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Factors controlling the three-decade long rise in cyanobacteria biomass in a eutrophic shallow lake

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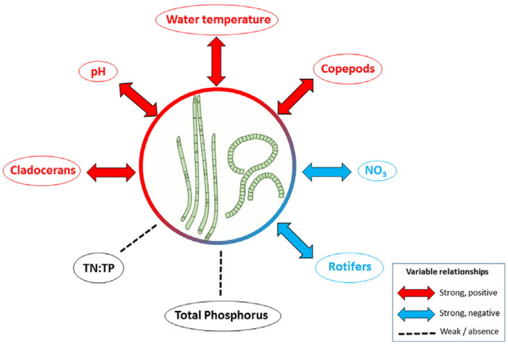
HIGHLIGHTS

- We assessed the influence of 28 variables on cyanobacteria.
- Cyanobacteria biomass did not respond to phosphorus concentration.
- Nitrates, temperature and pH had a major influence.
- Zooplankton could be positively or negatively correlated.
- Lake condition may deteriorate with global warming.

GRAPHICAL ABSTRACT



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ABSTRACT

We aimed at quantifying the importance of limnological variables in the decadal rise of cyanobacteria biomass in shallow hemiboreal lakes. We constructed estimates of cyanobacteria (blue-green algae) biomass in a large, eutrophic lake (Estonia, Northeastern Europe) from a database comprising 28 limnological variables and spanning more than 50 years of monitoring. Using a dual-model approach consisting in a boosted regression trees (BRT) followed by a generalized least squares (GLS) model, our results revealed that six variables were most influential for assessing the variance of cyanobacteria biomass. Cyanobacteria response to nitrate concentration and rotifer abundance was negative, whereas it was positive to pH, temperature, cladoceran and copepod biomass. Response to total phosphorus (TP) and total phosphorus to total nitrogen ratio was very weak, which suggests that actual in-lake TP concentration is still above limiting values. The most efficient GLS model, which explained nearly two thirds ($r^2 = 0.65$) of the variance of cyanobacteria biomass included nitrate concentration, water temperature and pH. The very high number of observations (maximum $n = 525$) supports the robustness of the models. Our results suggest that the decadal rise of blue-green algae in shallow lakes lies in the interaction between cultural eutrophication and global warming which bring in-lake physical and chemical conditions closer to cyanobacteria optima.

1. Introduction

Although occurring naturally in aquatic ecosystems and constituting the oldest oxygenic photoautotrophs, the recent proliferation of planktonic cyanobacteria is causing a growing concern about the ecological status of aquatic ecosystems (Brooks et al. 2016). Cyanobacteria

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biomass increase can turn into harmful algal blooms that deteriorate inland water quality and threaten animal and human health (Paerl et al. 2001). Additionally, the growing share of cyanobacteria in phytoplankton community triggers several bottom-up effects, especially in lacustrine systems. Cyanobacteria dominance among primary producers leads to declining light penetration into the water column, a modified zooplankton composition which elicits a reduction of piscivorous fish size and abundance (Jeppesen et al. 2012), and a shift of lake metabolism toward heterotrophy (Cremona et al. 2014). Several possible causes have been proposed for explaining the offset of cyanobacteria proliferation. Some researchers suggested that land-based fertilizer and manure export with low molar nitrogen to phosphorus ratios (TN:TP) to lakes might favor strains of cyanobacteria which are able to fix atmospheric N_2 and thus outcompete other phytoplankton producers (Schindler 1977; Smith 1983; Huisman and Hulot 2005). According to some other authors, cyanobacteria abundance is more tightly linked to quantitative changes in nutrient concentrations irrespective of their TN:TP ratios (Lathrop et al. 1998; Downing et al. 2001). There is however little disagreement on the decisive role played by global warming of surface waters in cyanobacteria expansion and persistence as the temperature optima of many cyanobacteria species is situated well above that of their eukaryote competitors (Kosten et al. 2012; Cremona et al. 2017). Typically, growth rate of diatom cells reaches maximum at 15 °C and declines at warmer temperatures while cyanobacteria attain their maximum growth rate above 25 °C (Paerl and Otten 2013).

Due to their generally larger surface to volume ratio and higher nutrient concentrations, shallow lakes have been considered particularly prone to cyanobacteria proliferation and its adverse effects (Jeppesen et al. 2014). Furthermore, as sediments in shallow lakes are in closer contact with the mixed layer, phosphorus can be remobilized more readily during the vegetation period and thus support photosynthesis for a longer time than in deeper lakes (Kalff 2002). Shallow lakes situated at higher latitudes are particularly sensitive to changes in the ice cover duration which drives the length of the growing season and phytoplankton dominance (Deng et al. 2016). Lake Võrtsjärv (Estonia) is among the most studied lakes in North-eastern Europe with a nearly continuous limnological monitoring since the late 1960s (Nõges et al. 2010). Despite a reduction of external nutrient loadings since the mid-1980s, the cyanobacteria abundance in the lake has kept growing (Nõges et al. 2010). Several reasons have been invoked for explaining this discrepancy: relative stability of the in-lake P and N concentrations (Nõges et al. 2008), high shade tolerance of the dominating species (Nõges et al. 2010) in the context of possible "brownification" of water, concomitant rise of temperature, or top-down control of grazer populations (Nõges, Cremona et al., 2016a; Nõges, Järvalt et al., 2016b); release of nutrients from the sediments and turbid-state resilience (Jeppesen et al. 2014), so that constructing a unified basin management policy has been out of reach to date. Additionally, the long-term monitoring on the lake has resulted in a vast amount of limnological data which defies a descriptive modelling approach (Nõges et al. 2010; Cremona et al. 2014). However, the advent of powerful statistical models and protocols has made possible the handling and hierarchizing of a growing number of variables simultaneously so that the most adequate ones could be singled out (Zuur et al. 2007). Recently, Feld et al. (2016) published a "cookbook" presenting an advisable protocol for treating large datasets and putative interactions between predictive variables which is suitable for the Võrtsjärv case study.

The objective of this research was to quantify the importance of limnological variables in determining the variance of cyanobacteria biomass (B_{CYAN}) in shallow hemiboreal lakes, using Lake Võrtsjärv as a case study. We used a dual-model approach consisting of two statistical models – Boosted Regression Trees (BRT) and Generalized Least Squares (GLS) model. BRT is a versatile and powerful statistical tool which allows non-parametric input data and non-linear relationships (Elith et al. 2008) whereas GLS is appropriate for analyzing time-series if complemented with an autoregressive term (Zuur et al. 2007). Our working hypothesis was that B_{CYAN} would be best explained by nutrient-related variables as the literature reported consistently their importance in the cyanobacteria proliferation in shallow lakes.

2. Methods

2.1. Study site

Lake Võrtsjärv is a large (270 km^2), shallow (mean depth: 2.8 m) and polymictic lake situated in central-southern Estonia. Forty percent of Võrtsjärv catchment (1313 km^2) is used for agriculture, followed by agricultural drained lands (799 km^2, 26.6%), forest (749 km^2, 24%), and bogs (243 km^2, 8%). Being located in the hemiboreal zone, Võrtsjärv is ice-covered on average 135 days per year. Water residence time approximates one year. Lake Võrtsjärv is highly eutrophic, with a mean total phosphorus (TP) concentration of 48 $\mu g\ L^{-1}$, mean total nitrogen (TN) of 0.91 $mg\ L^{-1}$, and persistent turbidity (Secchi depth < 1 m) during the ice-free period. The primary production in the lake is essentially (94%; Cremona et al. 2016a) carried out by phytoplankton dominated by cyanobacteria, which has durable ecological implications for the lake's carbon cycle and food web structure (Cremona et al. 2014). Although macrophytes are present, they are mostly abundant in a limited area of the Southern shore of the lake and play little functional role in the main water body. In Võrtsjärv, the most abundant cyanobacterial species are non-N_2 fixing *Limnothrix planktonica* (Wolosz.) Meffert, *L. redekei* (Van Goor) and *Planktolyngbya limnetica* (Lemm.) Kom.-Legn.; the principal N_2-fixing taxa, *Aphanizomenon skujae* Kom.-Legn. & Cronb. and *Anabaena* spp., have generally lower relative abundance (Nõges et al. 2008). Since the beginning of the 1980s, the mean annual cyanobacteria biomass has been rising despite a gradual reduction of phosphorus inputs. This growth of cyanobacteria has been accompanied by increasing water temperature, alkalinity and pH (Fig. 1).

In Lake Võrtsjärv, the most abundant metazooplankton taxa are rotifers *Anuraeopsis fissa* (Gosse), *Keratella cochlearis* (Gosse), *Keratella quadrata frenzeli* (Eckstein), *Keratella tecta* (Gosse), *Trichocerca rousseleti* (Voigt), *Polyarthra luminosa* Kutikova, in winter *Polyarthra dolichoptera* Idelson and *Synchaeta verrucosa* Nipkow. The dominant crustaceans (in biomass) are the cladocerans *Bosmina longirostris* (O. F. Müller), *Chydorus sphaericus* (O. F. Müller) and the juvenile forms of copepod genera *Mesocyclops* and *Thermocyclops*. The abundance of larger and more efficient grazers of algae, cladocerans *Bosmina berolinensis* Imhof, *Bosmina coregoni* (Baird) and a copepod *Eudiaptomus gracilis* (Sars), started to decrease in the 1980s and virtually disappeared from the zooplankton community. *Daphnia cucullata* Sars was earlier quite numerous in zooplankton (Haberman 1998), however, since the 2000s, only a few individuals have remained (Haberman and Haldna 2014).

2.2. Sampling and analyzing

Ecological monitoring on Lake Võrtsjärv dates back to the early 1960s and the study methods are described thoroughly by Nõges et al. (2010), Nõges, Cremona et al. (2016a), and Nõges, Järvalt et al. (2016b). Unless stated otherwise, all biomasses were given in wet weights (ww).

2.3. Statistical analyses

Data analysis was performed according to the methods described in Feld et al. (2016) "cookbook". In summary, the analysis was divided into three successive analytical steps: data preparation, exploratory and quantitative analyses. All the analyses were done with R