtration rate only equals the pumping rate when the retention efficiency for the particular particle size is 100%. Although the pumping rate has the same dimensions as the filtration rate (volume per time), it basically refers to something rather different i.e. to the water volume pumped through the feeding apparatus of the animal and not to the change in particle concentration (see e.g. Winter 1978).

b) Food uptake of suspension feeders can be described by two rates: the filtration rate (FR) and the ingestion rate (IR). These rates are not independent of each other but are linked by the food concentration $c$:

$$IR = FR \times c$$

At the same time, both IR and FR depend on $c$ in a quite characteristic way.

One of the first detailed studies devoted to this problem was that of Rigler (1961). He found that at moderately low food concentrations, the filtration rate estimated for *Daphnia magna* was independent of $c$. Consequently, the ingestion rate increases as more food is available. However, ingestion rate does not increase to infinity with $c$. At a particular concentration (called the incipient limiting concentration by subsequent authors; see e.g. Burns and Rigler 1967), the ingestion rate reaches its maximum and cannot increase further. Therefore, as a consequence of the formula given above, the filtration rates estimated in this range should decrease with increasing food concentration.

For *Mytilus edulis* larvae, Sprung (1984) found a similar relationship. He used the term "filtration capacity" for the particular filtration rate below the incipient limiting level and the term "ingestion capacity" above it. Both are concentration-independent characteristics of the feeding potential.

In bivalves, pseudofaeces can be formed on the gills in highly concentrated algal suspensions (see e.g. Foster-Smith 1975). By this means, surplus filtered food can be discarded. With *Mytilus edulis*, however, Winter (1973) found an algal concentration of 10–40 *Dunaliella* cells $\mu l^{-1}$ at which the ingestion rate was independent of the food concentration and the animal does not form pseudofaeces. There must therefore be a mechanism at the level of the gills to regulate the amount of food filtered from the water.

We examined food uptake of the freshwater bivalve *Dreissena polymorpha*. Questions addressed were (1) what is the size spectrum which *Dreissena* can filter out of the water? (2) Is there a range of food concentrations over which *Dreissena* can regulate food uptake without producing pseudofaeces? (3) If so, by what mechanisms may the process of filtration be regulated?

## Material and methods

### *Animals*

The mussels for the experiments were taken from a lake in the vicinity of Cologne (Fühlinger See) by SCUBA div-

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ing. They were detached from the stones by a knife, transported to the laboratory and stored at 12° C. Before the experiments the shells were thoroughly cleaned with a paper cloth. Water for storage and the subsequent experiments was made up from deionized water with 1% seawater added.

*Algal cultures*

Algae for the experiments were cultivated in aerated Erlenmeyer flasks. The following media were used for the algal strains (with their approximate diameter given):

a) medium of Chu (Müller 1972) for *Synechococcus elongatus* (1 µm)

b) medium of Kuhl (1962) for *Nannochloris coccoides* (2–3 µm), *Chlamydomonas reinhardii* (6 µm), *Chlamydomonas noctigama* (12 µm)

c) medium of Kuhl (1962) with vitamin B12 added for *Pandorina morum* (25–30 µm as a colony).

Most of the strains were bought from the Pflanzenphysiologischen Institut der Universität Göttingen. They were spun off and resuspended in freshwater before use.

*Retention spectrum*

Particle retention was estimated by means of a Coulter Counter (model TA II) following filtration rates in distinct channels. Experiments were conducted in aerated 500-ml beakers. Approximately the same volume (particle size × particle number) was established in each channel using the algal strains mentioned above.

The particle retention spectrum was recorded using 3 approaches:

1) with a 30-µm orifice tube at 12° C (undefined particles smaller than 1 µm in the water, *Synechococcus* and *Nannochloris* as food: 2 spectra for animals of 1.5–2 cm shell length and 2.5–3 cm shell length with 6 rates per channel)

2) with a 50-µm orifice tube at 12° C (*Nannochloris*, *C. reinhardii* and *C. noctigama* as food; a spectrum for animals of 2.5–3 cm shell length was recorded with 19 rates per channel)

3) with a 280-µm orifice tube after some days adaptation at 15° C (*C. reinhardii, C. noctigama* and *Pandorina* as food; 3 spectra with 1 rate each were recorded for mussels of 1.5–2 cm, 2–2.5 cm and 3–3.5 cm shell length).

Samples were diluted by a membrane (0.45 µm pore size)-filtered 16% NaCl solution to establish an adequate conductivity. The count was corrected by a blank using the salt solution alone. Alongside these beakers another blank (algae without mussels) was recorded and the filtration rates corrected by the particle change in it.

As most of the channels were evaluated with the 50-µm tube, the filtration rate in the channel of that tube with the highest estimate was defined as 100%. The mean rates of the 30- and 280-µm tubes were fitted to it by means of the overlapping channels.

*Food uptake*

Filtration and ingestion rates were recorded at defined concentrations of *Chlamydomonas reinhardii* using the same group of mussels of 2.5–3 cm shell length throughout this set of experiments. The animals were adapted to the food levels usually overnight. If more than one rate was recorded per day adaptation of the (in most cases neighbouring) food level took only about 1 h. The animals were transferred to aerated 500 ml beakers which were placed in a thermostatted water bath. Algal concentration was monitored by a Coulter Counter fitted with a 50-µm tube as described for the retention spectrum.

*Pumping behaviour*

Pumping (together with the ingestion and filtration rates) was followed with the same animal over the course of several days. It was adjusted roughly to the food concentration in the experiment the night before recording began.

The mussel was glued by one valve onto a stub. Its position could be changed so that the exhalant siphon when extended pointed directly into a tube of 2 cm length with an interior diameter of 0.3 cm. The tip of a 2 kΩ thermistor in the tube recorded the flow rate. Another thermistor of the same type was positioned in a similar tube mounted parallel to the first tube. It registered only temperature changes and water flow not caused by the animal. Both thermistors were part of a Wheatstone bridge which could be adjusted by a potentiometer. Changes in the resistance of the thermistor caused by the water flow were monitored on a chart recorder. The system was not calibrated. The mussels and the thermistor were situated in a circular flow-through chamber of 6 cm diameter and 2 cm height. The chamber and the tank supplying water to the chamber were placed in a thermostatted water bath. Algal concentration could be adjusted in the tank. Ingestion and filtration rates were recorded simultaneously in this system.

*Estimation of food uptake*

Food uptake was calculated by means of the decrease in particle number in the beakers. In most cases, five 5-ml samples were taken in the course of 1–2 h. Quite frequently, however, production of faeces interrupted the experiment. They disintegrated very rapidly causing a clear increase in particle number. In that case, the faeces were sieved off and a new run was started.

The filtration rate was calculated from the slope of the regression of log particle number versus time. The regression was fitted by the least squares method. Ingestion rates were calculated by multiplying this filtration rate with the geometric mean of the particle concentration registered.

In the flow-through chamber, ingestion (IR) was estimated from the flow rate (fl; by means of a graduated cylinder) the particle concentration in a bypass ($c_0$) and in the outflow of the chamber ($c_1$):

$$IR = (c_0 - c_1) \times fl$$

Filtration rate (FR) was estimated applying the formula discussed by Hildreth and Crisp (1976):

$$FR = IR\ c_1$$

*Observation of the gills*

The gills of specimens of 0.5–1 mm shell length could be observed under a compound microscope. These animals still had transparent shells so that the beat of the cilia could be monitored directly.

For scanning electron microscopy, one valve of a mussel of 1.5 cm shell length was removed. The animal was flooded in glutardialdehyde for 10 min, fixed in cacodylate buffer (2 h), dehydrated in a graded ethanol series, transferred to n-amyl acetate and dried by the critical point method. The whole specimen was given a thin coating of gold and viewed in a Hitachi S520 scanning electron microscope.

## Results

Relative particle retention efficiencies pooled from mean estimates from three sets of experiments are presented in Fig. 1: although only particles larger than 0.7 µm in diameter were removed from the water, maximum retention efficiency was only reached at 5 µm particle diameter and extended to at least 35 µm diameter.

A detailed description of the morphology of the *Dreissena* gill has been given by Morton (1969) according to microscopic studies. The scanning electron micrographs presented in Fig. 2 illustrate some details. Three types of cilia can be recognized:

1) The *frontal cilia*, in Fig. 2a at the distal end of the filament, but also in Fig. 2b as short densely packed structures: they effect particle transport over the gill surface.

2) The *lateral cilia*, which can be recognized in the interfilament space of Fig. 2b. Although the picture is not very clear for this type of cilia, they look quite similar to the frontal cilia; they are responsible for water transport across the gill (i.e. the pumping rate).

3) The latero-frontal cilia (or more precisely the *latero-frontal cirri*): they are much longer than the two other types. In Fig. 2b it can be seen that they are composed of a varying number of subunits which are split off towards the distal end.

Under the compound microscope, only the latero-frontal cirri could be recognized as more or less stiff structures covering the interfilament space (in contrast to the bent appearance indicated in the photographs). Neighbouring cirri on a filament beat alternately. This gives the impression of waves moving along the filaments, if the gill is not orientated exactly at right angles to the observer. The cirri cease beating when the shells are closed. When the shells are opened again, the gills apparently expand slightly and activity of the cilia is resumed. The latero-frontal cirri in one part of the gill may quite frequently be inactive while elsewhere (predominantly close to the mouth) they are still beating.

In Fig. 3, filtration and ingestion rates for different *Chlamydomonas reinhardii* concentrations are recorded. They show the tendency to be expected from Rigler's (1961) experiments: a maximum filtration rate (filtration capacity) at low particle concentrations and a maximum ingestion rate (ingestion capacity) at high algal concentrations. The incipient limiting concentration can be calculated from the quotient ingestion capacity/filtration capacity.

It is important to note that with these animals no pseudofaeces production was observed throughout the range of algal concentrations examined.

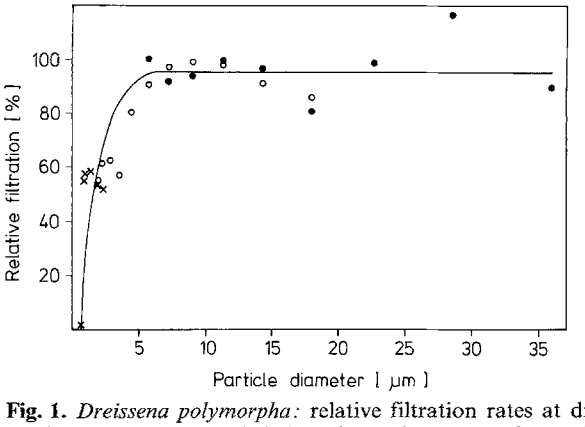


**Fig. 1.** *Dreissena polymorpha:* relative filtration rates at different particle diameters; pooled data from three sets of experiments, represented by different symbols. The graph is fitted by eye; for details see text

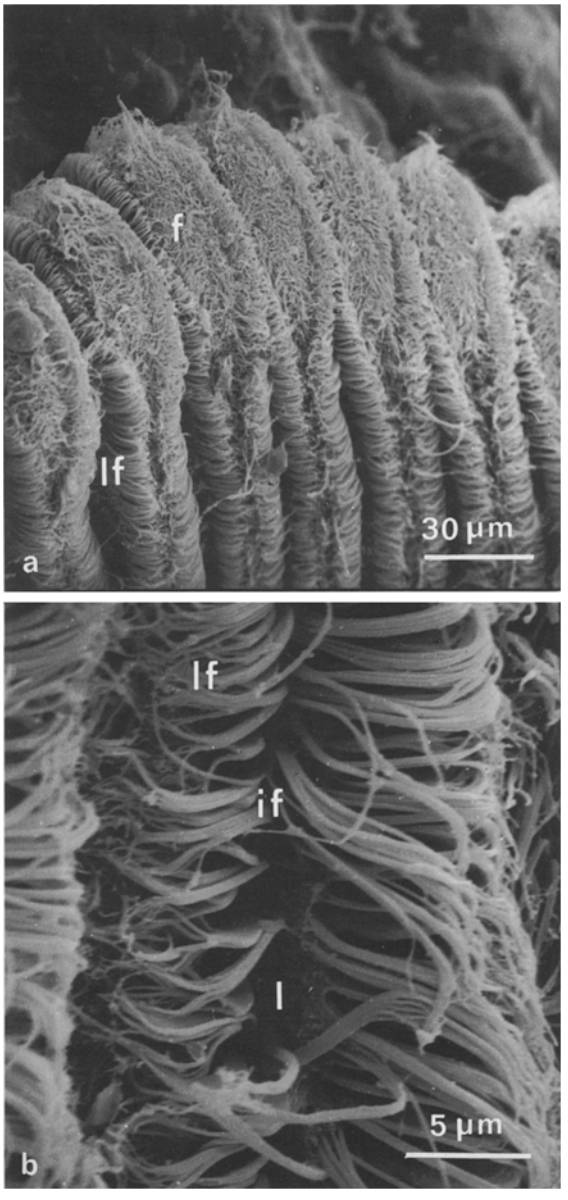


**Fig. 2a, b.** *Dreissena polymorpha:* Scanning electron micrographs of the gills. **a** distal end of the filaments of the outer demibranch **b** a closer view of the latero-frontal cirri emerging from the interfilament space. *f*, frontal cilia; *l*, lateral cilia; *lf*, laterofrontal cirri; *if*, interfilament space

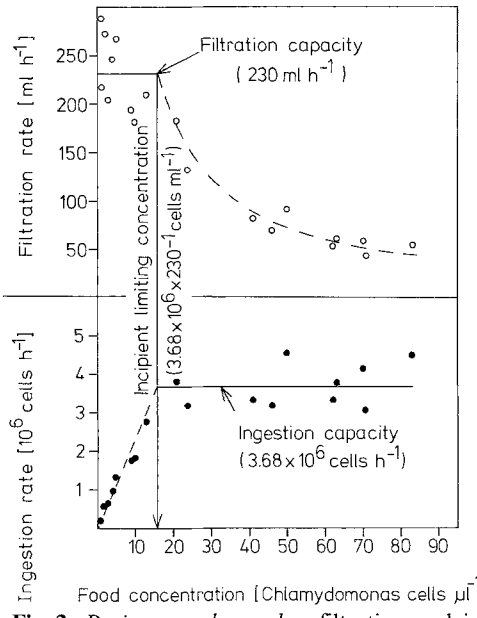


**Fig. 3.** *Dreissena polymorpha:* filtration and ingestion rates as a function of food density. The filtration and the ingestion capacity are calculated from the mean of the data points above and below the incipient limiting concentration respectively; the *dotted lines* represent the filtration rate to be expected at the ingestion capacity level and the ingestion rate at the filtration capacity level, respectively, at the food concentrations given

Pumping was typically not continuous, although the shells were open nearly all the time. Pauses of some seconds alternated with activity periods of up to several minutes duration. In Fig. 4 typical examples are presented: when the animal resumes activity after a longer period of shell closure, pumping typically shows peaks before it is fully active again. Pumping activity below the incipient limiting level is only infrequently interrupted. Interruptions become more frequent at dense concentrations of algae; it was also observed that the pumping activity could be depressed. The filtration rate is highest (although quite variable) at low food concentrations, and decreases at higher concentration; ingestion is at a maximum at dense concentrations, as also observed in the other set of experiments. Thus the filtration rate can be reduced by reduction of pumping activity at high particle concentrations.

## Discussion

The most detailed observations and experiments on the functioning of a bivalve gill refer to *Mytilus edulis* (see e.g. Dral 1967; Owen 1974; Jørgensen 1982; Silvester and Sleigh 1984). In spite of the fact that *Mytilus* has a filibranch and *Dreissena* a eulamellibranch structure, the gills of both these (and probably most other bivalve species) work on similar principles as briefly outlined in Results.

### *The latero-frontal cirri*

Most interest has been focused on the laterofrontal cirri, because they are responsible for the size spectrum and quantity of particles filtered out of the water. There has been a lot of confusion in the past about how bivalves (especially *Mytilus*) can filter out particles much smaller than the distance between the cilia as observed under the microscope (Jørgensen and Goldberg 1953). For this reason, Tammes and Dral (1955) and Dral (1967) suggested that these cirri might be sticky. This had already been suggested by Wallengren (1905); MacGinitie (1945) postulated a mucus sheet which would retain most of the particles. It was only quite recently that Moore (1971) and Owen (1974) discovered that the latero-frontal cirri are not single cilia but actually cirri which can form a much finer mesh than can be observed under the light microscope; that this is also the case with *Dreissena* has been demonstrated here. During the effective stroke they probably expand to featherlike structures; by this means they transport the particles to the frontal cilia which lead them to the distal end of the filament and from there to the labial palps and the mouth. In *Mytilus* the latero-frontal cirri beat alternately (Dral 1967); hence their position in Fig. 2 may be an artifact. However, their general orientation should be that found at the beginning of the recovery stroke.

Considering the pressure differences across the cilia, Jørgensen (1981, 1982, 1983) postulated shear forces that contribute to particle capture, although Silvester and Sleigh (1984) conclude from their calculations that these forces need not necessarily be involved.

### *Particle retention*

Bivalves whose gills have latero-frontal cirri generally retain particles down to about 1 µm in diameter (Møhlenberg and Riisgård 1978). As pointed out by Jørgensen et al. (1984), *Dreissena* takes a rather special position within the scale; they still found 90% particle retention at 1 µm particle diameter. Our graph (Fig. 1) modifies this picture only slightly.

Ten Winkel and Davids (1983) concluded from a comparison of the composition of the seston and the stomach contents that *Dreissena* positively selects particles of 15–40 µm in diameter and rejects larger particles (e.g. *Asterionella*), either by production of pseudofaeces or by not incorporating them in the digestive diverticula. Mikheyev (1967) indicates that *Dreissena* can even ingest particles of 80–450 µm diameter, which means that they can also ingest small zooplankton organisms such as rotifers.

### *Pumping rates*

Variations in pumping rate have been described for different bivalve species by Brand and Taylor (1974): in some (predominantly subtidal) species they found intermittent pumping activity with intervals of some minutes' duration, whereas in others (predominantly intertidal species) pumping was more or less continuous with only very short interruptions. *Dreissena* would belong to the latter group, because the animals showed pauses of only a few seconds' duration. The picture Davenport and Woolmington (1982) obtained from *Mytilus edulis* is quite similar to ours. They also report variations in pumping activity which were correlated with the presence or absence of food and the oxygen content of the water.

Several mechanisms could be involved in the variation of the pumping rate. Foster-Smith (1976) discusses a temporary or permanent restriction of the diameter of the exhalant siphon, which would be the most direct way. Hildreth (1976) and Famme et al. (1986) demonstrated that even

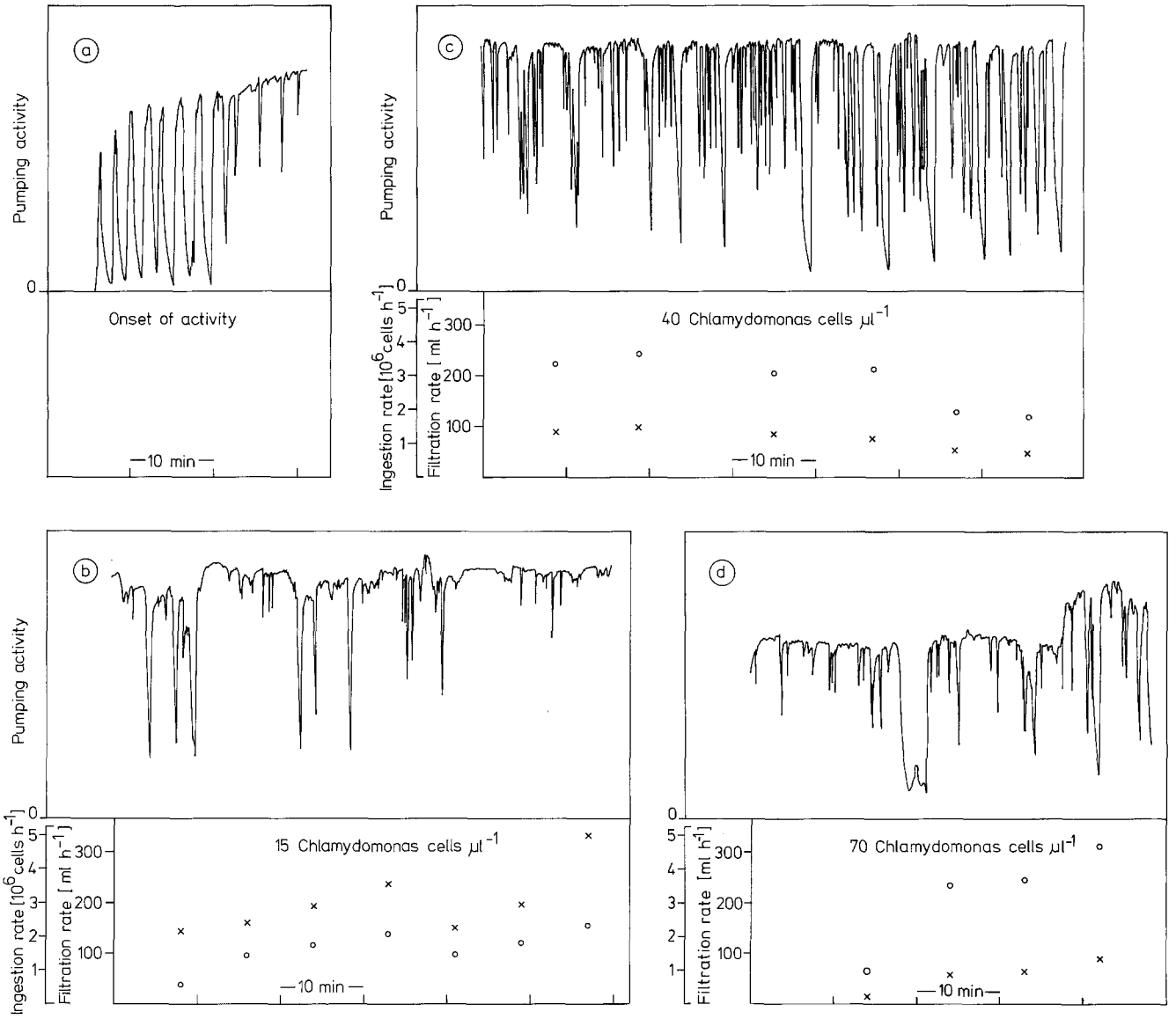


**Fig. 4a–d.** *Dreissena polymorpha:* Simultaneous registration of pumping activity (not calibrated), filtration rate (*crosses*) and ingestion rate (*circles*) under the conditions indicated

slight pressure changes across the gill would alter the pumping rate drastically. Dral (1968) also mentions a change in the orientation of the gills in the mantle cavity and inactivation of the lateral cilia.

Although variation in pumping rate should be reflected by variation in filtration rate, the reverse is not necessarily true: assuming a constant pumping rate, the mussel can theoretically remove quite different amounts of particles by inactivating groups of laterofrontal cirri (as observed here), shifting their beat trajectory, or widening the ostia (Dral 1968).

*Pseudofaeces*

Formation of pseudofaeces in *Dreissena* has frequently been reported in the literature (Stańczykowska et al. 1975; Ten Winkel and Davids 1983; Walz 1978). They are expelled from the mantle cavity via the inhalant siphon by means of a brief abrupt closure of the shells (Morton 1969). Walz (1978) recorded this in a *Nitzschia* suspension of 0.2 mg C $l^{-1}$, which was only one-tenth of the incipient limiting concentration in his experiments. We also observed production of pseudofaeces on various occasions e.g. when the animals had been left in the air for some time or when very dense suspensions (especially of *Dreissena* sperm) were present in the water.

There are two possible explanations for the formation of pseudofaeces. The first and most plausible is that the mussel needs to remove an excess of particles filtered out of the water just to keep the gills working. Thus formation of pseudofaeces is usually encountered in dense algal suspensions, although there are quite clear species-specific differences in the reaction (Foster-Smith 1975). The second is that pseudofaeces are involved in particle selection. This is important when the animal has to extract its food from a suspension which contains a large number of inorganic particles (Kiørboe and Møhlenberg 1981). Without pseudofaeces production, no such particle selection is possible

(Newell and Jordan 1983). Consequently, pseudofaeces production also depends on the quality of the particles in the water. From this point of view *Chlamydomonas* is an ideal tool to examine food uptake in *Dreissena*: it is retained with maximum efficiency and stimulates *Dreissena* to pseudofaeces production only above the incipient limiting concentration.

*Filtration and ingestion*

Filtration rates are usually considered when examining food uptake in bivalves. Many authors, however, have pointed out that the filtration rate frequently decreases with increasing food concentration for a large number of bivalve species examined: e.g. *Crassostrea virginica* (Loosanoff and Engle 1947; Loosanoff 1961), *Crassostrea gigas* (Gerdes 1983), *Ostrea edulis* (Wilson 1983), *Mya arenaria* (Stickney 1964) and *Mytilus edulis* (Davids 1964; Schulte 1975; Widdows et al. 1979). It is to Winter's (1973) credit that he pointed out that for bivalves there is also a range of algal concentrations over which the filtration rate is independent of the food concentration and another range over which the ingestion rate is independent of the food concentration. Walz (1978) has already described the same effect for *Dreissena polymorpha*.

This is probably a general phenomenon among suspension feeders. It has been demonstrated e.g. for the ciliate *Stentor coerulus* (Wenzel and Liebisch 1975), the rotifer *Brachionus plicatilis* (Chotiyaputta and Hirayama 1978), the larvae of the mussel *Mytilus edulis* (Sprung 1984), the brine shrimp *Artemia salina* (Reeve 1963), the copepod *Calanus pacificus* (Frost 1972), the cladocerans *Daphnia pulex* (Geller 1975), *Daphnia magna* (Kersting and van der Leeuw 1976; Porter et al. 1982) and *Daphnia hyalina* (Hopp and Horn 1984).

This does not apply at the extremes of the food concentration spectrum i.e. extremely dilute suspensions for which the animals may reduce their pumping or filtration rates (e.g. Loosanoff and Engle 1947; Davids 1964; Davenport and Woolmington 1982), or very dense suspensions, for which the ingestion rate of many bivalve species may drop owing to the formation of pseudofaeces (Foster-Smith 1975).

In this study, we wished to illustrate that almost every possible filtration rate and ingestion rate can be obtained below a certain maximum, depending on which food density has been chosen for the experiment. No doubt it is absolutely correct to call all these measured rates filtration or ingestion rates. However, a parameter is required that describes long-term potential food uptake under the given environmental conditions which is independent of the density of the suspension. Filtration capacity and ingestion capacity combined with the incipient limiting concentration describe this very well for *Dreissena* and certainly for most other suspension feeders.

It must also be pointed out that neither filtration capacity nor ingestion capacity necessarily vary strictly in parallel with internal or external factors (such as e.g. temperature or body size). Thus e.g. Walz (1978) found a temperature optimum at about 15° C for the filtration capacity and Morton (1971) found that ingestion capacity (filtration rates at high particle concentrations) continued to increase up to 31° C, at which point his animals died. In addition, Mayzaud and Poulet (1978) pointed out for copepod species that the feeding potential, i.e. the ingestion capacity, can adapt to certain food levels in the annual cycle. They relate this effect to the set of digestive enzymes detected. This in turn is not automatically reflected by the filtration capacity.

When allometry of growth processes is discussed in terms of weight exponents e.g. of respiration and food uptake, only the exponent of the filtration rate (or better: filtration capacity) is considered (Bayne and Newell 1983). Of course, this is a limiting factor in dilute suspensions; but does the ingestion capacity, the other limiting factor in dense food suspensions, necessarily follow the same laws?

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