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Research Article

Differences in efficiency of carbon transfer from dissolved organic carbon to two zooplankton groups: an enclosure experiment in an oligotrophic lake

Jan Karlsson[1,*], David Lymer[2], Katarina Vrede[2,3] and Mats Jansson[4]

[1] Climate Impacts Research Centre (CIRC), Department of Ecology and Environmental Science, Umeå University, SE-981 07 Abisko, Sweden
[2] Limnology/Department of Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Norbyv. 20, SE-752 36 Uppsala, Sweden
[3] Present address: The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning, P.O. Box 1206, SE-11 82 Stockholm, Sweden
[4] Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden

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Abstract. We added dissolved organic carbon (C) in various amounts to 6 enclosures in an oligotrophic subarctic lake to assess how bacterioplankton growth on dissolved organic C affects the growth of calanoid copepod (*Eudiaptomus graciloides*) and cladoceran (*Daphnia longispina*) zooplankton. Organic C was added as glucose (12.5 to 400 µgC L^{-1} d^{-1}) and was isotopically distinct (–11.7‰) from lakewater organic C (<–27.2‰). All enclosures were also enriched with the same amounts of inorganic nitrogen (30 µgN L^{-1} d^{-1} as NH_4NO_3) and inorganic phosphorus (2 µgP L^{-1} d^{-1} as Na_3PO_4). The results showed a direct relationship between bacterial growth on dissolved organic C and incorporation of bacterial biomass into crustacean zooplankton. After 9 days, *D. longispina* and *E. graciloides* contained glucose-C in all treatments and the incorporation of glucose-C by zooplankton was strongly correlated with bacterial growth on glucose-C. $\delta^{15}N$ data revealed different trophic positions of the two crustaceans, suggesting that *D. longispina* fed directly on bacteria while *E. graciloides* incorporated bacterial C by consumption of bacterivorus protozoans. Greater incorporation of glucose-C in *D. longispina* than in *E. graciloides* was explained by higher individual growth rates in *D. longispina*, and this difference between the two zooplankters increased as the bacterial production increased. Thus, the results show that the transfer of dissolved organic C through the food web can be more efficient via cladocerans than via calanoid copepods and that the effect becomes more pronounced as bacterial energy mobilization increases.

Key words. Bacterioplankton production; calanoida copepoda; cladocera; zooplankton growth.

Introduction

A major advance in aquatic research is the recognition that heterotrophic bacterioplankton play an important role in the productivity and function of pelagic food webs. Bacterial growth on phytoplankton exudates (via the microbial loop) can serve as an efficient remobilization of autoch-

* Corresponding author phone: +46 90 786 7769;
fax: +46 90 7866705; e-mail: Jan.Karlsson@emg.umu.se
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thonous carbon (C) for metazoans (Wyllie and Currie, 1991). Bacterial growth on allochthonous organic C (Tranvik, 1988) can also constitute a significant energy source for crustacean zooplankton (Grey et al., 2001; Karlsson et al., 2003). This source is of particular importance since bacterial growth on allochthonous organic C can be regarded as mobilization of new energy, for use by higher trophic levels, in analogy with photosynthesis (Jones, 1992).

The effect of high bacterial energy mobilization on the productivity of higher trophic levels is poorly known. However, the small size and high phosphorus (P) content of bacteria implies that bacteria based food webs may exert different effects on crustacean growth compared with phytoplankton based food webs. The transfer of dissolved organic C via bacteria occurs either by direct feeding on bacteria (e. g. cladocerans) or through intermediate bacterial consumers (e. g. protists to copepods) (Pace et al., 1990; Karlsson et al., 2004). Such differences in trophic position between crustaceans suggest that the transfer efficiency of bacteria generated organic C within the food web depends on the species composition of the crustacean zooplankton community (Pace et al., 1990; Wyllie and Currie, 1991). Also, different trophic routes of crustaceans suggest different responses in zooplankton growth along gradients in bacterial energy mobilization. It has been shown that cladocerans grow faster than copepods when algal food quantity increases and that the effect is more pronounced with greater food quality (Richman and Dodson, 1983; Lambert and Muck, 1985; Sterner and Hessen, 1994). However, it is not known how gradients in heterotrophic bacterial production or energy mobilization may affect the growth of crustaceans. Because of the presumed high P content of bacteria, it could be expected that high bacterial production should be particularly favourable for the growth of bacterivorous cladocerans such as daphnids, which have high P requirements relative to copepods (Sterner and Hessen, 1994).

This study tested the hypothesis that differences in bacterial growth on dissolved organic C should be reflected in zooplankton growth and that the response should be more pronounced in cladocerans than in copepods as bacterial productivity increases. We added dissolved organic C (glucose) and inorganic nutrients to lake water enclosures in an unproductive lake in northern Sweden to stimulate bacterial growth. The added glucose-C had a stable carbon isotope signal ($\delta^{13}C$) distinct from that of organic C present in the lake and we used stable isotopes to follow incorporation of glucose-C via bacteria into zooplankton.

Materials and methods

Experimental design

The experiment was conducted in a subarctic lake (lake Diktar Erik, mean depth 5 m, max. depth 16 m, area 0.1 km^2) near Abisko in northern Sweden (68°27′N, 18°36′E) during 9 days from June to July 2003. Eight epilimnion enclosures (300 L plastic bags, open top, closed bottom) were filled with lake water from 1 m depth and anchored in the lake. To ensure the same starting conditions in all enclosures, we added the water to the enclosures in portions of 30 L to all enclosures until all enclosures were filled (i. e. 10 rounds with 30 L in each enclosure). Analysis of the lake water at the start of the experiment revealed nutrient poor conditions (dissolved organic C: 4.2 mg C L^{-1}, total nitrogen (N): 270 µg N L^{-1}, dissolved inorganic N: 26 µg N L^{-1}, total P: 4 µg P L^{-1}) and no difference between enclosures (data not shown). The mid day water temperature in the enclosures during the course of the experiment was between 16.6 and 18.7 °C. Organic C in the form of glucose was added daily (12.5, 25, 50, 100, 200, 400 µg C L^{-1} d^{-1} during 9 days, $\delta^{13}C_{glucose}$ = –11.7‰) to 6 different enclosures (T2 to T6) forming a gradient (a total of 0.11 to 3.60 mg of added C L^{-1}, Table 1). The enclosures also received daily additions of N (30 µg N L^{-1} d^{-1} as NH_4NO_3, $\delta^{15}N$ = –0.2‰) and P (2 µg P L^{-1} d^{-1} as Na_3PO_4) in order to alleviate potential inorganic nutrient limitation, thereby revealing the flux of organic C between different trophic levels. One enclosure received no additions (control) and one enclosure (T1) received only N and P as a control for the effect of inorganic nutrient additions on primary production (PP), bacterioplankton production (BP) and isotopic composition of zooplankton.

The crustacean zooplankton community consisted of the cladoceran *Daphnia longispina* (1 ind. per L) and the calanoid copepod *Eudiaptomus graciloides* (5 ind. per L), two common species in lakes of the region (Nauwerck, 1994; Karlsson et al., 2004). The mean individual weight (W_1) of the zooplankton at the start of the experiment was small (*D. longispina* W_1 = 1.8 ± 0.9 µg C, *E. graciloides* W_1 = 3.4 ± 1.4 µg C) compared to what is observed later in the season for these species (Karlsson, unpubl. data); we assumed that an increase in zooplankton resources should be reflected in growth of individual zooplankton. We used stable isotopes to trace the incorporation of glucose-C into zooplankton during the experiment. The $\delta^{13}C$ of the added glucose (–11.7‰) was clearly ^{13}C enriched compared to natural organic C, but similar to inorganic C in the lake water (Karlsson et al., 2003; unpubl. data). Here we assumed that glucose addition changed the $\delta^{13}C$ of the external organic C source used by bacterioplankton but did not affect the $\delta^{13}C$ of phytoplankton generated organic C during the course of the experiment. Thus, changes in zooplankton $\delta^{13}C$ in the glucose treatments ($\delta^{13}C_{zoo}$) compared to that with only N and P added ($\delta^{13}C_{T1}$) is assumed an effect of incorporation of isotopically heavy glucose-C. The duration of the experiment (9 days) was presumed to be sufficient for incorporation of glucose-C into zooplankton biomass but

not long enough to let the zooplankton reach isotopic equilibrium with the $\delta^{13}C$ of their food source. The incorporation of glucose-C in zooplankton during the experiment should be due to zooplankton biomass increase and the glucose-C content in the zooplankton food. We use the results to estimate zooplankton growth rate and compare this estimate between species and treatments.

Analysis and calculations

Samples were collected from each enclosure on day 4, 7 and 10 for estimation of bacterial cell size (preserved with formaldehyde) and phytoplankton biomass and species composition (preserved with Lugol's solution). Determination of bacterioplankton cell size was performed with an epifluorescence microscope after staining lake water with acridine orange solution. Species composition and biomass of phytoplankton were determined using an inverted phase-contrast microscope, after overnight sedimentation in 10 mL of water (Olrik et al., 1998). The phytoplankton community was divided into obligate autotrophic, mixotrophic and heterotrophic functional groups following Jansson et al. (1996).

PP and BP were measured on day 1, 4, 7 and 10. The enclosures were gently mixed and a water sample was collected from each enclosure for analysis of PP and BP. PP was measured during mid-day (4 h) incubations at 0.1, 0.5 and 1.5 m depth using the ^{14}C method (Schindler et al., 1972), and is reported as net production of organic material. The production for the 4 h incubation period was extrapolated to daily values using the ratio of incident PAR irradiation during the incubation in relation to whole day irradiation of PAR (continuously measured at the Abisko Scientific Research Station situated 10 km from the study lake) following Karlsson et al. (2002). BP was measured by a modified version of the leucine incorporation method described by Smith and Azam (1992; see Karlsson et al., 2002 for details). Leucine saturation experiments were performed in a pilot study before the experiment started (nutrient additions as above) and during the experiment. The experiments showed that a final leucine concentration of 73 nM was enough to saturate leucine uptake in the enclosure experiment (data not shown). The leucine incorporation was converted into bacterial carbon production according to Simon and Azam (1989). From the PP and BP measurements, we calculated the total production of phytoplankton and bacterioplankton for the whole enclosure for the entire incubation period.

The total pelagic energy mobilization (PEM) was calculated by adding net PP and net BP based on exogenous C sources (allochthonous organic C and glucose-C). The calculation followed Jansson et al. (2003) and assumed a bacterial growth efficiency (BGE) of 26 % (del Giorgio and Cole, 1998) and that 37 % of net PP is available as a C source for BP (Lampert, 1978; Baines and Pace, 1991). The BP based on glucose-C ($BP_{glucose}$) in each treatment was estimated by subtracting BP on natural substrates (BP_{T1}) and the BP based on the PP increase in the treatment (assumptions as above) from measured BP ($BP_{glucose} = BP - (BP_{T1} + BP_{based\ on\ PP\ in\ treatment})$). The fractions of BP ($fBP_{glucose}$) and PEM ($fPEM_{glucose}$) supported by glucose-C in the treatments were estimated by division of $BP_{glucose}$ with the total BP ($fBP_{glucose} = BP_{glucose}/BP$) and PEM ($fPEM_{glucose} = BP_{glucose}/PEM$). All production calculations were based on integrated production values over the 9 days. We tested the uncertainty of the assumptions by using BGE of 5 to 37 % and an availability of PP for BP of 28 to 46 % (Jansson et al., 2003).

After 9 days zooplankton were collected by vertical hauling using a plankton net with a mesh size of 100 µm and stored in 0.2 µm filtered (tangential flow filtration) lake water (12 to 24 h) for gut evacuation. The crustacean zooplankton species were manually separated and washed with distilled water and dried (65 °C). Analyses of stable isotopes were carried out using a Carlo Erba EA 1108 elemental analyzer connected to a Fison Optima isotope ratio mass spectrometer at continuous flow. Results are expressed by the δ notation in per mil (‰) as $\delta = (R_{sample}/R_{standard} - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ or $^{15}N/^{14}N$. The analytical precision was below 0.3 ‰.

The fraction of the zooplankton C composed of glucose-C ($fZoo_{glucose}$) in each treatment was estimated as:

$$fZoo_{glucose} = (\delta^{13}C_{zoo} - \delta^{13}C_{T1})/(\delta^{13}C_{glucose} + (TP - 1) \times F - \delta^{13}C_{T1}) \quad (1)$$

assuming that the different $\delta^{13}C$ of zooplankton in the glucose treatments ($\delta^{13}C_{zoo}$) compared to that in the treatment with only N and P ($\delta^{13}C_{T1}$) was an effect of incorporation of glucose-C ($\delta^{13}C_{glucose}$). We adopted a trophic fractionation between zooplankton and its diet (F) of 0.4 ‰ (Post 2002) and assumed *D. longispina* and *E. graciloides* to be primary (trophic position (TP) = 2) and secondary consumers (TP = 3) respectively (Karlsson et al., 2004). The assumptions of TP involve a small potential error in the results presented (e. g. ±1 zooplankton TP corresponds to <1 % variation in $fZoo_{glucose}$).

The zooplankton individual specific growth rate (k) for the experimental period t was calculated from the increase in weight during the experiment ($k = \ln(W_{10}/W_1)/t$)). The mean individual weight of cladocerans and copepods in each glucose-C treatment at day 10 (W_{10}) was calculated as:

$$W_{10} = W_1 + W_1 \times (\delta^{13}C_{T1} - \delta^{13}C_{zoo})/(\delta^{13}C_{zoo} - (\delta^{13}C_{food} + (TP - 1) \times F)) \quad (2)$$

where we assume that the change in zooplankton $\delta^{13}C$ compared to in T1 was an effect of incorporation of new biomass. The $\delta^{13}C$ of the food ($\delta^{13}C_{food}$) of *D. longispina* and *E. graciloides* was set equal to the $\delta^{13}C$ of organic matter supplied by PEM in each enclosure (this was the

case in the control and in T1 as estimated following Karlsson et al., 2003). The $\delta^{13}C_{food}$ was calculated as:

$$\delta^{13}C_{food} = fPEM_{glucose} \times \delta^{13}C_{glucose} + (1\text{-}fPEM_{glucose}) \times \delta^{13}C_{PEM\ T1} \quad (3)$$

where the $\delta^{13}C$ of PEM in the T1 ($\delta^{13}C_{PEM\ T1}$) was set to –31.4‰ which is the mean for the food source of *D. longispina* (–31.5‰) and *E. graciloides* (–31.3‰).

Results and discussion

The mean size of bacteria showed a small variation among treatments (mean ± 1 SD: 0.045 ± 0.003 µm^3). The phytoplankton community was composed of a mixture of mixotrophic (mean ± 1 SD: 48.9 ± 7.3 µg C L^{-1}, e. g. *Dinobryon sp., Ochromonas sp.*), obligate autotrophic (33.8 ± 26.4 µg C L^{-1}, e. g. *Chlamydomonas sp., Snowella sp.*) and heterotrophic (1.4 ± 0.6 µg C L^{-1}, e. g. *Katablepharis ovalis*) functional groups with no significant ($p < 0.05$) correlations between absolute or relative composition of biomass and the glucose-C addition. BP and PP increased in the treatments with C addition (T2–T7) compared to the control and the treatment with only N and P (T1, Table 1, Fig. 1A). The BP increase per added C became progressively lower with increasing C addition, indicating increasing inorganic nutrient limitation of bacterial growth with increasing C addition. The bacterial C:P ratio (molar) increased from 16 to 111 from low to high C additions in our experiment (Jansson et al., 2006). Thus, the largest effect on both bacterioplankton and phytoplankton by the glucose and inorganic nutrients treatment was on biomass production (Table 1) and stoichiometry (only estimated for bacteria) rather than on the size structure or phytoplankton species composition. The increase in PP (Table 1) was not sufficient to support BP. Thus, the BP increase in the glucose treatments was mainly due to bacterial growth on the added glucose-C (Fig. 1B), causing an increase in PEM with C addition (Table 1). We estimated that glucose-C supported between 47 and 84 % of BP and between 31 and 66 % of PEM (Fig. 1B). These percentages are similar to what is typically measured for the allochthonous organic C contribution to BP and PEM in lake Diktar Erik (lake no. 5 in Jansson et al., 2003) and what was measured in the control of the present study (Table 1). The uncertainties introduced in the calculation of PEM, $fBP_{glucose}$ and $fPEM_{glucose}$ by assumptions of BGE and availability of PP for BP were low (Table 1 and Fig. 1B).

Daphnia longispina and *Eudiaptomus graciloides* had similar $\delta^{13}C$ in the treatment (T1) with only N and P (–31.1‰ v.s. –30.5‰) as in the control (–31.3‰ v.s. –31.1‰), although the BP and PP were doubled. Given the suggested large differences in $\delta^{13}C$ of allochthonous (–27.2‰) and autochthonous (–43‰) organic C in the lake water, this result showed that the proportion of the two C sources was the same in the food of the two species at isotopic equilibrium (cf Karlsson et al., 2003). Zooplankton $\delta^{13}C$ increased with increasing glucose-C addition (Table 1), suggesting that zooplankton acquired isotopically heavy glucose-C. The incorporation of glucose-C in *D. longispina* was approximately twice that by *E. graciloides* for most C enrichments (Fig. 1B). The $fZoo_{glucose}$ increase with the amount of added glucose was not linear (Fig. 1B). Instead we found a highly significant linear relationship ($r^2 = 0.97$, $p < 0.001$) between $fZoo_{glucose}$ and BP (Fig. 2). Since the BP was mainly supported by glucose-C (Fig. 1B), this result shows that glucose-C was incorporated in zooplankton via bacteria. Consequently, $fZoo_{glucose}$ was also linearly correlated to the estimated BP on glucose ($r^2 = 0.97$, $p < 0.001$).

Table 1. Enclosure experiment in lake Diktar Erik conducted during 9 days in June and July 2003. Total glucose-C addition, integrated values on bacterial production (BP), primary production (PP) and estimated pelagic energy mobilization (PEM, with ranges obtained by assuming different values on bacterial growth efficiency and PP availability for BP), and stable isotopic (C, N) composition of *Daphnia longispina* and *Eudiaptomus graciloides*. N (270 µg L^{-1}) and P (18 µg L^{-1}) were added to all enclosures except the control.

Enclosure	C-addition	BP	PP	PEM	*D. longispina*		E. graciloides	
	(mg C L^{-1})	(µg C L^{-1} d^{-1})	(µg C L^{-1} d^{-1})	(µg C L^{-1} d^{-1})	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Ctrl	0	5	4	9 (9–10)	–31.3	3.6	–31.1	5.4
T1	0	12	11	22 (21–23)	–31.1	0.7	–30.5	1.8
T2	0.11	23	14	35 (34–37)	–29.2	–0.2	–29.1	1.9
T3	0.23	33	13	45 (44–46)	–27.6	–0.2	–28.5	2.4
T4	0.45	43	15	57 (55–58)	–26.5	–0.3	–28.2	3.1
T5	0.90	54	24	76 (74–77)	–25.2	0.5	–27.7	3.5
T6	1.80	65	22	85 (83–87)	–23.5	1.3	–26.6	3.8
T7	3.60	83	25	106 (104–108)	–22.7	1.3	–26.1	3.9

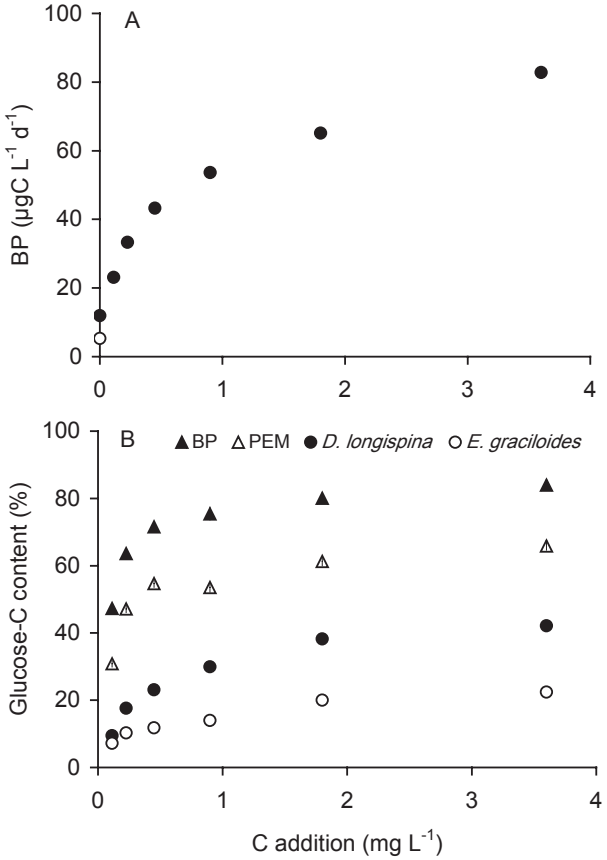

Figure 1. (A) Integrated bacterial production (BP), and (B) estimated fraction of glucose-C in BP, pelagic energy mobilization (PEM), *Daphnia longispina* and *Eudiaptomus graciloides* in enclosures receiving various C additions ((A) also includes control (open symbol) and T1 enclosures). The uncertainty introduced by the assumptions in calculating the glucose-C content in BP and PEM were below 2 % (i. e. too low to appear in all points in the figure).

The $\delta^{15}N$ of both *D. longispina* (–0.2–1.3‰) and *E. graciloides* (1.9–3.9‰) increased from low to high C-additions (Table 1). We interpret this increase as being mainly caused by increasing fractionation during N uptake in the energy mobilizers (bacteria and phytoplankton) rather than in variation in diet and trophic position of zooplankton. We base this interpretation on the assumption that both phytoplankton and bacterial N fractionation is lower during N-deficiency (Owens, 1987). Since all treatments in our experiment contained the same amount of N, the $\delta^{15}N$ of bacteria and phytoplankton should reflect a gradual increase in the relationship between N demand and N supply and can be expected to be higher with increasing C addition. However, despite the higher $\delta^{15}N$ of both zooplankters in high glucose-concentration treatments, the $\delta^{15}N$ was between 2.1 to 3.3‰ lower in *D. longispina* than in *E. graciloides* in enclosures with added glucose (Table 1). Although isotopic equilibrium was not obtained and the exact difference in $\delta^{15}N$ is not known, this result strongly suggests a higher trophic position of *E. graciloides* than *D. longispina* consistent with previous reports (Karlsson et al., 2004). Current data suggest that *D. longispina* derived a considerable portion of bacterial synthesized C by direct feeding on bacteria while *E. graciloides* mainly obtained bacterial C by feeding on bacterivores such as flagellates and ciliates.

The increase in zooplankton glucose-C content with increasing BP could have been an effect of an increasing proportion of glucose-C in the diet of zooplankton or an increasing zooplankton growth on the glucose-C with increasing BP. We calculated that *D. longispina* growth increased as the food supply (PEM) increased ($r^2 = 0.96$, $p < 0.001$, slope = 0.00114), while the growth rate of *E. graciloides* showed small variation among enclosures and a weaker relationship ($r^2 = 0.62$, $p = 0.065$, slope = 0.00022) with the food supply (Fig. 3). For this calculation we assumed that the proportion between the basal energy sources (phytoplankton and bacteria) was the same in the food of the crustacean species. Even if we assume that *D. longispina* fed on a high glucose-C diet corresponding to that of bacteria only (Fig. 1B), *D. longispina* still showed considerably higher growth rates than *E. graciloides* (Fig. 3, $p < 0.001$). Thus, the experiment showed that increased bacterial production likely caused increased individual growth rates in *D. longispina* but exerted little effect on *E. graciloides*.

The estimated differences in growth rates with increasing food concentration in the experiment are consistent with previously reported results showing increasing growth rates in daphnids but not in calanoid copepods as a response to increasing phytoplankton concentration (Richman and Dodson, 1983; Lambert and Muck, 1985). Here we show that this pattern also apply to bacterial based food webs. The strong increase in the growth rates

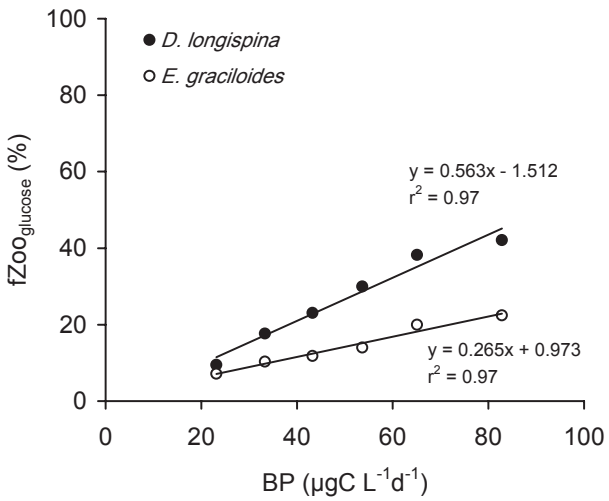

Figure 2. Zooplankton glucose-C content ($fZoo_{glucose}$) in relation to bacterial production (BP) in enclosures receiving glucose-C.

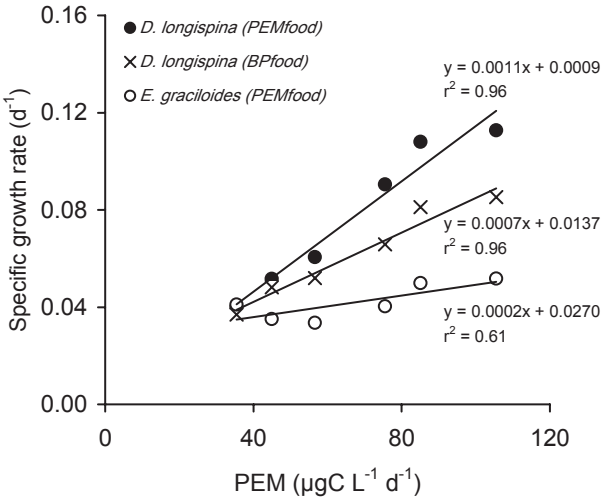

Figure 3. Estimated individual specific growth rate of zooplankton as a function of the pelagic energy mobilization by bacterioplankton and phytoplankton (PEM) in enclosures receiving glucose-C. Zooplankton food $\delta^{13}C$ were assumed to correspond to the $\delta^{13}C$ of organic carbon generated by PEM (PEMfood) or bacterioplankton production (BPfood).

of *D. longispina* in response to increasing bacterial growth may have been a consequence of high food quality (Sterner and Hessen, 1994). P is recognized as a key limiting element for the growth of daphnids. The C:P ratio of bacteria (C:P molar ratio = 16–111, Jansson et al., 2006) in the experiment were well below the critical threshold C:P ratio for P limited growth reported for *Daphnia* elsewhere (225–375, Brett et al., 2000), suggesting that the quantity rather than the quality of the food regulated the growth of *D. longispina* in the present experiment and allowed for a strong increase in the growth of *D. longispina* in response to increased food supply.

In conclusion, our experiment shows a direct relationship between bacterial growth and the incorporation of bacterial biomass into crustacean zooplankton. Although the results were formed by the enrichment with glucose-C, N and P that enhanced bacterial and phytoplankton production to unnatural levels, we had a ratio of bacterial to phytoplankton production similar to nearby lakes (Karlsson et al., 2002). The experiment should, therefore, be representative for how different planktonic energy mobilizers were used by the zooplankton grazers. In systems with high bacterioplankton energy mobilization from allochthonous organic C, heterotrophic food chains can contribute substantially to the production of higher trophic levels and sustain a higher secondary production than PP and the microbial loop alone (cf. Meili et al., 1996; Grey et al., 2001; Karlsson et al., 2003). Our study demonstrated different trophic positions of the crustaceans, which, together with previous studies (Karlsson et al., 2004), suggests that *D. longispina* were feeding directly on bacteria, while *E. graciloides* mainly obtained bacterial C via an additional link in the food chain. These differences in diet and trophic position imply a more efficient transfer of bacterial organic C to higher trophic levels via *D. longispina* than via *E. graciloides* (Pace et al., 1990; Wyllie and Currie, 1991). Moreover, *D. longispina* (but not *E. graciloides*) responded to increased bacterial production by increased individual growth rates in our experiment. Thus it is possible that daphnids, which feed directly on bacteria, are favoured relative to calanoid copepods, as *E. graciloides*, in lakes where the pelagic energy mobilization to a large extent is based on bacterioplankton use of allochthonous organic C, and that this effect becomes more pronounced as the bacterial production increase.

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