

Functional and taxonomical properties of the phytoplankton community of large and deep Lake Constance: Interannual variability and response to re-oligotrophication (1979-1993)

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with 7 figures

Abstract: In large and deep Lake Constance, total phosphorus concentrations during winter mixing (TP_{mix}) were reduced by a factor of three (exceeding 80 to ca. 30 $\mu\text{g/l}$) from about 1979 to 1993. This resulted in an amplification and lengthening of phosphorus (P) -depleted conditions throughout the season and water column. The response of the phytoplankton community depended on the time of the year and the level of aggregation under consideration. Total phytoplankton biomass quantified in terms of algal biovolume or chlorophyll concentrations decreased in summer, i.e., during the period of most severe P-depletion, to about half of the original values during the first decade. In subsequent years, summer chlorophyll concentrations remained at this lower level, whereas total biovolume increased again despite further decreases of TP_{mix} . Average algal biomass in spring and autumn fluctuated without a distinct relationship to TP_{mix} although P was depleted below the detection level during parts of these time intervals in recent years. This moderate response by community level parameters is attributed to shifts in the temporal and internal organization of the algal community. Population dynamics and the relative importance of various taxonomical and functional groups such as mixotrophs and less-edible forms clearly changed in spring and summer. The renewed increase in algal biovolume in summer is mostly caused by species which are able to exploit additional P-sources. For example, *Dinobryon* is an evidently mixotrophic organism which ingests P-rich bacteria, its strongest competitors for soluble reactive phosphorus (SRP). *Ceratium hirundinella* might be migrating between the euphotic zone and deeper, P-enriched water layers under suitable hydrodynamical conditions. At the level of genera and higher taxa, consistent trends in respect to TP_{mix} were observed in spring and summer mostly indicating an adaptation to more oligotrophic conditions. In contrast, the functional group of well-edible algae showed little interannual variability and did not alter in absolute numbers. This suggests that, in contrast to less-edible algae, well-edible forms are more strongly under top-down than bottom-up control, and that the nutritional basis of most herbivores changed less than it would be expected from the decrease in total algal biomass.

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Introduction

The ongoing re-oligotrophication process in Lake Constance represents a large-scale experiment delivering valuable information on the regulation, adaptability, and resistance of the system which is hardly obtainable otherwise. Owing to comprehensive long-term measurements, it provides an excellent case study for understanding the response of a pelagic food web to changing nutrient conditions at different levels of organization. Long-term studies at one lake are more suitable to detect fine-grained and causal responses to an altering nutrient regime than cross-system comparisons because numerous potentially interfering factors remain more constant with time than across lakes. Phytoplankton is widely regarded as the plankton group most sensitive to nutrient changes. Evidence on the long-term development of autotrophic picoplankton (APP), primary production, zooplankton, and fish are provided by GAEDKE & WEISSE (1998), HÄSE et al. (1998), STRAILE & GELLER (1998), and ECKMANN & RÖSCH (1998), respectively.

The phytoplankton community of Lake Constance was studied in great detail during the height of eutrophication (1975-1981, total phosphorus during winter mixing (TP_{mix}) exceeding $80\mu\text{g/l}$) (SOMMER 1987 and lit. cited therein). During the first decade of decreasing P-concentrations, annual averages of bulk parameters such as chlorophyll concentration and primary production hardly responded (e.g., SAS 1989, TILZER et al. 1991). Further measurements, selection of potentially sensitive periods of time and water layers, and investigations at lower levels of aggregation changed this picture (e.g., KÜMMERLIN 1991, GAEDKE & SCHWEIZER 1993, SOMMER et al. 1993). Nutrient limitation of autotrophic growth is only expected in those water layers and time periods where it is not more severely constrained by other factors such as light and grazing. Hence, a spatially and temporally resolved analysis increases the sensitivity for identifying potential responses to nutrient reduction. From November to about March, large proportions (20-50% per day) of the algal cells residing in the uppermost 8 m of the water column are mixed down below 20 m in deep Lake Constance, i.e., below the euphotic zone, where they remain on average for a relatively long period of time (GAEDKE et al. 1998). This implies that light limitation is the dominant factor for growth control during the non-stratified period which will thus be excluded from the present analysis. Another interval where nutrient limitation is likely to be overruled by another factor is the clear-water phase when algal biomass is strongly depressed by severe grazing pressure (SOMMER 1987) which will also be disregarded. Considerations of seasonal and interannual changes in nutrient concentrations are based on the values found in the uppermost water layer (0-8 m) since light limitation is likely to occur at greater depths.

The role of nutrient depletion for growth limitation during spring and autumn varied presumably between species, during the process of re-oligotrophication, and interannually dependent on hydrodynamic conditions. In summer, low concentrations of soluble reactive phosphorus (SRP) prevailed in the upper 8 m throughout the period of investigation (Fig. 1; cf. GAEDKE & SCHWEIZER 1993, GÜDE et al. 1998). However, they provide only rough indications of P-limitation because not all components of the measured SRP are biologically available and species with low P-demands such as pennate diatoms and Chrysophyta only become limited at SRP-concentrations below the normal detection limit of $1\text{--}2\mu\text{g/l}$. Cellular carbon (C) to P ratios of phytoplankton and bacteria vary according to their nutrient supply. They provide a reliable indicator of P-limitation if values are above 52:1 $\mu\text{gC}/\mu\text{gP}$, presupposed that N:P ratios are above 20:1 $\mu\text{gN}/\mu\text{gP}$ (HEALEY & HENDREL 1980). Such C:P-ratios were

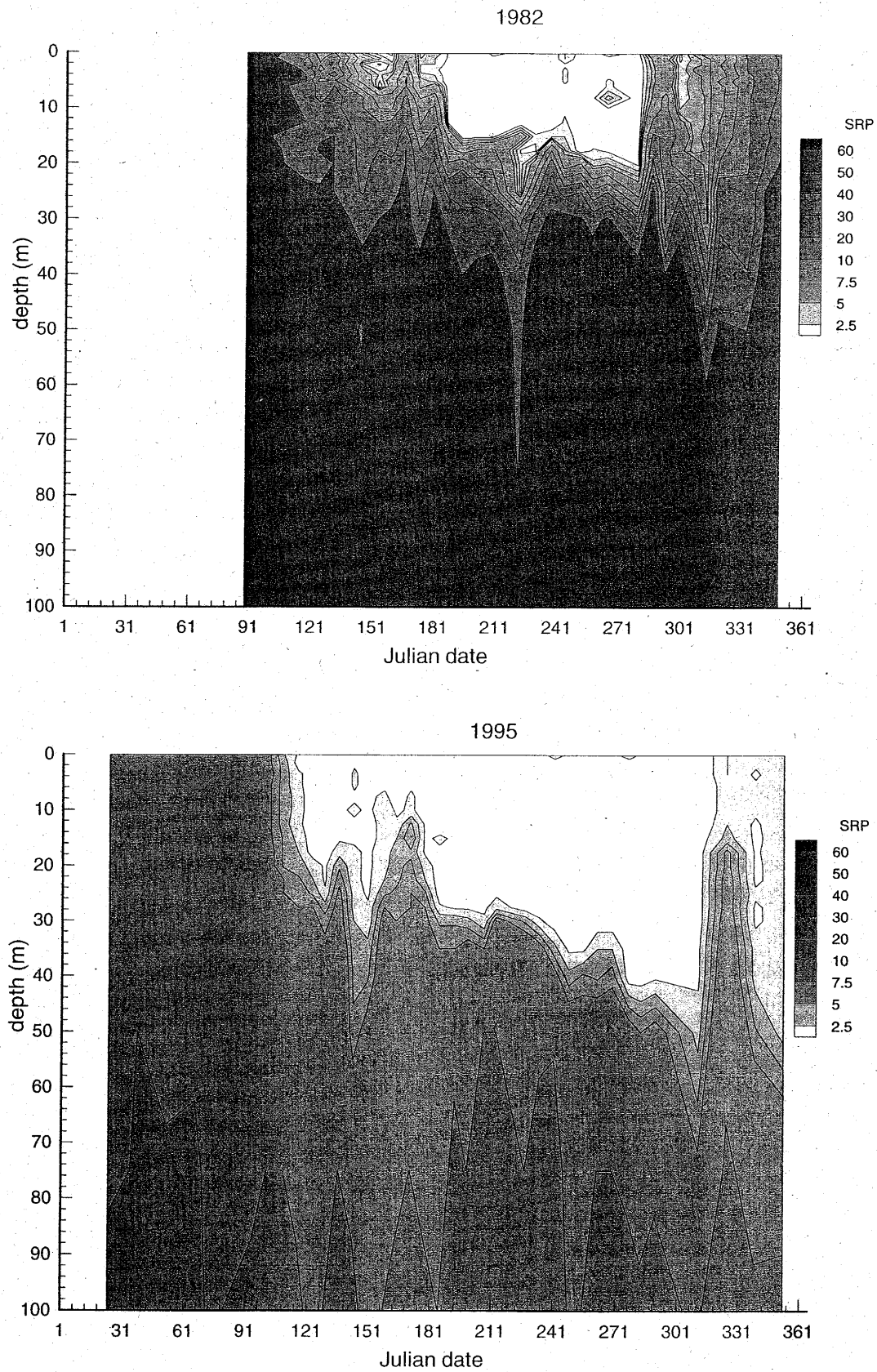


Fig. 1. Isopleths of SRP-concentrations in $\mu\text{gP/l}$ in Upper Lake Constance (Überlinger See) at the height of eutrophication (1982) (top) and after re-oligotrophication (1995) (bottom).

observed especially in the uppermost 8 m from May to November 1995 with an increasing trend until late summer (HOCHSTÄDTER 1997), i.e., a more or less pronounced P-limitation may be assumed for this time. For the summer period, this result is supported by nutrient enrichment bioassays (SCHWARZ 1991) and numerous previous studies on phytoplankton dynamics (e.g. SOMMER 1987). To account for these facts, spring, summer, and autumn are considered separately when investigating the response to nutrient changes.

The objectives of the present evaluations are to study the functional and taxonomical response of the phytoplankton community of Lake Constance to about fifteen years of re-oligotrophication characterized by a decline in TP_{mix} from more than 80 to about 30 $\mu\text{g/l}$, and to identify general mechanisms by which algal communities may respond to changing nutrient conditions (cf. GAEDKE 1998). The analysis is performed at different levels of aggregation: After consideration of the entire community, taxonomic groups are evaluated since related algal species often have similar physiological and functional properties (WATSON & MCCAULEY 1988, WATSON et al. 1997). Then, a bottom-up approach is used and all algal species are classified according to their ability to utilize bacteria as additional P-source (mixotrophy). Mixotrophy is increasingly recognized as a widespread phenomenon among phytoplankton species (SANDERS & PORTER 1988). Its quantitative importance exhibits a large temporal and cross-system variability even within species and apparently depends on numerous factors which are far from being understood (NYGAARD & TOBIESEN 1993). Finally, top-down aspects are considered and algal species are aggregated in respect to their edibility by zooplankton. The nutritional basis of different kinds of herbivores and the efficiency by which primary production is transferred to higher trophic levels depend on the edibility of the algal cells. It is, thus, of great importance for the overall food web structure and the pathways of energy flow. The edibility, in turn, influences also the grazing pressure to which algal species are potentially exposed. The biomass of herbivorous crustaceans did not exhibit a trend related to TP_{mix} during the study period (STRAILE & GELLER 1998). Hence, from 1979-1993, phytoplankton at Lake Constance was presumably subject to an approximately constant grazing pressure while P concentrations have been decreasing.

Study site, materials, and methods

Upper Lake Constance (in German: Bodensee) is a large and deep ($z_{max} = 253$ m, $z_{mean} = 101$ m), perialpine ($9^{\circ}18'E$, $47^{\circ}39'N$) lake of warm-monomictic character and approximately mesotrophic state on the northern fringe of the Alps (for details see GÜDE et al. 1998). Owing to its large size (472 km²) and mostly steep banks, Lake Constance has a relatively deep and well-mixed epilimnion and a true pelagic zone (for details see BÄUERLE et al. 1998).

Phytoplankton sampling was done weekly during the season (except 1981: every 2-3 days, 1987 on 2 consecutive days per week) and about biweekly in winter since 1979 at a central station ($z=147$ m) in the northwestern fjord-like arm of Upper Lake Constance (Überlinger See). No measurements are available for the second half of 1983. The phytoplankton community was assessed by enumerating all algal species using inverted microscopy by U. SOMMER (1979-1983), C. BRAUNWARTH (1984-1987), A. SCHWEIZER (1988-1990), J. FÜRST (1991-1993), and H. BINDER (1994-, first results became available during the revision of the paper). Great effort was made to get comparable results from all years. Analyses were conducted on the genus or a higher level of aggregation to maximize interannual comparability because the taxonomic resolution and microscopic equipment changed during the period of investigation. Cells smaller

than 3–4 μm in length were excluded from the present analysis since they were underestimated especially during the first years of investigation (for autotrophic picoplankton see GAEDKE & WEISSE 1998). The water column from the depth of 0–20 m was sampled with a 2 m long tube sampler ten times, and 2–4 integrated samples were counted. In accordance with numerous previous studies, average values of the uppermost 20 m are considered in the present investigation which roughly correspond to the euphotic zone (TILZER & BEESE 1988) omit if possible.

Vertical profiles of nutrient and chlorophyll concentrations were taken with about the same sampling frequency as phytoplankton (chlorophyll concentrations were not measured in 1979, 1984, and 1985, and some periods are now disregarded owing to potential errors in the nutrient analyses). SRP was determined with an automated molybdenum-blue method with ascorbic acid (Technician Auto-Analyzer II, Industrial Method No. 155-71 W). Soluble reactive silicate (SRSi) was measured by a standard molybdenum-blue method using oxalic acid to eliminate interference with SRP (Technician Auto-Analyzer II, Industrial Method No. 105-71 W). Chlorophyll *a* was assessed spectrophotometrically from hot ethanol extracts and corrected for phaeopigments by acidification (TILZER & BEESE 1988, TILZER et al. 1991, HÄSE et al. 1998).

All phytoplankton species were classified as either non-mixotrophic, potentially mixotrophic, or evidently mixotrophic (U. SOMMER, pers. comm; for details see MILANESI 1995). For species of the latter group, strong empirical evidence such as measurements of clearance rates exists for their mixotrophic capabilities. The classification of algal species into well-edible and less-edible was largely based on knowledge about the feeding behaviour of predominantly herbivorous crustaceans (e.g. KNISELY & GELLER 1986) since evidence from ciliates and rotifers is less available (MÜLLER et al. 1991). Typical representatives of well-edible species are small unicellular nanoplankters such as phytoflagellates, small centric diatoms (e.g. *Stephanodiscus parvus*), and *Chlorella*, whereas, e.g., large unicellulars, colonies, filaments (e.g. Cyanophyta), and pennate diatoms were classified as less-edible (for details see MILANESI 1995).

The relative contribution of individual groups of species to the total biovolume was first calculated for each sampling date and then averaged over the respective period of time, which gives equal weight to each sampling date. This technique delivers slightly different results than obtained by GAEDKE & SCHWEIZER (1993) and SOMMER et al. (1993) who first averaged the biovolumes over time and then calculated the relative share of individual groups.

The growing season was subdivided into three time intervals: spring, summer, and autumn (see introduction). The beginning of spring was taken as 15 March and the end of autumn as 15 November. The last date of the spring development prior to the clear-water phase, the onset of summer after the clear-water phase, and the beginning of autumn were chosen individually for each year according to the algal development and related parameters (for details see GAEDKE & SCHWEIZER 1993 and MILANESI 1995).

Results

Interannual and seasonal changes in epilimnetic nutrient depletion

For stratifying lakes, potential changes in inlake P-concentrations are most easily evaluated during winter mixing. However, in deep lakes such as Lake Constance, the vast majority of P

accumulates below the euphotic zone during stratification and is not available for primary production. Thus, measurements of TP and SRP throughout the season and water column provide better indicators for algal P-supply than concentrations during winter mixing. During the height of eutrophication in the late seventies and early eighties, hypolimnetic SRP-concentrations were far above 60 $\mu\text{g/l}$ throughout the year (Fig. 1, upper panel; GÜDE et al. 1998). Within the euphotic zone, SRP strongly decreased during the algal growing season. Values below 3 $\mu\text{g/l}$ occurred from about July to October in the uppermost 15 to 20 m (Fig. 1). They suggest P-limitation for numerous species if intracellular stores have been depleted. With ongoing re-oligotrophication, the temporal and spatial extent of SRP-depleted conditions has been amplified (Fig. 1, lower panel). Since the early nineties, hypolimnetic SRP-concentrations remained below 30 $\mu\text{g/l}$ year round. Epilimnetic SRP-concentrations dropped below 3 $\mu\text{g/l}$ as early as April and remained low until November or December. Additionally, the zone of severe P-depletion extended down to depths of 30 to 45 m in late summer. This implies that, firstly, in recent years low ambient nutrient concentrations prevailed already during the second part of the spring bloom and in early autumn. Secondly, nutrient imports during stratification from deep water have decreased since vertical P-gradients became less pronounced. This may have far-reaching consequences for the overall plankton community structure since, e.g., the relative P-uptake capabilities of bacteria and phytoplankton depend on the P-concentration and its spatio-temporal variability (ROTHHAUPT & GÜDE 1992, GÜDE & GRIES 1998).

Concentrations of soluble reactive silicate (SRSi) during winter mixing were on the order of 1300-1600 $\mu\text{g/l}$ and remained constant throughout the last decades (GAEDKE & SCHWEIZER 1993, and unpubl.) as they were hardly influenced by anthropogenic activities. Silicate limitation of diatom growth rates can safely be inferred from ambient SRSi-concentrations. During high summer, concentrations of SRSi below 300 $\mu\text{g/l}$ did occur in the uppermost part of the water column in all years of detailed investigations (1979, 1980, 1982, 1985, 1986, 1989-1995) which implies that diatom species with very high half-saturation constants such as *Synedra* (TILMAN et al. 1982) were likely to be silicate-limited during these periods. Concentrations below 150 $\mu\text{g/l}$ in the surface layer which may indicate silicate depletion for more diatom species (SAS 1989, WILLÉN 1991) were restricted to about one week in 1980, 1985, and 1995, and prevailed two or more partially non-consecutive weeks in 1979, 1980, 1986, 1989, 1990, 1991, and 1994. They were not found in 1992. Additionally, low SRSi-concentrations were observed in late spring 1986 and 1993. During all other years, silicate concentrations of at least several hundred $\mu\text{g/l}$ were measured throughout spring. To conclude, temporal reductions of individual diatom blooms by low ambient silicate concentrations in the uppermost water layers have presumably occurred. However, the small temporal and spatial extension of severe silicate depletion suggests that silicate was one of several factors determining the occurrence of diatoms throughout the growing season. No consistent trend in SRSi-concentrations was detectable during the re-oligotrophication process although diatom biovolumes changed considerably (see below).

Concentrations of nitrate were reliably assessed since 1989 (for longer time series measured in the main basin of Upper Lake Constance see GÜDE et al. (1998)). They varied little between years and were strongly anthropogenically enhanced (exceeding 1 mgN/l). During the growing season, a reduction of nitrate concentrations was observed in the upper water layer. However, minimum concentrations remained above 400 $\mu\text{gN/l}$ at all sampling dates and depths, well above the threshold commonly taken as indication for nitrogen limitation (ca. 150-300 $\mu\text{g/l}$) which was confirmed by nutrient enrichment bioassays (SCHWARZ 1991).

Interannual and seasonal changes in algal biomass

The average seasonal algal biomass (March, 15 to November, 15) as indicated by algal biovolume (fresh weight) and chlorophyll concentration decreased slightly from about 20 to approximately 13 cm³ biovolume/m², respectively 6 to 5 µg chlorophyll/l in the depth of 0-20 m during the period of re-oligotrophication (Fig. 2a). The high value of algal biovolume in 1992 originated from extended blooms in summer and autumn (see below). Fitting a straight line to the relationship between TP_{mix} and the average seasonal biovolume indicates a significant decline during re-oligotrophication ($p=0.03$, $r^2=0.42$; Spearman rank correlation coefficient: $r_s=0.62$, $p<0.05$) which, however, leaves a substantial part of the variance unexplained (Fig. 2a). The seasonal decrease in chlorophyll was not significant. A time-resolved analysis reveals that – as expected – a strong response occurred in summer, especially during the first decade (Fig. 2c). In summer, the average biovolume in the depth of 0-20 m decreased significantly from more than 30 to 16-23 cm³/m² ($p=0.006$, $r^2=0.59$; Spearman rank correlation coefficient: $r_s=0.73$, $p<0.01$; corresponding values for chlorophyll: $p=0.0001$, $r^2=0.82$). Average summer values of biovolume and chlorophyll declined to about 50% of the original level until the late eighties when TP_{mix} amounted to about 50 µg/l. Since then, chlorophyll concentrations remained almost constant with very little variability, whereas algal biovolume exhibited larger fluctuations and a renewed increase during recent years. In contrast, no distinct trends were visible in depth-integrated biovolume or chlorophyll concentrations during spring and autumn (Figs. 2b, 2d).

The seasonal course of the algal standing stock changed during the past 15 years (Fig. 3). During the height of eutrophication, maximum biovolumes in summer which occurred predominantly in July exceeded the spring bloom by a factor of 2 or more. During the mid-eighties, after a reduction of TP_{mix} by a factor of about two, summer blooms were approximately restricted to the spring level and weakened to even lower levels until 1990, i.e., when TP_{mix} had decreased by a factor of almost three. However, this rather oligotrophic pattern did not persist during the following years as higher biovolumes were observed again during summer. They were not reflected in corresponding increases of chlorophyll and primary production (Fig. 2c; HÄSE et al. 1998) and occurred about one month later than during maximum eutrophication. This caused an extension of the period with low biovolume between spring and summer in recent years (Figs. 1, 3; MILANESI 1995). Fitting a linear regression line to the monthly averaged biovolume in July versus TP_{mix} yielded a significant decrease by a factor of about 3, whereas no such relationship existed with averaged values in August. Adding a quadratic term to the regression equation improved the fit in July as the decrease was most pronounced during the first years and yielded a significant relationship in August. Average biovolume in August first diminished until the late eighties and re-enlarged afterwards (Figs. 1, 3).

Similarly, the maximum algal biomass at rather than on individual sampling dates and the temporal variability of biomass, which are also regarded as trophic indicators, consistently declined during summer until the late eighties, but exhibited higher values in the following years. The average of the 3 highest concentrations of biovolume measured within one year amounted to 51-82 cm³/m² in 1979-1984. Respective numbers were 27-40 for 1985-1990 and 41-57 in 1991-1993. To conclude, the unexpectedly fast change to an oligotrophic seasonal pattern of biomass development as it was observed during the first decade of lowered nutrient concentration (GAEDKE & SCHWEIZER 1993) did not persist during recent years despite further

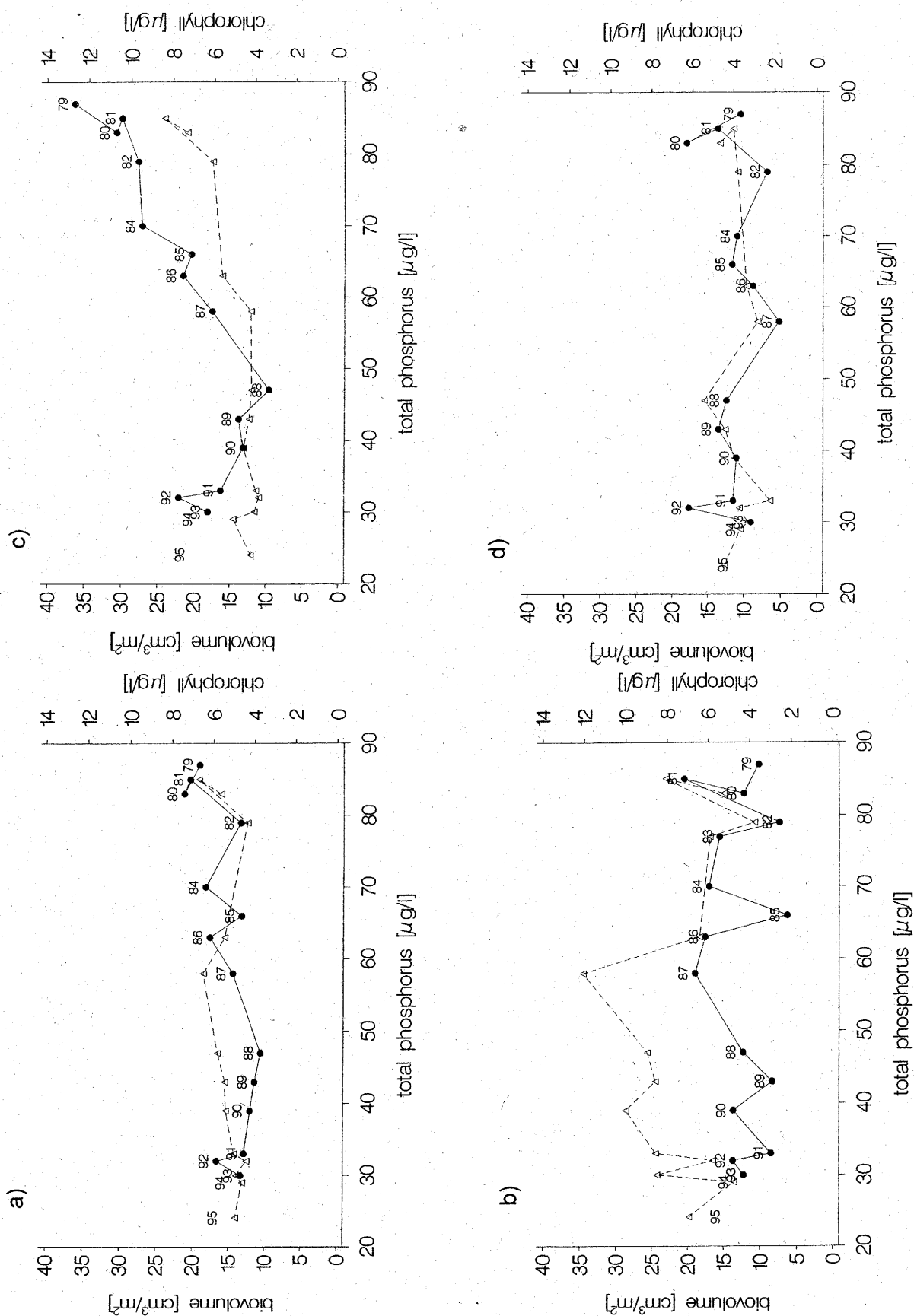


Fig. 2. Algal biovolume (full dots and full line) and chlorophyll concentrations (open triangles and broken line) in the uppermost 20 m of the water column in Upper Lake Constance (Überlinger See) averaged over a) the season (15.3. to 15.11.), b) spring, c) summer, and d) autumn in relation to total phosphorus concentrations during winter mixing. The latter decreased with time, i.e., the measurements at the left are the most recent ones.

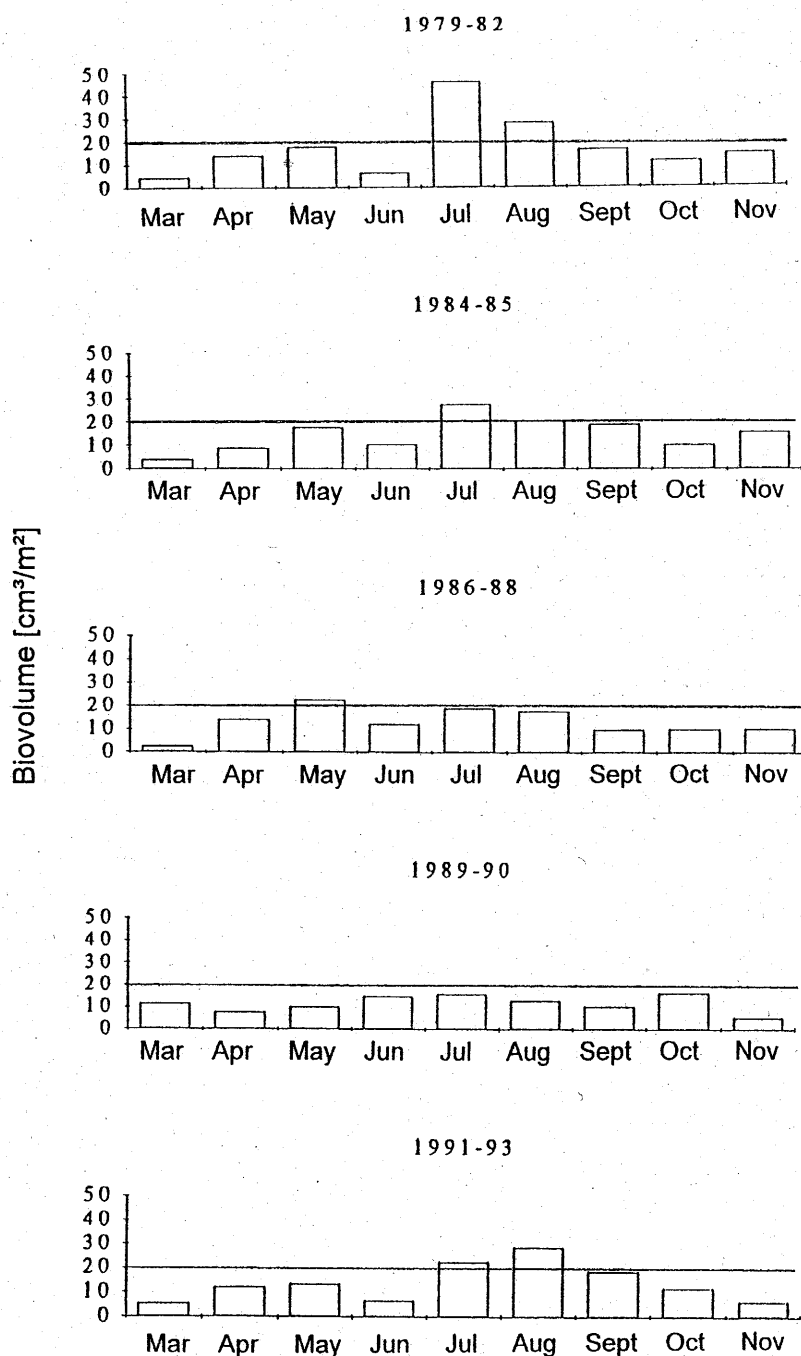


Fig. 3. Monthly averages of phytoplankton biovolume during different stages of the re-oligotrophication process.

reductions of TP_{mix} . Causal explanations of the reappearance of summer blooms demand a more detailed consideration of the taxonomical and functional phytoplankton composition which will be subsequently provided.

Interannual and seasonal variations in major taxonomical groups

Species composition changed greatly throughout the season which renders annual averages almost meaningless and demands the consideration of individual phases. (For the appearance and disappearance of species of quantitatively minor importance, see KÜMMERLIN & BÜRGI

(1989) and KÜMMERLIN (1998)). During spring, fast growing r-strategists such as *Rhodomonas* and *Cryptomonas* constituted a large portion during most years (Figs. 4a, 4b). Cryptophyta contributed 20-65% to the average spring biovolume. Their share was high during the most eutrophic years and in 1989 and 1990 which were characterized by exceptionally mild winters. In recent years, they made up about one third of the algal spring biovolume. *Cryptomonas* fluctuated widely without any trend. *Rhodomonas* decreased from very high levels (45-55% of total algal biomass) during the most eutrophic period to considerably lower values (around 10%) during the mid-eighties from which it increased in recent years contributing now almost 30% (Fig. 4b).

Diatoms, representing the other major group of the spring phytoplankton, exhibited the opposite trend with low values in the early eighties (ca. 30-45%) and higher ones (45-65%) during the following years (except for 1989/90). Important genera were *Stephanodiscus* (often small types such as *S. parvus*, but larger ones occurred as well) (Fig. 4c), *Asterionella* (until 1986) (Fig. 4d), *Fragilaria* (from 1984 onwards, but now probably declining) (Fig. 4e), *Synedra* (from 1982 onwards, less important since 1989) (Fig. 4f), and *Diatoma* (increasing, but still at a low level, up to 1, at most 3%) (Fig. 4g).

The last group which was occasionally quantitatively relevant in spring were Chlorophyta which contributed without a distinct trend 2-18% to the total biovolume. Important genera were *Chlamydomonas* (around 15% in 1980, 1987, and 1988) (Fig. 4h) and occasionally *Pandorina* (6-7% in 1984 and 1986) (Fig. 4i). At a very low absolute level (up to 1%), Chrysophyta clearly augmented owing to the larger abundance of *Dinobryon*. To conclude, some systematic changes in the taxonomic composition could be identified based on average spring values, but interannual variability was large for most genera.

In analogy to total algal biomass, the most pronounced changes in phytoplankton taxonomic composition occurred in summer. At the height of eutrophication, the average summer algal biomass was predominated by diatoms, constituting about 50% of the total community. The remaining fraction consisted mostly of Cryptophyta (15-30%), Dinophyta (7-25%), and Chlorophyta (5-20%). Cyanophyta were always of minor importance in Lake Constance except for some spatially and temporally restricted events. Their share of the average summer biovolume fluctuated between 1 and at most 10% without any trend. This stands in contrast to observations from many other eutrophied lakes.

During re-oligotrophication, diatoms lost their prevalence in summer and contributed regularly around 30% during recent years. *Stephanodiscus* strongly declined and was negligible since the late eighties (Fig. 5a). *Asterionella* decreased as well with large interannual fluctuations from less than 15 to roughly 3-7% (Fig. 5b). *Fragilaria* had its maximum development during the mid-eighties (up to 30%) and varied recently around 10% (Fig. 5c). The relative importance of *Diatoma* generally increased in summer (up to 5, maximum 13%), but some low values were observed in recent years (Fig. 5d). The share of *Synedra* varied between 0-1, at most 3%, without a consistent trend. In contrast to diatoms, Cryptophyta (dominated by *Cryptomonas*) revealed an increasing tendency in relative numbers (Figs. 5e, 5f) as did the Chrysophyta (maximum contribution: 17 and 19%). The latter augmented especially during the last years owing to the mixotrophic genus *Dinobryon* (Fig. 5g). The Dinophyta (dominated by *Ceratium hirundinella*) showed high values (above 20%) in 1979 at the height of eutrophication and in 1992/93 under more oligotrophic conditions, and lower values (ca. 5%) in between (Fig. 5h). Chlorophyta exhibited approximately the inverse trend (range 5-35%) since both relevant genera, *Pandorina* (Fig. 5i) and

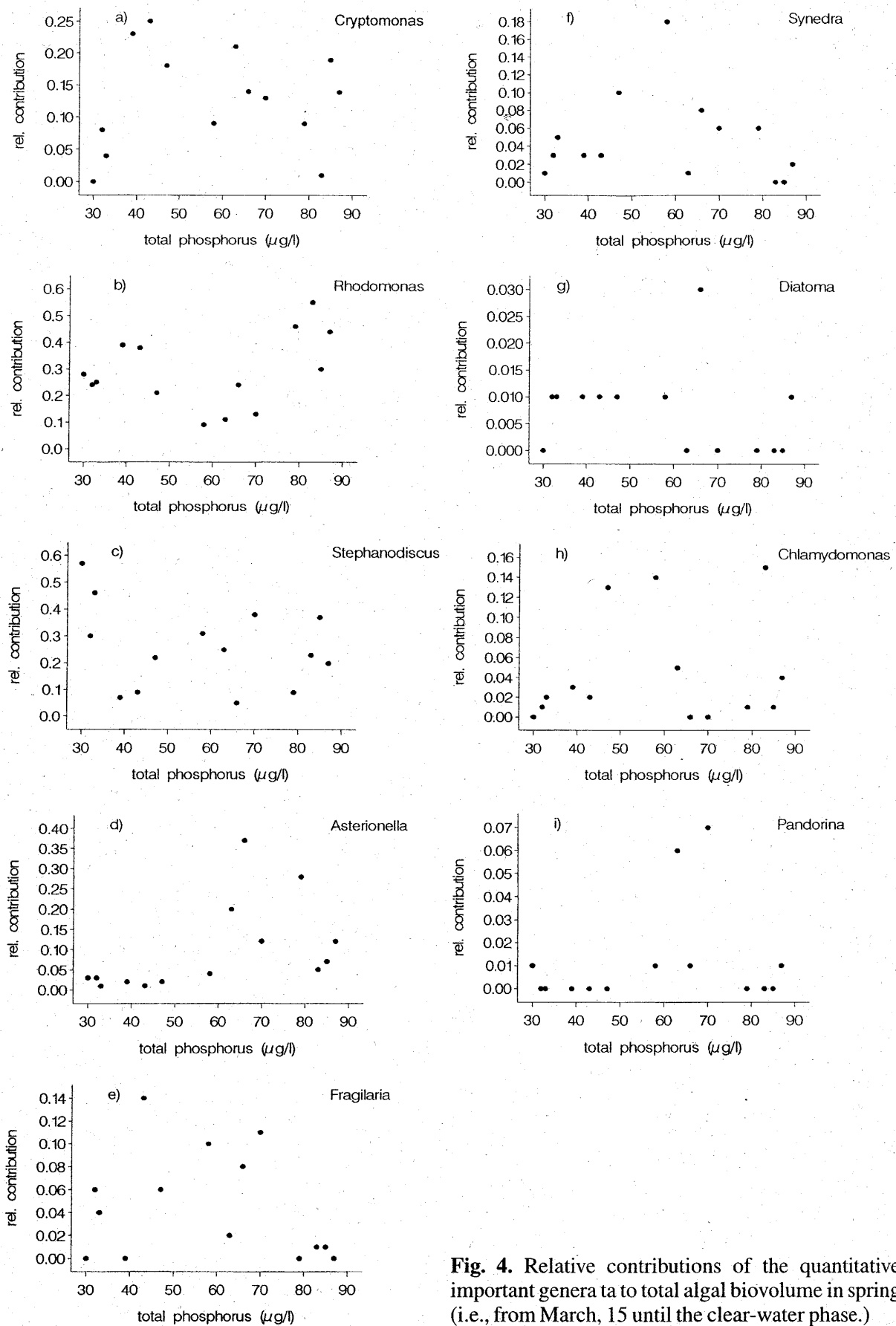


Fig. 4. Relative contributions of the quantitative important genera to total algal biovolume in spring (i.e., from March, 15 until the clear-water phase.)

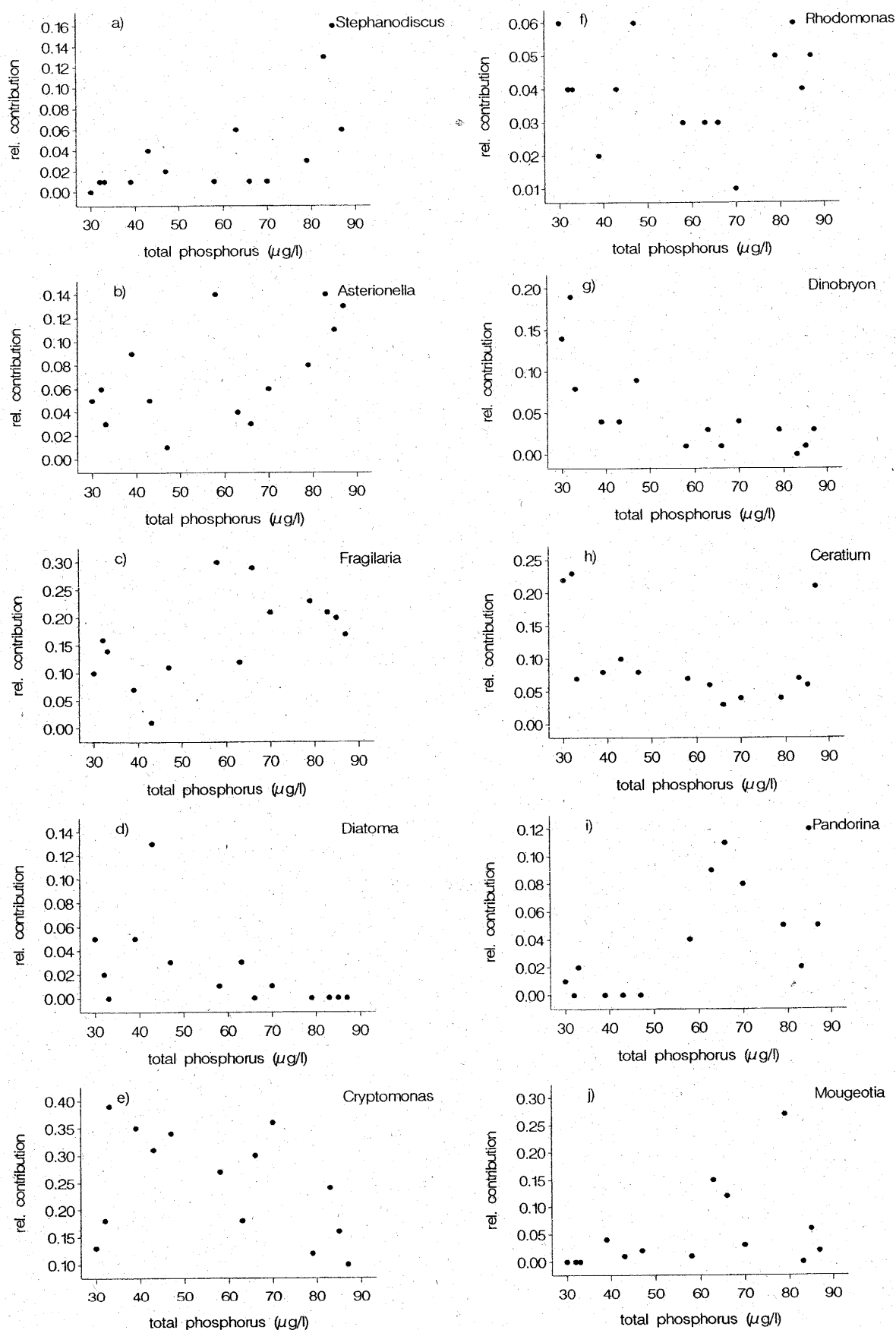


Fig. 5. Relative contributions of the quantitative important genera to total algal biovolume in summer (i.e., after the clear-water phase until the beginning of autumn, for details see text).

Mougeotia (Fig. 5j) declined after a relatively strong development in the early eighties to very low values since about 1988. The contribution of *Chlamydomonas* was low (generally 0-2%, in 1986: 7%).

Interannual and seasonal changes in major functional groups

In summer, the total biovolume of all potentially mixotrophic species remained constant during re-oligotrophication in contrast to the overall reduction of algal biomass. This implies a significant increase in the relative share of potentially mixotrophs with decreasing TP_{mix} ($r_s = -0.77$ $p < 0.001$). No such relationships were observed in spring or autumn. The evident mixotrophs showed a pronounced increase in absolute values which was significant in spring, summer, and autumn. During the last years, evidently mixotrophic species contributed 20-45% to total algal biovolume in summer (Fig. 6). They were responsible to a large extent for the unusually high biomass in summer 1992.

In spring, well-edible forms clearly dominated except for some years (i.e., 1983, 1984, 1986, and 1987) (Fig. 7a) when higher numbers of pennate diatoms occurred. During summer, a very constant amount of well-edible algae was recorded throughout the entire period of investigation, i.e., their relative share grew during re-oligotrophication (Fig. 7b). The variability of algal biovolume in summer was exclusively caused by less-edible forms. A similar pattern prevailed in autumn except for 1992 where both fractions were much higher than in other years (Fig. 7c).

Discussion

Some of the processes observed during the first decade of re-oligotrophication (GAEDKE & SCHWEIZER 1993, SOMMER et al. 1993), during which TP_{mix} was reduced from almost 90 to 42 $\mu\text{g/l}$, continued during recent years (TP_{mix} around 30 $\mu\text{g/l}$) whereas others did not. This illustrates once again that inference obtained from time series of eleven years (which is commonly regarded as long in plankton ecology!) may be subject to fluctuations caused by other factors. However, the present data suggest and future ones may prove that also some previously unexperienced phenomena appeared during the last years. The most striking event was the re-appearance of pronounced algal summer blooms in 1991-1993 (and also in 1994-1997) which resulted in higher average algal biovolumes, higher temporal variability, and higher maximum values than in the late eighties. However, these summer blooms differed in several respects from those observed at the height of eutrophication. They occurred later in the year (Fig. 3; MILANESI 1995) and had a different taxonomic composition and lower ratios between chlorophyll resp. photosynthetic activity and biovolume (Fig. 2c; cf. HÄSE et al. 1998). According to the PEG-model (SOMMER et al. 1986), a disappearance of summer blooms is to be expected during re-oligotrophication. However, the shift of seasonal patterns observed during the first decade of re-oligotrophication (Fig. 3) was unexpectedly fast as TP_{mix} decreased only by a factor of 2-3 during this period. This may challenge the idea that it was solely attributable to lower nutrient concentrations. Hence, it remains a matter of discussion whether or not to regard the recent reappearance of summer blooms as contradiction to the PEG-model. They now occur during the period of most severe P-depletion as judged by algal C:P-ratios (HOCHSTÄDTER 1997) and SRP-measurements (Fig. 1).

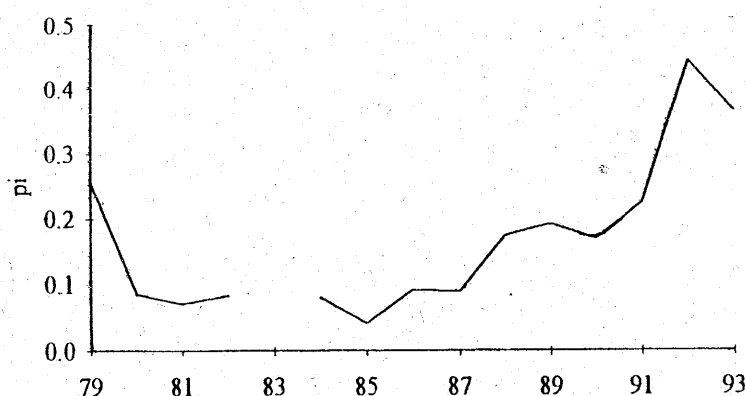


Fig. 6. Relative contribution of evidently mixotrophic species, p_i , to the total phytoplankton biovolume during summer.

A high temporal resolution enables to detect fine grained changes of the temporal organization of the community. However, the impact of the variability introduced by sampling and counting errors and other factors such as weather conditions increases with rising temporal resolution. The subdivision of the annual cycle into three periods was found to represent an efficient compromise between responsiveness and unexplained fluctuations, but it is too coarse for a detailed comparison of the results with the PEG-model (SOMMER et al. 1986). The present analysis focused on the potential effects of decreasing nutrient conditions. The presumably important impact of physical factors was partially accounted for by adjusting some of the starting and ending dates of the different seasonal periods according to the actual development. The frequently large variability may in parts be attributable to physical factors. Improvements may be made by replacing the rather arbitrary fixed onset of spring (15 March) and the end of autumn (15 November) by suitable dates according to the actual seasonal development especially of water column stability which may differ interannually by several weeks (GAEDKE et al. 1998).

During the period of investigation (1979-1993), nutrient conditions and large-scale weather patterns in winter covaried to some extent (GAEDKE et al. 1998). Winters were on average somewhat milder and the onset of algal growth often occurred earlier during recent, more oligotrophic years than at the beginning of the study period. Algal development responded quickly to reduced vertical mixing in March and April, but showed no correlation with weather conditions later in the season (GAEDKE et al. 1998). In contrast, daphnid biomass reacted sensitively to minimum winter temperatures throughout spring and summer (GAEDKE et al. 1998). Since daphnids are keystone species for the plankton community of Lake Constance (e.g. GAEDKE & STRAILE 1998), it cannot be ruled out that changes in the frequency of distinct weather types directly or indirectly influence phytoplankton dynamics and species composition in summer and that trends potentially linked to the re-oligotrophication process were affected by weather conditions. This difficult question can be tackled when further observations from colder years under relatively oligotrophic conditions become available (e.g. 1994-1997), and when the interplay between hydrodynamic processes and algal taxonomic composition is better understood.

The low average biovolume in summer 1988 can be partially explained by the omission of cells with degenerated chloroplasts which were to some extent included into the analysis during other years. However, this does not affect the general trend of the recent increase in algal biovolume during mid-summer. The underestimation was likely to be on the order of ten(s) of percent (inferred from long-term measurements of chlorophyll to biovolume ratios and the

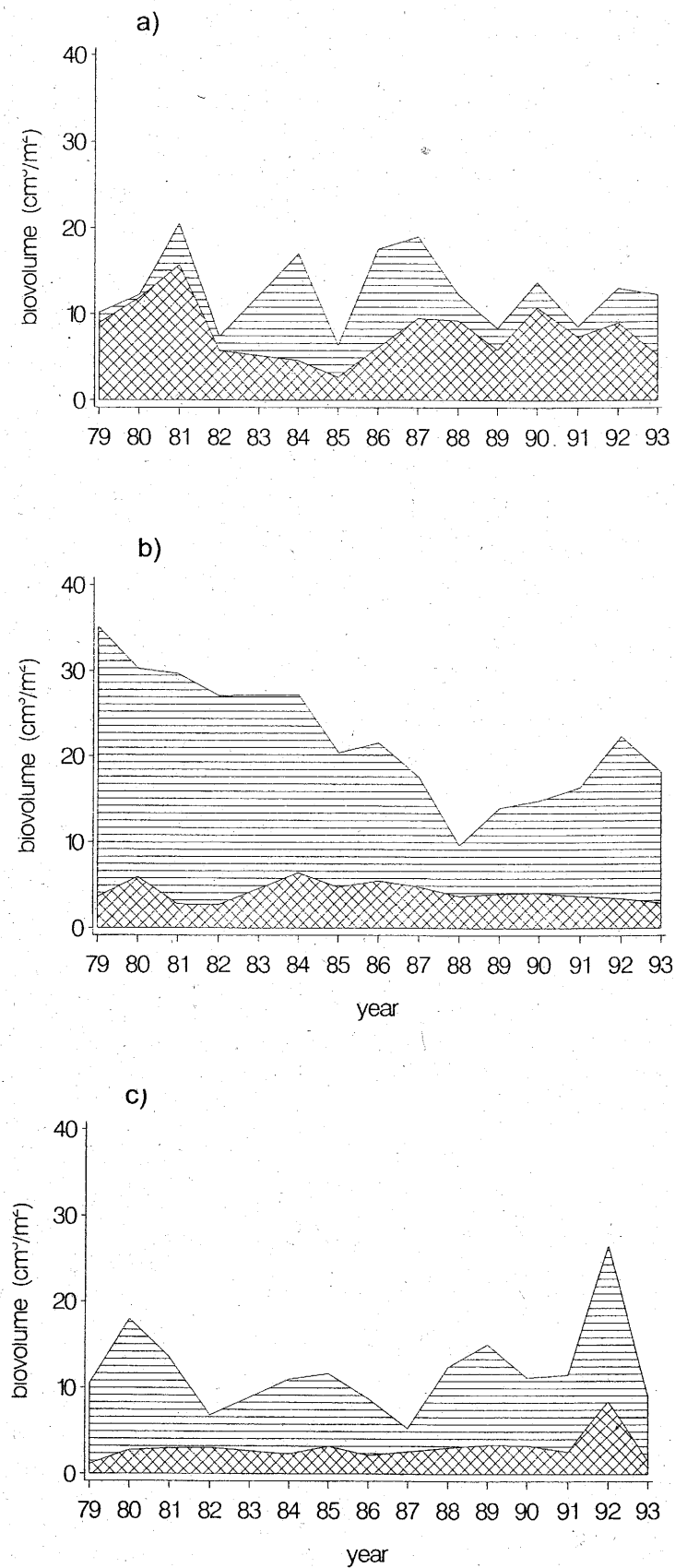


Fig. 7. Biovolume of well-edible (cross hatched) and less-edible (hatched) algae in a) spring, b) summer, and c) autumn.

ratios between cells with fully developed and degenerated chloroplasts observed during subsequent years). In 1991, a brief, but pronounced summer bloom of *Fragilaria* occurred. In 1992 and 1993, besides pennate diatoms, *Dinobryon* and *Ceratium* had mass developments. Abundances of *Dinobryon* were lower in 1994 and 1995, but of similar magnitude in 1996 (HENRICHS 1997, other species not yet analysed). *Ceratium hirundinella* and some related species are regarded as capable of migrating into deep, nutrient-rich water layers and back into the euphotic zone if turbulence is sufficiently small (FREMPONG 1984, KOIZUMI et al. 1996, STRAUSS 1996). Thus, their development is thought to depend on water column stability. However, further investigations including empirical studies and hydrodynamic modelling are required in order to show that this strategy is also applicable to large and deep Lake Constance where turbulence may be relatively high and P-depletion now extends down to depths of 30-40 m (Fig. 1). Alternatively, *Ceratium* might reach the sediment surface in the littoral zone which is considered as a potential P-source in summer (GÜDE & GRIES 1998). In summer, the relative importance of evidently mixotrophic species steadily augmented from the late eighties onwards (Fig. 6). However, in its beginning, this increase was not fast enough to compensate a pronounced decrease of other species which led to a temporal minimum in summer biomass during the late eighties.

The mass occurrence of an evidently mixotrophic genus, *Dinobryon*, which was only present in small quantities before, represented an interesting process for the entire nutrient cycle. Phagotrophy of bacteria can provide an additional P-source for autotrophs under P-depleted conditions (SANDERS & PORTER 1988, NYGAARD & TOBIESEN 1993). In high summer, C:P-ratios of bacteria were 4-5 times lower than those of the phytoplankton (HOCHSTÄDTER 1997). This entails that a relatively low weight-specific ingestion rate (in terms of carbon) can improve the P-supply of the predator considerably. Measurements of ingestion rates of *Dinobryon* conducted in 1996 support this point of view for Lake Constance (HENRICHS 1997). From an ecosystem perspective, predation of bacteria by phytoplankton implies that algae prey upon their most powerful competitors for nutrients and, thus, make use of the extremely efficient P-uptake capabilities of their prey at low nutrient concentrations. Model results on energy and nutrient cycling in the pelagic food web of Lake Constance (GAEDKE & STRAILE 1994, STRAILE 1995, 1998, HOCHSTÄDTER 1997) suggested that the mass occurrence of *Dinobryon* has far-reaching consequences for the overall nutrient cycle when the upper range of literature values for bacterial uptake rates (CARON et al. 1993) was supposed. However, for Lake Constance, mostly lower values were found (HENRICHS 1997). Comparisons between potential uptake rates of bacteria by *Dinobryon* and bacterial production indicate that *Dinobryon* may have exerted a pronounced grazing pressure during its recent blooms (MILANESI 1995, HENRICHS 1997). Assuming that vertical migration and mixotrophy provide additional P-sources for phytoplankton delivers an explanation for the observation that algal biomass in summer did not further decline, but rather increased despite further reductions of TP_{mix} and summer SRP-concentrations.

The responses established for most other functional and taxonomic groups during the first decade of reduced nutrient concentrations (GAEDKE & SCHWEIZER 1993, SOMMER et al. 1993) persisted during the following years, but some new trends were revealed as well. One may expect that the decreasing P-supply combined with unaltered concentrations of SRSi favoured diatom growth. In spring (but not in summer, see below), this effect was already observed after a few years of declining P-concentrations. Since then, diatoms have contributed around 50-60% to the total spring biovolume (except for 1989/1990 which were characterized by ex-

tremely mild winters and highest minimum winter water temperatures on record) without any further enhancement. *Stephanodiscus* provided a highly variable fraction to the total biovolume in spring which reached up to 50%. However, the pennate diatoms *Asterionella* and *Fragilaria* decreased in recent years from their mid-eighties level. This effect was not compensated by the slight concurrent increase of *Diatoma*. These diatom genera were known to vary in their competitive ability under different Si:P-ratios (e.g., TILMAN et al. 1982, SOMMER 1989). Constant concentrations of SRSi combined with falling P-concentrations caused an increasing Si:P-ratio (at least during homothermy) which gives rise to expectations of a gradual replacement of certain diatom species (i.e., *Stephanodiscus minutus* → *Diatoma elongatum* → *Fragilaria crotonensis* → *Asterionella formosa* → *Synedra filiformis*) (*S. minutus* is a synonym to *S. medius*, KRAMMER & LANGE-BERTALOT 1991). According to laboratory studies and other field observations, the large share of *Stephanodiscus* in spring and its rapid disappearance in summer indicate that P-depletion was on average not very pronounced in spring, but in summer. The reduction of centric diatoms in favour of, e.g. *Fragilaria*, under increasing Si:P-ratios fits well with experimental studies on nutrient physiology (summarized in SOMMER 1989). Considering the occurrence of individual pennate genera, however, field and laboratory studies agree less well. The observed temporal shift in the maximum development of individual species of pennate diatoms during re-oligotrophication points to a higher competitive ability of *Diatoma* and *Fragilaria* at increasing Si:P-ratios in spring and summer than it is expected from nutrient ratio experiments. The frequently high scatter in the data of the relative share of individual genera complicates such conclusions and suggests that other factors such as weather conditions and related hydrodynamical processes may have a large impact on species composition as well (see spring 1989/1990) and require further attention.

The absolute and relative amount of diatoms in summer diminished with decreasing P-concentrations despite increasing Si:P-ratios during winter mixing. It was hypothesized that enhanced spring growth of diatoms reduced silicate concentrations to such an extent that a more severe silicate limitation occurred in summer preventing further diatom growth (SOMMER et al. 1993). The argumentation was mostly based on decreasing SRSi-concentrations in summer during the late eighties. A careful re-evaluation of the quality of the measurements led to the exclusion of two years of SRSi-measurements (1987 and 1988) owing, e.g., to inconsistencies between individual profiles. Including most recent data, no trend was found in the SRSi-concentrations in the uppermost water layer during the vegetational period versus TP_{mix} . Hence, this potential mechanism of diatom growth control is no longer supported by the data. Individual diatom blooms were likely to be silicate-limited, but the overall halving of diatom occurrence throughout summer appears hardly explicable by this factor. This idea was corroborated by nutrient enrichment assays conducted from June to November 1990 which revealed hardly any silicon deficiency of diatom growth (SCHWARZ 1991). Lesser diatom growth in summer did not yield consistently higher SRSi-concentrations in surface waters. An alternative reason for reduced diatom growth might be that some diatom species may be more susceptible than other phytoplankton to high pH-values as they occurred in Lake Constance (pH 8.8 and higher). However, average and maximum pH-values in summer decreased during re-oligotrophication (GAEDKE, unpubl.) which is in accordance with measurements of lower primary production (HASE et al. 1998). Thus, the reason for the diminished share of diatoms in summer remains an open question. However, considering the average contribution of diatoms to total algal biovolume found in 91 temperate lakes differing greatly in size and trophic state

(TP in summer 3-1000 $\mu\text{g/l}$, WATSON et al. 1997) indicates that the share of diatoms observed in Lake Constance in recent years was only somewhat higher than in other systems with comparable trophic conditions. The contribution of diatoms found at maximum eutrophication was twice as high as the average value established by WATSON et al. (1997). Hence, the phytoplankton composition in Lake Constance exhibited some peculiarities such as a high fraction of diatoms and also Chlorophyta and a low one of Cyanophyta as compared to the average of a large number of small and large temperate lakes. We will further study the potential role of vertical mixing on the taxonomic composition.

The entirely dissimilar behaviour of well- and less-edible phytoplankton species during re-oligotrophication (Fig. 7) indicates that these different functional components were regulated in different ways. A strong bottom-up effect was visible for the less-edible forms especially during the first decade until mixotrophic species, which were mostly classified as less-edible, gained in importance. The reduction of blooms of less-edible algae in summer may imply lower sedimentation rates. In contrast, the higher share of diatoms in spring presumably intensified sedimentation during this period. The surprisingly small variability of the amount of well-edible and generally fast growing algae in summer suggests that they were predominantly top-down controlled, and that the nutritional basis of herbivores altered less than it is referred from the changes observed in total biovolume or chlorophyll concentrations. This hypothesis is supported by measurements of primary production which showed only a delayed, moderate reduction by about 25% in summer (HÄSE et al. 1998). It is also in accordance with corresponding long-term studies of the crustacean and rotifer community which revealed only little response to re-oligotrophication during the study period (STRAILE & GELLER 1998, STRAILE, pers. comm.). The interplay between the responses of algal biovolume and species compositions and of the other components of the pelagic food web to changing nutrient conditions was discussed in detail by GAEDKE (1998) and will not be repeated here.

For eutrophic Lake Arendsee, it became likewise apparent that net phytoplankton was more strongly bottom-up than top-down controlled (TITTEL 1997). Comparing lakes of very different trophic status, WATSON & MCCAULEY (1988) found that the biomass of "inedible" net phytoplankton increased more strongly with summer TP than that of "edible" nanophytoplankton (smaller than 35 μm). This was attributed to different susceptibility to grazing since the production of both fractions rose with TP in a similar way. The latter implies that the production to biomass ratio of nanoplankton augmented with trophy whereas that of netplankton did not, which contradicts the idea that net phytoplankton gained direct competitive advantages from a nutrient increase.

No relationship was found between TP_{mix} and the average algal biomass in spring and autumn. During the height of eutrophication and incipient recovery, P-depletion during spring and autumn never exceeded the point where P-limitation of major species is to be expected (SOMMER 1987, SAS 1989, GAEDKE & SCHWEIZER 1993). Up to now, the first part of the spring development was clearly controlled by an insufficient average light climate owing to frequently intensive vertical mixing (GAEDKE et al. 1998). During its second part when mixing below 20 m ceased, grazing pressure by herbivores was presumably of major importance throughout the study period since the community was still dominated by well-edible forms. Additionally, since about 1991, a reduction of SRP-concentrations below 3 $\mu\text{g/l}$ soon after the onset of the first pronounced algal growth (Fig. 1) suggests that nutrient limitation may play an increasing role during (late) spring. The marked depletion of SRP in late spring 1995 was moderately reflected by somewhat augmenting C:P-ratios of the phytoplankton (HOCHSTÄDTER 1997). Potential

responses of the algal community to changing nutrient conditions in spring and autumn may become better identifiable when time intervals dominated by low water column stability can be separated from others throughout the study period (cf. GAEDKE et al. 1998).

Long-term limnological investigations are also available for the main basin of Upper Lake Constance (cf., e.g., GÜDE et al. 1998, KÜMMERLIN 1998). The major sampling site at maximum depth ($z_{\max} = 253$ m) is about 40 km to the east from our sampling site in the Überlinger See. Differences in hydrodynamical conditions and fish abundances repeatedly gave rise to expectations of site-specific variations in other biological parameters. A comparison of the long-term data records from both sites on chemical and basic biological parameters revealed unexpectedly little systematic deviation between both parts of the lake which were consistent for substantial periods of time (SCHRÖDER 1994). Epilimnetic SRP-concentrations might be slightly higher in the Überlinger See. Differences of nitrate and silicate concentrations were within the range of uncertainty introduced by methodological differences (i.e., about 10% for silicate). Only during one (1986) out of eleven years of investigation, significantly deviating chlorophyll concentrations occurred (at least 11% higher in the Überlinger See), whereas GROSSART (1995) found no significant variations in chlorophyll concentrations within the Überlinger See and the adjacent main basin of Upper Lake Constance throughout 1993. His maximum deviations of mean concentrations within the euphotic zone were 1 µg/l between individual sampling stations. In some instances, a horizontal gradient of crustacean abundances was observed (SCHRÖDER 1994).

A comparison of the annual algal biovolumes obtained for the different sampling locations and by different institutions from 1979 onwards reveals comparable absolute values for most years and roughly decreasing overall trends in all data sets (cf., KÜMMERLIN 1998, STABEL & KLEINER 1995). The relative reduction of the seasonally averaged biovolume observed in this study (Fig. 2a) was similar to that of annual chlorophyll concentrations and photosynthetic activity (HÄSE et al. 1998) and to that of the annual biovolume recorded for the main basin of Upper Lake Constance (1976-81: ca. 25 cm³/m², but 13 cm³/m² in 1975 and 1982; 1991-93: 13 cm³/m², and some high values in between; KÜMMERLIN 1998, his Fig. 1). Data from the main basin of Upper Lake Constance exhibited a higher variability which may be related to the lower sampling frequency. Relatively high values were observed in 1988 and 1989 (cf. discussion in KÜMMERLIN 1998) which stands in contrast to our rather low values (see above). Annual averages of the algal biovolume measured by the Zweckverband Bodenseewasserversorgung at the same sampling location in the Überlinger See, but with a lower vertical and temporal resolution (biweekly in summer, every 3-4 weeks in winter, one integrated sample from 0-20 m) indicated for 1988 similar results as in the previous and following years (STABEL & KLEINER 1995). Annual averages were high for the years 1980 and 1981 and lower subsequently until 1993. In absolute values, they may be somewhat higher than those of the present data set. Chlorophyll concentrations were very similar in 1988 in the Überlinger See and the main basin of Upper Lake Constance except for a short, but very pronounced spring peak which took place in the Überlinger See (sampling frequency twice a week), but was not found in the main basin (sampling interval approximately one month during that period) (SCHRÖDER 1994).

Spatial heterogeneity in biovolumes may originate from deviations of the hydrodynamic, chemical, and biological conditions, but also from differences of the methodologies. For example, the average cell volumes assumed for individual taxa and other details of the counting techniques were consistent within each long-term data record, but varied partially between them. Furthermore, the threshold applied for the inclusion or exclusion of decaying cells with

strongly reduced chloroplasts may differ as it is difficult to define it objectively. Presumably more importantly, the different sampling frequencies caused deviations especially for individual years of investigation. To conclude, an overall decreasing trend of annual algal biovolume (and chlorophyll concentration) was ascertained in both parts of the lake by three independent studies, but fine-scale patterns differed. Changes in species composition and invasion or disappearance of species were observed largely simultaneously at both sampling locations (KÜMMERLIN & GAEDKE, in prep.). Little differences in taxonomic composition between sites were also obtained for planktonic ciliates (SCHWEIZER 1994).

Regression models between phytoplankton biomass and P-concentrations (e.g., DILLON & RIGLER 1974, OECD 1982, WATSON & MCCAULEY 1988, WATSON et al. 1997) were typically based on numerous different lakes and nutrient concentrations ranging over 3 orders of magnitude. In general, P-concentrations had to alter by a factor of 10 before the 95% confidence limits of algal biomass ceased to overlap, i.e., only responses to changes in nutrient concentrations by more than one order of magnitude could be clearly identified in cross-lake comparisons. Present results from long-term observations at an individual sampling site revealed a higher responsiveness. At Lake Constance, variations in TP_{mix} by a factor of 2-3 affected the algal biovolume, chlorophyll concentrations, and especially the taxonomical and functional composition during selected periods of the season. This finding is in accordance with expectations since many potentially influential factors such as morphology and hydrology remain unchanged. However, basing findings on one lake bears a higher risk that concurrently uncontrolled changing factors lead to wrong conclusions which needs to be counterbalanced by long time series.

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