Limnologica 46 (2014) 131–138

Contents lists available at ScienceDirect

Limnologica

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

The role of food availability and phytoplankton community dynamics in the seasonal succession of zooplankton community in a subtropical reservoir

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A R T I C L E I N F O

Article history:
Received 30 May 2013
Received in revised form
11 November 2013
Accepted 23 January 2014
Available online 1 February 2014

Keywords:
Food availability
Food composition
Seasonal succession
Physicochemical effects
Species interactions
Feitsui Reservoir

A B S T R A C T

Seasonal patterns of zooplankton succession have been explained by physical factors such as temperature and precipitation. While the influence of biological factors, such as food availability and composition, has been recognized in theory and studies in some temperate lakes, how food availability and composition affect the seasonal succession of zooplankton communities, especially in tropical/subtropical lakes, is still unclear and under debate. In this study, we applied multivariate analyses to a 3-year time series of physicochemical factors, various food sources (primary and bacterial production), and phytoplankton and zooplankton species composition in a subtropical reservoir in Taiwan. Our results demonstrated that (i) in addition to physical factors, seasonal variation of food availability partly explains zooplankton seasonal succession. In particular, inter-annual variation of food availability proved more important than physical factors in determining the inter-annual variation in zooplankton populations. Specifically, limited food supply amplifies the amplitude of seasonal variation of zooplankton community biomass and composition; (ii) the association between zooplankton and phytoplankton was stronger when regarding their species composition than when regarding their biomass, implying a strong interaction between zooplankton and phytoplankton at the community level.

Introduction

Seasonality is one of the important underlying factors structuring the dynamics of plankton communities in aquatic ecosystems. Many studies have shown that a change of season is accompanied by a regular succession of zooplankton species composition and total biomass (Saunders and Lewis 1988; Sommer et al. 1986; Yoshida et al. 2001). The seasonal succession of zooplankton communities has been reported worldwide, and its physical determinants vary across types of lakes. For example, the initiation of seasonal succession has been suggested to be more strongly associated with water temperature (Yoshida et al. 2001) in temperate lakes and with precipitation in tropical lakes (Nilssen 1984).

Biological factors, including food availability and composition, may also influence zooplankton seasonal succession (Zohary et al. 1994) in addition to the physical determinants. Food availability is one of the most critical factors affecting zooplankton population dynamics because of its influence on population growth rate (Vanni 1987) and life history traits (e.g. univoltine or multivoltine) (Twombly et al. 1998). Many critical life stages of zooplankton depend on the dynamics of food availability (Cushing 1990). Therefore, the seasonal variation of food availability may be expected to influence zooplankton seasonal succession. In many temperate lakes, the dynamics of phytoplankton biomass and composition profoundly affect zooplankton dynamics (Carpenter et al. 1985; Elser and Goldman 1991; Lampert et al. 1986). However, very few studies have explored how food availability influences zooplankton seasonal succession in tropical/subtropical lakes which have physicochemical properties distinctly different from those of temperate lakes (Lewis 1987). Moreover, the limited numbers of studies in tropical/subtropical lakes have demonstrated contrasting conclusions concerning the effects of phytoplankton

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0075-9511/$ – see front matter © 2014 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.limno.2014.01.002

biomass on zooplankton dynamics. For example, studies of Lake Okeechobee, Florida (Crisman and Beaver 1990; Havens et al. 2000) and lakes in southern China (Wang et al. 2007) have suggested weak zooplankton–phytoplankton interactions because of weak temporal correlations between the total biomass of zooplankton and phytoplankton. In contrast, studies of Australian (Hunt and Matveev 2005; Matveev 2003) and Brazilian lakes (de Cardoso and Marques 2004) demonstrated strong zooplankton–phytoplankton interactions which placed zooplankton as effective grazers of phytoplankton. The conflicting results in these studies may arise from a lack of detailed investigation of both phytoplankton and zooplankton species composition, and thus, the mechanisms determining how phytoplankton community composition affects zooplankton seasonal succession cannot be properly evaluated (Bergquist et al. 1985).

The pattern of seasonal succession is similar between years for most of zooplankton communities, but the amplitude of the seasonal variation of zooplankton biomass and composition, can vary from year to year (Dakos et al. 2009). Recent studies indicate that the effects of climate change have altered phenology and inter-annual variability of seasonal succession of zooplankton populations (Winder and Schindler 2004; Winder et al. 2009). Similarly, one might expect that at the community level, seasonal succession could also vary inter-annually in response to environmental changes. This inter-annual variability might be linked to the inter-annual variation of physicochemical environment and/or food availability. For example, Winder et al. (2009) showed that increased temperatures changed the number of generations of some zooplankton population from one to two generations per year. In addition, significant variation of food availability occurs on an inter-annual basis in lakes (Berman et al. 1995; Shade et al. 2007). When food is limited for a given year, one would expect a strong seasonal peak of zooplankton biomass associated with the peak of food concentration (large amplitude of seasonal variation); in contrast, when food is abundant in a given year, zooplankton can sustain their abundance throughout the year (McCauley and Murdoch 1987). Thus, years with low food availability have the potential to yield zooplankton community temporal dynamics which are less tied to the change of seasons with an expectation of small amplitude of seasonal variation. However, the effect of food availability on the inter-annual variability of the amplitude of seasonal variation of zooplankton still lacks empirical support.

To understand how food availability and composition (phytoplankton community) influence zooplankton seasonal succession in tropical/subtropical lakes, we investigated the potential determinants (food availability, phytoplankton species composition and physicochemical factors) of zooplankton community dynamics in a subtropical reservoir. In this study, we applied multivariate analyses in order to test the hypothesis that food availability influences inter-annual differences in zooplankton seasonal succession at least as much as physicochemical factors. Further, we compared the roles of food availability and food composition (phytoplankton composition) in order to assess which factor has a stronger association with the dynamics of zooplankton communities (i.e. how important are zooplankton–phytoplankton interaction at community level in tropical/subtropical lakes?).

Materials and methods

Study site

The Feitsui Reservoir is a deep, stratified subtropical reservoir located in northern Taiwan, 121°34′ E and 24°54′ N at an altitude of 160 m. The reservoir was constructed in 1987 in the valley of the Xindian River. It has a catchment of 303 km^2, an average depth of 90 m (max depth 100 m), and a total volume of 406 million m^3. Thermal stratification generally develops from May to September. Due to the important social–economical role of supplying drinking water for Taipei city, the reservoir has been well protected from human activities since its construction, and its trophic status is oligo- to mesotrophic (Wu and Chou 1998) according to the Carlson trophic state index (Carlson 1977).

Zooplankton community

To investigate the zooplankton community succession in Feitsui Reservoir, field sampling was carried out on a biweekly basis from January 2008 to October 2010 (60 samplings for 34 months). All fieldwork was carried out from a research vessel near a moored monitoring platform located 1-km off of the Feitsui Reservoir dam. Zooplankton samples were collected using a 50-μm mesh plankton net (equipped with a flowmeter) hauled vertically from the 50 m to surface. The average filtration efficiency of the net hauling is 53%, which the filtration efficiency is defined as the proportion of water passing through the net (recorded by the flowmeter) to the hauling water volume (net opening area * hauling depth). We chose to sample this depth layer in order to avoid the summer anoxic layer and hypolimion turbid inflow from upstream and because our pilot study found that zooplankton density is very low below 50 m. We note that the sampling method might not be optimal for sampling rotifers, chiefly because it risks the loss of eggs detaching from female adult, while its influence on abundance estimation is minor, Thus, this sampling method is useful for general rotifer community surveys (Likens and Gilbert 1970).

To avoid the deformation of rotifers in our samples, the zooplankton samples were first put into a refrigerator and then anesthetized by effervescing CO_2 tablets, and then fixed in 2% formalin. The preserved zooplankton sample was enumerated under the microscope. For each enumeration, on average 300 individuals were subsampled. All mature individuals were identified to species level under the microscope wherever possible. The zooplankton species identification follows published taxonomic keys (Chiang and Du 1979; Dussart and Defaye 2001; Koste and Shiel 1987; Shen and Song 1979; Wang 1961). The total length and width of each individual was measured by analyzing the image (Olympus analySIS®) taken by the microscopic CCD camera (Olympus DP71). Carbon biomass of zooplankton was estimated by using the empirical length-mass equations for crustacean plankton, and the length–biovolume equations for rotifers by assuming carbon to volume ratio of 0.05 (Andersen and Hessen 1991; Bottrell et al. 1976; Downing and Rigler 1984; Dumont et al. 1975). This is based on the assumption that the wet to dry weight ratio is 0.1 and that carbon contributes half of the dry weight of rotifers (Downing and Rigler 1984). Rotifer species with particularly small carbon to volume ratio (Dumont et al. 1975), such as *Asplanchna* spp., were rare in Feitsui Reservoir.

Food availability of zooplankton: bulk food variables

To determine the influence of food availability on the zooplankton community, bulk food variables including chlorophyll *a* concentration (Chl*a*), primary production rate (PP), cyanobacterial abundance (Cyano), bacterial abundance, bacterial production rate (BP), and particulate organic carbon (POC) were also measured biweekly. Chl*a* was measured by acetone extraction method (Parsons et al. 1984) of water samples filtered onto a glass fiber filters (Whiteman GF/F). PP was measured using the ^{14}C assimilation method (Parsons et al. 1984). For each PP measurement, we added $H^{14}CO_3$ to water samples and incubated the samples under nine different light intensities constructed by an artificial