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Review

Alternative stable states in large shallow lakes?

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ABSTRACT

Many lakes worldwide are experiencing great change due to eutrophication. Consequently, species composition changes, toxic algal blooms proliferate, and drinking water supplies dwindle. The transition to the deteriorated state can be catastrophic with an abrupt change from macrophyte to phytoplankton domination. This has been shown repeatedly in small lakes. Whether such alternative stable states also exist in large shallow lakes is less clear, however. Here we discuss the characteristics that give rise to alternative stable states in large shallow lakes either in the lake as whole or restricted to specific regions of the lake. We include the effect of *lake size*, *spatial heterogeneity* and *internal connectivity* on a lake's response along the eutrophication axis. As a case study, we outline the eutrophication history of Lake Taihu (China) and illustrate how *lake size*, *spatial heterogeneity* and *internal connectivity* can explain the observed spatial presence of different states. We discuss whether these states can be alternatively stable by comparing the data with model output (PCLake). These findings are generalised for other large, shallow lakes. We conclude that locations with prevailing *size effects* generally lack macrophytes; and, therefore, alternative stable states are unlikely to occur there. However, most large shallow lakes have macrophytes whose presence remains unexplained when only *size effect* is taken into account. By including *spatial heterogeneity* in the analysis, the presence of macrophytes and alternative stable states in large shallow lakes is better understood. Finally, *internal connectivity* is important because a high internal connectivity reduces the stability of alternative states.

Contents

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Introduction

Eutrophication drives numerous lakes worldwide to a deteriorated state where phytoplankton dominate over macrophytes (Smith et al., 1999). As a result, species composition changes (Jeppesen et al., 2000; Smith et al., 1999), toxic algal blooms proliferate (Paerl et al., 2011a) and drinking water supplies dwindle (Falconer and Humpage, 2005; Smith et al., 1999). The transition to a phytoplankton dominated state is often non-linear and in many cases catastrophic (Scheffer et al., 2000). In case of a catastrophic transition, a change from the macrophyte dominating state to the alternative phytoplankton state will be rapid and recovery may show hysteresis (alternative stable states) when positive feedbacks between macrophytes and phytoplankton are strong (Scheffer et al., 1993).

Small lakes are more likely to exhibit a macrophyte-rich state than large lakes (Van Geest et al., 2003) primarily because small lakes are less prone to destructive wind forces (Janse et al., 2008) and fish are less abundant (Scheffer and Van Nes, 2007). Examples of small lakes that shifted between the macrophyte and phytoplankton dominated state are the gravel pit lakes in England (<1 km^2, <2 m depth) (Scheffer et al., 1993; Wright and Phillips, 1992) and Lake Veluwe in the Netherlands (30 km^2, 1.5 m depth) (Meijer, 2000). But there are also larger lakes with macrophytes, and where alternative stable states are presumed. For example, Lake Apopka (125 km^2) in the USA became susceptible to disturbances due to increasing nutrient loading; the large macrophyte stands finally disappeared after a disruptive hurricane event (Bachmann et al., 1999; Lowe et al., 2001).

It is an intriguing question under which conditions large shallow lakes exhibit alternative stable states. The impression is often that these alternative states appear lake wide (Scheffer, 1990; Scheffer et al., 1993), though it is conceivable that in some cases these may be restricted to certain areas within a lake as well. This information is crucial because the type of transition (catastrophic or not) will determine the lake's response to restoration measures (Scheffer et al., 2001). It has been shown that it is difficult to restore large shallow lakes (Gulati et al., 2008). For instance Lake Okeechobee (USA, 1900 km^2, 2.7 m depth) (Beaver et al., 2013), Chaohu (China, 760 km^2, 2.5 m depth) (Shang and Shang, 2005) and Lake Markermeer (The Netherlands, 700 km^2, 3.2 m depth) (Kelderman et al., 2012b; Lammens et al., 2008) still suffer from water quality problems after restoration. The lasting water quality issues in these larger lakes often affect large populations that depend on their ecosystem services (Carpenter et al., 2011).

Here, we discuss the response of large shallow lakes to eutrophication. We aim to characterise conditions that promote alternative stable states within large shallow lakes (>100 km^2). First, we describe the effect of different lake characteristics on the lake response to eutrophication. We focus on *lake size*, *spatial heterogeneity* (spatial variation in patterns and processes within a lake) and *internal connectivity* (horizontal exchange between lake compartments; here defined as spatially distinct regions that are relatively homogenous in characteristics and processes). These characteristics are all recognised as key factors in understanding ecological systems (Cadenasso et al., 2006). Second, we will present the eutrophication history of Lake Taihu, China's third largest freshwater lake. Next, the effects of *lake size*, *spatial heterogeneity* and *internal connectivity* on the observed spatial development of this lake will be discussed in relation to model output. Finally, we discuss how we may generalise the effects of *lake size*, *spatial heterogeneity* and *internal connectivity* for other large shallow lakes.

Theory: *size effect*, *spatial heterogeneity* and *internal connectivity*

Alternative stable states are the result of strong reinforcing feedback loops that strengthen the competitiveness of the ruling state with other states (May, 1977; Scheffer et al., 2001). The dominant state is therefore not only dependent on the present conditions, but also on the prevalent state in the past (Scheffer and Carpenter, 2003). As a result of strong reinforcing feedback, multiple states are possible given the same conditions (Scheffer and Van Nes, 2007). Two important states distinguished in shallow lakes are the clear macrophyte state and the turbid phytoplankton state (Scheffer et al., 1993). These states are alternatively stable if the reinforcing feedback between algae and macrophytes is sufficiently strong to facilitate potential dominance of either of both (Hosper, 1989; Phillips et al., 1978; Scheffer et al., 1993).

PCLake is an ecosystem model that can be used as a tool to predict the state of lakes (e.g. macrophyte dominated or turbid) and indicate whether these states are stable or not (Janse, 1997). Previous studies showed that the presence of alternative stable states strongly depends on depth and fetch ('distance between any point in a lake and the shore in the wind direction') (Janse et al., 2008, 2010). Results of a bifurcation analysis using the general settings of PCLake illustrate that too great a depth or fetch prevents macrophyte dominance (Fig. 1) while very shallow lakes are likely to have unconditionally sufficient light conditions allowing macrophyte growth to impede algal domination (Fig. 1). Only lakes that meet the requirements for both states to dominate under the same conditions will show alternative stable states (Fig. 1). These requirements for alternative stable states can be fulfilled in a lake as a whole but also in regions (compartments) of a lake allowing different states to exist side by side. For details on the general settings used here see Janse (2005) and for details on the bifurcation analysis see Electronic Supplementary Materials ESM Appendix S1.

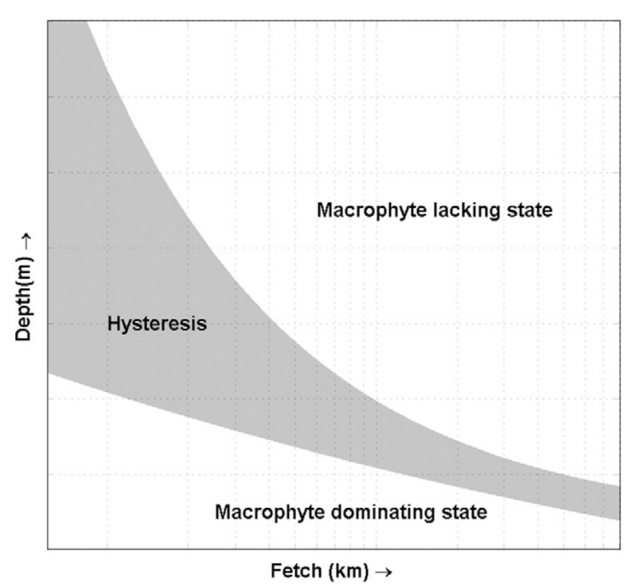

Fig. 1. Model output indicating the presence of alternative stable states depending on lake fetch and depth (PCLake, (Janse et al., 2010)). Alternative stable states are predicted in the grey area (labelled 'Hysteresis').