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Application of subfossil cladocerans (water fleas) in assessing ecological resilience of shallow Yangtze River floodplain lake systems (China)

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Abstract Majority of shallow floodplain lake ecosystems of the middle and lower reaches of the Yangtze River (China) have gone through serious eutrophication problems over the recent past. The severe environmental deterioration accompanied by cyanobacterial blooms have become major water resource management challenges in the region. An advanced research method is urgently needed to tackle these challenges. The concept of ecological resilience address pressing questions of non-linear dynamics, threshold effects and regime shifts in shallow floodplain lakes, and help manage the ecosystem effectively. Palaeolimnological techniques are important for assessing long term resilience and associated thresholds effects of shallow lake ecosystems. However, the lack of reliable proxy methods available, the assessment of long term ecological resilience of shallow Yangtze River lake systems has become increasingly difficult. Cladocerans (water fleas) play a central role in lacustrine food webs by responding to external drivers and internal ecosystem processes in lakes. Their subfossils are well preserved and becoming one of potential proxy indicators of lake ecosystems change for a longer time scale. This study explores the potential application of subfossil cladocerans and their ephippia in assessing a long term ecological resilience and help better management strategies of lake ecosystems and water resources of the middle and lower reaches of the Yangtze River in China.

Keywords Subfossil cladoceran, Yangtze River lake system, Food web, Ecological resilience, Regime shift, Threshold

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1. Introduction

The occurrences of alternative stable states behaviour are well documented phenomena in many shallow floodplain lakes of the large river systems worldwide (Scheffer et al., 1993; Hilt et al., 2011; Kattel et al., 2016). When shallow lakes are exposed to multiple environmental forces such as land use change, nutrient loading, fisheries activities and climate change, the cumulative impacts of these forcing can lead to non-liner responses of ecosystems (Scheffer and Carpenter, 2003). Better understanding of the mechanism behind such complex, non-linear ecosystem processes can help maintain ecological resilience of these lakes (Folke et al., 2004). Resilience is a degree in which a system is capable of self-organizing, when exposed to stressors (Holling, 1973). In growing environmental pressures, resilience can erode rapidly and the self-repairing capacity of ecosystems may be weakened, and the desirable goods and services of the ecosystems can also be lost (Folke et al., 2004). For example, a highly eutrophic, turbid lake system has limited

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value for drinking water, recreation and fisheries due to poor water quality. Resource managers are willing to achieve the clear-water state by putting more efforts to minimize the nutrient loads. However, the positive and negative feedback mechanisms in the lake system significantly hamper the successful management efforts for maintaining the ecological resilience (Folke, 2003).

In shallow lakes, the clear water, macrophyte-dominated state prevails at low nutrient levels, while the high level of nutrients is found at turbid water state with dominant phytoplankton (Scheffer and Jeppesen, 2007). The stabilization of clear water state and increased water transparency is strongly supported by sub-merged macrophytes (van Nes et al., 2002; Ibelings et al., 2007; Ziegler et al., 2015) by reducing sediment resuspension, trapping periphyton and competing for nutrients with algae and providing a refuge for zooplankton against fish predation (Jackson, 2003; Hilt et al., 2011). However, the turbid water state, where the dense bloom of filamentous algae can increase shading effects on underwater vegetation. The absence of under water plants and the feeding behaviour of benthivorous fish facilitate wind-driven sediment resuspension and increase eutrophication (Brönmark et al., 2010). An abrupt transition can occur any time when the intensity of external drivers exceeds a threshold that defines the limit (benchmark) of the capacity of feedback mechanisms to maintain stability of lake ecosystems (Figure 1). The alternative stabilizing factors also tend to remain in the same state despite the changes in external conditions, a process called 'hysteresis' and is dependent on resilience of the lake system (Carpenter and Cottingham, 1997). Hence, a resilient system is assumed to absorb disturbance without shifting to an alternative stable state (Folke et al., 2004).

The shallow lake systems in the middle and lower reaches of the Yangtze River are highly productive lake systems, which show increased interactions among physical, chemical and biological assemblages (Guo et al., 2013). Fisheries have been widely practiced in these lakes over the past century with strong cascading effects on trophic levels affecting dynamics of algal and submerged macrophyte populations. Overstocking of carps in many Yangtze River lake systems has caused intense water quality problems due to loss of submerged macrophytes and subsequent increase in algal biomass (Guo et al., 2013). The increased mobilization of

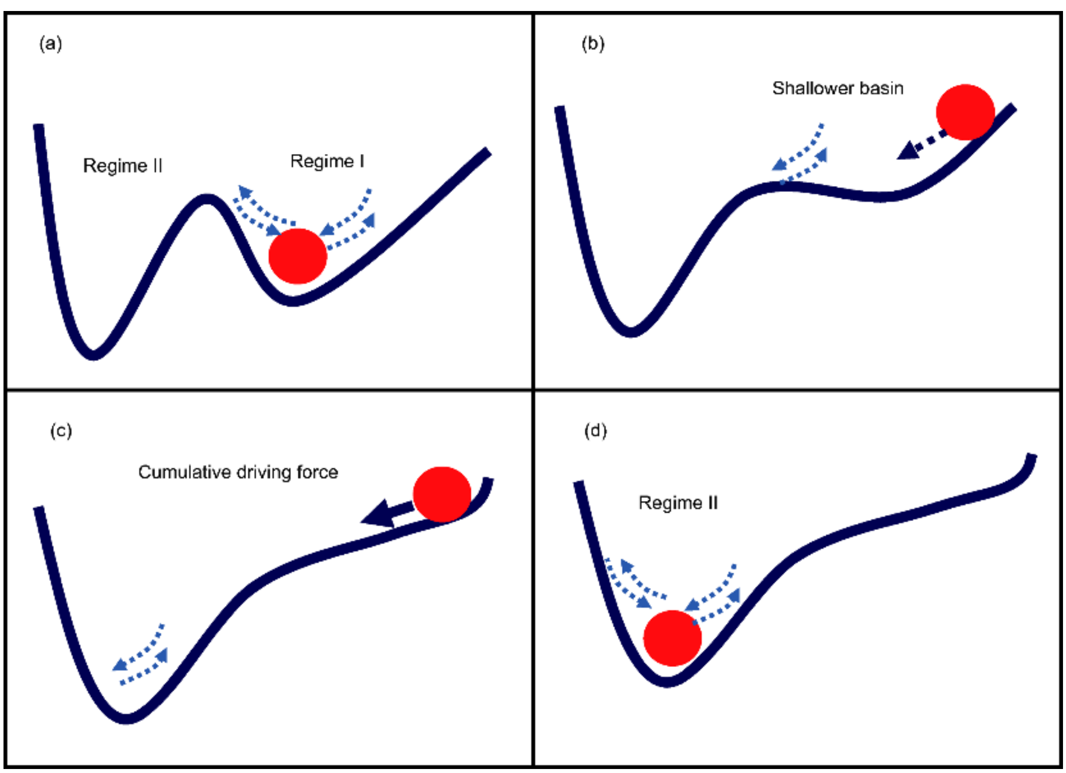


Figure 1 Schematic representation of the loss of positively consorted ecological resilience and regime shifts in shallow lakes caused by external driving forces and internal feedback mechanisms (adapted after Deutsch et al., 2003). Water clarity (a) remains stable until the nutrient loading (b) is exacerbated by, for example, extreme flood events (c) consequently pushing the system beyond a critical threshold when the lake shifts abruptly to a turbid or eutrophic state (d). The red ball represents the system moving from one regime to the other (or the basins of attraction). Cumulative changes in system variables can lead to a gradual loss of resilience the depth of the basin becomes shallower up to a point where even a small disturbance can push the system into a new basin of attraction, under a different regime. When a system shifts into a new regime, it reaches and is kept in a new state by internal feedback dynamics characteristic to that regime. This makes the recovery to the previous regime is very difficult, especially when lag effects in the system's response hinder its recovery (i.e., hysteresis, also see Figure 3). Transitions associated with drivers acting of shorter timescales may be cyclical in nature where the system resilience can be managed. However, those drivers acting over longer periods are less likely to get reversed (Lenton et al., 2008; Hughes et al., 2013).

nutrients from fisheries and catchments together with growing urbanisation and sewage disposal, all have profoundly implicated for the dynamics of macrophyte, zooplankton and fish populations in the region (Yin and Li, 2001; Wu et al., 2007; Yu et al., 2009; Guan et al., 2011; Zhang et al., 2012). Further, flow regulation by dams in rivers has disrupted natural hydrological regime and connectivity of lakes affecting the ecosystem processes (Yang et al., 2006). Many shallow floodplain lakes across the middle and lower reaches of the Yangtze River today are transformed into 'hypereutrophic' conditions with reduced ecological resilience (Liu et al., 2012).

Today, managing a lake together with the maintenance of ecological resilience of shallow Yangtze River lake systems has become an increasingly challenging task. A major problem is that lack of available long term monitoring data, which provide "anecdotal" support and offer improved understanding of underlying mechanisms of the lake ecosystem processes. In the absence of monitoring data, palaeolimnological methods provide the means to track centennial-and millennial-scale changes in the ecosystem structure and function of lakes, and help understanding the ecosystem responses to anthropogenic and climatic impacts. The palaeolimnological techniques are successfully applied for reconstructing past ecological conditions, and accurately tracked the regime shifts of shallow lakes in Europe and Australia (Davidson et al., 2010; Kattel et al., 2017). However, until recently, the multi-proxy application of lake sedimentary records for assessing ecological resilience of the Yangtze River lake system is rare.

Cladocerans (water fleas, Figure 2) play an intermediary role in food web structure and dynamics by showing strong sensitivity to lake environmental change (Persson et al., 2007; Kattel et al., 2008; Adamczuk, 2016). They transfer carbon energy and nutrient masses across the trophic system enhancing ecological stability and resilience (e.g. Figure 2; Post, 2002; Kuiper et al., 2015). The subfossil of cladocerans and their ephippial cover (Figure 2) are composed of chitin (chemical compound), which enables them to preserve in lake sediments after death (Korhola and Rautio, 2001). Hence, the ephippia, headshields, shells and post-abdomens of cladocerans retrieved from lake sediments have potential application for both qualitative and quantitative reconstructions of past environmental change and ecosystem processes over various time scales. For example, cladocerans have shown an extraordinary tolerance to low water temperature during the last glacial maximum (LGM) (Kattel and Augustinus, 2010) as well as resilience to progressive climate warming, catchment vegetation change, nutrient dynamics and eutrophication during the postglacial and the Holocene periods (Nevalainen and Luoto, 2012; Beck et al., 2018). Understanding of the long term ecological and hydrological processes and associated regime shifts of the shallow Yangtze River floodplains lakes using subfossil cladocerans can offer an excellent opportunity to assess ecological resilience of these lakes (Kattel et al., 2016). Cladoceran subfossils have been used to identify the deviation of lake ecosystems due to anthropogenic and other associated impacts including climate driven effects in the past (Jeppesen et al., 2001). However, the feedbacks, thresholds and resilience

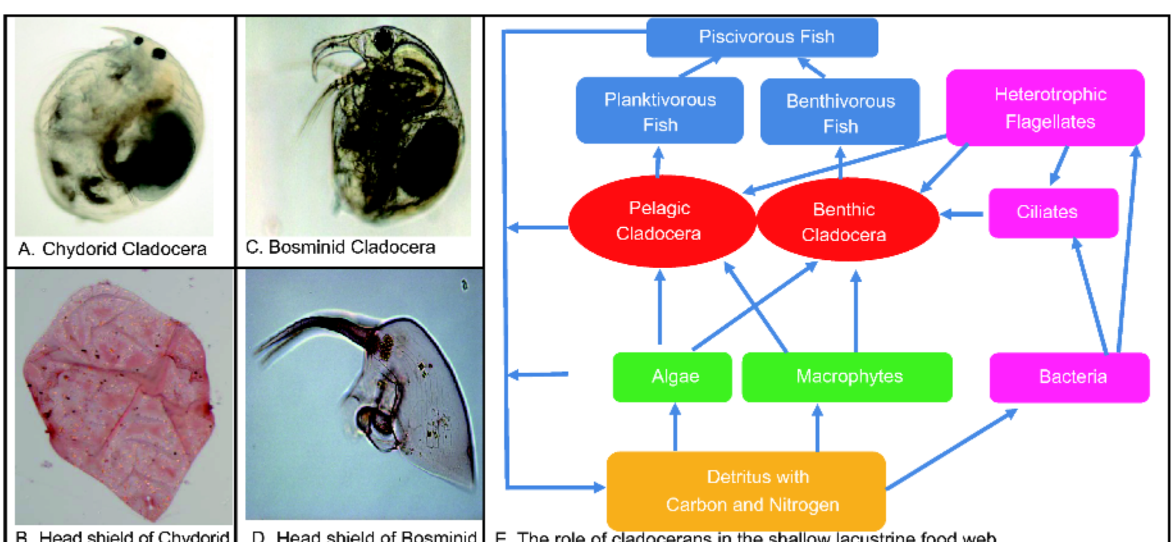


Figure 2 Cladocerans and their role in food web structure and dynamics of shallow large river floodplain lakes. A, B: Littoral species of Chydorid Cladocera (*Chydorus sphaericus*) and its fossil (Headshield of *Alona affinis*); C, D: Open water species of Bosminid Cladocera (*Bosmina coregoni*) and its fossil (Headshield of *Bosmina coregoni*). E: A simple schematic framework of the movement of carbon and nitrogen from the base of the food web, where cladocerans play a central role in carbon energy and nutrient mass flows via the macrophytes, algae and the microbial loop (bacteria, ciliates and heteotrophic flagellates) before transferring to the higher trophic levels such as planktivorous and benthivorous fish as well as piscivorous fish in shallow lakes. Carbon and nutrient mass will then recycled back to the system via detritus.

associated with ecosystem changes are not comprehensively investigated in the middle and lower Yangtze River system. Advancement of some methods using subfossil cladocerans and the stable isotope ratios of carbon and nitrogen extracted from chitin, have indicated the shift in ecological resilience due to changes in food web structure and functions of lakes in Europe and Australia during the past (Davidson et al., 2010; Perga, 2010; Kattel et al., 2014). Here, we explore the state of resilience of the middle and lower reaches of the Yangtze River lake system in China as well as the potential application of subfossil cladocerans and the stable isotopes of carbon and nitrogen in assessing the long term ecological resilience.

2. Loss of ecological resilience of the middle and lower Yangtze River lake systems

Over the millennia, the complex floodplain lake ecosystems across the middle to lower reaches of the Yangtze River have made significant, ecological and economic contributions to the society (Cui et al., 2013; Xu et al., 2017). However, today these lakes have experienced significant ecological transformation due to severe climatic, ecologic and hydrologic shifts including widespread land reclamation, irrigation, and domestic and industrial water usage (Wu et al., 2007; Yu et al., 2009; Zhang et al., 2012). The construction of dams and water impoundments has altered downstream hydrological regimes, modified channel morphology, and predictive concomitant increase in erosion and sedimentation (Liu et al., 2013). The sediment and nutrient loads have reduced flood retention capacity and enhanced eutrophication (Kong et al., 2015). Particularly after the c. 1960s river regulation, the natural flow regimes of the Yangtze River that maintained flood pulses and the healthy wetlands, are profoundly disrupted (Zhang et al., 2012). The nutrient enrichment in lake systems is thought to have led to regime shifts from clear (positively resilient) regime to turbid and eutrophic (negatively resilient) state (Kong et al., 2015; also see Figure 3).

3. History of ecological thresholds in Yangtze River lake systems

Thresholds exist in nonlinear ecosystem, which tend to collapse from more desirable (e.g. good water quality) to less desirable (poor water quality) state (Folke et al., 2004; Groffman et al., 2006). Thresholds are also scale-dependent and caused by multiple drivers, demonstrating increased need for knowledge and analyses to address pressing issues of the management of ecological resilience (Briske et al., 2010).

The middle and lower reaches of the Yangtze River lake systems have experienced severe "shocks" over the past century (Table 1), which may have lead the system to cross the thresholds (e.g. exceedance of total nutrient limit). The first evidence of a dramatic decline in the lake area during the 1860s in the lower basin was reported by Du et al. (2011). The rapid decline in lake area coincided with periods of land reclamation and increased sediment deposition. During the 1950s, the total phosphorous enrichment in the Yangtze

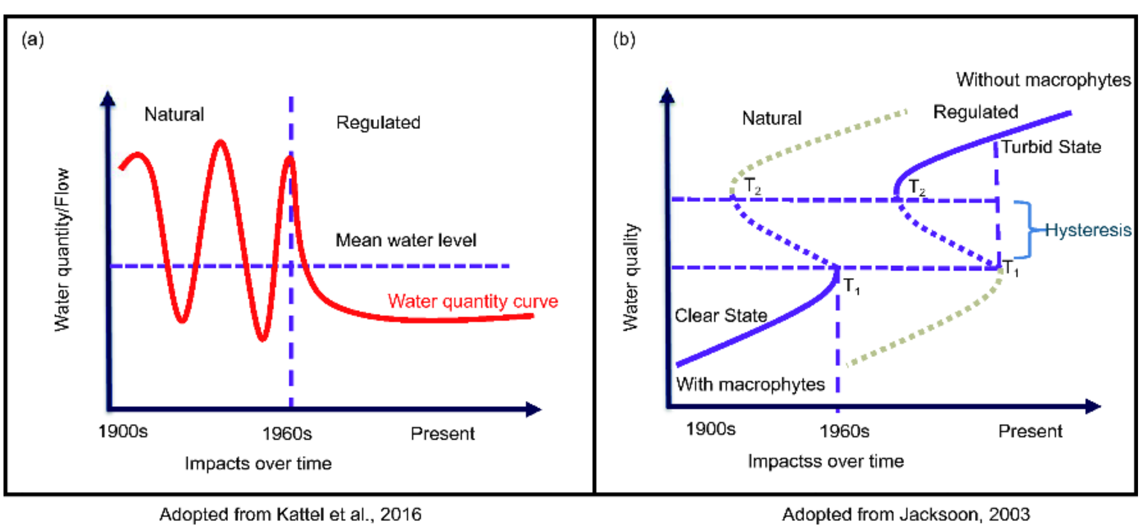


Figure 3 Conceptual frameworks on ecological resilience of the typical shallow Yangtze River floodplain lakes. (a) (Impacts over time vs water quantity) shows the changes in quantity of water or environmental flow regime (red curve) prior and after the river regulation over the past century. Following river regulation in the 1960s, many floodplain lakes have undergone lower water volume due to the construction of barrier in the upstream river and channel disconnectivity. (b) (Impacts over time vs water quality) shows the cumulative effects of nutrients on water quality and ecosystem regimes (blue curve). At around 1960 (T_1), the water quality and ecosystem began to switch from clear to turbid state. However, at the point T_2, the additional loads of nutrients (critical level) switched the ecosystem into a turbid state. The time between T_1 and T_2 (the dash line) is called 'hysteresis' when the ecosystem tried to recover to its original phase (clear water).

River lake systems exceeded 100 μg L^{-1} levels as a result of increased land use activities. These actions substantially reduced macrophyte density and benthic pathways of primary productivity (Zhang et al., 2012). The impacts on lake systems were severed during the Great Leap Forward (1960s). This period witnessed famine leading to widespread loss of natural resources across the catchments and increased eutrophication (Dong et al., 2012). By the 1970s, following the construction of dams and weirs in the river system, reservoirs and lakes were heavily used for commercial fisheries, which had significant implications for eutrophication and water quality (Guan et al., 2011; Kong et al., 2015). The economic reforms in the 1980s invested in development of water infrastructures leading to widespread ecological degradation (Dong et al., 2008). Further development in infrastructures in the 1990s significantly reduced river flow and river-lake connectivity resulting in unprecedented flood frequencies in the river system. The flood events have become catastrophic for lake ecosystems by bringing the large amount of carbon, salt, nutrients and sediments from the catchments (Wu et al., 2006). Since the early 2000s, the operation of large scale infrastructures such as the Three Gorges Dam (TGD) and the South to North Water Diversion Project (SNWDP) in the upstream Yangtze River system, have made basin wide changes of downstream habitats and ecosystem structure and function due to severe modification of river channels, hydrological flows and sedimentation (Sun et al., 2012; Akyuz et al., 2014; Yang et al., 2015; Huang et al., 2016). These large scale landscape level modifications for agricultural, industrial and urban development over the recent past are thought to have caused profound implications for ecosystem thresholds, regime shifts and resilience of the Yangtze River lake system (Kong et al., 2015; Table 1).

4. Application of subfossil cladocerans in assessing ecological resilience of the Yangtze River lake systems

Food-web theory increasingly elucidates the stability and resilience of shallow lake ecosystems. The presence of complex networks of trophic interactions in lacustrine ecosystems is thought to reflect the flow dynamics of carbon energy and nutrient masses across the system, which helps stabilize the ecosystem structure and functions for a longer period. Hence, the food webs provide an explicit link between the community structure and the maintenance of ecosystem processes in lakes (Kuiper et al., 2015). In this aspect, the cladocerans play a central role in food web structure, which is largely determined by the dynamics of nutrients, and fish and macrophyte community (Persson et al., 2007; Korosi et al., 2013). Increased nutrient loading and fish predation on larger cladocerans (such as *Daphnia*, *Eurycercus*), for instance, can induce eutrophication (Leavitt et al., 1989; Jeppesen et al., 2001). Pelagic *Daphnia* and *Bosmina* can depress microbial densities including bacteria, ciliata and heterotrophic nano-flagellates (DeMott, 1982) and contribute to food web, carbon cycling and nutrient remineralization (Adamczuk, 2016; also see Figure 1). However, due to variations in body size, food preferences and cyclomorophosis as well as the interactions with planktivorous fish, *Daphnia* and *Bosmina* can mobilize planktonic food webs and ecosystem processes differently. While *Daphnia* is selected primarily by planktivorous fish, smaller size *Bosmina* is vulnerable to invertebrate predation (Jeppesen et al., 2001). However, in absence of *Daphnia*, fish may rely on larger *Bosmina*. The competition for food resources for example phytoplankton dynamics and complex predator-prey interactions increase when both planktonic species co-exist (Korosi et al., 2013). Benthic cladocerans, on the other hand, also utilize the detritus and littoral submerged macrophyte community and significantly contribute to the predator-prey interactions in the benthic environment (Whiteside and Swindoll, 1988; de Eyto et al., 2003).

Hence, any deviation of planktonic and littoral cladoceran habitats can alter primary production, trophic pathways and food web dynamics (Liu et al., 2006). Both littoral and planktonic cladocerans are also able to reflect the internal dynamics (energy and nutrient mass flows) of the lake systems (e.g. Carpenter and Brock, 2004). In absence of monitoring data, subfossil cladocerans can have potential to infer the long term internally-mediated palaeo-food web structure and trophic dynamics of lakes (Leavitt et al., 1989; Jeppesen et al., 2000, 2002; Kattel et al., 2014). For instance, variability in mandible size (Kerfoot, 1974), length of carapaces and mucro of *Bosmina* (Hann et al., 1994; Alexander and Hotchkiss, 2010), ephippial size (Schilder et al., 2015a) and the proportion of *Daphnia* to total abundance of *Daphnia* and *Bosmina* (Kitchell and Kitchell, 1980) can show strong cascading effects of fish predation on cladoceran community. Studies suggest that lakes with moderate fish predation of planktivorous fish usually contain cladocerans (*Bosmina*) with short mucros (Korosi et al., 2013). Similarly, shift in the remains of Bosminid with long-appendaged morphotype to a short-appendaged morphotypes infer presence of dominant predators in the lake (Kerfoot, 1981). Extended dominance of forma cornuta is a response to low invertebrate predation, where the proportion of cornuta to morphotypes with long Bosminid antennules is an indicator of fish predation (Adamczuk, 2016). Increased composition of the remains of *Bosmina longirostris* in shallow lakes indicates elevated nutrient loads and eutrophication (Nevalainen and Luoto, 2012; Nevalainen et al., 2013). The replacement of the remains of *Bosmina coregoni* and *Bosmina longispina* by *B. longirostris* suggests the succession of clear water lakes into the eutrophic state (Adamczuk, 2016).

Table 1 Chronology of "shocks" and possible threshold effects on ecosystems of the Yangtze River lake system over the past century

Year	Shocks/Events	Possible threshold effects in lakes	Reference
1860s	Channel modification	Changes in sediment-water fluxes	Du et al., 2011
1950s	Use of fertilizer for agriculture	Increased load of total phosphorous	Zhang et al., 2012
1960s	Great Leap Forward	Famine and widespread loss of natural resources	Dearing et al., 2012
1970	Increased reservoirs and commercial fisheries	Eutrophication and changes in water quantity	Kong et al., 2015
1980s	Economic reforms, investment in agriculture	Increased ecological degradation	Dong et al., 2008
1990s	Large decline in flows and increased flood frequency	Mesotrophication to hyper-eutrophication of lakes	Wu et al., 2006
2000s	Rapid economic growth, large scale infrastructure development, operation of the Three Gorges Dam	Large scale aquatic habitat loss, impacts on fish movement, reduced ecosystem functioning	Sun et al., 2012 Huang et al., 2016
2010s	Large scale infrastructure development, operation of the south-to-north water transfer project	Significant downstream decline in water and sediment discharge	Akyuz et al., 2014 Yang et al., 2015

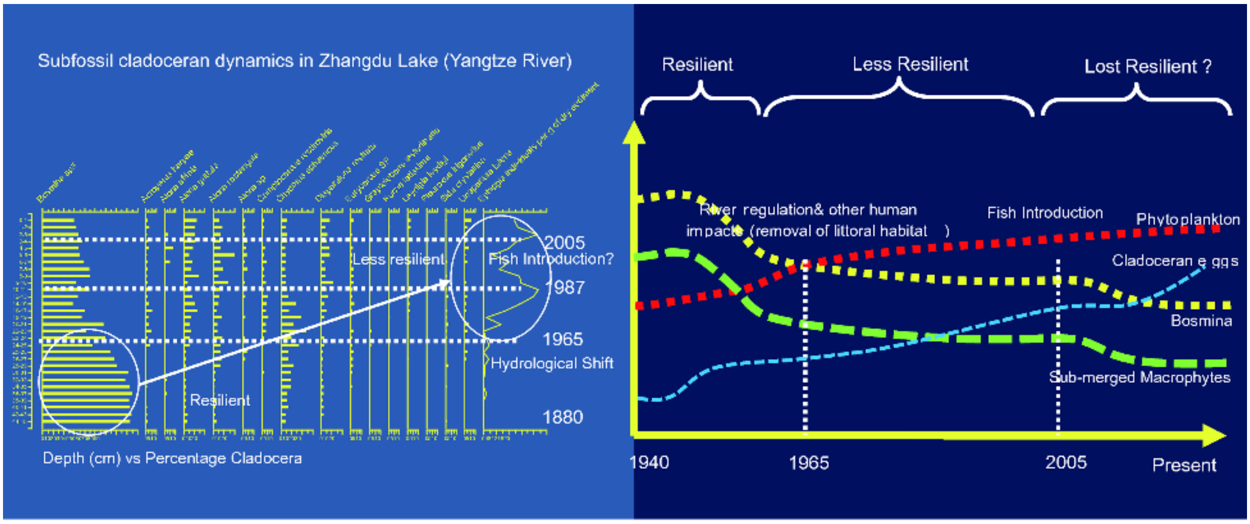
Bosmina coregoni and *B. longirostris* are dominant cladocerans, and the proportion of their remains is directly preserved in sediments of the Yangtze River lakes (Sun et al., 2012; Kattel et al., 2016). The proportion of the microfossils of *Bosmina longirostris* to the sum of *B. longirostris* and *B. coregoni* can serve as significant indicators of past changes in fish predation (Jeppesen et al., 2001). However, reconstruction of past food web based on *Bosmina* remains is difficult since Eubosmina is a species-complex of different species of cladocerans, such as of *Bosmina coregoni* and *Bosmina longispina*. As the body size including the length and shape of mucros and antennules of Eubosmina are largely determined by predation pressure of fish and invertebrates, identification of the remains of *Bosmina* based on species-specific predation by fish and feature of body parts makes difficult to detect shift of ecological resilience (Korosi et al., 2013). In addition, a number of abiotic factors (nutrients, pH, heavy metals and temperature) also influence the size and shape of cladocerans and their ephippia, and makes reconstruction of past food webs and ecosystem structures is difficult based on their remains. Further, cladoceran ephippia have potential to provide information regarding fish populations, feeding patterns and disturbances in the past. An inverse relationship between the density of fish and the concentration of *Daphnia* ephippia in sediments can be used for reconstruction of fish populations (Jeppesen et al., 2001). Similarly, the hatchability of fossilized ephippia isolated from the sediments can aid reconstruction of genetic changes associated with environmental perturbations including toxic algal blooms and inputs of toxic substances (Jeppesen et al., 2001). However, records available on long term dynamics of cladocerans and their ephippia in the middle and lower reaches of the Yangtze River lakes are rare. In addition, poor preservation of subfossil *Daphnia* in sediments is hindering the comprehensive understanding of a long term ecological resilience in the region.

River regulation, increased land reclamation and the use of fertilizers across the middle and lower reaches of the Yangtze River lake systems during the 1960s had considerable implications for river-lake connectivity, water depth and lake habitats. A framework (Figure 4a and b) for changes in ecological resilience is developed based on various studies in the region (Guo and Li, 2003; Dong et al., 2008; Guan et al., 2011; Kattel et al., 2016). For example, Kong et al. (2016) reported a decline of food web structure dynamics and ecosystem functioning of Chaohu Lake during the 1950s, 1980s and 2000s, where different functional groups indicated decreasing biodiversity and trophic interactions. Similarly, in Lake Taihu, since the 1980s, the chemical oxygen demand, the TP and TN all have increased with corresponding decline in littoral macrophytes, increased sediment resuspension, poor water quality and increased biomasses of phytoplankton and smaller zooplankton (Zhang et al., 2006; Guan et al., 2011). The palaeolimnological study of cladocerans in Zhangdu Lake by Kattel et al. (2016) has also showed that species preferring to shallow and nutrient rich water bodies such as small *Alona* (*A. guttata*) and their ephippia prevailed the system following the anthropogenic disturbances in the region. Climate change, river regulation together with eutrophication and intensive fisheries activities were thought to have played a major role. The cumulative effects, particularly after the early-to-mid-2000s may have caused significant loss of sub-merged vegetation and growth of phytoplankton leading to unprecedented eutrophication (Guan et al., 2011; Zhang et al., 2016). The widespread cage culture activities have enriched the exogenous nutrients such as TN and TP in the lake water. The food residues of fish from the cage were reported to release as high as 1532.9 kg (TN) and 339.2 kg (TP) within the 1000m^2 areas showing reduced diversity, composition and biomass of cladocerans (Guo and Li, 2003). In the recent past, the nutrient enrichment together with increased lake water temperature has led to the succession of cyanobacteria, such as *Mycrocystis* community in Lake Taihu (Deng et al., 2014; Shi et al., 2017). Diversity and composition of *Daphnia* sp. in Yangtze River lakes are rarely reported. However, a few studies, suggest that increased human activities and environmental changes may have led to genetic divergence of *Daphnia* *pulex* in the region. About 9% and 10.5% average genetic divergence of *D. pulex* found in 10 water bodies of the middle and lower reaches of the Yangtze River indicate that the species may have evolved into different subspecies due to the regional environmental changes (Wang et al., 2016). *Daphnia* no longer co-exists in lakes exposed to prolonged eutrophication. For example, the Taihu Lake show that smaller cladocerans, *Bosmina coregoni* and *Ceriodaphina cornuta* are dominant during *Microcystis* bloom indicating *Microcystis* may be favoured largely by these small-sized cladocerans (Sun et al., 2012). An analysis of cladoceran remains from Lake Taihu, also show that more than 95% of total cladocerans in the lake are composed by *Bosmina* (*B. coregoni* and *B. longirostris*). Retrieve of increasing number of cladcoeran ephippia from the sediment of Zhangdu and Liangzi Lakes (Kattel et al., 2016) together with toxic cyanobacterial bloom of *Mycrocystis* in Taihu and Chaohu Lakes (Sun et al., 2012; Kong et al., 2016) are an indicative of ecological stress and reduced resilience (see Figure 4). Studies suggest that cladocerans produce ephippia at a time of stress (Kattel et al., 2017).

In addition, cladocerans are also found to be powerful indicators for the internally-mediated food web structure and dynamics (carbon energy and nutrient mass flows across the trophic levels as shown by δ^{13}C and δ^{15}N values) in the past in Europe, Australia and North America (Struck et al., 1998; Post, 2002; Perga and Gerdeaux, 2006; Frossard et al., 2014; Kattel et al., 2014). The cladoceran community in the Yangtze River lake system is likely to be dependent on multiple sourced-food webs (Liu et al., 2006; Guo et al., 2013). Littoral cladocerans are dependent largely on detritus and macrophyte-derived-food from shoreline habitats, while the planktonic *Daphnia* and *Bosmina* are predominantly supplied by open water phytoplankton. Unravelling the internally-mediated food webs by advancing the more sophisticated methods of subfossil cladocerans would be crucial for the assessment of long term ecological resilience of these lakes (e.g. Kuiper et al., 2015).

5. Development of a conceptual framework on cladoceran-inferred internally-mediated food web dynamics and ecological resilience in Yangtze River lake system

Cladocerans show contrasting food and micro-habitat preferences (Jeppesen et al., 2001). A shift in functional group of these animals is an indicative of changes in food web structure and dynamics in an ecosystem over temporal and spatial scales (Jeppesen et al., 2001; 2002; Korosi et al., 2013; Liu et al., 2013). Stable isotope values of carbon and nitrogen (δ^{13}C and δ^{15}N) in subfossil cladocerans (e.g., Chydorids, Daphnids, Bosminids) provide one of the most sophisticated insights into the source of energy and nutrient mass flows in the food web (Post, 2002; Perga and Gerdeaux, 2006; Perga, 2010; Frossard et al., 2014; Kattel et al., 2014; Schilder et al., 2015b). A conceptual framework (Figure 5) is developed for an internally-mediated cladoceran-inferred food web structure and dynamics and ecological resilience of the Yangtze River lake systems. Unfortunately, no data are available on the δ^{13}C and δ^{15}N values of subfossil cladocerans in the region. However, with a view to improve the framework in future, the dynamics of the δ^{13}C and δ^{15}N values in shallow lake organic sediments in the region and elsewhere have been assessed (Wu et al., 2006; Kattel et al., 2014; Mao et al., 2012, 2014; Xu et al., 2016). Prior to the 1960s, existence of a diverse macrophyte-rich lake (resilient) system prevailed supporting the benthic chydorids, as well as the planktonic daphnids (Cui et al., 2013). In a resilient ecosystem, the increased standing phytoplankton biomass will be limited by *Daphnia* grazing and a macrophyte-dominated food web will persist in presence of light (Folke, 2003; Zhang et al., 2016). The increased abundance of biota also reflects their reproductive success and biological diversity. The δ^{13}C and δ^{15}N extracted from subfossil Chydorids and Daphnids can provide precise information of diet predominantly derived from the littoral submerged vegetation as well as planktonic algae (Kattel et al., 2014). However, nitrogen enrichment in cladocerans (mostly Bosminds and smaller Chydorids) may be evident when the lake is eutrophic and devoid of submerged macrophyte. In a shallow hypereutrophic lake, study suggests that plantkivorous fish would receive as high as 85% of δ^{15}N enriched zooplankton diet (Gu et al., 1996). Following the 1960s, the increased catchment disturbances including land reclamation, growing fisheries activities and increased sediment resuspension across the shallow Yangtze River lakes substantially altered the lake habitats and ecosystem processes (Zhang et al., 2006; Yang et al., 2015). An increased predation pressure by piscivores on planktovores, for example, can increase the impact on photic zone, as the control of *Daphnia* and chydorid cladocerans by planktivorours and benthivorous fish will be limited, inducing the growth of submerged macrophyte community or vice versa (Jeppesen et al., 2001). Data also suggest that fish such as carps can significantly affect species abundance and diversity of macrophytes and zooplankton and macro-invertebrate communities (Miller and Crowl, 2006; Kong et al., 2016). When the condition is persisted either way for a longer period an alternative stable state switch can occur in response to a shock with positive or negative feedback mechanism (Scheffer and Jeppesen, 2007). During the period of eutrophication (1960s–2000s), for example, the number of trophic species and trophic links in lakes are reported to have declined indicating that the food web structure of highly eutrophic lakes, such as Taihu had significantly low available carbon energy flow (Xu et al.,



Adopted from Kattel et al., 2016, Guo et al., 2013; Mao et al., 2012, 2014

Figure 4 Ecological resilience of the Yangtze River floodplain lake systems over the past century based on the evidence of fossil cladocerans in Zhangdu Lake (a) over the past century as well as the conceptual framework on the loss of resilience following the various literature reviews (b). The hydrological shift caused by river regulation in the1960s led to reduced water level followed by decline in the abundance of *Bosmina* (planktonic species) and increased concentration of cladoceran ephippia (left panel). Meantime, the increased abundance of small *Alona* (*A. guttata*) indicated eutrophication prevailing high density of phytoplankton and loss of sub-merged macrophyte density. Introduction of phytovorous and other omnivorous fish (e.g. carps) in some lakes may have triggered the loss of macrophyte density and reduced the ecological resilience further (right panel).

2016) while with rich nitrogen mass transfer in Longgan Lake from the base of the food web (Wu et al., 2008). Mao et al. (2014) reported more depleted δ^{13}C and enriched δ^{15}N isotope values of organic matter sources and consumers such as zooplankton (other than cladocerans) were found in the phytoplankton-dominated lake region than in the macrophyte-dominated region of the Lake Taihu. Such transformation of the depleted carbon energy, and enriched nitrogen mass from the base of the food web is likely to influence the more susceptible species (e.g. littoral chydorids) to extinction when eutrophication causes decline in their food sources (Xu et al., 2016). However, it is important to note that the dynamics of δ^{13}C and δ^{15}N isotope values in consumers including cladocerans in shallow Yangtze River lakes are largely dependent on the source of primary producers, which are influenced by various factors including type of littoral zone, suspended particles in the open water zone, catchment vegetation and land use change practices, seasonal changes, fish-zooplankton interactions and discrimination of carbon and nitrogen during assimmilation. For example, Wu et al. (2007) found differences in δ^{13}C and δ^{15}N enrichments in C_3 plants and organic soil dominated catchments. Li et al. (2010) reported the δ^{15}N enrichment in Yangtze River was from the high livestock waste release into the water. Mao et al. (2014) found that the suspended particulate organic matter contributed to depleted δ^{13}C and enriched δ^{15}N values among consumers in Taihu Lake. However, Wu et al. (2006) argued that the ^{13}C-enrichment of organic matter may also occur at periods of high productivity with limited aqueous CO_2 availability, causing a decrease in isotopic discrimination during photosynthesis.

Hence, the study of stable isotopes of carbon and nitrogen in subfossil cladocerans (Chydorids, Daphnids, and Bosminids) is significant, and can potentially reveal feedbacks at the molecular level over a temporal scale (Perga, 2010). Various literature suggest that the ecological resilience of the Yangtze River lake systems is thought to have declined significantly since the early 2000s as a result of the cumulative effects of multiple stressors including rapid development of infrastructures, commercial fisheries, and recent climate warming episodes (Mao et al., 2012, 2014; Kong et al., 2015). The widespread impacts on Yangtze River lake systems today have led to a new variant of cyanobacterial growth altering water quality, increased toxicity and health hazards in the local people (e.g. Zhang et al., 2009; de Kluijver et al., 2012). The application of subfossil cladoceran assemblages, their diversity as well as carbon and nitrogen stable isotopes extracted from their remains could be potentially powerful tool to assess ecological resilience, thresholds effects and regime shifts of the Yangtze River lake system over the longer time scale.

6. Conclusions

Conservation and management of biodiversity and ecosystem structure and function should be regarded as one of important management strategies for maximizing the large river floodplains lake ecosystems resilience and ecosystem services. Coupled human-climate disturbances have con-

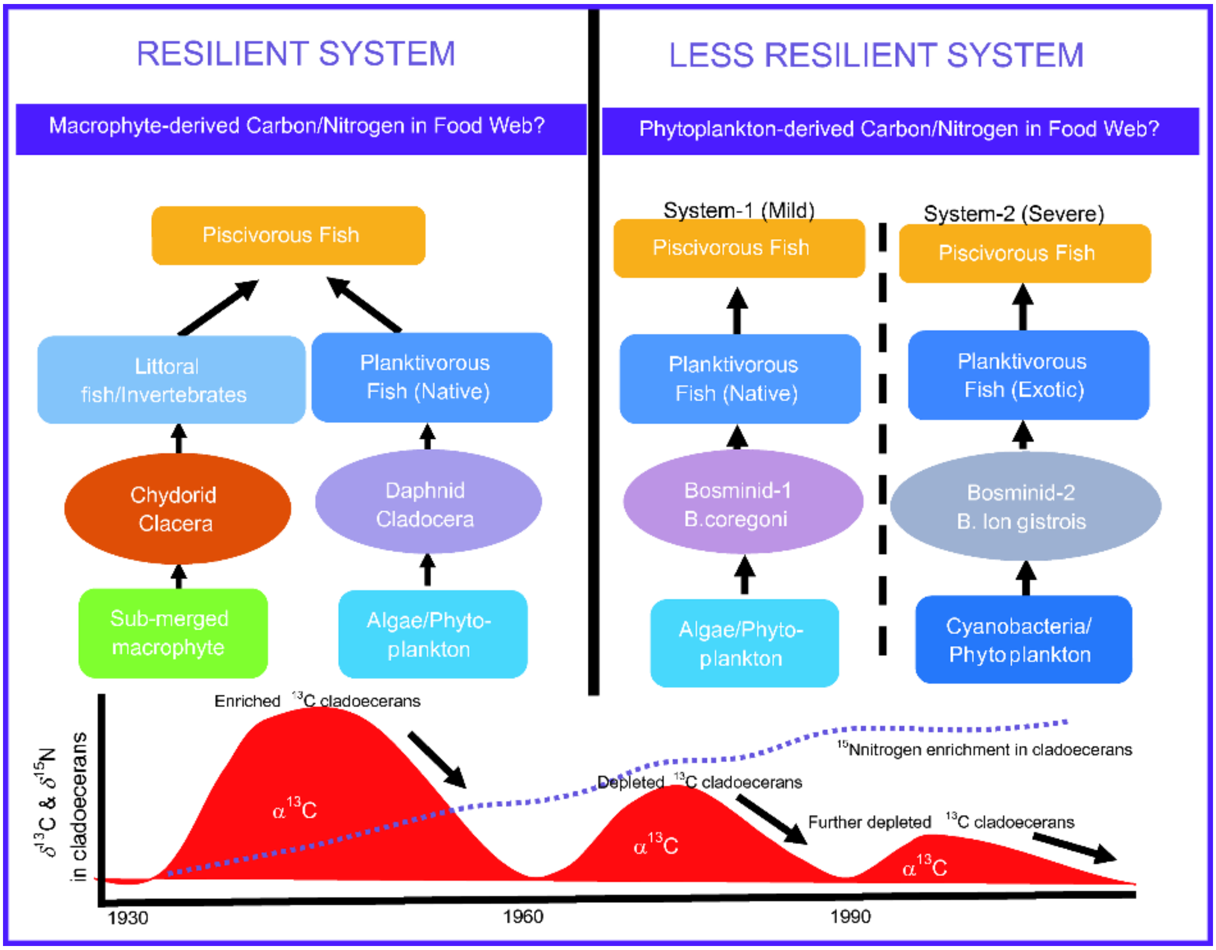


Figure 5 Development of a simple conceptual framework (after literature review) on carbon energy flow (δ^{13}C) and nitrogen mass transfer (δ^{15}N) in the food web of the shallow lowland eutrophic lake systems in the middle and lower Yangtze River, where the three functional groups of consumers (Chydorid, Daphnid or Bosmind) of cladocerans are thought to play a key role (see text for further details). Prior to the 1960s, the ecosystem was resilient, where the carbon energy flow from the base of the food web was considered relatively high (^{13}C-enriched cladocerans). Carbon derived from the submerged macrophytes and good quality algae were assimilated by benthic Chydorids and large filter feeding cladocerans (Daphnids), subsequently transferring to the higher trophic levels. However, following the 1960s, Daphnids and Chydorids are gradually replaced by smaller consumer zooplankton such as Bosminids (mesotrophic and eutrophic species) feeding preferentially ^{15}N enriched cyanobacteria (also see Mao et al. 2014). Further pressures in the system, such as the commercial fisheries activities during the 1990s and after, and development of infrastructures (dams and weirs in the river), have made positive feedbacks in the system with widespread loss of macrophyte community enhancing the cyanobacterial bloom such as *Mycrocystis* (e.g. Zhang et al., 2009) with depleted ^{13}C, but enriched ^{15}N, transferring primarily to Bosminids (*B. coregoni*) then to the higher trophic levels (also see Figure 2).

siderable implications for degradation of shallow floodplain lakes ecosystems in the middle and lower reaches of the Yangtze River. Rehabilitating these lakes as a healthy, functioning ecosystem is becoming increasingly challenging task as a result of the cumulative effects of multiple stressors. Palaeolimnology offers an excellent opportunity to understand the threats posed by external driving forces as well as the intrinsic ecological processes. Assessment of ecological resilience is essential to recognize disturbances in the past and associated feedback mechanisms, threshold effects and regime shifts. Subfossil cladocerans play a central role in the lake ecosystems and food web structure and dynamics through carbon energy and nutrient mass flows across the trophic levels. The fossil assemblages, diversity and the stable carbon and nitrogen isotopic records of cladocerans have potential application for assessing long term ecological resilience. The conceptual framework presented in this study is the first step to advance the method in their application in both temporal and spatial scales of the Yangtze River lake systems. The advancement of such sophisticated techniques is urgently needed to tackle the growing challenges of the water resource management and the maintenance of ecosystem services in the lower Yangtze River basin.

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