Breakage of cyanobacterial filaments by small- and large-sized *Daphnia*: are there any temperature-dependent differences?

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Abstract Filamentous cyanobacteria disturb food collection in *Daphnia* by mechanical interference with the filtering apparatus by the long trichomes. The intensity of this interference depends on the water temperature and the *Daphnia* body size. However, *Daphnia* are capable of breaking down the filaments, therefore improving the palatability of the cyanobacteria. The main objective of this study was to test whether the shortening of cyanobacterial filaments and the ensuing clearance rate of *Daphnia* would increase at higher temperatures to a greater degree in small-bodied *Daphnia* species than in large-bodied one. Laboratory feeding experiments were conducted in order to measure variation in the length of *Cylindrospermopsis raciborskii* trichomes and to calculate clearance rate. The filament length and the cyanobacteria clearance rate by *Daphnia* were calculated following their exposure to grazing by large-bodied *D. pulicaria* and small-bodied *D. longispina* in 20, 24, and 28°C. Rising temperature did not affect the

intensity of breakage of *C. raciborskii* trichomes by *D. pulicaria* and caused decrease in clearance rate of this species, whereas for *D. longispina*, the temperature increase enhanced both filament breakage and clearance rate. We suggest that these temperature-related changes may affect relative competitive performance of *Daphnia* species in the presence of cyanobacteria.

Keywords *Daphnia* · Cyanobacteria · Filament length · Zooplankton · Body size · Temperature

Introduction

Cyanobacteria are known to be an inadequate source of food for *Daphnia* for a variety of reasons, including low nutritional value and a lack of essential compounds (especially polyunsaturated fatty acids and sterols). They are also difficult for *Daphnia* to consume due to their size and shape (Porter & Orcutt, 1980; Lampert, 1987; von Elert & Wolffrom, 2001). Moreover, some cyanobacterial species or strains produce toxins (Leflaive & Ten-Hage, 2007). Cyanobacterial filaments and colonies can interfere with the food collection of daphnids by clogging their filtering apparatus, thus limiting *Daphnia* feeding efficiency. When cyanobacterial filaments are abundant, daphnids increase the frequency of rejection movements by their postabdominal claws (Gliwicz & Siedlar, 1980; Kirk & Gilbert, 1992). As a result, the presence of cyanobacterial filaments leads to higher

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rates of respiration as well as reduced rates of feeding and assimilation and may also cause egg abortion (Porter & McDonough, 1984; Hawkins & Lampert, 1989; DeBernardi & Giussani, 1990; Gilbert & Durand, 1990; Bednarska & Slusarczyk, 2013). Nevertheless, *Daphnia*, like other zooplankton taxa such as copepods and rotifers, are able to break down cyanobacterial filaments into small particles, thereby improving their palatability (Dawidowicz, 1990; Bouvy et al., 2001; Gulati et al., 2001). It has been shown that short non-toxic cyanobacterial filaments cause lower reduction in the growth rate and fecundity of *Daphnia* in comparison with longer ones (Bednarska et al., 2014). Cyanobacterial filaments could, therefore, serve as a supplementary food for zooplankton herbivores, especially under food-limiting conditions (DeBernardi & Giussani, 1990; Gilbert & Durand, 1990).

Both water temperature and cladoceran body size may affect the interference with cyanobacterial filaments. At higher temperatures, decreased water viscosity increases the flow through the filter screens, which in turn leads to more intensive mechanical interference by cyanobacteria filaments with *Daphnia* filtering combs (Abrusán, 2004). Small-bodied cladocerans are known to be more resistant to such interference than large-sized species, because they have a relatively narrow gap in their carapace, which prevents filaments from entering the filtration chamber (Gliwicz & Siedlar, 1980; Porter & McDonough, 1984; Panosso & Lüring, 2010). It has also been suggested that the food-gathering process is qualitatively different between *Daphnia* species which differ in body size, due to variation in the hydrodynamics of water flow through the filtering apparatus. Due to the lower values of the Reynolds number, the filtering combs of small-bodied species act more as paddles than sieves, which reduces clogging of the filters (Abrusán, 2004).

Additionally, in tropical and subtropical waters, high temperatures and selective grazing on other algae by some zooplankton taxa, e.g., copepods, promote cyanobacterial blooms (Hong et al., 2013), which results in small grazers (small-bodied cladocerans, copepods and rotifers) predominating in zooplankton communities; large cladocerans rarely occur there (Gillooly & Dodson, 2000). Furthermore, in temperate lakes during the summer, when there is a relatively high abundance of cyanobacteria, small-bodied

species dominate large-bodied ones, a phenomenon known as “*midsummer decline*” (Sommer et al., 1986; Müller-Navarra et al., 2000; Wagner et al., 2004).

We suggest that temperature-driven variations in cyanobacterial filament breakage and clearance rate may affect the competitive abilities of *Daphnia* species which differ in body size. An evaluation of the shortening of cyanobacterial filaments and the clearance rate was made by measuring the filament lengths of a non-toxic strain of *Cylindrospermopsis raciborskii*, which were exposed to grazing by two *Daphnia* species differing in body size, under various thermal conditions. The objective of the study was to test the hypothesis that shortening of cyanobacterial filaments, and the clearance rate would increase with rising temperature, due to increase the flow through the filter screens, for small-bodied *Daphnia*, but stay on the same level (or increase less) for large-bodied species that are more vulnerable to interference by cyanobacteria filaments.

Materials and methods

We carried out a laboratory feeding experiment using three clones of large-bodied *D. pulicaria* and three clones of small-bodied *D. longispina*. The origins and body sizes of the 4-day-old experimental *Daphnia* clones are presented in Table 1. We should mention that clones of *D. pulicaria* used in our experiments come from two genetically divergent clades: North American (clones DpBrA3, DpBrS) and European (clone DpBh; Colbourne et al., 1998). All of the clones had been maintained in the laboratory for many generations prior to the study. Prior to the experiment, the mothers from all the clones were maintained at experimental temperatures of 20, 24, and 28°C in 3 l glass beakers containing lake water (filtered through a 0.45 µm filter) under a summer light regime (16:8 h light:dark cycle, light: 20 µmol m⁻² s⁻¹). The lake water used in the experiment came from the small eutrophic Lake Szczęśliwice located in Warsaw, Poland, which had been filtered through a 1-µm filter and stored in aerated tanks for at least 2 weeks prior to its use. The *Daphnia* were fed green alga (*Scenedesmus obliquus*, strain no. 72, University of Texas Collection Center, Austin, USA), which had been batch cultured at 20°C (light: 90–100 µmol m⁻² s⁻¹) in aerated 2-l flasks in Bold’s basal medium

Table 1 Origin and body size (mm) of 4-day-old experimental *Daphnia* clones

Species	Clones	Origin	Body size (mm)	SD (mm)
<i>D. longispina</i>	DI6	Lake Roś, Poland	0.94	0.13
	DI4	Lake Roś, Poland	1.13	0.16
	DI5	Lake Roś, Poland	1.14	0.11
<i>D. pulicaria</i>	DpBh	Unknown Lake, Czech Republic	1.43	0.24
	DpBrA3	Lake Brome, Canada	1.27	0.16
	DpBrS	Lake Brome, Canada	1.31	0.14

Data are means ± 1 SD from 54 to 135 individuals

(Borowitzka & Borowitzka, 1988). Four-day-old *Daphnia* from their clonal mothers' second clutch were used to begin the experiment. Prior to the beginning of the experiment, the animals were kept for 24 h in lake water without food suspensions in order to empty their guts. The experiment was carried out in 30-ml plastic beakers filled entirely with filtered (0.2 μm) lake water containing *C. raciborskii* filaments (non-toxic strain no. 1.97, Sammlung von Algenkulturen, Universität Göttingen, Germany), batch-cultured at 24°C (light: 40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in aerated 1-l flasks in Z-4 medium (Zehnder & Gorham, 1960) at a density equivalent to 1 mg organic Cl^{-1} . Algal cells were harvested at late log phase, and the carbon concentration of the algal suspensions was estimated using photometric light extinction at 800 nm, making use of previously established carbon-extinction regressions. The experiment was conducted in a thermostatic chamber in the dark, in three thermal treatments: 20, 24, and 28°C. Additionally, control treatment without animals was also established. For each clone, we set up, respectively, three beakers containing 6 animals for *D. pulicaria*, and three beakers containing 15 animals for *D. longispina*. The experiment was carried out on a plankton wheel at 1 rpm in order to prevent sedimentation of the cyanobacteria during the 6 h of the experiment. Following completion of the experiment, samples of cyanobacterial filaments were preserved in a mixture of Lugol's solution and formalin. We then calculated the number of filaments in a Fuchs-Rosenthal haemocytometer. We measured the length of all the filaments in randomly selected subsamples of 32 μl under a dissection microscope using the video analysis software MultiScan 14.02. Clearance rate ($\text{ml}^{-1} \text{individual}^{-1} \text{h}^{-1}$) was based on the changes measured in cyanobacteria biovolume ($\mu\text{m}^3 \text{ml}^{-1}$) between the control and the experimental beakers according to the equation (Peters, 1984):

$$CR = \frac{V \cdot (\ln B_0 - \ln B_t)}{t \cdot N},$$

where V is volume of the experimental beakers (ml), B_0 is initial biovolume, B_t is final biovolume, t is length of the experiment (h), N is number of animals in the experimental beakers.

We used an analysis of variance (ANOVA) test followed by the Tukey-HSD test for multiple comparisons to investigate the effects of temperature and species on the differences in clearance rate and mean length of the filaments. The factor 'clone' was nested within the species. Prior to the analysis, data for filament length and clearance rate were log-transformed. We used the Kolmogorov–Smirnov two-sample test to check if the mean filament lengths of the samples had a divergent distribution. The mean filament lengths used in the analyses were divided into size class intervals of 30 μm . Both analyses were performed using Statistix 9.0 software.

Results

Reduction in the mean filament length was observed in both the *D. longispina* and *D. pulicaria* treatments. As indicated by the significant effect of the temperature * species interaction (ANOVA, $F = 2.79$, $P = 0.0366$), shortening of the filaments by both *Daphnia* species varied between the thermal treatments. Intensity of filament breakage for the large-bodied *D. pulicaria* was similar across the entire range of temperatures, whereas for the smaller-bodied *D. longispina*, this intensity increased with the rising temperature. At 20°C, the mean filament length of the samples with *D. longispina* treatments ($321 \pm 45 \mu\text{m}$) did not differ significantly from the control treatment ($323 \pm 28 \mu\text{m}$; Table 2), whereas it was significantly lower in the *D. pulicaria* treatments ($265 \pm 24 \mu\text{m}$, Table 2). The

Table 2 Mean length (μm) of cyanobacterial filaments *Cylindrospermopsis raciborskii* in three thermal regimes: 20, 24, and 28°C

Temperature	Species	Median	Mean	SD	Homogenous group
20°C	Control	257	323	28	A
	<i>D. longispina</i>	253	321	45	A
	<i>D. pulicaria</i>	211	265	24	B
24°C	Control	257	323	21	A
	<i>D. longispina</i>	198	259	44	B
	<i>D. pulicaria</i>	174	226	20	B
28°C	Control	262	326	33	A
	<i>D. longispina</i>	207	256	26	B
	<i>D. pulicaria</i>	198	252	35	B

Data are medians and means for three clones and three replicates for treatments with large-bodied *D. pulicaria*, small-bodied *D. longispina*, and control without any animals. Letters indicates homogenous groups between means of experimental treatments (Tukey-HSD test for multiple comparisons, $P < 0.05$)

frequency distribution of the mean filament lengths in both of the *Daphnia* treatments did not differ significantly from that of the control treatment (Kolmogorov–Smirnov Test, $P = 1.0000$ for *D. longispina* and $P = 0.2410$ for *D. pulicaria*; Fig. 1, Table 3). At 24 and 28°C, both *Daphnia* species broke down the cyanobacterial filaments intensively, as was indicated by a statistically significant decrease in their mean filament lengths (Table 2) and a divergent (more right-skewed) frequency distribution for the cyanobacterial filaments compared to the control treatment (Kolmogorov–Smirnov Test, $P \leq 0.05$; Fig. 1, Table 3). At 24°C, *D. pulicaria* treatments had an apparently lower mean cyanobacterial filament length than in treatments with *D. longispina* (226 ± 20 and 259 ± 44 μm , respectively), but this difference was not statistically significant (Table 2). At 28°C, both species broke cyanobacterial filaments with a similar intensity, which was indicated by nearly the same mean length of filaments: 252 ± 35 and 256 ± 26 μm for the *D. pulicaria* and *D. longispina* treatments, respectively (Table 2).

Shortening of the cyanobacteria filaments varied significantly among the clones within both of the *Daphnia* species (species * clone interaction; ANOVA, $F = 3.80$, $P = 0.0097$). Variation in the mean length of the cyanobacterial filaments, however, was observed only among the *D. longispina* clones (only clone DI6 differed significantly from clone DI4; clone DIE did not differed significantly from both of them), whereas *D. pulicaria* clones did not differ significantly.

The clearance rate for cyanobacteria of *D. pulicaria* was within the range of $0.38\text{--}0.64$ $\text{ml}^{-1} \text{ind.}^{-1} \text{h}^{-1}$ and was higher than that of *D. longispina*: $0.06\text{--}0.15$ $\text{ml}^{-1} \text{ind.}^{-1} \text{h}^{-1}$ (ANOVA, $F = 79.11$, $P < 0.0001$; Fig. 2). Similarly, as was the case for the shortening of the filaments, the clearance rate varied between thermal treatments in both species (temperature * species interaction; ANOVA, $F = 4.06$, $P = 0.0248$). With increasing temperature, the large-bodied *D. pulicaria* decreased its clearance rate, whereas the small-bodied *D. longispina* showed an increased clearance rate (Fig. 2). No variation was observed among clones (species * clone interaction; ANOVA, $F = 2.18$, $P = 0.0886$).

Discussion

Both studied *Daphnia* species investigated in the study broke up filaments of the cyanobacterium *C. raciborskii*, but with different intensities dependent on temperature. At 20°C, the effect of small-bodied *D. longispina* on mean cyanobacteria filament length was negligible, while *D. pulicaria* shortened the filaments significantly. Breakage of the cyanobacterial filaments remained unchanged for the large-bodied *D. pulicaria* across the range of temperatures tested, whereas for the small-bodied *D. longispina*, it increased. Similarly, as the temperature increased, the clearance rate for *D. pulicaria* decreased, whereas for *D. longispina*, the clearance rate increased. Consequently, the difference between the two species tended to decrease with

Fig. 1 Frequency distribution of cyanobacterial filaments in treatment with *D. pulicaria* (grey bar), *D. longispina* (white bar), and control treatment without animals (black bar) in thermal treatment **a** 20°C, **b** 24°C, and **c** 28°C

exposure to increasing water temperature. At 28°C, the reduction in cyanobacterial filament length was nearly identical for both *Daphnia* species, but the

clearance rate for cyanobacteria was still 2.5 times higher for *D. pulicaria*. We have observed only little variation among clones of both *Daphnia* species.

Table 3 Results of the Kolmogorov–Smirnov two-sample test comparing distribution of cyanobacterial filaments (*Cylindrospermopsis raciborskii*) length in treatment with large-bodied *D. pulicaria* and small-bodied *D. longispina* to the control treatment without any animals in three thermal regimes: 20, 24, and 28°C

Temperature	Treatment	Z	P
20°C	<i>D. longispina</i> vs control	0.06	1.0000
	<i>D. pulicaria</i> vs control	0.15	0.2410
24°C	<i>D. longispina</i> vs control	0.14	0.0084
	<i>D. pulicaria</i> vs control	0.21	<0.0001
28°C	<i>D. longispina</i> vs Control	0.17	0.0063
	<i>D. pulicaria</i> vs Control	0.18	0.0017

Significant results are emphasized in bold letters ($P < 0.05$)

Fig. 2 Clearance rate ($\text{ml}^{-1} \text{ individual}^{-1} \text{ h}^{-1}$) in three thermal treatments: 20, 24, and 28°C. Data are means $\pm$ 1SD for three clones and three replicates for *D. pulicaria* (grey bar) and *D. longispina* (white bar)

Although *D. pulicaria* clones come from two genetically divergent clades (Colbourne et al., 1998), we have not found statistically significant differences in shortening of cyanobacteria filaments as well as clearance rate.

The observed decreases in the mean lengths of cyanobacterial filaments could have contributed to the increase in ingestion rate of filaments by *Daphnia*, which generally prefer smaller-sized food particles within the range of 2–50 μm (Geller & Müller, 1981;

Sommer, 1988). A propensity to consume cyanobacterial filaments has been previously reported for a number of *Daphnia* species (Dawidowicz, 1990; Gilbert & Durand, 1990; Kurmayer, 2001; Reichwaldt & Abrusán, 2007). As demonstrated experimentally, another large-bodied *Daphnia* species, *D. magna*, was able to control the population growth of filamentous cyanobacteria (at a temperature of 20°C) as long as the density of the cyanobacteria remained low (Dawidowicz et al., 1988). Breakage of cyanobacterial trichomes was suggested as an important mechanism allowing *Daphnia* to maintain such population control (Dawidowicz, 1990). If we can generalize about our observations of *D. pulicaria*, one could expect a relative decrease in the efficiency of filamentous cyanobacteria breakage by large-bodied daphnids at elevated temperatures. In addition, it has been found that cyanobacterial filaments of *Aphanizomenon gracile* decrease in length in the presence of *Daphnia* infochemicals (Cerbin et al., 2013). Considering that cyanobacteria population growth increases with rising temperatures, and that some of the morphological characteristics of cyanobacterial trichomes change with increasing temperature (e.g., trichomes were shorter and wider; Soares et al., 2013), these changes would not be followed by an increase in filament processing and utilization by large-bodied *Daphnia*. The lack of positive effect of temperature on filament shortening and the decreasing cyanobacteria clearance rate by *D. pulicaria* could be explained by the susceptibility of this large-bodied species to mechanical interference.

On the other hand, filament breakage increased in the smaller *D. longispina* with increasing temperature, along with an increase in clearance rate for the cyanobacteria. Such an adaptation may allow *D. longispina* to graze on filaments more efficiently as the water warms up. Consequently, the relative performance of the small-bodied *Daphnia* species may increase, which would mitigate, but not reverse, the competitive superiority of the larger *D. pulicaria*. It has been suggested that the mere presence of cyanobacteria cannot reverse the competitive advantage of the larger-bodied species over the smaller-bodied ones (Kurmayer, 2001), even at higher temperatures (Sikora & Dawidowicz, 2014). Yet it is probable that the superior utilization of cyanobacterial filaments by small-bodied zooplankton compared to their larger-bodied congeners (Gulati et al., 2001)

contributes, along with other factors, not tested in the experiment: e.g., toxicity of cyanobacteria (Jiang et al., 2014a, b) or fish predation (Havens et al., 2015), to the dominance of small-bodied species in tropical and subtropical lakes and in temperate lakes during the “*midsummer decline*.” Such investigation of the interactions between *Daphnia* and cyanobacteria should be factored into the prediction of the potential effects of climate change on temperate lakes.

Conclusion

The results of our study show that small-sized *Daphnia* increase the intensity of filament breakage and the clearance rate for cyanobacteria with rising water temperature more than in the large-bodied species. Better utilization of cyanobacterial filaments with increasing temperature by small-bodied zooplankton could be, together with other factors, responsible for the observed dominance of small-bodied cladoceran species in warm-water lakes, where cyanobacteria are frequently the major food source for filter-feeding zooplankton.

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