

## Growth rate versus biomass accumulation: Different roles of food quality and quantity for consumers

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### Abstract

Population growth and biomass accumulation of *Daphnia magna* was studied in a two-stage continuous-culture system with light- and phosphorus-limited green algae (*Selenastrum capricornutum*) as food source. *Selenastrum* grown at saturating light conditions ( $70 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ) had on average 68% higher biomass yield and 103% higher C:P than algae grown under reduced light ( $10$  or  $36 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ). Initial *Daphnia* population response was affected by food quality, showing faster growth in the low-light treatments where food C:P was low and food quality was correspondingly high. When herbivore biomass became sufficiently high to deplete phytoplankton biomass to the threshold for net positive growth, the *Daphnia* carrying capacity appeared nevertheless to be determined primarily by the quantity of food. Thus, the high-light treatments, which yielded the highest algal biomass production, also gave twice as high asymptotic *Daphnia* biomasses as those with low light. This study demonstrates how short-term growth rate and long-term sustainability of populations may be affected differently by the quantity and quality aspects of their food. While high growth rate and reproduction require a diet that is balanced in terms of the grazer's demand for elements and macromolecules, a higher biomass of nongrowing individuals may still be sustained on a sufficiently plentiful supply of nutritionally deficient food.

Growth rate and carrying capacity for animal populations may be governed by different ecosystem properties. Both biomass and quality of plants have strong effects on grazers (Sternler and Elser 2002), and the relative effect of quantity versus quality is interrelated (cf. Boersma and Kreutzer 2002; Anderson and Hessen 2005). High food abundance may to some extent compensate for low quality, but food quality of plants may frequently be inversely related to food quantity since high biomass and low turnover commonly yields autotroph biomass with sub-optimal nutrient content relative to the grazers' demands. The effect of quantity relative to quality also strongly depends on the consumer's demands, which may also undergo ontogenetic shifts. Juvenile growth may have different requirements than those for reproduction or maintenance in adults (Færøvig and Hessen 2003). Correspondingly, changing demands at the individual level may sum up to responses at the population level.

The quality aspect of plant matter has several facets, including grazer repellents, structural defences, and biochemical constituents, such as essential fatty acids or amino acids. In this context, we will focus on the stoichiometry of plants relative to the grazer's demands, which strongly affects C utilization efficiency in both terrestrial and aquatic systems (Elser et al. 2000). Primary producers may exhibit a highly flexible cell stoichiometry with carbon (C) to element ratios (generally nitrogen, N, or phosphorus, P) spanning more than an order of magnitude (Andersen 1997). Metazoan herbivores in comparison have a much tighter regulation of their stoichiometry; both aquatic and terrestrial herbivorous invertebrates have far lower C to element ratios than that normally encountered in their food (Andersen and Hessen 1991; Elser et al. 2000; Sternler and Elser 2002). This dietary imbalance will make growth

efficiency in terms of C decline below a critical net intake of P relative to C, since an increasing amount of ingested C cannot be utilized for balanced somatic growth.

Several experiments have demonstrated how the growth of zooplankton herbivores, notably P-demanding species like *Daphnia* spp., may be constrained when the food source is autotrophs with low P content (Sternler 1993; Hessen et al. 2002). A growing body of literature suggests that a stoichiometric mismatch between grazers and their food source also may be a major determinant of food-web dynamics (Andersen 1997; Andersen et al. 2004), and that it may affect behavior and community composition of grazers both in aquatic and terrestrial habitats (White 1993; Sternler and Hessen 1994; Elser et al. 2000).

For plants, shifts in cellular P:C may be attributed both to ambient levels of P and photosynthetic active light (PAR) (Urabe and Sternler 1996; Sternler et al. 1997; Hessen et al. 2002). High light supports a high photosynthetic rate, leading to high accumulation of C-rich macromolecules, which results in a decreased P:C of autotroph biomass, especially under low P supply. Conversely, under conditions with light limitation and P saturation, biomass will be low, but the algal cells will have a high P:C (i.e., high food quality for herbivores). This shift in food quantity versus food quality could cause a trade-off scenario for grazers along a light gradient (Urabe and Sternler 1996). Along a gradient of increasing light with fixed total P, the herbivores' growth rate would be predicted to increase initially due to increased biomass of high-quality algae and then reach a peak growth rate at the optimum light:nutrient balance before finally declining due to decreasing food P:C (i.e., decreased quality).

The relative importance of food quality versus food quantity limitation will be of vital importance for assessments of ecosystem productivity. Nutritional constraints on growth hinge on an intake of elements in balanced

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Table 1. Experimental conditions, treatment levels, and initial conditions in three runs of the two-stage culture system.

Exp. run	Total P in medium ( $\mu\text{g P L}^{-1}$ )	High-light treatment ( $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ )	Low-light treatment ( $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ )	Treatment replicates (high/low)	Experiment duration (d)	Initial <i>Daphnia</i> addition ( $\text{mg C L}^{-1}$ )
1	155	70	36	2/2	79	0.9*
2	155	70	10	3/3	30	0.1†
3	78	70	10	3/3	37	0.08†

\* Added as juveniles.

† Added as adults.

proportions to the demands of somatic growth and reproduction. For maintenance metabolism, the dietary demands will shift and may to a greater extent be met by a stoichiometrically unbalanced diet, since the primary demand will be for C to meet respiratory demands (Anderson and Hessen 2005). When somatic growth ceases, the need for P, N, or essential macromolecules will also decrease, and the population may be regulated rather by food quantity than food quality. The elemental constraint as determinant for growth rate has been much explored by experiments and models. Less effort have been devoted to the balance between food quantity and quality as determinant of biomass accumulation and carrying capacity of consumers.

## Material and methods

The predicted contrasting effects of plant biomass quantity and quality on herbivore growth and carrying capacity was tested in experiments with the cladoceran *Daphnia magna* feeding on the unicellular chlorophyte *Selenastrum capricornutum*. The experiments were performed in a two-stage, flow-through culture system, consisting of an illuminated phototroph chamber connected to a darkened herbivore chamber (cf. Hessen et al. 2002).

The primary stage was a 2-liter glass vessel that received a nominal light intensity of  $70 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$  from 25-W blue-white fluorescent tubes. Low-light treatments were made by wrapping culture vessels in neutral-density screens. Peristaltic pumps supplied COMBO medium with reduced P content (Kilham et al. 1998) at a flow corresponding to a dilution rate of  $0.42 \text{ d}^{-1}$  in the phototroph stage. Timer-controlled magnetic stirrers mixed the primary chambers. Stirring was found to be preferable to bubbling because air bubbles tended to cause supersaturation problems in the downstream *Daphnia* cultures. All three experiments involved high- and low-light treatments, but with different levels of total P in the growth medium. The first experiment was run in duplicate; the others were run in triplicate (see Table 1 for further details on light intensities, nutrient levels, etc.). All experiments were run in a constant-temperature room at  $19^\circ\text{C}$ .

The phototroph growth chambers were sampled at least twice a week. One-hundred-milliliter subsamples were filtered on pre-ignited ( $500^\circ\text{C}$ , 2 h) GF/F-filters and analyzed for particulate C and N on a Carlo-Erba CHN 1106 elemental analyzer. Particulate P was measured on corresponding filters placed in 15-mL distilled water that

was acidified ( $150 \mu\text{L } 4.0 \text{ mol L}^{-1} \text{ H}_2\text{SO}_4$ ), supplemented with peroxydisulfate ( $0.15 \text{ g K}_2\text{S}_2\text{O}_8$ ), and autoclaved ( $121^\circ\text{C}$ , 1 h). Orthophosphate liberated by the wet oxidation was then analyzed spectrophotometrically by the standard molybdate-blue method. Algal cell numbers and size distributions were analyzed by flow cytometry (FCM). Samples of 1.0 mL were collected in Eppendorf vials, preserved with  $20\text{-}\mu\text{L } 50\%$  glutaraldehyde (1% final concentration), and stored in a refrigerator until analysis. FCM analyses were performed on a Skatron Argus 100 flow cytometer equipped with high-power mercury arc lamp (103 W) and a  $100\text{-}\mu\text{m}$  nozzle. The instrument was modified with gas-pressure-controlled sheath-flow delivery and a syringe-based sample-injection system, which minimized sample cross-contamination. Monodisperse latex beads (Polysciences No. 23517) were used for instrumental alignment and calibration. By using autofluorescence as trigger channel, egested cells would be excluded from FCM counts (cell autofluorescence was severely reduced by passage through the animal gut). Triggering on forward scatter and gating on fluorescence enabled differentiation between bacteria and *Selenastrum* in the FCM counts. Even under low light and high P, the share of bacteria was a minor contribution ( $<5\%$ ) to total biomass.

In order to obtain stable levels of cell numbers and elemental ratios of the food source, *Daphnia magna* were added to the downstream chamber when the primary stage had been running for 7 d. *Daphnia* biomass was monitored by a nondestructive image-analysis technique that allowed for regular observation of population growth without harvesting (details in Færøvig et al. 2002). The herbivore chamber had a grid covering the outlet so that detritus and uneaten food particles were washed out, while all *Daphnia* (including eggs and neonates) were retained in the system. This meant that the *Daphnia* population did not risk washout and that it could continue to grow until all supplied food was used for maintenance respiration and sufficient reproduction to replace biomass losses by natural mortality. Biomass increase of *Daphnia* was fitted with a logistic model:

$$x = \frac{K}{1 + \exp\left[-\mu\left(t - t_{1/2}\right)\right]}, (1)$$

where  $x$  is *Daphnia* biomass ( $\text{mg C L}^{-1}$ ),  $t$  is time (d), and  $K$  is the carrying capacity of the population ( $\text{mg C L}^{-1}$ ),  $\mu$  the maximal specific growth rate ( $\text{d}^{-1}$ ), and  $t_{1/2}$  is the half-time to maximum (d).

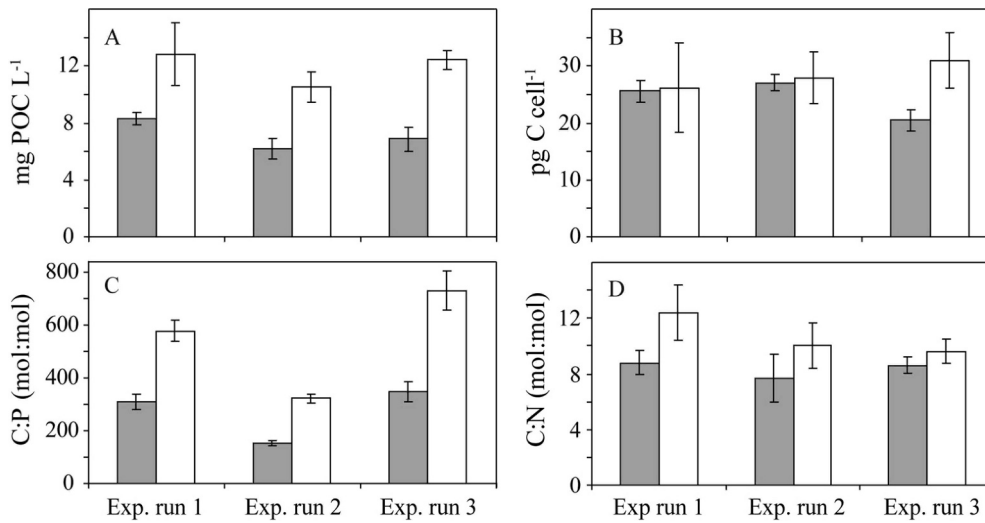


Fig. 1. Steady-state conditions in the primary (phototrophic) culture stage: (A) Particulate organic carbon (POC), (B) C per cell, (C) molar C:P, and (D) molar C:N. Bars are mean values with 95% confidence limits indicated by error bars, in relation to light treatments (low light: gray bars; high light: white bars) and experimental runs (Table 1).

We used the R statistical computing environment (<http://www.r-project.org>) to fit nonlinear and generalized additive models in this work. The nonlinear model fitting package for R (`nls`) has a built-in function (`SSlogis()` = self-starting logistic fit) for finding initial parameter estimates and fitting the logistic model (Eq. 1). The `nls` package also provides standard errors of parameter estimates based on profile likelihood theory under the assumption of normally distributed errors. Generalized additive models (GAM; Hastie and Tibshirani 1987) can represent any single-valued functional relationship between dependent and independent variables by the use of spline smoothers. Increasing the number of spline basis functions increases the number of model parameters and also increases the amount of “wiggleness” in the smoothing spline. A very flexible GAM model with many parameters will thus be able to fit the data well but may predict very badly on data points not included in the fit, while a very stiff GAM model with few parameters will behave much as a linear regression with little ability to represent nonlinearities in the data. We used the R package `mgcv` (Wood 2000), which fits a GAM using a generalized cross-validation scheme to find the optimal number of spline basis functions for balancing the concerns of goodness of fit and robustness.

## Results

Particulate organic C (POC) in the primary stage increased in proportion to light in all treatments, making the carbon biomass on average 68% higher in the high-light treatments compared with the low-light ones (Fig. 1A). The increase in particulate C was mainly due to increased cell abundance, as the carbon content of *Selenastrum* cells varied insignificantly between treatments in two of three experimental runs (Fig. 1B). Particulate P did not increase proportionally to biomass—the autotroph C:P was about

twice as high in the low-light treatments than in the ones with high light (Fig. 1C). The light-level treatment also had a small and consistent effect on the autotroph C:N, which was only statistically significant in one of three experimental runs (Fig. 1D).

All herbivore population responses went through a period of exponential increase that eventually levelled off to an asymptote, thus resembling a logistic function. As average *Daphnia* individual size was not significantly different among treatments or experimental runs, the main features of this growth response are independent of whether population size is expressed as abundance or biomass (Fig. 2; notice that the animals from the high-light treatments were consistently ~20% larger, even though this difference was not statistically significant). All experiments fit the logistic growth response model (Eq. 1) quite well (Fig. 3). If we look closer at the parameter estimates, we find that the high-light treatments had consistently significantly higher carrying capacities and longer half-

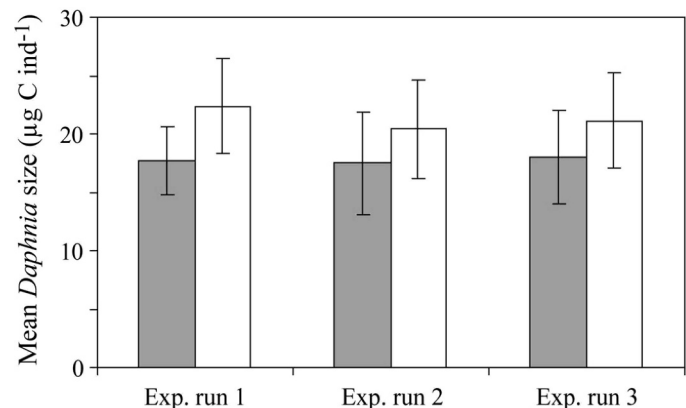


Fig. 2. Average individual *Daphnia* biomasses ( $\mu\text{g C ind}^{-1}$ ) in relation to light treatments (low light: gray bars; high light: white bars) and experimental runs (Table 1).

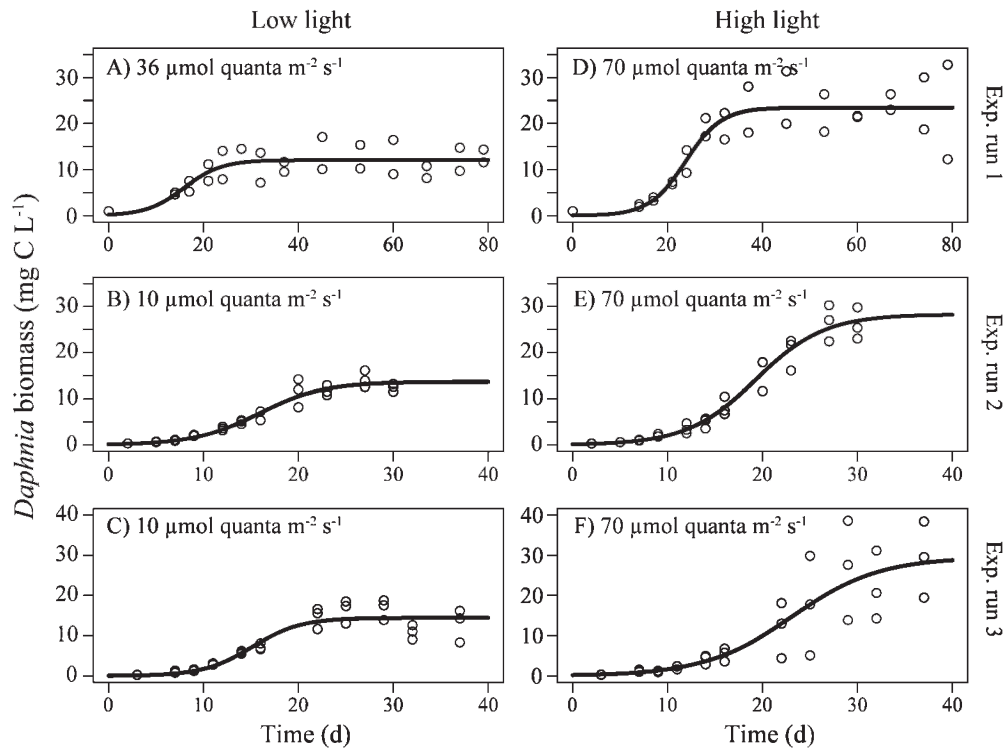


Fig. 3. Time development of *Daphnia* biomass ( $\text{mg C L}^{-1}$ ) in (A–C) low-light and (D–F) high-light treatments in three independent two-stage culture experiments (Table 1). Solid lines are predicted herbivore biomasses from a logistic model with parameters as given in Fig. 4. Notice differences in scales between experiments (both treatments in the same experiment are shown in identical scale).

times to maxima (Fig. 4A,B), while there were no significant differences in the third parameter (maximal specific growth rate; Fig. 4C). In other words, the high-light treatments reached a higher herbivore carrying capacity, but it took the population substantially longer time to reach this level.

If the volumes of the first and second culture stage are  $V_1 = 1.8 \text{ L}$  and  $V_2 = 1.0 \text{ L}$ , and the dilution rate of the autotroph stage is  $D = 0.42 \text{ d}^{-1}$ , then the average food supply to the herbivore stage would be  $D(V_1/V_2)C_1$ , where  $C_1$  is the average autotroph biomass in stage one (Fig. 1A;  $\text{mg C L}^{-1}$ ). Dividing the average food supply by the carrying capacity for *Daphnia* biomass (Fig. 4A;  $\text{mg C L}^{-1}$ ) gives the specific, or per capita, food-supply rate for the *Daphnia* population when it is at its carrying capacity. The specific food-supply rate at carrying capacity showed a consistent but statistically insignificant difference between light-level treatments (Fig. 5), which might be explained by the slightly larger body sizes in animals from the high-light treatments (Fig. 2). The average specific supply rate across all treatments and experimental runs was  $0.36 \text{ d}^{-1}$ , with an approximate 95% confidence interval from 0.29 to  $0.42 \text{ d}^{-1}$ .

The results in Figs. 3 and 4 indicate on a superficial level that the quantity of food supply has an overruling influence, since the high-light systems with the highest primary production also gave the highest accumulation of herbivore biomass. On the other hand, we already know

from previous studies (Hessen et al. 2002) that stoichiometric food-quality changes resulting from different light-level treatments have strong effects on juvenile *Daphnia* growth in the same system. In order to illuminate the quality effect in the early phase of the experiments, we can plot the ratio between average herbivore biomasses in the high- and low-light treatments against time for all experiments (Fig. 6). The ratios start off close to unity (as they should be since all treatments received the same inoculum), and then they drop after about 20 d: the high-light treatment develops the highest biomass, which then prevails to the end of the experiment.

We can substantiate this interpretation by fitting a generalized additive model (GAM; Fig. 6) with a 95% confidence belt that includes one initially, goes barely but significantly below one, and stabilizes at a plateau significantly above one. The low-light treatment leads initially (making the ratio  $< 1$ ) because of the lower food quality of algae from the high-light treatment. At a later stage, the low-light treatment has to give way because the buildup of herbivore biomass provides sufficient intraspecific facilitation to neutralize the quality effect of low light. In this changed situation, herbivore biomass production becomes just a question of food carbon supply, which will always be highest in the treatment where light is less limiting, and so the herbivore biomass ratio between treatments switches to values  $> 1$  and stays there throughout the experiment.

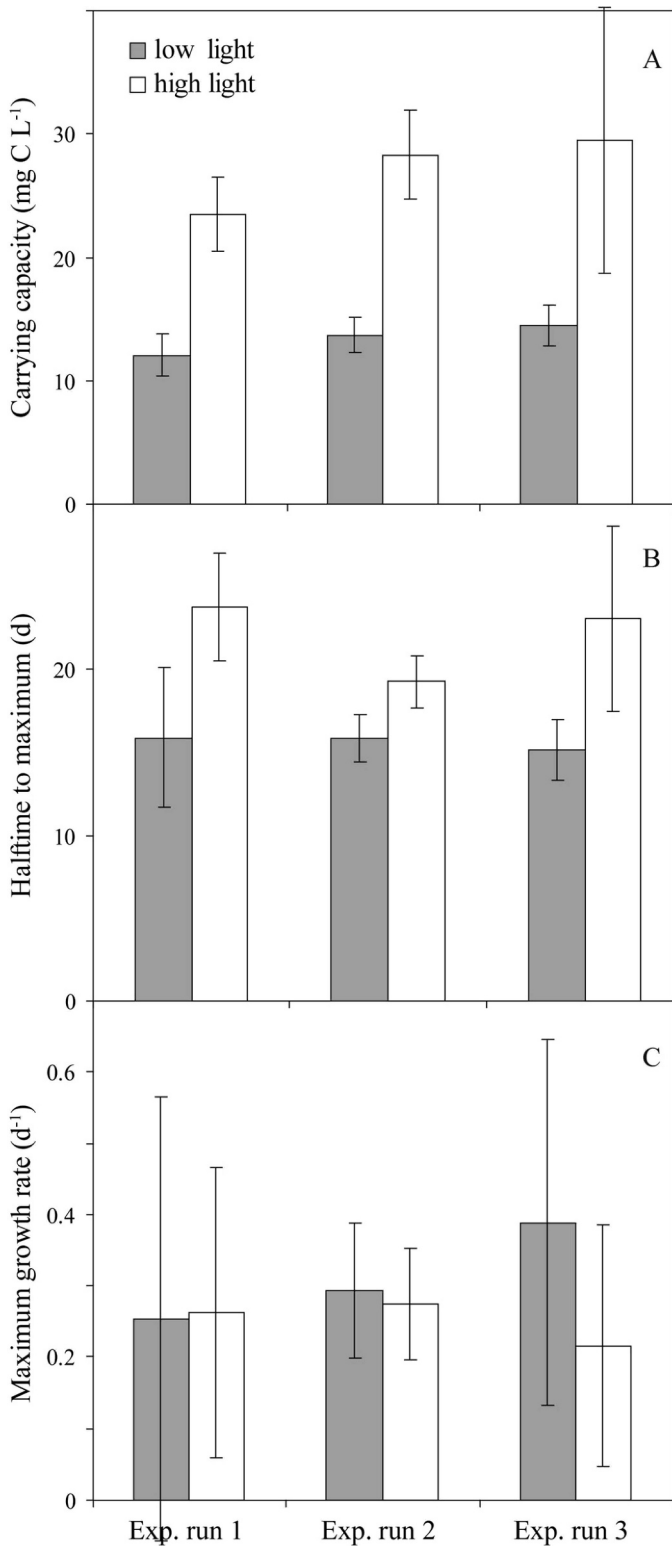


Fig. 4. Parameters of logistic models fitted to data in Fig. 3 with gray bars representing the low-light treatments: (A) carrying capacity (mg C L<sup>-1</sup>), (B) half-time to maximum (d), and (C) maximum growth rate (d<sup>-1</sup>). Error bars indicate 95% confidence limits.

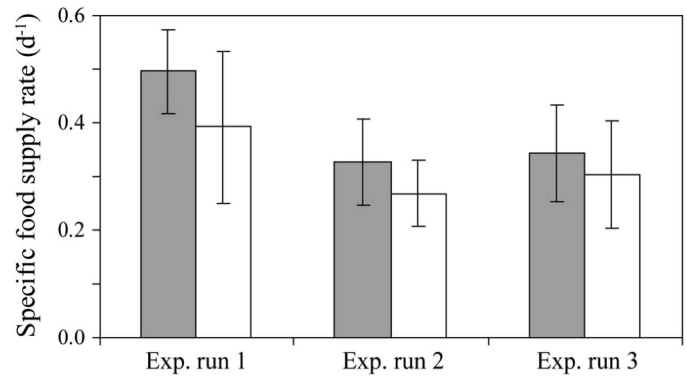


Fig. 5. Specific food-supply rate to the *Daphnia* population (d<sup>-1</sup>) computed as average biomass production rate in the phototroph stage divided by estimated *Daphnia* carrying capacity (Fig. 4A), in relation to light treatments (low light: shaded bars; high light: white bars) and experimental runs (Table 1). Error bars indicate approximate 95% confidence limits for the mean value.

Discussion

The general wisdom is that everything else being equal, increased inputs of solar energy will translate to higher primary production, which again means a higher capacity for secondary production. The innovative studies of Urabe and Sterner (1996) and Sterner et al. (1997) clearly demonstrated the kind of “paradox of energy enrichment” that occurs when the role of food stoichiometry is taken into consideration, where “too much” solar energy causes a reduced rate of individual growth due to food-quality constraints. The crucial question is how this affects consumer biomass and population dynamics. In our

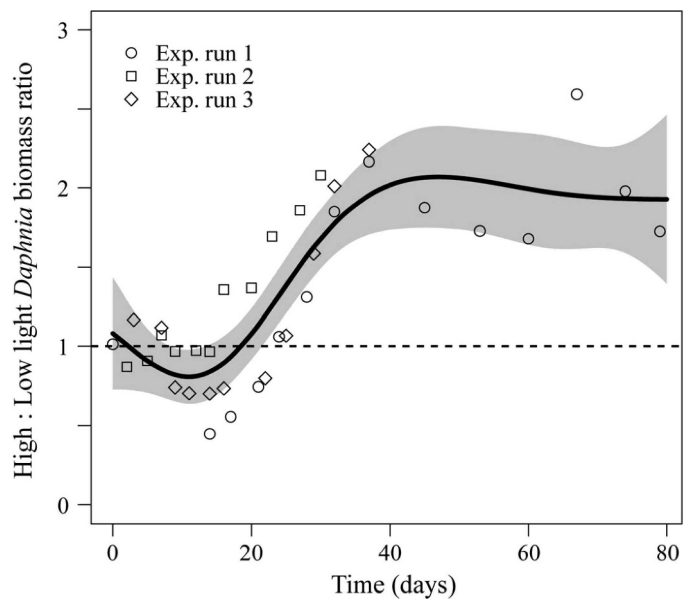


Fig. 6. Ratios of *Daphnia* biomasses in high- and low-light treatments as function of time, pooled for all three experiments. Smooth curve with shaded 95% confidence band is a generalized additive model (GAM) fitted to the observations using the mgcv package for R (Wood 2000). Dashed line indicates biomass ratio = 1 (i.e., no effect of light treatment).

experiments, biomass accumulation of *Daphnia* was initially faster in the low-light treatment, but eventually the biomass yield became highest in the high-light treatment, even though it could take a long time to reach this situation. The initial food-quality effect on the growth rate is fully concordant with the light:nutrient hypothesis (Urabe and Sterner 1996), while the observed positive effect of increased light on herbivore carrying capacity seems to indicate that this hypothesis is mainly valid for nonstationary populations.

Several experiments with zooplankton (notably P-demanding *Daphnia*) have demonstrated that if solar energy inputs are sufficiently high under low ambient nutrient content, the algal P:C may be too low for grazers to grow or even persist (Nelson et al. 2001; Urabe et al. 2002), leading to deterministic extinction of the grazer in line with theoretical predictions (Andersen 1997; Loladze et al. 2000). These events appear to occur only at extremely low P:C, however, while under less severe conditions, intraspecific facilitation may help *Daphnia* overcome P limitation and attain high biomass (Sommer 1992; Nelson et al. 2001; Urabe et al. 2002). This means that when grazer biomass builds up, increasing P recycling improves food quality by turning a large biomass of P-poor algae into a lower biomass with a higher P content (cf. Andersen et al. 2004). Thus, high light and low food quality may invoke a reversed (positive) density dependence in the consumer population, where a growing population may improve food quality via facilitation and thus increase secondary production until a point where food quantity becomes limiting and traditional (negative) density dependence sets in.

While there initially was some accumulation of algae in the grazer chamber, all inflowing biomass was entirely cropped down after 20 d or so. Thus, the specific food-supply rate at carrying capacity (Fig. 5) should also be a measure of the sum of all loss processes for a stationary population. Since losses due to moulting and natural mortality will be comparatively small, we can expect respiration and egestion to be the major carbon loss processes in a stationary *Daphnia* population (Andersen 1997). In other words, the specific food-supply rate in Fig. 5 will also be an upper limit for the specific maintenance respiration rate, and the calculated values fit well with those reported in the literature for *Daphnia* species (e.g., fig. 4.6 in Andersen 1997).

A system where the autotroph and the grazer growth chambers are separated is ideal for testing long-term grazer responses along food-quality and food-quantity gradients. At the same time, the two-stage design suffers from the weakness that recycling feedback effects from grazer to autotroph are not accounted for since autotrophs are unable to grow in the dark secondary stage. It can be shown, although we will not elaborate the proof here, that a two-stage system will unconditionally go through a facilitation phase as long as the system is sufficiently nutrient-rich and the through-flow rate is not too high. Thus, we expect a two-stage system to be unable to show the kind of dynamics that have been observed in single-stage systems (Nelson et al. 2001; Urabe et al. 2002), where

herbivores may end up in a quality- or quantity-limited state depending on the initial conditions.

Although the lack of recycling feedback on autotroph growth limits the extent to which the two-stage culture system can mimic a natural community, the distinct phases of quality and quantity limitation indicated in Fig. 5 give some idea what to look for. More specifically, if we accept the qualitative PEG model (Sommer et al. 1986) to describe the major steps in annual lake plankton succession, then events leading up to the spring clear-water phase would be roughly similar to the transition from quality to quantity limitation in a two-stage system. The subsequent events in the Plankton Ecology Group (PEG) sequence, when zooplankton abundance is limited by predation rather than food quality or quantity, would be outside the scope of what can be addressed in an experimental design where loss rate is not a treatment factor.

In pelagic ecosystems, high biomass of edible plankton and high biomass of herbivorous consumers do rarely coexist for long periods. Hence, in natural systems, it may be more correct to judge situations with high algal biomass of low quality as a transient situation and consider that high input of solar energy promotes higher peak biomass rather than a stable higher consumer biomass at carrying capacity. For littoral or terrestrial systems with far lower relative grazing losses (cf. Cebrian 1999), the scenario of a high biomass of grazers sustained on a high biomass of low-quality plants would be more likely. However the patchiness of food quality and quantity, as well as seasonal dynamics in the same parameters and selective foraging, makes it hard to predict the relative importance of food quality and quantity for growth and carrying capacity of herbivores (cf. Pastor et al. 1997). Moreover, the contrasting effects on growth rate and biomass accumulation are only valid if there is an inverse relationship between plant biomass and plant quality and if plant-quality constraints are important for the consumer. These assumptions are met for some systems, but certainly not all.

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