JOURNAL OF PLANKTON RESEARCH | VOLUME 24 | NUMBER 10 | PAGES 1047–1056 | 2002

Phenotypic plasticity in *Daphnia pulicaria* as an adaptation to high biomass of colonial and filamentous cyanobacteria: experimental evidence

ANAS GHADOUANI* [1] AND BERNADETTE PINEL-ALLOUL

GRIL-DÉPARTEMENT DE SCIENCES BIOLOGIQUES, UNIVERSITÉ DE MONTRÉAL, CP 6128, SUCC. CENTRE-VILLE, MONTRÉAL, QUÉBEC H3C 3J7, CANADA

[1]PRESENT ADDRESS: DEPARTMENT OF BIOLOGY, UNIVERSITY OF WATERLOO, 200 UNIVERSITY AVENUE WEST, WATERLOO, ONTARIO N2L 3G1, CANADA

*CORRESPONDING AUTHOR: aghadoua@sciborg.uwaterloo.ca

We investigated the ability of the water flea, Daphnia, to adapt the size and structure of its filtering apparatus as a response to experimentally increased biomass of inedible filamentous and colonial cyanobacteria in a large in situ enclosure experiment. Predator-induced phenotypic plasticity in Daphnia has been extensively documented, but only a small number of studies have focused on morphological changes induced by food quantity and quality. Here we show that Daphnia responded to increased biomass of inedible phytoplankton in its environment by enlarging the area and the mesh size of its filtering apparatus. These observations suggest that Daphnia responds to increased concentrations of inedible particles in the same fashion as it does in a very low food environment. In our study, daphnids exposed to a high biomass of inedible algae, in fertilized enclosures, had significantly larger (12–15%) filter screens attached to their third and fourth limbs in comparison to daphnids exposed to a low biomass of inedible algae. The mesh size also increased in the same conditions. These results suggest that daphnids used their phenotypic plasticity to respond to changes in their food quality and quantity. By using this strategy, daphnids can maximize their food uptake and hence compensate for the scarcity of suitable food encountered in very oligotrophic conditions or even in eutrophic conditions when phytoplankton communities are dominated by large inedible species.

INTRODUCTION

Some freshwater cladocerans, such as the water flea *Daphnia*, have been shown to reduce their body size in the presence of large size-selective predators such as fish (Stibor, 1992), and do just the opposite in the presence of small size-selective predators such as phantom midge *Chaoborus* (Stibor and Lüning, 1994). In lakes with planktivorous fish, the antipredator morphological plasticity is a result of a rather complex mechanism used by *Daphnia* to reduce egg size and produce neonates that mature at small size (Lampert, 1993). To moderate the effects of predation, cladocerans also use morphological changes such as helmet enlargement (Tollrian, 1990, 1994) or neck-teeth formation (Tollrian, 1993, 1995). The antipredator defences disappear rapidly in the absence of predators or their chemical cues because this defence mechanism has high energetic cost (Lampert, 1993; Tollrian and Dodson, 1999). In recent decades, ecologists have focused on predator-inducible defences such as diel vertical migration (Neill, 1992; De Meester *et al.*, 1995), changes in life history, and body shape and size (Lampert, 1993; Stibor and Lampert, 1993), but less on the response of these organisms to major changes in their food quality and quantity.

Zooplankton also use phenotypic plasticity to adapt to seasonal variations in bottom-up processes in terms of food quality and quantity (Lampert, 1994; Repka *et al.*, 1999). Laboratory studies have clearly shown that a number of *Daphnia* species are able to adapt to low food conditions by changing the size and structure of their filter screens on their third and fourth limbs (Geller and Müller,

1981; Koza and Korínek, 1985; Pop, 1991; Stuchlík, 1991; Lampert, 1994). This mechanism is used by *Daphnia* to optimize food gathering with moderate energy cost and hence compensate for occasional low food conditions in lakes (Lampert, 1994; Lampert and Brendelberger, 1996). Cladocerans with large filter screens have a higher filtering rate than animals with smaller ones (Egloff and Palmer, 1971; Stuchlík, 1991). On the other hand, cladoceran filter screens affect food selection, and could explain some zooplankton seasonal succession patterns in lakes (Geller and Müller, 1981). For example, species with coarser filter mesh tend to have lower retention efficiency for small particles (Brendelberger, 1991). Depending on the food environment, daphnids are capable of adjusting the area and/or mesh size of their filter screens (Brendelberger and Geller, 1985). The phenotypic plasticity in *Daphnia* can take place in a relatively short time (one or two generations) in natural populations as well as in monoclonal laboratory populations (Pop, 1991).

Previous studies of *Daphnia* phenotypic plasticity focused primarily on food quantity as a trigger for changes in filter screens (Lampert, 1994; Lampert and Brendelberger, 1996). Here we report the results of an *in situ* enclosure experiment in which we investigated the ability of daphnids to adapt to high biomass of large filamentous and colonial algae by changing particular morphological traits of their filtering apparatus. We anticipated that *Daphnia* populations exposed to high biomasses of colonial and filamentous cyanobacteria or large inedible algae would (1) enlarge their filter-screen area to compensate for the relative scarcity of small edible phytoplankton cells and (2) adjust their mesh size to be able to feed on smaller food particles, including bacteria, more efficiently. It has been suggested that eutrophic conditions are favourable for cladocerans with finer mesh size which are capable of filtering small particles, including bacteria (Geller and Müller, 1981; Brendelberger, 1991). We investigated these questions by comparing morphometric measurements of filter screens (filter-screen area, setular width and mesh size) of daphnids that were exposed to contrasting phytoplankton populations with low and high biomass of colonial and filamentous cyanobacteria in large *in situ* enclosures. One of the aims of this study was to evaluate whether or not daphnids display, in natural environments, phenotypic variations in their filter screens such as those observed in the laboratory under controlled conditions.

METHOD

Study site

The study was conducted in Steele Lake (54°39′N, 113°46′W), a relatively large (6.6 km^2 surface area) eutrophic lake in the northern boreal forest of Alberta, Canada. Steele Lake is shallow enough (3.2 m mean depth, 6.1 m maximum depth) to mix vertically during most of the summer. The drainage basin of Steele Lake is very large compared to that of many lakes on the boreal plain, representing 37 times the area of the lake (Mitchell and Prepas, 1990). Large amounts of nutrients are transported to the lake from the naturally rich drainage basin, which causes frequent cyanobacterial blooms during summer (Trimbee and Prepas, 1987). The blooms are usually dominated by species such as *Aphanizomenon* spp., *Anabaena* spp. and *Microcystis* spp., which make this lake an ideal site for these experiments.

Experimental set-up and nutrient manipulations

The experiments were performed in six large cylindrical enclosures, which were placed at the deepest part of the lake in a sufficiently quiet area to minimize the effect of the wind. The enclosures were closed off from the bottom of the lake and were made of clear thick woven polyethylene fitted to a flotation collar of ethafoam logs. The collars were ~50 cm above the surface of the water to keep enclosure and lake water from mixing. The stability of the enclosures was ensured by attaching each three enclosures to one side of a floating dock. The whole structure (enclosures + dock) was anchored at several points to ensure maximum stability. Water from the lake was pumped into each enclosure. The filled enclosures were then covered by a gill net to prevent fish from jumping into them. The enclosures had 2.5-m-diameter openings, were 2 m deep and contained ~10 m^3 of water each.

To enhance phytoplankton biomass, we fertilized four of the six enclosures by adding a combination of phosphorus (P) and nitrogen (N) to them, and left the remaining two as controls (no nutrient additions). We added P as potassium phosphate monobasic (KH_2PO_4) and N as ammonium nitrate (NH_4NO_3). We intended to create an exponential gradient in nutrients in comparison to the concentrations measured at the beginning of the experiments. Hence, we increased P concentration in the first two treated enclosures by ~3-fold, and hereafter refer to this treatment as nutrient addition (NA). In the last two enclosures, P concentrations were increased by ~7-fold in comparison with the control and were referred to as high nutrient addition (HNA). N was added in the proportions of 3:1 and 1:1 relative to P by weight in NA and HNA treatments, respectively. The nutrients were added as a single pulse at the beginning of the experiments and all the treated enclosures were fertilized at the same time.

Sampling and analytical methods

The experiments took place in summer 1996 and lasted for 5 weeks, including the pre-treatment period. Enclosures were sampled every fourth day. Water temperature, dissolved oxygen concentration and light penetration were measured in the enclosures and the lake during each visit to the site. Water samples for chemical analyses and chlorophyll (Chl *a*) estimation were collected with an integrated sampler made of tygon tubing. Water samples were taken and preserved in Lugol solution for phytoplankton identification and enumeration. P concentrations were determined following the modified Menzel and Corwin (Menzel and Corwin, 1965) potassium persulfate method (Prepas and Rigler, 1982). The ethanol extraction method was used to estimate Chl *a* concentration in water samples (Bergmann and Peters, 1980). Preserved subsamples were settled in a sedimentation chamber and identified with an inverted microscope according to the Utermöhl method (Lund *et al.*, 1958). Phytoplankton communities were regrouped here in three classes: cyanobacteria including all colonial and filamentous species; large diatoms considered as inedible for daphnids based on their large size (>30 μm); and all other species considered as edible due to their small size (<30 μm).

Daphnia filter screen measurements

Zooplankton were sampled by means of a Wisconsin plankton net of 53 μm mesh size, 29 cm diameter and 90 cm length. The samples were preserved in a buffered 4% sugar–formaldehyde solution (Haney and Hall, 1973; Prepas, 1978). *Daphnia pulicaria* individuals ranging from ~0.6 to ~3.0 mm in body length were picked out from preserved zooplankton samples. The animals used in this study all came from zooplankton samples taken at the end of the experiments to ensure that they were exposed to the different environments for sufficiently long periods. Between 30 and 40 daphnids belonging to the dominant cladoceran species, *D. pulicaria*, were taken from each treatment. Each individual was measured and dissected under a stereomicroscope to take out separately the pair of filter screens attached to the third and fourth limbs. The filters were identified and spread out on a microscopic slide. The projected filter areas, *sensu* Brendelberger and Geller (Brendelberger and Geller, 1985; Koza and Korínek, 1985), were plotted on paper with a stereomicroscope equipped with a drawing tube. The plots of the filters were scanned and the area determined precisely by computerized planimetry with image analysis software (SigmaScanpro 5.0).

Fine morphometric measurements of the filter screens, such as intersetal and intersetular distances, were made from scanning electronic microscope (SEM) photographs (Figure 1). Screen filters of large animals of the same size (3 mm) were selected from the different enclosures and prepared for SEM observations after critical point drying and metal coating (Brendelberger and Geller, 1985; Bozzola and Russell, 1992). Photographs were taken from each group of filter screens, scanned and specific measurements made. Between 150 and 300 measurements of intersetal (Figure 1a and b) and intersetular (Figure 1d) distances were made for each group of filter screens (control, NA, HNA) to ensure an accurate comparison.

Data analyses

Filter-screen areas of all the measured daphnids were plotted against their body length. Differences between the control and the treatments were tested with analysis of covariance (ANCOVA) after all the data were log transformed. Before the ANCOVA was calculated, we tested the assumption of homogeneity of slopes by making sure there was no significant interaction between the covariate (*Daphnia* size) and the treatment (control, NA and HNA). Since preliminary comparison of the area of filter screens of daphnids from NA and HNA treatments showed no significant difference, the two groups were pooled together. Further comparisons were made between control and treatment as one group (NA + HNA). Cases with high absolute Studentized residual were considered outliers and removed from the analysis (Velleman and Welsch, 1981). Hence, we were able to reduce the effects of outliers on the outcome of ANCOVA analysis. However, all data are shown on the figures including the outliers. ANCOVA was used to test the differences in filter-screen area of daphnids of all lengths (from 0.6 to ~3.0 mm), as well as small and large daphnids separately. The separation of the two groups was decided arbitrarily as 1.7 mm, based on visual examination of the relationships. A one-way ANOVA was used to test for possible changes in the intersetal and intersetular distances after exposure to high cyanobacterial biomass in NA and HNA enclosures in comparison with the control. All the data presented are from the six enclosures as well as the lake; however, the statistical tests were only used to compare the treatments (NA and HNA) with the control. We consider the lake to be different from the control, since the conditions of the lake were not the same as the control, and any comparison with the treatment would not be relevant and conclusive. However, we show the data from the lake in all tables and figures for indicative purposes only. All statistical analyses were performed with Systat version 8.0.

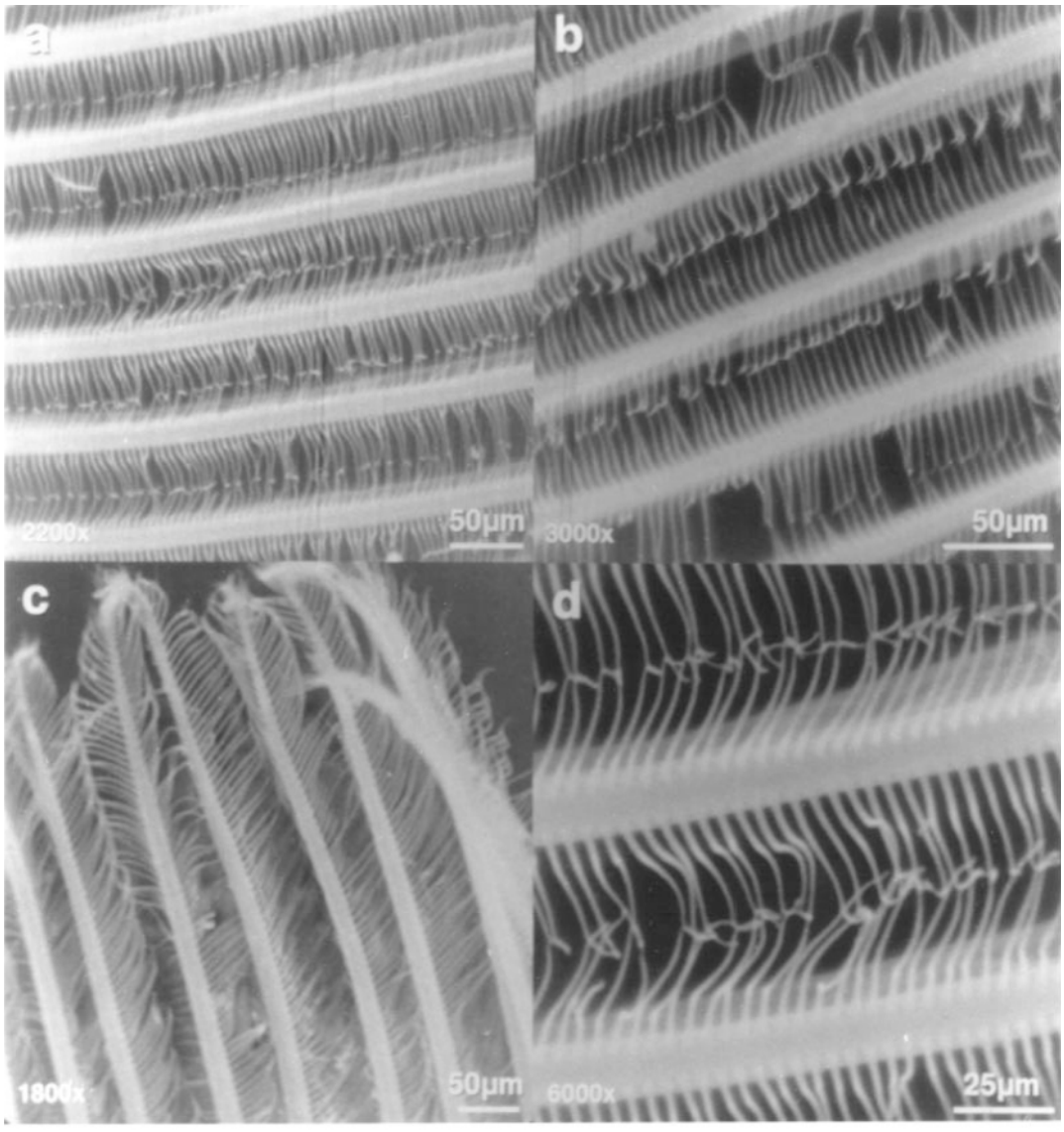

Fig. 1. SEM photographs showing the fine structure of *D. pulicaria* third and fourth limb filter screens at different magnifications ranging from ×1800 to ×6000. The first-order structures called setae support second-order structures called setules in a bird-plume-like fashion (c and d). Each setule appeared on the photograph (d) to be hooked at the end to the next setule, which is attached to the next seta. (Photograph by A.G.)

RESULTS

Phytoplankton response

The addition of nutrients (N, P) was responsible for doubling the biomass of phytoplankton, as estimated by Chl *a* biomass (Figure 2). The increase in Chl *a* biomass was caused by cyanobacterial blooms which occurred in the fertilized enclosures (NA and HNA) after the addition of nutrients. During the bloom events, Chl *a* reached peaks as high as 94 and 112 µg l^{-1} in NA and HNA treatments, respectively. Phytoplankton communities were dominated by large colonial and filamentous cyanobacterial species (*Microcystis aeruginosa*, *Aphanizomenon flos-aquae* and *Anabaena flos-aquae*) as well as large diatoms. These two groups, which are considered inedible food for *Daphnia*, accounted for an average of 80–90% of the total phytoplankton biomass, leaving only a small fraction of edible phytoplankton for the daphnids (Figure 2). The absolute biomass of the inedible fraction of phytoplankton was higher in the fertilized enclosures in comparison with the control. The biomass of large inedible filamentous and

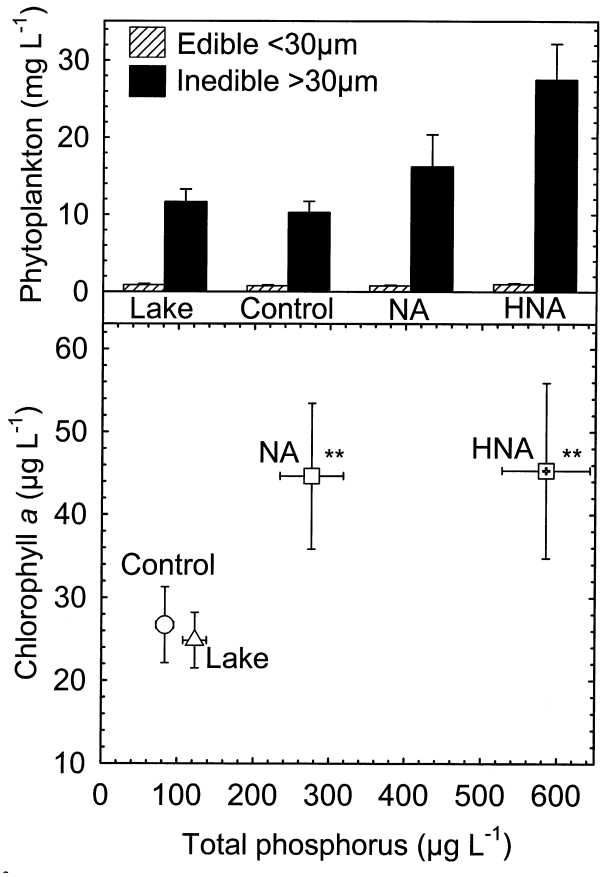

Fig. 2. Chlorophyll *a* biomass (µg l^{-1}) as a function of total phosphorus (µg l^{-1}) in the lake, control, NA and HNA enclosures. Data are presented as the mean of each group and bidirectional horizontal and vertical error bars (1 SEM). Phytoplankton are classified in two fractions: an edible fraction including all the unicellular species of size <30 µm (represented by hatched bars); and an inedible fraction including all the species of size >30 µm (represented by black bars). One standard error of the mean is presented on each bar. $^{**}P < 0.01$ (ANOVA comparison of control versus NA and HNA treatments).

colonial phytoplankton species was ~2–3 times higher in NA and HNA enclosures, respectively (Figure 2). These conditions allowed us to expose daphnid populations to an increasing gradient of dominance by large inedible phytoplankton species in conditions closer to natural conditions than common laboratory experiments with one or two species.

Changes in *Daphnia* filter-screen area

Daphnia total filter-screen area (mm^2) increased with body length in all the treatments; however, the increase was more rapid in *Daphnia* that were exposed to higher biomass of inedible cyanobacteria and diatoms (Figure 3). ANCOVA revealed that *Daphnia* total filter-screen area was significantly larger in hypereutrophic systems (NA + HNA) in comparison with moderately eutrophic systems (control) ($P = 0.008$; Table I). As the daphnids grew larger, the difference between the two groups became clear (Figure 3). The difference in filter-screen filter area was not statistically significant for daphnids <1.7 mm in body length ($P = 0.922$; Table I). When larger daphnids (>1.7 mm) were compared, the difference in total filter-screen area was statistically significant ($P = 0.017$; Table I).

We also compared separately the areas of each filter screen attached to the third and fourth limbs of *Daphnia*. The area of the third filter was generally two times larger than that of the fourth one, as shown by the fourth:third area ratio (Table II). The ratio was always very stable at around 0.55–0.58 with a standard error of <2% (Table II). The daphnids exposed to a high biomass of inedible algae appeared to have a higher ratio than the control; however, the difference was only marginally statistically significant, especially considering the high number of observations ($P = 0.0424$; Table II). The filter-screen area of the third limb was significantly larger in daphnids from the fertilized enclosures in comparison with the control (Figure 4a). The difference between the two groups was statistically significant ($P = 0.002$; Table I). As the daphnids from the treated enclosures grew, their third limb filter-screen area became larger (Figure 4a). The difference was statistically significant for large daphnids ($P = 0.001$; Table I), but not for small ones ($P = 0.404$; Table I). The same results were observed for fourth limb filter-screen area. Again, daphnids from the treated enclosures had larger filter screens in comparison with the control (Figure 4b). The difference was statistically

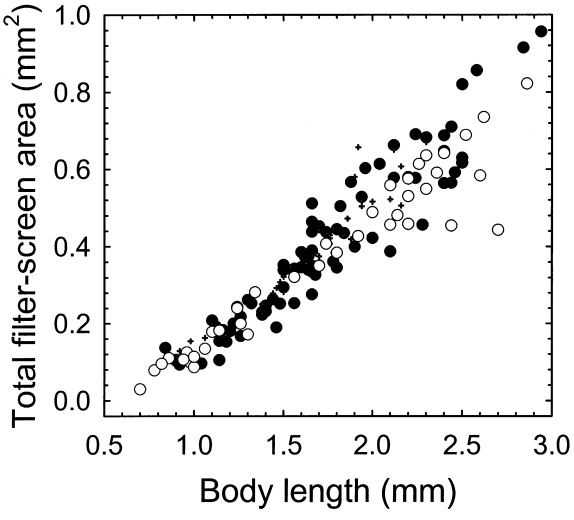

Fig. 3. Total filter-screen area (mm^2) of *D. pulicaria* from the lake (crosses), control enclosures (open circles), and NA and HNA treatment enclosures pooled together (solid circles), as a function of body length (top of the head to base of the spine). Outliers are shown on the graphs but not included in the ANCOVA analyses.

Table I: ANCOVA of (a) total filter-screen area, (b) third limb filter-screen area and (c) fourth limb filter-screen area for all measured daphnids, small daphnids (<1.7 mm) and large daphnids (>1.7 mm)

Source	All daphnids			Large daphnids (>1.7 mm)			Small daphnids (<1.7 mm)		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
(a) Total filter-screen area									
Treatment	1	7.3	0.008	1	6.0	0.017	1	<0.1	0.922
Body length	1	1277.0	<0.001	1	99.9	<0.001	1	319.0	<0.001
Treatment × body length	1	3.3	0.778	1	0.9	0.342	1	1.4	0.234
Error	116			53			60		
(b) Third limb filter-screen area									
Treatment	1	10.1	0.002	1	10.9	0.001	1	0.7	0.404
Body length	1	2572.9	<0.001	1	178.5	<0.001	1	729.8	<0.001
Treatment × body length	1	0.5	0.467	1	2.1	0.153	1	0.5	0.461
Error	237			109			124		
(c) Fourth limb filter-screen area									
Treatment	1	18.3	<0.001	1	9.9	0.002	1	1.9	0.169
Body length	1	1695.3	<0.001	1	153.1	<0.001	1	370.3	<0.001
Treatment × body length	1	4.3	0.038	1	1.3	0.256	1	7.9	0.006
Error	235			109			123		

Treatments represented control or NA + HNA pooled together and were coded 1 and 0, respectively. *Daphnia* body length was the covariate. The interactions between the two variables were used to test for homogeneity of slope, which is an assumption for ANCOVA analysis.

Table II: Averages (± 1 SEM) of the ratio of the filter-screen area (FSA) of the fourth to the third limb, setular density, intersetal and intersetular distances as well as ANOVA results of the comparison between control and NA + HNA treatments pooled together

Variables	Lake (mean ± 1 SEM)	Control (mean ± 1 SEM)	NA + HNA (mean ± 1 SEM)	*P* Control versus NA + HNA
Fourth FSA:third FSA	0.58 ± 0.01	0.55 ± 0.01	0.58 ± 0.01	0.0424
Setular density (no. per μm of setae)	0.16 ± 0.00	0.18 ± 0.00	0.16 ± 0.00	0.1254
Intersetal distance (μm)	91.83 ± 2.11	86.25 ± 1.40	82.66 ± 0.83	0.0189
Intersetular distance (μm)	5.52 ± 0.07	6.16 ± 0.10	6.49 ± 0.09	0.0221

significant for all daphnids ($P < 0.001$; Table I) and large daphnids ($P = 0.002$; Table I), but not for small ones ($P = 0.169$; Table I). Hence, the observed increase in the area of the filter screens of daphnids exposed to high cyanobacterial concentrations and large inedible diatoms was a result of a proportional increase in each of the two pairs of filter screens of the third and fourth limbs in large daphnids. The third and fourth limb filter-screen areas of daphnids in the fertilized enclosures were 12 and 15% larger than the control, respectively (Figure 5). ANOVA indicated that the difference was statistically significant for third ($P = 0.002$) and fourth limbs ($P < 0.001$).

Changes in filter-screen structure

In all the populations, the number of setulae per unit of setae did not increase as filter-screen area increased. The number of setulae attached to setae was stable at around 16–18/100 μm for all the lake, control and treatment populations (Figure 6). There was no detectable difference between control and treatment in setular density

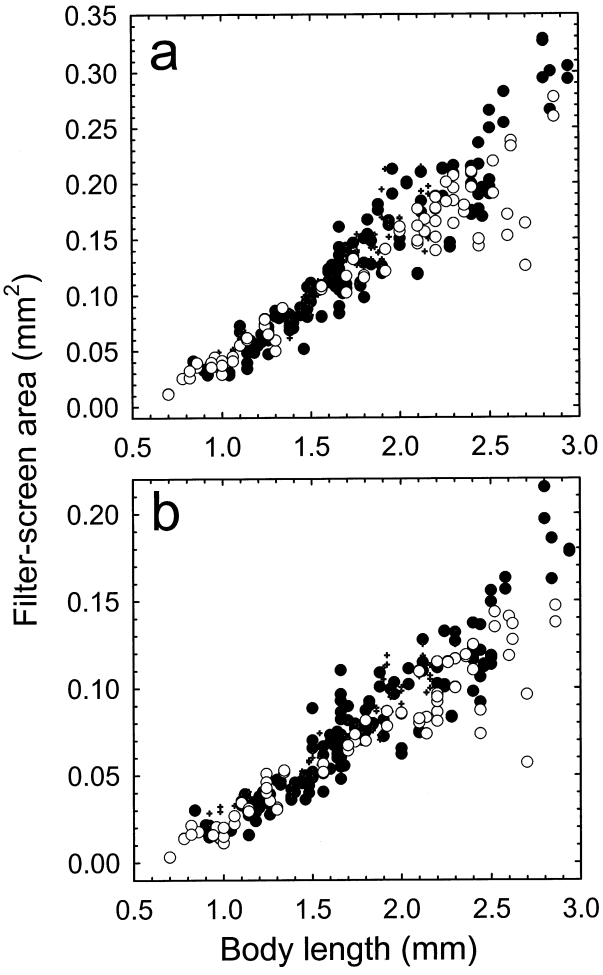

Fig. 4. Filter-screen area of the (a) third (top panel) and (b) fourth limb (bottom panel) of *D. pulicaria* from the lake (crosses), control enclosures (open circles), and NA and HNA treatment enclosures pooled together (solid circles), as a function of body length (top of the head to base of the spine). Outliers are shown on the graphs but not included in the ANCOVA analyses.

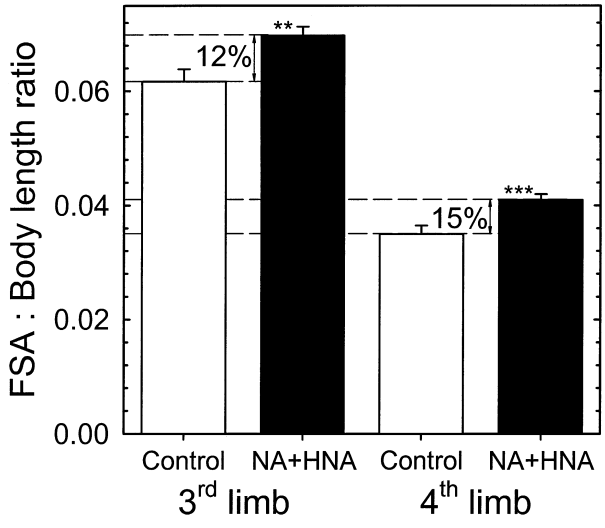

Fig. 5. Third and fourth limb filter-screen area (FSA): body length ratio of *D. pulicaria* from control and treatment enclosures NA and HNA pooled together. The average increase (%) in each FSA relative to the body length is shown. Bars represent means + 1 SEM. ANOVA probabilities are shown on the graph (**$P < 0.01$; ***$P < 0.001$).

($P = 0.125$; Table II). Intersetal distance appears to have decreased by 5% from an average of 86 to 82 μm in control and treatment populations, respectively (Figure 7). The change was statistically significant ($P = 0.019$; Table II). In contrast, intersetular distance showed a 5% increase from 6.2 μm in the control to 6.5 μm in the treatment (Figure 8). The increase was statistically significant ($P = 0.022$; Table II).

DISCUSSION

The phenomenon of enlarging the area of filter screens observed in daphnids and other cladocerans has been interpreted as an adaptive strategy in low food conditions (Koza and Korínek, 1985; Pop, 1991). More recently, Lampert demonstrated that several species of *Daphnia* grown in the laboratory in very low food conditions were able to enlarge the area of their filter screen from 19 to 83% relative to the same clones grown in high food conditions (Lampert, 1994). Here we show that *D. pulicaria* can enlarge their filter-screen area in hypereutrophic conditions with high phytoplankton biomass. These conditions are usually referred to as rich when one considers Chl *a* concentrations as the sole indicator of resource availability without looking at the phytoplankton species composition. In our experimental conditions, nutrient additions enhanced the biomass of large inedible colonial and filamentous species of cyanobacteria and large diatoms, leaving daphnids with only a small fraction of potentially edible particles. A high biomass of large colonial and filamentous cyanobacteria interferes with other algae and renders the gathering of suitable particles difficult for daphnids (Webster and Peters, 1978; Fulton and Paerl, 1987). Our results suggest that daphnids use the same adaptive response to increase the efficiency of food uptake as in very low food conditions or in environments dominated by large inedible phytoplankton. Experimental studies and mathematical modelling have suggested that an enlarged filtering area is a profitable strategy that allows the animals to increase their filtering rate without expending more energy (Lampert and Brendelberger, 1996).

Our results clearly show that both third and fourth limb area increased in the hypereutrophic systems by 12 and 15%, respectively (NA and HNA). In fact, the area of the

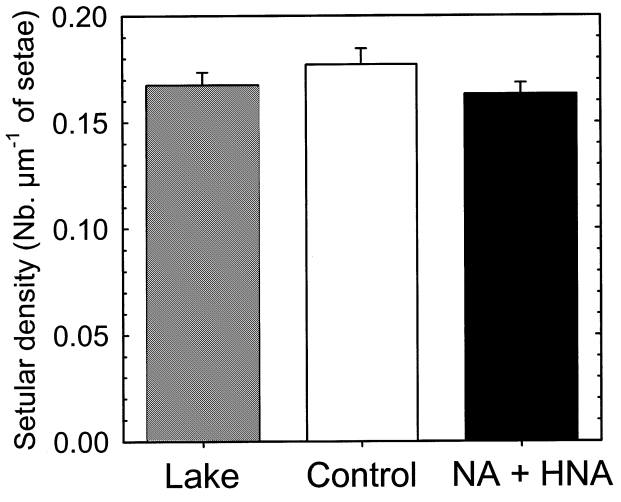

Fig. 6. Setular density expressed in number per micometre of setae for *D. pulicaria* from the lake, control, and NA and HNA enclosures pooled together. Bars represent means + 1 SEM.

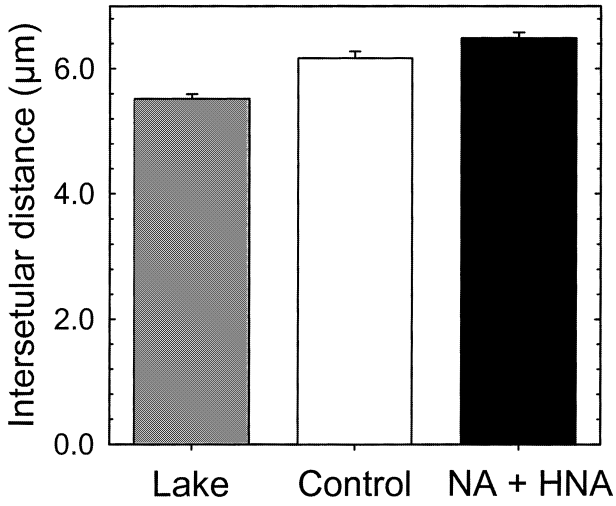

Fig. 8. Intersetular distance (µm) for *D. pulicaria* from the lake, control, and NA and HNA enclosures pooled together. Bars represent means + 1 SEM.

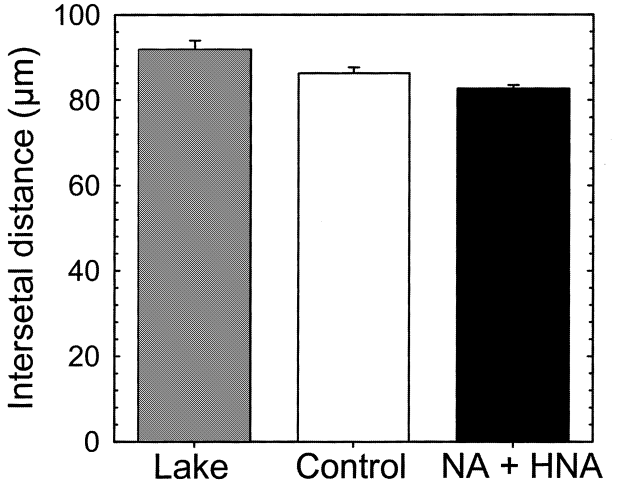

Fig. 7. Intersetal distance (µm) for *D. pulicaria* from the lake, control, and NA and HNA enclosures pooled together. Bars represent means + 1 SEM.

filter screens of the fourth limb is much smaller than that of the third one and any change may be difficult to detect, as reported previously (Pop, 1991). We demonstrate that the increase in the total filter-screen area is a contribution of both third and fourth filter screens. Pioneering studies by Koza and Kořínek have shown that *D. pulicaria* displayed the largest changes in the size of the filtering area in comparison with other species (Koza and Kořínek, 1985). In our experiments, *D. pulicaria* did not show a large change in comparison to species used by Lampert (Lampert, 1994) and which displayed between 19 and 89% increase of their filtering area in very low food conditions. However, our results are comparable to the changes observed in *D. pulicaria* and *Daphnia magna* by Lampert and Brendelberger (Lampert and Brendelberger, 1996). One possible explanation for the difference in response of different species and/or clones of the same species may be attributable to diverse ecological strategies used by particular species and clones in their respective habitats (Koza and Kořínek, 1985; Lampert *et al.*, 1994). A possible alternative explanation may be that daphnids enlarge their filter screen as a continuous function of food condition and in this case they may display greater plasticity in highly contrasted conditions. We believe that our *in situ* experimental conditions did not differ to the same degree as those used in previous laboratory studies, where the low food condition controls were 25-fold lower than the high food conditions (Lampert, 1994). It might be interesting to test whether or not the magnitude of the changes in the filtering area is actually a function of the food scarcity. The answer to this question may have important implications for understanding the evolution of daphnids. Hence, the plasticity of the filtering apparatus of daphnids may fall in the category of reaction norms, such as the predatory-induced cyclomorphic changes observed in several species of the water flea *Daphnia* (Dodson, 1989; Stearns, 1989; Tollrian and Dodson, 1999). Earlier field studies have reported smaller filtering areas for the same *Daphnia* species grown at high food concentration in the laboratory; this difference was explained by the fact that the seston concentration was much higher in the field than in the high food treatments

used in the laboratory experiments (Lampert, 1994). These observations support the hypothesis that the magnitude of the plasticity of the filtering apparatus is a continuous function of the food environment, which supports the reaction norm scenario. However, further experimental testing is needed before one can draw such a conclusion.

Our morphometric measurements show an increase in intersetular distance (or mesh size) with the increase in filtering area. This finding is consistent with the results of previous studies (Brendelberger and Geller, 1985; Lampert and Brendelberger, 1996); however, these authors reported a much smaller mesh size for *D. pulicaria* in comparison with our results. This discrepancy is probably due to the different feeding history and habitat of the daphnids. Geller and Müller proposed a scenario that could explain the highly variable mesh size they observed in their survey of a number of cladoceran species and which could also explain the highly variable mesh size reported in the literature (Geller and Müller, 1981). Their idea was that the seasonal succession of cladoceran species is controlled by the size of the seston available. In environments dominated by small particles, species with finer mesh size would dominate, while those species with coarser mesh size would dominate in large-particle environments. Based on this interpretation, one can speculate that species such as *D. pulicaria*, with a high ability for filtering apparatus plasticity, could adjust their mesh size to maximize their food uptake in a changing environment over the course of a season, for example. The consideration of such mechanisms, after further testing, in our interpretation of food webs would certainly lead to a better understanding of the interactions between zooplankton and their habitat.

Based on previous studies of the phenotypic plasticity of cladocerans and on our own observations, we can conclude that there is consistent evidence that aquatic organisms like daphnids gain benefits from allocating energy to adapt their body size, shape or behaviour to their environmental conditions. Daphnid reactions to environmental changes have been shown to be very rapid and usually take place within a single generation (Pop, 1991; Stibor, 1992; Tollrian, 1993; Lampert, 1994; Stibor and Lüning, 1994; Lampert and Brendelberger, 1996). In aquatic environments, phenotypic plasticity has been described for several different organisms and appeared to be a common strategy used by fish (Day *et al.*, 1994), cladocerans (Dodson, 1989), rotifers (Gilbert, 1966), and even in some phytoplankton species such as *Scenedesmus* (Hessen and Van Donk, 1993; Lampert *et al.*, 1994; Wiltshire and Lampert, 1999) to reduce the impact of predators on their communities. In the case of *Daphnia* filtering apparatus adaptation, it is actually the predator that adapts to the quantity and quality of the prey. While not as extensively studied as the predator-induced changes, this phenomenon is of fundamental ecological and evolutionary significance. In an elegantly designed study, Hairston *et al.* showed, by hatching individuals from ancient dormant ephippia, that *D. pulicaria* that lived in the early 1960s was less resistant to cyanobacteria than the late 1990s one (Hairston *et al.*, 1999). They have interpreted their results as evidence for a rapid evolution induced by the changes in the environment as Lake Constance became more eutrophic and more dominated by cyanobacterial species. However, the mechanisms that are responsible for this rapid evolution are not well known. One possible explanation could be that genotypes that have the ability to cope with cyanobacteria-dominated environments have been selected (Hairston *et al.*, 1999). Another alternative could be that genotypes with the ability to change the size and structure of their filtering apparatus have been favoured by the increasing eutrophication. Hence, it is clear that phenotypic evolution needs special attention and further studies because of the potential implications in theoretical ecology and evolution.

ACKNOWLEDGEMENTS

This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) collaborative special projects grant and University–Industry Cooperative Research and development grant, FCAR and the Québec Ministry of Education. Additional funds were provided by the Terrestrial Riparian Organisms Lakes and Streams project (TROLS) and the Groupe de Recherche Interuniversitaire en Limnologie et en Environnement Aquatique (GRIL) of the Université de Montréal. We are grateful to G. Lazure-Demers and M. Hugues for their help in the laboratory as well as to J. Burke, A. S. McNaught, E. Braun, K. Gibson, S. Manchour, A. Smart and C. Wichuk for field assistance. We warmly thank S. Paquet for analysing phytoplankton samples from this experiments. Our special thanks are extended to L. Pellettier for kindly providing her technical expertise in scanning electronic microscopy for our study and to J.-L. Verville for assistance with photographic processing.

REFERENCES

Bergmann, M. and Peters, R. H. (1980) A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus–chlorophyll–seston relationships. *Can. J. Fish. Aquat. Sci.*, **37**, 111–114.

Bozzola, J. J. and Russell, L. D. (1992) *Electron Microscopy: Principles and Techniques for Biologists*. Jones and Bartlett, Boston.

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

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

Day, T., Pritchard, J. and Schluter, D. (1994) A comparison of two sticklebacks. *Evolution*, **48**, 1723–1734.

De Meester, L., Weider, L. J. and Tollrian, R. (1995) Alternative antipredator defences and genetic polymorphism in a pelagic predator–prey system. *Nature*, **378**, 483–485.

Dodson, S. (1989) Predator-induced reaction norms. *Bioscience*, **39**, 447–452.

Egloff, D. A. and Palmer, D. S. (1971) Size relations of the filtering area of two *Daphnia* species. *Limnol. Oceanogr.*, **16**, 900–905.

Fulton, R. S., III and Paerl, H. W. (1987) Toxic and inhibitory effects of the blue-green alga *Microcystis aeruginosa* on herbivorous zooplankton. *J. Plankton Res.*, **9**, 837–855.

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

Gilbert, J. J. (1966) Rotifer ecology and embryological induction. *Science*, **151**, 1234–1237.

Hairston, N. G., Lampert, W., Caceres, C. E., Holtmeier, C. L., Weider, L. J., Gaedke, U., Fischer, J. M., Fox, J. A. and Post, D. M. (1999) Rapid evolution revealed by dormant eggs. *Nature*, **401**, 446.

Haney, J. G. and Hall, D. F. (1973) Sugar-coated *Daphnia*: a preservation technique for Cladocera. *Limnol. Oceanogr.*, **18**, 331–333.

Hessen, D. O. and Van Donk, E. (1993) Morphological changes in *Scenedesmus* induced by substances released from *Daphnia*. *Arch. Hydrobiol.*, **127**, 129–140.

Koza, V. and Kořínek, V. (1985) Adaptability of the filtration screen in *Daphnia*: Another answer to the selective pressure of the environment. *Ergebn. Limnol.*, **21**, 193–198.

Lampert, W. (1993) Phenotypic plasticity of the size at first reproduction in *Daphnia*: The importance of maternal size. *Ecology*, **74**, 1455–1466.

Lampert, W. (1994) Phenotypic plasticity of the filter screens in *Daphnia*: Adaptation to a low-food environment. *Limnol. Oceanogr.*, **39**, 997–1006.

Lampert, W. and Brendelberger, H. (1996) Strategies of phenotypic low-food adaptation in *Daphnia*: Filter screens, mesh sizes, and appendage beat rates. *Limnol. Oceanogr.*, **41**, 216–223.

Lampert, W., Rothhaupt, K. O. and Vonelert, E. (1994) Chemical induction of colony formation in a green alga (*Scenedesmus acutus*) by grazers (*Daphnia*). *Limnol. Oceanogr.*, **39**, 1543–1550.

Lund, J. W. G., Kipling, G. and LeCren, E. D. (1958) The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia*, **11**, 143–170.

Menzel, D. W. and Corwin, N. (1965) The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnol. Oceanogr.*, **10**, 280–282.

Mitchell, P. and Prepas, E. E. (1990) *Atlas of Alberta Lakes*. The University of Alberta Press, Edmonton, Alberta.

Neill, W. E. (1992) Population variation in the ontogeny of predator-induced vertical migration of copepods. *Nature*, **356**, 54–57.

Pop, M. (1991) Mechanisms of the filtering area adaptation in *Daphnia*. *Hydrobiologia*, **225**, 169–176.

Prepas, E. E. (1978) Sugar-frosted *Daphnia*: An improved fixation technique for Cladocera. *Limnol. Oceanogr.*, **23**, 557–559.

Prepas, E. E. and Rigler, F. H. (1982) Improvements in quantifying the phosphorus concentration in lake water. *Can. J. Fish. Aquat. Sci.*, **29**, 822–829.

Repka, S., Vesela, S., Weber, A. and Schwenk, K. (1999) Plasticity in filtering screens of *Daphnia cucullata galeata* hybrids and parental species at two food concentrations. *Oecologia (Berlin)*, **120**, 485–491.

Stearns, S. C. (1989) The evolutionary significance of phenotypic plasticity. *Bioscience*, **39**, 436–445.

Stibor, H. (1992) Predator induced life-history shifts in a freshwater cladoceran. *Oecologia (Berlin)*, **92**, 162–165.

Stibor, H. and Lampert, W. (1993) Estimating the size at maturity in field populations of *Daphnia* (Cladocera). *Freshwater Biol.*, **30**, 433–438.

Stibor, H. and Lüning, J. (1994) Predator-induced phenotypic variation in the pattern of growth and reproduction in *Daphnia hyalina* (Crustacea: Cladocera). *Funct. Ecol.*, **8**, 97–101.

Stuchlík, E. (1991) Feeding behaviour and morphology of filtering combs of *Daphnia galeata*. *Hydrobiologia*, **225**, 155–167.

Tollrian, R. (1990) Predator-induced helmet formation in *Daphnia cucullata* (Sars). *Arch. Hydrobiol.*, **119**, 191–196.

Tollrian, R. (1993) Neckteeth formation in *Daphnia pulex* as an example of continuous phenotypic plasticity: Morphological effects of *Chaoborus* kairomone concentration and their quantification. *J. Plankton Res.*, **15**, 1309–1318.

Tollrian, R. (1994) Fish-kairomone induced morphological changes in *Daphnia lumholtzi* (Sars). *Arch. Hydrobiol.*, **130**, 69–75.

Tollrian, R. (1995) *Chaoborus crystallinus* predation on *Daphnia pulex*: Can induced morphological changes balance effects of body size on vulnerability? *Oecologia (Berlin)*, **101**, 151–155.

Tollrian, R. and Dodson, S. (1999) Inducible defenses in Cladocera: Constraints, costs, and multipredator environments. In Tollrian, R. and Harvell, C. D. (eds), *The Ecology and Evolution of Inducible Defenses*. Princeton University Press, Princeton, pp. 177–202.

Trimbee, A. M. and Prepas, E. E. (1987) Evaluation of total phosphorus as a predictor of the relative biomass of blue-green algae with emphasis on Alberta lakes. *Can. J. Fish. Aquat. Sci.*, **44**, 1337–1342.

Velleman, P. F. and Welsch, R. E. (1981) Efficient computing of regression diagnostics. *Am. Stat.*, **35**, 234–242.

Webster, K. E. and Peters, R. H. (1978) Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. *Limnol. Oceanogr.*, **23**, 1238–1245.

Wiltshire, K. H. and Lampert, W. (1999) Urea excretion by *Daphnia*: A colony-inducing factor in *Scenedesmus*? *Limnol. Oceanogr.*, **44**, 1894–1903.

Received on April 1, 2001; accepted on February 1, 2002