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## THE ROLE OF FOOD CHAIN COMPOSITION AND NUTRIENT AVAILABILITY IN SHAPING ALGAL BIOMASS DEVELOPMENT<sup>1</sup>

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**Abstract.** With the aim of assessing the principal structuring forces for algal biomass development, I conducted field studies along a productivity gradient of Swedish and Antarctic lakes. In accordance with predictions from current ecological theory, the regression line of planktonic algal biomass vs. the concentration of total phosphorus shows a steeper slope for Swedish (functionally three trophic levels) than for Antarctic lakes (functionally two trophic levels). This difference suggests that, besides the effect of nutrients, the food chain composition in aquatic systems has a crucial impact on the biomass development of planktonic algae. However, at very high productivity, phytoplankton biomass in the Antarctic lakes approached levels similar to those in Swedish lakes, suggesting that the algae “grew away” from being grazer regulated and instead became nutrient limited. The mechanistic connections between the components in the food chain, suggested by theory and the descriptive field study, were evaluated in an enclosure experiment. It may be concluded that classical food chain theory can explain a great deal of the variation in the relation between phosphorus concentration and phytoplankton chlorophyll, frequently used by limnologists.

**Key words:** *algae; Antarctica; food chain; grazing; phytoplankton; trophic level.*

### INTRODUCTION

Determination of the hierarchy of forces structuring ecosystems has always been a fundamental goal for ecologists. With respect to limnology, the fluctuation in nutrient concentration (bottom-up effects) has traditionally been viewed as the major structuring factor in lake ecosystems (Persson et al. 1988, and references therein). An opposing view, which grew in strength during the seventies, stated that biomass and productivity of a certain trophic level may be regulated by predation/grazing from the level above (top-down effects) (Bendorff et al. 1984, Shapiro and Wright 1984). During later years both top-down and bottom-up forces have been considered important for the food chain structure (McQueen et al. 1986, Bartell et al. 1988).

A recent approach, used to identify which of the myriad of potentially structuring factors that are of importance in a certain system, is to, by whole lake experiments, study “complex interactions” between the components in a system (Carpenter et al. 1987, Kerfoot 1987, Carpenter 1988, Carpenter and Kitchell 1988, Kitchell and Carpenter 1988). This approach, mainly developed from early work by Hrbáček (1962), differs somewhat from traditional ecosystem ecology by focusing more on the hierarchy of key mechanisms structuring the food chain, than on energy and carbon flows (Odum 1959, 1977, Odum and Biever 1984).

A long-standing controversy has focused on the question of whether observed community structure mainly results from environmental factors (Connell 1978, 1980) and random colonizing events (Connor and Simberloff 1979), or from competition for limiting resources. With respect to phytoplankton community structure, Harris (1986) argued that variation in abiotic factors (temperature, nutrient input, currents) precludes competition from being important under most conditions (Harris 1986: Fig. 2.1). In contrast, laboratory and field experiments have shown that competition for limiting resources is by no means a negligible force in structuring algal communities (Tilman 1982, Tilman et al. 1982, Sommer 1983, 1985, 1988, Carney et al. 1988, Hansson 1988, Sterner 1989). Thus, as for the controversy concerning the importance of bottom-up and top-down effects, it is probably not a question of “this or that,” but “when and how much.”

In 1960, Hairston, Smith, and Slobodkin presented a verbal model concerning structuring factors in terrestrial food chains. The model (often named HSS) has been further developed for terrestrial systems (Fretwell 1977, Oksanen et al. 1981, Oksanen 1983), and recently for aquatic systems (Persson et al. 1988), and predicts that very low-production systems contain only primary producers, which are resource limited. When productivity eventually increases, grazers invade and the primary producers become grazer regulated (two-level systems). When productivity increases even more, predators invade (three-level systems), and the primary producers will be released from grazer regulation and again become resource limited. The predictions for

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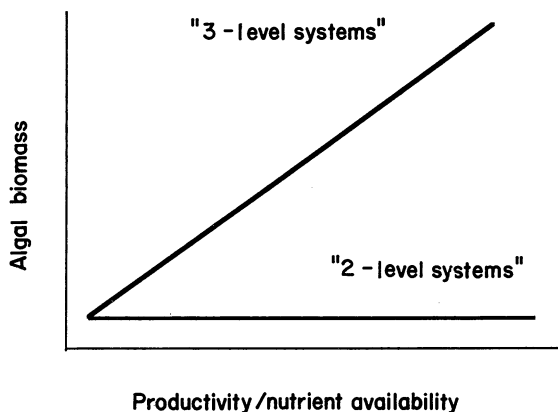


FIG. 1. Predictions revealed from current food chain theory about biomass development of phytoplankton along a productivity/nutrient gradient of lakes with two and three trophic levels, respectively. The graph shows a steep response of phytoplankton biomass in three-level lakes as nutrient availability increases, but no response in two-level systems as newly produced algal biomass is converted into grazer biomass.

aquatic systems will be that in three-level systems zooplankton are suppressed by fish predation, releasing algae from grazing, permitting them to grow as fast as nutrient availability and uptake permit, which can graphically be shown as in Fig. 1. In the two-level systems grazers are free to respond to any increases in algal biomass, and will therefore suppress algal biomass development, which will show no increase as nutrient availability increases along a productivity gradient.

Although food chain theory seems logical and simple, few empirical studies have been performed. A major reason for this may be that pure two-, three-, and four-level systems hardly exist in nature, but a two-level system eventually becomes a three-level system as productivity increases and predators invade, making it extremely difficult to test predictions from the theory. However, lakes may be suitable systems for food chain studies since migration of food chain components to and from the system is more restricted than in terrestrial systems.

In the present study I have utilized the special features of Antarctic lakes, combined with temperate and subarctic Swedish lakes, to test predictions from current theory. The Swedish lakes included in my study can be defined as functionally three-level systems (Persson et al. 1988), including primary producers and grazers (zooplankton), the latter regulated by planktivorous fish. For biogeographical reasons, Antarctic lakes totally lack fish (Heywood 1978, Hammar 1989), indicating low predation pressure on grazers. This suggests that the Antarctic lakes are very close to being "pure" two-level systems with primary producers and grazers as the major components. Moreover, as productivity increases no predators will invade these lakes, which makes it possible to test the specific food chain

hypothesis that there will be no increase in phytoplankton biomass in a two-level system with increasing nutrient availability (Fig. 1), since new algal biomass will be directly transferred into a growing zooplankton population. Hence, Antarctic lakes offer a rare opportunity to utilize natural two-level systems, ranging in productivity from extremely low-production meltwater lakes to highly productive guano lakes.

Although comparison between lakes along productivity gradients with respect to the biomass of primary producers is a useful tool in finding general patterns, such a correlative approach does not tell anything about mechanistic relations. Therefore I conducted an experimental study including enclosures with different predation pressures on zooplankton (simulating two and three trophic levels), where nutrient availability was gradually improved. If there is a mechanistic connection between predators, grazers, and primary producers in aquatic systems, the pattern evolved from the experiment will be the same as for the survey study of the Antarctic and Swedish lakes.

## MATERIAL AND METHODS

### Site description

Along a productivity gradient consisting of 12 lakes in temperate and 4 lakes in subarctic Sweden (55°50'–57°10' and 68°27' N, respectively), I measured the biomass of planktonic algae (as chlorophyll *a*) and the phosphorus content of the water. The studies were performed during July and August 1988 in the southern Swedish lakes and during August 1988 in the subarctic lakes. On the Antarctic peninsula (63°–68° S, 59°–62° W), 22 lakes were studied during February and March 1989. With few exceptions these lakes are situated on similar bedrock and in areas of similar climate, where lakes are ice free during 1–3 mo a year. All lakes investigated have separate drainage areas, and the Antarctic lakes lie in newly glaciated areas between moraine ridges, forming a mosaic lake landscape. Some drainage areas are very small, and such lakes only receive melt- and rainwater, leading to extremely low productivity. However, several lakes receive nutrients from breeding skuas (*Catharacta* sp.), whereas others are extremely productive due to penguin colonies and seals resting and swimming in the lakes. Hence, within a short distance a lake productivity gradient may be found, ranging from extremely low (total phosphorus [TP] 6 µg/L; chlorophyll *a* 0.5 µg/L) to extremely high productivity (TP 425 µg/L; chlorophyll *a* 407 µg/L) (Table 1). Although some of the Antarctic lakes are situated only 25 m from the seashore, the salinity is 0.19 g/kg (corresponding to 0.35 mS/cm), indicating that there is no influence from seawater (salinity: 35 g/kg) during summer. The dominant grazers in the Antarctic lakes are the copepod *Pseudoboeckella poppei* (Daday), and the anostracan *Branchinecta gaini* (Daday). During earlier larval stages *Branchinecta gaini* is

TABLE 1. Ranges in phytoplankton biomass (as chlorophyll *a*), total phosphorus (TP), total nitrogen (TN), phosphate (PO<sub>4</sub>-P), and temperature for temperate and subarctic Swedish, and Antarctic lakes.

	Temperate lakes	Subarctic lakes	Antarctic lakes
TP ( $\mu\text{g/L}$ )	5–306	5–7	6–425
TN (mg/L)	0.11–2.50	0.11–0.42	0.08–4.05
PO <sub>4</sub> -P ( $\mu\text{g/L}$ )	1–101	1	1–84
Phytoplankton ( $\mu\text{g/L}$ )	3.8–182.2	0.6–0.8	0.5–406.9
Water temperature ( $^{\circ}\text{C}$ )	15–24	6–18	1–4

probably eating phytoplankton (Heywood 1972), whereas the adult seems to focus more on the periphyton (L.-A. Hansson, *personal observations*). One predatory copepod (*Parabroteas sarsi* Daday) also occurs in low abundances in some lakes, although its predatory pressure is probably negligible compared to the fish predation in the Swedish lakes.

#### Sampling

All sampling was performed in macrophyte-free, unexposed littoral areas, at a water depth of 0.75 m. Phytoplankton was sampled in the surface water (0–20 cm), filtered on a GF/C filter, and frozen for later chlorophyll extraction in methanol (Holm-Hansen and Riemann 1978, Marker et al. 1980). Water samples for phosphorus analysis were taken from surface water (0–20 cm), fixed with HgCl<sub>2</sub> (4% [40 g/L], 0.1 mL per 100 mL sample), and stored in a refrigerator (+8°C). Samples for determination of total phosphorus were digested in potassium persulfate (50 g/L). Total phosphorus and phosphate were determined as molybdate reactive phosphorus on a Technicon Autoanalyzer II.

#### Experimental setup

Six cylindrical enclosures (2 m in diameter, volume 7.8 m<sup>3</sup>) were put in the littoral zone of the oligotrophic Long Lake (Michigan, USA, 46°13' N, 89°32' W). Enclosures were made of reinforced plastic attached to wooden posts driven into the sediment. The experiment was conducted from 10 June to 18 August 1990.

Besides direct predation on zooplankton, fish are known to affect nutrient levels by excretion (Threlkeld 1987), and by stirring up the sediment (Lamarra 1974). Since the aim of my study was to focus on predation effects, the same amount of fish was used in all six enclosures. In three of them fish were put in nylon cages (diameter 0.7 m, volume 0.4 m<sup>3</sup>) with a mesh size of 3 mm, allowing zooplankton to enter the cages (simulating three-level systems). In the other three enclosures the mesh size of the cages was 0.2 mm, excluding zooplankton from the fish (simulating two-level systems), but still exposing enclosures to the same amount of fish excretion. Once every 10th d fish were taken up and put in a solution of Prolong (nitrofurazone) to reduce infection by fungi. This treatment kept death rate among fish below 1% a day. After treatment (1 h), fish from fine mesh cages were put in coarse net cages and vice versa, a procedure assumed to smooth out

any differences in excretion and predation rate among fish individuals.

Fish abundance was eventually increased from 2 (10–21 June), 4 (21–28 June), 6 (28 June–20 July) to 8 (20 July–18 August). The fish species used were yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), and common shiner (*Notropis cornutus*), with sizes of 86.5 ± 13.6 mm, 62.8 ± 25.6 mm, and 80.1 ± 13.2 mm, respectively (means ± 1 SD). All species are common and reflect the fish community in the area.

With the aim of illustrating the development of algal biomass at different grazing pressures when nutrient availability gradually increases, phosphorus (3.33 g KH<sub>2</sub>PO<sub>4</sub>) and nitrogen (14.89 g NH<sub>4</sub>Cl) were added to each enclosure every 10th d.

Samples for zooplankton biomass and phytoplankton chlorophyll *a* were taken 5 times during the experimental period (3 July, 11 July, 23 July, 3 August, 18 August) with a plastic pipe (length 2 m, diameter 52 mm). Three subsamples were taken in each enclosure, mixed, and separated into a 4-L sample for zooplankton filtration (80  $\mu\text{m}$ ), and a 0.1–2.2 L sample for chlorophyll filtration. The zooplankton samples were filtered on an 80- $\mu\text{m}$  mesh net, fixed with Lugol solution for later counting, length measurements, and biomass calculations. Algal chlorophyll samples were filtered on GF/C filters (Whatman), which were frozen prior to extraction in methanol (Marker et al. 1980). Readings were made on a Turner 450 Fluorometer.

#### RESULTS

The range in total nitrogen and phosphorus concentrations in the water of the Swedish lakes was 0.11–2.50 mg/L and 5–306  $\mu\text{g/L}$ , respectively (Table 1). Ranges were somewhat broader for the Antarctic lakes: 0.08–4.05 mg/L and 6–425  $\mu\text{g/L}$  (TP). A higher portion ( $t = 2.87$ ;  $P < .007$ ) of available phosphorus (PO<sub>4</sub>-P) was found in the Antarctic than the Swedish lakes (33 and 17%, respectively). Both in Swedish three-level systems and Antarctic two-level systems phytoplankton biomass increased with increasing amounts of phosphorus in the water (Fig. 2). However, the slope was steeper for three-level (1.44), than for two-level systems (0.64), at phosphorus concentrations of up to 22  $\mu\text{g/L}$  ( $t = 15.7$ ;  $P < .001$ ). At higher phosphorus concentrations the two-level systems approached values of phytoplankton biomass similar to those of the three-level systems (Fig. 2). As the biomass of the ma-

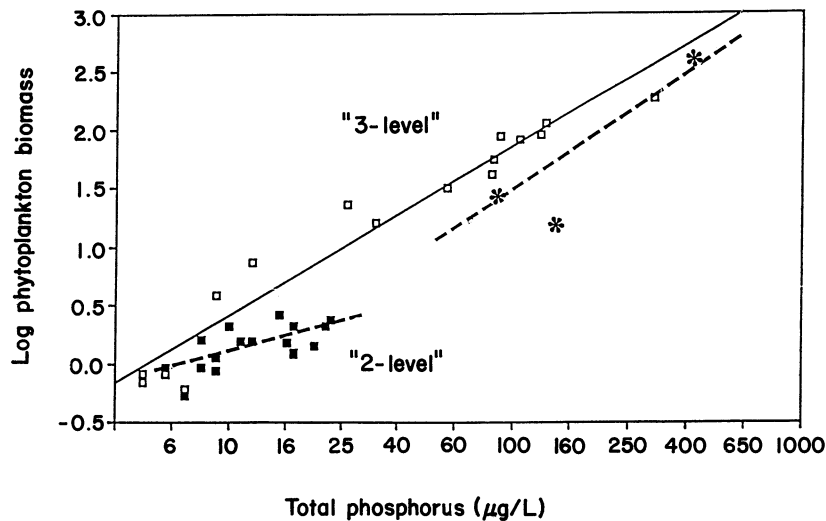


FIG. 2. Regression lines for log phytoplankton biomass (measured as chlorophyll *a* concentration, in micrograms per litre) vs. total phosphorus concentration (TP) in the water of Antarctic lakes (■, \*, ---) harboring two trophic levels (for TP < 22 µg/L:  $y = 0.64x - 0.56$ ;  $r^2 = 0.44$ ;  $F = 12.0$ ;  $P < .003$ . For TP  $\geq 22$  µg/L:  $y = 1.7x - 1.9$ ;  $r^2 = 0.89$ ;  $F = 15.9$ ;  $P = .057$ ;  $n = 4$ ), and three-level Swedish lakes (□, —:  $y = 1.4x - 1.0$ ;  $r^2 = 0.94$ ;  $F = 234.5$ ;  $P < .001$ ). Stars indicate the highly productive Antarctic lakes that can also be identified in Fig. 3. All equations are based on log-transformed values.

major grazer in the Antarctic lakes (*Pseudoboeckella poppei*) increased from 0 to  $\approx 100$  µg/L, the chlorophyll content of the lakes showed no increase (Fig. 3). In the three most eutrophic lakes, however, chlorophyll showed a substantial increase, despite the fact that grazer biomass was still high.

In the experimental enclosures without fish predation the zooplankton biomass at the end of the experiment had increased to 1575 µg/L (corresponding to 160 individuals/L), with *Daphnia*, *Bosmina*, and copepods as the main grazers (56, 19, and 25%, respectively; by numbers). In the presence of fish predation,

*Daphnia* abundance was reduced to zero within 3 wk, and the zooplankton community became dominated by small copepods and *Bosmina* (78 and 22%, respectively; by numbers). The experimental study showed different development of chlorophyll *a* in enclosures with and without fish predation (Fig. 4). As the biomass of *Daphnia* was reduced and the zooplankton community shifted into dominance by small, less efficient grazers, chlorophyll eventually increased 10 times. However, if *Daphnia* was released from the predation pressure, they were capable of keeping the chlorophyll level low, despite high nutrient concentrations. Fur-

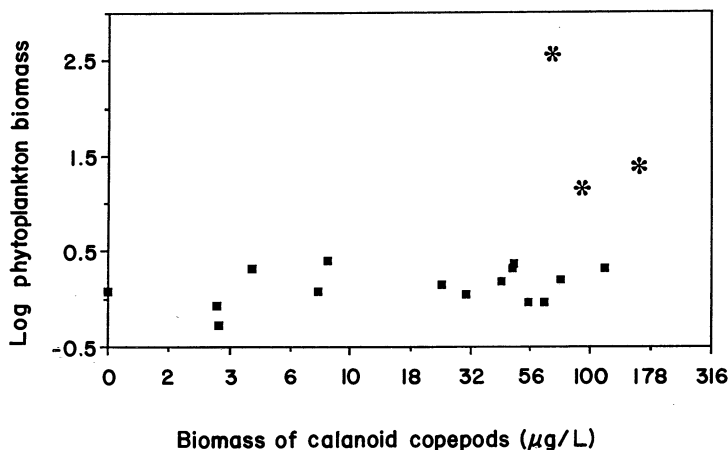


FIG. 3. Log biomass of phytoplankton (measured as chlorophyll *a* concentration, in micrograms per litre) in relation to biomass of the herbivorous calanoid copepod *Pseudoboeckella poppei* in the Antarctic lakes, showing no increase in phytoplankton biomass with increasing grazer biomass but a sudden increase when grazer biomass ceases to increase. Stars indicate the highly productive Antarctic lakes that can also be identified in Fig. 2.

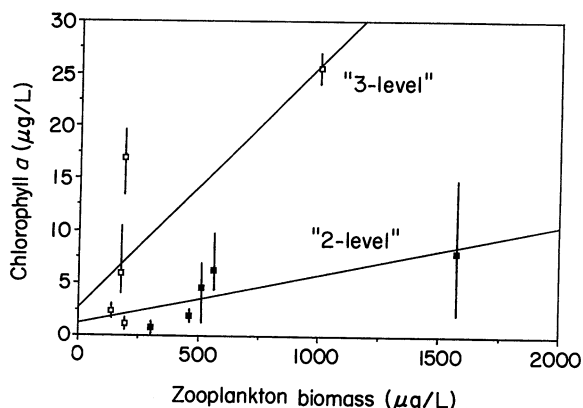


FIG. 4. The biomass development of phytoplankton (as chlorophyll *a*) in relation to the zooplankton biomass in the presence (□;  $y = 2.55 + 0.023x$ ;  $r^2 = 0.67$ ) and in the absence (■;  $y = 1.12 + 0.0046x$ ;  $r^2 = 0.63$ ) of predation from fish in enclosures simulating three- and two-level systems, respectively. The same amount of nutrients was added to all enclosures. Mean values and ranges are given. The number of replicates is three, except the three last sampling occasions in the "two-level enclosures" due to the presence of fish, which by mistake entered one of the enclosures, and the last sampling occasion in the "three-level enclosures" due to a rip in one of the plastic walls. Data from these occasions were discarded.

thermore, at similar nutrient availability, chlorophyll *a* levels differed more than threefold at the end of the experiment, depending on whether efficient grazers were present or not (Fig. 5).

DISCUSSION

My two data sets, including productivity gradients from Swedish three-level systems (major components: phytoplankton, zooplankton, and planktivorous fish), and Antarctic two-level systems (totally lacking fish; i.e., the third trophic level cannot invade at increasing productivity), may offer a rare opportunity to test the predictions from current food chain theory ( Hairston et al. 1960 [HSS], Fretwell 1977, Oksanen et al. 1981, Persson et al. 1988). One of the predictions revealed from the HSS model is that development of phytoplankton biomass along a productivity gradient of three-level systems should be a direct response of nutrient availability (i.e., bottom-up regulation) (Fig. 1). Furthermore, strictly applying HSS on two-level systems predicts that phytoplankton biomass should not respond to increased nutrient availability, since the increase in phytomass would be directly converted into grazer biomass (i.e., total top-down regulation) (Fig. 1). This is obviously not the case in natural systems (Fig. 2), but at phosphorus concentrations below 22 µg/L, the slope of the line is significantly less steep for two-level, than for three-level lakes, suggesting a lower phosphorus concentrations. That the grazers actually are responsible for the damped increase in phytoplankton biomass in the Antarctic lakes is suggested by the

lack of an increase in phytoplankton biomass when the biomass of grazers increased from 0 to ≈ 100 µg/L (Fig. 3). Comparison with International Biological Program data (Brylinsky 1980), mainly including temperate lakes with fish (three-level lakes), shows a clear liner relationship ( $r = 0.78$ , log-log scale) between the production of herbivorous zooplankton and phytoplankton. The notion is further strengthened by the experimental results from the enclosure study that show a poor biomass development of phytoplankton when zooplankton were allowed to respond to algal growth without being exposed to predation (simulating two-level systems), but a fast increase when fish reduced the biomass of efficient grazers (simulating three-level systems). Hence, differences in food chain composition, i.e., if grazers are a major regulating factor or not, may partly explain the variation within the classical and frequently cited regression between total phosphorus and planktonic algae (Sakamoto 1966, Vollenweider 1968, Dillon and Rigler 1974, Schindler 1978, Hansson 1988).

Assuming that the three-level line (Fig. 2) represents the exclusive response of phytoplankton to phosphorus availability (bottom-up response), i.e., the potential biomass when grazers have a negligible structuring function, the difference between this line and the two-level line represents the actual grazing pressure in the two-level lakes (i.e., the top-down effect). Actually, at a TP-concentration of 22 µg/L, phytoplankton biomass in the two-level lakes was only 26% of that in the three-level lakes (2.4 and 11.8 µg/L, respectively), illustrating the fact that grazing has a considerable impact on phytoplankton in two-level lakes. The difference between to two-level line (Fig. 2) and an imaginary line parallel to the *x* axis (slope = 0; predicted outcome by theory), represents the realized effect of increased phosphorus availability in the presence of unregulated grazing. However, an exclusive top-down control may not be expected in natural, dynamic systems, since the time scales of algal and zooplankton reproduction differ con-

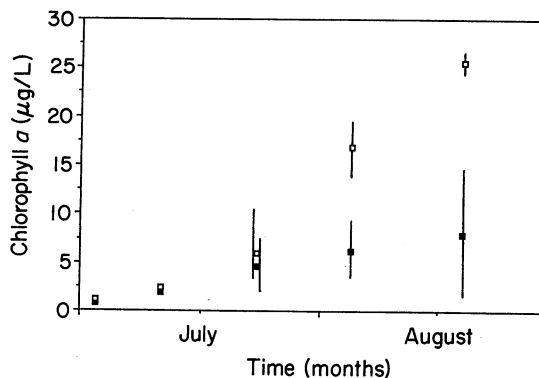


FIG. 5. Phytoplankton biomass development (measured by chlorophyll *a* concentration) over time in enclosures with (□) and without (■) fish predation on zooplankton. Mean values with ranges are given. Exceptions as in Fig. 4.

siderably (Walters et al. 1987, Kerfoot and DeAngelis 1989), which will induce a lag phase before grazers respond to alterations in the density of primary producers. The problem with different time scales is accentuated in the Antarctic data set where the dominant grazer is a copepod (*Pseudoboeckella poppei*), which has to go through several instars before reproduction, and an anostracan (*Branchinecta gaini*), which does not attain sexual maturity before 3 mo of age (Heywood 1972). Hence, phytoplankters respond quickly to alterations in nutrient availability, whereas the grazers may fail to directly follow changes in food availability (algae), and thus, to become the exclusive regulating factor for the phytoplankton assemblage. The time lag in zooplankton response to increased algal cell division seems to be even more pronounced at phosphorus concentrations above 22  $\mu\text{g/L}$ . Although only three data points are available, phytoplankton biomass seemed to increase in a pattern similar to that found in the three-level systems (Fig. 2), indicating that the grazers fail to control algal biomass at high nutrient availabilities. Besides the possible effects of time lags, this may be a result of changes in algal species composition towards inedible forms. The observations in the highly productive Antarctic lakes also show that phytoplankters in this harsh environment have the potential to attain similar biomass as in temperate lakes at similar nutrient availabilities, despite considerable differences in temperature, turbulence, and length of the growing season. Thus, the different slopes for Antarctic and Swedish lakes at TP concentrations below 22  $\mu\text{g/L}$  (Fig. 2) are not a result of differences in climatic or physical factors. This is in accordance with the suggestion of Priddle et al. (1986), that the low temperature does not consistently limit biomass production of phytoplankton in Antarctic lakes, but is contradictory to the concept that random disturbance is the major force limiting phytoplankton densities (Harris 1986).

If grazers, and not nutrients, are the main regulators for phytoplankton biomass development in two-level systems, then the fraction of phosphate (assumed as equal to bioavailable phosphorus) should be higher in two-level than in three-level systems. This was also the case in the Antarctic lakes where the portion of available phosphorus was 2 times higher than in the Swedish lakes (33 and 17% of total phosphorus, respectively). Furthermore, in the two-level lakes with highest productivity (Fig. 2), the fraction of available phosphorus was even lower (12%) than in three-level systems, suggesting that in highly productive two-level systems algae tend to "grow away" from grazing pressure, and instead become limited by nutrients. Hence, at total phosphorus concentrations of between 22 and 90  $\mu\text{g/L}$ , there seems to be a shift from grazing (top-down) to nutrient (bottom-up) regulation of phytoplankton biomass development in two-level Antarctic lakes. This notion is further strengthened by the sudden increase in phytoplankton biomass when grazer biomass ceases

to increase in very nutrient-rich Antarctic lakes (Fig. 3), indicating a mechanistic connection between grazer biomass and the complex shape of the algal-phosphorus regression (Fig. 2).

In summary, phytoplankton responded with a steep increase in biomass to improved nutrient conditions in lakes where grazing was of minor importance (three-level systems), but showed a less steep response to nutrient availability when grazers were not regulated by predators (two-level systems). Similar results were obtained in experiments simulating two- and three-level systems, suggesting that the mechanism behind the observed pattern involves differences in predation pressure on grazing zooplankton, "cascading" down to algae. Although food chain theory cannot explain all of the variation, this study clearly shows that the food chain composition in a lake has a crucial impact on the phytoplankton biomass development.

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