

Do alternative stable states exist in large shallow Taihu Lake, China?*

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Abstract Regime shifts from submersed macrophyte dominance to phytoplankton dominance have been widely reported in small- to medium-sized shallow lakes. However, alternative stable states in large shallow lakes (surface area >500 km²) remain unconfirmed. To understand the alternative stable states and the main influencing factors of submersed macrophytes in large lakes, the ecosystem states from monitoring data from 1959 to 2019 in large shallow Taihu Lake (2 338 km² in average depth of 2.12 m) in China were examined. Changes in submersed macrophyte coverage (C_{Mac}) and phytoplankton chlorophyll *a* (Chl *a*) in the time series and their relationships with environmental factors were analyzed. During the field investigation from August 2018 to May 2019, nutrients and Chl *a* showed obvious heterogeneity across the lake, being generally higher in the western and northern areas and lower in the southeast area, while C_{Mac} was only observed in the eastern areas, e.g., East Taihu Lake, Xukou Bay, and Gonghu Bay. During the long-term monitoring from 1959 to 2019 in the Central Region, Meiliang Bay, and East Taihu Lake, Chl *a* increased significantly in the time series. C_{Mac} varied slightly among different subareas, always at low levels (<10%) in the Central Region and Meiliang Bay but at relatively high levels in East Taihu Lake (10%–90%). Frequency distributions of response variables had no multimodality except for C_{Mac} in East Taihu Lake, with two peaks between 15% and 20% and between 55% and 60%. A dual relationship was found between Chl *a* and total phosphorus (TP) in the areas with and without macrophytes, while C_{Mac} showed no relationship with TP, and submersed macrophytes did not flourish in the Central Region and Meiliang Bay even when TP was at very low levels (≈ 10 mg/m³). Taihu Lake had similar algal turbidity (Turb_{Alg}) as small- to medium-sized lakes but generally presented with higher values of nonalgal turbidity ($\text{Turb}_{\text{NonAlg}}$), as did their contribution to total turbidity as a percentage. This study suggested that large shallow Taihu Lake may have no alternative stable states, but more evidence is needed for East Taihu Lake, which was dominated by macrophytes, as it remains unknown whether hysteresis occurs between the processes of eutrophication and oligotrophication. Unfavorable conditions caused by wind might be the main reason due to the absence of submersed macrophytes in Taihu Lake. These results demonstrate that stricter nutrient control is needed to maintain a healthy state or to recover from a decayed state for large lakes.

Keyword: alternative stable state; submersed macrophyte; phytoplankton; Taihu Lake; large shallow lake

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1 INTRODUCTION

Submersed macrophytes play an important role in maintaining a clear-water state (Jeppesen et al., 1998; Scheffer, 1998). Loss of submersed macrophytes and algal blooms in shallow lakes have occurred worldwide, mainly due to eutrophication (Scheffer, 1998; Wang et al., 2014; Jeppesen et al., 2020). The transition between macrophyte dominance and phytoplankton dominance is often nonlinear (Scheffer, 1998; Scheffer and Carpenter, 2003). The existence of alternative stable states has been widely reported in shallow lakes (e. g., Scheffer, 2001; Ibelings et al., 2007; Wang et al., 2014). Phosphorus loading is generally regarded as the driving variable for regime shifts between these two contrasting states in shallow lakes (Scheffer and Carpenter, 2003). Total phosphorus concentration (TP) thresholds for the forwards and backwards regime shifts in shallow lakes are generally 80–120 and 40–60 mg/m³, respectively (Jeppesen et al., 1990; Bachmann et al., 2002; Ibelings et al., 2007; Kosten et al., 2009; Wang et al., 2014). Previous studies on regime shifts have mainly focused on small- to medium-sized shallow lakes with a total area smaller than 500 km² (Wang and Dou, 1998; Wang et al., 2014). The existence of alternative stable states has not yet been verified in large lakes (>500 km²), although they have also experienced severe eutrophication and loss of macrophytes (Rosenmeier et al., 2004; Wu et al., 2007; Kong et al., 2015; Salmaso et al., 2018).

Regime shifts between the two contrasting states in shallow lakes were often delayed, resulting in feedback mechanisms. A lake would probably be in a clear state with rich submersed macrophytes initially. Increased nutrient loading may lead to the large disappearance of submersed macrophytes if a critical threshold is passed. Restoration of clear water occurs at substantially lower nutrient levels than those at which the collapse of the macrophytes occurred. Macrophytes could increase water clarity in several ways, such as reducing nutrient concentrations in the water column and preventing sediment resuspension, thereby enhancing their own growing conditions. This causes the clear state to be a self-stabilizing alternative to the turbid situation. In contrast, turbid water is also a self-stabilizing state. For example, internal nutrient loading is one of the most important reasons leading to the delay of restoration from eutrophication. In real ecosystems,

it is not easy to demonstrate the existence of alternative states. Scheffer and Carpenter (2003) once suggested three hints for field investigation: (1) sudden jumps of response variables in time series; (2) multimodality of the frequency distribution of states; and (3) dual relationship of response variables with control factors.

Regime shifts typically refer to the entire ecosystem change in small- to medium-sized lakes (Scheffer, 1990). However, submersed macrophytes could hardly dominate the whole ecosystem in large shallow lakes due to the long fetch, strong wave action, and strong sediment resuspension (Carpenter and Bachmann, 1984; Scheffer, 1998; van Geest et al., 2003; Cai et al., 2012; Janssen et al., 2014). Excess nutrient loading and consequently low underwater light availability are generally considered the underlying causes of submersed macrophyte recession in small- to medium-sized shallow lakes (Yu et al., 2015). Macrophytes usually fail to survive or reestablish at water depths where light is <1% of the surface value (Scheffer, 1998). In addition, graze pressure from herbivorous fishes and disturbance from omnivorous fish (such as cyprinid) could also damage the growth and reproduction of submersed macrophytes (van Donk et al., 1994; Lodge et al., 1998; Matsuzaki et al., 2009). However, submersed macrophytes in large shallow lakes face more adverse factors. Where fetches are >20 km, the effects of lake size on sediment resuspension become considerable (Cai et al., 2012). van Geest et al. (2003) suggested that the larger the surface area of a lake is, the lower the probability of maintaining submersed macrophyte dominance. Therefore, it is unlikely that unequivocal evidence indicates that alternative stable states occur in large shallow lakes. However, Janssen et al. (2014) pointed out that spatial heterogeneity plays a role in alternative stable states based both on their review of the eutrophication history of Taihu Lake and on modelling of large lakes. Therefore, the classical definition of alternative stable states may be somewhat constrained with regard to large lakes, which may undergo regime shifts in specific regions, although not in the whole lake simultaneously.

Taihu Lake is the third-largest freshwater shallow lake in China. The lake has a surface area of 2 338 km² in average depth of 1.9 m (Shen et al., 2011). Excessive nutrient inflow has led to massive proliferation of cyanobacteria along the western

shore and in northern bays. Macrophytes have gradually disappeared in these areas since the late 1980s, while the macrophyte coverage in the eastern part of the lake, where the nutrient concentrations were normally relatively low, changed little (Li et al., 2011b). This mosaic pattern among two different primary producers provided an excellent case for studying alternative stable states and regime shifts in a large, shallow lake (Zhao et al., 2017). In this study, a long-term field investigation was used to demonstrate the existence of alternative stable states, which involved a year-around field investigation from August 2018 to May 2019 and long-term monitoring data from 1960 to 2017 in Taihu Lake. The results were compared with those in thirty small- to medium-sized lakes located in the middle and lower Changjiang (Yangtze) River Basin to show the difference in lakes of different sizes. The purposes of this study were (1) to investigate the existence of alternative stable states in large shallow lakes using Taihu Lake as a case study and (2) to analyse the main controlling factors of submerged macrophytes in Taihu Lake.

2 MATERIAL AND METHOD

2.1 Study site

2.1.1 Taihu Lake

Taihu Lake is located in the Changjiang River

floodplain (119°52'32"E–120°36'10"E, 30°55'40"N–31°32'58"N). The lake was divided into six subareas for the field investigations: Zhushan Bay, Meiliang Bay, Gonghu Bay, Xukou Bay, Central Region, and East Taihu Lake (Fig.1). Field investigations were conducted seasonally from August 2018 through May 2019. Forty-five sites were sampled, ranging from 3 to 19 sites within each subarea (Fig.1). Submersed macrophytes were mainly distributed in East Taihu Lake (also in Xukou Bay), and the coverage and biomass varied spatially. Therefore, more samples were collected to evaluate the characteristics of the macrophyte community in this subarea. The long-term historical data (1959–2018) were collected from the published literature (Supplementary Table S1). Most of the samples were collected monthly or seasonally, and the sample sites ranged 2–10 in a specific subarea.

2.1.2 Small- to medium-sized shallow lakes along Changjiang River

Thirty small- to medium-sized shallow lakes (113°10'E–121°00'E, 29°30'N–32°00'N) located in the mid-lower Changjiang River Basin were investigated from 2002 to 2012. Thirty-four lakes were dominated by submerged macrophytes and twenty-nine lakes were dominated by phytoplankton. The limnological characteristics are shown in Table 1. Three to twelve sample sites were set in each lake, depending on lake

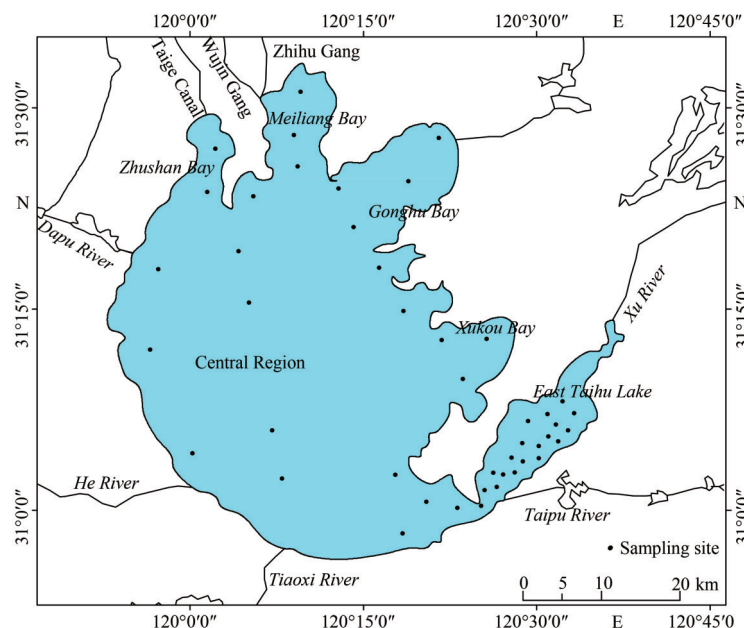


Fig.1 Location of the sampling sites in the six subareas of Taihu Lake during the field investigation from August 2018 through May 2019

Table 1 Statistical characteristics of the basic limnological parameters of the small- to medium-sized Changjiang River shallow lakes

Parameter	<i>n</i>	Mean (min.–max.)	SD
Surface area (km ²)	30	35.6 (0.5–355)	76.3
<i>Z_M</i> (m)	76	2.11 (0.63–4.24)	0.66
<i>Z_{SD}</i> (m)	76	1.14 (0.29–3.26)	0.69
TP (mg/m ³)	76	107 (5–970)	179
Chl <i>a</i> (mg/m ³)	76	23.2 (0.6–139)	31.2
<i>B_{Mac}</i> (g/m ²)	76	1 648 (0–13 150)	2 791

Z_M: mean water depth; *Z_{SD}*: Secchi depth; TP: total phosphorus concentration; Chl *a*: phytoplankton chlorophyll-*a* concentration; *B_{Mac}*: submerged macrophyte biomass; SD: standard deviation.

size. Detailed information about the distribution of the sites can be found in Wang et al. (2014).

2.2 Field sampling

In the field investigation in Taihu Lake and the small- to medium-sized shallow lakes, submersed macrophytes were sampled using a Scythe-type sampler (sampling area of 0.2 m², 1–3 replicates at each location). Water samples were taken at 0.5 m below the water surface and at half of the site depth. The pooled samples from the above two depths were stored in polyethylene bottles for chemical analysis at 4 °C.

2.3 Sample analysis

The fresh weight of submerged macrophytes at each sample site was measured with an electronic scale after removing the extraneous materials (such as sticks, macroinvertebrates, and sand). *C_{Mac}* was evaluated by remote underwater video. Phytoplankton chlorophyll *a* (Chl *a*) was determined by spectrophotometry within 2 d. First, the sample was extracted in 90% acetone (at 4 °C for 20–24 h) after filtration through GF/C filters (Whatman, GE Healthcare UK Limited, Buckinghamshire, UK), and the absorbance was then measured at two wavelengths of 665 nm and 750 nm, both before and after acidification using 10% HCl (Huang et al., 2000). An alkaline potassium persulfate digestion-UV spectrophotometric method was used to determine TN (total nitrogen) (PERSEE, TU-1810, Beijing, China), and TP was determined using an ammonium molybdate-UV spectrophotometric method (Huang et al., 2000). Both TN and TP were measured within 5–7 d after the samples were collected.

Water temperature (WT), dissolved oxygen

(DO), conductivity (Cond), total dissolved solids (TDS), salinity, and oxidation-reduction potential (ORP) were measured in situ using a YSI ProPlus (Yellow Springs Instruments Inc., USA). Water depth (*Z_M*) and Secchi depth (*Z_{SD}*) were measured with a sounding line and a Secchi disc, respectively.

For long-term monitoring during 1959–2018, surface (≤0.5 m) or integrated water samples were collected, and TN, TP, Chl *a*, and *Z_{SD}* were determined by methods similar to our field investigation. *C_{Mac}* was evaluated by a remote underwater video device or remote sensing and image interpretation. To avoid potential errors, those significantly different from the values of the previous and the next years were deleted.

Total turbidity (Turb_{Tot}) was estimated as the reciprocal of *Z_{SD}* (Portielje and van der Molen, 1999). Algal turbidity (Turb_{Alg}) and nonalgal turbidity (Turb_{NonAlg}) were calculated according to Wang et al. (2017) and Portielje and van der Molen (1999). Turb_{Alg} was calculated as 0.011×Chl *a*. Turb_{NonAlg} was calculated as follows:

$$\text{Turb}_{\text{NonAlg}} = 1/Z_{\text{SD}} - 0.18 - 0.011 \times \text{Chl } a.$$

2.4 Statistical analyses

In this study, TN, TP, and Turb were independent variables, while Chl *a*, *C_{Mac}*, and *B_{Mac}* were dependent, state or response variables. The sequential regime shift detection (SRS) method was used to test the variation in response variables in time series from 1959 to 2019 (Rodionov, 2004). The method was based on the sequential application of Student's *t*-test. If a newly arriving observation at time *t* is higher or lower than the critical level of the current mean value, time *t* would be marked as a potential changing point. A “running window” was used to check the time series data until all the data were processed. The regime shift index (RSI) represents a cumulative sum of normalized anomalies relative to the critical level:

$$\text{RSI} = \sum_{i=t_{\text{cur}}}^m \frac{(x_i - \bar{x}_{\text{crit}})}{L\bar{S}_L},$$

$$m = t_{\text{cur}}, t_{\text{cur}} + 1, \dots, t_{\text{cur}} + L - 1,$$

where *t_{cur}* is the current time, *L* is the cut-off length of the regimes to be tested and was set as 5 in this study, \bar{S}_L is the average standard deviation for *L*-year intervals in the time series, and *x_{crit}* is the critical level of the average value of the current regime.

SRS is written in Visual Basic for Application (Excel) (<https://sites.google.com/view/regime-shift>

test/downloads).

The spatial distributions of TN, TP, Chl *a*, and C_{Mac} for Taihu Lake were produced in ArcGIS using the Kriging interpolation. The correlations between the environmental variables were plotted using linear least squares regression analysis (R 3.4.0 and Microsoft Excel 2016).

3 RESULT

3.1 A year-around field investigation of Taihu Lake

The values of environmental variables in Taihu Lake from the sampling between August 2018 and May 2019 are shown in Supplementary Table S2. The spatial distributions of TN, TP, Chl *a*, and C_{Mac} showed obvious heterogeneity across the lake (Fig.2). Higher levels of TN (5 068.4 mg/m³) and TP (334.0 mg/m³) were recorded in the western and

northern sections of the lake as well as in the southern region. The distribution of Chl *a* had a similar pattern in spring, summer, and autumn. Higher levels were recorded in the northern section, while Chl *a* was higher in the southern section in winter. C_{Mac} was generally high in the eastern area from spring to autumn and high in the southeastern area during winter.

3.2 Long-term monitoring of Taihu Lake

The Chl-*a* concentration in Taihu Lake was very low before the 1980s and was lower than 10 mg/m³ in all subareas in 1959 (Fig.3). It began to increase in the 1980s in the Central Region and Meiliang Bay and increased to a considerable high level since the 2010s, especially in the Meiliang Bay (Fig.3a & c). In contrast, the East Taihu Lake had much lower Chl *a*, which stayed at relatively low levels until 2008, and the annual mean values were lower than 10 mg/m³. The mean value of Chl *a* in East Taihu

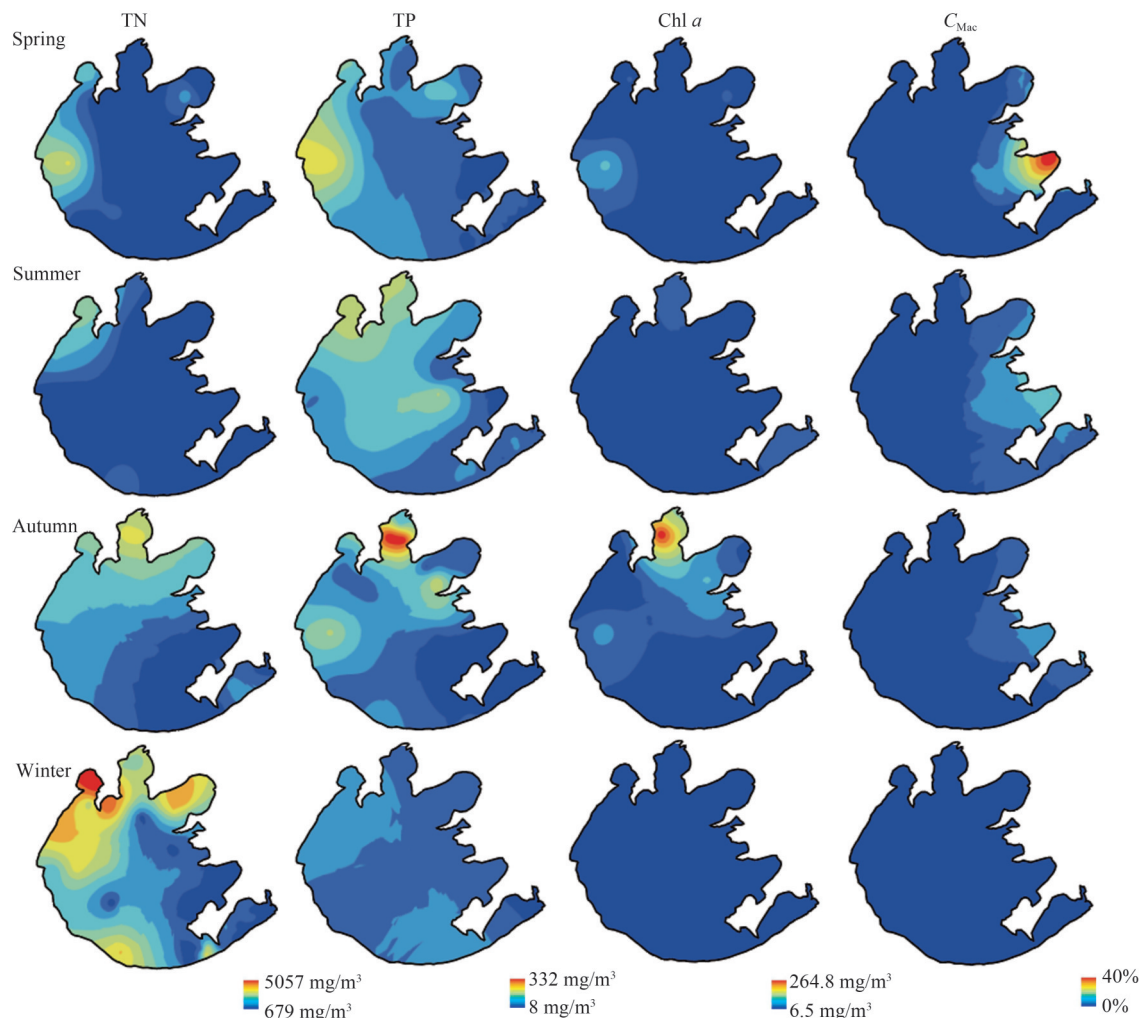


Fig.2 Spatial distribution of the environmental variables in Taihu Lake (August 2018–May 2019)

Lake during 2008–2019 was approximately 2 times greater than that during 1980s–1990s.

Unlike that of phytoplankton, the distribution of submersed macrophytes varied greatly among different subareas. The Central Region and Meiliang Bay had few macrophytes even under very low nutrient conditions before the 1980s (Fig.3b & d). East Taihu Lake had a large number of submersed macrophytes since 1959, while C_{Mac} decreased slightly since 1982 and stayed at ~20% in the last 5 years (Fig.3f).

The frequency distributions of response variables represented by the annual mean of all the sample sites in a specific subarea in the long-term monitoring (1959–2019) indicated spatial heterogeneity as well (Fig.4). $Chl\ a$ showed only one peak in the range of 5–10 mg/m³ in both the Central Region and East Taihu Lake. For Meiliang Bay, an obvious peak was found in the range of 20–25 mg/m³, while two peaks

in the range of 50–55 mg/m³ and 65–70 mg/m³ were indistinct (Fig.4c). Submersed macrophyte coverage showed different patterns with $Chl\ a$. A clear majority of C_{Mac} were in the range of 0–5% in the Central Region and Meiliang Bay (Fig.4b & d), while two distinct peaks were found between 15% and 20% and between 55% and 60% (Fig.4f).

3.3 Relationships between $Chl\ a$ and C_{Mac} with TP in Taihu Lake

$Chl\ a$ was significantly positively correlated with TP in the areas with no macrophytes ($P < 0.01$), and no such a correlation was found in the areas with macrophytes (Fig.5a). C_{Mac} had no relationship with TP in areas with macrophytes. In some subareas, there were no macrophytes across the range of TP (such as the Central Region), even at very low TP levels (TP ≈ 10 mg/m³) (Fig.5b).

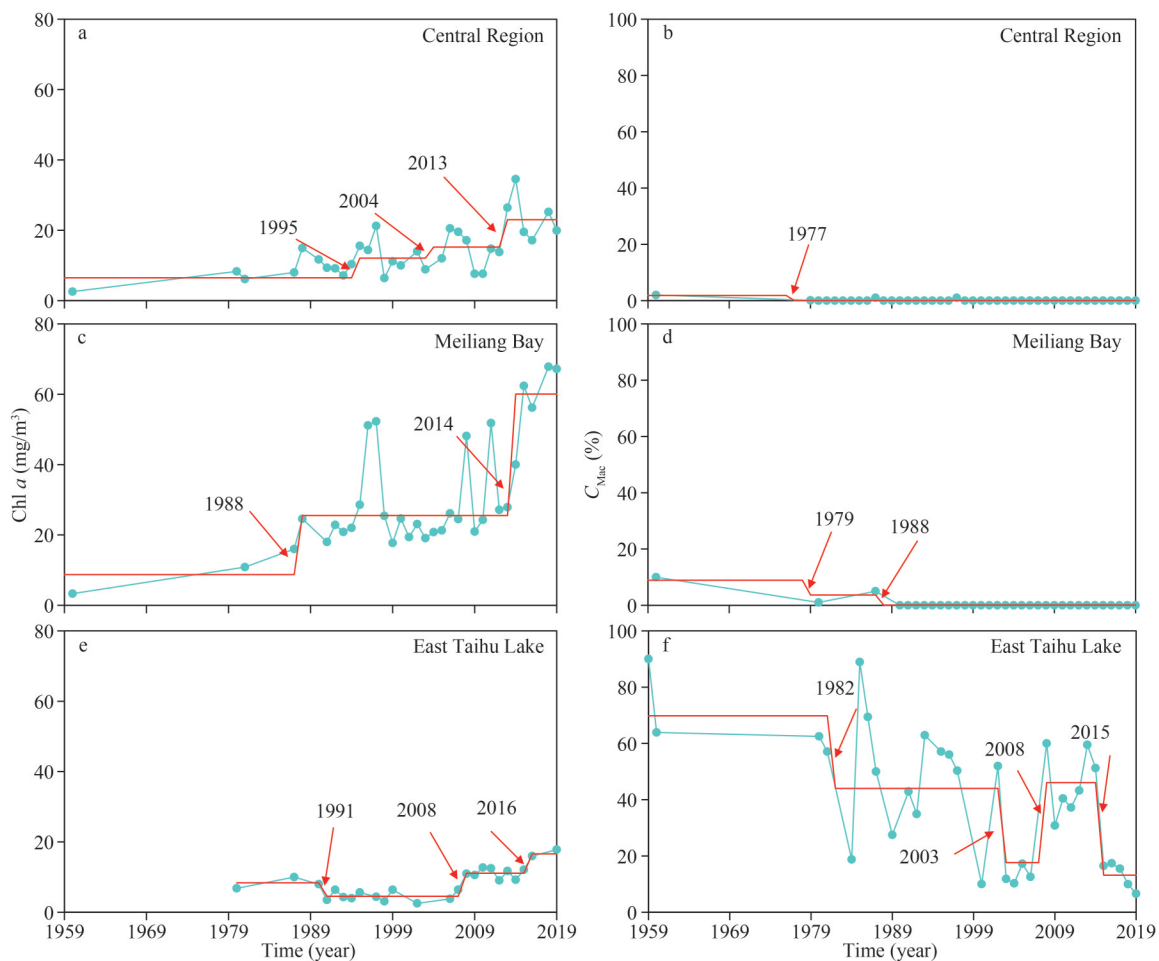


Fig.3 The interannual variations in phytoplankton chlorophyll a ($Chl\ a$, mg/m³) and submersed macrophyte coverage (C_{Mac} , %) of the Central Region, Meiliang Bay, and East Taihu Lake during 1960–2019

Red lines are the mean values of the response variables in the different regimes; blue lines are the actual values of the response variables, and arrows mark the change points. The data of 1959–2018 were collected from the literature, and the data of 2019 are from our field investigation.

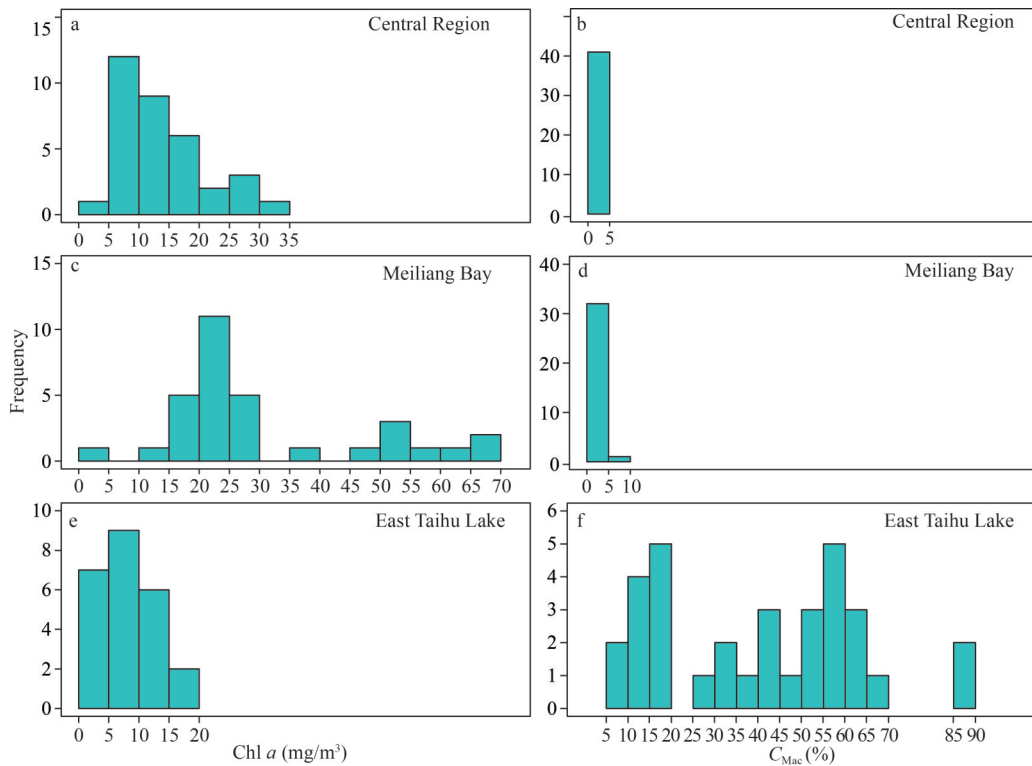


Fig.4 Frequency distribution of phytoplankton chlorophyll *a* (Chl *a*, mg/m³) and submersed macrophyte coverage (*C*_{Mac}, %) of the Central Region, Meiliang Bay, and East Taihu Lake during 1960–2019

The data of 1959–2018 were collected from the literature, and the data of 2019 were collected from our field investigation.

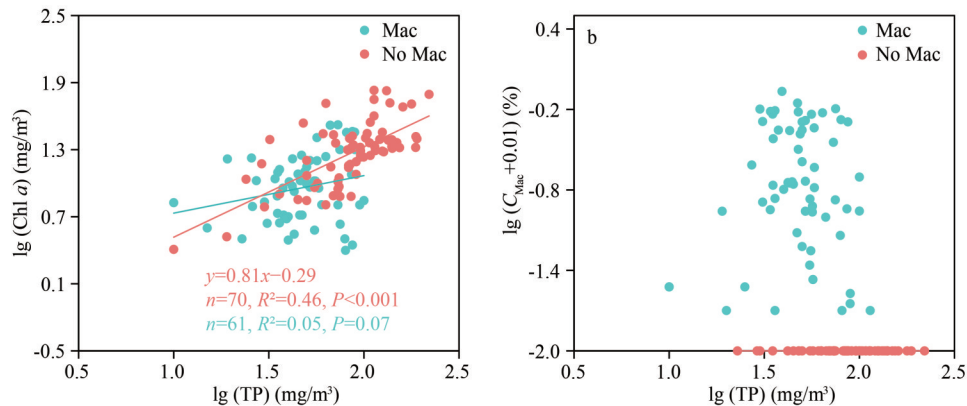


Fig.5 Relationships between phytoplankton chlorophyll *a* (Chl *a*, mg/m³) and submersed macrophyte coverage (*C*_{Mac}, %) and total phosphorus (TP, mg/m³)

The data of 1959–2018 were collected from the literature, and those of in 2019 were from our field investigation. Mac: regions with submersed macrophyte; No Mac: regions without submersed macrophyte.

3.4 Comparative analysis of Taihu Lake and small- to medium-sized Changjiang River lakes

Turb_{Alg} and its contribution to total turbidity were similar in lakes of different sizes (Fig.6b & d), while Turb_{NonAlg} and its contribution to total turbidity was higher in Taihu Lake (Fig.6a & c). For both Taihu Lake and the small- to medium-sized lakes, the lg(TP) vs. lg(Turb_{NonAlg}) and lg(TP) vs. lg(Turb_{Alg})

relationships presented similar trends (Fig.7). At the same TP levels, Taihu Lake generally presented with higher values of Turb_{NonAlg}, as did their contribution to total turbidity as a percentage (Fig.7). The contribution of Turb_{Alg} to total turbidity in Taihu Lake was lower than that in small- to medium-sized lakes, even with similar Turb_{Alg} at a specific TP level (Fig.7).

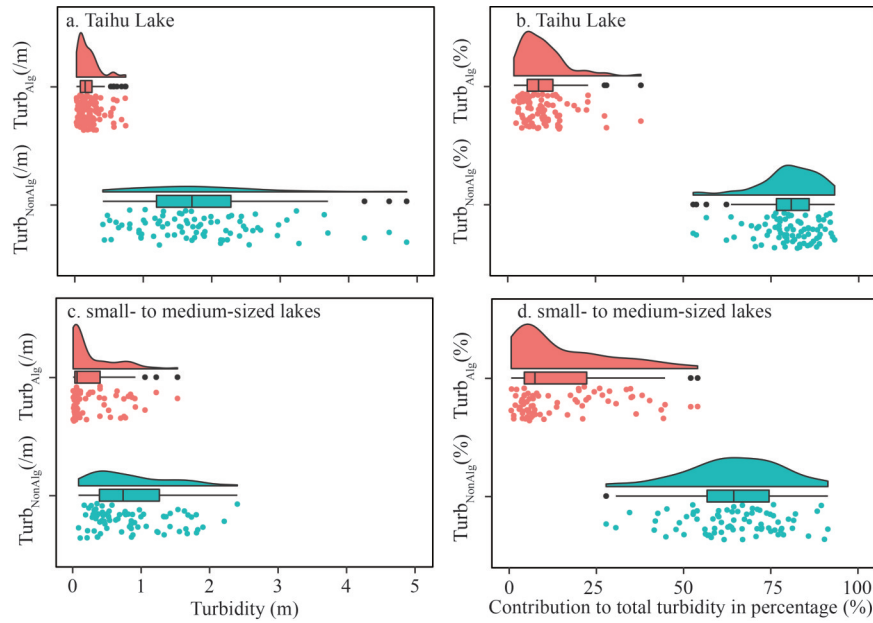


Fig.6 The algal (Turb_{Alg}/m) and nonalgal turbidity (Turb_{NonAlg}/m) and their contributions to total turbidity in percentage (Turb_{Alg}%, Turb_{NonAlg}%) for Taihu Lake (a, b) and small- to medium-sized shallow lakes of the Changjiang River floodplain (c, d)

For Taihu Lake: the data of 1959–2018 are from the literature, those of 2019 are from our field investigation; for small-to-medium-sized lakes: data span 2002–2012 are from Wang et al. (2014).

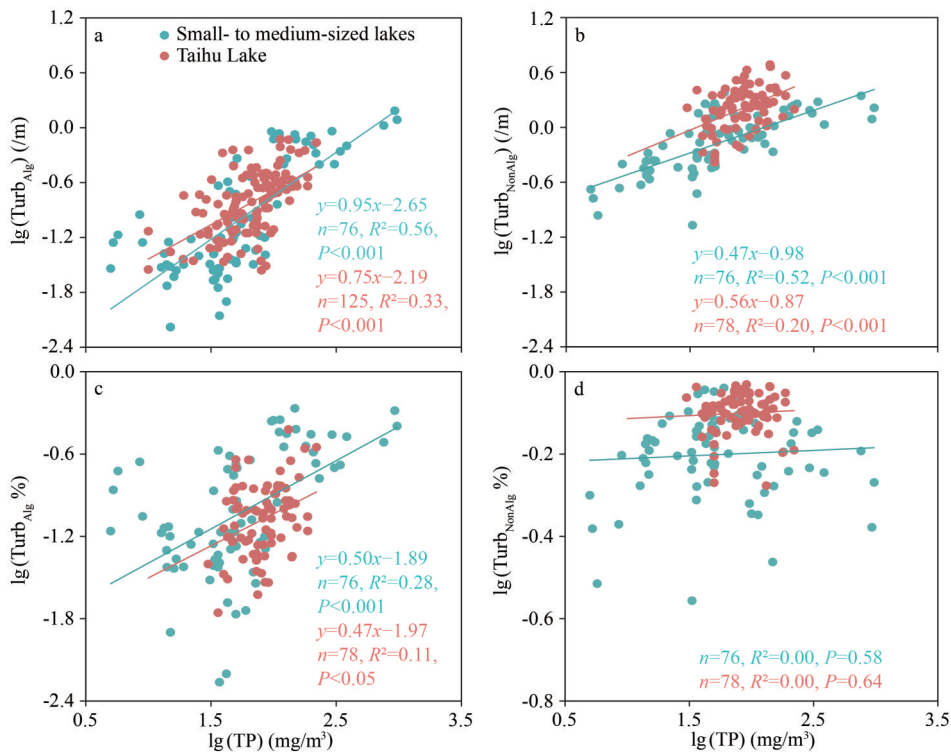


Fig.7 The relationships of total phosphorus (TP, mg/m³) vs. algal (Turb_{Alg}/m; a) and nonalgal turbidity (Turb_{NonAlg}/m; b) and their contribution to total turbidity in percentage (Turb_{Alg}%, Turb_{NonAlg}%; c, d) for Taihu Lake and the small- to medium-sized shallow lakes of the Changjiang River floodplain

For Taihu Lake, the data of 1959–2018 are from the literature, and those of 2019 from our field investigation; for small- to medium-sized lakes, data of 2002–2012 are from Wang et al. (2014) (those that have both Turb_{Alg} and Turb_{NonAlg} only).

4 DISCUSSION

4.1 Existence of alternative stable states in Taihu Lake

According to a year-around field investigation of Taihu Lake from August 2018 to May 2019 and long-term monitoring from 1959 to 2018, alternative stable states are unlikely to exist in Taihu Lake. For field data in real ecosystems, the following three pieces of evidence are usually used to demonstrate the existence of alternative stable states: sudden jumps in response variables along time series, multimodality of frequency distribution of response variables and dual relationship of response variables to control factors (Scheffer and Carpenter, 2003). In this study, time series of *Chl a* and C_{Mac} in the Central Region, Meiliang Bay, and East Taihu Lake showed several significant jumps. However, the ecosystem state before and after the jump points seemed to change little. For example, *Chl a* in Meiliang Bay was very low before 1988 and increased significantly in 1988 and 2014 (Fig.3c). However, the C_{Mac} has been at low levels since 1959, and the highest value was lower than 10%, which suggests that Meiliang Bay is always in a phytoplankton-dominated state (Fig.3d). Similar phenomena were also found in the Central Region (Figs.3a & 2b). In contrast, East Taihu Lake was dominated by submersed macrophytes throughout our investigation, even though the C_{Mac} decreased slightly recently (Fig.3f), which suggests that alternative stable states may potentially exist in this special subarea.

The frequency distributions of response variables (*Chl a* and C_{Mac}) are not multimodal except for the C_{Mac} in East Taihu Lake (Fig.4). The approximately bimodal distribution also supported the occurrence of alternative stable states in East Taihu Lake.

Dual relationships between *Chl a* and TP in the subareas with and without submersed macrophytes provided a more informative indicator for the existence of alternative stable states (Fig.5a). However, there was no folded curve for the relationships between C_{Mac} and TP, and no significantly negative relationship was found between these two variables in the areas with submersed macrophytes (Fig.5b), which greatly weakened the occurrence of alternative stable states.

The results suggest that, unlike small- to medium-sized shallow lakes, large shallow Taihu Lake may

have no alternative stable states. Although East Taihu Lake was dominated by submersed macrophytes, more convincing evidence is needed to draw a positive conclusion, as it remains unknown whether this subarea has hysteresis between the processes of eutrophication and oligotrophication. A lower possibility of submersed macrophyte dominance was also reported in other large lakes. In Chaohu Lake (780 km²), the 5th largest shallow lake in China, C_{Mac} did not exceed 30% (1931) in the last 100 years and decreased to less than 5% recently (Xie, 2009). In Kyoga (1 720 km²) of Uganda, macrophytes mainly consisted of invasive water hyacinth and were restricted to the shoreline in the 1990s when TP was between 48 and 62 mg/m³ (Ogutu-Ohwayo et al., 2013). The St. Clair-Detroit River system (1 113 km²) in the USA also had a coverage of 30% in 1978 (Schloesser and Manny, 1986). The submersed macrophytes in Okeechobee (1 900 km², USA) were concentrated in only two beds located in the south and west shoal regions, with a mean coverage of 7% during 1999–2000 (Havens et al., 2005). More cases were reported by Janssen et al. (2014).

4.2 Factors regulating submersed macrophytes in large shallow lakes

In Taihu Lake, unfavorable conditions caused by wind, such as the increased disturbance to the plant roots, the higher resuspension and the consequently lower underwater light availability, might be the main reason underlying the absence of submersed macrophytes, especially in the early years. Fetches usually grow longer with increasing surface area. A longer fetch could lead to larger wind-driven waves, resulting in a higher shear stress on the sediment surface and then stronger sediment resuspension (Carper and Bachmann, 1984). Taihu Lake generally had higher $Turb_{NonAlg}$ and $Turb_{NonAlg}\%$ or at a specific TP compared with small- to medium-sized lakes (Figs.6 & 7). The median $Turb_{NonAlg}\%$ in Taihu Lake was 81%; thus, $Turb_{NonAlg}$ was an important contributor to inhibiting macrophyte growth by light attenuation. Zhang et al. (2014) also reported that wind-driven sediment resuspension was the main factor determining the total suspended matter in this large shallow lake. Long-term wind forcing can also bring difficulties when submersed macrophytes struggle to root in the sediment. Evidence can be found in the Central Region of Taihu Lake, which always lacks macrophytes, especially in the limnetic zone, even

when nutrient concentrations and phytoplankton abundances were low before the 1980s (Fig.3; Supplementary Fig.S1).

Additionally, the distribution of submerged macrophytes is regulated by other physical, chemical and biological factors. For example, water-level variations could be a critical factor, especially in subtropical regions, where rainfall and net evapotranspiration vary greatly (Abtew, 2001). High water levels could generally induce large-scale loss of macrophytes (Havens et al., 2005). The water level of Taihu Lake has gradually risen in recent years, especially after 2011 (Wang et al., 2016; Chang et al., 2022). Increased nutrient inputs could promote the growth of phytoplankton and then lower the underwater light availability of macrophytes (Chamber and Kalff, 1987; Jones et al., 2002; Wang et al., 2014). TP in the Central Region arrived or exceeded the threshold (80–120 mg/m³) for a regime shift from a clear state to a turbid state since 2005, which brings more stress to the growth of macrophytes (Supplementary Fig.S1). Excessive grazing pressure from herbivorous fishes is also an important factor due to the absence of macrophytes (Wang et al., 1990; Zhong et al., 2017). Remarkably, large shallow lakes face more negative conditions than small- to medium-sized shallow lakes in addition to general factors.

Apart from the wide central area, large shallow lakes usually have several bays along the margin of the lakes, such as the Meiliang Bay and East Taihu Lake (Fig.1). They have similar surface areas and water depths with separated small shallow lakes, and macrophyte dominance seems possible in such areas. However, the variously shaped small bays seemed more complex when analyzing the existence of alternative stable states. Meiliang Bay, a phytoplankton-dominated subregion, is experiencing severe eutrophication and algal blooms (Zhu, 2009; Li et al., 2011a; Liu et al., 2018). It was oligotrophic before the 1980s, and the first algal blooms occurred in 1987 (Ma et al., 2008; Xie, 2009). Subsequently, algal blooms increased in coverage and frequency (Chen et al., 2003; Duan et al., 2009; Paerl et al., 2011). Submersed macrophytes were only limited in the littoral zone before the 1980s, and the coverage was always lower than 10% (Fig.3). Therefore, Meiliang Bay seemed to remain in a phytoplankton-dominated state even under very low nutrient levels (1960: TN, 60 mg/m³; TP, 20 mg/m³; Supplementary

Fig.S1) and did not show regime shifts between two contrasting states. High concentrations of suspended solids due to wind action might be an adverse factor for macrophyte growth. $Turb_{NonAlg}$ and $Turb_{NonAlg}^{\circ}/\%$ were 13.5 and 1.9 times higher on a specific TP than in small- to medium-sized lakes, respectively. As the surface area of Meiliang Bay is only approximately 110 km², which is similar to general small- to medium-sized lakes, the massive suspended solids more likely resulted from intense water exchange with the Central Region. The local regime shifts in this subregion were obstructed by water quality states elsewhere within a lake (Scheffer and van Nes, 2007; Hilt et al., 2011).

Contrary to Meiliang Bay, submersed macrophytes have flourished in East Taihu Lake, another subarea with a similar surface area (150 km²) in southeastern Taihu Lake, since the 1950s, which suggests that alternative stable states may exist in this area (Fig.3f). Most nutrient inputs come from the north and west of the Taihu Basin, where most cities and the major inflow rivers are situated (Yu et al., 2007; Li et al., 2011a). External loading of phosphorus in northwestern Taihu Lake was 1 509.6 t in 2018, approximately 17.6 times greater than that in the southeastern area (Taihu Basin Authority of Ministry of Water Resources, 2019). These nutrient concentrations decrease in a southeasterly direction from the input sources through the lake center towards the outlet rivers in the east (Chen et al., 2003; Kelderman et al., 2005; Li et al., 2011a; Paerl et al., 2011; Otten et al., 2012). According to a field investigation during 2018–2019, the annual TP in East Taihu Lake was 47.5 mg/m³, which was only 36% of that in Meiliang Bay (Table 1). The lower nutrient concentrations in East Taihu Lake were one of the most important factors allowing macrophytes to survive (Wang et al., 2014). In addition, East Taihu Lake is an elongated, relatively independent subregion and connects with the wild Central Region by a narrow channel. Therefore, submersed macrophytes were protected from wind forcing to some extent. Recently, the biomass of floating macrophytes has increased and is regarded as a sign of an upcoming shift to the phytoplankton-dominated state (Zhao et al., 2012; Poikane et al., 2018; Moi et al., 2021). 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 as submersed macrophytes (Scheffer and Carpenter, 2003).

5 CONCLUSION

Based on a study of Taihu Lake and a comparison with small- to medium-sized lakes, we present evidence to show that (1) in Taihu Lake, the existence of alternative stable states was not proven based on the long-term investigation during 1959–2019, while more evidence is needed to confirm alternative stable states in East Taihu Lake, a typically macrophyte-dominated subarea, as to whether hysteresis existed between two contrasting processes (e.g., eutrophication and oligotrophication) is still unknown; (2) wind forcing might be the main reason due to the absence of submersed macrophytes in Taihu Lake. Therefore, restoration could be more difficult for large lakes than for small- to medium-sized lakes, and nutrient reduction should be more critical to improve water quality. In addition, floating-leaved macrophytes can resist strong winds and waves and are usually distributed along the shoreline. Future studies may also focus on the dynamics of this macrophyte in large shallow lakes.

6 DATA AVAILABILITY STATEMENT

All data generated and/or analyzed during this study are available from the corresponding author upon request on reasonable request.

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Electronic supplementary material

Supplementary material (Supplementary Tables S1–S2 and Fig.S1) is available in the online version of this article at <https://doi.org/10.1007/s00343-022-1286-z>.