

# Integrated management to restore macrophyte domination

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### Abstract

Recent changes which have been observed at Alte Donau, a shallow urban lake within the city of Vienna, have been interpreted as a shift to a new stable state. The former macrophyte-dominated state changed to a turbid state dominated by high biomass of filamentous cyanobacteria, associated with a significant reduction in Secchi-depth. Phytoplankton was dominated by the filamentous cyanobacterial species *Cylindrospermopsis raciborskii* (Wolosz.), Seenayya et Subba Raju and *Limnothrix redekei* (Van Goor) Meffert. Integrated restoration plans included internal and external measures. Improvements in the catchment aim to minimize the input of nutrients from contaminated groundwater and from storm water and to reduce large numbers of water fowl. Internal restoration measures included water exchange, chemical flocculation and nitrate oxidation of the sediments. Additionally, macrophyte re-colonisation was enhanced through planting. A pelagic predator (*Aspius aspius* L.) was stocked to reduce bleak (*Alburnus alburnus* L.), the dominant cyprinid planktivore. Results from the period after water exchange and chemical treatment, showed significant reduction of nutrient and chlorophyll *a* concentrations. A shift in the phytoplankton species from cyanobacteria towards diatoms and greens was observed. Secchi depth greatly increased. Macrophyte growth became apparent both through re-colonisation, as well as from the planting.

### Introduction

Scheffer et al. (1993) showed that at intermediate nutrient concentrations shallow lakes are either dominated by macrophytes and characterized by clear water, or abundant phytoplankton biomass and low visibility. These two situations may be seen as alternative stable equilibria. This implies that the system, when in equilibrium, is resistant to disturbance and tends to return to equilibrium when disturbed (Blindow et al., 1993). The switch from one to the other stable state can occur as a catastrophic feature, or an ecosystem can oscillate between the two equilibria over longer time periods.

The recent changes in a shallow lake in Vienna, from a macrophyte-dominated state to a turbid state, dominated by high biomass of filamentous cyanobacteria, have been interpreted as a shift to a new equilibrium, and restoration measures have been instigated to reverse the process.

#### Site description

The Alte Donau, a backwater of the river Danube, was formed during the regulation of the river in the last century (1870–1875), when the former main course was cut off. The water body is subdivided into two main basins of almost equal size, connected by a narrow passage (Figure 1). Hydrological conditions of the Alte Donau are entirely dependent on groundwater exchange and precipitation, because there is no natural surface inflow or outflow. The nearby river Danube and especially the impoundment Neue Donau, which was built to protect the city from flood events, both influence the direction and dynamics of the groundwater. The Alte Donau nowadays is a shallow urban lake within the city of Vienna and a very popular recreation area.

The altitude of the lake is 157 m.a.s.l. It has an area of  $1.6 \text{ km}^2$  and an average depth of 2.3 m. The maximum depth is 6.8 m. A theoretial retention time of



Figure 1. Location of the study site. Arrows indicate direction of groundwater flow in the northern basin.

Table 1. Morphological and hydrological data of Alte Donau according to Löffler (1988) and Ripl (1995).

Parameter	Dimension	
Height above sea level	157 m	
Area of northern basin	0.62 km <sup>2</sup>	
Area of southern basin	0.97 km <sup>2</sup>	
Volume of northern basin	$1.43 \times 10^6 \text{ m}^3$	
Volume of southern basin	$2.227 \times 10^{6} \text{ m}^{3}$	
Mean retention time	180 days	
Maximum depth	6.8 m	
Mean depth	2.33 m	

150–210 days (mean value 180 d) was deduced from chloride dilution rates (Ripl, 1995). The Alte Donau is polymictic (Löffler et al., 1988), sometimes stratifies, but never for long periods. Morphological and hydrological data are summarized in Table 1.

## Conditions in the past and present changes

Evidence from the literature suggests that phytoplankton dominated in Alte Donau in the beginning of this century (Brunnthaler, 1907; Schiller, 1929). In the past decades, the water body was characterized by high transparency, low chlorophyll *a* concentrations and extensive macrophyte growth. The dominant species in the lake were *Myriophyllum spicatum* L. and *Potamogeton pectinatus* L. Charophytes like *Nitellopsis obtusa* (Desv. in Lois) J. Groves, *Chara tomentosa* L. and *Chara hispida* Wood were also abundant (Löffler, 1988). A similar macrophyte composition was reported from the swedish lakes – Lake Takern and Lake Krankesjon – which have shifted several times between a clear-water state and a turbid state (Andersson et al., 1990; Blindow et al., 1993).

Significant numbers of the blue-green algae *Limnothrix redekei* (Van Goor) Meffert were first recorded in water quality samples in the year 1992. Microscopical observations in the following year revealed a substantial domination of *Cylindrospermopsis raciborskii* (Wolosz.) Seenayya et Subba Raju. Average annual chlorophyll *a* concentrations increased substantially and secchi depth decreased (Dokulil, 1994; Mayer et al., 1997). Associated with these changes was a remarkable decline of submerged macrophytes. Within two years, only remnants of macrophyte and charophyte stands were left (Dokulil & Janauer, 1995).

Several reasons were believed to be responsible for the shift from a clear water state to a turbid state in Alte Donau. These were:

- 1. Changes in water level dynamics.
- 2. Increased nutrient input.
- 3. Insufficient lining of the sewage network.
- 4. High stocks of water fowl.
- 5. Extensive recreational activities.
- 6. High stocks of benthivorous and planktivorous fish.

Water level fluctuations for the period from 1958 to 1993 are shown in Figure 2. Reduced water level dynamics, in combination with a higher water level, can be seen from the late 1970s onwards. The mean water level calculated for the period from 1978 to 1993 was about 37 cm higher than in the period before. Similarly the range of water level fluctuations decreased by 1 m. The sharp transition in hydrological dynamics in 1978 are basically due to the nearby construction of a highway and the impoundment Neue Donau.

Nutrient input from non point sources is a major problem in the Alte Donau. Associated with the rise of the water level in the 1980s was a change in the direction of flow in the northern basin, such that nutrients were eluated from a former dump site (Figure 1). Leakage of septic tanks and insufficient sewerage in the catchment area also contributed to nutrient loading. Additional nutrient input originated from the excretion of water fowl and from recreation activities. Phosphorus input by water fowl was estimated to be 120 kg P (or 53  $\mu$ g l<sup>-1</sup>) in a winter period (Steiner, 1986). Estimation of phosphorus addition by



*Figure 2.* Water level fluctuations from 1958 to 1993. Upper and lower limits of the water level (unfilled area). Mean water level (thick line). Mean water level calculated for different periods (dashed line).

the 400 000 visitors in the summer period amount to approximately 38 kg P or 17  $\mu$ g l<sup>-1</sup> (Dokulil, 1993).

These changes seem to be correlated to the severe decline of the macrophytes similar to observations elsewhere (Scheffer et al., 1993; Blindow et al., 1993). Here, several factors may have combined to cause the loss. Macrophytes were extensively removed by the local authorities as a management practice for many years. Grazing by high densities of water fowl may also have contributed to the disappearence of submerged macrophytes in Alte Donau. According to Steiner (1986), water fowl grazed about 194 tons (wet weight) of macrophytes per year. The disappearence was accelerated through light limitation when phytoplankton began to dominate. The decisive environmental variable for macrophyte decrease is an altered underwater light climate (Chambers & Kalff, 1985).

Recent investigations of the fish community (Waidbacher et al., 1996) revealed a dominance of bleak (Alburnus alburnus L.). The cyprinids roach (Rutilus rutilus L.), rudd (Scardinius erythrophthalmus L.), bream (Abramis brama L.), white bream (Blicka bjoerkna L.) and tench (Tinca tinca L.) were abundant. Common carp (Cyprinus carpio L.) is the main fish stocked. Perch (Perca fluviatilis L.) is also abundant in Alte Donau and the piscivores pike (Esox lucius L.) as well as pike-perch (Stizostedion lucioperca L.) are stocked. An extensive grazing pressure on zooplankton was assumed by the fish community, especially from bleak. Confirmation came from zooplankton studies in 1994 (Dokulil, 1994). Abundances and species composition were typical for eutrophic conditions. Among the crustaceans, small species like Eubosmina coregoni Baird showed higher abundances than larger species such as Daphnia cucculata Sars. These results confirm investigations in 1987 (Löffler, 1988), but are in contradiction to earlier reports, where high species diversity amongst the cladocerans was reported (Pesta, 1928).

As a consequence of increased nutrient input, macrophyte decrease and grazing pressure on zooplankton, cyanobacteria became abundant in 1993 and 1994. The water showed a striking yellow colour and transparency decreased to 30 cm.

Investigations on the benthic communities (Waidbacher et al., 1996) showed a loss of characteristic species and poor diversity of macroinvertebrates in comparison to earlier studies (Löffler, 1988) and to similar backwaters. Lack of habitats in the littoral zone and loss of macrophytes were recognized to be responsible.

### **Restoration measures**

Integrated lake management strategies included external and internal measures. Rapid expansion of the sewerage network was initiated when the problem became apparent. To keep contaminated groundwater from the lake, four pumping wells were constructed between the former dump site and the lake. Recent investigations of groundwater fluxes showed that they have been successfully applied.

As a first step, artificial aeration combined with vertical mixing was performed in 1993 in areas where thermal stratification, and hence oxygen depletion near the sediment were expected to create problems. Substantial nutrient release from the sediment under anoxic conditions, shown by laboratory experiments, could thus be avoided (Dokulil, 1994).

Half of the water volume of the lake was exchanged by water low in nutrient concentrations from the impoundment Neue Donau in December 1993 (Dokulil & Gasser, 1994).

Attempts were made to concentrate most of the water fowl in a small appendix of the north-eastern basin which has been cut off from the rest of the lake. Collecting eggs from the ducks was proposed as a measure to reduce the high stock of water fowl (Steiner, 1986). In addition, people were asked not to feed the birds.

Great efforts were made by the local authorities to plant a reed belt to give more structure to the littoral zone in the southern basin and to enhance sedimentation of organic material. Approximately 10% of the shore line is now covered by a narrow reed belt in this basin. Structuring and revitalisation of the shore line is still in progress. Further investigations will show if restructuring of the shore line can supplement recovery of the benthic community.

Re-colonisation of submerged macrophytes was assisted by planting experiments in 1995. Macrophytes were taken from the impoundment Neue Donau and transferred into experimental areas in Alte Donau. The first results obtained for *Myriophyllum spicatum* L. and *Ceratophyllum demersum* L. are promising.

A pelagic predator (*Aspius aspius* L.) was introduced to the ecosystem to reduce bleak (Waidbacher et al., 1996). In the past three years, Alte Donau was stocked with juvenile as well as with adult fish, approximately 500 kg ann<sup>-1</sup>. It is expected that this biomanipulation will enhance the development of larger cladocerans.

After careful consideration of most of the restoration techniques commonly used, the Riplox-method was selected as the main restoration measure (Ripl 1976, 1978, 1986; Ripl & Lindmark 1978; Ripl & Wolter 1993a, b). It was implemented in spring 1995 in cooperation with the University of Berlin. The method consists of two steps which are performed in chronological sequence (Figure 3). In the first step, FeCl<sub>3</sub> buffered with limestone is added to remove phosphorus and suspended material by chemical and mechanical flocculation. The FeCl3 acts as a barrier against phosphorus release from sediments. In a second step, Ca(NO<sub>3</sub>)<sub>2</sub> is added to the sediments to enhance nitrate oxidation. Nitrate is reduced to elementary nitrogen by anaerobic denitrification. Organic mud is oxidized to carbon-dioxide and water. Consequently, the oxygen deficit caused by heterotrophic metabolism decreases. Thus prolonged anoxic conditions near the sediment surface can be avoided and internal loading reduces.



Figure 3. Scheme of the Riplox-treatment in Alte Donau in 1995.

Detailed descriptions of sampling intervals, sampling stations and methods for the investigation period from 1993 to 1995 are given in Dokulil (1993, 1994) and Mayer et al. (1997). Therefore only a brief description of the methods used is given here. Sampling was at fortnight intervals at ten sampling stations. At each of the sampling stations, water samples were collected near the surface and near the bottom. If not stated otherwise, all values in the figures and in the text are mean values of the different sampling stations and of depth.

Depth (m), temperature (°C), pH (-log H<sup>+</sup>), oxygen (mg l<sup>-1</sup> and % O<sub>2</sub>) and conductivity ( $\mu$ S cm<sup>-1</sup>) were measured with a multiple measuring probe (Hydrolog 2001, Grabner Instruments). Depth profiles were recorded at each sampling station in 50 cm intervals. Whatman GF/F filters were used for filtration of water samples. SRP (soluble reactive phosphorus), DP (total dissolved phosphorus) and TP (total phosphorus) were determined according to Strickland & Parsons (1968). After digestion with potassium persulphate, total phosphorus and DP were determined. Particulate phosphorus was calculated as the difference between total phosphorus and DP.

Chloride (Cl<sup>-</sup>), sulphate (SO<sub>4</sub>-S) and nitrateconcentrations, higher than 2 mg  $1^{-1}$  (NO<sub>3</sub>-N), were analysed by means of Ion-chromatography (Merck-Hitachi-HPLC equipment; column Merck polyspher IC AN-1; elution with phthalic acid and Tris-boric acid buffer). Nitrate concentrations below 2 mg  $1^{-1}$ were analysed according the method with sodiumsalicylate (Legler, 1988). Nitrite was analysed with sulphanylic acid and N-(1-naphthyl) ethylen-diaminedihydrochloride (Legler, 1988). TN (total nitrogen) and DN (dissolved nitrogen) were determined as NH<sub>4</sub>-N following digestion with sulphuric acid and hydrogen peroxide.

Chlorophyll *a* was extracted in 90% acetone after sample homogenisation and measured according the method of Lorenzen (1967). Phytoplankton counts were done from Lugol-fixed samples according to Utermöhl (1958). Cell dimensions were measured by means of an image analysing system (Lucia-M, Nikon) and volumes were calculated using simple geometric forms. For conversion of phytoplankton biovolumes into fresh weight, a specific gravity of 1 was assumed.

# Results

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The chloride concentrations for 1995 are shown in Figure 4 (bars indicate the treatment period). No immediate response of chloride concentrations to the addition of FeCl<sub>3</sub> was observed. In fact, the FeCl<sub>3</sub> showed almost no dissociation in the water column. A significant release of chloride ions took place after the deposition of the FeCl<sub>3</sub> in the sediments. Maximum chloride values reached almost 100 mg  $l^{-1}$ . As chloride is hardly used by organisms, the rapid decline of the chloride concentrations after the treatment indicate high dilution rates by the groundwater.

Changes in the nitrate concentrations are shown in Figure 5. Before treatment, the nitrate content was only about a few hundred  $\mu g l^{-1}$ . In contrast to the chloride values, an immediate reaction to the addition of Ca(NO<sub>3</sub>)<sub>2</sub> was observed. The nitrate content reached its highest amounts immediately after the addition. After the application was finished, a rapid de-

100 80



Figure 4. Chloride concentrations in 1995 (bars indicate the treatment period).



Figure 5. Nitrate-N concentrations from 1993 to 1995 (bars indicate the treatment period)

cline occurred, mainly due to denitrification and water exchange. At the end of the year, nitrate content was as low as in the years before. The degree of denitrification can be deduced from high nitrite concentrations, obtained after the addition of Ca(NO<sub>3</sub>)<sub>2</sub> (Figure 6). In general, nitrite is an intermediate product of bacterial metabolism. The high values in Alte Donau, up to 120  $\mu$ g l<sup>-1</sup>, originated from the pathway of denitrification, where nitrate is reduced to nitrite, nitric oxides (NO, N<sub>2</sub>O) and finally to molecular nitrogen (Rheinheimer, 1991). With decreasing nitrate concentrations, decreasing nitrite values were also measured.

Average total phosphorus concentration was 54  $\mu$ g  $1^{-1}$  in 1993 (Table 2, Figure 7). Cyanobacterial growth took place in late summer and autumn, associated with maximum total phosphorus concentrations of 70  $\mu g l^{-1}$ . No marked seasonal changes of total phosphorus concentrations were observed. Flushing of the ecosystem in winter 1993 was not accompanied by a significant reduction of total phosphorus. Contrary to



Figure 6. Nitrite-N concentrations in 1995 (bars indicate the treatment period).

Table 2. Changes in mean values of chlorophyll a, total phosphorus (both in  $\mu g l^{-1}$ ) and percentage chlorophyll *a* to total phosphorus from 1987 to 1995.

Year	Total phosphorus	Chlorophyll a	Chl <i>a</i> /total P as%
1987	35.1	5.2	15.0
1988	66.1	16.6	25.1
1989	110.0	15.2	13.8
1990	42.4	15.0	35.4
1991	47.1	20.3	43.0
1992	41.4	22.4	54.2
1993	54.2	43.1	79.6
1994	70.0	41.0	58.6
1995	27.3	12.0	43.9

*Table 3.* Mean values of phosphorus ( $\mu$ g l<sup>-1</sup>) and nitrogen (mg l<sup>-1</sup>) fractions from 1993 to 1995

Parameter	Mean value 1995	Mean value 1994	Mean value 1993
Total phosphorus	0.027	0.07	0.055
Soluble phosphorus	0.007	0.021	0.013
Particulate phosphorus	0.020	0.049	0.042
Soluble reactive phosphorus	0.002	0.003	-
Total nitrogen	1.88	1.75	1.69
Soluble nitrogen	1.63	0.93	-
Particulate nitrogen	0.25	0.83	_
Total N: Total P ratio	70	25	31



*Figure 7.* Total phosphorus from 1993 to 1995 (bars indicate the treatment period).



*Figure 8.* Chlorophyll *a* values from 1993 to 1995 (bars indicate the treatment period).

expectations, highest values were reached in summer 1994 (Figure 7), above 100  $\mu$ g l<sup>-1</sup> in late summer, when cyanobacterial abundance was highest. Internal loading, loss of macrophytes and suppression of zo-oplankton by planktivorous fish resulted in intensive phytoplankton growth, thus causing these high total phosphorus loadings. The chemical treatment resulted in a considerable decline of total phosphorus concentrations in 1995. The slight increase which occurred after the addition of Ca(NO<sub>3</sub>)<sub>2</sub> can be explained by phosphorus contamination of the used chemicals (Figure 3). In the remaining investigation period, values were about 25  $\mu$ g l<sup>-1</sup>. Concentrations of soluble reactive phosphorus were mostly depleted to trace levels by phytoplankton (data not shown).

As a consequence of cyanobacterial growth high chlorophyll *a* concentrations were observed in late summer 1993 (up to 60  $\mu$ g l<sup>-1</sup>) and 1994 (up to 125  $\mu$ g l<sup>-1</sup>; Figure 8). Chemical flocculation with FeCl<sub>3</sub> resulted in a decline of chlorophyll-*a* concentrations with a minimum value of 3  $\mu$ g l<sup>-1</sup>. The maximum

value of  $22 \ \mu g \ l^{-1}$  was observed in the summer period, but the typical chlorophyll *a* peak caused by cyanobacteria in late summer was lacking. The annual average of chlorophyll *a* for 1995 was  $12 \ \mu g \ l^{-1}$ . Chlorophyll *a* measurements for the different sampling stations in 1995 are given in Figure 9. In contrast to the untreated parts of Alte Donau, the majority of the chlorophyll *a* values were clustered near to the lower border of the eutrophic range with single values hypertrophic.

A very similar curve can be obtained from phytoplankton biomass values (Figure 10). Cyanobacteria, mainly *Cylindrospermopsis raciborskii* and *Limnothrix redekei*, were dominant throughout the year in 1993 and 1994, contributing 70% to 90% to total phytoplankton biomass. *Cylindrospermopsis raciborskii*, difficult to distinguish from closly related genera because of morphological variants (Singh, 1962; Cronberg, 1977; Horecka & Komarek, 1979; Hindak, 1988), was the main component of the phytoplankton in the years 1993 and 1994. *C. raciborskii* has been registered as the dominant species in a



Figure 9. Chlorophyll a concentrations of the different sampling stations in 1995. Trophic classification according to Forsberg & Ryding (1980).



*Figure 10.* Phytoplankton biomass from 1993 to 1995 (bars indicate the treatment period).

Brazilean reservoir by Cronberg (1977) and Branco & Senna (1994). This species has also been found as a common component in other water bodies in tropical and temperate regions forming blooms at high temperatures and elevated nutrient levels (Hill, 1970; Lind, 1984; Padisak et al., 1984; Lewis, 1986; Kalff & Watson, 1986). The dominance of *C. raciborskii* is favoured by a set of factors such as the ability to absorb rapidly phosphates at even low concentrations, the possibility for nitrogen-fixation by heterocyst formation, high water temperature, long retention time

and small predation by zooplankton (Cronberg, 1977; Branco & Senna, 1994).

After the chemical treatment, cyanobacteria were of minor importance. A dramatical shift in phytoplankton biomass composition towards diatoms and coccal chlorophyceans occurred. For short periods cryptophyceans, chrysophyceans, dinoflagellates and coccal cyanobacteria were also abundant. The shift in the phytoplankton composition may be due to the artificially altered N/P ratio. Among other factors, summarized by Varis (1993), low N/P ratios seem to favour cyanobacterial growth (Smith, 1986; Varis, 1993).

Transparency considerably improved in 1995 (Figure 11), re-establishing optimum light-conditions for new colonisation by submerged macrophytes.

# Discussion

Eutrophication of freshwaters is a well known and intensively studied problem, creating serious problems for water supply or recreational use (Harper, 1992). Numerous strategies and techniques have been developed in the past to cope with deterioration of fresh waters (e.g. Vollenweider & Kerekes, 1982; Shapiro & Wright, 1984; Sas, 1989). However, restoration of



Figure 11. Secchi depth from 1993 to 1995 (bars indicate the treatment period).

eutrophic or hypertrophic shallow lakes is often more complex than those of deep stratifying lakes (Sas, 1989; Moss, 1990). Integrated lake management practices, and detailed concepts, based on investigations of the whole ecosystem, are necessary to cope with these systems. Additionally mathematical modelling may serve as a tool for management in eutrophication control of shallow lakes (Van der Molen et al., 1994). The concept of alternative stable states in shallow lakes (Blindow et al., 1993), implying that the system, when in equilibrium, is resistant to disturbance and tends to return to equilibrium when disturbed, has strong implications for lake management. The impact of any applied restoration measures to an ecosystem must be greater than its resistence to disturbance. Knowledge of the lake's history, and detailed investigations of the ecosystem, are necessary to address problems and to set the objectives in a special case. Nutrient reduction serves as a prerequisite, but without considering trophic cascade effects of the food web (Carpenter & Kitchell, 1993), long term stabilisation of the ecosystem cannot be expected. Many case studies show that nutrient reduction itself is not sufficient to change conditions (e.g. Foy & Fitzsimons, 1987; Annadotter et al., 1999), especially when internal loading from the sediments is high. The importance of the structure of the food web is known from numerous investigations and biomanipulation experiments (Shapiro & Wright, 1984; Kasprzak et al., 1988; Benndorf, 1990; Hanson & Butler, 1990; van Donk et al., 1990a, b; Giussani et al., 1990; Jeppesen et al., 1990a, b; Lyche et al., 1990; Meijer et al., 1990; Vanni et al., 1990; Mazumder, 1994). However, appearence of filamentous cyanobacteria has been reported from different study sites, in response to biomanipulation (e.g. Kasprzak

et al., 1993). Due to different political and public interests, removal of fish on a large scale is impossible in many cases. Therefore, specific solutions have to be adopted for each case.

The management practices in Alte Donau are still in progress. From the results obtained so far, a success for restoration of a macrophyte dominated state can be expected (Figure 12, Table 1). Nevertheless, the conflicting interests of conservation, angling, swimming and other recreational activities will necessitate further monitoring and management measures to ensure sustainability. Although integrated management and continuous management practices need high funds, recovery of lakes may justify the high costs, especially in cases where public interest is high.



*Figure 12.* Log–log plot of mean chlorophyll *a* and mean total phosphorus from 1987 to 1995. Trophic classification according to Forsberg & Ryding (1980).

# Conclusions

From the results and observations obtained in this study, the following general conclusions can be drawn:

- Changes in the hydrological conditions, nutrient status and in the food-web structure are responsible for the catastrophic shift from the macrophyte dominated state to one characterized by abundant cyanobacterial appearance.
- Recovery of the clear state can be achieved by adopting both external and internal restoration strategies.
- 3. Phosphorus precipitation combined with sediment conditioning, proves to be a reliable technique to

reduce nutrient concentrations in the lake and internal loading from the sediment in groundwater seepage lakes.

- 4. Flocculation of seston improves the under-water light climate allowing re-colonization by submerged macrophytes.
- 5. Technical restoration measures should be supplemented by biomanipulation to ensure long-term stabilization of the desired ecosystem condition.
- 6. Integrated lake management practices, based on detailed investigations, must consider conflicting interests and the carrying capacity of the ecosystem.

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