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Potential effects of dam cascade on fish: lessons from the Yangtze River

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Abstract Construction of hydroelectric dams affect river ecosystems, fish diversity, and fisheries yields. However, there are no studies assessing the combined effects on fish caused by several adjacent dams and their reservoirs, as in a 'dam cascade'. This study predicts the potential effects that a cascade of ten dams currently under construction in the upper Yangtze River in China will have on local fishes, and uses such predictions to assess the effectiveness of possible fish conservation measures. We found that the dam cascade will have serious combined effects on fishes mainly due to impoundment, habitat fragmentation and blocking, flow regime modification, and hypolimnetic discharges. The impoundments will cause loss of critical habitats for 46 endemic species. The dams will fragment the populations of 134 species and will block migration routes for 35 potamodromous fishes. *Corieus guichenoti* will have a high risk of extinction due to the combined effects of impoundment and blocking. Modification of the flow regime will adversely affect the recruitment of 26 species that produce drifting eggs. The start of annual spawning for 13 fishes will be postponed by more than 1 month, and fish spawning and growth opportunities will be reduced due to low water temperatures associated with hypolimnetic discharges. Combined dam effects will further reduce the likelihood of successful recruitment of some endangered species, such as *Acipenser dabryanus* and *Psephurus gladius*. Three countermeasures hold promise to mitigate the near-term effects of the dam cascade, including preservation and rehabilitation of critical habitat, restoration of a semi-natural flow regime, and stock enhancement that respects genetic integrity. These conclusions can guide the development of protection plans for fishes in the upper Yangtze River. The approach undertaken in this study—by which the known and likely effects of present and future dams were simultaneously

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considered in light of the biology of the species—highlights the usefulness of ichthyology for fish conservation.

Keywords Combined effects · China · Conservation · Flow regime · Extinction · Biodiversity

Introduction

Construction of hydroelectric dams affect river ecosystems and undermine fish diversity and fisheries yields (Poff et al. 2007; Jiao et al. 2007; Wang et al. 2013). The effects of individual dams on fish diversity have been studied extensively and are now relatively well understood (López-Pujol and Ren 2009; Young et al. 2011; Azami et al. 2012). Nevertheless, economic growth in many regions of the world is spurring demand for renewable energy sources, leading to the construction of many additional hydroelectric dams. In some river basins, many large hydroelectric dams are being constructed downstream from each other, as in a 'dam cascade', to maximize energy production from available rivers. Although effects of dam cascade on fishes have been considered in some studies (e.g. Petesse and Petrere 2012; Petessea et al. 2014; Zhang et al. 2015), the effects of dam cascade on fish diversity and community in river systems have not been documented.

Previous studies on individual dams have revealed upstream and downstream effects on fish fauna. Upstream of the dams, impoundment modifies channel habitats by changing them from lotic to lentic, thereby increasing the risks of extirpation of habitat specialists and invasion of exotic species (Rahel 2002; Moyle and Mount 2007; Barletta et al. 2010). Dams block migration routes (e.g. *Acipenser sinensis*) and cause loss of spawning and nursery habitats for certain species (Wei et al. 1997; Xie et al. 2007; Gao et al. 2013), fragment genetic flows, reduce the fitness of subpopulations, and enhance the risk of species extinction (Lukas et al. 2001; Willi et al. 2007; Roberts et al. 2013). Downstream of the dams, the seasonality of water levels that characterizes many large naturally flowing rivers is altered, reducing spawning opportunities and survival rates of juveniles (Nesler et al. 1988; Dudley and Platania 2007; Young et al. 2011). Alteration of water temperature and water chemistry (e.g., in a hypolimnetic discharge) affects spawning of fish and development of fish larvae (Wolf and Willis 1996; Zhang et al. 2012).

The effects caused by dam cascade on fish are difficult to predict. Nevertheless, dam cascade are expected to cause effects on fish that are cumulative and therefore much stronger than those caused by individual dams alone. Dam cascade for hydropower production are increasingly common worldwide, such as in the Amazon, Mekong, and Yangtze River Basins (Yang et al. 2008; Kang et al. 2009; Castello et al. 2013). Scarcity of information about the cumulative effects of dam cascade on fish, however, is currently limiting the formulation of fish conservation measures.

This study predicts the effects that a cascade of ten dams under construction in the upper Yangtze River in China will have on local fishes, and uses such predictions to assess the effectiveness of potential fish conservation measures. The upper Yangtze River is located upstream from Yichang (30°41′N, 111°17′E) and is divided into three segments, i.e., the headstream, the Jinsha segment, and the upper mainstem. It harbors a diverse fish fauna (He et al. 2011; Cheng et al. 2013a) and is one of the "Global 200 Ecoregions" of the World Wildlife Fund (Olson and Dinerstein 1998). In this river, the construction of the Three Gorges Reservoir alone was thought to threaten 20 endemic species and to cause high extinction risk for six fish species mainly due to the environmental changes occurring in the reservoir after filling (Park et al. 2003), so the further ten dams that are under construction may be expected to cause even more-severe effects on fish fauna and biodiversity.

Study area and data collection

Study area

The study area includes the Jinsha and the upper mainstem segments and does not include the headstream segment in the Yangtze River. The Jinsha segment (or Jinsha River) is located between Yushu (32°31′N, 97°43′E) and Yibin (28°46′N, 104°37′E), whereas the upper mainstem segment is between Yibin and Yichang (Fig. 1). The Jinsha segment is about 2300 km in length. It is a deep canyon river with steep gradient, staggered shoals, and rapids. The

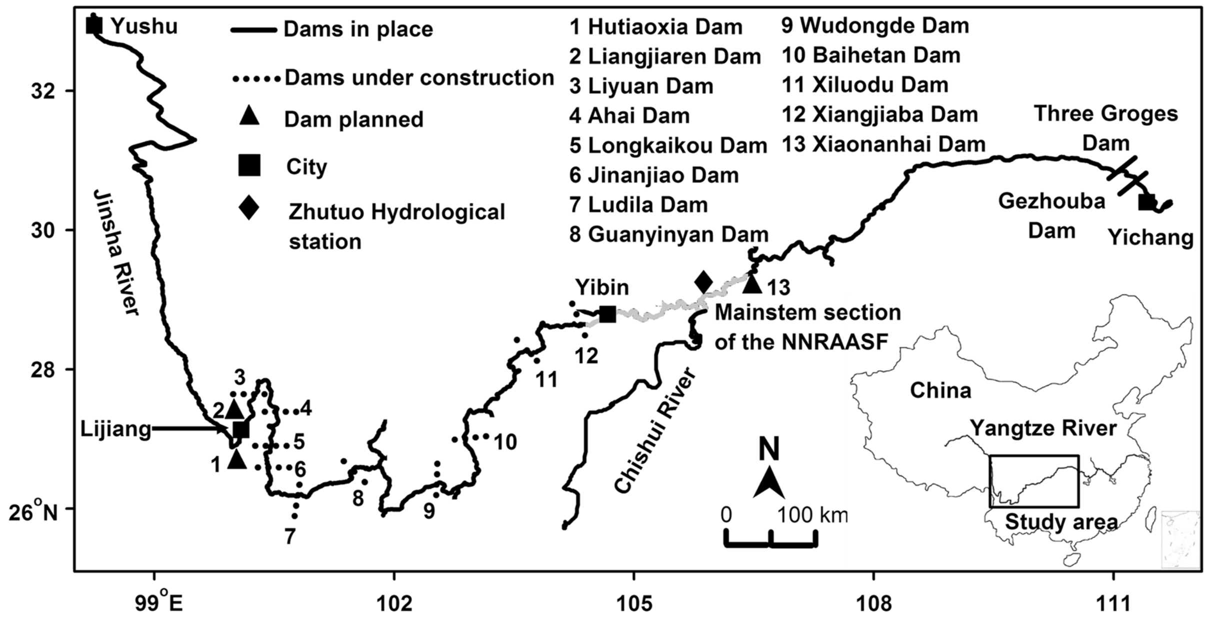

Fig. 1 Location of study area, dams, and the Zhutuo Hydrological station in the upper Yangtze River. The study area includes the Jinsha segment (or Jinsha River) is located between Yushu and Yibin, and the upper mainstem segment is located between Yibin and Yichang. Location of dam in place, dam under construction, dam planned, and the Zhutuo Hydrological station is labeled using *different symbols*. Mainstem section of the National Natural Reserve Areas of Rare and Special Fishes of the Upper Yangtze River (NNRARSF) is showed using *gray*. The Ahai Dam, the Longkaikou Dam, the Jinanjiao Dam, the Guanyinyan Dam, the Xiluodu Dam, and the Xiangjiaba Dam have begun electricity generation since December 2011, May 2013, March 2011, December 2014, July 2013, and October 2012, respectively. The Liyuan Dam and the Ludila Dam have begun impoundment since November 2014 and June 2013, respectively. The Hutiaoxia Dam, the Liangjiaren Dam, and the Xiaonanhai Dam are three planned dams in the upper Yangtze

channel of the Jinsha segment is usually narrower than 50 m. Water levels fluctuate strongly between flood and drought seasons. Flow velocity reaches up to 7 m/s during flood season (Ding 2006; Yi 2011). The upper mainstem segment is about 1100 km in length. It passes through undulating hilly land with staggered shoals and rapids, and has more moderate environmental conditions than the Jinsha segment. The channel of the upper mainstem segment is 300–400 m in width, and 10–35 m in depth. Fluctuations in water levels become smaller, and flow velocity slows down, as the river widens downstream (Liu and Cao 1992; Yi 2011). A major part of the upper mainstem segment had been impounded by the Three Gorges Reservoir. In this study, we mainly considered the lotic segment of the upper mainstem to analyze the effects of the proposed dam cascade.

The Gezhouba Dam and Three Gorges Dam built on the upper Yangtze River were impounded in 1981 and 2003 respectively. The Gezhouba Dam was the first dam constructed on the mainstem of Yangtze River, and is 38 km downstream of the Three Gorges Dam (Fig. 1). Upstream of the Three Gorges Reservoir, ten other dams are now already under construction in the middle and the low reaches of the Jinsha segment with six dams have been electricity generation, two dams have been impoundment, and other two dams still not impounded (Fig. 1). Another two dams are planned to be constructed in the middle Jinsha segment; and one dam is planned in the upper mainstem segment (Yang et al. 2008; Fig. 1).

Data collection and analysis

First, a comprehensive inventory of fish fauna in this section of the Yangtze River was compiled from the published literature. Discrepancies in nomenclature and taxonomy were resolved according to newly published literature. In some cases, qualified staff at the Hydrobiology Museum of the Institute of Hydrobiology, Chinese Academy of Sciences, was consulted to verify species identification. All scientific names were revised according to Nelson (2006) and FishBase (http://www.fishbase.org). Information on distribution, spawning grounds, characteristics of eggs, migratory behavior, spawning seasons, cues, and environmental conditions for spawning and duration of incubation was obtained from the literature. Endangered species were identified following Yue and Chen (1998), which were defined according to the system of the International Union for Conservation of Nature (1994). Endemic species in the Yangtze River were identified according to FishBase and Fu et al. (2003).

The ecological requirements of the fish fauna were analyzed to predict effects in light of the likely biophysical changes that will be caused by the dam cascade. Main types of biophysical effects considered were: river impoundment, habitat fragmentation and blocking, alteration of hydrological regime, and hypolimnetic discharge and nutrition retention. The extinction risk for each species was evaluated qualitatively based on available information on its biology and ecology, population size, and predicted effects of the dam cascade without considering effects of conservation measures and other threats. Daily river discharge (m^3/s) measured at the Zhutuo Hydrological station (29°00′N, 105°51′E) during 14 March 2012–22 November 2013 was obtained from National Hydrological Information of China (http://xxfb.hydroinfo.gov.cn) to analyze the alterations of flow regime following the impoundment of the Xiangjiaba and Xiluodu Dams.

The potential effectiveness of common proposed measures, i.e. preserving and rehabilitating habitat, restoring the natural flow regime, stock enhancement, and building of fish passages, to mitigate the negative effects of the dam cascade on local fishes was analyzed based on the biology and ecology of fishes and natural environment of the upper Yangtze River.

Fish fauna

A total of 223 fish species have been recorded in the Jinsha and upper mainstem segments of the Yangtze River; with 205 species in the Jinsha, and 154 species in the upper mainstem (Table 1, see Supplementary Material for detailed information of fish fauna). One-hundred-thirty-six species are found in both the Jinsha and the upper mainstem. Among them, two recorded diadromous fishes (*A. sinensis* and *Anguilla japonica*) had their migratory routes blocked due to the construction of the Gezhouba and Three Gorges Dams, and had disappeared in the Jinsha and upper mainstem segments. The fish fauna in the Jinsha is dominated by small-bodied species of the families of Cobitidae, Homalopteridae, Amblycipitidae and Sisoridae adapted to turbulent flow. Fish fauna in the upper mainstem possesses commercially important Cyprinidae species including the subfamilies Cultrinae (e.g. *Ancherythroculter wangi*), Gobioninae (e.g. *Corieus guichenoti*), and Cyprininae (e.g. *Procypris rabaudi*).

One-hundred-twenty-six species are endemic in the Yangtze River (Table 1). The Cyprinidae, Cobitidae, Homalopteridae, Bagridae, and Sisoridae are the most endemic species-rich families, accounting for 55, 25, 6, 4, and 4 % of the total endemic fishes respectively. For these endemic species, 45 species (e.g. *Liobagrus kingi*, *Nemacheilus obscurus*) are recorded only in the Jinsha, two species (*Ctenogobius szechuanensis* and *Megalobrama elongata*) only in the upper mainstem, and one species (*Triplophysa angeli*) only in the Jinsha and the upper mainstem segments (see Table 1 in Supplementary Material).

Fourteen species are identified as endangered with eleven of them endemic to the Yangtze River (Table 1). Thirteen of the fourteen species occur in the Jinsha with four species only in the Jinsha segment; and eight of them occur in the upper mainstem segment (see Table 1 in Supplementary Material). The endangered *A. sinensis* has disappeared from the Jinsha and upper mainstem segments.

Spawning grounds for 46 species have been reported only in the Jinsha, e.g. *C. guichenoti*, *L. kingi*, *Semilabeo notabilis*, three species (*C. szechuanensis*, *M. elongata* and *Ochetobius elongates*) have been reported to spawn only in the upper mainstem, and three species (*Acipenser dabryanus, Psephurus gladius* and *T. angeli*) have been reported to spawn only in the Jinsha and upper mainstem segments (Table 1). Meanwhile, some commercially important species have their spawning grounds in the upper mainstem segment such as *Corieus heterodon*, *Megalobrama pellegrini*, *Myxocyprinus asiaticus*, *Percocypris pingi*, and *P. rabaudi* (see Table 1 in Supplementary Material).

Thirty-eight species are potamodromous, conducting short-distance reproductive migrations (Table 1). Among them, 20 species are endemic; seven species

Table 1 Summary of the species number information on the biology and ecology of fishes and type of effects expected on the fishes from the proposed dam cascade in the Jinsha and upper mainstem segments of the Yangtze River

Biological and ecological characteristics of fishes and types of dam effects	Number of species
Recorded fishes	
The Jinsha segment	205
The upper mainstem segment	154
Across the Jinsha and upper mainstem segments	136
Endemic species	
Only in the Jinsha segment	45
Only in the upper mainstem segment	2
Only in the Jinsha and upper mainstem segments	1
Endangered species	
The Jinsha segment	13
The upper mainstem segment	8
Across the Jinsha and upper mainstem segments	8
Distribution of spawning grounds	
Only in the Jinsha segment	46
Only in the upper mainstem segment	3
Only in the Jinsha and upper mainstem segments	3
Potamodromous fishes[a]	
The Jinsha segment	37
The upper mainstem segment	35
The Jinsha and upper mainstem segments	38
Characteristics of eggs	
Drifting	26
Adhesive	50
Demersal	10
Pelagic	4
Impoundments	49
Fragmentation	134
Blocking migration between the Jinsha and upper mainstem segments	35
Hydrological regime	33
Hypolimnetic discharge	16

[a] Catadromous or anadromous fish has disappeared from the Jinsha and upper mainstem segments due to blocking of the Gezhouba and Three Gorges dams

are endangered. Thirty-five potamodromous species have been recorded migrating between the Jinsha segment and the upper mainstem segment. Fourteen potamodromous species (e.g. *C. guichenoti*, *Leptobotia elongate* and *O. elongates*) have their spawning grounds in the upper Yangtze, but they use other regions for growing and feeding, and migrate to spawning grounds.

Twenty-six species produce drifting eggs (excluding *A. japonica* which spawn in the sea), 50 species produce adhesive eggs, ten species produce demersal eggs, and four species produce pelagic eggs. There is no information on the ecology of the eggs of other 118 species (Table 1). Thirty-one species have their environmental requirements for spawning documented. They all spawn during April through July with the spawning season lasting for 2–4 months (Table 2). Typically, four endemic species (i.e. *Botia reevesae*, *Garra pingi*, *M. pellegrini*, *M. asiaticus*) have short spawning seasons lasting only 2 months (Table 2). Fifteen species are recorded to spawn at water temperature of 17.8 °C or higher (Table 2). The spawning of drifting-egg species occurs in turbulent flow with eddy currents. Rising water levels and flow velocity are general cues for the spawning of these species (Table 2). Duration of incubation usually lasts

Table 2 Thirty-one fishes in the upper Yangtze River and their spawning season, suitable water temperature, cue and environment conditions for spawning, and duration from fertilization to hatching of embryos

Species	Spawning season	Spawning temperature (°C)	Cue for spawning	Environmental conditions for spawning	Duration from fertilization to hatching	Sources
Myxocyprinus asiaticus (Bleeker)	March–April	≥13		Turbulent flow and mingled whirlpool current	166 h (18.7 °C)	Institute of Hydrobiology (IHB) (1976), Zhang and Zhao (2000)
Mylopharyngodon Piceus (Richardson)	May–July	≥20	Rising water level and increasing flow velocity	Turbulent flow, mingled whirlpool current and flow velocity 0.33–0.90 m/s	35 h (21–24 °C)	Yi and Liang (1964), Yi et al. (1988a, b)
Ctenonpharyngodon idellus (Cuvier et Valenciennes)	April–July	≥18	Rising water level and increasing flow velocity	Turbulent flow, mingled whirlpool current and flow velocity 0.33–0.9 m/s	35–40 h (19.4–21.2 °C)	Yi and Liang (1964), Yi et al. (1988a, b)
Squaliobarbus curriculus (Richardson)	April–August	≥26	Rising water level and flow velocity 1.4–1.6 m/s	Turbulent flow	16 h (28–28.5 °C)	Long et al. (2005)
Luciobrama macrocephalus (Lacepede)	April–July	18–28	Rising water level and intense increase of flow velocity	Turbulent low	33–35 h (18–24 °C)	Liang et al. (2003)
Ochetobius elongates (Kner)	May–June			Turbulent low	35 h (21–23.4 °C)	IHB (1976)
Elopichthys bambusa (Richardson)	April–July	20–27	Rising water level and flow increment 0.12–0.29 m/s	Turbulent flow and mingled whirlpool current	32 h (21 °C)	Liang et al. (1984)
Hypophthalmichthys molitrix (Cuvier et Valenciennes)	April–July	≥18	Rising water level and increasing flow velocity	Turbulent flow, mingled whirlpool current and flow velocity 0.33–0.90 m/s	35 h (20–23 °C)	Yi and Liang (1964), Yi et al. (1988a, b)
Aristichthys nobilis (Richardson)	May–July	≥18	Rising water level and increasing flow velocity	Turbulent flow, mingled whirlpool current and flow velocity 0.33–0.90 m/s	40 h (19–21 °C)	Yi and Liang 1964, Yi et al. (1988a, b)
Culter alburnus Basilewsky	June–August	≥20			44 h 30 min (22 °C)	IHB (1976), Zhang and Xiong (2005)
Parabramis pekinensis (Basilewsky)	April–July	≥20	Rising water level and increasing flow velocity	Turbulent flow and mingled whirlpool current	40 h (21–24 °C)	Wang et al. (2009b), Yi et al. (1966)

Table 2 continued

Species	Spawning season	Spawning temperature (°C)	Cue for spawning	Environmental conditions for spawning	Duration from fertilization to hatching	Sources
Megalobrama pellegrini (Tchang)	April–May	≥20	Rising water level and flow velocity 1.5–2 m/s	Running water	55 h (21–22 °C)	Wang et al. (2005)
Hemibarbus maculates Bleeker	March–May	≥16	Running water	Micro-flow, turbid water and shoal	140 h (18.2–19.8 °C)	Wang et al. (2008)
Corieus heterodon (Bleeker)	April–July	≥18	Rising water level	Turbulent flow and mingled whirlpool current	42 h (18–23 °C)	Xu et al. (1981)
Corieus guichenoti (Sauvage et Dabry)	Apr–Jul	≥18	Rising water level	Turbulent flow and mingled whirlpool current	45 h (18–23 °C)	Liu et al. (1990)
Rhinogobio ventralis Sauvage et Dabry	Mar–Jul	≥14.5	Turbulent flow			Zhou and He (1992)
Saurogobio dabryi Bleeker	March–May	≥15		Micro-flow and shoal	82 h (16 °C)	He et al. (1996)
Gobiobotia filifer (Garman)	May–June				40 h (21–25 °C)	Gao et al. (1988)
Spinibarbus sinensis (Bleeker)	April–July	19–28		Turbulent flow	43 h (23 °C)	Liang (2004)
Acrossochilus monticola (Günther)	April–June	≥17		Micro-flow and shoal	49 h 36 min (21 °C)	Yan et al. (1999)
Onychostoma sima (Cuvier et Valenciennes)	April–June	≥19.5		Turbulent flow and shoal	61–63 h (19.5–22 °C)	Chen et al. (2008)
Garra pingi (Tchang)	March–April	12–20		Turbulent low and complex flow pattern		IHB (1976)
Schizothorax prenanti (Tchang)	March–June	10–19		Turbulent flow	134 h (17 °C)	Ruo et al. (2001), Meng and Zhang (2011)
Lepturichthys fimbriata (Günther)	April–June	≥17.8		Turbulent low	34 h (22.5–23.5 °C)	Jiao et al. (1965) Xiong et al. (2008)
Botia superciliaris (Günther)	May–June	≥17.8		Turbulent flow		Yang and Xia (2010)
Botia reevesae Chang	June–July			Turbulent flow	27 h (23 °C)	Yue et al. (2011)
Parabotia fasciata Dabry	July–August	≥24			12 h (28 °C)	Yang et al. (2007)
Leptobotia elongate (Bleeker)	April–July	≥20			35 h (22–23 °C)	Institute of Hydrobiology (IHB) (1976), Liang et al. (2000)
Siniperca chuatsi (Basilewsky)	May–July	≥21		Running water, flow velocity 0.6–0.8 m/s and water depth 1–2 m	73 h (21–24 °C)	IHB (1976), Jiang (1959)

Table 2 continued

Species	Spawning season	Spawning temperature (°C)	Cue for spawning	Environmental conditions for spawning	Duration from fertilization to hatching	Sources
Siniperca kneri Garman	April–August				69 h (24–25 °C)	Wang et al. (2006)
Siniperca scherzeri Steindachner	May–August	≥20		Running water and water depth 20–60 cm	135 h (18–22 °C)	Zeng et al. (2005)

over 30 h depending on species and water temperature (Table 2).

Potential effects of the dam cascade on fishes

The ten dams in cascade under construction will have serious effects on recruitment of fish populations in the Jinsha and upper mainstem segments of the Yangtze River. These effects are mainly due to impoundment, habitat fragmentation and blocking, flow regime modification, and hypolimnetic discharge and nutrition retention.

Impoundment

Impoundment of the dam cascade will change the river segment between Lijiang (27°18′N, 100°13′E) and the Xiangjiaba Dam, creating 10 lentic reservoirs in cascade in this 1300-km segment (Fig. 1). Adaptation to turbulent current is common in fishes of the upper Yangtze (Chen et al. 1998). The impoundment of the dams will induce loss of critical lotic habitats for rapids-dwelling fish in this river segment, such as endemic fishes of Cobitidae, Homalopteridae, Amblycipitidae, and Sisoridae. Such effects will be strong for the 45 species that are endemic to the Jinsha segment (see Table 1 in Supplementary Material). Dramatic changes of fish communities through extirpation of endemic species and increases in generalists were reported from other impounded rivers (Rahel 2002; Clavero et al. 2004; Głowacki and Penczak 2013).

The disappearance of lotic environments will induce partial or even total loss of spawning grounds for fishes in this river segment, especially for the 46 species with spawning grounds only in the Jinsha (e.g., *C. guichenoti*, *L. kingi*, *S. notabilis*), and for the three species with spawning grounds only in the Jinsha and upper mainstem segments, including *A. dabryanus, P. gladius,* which are already endangered (Zhang et al. 2009; 2011). Loss of spawning grounds will increase their risk of extinction.

Habitat fragmentation and blocking

One-hundred-thirty-four species, including 61 endemic fishes and seven endangered fishes, were reported distributing across the river section where the cascade of dams will be located. Construction of the dams may fragment their populations. It is suggested that these fragmented populations will have their gene flows blocked, thereby increasing inbreeding, decreasing effective population size, and thus reducing fitness (Alo and Turner 2005; Cheng et al. 2013b; Roberts et al. 2013). Furthermore, commercial fisheries in the upper Yangtze have been mainly supported by some of these species, such as *A. wangi*, *C. guichenoti*, *P. pingi*, and *P. rabaudi* among others. Population declines of these species may affect fisheries yields substantially.

For the 35 potamodromous fishes migrating between the Jinsha and upper mainstem segments, their migration routes will be blocked by the dams. For species with spawning grounds in the Jinsha segment and above, blocking of their migratory routes will induce part or even total loss of spawning grounds upstream of the Xiangjiaba Dam (Fig. 1). This effect will be serious for 13 species such as *C. guichenoti*, *L. elongate*, *O. elongates*, and *Rhinogobio ventralis* which have spawning grounds only in the upper Yangtze (see Supplementary Material). Among them, spawning grounds of *C. guichenoti* are known only in the middle and low reaches of the Jinsha segment (Liu et al. 1990). Blocking its migration will result in the fish not arriving in its original spawning grounds. If no

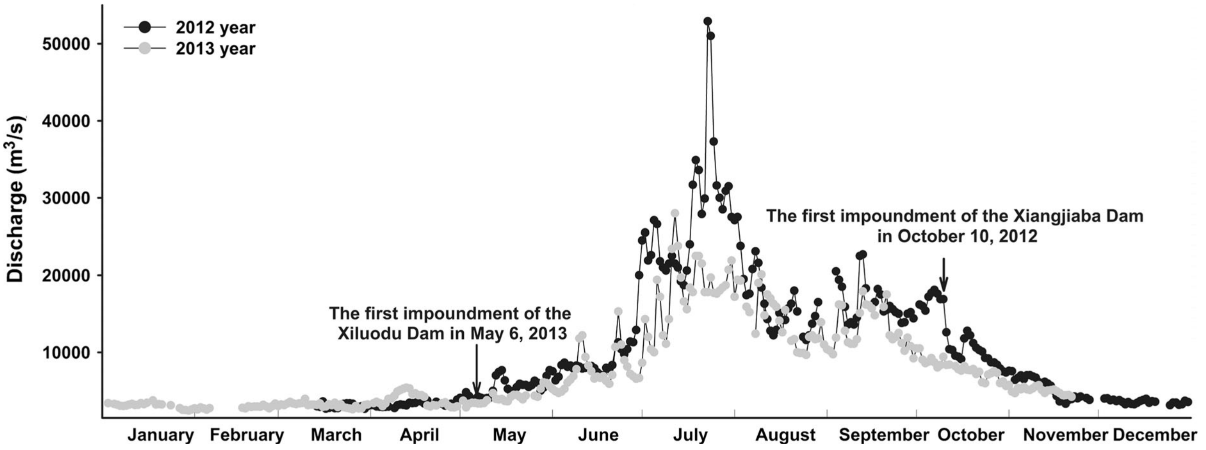

Fig. 2 Alteration of discharge (m^3/s) after the impoundment of the Xiangjiaba and Xiluodu dams

new spawning grounds are established, the risk of extinction for this species will be high.

The effects of impoundment, blocking of migrations, and habitat fragmentation may combine to induce additional effects on some species. For the 14 endemic potamodromous species, including 6 endangered species, their spawning grounds in the river segment between Lijiang and the Xiangjiaba Dam will disappear due to the impoundment and the blocking of migration routes. Meanwhile, populations below and upstream of the dams will be fragmented if new spawning grounds are established or maintained below the Xiangjiaba Dam in the upper mainstem and above Lijiang. Such combined effects on *A. dabryanus* will increase its risk of extinction; the situation for *P. gladius* will be similar or even worse (Zhang et al. 2009).

Alteration of hydrological regime

The river segment between the Xiangjiaba Dam and the headwater of the Three Gorges Reservoir will continue to be lotic. This segment ranges from 440 km (when the water level of the Three Gorges Reservoir is at 175 m) to 580 km (when the water level is at 145 m) in length. However, the dam cascade will dramatically modify the annual flow regime in this lotic segment by reducing the magnitude, frequency, and duration of flood peaks (Wang et al. 2009a; Poff and Zimmerman 2010). Following the impoundment of the Xiangjiaba Dam in October 2012 and the Xiluodu Dam in May 2013, the maximum flow peak observed below the Xiangjiaba Dam in the flood season of 2013 decreased by more than 50 % compared to 2012 (Fig. 2). Dramatic alterations of hydrological regime below some dams have been widely recorded (Batalla et al. 2004; Carlisle et al. 2011; Grantham et al. 2014). However, longer-term hydrological data will be needed to fully analyze modification of the hydrological regime following the impoundment of the dam cascade in the upper Yangtze River.

Modification of the natural flow regime may affect the recruitment success of fish populations, typically for the drifting-egg species. There are 26 drifting-egg fishes in this river segment with 11 endemic species, two endangered species (*L. elongate* and *Luciobrama macrocephalus*), and eight species with recorded spawning grounds only in the upper Yangtze. In natural flow conditions, there are 5–6 flow peaks during April through July in the Jinsha and upper mainstem segments (Wang et al. 2009a). At suitable water temperatures, flow peaks provide cues for spawning of these fishes (Table 2). A decline in magnitude, frequency, and duration of the flow peaks will result in decreased opportunity and magnitude of spawning. The spawning seasons of some endemic species (e.g. *O. elongates*, *Botia superciliaris*, *B. reevesae*, *Gobiobotia filifer*) in the upper Yangtze are usually about 2–3 months shorter than most other species (Table 2), so they may suffer even more consequential effects from the modification of the flow regime.

Sufficient drift duration is essential for embryo development of drifting eggs (Liang et al. 1984; Yi et al. 1988a; Agostinho et al. 2004); drifting eggs will sink and die if water current is less than 0.25 m/s (Tang et al. 1989). The shortened duration of flow peaks may not maintain drifting of the eggs, causing their mortality. The required drift time depends on the duration of embryo development, which in turn depends on the species, water temperature, and current velocity; so it is essential that lotic segments have enough distance for drifting eggs to finalize their development. Considering the four major carps (*Mylopharyngodon Piceus*, *Ctenonpharyngodon idellus*, *Hypophthalmichthys molitrix*, and *Aristichthys nobilis*) as examples, time duration of fertilization to active swimming larvae is 120 h at 20 °C (Yi and Liang 1964; Yi et al. 1988a, b). Thus, the minimum drifting distance in lotic segments should exceed 200 km if water current is 0.5 m/s, and exceed 400 km if water current is 1.0 m/s. The current in the upper Yangtze is general faster than 1.0 m/s and even up to 7 m/s during flood seasons (Jiang et al. 2010). So the lotic segment below the Xiangjiaba Dam may serve as a critical refuge for embryonic development of drifting carp eggs. Flow peak is also required for the spawning and development for many adhesive- and demersal-egg-producing fishes, e.g. *G. pingi, M. pellegrini*, *Onychostoma sima* (Table 2). Modification of the flow regime below the Xiangjiaba dam may also affect spawning and early development of these species.

Hypolimnetic discharge and nutrition retention

Hypolimnetic discharge from the dams will seriously affect the reproduction and development of egg of fishes below the Xiangjiaba Dam. Under natural flow regimes, water temperature in the Jinsha and upper mainstem segments can reach 18 °C (which is the lowest development temperature required for many fishes, especially those with drifting eggs) in early April (Table 2). Water will be vertically stratified by temperature in the reservoirs, and the dams are designed to discharge the cold bottom water. Considering cumulative effects on water temperature of the ten cascade dams, the time for the water temperature to rise to 18 °C has been predicted to be delayed to early May, postponing the start of fish spawning by more than 1 month (Deng et al. 2006; Wang et al. 2009a, b). Such effects will be typically strong for endemic species due to their beginning of spawning earlier and shorter spawning seasons, such as *L. elongate*, *C. guichenoti*, *Lepturichthys fimbriata*, *M. pellegrini*, *Spinibarbus sinensis*. Furthermore, the delayed spawning season will shorten the growing season for young-of-the-year juveniles before winter and decrease their energy accumulation, thereby reducing overwintering survival rates (Zhang et al. 2012).

Approximately 2.47×10^{12} kg of sediment per year is transported downstream in the Jinsha segment (Tan and He 2003; Dai and Lu 2014). Impoundment of the dam cascade will retain 82 % of that sediment (Hu et al. 2003), resulting in “clean water” flows downstream of the dams. Such “clean water” discharge can decrease food supply for fishes through retention of nutrients and lowered biological productivity. It can also degrade the benthic environment of fishes and alter physiochemical conditions (e.g. turbidity). However, more information is needed to clarify the effects of “clean-water” discharge.

The combined effects of flow-regime changes and delayed warming of water temperatures will dramatically decrease spawning and growth opportunities for fishes below the dams. This effect will be typically serious for some endemic fishes that have shorter spawning seasons and need specific environment conditions for spawning, e.g. *B. reevesae*, *B. superciliaris, C. guichenoti, M. pellegrini, S. sinensis* (Table 2). The combined effects of impoundment, blocking of migration and habitat fragmentation, alteration of hydrological regimes, and hypolimnetic discharges will have further reduced the likelihood of successful recruitment by many species, particularly for some endangered species such as *P. gladius*, *A. dabryanus, M. asiaticus*, *L. elongate*, *L. macrocephalus, L. kingi*, *P. rabaudi*, *Xenocypris yunnanensis*. *P. gladius* spawns only in the upper Yangtze (Billard and Lecointre 2001). The impoundment and blocking of the migration routes will induce loss of spawning grounds of *P. gladius* in the Jinsha segment; habitat fragmentation will isolate its population; and alteration of hydrological regime and water temperatures will change its spawning environment, likely for the worse. Based on our judgment for extinction risk of fishes, five species in the upper Yangtze are likely to go extinction following the completion of the dam cascade. Another 32 fishes have a moderate likelihood of extinction; while 27 fishes have a low likelihood (see Table 1 in Supplementary Material).

Countermeasures for conservation

Possible countermeasures to mitigate the negative effects of the dam cascade on fish include preserving and rehabilitating habitat, restoring the natural flow regime, stock enhancement, and building of fish passages. However, the suitability of these countermeasures depends on biology, the environment, the nature of the effects, and conservation objectives; and must consider local social and economic conditions as well as feasibility of implementation.

Enhancing management of protected areas

Protected area is an effective approach to preserve biological diversity (Saunders et al. 2002; Barmuta et al. 2011; Andam et al. 2013). The National Natural Reserve Areas of Rare and Special Fishes of the Upper Yangtze River (NNRARSF) were established to provide refuge for some endemic and endangered fish species in the upper Yangtze. It is composed of the river segment of upper Yangtze between Xiangjiaba Dam and Chongqing Diwei Bridge of the Yangtze River (29°20′N, 106°24′E), the whole channel of Chishui River, and partial river segments of six other tributaries (Official document of National Environment Protection Bureau, China, 2013 No. 161).

Conserving freshwater biodiversity requires management actions both inside and outside of protected areas (including both aquatic and terrestrial ecosystems) (Dudgeon et al. 2006; Linke et al. 2011; Castello et al. 2013). For the NNRARSF, the reserve only includes the channels of the river segments, but does not include the whole watershed catchment basin. The landscape of the Chishui River is in relatively pristine condition. Fish fauna of the Chishui River includes a major constituent of fishes in the upper mainstem of the Yangtze, including numerous endemic fishes, e.g. *O. sima*, *P. rabaudi, S. sinensis* (Liu and Cao 1992; Cao 2000; Wu et al. 2010). Reserve effectiveness would be increased by including the whole catchment of the Chishui River in the reserve. Furthermore, it would be highly beneficial to include more tributaries into the reserve (Wang et al. 2007).

However, a dam is proposed at Xiaonanhai downstream of the reserve in the upper mainstem segment (Fig. 1). If this dam is constructed, the reserve will be dramatically altered and fishes in the reserve will be further threatened.

Restoration of natural flow regime

Alteration of the hydrological regime is a major threat for the recruitment of fish populations (Nunn et al. 2007; Young et al. 2011; Cowx et al. 2012). Restoration of semi-natural flow regimes has been successfully accomplished for fish conservation purposes below dams in many river systems (Connor and Pflug 2004; Richter and Thomas 2007; Kondolf et al. 2013; Grantham et al. 2014). Flow regime can be somewhat naturalized at the dam cascade so as to meet the biological needs of fish. Such naturalization could have particular benefits for the protection of reproduction of those endemic endangered species. Four or five artificial flood pulses are needed and possible in the Jinsha and upper mainstem segments. Considering the negative effects of cold water discharge, operation of the dams should also consider surface water discharge through spillway during the major spawning season of fish, starting in April so as to mitigate the effect of the delayed increase of water temperature. Knowledge about life history and hydrological needs of various species of interest is still scarce, particularly for some endemic fishes in the Jinsha and upper mainstem segments. General investigation and more-detailed studies are necessary to assess biological and ecological requirements of threatened endemic species in the Yangtze River.

Artificial reproduction and hatchery release for threatened species

Release of juveniles from artificial reproduction is a possible approach for conservation for threatened fishes (Seddon 2010; Lawler and Olden 2011; Dudgeon 2012). This measure had been carried out as a major conservation strategy for over 20 vulnerable or endangered species in China, mainly in the Yangtze River (Yin and Zhang 2008; Yang et al. 2013). Artificially produced juveniles of *A. sinensis* have been released into the Yangtze River every year since 1983 after the Gezhouba Dam was completed (Wei et al. 2004; Stone 2008). The released individuals have apparently sustained the population of *A. sinensis* (Ban et al. 2011; Dudgeon 2011). Similarly, artificial propagation and release of *A. dabryanus* and *M. asiaticus* have shown good results (Zhuang et al. 1997; China Three Gorges Project Corporation 2007). But this approach to restoration can pose potential genetic and ecological risks to wild recipient populations (Theresa 2007; Holsman et al. 2012). Unsuccessful results for such releases have occurred due to lack of consideration of the status of recipient populations, genetic differentiation between the donor and recipient populations, and interaction among cultured individuals and the recipient populations and conservation targets (Hewitt et al. 2011; Olden et al. 2011; Holsman et al. 2012). Recent results in the Jupiá and Três Irmãos reservoirs, with better genetic control in artificial reproduction and larger size of juveniles at the time of release, have been relatively successful (Agostinho et al. 2008).

Although there are potential genetic and ecological risks associated with hatchery releases, there is no alternative for protecting some fishes of the Jinsha and upper mainstem segments, especially for species whose spawning grounds will be dramatically destroyed (such as *A. dabryanus*, *C. guichenoti*) (Dudgeon 2011). More research must be conducted in developing artificial-reproduction and fingerling-rearing techniques for important endemic fishes. Meanwhile, it is imperative to develop proper management protocols for conservation hatcheries to avoid the risk of reducing fitness of wild populations (Naish et al. 2008; Holsman et al. 2012).

Fish passages

Fish passages have been a major measure to mitigate the effects of blocking fish habitat and fragmenting fish populations (Williams et al. 2012; Cooke and Hinch 2013; McLaughlin et al. 2013). The efficiency of fish passages depends on the swimming ability of the target species (Gowans et al. 2003; Roscoe and Hinch 2010; Noonan et al. 2012). Passage efficiency of salmonids can be high with a mean value of 74.6 % for passing downstream and 61.7 % for passing upstream, but it varies widely (Noonan et al. 2012). Passage efficiency of other species, however, has been usually low with an average of 39.6 % for passing downstream and 21.1 % for passing upstream (Noonan et al. 2012). Fish passages can also act as ‘ecological traps’ for fishes typically in large tropical rivers (Pelicice and Agostinho 2008). With the hydrological and limnological environment being completely different from the original habitat conditions in the reservoirs, fish that pass the dams sometimes cannot spawn, and even cannot survive (Thornton et al. 1990; Okada et al. 2005). Meanwhile, dams also impose a blocking barrier for downstream fish migration as demonstrated in some large tropical rivers (Pelicice and Agostinho 2008; Pelicice et al. 2014).

Fish passages were constructed in some low-water dams built in 1960s and 1970s in China. Because of multiple reasons such as poor design and management of the passages and limited swimming ability of the target species, the efficiency of these passages was very low and most of them have now been abandoned (Wang and Guo 2005). Construction of the Gezhouba Dam caused a debate about the efficacy of fish passages in China, causing them to no longer be regarded as effective conservation measures (Chen et al. 2012). Since 2000, fish passages have been recommended again as important measures to protect fish diversity in China, so many have now been constructed (Chen et al. 2013). However, efficiency of these new passages has not been evaluated. It has been suggested that fish passages may not be effective for passing Chinese cyprinid fishes across high dams (Yi 1982). As a consequence, fish passage facilities are not designed for any dams in the mainstem of the Yangtze River, e.g. the ten cascade dams in the Jinsha, the Three Gorges Dam and the Gezhouba Dam. More research is needed to improve fish-passage design in China (Zhou et al. 2011).

Conclusions

This analysis showed that the dam cascade planned in the upper Yangtze River will have serious cumulative effects on fishes, mainly due to impoundment, habitat fragmentation and blocking, flow-regime modification, and hypolimnetic discharge. The impoundments will cause loss of critical habitats for 46 endemic species, fragment the populations of 134 species, and block migration routes for 35 potamodromous fishes. Modification of flow regimes will adversely affect the recruitment of 26 drifting-egg species. The initiation of annual spawning of 13 fishes will be postponed by more than 1 month, and fish spawning and growth opportunities will be reduced due to hypolimnetic discharge. The effects will be typically serious on endemic species. We suggested that five species (*A. dabryanus*, *P. gladius*, *C. guichenoti*, *L. macrocephalus*, and *P. pingi*) are likely to go extinct, and

32 species (*M. asiaticus*, *M. elongate*, *O. elongates*, *P. Rabaudi*, and *R. Ventralis*) may dramatically decline in abundance, inducing risk of extinction due to the combined effects of the dam cascade if no significant conservation measures are taken. However, three countermeasures appear to be relatively suitable to partially mitigate the near-term effects of the proposed dam cascade: enhancing management of protected areas, restoration of natural flow regime, and artificial reproduction and hatchery release of threaten species. These measures should be central components of the protection plan to avoid large-scale extinction of endemic fishes in the upper Yangtze River.

Our conclusions can guide further research on the combined effects of dam cascade in other large rivers. Grantham et al. (2014) developed a systematic screening approach to select proper dams for implementation of environmental flows to protect freshwater biodiversity in dam-regulated river systems. Scientists in many parts of the developing world have raised concerns about their ability to inform decision making while having only scarce information at their disposal. The approach undertaken in our study—by which the known and likely effects of present and future dams were simultaneously considered in light of the biology of the species—highlights the usefulness of available knowledge for fish conservation science.

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