Oecologia (2004) 141: 395–401
DOI 10.1007/s00442-004-1660-x

ECOPHYSIOLOGY

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Filamentous cyanobacteria, temperature and *Daphnia* growth: the role of fluid mechanics

Received: 15 December 2003 / Accepted: 22 June 2004 / Published online: 3 August 2004

Abstract Viscosity increases significantly with a fall in water temperature, thus temperature change affects not only the metabolic rates of aquatic suspension feeders, but also the physical properties of the surrounding fluid. This mechanistic effect of water temperature change on growth was separated from the effect of metabolism by using culture media with modified viscosity, while the temperature was kept constant. The effect of water viscosity on growth rate and feeding of four *Daphnia* species (*D. magna*, *D. pulicaria*, *D. hyalina*, *D. galeata*) was investigated. Increased viscosity decreased the growth rate significantly for three species, with the exception of *D. galeata*. Changing viscosity also affects growth qualitatively: the filamentous blue-green *Cylindrospermopsis raciborskii* reduces the growth rate of *D. pulicaria* at low viscosity, but its negative effect disappears when viscosity is higher. The findings are consistent with the hypothesis that it is the Reynolds number of the filtering appendages that determines the qualitative features of *Daphnia* filtration. The edibility of *C. raciborskii* at high water viscosity is most probably caused by lack of interference with filtering combs, and explains the coexistence of *D. pulicaria* with filamentous blue-green species in the field, and also the observed temperature dependence of growth inhibition of filaments.

Keywords Suspension feeding · Zooplankton · Fluid mechanics · Direct interception · Sieving

Electronic Supplementary Material Supplementary material is available for this article at http://dx.doi.org/10.1007/s00442-004-1660-x

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Introduction

When the temperature of water drops from 22 to 5°C its viscosity increases by 70%, thus the change in temperature alters not only the metabolic rate of organisms but also changes the physical characteristics of the ambient fluid. Such effects of temperature are potentially confounding at hydrodynamic scales where viscous forces dominate motion. It is the dimensionless Reynolds number (*Re*) that quantifies the relative importance of the two forces that matter during swimming: inertial forces and viscous forces. The *Re* is “the nearest thing we have to a completely general guide to what’s likely to happen when solid and fluid move with respect to each other” (Vogel 1994). When $Re < 1$, viscous forces dominate the flow. *Re* is the product of three variables: the velocity of flow (U), the kinematic viscosity of the fluid (ν) and the so-called characteristic length (l), which, in the case of swimming objects usually means the length measured in the direction of movement. Numerically *Re* is expressed as:

$$Re = lU\nu^{-1}$$

In this study, the feeding of the major freshwater herbivores, cladoceran zooplankton, was investigated from a biomechanical viewpoint. Suspension feeding of cladocerans is characterised by $Re \sim 10^{-1}$–10^{-4} (Porter et al. 1983). Therefore, it was expected that the efficiency of food collection (and in consequence, growth) of freshwater cladocerans (*Daphnia* sp.) would be strongly influenced by viscosity changes of the water.

The aim of this study is to test two hypotheses:

Hypothesis 1

First it was tested if, and if so to what extent water viscosity is responsible for the decline in the growth of *Daphnia* species observed with a decrease in temperature.

It is not just the viscosity that influences *Re*, but also the size of the animals (that is proportional to *l*). The size of herbivorous cladocerans has a tremendous impact on the effectiveness of filtration and their vulnerability to the interference of bloom-forming filamentous blue-greens. Filamentous algae, which often dominate in meso- and eutrophic lakes, can cause a considerable reduction in growth but they primarily inhibit large species. To this day the physiological causes of the influence of body size on the fitness of cladocerans are not known.

In laboratory experiments (Hawkins and Lampert 1989; Gliwicz and Lampert 1990; DeMott et al. 2001) interference was demonstrated many times; the long filaments are hypothesised to interfere with the feeding process, causing dramatic reductions in growth rate. The inhibition of growth is particularly strong in large daphnids (*D. pulicaria*), while small species (*D. galeata*, *D. cucullata*) are not, or only weakly influenced. At low food concentrations the addition of the non-toxic filamentous *Aphanizomenon flexosum* even improves growth of *D. galeata* (Kurmayer 2001). Von Elert et al. (2003) observed that the growth rate of *D. galeata* on the filamentous blue-green *Anabaena variabilis* was nearly equal to its growth rate on *Scenedesmus obliquus*, when *A. variabilis* was enriched with sterols. Field studies (Threlkeld 1986) have shown that at low temperatures the inhibitory effect of blue-green algae on growth and fecundity of *D. pulicaria* decreases dramatically; however, in these studies the direct cause of inhibition was not determined. Other studies show much less clear pattern. Filamentous species are often associated with large-bodied *Daphnia* (Lynch 1980), and there are well-documented cases of *D. pulicaria* feeding on filamentous cyanobacteria (Epp 1996; Paterson et al. 2002). The feeding experiments of Lampert (1981) and Kirk and Gilbert (1992) have shown that it is mainly the toxicity of blue-greens that is responsible for the reduction of fitness in *Daphnia*.

Hypothesis 2

The second hypothesis that was tested is that the body size and temperature dependence on cyanobacterial interference is caused basically by the same physical mechanism, the change in the Reynolds number (*Re*) of the feeding apparatus of *Daphnia*.

If one considers two objects with identical shape, then equality of *Re*s means that the physical character of the flow (streamlines) will be the same, regardless of the actual values of *l*, *U* or *ν*. This law of dynamic scaling was used in this study, to "virtually" reduce the size of large daphniids by increasing the viscosity of water. This reduces the *Re* of the filter screens just as the change in body size would. It was expected that large *Daphnia* species in water of higher viscosity (especially *D. pulicaria*, see Materials and methods and Fig. 1) will behave qualitatively like smaller *Daphnia*, and will not be sensitive to the interference of filaments of cyanobacteria (Fig. 1).

Materials and methods

Daphnia

Clones of four *Daphnia* species were used in the experiments: *D. magna*, *D. pulicaria*, (obtained from the Max-Planck Institute for Limnology, Plön), *D. hyalina* and *D. galeata*, (obtained from the Limnological Institute of the University of Konstanz, Konstanz). Prior to the experiments, the clones had been maintained in the laboratory for several months, fed with the green alga *S. obliquus*, and kept in constant, dim light at room temperature (20±2°C). The culture medium was membrane-filtered (0.45 µm) lake water from a hypertrophic lake in Warsaw.

Algae

The green alga *S. obliquus* (clone SAG 276-3a) and the filamentous blue-green *Cylindrospermopsis raciborskii* (originating from Lake Balaton, Hungary) were used in the experiments. Both species were grown in xenic (containing bacteria) batch cultures on Z/4 medium, with continuous illumination from white fluorescent lamps. *Scenedesmus* was grown at room temperature (18–22°C), while *Cylindrospermopsis* at 30±2°C. Most *Scenedesmus* in the culture was present in unicellular form, while *Cylindrospermopsis* forms short, straight trichomes of approximately 100 µm length, that are not coiled and do not form flakes. *Cylindrospermopsis* is a bloom-forming subtropical species, also found in southern Europe, which can produce the toxin cylindrospermopsin (Hawkins et al. 2001). There were two reasons for choosing this cyanobacterium as the interfering species: due to its straight shape it does not accumulate in the flow-through systems used in the experiments (see below), and secondly, previous studies have demonstrated that filtering rates (Hawkins and Lampert 1989), growth and life history parameters of *Daphnia* (Gliwicz and Lampert 1990) are strongly decreased in the presence of this cyanobacterium. The amount of algae and blue-greens used in the experiments reported here was determined spectrophotometrically (800 nm). The organic carbon content of *Scenedesmus* and *Cylindrospermopsis* suspensions was determined with a Shimadzu TOC analyser.

Viscosity modification

The viscosity of water was modified in two ways: by decreasing water temperature and by dissolving highly branched polymers (Fig. 1). Two polymers were used: dextran 500, a sucrose polymer produced by *Leuconostoc mesenteroides*, (molecular weight 500,000; SigmaAldrich), and ficoll, a synthetic polymer of sucrose and epichlorohydrin (molecular weight 400,000; SigmaAldrich). Both polymers have commonly been used in high

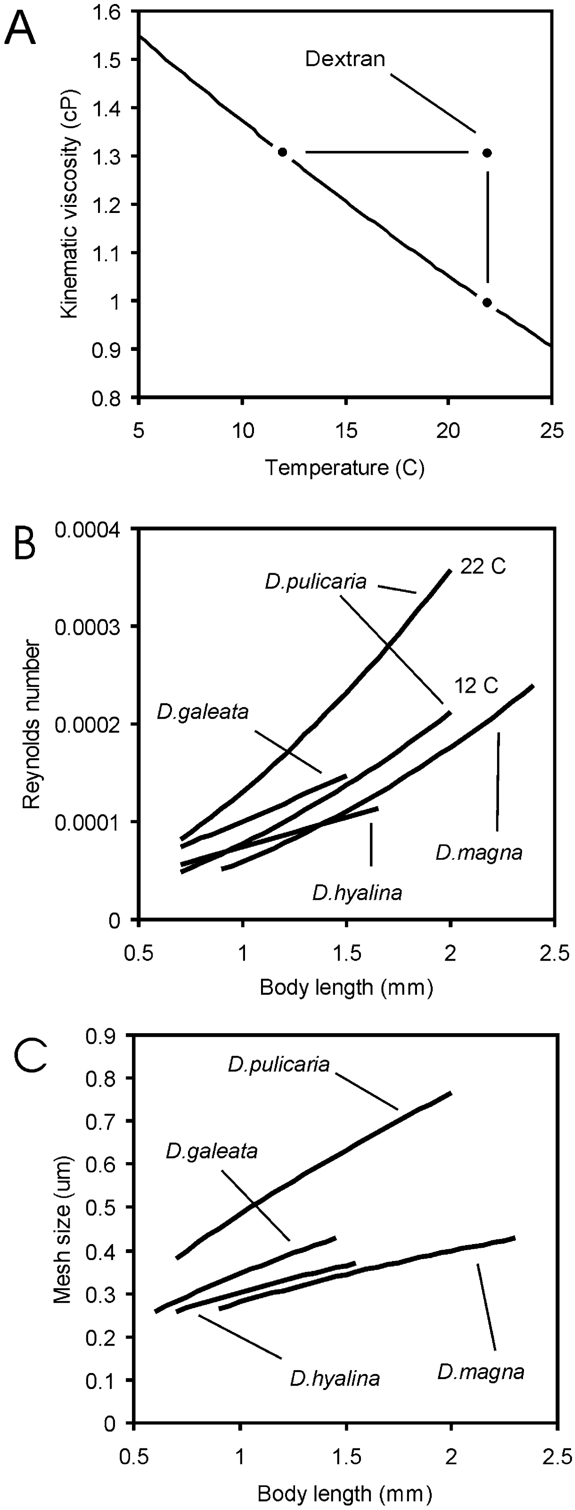

Fig. 1 **a** The change in the viscosity of water with temperature change, and the modification of viscosity with dextran. **b** Approximate Reynolds numbers (*Re*) of the setulae of the *Daphnia* species used. *Re* were calculated using morphological data from Brendelberger (1988). For all species the diameters of setulae of *D. pulicaria* were used as characteristic length. Flow velocity (*U*) was estimated as clearance rate/filtering area, thus the calculation ignores the fact that the flow is not steady but periodic. For *D. pulicaria* the *Re* for 12°C was also calculated. It was assumed that the 30% increase in viscosity that occurs when the temperature changes from 22°C to 12°C reduces *U* by 25%. **c** The mesh sizes of the filtering combs of the four species used (calculated after Brendelberger 1988)

concentrations to increase viscosity in studies of bacterial movement (Berg and Turner 1979). The small concentrations used in this study have a negligible effect on water density and osmotic pressure (Podolsky 1994).

The concentrations used were 0.54% (w/v) for dextran and 1.6% (w/v) for ficoll, and both increased the viscosity by 30%, from 1.0 cP (the viscosity of water at 22°C) to 1.3 cP (the viscosity of water at 12°C). Kinematic viscosity was determined with a Cannon-Ubbelohde viscometer. The reasons for choosing these polymers were the following: both are highly branched, their molecules are roughly spherical, and their solutions are Newtonian. The solutions of unbranched polymers (e.g. methylcellulose) are Newtonian only at very low concentrations; at higher concentrations the long branches form a “net” and the fluid becomes “elastic”: non-Newtonian (Berg and Turner 1979). Furthermore, two previous studies on the effects of viscosity on suspension feeding (Podolsky 1994; Bolton and Havenhand 1998) found these polymers to be non-toxic.

Experimental design

Two series of experiments were carried out, at constant, dim light, all in a flow-through system similar to the one described in Stich and Lampert (1984), which minimises the effect of sedimentation and makes it possible to maintain a constant food concentration. The general design of all experiments was similar: vessels of 250 ml with food suspension were kept in temperature-controlled water baths. Filtered lake water (0.45 µm) containing algal suspension was pumped into the vessels at a constant rate of 1.5 l day^{-1} vessel^{-1} with a peristaltic pump, from stirred reservoirs. The water in the controls and the polymer solutions used in the experiments were reused: they were refiltered on a 0.45-µm-membrane filter every 24 h and fresh food suspensions were added. The reasons for this practice were economic, due to the high cost of the polymers used. Although the secondary metabolites of *Daphnia*, *Scenedesmus*, *Cylindrospermopsis* and bacteria accumulate in this way, no signs of toxicity were found. All experiments were started with fresh water. To minimise the load of secondary metabolites, *Scenedesmus* was centrifuged at low speed (700 r.p.m.), and resuspended in membrane-filtered lake water prior to its addition.

At the start of each experiment *Daphnia* neonates younger than 24 h were pipetted into the vessels. The number of neonates in the vessels depended on the species used (eight *D. magna*, ten *D. pulicaria*, 15–12 *D. galeata* and *D. hyalina*). At the beginning of the experiments the dry weights of five subsamples of neonates were measured on a Cahn 25 microbalance. The experiments were ended after 5 days, the body size and clutch size of ovigerous animals were determined and all animals were dried and weighed on a Cahn 25 microbalance. Growth rates were calculated as $g=[\ln (W_t/W_0)]/t$, where W_0 and W_t are the weights of the animals at the beginning and the end of the experiments, respectively, and t is the duration of the experiment. In all experiments all treatments were done in three replicates.

In the first experimental series there were three treatments: high temperature (22±0.1°C, viscosity 1.0 cP), low temperature (12±0.1°C, viscosity 1.3 cP), and high temperature with artificially increased viscosity (22±0.1°C, viscosity 1.3 cP, only Dextran was used). In the first series *D. magna* and *D. pulicaria* were used. Ten experiments were performed, differing only in food (*Scenedesmus*) concentration. The food concentrations were 1.4, 1.0, 0.5, 0.35, 0.2, 0.125, 0.1, 0.0 (no food, experiment without the low-temperature treatment) mg C/l for *D. magna* and 0.4 and 1.4 mg C/l for *D. pulicaria*. The experiments were finished when the first clutches of daphnia appeared (after 5 days).

In the second experimental series all four *Daphnia* taxa were used. Similar temperatures and viscosities were used as in the first series, but with three more treatments, in which a mixture of *S. obliquus* and *C. raciborskii* was used as food. The concentration of *S. obliquus* was 0.4 mg C/l, the concentration of *C. raciborskii* was 0.25 mg C/l, (~1,600–1,800 filaments/ml). The concentration of blue-greens was kept moderate in order to minimise food quality (biochemical limitation) effects. The cold (12°C) treatments were done separately. Since at low temperatures the size of *Daphnia* at first reproduction increases significantly (at 22°C it was 1.8–1.9 mm, while at 12°C it was 2.6–2.8 mm for *D. pulicaria*) the cold treatments were ended after 10–14 days, when the animals were approximately 2-mm-long juveniles.

A Becton Dickinson flow cytometer (FACScalibur) was used in three flow-through experiments (with *D. magna* and *D. pulicaria*) to check whether dextran causes any deterioration of food particles (*Scenedesmus* and *Cylindrospermopsis*), or enhances bacterial growth (see supplementary figures). The FACS recorded four parameters: side scatter (SSC), forward scatter (FSC), fluorescence of fluorescein, (emission at 520 nm) and fluorescence of phycoerythrin (emission at 575 nm). The number of particles in the samples were counted with CellQuest software.

Results and discussion

The three marine studies that have separated the effect of a change in viscosity from a change in metabolism (Podolsky 1994; Bolton and Havenhand 1998; Hagiwara et al. 1998), found a strong effect of viscosity on the amount of collected particles in all cases. This also seems to be the case in large *Daphnia*, since at limiting food concentrations a 30% increase in viscosity decreases growth by 15–30% for *D. magna* and *D. pulicaria* (Fig. 2). The fact that at high food concentrations (1.0, 1.4 mg C/l) growth is reduced only marginally means that any toxicity of dextran or increased respiration rate is not the cause. This pattern of growth rates was expected if viscosity acts by reducing the flow through the filtering apparatus and in consequence reduces the amount of collected particles.

The growth when no food was added was probably caused by microbial growth in the experimental vessels due to dextran, but no decrease in viscosity was observed during the experiments. Dextran supported moderate microbial growth, with high bacterial concentrations appearing characteristically on the second day of the growth experiments (see Supplementary Figs. 1, 2 and 3). Prior to and subsequent to this, the amount of bacteria was higher with dextran than in the control, but the amounts in both were comparable (see supplementary figures). The positive growth of *D. magna* at 0.0 mg C/l with dextran suggests that the effect of viscosity on growth is underestimated in growth experiments.

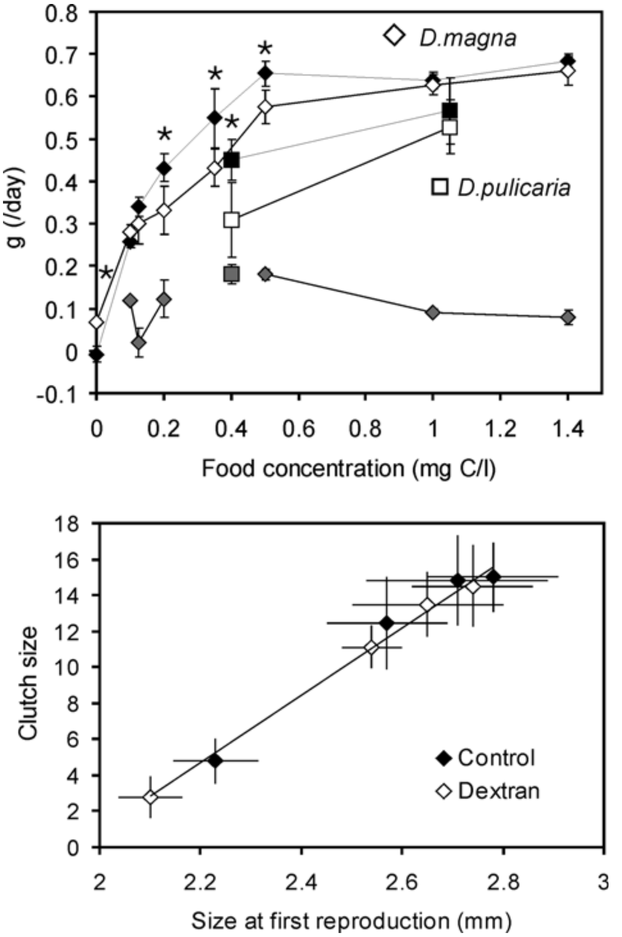

Fig. 2 **a** Growth rates of *D. magna* (*diamonds*) and *D. pulicaria* (*squares*) in different food concentrations. *Black symbols* show controls at the high temperature (22°C), *grey symbols* show controls at the low temperature (12°C), *open symbols* show growth rates at 22°C with viscosity adjusted to its level at 12°C. Significant ($P<0.05$; *t*-tests) differences between the high-temperature treatments are marked by an *asterisk*. **b** The life history parameters of *D. magna* in the experiments shown in (**a**). The regression lines of control and treatments with dextran do not differ significantly (analysis of covariance df=1, 169; F=0.652; P=0.42), thus the life history response of *D. magna* to dextran (elevated viscosity) cannot be distinguished from that to hunger

The slopes and intercepts of regressions between the size at first reproduction and clutch size of animals cultured with and without dextran do not differ from what would be expected in the case of hunger (Fig. 2b). Regardless of the efforts made to separate toxicity from food limitation, some sort of biochemical interaction of *Daphnia* metabolism and the polymers is possible (although theoretically dextran 500 does not penetrate cell membranes; supplier information).

No significant change of *Cylindrospermopsis* filament length (as reported in Gliwicz and Lampert 1990) was observed in any of the experiments. Overall, the negative effect of *C. raciborskii* on growth rates was much smaller than reported in previous experiments with the same species (Gliwicz and Lampert 1990), despite the comparable concentrations of algae used. In this study the only species for which *C. raciborskii* strongly inhibited growth was *D. pulicaria*, the species that has much larger intersetular distances (Brendelberger and Geller 1985) than the other species used. Contrary to this, the growth of the other "large" species, *D. magna* was weakly affected by filaments, what is in agreement with expectation based on its very dense filters (Brendelberger and Geller 1985; Geller and Müller 1981). *D. galeata* could utilize *C. raciborskii* under all experimental conditions used (Fig. 3).

Although filaments had a much smaller influence on growth than expected, there was a significant interaction between elevated viscosity/low temperature and the presence of filaments (Table 1). *D. pulicaria* and *D. hyalina* had significantly higher growth rates in the presence of both filaments and dextran, than in the presence of dextran alone; the filaments caused no growth reduction at a low temperature (*D. pulicaria*); and *D. magna* clone 1 is significantly less sensitive to filaments when cultured at an elevated viscosity (Table 1, Fig. 3.). Body size is clearly not the only factor influencing sensitivity to filaments: *D. hyalina* and *D. galeata* are nearly identical in size, whereas *D. magna* is slightly

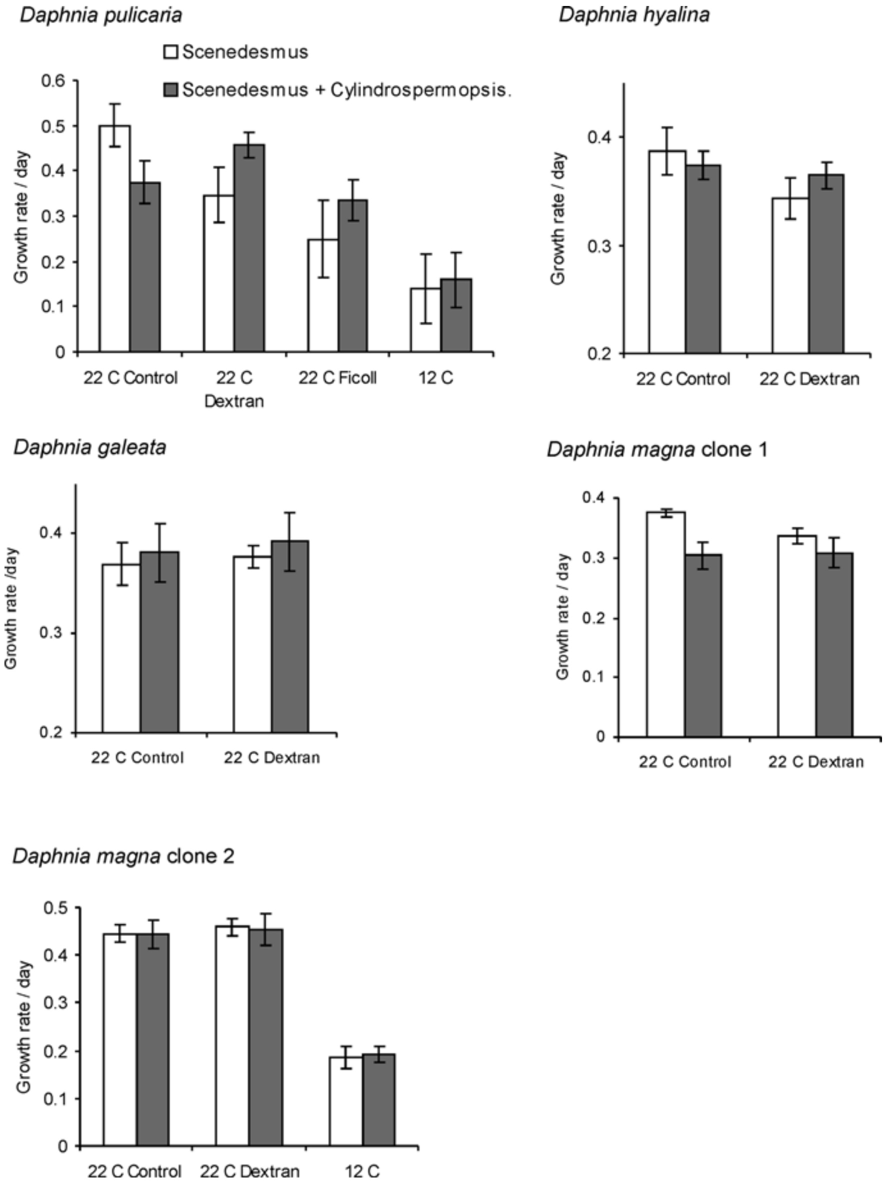

Fig. 3 Growth rates and life history parameters of *D. pulicaria*, *D. hyalina* and *D. galeata* and two clones of *D. magna*. The strongest interaction of blue-green filaments and increased viscosity is visible in *D. pulicaria*, where the presence of dextran, ficoll or low temperature made *Cylindrospermopsis* similarly edible. Growth rates and life history patterns of *D. hyalina* and *D. magna* clone 1 show qualitatively similar reactions to *D. pulicaria*, while *D. galeata* and *D. magna* clone 2 could feed on the filaments at both viscosities. *Note* the differences in scales

larger than *D. pulicaria*. Overall, the response of different *Daphnia* species was consistent with the *Re*s of their filters, and not their body size.

The result that higher water viscosity makes *D. pulicaria* and *D. hyalina* less sensitive to filament interference helps to explain several observations: the coexistence of *D. pulicaria* with filamentous species in the field (Lynch 1980; Epp 1996; Paterson et al. 2002) and the observed temperature dependence of growth inhibition due to filaments (Threlkeld 1986). The observation that during seasonal succession large-bodied *Daphnia* can delay cyanobacterial blooms but cannot prevent them (Kasprzak et al. 1999) is also consistent with the finding that interference by filaments depends on water viscosity (temperature).

At present there is no consensus on the particle-collection mechanisms of water fleas. Calculations and visual observations (Gerritsen et al. 1988, see also J. R. Strickler's website) suggested that only a minor portion of water goes through the filters, as the filtering appendages work like paddles rather than like rakes, and the main filtration mechanism is direct interception. Other studies (Brendelberger 1991; Gophen and Geller 1984) found strong correlations between filter mesh size and the minimum size of the collected particles that supports the sieve theory. The results of this study do not provide direct evidence for any of the collection mechanisms discussed above, but can be explained if both direct interception and sieving operate simultaneously on the filters (as discussed for copepods in Koehl 1996). The intersetular distances of *D. pulicaria* are much larger than those of *D. magna* (Brendelberger and Geller 1985), thus a possible cause for its filament sensitivity is that filaments clog the intersetular gaps. The strong positive effect of increased viscosity on growth of *D. pulicaria* in the presence of filaments may paradoxically be explained by decreased flow through the screens—which switches off sieving (see also Koehl 1996). This would reduce the amount of water filtered, but make possible the utilization of blue-greens, assuming that direct interception is not inhibited by the filaments. The correlation between the growth reduction in the presence of dextran (without filaments) and the growth reduction in the presence of cylindrospermopsis (without dextran) supports the hypothesis that the responses to viscosity and blue-green filaments have similar causes (Fig. 4.). Although these hypotheses are speculative at the present stage, it seems to be very difficult to explain the growth patterns of *D. pulicaria* and *D. hyalina* with reference to only one mechanism of particle retention.

Table 1 ANOVA table for the experiments shown in Fig. 3

Two-way ANOVA	*df*	MS	*F*	*P*
Daphnia. pulicaria				
Temperature (T)	1	0.15313	47.691	<0.001
Cylindrospermopsis (C)	1	0.01362	4.244	0.073
T×C	1	0.02298	7.157	0.028
Error	8	0.00321		
D. pulicaria				
Viscosity (V)	1	0.00214	4.52	0.066
Cylindrospermopsis (C)	1	0.00132	2.80	0.132
V×C	1	0.05379	113.77	<0.001
Error	8	0.00047		
Daphnia magna clone 1				
Viscosity (V)	1	0.00091	28.65	<0.001
Cylindrospermopsis (C)	1	0.00732	229.87	<0.001
V×C	1	0.00131	41.37	<0.001
Error	8	0.00003		
D. magna clone 2				
Viscosity (V)	1	0.00040	2.29	0.168
Cylindrospermopsis (C)	1	0.00003	0.20	0.664
V×C	1	0.00001	0.05	0.820
Error	8	0.00017		
D. magna clone 2				
Temperature (T)	1	0.19428	8598.87	<0.001
Cylindrospermopsis (C)	1	0.00003	1.45	0.263
T×C	1	000007	3.28	0.107
Error	8	0.00002		
Daphnia hyalina				
Viscosity (V)	1	0.00221	15.72	0.004
Cylindrospermopsis (C)	1	0.00004	0.31	0.591
V×C	1	0.00085	6.06	0.039
Error	8	0.00014		
Daphnia galeata				
Viscosity (V)	1	0.00028	3.06	0.118
Cylindrospermopsis (C)	1	0.00056	6.04	0.039
V×C	1	0.00001	0.11	0.745
Error	8	0.00009		

This study represents the first quantitative examination of the importance of physical properties of water in determining the competitive abilities of a freshwater suspension-feeding organism. The non-intuitive way in which temperature influences filtration through viscosity may be very important when the effects of global warming

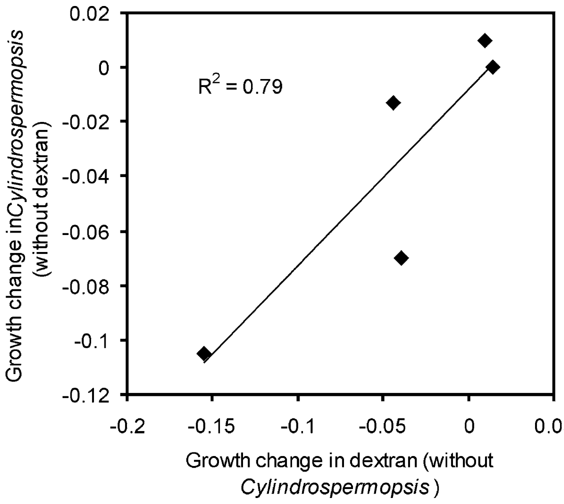

Fig. 4 Growth changes of the four *Daphnia* species compared to the high temperature (22°C)-low viscosity (no polymer) control. The correlation (P=0.043) between the response for elevated viscosity and the presence of blue-greens suggests that these two growth responses may have the same underlying cause

are considered on aquatic ecosystems, especially in freshwater, since they experience much wider temperature fluctuations than marine environments. (For the effect of viscosity on cladoceran filtration rate see also the paper of Loiterton et al. 2004, which was published after the submission of this manuscript).

Acknowledgement The research was supported by grants from KBN (6PO4F 04717) to György Abrusán and Piotr Dawidowicz (6PO4F 01821).

References

Berg HC, Turner L (1979) Movement of microorganisms in viscous environments. Nature 278:349–351

Bolton TF, Havenhand JN (1998) Physiological versus viscosity induced effect of an acute reduction in water temperature on microsphere ingestion by trochophore larvae of the serpulid polychaete *Galeolaria caespitosa*. J Plankton Res 20:2153–2164

Brendelberger H (1988) Untersuchungen zur funktionsmorpholgie des filterapparates von Cladoceren. PhD thesis. Christian-Albrechts University, Germany

Brendelberger H (1991) Filter mesh size of cladocerans predicts retention efficiency for bacteria. Limnol Oceanogr 36:884–894

Brendelberger H, Geller W (1985) Variability of filter structures in eight *Daphnia* species: mesh sizes and filtering areas. J Plankton Res 7:473–486

DeMott WR, Gulati RD, Van Donk E (2001) *Daphnia* food limitation in three hypereutrophic Dutch lakes: evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria. Limnol Oceanogr 46:2054–2060

Epp GT (1996) Grazing on filamentous cyanobacteria by *Daphnia pulicaria*. Limnol Oceanogr 41:560–567

Geller W, Müller H (1981) The filtration apparatus of Cladocera: filter mesh sizes and their implications on food selectivity. Oecologia 49:316–321

Gerritsen J, Porter KG, Strickler JR (1988) Not by sieving alone: observations of suspension feeding in *Daphnia*. Bull Mar Sci 43:336–376

Gliwicz ZM, Lampert W (1990) Food thresholds in *Daphnia* species in the absence and presence of blue green filaments. Ecology 71:691–702

Gophen M, Geller W (1984) Filter mesh size and food particle uptake by *Daphnia*. Oecologia 64:408–412

Hagiwara A, Yamamiya N, Belem de Araujo A (1998) Effect of water viscosity on the population growth of the rotifer *Brachionus plicatilis* Muller. Hydrobiologia 388:489–494

Hawkins P, Lampert W (1989) The effect of *Daphnia* body size on filtering rate inhibition in the presence of a filamentous cyanobacterium. Limnol Oceanogr 34:1084–1089

Hawkins PR, Putt E, Falconer I, Humpage A (2001) Phenotypical variation in a toxic strain of the phytoplankter, *Cylindrospermopsis raciborskii* (Nostocales, Cyanophyceae) during batch culture. Environ Toxicol 16:460–467

Kasprzak P, Lathrop RC, Carpenter SR (1999) Influence of different sized *Daphnia* species on chlorophyll concentration and summer phytoplankton community structure in eutrophic Wisconsin lakes. J Plankton Res 21:2161–2174

Kirk KL, Gilbert JJ (1992) Variations in herbivore response to chemical defenses: zooplankton foraging on toxic cyanobacteria. Ecology 73:2208–2217

Koehl MAR (1996) When does morphology matter? Annu Rev Ecol Syst 27:501–542

Kurmayer R (2001) Competitive ability of *Daphnia* under dominance of non-toxic filamentous Cyanobacteria. Hydrobiologia 442:279–289

Lampert W (1981) Inhibitory and toxic effects of blue-green algae on *Daphnia*. Int Rev Ges Hydrobiol 66:285–298

Loiterton B, Sundbom M, Vrede T (2004) Separating physical and physiological effects on zooplankton feeding rate. Aquat Sci 66:123–129

Lynch M (1980) Aphanizomenon blooms: alternate control and cultivation by *Daphnia pulex*. In: Kerfoot WC (ed) The evolution and ecology of zooplankton communities. University Press of New England, Hanover, N.H.

Paterson MJ, Findlay DL, Salki AG, Hendzel LL, Hesslein RH (2002) The effects of *Daphnia* on nutrient stoichiometry and filamentous cyanobacteria: a mesocosm experiment in a eutrophic lake. Freshwater Biol 47:1217–1233

Podolsky RD (1994) Temperature and water viscosity: physiological versus mechanical effects on suspension feeding. Science 265:100–103

Porter KG, Feig YS, Vetter EF (1983) Morphology, flow regimes and filtering rates of *Daphnia*, *Ceriodaphnia*, and *Bosmina* fed natural bacteria. Oecologia 58:156–163

Stich HB, Lampert W (1984) Growth and reproduction of migrating and non migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. Oecologia 61:192–196

Threlkeld ST (1986) Differential temperature sensitivity of two cladoceran species to resource variation during a blue-green algal bloom. Can J Zool 64:1739–1744

Vogel S (1994) Life in moving fluids—the physical biology of flow. Princeton University Press, Princeton, N.J.

Von Elert E, Martin-Creuzburg D, Le Coz JR (2003) Absence of sterols constrains carbon transfer between cyanobacteria and a freshwater herbivore (*Daphnia galeata*). Proc R Soc Lond B 270:1209–1214