



Review

Alternative stable states in large shallow lakes?

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ARTICLE INFO

Article history:

Received 16 April 2014

Accepted 10 September 2014

Available online 16 October 2014

Communicated by Robert McKay

Index words:

Size effect

Spatial heterogeneity

Internal connectivity

Large shallow lakes

Phytoplankton versus macrophytes

Taihu

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 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.

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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 km², <2 m depth) (Scheffer et al., 1993; Wright and Phillips, 1992) and Lake Veluwe in the Netherlands (30 km², 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 km²) 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 km², 2.7 m depth) (Beaver et al., 2013), Chaohu (China, 760 km², 2.5 m depth) (Shang and Shang, 2005) and Lake Markermeer (The Netherlands, 700 km², 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 km²). 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.

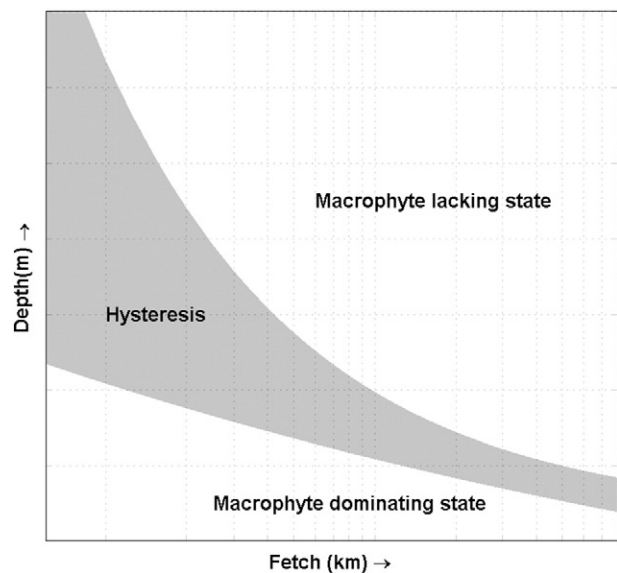


Fig. 1. Model output indicating the presence of alternative stable states depending on lake fetch and depth (PCLake, (Janse et al., 2010)). Alternative stable states are predicted in the grey area (labelled 'Hysteresis').

Size effect

Lake size is a very important factor in shaping the response of lakes to eutrophication, here further referred to as the *size effect*. As a result of the *size effect*, large shallow lakes are often presumed to lack alternative stable states (Janse et al., 2008). First, with larger lake size, fetch is increased (Fig. 2A, process 1) (Janse et al., 2008; Jeppesen et al., 2007). A longer fetch leads to larger wind-driven waves resulting in a higher shear stress on the sediment surface (Carper and Bachmann, 1984). Therefore, large shallow lakes are more prone to wind forces than small shallow lakes. As a result of high *size effect*, macrophytes are damaged by wave forces and sediment resuspension is more severe which inhibits macrophyte growth by light attenuation (Scheffer, 2004; Scheffer et al., 1993). A second example of a *size effect* is the depth, which tends to be deeper when lake size increases (Bohacs et al., 2003; Søndergaard et al., 2005). As depth increases, macrophytes can become light limited with their depth limit imposed by the euphotic zone depth. A third example of the *size effect* is the relatively small

littoral zone in larger lakes, due to a low perimeter to surface area ratio (Fig. 2A, process 2). Macrophytes growing in the littoral zone therefore have less impact on the limnetic zone of the lake ecosystem (Janse et al., 2001; Sollie et al., 2008b).

Spatial heterogeneity

According to Tobler's 'first law of geography' "everything is related to everything else, but near things are more related than distant things" (Tobler, 1970). This implies that the chance of *spatial heterogeneity* within a lake increases with *lake size*, a phenomenon known in spatial ecology as well (Wiens, 1989). With *spatial heterogeneity* is meant here the horizontal spatial variation in structure and biochemical processes within a lake. Examples of *spatial heterogeneity* are variation in depth and sediment type related nutrient storage (Fig. 2B, process 3), both influencing the potential for macrophyte growth (Canfield et al., 1985; Chambers and Kaiff, 1985; Jeppesen et al., 1990; Middelboe and Markager, 1997; Stefan et al., 1983).

Additionally, external drivers can be *spatially heterogeneous* such as allochthonous nutrient input. Data imply that eutrophication stress per unit of area experienced by lakes with similar land use is independent of lake size (Fig. 3). However, particularly in large lakes, the distribution of the nutrient input is often *spatially heterogeneous*. Allochthonous nutrient input enters the lake mostly via tributaries and overland flow (Fig. 2B, process 4) which exerts a higher eutrophic stress in the vicinity of inlets and lake shores, than further away. When eutrophication stress becomes excessive, the macrophytes that often grow luxuriously in the vicinity of the inlet and lake shores will retreat to only very shallow parts of the lake where light is not limited (Fig. 1, lower white region). Subsequently, these littoral macrophytes lose their capacity to reduce the impact of inflowing nutrients (Fisher and Acreman, 1999).

A last example of *spatial heterogeneity* is the irregular shape of the lake's shoreline or presence of islands which can result in unequal distribution of wind stress. The hypothetical lake in Fig. 2B for example, has a large fetch indicated by the dashed circle. At the same time the bay in the lower right corner forms a compartment with a shorter fetch and is thus more protected from strong wind forces (Fig. 2B, process 5). In this way the size of different lake compartments matters for macrophyte growth potential (Andersson, 2001).

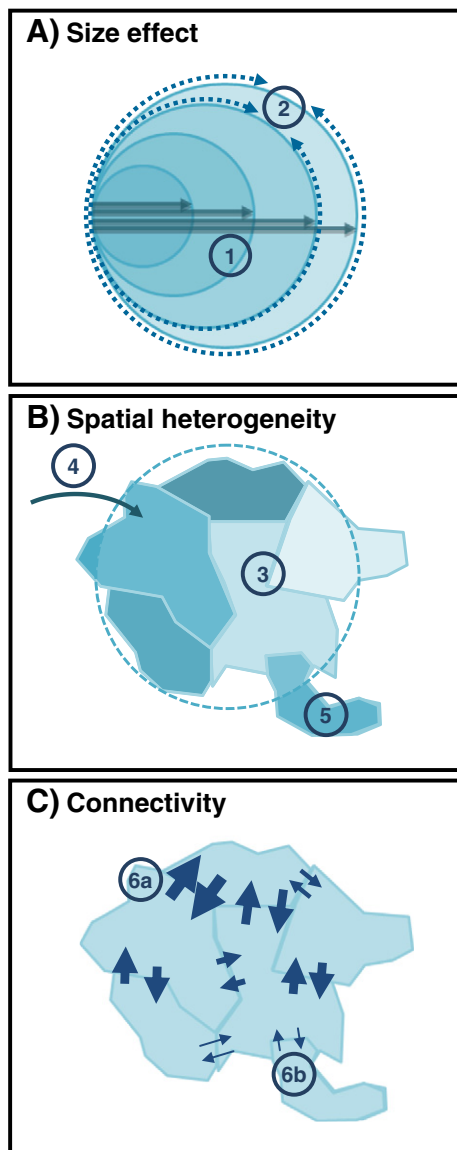


Fig. 2. Schematisation of the A) *size effect*, B) *spatial heterogeneity* and C) *internal connectivity* of lakes. Numbers denote the different processes including (1) fetch, (2) perimeter to surface area ratio, (3) heterogeneous distribution of input, (4) heterogeneity within the lake like depth, sediment etc. (5) heterogeneous shape /fetch and (6a) high and (6b) low connectivity.

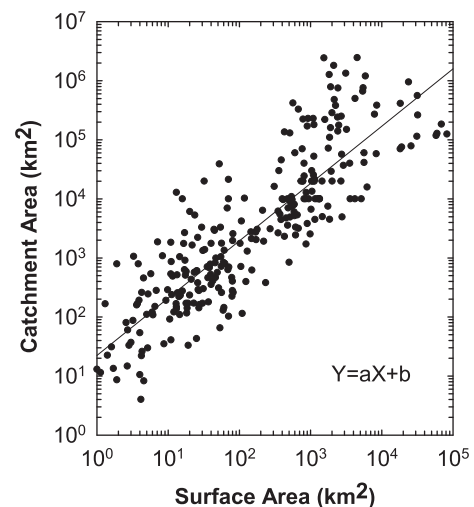


Fig. 3. Relationship between lake surface area and catchment area ($Y = aX + b$, $a = 0.965 \pm 0.07$, $b = 1.397 \pm 0.11$). With $a \approx 1$ on the log–log scale, the relationship is close to linear on normal scale as well ($y = 10^b x^a \approx 10^{1.4} x^{0.97} \approx 24x$), indicating on average a nearly constant lake area to catchment area ratio. Data from ILEC (1999).

Internal connectivity

The *internal connectivity* is defined here as horizontal exchange between different compartments ('connectivity') within a lake ('internal'). With respect to the earlier mentioned 'first law of geography' (Tobler, 1970), *internal connectivity* concerns the degree of relatedness of the different compartments and processes in a lake. A higher *internal connectivity* provides a higher relatedness and thus tends to minimise variability (Hilt et al., 2011; Van Nes and Scheffer, 2005). High *connectivity* (Fig. 2C, process 6a) leads therefore to a well-mixed lake in which transport processes (e.g. water flow, diffusion, wind driven transport) are dominant. On the other hand, with low connectivity (Fig. 2C, process 6b) the lake processes are biochemically driven and heterogeneity is maintained in different lake compartments (Van Nes and Scheffer, 2005). Intuitively, *internal connectivity* decreases though narrowing of the lake or dams in the lake, since they obstruct water flow between different lake compartments. Additionally, with increasing lake size, opposing shores become less connected because a longer distance needs to be spanned which requires increasing time for exchange. Depending on the connectivity of a lake, local regime shifts can be obstructed or, on the contrary, promoted by water quality states elsewhere within a lake (Hilt et al., 2011; Scheffer and Van Nes, 2007). In this way, events like state shifts can propagate as a domino effect throughout a lake (Hilt et al., 2011; Van Nes and Scheffer, 2005).

The combination of *size effect*, *spatial heterogeneity* and *internal connectivity* of large shallow lakes leads to a unique spatial response of these lakes to eutrophication. Given the relatively low number of large shallow lakes (Bohacs et al., 2003; Downing et al., 2006; ILEC, 1999) and the large differences between these lakes (e.g. in precipitation, altitude or latitude) it is difficult to make generalisations. Here, we will focus on a large shallow lake, Lake Taihu, located in eastern China (Fig. 4). Measured in terms of its depth to surface ratio, Taihu is among the shallowest of large lakes, only surpassed by Lake Eyre (Australia, which is ephemeral), Lake Chilwa (Malawi, temporarily dried out in 1968), Lake Taimyr (Russia, riverine and frozen for most of the year), Lake Hungtze (China, riverine) and during the dry season by Lake Tonlé Sap (Cambodia, riverine) (ILEC, 1999). Taihu is therefore a good model system to study the contribution of *size effect*, *spatial*

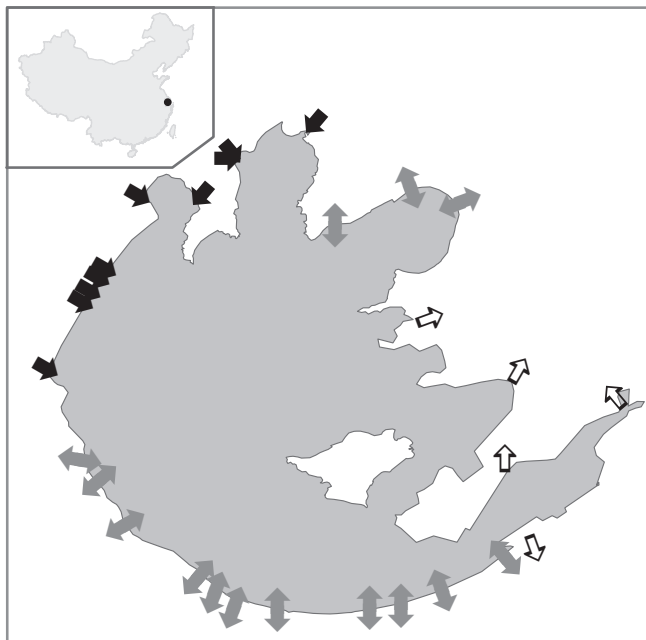


Fig. 4. Inflow (black arrows), outflow (white arrows) and bi-directional flow (grey arrows) of Taihu. Bi-directional flow of rivers means seasonally dependent alternating in- and out-flow of river water (after Li et al., 2011a).

heterogeneity and *internal connectivity* to the spatial variability and development of large shallow lakes.

Development in the Taihu Basin

Taihu is China's third largest freshwater lake (2338 km²) situated in the Yangtze River delta, approximately 100 km west of Shanghai (Qin et al., 2007). The lake is very shallow compared to its size with only 1.9 m average depth to a maximum of 2.6 m and is polymictic (Shen et al., 2011). More than 200 tributaries form a complex network that connects the lake with its own catchment. In the north, the catchment borders the Yangtze River. Since the 1980s, the lake has been plagued by algal blooms. The seriousness of the situation became particularly clear at the end of May to early June 2007 when more than 1 million people in the nearby city of Wuxi were without drinking water for up to a month due to large cyanobacterial scums at the water plant inlet (Guo, 2007; Qin et al., 2010). The current lake water quality with its cyanobacterial toxins is a direct health risk for the 40 million people that live in the Taihu Basin and depend on the lake ecosystem (Qin et al., 2010). The problem is of national significance since 10.3% of China's GDP (as determined in 2000) is produced in the watershed of Taihu (Duan et al., 2009). Up until now, measures to reduce the algal blooms in Taihu have had little effect (Chen et al., 2009, 2012a; Hu et al., 2008; Li et al., 2013).

Pristine situation

Prior to 6500 BC, farming societies established in the region of Lake Taihu (Smith, 1995). The fertile soils and the regular supply of nutrients and water by the Yangtze River were important conditions for the early agricultural development (Ellis and Wang, 1997). Anthropogenic pressures seem to have been low at that time (An and Wang, 2008). Information on the pristine state of the lake is sparse, however a Chinese song "Beautiful Taihu" (太湖美, Long-Fei) written in 1978 tells that the water was beautiful with flourishing fish swirling in the lake, with a mysterious water and green reeds along the shore. According to macrophyte records taken in the 1960s (Fig. 5), macrophytes were indeed present at the shores and bays with the east of the lake being most vegetated (Qin et al., 2007). However, it is likely that the lake has never been totally vegetated as a result of strong winds that act as a destructive force on the lake's centre. Remnants of long-term wind forcing can also be seen in the absence of fine sediments in the lake (Shen et al., 2011). Therefore it is arguable that the lake centre has always lacked macrophytes and appeared turbid on days of strong wind. Phytoplankton concentrations were thought to be low during this time (Zheng et al., 2009).

Anthropogenic pressure

Increasing anthropogenic pressure caused a change to this pristine situation. After the end of the Taiping rebellion (1850–1864) population grew exponentially, demanding a higher food production (Ellis and Wang, 1997). However, agricultural land in the Taihu Basin became limited, requiring a means to increase productivity (e.g. fertilisers, pesticides and higher irrigation efficiency) to meet the food demand (Ellis and Wang, 1997). In the end, agricultural innovation allowed for more than a tripling of population in 150 years to more than 40 million people at the start of the 21st century (An et al., 1996; Ellis and Wang, 1997; Tian et al., 2011; Zhang et al., 2008). Small villages and cities in the Taihu basin grew rapidly and merged into one of the world's largest "megalopolitan regions" (based on population) (Tian et al., 2011). Due to this urbanisation, waste water production has locally intensified and exceeded the increment in wastewater treatment capacity (Gao and Zhang, 2010). Cesspits that used to be emptied on the fields for fertilisation were replaced by flush toilets, resulting in better hygiene, but negatively impacting the nutrient cycle (Ellis and Wang, 1997;

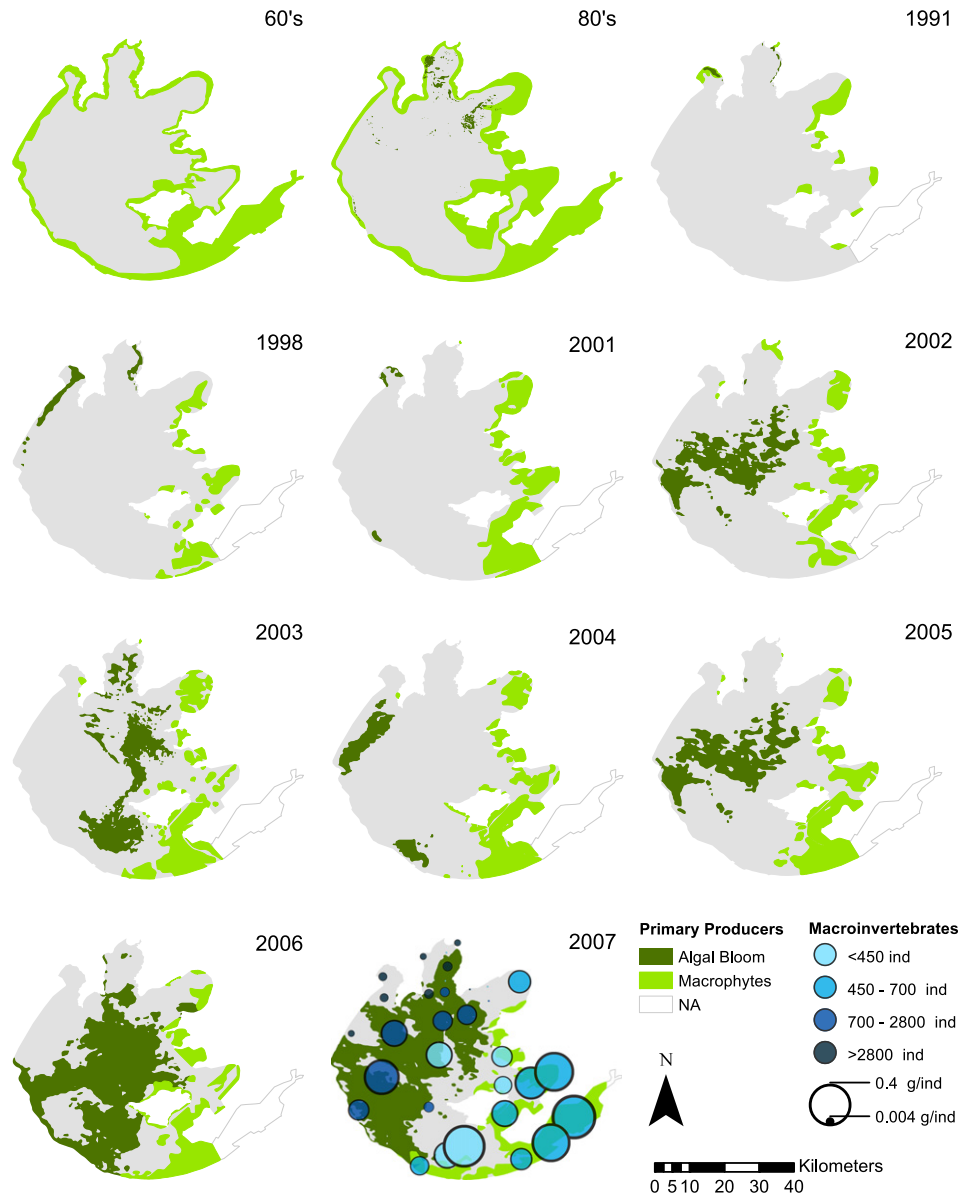


Fig. 5. Development of the ecosystem in Lake Taihu. Compilation of different maps with phytoplankton, macrophytes and macroinvertebrates data as available over time. Source for macrophyte data 1960s and 1980s from Qin et al. (2007) and 2002–2007 from Zhao et al. (2012b). Phytoplankton data originates from Ma et al. (2008) and Duan et al. (2009). Macroinvertebrates data of 2007 originates from Cai et al. (2012).

Gao and Zhang, 2010). In 2009, domestic wastes contributed more than 40% of the total waste input (Liu et al., 2013). Eutrophication has been further amplified by industries and the world's largest aquacultural fish production (Guo, 2007; Liu and Diamond, 2005; Qin et al., 2007). The construction of concrete embankment around most of the lake in 1991 as a response to flood events, destroyed the connection between the lake and its surrounding wetlands (Yang and Liu, 2010). Sluices are now regulating water levels within the lake which means a loss of the natural water level fluctuations (Yang and Liu, 2010).

Nutrients

Increasing amounts of nutrients have been discharged to the lake as a result of the anthropogenic pressure (Fig. 6). Fortunately, strict regulations for industrial waste loads (“zero-point-action”) starting from 1998 seemed to pay off, as could be seen from a decline in both nitrogen and phosphorus load between 1999 and 2001 in Fig. 6 (Li et al., 2011a; Liu et al., 2013). However, these regulations could not prevent the

nutrient load from increasing further after 2001. Most allochthonous nutrient input comes from the north and west of the Taihu Basin where most cities and the major inflow rivers are situated (Li et al., 2011a; Yu et al., 2007) (Fig. 4, black dots). As a result, high nutrient concentrations in the lake water can be found at the north and west side of Taihu. These nutrient concentrations decrease in a south-easterly direction from the input sources, through the lake centre towards the outlet rivers in the east (Fig. 4, white dots) (Chen et al., 2003a; Kelderman et al., 2005; Li et al., 2011a; Otten et al., 2012; Paerl et al., 2011b). The spatial decline in nutrient concentrations can be mainly explained by a loss of nutrients to the sediments and atmosphere. Nitrogen is removed mainly during summer by the large phytoplankton bloom populations and by denitrification (Paerl et al., 2011b; Xu et al., 2010). Phosphorus is immobilised in the sediments mainly during winter when pH levels are low (Xu et al., 2010). As a result, nitrogen and phosphorus are alternately limiting phytoplankton production in Lake Taihu (Paerl et al., 2011b). The removal of nutrients ‘en route’ is important to prevent algal blooms in the east of the lake, but has a drawback as well. Years of intensive nutrient input have led to accumulation of mainly

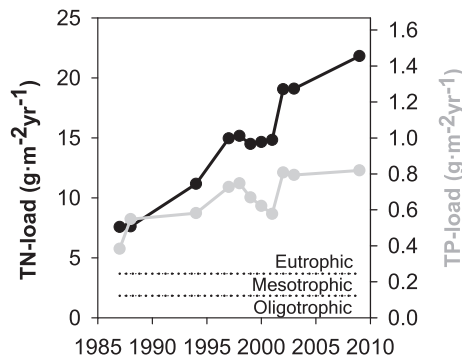


Fig. 6. Total nitrogen (black) and total phosphorus (grey) load from tributaries in Taihu. The dashed lines show the limits for different trophic states which are based on the input–output model of Vollenweider (1975) for phosphorus: $L_p = [P]/(10 + q_s)$ with L_p the areal nutrient load, $[P]$ the lake water phosphorus concentration (with upper limits for oligotrophic and mesotrophic respectively $[P] = 0.01 \text{ mg} \cdot \text{l}^{-1}$ and $[P] = 0.02 \text{ mg} \cdot \text{l}^{-1}$) and q_s the hydraulic loading rate (average depth z divided by the residence time τ_w) which is $2.24 \text{ m} \cdot \text{yr}^{-1}$ for Taihu. The limits for nitrogen are set with the ratio N:P = 15:1. Data 1987–2003 from Zhang (2007) and 2009 from Yan et al. (2011).

phosphorus in the lake sediments, forming a potential for internal nutrient loading once the external nutrient load has been reduced (Qin et al., 2006; Zhu et al., 2013).

Macrophytes

Until the 1980s, macrophyte coverage was around 25% of the lake surface (Fig. 5, excluding East Taihu Bay) but that decreased tremendously to approximately 5% at the end of the 1980s (Fig. 7). The disappearance of macrophytes can be mainly assigned to the massive mortality along the western shores and northern bays (Fig. 5). Meanwhile, macrophytes in the eastern part of the lake changed little, which could be explained by the lower nutrient concentrations, wind-shading and the shallowness providing more light for macrophytes (Li et al., 2011a; Zhao et al., 2012b). Despite the increasing eutrophication, the vegetated area in Taihu seems to have slowly increased since its minimum coverage in the late 1980s (Fig. 7), mainly due to increased macrophyte coverage in East Taihu (Zhao et al., 2013). Instead of being a sign of recovery, the increase of macrophyte coverage has been interpreted as a sign of an upcoming shift to the phytoplankton dominated state (Zhao et al., 2012b). This interpretation is based on the theory of alternative stable states that assumes macrophytes to respond non-linearly to eutrophication, showing first an increase due to higher fertility, prior to the collapse of the macrophyte stands (Janse et al., 2008; Timms and Moss, 1984). Another indication of an upcoming shift in this region can be found in the increasing dominance of floating macrophytes at the expense of the submerged macrophytes (Scheffer

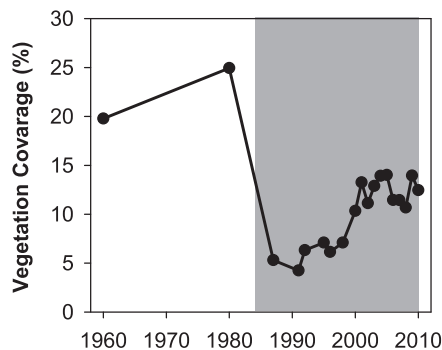


Fig. 7. Macrophyte coverage in Lake Taihu. East Taihu Bay is not included in the calculation since data was not available for all years, see Fig. 5. Grey area corresponds with the timespan of the increasing loads in Fig. 6.

et al., 2003; Zhao et al., 2012b). Floating macrophytes are able to better cope with lower light conditions than submerged macrophytes because they grow at the water surface. When light conditions deteriorate close to the shifting point, floating macrophytes will therefore predominate submerged macrophytes (Scheffer et al., 2003).

Phytoplankton

While macrophytes disappeared, the total primary production of Taihu increased more than twofold from 1960 ($5.46 \text{ t} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$) to 1990 ($11.66 \text{ t} \cdot \text{km}^{-2} \cdot \text{yr}^{-1}$) owing to the increasing phytoplankton biomass that bloomed due to the excessive nutrient input (Li et al., 2010). The first algal blooms occurred in 1987 in Meiliang Bay (Fig. 5, 1980s). Subsequently, algal blooms dominated by non- N_2 fixing cyanobacteria (*Microcystis*) increased in coverage and frequency, and appeared earlier in the season (Chen et al., 2003b; Duan et al., 2009; Paerl et al., 2011b). The presence of mainly non- N_2 fixing cyanobacteria indicates that external and internally-supplied nitrogen are sufficient to maintain proliferation over N_2 -fixers (Paerl et al., 2011b). The early blooms in the northern bays and western shores occurred right where enrichment was most severe and easterly winds drove algae to form thick scums (Chen et al., 2003b; Li et al., 2011a). At that time, high concentrations of suspended solids in the lake centre due to wind action (Fig. 8) might have prevented algal growth by light limitation (Li et al., 2011a; Sun et al., 2010). Despite this mechanism, blooms also emerged in the lake centre from 2002 onwards (Duan et al., 2009). Finally, in 2007 the problems with drinking water became so severe that it was not possible to ignore the blooms anymore (Qin et al., 2010).

Food web

The effects of excessive nutrient loads go beyond the shift in primary producers alone and appear also higher in the food web. As the biomass of primary producers and zooplankton grew over time, the biomass of higher trophic levels shrank and several species disappeared (Guan et al., 2011; Li et al., 2010). There are indications that in the presence of *Microcystis*, the zooplankton shifted their diet to the detritus-bacteria pathway rather than grazing on living phytoplankton (de Kluijver et al., 2012). A macroinvertebrate survey in 2007 by Cai et al. (2012) showed that small individuals (e.g. Tubificidae) appear in large numbers in the algal blooming zone (Fig. 5, 2007). The appearance of mainly small macroinvertebrate species might be related to the absence of refuges to prevent predation (e.g. macrophytes) (Cai et al., 2012) and the relatively low food quality due to the presence of toxic *Microcystis* (Chen et al., 2003b; De Bernardi and Giussani, 1990; Otten et al., 2012). In contrast, in East Taihu, where water quality is still relatively good, large individuals (e.g. Gastropoda) live in relatively low numbers as these species can hide from predators between macrophytes and have access to a relatively high food quality (e.g. periphyton and high-quality detritus) (Cai et al., 2012). Also fish are affected by the anthropogenic pressures. Large fish species almost disappeared from Taihu mainly due to overexploitation by fisheries, which is amplified by construction of flood protection dams and the destruction of spawning grounds by land reclamation (Guan et al., 2011; Li, 1999; Li et al., 2010). Also the exposure to different pollutants (e.g. DDT, POP and heavy metals) and the resulting bioaccumulation could have forced a decline in fish stocks (Feng et al., 2003; Rose et al., 2004; Wang et al., 2003).

Obviously, the safe operating space (cf. Rockström et al., 2009) with respect to e.g. nutrient cycles, land use and freshwater use needed for a healthy ecosystem in Taihu has been transgressed. While at first, water quality was negatively affected by the anthropogenic pressures, now human development is hampered by low water quality (Guo, 2007). According to the Chinese standards, which are based on physical and chemical parameters, acceptable drinking water has a total phosphorus concentration lower than 0.1 mg/l and total nitrogen concentration

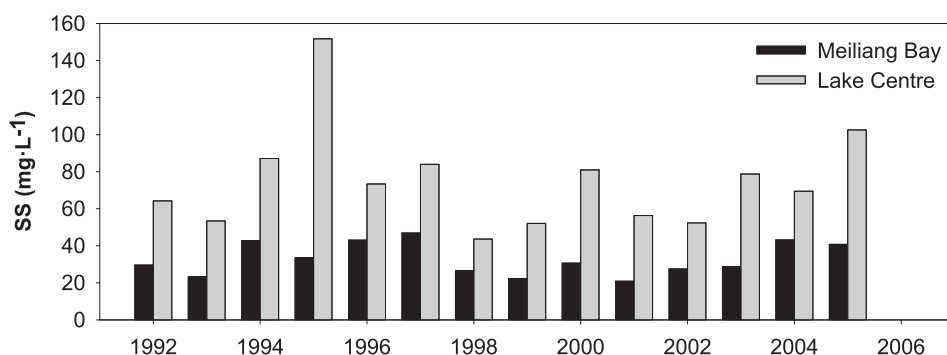


Fig. 8. Yearly average suspended solids concentration at Meiliang Bay (northeastern Lake Taihu) and the lake centre for 1992–2006 (Sun et al., 2010).

lower than 0.5 mg/l. Standards for biological parameters are not included in the Chinese classification; but, according to the European Water Framework Directive, the chlorophyll-a concentration (depending on the lake type) should not exceed $\sim 30 \mu\text{g/L}$ in order to ensure acceptable drinking water quality (Altenburg et al., 2007). At present, all these standards are exceeded at least some months during the year (TBA, 2014).

Insights from Taihu

Today, Taihu can be roughly divided into three zones: the wind-shaded phytoplankton blooming zone (north and west of the lake), the wind-disturbed phytoplankton blooming zone (lake centre), and the shallow wind-shaded macrophyte dominated zone (south-eastern part of the lake) (Cai et al., 2012; Zhao et al., 2012b). The development of Taihu reveals how the *size effect*, *spatial heterogeneity* and *internal connectivity* had its effect upon this spatial zonation.

The water quality model PCLake (Janse et al., 2010) is used for bifurcation analyses for different values of depth and fetch, to illustrate the possibility of alternative stable states in lakes (see Electronic Supplementary Materials ESM Appendix S1). In Fig. 9, the model generated grey domain indicates the possible existence of alternative stable states for a hypothetical set of lakes using the general PCLake settings (omitting horizontal exchange between lake compartments). Of course these model results depend on more factors than fetch and depth alone, but a full sensitivity analysis of the model for the setting of Taihu is beyond the scope of this study. However, a sensitivity analysis of the model for the default settings is available in Janse et al. (2008). For the purposes of this review, the output should be seen as an indication of what is possible rather than an exact prediction.

Combining the model output with Taihu's average depth and fetch (for details on fetch determination see ESM Appendix S2), the *size effect* seems to be too excessive for any macrophyte growth (Fig. 9A, red dot). However, this contradicts the observations showing macrophyte growth in parts of the lake. By using average values for fetch and depth and thereby ignoring the *spatial heterogeneity*, important explanatory information for macrophyte presence is neglected. Indeed, large parts of the lake do not behave according to the average. The frequency distribution shown on Fig. 9B accounts for the *spatial heterogeneity* considering the presence of shallow and wind shaded versus relative deeper windy regions. By including *spatial heterogeneity*, the presence of macrophytes in the bays in the north and east can be better understood because these regions are less prone to wind forces as result of a shorter fetch (Fig. 2B, process 5) or are relatively shallow (Fig. 2B, process 3). A comparison between the model simulations and the frequency distribution that depicts the *spatial heterogeneity* in depth and fetch of Taihu, suggests that nearly 40% of the lake has the potential for macrophyte growth and 15% may potentially have alternative stable states (Fig. 9B).

To examine whether the macrophyte-suitable area has indeed been macrophyte-dominated in the past, the frequency distribution is split

(according to the distribution data of the 1980s) into frequency distributions for macrophyte-dominated (Fig. 9C) and macrophyte-lacking (Fig. 9D) areas. Although the model results are only meant as indicative, this analysis imply that more than 75% of the vegetated area coincides with the potential suitable areas for macrophyte growth as indicated by the model output, of which more than 15% has the possibility of alternative stable states (Fig. 9C). The latter areas can be mainly found in near-shore areas around the lake, in Ghonghu Bay and southeast Taihu. Most northeasterly macrophyte stands have nowadays disappeared as result of *spatially heterogeneous* nutrient input (Fig. 2B, process 4). In contrast, macrophyte sites far away from the inlets were only moderately affected. The areas that lack macrophytes (Fig. 9D) are usually deeper and have a longer fetch. The areas where *size effects* prevail, are mainly restricted to the lake's centre where fetch length exceeds more than 20 km (Cai et al., 2012). This long fetch prohibits macrophyte growth due to the wind-driven waves that cause high concentrations of suspended solids and that would damage any macrophyte (Fig. 2A, process 1) (Cai et al., 2012; Pang et al., 2006; Zhao et al., 2012b). Additionally, the lake centre is deeper than other parts of the lake and has a mineral soil due to the ongoing resuspension (Fig. 8) which has prevented the development of an organic-rich lacustrine sediment (Shen et al., 2011). Due to unsuitability of the lake centre for macrophyte growth, alternative stable states are most likely not present here.

The large variation in nutrients and suspended solids indicate a low *internal connectivity* in Taihu, especially between the east and the rest of the lake (Li et al., 2011a). Likely, the variation in concentrations is the result of the long residence time of 300 days. The positive effect of low connectivity on water quality in East Taihu is enhanced by the prevailing winds that blow floating algae away from the east (Li et al., 2011b; Qin et al., 2010). If the flushing rate in the lake would be higher, nutrient concentrations would most likely be more equally distributed and macrophytes in the east would be more affected by eutrophication (Fig. 2C, process 6). A whole-lake flushing measure to reduce water age in Taihu (Li et al., 2011b) revealed the effect of *internal connectivity* on Taihu's water quality. The water age reduction was meant to flush out nuisance algae. However, the water age could not be shortened enough to overcome cyanobacterial growth (Qin et al., 2010). At the same time the most eutrophic bay (Meiliang) did not significantly improve in water quality as a result of flushing because local prevailing currents prevented inflow of the water into the bay (Li et al., 2013; Qin et al., 2010). In the past, the *internal connectivity* of this bay has been decreased by land reclamation; some islands became peninsula and thereby separated bays that were connected before (Hu et al., 2004; Li, 1999). Hence, the low *internal connectivity* prevents exchange between bays and restricts propagation of the phytoplankton towards the east where at present macrophytes still prevail. Consequently, Taihu has a modular response to eutrophication leading to different states side by side, some states conceivably alternatively stable, others probably not.

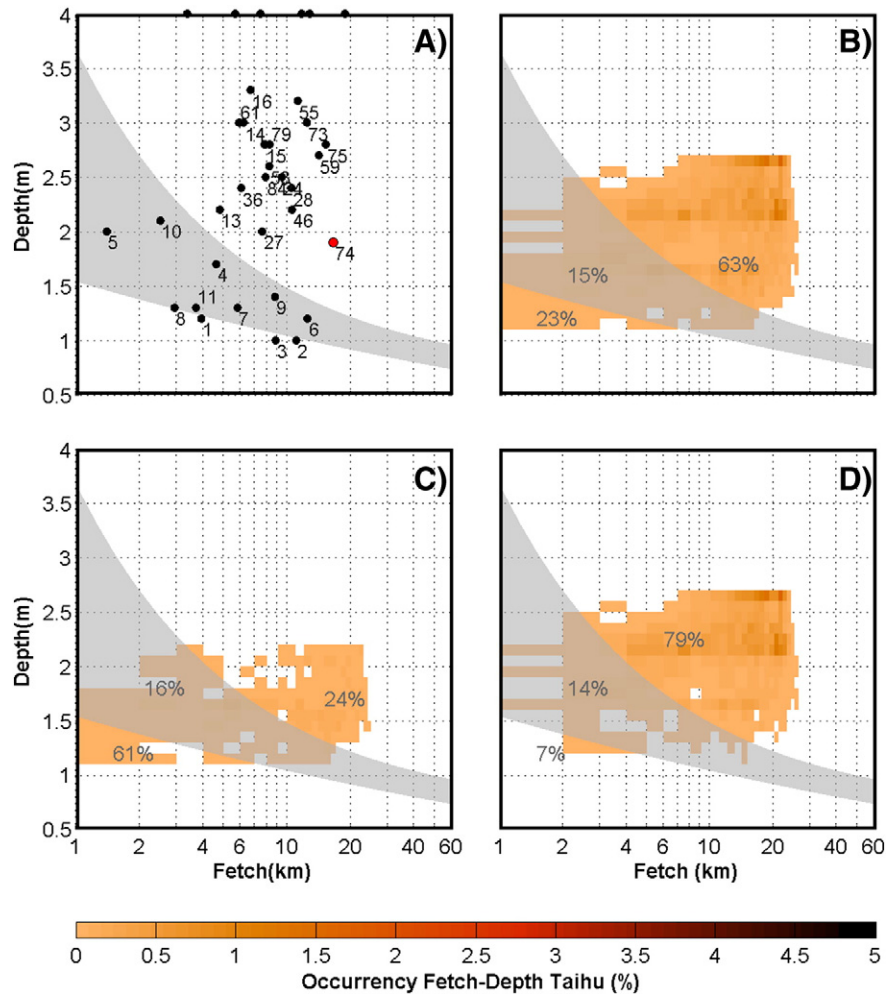


Fig. 9. A first estimation of alternative stable states (grey area) using a bifurcation analysis with PCLake, depending on fetch and depth (Janse et al., 2010). A) Expectation based on mean depth and fetch of different shallow lakes (black dots, with numbered items referring to Table 1) and for Taihu specific (red dot, number 74). B) Frequency distribution of the combination fetch–depth of areas within Taihu. C) Frequency distribution of fetch–depth restricted to only the macrophyte dominated areas in Taihu (according to the 1980s). D) Frequency distribution restricted to only the macrophyte-lacking areas in Taihu (according to the 1980s). The percentages denote the relative surface area that belongs to either the domain with possibility of alternative stable states or to the domain where only one of the two states are possible. Depth data from Liu (2013).

Other large shallow lakes

It is interesting to know whether *lake size*, *spatial heterogeneity* and *internal connectivity* acting in Taihu are exemplary for the existence and patterning of alternative stable states in other large shallow lakes. Based on a number of large shallow lakes listed in Table 1, the generality of these mechanisms will be discussed.

The estimated probability of other large shallow lakes to have macrophyte domination, and, if so, whether these have a potentially alternative stable state is shown in Fig. 9A. A comparison with the model outcomes indicate that 8 lakes might have alternative stable states (Table 1) including Lake Apopka (USA) where literature previously presumed alternative stable states (Bachmann et al., 1999; Lowe et al., 2001). The majority of the other lakes that are indicated by the model to potentially have alternative stable states are reported to support macrophytes, which in some lakes became too excessive, resulting in problems with boating access and flooding as in Lake Guiers (Senegal) (Cogels et al., 1997; Hellsten et al., 1999) and Loktak (India) (Singh and Khundrakpam, 2011). Other lakes are largely turbid such as the Boraphed Reservoir in Thailand (Mizuno and Mori, 1970). Whether these lakes indeed show alternative stable states has not been proven by this review and would require further research.

Model results also indicated 3 lakes to have habitats that are particularly suitable for macrophyte growth mainly because of their shallowness. These are Lake Upemba (Congo), Lake Istokpoga (USA) and Lake Tathlina (Canada). Indeed, macrophytes are abundantly present in Lake Upemba. Also in Lake Istokpoga macrophytes are flourishing. Despite great effort, removal of excess macrophytes from this lake had only a temporary effect (O'Brien and Hapgood, 2012) indicating that Lake Istokpoga has conceivably only one stable state which is macrophyte dominated. Whether Lake Tathlina (Canada) is also macrophyte dominated is not clear because data are not available.

The majority of the lakes fall outside the suggested domain with the possibility of having macrophytes. These large shallow lakes are expected to be prone to the *size effect*. This is not surprising, since they have a large fetch or depth reducing the window of opportunity for macrophytes (Fig. 2A, process 1). However, this contrasts to observations in the literature showing that in most of the lakes macrophytes had a chance to grow at least some time in history (Table 1). In some of the lakes this can be explained by natural water fluctuations. A drop in water level restricts the surface area where *size effects* prevail. For example, the water fluctuations in Lake Chad make the lake switch from a great large inland 'sea' in wet periods to a marshy macrophyte-rich area in dry periods (Leblanc et al., 2011). Additionally, in Lake Beyşehir and Lake Uluabat (both in Turkey) receding water levels made large

Table 1

Selected large shallow lakes of the world. A is surface area of lake in km², Z_{mean} and Z_{max} are mean and maximum depth in m, F_{mean} and F_{max} are mean and maximum fetch in km and M is model outcomes as YES (macrophytes present) or ASS (alternative stable states).

Lake	Country	Coordinates	A	Z _{mean}	Z _{max}	F _{mean}	F _{max}	M	
1 Istokpoga	USA	27°22'N, 81°17'W	113	1.2	3.0	3.9	15.3	YES	Although the lake is eutrophic, water level stabilisation caused excessive dense macrophyte stands in the large shallow littoral zone (Bunch et al., 2010) (O'Dell et al., 1995). Herbicide treatments led the macrophytes only temporally decline (O'Dell et al., 1995).
2 Tathlina	Canada	63° 32'N, 117° 35'W	573	1.0		11.0	83.8	YES	–
3 Upemba	Congo	8°37'S, 26°23'E	530	1.0	4.0	9.3	38.3	YES	Swampy-lake. Floating-mats of emergent macrophytes generally dominated by papyrus (Azza et al., 2006; Thompson et al., 1979).
4 Apopka	USA	28°37'N, 81°37'W	125	1.7		4.6	15.7	ASS	The entire lake shifted from macrophyte to phytoplankton dominance triggered by a hurricane, after long-term eutrophication (Bachmann et al., 1999, 2001; Lowe et al., 1999, 2001).
5 Boraphed	Thailand	15°42'N, 100°14'E	106	2.0	5.8	1.4	9.5	ASS	Southeast part of the lake is macrophyte rich. Here the lake is shallow. The rest of the lake is turbid (Mizuno and Mori, 1970).
6 Claire	Canada	58°35'N, 112°04'W	1410	1.2	2.0	12.5	86.6	ASS	–
7 Cross	Canada	54°59'N, 97°48'W	591	1.3	12.0	5.8	78.7	ASS	–
8 Guiers	Senegal	16°10'N, 15°52'W	228	1.3	2.5	2.9	43.3	ASS	Macrophytes have overgrown the shallow zone in the south completely after the construction of a dam causing problems for boating (Cogels et al., 1997; Hellsten et al., 1999; Thiam et al., 2013).
9 Hongze	China	33°20'N, 118°40'E	1960	1.8		8.7	60.6	ASS	Phytoplankton dominated lake (Hu et al., 2014)
10 Loktak	India	24°33'N, 93°47'E	289	2.1	4.6	2.5	13.1	ASS	Over 50% of the lake is overgrown by macrophytes, which proliferate after the construction of a dam (Singh and Khundrakpam, 2011).
11 Tisza (Kisköre)	Hungary	47°36'N, 20°40'E	127	1.3	17.0	3.7	24.1	ASS	Reservoir is covered with macrophytes (Kiss et al., 2003).
12 Abaya	Ethiopia	6°07'N, 37°38'E	1160	7.0	13.0	9.4	60.2	–	–
13 Abert	USA	42°37'N, 120°14'W	148	2.2	3.4	4.8	20.0	–	–
14 Abitibi	Canada	48°38'N, 79°48'W	904	3.0	10.0	6.2	66.3	–	–
15 Alexandrina	Australia	35°25'S, 139°07'E	570	2.8	5.0	7.8	45.7	–	Macrophytes were present before 2008, but a severe drought that went along with increasing salinity resulted in the disappearance of macrophytes (Skinner et al., 2014).
16 Balaton	Hungary	46°50'N, 17°42'E	593	3.3	12.2	6.7	72.2	–	Waves limit the distribution of macrophytes in the offshore and southern part of the lake. At the lee side in the north vegetation is present (Istvánovics et al., 2008).
17 Bangweulu	Zambia	11°05'S, 29°45'E	1510	4.0	10.0	12.8	72.2	–	–
18 Belaye Ozero	Russia	60°10'N, 37°38'E	1120	4.0	20.0	18.8	85.5	–	–
19 Beyşehir	Turkey	37°47'N, 31°33'E	650	5.0	9.0	8.5	48.6	–	<10% coverage when water level was high (before 1982) to 35% when water table had dropped in 1997 (Beklioglu et al., 2006).
20 Bositeng	China	42°0'N, 87°03'E	1010	7.7	16.0	10.2	67.0	–	Reeds present (Jun et al., 2001).
21 Buir	China	47°48'N, 117°40'E	610	8.0	11.0	12.1	42.6	–	–
22 Cedar	Canada	53°10'N, 99°60'W	1320	4.2	10.0	13.7	99.5	–	–
23 Chad	Cameroon	13°20'N, 14°10'E	1540	4.1	10.5	12.1	64.1	–	Chad is sensitive to water fluctuations. When water table is low, almost the entire lake is covered with macrophytes (Leblanc et al., 2011).
24 Chao Hu	China	31°30'N, 117°34'E	760	2.5	5.0	9.4	49.3	–	Around 30% of the lake has been covered by macrophytes in 1950 but after dam construction and increasing nutrient loading, there is less than 1% left (Kong et al., 2013; Zhang et al., 2014)
25 Chapala	Mexico	20°15'N, 103°0'W	1100	4.5	10.5	11.0	80.5	–	Submerged macrophytes are suppressed by high turbidity, however floating macrophyte species survive (Villamagna et al., 2010).
26 Churchill	Canada	55°58'N, 108°20'W	559	9.0	24.0	11.0	45.5	–	–
27 Colhué Huapi	Argentina	45°30'S, 68°45'W	810	2.0	5.5	7.6	43.0	–	–
28 Dauphin	Canada	51°16'N, 99°45'W	521	2.4	3.4	10.5	50.5	–	–
29 Derg	Ireland	53°00'N, 8°20'W	118	7.6	36.0	2.2	22.1	–	–
30 Deschambault	Canada	54°40'N, 103°33'W	542	6.2	22.4	5.0	37.1	–	–
31 Dongting	China	29°13'N, 112°55'E	2740	6.7	30.8	6.5	56.1	–	Inundation frequency determines macrophyte abundance (Deng et al., 2014)
32 Eğirdir	Turkey	38°01'N, 30°51'E	590	9.0	14.0	6.9	39.5	–	Marsh and reeds at the shores (Arslan, 2006).
33 Evans	Canada	50°51'N, 77°02'W	474	5.0	13.0	3.9	33.0	–	–
34 Frobisher	Canada	56°22'N, 108°14'W	516	5.5	19.0	2.6	25.9	–	–
35 Gaoyou	China	32°50'N, 119°15'E	663	7.9		8.0	57.7	–	'Transitional', macrophytes and phytoplankton present (Hu et al., 2014)
36 George	Uganda	0°00'N, 30°10'E	250	2.4	4.5	6.1	22.9	–	Surrounded by swamp macrophytes. Floating macrophytes are abundant but submerged macrophytes are absent in the center of the lake where phytoplankton dominate (Lock, 1973).

(continued on next page)

Table 1 (continued)

Lake	Country	Coordinates	A	Z _{mean}	Z _{max}	F _{mean}	F _{max}	M		
37	Hjälmaren	Sweden	59°13'N, 15°46'E	478	6.1	22.0	6.4	76.0	–	Before lowering the water surface, macrophytes were rare. After lowering the water table, macrophytes became more abundant. The northern shores and western basins have nowadays extensive macrophyte growth (Andersson, 2001).
38	Hulun	China	48°55'N, 117°22'E	1731	5.0	7.0	18.3	95.0	–	Macrophytes absent, phytoplankton dominates (Chen et al., 2012b).
39	IJsselmeer	The Netherlands	52°49'N, 5°15'E	1100	5.5	8.0	11.2	73.1	–	Diking with steep slopes and managed water levels reduced macrophyte growth (Sollie et al., 2008a).
40	Ilmen	Russia	58°16'N, 31°17'E	982	5.7	11.0	12.9	88.2	–	–
41	Kairakkumskoye	Tajikistan	40°17'N, 70°00'E	513	6.2	25.0	7.5	50.0	–	–
42	Kakhovskoye	Ukraine	47°30'N, 34°20'E	2150	8.5	24.0	10.4	121.9	–	–
43	Kasumigaura	Japan	36°00'N, 140°25'E	220	4.0	7.0	3.4	29.6	–	Construction of concrete levees has harmed littoral macrophytes with total disappearance of submerged macrophytes (Nishihiro and Washitani, 2009).
44	Khanka	China	44°55'N, 132°25'E	4190	4.5	6.5	28.3	92.5	–	–
45	Khar	China	48°04'N, 93°11'E	575	4.2	7.0	11.3	49.8	–	Macrophyte stands in the littoral zone (Krylov, 2012)
46	Khar us	China	48°02'N, 92°17'E	1578	2.2	4.5	10.5	62.9	–	–
47	Koka	Ethiopia	8°23'N, 39°05'E	250	9.1	13.0	4.1	23.0	–	–
48	Krementchugskoye	Ukraine	49°20'N, 32°35'E	2250	6.0	20.0	14.3	146.4	–	–
49	Kujbyshevskoe	Russia	54°30'N, 48°40'E	5900	9.8	41.0	10.0	123.3	–	–
50	Kyoga	Uganda	1°30'N, 33°0'E	1720	5.7	8.0	6.6	100.5	–	Macrophyte rich, except for the deeper areas. (Ogutu-Ohwayo et al., 2013).
51	Leopold II (Mai-Ndombe)	Congo	2°00'S, 18°20'E	2070	5.0	12.0	7.9	86.2	–	–
52	Lough Neagh	UK	54°36'N, 6°25'W	385	8.9	34.0	8.4	45.1	–	Due to depth, turbidity and exposure, macrophytes are restricted small sheltered areas close to the shore (Winfield and Winfield, 1994).
53	Louch Ree	Ireland	53°30'N, 7°57'W	105	6.2	35.0	2.6	22.1	–	–
54	Mangueira	Brazil	33°5'S, 52°45'W	817	2.6		6.7	82.3	–	Macrophytes mainly in the Taim wetland in the north northeast (Fragoso et al., 2008).
55	Manitoba	Canada	51°00'N, 98°50'W	4625	7.0	28.0	17.3	114.3	–	–
56	Markermeer	The Netherlands	52°34'N, 5°13'E	700	3.2	5.0	11.2	52.9	–	Almost no vegetation due to turbidity and depth (Kelderman et al., 2012a,b).
57	Moose	Canada	53°57'N, 100°09'W	1340	4.1	19.8	13.0	45.1	–	–
58	Mweru	Congo	9°00'S, 28°45'E	4350	7.0	37.0	26.1	124.3	–	–
59	Nipissing	Canada	46°14'N, 79°49'W	855	4.5	69.0	8.4	80.5	–	–
60	Okeechobee	USA	26°56'N, 80°48'W	1900	2.7	6.0	14.1	53.3	–	Vegetation mainly at the south and eastern shore. Water levels as well as sheltering are important for the macrophyte distribution (Carrick et al., 1994; Havens et al., 2005; Rodusky et al., 2013).
61	Oulujärvi	Finland	64°20'N, 027°15'E	900	7.0	38.0	7.2	83.4	–	–
62	Ozero Evoron	Russia	51°27'N, 136°30'E	590	3.0		5.9	22.8	–	–
63	Pátzcuaro	Mexico	19°38'N, 101°38'W	130	4.9	15.0	2.5	16.3	–	Around 42% of the lake used to be covered by macrophytes, mainly in the south of the lake growing at sheltered and shallow conditions (Torres A et al., 1989; Torres, 1993).
64	Peipsi	Estonia Russia	58°41'N, 27°29'E	3555	7.1	15.3	27.3	105.9	–	The water table of Lake Peipsi is unregulated with, despite the eutrophication, still macrophytes at the shores, mainly where till is present instead of sandstone. Lake center is dominated by algae (Mäemets et al., 2010).
65	Pielinen	Finland	63°13'N, 29°40'E	867	9.9	60.0	6.6	101.1	–	–
66	Playgreen	Canada	54°0'N, 97°55'W	653	4.0	18.0	5.7	51.3	–	–
67	Poyang	China	29°05'N, 116°17'E	3210	8.4	25.0	9.6	81.1	–	Rich in vegetation especially the shallow parts (Hui et al., 2008; Liao et al., 2013).
68	Pyasino	Russia	69°50'N, 87°40'E	735	4.0	10.0	11.7	78.5	–	–
69	Rio Hondo	Argentina	27°32'S, 64°57'W	330	5.3		4.2	24.1	–	–
70	Rybinsk	Russia	58°20'N, 38°40'E	4550	5.6	28.0	21.4	156.8	–	–
71	Tonlé Sap	Cambodia	12°53'N, 104°04'E	13000	–	12.0	15.8	115.6	–	Submerged macrophytes are uncommon due to turbidity and large water level fluctuations. The shallow shoreline of the lake consist of dense emergent and floating mat macrophytes (Campbell et al., 2006).
72	Skadar	Albania	42°10'N, 19°20'E	372	5.0	8.3	6.2	45.3	–	–
73	Saint Clair	USA Canada	42°28'N, 82°40'W	1113	3.0	6.0	12.4	58.4	–	Macrophytes dominate over phytoplankton except for the lake center (Schloesser and Manny, 1986; Schloesser et al., 1985).
74	Taihu	China	31°15'N, 120°15'E	2428	1.9	2.6	16.5	68.3	–	Macrophyte growth at the shores (in the past) and in the southeast (Zhao et al., 2012a,b, 2013)
75	Taimyr	Russia	74°35'N, 103°00'E	4560	2.8	26.0	15.2	326.5	–	No vegetation (Timm, 1996).
76	Tana	Ethiopia	11°59'N, 37°20'E	3600	9.0	14.0	20.4	76.5	–	–
77	Tsimlyanskoye	Russia	48°15'N, 43°05'E	2702	8.8	35.0	10.2	108.5	–	–
78	Tumba	Congo	0°50'S, 18°0'E	500	4.0	6.0	7.5	48.1	–	–
79	Uluabat	Turkey	40°10'N, 28°35'E	240	2.5	3.0	3.7	25.7	–	Submerged macrophytes were sparse during high water level but expanded to 55% of the lake's surface area during low water level (Beklioglu et al., 2006).

Table 1 (continued)

Lake	Country	Coordinates	A	Z _{mean}	Z _{max}	F _{mean}	F _{max}	M		
80	Võrtsjärv	Estonia	58°15'N, 26°3'E	271	2.8	6.0	8.3	34.0	–	In the south macrophytes grow in a sheltered condition (Feldmann and Nöges, 2007).
81	Vygozero	Russia	63°37'N, 34°38'E	1250	6.2	18.0	9.7	110.1	–	–
82	Winnebago	USA	44°01'N, 88°25'W	557	4.7	7.0	10.5	45.2	–	–
83	Winnipegosis	Canada	52°36'N, 99°50'W	5150	4.2	18.3	16.3	146.8	–	–
84	Yuqiao R.	China	40°2'N, 117°32'E	250	4.6	12.0	3.2	19.2	–	–
85	Ziway	Ethiopia	7°58'N, 38°50'E	485	2.5	9.0	7.9	31.4	–	Extensive vegetated shoreline (mainly emergent). Around 12% of the lake area is covered by macrophytes (Tamire and Mengistou, 2013).

areas suitable for macrophyte growth, whereas higher water levels prevented macrophytes to grow (Beklioglu et al., 2006). Water level fluctuations can thus lead to alternating behaviour of lakes to eutrophication, which will be showing a turbid state during high water levels, a macrophyte dominated state during extreme low water levels and possibly alternative stable states in between (Blindow et al., 1993; Van Geest et al., 2005). However, fluctuating water levels are not the sole explanation of macrophyte presence in all lakes.

So far, the effects of *spatial heterogeneity* have been ignored. If *spatial heterogeneity* is accounted for, as with the data of Taihu, there may well be compartments within large shallow lakes that are more sheltered or shallower and thereby being suitable for macrophyte growth. The *size effect* is then often restricted to the lake centre as has been reported for many lakes including Lake George (Uganda) (Lock, 1973) and Saint Clair (USA and Canada) (Schloesser and Manny, 1986; Schloesser et al., 1985). Lake shores are excellent examples of sheltered and often shallow areas that support macrophyte growth like in Lake Eğirdir (Turkey), Lough Neagh (UK) Tonlé Sap (Cambodia), Peipsi (Estonia, Russia) and Ziway (Ethiopia). However, not all shores are suitable for macrophyte growth. For example, in Lake Balaton (Hungary) prevailing northern winds cause high waves in the south, preventing macrophyte growth in this part of the lake while macrophytes are growing at the sheltered northern shores (Istvánovics et al., 2008). The same holds for Okeechobee (USA) where vegetation is restricted to the lee side in the south and west (Carrick et al., 1994; Havens et al., 2005; Rodusky et al., 2013) and Lake Võrtsjärv (Estonia) where most macrophytes grow at the lee side in the south of the lake. The sheltered conditions in Lake Võrtsjärv are enhanced by the natural narrowing of the lake's shores in the south (Feldmann and Nöges, 2007). Other lakes have unsuitable littoral regions for macrophyte growth due to the construction of firm dikes around the lake such as in Lake IJsselmeer (The Netherlands) and Lake Kasumigaura (Japan). Some lakes lack macrophytes because the general conditions are too harsh, as in Lake Alexandrina where a severe drought caused salinity to increase too high for macrophytes (Skinner et al., 2014), Lake Taimyr which is frozen most of the year (Timm, 1996) or the artificially created Lake Markermeer (The Netherlands) where the *size effect* is presumably too high, resulting in continuous resuspension of the soft sediment (Kelderman et al., 2012a; Kelderman et al., 2012b; Vijverberg et al., 2011).

The question remains whether the macrophyte-rich areas in large shallow lakes could be alternatively stable showing hysteresis between the processes of eutrophication and oligotrophication. As Fig. 9A illustrates, locations having the right characteristics for alternative stable states may exist. Of course, the model sensitivity to other factors besides fetch and depth has been omitted causing uncertainty in the exact positioning of the domain of alternative stable states. These uncertainties may lead to either extension (e.g. presence of a marsh zone) or reduction (e.g. more resuspension sensitive sediment) of the alternative stable state's domain (Janse et al., 2008). Additionally, the *internal connectivity* has been neglected so far. The *internal connectivity* is ignored in the analysis of Fig. 9, though its effect can be logically deduced. Take, for example, those lake compartments within the domain of alternative

stable states of Fig. 1. If these compartments are part of a homogeneous lake, *connectivity* will lead to local resistance to perturbations because other compartments will continuously supply inputs corresponding to the prevalent state, which leads to rehabilitation of the perturbed areas. Only when the entire lake has lost its resilience to perturbations, will a shift abruptly propagate through the lake like a 'domino effect' (Scheffer et al., 2012). This might be the case for Apopka (Florida), a lake that is rather homogeneous with respect to its depth; and several perturbations did not lead to a lake wide shift. However after persistent eutrophication a single hurricane event led to a whole lake shift from macrophyte to phytoplankton domination (Schelske et al., 2010).

Heterogeneous lakes, however, have most likely regions that only appear in a single stable state besides these potentially alternative stable compartments. These single stable state compartments will destabilise the alternatively stable compartments that appear in a contrasting state, but stabilise those that have the same state. Therefore, the regions that could potentially show alternative stable states tend to appear in the same state as their neighbouring compartments that only have a single state. As a consequence, high *internal connectivity* will enhance synchrony throughout the lake, through which edges of the grey domain in Fig. 9A will move towards each other, making the domain of alternative stable states more confined. In Lake Markermeer for example, the high turbidity in most of the lake can easily affect the more shallow parts and thereby prevent macrophyte growth (Kelderman et al., 2012b). In Lake Pátzcuaro (Mexico), however, which is highly heterogeneous with respect to depth, main water flow direction to the north prevents the turbid water of the north from affecting the macrophytes in the south (Torres, 1993). This *low connectivity* between the lake compartments leads to asynchronous response within the lake to eutrophication. *Low connectivity* may allow for alternative stable states to occur within certain lake compartments and not within others. Because shifts in such a lake will occur at different times, the lake as a whole will probably show a gradual response to eutrophication stresses (Scheffer et al., 2012). In Lake Balaton, for example, a natural narrowing in the lake prevents *connectivity* between the west and east side of the lake. Though alternative stable states are unlikely to occur in this lake, this narrowing leads to different eutrophic levels in different compartments of the lake (Pálffy et al., 2013).

Conclusion

The unique combination of *lake size*, *spatial heterogeneity* and *internal connectivity* determines the spatial extent of stable states in large shallow lakes. At locations where *size effects* prevail, macrophytes are generally absent and alternative stable states are unlikely to occur. However, the occurrence of macrophytes is inexplicable 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. Taking into account the *internal connectivity* is important in the evaluation whether the effect of *spatial heterogeneity* is either offset (high *internal connectivity*) or promoted (*low internal connectivity*).

Acknowledgments

We greatly thank Liu Sien for providing data on Lake Taihu. Furthermore we would like to thank the two anonymous reviewers for their constructive comments. This work is financed by the China–Netherlands Joint Scientific Thematic Research Programme (JSTP) of the Netherlands Organisation for Scientific Research (NWO) project no. 842.00.009. HWP was supported by US National Science Foundation Grants ENG/DEB 1230543 INSPIRE Program and DEB 1240851 Dimensions of Biodiversity Program. This is publication 5678 of the Netherlands Institute of Ecology (NIOO-KNAW).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2014.09.019>.

References

- Altenburg, W., Arts, G., Baretta-Bekker, J.G., Van den Berg, M.S., Van den Broek, T., Buskens, R.F.M., Bijkerk, R., Coops, H., Van Dam, H., Van Ee, G., Evers, C.H.M., Franken, R., Ietswaart, T., Jaarsma, N., De Jong, D.J., Joosten, A.M.T., Klinge, M., Knobben, R.A.E., Kranenborg, J., Van Loon, W.M.G.M., Noordhuis, R., Pot, R., Twisk, F., Verdonschot, P.F.M., Vlek, H., Wolfstein, K., 2007. Referenties en maatlaten voor natuurlijke watertypen voor de Kaderrichtlijn Water. Lakes (Dutch).
- An, S.Q., Wang, R., 2008. The human-induced driver on the development of Lake Taihu. The 93rd ESA Annual Meeting.
- An, S.Q., Yan, J.S., Yu, X.S., 1996. Grey-system studies on agricultural ecoengineering in the Taihu Lake area, Jiangsu, China. *Ecol. Eng.* 7, 235–245.
- Andersson, B., 2001. Macrophyte development and habitat characteristics in Sweden's large lakes. *Ambio* 30, 503–513.
- Arslan, N., 2006. Littoral fauna of Oligochaeta (Annelida) of Lake Eğirdir (Isparta). *Ege Univ. J. Fish. Aquat. Sci.* 23, 315–319.
- Azza, N., Denny, P., Van DE Koppel, J., Kansime, F., 2006. Floating mats: their occurrence and influence on shoreline distribution of emergent vegetation. *Freshw. Biol.* 51, 1286–1297.
- Bachmann, R.W., Hoyer, M.V., Canfield Jr., D.E., 1999. The restoration of Lake Apopka in relation to alternative stable states. *Hydrobiologia* 394, 219–232.
- Bachmann, R.W., Hoyer, M.V., Canfield, D.E., 2001. Evaluation of recent limnological changes at Lake Apopka. *Hydrobiologia* 448, 19–26.
- Beaver, J., Casamatta, D., East, T., Havens, K., Rodusky, A., James, R.T., Tausz, C., Buccier, K., 2013. Extreme weather events influence the phytoplankton community structure in a large lowland subtropical lake (Lake Okeechobee, Florida, USA). *Hydrobiologia* 709, 213–226.
- Beklioglu, M., Altinayar, G., Tan, C.O., 2006. Water level control over submerged macrophyte development in five shallow lakes of Mediterranean Turkey. *Arch. Hydrobiol.* 166, 535–556.
- 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.
- Bohacs, K.M., Carroll, A.R., Neal, J.E., 2003. Lessons from large lake systems—thresholds, nonlinearity, and strange attractors. *Spec. Pap. Geol. Soc. Am.* 75–90.
- Bunch, A.J., Allen, M.S., Gwinn, D.C., 2010. Spatial and temporal hypoxia dynamics in dense emergent macrophytes in a Florida lake. *Wetlands* 30, 429–435.
- Cadenasso, M.L., Pickett, S.T.A., Grove, J.M., 2006. Dimensions of ecosystem complexity: heterogeneity, connectivity, and history. *Ecol. Complex.* 3, 1–12.
- Cai, Y.J., Gong, Z.J., Qin, B.Q., 2012. Benthic macroinvertebrate community structure in Lake Taihu, China: effects of trophic status, wind-induced disturbance and habitat complexity. *J. Great Lakes Res.* 38, 39.
- Campbell, I.C., Poole, C., Giesen, W., Valbo-Jørgensen, J., 2006. Species diversity and ecology of Tonle Sap Great Lake, Cambodia. *Aquat. Sci.* 68, 355–373.
- Canfield, D., Langeland, K., Linda, S., Haller, W., 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. *J. Aquat. Plant Manag.* 23, 25–28.
- Carpenter, S.R., Stanley, E.H., Vander Zanden, M.J., 2011. State of the world's freshwater ecosystems: physical, chemical, and biological changes. *Annu. Rev. Environ. Resour.* 36, 75–99.
- Carper, G.L., Bachmann, R.W., 1984. Wind resuspension of sediments in a prairie lake. *Can. J. Fish. Aquat. Sci.* 41, 1763–1767.
- Carrick, H.J., Worth, D., Marshall, M.L., 1994. The influence of water circulation on chlorophyll-turbidity relationships in Lake Okeechobee as determined by remote sensing. *J. Plankton Res.* 16, 1117–1135.
- Chambers, P.A., Kaiff, J., 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. *Can. J. Fish. Aquat. Sci.* 42, 701–709.
- Chen, Y.W., Fan, C.X., Teubner, K., Dokulil, M.T., 2003a. Changes of nutrients and phytoplankton chlorophyll-a in a large shallow lake, Taihu, China: an 8-year investigation. *Hydrobiologia* 506–509, 273–279.
- Chen, Y.W., Qin, B.Q., Teubner, K., Dokulil, M.T., 2003b. Long-term dynamics of phytoplankton assemblages: microcystis-domination in Lake Taihu, a large shallow lake in China. *J. Plankton Res.* 25, 445–453.
- Chen, F.Z., Song, X.L., Hu, Y.H., Liu, Z.W., Qin, B.Q., 2009. Water quality improvement and phytoplankton response in the drinking water source in Meiliang Bay of Lake Taihu, China. *Ecol. Eng.* 35, 1637–1645.
- Chen, F.Z., Ye, J.L., Shu, T.T., Sun, Y., Li, J., 2012a. Zooplankton response to the lake restoration in the drinking-water source in Meiliang Bay of subtropical eutrophic Lake Taihu, China. *Limnologia* 42, 189–196.
- Chen, X., Chuai, X., Yang, L., Zhao, H., 2012b. Climatic warming and overgrazing induced the high concentration of organic matter in Lake Hulun, a large shallow eutrophic steppe lake in northern China. *Sci. Total Environ.* 431, 332–338.
- Cogels, F., Coly, A., Niang, A., 1997. Impact of dam construction on the hydrological regime and quality of a Sahelian lake in the River Senegal basin. *Regul. Rivers Res. Manag.* 13, 27–41.
- De Bernardi, R.D., Giussani, G., 1990. Are blue-green algae a suitable food for zooplankton? An overview—biomanipulation tool for water management. *Hydrobiologia* 29–41.
- de Kluijver, A., Yu, J.L., Houtekamer, M., Middelburg, J.J., Liu, Z.W., 2012. Cyanobacteria as carbon source for zooplankton in eutrophic Lake Taihu, China, measured by ¹³C labeling and fatty acid biomarkers. *Limnol. Oceanogr.* 57, 1245.
- Deng, F., Wang, X., Cai, X., Li, E., Jiang, L., Li, H., Yan, R., 2014. Analysis of the relationship between inundation frequency and wetland vegetation in Dongting Lake using remote sensing data. *Ecology* 7, 717–726.
- Downing, J., Prairie, Y., Cole, J., Duarte, C., Tranvik, L., Striegl, R., McDowell, W., Kortelainen, P., Caraco, N., Melack, J., 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* 51, 2388–2397.
- Duan, H., Ma, R., Xu, X., Kong, F., Zhang, S., Kong, W., Hao, J., Shang, L., 2009. Two-decade reconstruction of algal blooms in China's Lake Taihu. *Environ. Sci. Technol.* 43, 3522–3528.
- Ellis, E.C., Wang, S.M., 1997. Sustainable traditional agriculture in the Tai Lake Region of China. *Agric. Ecosyst. Environ.* 61, 177–193.
- Falconer, I.R., Humpage, A.R., 2005. Health risk assessment of cyanobacterial (blue-green algal) toxins in drinking water. *Int. J. Env. Res. Public Health* 2, 43–50.
- Feldmann, T., Nöges, P., 2007. Factors controlling macrophyte distribution in large shallow Lake Võrtsjärvi. *Aquat. Bot.* 87, 15–21.
- Feng, K., Yu, B., Ge, D., Wong, M., Wang, X., Cao, Z., 2003. Organo-chlorine pesticide (DDT and HCH) residues in the Taihu Lake Region and its movement in soil–water system: I. Field survey of DDT and HCH residues in ecosystem of the region. *Chemosphere* 50, 683–687.
- Fisher, J., Acreman, M., 1999. Wetland nutrient removal: a review of the evidence. *Hydrol. Earth Syst. Sci.* 8, 673–685.
- Fragoso, C.R., Marques, D.M.L., Collischonn, W., Tucci, C.E.M., van Nes, E.H., 2008. Modeling spatial heterogeneity of phytoplankton in Lake Mangueira, a large shallow subtropical lake in South Brazil. *Ecol. Model.* 219, 125–137.
- Gao, C., Zhang, T., 2010. Eutrophication in a Chinese context: understanding various physical and socio-economic aspects. *Ambio* 39, 385–393.
- Guan, B.H., An, S.Q., Gu, B.H., 2011. Assessment of ecosystem health during the past 40 years for Lake Taihu in the Yangtze River Delta, China. *Limnology* 12, 47–53.
- Gulati, R.D., Dionisio Pires, L.M., Van Donk, E., 2008. Lake restoration studies: failures, bottlenecks and prospects of new ecotechnological measures. *Limnologia* 38, 233–247.
- Guo, L., 2007. Doing battle with the green monster of Taihu Lake. *Science* 317 (5842), 1166.
- Havens, K.E., Fox, D., Gornak, S., Hanlon, C., 2005. Aquatic vegetation and largemouth bass population responses to water-level variations in Lake Okeechobee, Florida (USA). *Hydrobiologia* 539, 225–237.
- Hellsten, S., Dieme, C., Mbengue, M., Janauer, G., den Hollander, N., Pieterse, A., 1999. Typha control efficiency of a weed-cutting boat in the Lac de Guiers in Senegal: a preliminary study on mowing speed and re-growth capacity. *Hydrobiologia* 415, 249–255.
- Hilt, S., Köhler, J., Kozerski, H.P., Van Nes, E.H., Scheffer, M., 2011. Abrupt regime shifts in space and time along rivers and connected lake systems. *Oikos* 120, 766–775.
- Hosper, S., 1989. Biomanipulation, new perspectives for restoration of shallow, eutrophic lakes in The Netherlands. *Hydrobiol. Bull.* 23, 5–10.
- Hu, D., Yan, J.S., Liu, T.X., Chen, G.W., Yuan, S.J., Wang, R.S., 2004. An integrated analysis of sustainable human–water interactions in wetland ecosystems of Taihu Lake Basin, East China. *Wetlands ecosystems in Asia: function and management*. pp. 183–220.
- Hu, W.P., Zhai, S.J., Zhu, Z.C., Han, H.J., 2008. Impacts of the Yangtze River water transfer on the restoration of Lake Taihu. *Ecol. Eng.* 34, 30–49.
- Hu, Z., Guo, L., Liu, T., Chuai, X., Chen, Q., Shi, F., Jiang, L., Yang, L., 2014. Uniformisation of phytoplankton chlorophyll *a* and macrophyte biomass to characterise the potential trophic state of shallow lakes. *Ecology* 37, 1–9.
- Hui, F., Xu, B., Huang, H., Yu, Q., Gong, P., 2008. Modelling spatial-temporal change of Poyang Lake using multitemporal Landsat imagery. *Int. J. Remote Sens.* 29, 5767–5784.
- ILEC, 1999. ILEC: International Lake Environment Committee, 1999. Survey of the State of the World Lakes: Online-database. (Available at <http://wldb.ilec.or.jp/LakeDB2/>).
- Istvánovics, V., Honti, M., Kovács, Á., Osztóics, A., 2008. Distribution of submerged macrophytes along environmental gradients in large, shallow Lake Balaton (Hungary). *Aquat. Bot.* 88, 317–330.
- Janse, J.H., 1997. A model of nutrient dynamics in shallow lakes in relation to multiple stable states. *Hydrobiologia* 342, 1–8.
- Janse, J.H., 2005. Model Studies on the Eutrophication of Shallow Lakes and Ditches. Wageningen University.
- Janse, J.H., Ligtoet, W., Van Tol, S., Bresser, A.H.M., 2001. A model study on the role of wetland zones in lake eutrophication and restoration. *Sci. World J.* 1, 605–614.
- Janse, J.H., De Senerpont Domis, L.N., Scheffer, M., Lijklema, L., Van Liere, L., Klinge, M., Mooij, W.M., 2008. Critical phosphorus loading of different types of shallow lakes and the consequences for management estimated with the ecosystem model PCLake. *Limnologia* 38, 203–219.

- Janse, J., Scheffer, M., Lijklema, L., Van Lieere, L., Sloot, J., Mooij, W., 2010. Estimating the critical phosphorus loading of shallow lakes with the ecosystem model PCLake: sensitivity, calibration and uncertainty. *Ecol. Model.* 221, 654–665.
- Jeppesen, E., Jensen, J.P., Kristensen, P., Søndergaard, M., Mortensen, E., Sørtkjaer, O., Olrik, K., 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: Threshold levels, long-term stability and conclusions. *Hydrobiologia* 200, 219–227.
- Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., Landkildehus, F., 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshw. Biol.* 45, 201–218.
- Jeppesen, E., Meerhoff, M., Jacobsen, B., Hansen, R., Søndergaard, M., Jensen, J., Lauridsen, T., Mazzeo, N., Branco, C.W.C., 2007. Restoration of shallow lakes by nutrient control and biomanipulation—the successful strategy varies with lake size and climate. *Hydrobiologia* 581, 269–285.
- Jun, X., Qiting, Z., Jinwu, P., 2001. Enlightenment on sustainable management of water resources from past practices in the Bositeng Lake basin, Xinjiang, China. IAHS, Publication, pp. 41–48.
- Kelderman, P., Wei, Z., Maessen, M., 2005. Water and mass budgets for estimating phosphorus sediment–water exchange in Lake Taihu (China PR). *Hydrobiologia* 544, 167–175.
- Kelderman, P., Angweya, R., De Rozari, P., Vijverberg, T., 2012a. Sediment characteristics and wind-induced sediment dynamics in shallow Lake Markermeer, The Netherlands. *Aquat. Sci.* 74, 301–313.
- Kelderman, P., De Rozari, P., Mukhopadhyay, S., Angweya, R., 2012b. Sediment dynamics in shallow Lake Markermeer, The Netherlands: field/laboratory surveys and first results for a 3-D suspended solids model. *Water Sci. Technol.* 66.
- Kiss, M.K., Lakatos, G., Borics, G., Gidó, Z., Deák, C., 2003. Littoral macrophyte–periphyton complexes in two Hungarian shallow waters. *Hydrobiologia* 506, 541–548.
- Kong, X.-Z., Jørgensen, S.E., He, W., Qin, N., Xu, F.-L., 2013. Predicting the restoration effects by a structural dynamic approach in Lake Chaohu, China. *Ecol. Model.* 266, 73–85.
- Krylov, A., 2012. The species composition of zooplankton in waterbodies and water-courses of the great lakes depression. *Inland Water Biol.* 5, 266–273.
- Lammens, E., Van Luijn, F., Wessels, Y., Bouwuijs, H., Noordhuis, R., Portielje, R., Van der Molen, D., 2008. Towards ecological goals for the heavily modified lakes in the IJsselmeer area, The Netherlands. *Hydrobiologia* 599, 239–247.
- Leblanc, M., Lemoalle, J., Bader, J.-C., Tweed, S., Mofor, L., 2011. Thermal remote sensing of water under flooded vegetation: new observations of inundation patterns for the ‘Small’ Lake Chad. *J. Hydrol.* 404, 87–98.
- Li, K.M., 1999. Management and restoration of fish communities in Lake Taihu. *China Fish. Manag. Ecol.* 6, 1–8.
- Li, Y.K., Song, B., Chen, Y., Chen, L.Q., Yu, N., Olson, D., 2010. Changes in the trophic interactions and the community structure of Lake Taihu (China) ecosystem from the 1960s to 1990s. *Aquat. Ecol.* 44, 337–348.
- Li, Y.P., Acharya, K., Stone, M.C., Yu, Z.B., Young, M.H., Shafer, D.S., Zhu, J.T., Gray, K., Stone, A., Fan, L., Tang, C.Y., Warwick, J., 2011a. Spatiotemporal patterns in nutrient loads, nutrient concentrations, and algal biomass in Lake Taihu, China. *Lake Reserv. Manag.* 27, 298–309.
- Li, Y.P., Acharya, K., Yu, Z.B., 2011b. Modeling impacts of Yangtze River water transfer on water ages in Lake Taihu, China. *Ecol. Eng.* 37, 325–334.
- Li, Y.P., Tang, C.Y., Wang, C., Anim, D.O., Yu, Z., Acharya, K., 2013. Improved Yangtze River diversions: are they helping to solve algal bloom problems in Lake Taihu, China? *Ecol. Eng.* 51, 104–116.
- Liao, J., Shen, G., Dong, L., 2013. Biomass estimation of wetland vegetation in Poyang Lake area using ENVISAT advanced synthetic aperture radar data. *J. Appl. Remote. Sens.* 7(1) (1), 073579-1–073579-14.
- Liu, S., 2013. Numerical Modeling of Hydrodynamic Circulation in Lake Taihu. Delft University of Technology, TU Delft.
- Liu, J.Q., Diamond, J., 2005. China’s environment in a globalizing world. *Nature* 435, 1179–1186.
- Liu, B.B., Liu, H., Zhang, B., Bi, J., 2013. Modeling nutrient release in the Tai Lake basin of China: source identification and policy implications. *Environ. Manag.* 1–14.
- Lock, J., 1973. The aquatic vegetation of Lake George, Uganda. *Phytocoenologia* 250–262.
- Lowe, E.F., Battoe, L.E., Coveney, M., Stites, D., 1999. Setting water quality goals for restoration of Lake Apopka: inferring past conditions. *Lake Reserv. Manag.* 15, 103–120.
- Lowe, E.F., Battoe, L.E., Coveney, M.F., Schelske, C.L., Havens, K.E., Marzolf, E.R., Reddy, K.R., 2001. The restoration of Lake Apopka in relation to alternative stable states: an alternative view to that of Bachmann et al. (1999). *Hydrobiologia* 448, 11–18.
- Ma, R.H., Kong, F.X., Duan, H.T., Zhang, S.X., Kong, W.J., Hao, J.Y., 2008. Spatio-temporal distribution of cyanobacteria blooms based on satellite imageries in Lake Taihu, China (Chinese). *J. Lake Sci.* 20, 687–694.
- Mäemets, H., Palmik, K., Haldna, M., Sudnitsyna, D., Melnik, M., 2010. Eutrophication and macrophyte species richness in the large shallow North-European Lake Peipsi. *Aquat. Bot.* 92, 273–280.
- May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269, 471–477.
- Meijer, M.-L., 2000. Biomanipulation in The Netherlands: 15 Years of Experience. Wageningen Universiteit, The Netherlands (thesis).
- Middelboe, A.L., Markager, S., 1997. Depth limits and minimum light requirements of freshwater macrophytes. *Freshw. Biol.* 37, 553–568.
- Mizuno, T., Mori, S., 1970. Preliminary hydrobiological survey of some Southeast Asian inland waters. *Bot. J. Linn. Soc.* 2, 77–118.
- Nishihiro, J., Washitani, I., 2009. Quantitative evaluation of water-level effects on “regeneration safe-sites” for lakeshore plants in Lake Kasumigaura, Japan. *Lake Reserv. Manag.* 25, 217–223.
- O’Brien, K.R., Hapgood, K.P., 2012. The academic jungle: ecosystem modelling reveals why women are driven out of research. *Oikos* 121, 999–1004.
- O’Dell, K.M., VanArman, J., Welch, B.H., Hill, S.D., 1995. Changes in water chemistry in a macrophyte-dominated lake before and after herbicide treatment. *Lake Reserv. Manag.* 11, 311–316.
- Ogutu-Ohwayo, R., Odongkara, K., Okello, W., Mbabazi, D., Wandera, S.B., Ndawula, L.M., Natugonza, V., 2013. Variations and changes in habitat, productivity, composition of aquatic biota and fisheries of the Kyoga lake system: lessons for management. *Afr. J. Aquat. Sci.* 38, 1–14.
- Otten, T., Xu, H., Qin, B., Zhu, G., Paerl, H., 2012. Spatiotemporal patterns and ecophysiology of toxigenic *Microcystis* blooms in Lake Taihu, China: implications for water quality management. *Environ. Sci. Technol.* 46, 3480–3488.
- Paerl, H.W., Hall, N.S., Calandrino, E.S., 2011a. Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. *Sci. Total Environ.* 409, 1739–1745.
- Paerl, H.W., Xu, H., McCarthy, M.J., Zhu, G., Qin, B., Li, Y., Gardner, W.S., 2011b. Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): the need for a dual nutrient (N & P) management strategy. *Water Res.* 45, 1973–1983.
- Pálffy, K., Présing, M., Vörös, L., 2013. Diversity patterns of trait-based phytoplankton functional groups in two basins of a large, shallow lake (Lake Balaton, Hungary) with different trophic state. *Aquat. Ecol.* 47, 195–210.
- Pang, Y., Li, Y.P., Luo, L.C., 2006. Study on the simulation of transparency of Lake Taihu under different hydrodynamic conditions. *Sci. China Ser. D* 49, 162–175.
- Phillips, G., Eminson, D., Moss, B., 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4, 103–126.
- Qin, B.Q., Zhu, G.W., Zhang, L., Luo, L.C., Gao, G., Gu, B.H., 2006. Estimation of internal nutrient release in large shallow Lake Taihu, China. *Sci. China Ser. D Earth Sci.* 49, 38–50.
- Qin, B.Q., Xu, P.Z., Wu, Q.L., Luo, L.C., Zhang, Y.L., 2007. Environmental issues of Lake Taihu, China. In: Qin, B., Liu, Z., Havens, K. (Eds.), *Eutrophication of Shallow Lakes with Special Reference to Lake Taihu, China*. Springer Netherlands, pp. 3–14.
- Qin, B.Q., Zhu, G.W., Gao, G., Zhang, Y.L., Li, W., Paerl, H.W., Carmichael, W.W., 2010. A drinking water crisis in Lake Taihu, China: linkage to climatic variability and lake management. *Environ. Manag.* 45, 105–112.
- Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., 2009. A safe operating space for humanity. *Nature* 461, 472–475.
- Rodusky, A.J., Sharfstein, B., Hanlon, C.G., Donnelly, K.A., 2013. Ecological attributes of a native and exotic emergent subtropical marsh community in lake okeechobee, Florida (USA). *Wetl. Ecol. Manag.* 21, 87–105.
- Rose, N., Boyle, J., Du, Y., Yi, C., Dai, X., Appleby, P., Bennion, H., Cai, S., Yu, L., 2004. Sedimentary evidence for changes in the pollution status of Taihu in the Jiangsu region of eastern China. *J. Paleolimnol.* 32, 41–51.
- Scheffer, M., 1990. Multiplicity of stable states in freshwater systems. *Hydrobiologia* 200, 475–486.
- Scheffer, M., 2004. *Ecology of Shallow Lakes*. Springer.
- Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* 18, 648–656.
- Scheffer, M., Van Nes, E.H., 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Shallow Lakes in a Changing World*, pp. 455–466.
- Scheffer, M., Hosper, S., Meijer, M., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8, 275–279.
- Scheffer, M., Brock, W., Westley, F., 2000. Socioeconomic mechanisms preventing optimum use of ecosystem services: an interdisciplinary theoretical analysis. *Ecosystems* 3, 451–471.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Scheffer, M., Szabó, S., Gragnani, A., Van Nes, E.H., Rinaldi, S., Kautsky, N., Norberg, J., Roijackers, R.M.M., Franken, R.J.M., 2003. Floating plant dominance as a stable state. *Proc. Natl. Acad. Sci.* 100, 4040–4045.
- Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., van de Koppel, J., van de Leemput, I.A., Levin, S.A., van Nes, E.H., Pascual, M., Vandermeer, J., 2012. Anticipating critical transitions. *Science* 338, 344–348.
- Schelske, C.L., Lowe, E.F., Kenney, W.F., Battoe, L.E., Brenner, M., Coveney, M.F., 2010. How anthropogenic darkening of Lake Apopka induced benthic light limitation and forced the shift from macrophyte to phytoplankton dominance. *Limnol. Oceanogr.* 55, 1201.
- Schloesser, D.W., Manny, B.A., 1986. Distribution of submersed macrophytes in the St. Clair–Detroit River system, 1978. *J. Freshw. Ecol.* 3, 537–544.
- Schloesser, D.W., Edsall, T.A., Manny, B.A., 1985. Growth of submersed macrophyte communities in the St. Clair–Detroit river system between Lake Huron and Lake Erie. *Can. J. Bot.* 63, 1061–1065.
- Shang, G.P., Shang, J.C., 2005. Causes and control countermeasures of eutrophication in Chaohu Lake, China. *Chin. Geogr. Sci.* 15, 348–354.
- Shen, J., Yuan, H.Z., Liu, E.F., Wang, J.J., Wang, Y., 2011. Spatial distribution and stratigraphic characteristics of surface sediments in Taihu Lake, China. *Chin. Sci. Bull.* 56, 179–187.
- Singh, A.L., Khundrakpam, M.L., 2011. Phumdi proliferation: a case study of Loktak lake, Manipur. *J. Water Environ.* 25, 99–105.
- Skinner, D., Oliver, R., Aldridge, K., Brookes, J., 2014. Extreme water level decline effects sediment distribution and composition in Lake Alexandrina, South Australia. *Limnology* 15, 117–126.
- Smith, B.D., 1995. *The Emergence of Agriculture*. Scientific American Library, New York.
- Smith, V.H., Tilman, G.D., Nekola, J.C., 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* 100, 179–196.

- Sollie, S., Coops, H., Verhoeven, J.A., 2008a. Natural and constructed littoral zones as nutrient traps in eutrophicated shallow lakes. *Hydrobiologia* 605, 219–233.
- Sollie, S., Janse, J.H., Mooij, W.M., Coops, H., Verhoeven, J.T., 2008b. The contribution of marsh zones to water quality in Dutch shallow lakes: a modeling study. *Environ. Manag.* 42, 1002–1016.
- Søndergaard, M., Jeppesen, E., Jensen, J.P., 2005. Pond or lake: does it make any difference? *Arch. Hydrobiol.* 162, 143–165.
- Stefan, H.G., Cardoni, J.J., Schiebe, F.R., Cooper, C.M., 1983. Model of light penetration in a turbid lake. *Water Resour. Res.* 19, 109–120.
- Sun, H.I., Qin, B.Q., Hu, C.H., 2010. Ecosystem dataset of lakes and wetlands: Jiangsu Taihu Lake Station (1991–2006) (中国生态系统定位观测与研究数据集 湖泊湿地海湾生态系统卷: 江苏太湖站 (1991–2006)). (Chinese) China Agriculture Press.
- Tamire, G., Mengistou, S., 2013. Macrophyte species composition, distribution and diversity in relation to some physicochemical factors in the littoral zone of Lake Ziway, Ethiopia. *Afr. J. Ecol.* 51, 66–77.
- TBA, 2014. Provincial boundaries Taihu Lake Basin Water Resources Quality Bulletin. <http://www.tba.gov.cn/>.
- Thiam, A., Matty, F., Noba, K., Ba, A.T., 2013. Structural analysis of the vascular flora of Lake Guiers, the largest freshwater reservoir surface of Senegal. *Webbia* 68, 177–185.
- Thompson, K., Shewry, P.R., Woolhouse, H.W., 1979. Papyrus swamp development in the Upemba Basin, Zaire: studies of population structure in *Cyperus papyrus* stands. *Bot. J. Linn. Soc.* 78, 299–316.
- Tian, G.J., Jiang, J., Yang, Z.F., Zhang, Y.Q., 2011. The urban growth, size distribution and spatio-temporal dynamic pattern of the Yangtze River Delta megalopolitan region, China. *Ecol. Model.* 222, 865–878.
- Timm, T., 1996. Oligochaeta of Lake Taimyr: a preliminary survey. *Hydrobiologia* 334, 89–95.
- Timms, R., Moss, B., 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol. Oceanogr.* 29, 472–486.
- Tobler, W.R., 1970. A computer movie simulating urban growth in the Detroit region. *Econ. Geogr.* 234–240.
- Torres, A.C., 1993. Lake Patzcuaro, Mexico: watershed and water quality deterioration in a tropical high-altitude Latin American lake. *Lake Reserv. Manag.* 8, 37–47.
- Torres, A.C., Ross, L.G., Beveridge, M.C.M., 1989. Lake Patzcuaro, Mexico: results of a new morphometric study and its implications for productivity assessments. *Hydrobiologia* 184, 125–132.
- Van Geest, G., Roozen, F., Coops, H., Roijackers, R., Buijse, A., Peeters, E., Scheffer, M., 2003. Vegetation abundance in lowland flood plain lakes determined by surface area, age and connectivity. *Freshw. Biol.* 48, 440–454.
- Van Geest, G., Coops, H., Roijackers, R., Buijse, A., Scheffer, M., 2005. Succession of aquatic vegetation driven by reduced water-level fluctuations in floodplain lakes. *J. Appl. Ecol.* 42, 251–260.
- Van Nes, E.H., Scheffer, M., 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. *Ecology* 86, 1797–1807.
- Vijverberg, T., Winterwerp, J.C., Aarninkhof, S.G.J., Drost, H., 2011. Fine sediment dynamics in a shallow lake and implication for design of hydraulic works. *Ocean Dynam.* 61 (2–3), 187–202.
- Villamagna, A.M., Murphy, B.R., Trauger, D.L., 2010. Behavioral response of American coots (*Fulica americana*) to water hyacinth (*Eichhornia crassipes*) in Lake Chapala, Mexico. *Waterbirds* 33, 550–555.
- Vollenweider, R.A., 1975. Input–output models. *Schweiz. Z. Hydrol.* 37, 53–84.
- Wang, H., Wang, C., Wu, W., Mo, Z., Wang, Z., 2003. Persistent organic pollutants in water and surface sediments of Taihu Lake, China and risk assessment. *Chemosphere* 50, 557–562.
- Wiens, J.A., 1989. Spatial scaling in ecology. *Funct. Ecol.* 3, 385–397.
- Winfield, D.K., Winfield, I.J., 1994. Possible competitive interactions between overwintering tufted duck (*Aythya fuligula* (L.)) and fish populations of Lough Neagh, Northern Ireland: evidence from diet studies. *Hydrobiologia* 279, 377–386.
- Wright, R., Phillips, V., 1992. Changes in the aquatic vegetation of two gravel pit lakes after reducing the fish population density. *Aquat. Bot.* 43, 43–49.
- Xu, H., Paerl, H.W., Qin, B., Zhu, G., Gao, G., 2010. Nitrogen and phosphorus inputs control phytoplankton growth in eutrophic Lake Taihu, China. *Limnol. Oceanogr.* 55, 420.
- Yan, S.W., Yu, H., Zhang, L.L., Xu, J., Wang, Z.P., 2011. Water quantity and pollutant fluxes of inflow and outflow rivers of Lake Taihu, 2009 (Chinese). *J. Lake Sci.* 23, 855–862.
- Yang, S.-Q., Liu, P.-W., 2010. Strategy of water pollution prevention in Taihu Lake and its effects analysis. *J. Great Lakes Res.* 36, 150–158.
- Yu, G., Xue, B., Lai, G.Y., Gui, F., Liu, X.M., 2007. A 200-year historical modeling of catchment nutrient changes in Taihu basin, China. *Eutrophication of Shallow Lakes with Special Reference to Lake Taihu, China*. Springer, pp. 79–87.
- Zhang, L., 2007. An Integrated Ecosystem Model for Eutrophication in Lake Taihu, China. Unesco-IHE.
- Zhang, L.M., Xia, M.F., Zhang, L., Wang, C., Lu, J.L., 2008. Eutrophication status and control strategy of Taihu Lake. *Front. Environ. Sci. Eng. China* 2, 280–290.
- Zhang, X., Liu, X., Wang, H., 2014. Developing water level regulation strategies for macrophytes restoration of a large river-disconnected lake, China. *Ecol. Eng.* 68, 25–31.
- Zhao, D., Jiang, H., Yang, T., Cai, Y., Xu, D., An, S., 2012a. Remote sensing of aquatic vegetation distribution in Taihu Lake using an improved classification tree with modified thresholds. *J. Environ. Manag.* 95, 98–107.
- Zhao, D.H., Jiang, H., Cai, Y., An, S.Q., 2012b. Artificial regulation of water level and its effect on aquatic macrophyte distribution in Taihu Lake. *PLoS* 7.
- Zhao, D.H., Lv, M.T., Jiang, H., Cai, Y., Xu, D.L., An, S.Q., 2013. Spatio-temporal variability of aquatic vegetation in Taihu Lake over the past 30 years. *PLoS ONE* 8, e66365.
- Zheng, B.G., Xu, Q.J., Hua, Z.B., Zhang, L.J., 2009. Building nutrient and its response indications reference state for criteria enactment: on the case of Lake Taihu, a typical shallow lake in eastern China [J]. *J. Lake Sci.* 1.
- Zhu, M.Y., Zhu, G.W., Li, W., Zhang, Y.L., Zhao, L.L., Gu, Z., 2013. Estimation of the algal-available phosphorus pool in sediments of a large, shallow eutrophic lake (Taihu, China) using profiled SMT fractional analysis. *Environ. Pollut.* 173, 216–223.