No-linear dynamics of lake ecosystem in responding to changes of nutrient regimes and climate factors: case study on Dianchi and Erhai lakes, China

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Abstract: As different algae growths responding to a set of nutrients can occur under different conditions, the nutrient load management based on the relationship between chlorophyll a (Chla) and total phosphorus (TP) alone may not always effective for lake algae bloom control. It is not clear whether the lagged response of algae to reduced nutrients related to the utilization efficiency of algae to phosphorus (UEAP), and how UEAP could response to climate and water quality factors. Here we analyzed over 20 years monitoring data in two lakes with similar geology but different nutrient levels by using statistical and modeling methods. The aim was to reveal the impact of UEAP on lake algae dynamics and the driving factors of UEAP changes. The results showed that UEAP is one of the key factors affecting algae dynamics, the incorporation UEAP and its driving factors achieved greater modeling reliability. UEAP, Nitrogen phosphorus ratio (NPr) was the key driving factor in Dianchi Lake, while total nitrogen (TN) and air temperature (AT) were the key driving factors in Erhai Lake. The changes of nutrients and climate drove UEAP into the paralysis or sensitive phase depending on lake specific factors and conditions. This

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correlated to algae density dynamics, in particular to those characteristic of algae growth thresholds. The future trend of climate change will continue to promote the increase of UEAP in both lakes, but severer in Erhai Lake. The key finding here is of the value of a proxy index (UEAP) for phosphorus utilization was associated with the lagged response of algae to nutrient reduction. We demonstrated the related modeling procedures with two-function variable (UEAP) of both prediction and response can predict the trend of algae growth and determine the states of the lake ecosystem. Hence, the approaches are of great value for lake management policy making.

Keywords: algal bloom, climate change, lake eutrophication, phosphorus utilization efficiency, water quality

1. Introduction

Phosphorus is a necessary nutrient element for aquatic organisms to carry out biosynthesis and energy production, and it is also a major limiting factor for lake primary productivity (Kaiserli et al., 2002; Reeder, 2017). In the 1970s, some scholars put forward the concept of "phosphorus loading", which is based on the premise that the load of phosphorus influences the concentration of phosphorus in lakes, and higher concentration of phosphorus lead to higher primary production (Dillon, 1974; Rowland et al., 2020). The studies on the Chla-TP relationship in lakes around the world showed that the Chla concentration increases with the increase of TP concentration in a logarithmic linear function (Dillon and Rigler, 1974; Jones and Bachmann, 1976; Tang et al., 2019; Liang et al., 2020). These relationships suggest that phosphorus limits the primary productivity of most lakes, which has become a long-term paradigm for limnology (Canfield Jr., 1983; Filstrup et al., 2014; Smith and Shapiro, 1981). Based on this theory, people began to reduce external and internal loads of phosphorus according to load targets, so as to reduce biomass such as phytoplankton and lake eutrophication control (Ibisch et al., 2017; Søndergaard et al., 2005). However, this method is not always effective (Sas, 1990; Dodds et al., 1998; Oliver et al., 2017; Huang et al., 2018). As far as algae control is concerned, it is desirable to reveal the responding behaviors of lake ecosystems to environmental changes when setting the lake management strategy.

In the Chla-TP relationship, the UEAP reflects the nutrient and energy flow in the lake ecosystem, which is of great significance for understanding the state of the ecosystem (Abell et al., 2012; Huo et al., 2014). Although previous studies have expressed UEAP as the ratio of TP to Chla per mass unit (Huo et al., 2019a), this ratio does not truly reflect the availability of phosphorus. There is still no effective method in to quantify the change of UEAP on a long-term series and spatial scale. The impact of nutrients on algae depends on other growth conditions and environmental factors. Changes of the concentration of nutrients in water, or ratio between different nutrients, such as the ratio of nitrogen to phosphorus (NPr), can affect the interaction between nutrient and Chla (Hamilton and Mitchell, 1997). The relationship between nutrients and primary productivity is affected by meteorological conditions, which leads to changes of the utilization of algae to nutrients (Huo et al., 2019b; Davis et al., 2009; Wood et al., 2016). For example, temperature and light intensity determine the growth response of algae and its relationship with nutrients (Halldal and French, 1958). Water temperature is highly correlated with primary productivity and affects the relationship between nutrients and Chla significantly (Liu et al., 2018; Wang et al., 2016). Climatic warming can cause regime shifts in lake food webs (Scheffer et al., 2001). Light intensity is an important condition for the growth of phytoplankton and is related to absorption of phosphorus and other micronutrients (Paerl et al., 2011). Rainfall dilutes the lake water and brings nutrients into the lake (Huo et al., 2014), resulting in changes of the nutrients concentrations, which, in turn, alter the growth of algae. Climate change can effect on the water budget components and snow-melt runoff of lakes, which can change the hydrological conditions of algae growth (Kansoh et al. 2020; Javadinejad et al. 2020). Wind velocity affects the synthesis of gas vesicles in algae breeding and the distribution of algae cells, and also disturbs the water body to release nutrients from sediments (Yang et al., 2016). Broadly speaking, climate change is warming lakes, and the more frequent extreme precipitation events in many regions may be transport more nutrients to surface water (O'Reilly et al., 2015; Allan and Soden, 2008). At the same time, the flow of rivers entering the lake will also affect the hydrological conditions of the lake. Only by ensuring proper river flow and morphological quality can environmental goals be achieved (Ćosić-Flajsig et al., 2020). These changes are unevenly distributed in time and space, but all of these are expected to affect the effectiveness of lake eutrophication control. Determining the long-term characteristics of UEAP and its main driving forces are valuable in understanding how water ecosystems will change in a warmer and extreme climate.

In the world, one-third of the lakes are under considerable human pressure (Mammides, 2020). Water quality management is the main concern and research hotspot in current water pollution problems

(Zhang, 2019), many lakes still face algae bloom problem even with improved water quality (Sas, 1989; Dodds et al., 1998; Scheffer and Nes, 2007; Yang et al., 2008; Huang et al., 2018). and In China, with economic development and rapid urbanization, excessive external nutrient load causes the lake water quality to deteriorate drastically (Qin et al., 2010; Tong et al., 2017; Zhou et al., 2017). In order to improve the water quality of lakes, the Central Government of China issued a series of strict laws, plans and guidelines from 2005 to 2017, including a series of five-year plans, the Guidelines on Strengthening Water Environmental Protection for Key Lakes in 2008 and the Water Pollution Control Action Plan (Water Ten point Plan) in 2015. The investment in environmental restoration for improving the water quality of lakes and rivers has increased from nearly 0 in 1994 to 1 trillion yuan in 2014 (Huang et al., 2019; Zhou et al., 2017), especially for the three eutrophic lakes (Taihu, Chaohu and Dianchi Lakes). Eutrophication and harmful algal blooms of the three lakes have received great attention (Duan et al., 2017; Ni et al., 2016; Stone, 2011; Tong et al., 2017). At present, the water chemical quality of lake statue such as Taihu Lake, Chaohu Lake and Dianchi Lake has been improved to a certain extent, and the nutritional level has been reduced, but algal blooms have not been controlled effectively (Huang et al., 2018; Wu et al., 2017; Yang et al., 2008). Measures to reduce surface water pollution include the construction of sewage treatment plant, lakeside pollution interception, agricultural non-point source control, ecological restoration and dredging in the lake, and external load control (Liu et al., 2014), but the understanding of the impact of all these efforts on the lake ecosystem is still very limited.

In view of the huge cost of water quality management, we need to understand the reasons for the delayed response of algae to water quality improvement, and the relationship between the lake ecosystem and the staged characteristics of lake governance. As the response of algae growth to the nutrients are multi-factor controlled, nutrient load management based on the relationship between Chla and TP may not always effective for lake algae bloom control. Thus, is it possible that the current unexplained phenomenon of sustained algal blooms in water nutrients level improved or low-maintained lakes was the consequences of the changes of UEAP? In other words, was it possible the increased UEAP caused by nutrient factor and climate factor have offset the benefit of catchment management for reducing nutrient loads to lakes? If yes, what are the main drivers in controlling UEAP? When the threshold point and paralysis or active phase are? Is the change of UEAP the main driver for the change of algae?

Dianchi Lake and the Erhai Lake are the two climate-sensitive lakes with different nutritional states in Yungui Plateau of China. Before the 1980s, Dianchi Lake had a good water quality with lower nutrients contents. With the rapid economic development and urbanization in the lake basin, large amounts of external nutrient input has caused rapid deterioration of water quality and severe eutrophication (Chen et al., 2020). Erhai Lake is mainly affected by agricultural non-point source pollution. For a long time, Erhai Lake has maintained in the middle or low nutrition level and the water quality is at Grade II and III, but algal blooms have also occurred from time to time (Chu, 2020). In order to verify the above hypothesis, the two lakes were taken as examples for the study to investigate: (1) the relationships between UEAP and algae density, and significance of UEAP and other factors, (2) the main driving forces for lake UEAP in the past 20 years and their relevance and significance in individual lakes, (3) the improvement of modeling reliability for algae density by incorporation of UEAP and other factors (4) the simulation UEAP changes in response identified lake specific driving forces, explaining lake ecological status and stages, and speculating future trajectories of the lake ecology with possible interventions. Unlike our previous studies on the impact of sediment release on lake eutrophication (Chen et al., 2020; Ni et al., 2016), this study investigates the response of UEAP to nutrients and climate and discusses the mechanism of lake eutrophication from the perspective of changes in the water ecosystem. This result will reveal the impact of UEAP on lake algae dynamics and the driving factors of UEAP changes, therefore, provide a diagnosis method of lake ecosystem state, hence it is pertinent to the insights of algal blooms control from the perspective of water ecological changes.

2. Materials and methods

2.1. Study area

Dianchi Lake (24°40′-25°02′ N, 102°36′-103°40′ E) and Erhai Lake (25°36-25°58′N, 100°05′-100°17′E) are located in southwest of Kunming city and Dali Prefecture, Yunnan Province, respectively (Fig. 1). They are the largest and second largest freshwater lake in Yunnan-Guizhou Plateau in southwestern China, respectively. The area of the Dianchi watershed is 2920 km^2, and the area of lake is approximately 298 km^2 at an average water level of 1887.4 m. The area of the Erhai watershed is approximately 2565 km^2, and the area of lake is approximately 249.8 km^2 at an average water level of 1974 m. The hydraulic retention time of Dianchi Lake is about 4 years of the lake. Dianchi Lake has been divided into two parts artificially. Among them, Waihai is located in the south (299 km^2, with an average water depth of 5 m), and Caohai is located in the north (11km^2, with an average water depth of 2.5 m) (Wang et al., 2019). The average water depth of Erhai Lake is 10.5 m, and the hydraulic retention time is about 2.75 years. The average annual temperature in the Dianchi basin is 14.7 ℃, and the average annual rainfall is 1006 mm. For Erhai Lake, the average annual temperature of Erhai basin is 15.1℃ with the sufficient sunshine hours, and the annual dominant wind is southwest wind, and the annual precipitation is 1048 mm. More than 80% of precipitation is concentrated in May-October. There are 35 rivers flowing into Dianchi Lake, all of which converge into the lake along the north, east and south directions of the lake. However, there are 23 rivers enter the lake mainly, which accept all the incoming water in the basin. Xi'er River is the only river that flows out of the Erhai Lake (Wang, 2015). From the assessment reports of Five Year Plan (2006-2020) for Dianchi basin and Erhai basin, the soil types in the Dianchi Lake basin are mainly paddy soil and red soil, while the soil types in the Erhai Lake basin are mainly red soil, purple soil and brown forest soil. In recent years, the per capita GDP in the Dianchi Lake basin has increased year by year. The average per capita GDP (2005-2015) has increased by 3.2 times, and the annual growth rate was 12.34%. The average GDP growth rate of the Erhai Lake basin has reached more than 10% (2005-2015), and it is also one of the fastest growing regions in Yunnan Province. However, the overall industrial structure of the Erhai Lake basin is relatively low, and the development model is relatively extensive. The largest land use type in the Dianchi Lake basin is forest land, mainly coniferous forest, broad-leaved forest and mixed forest. With a wide variety of plants and rich in biodiversity, the Erhai Lake basin is an important biodiversity treasure house in China. The horizontal zonal vegetation in the Erhai Lake basin is semi-humid evergreen broad-leaved forest and Yunnan pine forest, and Yunnan pine forest is currently widely distributed.

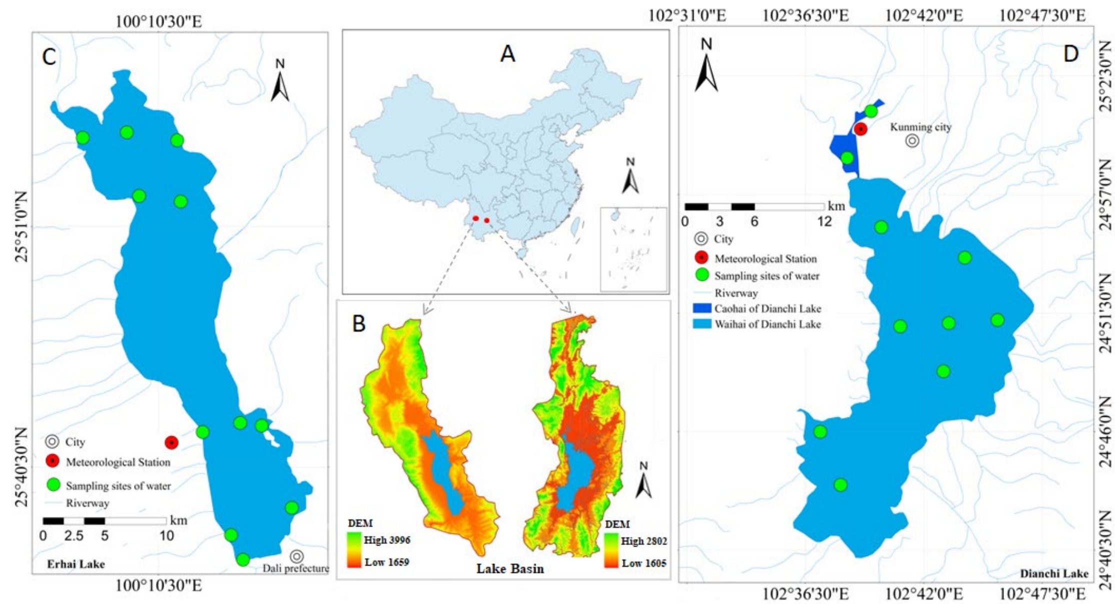


Fig. 1. Study area, the regularly sampled monitoring stations and meteorological stations in the Dianchi and Erhai Lakes. A is the locations of Dianchi and Erhai Lakes in China; B is the elevation map of the Dianchi Lake (right) and Erhai Lake (left); C is the location of Erhai Lake and the water quality indicator monitoring section; D is the location of the Dianchi lake and the water quality indicator monitoring section.

2.2. Data sources

The data of Kunming Meteorological Station (NO. 56778, 25°N, 102°38′24″E, altitude 1886.5 m) and Dali Prefecture Meteorological Station (NO. 56751, 25.7°N, 100°18′41″E, altitude 1990.5 m) were represented the climate of Dianchi Lake and Erhai Lake, respectively. The meteorological data of Dianchi Lake was obtained from the China Meteorological Data Center (CMDC), http://data.cma.cn/. The meteorological data of Erhai Lake was obtained from the National Greenhouse Data System (NGDC), http://data.sheshiyuanyi.com/WeatherData//. Meteorological indicators included air temperature (AT, °C), precipitation (PP, mm), wind velocity (WV, m/s) and sunshine hours (SH, h). The water quality of rivers and lakes in Dianchi Lake (1998-2019, 10 stations, month by month) and flow data were from Environmental Monitoring Center Station and Hydrological Bureau of Kunming city, respectively. The water quality of rivers and lakes in Erhai Lake (1994-2019, 11 stations, month by month) and flow data were from Environmental Monitoring Center Station of and Hydrological Bureau of Dali Prefecture, respectively. The TP load of the river entering the lakes was calculated using the W_i=C_i×Q_i formula (Zhao et al., 2013) , where W_i is the TP load into the lake in *i* year, t/a; C_i is the mean concentration of TP in the river inlet in *i* year, mg/L; Q_i is the average amount of water inflow into lake in *i* year, m^3/s. Water quality indicators include water temperature (WT, °C), dissolved oxygen (DO, mg/L), acidity and alkalinity (pH), servo disk depth (SD, m), total nitrogen (TN, mg/L), TP (mg/L) L), nitrogen phosphorus ratio (NPr), chemical oxygen demand (COD_{Cr}, mg/L), biochemical oxygen demand (BOD_5, mg/L) and Chla (mg/L). The relevant data for watershed water pollution control and load of lakes were from the assessment reports of the "Eleventh Five-Year Plan (2006-2010)", "Twelfth Five-Year Plan (2011-2015)" and "Thirteenth Five-Year Plan (2016-2020)" of Dianchi Lake basin and Erhai Lake basin. The abbreviations of the indicators were listed in the abbreviation table in the Supporting information files. According to the implementation of national governance measures and changes in pollution load, combined with the occurrence of algal blooms, the research time of Dianchi and Erhai Lakes were divided into three stages. Among them, Stage I from 1998 to 2005, Stage II from 2006 to 2012 and Stage III from 2013 to 2019 for Dianchi Lake, and Stage I from 1994 to 2002 Stage II from 2003 to 2012, and Stage III from 2013 to 2019 for Erhai Lake.

2.3. Statistical analysis

(1) Hierarchical Linear Model (HLM)

Multi-level/hierarchical modeling method can associate single observations with group-level variables and make statistical inferences based on group mean and population mean (Malve and Qian, 2006). A hierarchy structure was introduced into the data, including the observations nested in each year group and the year group nested in each lake. The log-log linear model was used as the basic model form of the Chla-TP relationship. Log-logarithmic linear regression represents the proportional change relationship between response and predictor variables (Qian, 2017). That is, the model assumes that a 1% increase in predictor variables will result in a fixed percentage increase in response variables. When using natural logarithm, the fitting slope (β) is the fixed percentage (β%) (Tang et al., 2019).

TP, Chla and meteorological data were grouped by year, where paired data of Chla-TP corresponds to the same sampling site. There were two lakes as types, and each lake was divided into *n* groups by year. There were 10 sampling monitoring sections in Dianchi Lake (Fig. 1C). The water quality indicators were sampled and monitored once a month for 12 months a year. Therefore, the annual Chla-TP paired data of

Dianchi Lake has 120 observation values. The monthly sampling sections of Erhai Lake were different (4-12 sections), and the water quality indicators were sampled and monitored once a month for 12 months a year. Therefore, the annual Chla-TP paired data of Erhai Lake has 53-144 observation values. The hierarchical nature of the data was formally assessed using 2-level models. The first layer was the observation value of *n* groups, and the relationship between Chla and TP was established. In the second layer, the relationship model between the influence factors and the intercept or slope of the first layer was established.

In the first level, after natural log-transforming, concentrations of Chla and TP were modeled linearly (Formula 1).

$$\text{Level 1:} \qquad \ln(Chla) = \beta_{0j} + \beta_{1j}\ln(TP)_{ijk} + \gamma_{ij} \tag{1}$$

Where β_0 and β_1 are the intercept and slope of the Chla-TP regression model in a certain type; ln(TP) is the natural logarithmic conversion of TP. Since the intercept and slope coefficients are random variables that vary across the lakes, they are often referred to as random coefficients. In our study, the specific values for the intercept and the slope coefficients are a lake characteristic (Hox, 2010). The intercept (β_0) is the expected natural logarithmic Chla concentration when the TP concentration is at the given level, a higher intercept indicates a higher Utilization Efficiency of Algae to TP (UEAP) (i.e., the same TP value resulting in a higher Chla) (Tang et al., 2019). In the previous study, some studies express UEAP as the ratio of TP to Chla per mass unit (Huo et al., 2019a), but a higher or lower value will affect the result. Here, regression model method provides a best fitting and makes UEAP comparable between different lakes objectively. Moreover, we established a relationship between Chla and TP data from point-to-point at each time point of the year to investigate that if TP is indeed supplying Chla productivity, this can better reflect the efficiency of phosphorus utilization. Therefore, we used the intercept of the Chla-TP relationship model to represent UEAP to achieve quantization the on long-term data sets. The slope (β_1) indicates the degree of changes of Chla in responding to TP increases or decreases in the lake, which represents the Response Rate of Algae to TP (RRAP); a higher slope indicates that the lake is more sensitive to TP; γ is the residual.

In the second level, we assume that the interannual change of the lnChla-lnTP relationship can be explained by changes in meteorological factors. Through Spearman correlation analysis, significant correlation factors were included as covariates in the model to illustrate the changes in the groups of intercepts and slopes of the Chla-TP relationship (Formulas 2 and 3).

$$\text{Level 2:} \quad \beta_{0j} = \gamma_{00} + \gamma_{01}(factor) + \mu_{0j} \tag{2}$$

$$\beta_{1j} = \gamma_{10} + \gamma_{11}(factor) + \mu_{1j} \tag{3}$$

Among them, γ_{00}, γ_{01}, γ_{10} and γ_{11} are the fixed coefficients (fixed effects) obtained in this process; γ_{ij}, μ_{0j}, and μ_{1j} are random errors (random effects). That is, in the HLM software operation result part, the value of γ_{00}, γ_{01}, γ_{10} and γ_{11} is the fixed effect part, and the variance of the residuals of γ_{ij}, μ_{0j} and μ_{1j} is the random effect part.

(2) Generalized Additive Model (GAM)

GAM is a non-parametric generalized multiple linear regression method based on the extension of the Generalized Linear Model (GLM). The advantage of GAM is that it can directly fit the non-linear relationship between the response variable and multiple explanatory variables (Guisan et al., 2002), add different forms of functions, find out the rules, and adapt to various function analysis of type distribution (Richard and Brent, 2008). Compared with linear models, the distribution of Y in GAM can be any form of exponential distribution (such as Gaussian distribution, Poisson distribution, binomial distribution), and the link function can be any monotonic differentiable function (such as logarithmic function or logistic function). The GAM method uses a smooth function s(x) instead of a linear function (Pearce et al., 2011; Capo et al., 2017), so the independent and dependent variables are not limited to linear relationships. These advantages enable the GAM model to deal with non-normally distributed response variables, while also including qualitative and semi-quantitative predictors. The general formula is:

$$g(y) = s_0 + s_1(x_1) + \ldots + s_m(x_m) + \varepsilon \tag{4}$$

where s(x) is a smooth function connecting explanatory variables and ε is a random residual.

The choice of explanatory variables is determined by the strength of the correlation between the response variable and the explanatory variable, and the principle is to select the index with the strongest correlation (Deng et al., 2015). In this study, meteorological and water quality factors were used as explanatory variables, UEAP and algae density were used as response variables, and the explanatory rate of the explanatory variables to the response variables was evaluated using the GAM method. For specific steps, refer to the literature by Deng et al. (Deng et al., 2015; Chen et al., 2020). First, calculate the variance expansion factor (VIF) by calling the *vif* function in the *bstats* package in the *R* language software to determine the collinearity of the predictor variables and eliminate the variables that may cause collinearity (When $0<\mathrm{VIF}<10$, there is no multicollinearity; when $10 \leqslant \mathrm{VIF}<100$, there is strong multicollinearity; when $\mathrm{VIF} \geqslant 100$, there is severe multicollinearity). Then, determine the connection function according to the probability density distribution type of the response variable. Next, all variables selected by collinearity diagnosis are analyzed by the *gam* function in the *mgcv* software package based on R software, and the best model is determined according to the principle of "r_{aj}^2 is the largest, AIC is the smallest". Finally, use the *gam check* function to evaluate the effect of the best model and the residual distribution. In this study, the GAM method was used to analyze the correlation between UEAP (and algae density) and influencing factors of two lakes.

(3) Principal Component Analysis (PCA)

PCA can replace the original indicators with some main components, and reorganize many related water quality and climate indicators into a set of unrelated new comprehensive indicators, thereby revealing the internal structure between multiple variables through several main components (Moore, 1981). The process of identifying driving factors for UEAP is as follows: First, Spearman correlation analysis was used to analyze the correlation between environmental variables and UEAP, and factors that are not related to UEAP were eliminated. Then, analysis, dimensionality reduction and factor analysis were performed in turn, and basic statistical information after selecting variables was output. After the main factors were extracted by PCA, the characteristic parameters were divided into several main components. Finally, based on the principal component method and the maximum variance rotation method, the interpretation rate of water quality and climate factors on the UEAP variance was obtained, and the influence and contribution of the main factors to UEAP were determined and quantified.

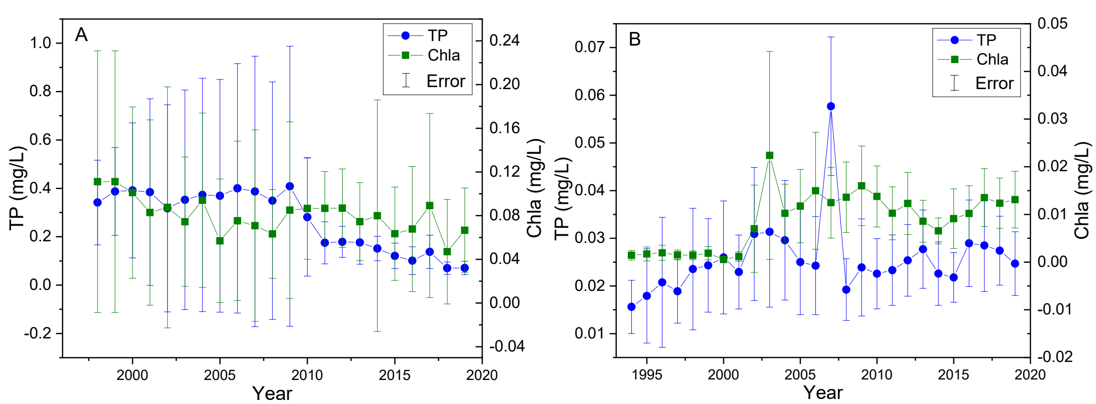
2.4. Data processing

The image (Fig. 1) of study area was performed in ArcGIS software. HLM analysis was performed by using HLM 6.08 software. GAM analysis was performed by using R language. Spearman and PCA analysis were performed by using the SPSS 20.0 statistical software, and the level of significance used was $p < 0.05$ for all tests. Plotting and regression analyses were completed using the Origin 2019.

3. Results

3.1. Relationships between TP and Chla

In the past 22 years, the average concentration scale of TP and Chla in Dianchi Lake were 0.070-0.480 mg/L and 0.047-0.111mg/L, respectively. The highest values of TP and Chla appeared in 2009 and 1999, respectively, while the lowest values all appeared in 2018 (Fig. 2A). TP concentrations of Dianchi have been in inferior Grade V water (national surface water quality standard) for many years. The water quality has improved in recent years, and most sites are superior to inferior category V water. In the past 26 years, the average concentration scales of TP and Chla in Erhai Lake were 0.015-0.058mg/L and 0.00058-0.023mg/, respectively (Fig. 2B). The highest values of TP and Chla appeared in 2007 and 2003, respectively, while the lowest values appeared in 1995 and 2000, respectively. Before 2003, the average concentration of Chla in Erhai Lake was lower than 0.007mg/L in each year, but after 2003, Chla increased significantly. Among them, the overall average concentration of Chla in 2003-2019 was 6 times higher than that in 1994-2002. The log-linear model between Chla and TP was established for Dianchi Lake and Erhai Lake based on more than 20 years data (Figs. 2CD, S1 and S2). A scatter plot showed that there is a linear relationship between on TP and Chla of the two lakes in most years over 20 years (*p*<0.05) (Table S1). However this general linear relationships model (*p*<0.05) (Table S1) could not explain the actual Chla fluctuations against TP over time (Fig. 2 A and 2B).



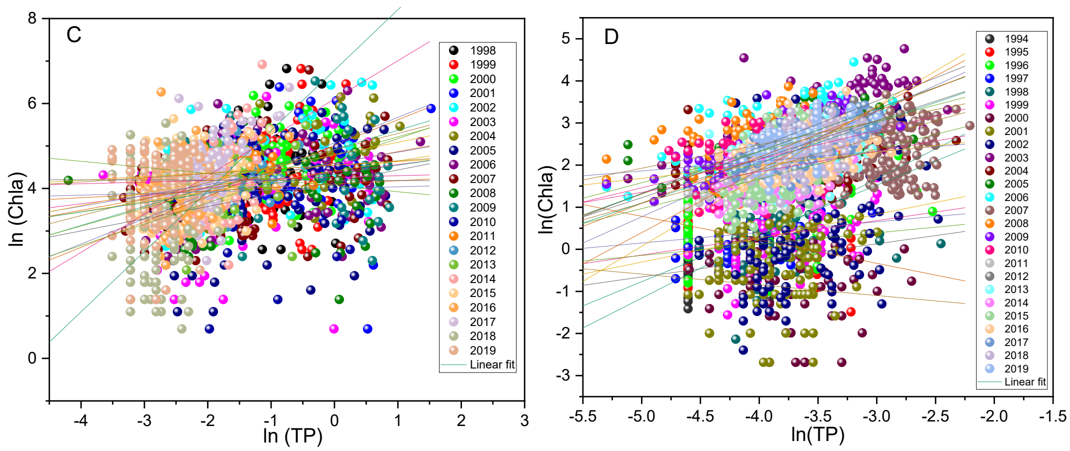


Fig. 2. Changes of the relationship between Chla and TP in the two lakes in the past two decades. (A) and (B) are the changes of measured Chla over time VS TP of Dianchi (A) and Erhai (B) Lakes. (C) and (D) are the relationship and fit lines between ln (Chla) and ln (TP) in Dianchi Lake (C) and Erhai Lake (D) based on the actual measure data for each year.

3.2. Relationships between UEAP and algal density

Fig. 3A shows that the scales of UEAP in Dianchi Lake were 4.00-6.79 (4.69±0.66) with a relatively small fluctuation ranges (2.79). Among them, UEAP fluctuated between 4 and 5 before 2013, but increased after 2013, especially in 2014 and 2017 (higher than 6). However, the scale of UEAP in Erhai Lake were -2.01 to 8.40 (4.26±2.71) and with a relatively large fluctuation ranges (10.41) (Fig. 3A). The UEAP with a lower intercept group was before 2003, and the higher group was after 2003. Before 2003, the UEAP of Erhai Lake was lower than Dianchi Lake, and then increased gradually and exceeded that of Dianchi Lake. The change trend of the RRAPs of the two Lake was similar to the change of their UEAPs, which increased after 2013 and 2003, respectively (Fig. 3B). After 2001, the RRAP of Erhai Lake was higher than that of Dianchi Lake significantly (p<0.05). All the fluctuations were correlated with the changes of algal density in the time serials (Fig. 3 and Table S2).

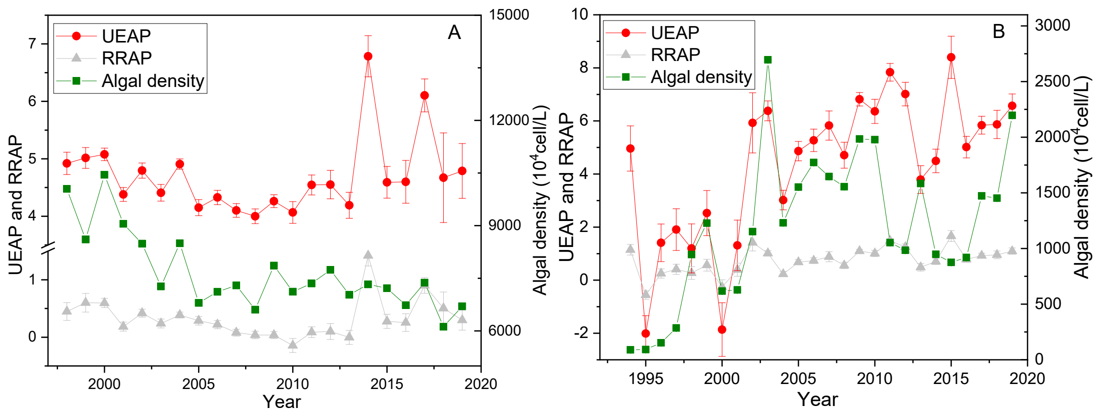


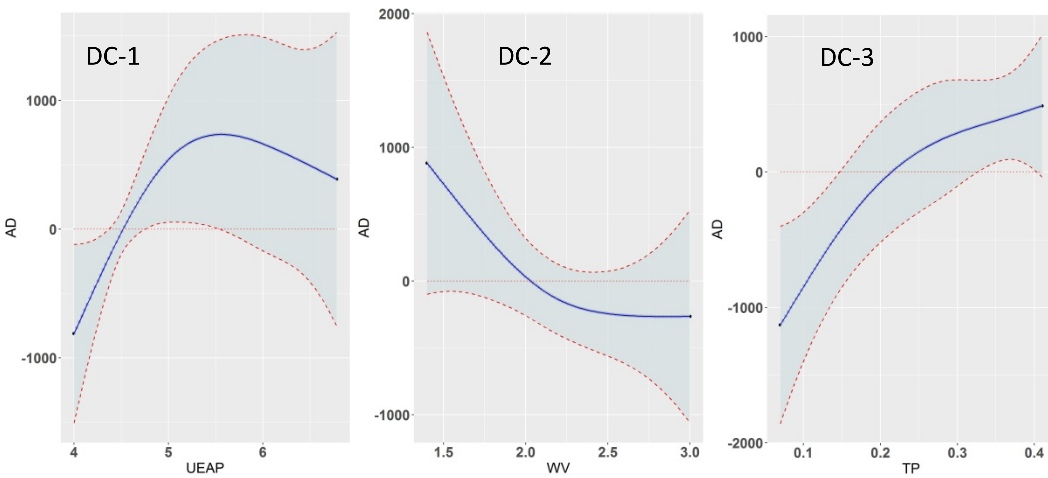
Fig. 3. Changes of UEAP and RRAP against Chla in 20 years in Dianchi Lake (A) and Erhai Lake (B).

In order to investigate the relationship between UEAP and algae growth, meteorological factors, water quality and UEAP were used as explanatory variables, and algal density was used as the response variable. Elimination of the irrelevant indicators to algal density was conducted by Spearman analysis in the meteorological and water quality indicator. After collinearity diagnosis, the remaining factors were arranged and combined as explanatory variables to construct the GAM nonlinear model. Figs. 4 and S3 showed the predictive model curves of univariate and multivariate for the changes of algal density in the two lakes. Table 1 showed the model and related parameters. The model R^2 is between 0.17 and 0.78. According to the principle of smaller AIC and higher DE, also combined with the value of Adj-R^2, GAM results showed that the interpretation rates of UEAP for algal density in Dianchi Lake and Erhai Lake were 65.67% and 58.93%, respectively. However, the combined model of UEAP, WV and TP was the best model of algal density variation in Dianchi Lake, and its interpretation rate was 75.76%. The combined model of UEAP and TN was the best model of algal density variation in Erhai Lake, and its interpretation rate was 85.44%. The model including UEAP can better explain the variation of algal density, indicating that UEAP has contributed to the change of algal density. A nonlinear correlation was observed between UEAP and algal density (Figs. 4DC-1 and EH-1), indicating the UEAP is a better parameter for explanation of algae dynamics. This relationship reflected the algal density fluctuations over time and the characteristic of threshold natures. When we consider other key factors, there may be a threshold for the response of algae to UEAP. For example, after exceeding the threshold (about 5.5) in Dianchi Lake, the promotion effect of UEAP on algae was diminishing.

Table 1 GAM related parameters for the changes of algal density in Dianchi and Erhai Lakes.

	Dianchi Lake				Erhai Lake			
EV	PV	Adj-R^2	DE (%)	AIC	PV	Adj-R^2	DE (%)	AIC
Algal density	UEAP	0.53	65.67	361.39	UEAP	0.47	58.93	402.65
	WV	0.61	66.27	355.21	AT	0.17	20.38	410.59
	TP	0.23	26.85	368.78	TN	0.61	62.26	391.18
	UEAP+WV	0.61	67.96	356.2	UEAP+AT	0.45	58.94	404.19
	UEAP+TP	0.66	73.12	353.06	UEAP +TN	0.78	85.44	381.9
	WV +TP	0.61	67.75	356.15	AT+TN	0.71	78.76	388.08
	UEAP+WV+TP	0.68	75.76	352.98	UEAP+AT+TN	0.59	64.29	394.45

Note: EV, Explanatory variables; PV, Predictor variable; DE, deviance explained; AIC, akaike information criterion.



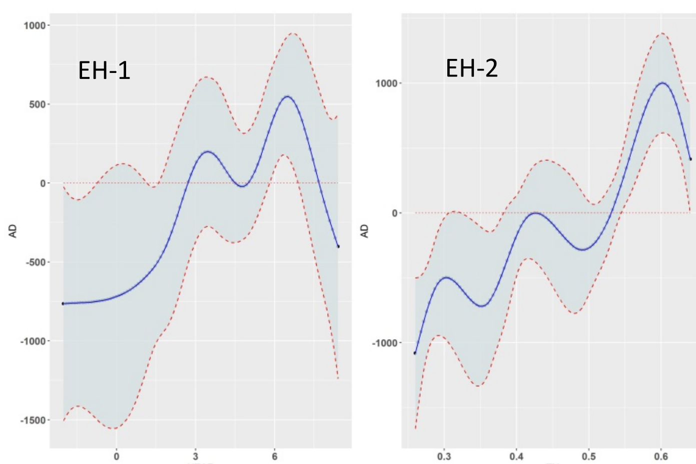


Fig. 4. GAM analysis results of the predictor variables on the changes of algal density in Dianchi (DC) and Erhai (EH) Lakes. AD is the algal density.

3.3. Factors driving UEAP

After Spearman analysis (Table S2) and extracting the main water quality and meteorological factors affecting UEAP, the parameters were divided into two principal components (PC1 and PC2) by PCA. For UEAP of Dianchi Lake (Fig. 5A), PC1 explained 45.87% of the total variance, while PC2 explained 29.64% of the total variance, respectively. Among them, TN, NH_3N and DO were the main components of PC1, and PP, WV, NPr and Chla were the main component of PC2 in Dianchi Lake. For UEAP of Erhai Lake (Fig. 5B), PC1 explained 58.60% of the total variance, while PC2 explained 19.00% of the total variance, respectively. Among them, TN, COD, BOD, pH, SD, and Chla were the main components of PC1, and AT, PP, NPr, and P_{Load} were the main component of PC2 in Erhai Lake. In general, regardless of Dianchi Lake or Erhai Lake, the water quality indicators were the main component of PC1 for the UEAP. In particular, changes of nutrients have an important contribution to changes of UEAP.

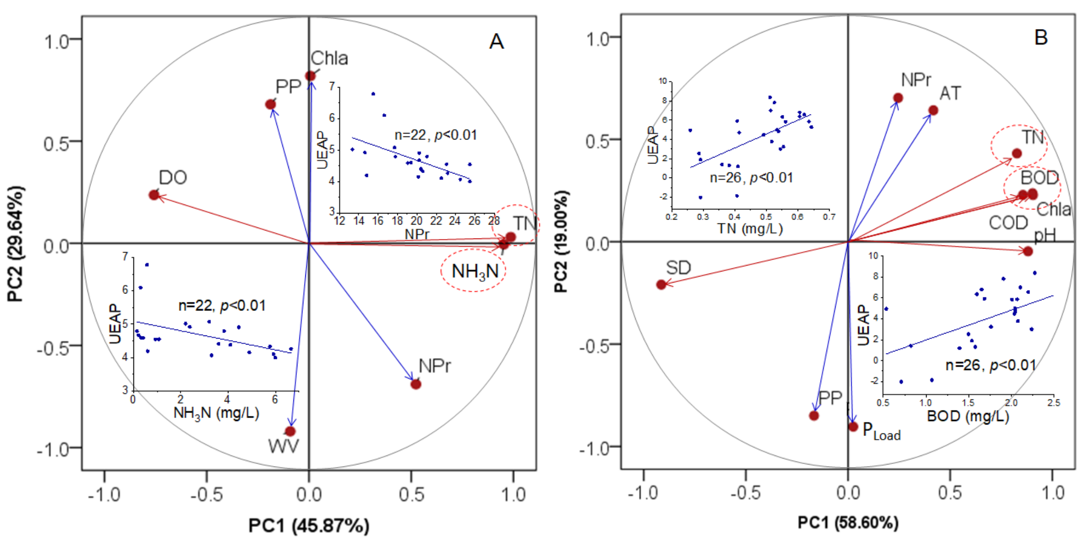


Fig. 5. Principal component loading diagrams of drive factors on UEAP of A Dianchi and B Erhai Lakes. The red arrow represents PC1, the blue arrow represents PC2, and the length of the arrow represents the correlation coefficient between the indicator and the common factor; The scatter-fitting line graphs selected the water quality index factor with the highest correlation with UEAP.

Although climate factors are the main component of PC2, it is obvious that climate factors will affect algae growth. In order to examine the impact of interannual climatic factors on UEAP, using AT, PP, and WV as the covariates to further populate the Chla-TP regression model first (SH was excluded due to insignificant relationship with the model parameters), a two-layer models of their relationship with UEAP (β_{0j}) was then established. The model reliability was between 0.803 and 0.997 (Table 2). The result showed AT did not show a significant effect on UEAP of Dianchi Lake (p>0.05), but showed a significant effect on that of Erhai Lake (p<0.05). From Figs. S4A and B, AT showed a significant linear positive correlation with UEAP of Erhai Lake (p<0.01) (Fig. S4A). PP showed a significant effect on UEAP of Dianchi and Erhai Lakes (p<0.05). Among them, PP showed a significant linear relationship with UEAP of both Dianchi and Erhai Lakes (p<0.01), which was positively correlated with UEAP of Dianchi Lake (Fig. S4C) and negatively correlated with UEAP of Erhai Lake (Fig. S4D). WV showed a significant effect on UEAP of Dianchi Lake (p<0.01), and showed a significant linear negative correlation with UEAP in Dianchi Lake (p<0.05, Fig. S4E), but did not show a significant relation to that of Erhai Lake (Fig. S4F). Therefore, PP and WV could explain the time-scale changes of the UEAP of Dianchi Lake partially, while AT and PP could explain that of Erhai Lake partially.

Table 2 The estimated between-group standard deviance in group-specific intercepts (β_{0j}) and slopes (β_{ij}), and the final estimation of fixed effects (with robust standard errors).

Lakes	Intercept	Reliability estimate	Fixed effect	Coefficient	Standard error	T-ratio	p-value
Dianchi Lake	For Intercept 1, β_{0j}	0.832	Intercept 2, γ_{00}	6.1385	4.7664	1.288	0.213
			AT, γ_{01}	-0.0915	0.2956	-0.309	0.760
	For Intercept 1, β_{0j}	0.803	Intercept 2, γ_{00}	3.5501	0.3287	10.800	0.000
			PP, γ_{01}	0.0011	0.0004	3.005	0.007
	For Intercept 1, β_{0j}	0.904	Intercept 2, γ_{00}	5.6015	0.2666	21.010	0.000
			WV γ_{01}	-0.4760	0.1148	-4.145	0.000
	For Intercept	0.908	Intercept 2,	-55.4437	12.6343	-4.388	0.000

Erhai Lake	1, β_{0j}		γ_{00}				
			AT, γ_{01}	3.8644	0.8086	4.779	0.000
	For Intercept	0.927	Intercept 2,	12.2588	2.927	4.138	0.000
	1, β_{0j}		γ_{00}				
			PP, γ_{01}	-0.0092	0.0036	-2.533	0.019
	For Intercept	0.997	Intercept 2,	2.5175	13.8100	0.182	0.857
	1, β_{0j}		γ_{00}				
			WV, γ_{01}	0.7419	5.6192	0.132	0.897

Abbreviations: DC, Dianchi Lake; EH, Erhai Lake.

3.4. Predictor variables and models for simulation of UEAP

Elimination of the irrelevant indicators to UEAP was contacted by Spearman analysis in the meteorological and water quality indicator. After collinearity diagnosis, the remaining factors were arranged and combined as explanatory variables to construct the GAM nonlinear model. Figs. 6 and S5 shows the fitting curve of the individual predictor variables to the changes of algal density in the two lakes. According to the principle of small AIC and high DE, combined with the value of Adj-R^2, it showed that NPr was the best explanatory variable for UEAP variation in Dianchi Lake, with an explanatory rate of 74.30%. While, the combined model of TN and AT was the best model for UEAP variation in Erhai Lake, with an explanation rate of 81.23% (Table 3). Therefore, NPr was the key predictor of UEAP changes in Dianchi Lake, and TN and AT were the key predictors of UEAP changes in Erhai Lake.

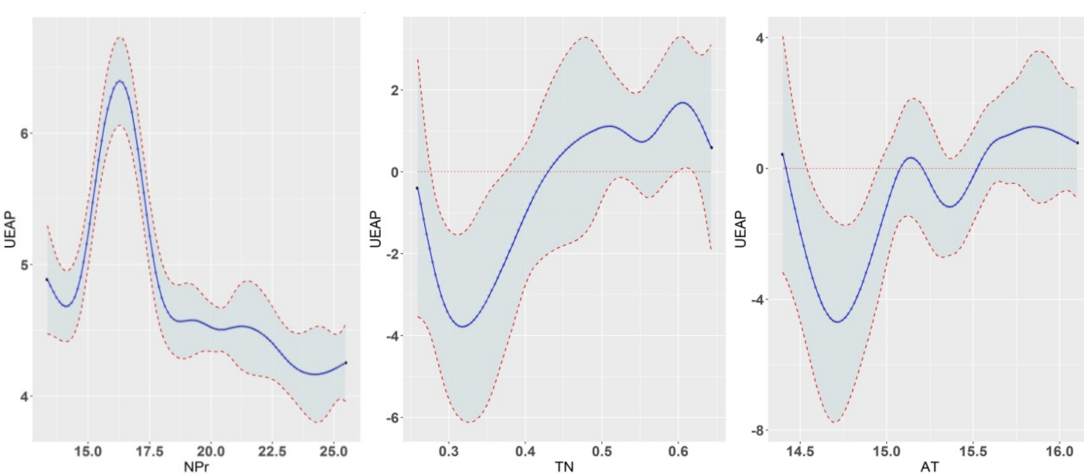


Fig. 6. GAM analysis results of the predictor variables on the changes of UEAP in Dianchi (DC) and Erhai

(EH) Lakes.

Table 3 GAM related parameters for the changes of UEAP in Dianchi and Erhai Lakes.

	Dianchi Lake				Erhai Lake			
EV	PV	Adj-R^2	DE (%)	AIC	PV	Adj-R^2	DE (%)	AIC
UEAP	NPr	0.59	74.30	32.52	TN	0.41	48.52	117.67
	DO	0.25	30.74	42.19	AT	0.38	40.13	117.21
	NPr+DO	0.34	41.02	39.53	TN +AT	0.66	81.23	107.79

Note: EV, Explanatory variables; PV, Predictor variable; DE, deviance explained; AIC, akaike information criterion.

4. Discussion

4.1. Drivers for UEAP changes

In the past 20 years, water quality in Dianchi Lake and Erhai Lake had undergone significant changes, ie the deterioration in Erhai Lake and improvement in Dianchi Lake. We found the similar result as those in previous studies that the nutrient levels alone could not explain the actual algae growth, while the UEAP of individual lake may be a better parameter to reflect the actual growth of the algae. UEAP has nonlinear positive correlation with algal density, showing more precise algal growth threshold phenomena. Fig. 7 is a schematic diagram showing the time serial plot of the UEAP, TN, TP, and algal density. The initial UEAP of Dianchi Lake was higher than that of Erhai Lake. However, UEAP of Erhai increased sharply after a threshold point around the year 2000 and kept increasing after that, and eventually succeeded the level of UEAP in Dianchi Lake. The increased UEAP of Erhai Lake correlated with the deterioration of water quality, while the UEAP of Dianchi Lake increased correlated with the improvement of water quality. For example, nitrogen and phosphorus concentrations of Erhai Lake increased in 2003, and UEAP also rose sharply. The concentrations of nitrogen and phosphorus of Dianchi Lake dropped significantly from 2010 to 2016, UEAP rose sharply in the period. This was in agreement with the actual algal density. Clearly, UEAP could better reflect the actual lake ecology, in terms of algae growth.

Further analysis of the two lakes' data, the key factors driving UEAP changes identified and showed the differences between the two lakes. Our statistic and modeling approaches found that the NPr of Dianchi, TN and AT of Erhai had the highest degree of explanation for the changes of UEAP. During the stage I-II of

Dianchi Lake, TP concentration decreased significantly as the nutrients load control progressed (Fig. S6), which resulted in an increase in NPr, while the UEAP gradually decreased in this period. This might be due to the predominance of phosphorus restriction. The insufficient phosphorus leads to a lower growth rate of algae due to higher NPr. Since 2010, nitrogen load control strengthened. Especially in the Stage III, TN reduced significantly. With the NPr dropped sharply, sufficient phosphorus leads to a higher utilization efficiency by algae. The changes of NPr caused by reduction in nitrogen and phosphorus at different levels drove the alternations of UEAP in Dianchi Lake temporarily. The response of UEAP to NPr was non-linear (Fig. 6-DC). It decreased sharply with the increasing of NPr between 16.25-17.5, and decreased slowly between 17.5-25. For Erhai Lake, TN and AT were the key factors driving UEAP changes. The UEAP of Erhai Lake in stage I was lower than that of Dianchi Lake, which might be related to the lower concentration of nutrients. Previous studies have shown that the higher the initial nutrient concentration within a certain range, the more nutrient salts are absorbed by algal cells (Janse and Aldenberg, 1991). This may be the main reason why the UEAP of Erhai Lake was lower than that of Dianchi Lake at first. When TN was higher than 0.35 (point a in Figs. 7 and 6EH-1) in Erhai Lake, UEAP increased rapidly with the increasing of TN. It might be that the nitrogen restriction was dominant, and UEAP began to respond to TN. In particular, compared with Dianchi Lake, despite the Erhai Lake had less nutrient level in general, its UEAP had exceeded that of Dianchi Lake after 2003 owing to its stage of sensitive response of UEAP to nutrients. Previous study demonstrated that high concentration of nutrients may inhibit the growth of phytoplankton (Wang, 2015). The growth kinetics experiments showed that the half-saturation constant of the maximum growth rate of microcystis cells was 0.53 mg/L for nitrogen and 0.02 mg/L for phosphorus (Baldia et al., 2007). The average concentrations of TN and TP were 0.259-0.643mg/L and 0.015-0.058mg/L in Erhai Lake, respectively. This was a more suitable nutrient concentration range for the growth of microcystis cells. This response dynamics of UEAP in different types of lakes is in line with the characteristics of the ecosystem of the specific lake. With the two sets of data, our approaches established the non-linear positive correlation between algae growth and UEAP. Using the long-term data sets, such a correlation has showed both in the high nutrient lake, the Dianchi Lake, which in the process of recovering from sever eutrophication, and a lake started deterioration from good ecological status, the Erhai Lake (Fig. 7). That is to say that the multi factors determined UEAP dynamics, which in turn explained the novel phenomena of lake ecology. Using this approaches can explain that for a lake ecosystems with a given nutrient level, reducing the load to a certain extent may either promote growth of algae by increased UEAP, or decrease of it by decrease UEAP, or even no response, depending on initial nutrients concentrations and their ratios (such as NPr). While a lake had relatively good ecological status in general, a small amount nutriment increase may cause significant increase in UEAP, and increase in algae growth. It is the first attempt using the approaches to explain the complicated lake systems. Further work on the new data coming from the two lakes together with study on different data sets and the mesocosm study to approve its versatility is desirable.

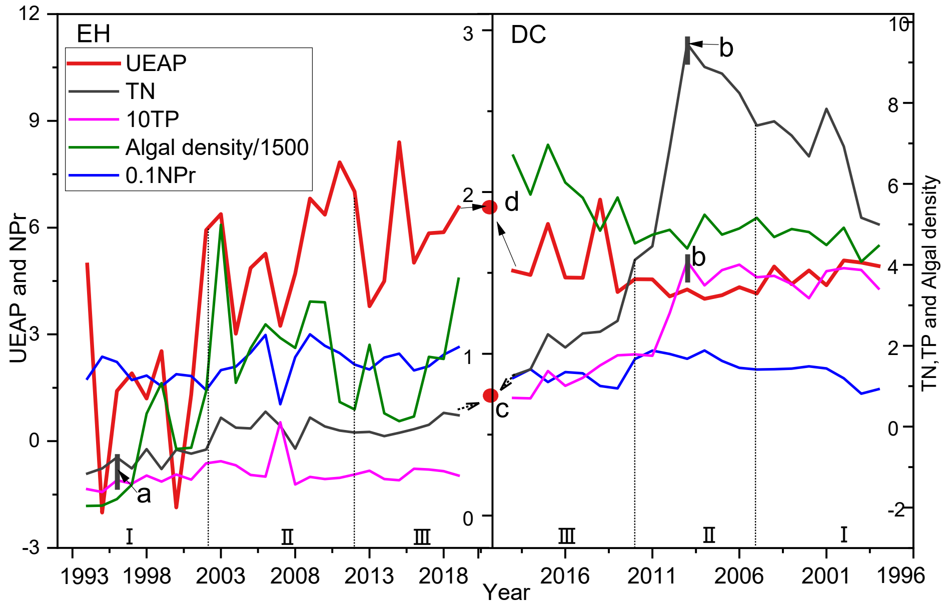


Fig. 7. Changes and relationship of UEAP, nutrients and algal density in Dianchi and Erhai Lakes. The left coordinate is the UEAP and NPr values of the two lakes, the middle and the right coordinates are the values of TN (mg/L), TP(mg/L) and algal density(10^4cell/L) of Erhai Lake and Dianchi Lake, respectively; In order to facilitate comparison in the same figure, TP and NPr were multiplied by 10, and 0.1, respectively, and algae density was divided by 1500; a and b are the possible threshold points of nutrient change (UEAP began to increase) in Erhai and Dianchi Lakes, respectively; c is the possible nutrient threshold that causes mutation of UEAP; d is a possible trend of UEAP; DC represents Dianchi Lake, EH represents Erhai Lake; I, II and III represents three stages.

GAM analysis of the two lakes' ecosystem changing processes showed that when TN is greater than 0.6

(mg/L), the effect on increase of UEAP slowed down in Erhai Lake (Fig. 6-EH). There was no a dataset available for Dianchi Lake when it was starting deterioration just like Erhai Lake today. However, it looks like the trajectories of the two lakes are at critical point because the nutrient levels, UEAP, and algal density are merging at “c” and “d” points shown in Fig. 7. If the two inverse trajectories of the two lakes mirrors each other are not by chance, this may be not a surprise as the two processes may be reflect each other because the two lakes have similar limnology and geography. Assuming it is true, we speculated that Dianchi Lake’s algae and UEAP will continues stay high for a while in the future if the water quality continues to improve, and finally reach the good ecological status. At the same time, if Erhai Lake’s nutrient level keeps going up, UEAP and algae may jump up to the level of current Dianchi Lake. Perhaps, between the high threshold point (point b in Fig. 7) and low threshold point (point a in Fig. 7) there is an inflection point (point c in Fig. 7) of nutrient concentration. Interestingly, UEAP increased with the increasing of nutrient in Erhai Lake (a-c), and decreased with the increasing of nutrient concentration in Dianchi Lake (c-b). It is easy to explain water quality deterioration leads to increased UEAP in Erhai Lake because there is a positive correlation between COD, BOD and SD (Table S2). The improvement of water quality in Dianchi Lake causing UEAP to increase may be indirect. The positive correlation between DO and UEAP may also support that the improved water quality increased the UEAP of Dianchi Lake (Table S2). Currently, both the improved water quality in Dianchi Lake and the deteriorated water quality in Erhai Lake are leading to the same direction of the increased UEAP if the speculated trajectory is true. If other factors remain unchanged, controlling the nutrients of Dianchi Lake may cause UEAP to rise to the threshold first and then decrease, and while controlling the nutrients of Erhai Lake can control UEAP directly and effectively pull the UEAP back to lower level. Therefore, the algae control in Dianchi Lake has a long way to go.

HLM analysis showed that among the meteorological factors, AT, WV and PP also affected UEAP. Again, the main factors affecting UEAP are lake specific. This differentiation made the identification of lake specific factor driven trajectory possible, which otherwise was impossible by using TP-Chla relationships. The WV in Dianchi Lake showed an increasing trend before 2010 and then decreased gradually, which showed a significant promoting effect on the UEAP in Dianchi Lake (Fig. S7). Decreased WV will reduce the exchange of oxygen between the water surface and the atmosphere, and help the algae particles drift along the wind direction, causing large amount of algae accumulation in a specific area of the water surface, thereby increasing the possibility of algal blooms (Whitehead et al., 2009). At the same time, taking 2010 as the demarcation point, PP of Dianchi Lake showed a trend of first decline and then gradually rise (Fig. S7). Precipitation, on the one hand, allows more runoff to enter the water body and dilutes the nutrients in the lake, on the other hand, it can bring many nutrients which are beneficial to algae absorption in the water body, thereby affecting the biomass of phytoplankton (Tang et al., 2019). PP showed a significantly positive correlation with the UEAP (p<0.05) of Dianchi Lake. This showed that the dilution effect of PP was greater than that of nutrient input. Increased PP is beneficial to dilute the concentration of nitrogen and phosphorus in the water body and make it tend to the optimum concentration for algae growth. This might also be related to the reduction of the nutrient content of the runoff into the lake body due to the reduction of the external load under the watershed water pollution control. In the past 26 years, the scale of annual average AT in Erhai Lake was 14.4-16.1℃ and showed an upward trend gradually (Fig. S7). This study found that AT promoted the UEAP of Erhai Lake significantly (Figs. 6 and S4A), and it will be severer if coupled with TN, the main driving force for the increase of UEAP. From the intercept of the AT-UEAP relationship, it can be speculated that a temperature increase of 1°C in the Erhai Lake would increase the UEAP by 3.25 times. On the one hand, warming can promote the absorption of ions by biofilm and the activity of related enzymes, and increase the utilization of nutrients by cyanobacteria (Wang et al., 2016). On the other hand, cyanobacteria can adjust their buoyancy to optimize nutrient and light access. Higher temperatures will reduce the viscosity of surface water, increase the settlement rate of eukaryotic phytoplankton, and further strengthen the competitive advantage of microcystis (Paerl and Huisman, 2009). Although currently the water chemical quality of Erhai Lake is still good, an increase of AT alone will promote the increase of UEAP. The Erhai Lake had less nutrient input, but its UEAP had exceeded that of Dianchi Lake after 2003, which might be related to the promotion of warming effect. The differences in UEAP level, amplitude and trend direction observed in this study may partly reflect the changes in the driving force of ecological destruction, which leads to the different responses of the ecosystem to environmental changes. The important point is the actual factor values and the combination of the factors in contribution to the changes of UEAP was different between the two lakes. The approaches we taken in this study were able to describe the individual ecological status of a specific lake. Further work using the same approaches on different data sets may approve its broad value.

4.2. Implications for lake eutrophication control and decision making

Reducing algal biomass is usually the goal of lake management, and decreasing nitrogen and phosphorus can reduce the primary production in surface waters (Oliver et al., 2017; Conley et al., 2009; Paerl et al., 2016; Schindler, 2012). Though the trends of TN of Erhai Lake and TP of Dianchi Lake were both positively correlated to Chla trends (Table S2), the magnitude of change in nutrients and algae can also be used to infer if trends are ecologically meaningful. For example, since the water pollution control began in 2006, nutrients of Dianchi Lake began to decline sharply in the middle stage II, but algae did not show a corresponding decline. The nutrient content of the Erhai Lake has always been in the water quality grade II and III, but algae has not recovered to the lower level like in the stage I (the green line was lower than the gray line in Fig. 7). The reductions in nutrients did not necessarily promote a similar shift in algal biomass decline. Previous studies have reported that the decline of TN has been enough to transform lakes from eutrophic to mesotrophic systems (Dodds et al., 1998), but reducing nutrients has not promoted a similar change in algal biomass, Even if, the nutrient load to such lakes was strongly reduced they often did not recover to their original clear state (Sas, 1990). The relationship of Chla and TP is bound to be changes when considering other ecological factors owning to nonlinear dynamics in ecosystem (Brown et al., 1999), which includes resilience and abrupt changes owing to thresholds and feedback processes (Walther, 2010). The lack of algae response to nutrient and the GAM analysis results indicate that other emerging environmental changes are affecting the ecosystem status of the lake (Oliver et al., 2017; Scheffer and Nes, 2007). Lake pollution control measures must related to specific endpoints, whether it is algae bloom or water quality, or both. These goals may be different between lakes and the same lake between different stages. Therefore, modeling work to identify the phase of the lake recovering or deterioration is crucial for decision making to achieve the goals.

Although algae biomass is affected by many factors, UEAP, WV and TP in Dianchi Lake, UEAP and TN in Erhai Lake all explained well the variation of algal density in the lakes. The two-lake study demonstrates that nutrients levels may not necessarily link to algae dynamic directly and climate change were driving the increasing of UEAPs. These assumptions were based on the contribution rate of the particular set of parameters to the change of algae density in the GAM results. UEAP successfully linked water nutrient factors and other environment and climate factors in defining the algae density. Our statistic and model approaches provided answers to phenomena of algae growth increase under the improvement of nutrient concentration because the decrease of concentrations of nutrients in Dianchi Lake will actually drive the increase of UEAP now, and the decreasing trend of WV is also conducive to the occurrence of algal blooms. In the past 22 years, the range of annual average AT in Dianchi Lake was 15.4-16.7°C. The annual WV was less than 3 m/s, and the average water exchange time was nearly 4 years. These conditions are favorable factors for the occurrence of algal blooms (Ibelings et al., 2016). Although the AT in Dianchi Lake did not show a significant increase and a significant impact on the UEAP in the past 20 years, the temperature still showed an upward trend (Fig. S7) from the perspective of long-term trend, which will become the catalyst for algal bloom. Unlike Dianchi Lake, the water quality in Erhai Lake has deteriorated in recent years, the increased nutrients concentration together with the increasing AT and the decreasing PP are all conducive to the increase of UEAP. This indicates that algal blooms may still occur even if the external load is reduced in the future, climatic conditions with more drying and warming period will increase the severity of lake eutrophication. At the same time, the fluctuation trends of algal density in each year in Dianchi Lake and Erhai Lake were basically consistent with UEAP dynamics. This makes UEAP a useful parameter to predict algae growth when a long term monitoring data is available. This showed that after controlling the nutrients level of the two lakes, the delayed response of algae to the reduction of external load may be due to the increased UEAP. Under the combined influence of UEAP and climate change, even if the nutrients are pressure significantly removed, the lake ecological response will delayed (McCrackin et al., 2017). Therefore, lake management based on the Chla-TP theory may not be achieved what we expected in time. The end targets of the lake management are impotent. Algae control is one and overall improvement of lake chemistry and ecology is another. Hence, the advantage of using UEAP is that one can incorporate many statistically significant factors as variables to increase the reliability of the modeling prediction. This was supported by statistical analysis and modeling work. However, this approach can only be possible with long term monitoring data sets. Of course, all these will need further studies to approve. Like most modeling and statistical analysis, there must be limitations of our work in incorporation of the details of complex natural phenomena. Future work on data sets form different lakes will improve the representation of adaptation in the modeling.

This also indicated that a lake specific and targeted restoration plan relies sound monitoring strategy.

In the past ten years, China has made considerable progress in improving lake water quality (Huang et al., 2019). However, the frequency and intensity of cyanobacteria blooms in many lakes such as Dianchi Lake, Chaohu Lake, Taihu Lake and Erhai Lake have not declined significantly (Jing et al., 2019; Zhang and Kong, 2015; Zhang et al., 2020; Yang et al., 2016). In other words, nutrient load management based on the Chla-TP relationship can reduce the external load to achieve water quality, but the algae response is variable. The phenomenon that the ecosystem cannot be restored to the original state after eliminating the disturbance also shows that only reducing the nutrient load is not enough, and the cost is huge. Our research found that UEAP has a high explanatory for algal density changes, which partly explains that the phenomenon of sustained algal blooms in water nutrients level improved or low-maintained nutrient level lakes. This is particularly impotent for those looks like no risk of lakes for algae blooms based on their low and medium level of nutrients. We need to treat the goals of overall eutrophication control and algae control separately and scientifically according to the progresses of dynamic lake ecology, consider setting algae control goals, and incorporate algae prevention and control into the governance. We summarized the pattern diagram in Fig. S8. Eutrophication control not only reduces the external source load, but also takes into account, the UEAP changes caused by climate and nutrient changes. For low nutrient lakes, reducing nutrient salts is beneficial to the reduction of UEAP and Chla, and nutrient control is the main method of lake management. For high-nutrient lakes, the interference itself has exceeded the ecological threshold, and recovery is difficult. Decreasing nutrients may not reduce algae in a short period of time, and it may even increase UEAP and make recovery more difficult. This type of lake management needs to consider controlling NPr while reducing nutrients, so that UEAP may be controlled in a lower range in coordinating control to nitrogen and phosphorus.

Our research showed that the UEAP incorporated nutrient and climate factors can predict the trend of algae dynamic. The incorporation of environment/climate factors into consideration dramatically increased the reliability of the model. The key finding here may be find a proxy index (UEAP) for phosphorus utilization and demonstrate a two-function variable of both predictor and response, and their related modeling procedures that can predict the response trend of algae growth and determine the state and stage of the lake ecosystem. The advantages of the approaches are, based on long-term monitoring dataset, a lake specific prediction produced and the insight of the lake ecological status identified, which otherwise would be difficult by just simple Chla-TP or Chla-NPr models. By our approaches, lake management may be strategic, informed, efficient, and relevant in response to future developing water quality and climate changes.

5. Conclusions

Our results showed UEAP was one of the major factors affecting algae density and had significant correlation with algae dynamics along the time serials. The incorporation of UEAP and other main factors into the modeling of the Chla-TP relationship achieved greater reliability. The time scale serial of the two contrary trajectories of the lake status showed, in the past 20 years, nutrients and meteorological factors driven the UEAP changes into the sensitive and paralysis phases between low and high threshold points, this was correlated to algal density. NPr was the key driving factor for UEAP changes in Dianchi Lake, while TN and AT were the key driving factors for UEAP in Erhai Lake. The approaches we took can explain the status of the lake, which otherwise would be difficult by just simple Chla-TP or Chla-NPr models. We also be able to quantify the threshold characters of UEAP, hence, explaining the resulted algae growth sensitive and paralyses stages. The study demonstrated that the nutrient levels of the two lakes were at critical points. We speculated that any future changes could cause changes in the lake UEAP, leading to different directions of ecological status. The holistic analysis on UEAP in responding the dynamics of nutrient regimes and environmental factors supported lake specific and phase specific pollution control measures. Our work indicated that the delayed algae response to changes of nutrient regimes might have partially offset the contribution of external load reduction from the expensive algae control measures. Therefore, the effectiveness of water quality control goals is able to achieve by reducing external nutrient load, while controlling algae is depended on the phase of the lake in the process trajectory and the environment/climate factors of the specific lake. The simulation of UEAP with multi factors is impotent. This approach can draw lake specific road maps for achieving the lake management goal and perhaps with more effective and targeted measures. The key finding here may be of the interest and value of a proxy index (UEAP) for phosphorus utilization and demonstrate the two-function variable of both predictor and response, and their related modeling procedures that can predict the response trend of algae growth and determine the state and stage of the lake ecosystem.

Acknowledgements

This research was jointly supported by the National Natural Science Foundation of China (No. U1902207), Yunnan Key Laboratory of Pollution Process and Management of Plateau Lake-Watershed (2020-02-2-W2), the National Major Science and Technology Program for Water Pollution Control and Treatment (2018ZX07701001-17), and Postdoctoral Science Foundation of China (2019M660521).

Appendix A. Supplementary material

Supplementary material files associated with this article can be found in the online version.

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Supplementary Material for

No-linear dynamics of lake ecosystem in responding to changes of nutrient regimes and climate factors: case study on Dianchi and Erhai lakes, China

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Abbreviated notation list

NO.	Abb.	Meaning	Unit	NO.	Abb.	Meaning	Unit
1	AT	Air Temperature	℃	16	P_{Load}	Phosphorus Load into the lake	Ton
2	PP	Precipitation	mm	17	N_{Load}	Nitrogen Load into the lake	Ton
3	WV	Wind Velocity	m/s	18	AD	Algal Density	10^4cell/L
4	SH	Sunshine Hours	h	19	UEAP	Utilization Efficiency of Algae to TP	-
5	WT	Water Temperature	℃	20	RRAP	Response Rate of Algae to TP	-
6	DO	Dissolved Oxygen	mg/L	21	PCA	Principal Component Analysis	-
7	pH	Acidity	-	22	GAM	Generalized Additive Model	-
8	SD	Secchi Disk Depth	m	23	HLM	Hierarchical Linear Model	-
9	TN	Total Nitrogen	mg/L	24	GLM	Generalized Linear Model	-
10	TP	Total Phosphorus	mg/L	25	PC1	First Principal Components	-
11	NH_3N	Ammonia nitrogen	mg/L	26	PC2	Second Principal Components	-
12	Chla	Chlorophyll A	mg/L	27	DC	Dianchi Lake	-
13	NPr	Ratio of TN to TP	-	28	EH	Erhai Lake	-
14	BOD	Biochemical Oxygen Demand	mg/L	29	AIC	Akaike Information Criterion	-
15	COD	Chemical Oxygen Demand	mg/L	30	DE	Deviance Explained	-

Note: "-"Represents no unit.

Table S1 Summary statistics of Chla-TP regression model for each year in Dianchi and Erhai Lake.

Group	Formula	N	Adj-R^2	*F*-value	*t*-value	*p*-value
DC_{1998}	$\ln(\text{Chl } a)=4.921+0.448\times\ln(\text{TP})$	120	0.0583	8.3724	25.2678	$p<0.01$
DC_{1999}	$\ln(\text{Chl } a)=5.016+0.600\times\ln(\text{TP})$	120	0.0960	13.6318	27.6388	$p<0.01$
DC_{2000}	$\ln(\text{Chl } a)=5.077+0.596\times\ln(\text{TP})$	120	0.3134	55.3088	46.6836	$p<0.01$
DC_{2001}	$\ln(\text{Chl } a)=4.379+0.185\times\ln(\text{TP})$	120	0.0367	5.5362	36.3090	$p<0.05$
DC_{2002}	$\ln(\text{Chl } a)=4.795+0.420\times\ln(\text{TP})$	120	0.2341	37.3762	36.0693	$p<0.01$
DC_{2003}	$\ln(\text{Chl } a)=4.409+0.239\times\ln(\text{TP})$	120	0.0662	9.4302	30.3380	$p<0.01$
DC_{2004}	$\ln(\text{Chl } a)=4.909+0.387\times\ln(\text{TP})$	120	0.3241	58.0527	55.0654	$p<0.01$
DC_{2005}	$\ln(\text{Chl } a)=4.150+0.287\times\ln(\text{TP})$	120	0.1028	14.6269	29.6024	$p<0.01$
DC_{2006}	$\ln(\text{Chl a})=4.327+0.220\times\ln(\text{TP})$	120	0.0660	9.4062	34.6003	$p<0.01$
DC_{2007}	$\ln(\text{Chl } a)=4.102+0.080\times\ln(\text{TP})$	120	0.0069	1.8212	34.4194	$p<0.05$
DC_{2008}	$\ln(\text{Chl } a)=4.000+0.039\times\ln(\text{TP})$	120	-0.0054	0.3600	31.4401	0.5496
DC_{2009}	$\ln(\text{Chl } a)=4.263+0.038\times\ln(\text{TP})$	120	-0.0053	0.3789	38.3190	0.5394
DC_{2010}	$\ln(\text{Chl } a)=4.066-0.143\times\ln(\text{TP})$	120	0.0032	1.3858	21.4425	0.2415
DC_{2011}	$\ln(\text{Chl } a)=4.545+0.088\times\ln(\text{TP})$	120	-0.0008	0.9005	26.1507	0.3446
DC_{2012}	$\ln(\text{Chl } a)=4.551+0.100\times\ln(\text{TP})$	120	-0.0041	0.5180	18.3564	0.4731
DC_{2013}	$\ln(\text{Chl } a)=4.191-0.003\times\ln(\text{TP})$	120	-0.0085	0.0006	18.5025	0.9809
DC_{2014}	$\ln(\text{Chl } a)=6.785+1.422\times\ln(\text{TP})$	120	0.3343	60.7511	18.9371	$p<0.01$
DC_{2015}	$\ln(\text{Chl } a)=4.591+0.276\times\ln(\text{TP})$	120	0.0329	5.0429	16.6559	$p<0.05$
DC_{2016}	$\ln(\text{Chl } a)=4.600+0.255\times\ln(\text{TP})$	120	0.0143	2.7303	12.3522	$p<0.05$
DC_{2017}	$\ln(\text{Chl } a)=6.104+0.902\times\ln(\text{TP})$	120	0.2644	43.7722	21.2937	$p<0.01$
DC_{2018}	$\ln(\text{Chl } a)=4.671+0.503\times\ln(\text{TP})$	120	0.0177	3.1446	5.9889	$p<0.05$
DC_{2019}	$\ln(\text{Chl } a)=4.790+0.298\times\ln(\text{TP})$	120	0.0161	2.9526	10.0464	$p<0.05$
EH_{1994}	$\ln(\text{Chl } a)= 4.962+1.146\times\ln(\text{TP})$	66	0.3263	32.4752	5.8160	$p<0.01$
EH_{1995}	$\ln(\text{Chl } a)= -2.009-0.559\times\ln(\text{TP})$	53	0.1760	12.1076	-2.9853	$p<0.01$
EH_{1996}	$\ln(\text{Chl } a)= 1.409+0.252\times\ln(\text{TP})$	66	0.0165	2.0917	1.9915	$p=0.05$
EH_{1997}	$\ln(\text{Chl } a)= 1.906+0.409\times\ln(\text{TP})$	66	0.0502	4.4318	2.4308	$p<0.05$

EH_{1998}	ln(Chl *a*)= 1.197+0.269×ln (TP)	54	0.0050	1.2651	1.2984	p<0.05
EH_{1999}	ln(Chl *a*)= 2.529+0.567×ln (TP)	66	0.0773	6.4459	2.9715	p<0.05
EH_{2000}	ln(Chl *a*)= -1.862-0.254×ln (TP)	62	-0.0017	0.8978	-1.8433	0.3472
EH_{2001}	ln(Chl *a*)= 1.310+0.394×ln (TP)	124	0.0122	2.5211	1.3744	0.1149
EH_{2002}	ln(Chl *a*)= 5.929+1.418×ln (TP)	124	0.1353	20.2473	5.2334	p<0.01
EH_{2003}	ln(Chl *a*)= 6.380+1.014×ln (TP)	135	0.4143	95.7649	16.9595	p<0.01
EH_{2004}	ln(Chl *a*)= 3.019+0.232×ln (TP)	144	0.0284	5.1720	8.1725	p<0.05
EH_{2005}	ln(Chl *a*)= 4.863+0.680×ln (TP)	143	0.2559	49.8392	13.2777	p<0.01
EH_{2006}	ln(Chl *a*)= 5.270+0.738×ln (TP)	142	0.2369	44.7781	12.4575	p<0.01
EH_{2007}	ln(Chl *a*)= 5.878+0.882×ln (TP)	144	0.2544	54.2151	12.3306	p<0.01
EH_{2008}	ln(Chl *a*)= 4.710+0.557×ln (TP)	132	0.1323	20.9731	9.6225	p<0.01
EH_{2009}	ln(Chl *a*)= 6.818+1.098×ln (TP)	132	0.6803	279.7656	26.9137	p<0.01
EH_{2010}	ln(Chl *a*)= 6.362+1.008×ln (TP)	132	0.3535	72.6232	13.9177	p<0.01
EH_{2011}	ln(Chl *a*)= 7.836+1.488×ln (TP)	132	0.6899	292.3867	23.5307	p<0.01
EH_{2012}	ln(Chl *a*)= 7.014+1.248×ln (TP)	132	0.4522	109.1186	15.7547	p<0.01
EH_{2013}	ln(Chl *a*)= 3.791+0.488×ln (TP)	132	0.0750	11.6199	7.2780	p<0.01
EH_{2014}	ln(Chl *a*)= 4.494+0.706×ln (TP)	132	0.2166	37.2197	10.1086	p<0.01
EH_{2015}	ln(Chl *a*)= 8.399+1.666×ln (TP)	132	0.3286	65.1030	10.5337	p<0.01
EH_{2016}	ln(Chl *a*)= 5.014+0.784×ln (TP)	132	0.2665	48.6037	12.3666	p<0.01
EH_{2017}	ln(Chl *a*)= 5.840+0.924×ln (TP)	132	0.4285	99.2072	17.3693	p<0.01
EH_{2018}	ln(Chl *a*)= 5.870+0.954×ln (TP)	132	0.2405	42.4872	11.0210	p<0.01
EH_{2019}	ln(Chl *a*)= 6.572+1.096×ln (TP)	132	0.3888	84.3218	14.7172	p<0.01

Note: DC represents Dicnhi Lake, EH represents Erhai Lake, and the subscript numbers represents the year.

Table S2 Spearman correlation between meteorology, water quality index, nitrogen and phosphorus load into lake and UEAP and RRAP. Red represents positive correlation, blue represents negative correlation, and green represents irrelevance, respectively. A is for Dianchi Lake, B is for Erhai Lake.

A

	UEAP	RRAP	AT	PP	WV	SH	P_{Load}	N_{Load}	TN	TP	NPr	NH_3N	COD	BOD	pH	DO	WT	SD	Chla	AD
UEAP	1																			
RRAP	.899**	1																		
AT	-0.082	-0.06	1																	
PP	.516*	.625**	-0.025	1																
WV	-.475*	-.583**	-0.01	-.435*	1															
SH	0.251	0.118	0.303	0.046	0.258	1														
P_{Load}	0.468	.593*	-0.154	.539*	-.886**	-0.418	1													
N_{Load}	0.386	0.368	-0.321	-0.093	-0.428	0.039	0.114	1												
TN	-.535*	-.438*	0.077	-0.271	-0.227	-.567**	0.032	-0.146	1											
TP	-0.257	-0.197	0.2	-0.153	-0.012	-.512*	0.277	0.009	.892**	1										
NPr	-.661**	-.685**	-0.155	-.594**	.507*	-0.293	-.568*	-0.211	.528*	0.215	1									
NH_3N	-.554**	-.440*	0.13	-0.284	0.009	-.522*	-0.061	-0.189	.984**	.857**	.547**	1								
COD	0.304	0.321	0.11	0.179	-.610**	-0.115	.777**	0.365	0.32	.518*	-.431*	0.312	1							
BOD	-0.112	-0.188	0.212	-0.2	-0.327	-.444*	0.471	0.189	.665**	.689**	0.262	.644**	0.387	1						
pH	-0.063	-0.253	0.299	-0.271	0.203	.476*	-0.189	-0.468	-133	-0.21	-0.028	-0.11	-0.171	0.001	1					
DO	.632**	.560**	-0.353	0.241	-0.309	0.302	0.471	0.146	-.811**	-.714**	-.536*	-.811**	-0.11	-.527*	0.077	1				
WT	0.121	0.265	0.311	0.296	0.130	0.368	-0.2	-0.171	-0.168	-0.097	-0.317	-0.067	0.244	-0.174	-0.042	-0.11	1			
SD	-0.259	-0.209	0.201	-0.259	0.209	0.154	-0.411	0.232	-0.125	-0.28	0.24	-0.034	-0.125	0.009	0.061	-0.302	0.195	1		
Chla	0.469*	0.293	0.075	0.136	-0.441*	-0.207	.614*	0.293	0.268	.501*	-0.169	0.224	.584**	.621**	-0.172	-0.2	-0.11	-0.226	1	
AD	0.488*	0.282	0.024	0.148	-0.427*	-0.189	0.275	0.636*	0.242	0.47*	-0.16	0.193	0.561**	0.617**	-0.158	-0.16	-0.131	-0.247	0.993**	1

B

	UEAP	RRAP	AT	PP	WV	SH	P_{Load}	N_{Load}	TN	TP	NPr	NH_3N	COD	BOD	pH	DO	WT	SD	Chla	AD
UEAP	1																			
RRAP	.935**	1																		
AT	.653**	.594**	1																	
PP	-.477*	-.413*	-.520**	1																
WV	0.031	0.03	-0.183	0.356	1															
SH	-0.05	0.082	-0.068	-0.087	0.204	1														
P_{Load}	-.584**	-.531**	-.638**	.892**	0.257	-0.061	1													
N_{Load}	-0.321	-0.245	-0.419	.837**	0.441	-0.247	.870**	1												
TN	.578**	0.324	.478*	-.461*	-0.093	-0.303	-.422*	-0.29	1											
TP	0.199	0.057	-0.034	-0.143	0.006	-0.05	-0.08	0.148	.582**	1										
NPr	.494*	0.307	.672**	-.425*	-0.233	-0.204	-.498**	-0.449	.549**	-0.204	1									
NH_3N	0.357	0.151	0.376	-0.268	0.131	-0.2	-0.27	0.028	.600**	0.298	.398*	1								
COD	.607**	0.383	.533**	-0.367	0.184	-0.34	-0.33	-0.141	.852**	0.355	.545**	.645**	1							
BOD	.552**	0.352	.432*	-.446*	-0.117	-0.122	-.458*	-0.412	.698**	.462*	.415*	.559**	.538**	1						
pH	.476*	0.325	0.196	-0.27	0.08	-0.14	-0.236	-0.046	.441*	.519**	0.091	.501**	.443*	.780**	1					
DO	-0.121	0.031	-0.023	0.049	-0.231	-0.068	0.048	0.112	-0.195	-0.007	-.422*	-.520**	-0.33	-0.038	-0.144	1				
WT	0.045	0.021	0.267	0.06	-.533**	-0.218	0.065	0.1	0.162	-0.247	0.363	0.147	0.076	-0.041	-0.336	0.079	1			
SD	-.500**	-0.255	-0.321	0.19	-0.088	0.297	0.208	-0.082	-.800**	-.471*	-.411*	-.672**	-.718**	-.737**	-.622**	0.147	-0.148	1		
Chla	.681**	.413*	.505**	-0.372	0.075	-0.222	-0.336	-0.121	.865**	0.385	.558**	.715**	.863**	.640**	.538**	-0.333	0.197	-.865**	1	
AD	.517**	0.272	.412*	-0.342	0.1	-0.175	-0.249	-0.216	.810**	.460*	.393*	.597**	.821**	.607**	.504**	-0.223	0.066	-.714**	.864**	1

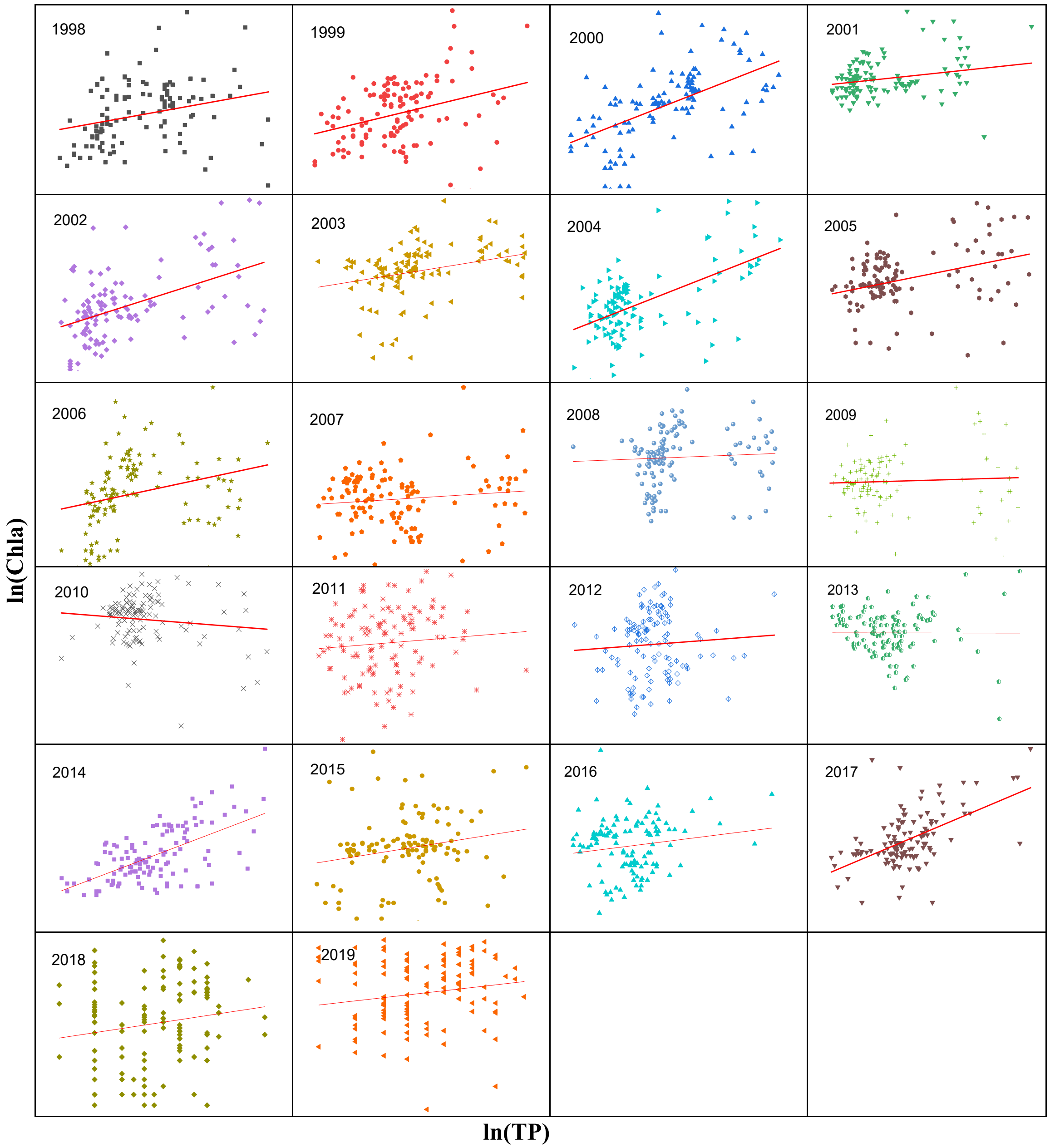


Fig. S1. Linear fitting between ln (Chla) and ln (TP) for Dianchi Lake from 1998 to 2019.

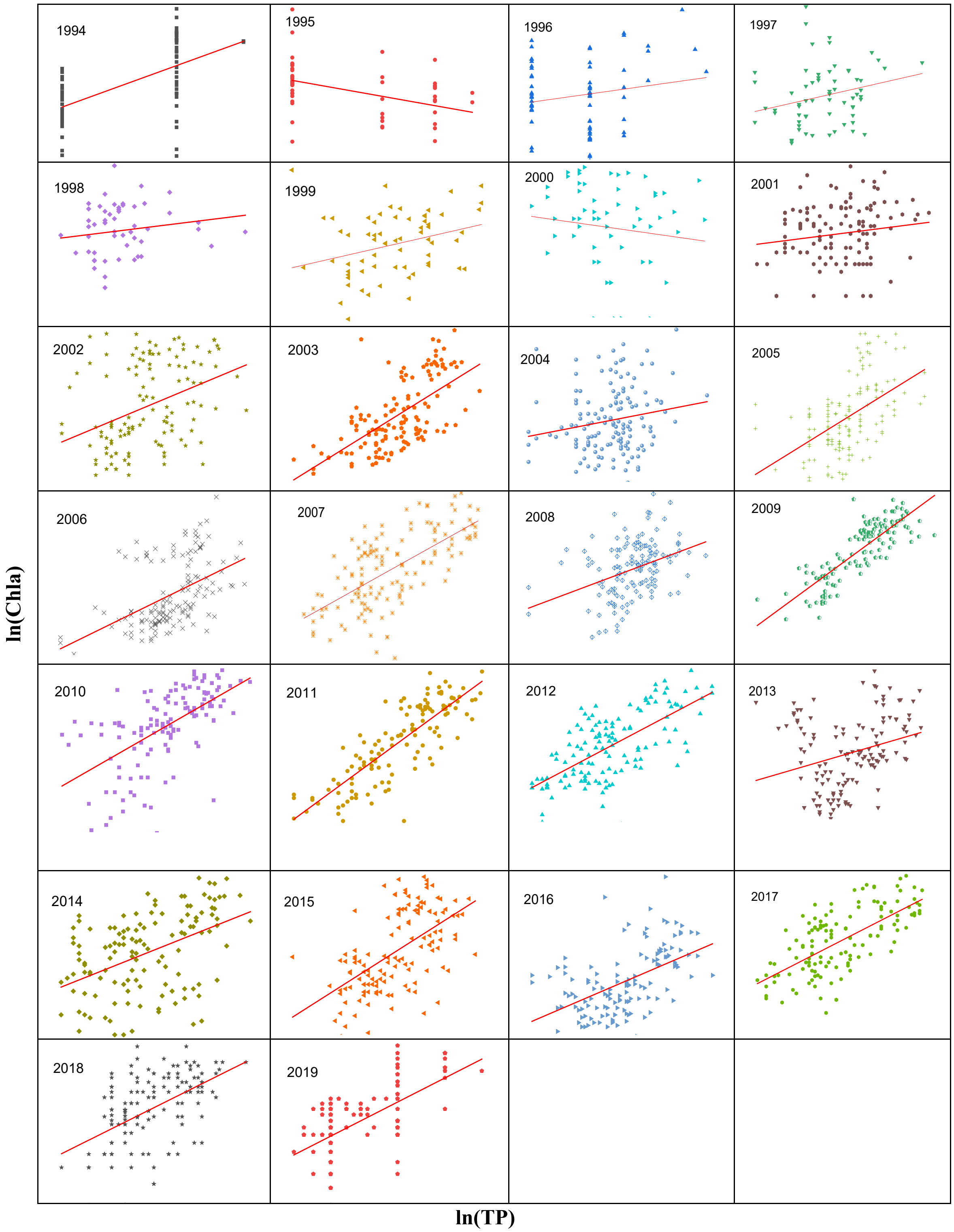
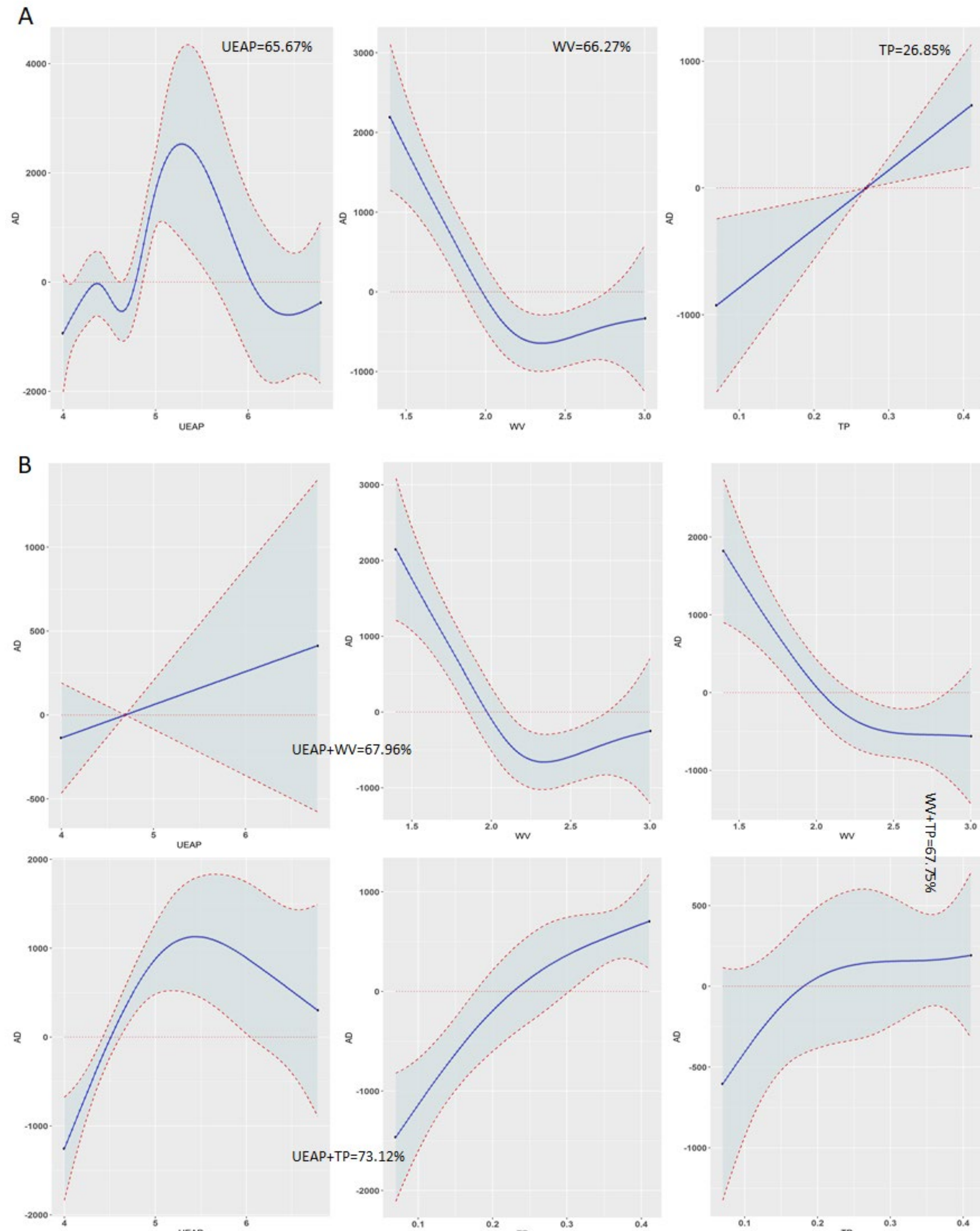


Fig. S2. Linear fitting between ln (Chla) and ln (TP) for Erhai Lake from 1994 to 2019.


A
UEAP=65.67%
WV=66.27%
TP=26.85%
B
UEAP+WV=67.96%
WV+TP=67.75%
UEAP+TP=73.12%
AD
UEAP
WV
TP

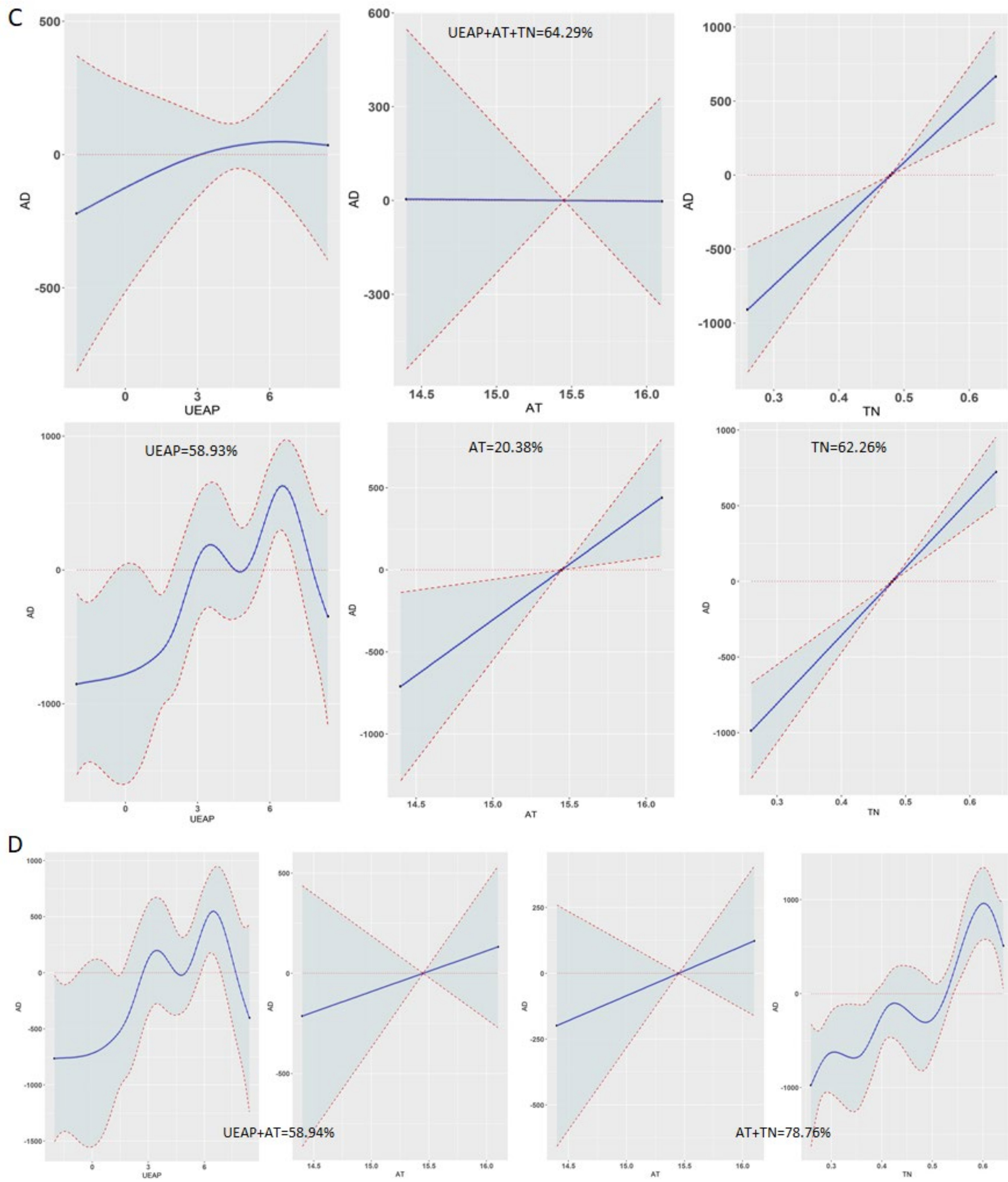


Fig. S3. GAM results of the predictive model curves of univariate and multivariate for the changes of algal density in Dianchi and Erhai Lakes. A and B are for Dianchi Lake, and C and D are for Erhai Lake.

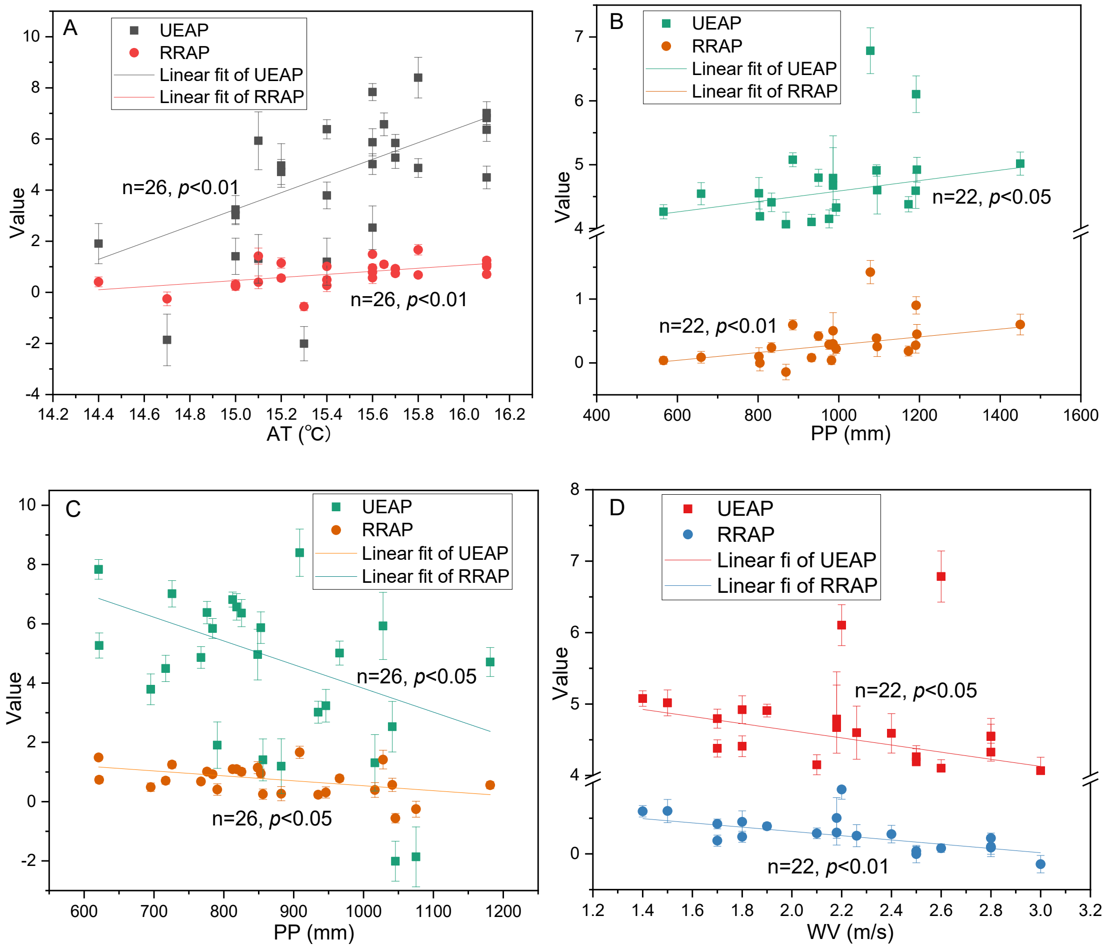


Fig. S4. The relationship between meteorological factors and UEAP or RRAP. A and B are the relationship between AT and the intercept and slope of Dianchi and Erhai Lakes; C and D are the relationship between PP and intercept and slope of Dianchi and Erhai Lakes, E and F are the relationship between WV and intercept and slope of Dianchi and Erhai Lakes.

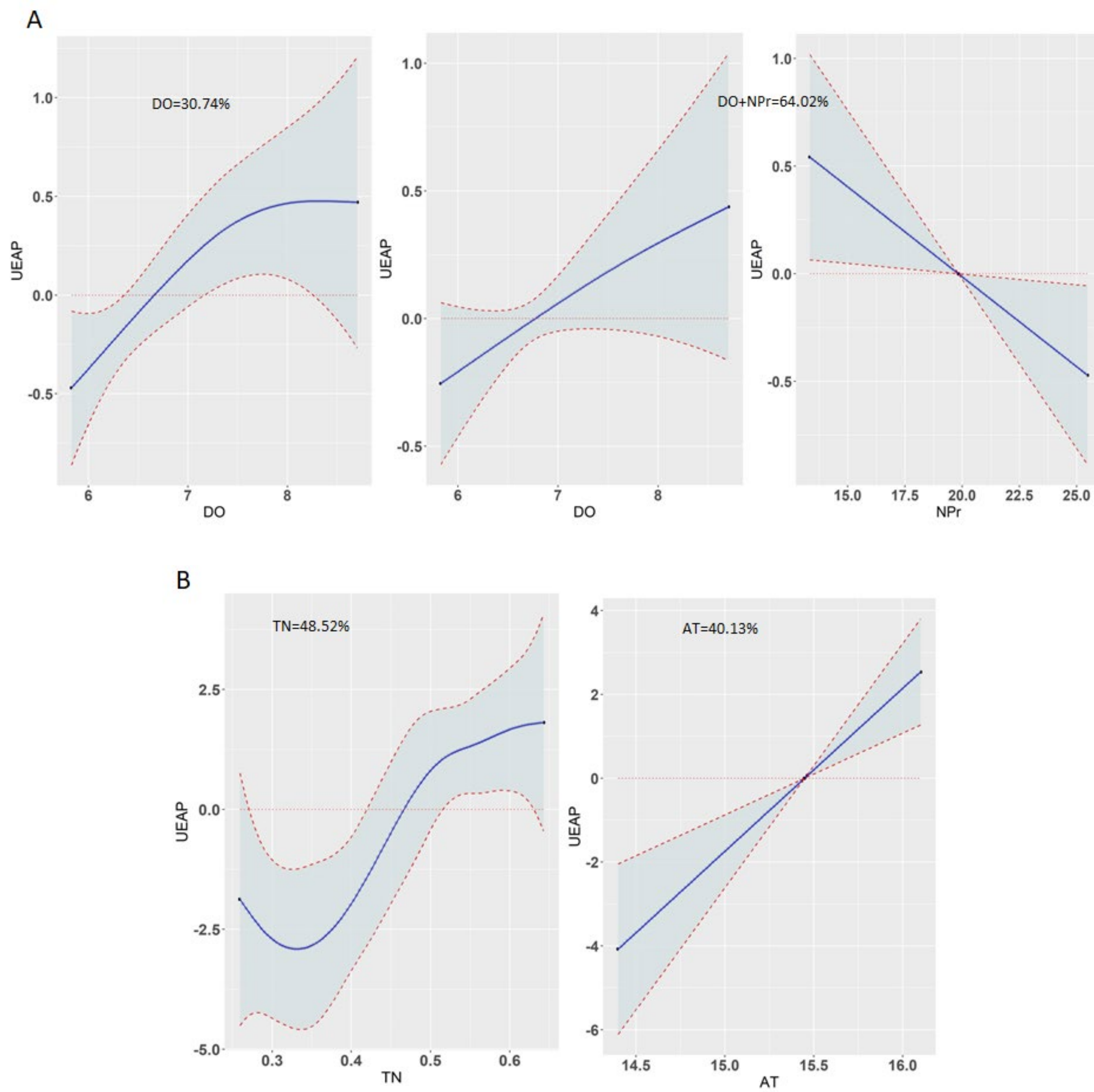


Fig. S5. GAM results of the predictive model curves of univariate and multivariate for the changes of UEAP in Dianchi and Erhai Lakes. A is for Dianchi Lake, and B is for Erhai Lake.

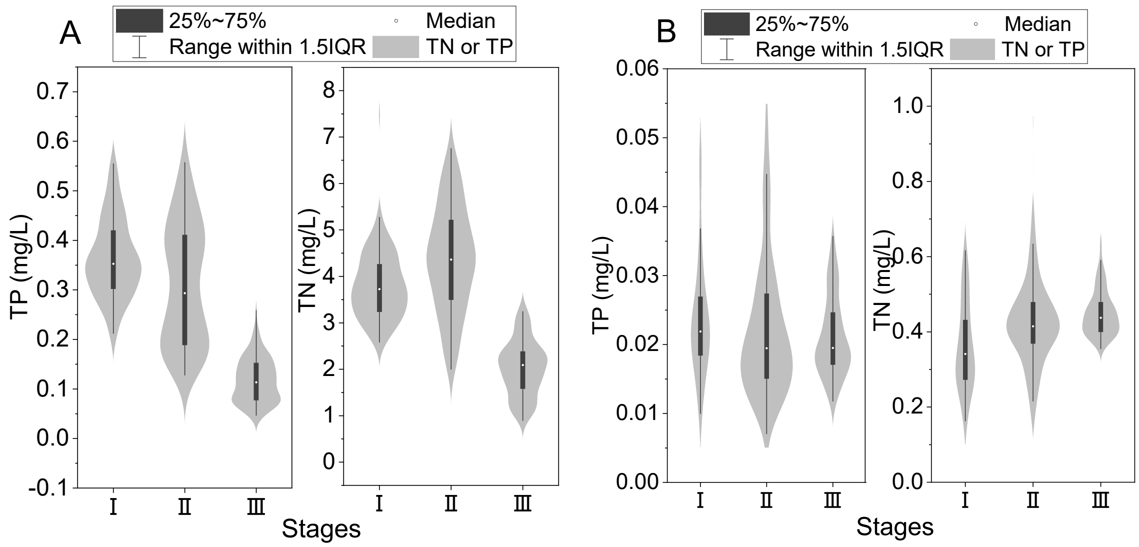


Fig. S6. Concentrations changes of TN and TP in Dianchi Lake (A) and Erhai Lake (B).

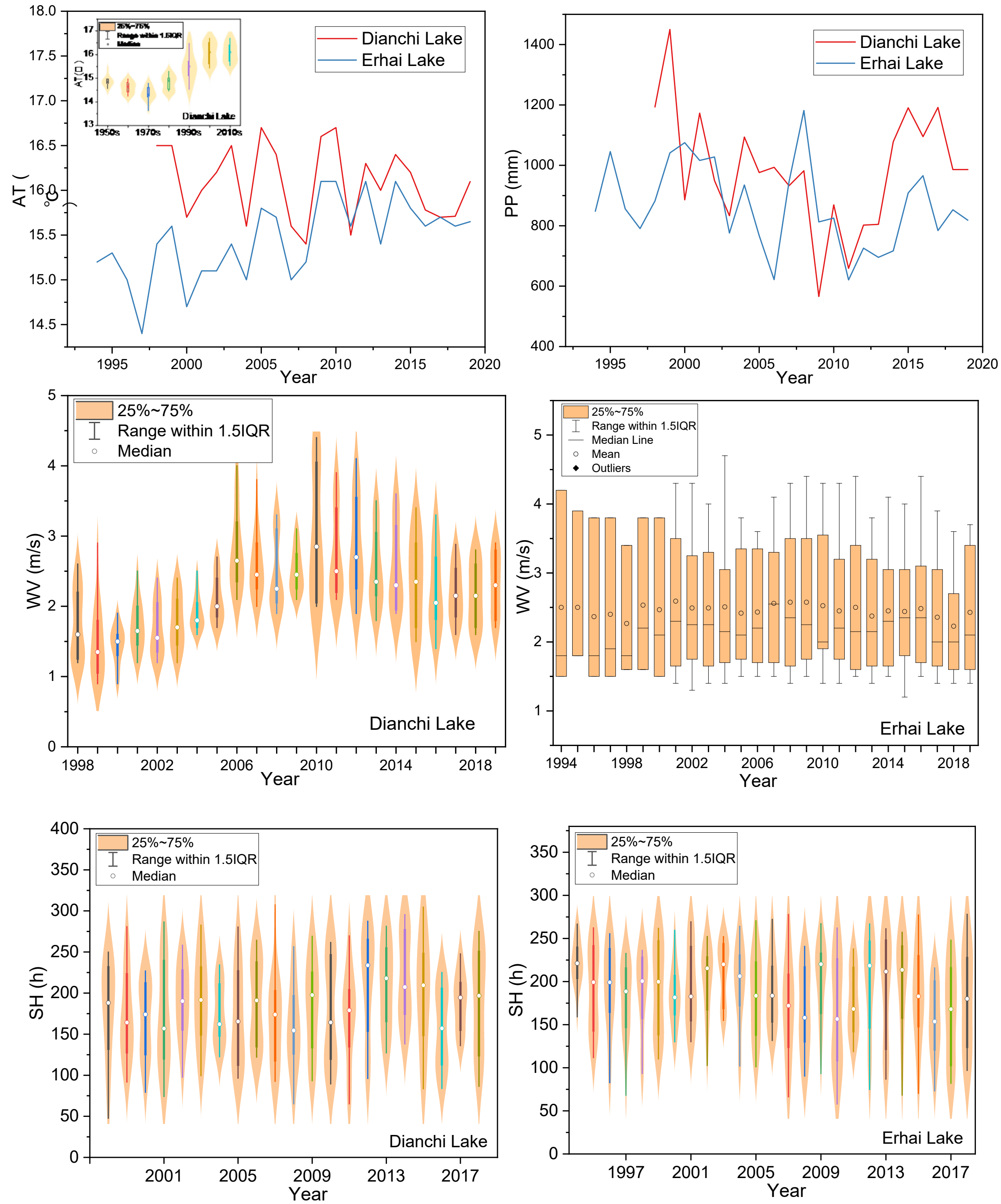


Fig. S7. Changes of AT, PP, WV and SH in Dianchi Lake and Erhai Lake.

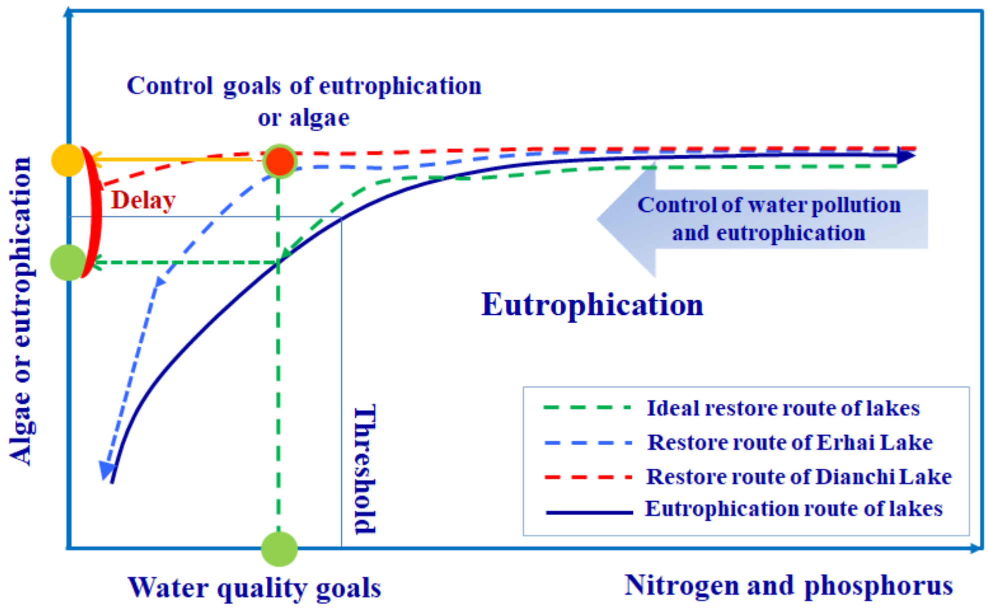


Fig. S8. Response patterns of water quality and algae under lake eutrophication control in China (taking Dianchi Lake and Erhai Lake as examples).