

Temperature-dependent effect of filamentous cyanobacteria on *Daphnia magna* life history traits

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ABSTRACT

Filamentous cyanobacteria are unsuitable food for *Daphnia* due to their poor manageability, poor nutritional value and, in some cases, toxicity. As the strength of harmful effects of cyanobacteria on filter-feeding zooplankton is temperature dependent, the global warming scenarios for eutrophic lakes in temperate zone might include an escalated suppression of *Daphnia* populations caused by the presence of cyanobacterial filaments. To test this assumption, we conducted life-table experiments with four clones of *Daphnia magna* fed either a green alga *Scenedesmus obliquus* or a non-toxic strain of filamentous cyanobacteria *Cylindrospermopsis raciborskii* in two temperatures (20 °C and 24 °C). Key life history parameters of *Daphnia*, i.e., age and size at first reproduction, fecundity, and individual growth rate, were measured. Both food and temperature significantly affected *Daphnia* performance, however, the effect of interaction of these two factors was ambiguous and highly genotype-dependent. We conclude that the temperature increase within the studied range will not necessarily strengthen the suppression of *Daphnia* growth by filamentous cyanobacteria, but may affect clonal selection within population of *Daphnia*, thus possibly triggering microevolutionary changes within affected populations.

Key words: inter-clonal differences, non toxic cyanobacteria, global warming, life history

1. INTRODUCTION

In the last decades, increased frequency and extended duration of cyanobacteria blooms can be seen in temperate lakes. It is commonly accepted that expansion of cyanobacteria in summer phytoplankton communities is associated with anthropogenic changes of environment, mainly with eutrophication (e.g., Lampert & Sommer 1993; Wetzel 2001). Cyanobacteria are an insufficient food source for filter-feeding zooplankton due to their toxicity (DeMott 1999), poor manageability due to interference with food gathering process (Gliwicz & Siedlar 1980), and nutritional inadequacy, i.e., deficiency in essential nutrients such as sterols, polyunsaturated fatty acids and others yet unidentified compounds (Von Elert *et al.* 2003). The presence of cyanobacteria can trigger various changes of behaviour, morphology and life history of herbivore planktonic cladocerans, especially of the genus *Daphnia* (Lampert 1987a; deBernardi & Giussani 1990).

It has been shown that negative effect of cyanobacteria on *Daphnia* is temperature-dependent. Claska & Gilbert (1998) showed that under elevated temperature, *Daphnia* are more sensitive to both toxic cyanobacteria and pure cyanotoxin than their conspecifics exposed to the same toxin at lower temperature. Moreover, sterol limitation of *Daphnia* fed with cyanobacteria can be intensified by elevated temperatures, due to increase in *Daphnia* demands for sterols with rising temperatures (Sperfeld & Wacker 2009). Increase in ambient temperature resulted in a decrease in growth rate of *Daph-*

nia fed cyanobacteria (Abrusán 2004). Reduced fecundity of daphnids as a result of interaction of elevated temperature with presence of filamentous cyanobacteria and algae was also demonstrated in *in situ* experiments (Threlkeld 1979).

Different climate scenarios predict the increase of global average temperature between about 1.1 °C and 6.4 °C, with average rise of 3.9 °C, by the end of this Century (IPCC 2007). The summer phytoplankton of eutrophic temperate lakes is already dominated by cyanobacteria, which generally grow well at elevated temperatures (Rapala & Sivonen 1998). Thus the temperature increase may strengthen the negative effect of cyanobacteria on *Daphnia* fitness, because (i) *Daphnia* are more affected by cyanobacteria at higher temperature and (ii) global warming is expected to promote cyanobacteria expansion and to lead to increased frequency and magnitude of cyanobacteria blooms (Paerl & Huisman 2008).

To test the hypothesis that a higher temperature increases the negative influence of cyanobacteria on *Daphnia*, four clones of *Daphnia magna* were fed with non-toxic strain of filamentous cyanobacterium *Cylindrospermopsis raciborskii* or green alga *Scenedesmus obliquus* at two temperatures, i.e. 20 °C, which represents averaged current thermal conditions in the epilimnetic zone of temperate lakes in summer, and 24 °C, which simulates conditions after forecasted global warming.

Cylindrospermopsis raciborskii, the cyanobacterium used in the study, is under a particular concern in rela-

tion to water quality management and the impact of the forecasted global warming on lakes phytoplankton assemblies. The species was originally described as subtropical but recently it has been found in growing number of mid-latitude lakes including many lakes across northern Europe (Padiśák 1997). Rapid spread of this cyanobacterium is usually linked with climate change as well as with its wide physiological tolerance (Briand *et al.* 2004; Wiedner *et al.* 2007).

2. MATERIALS AND METHODS

Four clones of *Daphnia magna* Strauss (K1, K2, K3, K4) were used in the experiments. All clones were hatched at least 1 year prior to the study from ephippia isolated in our laboratory from sediments originating from Książęca pond, Warsaw, Poland. The clones were maintained in laboratory batch cultures at room temperature (19–22 °C) and were fed with the green alga *Scenedesmus obliquus*. To establish clonal lineages used in the experiments, a single female from each clonal culture was selected. To standardize the animals from studied clones and to minimize the potential differences between clones, caused by differences in culturing conditions of the mothers, clonal lineages were precultured for at least 3 generations (second clutch offspring were always taken for further culturing) under standard conditions, i.e., in the temperature-controlled water bath (22 °C ± 0.5 °C), summer photoperiod (16L:8D), fed daily with *S. obliquus* (1 mg C L⁻¹), 50 ml of medium × ind⁻¹, culture medium changed every other day.

The experiments were performed under two temperatures, 20 °C and 24 °C. The filaments of non-toxic strain of cyanobacteria *Cylindrospermopsis raciborskii* or the green alga *Scenedesmus obliquus* as reference food, in concentrations of 1 mg C L⁻¹ were offered as a food source in the two temperatures.

The experimental media were prepared with lake water from a small eutrophic Lake Janówek located near Warsaw, prefiltered through 1-mm filter and conditioned in a large, aerated tank for 2 weeks before use. To prepare experimental media, the water was filtered again through 0.2-µm filter and enriched with suspension of food (either green algae or cyanobacteria). Both green algae and the cyanobacteria were cultured in xenic (containing bacteria) batch cultures on Z/4 algal medium, under room temperature (20 °C ± 0.5 °C), constant illumination, and aeration.

Second-clutch neonate females (aged ≤20h) were randomly assigned to one of the four experimental treatments (10 individuals kept separately in each treatment), and 25 additional newborns were dried and weighted to determine initial body mass. The experiments were performed in temperature-controlled water baths under summer photoperiod (16L:8D); the culture media were changed daily. All animals were kept individually in 100 mL glass vessels until first eggs were laid into brood chamber. Age at first reproduction

(AFR) was recorded. Primiparous *Daphnia* were photographed, the eggs were counted under the stereomicroscope, and the animals were dried and weighed (Orion Cahn C-35 Ultra-Microbalance, Thermo Electron Corporation, USA) to calculate growth rate. Dry masses were converted into somatic growth rates per day using the formula $g_s = (\ln[M_t] - \ln[M_0]) t^{-1}$, where M_0 and M_t are the masses of the animals at the start and at the end of experiment, respectively, and t is the experiment duration. The body length of *Daphnia* at first reproduction (SFR) was measured from the photographs using MultiScan image analysis software (Computer Scanning Systems, Warsaw, Poland). The statistical analysis of the data, three-way ANOVA followed by Tukey HSD post hoc analysis, was performed with the Statistix 9.0 software. The data concerning fecundity of *Daphnia* were ln-transformed to achieve homogeneity of variances.

3. RESULTS

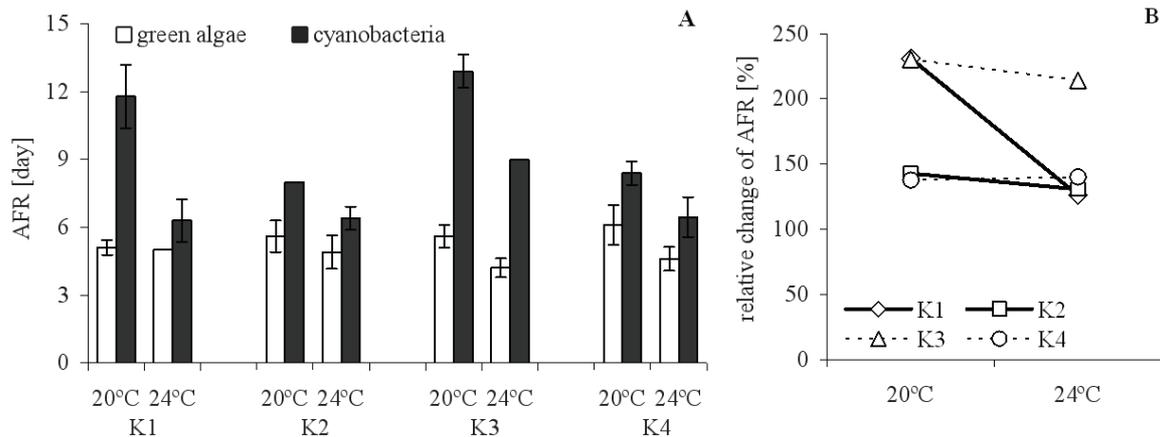
Food type, temperature and genotype (clone) significantly affected measured parameters of life history of *Daphnia* (Tab. 1, Figs 1, 2, 3 and 4). The animals fed with green algae matured earlier, at larger body size, they had almost four times more eggs, and grew more than two times faster than their clonemates fed with cyanobacteria. As expected, the temperature affected *Daphnia* life history as well. Animals reared at lower temperature (20 °C) grew slower, matured later, but attained larger body size and had more eggs than animals kept at higher temperature (24 °C). Clonal origin was also a significant source of variation in life history of studied *Daphnia* (Figs 1, 2, 3 and 4, Tab. 1).

Interactions of food type and genotype and temperature and genotype were significant sources of variation in all studied parameters of *Daphnia* life history (Tab. 1). Tukey HSD post hoc analysis (at $\alpha = 0.05$) revealed the biggest differences between food treatments in the clone K3 and the smallest in the clone K4. Only in the K1 clone the temperature significantly affected all measured life history parameters, whereas in the clone K2 only AFR and growth rate were slightly affected by temperature (Figs 1, 2, 3 and 4). Interaction of food type and temperature significantly affected only one of four studied life history parameters, age at first reproduction (Tab. 1). Although increase of temperature always resulted in shortening the age at first reproduction, the decrease of AFR due to higher temperature was stronger for animals kept in presence of cyanobacteria (Fig. 1 panel A and B).

Interaction of three parameters: food type, temperature and genotype, was a significant source of variation in all measured life history parameters (Tab. 1, Figs 1, 2, 3 and 4). In general, feeding on cyanobacteria prolonged time needed to reach maturity, and in animals fed with cyanobacteria significant differences between temperatures were found in all clones but when fed with green algae only animals from clones K3 and K4 matured sig-

Tab. 1. Three-way ANOVA testing the effects of genotype (Clone), type of food (*S. obliquus* vs *C. raciborskii*) and temperature on life history parameters of *Daphnia magna*.

Life history parameter	Source	df	F	<i>p</i>
AFR	Food	1	1097.49	<0.0001
	Temperature	1	383.94	<0.0001
	Clone	3	53.53	<0.0001
	Food × Temperature	1	118.31	<0.0001
	Food × Clone	3	83.44	<0.0001
	Temperature × Clone	3	13.50	<0.0001
	Food × Temperature × Clone	3	27.25	<0.0001
	Error	142		
SFR	Food	1	773.58	<0.0001
	Temperature	1	32.84	<0.0001
	Clone	3	101.37	<0.0001
	Food × Temperature	1	0.66	0.4194
	Food × Clone	3	15.51	<0.0001
	Temperature × Clone	3	5.93	0.008
	Food × Temperature × Clone	3	5.95	0.007
	Error	142		
Number of eggs	Food	1	875.50	<0.0001
	Temperature	1	35.70	<0.0001
	Clone	3	16.85	<0.0001
	Food × Temperature	1	0.15	0.7035
	Food × Clone	3	5.00	0.0025
	Temperature × Clone	3	8.53	<0.0001
	Food × Temperature × Clone	3	8.91	<0.0001
	Error	142		
g_i	Food	1	1995.49	<0.0001
	Temperature	1	175.65	<0.0001
	Clone	3	56.43	<0.0001
	Food × Temperature	1	0.54	0.4627
	Food × Clone	3	14.84	<0.0001
	Temperature × Clone	3	4.22	0.0068
	Food × Temperature × Clone	3	8.32	<0.0001
	Error	142		

**Fig. 1.** Age at first reproduction (AFR) of four clones of *D. magna* (K1, K2, K3, K4) fed with green algae or with cyanobacteria, at two temperatures (20 °C or 24 °C, left panel), and relative change of AFR (the value of the parameter in cyanobacteria treatment is expressed as a fraction of the value in green algae treatment at given temperature, right panel). Solid lines indicate a significant change; $p \leq 0.05$, Tukey).

nificantly earlier in higher temperature. Presence of cyanobacteria also resulted in a decrease of SFR of *Daphnia*, but the effect of cyanobacteria was more pronounced in elevated temperature only in one clone, K1. Significant differences in the number of eggs between temperature treatments were found in animals from

clones K1 and K3 but only when fed with cyanobacteria. The presence of cyanobacteria slowed down the growth rate of *Daphnia* but only in clones K1 and K4 this effect was significantly stronger under high temperature regime (Tukey HSD post hoc analysis, α threshold set at 0.05).

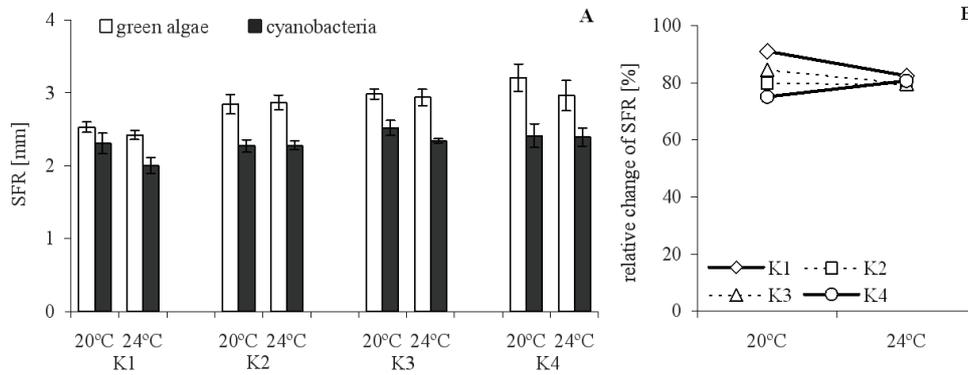


Fig. 2. Size at first reproduction (SFR) of four clones of *D. magna* (K1, K2, K3, K4) fed with green algae or cyanobacteria under two temperatures (20 °C or 24 °C, left panel) and relative change of SFR (right panel, see caption of Fig. 1 for description).

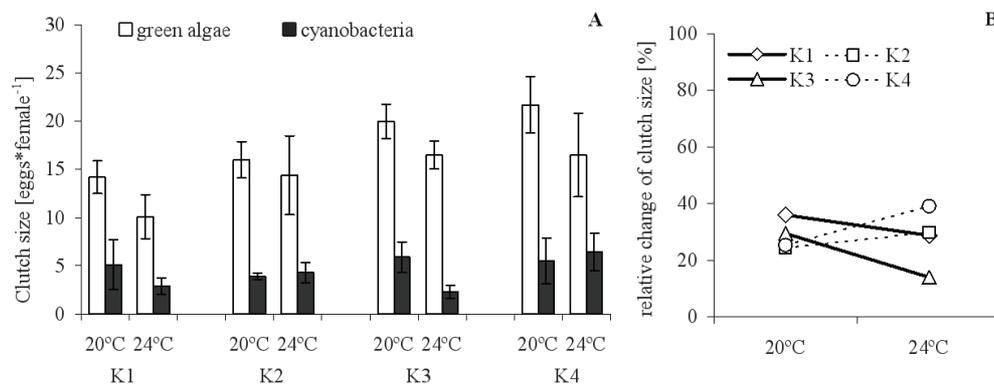


Fig. 3. Clutch size of four clones of *D. magna* (K1, K2, K3, K4) fed with green algae or cyanobacteria under two temperatures (20 °C or 24 °C, left panel) and relative change of numbers of eggs (right panel, see caption of Fig. 1 for description).

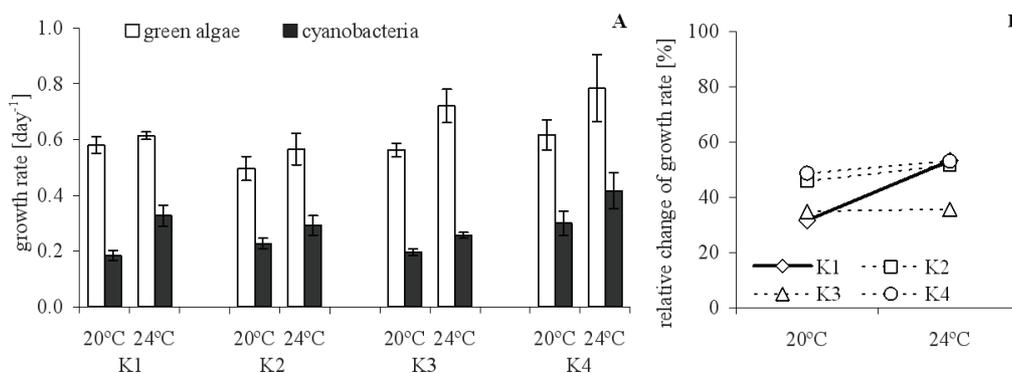


Fig. 4. Growth rate of four clones of *D. magna* (K1, K2, K3, K4) fed with green algae or cyanobacteria under two temperatures (20 °C or 24 °C, left panel) and relative change of growth rate (right panel, see caption of Fig. 1 for description).

4. DISCUSSION

In accordance with previous works (Porter & Orcutt 1980; Haney 1987; Lampert 1987a; deBernardi & Giusani 1990; Wilson *et al.* 2006), this study supports the view that filamentous cyanobacteria have a negative effect on *Daphnia* fitness. In the presence of *Cylindrospermopsis raciborskii* filaments individuals from all

studied clones grew slower, matured later and produced fewer eggs than in the absence of these filaments. However, unlike in few other studies (e.g., Von Elert & Wolffrom 2001; Martin-Creuzburg *et al.* 2008), our results show that cyanobacteria, at least in non-axenic conditions, can sustain growth and reproduction of *Daphnia*, although the decrease in key life history parameters was considerably high. One potential expla-

nation for the observed positive growth up to the reproductive age and ability to produce offspring by studied *Daphnia* is that the essential compounds absent in cyanobacterial food were transferred to animals by their well-fed mothers; similar maternal effects were described by Martin-Creuzburg *et al.* (2005). The maternal investment supplies the eggs with essential compounds, thus the suppressing effects of cyanobacterial food might be much stronger in later stages of life and later reproduction events, and particularly in subsequent generation(s). Secondly, Von Elert *et al.* (2003) found that the effect of feeding on low quality cyanobacterial food can be partly diminished when *Daphnia* can first feed on high-quality green algae at early life stage. The experimental animals in this study were born within 20 hours and stayed with their mothers in vessels containing green algae until the start of the experiments, therefore they had suitable feeding conditions in the first hours of life. Finally, our cultures were not axenic, and although the water was filtered through 0.2- μm filter before the medium was prepared to reduce the number of bacteria, we cannot exclude that their growth in the media provided additional food. Nevertheless, bacteria are considered poor-quality food source for *Daphnia* (see Lampert 1987b for review) and lack the same essential compounds (fatty acids and sterols) as cyanobacteria; it is therefore unlikely that they supplemented the cyanobacterial diet enough to allow positive growth rate of animals that would not be possible otherwise.

Some published data suggest that the strength of the negative effect of cyanobacteria on herbivorous zooplankton, particularly large-bodied *Daphnia*, is positively temperature-dependent. This is so because elevated temperature (1) increases sensitivity of *Daphnia* to cyanotoxins (Claska & Gilbert 1998), (2) decreases water viscosity and changes the hydrodynamics of filtering process towards strengthening the interference of cyanobacterial filaments with food collection mechanisms in *Daphnia* (Abrusán 2004), (3) increases sterol requirements in *Daphnia* (Sperfeld & Wacker 2009) and (4) increases metabolic rate and energetic demands of *Daphnia* (MacArthur & Baillie 1929) that can hardly be satisfied by cyanobacterial food of poor nutritional value. Indeed, it was suggested that observed epilimnion avoidance in *Daphnia* exposed to the presence of filamentous cyanobacteria (Forsyth *et al.* 1990; Berthon & Brousse 1995) is an adaptive behaviour that reduces the harmful effects of cyanobacteria due to low temperature in deepwater habitats (Bednarska & Dawidowicz 2007). One can further hypothesize that an increase in surface water temperature resulting from the global climatic trends can strengthen the inhibition of large-sized *Daphnia* population in temperate eutrophic lakes. Yet, this was not unambiguously supported by our results. Contrary to our expectations, the relative effect of cyanobacteria on the studied life-history parameters in our *D. magna* clones was in general not apparently

stronger in 24 °C than in 20 °C. Under higher temperature animals matured earlier and achieved higher growth rate. However, the relative decrease in growth rate caused by cyanobacteria was similar in the two studied temperatures and reached about half of the growth rate of animals fed with green algae. The relative delay of age at maturity due to feeding on cyanobacteria at 24 °C was similar or even smaller than at 20 °C. Panosso & Lüring (2010) studied the effect of *C. raciborskii* filaments on clearance rate of *D. magna* under two temperatures (20 °C and 27 °C) and did not find a significant effect of temperature. The difference in temperatures in our study was even smaller, so we can assume that the clearance rate of animals was also similar. Thus, the feeding inhibition in animals fed with cyanobacteria within given temperature range was not likely to produce differences in life history between the temperatures.

In two of the studied clones (K1 and K3), however, we found significant relative decrease of fecundity - the key parameter for fitness - in animals fed with cyanobacteria under higher temperature. In *Daphnia*, a significant inter-clonal variation was found in responses to factors such as temperature (Korpelainen 1986), food concentration (Pietrzak *et al.* 2010), food quality (Müller-Navarra & Lampert 1996; Weider *et al.* 2005), or food type (cyanobacteria vs green algae; Repka 1996). Similarly, we found that the pattern of responses to food type and/or cyanobacteria was genotype-dependent. Clone K3 was the most affected by the presence of cyanobacteria and performed poorly under higher temperature, whereas the effect of cyanobacteria and elevated temperature on clone K2 was negligible. The clones used in the studies originated from a shallow pond located near the center of Warsaw. During the growing season, the pond *Daphnia* population is exposed to varying - sometimes extremely high - temperatures. It is therefore not surprising that warm water-adapted clones, such as our clone K2, are present among the lineages raised from resting eggs collected in this pond. Although we have not performed any artificial selection experiments, we presume that continuous exposure of *Daphnia* populations to elevated temperature can result in clonal selection, similar to the enhanced microevolution driven by temperature rise alone reported by Van Doorslaer *et al.* (2009). Varying sensitivity to temperature may strongly interact with the differences in vulnerability to presence of cyanobacteria, and, consequently, may lead to rapid microevolutionary shifts in such populations.

5. CONCLUSION

We conclude that elevated temperature can strengthen the negative effect of cyanobacteria on large-sized cladoceran, *Daphnia magna*, but this result is not general for all studied clones and for all measured life history parameters. It is unlikely that increase of water

temperature and development of warm-water cyanobacteria will lead to elimination of *Daphnia magna* from surface waters, however, it will certainly lead to selection of better adapted clones and thus lead to micro-evolutionary changes in populations of this species.

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