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Can water level management, stock enhancement, and fishery restriction offset negative effects of hydrological changes on the four major Chinese carps in China's largest freshwater lake?

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ABSTRACT

Habitat degradation and fragmentation have been the leading cause of reduced fishery yields in many freshwater ecosystems around the world. In Poyang Lake, the largest freshwater lake in China, recent hydrological changes driven by the operation of Three Gorges Dam (TGD) and drought have caused a drastic loss of fishery resources. In response, managers have planned to build a sluice at Poyang Lake's outlet to manage the lake's water level and, as the sluice will unavoidably limit the river–lake migration of many fishery species, managers have also proposed implementing stock enhancement programs and restricting fisheries to sustain fisheries in the lake. In this study, we built and implemented a Poyang Lake Ecopath with Ecosim model to evaluate effects of water level management, stock enhancement, and fishery restriction on biomass of the four major Chinese carps: grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*H. nobilis*), and black carp (*Mylopharyngodon piceus*), of which all are river–lake migratory and important to fisheries. Results showed that the total biomass of the four major Chinese carps could increase with increases in water level, increases in stocking biomass, and decreases in fishing pressure. However, even in the best management effort scenario (i.e., highest water level, highest stocking biomass, and no fishing), simulated total biomass of the four major Chinese carps was still 16% lower than the biomass estimate in 2000, three years before the operation of TGD. These results suggest that a combination of managing water level, stocking, and restricting fisheries can substantially offset negative effects of hydrological changes on the four major Chinese carps, but may not be enough to restore the biomass of the four major Chinese carps to high levels that had occurred before the operation of TGD, because of the blockage of river–lake connectivity by the Poyang Lake sluice.

1. Introduction

Freshwater fisheries provide food security, nutrition, livelihoods, and recreation to billions of people around the world (Welcomme et al., 2010; Lynch et al., 2017). However, the majority of freshwater fisheries and their ecosystems have been stressed by human activities, especially by the construction of dams (Chen et al., 2009; Welcomme et al., 2010; Lynch et al., 2017). Dams have provided a range of social and economic benefits including irrigation, flood control, and hydropower generation, and the impoundment of some dams does support important fisheries, such as the Kariba dam between Zambia and Zimbabwe (Karenge and Kolding, 1995). However, effects of dams on fish habitats have been mostly negative and irreversible. The structure of the dam itself could block fish migration and sequester nutrients and sediments that support downstream fish habitats such as river deltas (Nilsson et al., 2005; Dudgeon et al., 2006; Suzuki and Pompeu, 2016). Flow regulation by the dams could eliminate floods that sustain floodplains for many fishes to use as spawning and nursery area (Fu et al., 2003; Ziv et al., 2012; Song et al., 2018). One giant dam (*sensu* Nilsson et al., 2005) could even result in profound changes in fish communities across the whole river

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system by altering the river's hydrological, thermal, and chemical regimes.

China is the country with the largest freshwater catches but the catches have been reportedly declining in recent years (FAO, 2016). The majority of China's freshwater catches are from the basin of middle and lower reaches of Yangtze River (MLYR, referring to Yangtze River below Three Gorges), where many fishery stocks have a long history of being stressed by pollution, overexploitation, and habitat fragmentation (Chen et al., 2009; Liu and Wang, 2018). Since 2003, fisheries in the basin of MLYR have been further stressed by Three Gorges Dam (TGD) and its operation for hydropower generation. The structure of TGD has disrupted the longitudinal connectivity of Yangtze River and the operation of TGD has changed the flow regime of MLYR, which both have negatively affected the recruitment of many fishery species (Xie et al., 2007; Duan et al., 2009). Additionally, sediment trapping by TGD resulted in deepened river bed of MLYR, which further lowered the water level of MLYR and the lateral connectivity between MLYR and its floodplain habitats during recent droughts (Lai et al., 2014). Coincided with these reported hydrological changes that have caused habitat degradation and fragmentation, decreases in fishery production have been reported across many fishing grounds in the basin of MLYR (Chen et al., 2009; Wang et al., 2014).

Changes in the flow regime of MLYR after the operation of TGD have especially strong negative effects on fish community and fisheries in Poyang Lake (Fig. 1), the largest freshwater lake in China. As a floodplain ecosystem, Poyang Lake drains into Yangtze River but also receives the backflow from Yangtze River when Yangtze River water level is at its seasonal high, usually between July and October (Ye et al., 2012). This river–lake interaction is important to the recruitment of migratory fishes in Poyang Lake (Fang et al., 2016), of which many are very important to fisheries such as the four major Chinese carps: silver carp (*Hypophthalmichthys molitrix*), bighead carp (*H. nobilis*), grass carp (*Ctenopharyngodon idella*), and black carp (*Mylopharyngodon piceus*). The four major Chinese carps feed and grow in Poyang Lake but migrate into Yangtze River for spawning in spring, usually between April and May, and then their larvae drift into Poyang Lake with the backflow from Yangtze River (Chen et al., 2009; Li et al., 2013). Comparing with the historical flow regime, the flow in MLYR has increased in the TGD drawdown period (April–June) but decreased in the TGD impoundment period (September–November) since the operation of TGD (Lai et al., 2014). The changes in the flow regime of MLYR have been linked to the decrease in larvae abundance of the four major Chinese carps (Duan et al., 2009).

In addition to changes in the flow regime of MLYR, Poyang Lake fisheries were also stressed by drought, which was widespread in the whole basin of Yangtze River in recent years (Lai et al., 2014). The average tributary inflow of Poyang Lake in 2003–2009 was 20% lower than that of 1957–2002, coincided with an 8% decrease in precipitation and a 10% increase in water consumption (Zhang et al., 2016a). The decrease in tributary inflow has been linked the decreases in water level (Zhang et al., 2014), aquatic habitat area (Wu and Liu, 2017), and nutrient (in terms of total phosphorus) inputs of Poyang Lake (Liu et al., 2014). Further, the operation of TGD might intensify negative effects of drought on the Poyang Lake ecosystem. For example, Zhang et al. (2012) showed that the impoundment of TGD has resulted in an increase in the difference between Yangtze River and Poyang Lake water levels, which, in turn, may result in an increase in the drainage and a decrease of the water level of Poyang Lake.

Managers have been concerned about habitat degradation and fragmentation associated with recent changes in the flow regime of MLYR and droughts that might have negatively affected the fisheries of the four major Chinese carps in Poyang Lake. Total catch of the four major Chinese carps decreased by 59% in Poyang Lake between 2000–2001 and 2008–2009 (Wang et al., 2014), which were two (hydrologically) normal years before the operation of TGD and two drought years after the operation of TGD, respectively (Zhang et al., 2016b). In response to the lake's recent loss of fishery resources, managers have proposed a Poyang Lake multi-faceted restoration project (PLMRP). The proposed project includes three main components: (1) building a sluice at the outlet of Poyang Lake to manage water level,

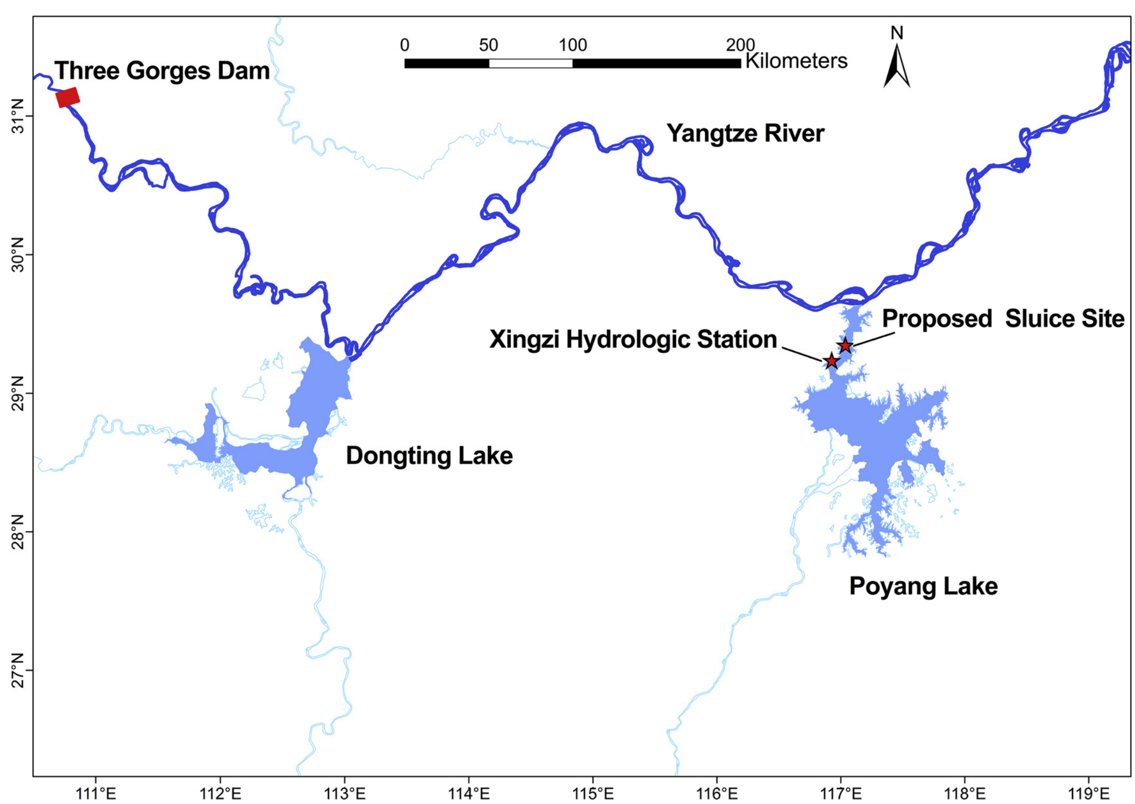

Fig. 1. The map of Yangtze River between Three Gorges Dam and Poyang Lake.

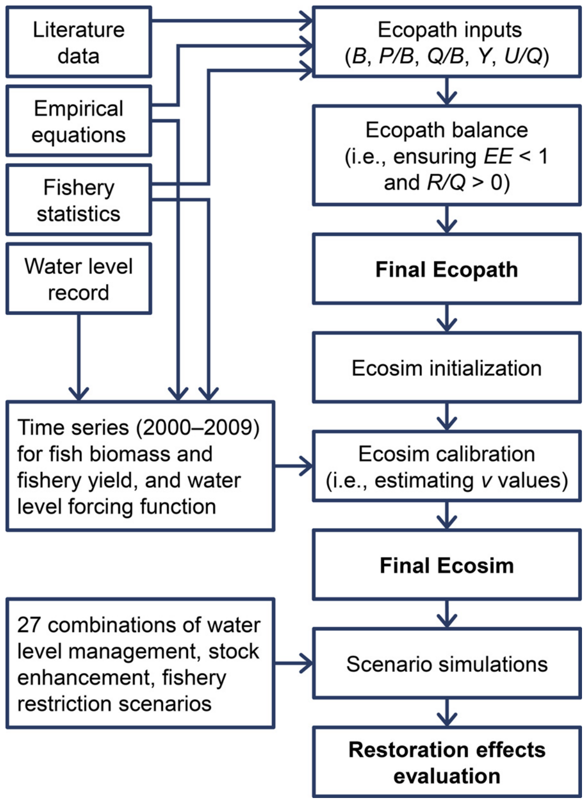

Fig. 2. The analytical flowchart of this study.

which is expected to restore the lake's floodplain habitats but will further limit the river–lake migration of animals, (2) implementing stock enhancement programs to stabilize recruitments of important fishery species; and (3) restricting fisheries (Zhao et al., 2011; Wu et al., 2014). However, the long-term benefit of this restoration project to Poyang Lake fisheries is still questionable and needs to be evaluated.

In this study, we built and implemented an Ecopath with Ecosim (EwE) model (Christensen and Walters, 2004) to evaluate effects of the PLMRP on the four major Chinese carps. While EwE models have been widely used to understand trophic flows among food web groups and simulate food web time-dynamics in many freshwater ecosystems around the world (e.g., Cremona et al., 2018; Guo et al., 2013; Shan et al., 2014; Kao et al., 2014, 2016, 2018), Ecosim, the scenario-simulation component of EwE, has been rarely implemented to support management decision-making for China's freshwater fisheries. To our understanding, only Li et al. (2009) and Zhao et al. (2018) implemented Ecosim to investigate fishery profits and fish community structure under a range of harvest and habitat-change scenarios in freshwater ecosystems in China. To evaluate effects of the PLMRP, we designed our EwE simulation analysis as a full factorial experiment that included three factors: water level, stocking, and fishery restriction. Each factor had three levels or scenarios that were developed based on managers' proposals in PLMRP. We simulated changes in biomass of the four major Chinese carps across all 27 combinations of water level management, stocking, and fishery restriction scenarios.

2. Materials and methods

2.1. Study area

Poyang Lake is located in Jiangxi Province and connected to the middle reach of Yangtze River via a 65-km channel at the north end (Fig. 1). The lake has an average area of 2933 km^2 and a mean depth of 8.4 m, but seasonal fluctuations of water level and lake area are both high. In flood season (April–August), the lake have an area of > 4000 km^2 and an average depth of about 11.6 m (Shankman et al., 2006). In the dry season (September–March), the lake can have an area of < 1000 km^2 and an average depth of about 3.7 m (Wang et al., 2011). The Poyang Lake basin has a subtropical climate, with an average rainfall of 1878 mm per year and > 50% of annual rainfall in the flood season (Guo et al., 2008). The trophic status of Poyang Lake is between mesotrophic and eutrophic (Liu et al., 2017).

2.2. Specifics of the PLMRP

Once again, the main components of PLMRP include (1) managing the lake's water level by building and operating a sluice at the lake's outlet, (2) implementing stock enhancement programs, and (3) restricting fisheries (Zhao et al., 2011; Wu et al., 2014). The proposed water level management plan is to keep the sluice open during Yangtze River's high-flow season (April–August) to allow the river–lake connection but keep the sluice closed otherwise to retain water in the lake. Although Poyang Lake's stock enhancement programs started in 2002, large-scale stocking did not begin until 2010. Proposed stock enhancement programs have a specific focus on the four major Chinese carps because of their river–lake migration and importance to fisheries. For fishery restrictions, currently fisheries in Poyang Lake are closed during the spring spawning season (Chen et al., 2009) but a 10-year ban on all fishing in the main stem of Yangtze River will start in 2020, as announced by China's Ministry of Agriculture and Rural Affairs (www.moa.gov.cn) in January 2019.

2.3. Modeling the Poyang Lake ecosystem

To evaluate long-term benefits of the PLMRP, we used the EwE modeling approach (Christensen and Walters, 2004) and its accompanied program software EwE version 6.5 (available from www.ecopath.org) to investigate effects of water level management, stock enhancement, and fishery restriction on the four major Chinese carps. As summarized in Fig. 2, our analyses included three main tasks. First, we built an Ecopath model to represent biomass flows in the Poyang Lake food web in 2000, which was the first year when we have enough data to estimate biomass inputs across all trophic levels. Second, we built and calibrated a Poyang Lake Ecosim model. Third, we implemented the Ecosim model to simulate food web dynamics over time under management scenarios, which were developed based on the PLMRP.

Based on Christensen et al. (2008), we modeled biomass flows among food web groups in our Poyang Lake Ecopath model as:

$$B_i \times (P/B)_i \times EE_i - \sum_j B_j \times (Q/B)_j \times DC_{ij} - Y_i = 0 \tag{1}$$

where B is biomass (g/m^2 in wet weight), subscript i and j indicate two specific groups, P/B is production to biomass ratio ($year^{-1}$), EE is the ecotrophic efficiency (dimensionless), Q/B is consumption to biomass ratio ($year^{-1}$), DC_{ij} is the proportion of group i in the diet of group j, and Y is fishery yield ($g \times m^{-2} \times year^{-1}$). In this Ecopath model, EE represented the fraction of production for each group lost to predation or fishing, and could be estimated after B, P/B, Q/B, and DC for all Poyang Lake food web groups were input (Christensen et al., 2008). We ensured the Ecopath model to achieve biomass balance ($EE < 1$) at parameterization.

The energy balance in an Ecopath model is modeled as:

$$(P/Q)_i + (U/Q)_i + (R/Q)_i = 1 \tag{2}$$

where $(P/Q)_i$ is production to consumption ratio, $(U/Q)_i$ is the proportion of unassimilated food in consumption, and $(R/Q)_i$ is respiration to consumption ratio (Christensen et al., 2008). In the Ecopath model, $(P/Q)_i$ was calculated based on input values of $(P/B)_i$ and $(Q/B)_i$, $(U/Q)_i$ was an input, and $(R/Q)_i$ was estimated using Eq. (2). We also ensured the Ecopath model to achieve energy balance ($R/Q > 0$) at parameterization.

Based on Christensen et al. (2008) and our Poyang Lake Ecopath model, we modeled the change in B_i over time in our Poyang Lake Ecosim model as:

$$dB_i/dt = G_i \times \sum_j Q_{ji} - \sum_j Q_{ij} - (M0_i + F_i) \times B_i \quad (3)$$

where G is gross conversion efficiency (dimensionless), Q_{ji} is consumption on group j by group i (g × m^{-2} × year^{-1}), Q_{ij} is predation on group i by group j (g × m^{-2} × year^{-1}), $M0$ is non-predatory natural mortality rate (year^{-1}), and F is fishing mortality rate (year^{-1}). In the Ecosim model, consumption was predicted based on the foraging arena theory (Ahrens et al., 2012). As did in Kao et al. (2016), the foraging arena equation could be expressed as:

$$Q_{ij} = \frac{p_{ij} \times v_{ij} \times B_i \times B_j \times f_1}{v_{ij} \times (1 + f_2) + p_{ij} \times B_j \times f_3} \quad (4)$$

where p_{ij} is predation rate on group i by unit biomass of group j (g^{-1} × year^{-1}), v_{ij} is vulnerability parameter (dimensionless), and f_1, f_2, and f_3 are functions representing effects of feeding time and handling time on consumption, which were kept as default settings (for details, refer to Christensen et al., 2008).

2.4. Parameterization of the Poyang Lake Ecopath model

We configured 19 food web groups in the Poyang Lake Ecopath model (Table 1). Input values of B, P/B, and Q/B (Table 2) were obtained from literature or estimated using empirical models. Due to lack of information, we set U/Q to the (Ecopath) default value of 0.20 for fish groups (Christensen et al., 2008) and following Kao et al. (2014), we set U/Q to 0.55, 0.55, and 0.40 for shrimps, benthos, and zooplankton respectively. As shown in Supplementary Table S1, diet composition inputs (DC) were either obtained from literature for Poyang Lake studies or based on studies of the same taxa in similar lake ecosystems in the basin of MLYR.

2.4.1. Fish groups

Our Poyang Lake Ecopath model included 13 fish taxa (Table 1). In order to simulate effects of stock enhancement in Ecosim, we parameterized the four major Chinese carps as multi-stanza groups with two stanzas—age zero (age 0) and age one and older (age 1 +)—and set the age-1 + stanza as the leading-stanza (Christensen et al., 2008). Additional input parameters required for multi-stanza groups include the von Bertalanffy (1938) growth parameter (K), which we obtained from literature (Supplementary Table S2), and the ratio of weight at maturity to asymptotic weight (w_m/w_∞), which we set to the default value of 0.09 (Christensen et al., 2008). Inputs for B and Q/B were only required for leading-stanza groups and B and Q/B for other stanza groups were estimated by Ecopath based on other input parameters (Christensen and others 2008).

We first estimated P/B for single-stanza groups or Z for the leading-stanza groups of the four major Chinese carps using the Beverton and Holt (1957) model based on K, asymptotic length (L_∞), average length (L_{ave}), and cut-off length at entry into fishery (L_{cut}). We set Z for age-0 groups of the four major Chinese carps to 3 year^{-1} based on Wang et al. (2017). Following Christensen et al. (2008), we estimated biomass inputs using fishery yield (Y) calculated from the catch statistics dataset used in Wang et al. (2014) as:

$$B = Y/F = Y/(Z - M) \quad (5)$$

where M is natural mortality rate. We estimated M using empirical model based on K, L_∞, and an annual average water temperature (T_{ann}) of 18 °C (Xu and Wang, 1989). We estimated Q/B using the empirical model from Palomares and Pauly (1998) based on T_{ann}, W_∞, and aspect ratio (A), the ratio of square of caudal fin height to its surface area. We obtained values for L_∞, L_{ave}, L_{cut}, and W_∞ from literature and estimated aspect ratios using images of Poyang Lake fish samples (Supplementary Table S2).

2.4.2. Shrimps

The biomass input of shrimps was estimated using fishery yield (Y) from the fishery catch dataset in Wang et al. (2014) and Equation (5). We estimated P/B for shrimps using Brey's (2012) empirical model for crustaceans in a lake habitat, with a mean temperature of 18 and a mean depth of 8.4 m. Another required input for Brey's empirical model is average individual weight in a unit of J, which we used 1000 J for shrimps based on an average individual weight of 1.25 g (Shi et al., 1995) and an energy density of 792 J/g (Cummins and Wuycheck, 1971). We estimated natural mortality rate for shrimps using Hoenig's (1983) empirical model based on a longevity of two years. We calculated Q/B for shrimps based on empirically estimated P/B and a P/Q of 0.19 (Li et al., 2018).

2.4.3. Lower-trophic-level groups

Biomass inputs of benthos, zooplankton, and producer groups were obtained from Cui and Li (2005), which were estimated based on survey data between 1997 and 1999. Similar to the estimation for P/B of shrimps, we estimated P/B for main taxa of benthos using Brey's (2012) empirical model and an average individual weight of 50 J, based on average individual weights from Cui and Li (2005) and energy densities from Cummins and Wuycheck (1971). We estimated P/B for main taxa of zooplankton using empirical models from Shuter and Ing (1997), based on an annual average temperature of 18. P/B values for phytoplankton and submerged macrophytes were obtained from Sun and Huang (1993) and Kao et al. (2014), respectively. We calculated Q/B for benthos and zooplankton based on empirically estimated P/B and a P/Q of 0.23 for benthos (Kao et al., 2014) and a P/Q of 0.26 for zooplankton (Straile, 1997).

2.4.4. Detritus

We used the empirical model from Pauly et al. (1993) to estimate detritus biomass in a carbon unit (gC/m^2), based on an annual primary production of 980 gC/m^2 and a euphotic depth of 2.4 m (Zhu and Zhang, 1997). To calculate the wet-weight biomass input of detritus, we

Table 1
Food web groups in the Poyang Lake Ecopath model.

Group (age stanza)	Scientific name or main taxa
Mandarin fish	*Siniperca chuatsi*, *Siniperca kneri*
Culters	*Culter alburnus*, *Culter mongolicus*, *Culter dabryi*, *Culterichthys erythropterus*
Amur catfish	*Silurus asotus*
Yellow catfish	*Pelteobagrus fulvidraco*, *Pelteobagrus vachelli*
Lake anchovy	*Coilia brachygnathus*
Silver carp (0, 1 +)	*Hypophthalmichthys molitrix*
Bighead carp (0, 1 +)	*Aristichthy nobilis*
Black carp (0, 1 +)	*Mytopharyngodon pious*
Grass carp (0, 1 +)	*Ctenopharyngodon idellus*
Common carp	*Cyprinus carpio*
Crucian carp	*Carassius auratus*
Chinese breams	*Megalobrama skolkovii*, *Parabramis pekinensis*
Small fishes	*Pseudorasbora parva*, *Sarcocheilichthys sinensis*, *Abbottina rivularis*, *Acheilognathus macropterus*
Shrimps	*Exopalaemon modestus*, *Macrobrachium nipponense*
Benthos	*Corbicula fluminea*, *Unio douglasiae*, *Limnoperna fortunei*, *Bellamya aeruginosa*, *Branchiura sowerbyi*, *Parafossarulus eximius*, *Polypedilum scalaenum*
Zooplankton	Cladocerans, copepods, rotifers, protozoans
Phytoplankton	Chlorophytes, Bacillariophytes, Cyanophytes, Euglenophytes, Cryptophytes, Dinophytes, Chrysophytes
Submerged macrophytes	*Vallisneria natans*, *Hydrilla verticillata*, *Potamogeton malaianus*, *P. crispus*, *Najas minor*, *N. marina*
Detritus	Dissolved and suspended organic matter

Table 2
Input parameters of the 2000 Poyang Lake Ecopath model.

Group (age stanza)	Biomass (g/m^2)	*P/B* or *Z* (year^{-1})	*Q/B* (year^{-1})	*EE*	Y (g × m^{-2} × year^{-1})
Mandarin fish	0.774	0.78	3.58	**0.56**	0.336
Culters	0.460	0.97	4.06	**0.73**	0.212
Amur catfish	0.537	2.09	7.00	**0.51**	0.571
Yellow catfish	0.685	2.19	7.72	**0.58**	0.710
Lake anchovy	0.816	1.20	8.50	**0.07**	0.040
Silver carp (0)	**0.049**	3.00	**46.71**	**0.00**	
Silver carp (1+)	0.392	1.36	14.26	**0.20**	0.109
Bighead carp (0)	**0.056**	3.00	**32.83**	**0.00**	
Bighead carp (1+)	0.288	1.44	11.67	**0.52**	0.215
Black carp (0)	**0.041**	3.00	**18.62**	**0.00**	
Black carp (1+)	0.429	0.90	6.00	**0.15**	0.057
Grass carp (0)	**0.081**	3.00	**26.54**	**0.00**	
Grass carp (1+)	0.402	1.13	10.47	**0.46**	0.139
Common carp	1.767	1.91	7.54	**0.92**	2.601
Crucian carp	1.491	1.75	14.88	**0.69**	1.440
Chinese breams	0.728	0.76	20.27	**0.53**	0.195
Small fishes	2.794	2.22	20.23	**0.98**	1.117
Shrimps	2.620	3.08	16.35	**0.97**	2.305
Benthos	148.095	5.83	25.00	**0.02**	
Zooplankton	2.127	31.69	120.00	**0.73**	
Phytoplankton	1.265	185.00		**0.93**	
Submerged macrophytes	450.000	10.00		**0.10**	
Detritus	10.906			**0.48**	

Bold parameters were calculated by Ecopath, *P/B* is production to biomass ratio, *EE* is the ecotrophic efficiency, *Q/B* is consumption to biomass ratio, *Y* is fishery yield.

multiplied the empirically estimated carbon biomass of detritus by a wet-weight-to-carbon ratio of 4 based on Kao et al. (2014).

2.5. Ecosim calibration

The objective of our Ecosim calibration was to estimate the vulnerability parameter in equation (4) for each consumer group by minimizing the overall sum of squares between predicted and observed biomass after logarithm transformation in the calibration period 2000–2009 (Christensen et al., 2008). We used observed fishery yields and water level in the calibration period as drivers of biomass time-dynamics of all modeled food web groups in our Ecosim calibration. Even though the stocking program started in 2002, the scale of stocking was small in the calibration period so that we assumed that stocking had no effect on fish biomass and did not include stocking in Ecosim calibration. In summary, inputs required for our Ecosim calibration included time series for observed biomass and fishery yield, and a forcing function that links primary productivity and observed water level.

For 12 out of 13 fish taxa in our Poyang Lake Ecosim model, we used the dataset in Wang et al. (2014) and the method described in 2.3.1 to calculate 2000–2009 time series for observed biomass and fishery yield. However, we were unable to obtain data to calculate observed biomass time series for lake anchovy and non-fish groups. Due to low catch rates, the management agency has stopped reporting catch statistics of lake anchovy since 2002. As a result, we assumed that there was no harvest on lake anchovy in the calibration period.

In our Poyang Lake Ecosim model, we represented effects of water level changes on the Poyang Lake food web as a control of primary productivity. Based on Christensen et al. (2008), we modeled the production (P) of producer group i as:

$$P_i = B_i \times SF \times (P/B)_{max,i} \times [Nf/(Nf + K_i)] \tag{6}$$

where $(P/B)_{max,i}$ is the maximum production to biomass ratio, SF is a seasonal forcing function that represents water level effects on primary productivity, Nf is the proportion of free nutrients, and K_i is a model constant. We calculated SF as:

$$SF(month) = [Depth(month) - 8.4]/8.4 \tag{7}$$

where $Depth(month)$ is average monthly depth (m) recorded at Xingzi hydrology station (Fig. 1) and 8.4 (m) is the average depth of Poyang Lake. We developed Eq. (7) based on a hypothesis that increases in water level can lead to increases in habitat availability, which, in turn, lead to increase in primary productivity. This hypothesis was developed based on Wu et al. (2013) and Liu et al. (2016b), which showed a strong positive correlation between water level and primary productivity (as indicated by chlorophyll *a*).

We kept all Ecosim parameters at default setting except (1) vulnerability parameters, which were estimated through calibration and (2) the "Base proportion of free nutrients", which was set to 0.75 to represent a mesotrophic ecosystem (Christensen et al., 2008). Notably, in Eq. (6), $(P/B)_{max,i}$ was set at default value of twice of Ecopath $(P/B)_i$ and Nf and K_i were estimated by Ecosim (Christensen et al., 2008). Finally, we calculated root-mean-square deviations between predicted and observed biomass after logarithm transformation (*RMSD*) to judge relative goodness of fit across groups in our Ecosim model.

2.6. Scenario simulations

Following the approach in Kao et al. (2018), we designed our scenario simulations as a full factorial experiment including three, three-level factors: water level management, stock enhancement, and fishery restriction. We chose to run all 27 scenario combinations, instead of using other methods such as the orthogonal experimental design to reduce the number of simulation runs, because computational time was not a limitation in this study. On average, it took us less than 1 min to run a scenario simulation on an average personal computer.

The four major Chinese carps were modeled as Ecosim hatchery groups (Christensen et al., 2008), whose recruitments were sustained by stocking fingerlings, in all of our scenario simulations. We assumed that there will be no natural recruitment for the four major Chinese carps after the sluice is built and operated to manage water level, because of the blockage of river–lake connectivity. Therefore, by comparing simulated biomass across scenarios with the biomass inputs in our 2000 Poyang Lake Ecopath model, we could identify the combinations of scenarios in PLMYR that can restore the biomass of the four major Chinese Carps to a level before the operation of TGD.

Our water level management scenarios included a pre-TGD

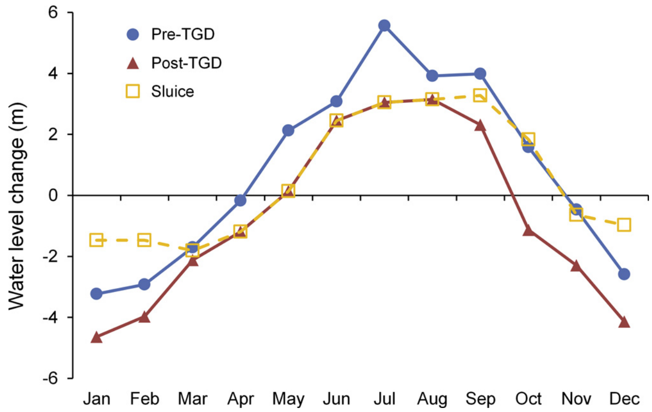

Fig. 3. Seasonal water level changes of three Poyang Lake water level management scenarios (0 = lake level at the mean depth of 8.4 m).

scenario, in which the sluice was operated to maintain average monthly water levels in 1999–2003; a post-TGD scenario, in which the sluice was operated to maintain average monthly water levels in 2005–2009; and a Sluice scenario, the sluice operation was based on the PLMRP: opening the sluice to connect the lake and Yangtze River in April–August and closing the sluice to maintain water level of the lake during the rest of the year (Fig. 3). The pre-TGD represented water level of Poyang Lake in a period (1999–2003) with normal to high precipitation (Zhang et al., 2016a) and no influence of TGD operation. The Post-TGD scenario represented water level of Poyang Lake in a period (2005–2009) with normal to low precipitation (Zhang et al., 2016b) and the influence of TGD operation. Finally, we calculated *SF* in each water level management scenario using Eq. (7).

Our stock enhancement scenarios were developed based on a goal of stocking at least 200 million fish (all species combined) across water bodies in Jiangxi Province per year, which was announced by the Department of Agriculture and Rural Affairs of Jiangxi Province (http://www.jxagri.gov.cn/) in September 2018. In the announced stocking plan, the majority of the 200 million stocked fish will be fingerlings of the four major Chinese carps that have a minimum size of 3 cm or about 0.5 g. Therefore, we assumed that the total biomass of stocked fingerlings of the four Chinese carps is about 100 tonnes across the Jiangxi Province. Accordingly, we developed low, medium, and high stocking scenarios as stocking 50, 100, and 150 tonnes of fingerlings of the four major Chinese carps, respectively, which represented a possible range of the total biomass of fingerlings of the four major Chinese carps stocked in Poyang Lake by Jiangxi Province. The total fingerling biomass in each stocking scenario was then apportioned to the four Chinese carps based on the biomass observed between 2007 and 2009, the last three years of the calibration period.

Our fishery restriction scenarios include high fishing pressure, low fishing pressure, and no fishing. The high fishing pressure scenario represented that there is no further restriction on fisheries in Poyang Lake and the average fishing mortality rates in 2007–2009, which were calculated in Section 2.4.1, were applied in simulations. The no fishing scenario represented the maximum achievable restoration effort, although the Jiangxi Province currently has no plan to further restricting fisheries. The low fishing pressure scenario, in which 50% of the average fishing mortality rates in 2007–2009 were applied in simulations, represented a middle ground between high fish pressure and no fishing scenarios.

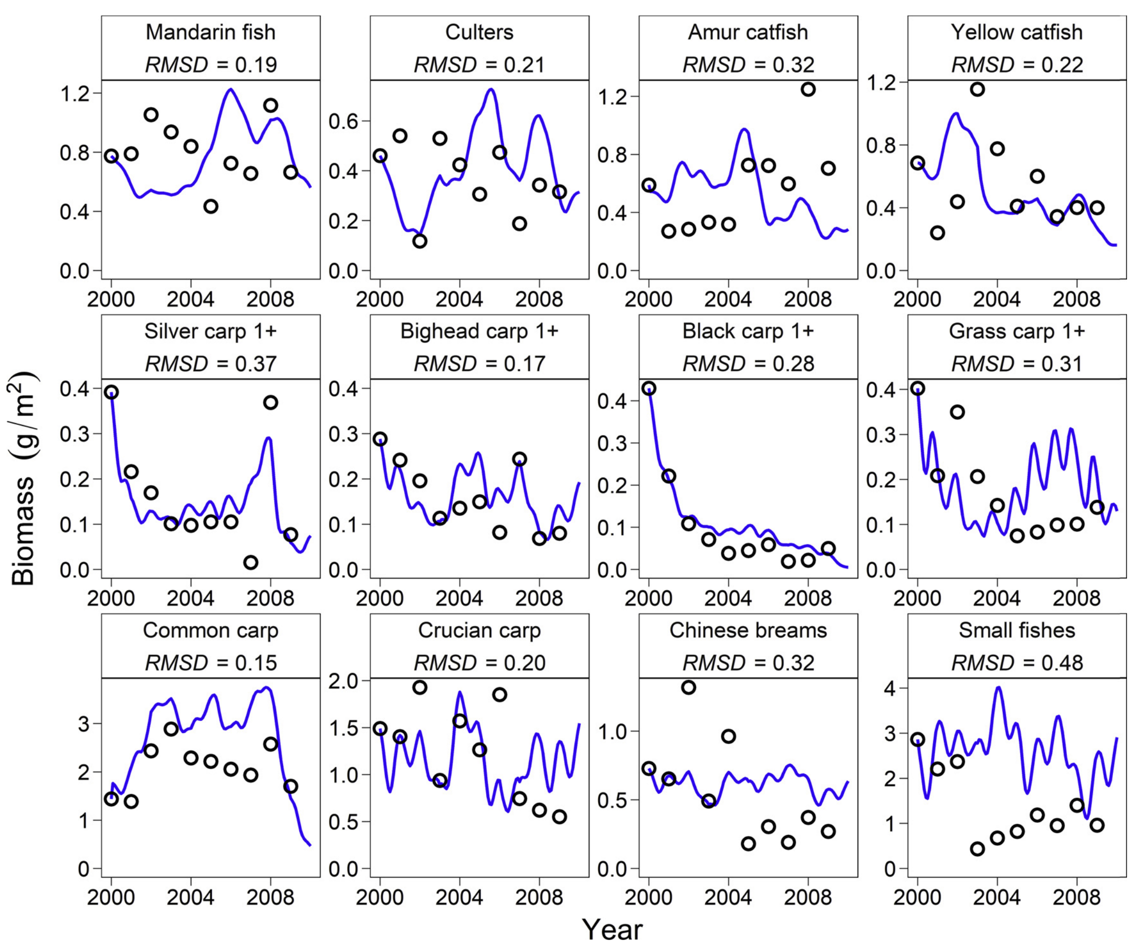

Fig. 4. Calibration results of the Poyang Lake Ecosim model. The line represents the best-fit biomass, and circles are observed biomass time series.

Across all 27 scenario combinations, we ran simulations for 110 years between 2010 (the first year after the calibration period of 2000–2009), and 2119. Simulated biomass of all food web groups reached equilibrium within 50 simulation years across all scenarios. We reported the equilibrium biomass for the four major Chinese carps across scenarios.

3. Results

3.1. Ecosim calibration

After calibration, biomass time series simulated by the Poyang Lake Ecosim model mostly fitted well with observed biomass time series (Fig. 4). Fits were best for mandarin fish, culters, yellow catfish, bighead carp 1 +, black carp 1 +, common carp, and crucian carp, with *RMSD* between 0.15 and 0.28. For Amur catfish, grass carp 1 +, and Chinese breams, simulated and observed biomass time series had opposite trends during part of the calibration period, with *RMSD* of about 0.32. Simulated biomass time series of Silver carp 1 + generally fitted well with observed biomass time series, but did not have the same large inter-annual variation as observed between 2006 and 2008, which resulted in a relatively higher *RMSD* of 0.37. Fits were relative poor for small fishes, with an *RMSD* of 0.48, mainly because simulated biomass time series did not have the same low-biomass period between 2003 and 2007.

3.2. Simulated biomass of the four major Chinese carps

Results (Fig. 5) showed that water level management, stock enhancement, and fishery restriction can all increase biomass of the four major Chinese carps in Poyang Lake but effects of fishery restriction could be the strongest. However, even in the best management effort scenario (i.e., highest water level, highest stocking biomass, and no fishing), simulated total biomass of the four major Chinese carps was still 16% lower than the biomass estimates used in the 2000 Poyang Lake Ecopath model.

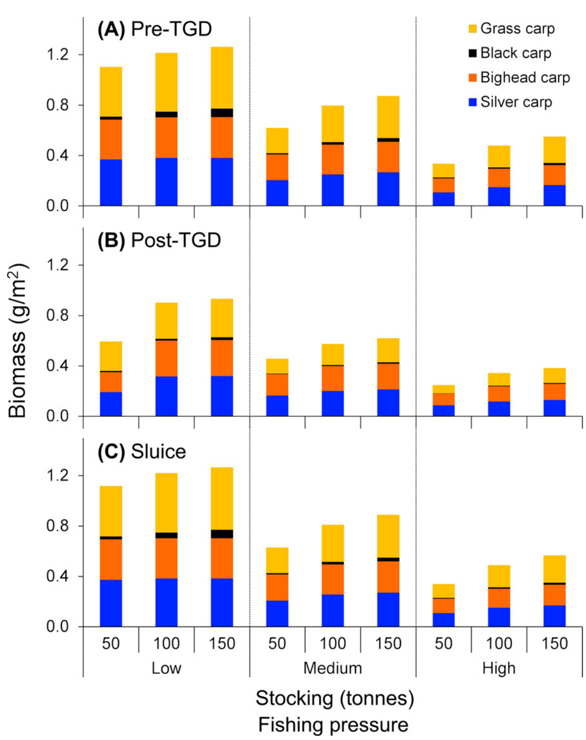

Fig. 5. Simulated equilibrium biomass for the four major Chinese carps across 27 scenarios of water level management, stock enhancement, and fishery restriction.

Equilibrium (total) biomass of the four major Chinese carps increased by 30–78% across all (water level management and stock enhancement) scenarios where fishing pressure decreased from the high to the low level, and increased by another 57–85% across all scenarios where fishing pressure decreased from the low level to no fishing. Results also showed that positive effects of fishery restriction on biomass of the four major Chinese carps increased with increases in water level and decreases in stocking rate. Between scenarios of the same level of decrease in fishing pressure (e.g., decreased from scenarios of high fishing pressure to low fishing pressure), the largest increases in equilibrium biomass of the four major Chinese carps occurred under the scenario of low stocking and Pre-TGD water level.

Equilibrium biomass of the four major Chinese carps increased by 35–88% across all (stock enhancement and fishery restriction) scenarios where water level management scenarios changed from Post-TGD to Sluice, but increased by only 0.2–3% across all scenarios where water level management scenarios changed from Pre-TGD to Sluice (Fig. 5). Across all scenarios where water level management scenarios changed from Post-TGD to Sluice, the largest increase in equilibrium biomass of the four major Chinese carps occurred under the scenario of lowest stocking rate and no fishing while the least increase occurred under the scenario of no fishing and largest stocking.

Equilibrium biomass of the four major Chinese carps increased by 9–52% across all (water level management and fishery restriction) scenarios where stocking increase from the low to the medium level, and increased by another 3–16% across all scenarios where stocking increased from the medium to the high level (Fig. 5). Results also showed that positive effects of stock enhancement on biomass of the four major Chinese carps generally increased with increases in fishing restriction and water level. However, between scenarios of low and medium stocking level, the largest increases in equilibrium biomass of the four major Chinese carps occurred under the scenario of no fishing and Post-TGD water level.

4. Discussion

4.1. Overview and synthesis

In this case study of Poyang Lake, we found that a combination of maintaining a relatively high water level, stocking fingerlings, and restricting fisheries can substantially offset negative effects of hydrological changes on the four major Chinese carps. However, even though managing water level and stocking fingerlings are both more direct management responses to habitat degradation and fragmentation caused by recent hydrological changes, we found that restricting fisheries could be the most effective way to restore the four major Chinese carps. These results suggest that the four major Chinese carps have been stressed by overfishing, even with the enforcement of a breeding season fishing bang. Further, overfishing may exacerbate the negative effects of habitat degradation and fragmentation on the four major Chinese carps. For example, when water level decreased from Pre-TGD scenario to Post-TGD scenario (Fig. 3) and stocking was maintained at the highest level (i.e., 150 tonnes of fingerlings), simulated total biomass of the four major Chinese carps decreased by 26% under the low fishing pressure scenario but by 32% under the high fishing pressure scenario.

While the proposed sluice may maintain the size and quality of habitat during droughts and in the dry season, it may also eliminate the potential for strong year classes of the four major Chinese carps in Poyang Lake, which usually occurred alongside with Yangtze River flooding (Duan et al., 2009), because of the blockage of river–lake connectivity. Even in our best management effort scenario (i.e., highest water level, highest stocking biomass, and no fishing), simulated total biomass of the four major Chinese carps was still 16% lower than the biomass estimate used in our 2000 Poyang Lake Ecopath model. The main difference between the Poyang Lake ecosystem represented in all of our scenario simulations and in our 2000 Ecopath model was that we assumed that there will be no natural recruitment for the four major Chinese carps after the proposed sluice is built and operated to manage water level. Additionally, the biomass of the four major Chinese carps in 2000 could be at a relatively high level because the high Yangtze River water level in 1997–1999 might result in strong year classes of the four major Chinese carps in Poyang Lake (Duan et al., 2009). These results also suggest the proposed PLMRP may stabilize the biomass of the four major Chinese carps but may not restore their biomass to high levels that had occurred before the operation of TGD, because of the blockage of river–lake connectivity by the Poyang Lake sluice.

We hypothesized that increases in water level will result in increases in primary productivity of the Poyang Lake ecosystem. Accordingly, we used a simple equation (7) to model effects of water level on primary productivity in our Poyang Lake Ecosim model. This hypothesis was supported by empirical studies from Liu et al. (2016b) and Wu et al. (2013). Both studies suggested that the observed positive correlation between water level and primary productivity in Poyang Lake could be explained by a better light condition for the primary producers to grow at a higher water level. Because of the low water depth of Poyang Lake, water level could be an important control on sediment resuspension and water transparency, especially during the dry season (Liu et al., 2016b; Wu et al., 2013). Additionally, this hypothesis was also supported by this study. We were able have our Ecosim-predicted biomass time series fit well with observed biomass time series (Fig. 4), which indicates that it should be reasonable to use equation (7) to model the relationship between water level and primary productivity in the Poyang Lake ecosystem.

As water level can be a main control on primary productivity, the four major Chinese carps in Poyang Lake can be stressed by food limitation in drought years. Our results showed that when water level increased from Post-TGD scenario (i.e., low water levels in a dry period after TGD operation) to Sluice scenario (i.e., the proposed water level management plan through sluice operation), the simulated biomass increased across food web groups in all trophic levels. These results suggest strong bottom-up (resource) controls in the Poyang Lake ecosystem at low water levels. Other studies also showed that biomass of organisms across trophic levels decreased with water level in the Poyang Lake ecosystem, including phytoplankton (Qian et al., 2017), zooplankton (Liu et al., 2016a), benthos (Cai et al., 2014), and submerged macrophytes (Wu et al., 2009). These studies support our hypothesized relationship between water level and primary productivity and also suggest strong bottom-up controls in the Poyang Lake ecosystem, at least, at low water levels.

Although the importance of lake level fluctuation to nutrient recycling and primary productivity has been documented in other ecosystems (e.g., Gownaris et al., 2018; Kolding and van Zwieten, 2012), we could not find any previous study supporting this hypothesis for the Poyang Lake ecosystem. One plausible explanation is that even though the fluctuation of water level can facilitate nutrient recycling, the quantity of recycled nutrients is small relatively to the nutrient inputs from tributaries for the Poyang Lake ecosystem. On an annual basis, about 240 tonnes of phosphorus was released from Poyang Lake sediments (Wu, 2014), which was about 6.4% of phosphorus inputs (3700 tonnes) from Poyang Lake tributaries (Chen et al., 2016). Therefore, effects of water level on primary productivity could be much stronger than effects of water level fluctuation in the Poyang Lake ecosystem.

While our fishery restriction scenarios included a scenario representing the maximum achievable restoration effort (i.e., no fishing), it is possible to increase restoration effort above our best restoration effort scenario of either water level management or stock enhancement. However, we found that there might be an upper limit, above which stocking more fingerlings of the four major Chinese carps or maintaining water level at an even higher level will have little positive effects on the biomass of the four major Chinese carps in Poyang Lake. For example, our scenario simulations showed that increasing stocking rate from 100 tonnes to 150 tonnes fingerlings per year did not result in the same level of biomass increases for the four major Chinese carps as increasing in stocking rate from 50 tonnes to 100 tonnes fingerlings per year (Fig. 5). Although identifying an optimal biomass of the four major Chinese carps to stock in Poyang Lake is beyond the scope of this study and the capacity of our EwE model, more research (e.g., understanding the relationship between water level and primary productivity, survival rates of stocked fingerlings) is needed so that the Poyang Lake ecosystem can be better understood and the valuable resource can be better spent on restoration.

4.2. Potential model biases

We first acknowledge that Poyang Lake is a data-poor ecosystem so that while our EwE input parameters were developed based on our best effort, the parameterization of this EwE model can be improved with more researches. Similar to many other EwE models built for aquatic ecosystems in developing countries (e.g., Chea et al., 2016; Downing et al., 2012; Guo et al., 2013; Shan et al., 2014), our EwE biomass inputs for fish groups were largely based on fishery-dependent data and empirical estimations of mortality rates and our *P/B* and *Q/B* inputs for lower trophic level groups were largely based on empirical models developed based on global dataset. These model input parameters can be improved by, for example, developing statistical catch-at-age population models (e.g., He et al., 2015) and conducting monitoring surveys (e.g., Bunnell et al., 2014).

We used *RMSD*, which suggests a goodness of fit between simulated and observed biomass time series in Ecosim calibration, as an indicator of potential model biases for a food web group within our Poyang Lake Ecosim model. Following Kao et al. (2018), we diagnosed a relatively high *RMSD* of silver carp 1 + as noninfluential because it was driven by a year (2007) of poor fit and the simulated biomass could emulate the general trend of observed biomass changes in the Ecosim calibration period of 2000–2009. Relatively high *RMSD* for Amur catfish, Grass carp 1 +, Chinese breams, and small fishes indicated potential biases for these groups. However, these relatively high *RMSD* could also be caused by inaccurate fishery statistics in some years, as these biomass time series were based on fishery-dependent data. For example, due to low economic value small fish catches often under reported (Qian et al., 2002; Fang et al., 2016).

4.3. Management implications

While we showed that water level management and stock enhancement could both offset negative effects of hydrological changes on the four major Chinese carps in Poyang Lake, we highlight the importance to incorporate fishery restriction into restoration planning. We found that overfishing may not only stress the four major Chinese carps more than habitat degradation and fragmentation but also exacerbate the negative effects of habitat degradation and fragmentation on the four major Chinese carps in Poyang Lake. Our results also implied that current breeding season fishing ban, with focuses of protecting reproduction and enhancing juvenile survival rates, may not be enough to sustain fisheries of the four major Chinese carps in Poyang Lake. However, it is uncertain whether a stricter fishery restriction than current breeding season fishing ban can be achieved. Therefore, future fishery management may use different approaches to reduce fishing pressure, such as regulating landing size, fishing gear, catch quota, and fishing area (Chen et al., 2012; Allan et al., 2005).

We also highlight the importance of maintaining water level during the dry season to the four major Chinese carps in Poyang Lake, as our results suggest that low water levels during the dry season can result in food limitation and become a recruitment bottleneck to them. Similar recruitment bottleneck resulted from low dry-season water level was also observed for fishery species in other floodplain ecosystems—after drought fish abundance sharply dropped in floodplain lakes in both central Amazon (Ropke et al., 2017) and Australia (Arthington et al., 2005). However, the dry-season water level of Poyang Lake may be negatively affected by the operation of TGD. The dry season of Poyang Lake begins (usually in September) during the TGD impoundment period (September–November) and the impoundment of TGD has resulted in an increase in the difference between Yangtze River and Poyang Lake water levels, which lead to an increase in the drainage and a decrease of the water level of Poyang Lake (Zhang et al., 2012). In a long term, sediment trapping by the TGD may further lower the water level in MLYR and increase in the difference between Yangtze River and Poyang Lake water levels during the dry season (Lai et al., 2014). In this respect, even though proposed Poyang Lake sluice will unavoidably block the Yangtze River–Poyang Lake connectivity, it might be needed to maintain the size and quality of habitat for the four Chinese carps in the dry season.

Stock enhancement is a direct management response to reported recruitment decreases of the four major Chinese carps in Poyang Lake (Huang et al., 2013). However, our results implied that there is an upper limit about which stocking more fingerlings of the four major Chinese carps is not cost effective. Additionally, the efficacy of stock enhancement in Poyang Lake may be also negatively affected by high juvenile fishing mortality rates. As currently lots of harmful fishing gears and methods are used for Poyang Lake fisheries, recent decreases in fishery resources have resulted in increases in fishing pressure on juveniles of the four major Chinese carps (Wang et al., 2017). Our study also suggests that managers in other lake ecosystems connected to MLYR, such as Dongting Lake, to incorporate fishery regulation into stock enhancement planning.

Finally, to our understanding, this is the first study using the EwE modeling approach to investigate simultaneous effects of multiple restoration practices in a proposed multi-faceted restoration project for a Chinese freshwater ecosystem. We demonstrated that using an ecosystem model can provide evaluations of management scenarios in a timely manner. We suggest that EwE and other ecosystem models should be utilized more often to support ecosystem-based management.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2019.03.020.

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