The first decade of oligotrophication of Lake Constance

II. The response of phytoplankton taxonomic composition

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Abstract. In Lake Constance, after several decades of eutrophication, a decrease in phosphorus loading over the last decade has lead to a partial recovery from eutrophication. Here we analyse the shift in the taxonomic composition of phytoplankton during the first decade of oligotrophication in Lake Constance. During the 1980s, spring total P concentrations decreased from ca. 130 to less than $50\ \mu \cdot l^{-1}$. This decrease was reflected by an approximately proportional decrease in summer phytoplankton biomass while spring phytoplankton biomass seemed unresponsive. Major taxonomic changes occured during both growth seasons. In spring, the proportion of diatoms, green algae and Chrysophyta increased while the proportion of Cryptophyta decreased. The summer trend was very different: the relative importance of diatoms decreased and Cryptophyta and Chrysophyta increased, while Chlorophyta reached their peak around 1985. These trends are also analysed at the genus level. Comparison with taxonomic trends during the eutrophication period shows the expected reversals in most cases. Comparison with other lakes shows general similarities, with the notable exception that *Planktothrix rubescens* has never been important in Lake Constance. The increase of diatoms during spring is attributed to their improved competitive performance with increasing Si:P ratios. Their decrease during summer is explained by the increasing silicate removal from the epilimnion by increasing spring populations.

Key words: Phytoplankton – Recovery from eutrophication – Species composition

In spite of a more than twofold reduction in total P concentration (Gaedke and Schweizer 1993) several researchers have considered the response of phytoplankton and related variables (annual mean chlorophyll, annual maximal chlorophyll, annual primary productivity, annual mean water transparency) to the first decade of oli-

gotrophication disappointingly weak or even insignificant (Sas 1989; Tilzer et al. 1991). Changes in taxonomic composition, however, have been reported. Besides several institutional reports there are two publications in international journals (Kümmerlin 1991; Stabel 1991) which deal with the taxonomic response of phytoplankton in Lake Constance to the incipient recovery from eutrophication. Stabel's study encompasses the period 1977 to 1989 and is based on annual averages and depth intervals from 0 to 140 m. He concluded that there is no significant response of total phytoplankton biovolume to oligotrophication, that the relative importance of Bacillariophyceae tended to increase while the relative importance of Cyanophyta (= Cyanobacteria), Dinophyta, and Chlorophyta tended to decrease with oligotrophication, despite strong fluctuations of all taxa around the general trend. Chrysophyceae showed no consistent trend; data for Cryptophyta were not given. Kümmerlin (1991) presents a summary of plankton studies from 1896 to 1986 (with extended interruptions) and a figure which illustrates monthly averages for several species from 1965 to 1986. In the text he notes a shift of the main growth period of *Asterionella formosa* from summer to spring and the reappearance of *Tabellaria fenestrata*, *Cyclotella* spp. and *Cryptaulax vulgaris* as major taxonomic changes related to recovery from eutrophication.

The comparison of Kümmerlin's and Stabel's studies shows the critical importance of temporal averaging for conclusions. A seasonal shift like the one shown for *Asterionella* by Kümmerlin would remain undetetected if only annual averages were considered. Averaging over extended periods has advantages and disadvantages. The major advantage is that most of the noise caused by sampling and counting errors and by changing weather conditions is removed. The major disadvantage is that phytoplankton growth and biomass accumulation are controlled by nutrients only during restricted periods of the year (Sommer 1987). Phytoplankton is expected to be responsive to changes in the trophic state only during periods of nutrient limitation. Temporal averaging over

too great an interval would dilute the data from the nutrient-limited periods with data from periods when phytoplankton is not responsive to the trophic state of the lake. In our study, we try to reach a compromise between fine-grained temporal resolution and annual averaging. We base our analysis on separate averages for those parts of the year where nutrient limitation may occur occasionally to a small extent (spring bloom) and where it occurs more regularly (summer period). The extended winter minimum, the clear-water phase in June and the autumn period when phytoplankton are either controlled by physical conditions (winter, autumn) or by grazing (clear-water phase) are therefore not considered here. Our analysis is based on separate averages for the spring and the summer growth periods of phytoplankton. We thus hope to make the best compromise between the conflicting aims of increasing responsiveness and decreasing noise.

Material and methods

Our analysis is based on data collected by the Limnological Institute of the University of Constance between 1979 and 1990 (see also Gaedke and Schweizer 1993). The phytoplankton samples were not collected primarily for the purpose of long-term monitoring, but rather for a diverse array of projects. Therefore, there are temporal inconsistencies in the vertical resolution of samples, in the counting effort and in the details of taxonomic resolution. This forces us to use averaging and lumping procedures which maximize interannual comparability.

The data used in our study comprise chemical data [dissolved Si, soluble reactive phosphorus (SRP), total phosphorus (TP)], and phytoplankton biovolume estimates. Nutrients were measured according to widespread standard methods (Strickland and Parssons 1972). The detection limit for P was $1 \, \mu g \cdot l^{-1}$, and for Si was ca. $5 \, \mu g \cdot l^{-1}$. Phytoplankton counts and biovolume estimates were obtained by Utermöhl's (1985) inverted microscope technique. The data cover the years 1979–1989 (spring and summer period) and 1990 (spring period only, see Gaedke and Schweizer 1993). Phytoplankton data for summer 1983 are lacking. The identification of several phytoplankton species was inconsistent between the different investigators while the identification of genera was consistent. Therefore, we decided to use the genus as the smallest taxonomic unit in our analysis. In addition we also analysed higher taxa (Cyanophyta, Cryptophyta, Dinophyta, Chrysophyceae, Bacillariophyceae, Chlorophyta). Several phytoplankton species had been entirely neglected during some of the years (e.g. Chrysochromulina, picoplankton). These were excluded when calculating aggregate biomasses (total phytoplankton biomass or biomass of higher taxa). Phytoplankton biomass was expressed as cell volume (biovolume) per lake surface area integrated from the surface to 20 m depth $(cm^3 \cdot m^{-2})$. This depth integral was chosen for two reasons: it could be calculated from the data sets of all years under study and it corresponds roughly to the maximum extension of the euphotic zone in Lake Constance (Tilzer 1983).

Temporal averages were calculated for two of the three major growth periods of phytoplankton in lake Constance (Sommer 1987): the spring bloom and the summer growth period. The minor biomass peak in autumn was not considered here, because up to now there has been no indication of nutrient shortage during that period and no response to oligotrophication would be expected. The definition of periods is the same as in Gaedke and Schweizer (1993). While the end of the spring bloom and the start and end of the summer growth period were assessed for each year individually, insufficient sampling forced us to take an arbitrary starting point of the spring bloom (15 March). This arbitrary starting point for

the spring bloom certainly led to erroneous impressions in the years 1989 and 1990. In these years an unusually warm and calm period before mid-March caused continuously high biomass levels to start 1 month earlier. Therefore, spring data for these years are shown in the Results but excluded from the analysis.

Temporal averages of the relative contribution of individual taxa (p_i) to total biomass were calculated by first calculating the period means of taxon biomass (B_i) and total biomass (B_{tot}) and then calculating p_i as mean B_i/mean B_{tot}. This procedure gives more weight to sampling dates with higher biomass, while calculating p_i for individual sampling dates and then averaging p_i would have given equal weight to all sampling dates. Our procedure reduces the error introduced by the arbitrary character of period definition.

Results

Nutrients and biomass

Under phosphorus-limited conditions the trophic state of a lake can best be characterized by total phosphorus concentrations during the last full circulation period before the start of the vegetation period (Dillon and Rigler 1974). In Lake Constance winter circulation TP concentrations reached a peak of nearly $130 \, \mu g \cdot l^{-1}$ in 1980 and 1981 (Fig. 1). Thereafter they declined to $47 \, \mu g \cdot l^{-1}$ in 1989 and $48 \, \mu g \cdot l^{-1}$ in 1990. Soluble reactive phosphorus showed a similar trend to TP. The remarkable interannual fluctuations in the TP–SRP differences are probably due to different amounts of phytoplankton and other P-containing components of the seston surviving through winter. In contrast to P, there was no trend in
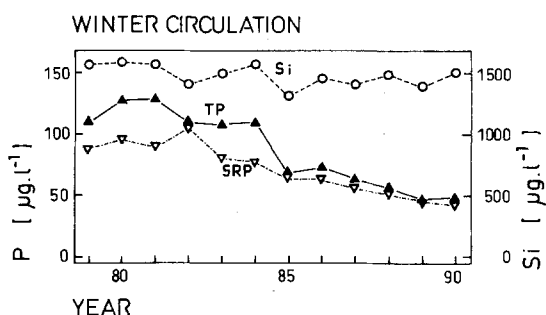

Fig. 1. Total phosphorus (TP), soluble reactive phosphorus (SRP) and dissolved Si concentrations during the winter circulation in Lake Constance
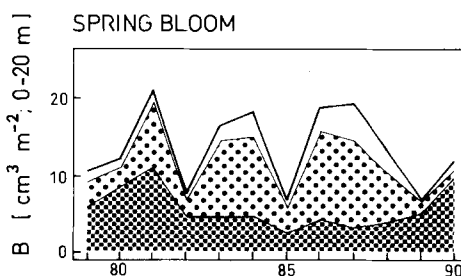

Fig. 2. Mean phytoplankton biomass (total and most important higher taxa) during the spring bloom in Lake Constance. Chequered area, Cryptophyta; spotted area, Bacillariophyceae

the dissolved Si concentrations during winter circulation. They fluctuated between 1300 and 1580 µg · l^{-1}. The differences in the behaviour of the two limiting biogenic elements lead to an increase in Si:P ratios. According to the competition theory of Tilman et al. (1982) and experimental evidence (summarized in Sommer 1989a) an increase in Si:P ratios is expected to favour diatoms over non-silicified algae and to favour araphid, pennate diatoms (family Fragilariaceae) and particularly *Synedra* sp. over other (mainly centric) diatoms.

The mean biomass of the phytoplankton spring bloom showed no response to the decrease in P concentrations (Fig. 2). It fluctuated irregularly between 6.3 and 20.3 cm^3 · m^{-2}. There was no statistical relationship with TP or any other nutrient parameter.

The mean summer biomass, however, declined at roughly the same rate as TP during the spring circulation (Fig. 3). Initially summer biomass levels were much higher than spring levels (30–40 cm · m^{-2}) but entered the range of interannual spring biomass fluctuations in 1987. The conventional log-log regression (Fig. 4) showed a significant ($r^2 = 0.79$; $P < 0.001$) and almost linear relationship with circulation TP ($B = 0.27$ $P^{0.99}$).
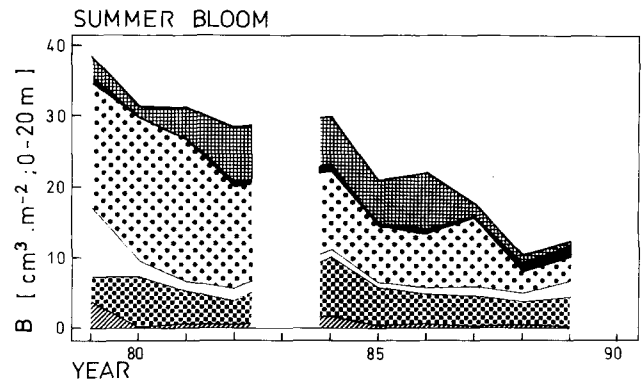

Fig. 3. Mean phytoplankton biomass (total and important higher taxa) during the summer growth period in Lake Constance. *Shaded area,* Cyanophyta; *chequered area,* Cryptophyta; *clear area,* Dinophyta; *spotted area,* Bacillariophyceae; *cross-hatched area,* Chlorophyta; *solid area,* Chrysophyceae

The relationship to the mean TP (0–20 m) in the clear-water phase which immedeately precedes the summer growth period shows more scatter, but is still significant ($r^2 = 0.62$; $P < 0.05$; values for some years missing) and less steep ($B = 1.66$ $P^{0.55}$).
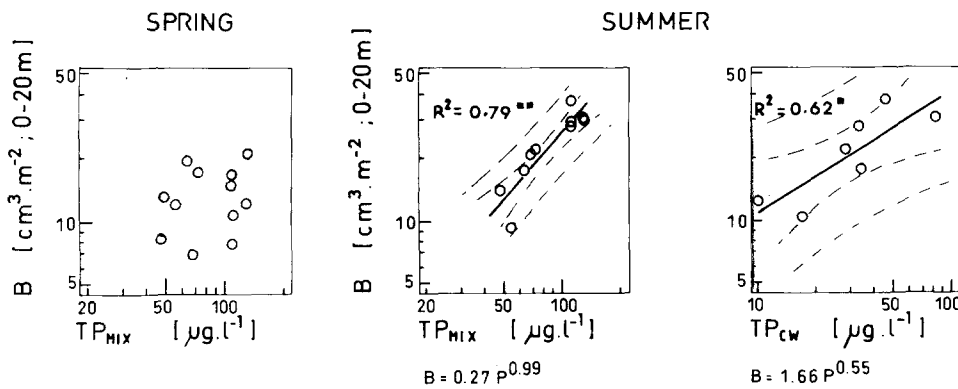

Fig. 4. Log-log relationship between circulation TP and the mean spring-bloom biomass *(left),* circulation TP and the mean summer biomass *(center),* and TP in the clear-water phase and mean summer biomass *(right)*
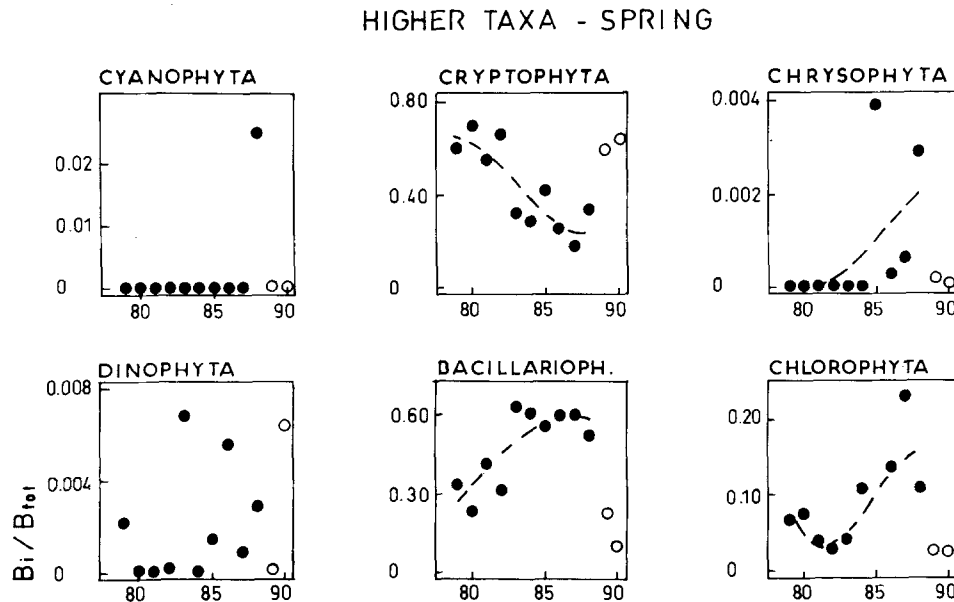

Fig. 5. Relative contribution of higher phytoplankton taxa to the mean spring-bloom biomass. *Solid circles,* original values 1979–88; *empty circles,* original values 1989/90; *broken line,* trend obtained by 3rd-order polynomial smoothing of time series (1989/90 exluded)
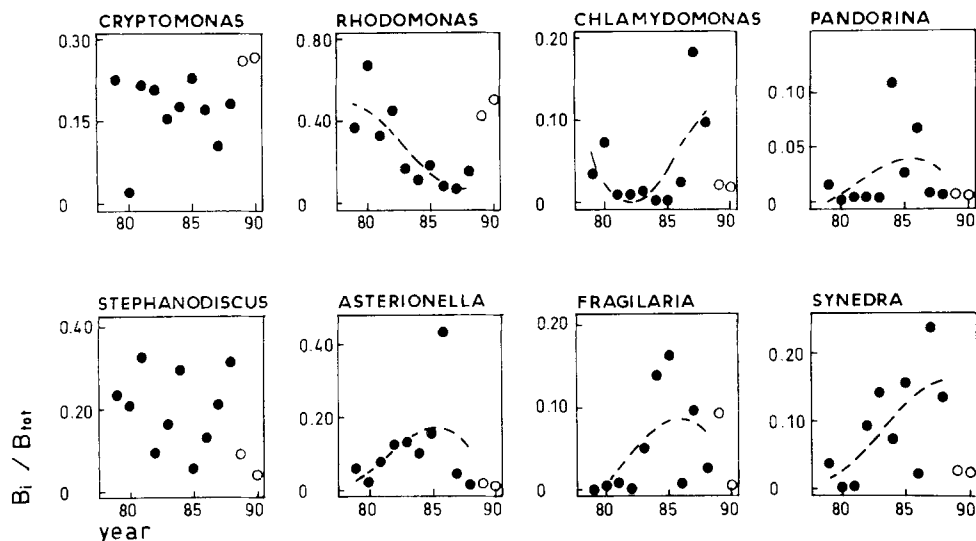
GENERA - SPRING

Fig. 6. Relative contribution of important genera to the mean spring bloom biomass. *Symbols* as in Fig. 5

Taxonomic composition during the spring bloom

During the period of this investigation the phytoplankton spring bloom was mainly composed of Cryptophyta and Bacillariophyceae (Figs. 2 and 5). Together, they always made up > 75% of total phytoplankton biomass. The only other group of importance was the Chlorophyta, while Cyanophyta, Dinophyta and Chrysophyceae (including Synurophyceae) contributed only insignificantly to phytoplankton biomass. Temporal trends of the p_i values of the individual taxa were visualized by 3rd-order polynomial smoothing (Fig. 5) excluding the years 1989 and 1990. These years are nevertheless shown in Fig. 5.

The relative importance of Cryptophyceae in spring tended to decline with the recovery from eutrophication, while the relative importance of diatoms tended to increase. An increasing trend was also found for Chlorophyta and for the Chrysophyceae. The latter were represented practically only by *Dinobryon* spp. No temporal trend was observed for the Cyanophyta and the Dinophyta. The exceptional years 1989 and 1990 lie outside the general trend and seem to recapitulate the situation of the most eutrophic years around 1980.

Figure 6 shows those genera which at least once contributed > 10% to the mean spring biomass. The declining trend of the Cryptophyta is entirely due to the decrease in *Rhodomonas* while the other important genus, *Cryptomonas*, shows wide fluctuation without any consistent trend. The increasing trend for diatoms is the composite result of quite different trends in the important diatom genera. *Stephanodiscus* fluctuated widely without consistent trend. *Fragilaria* initially increased and then decreased after a maximum in 1985. *Asterionella* had an unimodal trend with a maximum in 1986. *Synedra* increased with oligotrophication. Among the green algae, *Chlamydomonas* increased after a period of minimal importance from 1981 to 1985. *Pandorina* was always unimportant except during the years 1984–1986.

Taxonomic composition during summer

In contrast to findings from many other eutrophic lakes, Cyanophyta (mainly represented by *Anabaena*) were never important contributors to mean summer phytoplankton biomass in Lake Constance (Fig. 7). This contrasts with the occurrence of conspicuous surface blooms during several years. However, the temporal and spatial restriction of those blooms (only near the surface, only a few weeks) led to low scores in our averaging procedure. No temporal trend was observed for the Cyanophyta. The temporal trend of the Dinophyta does not seem to be related to oligotrophication. They made their greatest contribution to summer mean biomass during the beginning and the end of the study period but were quite unimportant during the middle. This U-shaped pattern cannot be explained by species shifts within the dinoflagellates, because during the entire study period most of the dinoflagellate biomass (> 90%) consisted of only one species, *Ceratium hirundinella*.

The four other higher taxa exhibited clearer trends (Fig. 7). The Cryptophyta and the Chrysophyceae tended to increase with oligotrophication. The increase of the p_i of Chrysophyceae was due to an increase in absolute biomass while the relative increase of the Cryptophyta was due to a slower decrease of their biomass than the decrease of total biomass (see also Fig. 2). The diatoms tended to decrease both in absolute biomass and in p_i. The Chlorophyta reached their maximal relative importance in the middle of the study period with rather low levels at the beginning and the end.

The analysis at the genus level (Fig. 8) shows that the increasing trend for the Cryptophyta is mainly due to *Cryptomonas*, while *Rhodomonas* is quite unimportant during summer. The trends for the *Dinobryon* (the only important chrysophyte) and *Ceratium* (the only important dinophyte) have already been discussed. The different diatom genera responded differently to recovery from eutrophication. The relative importance of *Stepha-*

HIGHER TAXA - SUMMER
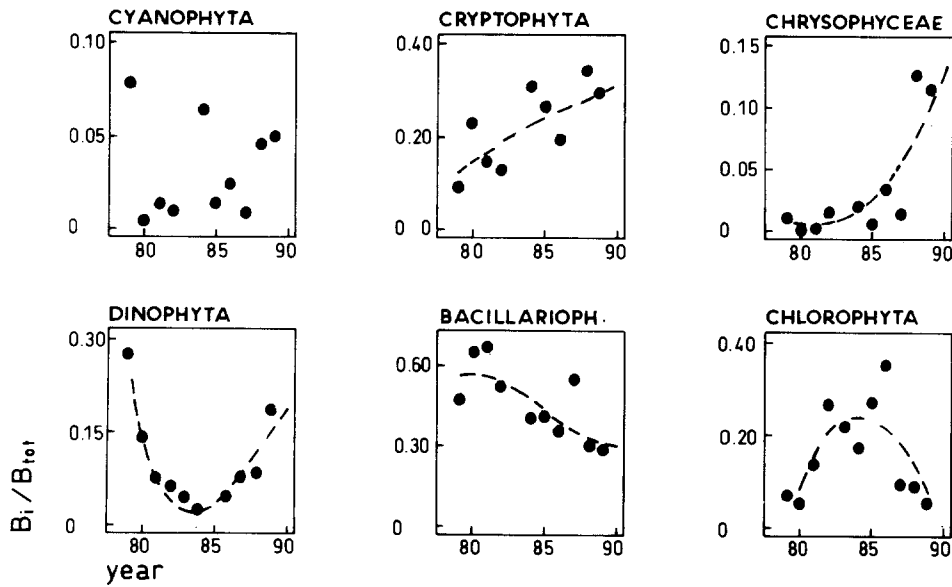

Fig. 7. Relative contribution of higher taxa to mean summer biomass. *Circles*, original values; *broken line*, trend obtained by 3rd-order polynomial smoothing of time series
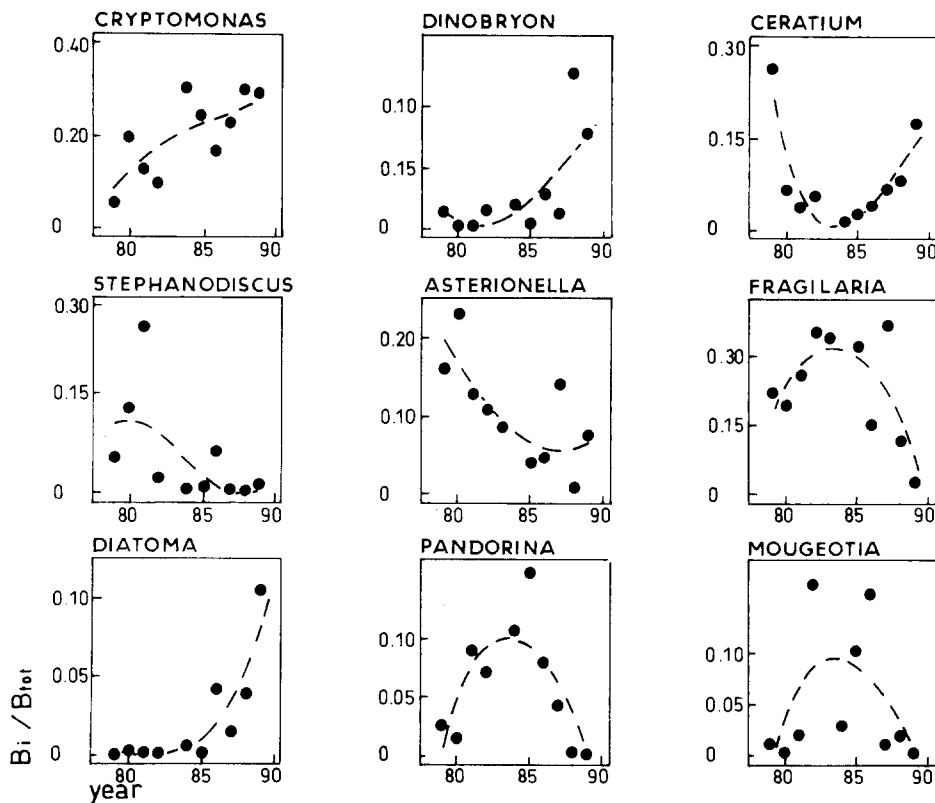
GENERA - SUMMER

Fig. 8. Relative contribution of important genera to mean summer biomass. Symbols as in Fig. 7

nodiscus and *Asterionella* decreased, *Fragilaria* showed an unimodal pattern with high levels during the middle of the study period and *Diatoma* increased steadily from 1985 onwards. The two most important green algal genera, *Mougeotia* and *Pandorina*, followed the general unimodal pattern of the Chlorophyta with peak values in the mid-eighties. Other genera never contributed > 10% to mean summer biomass.

Discussion

Comparison with the eutrophication period

The recovery from eutrophication since 1980/81 has so far led to a 2.5-fold decrease of total P concentrations during the spring circulation. This is much less than the spread of the nutrient axis in the well known regression

models (Sakamoto 1967; Dillon and Rigler 1974; Vollen-weider and Kerekes 1982) which predict phytoplankton biomass (expressed as chlorophyll) as a function of P concentrations in the lake. These regression models are based on lakes which differ in total P concentrations by 3 orders of magnitude. Phosphorus concentrations usually have to change by 1 order of magnitude before the 95% confidence limits of the biotic response variable cease to overlap. In Lake Constance this change of TP by 1 order of magnitude would imply a nearly complete return to the situation before cultural eutrophication. The response of an individual lake, however, would be expected to yield less scatter and therefore narrower confidence limits than a collection of lakes with different hydrography, climate and so on. Still, not too much response would be expected at the present stage of oligotrophication, given the interannual variability in physical conditions and the relative shortness of the periods when phytoplankton is mainly controlled by nutrients (Sommer 1987).

The absence of response of the spring bloom biomass to decreased P availability is not surprising. During the most eutrophic years P depletion by algal growth never proceeded to the point where P limitation of the major species would be expected (Sommer 1987). The increases and decreases in biomass during the first half of the spring bloom are assumed to be primarily controlled by changes in the stability of vertical stratification, while the termination of the spring bloom and the biomass accumulation towards the end of the spring bloom are controlled by grazing (Lampert and Schober 1978; Geller 1980). After the mid-1980s P depletion increased considerably and a modest amount of P limitation could be expected (Gaedke and Schweizer 1993). At present, grazing appears to play its previously predominant role only in years with a relatively warm spring and an early onset of *Daphnia* growth (Geller, unpubl. data). The increasing importance of relatively large and not very edible diatoms during the spring bloom might further restrict the impact of grazing on the quantity and duration of the spring bloom.

The taxonomic trends shown for the spring period (Figs. 4 and 5) only become apparent if the years 1989 and 1990 are excluded. These most oligotrophic years of the study period strongly resembled the most eutrophic years from 1979 to 1982. How justified we are in omitting 1989 and 1990 can only be judged when oligotrophication has proceeded further. At present, it is at least possible to test to what extent the trends presented here are a reversal of trends during the eutrophication period, and how then data compare with those from lakes of different trophic states.

The main source of comparison with the past in Lake Constance is the report by Kümmerlin and Bürgi (1989) (also summarised in Kümmerlin 1991) based on data from 1961 (SRP concentration during the winter circulation ca. 12 μg · l^{-1}) to 1986. Phosphorus levels similar to those found in 1990 were reached around 1970. Thus, the period from 1970 to 1981 is taken as the "symmetrical" counterpart to our study. The comparison with our data can only be rough and has to be done by eye, because the

data of Kümmerlin and Bürgi are presented in a different way (monthly means of absolute biomass, only discrete classes of log$_2$ shown). Moreover, phosphorus data for the period prior to 1979 in the sources cited here (Kümmerlin 1991; Kümmerlin and Bürgi 1989; Tilzer et al. 1991) are restricted to SRP. In our study period SRP and TP during the mixing period were strongly correlated (SRP = 2.45 TP$^{0.75}$; $r^2 = 0.93$; $P = 0.00001$).

The major trend related to entrophication distinguished by Kümmerlin (1991) is a gradual shift of the main growth period of colonial diatoms. During the oligotrophic period they tended to be the dominant group of spring phytoplankton. With increasing eutrophication their relative importance during spring declined while a summer bloom of diatoms began to appear. During oligotrophication a reversal began to be seen, as documented by the tendency of diatoms to increase in p_i during the spring bloom and to decrease during the summer bloom. A reverse pattern for the second most important fraction of phytoplankton, the Cryptophyta, is a logical consequence.

At the genus level the majority of trends for the oligotrophication period and the eutrophication period after 1970 are symmetrical (Table 1). There are at least two reasons for the lack of symmetry in some cases. First, there are some differences between the central region of Obersee (the site studied by Kümmerlin and Bürgi) and the Überlinger See. Among other examples, Kümmerlin

Table 1. Comparison of genus-level trends in relative biomass during the eutrophication and the oligotrophication period in Lake Constance

Genus	Eutrophication		Oligotrophi-cation
	Before 1970	After 1970	
SPRING			
Cryptomonas	○	○	○
Rhodomonas	○	+	+
Chlamydomonas	○	u	u
Pandorina	.	.	u
Stephanodiscus	+	○	○
Asterionella	−	−	u
Fragilaria	.	.	u
Synedra	.	.	−
SUMMER			
Anabaena	.	+	○
Cryptomonas	○	−	−
Dinobryon	○	○	−
Ceratium	+	○	○
Pandorina	.	○	u
Mougeotia	.	u	u
Stephanodiscus	○	+	+
Asterionella	○	+	+
Fragilaria	○	u	u
Diatoma	.	.	−

Response types:
+ increasing with trophic state
− decreasing with trophic state
u unimodal response, maximum at medium level
○ unresponsive or irregular
. no data or unimportant

and Bürgi noted a considerable mass development of *Microcystis* in 1980 which was not marked in the Über-linger See. Second, community composition would be expected to react to environmental changes with some inertia because population replacements take time. When comparing one year with another, this inertia cannot be due to the phytoplankton because phytoplankton species replacements take place on a scale of weeks, and most phytoplankton species build up to their annual maxima from overwintering inoculum populations which are at least 4 orders of magnitude smaller than the peak popula-tion. However, if the phytoplankton is affected by the zooplankton and the zooplankton by fish, the inertia of the much slower reacting fish community may cascade downwards to phytoplankton.

Comparison with other lakes

The seasonal biomass trends seen in Lake Constance conform well with widespread differences between eutro-phic and oligotrophic lakes or changes within the same lake in the course of eutrophication (Davis 1964). A number of examples for oligotrophic lakes with a spring peak and a summer depression of biomass and eutrophic lakes with a spring peak, a clear-water phase and an annual maximum in summer are summarised in Sommer (1986) and Sommer et al. (1986). The current pattern in Lake Constance is half-way between the eutro-phic and the oligotrophic type.

The taxonomic trends in Lake Constance also con-form to widespread trends for hardwater lakes (Reynolds 1984; Harris 1986), but there is one notable exception. The importance of summer blue-green algae *(Anabaena, Aphanizomenon, Microcysts)* was unexpectedly low even during the most eutrophic years and *Planktothrix (= Os-cillatoria) rubescens* has been completely absent. In most other subalpine lakes, *P. rubescens* is characteristic of the early stages of eutrophication. In those lakes it forms a conspicuous part of the spring bloom and dense meta-limnetic layers during summer. The relatively poor per-formance of blue-green algae in Lake Constance might be due to the rather unstable summer stratification (Rey-nolds 1987). The other subalpine lakes are either much smaller (less wind fetch), are surrounded by higher mountains (better wind protection, e.g. the North Italian great lakes) or are warmer during summer (Lake Geneva, south Alpine lakes).

Changes in competitive relationships

It seems safe to conclude that the taxonomic changes in Lake Constance phytoplankton cannot be explained by purely independent responses of taxa to the changes in trophic state without invoking biotic interactions. The difference between the conditions at the peak of eutrophi-cation and the present state is simply too small to assume that species that thrive at one end of the spectrum would encounter adverse conditions at the other end of the spectrum. The biotic interactions within the plankton that have received most attention during recent years are

grazing by herbivorous zooplankton and competition for resources. The first one is beyond the scope of this paper and will be the subject of a later analysis. The potential impact of the latter will be illustrated by the response of the diatoms.

Before discussing resource competition, the limiting resources for which competition takes place must be identified. It is the limitation of reproductive rates that is critical in identifying competition; it is not necessary for the population to reach carrying capacity for a re-source to be considered limiting. Indeed, the carrying capacity as defined by resources (nutrients, light) is never attained in Lake Constance (Tilzer et al. 1991). There is, however, evidence for resource limitation of growth rates and/or physiological rates. Light limitation below the depth of optimal photosynthesis has been documented by numerous photosynthesis depth profiles (e.g. Tilzer 1984). Silicate limitation of diatom growth rates can safely be inferred from dissolved Si concentrations. Several important diatom species have very high half-saturation constants for Si-limited growth *(Synedra:* $550 \, \mu g \cdot l^{-1}$, *Asterionella:* $110 \, \mu g \cdot l^{-1}$; Tilman et al. 1982) which leads to incipient silicate limitation even at modest Si depletion if other limiting factors can be ex-cluded.

Phosphorus limitation of species with high require-ments (e.g. Cryptophyta, large Volvocales) becomes possible if SRP concentrations fall below $10 \, \mu g \cdot l^{-1}$ and intracellular stores have been depleted. Species with low P demand (pennate diatoms, Chrysophyta) would only become limited at undetectable SRP concentrations. Be-cause of the possibility of intracellular storage, cellular stoichiometry is a safer indicator of P limitation than dissolved concentrations (Droop 1983). Sestonic C:P ratios clearly in excess of 100:1 (atom:atom) are a fairly safe indication of P limitation (Sommer 1988a, 1989b). Chemical evidence for nutrient limitation can only be found in the top few meters of Lake Constance because in the lower part of the euphotic zone light imposes a stronger restriction on growth rates than nutrients and therefore prevents their full exploitation. The depths of maximum nutrient depletion, however, roughly coincide with the depth of maximum biomass and therefore have the strongest influence on the p_i values calculated by our averaging method. Silicate limitation of diatoms and P limitation of other phytoplankton species have been doc-umented for parts of the summer period (Sommer 1987; Gaedke and Schweizer 1993).

The situation for the spring bloom is more am-biguous. The nutrient concentrations prior to massive algal growth would easily support maximal reproductive rates except for a modest degree of Si limitation in *Syne-dra*. The depletion of P did not proceed to limiting levels during the years of maximal eutrophication but, after the mid-1980s some P limitation of algae with high demands seems plausible. Since 1986 minimum spring SRP con-centrations (mean for 0–8 m $< 10 \, \mu g \cdot l^{-1}$) have occurred regularly together with correspondingly lower values at the depths of maximum biomass.

Experimental evidence shows that if algae are compet-ing for Si and P the proportion of diatoms in the popula-

tion increases with increasing Si:P ratios (Sommer 1983). Among the diatoms *Synedra* is commonest at the highest Si:P ratios, *Asterionella* follows next, *Fragilaria* is third, *Diatoma* fourth, and centric diatoms are commonest at relatively low ratios (Tilman et al. 1982). The tendency of diatoms to increase in importance during the spring bloom corresponds well with the increasing Si:P ratios during the circulation period resulting from declining P levels and fairly constant Si levels. Additionally, the years in which the different diatom genera reached their highest proportion in the spring follows the pattern predicted from experiments. The centric diatom *Stephanodiscus* had its maximum spring p_i in 1981 when the molar ratio of dissolved Si:P during the circulation was 19.4. *Diatoma* had its maximal p_i in 1983 (Si:P = 20.6), *Fragilaria* in 1985 (Si:P = 22.8), *Asterionella* in 1986 (Si:P = 25.5) and *Synedra* in 1988 (Si:P = 27.7). The years 1989 and 1990 do not fit this pattern, which might be because SRP ratios during the circulation period are only a good indicator of the Si:P ratio available for the buildup of the spring bloom if no major algal growth has intervened.

During summer the sequence of pennate diatoms was partially reversed: *Asterionella* declined first in response to oligotrophication, *Fragilaria* had a peak in the middle and *Diatoma* increased. *Synedra* was unimportant during summer. How can this reversal between summer and spring be explained? Resource ratios during the circulation period have already been shown to be an inadequate predictor of the taxonomic pattern of spring bloom if too much growth of algae has occurred before the spring bloom *sensu stricto* (1989/90). Obviously, they are even more inadequate predictors of the summer bloom. Dissolved phosphorus during the clear-water phase cannot serve as a basis for the calculation of a resource ratio prior to the onset of summer growth. This is because SRP during the clear-water phase fluctuates widely between 17 and nearly 100% of TP, contrary to the relatively narrow range of 70–98% during the spring circulation. Phosphorus present in the particulate fraction during the clear-water phase may become available again by recycling or may be lost by sedimentation. The best choice to test the resource ratio hypothesis for the summer period would be the mean total Si: mean total P ratio over that period. Unfortunately total Si was not measured. Dissolved Si cannot serve as a surrogate for total Si, because during diatom blooms it measures only the amount of Si which diatoms have left in solution, but not the amount of Si which has been available for their biomass formation. On the other hand, dissolved Si prior to diatom increase is a good measure because, unlike particulate P particulate Si is not usually recycled for repeated diatom growth within the epilimnion (Sommer 1988b). Thus it seems possible to relate the biomass of summer diatoms to the dissolved Si concentration during the clear-water phase. The Si concentration during the clear-water phase can then be explained by the removal of dissolved Si by the spring growth and subsequent sinking of diatoms. Indeed, there is a positive correlation between the difference between circulation Si and clear-water phase Si with the biomass of spring diatoms and a positive correlation between the Si concentrations
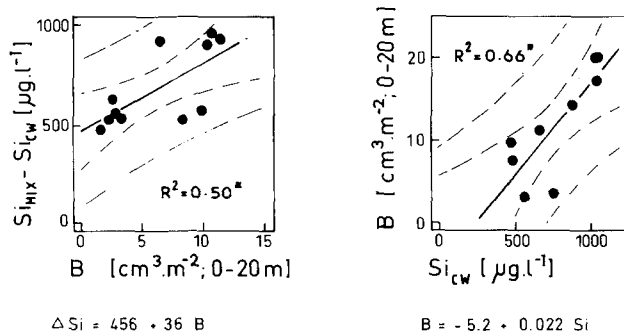

Fig. 9. *Left:* Correlation of the Si depletion during the spring bloom (Si during the mixing period minus Si during the clear water phase) and diatom biomass during the spring bloom. *Right:* Correlation between the summer biomass of diatoms (*B*) and the Si concentration during the clear-water phase

during the clear-water phase and the summer biomass of diatoms (Fig. 9). Thus, the response of diatom biomass during spring and during summer can be accounted for. The considerable scatter in both graphs probably has two reasons. First, diatoms have been treated as a unit instead of considering different Si requirements of different taxa. Second, mid-seasonal partial mixing events may import additional Si into the epilimnion, probably with strong year-to-year variability.

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