



Temporal variations in a phytoplankton community in a subtropical reservoir: An interplay of extrinsic and intrinsic community effects



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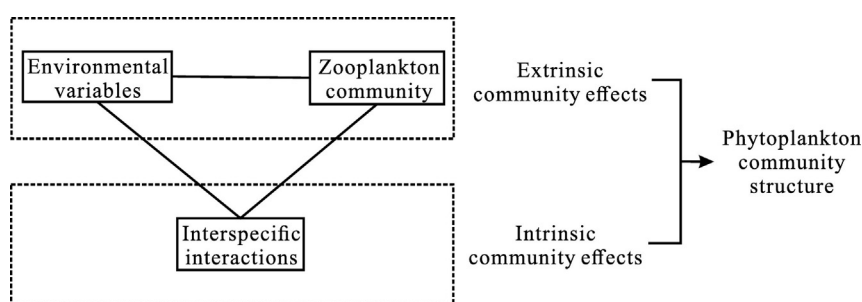
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HIGHLIGHTS

- Extrinsic factors originated from the surrounding environment were incomplete predictors of phytoplankton community dynamics
- Interspecific interactions were widely existed in phytoplankton community and had significant influences on shaping phytoplankton community structure.
- Phytoplankton community dynamic is a multifactorial process regulated by an interplay extrinsic and intrinsic community factors.
- Intrinsic associations dominated the network rather than extrinsic associations.

GRAPHICAL ABSTRACT



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ABSTRACT

The phytoplankton community structure is potentially influenced by both extrinsic effects originating from the surrounding environment and intrinsic effects relying on interspecific interactions between two species. However, few studies have simultaneously considered both types of effects and assessed the relative importance of these factors. In this study, we used data collected over nine months (August 2012–May 2013) from a typical subtropical reservoir in southeast China to analyze the temporal variation of its phytoplankton community structure and develop a quantitative understanding of the extrinsic and intrinsic effects on phytoplankton community dynamics. Significant temporal variations were observed in environmental variables as well as the phytoplankton and zooplankton communities, whereas their variational trajectories and directions were entirely different. Variance partitioning analysis showed that extrinsic factors significantly explained only 31% of the variation in the phytoplankton community, thus suggesting that these factors were incomplete predictors of the community structure. Random forest-based models showed that 48% of qualified responsible phytoplankton species were more accurately predicted by phytoplankton-only models, which revealed clear effects of interspecific species-to-species interactions. Furthermore, we used association networks to model the interactions among phytoplankton, zooplankton and the environment. Network comparisons indicated that interspecific interactions were widely present in the phytoplankton community and dominated the network rather than those between phytoplankton and extrinsic factors. These findings expand the current understanding of the underlying mechanisms that govern phytoplankton community dynamics.

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1. Introduction

Phytoplankton constitute the base of aquatic food webs, thereby determining the development of ecosystem stability and function (Behrenfeld and Boss, 2014; Falkowski et al., 2003; Kazamia et al., 2016). Unlike systems that are at equilibrium or at steady state, phytoplankton communities are constantly undergoing rapid temporal and spatial change, thus prompting the examination of how different species are associated with ambient conditions and the ecological causal feedback in aquatic ecosystems (Fuhrman et al., 2015).

Longitudinal dynamics in a phytoplankton community are often assumed to be controlled by bottom-up effects of environmental variables, e.g., temperature (Chen et al., 2016; Dai et al., 2016; Vogt et al., 2015), light and nutrients (Becker et al., 2010; Lv et al., 2014) and top-down effects of zooplankton (van Gremberghe et al., 2008; Xiong et al., 2016). Nevertheless, no consensus has emerged regarding the unique roles of these effects. For example, some studies have proposed that, in general, a monsoon climate and nutrition limitation, along with the specific morphology and hydrology of the water body, constrain the variation in phytoplankton community assembly, especially in subtropical and temperate aquatic systems (Cottenie, 2005). Other studies have demonstrated that there is still a larger proportion of variation unconstrained by these factors (Beisner et al., 2006; Nabout et al., 2009; Wiltshire et al., 2008). A plausible explanation for these contradictory patterns is that the factors previously considered were all extrinsic (exogenetic) factors that originated outside the community. However, community dynamics is multifactorial and is conjointly regulated by extrinsic and intrinsic (endogenetic) factors, e.g., intraspecific and interspecific interaction (Dai et al., 2017a; Xiong et al., 2016). Few studies have simultaneously considered the relative importance of extrinsic and intrinsic factors, thus making it difficult to explore the underlying mechanisms of phytoplankton community dynamics (Lima-Mendez et al., 2015).

In a given community, every member frequently interacts with others to form a complex ecological network through various types of interactions, that are either positive (e.g., mutualism and symbiosis) or negative (e.g., competition and parasitism), ranging from mutually beneficial through neutral to mutually harmful (Dai et al., 2017b; Faust and Raes, 2012). An organism's interactions are fundamental to the survival of that organism and the functioning of the ecosystem as a whole. In the past two decades, research into organismal interactions has received great attention in plant and animal ecology (Allesina et al., 2008; Bastolla et al., 2009; Martin et al., 2017), but has been restricted in microbial ecology (Luo et al., 2007), probably because of the difficulties in directly observing and quantifying microbial interactions under natural conditions (Deng et al., 2016). Recently, as time series analyses of microbial communities become increasingly available, identifying and quantifying complex relationships among community members should become easier (Faust et al., 2015; Steele et al., 2011). For example, a network model can be built from co-occurrence or antagonism, with nodes representing taxa and connecting edges representing correlation over time (Ryan et al., 2006). Given the potential for interactions among species, appreciation for bacterial interactions is growing (Dai et al., 2017a; Eiler et al., 2012; Liu et al., 2014; Xiong et al., 2015a; Zhu et al., 2016), whereas information on how their close microbial relatives, phytoplankton species, respond to one another is scarce.

A reservoir is a suitable freshwater ecosystem to study the succession of phytoplanktonic events, because its highly dynamic environment and shifts in ecosystem state threaten biodiversity and cause large losses in sustainable ecosystem goods and services (Palmer, 2010; Yang et al., 2016). Here, we used multi-statistical and association network analysis methods to address the following questions: (i) How do extrinsic factors affect phytoplankton community dynamics? (ii) Do interspecific interactions at the species level have a significant influence on the formation of a phytoplankton community? and (iii) How important are these intrinsic effects compared with extrinsic effects?

To this end, we examined a phytoplankton community and its driving factors in a typical subtropical reservoir, Siminghu Reservoir in south-east China, as a classic example for studying the temporal patterns of phytoplankton community succession and its ecological interpretation.

2. Materials and methods

2.1. Study area

Siminghu Reservoir is a shallow polymictic reservoir located in Ningbo, Zhejiang, eastern China (29° 56' N, 121° 03' E) (Fig. 1). This reservoir was impounded in 1958 and has a catchment area of 1.031 km², mean and maximum depth of 8.4 m and 13 m, respectively, and a total storage capacity of 0.123 km³. It is one of the most important sources for flood control, drinking water and power generation functions. The area has a subtropical humid monsoon climate with an annual mean precipitation of 2125 mm and an annual mean temperature of 21 °C.

2.2. Sampling and analysis

To obtain the best picture of the structure of the phytoplanktonic organisms in a manner compatible with the practicalities of sampling and analysis, four sampling sites were chosen: site 1# (29° 55' 45.8'' N, 121° 04' 28'' E) and site 2# (29° 55' 54.5'' N, 121° 03' 27.1'' E) receive water from two inflow rivers, Liangnong River and Hengao River, respectively; site 3# (29° 56' 16.0'' N, 121° 03' 28.4'' E) is approximately in the middle of the reservoir; site 4# (29° 56' 49.9'' N, 121° 03' 08.2'' E) is a relative lentic ecosystem near the dam (Fig. 1). Samples were taken at monthly intervals from August 2012 to May 2013, except for January 2013.

Water temperature (WT), pH, and dissolved oxygen (DO) were recorded in situ with a YSI 6000 multi-parameter probe (Hydrolab Datasond 4α, Hach Corporation, Loveland, USA) at a depth of 50 cm. Secchi depth (SD) was measured by using a 20-cm diameter black and white Secchi disk.

All water samples were mixed with water taken with an integrator tube from the surface layer (50 cm below the surface), mid-layer (half-way water depth) and bottom layer (50 cm above the bottom). Unfiltered samples were stored in polypropylene bottles to analyze the concentrations of total phosphorus (TP), total nitrogen (TN) and chemical oxygen demand (COD) following standard methods (Rand et al., 1991). For the analysis of ammonia (NH₄⁺-N), nitrite (NO₂⁻-N), nitrate (NO₃⁻-N), and orthophosphate (PO₄³⁻-P), samples were filtered through glass fiber filters (GF/F, 25 mm, 0.7 μm) with a filtration system (Vacuum Pump XF5423050, Millipore, Darmstadt, Germany), and measured with an automated spectrophotometer (Smart-Chem 200 Discrete Analyzer, Westco Scientific Instruments, Brookfield, USA). N/P was determined as the ratio of dissolved inorganic nitrogen (the sum level of NH₄⁺-N, NO₂⁻-N and NO₃⁻-N, expressed in mg/L) and PO₄³⁻-P. For chlorophyll-a (Chl-a), known volumes of water were filtered by GF/F filters in replicate and the filters were frozen until extraction. Chlorophyll-a extraction was performed in 90% hot ethanol, and further reading was performed with a spectrophotometric method (Jespersen and Christoffersen, 1987).

For phytoplankton, a 1000-mL integrated sample was taken vertically at three different depths: surface, euphotic (2.7 times the SD) and 1/2 euphotic layer. Samples were fixed with Lugol's solution. Quantitative samples for zooplankton were collected by filtering a 15-liter integrated water sample and immediately preserving in 4% buffered formaldehyde.

Phytoplankton taxa were counted in sedimentation chambers (Hydro-Bios Apparatebau GmbH Kiel, Germany) with an inverted microscope (CK2, Olympus Corporation, Tokyo, Japan) according to Utermöhl (1958). Phytoplankton biomass was calculated by geometric approximations by using the computerized counting program (OPTICOUNT, http://science.do-mix.de/software_opticount.php).

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