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Fish assemblage structure in relation to seasonal environmental variation in sub-lakes of the Poyang Lake floodplain, China

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Abstract

The Yangtze River and its watershed have undergone vast changes resulting from centuries of human impacts, yet ecological knowledge of the system is limited. The seasonal variation and spatial variation of three sub-lakes of Poyang Lake, a huge wetland in the middle Yangtze Basin, were investigated to examine how fish assemblages respond to seasonal hydrology and associated environmental conditions. In all three sub-lakes, fish assemblage structure revealed strong variations associated with seasonal water level fluctuation. Fish species richness in all sub-lakes was highest during the middle of the monsoon season and lowest during the dry season. Fish numerical abundance and biomass varied significantly, with several of the most common species having inconsistent patterns of seasonal variation among sub-lakes. Fish assemblage structure was significantly associated with environmental gradients defined by water level, aquatic macrophyte coverage, conductivity and dissolved oxygen concentration. Assemblage composition in all three sub-lakes underwent strongest shifts between December and April, the period when water levels were lowest and fishing has the greatest impact on fish stocks. Future impacts that change the hydrology of the middle Yangtze would alter the dynamics of habitat connectivity and affect environmental conditions and fish assemblages of the Poyang Lake wetland system.

KEYWORDS
conductivity, dissolved oxygen, hydrological connection, macrophytes, water level, Yangtze River

1 | INTRODUCTION

A central issue in community ecology is understanding and predicting the structure of species assemblages and their spatio-temporal variation across multiple scales (Fitzgerald, Winemiller, Sabaj Perez & Sousa, 2017; Hutchinson, 1959; Pacala & Tilman, 1994). Local assemblages of aquatic organisms in fluvial ecosystems are particularly variable in response to dynamic hydrology that affects physical disturbance (e.g. erosion, sediment transport, water chemistry), habitat quality, availability and connectivity, primary production, and other ecological factors.

Species richness in sub-lakes was assumed to be positively associated with water depth, and aquatic habitat availability and connectivity, all of which increase during the wet season. In addition, biomass density should peak during the period of water recession when fishes have gained weight and are concentrated within shrinking and increasingly isolated aquatic habitats (Halls & Welcomme, 2004). Fish assemblage structure was investigated in a major floodplain of the middle Yangtze River Basin in central China, a region that has received relatively little attention from ecologists despite its importance in supporting aquatic and avian diversity and important fisheries.

Floodplains are among the most productive and biologically diverse landscapes on Earth and provide valuable ecosystem services, such as nutrient cycling and production supporting fisheries, forest products and agriculture (Amoros & Bornette, 2002; Bond et al., 2014; Junk, Bayley & Sparks, 1989; Ropke, Amadio, Winemiller & Zuanon, 2016; Tockner & Stanford, 2002). Despite their valuable services, river–floodplain ecosystems throughout the world have been modified for flood control, energy production, navigation and other human benefits (Stoffels, Clarke, Rehwinkel & McCarthy, 2014). Previous studies of floodplain ecosystems have revealed the importance of flood pulses for aquatic food web dynamics and lateral habitat connectivity that allows fishes and other aquatic organisms to disperse among habitats for feeding or reproduction (Daga et al., 2009; Ou & Winemiller, 2016; Thomaz, Bini & Bozelli, 2007; Welcomme, 1979, 1985; Winemiller, Tarim, Shormann & Cotner, 2000).

During high-flow pulses, aquatic floodplain habitats tend to become more homogeneous and interconnected, which enhances dispersal of aquatic organisms, often leading to increases in alpha diversity and a reduction in beta diversity (Amoros & Bornette, 2002; Espinola et al., 2017; Miranda, 2005). Habitat heterogeneity created by aquatic macrophytes is a major factor that structures floodplain fish assemblages, especially during low-water periods when dispersal is lower and local densities are higher in increasingly isolated aquatic habitats (Dembkowski & Miranda, 2014; Gomes, Bulla, Agostinho, Vasconcelos & Miranda, 2012; Petry, Agostinho & Gomes, 2003; Ropke et al., 2016). Water depth and physicochemistry vary in response to hydrology and may further influence the structure of local fish assemblages (Petry, Agostinho, et al., 2003; Winemiller et al., 2000). Analysis of long-term survey data for the fish assemblage of a natural lake in the floodplain of the Amazon and Negro rivers in Brazil revealed that species richness, abundance and assemblage composition were strongly influenced by patterns of discharge that affected water conductivity and temperature (Ropke et al., 2016). The structure of fish assemblages from oxbow lakes in floodplains of the Brazos River in Texas (temperate region) showed large between-lake variation that was associated with differences in water depth, dissolved oxygen (DO), dissolved nutrients, turbidity and plankton density (Winemiller et al., 2000).

The middle and lower reaches of the Yangtze River are in the sub-tropical region of China where floodplains contain numerous lakes that support high biodiversity and major artisanal and commercial fisheries (Wang, Liu & Wang, 2016). Historically, most lakes had either permanent or periodic connections with the mainstem of the Yangtze River, and floods pulses occurred annually (Pan, Wang, Liang & Wang, 2011). Since the 1950s, fish diversity in the Yangtze Basin has declined at an accelerating rate owing to a series of direct and indirect effects of environmental impacts from human activities (e.g. loss and fragmentation of habitat, overfishing, pollution, and construction of dams) (Ye, Li, Liu, Zhang & Xie, 2011). Some lakes are now isolated from the river channel and its tributaries, thereby restricting lateral fish migration and further contributing to reductions in local and regional fish stocks (Fang et al., 2006). At present, the Poyang Lake is one of only three major floodplain lake systems that remain connected to the mainstem of Yangtze River. During the summer rainy season, Poyang Lake expands to more than 3,000 km^2 as its sub-lakes coalesce into a single, large, shallow waterbody. As water levels recede during the dry season, shallow sub-lakes are again isolated within the Poyang Lake floodplain (Wang et al., 2016).

Despite its national and global importance as a major wetland supporting aquatic and avian diversity and fisheries, little information has been gathered concerning relationships between hydrology, environmental conditions and local fish assemblages of the Poyang Lake floodplain. Yang, Li, Zhu, Wang and Liu (2015) investigated spatial and temporal variations of fish assemblages in open-water areas of Poyang Lake. Relationships between fish assemblage structure and environmental factors have been studied in floodplain lakes in other regions of the middle Yangtze Basin (Xie, Cui & Li, 2001; Xie, Cui, Zhang, Fang & Li, 2000; Xie, Li, Cui & Murphy, 2005; Ye et al., 2006). To understand the value of floodplain lakes for sustaining biodiversity and ecosystem services in the Yangtze Basin, research is urgently needed to facilitate better management. The purpose of the present study was to describe seasonal variation in fish assemblages within three sub-lakes of Poyang Lake floodplain, to investigate between-lake differences and relationships between local environmental conditions and fish species richness, abundance and assemblage structure. It was hypothesised that species richness in sub-lakes would be positively associated with water depth and expansion of aquatic habitat, an expectation founded in the species–area relationship. It was further predicted that biomass would peak during the period of water recession when fishes have gained weight and are concentrated within shrinking and increasingly isolated aquatic habitats (Halls & Welcomme, 2004).

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in a 224 km^2 area in the north-western part of the Poyang Lake National Nature Reserve, a major wetland in central China. When completely filled, Poyang Lake is the largest freshwater lake within the middle-lower Yangtze River Basin. Five major rivers flow into Poyang Lake, and water eventually flows northward to enter the Yangtze via a narrow channel (Figure 1). Average annual temperature in the region varies from 16.7 to 17.7°C, and average precipitation is 1,400–1,900 mm, with a strong influence from sub-tropical monsoons (Zhang, 1988). During the summer monsoon (May to September), the area floods and sub-lakes within the floodplain coalesce into a single lake with an area >3,000 km^2 (Xu & Qin, 1998). Floodplain inundation results from inflows from the tributary rivers as well as reverse flow from the Yangtze River, the latter usually occurring between July and September. During the dry season (October to March), the lake level falls 8–10 m and the area of surface water shrinks to <1,000 km^2 with a narrow meandering channel and many isolated small and medium-sized sub-lakes separated by grassland and mudflats (Feng et al., 2012).

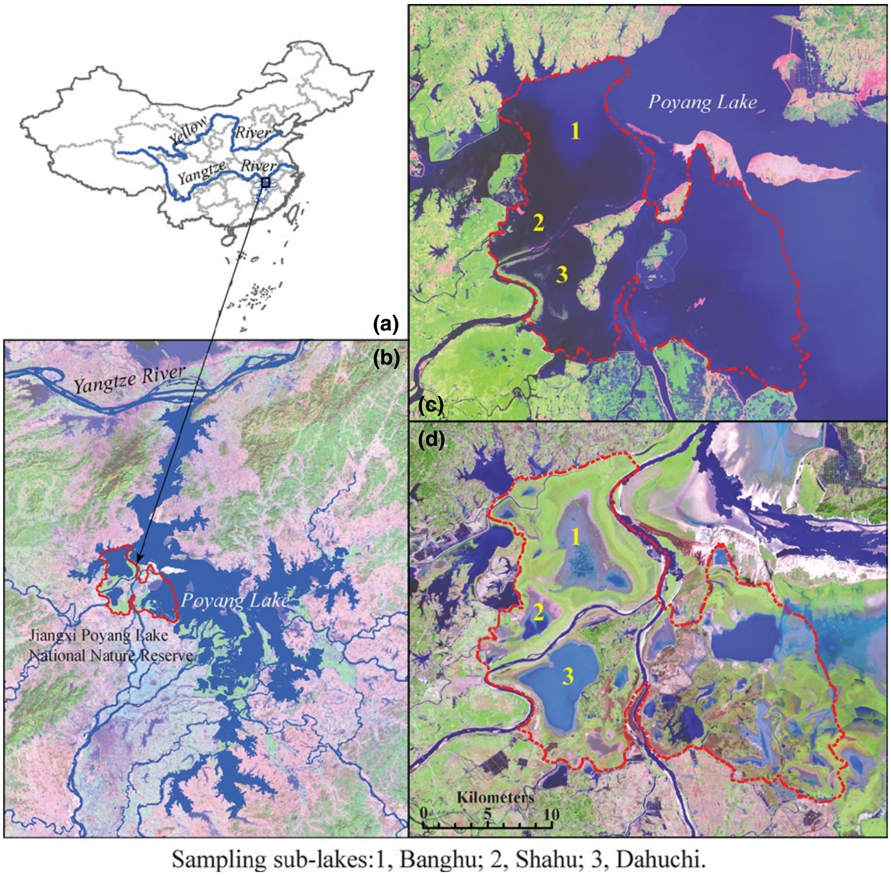

FIGURE 1 Location of Poyang Lake in the Yangtze River Basin (a), the study area in the north-west region of the lake (b) and three sub-lakes (1-Banghu, 2- Shahu, 3-Dahuchi) that were surveyed during wet (September, c) and dry seasons (March, d) [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Fish surveys

Fishes were surveyed on 5–9 July 2015, 16–21 September 2015, 27–29 December 2015, and 17–19 April 2016, from three sub-lakes (Banghu, Shahu and Dahuchi) located in the Poyang Lake National Nature Reserve (Figure 1). During June and July, the water level was high; then, water level began to decline, in October sub-lakes were disconnected with the main lake; from April, the water level was rising, but still low (Figure 2). Eight stations in both Banghu and Dahuchi and five sampling stations in Shahu were selected for sampling fish assemblages. Fishes were collected using a beach seine (10 m × 1.5 m; 0.5 mm mesh). Three, 30-m seine hauls were done at each station on each survey date. Hauls were done near shore with hauls separated by at least 100 m. Each haul was from deep water (1–1.5 m) to the shoreline through areas of open water and/or submerged and emergent aquatic vegetation in proportions approximating their areal coverage at locations. Some fishes, such as large and mobile fish, could have evaded capture by the seine, and surveys likely failed to capture some extremely rare species. Nonetheless, the many seine hauls that were made within a given sub-lake during a given survey period yielded fish samples with fairly consistent composition, and in most cases, no additional species were obtained after the fifth consecutive haul. During each of four sampling periods, water pH, conductivity, temperature, turbidity and DO were measured using portable multiparameter water quality metres (YSI 6600). The bankfull area of each

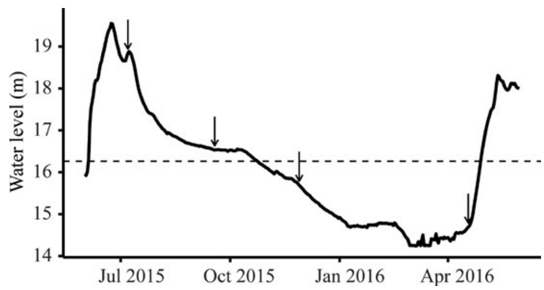

FIGURE 2 Daily variation of water levels of the sub-lake from June 2015 to May 2016, measure at the Dahuchi hydrometric station. Arrows represent the sampling time; dashed line indicates water level required for initial connect between sub-lakes and Poyang Lake floodplain

lake and area covered by macrophytes in each lake were recorded (data were provided by Poyang Lake National Nature Reserve Authority). The standard length (cm) and mass (g) of each captured fish specimen were measured in the laboratory. Nomenclature follows Froese and Pauly (2017).

2.3 | Data analysis

The index of relative importance (IRI) was used to assess the relative dominance of species in each sample. IRI was calculated based on abundance, biomass and frequency of occurrence as follows:

IRI = (%N + %W) × %FO, where %N, %W and %FO are percentage contribution of abundance, contribution of biomass and frequency of occurrence (Jin, Xu, Guo, Chen & Fu, 2014; Jin et al., 2007, 2010; Pinkas, Ouphant & Iverson, 1971). Mean abundance of each species in the three seine hauls at each survey station on each date was standardised as catch-per-unit-effort (CPUE). Data for environmental variables, including pH, turbidity, conductivity and DO, were compared using two-way analysis of variance (ANOVA). Two-way ANOVA also was used to evaluate the effect of sampling month and lake on abundance, biomass and species richness. When necessary, numerical data were log transformed prior to statistical analyses to meet ANOVA assumptions for data distribution.

Canonical redundancy analysis (RDA) was performed to evaluate the relationship between fish assemblage structure and lake environmental variables using CANOCO software (version 4.56). Prior to analysis, abundance (CPUE) data were log (x + 1) transformed, and rare species (individuals <5% of the total catch) were excluded from the data matrix (McGarigal, Cushman & Stafford, 2000). A Monte Carlo test was done for each canonical axis to determine the statistical significance of the species–environment relationship.

3 | RESULTS

3.1 | Environmental variables

Two-way ANOVA revealed significant difference in pH, turbidity, conductivity and DO between survey periods and sub-lakes. Water temperature was significantly different among sampling month (mean = 24°C in July, 23°C in October, 10°C in October and 20°C in April) and pH was higher during April (mean = 8.16) than other months, and Dahuchi Lake had higher pH (mean = 8.43) than the other sub-lakes during April (Figure 3a). Overall, conductivity, turbidity and DO were higher during December than other periods. Conductivity was higher in Banghu Lake than the other lakes during July (mean = 127.5 μS/cm), October (mean = 203 μS/cm) and December (mean = 344 μS/cm; Figure 3b). In Shahu Lake, turbidity was significantly higher during December (mean = 265 NTU) than other periods (Figure 3c).

3.2 | Fish assemblage structure

Seine surveys produced 9,440 fish specimens weighing 8.63 kg and belonging to 11 families, 31 genera and 36 species. Eighteen of these species have significant commercial value (Table 1). The most

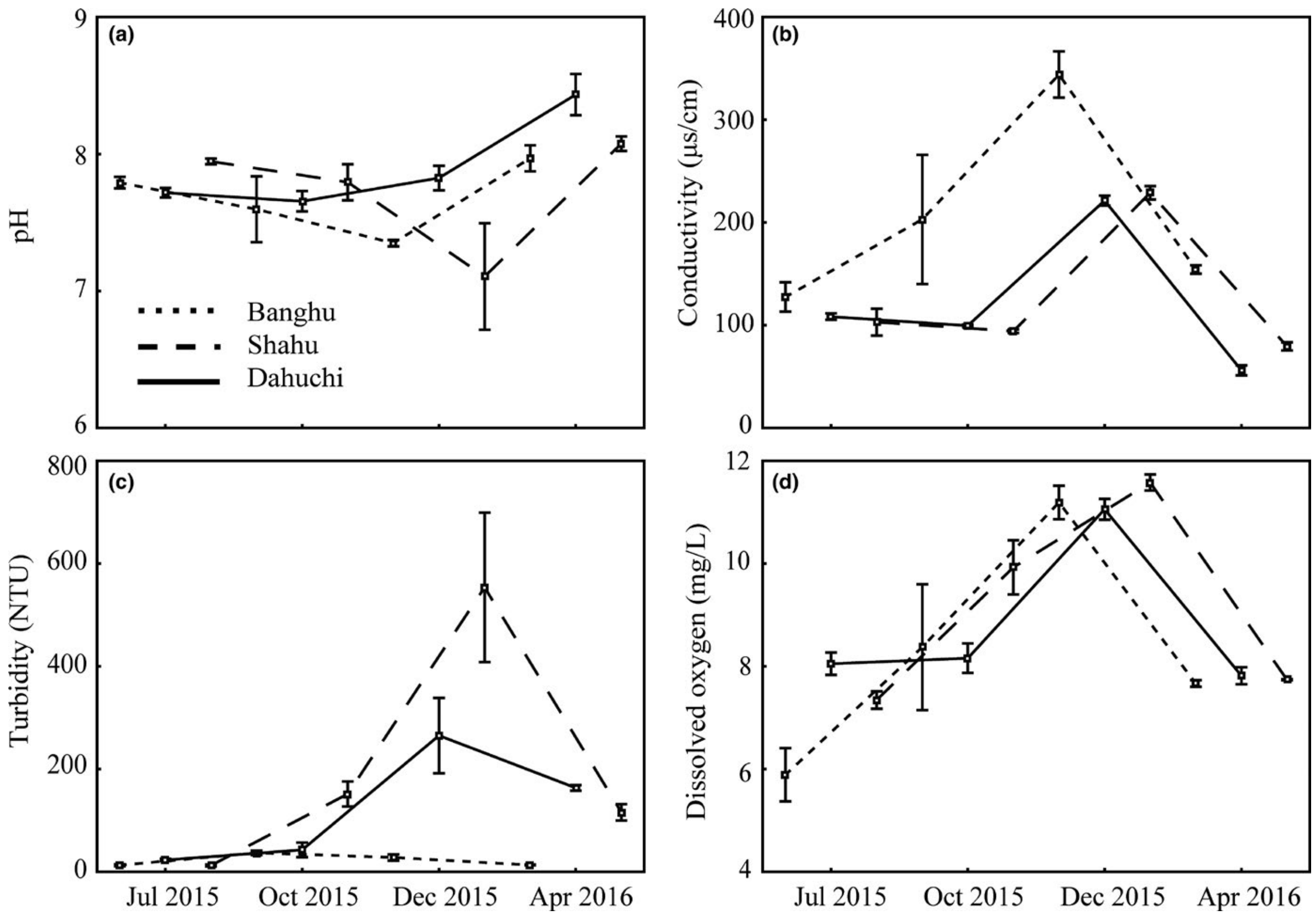

FIGURE 3 Mean values of environmental variables (pH, conductivity, turbidity and dissolved oxygen) recorded in three sub-lakes of Lake Poyang during surveys conducted from July 2015 to April 2016. Error bars represent ±1 *SE*

TABLE 1 Fish families and species with total catch (*N*), total biomass (W), range of standard length (L), index of relative importance (IRI)

Family	Species	July 2015			October 2015			December 2015			April 2016			IRI
		N	W	L	*N*	W	L	*N*	W	L	*N*	W	L	
Salangidae	*Protosalanx hyalocranius*	2	0.6	3.9–3.9	11	5.0	2.6–5.2	271	213.1	3.0–6.4	4	0.6	3.3–3.6	97
Cyprinidae	*Ctenopharyngodon idella*	79	29.0	1.2–5.1	11	12.5	2.1–7.0	19	10.6	2.6–4.4				67
	Mylopharyngododon piceus	93	66.0	1.5–5.4	1	0.3	2.7–2.7							28
	Squaliobarbus curriculus	1	39.2	13.4–13.4										0.57
	Hemiculter leucisculus	2,060	652.4	0.9–10.0	610	913.4	2.4–10.5	874	1155.0	2.6–10.6	174	444.2	3.7–10.0	6,291
	Pseudolaubuca sinensis	80	100.1	1.5–6.6	18	26.0	3.2–6.1							40
	Chanodichthys mongolicus				1	0.8	3.7–3.7	1	1.6	5.2–5.2	1	2.7	6.0–6.0	0.33
	Chanodichthys erythropterus	6	17.4	2.2–9.2	14	24.9	4.6–6.7	4	46.4	14.5–14.5	5	41.9	5.9–13.6	25
	Parabramis pekinensis							3	3.4	2.9–4.7	1	5.4	7.5–7.5	0.53
	Carassius auratus	164	246.0	1.5–5.3	154	429.0	2.5–6.0	375	1082.8	3.0–8.2	6	41.7	1.5–9.9	1,395
	Cyprinus carpio	26	81.0	3.0–6.2										9
	Hypophthalmichthys molitrix	22	30.2	2.9–4.9	1	1.5	4.0–4.0							4
	Rhodeus lighti	254	68.6	1.0–4.4	8	2.3	1.9–2.6	8	1.0	1.4–2.1	33	1.2	1.0–2.4	115
	Rhodeus sinensis	176	110.3	1.2–4.1	9	14.4	2.8–4.5	2	5.4	4.1–4.8				34
	Acheilognathus macropterus				5	1.9	2.4–2.7				2	6.8	4.4–5.6	0.26
	Xenocypris macrolepis	31	39.9	2.0–7.0	183	413.5	2.9–10.2	60	77.6	2.8–5.3	30	164.8	4.4–8.0	334
	Distoechodon tumirostris	7	4.2	3.0–3.6										0.30
	Pseudobrama simoni				47	105.3	3.7–6.2	305	367.6	3.2–7.3				125
	Saurogobio dabryi	53	29.7	1.5–6.0	2	2.0	3.5–4.2	31	94.3	4.3–6.5				35
	Squalidus argentatus	4	1.3	2.0–3.2										0.07
	Pseudorasbora parva				48	49.5	2.2–6.6	84	153.5	2.5–7.4	11	29.9	4.1–6.8	135
	Hemibarbus maculatus				9	17.0	3.4–6.0	26	58.7	3.2–7.1	2	7.3	5.4–5.5	23
Cobitidae	*Misgurnus anguillicaudatus*				1	2.1	6.5–6.5				53	42.6	1.7–7.2	12
	Sinibotia superciliaris	2	2.6	4.6–4.8	1,918	471.0	2.3–4.1	1	0.1	2.5–2.5	5	1.4	2.3–3.0	320
Bagridae	*Tachysurus fulvidraco*	6	25.0	2.4–9.2	1	3.4	5.4–5.4				38	161.6	2.6–12.0	40
Cyprinodontidae	*Oryzias latipes*	195	24.1	1.2–2.4	3	0.3	1.0–1.9	5	0.4	1.5–1.8	34	7.3	1.8–2.6	78
Hemiramphidae	*Hyporhamphus intermedius*	30	57.9	7.2–11.4	18	22.0	7.0–10.8	1	2.0	9.6–9.6				25
Synbranchidae	*Monopterus albus*										1	0.6	6.8–6.8	0.02
Gobiidae	*Mugilogobius myxodermus*				24	9.8	1.8–3.4	1	0.4	2.6–2.6	13	4.1	1.7–2.8	9
	Rhinogobius giurinus	156	33.4	1.1–3.9	329	164.4	1.5–4.7	29	13.9	1.7–3.8	3	3.1	2.0–4.6	403
Eleotridae	*Micropercops cinctus*				8	2.7	1.5–3.4	10	2.7	1.6–3.5				2

(*Continues*)

TABLE 1 (Continued)

Family	Species	July 2015			October 2015			December 2015			April 2016			IRI
		N	W	L	N	W	L	N	W	L	N	W	L	
Channidae	*Channa argus*	28	17.8	1.7–3.7										0.62
Percichthyidae	*Siniperca chuatsi*	2	0.3	1.7–1.8										0.06
	Siniperca scherzeri	1	0.6	2.7–2.7										0.02
	Siniperca knerii	1	0.1	1.3–1.3										0.01
	Siniperca undulata	1	0.7	2.7–2.7										0.02

species-rich family was Cyprinidae (23 species). The eight most abundant species (IRI > 100) comprised 84.34% of the total catch, that is, *Hemiculter leucisculus* (Basilewsky), *Carassius auratus* (L.), *Rhinogobius giurinus* (Rutter), *Xenocypris macrolepis* Bleeker, *Sinibotia superciliaris* (Günther), *Pseudorasbora parva* Temminck & Schlegel, *Pseudobrama simoni* (Bleeker), *Rhodeus lighti* Wu. Goldfish, *C. auratus*, was abundant (IRI = 1,395) and is one of the most important fishery species in Yangtze Basin.

When data were combined for all lakes, fish species richness was highest in the July sample (26) taken during the middle of the monsoon season and lowest in the April sample (18) taken during the late dry season. Only nine species were captured during all four sampling periods (Table 1). Mean numerical abundance was greatest during October (late monsoon season), and mean fish biomass was greatest during October and December (Figure 4). Species richness varied significantly among survey periods, as did total abundance, total biomass and abundances of dominant fish species (Table 2). Abundances of *H. leucisculus* and *R. lighti* were greatest during July, and *S. superciliaris*, *R. giurinus* and *X. argentea* were most abundant during October. *Carassius auratus* and *P. simoni* had greatest abundance during December, and *P. parva* was most abundant during October and December.

Fish species richness and total abundance, but not total biomass, varied significantly between sub-lakes (Figure 4). Species richness was significantly higher in lakes Banghu and Dahuchi than Shahu during July and October. Total abundance tended to be higher in Banghu than Dahuchi and Shahu during July and October (Figure 4b). Seven of the eight dominant species tended to be most abundant in Banghu Lake, with *P. parva* most abundant in Dahuchi.

The RDA analysis revealed separation of fish samples obtained during different periods (Figure 5). The relationship between assemblage structure and environmental variables indicated by axes 1 and 2 cumulatively accounted for 64.7% of total environmental variation. The first axis was most strongly influenced by bankfull area, macrophytes area, turbidity and DO. The second axis was most strongly influenced by water level and conductivity. The second axis separated July (middle monsoon season) from April (late dry season) (Figure 5a). The first axis separated Banghu Lake, having more vegetated area, from Dahuchi Lake (Figure 5b).

The Monte Carlo permutation procedure revealed significant associations of water level ($p = 0.002$), conductivity ($p = 0.002$), DO ($p = 0.008$) and vegetated area ($p = 0.008$) with fish assemblage structure. Abundance of most fish species was positively correlated with water level and vegetated area, but *Protosalanx hyalocranius* (Abbott) was negatively correlated with these variables, and *Misgurnus anguillicaudatus* (Cantor) was positively correlated with pH and negatively correlated with water level (Figure 5c).

4 | DISCUSSION

Fish assemblages of sub-lakes within the Poyang Lake floodplain underwent major compositional changes in relation to seasonal

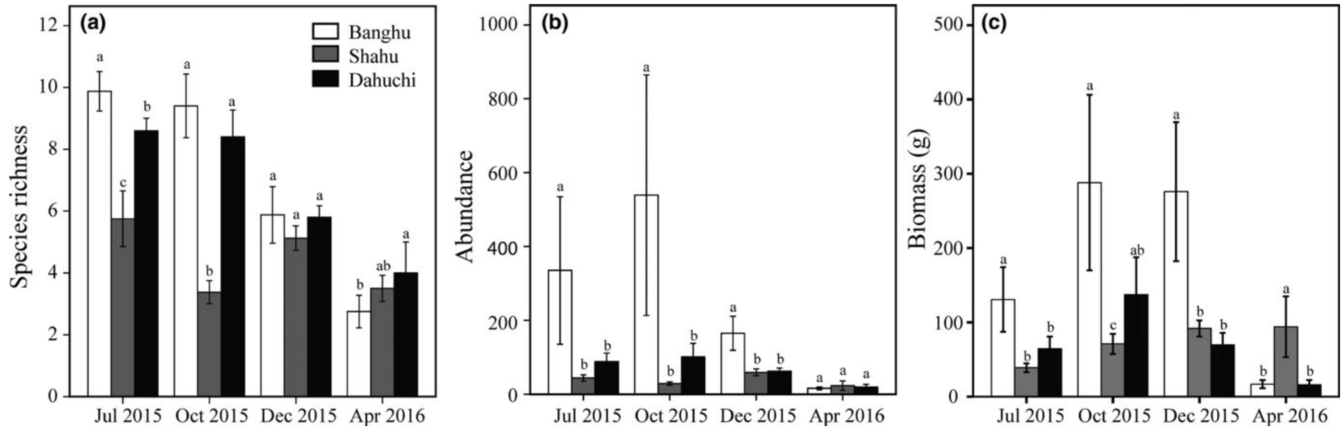

FIGURE 4 Mean fish species richness (a), abundance (b) and biomass (c) during each survey period in each sub-lake (*y*-axis values are CPUE). Different letters (a, b, c) indicated significant difference ($p < 0.05$) among sub-lakes at each month. Error bars represent ±1 *SE*

TABLE 2 Summary of two-way ANOVA for testing the effects of month and location (sub-lakes) on species richness, total abundance, total biomass and abundance of dominant fish species (IRI > 100)

	Month			Location			Month×Location		
Variables	*F*	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
Species richness	22.93	3	***	10.714	2	<0.001	5.284	6	***
Total abundance	19.227	3	***	12.344	2	<0.001	2.223	6	ns
Total biomass	12.771	3	***	1.317	2	0.275	2.823	6	*
Dominant fishes									
Hemiculter leucisculus	9.737	3	***	0.338	2	0.714	1.171	6	ns
Sinibotia superciliaris	10.288	3	***	11.181	2	<0.001	14.781	6	***
Carassius auratus	3.861	3	*	1.934	2	0.152	2.64	6	*
Rhinogobius giurinus	9.556	3	***	8.735	2	<0.001	5.682	6	***
Pseudobrama simoni	4.857	3	**	4.632	2	0.013	4.554	6	**
Xenocypris macrolepis	1.508	3	ns	2.749	2	0.071	4.381	6	**
Rhodeus lighti	10.74	3	***	4.748	2	0.012	1.532	6	ns
Pseudorasbora parva	6.82	3	***	6.217	2	0.003	2.348	6	*

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns, $p > 0.05$.

variation in water level. Species richness was highest during the middle of the monsoon season and lowest during the dry season. Considerable between-lake variation was also found, for example, total fish abundance and biomass tended to be higher in Banghu than Dahuchi and Shahu during October and December. Fish assemblages in other river–floodplain systems have been shown to undergo compositional changes in response to pulsing hydrology (Ropke et al., 2016; Zeug, Winemiller & Tarim, 2005). Flood pulses create critical connections between the main channel and adjacent floodplain habitats that provide fish access to shelter, food resources and spawning habitat (Amoros & Bornette, 2002; Couto, Zuanon, Olden & Ferraz, 2018; Ropke et al., 2016). These lateral connections also allow fishes to return the main channel as water levels begin to drop and floodplain habitats shrink (Junk et al., 1989).

The Poyang Lake floodplain undergoes annual water level fluctuations of 8–10 m. During the flood season (spring and summer), sub-lakes coalesce into a single, large waterbody. Fish species richness and abundance in sub-lakes were greater during the flood season. Within this open system, fishes are able to disperse into newly available habitats located at higher elevations in the floodplain. Fish migration in response to lateral connectivity has been shown to be a primary determinant of fish species richness and assemblage composition at local scales in many river–floodplain systems. For example, Fernandes (1997) described three lateral migration patterns of fishes in Amazon floodplain associated with water level fluctuations. Galat et al. (1998) described how connected floodplain habitats of the Missouri River contained more fishes with periodic life history strategies than isolated habitats. In excavated ponds in floodplains of the lower Mississippi River, pond morphology affected access for pre-spawning fishes as well as larval survival and growth (Sabo & Kelso, 1991).

During the dry season (autumn and winter), water levels fall in the Yangtze River and Poyang Lake, and sub-lakes become separated by

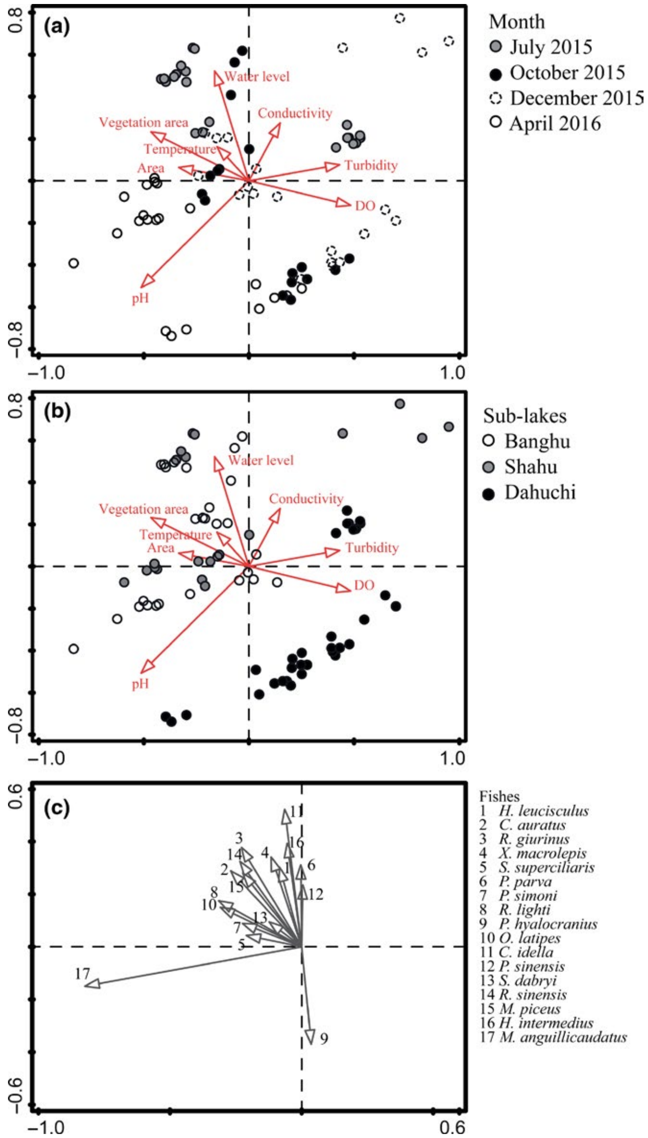

FIGURE 5 Ordination diagrams from redundancy analysis. (a) Biplot of fish assemblages according to survey periods and showing correlations of environmental variables with the two axes as vectors; (b) biplot of fish assemblages according to sub-lakes with environmental correlations again shown as vectors; (c) plot showing correlations of fish species with the two axes as vectors. Species with fewer than 5% individual observation were excluded from the analysis [Colour figure can be viewed at wileyonlinelibrary.com]

extensive areas of exposed mudflats (Hu, Ge, Liu, Chen & Li, 2010; Wang, Yu, Zhang & Lei, 2013). As sub-lakes become smaller and more isolated, environmental conditions gradually change and diverge among sub-lakes. This spatial habitat heterogeneity apparently has a significant influence on local fish assemblage diversity and structure. Aquatic macrophytes appear to play a particularly strong role in structuring fish assemblages in the Poyang Lake system. Macrophytes increase habitat structural complexity and productivity of many types of aquatic macroinvertebrates that are important food resources for fish (Agostinho, Thomaz, Gomes & Baltar, 2007; Dias, da Silva, Gomes & Agostinho, 2017; Gomes et al., 2012; Winemiller & Jepsen, 1998). Interactions between fishes and macrophytes have been widely investigated, but much remains to be understood (Dias et al., 2017; St. Pierre & Kovalenko, 2014). Aquatic macrophytes can influence fish feeding (Guo et al., 2013; Yu et al., 2016) and provide refuge from predators (Warfe & Barmuta, 2006) and nursery areas that enhance early life stage feeding, growth and survival (Bulla, Gomes, Miranda & Agostinho, 2011; Sabo & Kelso, 1991). All these influences are affected by water level fluctuations in floodplains (Dias et al., 2017; Shima, Osenberg & St Mary, 2008; Oliveira, Martinelli, Moreira, Soares & Cyrino, 2006).

Previous studies from lakes of the middle and lower reaches of the Yangtze Basin show that macrophyte cover had a high impact on assemblages of small fishes, with species richness, diversity, density and biomass higher in vegetated areas of the lake (Xie et al., 2001). A dominant species, *C. auratus*, preferred dense beds of submerged macrophytes where it not only obtains food and shelter from predation but also spawns (Xie, Cui, Zhang & Li, 2000; Xie, Cui, Zhang, Fang, et al., 2000; Xie et al., 2001, 2005; Ye et al., 2006). Using stable isotope analysis, Wang, Yu, Xu, Li and Fan (2012) showed that during high water conditions of summer, the submerged macrophyte *Ceratophyllum demersum* (L.) was the most important primary production source supporting fish biomass. During the high-water period, the Poyang Lake systems contain 102 sub-lakes within an area of 816.32 km^2, with approximately 54% of that area covered with submerged macrophytes mainly within the sub-lake basins (Hu, Zhang, Liu, Ji & Ge, 2015). This study found highest fish species richness during July and October when sub-lakes had high connectivity and Poyang Lake systems were well connected to the Yangtze River, and dense growth of aquatic macrophytes probably played an important role in supporting high fish diversity.

From October to December, when the water level falls, sub-lakes become more isolated from the main lake, and conductivity and DO concentrations reached their highest levels during the year. Conductivity and DO then decline from December to April. Environmental gradients influenced by aquatic vegetation, conductivity and DO were significantly associated with fish abundance, diversity and assemblage structure. This finding is similar to that of Petry, Bayley and Markle (2003) in which shallow water, high conductivity and low DO were associated with high fish abundance and diversity. In Ropke et al. (2016), long-term study of an Amazonian floodplain lake, fish species richness, abundance and assemblage structure were strongly associated with water conductivity and temperature that were influenced by discharge. In this study, two species (*M. anguillicaudatus*, *P. hyalocranius*) were negatively correlated with the environmental variables that were analysed. Relative abundance of *M. anguillicaudatus* was inversely correlated with water level, and this species apparently prefers shallow habitats with mud and silt substrates (Yamamoto & Tagawa, 2000), whereas little is known about the ecology of *P. hyalocranius*.

Disconnected sub-lakes of Poyang Lake had a similar number of fish species but assemblage structure differed depending on local habitat conditions (Figures 4a and 5), a finding similar to those from other studies of floodplain fish assemblages (Thomaz et al., 2007; Ward, Tockner & Schiemer, 1999). During the low-water periods when sub-lakes were isolated, ecological dynamics are more strongly influenced by local environmental conditions, which leads to differentiation of local species assemblages. Fernandes (1997) suggested that environmental conditions of floodplain lakes during the dry season could function like a filter that selects for subsets of species adapted to certain conditions. From December to April, composition of fish assemblages in all three Poyang sub-lakes underwent strong changes (Figure 5a). These compositional shifts likely were influenced by fishing (Zeng et al., 2015). Each year from the end of November through January, fishermen target fish exiting sub-lakes as waters drain from them. Although the Poyang Lake system retains a fairly natural flood regime, humans are nonetheless impacting fish stocks via fishing pressure. Future impacts that change the hydrological regime of the middle Yangtze River would affect the dynamics of habitat connectivity and have a significant impact on fish assemblages of the Poyang Lake system. Findings from the current study can help guide river management and fish conservation in floodplain regions of the Yangtze Basin.

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REFERENCES

Agostinho, A. A., Thomaz, S. M., Gomes, L. C., & Baltar, S. L. S. M. A. (2007). Influence of the macrophyte Eichhornia azurea on fish assemblage of the Upper Parana River floodplain (Brazil). *Aquatic Ecology*, *41*, 611–619.

Amoros, C., & Bornette, G. (2002). Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, *47*, 761–776.

Bond, N., Costelloe, J., King, A., Warfe, D., Reich, P., & Balcombe, S. (2014). Ecological risks and opportunities from engineered artificial flooding as a means of achieving environmental flow objectives. *Frontiers in Ecology and the Environment*, *12*, 386–394.

Bulla, C. K., Gomes, L. C., Miranda, L. E., & Agostinho, A. A. (2011). The ichthyofauna of drifting macrophyte mats in the Ivinhema River, upper Parana River basin, Brazil. *Neotropical Ichthyology*, *9*, 403–409.

Couto, T. B. D., Zuanon, J., Olden, J. D., & Ferraz, G. (2018). Longitudinal variability in lateral hydrologic connectivity shapes fish occurrence in temporary floodplain ponds. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*, 319–328.

Daga, V. S., Gogola, T. M., Sanches, P. V., Baumgartner, G., Baumgartner, D., Piana, P. A., & Delariva, R. L. (2009). Fish larvae assemblages in two floodplain lakes with different degrees of connection to the Parana River, Brazil. *Neotropical Ichthyology*, *7*, 429–438.

Dembkowski, D. J., & Miranda, L. E. (2014). Environmental variables measured at multiple spatial scales exert uneven influence on fish assemblages of floodplain lakes. *Hydrobiologia*, *721*, 129–144.

Dias, R. M., da Silva, J. C. B., Gomes, L. C., & Agostinho, A. A. (2017). Effects of macrophyte complexity and hydrometric level on fish assemblages in a Neotropical floodplain. *Environmental Biology of Fishes*, *100*, 703–716.

Espinola, L. A., Rabuffetti, A. P., Abrial, E., Amsler, M. L., Blettler, M. C. A., Paira, A. R., & Santos, L. N. (2017). Response of fish assemblage structure to changing flood and flow pulses in a large subtropical river. *Marine and Freshwater Research*, *68*, 319–330.

Fang, J., Wang, Z., Zhao, S., Li, Y., Tang, Z., Yu, D., & Zheng, C. (2006). Biodiversity changes in the lakes of the Central Yangtze. *Frontiers in Ecology and the Environment*, *4*, 369–377.

Feng, L., Hu, C. M., Chen, X. L., Cai, X. B., Tian, L. Q., & Gan, W. X. (2012). Assessment of inundation changes of Poyang Lake using MODIS observations between 2000 and 2010. *Remote Sensing of Environment*, *121*, 80–92.

Fernandes, C. C. (1997). Lateral migration of fishes in Amazon floodplains. *Ecology of Freshwater Fish*, *6*, 36–44.

Fitzgerald, D. B., Winemiller, K. O., Sabaj Perez, M. H., & Sousa, L. M. (2017). Seasonal changes in the assembly mechanisms structuring tropical fish communities. *Ecology*, *98*, 21–31.

Froese, R., & Pauly, D. (2017). *FishBase: World wide web electronic publication*. Rome, Italy: FAO.

Galat, D. L., Fredrickson, L. H., Humburg, D. D., Bataille, K. J., Bodie, J. R., Dohrenwend, J., … Semlitsch, R. D. (1998). Flooding to restore connectivity of regulated, large-river wetlands - Natural and controlled flooding as complementary processes along the lower Missouri River. *BioScience*, *48*, 721–733.

Gomes, L. C., Bulla, C. K., Agostinho, A. A., Vasconcelos, L. P., & Miranda, L. E. (2012). Fish assemblage dynamics in a Neotropical floodplain relative to aquatic macrophytes and the homogenizing effect of a flood pulse. *Hydrobiologia*, *685*, 97–107.

Guo, C. B., Ye, S. W., Lek, S., Liu, J. S., Zhang, T. L., Yuan, J., & Li, Z. J. (2013). The need for improved fishery management in a shallow macrophytic lake in the Yangtze River basin: Evidence from the food web structure and ecosystem analysis. *Ecological Modelling*, *267*, 138–147.

Halls, A. S., & Welcomme, R. L. (2004). Dynamics of river fish populations in response to hydrological conditions: A simulation study. *Rivers Research*, *20*, 985–1000.

Hu, Z., Ge, G., Liu, C., Chen, F., & Li, S. (2010). Structure of Poyang Lake wetland plants ecosystem and influence of lake water level for the structure. *Resources and Environment in the Yangtze Basin*, *19*, 597–605. (in Chinese with English abstract).

Hu, Z., Zhang, Z., Liu, Y., Ji, W., & Ge, G. (2015). The function and significance of the Shallow-Lakes in the Poyang Lake wetland ecosystem. *Jiangxi Hydraulic Science and Technology*, *41*, 318–323. (in Chinese with English abstract)

Hutchinson, G. E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, *93*, 145–159.

Jin, B. S., Fu, C. Z., Zhong, J. S., Li, B., Chen, J. K., & Wu, J. H. (2007). Fish utilization of a salt marsh intertidal creek in the Yangtze River estuary, China. *Estuarine Coastal and Shelf Science*, *73*, 844–852.

Jin, B. S., Qin, H. M., Xu, W., Wu, J. H., Zhong, J. S., Lei, G. C., … Fu, C. Z. (2010). Nekton use of intertidal creek edges in low salinity salt marshes of the Yangtze River estuary along a stream-order gradient. *Estuarine Coastal and Shelf Science*, *88*, 419–428.

Jin, B., Xu, W., Guo, L., Chen, J., & Fu, C. (2014). The impact of geomorphology of marsh creeks on fish assemblage in Changjiang River estuary. *Chinese Journal of Oceanology and Limnology*, *32*, 469–479.

Junk, W., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. In D. P. Dodge (Ed.), *Proceedings of the International Large River Symposium*.

McGarigal, K., Cushman, S., & Stafford, S. (2000). *Multivariate statistics for wildlife and ecology research*. New York, NY: Springer-Verlag.

Miranda, L. E. (2005). Fish assemblages in oxbow lakes relative to connectivity with the Mississippi River. *Transactions of the American Fisheries Society*, *134*, 1480–1489.
Oliveira, A. C. B., Martinelli, L. A., Moreira, M. Z., Soares, M. G. M., & Cyrino, J. E. P. (2006). Seasonality of energy sources of *Colossoma macropomum* in a floodplain lake in the Amazon - lake Camaleao, Amazonas, Brazil. *Fisheries Management and Ecology*, *13*, 135–142.
Ou, C., & Winemiller, K. O. (2016). Seasonal hydrology shifts production sources supporting fishes in rivers of the Lower Mekong Basin. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1342–1362.
Pacala, S. W., & Tilman, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *American Naturalist*, *143*, 222–257.
Pan, B. Z., Wang, H. J., Liang, X. M., & Wang, H. Z. (2011). Macrozoobenthos in Yangtze floodplain lakes: Patterns of density, biomass, and production in relation to river connectivity. *Journal of the North American Benthological Society*, *30*, 589–602.
Petry, A. C., Agostinho, A. A., & Gomes, L. C. (2003). Fish assemblages of tropical floodplain lagoons: Exploring the role of connectivity in a dry year. *Neotropical Ichthyology*, *1*, 111–119.
Petry, P., Bayley, P. B., & Markle, D. F. (2003). Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology*, *63*, 547–579.
Pinkas, L., Ouphant, M., & Iverson, I. (1971). Food habits of albacore, bluefin tuna, and bonito in California water. *California Fish, and Game, Fish Bulletin*, *152*, 1–105.
Ropke, C. P., Amadio, S. A., Winemiller, K. O., & Zuanon, J. (2016). Seasonal dynamics of the fish assemblage in a floodplain lake at the confluence of the Negro and Amazon Rivers. *Journal of Fish Biology*, *89*, 194–212.
Sabo, M. J., & Kelso, W. E. (1991). Relationship between morphometry of excavated floodplain ponds along the mississippi river and their use as fish nurseries. *Transactions of the American Fisheries Society*, *120*, 552–561.
Shima, J. S., Osenberg, C. W., & St Mary, C. M. (2008). Quantifying site quality in a heterogeneous landscape: Recruitment of a reef fish. *Ecology*, *89*, 86–94.
St. Pierre, J. I., & Kovalenko, K. E. (2014). Effect of habitat complexity attributes on species richness. *Ecosphere*, *5*, 1–10.
Stoffels, R. J., Clarke, K. R., Rehwinkel, R. A., & McCarthy, B. J. (2014). Response of a floodplain fish community to river-floodplain connectivity: Natural versus managed reconnection. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*, 236–245.
Thomaz, S. M., Bini, L. M., & Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, *579*, 1–13.
Tockner, K., & Stanford, J. A. (2002). Riverine flood plains: Present state and future trends. *Environmental Conservation*, *29*, 308–330.
Wang, H. Z., Liu, X. Q., & Wang, H. J. (2016). *The Yangtze River Floodplain: Threats and Rehabilitation. Fishery Resources, Environment, and Conservation in the Mississippi and Yangtze (Changjiang) River Basins*, *84*, 263–291.
Wang, Y. Y., Yu, X. B., Xu, J., Li, W. H., & Fan, N. (2012). Temporal variation of energy sources in a floodplain lake fish community. *Journal of Freshwater Ecology*, *27*, 295–303.
Wang, Y. Y., Yu, X. B., Zhang, L., & Lei, G. C. (2013). Seasonal variability in baseline delta N-15 and usage as a nutrient indicator in Lake Poyang, China. *Journal of Freshwater Ecology*, *28*, 365–373.
Ward, J. V., Tockner, K., & Schiemer, F. (1999). Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regulated Rivers-Research & Management*, *15*, 125–139.
Warfe, D. M., & Barmuta, L. A. (2006). Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia*, *150*, 141–154.
Welcomme, R. L. (1979). *Fisheries ecology of floodplain rivers*. New York, NY: Longman.
Welcomme, R. L. (1985). *River Fisheries. FAO Fisheries Technical Paper*, No.262, (pp. 330).
Winemiller, K. O., & Jepsen, D. B. (1998). Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, *53*, 267–296.
Winemiller, K. O., Tarim, S., Shormann, D., & Cotner, J. B. (2000). Fish assemblage structure in relation to environmental variation among Brazos River oxbow lakes. *Transactions of the American Fisheries Society*, *129*, 451–468.
Xie, S., Cui, Y., & Li, Z. (2001). Small fish communities in two regions of the Liangzi Lake, China, with or without submersed macrophytes. *Journal of Applied Ichthyology*, *17*, 89–92.
Xie, S., Cui, Y., Zhang, T., Fang, R., & Li, Z. (2000). The spatial pattern of the small fish community in the Biandantang lake – A Small shallow lake along the middle reach of the Yangtze River, China. *Environmental Biology of Fishes*, *57*, 179–190.
Xie, S., Cui, Y., Zhang, T., & Li, Z. (2000). Seasonal patterns in feeding ecology of three small fishes in the Biandantang Lake, China. *Journal of Fish Biology*, *57*, 867–880.
Xie, S. G., Li, Z. J., Cui, Y. B., & Murphy, B. R. (2005). Distribution, feeding and body condition of four small fish species in the near-shore and central areas of Liangzi Lake, China. *Environmental Biology of Fishes*, *74*, 379–387.
Xu, G. X., & Qin, Z. Q. (1998). Flood estimation methods for Poyang lake area. *Journal of Lake Sciences*, *10*, 31–36.
Yamamoto, M. N., & Tagawa, A. W. (2000). *Hawai'i's native and exotic freshwater animals*. Honolulu, HI: Mutual Publishing.
Yang, S., Li, M., Zhu, Q., Wang, M., & Liu, H. (2015). *Spatial and temporal variations of fish assemblages in Poyang Lake. Resources and Environment in the Yangtze Basin*, 54–64.
Ye, S. W., Li, Z. J., Lek-Ang, S., Feng, G. P., Lek, S., & Cao, W. X. (2006). Community structure of small fishes in a shallow macrophytic lake (Niushan Lake) along the middle reach of the Yangtze River, China. *Aquatic Living Resources*, *19*, 349–359.
Ye, S. W., Li, Z. J., Liu, J. S., Zhang, T. L., & Xie, S. G. (2011). Distribution, endemism and conservation status of fishes in the Yangtze River basin, China. In O. Grillo (Ed.), *Ecosystems biodiversity* (pp. 41–66). Rijeka: InTech.
Yu, J. L., Liu, Z. W., He, H., Zhen, W., Guan, B. H., Chen, F. Z., & Jeppesen, E. (2016). Submerged macrophytes facilitate dominance of omnivorous fish in a subtropical shallow lake: Implications for lake restoration. *Hydrobiologia*, *775*, 97–107.
Zeng, Z., Zhang, X., Liu, G., Jin, J., Chen, J., & Jin, B. (2015). Structure and features of fishery resources of sub-lakes in Poyang Lake, Jiangxi, China. *Resources and Environment in the Yangtze Basin*, *24*, 1021–1029.
Zeug, S. C., Winemiller, K. O., & Tarim, S. (2005). Response of Brazos River oxbow fish assemblages to patterns of hydrologic connectivity and environmental variability. *Transactions of the American Fisheries Society*, *134*, 1389–1399.
Zhang, B. (1988). *Studies on Poyang lake*. Shanghai, China: Shanghai Scientific and Technical Publishers. (in Chinese).

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