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Nutritional quality of seston for the freshwater herbivore *Daphnia galeata* × *hyalina*: biochemical versus mineral limitations

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Abstract The quality of natural seston as food for zooplankters can be highly variable. Thus far, experimental evidence on the factors affecting food quality under natural conditions is scarce. Hence, in this study, we set out to investigate how *Daphnia galeata* × *hyalina* responded to qualitative variation in natural seston. This was done in laboratory experiments where we supplement natural seston from a mesotrophic lake with dissolved phosphorus and emulsions of highly unsaturated "essential" fatty acids. The growth rate of juveniles increased upon the supply of both phosphorus and fatty acids. These results suggest that these phosphorus and highly unsaturated fatty acids are substitutable and thus challenge our existing interpretation/understanding of how herbivore growth is "limited".

Keywords Assimilation · Highly unsaturated fatty acids · Fatty acid · Phosphorus · Seasonal dynamics

Introduction

In the current literature on the effects of food quality on zooplankton growth and reproduction, two classes of substances have been identified to be of major importance. Both the mineral and the biochemical content of the seston influence growth rates of herbivorous zooplankton. In freshwater systems, phosphorus seems to be the major limiting mineral. If the phosphorus concentration of algae is low, nutritional quality of the food is low (Urabe et al. 1997; DeMott et al. 1998). On the other hand, several studies have indicated the importance of highly unsaturated fatty acids (HUFAs), such as eicosapentaenoic acid (EPA), and docosahexaenoic acid (DHA) for herbivorous zooplankton (Müller-Navarra 1995; Brett and Müller-Navarra 1997; Sundbom and Vrede 1997; Weers and Gulati 1997b). The empirical support comes mainly from laboratory experiments with algal monocultures grown under different conditions (e.g. Sterner 1993; DeMott et al. 1998), from correlation studies between lake seston characteristics and *Daphnia* growth in the laboratory (Müller-Navarra 1995; De Lange and Arts 1999; Wacker and von Elert 2001), or from correlations between lake seston characteristics and densities of different zooplankton species (e.g. Elser and Hassett 1994; Sterner et al. 1997).

It is generally accepted that phosphorus and polyunsaturated fatty acids are essential resources for zooplankters and as such are non-substitutable (sensu Tilman 1982). Phosphorus is needed in the energy carrier ATP, and probably even more important in RNA as a large proportion of phosphorus in an organism is found in RNA (Vrede et al. 1999; Elser et al. 2000a). Polyunsaturated fatty acids are used in membranes and are precursors for hormones. Although there are a few studies which have investigated more than one essential resource under laboratory conditions (DeMott and Müller-Navarra 1997; Sundbom and Vrede 1997; Boersma 2000; Plath and Boersma 2001), this information was until very recently non-existent for natural systems. In contrast to what seems to be a standard procedure to assess limitations and the nature of different resources for phytoplankton (Suttle and Harrison 1988; Grover et al. 1999), thus far only one supplementation experiment has been carried out with zooplankters, even though DeMott (1998) suggested this a few years ago (Elser et al. 2001). The study by Elser et al. incorporated only the effect of phosphorus additions and not of fatty acid additions. Therefore, here we set out to assess whether phosphorus

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and polyunsaturated fatty acids are essential resources, and to what extent they limit zooplankton growth. Hence, we supplied natural seston with spikes of either phosphorus or emulsions with a high content in HUFAs. If HUFAs and phosphorus are truly non-substitutable resources we expect that in any one case only the addition of one of the resources will yield an increase in the growth rates of daphnids.

Materials and methods

In the summer of 1998, we carried out growth experiments every 2 weeks from April to October. A laboratory clone of *Daphnia galeata* × *hyalina* was provided with natural lake water from Schöhsee, a mesotrophic lake near the Institute. The lake water was pre-filtered through a 30 µm filter. Water was taken from 1, 5 and 12 m to be able to integrate the results over the whole water column, and the depth at which we observed most animals during the day (variable depth). From the sample, we established particulate phosphorus and particulate carbon content of the seston. POC was established after filtration onto pre-combusted glass-fibre filters (GF/F), using a LECO carbon analyser, and particulate P after oxidation using the molybdate-sulfuric acid method.

The mothers of the experimental animals were grown in batch-cultures, and fed *Scenedesmus obliquus* daily. Third brood neonates of these mothers were collected within 10 h after birth, and used for the growth experiments. All growth experiments were done under constant conditions (20°C, dimmed light). The experiments were carried out in the flow-through chambers (180 ml) described by Lampert et al. (1988), with a flow rate of 40 ml h^{-1}. Fresh water was collected from the lake every day between 9 and 10 a.m., brought to the laboratory, and used to fill the reservoirs of the flow-through systems. These reservoirs were placed in the dark to avoid photosynthesis and algal growth, and stirred continuously to prevent sedimentation. Ten neonates were collected and transferred to pre-weighed aluminium weighing boats. Initial weights were established using four replicates. Five neonates were introduced in the flow-through vessels. After 3 days, these animals were removed from the vessels and placed in pre-weighed aluminium boats. The boats were dried overnight at 60°C and weighed to the nearest 0.1 µg with a Satorius ultramicrobalance. All animals of a vessel were pooled. Dry weights were converted into somatic growth rates per day using the formula $g=[\ln(W_3)-\ln(W_0)]/3$, where W_0 is the mass of the animals at day zero, W_3 the mass at the end of the experiment and 3 is the duration of an experiment in days. This part of our experiments was nearly identical to the experimental set-up described by Müller-Navarra (1995), the main difference being that we used newly born animals, whereas Müller-Navarra worked with animals that were pre-cultured on *S. obliquus* under non-limited conditions for 3 days.

Phosphorus and HUFAs were added to the water from the different depths, resulting in an experimental set-up with 4(depth).3(control, P addition, HUFA addition).3(replicates)=36 vessels. Phosphorus-limited algae take up phosphorus very rapidly (Rothhaupt 1995; DeMott 1998; Plath and Boersma 2001). Hence, we added 3.2 µM (100 µg l^{-1}) dissolved phosphorus (K_2HPO_4 solution) to the seston. Previous experiments (Boersma 2000) have shown that the C:P ratio of phosphorus-limited *Scenedesmus* changed as a consequence of the P uptake, but that the biochemical composition, measured as the fatty acid spectrum of the algae, changed much more slowly. Moreover, recently Elser et al. (2001) showed that this is also the case for natural seston. Hence, in this way one can assess the degree of phosphorus limitation in natural seston. Particulate-P was established in the flow-through vessels after 1 day of incubation, and C:P values of the pulsed seston computed. At the same time, we added an emulsion rich in HUFAs, especially EPA and DHA. Every day, fresh emulsions of ICES 30/0.6/C, supplied by INVE technologies Belgium (Coutteau et al. 1996; Boersma 2000), were prepared by adding 0.5 mg wet weight of emulsion (0.4 mg C) per litre of lake seston. Analysis of the particle size showed that the emulsion particles were in the range of 1–2 µm, but that they were readily taken up by daphnids (see also Weers and Gulati 1997a). For details of the fatty acid content of the emulsions see Boersma (2000). Both additions were made in excess, to ascertain that the added substance was no longer present in limiting amounts. Previous experiments (Boersma and Stelzer 2000; Plath and Boersma 2001) showed that these added quantities significantly increased growth under laboratory conditions. The level of fatty acid additions was chosen such that it was maximally 50% of the total food carbon, a level at which Elendt (1990) observed no changes in reproduction in *Daphnia*.

Results

In 1998, the POC values of the seston in Schöhsee were relatively high, ranging from 0.3 to 0.75 mg C l^{-1} (Fig. 1). This implies that during the largest part of the year these values were above the incipient limiting level. Hence, one would expect that quantitative limitations of *Daphnia* would not occur. However, we still found a significantly positive correlation between growth rates of the animals and the POC content in the lake (r=0.41; P=0.004; n=47), indicating that changes in the quantity of the food explain a significant proportion of the variation in the growth rates. We observed no significant correlations between the somatic growth rates and the P content or the C:P ratios of the seston (r=0.13, 0.07, respectively), and only a marginally significant relationship with the total fatty acid content (r=0.26; P=0.06).

The addition of P to seston caused a significant increase in the particulate P content of the food media. As a result, the C:P ratio decreased significantly, and 85% of the values were now between 95 and 155 (Fig. 2). The growth rates of the animals were significantly affected by the treatment they were exposed to (Table 1). Figure 3 shows that both the addition of fatty

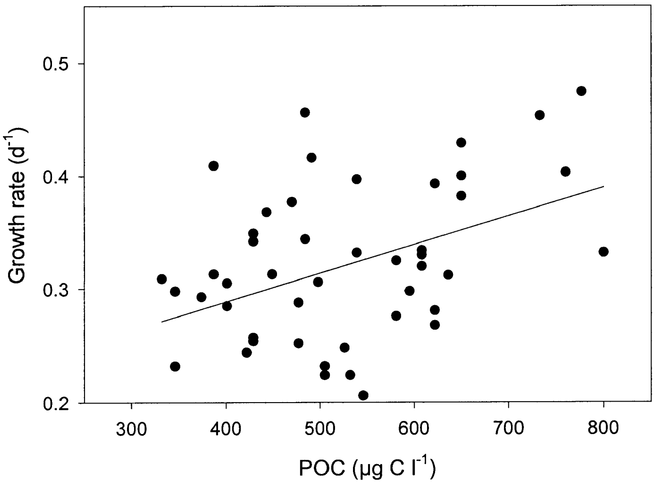

Fig. 1 Somatic growth rates of the experimental animals in relation to the POC content of the seston. The correlation between the growth rate and the POC content is highly significant (r=0.41; P=0.04)

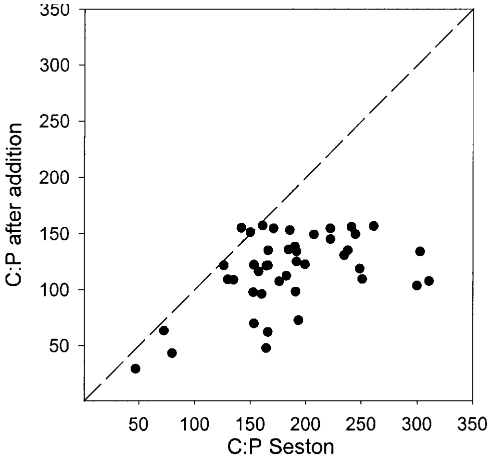

Fig. 2 C:P ratios (molar) of the seston before adding the P pulse, and after the addition. The *diagonal line* indicates the 1:1 line

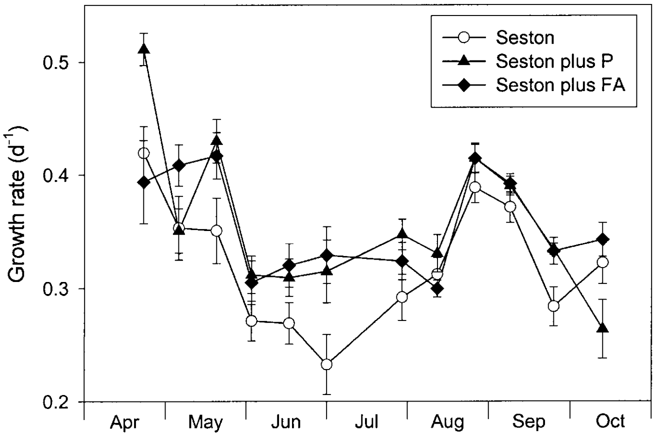

Fig. 3 Seasonal changes in the growth rate of experimental animals cultured on natural seston, natural seston with phosphorus added, and natural seston with emulsions of fatty acids added. For graphical clarity, the average of all depths is shown. *Error bars* indicate standard errors

Table 1 Summary ANOVA table of growth rates of experimental animals as the dependent variable, and date (random), depth (fixed), and treatment (fixed) as independent factors

	df	MS	*df* error	MS error	*F*	*P*
Date	10	0.0665	261	0.0020	32.57	<0.001
Depth	3	0.0109	30	0.0198	0.55	0.652
Treatment	2	0.0598	20	0.0060	9.98	<0.001
Date × Depth	30	0.0198	261	0.0020	9.68	<0.001
Date × Treatment	20	0.0060	261	0.0020	2.93	<0.001
Depth × Treatment	6	0.0054	60	0.0031	1.74	0.127
3-way	60	0.0031	261	0.0020	1.52	0.014

acids and the addition of phosphorus significantly increased the growth rates of the experimental animals. A Tukey post hoc comparison showed that there were no differences between the two additions (P=0.95), but that the growth rates were significantly increased as a result of the additions (P<0.001 for both) when compared to the natural seston. We observed a significantly negative correlation between the growth rates on natural seston and the change as a result of the supplementations (r=–0.32; P=0.03 and r=–0.48; P<0.001 for P and fatty acid additions, respectively). This indicates that when growth on natural seston was low, the effect of the additions was larger. Even though there was a significant effect of date, and a significant interaction between date and treatment (Table 1), our results indicate that there were no specific periods when phosphorus limited zooplankton growth, or when essential fatty acids limited zooplankton growth. There were some sampling dates where the two supplementations yielded different growth rates, but the main pattern was that supplementing either P or fatty acid emulsions increased growth of the daphnids. The increase in growth of the daphnids as a result of P addition and fatty acid addition was highly correlated (r^2=0.47; P<0.001; Fig. 4).

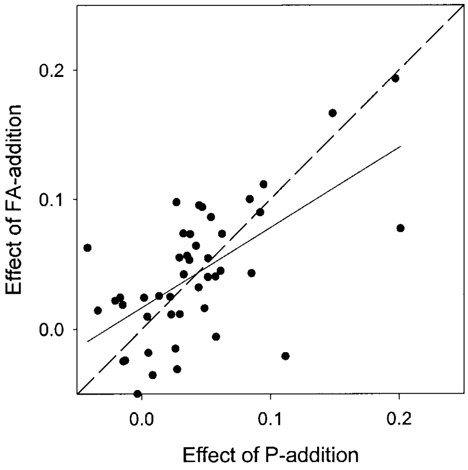

Fig. 4 The relation between the absolute increase in growth rate (day^{-1}) of P addition and the absolute increase in growth rate (day^{-1}) of FA addition. The correlation is highly significant (r^2=0.39; P<0.001). The line is not significantly different from the 1:1 line (*dashed line*)

Discussion

In this study, we have shown that the feeding conditions for zooplankters in mesotrophic Schöhsee varied throughout the year. Feeding conditions were good in spring, decreased during summer and increased again in August–September (Fig. 3). This finding is not new. Using a plethora of different techniques, similar observations were made by Vijverberg and Richter (1982), Larsson et al. (1985), Boersma and Vijverberg (1994b) and Müller-Navarra (1995) in a range of different lakes. Most of our correlations of somatic growth rates with seston parameters were smaller and less significant than those of Müller-Navarra (1995) for the same lake. This is most likely caused by the high POC values in Schöhsee in 1998. Müller-Navarra reported that in about half of her observations the sestonic POC levels were lower than 300 µg l^{-1}. These values were largely responsible for all of the significant correlations between growth rates and seston characteristics. In contrast, all of our POC values were higher than 300 µg l^{-1}. Hence, the lake seems to have changed considerably in the 8 years between the two studies. Nevertheless, still a significant part of the variation in growth rates was explained by the variations in food quantity, even though most the POC values were above the incipient limiting level, which is somewhere in the order of 0.2–0.5 mg C l^{-1} (Lampert 1987).

We set out to investigate the potential factors limiting zooplankton growth, using the supplementing approach, which is commonly used in phytoplankton ecology (e.g. Grover et al. 1999), and recently for the first time and almost concurrently with our study for zooplankton (Elser et al. 2001). Although much has been written about nutritional limitations in natural communities of zooplankton, there have been attempts to supplement zooplankton with specific elements of their food only under laboratory and semi-natural conditions (enclosures) (DeMott and Müller-Navarra 1997; Sundbom and Vrede 1997; Goulden et al. 1999; Boersma and Stelzer 2000), but see Elser (Elser et al. 2001).

In our study, we observed that either the addition of dissolved phosphorus to natural seston or the addition of emulsions with high amounts of HUFAs increased growth of the *Daphnia* individuals (Fig. 3). The increase in growth rates as a result of P supplementation was highly correlated with the increase in growth rate caused by the supplementation with fatty acids (Fig. 4). This was highly unexpected, as it is generally accepted that both P and HUFAs are non-substitutable resources, and of those only one nutrient can be limiting at the same time (von Liebig 1855; Tilman 1982). We had expected to find that on any one given date, the growth of the experimental animals would be increased only by the addition of one substance, and that the addition of the other substance would have made no difference. Therefore, we must conclude that in our experimental set-up phosphorus and the fatty acid emulsions were substitutable resources (Tilman 1982).

There are several explanations for our observation. First of all, there are some experimental features that need to be considered. The fatty acid emulsions contained some phosphorus, and with the emulsions we added 0.5 µg P l^{-1}. This is very small in comparison with the P additions, and the total phosphorus content of the seston, which was always in the range of 10 µg l^{-1}, and hence probably did not play an important role. Another possibility is that the increase in available phosphorus in the treatments with P addition caused the phytoplankton in the seston to grow and hence increase the food quantity. This is unlikely, as the containers with the media were placed in the dark to avoid photosynthesis and algal growth. Alternatively, an increase in bacterial growth in the containers with the food media, as a result of the additions, could have increased food availability in both additions. This is possible, but given the relatively low C:P ratios in the natural seston most likely the bacteria were not very P-limited (Vrede 1998), and most likely the differences in bacterial growth rates between treatments will have been low.

Hence, our observation that P and HUFAs seem to be substitutable resources needs an adaptive or mechanistic explanation. When adding the emulsions of fatty acids we added both the essential component of the food and energy. This does not change the premise of our experimental set-up, as phosphorus and energy should also be non-substitutable resources. However, in a recent study, Plath and Boersma (2001) observed that both the addition of dissolved P and the addition of emulsions with HUFAs increased growth in their experimental animals. They observed that when supplied with inferior quality (low P) food, daphnids reacted by increasing their appendage beat rate, and hence their food uptake rates. They argued that the added fatty acids served as an additional, easily accessible carbon source. This additional energy was used in the behavioural response, the higher appendage beat rates, and thus a higher uptake of phosphorus. The above explanation argues that energy facilitates the uptake of phosphorus, an argument based on the observation that the appendage beat rate increases when the C:P ratio of the food increases (Plath and Boersma 2001), and secondly that the C assimilation decreases with decreasing phosphorus content of the food (DeMott et al. 1998). Obviously, one of the assumptions of this explanation is that increasing the appendage beat rate comes with substantial costs. This, however, has not been measured as yet, and the estimates of 5–60% of basic metabolism are largely based on circumstantial evidence or modelling (Brendelberger et al. 1986; Bohrer and Lampert 1988; Gerritsen et al. 1988; Philippova and Postnov 1988; Urabe and Watanabe 1990; Fryer 1991; Plath 1998).

An interesting alternative is that *Daphnia* are actually energy limited and the supplementation of phosphorus in their diet increases the assimilation efficiency for carbon. It is a commonly described pattern that consumers reduce their assimilation efficiency for carbon when phosphorus (Andersen 1997; DeMott et al. 1998) or nitrogen (White 1993) is limiting. The general assumption seems to be that in situations where phosphorus or nitrogen is limiting, homeostatic zooplankton reduce their carbon assimilation in order to maintain homeostasis (DeMott et al. 1998; Elser et al. 2000b). However, it could well be that the amount of nutrients, *in casu* phosphorus in the food directly affects the carbon assimilation rates. Using a model of individual growth that takes into account the scaling of physiological rates (ingestion, maintenance, moulting etc.), we investigated how much of a change in assimilation efficiency would be required to sustain the differences in growth rates observed between treatments. Figure 5 shows that only a 3–5% change in the assimilation efficiency is required and this level of difference is small relative to the large variation in assimilation efficiencies reported for *Daphnia* (e.g. Urabe and Watanabe 1991a; DeMott et al. 1998). Unfortunately, little is

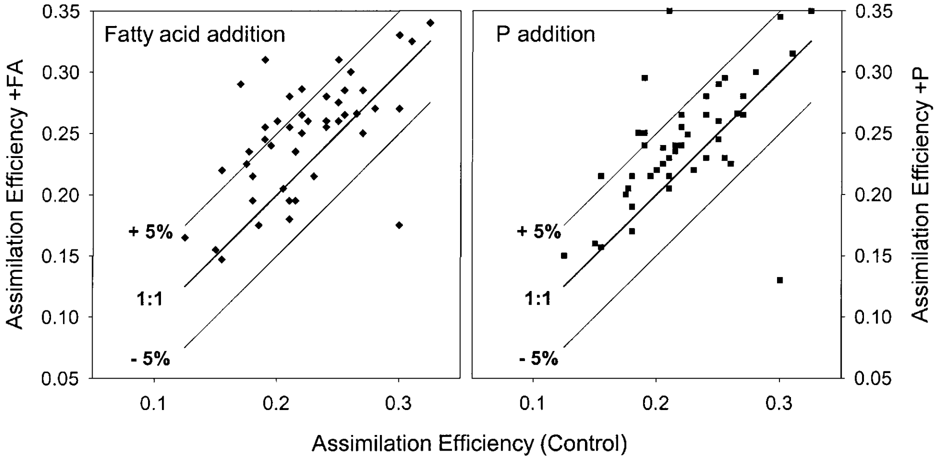

Fig. 5 Changes in assimilation efficiency required to produce the differences observed in somatic growth rates between control versus supplemented treatments. A dynamic energy budget model (Gurney et al. 1990; McCauley et al. 1990) was used to determine the differences in assimilation efficiency. The model is a mixture of continuous (feeding, assimilation, respiration) and discrete processes (i.e. moulting, brood production). Functional dependencies for all rate processes (e.g. length- or food-dependence in ingestion rates etc) were estimated from independent physiological observations (Muck and Lampert 1980; Urabe and Watanabe 1990, 1991b; McCauley et al. 1996) and the model was tested against independent data (Boersma and Vijverberg 1994a) for growth and reproduction of *D. galeata* (E. McCauley, R. Nisbet, W. Lampert, unpublished data). Here, we use the model in a strategic sense, by adopting assimilation efficiencies required to match the growth trajectories of individuals experiencing the control treatment. We then determined how much the assimilation efficiency (the test parameter) would have to be altered to sustain the somatic growth rates observed by individuals in the manipulated treatment. Since food levels vary over the growing season, there is not necessarily a 1:1 mapping of the change in assimilation efficiency required and the change in somatic growth rate between treatments. The model allows us to perform this mapping correctly

known about the physiology of digestion in daphnids, or more specifically, how and where in the gut they take up their food. Anatomical studies have suggested that the different gut regions perform different functions and that there are complex uptake processes associated with phagocytosis (e.g. Schultz and Kennedy 1976; Peters 1987; Brunet et al. 1994). Hence, phosphorus availability in the diet may directly affect carbon assimilation by digestive cells. If this were the case then one would expect both the addition of phosphorus and the addition of energy to increase growth, which indeed it did. Hence, the extra carbon is not used to take up more phosphorus, but the extra phosphorus enables the uptake of more carbon.

It is important to note that in both our adaptive explanations of the phenomenon observed, we conclude that in our experiments the emulsions of fatty acids served as additional energy and not as sources of essential food items. Until we can supply daphnids with single fatty acids and avoid the additional energy addition it will be difficult to truly assess the importance of essential fatty acids under natural conditions. The approach of von Elert and Stampfl (2000), by which they were able to manipulate the fatty acid content of cultured algae experimentally is certainly a major step forward. Nevertheless, we have been able to explain why we still observed a significantly positive correlation between growth rates of the animals and the POC content in the lake.

Hence, we believe that we have to rethink our ideas on limiting resources and perhaps focus on a more mechanistic view of how food supply affects growth rate of herbivores. The recent approach of Kooijman and coworkers on synthesising units (e.g. Kooijman 1998; Muller et al. 2001), by which features of resources are combined with levels of availability to determine herbivore growth rates, seems to be a very promising approach. In natural systems, herbivore growth can be related to the abundance and size distribution of particles, as well as their chemical and nutritional value. Given our relatively poor understanding of compensatory foraging by zooplankton and the physiological flexibility of individuals in achieving the imperfect homeostasis to grow, we have to move away from the quest for single-factor explanations and consider how herbivore growth is achieved when individuals are foraging on diverse resources that vary significantly over time and space.

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