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Feeding behaviour and morphology of filtering combs of *Daphnia galeata*

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Abstract

The population of *Daphnia galeata* Sars from the fish pond Velký Pálenec (Blatná, Czechoslovakia) living in high food conditions (7 mgC l^{-1}) was characterized by a small size of the filtering comb on the thoracic limb 3, measured as seta length, length of the base of the comb and number of setae (population 1). One month cultivation of this population in low food conditions (1.5 mgC l^{-1}) in the laboratory resulted in twofold increase in size of the filtering comb (population 2). Filtering and ingestion rates of both populations were measured at eight concentrations of food (approximately 0.025–3.2 mgC l^{-1}) using ^{14}C labeled *Scenedesmus acutus*. The results show that size of the filtering combs influences considerably feeding behavior of *Daphnia*. The comparison of animals with the same body length suggests that the population with a large comb feeds at concentration of food below 0.4 mgC l^{-1} more intensively and reaches the maximum of the filtering rate at a lower concentration than the population with a small comb. The situation is opposite at concentration above 0.4 mgC l^{-1}. The higher values of theoretical flow in population with a small projection of filtering area suggest that this population has to compensate disadvantage of a small comb with the higher appendages beat frequency.

Introduction

Egloff & Palmer (1971) first showed the possible positive correlation between the area of the filtering combs of limbs 3 and 4 and the filtering rate in *Daphnia*. They suggested a very complex approach to investigation of morphology and feeding behavior that had unfortunately only a few followers. Nevertheless very important discoveries were made in the field of morphology of the filtering combs of the thoracic limbs concerning a large scale change of these structures under variable food conditions (Kořínek *et al.*, 1981, 1986; Koza & Kořínek, 1985). The aim of this study was to find appropriate consequences of the change of morphology of the filtering comb on feeding behavior of *Daphnia galeata*.

Materials and methods

The experiments presented in this paper were conducted at the Hydrobiological station of Charles University near the town Blatná in south-western Bohemia from August to September of 1986.

Experimental animals

Two populations of *Daphnia galeata* Sars were used in experiments. The first population (population 1) was collected from the fish pond Velký Pálenec (area 31 ha, mean depth 1.4 m) August 30, 1986, 24 hours before the experiment. Mean concentration of seston varied about 7 mgC l^{-1}

in this pond. Approximately 300 animals were immediately separated from other zooplankton with a wide pipette and placed in water from the locality filtered through a 39 μm mesh, at a temperature 20 °C and natural illumination. The second population (population 2) coming from the same lake was collected August 17, 1986, kept under laboratory conditions at a temperature of 20 °C and natural illumination and fed with *Scenedesmus acutus* at a concentration of about 1.5 mgC l^{-1} till September 21, 1986 when the experiment was carried out.

Feeding suspension

The axenic culture of *Scenedesmus acutus* Mayen used for preparation of both active and non-active feeding suspensions was received from the collection of algae of the Institute of Botany, Czechoslovak Academy of Sciences, Třeboň.

Non-active suspension was produced on Bold basal medium – Bristol (Nichols, 1975) in a semi-continual sterile cultivator (a glass tube 60 cm long and 6 cm in diameter with two parallel fluorescent tubes, aeration and peristaltic pump for input of fresh medium) and harvested daily. To be received more easily, the required concentration of food was prepared according to the calibration graph between extinction (5 cm cuvette, 750 nm) and total particulate volume (TPV, mm^3 l^{-1}) of cells in the peak of size distribution, and between extinction and organic carbon (C, mg l^{-1}). In the log-log plot the relation was linear in the range of concentrations 1–100 mgC l^{-1}. The same size distribution is essential for validity of this relation. I took care the feeding suspension was composed only from single cells; in other case, sonication was used to destroy two or four cell cenobia. Besides, the feeding suspension used in the experiment was checked directly for content of organic carbon and size distribution.

A Coulter counter – model ZB extended with an 18 channel analyzer of our own construction, microcomputer and dot-matrix printer was used to analyze cell-size distribution and TPV of non-active algal culture (Fig. 1). Samples were gently prefixed with the Lugol solution (100 μl to 100 ml) at first and then a solution containing NaCl and formalin was added. Final concentrations of NaCl and formalin in samples were 2% and 0.9%, respectively. The electrolyte with formalin was filtered carefully through nitro-cellulose membrane filters Synpor® (Barvy a laky, Praha), finishing this procedure with a 0.3 μm pore sized filter (Synpor No 7).

Organic carbon was estimated by multiplication of the value of dichromate reducing capacity of organic material by factor 3 according to Mackereth *et al.* (1978).

Active suspension of *Scenedesmus acutus* was prepared from cultures growing on Bristol in 100 ml Erlenmayer flasks under controlled axenic conditions. Flasks were placed in a shaker at 20 °C, under continuous illumination of 1000 Lux. About one week before the experiment an appropriate volume of the culture was resuspended in a flask filled with the minimum maintenance medium (MMM) prepared by

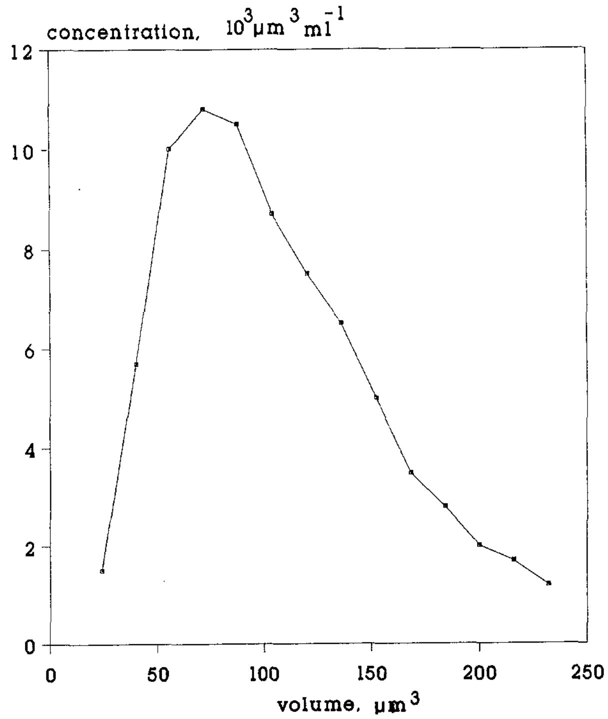


Fig. 1. Arithmetical size spectrum of the culture of *Scenedesmus acutus* (single cells) used in experiments.

Thompson *et al.* (1982). This medium is free of inorganic carbon and pH 8.6 is maintained by TRIS. After some days 5.5–11 kBq ^{14}C-labelled $NaCO_3$ was added to 50 ml of the culture. Immediately before the beginning of the experiment, the labelled culture was checked under microscope (if necessary, sonication was carried out), centrifuged three times (15 min, 2000 RPM) and redispersed again in the fresh MMM. After this procedure all activity was in cells only. Extinction was measured and concentration of the basic suspension was calculated from the calibration graph; required concentrations were prepared then by diluting the basic suspension. Mean activity in experiments ranged, depending on food concentration, from 16.7 to 200 Bq ml^{-1}.

Diluting water for the experiment was taken from the fish pond Smyslov, near the Hydrobiological station, which was in a clear water phase during the experimental period. Water was filtered through a Whatman GF/C filter and a series of Synpor filters, diluted ten times with distilled water to decrease the content of dissolved organic carbon and finally filtered through Synpor No 7. After several hours of aeration in a thermostat the temperature of the water was 20 °C, pH 7.1, calcium about 7 mg l^{-1}, DOC 0.9 mg l^{-1} and the water was saturated with oxygen to 100%.

Experimental design

Eight hours before the planned start of each experiment, the logarithmic scale of eight concentrations of the feeding suspension (approximately 3.2, 1.6, 0.8, 0.4, 0.2, 0.1, 0.05 and 0.025 mgC l^{-1}) was prepared using non-active suspension and diluting water. About 150 individuals of *Daphnia* were transported with a pipette to 120 ml narrow necked stoppered glass bottles containing feeding suspensions through several 'washing baths' with diluting water. *Daphnia* were sorted to have all size groups proportionally represented in each concentration. There were 15–20 animals in a bottle to keep the possible effect of crowding on the filtering rate constant (Helgen, 1987). Bottles were not closed with stoppers but their narrow necks protected *Daphnia* from catching on the surface of the water. Then all bottles were put into the thermostat (20 °C, 1000 Lux) for *Daphnia* adaptation to a new concentration of food. Time of adaptation was set according to data of Muck & Lampert (1984) who found a dramatic increase in the filtering rate in animals transferred from high to low concentrations of food, with the maximum two hours after the change. During the adaptation the content of the bottles was gently mixed with a pipette several times to protect sedimentation of cells. After 4–6 hours the bottles were brought to the laboratory where the same experimental conditions were arranged (20 °C, 1000 Lux). Approximately 30 minutes before the experiment all bottles were mixed again, almost the whole volume of feeding suspension were gently sucked off from each bottle (with a 200 ml capacity syringe with a rubber tube, covered with a 100 μm mesh on the mouth) and refilled with a fresh feeding suspension. This step was essential to return oxygen saturation and concentration of food to original values.

The proper measuring of feeding activity took place at midnight to avoid the influence of diurnal variations of feeding behavior (Starkweather, 1983) though in experiments with *Daphnia* from shallow lakes no significant diurnal rhythms were found (Stuchlík, 1982). The exposure started with replacement of an appropriate volume of the feeding non-active suspension with the ^{14}C-labelled one. The time of exposure was 6 minutes for concentrations 3.2–0.4 mgC l^{-1}, 20–30 minutes for 0.2–0.1 mgC l^{-1} and 40–60 minutes for concentrations 0.05–0.025 mgC l^{-1}. As it follows from published data (Geller, 1975; Muck & Lampert, 1984) and from conducted methodical experiment (Fig. 2), these times of exposure did not probably exceed the gut passage time. During the exposure the content of the bottles was mixed gently several times to protect sedimentation of food. After a fixed time period the content of each bottle was filtered through a sieve with 99 μm mesh. *Daphnia* remaining on the sieve were narcotized in soda water, gently but thoroughly

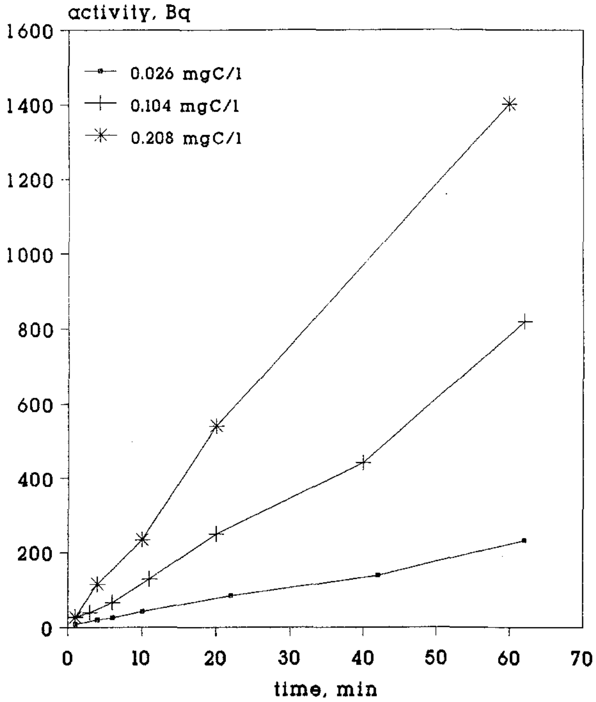


Fig. 2. Dependence of activity of adult *Daphnia pulicaria* on time of exposure at various concentrations of food.

rinsed with soda water again and placed with a pipette into Petri dishes on small GF/C filters with a diameter of 8 mm which layed on a wet filter paper. Closed dishes were stored in a refrigerator. 250 μl of the feeding suspension was pipetted into the vial and mixed with 1 ml of NCS tissue solubilizer (Amersham). Alternatively 1 ml of the feeding suspension was filtered through a GF/C filter to assure the measurable part of activity was not released from the labelled cells.

When the experiment was finished but not later than in two following days, body length of animals without a spine was measured under a microscope, directly on the wet small GF/C filters that are sufficiently transparent. The whole filter with *Daphnia* was then put into the vials. An appropriate volume of the tissue solubilizer (0.4 ml as a rule) was added immediately. 3–5 filters with a drop of water but without *Daphnia* were used as a blank.

All samples with the solubilizer were heated to 50 °C overnight. After completing 10 ml of the scintillation cocktail SLT 61 (Spolana Neratovice), the activity of samples was measured by the liquid scintillation counter Tri-Carb 300C (Packard Canberra).

The proposal of the method for storing *Daphnia* in a refrigerator within a period before measuring is based on the supposition that labelled cells in the gut or in the food grove of *Daphnia* will lose their activity more slowly than after preservation with formalin, ethanol or Lugol solution. Several experiments were conducted to find time dependent losses of activity. The results showed that the percentage of losses is linear in time and can be described with the following relation:

$$\% \text{ of losses} = 12.44 + 10.36 \log t,$$

where t = time in hours. Correction factors calculated according to this relation ranged from 1.35 to 1.44 for the presented experiments. In spite of the fact that the losses were lower than in formalin or ethanol (Holtby & Knoechel, 1981; Mourelatos, 1990), the method does not satisfy requirements regarding the losses of activity and can be recommended only if animals are measured within one hour. In this case losses do not exceed 15%. Manipulation with animals laying on small GF/C filters is extremely fast and easy. In any case the filters protect against next contingent losses of activity in particles that can be released from gut and food grove. Handling animals on filters could be combined with rapid freezing on dry ice (Sierzen & Waltras, 1987) or with freezing and lyophilization (Berberovic & Pinto-Coelho, 1989), thus providing a good tool for individual

Filtering rate (FR) was calculated according to the following relation:

$$FR = \frac{(A_D - B_D) \cdot 60}{(A_{FS} - B_{FS}) \cdot t} \ (\text{ml ind}^{-1}\,\text{h}^{-1}),$$

where A_D and A_{FS} are activities in *Daphnia* and feeding suspension (ml^{-1}), resp., B_D and B_{FS} are appropriate blanks and t is time of exposure in minutes. Ingestion rate is then:

$$IR = FR \cdot c \ (\text{mgC ind}^{-1}\,\text{h}^{-1}),$$

where c is concentration of food in mgC l^{-1}.

Morphology of the filtering screen

Total body length, length of the base of the comb (comb length), seta length and number of setae of the filtering comb of the thoracic limb 3 within the whole range of size of both populations were measured under a microscope. Usually about 12 animals were used. Parameters listed above were found to be the most important for the change of projection of filtering area (Kořínek *et al.*, 1986). Relative (size specific) comb length and seta length recognized as closed to constant for a population (Pop, 1991) were then calculated.

Results

Experimentally induced change of the filtering screen

Transferring *Daphnia galeata* from the fish pond, with high concentration of food and with heavy fish predation to a laboratory and, 35 days of cultivation under conditions of relatively low concentration of food and without predation, changed the original population completely. Compared populations 1 and 2 differ significantly both in range of size and length-weight relationship (Novotná, 1987) and especially in morphology of the filtering comb of thoracic appendages (Table 1). Length of the base of the comb and length of seta of the comb on limb 3 depend linearly on body length with the slope close to 1. The mean number of setae in the comb, just like relative comb and seta lengths, are independent of body length and thus are advantageous criteria for investigations of morphology of the filtering screen (Kořínek *et al.*, 1986; Pop, 1991). Mean values of these parameters within the population have very narrow confidence intervals (Table 1) and they are usually expressed in percentage of body length (Fig. 3). The results presented here show that population 2, coming from a lower concentration of food, exceeds population 1 in all parameters under investigation.

Feeding behavior of population 1

Unfortunately I could not secure all size groups of this population to be significantly distributed in the experiment and thus mean values only for animals in the range of size 1.15–1.40 mm were finally calculated (Table 2). If concentration of food decreased, the mean filtering rate increased reaching the maximum at 0.14 mgC l^{-1}. The next

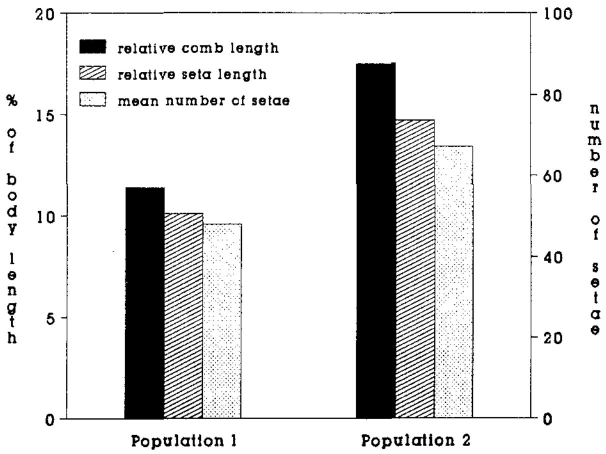


Fig. 3. Comparison of size of the filtering comb between populations 1 and 2 of *Daphnia galeata*.

Table 1. Coefficients of power regression of the comb length (CL) and seta lengths (SL), both in μm, on body length (L) in mm and mean size specific comb length (CL/L) and seta length (SL/L) and number of setae (NS) including 95% confidence limit of limb 3 in both populations.

	CL			SL			CL/L	± cl	SL/L	± cl	NS	± cl
	a	b	r	a	b	r						
Population 1	112.17	0.82	0.98	99.48	0.89	0.98	114.50	5.02	101.80	3.55	47.60	1.15
Population 2	181.27	0.85	0.99	149.91	0.91	1.00	175.00	6.88	146.90	3.68	66.70	2.44

Table 2. Experimental conditions and feeding behaviour of population 1. Animals in the range of size 1.15–1.40 mm.

Concentration, mgC l^{-1}	4.16	2.08	0.37	0.53	0.27	0.14	0.07	0.038
Mean L, mm	1.23	1.24	1.24	1.24	1.25	1.26	1.24	1.26
(± 95% cl)	(0.04)	(0.07)	(0.04)	(0.04)	(0.05)	(0.04)	(0.04)	(0.05)
Mean FR, ml ind^{-1} h^{-1}	0.07	0.11	0.20	0.21	0.18	0.39	0.20	0.14
(± 95% cl)	(0.01)	(0.02)	(0.03)	(0.03)	(0.01)	(0.12)	(0.04)	(0.04)
Number of animals	5	6	7	8	11	6	9	9

Table 3. Experimental conditions and coefficients of power regression of filtering rate on body length of population 2.

Concentration, mgC l^{-1}	0.03	0.05	0.10	0.19	0.37	0.72	1.44	2.84
Number of animals	6	15	16	13	18	18	17	17
a	0.05	0.04	0.06	0.15	0.17	0.21	0.23	0.30
b	2.23	3.19	2.82	2.28	3.07	3.14	2.76	2.81
r	0.95	0.92	0.76	0.78	0.98	0.92	0.91	0.93

reduction of food concentration was accompanied with a drop of the filtering rate. Ingestion rate grew together with concentration of food, identically to the known model. It seems to reach saturation at concentration about 0.7 mgC l^{-1} but next two points defy this idea.

Feeding behavior of population 2

This experiment provided me with more detailed information about feeding behavior of *Daphnia galeata*. Filtering rate is a power function of the body length with a slope ranging from 2.23 to 3.19 (Fig. 4, Table 3). There is no relation of value of the slope to the concentration of food while the value of the intercept increases with the concentration of food. Filtering and ingestion rates for animals with a size of 0.8, 1.0, 1.5 and 2.0 mm were calculated then and plotted against the concentration of food (Fig. 5). Filtering rate increases in relation to the drop of the concentration of food but does not reach the plateau. Ingestion rate, like in the experiment with population 1, fit the saturation model rather well excluding last two points. The model I used had to suit the following assumptions: 1. saturation course is used for ingestion rate, 2. the drop after reaching the maximum occurs if it is used for the filtering rate, 3. it must go through the origin in both the cases. Then

$$IR = \frac{k_1 \cdot c^2}{k_2 + c^2} \text{ and } FR = \frac{k_1 \cdot c}{k_2 + c^2},$$

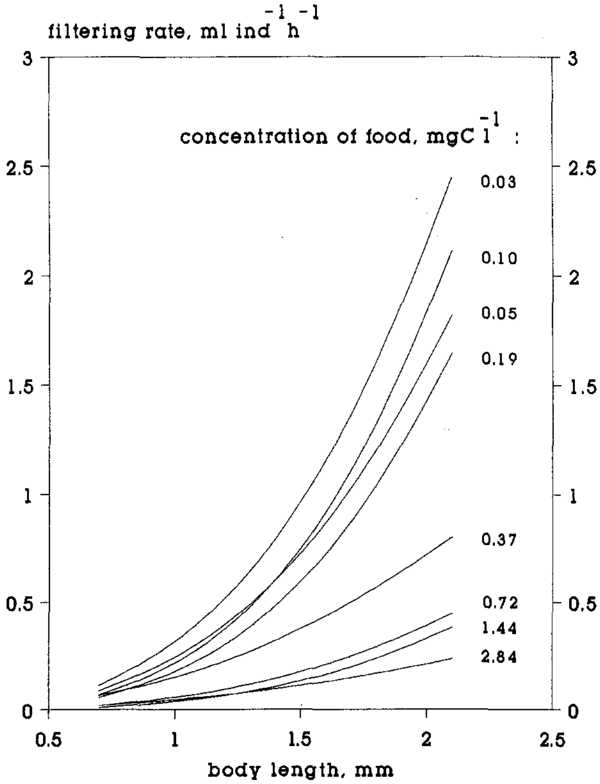


Fig. 4. Power curve fit of filtering rate on body length at eight concentrations of food in population 2.

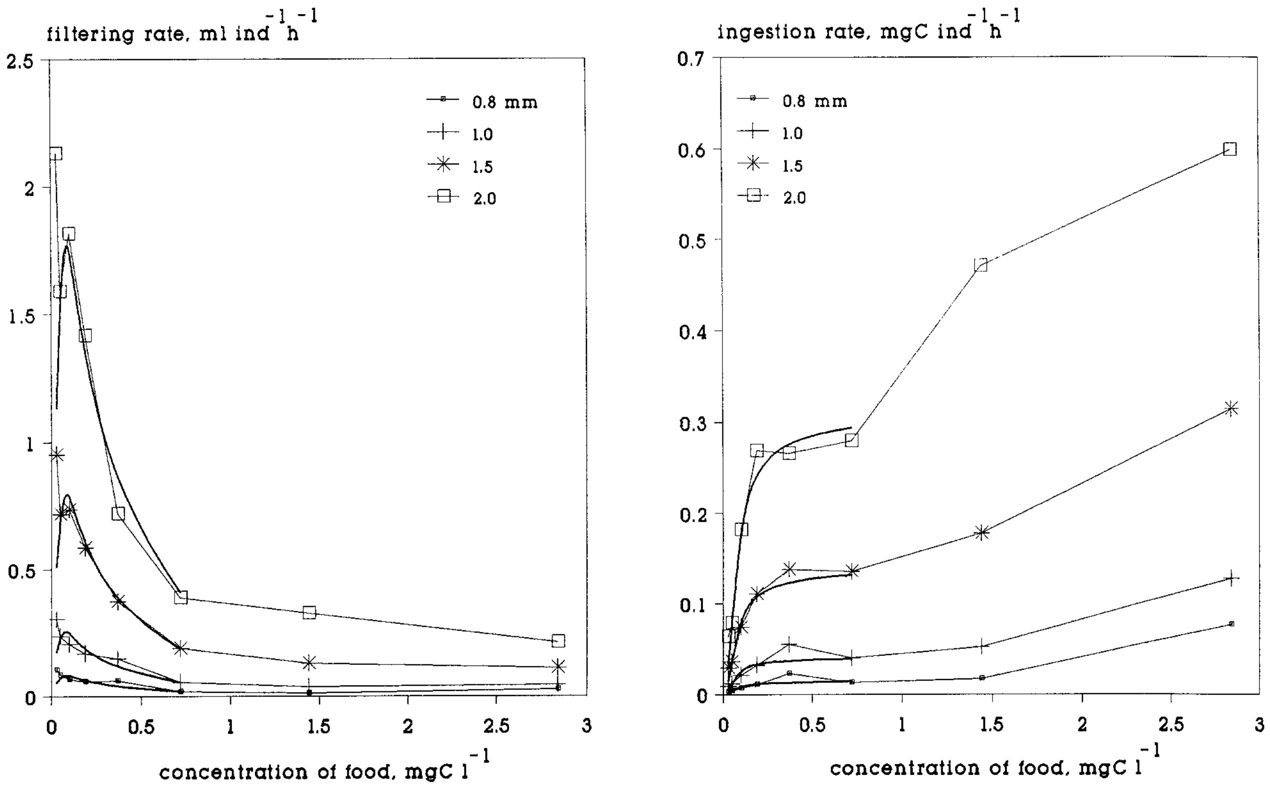


Fig. 5. Plots of filtering and ingestion rates on concentration of food within animals of population 2 with varied body length. Calculation of the points based on parameters of power regression from Table 3 (thin lines). Coefficients of the curves provided by the model (thick lines) are in Table 4.

where c is concentration of food and k_1, k_2 are coefficients. To estimate values of the coefficients k_1, k_2, I plotted 1/IR against $1/c^2$ and calculated intercept and slope of the linear regression, where $a = 1/k_1$ and $b = k_2/k_1$. The last two points lay out of this model and the first one had to be excluded because it affected unrealistically the fitting of the model after the linearization (Fig. 5, Table 4).

Table 4. Coefficients (a, b, r) of linear regression of 1/IR on $1/c^2$ and coefficients (k_1, k_2) of relation IR = $(k_1 \cdot c^2)/(k_2 + c^2)$, where $a = 1/k_1$ and $b = k_2/k_1$, IR is ingestion rate, in mgC ind^{-1} h^{-1}, c is concentration of food, in mgC l^{-1}. Calculation based on concentrations 0.05–0.72 mgC l^{-1}.

Size, mm	a	b	r	k_1	k_2
0.8	71.118	0.463	0.966	0.014	0.007
1.0	24.863	0.151	0.976	0.040	0.006
1.5	7.467	0.051	0.998	0.134	0.007
2.0	3.359	0.023	0.998	0.298	0.007

Comparison of both populations

It is not easy to decide whether the feeding behavior is to be compared for animals with the same body size, or body mass or finally with the same filtering combs size. As regards population 1, I have only the size group 1.15–1.40 mm at my disposal. The mean body length is about 1.25 mm (Table 2), dry weight 8.85 μg (Novotná, 1987) and the average length of the seta is 121 μm. The members of population 2 with equal length of seta have, however, body length of only 0.8 mm. Finally I computed filtering and ingestion rates and morphological parameters for population 2 as a mean of values calculated in the range of size 1.15–1.40 mm, using appropriate regression equations (mean body length 1.28 mm and dry weight 8.47 μm – Novotná, 1987). The fact that dry weights of both populations are close allows me to suppose that the filtering and ingestion rates presented for animals with the same body length are in a similar ratio as their size-specific values (Fig. 6). The same equation and method were applied to fit data with the model as described above. Filtering and ingestion rates of the population with a large filtering comb (population 2) significantly exceed values of population 1 below concentration of food 0.4 mgC l^{-1}. At a concentration where the filtering rate of population 1 is decreasing, that of population 2 still increases and does not reach the true plateau. Starting from the data provided by the model, the maximum of the filtering rate of population 2 is almost two times higher and incipient limiting level nearly at half concentration if compared with population 1. This means the ingestion rate at incipient limiting level is practically the same in both populations (Fig. 7). Different results were recorded at the concentration above 0.4 mgC l^{-1}. Population 1 tends to higher filtering and ingestion rates but differences are not so manifest (Fig. 6).

Flow regimes

Considering that the true projection of filtering area (PFA) was not measured for populations under study, I used a converting equation for the relation between seta length and projection of filtering area which is available for the limb 3 of *Daphnia pulicaria* (Pop, 1991). On the supposition that projection of filtering area of limb 4 is 55.4% of limb 3 (calculation based on data of Křepelová (1980)), total projection of filtering area can be estimated from seta length of the filtering comb of limb 3 (SL):

$$\text{PFA} = 5.840\ \text{SL}^{1.996}.$$

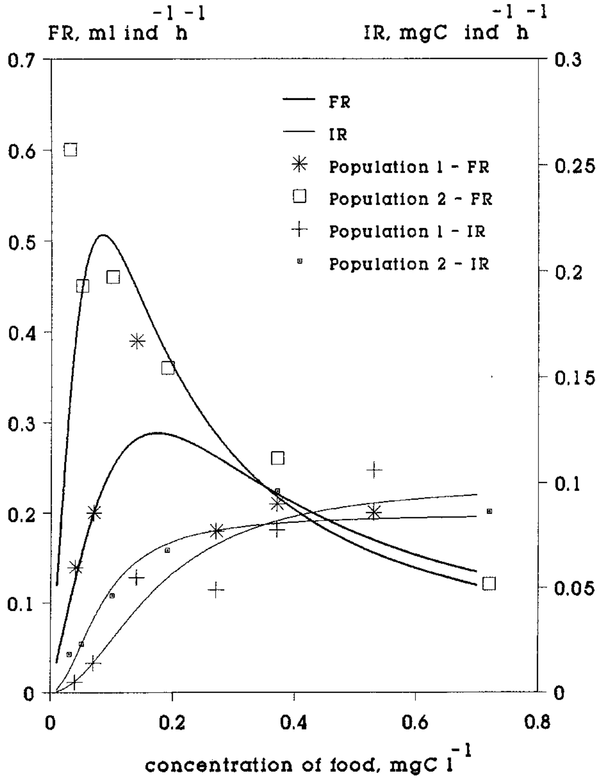


Fig. 6. Comparison of feeding behavior of populations 1 and 2 of *Daphnia galeata* with the same body length.

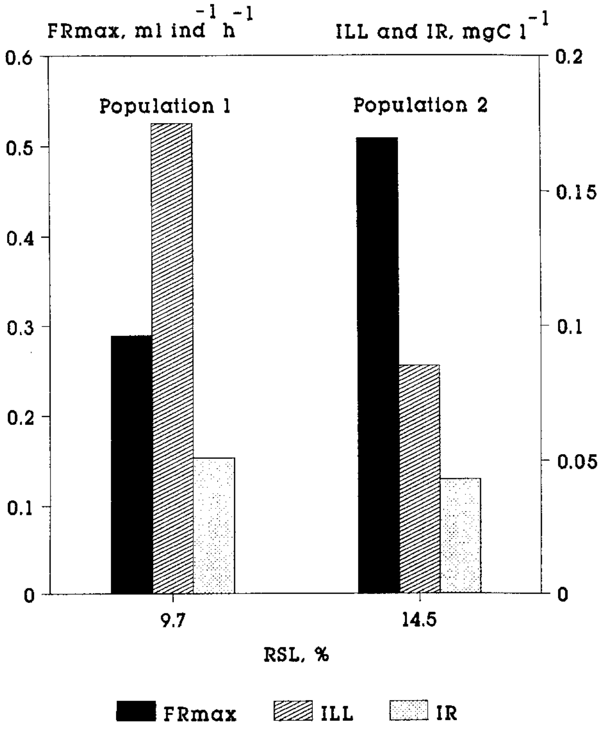
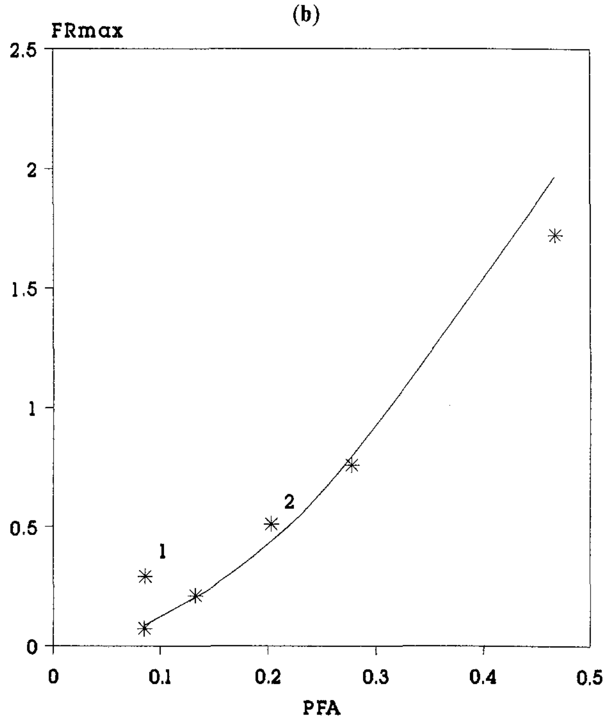


Fig. 7. Basic parameters of feeding response curves and relative seta length summarized for populations 1 and 2 of *Daphnia galeata*.

The ratio of the filtering rate to projection of filtering area sets the value of a theoretical flow. Plots of maximal filtering rate, projection of filtering area and flow vs. body length, maximal filtering rate vs. projection of filtering area and flow vs. concentration of food are presented in Fig. 8. For the values of coefficients of the power regression see Table 5. Excluding the dependence of projection of filtering area on body length, the slopes of the relations are somewhat higher than could be expected from theoretical considerations. There are manifest differences between populations 1 and 2 within all relations shown. In plots of flow on body length and on concentration of food, the values of a theoretical flow calculated for population 1 exceed those for population 2 with one exception at the lowest concentration. This means that population 1, which is handicapped by smaller projection of filtering area, has to compensate for it, probably by a higher beat frequency of limbs.



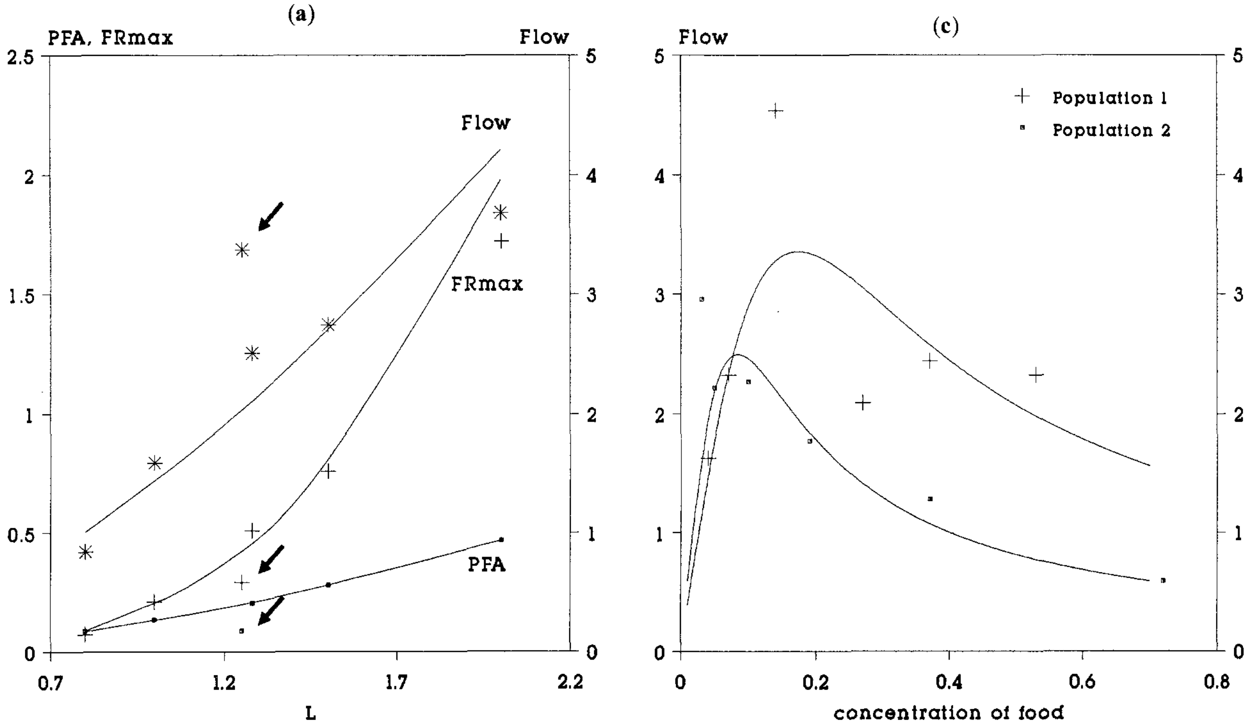


Fig. 8. Relations of projection of filtering area (PFA), maximal filtering rate (FR_{max}) and flow to body length (L) – a; relation of maximal filtering rate to projection of filtering area – b and relation of flow to concentration of food – c for both populations of *Daphnia galeata*. PFA is in mm^2, FR_{max} is in ml ind^{-1} h^{-1}, flow is in ml mm^{-2} h^{-1}, concentration of food is in mgC l^{-1} and L is in mm. Arrows indicate points for population 1, figures 1 and 2 are points for animals from populations 1 and 2 with the same body length. For parameters of power regression curves, see Table 5.

Table 5. Coefficients of power regression of dependence of maximum filtering rate (FR_{max}), in ml ind^{-1} h^{-1}, on body length (L), in mm, and projection of filtering area (PFA), in mm^2, and projection of filtering area and flow, in ml mm^{-2} h^{-1}, on body length of population 2.

Dependent variable	Independent variable	a	b	r
FR_{max}	L	0.18	3.42	0.99
PFA	L	0.13	1.85	1.00
Flow	L	1.42	1.56	0.96
FR_{max}	PFA	8.03	1.85	0.99

Discussion

Today there is not doubt that cladocerans can change the morphology of their filtering screen (especially the area of the combs of limbs 3 and 4) depending on the change of concentration of food (Kořínek *et al.*, 1981, 1986). This ability is specific to some species and reflects their ecological strategy and is the most developed in the species *Daphnia pulicaria*. Its ratio of minimal to maximal projection of filtering area is more than two (Koza & Kořínek, 1985). An experimentally induced change and recorded differences within populations 1 and 2 show this ability is practically the same in *Daphnia galeata*. Projection of filtering area calculated for population 1 is the lowest which has ever been found for this species while projection of filtering area calculated for population 2 is equal to the maximal values published for the population from Lake Constance (Brendelberger & Geller, 1986) and from the drinking water reservoir Želivka, in Czechoslovakia (Kořínek *et al.*, 1986). In the past it was supposed that the maximal change of projection of filtering area within a natural populations need several weeks to manifest itself (Kořínek *et al.*, 1986); a more recent study showed however that the reaction of an individual animal is immediate (Pop, 1991). Nevertheless the data presented here for *Daphnia galeata* are the first data recording such a dramatic increase of projection of filtering area, the comb and the seta length and number of setae. The observations published formerly present rather the decrease of projection of filtering area as a result of a growth of food concentration (Kořínek *et al.*, 1986).

The original rectilinear model of the dependency of filtering and ingestion rates on concentration of food in daphnids according to which each filtering rate below incipient limiting level is equal to maximal filtering rate (McMahon & Rigler, 1965) became invalid when data appeared that filtering rate can decrease again after reaching its maximum (Horton *et al.*, 1979; Muck & Lampert, 1980; Nikolaev & Postnov, 1981; Filippova & Postnov, 1988), as described in calanoids (Frost, 1975). Muck & Lampert (1980), who worked with daphnids from Lake Constance (probably a mixture of *Daphnia galeata* and *D. hyalina*), explained the drop of filtering rate at very low concentrations of food as exhaustion of animals in the process of adaptation and supported this hypothesis experimentally (Muck & Lampert, 1984; Lampert & Muck, 1985). In my experiments I tried to minimize the possible effect of exhaustion by an appropriate time of adaptation. In experiments by Nikolaev & Postnov (1981) and Filippova & Postnov (1988) with *Daphnia longispina*, *Ceriodaphnia quadrangula*, *Moina macrocopa*, *Daphnia magna* and *Simocephalus vetulus* where the cell count method and 5–10 hour exposures were used, the mechanism of exhaustion is improbable. This drop in filtering rate was also recorded by Ganf & Shiel (1985) in *Daphnia carinata* and *Ceriodaphnia quadrangula* (Coulter counter method and 2–4 hour exposures), by Holm *et al.* (1983) in *Daphnia pulex* (cell count method) and by several authors who used the radio-isotopic method: Horton *et al.* (1979) in *Daphnia pulex* (only one hour adaptation) and Porter *et al.* (1982) in *Daphnia magna* where moreover the decrease of beating rate of thoracic appendages and mandibles was recorded, too. The first data regarding retardation of thoracic appendages and mandibles beat frequency at very low concentrations of food were published by Burns (1968). This mechanism seems to be involved in the drop of filtering rate mentioned, though the beating of thoracic limbs does not have to be connected with filtering of food (M. Gophen, pers. com.). In my opinion, whether the drop of filtering rate was found or not depended 1. on the range of concentrations in the experiment and 2. on the feeding history of the examined population which also conspicuously influences morphology of the filtering screen (Fig. 6). Population 2 probably did not reach this point and its filtering rate curve is similar to the response found in starved *Daphnia magna* (Ringelberg & Royackers, 1985). Geller (1975) in experiments with *Daphnia pulex* also found filtering rate at very low concentrations to be higher for starved than for prefed animals though typical response curves were not reached in either cases.

The curves of ingestion rate seem to reach saturation at concentration 0.7 mgC l^{-1}. The high values of ingestion rates at higher concentrations indicate possible influence of so called excessive feeding (Ivanova, 1970). Animals probably can not decrease filtering rate because it may be necessary for respiration (Gutelmacher *et al.*, 1988), and postabdomen rejection rate, although it grows with concentration of food, is not able to prevent from gut filling. Thus I suppose short retention time and partial digestion of food in the gut are mechanisms that regulate real ingestion rate. Ingestion without saturation is also typical for hungry animals (Geller, 1975; Ringelberg & Royackers, 1985). Paffenhöfer & Orcutt (1986) received similar results in an experiment with juveniles of *Penilia avirostris*; they explain this phenomenon as an absence of food satiation.

There are many equations which were used to describe the relation between filtering and ingestion rates and concentration of food (Mullin *et al.*, 1975; Nikolaev & Postnov, 1981; Porter *et al.*, 1982; Peters, 1984; Lampert, 1987; Gutelmacher *et al.*, 1988). I also tried to find the 'true' model to fit my data. The generalization was finally done after excluding the two highest concentrations and the lowest concentration (in both populations) provided the best fitting of data. The most questionable point of the presented models was excluding of the lowest concentration which was necessary because of the method used for computation of the coefficients. The low number of points did not allow distinguishing what is the trend of filtering rate of population 2 – whether it is still growing or falling already. In any case the model supposes the final drop of filtering rate at the end.

The fact that the population with a smaller projection of filtering area gathers food with a lower efficiency below food concentration about 0.4 mgC l^{-1}, and is limited by deficiency of food earlier than the population with a larger projection of filtering area, in contrast to the situation above this concentration, corresponds to 'oligotrophic' and 'eutrophic' types of feeding behavior recognized by Kasprzak *et al.* (1986). The data presented demonstrate that *Daphnia galeata* is able to change from the first type to the second one within one month.

Regarding the positive correlation between filtering rate and projection of filtering area my findings are rather close to the older data (Egloff & Palmer, 1971; Arruda, 1983; Ganf & Shiel, 1985) though there are some slight differences in the values of slopes. The fact that *Daphnia* with larger area of the filtering comb also has a higher filtering rate was recorded for the first time by Egloff & Palmer (1971). Unfortunately they did not measure filtering rate regularly and used only published data. The following authors were more skeptical in evaluating the influence of area of the filtering comb on filtering rate. They ascribed the main effect rather to some other factors such as gut fullness and/or capture efficiency (Arruda, 1983; Porter *et al.*, 1983 and Ganf & Shiel, 1985). On the other hand, if any concentration below incipient limiting level is used, we can hardly expect to measure the true maximal filtering rate. Moreover, it is really difficult to carry out measurements of filtering rate where only one simple factor varies and the other remain constant. This may results in poor comparability of data.

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