

Estimation of minimum area requirement of river-connected lakes for fish diversity conservation in the Yangtze River floodplain

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ABSTRACT

Aim Hydrological disconnection of floodplains from rivers is among the top factors threatening river-floodplain ecosystems. To keep enough floodplain area is of great importance to biodiversity conservation. In the Yangtze River floodplain, most lakes were disconnected from the mainstream by dams in 1950–1970s. By analysing fish diversity data, we aim at determining the effects of river-lake disconnection on fish diversity, at estimating the minimum protected area of river-connected lakes and at proposing a holistic strategy for fish conservation in the mid-lower reaches of the river.

Location The Yangtze River floodplain, China.

Methods We collected recorded data of fish diversity of 30 Yangtze floodplain lakes. Species–area relationships were analysed and compared between river-connected and river-disconnected lakes. Cumulative species–area models were constructed to estimate the minimum protected area of river-connected lakes.

Results River-lake disconnection reduced fish diversity of Yangtze lakes by 38.1%, so that the river-connected lakes play an important role in maintaining the floodplain biodiversity. The minimum protected area of river-connected lakes was estimated to be 14,400 km². Therefore, we should not only protect the existent connected lakes of 5500 km², but also reconnect disconnected lakes of at least 8900 km² in the Yangtze basin.

Main conclusions Species–area relationships are of importance in reserve design. We suggest that cumulative species–area model might be more suitable for ecosystems with high connectivity among regions such as floodplains. As the Yangtze River floodplain is an integrative ecosystem, we suggest establishing a holistic nature reserve in the mid-lower basin for effective conservation of biodiversity.

Keywords

Cumulative species–area model, holistic conservation strategy, hydrological connectivity, protected area, river-lake disconnection, species diversity.

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INTRODUCTION

Floodplains are among the most threatened ecosystems in the world because of high levels of biodiversity and bioproduction (Tockner & Stanford, 2002; Revenga *et al.*, 2005). Their rich resources have attracted human use and occupancy, often to the detriment of the very processes that generate valued ecosystem benefits (Sala *et al.*, 2009; Tockner *et al.*, 2010). Floodplain ecosystems are particularly vulnerable to flow

regime alteration and other stresses associated with human occupancy and use of catchment resources (Tockner *et al.*, 2008). Obstruction of lateral hydrological connectivity, i.e. river-floodplain disconnection, is one of the top threats to floodplains (Saunders *et al.*, 2002; Revenga *et al.*, 2005). The negative effects of such disconnections on floodplain ecosystems include blocking the exchange of matter, energy and organisms between a river and its floodplain, decreasing habitat area and heterogeneity, reducing opportunities for fish

to exploit rich floodplain resources during early life history stages and eliminating the benefits of intermediate disturbance of river dynamics on floodplain biological communities (e.g. Amoros & Bornette, 2002; Wang & Wang, 2009). Among the affected organisms, fishes are one of the most vulnerable groups (Heiler *et al.*, 1995; Welcomme *et al.*, 2006). Therefore, the maintenance of natural hydrological connectivity is of great importance to the conservation of fishes and other organisms (Saunders *et al.*, 2002; Dudgeon *et al.*, 2006).

Establishing protected areas is widely regarded as one of the most effective strategies for biodiversity conservation (Saunders *et al.*, 2002; Dudgeon *et al.*, 2006). However, determination of the minimum area requirement is considered to be difficult in freshwater systems (Saunders *et al.*, 2002). One approach used for estimating the minimum protected area in terrestrial reserve design is based on the estimation of minimum viable population (MVP) of target or keystone species (e.g. Soule & Simberloff, 1986; Brito & Grelle, 2006). As it requires long-term monitoring data (30–40 years for most vertebrates) (Jiang *et al.*, 1997; Reed *et al.*, 2003), MVP was seldom used for fishes, especially those in large floodplains, because fish population sizes are more difficult to determine, and the long-term data are scarce (Tockner & Stanford, 2002). Furthermore, MVP deals with the target species rather than entire biota. The estimated area (MVP/density) could not ensure the existence of the total biodiversity even though the target species are well protected. An alternative approach for the estimation of minimum protected area is based on the species–area relationship, which is regarded as one of the few generalizations in ecology (Schoener, 1976; Green *et al.*, 2004). It is most commonly expressed by the power model ($S = cA^z$) or the semi-log model ($S = c + z\log_{10}A$) (Lomolino, 2000), where S is species number, A is area, c and z are fitted constants. Species–area relationships were usually applied in terrestrial reserve design (e.g. Shafer, 1990; Gurd *et al.*, 2001). The approach is also applicable in floodplain waters such as river-connected lakes that are relatively homogenous under similar flow regimes (Liu, 1984). The species–area relationship approach is very simple and robust. It needs only two simple parameters, i.e. the species richness and the size of area. This advantage makes it possible to estimate the minimum protected area for those waterbodies where fish diversity is seriously threatened but the ecology is not well understood.

The Yangtze River floodplain is one of the largest floodplains of the world, where hundreds of shallow lakes were connected with the mainstream. Fish fauna of this region was rich in species, with the presence of about 3% of known freshwater fish species of the world (Chen *et al.*, 2002). From 1950s to 1970s, most lakes were disconnected from the Yangtze River by dams or sluice gates, leaving few connected lakes at present. The dams or gates not only form physical barriers between the river and its floodplain lakes, but also reduce or eliminate hydrological connectivity of the floodplain ecosystem (Wang & Wang, 2009). Previous studies on the effects of river-lake disconnection in this area were concentrated on migratory fishes (e.g. Liu & Cao, 1992; Chang & Cao, 1999; Li, 2001; Wang *et al.*, 2005), and conservation practices have been

focused on a few species of high economic value such as the four Chinese carps (e.g. Li, 2001). The impact of disconnection on the others including about 20% endemic fishes was neglected, but it is very likely to be negative. Hence, the present study attempts to examine the effects of river-lake disconnection on all fishes of the Yangtze floodplain lakes and to estimate the minimum requisite area of protected river-connected lakes for the conservation of total fish diversity using species–area models.

METHODS

We collected fish diversity data for mid-lower Yangtze floodplain lakes from published fish surveys since 1950s. To ensure good quality of the dataset, we excluded those studies with poor sampling efforts (survey time less than 1 year). If a lake was surveyed for several times under similar hydrological connectivity, we chose the earliest data as they may represent a state with fewer disturbances. Finally, we used fish diversity data of 30 Yangtze lakes to analyse the effects of river-lake disconnection (Fig. 1, see Appendix S1 in Supporting Information).

The lakes are located in the mid-lower reaches of the Yangtze River, covering a narrow range of latitude (29°51′–32°50′) and a wide range of longitude (111°53′–120°48′) (Fig. 1; Appendix S1). The altitude of these lakes ranges from 3.0 to 34.5 m above Huang Hai mean sea level. The annual mean air temperature is 15.0–18.5°C, and rainfall is 867–1570 mm. They are all shallow lakes with a mean water depth of 1.2–6.4 m. Lake areas covered a wide range of 1.9–4554.7 km² at ordinary water level. The lakes were classified into two groups: (1) river-connected lakes, freely connected with the Yangtze mainstream and (2) river-disconnected lakes, severed from the mainstream by dams or sluice gates. The disconnected lakes discharged into the mainstream and occasionally received river water for irrigation in dry years and for diversion in flood disasters. The dataset examined in the present study includes 10 river-connected lakes and 23 river-disconnected lakes. For three lakes, i.e. Lake Zhangduhu, Lake Honghu and Lake Taihu, data are available both before and after disconnection.

Fish surveys were carried out in 1950–1990s for river-connected lakes, and in 1990–2000s for disconnected lakes. Field survey of each lake was conducted for more than 1 year (most surveys > 3 years), ensuring that almost all fishes inhabiting the lakes would have been collected (Appendix S1). Fishes were caught by fish trap, gill net and trawl net. The validity of fish species was checked using recent taxonomical monographs (Chen, 1998; Chu *et al.*, 1999; Yue, 2000). Most species are distributed all over the Yangtze River floodplain. Fish stocking was common in the disconnected lakes, and some species (mainly four Chinese carps) were released to the mainstream annually to enhance the population size (Li, 2001). We are incapable of distinguishing stocked species from natural ones; however, this might have little effect on our results because stocked species were mostly native, and the number was rather small (usually 3–5 species for a lake). Exotic species were excluded for analyses.

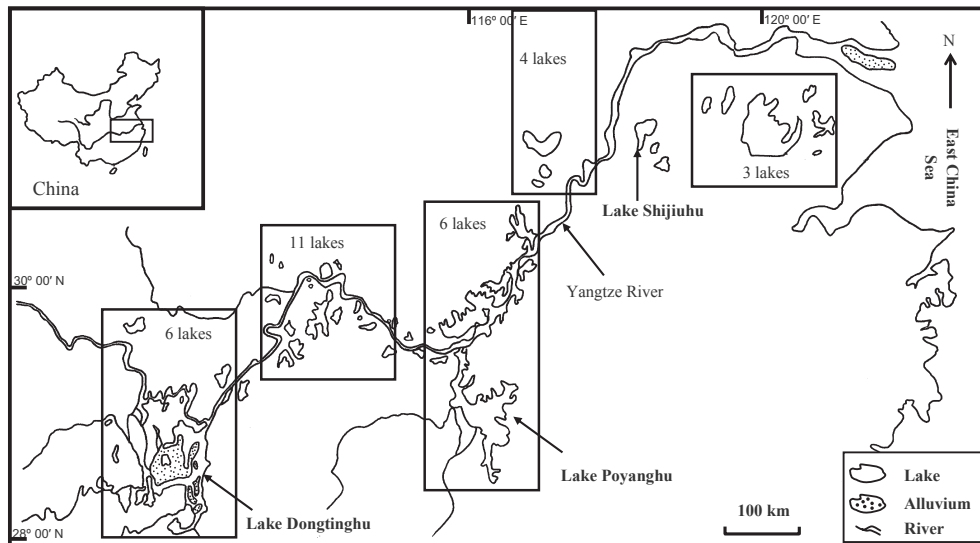


Figure 1 Distribution of lakes used for analyses in the Yangtze River floodplain.

Species number ranged from 33 to 116 in each lake. Fish species were classified into four habitat guilds, viz. river-sea migratory fishes, river-lake migratory fishes, riverine fishes and lake resident fishes (Chen, 1998; Chu *et al.*, 1999; Yue, 2000). River-sea migratory fishes include anadromous and catadromous species. River-lake migratory fishes spawn in the Yangtze mainstream and grow in the floodplain waters. Riverine fishes are rheophilic species and occurred in both river channel and associated lakes. Lake resident fishes (i.e. limnophilic species) mainly inhabit lentic waters. In disconnected lakes, the occurrence of some migratory fishes was mainly because of fish stocking and river water input through sluice gates. Three species of marine fishes (*Odontamblyopus rubicundus* (Hamilton), *Taenioides anguillar* (B. et T.), and *Taenioides cirratus* (Blyth)) were also found in a lake, but they were excluded for analysis because of their rarity.

To examine the effects of river-lake disconnection, we plotted fish species richness of river-connected lakes and river-disconnected lakes on the areal gradient; lake area was shown to be the only factor significantly correlated with species richness ($P < 0.05$) among the geographical and climatic factors. The data were fitted to the commonly used power model ($\log_{10}S = c + z \log_{10}A$) (Lomolino, 2000).

To estimate the minimum protected area, we constructed species–area model (Lomolino, 2000) and cumulative species–area model (Scheiner, 2003; Magurran, 2004) in which species richness was cumulated by progressively adding the number of new species gained with each increase in lake area. For each model, three kinds of submodels were tested as linear regression (S/A), semi-log model ($S/\log_{10}A$) and power model ($\log_{10}S/\log_{10}A$) (Sfenthourakis, 1996). The optimum models were determined to estimate the minimum protected areas for the total fish species and each habitat guild.

Data analyses were conducted with STATISTICA 8.0 and EXCEL 2007.

RESULTS

Table 1 and Fig. 2 present the species–area relationships of each habitat guild and the number of all fishes in the river-connected and river-disconnected lakes. Data for the disconnected lakes were better fitted by the power model than that of the river-connected lakes (Table 2). Fish diversity was lower in disconnected lakes (Fig. 2). A *t*-test also showed that the differences of mean species richness between the two lake groups were significant ($P < 0.05$, Table 1). The total species number in disconnected lakes attained a reduction of 38.1% on average (Fig. 2e). This was also the case when a single lake was concerned. For example, fish species of Lake Taihu has been reduced from 106 to 57 species as disconnection (see Appendix S1). In terms of habitat guilds in disconnected lakes, river-sea migratory fishes was reduced by 87.5%, riverine fishes by 71.7%, river-lake migratory fishes by 40.6% and lake resident fishes by 25.4% (Fig. 2a–d).

To determine the optimum models for estimating the requisite minimum protected area of river-connected lakes, species–area models and cumulative species–area models were constructed and compared (Table 2). Models for all habitat guilds except river-lake migratory fishes indicated significant relationships between species richness and lake area. Cumulative species–area models were more powerful (much higher R^2 values) than species–area models for all habitat guilds, thus were used to estimate the minimum protected areas. Among the three submodels of cumulative species–area models, semi-log models were the best fitted models, followed by power models and linear regressions (Table 2). The minimum protected areas calculated by the submodels were compared (Table 3). Although semi-log models were the best fitted models for the total fishes, lake resident fishes and riverine fishes, the minimum protected areas calculated accordingly were too large to exceed the total area of present lakes (about

Table 1 Species–area regression models of fishes in river-connected and river-disconnected lakes in the Yangtze River floodplain.

Habitat guilds	Regression models ($\log_{10}S = c + z \log_{10}A$)				Difference of mean species richness between two lake groups (<i>t</i> -test) (df = 31, $t_{0.05,31} = 2.040$)
	<i>c</i>	<i>z</i>	<i>P</i>	<i>R</i> ²	
River-disconnected lakes (<i>n</i> = 23)					
River-sea migratory fishes	−0.0378	0.1298	0.0073*	0.2962	7.219*
River-lake migratory fishes	0.7352	0.0156	0.7485	0.0050	6.893*
Lake resident fishes	1.5032	0.0674	0.0020*	0.3713	4.478*
Riverine fishes	0.0162	0.2664	0.0006*	0.4346	5.304*
Total species	1.5831	0.0772	0.0010*	0.4076	6.269*
River-connected lakes (<i>n</i> = 10)					
River-sea migratory fishes	0.3898	0.1545	0.0105*	0.5801	
River-lake migratory fishes	1.0131	0.0013	0.9009	0.0021	
Lake resident fishes	1.6757	0.0298	0.2128	0.1864	
Riverine fishes	0.6709	0.1532	0.1249	0.2685	
Total species	1.7972	0.0531	0.0790	0.3370	

*Significant correlation or difference (*P* < 0.05).

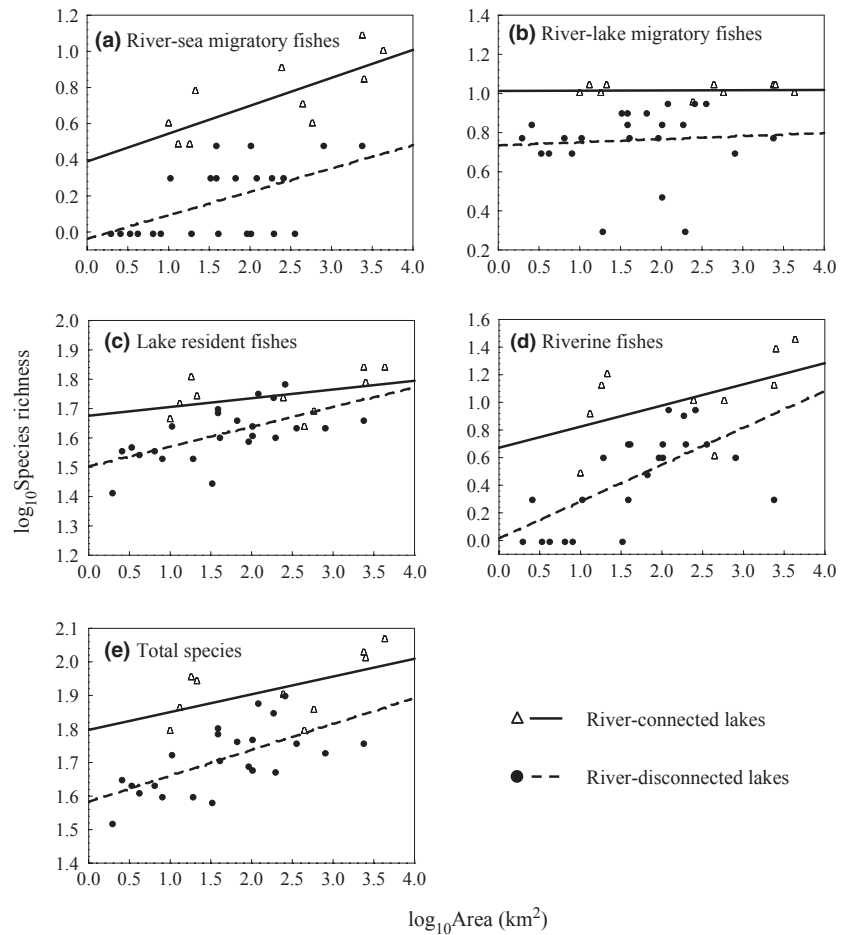


Figure 2 Species–area relationships of fishes in river-connected and river-disconnected lakes in the Yangtze River floodplain. The regression equations are given in Table 1.

16,600 km²), thus were inapplicable. We then used the power models according to which the minimum protected area was estimated to be 14,400, 13,500 and 11,400 km² for conservation of the total fish diversity, lake resident fishes and riverine

fishes, respectively (Fig. 3a,d,e). The minimum protected area for conservation of river-sea migratory fishes was estimated to be 7500 km² by the power model (Fig. 3b). Regarding the river-lake migratory fishes, the three submodels were not

Table 2 Comparison of different models used to estimate the minimum areal requirement of river-connected lakes for fish diversity conservation in the Yangtze River floodplain.

Habitat guilds	Models ($y = c + zx$) [S = species richness, A = area (km^2), $n = 10$]								$\frac{R_2^2}{R_1^2}$
	Species–area models				Cumulative species–area models				
	c	z	P_1	R_1^2	c	z	P_2	R_2^2	
Total species richness									
S/A	74.0100	0.0098	0.003	0.70	105.0041	0.0067	0.006	0.63	0.9
$S/\log_{10}A$	59.5149	11.0049	0.059	0.38	49.9162	27.6309	<0.001	0.90	2.4
$\log_{10}S/\log_{10}A$	1.7972	0.0531	0.079	0.34	1.7905	0.1076	<0.001	0.84	2.5
River-sea migratory fishes									
S/A	3.5937	0.0015	0.013	0.56	6.1051	0.0010	0.003	0.69	1.2
$S/\log_{10}A$	0.1572	2.1861	0.014	0.55	-1.2848	3.7540	<0.001	0.90	1.6
$\log_{10}S/\log_{10}A$	0.3898	0.1545	0.011	0.58	0.3122	0.2152	<0.001	0.92	1.6
River-lake migratory fishes									
S/A	10.3532	4.2315E-5	0.793	0.01	10.8537	1.925E-5	0.529	0.05	5.6
$S/\log_{10}A$	10.3246	0.0327	0.894	0.002	10.5147	0.1494	0.132	0.26	108.7
$\log_{10}S/\log_{10}A$	1.0131	0.0013	0.901	0.002	1.0213	0.0062	0.132	0.26	124.2
Lake resident fishes									
S/A	51.6389	0.0041	0.023	0.50	70.9491	0.0028	0.022	0.50	1.0
$S/\log_{10}A$	46.8020	4.0742	0.183	0.21	45.4162	12.5138	<0.001	0.84	4.0
$\log_{10}S/\log_{10}A$	1.6757	0.0298	0.213	0.19	1.6860	0.0760	<0.001	0.77	4.1
Riverine fishes									
S/A	8.3630	0.0041	0.005	0.65	17.0465	0.0027	0.003	0.69	1.1
$S/\log_{10}A$	2.5506	4.4867	0.078	0.34	-3.5118	10.5090	<0.001	0.87	2.6
$\log_{10}S/\log_{10}A$	0.6709	0.1532	0.125	0.27	0.6018	0.2660	0.002	0.72	2.7

suitable for the estimation of minimum protected area because of the poor relationship between species richness and lake area (Table 2). According to the scatter plot, the river-lake migratory fishes reached the maximum species number when lake area increased to about 30 km^2 , which was probably the minimum area requirement of the fish (Fig. 3c).

DISCUSSION

By comparing species–area relationships of fishes in river-connected and river-disconnected lakes (Fig. 2), our study shows that river-lake disconnection has seriously reduced fish diversity in lakes on the Yangtze River floodplain. River-lake disconnection significantly affects all four fish guilds, with species preferring lotic waters suffering most. Previously, negative effects of hydrological disconnection on fish diversity were also reported from river floodplains in the USA and Europe (Schiemer & Waidbacher, 1992; Guti, 1995; Galat & Zweimüller, 2001). The reduction in fish diversity after river-lake disconnection should be attributed mainly to the blockage of migration routes, the loss of fluvial environments in which some species spend a part of their life cycle and decreased habitat heterogeneity. Therefore, river-connected lakes play an important role in maintaining the Yangtze River's floodplain biodiversity, and it is crucial to keep sufficient area of such waters for biodiversity conservation.

Considering that each river-connected lake is a part of the whole floodplain ecosystem and most fish species are widely

distributed along the mid-lower reaches of the Yangtze River (Liu, 1984), we construct the cumulative species–area model to estimate the minimum area requirements of river-connected lakes. Such a regional scale model may largely reflect the relationship of species number with habitat diversity (Neigel, 2003). In comparison with the species–area model, we believe that the cumulative one is more suitable for estimating protected area requirements. First, the estimated area is the sum of river-connected lakes to be protected and restored, and thus, is a cumulative value itself. Second, the cumulative species–area model is more powerful, and the result may be more reliable. In other ecosystems with high connectivity among different regions, cumulative species–area relationships could be applicable in the estimations of area requirements for biodiversity conservation.

The minimum protected areas of river-connected lakes were determined to be different among habitat guilds in the Yangtze River floodplain. Lake resident fishes have the highest area requirement, indicating that their protection may need a larger area of lake habitats that is still connected to lotic habitats. The river-lake migratory fishes have the lowest area requirement, suggesting that lake area is not the chief factor limiting their diversity in floodplain waters. It may be more important to maintain free (unblocked) passage (i.e. connectivity) along their migration routines between the river and individual lakes (Wang *et al.*, 2005; Wang & Wang, 2009). Dealing with the conservation of total fish fauna of the mid-lower Yangtze River, the minimum protected area of river-connected lakes

Table 3 Comparison of minimum protected area estimated by different cumulative species–area models.

Habitat guild	Conservation target	Minimum protected area estimated (km ²)		
		S/A	S/log ₁₀ A	log ₁₀ S/log ₁₀ A
Total species	173	10,100	28,500	14,400
River-sea migratory fishes	14	7900	11,800	7500
River-lake migratory fishes	11	–	–	–
Lake resident fishes	100	10,400	23,000	13,500
Riverine fishes	48	11,500	79,800	11,400

–, not estimated because of poor relationship between the two variables.

was estimated to be 14,400 km². Such an area can also meet the requirements of all habitat guilds. Therefore, we recommend that at least 14,400 km² of river-connected lakes should be preserved for total fish conservation in the Yangtze floodplain lakes.

The World Conservation Union (IUCN) recommended that at least 10% of the land area should be set aside for biodiversity conservation (IUCN, 1993). However, such a target is clearly

insufficient for fish diversity conservation in the Yangtze River floodplain. The minimum protected area estimated in this study accounts for 55.8% of the total area of lakes before the heavy reclamation of land from lakes in the 1950s, and up to 86.7% of the total area that remains today (Shi & Qin, 2007). As the total lake area presently connected to the river is only about 5500 km², at least 8900 km² of disconnected lakes need to be reconnected with the Yangtze mainstream. For effective conservation of fish diversity, we should take into account not only the protection of existing connected lakes but also the restoration of connectivity between disconnected lakes and the main river channel.

The existing river-connected lake area in the Yangtze River floodplain is contributed mainly by two large-sized lakes, Lake Poyanghu (current area 2520 km²) and Lake Dongtinghu (current area 2625 km²), and one medium-sized lake, Lake Shijiuhu (current area 210 km²) (see Fig. 1). They could be regarded as ‘hotspots’ while considering fish diversity conservation in the floodplain because they maintain rich species (Please see Appendix S1) and diverse habitats (Dou & Jiang, 2000; Zhang & Li, 2007). However, fishes in these lakes are facing serious threats, such as overfishing, sand excavation, water pollution and unusually low water level in dry seasons because of flow regulations by upstream reservoirs and climate change (e.g. Shen *et al.*, 2007; Li *et al.*, 2008; Ru *et al.*, 2008;

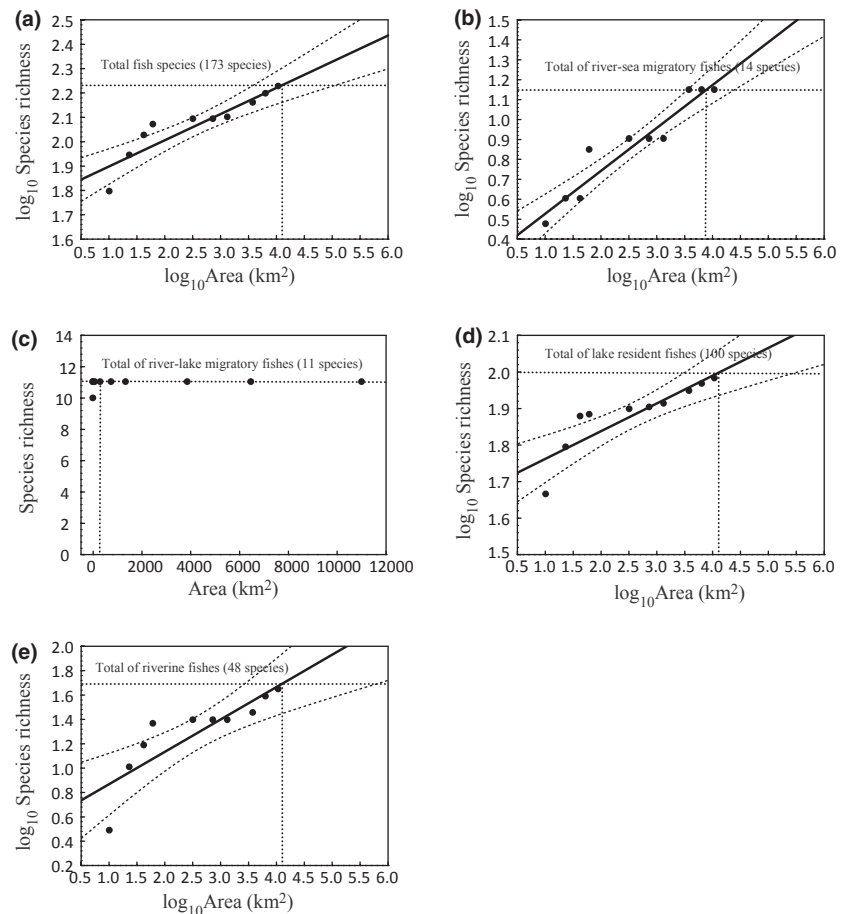


Figure 3 Estimation of minimum protected area for fish diversity conservation in Yangtze floodplain lakes. The regression equations are given in Table 2.

Zhang & Huang, 2008). Although the central government has banned fishing in spring in the Yangtze and connected lakes since 2002, the protection achieved appears to be rather limited. Numerous juvenile fish are being caught in the open fishing seasons with illegal fishing gears (Wang *et al.*, 2005), and the fish yield (only 0.2% of that in the country at present) has decreased from 4.3×10^5 to 1.0×10^5 t/a between the 1950s and 2000s. We propose that commercial fishing in the Yangtze and connected lakes should be banned all the year round, and a core protected area, where all human activities are forbidden, should be demarcated. In addition, it is necessary to re-operate the upstream dams to meet the ecohydrological requirements and connectivity of the connected lakes.

Regarding the disconnected lakes, as the river-lake dams and sluice gates are significantly important to flood control, water supply, irrigation, etc. (Wu, 2000), it is inappropriate to remove them completely. A feasible solution is to open particular dams periodically to restore fish migration routes and to increase habitat heterogeneity. We suggest that those lakes considered as potential hotspots and with relatively good conservation potential, such as the wetland nature reserve (a group of lakes) along the Yangtze River in Anqing (Hu & Wang, 2003), should be given priority.

Protection of lake area is not sufficient to protect the fish diversity of the mid-lower Yangtze floodplain ecosystem. We need also to determine the optimum selection of reconnected lakes and their spatial pattern in the landscape, and how to reconnect them with the Yangtze mainstream. To address these issues, we should further study (1) life history processes of fishes, especially spawning grounds and seasonal patterns of recruitment from different habitats, migration routes, the timing of migration of the different fish habitat and life history guilds into and out of lakes and (2) environmental flow requirements of fishes and related organisms (e.g. macrophytes, benthos) in the river system, including flow magnitudes and frequencies required to maintain the diversity of habitats and the connectivity pathways required by fish guilds and species. As tentative measures to meet the urgent need of fish conservation, we may first construct a restoration framework on the basis of the fish diversity patterns, ecological health and spatial distribution patterns of disconnected lakes and then reconnect these lakes with the Yangtze mainstream as frequently as possible.

As an integrated ecosystem, the Yangtze River floodplain should be restored and protected as part of a restoration strategy for the whole river basin. However, current restoration measures are largely restricted to limited areas, with the focus upon a few endangered species (Li, 2001). In the present paper, we suggest a holistic strategy of restoration to protect the entire fish assemblage of the mid-lower river-floodplain ecosystem and estimate the minimum protected area of river-connected lakes using the cumulative species–area model of fishes. As fishes are on the higher trophic level relative to most aquatic organisms, the estimated area of connected lakes could also be applied to a majority of other taxa. By incorporating the needs

of wetland birds, dolphins and other taxa, we hope to establish a holistic nature reserve to protect the Yangtze River–floodplain ecosystem in the near future, through joint efforts of governments, NGOs (nongovernment organizations), scientists, stakeholders and the public.

ACKNOWLEDGEMENTS

The research was funded by the State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology (2008FBZ03), Chinese Academy of Sciences (KZCX2-YW-426-02) and World Wild Fund for Nature (WWF) (CN087901-2.3.02.03). We thank Profs Yanling Liang, Angela Arthington and Dr Robert Rolls for their invaluable comments on the manuscript and help during X.L.'s visit to Australian Rivers Institute, Griffith University, Australia. Thanks to Dr Mathieu Rouget and two anonymous reviewers for their invaluable comments on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Fish species richness and lake area used for analyses in the study. Data were arranged by lake area.

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Editor: Mathieu Rouget