

Miquel Lürling · Ellen Van Donk

Zooplankton-induced unicell-colony transformation in *Scenedesmus acutus* and its effect on growth of herbivore *Daphnia*

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Abstract The effects of colonial ecomorphs of the green alga *Scenedesmus acutus* on growth of *Daphnia cucullata* and *D. pulex* were examined. In ecologically relevant densities (up to 200 animals l⁻¹) the relatively small *D. cucullata* did not induce colony formation in *Scenedesmus acutus*, whereas the larger congener *D. pulex* significantly promoted colony formation. Both clearance rate and population growth rate (*r*) were significantly lower in *D. cucullata* when fed colonial *Scenedesmus* than when fed unicellular food. However, for *D. pulex* no effects of food type were observed. These results show that large *Daphnia* may influence its food in such a way that smaller congeners and competitors are negatively affected.

Key words Colony formation · *Daphnia* · Life history · *Scenedesmus* · Infochemicals

Introduction

In aquatic ecosystems planktonic herbivores encounter a broad range of both edible and inedible algal taxa. An important and central position in freshwater systems is occupied by the suspension-feeding members of the genus *Daphnia*. It is commonly accepted that their success depends on the ability to feed efficiently on a wide size range of available resources. Clear relationships exist between the grazer's body-size and the size of grazable particles (Burns 1968). The upper limit of grazable particles depends on the structure of a grazer's filtering apparatus, and generally this limit is lower for smaller daphnids. The dietary breadth with respect to algae is mainly determined by the upper limit. Although the lower size limit differs between species (Geller and Müller 1981), and is phenotypically variable according to trophic con-

ditions (Brendelberger and Geller 1985), it is of no relevance when food mainly consists of phytoplankton particles $\geq 3 \mu\text{m}$. This means that in situations where large algae, inedible for a small species A, but still edible for a larger species B, are more abundant, species B will eventually dominate the zooplankton community. Natural phytoplankton assemblages can be highly variable in species composition and there is a broad consensus that dominance of inedible algal species is favoured when grazing pressure on edible algal taxa is high (Sommer et al. 1986).

Besides shifts from edible to inedible species, two types of intraspecific morphological changes may also occur. Changing environmental conditions, favouring different clones of the same species, could lead to the replacement of one clone by another one (Wood and Leatham 1992), possibly with a different morphology. The second type, phenotypic plasticity, occurs when changed environmental variables alter the morphology of cells belonging to the same clone. For example, phenotypically plastic species are common in members of the genus *Scenedesmus* in which nutrients, pH and temperature all affect *Scenedesmus* phenotypes (Trainor and Egan 1990, 1991; Trainor 1992, 1993).

It is known from several studies that the presence of *Daphnia* can alter morphological appearance of phytoplankters. *Aphanizomenon* showed a shift from flakes in the presence of *Daphnia* to single filaments or smaller flakes in its absence (Lynch 1980; Holm et al. 1983). *Synedra* also occurred as colonies consisting of dozens to hundreds of cells in presence of *Daphnia*, but as single cells in its absence (R.W. Sterner, personal communication). However, these studies do not elucidate whether the observed effect is the result of a direct grazing impact on smaller flakes and single cells or the effect of some kind of colony/flakes-inducing infochemical.

It has recently been discovered that an infochemical (for terminology see Dicke and Sabelis 1988) released from grazing *Daphnia* induced the formation of colonies in *Scenedesmus* (Hessen and Van Donk 1993; Lampert et al. 1994). The presence of large four- and eight-celled

M. Lürling (✉) · E. Van Donk
Department of Water Quality Management & Aquatic Ecology,
Agricultural University Wageningen,
PO Box 8080, 6700 DD Wageningen, The Netherlands
fax: +31 317 484411; e-mail: miquel.lurling@aqec.wkau.wau.nl

colonies of *S. subspicatus*, with more rigid and longer spines than unicells, reduced grazing by *D. magna* (Hessen and Van Donk 1993), but when they were fed spineless colonies of *S. acutus* grazing by *D. magna* was not depressed (Lampert et al. 1994). The colonies of the spineless *S. acutus* may, however, exceed the size of grazable particles for juveniles and small zooplankters.

Up to now, the induction of colonies in *Scenedesmus* has been demonstrated in the cladoceran *D. magna* (Hessen and Van Donk 1993; Lampert et al. 1994), *D. galeata*, *Bosmina longirostris*, the copepod *Eudiaptomus gracilis* and the rotifer *Brachionus calyciflorus* (M. Lüring and E. Van Donk, in press). Only short-term grazing experiments have been performed with *D. magna*. This study is a first attempt to discover the effect of algal phenotypic changes on growth of different species of *Daphnia*. In a first experiment we investigated the ability of the relatively small *D. cucullata* and the relatively large *D. pulex* to induce colony formation at several ecologically relevant densities. Secondly, a short-term grazing experiment was conducted with both daphnids fed either unicellular or colonial *Scenedesmus*. Finally life table experiments were performed, investigating the effect of feeding unicellular or colonial *Scenedesmus* on the life history of these two *Daphnia* species.

Methods

Algae

The green alga *Scenedesmus acutus* Meyen was obtained from the chemostat culture of the Max-Planck Institut für Limnologie (Plön, Germany). The algae were cultured axenically in two 1.0-l chemostats on either 20% Z8 medium (Skulberg and Skulberg 1990) or on water from Lake Zwemlust (The Netherlands) filtered through a 0.2- μm membrane filter enriched with Z8 nutrients. During the course of the experiments $81 \pm 7\%$ of *S. acutus* cultured in the chemostat on 20% Z8 medium occurred as unicells with cell dimensions of $(10 \pm 2) \times (4 \pm 1) \mu\text{m}$. The average number of cells per colony was 1.30 ± 0.12 with a mean volume of $85.0 \pm 6.6 \mu\text{m}^3$. Lake water was able to induce colonies in *Scenedesmus* and the inductive strength is related to zooplankton abundance (M. Lüring and E. Van Donk, in press). The zooplankton abundance and composition of Lake Zwemlust during the experimental period were comparable. The lake contained c. 60 *Daphnia galeata* l⁻¹, c. 450 *Bosmina longirostris* l⁻¹, c. 300 copepoda l⁻¹ and c. 1000 rotifera l⁻¹ (mainly *Keratella cochlearis*). In the *S. acutus* chemostat on membrane-filtered lake water 30 \pm 5% of the algal population remained unicellular, 21 \pm 8% was four-celled, 22 \pm 10% occurred as eight-celled coenobia, while the remaining colony sizes (i.e. 2, 3, 5, 6 and 7 cells per colony) made up 1–10% of the population. The mean dimensions of an eight-celled coenobium were $(27 \pm 8) \times (21 \pm 3) \mu\text{m}$. On average 4.03 ± 0.47 cells formed a colony with a mean volume of $413.0 \pm 79.9 \mu\text{m}^3$. Both chemostats were continuously illuminated by circular fluorescent tubes (Philips TLEM 40 W/33RS) at an irradiance of $125 \mu\text{E m}^{-2} \text{s}^{-1}$ in a temperature controlled chamber at 20°C and with a dilution rate of 1.2 day^{-1} .

Animals

The cladoceran *Daphnia pulex* (adult female c. 3–4 mm) was isolated from Lake Zwemlust (The Netherlands) and has been cultured for over a year in the laboratory. A clone (Tj33) of the small-

er species *D. cucullata* (adult female c. 0.8–1.1 mm) was obtained from the culture collection of the Centre for Limnology (Nieuwersluis, The Netherlands). Animals were cultured at 20°C in 1-l jars containing a suspension of *S. acutus* (from the 20% Z8 chemostat) in 0.45- μm membrane filtered lake water from Lake Marsseveen (The Netherlands).

Induction experiments

In the first experiment the two *Daphnia* species were tested for their ability to induce colonies in *S. acutus* at ecologically relevant densities of the daphnids. For production of the colony inducing exudates animals were transferred into sterile 100 ml Erlenmeyer flasks containing axenic *Scenedesmus* (c. 10^5 cells ml⁻¹) in 20% Z8 medium. Both species were incubated at 10, 50, 100 and 200 individuals per litre and allowed to graze for 24 h in the dark at 20°C. An algal suspension without zooplankton served as additional control. Water from all incubations was filtered through a 0.1- μm membrane-filter before it was added to the algal test cultures.

An inoculum of exponentially growing unicellular algae was transferred in 100 ml Erlenmeyer flasks containing 50 ml of medium and sealed with Parafilm. Each batch culture contained 43 ml autoclaved 20% Z8 medium, 2 ml algal inoculum and either 5 ml additional 20% Z8 medium filtered through a 0.1- μm membrane-filter or 5 ml membrane-filtered test water. The batches were incubated at 20°C on a shaking table and illuminated from above by cool-fluorescent white tubes at $175 \mu\text{E m}^{-2} \text{s}^{-1}$ using a 16/8 h light-dark cycle. The tests were run in triplicate for 48 h. Algal densities and particle size distributions were determined routinely in the size range 3.0–20.0 μm ESD (100 μm capillary) using a Coulter Multisizer II. For each incubation after 48 h at least 100 aggregates (i.e. single cells as well as colonies) of test algae were counted microscopically and the number of cells per colony determined.

To reveal whether possible metabolic costs associated with colony formation were reflected in decreased growth, growth rates $\{\mu = [\ln(V_{t_2}) - \ln(V_{t_0})] \times (t_2 - t_0)^{-1}, \text{ day}^{-1}\}$ were calculated from increase in biovolumes and total cell numbers by Coulter analysis; where μ is algal growth rate (d⁻¹), V_{t_0} is the initial algal volume, V_{t_2} is the algal volume after 48 h of incubation and t is time in days. Total cell numbers were computed by multiplying the number of particles (determined by Coulter) by the mean number of cells per colony (determined by microscope). Growth rates were statistically compared by two-way ANOVA. After an F_{max} -test to check homogeneity of variance, two-way ANOVA was also used for statistical comparison of mean particle volumes and of mean cells per aggregate. Significant differences between treatments were detected by the Tukey test.

Grazing experiments

Short time grazing experiments were performed with two size classes of *D. pulex* and *D. cucullata*. The animals were fed with either unicellular algae from the 20% Z8 chemostat or colonial algae derived from the lake water chemostat. A cohort of *D. pulex* and one of *D. cucullata* were transferred into separate 1 litre beakers containing lake water filtered through 0.2 μm . After c. 1 h 10 *D. pulex* and 20 *D. cucullata* were selected and transferred separately into 100-ml algal suspensions (unicellular algae c. 1 mg C l⁻¹). The used algal biovolumes were similar for both treatments (i.e. $6.5 \cdot 10^6 \mu\text{m}^3 \text{ ml}^{-1}$). The tests were run for 3 h in the dark at 20°C in triplicate. The experimental set-up (i.e. 3 h in dark) allowed no induction of colonies during the course of the experiment. Total algal volumes between 3.0 and 20.0 μm ESD were determined at the beginning of the experiments and after 3 h of grazing using the Coulter Multisizer II. Clearance rates (CR, ml individual⁻¹ h⁻¹) were computed from Coulter data and statistically compared by applying two-way ANOVA.

Life table experiments

Life table experiments with both *Daphnia* species were conducted to investigate the influence of altered algal morphology on growth and reproduction. Animals belonging to the same cohort were placed individually in 100 ml tubes containing log-phase *S. acutus* in 0.45- μm filtered lake water (Lake Maarsseveen, The Netherlands). Newborns from the third clutch were collected within 20 h of birth and put together in a 500-ml beaker. For each series neonates of *D. pulex* and *D. cucullata* (15 respectively 14) were selected from this beaker and placed individually in 100 ml test tubes containing 60 ml of a unicellular or colonial *S. acutus* suspension in 0.45 μm membrane filtered lake water. Both *Daphnia* species were fed with equivalent biovolumes of unicellular or colonial algae (i.e. $8 \times 10^6 \mu\text{m}^3 \text{ml}^{-1}$). The tubes were incubated at 20°C in the dark to prevent algal growth and consequently induction of colonies in the control tubes. The animals were transferred daily into clean tubes containing fresh medium. Length was recorded and the animals were examined daily for moulting. Time needed to reach maturity, survival and number of newborns were recorded. Newborns were removed from the tubes. Growth and reproduction were measured until the animals reached the fourth adult instar and consequently had released their third clutch, because the population growth rate is mainly determined by the first three clutches (Porter et al. 1983; Vanni and Lampert 1992). The intrinsic rate of population increase (r) was estimated using the Euler equation:

$$1 = \sum_{x=0}^N e^{-rx} l_x m_x$$

where r = rate of population increase (day^{-1}), x = age class (0... N), l_x = probability of surviving to age x , m_x = fecundity at age x . Because of the impossibility of computing standard errors of the population parameter r directly, a jackknifing method was used to calculate them (Meyer et al. 1986). For both daphnids r values, age and length at maturity of animals grown on unicellular and colonial food were compared by t -test. Numbers of newborns were statistically compared applying two-way ANOVA with repeated measurements.

Results

Induction experiments

When exponentially growing unicells were harvested from the 20% Z8 chemostat and incubated for 48 h with filtrate from cultures of *D. pulex*, both the mean number of cells per colony and the mean particle volume increased. However, incubation with filtrate from cultures of *D. cucullata* triggered no unicell-colony transformation in *S. acutus* (Fig. 1). This resulted in a significant species ($F = 46.0$; $P < 0.001$), density ($F = 10.0$; $P < 0.001$) and interaction effect ($F = 5.4$; $P = 0.004$) for colony formation based on mean number of cells per colony (similar for colony formation based on mean particle volumes). Tukey post hoc comparisons showed that colony formation was significantly promoted in algal incubations with water from the two highest *D. pulex* densities. The algal growth rates of the controls and the different treatments based on volumes were similar, on average $0.93 \pm 0.13 \text{ day}^{-1}$. Two-way ANOVA indicated no significant species ($F = 0.38$; $P = 0.542$), *Daphnia* density ($F = 2.11$; $P = 0.118$) and interaction effect ($F = 0.42$; $P = 0.791$). Based on total cell numbers, growth rates were slightly higher, on average $1.01 \pm 0.13 \text{ day}^{-1}$, but

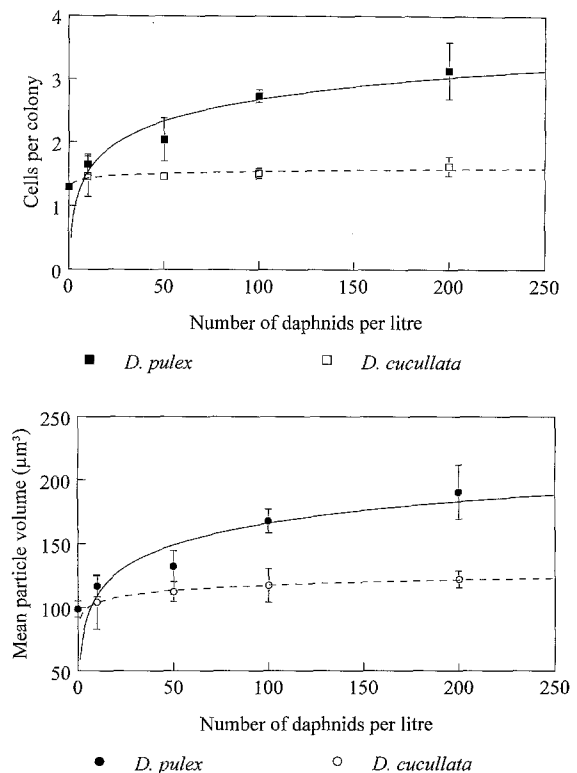


Fig. 1 Effect of 5 ml filtrate (0.1 μm) from *Daphnia* cultures varying in density on colony formation in *Scenedesmus acutus*. Upper panel mean number of cells per colony ($\pm 1\text{SD}$), lower panel mean particle (colony) volume ($\pm 1\text{SD}$) of *S. acutus*

again no significant effect of *Daphnia* density on growth rate was found ($F = 2.21$; $P = 0.105$). Hence, no metabolic costs seem to be associated with colonial growth.

Grazing experiments

Algae harvested from both chemostats and fed to two size-classes of each *Daphnia* revealed great differences in clearance rate between the two zooplankters (Fig. 2). *D. pulex* showed no differences in clearance rate when fed unicellular or colonial *Scenedesmus*, while *D. cucullata* showed depressed clearance rates when fed colonies compared to unicells. This resulted in a significant species ($F = 49.8$; $P < 0.001$) and food type ($F = 18.8$; $P < 0.001$) effect, but no significant interaction effect ($F = 3.1$; $P = 0.057$). Posthoc comparisons showed that only *D. cucullata* had significantly lower clearance rates when feeding on colonies instead of unicells. Comparison between the smaller size class of *D. pulex* and the larger size class of *D. cucullata*, which in fact are similarly sized, reveals that both species had clearance rates which did not differ significantly when fed colonies, but that adult *D. cucullata* had a significantly higher clearance rate than juvenile *D. pulex* when fed unicells.

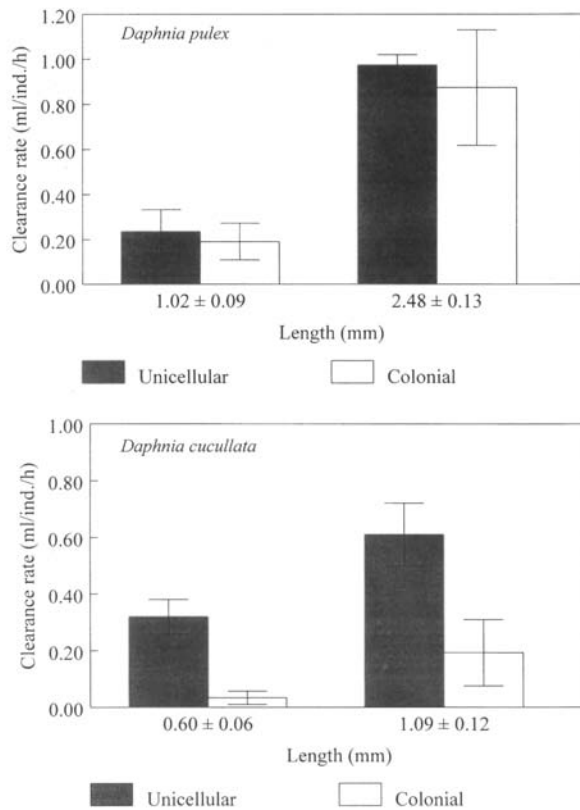


Fig. 2 Effect of colonial *S. acutus* on clearance rate (ml h⁻¹) (\pm ISD) of *D. pulex* (upper panel) and *D. cucullata* (lower panel)

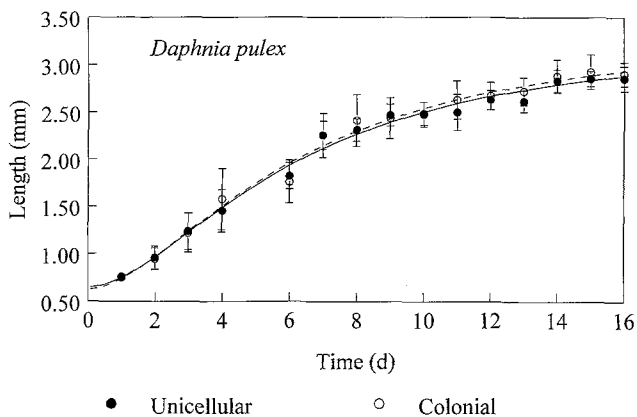


Fig. 3 Relationship between age and carapace length (\pm ISD) of *D. pulex* grown on unicellular or colonial *S. acutus*

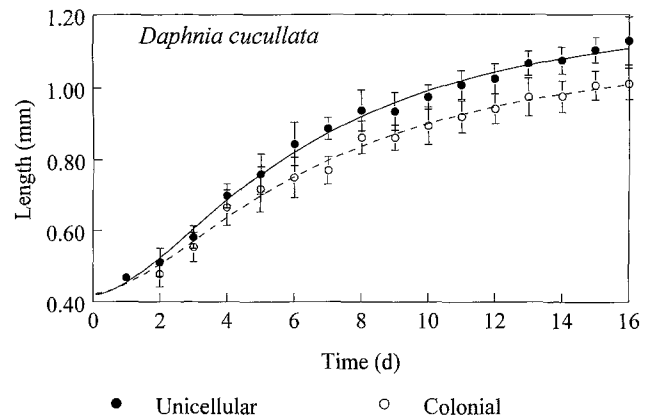


Fig. 4 Relationship between age and carapace length (\pm ISD) of *D. cucullata* grown on unicellular or colonial *S. acutus*

Life history experiments

Growth of *D. pulex*, as increase in body length in time, shows no differences between animals fed unicellular or animals fed colonial *Scenedesmus* (Fig. 3). This in contrast with *D. cucullata* in which a significant difference in increase in body length occurred (Fig. 4). After 16 days, body size of *D. cucullata* fed with colonies was significantly smaller than that of animals reared on unicells (*t*-test; $P < 0.001$), at 1.01 ± 0.04 and 1.13 ± 0.07 mm, respectively.

Age at maturity was not affected by the different food types in both *Daphnia* species (*t*-test; $P = 0.760$ and $P = 0.767$ for *D. pulex* and *D. cucullata*, respectively) neither was length at maturity in *D. pulex* ($P = 0.595$), but the length at maturity was significantly lower in *D. cucullata* when fed colonies ($P = 0.008$; Table 1).

The number of live neonates released per mature female differed significantly between successive clutches in *D. pulex* ($F = 43.8$; $P < 0.001$). However, no significant effect of unicellular or colonial food ($F = 0.34$; $P = 0.565$) was found. *D. cucullata* had more offspring in all three clutches when fed unicells compared to clutch size of animals grown on colonial *Scenedesmus* (Fig. 5). Repeated-measures ANOVA indicated no significant clutch (brood number: $F = 2.2$; $P = 0.123$) and interaction effects ($F = 1.1$; $P = 0.361$), but a significant food type effect ($F = 21.5$; $P < 0.001$). Tukey posthoc comparison revealed that there were significantly more

Table 1 Population growth rate ($r \pm 1$ SD), age and length at maturity (± 1 SD), inter-clutch duration (± 1 SD) and survival to day 16 of *Daphnia pulex* and *D. cucullata* fed unicellular or colonial *Scenedesmus acutus*.

<i>Scenedesmus</i> morphology	Growth rate (r , day ⁻¹)	Age at maturity (day)	Length at maturity (mm)	Interclutch duration (day)	Survival to day 16 (%)
<i>D. pulex</i>					
Unicellular	0.44 \pm 0.06	5.4 \pm 0.7	2.29 \pm 0.07	2.82 \pm 0.39	67
Colonial	0.42 \pm 0.07	5.4 \pm 1.4	2.31 \pm 0.09	2.86 \pm 0.64	73
<i>D. cucullata</i>					
Unicellular	0.25 \pm 0.05	6.8 \pm 1.9	0.92 \pm 0.05	2.78 \pm 1.00	86
Colonial	0.18 \pm 0.05	6.6 \pm 1.4	0.86 \pm 0.05	2.77 \pm 0.61	78

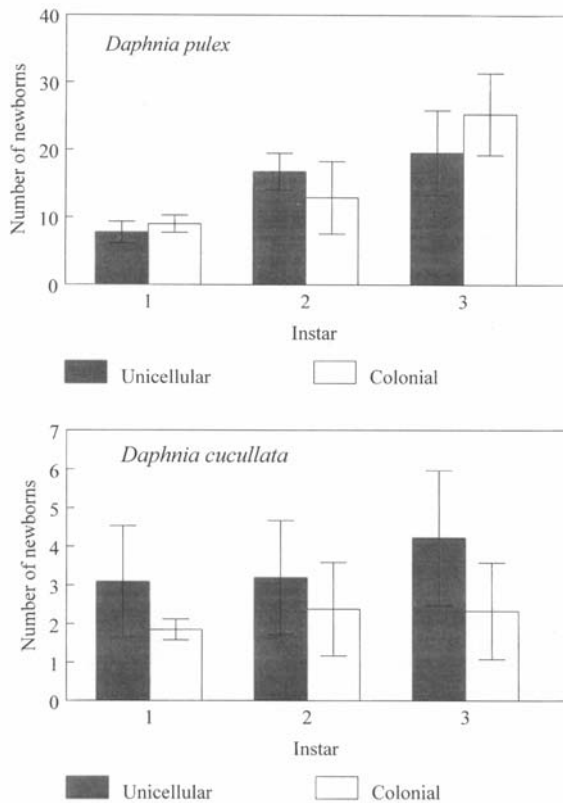


Fig. 5 Mean clutch sizes (± 1 SD) of *D. pulex* (upper panel) and of *D. cucullata* (lower panel) grown on either unicellular or colonial *S. acutus*

D. cucullata offspring in the third clutch when they were fed unicells than for animals feeding on colonies.

The *Daphnia* intrinsic rate of population increase (r) was similar for *D. pulex* on both food types (t -test; $P = 0.757$), but significantly different for *D. cucullata* (t -test; $P = 0.020$). Feeding on colonial *Scenedesmus* resulted in a lower *D. cucullata* growth rate (Table 1).

Discussion

Our results provide evidence that large *Daphnia* can influence its algal food in such a way that the life history of smaller congeners is affected. This implies that both phytoplankton-zooplankton and zooplankton-zooplankton interactions are altered by the induced colony formation. At ecologically relevant densities (up to 200 animals l^{-1}) the small *D. cucullata* induced no colonies in *Scenedesmus* probably due to the relative low biomass of *D. cucullata* instead of really lacking the ability to induce colonies. A number of grazers, including small ones like *Bosmina* (1000 animals l^{-1}), were able to induce colonies in *S. acutus* (M. Lüring and E. Van Donk, in press). Hence, colony formation in *Scenedesmus* can be interpreted as an adaptive anti-grazer strategy governed by the algae, and one can hardly claim that this

strategy is a coevolutionary conspiracy of large daphnids and algae to be protected against smaller grazers, even though at ecologically relevant densities it has exactly that effect.

One would expect a trade-off between grazer-induced colony formation and some metabolic cost (Dodson 1989). However, no differences between volume-specific algal growth rates and cell multiplication rates were found. Costs seem, therefore, not to be associated with algal growth rate. This was also observed by Hessen and Van Donk (1993) and Lampert et al. (1994).

Although the proportion of eight-celled coenobia was relatively small (c. 25%), a significant reduction in population growth of *D. cucullata* was observed. Previous induction experiments showed *S. acutus* populations consisting of over 50% of eight-celled coenobia (Lampert et al. 1994; M. Lüring and E. Van Donk, in press). We hypothesize that differences in life history parameters of small zooplankters will be even larger when large coenobia are more abundant. In fact, McCauley and Downing (1985) reported a significant underrepresentation of spheric beads in the range 12.5–17.5 μm in the guts of *D. cucullata*, and eight-celled coenobia with dimensions of 30 \times 20 μm clearly exceed this size range. Bern (1990) found that *D. cucullata* fed nonselectively on small particles, but noted selectivity against beads near the upper size limit of ingestible particles. His data showed a decreased filtering rate with increasing particle size. Filtering rates of small (0.6–0.75 mm) *D. cucullata* were c. 35% lower when fed 19- μm algae, compared with rates found when fed 2- μm algae. DeMott (1995) observed that not only the size of the food but also the hardness influences the ingestibility by *Daphnia*. He found that *Daphnia* can feed effectively on algae (relatively soft) exceeding the size of the largest ingestible bead (relatively hard) by a factor 2–5. This implies that eight-celled coenobia could be ingestible by *D. cucullata*, but our data indicate otherwise. In the presence of coenobia the clearance rate of both juvenile and adult *D. cucullata* was lower than when feeding on unicellular *Scenedesmus*.

The possibility of negative *Daphnia-Daphnia* interactions mediated by allelochemicals exuded from *Daphnia* in the lake (Matveev 1993) can not be excluded, but those allelochemicals are probably not present or at concentrations too low in the algal suspension grown on filtered lake water to be responsible for the observed effects. *D. pulex* did not show a depressed clearance rate or population growth rate, though this animal has been shown to respond to chemicals released from conspecifics (Helgen 1987).

The intrinsic rate of population increase of *D. pulex* resembled the value of 0.40 day^{-1} at the similar food carbon level of 1.5 $mg l^{-1}$ reported by Lynch (1989). The population growth of *D. cucullata* was slightly higher than values reported in literature of 0.12–0.15 day^{-1} at similar food carbon contents but at lower temperatures (Ebert and Jacobs 1991; Boersma and Vijverberg 1994).

This difference in r from literature data was mainly caused by a shorter generation time for *D. cucullata* in our experiment (~9.5 vs. ~11 days) as a result of the higher temperature. The generation time of *D. pulex* was shorter (~8.2 days) than that of *D. cucullata*, and the r value almost twice as high. Our results suggest that even when fed unicellular algae *D. cucullata* will be outcompeted by *D. pulex* (of course only in situations with low predation pressure on the larger species). Nevertheless, *D. pulex* may gain a competitive advantage from manipulating its algal food. In the field, predation pressure on large *Daphnia* will be higher than on smaller zooplankters, but grazing on larger algae and even triggering the unicell-colony transformation in some algae will result in more available food for the larger species and less for the smaller herbivorous zooplankton. Moreover, the colonial algae will exceed the size of vulnerability to grazing by small zooplankters like rotifers. Hence total grazing pressure on the algae in concern may very likely decrease. Often exudates (infochemicals) of one aquatic animal that evoke a behavioural or physiological response in another individual have been called kairomones (e.g. Tollrian 1993; Reede 1995), implying that the emitted infochemical evokes a response in a receiving organism that is adaptive in a manner favourable to the receiver. In the *D. pulex* - *Scenedesmus* interaction, however, the infochemical appears to act like a synomone (Dicke and Sabelis 1988), since both the emitter and the receiver may gain an advantage from the chemical interaction.

Further research will focus on life-history shifts in *Daphnia* and other zooplankters induced by altered algal morphology. Other polymorphic green algae like *Coelastrum* will be examined. Special attention will be paid to the possession of spines by algae, since preliminary experiments revealed an increased grazing resistance of spine-bearing morphs compared to spineless algae.

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