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EXPLOITATIVE COMPETITION IN DIFFERENTLY SIZED *DAPHNIA* SPECIES: A MECHANISTIC EXPLANATION

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Abstract. The concept of the threshold food concentration that allows metabolic maintenance of an animal (C_0) has been used as an analogy to Tilman's R^* (equilibrium resource requirements) to explain competitive abilities of cladoceran species. Until now, however, theoretical analysis has been hampered because C_0 was measured in experiments where cladoceran growth was determined in response to fixed, low food concentrations, not as a result of the cladocerans' grazing activity. C_0 is an indirect estimate from nonequilibrium conditions. It still needs to be shown that growing *Daphnia* are efficient enough to suppress resource concentrations to levels equivalent to their C_0 . We designed flow-through experiments to establish equilibrium conditions between algal inflow and cladoceran population biomass with three differently sized *Daphnia* species. The equilibrium food concentration resulting from the daphniids' grazing activity was labeled C^* , as it can be used to predict competitive abilities in analogy to Tilman's R^* . Equilibrium was reached in each experiment. *Daphnia* grew to carrying capacity without fluctuations in numbers or biomass, and biomass remained constant after this level was reached. Mortality was compensated for by somatic growth or, in the case of the small species *D. ambigua*, by production of offspring. When the carrying capacity was reached, algal concentrations remained constant at C^* . As predicted from previous growth experiments, larger species suppressed algal concentrations to lower levels, i.e., they were predicted to have higher competitive ability. This prediction was tested in a mixed-species experiment with *D. pulicaria* and the smaller *D. galeata*. That experiment clearly demonstrated the mechanism of exploitative competition. In the beginning, the smaller *D. galeata* performed better, but as soon as the food concentration fell below *D. galeata*'s individually determined C^* , the smaller species suffered mortality. At this point, *D. pulicaria* had not yet reached its C^* . It continued to grow and replaced *D. galeata*. Numerical values of *D. pulicaria*'s C^* were slightly higher than the independently determined, corresponding C_0 values. This was to be expected as C_0 applies to zero mortality. However, the rank order among species was identical for both characteristics. We propose that both C^* and C_0 have strong predictive power for mechanistic models of competitive interactions.

Key words: body size; carrying capacity; competitive ability; *Daphnia*; resource equilibrium; threshold concentration.

INTRODUCTION

Cladocerans like *Daphnia* are key species in pelagic freshwater food webs. Because they are relatively non-selective filter feeders (Lampert 1987), the food spectra of different species overlap to a large degree (Kerfoot et al. 1985) and hence there is a considerable range of seston particles that can be considered a single shared resource. This makes it possible to use Tilman's (1982) concept of R^* to predict competitive relationships among various species of *Daphnia*. In Tilman's mechanistic theory of resource competition, R^* represents the amount of resource that a species requires in order to maintain a stable equilibrium population. The main advantage of Tilman's theory is that R^* is a species-specific physiological characteristic that can be measured for individual species and can be applied to pre-

dict the outcome of competition between species. The species with the lowest R^* will always be the superior competitor.

Until today, Tilman's models have been tested for plankton exclusively in chemostats, which cannot be used for crustaceans because these animals are strong swimmers and can avoid being washed out. Rotifers are the only metazoans small enough to be cultured in chemostats and, thus, they have been used successfully to test the resource competition theory (Rothhaupt 1988).

A possibility to estimate the competitive abilities of different *Daphnia* species without using chemostats (Rothhaupt 1990) is the "threshold food concentration" concept (Lampert 1977), a special case of Tilman's R^* concept. The threshold food concentration (C_0) is the ambient concentration of food that allows an individual to meet its metabolic demands but not grow. Both R^* and C_0 indicate resource concentrations

at a zero net change in the consumer's biomass, but basic differences between the two characteristics originate from the way they are measured. R^* is calculated from the residual resource concentration in a chemostat at equilibrium. C_0 is determined by measuring individual growth rates in a series of constant low food concentrations. The intersection of a regression of growth rate vs. food concentration (growth rate = zero) defines R^* and C_0 . Thus, the growth rate is kept constant experimentally for estimating R^* and the residual food concentration is measured in response, whereas the food concentration is kept constant and the resulting growth rate is measured when C_0 is determined. As a consequence R^* cannot be determined for zero mortality (chemostat flow rate zero) while C_0 applies always to zero mortality, i.e., it predicts the competitive ability in a predator free environment.

The C_0 concept has been used in various ways. Lampert (1977) studied the effect of environmental conditions and body size on C_0 of *Daphnia pulex*, but did not consider differences among species. He calculated C_0 as the difference between carbon assimilation and respiration rate. Stemberger and Gilbert (1987) used population growth rates to compare food thresholds of differently sized rotifers. A clear negative relationship between body size and the C_0 of various cladocerans was found by Gliwicz (1990), confirming the competition part of the Size Efficiency Hypothesis (Hall et al. 1976). Gliwicz and Lampert (1990) demonstrated the differing effects of algal filaments interfering with the filtering process on C_0 of differently sized *Daphnia*. They used these data to explain the dominance of small cladocerans under hypertrophic conditions. Finally Achenbach and Lampert (1997) showed that temperature does not affect the rank order of C_0 in various cladocerans, hence concluding that changing competitive ability cannot explain the dominance of small species in subtropical waters.

Although R^* and C_0 are theoretically similar, they differ in the predictive power of the conclusions. R^* is a direct measure of the minimum resource concentration that can result from the consumption by organisms. C_0 in contrast is an indirect estimate from non-equilibrium conditions, and it still needs to be shown that growing *Daphnia* are efficient enough to suppress environmental resource concentrations to levels equivalent to their C_0 . At this point, they would no longer grow and be in equilibrium with the growing algal resource.

The aim of this study was to establish equilibrium conditions between *Daphnia* and its food resource and to measure the resulting equilibrium food concentration directly. If a *Daphnia* population at a fixed resource renewal rate grows towards its carrying capacity the food concentration will decrease until no further *Daphnia* growth is possible. *Daphnia* biomass and food concentration will remain constant. Although mortality in this case is not predetermined by the chemostat flow

rate (only natural mortality is involved), the equilibrium food concentration results from the resource uptake of the daphniids. Hence it is equivalent to Tilman's R^* . In order to point out the analogy we will call the resulting equilibrium resource concentration C^* . C^* and C_0 should be numerically identical at zero mortality.

Having determined C^* of individual *Daphnia* species we would be able to make predictions about their competitive abilities and to test the predictions in mixed species experiments. In addition, we wanted to compare the C^* values with independent estimates of C_0 for the same clones. If, in fact, C_0 and C^* are numerically similar, C_0 is a reliable predictor of competitive ability. This would support the conclusions drawn from earlier studies based on the C_0 concept (e.g., Gliwicz 1990, Achenbach and Lampert 1997).

MATERIAL AND METHODS

Experimental design

The basic idea of the experiments was to introduce daphniids into a flow-through system at a particulate organic carbon (POC) concentration slightly above their assumed threshold food concentration C_0 at a low flow rate that exceeded the population grazing rate. The animals would then grow, i.e., the population grazing rate would increase. As a result, the POC concentration in the flow-through vessel would decrease until the daphniids' C_0 was reached. At this point, the daphniids could not grow further, i.e., the *Daphnia* biomass and the consequent population grazing rate would remain constant, and an equilibrium between the rate of inflow and the grazing rate would be established. *Daphnia* biomass and POC concentration in the vessel would have to be monitored over time to show that an equilibrium was reached. Due to the time lag between food uptake and reproductive output, *Daphnia* populations tend to fluctuate around the carrying capacity (e.g., Frank 1952, McCauley et al. 1988, Van der Hoeven 1989). In order to avoid such fluctuations we tried to adjust the experimental conditions in a way that the daphniids would grow somatically but not reproduce before they reached the equilibrium (where no reproduction is possible).

We used clonal cultures of three differently sized *Daphnia* species that have been maintained in our laboratory for many years. They were the same clones as used by Gliwicz (1990). All experiments were run with the same unialgal food source, the chlorococcal *Scenedesmus acutus* Meyen taken directly from the outlet of a chemostat and diluted to the appropriate concentration with membrane-filtered (0.45 μm) lake water.

We performed three successive experiments with this basic design:

Experiment 1 was designed to test if an equilibrium could be established. We introduced 30 neonates of *D. pulex* into each of 12 flow-through vessels.

TABLE 1. Body size characteristics of the three *Daphnia* species when grown at high food concentrations and 20°C (following Gliwicz 1990).

<i>Daphnia</i> species	Size at birth (mm)	Size at maturation (mm)
<i>D. pulicaria</i>	0.7	1.6
<i>D. galeata</i>	0.6	1.2
<i>D. ambigua</i>	0.4	0.8

Note: Clones were identical in our work and in the study of Gliwicz (1990).

In addition, three subsamples of ten neonates each were randomly selected from the original population, and they were measured and weighed to determine the initial mass. The algal concentration in the vessels was monitored every other day. Three randomly selected vessels were sacrificed per day on days 9, 13, 18, and 23, and the *Daphnia* mass was determined.

Experiment 2 tested three differently sized *Daphnia* species, *D. pulicaria*, *D. galeata* Sars, and *D. ambigua* Scourfield (Table 1). Species were kept in separate vessels, five replicates of *D. pulicaria* and *D. galeata*, and four of *D. ambigua*. Due to the smaller size of the latter species we started with 30 neonates per vessel of *D. pulicaria*, 40 neonates/vessel of *D. galeata*, and 50 neonates/vessel of *D. ambigua* to achieve similar initial grazing rates. Algal concentration was monitored every second day, but *Daphnia* mass was only determined after 21 d, when the experiment was terminated.

The third experiment was designed as a competition experiment. *D. pulicaria* (15 neonates/vessel) and *D. galeata* (20 neonates/vessel) were combined in 15 vessels. The experiment was run for 27 d, and three vessels per day were sacrificed on days 3, 6, 13, 20, and 27 to determine *Daphnia* masses. Every third or fourth day, when they were transferred to clean vessels, all surviving daphniids were counted. The algal concentration was determined after periods of 1 or 2 d.

Culture system

The experiments were carried out in a flow-through system as described by Lampert et al. (1988). The only difference was that we did not intend to keep the food concentration constant by applying a high flow rate, but rather we reduced the flow rate to only 20 mL/h. Preliminary calculations (Lampert 1987) had shown that this flow rate exceeded the total filtering rate of daphniids in a vessel as long as they were small, but was lower than the filtering rate for daphniids growing towards maturity. Four vessels were supplied with algal suspension from the same reservoir by a multi-channel peristaltic pump. As flow rates of the individual channels varied by a factor of 5%, inflows were randomly assigned to the different flow-through vessels every 12 h. Fresh food suspension of 0.1 mg C/L was prepared every day in one batch and then distributed to the reservoirs. All flow-through vessels were maintained in a water bath at $20 \pm 0.1^\circ\text{C}$ under dim continuous room

light. To avoid *Daphnia* grazing on bacteria growing at the walls or material settling on the mesh screens, daphniids were transferred to clean flow-through vessels every third or fourth day. Care was taken to also transfer the water from the old vessel to the clean one in order to avoid a change in food concentration for the animals due to the transfer.

Determination of algal concentration and *Daphnia* mass

We measured the particulate carbon (POC) concentration of the *Scenedesmus* stock suspension in an infrared carbon analyzer and established a calibration curve POC vs. light absorbance (at 800-nm wavelength) measured in a photometer. As we found low variability ($\pm 1\%$) for the POC vs. light absorbance relationship we used absorbance to prepare the daily food suspension of 0.1 mg C/L. A direct determination of carbon at the very low food concentrations in the experimental vessels ($\sim 50 \mu\text{g C/L}$) was not possible as the low flow rate did not permit removal of sufficiently large quantities of algal suspension for a direct determination of POC. Also the low concentrations used and the small quantities available made direct microscopic counts of algal cells unsuitable. Therefore, we determined the total particle volume of the algal suspension by using an automatic particle counter (Casy I, Schärfe System GmbH, Reutlingen, Germany) adjusted to measure low particle densities. Algal volume is closely related to carbon content, particularly in unialgal suspensions (Strathmann 1967, Rocha and Duncan 1985). We usually withdrew 5 mL of algal suspension from a flow-through vessel by a syringe, diluted 2 mL of the sample to 10 mL, and averaged four measurements of 0.4 mL from each sample. As our *Scenedesmus* has an equivalent spherical diameter of $\sim 6 \mu\text{m}$ we set the size range of particles to be counted to 3.5–10 μm . Every morning when the fresh food suspension of 0.1 mg C/L had been prepared, we determined a new calibration factor (F_d) for the particle counter biovolume by measuring the particle volume in the food suspension (B_d , in cubic micrometers per milliliter): $F_d = (0.1 \text{ mg C/L})/B_d$.

We used F_d (in grams of carbon per cubic micrometer) to convert the algal volume measured in the experimental vessels to POC.

All *Daphnia* removed from the experimental vessels were measured from the upper edge of the eye to the base of the tail spine to the nearest 0.01 mm using a video imaging system (SIS) under a dissecting microscope. They were then pooled in preweighed aluminum containers, dried at 60°C overnight, and weighed to the nearest 0.1 μg on an electronic microbalance. If neonates were released in the experimental vessel they were weighed separately. Individual masses always refer to the daphniids introduced at the beginning of the experiments while total *Daphnia* masses are the sum of surviving daphniids and their offspring.

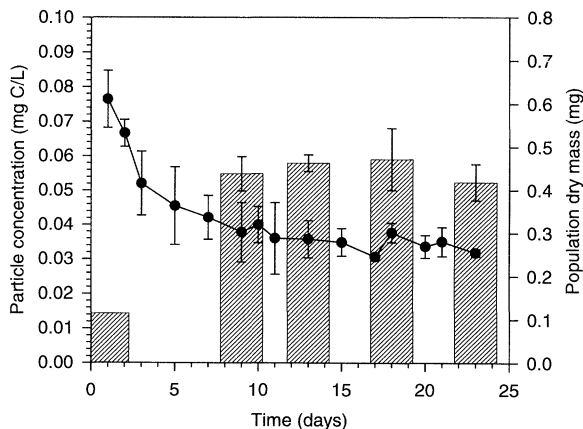


FIG. 1. Particle concentration (●) and mean consumer dry mass per vessel of *Daphnia pulicaria* (columns) in experiment 1. Error bars are ± 1 SD.

The equilibrium phase was determined by linear regression analysis. We calculated a linear regression of particle concentration vs. time and omitted successive days beginning with day 0 until the slope was no longer different from zero ($P \geq 0.05$). We averaged all particle volumes after the last omitted day to calculate the equilibrium POC concentration (C^*). We compared the equilibrium concentrations for different *Daphnia* species by a repeated-measures two-way ANOVA (factors: day of experiment, species) and a post hoc test (Tukey hsd).

Grazing and filtering rates of *D. pulicaria*

Propp et al. (1982) provide a formula to calculate the concentration of a substance in a mixed dynamic system. If the concentrations in the inflow and the outflow of the system are known, this formula can be used to estimate the rate of consumption of the substance. We used it to estimate the rate of food uptake (R) by the *Daphnia* population in the vessel between two measuring dates (t_0 and t_n):

$$R = V \times [C(t_n) - C_i \times (1 - k) - k \times C(t_0)] / (k - 1)$$

with $k = \exp(-V \times t_n / \omega)$, where R = consumption rate (in milligrams of carbon per hour), C_i = inflow concentration (in milligrams of carbon per liter), $C(t_0)$ = concentration in the vessel at time t_0 (in milligrams of carbon per liter), $C(t_n)$ = concentration in the vessel at time t_n (in milligrams of carbon per liter), t_n = time period (in hours), V = rate of flow (in milliliters per hour), ω = volume of container (in milliliters).

The mean grazing rate (G , in milliliters per hour) was then calculated assuming a linear change of the algal concentration during the short time interval $t_0 - t_n$ (Geller 1975):

$$G = R / [C(t_0) + C(t_n)] / 2.$$

The individual filtering rate (F , in milliliters per hour) was calculated by dividing G by the number of

Daphnia in the vessel. If neonates had been released, they were not included in the population number due to their small size. Instead, an empirical value of 0.35 mL/h per neonate was subtracted from G before the division.

RESULTS

Experiment 1: Initial feeding experiment

The experiment with *D. pulicaria* confirmed our expectations of an equilibrium (Fig. 1). The algal concentration declined from the initial of 0.1 mg C/L at day zero to ~ 0.04 mg C/L at day 9. No decrease was found afterwards as the slope of the calculated regression line did not differ significantly from zero ($P = 0.39$). Algal concentration during this equilibrium phase was 0.036 ± 0.004 mg C/L (mean ± 1 SD, $n = 10$ sampling dates).

At the same time, mean *Daphnia* body size increased from 0.66 mm to 1.45 mm at day 9 and then increased at a much lower rate to 1.72 mm at day 23 (Table 2). Mortality was low (6%) during the first nine days and increased to a maximum of 40% after 23 d. Despite the low food concentration, the daphniids produced a few neonates after day 18. Individual body mass of the surviving daphniids increased at first and then remained fairly constant after day 13. The population biomass per vessel increased sharply until day 9, but afterwards it did not change significantly (ANOVA, $P = 0.35$) until the end of the experiment (Table 2). Fig. 1 demonstrates that the *Daphnia* population biomass increased as long as the algal concentration decreased, but both algal concentration and daphniid biomass remained constant after day 9; i.e., an equilibrium was reached between algae and daphniids. Mortality losses of *Daphnia* were compensated for by individual growth of the survivors and the few neonates added to the population.

Experiment 2: Feeding experiment with three species

We repeated experiment 1 with the three differently sized *Daphnia* species in separate flow-through vessels. Due to the lower numbers of replicates per species we were not able to sacrifice daphniids for mass determination during the experiment, but we counted all individuals and measured their body length every 3–4 d when they were transferred to clean vessels. All three

TABLE 2. Results of initial feeding experiment (experiment 1) with *Daphnia pulicaria*. Data from days 9–23 are means (with 1 SD in parentheses) of three sacrificed vessels.

Day	Body size (mm)	Individual dry mass (μ g)	No. of survivors	No. of neonates	Total dry biomass (μ g)
0	0.66	3.8	30	0	114
9	1.45 (0.07)	15.5 (0.7)	28.3 (2.9)	0	438 (39)
13	1.57 (0.08)	20.2 (6.3)	24.3 (7.4)	0	463 (19)
18	1.66 (0.12)	21.7 (5.0)	22.3 (7.2)	3.6 (5.5)	471 (71)
23	1.72 (0.08)	23.1 (3.2)	18.0 (1.0)	1.7 (1.5)	418 (42)

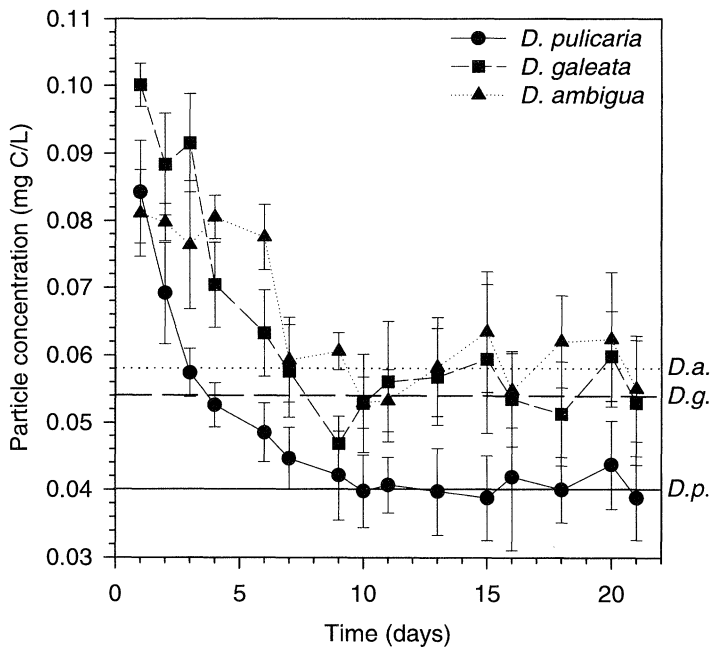


FIG. 2. Particle concentrations in vessels with different individual *Daphnia* species in experiment 2. Horizontal lines indicate equilibrium concentrations (C^*) of the individual species: Dotted line, *D. ambigua* (*D.a.*); dashed line, *D. galeata* (*D.g.*); solid line, *D. pulicaria* (*D.p.*). Error bars are ± 1 SD.

species reached equilibrium within 9 d (Fig. 2). The pattern of food concentration for *D. pulicaria* was remarkably similar to experiment 1. The two other species reduced the food concentration more slowly, reaching equilibrium on the same day but at higher algal concentrations. A two-way repeated-measurement ANOVA (date, species) revealed significant differences in equilibrium algal concentrations among species ($P < 0.001$). The post hoc test (Tukey hsd) showed that *D. pulicaria* differed from both *D. galeata* ($P = 0.0003$) and *D. ambigua* ($P = 0.0002$), but the two smaller species did not differ significantly from each other ($P = 0.32$).

Individuals of all three species grew during the course of the experiment (Table 3). This time, *D. pulicaria* did not release neonates within 21 d. Mortality was $\sim 33\%$, but the increase in body mass of the surviving daphniids compensated for the losses. Using the length-mass data of Table 1, we estimated total biomass on the successive dates, when the daphniids had been measured. As in expt. 1, total biomass did not change during the equilibrium phase. Mortality in *D. galeata* amounted to 45%, but a few neonates were released after day 13 and contributed to the biomass in addition to the growth increment.

A different pattern appeared in the smallest species, *D. ambigua*, which had a much shorter generation time. The first juveniles were observed on day 6 and the total number per vessel increased considerably until day 13 when it leveled off at ~ 120 individuals/vessel. Discrimination from the parental generation was possible until day 10; afterwards it was impossible due to size overlap.

Experiment 3: Two-species resource competition experiment

When *D. pulicaria* and *D. galeata* competed for *Scenedesmus*, they quickly reduced the food concentration as in the single-species experiments. At day 6, the algal concentration fell below the C^* of *D. galeata* (0.054 mg C/L) determined previously in expt. 2 (Fig. 3). Thereafter, the algal concentration fluctuated around a value of 0.048 ± 0.003 mg C/L (mean ± 1 SD) but never dropped below the measured C^* of 0.04 mg C/L for *D. pulicaria*, although it came close at days 25 and 27.

Numbers of both species decreased during the first 6 d, but after that date, when the food concentration remained between the C^* values for the two species, the population density of *D. galeata* continued to decrease steadily, while *D. pulicaria* stabilized (Fig. 4). On average only one individual per vessel of *D. galeata* survived to day 27. In contrast, *D. pulicaria* maintained its population density and started to increase in numbers towards the end of the experiment as neonates were born into the population (Table 4).

Individuals of both species were of nearly the same size until day 6, but afterwards *D. galeata* ceased growing while *D. pulicaria* continued growing until day 27 (Table 4). The trend in body mass was even stronger. Both species were of equal mass until day 6, but an increase in mass difference developed later as *D. galeata* showed only a very minor individual increase in mass. Individuals of *D. pulicaria* grew in size considerably and reached about three times the mass of *D. galeata* on day 27. Changes in numbers and individual

TABLE 3. Results of feeding experiment with three *Daphnia* species foraging in separate vessels (experiment 2). Data are means (with 1 SD in parentheses) of replicate vessels at day 21, except for algal concentration ($n = 9$ sampling dates).

Measure	Species		
	<i>D. pulicaria</i>	<i>D. galeata</i>	<i>D. ambigua</i>
Replicate vessels	5	5	4
Initial number	30	40	50
Final number of adults	21 (4)	24 (5)	...†
Total number	21 (4)	32 (3)	122 (4)
Adult body size (mm)	1.59 (0.06)	1.28 (0.03)	0.89 (0.05)†
Adult individual dry mass (μg)	17.65 (1.67)	13.31 (1.77)	2.61 (0.23)
Total biomass ($\mu\text{g}/\text{vessel}$)	362.2 (63.7)	335.6 (44.6)	323.4 (25.0)
Equilibrium algal concentration, C^* (mg C/L)	0.040 (0.002)	0.054 (0.004)	0.058 (0.004)

† Adult body size for *D. ambigua* is reported for day 10, as discrimination of the parental generation was not possible after time. For the same reason, final number of adults is not known for this species.

masses resulted in a striking shift in the fractions of the two species of the total biomass per vessel. They started with about equal biomasses and *D. galeata* doubled its share during the first 6 d, while the biomass of *D. pulicaria* did not change. After day 6, however, the biomass of *D. galeata* did not increase further and finally decreased, while that of *D. pulicaria* increased steadily (Table 4). *D. pulicaria* reached 93% of the total biomass on day 27, hence it was the dominant species both in numbers and biomass.

Mechanisms

The decrease in the algal concentration in the flow-through vessels is a consequence of the daphniids' grazing rate, i.e., the sum of all individual filtering rates. Fig. 5 demonstrates the change in the grazing over time in expt. 1. This pattern is similar to the development of the daphniids' body size and total biomass. The grazing rate reaches a plateau at day 14 and

does not increase further, i.e., the equilibrium has been established.

The shape of the grazing curve is the result of decreasing numbers but increasing size of the daphniids. We calculated individual filtering rates for all periods with length measurements of *D. pulicaria* in expts. 1 and 2 and two preliminary studies (not reported). Plotting individual filtering rates (F) vs. body length (L) results in the well-known function (Fig. 6), which can be linearized using a log-log model. The highly significant ($P < 0.0001$) regression yields the following equation:

$$\log F = -0.32 + 2.39 \log L$$

($r^2 = 0.93$, $n = 65$ calculations).

DISCUSSION

All experiments confirmed our expectations that we would be able to establish an equilibrium between algal renewal rate and *Daphnia* grazing. We did not see fluctuations in *Daphnia* numbers and biomasses. Instead, the daphniid populations approached their carrying ca-

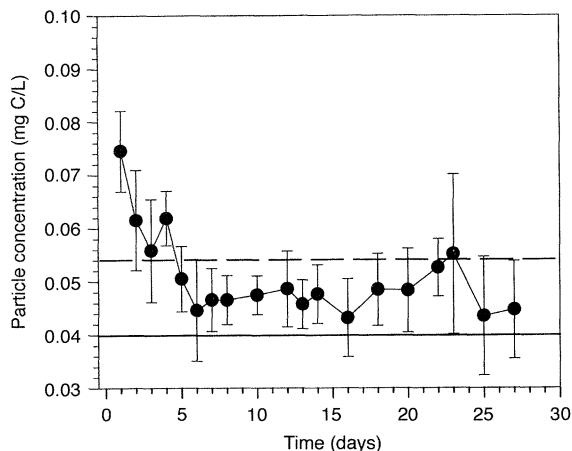


FIG. 3. Particle concentration in the two-species resource competition experiment (experiment 3) with populations of *Daphnia pulicaria* and *D. galeata* grazing in shared vessels. Horizontal lines indicate equilibrium concentrations (C^*) determined with individual species in experiment 2: dashed line, *D. galeata*; solid line, *D. pulicaria*. Error bars are ± 1 SD.

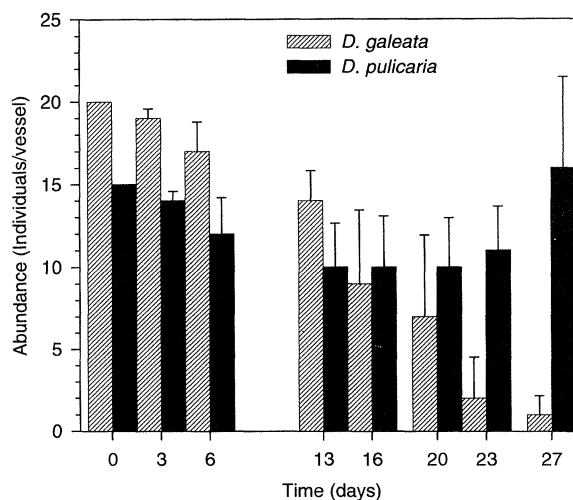


FIG. 4. Numbers of *D. pulicaria* and *D. galeata* in experiment 3. Error bars are $+1$ SD.

TABLE 4. Characteristics of *Daphnia pulicaria* (*D.p.*) and *D. galeata* (*D.g.*) after foraging on *Scenedesmus* for 27 d in 15 shared vessels during the competition experiment (experiment 3).

Day	No. survivors		No. offspring		Total number		Survivors			
	<i>D.p.</i>	<i>D.g.</i>	<i>D.p.</i>	<i>D.g.</i>	<i>D.p.</i>	<i>D.g.</i>	Body size (mm)		Individual mass (μg)	
							<i>D.p.</i>	<i>D.g.</i>	<i>D.p.</i>	<i>D.g.</i>
0	15	20	0	0	15	20	0.60 (0.01)	0.64 (0.02)	2.73	2.10
3	14	19	0	0	14	19	0.81 (0.01)	0.88 (0.02)	3.49 (0.08)	3.82 (0.24)
6	12	17	0	0	12	17	0.98 (0.05)	0.98 (0.03)	5.52 (0.54)	5.42 (0.55)
13	10	14	0	0	10	14	1.32 (0.03)	1.13 (0.02)	11.84 (1.33)	7.67 (1.55)
20	10	7	0.33 (0.47)	0	10	7	1.64 (0.06)	1.26 (0.02)	22.06 (6.24)	8.67 (0.14)
27	8.7	1	8 (5.88)	0	16	1	1.77 (0.10)	1.23 (0.11)	31.39 (6.61)	10.08 (3.50)

Notes: Data are means (with 1 SD in parentheses) for three sacrificed vessels. The term "survivors" refers to the parental generation introduced at day zero.

capacities and then remained constant. This pattern of population growth is consistent with the conclusions of Van der Hoeven (1989), who (based on a literature review of population dynamics under constant food supply) concluded that most of the reported fluctuations were a result of discontinuous food provision and external factors, such as temperature deviations, food quality changes, or light shocks when the animals were handled. One prerequisite for our result is the choice of initial conditions. The food concentration of 0.1 mg C/L was limiting from the beginning of the experiment, as the incipient limiting concentration is ~ 0.25 mg C/L (Lampert 1987). There was no possibility that the food concentration could exceed this value in the flow-through system. Hence, the daphniids would not accumulate internal energy reserves during initial phases of the experiment and overshoot the carrying capacity when they released offspring with a time lag.

The carrying capacity is indicated by the constant population biomass during the second half of the experiments. However, the three *Daphnia* species achieved the constant biomass in different ways. *D. pulicaria* and *D. galeata* produced very few offspring as they matured only when the food supply was already at its minimum. The constant biomass was mainly the result of somatic growth of the individuals. Biomass losses through mortality were immediately compensated for by additional growth of the survivors using the free resources as in the experiments of Enserink et al. (1996). In contrast, the small *D. ambigua* showed numerical compensation. They matured much faster than the larger species and were able to use the relatively high, although limiting, food concentrations during the first days for offspring production. The number of daphniids per vessel increased until reproduction stopped, but not at a rate sufficiently high to overshoot the carrying capacity.

All species were able to suppress the algal concentration considerably, but the equilibrium food levels

(C^*) depended on species. The large *D. pulicaria* created a lower equilibrium concentration than the smaller *D. galeata* and *D. ambigua*. The C^* ranking of the three species is consistent with the results of Gliwicz (1990), Lampert (1994), and Achenbach and Lampert (1997). These authors calculated C_0 from individual growth, but did not measure the residual algal concentrations (Table 5). The negative relation observed between cladoceran body size and C_0 caused Gliwicz (1990) to propose that there is competitive superiority by larger species over small ones under conditions of food limitation; this trend supports the competition part of the Size Efficiency Hypothesis (Hall et al. 1976). The efficiency to use a limiting resource has often been used to define competitive abilities of species (e.g., Neill 1975). As the energy input into our system was identical for all species, resource use efficiency was reflected by the total biomass accumulated in the equilibrium phase. In fact, the order of biomasses of the differently sized species is consistent with the order of competitive abilities estimated by C^* , although the differences in biomasses are not significant (ANOVA, $P = 0.16$). *D. pulicaria* reached the lowest C^* as well as the highest biomass. Efficiency of resource utilization and C_0 are interconnected, as an animal with the higher resource use efficiency must have the lower C_0 (it can grow at a lower ambient food concentration). This justifies the use of C_0 to predict competitive abilities. However, a lower efficiency will not lead to a given species' extinction as long as the resource concentration is above its minimum demands (C^*). The mechanism of competitive exclusion ultimately requires C^* , hence C^* is a more direct, quantitative predictor of competitive success than C_0 .

Our competition experiment has provided independent evidence that Gliwicz's (1990) conclusions are correct. *D. galeata* grew even better than *D. pulicaria* as long as the algal concentration was above its C^* . At this time the algal concentration was suppressed by the

TABLE 4. Extended.

Total dry mass per vessel (μg)		Percentage of total biomass	
<i>D.p.</i>	<i>D.g.</i>	<i>D.p.</i>	<i>D.g.</i>
41	42	50	50
50.03 (1.05)	74.00 (6.56)	40	60
49.67 (7.37)	100.00 (18.19)	34	66
116.00 (25.38)	114.93 (22.09)	50	50
199.00 (55.53)	89.80 (43.69)	68	22
286.67 (71.96)	20.15 (7.00)	93	7

activity of both species. However, as soon as the algal concentration dropped below the C^* for *D. galeata*, this species ceased growth, and its mortality losses were no longer compensated for. The algal concentration subsequently remained below the C^* of *D. galeata* (but above that of *D. pulicaria*), and *D. pulicaria* reached its carrying capacity later than in the single-species experiment due to lower initial numbers. At the end of the experiment, *D. galeata* went extinct, but the competitively superior *D. pulicaria* was still growing.

Although we found the same rank order of the three species for C^* as Gliwicz (1990), Lampert (1994), and Achenbach and Lampert (1997) found for C_0 , our absolute values are slightly higher (Table 5). This may be expected as the thresholds determined in earlier studies (C_0) and in this study (C^*) are related to different levels of mortality. Lampert (1977) pointed out that food thresholds can be defined either for the maintenance of body mass of an individual or for the growth of a population. The population threshold must in the-

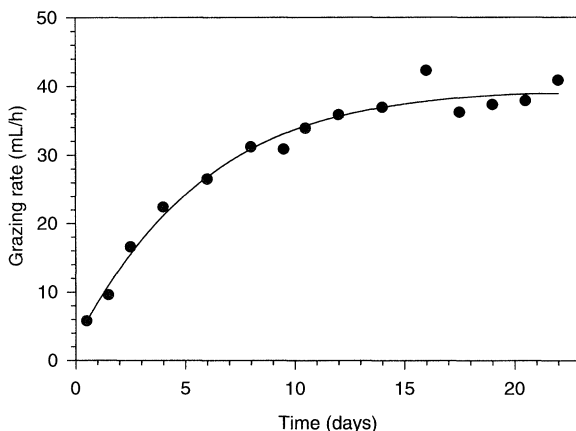


FIG. 5. Community grazing rates of *Daphnia pulicaria* in experiment 1. Data points are plotted between sampling dates, as they were calculated from particle densities at successive dates. The line is a quadratic fit to the data.

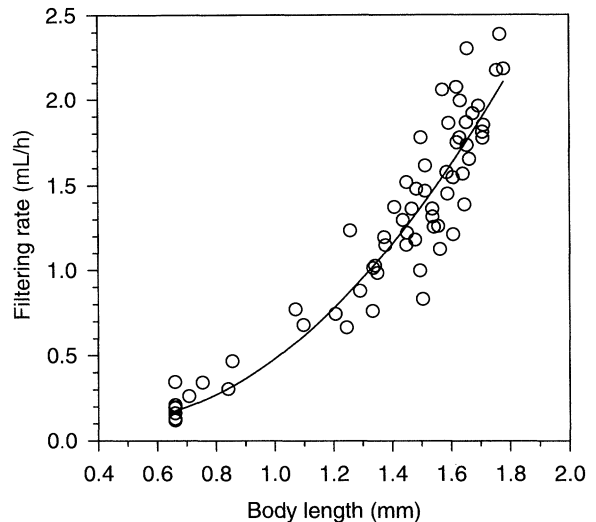


FIG. 6. Size-dependent individual filtering rates of *Daphnia pulicaria*. Data of four experiments are pooled. Size represents the mean body size of daphniids in a vessel. The regression line was calculated with a log-log model.

ory be higher, however, as compensating for mortality requires additional energy (Lampert and Schober 1980, Rothhaupt 1990). The higher the mortality losses, the higher the population-based threshold must be. Earlier studies have estimated C_0 from individual growth directly, and hence C_0 provides an estimate of the individual threshold. Our study measured the population threshold, although only natural mortality was included; hence, the higher absolute values of C^* are consistent with the theoretical expectations.

A technical difference may also contribute to the higher absolute values in our study. Previous studies to estimate C_0 used high flow rates to avoid any reduction of the food concentration by grazing. An additional effect of this high flow rate is the immediate removal of defecated particles of lower nutritional val-

TABLE 5. Comparison of the equilibrium food concentrations of three *Daphnia* species at 20°C determined in this study (C^*) with threshold food concentrations (C_0) reported in the literature.

<i>Daphnia</i> species	C^* (this study)	C_0		
		Gliwicz (1990)	Achenbach and Lampert (1997)	Lampert (1994) (uncorrected)
<i>D. pulicaria</i>	40 ± 2	17 (16–20)	29 (5–32)	35
<i>D. galeata</i>	54 ± 4	28 (25–32)	37 (23–46)	52
<i>D. ambigua</i>	58 ± 4	31 (27–37)	42 (33–56)	55

Notes: All values are reported in micrograms of carbon per liter; C^* results are reported as means (± 1 SD), C_0 results are reported as means (with lower and upper 95% fiducial limits in parentheses).

ue from the vessels (Vijverberg 1989). As a result, the daphniids were supplied high-quality food continuously. In contrast, the flow rate must be held low if C^* is to be estimated from the residual algal concentration as a result of the animals' feeding activity. Under these conditions, the particle concentration in the water is a mixture of fresh food and partly digested algal cells, which can be reingested (Kersting and Holtermann 1973), i.e., the food quality in the vessels must be lower than in the inflow. Direct determination of carbon at the extremely low equilibrium concentration is not possible (note that a 1-mL sample contains only $0.05 \mu\text{g}$ particulate carbon). Only the particle volume can be measured under these conditions, but the particle counter cannot determine the particle quality. However, lower food quality at low flow rates must result in higher thresholds expressed in mass of carbon.

We have shown with this study that the threshold concept can be used to construct mechanistic models of competitive interactions in zooplankton based on C_0 , food-dependent growth rates and size-specific filtering rates. The function describing the individual filtering rates in dependence of body length calculated from the flow-through system (Fig. 6) is remarkably similar to functions measured with individual daphniids and various other methods (e.g., radiolabeled algae). The exponent of 2.39 is typical for such relationships (Geller 1975, Lampert 1987). Mechanistic models may help our understanding of the controversial results of classical competition experiments with cladocerans. These experiments are usually performed in batch cultures with periodic renewal of the food medium or the addition of a fixed "ration." Algal concentrations fluctuate widely over time under these conditions (Tillmann and Lampert 1984). We suspect that some of the observations when small cladocerans were competitively superior (e.g., Goulden et al. 1982, Tillmann and Lampert 1984, Romanovsky and Feniova 1985) were the result of fluctuating food conditions. Expt. 2 shows that the small *D. ambigua* can use the initial relatively high food concentration to grow to maturity and produce offspring before the food is seriously limiting. Also, in expt. 3, *D. galeata* grew better than *D. pulicaria* in the initial phase. Hence, small cladocerans may be able to better utilize short pulses of high food and may, therefore, be favored in batch systems. Our flow-through system provides a more realistic method for testing competitive abilities.

We have demonstrated that both the threshold food concentration (C_0) and the residual food concentration (C^*) are useful mechanistic concepts. Applying them to species competing for a single resource is easy with cladocerans that have a broad overlap in food resources. For future competition studies we suggest a combined use of C_0 and C^* . As it is relatively easy to measure C_0 , threshold food concentrations can be calculated under various environmental conditions and the results can be used to predict competitive abilities. Se-

lected predictions can be tested in competition experiments based on C^* using our experimental design.

Although our experiments have been made in a predator-free environment with a single resource, the concept is also valid if the food resource is not uniform (Gliwicz and Lampert 1990). In principle it can be applied for species competing for multiple resources as in Tilman's (1977, 1981) and Sommer's (1989) work with algae. The experiments of Rothhaupt (1988) with rotifers were the first step in this direction.

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