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Changes in food web structure and ecosystem functioning of a large, shallow Chinese lake during the 1950s, 1980s and 2000s

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A B S T R A C T

Food web structure dynamics and ecosystem functioning are strongly linked, and both are indispensable in evaluating ecosystem development in lakes under multiple anthropogenic stressors. However, model-based approaches concerning the changes in food web structure and ecosystem functioning in a certain lake during distinct periods are scarce. In this study, we focus on Lake Chaohu, the fifth-largest lake in China, which has undergone drastic changes over the last several decades. Data from the 1950s, 1980s and 2000s were used to create three Ecopath mass-balance models. These Ecopath models were validated by the stable isotope-determined trophic level (TL) for each functional group, which indicated an acceptable model performance. Over time, we observed a collapse of the food web toward a simplified structure and decreasing biodiversity and trophic interactions. The lake ecosystem was approaching an immature but stable status from the 1950s to the 2000s, as indicated by the multiple related indicators and the distribution of energy flows in slow detrital-based and fast primary producer-based channels. We further discuss the potential driving factors and underlying mechanisms, hypothesizing that hydrological regulation may play a significant role in driving all of these changes in Lake Chaohu in addition to eutrophication and intensive fishery. Overall, we strongly advocate the identification of a threshold in abundance of zooplanktivorous fish, an integrated strategy for future ecological restoration in Lake Chaohu, and the consideration of using Ecopath as a new management tool for other lakes, thereby bridging the strategies from both environmental and ecological perspectives.

1. Introduction

It is commonly accepted that natural and human systems are strongly coupled and that human activities have currently reached a level that may damage the natural system beyond its adaptive capacity (Liu et al., 2007; Rockström et al., 2009). Many subsystems on the planet, such as aquatic ecosystems, will exhibit nonlinear behavior as certain thresholds are crossed (Casini et al., 2009; Scheffer et al., 2001). For lake ecosystems, multiple anthropogenic stressors may have synergetic effects that lead to drastic ecological degradation (Yang and Lu, 2014). In addition to fertilization-induced nutrient enrichment and hydrological regulation, fishery in lakes provides important ecological services to local communities, but it is rarely sustainable around the globe (Pauly et al., 2002). Intensive fishery leads to biodiversity loss and simultaneous erosion of the structure and processes that confer stability in the food web (de Ruiter et al., 1995; Rooney et al., 2006), resulting in disastrous consequences, such as "fishing down the food web" (Pauly et al., 1998), food web collapses (Downing et al., 2012) and ultimately catastrophic regime shifts (Casini et al., 2009; Folke et al., 2004).

Over the last several decades, lakes along the Yangtze River floodplain in China have witnessed a strong ecological degradation (Dearing et al., 2012). Lake Chaohu, the fifth-largest freshwater shallow lake in China, is one of the three lakes in China (along with Lake Taihu and Lake Dianchi) that have attracted public concern regarding harmful cyanobacterial blooms (Shan et al., 2014). This lake has suffered from gradual nutrient enrichment from the 1950s

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onwards (Kong et al., 2015), hydrological regulation, which disconnected the lake from the Yangtze River since 1963 (Xu et al., 1999b; Zhang et al., 2014) and intensive fishery since the 1980s (Zhang et al., 2012). Consequently, drastic changes have occurred in Lake Chaohu's ecosystem, resulting in significant changes in the food web structure, a decreasing biodiversity and catastrophic regime shifts toward an unfavorable turbid state dominated by phytoplankton and small-sized planktivorous fish (Kong et al., submitted; Liu et al., 2012; Zhang et al., 2015). A significant fourfold to fivefold increase in total biomass was observed, with an increasing dominance of the lower trophic levels (TLs) throughout these years. These changes in the food web structure may strongly influence the functioning of the ecosystem. To date, however, the quantitative changes in ecosystem functioning have not been documented for Lake Chaohu.

The Ecopath model is a well-established modeling tool with a user-friendly interface and a standard modeling procedure to analyze and document food web structure and ecosystem functioning (Christensen et al., 2005). These features of the model and the availability of relevant data from the 1950s, 1980s and 2000s make the present study feasible. Several studies have already used Ecopath for lakes in the Yangtze River floodplain (Guo et al., 2013; Jia et al., 2012; Li et al., 2010) and even a preliminary Ecopath model for Lake Chaohu (Liu et al., 2014), but studies that investigate the changes in the food web structure and ecosystem functioning over a long time span are scarce. The drastic changes in the Lake Chaohu ecosystem, however, urgently call for a quantitative analysis of food web dynamics and ecosystem functioning comparable with studies conducted in, e.g., Lake Taihu (Hu et al., 2011; Li et al., 2010), Lake Chozas (Marchi et al., 2011, 2012) and the Baltic Sea (Casini et al., 2009), to provide deeper insights into the effect of multiple anthropogenic stressors. Furthermore, the development of an integrated modeling tool is becoming imperative to support a sound policy for lake management with both environmental and ecological perspectives (Jørgensen and Nielsen, 2012).

In the present study, we built three Ecopath mass-balance models for Lake Chaohu that represent the 1950s, 1980s and 2000s. We attempted to investigate the changes in ecosystem properties and to analyze the potential driving factors and underlying mechanisms. In addition, Ecopath requires data of which it is difficult to obtain good empirical estimates (e.g., diet composition). Thus, a validation of the Ecopath model is strongly recommended. We provide a reliable method to validate the diet composition of the Ecopath model for Lake Chaohu using lab- and literature-based estimations of TLs from stable isotopes' determination for each functional group in the food web.

The goals of this study are as follows: (1) to establish three validated Ecopath mass-balance models for Lake Chaohu corresponding to the 1950s, 1980s and 2000s, (2) to quantify the changes in food web structure in Lake Chaou during different periods, (3) to evaluate the changes in the ecosystem functioning of Lake Chaohu during the 1950s, 1980s and 2000s, (4) to discuss the potential key factors driving the changes in the food web structure and ecosystem functioning, and (5) to provide a sound modeling basis for an integrated management tool with an illustrative example in Lake Chaohu.

2. Materials and methods

2.1. Study site

Lake Chaohu (31°33′59″N, 117°26′40″E) is the fifth-largest shallow lake in China. It covers an area of 760 km^2 and has a depth of 3 m on average (Fig. 1). Before the 1950s, the lake was famous for its beautiful scenery with a high water quality, a large amount of vegetation (30% of the surface area) and a high level of biodiversity (Kong et al., 2013; Xu et al., 1999a; Zhang et al., 2012; Zhang et al., 2014). However, in 1963, the connection of the lake with Yangtze River was blocked by the "Chaohu Sluice" on the Yuxi River, and as a result, the water level fluctuation in the lake was largely reduced. Since 1980, the rapid socio-economic development in the drainage area of the lake led to a gradual elevation in nutrient loading and a deterioration of the water quality (Kong et al., 2015). Intensive fishery from the 1980s onwards exacerbated the effect of eutrophication and water level control, resulting in rapid loss of ecological services. Natural riparian areas were reduced to less than 1% of the total area (Ren and Chen, 2011). The west part of the lake could no longer provide drinking water for the city of Hefei, primarily due to frequent cyanobacterial blooms. As the total fishery yield increased rapidly over the past decades (Fig. 2A, $p < 0.01$; approximately 2000 t from the 1950s to the 1970s and nearly 20,000 t in 2009), the total number of species in the fish community decreased from 84 (1963) to 62 (1973) to 78 (1981) to 54 (2002), indicating a considerable loss of biodiversity (Lv et al., 2011).

2.2. Model construction and parameterization

We have built three static mass-balance models for Lake Chaohu, representative of the 1950s, 1980s and 2000s, using Ecopath with Ecosim, version 6.4.3 (freely available at http://www.ecopath.org). The reasons we focus on these three different periods in the present study are that these three periods (1) represent three distinct stages in the development of the lake ecosystem, and (2) correspond to the times when intensive investigations were conducted in Lake Chaohu, with abundant data available in the literature. The basic equation for this model is given in Eq. (1):

$$B_i \cdot \left(\frac{P_i}{B_i}\right) \cdot \mathrm{EE}_i - \sum_{j=1}^{n} B_j \cdot \left(\frac{Q_j}{B_j}\right) \cdot \mathrm{DC}_{ji} - \mathrm{EX}_i = 0 \quad (1)$$

where B_i (t/km^2) and B_j (t/km^2) are the biomass of group i and j, respectively, P_i/B_i (per year) is the production/biomass ratio of group i, EE_i (−) is the ecotrophic efficiency of group i, Q_i/B_i (per year) is the consumption/biomass ratio of group j, n is the number of groups, DC_{ji} (−) is the contribution of prey i in the diet of predator j, and EX_i (t/km^2) is the export of group i.

Based on their feeding habits, fish can be categorized into several groups: planktivores, planktivores/benthivores, benthivores, benthivores/piscivores, piscivores, omnivores, detritivores and herbivores. In Lake Chaohu, small-sized fish are dominated primarily by small pelagic and planktivorous fish, including *Coilia ectenes taihuensis* and *Neosalanx taihuensis*. Large-sized fish include piscivorous fish (e.g., *Erythroculter ilishaeformis*), planktivorous fish (e.g., *Aristichthys nobilis*), benthivorous fish (e.g., *Mylopharyngodon piceus*), herbivorous fish (e.g., *Ctenopharyngodon idella*), and omnivorous fish (e.g., *Hypophthalmichthys molitrix*, *Cyprinus carpio* and *Carassius auratus*). We defined 24 functional groups in total for the Ecopath model in Lake Chaohu based on a previous study of the food web structure of Lake Chaohu (Zhang et al., 2012). All important biota components are covered by these 24 groups. We separated the phytoplankton group into three sub-groups, i.e., Cyanobacteria (Cyan), Chlorophytes (Chlo) and Bacillariophytes (Baci), and added a new group accounting for macrocrustacean shrimp (MacS). For each model, the input data included biomass in certain period of time (B), the landings of fishery, diet composition, the parameter values for the production/biomass ratio (P/B), the consumption/biomass ratio (Q/B) and the ecotrophic efficiency (EE) for each functional group. The landing data were collected primarily from peer-reviewed publications, stock assessments and government reports. Biomass was estimated based on the quote of landing data and estimated fishing mortality (Liu et al., 2014). P/B and Q/B