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Seston food quality and *Daphnia* production efficiencies in an oligo-mesotrophic Subalpine Lake

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Abstract

Because of major biochemical imbalances between plants and animals, ecological efficiency at this interface may have a major impact on overall energy flow in ecosystems. In order to study relationships between seston food quality and energy transfer between primary producers and herbivores, we conducted five microcosm experiments in Castle Lake, California, USA during the summer of 1996. We simultaneously performed life table experiments to determine the effects of highly unsaturated fatty acids (HUFA) on *Daphnia rosea* growth, reproduction and survival. The results of these experiments suggest strong energy limitation of *D. rosea* growth in Castle lake during the study. *D. rosea* production was coupled with primary production in Castle Lake and in the microcosm experiments. *D. rosea* production efficiencies, i.e., the ratios of *D. rosea* productivity to primary productivity, decreased towards the end of the summer. A food quality index based on phytoplankton species composition and seston carbon to phosphorus (C:P) ratio were good predictors of *D. rosea* production efficiencies. The predicted *D. rosea* production pattern based on phytoplankton composition and primary productivity matched the zooplankton biomass dynamics in Castle Lake during 1991. Life table experiments showed HUFA effects on *D. rosea* population growth rates, reproduction and survival in support of the HUFA limitation hypothesis.

Abbreviations: C:P – Carbon to Phosphorus, HUFA – Highly Unsaturated Fatty Acids, SAMUFA – Saturated and Mono-Unsaturated Fatty acids, SFQI – Species Food Quality Index

Introduction

Energy in pelagic ecosystems flows from phytoplankton, the primary producers, to zooplankton consumers through the classical food chain and microbial food webs (Weisse and Stockner 1993). The interface between zooplankton and the next lower trophic level shows much variability in energy transfer processes and the factors affecting the energy transfer efficiency are still poorly understood (Hilbricht-Ilkowska 1977; Brett and Müller-Navarra 1997). Energy flow at the primary producer and herbivore interface is influenced by both the quality and quantity of food available for zooplankton (Müller-Navarra and Lampert 1996; Brett and Müller-Navarra 1997; Sterner and Schulz 1998). While food quantity can be easily defined and studied, limnologists have debated what determines seston food quality for zooplankton (Brett 1993; Urabe and Watanabe 1993; Hessen 1993; Müller-Navarra 1995a; Gulati and DeMott 1997).

It is generally accepted that *Daphnia*, large cladoceran filter feeders, play a central role in many freshwater pelagic food webs (Weisse and Stockner 1993; Gaedke and Straile 1998). For *Daphnia*, phytoplankton is a major food source due to its dominance of the seston biomass amongst other possible foods such as detritus, bacteria, flagellates, and ciliates (Lampert 1987; Gaedke 1992). Algal size, secondary metabolites, digestibility, elemental and biochemical composition have previously been used to

explain food quality for zooplankton (Müller-Navarra and Lampert 1996; Lampert and Sommer 1997). While algal physiological status may affect food quality via nutrient limitation, especially phosphorus limitation (Hessen 1992; Urabe and Watanabe 1992; Sterner 1993; Schulz and Sterner 1999), phytoplankton species composition is also important in the food quality of the seston in most aquatic environments (Infante and Litt 1985; Lundstedt and Brett 1991; Brett and Müller-Navarra 1997; Brett et al. 2000). In addition, highly unsaturated fatty acids (HUFA) may be crucial compounds that determine food quality based on phytoplankton composition since each algal phylum tends to have a distinct HUFA composition (Ahlgren et al. 1990; Napotalino 1999). We defined HUFA as a subset of PUFA molecules with 20 or more carbon atoms in this study. Since phytoplankton communities typically show dramatic changes in their composition in temperate waters (Sommer et al. 1986), zooplankton growth in nature may depend on the quality of the food available as the phytoplankton community changes.

Despite the many field studies of phytoplankton and zooplankton dynamics, there are few studies dealing directly with the food quality impacts of phytoplankton composition on zooplankton dynamics in nature (however, see Kerfoot et al. (1988) and De Stasio et al. (1995)). The purposes of this study are: 1) to study the relationships between food quality and production efficiency at the plant-herbivore interface, and 2) to examine whether HUFA are an important component of seston food quality using *D. rosea* life table experiments. We hypothesized that phytoplankton composition (thus HUFA) and seston carbon to phosphorus (C:P) ratios are important factors in determining seston food quality. We estimated seasonal changes in incubated and *in situ D. rosea* production efficiencies and related them with a food quality index based on the phytoplankton community composition and C:P ratios. We evaluated the relationship between production efficiency and this food quality using an independent data set collected from Castle Lake in 1991.

Material and methods

Study site

Castle Lake is a dimictic, oligo-mesotrophic, subalpine lake located in northern California, USA. It has a mean depth of 11.4 m, a maximum depth of 35 m, and a surface area of 0.2 km^2. The lake has a continuous limnological sampling record dating back to 1959. During summer stratification, dissolved inorganic nitrogen and phosphorus levels are typically below 10 $\mu g\ L^{-1}$ in the epilimnion. Total phosphorus concentrations are on average 10 $\mu g\ L^{-1}$ during summer (Brett et al. 1999). Detailed information describing Castle Lake can be found in Goldman and DeAmezaga (1984) and Elser et al. (1990), Jassby et al. (1990).

Lake monitoring

Physical, chemical, and biological parameters in Castle Lake were monitored weekly from a central sampling station during the months of June to September 1996. Chlorophyll *a* was measured at almost daily intervals from epilimnetic water collected with a Van-Dorn water sampler and pooled from 1, 3, 5, and 7 m depths. 100–150 ml of the water was filtered through glass fiber filters (Whatman GF/C), and measured for chlorophyll *a* concentration using the fluorometric method with acid correction after methanol extraction (Marker et al. 1980). Phytoplankton samples were collected weekly from the same epilimnetic waters and preserved with a 1% Lugol's solution for future identification. Crustacean zooplankton and their nauplii were sampled using vertical tows from the bottom to the surface of the lake during both day and night, and fixed with a sucrose and 1% Lugol's solution. The macrozooplankton were counted and converted to biomass using previously determined dry weights for Castle Lake zooplankton (Redfield 1979).

Incubation experiment

Five experiments were conducted during the summer of 1996. Each experiment had control (C) and *D. rosea* addition (D) treatments. 10 L Cubical polyethylene containers (i.e., cubitainers®) were used as the experimental vessels. Each treatment had four replicates except for Exp. 1 which had 5 replicates. Epilimnetic water was collected from 1, 3, 5, and 7 m depths, filtered through an 80 μm zooplankton net to remove macrozooplankton, and mixed in two 100 L plastic containers before being transferred to the containers. *Daphnia rosea* with eggs were picked by Pasteur pipette from lake water collected by vertical and horizontal tows ($n > 500$) and then 100 of these were added randomly to each experimental unit in the *D.*

rosea addition treatments to a final density of 10 *Daphnia* L^{-1}. *D. rosea* density varied between 0.5 to 15 individual per liter in the epilimnion of Castle Lake during these experiments. One hundred *D. rosea* were fixed with a 1% Lugol's and sucrose solution for initial biomass estimates. All cubicontainers were hung on a rectangular PVC pipe rack and incubated *in situ* at 4 m depth for 7 d. At the end of the 7-d incubation, primary productivity in each container was measured by the ^{14}C method with a 4-h incubation from 1100 to 1500 h. 100–150 ml of experimental water was filtered for chlorophyll *a* as previously described. Phytoplankton were collected and fixed with 1% Lugol's solution. Phytoplankton were counted and measured with a Wild inverted microscope using the Utermöhl technique (Utermöhl 1958). Crustacean zooplankton were collected by pouring the contents of the cubicontainers into a bucket with a 63 μm mesh size screen at the end of the experiments and fixed with a sucrose and 1% Lugol's solution. Soluble reactive phosphorus in lake water and water from incubation experiments was analyzed within 24 h of collection using the phenolhypochlorite method (Solórzano 1969). Total phosphorus was determined by the persulfate digestion method (Strickland and Parsons 1972). Particulate phosphorus concentration was estimated from the difference between total phosphorus and soluble reactive phosphorus concentration in the Lake. Seston carbon concentrations were estimated from the relationship between chlorophyll *a* and seston carbon data obtained from Castle Lake during 1997 and 1998. Seston C:P ratios were calculated from particulate phosphorus concentrations and estimates of seston carbon concentrations for Castle Lake water. Since we estimated particulate phosphorus concentration indirectly, our C:P ratios may be underestimated.

Energy transfer efficiency

Production efficiency was used as energy transfer efficiency in this study according to Hilbricht-Ilkowska (1977):

$$\text{Production efficiency:} \quad P_n/P_{n-1}$$

where P indicates productivity, n denotes the herbivore level and $n - 1$ denotes the primary producer trophic level.

The measurement of secondary production in the field is complex due to difficulties in measuring the zooplankton mortality rate (Brett et al. 1992). For incubation experiments, we used *D. rosea* biomass increase during incubation as a measure of *D. rosea* production. Egg production and neonate biomass increase were regarded as new biomass production during incubation assuming no weight increase in adults. Therefore, our estimates for new biomass production were partial production estimates. We assumed that a second clutch would be produced in 4 days and that neonates were 3 to 7 days old at the end of the experiment. 3- and 7-d-old juvenile dry weights were estimated using average dry weights of *D. rosea* adults (8.2 μg DW from Redfield (1979)) and eggs (2.5 μg from D.C. Müller-Navarra, unpublished data) in Castle Lake, and average time for *D. rosea* to mature (25 d; data in this study) assuming the dry weight of neonate linearly increase during a given experimental period. We used average dry weight estimates of 3- and 7-day-old neonates to calculate juvenile biomass. For the calculation of production efficiencies, *D. rosea* carbon content was calculated from zooplankton dry weight using a conversion factor of 0.4 (Peters 1983). Mean primary productivity per hour during the experiment was estimated from the average of initial and final primary productivity. The primary productivity in the incubated water at the end of each experiment was measured with ^{14}C, while initial primary productivity was estimated using the ratio between chlorophyll *a* concentration and primary productivity from the control treatment in each experiment. Calculated mean hourly primary productivity was projected to total primary production during the experiment by the ratio of total irradiance during the experiment to the irradiance during primary productivity measurement (4 h).

In the monitoring study, productivity of *D. rosea* was estimated from the products of their biomass and estimated growth rates (Sanders and Lewis 1988) during the summer growth season. Population birth rate (b) was used to estimate growth rate (g). It should be noted that we used the numerical increase rate to estimate the biomass growth rate (Paterson et al. 1997). All intact and loose eggs and embryos of *D. rosea* from pooled epilimnetic samples collected during the day (around 1300 h) and at night (around 2200 h) were counted for estimation of egg ratios following the equation of Paloheimo (1974). Primary productivity in the lake was measured in duplicate with the standard *in situ* ^{14}C technique (Goldman 1963, 1968). Samples were incubated in the lake from 1000 h to 1400 h, and daily productivity was estimated from the

ratios of solar radiation during the entire day to that during the incubation period.

Food quality index

Phytoplankton community composition in a lake is not constant, and typically shows dynamic seasonal changes (Harris and Piccinin 1980). Many laboratory growth experiments have shown that different phytoplankton taxa have different food quality for zooplankton growth (Infante and Litt 1985; Lundstedt and Brett 1991). Brett and Müller-Navarra (1997) present a food quality rank for 10 species from 5 major phytoplankton groups based on the average of the observed change in individual zooplankter abundance in growth bioassays using *Daphnia*, *Bosmina* and *Chydorus*. For these food quality ranks, we averaged these taxa as follows: cyanobacteria: 0.2, green algae: 0.525, diatoms: 0.7, cryptomonads: 0.95, on a scale of 0–1. A high value in the food quality rank means high food quality and vice versa. These average food quality ranks were then multiplied by the relative biovolume of each edible phytoplankton group. This produced a food quality index for the whole phytoplankton community (species food quality index) with a range of 0–1. Since most chrysophytes (especially *Dinobyron* spp.) and dinoflagellates in this study were inedible for *D. rosea* due to their large size, they were assigned 0 in the calculations of the species food quality index. For phosphorus limitation calculations, the stoichiometry model for phosphorus and carbon was used to calculate the expected growth reduction for *D. rosea* (Brett et al. 2000). Assuming 300 as the critical C:P ratio in food and 86 as the *D. rosea* C:P ratio (Sterner and Hessen 1994), the predicted reduction for *D. rosea* growth would be:

$$\begin{aligned}\text{Predicted reduction} &= 1 - K_c(predicted)/K_c(theoretical)\\ &= 1 - (C{:}P_z/C{:}P_s)/(C{:}P_z/300)\\ &= 1 - 300/C{:}P_s\end{aligned}$$

where K_c is carbon growth efficiency of *D. rosea*, $C{:}P_z$ is molar C:P ratio in *D. rosea*, and $C{:}P_s$ is molar C:P ratio in seston. Thus, we used a function of min (1, $300/C{:}P_s$) to estimate P limitation impacts on seston food quality. Overall food quality index used in this study was as follows:

$$\begin{aligned}\text{Food quality index} &= \text{Species Food Quality Index} \cdot \text{Reduction by P limitation}\\ &= (Rb_{bluegreen}\cdot 0.2 + Rb_{green}\cdot 0.525 + Rb_{diatoms}\cdot 0.7 + Rb_{crypto}\cdot 0.95)*(\min(1, 300/C{:}P_s))\end{aligned}$$

where Rb stands for relative biomass of each phytoplankton group.

Life table experiment

Since our hypothesis was that HUFA are important in determining food quality of phytoplankton, the species food quality index was expected to be related to algal HUFA content. In this study, we tried to assess the importance of HUFA for seston food quality by adding HUFA emulsions to lake water and feeding these mixtures to *Daphnia* in life table experiments. Three consecutive life table experiments were performed in addition to the incubation experiments conducted during the same field season. Each experiment had 3 treatments in which *D. rosea* neonates received lake water (CONTROL treatment), lake water with HUFA emulsions added (HUFA treatment), and lake water with saturated fatty acids (SAFA) and monounsaturated fatty acids (MUFA) emulsions added (SAMUFA treatment). We collected epilimnetic water at 1, 3, 5, and 7 m depths from the central sampling station. For each treatment, we used 15–18 neonates (< 12 h old) that had been born from *D. rosea* collected from Castle Lake the previous night. Each neonate was placed in a 250 ml beaker containing treatment water. We used ICES 30/0.6/C for the HUFA treatments and ICES 0/-/C for the SAMUFA treatments (Table 1). These standardized emulsions were made available through the International Council for the Exploration of the Sea (ICES)-Working Group on Mass Rearing of Juvenile Fish (ICES 1994). These enrichment emulsions have been designed to manipulate ω3 HUFA concentrations in live feed organisms for aquaculture (Coutteau and Sorgeloos 1997). According to Han et al. (2000), the total lipid content of ICES 30/0.6/C and ICES 0/-/C were quite similar while ICES 0/-/C was missing ω3 PUFA, especially ω3 HUFA. These ICES emulsions have been used for enriching brine shrimp (*Artemia*) (Coutteau and Sorgeloos 1997), *Daphnia* (Boersma 2000) and freshwater zooplankton communities (Boersma and Stelzer 2000). We used standard HUFA

and SAMUFA emulsions from Laboratory of Aquaculture and Artemia Reference Center (University of Ghent, Belgium) which contained about 37% and 1% HUFA as a percent of total fatty acid, respectively (Table 1). The fatty acids in both emulsions are bound in triacilglycerides (TAG) (Boersma and Stelzer 2000) and contain emulsifiers, antioxidants and liposoluble vitamins (Han et al. 2000). The particle size of the ICES emulsion are in the range of 1–2 μm and is readily taken up by *Daphnia* (Boersma 2000). For the HUFA and SAMUFA treatments, we prepared fresh ICES 30/0.6/C or ICES 0/-/C emulsions each day by adding 0.5 g FA L^{-1} to dionized water. We then added 1 ml of these mixtures to raw lake water in a 250 ml beaker for a final concentration of 2 mg FA L^{-1} (0.6 mg HUFA L^{-1} in HUFA treatment). The intent with these additions was to increase the HUFA composition of the seston to about 40% HUFA relative to the original dry wt (assuming seston particulate concentrations of 1.5 mg L^{-1}) which is similar to the HUFA content of highly nutritious cryptophytes (Brett and Müller-Navarra 1997). Since we added fresh emulsions and changed the lake water daily, oxidation of unsaturated fatty acids was expected to be low (McEvoy et al. 1995). SAMUFA treatment was regarded as a reference treatment for lipids since the HUFA treatment received more lipids than did the CONTROL treatment. Neonates were examined daily for survival, reproduction, and molting. The first life table experiment was carried out between June 23rd and August 13th (51 d) while the second was performed between July 10th and September 12th (64 d) in 1996. The third experiment was carried out from August 17th until September 18th (32 d) in 1996. This experiment was terminated early because the field season ended.

Life history traits

The intrinsic rates of population increase (r) were estimated from reproductive rates (R_0) and cohort generation time (T_c):

$$r = R_0/T_c,$$

$$T_c = \Sigma x l_x m_x / \Sigma l_x m_x, \quad \textit{and}$$

$$R_0 = \Sigma l_x m_x,$$

where l_x indicates the proportion of original cohort surviving to day x and m_x indicates the offspring produced per survivor on day x. The Jackknife method was used to generate pseudo r values and to calculate their standard errors (Meyer et al. 1986). We used

Table 1. Fatty acid (FA) profiles of ICES 0/-/C/2 (30.03.94) and ICES 30/0.6/C/1 (19/4/96) that we used for our life table experiments. Fatty acid contents are shown in mg g dry weight^{-1}. ND stands for not detected, SAFA is for saturated fatty acid, UFA is for unsaturated fatty acid, PUFA is for polyunsaturated fatty acid, and HUFA is for highly unsaturated fatty acid.

FA	ICES 0/-/C/2	ICES 30/0.6/C/1
14:0	129.8	58.6
14:1ω5	0.0	1.8
15:0	0.2	4.6
15:1ω5	0.1	0.7
16:0	85.7	136.6
16:1ω7	0.8	68.1
17:0	0.2	9.2
17:1ω7	0.1	ND
18:0	24.0	19.2
18:1ω9	64.0	92.7
18:1ω7	1.8	38.0
18:2ω6-tras	0.0	1.0
18:2ω6-cis	45.8	44.7
18:3ω6	ND	1.6
18:3ω3	4.1	10.6
18:4ω3	0.1	16.3
20:0	0.8	1.2
20:1ω9	0.5	6.7
20:2ω6	0.1	1.2
20:3ω6	ND	0.8
20:4ω6	ND	9.5
20:4ω3	ND	6.2
22:0	0.5	ND
20:5ω3	1.4	147.9
21:5ω3	ND	6.4
22:4ω6	ND	1.0
22:5ω6	ND	4.0
22:4ω3	ND	0.7
24:0	0.3	ND
22:5ω3	0.2	22.3
24:1ω9	ND	3.2
22:6ω3	1.3	107.5
FA	361.8	822.3
SAFA	241.5	229.4
UFA	120.3	592.9
PUFA	53.0	381.7
ω3-PUFA	5.8	317.9
ω3-HUFA	3.0	307.5
ω3-HUFA/FA (%)	0.83	37
DHA/EPA		0.73

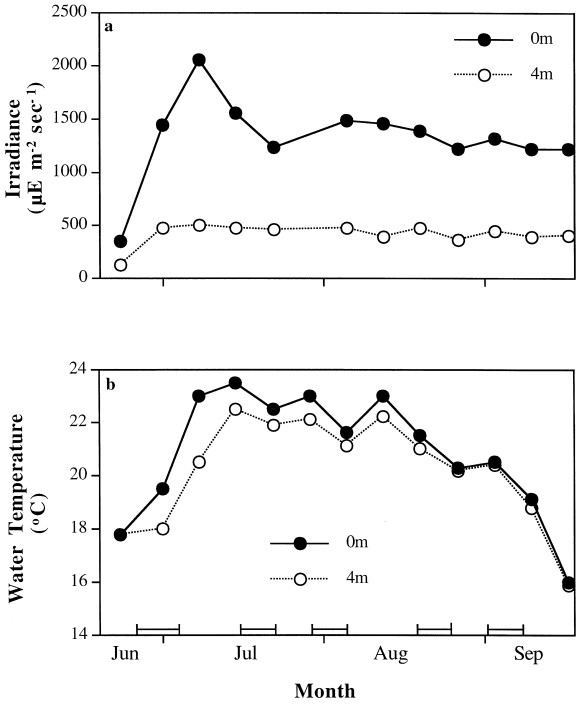

Figure 1. (a) Irradiance and (b) water temperature at 0 m and 4 m depth in Castle Lake in 1996. Bars in lower panel indicate incubation experiment periods.

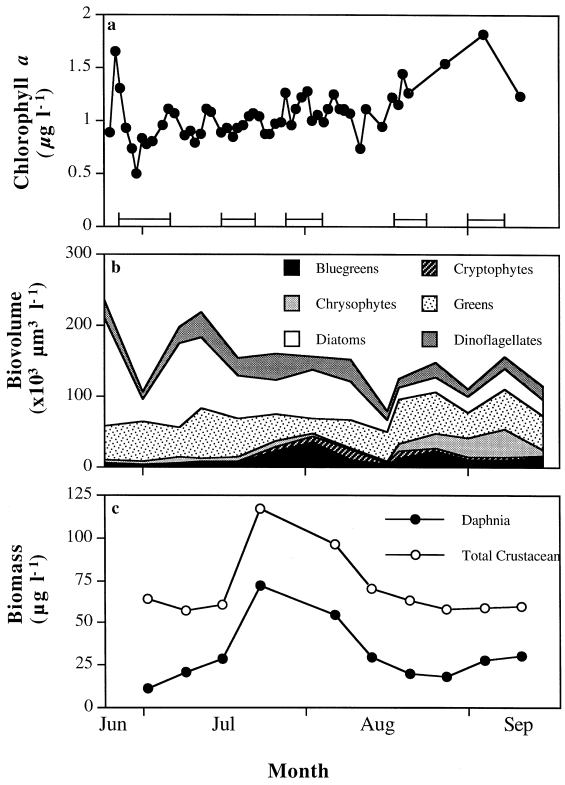

Figure 2. (a) Chlorophyll *a*, (b) phytoplankton assemblage, and (c) crustacean macrozooplankton biomass in Castle Lake during summer 1996. Bars in the top panel indicate incubation experiment periods.

pseudo r values generated by Jackknifing for statistical comparisons of the intrinsic population growth rates. Scheffe's F test was used to compare each treatment using Statview™ II.

Results

Light and water temperature in Castle Lake

Light and water temperatures were quite stable during experimental periods except for Experiment 1 (Figure 1), when both epilimnetic irradiance and water temperature were lower compared to other experimental periods. For the rest of the experimental period, irradiance and water temperature were around 500 µE m^{-2} sec^{-1} and 20–21 °C, respectively, at 4 m depth.

Phytoplankton and zooplankton assemblage changes in the lake

Chlorophyll *a* levels in the pooled epilimnetic samples from Castle Lake averaged $\approx$ 1 µg L^{-1} in early summer and increased to $\approx$ 2 µg L^{-1} in late summer (Figure 2a), which is fairly typical for Castle Lake (Müller-Solger et al. 1997). This suggests the availability phytoplankton as food for zooplankton was very limited during these experiments. During this period, the phytoplankton community showed significant changes in its species composition (Figure 2b). Diatoms dominated the phytoplankton community during early summer, while cyanobacteria and chrysophytes dominated towards end of summer. The dominant taxa in the chrysophyte group were *Dinobryon* sp., which form large, inedible colonies. The *D. rosea* population and total crustacean biomass was relatively high in the early summer and decreased towards the end of summer (Figure 2c).

Food quality and production efficiency in Castle Lake

As expected, phytoplankton species food quality decreased toward the end of summer 1996 as diatoms were replaced by cyanobateria and chrysophytes.

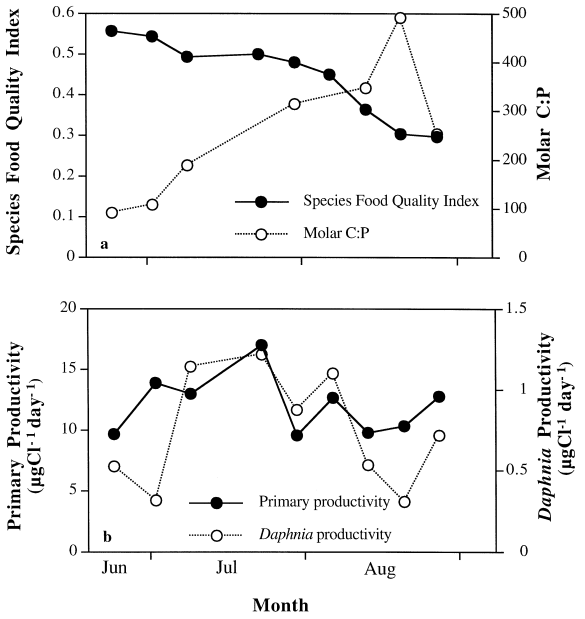

Figure 3. Temporal change of (a) the species food quality index (SFQI) and molar C:P ratios of seston, and (b) primary and *Daphnia rosea* productivity in the epilimnion of Castle Lake, 1996.

Also, seston C:P ratios increased to values higher than 300 by the middle of August 1996 (Figure 3a). In Castle Lake, primary productivity and *D. rosea* productivity exhibited considerable variability in the summer of 1996 (Figure 3b). They showed similar patterns in July and in the beginning of August, but showed large discrepancies in June and after the middle of August. The estimated food quality index from the species food quality index and seston C:P ratio matched with change in *D. rosea* production efficiency in Castle Lake, although early *D. rosea* production efficiencies were lower than expected based on seston food quality (Figure 4). Including seston C:P ratio when calculating the estimated food quality strengthened this correlation, especially in the late summer.

Food quality and production efficiency in incubation experiments

In the incubation experiments, primary production and *D. rosea* production showed similar unimodal patterns, with the highest values in the third experiment (Figure 5a). Estimated *D. rosea* production showed patterns similar to that of primary production in the incubation experiments (Figure 5b). *Daphnia rosea* production efficiencies in the incubation experiments showed a pattern very different from primary productivity and *D. rosea* production patterns, decreasing until the 4th experiment (Figure 5c). The lower production efficiencies might be due to higher abundance of inedible species such as the large-colony forming chrysophyte *Dinobryon* sp. and the large-celled dinoflagellate *Gymnodinium* sp. However, the edible fraction of phytoplankton biovolume did not correlate well with production efficiency. *D. rosea* production efficiency in the incubation experiments was significantly correlated with seston food quality as estimated by the species food quality index and C:P ratio, although *D. rosea* production efficiency in the second experiment (2nd in seston food quality) was lower than that expected based on this index (Figure 6). Also, *D. rosea* production efficiencies in the microcosm experiments were somewhat lower than those observed in Castle Lake.

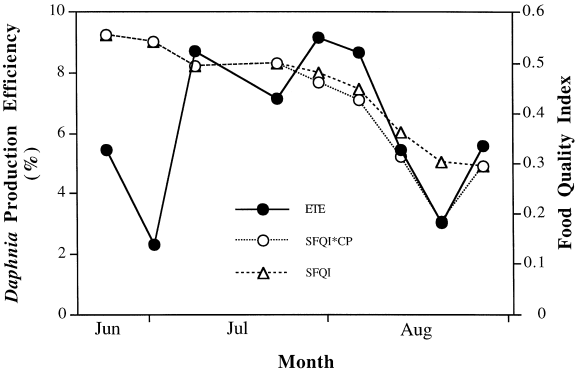

Figure 4. Daphnia rosea production efficiency (ETE) in the epilimnion of Castle Lake, 1996. Food quality index was calculated from the Species Food Quality Indices modified with seston C:P ratio (SFQI*CP) or from only species food quality indices (SFQI).

Projection to 1991 data set

To evaluate the relationship between seston food quality and zooplankton production efficiency found from *D. rosea* treatments, we examined unpublished Castle Lake 1991 data (Figure 7). From the 1991 data set, primary productivity, *D. rosea* biomass and phytoplankton composition data were all available. First, we calculated production efficiencies from phytoplankton composition in 1991, using the linear relationship between the species food quality index and production efficiencies from the 1996 experiments. Since Seston C:P ratios were not available for this data set, we could not consider phosphorus limitation for these data. Next, *D. rosea* productivity in 1991

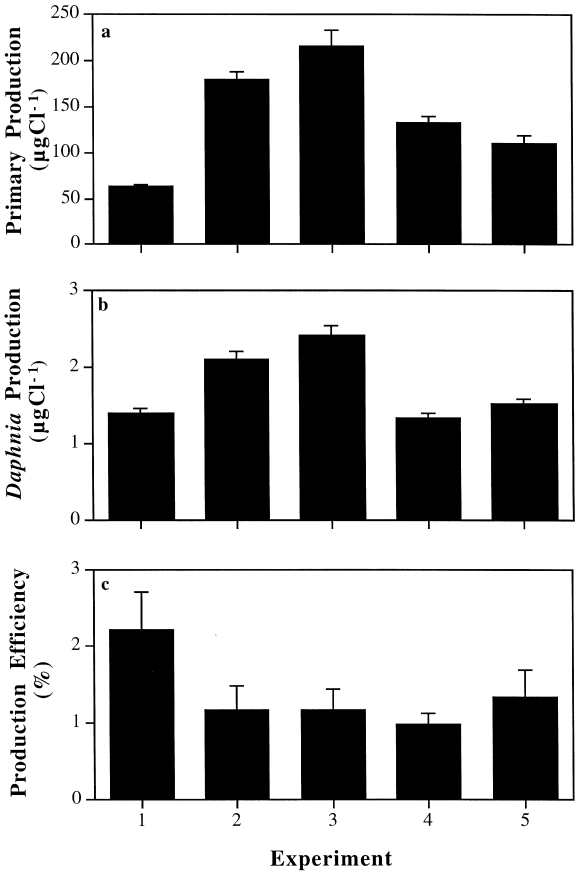

Figure 5. Temporal change of (a) primary production, (b) *Daphnia rosea* production, and (c) *Daphnia* production efficiency during incubation experiments over summer 1996. Bars indicate standard deviation (n = 4 except for Exp. 1 (n = 5)).

was projected from primary productivity in the epilimnion and the calculated production efficiencies.

Although it is not entirely appropriate to compare the projected secondary productivity and zooplankton biomass directly since they are in different units, the patterns for *D. rosea* biomass and projected production were quite similar. Both zooplankton biomass and projected secondary productivity showed higher peaks in early summer, then decreased as summer progressed. A regression analysis showed a significant correlation between projected secondary production and zooplankton biomass (*D. rosea* Biomass = 36.42 * (projected *D. rosea* productivity) – 2.68; $r^2 = 0.55$, $n = 11$, $p < 0.01$).

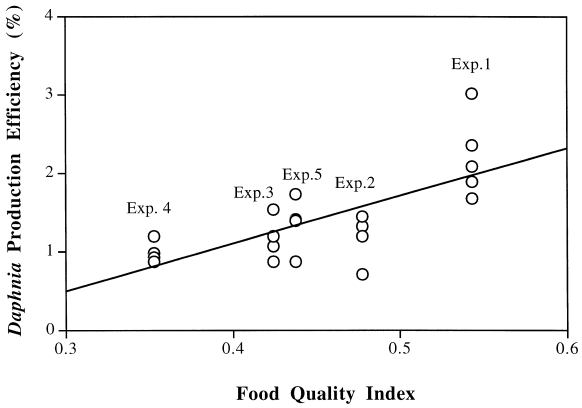

Figure 6. Relationship between seston food quality index and *Daphnia rosea* production efficiency. Seston food quality index was calculated from species food quality index and seston molar C:P ratios. Slope and intercept for the regression line was 6.114 and −1.343 ($r^2 = 0.511$; $n = 21$; $p = 0.0003$).

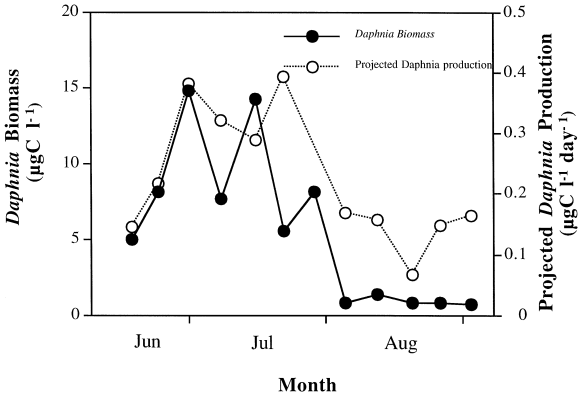

Figure 7. Projected *D. rosea* productivity and observed *D. rosea* biomass in Castle Lake, 1991. *Daphnia rosea* productivity was projected by multiplying production efficiency (from phytoplankton composition) to primary productivity.

Life table experiments

The three life table experiments supported our hypothesis that seston HUFA content is an important food quality factor for *D. rosea* growth although the effects of HUFA were rather modest (Table 2). *Daphnia rosea* in the HUFA treatment showed the highest population growth rates of (r) in all experiments. The SAMUFA treatment showed significantly higher growth than the CONTROL treatment in two of the three experiments. At the end of each experiment, significantly more *D. rosea* survived in the HUFA treatment than in any other treatments except for Exp. 3 which had shorter experimental period than others. However, there was no statistically significant difference in age at first reproduction (AFR) between the

Table 2. Rates of population increase (r, ± S.E. of the jack-knife method), age at first reproduction (AFR, ± S.E.), and survival until the end of the experiment (*S*) of *Daphnia rosea* grown in lake water (CONTROL), lake water with HUFA emulsion (HUFA), and lake water with SAFA and MUFA (SAMUFA). The results of Scheffe's multiple comparison are shown as a, b, and c at the 95% significance level for *r* and AFR. We did binomial test of significance for *S*. For *S*, we just showed significance between HUFA and SAMUFA treatment.

	Treatment	r (d^{-1})	AFR (d)	S (%)
Exp. 1				
	CONTROL	−0.012 (0.0000)^{a}	32.00 (0.000)^{a}	7
	HUFA	0.058 (0.0006)^{c}	25.83 (1.493)^{a}	38***
	SAMUFA	0.034 (0.0012)^{b}	24.33 (1.667)^{a}	13
Exp. 2				
	CONTROL	0.036 (0.0010)^{b}	22.25 (0.854)^{b}	13
	HUFA	0.066 (0.0006)^{c}	19.00 (0.365)^{a}	44***
	SAMUFA	0.024 (0.0024)^{a}	21.67 (1.202)^{ab}	7
Exp. 3				
	CONTROL	−0.025 (0.0015)^{a}	21.60 (2.561)^{a}	33
	HUFA	0.050 (0.0006)^{c}	18.69 (1.247)^{a}	61
	SAMUFA	0.031 (0.0007)^{b}	18.75 (1.473)^{a}	56

*for $p \leq 0.05$, ** for $p \leq 0.01$ and ***for $p \leq 0.001$

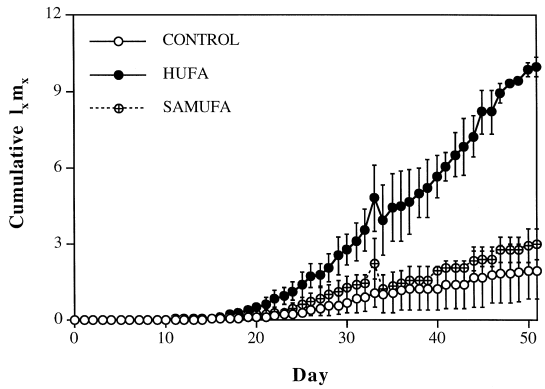

Figure 8. Averaged cumulative $l_x m_x$ of *D. rosea* at each day from life table experiment 1, 2 and 3 in 1996. Final values of cumulative $l_x m_x$ equal to reproductive rate (R_0). Values are averages of Exp. 1, 2, and 3 from day 1 through day 32, and averages of Exp. 1 and 2 between day 33 and day 51. Data are expressed as means ± S.E. CONTROL; lake water treatment, HUFA; lake water with the addition of ICES 30/0.6/C emulsion, and SAMUFA; lake water with the addition of ICES 0/-/C emulsion.

HUFA and the SAMUFA treatment. In all experiments, the cumulative $l_x m_x$ at all ages and reproductive rate (R_0) were always the highest in the HUFA treatment (Figure 8).

Discussion

The results of this study have important implications for planktonic food web studies. First, production of filter feeding cladoceran *D. rosea* appeared to be coupled to primary production in Castle Lake. Second, the ecological efficiency, or energy (carbon) transfer efficiency between primary producers and consumers, can be predicted from seston food quality using phytoplankton species composition and the seston C:P ratio. Finally, highly unsaturated fatty acids (HUFA) appear to play a significant role in determining seston food quality for *D. rosea*.

Daphnia rosea in Castle Lake appeared to be strongly carbon (energy) limited. Many researchers assume, in accordance with Liebig's law of minimum, that only a single factor determines the growth rate of animals at any given time. In fact, recent works on stoichiometric theory of essential fatty acids and field study also assume that only one factor at a time determines marine copepod growth (Anderson and Pond 2000; Wacker and von Elert 2001). However, this assumption, while logical, is simply an assumption. Under a strong energy limitation, HUFA limitation may not be important if only one factor can limit zooplankton growth (Boersma and Stelzer 2000; Wacker and von Elert 2001). However, the alternative assumption that two or more resources can be simultaneously limiting is also quite plausible. Park et al. (2002) showed that P-limited *Synechococcus* sp. supported lower *Daphnia magna* growth rates than did P-saturated *Synechococcus* sp. It is certainly possible that growth depression by insufficient multiple resources is common in nature. In the present study, the population rates of increase (r) for *D. rosea* was slightly higher in the SAMUFA (lipid addition) treatment than in the Lake seston treatment. Furthermore, the HUFA treatment showed substantially higher *D. rosea* growth rates than either of the other treatments, which suggests both HUFA and energy co-limited *D. rosea* growth.

The *D. rosea* production pattern was overall similar to the pattern of primary production in this study, supporting previous findings that primary and secondary production are highly correlated (Lacroix et al. 1999). There is a possibility that this unimodal pattern of *D. rosea* production might be due to the direct effect of water temperature (Shuter and Ing 1997; Stockwell and Johannsson 1997). Temperature could affect zooplankton production directly through physiological processes as zooplankton metabolism is

highly temperature-dependent in addition to indirect effects via primary production (Bottrell et al. 1976). In the present study, low water temperatures probably lowered *D. rosea* production during the early summer (Figure 3b). However, during similar temperature periods later in the summer, *D. rosea* production showed considerable variability. Therefore, overall, water temperature did not appear to be the major factor for *D. rosea* production. We infer that *D. rosea* in a food-limited situation would primarily respond to the rate of food supply (primary productivity) after water temperatures reached a certain threshold.

The second implication of our results is that phytoplankton composition and their physiological status (i.e., carbon to phosphorus ratio) may predict energy transfer efficiency between primary producers and herbivores. Although *D. rosea* production followed the pattern of primary production, the production efficiencies showed considerable variability with season rather than a seasonal independence (Figures 4 and 5). This result indicates food availability was not the sole factor for *D. rosea* production. From the present study, we showed correlative evidence suggesting phytoplankton food quality influenced *D. rosea* production efficiencies in Castle Lake. The species food quality index in this study used the relative biovolume of each edible phytoplankton taxon to total biovolume of phytoplankton, which could reflect the inedible phytoplankton abundance. Therefore, the species food quality index in the present study includes ingestibility (size) in addition to biochemical content (Brett and Müller-Navarra 1997). Seston phosphorus content appeared to be important especially in the late summer when the epilimnion water was depleted of phosphorus due to stratification (Figure 3a); (Elser and George 1993). Many other factors such as temperature, competition among zooplankton, and fish predation can affect zooplankton biomass in addition to seston food quality (Achenbach and Lampert 1997; Mumm 1997). The application of phytoplankton species food quality index for estimating secondary production for the 1991 Castle Lake data set resulted in a good match although in late summer, the discrepancy between the projected *D. rosea* production and biomass increased (Figure 6), suggesting possible top-down effects from fish predation. It has previously been suggested that fish predation on *D. rosea* by brook trout, rainbow trout and golden shiners becomes more intense toward late summer (Elser et al. 1995).

The production efficiency of *D. rosea* in the present study was in the range of 2–9% in the *in situ* determinations and between 1–3% in the incubation determinations. Since the *in situ* determinations did not consider mortality of *D. rosea* and the incubation determinations did not consider adult growth, the actual production efficiencies would have been higher than values from the incubation determinations and lower than the values from the *in situ* determinations. Hilbricht-Ilkowska (1977) suggested that most lakes with primary productivity under 200 kcal m^{-2} $season^{-1}$ have less than 10% of production efficiencies. Considering that we did not determine the production efficiencies for total zooplankton, our estimates of *D. rosea* production efficiencies appears to be realistic.

Food quantity and quality act together in driving zooplankton dynamics (Müller-Navarra and Lampert 1996). We used primary productivity and phytoplankton composition to project secondary productivity. It is not novel to use phytoplankton composition as a food quality descriptor (Kerfoot et al. 1988; Kleppel and Burkart 1995; Schmidt et al. 1998). While primary productivity appears to be a good representation of food availability, the phytoplankton species composition component in projecting secondary productivity still needs improvement. Although phytoplankton may represent the majority of edible seston sometimes (Gaedke 1992), a food quality index based on phytoplankton composition would probably be only a very coarse indicator of zooplankton growth. For example, diatoms may not always be a good food for marine copepods (Ban et al. 1997; Jónasdóttir et al. 1998), while bluegreens sometimes enhance marine copepod production (Schmidt and Jónasdóttir 1997). Also, it has been known that viable gut passage of gelatinous algal taxa (Porter 1975; Vanni and Lampert 1992) and thickened cell walls in phosphorus limited algae (Van Donk and Hessen 1993, 1995; Van Donk et al. 1997) reduce digestibility for *Daphnia*. Therefore, digestibility appears to be another important factor in determining algal food quality in addition to edibility and biochemical composition. However, at this stage, we regard highly unsaturated fatty acid (for example EPA) content and phosphorus content in seston as the most promising and easily measurable indices of seston food quality for *Daphnia*.

Hairston and Hairston (1993) argue that ecological efficiency is a product of trophic structure. According to them, terrestrial communities usually have

3 trophic levels and low consumption efficiencies for herbivores while pelagic communities generally have 4 trophic levels with higher consumption efficiencies by herbivores. Their explanation can be regarded as a top-down position on energy transfer efficiency. Our results suggest that ecological efficiency may also be influenced by bottom-up forces determined by seston food quality. Our results further suggest that ecological efficiency is variable within the same trophic configuration. We are convinced that both bottom-up and top-down forces affect energy transfer efficiency and secondary production (Hunter and Price 1992; Power 1992; Brett and Goldman 1997). It is also likely that herbivores such as *Daphnia* have impacts on phytoplankton composition and production by selectively grazing edible species and recycling nutrients. Kerfoot et al. (1988) tried to classify algal species by the Principal Components Analysis with the algal response to *Daphnia* density. They showed that *Daphnia* cause rapid shifts within algal community from accessible and edible algae to refractory digestion-resistant species.

Seston HUFA content has been proposed to be a determinant of seston food quality (Ahlgren et al. 1990; Müller-Navarra 1995a), while the seston carbon to phosphorus (C:P) ratio has been proposed by others (Urabe and Watanabe 1992). Our results lead us to the opinion that phytoplankton species composition and phosphorus content determine zooplankton food quality. HUFA in algae are thought to be more strongly related to species composition than algal P content or other factors (Napotalino 1999). Thus, factors like HUFA specific to the taxonomic phytoplankton group appear to play an important role in food quality for zooplankton. The life table experiments in the present study provided support for the HUFA limitation hypothesis by demonstrating that HUFA additions enhanced *D. rosea* population growth rates, reproduction and survival (Table 2). A recent study shows that biomass transfer efficiency to *Daphnia* seems to be related to a highly unsaturated fatty acid, eicosapentaenoic acid (EPA), content in a hypereutrophic system (Müller-Navarra et al. 2000). However, in a similar HUFA addition study using mesocosms, *Daphnia* reached the highest number only in the saturated fatty acid addition treatment (Boersma and Stelzer 2000). Our life table experiments were substantially different from their study in the way we added the emulsions. We added fresh emulsions daily to new lake water in the life table experiments, whereas Boersma and Stelzer (2000) did not change the water in their experiments but simply added new emulsions daily. Continually adding new emulsions to the same solutions is highly problematic because it has been previously pointed out that the emulsions employed in our and Boersma and Stelzer (2000) experiments rapidly degrade when incubations exceed 24 hr (McEvoy et al. 1995). It is also quite likely that HUFA produce toxic metabolites when they degrade. Thus it may not be possible to test the nutritional importance of HUFA using the design employed by Boersma and Stelzer (2000). High seston C:P ratios also appeared to be related to reduced production efficiencies in the present study (Figure 5). This supports the notion that increasing C:P ratio in seston could reduce carbon transfer efficiency at the plant-herbivore level (Urabe and Sterner 1996; Hessen and Faafeng 2000). Overall, as summer progressed, the seston's HUFA and phosphorus content declined, and the proportion inedible phytoplankton species increased.

It is also possible that other factors, not measured in this study, such as toxins (Jónasdóttir and Kiørboe 1996), amino acids (Kleppel et al. 1998), phospholipids (De Lange and Arts 1999), ω3-PUFA (Wacker and von Elert 2001), trace elements, proteins or vitamins co-vary with seston HUFA or P content and may explain additional zooplankton growth. To improve our understanding of seston food quality for zooplankton, it will be necessary to conduct more direct studies of zooplankton production relative to the seston fatty acid composition and C:P ratio in natural systems.

Conclusions

In conclusion, this study has shown the importance of phytoplankton species composition in addition to P limitation in determining seston food quality daphnid growth. We also showed that food quality based on phytoplankton species composition and seston C:P ratio correlated well with *D. rosea* production efficiencies. This suggests that combining food quality and primary productivity might be useful in predicting secondary productivity and energy flow in pelagic ecosystems. Finally, this study suggests that an index of seston highly unsaturated fatty acid (HUFA) content is a promising candidate for a food quality index that, in turn, may determine the efficiency of energy transfer processes in pelagic ecosystems. Further studies should focus on the role of seston food quality in terms of seston essential fatty acid content and

phosphorus content in determination of energy transfer efficiency in pelagic ecosystems.

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References

Achenbach L. and Lampert W. 1997. Effects of elevated temperatures on threshold food concentrations and possible competitive abilities of differently sized cladoceran species. Oikos 79: 469–476.

Ahlgren G., Lundstedt L., Brett M. and Forsberg C. 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. J. Plankton Res. 12: 809–818.

Anderson T.R. and Pond D.W. 2000. Stoichiometric theory extended to micronutrients: Comparison of the roles of essential fatty acids, carbon, and nitrogen in the nutrition of marine copepods. Limnol. Oceanogr. 45: 1162–1167.

Ban S., Burns C., Castel J., Chaudron Y., Christou E., Escribano R. et al. 1997. The paradox of diatom-copepod interactions. Mar. Ecol. Prog. Ser. 157: 287–293.

Boersma M. 2000. The nutritional quality of P-limited algae for *Daphnia*. Limnol. Oceonogr. 45: 115–1161.

Boersma M. and Stelzer C. 2000. Response of a zooplankton community to the addition of unsaturated fatty acids: an enclosure study. Freshwater Biol. 45: 179–188.

Bottrell H.H., Duncan A., Gliwicz Z.M., Grygierek E., Herzig A., Hillbricht-Ilkowska A. et al. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419–456.

Brett M.T. 1993. Comment on "Possibility of N or P limitation for planktonic cladocerans: An experimental test" (Urabe and Watanabe) and "Nutrient element limitation of zooplankton production" (Hessen). Limnol. Oceanogr. 38: 1333–1337.

Brett M.T. and Goldman C.R. 1997. Consumer versus resource control in freshwater pelagic food webs. Science 275: 384–386.

Brett M.T., Lubnow F.S., Villar-Argaiz M., Müller-Solger A. and Goldman C.R. 1999. Nutrient control of bacterioplankton and phytoplankton dynamics. Aquat. Ecol. 33: 135–145.

Brett M.T. and Müller-Navarra D.C. 1997. The role of highly unsaturated fatty acids in aquatic food-web processes. Freshwater Biol. 38: 483–499.

Brett M.T., Martin L. and Kawecki T.J. 1992. An experimental test of the egg-ratio method: estimated versus observed death rates. Freshwater Biol. 28: 237–248.

Brett M.T., Müller-Navarra D.C. and Park S.K. 2000. An empirical analysis of mineral P limitation's impact on algal food quality for freshwater zooplankton. Limnol. Oceanogr. 45: 1564–1575.

Coutteau P. and Sorgeloos P. 1997. Manipulation of dietary lipids, fatty acids and vitamins in zooplankton cultures. Freshwater Biol. 38: 501–512.

De Lange H.J. and Arts M.T. 1999. Seston composition and the potential for *Daphnia* growth. Aquat. Ecol. 33: 387–398.

De Stasio B.T. Jr, Rudstam L.G., Haning A., Soranno P. and Allen Y.C. 1995. An *in situ* test of the effects of food quality on *Daphnia* population growth. Hydrobiologia 307: 221–230.

Elser J.J. and George N.B. 1993. The stoichiometry of N and P in the pelagic zone of Castle Lake, California. J. Plankton Res. 15: 977–992.

Elser J.J., Carney H.J. and Goldman C.R. 1990. The zooplankton-phytoplankton interface in lakes of contrasting trophic status – an experimental comparison. Hydrobiologia 200: 69–82.

Elser J.J., Lueke C., Brett M.T. and Goldman C.R. 1995. Effects of food web compensation after manipulation of rainbow trout in an oligotrophic lake. Ecology 76: 52–69.

Gaedke U. 1992. The size distribution of plankton biomass in a large lake and its seasonal variability. Limnol. Oceanogr. 37: 1202–1220.

Gaedke U. and Straile D. 1998. Daphnids: keystone species for the pelagic food web structure and energy flow – a body sized-related analysis linking seasonal changes at the population and ecosystem levels. Arch. Hydrobio. Spec. Issues Advanc. Limnol. 53: 587–610.

Goldman C.R. 1963. The measurement of primary productivity and limiting factors in freshwater with carbon-14. In: Primary productivity measurements, marine and freshwater, Proc. Conf. Div. Technol. Inform. Rep. TID-7633. U.S., pp. 103–113.

Goldman C.R. 1968. The use of absolute activity for eliminating serious errors in the measurement of primary productivity with C14. J. Cons. Cons. Int. Explor. Mer. 32: 172–179.

Goldman C.R. and DeAmezaga E. 1984. Primary productivity and precipitation at Castle Lake and Lake Tahoe during twenty-four years, 1959–1982. Int. Ver. Theor. Angew. Limnol. Verh. 22: 591–599.

Gulati R.D. and DeMott W.R. 1997. The role of food quality for zooplankton: remarks on the state-of-the-art, perspectives and priorities. Freshwater Biol. 38: 753–768.

Hairston N.G. Jr and Hairston N.G. Sr 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. Am. Nat. 142: 379–411.

Han K., Geurden I. and Sorgeloos P. 2000. Enrichment strategies for *Artemia* using emulsions providing different levels of n-3 highly unsaturated fatty acids. Aquaculture 183: 335–347.

Harris G.P. and Piccinin B.B. 1980. Physical variability and phytoplankton communities. IV. Temporal changes in the phytoplankton community of a physically variable lake. Arch. Hydrobiol. 89: 447–473.

Hessen D.O. 1992. Nutrient element limitation of zooplankton production. Am. Nat. 140: 799–814.

Hessen D.O. 1993. The role of mineral nutrients for zooplankton nutrition: Reply to the comment by Brett. Limnol. Oceanogr. 38: 1340–1343.

Hessen D.O. and Faafeng B.A. 2000. Elemental ratios in freshwater seston, implications for community structure and energy transfer in food webs. Ergebnisse der Limnologie 55: 349–363.

Hilbricht-Ilkowska A. 1977. Trophic relations and energy flow in pelagic plankton. Pol. Ecol. Stud. 3: 3–98.

Hunter M.D. and Price P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724–732.

ICES 1994. Report of ICES Working Group on Mass Rearing of Juvenile Marine Fish. International Council for the Exploration of the Sea, Committee Meeting, Mariculture Committee. F, 6.

Infante A. and Litt A.H. 1985. Differences between two species of *Daphnia* in the use of 10 species of algae in Lake Washington. Limnol. Oceanogr. 30: 1053–1059.

Jassby A.D., Powell T.M. and Goldman C.R. 1990. Interannual fluctuations in primary production, direct physical effects and the trophic cascade at Castle Lake. Limnol. Oceanogr. 35: 1021–1038.

Jónasdóttir S.H. and Kiørboe T. 1996. Copepod recruitment and food composition: do diatoms affect hatching success? Marine Biol. 125: 743–750.

Jónasdóttir S.H., Kiørboe T., Tang K.W., St John M., Visser A.W., Saiz E. et al. 1998. Role of diatoms in copepod production: good, harmless or toxic? Mar. Ecol. Prog. Ser. 172: 305–308.

Kerfoot W.C., Levitan C. and DeMott W.R. 1988. Daphnia-phytoplankton interactions: density-dependent shifts in resource quality. Ecology 69: 1806–1825.

Kleppel G.S. and Burkart C.A. 1995. Egg production and the nutritional environment of *Acartia tonsa*: the role of food quality in nutrition. ICES J. Mar. Sci. 52: 297–304.

Kleppel G.S., Burkart C.A. and Houchin L. 1998. Nutrition and the regulation of egg production in the calanoid copepod *Acartia tonsa*. Limnol. Oceanogr. 43: 1000–1007.

Lacroix G., Lescher-Moutoué F. and Bertolo A. 1999. Biomass and production of plankton in shallow and deep lakes: are there general patterns? Annls. Limnol. 35: 111–122.

Lampert W. 1987. Feeding and nutrition. In: Peters R.H. and De Bernardi R. (eds), Daphnia. Vol. 45. Memorie Dell'istituto Italiano di Idrobiologia Dott, Marco De Marchi, pp. 143–192.

Lampert W. and Sommer U. 1997. Limnoecology – the Ecology of Lakes and Streams. Oxford University Press, Inc., New York, Translated by Hanley J.F.

Lundstedt L. and Brett M.T. 1991. Differential growth rates of three cladoceran species in response to mono- and mixed-algal cultures. Limnol. Oceanogr. 36: 159–165.

Marker A.F., Crowther C.A. and Gunn R.J.M. 1980. Methanol and acetone as solvents for estimating chlorophyll *a* and phaeopigments by spectrophotometry. Arch. Hydrobiol. Beih. Ergebn. Limnol. 14: 52–59.

McEvoy L.A., Navarro J.C., Bell J.G. and Sargent J.R. 1995. Autoxidation of oil emulsions during the Artemia enrichment process. Aquaculture 134: 101–112.

Meyer J.S., Ingersoll C.G., McDonald L.L. and Boyce M.S. 1986. Estimating uncertainty in population growth rates: Jackknife vs. Bootstrap techniques. Ecology 67: 1156–1166.

Müller-Navarra D.C. 1995a. Biochemical versus mineral limitation in *Daphnia*. Limnol. Oceanogr. 40: 1209–1214.

Müller-Navarra D.C. 1995b. Evidence that a highly unsaturated fatty acid limits *Daphnia* growth in nature. Arch. Hydrobiol. 132: 297–307.

Müller-Navarra D.C. and Lampert W. 1996. Seasonal patterns of food limitation in *Daphnia galeata*: separating food quantity and food quality effects. J. Plankton Res. 18: 1137–1157.

Müller-Navarra D.C., Brett M.T., Liston A.M. and Goldman C.R. 2000. A highly-unsaturated fatty acid predicts carbon transfer between primary producers and consumers. Nature 403: 74–77.

Müller-Solger A., Brett M.T., Lueke C., Elser J.J. and Goldman C.R. 1997. The effects of planktivorous fish (golden shiners) on the ciliate community of a mesotrophic lake. J. Plankton Res. 19: 1815–1828.

Mumm H. 1997. Effects of competitors and *Chaoborus* predation on the cladocerans of a eutrophic lake: an enclosure study. Hydrobiologia 360: 253–264.

Napotalino G.E. 1999. Fatty acids as trophic and chemical markers in freshwater ecosystems. In: Arts M.T. and Wainman B.C. (eds), Lipids in Freshwater Ecosystems. Springer, New York, pp. 21–44.

Paloheimo J.E. 1974. Calculation of instantaneous birth rate. Limnol. Oceanogr. 19: 692–694.

Park S., Brett M.T., Müller-Navarra D.C. and Goldman C.R. 2002. Essential fatty acid content and the phosphorus to carbon ratio in cultured algae as food quality indices for *Daphnia*. Freshwater Biol. 47.

Paterson M.J., Findlay D., Beaty K., Findlay W., Schindler E.U., Stainton M. et al. 1997. Changes in the planktonic food web of a new experimental reservoir. Can. J. Fish Aquat. Sci. 54: 1088–1102.

Peters R.H. 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge, England.

Porter K.G. 1975. Viable gut passage of gelatinous green algae ingested by *Daphnia*. Verh. Internat. Verein. Limnol. 19: 2840–2850.

Power M.E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology 73: 733–746.

Redfield G.W. 1979. Temporal Variation in Diel Vertical Migration and the Ecology of Zooplankton in Castle Lake, California. PhD Dissertation, University of California-Davis.

Sanders J.F. III and Lewis W.M. Jr. 1988. Dynamics and control mechanisms in a tropical zooplankton community (Lake Valencia, Venezuela). Ecol. Monogr. 58: 337–353.

Schmidt K. and Jónasdóttir S.H. 1997. Nutritional quality of two cyanobacteria: how rich is 'poor' food? Mar. Ecol. Prog. Ser. 151: 1–10.

Schmidt K., Kähler P. and von Bodungen B. 1998. Copepod egg production rates in the Pomeranian Bay (Southern Baltic Sea) as a function of phytoplankton abundance and taxonomic composition. Mar. Ecol. Prog. Ser. 174: 183–195.

Schulz K.L. and Sterner R.W. 1999. Phytoplankton phosphorus limitation and food quality for *Bosmina*. Limnol. Oceanogr. 44: 1549–1556.

Shuter B.J. and Ing K.K. 1997. Factors affecting the production of zooplankton in lakes. Can. J. Fish. Aquat. Sci. 54: 359–377.

Solórzano L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr. 14: 799–801.

Sommer U., Gliwicz Z.M., Lampert W. and Duncan A. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106: 433–471.

Sterner R.W. 1993. *Daphnia* growth on varying quality of *Scenedesmus*: mineral limitation of zooplankton. Ecology 74: 2351–2360.

Sterner R.W. and Hessen D.O. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. Ann. Rev. Ecol. Syst. 25: 1–29.

Sterner R.W. and Schulz K.L. 1998. Zooplankton nutrition: recent progress and a reality check. Aquat. Ecol. 32: 261–279.

Stockwell J.D. and Johannsson O.E. 1997. Temperature-dependent allometric models to estimate zooplankton production in temperature freshwater lakes. Can. J. Fish. Aquat. Sci. 54: 2350–2360.

Strickland J.D.H. and Parsons T.R. 1972. A Practical Handbook of Seawater Analysis. Bulletin 167. Fisheries Research Board of Canada, Ottawa.

Urabe J. and Sterner R.W. 1996. Regulation of herbivore growth by the balance of light and nutrients. Proc. Natl. Acad. Sci. USA 93: 8465–8469.

Urabe J. and Watanabe Y. 1992. Possibility of N or P limitation for planktonic cladocerans: An experimental test. Limnol. Oceanogr. 37: 244–251.

Urabe J. and Watanabe Y. 1993. Implications of seston elemental ratio in zooplankton ecology: Reply to the comment by Brett. Limnol. Oceanogr. 38: 1337–1340.

Utermöhl H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. Mitt. Int. Ver. Limnol. 9: 1–38.

Van Donk E. and Hessen D.O. 1993. Grazing resistance in nutrient-stressed phytoplankton. Oecologia 93: 508–511.

Van Donk E. and Hessen D.O. 1995. Reduced digestibility of UV-B stressed and nutrient-limited algae by *Daphnia magna*. Hydrobiol. 307: 147–151.

Van Donk E., Lürling M., Hessen D.O. and Lockhorst G.M. 1997. Altered cell wall morphology in nutrient-deficient phytoplankton and its impact on grazers. Limnol. Oceanogr. 42: 357–364.

Vanni M.J. and Lampert W. 1992. Food quality effects on life history traits and fitness in the generalist herbivore *Daphnia*. Oecologia 92: 48–57.

Wacker A. and von Elert E. 2001. Polyunsaturated fatty acids: evidence for non-substitutable biochemical resources in *Daphnia galeata*. Ecology 82: 2507–2520.

Weisse T. and Stockner J.G. 1993. Eutrophication: the role of microbial food webs. Mem. Ist ital. Idrobiol. 52: 133–150.