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Boqiang Qin[1, 2]*, Jian Zhou[1], James J. Elser[3], Wayne S. Gardner[4], Jianming Deng[1], Justin D. Brookes[5]

[1] State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, 73 East Beijing Road, Nanjing 210008, P. R. China.

[2] School of Geography & Ocean Science, Nanjing University, 163 Xianlin Street, Nanjing 210023, P. R. China.

[3] Flathead Lake Biological Station, University of Montana, Polson, MT 59860, School of Life Sciences & School of Sustainability, Arizona State University, Tempe, AZ 85287-4501.

[4] Marine Science Institute, University of Texas at Austin, Port Aransas, TX 78373, USA.

[5] Water Research Centre, School of Biological Sciences, The University of Adelaide, Benham Building, South Australia 5005, Australia.

*Correspondence to: qinbq@niglas.ac.cn.

20   **Abstract:** Eutrophication mitigation is an ongoing priority for aquatic ecosystems. However, the

21   current eutrophication control strategies (phosphorus (P) and/or nitrogen (N)) are guided mainly

22   by nutrient addition experiments in small waters without encompassing all in-lake biogeochemical

23   processes that are associated largely with lake morphological characteristics. Here we use a global

24   lake data set (573 lakes) to show that the relative roles of N vs. P in affecting eutrophication are

25   underpinned by water depth. Mean depth and maximum depth relative to mixing depth were used

26   to distinguish shallow (mixing depth > maximum depth), deep (mixing depth < mean depth), and

27   transitional (mean depth $\leqslant$ mixing depth $\leqslant$ maximum depth) lakes in this study. TN:TP ratio (by

28   mass) was used as an indicator of potential lake nutrient limitation, i.e. N only limitation if N:P <

29   9, N+P co−limitation if $9 \leqslant$ N:P < 22.6 and P only limitation if N:P $\geqslant$ 22.6. The results show that

30   eutrophication is favored in shallow lakes, frequently (66.2%) with N limitation while P limitation

31   predominated (94.4%) in most lakes but especially in deep ones. The importance of N limitation

32   increases but P limitation decreases with lake trophic status while N and P co-limitation occurs

33   primarily (59.4%) in eutrophic lakes. These results demonstrate that phosphorus reduction can

34   mitigate eutrophication in most large lakes but a dual N and P reduction may be needed in

35   eutrophic lakes, especially in shallow ones (or bays). Our analysis helps clarify the long debate

36   over whether N, P, or both control primary production. While these results imply that more

37   resources be invested in nitrogen management, given the high costs of nitrogen pollution reduction,

38   more comprehensive results from carefully designed experiments at different scales are needed to

39   further verify this modification of the existing eutrophication mitigation paradigm.

40

41   **Key words**: Eutrophication, Water depth, P-limitation, N and P co-limitation

42

43   **Table of Contents graphic**

Shallow lake   Deep lake
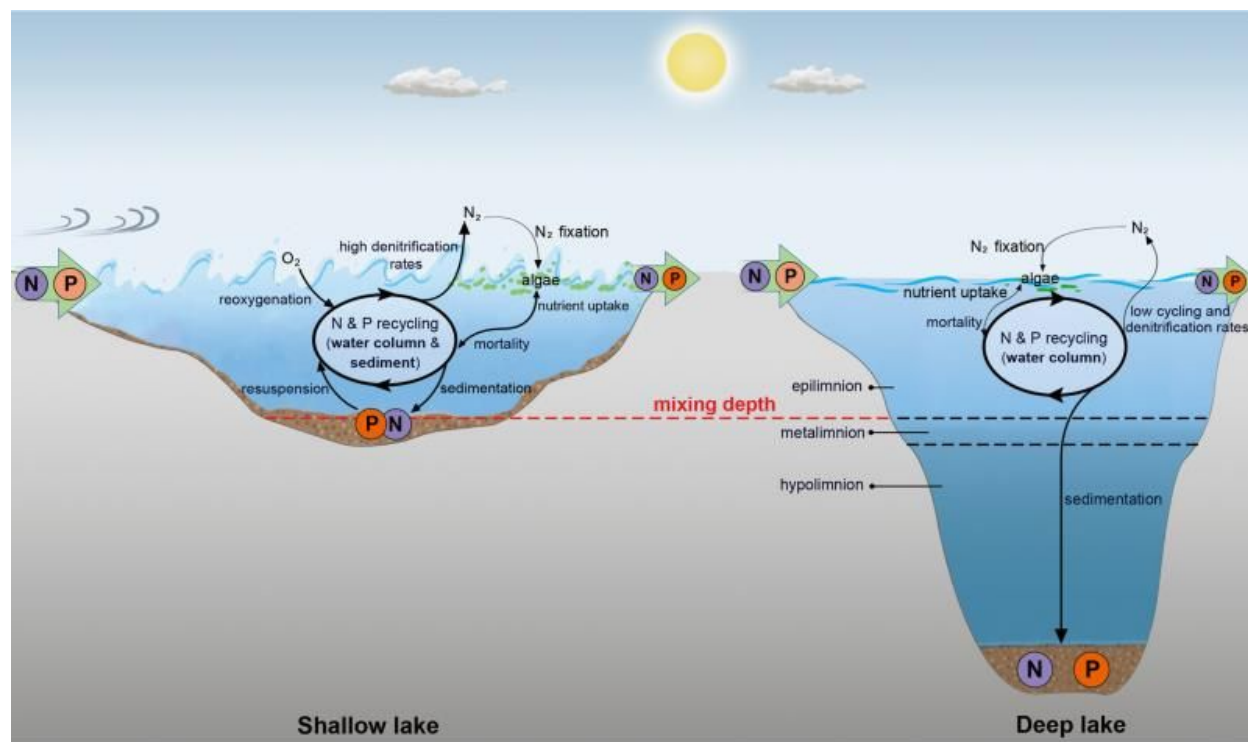
45   Water depth differentiate the effects of in-lake biogeochemical processes between shallow and

46   deep lakes.

47

1. INTRODUCTION

48

49   Increased nutrient loading combined with global climate change has increased the frequency

50   and global proliferation of harmful algal blooms, harming biodiversity, water quality, and human

51   health.[1] Economic losses due to this eutrophication have been estimated as at least $2.2 billion

52   annually in U.S. fresh waters.[2] Despite considerable investment to control nutrient input,

53   particularly phosphorus (P) and nitrogen (N), this problem has not abated; even some restored

54   lakes have re-experienced cyanobacteria blooms in recent years.[3] This observation suggests that

55   current controls on nutrient inputs are not sufficient, particularly nutrients derived from fertilizer

56   use in agriculture production[4] and/or that current eutrophication control strategies lack a full

57   understanding of the internal cycling and impacts of nutrients in lakes, especially in eutrophic

58   shallow lakes. The current eutrophication control paradigm is built mainly on nutrient addition

59   experiments in small bodies of water, which simulated the effects of external input without

60   encompassing all in-lake biogeochemical processes. For example, in-lake processes that remove

61   nutrients such as sedimentation and denitrification are associated with lake morphologic

62   characteristics that are reflected in water residence time and aeration of bottom waters.

63   Summarizing past experiences of lake eutrophication mitigation, the interesting and puzzling

64   observation can be noted that most successfully-restored systems involving P-only reduction were

65   in deep lakes such as Lakes Geneva and Zurich (Switzerland), Lago Maggiore (Italy), Lake

66   Constance (Germany, Switzerland and Austria),[5,6] while dual N and P reduction was successful in

67   shallow systems such as Lake Wuli (China), Tampa Bay (USA), Lake Tohopekaliga (USA), Lake

68   Albufera (Spain), Scheldt Estuary (Netherlands).[3] This observation implies that lake

69   morphological characteristics such as water depth may play a critical role in lake eutrophication.

70   This possibility highlights the need for improving understanding of in-lake nutrient dynamics with

71   lake morphology to achieve desired eutrophication solutions. Here a global lake data base with

72   total 573 lakes (Figure 1) was analyzed to investigate the potential role of lake morphology,

73   specifically water depth, in relation to lake trophic status and relative importance of N and P

74   limitation.

75   **[Figure 1 is here]**

76   **2.   MATERIALS AND METHODS**

77   **2.1. Data Collection.** We searched published papers as well as regional databases of lake

78   monitoring data (European Environment Agency and the LAke multi-scaled GeOSpatial and

79   temporal (LAGOS) databases).[7] To minimize the dramatic effect of external input and focus on

80   the in-lake biogeochemical processes, the sites of small lakes (area < 1 km^2) were excluded from

81   our global lake data set. In addition, only the growing season data (northern hemisphere, May-

82   September; southern hemisphere, November-March) of lakes were collected to explore nutrient

83   conditions during summer periods to minimize the influence of temperature discrepancy (seasonal

84   change of total nitrogen (TN) : total phosphorus (TP)) on primary production across the diverse

85   latitudinal and altitude systems. To investigate the relation between nutrient conditions and lake

86   morphology, only those sites which were documented simultaneously with lake morphometries

87   (geographical locations, area, maximum and mean depth) and TN, TP, and chlorophyll *a* (Chl *a*)

88   concentrations during the growing season (more than 2 sample times in each lake) were included.

89   In total, 573 lakes were extracted from the database (Figure 1) in which 562 sites are lakes and 11

90   sites are reservoirs. Our database includes 4 sites from Asia, 240 sites from Europe, 313 sites from

91   North America, and 16 sites from South America (Figure 1). The database covers lakes ranging

92   from shallow to deep, oligotrophic to hypertrophic, and subtropical to temperate (Table S1).

93   Specifically, 204 lakes were collected from the Web of Science database, 146 lakes from European

94 Environment Agency, and 223 lakes from LAGOS. Moreover, the data of denitrification rate in

95 lakes during the growth periods were also collected, and total of 44 lakes were screened from the

96 database.

97 **2.2. Trophic Status Categorization and Nutrient Limitation Definition.** Based on their Chl *a*

98 concentrations in the database, the lakes were categorized into three major trophic state categories

99 following the standards set by the Organization for Economic Co-operation and Development

100 (OECD): oligotrophic (Chl $a \leqslant 2.5\ \mu g\ L^{-1}$), mesotrophic ($2.5 < $ Chl $a \leqslant 8.0\ \mu g\ L^{-1}$), and eutrophic

101 (Chl $a > 8.0\ \mu g\ L^{-1}$).[8] Changes in TN:TP stoichiometry can indicate altered patterns of

102 phytoplankton nutrient limitation.[9] According to thresholds derived from global patterns of

103 phytoplankton stoichiometry, potential N only limitation is indicated when N:P ratio (by mass) <

104 9.0, N+P co-limitation when $9 \leqslant $ N:P < 22.6 and P only limitation when N:P $\geqslant 22.6$.[10]

105 **2.3. Lake Mixing (epilimnion) Depth and Classification.** To deal with the possible influence of

106 lake shape on sediment-water interactions and spatial distributions of nutrients and oxygen, we

107 delineated the three traditional lake stratification layers: hypolimnion (non-turbulent and isolated

108 from the atmosphere); the surface, epilimnion (turbulent, in contact with the atmosphere) and,

109 between the hypolimnion and epilimnion, the metalimnion (strong temperature gradient or

110 thermocline). In practice, the surface mixing depth is defined as epilimnion depth (*EPI*, m),

111 determined by the wind-induced disturbance intensity, which is associated directly with lake

112 surface area.[11] Many empirical expressions estimate the epilimnion depth as a function of lake

113 morphologic variables such as maximum length, maximum width, maximum effective length,

114 maximum effective width, shoreline length, area, maximum depth, mean depth, etc.[11] For data

115 availability, lake area was used to estimate the mixing depth (*EPI*):

$$EPI\ =\ (10^{0.185 \mathrm{Log}(A)\ +\ 0.842}\text{-}2.37)\ /\ 1.05 \tag{1}$$

117   where A is the lake area (km^2). Data from more than one hundred lakes representing a range of

118   lake sizes and shapes over an extensive geographical region were used to verify the mixing depth

119   prediction; many calculated and measured mixing depths were related, with correlations as high

120   as 0.9.[11]

121   In addition to the mixing depth, the sediment area exposed to overlying water in relation to

122   mixing depth can play a key role in oxygen penetration downward and nutrient release from the

123   sediment. A lake is usually not rectangular with sediments exposed to water at the deepest part.

124   The area at depth h can be approximated according to following expression:[12,13]

125
$$A_h = A_H (\frac{h}{H})^\eta$$

126   where H is maximum depth; A_H, A_h are areas at surface and depth h, respectively; η is the

127   nondimensional topographic exponent between 0.5 and 1.5[12,13]. Considering that water depth

128   changes continuously from shallow to deep lakes, we define shallow lakes as those with mixing

129   depth exceeding the maximum depth, which means that a lake is often completely mixed. In

130   contrast, we define deep lakes as those with mixing depth less than mean depth. They are

131   considered to be incompletely mixed vertically if the lower boundary of the mixed layer touches

132   the sediment at less than half of surface area of the lake. Finally, we classify lakes as transitional

133   if mean depth $\leqslant$ mixing depth $\leqslant$ maximum depth, which indicates a part of lake bottom (more

134   than half of surface water area) is exposed to mixing.

135   **2.4. Statistical Analysis.** Relationships among water depth, TN, TP, Chl a, and TN: TP mass ratio

136   were explored by Pearson's correlation coefficient, and a One-way analysis of variance (ANOVA)

137   was used to analyze the differences. These analyses were performed in Statistical Product and

138   Service Solutions (SPSS 22.0) statistical package for personal computers, and the level of

139   significance used was $p < 0.05$ for all tests. Statistical tests of the difference of nutrient limitations

140   and trophic status between shallow and deep lakes were examined with non-parametric statistical

141   test (Chi-square χ^2), and the differences between slopes of Log (TN) ~ Log (Depth) and Log(TP)

142   ~ Log(Depth) regressions were tested with standardized major axis test (SMA) using package

143   smart[14,15] in R 3.6.[16]

3.   RESULTS

3.1. Trophic Status in Differential Depth Lakes

[Figure 2 is here]

147   TN, TP, and Chl *a*, the three typical water quality indicators, were chosen to evaluate the

148   lake trophic status as a function of water depth. Mean growing season concentrations of TN, TP,

149   and Chl *a* decreased uniformly with increasing water depth (*t*-test, $p < 0.01$, Figure 2). Interestingly,

150   the decreases of TN, TP and Chl *a* concentrations were not linear with water depth. However,

151   although trophic status is distributed widely in lake systems, it is notable that most of the high

152   values were confined to lakes with maximum depth less than 20 m (Figure 2). As water depth

153   increased, concentrations of TN, TP, and Chl *a* decreased sharply with a transition occurring

154   around 20 m (Figure 2), suggesting a functional shift from shallow to deep lakes.

[Table 1 is here]

156   Our database contains 77 shallow, 285 transitional, and 211 deep lakes, accounting for

157   13.4%, 49.7% and 36.8%, respectively (Table 1). On average 69% shallow lakes and 21% deep

158   lakes were classified as eutrophic (Table 1), which clearly shows that trophic status is related to

159   water depth (χ^2-test, $p < 0.01$) and that shallow lakes are more susceptible to eutrophication

160   (ANOVA, $p < 0.01$). In addition, 61 lakes (10.6% of all lakes) had Chl *a* concentrations above 40

161   µg L^{-1} (frequently given as a threshold for algal blooms[17]), which occurred mostly in shallow lakes

162   (44.2% in shallow lakes, 37.7% in transitional lakes and 18.0% in deep lakes) (Figure 2C). These

163   results suggest that shallow lakes are more susceptible to eutrophication and algal blooms than

164   deep systems.

3.2. Nutrient Limitation in Differential Depth Lakes

166   Based on TN:TP ratios in our dataset, 38.7% of all lakes showed potential N limitation (N

167   only and N + P co-limitation), while 94.4% indicated potential P limitation (P only and N + P co-

168   limitation; Table 1), suggesting that P limitation predominated across a diverse range of lakes over

169   broad climatic and latitudinal zones. Based on TN:TP ratios, the frequency of P limitation was

170   87% in shallow lakes, 91.9% in deep lakes and 97.5% in transitional lakes, but N limitation was

171   evident in 66.2% shallow lakes, 33.2% deep lakes and 35.4% transitional lakes (Table 1). The

172   difference between shallow and deep lakes are statistical significance (χ^2-test, $p < 0.01$).

173   Since Chl a concentration decreased with water depth, trophic status changes with water

174   depth are also considered. Based on trophic status categorization, the importance of P limitation

175   decreases and N limitation increases with lake trophic state (Table 1). In our dataset, P limitation

176   dominated in all classes (85.5~100%), while N limitation dominated in eutrophic lakes

177   (63.8~79.2%) (Table 1). In particular, 86.9% of lakes with algal blooms (Chl $a \geq 40$ μg L^{-1}) were

178   classified as potentially N-limited based on TN:TP ratio (Figure S1), indicating that severe algal

179   blooms generally occur in N limited or N and P co-limited systems.

4. DICUSSION

181   Our analysis of a global database of lake characteristics revealed that, in addition to the

182   quantity and composition of nutrient inputs, water depth influences trophic status as well as the

183   prevalence of N and P limitation, although the consistency and magnitude of these impacts varies

184   in lakes. Concentrations of TN, TP, and Chl a decrease with depth, indicating that deep lakes are

185   less eutrophic than shallow ones.[18] Eutrophication and algal blooms occurred mostly in shallow

186   systems that were more likely to be N and P co-limited, while P limitation predominated in most

187   lake ecosystems and especially in deep lakes. Differences in TN:TP in shallow and deep lakes

188   likely reflect contrasting nutrient processing regulated by complex in-lake biogeochemical

189   processes that depend on water depth. Interestingly, with increased nutrient concentrations, N + P

190   co-limitation increased and predominated in eutrophic lakes. These results revealed that

191   eutrophication mitigation in lakes likely requires different strategies depending on lake

192   morphometry. Nutrient control should be of particular concern in shallow lakes where dual

193   reductions of both N and P might be needed to achieve water quality goals.

194   **[Figure 3 is here]**

195   **4.1. Mixing Depth and Its Relation to In-lake Biogeochemical Processes.** Many basin

196   morphological characteristics can affect lake trophic status and internal biogeochemical processes.

197   It is necessary to find simple criteria that allow classification of lakes with respect to their likely

198   responses to changes to nutrient loading. Our analyses as well as previous studies[13] indicate that

199   mixing depth and the area of sediment interacting with overlying water are likely two critical

200   attributes regulating in-lake nutrient dynamics. Biogeochemical processes related to mixing depth

201   determine the penetration of dissolved oxygen (DO) and other nutrients downward to sediment

202   while the area of sediment exposed to mixing regulates the DO and nutrient exchange flux across

203   water-sediment interface. We suggest that the degree into which turbulent mixing extends towards

204   the lake bottom area may be the best classification criterion for assessing in-lake nutrient cycling

205   processes.[13]

206   The theoretical mixing thickness of a lake is determined by lake geomorphological attributes

207   such as area, basin shape, wind fetch, and wind speed. According to Hanna's[11] empirical formula,

208   the epilimnetic (mixing) depth is 9.7 ± 4.8 m in our lake data set, which resembles a key threshold

209   seen in the relations of TN, TP, and Chl *a* with water depth (Figure 2). If water depth is deeper

210   than the mixing depth, the hypolimnion of lake is undisturbed seasonally by hydrodynamic actions

211   with only epilimnion processes staying active (Figure 3). However, if the physical depth is

212   shallower than the mixing depth, the water column and sediment are maintained in dynamic

213   contact (Figure 3). That is why the water depth compared to mixing depth is used to classify lakes

214   in this study. In deep lakes, in-lake biogeochemical processes that remove nutrients (such as

215   sedimentation and denitrification) no longer correspond with water depth in the hypolimnion. In

216   shallow lakes, the interactions between water column and sediment cause in-lake biogeochemical

217   processes to regulate nutrient dynamics effectively (Figure 3). Indeed, the concentrations of TN,

218   TP, and Chl *a* decrease sharply with lake depth in shallow lakes, with high values confined to lakes

219   shallower than 20 m, but descend gently to low values in lakes deeper than 20 m (Figure 2).

220   **4.2. Different Nutrient Dynamics in Shallow and Deep Lakes.** By the 1960s, lake trophic status

221   was related to the input concentration of P and water residence time.[19] The magnitude of in-lake

222   biogeochemical processes as well as their impacts on lake trophic status depend on depth-

223   dependent conditions beyond just water residence time and include processes associated with

224   surface area that affect water mixing depth, re-oxygenation, and sediment resuspension (Figure 3).

225   These in-lake biogeochemical processes play critical roles in determining trophic status in shallow

226   systems. However, massive efforts were devoted to identify the relative importance of N and P in

227   lake eutrophication by linking lake N:P ratios to the relative amounts of N and P coming from

228   external sources.[20-24] As a crucial example, fertilizers including manure from increased agricultural

229   production results in non-point source pollution, which plays an increasingly predominant role in

230   the eutrophication of receiving waters.[4] However, few researchers paid attention to the role of lake

231   morphology, particularly the water depth, and its impacts in-lake biogeochemical processes, which

232   affect the internal fate of N and P (Figure 3). Indeed, the effects of external inputs on trophic status

233   and N:P ratio (imbalanced supply) are modified by in-lake biogeochemical processes.

234   P enrichment in the water column depends on the balance between input, outflow, and loss

235   *via* sedimentation, which is controlled by water residence time, and related positively to water

236   depth (Figure S2).[19] In deep lakes, residual P in non-metabolized particles settle to and are often

237   buried in bottom sediments (Figure 3). However, in shallow lakes, frequent hydrodynamic

238   disturbance re-suspends more of the P in surficial sediments into the water column (Figure 3),

239   slowing the decline of P concentration in the water column.[25] Nitrogen is also lost from the

240   epilimnion *via* sedimentation similar to P but is often less efficiently removed from the water

241   column by sedimentation because much N remains in bioavailable dissolved forms[26] while any P

242   that is not recycled generally remains in particulate forms.[27] This conclusion is supported by the

243   differential decline in N and P concentrations with depth (as the slope of Log (max depth) ~ Log

244   (TN) > Log (max depth) ~ Log (TP), SMA, $p < 0.001$, Figure 2). Importantly, N is lost to the

245   atmosphere in gaseous forms (e.g., N_2) *via* denitrification under biogeochemically reduced

246   conditions. Generally, the efficiency of N removal from the water-sediment system *via*

247   denitrification is determined by availabilities of nitrate, labile organic matter[28] and alternating

248   anaerobic/aerobic conditions.[29] Hypolimnetic redox conditions are stable in deep lakes[30] but, in

249   shallow lakes, wind-induced mixing in the water column transports oxygen frequently to the lake

250   bottom and favors *facultative* (oxic/anoxic) conditions[29] at the water-sediment interface (Figure

251   S3). High concentrations of labile organic matter provide biogeochemical energy for metabolic

252   conversion of nitrates to nitrogen gas *via* denitrification,[31] particularly in shallow eutrophic lakes.

253   Thus, denitrification is a critical in-lake biogeochemical process of N removal in shallow systems,

254   which can sometimes remove up to 90% of TN inputs in shallow eutrophic lakes with short

255   particle-settling times.[32] In addition, although some dominant bloom-forming cyanobacteria (e.g.

256   *Microcystis*) are not capable of N_2 fixation, biological controls on N inputs *vs.* outputs, or the

257   balance between N_2 fixation *vs.* denitrification, often favor the latter, especially in shallow lakes

258   undergoing accelerating eutrophication.[33] Nitrogen loss *via* denitrification is often higher in

259   shallow than in deep lakes (Figure S4). This tendency is supported by denitrification rate

260   measurements in a variety of lakes with different depths such as Lakes Taihu, Erie, Huron, and

261   Superior.[34,35]

262   The dynamics of N and P are distinct in lakes with different water depths, as indicated by

263   differences in N:P ratio in shallow and deep lakes (Table 1). In shallow lakes, enhanced N loss,

264   dampened P loss, and P supply from sediments lead to lower N:P ratios and thus greater potential

265   for N limitation, while the opposite occurs in deep lakes, favoring P limitation (Table 1). In

266   addition, N:P ratio correlates significantly with Chl *a* concentrations in our dataset (Figure S1,

267   Pearson's Correlation Analysis, $p < 0.001$), indicating that potential nutrient limitations shifts with

268   trophic status changes that are associated with water depth. In shallow productive lakes or bays,

269   high nutrient loading accelerates nutrient recycling and boosts phytoplankton proliferation even

270   during cyanobacteria blooms. Algae blooms provide abundant organic carbon sources that

271   degrade and result in bottom-water hypoxia,[36] stimulating P regeneration by mobilizing P from

272   sediments[37] and amplifying N loss by increasing denitrification rates,[32] and a higher rate of P

273   supply and N removal[32] and finally lowering N:P ratio. Thus, we propose that in-lake

274   biogeochemical processes associated with water depth help explain the transition from P

275   limitation in deep systems to N and P co-limitation in shallow eutrophic lakes.[25,38,39]

276   The number and percentage of N limitation (N only and P + N colimitation) *vs.* P limitation

277   (P only and N + P colimitation) in transitional lakes (35.4% vs 97.5%) are similar to those of deep

278   lakes (33.2% vs 91.9%) (Table 1). According to the definition of transitional lake, sediment area

279   is less than water surface area but greater than half of the lake surface area exposed to mixing,

280   which means only a small part (less than half of the lake surface) is free from water mixing. The

281   water depth influence on nutrient biogeochemical processes in the transitional lakes, therefore, is

282   supposed to be similar to the shallow lakes. This result likely suggests that sedimentation is more

283   widespread and pervasive than denitrification, because the former enhances P-loss or P limitation

284   whereas the later causes more N loss and N limitation. It also may explain why P limitation widely

285   occurs in most lakes, and N limitation is less extensive present in our lake dataset.

286   **4.3. Different N, P Limitation and Corresponding Control Strategies**. Current nutrient

287   reduction strategies are informed mainly by nutrient addition experiments, in mesocosms, flasks,

288   or small deep lakes, which neglect the importance of in-lake biogeochemical processes. Thus,

289   inferences about limitations derived from these experiments are *proximate* at the temporal scale

290   from hours to days, months or years, whereas nutrients that provide long-term controls on

291   ecosystem productivity and phytoplankton biomass can be termed as *ultimate* limiting nutrients.[6]

292   Although useful, measures of proximate nutrient limitation do not necessarily provide critical

293   information about ultimate nutrient limitation in eutrophic waters.[6] That is, extrapolations from

294   small water-volume experiments to large systems can be misleading.[6] In fact, many factors beyond

295   TN:TP organism ratios can affect nutrient deficiency and limit ecosystem production, such as

296   phytoplankton assemblage features,[40] the unavailability of some forms of TP or TN[41], the

297   composition of dissolved organic nitrogen,[42] limitations by silicon or trace metals, or biotic

298   interactions like grazing by zooplankton[43]. These influences are likely intensified in nutrient

299   addition experiments in small water bodies or enclosures due to the short-term duration and

300   weakened effects of in-lake biogeochemical processes.

301   Our analyses emphasize the importance of in-lake biogeochemical processes. They help

302   explain why some long-standing efforts to control lake eutrophication have resulted in frustratingly

303   slow or modest effects in shallow productive lakes and why P-only reduction strategies are more

304   effective in deep lakes. Our findings help clarify a long-standing concern over the relative

305   importance of N vs P in limiting lake productivity,[3,5] i.e. nutrient limitation depends on

306   biogeochemical effects on N vs. P, which is related to lake morphology. More comprehensive

307   results from carefully designed experiments are needed to confirm this inference and test the

308   mechanisms we propose. Overall, our findings imply that alleviation of eutrophication based on

309   nutrient management requires different strategies in lakes depending on their depths and mixing

310   characteristics. Because of the different costs of N vs. P reduction strategies, particularly the high

311   cost of nitrogen removal,[44,45] empirical verification is necessary before the proposed new nutrient

312   reduction paradigm is put into widespread use.

313

314   **ASSOCIATED CONTENT**

315   **Supporting Information.** Table S1. Frequency distribution of lake morphometric and chemical

316   data in the global lake data set. Figure S1. Scatter diagrams showing the relationships between Chl

317   *a* and TN:TP mass ratio during the growing season. Figure S2. The distribution of water residence

318   time as a function of mean depth in lakes (n = 85). Figure S3. Relationships between daily mean

319   wind speed and daily minimum dissolved oxygen (DO) in Lake Taihu over the period of 2007-

320   2017 to demonstrate that the extreme shallow system can still experience hypoxia during

321   summertime. Figure S4. Scatter diagrams showing the relationships between denitrification rate

322   and maximum depth in lakes (n = 46).

323

324   **AUTHOR INFORMATION**

Corresponding Author

*Phone +86 (025) 86882192 . E-mail: qinbq@niglas.ac.cn.

 Notes

The authors declare no competing financial interest.

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466

467 **Table 1. Numbers and percentages of N only limitation, P only limitation , N and P co-**

468 **limitation sites respectively in shallow (mixing depth > maximum depth), deep (mixing depth**

469 **< mean depth) and transition (mean depth ⩽ mixing depth ⩽ maximum depth) lakes with**

470 **oligotrophy, mesotrophy, and eutrophy.** The mixing (epilimnetic) depth is estimated in terms of

471 Hanna[11]. The threshold values of trophic status were defined by Organization for Economic Co-

472 operation and Development[8].

Lake type	Trophic status	Total	N only limitation (TN/TP < 9)	N and P co-limitation (9 ≤ TN/TP < 22.6)	P only limitation (TN/TP ≥ 22.6)	N limitation (N and N+P) vs P (P and N+P) limitation
				Number of sites (Percentage)		
Shallow lakes	Oligotrophic lake	2 (2.6%)	0	0	2 (100%)	0 vs 100%
	Mesotrophic lake	22 (28.6%)	0	9 (40.9%)	13 (59.1%)	40.9% vs 100%
	Eutrophic lake	53 (68.8%)	8 (15.1%)	34 (64.2%)	11 (20.8%)	79.2% vs 84.9%
	Subtotal	**77**	8 (10.4%)	43 (55.8%)	26 (33.8%)	66.2% vs 89.6%
Transition al lakes	Oligotrophic lake	45 (15.8%)	1 (2.2%)	5 (11.1%)	39 (86.7%)	13.3% vs 97.8%
	Mesotrophic lake	135 (47.4%)	1 (0.7%)	27 (20%)	107 (79.3%)	20.7% vs 99.3%
	Eutrophic lake	105 (36.8%)	5 (4.8%)	62 (59%)	38 (36.2%)	63.8% vs 95.2%
	Subtotal	**285**	7 (2.5%)	94 (33.0%)	184 (64.6%)	35.4% vs 97.5%
Deep lakes	Oligotrophic lake	69 (32.7%)	10 (14.5%)	8 (11.6%)	51 (73.9%)	26.1% vs 85.5%
	Mesotrophic lake	98 (46.4%)	2 (2%)	21 (21.4%)	75 (76.5%)	23.5% vs 98%
	Eutrophic lake	44 (20.9%)	5 (11.4%)	24 (54.5%)	15 (34.1%)	65.9% vs 88.6%
	Subtotal	**211**	17 (8.1%)	53 (25.1%)	141 (66.8%)	33.2% vs 91.9%
Total		**573**	32 (5.6%)	190 (33.2%)	351 (61.3%)	38.7% vs 94.4%

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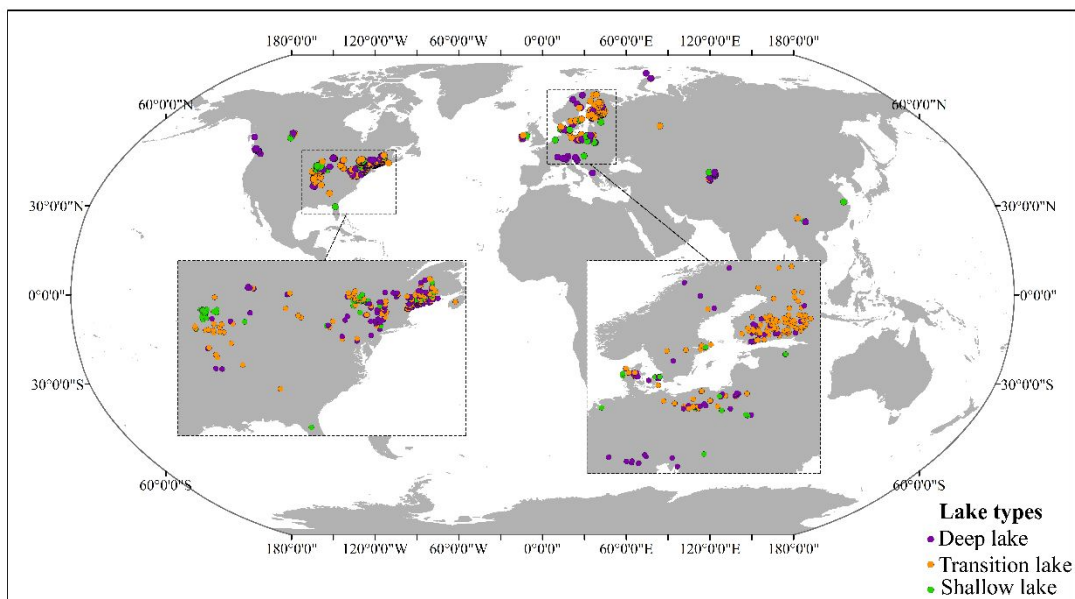477   **Figure legends**

478   **Figure 1. The distribution of lakes in our lake data set. Lakes were defined by comparing the**

479   **maximum and mean depth to the mixing (epilimnion) depth.** For shallow lakes, mixing depth

480   > maximum depth; for deep lakes, mixing depth < mean depth; for transition lakes, mean depth $\leq$

481   mixing depth $\leq$ maximum depth. Blue circles represent deep lakes, red circles represent transition

482   lakes, and green circles represent shallow lakes.

483

484   **Figure 2. The distribution of total nitrogen (TN, A), total phosphorus (TP, B) and chlorophyll**

485   ***a* (Chl *a*, C) as a function of lake maximum depth during the growing season.** The

486   concentrations of TN, TP and Chl *a* uniformly decreased with lake maximum depth (*t*-test, *p* <

487   0.01), indicating that strong eutrophication and algal blooms are largely confined to shallow lakes.

488

489   **Figure 3. The in-lake biogeochemical processes associated with water depth regulate**

490   **remarkably the nutrient dynamic in shallow (left) and deep (right) lakes.** In shallow systems,

491   defined as mixing depth > maximum depth, water column and sediment are dynamic with

492   enhanced N loss (denitrification), dampened P loss (sedimentation), and P supply from sediment,

493   leading to a decline of N:P ratio with frequently N limitation. Correspondingly, in deep systems,

494   defined as mixing depth < mean depth, the hypolimnion of lake are seasonally undisturbed by

495   hydrodynamic actions with only the epilimnion staying active. Dampened N loss and High

496   removal efficiency of P through sedimentation lead to an increase of N:P ratio with frequently P

497   limitation predomination.

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Figure 1. The distribution of lakes in our lake data set. Lakes were defined by comparing the

maximum and mean depth to the mixing (epilimnion) depth. For shallow lakes, mixing depth >

maximum depth; for deep lakes, mixing depth < mean depth; for transition lakes, mean depth $\leqslant$

mixing depth $\leqslant$ maximum depth. Blue circles represent deep lakes, red circles represent

transition lakes, and green circles represent shallow lakes.

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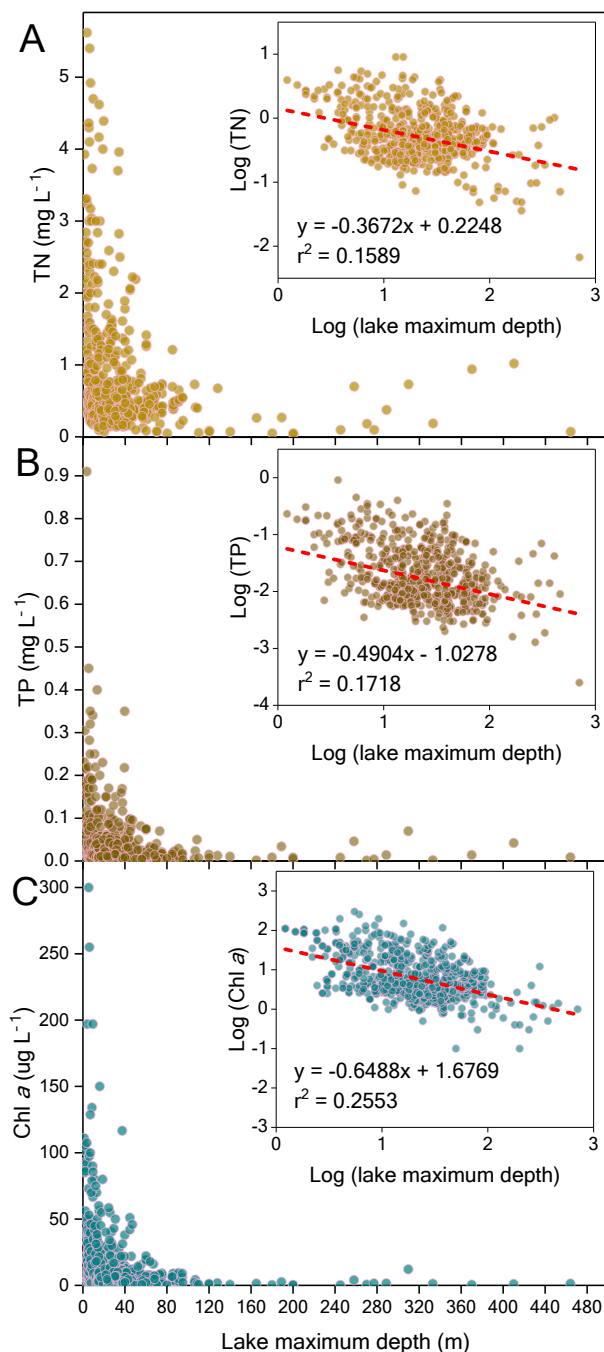
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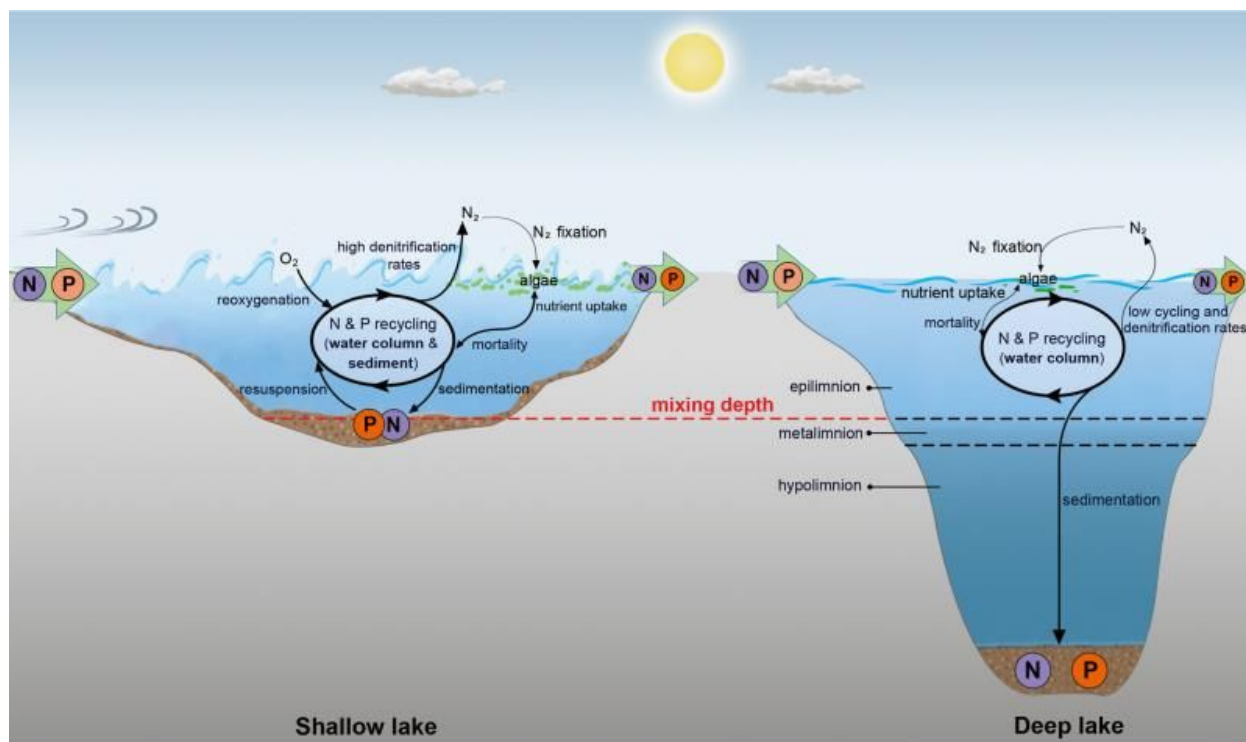
Figure 3. The in-lake biogeochemical processes associated with water depth regulate remarkably the nutrient dynamic in shallow (left) and deep (right) lakes. In shallow systems, defined as mixing depth > maximum depth, water column and sediment are dynamic with enhanced N loss (denitrification), dampened P loss (sedimentation), and P supply from sediment, leading to a decline of N:P ratio with frequently N limitation. Correspondingly, in deep systems, defined as mixing depth < mean depth, the hypolimnion of lake are seasonally undisturbed by hydrodynamic actions with only the epilimnion staying active. Dampened N loss and High removal efficiency of P through sedimentation lead to an increase of N:P ratio with frequent P limitation predomination.