

Enhanced phosphorus accumulation efficiency by the pelagic community at reduced phosphorus supply: A lake experiment from bacteria to metazoan zooplankton

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Abstract

The effects of experimentally reduced total phosphorus concentrations (TP) from 2.4 to 0.6 $\mu\text{mol L}^{-1}$ on plankton community in a shallow lake were evaluated from the proportion between dissolved reactive P (DRP), dissolved nonreactive P (DOP) and particulate organic P (POP), and the stoichiometry among particulate organic carbon (POC), nitrogen (PON), and POP. In both triple ratios, DRP:DOP:POP and POC:PON:POP, we used POP as a key component to indicate shifts between P fractions and between nutrients in particulate organic matter. The enhanced P accumulation by the planktonic assemblage by 14% at reduced P supply was achieved by two steps, in the first year mainly at the expense of DOP and in the second year by DRP. The evidence that this increase of %POP of TP reflects the adaptive P utilization of the organisms under low P supply was substantiated by significant relationships between P fractions and changes in the community. A higher %POP of TP was associated with higher specific alkaline phosphatase activity and with tighter coupling between producers and consumers respectively—that is, driven from both the nutrient-producer and the producer-consumer interface. A lowered %DOP of TP was significantly related to smaller overall loss rates for the carbon pool of bacteria and algae, whereas %DRP of TP was correlated to the decrease of the biomass of most organism groups. Stoichiometric shifts toward a P-rich assemblage under low TP have been justified by compositional shifts from N-rich cyanobacteria to P-rich eukaryotic algae and bacteria. The shifts toward POP in both triple ratios strongly indicated that the plankton community acted as a sink for phosphorus under reduced total pool size.

Ecosystems are regulated by abiotic and biotic factors. The controversial debate over which of the two is more important finally led to the concept of bottom-up and top-down control. These are not mutually exclusive but act alternatively or simultaneously. Abiotic factors such as nutrient supply establish potential biomass increases of producers, whereas food web structure determines actual biomass increase. The concept is complicated by feedback and coupling

effects of organism groups in the microbial loop. Interactions within the plankton community largely depend on pool sizes of resources. In resource-limited environments, plankton dynamics mainly rely on internal mechanisms that recycle nutrients many times within surface waters. As nutrient pools decrease, turnover rates and cycling through the microbial loop become increasingly important (e.g., Thingstad et al. 1998). There is strong evidence that food web interactions at the microbial level strongly affect the production of carbon and the regeneration of nutrients in the pelagic zone (Sherr and Sherr 1987; Capblancq 1990; Weisse 1991).

A number of whole lake or enclosure experiments have demonstrated that regulatory factors of food web interactions vary across gradients of productivity in lake ecosystems (Pace and Funke 1991). The effects of nutrient reduction during oligotrophication on pelagic food-webs have, how-

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Acknowledgments

We thank Dan Danielopol, Gernot Falkner, Martin Hahn, Alois Herzig, Thomas Posch, and Bettina Sonntag for discussion on adaptation of organisms, ratios, and food chain structure. We are very grateful to Thomas Weisse, Richard Robarts, and two anonymous reviewers for improving an earlier draft of the manuscript.

ever, mainly been deduced from field observations (Manca and Ruggiu 1998). The implications of experimental nutrient stripping on pelagic interactions are not common but suggest that nutrients appear to regulate bacteria in oligotrophic waters, whereas protozoan regulation is more complex and is related to nutrients and community structure.

In freshwater systems, phosphorus is usually the major bottom-up element controlling productivity (e.g., Hecky and Kilham 1988). The absolute concentration of particulate organic P (POP) is a function of total biomass. As a consequence, POP can be seen as a key-parameter in P limited ecosystems. POP, however, can not be seen independently but is linked to other fractions (dissolved reactive P [DRP], dissolved nonreactive P [DOP], mainly dissolved organic P, and some inorganic polyphosphates) within the total P pool (TP) and to other nutrients within particulate organic matter (POM). In terms of ratios, these two relationships are expressed by DRP:DOP:POP and particulate organic carbon (POC):particulate organic nitrogen (PON):POP, respectively. Portions between the P fractions, as described by the first triple ratio (Teubner 2003), reflect biomass, P availability for producers (Cotner and Wetzel 1992; Coveney and Wetzel 1995), and P release by producers and consumers (Lampert 1978; Jones and Cannon 1986). The second triple ratio concerns the stoichiometric relationship between nutrients in planktonic matter. The significance of stoichiometry, proposed first by Redfield (1958) by C:N:P = 106:16:1 for marine net samples, has been assessed as an indicator for the nutrient limitation of phytoplankton composition at the species, community, and ecosystem levels (e.g., Hecky and Kilham 1988; Hillebrand and Sommer 1999; Teubner and Dokulil 2002), of community structure and food web interactions (e.g., Tilman et al. 1982; Behrendt 1990; Sterner et al. 1993; Urabe et al. 1995; Elser and Urabe 1999).

Phosphorus was experimentally reduced by internal precipitation in a shallow urban lake (Alte Donau, Vienna). The effects of reduced P supply on the planktonic community from bacteria to metazoans are central for our lake experiment in Alte Donau. We wanted to test how powerful these effects were as reflected by shifts in DRP:DOP:POP and POC:PON:POP. We hypothesized that the portion of POP in both triple ratios is a key component in showing adaptive P utilization of plankton communities under low P supply. In particular, we want to test how possible shifts between the P fractions and the stoichiometry of nutrients are related to changes in structures and processes at the nutrient-producer and the producer-consumer interfaces and the community structure, production, turnover, and overall loss rates (Tilzer 1984; Garnier and Mourelatos 1991; Thingstad et al. 1998). We hypothesize that shifts toward POP in both triple ratios signal enhanced P accumulation efficiency by plankton assemblages under reduced P supply.

Materials and methods

Alte Donau is a shallow groundwater-seepage lake (area, 1.5 km²; mean depth, 2.3 m) that was cut off from the main river ~150 yr ago during river regulation. P was precipitated with FeCl₃ during the whole lake experiment in April 1995

Table 1. Abbreviations, descriptions, methods, and units for biotic variables. All rates were calculated from biweekly intervals.

		Notation
<i>BP</i>	Heterotrophic bacterial production rate estimated from ³ H-leucine incorporation (areal) (g C m ⁻² h ⁻¹)	
<i>BP/C</i>	Turnover rate of bacterial carbon (g C g ⁻¹ C d ⁻¹)	
μ_b	Bacterial potential growth rate [$\mu_b = \ln(1 + BP/C)$ as d ⁻¹]	
k_b	Apparent growth rates from areal bacterial carbon net change, time interval as <i>BP/C</i> [$k_b = (\ln C_{b2} - \ln C_{b1}) / (t_2 - t_1)$ as d ⁻¹]	
$\mu_b - k_b$	Bacterial overall loss rate (d ⁻¹)	
<i>PP</i>	Primary production rate of phytoplankton as ¹⁴ C incorporation (areal); acid bubbling method (g C m ⁻² h ⁻¹)	
<i>PP/C</i>	Turnover rate of phytoplankton carbon (g C g ⁻¹ C d ⁻¹)	
μ_p	Potential growth rate of phytoplankton [$\mu_p = \ln(1 + PP/C)$ as d ⁻¹]	
k_p	Apparent growth rates from areal phytoplankton carbon net change [$k_p = (\ln C_{p2} - \ln C_{p1}) / (t_2 - t_1)$ as d ⁻¹]	
$\mu_p - k_p$	Phytoplankton overall loss rate (d ⁻¹)	
C_{b+p}	Pooled carbon of bacterioplankton and phytoplankton as ($\mu\text{mol C L}^{-1}$)	
C_z	Zooplankton carbon as the sum of carbon content of ciliates, rotifers, cladocerans, and copepods ($\mu\text{mol C L}^{-1}$)	
C_z/C_{b+p}	Ratio of carbon of zooplankton to pooled carbon of bacteria and phytoplankton ($\mu\text{mol C L}^{-1} : \mu\text{mol C L}^{-1}$)	
APA	Total alkaline phosphatase activity, fluorometrically determined by 4-methyl-umbelliferyl-phosphate hydrolysis ($\mu\text{mol P L}^{-1} \text{ h}^{-1}$)	
APA/C_{b+p}	Specific APA per pooled carbon of bacterio- and phytoplankton ($\mu\text{mol P L}^{-1} \text{ h}^{-1} : \mu\text{mol C L}^{-1}$)	
k_{b+c}	Net change of pooled carbon of bacterio- and phytoplankton (C_{b+p}) [$k_{b+p} = (\ln C_{b2+p2} - \ln C_{b1+p1}) / (t_2 - t_1)$ as d ⁻¹]	
k_z	Net change of zooplankton carbon [$k_z = (\ln C_{z2} - \ln C_{z1}) / (t_2 - t_1)$ as d ⁻¹]	

and again in April 1996. Integrated samples of the top 2 m were taken at biweekly intervals throughout both treatment years and the year before (1994–1996). Methods, abbreviations, and descriptions for biotic variables including productivity and phosphatase are shown in Table 1. Organisms were microscopically enumerated. Biovolumes were calculated and translated into carbon content using volume-conversion factors: heterotrophic bacteria (Norland 1993), ciliates (Putt and Stoecker 1989), metazoan zooplankton, and phytoplankton (Behrendt 1990) and separately for cyanobacteria, diatoms, and other eukaryotic algae. Unpublished fish stocking data suggest that the total fish population remained the same during the investigation period. Temperature was not significantly different between years (annual averages: 1994, 16.2°C; 1995, 17.0°C; and 1996, 16.1°C).

TN, PON, dissolved N compounds, TP, total dissolved P (DP), DRP, DOP (DP – DRP, probably mainly dissolved organic P; Psenner and Pucsko 1988), POP (TP – DP), dissolved organic carbon (DOC), and POC were estimated from epilimnetic samples using standard techniques (American Public Health Association 1992). Dissolved and particulate matter were separated by cascade filtration through Whatmann GF/F and Satorius membrane filters of 0.45 μm pore size.

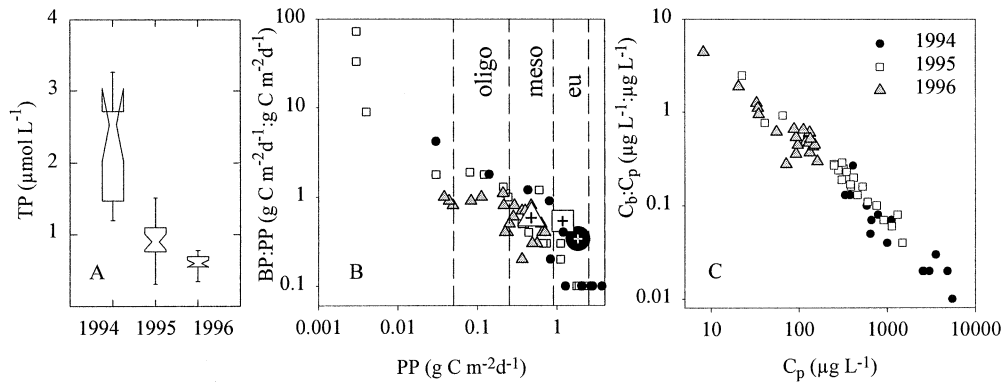


Fig. 1. (A) TP as notched box-whisker plots for 1994–1996. Boxes are notched at the median, with the length of the notches indicating the 95% confidence intervals. (B) Relation between PP and the ratio of bacterial production to primary production 1994–1996 (BP:PP; crosses mark the annual averages, trophic delineation according to Felföldy 1978 shown by dashed vertical lines). (C) Same as B but carbon content of phytoplankton (C_p) vs. $C_b:C_p$. Regression statistics for BP:PP vs. BP and $C_b:C_p$ vs. C_p were not calculated, to avoid problems with autocorrelations.

Results and discussion

Decrease of TP and changes of community structure—TP was stepwise reduced from 2.37 $\mu\text{mol L}^{-1}$ in 1994 to 0.63 $\mu\text{mol L}^{-1}$ in 1996. The changes from highly eutrophic to mesotrophic conditions were significant year by year, as indicated by the nonoverlapping notches in the box-whisker plot of Fig. 1A. Annual averages of primary productivity switched in the same way from 7.45 to 0.47 $\text{g C m}^{-2} \text{d}^{-1}$ (Fig. 1B). Annual changes for most variables and derived

parameters are summarized as box plots in Fig. 2. Significant downward shifts were observed year by year for DOP, POP, and DOC. DRP, POC, primary production (PP), and phytoplankton biovolume (not shown) followed the same trend but reached significantly lower levels only in 1996. Phytoplankton composition changed from cyanobacterial dominance (63% of *Cylindrospermopsis raceborski* Seenayya et Subba Raju) to a mixed assemblage of diatoms, chrysophytes, cryptophytes, and chlorophytes, with a 15% contribution of cyanobacteria after phosphorus reduction.

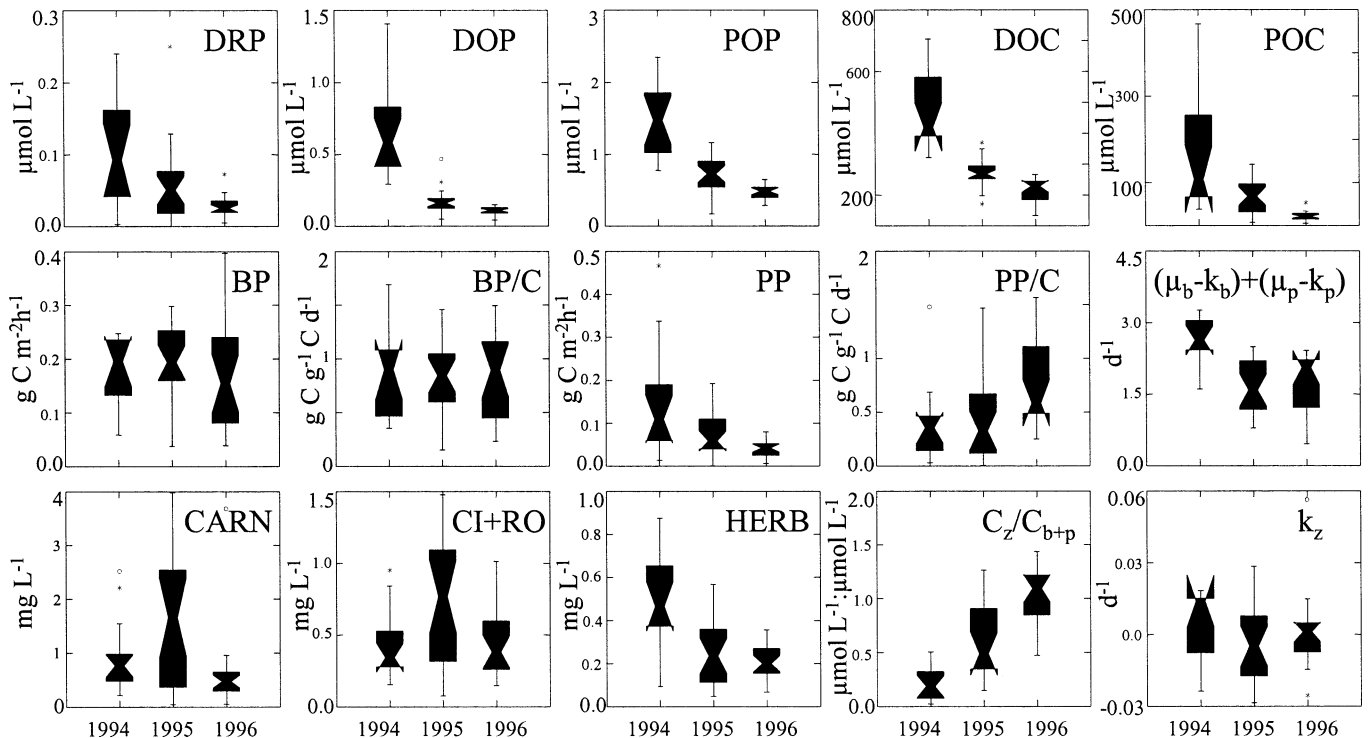


Fig. 2. Summary of variables and derived parameters as notched box-whisker plots for 1994–1996. Significant changes are indicated by nonoverlapping confidence limits as in Fig. 1.

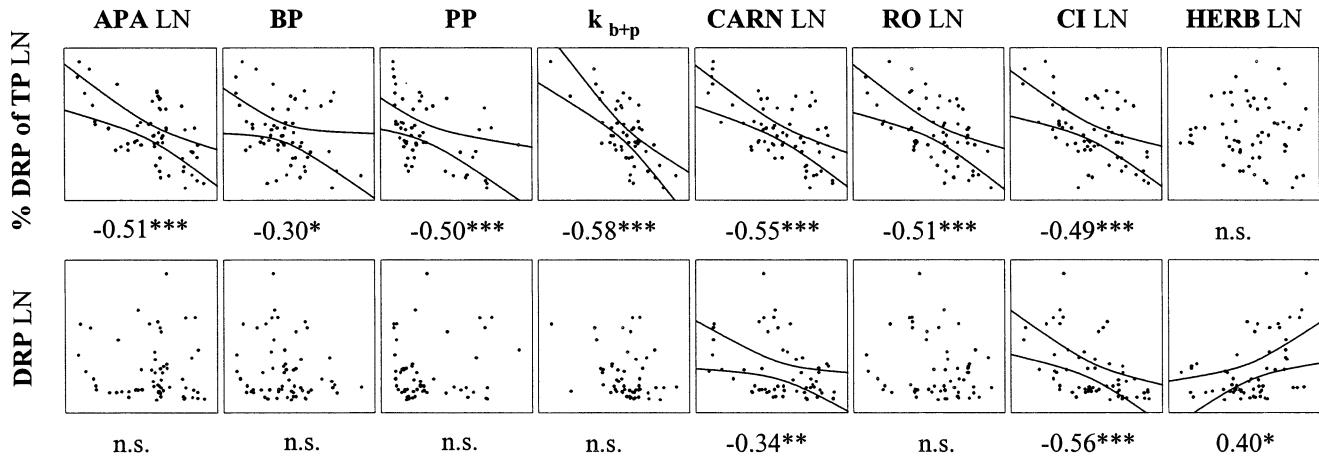


Fig. 3. Pairwise Spearman rank-correlation coefficients between variables and %DRP of TP and absolute DRP in $\mu\text{mol L}^{-1}$, respectively. Data cover all 3 yr ($n = 60$). Coefficients and 0.95 confidence intervals of regression lines are shown only for significant correlations. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. n.s. = not significant. Variables that are log-transformed have “LN” as suffix. Rotifers (RO) and ciliates (CI) are given as $\mu\text{g L}^{-1}$, for other abbreviations, see “Materials and methods” section and Table 1.

Bacterial biovolume and production (BP) did not follow this general trend. BP remained almost the same during the first 2 yr and then dropped slightly. Bacteria gained relative importance over phytoplankton—PP and algal biomass declined, whereas those of bacteria remained unchanged (Fig. 1B,C). The ratio of BP:PP increased from 0.06 to 0.71 (Fig. 1B) and the ratio of bacterial carbon (C_b) to phytoplankton carbon (C_p) from 0.07 to 0.81 (Fig. 1C). Therefore, C_b was the same order of magnitude as C_p under reduced nutrient supply, corresponding to mesotrophic conditions. These findings are consistent with observations of enhanced bacterial biomass and production relative to algal biomass and production in oligotrophic compared to eutrophic systems (Cole et al. 1988; Simon et al. 1992; Coveney and Wetzel 1995).

The turnover rate of bacterial carbon (BP/C) remained more or less constant during the investigation period (Fig. 2). Carbon-based turnover rates of phytoplankton (PP/C), however, became higher, suggesting a reduced P availability at low P levels only for algae, similar to observations by Thingstad et al. (1998). Nevertheless, under low P conditions, BP/C exceeded PP/C by 60%.

Interannual patterns differed among the functional zooplankton groups. The greatest development of herbivorous metazooplankton coincided with phytoplankton blooms in 1994 and the lowest was during the third year (Fig. 2). The decline corresponded with a pronounced shift from cladocerans (*Bosmina longirostris*, *Eubosmina coregoni*, *Daphnia cucullata*, *D. hyalina*, and *D. longispina*) to herbivorous calanoids (*Eudiaptomus gracilis*) and nauplii of carnivorous copepods. Carnivorous metazooplankton (CARN), rotifers and ciliates (CI+RO) showed their highest biomass variability in the first year of P reduction, with their medians significantly higher than before (1995 in Fig. 2). The temporal enhancement of bacterio-herbivorous zooplankton, concomitant with the increase of CARN, indicated that small-sized phytoplankton and bacteria were subsequently consumed by micro- and macrozooplankton. It is now widely accepted that the relative significance of the microbial loop to the pelagic carbon flux becomes higher in nutrient-limited ecosystems

and could be linked to the classic pelagic food chain (Sherr and Sherr 1987; Weisse 1991). In summary, the plankton community structure in Alte Donau shifted during the period of phosphorus reduction, evidently within both the producer and the consumer assemblages.

Correlation of biotic variables with DRP and %DRP of TP—Spearman rank correlation was used to examine pairwise relationships between P fractions and the organism groups mentioned above. For DRP as $\mu\text{mol L}^{-1}$, significant relationships were only found with zooplankton groups (Fig. 3, lower panel). Many more significant relations were obtained between the portion of inorganic phosphorus (%DRP of TP) and organism groups. The higher the %DRP of TP was, the lower the alkaline phosphatase activity, the BP and PP, the biomass of carnivorous metazooplankton, rotifers, and ciliates, and the net changes of carbon content of bacterioplankton and phytoplankton. The only non-significantly correlated group was herbivorous metazooplankton.

As exemplified by DRP, the portion of a total pool and not its absolute concentration was of higher explanatory value for biotic parameters in a system of reduced nutrient supply. From that view, we focus below on the proportion between P fractions for assessing the effects of P reduction on biota.

Shifts toward POP within DRP:DOP:POP and links to nutrient-producer-consumer interfaces—Shifts between P fractions were evaluated by DRP:DOP:POP as displayed in ternary diagrams (Fig. 4A–D). The %DOP of TP was highest during highly eutrophied conditions, as indicated by the points in sector a (Fig. 4A) and coincided with the phytoplankton summer bloom. Among the three fractions, POP was relatively invariant, whereas both dissolved fractions highly fluctuated, which is seen by the scatter of points along line d, parallel to the DOP:DRP axis. The relative stability of %POP of TP throughout the year is in accordance with longer turnover rates and weakened coupling of both dis-

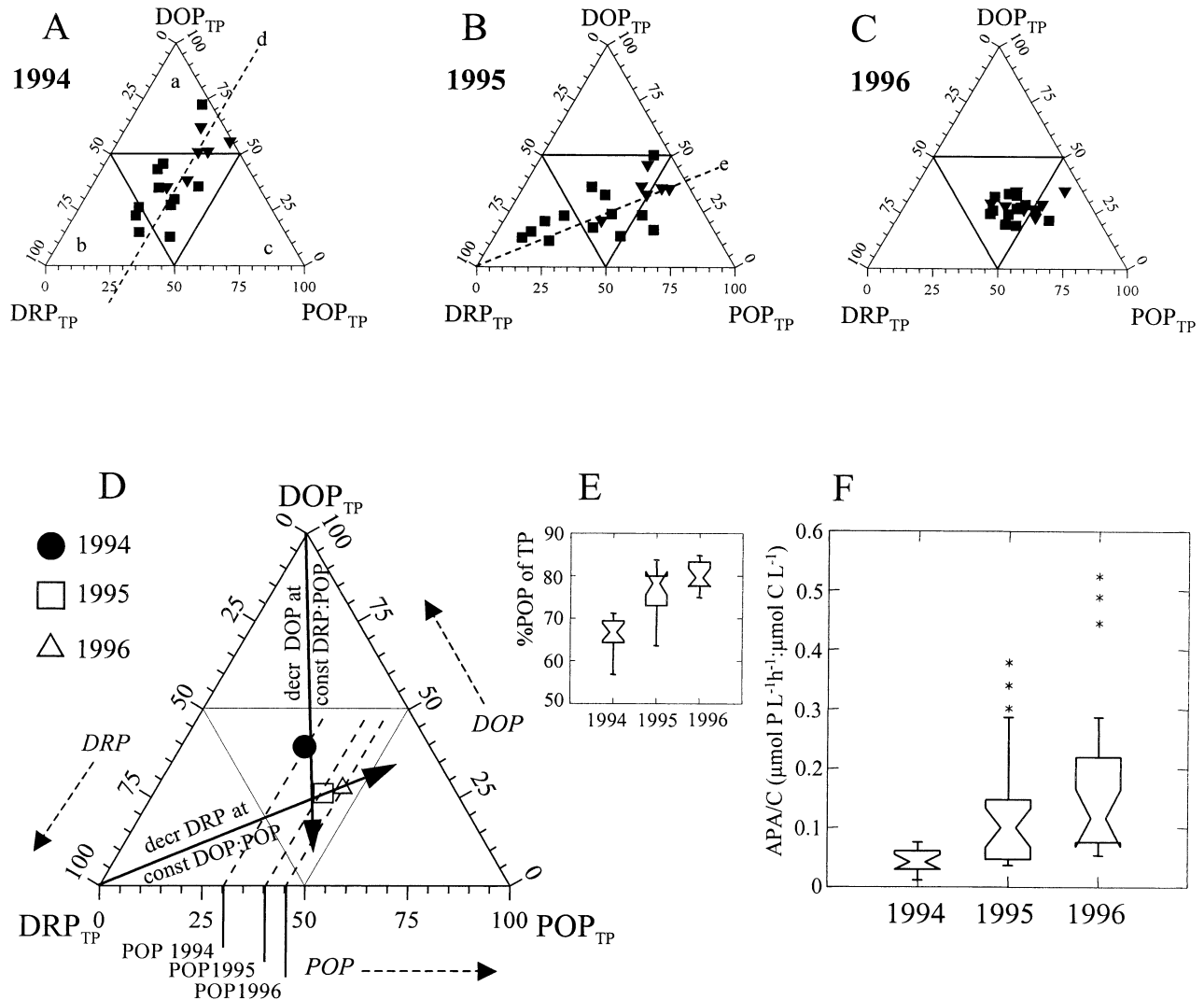


Fig. 4. P accumulation efficiency (A–E) and specific APA (F, APA/C_{b+p}) for 1994–1996. (A–D) Proportion between P fractions as DRP:DOP:POP. Biweekly data (A–E); triangles = summer, squares = other seasons. Sector a indicates relatively a high portion of DOP, b indicates high DRP, and c indicates high POP in the P pool. Sectors are valid for A–E but are shown only in A. Lines d and e are explained in the text. (D) Annual means. Relative increases of POP from year to year are marked by lines on the POP axis. Arrows inside triangles indicate the decrease of DOP at a constant ratio of DRP:POP (decrease in DOP at constant DRP:DOP) and the decrease of DRP at a constant ratio of DOP:POP (decrease in DRP at constant DOP:POP). Data in A–D are normalized as $C_{TP} = (C_{orig}/\sum_{i=1}^n C_i)$. (E) Significance of the increase of %POP. E and F, box plots as in Fig. 1.

solved fractions to biomass when total pool size is higher (Capblancq 1990).

After internal P reduction in 1995, %DOP of TP was reduced, whereas %POP increased (Fig. 4B, points in sector c but not a). A more stable DOP:POP ratio was established throughout the year at highly fluctuating DRP, as indicated by the scatter along line e, which intersects at the DRP corner. Especially during autumn, relatively high concentrations of DRP at low POP indicated that DRP was not utilized (autumn points in sector b). Under a further reduced P supply in 1996, the variability of DOP:POP remained the same as during the previous year (Fig. 4C). The ratios DRP:POP and DRP:DOP, however, became also less variable. The low scatter of the points in Fig. 4C indicated a more rapid cycling of all fractions in the P pool.

The increases of annual averages of %POP, marked on the DOP:POP axis in Fig. 4D, were significant, as indicated by the box plots in Fig. 4E. The %POP within the pool increased from 66% to 80% and is seen as an enhanced P accumulation efficiency by the organism assemblages. Among the three fractions, the share of POP was most sensitive to pool size reduction and was charged by the relative decrease of both dissolved fractions, DRP and DOP (molar ratios given in Table 2). The increase of accumulation efficiency in terms of annual averages, however, is again recognized as a two-step process. During the first year, POP was built mainly at the expense of DOP and, in the second, only by DRP, as seen graphically by arrows in Fig 4D.

The accumulation of P by organisms (%POP of TP) at the expense of DOP in the first step of pool size reduction is

Table 2. Annual averages for the molar triple ratios DRP : DOP : POP and POC : PON : POP.

Year	DRP : DOP : POP	POC : PON : POP
1994	0.080 : 0.425 : 1	119 : 36 : 1
1995	0.062 : 0.206 : 1	97 : 25 : 1
1996	0.047 : 0.206 : 1	62 : 24 : 1

mainly due to two processes: the enzymatic mobilization of substrate in the DOP pool and the smaller release of DOP because of lower producer biomass, mainly algae (Jones and Cannon 1986). By assuming that the alkaline phosphatase activity (APA) was linked only to producers, the effort of producers to mobilize P resources from the DOP pool can be expressed by the relationship of APA per pooled cell carbon of bacteria and algae (APA/C_{b+p} , Fig. 4F). Both APA/C_{b+p} and %POP of TP were directly related to each other ($r = 0.67$, $P < 0.001$). Significant increases of APA/C_{b+p} were observed during the first year of P reduction, corresponding with the first step of significant increase of the accumulation efficiency, which was mainly at the expense of DOP, as mentioned above (Fig. 4D–F). APA/C_{b+p} and %POP of TP during the third year validate each other by slight increases and can be interpreted as a high affinity to low portion of both DRP and DOP within the P pool. The significant correlation between the APA and the cell carbon of producers refers to the control of DOP by extracellular enzymes released from both algae ($r = 0.71$, $P < 0.001$) and bacteria ($r = 0.39$, $P < 0.005$). This relationship is consistent with observations that APA was associated with particles of both algal and bacterial sizes (Coveney and Wetzel 1995; Jamet et al. 1997) and plays an important role for nutrient recycling at the nutrient-producer interface.

We found further justification of increased P accumulation efficiency by the community at the producer-consumer interface (Fig. 5A–D). Net carbon changes of bacterioplankton plus phytoplankton (k_{b+p}) were high and uncorrelated to zooplankton (k_z) during the nutrient-rich condition in 1994 (Figs. 2, 5A). Rates were much lower in 1995, the first year of P reduction, and became correlated ($r = 0.47$, $P < 0.05$). The correlation of 0.73 ($P < 0.001$) during the third year can be interpreted as a close functional coupling between both carbon net change rates coinciding with the highest P accumulation efficiency by the pelagic community. The ratio of zooplankton carbon to producer carbon (C_z/C_{b+p} ; Figs. 2, 5B) rose from 0.21 to 1.1 over the years and was directly related to the increase of %POP of TP ($r = 0.64$, $P < 0.001$). This relative enhancement of zooplankton implies an accelerated circulation of matter within Alte Donau, as has been shown by experiments for other ecosystems (Queimaliños et al. 1998) and theoretically reinforced (Loreau 1995).

The control of %DOP at the producer-consumer interface can be deduced from the significant relation to the overall loss rates of producers (Fig. 5C,D; $r = 0.60$, $P < 0.001$). The loss rates of bacterioplankton were the same order of magnitude (annual averages 1994–1996, 48%, 62%, and 52%) as those of phytoplankton and became even slightly higher than those of phytoplankton under reduced phosphorus levels. These increased relative loss rates are taken as

indirect evidence of enhanced grazing of bacteria, although the biomass remained constant, as has been observed in other ecosystems (e.g., Berman 1990). The same trend of averaged net zooplankton carbon changes and overall producer loss rates [Fig. 2; $(\mu_b - k_b) + (\mu_p - k_p)$ and k_z] confirm observations by Tilzer (1984) and Garnier and Mourelatos (1991) that losses can largely be explained by grazing. Enhanced loss rates and high %DOP of TP during the first year were accompanied by a dominance of cladocerans, which are known for their sloppy feeding (Lampert 1978). The decreased overall loss rates after P reduction during the following years for both algae and bacteria were associated with pronounced internal shifts in zooplankton from bacterioalgalivorous to carnivorous assemblages. The ratio of herbivorous zooplankton to carnivores correlated with prey overall loss rates as $r = -0.41$, $P < 0.005$. Evaluated at the producer-consumer interface, the higher %POP of TP at the expense of DOP was related to lower overall loss rates, which were associated with the shift from a direct food chain toward a multistep food web—in other words, a shift from new production to regenerated production (Capblancq 1990).

To conclude, the increased P accumulation by organisms was driven from both the nutrient-producer and producer-consumer interface. The first was associated with higher specific APA and the second with a tighter coupling between producers and consumers and lower overall loss rates of producers.

Shifts toward POP within POC : PON : POP and pelagic community compositional changes—With increasing %POP of TP over the years of reduced P supply, the stoichiometry among C, N, and P shifted successively toward P-rich organic matter, as indicated by the scatter toward the POP corner in Fig. 5E (annual averages in Table 2). We assume that the Redfield ratio was valid for Alte Donau, because the scatter areas covered the point of the optimum ratio of 106 : 16 : 1 (Fig. 5E). If nutrients are scaled in optimum proportions (Teubner and Dokulil 2002; Teubner 2003), stoichiometric shifts were mainly associated with the increase of P, whereas C decreased slightly and N remained almost the same relative to P and C. In terms of ratios, POC : POP was mainly affected (extent of variation is displayed by the length of the black bar on the POC : POP axis in Fig. 5E).

The stoichiometric shift toward P-rich organism assemblage in Alte Donau at reduced P supply seemed a priori to be paradoxical. The restructured pelagic community can explain it, however. Stoichiometric data from eutrophied Großer Müggelsee by Behrendt (1990), reevaluated as C : N : P in Fig. 5F, evidently show that diatoms and other eukaryotic algae contain more P than relatively N-rich cyanobacteria. Metazooplankton is considerably lower in C than phytoplankton (Behrendt 1990) or seston mainly containing algae (Urabe et al. 1995). Heterotrophic bacteria under balanced nutrient conditions are low in C but rich in P in comparison to other organisms (Fig. 5F; Goldman et al. 1987; Vadstein et al. 1988; Eccleston-Parry and Leadbeater 1995). Shifts in stoichiometry toward P-rich assemblages in Alte Donau can therefore be explained by pronounced shifts toward P-rich producers, the replacement of cyanobacteria by P-rich eukaryotic algae, and the increase of the relative im-

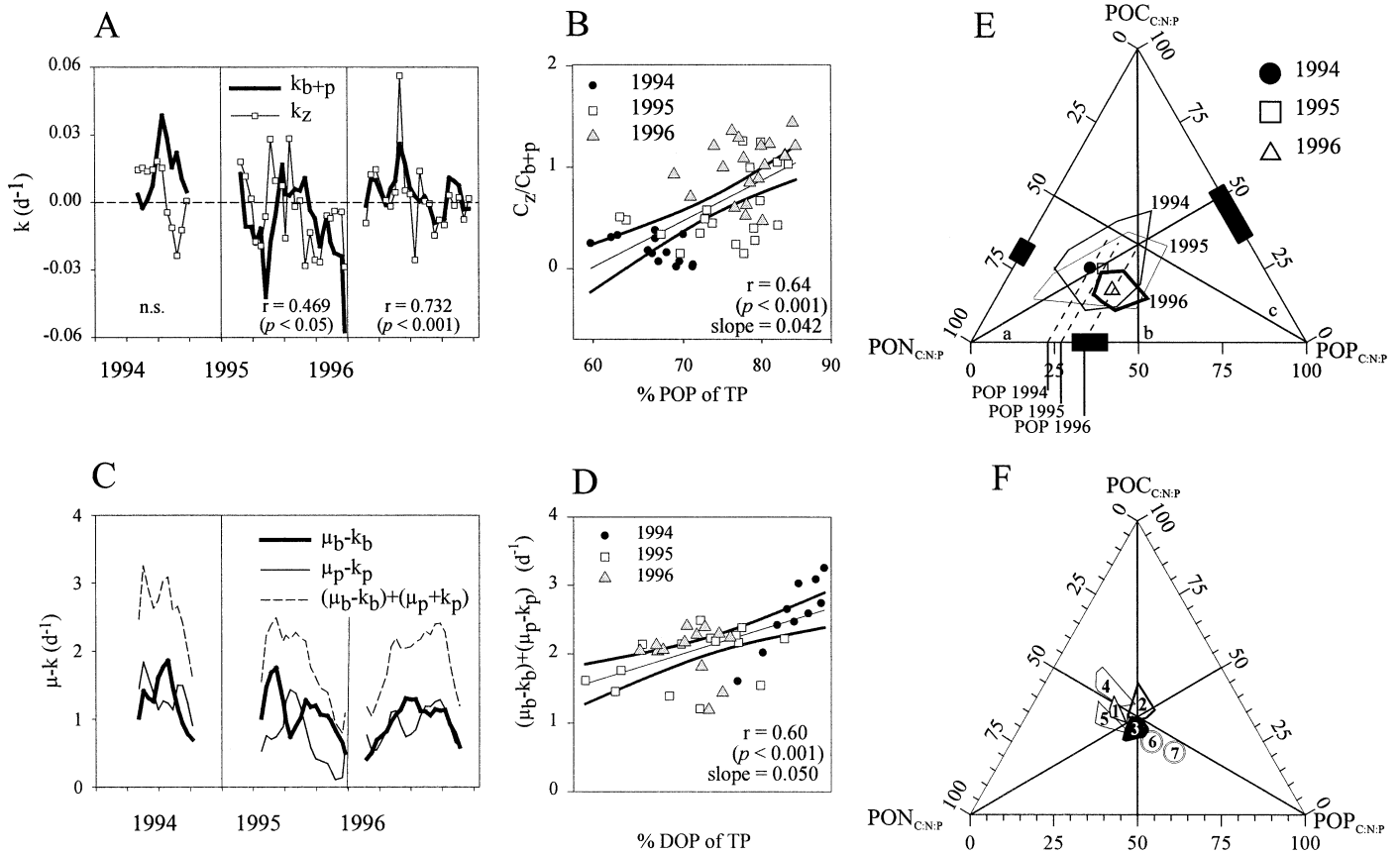


Fig. 5. Producer-consumer relationships (A–D) and stoichiometry of POM (E and F). (A) Net change rate for pooled C of bacterioplankton and phytoplankton (k_{b+p}) and zooplankton (k_z). Correlations between both rates were estimated separately for each year (1994, $n = 11$; 1995 and 1996, $n = 21$). (B) Ratio of zooplankton C to bacterioplankton C ($C_z:C_{b+p}$) in relation to %POP of TP. (C) Overall loss rates for bacterioplankton and phytoplankton and for the sum of both. (D) Overall loss rates for pooled bacterioplankton and phytoplankton in relation to %DOP of TP. A, B, and D, Spearman rank-correlation coefficients. (E) Ratio of POC:PON:POP for Alte Donau. Annual averages as points and distribution of original data as areas. Scaling according to Redfield's ratio ($POC_{C:N:P} = POC_{orig}/106$, $PON_{C:N:P} = PON_{orig}/16$, and $POP_{C:N:P} = POP_{orig}/1$), line a indicates the constant ratio of POC:POP = 106:1, b of PON:POP = 16:1, and c of POC:PON = 106:16; the intersection of these three lines is 106:16:1. The length of the thick black bar on the POC:POP axis indicates the relative variability of C:P between annual averages, and black bars on the other axes are the variability for C:N and N:P, respectively. (F) Scaling and lines as in E, but data from the following: Lake Müggelsee (Behrendt 1990), 1 = cyanobacteria (contribution of >76% to phytoplankton biovolume, from summer), 2 = eukaryotic algae (>61%, from spring), and 3 = metazooplankton; Lake Biwa (Urabe et al. 1995), 4 = seston <98 μm and <20 μm and 5 = metazooplankton; cultures of heterotrophic bacteria, 6 = single freshwater strain at balanced nutrient conditions (Eccleston-Parry and Leadbeater 1995) and 7 = marine assemblage (Goldman et al. 1987).

portance of P-rich bacteria. Under reduced P supply, the ratio of $C_b:C_p$ increased by about an order of magnitude, emphasizing the contribution to biotic P by heterotrophic bacteria in Alte Donau. Commonly, their contribution to particulate P is sevenfold higher than that of particulate carbon, whereas the contribution of particulate P is less than half in algae than that of particulate C (Vadstein 2000). The stoichiometric decrease of POC was further triggered by the relative increase of animal biomass versus plants. The lower POC:POP ratio under reduced TP conditions therefore corresponded well with simultaneous changes of both the relative increase of heterotrophic bacteria among producers and the increase of zooplankton among the pelagic community.

The stoichiometric shift toward the limiting element is a common phenomenon of individual adaptation of producer organisms. The elemental composition of individual bacterial and algal cells can vary strongly in contrast to consumers

keeping their elemental composition within a limited range, even if the elemental composition of ingested food is much different from their body tissue (Sternner et al. 1993; Elser and Urabe 1999). The uptake systems of bacteria and algae adapt sensitively to reduced external nutrient concentrations by changes in affinity, threshold values, and storage capacity (Falkner et al. 1989). Bacteria that appear to have especially higher affinities and more rapid specific uptakes for DRP than algae could outcompete larger-celled phytoplankton under P-limited conditions and be P-rich organisms through the high storage capacity of polyphosphates under natural conditions (Rhee 1973; Berman 1985; Vrede 1998; Vadstein 2000). A reevaluation of data from Behrendt (1990), Teubner et al. (1999), and Teubner and Dokulil (2002) shows that N-rich algae (cyanobacteria) dominate under N limitation and that P-rich organisms (diatoms and other eukaryotic algae) dominate under P limitation (Fig. 5; fig. 1A in Teubner

et al. 1999; fig. 5, triangle for MUES, in Teubner and Dokulil 2002). Cyanobacteria are relatively N rich because of N storage in cyanophycin and phycobiliproteins in addition to P storage by polyphosphates.

Our hypothesis that the P accumulation efficiency of the pelagic community (%POP of TP) was enhanced under reduced P supply and was also reflected in the stoichiometry of C:N:P by shifts toward a P-rich pelagic community was experimentally supported. The coupling between both trends was mirrored by shifts toward POP simultaneously in the both DRP:DOP:POP and POC:PON:POP ratios. The evidence that the increased %POP of TP reflects the adaptive P utilization of a planktonic community under low P supply was substantiated by correlative relationships to changes in the structure and processes at the nutrient-producer and producer-consumer interfaces (biomass parameters, turnover rates, and overall loss rates). The stoichiometric shift toward a P-rich community can be explained by compositional changes. As a consequence, both shifts toward POP suggest that the pelagic community acted as a sink for phosphorus under conditions of reduced P supply.

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Received: 4 March 2002

Accepted: 9 January 2003

Amended: 3 February 2003