Change of phytoplankton composition and biodiversity in Lake Sempach before and during restoration

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Abstract

Lake Sempach, located in the central part of Switzerland, has a surface area of 14 km², a maximum depth of 87 m and a water residence time of 15 years. Restoration measures to correct historic eutrophication, including artificial mixing and oxygenation of the hypolimnion, were implemented in 1984. By means of the combination of external and internal load reductions, total phosphorus concentrations decreased in the period 1984–2000 from 160 to 42 mg P m⁻³. Starting from 1997, hypolimnion oxygenation with pure oxygen was replaced by aeration with fine air bubbles. The reaction of the plankton has been investigated as part of a long-term monitoring program. Taxa numbers, evenness and biodiversity of phytoplankton increased significantly during the last 15 years, concomitant with a marked decline of phosphorus concentration in the lake. Seasonal development of phytoplankton seems to be strongly influenced by the artificial mixing during winter and spring and by changes of the trophic state. Dominance of nitrogen fixing cyanobacteria (*Aphanizomenon* sp.), causing a severe fish kill in 1984, has been correlated with lower N/P-ratio in the epilimnion. Buoyant algae such as *Planktothrix rubescens* (syn. *Oscillatoria rubescens*) increased in abundance due to enlargement of the trophogenic layer and extended mixing depth during winter. The interactions between zoo- and phytoplankton seemed to be depressed as a result of restoration measures. Zooplankton composition changed to more carnivorous and less herbivorous species. Oxygenation of the hypolimnion induced bioturbation of sediments, mainly by oligochaetae worms, and stimulated germination of spores and cysts and hatching of resting eggs.

Abbreviations: E_n – evenness index based on species numbers; FW – fresh weight; H_b – diversity index based on biomass; H_n – diversity index based on species numbers; I_k – saturation value of light intensity; WWTP – waste water treatment plant

Introduction

Since the International Symposium on Eutrophication at Madison, Wisconsin, in 1967 various recommendations and guidelines were established for lake rehabilitation and techniques have been developed for controlling effects of eutrophication (Bartsch, 1980). Since then, many lakes have been restored by reduction of nutrient loading. Long-term studies of European lakes with successful reduction of P loading are documented for Lake Lucerne, Lake Walenstadt and Lake Constance (Sas, 1989; Gaedke & Schweizer, 1993; Bloesch et al., 1995).

Besides external measures to limit nutrient inputs (ban of phosphate in detergents, P removal in sewage treatment plants, regulations for fertilizer in agriculture, internal measures have also been recommended to control the effect of eutrophication:

1. Increased nutrient export out of the system (removal of plants, dredging of nutrient-loaded sediments, hypolimnion drainage).
2. Diminishing nutrient availability and phosphorus mobilisation (*in situ* phosphorus precipitating, aeration of hypolimnion and injecting pure oxygen into deep layers).

3. Decrease of algae biomass by artificial mixing or flushing.
4. Biomanipulation to change the phytoplankton or zooplankton densities or to increase grazing of plants including algae.
5. Enforcement of sedimentation including phytoplankton.

Prior to implementing internal measures, the critical nutrient loading to a lake should be defined and, for deciding best management practices, a cost-benefit analysis should be undertaken. The effects of the various measures on primary production, algal biomass, oxygen concentrations in the hypolimnion, reaction of benthic fauna and fish population should be predicted (EAWAG, 1979). Ecotechnologies always depend on the properties of a lake. Jaeger & Koschel (1995) summarize the effects of many lake restoration techniques. Hypolimnetic drainage and oxygenation of the hypolimnion should be operated without destroying the summer stratification and without causing upwelling of nutrients.

Some restoration measures, especially biomanipulation, may have unexpected effects on the limnology of a lake (Van Donk et al., 1990). One of the main problems in ecotechnology and biomanipulation is stability and resilience (Benndorf, 1988). Some procedures of biomanipulations are connected with ethic problems as for instance poisoning of animals (Shapiro & Wright, 1984). The stocking of just one new species can change an ecosystem completely. Biomanipulation with Nile perch in Lake Victoria resulted in the extinction of a lot of fish taxa (Kaufman, 1992; Goldschmidt, 1996). Artificial mixing of deep lakes has effects on alga growth due to light limitation and on water transparency (Lorenzen & Mitchell, 1975). Nutrient upwelling increases primary production. The response to artificial mixing was some times so dramatic that the measure had to be stopped as for instance in the Swiss lakes Pfäffikersee (Thomas, 1966) and Wilersee (Keller, unpublished), where a fish kill occurred. Circulation of lakes during summer can increase the heat budget and may result in higher water temperatures, which are harmful for fish as salmonids (Fast & St. Amant, 1971).

There are few biological studies about the restoration of deep lakes, especially regarding the combination of artificial destratification and hypolimnion oxygenation, and little is known about the impacts of these measures on plankton and benthic fauna.

Unfortunately lake restoration with internal manipulations, are unreplicable experiments, and changing phosphorus concentrations, oxygenation of the hypolimnion and mixing of a lake have synergetic effects. Thus, it is difficult to ascribe changes in the plankton community to any particular cause. Based on the literature, we hypothesise that the most important influences on the behavior of Lake Sempach, include the following:

1. Oxygenation of the hypolimnion changes the redox conditions and extends the oxic habitat available to zooplankton and fish, which expand their vertical distribution (Brynildson & Serns, 1977; Schumpelick, 1995; Bürgi & Stadelmann, 2000). Specialists as *Chaoborus* sp., that are tolerant of low oxygen concentration, partly lose their refuge in the deep anoxic water layers (Akeret, 1993). Resting eggs and cysts in the sediment are driven to hatch by changes of temperature and oxygen concentration and the seasonal course of plankton community gets chaotic (Bürgi & Stadelmann, 1991).
2. Forced destratification and expanded overturn periods alters the buoyancy and shortens the light exposition for phytoplankton. Oligophotic cyanobacteria with gas vacuoles become more abundant during wintertime (Bürgi & Stadelmann, 1991).
3. Decrease of nutrients influences plankton community and the potential for algae to form blooms. In a less eutrophic environment, bottom up control gives a chance to K-strategists (beside the robust *r*-strategists) and therefore increases the species richness and evenness. Consequently the α -diversity of phytoplankton is expected to increase. Decreasing phosphorus concentration influence the transparency in the epilimnion and visual-hunting fish can better detect their prey (Uehlinger et al., 1996).

The purpose of this overview of the long-term study of Lake Sempach is to describe changes in plankton composition that have occurred since the beginning of lake-restoration in 1984 and to compare our results with earlier investigations.

The main goal of this paper is to subdivide the seasonal and long-term development of plankton as a reaction of the combined restoration measures.

We would like to answer following questions:

1. How does lake-restoration of L. Sempach influence composition and biomass development of plankton?
2. How does phytoplankton community change in respect to biomass, size, buoyancy, species richness, evenness and biodiversity over seasons?

Eutrophication of Lake Sempach

The first inventories of phytoplankton species were reported by Heuscher (1895) and Bachmann & Hotz (1922). Further investigations of phytoplankton were made by Pavoni (1963), Zimmermann (1969) and August Schwander (unpublished), who counted plankton in depth profiles from 1972 to 1976. The limnological state of Lake Sempach can be followed up over 60 years by means of physical and chemical measurements. Züllig (1982) described the eutrophication history for the period 1800–1978, using algae pigments in a sediment core collected at depth of 87 m. Based on these pigment remains, the cyanobacteria *Planktothrix rubescens* has been reported to appear in 1963. Investigations of sediment cores taken in 1984 from the deepest location (Sturm, 1993) revealed already anoxic conditions around 1936, even though at this time the lake was in an oligotrophic state. Lake Sempach exhibits mostly complete mixing during wintertime but, in some winters – under disadvantageous climatic conditions – circulation may be incomplete or very short. Based on available measurements, this was the case in 1947, 1969, 1971, 1972, 1976, 1977, 1980 and, 1982. Since 1985, the lake has been artificially destratified in winter by bubbling compressed air and therefore Lake Sempach exhibits complete mixing every winter.

In a recent sediment core, collected in May 1994, Ambühl (1995) demonstrated that the earlier lamellar layers were disturbed by bioturbation, after internal measures were in operation (Fig. 1). Rodrigues (1996) found oligochaetae down to 85 m, which explains the bioturbation by these worms.

Due to its progressive enrichment with nutrients, the lake changed from an oligotrophic state prior to 1950 to a mesotrophic one around 1965 and reached highly eutrophic conditions in 1984 (Stadelmann, 1988). Because of high phosphorus concentrations, algae densities increased and heavy algae blooms occurred, so the drinking water supply from L. Sempach was affected. This required additional steps in purifying lake water taken from 40 m depth.

Figure 1. Sediment core from a depth of 87 m from Lake Sempach, 5th August 1994 (Ambühl, 1995).

In the course of eutrophication changes in algae, zooplankton and fish species composition were detected. Since 1883, Lake Sempach has been stocked with large numbers of hatchery-reared white fish larvae (*Coregonus* sp.) and there is still today a commercial fishery yielding mainly white fish ($10\text{--}95\text{ kg ha}^{-1}\text{ yr}^{-1}$; Heer, 1993).

During the period 1965–1985, sewage discharge, extended use of phosphate detergents and high animal densities in agriculture each contributed to fast increase of total phosphorus concentration from 30 to 160 mg m^{-3} (Fig. 2a). Since then, the sewer systems have been completed and the waste water treatment plants (WWTP) were equipped with phosphorus removal steps. A part of the sewage load has been diverted to a WWTP outside of the drainage basin

Figure 2. Total phosphorus and dissolved inorganic nitrogen concentrations in Lake Sempach for the period 1952–1999. The values are mean concentrations during spring overturn (a) Total phosphorus concentration in mg P m^{-3} . (b) Total dissolved inorganic nitrogen (DIN as nitrate- and ammonia-N) in g N m^{-3} .

of Lake Sempach. In 1986, the use of phosphates in textile detergents was forbidden in Switzerland. As a result of these measures, P concentrations in the lake declined slowly.

Investigation and sampling location

Lake Sempach (504 m above sea level.), situated in central Switzerland, has a surface area of 14.4 km^2 , a maximum depth of 87 m and a mean depth of 46 m. The water residence time is 15 years, so the lake reacts to changes of nutrient loading with a prolonged lag time. Since 1984, the lake has been (1) oxygenated with pure oxygen in summer in order to prevent anoxic conditions in the hypolimnion and (2) artificially destratified during wintertime by bubbling compressed air at depths of about 85 m (Gaechter & Stadelmann, 1993).

Before lake restoration started in 1984, an intensive physical and chemical monitoring program was initiated and accompanied by phyto- and zooplankton

investigations. From 1984 until now, plankton samples have been taken first biweekly later monthly at the deepest location of Lake Sempach.

Methods of plankton enumeration

Phytoplankton and microzooplankton were sampled from 0 to 15 m with an integrated sampler according to Schroeder (1969) and preserved with Lugol's solution. The species were counted using the Utermöhl (1958) technique with an inverted microscope.

Crustaceans were sampled quantitatively with a tilt closing net (mesh size $95 \mu\text{m}$, with a ratio of net mouth-net area of 1:50) according to Bürgi (1983). The samples were collected from two depth layers: 0–15 m and 15–85 m (6 duplicates). The zooplankton species were enumerated under a dissecting microscope of 10–75 magnification.

Diversity indices were calculated according to Shannon & Weaver (1949), based on numbers of data set has to be acquired with the same method and – if possible – by the same person. We are using the terms H_n (numerical based diversity) and H_b (biomass based diversity) according to the following equations (Bürgi & Stadelmann, 2000):

$$H_n = -\sum (\text{Ind}_i \cdot \text{Ind}_{\text{total}}^{-1} *^2 \text{Log}(\text{Ind}_i \cdot \text{Ind}_{\text{total}}^{-1}))$$

where Ind_i is the number of individuals of the i th type, $\text{Ind}_{\text{total}}$ is the number of total individuals.

$$H_b = -\sum (\text{biom}_i \cdot \text{biom}_{\text{total}}^{-1} *^2 \text{Log}(\text{biom}_i \cdot \text{biom}_{\text{total}}^{-1}))$$

where biom_i is the biomass of the i th type, $\text{biom}_{\text{total}}$ is the total biomass of all individuals.

The index of evenness was calculated according to Krebs (1993):

$$E_n = (H_n - H_{n \min})(H_{n \max} - H_{n \min})^{-1}$$

where $H_{n \min}$ is the minimal possible numerical based diversity (totally uneven abundance),

$H_{n \max}$ is the maximal possible numerical based diversity (all species have the same abundance).

Results

Phosphorus and nitrogen in Lake Sempach

The first systematic measurements of phosphorus and dissolved inorganic nitrogen in Lake Sempach were performed in 1952 by Thomas (1953), who reported

spring mean concentrations of about 15 mg m^{-3} and of $300 \text{ mg m}^{-3} \text{ NO}_3\text{-N}$, respectively (Fig. 2a,b).

The combination of external measures (improved sewage treatment with P-removal, regulations of fertilizing agricultural land and on storage of manure) and internal measures resulted in oxic conditions in the whole lake and in lower P-concentrations. The actual yearly loading of about 12 tons total P and 6 tons of dissolved P (mean 1992–1999) is dominated by runoff, leaching and erosion of agricultural land (Mathis, 1999). Based on this mean loading, Wehrli & Wüest (1996) assumed a steady state phosphorus concentration of 65 mg P m^{-3} . In the year 2000, already 42 mg P m^{-3} measured during complete overturn in spring, less than the predicted value. This indicates that the improved oxic conditions by internal measures decreased the remobilisation of P from the sediments.

In the period 1955–1985, dissolved inorganic nitrogen (DIN consisting of nitrate and ammonia) increased from 300 to 900 mg N m^{-3} . Since the internal measures have been in operation, DIN exists mainly in the form of nitrate-N. From 1985 to 1999, nitrate concentrations fluctuated between 500 and $800 \text{ mg m}^{-3} \text{ NO}_3\text{-N}$ with a tendency to lower values during spring overturn (Fig. 2b).

Figure 3 shows a three-dimensional graphs of soluble phosphorus in mg P m^{-3} in Lake Sempach based on monthly measurements at a depth of 85 m. A significant decrease of dissolved phosphorus is evident in the epilimnion due to P-uptake by algae, which extended steadily to deeper layers. Because of good oxygen conditions above the lake bottom, P-accumulation in the hypolimnion at the end of stratification became less significant than in earlier years.

Figure 4 shows a three-dimensional graph of nitrate in $\text{mg m}^{-3} \text{ NO}_3\text{-N}$ based on monthly measurements at a depth of 85 m. Before 1984, ammonia peaked regularly in the deeper hypolimnion, where lower values of nitrate due to denitrification processes were observed. The decrease of nitrate in the epilimnion is less pronounced compared to dissolved phosphorus. This may be explained by the fact that nitrogen is not limiting at the present time for algae growth. Only during periods with higher phosphorus concentrations (1980–1985) nitrogen could limit algae growth. During this period, large blooms of nitrogen fixing cyanobacteria occurred too.

Plankton composition and seasonal succession

In the last 30 years, the plankton community changed significantly (Fig. 5). Since 1972, three dominant algae blooms (with maxima over 150 g m^{-2} fresh weight) were recorded in Lake Sempach: in 1975/76 *Ceratium hirundinella*, in 1988 *Staurostrum* sp. and in 1996 *Planktothrix rubescens*. Blooms of cyanobacteria are reported from many Swiss lakes. *Ceratium* blooms are not so frequent but known for Lake Walenstadt (Florin & Ambühl, 1978) and Lake Lucerne (Buerger, unpublished). An anomaly was the bloom of *Staurostrum* in 1988, which lasted for several months. Besides excessive fluctuations in plankton community, there are some trends concerning systematic plankton groups:

1. Decrease of dinoflagellates and chlorophytes,
2. Increase of cyanobacteria and diatoms,
3. Increase of carnivorous crustaceans,
4. Decline of herbivorous crustaceans.

Generally 10–20% of the total zooplankton biomass consists of carnivorous crustaceans. But unexpectedly in 1997 the carnivorous zooplankton biomass (e.g. *Leptodora Kindtii* and *Cyclops* spp.) extended almost to the same magnitude as the herbivorous crustaceans (Fig. 5).

Seasonal phytoplankton changes

Compared with the phytoplankton records of the years 1972–1976, when similar nutrient conditions existed as nowadays, the recent plankton enumeration showed a quite different community structure and seasonal sequence. The higher areal biomass since 1990 has been mainly caused by large cyanobacteria occurring in fall and winter (Fig. 6). Since internal measures are in operation, the biomass minimum observed in earlier years during wintertime, is less distinct. On the other hand, maximum biomass in spring and summer is still in the same magnitude as before. In the period 1989–1997, phytoplankton was dominated by *Planktothrix rubescens*, this often contributed more than 50% of total phytoplankton biomass. This cyanobacteria is known as an oligophotic species indicating moderate eutrophication.

Buoyancy, size and motility of phytoplankton

In Figure 7, the relative portions of functional phytoplankton groups, based on motility, buoyancy and size (two fractions: nano < $30 \mu\text{m}$; net > $30 \mu\text{m}$), are shown.

Figure 3. Three-dimensional graph of total soluble phosphorus in mg P m^{-3} based on monthly measurements at locations with maximum depth of 85 m in Lake Sempach.

Before 1984, motile net-plankton as dinoflagellates had been abundant. Due to internal measures, we observed a shift from motile plankton to buoyant and non-motile net-plankton.

With the invasion of *Planktothrix rubescens*, the buoyant phytoplankton became a substantial fraction of phytoplankton biomass. Non-motile nanoplankton contributed normally less than 3 g FW m^{-2} . During the period 1996–1998, this portion increased from 10 to 15 g FW m^{-2} . Contrasting to the situation between 1984 and 1986, the motile nanoplankton fraction (e.g. cryptomonads) contributed more and more to the total biomass in wintertime. The preferred seasons for motile nanoplankton are still spring and summer; its biomass varied between 1 and 7 g FW m^{-2} in winter and reached 18 g FW m^{-2} in spring. Motile nanoplankton is the most important food source for filter-feeding zooplankton.

Clear water stages caused by zooplankton overgrazing on algae are nowadays less distinct than in the earlier years, but the phytoplankton biomass often showed minimal values in June/July.

Phytoplankton reaction with changing N/P ratios

In Figure 8, the variation of N/P ratios are compared with the biomass of nitrogen-fixing cyanobacteria, which can overcome N-limitation. During the period of phosphorus increase (from 1975 to 1984), the N/P-ratio decreased and nitrogen could limit algae growth. Nitrogen-fixing cyanobacteria peaked with periods of low N/P ratio (Fig. 8). Maximum biomass of cyanobacteria (50 g FW m^{-2}) was recorded in August 1984, just before a serious fish kill occurred on 7/8th of August. Approximately 400 000 fish died, mainly cyprinids, perch and pikes. The reason for this enormous event ever reported in a Swiss lake

Figure 4. Three-dimensional graph of nitrate in $\text{mg NO}_3\text{-N m}^{-3}$ based on monthly measurements at locations with maximum depth of 85 in Lake Sempach.

Table 1. Biomass of total phytoplankton and Cyanobacteria including the most prominent species *Planktothrix rubescens* and *Aphanizomenon flos-aquae* during the period with the most prominent fish kill in Lake Sempach

	Biomass of total phytoplankton g FW m^{-2}	Biomass of all cyanobacteria g FW m^{-2}	Cell densities of <i>Planktothrix</i> Cells l^{-1}	Cell densities of <i>Aphanizomenon</i> cells l^{-1}
July 2, 1984	29.5	27.5	28 000 000	Not observed
July 16, 1984	37.8	32.3	30 000 000	500 000
July 30 1984	75.8	53.9	24 000 000	22 000 000
Aug. 7, 1984	Fishkill			lysis
Aug. 8, 1984	84.6 ^a	55.2 ^a	22 000 000	260 000*)
Aug. 13, 1984	55.2	27.6	7 100,000	670 000
Aug. 27, 1984	27.9	10.9	17 000 000	180 000
Sept. 10, 1984	34.4	16.0	14 000 000	120 000

^a Sample from lake surface.

Figure 5. Long-term development of plankton in Lake Sempach. Biomass as fresh weight in g FW m^{-2} for systematic groups of phytoplankton (0–15 m) and functional groups of zooplankton in g FW m^{-2} (0–85 m).

was a biological collapse. Immediately prior to the fish kill, a massive lysis of the cyanobacteria mainly *Aphanizomenon flos-aquae* (35 g FW m^{-2}) was recorded (Table 1). *Aphanizomenon flos-aquae* can produce neuro-toxins. An estimation showed, that within a few days, about 400 tons of organic material was released (Stadelmann et al., 1985). The question has to be discussed, why cyanobacteria were so abundant and toxic.

During the fish kill, huge quantities of *Planktothrix rubescens* were also present in L. Sempach. Recently, Mez (pers. comm.) found active toxic strains of *Planktothrix rubescens* in the nearby Lake Baldeg.

Richness, evenness and biodiversity of phytoplankton

In Figure 9, species richness as phytoplankton taxa numbers are plotted. Regarding all species or taxa (including periphyton) in Lake Sempach, more than 200 taxa have been found during our studies. The taxa numbers reported in Figure 9 contribute more than 99% of the biomass. With decreasing phosphorus concentrations, we found a clear trend to higher taxa numbers. Before restoration only about 10–30 taxa were found in each sample. After 1984, the number of taxa usually surpassed 20–60 taxa. Species rich-

ness fluctuated within a year about $\pm 50\%$ around the mean.

Besides species richness, the evenness is a further component of diversity. Completely even distribution (each species has the same abundance) gives an evenness index of 1. Dominance of only one species gives an index of 0. The evenness index shows no clear correlation with phosphorus decline. We found similar maxima of evenness indices over the entire investigated period but extreme minima are less frequent since 1989, consequently the mean values show a trend to better evenness (Fig. 10).

Biodiversity indices imply species richness and evenness. More species and a more balanced evenness increase diversity indices. If only one species is present the diversity index is zero. About 30 species in balanced portions originate an index ($H_{\max}$) of about 5.

Figure 11 shows phytoplankton α -diversity indices based on species numbers (H_n) and biomass (H_b) of phytoplankton in Lake Sempach for the period 1984–1999, when the analysis were done by the same scientist with the same method. Earlier countings were made by other investigators, who used not the same method. The trend is towards higher biodiversity indices. Blooms of cyanobacteria and chlorophytes (e.g.

Figure 6. Seasonal development of buoyant phytoplankton biomass in Lake Sempach (0–15 m) before and during internal measures.

Figure 7. Long-term development of phytoplankton biomass separated in different size and motility classes in L. Sempach (0–15 m).

Figure 8. N/P ratio (weight based) in the epilimnion and biomass of nitrogen fixing cyanobacteria in L. Sempach.

Figure 9. Phytoplankton richness (taxa numbers) before (1972–1976) and during restoration measures (1984–1998) in Lake Sempach.

Figure 10. Phytoplankton evenness in Lake Sempach.

Figure 11. Diversity indices based on taxa numbers (H_n) and on biomass (H_b) of phytoplankton in Lake Sempach for the period 1984–1999, when the enumerations were done with the same method by the same scientist.

Figure 12. Monthly fluctuations of nanoplankton in Lake Sempach.

Figure 13. Distribution of *r*- and *K*-strategists for the period 1972–1976 and 1984–1999 in Lake Sempach.

Planktothrix rubescens and *Staurostrum* sp.) caused distinct minimal indices. In Lake Sempach, phytoplankton diversity (H_n) seems to be closer correlated to evenness than to species richness. Numerically based biodiversity index (H_n) is usually 1 point lower than biomass-related diversity (H_b), indicating that the most frequent species belong to the small nanoplankton. These typically *r*-strategists are able to produce huge cell densities within a few days (Fig. 13). The biomass of this nanoplankton is often in the same magnitude as the biomass of larger ones but less abundant taxa.

Coupling between phyto- and zooplankton

The monthly variation of phytoplankton biomass has changed due to a decrease of phosphorus concentrations and lower zooplankton grazing pressure. Short-time fluctuations of nanoplankton (calculated as ratio of biomass at time x · (biomass at time $x + 1$)⁻¹) are more significant during the period of higher phosphorus concentrations (Fig. 12). Drastic rates of changes are inferred from the graph from 1972 to 1976 and from 1984 to 1988.

From 1989 to 1995, when the plankton succession was smoothed, only moderate rates are recorded. Most of the chaotic changes took place in the period of spring and early summer, including clear water phases, caused by zooplankton grazing.

Discussion

Phosphorus and nitrogen

Through a combination of external and internal measures, P concentration in L. Sempach has declined to 42 mg m⁻³. The formerly highly eutrophic lake has become only moderately eutrophic and there is still a trend to lower P concentrations. This is below the predicted value of Wehrli & Wüest (1996). We suggest that aeration of hypolimnion is the reason for further decrease of P concentrations, which can be explained by better P-retention in the sediments. Sediment cores taken by Ambühl (1995) show that the typical lamellar structure before restoration, has been destroyed by bioturbation since 1985. The surface of sediment changed to a more flocculated structure and therefore the active boundary layer between sediment and hypolimnion water increased.

Due to better mineralization of the settled material, the oxygen demand has been lowered and the capacity of P retention may be increased. Algae incorporation of P and N in the epilimnion demonstrates that the trophogenic layer extended to deeper zones.

Dissolved inorganic nitrogen (DIN) shows a similar trend to phosphorus. Since the beginning of restoration DIN stabilized at concentration of 0.6–0.9 mg N l⁻¹. Nowadays, P once again is the limiting growth factor for algae.

Effects on plankton community and their seasonal succession

Pavoni (1963) counted on 3rd August 1961, 30 algae species: chlorophytes (13 taxa), cyanobacteria (5 taxa), diatoms, (4 taxa), chrysophyceae (3 taxa), peridineae (3 taxa) and cryptophyceae (2 taxa), *Planktothrix rubescens* had not yet been observed. August Schwander (unpublished) mentioned 31 taxa, including *Planktothrix rubescens* in 1963. His data of the period 1972–1976 are included in our study. During the long-term investigations, we found up to 58 taxa in a single sample, with a clear trend to higher taxa numbers in recent years. Samples with less than 20 taxa were recorded only 4 times in the last 10 years (Fig. 9).

The long-term development of phytoplankton did not correspond with the decrease of phosphorus concentrations. The response of plankton to the environment changes can be understood only in a holistic approach. There was a shift in phytoplankton community but total biomass m^{-2} is still in same magnitude. Changing physical and chemical factors influence the seasonal succession of phytoplankton. After starting internal measures in 1984, the plankton became stressed. Due to altered environmental conditions, the formerly balanced plankton community destabilized. Several alga blooms occurred and during highest P concentration nitrogen-fixing cyanobacteria as *Aphanizomenon* coincided with low N/P ratios.

Observed fluctuations of phytoplankton biomass seem to be affected by top-down effects as well as bottom up control. Nanoplankton biomass especially benefits from better nutrient situations and less grazing pressure. The strength of coupling between phyto- and zooplankton seems to be weakened due to lake-internal measures.

Clear trends in zooplankton biomass are recorded: camivorous zooplankton increased, herbivorous zooplankton generally decreased. Expanding oxic habitat and better transparency in the epilimnion changed the migratory behavior of zooplankton. This is also reported for Lake Lucerne (Bürgi et al., 1999). Because edible algae decreased, herbivorous zooplankton found less suitable food than in earlier times. The spatial overlap between filter feeding zooplankton and their preferred nanoplankton food was lowered.

Visual predators such as whitefish could benefit from the increased transparency by catching more zooplankton, and therefore the grazing pressure on

phytoplankton decreased too. Under these conditions, nanoplankton should become common.

In contrast, phytoplankton composition showed a quite different pattern. Large and buoyant cyanobacteria biomass became dominant. As a consequence, filter feeding zooplankton avoided layers with high densities of filamentous algae. As a consequence small algae living together with cyanobacteria had a lower grazing pressure too. Since internal measures extended oxic habitat, sensible zooplankton are more evenly distributed over the whole water column during daytime and grazing pressure on phytoplankton weakened.

Planktothrix rubescens, a keystone species

As in many Swiss and Austrian lakes *Planktothrix* (*Oscillatoria*) *rubescens* emerged as a keystone species (Jaag, 1972; Deisinger, 1987). *Planktothrix rubescens* is oligophotic and prefers higher temperatures (Zimmermann, 1969). Zones of warmer water together with low light intensities occur in lake only in the metalimnion during fall (Ramberg, 1979). As a buoyant species with gas vacuoles, *Planktothrix* needs also minimal density gradients ($50\text{-mg l}^{-1} \text{ m}^{-1}$) to stay in a distinct water layer. Even though all these factors are seldom fulfilled at the same time, *Planktothrix* has a robust fitness and can concur with other species.

How can algae survive during complete mixing, when each cell is drifted up and down in a water column under different light intensities? They need an effective light harvesting system. *Planktothrix* has this potential because of its pigments as phycoerythrin and carotenoids, which have a high light-harvesting efficiency (Govindjee & Braun, 1974).

Reynolds (1994) mentioned the important role of turbulence and of the vertical extent of mixing, which favors good 'light-antenna' species. L. Sempach has during complete overturn conditions a euphotic zone of about 15 m. During this period, the mixed zone corresponds to the critical mixing depth according to Tilzer & Beese (1988), so *Planktothrix rubescens* can survive these unfavorable conditions. *Planktothrix* has an I_k value of only $10 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Mur & Bejrdorff, 1978). The mean light intensity used up by this vertical drifting species is therefore still sufficient for primary production to compensate for respiration loss, and it can even increase its biomass. Similar environment was found in Lake Hallwil and Lake Baldegg with maximum depth of 48 m and 65 m,

respectively (Bürge & Jolidon, 1998; Bürge & Stadelmann, 2000). Most of these lakes, which nowadays are less eutrophicated, supported this species. During the stagnation period, *Planktothrix* lives in the metalimnion, where the photosynthetic active radiation (PAR) reaches about 1–5% of surface values. During the circulation period, *Planktothrix* can survive due to the low light demand and due to its buoyancy.

The first record of *Planktothrix rubescens* in Lake Sempach dated from 1963 (Stadelmann, 1980). Züllig (1982) could identify Oscillaxanthin in the lake sediments of L. Sempach starting in 1964. Since 1977, higher concentration of this pigment is reported.

In deeper lakes such as Lake Constance, the mixing depth goes beyond the critical value for *Planktothrix* each winter (Tilzer & Beese, 1988). The absence of *Planktothrix* in L. Constance may also be explained by unstable stratification during summer (Sommer et al., 1993). With the onset of stratification in Lake Zürich, *Planktothrix* filaments remain only vital in the euphotic zone, while under light limitation the filaments die off in the hypolimnion (Gammeter et al., 1997). The massive reappearance of *Planktothrix rubescens* in L. Sempach, L. Hallwil and L. Baldegg, when internal measures were installed corresponds to a decline of phosphorus concentrations and to an enlarged artificial mixing during winter. Now all three lakes exhibit reddish blooms of *Planktothrix rubescens* as in earlier decades, when comparable P-concentrations were measured. The same is true for Lake Zürich (Zimmermann et al., 1993).

Evenness and biodiversity of phytoplankton

Diversity of freshwater habitat is poorly investigated. Ecosystems stability and biodiversity depend on the kind and degree of disturbance (Wetzel, 1999). There are a variety of disturbances (catastrophic or gradual ones). According to the intermediate disturbance hypothesis (IDH), there are all times more species existing in a lake than it would be feasible under stable conditions. Hutchinson (1961) called this “The Paradox of the Plankton”. Many phytoplankton species are able to produce within a few days large biomass but they are also capable of persisting through an extended period of unfavorable conditions.

Variation of species richness was markedly smaller than variation of evenness indices. Dominant species can obviously not completely rival other species. During blooms of *Ceratium* in 1975, of *Aphanizomenon* in 1984, and of *Planktothrix* in 1997, the evenness index

declined to values below 0.1, although taxa numbers were in the same range as before.

Plankton composition needs time to adapt to a new situation. After internal measures, diversity indices were about 1.5 lower in the first two years, than in the following years. Later, the diversity improved due to larger species richness and better evenness. Only in winter 1996/97 did a bloom of *Planktothrix* decrease the diversity index again.

Due to oxic conditions above the sediments, resting spores and cysts have probably been permitted to survive and to hatch. Only a short time after the beginning of hypolimnion oxygenation in July 1984, *Aphanizomenon flos-aquae* emerged and formed a bloom with heterocysts in August 1984. After a few days, the huge biomass of *Aphanizomenon flos-aquae* collapsed (Table 1). Before its breakdown, the filaments produced resting stages (akinetes). This might be a reaction of *Aphanizomenon* to unfavorable conditions.

The extent of community dynamics can be positively correlated with primary production and rates (Jassby & Goldman, 1974; Lewis, 1978). Bürge et al. (1999) pointed out that the strength of coupling between phytoplankton and herbivorous zooplankton depends on the trophic state of a lake. Fluctuations of nanoplankton in Lake Sempach are of the same size as in Lake Lucerne, indicating top-down regulation of the plankton food web. During overgrazing periods, decrease and increase of nanoplankton are in the similar range, though phytoplankton was not heavily limited by nutrients.

During periods of *Planktothrix rubescens* abundance, seasonal variations of nanoplankton biomass are retarded. Nanoplankton growth is now limited by competition between algae in such a way that immobilization of nutrients occurs by filaments constituting non-consumable algae. The decrease of herbivorous zooplankton supports our hypothesis that high densities of filamentous algae can limit the growth of filter feeding zooplankton (Gliwicz, 1990).

Conclusions

The main goal of restoration measures was to decrease phosphorus concentrations in Lake Sempach. Decrease of eutrophication influenced plankton community in following ways:

1. Enlargement of the trophogenic layer.

2. Raising the N/P ratios in the euphotic zone and, therefore, less dominance of nitrogen-fixing cyanobacteria as *Aphanizomenon* sp.
3. Increase of phytoplankton richness from about 20 to 60 taxa.
4. Increase of phytoplankton biomass as fresh weight m^{-2} (in the layer 0–15 m).
5. Increase of evenness indices and less periods with minimum values.
6. Increase of phytoplankton diversity indices based on taxa numbers (H_n) or on biomass (H_b).
7. Decrease of herbivorous zooplankton biomass per m^2 , caused by the presence of more filamentous algae.

The internal measures consisting of hypolimnion oxygenation and of forced mixing during wintertime caused following effects on plankton and benthic fauna:

1. Increased oxic habitat.
2. Shift to higher phytoplankton biomass in winter.
3. Shift to more buoyant algae as *Planktothrix rubescens*.
4. Shift to non-motile net plankton (greater than 30 micrometer) as Diatoms and Conjugates.
5. Induced germination of spores and cysts and hatching of resting eggs.
6. Zooplankton migrated to deeper layers and lowered grazing pressure on algae in the euphotic zone.
7. Supporting populations of oligochaetae and chironomids due to better oxic conditions.
8. Bioturbation and mineralisation of the upper sediment layers.

This studies show clearly that, if a lake endures restoration or rehabilitation measures, a long term monitoring program has to be planned and that physical and chemical measurements have to accompanied by investigations of phytoplankton, zooplankton, fish and benthic fauna. The biological reaction of Lake Sempach has a long lag time and the question of resilience is not answered yet.

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