

Light-induced changes of plankton growth and stoichiometry: Experiments with natural phytoplankton communities

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Abstract

Both low and high rates of light supply can restrict herbivore growth rates by limiting either the quantity (photosynthetically fixed carbon) or the nutritional quality (nutrient content per fixed carbon) of the herbivores' food. The "light–nutrient hypothesis," therefore, predicts that, if phosphorus (P) supply is sufficiently low, production of herbivorous zooplankton should be unimodally related to light intensity. We manipulated the light regime of six different algal communities in a field experiment and investigated the effect of these manipulations on *Daphnia* growth. The algal communities came from six lakes having different total phosphorus concentrations, ranging from oligotrophic to eutrophic. Seston carbon (C) and seston carbon-to-phosphorus ratios in communities from oligotrophic and mesotrophic lakes increased with higher light availability. Across all lakes, the strength of these responses was related to algal diversity. More diverse algal communities showed a stronger increase than less diverse communities in both their carbon biomass and their C:P ratio with increasing light. Furthermore, in oligotrophic and mesotrophic treatments, *Daphnia* growth was highest at intermediate light intensities. In contrast, seston parameters and *Daphnia* growth were only weakly related to light supply in communities from eutrophic lakes.

In pelagic ecosystems, primary production is determined by the supply of light and dissolved mineral nutrients. In lakes, the nutrient that limits primary production is often phosphorus (P) (Vollenweider 1976). The loose coupling between algal nutrient uptake and photosynthesis allows for highly flexible C:P ratios of algal biomass. It is therefore common that the P content of algal biomass relative to carbon (C) fixed by photosynthesis decreases with increasing light input (Sterner et al. 1997; Diehl et al. 2005; Berger et al. 2006). In contrast, the elemental composition of herbivorous zooplankton is largely homeostatically regulated (Andersen and Hessen 1991; Main et al. 1997; Elser et al. 2000). Zooplankton with high specific growth rates, such as *Daphnia*, tend to have a high body phosphorus content and, therefore, a C:P ratio that is considerably lower than that of phytoplankton (Elser et al. 1996; Main et al. 1997; Weider et al. 2004). If this mismatch in the elemental composition between autotrophs and herbivores becomes sufficiently strong, herbivore growth could become limited by the nutrient rather than by the carbon content of their food. For example, *Daphnia* growth has been reported to be limited by P at molar seston C:P ratios >300 (Hessen 1992; Urabe and Watanabe 1992; Urabe et al. 2002a), whereas only weak P limitation and stronger energy limitation is usually observed at molar

seston C:P ratios <300 (DeMott and Tessier 2002; DeMott et al. 2004).

The degree of mismatch in the elemental composition between autotrophs and herbivores has implications for the efficiency with which biomass and energy are transferred up the food chain, summarized in the "light–nutrient hypothesis" (Sterner et al. 1997). In short, although increased light supply usually promotes phytoplankton growth, the resulting increase in primary production can only be fully transferred to the herbivore level if herbivore growth is predominantly carbon (energy) limited. In contrast, if herbivore growth is predominantly nutrient limited, increased light supply could actually decrease herbivore production because any light-induced increase in food quantity could be offset by a disproportional decrease in the food's nutrient content (Andersen et al. 2004; Diehl 2007). The latter phenomenon has been termed the "paradox of energy enrichment" (Loladze et al. 2000) and has been observed in several laboratory experiments with *Daphnia* and monocultures of chlorophytes (Urabe and Sterner 1996; Sterner et al. 1998; Urabe et al. 2002a). Still, to date, only very few attempts have been made to investigate experimentally how widely applicable the light–nutrient hypothesis (LNH) is to the description of natural phytoplankton–zooplankton interactions with diverse algal communities.

To our knowledge only one field experiment to date (Urabe et al. 2002b) has investigated the response of the plankton community of an oligotrophic lake to the factorial manipulation of light (shading) and nutrients (P enrichment) in field mesocosms. These manipulations had major effects on seston C:P stoichiometry and on zooplankton production and growth over the 4-week experiment, consistent with the predictions of the LNH. However, the short-term response of an algal community to an experimental manipulation can be constrained by its

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Acknowledgments

We thank Sebastian Diehl, William DeMott, and two anonymous reviewers for comments that improved this manuscript; Angelika Wild and Achim Weigert for technical support; and Christian Matauschek, Johanna Vilsmaier, and Ferdinand M. Neuberger for help during the field experiment.

This study was supported by funding from Deutsche Forschungsgemeinschaft (STI 180/2-1).

Table 1. Characteristics of the lakes and the algal communities deriving from these lakes at the start of the experiment. Seston N:P ratios (marked with *) are from samples obtained in 2005.

Lake	Förchensee	Brunnensee	Klostersee	Langbürgenersee	Thalersee	Bansee
Total P ($\mu\text{g L}^{-1}$)	6.0	9.4	14.2	17.2	55.0	81.0
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	0.2	2.5	3.1	4.5	26.9	53.4
POC (mg L^{-1})	0.18	0.46	0.54	1.10	1.38	1.79
Seston C:P (molar)	559	278	178	299	104	107
Seston N:P (molar)*	42	40	38	29	29	16
Mean depth (m)	4.0	8.5	5.9	9.2	4.4	2.4
Surface area (km^2)	0.04	0.06	0.47	1.04	0.04	0.03
Diversity (<i>H</i>)	0.07	0.29	0.85	0.53	0.59	0.39
Evenness ($H^* \ln S^{-1}$)	0.07	0.28	0.68	0.42	0.54	0.33
Proportion of algal biovolume						
Cyanophyceae	0.0	8.5	0.0	0.4	60.0	0.0
Chlorophyceae	97.9	84.1	72.7	83.3	33.6	2.5
Dinophyceae	0.0	2.0	6.9	1.2	0.0	0.0
Bacillariophyceae	0.3	0.9	1.9	3.2	1.6	1.6
Cryptophyceae	0.0	1.3	3.4	0.4	0.0	84.4
Chrysophyceae	0.0	0.0	3.2	2.7	0.0	1.5
Other flagellates	1.8	3.0	11.6	8.8	4.0	9.7

initial characteristics, such as species richness and taxonomic composition.

Here, we report from a field study in which we exposed different natural algal communities to a gradient of light intensities. The algal communities originated from six lakes chosen along a gradient of total phosphorus (TP) concentration. By using different natural algal communities, we furthermore assured realistic species combinations and algal communities with shared evolutionary histories as experimental systems. The LNH predicts a unimodal relation between light intensity and *Daphnia* growth over some range of the light–nutrient supply space. Such a response can only be captured with a gradient design. We therefore exposed the algal communities and the herbivores to a gradient of five light levels. We investigated how the different algal communities responded to light manipulation and to what extent these responses and subsequent effects of light manipulation on *Daphnia* growth could be described by the LNH and other, alternative or complementary, mechanisms.

Materials and methods

Algal communities—We exposed natural algal communities originating from six lakes in Bavaria, covering a broad range of nutrient conditions (Table 1) to different light intensities in outdoor mesocosms. On the basis of total phosphorus concentration, Lake Förchensee and Lake Brunnensee can be defined as oligotrophic, Lake Klostersee and Lake Langbürgenersee as mesotrophic, and Lake Thalersee and Lake Bansee as eutrophic lakes. All lakes are located near the Limnological Research Station of the University of Munich at Seon (Bavaria, Southern Germany).

Experimental design—On 26 August 2004, we took from each lake a pooled sample of the epi- and hypolimnion and filtered it through a 224- μm mesh nylon screen to remove

mesozooplankton. The samples were immediately transferred into rectangular 20-liter mesocosms of clear polyethylene (PE). To ensure equal temperature and light conditions, all mesocosms were exposed in Lake Brunnensee at a water depth of 1 m. At that depth, water temperature was about 21°C during the experiment, which lasted from 26 August to 23 September 2004. We wrapped the mesocosms with one or more layers of white PE foil (Renoplan foil) to establish the following light gradient for each algal community: 90%, 70%, 45%, 25%, and 5% of ambient light. Each treatment was replicated twice (yielding a total of 60 mesocosms). Light intensity 1 m below water surface at noon ranged between 150 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ on cloudy days and 1,400 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ on clear, sunny days. The mesocosms were exposed for 2 weeks to allow the algal communities to respond to the different light intensities in the absence of grazing from mesozooplankton. After these 2 weeks, we stocked juvenile *Daphnia magna* (one individual per liter) into the mesocosms and continued the experiment for another 2 weeks. The juvenile *Daphnia* came from a synchronized stock culture and were put into the mesocosms 12 h after they were released from their mothers. We obtained an initial value of *Daphnia* biomass by determining the particulate organic carbon (POC) content of an aliquot of the juvenile *Daphnia*.

Sampling and measurement—We took samples from each mesocosm at the beginning and at the end of the experiment and once per week during the experiment. These samples were immediately filtered through a 224- μm mesh nylon screen. We measured POC, particulate phosphorus (PP), total phosphorus (TP), total algal biovolume, and algal species composition. To estimate POC and PP, we filtered water from each mesocosm onto precombusted and acid-washed glass fiber filters (Whatman GF/F). POC was determined after filtration and combustion by infrared spectrometry (C-Mat 500, Ströh-

lein). PP was measured after sulfuric acid digestion followed by molybdate reaction. TP was quantified by persulfate digestion followed by molybdate reaction.

We identified and counted different algal species from samples fixed with Lugol's iodine in an inverted microscope using Utermöhl chambers (Utermöhl 1958). To determine phytoplankton diversity of the initial samples from the six algal communities, the entire counting chamber was screened, and each algal species occurring in these samples was recorded. If present, at least 400 units (cells or colonies) of each species were counted to keep the counting error at <10% (Lund et al. 1958). Because the total number of counted algal units differed among the six lakes, we conducted a rarefaction analysis to check the robustness of our diversity measures. The results of this analysis showed that our diversity estimates were robust against sampling efforts. In the samples from weeks 2 and 4, we counted at least 400 units (cells or colonies) of every abundant species by scanning a minimum of two perpendicular transects or 20 distinct fields randomly distributed on two such transects. Biovolume of the different algal species was calculated according to Hillebrand et al. (1999). The taxonomic composition of an algal community can affect its quality as food for *Daphnia*. Although some species are completely inedible, others can be ingested by *Daphnia* but are resistant to digestion. We categorized the algal species in our mesocosms as edible or inedible algae. We defined inedible algae as those, which, according to literature, either cannot be easily ingested or digested by *Daphnia*. According to these criteria, we assumed that Cyanophyceae, large diatoms, defended (spiny) algae, and filamentous or gelatinous green algae were inedible (Burns 1968; Burns et al. 1989; DeMott et al. 2001).

At the end of the experiment, we counted the *Daphnia* in each mesocosm and determined their carbon biomass by infrared spectrometry after combustion. We calculated the population growth rate (R) of *Daphnia* with Eq. 1,

$$R = \left(\frac{\ln N_{\text{End}} - \ln N_{\text{Start}}}{t_{\text{End}} - t_{\text{Start}}} \right) \quad (1)$$

where N_{Start} and N_{End} are the biomasses of *Daphnia* (measured as POC) on the day of *Daphnia* stocking ($t_{\text{Start}} = \text{day 14}$) and the final day ($t_{\text{End}} = \text{day 28}$) of the experiment.

Using stepwise multiple regression (with backward elimination), we related *Daphnia* growth rates to seston biomass (as POC and as POC² to account for the possibility of saturation of the growth response), the seston C:P ratio, and the proportion of edible algae. For these parameters, we used the average of days 14, 21, and 28. Standardized coefficients for the regression parameters were estimated according to Sokal and Rohlf (1981). We analyzed the responses of algal communities and *Daphnia* to light manipulation with the regression analysis tools of Sigma Plot (8.0). When visual inspection of the data suggested a unimodal relationship between a response variable and the light gradient, we fitted the following Weibull function,

$$y(x) = m \left[\frac{b}{a} \left(\frac{x}{a} \right)^{b-1} e^{-\left(\frac{x}{a} \right)^b} \right] \quad (2)$$

where y is the response variable, x is light treatment (percentage of ambient light intensity), and a , b , and m are fitted constants. We used this equation because it can describe unimodal distributions with both symmetric and asymmetric peaks.

Results

Seston biomass and C:P ratio—Initial concentrations of seston POC ranged from 0.18 to 1.79 mg C L⁻¹. They differed among the initial communities and were positively related to lake phosphorus status (Table 1; Pearson correlation of POC vs. log(TP), $r = 0.966$, $p = 0.002$). The relative ranking of the lake communities with respect to seston POC remained similar throughout the experiment, with Förschensee and Brunnensee having the lowest and Thalersee and Bansee having the highest values (Fig. 1). With one exception, seston POC concentrations in the treatments from the different lakes were positively related to the experimentally manipulated light supply both on day 14 (before *Daphnia* stocking) and at the end of the experiment (Fig. 1A,B,E,F; Table 2). Described by linear regression, these relationships were statistically significant or marginally significant in treatments from Brunnensee, Klostersee, and Langbürgenersee on both dates and in treatments from Förschensee and Bansee on the final date (Table 2).

The initial molar seston C:P ratios ranged from 103.5 to 559.2. They differed among the starting communities and were negatively related to lake phosphorus status (Table 1; Pearson correlation of C:P vs. log(TP), $r = -0.837$, $p = 0.038$). Seston C:P ratios increased in many treatments over time, extending the overall range of molar C:P values to 67–986 (Brunnensee, 5% ambient light, to Thalersee, 70% ambient light, respectively) on day 28 (Fig. 1G,H). In all lake treatments, seston C:P ratios were positively related to the experimentally manipulated light supply on both day 14 (before *Daphnia* stocking) and at the end of the experiment, but the statistical support for these relationships was weaker in most treatments on day 14 (Fig. 1C,D,G,H; Table 2). Described by linear regression, the positive relationships were statistically significant in Klostersee treatments on both dates and in treatments from Förschensee, Brunnensee, and Langbürgenersee on the final date, but not in treatments from eutrophic Bansee and Thalersee (Table 2).

Daphnia abundance and growth—*Daphnia* biomass increased in most treatments from an initial value of 6.7 µg C L⁻¹ to final values ranging from 16.5 to 173.1 µg C L⁻¹, corresponding to daily growth rates of 0.076 to 0.243 (Fig. 2). As suggested by the good fit of Weibull functions, *Daphnia* growth rates were unimodally related to light availability in the treatments from Förschensee, Klostersee, and Langbürgenersee (Fig. 2A), the latter one being only marginally statistically significant (Table 3). In all these treatments, the highest *Daphnia* growth rates occurred at intermediate light availability (35–45% of available light). The treatments from Bansee suggested a U-shaped relationship between light availabil-

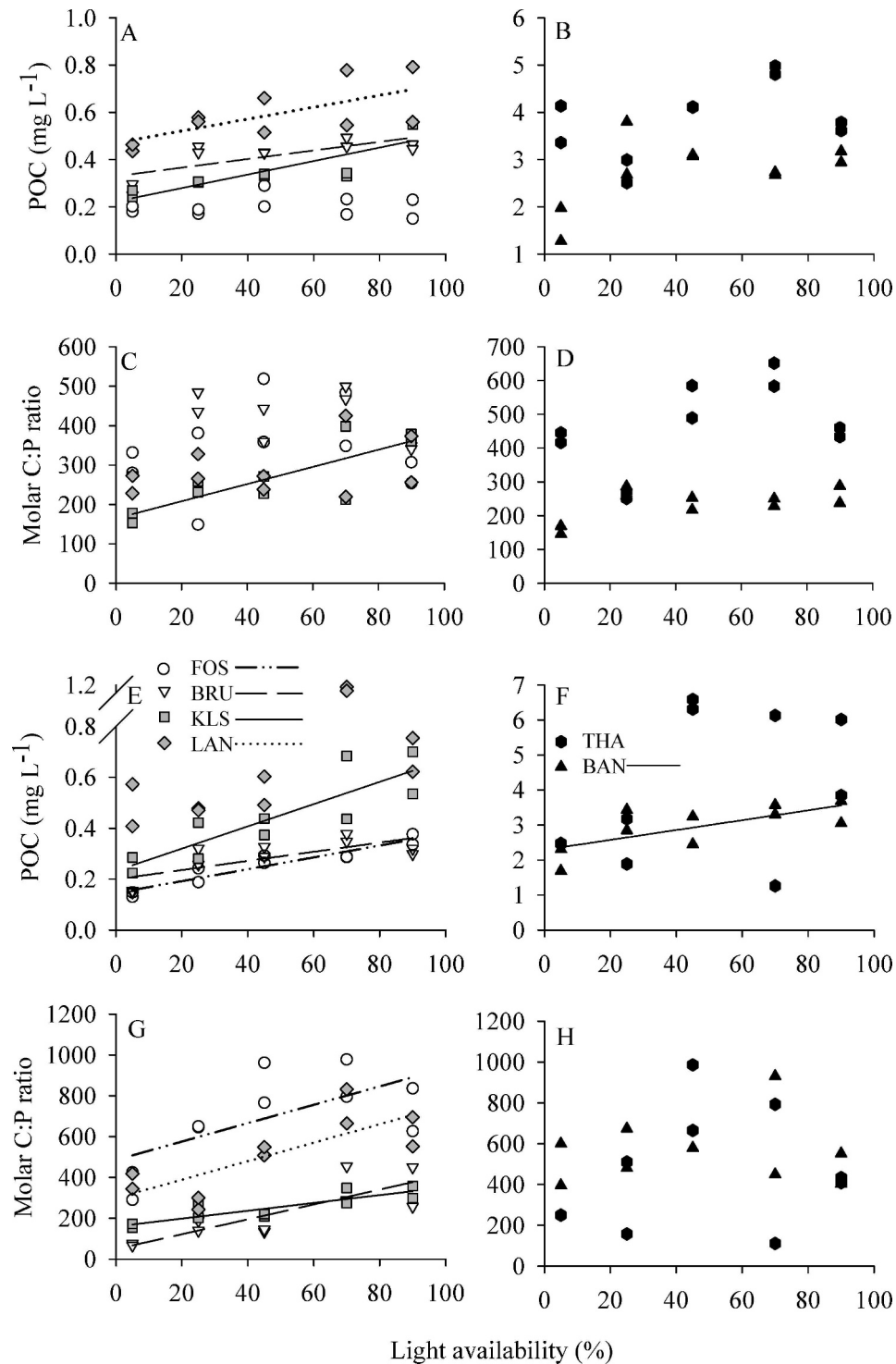


Fig. 1. Effects of different light treatments on seston biomass (POC, mg L⁻¹) of communities (A) from oligotrophic Förschensee and Brunnensee, mesotrophic Klostersee and Langbürgenersee and (B) from eutrophic Thalersee and Bansee after 2 weeks of exposure. Effects of different light treatments on the molar seston C:P ratios of the communities (C) from oligotrophic Förschensee and Brunnensee and mesotrophic Klostersee and Langbürgenersee and (D) from eutrophic Thalersee and Bansee after 2 weeks of exposure. Effects of different light treatments on the seston biomasses (POC, mg L⁻¹) after 4 weeks of exposure in communities (E) from Förschensee, Brunnensee, Klostersee, and Langbürgenersee and (F) from eutrophic Thalersee and Bansee. Effects of different light treatments on the molar seston C:P ratios after 4 weeks of exposure in communities (G) from Förschensee, Brunnensee, Klostersee, and

Table 2. Summary of linear regression statistics of algal biomass and molar seston C:P ratio against light treatment (% ambient light intensity) after 2 weeks of exposure without *Daphnia* and after 2 weeks of exposure with *Daphnia*. Values in brackets are \pm SE.

Lake	After 2 weeks of exposure and before the introduction of <i>Daphnia</i>					After 2 weeks of exposure with <i>Daphnia</i>				
	Intercept	Slope	r^2	$F_{1,8}$	p	Intercept	Slope	r^2	$F_{1,8}$	p
Förchensee										
Biomass (mg C L ⁻¹)	0.2 (0.03)	-0.0001 (0.0004)	0.003	0.02	0.89	0.2 (0.02)	0.002 (0.0003)	0.89	65.1	<0.0001
C:P molar	319.9 (65.5)	0.5 (1.2)	0.02	0.15	0.71	485.6 (101.5)	4.5 (1.8)	0.44	6.2	0.04
Brunnensee										
Biomass (mg C L ⁻¹)	0.3 (0.03)	0.002 (0.0006)	0.56	10.0	0.01	0.2 (0.03)	0.002 (0.0006)	0.56	10.1	0.01
C:P molar	357.1 (49.7)	0.8 (0.9)	0.08	0.7	0.42	48.7 (48.6)	3.7 (0.9)	0.69	17.7	0.003
Klostersee										
Biomass (mg C L ⁻¹)	0.2 (0.03)	0.003 (0.0006)	0.74	22.7	0.001	0.2 (0.05)	0.004 (0.0009)	0.75	23.4	0.001
C:P molar	164.3 (30.0)	2.2 (0.5)	0.67	16.6	0.004	159.9 (21.3)	1.9 (0.4)	0.76	25.4	0.001
Langbürgenersee										
Biomass (mg C L ⁻¹)	0.8 (0.006)	0.003 (0.001)	0.45	6.6	0.03	0.4 (0.1)	0.005 (0.002)	0.37	4.74	0.06
C:P molar	253.3 (38.8)	0.7 (0.7)	0.12	1.1	0.32	297.8 (72.9)	4.5 (1.3)	0.60	12.11	0.008
Thalensee										
Biomass (mg C L ⁻¹)	3.4 (0.4)	0.01 (0.008)	0.17	1.6	0.24	2.7 (1.2)	0.03 (0.02)	0.18	1.7	0.23
C:P molar	372.1 (71.2)	1.8 (1.3)	0.21	2.1	0.19	364.9 (172.3)	1.9 (3.1)	0.05	0.4	0.55
Bansee										
Biomass (mg C L ⁻¹)	2.3 (0.4)	0.01 (0.007)	0.23	2.4	0.16	2.3 (0.3)	0.01 (0.005)	0.50	8.1	0.02
C:P molar	195.4 (23.6)	0.8 (0.4)	0.31	3.6	0.09	547.4 (96.9)	0.4 (1.7)	0.005	0.04	0.85

ity and *Daphnia* growth rates, but the variance among replicates was very high (Fig. 2B). Because zero survival occurred in several replicates of the Brunnensee and Thalensee treatments, we did not relate *Daphnia* growth rates to light availability in these treatments.

To ascertain whether the relationships of *Daphnia* growth to seston biomass and seston C:P stoichiometry could have been confounded by differences in algal ingestibility and digestibility, we categorized algae as edible and inedible, as described in the *Materials and methods* section. In spite of large differences in the initial composition of the algal communities from the different lakes, between 80% and 95% of total algal biovolume was categorized as edible. The proportional contribution of edible algae to total algal biovolume decreased in several treatments during the first 2 weeks of incubation (Fig. 3A,B). In each of the three lake treatments in which we found a unimodal relationship between *Daphnia* growth and light availability (Förchensee, Klostersee, Langbürgenersee), the proportion of edible algae tended to be weakly positively related to light availability before and 2 weeks after *Daphnia* stocking, but these relationships were not statistically significant (Fig. 3). Given that food quantity (seston POC) was positively related to light

availability in these treatments, light-dependent differences in algal ingestibility and digestibility seemed unlikely to explain the declining limbs of the *Daphnia* growth responses to light availability.

The latter was confirmed in the stepwise multiple regression in which we regressed *Daphnia* growth rates from all treatments on seston C:P ratio, seston POC content, and the proportion of edible algae. The proportion of edible algae was not retained in the final model. Instead, *Daphnia* growth rate was negatively related to seston C:P ratios and in an upward convex manner to seston POC content, suggesting saturation of *Daphnia* growth rate at higher POC values (*Daphnia* growth rate [d⁻¹] = 0.14 - [0.0001 × C:P ratio] + [0.08 × POC] - [0.03 × POC²]; $r^2 = 0.32$, $F_{3,46} = 6.76$; $p = 0.0008$; Fig. 4).

Algal diversity and seston C:P ratios—Taxon richness (S), diversity (Shannon–Wiener Index, H) and evenness ($H'/\ln S$) of the initial algal communities differed among the lakes (Table 1). The highest species richness occurred in mesotrophic lakes, and both Shannon diversity and evenness were highest in the initial algal community from mesotrophic Lake Klostersee (Table 1). Diversity and evenness of the initial algal communities were positively

←

Langbürgenersee and (H) from Thalensee and Bansee. Linear regressions are shown when they are statistically significant ($p \leq 0.05$). Förchensee (FOS), Brunnensee (BRU), Klostersee (KLS), Langbürgenersee (LAN), Thalensee (THA), Bansee (BAN).

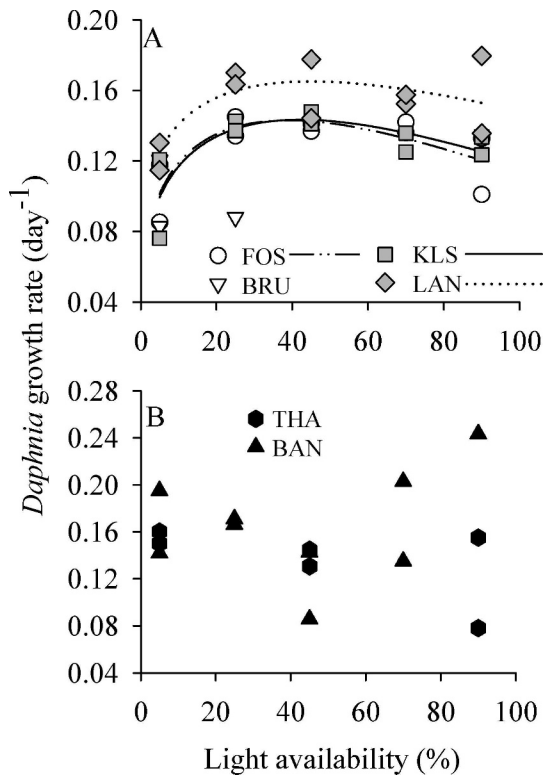


Fig. 2. Effects of different light treatments on *Daphnia* growth rates (d^{-1}) in treatments (A) from oligotrophic Förschensee and Brunnensee and mesotrophic Klostersee and Langbürgenersee and (B) from eutrophic Thalersee and Bansee. Fits of nonlinear Weibull functions are shown when $p < 0.1$. Förschensee (FOS), Brunnensee (BRU), Klostersee (KLS), Langbürgenersee (LAN), Thalersee (THA), Bansee (BAN).

related to their stoichiometric responses to light enrichment in the absence of *Daphnia*. We calculated the size of the effect of light enrichment on the molar C:P ratios of the algal communities as the slopes of the regressions of light availability versus seston C:P ratio on day 14 (see Table 2). This measure of effect size was positively related to both Shannon diversity (Fig. 5A; effect size = $2.2 \times \text{Diversity} + 0.13$; $r^2 = 0.74$; $F_{1,4} = 11.3$; $p < 0.05$) and to evenness (Fig. 5B; effect size = $2.9 \times \text{Evenness} - 0.02$; $r^2 = 0.79$; $F_{1,4} = 15.1$; $p < 0.05$) of the algal communities. A similar relationship between initial algal diversity and stoichiometric response to the light gradient was no longer found after 2 weeks of *Daphnia* grazing.

Discussion

Possible mechanisms of unimodal relationships between Daphnia growth and light supply—Urabe and Sterner (1996) have demonstrated unimodal relationships between light availability and zooplankton production in laboratory experiments. Our experiment, which covers a very broad range of natural algal communities, suggests that such patterns of light–nutrient interactions might also occur under field conditions. In the two eutrophic treatments, seston POC and seston C:P were only weakly (and mostly nonsignificantly) related to the light gradient. Consistent with this lack of clear light–seston relationships, *Daphnia* growth rates were unrelated to light intensity in the eutrophic treatments. In contrast, seston POC and seston C:P were positively related to the light gradient in most oligotrophic and mesotrophic treatments, and *Daphnia* growth rates in Förschensee and Klostersee were best described by unimodal relationships with light availability. In addition, mesotrophic Langbürgenersee treatments suggested a unimodal relationship between *Daphnia* growth rate and light supply, but here the descending limb of the relationship hinges critically on a single data point.

The rising limbs of these relationships are likely a consequence of food (C) limitation being alleviated with increasing light availability in the oligotrophic and mesotrophic lake communities. The quantity of food (amount of seston POC) increased with higher light availability, and more food resulted in faster zooplankton growth. Using natural lake seston as food for *Daphnia*, Müller-Navarra and Lampert (1996) observed moderate food (C) limitation at 0.3–0.6 mg C L⁻¹. When estimates of food quantity are based on the amount of edible algae (see Figs. 1, 3), carbon limitation of *Daphnia* might have occurred in oligotrophic and mesotrophic treatments, especially in mesocosms with low light availability. In contrast, carbon limitation seems unlikely in eutrophic treatments (Figs. 1, 3), which could explain the absence of a positive effect of light supply on *Daphnia* growth rates in these treatments.

Several mechanisms can be put forward that could explain the observed decline in *Daphnia* growth rates at high light availabilities in Förschensee, Klostersee, and Langbürgenersee treatments. Our data support a significant contribution of elemental food quality (C:P ratio) with changing light availability, as indicated by the multiple regression analysis of *Daphnia* growth rates across all treatments (Fig. 4). Light and nutrient supply might,

Table 3. Standard Weibull regression (Eq. 2) parameters of unimodal relationships between *Daphnia* growth rates (d^{-1}) and light availability (% incident light). Values in brackets are standard errors.

Lake		m	a	b	r^2	$F_{2,7}$	p	Peak
Förschensee	Coefficient	26.0 (5.9)	134.4 (36.0)	1.3 (0.07)	0.65	6.4	0.02	38.9
	p	0.003	0.007	<0.0001				
Klostersee	Coefficient	28.3 (7.1)	145.7 (45.6)	1.3 (0.07)	0.67	7.1	0.02	42.2
	p	0.005	0.001	<0.0001				
Langbürgenersee	Coefficient	44.3 (19.5)	202.2 (101.2)	1.2 (0.08)	0.53	3.9	0.07	44.8
	p	0.06	0.09	<0.0001				

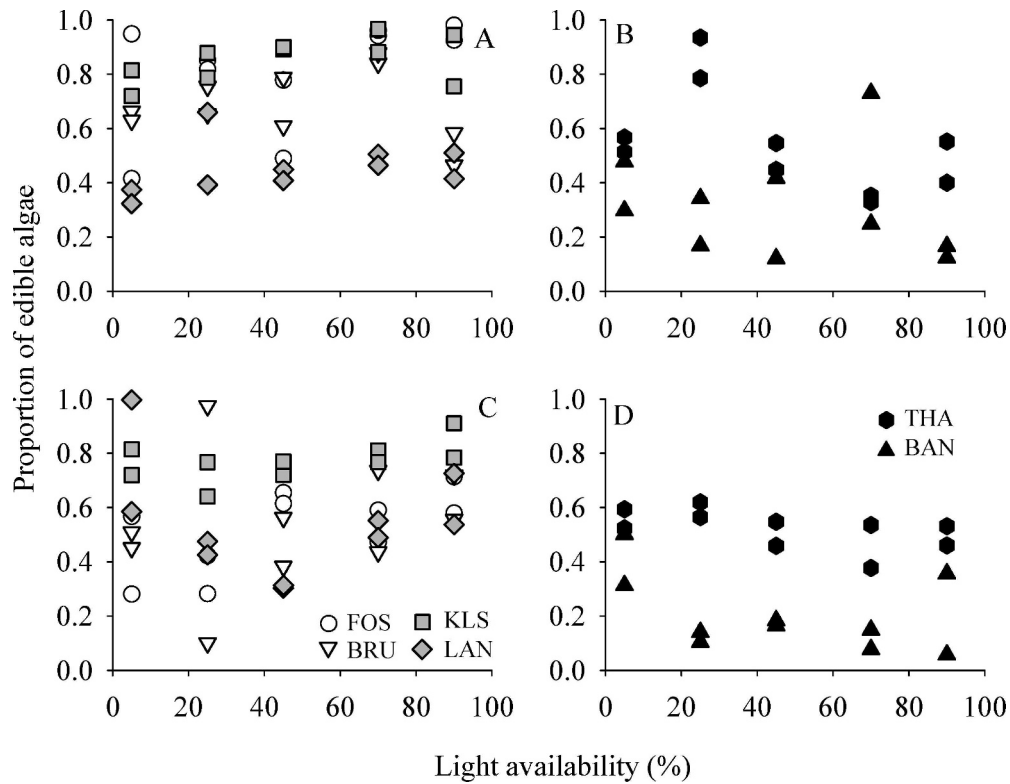


Fig. 3. Proportions of edible algae in different light treatments before *Daphnia* stocking (A, B) and after 2 weeks of exposure with *Daphnia* (C, D). Communities from oligotrophic Förschensee (FOS) and Brunnensee (BRU) and mesotrophic Klostersee (KLS) and Langbürgenersee (LAN) are shown in panels A and C. Communities from eutrophic Thalersee (THA) and Bansee (BAN) are shown in panels B and D.

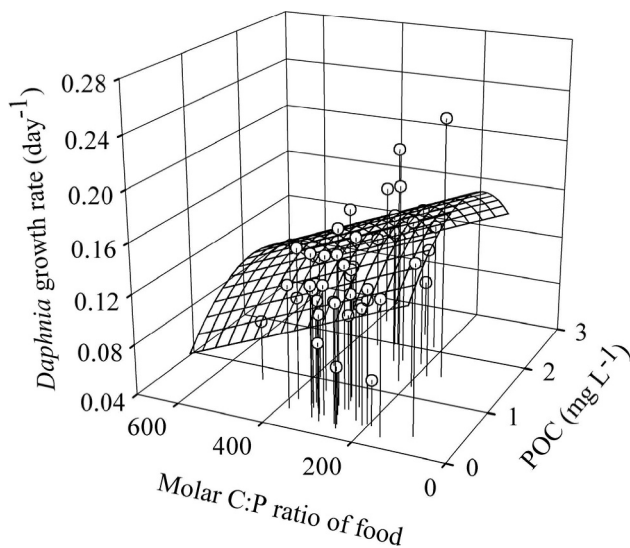


Fig. 4. *Daphnia* growth rates (d^{-1}) from all lake treatments plotted against abundance (POC, mg L^{-1}) and C:P ratio (molar) of seston. The plane describes the multiple regression *Daphnia* growth rate (d^{-1}) = $0.14 - (0.0001 \times \text{C:P ratio}) + (0.08 \times \text{POC}) - (0.03 \times \text{POC}^2)$; $r^2 = 0.32$, $F_{3,46} = 6.76$; $p = 0.0008$.

however, affect other algal traits than just C:P ratios. For example, light inhibition might cause a unimodal response of algal photosynthesis to light availability. In addition, light-dependent changes in phytoplankton taxonomic composition toward less nutritious or less edible taxa at high light levels should be considered.

Our data show no evidence for a saturation of photosynthetic activity at higher light intensities. Carbon-to-chlorophyll *a* ratios (as an indicator of photosynthetic characteristics) showed no significant relationships to light availability (Striebel unpubl. data). Additionally, phytoplankton biomass increased with increasing light levels in all treatments except for those from eutrophic Thalersee. Similarly, we found no evidence that edibility was negatively related to light availability in any of the treatments. If anything, the contribution of edible algae to total phytoplankton biomass increased at light levels beyond 50% ambient light in Förschensee, Klostersee, and Langbürgenersee, which is opposite to the observed decline in *Daphnia* growth rates over the same range of light supplies (Figs. 2, 3).

We considered the proportional contributions of three important algal classes (Chrysophyceae, Bacillariophyceae, and Chlorophyceae) to the total biovolume of each algal

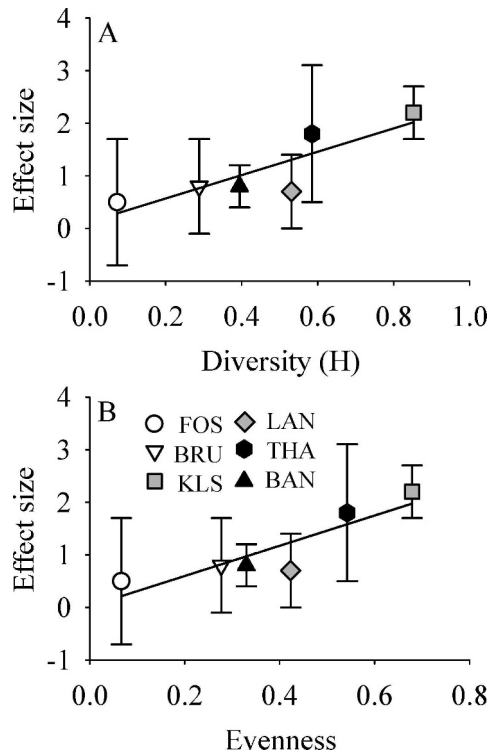


Fig. 5. Relationships between the size of light enrichment effects on seston C:P ratios after 2 weeks of exposure without *Daphnia* and (A) diversity and (B) evenness of the algal communities on the day before *Daphnia* stocking. The effect of light enrichment on the C:P ratios of the algal communities (effect size) was calculated with the use of slopes (with standard error) of light availability versus C:P ratio regressions before the addition of *Daphnia*. Förchensee (FOS), Brunnensee (BRU), Klostersee (KLS), Langbürgenersee (LAN), Thalersee (THA), Bansee (BAN).

community as an additional potential food quality parameter and investigated how these were related to light availability. Cyanophyceae and Cryptophyceae represented at the time of *Daphnia* stocking <1% of total algal biovolume in all treatments. The proportional contribution of presumably less edible Chlorophyceae to total algal biovolume was either unrelated (four cases) or negatively related (two cases) to light availability; the potentially more edible classes Bacillariophyceae and Chrysophyceae were instead mostly unrelated (nine cases) or positively related (three cases) to light availability (Fig. 6). Accordingly, changes in the taxonomic composition of the algal communities seem an unlikely explanation for declining *Daphnia* growth rates at the highest light availabilities.

Additional aspects of food quality—It is clearly insufficient to characterize the food quality of different algal communities only by the seston C:P ratio, which could explain the relatively weak explanatory power of the multiple regression relating *Daphnia* growth to seston C:P and POC ($r^2 = 0.32$; Fig. 4). Most probably, variation in the assimilation efficiency of *Daphnia* for the carbon

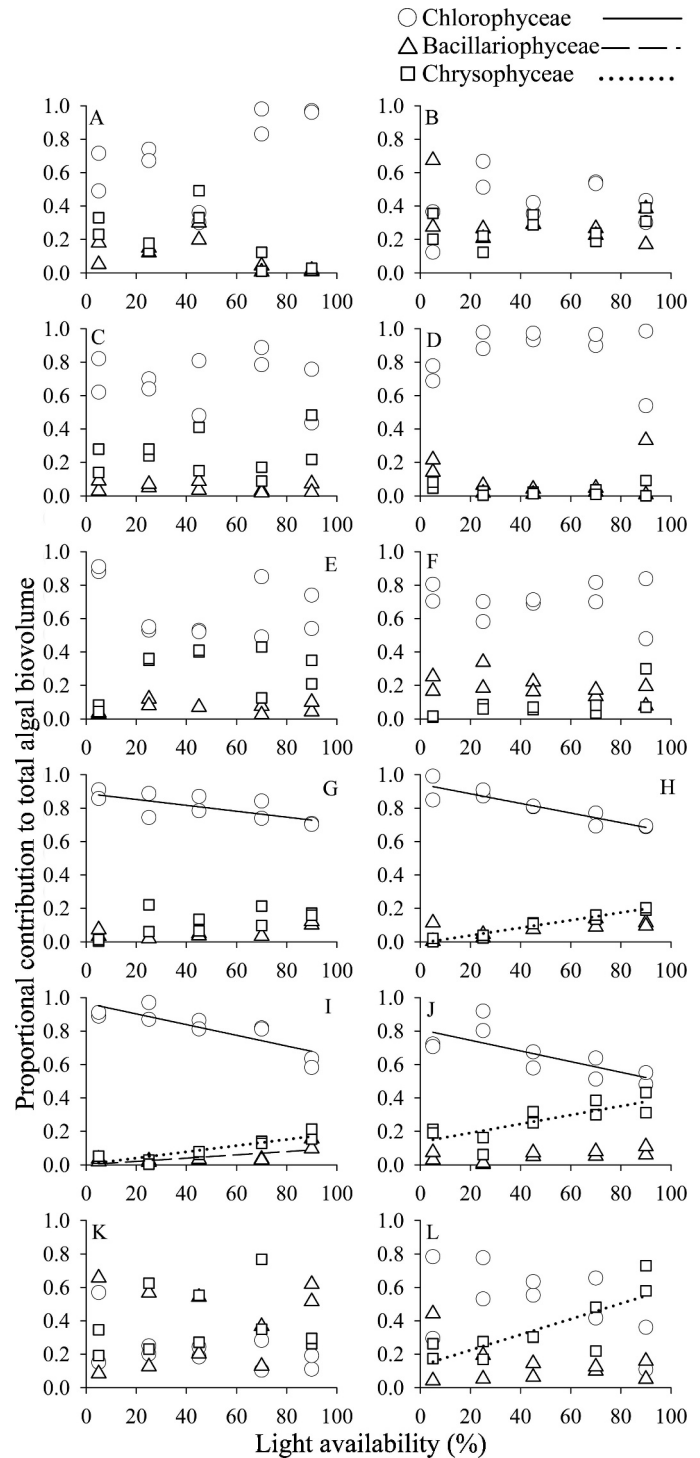


Fig. 6. Proportions of the three dominant algal classes in the treatments from Lake Förchensee (A, B), Lake Brunnensee (C, D), Lake Klostersee (E, F), Lake Langbürgenersee (G, H), Lake Thalersee (I, J), and Lake Bansee (K, L). Data after 2 weeks of exposure are displayed as panels A, C, E, G, I, K and data after 4 weeks of exposure are displayed as panels B, D, F, H, J, L. Statistically significant relationships (linear regression $p < 0.05$) are indicated by straight lines.

fraction of their food will determine the food's critical C:P ratio. If much of algal carbon is located in structures (such as cell wall structures with a high amount of cellulose) that *Daphnia* cannot assimilate with high efficiency (Van Donk et al. 1997), P limitation should occur at higher C:P ratios compared with communities in which algal carbon is easier to assimilate. The assimilation efficiency for carbon is probably considerably more variable than the assimilation efficiency for the phosphorous fraction of the algal biomass. Therefore, C:P ratios might be most valuable as a component measure of algal food quality once the suitability of the carbon fraction has been characterized. Obviously, this should be studied in more detail in further studies.

Responsiveness of different algal communities to the light supply—Our approach of using different algal communities from lakes of different nutrient status (rather than manipulating nutrient supply to a single algal community) brought additional insights into how different algal communities respond to light manipulation. In particular, we found that, in the absence of *Daphnia*, the size of light effects on seston C:P ratios (measured as the slope of the relationship between seston C:P ratio and light supply) was positively related to two measures of diversity: the Shannon–Wiener indices of diversity and evenness of the algal communities. Light-mediated changes in seston C:P ratios were stronger in more diverse algal communities (Fig. 5). A similar pattern was observed by Dickman et al. (2006) in a study of light-mediated changes in seston C:P ratios of three different natural algal communities. Such relatively small datasets cannot give conclusive evidence that the observed relationship is general. Characterizing these relationships and unraveling the mechanisms behind them require the study of a broader range of natural algal communities.

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Received: 19 February 2007

Amended: 12 October 2007

Accepted: 24 October 2007