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Convergent succession of phytoplankton in microcosms with different inoculum species composition

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Summary. Different initial mixtures of phyto- and zooplankton from different lakes were grown under identical chemical and physical conditions in medium size (8- and 12-l) laboratory microcosm cultures until convergence of phytoplankton species composition was attained. Five such experiments with four (four experiments) or three (one experiment) microcosm cultures were run. Three experiments were performed with weak stirring which permitted sedimentary elimination of the diatoms. Two experiments were conducted with stronger stirring to prevent sedimentation. In the three "sedimentation intensive" experiments, the final phytoplankton community was composed of the filamentous chlorophyte *Mougeotia thylespora* together with a smaller biomass of nanoplanktic algae. In the two "sedimentation free" experiments the final phytoplankton community consisted of pennate diatoms. Both dissolved nutrient concentrations and the chemical composition of biomass suggested strong nutrient limitation of algal growth rates in the final phase of the experiments. The zooplankton communities at the end of the experiments were composed of species that were apparently unable to ingest the large, dominant algae and that presumably fed on the nanoplanktic "undergrowth" and the bacteria. There was a distinct sequence of events in all experiments: first, the large zooplankton species (*Daphnia* and Copepoda) were replaced by smaller ones (*Chydorus*, *Bosmina*, rotifers); second, all cultures within one experiment developed the same nutritional status (limitation by the same nutrient); and third, the taxonomic composition of phytoplankton of the different cultures within one experiment converged. The last took 7–9 weeks, with is about 2–3 times as long as the time needed in a phytoplankton competition experiment to reach the final outcome.

Key words: Phytoplankton – Zooplankton – Microcosm – Succession – Competition

Current views explaining the species composition of phytoplankton fall on a continuum. One extreme position holds that phytoplankton species composition can be explained by species-specific requirements for resources, abilities to harvest resources, and abilities to withstand mortality and the dependence of these requirements and abilities on physical conditions. This view has gained considerable momentum from Tilman's (1982) competition theory and from increasing knowledge about grazing selectivities (for a review see Sterner 1989). According to this view, phytoplankton communities will be dominated by species best suited to the current combination of growth and loss factors. The other position (e.g. expressed in Harris 1986) denies that there will ever be enough time for "best suited" species to displace less well suited ones before conditions change and alter the competitive hierarchy. Community composition at any moment will therefore be codetermined by the abundance of species before the last reversal in conditions.

By analogy to economic theory, these views may be characterized as the "supply side" (Roughgarden et al. 1987) and the "demand side" hypothesis. The "supply side" hypothesis predicts that community composition will primarily be determined by the availability of species either supplied by immigration and physical transport or supplied as residual populations from previous successional stages. The "demand side" hypothesis predicts that community composition will be determined by the environmental requirements and physiological abilities of the different species. At first sight it seems plausible that the relative validity of both hypothesis depends on the time elapsed since the last change in external conditions. Early on the "supply side" hypothesis will explain more and later on the "demand side" hypothesis will explain more.

Unfortunately, experimental investigations of the time needed to obtain communities of "best suited" species and, conversely, of the temporal persistence of inoculum effects are scarce. The time required for competitive exclusion in the absence of differential mortality can be extracted from published chemostat experiments. Although competitive exclusion can in theory be an infinite process, some operational end-points can be defined arbitrarily. If a physiologically superior competitor invades an already existing equilibrium population of an

inferior competitor it takes only 1–3 days before the population of the resident species starts to decline (Tilman and Sterner 1984). If chemostats are inoculated with a natural multispecies phytoplankton assemblage (Smith and Kalff 1983; Sommer 1983, 1986) it takes 14 ± 3 (SD) days before the last losing species starts to decline and 23 ± 5 days for the winning species or winning couple of species to reach 95% of total phytoplankton biomass. These times were independent of dilution rate, nutrient conditions and the initial abundance of the winning competitors. In a series of competition experiments with periodic disturbances by addition of the limiting nutrient in weekly pulses instead of a continuous supply, the number of coexisting species increased dramatically (Sommer 1985) but the approach to the final species composition was only slightly retarded: 18 ± 4 days till the last loser started to decline and 27 ± 4 days till the species classified as persisting made up > 95% of total biomass. This means that any disadvantage imparted by initial rarity and any advantage imparted by initial dominance will vanish and that communities with initially different relative abundances will converge within a few weeks if only phytoplankton-resource interactions are important.

In the presence of herbivorous zooplankton, a different outcome may be expected if inoculum effects within the zooplankton community perist longer and propagate "top-down" to phytoplankton. The experiments reported in this paper are intended as a first step into the experimental investigation of this question. Microcosm cultures with initially different relative abundances of algae and zooplankton were subjected to identical and unperturbed physical and chemical conditions and maintained until the species composition of phytoplankton had converged. Three possible outcomes can be expected: (1) Zooplankton do not delay the convergence of phytoplankton; (2) zooplankton delay the convergence of phytoplankton; (3) zooplankton prevent the convergence of phytoplankton.

Methods

Each experiment consisted of four (in experiment 2 only three) microcosm cultures which received different inocula but identical physical (light, temperature, stirring) and chemical (medium) treatment. The experiments are designated by numbers; the individual microcosms within each experiment are designated by letters. The different inocula were obtained by mixing plankton samples from different lakes in different proportions. In experiment 3 there were two different treatments with two replicates each. In the other experiments each individual microcosm received a different inoculum (Table 1). Bottle samples (half epilimnion, half hypolimnion) were used in experiments 1 and 3. The inoculum made up half of the culture volume. For the experiments started in periods of low plankton densities (2, 4, 5) net-samples (10 µm mesh size) were used as inoculum. Otherwise complete absence of important zooplankton species in some, but not all of the cultures could have precluded convergence of species composition. The medium was sterile filtered water from the mesotrophic lake Schöhsee enriched with silicate, phosphate and ammonium nitrate to the final concentrations given in Table 1. Once per week 25% of the culture volume was sampled and replaced by fresh medium. A 25% renewal per week corresponds to a daily instantaneous dilution rate of about 0.04 d^{-1}. This rate is extremely low relative to phytoplankton growth and loss processes and guarantees that internal cycling of nutrients is far more important than external renewal.

Experimental temperatures were 18° C; the light measured in the center of the culture bottles was 270–320 $\mu E \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation at a light : dark cycle of 12 : 12 h. Air was continuously blown to the surface of the cultures. Bubbling of the cultures was avoided, to prevent selective mortality of zooplankton species with a hydrophobic surface (e.g. *Daphnia*). Experiments 1, 2, and 3 were conducted in polycarbonate containers of 14 l total volume (12 l culture volume). The cultures were mixed with a floating magnetic stirring bar (Nalgene labware) at 10 rpm. This mixing regime was insufficient to avoid sedimentation of diatoms and the subsequent formation of a bottom sediment in the containers. For the sake of brevity, these experiments shall be called "sedimentation intensive". Experiments 4 and 5 were conducted in glass reaction flasks (Schmizo, Zofingen, Switzerland, type 50) of 10 l total volume and 8 l culture volume. The cultures were mixed with a motor-driven anchor-shaped glass stirrer at 20 rpm. This mixing regime was sufficient to avoid sedimentation and shall be called "sedimentation free".

Chemical analyses of dissolved nutrients (silicate, soluble reac-

Table 1. Summary of the experimental treatments: number of experiment (No.); time; dissolved silicate (Si), dissolved reactive phosphorus (P) and dissolved inorganic nitrogen (N) in the medium (µM); source of the inoculum; and proportions in which inoculum was mixed

No.	Time	Medium			Inoculum				
					Source	Proportions			
		Si	P	N		A	B	C	D
1	21.05.–05.08.87	15.9	1.3	22.0	Schöhsee	1	10	1	1
					Kellersee	1	1	10	1
					Gr. Binnensee	1	1	1	10
2	30.03.–03.06.88	25.2	0.8	12.1	Schöhsee	10	1	1	
					Gr. Plöner S.	1	1	10	
3	26.06.–17.08.88	67.0	0.17	23.2	Schöhsee	10	10	1	1
					Gr. Plöner S.	1	1	10	10
4	01.02.–05.04.89	108.0	0.75	20.5	Suhrer See	20	1	1	1
					Edebergsee	1	20	1	1
					Schöhsee	1	1	20	1
5	26.04.06.07.89	110.0	0.35	8.5	Suhrer See	20	1	1	1
					Gr. Plöner S.	1	20	1	1
					Schöhsee	1	1	20	1

tive phosphorus, nitrate, nitrite, ammonium) were performed according to standard techniques (Strickland and Parsons 1972). Particulate organic carbon (POC) and particulate organic nitrogen (PON) were measured with a Carlo-Erba CN analyzer. Particulate phosphorus was measured by filtering an appropriate volume of plankton suspension onto a cellulose nitrate membrane filter (0.2 µm pore size). The entire filter was then used for the standard total phosphorus technique, which completely extracted P from the filters without dissolving them. Similarly particulate opaline silicate was extracted from Nuclepore filters and measured according to Tessenow (1966). Zooplankton were excluded from particulate element analysis by sieving through plankton gauze of appropriate mesh size.

Phytoplankton counts were performed according to the inverted microscope technique. About 400 individuals were counted per important species, thus giving a counting precision of ± 10% within 95% confidence limits. Rare species were counted in correspondingly lower numbers. Biomass was estimated as cell volume, which was calculated by approximation to the nearest standard geometric solid after microscopic measurements of at least 20 individuals per species. Total phytoplankton carbon recalculated from total biovolume according to Rocha and Duncan (1985) agreed well with chemically measured POC, differences being always < 25%.

Pairwise taxonomic similarity between the different cultures within one experiment was expressed by a biomass-based version of the similarity index according to Bray and Curtis (1957). This index is obtained by calculating the relative contribution of individual species to total biomass ($p_i = B_i/B_{tot}$), selecting those species which are common to both samples, selecting the smaller of both p_i values for each species, and calculating their cumulative sum.

Due to the insufficient sample size (1 l) crustacean zooplankton could not be counted at the same precision as phytoplankton. Zooplankton abundance data should therefore be taken only as rough estimates.

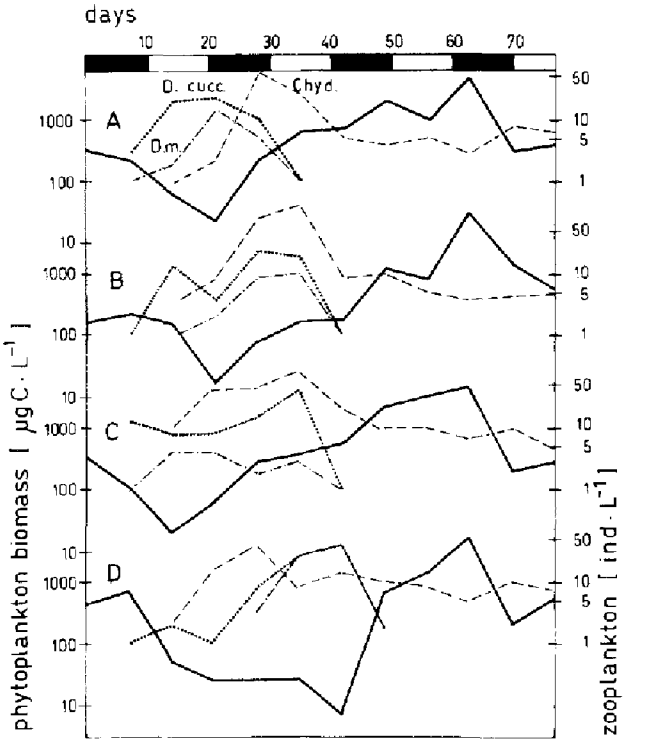

Fig. 1A–D. Phytoplankton biomass (µg C · l⁻¹, *thick line*) and abundances of important zooplankton species (*D.m.* –.–.: *Daphnia magna, D. cucc.* .....: *Daphnia cucculata, Chyd;* – – – : *Chydorus sphaericus;* other zooplankton not shown, (but see Fig. 10) in experiment 1. A, B, C and D designate the different microcosm cultures within experiment 1 (for treatments see Table 1)

Results

Phytoplankton biomass

The phytoplankton biomass in experiment 1 declined from initially several hundred µg C · l⁻¹ to minimal levels of 8–20 µg C · l⁻¹ (Fig. 1). This minimum was attained at different times in the different cultures and coincided roughly with the peak in the abundances of *Daphnia* spp., apparently similar to the well known mid-seasonal clear-water phase in many natural lakes (Lampert and Schober 1978; Sommer et al. 1986). After the clear-water phase biomasses increased again and reached peaks at day 63 in all cultures. From day 49 on biomass differences between the four different cultures had become rather low (usually within a ratio of 1:4) and the temporal trend of change had become uniform within the cultures.

Pronounced clear-water phases were also observed in culture A of experiment 2, in cultures C and D of experiment 3 and quite late (day 49) in all cultures of experiment 5. In all experiments phytoplankton biomass of the different cultures tended to become similar towards the end of the experiments, after there had been some spectacular cases of intitial divergence (Fig. 2). In experiment 2, culture A had a biomass 1.5 orders of magnitude smaller than the other cultures on day 21. In experiment 4 a similar difference was observed between culture C and the rest. In experiment 3, where culture A received the

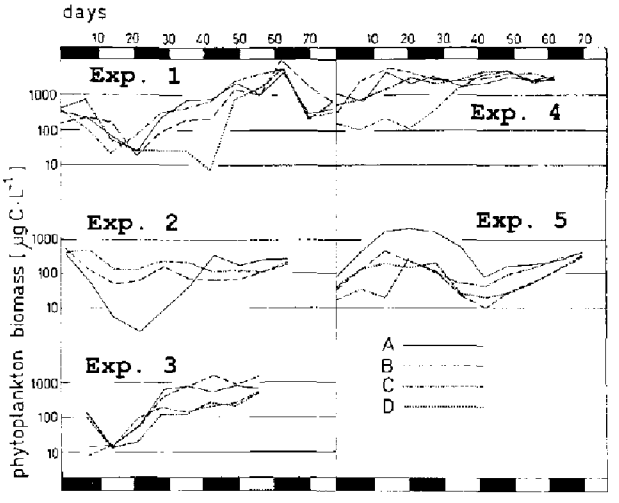

Fig. 2. Time course of phytoplankton biomass (µg C · l⁻¹; logarithmic scale) in the five experiments; individual microcosms designated by different lines: A: ———; B: – – –; C: –.–.–; D: .....

same inoculum as culture B and culture C the same as culture D, there were very small differences between the replicates as opposed to much bigger differences between the different treatments. The time needed for convergence of the phytoplankton biomass between the different cultures varied strongly between experiments. In experiment 4 it was already achieved after 5 weeks, in

experiment 3 it was not yet completely achieved at the termination of the experiment (9 weeks).

Phytoplankton species composition

In experiment 1 (Fig. 3) the initial algal assemblage consisted of nanoplanktic green algae (*Dictyosphaerium botryella* Kom. et Perm., *Scenedesmus* spp., *Monoraphidium* spp., cryptophytes (*Cryptomonas ovata* Ehr., only important in culture 3), and centric diatoms (*Stephanodiscus* spp., *Chaetoceros gracile* Schütt, only important in culture D). Initially the phytoplankton species compositions diverged. This can be seen from the fact that the pairwise similarity indices had a pronounced minimum between 1 week (C–D) and 5 weeks (A–C) after the start of the experiment. Subsequently the inititial assemblage of nanoplanktonic algae was replaced by the filamentous green alga *Mougeotia thylespora* Skuja, which became the dominant phytoplankton species in all cultures. Later it was accompanied by the amoeboid chrysophyte *Rhizochrysis* sp. Depending on the timing of the *Mougeotia* dominance, pairwise similarity indices >0.9 were attained after 5–7 weeks.

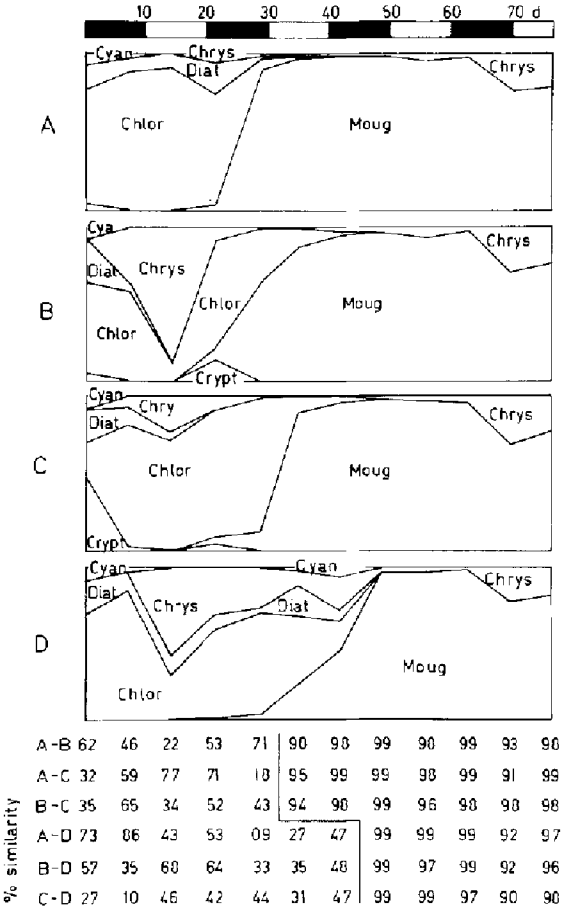

Fig. 3A–D. Taxonomic composition of phytoplankton in experiment 1. The height of one *block* corresponds to 100% of biovolume; linear scale. *Cyan:* Cyanobacteria; *Chrys:* Chrysophyceae, *Diat:* diatoms, *Chlor:* Chlorophyta (without *Mougeotia*), *Crypt:* Cryptophyta, *Moug:* *Mougeotia thylespora*. *Numbers* at bottom: pairwise similarity index (%) between the different cultures. The *thick line* marks the attainment of complete convergence

The phytoplankton in experiment 2 (Fig. 4) was initially dominated by an unidentified chrysophycean flagellate (more prominent in cultures A and B) and by the diatom *Asterionella formosa* Hassal (more prominent in culture C). As in experiment 1 there was an initial decrease in the pairwise similarity indices. After an intermediate peak of an unidentified spherical picoplanktonic alga (ca. 2 µm diameter), *Mougeotia thylespora* and *Rhizochrysis* became dominant in all cultures. In spite of its occurrence in all cultures, the picoplankton peak did not lead to a convergence of taxonomic composition because it occurred at different times in the different cultures. Final convergence of phytoplankton species composition was achieved after 7–9 weeks.

Experiment 3 (Fig. 5) differed from the other experiments in that it consisted of two pairs of cultures receiving the same inoculum. The phytoplankton in cultures A and B was initially dominated by the prymnesiophyte *Chrysochromulina parva* Lackey which was replaced by *Rhizochrysis* and then by *Mougeotia*. In cultures C and D *Rhizochrysis* was dominant initially, declined in relative importance during the first 2 weeks, recovered again and was finally replaced by *Mougeotia*. The replicate cultures showed a divergence in species composition during the intermediate phase of the experiment, in spite

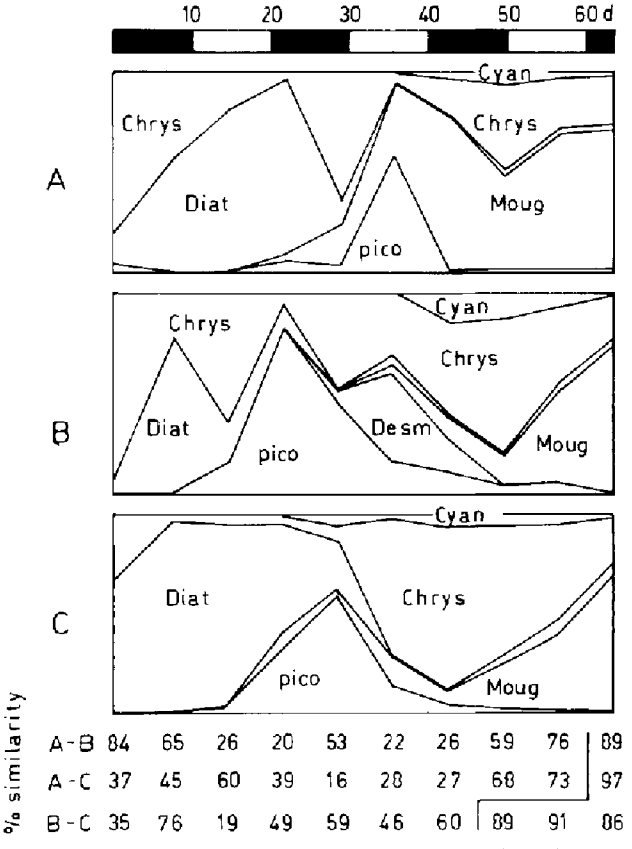

Fig. 4A–C. Taxonomic composition of phytoplankton in experiment 2. The height of one *block* corresponds to 100% of biovolume; linear scale. *Cyan:* Cyanobacteria, *Chrys:* Chrysophyceae, *Diat:* diatoms, *pico:* unidentified picoplankton, *Desm:* desmids, *Moug:* *Mougeotia thylespora*. *Numbers* at bottom: pairwise similarity index (%) between cultures. The *thick line* marks the attainment of complete convergence

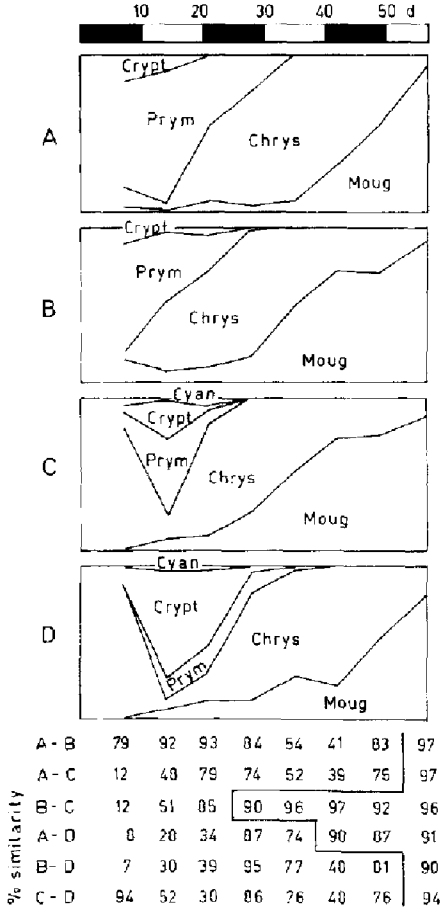

Fig. 5A–D. Taxonomic composition of phytoplankton in experiment 3. The height of one *block* corresponds to 100% of biovolume; linear scale. The samples of day 1 were lost. *Cyan:* Cyanobacteria, *Crypt:* Cryptophyceae, *Prym:* Prymnesiophyceae, *Chrys:* Chrysophyceae, Moug: *Mougeotia thylespora. Numbers* at bottom: pairwise similarity index (%) between cultures. The *thick line* marks the attainment of complete convergence

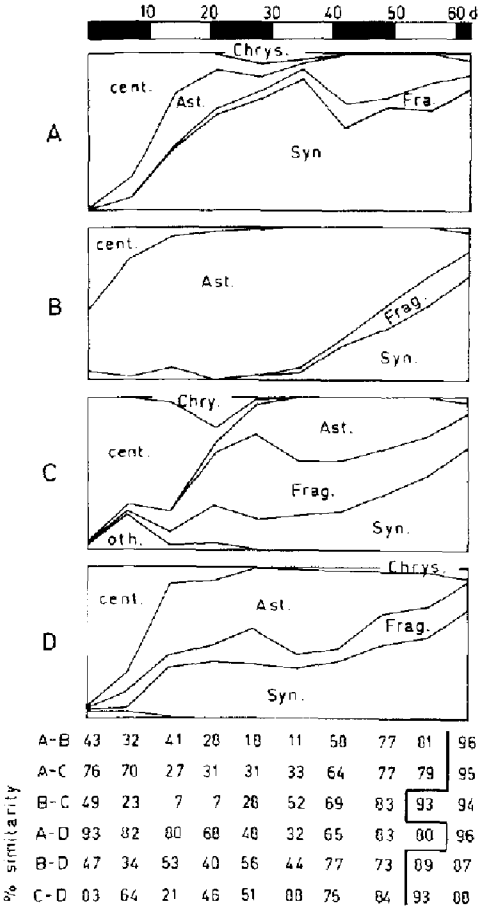

Fig. 6A–D. Taxonomic composition of phytoplankton in experiment 4. The height of one *block* corresponds to 100% of biovolume; linear scale. *Chrys:* Chrysophyceae, *cent:* centric diatoms, *oth:* others, *Ast: Asterionella formosa; Frag: Fragilaria crotonensis, Syn: Synedra* spp. *Numbers* at bottom: pairwise similarity index between cultures. The *thick line* marks the attainment of complete convergence

of a qualitative agreement of the patterns of species replacement. The divergence between cultures A and B was only caused by a slight time-shift in the species replacements; the divergence between cultures C and D was also caused by differences in the proportions of *Chrysochromulina* and *Cryptomonas ovata* which formed transient peaks during the the second and third weeks. With the rise of *Mougeotia* the species composition of the four cultures became more similar again, reaching pairwise similarity indices around 0.9 after 4–8 weeks.

The phytoplankton in experiment 4 (Fig. 6) was mainly composed of diatoms throughout the entire course of the experiment. The originally dominant species were *Melosira islandica* O. Müller in culture A, *Asterionella formosa* in culture B, a large (35 µm) *Stephanodiscus* in culture C, and *Melosira* and *Stephanodiscus* together in culture D. Quite rapidly the centric diatoms *(Melosira* and *Stephanodiscus)* were replaced by *Asterionella* which was in turn replaced by *Fragilaria crotonensis* Kitton, *Synedra acus* Kütz., and *Synedra minuscula* Grun. Final convergence between the four cultures was achieved after 8–9 weeks.

The initial phytoplankton assemblages in experiment 5 (Fig. 7) were more diverse than in the other experiments. *Asterionella formosa* was dominant in culture A, accompanied by *Melosira islandica.* In culture B *Stephanodiscus* sp., *Asterionella* and *Melosira* were important initially, with *Stephanodiscus* being dominant. The initial assemblage in culture C was an equitable mixture of *Stephanodiscus, Asterionella* and *Ceratium hirundinella* Schrank. In culture D *Asterionella* was initially dominant, *Melosira, Stephanodiscus,* and *Fragilaria crotonensis* were subdominant. As in experiment 4, centric diatoms were displaced during the first weeks. Later, *Asterionella* was displaced by *Fragilaria,* which was accompagnied by a smaller biomass of the small green alga *Coccomyxa* sp. After an initial decline in pairwise similarity indices final convergence was achieved after 5–9 weeks.

The nutritional status of phytoplankton

In all experiments at least one of the classic nutrients P, N, and Si was depleted to levels potentially limiting for

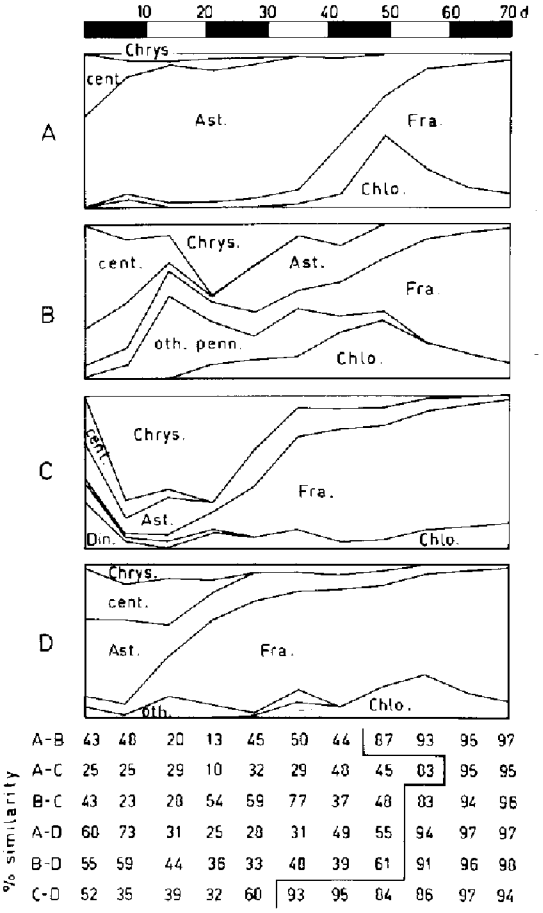

Fig. 7A–D. Taxonomic composition of phytoplankton in experiment 5. The height of one *block* corresponds to 100% of biovolume; linear scale. *Chrys:* Chrysophyceae, *cent:* centric diatoms, *Din:* dinoflagellates, *Chlo:* Chlorophyta, *Ast: Asterionella formosa, Fra: Fragilaria crotonensis, oth. penn.:* other pennate diatoms. *Numbers* at bottom: pairwise similarity index (%) between cultures

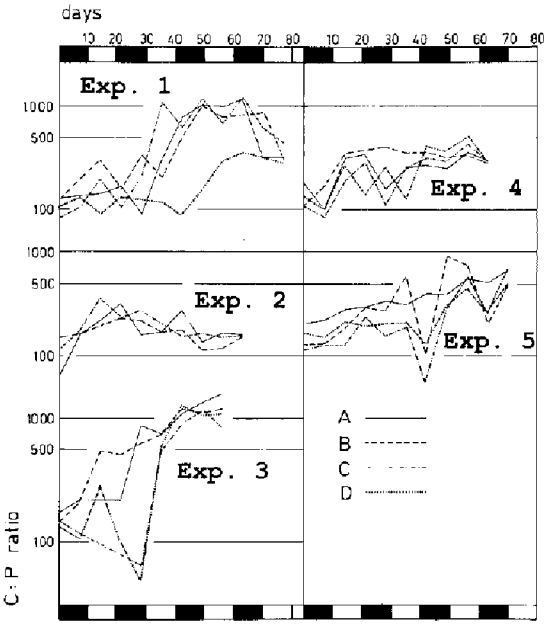

Fig. 8. C:P ratios (mol/mol) of the particulate matter in experiments 1 to 5

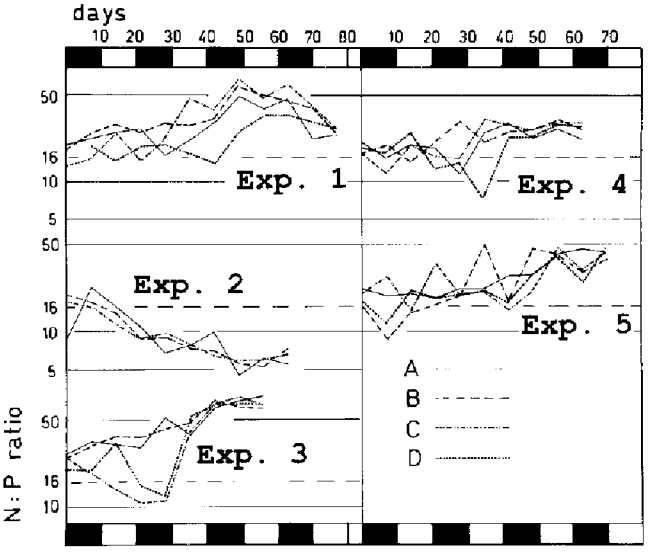

Fig. 9. N:P ratio (mol/mol) of the particulate matter in experiments 1 to 5

growth rates. The half-saturation constant of phosphorus-limited growth of *Mougeotia thylespora*, the dominant alga at the end of experiments 1, 2, and 3, has been reported to be 0.074 µM (Sommer 1986). Concentrations of soluble reactive phosphorus lower than that were attained in nearly all cultures within the first 4 weeks. Only in cultures B and C of experiment 1 were they not attained before day 49. The half-saturation constants of Si-limited growth of the diatoms *Synedra acus*, *Synedra minuscula* and *Asterionella formosa* are 8.9, 7.2, and 2.5 µM (Sommer 1988a), respectively. Concentrations of dissolved Si lower than the last value were attained in experiments 1, 2, and 4 within the first 5 weeks. In experiments 3 and 5 the silicate concentrations always remained above that limit. Dissolved inorganic nitrogen (DIN) concentrations suggestive of potential growth limitation (< 1.5 µM; cf. Table 5–21 in Kohl and Nicklisch 1988) were only reached during the late stages of most cultures except for experiment 2, where DIN fell below 1 µM during the first week.

In the case of nitrogen and phosphorus, dissolved nutrient concentration may be an unreliable predictor of growth limitation if nutrient supply to the algae is variable in time (Goldman et al. 1979). In this case, the stoichiometry of biomass is considered to be a more reliable indicator of the nutritional status of algae. According to Goldman et al. (1979) a stoichiometry C:N:P = 106:16:1 ("Redfield" ratio) indicates nutrient saturated growth. The nutrient falling short most strongly of this ratio would then be the limiting one. C:P ratios of the order of 1000 and C:N ratios of about 20–30 indicate extreme nutrient stress, i.e. near-zero growth rates. These values originally obtained in marine studies were roughly confirmed for freshwater algae in a series of studies with phytoplankton from Schöhsee and Gr. Binnensee (Sommer 1988b, 1989b, in press). Particulate C:P ratios suggestive of strong P limitation were

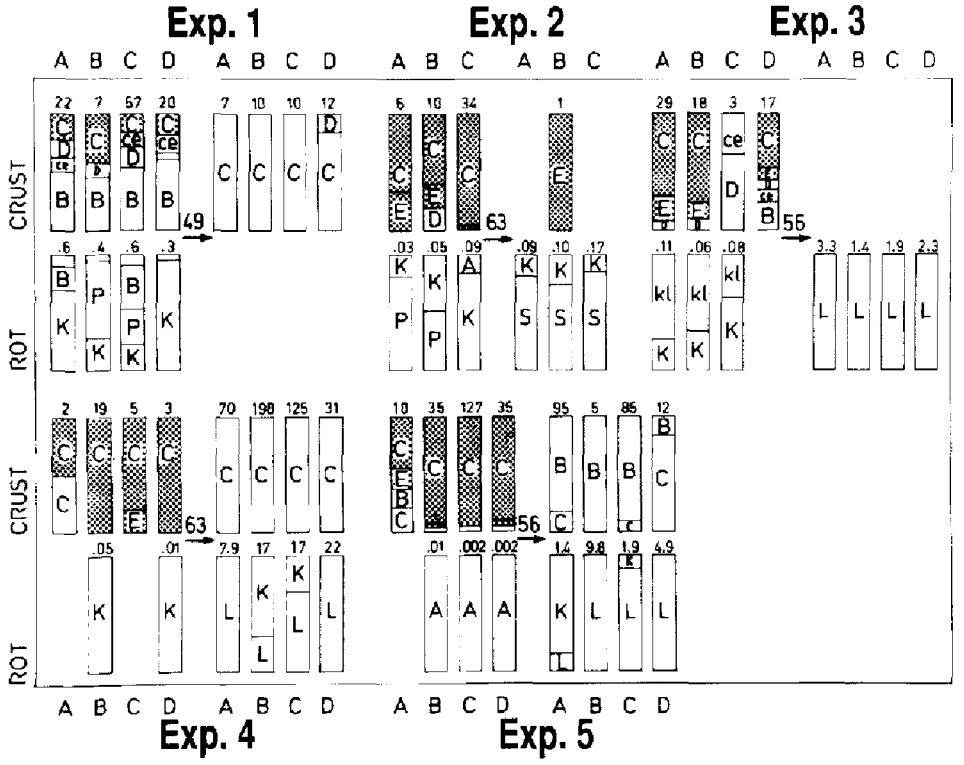

Fig. 10. Composition of zooplankton communities 1 week after the start of the experiments and at the time when convergence of phytoplankton had been achieved (number of days above *horizontal arrows*). *Bars:* Relative abundance (height of bar corresponds to 100%; linear scale) of Crustacea *(first line)* and of rotifers *(second line)*; *stippled part* of crustacea: copepods (*C:* cyclopoid copepods, *e: Eudiaptomus*); *white part* of Crustacea: Cladocera *(B: Bosmina, C: Chydorus, ce: Ceriodaphnia, D: Daphnia)*; *rotifers: A: Asplanchna, B: Brachionus, K: Keratella, kl: Kellikottia, L: Lecane, P: Polyarthra, S: Synchaeta. Numbers above bars:* total individual numbers of crustacea (l^{-1}) and of rotifers (ml^{-1})

reached in all experiments except experiment 2 (Fig. 8). In this experiment, nitrogen was probably the limiting nutrient, as suggested by N:P ratios clearly below the optimal ratio of 16 (Fig. 9). In all other experiments N:P ratios in excess of the optimal ratio suggested that nitrogen limitation played no role, at least during the second half of the experiments.

Zooplankton (Fig. 10)

During the first few days there was a considerable mortality of zooplankton, probably of individuals injured during sampling. Therefore, the zooplankton abundances after 1 week are shown as starting point in Fig. 10. In experiment 1 there was initially a quite diverse crustacean zooplankton together with rotifers which were more than 10 times as abundant. In the course of the experiment, the rotifers completely disappeared and the cladoceran species *Chydorus sphaericus* O.F. Müller became the only important zooplankton species in all cultures. Initially it had been undetectably rare. In experiment 2, crustaceans virtually disappeared from the cultures and the rotifers *Keratella cochlearis* Lauterborn (already common at the beginning) and *Synchaeta* sp. (initially rare) made up the final zooplankton assemblage. A complete displacement of crustaceans also took place in experiment 3, where the initially undetectable rotifer *Lecane luna* O.F. Müller became the only important zooplankton species. In experiment 4 the final assemblage consisted of crustaceans *(Chydorus)* and rotifers (*Lecane* alone in cultures A, D; *Lecane* and *Keratella* in cultures B and C). In experiment 5 the final assemblages in the different cultures were quite different. In cultures B and D a fungal infection had strongly depressed the abundance of crustaceans (*Bosmina longirostris* O.F. Müller in culture B; *Bosmina* and *Chydorus* in culture D). In these cultures the rotifer *Lecane* reached high abundances (9000 and 4900 ind · l^{-1}). In cultures A and C this infection did not take place, and a high abundance of crustaceans (near 100 ind · l^{-1}; mainly *Bosmina longirostris*, but also *Chydorus*) was accompanied by relatively low numbers of the rotifers *Keratella* and *Lecane* (1400 and 1900 ind · l^{-1}). *Daphnia, Ceriodaphnia, Eudiaptomus* and cyclopoid copepods had been displaced in all cultures.

Discussion

Functional characterization of succession patterns

There was a remarkable similarity in the phytoplankton succession between experiments. In the three sedimentation-intensive experiments *Mougeotia thylespora* became the dominant algal species. Previous experience has shown that *Mougeotia* is a good competitor for phosphorus after exclusion of diatoms by low Si:P ratios under steady-state conditions (Sommer 1983); with temporally variable P supply it is an even more powerful competitor, by extending its range of dominance to higher Si:P ratios (Sommer 1985). It became also dominant in two-chamber microcosm experiments where algae were subjected to simultaneous competition for P and grazing pressure by *Daphnia* (Sommer 1988a). Its performance in competition for nitrogen (relevant to experiment 2) is not known. In the microcosm experiments of Sommer (1988a) it was not much eaten, though not completely inedible, by *Daphnia magna* and *D. lon-*

gispina. Similar results have been reported for *D. hyalina* Leydig and *D. galeata* Sars (Knisely and Geller 1986). The known relationships between the body-size and the food-size spectrum of crustacean zooplankton (Burns 1969; Geller and Müller 1981) suggest that *Mougeotia* should be inedible for *Chydorus* and *Bosmina*. In experiment 3 *Mougeotia* would probably have lost in competition for P against similarly grazing-resistant diatoms (e.g. *Asterionella, Synedra, Fragilaria*), but sedimentation eliminated the diatom populations in spite of Si concentrations sufficient for near maximal growth rates (> 40 µM).

Diatoms of the family Fragilariaceae became dominant in experiments 4 and 5 where stirring was sufficient to preclude significant sedimentary losses. Fragilariaceae are well known as successful competitors for P when Si supply is sufficient (Tilman 1982; Tilman et al. 1982; Sommer 1983; Tilman et al. 1986). Among them, *Fragilaria crotonensis* is highly resistant against grazing by *Daphnia, Asterionella formosa* and *Synedra acus* are about as resistant as *Mougeotia*, and only the much smaller *Synedra minuscula* is very edible (Knisely and Geller 1986; Sommer 1986). Probably all of them except. *S. minuscula* are quite inedible for the small Cladocera *Chydorus* and *Bosmina*.

A remarkable feature of the zooplankton succession in all experiments was the displacement of the larger crustacean species, such as *Daphnia* spp., *Eudiaptomus* spp. and cyclopoid copepods. The displacement of large by small crustacean zooplankton species frequently occurs during the seasonal zooploplankton succession in meso- and eutrophic lakes (Gliwicz 1977; Sommer et al. 1986). This shift is either explained in a "top-down" manner by fish predation or in a "bottom-up" manner by seasonal shifts in the food. The former hypothesis can be excluded for these experiments. For *Daphnia* artificial exclusion by the mechanical regime in the cultures (stirring) can also be excluded, because in the experiments reported by Sommer (1988a) *D. magna* Straus and *D. longispina* O.F. Müller did well under identical physical conditions in the absence of competing zooplankton species. This does not necessarily apply to the copepods. At least the shift from *Daphnia* to smaller zooplankton species is therefore best explained by Gliwicz's (1977) hypothesis: filamentous and colonial algae interfere with the feeding process of herbivorous zooplankton and thus reduce their ability to ingest highly edible nanoplankton algae. This effect is stronger for larger species than for smaller ones, as has been confirmed by further experiments (Webster and Peters 1978; Hawkins and Lampert 1989). Gliwicz (in press) has shown that the interference effect is found even when the filamentous algae are partly edible. If the density of interfering algae is sufficiently high the competitive hierarchy suggested by the "size-efficiency hypothesis" (Brooks and Dodson 1965) can be reversed to the advantage of small zooplankton.

An additional mechanism which could have contributed to the exclusion of *Daphnia* spp. is the severe phosphorus limitation of phytoplankton in experiments 1, 3, 4, and 5. Current experiments (U. Sommer, unpubl. data; R.W. Sterner, pers. comm) have shown that *Daphnia* spp. are unable to grow when fed with otherwise edible algae of low phosphorus content (C:P > 300–400).

Functionally, the late successional communities in all experiments can be characterized as in step 8 of the PEG model of plankton succession (Sommer et al. 1986). Phytoplankton biomass is dominated by algae which are hardly consumed by zooplankton and which grow under severe nutrient limitation. These "canopy species" are accompanied by a smaller biomass of highly edible algae (*Rhizochrysis, Coccomyxa*, and possibly *Synedra minuscula*). In addition it may be suspected that the zooplankton species dominant in the final phase also feed on bacteria. *Chydorus sphaericus* has been chracterized as a "high-efficiency bacteria feeder" on the basis of intersetular distances (Geller and Müller 1981). Without experimental evidence in support, I suggest that the rotifers dominant in the final phase of some of the cultures were functionally comparable to the late successional cladocerans.

Duration of convergence

Within my experiments, initally dominant species were not able to prevent the establishment of populations better suited to the prevalent conditions. "Supply side" arguments seem to explain only the composition of early and intermediate successional stages but not of late ones. It might be argued, however, that differences in inoculum species composition were not big enough to produce persistent inoculum effects. Unfortunately, more extreme differences could not be tested because of restrictions imposed by the culture volume. Inoculum mixtures of say 100:1:1 instead of 10:1:1 or 20:1:1 would risk complete absence of key zooplankton species in one or more of the cultures. Certainly, such experiments should be repeated with much bigger culture volumes. Nevertheless, I do not expect a qualitatively different outcome. First, there was no correlation between initial dissimilarity and time needed for convergence between pairs of cultures within the same experiment. Second, in most cases (23 of 27 pairwise comparisons) there was an initial divergence of species composition leading to similarity minima much lower than the intial condition. Third, in most cultures the dominant phytoplankton species at the end of an experiment were initially undetectable (*Mougeotia*; < 0.1 filaments · ml^{-1}) or rare (diatoms in experiments 4 and 5).

Convergence of phytoplankton species composition took a longer time than in competition experiments without a consumer trophic level. Convergence was considered "complete" when the similarity index between two microcosms had reached a saturation plateau where it changed only little and undirectionally. This arbitrary endpoint of convergence is marked in Figs. 3 to 7. Usually the similarity index after this endpoint was > 0.9. The average time to full convergence between two cultures within one experiment was 52 ± 10 (SD) days; the time needed to achieve convergence between all cultures of an experiment was 59 ± 6 days. This delay relative to pure competition experiments indicates a certain "top-down" influence of the slower reacting zooplankton on phytoplankton dynamics. It is remarkable, however, that

convergence of zooplankton composition was not required before phytoplankton converged. Zooplankton convergence was more or less achieved in experiments 1 to 4, but not in experiment 5 (Fig. 10). Apparently, different zooplankton species may be functionally equivalent in their effect on phytoplankton, although it takes a much higher number of rotifers than of *Chydorus* or *Bosmina* to have the same effect on phytoplankton. In all experiments there was a characteristic sequence of events: First, the large zooplankton species (*Daphnia* and the copepods) declined (22 ± 10 days); second, all cultures within one experiment reached the same nutritional status (i.e. limitation by the same nutrient; 33 ± 14 days; third, phytoplankton species composition converged.

I take the presented results only as preliminary support for a "demand side" view of phytoplankton ecology; i.e. in the long run phytoplankton species composition will be determined by the abilty to cope with the physical environment, to compete for resources and to resist grazing, and not by "inoculum effects". The time to convergence is clearly shorter than the growth season of phytoplankton in temperate lakes. It is however longer than the duration of undisturbed external conditions (water temperature, turbulence, mixing depth) in temperate lakes. It is a straightforward extension of the experiments presented here to test whether external disturbances would delay the convergence of phytoplankton. A further question, which cannot be studied in laboratory microcosms, is how further trophic levels (fish) would influence the convergence of phytoplankton succession.

References

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecol Monogr 27:325–349

Brooks JL, Dodson SI (1965) Predation, body size and composition of plankton. Science 150:28–35

Burns C (1969) The relationship between body size of filter-feeding Cladocera and the maximum size of particles ingested. Limnol Oceanogr 13:675–678

Geller W, Müller H (1981) The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food-selectivity. Oecologia 49:316–321

Gliwicz ZM (1977) Food-size selection and seasonal succession of filter feeding zooplankton in a eutrophic lake. Ekol Polska 25:179–225

Gliwicz ZM (in press) *Daphnia* growth at different concentrations of filaments. Arch Hydrobiol

Goldman JC, McCarthy JJ, Peavey DG (1979) Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature 279:210–215

Harris GP (1986) Phytoplankton ecology. Chapman and Hall, London

Hawkins P, Lampert W (1989) The effect of *Daphnia* body size on filtering rate inhibition in the presence of a filamentous cyanobacterium. Limnol Oceanogr 34:1084–1089

Knisely K, Geller W (1986) Selective feeding of four zooplankton species on natural lake phytoplankton. Oecologia 69:86–94

Kohl JG, Nicklisch A (1988) Ökophysiologie der Algen. Akademie Verlag, Berlin

Lampert W, Schober U (1978) Das regelmäßige Auftreten von Frühjahrsblüte und "Klarwasserstadium" im Bodensee als Folge klimatischer bedingungen und Wechselwirkungen zwischen Phyto- und Zooplankton. Arch Hydrobiol 82:364–386

Rocha O, Duncan A (1985) The relationship between cell carbon and cell volume in freshwater algal species used in zooplankton studies. J Plankton Res 7:279–294

Roughgarden J, Gaines SD, Pacala SW (1987) Supply side ecology: The role of physical transport processes. In Gee JHR, Giller PS (eds) Organisation of communities past and present. Blackwell, Oxford, pp 491–518

Smith RE, Kalff J (1983) Competition for phosphorus among co-occurring freshwater phytoplankton. Limnol Oceanogr 28:448–464

Sommer U (1983) Nutrient competition between phytoplankton species in multispecies chemostat experiments. Arch Hydrobiol 96:399–416

Sommer U (1985) Comparison between steady state and non-steady state competition: Experiments with natural phytoplankton. Limnol Oceanogr 30:335–346

Sommer U (1986) Phytoplankton competition along a gradient of dilution rates. Oecologia 68:503–506

Sommer U (1988a) Phytoplankton succession in microcosm experiments under simultaneous grazing pressure and resource limitation. Limnol Oceanogr 33:1037–1054

Sommer U (1988b) Does nutrient competition among phytoplankton occur in situ? Verh Internat Verein Limnol 23:707–712

Sommer U (1989a) The role of competition for resources in phytoplankton succession. In Sommer U (ed) Plankton ecology: Succession in plankton communities. Springer, Berlin, pp 57–106

Sommer U (1989b) Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake. Limnol Oceanogr 34:1162–1173

Sommer U (in press) The application of the Droop-model of nutrient limitation to natural phytoplankton. Verh Internat Verein Limnol 24: –

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

Sterner RW (1986) Herbivores direct and indirect effects on algal populations. Science 231:605–607

Sterner RW (1989) The role of grazers in phytoplankton succession. In Sommer U (ed) Plankton Ecology: Succession in plankton communities. Springer, Berlin, pp 107–170

Strickland JDH, Parsons DR (1972) A practical handbook of seawater analysis. 2nd edn. Bull Fish Res Board Can 167

Tessenow U (1966) Untersuchungen über den Kieselsäuregehalt der Binnengewässer. Arch Hydrobiol Suppl 32:1–136

Tilman D (1982) Resource competition and community structure. Princeton Univ Press, Princeton

Tilman D, Sterner RW (1984) Invasions of equilibria: test of resource competition using two species of algae. Oecologia 61:197–200

Tilman D, Kilham SS, Kilham P (1982) Phytoplankton community ecology: The role of limiting nutrients. Ann Rev Ecol Syst 13:349–372

Tilman D, Kiesling R, Sterner RW, Kilham SS, Johnson FA (1986) Green, bluegreen and diatom algae: Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch Hydrobiol 106:473–485

Webster KE, Peters RH (1978) Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. Limnol Oceanogr 23:1238–1245