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High temperature favors elimination of toxin-producing *Microcystis* and degradation of microcystins by mixotrophic *Ochromonas*

Lu Zhang, Lei Gu, Qian Wei, Xuexia Zhu, Jun Wang, Xiaojun Wang, Zhou Yang*

Jiangsu Key Laboratory for Biodiversity and Biotechnology, School of Biological Sciences, Nanjing Normal University, 1 Wenyuan Road, Nanjing, 210023, China

HIGHLIGHTS

- The effect of temperature on *Ochromonas* degrading microcystins was evaluated.
- High temperature favors *Ochromonas* to eliminate *Microcystis.*
- High temperature boosts *Ochromonas* to degrade microcystins.
- Both intracellular and extracellular microcystins can be degraded by *Ochromonas.*
- More extracellular microcystins were released at 20 °C than at higher temperatures.

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ABSTRACT

This study aimed to investigate the influence of temperature on the ability of the mixotrophic flagellate *Ochromonas* to eliminate a toxic *Microcystis* population and degrade microcystins. We exposed *Microcystis* to cultures with or without *Ochromonas* YZ1 at 20, 25, and 30 °C for 10 days. Results showed that increased temperature promoted the growth of *Ochromonas* YZ1 and *Microcystis*, with the latter achieving high abundance without grazing. With increased temperature, *Ochromonas* YZ1 clearance rate increased, and *Microcystis* populations were earlier eliminated. Importantly, *Ochromonas* YZ1 degraded both intracellular and extracellular microcystins by grazing effects. The reduction ratios of *Microcystis* abundances and microcystins were both approximately 100% after 6 days at high temperature. In addition, more microcystins were released outside at 20 °C than at the higher temperatures. Overall, this study showed that high temperature favors elimination of toxin-producing *Microcystis* and degradation of microcystins by mixotrophic *Ochromonas*.

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1. Introduction

Cyanobacterial blooms are prevalent in many eutrophic lakes (Wu et al., 2013; Keating, 1977; Beversdorf et al., 2013). Some studies have indicated that high temperatures directly increase the growth rates of cyanobacteria (Robarts and Zohary, 1987; Jöhnk et al., 2008) and especially yields higher growth rates of toxic cyanobacteria than those of nontoxic cyanobacteria and increases the cyanotoxin concentration in lakes (Davis et al., 2009; Li et al., 2014). When the nutrients are sufficient to support cyanobacterial populations, warmer waters promotes cyanobacterial blooms even occurring in the early spring (Deng et al., 2014). In addition, blue-green algae have more advantages over other microalgae in shallow eutrophic lakes when the temperature increases (Rigosi et al., 2014). Thus, warming favors proliferation of toxic cyanobacteria and promotes them dominated in many aquatic ecosystems (Petchey et al., 1999).

Currently, cyanobacterial blooms are garnering particular attention because of their negative effects on aquatic ecosystems and health. The massive growth of cyanobacteria may lead to water hypoxia and produce more competition for the limited resources, thus disrupting the living conditions of other organisms (Timmermann et al., 2012; Suikkanen et al., 2013). Furthermore, cyanotoxins are the secondary metabolites of toxic cyanobacteria with severe toxic damages to zooplankton and fishes, and even they can be transferred into humans through the food chains

* Corresponding author.
E-mail address: yangzhou@njnu.edu.cn (Z. Yang).

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(Carmichael et al., 2001; Ferrão-Filho and Kozlowsky-Suzuki, 2011). Several measures have been proposed to control the blooms and remove cyanotoxins. Paerl et al. (2004) previously proposed a dual nutrient management strategy by reducing both nitrogen and phosphors inputs in long terms. Besides, chemical and physical treatments mainly include sonication, ozonation, maghemite catalyzation under visible light, and algicides, however, these methods are usually expensive, short-lived, and inefficient, and they may even aggravate pollution (Rajasekhar et al., 2012; Chang et al., 2014; Fang et al., 2014; Jones and Orr, 1994). By contrast, biological control is considered as an environment-friendly and acceptable method because of its nontoxic byproducts and long-lasting control. For instance, allelochemicals in periphyton biofilms inhibits cyanobacterial growth by reducing photosynthesis and controlling the phosphorus release (Li et al., 2012). Water samples from eutrophic lake were demonstrated to be able to degrade of mixed cyanotoxins (Edwards et al., 2008). Particularly, several studies reported that protozoan grazing has effective effects on the reduction both the cyanobacterial populations and cyanotoxin (Sugiura et al., 1990; Ou et al., 2005; Zhang et al., 2010).

In aquatic ecosystems, protozoans are the major grazers of cyanobacteria (Caron et al., 2009). Climate warming not only promotes cyanobacterial growth, but also importantly boosts protozoan growth and grazing. Kratina et al. (2012) and Yang et al. (2016) indicated that increased temperature strengthens the consumers controlling the primary producers in aquatic ecosystems. However, to date, little study focuses on the temperature-driven effects on reducing total cyanotoxin in culture with protozoan as predators.

Microcystis is the most prevalent and major bloom-forming cyanobacteria (Chen et al., 2010; Joung et al., 2011). In the present study, we exposed toxic *Microcystis* in two sets of cultures: one set contained mixotrophic protist *Ochromonas*, whereas the other set did not. Both sets were subjected to temperatures of 20, 25, and 30 °C for 10 days to determine the *Ochromonas-Microcystis* dynamics, *Ochromonas* grazing and clearance rates, reduction ratio of toxic *Microcystis*, and degradation ratio of microcystins, which were enough for evaluating the effects of temperature on *Ochromonas* eliminating on *Microcystis* populations and degrading microcystins.

2. Materials and methods

2.1. Microorganism strains and cultures

The mixotrophic flagellate *Ochromonas* sp. (strain YZ1) was originally sampled from Lake Taihu which has many different species of protozoans (Chen et al., 2008; Table S1). *Ochromonas* YZ1 was isolated and cultured as a monoclonal population in the laboratory. The microcystin-producing cyanobacteria *Microcystis aeruginosa* (PCC7806) was obtained from the Freshwater Algae Culture Collection at the Institute of Hydrobiology, China. These two experimental populations were both maintained in BG-11 medium (Stanier et al., 1971) at 25 °C under fluorescent light at 40 μmol photons m^{-2} s^{-1} with a light-dark period of 12 h:12 h. The *M. aeruginosa* strain was grown as a single cell or paired cells under laboratory conditions. Before the experiment, *Ochromonas* YZ1 and *M. aeruginosa* were cultured in respective fresh media to maintain the exponential phase.

2.2. Identification of Ochromonas

Ochromonas YZ1 was identified by morphological characteristics and 18s rRNA gene sequencing. The morphological characteristics (Fig. 1) was observed by light microscopy (Nikon Eclipse Ci-S; Tokyo, Japan) and photographed with a Nikon digital camera (Nikon Digital Sight DS-U3; Tokyo, Japan) through a microscope imaging software (Nikon NIS-Elements; Tokyo, Japan). Genomic DNA of *Ochromonas* YZ1 was isolated using an EasyPure Genomic DNA Kit (EE101-01, Transgen Biotech, China). The PCR-based amplification process and the specific primers were conducted according to Lara et al. (2007). DNA analysis included PCR amplification of the 18s rRNA gene, Blast analysis, and comparison with sequences found in the GenBank nucleotide database (http://www.ncbi.nlm.nih.gov/blast/). The phylogenetic analysis between *Ochromonas* YZ1 and other strains were described by polygenetic tree shown in Fig. 2 (MEGA 6.0, Arizona State University, USA). Alignments and phylogenetic analysis showed that the gene sequences of *Ochromonas* YZ1 had 99% maximum identification with the *Ochromonas gloeopara* strain CCMP2718 (GenBank accession: EF165112) and CCMP2060 (GenBank accession: EF165113). Therefore, YZ1 was identified as *Ochromonas gloeopara*, a species of the *Ochromonas* genus.

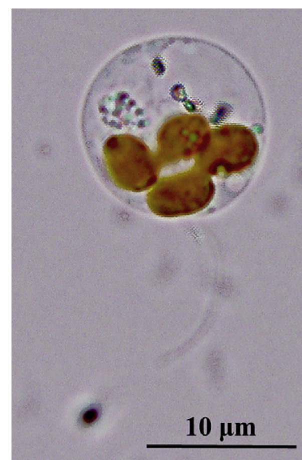

Fig. 1. Light micrograph of *Ochromonas* strain YZ1.

2.3. Grazing experiments

In this experiment, two groups were set at 20, 25, and 30 °C, that is, the control group contained *M. aeruginosa* only, and the grazing group contained both *Ochromonas* YZ1 and *M. aeruginosa* as predator and prey, respectively. The initial prey concentrations of *M. aeruginosa* were approximately 3.0×10^5 cells mL^{-1} in all the treatments, and the initial predator abundances of *Ochromonas* YZ1 were approximately 1.0×10^3 cells mL^{-1}. All experiments were each performed in 250 mL flasks with 150 mL sterilized BG-11 medium, and incubated at three temperatures under fluorescent light at 40 μmol photons m^{-2} s^{-1} with a 12 h:12 h light-dark period. Six treatments were used, and each was performed in triplicate. All flasks containing the samples were shaken every 12 h to avoid sedimentation. According to the pre-experiments, the entire experiment lasted for 10 days.

2.4. Population dynamics

To determine the population dynamics of *Ochromonas* YZ1 and *M. aeruginosa* in response to three temperatures, 2 mL of sample was collected daily for 10 days and fixed with Lugol's solution (2%). Abundances were counted using a hemocytometer (Tianlong XB-K-25; Jiangsu, China) under a microscope (Olympus 6V20WHAL; Tokyo, Japan). Such data were used to calculate the specific growth rates, clearance rates, and grazing rates and to fit population models (see 2.6 *Data analysis*).

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