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Long-term dynamics of phytoplankton assemblages: *Microcystis*-domination in Lake Taihu, a large shallow lake in China

YUWEI CHEN*, BOQIANG QIN, KATRIN TEUBNER[1] AND MARTIN T. DOKULIL[1]
NANJING INSTITUTE OF GEOGRAPHY AND LIMNOLOGY, CHINESE ACADEMY OF SCIENCES, NANJING 210008, CHINA AND [1]INSTITUTE FOR LIMNOLOGY, AUSTRIAN ACADEMY OF SCIENCES, A-5310 MONDSEE, AUSTRIA

*CORRESPONDING AUTHOR: njchenyuwei@hotmail.com; ywchen@niglas.ac.cn

Long-term phytoplankton assemblages in a large shallow Chinese lake, Lake Taihu, were presented using the monthly monitoring data from October 1991 to December 1999. Earlier research results (1960, 1981 and 1988) were applied to discuss the different trophic stages of the lake. The species composition in the lake was more closely related to eutrophication level than to lake-size, shallowness, or turbidity. Each summer, a single peak of phytoplankton biovolume appeared in Meiliang Bay. The results of principal components analysis showed a distinct temporal shift in species composition between summer and winter. A clear spatial difference in phytoplankton occurred between Meiliang Bay and the lake centre. Wind speed and direction affected the horizontal distribution of phytoplankton, especially Microcystis, in the lake. Temperature, underwater light climate, nutrients and grazing by zooplankton and by fish were discussed to explain the overwhelming dominance of Microcystis. Four nutrient-phytoplankton stages were identified in the lake: an oligo-mesotrophic stage with low algal biomass until 1981, a eutrophic situation with blooms of Microcystis during 1988–1995, hypertrophic conditions with the dominance of Planctonema and total phosphorus up to 200 mg m^{-3} from 1996 to 1997 and the restoration period after 1997. The wax and wane of the phytoplankton assemblages were mainly controlled by temperature, wind and turbidity while long-term biomass dynamics were influenced by the level of nutrients.

INTRODUCTION

China has a large number of freshwater ecosystems. Nevertheless, freshwater resources of good quality are not abundant and hence water availability per capita is only a quarter of the worlds average (Dokulil *et al.*, 2000). Historically, human populations in China have always lived close to lakes, which recently has resulted in increased water consumption and, as a consequence, water pollution and water shortage. Many of Chinas lakes are shallow, situated in the densely populated lowlands and are used for drinking and irrigation among several other purposes.

World-wide, shallow water ecosystems are much more numerous than deep lakes and hence are of great importance. Such shallow systems usually have specific characteristics influencing their management. About 35 lakes are situated between 22.5º and 35º latitude north and south of the equator, with surface areas larger than 500 km^2. This number includes 20 saline or brackish waters and 15 freshwater lakes, of which five are located on the Qinghai–Tibet–Altiplano at elevations higher than 4000 m (Herdendorf, 1990). From the remaining ten lakes, seven (including Lake Taihu) are located in central-east China which is the region of fastest development. All are shallow with mean depths less than 10 m (Chang, 1987). Most of them are used as sources of drinking water, although they are eutrophic because of nutrient overdose and therefore have become cyanobacteria-dominated ecosystems.

The large shallow lake, Taihu, located in the vicinity of two large cities and about 100 km west of Shanghai, which is the biggest city in China, is a good example because of its multiple uses, among which drinking water abstraction, wastewater discharge and fisheries are the most important. Irregular observations in the lake are available from the years 1960, 1981 and 1988 (Sun and Huang, 1993). Eutrophication as a result of enhanced nutrient input from the catchment began in the 1980s (Shi and Zai, 1994). Studies of the trophic relations and monthly monitoring to find remedies against eutrophication began in October 1991, focusing on effects in the northern part of the lake (Cai *et al.*, 1994).

This paper concentrates on long-term changes using the monthly monitoring data covering the period 1991–1999. The main aim is to extract from this long-term data set differences from or similarities to other lakes in the regulation of the phytoplankton assemblages.

METHOD

Site description

Lake Taihu is located between 30º05′ and 32º08′N and between 119º08′ and 121º55′E, downstream of the Changjiang River (Figure 1). It is the third largest freshwater lake in China, with an area of 2338 km^2 and an average depth of 2.0 m (Jin *et al.*, 1990). According to Li *et al.*, the drainage basin of the lake is about 36 500 km^2 (Li *et al.*, 1994). More than 200 brooks, canals and rivers discharge some 7.6 billion m^3 water into the lake each year (Zhu, 1994).

Meiliang Bay is one of the most eutrophic bays in the northern part of the lake. The surface area of the bay is about 100 km^2. There are two main rivers, the Liangxi and the Lujiang, connected to the bay (Figure 1). These two rivers sometimes function as inflow, sometimes as outflow depending on the water level differences between the Changjiang River and the lake. They discharge the effluents from the cities of Wuxi and Changzhou. Morphological and hydrological properties of the lake are summarized in Table I.

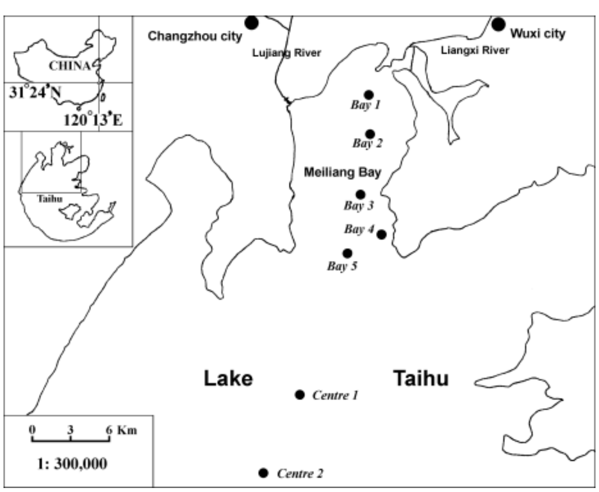

Fig. 1. Location of Lake Taihu, China and the sampling stations in the northern part (Meiliang Bay).

Analytical methods

Seven sampling stations, Bay 1 to 5 and Centre 1 and 2, were selected covering the Meiliang Bay and the open lake (Figure 1).

Integrated water samples were taken using a 2 m long and 10 cm diameter plastic tube. Physical and chemical variables such as suspended solids, Secchi-depth, water temperature, pH, alkalinity and nutrient concentrations were analysed according to standard techniques used in China (Jin and Tu, 1990). Chlorophyll *a* concentration (Chl *a*) was calculated according to Lorenzen from spectrophotometric measurements after extraction in 90% hot ethanol (Lorenzen, 1967).

Phytoplankton samples were fixed with Lugol's iodine solution and sedimented for 48 h prior to counting on a microscope. Phytoplankton species were identified according to Hu *et al.* (Hu *et al.*, 1980). Algal biovolumes were calculated from cell numbers and cell size measurements. Conversion to biomass assumes that 1 mm^3 of volume is equivalent to 1 mg of fresh-weight biomass.

Seasonal averaging of phytoplankton biovolume used fixed time periods for all years (spring, March–May; summer, June–August; autumn, September–November; winter, December–February). Differences in spatial distribution were simplified by calculating the means for 'Bay' (Bay 1–5) and 'Centre' (Centre 1 and 2).

Annual average data of total phosphorus, Chl *a* and phytoplankton biovolume are compiled as 'bubble plots' with the size of each bubble equivalent to the biovolume. These plots are augmented by pie charts showing the contribution of individual algal groups. Data prior to 1990 were extracted from Sun and Huang (Sun and Huang, 1993).

Multivariate analyses were based on the biovolume of single algal taxa. The phytoplankton composition between sampling stations was studied on annual averages (n = 63) and the seasonal phytoplankton pattern was

Table I: Morphological and hydrological properties of Lake Taihu, China

Properties	Lake Taihu	Meiliang Bay
Surface water area (km^2)	2338	~100
Catchment area (km^2)	36500	–
Maximum depth (m)	4.5	3.8
Mean depth (m)	2.0	1.8
Retention time (days)	264	–
Shore line (km)	465	–
Volume (km^3)	4.44	~0.20

After (Jin *et al.*, 1990; Cai *et al.*, 1994).

obtained from the seasonal averages as described above (n = 252). Logarithmic data were standardized for multivariate statistical analyses using STATGRAPHICSplus. A step-wise species extraction was repeated with the principal component analysis (PCA) until the first two components represented more than 40% of total variance (seven taxa in Figure 7A, eight taxa in Figure 7B).

RESULTS

Higher average concentrations of physical and chemical variables were usually associated with stations in the Meiliang Bay except for the content of suspended solids (Table II). The mean concentration for suspended solids was 35.8 mg l^{-1} in the bay and 63.2 mg l^{-1} in the centre. Correspondingly, average Secchi-depth was 0.49 m in the bay and 0.43 m in the centre. Figure 2 shows the correlation between suspended solids and Secchi-depth in Lake Taihu (Secchi-depth = 2.71 × suspended solids$^{-0.54}$; R^2 = 0.73, n = 997, $P < 0.001$). About 98% of the Secchi-depth measurements were below 1.0 m. High water temperatures, up to 32.5°C, were recorded in the bay during the summer, dropping to 1.5°C during winter. Similar values (2.0–32.3°C) were measured in the centre of the lake (Table II). The annual cycles of water temperature in Meiliang Bay showed one regular summer peak each year while Secchi-depth randomly fluctuated in accordance with turbidity and wind speed (Figure 3).

Total phosphorus concentration averaged 113 mg m^{-3} in the bay and 76 mg m^{-3} in the centre. The concentrations of orthophosphate (PO_4-P) in the bay ranged from

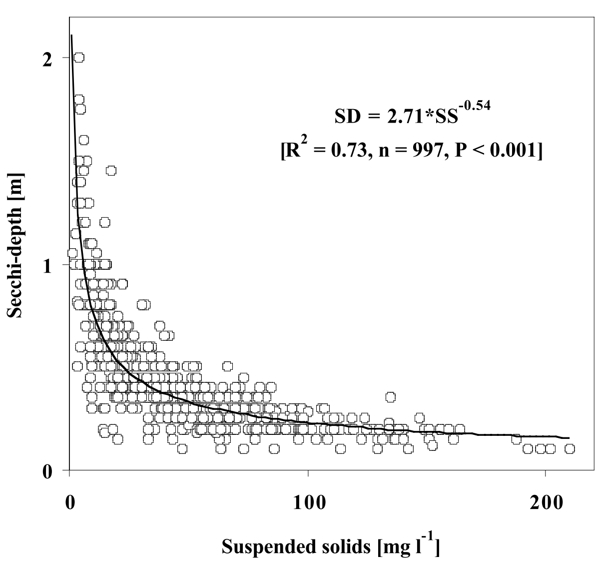

Fig. 2. Correlation between suspended solids and Secchi-depth in Lake Taihu, China.

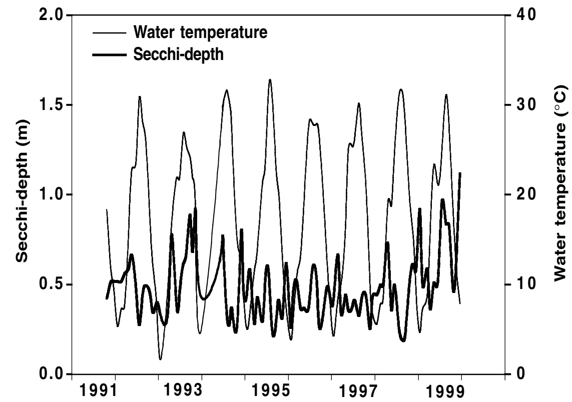

Fig. 3. Annual cycles of water temperature and Secchi-depth in Meiliang Bay, Lake Taihu, China.

1 to 273 mg m^{-3} (Table II). Similarly, the total nitrogen concentration, as well as ammonium (NH_4-N), nitrite (NO_2-N) and nitrate (NO_3-N), were higher in the bay than in the centre (Table II).

Seventy-four algal species were recorded among the phytoplankton assemblages in the lake during our sampling period, comprising four main groups: cyanobacteria, 16 species; diatoms, 16 species; green algae, 28 species; and flagellates, 14 species (Table III). Several species of *Microcystis* dominated not only among the cyanobacteria but also among the whole phytoplankton assemblages. Besides the *Microcystis* species and *Anabaena flos-aquae*, the diatom *Aulacoseira granulata*, the flagellate *Cryptomonas* spp. and several species of green algae, belonging mainly to such genera as *Scenedesmus* and *Pediastrum*, could be regarded as the dominant species among each phytoplankton group (Table III; see Hu *et al.*, 1980 for a taxon list).

Long-term development of total phytoplankton biovolume in the bay and in the centre is presented in Figure 4, together with the dynamics of several dominant genera in the bay for the period from October 1991 to December 1999. Regular peaks of total biovolume appeared in the summer of each year, as shown for both sites in Figure 4A. On average, total biovolume in the bay was five times higher than that in the centre. The summer maxima were usually associated with blooms of *Microcystis* in the bay, peaking at 118 mm^3 l^{-1} in August 1998 (Figure 4B). In contrast, the summer peaks of total biovolume in the two previous years were mainly composed of green algae (99% in 1996, 94% in 1997, Figure 4E). Lower values of biovolume occurred during the period December to March of each year (Figure 4A). The lowest biovolume was observed during the winter of 1992–1993 at both sites (Figure 4A).

Table II: Mean and ranges of physical and chemical measurements in Lake Taihu, China

	Meiliang Bay		Lake centre	
Variables	Mean	Range	Mean	Range
Suspended solids (mg l^{-1})	35.8	1.6–134	63.2	3.6–499
Secchi-depth (m)	0.49	0.1–1.5	0.43	0.1–2.0
Water temperature (°C)	17.6	1.5–32.5	17.3	2.0–32.3
pH	8.44	6.9–10.1	8.23	7.0–9.67
Alkalinity (mg l^{-1})	1.49	0.69–2.64	1.12	0.87–1.68
Total phosphorus (mg m^{-3})	113	8–750	76	5–670
PO_4-P (mg m^{-3})	3	1–273	7	1–39
Total nitrogen (mg l^{-1})	2.71	0.16–9.94	1.84	0.38–4.93
NH_4-N (mg l^{-1})	0.647	0.002–5.68	0.127	0.002–0.426
NO_2-N (mg l^{-1})	0.037	0.0–0.737	0.013	0.001–0.078
NO_3-N (mg l^{-1})	0.842	0.006–2.89	0.740	0.017–3.05

Table III: Phytoplankton groups and dominant species in Lake Taihu, China

Phytoplankton groups		Species	Dominant species
Cyanobacteria	Cyanophyta	16	*Microcystis aeruginosa, M. flos-aquae, M. wesenbergii, Anabaena flos-aquae*
Diatoms	Bacillariophyta	16	*Aulacoseira granulata, Cyclotella bodanica*
Green algae	Chlorophyta	28	*Scenedesmus bijuga, S. obliquu, S. quadricauda Pediastrum duplex, P. simplex, Planctonema* sp.
Flagellates	Euglenophyta	5	*Euglena acus, E. oxyuris*
	Cryptophyta	3	*Cryptomonas ovata, C. erosa*
	Pyrrophyta	4	*Ceratium hirundinella*
	Chrysophyta	2	*Dinobryon sertularia*

Different species of *Microcystis* contributed more than 40% and up to 98% of total biovolume from May to October each year (Figure 4B). The diatom *Aulacoseira* spp. contributed significantly to total biovolume a month later than *Microcystis* in most years (Figure 4C). The highest biovolume of *Cryptomonas* spp. appeared either shortly before or after the *Aulacoseira* peak. In some years another peak appeared in April or May (Figure 4D). Green algae, comprising several species of *Scenedesmus* and *Pediastrum*, did not contribute significantly to total biovolume in most of the years but produced blooms of *Planctonema* sp. in 1996 and 1997 (Figure 4E).

Spatial distribution of total phytoplankton biovolume is shown for all stations in Figure 5. In general, biovolume tended to decrease from the inner parts of the bay (Bay 1) towards the centre of the lake (Centre 2) with values significantly higher in the bay. Even within the bay, significant differences occurred, e.g. between the Bay 1 and Bay 5 stations (Figure 5).

The long-term development of eutrophication in Lake Taihu is shown as annual averages for the bay and the centre in Figure 6. The early years of the observation period (1960, 1981) were characterized by a rapid increase of total phosphorus, Chl *a* and phytoplankton biovolume. Values in the centre of the lake, however, were about half of those in the bay (Figure 6B). Phytoplankton species composition changed concomitantly from diatom dominance to a predominance of cyanobacteria in 1988. Cyanobacteria prevailed from 1988 to 1995. During the same period, total phosphorus fluctuated between 50 mg m^{-3} and 150 mg m^{-3} while Chl *a* remained more or less the same in the bay (Figure 6A). In the following period all

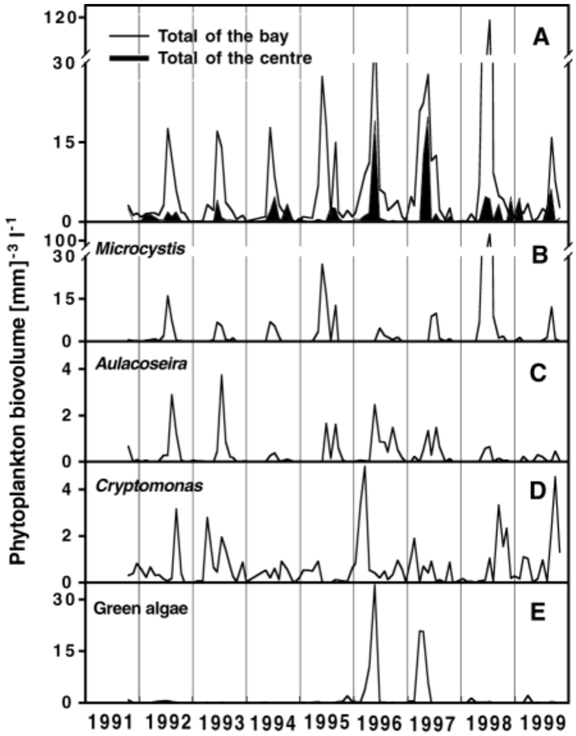

Fig. 4. Long-term development of monthly average phytoplankton biovolume in Lake Taihu, China. (**A**) Total biovolume in Meiliang Bay and Lake Centre, (**B**) *Microcystis* spp., (**C**) *Aulacoseira* spp., (**D**) *Cryptomonas* spp., (**E**) total green algae. (**B–E**) in Meiliang Bay.

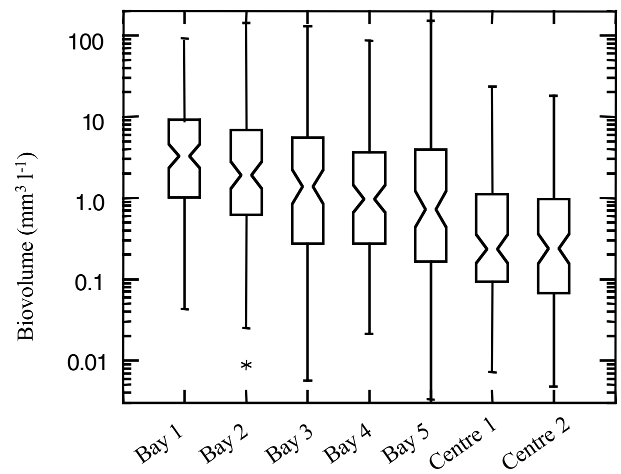

Fig. 5. Spatial distribution presented as log biovolume in Lake Taihu, China. Further explanation in the text.

variables increased again, peaking in 1996 or 1997 throughout the lake. This and the previous year saw an exceptional appearance of green algae as described already. Finally, total phosphorus and Chl *a* began to decline and the biovolume reached levels similar to those recorded in 1991. Cyanobacteria became the dominant algal group again. The greatest annual average biovolume ever was observed in 1998 in the Meiliang Bay (see also Figure 4) as a result of the heavy *Microcystis* bloom in that year.

PCA analysis

The phytoplankton species in Lake Taihu differed among the four seasons and among the sampling stations as shown by the PCA in Figure 7. The phytoplankton composition observed in summer was distinct from that seen in winter, as indicated by the separation of points of the respective seasons in Figure 7A. *Microcystis* spp., *Aulacoseira* spp. and *Ceratium hirundinella* were typical summer algae while *Dinobryon sertularia* appeared mainly in winter. Various species of *Cryptomonas* and *Euglena* contributed most to the phytoplankton in spring while no single algal group was typical for autumn. Between-site differences

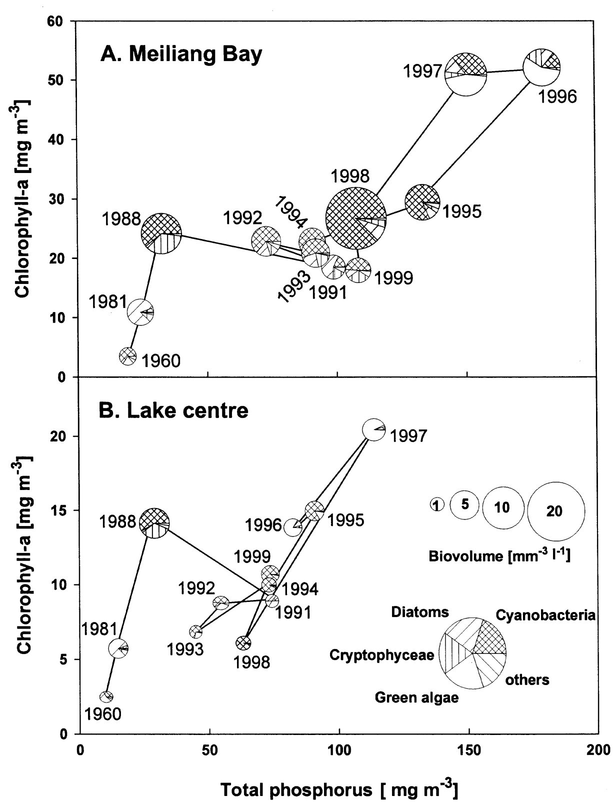

Fig. 6. Multivariate bubble-plot of long-term development of total phosphorus, Chl *a*, biovolume and algal groups in Lake Taihu, China: (**A**) for Meiliang Bay, (**B**) for the lake centre.

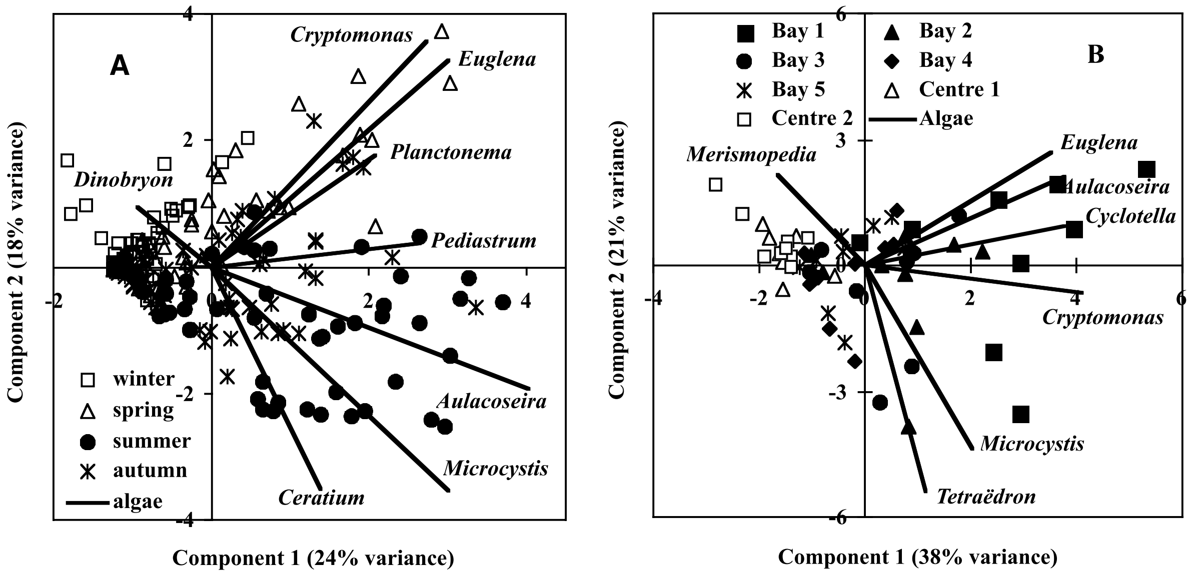

Fig. 7. Results of principal component analysis (PCA) in Lake Taihu, China. (**A**) Differences among the four seasons, (**B**) differences among the seven sampling stations.

are shown in Figure 7B. The separation of the points for Bay 1–5 from the points for Centre 1–2 indicated a quite different algal composition in Meiliang Bay compared with the lake centre. Furthermore, high biovolumes of *Euglena* spp., *Aulacoseira* spp., *Cyclotella* spp. and *Cryptomonas* spp. were common at Bay 1 and Bay 2 while *Microcystis* spp. and *Tetraedron* sp. mostly appeared at Bay 2 and Bay 3 (Figure 7B). Phytoplankton at the lake centre was mainly characterized by the low biovolume of the species mentioned above for Bay 1–3. The two stations in the centre did not show a clear difference of species composition.

DISCUSSION

The overwhelming dominance of *Microcystis* in various lakes of the world has been explained by water temperature, underwater light climate (turbidity or suspended solids or Secchi-depth), nutrients, buoyancy regulation and zooplankton grazing or fish grazing (Okino, 1973; Smith, 1983; Reynolds *et al.*, 1987; Robarts and Zohary, 1987; Ibelings *et al.*, 1991; Schreurs, 1992; Wood, 1993; Scheffer, 1998; Brookes and Ganf, 2001).

Temperature plays an important role in the phytoplankton composition in Lake Taihu. It is commonly observed that warm temperatures favour cyanobacteria (Wood, 1993). Robarts and Zohary concluded that temperature was the second most important factor affecting the *Microcystis* bloom in Hartbeesport Dam (Robarts and Zohary, 1987). *Microcystis aeruginosa* appeared every year at temperatures above 20°C in the Japanese lake Suwa (Okino, 1973). Similarly, the water temperature from May to October in Lake Taihu is in the range of 18.2–32.5°C (Figure 3). Thus *Microcystis* developed mainly during this period.

Many previous studies in shallow lakes discussed the effect of turbidity on phytoplankton assemblages [e.g. summarized by (Scheffer, 1998)]. Dokulil suggested that the most obvious feature of turbid lakes like Neusiedlersee was the profound influence on underwater light, which was rapidly attenuated and altered in its spectral composition according to the nature of the suspended particles (Dokulil, 1984). In turbid underwater environments, algal species with gas vesicles, such as *Microcystis*, can either move down to avoid the high light intensity at the water surface, or float up when underwater light conditions are poor (Ibelings *et al.*, 1991; Brookes and Ganf, 2001). Our Secchi-depth and suspended solids data showed the high turbidity in Lake Taihu (Figures 2 and 3). As a consequence, *Microcystis* spp. became dominant. Therefore, the underwater light climate seems to be one of the selective environmental factors that strongly influenced the species composition and biomass of phytoplankton in the lake.

Wind speed and direction affected the horizontal distribution of phytoplankton, especially *Microcystis*, in Lake Taihu. The summer wind direction in the region, in general, was from the south (unpublished data from the authors). The difference in species composition between Meiliang Bay and the lake centre was one of the consequences of the wind (Figure 7B). The bloom of *Microcystis* in 1998 can be regarded as wind accumulation from the open lake to the bay because we found a low phytoplankton biovolume in the lake centre but comparably high values in the bay in 1998 (Figure 4A,B). The large variability of biovolume at sampling station Bay 5 was also the result of wind shifting the distribution of *Microcystis* blooms (Figure 5) as confirmed by the model of Zhu and Cai (Zhu and Cai, 1998).

As Schreurs summarized, cyanobacteria dominated lakes either when their average depth was less than 2 m or total phosphorus ranged from 100 to 800 mg m^{-3} or total nitrogen was in the range of 2.5–3.5 mg l^{-1} (Schreurs, 1992). With a mean depth of 2.0 m, average total phosphorus of 113 mg m^{-3} and average total nitrogen of 2.71 mg l^{-1} (Tables I and II), Lake Taihu thus fits very well to a suitable situation of cyanobacterial dominance (Chen *et al.*, 2003).

According to studies on zooplankton composition and feeding rates of crustacean in Lake Taihu by Chen and Nauwerck (Chen and Nauwerck, 1996), the zooplankton in the lake could never reach values high enough to control *Microcystis* production and to produce a situation of clear water. Furthermore, the dominant fish populations in Lake Taihu were zooplankton-feeding fish (~46% of fish capture in 1993; unpublished data from the Chinese Fishery Administration of Lake Taihu). Phytophagous fish abundance was insignificant to control the *Microcystis* bloom. Phytoplankton in Lake Taihu should therefore not be controlled either by zooplankton or by fish grazing.

Our results suggest that phytoplankton species composition in Lake Taihu does not differ from that of other eutrophic lakes of the globe [e.g. (Scheffer, 1998)]. The dominant algal genera such as *Microcystis* in the lake are typical for eutrophic lakes as described by Hutchinson (Hutchinson, 1967). The size of the lake, its shallowness, or its turbidity seem to have less influence on species composition or the dominance of cyanobacteria than the trophic level (Tilzer and Serruya, 1990). Shallow turbid lakes, like Neusiedlersee, only had cyanobacterial dominance during the eutrophic period (Dokulil and Padisák, 1994).

Comparing a large number of Danish lakes of different trophic levels, Jensen *et al.* concluded that cyanobacteria were often replaced by green algae when total phosphorus in the lake water reached values above 1000 mg m^{-3} (Jensen *et al.*, 1994). In Lake Taihu, however, the filamentous green alga *Planctonema* sp. dominated the phytoplankton assemblage already, at a total phosphorus of 150–200 mg m^{-3}. A similar result was also discussed by Laugaste *et al.* that the green alga *Planctonema lauterbornii* was quite abundant and even belonged to the dominant species in the strongly eutrophic large, shallow lake Pihkva in the 1960s (Laugaste *et al.*, 1996). For a short period in the 1970s, *Planctonema* made an appearance in Lough Neagh but then disappeared again (Gibson, personal communication). In the deep-alpine lake Constance, another filamentous green alga, *Mougotia thylespora*, became significant during the most eutrophic phase, with highest total phosphorus around 80 mg m^{-3} (Gaedke, 1998; Güde *et al.,* 1998). At present, there is no generally accepted explanation for all these phenomena. It might be considered as a separate 'stable state' within phytoplankton (Scheffer, 1998) depending on the nature and latitude of the lake.

As pointed out by Reynolds, one phytoplankton biovolume summer peak each year was the simplest case observed in many lakes (Reynolds, 1984). Peak biovolume in Lake Taihu occurred when the physical conditions were most favourable (e.g. water temperature reached its maximum in summer) and phytoplankton abundance is subject to a lasting and overriding control by chronic nutrient deficiency. The very low value of phytoplankton total biovolume during winter 1992/1993 was a reflection of a weather situation that was unusual for the region, with air temperatures below freezing point and heavy snowfall (Figure 3).

From the long-term sequence of total phosphorus, phytoplankton Chl *a* and biovolume, four developmental phases of Lake Taihu can be identified (Figure 6).

In the first phase, moderate total phosphorus before 1981 was associated with a lower annual average biovolume of less than 5 mm^{-3} l^{-1} and Chl *a* lower than 12 mg m^{-3}. According to the classification proposed by Vollenweider and Kerekes (Vollenweider and Kerekes, 1982); this period was oligo-mesotrophic. Unfortunately, no detailed phytoplankton compositional data were found in Sun and Huang (Sun and Huang, 1993). However, the change in dominant group from diatoms to cyanobacteria during this stage is common in other lakes world-wide (Padisák, 1992). The rapid growth of phytoplankton until 1988 was mainly the result of the increase of nutrient concentrations at increasing trophic level.

The second phase, characterized by *Microcystis* dominance, started in 1988 and lasted until 1995. The relatively low biomass in relation to total phosphorus levels and stable species composition during this stage reflect the light limitation of the phytoplankton assemblage similar to other turbid lakes (Dokulil and Teubner, 2003).

The third phase in Lake Taihu occurred during 1996 and 1997 when hypertrophic conditions were clearly evident. With total phosphorus reaching the highest values, *Microcystis* became less dominant and the green algae appeared in very high percentage in 1996 and 1997. Although the general sequence of the bay and the lake centre was similar, the total phosphorus started decreasing in 1996 in Meiliang Bay while it still increased rapidly from 1996 to 1997 in the lake centre. This indicated the time delay of nutrient transport from the bay to the centre.

The last phase in our study was the possible restoration stage. The decrease of both total phosphorus and Chl *a* was mainly the result of a decline in nutrient input from the catchment. The local government carried out strong action to reduce the nutrient input from the catchment in 1995 (Chen *et al.*, 2003). Thus, both Meiliang Bay and the lake centre showed a recovery process from 1997 and onwards (Figure 5). As shown for Lake Constance (Gaedke, 1998) or other eutrophic lakes, the first step to restoring Lake Taihu must be to cut the nutrient loading from the catchment, even if it will take a long time to get a response from such a large waterbody.

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