

Phytoplankton phosphorus limitation and food quality for *Bosmina*

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Abstract

Recent studies have demonstrated that *Daphnia*, a cladoceran (anomopod) zooplankton species with a high phosphorus content, can become P limited when fed algae deficient in phosphorus. *Bosmina* is another common anomopod zooplankton, but its body has a lower percentage of P than does that of *Daphnia*, and *Bosmina* might therefore be less susceptible to P mineral limitation. To test for this hypothesized interspecific difference in nutrition, *Bosmina* and *Daphnia* were raised on two food types: P-deficient or P-sufficient *Scenedesmus acutus* in two concentrations (0.2 or 1.0 mg C L⁻¹). As predicted by its lower P content, *Bosmina* growth and fecundity were not affected by the P content of algal food, even though P-deficient food caused significant declines in these life history parameters for *Daphnia*. Results suggest that *Bosmina* has a lower P requirement than does *Daphnia* and that *Bosmina* may process phosphorus more efficiently or be better able to survive losses in body P content. The outcome of competition between *Bosmina* and *Daphnia* therefore might shift in favor of low-P-content zooplankton such as *Bosmina* under conditions of seston P mineral limitation.

“Food quality” can be a nebulous term. Historically, investigators categorized an algal species as high in food quality if zooplankton grew well on a laboratory-cultured clone of that species (e.g., Taub and Dollar 1968; Schwartz and Ballinger 1980). Clearly many factors are important in determining algal food quality for zooplankton. For example, algal size (e.g., Burns 1968; Holm et al. 1983; Knisely and Geller 1986), edibility or digestibility (Porter 1973, 1975; Horn 1981; Burns et al. 1989; van Donk and Hessen 1993), toxin production (Porter and Orcutt 1980; Lampert 1981; Burns et al. 1989), and biochemical composition (fatty acids, Ahlgren et al. 1990; Müller-Navarra 1995; DeMott and Müller-Navarra 1997; Weers and Gulati 1997; Weers et al. 1997) have all been shown to influence food quality for zooplankton. Recently, several studies have demonstrated that algal mineral phosphorus (P) content is another potentially important contributor to zooplankton food quality (e.g., Sterner 1993; Sterner and Hessen 1994).

Several observations led to the hypothesis that the P content of algal food is important for zooplankton. First, despite a large (10-fold) variation in freshwater algal carbon:phosphorus (C:P) ratio (Hecky and Kilham 1988), individual zooplankton species sampled at different locations and seasons have relatively constant body C:P (Andersen and Hessen 1991; Sterner and Hessen 1994). Furthermore, the intraspecific differences in zooplankton C:P are less than the interspecific differences (Hessen and Lyche 1991), suggesting that individual zooplankton species maintain relatively stable and unique C:P body ratios despite widely varying algal stoichiometry (Sterner 1990).

Acknowledgments

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The anomopod zooplankton *Daphnia* has a particularly high body P content (~1.5% dry weight; Hessen and Andersen 1990; Main et al. 1997; DeMott et al. 1998). Many studies have demonstrated that *Daphnia* growth, age at first reproduction, fecundity, and survivorship are depressed when the animal is fed low-P food (Hessen 1992; Sterner 1993; Sterner et al. 1993). Under experimental conditions of extremely high soluble reactive phosphorus, *Daphnia* uptake of inorganic P remediates growth limitation. This growth enhancement with inorganic P addition lends support to the hypothesis that mineral P, and not some biochemical correlate of algal P limitation, is responsible for the observed food quality responses in *Daphnia* (Urabe et al. 1997).

Models based on optimal nutrient ratios have been used successfully to predict phytoplankton species composition (e.g., Tilman 1982; Tilman et al. 1982; Smith 1983; Sommer 1983), indicating the importance of the ratio of available nutrients to phytoplankton dynamics. Because zooplankton are homeostatic and may have specific elemental requirements (Sterner 1990; Hessen 1992), nutrient ratios may influence zooplankton competition as well. Clearly, the high P content of *Daphnia* is influenced strongly by mineral P limitation of its phytoplankton food. Based on the homeostatic model, one would predict that zooplankton with a lower P content would have a lower P requirement than does *Daphnia*. *Bosmina* is also an anomopod crustacean, but it has a much lower P content (~0.7% dry weight; Hessen and Lyche 1991), so one would predict that it should not be as easily limited by low-P algal food. We investigated *Bosmina* responses to food quantity and food P concentration, using experiments similar to those demonstrating P limitation in *Daphnia* (Sterner 1993). Based on stoichiometry, we predicted that *Bosmina* life history parameters (growth and fecundity) should be less susceptible than those of *Daphnia* to limitation of mineral P.

Methods

The experiment was set up in a 2 × 2 × 2 factorial design, with two levels of phytoplankton P content (food quality),

two phytoplankton density treatments (food quantity), and two experimental species (*Bosmina* and *Daphnia*). The phytoplankton *Scenedesmus acutus* (Chlorophyta) was grown in chemostats on COMBO medium (Kilham et al. 1998) under different nutrient loading ratios to produce foods of different C:P ratios, as described elsewhere (Sterner et al. 1993). One benefit of the COMBO medium is that it can be used for culturing both phytoplankton and zooplankton. The *Bosmina* therefore were raised in basal COMBO (COMBO medium without nitrogen or P) with added phytoplankton food from the chemostats.

The two food types used were high P content (HIP, identical to "MON" of Sterner et al. 1993), with a C:P of ~150:1, and severely P limited (LOP), with a C:P of ~1,600:1. The C:P of the food was measured by filtering chemostat outflow onto replicate precombusted (550°C) acid-washed GF/F filters. The C analysis was performed on a CHN analyzer (Perkin Elmer), and P was measured spectrophotometrically after digestion with potassium persulfate (Langner and Hendrix 1982). The two food quantities were 200 $\mu\text{g C L}^{-1}$ and 1000 $\mu\text{g C L}^{-1}$. These concentrations bracket the incipient limiting levels reported for *Bosmina longirostris* (somewhat above 250 $\mu\text{g C L}^{-1}$; Urabe 1991a) and for *Daphnia* (200–500 $\mu\text{g C L}^{-1}$; Lampert 1987), without being so low as to result in starvation. Phytoplankton concentrations were estimated from standard curves of *S. acutus* chemostat culture absorbance at 800 nm versus C concentration of the culture for each food type. Published clearance rates for *B. longirostris* indicate that <5% of the added phytoplankton should have been cleared each day (Urabe 1991b). In vivo fluorescence and cell counts of the cultures also confirmed that phytoplankton concentrations did not decrease substantially in any treatment (daily decreases during incubation averaging only 4%).

Three experimental trials were run with the bosminid *Bosmina* (*Sinobosmina*) *leideri* (formerly identified as *Bosmina longirostris* complex but reclassified by De Melo and Hebert 1994), for a total of 45 animals per treatment. One *B. (S.) leaderi* trial was run simultaneously with a trial of *Daphnia magna* (10 *Daphnia* per treatment). The purpose of testing both species was twofold: (1) to verify that *Scenedesmus acutus* used in these experiments induced the same dramatic responses in *Daphnia* as had been observed previously and (2) to determine whether the batch culture conditions used in the *Bosmina* trials produced different responses in *Daphnia* than did the continuous culture methods employed in the original study of *Daphnia* (Sterner 1993).

Females from laboratory cultures of *Bosmina* (*Sinobosmina*) *leideri* and *D. magna* were isolated and raised on HIP at 1,000 $\mu\text{g C L}^{-1}$. Prior to the experiments, females with late stage embryos (stage 5, black-eyed; Threlkeld 1979) were identified and isolated, and neonates were added to the treatment vials within 12 h of parturition. Siblings were assigned randomly to different treatments. Individual *B. leaderi* were raised in glass scintillation vials (~25 ml volume) with polyseal caps. These vials were filled completely to avoid air bubbles because air bubbles often trap *B. leaderi* in the surface tension. Individual *D. magna* were reared in sealed 60-ml culture tubes with Teflon-lined caps. Although air bubbles did not appear to pose a hazard to the larger *D.*

magna, these culture tubes were also filled to the top. Both types of vials were placed in roller bottles on a roller deck turning horizontally at 1 rpm and were incubated at 20°C in the dark.

Every day, zooplankton were removed from the vials with a pipette and examined under a compound microscope; organism length was measured with an ocular micrometer, and visual lipid-ovary index (Tessier and Goulden 1982), fecundity, and overall condition were noted. The medium in each vial was discarded and replaced with appropriate fresh treatment medium. Zooplankton were returned to the vials by pipetting. Any *B. leaderi* that became stuck in the surface tension were released by dropping additional medium on top of them, and the vials were filled and resealed.

Trials proceeded until the first animals reached maturity (5–6 days). At this point, the daily animal length, lipid, and fecundity measurements were taken again, and then the animals were used for dry mass determination in two of the three trials. The zooplankton to be weighed were placed on aluminum boats and dried in a 60°C oven for at least 24 h. The dried animals were stored in a desiccator until weighed individually on a Mettler UMT2 ultramicrobalance ($\pm 0.2 \mu\text{g}$). Growth rate (g) was determined as:

$$g = [\ln(M_t) - \ln(M_0)]/t \quad (1)$$

where M_t is the final measured body mass, M_0 is the initial body mass (estimated from initial lengths and a length-weight regression of animals in the laboratory culture), and t is the duration of the experimental trial (in days). The results of the three *Bosmina* trials were combined for analysis. Statistical tests were performed using STATISTICA (Statsoft) and SYSTAT version 7.0 (SPSS). Residuals of all ANOVAs were examined to ensure that they met model assumptions.

Results

There were differences in the patterns of growth, as measured by length over time, between *D. magna* and *B. leaderi* (Fig. 1). Over the course of the entire experiment, *D. magna* length was affected significantly by food treatment (repeated measures ANOVA between-subjects effects, $n = 38$, $F = 13.522$, $P < 0.001$). The overall food quality (P content) effect was significant, but food quantity was not (repeated measures ANOVA between-subjects effects, $n = 38$: quality effect $F = 17.869$, $P < 0.001$; quantity effect, $F = 0.178$, $P = 0.178$). Specifically, *D. magna* grown in the HIP treatments were significantly longer than those raised on LOP food (Bonferroni post hoc pairwise comparison with adjusted significance levels, $df = 35$, $P < 0.001$). Similarly, *D. magna* fed high quantity HIP were significantly longer than those in the low quantity treatment (Bonferroni, $df = 35$, $P < 0.001$); however, there was no significant difference between length in the low and high quantity LOP treatments (Bonferroni, $df = 35$, $P = 0.959$; Fig. 1A). In contrast, *B. leaderi* showed no significant differences in length between any of the food quality (P content) or food quantity treatments (repeated measures ANOVA between-subjects effects, $n = 101$, $F = 0.402$, $P = 0.752$, Fig. 1B).

Growth rates (g , Eq. 1) calculated from mass gain showed

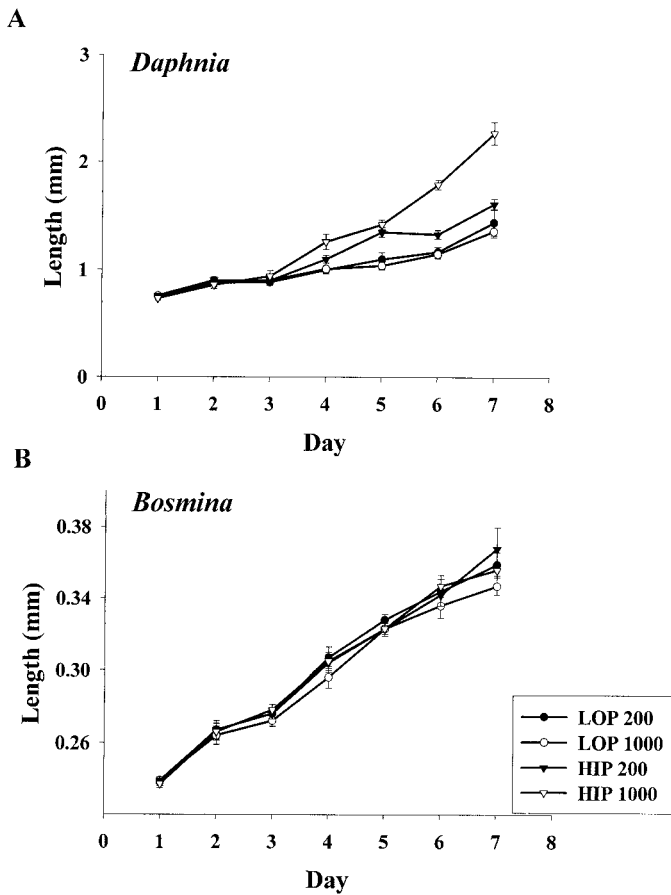


Fig. 1. Daily growth (mm) for (A) *Daphnia magna* and (B) *Bosmina (Sinobosmina) leideri* under four food regimes. Error bars are standard error of the mean.

patterns similar to those of body length increase (Fig. 2; Table 1). Again, growth of *D. magna* was significantly affected by both food quantity and food quality (Table 1). There was also a significant interaction between food quality and quantity on *D. magna* growth rate (Table 1). Even when *D. magna* was fed high quantities of LOP food, growth was lower than on low quantity HIP food (Bonferroni, $df = 35$, $P = 0.048$). These growth rates are numerically similar to those found by Sterner (1993) in the same treatments using a flow-through culture apparatus. *Bosmina leideri* showed a slight trend toward a food quantity effect, but the differences were not significant at $\alpha = 0.05$ (Fig. 2; Table 1). Unlike *D. magna*, *B. leideri* showed no food quality effect on growth ($n = 73$, Fig. 2; Table 1).

Lipid and ovary indices were added and expressed as a composite lipid-ovary index for each species (Fig. 3). There was no variance in visual lipid-ovary index patterns among treatments for *D. magna* through day 5 (Fig. 3A). On days 6 and 7, the *D. magna* in the HIP low-quantity food treatment had lower lipid-ovary index values than did those fed the other treatment algae (Bonferroni, $df = 35$, $P < 0.001$). Those *D. magna* in the HIP high-quantity food treatment had higher lipid-ovary index values than did the other animals on day 6 (Bonferroni, $df = 35$, $P < 0.001$). However, overall

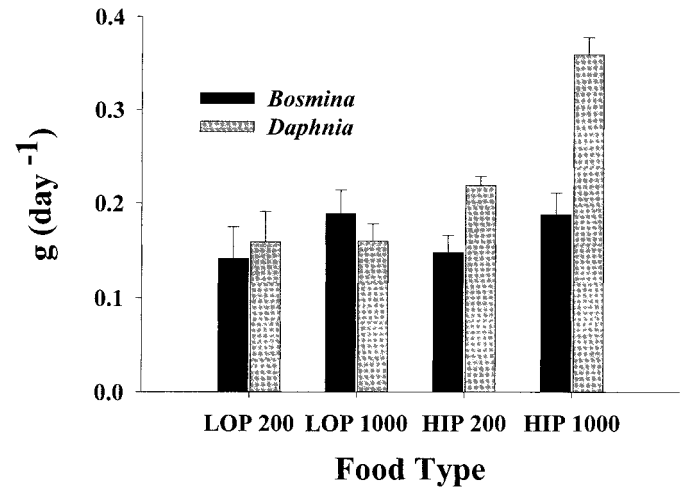


Fig. 2. Growth rates (g) for *Daphnia magna* and *Bosmina (Sinobosmina) leideri* under the same four food regimes. Error bars are standard error of the mean.

there was no significant effect of food quality on lipid and ovary indices (repeated measures ANOVA between-subjects effects, $F = 0.208$, $P = 0.651$). *Bosmina leideri* lipid and ovary indices (Fig 3B) also showed no significant differences with either food quality or quantity treatment over the experiment (repeated measures ANOVA between-subjects effects, $n = 69$, $F = 0.582$, $P = 0.752$).

The effect of food treatment on fecundity, calculated as the number of eggs per female on the day when animals first started producing eggs, showed different patterns for the two zooplankton species (Fig. 4). For *D. magna*, there were significant food quality, quantity, and treatment interaction effects (Table 1), with only HIP high-quantity food resulting in significant egg production within 7 d (Fig. 4). *Bosmina leideri* showed no significant food quantity or quality effects

Table 1. ANOVA results for the effects of foods of different quality (P content) and quantity on *Daphnia magna* and *Bosmina (Sinobosmina) leideri* growth rate and fecundity. Fecundity data were log transformed to permit analysis of the interaction term (Hurlbert and White 1993).

Genus	Parameter	Source	SS	df	F	P
<i>Daphnia</i>	g	quality	0.190	1	41.285	<0.001
		quantity	0.065	1	14.097	0.001
		interaction	0.028	1	6.168	0.018
		error	0.157	34		
<i>Bosmina</i>	g	quality	0.000	1	0.011	0.917
		quantity	0.032	1	3.045	0.085
		interaction	0.000	1	0.021	0.886
		error	0.723	69		
<i>Daphnia</i>	fecundity	quality	3.190	1	9.159	0.005
		quantity	3.190	1	9.159	0.005
		interaction	6.741	1	19.359	<0.001
		error	11.840	34		
<i>Bosmina</i>	fecundity	quality	0.177	1	1.560	0.224
		quantity	0.063	1	0.552	0.465
		interaction	0.300	1	2.652	0.117
		error	2.605	23		

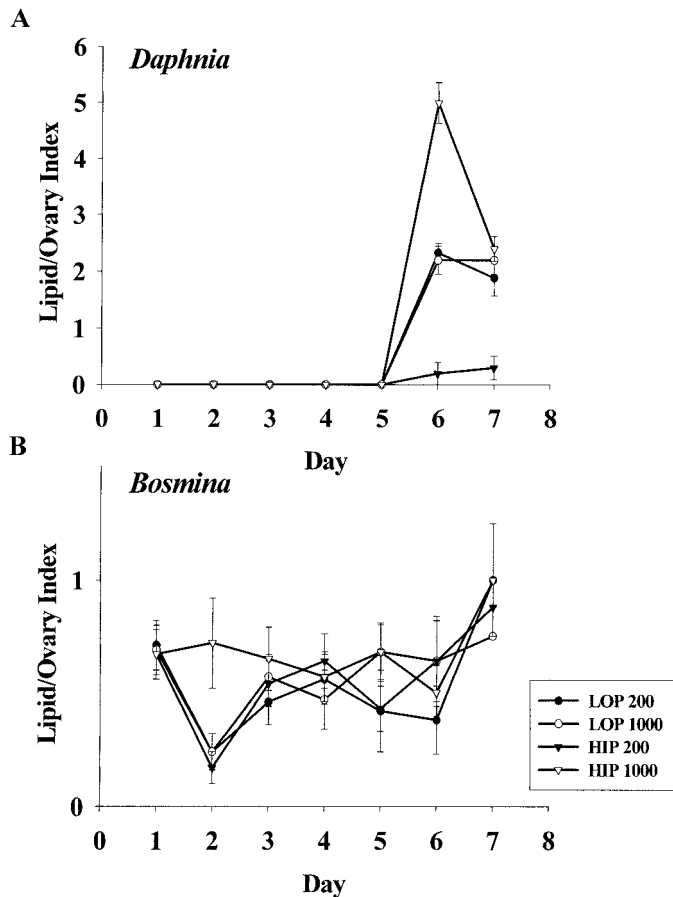


Fig. 3. Daily patterns of lipid-ovary index for *Daphnia magna* and *Bosmina (Sinobosmina) leideri* under the same four food regimes. Error bars are standard error of the mean.

(Table 1), with all treatments containing some fecund animals (Fig 4) on the date of first reproduction.

Daphnia magna survivorship was 100% for all treatments except low-quantity LOP, where 1 of 10 animals in this treatment died. For *B. leideri*, approximately 15–20% mortality was caused directly by losses due to handling or inadvertent capture in bubbles. This procedural mortality was uniformly distributed among treatments and did not account for all recorded mortality. An additional 32% mortality in the LOP low-quantity treatment, 21% mortality in the LOP high-quantity treatment, 12% mortality in the HIP low-quantity treatment, and 17% mortality in the HIP high-quantity treatment were observed. In this experiment, *B. leideri* therefore exhibited a lower survivorship in the LOP low-quantity food treatments than in the other treatments. Additional trials would be needed to determine if this result is repeatable and significant.

Discussion

Although this experiment used batch instead of continuous culture techniques, the *Daphnia* results for growth, fecundity, and survivorship agree with previous results (Sterner 1993, Sterner et al. 1993). Apparently, the change in culture

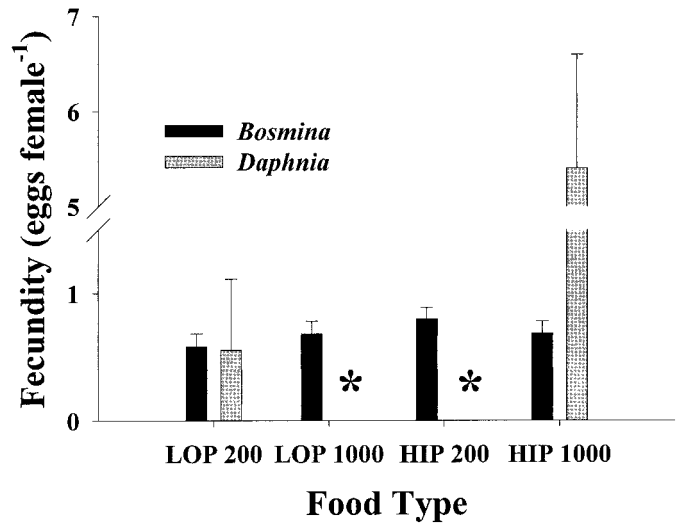


Fig. 4. Fecundity of *Daphnia magna* and *Bosmina (Sinobosmina) leideri* after being raised to maturity on the same four food regimes. Error bars are standard error of the mean. * indicates a zero value (not missing data).

technique did not affect food quality as perceived by *Daphnia*. These results should therefore be directly comparable with those of previous studies.

Based solely on the differences in P content of the two zooplankton taxa, we predicted that the low-phosphorus-content zooplankton *Bosmina* would be less affected by LOP food than would the high-phosphorus-content *Daphnia*. *Bosmina* growth, as measured by changes in both length (Fig. 1) and body mass (g, Fig. 2), was not affected at all by a LOP diet, but the growth of *Daphnia* was strongly depressed in the LOP treatments. The observed patterns for *Daphnia* are similar to those in previous studies (Sterner 1993, Sterner et al. 1993), with both low- and high-quantity P-deficient foods resulting in less growth than HIP food of either quantity (Fig. 2). *Daphnia g* values in Fig. 2 are almost identical to those recorded in previous experiments with the same food treatments. Although there was a trend toward higher growth at higher food quantities, *Bosmina* growth did not exhibit a significant food quantity effect. Perhaps the incipient limiting level for *B. leideri* is somewhat less than that reported for *Bosmina longirostris* ($>250 \mu\text{g C L}^{-1}$; Urabe 1991a) or is not near the level of C growth limitation in this species. The low-quantity ($200 \mu\text{g C L}^{-1}$) food treatment, therefore, may not have been as limiting as originally intended. As is typical for bosminids, the measured g of 0.15 d^{-1} for *Bosmina* was lower than that of *Daphnia* in high-growth conditions (DeMott and Kerfoot 1982; Goulden et al. 1982; Urabe and Watanabe 1992). Urabe and Watanabe (1992) reported growth rates higher than 0.15; thus, even in the high-quantity HIP treatment, experimental conditions were not optimal for *Bosmina* growth.

These results corroborate those of other recent studies connecting zooplankton P content to growth rate (Main et al. 1997; DeMott et al. 1998). The high-P-content *Daphnia* has a high potential growth rate, but that rate is realized only under conditions of nutritionally balanced food (Fig. 2). In

contrast, the low-P-content *Bosmina* has a relatively low growth rate (compared with that of *Daphnia*) on all foods (Fig. 2). However, measured by growth alone, *Bosmina* did not outperform *Daphnia* on low-quality foods: absolute *Daphnia* growth rate on poor food was similar to *Bosmina* growth on all foods. The difference in P content between *Daphnia* and *Bosmina* might allow for the additional growth increment on balanced foods, suggesting that *Daphnia* life histories are more oriented than those of *Bosmina* toward rapid colonization and quick usurpation of high-quality resources.

The lipid–ovary index of *Bosmina* also did not show significant food quantity or quality effects (Fig. 3). In previous studies, equal lipid indices under the different food treatments have been reported for *Daphnia* (Sterner et al. 1992). Although the low-quantity HIP food resulted in a significantly lower lipid index than did the other treatments after 2 d, no significant overall food quality effects on the lipid–ovary index were found. As in earlier studies (Sterner et al. 1992, Sterner 1993), the accumulation of lipids in the LOP treatments indicates that *Daphnia* were not starving for carbon, despite their low growth. Therefore, even if low- and high-P *Scenedesmus* are not equally edible, as might be indicated by differences in cell wall structure under algal nutrient limitation (van Donk and Hessen 1993), the potentially poorer edibility of low-P algae did not prevent digestion and assimilation by *Daphnia*. The successful growth of *Bosmina* on this low-P *Scenedesmus* is further evidence that any cell wall differences are not generally inhibitory to digestion by anomopod crustaceans.

Patterns of fecundity for these two species also matched predictions (Fig. 4). Consistent with prior results (Sterner 1993, Sterner et al. 1993), HIP food resulted both in higher fecundity and shorter time to first reproduction for *Daphnia* than did LOP food. *Bosmina*, however, showed no significant food quantity or quality effects on either fecundity or time to first reproduction, although there was a trend toward higher fecundity with HIP food at low quantity.

The small *Daphnia* sample size in this experiment ($n = 10$ for all treatments) precludes strong conclusions about survivorship effects, although no differences in *Daphnia* survivorship on the different foods were observed. Sterner (1993) found a slightly reduced survivorship of *Daphnia* on LOP food (average mortality of 1.3% for HIP and 6.1% for LOP). *Bosmina* did show a 20% survivorship reduction on LOP low-quantity food compared with that on HIP low-quantity food. Overall, survivorship was 12% higher for *Bosmina* on HIP food. This difference in survivorship is larger than the ~5% difference for *Daphnia* reported by Sterner (1993) and might translate into a substantial disadvantage for *Bosmina* on LOP food relative to HIP food. The relatively high mortality rate for *Bosmina* in this experiment suggests again that the culture environment was not optimal for this species. More work is necessary on larger numbers of organisms over longer time periods to quantify the treatment survivorship effects more fully for both species.

The results of this study agree qualitatively with our initial predictions. *Bosmina*, an organism with a lower body P content, does not exhibit the same dramatic negative effects of LOP food on its growth and reproduction as does *Daphnia*.

However, the LOP food in this study is extremely low in P (C:P = ~1,600:1). The only demonstrable effect of the LOP diet on *Bosmina* was a 12% reduction in survivorship, which may be surprising in a quantitative sense. Based on published metabolic parameters, the expected theoretical boundary for P limitation in *Bosmina*, can be calculated in a manner similar to that done for *Daphnia* (Hessen 1992, Sterner 1997). Assuming homeostasis of body composition (Sterner 1990), then the food P content threshold at which P limitation for a zooplankton should occur (given high food quantity) can be calculated as

$$\frac{C_{\text{food}}}{P_{\text{food}}} = \frac{C_{\text{zooplankton}}}{P_{\text{zooplankton}}} \cdot \frac{A_P}{A_C} \quad (2)$$

where $C_{\text{food}}/P_{\text{food}}$ is the molar ratio of C to P in the algal food, $C_{\text{zooplankton}}/P_{\text{zooplankton}}$ is the molar ratio of C to P in the animal, A_P is the assimilation efficiency of P uptake, and A_C is the assimilation efficiency of C uptake (Sterner 1997).

The C:P of *B. leideri* is approximately 150 (147: Schulz unpubl. data, a value remarkably similar to 150 for *B. longirostris*; Hessen and Lyche 1991). Given this body C:P and assimilation efficiencies for C (Urabe 1991b) and P (as in Sterner 1997) of 0.766 and 0.9, respectively, the predicted C:P of food that would induce P limitation for *Bosmina* is 176 (Eq. 2). This threshold is similar to that predicted for *Daphnia* (171, Sterner 1997). If we use a lower C assimilation efficiency of 0.5, the maximum value reported in a eutrophic lake (Lair 1991), then the predicted threshold becomes 270. Given *Bosmina* homeostasis, even if assuming a maximal P efficiency of 100, the theoretical boundary of P limitation is 300, which is twice that predicted for *Daphnia* (Sterner 1997) but close to the threshold of 320 estimated by Urabe and Watanabe (1992). A threshold of 300 is, however, still far below the ~1,600 C:P of the LOP food used in this study.

Until recently, evidence suggested that even when *Daphnia* is raised under different P conditions or starved, it maintains a strict homeostasis of zooplankton P content (Hessen 1990a, 1992; Andersen and Hessen 1991; Sterner 1993; Sterner and Hessen 1994). New evidence, however, suggests that when fed LOP food, *Daphnia* reduces its C assimilation yet is unable to maintain strict homeostasis (DeMott et al. 1998). *Daphnia* percentage P may be reduced by 33% when fed low C:P food, although this comes at a high cost in reduced growth rate (DeMott et al. 1998). These studies suggest two possibilities for the discrepancy between the theoretical and observed P limitation thresholds for *Bosmina*. First, *Bosmina* may effectively reduce its C assimilation efficiency relative to P assimilation efficiency. If A_P approaches 1 and A_C approaches 0.2 (similar to values found for *Daphnia* fed high C:P food; by DeMott et al. 1998), then the theoretical threshold becomes 750. Such a change, however, should come only at a large cost to overall growth rate. Because *Bosmina* growth in this study was not maximal, the P limitation threshold should have been higher (due to increased metabolic loss of C and thus a reduced C use efficiency). Still, Urabe and Watanabe (1992) found that even at low growth rates the threshold did not exceed 350 and

that *Bosmina* was less prone to changes in threshold due to lowered growth rates than was *Daphnia*. Second, *Bosmina* may be less homeostatic than *Daphnia* and may not suffer a similar severe growth penalty for not maintaining homeostasis. For *Bosmina* to have a threshold for P limitation of 1,000 C:P in its food, its body P content would have to decline by a factor of 3.7 (Eq. 2). For the threshold to decrease to 1,500 C:P, its body P content would have to decrease by a factor of 5.5 (i.e., from 150 to 825). These values are extreme shifts and seem implausible. More work is needed to quantify *Bosmina* homeostasis and evaluate the possible magnitude of changes in body composition. The exact empirical threshold is not clear from this study because only LOP and HIP food was used, and some survivorship effects were observed at 1,600 C:P. The threshold for the initiation of P limitation must therefore be below 1,600, but how far below is unclear.

One additional possible explanation for the success of *Bosmina* under low algal P conditions would be if *Bosmina* were able to use bacterial P and *Daphnia* were unable to feed on this source. If this were the case, then the effective P concentration of food available to *Bosmina* might actually be greater than that for *Daphnia*, in part explaining the differences in their responses to the food treatments. This scenario of preferential use of bacteria in the food cultures seems unlikely, however. Contrary, perhaps, to expectations based on body size, *D. magna* is an effective grazer on bacteria (Brendelberger 1985). The preferential utilization of bacteria as a food source by *Bosmina* is uncommon, although there are a few reports of some non-North American Bosminidae effectively grazing bacteria when offered natural or cultured bacteria as a food source (Tóth and Kato 1997). In one study, *Bosmina longispina* (from Europe) was able to graze bacteria and preferred it to *Scenedesmus* (Borsheim and Andersen 1987). Conversely, many authors have demonstrated that *Bosmina* is much less efficient when feeding on bacteria than is *Daphnia* (Geller and Müller 1981; DeMott 1982; Haney and Trout 1985; Hessen and Andersen 1990; Urabe 1990; Hart and Jarvis 1993). Even if the *B. leideri* in this study did consume substantial quantities of bacteria, the *D. magna* should have been able to feed on these bacteria as well. Further, because the LOP cultures were being supplied with a very low proportion of P, not only the algae but also the bacteria in these cultures should have been P deficient. Culture C:P was measured on GF/F-filtered samples (0.7 μm), and thus includes both phytoplankton and large bacteria. Thus, LOP bacteria should not have contributed a large amount of P, even if ingested, and *Daphnia* should have been more likely than *Bosmina* to ingest particles <0.7 μm . Bacterial feeding therefore does not explain the differential effect of P food treatment on life history parameters for the two species.

Another explanation for the low quality of P-limited *Scenedesmus* is that because these nutrient-stressed algae are low in essential fatty acids (HUFA), it is actually HUFA limitation and not mineral P limitation that impedes daphnid growth on LOP food (Brett and Müller-Navarra 1997). Because there is no known reason that *Bosmina* should have a lower physiological requirement for HUFA than does *Daphnia*, the HUFA hypothesis would predict that LOP *Scene-*

desmus should be just as poor food for *Bosmina* as they are for *Daphnia*. On the contrary, the results of the present study clearly demonstrate that LOP food is not as detrimental to *Bosmina* as it is to *Daphnia* and therefore do not support the HUFA food quality hypothesis.

Elemental stoichiometry provides a framework for making a priori predictions about the growth of consumers and their resources. In this study, we observed qualitative agreement with stoichiometric theory. The low-P zooplankton did not suffer the large growth penalty from feeding on LOP foods that the high-P zooplankton did. The possibility that something as potentially complex as the production of animal biomass feeding on live algal foods can be a function of a simple mass-balance problem is encouraging.

The effective algal C:P that limits *Daphnia* growth appears to be approximately 180–300 (Sterner 1993, 1997), whereas *Bosmina* is able to maintain growth and reproduction even when fed extremely high C:P algae (this study). This difference in the threshold food C:P required to maintain growth and reproduction implies that there may be a range of lakes with high seston C:P where *Bosmina* have a competitive advantage over *Daphnia* because *Daphnia* fecundity is so depressed on LOP food. In a review of seston C:P in some North American lakes (Elser and Hassett 1994), ~50% of the lakes surveyed had a C:P greater than the threshold for *Daphnia* P limitation. Perhaps the range of *Daphnia* abundance and overlap of *Bosmina* and *Daphnia* is partially constrained by P mineral limitation of *Daphnia*. Good tests of this hypothesis are lacking. However, three correlational studies have provided tentative support for this hypothesis. First, in a survey of 47 lakes in which daphnid abundance was correlated with particulate P, Hessen (1992) suggested that C:P sestonic ratios may limit *Daphnia* distribution. Second, a comparison of the stoichiometry of N and P in lakes and oceans also showed a negative correlation between *Daphnia* percentage dominance and seston C:P (Hassett et al. 1997). Third, in conditions of low seston P, *Daphnia* establishment may be inhibited (Elser et al. 1998), although growth penalties may be small (Sterner 1998). Traditionally, competition experiments between *Daphnia* and *Bosmina* have concentrated on selective feeding (e.g., DeMott and Kerfoot 1982; Burns et al. 1989) or on the ability of *Bosmina* to withstand periods of low food (for review of zooplankton competition, see DeMott 1989). This study supports the hypothesis that mineral limitation may also influence zooplankton species distributions (Hessen 1990b), particularly when the species in question have very different P requirements, as is clearly the case for *Daphnia* and *Bosmina*.

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