J. Limnol., 2013; 72(3): 505-511
DOI: 10.4081/jlimnol.2013.e41

Aphanizomenon gracile increases in width in the presence of *Daphnia*. A defence mechanism against grazing?

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ABSTRACT

Filamentous cyanobacteria are frequently consumed by grazers like Daphnia*, which can break filaments and make them more readily available to filter-feeders. However, various defence mechanisms against grazing have also been observed in cyanobacteria. Data concerning changes in the morphology of filamentous algae, especially their width in the presence of a grazer, are scarce. Field studies of filament morphology of cyanobacteria relate their changes to nutrient availability and temperature. Moreover, filament morphology displays significant differences in filament length and width among seasons. We hypothesised that the morphological changes in filament observed in the field – especially their width – could be a defence mechanism that is induced by the presence of a grazer, such as* Daphnia*. Thus, two experiments were conducted in order to test the influence of* Daphnia *(direct grazing and infochemicals together in the first experiment) and the chemicals it released (grazing excluded, only chemicals present in the second experiment) on* Aphanizomenon gracile*'s morphology, in controlled laboratory conditions.* Aphanizomenon *filaments became significantly shorter and thicker in both experiments. However,* Daphnia*'s grazing combined with excreted chemicals had stronger effect than chemicals alone. To our knowledge, this is the first report describing the shortening and thickening of filaments in the presence of* Daphnia *infochemicals. It seems that the* Aphanizomenon *filaments in the presence of* Daphnia *switch their growing mode and invest more heavily in width than length. Our results support the hypothesis that* Daphnia *is at least partly responsible for the changes in filament width observed in the field. This could be a strategy that helps* Aphanizomenon *to withstand grazer's pressure during early stages of a bloom.*

Key words: filamentous cyanobacteria, grazing, induced defence, mechanical interference, infochemicals.

Received: March 2013. Accepted: May 2013.

INTRODUCTION

The necessity to minimise the risk of predation and the ability to defend against predators are believed to be driving forces in the evolutionary histories of organisms at lower trophic levels (Tollrian, 1995). Thus, many organisms have evolved a variety of defence mechanisms. Van Donk *et al.* (2011) reviewed various induced defences in phytoplankton against grazing by herbivorous zooplankton. They distinguished three mechanisms of defence: i) morphological, such as forming colonies and developing spines (Hessen and Van Donk, 1993), bristles (Luo *et al.*, 2006) or thicker cell walls (Pondaven *et al.*, 2007); ii) chemical, such as toxic metabolites (Jang *et al.*, 2003); and iii) changes in life history, such as vertical migration (Latta *et al.*, 2009) or cyst formation (Toth *et al.*, 2004). A good example of these defences occurs in phytoplankton with flexible morphologies (Lürling and Van Donk, 1996) or colony sizes (Jakobsen and Tang, 2002). For example, the green alga *Scenedesmus* sp., in the presence of a grazer such as *Daphnia*, produces many-celled cenobia that prevent it from entering the filtering chamber of a filter feeder (Lürling and Van Donk, 1996).

Various defence mechanisms against grazing have also been observed in cyanobacteria. Cyanobacterial toxins are known to have adverse effects on *Daphnia*: Jang *et al.* (2003) observed the induction of toxin production in *Microcystis aeruginosa* in the presence of *Daphnia*. Moreover, Jang *et al.* (2007) demonstrated that grazing pressure and infochemicals that are released by grazers can induce toxin production and secretion in filamentous *Planktothrix agardhii*. There are many examples of the negative influence of cyanobacteria's morphology on *Daphnia*. Filamentous blue-green algae strongly disrupt food collection in daphnids, which are forced to clean their filtering apparatuses (Gliwicz and Siedlar, 1980; Burns, 1968).

However, filamentous cyanobacteria are frequently consumed and can support the growth of *Daphnia*; for example, at low food levels, the addition of non-toxic filamentous *Aphanizomenon flexuosum* improved the growth of *Daphnia galeata* (Kurmayer, 2001). Moreover, Von Elert *et al.* (2003) observed that the growth rate of *D. galeata* that were fed filamentous *Anabaena variabilis* enriched with sterols was nearly equal to the growth of daphnids that were fed *Scenedesmus obliquus*.

Data concerning changes in the morphology of fila-

mentous algae, especially their width in the presence of a grazer, are scarce. *Daphnia* can break filaments and make them shorter, which may increase their availability to filter-feeders (Dawidowicz, 1990). Oberhaus *et al*. (2007) reported that *D. pulicaria* preferentially graze on filaments of *P. rubescens* that are shorter than 100 µm. Conversely, Chen *et al*. (2011) reported no preference in *Daphnia* for shorter or longer filaments of *Ulothrix*. The length distribution of filaments in daphnids' guts was related to their length in lake water. Moreover, Nadin-Hurley and Duncan (1976) found that a limiting factor for ingestion was the width, rather than length, of a particle, and most of the very large particles that were found in the daphnid's gut were long, narrow, pliant filaments, such as those in *Tribonema*. Some Cyanobacteria can defend themselves by changing their filament morphology. Fijałkowska and Pajdak-Stós (1997) described the withdrawal of the *Phormidium* trichomes into their sheaths when they were disturbed by grazing ciliates. Moreover, Pajdak-Stós *et al*. (2001) reported that *Phormidium autumnale* produced an extracellular polysaccharide (EPS) envelope that was surrounded by filaments, thus protecting them from grazing by ciliates that could not penetrate the EPS mucilage. It has also been suggested that *Aphanizomenon* produces grass-like blades as an adaptation to avoid grazing by *Daphnia* (Lynch and Shapiro, 1981).

On the other hand, field studies of filament morphology relate their changes to nutrient availability and temperature, *e.g*. *Planktothrix agardhii's* filament morphology displayed significant differences in filament length and width among seasons, with the longest and widest occurring during summer and autumn (Pouličkova *et al*., 2004). A different pattern was reported by Kokociński *et al*. (2010), who observed the longest and widest trichomes during winter and spring. Laamanen *et al*. (2001) noticed that the same strain of *Nodularia,* when grown under different chemical or physical conditions, differed in its cell dimensions. Hašler and Pouličkova (2003) noted that the widest trichomes of *P. agardhii* coincided with the highest phosphorus (P) concentrations during their experiments. The trichome width was demonstrated to be the significant feature that differentiated different populations of *P. agardhii*, while the length was positively correlated with nutrient availability and temperature (Gonzalez, 1981; Romo, 1994).

We hypothesised that the seasonal morphological changes in filaments, especially increase of their width, that were observed in the field could be a defence mechanism that is induced by the presence of a grazer, such as *Daphnia*. Therefore, we wanted to test how the physical disturbance that is caused by filtering influences filament morphology. However, if the widening of filaments is a defence response to grazing, it could also be induced by infochemicals that are secreted by a herbivore. To test our predictions and separate the mechanical interference from chemical induction, we conducted two experiments. The first experiment tested the influence of *Daphnia* that was physically present in the culture of filamentous *Aphanizomenon gracile*. In the second experiment, we cultured *A. gracile* with daphnids that were kept in cages to avoid direct contact with filaments to test the induction of morphological changes by chemicals alone. Even though filamentous algae are avoided by *Daphnia,* they are frequently a part of their diet. *Daphnia* can suppress cyanobacterial blooms at the initial stage. It is important to understand the role of morphological changes of filamentous cyanobacteria observed in the field for evaluating possibilities of suppressing their developement.

METHODS

Experimental organisms

The cyanobacterium *Aphanizomenon gracile* (Lemmermann, 1910) SAG 31.79 was obtained from the culture collection of algae (Sammlung von Algenkulturen - SAG) at the University of Göttingen. The stock of Aphanizomenon was cultivated in a phytotron (Conviron, Winnipeg, Canada) at 20°C in a 2 L chemostat on Wilkins-Chalgren (WC) medium (Guillard and Lorenzen, 1972) at a light intensity of 17.5 µmol quanta m^{-2} s^{-1} for a cycle of 16 h darkness and 8 h light. The photosynthetically active radiation (PAR) intensity was measured using a light meter (LI-192 quantum sensor; LI-COR Biosciences, Lincoln, NE, USA).

A laboratory clone of *Daphnia magna* (Straus, 1820) was used in this study as a grazer and infochemical producer. Daphnids were cultured in an incubator at 20°C in 1 L glass beakers that were filled with 0.45 µm filtered lake water. We used the green alga *Scenedesmus obliquus* (Kützing, 1833), strain SAG 276-3a, as a food source for the daphnids. However, during the experiments, no *Scenedesmus* cells were present.

Experimental design

Mechanical interference

This experiment lasted 12 days and consisted of 3 treatments that were replicated 5 times: control with *Aphanizomenon* alone (control), *Aphanizomenon* grown with *Daphnia* present from the start of the experiment (D-12) and, additionally, a third treatment in which *Daphnia* was added after 6 days of the experiment (D-6). All daphnids were able to graze on *Aphanizomenon*. Daphnids were replaced every second day with new individuals of a similar size. All of the daphnids were mature, and their sizes ranged from 3 to 4 mm. Newborns, if present, were removed from the experimental vials as soon as they appeared. The experiment was performed in vials that were

filled with 20 mL of WC media, placed in an incubator at 20°C with PAR intensity of 44 µmol quanta m^{-2} s^{-1} using a 16:8 h light-dark cycle. Each treatment was replicated five times, and one individual of *Daphnia* was assigned to each flask of D-12 and D-6 treatments. The concentration of cyanobacteria in the experimental vessels was $2.714x10^{-6}$ filaments/mL, while their average length was 225.2 µm (±16.45 SD) at the beginning of the experiment.

During the experiment, 1 mL samples were taken at the beginning and at the end (12 days). In the treatment in which daphnids were added after 6 days, the samples were taken before the daphnids were put into the vials.

Infochemicals

In the second experiment – which was also held for 12 days – we tested the influence of *Daphnia*'s infochemicals on the morphology of *Aphanizomenon*. We distinguished 3 treatments, similar to the first experiment: control with *Aphanizomenon* only (control), *Aphanizomenon* grown with grazer infochemicals present from the start of the experiment (D-12), and a third treatment in which grazer infochemicals were added after 6 days of the experiment (D-6). The daphnids were not able to graze on *Aphanizomenon* because they were placed in 10 cm^3 Falcon tubes with a mesh mounted at the bottom (size 500 µm). The *cages* were immersed in containers with *Aphanizomenon*. Each treatment was replicated five times, and three individuals of *Daphnia* were assigned to each container of D-12 and D-6 treatments. The daphnids that were used for this experiment were mature and their sizes ranged from 3 to 4 mm. The daphnids in cages were replaced with new individuals of a similar size every second day. All newborns were removed from the experimental containers as soon as they appeared. The experiment was performed in containers with 50 mL of WC media, placed in an incubator at 20°C, with a PAR intensity of 44 µmol quanta m^{-2} s^{-1} using a 16:8 h light-dark cycle. All of the containers were gently stirred every day. The concentration of *Aphanizomenon* in the experimental containers was $4.524x10^{-6}$ filaments/mL, while the average length of filaments was 145.9 µm (±20.2 SD) at the beginning of the experiment.

During the experiment, 1 mL samples were taken at the beginning, after 6 days and at the end (12 days). In the treatment with grazer infochemicals added, the samples were taken after 6 days, before the daphnids were caged.

Procedural control

Because there were cages immersed in an *Aphanizomenon* culture in the second experiment and they were shaken gently every day, a procedural control was employed to exclude the possibility that mechanical disturbance could influence the filaments' morphologies. The procedural control consisted of treatments with *Aphanizomenon* cultures without cages and with empty cages (*i.e.* no *Daphnia*). This experiment did not result in significant differences in filament length between the two treatments, either at the beginning or at the end of the experiment (ANOVA: $F_{1,8}$=1.09, P=0.32; $F_{1,8}$=1.13, P=0.31, respectively). This result proves that the presence of the cages in the experimental containers with *Aphanizomenon* cultures did not have any effect on the length of the trichomes. Moreover, in order to confirm that daphnids had significantly reduced mechanical contact with filaments, we also examined filtering apparatuses and guts of daphnids present in cages during the infochemical experiment. There were no clumps detected and only a few filaments in the guts. This number of filaments can be neglected comparing to almost 3 millions of filaments per mL present outside of the cage.

Statistical analyses

The lengths of 50 filaments were measured in each sample at 400× magnification, and a total of 250 measurements per treatment were made. Widths of 30 filaments were measured at a magnification of 400×, and a total of 150 measurements per treatment were made. The measurements from each replicate were averaged, and the resulting means were used for statistical analyses (*i.e.* 15 lengths and 15 widths). The statistical analyses were performed with STATISTICA 7.1. The lengths and widths of the *Aphanizomenon* filaments were compared between the different treatments separately for the beginning and end of the experiment using one-way ANOVA. If the ANOVAs detected overall significant differences, Tukey's post-hoc tests were run for pair-wise comparisons. The data were not normally distributed; however, ANOVAs are quite robust to non-normality (Underwood, 1997). The homogeneity of variance in all of the data was tested with Levene's test, and all of the data met this assumption.

RESULTS

Mechanical interference

The experiment began with filaments that did not differ significantly from one another, both in length and width, in any of the treatments (ANOVA: $F_{2,12=}$3.518, P=0.07; $F_{2,12=}$0.18, P=0.83, respectively). However, *Daphnia* grazing had significant effects on the length of *Aphanizomenon* filaments at the end of the experiment (ANOVA: $F_{2,12=}$102.9, P<0.0001). The controls had longer filaments than D-6 and D-12 (Tukey HSD test: P=0.0002; P=0.0001, respectively) (Fig. 1A). Moreover, the filaments in the D-6 treatment were longer than those in the D-12 treatment [Tukey honestly significant difference (HSD) test: P=0.0002].

Daphnia grazing also affected the width of the filaments

(ANOVA: $F_{2,12=}116.4$, P<0.0001). The filaments in the D-12 treatment were thicker than those in the control and D-6 (Tukey HSD test: P=0.0001; P=0.0001, respectively), but no differences were observed between the control and D-6 treatments (Tukey HSD test: P=0.97) (Fig. 1B).

Infochemicals

All of the filaments were of similar length and width at the beginning of the experiment that tested the influence of grazers' infochemicals on *Aphanizomenon* (ANOVA: $F_{2,12=}1.7$, P=0.22; $F_{2,12}$=0.08, P=0.92, respectively). However, at the end of the experiment, significant differences were observed in the length of filaments (ANOVA: $F_{2,12=}8.1$, P=0.006). The *Aphanizomenon* in the control had longer filaments than D-6 and D-12 (Tukey HSD test: P=0.006; P=0.02, respectively) (Fig. 2A). However, no differences were noted between D-6 and D-12.

Significant differences were also observed for the width of filaments (ANOVA: $F_{2,12=}71.3$, P=0.00001). The D-12 and D-6 treatments had thicker filaments than the control (Tukey HSD test: P=0.0001; P=0.0006, respectively). The filaments in D-12 were also thicker than those in D-6 (Tukey HSD test: P=0.0002) (Fig. 2B).

DISCUSSION

Our results support the hypothesis that *Daphnia* is responsible for the changes in filament width. *Aphanizomenon gracile* changed its morphology significantly when exposed to *Daphnia*'s grazing or infochemicals. To our knowledge, this is the first report describing the shortening and thickening of filaments in the presence of *Daphnia* infochemicals.

During the first experiment, in the treatment in which daphnids were able to graze on *Aphanizomenon,* we observed shorter filaments in the treatment than in the controls (Fig. 1A). This result was expected and is associated with the mechanical interference in the filtering apparatus of *Daphnia*, where longer filaments break as a result of increased postabdominal rejection movements (Gliwicz and Siedlar, 1980; Hartmann and Kunkel, 1991). Therefore, previously inedible filaments may be efficiently eaten because they are shorter (Dawidowicz, 1990). This

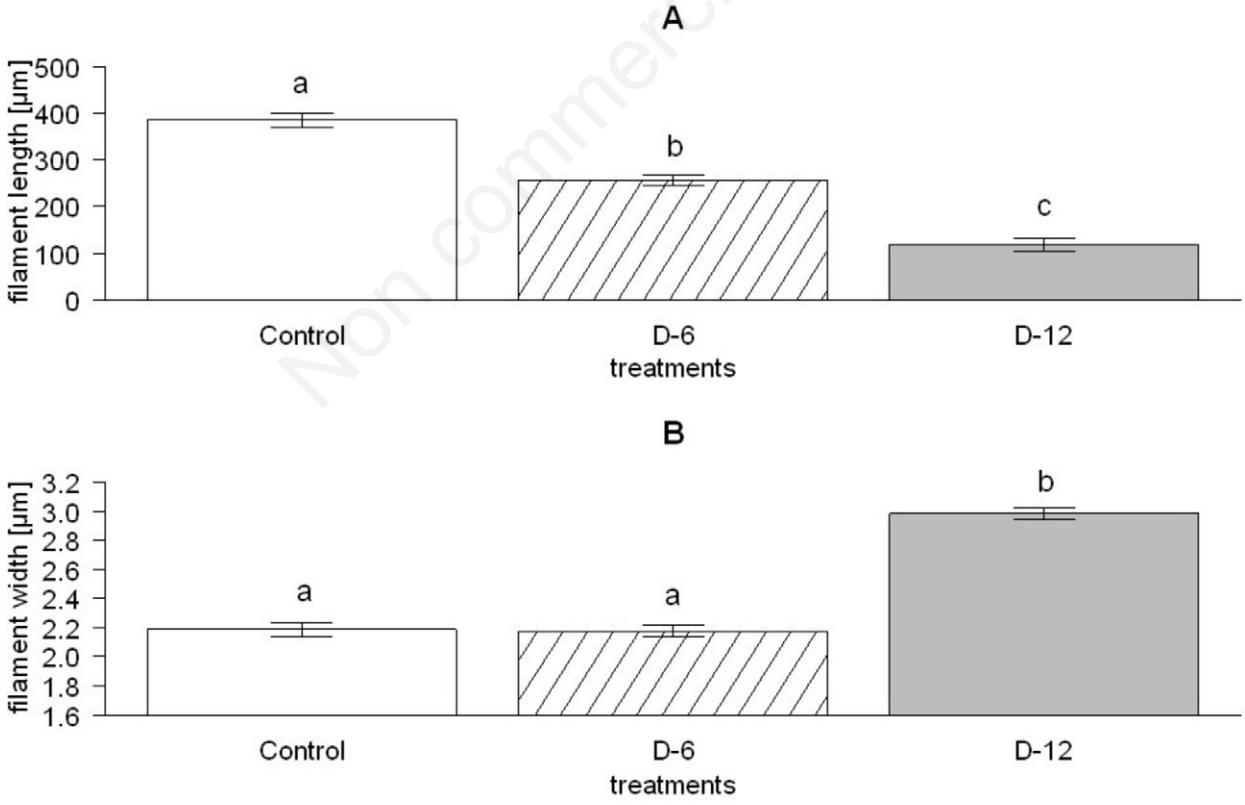

Fig. 1. Differences of *Aphanizomenon*'s filaments in (A) length and (B) width at the end of the mechanical interference experiment (mean±standard deviation). Treatments: open boxes=control without a grazer (control); dashed boxes=grazer present since the 6th day (D-6); filled boxes=grazer present since the start of the experiment (D-12). The same letters above the bars indicate that the values do not differ significantly (Tukey, P<0.05).

is consistent with the findings of Oberhaus *et al*. (2007), who reported that *D. pulicaria* grazed preferentially on filaments of *P. rubescens* that were shorter than 100 µm. However, the mechanical interference was not the only factor causing shorter filaments in our experiments. Although to a lesser extent, shorter filaments were also observed when daphnids were placed in cages to exclude grazing (Fig. 2A). Shortening could be a result of reduced growth under P-limitation. Such limitation in the presence of *Daphnia* was observed by Paterson *et al.* (2002). They suggested that P excreted by daphnids is less available for uptake by phytoplankton. The suppression of growth of some *Microcystis* strains by *Daphnia* infochemicals was also observed (van Gremberghe *et al.*, 2009). It is worth noting that the mechanical disturbance caused by stirring in *Aphanizomenon* cultures during the experiment can be excluded as a cause of shortening because it was ruled out in the procedural control experiment. The changes in the width of filaments were also observed in both experiments. Thicker filaments were noted both in the treatments that had the direct pressure of grazers (Fig. 1B) and in the treatments in which grazing was excluded (Fig. 2B).

Considering the filament length alone, one can assume a negative influence of *Daphnia* on *Aphanizomenon* by both physical and chemical mechanisms. However, when considering the length and width of filaments together, we note in both experiments that trychomes became thicker and shorter simultaneously after 12 days of exposure. We speculate that the thickening and shortening of *Aphanizomenon* filaments help individuals to avoid mechanical destruction. Bednarska and Dawidowicz (2007) observed in *Daphnia* a reduction in intersetal and intersetular distances in the filtering apparatus to reduce the interference from filamentous cyanobacteria. The shortening and thickening of a filament may make it easier to pass through the filtering chamber without being destroyed or eaten. The ability of *Daphnia* to collect food particles is determined by the Reynolds number (Re). At low Re, viscous forces dominate the flow, filtering appendages act as paddles (Abrusan, 2004), and the majority of water with suspended particles (including cyanobacterial filaments) flows tangentially to the surface of filter screens (Gerrit-

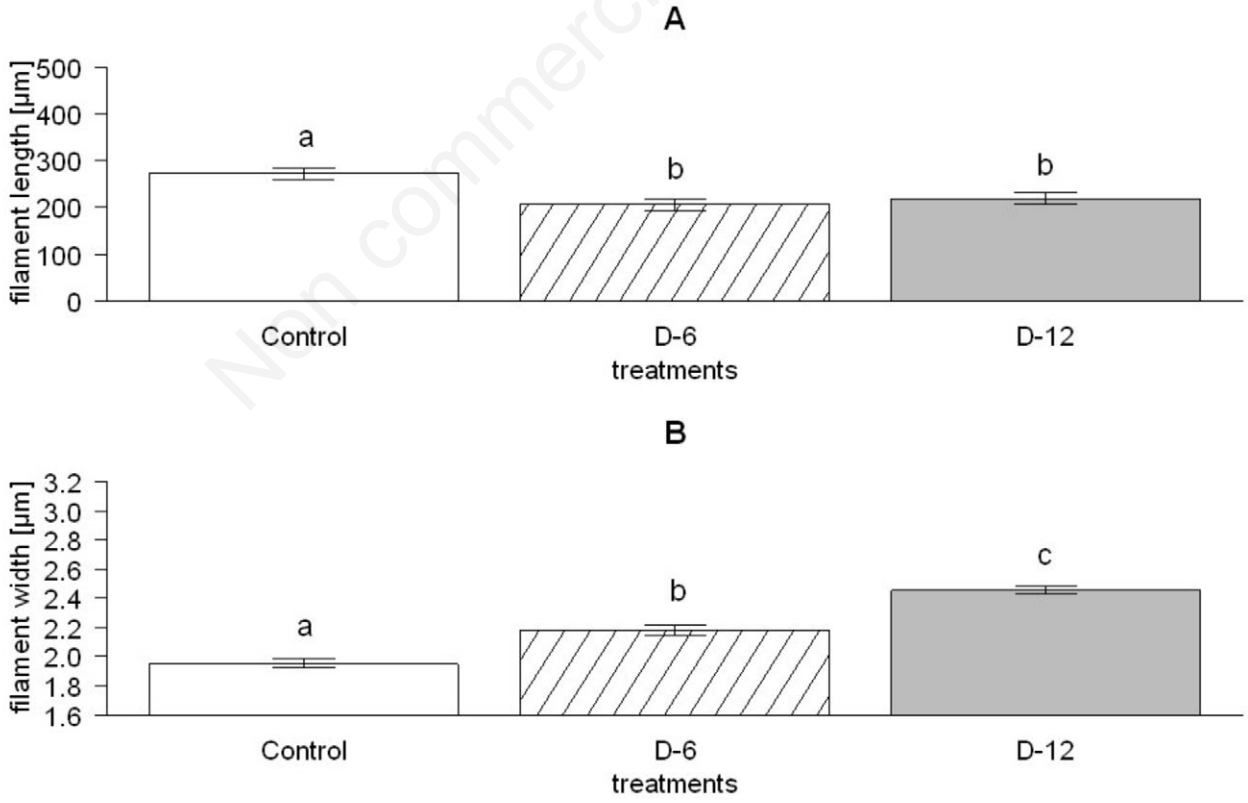

Fig. 2. Differences of *Aphanizomenon*'s filaments in (A) length and (B) width at the end of the the experiment with Daphnia's infochemicals only (mean±standard deviation). Treatments: open boxes=control without grazer (control); dashed boxes=grazer presence since the 6th day (D-6); filled boxes=grazer presence since the start of the experiment (D-12). The same letters above the bars indicate that the values do not differ significantly (Tukey, $P<0.05$).

sen *et al*., 1988). In such conditions, food gathering is predominantly based on direct interception (adhesion) rather than filtration (Rubenstein and Koehl, 1977; Koehl, 1996). The width of filaments is particularly important in light of the results of Nadin-Hurley and Duncan (1976), who reported that a limiting factor for ingestion was the width, rather than the length, of a particle, and most of very large particles found in the daphnid's gut were long, narrow, pliant filaments, such as those of *Tribonema*. However, long filaments of cyanobacteria inside the filtering apparatus of *Daphnia* can tangle and form irregular complexes (Hartmann and Kunkel, 1991). In this form, the filamentous cyanobacteria cannot be eaten; in fact, the postabdominal rejection movements can tear and break them. It seems reasonable that reducing mechanical interference is convenient for both *Daphnia* and *Aphanizomenon*. *Daphnia* can filter more efficiently without rejecting food particles, while avoiding destruction is advantageous to cyanobacteria. Unfortunately, we do not have data concerning the differences in the grazing efficiency of *Daphnia* that are fed with two morphological forms of filaments.

Another explanation for our findings could be related to nutrients. It is highly possible that thicker filaments allow cyanobacteria to store more nutrients per unit of length than thinner ones. Moreover, thicker filaments have a larger area that can be used for nutrient intake when in contact with *Daphnia*. This possibility is predicted by mathematical models (Ramin *et al*., 2012), and Doblin *et al*. (2012) reported that *Cylindrospermopsis* is subsidised by nutrients that are recycled by zooplankton and, thus, obtains a competitive advantage over other phytoplankton species. The nutrient hypothesis is at least partly supported by the results from the infochemical experiment – that excluded mechanical interference – in which the filaments grow wider when they are exposed to *Daphnia* chemicals for a longer time (D-6 *vs* D-12) (Fig. 2). This result is consistent with the findings of Hašler and Pouličkova (2003), who related the increase in width of trichomes in *P. agardhii* with the highest concentrations of P during their experiments. Additionally, Laamanen *et al.* (2001) demonstrated that the same strains of *Nodularia* express different cell dimensions when grown under different chemical or physical conditions.

CONCLUSIONS

Our experiments confirm that the changes in morphology of filaments are the reaction to the presence of a grazer such as *Daphnia*, which could be at least partly responsible for changes in width observed in the field. However, the results revealed more complicated interactions than we suspected. *Daphnia* has a negative mechanical influence on filamentous *Aphanizomenon,* but the presence of infochemicals alone also causes the decrease in length and increase in width. Decrease in length of filaments, despite the mechanical interference, could be also explained by nitrogen (N) excreted by daphnids and less available P for uptake by phytoplankton which increases the N:P ratio (Paterson *et al*., 2002). Such conditions are not preferable for most of cyanobacteria. The strategy of switching their growing mode and invest more heavily in width than in length is perplexing. It can either allow *Aphanizomenon* to withstand grazer's pressure during early stages of a bloom or be a response to the reduction of nutrient availability due to the presence of *Daphnia* infochemicals. Further studies are needed to determine the role of nutrient levels in changing the life history of cyanobacteria in the presence of *Daphnia* and to compare the resistance of thick and narrow filaments to the pressure of a grazer.

ACKNOWLEDGMENTS

We thank Maciej Bartosiewicz and Jakub Kosicki for their criticism and valuable comments on the manuscript. We would also like to thank the two anonymous reviewers whose comments and doubts greatly improved the manuscript. The financial support was provided by the National Science Centre through research grant No. NN 304 014 539. The purchase and maintenance of phytoplankton cultures was financed from the Marie-Curie Reintegration Grant *Contrastress* No. PERG05-GA-2009-249273.

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