Chapter 14

Successful Restoration of a Shallow Lake: A Case Study Based on Bistable Theory

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Abstract Eutrophication of shallow lakes provides an excellent example of alternative stable states. Clear water, macrophyte-dominated stages can alternate with turbid conditions characterized by high algal concentrations. Stable states can switch from one to the other domination through alterations of natural factors such as changes in water level and reduction in throughflow. Forward switches are often associated with anthropogenic pressure. In such cases, backward shift to the original, macrophyte-dominated stage may be difficult. Return times are often prolonged due to hysteresis as a result of resilience. The theory is exemplified with results from a shallow, urban, seepage lake 'Old Danube,' which is within the city limits of Vienna. Causes and consequences of switches between stable states including resilience and hysteresis are discussed. The remediation measures are explained and the success of the restoration is explained in detail.

Keywords Urban lake · Remidiation · Whole lake approach · Australia

14.1 Defining the Problem

Lake eutrophication is a worldwide environmental problem. The process of eutrophication and (re)-oligotrophication has manifold facets including many moderate and continuous disturbances originating in the lake, its watershed, or its airshed. In the normal dynamics of lakes, systems tend to maintain a given state through resilience against environmental perturbations (Carpenter and Cottingham 1997). Such 'resilient systems' have several mechanisms with different ecosystem components, distinctive temporal and spatial extents, and return times. These mechanisms buffer lake ecosystems against fluctuating perturbations. They maintain the reliability of ecosystem services, water quality, and productivity. Perturbations of freshwater systems are usually brief in duration, but may be extensive in space. Fluctuations of environmental variables in the catchment or lake influenced by weather conditions, variability of interacting populations, or fires that sweep through the watershed are examples. Resilience mechanisms that tend to restore the normal dynamics involve longer or larger scales, e.g., nutrient pulses which can be absorbed by food web dynamics or retained in wetlands. Extreme perturbations can destroy resilience but may also give rise to new resilience mechanisms and qualitative changes in the ecosystem.

Oligotrophic conditions are usually stable, because the growth of algae is limited by the nutrient input from the watershed and practically no return of nutrients from the sediments. Eutrophic conditions are stabilized by internal recycling of phosphorus within the lake particularly in shallow, thermally unstratified lakes. Many such lakes remain eutrophic for extended periods of time. Their persistent eutrophication can be due to many factors because the process of recovery from eutrophication is not entirely understood, can be slow, or do not succeed. Environmental fluctuations and natural or human-induced perturbations can result in big changes that occur during a relatively short period of time. These regime shifts are infrequent, modify ecosystem organization and dynamics, with prolonged

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consequences which may have large ecological and social consequences. Such regime shifts are difficult to predict in advance.

In some cases, a threshold may separate different regimes. When an ecosystem crosses a threshold it may switch from one alternative stable state to another. Therefore regime shifts are an important topic for ecosystem management (Carpenter 2003, 2005).

14.2 The Theory of Stable States – Reloaded

The existence of alternative stable states in natural ecosystems has already been hypothesized half a century ago (Dokulil and Teubner 2003). According to Lewontin (1969) a system possesses alternative stable states if it can return to one or more equilibrium after a disturbance. In several cases, compound disturbances may play a key role in changing ecosystem structure or composition of the community. Changes only occur when the severity of the disturbance exceeds the tolerance level, e.g., the 'normal' intensities a species assemblage may typically experience (Sousa 1984). Regime shifts can be caused by natural or anthropogenic perturbations and may be gradual or catastrophic (Scheffer et al. 2001, Scheffer and Carpenter 2003, Van Nes and Scheffer 2005). Two perspectives have developed to describe how communities shift from one stable state to another. One assumes a constant environment with shifts in variables such as population density, and the other anticipates changes to underlying parameters or environmental 'drivers.' Regeneration or recovery of the ecosystem is ensured by species adapting to a certain disturbance regime (Paine et al. 1998). The possibility of alternative stable states has been supported by ecological models (Holling 1973, Sutherland 1974) but their presence in the 'real' world has been much debated (Conell and Sousa 1983, Peterson 1984, Jasinski and Asselin 2004). Experimental evidence shows the alternating presence of persistent communities which are often difficult to observe directly (Petraites and Latham 1999, Bertness et al. 2002). The presence of alternative equilibria has been demonstrated for a number of aquatic and terrestrial ecosystems using a multitude of analytical and experimental techniques (Knowlton 1992, Hughes 1994, Baker and Walford 1995, Steele 1998, Hare and Mantua 2000, Van de Koppel et al. 2001, Bertness et al. 2002, Sedia and Ehrenfeld 2003, Rietkerk et al. 2004, Jasinski and Payette 2005). In freshwaters, especially when shallow, the theory of bistable states has been widely used, accepted, and modified (Scheffer 1990, 1991, 1998, Scheffer et al. 1993). Moreover, the concept has been adopted and expanded for use in lake management and restoration (Moss et al. 1996, 1997).

Two different situations can exist in lakes, as has already been pointed out by Uhlmann (1980): dense stands of submerged plants and clear water or algal blooms associated with high turbidity. Such stable states usually change gradually with changing environmental conditions in deep lakes. In shallow lakes, however, more abrupt switches from one situation to the other are common allowing alternative states at almost identical conditions (Fig. 14.1). The equilibrium trajectory is folded producing an unstable, never realized region (dotted line in Fig. 14.1) which marks the 'turning point' of the system called 'bifurcation.' Two mechanisms are involved: environmental disturbances partly absorbed by the resilience of the system (Gunderson et al. 2002), gradually modify internal structures. When the 'break-point' region is reached, a small further alteration may result in a 'catastrophic' shift to another stability domain. The folded region of the trajectory is therefore called 'catastrophic fault.' Strong perturbations can flip an ecosystem across the unstable region when disturbances are large enough to exceed resilience.

Natural ecosystems are never in equilibrium or steady state, because unpredictable changes in weather and hydrology, seasonal changes of light and temperature, and internal mechanisms in populations continuously affect the structure and function of freshwater systems. The theory of alternative stable states nevertheless is applicable if two main questions can be resolved:

- What are the reasons for the disappearance of macrophyte beds?
- Which factors are necessary to stabilize the macrophyte domination?

One reason for a forward switch from clear water and macrophyte domination to the turbid, algal-dominated state is an increase in nutrient concentration leading to enhanced growth of planktonic and epiphytic algae which in turn affects the underwater vegetation, especially when combined with an increase

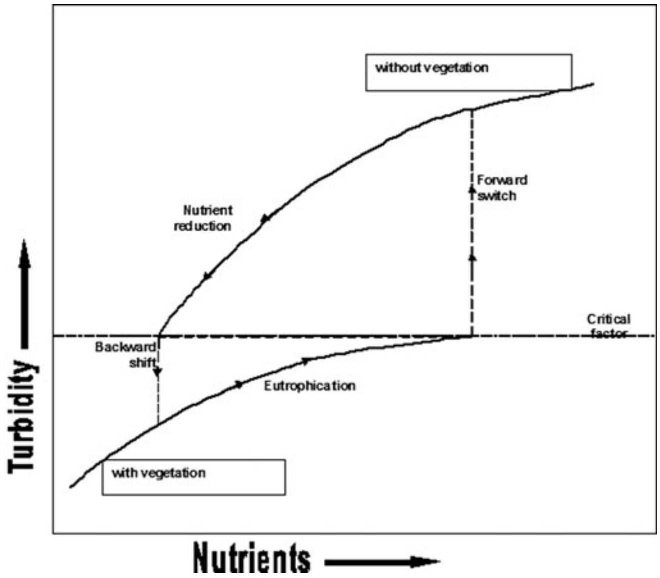

Fig. 14.1 Conceptual diagram of regime shifts (forward and backward switches) leading to alternative stable states under nutrient enrichment and decline

of algivorous and benthivorous fish species (Scheffer 1998). Massive stocking with carp and grass carp can result in abrupt changes in equilibrium conditions leading to a forward switch inducing a turbid algal-dominated situation. Grazing by waterfowl during summer, however, is considered to be of minor importance while migrating birds can damage overwintering macrophytes severely. Grazing by waterfowl may also strongly affect re-colonization by water plants. Other factors causing destruction and loss of macrophytes are disturbances by heavy storms, extreme frost at low water level, or a permanent increase in water depth.

The macrophyte-dominated stage is stabilized essentially by two mechanisms: uptake and incorporation of nutrients by macrophytes and their associated periphytic algae. Both strongly reduce nutrient availability for algae in the pelagic. Moreover, such systems have greater potentials for top-down control of the phytoplankton (Jeppesen et al. 1998).

14.3 The Study Site

Regulation of the river Danube at Vienna in 1875 resulted in the isolation of parts of the main river channel (Fig. 14.2)

The remaining backwater, now known as 'Old Danube,' became almost entirely dependent on groundwater seepage and precipitation because of no natural surface inflow or outflow. The lake soon developed into a famous recreational resort and has progressively been engulfed by the city. The nearby river Danube and especially the impoundment New Danube, which was built to protect the city from flood events, both influence the direction and dynamics of the groundwater. Today, the Old Danube is a shallow urban lake within the city of Vienna and a very popular recreation area (Fig. 14.1 and Table 14.1).

Before about 1990 water was clear with high Secchi disk transparencies, frequently down to the bottom. Large areas were covered with submerged macrophytes substantially influencing nutrient dynamics by their storage capacity. The abundant species were *Myriophyllum spicatum* L. and *Potamogeton pectinatus* L. The Charophytes *Nitellopsis obtusa* (DESV. IN LOIS) J. GROVES, *Chara tomentosa* L., and *Chara hispida* WOOD dominated macrophyte biomass. Over the years organic-rich sediments accumulated in several areas on top of the fluvial deposits as a result of internal processes. Parts of these sediments became anoxic because of respiration and reduced water exchange (Löffler 1988).

14.3.1 *What Happened? Causes of Change*

Available information on long-term changes in phytoplankton biovolume and submerged macrophyte biomass is summarized for Old Danube in Fig. 14.3, an

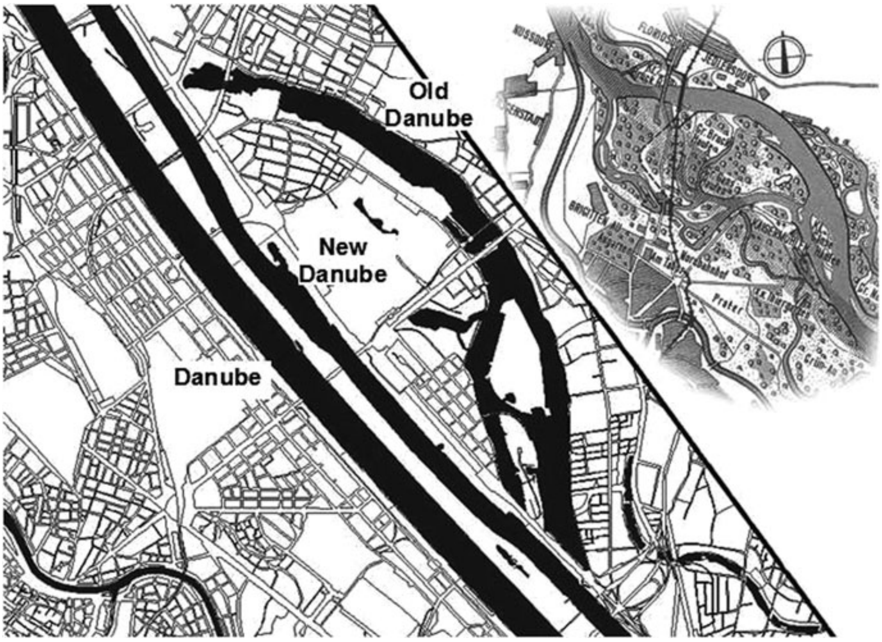

Fig. 14.2 Map showing the natural meandering situation of the river Danube in the mid-nineteenth century in Vienna (*upper right*) and the situation as it appears at present in 2009

Table 14.1 Morphometric and basic chemical data for Old Danube

Altitude [m a.s.l.]	157
Area [km^2]	1.583
Volume [10^6 m^3]	3.697
Maximum depth [m]	6.8
Mean depth [m]	2.3
Average retention time [days]	190
Mixing type	Polymictic
pH	7.0–8.5
Conductivity [$\mu S\ cm^{-1}$]	321–608
Alkalinity [meq L^{-1}]	1.96–4.72
Ca^{++} [meq L^{-1}]	1.03–4.15
Mg^{++} [meq L^{-1}]	1.09–3.07
Cl^- [meq L^{-1}]	15.2–38.7

updated version from Donabaum et al. (1999). In 1987 the lake was in the clear water, macrophyte-dominated state as indicated by the high macrophyte biomass (721 tons dry weight biomass) and the low phytoplankton biovolume of 1.7 mm^3 L^{-1}. Phytoplankton composition at that time was dominated by cryptophytes (39%), dinophytes (17%), and chrysophytes (12%) while cyanobacteria comprised as little as 4%. Macrophyte biomass was mainly made up by a variety of Charophyte species almost entirely covering the bottom sediments. For the following 5 years we only have fragmented information. Certainly algal biovolume gradually increased at a moderate rate from 3 to 4 mm^3 L^{-1}. First symptoms of severe deterioration of water quality were detected during routine monitoring in the late 1980s. The filamentous cyanobacteria *Limnothrix redekei* (VAN GOOR) MEFFERT was first recorded in water quality samples in the year 1992. By early 1993 the lake had suddenly shifted to a turbid state dominated by the filamentous, cyanobacterial species *Cylindrospermopsis raciborskii* (WOLOSZ.) SEENAYYA ET SUBBA RAJU which potentially can fix atmospheric nitrogen and is also able to produce cyanotoxins harmful to men affecting also trophic interactions (Dokulil and Mayer 1996, Mayer et al. 1997). This compositional change was accompanied by a sixfold increase in annual average biovolume and a dramatic loss of macrophytes. In the years 1993 and 1994 only remnants of the previous submerged macrophyte stands and the extensive bottom cover of Charophytes were left (Dokulil and Janauer 1995).

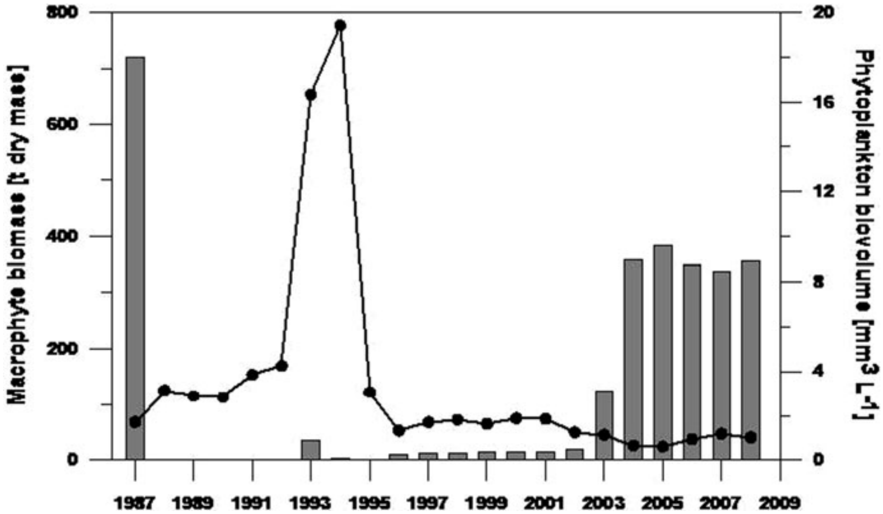

Fig. 14.3 Long-term changes of macrophyte biomass (*bars*) and phytoplankton biovolume (*line*) in Old Danube from 1987 to 2008

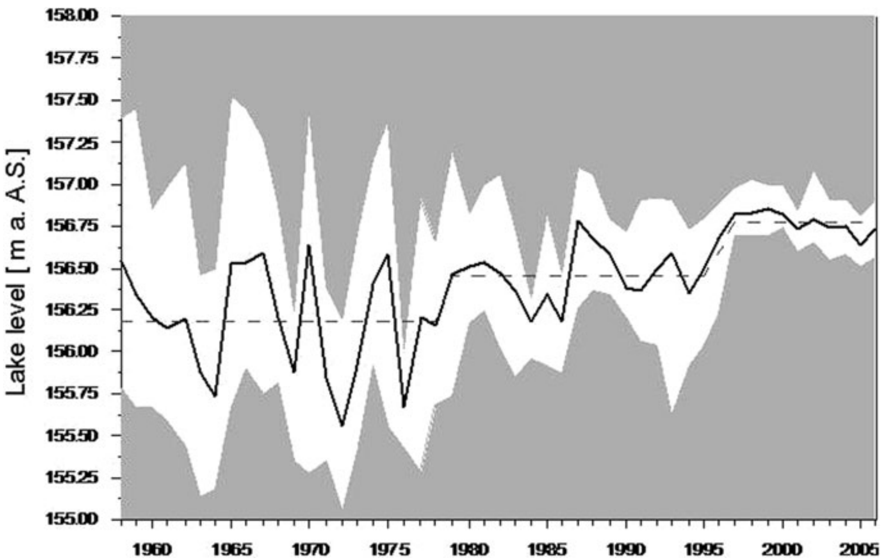

Fig. 14.4 Maximum, mean, and minimum water levels in Old Danube for the years 1958–2003. Water level is in meters above the Adriatic Sea

Reasons responsible for the rapid shift from clear water to the turbid state were believed to result from substantial nutrient flux from non-point sources such as leaking septic tanks and elution from a former dump site nearby. Nutrient input originating from the excretion of water fowl and from recreational activities was assumed to be of minor importance. Due to large stocks of benthivorous (cyprinids) and planktivorous fish in Old Danube, background turbidity was high and abundance of larger zooplankton species was low. The zooplankton was dominated by rotifers, small cladocerans, and copepods. The main trigger for the shift, however, was seen in the changes in water level dynamics in the second half of the twentieth century (Fig. 14.4.). The reduction in water level fluctuation and a permanent higher water level since the late 1970s in combination with nutrient influx were assumed to be the main reasons for the vanishing of the macrophytes similar to observations by Blindow et al. (1993).

14.3.2 How to Restore? The Concept of Remediation

As a consequence of the associated drop in water quality, the municipality asked for quick action and restoration early in 1993. As an immediate short-lived action, the lake was diluted with water of better quality which reduced algal biomass considerably in the first half year of 1994. After running a number of different pilot projects in 1994, we decided to use internal phosphorus precipitation as a restoration technique (Ripl 1976). As a whole-lake experiment, ferric chloride and calcium nitrate were successfully applied in a two-step process in spring 1995 and 1996 resulting in a drastic backward shift of all parameters. For details refer to Donabaum et al. (1999) or Donabaum et al. (2004). Secchi depth increased significantly mainly because algal biovolume declined to about 1 mm^3 L^{-1} and macrophytes started to re-colonize the system (Fig. 14.3). A period of 6 years from 1997 to 2002 and several additional measures including biomanipulation were necessary to finally re-establish macrophyte biomass. During this period phytoplankton composition changed from cyanobacterial dominance to a more mixed composition of various algal classes (Fig. 14.5.). Similarly, zooplankton biomass declined and the composition shifted from rotifer dominated to a greater preference of cyclopoida (Fig. 14.6). The main increase of macrophyte biomass occurred in 2003 and 2004 after growth has been promoted every spring through water level drawdown since 2002. This drawdown, to some extent, mimics the previous water level dynamics thereby providing better light conditions in shallow areas enhancing macrophyte growth. As a consequence, annual mean submerged macrophyte biomass has now stabilized around 350 tons dry weight (Fig. 14.3) which is less than in the 1980s. Species composition has changed and *M. spicatum* is now dominating making weed management necessary to avoid interference with swimming and boating. Therefore, the biomass stabilization is mainly a consequence of the aquatic weed control by cutting and removing aquatic weeds. At the moment, Charophytes are coming back at increased rates. The final goal therefore is to get a bottom cover of stonewort back similar to what it was previously.

Following Scheffer (1998), shifts in stable states can be visualized using conventional phosphorus–chlorophyll diagrams. The development of annual average TP versus chlorophyll-a is plotted for Old Danube in Fig. 14.7. The diagonal line in the graph separates macrophyte from algal-dominated years. The shift from one stable state to the other occurred in 1992. Trophic state dropped from hypertrophic to lower eutrophic in 1995 after the first phase of internal restoration. Mesotrophic conditions were reached in 2004. The development of chlorophyll-a versus

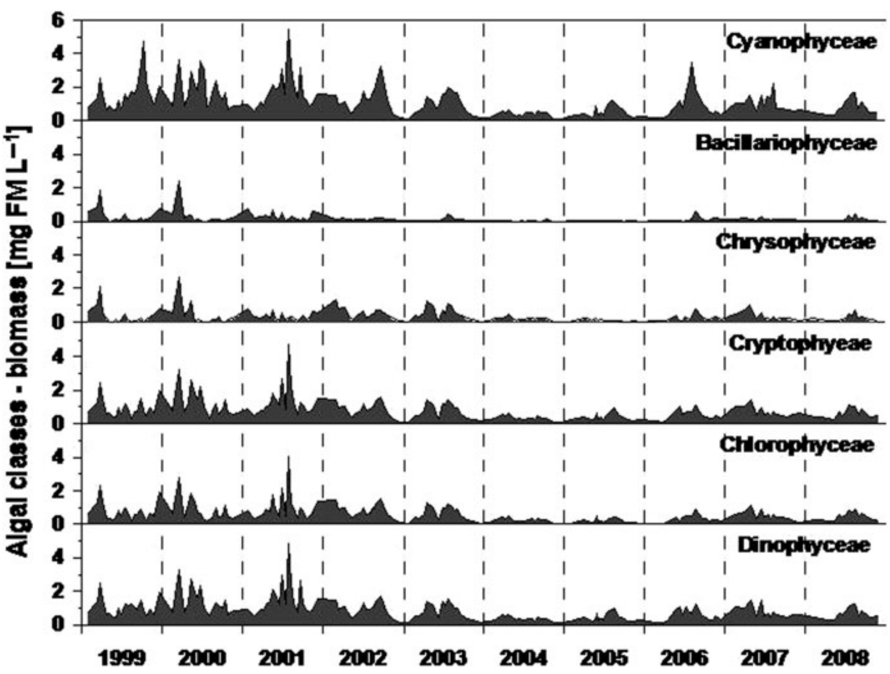

Fig. 14.5 Long-term succession of phytoplankton algal classes in Old Danube for the years 1999–2008

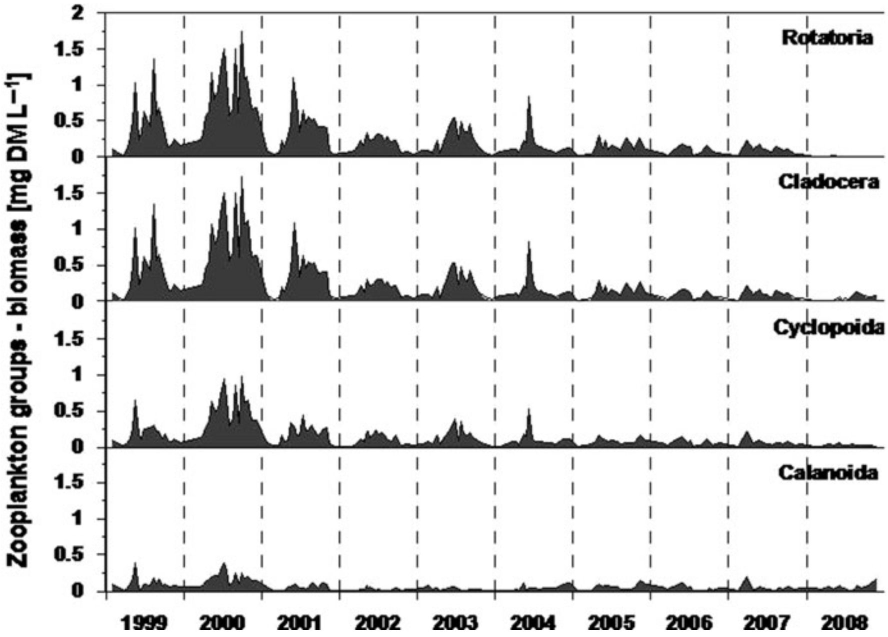

Fig. 14.6 Long-term changes of zooplankton biomass and groups in Old Danube for the years 1999–2008

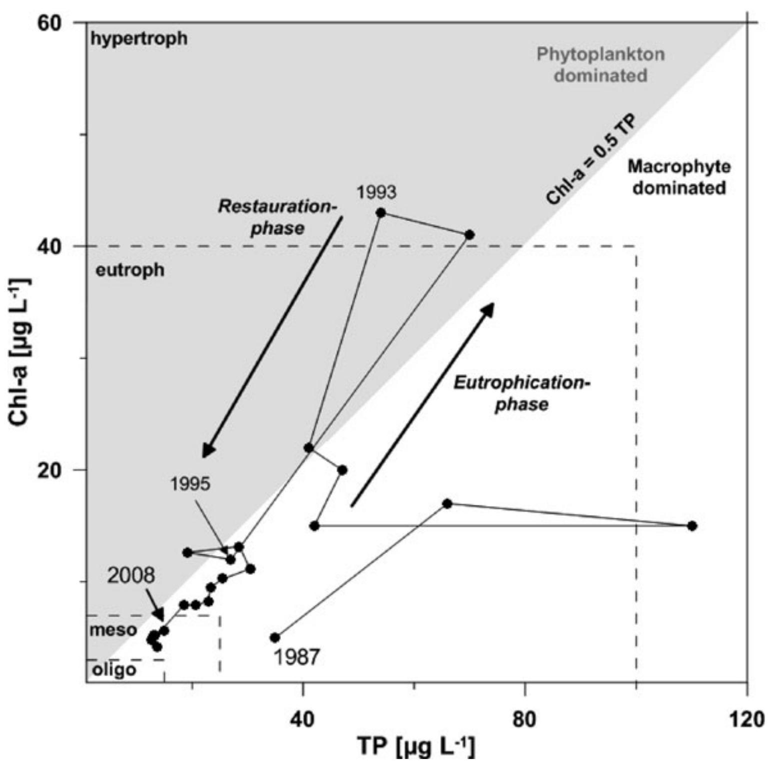

Fig. 14.7 Trophy plot of Chl-a versus TP for Old Danube for the years 1987–2008. Delineation of trophic levels follows Forsberg and Ryding (1980). Separation of phytoplankton from the macrophyte domination by Chl-a = 0.5 TP

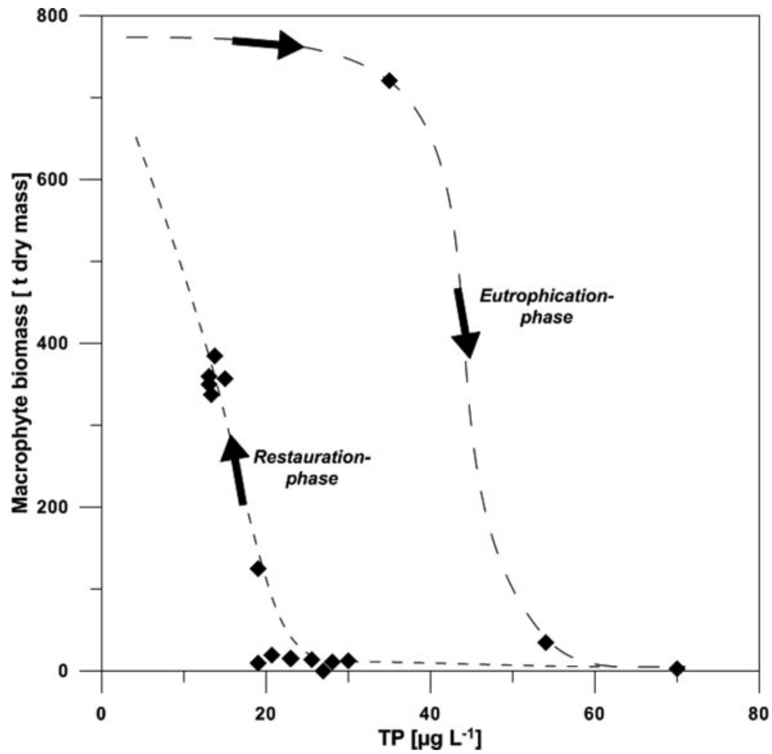

Fig. 14.8 Annual total macrophyte biomass in tons of dry matter versus annual mean total phosphorus concentration (TP) for the year 1987 and for the period 1993–2008

TP over time in this graph, however, does not show a great deal of hysteresis due to resilience of the system, most likely because of the rapid internal restoration.

In contrast to the phytoplankton, the history of macrophyte development clearly indicates considerable hysteresis in switching between stable states (Fig. 14.8). Also only limited information is available for the eutrophication phase; the switch from macrophyte dominated to the dominance of phytoplankton is clearly separated from the backward switch. Macrophyte development did not immediately respond to the reduction in total phosphorus concentrations. The resilience of the system produced strong hysteresis which to some extent probably was a result of the chemical perturbation during remediation forcing the system to switch back through technical intervention. Natural cyclic shifts between stable states have been recently observed and modeled by Van Nes et al. (2006).

14.4 Conclusions from a Successful Story

Alternative stable states and regime shifts can occur in shallow lakes as a result of natural or anthropogenic forcing. Such stable equilibria can occur within the same water body at various locations, at different times of the year, or during trophic development (Scheffer et al. 1994). The theory of alternative stable states and regime shifts can be applied successfully to the recovery of urban lakes as a consequence of ecohydrological changes (Hosper 1998). When systems are forced back to the original, macrophyte-dominated stage through, e.g., internal technical intervention resilience produces hysteresis and consequently return times become longer, particularly for macrophytes. Here we have shown that state transitions from one stable state to another were associated with significant changes in species composition of the phytoplankton assemblage. Shifts in either direction immediately altered total biovolume and algal composition without hysteresis. In contrast, considerable hysteresis occurred during macrophyte recovery making additional remediation measures necessary. Regime shifts induced by internal restoration techniques may require many years of monitoring for improvement and additional efforts to return to the previous stable state. Summarizing the experiences of the remediation project Old Danube, the theory of alternative stable states can be applied successfully to the restoration and recovery of shallow urban lakes.

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References

Baker WL, Walford GM (1995) Multiple stable states and models of riparian vegetation succession on the Animas River, Colorado. Ann Assoc Am Geogr 85:320–338

Bertness MD, Trussell GC, Ewanchuk PJ, Silliman BR (2002) Do alternative stable community states exist in the Gulf of Maine rocky intertidal zone? Ecology 83:3434–3448

Blindow I, Andersson G, Hargeby A, Johansson S (1993) Long-term pattern of alternative stable states in two shallow eutrophic lakes. Freshw Biol 30:159–167

Carpenter SR (2003) Regime shifts in lake ecosystems: pattern and variation. Excellence in ecology series, vol 15. Ecology Institute, Oldendorf/Luhe

Carpenter SR (2005) Eutrophication of aquatic ecosystems: bistability and soil phosphorus. PNAS 102:10002–10005. http://www.pnas.org/content/102/29/10002.full.pdf+html

Carpenter SR, Cottingham KL (1997) Resilience and restoration of lakes. Conservation Ecology [online] 1(1):2. http://www.consecol.org/vol1/iss1/art2/

Conell JH, Sousa WP (1983) On the evidence needed to judge ecological stability or persistence. Am Nat 121:789–824

Dokulil MT, Janauer GA (1995) Alternative stable states during eutrophication of a shallow urban lake in Vienna, Austria. Proc 6th Int Conf Conserv Manag Lakes – Kasumigaura'95 2:730–733

Dokulil MT, Mayer J (1996) Population dynamics and photosynthetic rates of a Cylindrospermopsis – Limnothrix association in a highly eutrophic urban lake, Alte Donau, Vienna, Austria. Algol Stud 83:179–195

Dokulil MT, Teubner K (2003) Eutrophication and restoration in shallow lakes – the concept of stable equilibria revisited. Hydrobiologia 506–509:29–35

Donabaum K, Schagerl M, Dokulil MT (1999) Integrated lake management to restore macrophyte domination. Hydrobiologia 395/396:87–97

Donabaum K, Pall K, Teubner K, Dokulil MT (2004) Alternative stable states, resilience and hysteresis during recovery from eutrophication – a case study. SIL-News 43:1–4. http://www.limnology.org/news/silnews43.pdf

Forsberg CG, Ryding SO (1980) Eutrophication parameters and trophic state indices in 30 Swedish waste-receiving lakes. Arch Hydrobiol 89:189–207

Gunderson L, Holling CS, Pritchard L, Peterson GD (2002) Resilience. In: Mooney HA, Canadell JG (eds) Encyclopedia of global environmental change, Vol. 2, The Earth system: biological and ecological dimensions of global environmental. John Wiley & Sons ISBN 0-471-97796-9

Hare SR, Mantua NJ (2000) Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progr Oceanogr 47:103–145

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Hosper SH (1998) Stable states, buffers and switches: an ecosystem approach to the restoration and management of shallow lakes in The Netherlands. Wat Sci Tech 37:151–164

Hughes TP (1994) Catastrophes, phase shifts, and largescale degradation of a Caribbean coral reef. Science 265:1547–1551

Jasinski JPP, Asselin H (2004) Alternative view of alternative stable states. Front Ecol Environ 2:10–11

Jasinski JPP, Payette S (2005) The creation of alternative stable states in the southern boreal forest, Quebec, Canada. Ecol Monogr 75:561–583

Jeppesen E, Søndergaard M, Søndergaard M, Christoffersen K (eds) (1998) The structuring role of submerged macrophytes in lakes. Ecological studies, vol 131. Springer, New York, NY

Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. Am Zool 32:674–682

Lewontin RC (1969) The meaning of stability. Brookhaven Symp Biol 22:13–24

Löffler H (1988) Alte donau limnologische projektstudie ökosystem alte donau. Final project report, University of Wien

Mayer J, Dokulil MT, Salbrechter M, Berger M, Posch T, Pfister G, Kirschner AKT, Velimirov B, Steitz A, Ulbricht T (1997) Seasonal successions and trophic relations between phytoplankton, zooplankton, ciliophora and bacteria in a hypertrophic shallow lake in Vienna, Austria. Hydrobiologia 342/343:165–174

Moss B, Madgwick J, Phillips G (1997) A guide to the restoration of nutrient-rich shallow lakes. Broads Authority, UK

Moss B, Stansfield J, Irvine K, Perrow M, Phillips G (1996) Progressive restoration of a shallow lake: a 12-year experiment in isolation, sediment removal and biomanipulation. J Appl Ecol 33:71–86

Paine RT, Tegner MJ, Johnson EA (1998) Compound perturbations yield ecological surprises. Ecosystems 1:535–545

Peterson CH (1984) Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? Am Nat 124:127–133

Petraites PS, Latham RE (1999) The importance of scale in testing the origins of alternative stable states with examples from marine and terrestrial ecosystems. Ecology 80:429–442

Rietkerk MS, Dekker C, de Ruiter PC, van de Koppel J (2004) Self-organized patchiness and catastrophic shifts in ecosystems. Science 305:1926–1929

Ripl W (1976) Biochemical oxidation of polluted lake sediment with nitrate. A new restoration method. Ambio 5:112–135

Scheffer M (1990) Multiplicity of stable states in freshwater systems. Hydrobiologia 200/201:475–486

Scheffer M (1991) On the predictability of aquatic vegetation in shallow lakes. Mem Ist Ital Idrobiol 48:207–217

Scheffer M (1998) Ecology of shallow lakes. Chapman and Hall, London

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. TREE 18:648–656

Scheffer M, Carpenter SR, Foley JA, Folkes C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413: 591–596

Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in shallow lakes. TREE 8: 275–279

Scheffer M, van den Berg M, Breukelaar A, Breukers C, Coops H, Doef R, Meijer ML (1994) Vegetated areas with clear water in turbid shallow lakes. Aquat Bot 4: 193–196

Sedia E, Ehrenfeld J (2003) Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. Oikos 100:447–458

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Steele JH (1998) Regime shifts in marine ecosystems. Ecol Appl 8:S33–S36

Sutherland JP (1974) Multiple stable points in natural populations. Am Nat 108:859–873

Uhlmann D (1980) Stability and multiple steady states of hypereutrophic ecosystems. In: Barica J, Mur R (eds) Hypertrophic ecosystems. Develop Hydrobiol 2:235–247

Van de Koppel J, Herman PMJ, Thoolen P, Heip CHR (2001) Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. Ecology 82:3449–3461

Van Nes EH, Scheffer M (2005) Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. Ecology 86:1797–1807

Van Nes EH, Rip WJ, Scheffer M (2006) A theory for cyclic shifts between alternative states in shallow lakes. Ecosystems 10:17–27 DOI 10.1007/s 10021-006-0176-0