Science of the Total Environment 645 (2018) 876–886

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Long-term dynamics and drivers of phytoplankton biomass in eutrophic Lake Taihu

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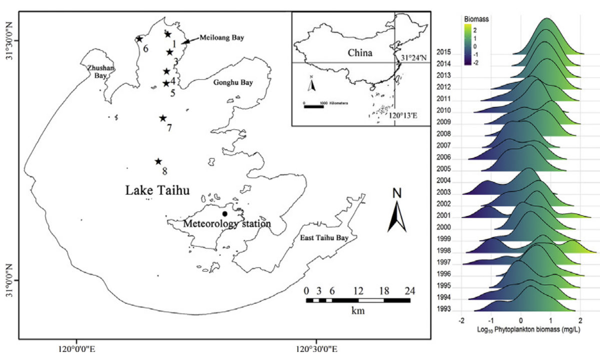
HIGHLIGHTS

- Phytoplankton expanded towards central lake area, and towards autumn and winter.
- Nutrients were the primary predictors of phytoplankton biomass trend.
- The effect size of climate variables on biomass was close to that of nutrients.
- Wind speed and I_m were more important predictors than temperature.
- Compensatory dynamics were weak, and synchronous dynamics drive variation in biomass.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 3 May 2018
Received in revised form 15 July 2018
Accepted 16 July 2018
Available online xxxx

Editor: Jay Gan

Keywords:
Lake Taihu
Phytoplankton biomass
Nutrients
Photothermal processes
Wind speed

ABSTRACT

Understanding the relative effect sizes of climate-related environmental variables and nutrients on the high annual variation in the phytoplankton biomass in eutrophic lakes is important for lake management efforts. In this study, we used a data set of phytoplankton dynamics in eutrophic Lake Taihu that cover more than two decades (1993–2015) to show the variation in and the drivers of phytoplankton biomass under complex, fluctuating environmental conditions. Our results showed that the phytoplankton biomass increased slowly over the studied period despite the recent decrease in nutrient levels. The distribution of the phytoplankton biomass expanded spatially towards the central lake region, and seasonally towards the autumn and winter. Nutrients were still the primary predictors of the long-term phytoplankton biomass trend. The effect size of climate-related variables was also high and close to the effect size of nutrients. Among the climate-related variables, wind speed and underwater available light were more important predictors than temperature. The biomass of the phytoplankton taxonomic groups showed different responses to the environmental variables based on their niches. However, the compensatory dynamics affecting biomass were weak at phylum level, and synchronous dynamics drove the variation in total biomass. Our findings highlight the effect of climate-related variables on the phytoplankton biomass in Lake Taihu, which has experienced high nutrient loadings and concentrations for more than two decades. Therefore, changes in climate-related variables, such as wind speed and underwater available light, should be considered when evaluating the amount that nutrients should be reduced in Lake Taihu for future lake management.

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https://doi.org/10.1016/j.scitotenv.2018.07.220
0048-9697/© 2018 Published by Elsevier B.V.

1. Introduction

Annual phytoplankton biomass within individual ecosystems is highly variable from year to year (Cloern and Jassby, 2010; Winder and Cloern, 2010). Understanding the patterns of phytoplankton biomass and primary production in lakes has been a central concern of limnologists for both theoretical and practical reasons (Carpenter et al., 1998). Among the various factors that influence phytoplankton biomass, variations in nutrients are generally emphasised as the primary driving factors (Schindler and Eby, 1997). Recently, the effect of climate-related environmental variables on phytoplankton biomass has attracted increasing attention due to the influence of these variables on the expansion of harmful cyanobacterial blooms (Padisák et al., 1990; Paerl and Huisman, 2008; Wagner and Adrian, 2009). Most importantly, climate-related environmental variables are hypothesised to mimic and worsen the effects of eutrophication (Moss et al., 2011; Paerl and Huisman, 2008). Therefore, it is important to understand the relative effect sizes of these climate-related environmental variables and nutrients on the high annual variation in phytoplankton biomass, especially in eutrophic lakes.

The regulation of phytoplankton biomass by multiple processes operating at multiple time scales adds complexity to the challenge of detecting trends in phytoplankton biomass in aquatic ecosystems where the noise to signal ratio is high (Winder and Cloern, 2010). Some scientists have addressed this challenge by analysing cross-sectional field data (e.g., Jeppesen et al., 2005; Rigosi et al., 2014; Watson et al., 1997), and selecting out the primary climate-related environmental variables influencing phytoplankton biomass such as temperature, light condition and mixing events. IN addition, one study revealed that the relative importance of these variables was dependent on the trophic state of a lake, and increased with increasing nutrients level (Rigosi et al., 2014). However, these cross-sectional field data generally came from multiple lakes, which might have increased the gradient of these environmental variables exceeding the inter-annual amplitude of the variation in these variables within one lake. The increased gradient will further increase the detectability of the effects of these variables on phytoplankton biomass. In addition, even using long-term data within a single lake, the results of these studies on the factors influencing the variation in phytoplankton biomass were not consistent (Anneville et al., 2005). For example, a study in Lake Constance with a 43-year data series found that the nutrients were the primary factor driving the variation in phytoplankton biomass, and temperature was statistically unrelated to the variation (Jochimsen et al., 2012). However, a study in Lake Zurich with a 30-year data series determined that both nutrients and temperature were significant factors driving the variation (Pomati et al., 2012).

Generally, the previously mentioned studies of a single lake were performed in deep lakes. In large, eutrophic, shallow lakes, the regulatory process of phytoplankton biomass might be more complex than that in deep lakes. On the one hand, the shallow lake was frequently mixed. Mixing events can produce large increases in phytoplankton production and shifts in community composition by increasing the pulse release of nutrients from the sediment and the availability of light (Padisák et al., 1990). However, stability conditions favour cyanobacteria, which is the main contributor to phytoplankton biomass in the eutrophication process (Wagner and Adrian, 2009). On the other hand, the negative feedback from high phytoplankton biomass in eutrophic lakes will decrease underwater available light and limit the increase in phytoplankton biomass (Zhang et al., 2012b). These complex processes also further increase the difficulty of detecting trends in phytoplankton biomass and their driving factors. Although these processes are complex and challenging, we can summarise several primary processes that influence the variation in phytoplankton biomass based on the previously mentioned studies, such as nutrients (nitrogen, phosphorus, and their ratio), photothermal processes (temperature and available light), and water stability (mixing events).

The response of phytoplankton biomass to environmental changes is dependent on their taxonomic community (Rigosi et al., 2014). Likewise, some taxa, such as large diatoms, are more sensitive to stabilisation, while others, such as cyanobacteria, are more tolerant to low light (Salmaso, 2010). In a changing environment, phytoplankton composition shifts due to the differences in competitive ability arising from niches differences (Cardinale et al., 2011). Species abundance may decreases for species negatively affected by a specific environmental driver, but the decrease may be offset by increased population growth in less sensitive taxa (compensatory dynamics). In addition, phytoplankton groups also might show synchronous dynamics (synchronous fluctuations in population abundance) in response to a specific environmental change (Jochimsen et al., 2012). Therefore, understanding the trends and driving factors of different taxonomic biomasses will be helpful for detecting the response mechanism of total phytoplankton biomass to environmental changes.

Lake Taihu is the third largest freshwater lake in China and is an important drinking water source for four million people. This lake also supports important economic activities, such as tourism, fisheries, and shipping (Qin et al., 2010). It is a very shallow lake with a mean depth 1.9 m, which makes it (and its dynamics) different from many other large lakes. This lake has been eutrophic since the 1990s, and it experiences massive cyanobacterial blooms that are dominated by *Microcystis* each year during the warm season (Zhang et al., 2012a). During the past two decades, the eutrophic lake has exhibited considerable variability in nutrient levels, accompanied by changes in climate-related environmental variables. However, a recent reduction in nutrients did not lead to a decrease in phytoplankton biomass, which lead to confusion of policy-makers and lake managers over their treatment efforts.

In this study, we use a 24-year data series from Lake Taihu to examine: (1) trends in the biomass of different phytoplankton taxonomic groups, (2) temporal variability in the environmental physical conditions and available resources, (3) variation in the annual patterns of phytoplankton biomass, and (4) the primary driving factors of variation in phytoplankton biomass.

2. Methods

2.1. Study lake

Lake Taihu is the third largest freshwater lake in China (latitude 30°55′40″–31°32′58″N; longitude 119°52′32″–120°36′10″E, Fig. 1), with an area of 2338 km^2, a maximum and mean depth of 2.6 and 1.9 m, respectively, and a mean water residence time of approximately 309 days (Qin et al., 2004). Lake Taihu receives inflows from nearby riverine networks, including over 200 streams, canals and rivers (Chen et al., 2003b). In response to heavy industrial and agricultural pollution, blooms of *Microcystis* have been dominant over the past few decades (Liu et al., 2011). Generally, the phytoplankton production has presented a unimodal pattern, with a peak in the summer. Phosphorus is the primary limiting nutrient for phytoplankton production (Chen et al., 2003b).

2.2. Sampling and analyses

The long-term data series (1993–2015) on water quality and phytoplankton biomass (except for that in 2004 and the biomass of taxonomic groups in 2007–2009) was obtained from the Taihu Laboratory for Lake Ecosystem Research (CERN TLLER). The observations of water quality and phytoplankton community structure were conducted monthly at sites 1 and 3–8 from 1993 to 2015. Twenty-four years of continuous monthly sampling at the seven stations provided 2016 samples. At each site, water samples were taken by mixing the surface (0.5 m below the surface), middle, and bottom (0.5 m above the bottom) layers of the water. Physicochemical variables such as transparency, water temperature, pH and nutrient concentrations (total nitrogen: TN and