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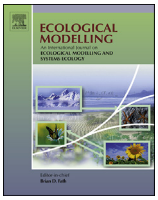

Modelling ecosystem structure and trophic interactions in a typical cyanobacterial bloom-dominated shallow Lake Dianchi, China

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ABSTRACT

Lake Dianchi is the largest shallow lake in Yunnan-Guizhou plateau and the sixth largest one in China. The lake has been experiencing cyanobacterial blooms in the last two decades. Although a few studies have investigated the tempo-spatial dynamics of cyanobacterial blooms and their underlying mechanisms, knowledge regarding the food web structure and trophic interactions in bloom-dominated ecosystems is scarce. In the present study, an Ecopath model was developed to assess the entire lake ecosystem on the basis of historical and survey data obtained between 2009 and 2010 at Lake Dianchi. The results showed that the aggregation of flows *sensu* Lindeman refers to six trophic levels (TLs), and most biomasses and trophic flows were primarily concentrated at the first three levels. About 77.5% of the trophic flows from TLI to TLII originated from detritus, whereas high proportions of under-utilised zooplankton biomass returned to the detritus because of low transfer efficiencies (2.9%) in TLII. The microbial loop was considered to be involved in linking the transfer between detritus and TLII. In addition, low values of connectance index and average mutual information implied that the food web tended to be lost in information diversity and had a less complicated structure. High cycling flows concentrated in the microbial loop reflected that the ecosystem enhanced recycling to forms positive feedback by which ecosystem locked the nutrients and promoted the inflation of biomass in plankton communities. Thus, Dianchi Lake was clearly thought to be a bottom-up control ecosystem. These characteristics of the food web partly explained why cyanobacterial blooms were exceptionally heavy and durable in this lake. Finally, the implications of artificially stocking filter-feeding fish (bighead and silver fish) and exotic zooplantivorous icefish on the ecosystem structure and function are discussed herein.

1. Introduction

The structure, function, and stability of aquatic ecosystems are supposed to be susceptible to a wide array of human activities, including anthropogenic nutrient enrichment, over-exploited fishery activity, and alien species introduction (Wilcove et al., 1998; Pauly et al., 1998; Capriulo et al., 2002; Heisler et al., 2008). To date, early signs of climate-related changes in lake ecosystems have been reported (Straile, 2002; Livingstone, 2003); ecologists have begun to pay more attention to the effects of climate variability, especially temperature increase (Carpenter et al., 1992; Garten and Adrian, 2002; Beardall and Raven, 2004; Wrona et al., 2006). The propagation of cyanobacteria has been proposed to have steadily intensified with the increase of water temperature in lakes, rivers, and reservoirs worldwide during the last decades (Carey et al., 2012; Paerl and Paul, 2012).

Microcystis, the genus with the most ubiquitous and harmful blooms of cyanobacteria (CyanoHABs), blooms have widely threatened the safety and health of aquatic ecosystems (Paerl and Huisman, 2008). In the period of blooms, scums of *Microcystis* species accumulate on the surface of water and regulate buoyancy for the optimum utilisation of nutrients and light resources (Xiao et al., 2012); this is responsible for water quality deterioration and ecological degradation by severe changes in ecosystem properties (Carpenter et al., 1998; Paerl and Huisman, 2009). Negative impacts

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Abbreviations: EE, ecotrophic efficiency; DOC, dissolved organic carbon; POC, particulate organic carbon; AODC, acridine orange direct count; GPP, gross primary production; TL, trophic level; OI, ominivory indices; CI, connectance index; TEs, transfer efficiencies; TST, total system throughput; FCI, Finn's cycling index; AMI, average mutual information; MTI, mixed trophic impact.

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of bloom formation and collapse are well known on aquatic ecosystems, including high turbidity and shading the light needed by aquatic plants (Berger, 1989), changing physico-chemical factors (elevated pH and reduced CO_2), and producing toxins called microcystins (MCs) that affect the habitats of other biological communities (Kann and Smith, 1999; Hessen et al., 2005). Therefore, some studies have focused on different levels of aquatic organisms along with life cycle of *Microcystis* (Ke et al., 2008) and even the involved dynamics of the 'microbial loop' (Sommaruga, 1995) to postulate the possible relationship between cyanobacteria and community structure of bacteria and flagellates (Xing et al., 2007; Wilhelm et al., 2011). However, predicting the overall effects of blooms on ecosystem seems difficult. The community changes of different organisms can indirectly cause changes in the pathways and magnitude of material flows in food webs. These flows have been considered to reveal important features and functions of natural food webs (Berlow et al., 2004; Van Oevelen et al., 2010).

In China, typical cases for *Microcystis* blooms are mainly found in three large shallow lakes: Lakes Taihu, Chaohu, and Dianchi; at these sites, the government has invested billions of funds over the last decade in order to prevent the occurrence of blooms. At Lake Dianchi, despite the implementation of various measures, including cutting down the point and non-point nutrients, re-establishing aquatic macrophytes in lakeside zones, and introducing artificially cultured carp (bighead and silver carp), successfully decreased the nutrient concentration to some extent (Lu et al., 2012), the *Microcystis* blooms still remained a severe problem. These blooms could persist for up to 10 months and cover the majority of the lake's surface (Wan et al., 2008). Reasons for the persistence of cyanobacterial blooms and mechanisms of nutrient cycling at the ecosystem level in shallow eutrophic lakes have fascinated many ecologists (McCarthy et al., 2007; Paerl et al., 2011). Recent research has revealed the importance of internal nutrient dynamics (McDonald et al., 2010). Therefore, quantitative trophic interaction analyses at the ecosystem level are crucial for lakes with cyanobacterial blooms to better understand the effect on nutrient cycling from the food web structure.

Icefish (*Neosalanx taihuensis* Chen) are small transparent fish that are distributed widely in both coastal and inland waters of China. It was first introduced from Yangtze River Basin to Lake Dianchi in 1979 and has rapidly dominated and become the primary economic fishery species. This species was introduced at a large scale in some Yunnan Plateau Lakes (Guo et al., 2009). Nevertheless, recently, with the widespread degeneration of lake ecosystems in Yunnan Plateau, many studies have focused on the influence of eutrophication and icefish introduction on the ecosystem structure (Liu et al., 2009; Li et al., 2011). Some ecologists have suggested that the introduction of icefish from the Yangtze River to lakes in Yunnan-Guizhou Plateau often has detrimental impacts on the ecological structure (Zhang et al., 2005). The hypothesis was based on the trophic cascading interactions that increase the zooplantivorous biomass, resulting in decreased herbivorous zooplankton biomass and increased phytoplankton biomass (Drenner and Hambright, 2002). Thus, an ecosystem-based approach is essential for the Yuannan Plateau Lakes to maintain the sustainable exploitation of exotic fisheries and health of ecosystems (Garcia, 2003; Villanueva et al., 2008).

To better understand the above-mentioned issues and to assess the trophic structure and interactions in Lake Dianchi, we used the ecological network analysis (ENA) method. This analysis has been successfully used in various lakes worldwide (Moreau et al., 2001; Fetahi and Mengistou, 2007; Thapanand et al., 2007), but it is an emerging field for lake research and management in China. The most commonly used software packages for ENA are NETWRK4 (Ulanowicz, 1987) and Ecopath (Christensen and Pauly, 1992). The differences in their output are so small that modellers would interpret the results and obtain the same qualitative conclusions (Heymans and Baird, 2000). Ecopath software was used in this study since it is user-friendly and has a standardised interface. The model definitely required large amounts of input data that directly obtained in Lake Dianchi in order to ascertain the quality of model. Our objectives were to (1) quantify the food web structure and trophic interactions in a cyanobacterial bloom-dominated ecosystem, (2) reveal ecosystem properties and development status, and (3) evaluate the ecological consequences of cyanobacterial blooms and exotic fish in Lake Dianchi.

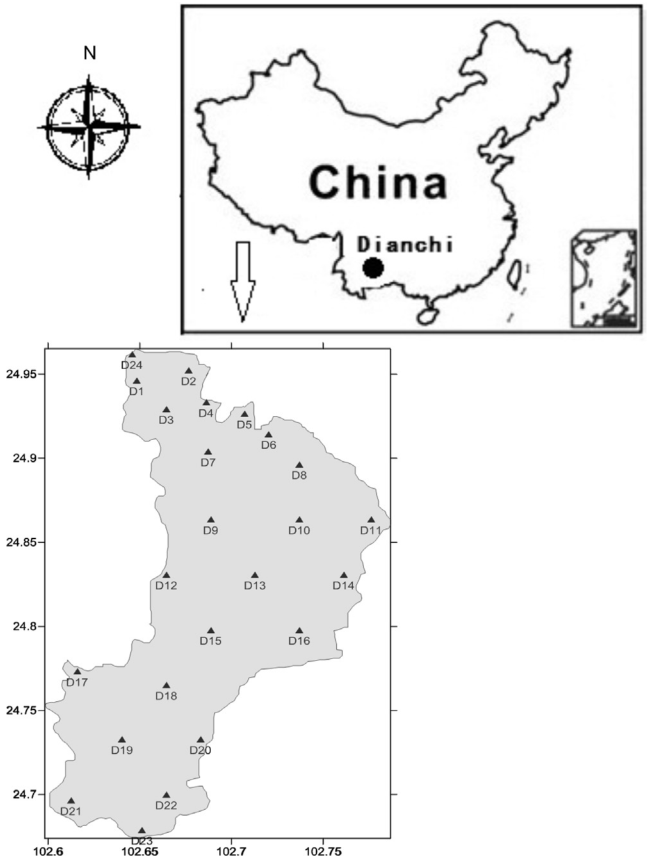

Fig. 1. Location of Lake Dianchi with the 24 sampling sites.

2. Materials and methods

2.1. The study site

Lake Dianchi (24°29′–25°28′ N, 102°29′–103°01′ E) is located at the south-west region of Kunming City, Yunnan Province, China (Fig. 1). It is a typical shallow plateau lake at an altitude of 1886.5 m, with an area of approximately 300 km^2; mean depth, 4.7 m; and maximum depth, 11 m (Hou et al., 2004), as well as covering a total basin area of 2920 km^2. Lake Dianchi is regarded as the sixth largest freshwater lake in China and the largest lake in Yunnan Plateau, which has a distinctive monsoon climate with an annual mean temperature of 15 °C; an annual mean precipitation of about 1000 mm; and annual evaporation of 1870–2120 mm (Gong et al., 2009). Lake Dianchi also provides various natural resources for local inhabitants, in terms of fishery, reserved drinking water, and tourism industry.

Before the 1960s, the nutrient concentrations in Lake Dianchi were low; submerged macrophyte communities covered more than 80% area of the lake, and indigenous fish dominated the fish community. However, between the 1970s and 1980s, the amounts