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Effects of hydrologic regulation on icefish population dynamics, assemblage structure and fishery yield in Lake Nanyi, China

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Abstract – Stock dynamics and demographic parameters of a family of annual icefishes (Salangidae) were investigated in Lake Nanyi in eastern China before and after construction of irrigation infrastructure. After hydroregulation, two of four icefish species, a migratory species (*Hemisalanx brachyrostralis*) and a previously rare species (*Neosalanx tangkahkeii*) were absent from survey samples. The relative abundance of the remained icefish stocks changed greatly. The spring and autumn stocks of *N. taihuensis* increased from 9.9% and 1.7% to 74.8% and 4.8%, respectively, and *N. oligodontis* decreased from 84.8% to 20.4%. Total icefish density (CPUE) and yield doubled under the new hydrologic regime. Average adult body size and absolute fecundity of the three persistent icefish stocks decreased, and this could have resulted from slower rates of growth and development of larvae and juveniles in response to greater density of icefishes overall and more intense competition for planktonic food resources during summer and fall.

Key words: biodiversity; dam; fishery; growth rate; habitat fragmentation; hydrology

Introduction

Anthropogenic changes to hydrologic processes have impacted ecological processes and fish species assemblages in fluvial ecosystems worldwide (Dynesius & Nilsson 1994; Fulton et al. 2011; Pool & Olden 2012). Dams and other water-control structures change natural flow regimes, alter the quality and quantity of aquatic habitats and reduce longitudinal and lateral connectivity of habitats within drainage basins (WCD 2000; Morita & Yamanoto 2002; Mims & Olden 2013). Reduction of longitudinal connectivity is a particularly severe problem for migratory fishes (Bain et al. 1988; Dudgeon 2000; Katono et al. 2006), but lateral connectivity between the river channel and floodplain habitats also is critically important for many fish stocks worldwide (Agostinho et al. 2004; Poff & Zimmerman 2010). Following dam construction, fish community structure within the upstream impoundment will change, oftentimes radically, with lentic-adapted species becoming dominant (Park et al. 2003; Quinn & Kwak 2003; Arthington 2009). Frequently observed changes within newly regulated water bodies include shifts in body size and fecundity distributions of fish populations, changes in fishery yields and reduced value of fish catches (Weitzman & Vari 1988; Hanken & Wake 1993; Rũber et al. 2007; Hoeinghaus et al. 2009; Pool & Olden 2012).

Fish species with divergent life histories and habitat requirements generally respond in different ways to dam construction and resulting hydrologic modification (Zhong & Power 1996; Bradford et al. 2011; Mims & Olden 2012, 2013). Long-lived fishes have populations with age and size structures that are more complex than those of annual fishes, and therefore responses of the former to environmental alterations are more difficult to characterise (Gehrke et al. 2002; Duan et al. 2009). In contrast, annual fish populations generally are comprised of cohorts with limited age and size structure, which facilitates analysis of population dynamics (Wang et al. 2004). Changes in

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abundance of annual fish populations in response to environmental alteration can be rapid (Quist et al. 2005; Han et al. 2008), which makes them sensitive indicators of impacts, such as flow regulation. The relationship between flow alteration and population dynamics of annual fishes has rarely been investigated, and the present study examines this relationship with a family of annual icefishes (Salangidae) in Lake Nanyi in eastern China. Icefishes (Salangidae) are annual fishes with a lifespan of about 13 months (Wang et al. 2004). All icefish adults die after completion of spawning (Chen 1956). Larval recruitment and population abundance reveal high interannual variation in response to water-level fluctuations and the quality and availability of habitat during spawning periods (Zhu 1982; Liu & Zhu 1994; Tang et al. 2000; Islam et al. 2006).

Seventeen icefish species inhabit marine and inland waters in the northwestern Pacific region (Nelson 2006), but greatest species richness (five spp.) and commercial yield (>4000 metric tonnes) of icefishes are found in natural lakes within the floodplains of the middle and lower Yangtze River (Zhu 1982; Wang et al. 2005a, 2009). In Lake Nanyi, average yield of icefishes was 66.6 ± 54.6 (SD) metric tonnes over the past three decades, with a peak yield of 260 metric tones in 1982 (Wang et al. 2004, 2009).

Hydrology of the Yangtze River has been disrupted by extensive irrigation systems (Park et al. 2003; Stone 2008). Most floodplain lakes have lost their natural connectivity with the Yangtze River channel, and this has impacted fish species diversity in the lakes as well as the river channel (Xie & Chen 1999; Zhang & Zhao 2001; Xie et al. 2003; Duan et al. 2009). Over the past five decades, many fishes, including nonmigratory species, have been severely reduced in abundance within the river basin, and some have been extirpated (Zhong & Power 1996; Park et al. 2003). During the past three decades, the degradation of icefish populations has accelerated on a large scale within the mid-lower Yangtze as well as in the other river basins within their native range (Dou & Chen 1994; Tang et al. 2000; Islam et al. 2006; Wang et al. 2009). Some reports have identified localised overfishing as the primary cause for the overall decline and body size reduction in icefish stocks (Dou & Chen 1994; Wang et al. 2006), and others concluded that reduced icefish diversity was caused by habitat degradation and fragmentation within the river network (Wang et al. 2005b, 2009; Islam et al. 2006). These conclusions, however, are mainly based on short-term investigations. Here, we report results from a long-term investigation that analyses a multiyear data set of icefish stocks in Lake Nanyi to assess impacts of water-control infrastructure on wild fish assemblage. Icefishes were surveyed and environmental variables were recorded during two periods of 2001–2003 (preregulation) and 2006–2008 (postregulation), and demographic and life history variables were compared.

Methods

Study area

Lake Nanyi is located within the lower reaches of the Yangtze River, situated at 31°03′–10′ N, 118°50′–119°02′ E (Fig. 1). The lake surface area is 203 km^2

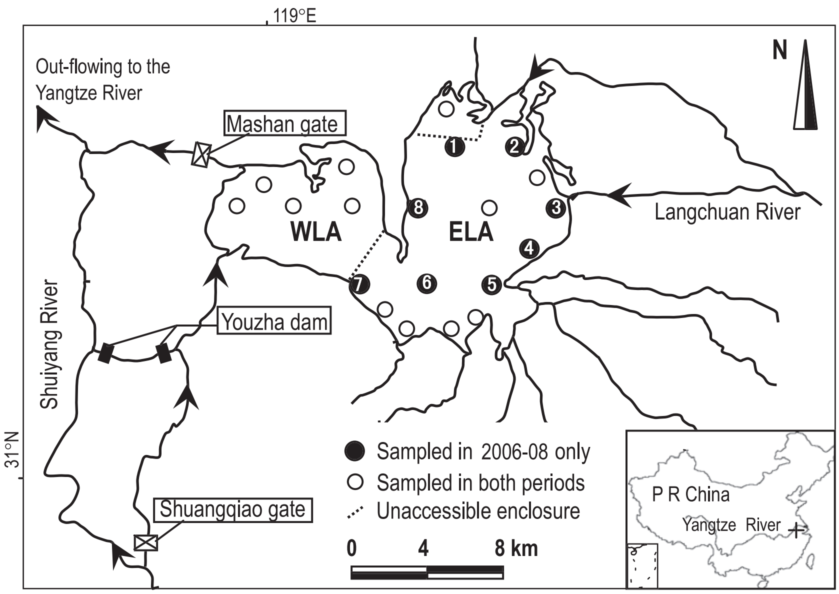

Fig. 1. Sketch map of Lake Nanyi, with the illustration of dams, weirs and icefish survey sites. WLA and ELA are the Western and Eastern Lake Area, respectively.

at median water level, and the lake has two main bodies, the Eastern Lake Area (ELA) and the Western Lake Area (WLA). The ELA is deeper and broader, with a sandy substrate that favours icefish spawning and development (Zhang 1987). The WLA is relatively shallow with thick beds of aquatic macrophytes and thus is not suitable for icefishes (Zhang 1987; Wang et al. 2004, 2006).

Water discharges northwest into the out-flowing Shuiyang River and then flows into the Yangtze River channel (Fig. 1). Since the spring of 2004, this natural connection between the Yangtze River and Lake Nanyi has been obstructed by the Nanyi flood-control engineering (NFCE) project. NFCE consists of the Mashan and Shuangqiao floodgates and two dams at the Youzha channel (Fig. 1). The Mashan floodgates regulate outflow from the lake, and the Shuangqiao floodgates regulate inflow from the upper Shuiyang River during the flood season. With flow regulation by NFCE, the water level has become more stable within the lake, with a lower summer peak and more water during the normally dry winter and spring (Fig. 2). Stabilized water levels facilitated growth and dispersal of aquatic macrophytes in the WLA and southern ELA.

Fish sampling method

Icefishes and environmental data were collected during two periods, 2001–2003 (preregulation) and 2006–2008 (postregulation). Twenty sites were sampled during the first period (Wang et al. 2004), and eight of the 20 sites were chosen for sampling during the second period. The other sites yielded lower densities of icefishes, and some of them were shallow and covered by dense beds of aquatic macrophytes that made boat access impossible (Wang et al. 2004; Fig. 1). Monthly sampling was conducted during August 2001–August 2002 and August 2006–August 2007, with additional weekly sampling at the key spawning ground of sites 4 and 5 during spawning

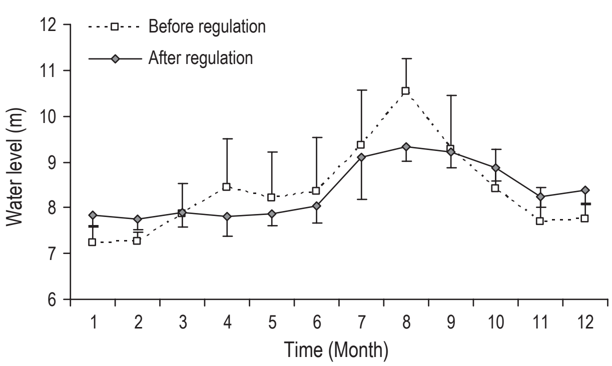

Fig. 2. Monthly variation of lake water level (Mean ± SD) before and after the construction of water-control infrastructure at Lake Nanyi.

period. These two sites had been identified as major spawning grounds for icefishes. During 2003 and 2008, icefish sampling was conducted in August only.

Icefishes were collected with a specially designed trawl during each survey. The trawl was 8 m long with a 4-m- × 1.2-m rectangular mouth and a 4-mm- × 4-mm mesh wings and a 1-mm- × 0.5-mm mesh cod end. Two trawl nets were towed simultaneously, one on each side of the vessel, at 2.8 $km \cdot h^{-1}$. A global positioning system (GPS) was used to mark locations of sampling sites and to monitor vessel speed. Duration of each trawl run was 30 min. The two trawls were combined as one sample, and the sample area at each site was approximately 11 200 m^2. Icefishes were identified to species immediately following capture. Individuals were counted (in the case of a low catch), or abundance was estimated (in the case of large catch) using the total weight and the mean body weight of 100 randomly selected individuals. CPUE (catch per unit effort) of a sample was estimated as the number of icefish specimens collected by the two trawl nets during one tow. A subsample of each sample was preserved in 5% formalin for subsequent laboratory analysis.

Data analyses

We estimated richness (S), relative abundance (P_i) and individual density (CPUE) of stocks (populations) rather than species based on taxonomy. This was because the species of *N. taihuensis* in Lake Nanyi is comprised of two populations with nonoverlapping spawning periods that, therefore, do not interbreed (Chen 1956; Wang et al. 2004). Relative abundance (P_i) was the percentage of the total icefish catch composed of population i. Analysis of P_i and CPUE was based on August samples to avoid bias from postspawning parental mortality, recruitment of the next cohort and mortality from commercial fishing that begins each year in September (Wang et al. 2004). A paired *t*-test was used to assess significance of CPUE differences between the 2001 and 2006 cohorts, representing typical pre- and postregulation year, respectively.

Commercial fishery yield data were examined to evaluate variation in icefish biomass across years and to determine if there was a relationship with hydrology. Icefish yield data were provided by the Municipal Bureau of Fisheries of Xuancheng, and water-level data were obtained from the Municipal Bureau of Hydrology of Wuhu. Annual icefish yield was regressed against mean water level in the lake during the icefish wintering and spawning seasons (December–March) to indicate the potential influence of water-level dynamics (Zhu 1982).

Body mass (g) and standard length (SL, mm) were measured on randomly selected formalin-preserved specimens, that is, *N. oligodontis* (NO), the spring stock of *N. taihuensis* (NTs) and autumn stock of *N. taihuensis* (NTa), from each survey period ($n_{NTs} = n_{NO} = 150$ fish, $n_{NTa} = 40$ fish). In this analysis, specimens of NTs and NO were collected in April of 2002 and 2007, and NTa specimens were collected in August of 2001 and 2006, respectively, when all individuals of these stocks were mature. Body size differences between different annual cohorts of the same stock were compared with a *t*-test.

Absolute fecundity of female icefishes was calculated by the total mass, and the mean mass of 100 randomly selected eggs of individual specimens preserved in formalin. To evaluate potential effects of hydrologic regulation and stock density on reproductive potential, the fecundity difference between the 2001 and 2006 cohorts of the three persistent icefish stocks ($n_{NTs} = n_{NO} = 50$ specimens, $n_{NTa} = 20$ specimens) were further compared, respectively, with analysis of covariance (ANCOVA). Because absolute fecundities of the three stocks were significantly correlated with body mass (simple linear regression, $P < 0.001$), the variable of body mass was used as covariate in ANCOVA to account for the potential influence of temporal change in the body size distribution. The spawning period of each stock was estimated as the interval between the first and last dates when early stage larvae (SL < 10 mm) were collected over the course of the weekly surveys. Statistical analyses were conducted with SPSS 16.0 (SPSS Inc., Chicago, IL, USA) and Microsoft Excel 2007 for windows.

Results

Assemblage structure

In the first sampling period of 2001–2003, four icefish species, *Neosalanx taihuensis* Chen (1956), *N. oligodontis* Chen (1956), *N. tankahkeii* Wu (1931) and *Hemisalanx brachyrostralis* Fang (1934), were collected from Lake Nanyi (Table 1). In addition, *N. taihuensis* had distinct cohorts that spawn during spring (NTs) and autumn (NTa). Given that the NTs and NTa have nonoverlapping spawning periods and do not interbreed (Table 1), five icefish stocks, or populations, were recognised within the lake. After construction of the irrigation infrastructure, the previously rare *N. tangkahkeii* and the migratory *H. brachyrostralis* were not collected during surveys, and the number of icefish stocks was reduced to three (Table 1).

Through the hydroregulation, relative abundances (P_i) of NTs, NTa and *N. oligodontis* (NO), changed, but patterns differed among stocks. The relative abundance of NO (P_{NO}), the previously predominant species, declined from a mean of 84.8 ± 1.4% (±SD) to 20.4 ± 4.1%. P_{NTs} increased from 9.9 ± 1.2% to 74.8 ± 4.3% between the two periods. Over the same

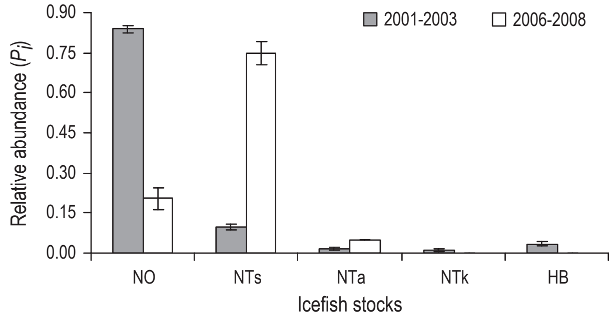

Fig. 3. Comparison of relative abundances (P_i) of the icefish stocks in Lake Nanyi before and after hydrologic regulation. Vertical bars indicate ± SD of the mean P_i of each population.

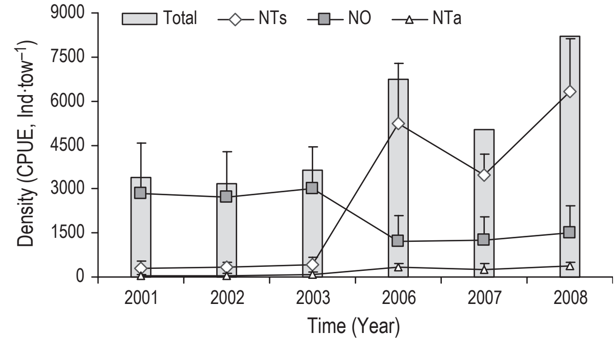

Fig. 4. Density (CPUE) of icefish stocks before (2001–2003) and after (2006–2008) hydrologic regulation. Vertical bars indicate + SD of mean CPUE of each population.

Table 1. Basic biological characteristics and presence/absence of icefish taxa in Lake Nanyi. + presence; – absence.

Taxa (Abbreviation)	Migratory or not	Occurrence 2001–2003	Occurrence 2006–2008	Spawning duration* 2001–2003	Spawning duration* 2006–2008
Neosalanx					
N. oligodontis (NO)	Resident	+	+	May 09–June 13	May 07–June 11
N. taihuensis Spring (NTs)	Resident	+	+	March 28–May 02	March 25–May 06
N. taihuensis Autumn (NTa)	Resident	+	+	September 27–October 11	September 22–October 06
N. tangkahkeii (NTk)	Resident	+	–	March 25–April 03	–
Hemisalanx					
H. brachyrostralis (HB)	Migratory	+	–	February 24–March 19	–

*Earliest to latest dates on which earliest larval stages were collected, based on weekly surveys.

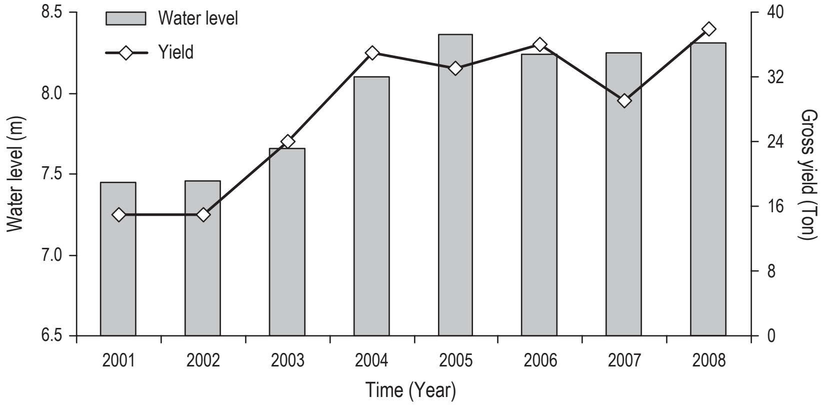

Fig. 5. Variation in the annual yield of the icefish commercial fishery of Lake Nanyi and its relationship with the fluctuation of mean water level in winter and early spring.

period, P_{NTa} became slightly more abundant, from 1.7 ± 0.7% to 4.8 ± 0.2% (Fig. 3).

Individual density and fishery stocks

Total icefish density (CPUE) increased significantly (paired *t*-test, $t_7 = 3.14$, $P_{\text{two-tailed}} = 0.016$) from 3377 ± 2015 (mean ± SD) ind·tow^{-1} in August 2001 to 6757 ± 2987 ind·tow^{-1} in August 2006, and then reached a peak of 8203 ± 2824 ind·tow^{-1} in August 2008 (Fig. 4). An increase in NTs density was apparent, from 339 ± 58 (mean ± SD) ind·tow^{-1} in 2001–2003 to 5015 ± 1425 ind·tow^{-1} in 2006–2008, which contributed greatly to the increase in total icefish density. Over the same period, NTa increased from <60 ± 28 to 318 ± 67 ind·tow^{-1}, whereas NO declined from 2853 ± 147 to 1322 ± 158 ind·tow^{-1} (Fig. 4).

After hydroregulation, icefish fishery yield (*Y*) increased from 15.0 metric tones in 2001 to 36.0 metric tones in 2006 (Fig. 5). Simple linear regression indicated that the increase of icefish yield was significantly and positively correlated with the gain of mean water level in winter and early spring in the lake ($R^2 = 0.867$, $F_{1,7} = 39.13$, $P = 0.001$; Fig. 5).

Body size and fecundity

Spawning periods of the three persistent stocks did not change between pre- and postregulation periods (Table 1). However, their body size declined during the postregulation period (Fig. 6). Average body length (SL) of NO decreased significantly ($t_{148} = 19.38$, $P < 0.001$) along with a significant decrease ($t_{148} = 19.33$, $P < 0.001$) of its body mass (Fig. 6). Similarly, NTs underwent significant reductions in average SL ($t_{148} = 3.92$, $P = 0.008$) and body mass ($t_{148} = 3.24$, $P = 0.018$; Fig. 6). For NTa, the apparent pattern of reduction was not statistically significant ($P > 0.05$) for either body length or body mass (Fig. 6).

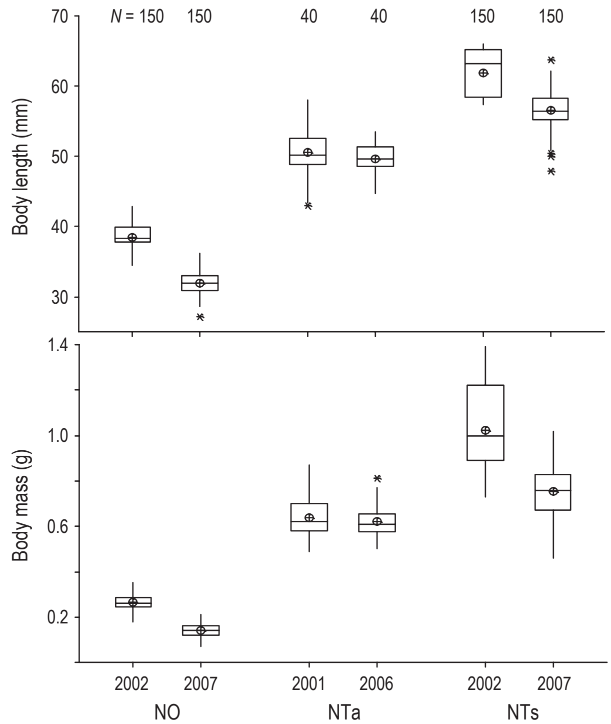

Fig. 6. Variation in average body size of three persistent icefish stocks of NTs, NTa and NO in Lake Nanyi. Icefish adults were collected in August 2001 and 2006 (NTa) and April 2002 and 2007 (NTs and NO), respectively.

Given the observed reductions in body size of the three persistent stocks, absolute fecundity of these populations changed in a predictable manner when pre- and postdam periods were compared (Table 2). Absolute fecundity of NTs, NTa and NO decreased by 25.7%, 24.8% and 26.4%, respectively (Table 2), and absolute fecundity was significantly correlated with body mass (linear regression; $P < 0.001$). When the influence of body mass was removed using ANCOVA, the decline in fecundity was statistically significant ($P < 0.05$) for NTs and NO, but not significant for NTa (Table 2).

Table 2. Comparison of icefish absolute fecundity before and after hydrologic regulation in Lake Nanyi. Date means sampling month, *N* indicates specimen number used in analysis. Results of ANCOVA illustrate the fecundity difference between the pre- and postregulation samples of each stock.

	Before regulation			After regulation			
Taxa	Date	*N*	Mean ± SD	Date	*N*	Mean ± SD	ANCOVA result
NTs	April 2002	50	1570 ± 362	April 2007	50	1165 ± 160	$R^2 = 0.992$, $F_{1,97} = 4.162$, $P = 0.044$
NTa	September 2001	20	1085 ± 257	September 2006	20	816 ± 118	$R^2 = 0.999$, $F_{1,37} = 0.141$, $P = 0.709$
NO	April 2002	50	461 ± 22	April 2007	50	306 ± 20	$R^2 = 0.986$, $F_{1,97} = 248.7$, $P < 0.001$

Discussion

The icefish assemblage structure in Lake Nanyi changed very soon after the construction of the irrigation infrastructure and followed hydroregulation in the lake area. The water regulation began in spring 2004, and the changes of icefish population dynamics, assemblage structure and commercial yield had been observable by the start of our postregulation survey period in 2006, which implies that these changes of the annual fish assemblage may be sensitive indicators to the environmental alteration in the lake (Geist 2011).

Dams and floodgates reduced channel connectivity and probably prevented the migratory icefish, *Hemisalanx brachyrostralis*, from entering the lake to spawn (Dugan et al. 2010). Dispersal limitation can be a strong ecological filter for freshwater fish assemblages (Brakou et al. 2009; Mims & Olden 2013). Dams on large rivers in many regions of the world, such as the Colorado in North America, the Nile in Africa and the Volga in Europe, have severely impacted stocks of large migratory fishes (Park et al. 2003; Stone 2008; Snelder & Lamouroux 2010). *H. brachyrostralis* is probably among the smallest truly migratory freshwater fishes. Mature *H. brachyrostralis* migrates upstream to the lake prior to spawning during late winter, and most larvae and juveniles swim downstream with the outflow during summer flooding (Wang et al. 2005b). The dams and weirs on the Mashan, Shuangqiao and Youzha channels appear to have prohibited adults from reaching spawning habitat in the lake, and the result was its local extirpation.

In addition to reduced fluvial connectivity, the altered flow regime following construction of water-control infrastructure likely contributed to the changes observed in icefish stocks in Lake Nanyi. Fishes with different life histories respond in different ways to hydrologic alteration, with some populations increasing and others decreasing (Lamouroux et al. 2006; Taylor et al. 2008; Mims & Olden 2012; Pool & Olden 2012). The new hydrologic regime in Lake Nanyi favoured both the spring and autumn stocks of *N. taihuensis* and resulted in the considerable increase of their individual density (CPUE; Fig. 4) and the overall yield of the icefish fishery (Fig. 5). After hydroregulation, the water level in Lake Nanyi was more stable with higher water levels during the winter and early spring (Fig. 2). Deeper water during the winter probably favoured feeding, growth and overwinter survival of juvenile icefishes, which in turn would enhance the reproductive stocks and larvae recruitments during the ensuing spawning seasons. Moreover, lower flood peaks during summer undoubtedly reduced outflows and exporting loss of larval and juvenile icefish from the lake, which would have further contributed to increased icefish density and biomass in the lake (Fig. 5).

Although the higher water level in winter and early spring may have also favoured the overwinter survival of juvenile NO, seasonal degradation of spawning habitat would have affected its reproductive success and larvae recruitment in the regulated stable conditions. Sandy substrate without vegetation cover is necessary for successful spawning by most icefish species, including NO (Zhang 1987; Wang et al. 2005a, 2006). After hydrologic regulation, most of the icefish spawning habitat, in the vicinity of sites 4 and 5 within the ELA, was covered by dense macrophytes from May to November (Chen et al. 2008; Wu et al. 2008), which encompasses the period when NO spawns (May–June; Table 1). As result, the density of NO declined during summer and autumn, which reduced its relative abundance (P_i) and relatively improved the P_is of the other two stocks of NTs and NTa in the August samples (Figs 3,4).

Food availability strongly influences growth and development of larval and juvenile fishes (Christensen 2009; Lobón-Cerviá 2009; Sethi 2010). In Lake Nanyi, annual average densities of zooplankton and phytoplankton were not significantly different during pre- and postregulation periods (Chen et al. 2005, 2008), which suggests little change in water-column productivity in response to hydrologic regulation. However, food availability for planktivorous *Neosalanx* decreased during critical feeding season of summer and autumn. This may have been caused partly by the increased icefishes density, and partly by the reduced water volume and habitat area, because that water level in the feeding season was lower in the lake after hydroregulation than before (Fig. 2) and macrophytes spread to larger area during the same period (May–November; Zhang 1987; Wu et al.

2008). And thus, food competition intensified, which probably caused reductions of mean body sizes that were observed in all of the three persistent icefish stocks (Fig. 6). Smaller adult body size yields lower absolute fecundity (Bradford et al. 2011), and therefore the smaller average body masses of the three *Neosalanx* stocks yielded lower absolute fecundities. Even after adjusting for the influence of body mass, ANCOVA results indicated that fecundity of NTs and NO was significantly lower during the postregulation period (Table 2). This result further implies that increased competition for planktonic prey probably reduced allocation of surplus energy to reproduction, which then would imply that total icefish density could be near the carrying capacity of the lake under new regulation regime.

In summary, the icefish assemblage of Lake Nanyi underwent large-scale changes following construction of the flood-control system. The disappearance of two icefish species, the increase of the spring stock of *N. taihuensis* and decrease of the *N. oligodontis* resulted in an altered icefish assemblage structure. Large increases in total icefish density and fishery yield indicate that the changed hydrologic regime favours icefishes in general. A reduction in average body size and absolute fecundity of the persistent icefish stocks may indicate that icefish stocks may be approaching the lake's carrying capacity. Although other factors could have contributed to these changes, a less variable water level in the lake probably is a key driver. Further research is needed to elucidate the influence of hydrology on habitat quality and quantity and dynamics of not only icefish stocks, but also the entire fish community of Lake Nanyi.

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