A probabilistic method to enhance understanding of nutrient limitation dynamics of phytoplankton

Zhongyao Liang a, Sifeng Wu a, Huili Chen a, Yanhong Yu b, Yong Liu a,∗

a College of Environmental Science and Engineering, Key Laboratory of Water and Sediment Sciences (MOE), Peking University, Beijing 100871, China
b Yunnan Key Laboratory of Pollution Process and Management of Plateau Lake-Watershed, Kunming 650034, China

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A B S T R A C T
The determination of the limiting nutrient of phytoplankton is critical to the lake eutrophication management. The average value of total nitrogen/total phosphorus (TN/TP) ratio is widely used to determine the limiting nutrient; while it suffers from the risk of the incorrect description of data and neglecting dynamics of the nutrient limitation. A probabilistic method was thereby proposed in this study to explore dynamics of nutrient limitation, including (a) indicator definition as the probability of TN/TP ratio falling in Redfield ratio line (PFR), indicating the possibility of TN limitation, to improve a probabilistic measure for the nutrient limitation; (b) Bayesian ANOVA analysis for posterior distributions of different treatments; and (c) dynamics determination as PFRs to show dynamics of nutrient limitation. Lake Xingyun in Southwestern China was taken as a case to explore the interannual and seasonal dynamics of the nutrient limitation. According to modeling results, we deducted that (a) for the interannual dynamics, the limiting nutrient shifted from TP to TN, and (b) for the seasonal dynamics, TN and TP were co-limiting. Deductions were further confirmed by the observed data. With the proposed probabilistic method, the co-limitation of TN and TP was identified for the seasonal dynamics; while using the average ratio solely denied the possibility of co-limitation. The current study also revealed that, due to neglecting the interannual and seasonal dynamics of nutrient limitation, the average ratio might mislead the eutrophication management strategy by recommending reducing TN and TP concentration together. The proposed probabilistic method demonstrated that TN was the limiting nutrient during the growing season of the phytoplankton in recent years and actions should focus on the TN concentration reduction.

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1. Introduction
Eutrophication has become the primary problem for freshwater and marine ecosystems (Smith et al., 2006), leading to the deterioration of water quality, damages of ecosystem structure and function, and huge economic losses (Dodds et al., 2009; McDowell and Hamilton, 2013; Paerl and Otten, 2013). Excessive phosphorus and nitrogen, are main drivers of eutrophication (Conley et al., 2009). To maximize the efficiency of restoration measurements, it is critical to distinguish the limiting nutrient of phytoplankton (Dodds, 2007). In spite of increasing doubts in recent years, the total nitrogen/total phosphorus (TN/TP) ratio has been widely used to determine the limiting nutrient of waterbody (Bergstrom, 2010; Persic et al., 2009; Symons et al., 2012; Xu et al., 2010), with respect to the Redfield ratio (16:1 by molar) (Redfield, 1934, 1958). Generally, if the ratio is above the Redfield ratio, the waterbody is TP limited, and if the ratio is smaller than the Redfield ratio, TN is the limiting nutrient.

When there are more than one group of data, averaging TN/TP ratios seems like a natural way to determine the limiting nutrient (Li et al., 2013; Pelechata et al., 2016). However, the average ratio loses information of the observed data and may lead to an incorrect description of the data (de Fouquet, 2012). For example, if there are four groups of data whose average ratio is above the Redfield ratio, it can jump into the conclusion of TP limitation. Unfortunately, under that condition, it is possible that three of them are smaller than the Redfield ratio while the rest one is very large, and the lake is actually TN limited for most of the chances. Moreover, the average ratio may also neglect dynamics of nutrient limitation when data is aggregated from different sources (e.g. different years, months, or sites), because the TN/TP ratio varies temporally and spatially (Cha et al., 2016; Frigstad et al., 2011; Sterner et al., 2008). The temporal trend of the ratio is impacted by atmospheric deposition (Miyazako et al., 2015), runoff diversion and internal loading release (Cruz

* Corresponding author.
E-mail address: yongliu@pku.edu.cn (Y. Liu).

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et al., 2015). The relative more internal release of TP than TN always lead to significantly seasonal variations (Davies et al., 2010; Dolman et al., 2016). Since the growth rate of phytoplankton varies with season, mainly caused by the water temperature (Paerl et al., 2016), exploring the limiting nutrient in the growing season is critically important for the eutrophication control. The ratio is always larger in upstream than downstream (Green and Fritsen, 2006) and varies spatially both in lakes and oceans (Caccia and Boyer, 2005; Smith and Bennett, 1999).

While aggregated environmental data for status and trend assessments has been increasingly used (Maas-Hebner et al., 2015), new methods, which overcome these two shortcomings of using the average ratio solely, are required to determine the limiting nutrient. While using the average solely could be misleading, the distribution would give a full view of the TN/TP ratio. That is, the determination of nutrient limitation should be distribution based. We defined an indicator, the probability of TN/TP ratio failing in Redfield ratio line (PFR), to extract useful information from the distribution of the TN/TP ratio to identify the limiting nutrient. It is the probability when the ratio is smaller than the Redfield ratio, indicating the possibility of TN limitation. Thus, it improves a probabilistic measure for the nutrient limitation. The larger PFR indicates that TN is more likely to be the limiting nutrient.

Exploring dynamics of the nutrient limitation is critical to making the proper strategy for the watershed load reduction (Alam et al., 2018; Niemisto et al., 2008). The Bayesian Analysis of Variance (Bayesian ANOVA) method is an effective tool to estimate treatment effects using a hierarchical regression (Gelman, 2005; Qian and Shen, 2007), and thus is suitable to explore dynamics of the TN/TP ratio. Compared with the conventional ANOVA approach, Bayesian ANOVA is more flexible in model formulation, easier to set up and easier to present graphically (Qian et al., 2009). More importantly, based on the Bayesian Theorem, it gives the distribution of the TN/TP ratio for every treatment conveniently (Ellison, 2004; Qian, 2015), which is exactly the basis for calculating the PFR. Therefore, integrating the PFR and the Bayesian ANOVA method, we propose a probabilistic method to explore dynamics of the nutrient limitation. By which, the distributions of TN/TP ratio for different treatments can be obtained via the Bayesian ANOVA model and then corresponding PFRs can be calculated to explore dynamics of the nutrient limitation.

Dynamics of the nutrient limitation in hyper-eutrophic Lake Xingyun (Southwestern China) was taken as an example to verify the applicability of the proposed probabilistic method. The eutrophication of Lake Xingyun calls for exploration of the limiting nutrient for proper management strategy. Due to the relatively small lake size, the spatial dynamics was not explored in this study. It is hypothesized that dynamics of the nutrient limitation has both interannual and seasonal differences in Lake Xingyun. Therefore, it was important to explore interannual and seasonal dynamics of the nutrient limitation for proper eutrophication management strategy. The proposed probabilistic method was applied to test the hypothesis, to facilitate the efficient eutrophication management, and to verify the applicability of the proposed probabilistic method.

2. Material and methods

2.1. Study area

Lake Xingyun (24°17′23″–24°23′11″N, 102°45′19″–102°48′12″E) is located in Yuxi City, Yunnan Province, southwestern China, with an average depth of 7 m, and a maximum depth of 11 m. The catchment area is 386 km², and the lake surface area is 34.7 km². The watershed belongs to the subtropical monsoon climate, characterized by wet summers and dry winters. The mean annual temperature is 16.1 °C, with a mean July temperature of 21 °C and a mean January temperature of 9 °C. The mean annual precipitation is 879 mm, and the wet season, from May to October, contributes approximate 85% of the annual precipitation (Chen et al., 2014). July is the month with maximum rainfall, accounting for 20% of the annual precipitation. The surface runoff (about 82 million m³/a) accounts for 73% of the total lake water supply (People’s Government of Yuxin City, 2016).

With the development of the agriculture and phosphate industry, the lake water quality has deteriorated since the 2000s, together with the cyanobacterial bloom (Li et al., 2007). The runoff brings heavy nutrients loading into the lake, and total loadings of TN and TP are approximately 1060 t/a and 230 t/a, respectively. Besides, as a semi-enclosed lake, pollutants tend to accumulate within the lake (Zhang et al., 2016). Consequently, the lake is susceptible to eutrophication. Last decade has witnessed the significant degradation of water quality, especially for the increase of TP concentration (Fig. S1). It is now in a hyper-eutrophic state with a mean Chlorophyll a (Chla) concentration of 56 μg/L (Table 1).

The interannual trend of water quality over the last decade and the seasonal fluctuations of nutrients (Fig. S1) make Lake Xingyun a proper example to show interannual and seasonal dynamics of the nutrient limitation. More importantly, the eutrophication calls for the identification of the limiting nutrient to help set proper management strategy, and that is also what we try to provide. The data was from the monthly routine monitoring by Environmental Monitoring Station of Yunnan Province from 2006 to 2014, with 108 groups of data in total.

2.2. Methods

The proposed probabilistic method to explore interannual and seasonal dynamics of nutrient limitation in Lake Xingyun includes four steps (Fig. 1):

(1) Transformation of original data as normal distribution;
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