Oecologia (Berlin) (1986) 71:25–28

Oecologia

The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity

A. Gaedeke[1] **and U. Sommer**[2]

[1] Institute of Limnology, University of Konstanz, P.O.Box 5560, D-7750 Konstanz, Federal Republic of Germany
[2] Max Planck Institute of Limnology, P.O.Box 165, D-2320 Plön, Federal Republic of Germany

Abstract. The influence of periodic disturbances of various frequency on the maintenance of the phytoplankton diversity was studied by semicontinuous competition experiments. Disturbances consisted of dilution events, which meant both addition of fresh nutrients and elimination of organisms. The intervals between dilution events varied from 1 to 14 days. Diversity was found to increase with increasing intervals between disturbances. Coexisting species belonged to different strategy types: (a) species with rapid growth under enriched conditions, (b) species with good competitive abilities under impoverished conditions, (c) species with the ability to build up storage pools of the limiting nutrient. An increase of the number of coexisting species over the number that would have coexisted in steady state was only found when the interval exceeded one generation time.

Key words: Diversity – Disturbances – Nutrient pulses – Population reductions – Varying frequency and intensity – Growth strategies

Phytoplankton competition research has successfully used the the Monod (1950) equation to predict the outcome of interspecific competition for limiting nutrients in chemostat cultures from the parameters k_s and μ_{MAX} (Tilman 1977, 1981, 1982; Kilham 1984). One of the consequences of the steady state model is the conclusion, that only as many species can coexist as there are limiting resources. The number of potentially limiting resources (light, N, P, Si and some trace elements) usually is much lower than the number of coexisting species of phytoplankton. Therefore, coexistence of species limited by different resources is not yet a sufficient solution to Hutchinson's (1961) paradox of the plankton.

However, theoretical considerations (Armstrong and McGehee 1977) and pulsed nutrient competition experiments (Robinson and Sandgren 1983; Sommer 1984, 1985) have shown that deviation from perfect steady state permits the persistence of more species than there are limiting resources. Under non steady state conditions the simple Monod relationship between the growth rate and the external nutrient concentrations breaks down, if the maximum uptake velocity of the limiting nutrient is relatively higher than the maximum growth rate of biomass (this is true for P and N). In that case, transient nutrient pulses permit the build-up of intracellular storage pools which permit temporary maintenance of a growth rate higher than predicted from ambient nutrient concentrations (Droop 1968, 1983). Alternatively, a species might use a nutrient pulse for rapid build-up of a big population stock which compensates for decline during intense competition. Thus, fluctuating nutrient conditions permit three different types of strategy: rapid growth under rich conditions, storage under rich conditions, or good competitive abilities under impoverished conditions.

The difference between a temporally heterogenous and a "steady state" environment is a question of temporal scale. Environmental fluctuation around a long term mean may be perceived by the organisms or not, depending on their frequency and intensity. The threshold of perception of heterogeneity may be different at different levels of organisation, e.g. small heterogeneity in nutrient supply may have consequences for nutrient uptake but not necessarily for the outcome of competition.

In this study we are mainly interested in the response on the level of species numbers. In order to study the consequences of disturbance frequency and intensity on the number of coexisting phytoplankton species, we used the well known technique of semicontinuous culture (dilution at discrete intervals, here from 1 to 14 days). Each dilution event is a two-fold disturbance: reduction of the population size and addition of fresh nutrients. In order to obtain the same long term average of the dilution rate, the intensity of disturbance increases with decreasing frequency.

Methods

The experiments were carried out in a "Kniese incubator" according to the principles of "semicontinuous culture" (stepwise dilution). In each series of the experiments seven 400 ml culture glass tubes with modified Chu-12 (Müller 1972) were incubated at the same time. A total of four series was employed. For two series the media were silicon-free. The surface light was a constant 0.78×10^{16} quanta $\times$ cm^{-2} $\times$ s^{-1}, the temperature was 18°. The tubes were aerated in order to keep the cultures mixed and to supply CO_2.

Dilution was discontinous at regular intervals. The long-term average of the dilution rate $[-\log \cdot (v_t/v_o)/t)$ was con-

Offprint requests to: U. Sommer

Table 1. List of species

DIATOMS	
Asterionella formosa	
Synedra acus	
Fragillaria crotonensis[b]	
Stephanodiscus astrea[b]	
Nitzschia acicularis[a]	
CHLOROPHYCEAE	
Chlamydomonas sp. I, II[b], III[b] (distinguished only by size)	
Pandorina morum[a]	
Chlorella sp.	
Scenedesmus sp.	
Ankistodesmus acicularis[b]	
Monoraphidium contortum[a]	
Koliella spiculiformis	
Oocystis parva[b]	
Golenkiniopsis solitaria[b]	
Cosmarium cf. margaritiferum[a]	
CYANOPHYCEAE	
Pseudanabaena catenata	

[a] Species comprised in the graphs as "others"
[b] Species being excluded right after the start for the cell counts

stant ($0.3\ d^{-1}$), v_o being the total culture volume, v_t the volume of the algal suspension remaining in the culture tube at dilution, t the length of the interval between dilution events. The interval varied between different experimental treatments (1, 2, 3, 5, 7, 10, 14 days). Cell counts were done every day throughout the entire experiments as described in Sommer (1983). The cell volumes for biomass estimates are taken from the same source. Standardized species biomass in the figures is shown as percent of the maximum total biomass within one interval from dilution to dilution. Diversity was determined according to Shannon and Weaver 1949.

Results

Throughout all experiments the communities were built up by a comparable set of species (Table 1). This fact permitted to compare the growth behavior of the species between the different experiments.

Figure 1 shows the example of the time course of an experiment with daily dilution (1d culture). Figure 2 shows in contrast to it an experiment with a seven day interval (7d cultures) and Fig. 3 an experiment with 14 days in between dilution events (14d cultures). In the 1d cultures one single species outcompeted all other species and reached absolute dominance. Conversely, in the 7d cultures and the 14d cultures several species were able to coexist. The dominant species of the one day cultures, however, were not excluded in the 7d and the 14d cultures but were able to coexist in low umbers throughout all these experiments. Each of the coexisting species showed a characteristic growth and decline pattern during the time period between dilution.

The bluegreen alga *Pseudanabaena catenata* dominated the silicon enriched 1 day cultures while the silicon-free cultures were dominated by *Koliella spiculiformis*, a species that had been a successful non-diatom competitor for phosphorus in previously reported steady-state experiments

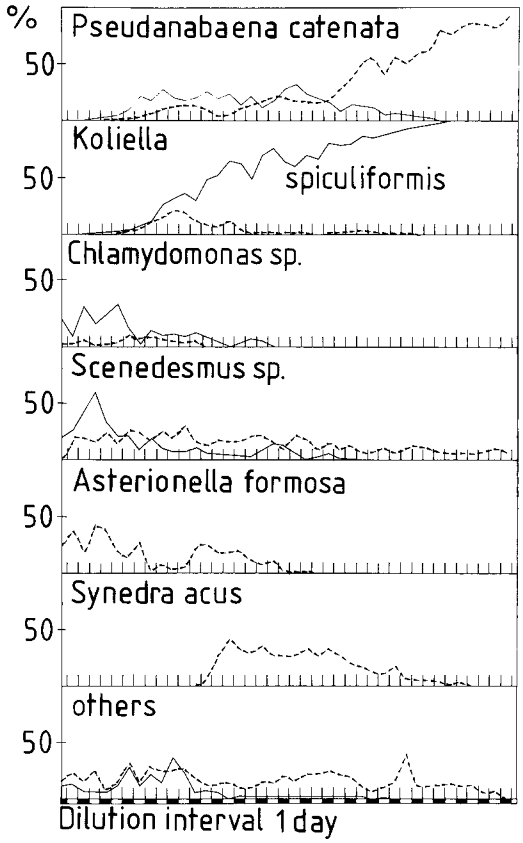

Fig. 1. Competition experiments with a 1 day dilution intervals. Biomass expressed in % of maximal total biomass within each dilution interval. Vertical lines: dilution events. *Solid line* Experiments without Si, *broken line* experiments with Si

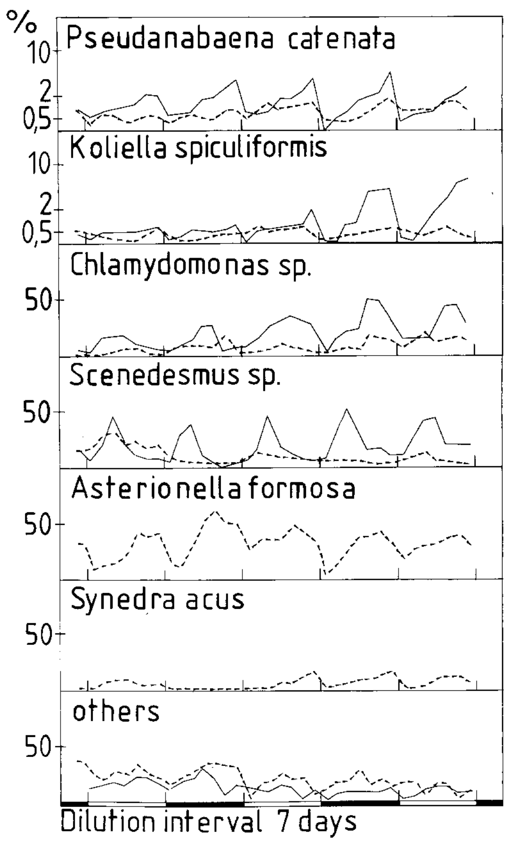

Fig. 2. Competition experiments with 7d dilution intervals. Symbols as in Fig. 1

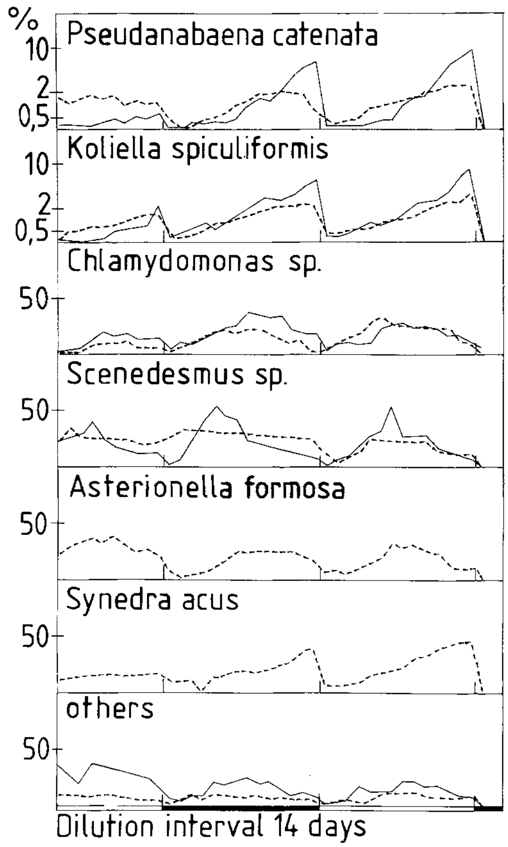

Fig. 3. Competition experiments with 14d dilution intervals. Symbols as in Fig. 2

(Sommer 1983). Cultures with a dilution interval of two days (2d cultures) also were dominated by single species (*Pseudanabaena catenata* in both the Si-free and the Si enriched cultures). However, the diatom *Synedra acus* never got excluded completely from the Si-enriched 2d cultures. In steady state experiments *Synedra* is the typical winner at high Si: P ratios, when only phosphorus is limiting (Tilman 1981; Sommer 1983; Kilham 1986). In the 3d cultures *Synedra* reached only a very low level of biomass. Its importance increased with longer dilution intervals. Within the intervals between dilution events *Synedra* became increasingly important towards the end of each period (i.e. with intensifying competition) and achieved the highest numbers at the end of the periods of the 14d cultures. The same growth pattern was also followed by *Pseudanabaena* and *Koliella*. They achieved very low population densities throughout all the experiments with a dilution interval of more than 2 days and always increased towards the end of the longer periods.

In the experiments with three days intervals the number of coexisting species was already higher than in the cultures with more frequent dilution events. In the Si-free culture *Chlamydomonas sp.* and in the Si-enriched cultures *Asterionella formosa* reached relative dominance. No species, however, was able to outcompete all other species.

In the experiments with a dilution interval of five days it was *Scenedesmus sp.* for the Si-free and again *Asterionella formosa* for the Si-enriched cultures to reach highest biomass. In the 7d and the 10d cultures *Scenedesmus, Asterionella* and *Chlamydomonas* were about equally important. *Scenedesmus* always reached its peak first, next was *Asterionella, Chlamydomonas* following last. In the 14d the pattern was less less clear. Here, *Pseudanabaena, Koliella* and *Synedra* grew steadily till the end of each period.

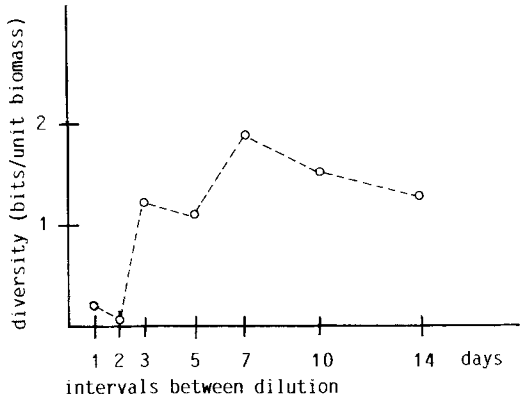

Fig. 4. Diversity index in dependence of the interval between dilutions

The diversity index was close to zero for the 1d and the 2d cultures. It was clearly higher for the 3d and the 5d cultures, reaching a maximum for the 7d cultures. Cultures with a longer interval than 7 days between dilutions again had a slightly lower diversity (Fig. 4).

Conclusions

The maintained diversity of periodically diluted phytoplankton cultures, grown from the same inocculum depends on frequency (and intensity) of the dilution events. Each dilution event may be conceived as a "disturbance": It reduces the size of the populations, supplies fresh nutrient, decreases or completely removes nutrient limitation and competitive pressure. With increasing intervals between dilutions the temporal variability of growth conditions increases. Disturbances of short frequency and low intensity create constantly moderate nutrient limitation with only small changes in the intensity of competition for the cultures. Cultures with longer intervals experience with increasing length of the interval increasingly intense nutrient limitation alternating with with increasingly rich nutrient availability and increasingly drastic population reductions. This variation of growth conditions prevents competition to proceed until equilibrium ("competitive exclusion") and permits the persistence of species that would have been excluded under steady-state conditions.

The diversity first increased with the length of the interval but reached a maximum for cultures that got diluted at a moderate interval. The slight decrease in diversity in the 14d cultures might have been an artifact because of the small culture volume and the hereby increased probability of random extinctions of rarer species by the radical dilution events.

It turned out that in the 1d and the 2d cultures the differences in the nutrient supply and the intensity of the population reductions were not sufficient to increase the diversity beyond the level of steady state experiments. The diversity was close to zero. Both, the 1d and the 2d cultures were dominated by algae with good competitive abilities under impoverished conditions. In the cultures with 3 and 5 days dilution interval species with high μ_{MAX} became relatively more important, probably because of the increased intensity of the nutrient pulses at dilution.

In the 7d and the 10d cultures the gradual changes within the period prevented the elimination of the at a time inferior competitors. The disturbances here supplied the fast growers with enough nutrients to build up high cell numbers and therefore they were able to compensate the decline during low concentration periods and the population reductions. Species with high competitive abilities like *Synedra, Pseudanabaena,* and *Koliella* were favoured by the increasing nutrient limitation toward the end of each period. The coexistence of the species was possible following a certain succession from period to period that was given by the gradual changes of the conditions within the period. These gradual changes were maintained by the moderate disturbances.

The coexistence of several species as in the experiments stands in accordance to the theoretical predictions of Stewart and Levin (1974) as well as with the experiments of Sommer (1984) with one fluctuating resource. The results confirm the "Intermediate disturbance hypothesis" of Connell (1978) which claims that disturbances have a positive influence on the diversity of communities as long as they are intermediate in frequency and intensity.

It is interesting that persistence of more species than under steady state conditions was only found when the the length of the interval between disturbances exceeded the average generation time. This would indicate that the natural 24h periodicity in lakes (photosynthesis and grazing) could prevent competitive exclusion only during periods of extremely high turnover rates.

References

Armstrong RA, McGehee R (1977) Competitive exclusion. Am Nat 115:151–170

Conell J (1978) Diversity in tropical rainforests and coral reefs. Science 199:1304–1310

Droop MR (1968) Vitamin B_{12} and marine biology. IV. The kinetics of uptake, growth, and inhibition in *Monochrysis lutheri.* J Mar Biol Ass U K 48:689–733

Droop MR (1983) 25 years of algal growth kinetics. Bot Marina 26:99–112

Hutchinson GE (1961) The paradox of the plankton. Am Nat 95:137–145

Kilham SS (1984) Silicon and phosphorus growth kinetics and competitive interactions between *Stephanodiscus minutus* and *Synedra* sp. Verh internat Verein Limnol 22:435–439

Kilham SS (1986) Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si: P loading gradient. Can J Fish Aquat Sci 43:351–360

Monod J (1950) La technique de la culture continue: theorie et applications. Ann Inst Pasteur Lille 79:390–410

Müller H (1972) Wachstum und Phosphatbedarf von *Nitzschia actinastroides* in statischer und homokontinuierlicher Kultur unter Phosphatlimitierung. Arch Hydrobiol Suppl 33:206–236

Robinson JV, Sandgren CD (1983) The effect of temporal environmental heterogeneity on community structure: a replicated experimental study. Oecologia 57:98–112

Shannon CE, Weaver W (1949) The mathematical theory of communication. Univ Illinois Press

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

Sommer U (1984) The paradox of the plankton: Fluctuations of the phosphorus availability maintain diversity of phytoplankton in flow-through cultures. Limnol Oceanogr 29:633–636

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

Stewart FM, Levin BR (1973) Partitioning of the resources and the outcome of interspecific competition: A model and general considerations. Am Nat 107:171–198

Tilman D (1977) Resource competition between planktonic algae: An experimental and theoretical approach. Ecology 58:338–348

Tilman D (1981) Test of resource competition theory using four species of Lake Michigan algae. Ecology 62:802–815

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

Received June 9, 1986