

## Change in filter-screen morphology and depth selection: Uncoupled responses of *Daphnia* to the presence of filamentous cyanobacteria

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### Abstract

In many eutrophic lakes, ability to cope with filamentous cyanobacteria is crucial to *Daphnia* fitness, as the filaments can reduce food intake by interference with food-particle retention. Two basic mechanisms were proposed to explain food collection by *Daphnia*: mechanical sieving, in which filtering appendages act as sieves, and direct interception, in which appendages act as paddles and water does not pass through. As was recently suggested, both mechanisms may be active, and their relative importance is determined by the Reynolds number on filtering appendages. Mechanical sieving seems particularly sensitive to the interference from filamentous cyanobacteria, which can clog the meshes while passing through the filtering chamber. We therefore hypothesized that in the presence of filaments, *Daphnia* minimizes the interference with filtration by decreasing the Reynolds number on the filters and by thus reducing the relative importance of sieving. To test this hypothesis, we examined the responses of nine clones of the *Daphnia longispina* group to the presence of nontoxic, filamentous cyanobacteria. The presence of cyanobacteria triggered in *Daphnia* responses of both behavioral (descending to deep, cold waters) and morphological nature (decreased intersetal and intersetular distances in the filtering apparatus). Both responses led to a decrease in the Reynolds number on the filters. Moreover, the two responses were inversely correlated: individuals with larger meshes descended to colder strata than did those with smaller meshes. These modifications of phenotype are regarded as adaptive, since they allow for minimized filament-induced interference with the filtration process.

Cyanobacteria are generally considered low-quality food for zooplankton, being toxic, of poor nutritional value, and/or of filamentous morphology; the last quality renders cyanobacteria capable of interfering with food-collection mechanisms in filter-feeding species (Haney 1987; Lampert 1987). Most vulnerable to such interference are large-bodied *Daphnia*, whose mode of feeding is nonselective, while the width of their carapace gape allows filaments to enter the filtering chamber (Gliwicz and Siedlar 1980; Gliwicz and Lampert 1990; Kirk and Gilbert 1992). However, *Daphnia* are shown to be less affected by interfering cyanobacterial filaments at low temperature (Threlkeld 1986), and Abrusán (2004) has advanced a hypothesis to explain such temperature-dependent vulnerability of *Daphnia* to cyanobacterial filaments.

According to this hypothesis disturbances to food gathering are markedly dependent on whichever is the prevalent mechanism of food collection (i.e., mechanical sieving or direct interception). This factor in turn depends on hydrodynamic characteristics of flow through the *Daphnia* feeding apparatus, which is best described by the Reynolds number ( $Re$ ).  $Re$  is a dimensionless parameter dependent on flow velocity ( $U$ ), characteristic length ( $l$ , a crude measure of the size of the object, in our case the

pore diameter), and kinematic viscosity of the fluid ( $\nu$ ) and is expressed numerically as

$$Re = U l \nu^{-1}$$

Reynolds numbers on cladoceran filters were estimated to vary between relatively low values of  $10^{-3}$ – $10^{-5}$  (Porter et al. 1983). This is a very limited range for  $Re$ , and theory predicts that there is no flow through the filters at any of these values (Gerritsen et al. 1988). This would strongly contradict the classical definition of feeding mechanism in *Daphnia* as mechanical sieving (Cannon 1933). Still, the sieving hypothesis gains support from a number of experimental and theoretical studies (e.g., Gophen and Geller 1984; Hessen 1985; Brendelberger 1991) that demonstrate apparent particle selectivity depending on *Daphnia* mesh size (presumably as a result of the filtering chamber wall effect). Hence, mechanical sieving cannot be excluded from considerations of food-collection mechanisms in cladocerans (see Bednarska [2006] for recent review of feeding mechanisms in *Daphnia*). Abrusán (2004) reconciles the two opposing views on the mechanism of particle retention in filter-feeding cladocerans: *Daphnia*'s filter combs function as both sieves and paddles at any time, but the relative importance of the two mechanisms varies in accordance with the  $Re$ .

When filtering appendages act more like sieves, at high  $Re$ , *Daphnia* are sensitive to the interference caused by filaments of cyanobacteria. Entangling of filter limbs with filaments makes frequent cleaning of the filtering apparatus by combing movements of postabdominal claws necessary. Although the cleaning process allows for continuous filtration, it entails the loss of the edible food particles

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already retained on the filters and in the food groove, thereby resulting in a decrease in food uptake.

At low *Re*, viscous forces dominate the flow and filtering appendages act principally as paddles, not as rakes (Abrusán 2004). The majority of water with suspended particles (including cyanobacterial filaments) flows tangentially to the surface of filter screens (Gerritsen et al. 1988). In such conditions, food gathering is based mostly on direct interception (adhesion) rather than on filtration (Rubenstein and Koehl 1977; Koehl 1996), and most of the filaments that enter the *Daphnia* filtering chamber bypass the filter screen, and so do not clog the meshes. Consequently, the filtering apparatus does not have to be cleaned frequently, and *Daphnia* are relatively well protected against interference from filamentous cyanobacteria.

If this hypothesis is true, large-bodied filter-feeding cladocerans that are unable to prevent filamentous cyanobacteria from entering the filtering chamber should aim to lower the *Re* on their filter screens in order to reduce interference with the filtration process. *Daphnia* could achieve reduced *Re* (1) through the use of depth selection in a thermally stratified lake, in order to experience a reduction in ambient temperature that increases the viscosity of water, (2) through a reduction in the so-called "characteristic length," achieved by decreasing filter mesh size, or (3) through a reduction in the velocity of flow through the filtering apparatus (not tested in this study). The aim of our research was to determine whether *Daphnia* responds to the presence of filamentous cyanobacteria in a manner associated with the above predictions (i.e., by reducing *Re* on the filter screen via morphological and behavioral changes). As *Daphnia* displacement to colder waters incurs distinct fitness costs (Dawidowicz and Loose 1992), individuals already protected against interference from filaments by small meshes were expected to constrain their descents to deep, cold waters. A negative correlation between filter mesh size (the morphological response) and temperature preferences (the behavioral response) was thus expected in *Daphnia* exposed to the presence of filaments.

## Materials and methods

We used nine clones comprising *Daphnia galeata* (GAd22, GAd24, and GA002), *Daphnia hyalina* (HYd47, HYd19, and HY014), and the interspecific hybrids between the two species (*D. hyalina* × *galeata*: HG001, HGd69, and HGd15). Clones GAd22, HYd47, and HG001 originated from Lake Constance (Switzerland/Germany) and the remainder from the eutrophic Lake Roś (North Poland). The identities of the parental species and hybrid clones were diagnosed using electrophoretic analysis of AAT isoenzymes (Wolf and Mort 1986; see Hebert and Beaton [1989] for the electrophoresis protocol). The clones were isolated at least 1 yr prior to the study and were subsequently maintained in laboratory batch cultures at room temperature (19–22°C) and were fed with the green alga *Scenedesmus obliquus*.

The offspring of single *Daphnia* individuals isolated from each clonal culture were assigned at random to two groups, which were cultured in 250-mL glass beakers under

a summer photoperiod (16:8 light:dark [L:D]) in a temperature-controlled room (20°C ± 1°C) and in one of the two experimental media. The media were prepared with a mixture of dechlorinated tap water and water from a small eutrophic lake, Lake Szczęśliwice (3:1 ratio). The lake water was prefiltered through a 1-µm sieve, diluted with the tap water, and stored in a large, aerated glass tank for 4 weeks before use. The water was subsequently refiltered through an 0.45-µm membrane and enriched with either *S. obliquus* to a concentration of 0.6 mg carbon (C) L<sup>-1</sup> (henceforth referred to as the "Scenedesmus medium") or a mixture of *S. obliquus* (0.6 mg C L<sup>-1</sup>) and the cyanobacterium *Cylindrospermopsis raciborskii* (0.6 mg C L<sup>-1</sup>) (henceforth referred to as the "Cylindrospermopsis medium"). The culture media were refreshed daily. After 4 weeks of preculturing, three adolescent females were chosen at random from each of the 18 *Daphnia* cultures (nine clones × two food media). These females were further cultured under the same conditions, and their synchronized (i.e., born within 10-h period) second-clutch offspring were used for the purpose of the experiments.

In a factorial experiment we tested the depth preferences of *Daphnia* precultured in the two media and then transferred to either the *Scenedesmus* or *Cylindrospermopsis* media in the "plankton organ," a device similar to that described by Dawidowicz and Loose (1992). This "organ" has proved a useful tool in the study of depth-selection patterns in zooplankton (e.g., Loose et al. 1993; Boriss et al. 1999). It consists of a set of glass tubes (55 cm long, 1 cm in diameter) filled with the respective medium and placed vertically in a transparent water bath that maintains thermal stratification within the tubes, the temperature being 22.9°C at the surface and 10.1°C at the bottom (Fig. 1). The system is illuminated from above with a set of 12 halogen lamps (20 W, 12 V) shining through a frosted glass diffuser, with a 16:8 L:D photoperiod. Primiparous, synchronized (5 d ± 5 h old) *Daphnia* precultured in each of the two media were placed into tubes with the *Scenedesmus* medium and with the *Cylindrospermopsis* medium. Twenty-four *Daphnia* from each clone were exposed at a time in four tubes (six individuals per tube × four combinations of preculture medium and the plankton organ medium), randomly assigned at the "organ" 3 h before the simulated sunset. The depth distribution of *Daphnia* was recorded the next midday, 8 h after "sunrise," by visual counting of the animals in each tube. This procedure was repeated four times, each time with a new set of *Daphnia*, giving a total of 24 individuals (six individuals per tube × four replicates of the exposure) tested for each of four combinations of preculture medium and the medium used in the plankton organ.

The animals that were staying in the same medium during preculturing and in the plankton organ were further maintained in adequate medium until their third adult instar. Then three egg-bearing (third clutch) *Daphnia* from each clone were anesthetized and fixed in 4% sugar formaldehyde. The endopodites were dissected from each individual's third pair of thoracic legs (giving two endopodites per individual *Daphnia*) and were transferred

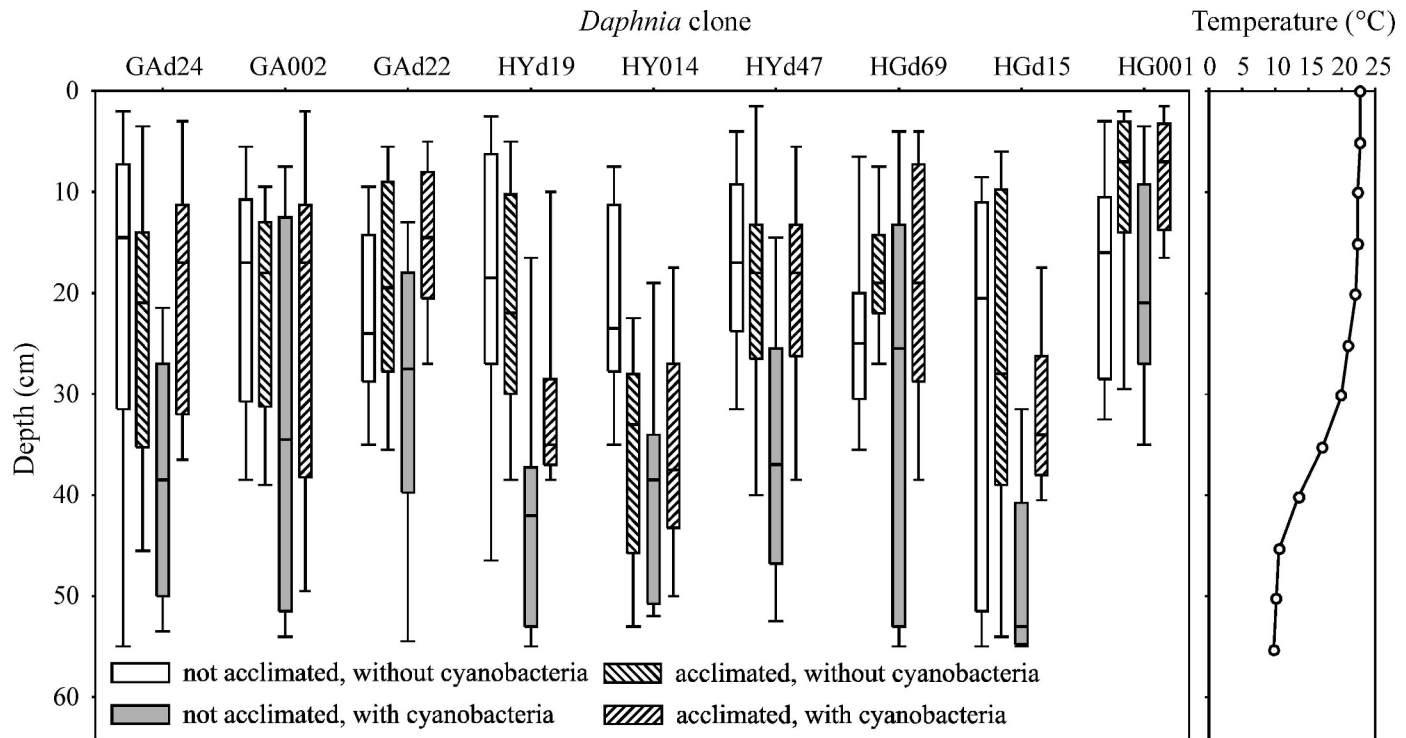


Fig. 1. Box plot of the depth distribution of *Daphnia* clones raised in *Scenedesmus* medium or acclimated for 4 weeks in the *Cylindrospermopsis* medium and then exposed in the “plankton organ” with *C. raciborskii* or without the species. Each box is bisected at the median depth; 50% of the counts fit within the box, the whiskers extending to 90% of counts. Clone names are on the x-axis. The temperature profile in the plankton organ is visible in the right panel.

with a drop of glycerol to a microscope slide. The filter screens were photographed ( $100 \times 16$  magnification) at 10 random places, intersetal and intersetular distances being measured from each photo using MultiScan image analysis software (Computer Scanning Systems). The intersetal distance was measured at the bases of the setae, while the intersetular distance was determined for the setulae located in the middle of the setae. The statistical analysis of the data was performed with Statistix 8.0 software.

## Results

*Filter screen structure*—Exposure to *C. raciborskii* filaments resulted in changes in filter screen morphology in the studied *Daphnia* clones (Table 1). Both intersetal and intersetular distances in general decreased ( $F = 865.74$ ,  $df = 1$ ,  $p < 0.0001$  and  $F = 1299.86$ ,  $df = 1$ ,  $p < 0.0001$ , respectively, two-way analysis of variance [ANOVA]), although the extent of this response was clone dependent,

Table 1. Intersetal and intersetular distances (mesh size) of the filter appendages of adult *Daphnia* reared with and without cyanobacteria (values are mean  $\pm$  standard deviation [SD]). Tukey post-hoc comparisons: \*  $p = 0.05$ ; \*\*  $p = 0.005$ ; ns, nonsignificant.

Taxon	Clone	Intersetal distance ( $\mu\text{m}$ )			Mesh size ( $\mu\text{m}$ )		
		<i>Scenedesmus obliquus</i>	<i>S. obliquus</i> + <i>Cylindrospermopsis raciborskii</i>	<i>p</i>	<i>S. obliquus</i>	<i>S. obliquus</i> + <i>C. raciborskii</i>	<i>p</i>
<i>Daphnia galeata</i>	GAd24	6.151 $\pm$ 0.160	6.126 $\pm$ 0.187	ns	0.467 $\pm$ 0.013	0.448 $\pm$ 0.011	**
	GA002	6.726 $\pm$ 0.068	6.651 $\pm$ 0.057	*	0.489 $\pm$ 0.004	0.469 $\pm$ 0.004	**
	GAd22	6.680 $\pm$ 0.092	6.546 $\pm$ 0.124	**	0.468 $\pm$ 0.009	0.450 $\pm$ 0.013	**
<i>Daphnia hyalina</i>	HYd19	6.355 $\pm$ 0.167	6.303 $\pm$ 0.119	ns	0.505 $\pm$ 0.012	0.496 $\pm$ 0.010	**
	HY014	7.341 $\pm$ 0.065	7.293 $\pm$ 0.053	ns	0.531 $\pm$ 0.007	0.515 $\pm$ 0.004	**
	HYd47	6.609 $\pm$ 0.063	6.323 $\pm$ 0.047	**	0.485 $\pm$ 0.005	0.473 $\pm$ 0.005	**
<i>D. galeata</i> $\times$ <i>D. hyalina</i>	HGd69	6.412 $\pm$ 0.129	6.361 $\pm$ 0.124	ns	0.451 $\pm$ 0.008	0.425 $\pm$ 0.009	**
	HGd15	7.365 $\pm$ 0.078	6.592 $\pm$ 0.100	**	0.479 $\pm$ 0.006	0.451 $\pm$ 0.012	**
	HG001	6.514 $\pm$ 0.073	6.239 $\pm$ 0.064	**	0.447 $\pm$ 0.005	0.425 $\pm$ 0.007	**

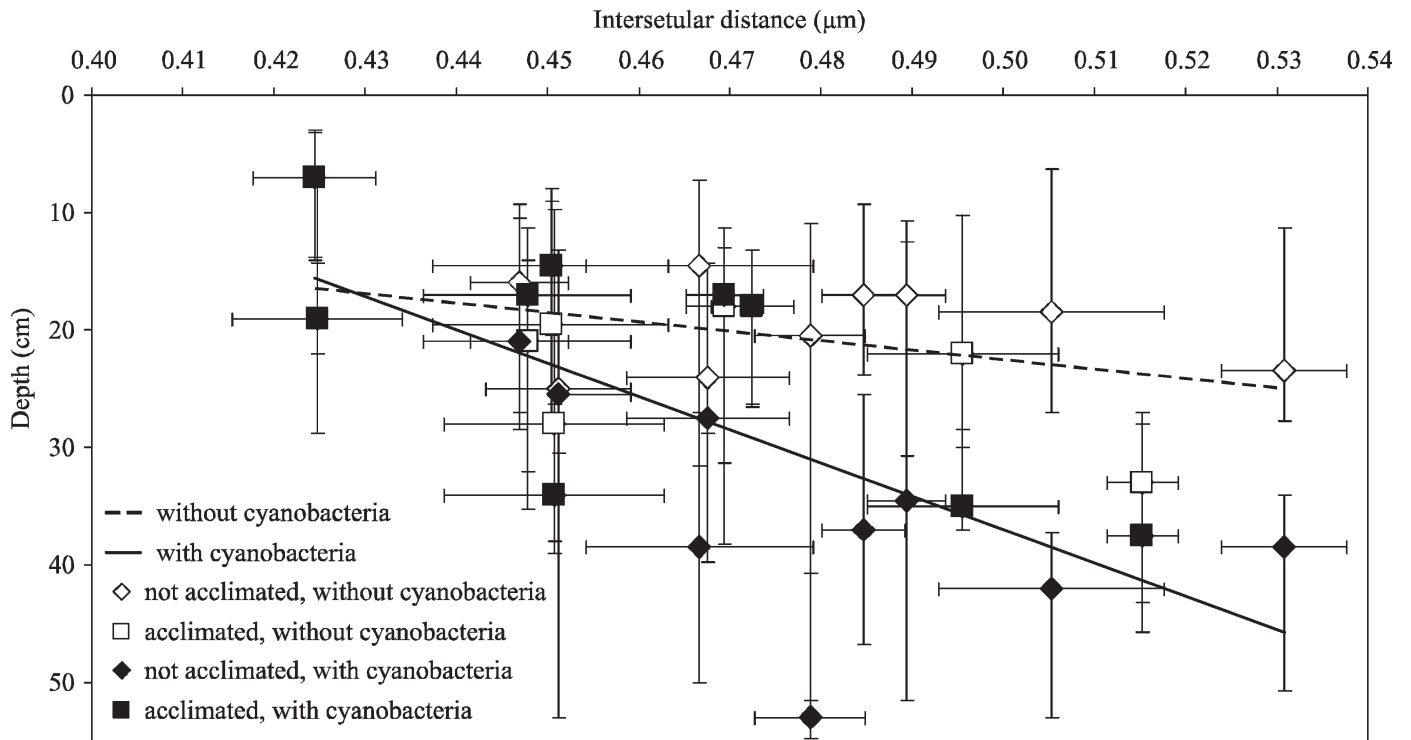


Fig. 2. Scatter plot of depth preference versus mesh size in *Daphnia* kept in the “plankton organ” with or without cyanobacterial filaments. The *Daphnia* precultured in *Scenedesmus* medium (not acclimated) and *Cylindrospermopsis* medium (acclimated) are pooled into one category.

as indicated by a significant clone  $\times$  filament interaction ( $F = 150.97$ ,  $df = 8$ ,  $p < 0.0001$  and  $F = 15.10$ ,  $df = 8$ ,  $p < 0.0001$ , respectively, two-way ANOVA). In five (out of nine) clones, the decrease in the intersetal distance attained statistical significance, while the intersetal distance was found to change significantly in all clones (Table 1). The relative decreases in the intersetal and intersetal distances in the studied clones varied from 0.4% to 10.5% and from 1.9% to 5.9%, respectively.

**Daphnia depth preference**—The studied *Daphnia* changed their depth-selection behavior in response to the presence of cyanobacterial filaments (Fig. 1). Both clone (Kruskal–Wallis statistic, 114.579;  $p < 0.0001$ ) and presence/absence of filaments (Kruskal–Wallis statistic, 99.2768;  $p < 0.0001$ ) were shown to have affected the animals’ preferred depths significantly. The *Daphnia* that had their first contact with cyanobacteria in the plankton organ stayed deeper than their clonal sisters that were kept constantly in green alga, and they stayed still deeper than those clone mates that had experienced a prior exposure to the filaments that was long enough to allow them to respond morphologically (Fig. 1).

**Relationship between filter screen structure and depth preference**—The depth preferences (median depth) of the *Daphnia* exposed to the cyanobacterial filaments in the “plankton organ” were strongly correlated with the individual’s filter mesh size (Fig. 2), the animals with fine meshes staying closer to the surface than those with larger

mesh size (Pearson correlation between mesh size and depth,  $r = 0.6923$ ,  $p = 0.0015$ ). In contrast, there was no association between depth of residence and filter mesh size in the *Daphnia* that had been exposed to cyanobacterium-free medium in the plankton organ (Pearson correlation,  $r = 0.4180$ ,  $p = 0.0829$ ).

## Discussion

There are three conceivable ways for *Daphnia* in a stratified lake to lower  $Re$  on the filtering appendages: first, they can do so by descending to the deeper (and thus colder) waters; second, they can do so by reducing the mesh size of the filter screens; and third, they can do so by slowing down the motion of filter appendages.

With a decrease in ambient temperature the viscosity of surrounding fluid increases and the character of flow through the filter chamber change. Reducing the pore size of filters affects the flow in a similar way as a result of a reduction in “characteristic length.” As a consequence of the reduction in  $Re$ , a smaller proportion of the fluid goes through the filter.

Threlkeld (1986) found that the growth rate of *Daphnia* was less affected by the presence of filamentous cyanobacteria, at lower temperature. It has been stated that in the presence of (toxic) cyanobacteria at the surface, *Daphnia* attempt to stay away from them, preferring deeper water layers (Gliwicz and Siedlar 1980; Forsyth et al. 1990). In our study, the *Daphnia* also descended in the water column when exposed to filamentous cyanobacteria. Moreover, we

detected a negative correlation between mesh size and preferred depth; such a correlation would be hard to explain if descending was the mechanism used by *Daphnia* to avoid contact with filaments aggregated at the surface, as has been proposed by Gliwicz and Siedlar (1980). The dependence of depth distribution on filter-screen morphology in *Daphnia*, observed in the presence of cyanobacterial filaments (but not where they are absent), indicates that the animals with finer meshes do not have to descend because of their lesser sensitivity to the filaments' interference.

Previous studies have shown that in eutrophic lakes (in the presence of colonial or filamentous cyanobacteria and algae), planktonic cladocerans display a finer mesh size of their filtering apparatus than do the cladocerans from oligotrophic lakes (Geller and Müller 1981; Brendelberger and Geller 1985). This phenomenon has commonly been explained in terms of starvation avoidance (Brendelberger 1991), small-sized meshes being more efficient at gathering fine food particles (e.g., bacteria). Where the quantity of available food is limited *Daphnia* are seen to modify the size and structure of their filter screen to maximize food uptake (Lampert and Brendelberger 1996; Repka et al. 1999). However, the adaptive significance of such a modification may not be restricted to increased efficiency in the gathering of fine particles; it may also (or perhaps even mainly) serve in the "immunization" of *Daphnia* to the interfering effects of filaments during cyanobacterial bloom events. We did not find any signs of starvation in animals reared in the presence of filamentous cyanobacteria for 4 weeks, a time period that is long enough for a change in filter morphology to be obtained.

We suggest that the small mesh size observed in *Daphnia* from eutrophic environments and in animals exposed to filamentous cyanobacteria in our experiments is a way of building up resistance to filament interference. The issue of whether the resistance against cyanobacteria observed in *Daphnia* is a constitutive feature of certain genotypes (clones), as opposed to an expression of phenotypic plasticity, is debatable. The results of Hairston et al. (2001) indicate that resistance on the part of *Daphnia* could develop through the selection of genotypes differing in their performance in the presence of cyanobacteria. On the other hand, just 4 weeks of acclimation of a natural population of *Daphnia* to the presence of cyanobacteria is shown to suffice to significantly reduce the harmful effects of cyanobacteria on the animals (Gustafsson and Hansson 2004). Such an increase in resistance could probably be achieved through phenotypic plasticity. Further research by Gustafsson et al. (2005) showed that an increased tolerance to toxic *Microcystis* can indeed develop during an individual *Daphnia* life span. Ghadouani and Pinel-Alloul (2002) observed changes in filtering-structure morphology in a lake population of *Daphnia pulex* exposed in situ enclosures to an artificially induced bloom of colonial and filamentous cyanobacteria. They attributed these changes to phenotypic plasticity, though selection might have operated in their experiments as well. The present study has clearly demonstrated that adaptive shifts in morphology and behavior can be induced within a single *Daphnia* lineage by the presence of filamentous cyanobacteria. At

the same, we show that clones differ in their responses to cyanobacteria.

Changes in mesh size observed in this study indicate that *Daphnia* use the same adaptive strategy (filter mesh-size reduction) in response to low food quality (i.e., presence of filaments in the food particle suspension) and quantity (as described earlier in the literature; Lampert and Brendelberger 1996; Repka et al. 1999). On one hand, the decrease in mesh size may allow for the utilization of bacteria (abundant in eutrophic waters) and other small organic particles as food, while on the other hand *Daphnia* may be made less vulnerable to cyanobacterial filament interference via these changes.

The third way of lowering *Re* on the filter screen would be to achieve reduced velocity of flow through the *Daphnia* feeding apparatus. While this parameter was not measured in the course of the present study, there are a few reports indicating a decrease in *Daphnia* appendage beat rate in the presence of filamentous and colonial cyanobacteria (Haney et al. 1995; Ghadouani et al. 2004). These findings are consistent with those of Abrusán (2004), notwithstanding the facts that (1) the studies were conducted with toxic strains of cyanobacteria, such that intoxication of animals cannot be excluded as a possible explanation behind changes in appendage beat rate; and (2) it remains unclear whether the decrease in beat rate results from a slowing down of motion on the appendages (bringing about reduced *Re*) or from a decrease in the frequency of appendage movements without any change in their intensity (which would not affect *Re*). To our knowledge, there is only one study, by Burns (1968), reporting a decrease in *Daphnia* appendage beat rate via the presence of nontoxic filamentous or colonial cyanobacteria. However, that decrease was accompanied by a significant increase in the frequency of the labral and postabdominal rejection movements occurring between limb beats. It is thus difficult to judge whether the decreased appendage beat rate was caused by a slowing down of movement by the thoracic limbs.

We found a genotype effect on filter mesh-size change among the studied *Daphnia*. In the presence of cyanobacterial filaments the mesh sizes and the intersetal distances decreased more in *D. galeata* (and the hybrids) than in *D. hyalina* clones, while the latter responded to the filaments' presence by moving deeper in the water column. This pattern of response is in agreement with earlier studies of antipredator defenses of those taxa, in which *D. galeata* undergo cyclomorphosis and *D. hyalina* are known to use diel vertical migration (Stich and Lampert 1981). However, the low number of replications within a taxon (three clones of each) in our experiments does not permit any conclusive statements with regard to the differences in strategies used by the studied taxa to cope with filamentous cyanobacteria.

Our results indicate a switch between the behavioral and morphological responses of *Daphnia* to the presence of nontoxic cyanobacterial filaments. It would seem that when the abundance of cyanobacterial filaments is increasing rapidly (e.g., during bloom events), the animals not yet "morphologically prepared" to cope with the filaments can take shelter from interference thanks to an immediate

behavioral response involving descent to colder water layers. Such a response incurs metabolic costs related to the effect of low ambient temperature on metabolic rates (Dawidowicz and Loose 1992). If animals co-occur with cyanobacteria long enough to allow for a buildup in morphological resistance, they may once again return to favorable and warm surface waters.

To conclude, in light of Abrusan's (2004) hypothesis, the observed morphological and behavioral reactions to the presence of filamentous cyanobacteria can be regarded as adaptive, because they "immunize" *Daphnia* against filament-induced interference. Moreover, our results show that development of tolerance to filamentous cyanobacterial interference can be acquired through phenotypic plasticity within a single clonal lineage, such that phenotypic responses may be responsible for the ability of large-bodied *Daphnia* to coexist with filamentous cyanobacteria in the field.

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