Feeding in *Daphnia galeata* on *Oscillatoria limnetica* and on detritus derived from it

RAMESH D. GULATI, MONIQUE BRONKHORST AND ELLEN VAN DONK
NETHERLANDS INSTITUTE OF ECOLOGY, CENTRE OF LIMNOLOGY, 3631 AC NIJEWETSALS, THE NETHERLANDS

Oscillatoria spp. are generally very abundant in many shallow, eutrophic lakes in the Netherlands. However, this is less true for *Daphnia galeata*. The main aim of this study was to investigate whether the edibility of live Oscillatoria limnetica by *Daphnia galeata*, and of the detritus derived from this filamentous cyanobacterium, was, among others, an important limiting factor for the daphnids. We measured the consumption and assimilation rates of *Daphnia* using dual-labelling radio-tracer techniques ($^{14}C$ and $^{32}P$) to label separately the live Oscillatoria filaments and detritus prepared from these filaments. The two food types were mixed in different proportions, and both the food ingestion and food incorporation rates by daphnids were measured. The main findings of this study were that specific clearance rates of *Daphnia* on shorter Oscillatoria filaments were significantly higher than on the longer filaments, in other words the weight-specific ingestion rates were higher on the shorter Oscillatoria filaments than on the longer filaments from the batch cultures. The longer Oscillatoria filaments are more likely to clump and, therefore, are more liable to be rejected by *Daphnia* during the food collection and ingestion processes. The shorter filaments, in comparison, are apparently less prone to clumping and, therefore, are cleared by the daphnids at higher rates than the longer filaments. Feeding the daphnids on double-labelled ($^{14}C$ and $^{32}P$) shorter filaments revealed that the assimilation efficiency of shorter Oscillatoria filaments was generally higher for $P$ than for $C$, probably because of a high $C/P$ ratio of Oscillatoria. *Daphnia* (0.75–1.85 mm in size) fed significantly better on dead (detritus) Oscillatoria filaments than on live Oscillatoria filaments, even if the relative proportion of detritus in the food was only about one-quarter that of the live filaments. This preference for detritus over live Oscillatoria, as indicated by Chesson’s selectivity coefficient $a$, was apparently a passive process, rather than a case of active food selection. This ‘selective’ feeding on detritus was apparently facilitated by the relatively greater rejection of the live filaments than the detrital filaments. At very high food concentrations (15–25 mg C l$^{-1}$), with the share of the live Oscillatoria filaments 2 to 2.5 times greater than that of the detritus, the ingestion rates increased proportionally less with increase in daphnid size than was expected on the basis of the allometric relationship between the length and weight of these animals. This implies that the larger animals had greater interfering effects of the Oscillatoria filaments on the food collection and ingestion processes.

INTRODUCTION

The eutrophication-related increases of filamentous cyanobacteria (blue-green algae) and detritus in lakes are now well known. However, the edibility of cyanobacteria for filter-feeding zooplankton, especially *Daphnia* spp. (see reviews [Burns, 1987; Lampert, 1987a]), and the role of cyanobacteria in the nutrition of planktonic crustaceans, are quite controversial [Haney, 1987]. Coexistence of some large-bodied *Daphnia* spp. with filamentous cyanobacteria in some lakes may be facilitated by undeterred consumption of some groups in the *in situ* phytoplankton (diatoms, flagellates and chlorococcales) and avoidance of cyanobacterial filaments without substantial interference [Epp, 1996]. That the cyanobacterial filaments may be important for *Daphnia* as a source of nutrition (positive), but may interfere with the process of food collection, related to the filament concentration and length (negative), has been analysed thoroughly by Glowińc (Gliwicz, 1990a,b; Gliwicz and Lampert, 1990). The nutritive value of detritus compared with that of the live algae often appears to be low (Starkweather and Bogdan, 1980). Despite the
dominance of detritus in some lakes, its share in the nutrition of daphnids may be negligible (Ojala et al., 1995). However, daphnids appear to be indifferent to detritus and algae (Bossemann and Räimann, 1986), primarily because they are non-selective in their feeding behaviour. When good-quality food is scarce there may be a weaker selection for the low-quality food, e.g. detritus. This latter has been shown for copepods using dialabelling with live and dead algae (DeMott, 1988). Thus, detritus may, in such cases, contribute a substantial proportion to the energy requirements of grazing zooplankton and form an important food source for cladocerans (Toth et al., 1987).

In smaller-bodied cladocerans (Chydrorus sphaericus), cyanobacterial detritus, added to laboratory cultures of green alga, has been reported to even increase the fitness of these animals (Vijverberg and Boersma, 1997). It was also reported that the juveniles of 11 clones of Daphnia cucullata from Dutch lakes of varying trophy grew and reproduced in the laboratory on a sole diet of Oscillatoria limnetica (Repka, 1998). However, it was observed that this cyanobacterium was a poor food compared with Scenedesmus.

Some cyanobacteria are known to possess morphological defences (size) or chemical defences (toxins) against herbivory by zooplankton (Kirk and Gilbert, 1992). The relative edibilities of the cyanobacteria for the taxa of filter-feeding zooplankton of different sizes, and the effect of variance in the assimilation efficiency of different algae on the growth and reproduction of the filter-feeding zooplankton are important. Mechanical aspects of food particle interception, collection and enmeshment to the feeding cross-sectional area, using a digitizing tablet (Hoogveld and Moed, 1984), show increased handling time of filaments, as well as their entanglement with the feeding limbs of Daphnia.

Daphnia galeata (erroneously cited as D. hyalina in some earlier papers) is commonly encountered in both deep and shallow Dutch lakes, irrespective of the trophic state of the lakes. Nevertheless, it is virtually absent in certain highly eutrophic water bodies, e.g. Loosdrecht lakes (Gulati, 1990; Lammens et al., 1992). These lakes are dominated by cyanobacteria spp. (mainly Oscillatoria limnetica) and detritus (Otten et al., 1992). Dawidowicz fed Daphnia magna in a flow-through system containing the Lake Loosdrecht water, very rich in Oscillatoria limnetica filaments (Dawidowicz, 1990). He not only observed a significant decrease in these filaments but also a significant reduction in the filament length, caused by the Daphnia feeding activity. Nevertheless, the existing circumstantial evidence shows that the quality of sestonic food, dominated by these filamentous cyanobacteria, for Daphnia spp. in these lakes is poor (Gulati, 1990; Gulati et al., 1992).

More recently it was confirmed that the high C/P ratios of the seston in the Loosdrecht lakes limited the abundance of Daphnia spp., especially of the D. galeata (DeMott and Gulati, 1999). Also, size selective predation on zooplankton by planktivorous fish, particularly by the bream which are abundant in these lakes, could contribute importantly to the scarcity of daphnids in these lakes (see papers in Van Liere and Gulati, 1992). What we do not know, however, is how, when and to what extent the two factors, edibility and quality of food and predation, are important for Daphnia spp. in these lakes?

As a part of the food-chain research we examined the effects of food quality on growth and reproduction rates of Daphnia species, and edibility and assimilation rates of Daphnia spp. feeding on cyanobacteria and the detritus originating from these cyanobacteria (Vijverberg et al., 1993; Bronkhorst, 1994; Repka et al., 1998). In the present study, we determined the grazing and assimilation rates and assimilation efficiencies of a D. galeata clone in the laboratory. The animals, including those in the length range 0.75–1.9 mm, were concurrently fed mixtures of O. limnetica and detritus filaments, of the same length range, in order to study if the physiological differences in the food types affected the ingestion and assimilation by the daphnids differently. Notably, in the Loosdrecht Lakes, the abundance of cyanobacteria and of the smaller-bodied cladocerans, D. cucullata and Bosmina spp. goes hand in hand. We, therefore, expect that the present study, comparing the food-size-related edibility for the daphnids of these filaments, could provide a clue to the disadvantage the larger animals might have in such lakes.

**METHOD**

**Cultures, filament size and detritus preparation**

*Culture of Oscillatoria*

In the feeding experiments, a strain of Oscillatoria limnetica was used that was originally isolated from Lake Loosdrecht and is now maintained in cultures in laboratory-scale enclosures (LSE), which are designed to simulate the growth conditions for this cyanobacterium in the lake (Gons et al., 1993). For our experiments, we obtained Oscillatoria from the ‘overflow’ of the LSE and centrifuged and resuspended it in GF/F-filtered lake water.

*Effect of filament length on feeding*

The length frequency distribution of about 100 live Oscillatoria filaments was measured at random under a microscope, using a digitizing tablet (Hoogveld and Moed, 1993). Roughly comparable length classes of the live filaments and detritus (see below) were obtained by sonifying...
both food types for 50 s at a sonifier intensity of 3 (Sonifier B-12, Branson Sonic Company, CT, USA). Non-sonified and sonified *Oscillatoria* filaments are hereafter distinguished as long filaments and short filaments, respectively.

The length frequency distributions of the long and short filaments differed significantly ($\chi^2 = 34.39; \text{DF } 5; P < 0.001$). Only about 20% of the long *Oscillatoria* filaments were <50 µm (range 10–190 µm), while >55% of the short filaments were <50 µm (Figure 1a). Live, long filaments were longer than the detrital filaments, with a greater tendency to aggregate. However, after sonification, between 64% and 73% of filaments of both detritus and live *Oscillatoria* were <30 µm and in both cases, between 46 and 50% of the filaments varied in length between 10 and 30 µm (Figure 1b). Thus, the length frequency distributions of detritus and live filaments did not differ significantly from one another after sonification ($\chi^2 = 7.73; \text{DF } 5; P > 0.05$).

**Preparation of detritus:**

We know that when growth is prevented, the cyanobacteria decompose rather rapidly (Fallon and Brock, 1979), and that the detritus thus formed can be an important

---

**Fig. 1.** Effect of sonification (50 s) on the filament lengths of *Oscillatoria limnetica*. (a) Length frequency distribution: non-sonified filaments, black bars; sonified filaments, hatched bars; (b) a comparison of the length frequency distribution of the filament lengths of sonified detritus (black bars) and sonified *O. limnetica* (hatched bars).
Food source for cladocerans in lakes (Toth et al., 1987). Detritus was prepared by placing Oscillatoria filaments in beakers in complete darkness and incubating the beakers at 30°C with continuous stirring. After incubating the filaments for between 3 and 6 days, usually 4 days, the detritus was ready. This was indicated by the colour of the suspensions, which turned from blue-green to yellow to yellowish-brown during the incubation. Microscopic examination confirmed that the filamentous material in suspension did not have any viable filaments. The detritus was centrifuged twice for 10 min at 4000 r.p.m. and the supernatant medium was decanted. The concentrated detritus was then resuspended in GF/F-filtered lake water. Clumps, if any, were broken up by sonification as for the live filaments, using intensities of between 5 and 7 for 5–60 s, with a stepwise increase of 5 s. An intensity of 3 for 50 s was usually found to be adequate to break up any left-over clumps, without causing notable damage to the filament morphology or leaching loss of the cell contents. The detritus was then filtered through a 33-µm-mesh sieve to remove any clumps. The filtrate with detritus was stored in a refrigerator. The sonifying and filtration procedures prevented the detritus in suspension from sedimenting. Some contamination with clathers of both the live filaments and the detritus was observed but was unavoidable.

Culture of Daphnia

The Daphnia pulex used in the experiments belonged to a clone derived from a single female. The animals were fed a 1:1 food mixture (4 mg C l–1) of Oscillatoria and detritus suspended in fresh GF/F-filtered lake water. The carbon concentrations of Oscillatoria and of detritus were derived from separate calibration curves between spectrophotometric extinction (772 nm) values and the corresponding carbon contents of Oscillatoria and detritus in the suspensions. The carbon content was computed from the measurements of Chemical Oxygen Demand using a modified method (Gulati et al., 1982). The culture was refreshed daily and maintained at an experimental temperature of 20°C in subdued light. Prior to the experiments, the daphnids were sorted into length classes, and acclimatized for 24 h to the experimental food mixture and temperature (20°C).

Grazing and assimilation experiments

Dual labelling

The uptake and assimilation rates of detritus and live filaments by daphnids were compared using both 14C-labelled detritus and 32P-labelled live algae in mixture or 32P-labelled detritus and 14C-labelled live algae. This enabled us to measure possible discrepancies due to differential leakage losses of C and P during the handling and collection of the filaments by the daphnids. It also allowed comparison of the assimilation rates of C and P by the daphnids, because it is known that P is better assimilated than C by D. magna, using P-deficient diets (DeMott et al., 1998) such as the cyanobacteria populations from these lakes (personal observations R. D. Gulati). In addition, we concurrently measured in an experiment the assimilation efficiencies of C and P in the dual-labelled detrital food, by simultaneously incubating the live Oscillatoria filaments with both 14C and 32P. The detritus was thereafter prepared from these filaments in the same way as explained in the section above.

Preparation of tracer foods

A 500 ml suspension of Oscillatoria obtained from the LSE was mixed with 600 ml fresh culture medium (Rijkeloer et al., 1988). The suspension was split into two equal parts: to one part 3.7 MBq NaH14CO3 was added and to the other part 4 MBq 32PO4 was added. For measuring assimilation efficiencies of C and P, the detritus filaments in suspension were dual-labelled. These suspensions were then incubated in a culture cabinet at 20°C in a light intensity of 8.4 W m–2, using white luminescent light. A 14 : 10 h light : dark cycle was used for the incubation, which lasted 4 days. We assumed that this 4-day labelling period was long enough to ensure uniform distribution of the label over the different cell parts. Thereafter, the algae in both beakers were filtered and centrifuged, as mentioned under the procedure for preparing the detritus. The detritus tracers (14C or 32P) were prepared by placing the labelled algae in the dark at 30°C, proceeding in the same way as for the manufacturing of detritus. Both the tracer foods, the live filaments and the detritus, were centrifuged twice and resuspended in GF/F-filtered lake water from Lake Loosdrecht and sonified and sieved (33 µm).

Measurement of clearance and assimilation rates

The procedures for measuring clearance and assimilation rates are essentially the same as those used previously (Gulati et al., 1982). On the day of the experiment, 10 daphnids were transferred to 100 ml fresh food suspension (4 mg C l–1) in a beaker, and placed in a culture cabinet at the same temperature and light settings as for culturing and acclimatization of the animals. About 2–3 ml each of the two tracers, 14C-labelled detritus and 32P-labelled O. limnetica or 14C-labelled O. limnetica and 32P-labelled detritus, were added to the beakers containing the daphnids. This caused only a negligible increase in the food concentration for the animals (Gulati et al., 1982). A feeding period of between 10 and 15 min was used to measure the clearance rates (CR). This time is shorter than the gut passage time (Gulati et al., 1982; Muck and Lampert, 1984). Thereafter, the animals were transferred...
to a 100 µm sieve, rinsed with filtered lake water, back-washed from the sieve to scintillation vials, and immediately killed by adding a few drops of 96% ethanol to prevent possible 14C loss due to respiration. The assimilation rates of *Daphnia* were determined the same way as the CR, except that the daphnids were fed for 30 min instead of 10–13 min, and were subsequently fed for 45 min on unlabelled food to clear their guts, appendages and carapace of labelled food, before transferring the animals to the vials and adding ethanol.

The radioactivities of animals in the vials and the tracer food were measured using a Packard Liquid Scintillator Counter (Model 4530) and a standard procedure for counting the two tracers simultaneously, and for deriving the respective radioactivities (DPM) of these tracers.

**Daphnia biomass**

The length (L, mm) and weight (W, µg C daphnid⁻¹) of individual daphnids were obtained from the L : W regression relationship (W = 5.29 \( \times \) \( L^{2.65} \)) computed by us for *D. galeata* grown in the lake water at high food concentrations in the laboratory.

**Feeding parameters and calculations**

The calculation procedures are summarized below [for details see (Gulati et al., 1982)].

**Clearance rate**

The clearance rate (CR, ml daphnid⁻¹ day⁻¹) is equivalent to the volume of suspension from which food is removed by the daphnids in 24 h, such that CR = \( \frac{\left( \frac{R_z}{R_f} \right)}{t} \times 60 \times 24 \) ml daphnid⁻¹, where \( R_z \) is the radioactivity in DPM daphnid⁻¹; \( R_f \) is the activity in the food suspension in DPM ml⁻¹; and \( t \) is the experimental feeding time in minutes.

**Specific clearance rate**

The specific clearance rate (SCR, ml µg⁻¹ daphnid C day⁻¹) is given by CR/W, where W is the weight (µg C) per individual daphnid.

**Ingestion rate**

The ingestion rate (IR, µg C ingested daphnid⁻¹ day⁻¹), or feeding rate, by the animals is CR \( \times F_f \), where \( F_f \) is food concentration (µg C ml⁻¹).

**Specific ingestion rate**

The specific ingestion rate (SIR in per cent: µg C food ingested per µg⁻¹ C daphnid day⁻¹ \( \times 100 \) or % daily ration) is given by IR/W, where W is the weight of daphnid in µg C.

**Net clearance rate**

The net clearance rate (NCR), or assimilation, is measured in ml daphnid⁻¹ day⁻¹, i.e. fraction of the CR from which food is incorporated into the body tissues. It is calculated like CR, but replacing \( t \) with the corresponding feeding period value (i.e. 30 min).

**Assimilation efficiency**

The assimilation efficiency is the ratio between NCR and CR expressed in per cent.

**Statistical analysis**

A \( \chi^2 \) test was used to test for differences in length frequency distribution between the short and long filaments of *Oscillatoria* and between short *Oscillatoria* filaments and sonified detritus filaments. In addition, the differences in grazing rates and assimilation rates were tested statistically (two sample analysis of variance, \( t \)-test of the differences between two means) using the computer program CSS (Statsoft, 1992). Because in the daphnids the relationship between L and CR is known to be of the form CR = aLb (Lampert, 1987b), the data were log-transformed for regression analysis.

**Food selectivity coefficient**

Food selection for detritus was quantified by the selectivity coefficient \( \alpha \) (Chesson, 1983). This \( \alpha \) is a measure of CR for detritus compared with live filaments. All values of \( \alpha > 0.5 \) indicate a preference for the detritus and those <0.5 indicate a preference for the live filaments. A one-sample \( t \)-test was used to examine the confidence limits of \( \alpha \) and to test if this coefficient was significantly >0.5 at \( P < 0.01 \).

**RESULTS**

A total of 10 experiments was carried out. The first three were introductory trials (see Figures 2 and 3a,b) and the remaining seven concerned the different aspects of ‘grazing’ (see Table 1 and Figures 4–7).

**Introductory trials**

**Effects of Oscillatoria filament size on the SCR of daphnids**

The SCR for daphnids on shorter (S, sonified) *Oscillatoria* filaments was nearly twice as high as for longer filaments (NS, not sonified), irrespective of the tracer used to measure the SCR (Figure 2). The variation between the SCR replicates of longer filaments was high for both the tracer foods. The assimilation efficiencies on shorter filaments were higher than on longer filaments for both tracer foods. The assimilation efficiencies on shorter filaments were higher than on longer filaments for both tracer foods (\( ^{32}P \): shorter filaments, 31.5 ± 4.4%; and longer filaments, 32.8 ± 11.2%; and \( ^{14}C \): shorter filaments, 37.7 ± 9.5%; and longer filaments, 36.8 ± 15.2%).
Assimilation efficiency of short Oscillatoria filaments

This experiment was carried out using non-labelled Oscillatoria and detritus in the ratio of about 1:1 (total food, 4.2–4.7 mg C l⁻¹). The shorter Oscillatoria filaments were double-labelled to measure CR and NCR of the daphnids (L, 1.67 mm) to derive their assimilation efficiencies for C and P (Figure 3a). The CR for Oscillatoria based on the 14C tracer (4.48 ± 0.21 ml daphnid⁻¹ day⁻¹) and 32P tracer (4.04 ± 0.34 ml daphnid⁻¹ day⁻¹) did not significantly differ. The NCR for 32P tracer was, however, about 20% higher, resulting in a clearly higher assimilation efficiency for P than for C, i.e. 65.8 ± 0.8% versus 46 ± 3.6%, respectively (Figure 3a).

### Table 1: Summary of grazing experiments with Daphnia galeata, using food mixtures of Oscillatoria limnetica and detritus in different concentrations and parameters measured

<table>
<thead>
<tr>
<th>Exp. no.</th>
<th>Food conc. (mg C l⁻¹)</th>
<th>Ratio Osc.:Detr.</th>
<th>Daphnia length (mm)</th>
<th>Measured parameters</th>
<th>Detritus label</th>
<th>Figure no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>6.40</td>
<td>NS S 1:1</td>
<td>1.67</td>
<td>IR</td>
<td></td>
<td>32P4 (a)</td>
</tr>
<tr>
<td>2</td>
<td>6.80</td>
<td>NS S 1:1</td>
<td>1.67</td>
<td>IR</td>
<td>14C</td>
<td>4(a)</td>
</tr>
<tr>
<td>3</td>
<td>15.80</td>
<td>NS S 4:6:1</td>
<td>1.80</td>
<td>IR</td>
<td></td>
<td>32P4 (a,b)</td>
</tr>
<tr>
<td>4</td>
<td>24.40</td>
<td>NS S 2:5:1</td>
<td>0.70–1.80</td>
<td>IR</td>
<td>14C</td>
<td>5(a)</td>
</tr>
<tr>
<td>5</td>
<td>14.00</td>
<td>NS S 1:1</td>
<td>0.70–1.80</td>
<td>IR</td>
<td>14C</td>
<td>5(b)</td>
</tr>
<tr>
<td>6</td>
<td>4.00</td>
<td>S S 1:1</td>
<td>1.65</td>
<td>CR, NCR</td>
<td>14C</td>
<td>6(a)</td>
</tr>
<tr>
<td>7</td>
<td>4.00</td>
<td>S S 1:1</td>
<td>0.90–1.90</td>
<td>CR, NCR</td>
<td>14C</td>
<td>6(b)</td>
</tr>
</tbody>
</table>

Detritus (Detr.) was sonified (S) in all experiments but Oscillatoria filaments (Osc.) were not sonified (NS) in the first five experiments, they were sonified in the last two experiments only.

IR, ingestion rate; CR, clearance rate; and NCR, net clearance rates.

**Fig. 2.** Specific clearance rates of Daphnia galeata on sonified (S) and non-sonified (NS) filaments labelled with two tracers: 14C (black bars); 32P (hatched bars).

**Assimilation efficiency of short Oscillatoria filaments**

This experiment was carried out using non-labelled Oscillatoria and detritus in the ratio of about 1:1 (total food, 4.2–4.7 mg C l⁻¹). The shorter Oscillatoria filaments were double-labelled to measure CR and NCR of the daphnids (L, 1.67 mm) to derive their assimilation efficiencies for C and P (Figure 3a). The CR for Oscillatoria based on the 14C tracer (4.48 ± 0.21 ml daphnid⁻¹ day⁻¹) and 32P tracer (4.04 ± 0.34 ml daphnid⁻¹ day⁻¹) did not significantly differ. The NCR for 32P tracer was, however, about 20% higher, resulting in a clearly higher assimilation efficiency for P than for C, i.e. 65.8 ± 0.8% versus 46 ± 3.6%, respectively (Figure 3a).

**Fig. 3.** A comparison of assimilation efficiencies of Daphnia galeata on short filaments (sonified) of Oscillatoria limnetica using two radioisotopes (a). Regression relationship between the specific ingestion rates on detritus and Daphnia galeata of different weights; 14C, + and unbroken line; 32P, ● and broken line. b.
Feeding on detritus in the presence of Oscillatoria

In this experiment, double-labelled and sonified detritus was fed to six size (weight) classes of daphnids (Figure 3b) to examine the specific ingestion rates (SIR) of detritus in the presence of Oscillatoria in the food mixture. The SIR for detritus was markedly higher for detrital C than for detrital P for the smaller daphnids, <5 µg C animal⁻¹, but only marginally for the larger daphnids, >5 µg C animal⁻¹ (Figure 3b). However, all the SIR values for detritus lay below 20% day⁻¹, and were, except for the two smallest size classes, <5% day⁻¹. Such low daily rations are apparently due to very high rejection rates of the food comprising mixed live and dead filaments of Oscillatoria, especially by the larger animals.

Grazing experiments

The protocol of the seven grazing experiments carried out using mixed food comprising detritus and Oscillatoria is summarized in Table 1. The purpose of these experiments was to examine the following: firstly, whether the differences in filament size of mixed detritus and live Oscillatoria affect their relative uptake rates by the daphnids; secondly, if the relative or absolute concentrations of detritus and Oscillatoria in the mixture influence selection

![Feeding of Daphnia galeata on mixtures of sonified detritus and long (non-sonified) Oscillatoria limnetica in three experiments (a; see also Table 1 for details of the experiments 1, 2 and 3). Feeding replicates (Exp. 3) of ³²P-labelled detritus (shaded bars) and ¹⁴C-labelled O. limnetica (unshaded bars) (b). The concentrations of the two food types in the mixture are shown.](image-url)
2.4-fold and the
In the third experiment, total food level was raised about
tus at significantly higher rates, irrespective of the tracer.
toria
examine if a much higher proportion of
panel of Figure 4a, and Figure 4b). This enabled us to
mixture was markedly higher, 4.60 : 1.00 (Table 1; right
switching of the labels between the detritus and
main difference between these two experiments was the
length (the left and middle sets of bars, Figure 4a). The
roughly a 1 : 1 ratio, and the daphnids were 1.67 mm in
respectively, comprised detritus and long
Evidence that
the much higher concentration of live filaments (right
for detritus was between 1.4- and 1.8-fold higher, despite
specific uptake rates of detritus by larger animals relative
to those generally prevailing in Lake Loosdrecht at the time of
Oscillatoria blooms. Even though the share
of total food, the IR was 3.3 and 5.2 times higher for the
detritus, for the small and large animals, respectively. The
intercepts of the regressions indicate that even the 1 mm
length animals ingested about four times more detritus
than live Oscillatoria filaments. The regressions for IR upon
L (animal length) were significant (P < 0.05) for both food
types. The regression slopes of less than 2, for both detri-
tus and Oscillatoria, imply that IR increased proportion-
ately less with size than expected on the basis of the
length- related increase of the daphnid weights. This was
especially true in Exp. 4 (Table 1; Figure 5a) for IR of
larger animals on detritus (slope 1.01), the concentration
of Oscillatoria being approximately 1.8 times higher than
in Exp. 5.

Detritus vs. Oscillatoria: filament size effect (Exp. 1, 2 and 3)
The labelled detritus and long Oscillatoria filaments were
offered together to the animals. In the first two experi-
ments, food concentrations, 6.4 and 6.8 mg C l–1, respec-
tively, comprised detritus and long Oscillatoria filaments in
roughly a 1 : 1 ratio, and the daphnids were 1.67 mm in
length (the left and middle sets of bars, Figure 4a). The
main difference between these two experiments was the
switching of the labels between the detritus and Oscilla-
toria. In both experiments, the daphnids ingested the detri-
sus at significantly higher rates, irrespective of the tracer.
In the third experiment, total food level was raised about
2.4-fold and the Oscillatoria to detritus ratio in the food
mixture was markedly higher, 4.60 : 1.00 (Table 1; right
panel of Figure 4a, and Figure 4b). This enabled us to
examine if a much higher proportion of Oscillatoria in the
food mixture than in the preceding two experiments would interfere with the ingestion of detritus. The CR (i.e. IR/food concentration) for detritus was between 6.6- and 8.6-fold higher than that for the live filaments. Also, the IR for detritus was between 1.8- and 1.8-fold higher, despite the much higher concentration of live filaments (right panel of Figure 4a, and Figure 4b). Thus, there was no evidence that Oscillatoria in any way interfered with the ‘selective’ higher uptake of detritus by the daphnids.

Effects of daphnid size on feeding (Exp. 4 and 5)
We compared the IR of different size classes of the daph-
nids on a mixture of live and dead filaments. The concen-
tration of long Oscillatoria filaments was kept between 1.9- and 2.5-fold higher than the detritus in the food suspen-
sion. The total food concentrations used were much higher than those generally prevailing in Lake Loosdrecht
at the time of Oscillatoria blooms. Even though the share
of live filaments was much greater, between 66% and 71%
DISCUSSION

Daphnia feeding on Oscillatoria versus detritus

The main objective of this study was to examine in Daphnia their ingestion rates of live Oscillatoria filaments and to compare these with those of detritus. We used the two diets together in concentrations that are higher than those observed at the peak densities of the filamentous cyanobacteria in most of our eutrophic lakes (VanTongeren et al., 1992). To start with, we offered the daphnids relatively long Oscillatoria from the laboratory cultures in combination with the Oscillatoria detritus manufactured in the laboratory. The detritus had to be sonified to prevent clumping and to keep it in suspension. The use of two tracer foods in the mixture enabled us to concurrently measure the uptake and assimilation rates of the live cyanobacterial filaments and the detritus.

The clearance rates (CR) of daphnids on detritus are
significantly higher than on Oscillatoria filaments. Even though the share of detritus in the food menu was kept to as low as one-fifth of the total food mixture, both CR and NCR were much higher for detritus than for Oscillatoria. Also, irrespective of their size and the proportions of the two foods in the mixed diet, the daphnids are able to ingest disproportionately more detritus than Oscillatoria. That there is a strong preference for detritus is also confirmed by the high selectivity coefficients (Chesson, 1983). An active selection of detritus is, however, not expected because daphnids, unlike Bosmina and copepods, are considered non-selective feeders (DeMott, 1988). Moreover, this selection is less likely for long, solitary trichomes, which are known to be effectively grazable (Schaffner et al., 1996). Because the experimental duration was short, 10–12 min, we did not observe any increased sinking or floating of Oscillatoria in food suspension that might result in its poor availability and, therefore, its reduced uptake compared with detritus. Thus, the relatively higher clearance of detritus than of the Oscillatoria filaments by the daphnids can be explained by “selective” rejection of Oscillatoria during the food collection process. This is, however, hard to conceive if Oscillatoria filaments and detritus are homogeneously mixed, as we had assumed because the...
filaments were shortened and were in a similar size range. This shortening of the Oscillatoria filaments was necessitated because the long filaments (200 µm) tended to clump. The increase in filament length could be an important factor in the field. The nutrient bioassays using laboratory-scale enclosures (LSE) indicate that this increase is caused by nutrient limitation (personal communication, Dr H. Gons). Also, Smith and Gilbert attributed changes in the filament length of Anabaena to changes in the growth phase and culture medium (Smith and Gilbert, 1995). Apparently, despite the measures taken to overcome clumping, it is difficult to quantify the adverse effects of these clumps in preventing food particles from entering the gape of the food chamber or causing their rejection. The high filament densities used, which reflect the prevailing concentrations in many Dutch lakes, may not only interfere with the process of food collection but also promote rejection of these filaments (DeMott, 1993).

Thus, the increased rejection of live filaments during the food collection process, must go hand in hand with greater ingestion of detritus. In other words, the daphnids must possess the mechanical ability to reject certain food particles much more than the other particles in the food mixture. Discreet rejection of live filaments is quite conceivable if these form some sort of flakes, stacks, or clumps, from which the detritus is generally excluded. It is most likely that in our study, the detritus and live filaments did not homogeneously mix with one another in the suspension. There is some evidence now that some Daphnia species can discriminate between hard and soft food particles (DeMott, 1995) as well as exhibit weak discrimination between beads and algae in the upper size range (Bern, 1990). Thus, the unexpectedly higher uptake of detritus is the result of some sort of selection, passive or "active", because of the greater pliability of detritus than the Oscillatoria filaments. The latter are seemingly more rigid and, therefore, less easily broken, or more difficult to handle. This, together with similarities in physical properties (length, narrow width and form) of these filaments within a food mixture will probably facilitate their affinity for greater adherence to one another in the mixture, than to detrital filaments, thus preventing their uniform mixing with the detrital particles. In an analogous study, we fed the daphnids a mixture of Oscillatoria and Scenedesmus in varying concentrations. The CR for Scenedesmus, as detritus in the present study, was not adversely influenced, by the stepwise increase in the proportion of live Oscillatoria from 25% to 50% and 75% [R. D. Gulati unpublished results; (Buenk, 1993)].

We observed that the increase in the ingestion rate and assimilation rate with increase in animal size was greater for detritus than for live Oscillatoria filaments. The IR of smaller animals (L 0.74 mm; W 2.4 µg C ind⁻¹ day⁻¹) and larger animals (L 1.8 mm; W 25.1 µg C ind⁻¹ day⁻¹) for the two food types were derived from regressions (Figure 5b). The computed ratios of detritus to live filaments for the Daphnia IR (µg C ind⁻¹ day⁻¹) were: large animals, 13:2.5 and small animals, 2.3:0.7. Thus, the large animals, that weighed an order of magnitude more, consumed

![Fig. 7. Mean values with SE of Chesson’s α for food selectivity with y axis, detritus Oscillatoria limnetica by Daphnia plates of different lengths, a preference for detritus is seen for all size classes of the daphnids.](image-url)
detritus 3.2 times (13.1/2.5) more than the live filaments, but this difference was only 3.3 times for the smaller animals. The size-related disparity (SRD) between the daphnids for the total food ingested (detritus + live) was about a factor of 2 (1.25/0.62). Thus, their weight-specific ingestion, or daily ration, was just one-half of that for smaller daphnids. In other words, the larger animals would lag behind their smaller counterparts in their food uptake for both food types, probably because of the lower assimilation efficiency of shorter filaments of *Oscillatoria* filaments: the size-related effects

As mentioned above, it is now well known that the clearance rates of large-bodied daphnids are more likely to be depressed by cyanobacterial filaments than those of the smaller ones (Gliwicz and Siedlar, 1980). On the other hand, Dawidowicz, who fed *Daphnia magna* on *Oscillatoria* filaments from Lake Loosdrecht (Dawidowicz, 1980), observed that the daphnids caused both reduction in filament numbers and the filament length. This implies that the feeding activity of the daphnids makes these filaments more accessible to other filter-feeding cladocerans, and that the detritus formation is likely to make these filaments more vulnerable to be used as a substrate by heterotrophic bacteria. We examined whether the reduced filament length of live *Oscillatoria* could enhance the uptake of these filaments size-related the longer *Oscillatoria* filaments and detritus particles (discussed above). We offered the daphnids the live filaments and detrital particles of comparable length. The detrital filaments, however, are probably less consistently elongated in the suspension than are the live filaments. It is, however, assumed that the size comparability would preclude the inhibitory effect of length-related factors. Despite the difficulties of preparing shorter, live filaments of reproducible length, the disparity between the uptake rates of detritus and live filaments was substantially reduced. All the food uptake rate parameters are significantly higher for *Daphnia* feeding on the shorter *Oscillatoria* filaments than on the longer filaments. Thus, in *D. galeata* the filament length, indeed, appears to interfere with the collection and ingestion of the long filaments, which had an average length of 100 µm in our case. Lower ingestion and filtering (clearance) rates for *D. pulex* feeding on *Aphanizomenon fluo-aquae* with colonies >1.5 mm compared with colonies <1.5 mm have been reported (Holm et al., 1983). Also, DeBernardi et al. found that *Microcystis aeruginosa* is consumed better if its colonies are small (DeBernardi et al., 1981).

Shorter filaments also result in an increase in SCR than long filaments, notwithstanding the presence of P or C tracers in the food (Figure 2a). Nevertheless, the assimilation efficiency of shorter filaments of *O. flos-aquae* was higher for P than for C (Figure 3a). If this was achieved by egesting relatively more C or by incorporating relatively more P in the gut to keep the body’s C:P ratio constant (about 30:1), has been the subject of our other study. This is certainly quite likely in homeostatic consumers such as *Daphnia* (Sternier and Hessen, 1994). Thus, the shorter filaments do appear to improve food uptake but this does not change our conclusion that the detritus was ingested much better than live filaments. On the other hand, assimilation efficiency of *Daphnia* feeding on detritus and shorter *Oscillatoria* filaments did not differ, though we had expected a clearly lower assimilation efficiency for detritus because of the expected lower nutritive value of detritus compared with live filaments. Lastly, our data confirm that the difference in nutritive value between live *Oscillatoria* and detritus did not play an important role in the latter’s greater uptake.

Detritus uptake: its quality and consequences for *Daphnia* growth and reproduction

Because the daphnids are relatively insensitive to food quality in their food collection mechanisms, they are likely to feed more efficiently on (finer) detrital particles so that they are categorized as detritivores rather than as herbivores (Kerfoot and Kirk, 1991). The quality of detritus can vary markedly with its origin, age and colonization by microbes (DeMott, 1988), and it is generally regarded as inferior to live algae as food for daphnids (Lampert, 1987b). Thus, the ‘preferential’ uptake of detritus – the low-quality food – by *D. galeata* in our study, further
corroborates the prevailing view that daphnids cannot select food based on quality. However, the observations that daphnids derived from dying and decaying cyanobacteria can be effectively ingested and assimilated can have important consequences for the growth and reproduction of daphnids in the field. Interestingly, in an other study from our laboratory it has been demonstrated that the daphnids derived from *O. limnetica* supports growth and reproduction in *D. galeata* (Repa et al., 1990, comparable to that on *Synechocystis* elongata. Gliwicz (1990) observed that filaments of *Aphanizomenon* in ‘poor physiological condition’ had a lower interfering effect than healthy filaments. In other words, these decaying filaments overgrown by bacteria were found to become a better food source for filter-feeding cladocerans. Also laboratory studies demonstrated increased reproduction of cladocerans concomitant with the decline of cyanobacteria, e.g., *Microcystis* overgrown by bacteria were found to become a better food source for filter-feeding cladocerans. Such studies complement our findings that daphnids derived from Oscillatoria is both ingested and assimilated better by the daphnids.

Conclusions

Both the present study and the published literature on the edibility of filamentous cyanobacteria for *Daphnia* show that despite the interference with the food collection and ingestion processes, cyanobacteria can be an important food source for daphnids in lakes. That the cyanobacterial daphnids and shorter cyanobacterial filaments can be relatively better ingested, are important findings of this study. The cyanobacteria may form an important link in the food chain in lakes in which they are very abundant, especially considering that daphnids formation considerably improves the edibility as well as nutritional value of cyanobacteria for daphnids. It is quite likely that in lakes dominated by filamentous cyanobacteria, it is not the interference or edibility of these organisms alone, but more importantly, the low nutritive value of the cyanobacteria and increase in predation by fish, or both, that would help us explain better the virtual absence of daphnids, particularly of the larger-bodied *Daphnia* spp.

**ACKNOWLEDGEMENTS**

The manuscript benefited greatly from the constructive criticism and suggestions of especially Bill deMott and Michael Arts and the reviewers’ comments. Also, two colleagues at the Centre of Limnology (Nieuwersluis), Koos Vijverberg and Wolf Moos, read an earlier version of the typescript. Klas Siewertsen helped in preparing the illustrations and Irma Breek in some of the grazing experiments. Publication No. 2777, Netherlands Institute of Ecology.

**REFERENCES**


