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EUTROPHICATION PROBLEMS AND THEIR POTENTIAL SOLUTIONS IN THE ARTIFICIAL SHALLOW LAKE ALTMÜHLSEE (GERMANY)

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Abstract

Lake Altmühlsee in Middle Franconia, Germany, was constructed as part of a water transportation system and flooded in 1986 by River Altmühl. Supply of nutrient rich water resulted in a hypertrophic state characterized by low Secchi depth (<0.5 m in summer). Massive blooms of phytoplankton in summer were mainly caused by cyanobacteria (*Aphanizomenon flos-aquae*, *Anabaena flos-aquae*, *Microcystis aeruginosa*) and by chlorophytes (*Oocystis* ssp., *Monoraphidium* ssp., *Planktosphaeria gelatinosa*), respectively. Fish assemblage was characterized by the dominance of planktivorous bream. Hence, zooplankton community mostly consisted of small-bodied cladocerans due to predation pressure by fish. Investigations of the phosphorus (P) cycle of Lake Altmühlsee revealed high P-turnover rates in the water body and at the immediate sediment-water interface, an outstanding importance of external P-load, and a minor importance of the internal P-load. The lake supports recreational and social functions which, however, are restricted due to the low water quality. Improvement of water quality is necessary to increase attractiveness. Our study presents some proposals for an effective and economically justifiable water quality management, especially, biomanipulation in accordance to the holder of the fishing rights and local establishment of macrophytes.

Key words: nutrient loading, internal P-turnover, food chain, biomanipulation, restoration, shallow lake

INTRODUCTION

Water reservoirs, primarily designed for technical water quantity management, often gain socio-economic importance for recreational use and nature conservation. If the reservoirs are supplied from eutrophic rivers their water quality will be negatively impacted by eutrophication. Lake Altmühlsee is such an artificial shallow lake characterized by high turbidity due to high phytoplankton biomass. Shallow lakes can exist in two alternative equilibria. The turbid state is characterized by nutrient enrichment, low Secchi depth, high phytoplankton biomass, a lack of macrophytes and the dominance of planktivorous fish. On the other hand, at low nutrient concentrations there exists a clear water state with high Secchi depth, rich abundance of macrophytes, and piscivorous fish controlling the food web. Both states have different feed-back mechanisms with self-stabilizing effects. In turbid lakes, algae development and sediment resuspension reduce light availability which further improves living conditions for phytoplankton, especially cyanobacteria (Meijer *et al.* 1990, Lammens 1999). Additionally, sediment resuspension may increase internal nutrient load (Lammens 1999). Planktivorous fish feed on large grazing zooplankton, which, in turn, is not able to control phytoplankton growth (Brooks, Dodson 1965). Pike is missing due to a lack of places for predation by ambush and for nurturing offspring (Lammens 1999). In clear water lakes, macrophytes have a stabilizing effect on the clear water state due to effective competition for nutrients (Ozimek *et al.* 1990, van Donk, Gulati 1995), offering refuges to herbivorous zooplankton (Lauridsen *et al.* 1996, Stansfield *et al.* 1997) and young piscivorous fishes (Skov, Berg 1999), stabilizing the sediment and reducing resuspension (Barko, James 1998, Stephen *et al.* 1998, van den Berg *et al.* 1998), promotion of macroinvertebrates as grazers (Diehl, Kornijów 1998, Brönmark, Vermaat 1998), enhanced denitrification (Stephen *et al.* 1998), and potential allelopathy (Stansfield *et al.* 1997, Stephen *et al.* 1998, Leu *et al.* 2002). These findings of alternative stable states are based on empirical observations (Jeppesen *et al.* 1990, Blindow *et al.* 1993, Meijer *et al.* 1994, Moss *et al.* 1996a) and on deductions from theoretical mathematical models (Scheffer 1990, Scheffer *et al.* 2001). The clear water state will persist over a wide range of nutrient concentrations, but once the critical turbidity is attained, the system is thought to switch to the tur-

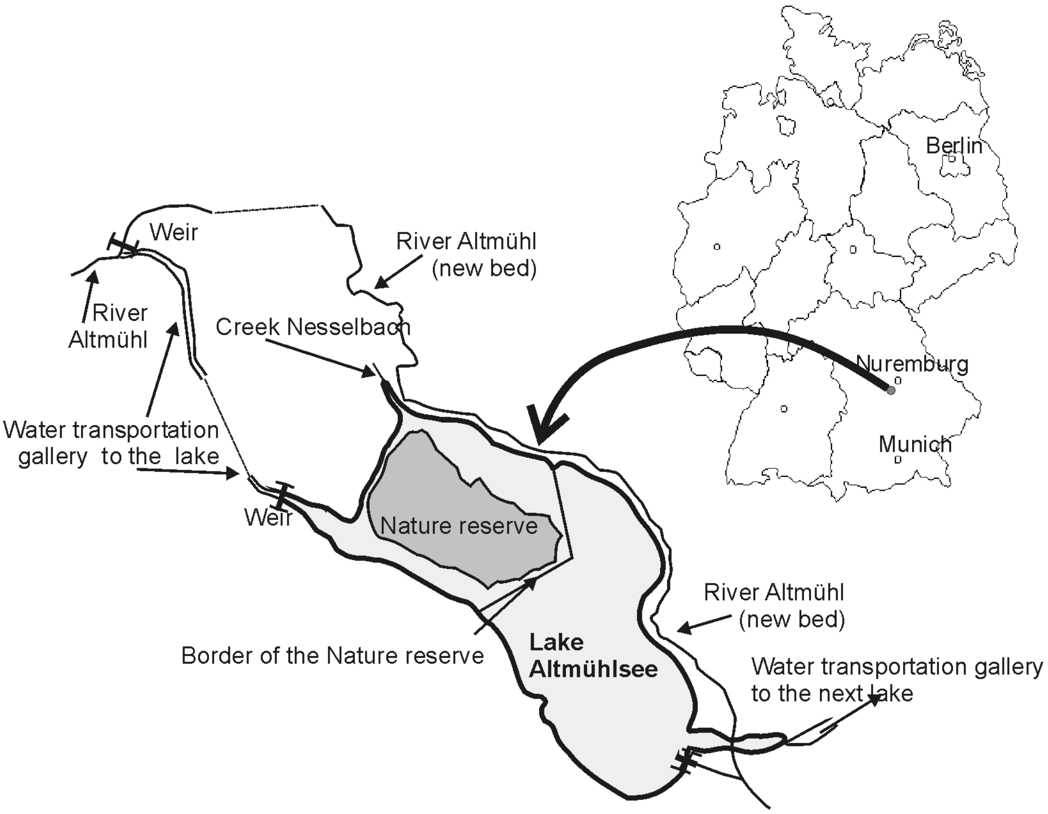

Fig. 1. Geographic location and topography of Lake Altmühlsee.

bid state (Scheffer *et al.* 1993, 2001). According to the 'marble-in-a-cup' model of Scheffer (1990), the stability of a system is decreasing with increasing nutrient enrichment. The feed-back mechanisms stabilize the system, and a reduction of the nutrient level alone will not necessarily allow a switch from turbid to clear (hysteresis) (Zhang *et al.* 2003). A presumably strong perturbation is needed to push the system from one equilibrium to another (Perrow *et al.* 1997). To re-establish a macrophyte-dominated state, the perturbation must allow a temporary increase of Secchi depth to enable the (re)colonization of macrophytes (Scheffer *et al.* 1993). Once submerged vegetation has established, the system should be stable in the clear water state. One crucial measure of such a perturbation is the specific adjustment of the fish assemblage called biomanipulation, including a strong reduction of planktivorous fish and the support of piscivorous ones. Biomanipulation became an important technique in lake restoration over recent last years. For more details see de Bernardi, Gussani (1995), Kufel *et al.* (1997), Harper *et al.* (1999), Walz, Nixdorf (1999) and the special issue of *Freshwater Biology* 47(12) of December 2002.

In this contribution, we try to reconstruct the reasons leading to the turbid state of the Lake Altmühlsee to gain detailed knowledge of food-web and ecosystem structure using data sampled routinely in 1994–2002. For a more detailed analysis, we additionally examined the phosphorus fractions in the sediment, the dissolved substances in the pore water, and the gut content of potentially planktivorous fish. The aim of our study was to derive in detail effective and economically justifiable strategies for water quality improvement.

MATERIAL AND METHODS

Study site

Lake Altmühlsee is an artificial, eutrophic, shallow lake in Middle Franconia, Germany, situated about 50 km southwest of Nuremberg (Fig. 1).

The lake was originally constructed in the middle of the 1980ies for water storage as part of a water transfer system from the water-rich Altmühl-Danube area to the Regnitz-Main area in North Bavaria, a region with scarce precipitation. Additional purposes of the reservoir were the protection of the central Altmühl valley against summer flooding, and water supply in dry seasons (StMLU 2000). Due to the lack of natural lakes in the Greater Nuremberg area the lake also supports a host of recreational and social functions:

– Tourists and inhabitants of the surrounding area use the lake for sporting activities. The dam is part of a road network for walker and bicyclists. Beaches are subdivided for swimming, sailing, and windsurfing.

– Fishing rights are given to the regional sports fishing association ("Mittelfränkischer Fischereiverband"), selling fishing rights to individuals.

– About 200 ha of Lake Altmühlsee are established as a nature reserve for waterfowls. It consists of small islands and very shallow areas. Entrance by boat, for swimmers and anglers is forbidden. A circular wooden walk of about one km allows bird watching from several outlook posts.

The lake was constructed by building a 12.5 km ring dam, since a natural drop in the valley was lacking and a dam across the valley would have created a large flood-plain. The lake is of considerable economical importance for the surrounding municipalities.

In summertime, the total lake surface is approximately 4.5 km^2, and total lake volume is approximately 9.1 10^6 m^3. River Altmühl was moved to a new bed around the lake and is connected with the lake by a 5 km gallery (StMLU 2000). The lake was flooded in 1986 with nutrient-rich water from River Altmühl. Up to now, the catchment area (523 km^2) is under intensive agricultural use with extensive fertilizer application. P-input from municipal wastewater treatment plants was reduced as far as possible by technical improvement over recent years. P-concentration in River Altmühl consequently decreased, and the annual mean of TP is now approximately 0.3 mg L^{-1}. An additional permanent, but negligible inflow comes from creek Nesselbach. The main inflow occurs in winter during flood periods of River Altmühl with discharges >4.5 m^3 s^{-1} entering the lake via the water transportation gallery. The water level of the lake is alternating 0.5 to 0.75 m in the course of the year. Inflowing waters theoretically cause a complete water exchange in most years. However, water retention times cannot be calculated, as there is no flow-through under normal conditions. The basin outside the nature reserve has a flat bed topography with a mean depth of 2.0 m and a maximum depth of 2.2 m. Consequently, the lake is polymictic, and stratification may appear only for some hours or days.

During its first few years, Lake Altmühlsee was non-turbid and dominated by the macrophyte *Polygonum amphibium*, a typical plant of eutrophic lakes (Carpenter *et al.* 1998). The vegetation was cut, and later the lake water became increasingly turbid. Cyanobacteria started occurring and long-lasting blooms became a nuisance to visitors seeking recreation. During summer months, Secchi depth is often below 0.5 m.

Water sampling and analyses

Sampling was carried out biweekly from one location (landing-pier Muhr) in the 0–1 m water column. Previous investigations have established this location as representative for the whole lake. Temperature and dissolved oxygen were measured in the field using a Multiline P4, pH and conductivity were measured in the laboratory at 20 °C using an LF 191 and pH 330 respectively (all WTW, Weilheim). Analyses of chlorophyll, phosphorus (total phosphorus = TP, soluble reactive phosphorus = SRP), nitrogen (total nitrogen = TN) and ion concentrations were performed at the Wasserwirtschaftsamt Ansbach in accordance to standard methods (DIN 38 405). Secchi depth was determined occasionally in earlier years, since 2000 fortnightly.

Sediment

A sediment core was sampled from a central location in June 2000 using a Kajak-sampler (Uwitec) and sliced into 1-cm sections. Dry weight (DW) was determined after drying at 105 °C to constant weight, loss of ignition (LOI) by burning at 450 °C for three hours. TP content was analyzed photometrically as SRP after extraction of the dried, ground sediment samples with H_2SO_4-acid peroxide for 12 hours at 105 °C. Binding forms of phosphorus were studied applying the sequential fractionation from Psenner *et al.* (1984; modified by Hupfer *et al.* 1995; see Ulrich 1997). P-fractions were separated as $P_{(NH4Cl)}$ [loosely adsorbed P], $P_{(BD)}$ [reductant soluble P mainly bound to Fe(III)- and Mn(IV)-hydroxides], $SRP_{(NaOH)}$ [P superficially bound to metal oxides (Fe, Al) and exchangeable against OH^-], $NRP_{(NaOH)}$ [organic and humic P] and $P_{(HCl)}$ [Ca-bound and Apatit-P]. The residual P-fraction $P_{(Res)}$ included mineral and refractory organic P. The fractions do not correspond to chemically exactly defined compounds, but are characterized by eluation medium and conditions. Thus, they are operational phases (Psenner, Pucsko 1988).

Vertical distribution of dissolved substances at the sediment-water interface was investigated in June 2003 using *in-situ* dialysis pore water samplers according to Hesslein (1976). Two samplers with a spatial resolution of 1 cm were exposed for 14 days along the borderline of the nature reserve for birds (Vogelinsel) with a distance of approximately 150 m. The method is described in detail by Lewandowski (2002). Pore water analysis was conducted according to the methods described for the water samples. Turnover rates were calculated with the program Profile V 1.0 merely on the basis of molecular diffusion since biodiffusivity and irrigation coefficient were not measured (Berg *et al.* 1998). For the calculation of fluxes according to Fick's first law pH, temperature, water content, and loss on ignition were taken into account (Lewandowski *et al.* 2002) and the smoothed profiles calculated with Profile V 1.0 were used since a random scattering of the values would cause a large variation of calculated fluxes.

Plankton

Two phytoplankton samples were collected with a 0.5 m tube sampler with 5 L (HydroBios), pooled and preserved with Lugol-solution. Cells were estimated quantitatively using an inverted microscope (Utermoehl 1958). Determinations were done according to Huber-Pestalozzi (1941–1983), Geitler (1985), and Ettl & Gärtner (1988).

Depth-integrated zooplankton samples of 50 L were pumped through a 55 µm net and fixed in 4% sugar/formalin. Metazooplankton was identified and counted using an inverted microscope. Species of nauplii were not further determined. Zooplankton composition and abundance was studied in 1994, 1996, 1997, and 1999–2001. Determinations were done according to Ruttner-Kolisko (1972), Einsle (1993), and Flössner (1972, 2000).

Fish

A fish survey was conducted in April 2000 to determine fish stock composition and to identify the main predators of daphnids in spring, since the decline of daphnids was thought to be one of the main reasons for the high phytoplankton biomass observed during the summer season. Two sets of gillnets comprising 16 different mesh widths ranging from 5 to 90 mm were placed at 6 sampling sites during the day and at one site overnight. The sets were 266.5 m or 284 m, respec-

Table 1

Annual concentrations of TP [mg L^{-1}], and chlorophyll *a* [µg L^{-1}] in Lake Altmühlsee in 1994–2002, data are means ±s.d.

	TP-year	TP-summer[1]	TN-year	TN-summer[1]	Chl *a*-year	Chl *a*-summer[1]
1994	0.184±0.086	0.189±0.070	2.0±1.7	2.6±1.2	36.3±29.5	45.9±31.7
1995	0.157±0.074	0.154±0.045	2.4±1.5	2.0±0.9	29.3±19.7	31.8±24.8
1996	0.184±0.080	0.162±0.053	3.2±2.2	1.7±0.5	48.0±54.0	37.3±16.8
1997	0.199±0.109	0.226±0.130	2.6±1.3	2.0±1.0	38.0±26.5	38.1±23.4
1998	0.219±0.110	0.260±0.133	2.7±1.6	2.0±1.3	55.5±78.2	75.7±98.6
1999	0.182±0.059	0.192±0.066	2.8±1.6	2.3±1.1	34.4±24.8	40.5±31.7
2000	0.189±0.057	0.183±0.061	2.9±1.9	2.2±1.2	56.2±38.0	63.8±32.3
2001	0.172±0.088	0.205±0.102	2.6±1.4	2.7±1.5	72.0±61.1	86.6±76.7
2002	0.184±0.046	0.188±0.042	3.0±1.1	2.3±1.0	43.3±30.7	53.5±34.4

[1] summer: April - September

tively, in length with depths ranging from 1.25 m to 2.4 m. Catches of each net were related to a standardized net size of 20 m˛. Additionally, fishes in the littoral zone were sampled at 8 sites by electrofishing. The total length of the fishes was measured to the nearest 0.5 cm.

Diet composition of three potentially planktivorous species, namely bream [*Abramis brama* (L.)], roach [*Rutilus rutilus* (L.)], and white bream [*Abramis bjoerkna* (L.)], was determined semi-quantitatively. Diet was categorized in the four groups zooplankton, zoobenthos, plant material, and miscellaneous (mainly freshwater mites).The proportional volume of each category was estimated using a binocular microscope. The degree of filling of the gut was classified in five groups according to Bohl (1979).

RESULTS AND DISCUSSION

Physical and chemical parameters

Maximum water temperature went up to around 25 °C in late summer months. During the winter months, the lake is frequently ice-covered. Lake water was alkaline with pH from 8.5 to 9.5 during the summer due to autotrophic production. Integral measurements from three different depths (near-surface, mid-depth, bottom) in 2002 showed no stratification for temperature or pH. Oxygen concentrations never dropped below 4 mg L^{-1}, and saturation was around 100% (samples were taken mostly in the morning hours). O_2-depletion, if any, probably occurred only during the night or early morning hours. Low O_2-content was found only for a single sampling date in August.

Annual and seasonal concentrations of both nutrient and chlorophyll *a* showed high variability (Table 1, Fig. 2).

External nutrients mainly entered the lake during high water events in winter. Thus, the long-term trophic state of the lake was caused by the actual state of River Altmühl during high waters, normally lasting for 10–30 days. Incoming waters were heavily loaded with eroded material. The mean in-lake concentration of total nitrogen (TN) was highest in February (4.33±1.56 mg L^{-1}) and declined to 1.49±0.35 mg L^{-1} in October. Loss of nitrogen probably occurred due to sedimentation and denitrification at the sediment-water interface. Mean concentration over the whole study period was 2.77±1.60 mg L^{-1} with an annual minimum in 1995 and annual maxima in 1994 and 2002. Annual fluctuations of summer values were less pronounced. Ammonium and nitrate concentrations displayed a seasonal minimum during the summer and dropped below detection limits in July/August of certain years.

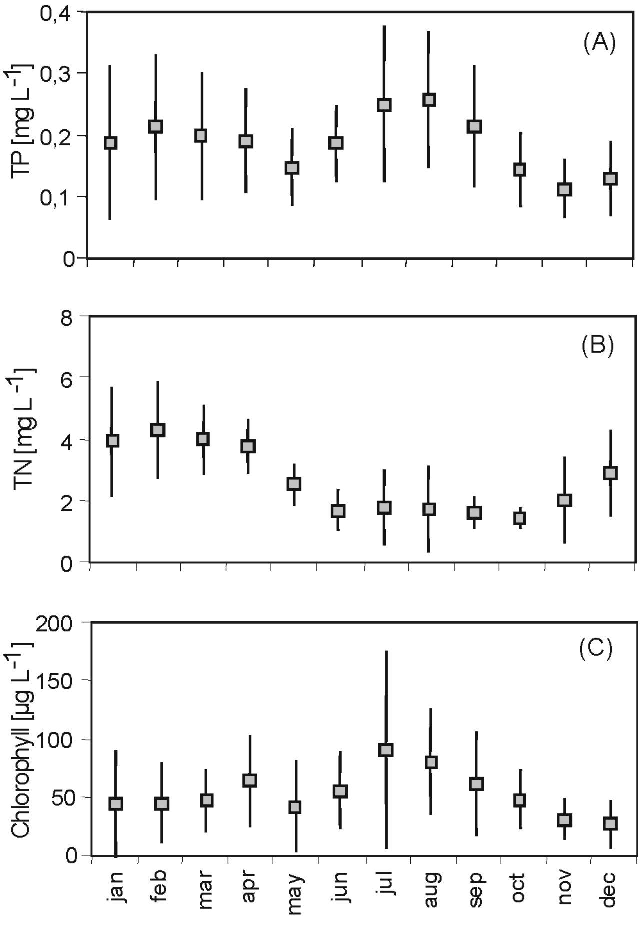

Fig. 2. Seasonal concentrations of TP (A), TN (B), and chlorophyll *a* (C) in Lake Altmühlsee in 1994–2002, data are means ± s.d.

The mean concentration of total phosphorus (TP) showed a first maximum in February (0.21 mg L^{-1}) and a second one in August (0.26 mg L^{-1}) (Fig. 2). An increase of TP

Table 2

Sediment characteristics of a core of Lake Althühlsee taken in June 2002

	Sediment layer [cm]		
	0–5	9–10	20–22
DW [%]	15.3	23.0	28.6
LOI [%]	12.1	14.4	13.7
TP [mg g^{-1} DW]	1.4*	1.2	0.99
BD-TP [mg g^{-1} DW]	0.29	0.22	0.14

* layer 0–4 cm

during the summer was probably caused by evaporation of water and P-release from the sediment. Monthly water concentrations of SRP ranged from 0.025 mg L^{-1} in May to 0.088 mg L^{-1} in February. The average concentration of SRP for nine years was 0.053 mg L^{-1} changing from 0.039 mg L^{-1} in 1995 to 0.071 mg L^{-1} in 1996. Mean values of chlorophyll-*a* fluctuated from 26 µg L^{-1} in December to 90.2 µg L^{-1} in July with intense within-month deviations. Interannual variations were less intensive than variations within the years. Mean values for the whole study period were 0.19 mg TP L^{-1} and 45.1 µg Chl *a* L^{-1}. According to the OECD classification (Vollenweider, Kerekes 1982) the trophic state of Lake Altmühlsee is hypertrophic (TP>0.1 mg L^{-1}, Chl $a_{\max}$ >75 µg L^{-1}).

Over the 15 year period since construction of the lake, on the average 5–10 cm of sediment were deposited, with a maximum of 25 cm in areas near the islands with low turbulence. Sediment characteristics are shown in Table 2.

Dry weight (DW) of sediment increased with depth from 15.3 to 28.6% of fresh weight. The content of organic matter determined as loss of ignition (LOI) was below 15% in all depth. TP concentrations decreased toward the deepest layers from 1.4 to 0.99 mg g^{-1} DW. For a hypertrophic lake with its high productivity, but also with high mineralization in the water column, the sediment of Lake Altmühlsee had a high dry weight, a low loss on ignition, and a low TP. It appears that the major part of the sediment was allochthonous more or less inorganic material eroded from the agriculturally used catchment area and transported into the lake during high waters.

P-fractionations of different layers showed a quite constant pattern. Significant fractions could be attributed equally to three different P-forms. 19.7–29.6% TP could be found as $P_{(BD)}$ decreasing with depth. $SRP_{(NaOH)}$ came to 21.1–33.5% TP increasing with depth. Finally 22.7–27.2% TP consisted of $NRP_{(NaOH)}$. Less than 0.5% TP ($P_{(NH4Cl)}$) were dissolved in interstitial water or loosely adsorbed. About one tenth (10.0–13.8% TP) was attributed to $P_{(HCl)}$ and another (8.4–10.9% TP) to $P_{(Res)}$. The mobilization of the different P-fractions occurs under different milieu conditions, *e.g.* $P_{(BD)}$ might be released under reducing conditions and $NRP_{(NaOH)}$ might be released due to mineralization. Nevertheless, not the total, but only a part of each fraction is really released during diagenesis. In Lake Altmühlsee, the released part appears to be very small. There was only little decrease of TP with depth and little change of P-fractions when the actual sediment composition was compared with the earliest sediment layers settled about 1986. Even the P-content of the uppermost layer was not increased (Fig. 3). Thus, the P-turnover in Lake Altmühlsee seems to be extremely fast and occurred already in the water above sediment during the sedimentation of the particles and during sediment-resuspension. Another explanation for the quite constant pattern might be intensive sediment mixing due to bioturbation or resuspension.

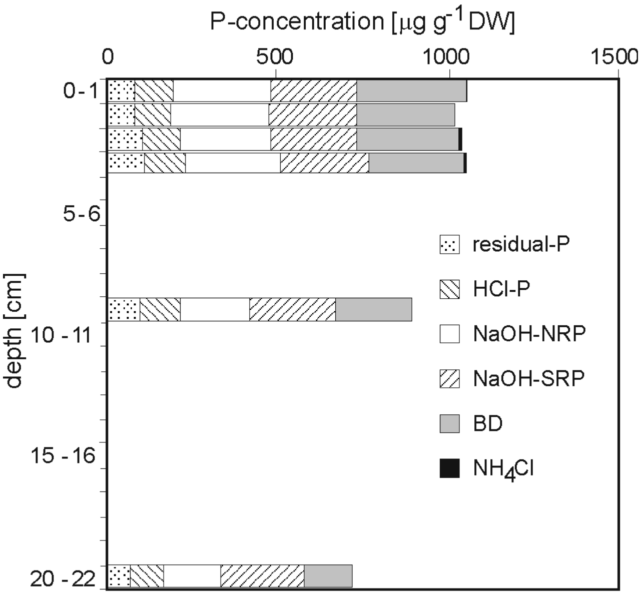

Fig. 3. Different P-fractions according to Psenner *et al.* (1984) of a core of Lake Altmühlsee taken in June 2000.

Lake Altmühlsee revealed an increase of TP during the summer (Fig. 2), and P-release was calculated for all periods without water exchange (Table 3). The calculated net releases were extremely high confirming the intense P-turnover of the lake. However, the periods without water exchange are by no means uniform, they include calm periods with short-term stratification and anoxic sediment-water interface as well as stormy periods with sediment resuspension. Hence, completely different mechanismus for P-release (pH- and redox-mediated as well as physical mechanisms) account for the figures in Table 3.

In shallow lakes, internal P-load might temporarily be as important as external P-load (*e.g.* Søndergaard *et al.* 1996). However, in the annual balance sediments of shallow lakes are always a P sink unless an adaptation to a new steady state causes a temporal imbalance (Søndergaard *et al.* 2003). P-release in Lake Altmühlsee might be mostly caused by mineralization of detritus and pH-controlled desorption after sediment resuspension. High temperature in the whole water column (20 °C in summer) warmed up the upper layers of sediment. Increasing bacterial activity enhance the mineralization of both newly settled detritus and organic matter settled during winter (Søndergaard *et al.* 1999). The degradation process leads to an increase of SRP in the pore water and of SRP-fluxes into the water body. In summer months, pH in Lake Altmühlsee reached values up to 9.5 due to high photosynthetic activity. In case sediment particles come into contact with water of high pH increased concentrations of

Table 3

Phosphorus release in Lake Altmühlsee as total load [kg] and flux rate [mg m^{-2} d^{-1}] for TP and SRP calculated for periods without water exchange

Period without water exchange	TP		SRP	
	[kg]	[mg m^{-2} d^{-1}]	[kg]	[mg m^{-2} d^{-1}]
20/06 – 06/07/1994	1154.8	22.6	23.8	0.5
14/08–30/08/1995	742.4	14.5	80.7	1.6
30/07–27/08/1996	1148.5	12.8	984.4	11.0
14/07–30/07/1997	695.9	13.6	282.0	5.5
27/08–08/09/1997	1291.8	33.6	1527.5	39.8
03/06–15/06/1998	1948.5	50.7	577.6	15.0
14/06–30/06/1999	768.4	15.0	-227.6	-4.4
28/07–09/08/1999	1129.8	29.4	394.7	10.3
29/05–14/06/2000	744.6	14.5	383.0	7.5
25/06–09/07/2001	1028.1	22.9	827.2	18.5
20/08–03/09/2001	1294.4	28.9	-16.4	-0.4
19/08–02/09/2002	922.4	20.6	439.9	9.8

Table 4

Fluxes [mg m^{-2} d^{-1}] at the sediment-water interface of Lake Altmühlsee in June 2003

	Dialysis sampler West	Dialysis sampler East
SRP	9.1	6.8
Mn	5.3	2.7
Fe	3.6	4.6

OH^--ions reduce the binding capacity of iron and, in turn, the adsorption capacity of metal hydroxides is diminished (Ohle 1938, Lijklema 1977, Søndergaard 1988). Usually, pore water pH remains low due to respiration of organic matter near the sediment surface and a subsequent weak lowering of the pH (Søndergaard 1988). In Lake Altmühlsee wind-induced sediment resuspension might have caused a contact of sediment particles and lake water resulting in intense P-mobilization. Furthermore, foraging benthivorous fish, especially bream, are known to stir up sediment during their search for food. Sediment, taken in by sucking, is filtered through the gill raker system. Food particles are retained and sediment particles are discharged through the gill to the water column where they become suspended. Reductive dissolution of iron-bound P in the anoxic sediment might be an additional P-mobilization mechanism during calm periods and subsequent stratification and reduction of the physical and chemical oxygen depots. The mobilized P was transported into the water body by molecular diffusion, bioirrigation and convective water transport due to resuspension.

Fig. 4 shows the pore water profiles at two locations of Lake Altmühlsee for SRP, dissolved Fe and dissolved Mn. At the west located dialysis sampler SRP-turnover was estimated as a P-mobilization of 2.35 µg m^{-3} s^{-1} in the upper 3.7 cm and a smaller P-mobilization of 0.13 µg m^{-3} s^{-1} in the following 14.8 cm. At the east located dialysis sampler SRP-turnover was estimated as a P-mobilization of 1.25 µg m^{-3} s^{-1} in the upper 6.4 cm followed by a P-fixation, another P-mobilization and another P-fixation zone. Manganese and iron showed a similar pattern with an intense mobilization zone at the sediment-water interface and an underneath layer with little fixation or mobilization. Fluxes at the sediment-water interface were calculated on the basis of the smoothed profiles (Table 4). Smoothing using Profile V 1.0 eliminated the random scattering of the measured values and, thus, resulted in a qualitatively better estimation of the P-fluxes across the sediment-water interface. Nevertheless, the course of the smoothed profiles depends on the chosen boundary conditions. Another problem of using pore water profiles in shallow lakes is the intense small scale heterogeneity (Lewandowski *et al.* 2002). Thus, few deployments of dialysis samplers are not representative and calculated fluxes might vary with a factor of more than 10 (Lewandowski *et al.* 2003).

The uppermost layers of P-mobilization (Fig. 4) were much broader than expected according to the P-fractionation results (Fig. 3). This contradiction might be a consequence of pore water heterogeneity or further transport processes operating in addition to molecular diffusion on which Fick's first law, and the calculation using Profile V. 1.0 are based on. Bioirrigation and convective water transport caused by resuspension might cause a flattening of pore water profiles and broadening of turnover zones. Comparing the SRP-release rates calculated on the basis of pore water profiles (Table 4) and the TP-release rates calculated on the basis of the mass balances (Table 3) shows that fluxes calculated on the basis of molecular diffusion (dialysis sampler) were much lower than fluxes on the basis of a mass balances. SRP release rates are compared here with TP release rates, since P released as SRP is soon transformed into TP in the water body. The discrepancy of the two rates indicates, that, bioirrigative fluxes and convective fluxes were very important in addition to diffusive fluxes taken into account with a dialysis sampler.

Summarizing, external load into Lake Altmühlsee was high. P-turnover (decomposition, ligand exchange, redox-induced P-mobilization) processes in the water body and at the sediment-water interface were very fast. Transport limitation did not occur due to intensive bioirrigation and resuspension operating in addition to molecular diffusion. The P-pool stored in the sediment was of minor importance.

Plankton

Despite its hypertrophic state, Lake Altmühlsee showed a high diversity of phytoplankton (more than 85 species). Composition and total biomass changed over the study period. During the earlier years (1994–1998), the phytoplankton of Lake Altmühlsee was mainly composed of cyanobacteria and cryptophyte, together comprising 40–80% of total biomass. Excluding cyanobacteria, biomass normally averaged 1.5–1.8 mg L^{-1}, except in 1998 (2.9 mg L^{-1}) due to an intense bloom of the dinophyte *Gymnodinium tenuissiinum* in February (Fig. 5). Maximum biomass (3.3–9.4 mg L^{-1})

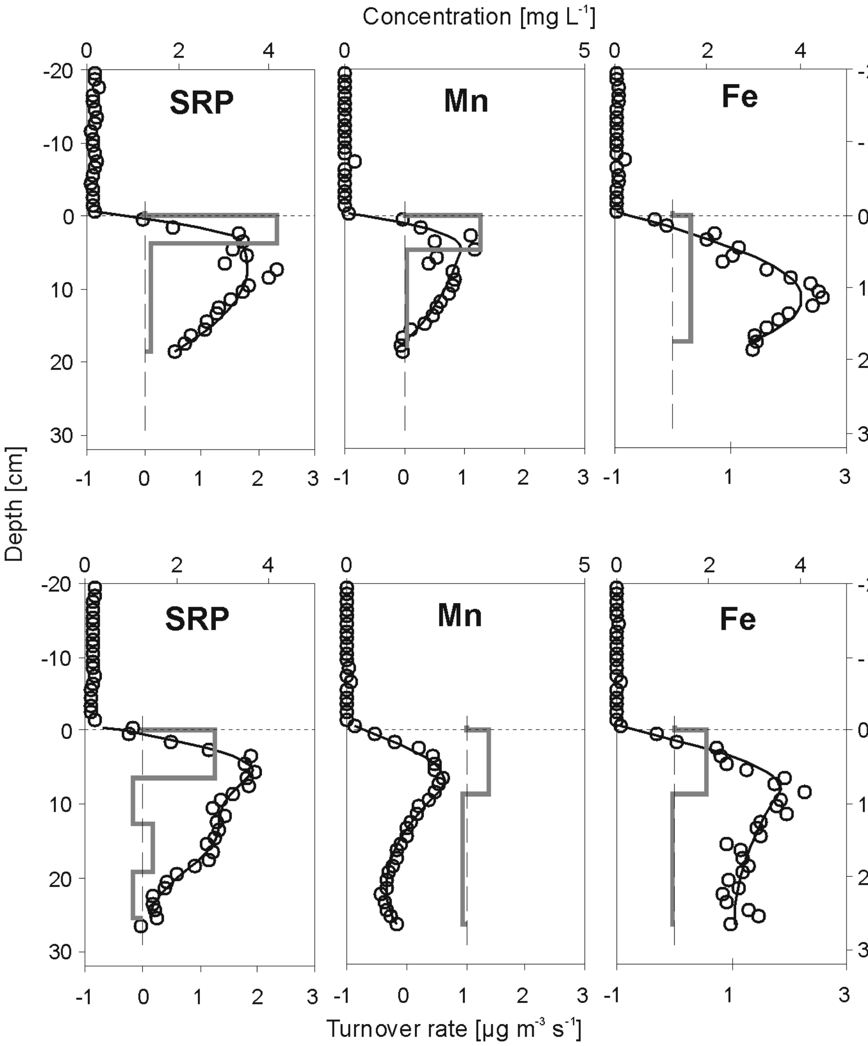

Fig. 4. Pore water concentration profiles of SRP, dissolved Fe, and dissolved Mn for two sampling locations (upper row: west located dialysis sampler, lower row: east located dialysis sampler) taken in June 2003. The mobilization rates, the fixation rates, the smoothed graphs and the coefficients of determination R^2 were calculated with the program Profile V 1.0 (Berg *et al.* 1998).

usually occurred during fall and winter. Starting in 1999, the chlorophyte *Planktosphaeria gelatinosa* became a prominent species with single maxima up to 3.3 mg L^{-1}. Only during massive cyanobacteria blooms, maxima of 20–74 mg L^{-1} were measured.

During the winter/spring period the phytoplankton was dominated by fast-growing edible species, mostly cryptophytes *Cryptomonas* ssp. and, to a lesser extent, by *Rhodomonas* spp. Breakdown coincided with SRP-depletion (SRP below detection limit). Cryptophytes were replaced by diatoms, especially *Stephanodiscus* ssp., and dinophytes belonging to the genera *Gymnodinium* and *Peridinium*. In most years a short lasting clear water period of 5–10 d followed. Later in the year, edible plankton was replaced almost every year by species resistant to grazing. Succession of phytoplankton continued with the development of chlorophytes mainly consisting of *Oocystis* ssp., *Monoraphidium* ssp., *Planktosphaeria gelatinosa* and some chlorococcales. The N:P-ratio was very low during the summer, and below the physiological optimum for most phytoplankton. Starting in June/July the ratio of dissolved inorganic nitrogen (DIN) to bioavailable phosphorus (SRP) was far below the Redfield ratio of 5.7 (weight/weight) favoring N_2-fixing cyanobacteria. Actually, cyanobacteria, mainly *Aphanizomenon flos-aquae* and sometimes *Anabaena flos-aquae* with some co-occurrence of *Microcystis aeruginosa*, became dominant, often resulting in heavy blooms in July and August. Cyanobacteria were additionally favored by low transparency and high pH. From 2001, cyanobacteria competed against inedible chlorophyceae. At high P-concentrations there are alternative states of dominance of cyanobacteria and green algae depending on turbidity and flush rate (Scheffer 1998). Obviously, there was a switch to the dominance of green algae (2002) with a transition state in 2001. Phytoplankton in fall was dominated by the chlorophyte *Oocystis* ssp. and the cryptophytes *Cryptomonas* ssp. or the chlorophyte *Planktosphaeria gelatinosa* respectively. In some years, euglenophytes (*Phacus* ssp., *Trachelomonas* ssp., *Euglena* ssp.) reached individual peaks (1994: 2.9 mg L^{-1}; 2001: 3.0 mg L^{-1}; 2002: 1.6 mg L^{-1}) in late summer and fall.

The zooplankton community in Lake Altmühlsee is dominated by only a few genera, *e.g. Daphnia* spp., *Bosmina* spp. (two cladocerans), as well as some rotifers (*Asplanchna* spp, *Keratella* spp, *Polyarthra* spp), and copepods. This

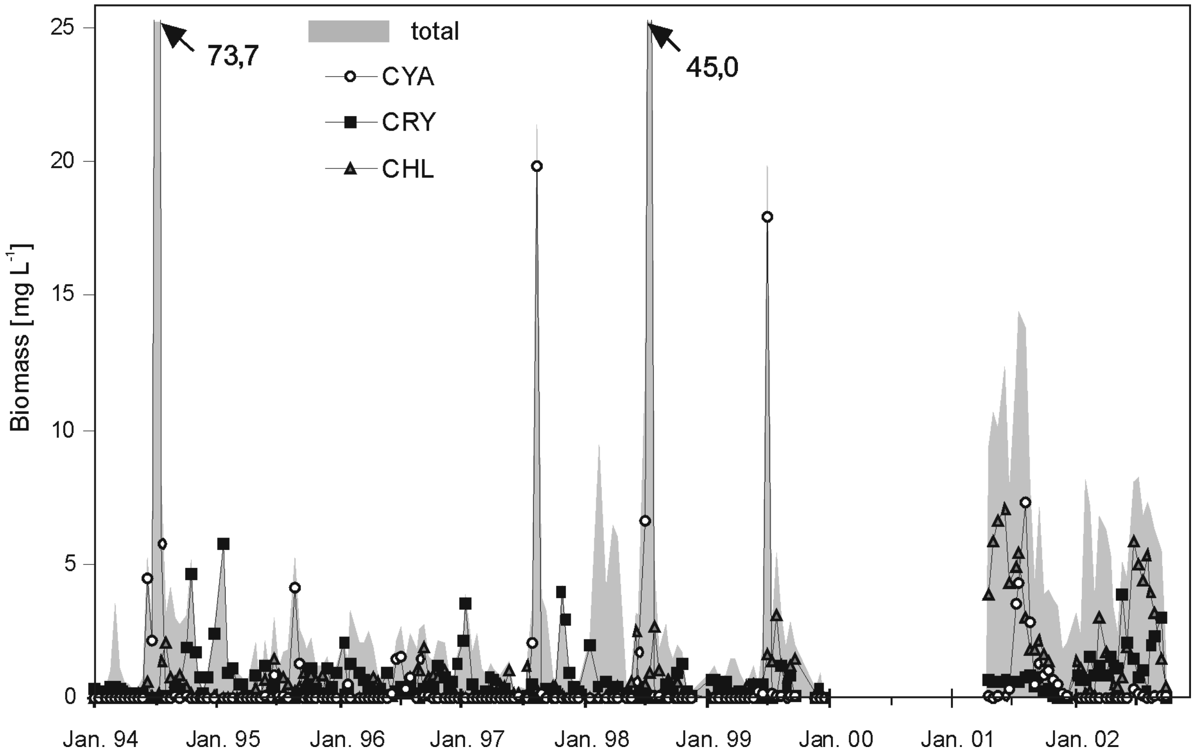

Fig. 5. Biomass of phytoplankton in Lake Altmühlsee for 1994–2002. CYA = Cyanobacteria, CRY = Cryptophytes, CHL = Chlorophytes.

community is typical for shallow eutrophic lakes with strong fish predation (Jeppesen *et al.* 1996). Most species are microfilter feeders which consume on small algae and detritus. Among the effective filterfeeders only D. *galeata* was of some importance. Maximum edible particle size was determined as 50 µm by measuring the intersetulae (Schatz 1997). During wintertime and in early spring the abundance of zooplankton was very low, mainly consisting of the rotifers *Polyarthra remata*, *Keratella* spp. as well as cyclopoid nauplii and copepodits (Fig. 6).

Cyclops vicinus or its copepodits dominated the zooplankton during March/April. In May, *Daphnia* spp. had a first small maximum followed by a fast breakdown. The main zooplankton peak occurred in June/July, mainly composed of rotifers. Particularly highly abundant were the herbivorous *Brachionius* spp., *Polyarthra dolichoptera/remata*, and *Asplanchna priodonta*. both known as unselective microfiltrators and equally herbivorous and carnivorous/omnivorous (Kohmann, Steinberg 1982). The extreme maximum in June 1996 was comprised by a unique mass occurrence of *Polyarthra vulgaris* with 2,390 Ind. L^{-1}. Cladocerans almost simultaneously had a summer maximum, yet not quite reaching such high levels. The community was alternatively dominated by daphnids and bosmids. *Bosmina* spp. was favored in times of low food conditions. The edible algae concentration was temporarily below 0.1 mg C L^{-1} where *Daphnia* should be growth limited. The small cladocerans were obviously favored in these periods of times. Mostly there was a co-occurrence of unselective microfilter feeders like the rotifers *Brachionius* and *Keratella* which may feed flagellates, bacteria, and ciliates (Arndt 1993). Suppression of daphnids might additionally be due to low food quality. Non-toxic cyanobacteria reduce the growth under non-limited conditions (Kurmayer 2001). Cyanobacteria are nutritionally inadequate due to a deficiency in polyunsaturated fatty acids and P (Gulati, DeMott 1997, von Elert 2002, Wacker *et al.* 2002). A low P content in the diet promotes the abundance of zooplankton with low P-requirement like cyclopoid copepods, *Bosmina* spp. and possibly *Chydorus* (DeMott, Gulati 1999, Gulati, van Donk 2002). Additionally, the small cladocerans might benefit from detritus and bacteria attached to the filaments of *Aphanizomenon flos-aquae* (Kurmayer 2001). Normally, *Daphnia* spp. dominated after a short peak of *Bosmina* spp. As *Bosmina* is a size-specific grazer in a narrow size range, edible algae out of this range might be available to *Daphnia* (Cyr, Curtis 1999). Yearly maxima of dominating *Bosmina longirostris* were between 194 and 546 Ind. L^{-1} occurring in July/August with the exception of July 14, 1997 (2,326 Ind. L^{-1}). Highest amounts of *Daphnia* spp. fluctuated from 92–210 Ind. L^{-1}. *Daphnia* spp. consisted mainly of *D. galeata*, *D. cucullata* and to a lesser extent of *D. parvula* (Fig. 7). *D. pulex* and *D. ambigua* were neglected due to only short-term appearance in certain years, and their disappearance since 1997.

Body size of all three species was smaller than described in the literature (Schatz 1996). Reasons may lie in size-specific predation or fish kairomone (Mikulski 2001). The presence of fish may induce cladocerans to spend their energy for reproduction instead of somatic growth to mature earlier at smaller sizes (Ślusarczyk 1997). The occurrence of small *Daphnia* might, however, also result from food-limiting conditions. Large adults may starve due to a time lag in adaptation of the combs to decreasing food supply (Hülsmann, Weiler 2000). *D. galeata* additionally showed a strong decrease in June which is was not seen for *D. cucullata*. While in the early years, the *Daphnia* community was domi-

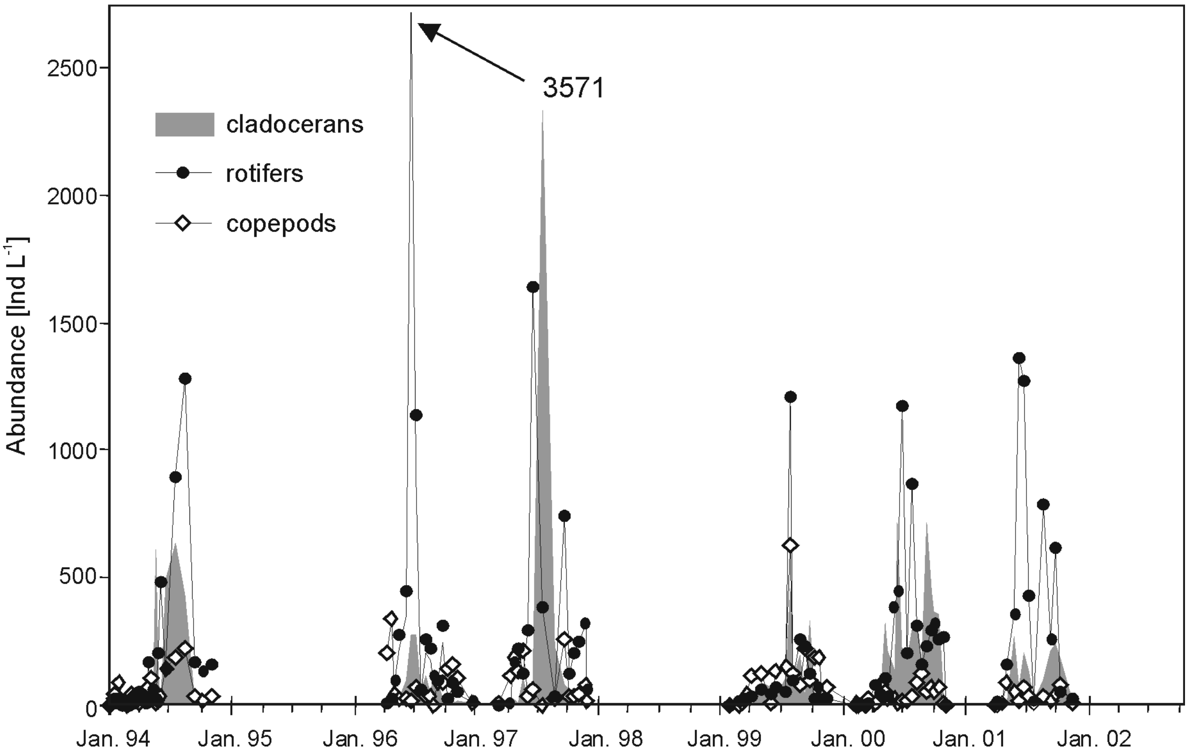

Fig. 6. Abundance of zooplankton in Lake Altmühlsee for 1994–2002; data not shown were not determined.

nated by *D. galeata*, the smaller *D. cucullata* gradually tool over and dominated in later years. This may be an indication of increasing predatory pressure by fish (Lammens 1999).

Fish

Gillnetting and electro-fishing in Lake Altmühlsee resulted in a cath of 701 fishes with a total biomass of 226 kg. The fish assemblage consisted of 17 species. Bream dominated by numbers and by biomass (Table 5). Other important species were carp, white bream, and pikeperch. Pike was mainly caught in the littoral by electro-fishing.

Dominance of the cyprinids is quite common in shallow eutrophic lakes due to their capability to filter-feed in turbid waters, their high nutritional plasticity, a high reproduction rate with low demands on the quality of spawning locations and the low predatory pressure in such lakes (see Peltonen *et al.* 1999, Olin *et al.* 2002).

Bream and white bream showed a broad size distribution with a remarkably high proportion of large individuals.

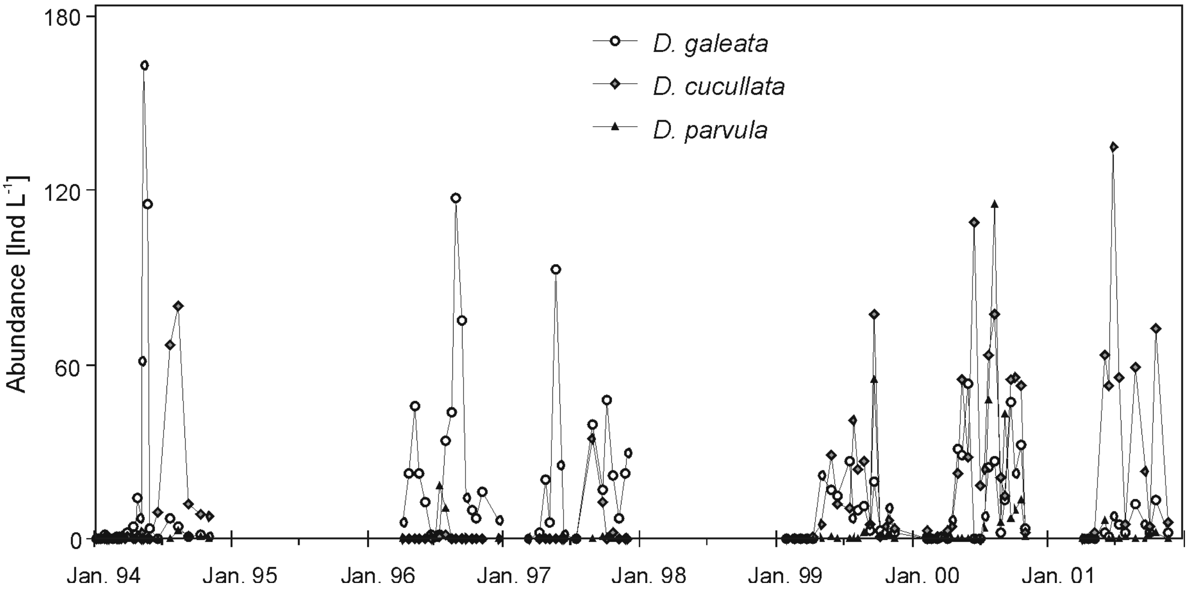

Fig. 7. Co-existence of three *Daphnia* species, *D. galeata*, *D. cucullata*, and *D. parvula* in Lake Altmühlsee.

Table 5

Fish species composition in Lake Altmühlsee in April 2000; gillnet catches, mesh widths 5–90 mm

	numbers %	biomass %
Bream (*Abramis abramis* L.)	83.7	43.8
White bream (*Abramis bjoerkna* L.)	3.3	7.0
Pike (*Esox lucius* L.)	0.2	1.5
Ruffe (*Gymnocephalus cernuus* L.)	2.0	0.3
Carp (*Cyprinus carpio* L.)	0.5	20.4
Roach (*Rutilus rutilus* L.)	6.5	1.7
Asp (*Aspius aspius* L.)	0.7	9.7
Pike-perch (*Sander lucioperca* L.)	2.4	14.4
Miscellaneous	0.7	1.1
Total	100.0	100.0

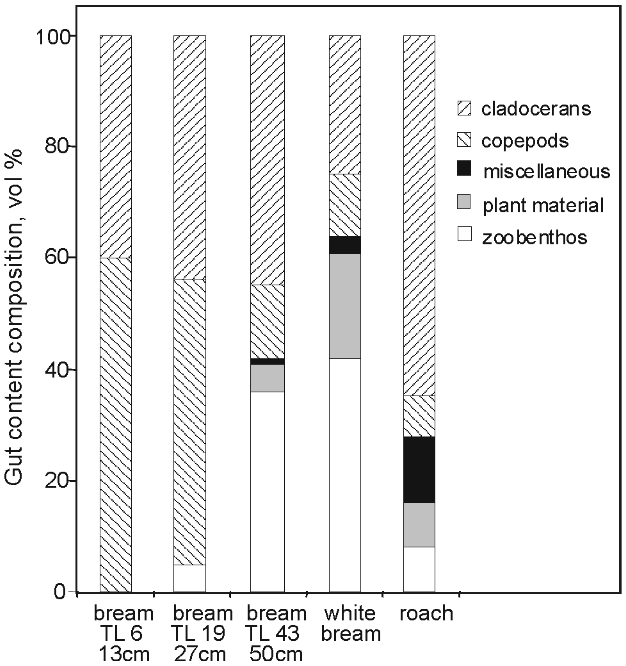

Fig. 8. Diet composition of different cyprinids of Lake Altmühlsee in April 2000. TL = total length.

Bream and white bream are known to switch from benthos to zooplankton in times of food shortage or high *Daphnia* density. Therefore, the diet composition of the potentially planktivorous species was investigated. In Lake Altmühlsee only bream, white bream, and roach were sufficiently abundant to potentially control the daphnids. To prove this assumption, the gut content of 126 breams in three different size classes, 9 white breams and 15 roaches were analyzed.

Zooplankton was separated into copepods and cladocerans, >80% of which belonged to *Daphnia* spp.. Zoobenthos was made up mostly by Chironomid larvae. All groups investigated included zooplankton in their diet to different proportions (Fig. 8). The gut content of the mainly planktivorous roach consisted of 70% zooplankton and 12% fresh water mites. The diet of adult white bream consisted of almost equal amounts of zooplankton and zoobenthos. All length classes of bream intensively fed on cladocerans, accounting for 85% of the overall cladoceran consumption (Fig. 9).

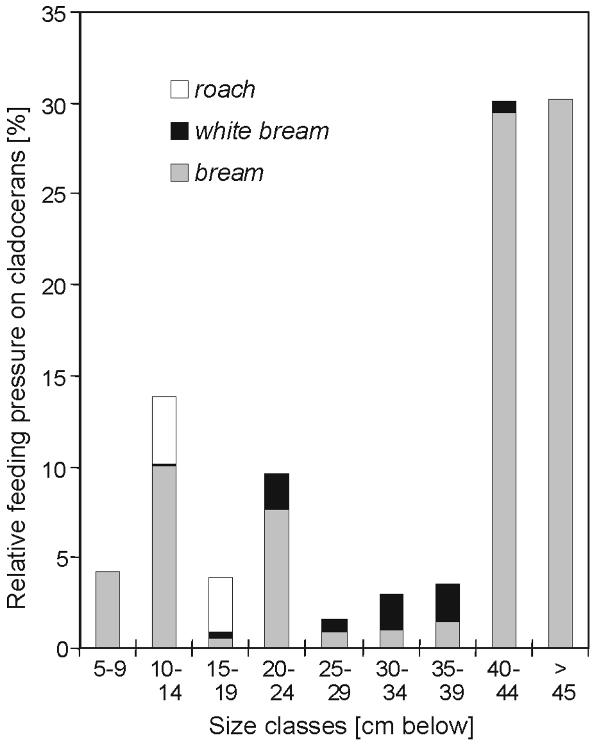

Fig. 9. Distribution of cladoceran consumption in April 2000 between the different planktivorous fish species and length classes. Data are calculated by multiplying (a) the biomass of the fish species or length class in the gill net catches, with (b) the proportion of cladocerans in the gut content, and with (c) the maximum daily ration per g wet weight following Hölker (1999).

As fish matured, they relied more heavily on zoobenthos and plant material for food; nevertheless cladocerans made up 40–45% of this diet. These results were supported by corresponding investigations in 2001 (unpublished results). Remarkable is the importance of the large size groups for total cladoceran consumption: bream and white bream with a total length of more than 40 cm accounted for more than 60% of the cladoceran consumption (Fig. 9).

PROPOSALS FOR LAKE MANAGEMENT

Lake Altmühlsee is very well fulfilling its primary purposes as a water storage and flood protection reservoir. Secondary use of the lake for recreational purposes is restricted due to low water quality. At present, Lake Altmühlsee is characterized by low Secchi depth for most time of the year due to distinct phytoplankton development. High turbidity is intensified by sediment resuspension. Inflow of P occurs mainly via particle-bound P in eroded material settling in the lake, which may be released during the summer as described above. TP is oscillating over the course of each year with peaks in winter from water inflow and in summer due to internal load from sediments.

Due to the intense algal blooms there is a need to improve overall water quality to increase attractiveness and utility value. However, the primary functions of the lake somewhat limit the options for remedial actions. Particularly, hydrological management of water quality may not be employed. Wastewater treatment is already optimized and cannot lead to a further substantial decrease in P-inflow. Flushing with nutrient-poor water is nearly impossible and will be rendered ineffective by the subsequent flood. For similar reasons, chemical P-fixation would be ineffective, besides being very expensive. The quality of the water in Lake Altmühlsee is mainly determined by its inflow, and its eutrophication is largely a result of the high P load from its agricultural catchment area. Therefore, improvement in water quality should concentrate on a reduction of nutrient inflow to the lake. To reduce the input of P bound to suspended solids, extended buffer zones of vegetated strips could be established along river banks in the intensively agriculturally exploited catchment area. However, such measures would only partially lie within the responsibilities of the lake authorities, and may become severely hampered by opposition from local farmers. That means that external measures in the catchment are very limited. Hence, only internal biomanipulation measures will be discussed with respect to their appropriateness.

Moss *et al.* (1996b) present a nice shopping list of measures. According to their 6-step restoration strategy, implementation of the following steps may help to improve water quality:

– remove any forward switches to turbidity

– reduce nutrient load as far as possible to increase the change of stable recovery

– manipulate fish community to favor algae grazing species (biomanipulation)

– re-introduce plants, where appropriate, and protect against damage (birds, waves)

– re-introduce an appropriate fish stock (high piscivorous:planktivorous fish ratio) when plants are established

– monitor the situation.

Forward switches of plant damage include activity of fish such as common carp (*Cyprinus carpio* L.), of aggregations of birds, as well as mechanical cutting and pesticide applications (Moss *et al.* 2002). Even a few large carps can disturb sediments by foraging, plant eating, and uprooting and, hence, enhance P-release from sediment (Moss *et al.* 1996b). In Lake Altmühlsee, common carp was only stocked in early years. In agreement with the fishing rights holders, carp will need to be completely removed; there are sufficient carp ponds for fishing in the surrounding area. High bird aggregation occurs only in the nature reserve, especially in fall, but total bird numbers are low and not considered to have a major impact.

Reduction of internal P-turnover is desirable in order to increase the DIN:SRP ratio. This will suppress one mechanism which promotes the development of N_2-fixing cyanobacteria. As described above, P-release is maintained by several factors, and one key factor in restoration will be the removal of benthivorous and planktivorous fish resulting in:

– reduced predation pressure on cladocerans improves the filtering capacity of effective grazers, and thus reduces the turbidity caused by phytoplankton;

– fish reduction will lead to an increase of Secchi depth due to the suppression of sediment resuspension from foraging;

– improved light climate will cause phytoplankton, especially cyanobacteria, to be less competitive and allows development of macrophytes;

– decreased phytoplankton growth will help to keep pH below the critical levels for P-release by ligand exchange and development of cyanobacteria; less detritus will cause a decrease of bacterial degradation activity, hence P-release from the anoxic sediment will be less intensive.

Lake Altmühlsee is well suited for fish reduction due to its flat pool form. Total mortality of bream should be increased to at least 0.5, as otherwise this species can compensate losses by high recruitment (Lammens *et al.* 2002). Biomanipulation at a nutrient level as high as in Lake Altmühlsee may result in only a temporal switch to a clear water state, and repeated fish stock reduction may be required for stabilization (Meijer 2000). On the other hand, biomanipulation may lead to a decrease of in-lake P-concentrations (Hansson *et al.* 1998, Annadotter *et al.* 1999), resulting in a stable fish stock (Meijer 2000).

Macrophytes establishment will be very complicated in Lake Altmühlsee. *Polygonum amphibium* is the only plant previously established in the lake. The floating macrophyte descended from sediment of the former river and completely disappeared after a mechanical cut. Swimmers, surfers, and sailors would oppose re-establishment. There are two major obstacles to macrophyte establishment: First, the water level is changing approximately 0.5–0.75 m over the year. Secondly, littoral zones almost do not exist due to the pool form of the lake. Initial biomasses of seed banks and propagules have to exceed a critical threshold level for successful plant colonization (van Nes *et al.* 2002). A plant volume infested (PVI) of 15–20% was demonstrated to be sufficient for cladoceran survival in one specific case study (Schriver *et al.* 1995). Perrow *et al.* (1999), however, found a PVI of 40% required as an adequate refuge especially at high fish density (1 m^{-2}) in another case study. Concluding, the PVI has to be figured for each individual lake. In case of Lake Altmühlsee, costs of establishing such a quantity are prohibitive. Only specific areas should be planted where macrophytes can grow in sheltered areas and spread out (Moss *et al.* 1996b). At several regions of the shore, artificial lake banks should be built to allow the growth of emergent and floating-leafed plants. The emergent plants are advantageous under changing water levels as they are able to tolerate situations when the water table falls below the soil surface. Reed (*Phragmites australis*) is recommended as it already grows on the shore, together with cattail (*Typha latifolia*, *T. angustifolia*). Floating-leaved plants should be planted in parts with a permanent water body, because they are usually not able to survive times of drying out. Water lily beds may act as refuges against predation for *Daphnia* particularly in lakes dominated by bream and roach (Moss *et al.* 1998). These weed beds will later provide lurking habitat at their edges for pike (Moss 1990, Skov, Berg 1999). Beds of submerged macrophytes should be established around recreational areas as they can aid to substantially increase Secchi depth by enhanced sedimentation while not being in the way of swimmers, surfers, and sailors if kept deep enough below the water surface. Best development can be expected in slightly wind-exposed sites due to less epiphyte growth, less intense waterfowl grazing and higher densities of the sediment (Weisner *et al.* 1997). A pioneer plant community may be built up by *Potamogeton pectinatus* and *Myriophyllum spicatum* which both already exist in the River Altmühl. Dredged sediment of the river from renaturation measures should have high inoculum and can be used as a cheap and adequate source. Later on, sediment with inocula of the macroalga *Chara* spp. might be added to get dense meadows. The establishment of strips with submerged macrophytes may result in local clarity of the water (van den Berg *et al.* 1998, van Nes *et al.* 2002). This will be sufficient for water-sportsmen and possibly allow a further spreading out of plants.

The adjustment of the fish stock will need to be left to the owners of the fishing rights. However, qualified recommendations for the owner of the fishing rights are advisable. Increase of piscivory should focus on the establishment of pike as a large and effective predator. Smaller fish are already hunted by pike-perch which is well established. Stocking can be done by 0^+- or 1^+-pike. A small community of pike already exists in the nature reserve which is more structured by small islands macrophyte belts. Pike may be rather hampered by missing vegetation than by turbidity. Jepsen *et al.* (2001) found pike in a turbid reservoir closely related to restricted areas of vegetation and in good food conditions. Newly created weed beds should offer more hiding places. Additionally artificial refuges like fresh felled spruce trees will enhance the survival of 0^+-pike, which otherwise may be poor (Skov, Berg 1999, Skov *et al.* 2002), and may therefore also ease the stocking effort. Fish stock management must be combined with regulation of fish removal by sport anglers. Catches of piscivorous fish must be restricted by size and amount per day. At present, bream has a low market value in Franconia, hence its attractiveness needs to be increased. In the Netherlands living bream are now caught for stocking angling ponds (Lammens *et al.* 2002).

CONCLUSIONS

Remedial of Lake Altmühlsee eutrophication will likely not result in complete restoration but rather in a partial improvement of water quality since external nutrient load can hardly be decreased. Realistic goals include an enhancement of Secchi-depth to approximately 1 m and suppression of cyanobacteria blooms. A combination of planktivorous fish reduction, increase of pike community, and establishment of macrophytes may lead to a local clear water state which may stabilize itself over coming years and spread. Adequate measures may result in indirect P-reduction due to feed-back mechanisms. Monitoring the system is necessary to repeat the applications if turbidity increases. The lake will probably require frequent adjustment of the fish community. Successful and long-lasting recovery can only be reached by co-operation between the responsible authorities and the various special interest groups (Mehner *et al.* 2002).

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