Freshwater Biology

Freshwater Biology (2014) doi:10.1111/fwb.12372

Total phosphorus thresholds for regime shifts are nearly equal in subtropical and temperate shallow lakes with moderate depths and areas

HAI-JUN WANG, HONG-ZHU WANG, XIAO-MIN LIANG AND SHI-KAI WU
State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China

SUMMARY

1. Published research suggests that the total phosphorus (TP) thresholds for the regime shifts between a clear-water state dominated by submersed macrophytes and a turbid-water state dominated by phytoplankton in shallow lakes vary with forms of lake basins and climates. However, such hypotheses remain untested by direct field evidence. We therefore tested the hypotheses with empirical data from subtropical lakes on the Yangtze floodplain and also from other lakes in temperate to tropical zones.
2. TP thresholds were found to vary little at moderate depths, but to decrease notably when depth exceeds a level of probably 3–4 m, and increase sharply when depth is below a level of around 1–2 m.
3. TP thresholds were found to be nearly equal in shallow lakes (1–2 m <mean depth <3–4 m; *c.* 0.1 km^2 <area <at least 350 km^2) from temperate to subtropical (probably to tropical) zones, being 80–120 mg m^{-3} for the forward shift from a clear-water state to a turbid-water state and 40–60 mg m^{-3} for the backward shift.
4. The threshold of turbidity for the forward shift was found to be higher than that for the backward shift, amending the previous hypothesis of the equality of turbidity thresholds for both shifts.
5. Our findings suggest that according to the subequality of TP thresholds, similar target concentrations for in-lake TP can be set in most shallow lakes world-wide to mitigate eutrophication.

Keywords: mechanisms, regime shifts, subtropical lakes, TP thresholds, turbidity thresholds

Introduction

Research into the underlying mechanisms and thresholds for regime shifts between contrasting states is important from theoretical and practical perspectives. The shifts in shallow lakes between a clear-water state dominated by submersed macrophytes and a turbid-water state dominated by phytoplankton, or back, are a well-known example of a regime shift. To explain regime shifts in shallow lakes, Scheffer *et al.* (1993) presented a graphical model on the basis of three assumptions: (i) turbidity increases with nutrient levels; (ii) vegetation reduces turbidity; and (iii) vegetation disappears when a critical turbidity is exceeded and recovers when turbidity drops below the threshold. Much evidence from north temperate shallow lakes has been presented to support this theory (as reviewed by Scheffer, 1998, 2001), but its validity for lakes in other climatic zones remains uncertain. Furthermore, the assumption that submersed vegetation disappears and recovers at the same critical turbidity requires direct field evidence.

Phosphorus loading is generally regarded as the driving variable for regime shifts between clear-water and turbid-water states in shallow lakes (Scheffer & Carpenter, 2003). However, total phosphorus concentration in lake water (TP) is usually used as a surrogate, because phosphorus loading is often difficult to measure. Previous research into TP thresholds has concentrated on European temperate lakes (Jeppesen *et al.*, 1990; Ibelings *et al.*, 2007). Thresholds of phosphorus have generally been suggested to vary with forms of lake basins (area and depth) and climate (Genkai-Kato & Carpenter, 2005; Mooij & Janse, 2007;

Correspondence: Hong-Zhu Wang, 7 South Donghu Road, Wuchang District, Wuhan 430072, Hubei Province, China.
E-mail: wanghz@ihb.ac.cn

Scheffer & van Nes, 2007; Janse *et al.*, 2008). However, direct field evidence is rare (e.g. Jeppesen *et al.*, 1990).

The subtropical Yangtze River floodplain is a mosaic of numerous shallow lakes with different nutrient levels, providing excellent opportunities for research into regime shifts. Based on a combination of multi-lake comparisons and long-term monitoring, we aimed the following: (i) to analyse the existence of alternative states in subtropical lakes; (ii) to test the hypothesis that submersed vegetation disappears and recovers at the same critical turbidity; (iii) to analyse the mechanisms underlying the regime shifts in subtropical lakes; (iv) to estimate TP thresholds for the regime shifts in subtropical shallow lakes and analyse effects of lake area and depth on the thresholds; and (v) to explore the general rules governing the variation in TP thresholds through comparisons of lakes from different climatic zones.

Methods

All the lakes studied (E 113°10′–121°00′, N 29°30′–32°00′) are located in the mid-lower Yangtze Basin (Fig. 1), characterised by a dominant warm, humid subtropical monsoon climate, annual mean air temperature ranging between 14 and 18 °C and precipitation between 1000 and 1400 mm. All the lakes in this basin are shallow floodplain lakes, isolated from the Yangtze River by embankments and sluice gates, with elevations generally lower than 50 m ASL.

A data set of 76 lake-years from 30 lakes was used for multi-lake analyses (Fig. 1a). Fifty-seven lake-years of 28 lakes were investigated by this study during 2002–2012, and 19 lake-years of 10 lakes were gathered from the literature (Hu & Huang, 1991; Liang & Liu, 1995; Cui & Li, 2005). Long-term investigations (1987–2012) were carried out in two adjacent subareas (Shuimiao, 1.6 km^2, 2.3 m; Changlingtou, 1.5 km^2, 1.9 m) of Lake Bao'an (40.0 km^2) (Fig. 1b).

The number of water samples collected from each lake during each sampling period ranged from 3 to 12, depending on lake size. One additional station, located between each set of two adjacent sampling sites, was used to measure water depth (Z), Secchi depth (Z_{SD}) and submersed macrophyte biomass (B_{Mac}). A sounding lead was used to measure water depth. Water samples were taken from 0.5 m below the surface and from the layer with a depth of half the water column depth at each site, and the two samples were mixed for analyses. Analyses for phytoplankton chlorophyll *a* (Chl *a*) and total phosphorus (TP) followed those presented in Chinese Water Analysis Methods Standards (Huang, Chen & Cai, 1999). Chl *a* was extracted without grinding from

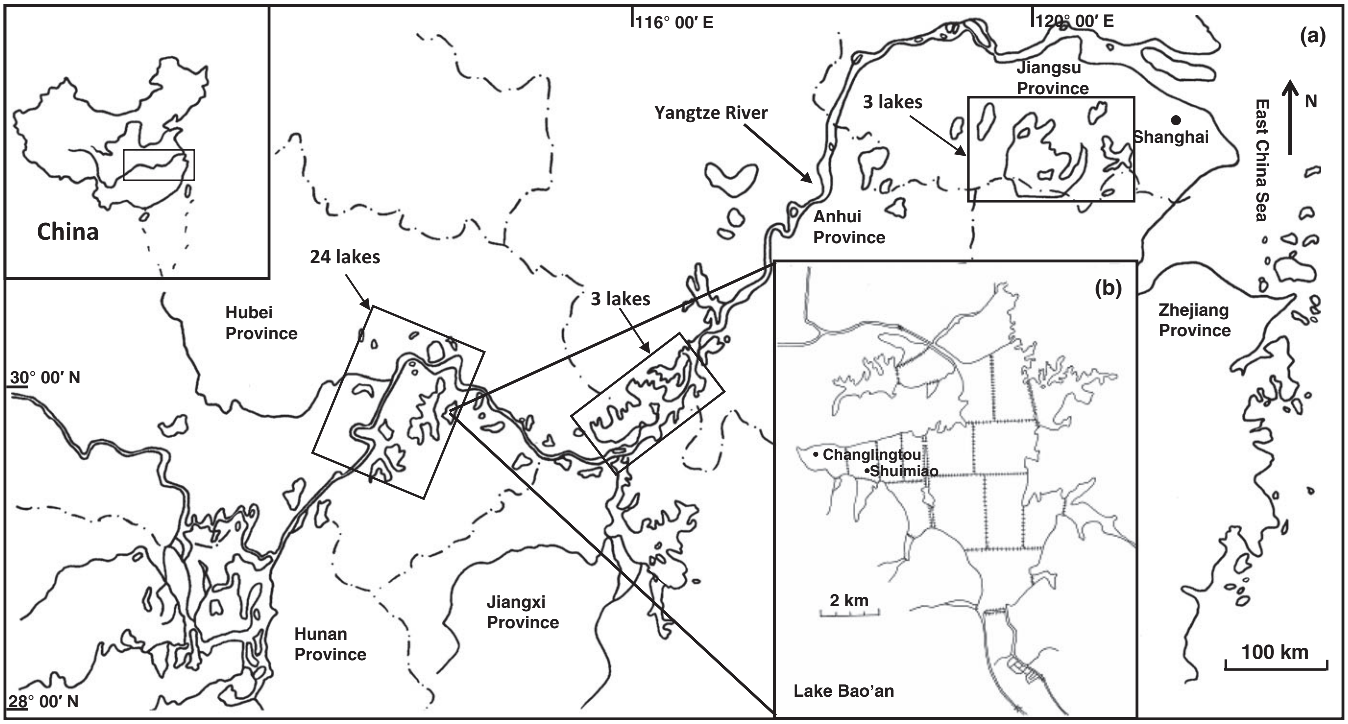

Fig. 1 Distribution of the subtropical lakes studied in the mid-lower basin of the Yangtze River (Hubei, Anhui and Jiangsu provinces, Shanghai, China). The dashed lines in Lake Bao'an represent networks or dykes isolating the lake into subareas.

filters (GF/C, Whatman, GE Healthcare UK Limited, Buckinghamshire, UK) using 90% acetone (at 4 °C for 20 h); absorbance was then read at 665 and 750 nm, both before and after acidification (with 10% HCl) using a spectrophotometer (Unico UV-2000, Shanghai, China). TP was measured by an ammonium molybdate-ultraviolet spectrophotometric method after potassium persulphate digestion (at 120 °C for 30 min).

The diversity and abundance of submersed macrophytes were measured by random sampling (2–4 replicates) at each site using a scythe-type sampler (0.2 m^2 in sampling area) with a long handle. Samples were then combined, cleaned (removal of extraneous material such as sticks, macroinvertebrates and substrates), dewatered and then weighed for wet biomass.

Turbidity (Turb) was estimated as the reciprocal of Secchi depth. Measured turbidity is strongly correlated with reciprocal of Secchi depth in Yangtze lakes (authors' unpublished data). For the thresholds of TP and Turb, the highest values in the data set of vegetation-present lakes and the lowest values in the data set of vegetation-absent lakes were defined as the thresholds for disappearance and recovery of macrophytes, respectively. In the analyses of multi-year monitoring, the values of the year in which macrophyte abundance decreased greatly (and sometimes to zero) were defined as the thresholds for the disappearance of macrophytes.

To explore relative contributions of non-algal components to changes in total turbidity during regime shifts, ratios of turbidity to chlorophyll *a* were analysed: $\log_{10}(\text{Turb})/\log_{10}(10\ \text{Chl}\ a)$. In the calculation, prior to log-transformation, Chl *a* was multiplied by 10, as in some cases, a $\log_{10}(\text{Chl}\ a)$ close to zero could result in an extremely high $\log_{10}(\text{Turb})/\log_{10}(\text{Chl}\ a)$. In such cases, $\log_{10}(\text{Turb})/\log_{10}(\text{Chl}\ a)$ fails to reflect the true situation.

To compare the difference in grazing stress of zooplankton on phytoplankton (measured as biomass ratio of cladocerans to phytoplankton) between lakes with and without vegetation, a data set of 31 lake-years collected from 26 lakes was summarised from results presented in the literature (Liu, 1990; Yang & Huang, 1994; Liang & Liu, 1995; Cui & Li, 2005; Xiong, 2005).

The basic limnological characteristics of the lakes used for the multi-lake comparisons are given in Table 1. Lake areas ranged from 0.5 to 355 km^2, maximum water depth from 1.0 to 5.0 m and mean water depth from 0.6 to 4.2 m. TP ranged from 5 to 970 mg m^{-3}, Chl *a* from 0.6 to 139 mg m^{-3} and Z_{SD} from 0.3 to 3.3 m. Submersed macrophyte biomass (B_{Mac}) ranged between 0 and 13 200 g m^{-2}. Lake-years with $B_{Mac} = 0$ g m^{-2}, $B_{Mac} \leq 1000$ g m^{-2} (>0) and $B_{Mac} > 1000$ g m^{-2} were 36.8%, 27.6% and 35.5%, respectively (see Appendix S1 for more information about biological assemblages from these lakes and Appendix S2 for a description of two subareas (Shuimiao and Changlingtou) of Lake Bao'an).

Table 1 Statistical characteristics of the basic limnological parameters of lakes for multi-lake comparisons

	n	Mean	Median	Min	Max	SD	CV
Area (km^2)	30	44.9	9.0	0.5	355.0	81.4	181
Z_{Max} (m)	30	2.74	2.55	1.00	5.00	0.92	34
Z_M (m)	76	2.11	1.99	0.63	4.24	0.66	31
TP (mg m^{-3})	76	107	48	5	970	179	167
B_{Mac} (g m^{-2})	76	1648	355	0	13 150	2791	169
Chl *a* (mg m^{-3})	76	23.3	6.0	5.3	139.1	0.31	135
Turb (m^{-1})	76	1.29	1.07	0.31	3.45	0.79	62

Area, lake surface area; Z_{Max}, maximum water depth; Z_M, mean water depth; TP, total phosphorus of lake water; B_{Mac}, submersed macrophyte biomass; Chl *a*, phytoplankton chlorophyll *a*; Turb, turbidity, calculated as a reciprocal of Secchi depth ($1/Z_{SD}$); SD, standard deviation; CV, coefficient of variation,%. The sample size n indicates the number of lakes sampled for Area and Z_{Max} and the number of lake-years in the data set for the other parameters.

STATISTICA 8.5 and Microsoft Excel 2007 were used for data processing and analyses. *t*-tests were used to analyse the differences between regression lines. Unequal N *Post hoc* ANOVA was used to test the differences between group means if group *n* values were not equal.

Results

Multi-lake comparisons

A linear relationship was found between $\log_{10}(\text{Chl}\ a)$ and $\log_{10}(\text{TP})$ ($r = 0.75$, $n = 76$, $P < 0.001$). The regression equations were not significantly different between lakes with and without vegetation (slope, $P > 0.1$; intercept, $P > 0.5$) (Fig. 2a). $\text{Log}_{10}(\text{Turb})/\log_{10}(10\ \text{Chl}\ a)$ in vegetation-present lakes (-0.09 ± 0.02) was significantly lower than that in vegetation-absent lakes (0.11 ± 0.02) ($P < 0.001$), and a significant negative correlation was found between the ratio and $\log_{10}(B_{Mac}+1)$ (Fig. 2b) in vegetation-present lakes. A linear relationship was also found between $\log_{10}(\text{Turb})$ and $\log_{10}(\text{TP})$ ($r = 0.81$, $n = 76$, $P < 0.001$), and the regression equations were significantly different in intercept ($P < 0.001$), but not in slope ($P > 0.05$), between lakes with and without vegetation (Fig. 2c). A relationship described by a folded curve was evident between $\log_{10}(B_{Mac}+1)$ and $\log_{10}(\text{TP})$ (Fig. 2d): when TP was higher than *c*. 120 mg m^{-3}, submersed macrophytes were absent in all lakes; when TP

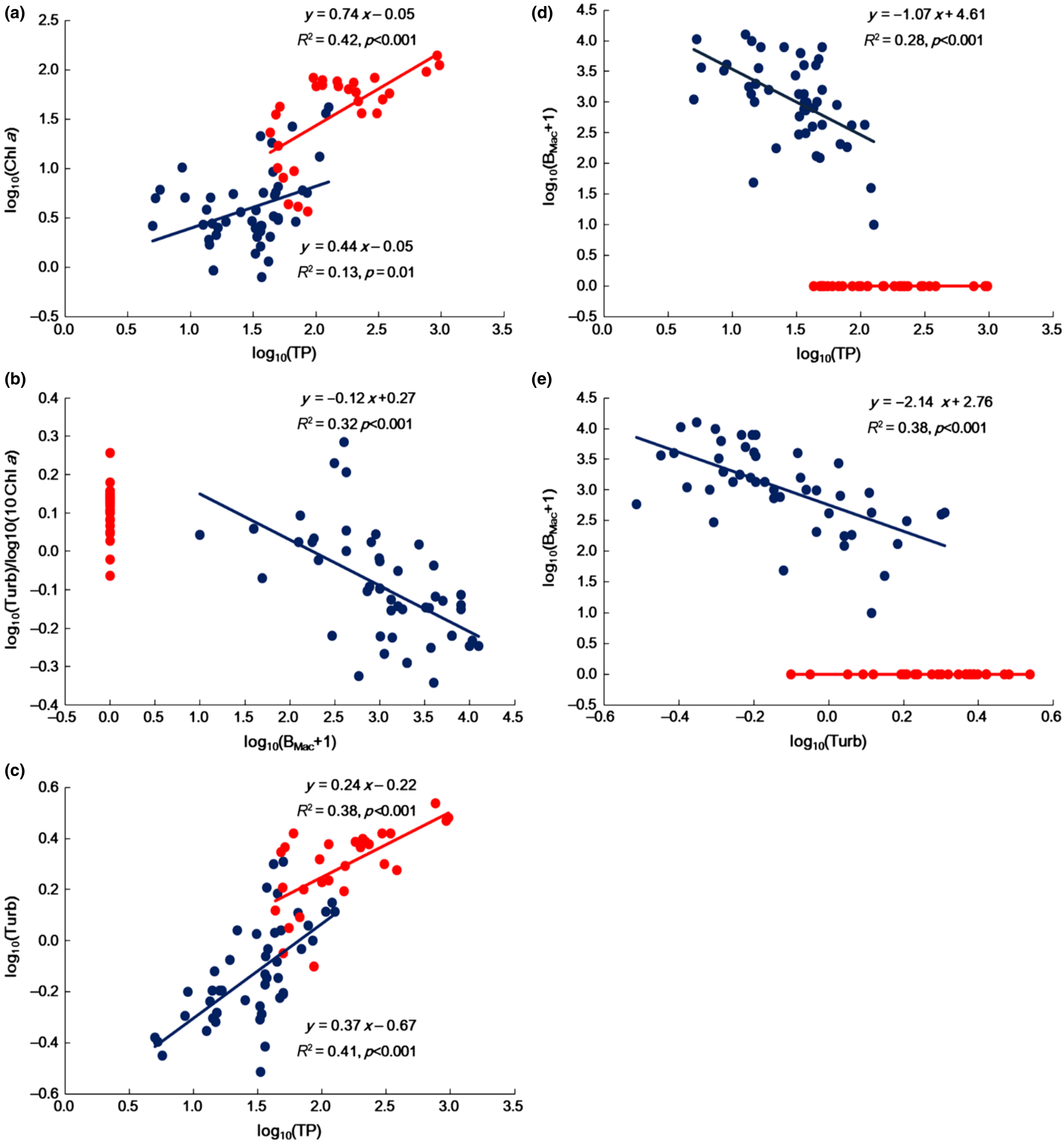

Fig. 2 Relationships between total phosphorus (TP, mg m^{-3}), phytoplankton chlorophyll *a* (Chl *a*, mg m^{-3}) indicating algal turbidity, ratio of turbidity to Chl *a* ($\log_{10}$(Turb)/$\log_{10}$(10 Chl *a*)) indicating non-algal turbidity, turbidity (Turb, m^{-1}) and submersed macrophyte biomass (B_{Mac}, g m^{-2}). Blue, vegetation-present, n = 48; Red, vegetation-absent, n = 28.

was lower than *c.* 50 mg m^{-3}, macrophytes were abundant in all lakes; when TP was between 50 and 120 mg m^{-3}, macrophytes were either absent or abundant. A relationship described by a folded curve was also found between $\log_{10}(B_{\mathrm{Mac}}+1)$ and $\log_{10}$(Turb) (Fig. 2e), and the Turb thresholds for disappearance and recovery of macrophytes were *c.* 2.0 and 0.8 m^{-1}, respectively.

Total phosphorus thresholds for disappearance and recovery of macrophytes did not differ notably between deeper and shallower lakes and between larger and smaller lakes (Fig. 3a,b). Markedly higher Turb thresholds for disappearance and recovery of submersed macrophytes were found in shallower lakes (*c.* 2.0 and 1.1 m^{-1}, respectively) than in deeper lakes (*c.* 1.5 and 0.8 m^{-1}) (Fig. 3d). Markedly different Turb thresholds for disappearance and recovery of submersed macrophytes were also found between larger (*c.* 2.0 and 0.8 m^{-1}) and smaller (*c.* 1. 4 and 1.1 m^{-1}) lakes (Fig. 3c).

Long-term monitoring

In the two subareas (Shuimiao and Changlingtou) of Lake Bao'an during the period from 1987 through 2006, TP levels were low (15–51 mg m^{-3} for Shuimiao, 15–47 mg m^{-3} for Changlingtou) (Fig. 4a,c,d,f,h,i), Turb was correspondingly low (0.4–0.9, 0.5–0.8 m^{-1}) (Fig. 4c,e,h,j), and B_{Mac} levels were high (1100–13 200, 900–9600 g m^{-2}) (Fig. 4b, d,e,g,i,j). In 2007, TP increased to 120–125 mg m^{-3}, Turb to 1.3–1.4 m^{-1} and B_{Mac} decreased to zero. Afterwards (2008–2012), TP and Turb levels were high (51–200 m m^{-3}, 48–180 mg m^{-3}; 1.6–2.4, 1.7–2.5 m^{-1}), and macrophytes did not recover. Although TP dropped once in 2010 to a low value, the waters remained in the turbid state. During the whole period, $\log_{10}$(Chl *a*) was sensitive to the variation in $\log_{10}$(TP), with linear relationships ($r = 0.86$, 0.91, $n = 13$, $P < 0.001$) (Fig. 4a,f). Significantly different $\log_{10}$(Turb)/$\log_{10}$(10 Chl *a*) was found between the periods before (0.11 ± 0.04, 0.12 ± 0.04) and after (−0.14 ± 0.03, −0.14 ± 0.03) macrophyte disappearance ($P = 0.001$, d.f. = 11) (Fig. 4b,g).

Discussion

Existence of alternative stable states in the subtropical shallow lakes on the Yangtze floodplain

Shallow lakes along the Yangtze River can shift between clear-water and turbid-water states. There is evidence

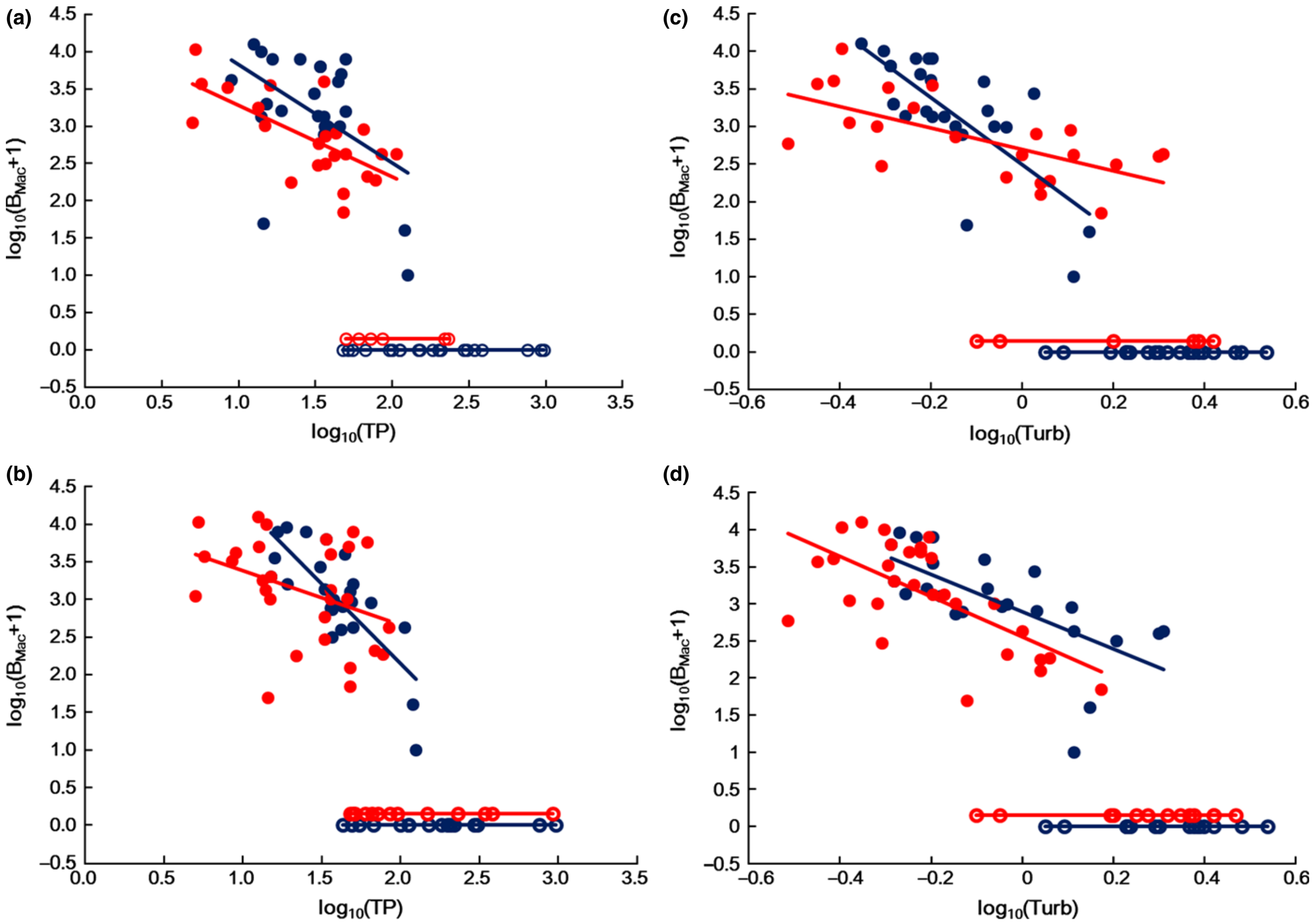

Fig. 3 Relationships between submersed macrophyte biomass (B_{Mac}, g m^{-2}) (closed dots, vegetation-present; open dots, vegetation-absent) and total phosphorus (TP, mg m^{-3}) and turbidity (Turb, m^{-1}) for lakes with different surface area (a, c) (blue, <10 km^2; red, ≥10 km^2) and water depth (b, d) (blue, <2 m; red, >2 m).

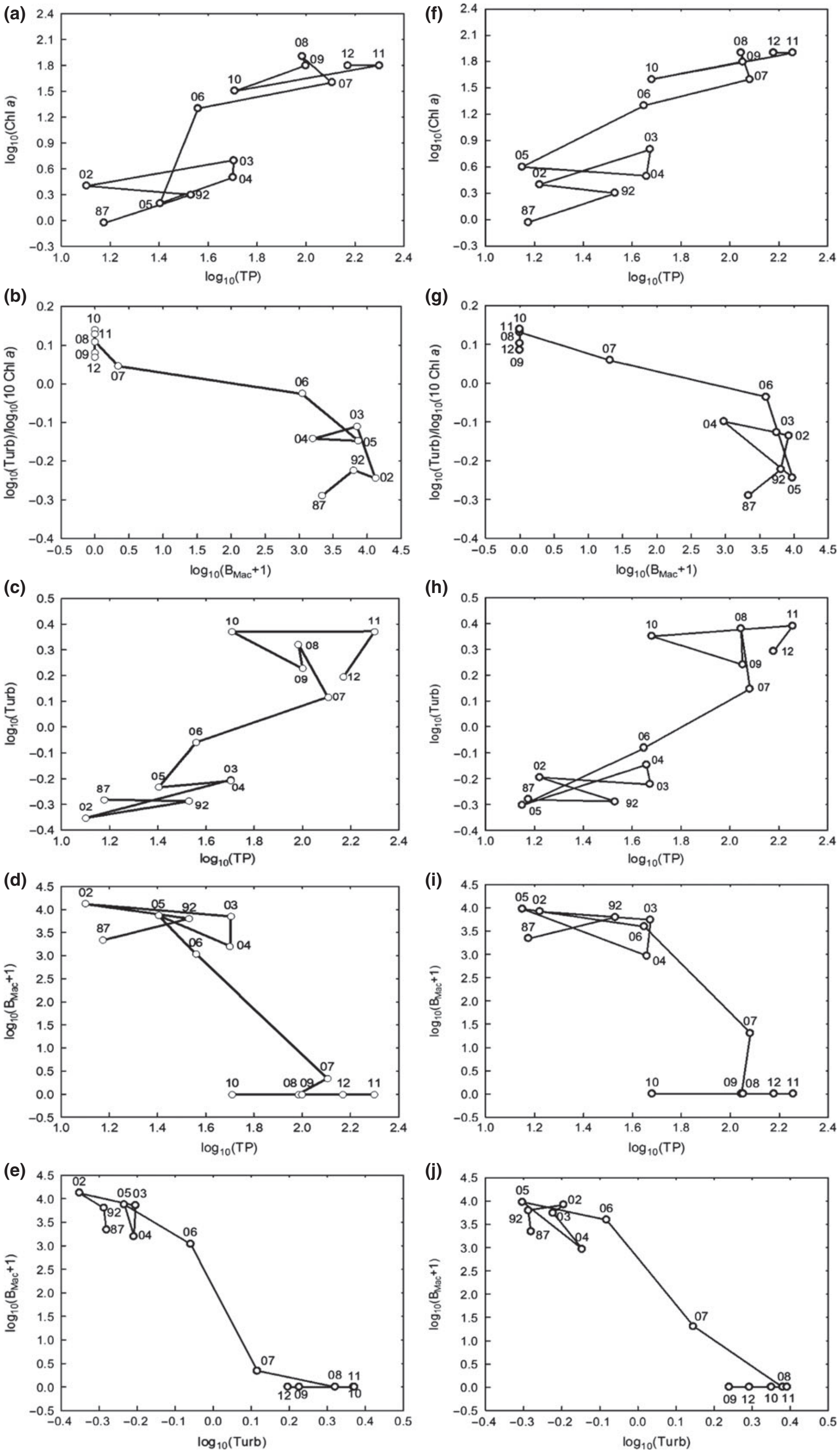

Fig. 4 Responses of phytoplankton chlorophyll *a* (Chl *a*, mg m^{-3}) indicating algal turbidity (a, f) and turbidity (Turb, m^{-1}) (c, h) to changes in total phosphorus (TP, mg m^{-3}); responses of ratio of turbidity to Chl *a* ($\log_{10}$(Turb)/$\log_{10}$(10 Chl *a*)) indicating non-algal turbidity (b, g) to changes in submersed macrophyte biomass (B_{Mac}, g m^{-2}); and responses of B_{Mac} to changes in TP (d, i) and Turb (e, j) in Shuimiao (a–d) and Changlingtou (e–h) of Lake Bao'an during 1987–2012.

for hysteresis in the relationships between the control factor TP and the state variables B_{Mac} and Turb. A relationship described by a folded curve was evident between $\log_{10}(B_{\mathrm{Mac}}+1)$ and $\log_{10}(\mathrm{TP})$ in multi-lake comparisons (Fig. 2d), and a hysteresis in the response of B_{Mac} to TP seems to exist in multi-year monitoring (Fig. 4d,i). The intercept of the $\log_{10}(\mathrm{TP})-\log_{10}(\mathrm{Turb})$ regression equation for vegetation-present lakes was significantly lower than for vegetation-absent lakes (Fig. 2c), and a hysteresis in the response of Turb to TP is suggested in multi-year monitoring (Fig. 4c,h).

Do forward and backward shifts occur at the same turbidity threshold?

The turbidity threshold for the forward shift was found to be about twice as high as that for the backward shift. Based on multi-lake comparisons, submersed macrophytes were absent when Turb exceeded 1.5–2.0 m^{-1} and abundant when Turb was lower than 0.8–1.1 m^{-1} (Figs 2e & 3c,d). The hysteresis in responses of macrophytes to turbidity is attributed to the different plant heights between contrasting stages. Prior to disappearance, taller plants can reach the upper water layer and hence withstand higher turbidity; in recovery, turbidity must be reduced to lower levels to meet the light demands of germination and seedlings.

The third assumption supporting the theory of alternative states suggested an identical critical turbidity level for forward and backward shifts, based mainly on the empirical inverse relationship between the light attenuation coefficient and the maximum colonisation depth of submersed macrophytes (Z_C) (Scheffer *et al.*, 1993; Scheffer, 1998). According to our analyses, we suggest amending the third assumption as follows for the situation of subtropical lakes where perennial macrophytes are dominant: macrophytes disappear once turbidity exceeds a critical level K_f and recover at another critical level K_b, which is lower than K_f.

Mechanisms maintaining alternative stable states in subtropical shallow lakes

Reduction in algal turbidity by submersed macrophytes via non-nutrient means is considered to be one of the important ways to maintain the clear-water state. In northern temperate lakes, the TP–Chl *a* relationships in vegetation-present lakes have a gentle slope (Scheffer, 1998). In the Netherlands, both Chl *a* ($P = 0.002$) and $\log_{10}(\mathrm{Chl}\ a)/\log_{10}(\mathrm{TP})$ ($P < 0.001$) were significantly lower in vegetation-present lakes ($n = 9$) than in vegetation-absent lakes ($n = 6$) at a same TP range (TP = 60–160 mg m^{-3}) (reanalysed from Janse, 2004). No such marked effect was identified in Yangtze subtropical lakes, according to the not significantly different $\log_{10}(\mathrm{TP})-\log_{10}(\mathrm{Chl}\ a)$ regressions between lakes with and without vegetation (Fig. 2a) and the not significantly different Chl *a* ($P = 0.08$) and $\log_{10}(\mathrm{Chl}\ a)/\log_{10}(\mathrm{TP})$ ($P = 0.06$) between lakes with and without vegetation over the same TP range (TP = 50–120 mg m^{-3}).

In northern temperate lakes, macrophytes provide refuges for large zooplankton, such as *Daphnia*, protecting them from grazing by fish in the daytime and thereby inducing overexploitation of phytoplankton by zooplankton (Scheffer, 1998). Such an effect may be minor in Yangtze subtropical lakes according to the not significantly different biomass ratios of cladocerans to phytoplankton (0.29 ± 0.07 versus 0.27 ± 0.05) between vegetation-present ($n = 12$) and vegetation-absent ($n = 19$) lakes ($P = 0.88$) (reanalysed from literature data).

Reduction in nutrient availability is probably another means by which macrophytes suppress algal turbidity. Regarding the overall effects of macrophytes on TP, it is difficult to draw a consistent conclusion from the investigations undertaken in northern temperate lakes (Meijer *et al.*, 1994; Scheffer, 1998). The effects of submersed macrophytes on TP can be either positive or negative (Kufel & Ozimek, 1994; Scheffer, 1998; Madsen & Cedergreen, 2002). The positive effects include translocation of nutrients from sediments to water column and stimulation of sediment phosphorus release under anaerobic and high pH conditions. The negative effects include absorption of phosphorus from the water column and inhibition of sediment phosphorus release due to reduced resuspension and aerobic conditions with oxygen release from canopy and roots. According to our research, the effects of macrophytes on TP in Yangtze subtropical lakes seem to be more negative than positive. A significant negative correlation was found between $\log_{10}(B_{\mathrm{Mac}}+1)$ and $\log_{10}(\mathrm{TP})$ (Fig. 2d), while there was no significant relationship between vegetation coverage and TP in temperate lakes (Scheffer, 1998). The negative effects in Yangtze lakes are probably due to dominance of perennial plants which could retain nutrients in their tissues at most times.

Reduction in detritus and inorganic particles by submersed macrophytes is another important way to maintain the clear-water state (Van den Berg *et al.*, 1998; Scheffer, Portielje & Zambrano, 2003). In Yangtze lakes, such an effect could be detected from significantly lower $\log_{10}(\mathrm{Turb})/\log_{10}(10\ \mathrm{Chl}\ a)$ in vegetation-present lakes than in vegetation-absent lakes and a significant negative correlation between the ratio and $\log_{10}(B_{Mac}+1)$ (Fig. 2b) and also from significantly increased $\log_{10}$(-Turb)/$\log_{10}$(10 Chl *a*) after disappearance of vegetation in Shuimiao and Changlingtou (Fig. 4b,g).

Based on our analyses, we present a diagrammatic model to explain the mechanisms and processes of regime shifts in Yangtze subtropical shallow lakes (Fig. 5a). The model is based on three assumptions: (i) algal turbidity (Chl *a*) increases with TP and levels off when TP approaches a high level probably due to self-shading effects caused by excessive algae growth (Stauffer, 1991) (Fig. 5a_1); (ii) submersed macrophytes reduce non-algal turbidity (Fig. 5a_2); and (iii) macrophytes disappear when Turb exceeds a critical level K_f and recover when Turb is lower than K_b (Fig. 5a_3). Combining Fig. 5a_1,a_2 produces two curves as presented in Fig. 5a, showing separate TP–Turb relationships for the contrasting cases with and without vegetation; the curve is steeper for the vegetated state because non-algal turbidity decreases with the increase in macrophytes. When TP > TP_f and Turb > K_f (Fig. 5a_3), macrophytes disappear and the lake shifts to a turbid-water state dominated by phytoplankton (the upper equilibrium line) (Fig. 5a). When TP < TP_b and Turb < K_b (Fig. 5a_3), macrophytes recover and an opposite shift takes place (the lower equilibrium line) (Fig. 5a). In the shifting processes, TP varies because macrophytes reduce TP. When TP = TP_b–TP_f, two states exist: the lake tends to be in a clear-water state when Turb < K_b and in a turbid-water state when Turb > K_f; when Turb = K_b–K_f, the lake tends to be in a clear-water state when forward shifting and in a turbid-water state when backward shifting.

TP thresholds for the regime shifts in subtropical shallow lakes and effects of lake area and depth on the thresholds

In multi-lake comparisons, the TP thresholds were estimated to be *c*. 120 and 50 mg m^{-3} for the forward and backward shifts, respectively (Fig. 2d). According to the long-term monitoring, the TP threshold for the forward shift was estimated to be *c*. 120 mg m^{-3}; although macrophytes did not occur, the TP threshold should be lower than the minimum of *c*. 50 mg m^{-3}, the lowest level of TP after macrophyte disappearance (Fig. 4d,i). Through reconstruction of long-term (1786–2003) changes in a mid-Yangtze lake, Yang *et al.* (2006) estimated the TP threshold for shifting from macrophyte- to algae-dominated stage to be 70–110 mg m^{-3}. Combining the above results, TP thresholds in Yangtze subtropical shallow lakes are ascertained to be 70–120 mg m^{-3} for the forward shift and *c*. 50 mg m^{-3} for the backward shift.

Our multi-lake comparisons indicate that water depth affects turbidity thresholds, with lower thresholds in deeper lakes than in shallower lakes (Fig. 3d). This is in agreement with the prediction by Scheffer & van Nes (2007) that turbidity thresholds decrease with increasing water depth. However, TP thresholds for deeper and shallower lakes are almost equal (Fig. 3b), which contradicts the prediction that nutrient thresholds decrease with increasing water depth (Scheffer & van Nes, 2007; Janse *et al.*, 2008).

To explain the effects of water depth on TP thresholds, we present a diagrammatic model (Fig. 6) based upon two assumptions. First, turbidity thresholds decrease with increasing water depth (Fig. 3d) because, at a given turbidity, the light intensity in the layer where submersed macrophytes grow is lower in a deeper lake than in a shallower lake. Secondly, turbidity decreases with increasing water depth within a certain range of water depth. The negative relationship between turbidity and depth has been demonstrated by previous modelling and empirical work. (i) The area eroded by wave action decreases rapidly with increasing water depth, resulting in obvious decreases of suspended substances and TP (Kristensen, Søndergaard & Jeppesen, 1992; Scheffer, 1998); our results also showed a significant negative correlation between $\log_{10}$(Turb) and Z_M ($r = -0.51$, $P < 0.001$, $n = 76$). (ii) At high nutrient levels, algal turbidity also decreases with increasing water depth, because light is the only limiting factor and the density of phytoplankton can decrease in such a way that the light reaching bottom remains the same (Scheffer, 1998; Phillips *et al.*, 2008). However, once water depth is beyond the upper and lower limits, turbidity should not be affected by water depth for two reasons. (i) Resuspension ceases when water depth exceeds one half of wavelength of wind-driven wave (Carper & Bachmann, 1984), and its intensity should reach a maximum when shallower than a depth (Scheffer, 1998). (ii) Phytoplankton abundance declines rather slowly with depth when the water column is very deep, and it is not affected when the water column is very shallow due to no light limitation (Scheffer, 1998).

According to our model (Fig. 6), at moderate water depths, both turbidity thresholds and turbidity decrease with increasing water depth, and the two effects almost balance. Therefore, the TP thresholds vary slightly. In this study, water depths did not vary widely; hence, TP thresholds were nearly equal. If water depth exceeds the lower limit, the turbidity thresholds decrease with increasing depth, whereas turbidity ceases to decrease, thus resulting in an apparent decrease in the TP thresh-

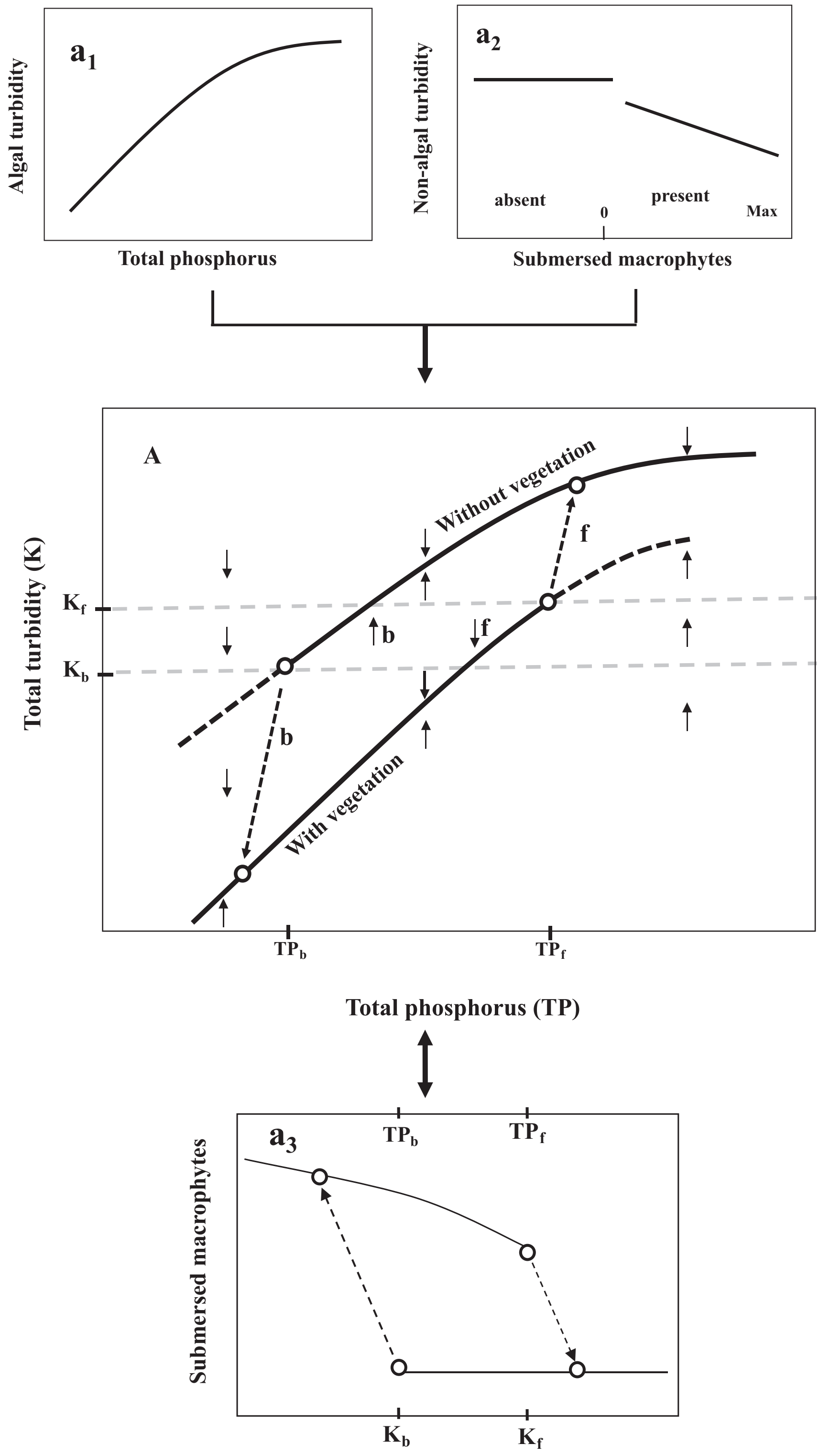

Fig. 5 Schematic diagram interpreting the triggering of regime shifts and maintenance of alternative stable states in subtropical shallow lakes. f, Forward shifts from a clear-water state to a turbid-water state; b, backward shifts from turbid-water state to a clear-water state.

olds. If depth exceeds the upper limit, the turbidity thresholds increase, whereas turbidity ceases to increase, thus resulting in an apparent increase in the TP thresholds. When depths are very shallow, the turbidity thresholds reach or surpass the curved section with a gentle (and flat) slope, and the TP thresholds increase sharply, even to such a high level that forward shifting cannot occur. In European lakes shallower than 1 m, the macrophyte-dominated clear-water state stabilised even when TP reached 700–2500 mg m^{-3} (Carvalho, 1994;

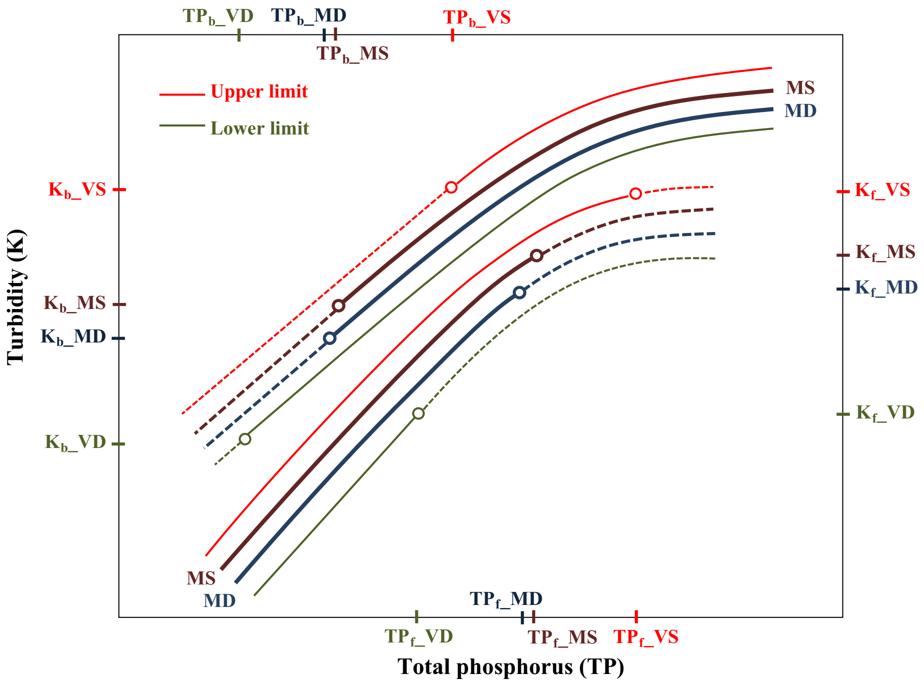

Fig. 6 Schematic diagram depicting the effects of water depth on the critical thresholds for regime shifts in shallow lakes. f, Forward shifts from a clear-water state to a turbid-water state; b, backward shifts from a turbid-water state to a clear-water state. VS, very shallow; MS, moderately shallow; MD, moderately deep; VD, very deep.

Perrow, Moss & Stansfield, 1994), agreeing well with the prediction of our model.

To quantify the upper and lower limits of water depth in Fig. 6, systematic surveys of lakes with different depths will be needed. For the time being, we make a preliminary analysis as follows. A worldwide synthesis of lake data (Middelboe & Markager, 1997) showed that when Z_{SD} was lower than 1 m, Z_C (maximum colonisation depth) of charophytes and caulescent angiosperms was generally lower than 1–1.5 m independent of Z_{SD}. This indicates that the plants can avoid light limitation when water depth is lower than 1–1.5 m. According to data compiled by Kosten *et al.* (2009), for lakes with a median depth of 1.1–1.5 m, submersed macrophytes still predominated in some lake-years even when TP > 100 mg m^{-3}; for lakes of 1.9–3 m, macrophytes almost never predominated when TP > 100 mg m^{-3}; for lakes of 3.5 m, macrophytes did not predominate when TP > 32 mg m^{-3}. Table 2 also shows that there is no obvious difference in TP thresholds among lakes with depths between 1.2 and 3.6 m from various climatic zones. In summary, the upper limit of depth in Fig. 6 could be between 1 and 2 m, and the lower limit seems to be between 3 and 4 m.

Our multi-lake comparisons did not show any difference in TP thresholds between larger and smaller lakes (Fig. 3a). Although a difference in turbidity thresholds was shown between larger and smaller lakes (Fig. 3c), it should be attributed to effects of water depth rather than those of lake area. In larger lakes, the two dots representing the turbidity threshold for the forward shift were shallower (0.6, 1.5 m), while the two dots for the backward shift were much deeper (2.9, 3.5 m), thus leading to the divergence of the two thresholds in opposite directions (Fig. 3d). Therefore, we found no marked effects of lake area (0.5–355 km^2) on the thresholds of turbidity and TP in our study. Table 2 also shows no difference in the TP thresholds among northern temperate lakes with various sizes (0.1–30.5 km^2). The main reason should be the minor effect of area on turbidity: we found no significant correlation in our lakes between log$_{10}$(Turb) and log$_{10}$(Area) (r = –0.09, P = 0.55, n = 48); according to the model by Scheffer (1998), the increasing rate of resuspension with area is much lower than the decreasing rate of resuspension with water depth. Larger lakes are generally deeper (Lewis, 2011), so effects of area and depth may balance; larger lakes should have a larger area of hard bottom, reducing the effect of greater resuspension by wind. Assuming higher settling and lower resuspension rates in smaller lakes, the model of Janse *et al.* (2008) suggested that the thresholds of phosphorus loading for regime shifts should decrease with increasing fetch, but such a prediction evidently does not hold for lakes with area of 0.1–355 km^2.

In the northern temperate zone, mini lakes with area <0.05 km^2 (0.7–1.5 m in depth) were found to be in the clear-water state when TP was 650–2500 mg m^{-3} (Jeppesen *et al.*, 1990; Van Donk *et al.*, 1990; Carvalho, 1994; Perrow *et al.*, 1994). Such a 'mini-lake phenomenon' may be attributed to various reasons (Jeppesen *et al.*, 1990),

Table 2 Total phosphorus (TP) thresholds for regime shifts in shallow lakes

TP thresholds (mg m^{-3})					
Forward	Backward	Lakes [area, mean water depth: median (min-max)]	Location	Methods	Sources
125	50	Lakes, number unknown (>0.03 km^2, <3 m)	Temperate, Denmark (54°–57°N)	Multi-lake	Jeppesen *et al.* (1990)
50–100*		Lake Væng (0.15 km^2, 1.2 m) and 14 additional experiments	Temperate, Denmark (54°–57°N)	Multi-year (1978–1995) and multi-lake	Jeppesen *et al.* (1999)
100	40–60	Lake Veluwe (30.5 km^2, 1.5 m)	Temperate, the Netherlands (52°N)	Multi-year (1965–2002)	Ibelings *et al.* (2007)
120	50	50 lake-years (10 (0.5–355) km^2, 2.0 (0.6–3.6) m)	Subtropical, China (28°–32°N)	Multi-lake	This study
120	<50	2 sub-areas of Lake Bao'an (1.6 km^2, 2.3 m; 1.5 km^2, 1.9 m)	Subtropical, China (30°N)	Multi-year (1987–2012)	This study
70–110		Lake Taibaihu (25.1 km^2, 3.2 m)	Subtropical, China (29°N)	Sediment fossil diatom-TP transfer function (1796–2003)	Yang *et al.* (2006)
100†		434 lake-years (0.7 (0.01–198) km^2, 2.7 (0.4–9.9) m)	Subtropical, Florida (24°–30°N)	Multi-lake	Bachmann *et al.* (2002)
100‡		64 lake-years (0.45 (0.09–2.43) km^2, 1.9 (0.8–4.5) m)	(Sub) Tropical, Brazil-Uruguay (5°–25°S)	Multi-lake	Kosten *et al.* (2009)

*Below which, fish manipulation had a long-term effect.

†Below which, submersed macrophytes were present in 360/433 lake-years; above: in only 7/24 lake-years.

‡Below which, submersed macrophytes dominated (coverage > 30%) in 13/42 lake-years: above: in only 2/22 lake-year.

among which frequent fish-kills and shallow water depth seem to be most important (Van Geest *et al.*, 2003; Scheffer & van Nes, 2007). According to data from 796 Danish lakes, many lakes with area <0.1 km^2 and around 1 m in depth were fishless or had lower species richness and biomass of fish, and macrophyte coverage was correspondingly much higher in smaller lakes despite a generally higher TP level (Søndergaard, Jeppesen & Jensen, 2005). Combining this phenomenon with our research, it could be concluded that with the exception of very small lakes or lakes with strong wind-driven sediment resuspension, area does not substantially affect TP thresholds for regime shifts.

Comparisons of TP thresholds among lakes from different climatic zones

In temperate lakes, TP thresholds for the forward and backward shifts were estimated to be 100 and 40–60 mg m^{-3}, respectively (Jeppesen *et al.*, 1990; Jeppesen, Søndergaard & Kronvang, 1999; Ibelings *et al.*, 2007) (Table 2). In subtropical to tropical lakes, submersed macrophytes were found to be distributed mainly in areas with TP < 100 mg m^{-3} (Bachmann *et al.*, 2002; Kosten *et al.*, 2009) (Table 2). These thresholds are in agreement with our results. Therefore, except for very small lakes, at moderate water depths, TP thresholds for the forward and backward regime shifts in shallow lakes located in temperate to subtropical (probably to tropical) zones are generally 80–120 and 40–60 mg m^{-3}, respectively, which implies that there is no noticeable effect of climate on TP thresholds for regime shifts. This does not contradict the prediction by Genkai-Kato & Carpenter (2005) that the thresholds of phosphorus loading for regime shifts decreased with increasing temperature, as their prediction was based on an assumption that internal P recycling increased with warmer climate.

The mechanisms underlying the subequality of TP thresholds among different climatic zones are inferred as follows. (i) $\log_{10}(\text{TP})-\log_{10}(\text{Chl } a)$ relationships do not differ markedly among shallow lakes at least from temperate to subtropical zones, with the regression equation as $\log_{10}(\text{Chl } a) = 0.89\ (0.73\text{–}1.05)\ \log_{10}(\text{TP}) - 0.38(-0.15 \text{ to } 0.97)$ (Canfield, 1983; Nürnberg, 1996; Brown *et al.*, 2000; Flanagan *et al.*, 2003; Huszar *et al.*, 2006; Wang *et al.*, 2008). (ii) The reduction in non-algal turbidity by submersed macrophytes through resuspension prevention can be regarded as a general rule in shallow lakes. (iii) The shade tolerance of submersed macrophytes in the process of regime shifts differs little between lower and higher latitudes (Duarte & Kalff, 1987; Middelboe & Markager, 1997; Kosten *et al.*, 2011). (iv) Within a certain range, the positive and negative effects of water depth on TP thresholds for regime shifts can balance, and the effects of lake area are minor. (v) Combining the above four points, a plausible explanation can be drawn from the diagrammatic model of mechanisms depicted in Fig. 6.

Our conclusions hold practical importance. According to the inequality of TP thresholds, we suggest that similar target concentrations for in-lake TP can be set to mitigate eutrophication for most shallow lakes in the world.

Acknowledgments

The project is supported by National Natural Science Foundation of China (30900194), 973 Programs (2008CB418006 and 2002CB412309), Chinese Academy of Sciences (KZCX1-SW-12) and State Key Laboratory of Freshwater Ecology and Biotechnology (2011FBZ14). We thank Jian-Kang Liu (Institute of Hydrobiology, Chinese Academy of Sciences), John Melack (University of California, Santa Barbara, USA) and Martin Søndergaard (Aarhus University, Denmark) for their inspired comments on the manuscript and Anne Mette Poulsen (Aarhus University, Denmark) and Mark J. Wetzel (Illinois Natural History Survey, USA) for their assistance in English correction. We also thank Bao-Zhu Pan, Ping-Hong Jiang, Zong-Xing Wang, Ai-Ping Wu and Song-Bo Wang for their help with fieldwork.

References

Bachmann R.W., Horsburgh C.A., Hoyer M.A., Mataraza L.K. & Canfield D.E. Jr (2002) Relations between trophic state indicators and plant biomass in Florida lakes. *Hydrobiologia*, **470**, 219–234.

Brown C.D., Hoyer M.V., Bachmann R.W. & Canfield D.E. Jr (2000) Nutrient-chlorophyll relationships: an evaluation empirical nutrient-chlorophyll models using Florida and north-temperate lake data. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1574–1583.

Canfield D.E. Jr (1983) Prediction of chlorophyll *a* concentrations in Florida lakes: the importance of phosphorus and nitrogen. *Water Resources Bulletin*, **19**, 255–262.

Carper G. & Bachmann R.W. (1984) Wind resuspension of sediments in a Prairie Lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1763–1767.

Carvalho L. (1994) Top-down control of phytoplankton in a shallow hypertrophic lake Little Mere (England). *Hydrobiologia*, **276**, 53–63.

Cui Y.B. & Li Z.J., eds (2005) *Fishery Resources and Conservation of Environment in Lakes of the Changjiang River Basin*. Science Press, Beijing, China (in Chinese with English abstracts).

Duarte C.M. & Kalff J. (1987) Latitudinal influences on the depths of maximum colonization and maximum biomass of submerged angiosperms in Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 1759–1764.

Flanagan K.M., McCauley E., Wrona F. & Prowse T. (2003) Climate change: the potential for latitudinal effects on algal biomass in aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 635–639.

Genkai-Kato M. & Carpenter S.R. (2005) Eutrophication due to phosphorus recycling in relation to lake morphology, temperature and macrophytes. *Ecology*, **86**, 210–219.

Hu C.L. & Huang X.F., eds (1991) *Collected Papers on the Fishery Ecology and Exploitation Technology of the Bao'an Lake*. Science Press, Beijing (in Chinese).

Huang X.F., Chen W.M. & Cai Q.M. (1999) *Standard Methods for Observation and Analysis in Chinese Ecosystem Research Network-Survey, Observation and Analysis of Lake Ecology*. Standards Press of China, Beijing, China (in Chinese).

Huszar V.L.M., Caraco N.F., Roland F. & Cole J. (2006) Nutrient-chlorophyll relationships in tropical-subtropical lakes: do temperate models fit? *Biogeochemistry*, **79**, 239–250.

Ibelings B.W., Portielje R., Lammens E.H.R.R., Noordhuis R., Van den Berg M.S., Joosse W. *et al.* (2007) Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. *Ecosystems*, **10**, 4–16.

Janse J.H. (2004) *Model Studies on the Eutrophication of Shallow Lakes and Ditches*. PhD Thesis, Wageningen University, Wageningen, the Netherlands.

Janse J.H., Domis L.N.D.S., Scheffer M., Lijklema L., Van Liere L., Klinge M. *et al.* (2008) Critical phosphorus loading of different types of shallow lakes and the consequences for management estimated with the ecosystem model PCLake. *Limnologica*, **38**, 203–219.

Jeppesen E., Jensen J.P., Kristensen P., Søndergaard M., Mortensen E., Sortkjær O. *et al.* (1990) Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. *Hydrobiologia*, **200/201**, 219–227.

Jeppesen E., Søndergaard M. & Kronvang B. (1999) Lake and catchment management in Denmark. *Hydrobiologia*, **395/396**, 419–432.

Kosten S., Jeppesen E., Huszar V.M., Mazzeo N., van Nes E.H., Peeters E.T.H.M. *et al.* (2011) Ambiguous climate impacts on competition between submerged macrophytes and phytoplankton in shallow lakes. *Freshwater Biology*, **56**, 1540–1553.

Kosten S., Kamarainen A., Jeppesen E., van Nes E.H., Peeters E.T.H.M., Mazzeo N. *et al.* (2009) Climate-related differences in the dominance of submerged macrophytes in shallow lakes. *Global Change Biology*, **15**, 2503–2517.

Kristensen P., Søndergaard M. & Jeppesen E. (1992) Resuspension in a shallow eutrophic lake. *Hydrobiologia*, **228**, 101–109.

Kufel L. & Ozimek T. (1994) Can *Chara* control phosphorus cycling in Lake Luknajno (Poland)? *Hydrobiologia*, **275/276**, 277–283.

Lewis W.M. Jr (2011) Global primary production of lakes: 19th Baldi Memorial Lecture. *Inland Waters*, **1**, 1–28.

Liang Y.L. & Liu H.Q., eds (1995) *Resources, Environment and Fishery Ecological Management of Macrophytic Lakes*. Science Press, Beijing, China (in Chinese with English abstracts).

Liu J.K. (1990) *Ecology of East Lake (I)*. Science Press, Beijing, China (in Chinese).

Madsen T.V. & Cedergreen N. (2002) Sources of nutrients to rooted submerged macrophytes growing in a nutrient-rich stream. *Freshwater Biology*, **47**, 283–291.

Meijer M.L., Jeppesen E., van Donk E., Moss B. & Scheffer M. (1994) Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark. *Hydrobiologia*, **275/276**, 457–466.

Middelboe A.L. & Markager S. (1997) Depth limits and minimum light requirements of freshwater macrophytes. *Freshwater Biology*, **37**, 553–568.

Mooij W.M. & Janse J.H. (2007) Predicting the effect of climate change on temperate shallow lakes with the ecosystem model PC Lake. *Hydrobiologia*, **584**, 443–454.

Nürnberg G.K. (1996) Trophic state of clear and colored, soft- and hard-water lakes with special consideration of nutrients, anoxia, phytoplankton and fish. *Lake Reservation and Management*, **12**, 432–447.

Perrow M.R., Moss B. & Stansfield J. (1994) Trophic interactions in a shallow lake following a reduction in nutrient loading: a long-term study. *Hydrobiologia*, **275/276**, 43–52.

Phillips G., Pietiläinen O.P., Carvalho L., Solimini A., Solheim A.L. & Cardoso A.C. (2008) Chlorophyll-nutrient relationships of different lake types using a large European dataset. *Aquatic Ecology*, **42**, 213–226.

Scheffer M. (1998) *Ecology of Shallow Lakes*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Scheffer M. (2001) Alternative attractors of shallow lakes. *The Scientific World Journal*, **1**, 254–263.

Scheffer M. & Carpenter S.R. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution*, **18**, 648–656.

Scheffer M., Hosper S.H., Meijer M.L. & Moss B. (1993) Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution*, **8**, 275–279.

Scheffer M., Portielje R. & Zambrano L. (2003) Fish facilitate wave resuspension of sediment. *Limnology and Oceanography*, **48**, 1920–1926.

Scheffer M. & van Nes E.H. (2007) Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia*, **584**, 455–466.

Søndergaard M., Jeppesen E. & Jensen J.P. (2005) Pond or lake: does it make any difference? *Archive fur Hydrobiologia*, **162**, 143–165.

Stauffer R.E. (1991) Environmental factors influencing chlorophyll v. nutrient relationships in lakes. *Freshwater Biology*, **25**, 279–295.

Van den Berg M.S., Coops H., Meijer M.L., Scheffer M. & Simons J. (1998) Clear water associated with a dense *Chara* vegetation in the shallow and turbid Lake Veluwemeer, the Netherlands. In: *Structuring Role of Submerged Macrophytes in Lakes* (Eds E. Jeppesen, M.A. Søndergaard, M.O. Søndergaard & K. Kristoffersen), pp. 339–352. Springer-Verlag, New York.

Van Donk E., Grimm M.P., Gulati R.D. & Klein Breteler J.G.P. (1990) Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. *Hydrobiologia*, **200/201**, 275–290.

Van Geest G.J., Roozen F.C.J.M., Coops H., Roijackers R.M.M., Buijse A.D., Peeters E.T.H.M. *et al.* (2003) Vegetation abundance in lowland flood plan lakes determined by surface area, age and connectivity. *Freshwater Biology*, **48**, 440–454.

Wang H.J., Liang X.M., Jiang P.H., Wang J., Wu S.K. & Wang H.Z. (2008) TN: TP ratio and planktivorous fish do not affect nutrient-chlorophyll relationships in shallow lakes. *Freshwater Biology*, **53**, 935–944.

Xiong J.L. (2005) *Community Diversity of Plankton and Zoobenthos in Lakes of Different Nutrient Levels*. PhD thesis, Huazhong Agriculture University, Wuhan, China.

Yang X.D., Shen J., Dong X.H., Liu E.F. & Wang S.M. (2006) Historical trophic evolutions and their ecological responses from shallow lakes in the middle and lower reaches of the Yangtze River: case studies on Longgan Lake and Taibai Lake. *Science in China Series D*, **49**(Suppl 1), 51–61.

Yang Y.F. & Huang X.F. (1994) Structure of zooplankton community in Donghu Lake of China. *Chinese Journal of Appllied Ecology*, **5**, 319–324 (in Chinese with an English abstract).

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Basic characteristics of biological assemblages of lakes for multi-lake comparisons.

Appendix S2. Description of two subareas (Shuimiao and Changlingtou) of Lake Bao'an.

(Manuscript accepted 10 March 2014)