

TN : TP ratio and planktivorous fish do not affect nutrient-chlorophyll relationships in shallow lakes

HAI-JUN WANG*, XIAO-MIN LIANG*, PING-HONG JIANG*[†], JIAN WANG*,
SHI-KAI WU*[†] AND HONG-ZHU WANG*

*State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China

[†]Graduate School of Chinese Academy of Sciences, Beijing, China

SUMMARY

1. In previous work, phytoplankton regulation in freshwater lakes has been associated with many factors. Among these, the ratio of total nitrogen to total phosphorus (TN : TP) has been widely proposed as an index to identify whether phytoplankton are N- or P-limited. From another point of view, it has been suggested that planktivorous fish can be used to control phytoplankton.
2. Large-scale investigations of phytoplankton biomass [measured as chlorophyll *a*, (chl-*a*)] were carried out in 45 mid-lower Yangtze shallow lakes to test hypotheses concerning nutrient limitation (assessed with TN : TP ratios) and phytoplankton control by planktivorous fish.
3. Regression analyses indicated that TP was the primary regulating factor and TN the second regulating factor for both annual and summer phytoplankton chl-*a*. In separate nutrient–chl-*a* regression analyses for lakes of different TN : TP ratios, TP was also superior to TN in predicting chl-*a* at all particular TN : TP ranges and over the entire TN : TP spectrum. Further analyses found that chl-*a* : TP was not influenced by TN : TP, while chl-*a* : TN was positively and highly correlated to TP : TN.
4. Based on these results, and others in the literature, we argue that the TN : TP ratio is inappropriate as an index to identify limiting nutrients. It is almost impossible to specify a 'cut-off' TN : TP ratio to identify a limiting nutrient for a multi-species community because optimal N : P ratios vary greatly among phytoplankton species.
5. Lakes with yields of planktivorous fish (silver and bighead carp, the species native to China) >100 kg ha⁻¹ had significantly higher chl-*a* and lower Secchi depth than those with yields <100 kg ha⁻¹. TP–chl-*a* and TP–Secchi depth relationships are not significantly different between lakes with yields >100 kg ha⁻¹ or <100 kg ha⁻¹. These results indicate that the fish failed to decrease chl-*a* yield or enhance Z_{SD} . Therefore, silver carp and bighead carp are not recommended as a biotic agent for phytoplankton control in lake management if the goal is to control the entire phytoplankton and to enhance water quality.

Keywords: chlorophyll-*a*, phytoplankton, planktivorous fish, total nitrogen : total phosphorus ratio, total phosphorus

Correspondence: Hong-Zhu Wang, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, Hubei Province, China. E-mail: wanghz@ihb.ac.cn

Introduction

Phytoplankton abundance [measured as chlorophyll-*a* (chl-*a*)] in freshwater lakes has been associated with many factors in previous studies. Among these

factors, phosphorus (P) is usually regarded as the primary limiting nutrient. Many total P (TP)–chl-*a* relations have been published (Dillon & Rigler, 1974; Peters, 1986; Florida LAKEWATCH, 2000). However, large unexplained variations usually occur in the relations. The variations have been often regarded as the results of total nitrogen (TN) limitation. Accordingly, ratio of TN : TP was proposed as an index to divide lakes into N- and P-limited categories (Canfield, 1983; Florida LAKEWATCH, 2000). Generally, lakes have been regarded as limited by TP if TN : TP was relatively large, limited by TN if TN : TP was relatively small and co-limited by TN and TP when TN : TP was intermediate. However, the thresholds of TN : TP to indicate nutrient limitation have varied greatly in the literature, being, for instance, 10–17 by Sakamoto (1966), 10–30 by Huber *et al.* (1982) and 7–15 by OECD (2006). Further research is necessary to test whether TN : TP might be used as an index to indicate the nutrient limitation of phytoplankton.

Planktivorous fish have also been regarded as an important factor regulating phytoplankton growth. Silver carp [*Hypophthalmichthys molitrix* (Cuvier et Valenciennes)] and bighead carp [*Aristichthys nobilis* (Richardson)] are two of the species that have received attention. These Chinese species have been proposed to be effective in controlling scum-forming phytoplankton (Starling & Rocha, 1990; Datta & Jana, 1998). However, when the focus is on the entire phytoplankton community (represented as chl-*a*), the effectiveness of using these fish to control phytoplankton is still debated. Some studies (Starling, 1993; Datta & Jana, 1998) found a decrease in chl-*a* when fish were present while others found an increase (Laws & Weisburd, 1990; Lieberman, 1996). Further work is needed to test whether planktivorous fish are effective in controlling phytoplankton chl-*a*. Because all previous conclusions have been deduced from small-scale experiments, large-scale field investigations are needed.

In the Yangtze Basin of China there are hundreds of shallow lakes, with a combined total area exceeding 20 000 km² (Liu, 1984). They play an important role in drinking water abstraction, aquaculture, sightseeing and so on. Many lakes in the basin have suffered for decades from man-made eutrophication, causing increased production of phytoplankton, resulting in toxic algal blooms, fish kills and lowered water clarity (Jin, 2003). However, research on chl-*a* regulation in

Yangtze lakes is at an early stage. Relevant work has only been carried out in a few specific lakes, such as Lake Taihu (Chen *et al.*, 2003) and Lake Donghu (Li *et al.*, 1995), and it is difficult to extrapolate results to other lakes. Jin *et al.* (1992) established nutrient–chl-*a* models based on research material from 16 Chinese lakes and reservoirs. Their models, however, included data from 9 non-Yangtze lakes, and the models may have little power to predict chl-*a* variations in mid-lower Yangtze lakes.

The universal overgrowth of phytoplankton and the scarcity of relevant research in the Yangtze Basin make it urgent to discover the general mechanisms of phytoplankton regulation in the basin. Moreover, the abundance of shallow lakes in the Yangtze Basin provides the basis for a contribution to understanding phytoplankton regulation in shallow lakes worldwide. The present study was conducted in 35 shallow lakes and 10 fishponds in the mid-lower Yangtze Basin. Our objectives are (i) to determine the key factor regulating phytoplankton in the basin and establish general empirical chl-*a* models; (ii) to test whether TN : TP can be used as an index of nutrient limitation of phytoplankton and (iii) to test whether planktivorous fish are effective in controlling phytoplankton in these natural lake ecosystems.

Methods

All the 35 shallow lakes and 10 fishponds are located in the mid-lower Yangtze Basin (Fig. 1). The annual air temperature is 15–20 °C and precipitation 1200–1600 mm (Changchun Institute of Geography and Chinese Academy of Sciences, 1998).

Field investigations were conducted in the period December 2001–05. Samples were taken seasonally or bimonthly. Water samples were taken near the surface and at the bottom at each site, combined and brought back for laboratory analysis. Chl-*a*, TN and TP were determined according to Chinese Water Analysis Methods Standards (Huang, Chen & Cai, 1999). Chl-*a* was measured after acetone extraction by reading absorbance at 665 and 750 nm using a spectrophotometer (Unico UV-2000, Shanghai, China). TN was determined using an alkaline potassium persulfate digestion-UV spectrophotometric method and TP by the ammonium molybdate-ultraviolet spectrophotometric method. Water depth and Secchi depth were measured once at each site. Water temperature, pH

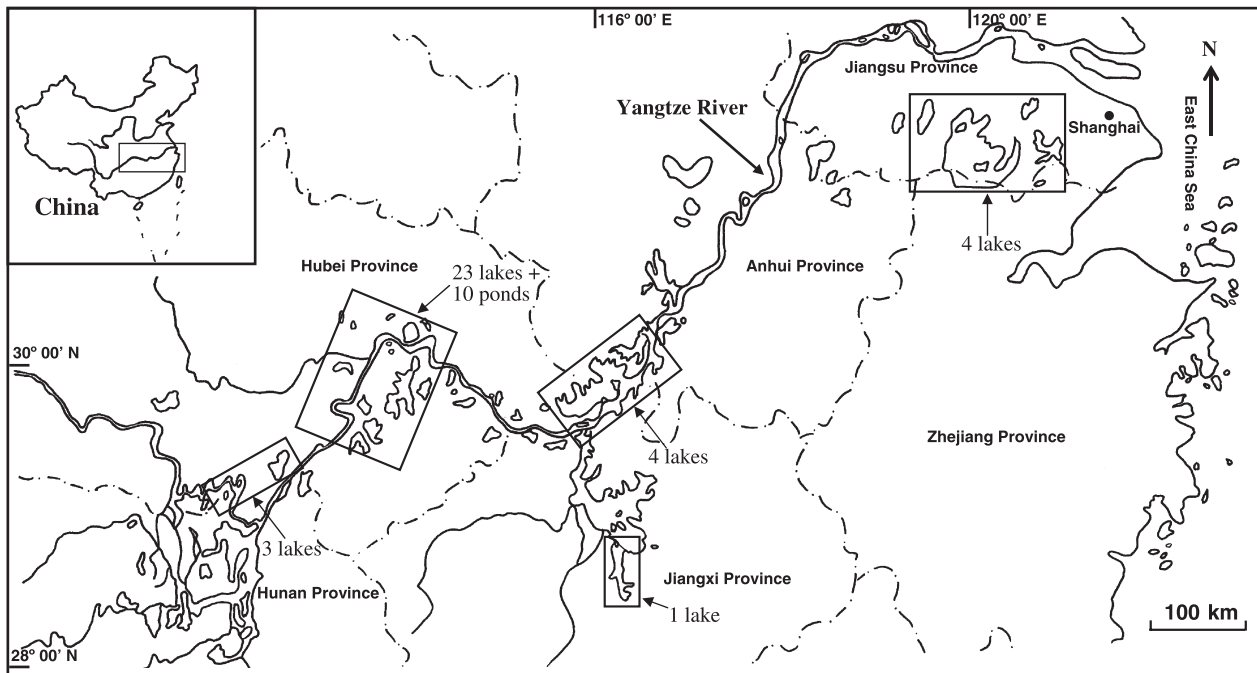


Fig. 1 Distribution of research lakes along the Yangtze River.

and conductivity were measured in the field with a probe (YSI Environmental Monitoring System 6600; YSI Incorporated, Yellow Springs, OH, U.S.A.). Submersed macrophytes were sampled 2–4 times at each site using scythes, then cleaned, superfluous water removed and weighed for wet mass. We obtained fish yield data from detailed records held by local fish culture farms and dealers in food fish.

To test the effects of TN : TP ratio on nutrient–chl-*a* relationships over the full range, we performed regression analyses for data of all the lakes and years following the procedures of Prairie, Duarte & Kalff (1989): (i) all lakes were ordered by their TN : TP ratios, starting at the lower end of the TN : TP spectrum; (ii) one natural log unit was set as a window width and 15 lakes were randomly selected within each TN : TP ratio window width; (iii) linear regressions between $\log_{10}(\text{TP})$, $\log_{10}(\text{TN})$ and $\log_{10}(\text{chl-}a)$ were performed, and regression statistics (coefficient of determination and mean TN : TP ratio) for the selected lakes were determined; (iv) steps 2–3 were repeated five times per window; (v) the window was moved forward along the TN : TP spectrum by a distance of 0.25 \log_{10} -unit and (vi) steps 2–4 were repeated until the complete spectrum had been covered.

Lakes were divided into two groups [planktivorous fish yield ($\text{FY}_{\text{Plankt}}$) $< 100 \text{ kg ha}^{-1}$ and $\text{FY}_{\text{Plankt}} > 100$

kg ha^{-1}] to analyse the effects of planktivorous fishes on absolute chl-*a* and nutrient–chl-*a* relationships. The regressions were performed based on monthly data. All lakes containing macrophytes were excluded to avoid potential confounding effects of macrophytes.

To evaluate the predictive abilities of the models, we calculated the percentage model error (PE) using the formula in Canfield & Bachmann (1981): $\sum |P/O - 1| \times 100/n$. In the formula, P is untransformed predicted chl-*a* and O is observed chl-*a*. In this calculation of PE, division by observed chl-*a* (O) and sample size (*n*) allows us to compare the precision of different models based on different sample sizes and absolute chl-*a* levels.

STATISTICA 6.0 was used for analyses of Pearson's correlation, Spearman's rank correlation, simple regression, stepwise multiple regression and ANOVA. We tested the data for normal distribution and transformed where necessary. A *t*-test was used to test for differences between regression lines.

Results

Limnological characteristics of the lakes

The lakes in this study represent a wide range of limnological conditions (Table 1). According to the

Table 1 Limnological characteristics of the research lakes

Parameters	<i>n</i>	Mean	Median	Min.	Max.	SD	CV (%)
L_{Max} , maximum length of lakes (km)	45	9.44	4.43	0.03	68.50	12.12	128
Area, lake surface area, A_o (km ²)	45	88.6	7.9	0.0004	2338	350.5	395
Z_{Max} , maximum depth of lakes (m)	45	3.31	2.32	0.60	25	4.29	130
Z_{Mean} , lake-specific mean depth calculated as V/A_o (m)	45	1.91	1.80	0.60	6.00	1.02	53
D_V , development of lake volume, $3Z_{Mean}/Z_{Max}$	45	2.24	2.31	0.54	3.00	0.63	28
Chl- <i>a</i> , phytoplankton chlorophyll <i>a</i> (mg m ⁻³)	80	30.0	5.7	0.7	294.6	55.4	185
<i>Z</i> , site-specific water depth (m)	71	2.11	1.97	0.60	7.03	1.07	51
Z_{SD} , Secchi depth (m)	78	1.00	0.79	0.08	3.26	0.72	72
<i>T</i> , water temperature (°C)	76	21.31	21.08	11.42	30.38	4.62	22
Cond, conductivity of lake water (mS cm ⁻¹)	64	0.32	0.28	0.11	1.08	0.17	53
pH	75	8.01	7.98	7.22	8.93	0.30	4
TN, total nitrogen concentration of water (mg m ⁻³)	66	2586	1151	74	13 690	3011	116
TP, total phosphorus concentration of water (mg m ⁻³)	70	200	54	5	1424	328	164
TN : TP, ratio of TN to TP by mass	66	27.0	19.3	5.1	231.9	30.7	114
B_{Mac} , submersed macrophyte biomass, wet mass (g m ⁻²)	78	852	50	0	9484	1817	213
FY _{Herb} , yield of herbivorous fishes (kg ha ⁻¹)	12	76	26	2	341	105	138
FY _{Carn} , yield of carnivorous fishes (kg ha ⁻¹)	12	175	9	2	1787	511	292
FY _{Plankt} , yield of planktivorous fishes (kg ha ⁻¹)	14	425	99	1	3000	818	192
FY _{Omn} , yield of omnivorous fishes (kg ha ⁻¹)	15	143	57	2	1115	291	203
FY _{Other} , yield of other fishes (kg ha ⁻¹)	10	51	44	6	182	52	102
FY _{Tot} , yield of entire fish assemblage (kg ha ⁻¹)	37	1076	250	59	15 544	2666	248
FY _{Herb} %	12	12.4	11.5	0.1	36.3	10.2	82
FY _{Carn} %	12	8.1	4.0	0.1	38.5	10.5	130
FY _{Plankt} %	14	40.5	32.4	1.7	95.2	29.2	72
FY _{Omn} %	15	24.8	24.0	1.0	74.6	21.5	87
FY _{Other} %	10	16.7	7.6	0.6	62.6	20.1	120

n, sample number; SD, standard deviation; CV, coefficient of variation.

Table 2 Pearson (upper triangle) and Spearman's rank (lower triangle) correlation coefficients (*r*) between annual variables

	Chl- <i>a</i>	L_{Max}	A_o	D_V	<i>Z</i>	Z_{SD}	pH	Cond	TN	TP	TN : TP	B_{Mac}	FY _{Plankt}	FY _{Tot}
Chl- <i>a</i>		-0.28*	-0.07	0.52***	-0.37**	-0.46***	0.58***	0.50***	0.72***	0.91***	-0.42**	-0.23*	0.95***	0.62***
L_{Max}	-0.45***		0.86***	-0.42***	0.24*	0.10	-0.13	-0.39**	-0.26*	-0.30*	0.13	-0.03	-0.38	-0.26
A_o	-0.45***	0.97***		-0.07	-0.03	-0.11	-0.11	-0.15	-0.07	-0.11	0.14	-0.07	-0.25	-0.11
D_V	0.44***	-0.72***	-0.70***		-0.40**	-0.26**	-0.12	0.40**	0.50***	0.53***	-0.20	-0.14	0.37	0.44**
<i>Z</i>	-0.29*	0.39*	0.35**	-0.20		0.49***	-0.13	-0.32*	-0.34**	-0.40**	0.05	0.11	-0.22	-0.14
Z_{SD}	-0.76***	0.43***	0.46***	-0.45***	0.50***		-0.06	-0.62***	-0.50***	-0.49***	0.41**	0.56**	-0.36	-0.34*
pH	0.03	0.00	0.01	0.01	0.03	0.05		0.081	0.32*	0.52***	-0.28*	0.03	0.16	-0.08
Cond	0.65***	-0.54***	-0.54***	0.28*	-0.46***	-0.72***	-0.05		0.72***	0.58***	-0.23	-0.30*	0.82**	0.56***
TN	0.77***	-0.44***	-0.44***	0.47***	-0.28*	-0.72***	0.18	0.63***		0.84***	-0.23	-0.30*	0.94***	0.30
TP	0.85***	-0.40**	-0.42***	0.41***	-0.33**	-0.86***	0.15	0.65***	0.82***		-0.43**	-0.27*	0.98***	0.38*
TN : TP	-0.44***	0.31*	0.35**	-0.29*	0.20	0.51***	-0.26*	-0.39**	-0.14	-0.59***		0.14	-0.49	-0.31
B_{Mac}	-0.77***	0.32**	0.35**	-0.40***	0.13	0.79***	0.01	-0.55***	-0.63***	-0.80***	0.41***		-0.33	-0.19
FY _{Plankt}	0.45***	-0.74***	-0.81***	0.23	-0.40	-0.49*	-0.43	0.71*	0.18	0.54*	-0.77**	-0.58*		0.80***
FY _{Tot}	0.36*	-0.79***	-0.83***	0.34*	-0.47**	-0.53**	-0.46**	0.77***	0.29	0.37*	-0.27	-0.31	0.93***	
<i>n</i>	80	80	80	80	80	78	75	63	66	70	64	78	14	37

chl-*a*, phytoplankton chlorophyll *a*; L_{Max} , maximum lake length; A_o , lake surface area; D_V , development of lake volume; *Z*, site-specific water depth; Z_{SD} , Secchi depth; Cond, conductivity; TN, total nitrogen; TP, total phosphorus; B_{Mac} , submersed macrophyte biomass; FY_{Plankt}, yield of planktivorous fishes; FY_{Tot}, yield of entire fish assemblage.

Significant correlations (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$) in bold letters.

fixed boundary classification system for lake trophic states accepted by OECD (2006), many lakes (98% assessing by Secchi depth, 54% by annual chl-*a* and

39% by summer chl-*a*) are in eutrophic–hypertrophic states. Dominant algae in these waters are Cyanophyta (mainly *Microcystis*), Bacillariophyta

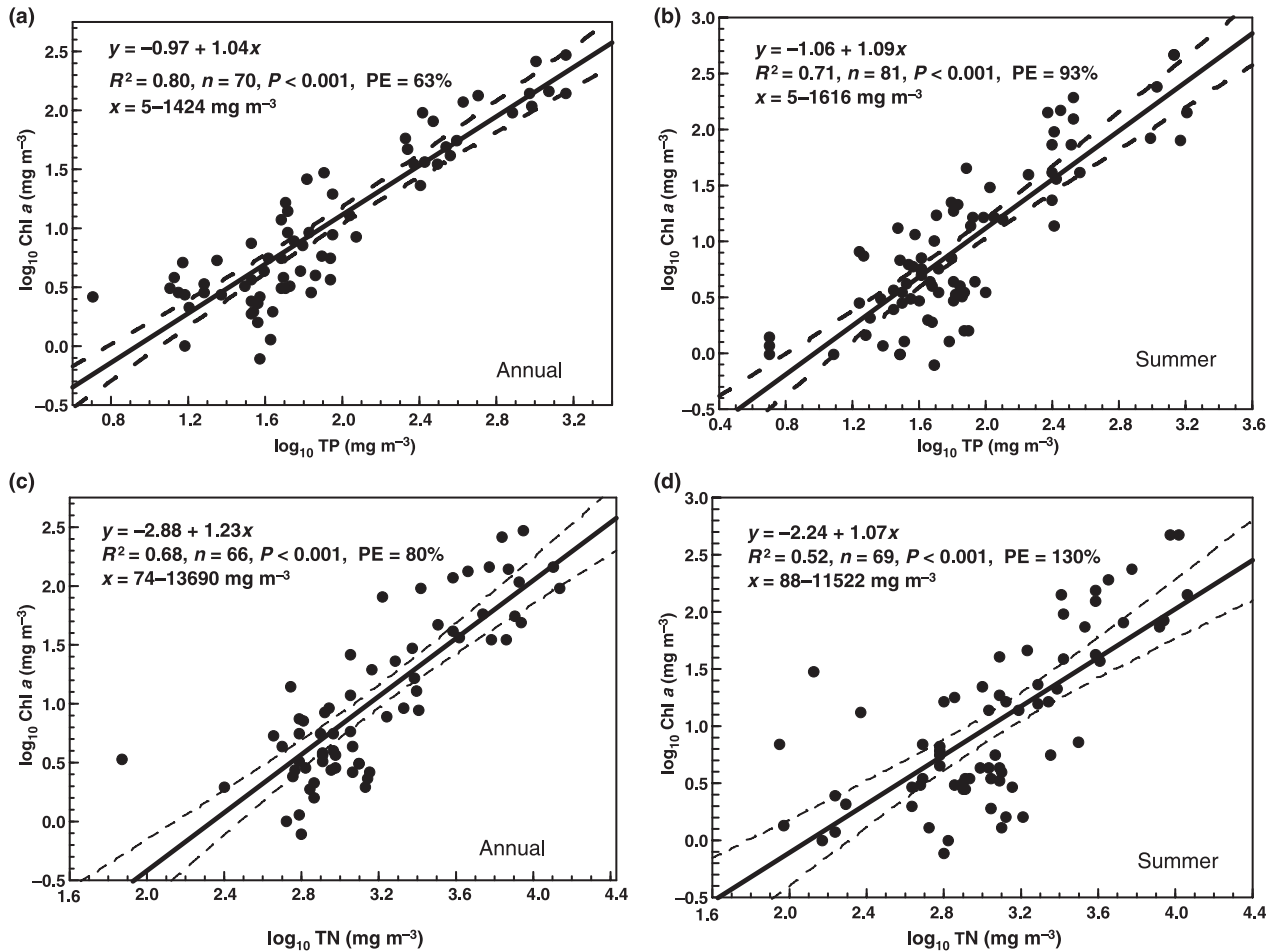


Fig. 2 Relationships between phytoplankton chlorophyll *a* (chl-*a*) and total nitrogen (TN) (a) overall and (b) in summer, and between chl-*a* and total phosphorus (TP) (c) overall and (d) in summer. PE, percentage error, calculated by the formula in Canfield & Bachmann (1981): $\sum |P/O - 1| \times 100/n$, where P is untransformed predicted chl-*a* and O is observed chl-*a*. Dashed lines indicate the 95% confidence limits.

(mainly *Cyclotella*) and Chlorophyta (mainly *Scenedesmus*). Fish assemblages in most lakes are dominated by planktivores, mainly silver and bighead carps (Table 1).

Key factor analyses and nutrients–chl-*a* models

Chlorophyll-*a* is significantly correlated with most environmental factors (Table 2). It is positively related to lake volume (D_V), conductivity, TN, TP, planktivorous fishes yield (FY_{Plankt}), total fish yields (FY_{Tot}) and negatively related to site-specific water depth (Z), Secchi depth (Z_{SD}), TN : TP and submersed macrophyte biomass (B_{Mac}). Both Pearson and Spearman's rank correlations yielded closest relations between TP and chl-*a*. Factors that are correlated significantly with

chl-*a* are also significantly correlated with TP. Stepwise multiple regressions made for absolute and normalized data both showed that TP entered first, making the greatest contribution to explaining chl-*a* variations. All the analyses based on summer (June–September) data also determined TP to be the factor most closely related to chl-*a*. In addition, TN had a highly significant correlation with chl-*a* (Table 2). Figure 2 shows the regression models of chl-*a* based on TP and TN.

Effects of TN : TP ratios on nutrient–chl-*a* relations

Separate nutrient–chlorophyll regressions were analysed for lakes with different TN : TP ratios by mass (according to the TN : TP thresholds proposed by

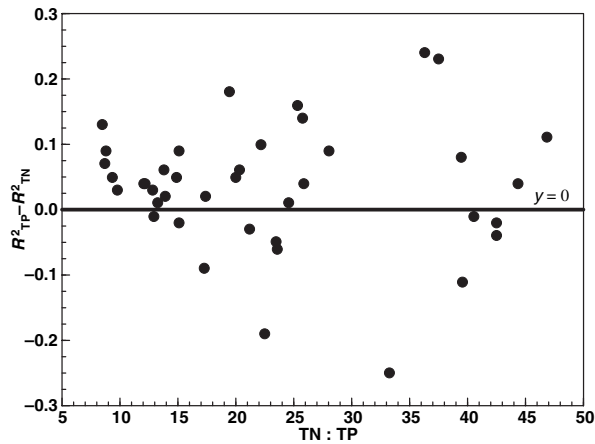


Fig. 3 The differences between R^2 values for regressions of total phosphorus (TP) against chlorophyll *a* (chl-*a*) and total nitrogen (TN) against chl-*a* over the complete TN : TP spectrum.

Sakamoto, 1966) (Table 3). Almost all the TP–chl-*a* regressions had higher coefficients of determination (R^2) and lower PE than the TN–chl-*a* regressions.

We further compared the differences between R^2 -values based on TP–chl-*a* and TN–chl-*a* regressions over the complete TN : TP spectrum, according to the method described by Prairie *et al.* (1989). The results (Fig. 3) show that 28, or 70% of R^2 -values for TP–chl-*a* regressions were higher than R^2 -values for TN–chl-*a* regressions over the entire TN : TP spectrum. The 28 points were not confined to any specific region of higher TN : TP ratios.

For a given amount of TP, chl-*a* varied regardless of the changes in TN (Fig. 4a,b). Within the TN : TP

range of the present research, chl-*a* : TP trended towards a specific value, namely the median value of 0.13 (for both annual and summer cases). For a given amount of TN, chl-*a* increased rapidly with an increase in TP (Fig. 4c,d). Further analysis showed that TN changes simultaneously with TP (Fig. 5).

Effect of planktivorous fish on water quality

The lakes with high yields of planktivorous fish ($FY_{\text{Plankt}} > 100 \text{ kg ha}^{-1}$) had significantly higher chl-*a* ($P < 0.001$, $t = 7.40$, $t_{0.001,35} = 3.60$) and lower Z_{SD} ($P < 0.001$, $t = 5.93$, $t_{0.001,34} = 3.60$) than those with low fish yields ($FY_{\text{Plankt}} < 100 \text{ kg ha}^{-1}$). The separate regression lines in both Fig. 6a,b did not differ significantly from each other (Fig. 6a, $t = 0.40$ for the slope difference and 0.52 for the intercept difference, $P > 0.50$; in Fig. 6b, $t = 0.67$ for the slope difference and 0.22 for the intercept difference, $P > 0.05$; $t_{0.50,70}$, $t_{0.50,80} = 0.68$).

Discussion

All the analyses of Pearson and Spearman's rank correlations and stepwise multiple regressions based on summer and annual data indicated that TP makes the greatest contribution to explain variations in chl-*a*. Therefore, TP can be statistically regarded as the most important factor regulating chl-*a* in these waters.

Traditionally, TN : TP was proposed as an index to divide lakes into N- and P-limited categories

Table 3 Predictive power (R^2 and PE) of nutrient-chlorophyll *a* models ($y = b_0 + b_1x$) for lakes with different TN : TP ratios

Condition	y (mg m^{-3})	x (mg m^{-3})	b_0	b_1	R^2	PE(%)
Annual						
TN : TP < 10, $n = 14$	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TP})$	-1.34	1.20	0.86	59
	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TN})$	-1.96	1.08	0.82	77
10 < TN : TP < 17, $n = 15$	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TP})$	-1.75	1.34	0.83	52
	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TN})$	-3.48	1.42	0.80	57
TN : TP > 17, $n = 37$	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TP})$	-0.87	1.00	0.73	54
	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TN})$	-2.60	1.10	0.66	59
Summer						
TN : TP < 10, $n = 20$	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TP})$	-1.11	1.09	0.79	78
	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TN})$	-1.39	0.90	0.65	104
10 < TN : TP < 17, $n = 22$	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TP})$	-1.99	1.59	0.74	99
	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TN})$	-3.72	1.57	0.72	109
TN : TP > 17, $n = 27$	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TP})$	-0.65	0.82	0.50	75
	$\log_{10}(\text{chl-}a)$	$\log_{10}(\text{TN})$	-1.88	0.84	0.48	69

R^2 represents the explanation of $\log_{10}(\text{TP})$ or $\log_{10}(\text{TN})$ on the variations of $\log_{10}(\text{chl-}a)$. PE represents the percentage predictive error of chl-*a* by TP or TN, calculated as the differences between absolute predicted (P) and observed (O) chl-*a* by the following formula (Canfield & Bachmann (1981): $\sum |P/O - 1| \times 100/n$.

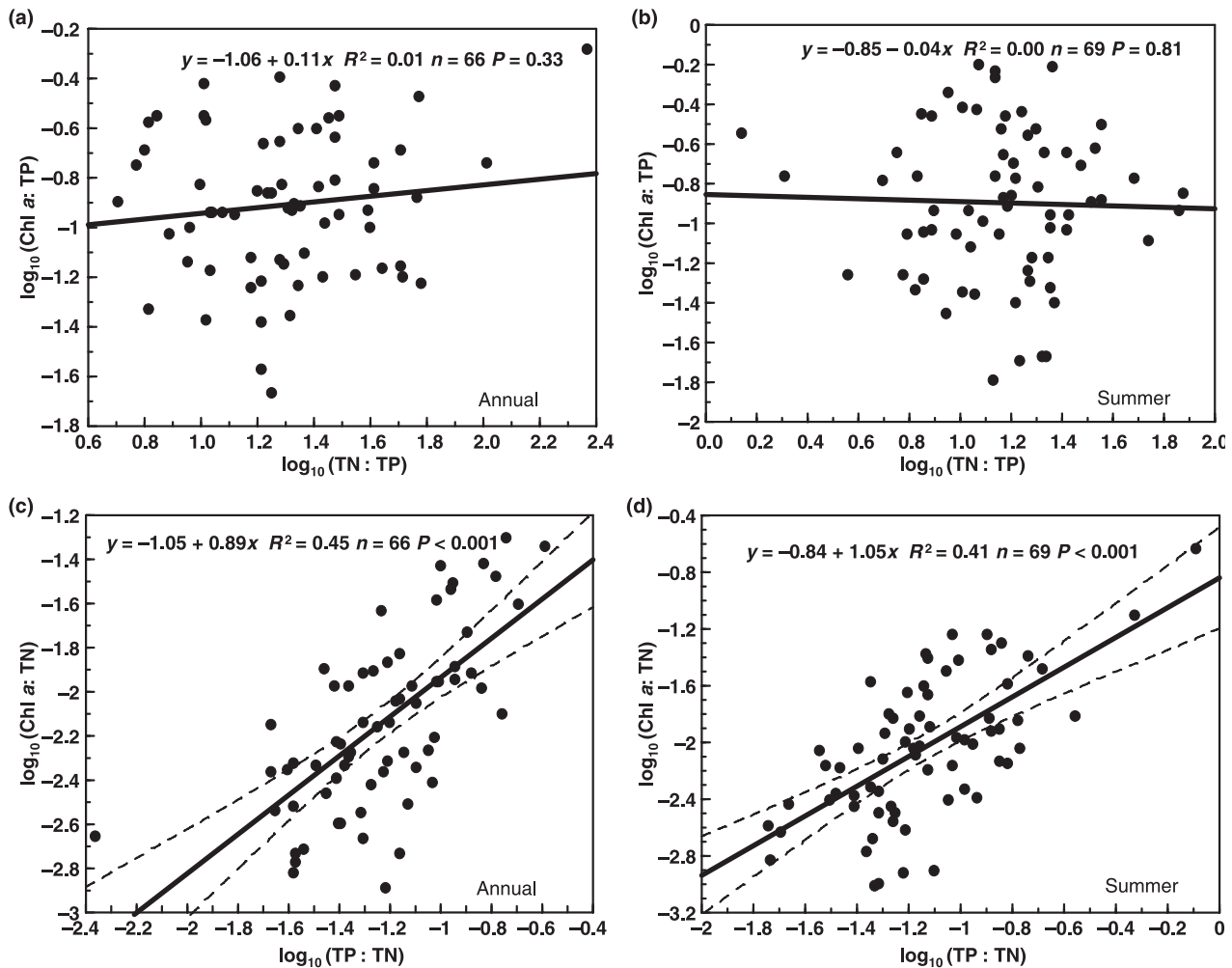


Fig. 4 Relationships between the ratio of chlorophyll *a* to total phosphorus (chl-*a* : TP) and the ratio of total nitrogen to total phosphorus (TN : TP) (a) overall and (b) in summer, and between chl-*a* : TN and TP : TN (c) overall and (d) in summer. Dashed lines indicate the 95% confidence limits.

(Canfield, 1983; Florida LAKEWATCH, 2000; OECD, 2006). Generally, phytoplankton in lakes have been regarded as limited by TP if TN : TP was relatively large, limited by TN if TN : TP was relatively small. In the current research, separate regressions for lakes with different TN : TP ratios shows that all the TP–chl-*a* regressions had higher coefficients of determination (R^2) and lower PE than those of TN–chl-*a* regressions. This emphasizes the superiority of TP over TN as a predictor in all cases and also the failure of TN : TP to indicate nutrient limitation.

Because different TN : TP thresholds have been proposed to indicate N or P limitation in literature, we further compared the differences of R^2 -values between TP–chl-*a* and TN–chl-*a* regressions over the complete TN : TP spectrum. Seventy per cent of

R^2 -values for TP–chl-*a* regressions were higher than those for TN–chl-*a* regressions over the entire TN : TP spectrum (Fig. 3). According to the conventional expectation, the lakes involved should have relatively higher TN : TP ratios. However, the cases in point were not confined to any specific region of higher TN : TP ratios. These results demonstrate a failure of TN : TP to indicate nutrient limitation.

Some limnologists use the ratio C : N : P (106 : 16 : 1 by atoms, 41 : 7 : 1 by mass) proposed by Redfield, Ketchum & Richards (1963) as a criterion to assess nutrient limitation. However, this does not take into account that the Redfield ratio is not a universal optimum ratio, but an average of species-specific ratios. Optimal N : P ratios vary greatly among various freshwater phytoplankton species, ranging

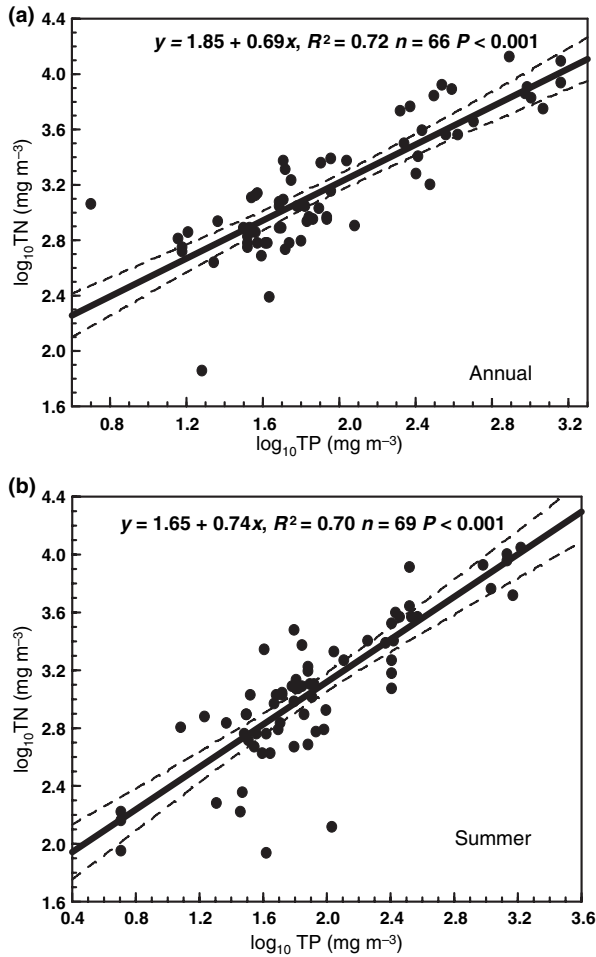


Fig. 5 Relationships between total nitrogen (TN) and total phosphorus (TP) (a) overall and (b) in summer. Dashed lines indicate the 95% confidence limits.

from 4.1 to 133.3 (cf. Smith, 1982; Klausmeier *et al.*, 2004). Therefore, it is almost impossible to set a specific 'cut-off' ratio to identify a limiting nutrient(s) for a multiple-species community.

To differentiate the effects of TN and TP on chl-*a*, we regressed chl-*a* : TP to TN : TP and chl-*a* : TN to TP : TN. The results show that chl-*a* varies regardless of the changes of TN for a given amount of TP (Fig. 4a,b) but increases rapidly with an increase of TP for a given amount of TN (Fig. 4c,d). This means that TN itself does not limit chl-*a* in these lakes. The close relationship between TN and chl-*a* is actually due to the simultaneous changes of TN with TP (Fig. 5).

Based on the analyses above, we suggest that it is inappropriate to use the TN : TP ratio to classify lakes

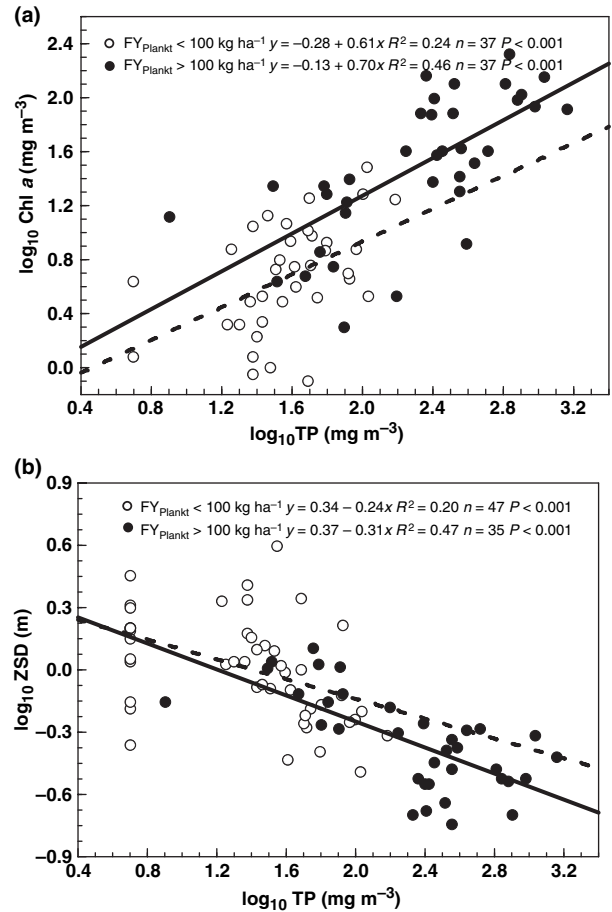


Fig. 6 Regressions between total phosphorus (TP) and chlorophyll *a* (chl-*a*) (upper panel) and between TP and Secchi depth (Z_{SD}) (lower panel) for lakes with different yields of planktivorous fish (FY_{Plankt}). The regressions were performed based on monthly data. All lakes containing macrophytes were excluded to avoid potential confounding effects of macrophytes.

into N- or P-limited classes, and that TP is the primary nutrient limiting phytoplankton over the entire TN : TP spectrum. The results from whole-lake enrichment experiments (Schindler, 1977) also suggest TP as the primary limiting nutrient. The lack of a mechanism to correct for P deficiency has been attributed to widely occurring P limitation (Schindler, 1977). On the other hand, there are natural compensating mechanisms for nitrogen, such as N₂ fixation from the atmospheric cycle.

We also tested whether planktivorous fish are effective in controlling phytoplankton. The lakes with yields of planktivorous fish (FY_{Plankt}) $> 100 \text{ kg ha}^{-1}$ had significantly higher chl-*a* and lower Z_{SD} than those with $FY_{\text{Plankt}} < 100 \text{ kg ha}^{-1}$. The regression

lines of $\log_{10}(\text{TP})$ with $\log_{10}(\text{chl-}a)$ and $\log_{10}(Z_{\text{SD}})$ for lakes with different $\text{FY}_{\text{Plankt}}$ do not differ significantly from each other. This indicates the failure of the fish species concerned to reduce chl-*a* yield and enhance Z_{SD} . Lieberman (1996) obtained similar results in his 3-year experiments. The mean chl-*a* concentrations increased from 42.60 to 78.79 mg m^{-3} and the turbidity increased from 9 to 15 NTU in his ponds containing silver and bighead carps, though the scum-formed phytoplankton (*Rhizoclonium* spp.) had all but disappeared. On the other hand, a decrease in chl-*a* was reported by Starling (1993). However, this conclusion was based on a 38-day experiment in fiberglass tanks (2 m in diameter and 3 m in height). Such a result from limited time and limited space may not adequately reflect the long-term response of natural phytoplankton under grazing pressure.

The failure of these fish to reduce chl-*a* may mainly be due to mechanisms related to size-dependent grazing efficiency. Both silver and bighead carps are highly opportunistic omnivores. They are ineffective in filtering particles $<10 \mu\text{m}$ (Smith, 1989). By eliminating large-sized phytoplankton (competitors of small-sized species) and zooplankton (grazers of small-sized species), they may shift the phytoplankton assemblages from large-sized, highly vulnerable individuals to small-sized, less vulnerable forms (Smith, 1989; Lieberman, 1996). Many reports have pointed out that dominance of small-sized species is a general result of stocking of silver and bighead carps (Laws & Weisburd, 1990; Miura, 1990; Xie, 2003). Briefly, the compensatory shifts mean we can expect a constant increase in chl-*a* from inedible phytoplankton assemblages. Another mechanism may also explain the failure of these fishes to reduce chl-*a*: feeding and excretion by planktivores may accelerate nutrient cycling (Opuszyński, 1981; Chen, Liu & Hua, 1991) and an increased rate of nutrient circulation may lead to higher algal growth. For lake management, these two fish species cannot be recommended as a biotic agent for phytoplankton control if the goal is to control the entire phytoplankton and enhance water quality.

In conclusion, based on large-scale field investigations, we argue that the TN : TP ratio is inappropriate to be used as an index to discriminate lakes as N- or P-limited. For all our TN : TP cases, TP was the primary factor regulating phytoplankton chl-*a*. Stocking with planktivorous fishes (silver and bighead carp), cannot reduce chl-*a* and enhance Z_{SD} and, in

fact biomanipulation by stocking might result in an increase in biomass of small-sized taxa and the entire phytoplankton and hence a reduction in water quality. For lake management for phytoplankton control, nutrients abatement should be the primary target.

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