Contrasting effects of different types of resource depletion on life-history traits in *Daphnia*

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Summary

1. Life-history traits of animals are known to change according to food quantity, but there is another type of resource depression, namely depletion of food quality. To examine life-history responses of herbivores to changes in resource quality, *Daphnia obtusa* Kurz, a common planktonic herbivore, were reared individually under several algal food regimes with different quantity and quality in terms of chemical composition.

2. Compared with *Daphnia* fed on a small quantity of nitrogen (N) and phosphorus (P) sufficient food, *Daphnia* fed on a large amount of P deficient food grew more slowly at young ages but continually grew until older ages. This trend was also found for *Daphnia* fed on a large amount of N deficient food.

3. However, the size-specific reproductive investment (measured as biomass accrued per unit time) of *Daphnia* fed on a large amount of N or P deficient algae was similar to those fed on a small amount of N and P sufficient food, indicating complex life-history responses to food quality and suggesting that nutritional requirements for reproduction differ from somatic growth.

4. Compared with individuals fed high-quality and high-quantity food, *Daphnia* fed on a large amount of P deficient food produced smaller eggs, while individuals fed on a small amount of P and N sufficient food produced larger eggs. Furthermore, 15–30% of eggs produced by individuals fed on P or N deficient food ceased to develop and were aborted.

5. These results demonstrate that life-history responses to food quality differ from responses to food quantity. Since the chemical composition of algae is highly variable in nature, herbivorous plankton demographics may not be predictable from resource quantity alone.

Key-words: Algal food, C : N : P ratio, food quality, herbivorous plankton

Introduction

Studies of life-history traits of animals have played a central role in the development of modern ecology. A life history is a schedule of a suite of parameters, which may include somatic growth, development time, age and size at maturation, egg and brood size, and survivorship. These parameters bridge the gap between physiology at the individual level and demography at the population level. Laboratory studies and field observations on plankton have shown that life-history parameters determine population dynamics of consumers and prey (Gurney *et al*. 1990; McCauley *et al*. 1996). Life-history parameters also provide basic information about the reasons for success or failure of plankton species in a community (Threlkeld 1976; Lynch 1980; Taylor & Gabriel 1992).

Within a single genotype, life-history parameters of planktonic herbivores are not fixed but rather change according to environmental conditions. Some of these changes may be adaptive adjustments to optimize fitness under the set of conditions experienced by the species (Tessier & Consolati 1989, 1991; Gilwicz & Guisande 1992; Boersma 1995, 1997). Others may be due to unavoidable physiological or thermodynamic
constraints. Among environmental factors affecting life-history parameters of planktonic herbivores, food availability has received much attention. In aquatic habitats, algal food is not always supplied sufficiently and constantly, forcing planktonic herbivores to respond to resource depression (Taylor 1985; Urabe 1988; Lynch 1989, 1992; Tessier & Consolati 1991; Gliewicz & Guisande 1992; Ebert 1993; Lampert 1993; Boersma 1995, 1997).

However, there are two different kinds of resource depressions: quantity and quality. Poor food quantity is characterized by an insufficient availability of all essential resources for the consumer, including energy. Many studies on life-history plasticity of planktonic herbivores have examined responses to poor food quantity. Poor food quality, however, is characterized by insufficiency of only a subset of all essential resources. Energy may be in surplus, while a single material such as protein is in deficient supply. Though poor food quality is thought to be a major factor in the ecology of many animals, little is known about the response of multiple life-history traits of planktonic herbivores to changes in algal food quality (Sterner & Schulz 1998). If some elements or biochemicals are deficient in the food, planktonic herbivores may not perform optimally or in a way that is predicted from food quantity alone.

In aquatic habitats, it is well known that the elemental and biochemical composition of algal changes depending on regimes of light and nutrient supplies (Wynne & Rhee 1986; Harrison, Thompson & Calderwood 1990; Urabe & Sterner 1996). Field studies demonstrate that nitrogen (N) and phosphorus (P) content relative to carbon (i.e. the C : N or C : P ratios) in suspended particles (mainly planktonic algae) differs by one or two orders of magnitude among lakes (Hessen 1992; Hecky, Campbell & Hendzel 1993; Elser & Hassel 1994; Downing 1997; Hassett et al. 1997; Sterner et al. 1997). In contrast, the elemental composition of planktonic herbivores appears to be less varied than that of algal species regardless of environmental conditions (Andersen & Hessen 1991; Elser & Urabe 1999). Thus, planktonic herbivores are expected to be frequently confronted with an imbalance between chemical composition in food and their demand (Hessen 1992; Urabe & Watanabe 1992; Sterner & Schulz 1998). Recent field studies have confirmed this imbalance in nature (DeMott & Gulati 1999; Elser, Hayakawa & Urabe 2001).

Previous studies showed that Daphnia, a common planktonic herbivore in lakes and ponds, grew slowly and produced a smaller number of offspring when they fed on algae with a high C : P or C : N ratio (Sterner 1993; Sterner et al. 1993; Schulz & Sterner 1999). These studies examined Daphnia growth for less than 14 days after birth; the response of adults, and details about reproductive output, thus were not observed (Daphnia take more than 10 days to mature in poor food regimes). If the suite of elements or biochemicals required for reproduction differs from somatic growth requirements, animals may alter their growth and reproduction patterns differently depending on the chemical composition of food. Some Daphnia species are known to produce larger eggs when food quantity is low. Such changes in egg size are believed to be an adaptive response, because neonates from larger eggs can survive longer without food (Tessier et al. 1983; Goulden, Henry & Berrigan 1987; Gliewicz & Guisande 1992). However, when they feed on food with sufficient energy but some nutrient deficiency, production of large eggs may not be advantageous because neonates can gain energy from surrounding food. Thus, food quality may differentially affect a number of life-history traits in addition to body growth and fecundity.

To address these uncertainties, we reared Daphnia individuals from birth to sixth adult instars under several food regimes with different quantity and quality in terms of chemical composition. The specific objectives were to examine how the life-history traits of Daphnia fed on a large amount of low-quality food differ from the traits of those fed on a small amount of high-quality food.

Materials and methods

Individuals were used from a strain of Daphnia obtusa Kurz and a strain of Scenedesmus acutus Uherkovich, which have been examined in previous studies (Sterner 1993; Sterner et al. 1993). Daphnia were originally isolated from a natural population in north-central Texas and have been maintained for 5 years in laboratory stock cultures with filtered lake water and S. acutus.

Scenedesmus acutus with high P and N contents (HIP, same as MON in Sterner et al. 1993), low N content (L-LOP) and low P content (LOP) were cultured at 20°C in continuous flow cultures (chemostats) using modified MPI growth media (N and P concentrations were adjusted). Details of culturing methods and analytical methods for C, N and P contents of algae are described elsewhere (Sterner et al. 1993). Experiments were run with four different feeding suspensions (Table 1), a low amount (0·2 mg C l⁻¹) of HIP algae (L-HIP), and high amounts (1 mg C l⁻¹) of HIP algae (H-HIP), LON algae (H-LON), and LOP algae (H-LOP).

An artificial growth medium (basal COMBO) which is COMBO (Kilham et al. 1998) without N and P nutrients was used as an experimental medium to reduce changes in C : N : P ratio of each algal food.

Table 1. Food regimes showing density and C : N : P atomic ratios of algal food

<table>
<thead>
<tr>
<th>Food regime</th>
<th>Density (mg C l⁻¹)</th>
<th>C : N</th>
<th>C : P</th>
<th>N : P</th>
</tr>
</thead>
<tbody>
<tr>
<td>H-HIP</td>
<td>1.0</td>
<td>7</td>
<td>110</td>
<td>16</td>
</tr>
<tr>
<td>H-LON</td>
<td>1.0</td>
<td>15</td>
<td>270</td>
<td>18</td>
</tr>
<tr>
<td>H-LOP</td>
<td>1.0</td>
<td>11</td>
<td>1100</td>
<td>100</td>
</tr>
<tr>
<td>L-HIP</td>
<td>0.2</td>
<td>7</td>
<td>110</td>
<td>16</td>
</tr>
</tbody>
</table>
The pH of the medium was adjusted to 8 by dilute HCl. The use of the artificial growth medium enabled the experimental conditions to be normalized and a constant algal quality maintained. Before each run, five to eight preadult individuals were isolated into 1-l bottles containing basal COMBO with 0 5-mg C 1–

\[ HIP \]

alga. The food and culture medium was replaced every day and neonates hatched from the second brood of these individuals were used for the experiments.

Daphnia were reared individually at 20 °C in 50 ml continuous-flow chambers that were similar to those used by Lampert, Schmitt & Muck (1988). The medium with food was pumped from a food reservoir by a multichannel peristaltic pump to the zooplankton chambers. According to microscope inspection, algae were not damaged by the peristaltic pump. The flow rate of feeding suspension was set at 10 4 ml h 1 chamber. Thus, 250 ml of feeding suspension was passed through one zooplankton chamber daily. Foods and growth medium in the food reservoir were replaced daily. Fresh algae were obtained from the outflow of the algal culture, centrifuged, washed twice with basal COMBO, enumerated and suspended with basal COMBO medium to create the correct food. Both the food reservoir and zooplankton chambers were placed under dim light to minimize photosynthetic activity of algae. A preliminary check showed no significant changes in elemental composition of algae between the inflow and outflow. For each food regime, 14–16 neonates born within 10 h were placed individually in 50 ml zooplankton chambers and were reared until they had produced at least their sixth brood. During the experimental run, the entire contents of the zooplankton chambers were withdrawn once a day to allow washing of the chambers, and a number of measurements, described below, were recorded for each individual under a microscope.

Body length was measured from the head to the base of the tail spine. In the present study, maturation of Daphnia is defined as the time of first appearance of egg(s) in the brood pouch. After maturation, the numbers of live and dead eggs or embryos in the brood pouch were recorded. For each brood, the length and width of three to five eggs and the diameter of their yolk (Kerfoot 1974) were also measured through the transparent carapace when the egg membrane was still intact. Appearance of moulting cast (exuviae) and the number of newly born neonates were also recorded. After removing neonates and any moulting cast from the growth medium, daphnids were returned to the zooplankton chambers.

The time course changes of body length (Lx) were fitted to the following equation, where L∞ is asymptote length, α and β are growth coefficients, and x is age:

\[ L_x = \frac{L_{\infty}}{1 + \exp (-\beta x)} \quad \text{eqn 1} \]

The coefficient α represents body length at age 0 in combination with L∞ and a larger value of the coefficient β means that animals approach L∞ at a younger age. Fitting to this equation was made for each individual survived until 20 days using the Quass-Newton method (SYSTAT 5.2, Systat Inc.), and the average value of the coefficients were estimated for each food regime. The intrinsic rate of population increase was calculated as an iterative solution to Euler’s equation:

\[ 1 = \sum_{x=0}^{\infty} m_x \exp (-rx) \quad \text{eqn 2} \]

Here \( m_x \) is the age-specific fecundity (number of newly born individuals per day) and \( l_x \) is age-specific survivorship. Significant differences in life-history parameters among the food regimes were examined by one-way ANOVA and Tukey pairwise comparison tests after log-transformation to stabilize variance in all parameters except growth coefficients α and β.

Results

Animals grew in length in all food regimes (Fig. 1). However, patterns of growth as measured by the growth parameters differed greatly among the food regimes (Table 2). The \( L_x \) in L-LOP was smaller than that in H-HIP, but larger than that in H-LOP or L-LOP. Similarly, the largest coefficient \( L_x \) was found in H-HIP and the smallest one in H-LOP. To illustrate these differences in the growth parameters, the relative increment rate of body length (\( L_{x+1}/L_x \)) was calculated using the parameters shown in Table 2 and plotted against \( L_x \) (Fig. 2). The relative increment rate decreased monotonically with body length in all food regimes, and was always highest in H-HIP at a given body size. The relative increment rate in H-LOP was similar to that in L-HIP at a small size but approached that in H-HIP with increasing body length. In contrast, the relative increment rate in H-LOP was lower than in all other food regimes for neonates but approached those in L-HIP with increasing body size. These results imply that Daphnia fed on HIP algae exhibit a very rapid growth rate during juvenile stages that quickly decelerates with size, whereas Daphnia fed on LON and LOP algae grow at a slower and more even rate throughout their life span. As expected from the body growth curves, Daphnia in H-HIP matured at the largest length at the youngest age with the fewest juvenile instars (Table 2). The maturation age and size of Daphnia in H-LOP were comparable to those in L-HIP, although \( L_x \) was much larger in H-LOP than in L-HIP. Daphnia in H-LOP matured at a smaller length at an age that was twice as old as in H-HIP.

After maturation, Daphnia produced eggs into their brood pouch at each moult. Intermoult duration of the adult instars was slightly but significantly shorter in H-HIP than in other food regimes (Table 2). In all food regimes, the number of eggs produced per brood increased exponentially with body length (r² > 0 63, P < 0 001) (Fig. 3). In H-HIP, it exceeded 25 eggs after the 5th adult instar. The maximum brood size...
of *Daphnia* for the first six adult instars was, however, less than 20 eggs in H-LON, 12 eggs in H-LOP and 8 eggs in L-HIP, partly because of smaller adult size in these food regimes. Analysis of covariance (ANOVA) showed that the elevation of log-log regression lines between brood size and body length was significantly different among the food regimes ($F_{3,216} = 34.78, P < 0.001$), but the slope was not ($F_{3,213} = 1.61, P = 0.187$). At a given adult length, the brood size of *Daphnia* in H-LON and H-LOP tended to be larger than in L-HIP but smaller than in H-HIP.

Significant differences were also found in egg size among the food regimes. Although egg size was not significantly related to the body length of the maternal individual in any food regime (Fig. 4), mean egg size produced in the first five broods was slightly but significantly larger for individuals in L-HIP than H-HIP (Table 3). Similarly, absolute and relative yolk content within an egg were not correlated with maternal size but were higher in L-HIP than H-HIP. In contrast, *Daphnia* in H-LOP produced significantly smaller eggs compared with those in H-HIP. These smaller eggs, however, had more yolk than those in H-HIP.

![Fig. 1. Temporal trends in body length of *Daphnia obtusa* grown under food regimes with 1 mg C l$^{-1}$ of N and P sufficient food (H-HIP), N deficient food (H-LON) and P deficient algae (H-LOP), and 0.2 mg C l$^{-1}$ of N and P sufficient food (L-HIP). In each individual, instars are denoted by open circles.](image1)

![Fig. 2. Relationship between the relative increment rate of somatic growth ($L_{x+1}/L_x$, day$^{-1}$) and body length of *Daphnia obtusa* grown under four different food regimes. Growth parameters used in estimating the increment rate are shown in Table 2.](image2)

### Table 2. Parameters of somatic growth. (Mean ± 1 SE). Growth curve is given as $L_x = L_\infty (1 + \exp (\alpha - \beta x))$, where $L_x$ is body size at age $x$ (day) and $L_\infty$ is asymptotic size. Lack of significant difference is denoted by superscript letters.

<table>
<thead>
<tr>
<th></th>
<th>H-HIP</th>
<th>H-LON</th>
<th>H-LOP</th>
<th>L-HIP</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth curve</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$L_\infty$ (mm)</td>
<td>2.10 ± 0.03</td>
<td>1.92 ± 0.02</td>
<td>1.65 ± 0.04$^*$</td>
<td>1.68 ± 0.03$^*$</td>
<td>3.37</td>
<td>60.8</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>0.98 ± 0.03</td>
<td>0.94 ± 0.09</td>
<td>0.78 ± 0.05</td>
<td>0.89 ± 0.04$^*$</td>
<td>3.37</td>
<td>2.4</td>
<td>0.08</td>
</tr>
<tr>
<td>$\beta$</td>
<td>0.33 ± 0.02</td>
<td>0.19 ± 0.01$^*$</td>
<td>0.17 ± 0.03$^*$</td>
<td>0.21 ± 0.01$^*$</td>
<td>3.37</td>
<td>41.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Maturation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Size ($L_m$ mm)</td>
<td>1.55 ± 0.03</td>
<td>1.33 ± 0.02$^f$</td>
<td>1.20 ± 0.01</td>
<td>1.34 ± 0.02$^d$</td>
<td>3.43</td>
<td>51.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Instar (days)</td>
<td>5.6 ± 0.2$^e$</td>
<td>6.2 ± 0.1$^d$</td>
<td>7.9 ± 0.4</td>
<td>7.0 ± 0.2</td>
<td>3.43</td>
<td>18.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Age (days)</td>
<td>5.8 ± 0.2</td>
<td>9.6 ± 0.4$^d$</td>
<td>11.7 ± 0.9</td>
<td>10.8 ± 0.5$^e$</td>
<td>3.43</td>
<td>26.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Intermoult duration of adult instars (days)</td>
<td>2.31 ± 0.05</td>
<td>2.64 ± 0.07$^d$</td>
<td>2.51 ± 0.07$^d$</td>
<td>2.66 ± 0.07$^d$</td>
<td>3.231</td>
<td>7.80</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

result, the ratio of yolk to egg volume in H-LOP was much higher than in H-HIP and as high as in L-HIP. Daphnia in H-LON tended to produce smaller eggs than those in H-HIP, but mean egg size and relative yolk content in the first five broods did not significantly differ between these two food regimes.

Based on brood size, mean egg size and intermoult duration of adult individuals, daily reproductive investment was estimated for each food regime (Fig. 5). Here, the reproductive investment was expressed as a carbon unit, assuming that carbon to egg volume ratio (0.0152 mg C 10⁻⁵ m⁻³) was not affected by the food regime (Urabe 1988). As with brood size, the daily reproductive investment increased exponentially with adult body size in all food regimes (r² > 0.623, P < 0.001). In contrast with brood size, however, the reproductive investment of Daphnia in L-HIP was almost the same as that in H-LOP and H-LON because of the production of larger eggs in L-HIP.

During the experiments, one to several eggs within a brood often failed to develop and were aborted (Fig. 6). In some cases, all eggs in a brood were aborted. The stage and form of the aborted eggs varied. Some of the aborted eggs appeared to be darkened in colour and congealed, and remained at an early stage in the brood pouch without further development, similar to the description given by Boersma & Vijverberg (1995). In other cases, eggs developed to the mid-egg stage when red eye pigments appeared, but did not complete further somatic segmentation and finally collapsed, appearing to ‘melt down’. In the latter case, yolk droplets were observed to be left in the brood pouch.

Aborted eggs were frequently seen in Daphnia fed on LOP and LON algae. In H-LOP, 80% of the 1st brood contained at least one aborted egg and more than 40% of eggs produced in this brood failed to develop normally (Fig. 6). In this food regime, the frequency of aborted eggs and broods containing aborted eggs decreased with age. In H-LON, however, all eggs produced in the 1st brood developed normally, and the frequency of aborted eggs and broods containing aborted eggs increased with age. On average, Daphnia in H-LOP produced a total of 23.7 eggs per matured female from birth to 5th brood, and 32.6% of the eggs failed to develop into neonates (Table 4). In H-LON, 14.3% of eggs were aborted. For Daphnia fed HIP algae, aborted eggs were found only in less than 4% of the eggs produced in the first five broods.

The mortality of Daphnia in H-HIP was low throughout the observed life span (Fig. 7); 93% of individuals survived to maturity (Table 4). In H-LOP, however, there was considerable early mortality, with 35% of Daphnia dead before maturation. Most mature H-LOP individuals survived until the 6th adult instar (at 27 days) when the experiment was terminated. In H-LON mortality was elevated over the whole observed life span; 29% of individuals died before maturation and 20% of matured individuals died before the 6th adult instar (at 24 days). Among food regimes, overall survivorship from birth to the 6th adult instar (at 25 days) was lowest in L-HIP, where 60% of individuals died within the observation period, most after maturation.

From the survivorship and time schedules of the

Table 3. Mean egg volume, yolk volume and ratio of yolk to egg volume (mean ± 1 SE). Lack of significant difference is denoted by superscript letters

<table>
<thead>
<tr>
<th></th>
<th>H-HIP</th>
<th>H-LOP</th>
<th>H-LON</th>
<th>L-HIP</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg volume (×10⁵ μm³)</td>
<td>35.10 ± 0.77ab</td>
<td>32.97 ± 0.51a</td>
<td>29.08 ± 1.03</td>
<td>38.99 ± 0.80</td>
<td>3,164</td>
<td>21.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Yolk volume (×10⁵ μm³)</td>
<td>2.53 ± 0.08b</td>
<td>2.48 ± 0.06b</td>
<td>2.86 ± 0.13</td>
<td>3.70 ± 0.15</td>
<td>3,164</td>
<td>19.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Yolk : egg ratio</td>
<td>0.072 ± 0.002c</td>
<td>0.075 ± 0.002c</td>
<td>0.100 ± 0.003d</td>
<td>0.098 ± 0.003d</td>
<td>3,164</td>
<td>36.300</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

number of neonates liberated from birth to 5th brood, the net reproductive rate ($R$) and intrinsic rate of natural increase ($r$) were computed. Both rates were lowest in H-LOP (Table 4). In H-HIP, the net reproductive rate was seven times higher, and the intrinsic rate of increase was three times higher than in H-LOP. 

Daphnia in H-LON and L-HIP had rates intermediate between these regimes. When aborted eggs were included in the estimation by assuming that they developed normally, the intrinsic rate increased to 0.196 day$^{-1}$ in H-LON and 0.149 day$^{-1}$ in H-LOP. Thus, aborted eggs reduced the intrinsic rate of population increase in H-LON and H-LOP by 4% and 13%, respectively. The low contribution of aborted eggs to the intrinsic rate in H-LON is because aborted eggs were produced mainly by late-instar adults.

**Discussion**

Previous studies have shown that Daphnia obtusa fed on LOP or LON algae grew more slowly and produced a smaller number of offspring compared with Daphnia fed on the same amount of HIP algae (Sterner 1993; Sterner et al. 1993). However, these studies did not collect data in a means conducive to life-table analysis. The present study shows that Daphnia fed on N or P deficient algae not only grow slowly but they also produce a substantial number of eggs that cease to develop, and they have reduced survivorship, especially before maturation. As a result, the intrinsic rate of population increase for Daphnia fed on N or P deficient algae was much lower than those fed on the same amount of

<table>
<thead>
<tr>
<th>Table 4. Summary of population parameters</th>
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<tr>
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<tr>
<td><strong>H-HIP</strong></td>
</tr>
<tr>
<td>% matured</td>
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<tr>
<td>Egg production rate* (eggs/matured female)</td>
</tr>
<tr>
<td>% of non-viable eggs</td>
</tr>
<tr>
<td>Net reproductive rate* (R/offspring/female)</td>
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<tr>
<td>Intrinsic rate of population increase* (r/day)</td>
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<td></td>
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<tr>
<td><strong>H-LON</strong></td>
</tr>
<tr>
<td>% matured</td>
</tr>
<tr>
<td>Egg production rate* (eggs/matured female)</td>
</tr>
<tr>
<td>% of non-viable eggs</td>
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<tr>
<td>Net reproductive rate* (R/offspring/female)</td>
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<tr>
<td>Intrinsic rate of population increase* (r/day)</td>
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<td></td>
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<tr>
<td><strong>H-LOP</strong></td>
</tr>
<tr>
<td>% matured</td>
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<tr>
<td>Egg production rate* (eggs/matured female)</td>
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<td>% of non-viable eggs</td>
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<td>Net reproductive rate* (R/offspring/female)</td>
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<td>Intrinsic rate of population increase* (r/day)</td>
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<tr>
<td><strong>L-HIP</strong></td>
</tr>
<tr>
<td>% matured</td>
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<tr>
<td>Egg production rate* (eggs/matured female)</td>
</tr>
<tr>
<td>% of non-viable eggs</td>
</tr>
<tr>
<td>Net reproductive rate* (R/offspring/female)</td>
</tr>
<tr>
<td>Intrinsic rate of population increase* (r/day)</td>
</tr>
</tbody>
</table>

*From birth to 5th brood.
Food quality and Daphnia life history


Fig. 6. Abortion rate and percentage of individuals with aborted eggs in successive brood numbers in Daphnia obtusa grown under four different food regimes.

Fig. 7. Survivorship of Daphnia obtusa in four different food regimes.

H-LON matured at the same length and age as those in L-HIP, but they grew more after maturation. In contrast, size-specific investment for reproduction in terms of carbon was similar among H-LON, H-LOP and L-HIP (Fig. 5). These results suggest that the suite of elements or biochemicals demanded for somatic growth of young individuals differ from the suite demanded by adult individuals for reproduction. It is known that N and P content relative to C in body tissues are higher for smaller Daphnia individuals (Tessier & Consolati 1991; Main, Dobberfuhl & Elser 1997; DeMott, Gulati & Siewertsen 1998). In addition, C : N and C : P atomic ratios of D. obtusa eggs are 20 and 300, much higher than the ratios in postembryonic individuals (C : N = 6 and C : P = 80) (Sterner & Schulz 1999). The high C : N and C : P ratios in eggs is probably related to the fact that yolk is the energy source for embryonic development. This marked difference in C : nutrient ratio between eggs and postembryonic individuals implies that young individuals require more N and P relative to C for their growth, while less N and P relative to C are required for the development of eggs. It should be noted that survivorship before maturation was lowest in individuals fed on P deficient food and was also reduced in individuals fed on N deficient food. However, these individuals survived at a relatively high rate after maturation. Thus, it is likely that low survivorship is linked to relatively higher N or P demand at younger ages. In Daphnia, young individuals may be more vulnerable to N or P deficient food than adult individuals.

When Daphnia were fed on a small amount of N and P sufficient food (L-HIP treatment), they produced larger eggs with a larger amount of yolk. Yolk of Daphnia eggs is a maternal investment for egg development and is used partly for postembryonic development (Goulden et al. 1984). In cladocerans, large eggs generally contain more yolk (Goulden et al. 1987). Thus, neonates from large eggs can resist starvation for longer periods because a substantial amount of yolk is left for postembryonic development (Tessier et al. 1983; Goulden et al. 1987). Alternatively, since individuals from larger eggs develop into larger neonates with a lower mass-specific metabolic rate (Threlkeld 1976), they can survive longer without food (Gliwicz & Guisande 1992). In either case, production of larger eggs with a relatively high amount of yolk is advantageous at low food abundance and is therefore believed to be an adaptive response to decreased food density (Gliwicz & Guisande 1992; see also Ebert 1993, 1994). A greater lipid content in eggs both in absolute and relative terms in animals fed on LOP algae corresponds to an overall higher level of lipids in those animals (Sterner et al. 1992).

In contrast to Daphnia fed on a small amount of HIP algae, Daphnia fed on a high amount of P deficient algae produced smaller eggs. Since P deficient food contains plenty of energy (carbon), there is little chance that neonates will starve due to respiration cost.
even if they cannot grow (Sterner & Robinson 1994). Therefore, it may be more advantageous for Daphnia fed on a high amount of P deficient algae to increase brood size by producing small eggs. However, such an adaptive explanation is not consistent with the observation that Daphnia fed on N deficient algae did not produce small eggs. Moreover, eggs produced in H-LOP contained an amount of yolk comparable to those of eggs in H-HIP. Thus, production of small eggs by Daphnia fed on P deficient food cannot be explained by a decrease in maternal investment of reserved material. Considering these facts, production of small eggs by Daphnia fed on LOP algae may be a maternal constraint induced by the chemical composition of food rather than an adaptive response.

In previous studies with similar food regimes (Sterner 1993; Sterner et al. 1993), egg abortion was not noted, because all released maternal individuals was examined, eggs were not counted in the brood pouch. The present study showed that 15–32% of eggs produced by Daphnia fed on N or P deficient algae ceased to develop and were aborted. Vuijverberg, Kalf & Boersma (1996) showed that some eggs produced by Daphnia are aborted at pH > 9.5. In the present study, pH was adjusted to 8. Bell (1983) suggests that there is a minimum size of Daphnia eggs necessary for successful development. However, egg abortion in our experiments cannot be explained by insufficient egg size because eggs produced by Daphnia fed on N deficient food were as large as those fed on N and P sufficient food. Similar to the present results, Weers & Gulati (1997) found that more than 50% of eggs in the 1st brood of Daphnia galeata G. O. Sars fed on P deficient Chlamydomonas were not developed. These results imply that N- or P-limited algae are a nutritionally inadequate diet for production of healthy eggs. In natural habitats, degeneration or abortion of parthenogenetic eggs is frequently observed in Daphnia populations (Brooks 1946; Hall 1967; Redfield 1981; Threlkeld 1985). In some cases, more than 50% of eggs in Daphnia populations are non-viable (Boersma & Vuijverberg 1995). These observations imply that chemical composition of food is not always suitable for Daphnia populations in nature.

There is evidence that P deficiency limits juvenile growth of Daphnia (Urabe, Clasen & Sterner 1997). However, deficiency of P itself within the food could not explain production of non-viable eggs by Daphnia fed on N deficient algae because these algae contained high P relative to C and N. In general, the biochemical composition of algae changes according to nutritional condition (Müller-Navarra 1995; Weers & Gulati 1997). Thus, LON and LOP algae might be deficient in a substance essential to healthy egg development. Elenkoff & Bias (1990) showed that lack of selenium in growth media may cause egg abortion; however, the growth medium used in the present study contained this element. Rice & Kennedy (1988) noted that detrimental effects of selenium deficiency on animals are related to increased dietary intake of polyunsaturated fatty acids (e.g. the n-3 and n-6 series). Müller-Navarra (1995) showed that P deficient Scenedesmus cells contained higher amounts of polyunsaturated fatty acids, especially the n-6 series, than P sufficient cells. These facts suggest that egg abortion of Daphnia fed on LON and LOP algae may be caused by a disproportionate intake of some trace nutrients and biochemicals within the food.

If egg abortion was due to a disproportionate intake or deficiency of some substance necessary for healthy egg development, why did Daphnia not decrease brood size such that all eggs in a brood are able to develop? Since brood size of Daphnia fed on P deficient algae was more than two and up to six, it is possible that they invested more into each egg by decreasing brood size. Boersma (1995) speculated that Daphnia can decrease brood size only when they can insert more than two eggs but not by an odd number (e.g. one egg) because of the paired nature of the ovaries. This possibility implies that at a small brood size, it is not feasible to adjust a nutritional or material investment into eggs by changing brood size (Boersma 1995). Since broods with odd egg numbers have frequently been observed by us and others, however, it does not seem likely that paired ovaries present a physiological constraint for Daphnia brood sizes.

It should be noted that although the egg abortion rate was substantial (14–32%) for Daphnia fed on N or P deficient algae, abortion decreased the intrinsic rate of population growth by only 3–12%. This difference is because all eggs within a brood were not necessarily aborted and, as is well known, the intrinsic rate of population increase is more sensitive to age at maturation rather than brood size. Fitness reductions due to egg abortion therefore are complex, and may not be as large as simple observation of high percentages of abortion would suggest. When fed on low-quality food, Daphnia may determine brood size more relative to nutritional gain at early stages of the reproductive cycle (Tessier & Honnef 1988). If food quality is improved or they encounter patches of high-quality food during the reproductive cycle, Daphnia could assimilate substances essential to egg development and allocate them equally into each egg within the brood. Even if this were not to happen, Daphnia could reduce fitness loss by allocating a limited amount of an essential substance unequally into eggs, which would enable some eggs within the brood to develop. According to this speculation, production of non-viable eggs can be regarded as a cost of fitness that may be gained when food condition is improved. Alternatively, Daphnia may use egg abortion to balance the elemental or biochemical composition of their body tissues. When they feed on food with excess carbon, Daphnia may assimilate more carbon than they require, in order to concentrate other elements or biochemicals from the food. If this is the case, the abortion of eggs by Daphnia could be a way to discard carbon that was once assimilated in excess.
In conclusion, there are a number of differences in life-history traits among *Daphnia* that consume food of different chemical composition, which are not explained from knowledge of responses to changes in food quantity. Effects of low food quality on life-history traits probably differ among herbivorous plankton because of difference in relative nutritional requirements (Shulz & Sterner 1999). It should be noted that *Daphnia* used in the present study were of a single genotype and were the first generation exposed to a given food regime. A number of studies have shown that responses of *Daphnia* to changes in food abundance differ somewhat among genotypes (Tessier & Consolati 1989; Ebert et al. 2001). On the one hand, low-quality food in terms of chemical composition constrains the maternal basis of life-history traits in animals. On the other hand, if animals have frequently faced food with low quality, they may be able to adjust their life-history traits to partially overcome growth penalties. Since both field data on the effects of food quality and physiological knowledge of *Daphnia* nutrition are still limited, we could not ascertain whether any of the changes we observed were adaptive responses. Implications of the quality or chemical composition of food resources on population and trophic dynamics have been pointed out by several authors (Sterner & Schulz 1998; Elser et al. 2001). In addition, however, studies incorporating food quality into population and trophic dynamics are still limited (e.g. Andersen 1997). Thus, we encourage experimental, field and theoretical studies on the response of herbivore life-history traits to changes in food quality and the implications of these responses for population and trophic dynamics.

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References


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