Chapter 13

Long-Term Ecological Research in Freshwater Ecosystems

Jan Köhler

Abstract Long-term changes of freshwater ecosystems are mainly caused by immissions from drainage basin and atmosphere (nutrients, acid substances, etc.) and by changing climatic conditions. Freshwater ecosystems often react in non-linear ways to these external forces. Beyond a certain threshold, gradual shifts may cause catastrophic switches to another state. The way back to the previous state rarely corresponds to the past changes because of memory effects of the system. Long-term studies are necessary, but they do not allow for a simple extrapolation of past observations into the future.

Freshwater systems are also influenced by rare events like invasion of new species, spates or droughts. Effects of perturbations should be studied until the system establishes a new equilibrium.

The analysis of long-term processes needs sound knowledge about natural oscillations or gradual changes of the baseline. Monitoring programmes of German lakes and reservoirs rarely last longer than 30 years. They usually started after serious environmental problems had emerged; they do not cover periods without human impacts (baseline conditions). Therefore, long-term monitoring should be accompanied and extended by palaeolimnological approaches.

Keywords Lake ecology · Long-term studies · Eutrophication · Acidification · Invasive species · Climate change · Feedback mechanisms · Hysteresis · Palaeolimnology

J. Köhler (✉)
Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 301, 12587 Berlin, Germany
e-mail: koehler@igb-berlin.de

13.1 Introduction

German lakes were formed after the retreat of the last glaciation about 10,000–15,000 years before present. Since then, they underwent permanent developments caused by sediment accumulation, invasion by new and extinction of 'native' species, changes in vegetation, soil properties and hydrology of the drainage basin, or large-scale climatic shifts. Human activities influenced lake and river systems in many ways for at least the last millennium. First systematic studies of lakes were performed in the late 19th century. In the first decades of the 20th century, most limnological studies were focused on descriptions of several aspects of single lakes and attempts to compare lakes by different schemes of lake classification. Deep lakes were more frequently studied than shallow ones, and running waters were nearly neglected. Lakes were seen as microcosms or superorganisms; the effects of drainage basin and the atmosphere came into focus only in the 1970s (Kalff, 2002). Popularity of research topics and funding policy is always changing. Therefore, systematic studies of lakes or rivers rarely cover more than the last 30 years. This is a long time relative to the life span of the researcher but just a snapshot given the thousands of years' development time of the studied systems.

Man usually tries to extrapolate the own experience in order to understand past changes or to predict future developments. This strategy is of limited value, however, in case of rare events or slow shifts which eventually cause catastrophic switches. Obviously, even an extended study period will never cover all important timescales. But the reliability of extrapolations will increase with the duration of included

F. Müller et al. (eds.), *Long-Term Ecological Research*,
DOI 10.1007/978-90-481-8782-9_13, © Springer Science+Business Media B.V. 2010

observations. Even more important, long-term investigations are needed to understand the processes which shape ecosystems in the long run. Main driving forces for freshwater systems are immissions of nutrients and acid substances, invasion of new species and climatic conditions. In this chapter, I discuss the timescale of direct and indirect processes determining these driving forces and compare them with known monitoring programmes of German lakes and reservoirs.

13.2 Effects of Perturbations

Rare events or catastrophes may completely alter species composition or habitat structure of aquatic ecosystems. Running waters are especially prone to occasional floods or droughts. Obviously, long-term observations are necessary to estimate the frequency of rare events and to study their impact on the ecosystem.

We need to observe the effects even of frequent perturbations at least until the system reaches a new equilibrium. The response of an aquatic ecosystem to loading with nutrients or toxic substances depends on flushing rate or retention time. Rivers or flushed lakes will recover from perturbations much faster than isolated lakes. A new equilibrium appears only after some generations, i.e. it needs several years for fish or macrophytes but only few weeks for bacteria, algae or protozoa. Speed of equilibration also depends on reproductive strategies of the key species. On the other hand, environmental changes in temperate lakes or rivers follow an annual pattern, so that investigations even of quickly reproducing organisms should last whole years. Weather conditions (temperature, irradiance, precipitation and the related fluxes from the drainage basin) usually vary from year to year, i.e. observations from single years are not valid for longer periods.

Oscillations and long-term shifts are essential parts of dynamic systems. A serious analysis of any change in the system requires sound knowledge on temporal variations in the baseline from which the change occurred (see Elliott, 1990). In an ideal world, the system under investigation should be studied for some years before a perturbation starts.

Other processes cause gradual changes over long time periods, like nutrient enrichment (eutrophication), acidification and invasion of non-native species or climate change. These long-term changes may occur without any human activities so it is important to differentiate between natural dynamics and anthropogenic impacts. Apart from this baseline problem, the non-linear response to external forces requires long-term studies of aquatic ecosystems.

13.3 Eutrophication

Productivity and structure of most aquatic ecosystems depend on nutrient supply. In most freshwater systems, phosphorus availability limits growth of primary producers. Other potentially important nutrients are nitrogen and silicon. Nutrient immissions into lakes and rivers result from import to the drainage basin and release and retention processes within the basin. Release and retention of nutrients are influenced by properties of the catchment (relief, vegetation cover, geology, soil type, etc.), by hydrological and climatic conditions. Most of these factors are subject to permanent natural as well as anthropogenic changes. After the last glaciation, nutrient emissions from the catchment changed slowly due to soil formation, vegetation succession and development of stream systems. These long-term shifts were modified by climate changes. Human activities like deforestation, farming and stockbreeding, drainage of wetlands or construction of watermills influenced nutrient emissions in European catchments for at least the last millennium. Nutrient input increased dramatically after introduction of flushing toilets and sewer systems in urban areas and of artificial fertilisers in agriculture and horticulture. Phosphorus loading of European rivers and lakes was highest in the 1960s–1980s. It declined after the ban of P-containing washing powders and detergents and the construction of advanced sewage treatment plants which remove most phosphorus and nitrogen from wastewater. Nitrogen loading did not decline in many catchments due to still intensive use of fertilisers. Additionally, nitrate often travels some decades from application in agriculture via groundwater to the next river.

Aquatic ecosystems respond to changes in nutrient loading more or less delayed and often in non-linear ways. Lake sediments act as phosphorus sink. They accumulated large P amounts in decades of increased loading. This P pool delays the decline of in-lake P concentration despite reduced external loading. P remobilisation from sediments was enhanced by the positive feedback between high phytoplankton biomass and high oxygen demand at the sediment–water interface. In most lakes, a new equilibrium was attained only 10–15 years after reduction of external nutrient loading (Jeppesen et al., 2005). The length of this delay depends on flushing rate, P concentration in sediment and water and binding form of P. Often, lakes recovered initially at slow rates but improved once phosphorus concentration fell below a critical value (Moosmann, Gächter, Müller, & Wüest, 2005). Lakes respond nearly immediately to reductions in nitrogen loading because N accumulation in sediments is low and surplus N is removed from the system via denitrification (Jensen, Jeppesen, Kristensen, Christensen, & Sondergaard, 1992; Köhler et al., 2005).

Non-linear responses to changing nutrient loading are also caused by biotic interactions. Under eutrophic conditions, fish community was dominated by whitefish feeding on zooplankton and zoobenthos. A shift back to a higher proportion of piscivores is usually delayed and may be accelerated by artificial stocking. Shallow regions of lakes and rivers are often covered by aquatic vegetation. Dense stands of plants reduce resuspension of settled particles and provide shelter to planktonic and substrate to benthic filter-feeders. In this way, they reduce the turbidity of the water column and improve their own light supply. Increased nutrient loading caused higher biomass of planktonic and epiphytic algae which shaded the submersed macrophytes. As a consequence, higher plants disappeared and algal growth further accelerated. At reduced nutrient concentrations, submersed macrophytes re-appeared. This switch between macrophyte- and phytoplankton-dominated states may occur from one year to the next. The nutrient concentrations which trigger this switch are much lower for the re-colonisation by macrophytes than for their disappearance. Due to this hysteresis, two stable but completely different states of lake systems may occur at the same nutrient concentration (Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993). Hysteresis implies a delayed response of shallow lakes to reductions of nutrient loading.

13.4 Acidification

After the last glaciation, pH of soft-water lakes decreased slowly, caused by development of vegetation and soils releasing organic acids. During the last 2,000 years, man-made eutrophication produced a pH increase, followed by recent acidification (Psenner & Catalan, 1994). Acidification of rivers and lakes is caused by wet or dry deposition of acidic components like sulphur dioxide or nitrogen oxides in the drainage basin. Emissions of these gases to the atmosphere have increased since the industrial revolution, mainly due to burning of sulphur-containing coal in power plants or households and to oxidation of atmospheric nitrogen in combustion engines. Acid rain was first described by Smith (1872, cit. in Lenhart & Steinberg, 1992). Due to the long time lag between start of acidification (19th century) and public awareness of its consequences (second half of the 20th century), reconstruction of background conditions or a baseline is even more difficult than for eutrophication. Additionally, a large amount of sulphur dioxide stems from natural processes like volcano emissions, oxidation of biogenic dimethyl sulphide or sulphur-containing minerals. Acid substances are partly neutralised by dust which originates from natural (e.g. deserts) as well as anthropogenic sources (power plants, traffic, agriculture, etc.). Dust emission from power plants was earlier and more strongly diminished than emission of sulphur dioxide or nitrogen oxides, so a temporary more severe acidification resulted in regions affected by power plant emissions. During the last decades, sulphuric acid deposition declined drastically in Germany but was partly replaced by nitric acid. In many forest regions, the deposited NO_3- had been retained by soils and taken up by vegetation until the system became N-saturated. This process may cause a delayed, but sudden decline in pH. Decreases in acid deposition result in an incomplete or delayed recovery because large amounts of calcium and magnesium have been washed out from the soils so that their buffer capacity was reduced (Likens, Driscoll, & Buso, 1996).

Many aquatic organisms disappear if pH declines below 6.0–6.5 (Psenner & Catalan, 1994). Acidification affects certain stages of the life cycle, e.g. larval phases of fish or emergence of aquatic insects. Abundance of the affected species often declines only after some delay. Pulses of acid substances may reach the stream or lake only occasionally, e.g. after snow melt or heavy rain. Such pulse may or may not coincide with sensitive life stages.

In some lakes, a temporary recovery from acidification was produced by liming. The rate of recovery of aquatic organisms depends on their dispersal ability and reproductive strategy. Zooplankton recovery needed 10 years after liming in a moderately acidic Canadian lake, but more than 15 years in more acidic lakes (Yan, Keller, Somers, Pawson, & Girard, 1996). Molluscs and fish need an inoculum from refuges or artificial stocking. In any case, a time lag of several years occurs between chemical and biological recovery.

Global warming enhanced weathering of minerals and increased biological activity. Sommaruga-Wögrath et al. (1997) found a strong positive correlation between pH of alpine lakes and air temperature.

Sensitivity of a stream, reservoir or lake to import of acidic substances mainly depends on the geochemistry of its catchment. Most of northern Germany is covered by easily weathered carbonate-rich rocks and soils which neutralise incoming acids. Much more vulnerable to acidification are mountainous areas with insoluble surface material like granite, gneiss, basalt or sandstone. Streams, lakes and reservoirs with small drainage basin are most at risk. Therefore, acidified water bodies are concentrated in upper regions of the Ore Mountains, Bavarian Forest and Black Forest.

13.5 Invasion by Non-native Species

Compared to terrestrial or marine systems, freshwater ecosystems are more separated (less coherent) under natural conditions. Micro-organisms may spread by wind or birds over long distances. Many higher plants or animals, however, can migrate only within their river basin. Human activities (intended or accidental import, connection of river basins by canals, ship traffic, etc.) enabled or favoured invasion of new areas. Invasive species have large effects on diversity and structure of native communities, but also on pool sizes and main processes in aquatic ecosystems. Climate change favoured the northward spreading of warm-adapted species during the last decades.

Effects of many invaders are not constant over time. Processes like evolution, shifts in species composition, accumulation of materials and interactions with abiotic variables can increase, decrease or qualitatively change the impacts of an invader through time. Strayer, Eviner, Jeschke, and Pace (2006) differentiate between an acute phase just after arrival of a new species and a chronic phase after various ecological and evolutionary processes. The latter may last for decades or centuries. However, most studies of the effects of invasive species have been brief and lack a temporal context; 40% of recent studies did not even state the amount of time that had passed since the invasion (Strayer et al., 2006).

In the following, main processes requiring long-term studies of invasions are briefly discussed: Invasive species often have to acclimate to their new surrounding. This acclimatisation can occur quickly in the initial phase or as a response to changes developing later in the invasion process. The need to acclimate often causes a time lag between invasion and explosive population growth. On the other hand, the community that has been invaded also changes over time. Invaders often arrive in a new system without their associated enemies. Introduced populations host on average half the number of parasite species of native populations (Torchin, Lafferty, Dobson, McKenzie, & Kuris, 2003). Predators, parasites or competitors may follow from previously occupied regions or old established species may adapt to the invader. The time lag between invasion and arrival of the old or adaptation of new enemies often causes an initial mass development of the invasive species followed by a regulation to lower population densities. Additionally, composition of the invaded community can shift towards species resistant to effects of the invader or native species can adapt to reduce own losses caused by the invader.

The zebra mussel (*Dreissena polymorpha*) is a good example for many of the mentioned long-term processes. It expanded after construction of the Pripyat-Bug canal in 1780 from tributaries of the Black Sea to central Europe (Kinzelbach, 1995). Man-made changes favoured *Dreissena* during the last century: eutrophication increased the food concentration of this filter-feeder; hydraulic engineering provided hard substrates to settle. Zebra mussel filtration reduced the biomass (Makarewicz, Lewis, & Bertram, 1999; Caraco, Cole, & Strayer, 2006) and altered the species composition of phytoplankton (Vanderploeg et al., 2001). This species also creates new habitats by 'paving' soft sediments (Beekey, McCabe, & Marsden, 2004). The zebra mussel was followed by a specialised parasite, the trematode *Bucephalus polymorphus* (Kinzelbach, 1995). Some native waterfowls have adapted to feed on this mussel and may control its abundance (Petrie & Knapton, 1999). Ironically, water fowl foraging was facilitated by increased water clarity caused by filter-feeding mussels. Molloy, Karatayev, Burlakowa, Kurandina, and Laruelle (1997) reviewed the old and new predators, parasites and competitors of *Dreissena*. The zebra mussel was the most important filter-feeder in the Rhine during the 1980s but is now diminished by competition from new invaders, mainly the amphipod *Corophium curvispinum* (Kinzelbach, 1995).

13.6 Climate Change

'Climate change' means a significant change in mean temperature, precipitation or wind patterns during time periods of decades to millions of years. At the geological timescale, continental drift, uplift and erosion of mountains and CO_2 uptake by sedimentary rocks caused shifts in climatic conditions. At a shorter timescale, changes in the Earth's orbit and in solar energy output trigger glacial and interglacial phases. Volcano eruptions may cause short-term climatic changes. Human activities like deforestation, irrigation and fuel burning influenced the climate, at least locally, for many centuries. After the industrial revolution, emissions of greenhouse gases (CO_2, CH_4, etc.) increased dramatically, so that human activity is the main reason for the current rapid climate changes. Mean global surface temperature increased 0.74 K from 1906 to 2005 and will likely rise a further 1.1–6.4 K during the 21st century (IPCC, 2007). Several complex feedbacks may cause non-linear behaviour and rate-independent memory (hysteresis) of the climate system.

Higher temperature and lower discharge effect nutrient loading of rivers and lakes. Increasing evaporation and decreasing discharge may contribute to eutrophication of lakes which receive nutrients mainly from point sources. In contrast, lower discharge causes reduced P input from non-point sources. Lower precipitation reduces weathering and stream flow, resulting in lower silica concentrations in lakes (Schindler et al., 1996). Lakes in pristine catchments thus received less P and Si, resulting in a slight oligotrophication despite reduced water renewal (Schindler et al., 1996). Lower discharge and higher temperature favour nitrogen retention in the river system by denitrification.

In recent decades, water temperatures increased in many northern temperate lakes, especially in winter and spring (Gerten & Adrian, 2002). Duration of ice cover declined and the spring growth period of phytoplankton started earlier. Paradoxically, the shift of the spring growth period favoured phytoplankton species adapted to lower temperature, shorter day length, lower irradiance and, under high Si:P ratios, filamentous cyanobacteria (Shatwell, Köhler, & Nicklisch, 2008). Timing of zooplankton was relatively independent of the winter conditions (Shatwell et al., 2008), so that longer time was available for phytoplankton spring growth and less phytoplankton fuelled the trophic cascade from zooplankton to fish. Higher water temperatures also cause earlier and more stable stratification of the water column from late spring to autumn. In deep lakes, temperature of the epilimnion and gradients in the metalimnion increased. Moderately shallow lakes stratified more permanently and their hypolimnion tended to become colder (Gerten & Adrian, 2001), whereas the whole water column of very shallow, polymictic lakes became warmer. More stable stratification favours mobile phytoplankton species, enhances settling and reduces resuspension of particles. Higher temperatures at the sediments increase oxygen consumption and remobilisation of nutrients (P, Si) and heavy metals.

Lower silica input from the catchment, more stable stratification and higher temperatures favour some cyanobacteria and aggravate nuisance bloom formation (Schindler, 2006). In general, the aquatic organisms respond to climate changes in species-specific ways. The complex, often time-lagged, direct and indirect responses in biotic structure and trophic interactions are not fully understood yet.

13.7 Disadvantages and Limitations of Long-Term Investigations

Most limnologists agree that long-term investigations are necessary, but few of them want to spend time for repetitive monitoring. Less paper in high-ranking journals can be distilled per unit effort from long-term investigations than from studies on single processes. Once a long-term data series is accumulated, its utilisation is often profitable but its analyser stands on the shoulders of former colleagues which earned less for long efforts. Papers on popular topics are most cited. Researchers have to follow the fashion for funding. Of course, popularity of topics changes and so investigations are usually terminated after few years. Additionally, methods will advance but comparability within a data series often requires sticking on old methods. Therefore, data series without interruptions are very rare in research institutes.

Only few institutions can achieve to commit staff and facilities continuously for decades.

On the other hand, there are also theory-based arguments against long-term studies. Often, episodic, seasonal and interannual variations are higher than long-term directional changes. Stochastic disturbances can mask long-term shifts; in some freshwater systems frequent disturbances may prevent any steady state. On the community level, return intervals for the next disturbance are usually too short to attain a new equilibrium (Reice, 1994).

Even long-term studies do not allow for a simple extrapolation of past observations into the future. Freshwater ecosystems often react in non-linear ways to external forces. Beyond a certain threshold, gradual shifts may cause catastrophic switches to another state. The way back to the previous state rarely corresponds to the past changes because of memory effects of the system.

Research and corresponding management usually ignores timescales in the natural dynamics of lakes and rivers which exceed the human life span and experience. An assessment of the current state and of human influences should be based, however, on its deviation from natural reference conditions (European Union, 2000). Long-term monitoring usually started after serious environmental problems have emerged. They rarely cover the periods of nearly undisturbed conditions and even seldom the phase of deterioration. Therefore, long-term monitoring should be accompanied and extended by palaeolimnological approaches. Stratigraphical analyses of sediments or ice cores can cover much longer timescales than the most persistent limnological monitoring. On the other hand, the comparison between long-term observational data and recent sediment stratigraphy is very valuable for calibration of palaeolimnological methods (Battarbee, Anderson, Jeppesen, & Leavitt, 2005).

In some cases, we can change space for time. We can deduce the response of one system to temporal changes by comparing similar systems which experience the same impact at different degrees at the same time.

13.8 Long-Term Investigations of German Lakes and Reservoirs

In Germany, first freshwater laboratories were established in the late 19th century at Plön (1891) and Friedrichshagen (1893). These institutions were not intended to analyse certain lakes for longer time periods. In fact, comprehensive studies of lakes around Plön and Berlin-Friedrichshagen were occasionally organised by staff members, but these analyses lasted only a few years each, were not part of longer-lasting programmes and often used outdated or not well-documented methods. Lake Constance as the largest German lake and an important drinking water source of south-western Germany was regularly studied by the Institute of Lake Research at Langenargen since 1952, by the International Commission for the Protection of Lake Constance since 1961 and by the Limnological Institute of the University of Constance since 1979, although some programmes had been terminated or interrupted in the meantime [Arch Hydrobiol. Spec. Issues Advanc. Limnol. 53 (1998)]. Since the late 1950s, Lake Stechlin has been comprehensively and continuously monitored because of a small nuclear power plant which took lake water for cooling (Casper, 1985). Apart from these exceptions, monitoring programmes were not started before 1970. They were usually motivated by eutrophication problems and thus focused on growth and production of phytoplankton, nutrient budgets and trophic interactions in the pelagic zone. The benthic community was studied only occasionally and usually in qualitative terms. Long-term data on the fish stock of some lakes are (cautiously) extractable from catch statistics of commercial fishermen. Until now, consistent analyses comprising the major groups of organisms and most important processes at the same lake and during the same time are very rare.

Different institutions run long-term monitoring programmes for different purposes. Water authorities often monitor chemistry and some hydrological and biological parameters in large river systems. Reservoirs (and few lakes) serving as source of drinking water are analysed by the water suppliers. Many lakes are occasionally sampled by the local water authorities, often to test the suitability for bathing. Very few German lakes have been intensively investigated in high frequency for long time. Table 13.1 gives examples for monitoring programmes which have been

Table 13.1 Long-term monitoring of German lakes and reservoirs (selected sites): start, termination (if applicable) and frequency of regular measurements

Parameter	Lake Müggelsee	Lake Stechlin	Lake Constance	Saidenbach reservoir	Lake Haussee	Lake Luzin	Lake Tollense
Phytoplankton biovolume + species composition	1977-	1959-	1952-	1975-	Occasionally	–	–
Phytoplankton chlorophyll a	1994-	1980-	1976-	1994-	1978-	1981-	1981-
Zooplankton biovolume + species composition	–	1978-	1952-	1975-	1978-	1981-	1981-
Zooplankton abundance	1979-	1978-	1952-	1975- (without ciliates)	1978-	1981-	1981-
Fish stock	–	1995-	1909-	1981, 1998	Few observations	–	–
Macrozoobenthos abundance	1991–1992, 2001	Few observations	1968, 1972, 1978, 1985, 1993, 2005	–	–	–	–
Macrophytes coverage	1999, 2000, 2006, 2008	Few observations	1968, 1978, 1993, 2008	–	–	–	–
Periphyton biomass	–	–	–	–	–	–	–
Primary production (phytoplankton)	1978-	1970-	1979–1997	–	Few observations	–	–
Bacterial production (pelagic)	–	1976-	1980–1997, 2005	–	–	–	–
Water temperature	1976-	1958-	1961-	1975-	1978-	1981-	1981-
Ice coverage	1977-	1958-	875-	1975-	–	–	–
Secchi disc depth	1979-	1958-	1920–24, 1951-	1975-	1978-	1981-	1981-
Light attenuation	1976-	1970-	1979–1997	1975–1990, rarely	–	–	–
Discharge/retention time	1976-	–	1951-	1975-	–	–	–
Total phosphorus	1979-	1971-	1961-	1975-	1978-	1981-	1981-
Dissolved reactive phosphate	1979-	1971-	1961-	1975-	1978-	1981-	1981-
Total nitrogen	1976-	1993-	1961-	–	1993-	1993-	1993-
Dissolved inorganic nitrogen	1976-	1971-	1961-	1975- (only nitrate)	1978-	1981-	1981-
Dissolved reactive silica	1977-	1971-	1961-	1981-	1978-	1981-	1981-
Conductivity	1994-	1970-	1961-	1991-	1978-	1981-	1981-
pH	1991-	1970-	1961-	1991-	1978-	1981-	1981-
Oxygen content	1979-	1971-	1961-	–	1978-	1981-	1981-
Dissolved inorganic carbon	1978-	1971-	1976-	–	1978-	1981-	1981-
Sampling frequency summer (winter) in d	7 (14)	14 (28)	14	1975–1986: 7, 1987-: 14	14 (28)	14 (28)	14 (28)
Institution	IGB	IGB	IGKB, Uni Konstanz	TU Dresden	IGB	IGB	IGB

performed for more than 20 years at German lakes and reservoirs. This compilation is not complete, especially regarding reservoirs.

Due to the federal organisation of environmental protection, Germany lacks a central institution to coordinate monitoring programmes, to validate and standardise the used methods and to centralise data collation.

13.9 Conclusions

Natural systems are always changing. There is no constant baseline. Observed temporal changes are never exclusively caused by human activities. Long-term observations are necessary to understand natural fluctuations and shifts and to differentiate them from human impacts.

The temporal scale of investigations generally depends on the processes under study. Spatial scale and temporal scale determine tools and approaches which are effective at that level. The results and interpretations made at one scale may be wrong or inappropriate at another (Fisher, 1994). Long-term changes usually occur at the spatial scale of whole ecosystems. Long-term studies of lakes or rivers have to include the processes in its catchment and interactions with the atmosphere. On the other hand, it is often defensible to neglect the processes acting at lower scales of space or time. Statistical models with seasonal averaged responses of aggregated properties or proxies are appropriate for many long-term studies.

Long-term observations of lakes and rivers are not replaceable by palaeolimnological studies or by the comparison of systems at different development stages. Instead, these approaches should be combined to overcome limitations of the single concepts.

Acknowledgements Rainer Koschel, Reiner Kümmerlin, Hans Güde and Wofgang Horn provided information about long-term monitoring programmes at lakes Stechlin, Haussee, Luzin and Constance and at the Saidenbach reservoir.

References

Battarbee, R. W., Anderson, N. J., Jeppesen, E., & Leavitt, P. R. (2005). Combining palaeolimnological and limnological approaches in assessing lake ecosystem response to nutrient reduction. *Freshwater Biology, 50*, 1772–1780.

Beekey, M. A., McCabe, D. J., & Marsden, J. E. (2004). Zebra mussel colonization of soft sediments facilitates invertebrate communities. *Freshwater Biology, 49*, 535–545.

Caraco, N. F., Cole, J. J., & Strayer, D. L. (2006). Top down control from the bottom: Regulation of eutrophication in a large river by benthic grazing. *Limnology & Oceanography, 51*, 664–670.

Casper, S. J. (1985). *Lake Stechlin: A temperate oligotrophic lake*. Dordrecht: Junk Publishers.

Elliott, J. M. (1990). The need for long-term investigations in ecology and the contribution of the Freshwater Biological Association. *Freshwater Biology, 23*, 1–5.

European Union (2000). Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Amtsblatt der Europäischen Gemeinschaften, L327*, 1–72.

Fisher, S. G. (1994). Pattern, process and scale in freshwater systems: Some unifying thoughts. In P. S. Giller, A. G. Hildrew, & D. G. Raffaelli (Eds.), *Aquatic ecology: Scale, pattern and process* (pp. 575–591). Oxford: Blackwell.

Gerten, D., & Adrian, R. (2001). Differences in the persistency of the North Atlantic Oscillation signal among lakes. *Limnology & Oceanography, 46*, 448–455.

Gerten, D., & Adrian, R. (2002). Effects of climate warming, North Atlantic Oscillation, and El Nino-Southern Oscillation on thermal conditions and plankton dynamics in northern hemispheric lakes. *The Scientific World Journal, 2*, 586–606.

IPCC (2007). Summary for policymakers. In S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, & H. L. Miller (Eds.), *Climate change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1–18). Cambridge: Cambridge University Press.

Jensen, J. P., Jeppesen, E., Kristensen, P., Christensen, P. B., & Sondergaard, M. (1992). Nitrogen loss and denitrification as studied in relation to reductions in nitrogen loading in a shallow, hypertrophic lake (Lake Sobygard, Denmark). *Internationale Revue der gesamten Hydrobiologie und Hydrographie, 77*, 29–42.

Jeppesen, E., Sondergaard, M., Jensen, J. P., Havens, K. E., Anneville, O., Carvalho, L., et al. (2005). Lake responses to reduced nutrient loading – an analysis of contemporary long term data from 35 case studies. *Freshwater Biology, 50*, 1747–1770.

Kalff, J. (2002). *Limnology: Inland water ecosystems*. Upper Saddle River, NJ: Prentice Hall.

Kinzelbach, R. (1995). Neozoans in European waters – Exemplifying the worldwide process of invasion and species mixing. *Experientia, 51*, 526–538.

Köhler, J., Hilt, S., Adrian, R., Nicklisch, A., Kozerski, H. P., & Walz, N. (2005). Long-term response of a shallow, moderately flushed lake to reduced external phosphorus and nitrogen loading. *Freshwater Biology, 50*, 1639–1650.

Lenhart, B., & Steinberg, C. E. W. (1992). Gewässerversauerung. In W. K. Besch, A. Hamm, B. Lenhart, A. Melzer, B. Scharf, & C. E. W. Steinberg (Eds.), *Limnologie für die Praxis – Grundlagen des Gewässerschutzes* (pp. 347–404). Landsberg/Lech: ecomed.

Likens, G. E., Driscoll, C. T., & Buso, D.C. (1996). Long-term effects of acid rain: Response and recovery of a forest ecosystem. *Science, 272*, 244–246.

Makarewicz, J. C., Lewis, T. W., & Bertram, P. (1999). Phytoplankton composition and biomass in the offshore waters of Lake Erie: Pre- and post-Dreissena introduction (1983–1993). *Journal of Great Lakes Research, 25*, 135–148.

Molloy, D. P., Karatayev, A. Y., Burlakowa, L. E., Kurandina, D. P., & Laruelle, F. (1997). Natural enemies of zebra mussels: Predators, parasites, and ecological competitors. *Reviews in Fisheries Science, 5*, 27–97.

Moosmann, L., Gächter, R., Müller, B., & Wüest, A. (2005). Is phosphorus retention in lakes controlled by oxygen or phosphorus? *Limnology & Oceanography, 51*, 763–771.

Petrie, S. A., & Knapton, R. W. (1999). Rapid increase and subsequent decline of zebra and quagga mussels in Long Point Bay, Lake Erie: Possible influence of waterfowl predation. *Journal of Great Lakes Research, 25*, 772–782.

Psenner, R., & Catalan, J. (1994). Chemical composition of lakes in crystalline basins: A combination of atmospheric deposition, geologic background, biological activity and human action. In R. Margalef, (Ed.), Limnology now: Paradigms of planetary problems (pp. 255–314). Amsterdam: Elsevier.

Reice, S. R. (1994). Nonequilibrium determinants of biological community structure. *American Scientist, 82*, 424–435.

Scheffer, M., Hosper, S. H., Meijer, M. L., Moss, B., & Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution, 8*, 275–279.

Schindler, D. W. (2006). Recent advances in the understanding and management of eutrophication. *Limnology & Oceanography, 51*, 356–363.

Schindler, D. W., Bayley, S. E., Parker, B. R., Beaty, K. G., Cruikshank, D. R., Fee, E. J., et al. (1996). The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. *Limnology & Oceanography, 41*, 1004–1017.

Shatwell, T., Köhler, J., & Nicklisch, A. (2008). Warming promotes cold-adapted phytoplankton in temperate lakes and opens a loophole for Oscillatoriales in spring. *Global Change Biology, 21*, 2194–2200.

Sommaruga-Wögrath, S., Koinig, K.A., Schmidt, R., Sommaruga, R., Tessardi, R., & Psenner, R. (1997). Temperature effects on the acidity of remote alpine lakes. *Nature, 387*, 64–67.

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution, 21*, 645–651.

Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J., & Kuris, A.M. (2003). Introduced species and their missing parasites. *Nature, 421*, 628–630.

Vanderploeg, H. A., Liebig, J. R., Carmichael, W. W., Agy, M. A., Johengen, T. H., Fahnenstiel, G. L., et al. (2001). Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences, 58*, 1208–1221.

Yan, N. D., Keller, W., Somers, K. M., Pawson, T. W., & Girard, R. E. (1996). Recovery of crustacean zooplankton from acid and metal contamination: Comparing manipulated and reference lakes. *Canadian Journal of Fisheries and Aquatic Sciences, 53*, 1301–1327.