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Rapid change of Yangtze fisheries and its implications for global freshwater ecosystem management

Running title: Fishery change in Yangtze & implications

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Abstract: Freshwater capture fisheries are globally essential for food security and aquatic biodiversity conservation. The Yangtze River Basin is the third longest, and one of the most human-influenced drainage basins worldwide. Since the founding of P. R. China in 1949, this large river system has suffered increasing human perturbation and its sustainable development is now severely challenged. Meta-analysis showed that Yangtze River fisheries have experienced an extraordinary process of utilization-overexploitation-protection during the past 70 years, to the extent that other globally important rivers may never have encountered. Its fisheries appear to have collapsed over the past four decades, with yield decreasing to only 25% of an historic peak of 400,000 metric tonnes in the late 1950s. Endemic, migratory and rare fishes have been highly threatened with obvious changes in fish community structure and aquatic biodiversity. Anthropogenic activities, including impoundment of water in dams, discharge of pollutants, and riverine modification for vessel navigation, have caused large decreases in fisheries yields. Projections from surplus production modelling showed potential for improvement under fishing ban scenarios, but without any prospect for full recovery to historical stock status. This study revealed that the change in fisheries resources was dominated by the social-ecological watershed system, and an integrated approach to river basin management is warranted. Better management of freshwater ecosystems to integrate food security with biodiversity conservation is urgently needed throughout the world, and the changes evident in the Yangtze River fish populations can serve as an informative global

reference.

Key words: biodiversity conservation, China, fishing ban, food security, human impact, inland fishery

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1 INTRODUCTION

Freshwater capture fisheries are essential for food security and biodiversity conservation worldwide (Food and Agriculture Organization of the United Nations [FAO], 2016; Funge-Smith & Bennett, 2019; Lynch et al., 2017; McIntyre, Reidy Liermann, & Revenga, 2016; Welcomme, Valbo-Jorgensen, & Halls, 2014; Youn et al., 2014). Global production from inland capture fisheries was approximately 11.9 million metric tonnes in 2014, accounting for 7.1% of the total global production according to a report by FAO (2016). Freshwater capture fisheries provide a source of animal protein which is equivalent to the total requirements of approximately 119.1 million people, based on 36 countries where protein consumption data were available (Fluet-Chouinard, Funge-Smith, & McIntyre, 2018); moreover, these fisheries account for up to 81% of the nutrient supply to low-income countries where other protein sources are too expensive (McIntyre et al., 2016). In addition to sustaining target species production for human needs, conserving freshwater fish diversity is critically important for maintaining ecosystem function and provision of ecosystem services (Harrison et al., 2014). Freshwater areas represent less than 1% of the entire surface area of the Earth, yet contain 40% (i.e. 13,000 strictly freshwater species) of all fish species, whereas saline waters covering 70% of the Earth's surface, contain the remaining 60% (i.e. 16,000 species) (Lévêque, Oberdorff, Paugy, Stiassny, & Tedesco, 2008; Tedesco et al., 2017). Freshwater fishes are highly evolved and specialized with some only able to live in specific local habitats (Tedesco et al., 2012). In Western Europe and the USA, riverine fish extinction rates are ~112 times higher than background extinction rates (Dias et al., 2017). Human influences such as fishing

pressure can lead to precarious circumstances for aquatic animals already in low abundance. It has been predicted that freshwater biodiversity and ecosystem services will be severely reduced by 2050; thus, a systematic and effective protection framework is urgently needed if this predicted situation is to be averted (Jenkins, 2003; Nguyen et al., 2016; Vörösmarty et al., 2010; Zhou et al., 2010).

The Yangtze River is the third longest, and third most water-rich river system, yet it is also one of the most human-impacted large rivers in the world (Liu & Diamond, 2005; Yang, Ma, & Chang, 2009; Yang, Wen, & Li, 2007; Yang, Zhu, & Jiang, 2011). The Yangtze River has experienced large perturbations and severe overall stress from anthropogenic activities during the past 70 years as a consequence of China's economic development and modernization (Liu & Diamond, 2005; Qiu, 2012; Wu et al., 2004; Xie, Wu, Huang, & Han, 2003). The drainage basin crosses the western, middle and eastern parts of China, comprising one-fifth of the land area and traverses 19 provincial administrative units (56% of all units) (Yang et al., 2007, 2009, 2011). The basin is home to more than 0.4 billion people (one-third of the Chinese population) and generates approximately two-fifths of China's gross domestic product (GDP). Also, the Yangtze River is the busiest river in the world in terms of inland vessel navigation with numerous diverse watercraft ranging from bamboo rafts to large cruise ships. It has made great contributions to China's rapid economic growth both historically and currently. The river is presently under a new development plan called the "Yangtze River Economic Belt" to further promote the economic development of China (Central Government of China, 2014; Yang et al., 2007, 2009, 2011).

Fishes in the Yangtze River are very important for both fisheries development and aquatic biodiversity conservation (Yang et al., 2007, 2009, 2011; Zeng, 1990). Like the Amazon, Mekong and Niger rivers, the wild capture fishery in the Yangtze River supplies a vital food source for local residents in a myriad of communities in its catchment (FAO, 2016; Welcomme et al., 2014; Zeng, 1990). In the 1950s, yields from wild capture fisheries in the

Yangtze River accounted for approximately 60% of inland fish production in China (Yang et al., 2007, 2009, 2011). Currently, among the 35 major freshwater aquaculture species in China, 26 species are distributed in the Yangtze River (Yang et al., 2007). Furthermore, the quality of the four major Chinese domestic carps (i.e. black carp (*Mylopharyngodon piceus*, Cyprinidae), grass carp (*Ctenopharyngodon idella*, Cyprinidae), silver carp (*Hypophthalmichthys molitrix*, Cyprinidae), and bighead carp (*H. nobilis*, Cyprinidae)) are considered to be the best among all aquatic systems in China. Prior to success in artificial propagation techniques for the four major Chinese carp species, more than 10 billion fish larvae and juveniles were caught each year from the middle reaches of the Yangtze River for aquaculture during the period of 1958–1962, with the highest number of 20 billion reported in 1960 (Hubei Provincial Water Resources and Electric Power Bureau, 1975). Thus the Yangtze River has been greatly supporting development of China's freshwater culture as well as capture fisheries. Currently, fisheries production (i.e. wild capture and aquaculture) in the Yangtze River Basin accounts for 60% of China's total freshwater fisheries production (Yang et al., 2007, 2009, 2011). There are approximately 416 fish species and subspecies in the Basin, of which 362 are strictly freshwater species and 178 are endemic (Ye, Li, Liu, Zhang, & Xie, 2011). In addition, there are some unique aquatic mammals, amphibians and reptiles, such as Baiji (*Lipotes vexillifer*, Lipotidae), Yangtze finless porpoises (*Neophocaena asiaeorientalis*, Phocoenidae), Chinese giant salamander (*Andrias davidianus*, Cryptobranchidae), and Chinese alligator (*Alligator sinensis*, Alligatoridae) (Yang et al., 2007, 2009, 2011).

Fisheries sustainability and biodiversity conservation in the Yangtze River have both faced great challenges, in common with most large-river systems throughout the world (Dudgeon, 2010, 2011; Jackson, Loewen, Vinebrooke, & Chimimba, 2016; Vörösmarty et al., 2010; Youn et al., 2014). With continual socio-economic development associated with the Yangtze River Basin, various human activities have adversely affected the Yangtze River's aquatic organisms and their habitats (Chen, Duan, Liu, & Shi, 2003; Chen, Xiong, Wang, & Chang, 2009; Lu et al., 2016; Yang et al., 2007, 2009, 2011; Zhang et al., 2017). The major

threatening elements include damming (Cheng, Li, Castello, Murphy, & Xie, 2015; Liu, Qin, Xu, Ouyang, & Wu, 2019; Wang, Li, Duan, Chen, et al., 2014; Wang, Li, Duan, Luo, et al., 2014), legal overfishing and illegal fishing (Ma et al., 2018; Zhu & Chang, 2008), water pollution (Müller et al., 2008), reclamation of lakes for farmland, isolation of lakes from rivers (Cheng et al., 2014; Fang et al., 2006), waterway channel construction, and vessel navigation (Huang & Li, 2016; Xie, 2017a, 2017b). To date, wild capture fisheries production has already decreased to less than 100 thousand tonnes, falling well short of the maximum production of 427 thousand tonnes in 1954 (Zeng, 1990). The quantity of newly produced eggs and larvae of the four major Chinese carp species (i.e. the dominant commercial species in the Yangtze River) was approximately 1.11 billion in 2015, accounting for only 1% of historic production (118.4 billion) estimated for 1964–1965 (Yi, Yu, & Liang, 1988; Zhang et al., 2017). Sixty-five Yangtze River fish species (15.6% of total) were registered in various threatened categories of the China Species Red List (Ye et al., 2011). The Baiji (Turvey et al., 2007), Chinese paddlefish (*Psephurus gladius*, Polyodontidae) (Zhang et al., 2020), and Reeves shad (*Tenualosa reevesii*, Clupeidae) are thought to be functionally extinct because no living specimens of these species have been found for over 15 years (Yang et al., 2007, 2009, 2011). The Yangtze finless porpoise and Chinese sturgeon (*Acipenser sinensis*, Acipenseridae) are highly endangered (Mei et al., 2014; Wu et al., 2015). In particular, the natural spawning activity of Chinese sturgeon has been interrupted several times in the year of 2017–2019 (Wei et al., unpublished data), which may be due to the decline of its breeding population and the degeneration of its spawning habitat, which have led to a strong signal of a near-extinction status (Huang & Wang, 2018; Wu et al., 2015).

Currently, ecological issues in the Yangtze River, especially fisheries sustainability and aquatic biodiversity conservation, have received considerable attention, which is unprecedented for this system as the emphasis in the past was on how to greater utilize fisheries resources (Bryan et al., 2018; Yang et al., 2007, 2009, 2011). The new principle for more ecologically sustainable development of the Yangtze River is “Go together for conservation, No excessive development”. In response to this shift in policy, a systematic and

ambitious fisheries adjustment plan, involving 278.3 thousand fishermen and 113.3 fishing boats, has been proposed, and some of the planned actions are already being implemented (Yi & Yu, 2018). Other comprehensive protection plans for the river, which directly or indirectly benefit particular aquatic organisms and their habitats or the entire aquatic ecosystem, have also been implemented, with others to be conducted in the near future (Bryan et al., 2018; Yang et al., 2007, 2009, 2011). This new policy is critical for recovering depleted fisheries resources and halting declines in aquatic biodiversity as further delay will limit the extent to which the Yangtze River ecosystem and the services it provides can be restored.

The Yangtze River has experienced an extraordinary process of utilization-overexploitation-protection in the past 70 years, and this process is one that many other large river systems may have never encountered, or at least not to the same extent. Globally, although each river basin has its own unique characteristics among its social (population, diet habits, etc.), economic (GDP, agriculture, industry, etc.), and natural (climate, hydrology, topography, biology, etc.) dimensions, most will nevertheless experience a similar sequence of utilization, overexploitation, and rehabilitation at some stage. The Yangtze River Basin can therefore serve as an informative example from which riverine managers in other countries can learn. In this study of the socio-ecological watershed system of the Yangtze River (Figure 1), first changes in wild capture fisheries production and fish community composition were reviewed from the inception of the People's Republic of China in 1949 until 2016. Second, to determine the impacts of human activities the influence of environmental factors (e.g. run-off, water impoundment, water pollution and navigation) on fisheries resources between 1997 and 2016 were investigated, and their impacts on fisheries yields were examined. Third, fish biomass under three different fishing regulation scenarios up to 2030 was predicted. Finally, fishing pressure and biodiversity threats faced by the 30 largest river systems in the world were reviewed. The objective of this study was to explore changes in Yangtze River fisheries including their interactions with human activities in such a highly human-dominated ecosystem over the past 80 years, and ultimately to provide meaningful management guidance for large river systems worldwide.

213

214 2 MATERIALS AND METHODS

215 2.1 Study area

216 The Yangtze River stretches from Tibet to Shanghai (24°30'–35°45' N, 90°33'–122°25' E)
217 where it finally flows into the East China Sea (Figure 2) (Yang et al., 2007, 2009, 2011). The
218 mainstream is more than 6,300 km long within a catchment area of 1.8×10^6 km². Most areas
219 of the basin have a subtropical monsoon climate. The total annual flow and sediment
220 discharge at Datong station averaged 8.93×10^{12} m³ (1950–2015) and 3.68×10^9 t (1951–2015),
221 respectively (Changjiang Water Resources Commission of the Ministry of Water Resources,
222 P. R. China, 2017). The elevation difference from the headwater to the estuary is
223 approximately 5,400 m, with riverbed gradients ranging from 54×10^{-4} to 0.097×10^{-4} (Yu &
224 Lu, 2005). The basin has more than 10,000 tributaries; among them 437 have catchment areas
225 larger than 1,000 km², and 22 have catchment areas larger than 10,000 km² (Yu & Lu, 2005).
226 Approximately 4,000 lakes are included in the basin area, 27 of which are larger than 100 km²,
227 and 5 are larger than 1,000 km² (Zeng, 1990). In particular, Dongting Lake (2,625 km²) and
228 Poyang Lake (3,750 km²), located in the middle reach, are the two largest freshwater lakes in
229 China (Yu & Lu, 2005).

230

231 In the Yangtze River, historically 361–370 species and subspecies have been reported (Chen
232 et al., 2003; Fu, Wu, Chen, Wu, & Lei, 2003; Fu, Wu, Wang, Lei, & Chen, 2004), but the
233 latest research identified approximately 416 fish species and subspecies, 362 of which are
234 strictly freshwater species (Ye et al., 2011). The number of endemic fish species is 178
235 (42.8%), out of which 65 are on the China Species Red List (Ye et al., 2011). The most
236 species-rich phylogenetic orders in the river are Cypriniformes (280 species), Perciformes (50
237 species), and Siluriformes (40 species). The Yangtze River mainstream can be divided into
238 five sections (Figure 2): riverhead (above Batang), upper reach (Batang–Yichang), middle
239 reach (Yichang–Hukou), lower reach (below Hukou), and estuary. The number of fish species
240 (endemic species) in each section is 14 (8), 279 (147), 227 (70), 158 (23), and 142 (10),
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respectively (Ye et al., 2011). The number of species registered in various threatened categories of the China Species Red List is 4, 48, 20, 9 and 12, for the five sections respectively (Ye et al., 2011).

The Yangtze River Basin is one of the most exploited regions in China (Liu & Diamond, 2005; Yang et al., 2007, 2009, 2011). For example, the river has tens of thousands of dams on its mainstream and tributaries. The Gezhouba Dam at the end of the upper reach was closed in 1981 and is currently the lowermost dam on the Yangtze mainstream (Zhang et al., 2017). There is no fish passage on the dam, although a nation-wide debate has been triggered over this situation. The Three Gorges Dam, which supports the largest power station in the world, was completed in 2002, and a trial operation began in 2003 before becoming fully operational in 2009; this dam is located approximately 40 km upstream from the Gezhouba Dam. Accordingly, the enormous dam created a reservoir which is 600 km in length and has greatly changed the fluvial environment and aquatic ecosystem (Liu, Wang, & Cao, 2012; Wu et al., 2004; Wu, Huang, Han, Xie, & Gao, 2003; Yang, Gao, Li, Ma, & Liu, 2012). A number of issues, such as isolation of lakes from the river and reclamation of some of them for farmland, have been controversial. To date, only two large lakes remain connected to the Yangtze mainstream (Huang, Wu, & Li, 2013; Xie, 2017a, 2017b). Furthermore, other human activities, including overfishing, water pollution, waterway construction and vessel navigation, river channelization, port construction, and sand and gravel extraction, have seriously affected the aquatic ecosystem of the Yangtze River (Yang et al., 2007, 2009, 2011).

2.2 Data on fisheries yields and fish communities

To explore for changes in fisheries resources and fish community composition in the Yangtze River, we extensively investigated the literature regarding wild fisheries production (no previous estimates of fish population or stock biomass were available), fish community structure and aquatic biodiversity in the river since the 1970s (Chen et al., 2009; Fish Laboratory, Institute of Hydrobiology, Hubei Province, 1976; Liu & Gao, 2012; Zeng, 1990).

Relevant data from a large body of publicly available literature were transcribed and utilized in our analyses. The data on fisheries yields in the Yangtze River were mainly obtained from Zeng (1990) and a series of the *Bulletin on the Ecological and Environmental Monitoring Results of the Three Gorges Project* (Abbreviation: *Bulletin of the Three Gorges Project*) from 1997 to 2017. During 1949–1995, the yield data were based on provincial areas (Chen et al., 2003; Zeng, 1990), and since 1996, they have been based on four major yield producing areas (Liu & Gao, 2012; Lu et al., 2016; Table S1): Three Gorges Reservoir, middle reach of Yangtze, Dongting Lake and Poyang Lake. The data on fisheries production (wild capture and aquaculture) were obtained from a series of the *China Fisheries Statistical Yearbook* from 1979 to 2017. Data on fish community structure were compiled chiefly from Zeng (1990), Yang et al. (2007, 2009, 2011), Ye et al. (2011), Liu and Gao (2012), and a series of the *Bulletin of the Three Gorges Project* from 1997 to 2017, which included special reports. The list of references is provided in Table S1.

2.3 Environmental factors and their impacts

To understand the impacts of anthropogenic activities on fisheries resources, four categories (12 factors) of environmental variables were selected based on present knowledge (Yang et al., 2007, 2009, 2011; Zeng, 1990). These categories included i) river runoff (i.e. total discharge and mean sediment concentration at three representative sites: Yichang, Hankou and Datong; locations in Figure 2); ii) water impoundment (i.e. number of reservoirs and total reservoir capacity); iii) water pollution (i.e. the total volume of waste water emissions and ratio of low water quality reach, that is, the ratio of river reach with water quality belonging to Categories IV, V, and above, according to *Environmental Quality Standards for Surface Water* (GB 3838-2002) issued by China); and iv) vessel navigation (i.e. ship cargo volume and total passenger traffic). Because the total biomass of fish in the Yangtze River is difficult to estimate, we used wild capture fisheries yields, which are highly correlated with biomass. Data on key environmental factors were mainly obtained from a series of the *Changjiang Sediment Bulletin* from 2000 to 2016 and the *Yangtze River Yearbook* from 1998 to 2017. To understand the relationships between wild capture fisheries yields and environmental factors,

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as well as the interconnections among the environmental factors themselves, the Spearman correlation analysis was used. To exclude co-correlations of factors and identify key environmental factors, a stepwise regression analysis in the PASW Statistics 18 (IBM, USA) was performed.

2.4 Biomass estimation and future projections

2.4.1 Surplus production model

The middle reach of the Yangtze and the two largest lakes (Dongting and Poyang lakes) have been the major fishing areas since 1990s (Figure 2). Since a number of large lakes in the lower Yangtze (i.e. in Jiangsu and Anhui provinces) have become isolated from the Yangtze main stream by sluice and were used for aquaculture these can no longer be treated as natural resources. Despite rich biodiversity in its headwaters, commercial fisheries production in the Yangtze's upper reaches is relatively low and so is not an important fishing area. A surplus production model was selected to estimate fish biomass in the three major fishing areas. This model was selected because it only requires catch and effort data (Hoggarth et al., 2006). It was considered to be the most suitable model for the Yangtze River due to a general lack of biological information which would be needed as inputs and parameters for more complex models. The fundamental concept of this model is that fish populations follow a depletion curve with population size decreasing as more fish in the population are caught than are replaced through recruitment. Assuming that fishing success is related to abundance, changes in fish populations can be reflected in trends in catch per unit effort (CPUE), which will decrease in proportion to decreasing exploitable biomass (Hilborn & Walters, 1992). The biomass estimation was conducted using the CEDA 3.0.1 package (MRAG Ltd, UK), which is based on the standard dynamics of surplus production models but uses non-equilibrium fitting methods and three different error models (Hoggarth et al., 2006). After test running, the Schaefer and Fox production models were used to conduct the estimation (Equations 1–3):

$$B_{t+1} = B_t + f(B_t) - C_t \quad (1)$$

$$\text{Schaefer: } f(B_t) = rB_t(1 - B_t/K), \text{ MSY} = rK/4 \quad (2)$$

$$\text{Fox: } f(B_t) = rB_t \ln(K/B_t), \text{ MSY} = rKe^{-1} \quad (3)$$

where B is the fish stock biomass, t is the time (year), C is the catch, r is the intrinsic rate of growth, K is the carrying capacity of the population, and MSY is the maximum sustainable yield.

For conducting sensitivity analysis, the Schaefer and Fox production models, including two error assumptions (LSQ, least squares; and Log, log transform) and an initial proportion (IP) from 0.1 to 1.0, were used. In each area, the model and parameter combinations produced 40 estimates of biomass and population characteristics. The goodness-of-fit was determined using plots of residuals, coefficients of determination, and reasonable projections. The CPUE data in the three areas were calculated from the *Bulletin of the Three Gorges Project* from 1997 to 2017, which included special reports.

2.4.2 Scenario settings

Three scenarios were set with different catches and fishing effort in the three areas. The projection period was from 2017 to 2030 based on the following considerations: 1) the latest available data were in 2016, and since 2017 the fishing ban policy was implemented in some tributaries and protected areas with variability in implementation among areas complicating the situation, so for simplicity the projection period was set to start in 2017; and 2) because confidence intervals widen as the projection period increases, a limitation on model prediction of 10 years was deemed suitable, so the projection period ended in 2030.

Scenario one: maintaining current fishing pressure

It was assumed that there was no change in fisheries management policy. The annual catch during 2017–2030 was the same as the average yield since the trial operation of the Three Gorges Project (2003) to 2016.

Scenario two: fishing ban in protected areas

It was assumed that there was no fishing in all aquatic protected areas since the Chinese government announced a ban on any kind of fishing in the 332 aquatic protected areas in the Yangtze River as of 2018 (Yi & Yu, 2018). The protected areas include 53 natural protected areas and 279 aquatic germplasm protected areas (for protecting species with potential commercial benefit) at national, provincial and municipal levels. The proportion of the combined total of these two kinds of protected areas to the entire water area was estimated. This ratio was then used to predict the extent to which fishing pressure (i.e. so-called catch weight) would decrease in the 2017–2030 period.

Scenario three: fishing ban in the entire Yangtze River

It was assumed that any fishing activity was prohibited and that no fish were caught from the entire Yangtze River during the period 2017–2030.

2.5 Synthesizing fishing and biodiversity threats in global rivers

Pressure from fishing and biodiversity threats from other anthropogenic activities have been quantitatively evaluated on a global scale by Vörösmarty et al. (2010). The spatial distribution status of fishing pressure and biodiversity threats throughout the world was described in the form of a raster (using 30' latitude/longitude grids). In contrast, we chose to use a raster comprising river basin spatial units in accordance with Tedesco et al. (2017), as we consider that river basin/watershed units are more appropriate as an integral part of river ecosystems and more meaningful for riverine fisheries management. To make the river basins comparable, we chose only the 30 largest river basins which have their watershed areas proximal to the Yangtze River. The spatial analysis was conducted using ArcGIS (ESRI, USA).

3 RESULTS

3.1 Fisheries yields in time and space

Fisheries yields in the Yangtze River showed declining trends during 1949–2016 (Figure 3). The average decadal yields from 1950s to 2010s were 324.65, 252.77, 166.96, 242.33, 149.85, 64.35, and 58.37 thousand tonnes, respectively. The maximum yield of 427.22 thousand tonnes was reported in 1954, and the minimum yield of 46.50 thousand tonnes in 2011. The trend of gradual decline in wild fisheries production was expressed as (assumed $x=1$): $y = 393.08e^{-0.027x}$, $R^2 = 0.71$. The ratios of the yields from fisheries in the Yangtze River to the total fisheries production in China presented an obvious declining trend. The maximum ratio of the yield from the Yangtze River to the freshwater capture yield in China was 67.40%; that to the freshwater capture and aquaculture in China was 44.39%; and that to the total fishery production in China was 31.63%. However, in 2016, the above three ratios were 2.86%, 0.19%, and 0.10%, respectively, indicating that the contribution of the capture fishery in the Yangtze River to food security in China was extremely low at that point in time.

In Dongting Lake, wild capture production was 24.22 ± 8.96 (10.37–55.00) thousand tonnes during 1950–2016, with a coefficient of variation (CV) of 37.0% (Figure 3). In Poyang Lake, the production was 25.55 ± 10.83 (10.02–71.90) thousand tonnes during 1949–2016, with a CV of 42.4%. It is noteworthy that yield from the Three Gorges Reservoir increased, whereas in the middle Yangtze it clearly decreased. The spatio-temporal pattern of yields associated with the provincial area had no obvious change; however, there was clearly observable annual variation in each area (Figures 3 and 4). The spatial distribution of average yield density (1949–1985) among seven provinces declined from the estuary to the upstream region (Figure 4). Until 1985, the latest available data, the areas near the estuary, such as Shanghai and Jiangsu, had the highest yield densities (1,125.21 and 949.30 kg/km², respectively). The areas in the middle and lower reaches, such as Hubei and Anhui, had the second highest yield densities, and those in the two large-lake provinces (i.e. Dongting Lake in Hunan and Poyang Lake in Jiangxi) had the third highest yield densities. Finally, the upper reach (Sichuan) had the lowest yield density (only 15.14 kg/km²).

3.2 Structural changes in fish community

The community structure of fishes, such as the proportions of endemic and migratory species, and the number of rare and endangered species have been considerably altered during the fisheries development process (Figure 5). During 1997–2016, the percentage of endemic fish species among all fishes in the upper Yangtze reach was $22.8 \pm 2.9\%$ (18.6–30.8%), showing a declining trend with a slope of -0.32 (Figure 5a). In Mudong (i.e. at the tail of the Three Gorges Reservoir) (Figure 2), a decreasing trend with a slope of -0.60 was clearly observed. It could reasonably be assumed that the aquatic habitat was highly affected by the operation of the dam, accordingly endemic fishes decreased because most of them being rheophilic required flowing water. From the 1950s to the 2010s, the biomass percentages of the four major Chinese carp species (i.e. the most commercially important migratory fishes in the Yangtze River; the biomass percentage is based on their proportion of total catch weight) in Dongting and Poyang lakes were $12.8 \pm 5.0\%$ (6.7–21.0%) and $8.4 \pm 2.8\%$ (5.9–12.5%), respectively (Figure 5b). Both showed decreasing trends, with the trend in Dongting Lake was more obvious than that in Poyang Lake. It was concluded that either physically disconnected (sluice) or biologically disconnected (streamflow is unimpeded, but fish migration behavior is changed due to hydrological alteration) would have effects on species composition in the lakes. Those such as Dongting Lake and Poyang Lake, although still physically connected nevertheless showed changes in species composition. In addition, fishing activities also altered fish composition due to their selectivity of specific fish species.

Owing to the Gezhouba Dam impeding the river since 1981, the number of rare and endangered fishes diminished rapidly (Figure 5c and 5d). The number of mature Chinese sturgeons below the Gezhouba Dam was estimated to be approximately 2,500 individuals in the early 1980s but declined to approximately 50 by 2014–2016 (Figure 5c). Bycatch numbers of Chinese paddlefish and Yangtze sturgeon (*Acipenser dabryanus*, Acipenseridae) peaked in 1985 and then dropped dramatically (Figure 5d). These two fishes are migratory species that were widely distributed in the upper, middle and lower reaches of the Yangtze River, although their spawning areas were located in the upper reach. As the Gezhouba Dam in the

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middle reach blocked the migration route of these two fishes in 1981, their juveniles of various age classes (0+ and above) became restricted to the middle and lower reaches of the Yangtze River. These juveniles gradually matured and swam upstream but were blocked below the Gezhouba Dam. As the maturation age of Chinese paddlefish is 5–7 years, and 4–6 years for Yangtze sturgeon (Wei et al., 1997), 4–5 years after the dam closed the number gradually increased to its peak then started to decrease. The decrease implies that their populations were declining, and the last living specimen of the Chinese paddlefish was found in 2003 in the upper Yangtze. No Yangtze sturgeon was found below the Gezhouba Dam during 1995–2000, indicating the rapid decline of its favored habitat. Currently, 70 aquatic animals in the Yangtze River Basin have been listed as nationally and/or internationally protected species (Table 1, Table S2), which implies a serious loss in aquatic biodiversity.

3.3 Environmental factors and their impacts on capture yields

The environmental factors in each of the four categories varied greatly during 1997–2016 (Figure 6, Table 2). The total flow discharged at the three stations varied among years, yet there was no clear trend, while the mean sediment concentration at the stations has obviously decreased since 2003 (i.e. the trial operation of the Three Gorges Project). In particular, the mean sediment concentration at Yichang, which is located just below the Three Gorges Dam, decreased considerably (Figure 6a). Both the reservoir number and the total reservoir capacity clearly increased (Figure 6b). The total volumes of wastewater emissions clearly increased, while the ratio of low water quality has decreased since 2010 (Figure 6c). This result implied that water pollution prevention work has become more effective than it was before. Ship cargo volume increased, while total passenger traffic decreased (Figure 6d). This decrease in passengers might have resulted from diversified transport methods; hence, passengers could choose other transport methods, such as railways and highways, rather than ships.

Correlation analysis between wild capture fisheries production and environmental conditions showed significant associations with many of those factors (Table 2). Significant positive

correlations were found between production and runoff characteristics, e.g. the total discharge ($r=0.50-0.62$, $P<0.05$) and the average sediment concentration ($r=0.57-0.75$, $P<0.05$), at the three stations. Correlations between capture production and water impoundment ($r=-0.63$, -0.68 , $P<0.01$) as well as between capture production and water pollution ($r=-0.72$, -0.72 , $P<0.01$) were significantly negative. Ship cargo volume was negatively correlated with capture production ($r=-0.69$, $P<0.01$), whereas total passenger traffic had a positive correlation with capture production ($r=0.80$, $P<0.01$). In addition, weak positive correlations were found between the two runoff variables because they were inherently related. Water retention in dams showed significant negative correlation with sediment concentration because of its effects on the runoff process. Note that although some environmental variables were significantly correlated, they did not have inherent cause and effect relationships with each other and were more likely to have similarly developing trends with time.

The stepwise regression method built two effective regression formulae (Table 3). Two variables (i.e. the sediment concentration (Datong) and the ratio of low water quality reaches), which were selected from the 12 variables, built the better formula, with $F(2, 14)=34.283$ ($P<0.001$, adjusted $R^2=0.83$). This result implied that sediment concentration and water pollution had a significant influence on fishing yields with year.

3.4 Biomass projection in the future

Dongting Lake had the highest average CPUE of 11.70 ± 4.19 kg/boat-day, with a drastic range in the variation of 5.24–21.34 kg/boat-day and a CV of 35.8% (Figure 7). The average CPUE values in the middle reach of the Yangtze River and Poyang Lake were 7.05 ± 2.54 (range 4.70–15.20) kg/boat-day and 5.84 ± 1.66 (range 3.33–8.76) kg/boat-day, respectively and were relatively close. Overall, the CPUE in Dongting Lake showed a downward trend, while that in the middle reach and in Poyang Lake had slightly upward trends.

The spatial analysis showed that the 332 aquatic protected areas were distributed in 13 provincial areas of the Yangtze River (Figure 8). The number of protected areas in each province was highly dependent on the proportion of the area included in the Yangtze River. For instance, Hubei had the largest number of 83, while Shanghai had the smallest number of only two. It revealed that these 332 protected areas occupied approximately 1/3 of the entire water area in the basin. Accordingly, the scenario settings for future biomass estimation are described in Table 4.

The surplus production model estimated past and future biomass in three areas (Table 5, Figure 9). In each area, two of 40 estimates were selected according to the standard of the goodness-of-fit (Table 5). The two lakes have a larger carrying capacity (78,054.91–96,321.65 t in Dongting Lake and 92,974.70–135,020.60 t in Poyang Lake) than that of the middle Yangtze (22,377.51–23,943.21 t). The maximum sustainable yield (MSY) and the final biomass in the two lakes were higher than those in the middle reach of the Yangtze. Under the three management scenarios, the three areas showed very similar variation in biomass (Figure 9). If fishing activity were to continue under the present situation, then the biomass would not change, remaining at its relatively low current level. If fishing was banned in the protected areas, then the biomass would slightly increase. If fishing was completely banned from all areas of the river, then the biomass would rapidly increase and remain at a relatively high level. However, as indicated by difference in the estimates of the population growth rate parameter r (Table 5), the recovery period for fisheries resources in the two lakes would be much faster (3–5 years) than that for the middle reach (8 years). In comparison, the sum of the MSY in the three areas was ~76.17 thousand tonnes, which was still far less (26.1%) than the average yield of 103.06 thousand tonnes reported during 1949–1985 in the corresponding provinces (i.e. Hubei, Jiangxi, and Hunan) (Figure 4).

3.5 Fishing and biodiversity threats in global large rivers

Based on data from Vörösmarty et al. (2010), evaluations of fishing pressure and biodiversity

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threats on thirty large rivers globally were analyzed (Figure 10, Table S3). The analysis showed that the Mekong, Ganges, and Yangtze rivers had the first, second, and third highest fishing pressures, respectively. The Danube, Mississippi, and Shatt al-Arab rivers had the first, second, and third highest biodiversity threats, respectively, and the Yangtze River ranked in 6th place. By simply summing the two indices of fishing pressure and biodiversity threat, the Shatt al-Arab, Yangtze, Ganges, Mekong, and Niger rivers occupied the top five positions, respectively.

4 DISCUSSION

4.1 Limitations of methods

Systematic and long-term monitoring of the Yangtze aquatic ecosystem has been insufficient due to the huge spatio-temporal scale and lack of research effort (Chen et al., 2009; Liu & Gao, 2012). Hydrological monitoring of the Yangtze River, which started in the late 19th century, is more comprehensive than biological monitoring of its aquatic ecosystem (Yang, Xu, Milliman, Yang, & Wu, 2015). The commencement of the Three Gorges Project in the middle 1990s, prompted more extensive monitoring of natural resources and the aquatic environment of the Yangtze River Basin (Chen et al., 2009; Liu & Gao, 2012). The reason that the correlation and projection analyses in this study were performed only from the late 1990s was because of limited data availability prior to then. However, to target the entire Yangtze River, comprehensive fisheries surveys could not be undertaken due to deficiencies in past investments in data collection, and a lack of systematic organization including data sharing mechanisms. In this study, the surplus production model seemed to be the only feasible method which allowed the exploitable biomass to be estimated for such an enormous study area (Hoggarth et al., 2006). The model assumed that fish migration in the evaluated area was negligible. In fact, some fishes migrated to the middle reach and the two lakes, yet their number and biomass were very low (Xie, 2007a, 2007b). Hence, it was reasonable to use this model in the present study. Further monitoring using direct measurements like acoustic detection of fishes, could possibly improve the biomass estimation results in this study. Other

anthropogenic activities directly related to the fishery, such as artificial fish propagation and release (i.e. stocking), recreational fishing, illegal fishing, and dam ecological operations, were excluded from this analysis due to limitations in the available data which are not well elucidated at such large temporal and spatial scales. The prediction is nevertheless worthwhile and the results meaningful despite the omission of these extrinsic factors that may be influencing production. Our models predicted trends in fish biomass under three future fishing scenarios, i) maintaining the current level of fishing pressure, ii) banning fishing in protected areas, and iii) banning fishing in the entire Yangtze River; results that can provide guidance for future fisheries management in the Yangtze River. Moreover, it is hoped that future studies will be able to include more variables (Yang et al., 2007, 2009, 2011).

4.2 Fisheries utilization and protection in the Yangtze

The Yangtze River Basin has experienced great changes in the utilization and protection of its fisheries during the past 70 years (Table 6) (Chen et al., 2003; Lu et al., 2016; Zeng, 1990). From the 1950s to the 1970s, the main role of the Yangtze River was to provide protein-rich food (Zeng, 1990). Since the 1970s, after the construction of the Gezhouba Dam, the protection of migratory fishes (such as the four major Chinese carp species, Chinese sturgeon, and others) started to receive more attention (Yi et al., 1988; Zhang et al., 2017). However, the first fisheries law in China was not decreed until 1986, and in the Yangtze River, the first regulation was issued in 1988. The protection of rare, endangered, and endemic species as well as their habitats has gradually been recognized as an important issue. In 2002, a tentative fishing ban policy was trialed in the middle and lower reaches of the Yangtze River (Yi & Yu, 2018). In 2003, the fishing ban policy was officially implemented and became an important national-level policy for all inland waters of China following on from a marine fishing moratorium. Since 2006, artificial fish propagation and release (i.e. stocking) projects involving many species have been conducted after implementing conservation programs on living aquatic resources (Chen et al., 2009). In general, stocking is for commercial harvesting or rehabilitation of endangered or endemic species. For instance, stocking of Chinese mitten crab (*Eriocheir sinensis*, Varunidae), and the four major Chinese domestic carps, within the

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lakes in the middle and lower Yangtze Basin is mainly for harvesting, whereas stocking of protected species, such as Chinese sturgeon, Yangtze sturgeon and Chinese sucker, etc., is aimed at rehabilitating wild populations. Since 2015, three rescue action plans on flagship species in the Yangtze River, such as Chinese sturgeon, Yangtze finless porpoise, and Yangtze sturgeon, have been successively implemented (Yi & Yu, 2018). Since 2017, a long-term fishing ban policy was implemented, first in a tributary of the upper Yangtze and subsequently extended to 332 nature and germplasm protected areas throughout the entire river basin. To protect wild populations and genetic germplasm resources of three migratory species including Chinese mitten crab, the issuing of a special fishing permit to fish for them, which began in 2002, ceased in late 2018. Currently, more integrated and comprehensive protection plans (a 10-year fishing ban) for the entire Yangtze aquatic ecosystem are being designed (Ministry of Agriculture and Rural Affairs of China, 2019; Yi & Yu, 2018).

4.3 Challenges for Yangtze aquatic biodiversity

Yangtze River aquatic biodiversity is still facing a number of challenges even though the fishing ban policy has been implemented (Chen et al., 2003, 2009; Huang & Li, 2016; Liu et al., 2019; Ye et al., 2011). First, habitat fragmentation and its loss due to damming and sluice construction are difficult to remediate, while some endemic fishes remain exposed to a high risk of extinction (Cheng et al., 2015; Zhang et al., 2013; Zhang, Gao, Wang, & Cao, 2015). The Three Gorges Dam and upstream dams without fish passages have directly blocked the migration of fishes and altered the fluvial river reach into artificial reservoirs (Wu et al., 2003, 2004). This greatly decreased the diversity of endemic fishes as most of them were rheophilic so required flowing water. Currently, there is a plan to build 27 dams along the 2,290 km of the Jinsha River (i.e. the upper reach of the Yangtze and the most species-rich area in the river). Once these dams have been built nearly no river flow will remain (Yang et al., 2007, 2009, 2011). Moreover, a plan to construct a sluice at the confluence of Dongting Lake and Poyang Lake, which are the only lakes still connected to the mainstream of the river, has been proposed, although there has been considerable debate about the merits of this project (Huang et al., 2013; Xie, 2017a, 2017b). In addition, although reclaiming lakes for farmland is now

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strictly forbidden, areas that have already been converted into farmland cannot be reverted to lakes. Second, habitat alterations and deterioration due to reservoir operations and various human activities are difficult to remediate. Reservoir operations largely changed hydrological processes such as flow and sediment transport and deposition (Wu et al., 2004; Yang et al., 2015), and altered the water temperature regime (Wang, Li, Duan, Chen, et al., 2014; Wang, Li, Duan, Luo, et al., 2014) which is critical for fishes throughout the entire Yangtze River. This study revealed that the sediment concentration had important impacts on the yields from capture fisheries. In addition, issues of water pollution, waterway construction and channelization, sand and gravel extraction, port construction, and noise and vibration from vessel navigation are extremely difficult to completely resolve (Yang et al., 2007, 2009, 2011). Third, the recreational fishery and exotic species should be given more attention. Based on our experience, the recreational fisheries catch could be very high; thus, effective regulatory management will be required in the near future (Ma et al., 2018). According to a basin-wide capture survey during 2017–2018 in the Yangtze River, a total of 25 exotic species have been recorded, out of which 11 had never been previously observed in the basin, such as several kinds of tilapia, largemouth bass (*Micropterus salmoides*, Centrarchidae), freshwater pompano (*Piaractus brachypomus*, Serrasalminidae) (Zhang et al., 2020, unpublished data). Moreover, the abundance of exotic species gradually increases from the Yangtze estuary to the headwater, implying that the upstream regions are of greater concern in this regard. In the past, although exotic fish species were occasionally caught in the Yangtze River, due to fishing pressure their influence on the aquatic ecosystem was low. However, the fishing ban policy may be allowing them to flourish, as evidenced by the buildup of an enormous quantity of red swamp crayfish in Dongting Lake. In 2017, its catch reached 11,300 tonnes, accounting for nearly 30% of the total capture production (FB-MARA-PRC, NFTECC, & CFA, 2019). If fishing activities in this lake ceased, then the ecological impacts would be incalculable. Accordingly, measures for controlling their possible sources should be instigated (Liu, McGarrity, Bai, Ke, & Li, 2013). Lastly, an integrated and scientifically based strategic management system for the entire Yangtze River aquatic ecosystem is urgently required (Chen et al., 2009; Liu and Gao, 2012).

632

633 It is speculated that the current protection measures can only rehabilitate Yangtze River
634 fisheries resources to a certain degree. Once a fish community structure is severely disrupted,
635 it is almost impossible to restore. Functionally extinct species (i.e. Baiji, Chinese paddlefish,
636 and Reeves shad) (Turvey et al., 2007; Zhang et al., 2020) will become completely extinct if
637 no further rescue measures are undertaken.

638

639 **4.4 Fishing pressure and biodiversity threat of global rivers**

640 The circumstance of each river is different, not only because it differs in geographic location
641 and associated environment, but also in economic development, fisheries (especially
642 aquaculture) development status, and even the various consumptive habits of the local people
643 (Castello & Macedo, 2016; FAO, 2016; Welcomme et al., 2014). Some rivers face concerns
644 related to food supply (McIntyre et al., 2016), whilst others are confronted by a need for
645 biodiversity conservation (Kominoski et al., 2018). Nevertheless, in all drainage areas, human
646 perturbations have become generally high (Jackson et al., 2016; Vörösmarty et al., 2010) and
647 human population growth has created increased dependency on their natural resources, which
648 in turn leads to increased fishing pressure and biodiversity threats.

649

650 The rapid change in fisheries development and biodiversity conservation in the Yangtze River
651 has many management implications for other large-river systems in the world (Castello &
652 Macedo, 2016; Jackson et al., 2016; Kominoski et al., 2018), as the river has experienced a
653 challenging process of utilization-overexploitation-protection of its fisheries during the last 80
654 years; moreover, other large rivers may have similar issues. Given the similarity in
655 circumstances between these large rivers and the Yangtze River in terms of fishing pressure
656 and biodiversity threats (Figure 10, Table S3), ecosystem management initiatives in the
657 Yangtze River could be informative for other globally large rivers to improve the
658 management outcomes for their ecosystems.

660 4.5 Future management implications

661 In the Yangtze River Basin, five aspects of future management are strongly recommended.
662 First, the present cascaded dam development plan at the basin scale should be reconsidered
663 and revised (Cheng et al., 2015; Kominoski et al., 2018; Winemiller et al., 2016). The
664 cumulative and long-term effects of the dams at the basin scale should be re-evaluated to
665 develop a more ecologically sustainable plan (Castello & Macedo, 2016; Ziv, Baran, Nam,
666 Rodríguez-Iturbe, & Levin, 2012). Some tributaries are important for biodiversity
667 conservation so that the excessive number of small dams located in tributaries should be
668 removed or modified by adding fish passages. Second, a more natural run-off process should
669 be created through strategic reservoir operations. Under the increasing impacts of climatic
670 change and human activities, more components of favorable ecosystems such as water
671 temperature regimes, flood pulses, and sedimentation processes should be designed based on
672 the needs of aquatic organisms (Sabo et al., 2017; Wang, Li, Duan, Chen, et al., 2014; Wang,
673 Li, Duan, Luo, et al., 2014; Yang et al., 2015). Third, the need for appropriate and stringent
674 fisheries policies, to ensure sustainable wild capture and aquaculture practices, must be
675 addressed (Kang et al., 2017; Ma et al., 2018; Wang, Cheng, et al., 2015; Wang, Li, &
676 Waerebeek, 2015), and ecosystem-based fisheries management in light of selective fishing
677 policies should be implemented (Goulding et al., 2019; Zhou et al., 2010). The lakes
678 (reservoirs) in the Yangtze River Basin potentially suitable for aquaculture should be
679 scientifically differentiated, and sustainable fisheries should be ensured by encouraging
680 responsible well-managed fishing activities compatible with engaging local communities in
681 generating socio-ecological benefits. Fishing related tourism, incorporating the catering
682 industry, recreational angling, and cultural activities needs to be encouraged in a balanced
683 manner to maximize long-term economic and ecological benefits. More importantly,
684 aquaculture and species conservation in lakes should be integrated with flood control, water
685 supply, etc., through support from all relevant stakeholders. In addition, recreational angling
686 in natural waters should be scientifically managed via restrictions that limit equipment,
687 thereby curtailing the take of particular species, as well as imposing moratoria and temporal

closures where appropriate to protect endangered and threatened species, ecosystems at risk, and vulnerable habitats (Ma et al., 2018). In addition, aquaculture in the basin should have effective ways to prevent the introduction of exotic species, with stocking required to use local species, and not permitting release of hybrids, gene-modified species, and species that don't meet ecological requirements (Kang et al., 2017; Wang, Cheng, et al., 2015). Fourth, a scientific-based systematic management system should be implemented at the basin scale (Chen et al., 2009; Heiner, Higgins, Li, & Baker, 2011; Wang, Gao, Jakovlić, & Liu, 2017). Finally, public education imparting knowledge and promoting understanding about the critical roles and importance of the ecosystem of the Yangtze River and ecosystem services it provides for human well-being is also necessary, including changing the way people interact with the river system e.g. avoidance of risks from releasing exotic species by ceasing this practice as a religious activity or irresponsible release of unwanted ornamental fish or fish pets by the public (Liu et al., 2013). It is noteworthy that recovery of fisheries resources will not directly result in the rehabilitation of aquatic biodiversity, which requires a much more sophisticated approach to deal with the complexities of ecological interactions.

This study demonstrated that overexploited fisheries resources could be recovered by enforcing a fisheries protection policy including drastic measures such as a complete ban on fishing in the entire river. However, once aquatic habitats are lost or seriously degraded, it will be extremely difficult if not impossible for them to be fully restored. The structure of the fish communities, which is strongly related to biodiversity, is likely to be transformed by indiscriminate fishing and will be challenging to rehabilitate. Of paramount importance is that the rare and endangered, endemic and migratory aquatic species of the Yangtze River Basin require urgent intervention to prevent their extinction.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in this published article and its supporting information.

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Table 1 Protected species in the Yangtze River basin; a detailed list is found in Table S2.

Type of protection list	Category and number	Total
The IUCN Red List of Threatened Species	Critically Endangered, 16;	29
	Endangered, 3;	
	Vulnerable, 1;	
	Near Threatened, 4;	
	Least Concern, 5	

Convention on International Trade in Endangered Species of Wild Fauna and Flora	Appendix I, 5; Appendix II, 3	8
National Protected Wildlife in China	Top Level, 5; Second Level, 9	14
China Species Red List (Fishes)	Extinct, 2; Extinct in the Wild, 2; Critically Endangered, 5; Endangered, 36; Vulnerable, 20	65

1088 **Table 2** Spearman correlations between wild capture fisheries production and environmental factors in the Yangtze River during 1997–2016.

Theme	Mean	SD	Capture production	Runoff process							Water impoundment		Water pollution		Navigation		
			(n=20)	(n=17)							projects (n=20)		(n=20)		(n=20)		
Production and factor	#		1	2	3	4	5	6	7	8	9	10	11	12	13		
Capture production	1	7.16	2.64	X	0.50*	0.62**	0.61**	0.57*	0.57*	0.75**	-0.63**	-0.68**	-0.72**	-0.72**	-0.69**	0.80**	
Summed discharge (Yichang) (×10 ⁹ m ³)	2	406.62	46.77		X	0.64**	0.59*	0.35	0.38	0.50*	-0.13	-0.12	-0.07	-0.36	-0.16	0.21	
Summed discharge (Hankou) (×10 ⁹ m ³)	3	684.67	70.98			X	0.93**	0.32	0.33	0.53*	-0.03	-0.04	0.04	-0.56*	-0.10	0.11	
Summed discharge (Datong) (×10 ⁹ m ³)	4	868.18	113.06				X	0.17	0.16	0.42	0.13	0.10	0.16	-0.62**	0.03	0.03	
Sediment concentration (Yichang) (kg/m ³)	5	0.201	0.256					X	0.96**	0.93**	-0.81**	-0.87**	-0.83**	0.10	-0.91**	0.78**	
Sediment concentration (Hankou) (kg/m ³)	6	0.195	0.109						X	0.94**	-0.80**	-0.86**	-0.80**	0.07	-0.88**	0.74**	
Sediment concentration (Datong) (kg/m ³)	7	0.190	0.075							X	-0.71**	-0.77**	-0.73**	-0.10	-0.81**	0.73**	
Reservoir number (×10 ³ ind.)	8	55.74	11.33								X	0.95**	0.92**	0.11	0.92**	-0.89**	
Total reservoir capacity (×10 ⁹ m ³)	9	335.43	186.37									X	0.97**	0.13	0.98**	-0.94**	
Waste water emissions (×10 ⁹ t)	10	29.30	5.53											X	0.96**	-0.97**	
Low water quality reach (%)	11	26.01	5.38												X	0.13	-0.26
Ship cargo volume (×10 ⁶ t)	12	54.34	37.97													X	-0.94**
Total passenger traffic (×10 ⁶)	13	1.59	1.25														X

1089 * Correlation is significant at the 0.05 level (2-tailed)
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1090 ** Correlation is significant at the 0.01 level (2-tailed)

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Table 3 Stepwise regression between the capture production (CP) and the environmental factors in the Yangtze River. Two factors were selected from the 12 environmental variables (Table 2).

Model	Variables entered	Regression formula	R	R ²	Adjusted R ²	F	Sig.
1	Sediment concentration (Datong) (SC _{DT})	CP = 41.930 + 104.954 × SC _{DT}	0.795	0.63	0.61	25.776	<0.001
2	Sediment concentration (Datong) (SC _{DT}), Low water quality reach (R _{LWQR})	CP = 67.695 + 95.749 × SC _{DT} − 0.885 × R _{LWQR}	0.911	0.83	0.81	34.283	<0.001

Table 4 Scenario settings for catches in three major fishing areas in the Yangtze River.

Area	Middle reach (t)	Dongting Lake (t)	Poyang Lake (t)
Scenario 1 (No fishing ban, assumed catch was the average yield during 2003–2016)	1706	23651	28829
Scenario 2 (Ban fishing in protected areas, which means the catch decreases by 1/3)	1137	15767	19219
Scenario 3 (Ban fishing in all water areas, no catch at all)	0	0	0

Table 5 Parameter estimates for the catch and effort data in the three major fishing areas in the Yangtze River using the Schaefer and Fox production models, including two error

assumptions (LSQ, least squares; and Log, log transform). IP, initial proportion; K, carrying capacity of the population; q, catchability coefficient; r, intrinsic rate of growth; MSY, maximum sustainable yield; R. Yield, replacement yield; R², coefficient of determination.

Area	Model	Fit	IP	K (t)	q($\times 10^{-4}$)	r	MSY (t)	R. yield (t)	Final biomass (t)	R ²
Middle reach	Schaefer	LSQ	0.5	22377.51	5.71	0.395	2208.94	1947.48	15038.15	0.156
	Schaefer	Log	0.5	23943.21	5.39	0.367	2194.44	1967.41	15822.29	0.137
Dongting Lake	Fox	LSQ	0.4	78054.91	2.15	1.297	37247.91	28985.09	49863.66	0.686
	Fox	LSQ	0.5	96321.65	1.69	1.116	39530.38	28804.40	64577.12	0.681
Poyang Lake	Fox	LSQ	0.2	92974.70	1.17	1.119	38279.83	27435.70	63008.21	0.907
	Fox	Log	0.3	135020.60	1.05	0.662	32884.25	28016.19	79052.20	0.938

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Table 6 Key events affecting Yangtze River fisheries and aquatic biodiversity since the 1980s.

Date	Event
Jul 1, 1986	Issued the “Fisheries Law of the People's Republic of China”
Jul 2, 1988	Issued the “Provisional Regulations on the Management of Fishery Resources in the Middle and Lower Reaches of Yangtze River”
Dec 10, 1988	Issued the list of key protected wildlife in China. In the Yangtze River, 5 species were listed at the top protection level and 8 at the second highest level
Sep 28, 1995	Issued the “Yangtze River Fishery Resource Management Regulations”
Apr 4, 2000	Built a national protected area (between Hejiang and Leibo) for protecting rare species in the upper Yangtze. In 2005, this protected area was enlarged and renamed as the Upper Yangtze National Protected Area for Endangered

and Endemic Fishes, which is the largest protected area (3.32×10^4 ha) for freshwater fishes in China

Jan 6, 2003	Started the fishing ban policy in the Yangtze River. The fishing ban period was 3 months: Feb-Apr above the Gezhouba Dam and Apr-Jun below the dam
Feb 14, 2006	Issued the “Program of Action on the Conservation of Living Aquatic Resources of China”, including the Yangtze River as a key area
Sep 28, 2015	Issued the “Rescue Action Plan for Chinese Sturgeon (2015–2030)”
Jan 1, 2016	Adjusted and improved the fishing ban policy. The fishing ban area was enlarged to cover the major mainstream, tributaries and lakes, and the period was extended to 4 months (March to June)
Dec 13, 2016	Issued the “Rescue Action Plan for Yangtze Finless Porpoise (2016–2025)”
Jan 1, 2017	The full fishing ban was applied in a tributary (Chishui River, 436 km) in the upper reach for ten years (2017–2026) (Liu et al., 2012)
Nov 23, 2017	The full fishing ban was applied in 332 aquatic protected areas in the Yangtze River, which accounted for 1/3 of the water areas in the entire drainage area
Mar 22, 2018	Issued the “Key River Basin Aquatic Biodiversity Conservation Program”, which included 7 basins. The first basin was the Yangtze River
May 15, 2018	Issued the “Rescue Action Plan for Yangtze Sturgeon (2018–2035)”
Oct 15, 2018	Issued the "Opinions on Strengthening the Protection of Aquatic Organisms in the Yangtze River"
Dec 28, 2018	Special fishing permit for longjaw grenadier anchovy (<i>Coilia macrognathos</i> , Engraulidae), phoenix-tailed anchovy (<i>Coilia mystus</i> , Engraulidae), Chinese mitten crab, introduced on Feb 8, 2002, was ceased

Figure legends:

Figure 1 Conceptual framework, logical ideas and research content in the present study. Human activities, aquatic organisms, and aquatic environments interact with each other, and policies, such as fisheries law, fishing moratorium policy, rescue action plan, biodiversity conservation program, etc. are used to regulate these to get the best ecosystem services. Figure appears in colour in the online version only.

Figure 2 The study area that is the Yangtze River Basin, showing cities, dams, rivers and lakes. The geographic data are from the National Fundamental Geographic Information System of China. Dam information (associated with reservoirs that have a storage capacity greater than 0.1 km³) in the drainage basin is from the NASA Socioeconomic Data and Applications Center (SEDAC) (Lehner et al., 2011a, b). Based on this dam information, a few dams on the mainstream have been added that reflect recent developments. Figure appears in colour in the online version only.

Figure 3 Fisheries capture production in the Yangtze River Basin and its percentage of China's fisheries production during the period of 1949–2016. Yields in the four major production areas of the basin are indicated separately when the data are available. Figure appears in colour in the online version only.

Figure 4 The spatial distribution of fisheries capture production in the Yangtze River during the period of 1949–1985 (n = 27–37, Zeng, 1990). Map shows the mean yield density (kg/km²) in 7 provinces (Chongqing municipality belonged to Sichuan Province at that time). The

vertical bars in the 7 boxes indicate the capture yields ($\times 10^3$ t) by year (1949–1985). The average yield is seen in the title of the box. TGR-Three Gorges Reservoir, MR-middle reach, DTL-Dongting Lake, and PYL-Poyang Lake. Figure appears in colour in the online version only.

Figure 5 Variations in fish community and number in the Yangtze during capture fisheries development. Refer to Figure 2 for the locations. (a) Percentage of endemic species monitored in the upper reach and number monitored in Mudong, (b) biomass percentage of representative migratory species (the four major Chinese carp species) in the two largest lakes in the middle reach, (c) estimated number of adult Chinese sturgeon below the Gezhouba Dam since the dam was closed in 1981 (Figure S1), (d) bycatch number of Chinese paddlefish in the entire Yangtze, and bycatch number of Yangtze sturgeon below the Gezhouba Dam. Figure appears in colour in the online version only.

Figure 6 Variations in environmental factors in the Yangtze River. (a) Run-off process, refer to Figure 2 for the locations of the monitoring sites; (b) water impoundment; (c) water pollution, data from the entire Yangtze River; (d) navigation, data from the Gezhouba Dam and the Three Gorges Dam. Figure appears in colour in the online version only.

Figure 7 Catch per unit effort (CPUE) in three major fishing areas in the Yangtze River during 2001–2016. Figure appears in colour in the online version only.

Figure 8 The spatial distributions of the aquatic protected areas in the Yangtze River. The numbers before and after the slash represent the quantities of nature and aquatic germplasm protected areas, respectively. The green color scale indicates the total number of protected areas. Figure appears in colour in the online version only.

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1158 **Figure 9** Future stock biomass in the three major fishing areas in the Yangtze River under
1159 three different catch scenarios. Refer to Table 4 for scenario settings. Figure appears in colour
1160 in the online version only.

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1162 **Figure 10** Index of fishing pressure and biodiversity threat in the 30 largest global river
1163 basins. The index is between 0 and 1 (lowest to highest) and is calculated by further analyzing
1164 data from Vörösmarty et al. (2010) and Tedesco et al. (2017). (a) Fishing pressure, roughly
1165 estimated based on capture production and net primary productivity; (b) biodiversity threat, a
1166 combination index based on 23 catchment stressors (factors) including fishing pressure; (c)
1167 scatter plots. Figure appears in colour in the online version only.

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