Phytoplankton response to re-oligotrophication in large and deep Lake Constance: Photosynthetic rates and chlorophyll concentrations

Clivia Häse, Ursula Gaedke, Angelika Seifried, Bärbel Beese, and Max M. Tilzer

with 7 figures and 2 tables

Abstract: In Lake Constance, phytoplankton productivity, together with parameters relevant for the production process, was assessed year-round at about 500 dates between 1980 and 1995/1996. During this period, the concentration of total phosphorus during winter circulation decreased from more than 80 to 22 µg/l as a consequence of sewage diversion and waste water treatment within the catchment area. By contrast, annual photosynthetic rates remained virtually unchanged for about 10 more years following phosphorus decline (mean value 288 ± 21 gC m^{-2} a^{-1}), and thereafter diminished only by about 25% until 1996. The aim of this study is to analyse factors responsible for this pronounced resilience.

The time-course of phytoplankton productivity, biomass, and taxonomic composition during the growing season in Lake Constance exhibits three characteristic phases which reacted differently to the decrease in phosphorus concentrations. The dampened response of annual photosynthetic rates to phosphorus reduction in Lake Constance, including the observed time lag of about one decade, can be explained by the cumulative effect of the changes occurring during these phases. In spring, chlorophyll concentrations reached maximum values during intermediate years of the study period (1986-1991). Presumably owing to taxonomic shifts within the phytoplankton community and to increased self-shading within the water column, depth-integrated photosynthetic rates in spring basically remained unchanged until 1991, and decreased markedly by about 40% thereafter. This coincided with the fact that since 1992, contrary to previous years, phosphorus became depleted already during spring. In contrast in summer, phosphorus concentrations within the uppermost 8 meters were below the detection limit during the entire study period. Chlorophyll concentrations in summer declined from the outset which, however, slowed down during the course of the study period. The response of depth-integrated photosynthetic rates in summer to re-oligotrophication was dampened by a factor of 2 due to reduced self-shading within the water column. The phytoplankton development in autumn apparently was not yet affected by the re-oligotrophication process.

Authors' addresses: C. Häse, U. Gaedke, A. Seifried, B. Beese, M.M. Tilzer, Limnological Institute, University of Constance, D-78457 Konstanz, Germany. C. Häse at present: Interuniversity Institute Eilat, P.O.B. 469, Eilat 88103, Israel.

Introduction

Accelerated eutrophication represents one of the most important responses of lakes to anthropogenic impacts. It has been studied extensively in order to improve our understanding of the effects of increasing nutrient concentrations on water quality and the community structure of lakes (e.g., DILLON & RIGLER 1974, WATSON & MCCAULEY 1988, BAYNE et al. 1990, BERMAN et al. 1995, JASSBY et al. 1995). However, only little is known to date on how phytoplankton in large lakes responds to re-oligotrophication. For example, in Lake Washington, phytoplankton biomass responded immediately to nutrient reduction, and the lake was considered to be recovered from eutrophication within a period of about 10 years (EDMONDSON & LEHMAN 1981). In Lake Mondsee, phytoplankton reacted without a remarkable delay to nutrient decline by a decrease in biomass and taxonomic changes in spring and summer (DOKULIL 1993). In Lake Lugano, annual primary productivity decreased considerably within 10 years during re-oligotrophication (POLLI & SIMONA 1992). By contrast, in Lago Maggiore, annual primary productivity declined only gradually during re-oligotrophication after a rapid increase within 5 years during eutrophication (MANCA et al. 1992). Especially long-term records of phytoplankton productivity in large lakes are rare and, moreover, some of them are still in the process of eutrophication (GOLDMAN 1988, BAYNE et al. 1990, BERMAN et al. 1995). However, it became evident that re-oligotrophication can rarely be predicted by the reverse course of eutrophication (e.g. MANCA et al. 1992).

In Lake Constance, phosphorus was repeatedly identified as the main nutrient limiting phytoplankton growth during the past decades (GRIM 1955, ELSTER, 1977, SCHWARZ 1991, TILZER et al. 1991). Between 1951 and 1980, the concentration of total phosphorus during winter circulation (TP_{mix}) rose by a factor of 10 (see Fig. 3 in GÜDE et al. 1998). Mainly as a result of sewage diversion and waste water treatment in the catchment area, the annual rate of increase of TP_{mix} was reduced during the mid and late seventies, and TP_{mix} reached maximum values of more than 80 µg/l in the late seventies and early eighties. Since then, TP_{mix} has decreased by a factor of almost four to 22 µg/l by 1996 (for details see GÜDE et al. 1998), whereas inorganic nitrogen continued to augment. As a major consequence of the decline in phosphorus concentrations, the spatio-temporal "window" of severe depletion of soluble reactive phosphorus (SRP) widened considerably during the past 15 years (cf. Fig. 1 in GAEDKE 1998, GÜDE et al. 1998). During the height of the accelerated eutrophication process, SRP-concentrations in Lake Constance dropped below 3 µg/l between July and September/ October within the uppermost 8 meters of the water column. In contrast, during recent years, SRP already became undetectable during the spring bloom in surface waters, and remained low until November or December. Recent measurements of algal C:P-ratios as performed in 1995 suggested moderate phosphorus limitation of phytoplankton growth prior to the clear-water phase (HOCHSTÄDTER 1997).

During the first decade of re-oligotrophication, a decline of average and maximum phytoplankton biomass was observed in summer, but not during other seasons (MÜLLER & STICH 1991, GAEDKE & SCHWEIZER 1993). In addition, the taxonomic composition and the timing of mass abundances of individual species changed in spring and summer (SOMMER et al. 1993, KÜMMERLIN 1998). However, in annual averages of phytoplankton productivity, chlorophyll concentrations, and water transparency no response was detected during the first decade of re-oligotrophication (TILZER et al. 1991).

The aim of the present study is to identify factors responsible for the observed discrepancy between the time-course of total phosphorus concentrations and phytoplankton biomass and productivity. For that purpose, we complement and update previous investigations by evaluating approximately 500 depth profiles of photosynthetic rates and chlorophyll concentrations recorded during 15 years of investigation (1980-1983 and 1986-1996). Their seasonal and interannual variability was analysed with respect to decreases in phosphorus concentrations. Special emphasis was layed on mechanisms underlying the changes of temporally and vertically averaged bulk parameters.

On the temporal scale, our analyses focused on three main phases of phytoplankton development in Lake Constance during the course of the year. Phytoplankton biomass and productivity during these phases generally were controlled by different ecological factors, among which nutrients played a major role only during restricted periods of the year (SOMMER 1987, TILZER & BEESE 1988 and references therein): The spring bloom was terminated by intense zooplankton grazing leading to the clear-water phase. The ensuing summer bloom was governed mainly by nutrient depletion and grazing, whereas the phytoplankton development in autumn was terminated by declining solar energy supply, in spite of increasing nutrient inputs into the euphotic zone from deeper waters due to mixing events.

On the vertical scale, we considered self-shading as a possible mechanism that may have dampened the response of depth-integrated photosynthetic rates and, hence, that of annual photosynthetic rates to re-oligotrophication. As phytoplankton in Lake Constance exhibits a high seasonal variability in both biomass and productivity, and non-algal turbidity is relatively low, the extension of the euphotic zone in Lake Constance is mainly determined by variations in chlorophyll concentrations (TILZER 1983). Due to self-shading within the water column, depth-integrated photosynthetic rates are less responsive to changes in the nutrient regime than maximum photosynthetic rates within the water column (SMITH 1979, TILZER 1983). Therefore, in the present study, both parameters were compared in their response to decreases in TP_{mix}.

Methods

Upper Lake Constance is a large (472.3 km^2) and deep (mean depth 101 m) lake of warm-monomictic character on the northern fringe of the Alps. Samples were collected on about 35 to 40 dates per year (weekly during the growing season and biweekly to monthly in winter) between 1980 and 1996 with a gap of measurements in 1984 and 1985. The sampling station was located in the middle of the 'Überlinger See', a fjord-like basin in the north-western part of Upper Lake Constance.

A first rough estimate of the euphotic depth was obtained on board from Secchi readings by applying the non-linear empirical relationship between Secchi and euphotic depth observed in Lake Constance (TILZER 1988) in order to determine the incubation depths for photosynthesis measurements for the respective day. Water samples were collected from 15 depths covering the euphotic zone. Photosynthetic rates were evaluated using a modified radiocarbon method: Duplicate light bottles and one dark bottle were incubated in situ at the respective sampling depths for 4 hours around local noon time. The samples were filtered onto membrane filters (0.45 mm) after withdrawing an aliquot for measuring the added activity. Particular care was taken to minimize light exposure of the samples during handling. During the incubation period, a concomitant profile of the photosynthetically available radiation (PAR) was recorded
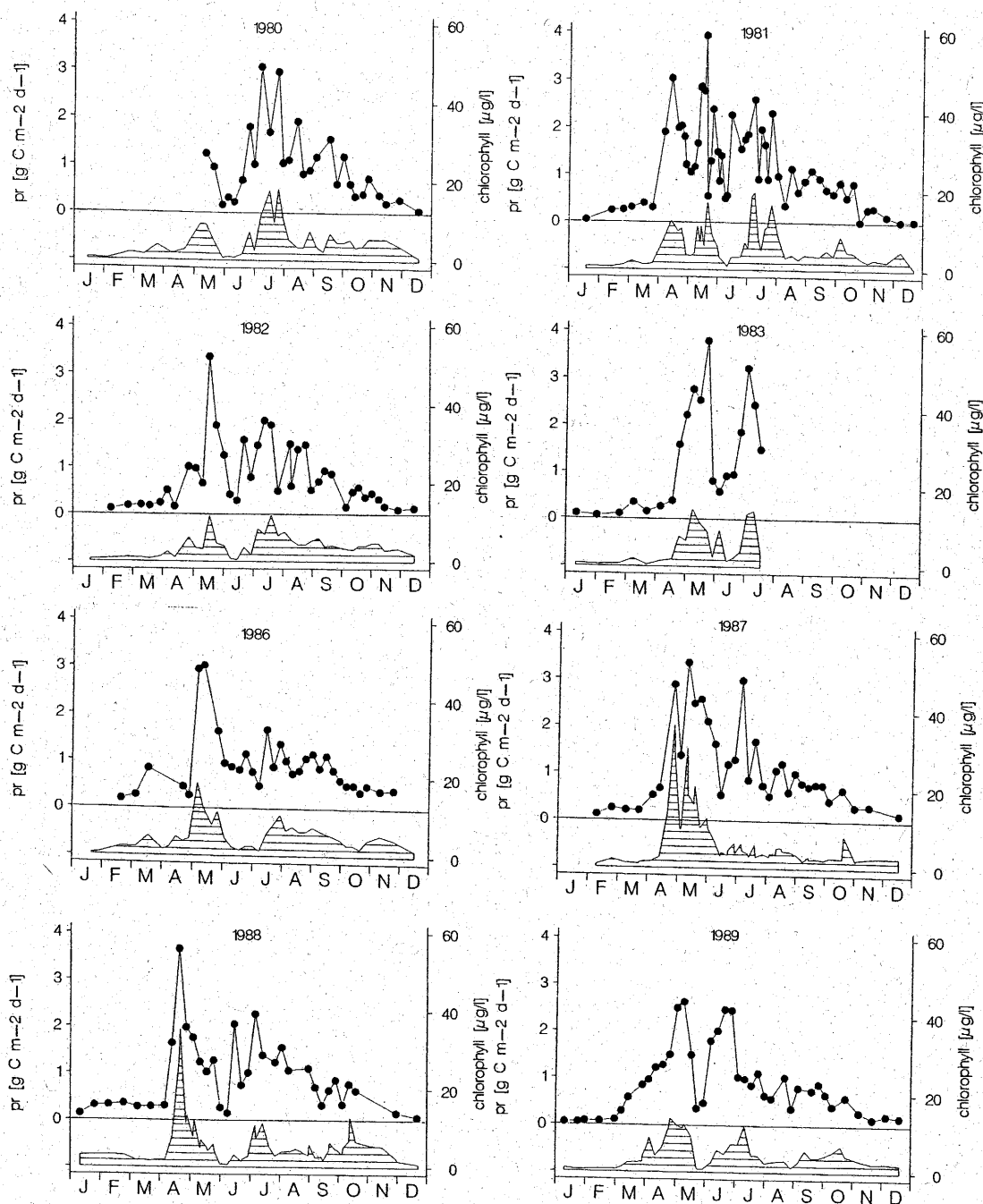
Fig. 1. Seasonal course of mean chlorophyll concentration within the uppermost 20 m of the water column (lower line, hatched area) and photosynthetic rates within the euphotic zone per day (upper line, dots) in Lake Constance from 1980 to 1995.

by an underwater scalar irradiance meter. From this profile, the euphotic depth was determined by the depth where 1% of the surface irradiance penetrated. Chlorophyll a was analysed spectrophotometrically after extraction in hot ethanol, and was corrected for pheopigments by acidification. For further methodological details of light, chlorophyll, and photosynthesis measurements, see TILZER (1983) and TILZER & BEESE (1988).
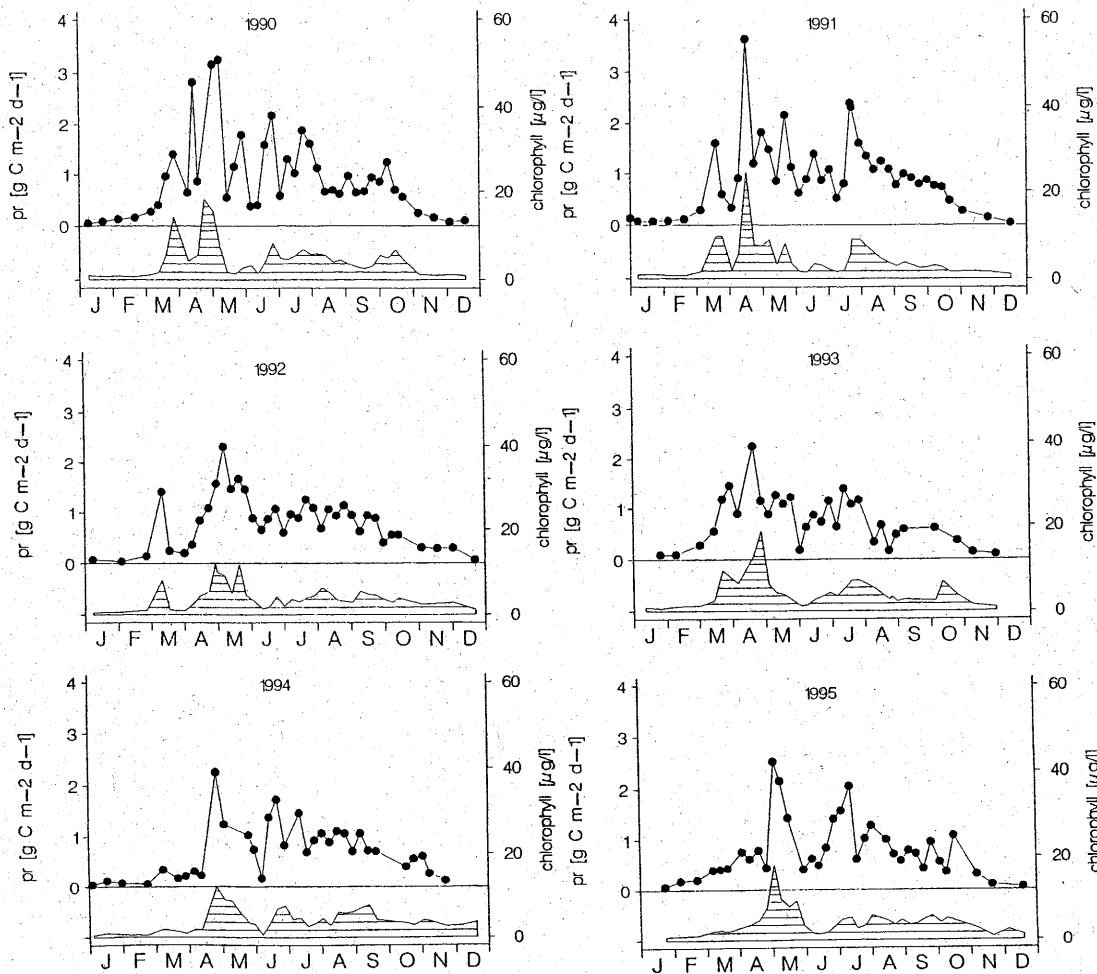
Fig. 1. (Continued).

For our analyses, we subdivided the growing season into a number of phases in the same fashion as GAEDKE (1998): Spring was defined as the period from March 15 until the onset of the clear-water phase, the date of which changed interannually. During the clear-water phase, phytoplankton was assumed to be controlled mainly by zooplankton grazing. Therefore, this phase was excluded from present analyses focusing on nutrient effects. Summer was specified as the period following the clear-water phase until the beginning of autumn, the date of which was – sometimes somewhat arbitrarily – chosen individually for each year according to the temporal course of phytoplankton biomass and related parameters. Autumn was determined as the remaining interval until November 15.

Daily and annual photosynthetic rates were extrapolated from vertical integrals of the 4-hour incubations using Talling's light division hours as described in detail by TILZER & BEESE (1988). Annual averages of chlorophyll concentrations and the annual total of photosynthetic rates (pr_{tot}) were corrected for differences in time intervals between the respective sampling dates. Since sampling was almost consistently performed weekly during the growing season, mean values of photosynthetic rates and chlorophyll concentrations for spring, summer, and autmn were obtained by simply averaging the observed values of the corresponding sampling dates. Note that in many figures the mean chlorophyll concentration within 0-20 m is given, which we consider as a measure for depth-integrated chlorophyll concentrations.
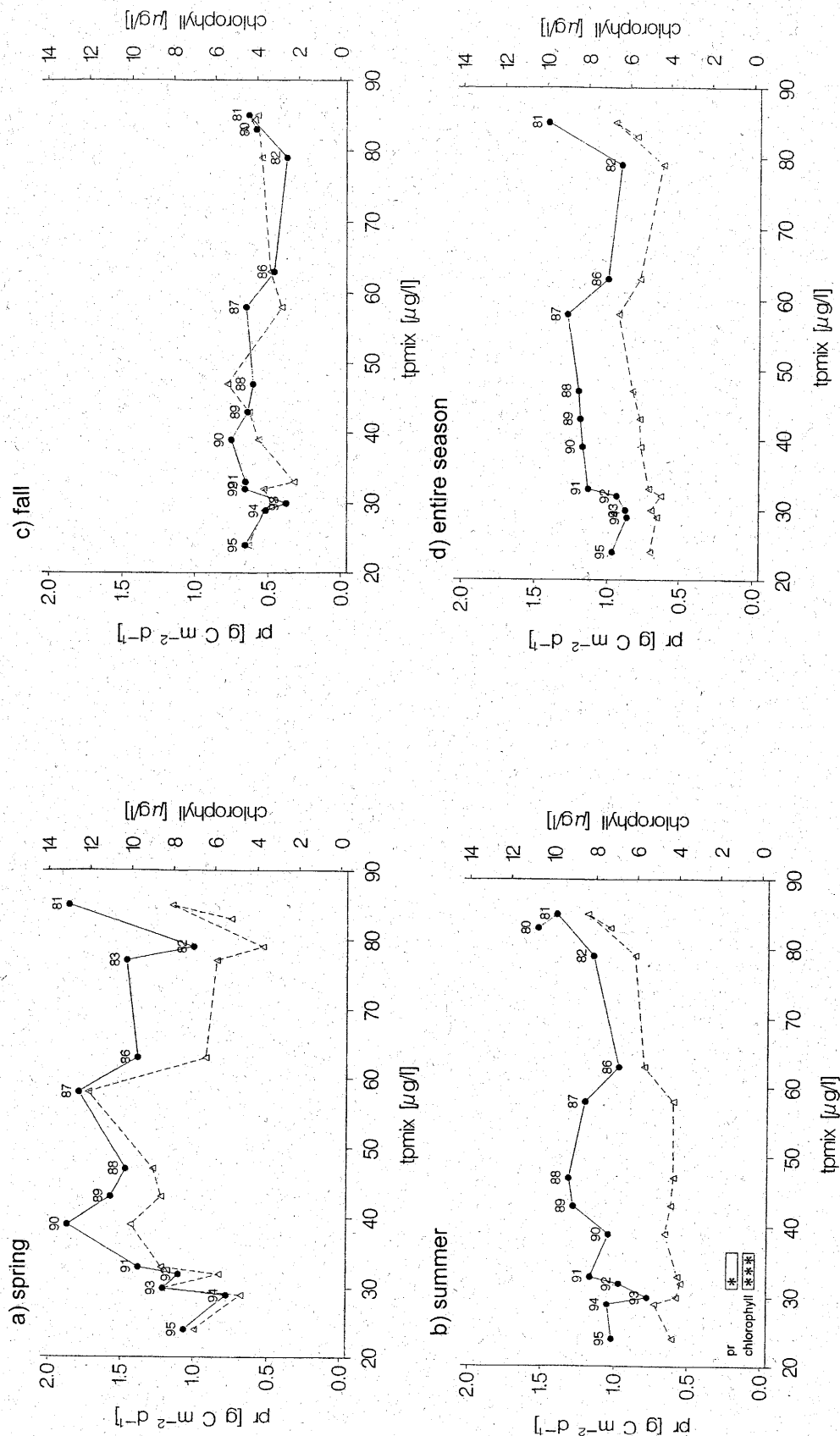
Fig. 2. Averages of mean chlorophyll concentrations within the depth of 0-20 m (triangles) and of daily photosynthetic rates within the euphotic zone (dots) during a) spring, b) summer, c) fall, and d) the growing season (15.3.-15.11.) versus maximum concentrations of total phosphorus during winter circulation (TP_{mix}). Significance levels of the linear relationships are marked by asterisks: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Results

The seasonal cycle of depth-integrated chlorophyll concentrations and photosynthetic rates

Depth-integrated chlorophyll concentrations and photosynthetic rates covaried closely in Lake Constance (Fig. 1; cf. TILZER et al. 1991). Both parameters revealed a high, but largely recurrent seasonal variability (Fig. 1). The spring bloom occurred between mid-March and the end of May. Depending presumably on weather conditions and the vertical mixing intensity within the water column (GAEDKE et al. 1998), one to three peaks of phytoplankton biomass appeared until the bloom was terminated by severe grazing which caused the clear-water phase in late May or June. Highest chlorophyll concentrations (mean within 0-20 m) in spring usually varied between 12 and 25 µg/l. During 1987 and 1988, extremely high spring chlorophyll concentrations of about 30-35 µg/l were reached (Fig. 1). During some early years of observation (1980-1983), the chlorophyll maximum was in the same range in spring and summer. The spring chlorophyll maximum did not show any consistent trend, while the summer chlorophyll peak diminished significantly during the study period ($r^2=0.63$, $p=0.001$) (Fig. 1). Maximum photosynthetic rates always occured in spring (Fig. 1) and decreased

Table 1. Changes of trophic indicators in percent throughout the study period. Values indicate the relative deviations of the observations in 1994/1995 from those made in 1980/198 . If changes were observed only during recent years, comparisons were made between the years 1990/91 and 1994/95 which ist marked by '*'. If the linear relationship versus TP_{mix} was significant for the entire study period, the correlation coefficient and the significance level are provided.

Phase averages	spring	summer	fall
Depth-integrated values			
Photosynthetic rates	- 40% *) n.s.	- 30% $r^2=0.45$ p=0.01	n.s.
Chlorophyll (0-20m)	- 40% *) n.s.	- 50% $r^2=0.73$ p=0.0002	n.s.
Maxima within the water column			
Photosynthetic rates	- 40% $r^2=0.31$ p=0.05	- 60% $r^2=0.74$ p=0.0002	- 40% $r^2=0.42$ p=0.02
Chlorophyll concentrations	- 40% *) n.s.	- 50% $r^2=0.80$ p=0.0001	n.s.
Water transparency			
Secchi depths	n.s.	+ 30% $r^2=0.62$ p=0.001	n.s.
Euphotic depths	n.s.	+ 20% $r^2=0.47$ p=0.009	n.s.

significantly during the study period (r^2=0.42, p=0.02). During the first decade of re-oligotrophication, maximum photosynthetic rates between 3 and 4 gC m^{-2} d^{-1} were measured regularly in spring, while rates did not exceed 2.5 gC m^{-2} d^{-1} since 1992 (Fig. 1). In summer, variations in the photosynthetic rates became less pronounced than in the years 1980-82 (Fig. 1). In autumn, phytoplankton development did not exhibit a distinct peak in every year of the study period (Fig. 1).

Chlorophyll concentrations and photosynthetic rates versus TP$_{mix}$

Only in summer did depth-integrated chlorophyll concentrations and photosynthetic rates decrease significantly with TP$_{mix}$ during the study period (Table 1). Depth-integrated chlorophyll concentrations (0-20 m) in summer declined by about 50% between 1980 and 1987 (Table 1, Fig. 2b). During the same period, TP$_{mix}$ lessened by about 30%. Thereafter, chlorophyll concentrations in summer remained nearly constant, although TP$_{mix}$ diminished further by almost 60% between 1987 and 1995. Depth-integrated photosynthetic rates in summer declined by only 30% during the study period (Table 1, Fig. 2b) and did not closely follow the trend of chlorophyll concentrations. In spring and autumn, no significant tendency was observed for depth-integrated chlorophyll concentrations and photosynthetic rates. In spring, photosynthetic rates remained approximately at the same level during the first decade of the re-oligotrophication period, and decreased by about 40% thereafter (Fig. 2a, Table 1). In autumn, both parameters varied little without any tendency during the study period (Fig. 2c). Considering the entire growing season from March 15 until November 15, depth-integrated chlorophyll concentrations and photosynthetic rates varied moderately and almost in parallel. Both parameters exhibited a decreasing trend during the study period (Fig. 2d), which was significant only at the 10% level, so far.

Maximum photosynthetic rates within the water column responded more strongly to declining phosphorus concentrations than did depth-integrated photosynthetic rates (Table 1, Figs. 2, 3). This was most pronounced in summer (Figs. 2b, 3b), when maximum photosynthetic rates within the water column diminished approximately in proportion to maximum chlorophyll concentrations by about 60% during the study period (Table 1).

Covariation between photosynthetic rates and chlorophyll concentrations

Maximum photosynthetic rates within the water column covaried almost proportionally with maximum chlorophyll concentrations (Figs. 4a-c). In spring, photosynthesis in the light-saturated portion of the water column on average was performed more effective per unit of chlorophyll during the early eighties (1980-83) than during subsequent years of the study period (Fig. 4a): The mean ratio between maximum photosynthetic rates and maximum chlorophyll concentrations was significantly higher during the early eighties than during the following years. The same was observed in summer (Fig. 4b), but it was significant at the 10% level only. In autumn, no significant changes in the mean ratio between both parameters were found (Fig. 4c).

In accordance with theory (BANNISTER 1974, MEGARD et al. 1979, TILZER 1983), the relationship between depth-integrated photosynthetic rates and euphotic chlorophyll concentrations followed a saturation curve (Figs. 4d-f). This was most evident in spring and summer, when high chlorophyll concentrations enhanced the self-shading within the water column. In spring, self-shading was more pronounced during intermediate years of the study period than
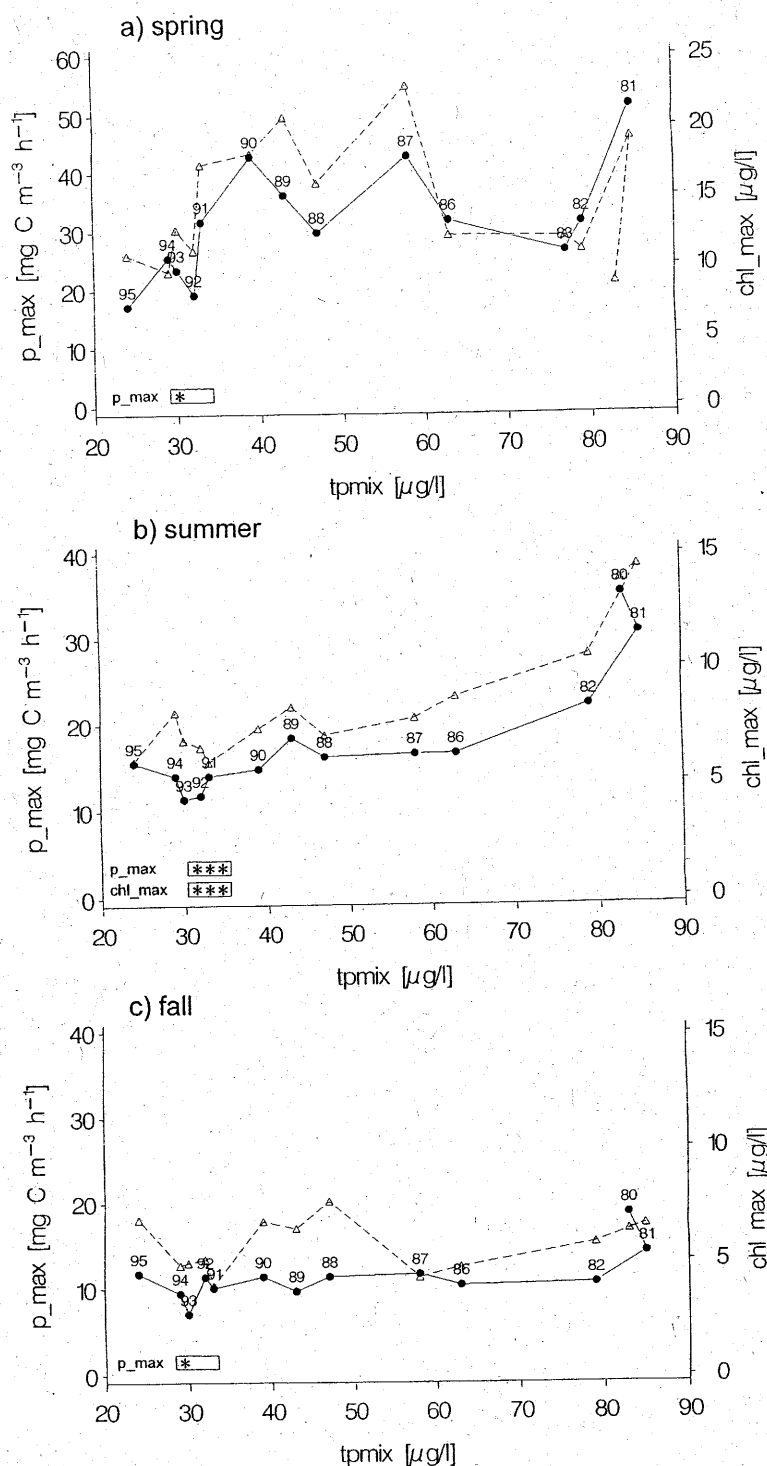
a) spring

b) summer

c) fall

Fig. 3. Averages of maximum chlorophyll concentrations (triangles) and maximum photosynthetic rates (dots) within the water column, during a) spring, b) summer, and c) fall versus TP_{mix}. The maxima within the water column were calculated as averages of the three highest values within individual depth profiles. Significance levels are marked as in Fig. 2. Please, note the differences in scale.

during the early eighties due to an increase in chlorophyll concentrations (Fig. 4d). By contrast, in summer, self-shading was strongest during the early eighties: The highest euphotic chlorophyll concentrations recorded during the early eighties were associated with only moderately high values of depth-integrated photosynthetic rates compared to the values during subsequent years (Fig. 4e).
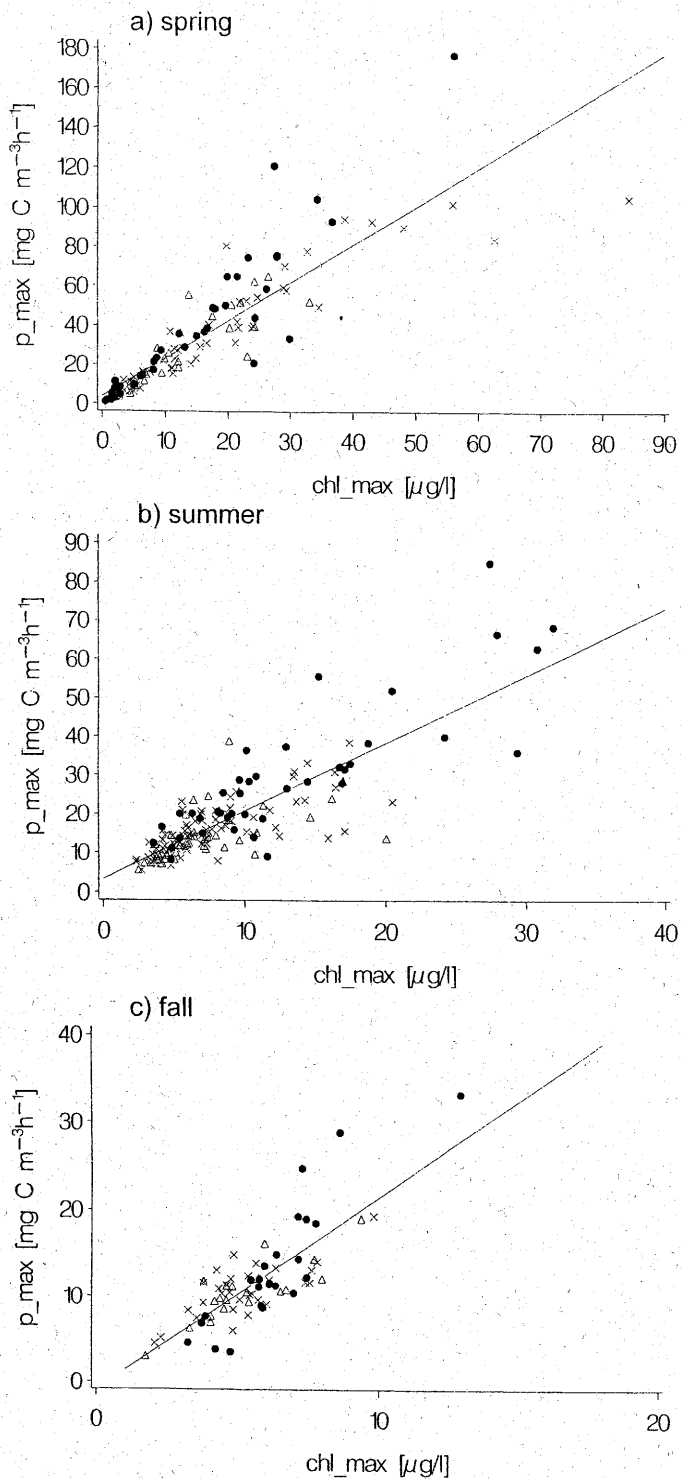
Fig. 4. Photosynthetic rates versus chlorophyll concentrations during spring, summer, and autumn. In panels a to c, the maximum photosynthetic rates within the water column were plotted against the maximum chlorophyll concentration within the water column. Solid lines represent the linear regression line for all data points within the respective phase of the seasonal cycle (in autumn, 2 outliers were omitted). In panels d to f, depth-integrated photosynthetic rates were plotted against the mean euphotic

d) spring

e) summer

f) fall
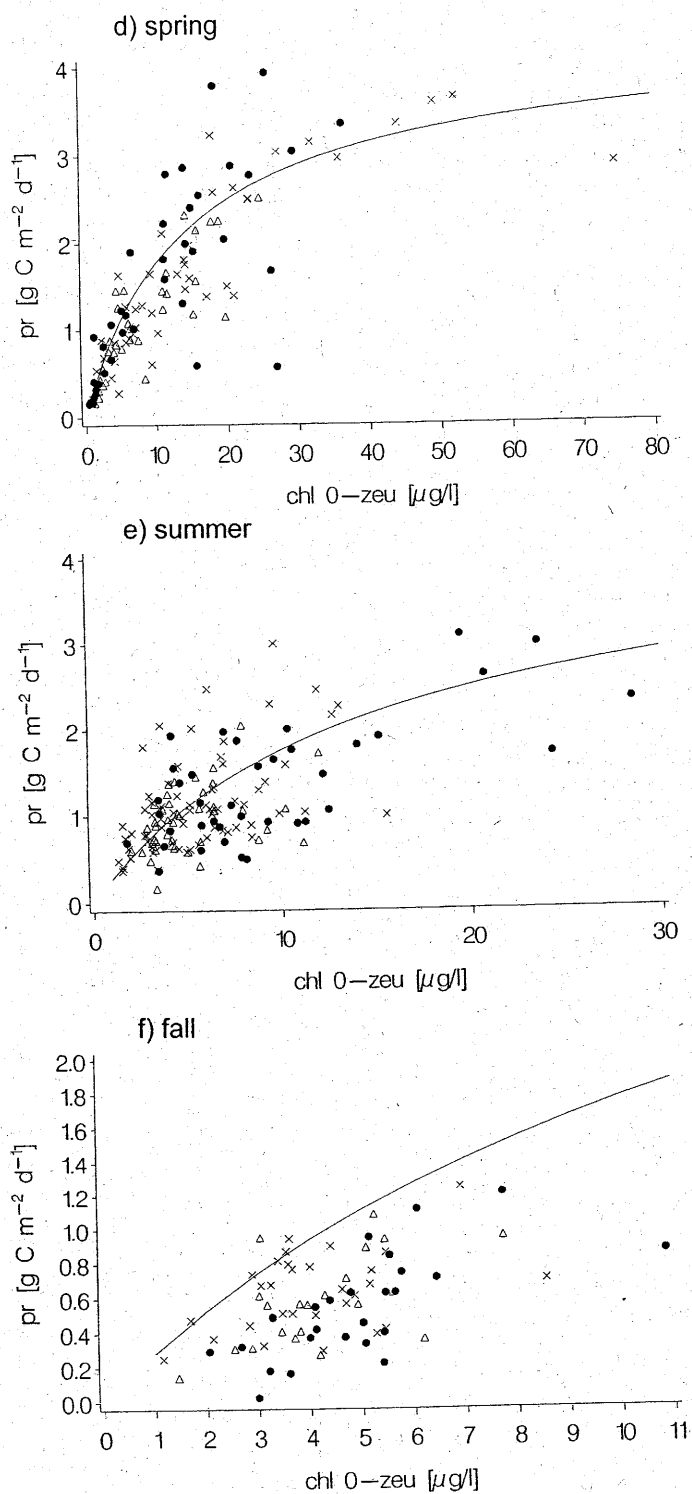
chlorophyll concentrations. Solid lines represent the theoretical relationship between both parameters based on annually averaged measurements for 1981 in Lake Constance (TILZER 1983, TILZER & BEESE 1988). The years under observation were divided into subgroups according to the response of chlorophyll concentrations and photosynthetic rates to re-oligotrophication. Full dots represent the years 1980-83, crosses 1986-91, and triangles 1992-95. Please, note the differences in scale.

Water transparency

Water transparency was inversely related to chlorophyll concentrations during the study period (Figs. 2, 5, Table 1; TILZER 1983, TILZER et al. 1995). Secchi depths and euphotic depths exhibited a significant correlation with TP_{mix} during the entire study period only in summer (Fig. 5b, Table 1). In summer, average values of Secchi and euphotic depth increased significantly during the study period from 4.5 to about 6.5 m and from 10.5 to 13 m, respectively. In spring, no Secchi depths of less than 2.5 m and no euphotic depths of less than 6 m have been observed since 1991 which had occurred regularly during the years before. Average Secchi depths in spring were considerably higher during recent years (1992-1995) than before (Fig. 5a) except in 1993, where the effect of diminished chlorophyll concentrations on water transparency was compensated for by prolonged precipitation of calcite in April (GRIES 1995). Values were extremely low also in 1981 presumably due to a pronounced sedimentation event in May (H.-H. STABEL, pers. comm.). In autumn, no consistent temporal changes in water transparency were detected during the study period (Fig. 5c).

Annual chlorophyll concentrations and photosynthetic rates

Annual averages of chlorophyll concentrations exhibited a significant correlation with TP_{mix} during the entire study period only at the 10% level (p=0.08, r^2=0.24), so far (Fig. 6). The annual averages of chlorophyll concentrations in 1986-88 were significantly higher than during the following years.

Fitting a linear regression line versus TP_{mix} revealed a significant decrease of annual photosynthetic rates between 1980 and 1995 (r^2=0.44, p=0.01). During the first decade of the re-oligotrophication period, annual photosynthetic rates revealed no response to lowered phosphorus concentrations (Fig. 6; TILZER et al. 1991). However, in recent years, a significant drop in annual photosynthetic rates was observed (Fig. 6). Since 1992, the values varied around 220 $\pm$ 16 gC m^{-2} a^{-1}. Compared to the higher level of 288 $\pm$ 21 gC m^{-2} a^{-1} during the previous years, this was equivalent to a reduction of the annual photosynthetic rates by almost 25%. The results from 1996 indicated a further decline in annual photosynthetic rates which, however, has to be confirmed by further measurements. A decrease in annual photosynthetic rates was noticed only since that time, when depth-integrated photosynthetic rates in spring declined in addition to those in summer.

The relative contributions of the different phases, i.e., spring, summer, and autumn, to the annual total of photosynthetic rates (pr_{tot}) varied moderately during the study period (Fig. 7, Table 2). In particular, no significant linear relationship with TP_{mix} during the study period was observed.

Discussion

Restrictions of the present analysis

When interpreting the response of the phytoplankton community to re-oligotrophication as quantified in Table 1, the following restrictions and uncertainties have to be kept in mind. First, the subdivision of the growing period into three different phases allowed roughly to account for the seasonal changes of the factors controlling algal productivity and biomass. The definition of the end of summer and beginning of autumn was arbitrary to some extent, and may have contributed to the fact that almost no response to re-oligotrophication was observed in fall.
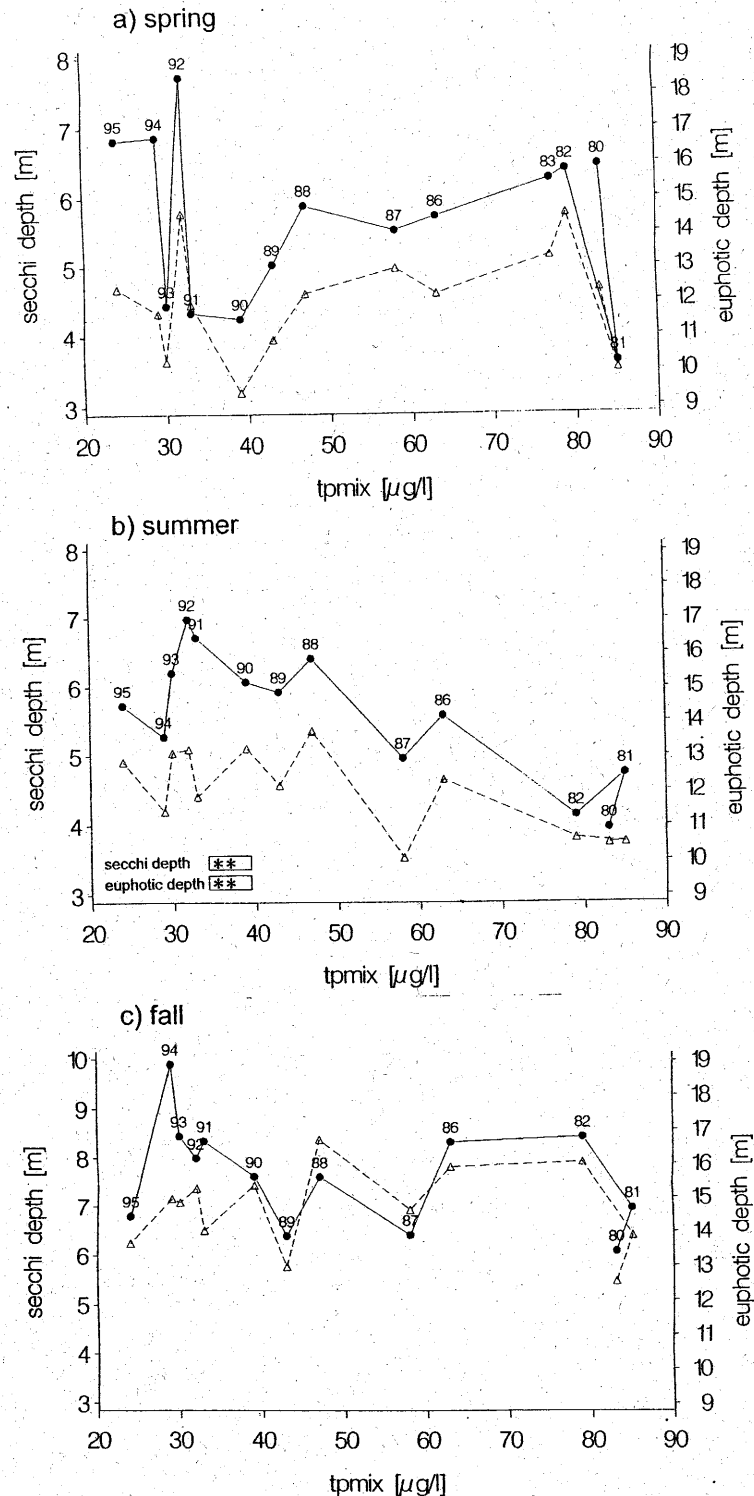
Fig. 5. Averages of Secchi depths (dots) and euphotic depths (triangles) in a) spring, b) summer, and c) fall versus TP_{mix}. Significance levels are marked as in Fig. 2. Please, note the differences in scale.

Secondly, simple linear regression models were used for the entire study period to establish potential responses of the phytoplankton community to decreases in TP_{mix} which was not appropriate in all cases. Thirdly, phytoplankton dynamics were not only controlled by nutrients, but to a large extent also by grazing (TILZER et al. 1991, GAEDKE & STRAILE 1994). In addition, weather conditions were likely to impose some variation on the response of the phytoplankton community to re-oligotrophication (GAEDKE et al. 1998).
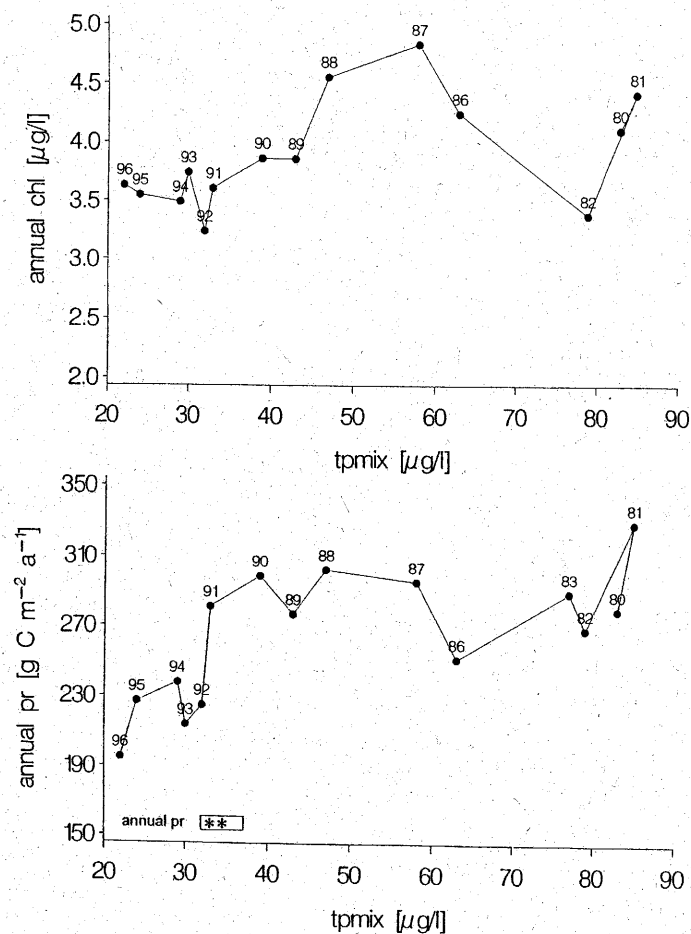
Fig. 6. Annual averages of chlorophyll concentrations (upper panel) in Lake Constance between 1980 and 1996 versus TP_{mix}. Values were calculated as temporal weighted averages of all observations during the respective years. Annual photosynthetic rates (lower panel) were calculated from mean daily photosynthetic rates per month, which were corrected for the average incoming irradiance during the respective months by Talling's Light Division Hours (for details see TILZER & BEESE 1988). Significance levels are marked as in Fig. 2.
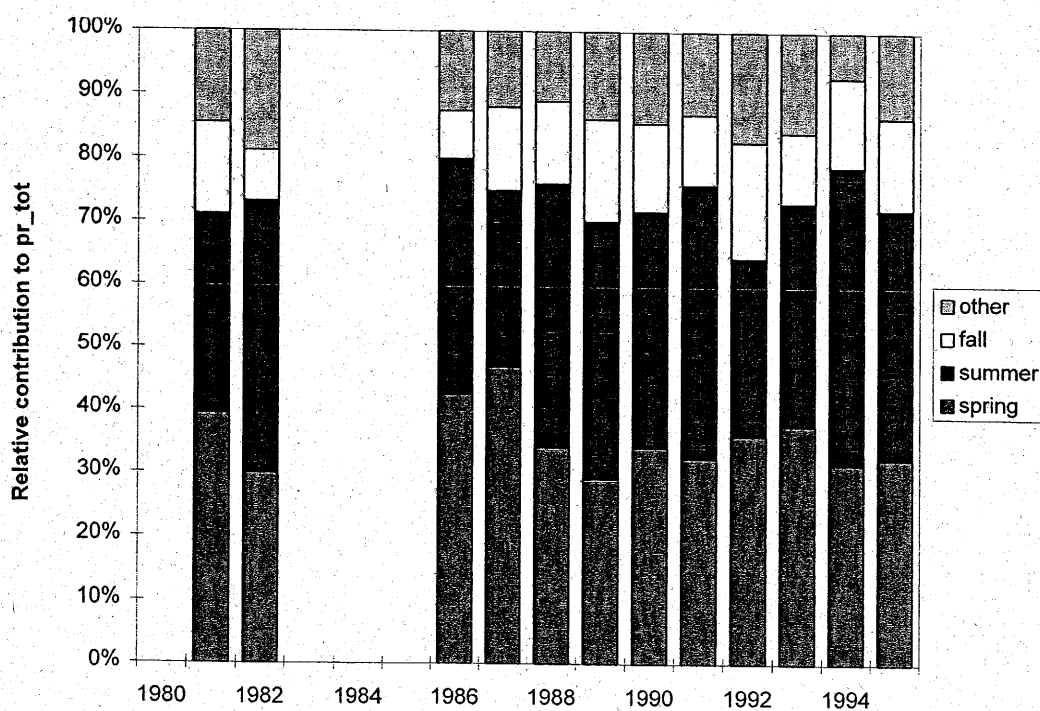

Fig. 7. The relative contributions of spring, summer, and fall to the annual total of photosynthetic rates, pr_{tot}, exhibited some variability, but no significant trends with TP_{mix} during 1981-95. Data from 1980 and 1983 were excluded since measurements did not cover the entire growing season during these years (Fig. 1).

Potential effects of decreasing phosphorus concentrations

Photosynthetic rates are sensitive to changes in nutrient supply in different fashions. On the cellular level, nutrient deficiency possibly directly affects the process of photosynthesis (e.g. TURPIN 1991). Indirect effects might result from decreasing cellular pigment contents which usually are found in algal cultures under both nitrogen and phosphorus limitation (e.g., TURPIN 1991, LATASA & BERDALET 1994). In the natural environment, photosynthetic rates per volume covary proportionally with the respective chlorophyll concentrations in the water (e.g. Fig. 4), the accumulation of which might be under nutrient control. In a stratified water column, the effects of reduced phosphorus concentrations on photosynthetic rates are expected to be much more pronounced in the upper part of the water column because photosynthesis in deeper water layers is limited by the availability of photons. In addition, the phytoplankton community may respond to changes in the nutrient regime by shifts in the taxonomic composition which, in turn, may lead to alterations of photosynthetic characteristics and pigmentation.

In Lake Constance, most of the variability observed in photosynthetic rates was due to variations in chlorophyll concentrations: Maximum (i.e. light-saturated) photosynthetic rates measured in situ close to the water surface varied by a factor of about 100 throughout the year. After normalizing photosynthetic rates to the respective chlorophyll concentrations, their variability was diminished to a factor of about 5, and further to a factor of about 2-3, when chlorophyll-specific values were corrected for temperature variations (TILZER et al. 1993, HÄSE 1996). The remaining variability was presumably attributable to variations in the taxonomic composition of phytoplankton and nutrient supply (TILZER 1989). According to nutrient enrichment bioassays conducted in 1990, the assimilation numbers of Lake Constance phytoplankton, i.e., the light-saturated chlorophyll-specific photosynthetic carbon uptake rates, were stimulated by phosphorus addition during summer (SCHWARZ 1991).

Observed response of the phytoplankton community to decreasing phosphorus concentrations

In the following, we summarize the main findings of the present study which will be discussed subsequently:

1. The seasonal cycle of phytoplankton growth was subdivided into characteristic phases which were different with respect to the main controlling factors and the taxonomic composition of phytoplankton. The relative contributions of these phases to the annual total of photosynthetic rates (pr_{tot}) did not change significantly with TP_{mix} during the study period and amounted in average to $36 \pm 5\%$ in spring, $38 \pm 6\%$ in summer, and $13 \pm 3\%$ in autumn (Table 2, Fig. 7).

2. In spring, chlorophyll concentrations were higher during intermediate years of the study period (1987-90) than during the early eighties and during recent years (Fig. 2a, Table 1). Depth-integrated photosynthetic rates in spring remained approximately at the same level between 1980 and 1991, and thereafter decreased by about 40% (Fig. 2a, Table 1).

3. In summer, maximum chlorophyll concentrations and maximum photosynthetic rates within the water column declined by at least 50% during the study period (Fig. 3b, Table 1). Depth-integrated chlorophyll concentrations in summer diminished proportionally with maximum chlorophyll concentrations by 50%, whereas depth-integrated photosynthetic rates declined by only 30% due to reduced self-shading within the water column (Figs. 2b, 3b, 4e, Table 1).

4. In autumn, no consistent long-term trends in chlorophyll concentrations and photosynthetic rates were observed during the study period (Fig. 2c, Table 1).

5. A marked decrease in annual photosynthetic rates became apparent only about 10 years after the onset of the decline in TP_{mix}. Between 1980 and 1996, TP_{mix} lessened by a factor of four, whereas the annual photosynthetic rates diminished only by 25%. By contrast, annual averages of chlorophyll concentrations revealed no consistent response to re-oligotrophication.

The observed increase in **spring** chlorophyll concentrations during the years 1987-1991 was coincident with taxonomic changes within the phytoplankton community and temporally associated with relatively low grazing pressure by herbivores: Unusual weather conditions in 1987 and 1988 enabled a sudden onset of autotrophic growth (Fig. 1; GAEDKE et al. 1998) that was presumably able to run away from the corresponding development of herbivores for a few weeks. That photosynthetic rates in spring did not intensify with rising chlorophyll concentrations during these years (Figs. 2a, 3a), we attribute mainly to the following two processes: First, with augmenting chlorophyll concentrations, self-shading within the water column increased (Fig. 4d) which was confirmed by decreases in water transparency (Fig. 5a). Secondly, in comparison to the early eighties, the phytoplankton community in spring presumably became dominated by less effective species during intermediate years of the study period (Table 1, Figs. 2a, 3a). This was consistent with taxonomic changes in the phytoplankton community: During the early eighties, small, fast-growing Cryptophyceae dominated the spring phytoplankton community (SOMMER 1987, GAEDKE 1998 and literature therein), whereas the relative share of diatoms and Chlorophyceae was lower than in subsequent years. Cryptophyceae are expected to yield high photosynthetic rates per unit chlorophyll due to the presence of phycobilisomes (A. POST, pers. comm.). Diatoms are known for low photosynthetic rates per unit of chlorophyll (S. WEILER, pers. comm.) and for Chlorophyceae as chlorophyll-rich algae (R. KÜMMERLIN, pers. comm.) we assume the same. To explain the observed decline in depth-integrated chlorophyll concentrations and photosynthetic rates during recent years, we suggest that both parameters got partially under nutrient control in spring. Since 1991, SRP in the uppermost water layer was depleted already during the last weeks of spring which had not occurred during the years before.

In **summer**, SRP-concentrations in the uppermost 8 m of the water column were consistently below 3 µg/l (GAEDKE 1998), which suggests that phytoplankton growth was phosphorus limited during the entire study period. Thus, chlorophyll concentrations responded from the outset to phosphorus reduction (Figs. 2b, 3b). Only maximum photosyn-

Table 2. Relative contributions of the different phases of the phytoplankton growing season to the annual total of photosynthetic rates (pr_{tot}). Given are the averages for the entire study period. Data from 1980 and 1983 were excluded since measurements did not cover the complete growing season during these years (Fig. 1).

Phase of the seasonal cycle	Relative contribution to pr_{tot}
spring	36 ± 5%
summer	38 ± 6%
autumn	13 ± 3%

thetic rates within the water column (i.e. at the light optimum) decreased proportionally with chlorophyll concentrations. The response of depth-integrated photosynthetic rates was dampened by reduced self-shading within the water column. This was confirmed by a significant increase in water transparency during the study period (Table 1, Fig. 5b). Another reason for the more pronounced decline in depth-integrated chlorophyll concentrations compared to depth-integrated photosynthetic rates in summer may be enhanced phosphorus recycling within the euphotic zone (GÜDE & GRIES 1998). This agrees well with taxonomic shifts in the phytoplankton community in summer as, e.g., the relative share of easily grazeable and mostly fast growing taxa rose during the period of re-oligotrophication (GAEDKE 1998). The relative increase of easily grazeable taxa may also partially be responsible for the observed deceleration in the decline of summer chlorophyll concentrations (Fig. 2b). It corresponds to findings of other studies where changes in the summer biomass of this fraction along a trophic gradient were much less pronounced than in the fraction of "inedible" taxa mainly due to grazing losses (WATSON & MCCAULEY 1988).

In **autumn**, the significance of the decreasing trend of maximum photosynthetic rates within the water column relied strongly on two relatively high values during the early eighties (Fig. 3c). As this was the only indication for a possible response to decreases in TP_{mix} in autumn, we assume that photosynthetic rates were hardly affected by the re-oligotrophication process, although phosphorus concentrations remained depleted for an increasing period within autumn during recent years.

The following calculations demonstrate that the combination of the respective decline of depth-integrated photosynthetic rates in spring and summer during the study period is sufficient to explain the observed time course in annual photosynthetic rates, including the time lag of about one decade. The decrease in photosynthetic rates ascertained in spring and summer (Table 1) was multiplied by the mean relative contribution of spring and summer to pr_{tot}, respectively (Table 2). Then the two fractions were added. Over the **entire** study period, a decrease in pr_{tot} by 26% results:

$$\Delta\, pr_{tot} = -\,(\,0.30 * 0.38 + 0.40 * 0.36\,) = -\,0.26\,.$$

The corresponding value for the **first decade** of the study period amounts only to 10% since the depth-integrated photosynthetic rates merely diminished in summer, and by not more than 25% (Fig. 2b):

$$\Delta\, pr_{tot} = -\,0.25 * 0.38 = -\,0.10.$$

The interannual variability in annual photosynthetic rates hardly allows to detect a decrease of 10% (Fig. 6). Finally, we are focusing on the effect of self-shading. In summer, reduced self-shading was most likely the main factor that caused the difference in the responses of depth-integrated photosynthetic rates and maximum photosynthetic rates within the water column. Let us assume for the moment that depth-integrated photosynthetic rates in summer declined at the same rate as maximum photosynthetic rates which decreased by almost 60% already during the first decade of the study period (Fig. 3b, Table 1). This would result in a reduction of pr_{tot} by 23% during the first decade of the re-oligotrophication period:

$$\Delta\, pr_{tot} = -\,0.60 * 0.38 = -\,0.23,$$

and by 37% during the entire study period:

$$\Delta\,pr_{tot} = -\,(\,0.60 * 0.38 + 0.40 * 0.36\,) = -\,0.37.$$

These values indicate that reduced self-shading in summer contributed considerably to the dampened response of annual photosynthetic rates to re-oligotrophication. A decrease of 23% in annual photosynthetic rates during the first decade of the study period would not have passed unnoticed.

Conclusions

By refining the temporal and vertical resolution, the main mechanisms responsible for the resilience in the phytoplankton response to re-oligotrophication based on annual averages could be identified in Lake Constance. The observed time lag and the dampened response of annual photosynthetic rates to phosphorus reduction are the cumulative result of the changes in depth-integrated photosynthetic rates occurring during the different phases of the year. Depth-integrated photosynthetic rates in spring became affected by phosphorus reduction only during recent years, whereas their response in summer was dampened by a factor of 2 due to lessened self-shading within the water column. By contrast, photosynthetic rates in autumn were not significantly influenced by the re-oligotrophication process during the study period.

Acknowledgements

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