OLM12.3 Hysteresis in a high productivity shallow lake

One of the earliest dynamical systems in which *hysteresis* (Ch12Divers, p.272) – the phenomenon that the values of an environmental variable at which forward and backward regime shift occurs differ – was described was an artificial lake in the Netherlands (Scheffer et al. 2001). This is still the prototype study regarding such transitions. Relying on two review articles (Ibelings et al. 2007; Kéfi et al. 2016) the mechanisms of this interesting – and not nearly exceptional, see also OLM 12.4 – phenomenon will be discussed briefly.

The hysteresis of ecosystems containing keystone species is an important dynamical issue because the loss of such species due to a major (or gradually accumulating) environmental change may induce the collapse of a complete community which they dominate (McMahon 1973; Bruno et al. 2003). A well-known example of such a dynamical system is shallow-lake macrophyte communities (Van den Berg et al. 1999). Ibelings et al. (2007) have studied the state changes of Veluwe Lake, an artificial shallow lake created in the Netherlands in 1957, during the period between 1969 and 2000. Due to the nutrient-rich waters drained into the lake it had become eutrophic by 1969, and – following external intervention – it took a quarter of century for it to regenerate (Figure 12.3.1).

Pásztor L., Z. Botta-Dukát, G. Magyar, T. Czárán and G. Meszéna (2016)
Theory-based ecology: A Darwinian approach, Oxford University Press. OLM 12.3.
Hysteresis in a high poductivity shallow lake. pp. 1-5.

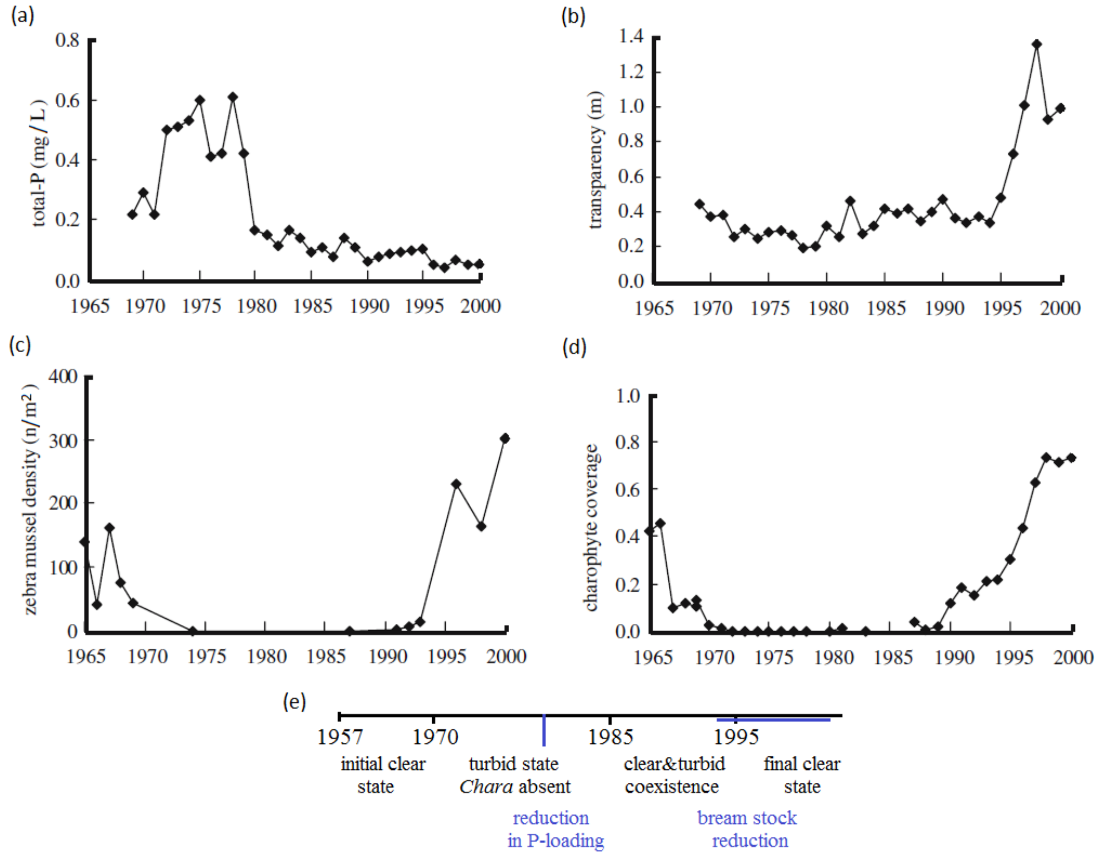

Figure 12.3.1: Monitoring the changes in Lake Veluwe between 1965 and 2000 (Ibelings et al. 2007).

Figure a) and b): The transparency of the lake remained low during the period 1969-95 despite the P-load having been drastically reduced in 1980 and the lake regularly flushed by the water of a nearby polder. c) and d): The density of submerged aquatic plants and zebra mussels started radically increasing only after 1993, when the bream population was decimated. The cover of stoneworts (Charophytes) (d) and the density of zebra mussels (*Dreissena polymorpha*) (c) have returned to their original values at a P-load (a) that was much lower than the value at which their populations collapsed.

The ecological state of the lake can be reliably followed by measuring the coverage by stoneworts (*Chara sp.*) and the turbidity (or transparency) of the water body. All the relevant external effects (spontaneous and planned alike) affected the total phosphorus content of the water directly. Following a steady increase in the P-content of the water the transparency of the lake has dropped by the seventies, because planktonic algae have boomed while *Chara* and zebra mussel (*Dreissena polymorpha*) have essentially been wiped out of the lake. (Zebra mussel had been introduced and spread over the Great Lakes in which, among other effects, it decreased turbidity considerably (Cuhel and Aguilar, 2013). Decreasing the P-influx to a quarter of its previous level was still not sufficient for *Chara* to recolonize the lake from the shallows. Reinstating the original state of the lake was facilitated from 1994 by the stepwise culling to a third of its density of the bream population that had increased the turbidity of the water by convection, decreased zooplankton density, and impeded the colonization of zebra mussel that could have filtered the water.

The lake has re-gained its high transparency by 2000, and it has proven to be resilient against temporary disturbances (dredging that results in high turbidity).

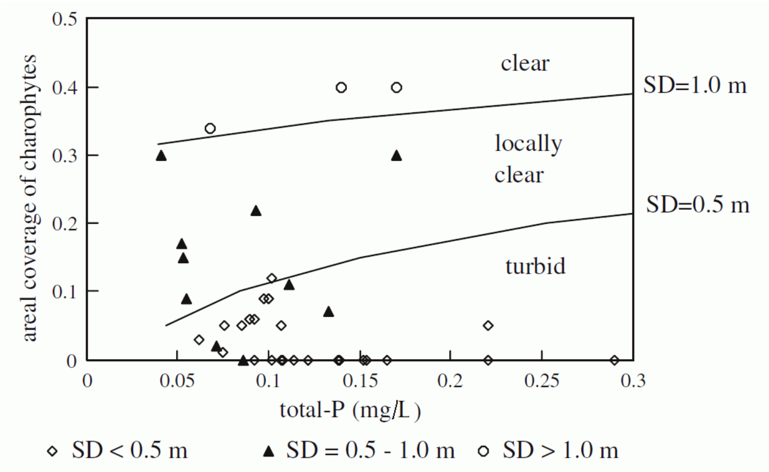

Figure 12.3.2: Alternative stable states in Lake Veluwe (Ibelings et al. 2007).

Decreasing phosphorus concentration is not sufficient in itself to increase water transparency and *Charophyta* cover. The two lines on the plot are the average simulated water transparencies of 0.5 and 1.0 meter. The actual transparency measurements are represented by the three different symbols. The condition of 1.0 m transparency is that the cover of green algae exceed 30%. At high plant cover values the water remains transparent even at relatively high phosphorus loads.

The textbook examples show that positive interactions may result in alternative stable states, but they need not to. Positive interactions are necessary, but not sufficient for alternative stable states to occur; we have seen this in the example of weak Allee effects (Ch6Regul, Figure 6.3, p.98). The previous example is typical in that there are more than one interactions leading to positive feedback between the growth rates and the density of foundation species (Figure 12.3.3).

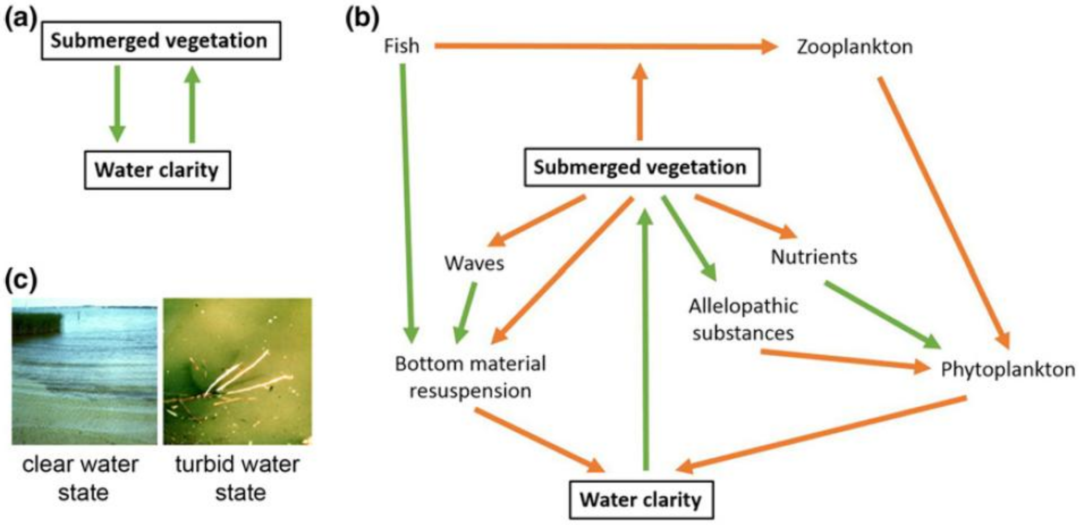

Figure 12.3.3: Positive feedback loops stabilizing alternative stable states in shallow lakes (Kéfi et al. 2016).

a): The main positive feedback effect determining community composition in shallow lakes; b): Interactions resulting in feedback effects. The sign of the complete feedback loop is the product of the signs of the interactions making up the loop. Negative effects are represented by orange lines, positive ones are green; c): Typical pictures of the two states.

High abundance of the light-limited stoneworts reduces the intensity of waving and thus the turbidity of water, which has a positive effect on their own growth through providing more light (positive feedback). They also excrete allelopathic substances which decrease the growth of phytoplankton that has a negative effect on water transparency – another positive feedback between stoneworts density and growth rate. Stonevorts decreases the equilibrium concentration of nutrients by consuming them and by hindering their influx through slowing down the stirring up of the sediment. These are also positive effects on their own growth and negative on that of their competitors. On the other hand, benthic fish have two different positive effects on the growth of phytoplankton species: by decreasing the density of zooplankton and by increasing water turbidity. The trigger of the forward shift phase is the eutrophication due to high nutrient load, and it results in low transparency and the extinction of stoneworts. This state is stabilized by the increase of the benthic fish population by stirring up the sediment and removing the mussels filtering the water. Therefore, decreasing the nutrient load is not sufficient to regenerate the original vegetation of the lake – hence the hysteresis of the dynamics.

References

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