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Regime Shifts in Shallow Lakes

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Every now and then the usual scenario of fluctuations around trends in ecosystems is interrupted by sharp shifts to a different regime (Scheffer and others 2001; Carpenter 2003). Similarly, reconstructions of past climatic dynamics reveal various spectacularly rapid changes punctuating episodes of relative stability (Rial and others 2004), and also societies are notorious for going through occasional drastic shifts (Brock 2006). The term '*regime shift*' originally proposed to describe sharp changes in oceanic ecosystems (Steele 1996; Hare and Mantua 2000), is increasingly used in a general sense to refer to such sudden drastic transitions from one persistent dynamical regime to another.

Regime shifts may be due to different mechanisms, such as a drastic impact on the system, or a stepwise change in some important external condition. However, of particular interest are regime shifts that arise because the system reacts sensitively to changing conditions around some critical threshold. One reason for this can be the existence of alternative attractors in a system over some range of conditions. Although this possibility has been postulated and intensively discussed during various episodes in the history of ecology (Holling 1973; May 1977), interest increased sharply after this phenomenon was convincingly demonstrated for the ecosystems of shallow lakes. In those ecosystems submerged macrophytes can become abundant if the water is clear enough, but the macrophytes also affect many key processes promoting water clarity (Jeppesen and others 1997). This implies a positive feedback that can cause the turbid and a clear state to be alternative attractors (Scheffer and others 1993).

Much of the work on shallow lakes over the years has focused on understanding how the alternative states work, and how manipulation of fish stocks can be used to tip lakes from a turbid to a clear state (Moss and others 1996; Jeppesen 1998; Scheffer 1998). There have been anecdotal descriptions of lakes shifting in response to an exceptionally heavy storm (Hamilton and Mitchell 1988), a change in water level (Wallsten and Forsgren 1989), or unknown causes (Blindow and others 1997). However, little work had been done so far on unraveling the mechanisms behind natural regime shifts in shallow lakes.

In this issue we present a cluster of papers that address this topic from different perspectives. Although some studies illustrate that speculations can remain inconclusive even after years of investigation, others arrive at fundamentally new insights and hypotheses that, just like the finding of alternative stable states, may have parallels and implications far beyond the realm of limnology.

First, a 30-year in-depth study of Lake Veluwe provides a detailed view of a classical scenario of eutrophication and recovery of a shallow lake (Ibelings and others 2007). Hysteresis between alternative states is apparent in this case study, and it is argued that the resilience of the clear state depends critically on a few key species. The remaining studies all highlight deviations from this classical scenario.

Two of the papers highlight the remarkable phenomenon of lakes oscillating between the contrasting states in a cyclic way. A Dutch and an English lake seem to have moved from a turbid

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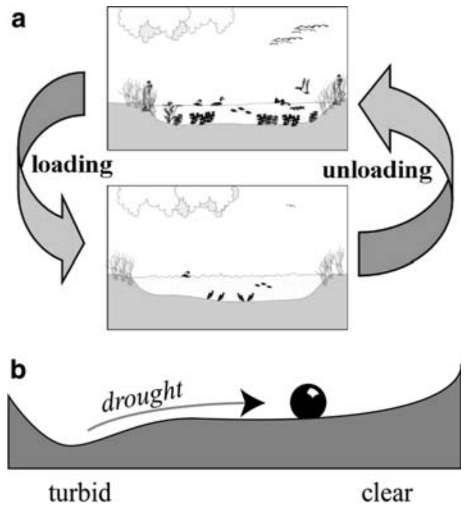

Figure 1. Two newly proposed scenarios of regime shifts in shallow lakes. (**A**) Oscillations between a vegetated and a turbid state may be due to intrinsic differences in accumulation of phosphorus and organic matter in the two (van Nes and others 2007). (**B**) Occasional droughts push the system to an unstable clear state that represents the ghost of a stable state. Because droughts happen every now and then, and the dynamics around such a ghost are very slow, the lake may be in a transient state most of the time. Note that the way to interpret such stability landscapes is that the movement of the ball is always damped. Imagine that the ball rolls through a heavily viscous fluid (Van Geest and others 2007).

state to such a cyclic regime upon restoration efforts (van Nes and others 2007*)* (Figure 1A) whereas two Swedish lakes appear to have oscillated in an irregular fashion for a century or more already (Hargeby and others 2007). Van Nes and others (2007) suggest a mechanism explaining why under particular conditions lakes with alternative states may become cyclic. Although the field data from Swedish and Dutch cyclic lakes are consistent with this hypothesis, both studies also suggest that external events such as extreme weather conditions may have played a role in triggering the shifts. The emerging picture is that of a 'noisy clockwork' (Bjornstad and Grenfell 2001). Slow processes undermine the resilience of each of the alternative states in turn, allowing stochastic events to trigger quasi cyclic shifts. Although various studies have highlighted cyclic shifts in ecosystems, these lake studies seem to be the first to show how such a cyclic scenario may arise from an alternative stable states scenario in a single ecosystem.

A study of 70 floodplain lakes also reveals frequent shifts between alternative states (Van Geest and others 2007). Here, draw-down of water levels in dry summers seems to be the main trigger for an occasional shift from a turbid to a clear state. The authors suggest that in the absence of such incidental disturbance most of those lakes would be turbid in view of the high nutrient levels. They also show that part of the lakes can remain in a transient clear state for years after the disturbance. They use models to show that this might theoretically be explained as the result of a 'ghost' of the clear equilibrium. Such a ghost is not stable, but may still slow down the development towards the turbid state (Figure 1B). The study supports the view that transients rather than equilibria may be the key to understanding some ecological systems (Hastings 2004). A practical implication is that the artificial stabilization of water levels in many shallow lakes in agricultural areas may aggravate the tendency of such lakes to be in a permanently turbid state, emphasizing the importance of restoring the natural regime of fluctuating water levels.

Most work on shallow lakes has focused on the role of nutrient levels, water fluctuations and fish kills in driving shifts between alternative states. A Danish study in this issue reminds us that large scale ecosystem shifts may occur if any key-species is sensitive to an environmental factor that varies around a critical range (Jeppesen and others 2007). Combining experiments and field data from 60 brackish lagoons, the authors show that *Daphnia*, which is the main grazer controlling phytoplankton in most lakes, disappears if salinity increases above some threshold (typically < 2‰). This implies that brackish systems can be quite sensitive to freshwater input, and that this is another variable that might be used for managing the ecological state of such lakes. It also implies that fish-stock manipulations aimed at cascading effects may not be successful if salinity levels are too high to allow *Daphnia* to become abundant.

The papers in this issue illustrate that our insight into the dynamics of shallow lakes around their 'stable states' has become much richer over the years. Other lines of work are revealing the different role of fish in (sub)tropical lakes (Lazzaro 1997), the possibility of floating plant dominance as a third state (Scheffer and others 2003) and the fact that various lakes appear to show a rather smooth shift towards the clear state when subjected to nutrient loading reduction (Jeppesen and others 2005, 2006, in press and unpublished data). We hope that such elaborations of the theory for the archetypical system of shallow lakes may keep inspiring fresh looks at other ecosystems, and help move the discussion away from the rather simplistic question of whether alternative attractors exist or not, towards more realistic visions of when and how alternative attracting regimes may dominate dynamics.

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