



Modeling trophic interactions and impacts of introduced icefish (*Neosalanx taihuensis* Chen) in three large reservoirs in the Yangtze River basin, China

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Abstract Non-native fish introductions may damage aquatic ecosystems. To assess the ecological impacts of the introduced icefish (*Neosalanx taihuensis* Chen), three reservoirs in a cascade, including the Shuibuya Reservoir (SBYR), which is devoid of icefish, and the Geheyan Reservoir (GHYR) and the Gaobazhou Reservoir (GBZR), which have large and small icefish populations, respectively, were selected for this study. Three mass-balance trophic models were established using the Ecopath approach. The results indicated that

(1) the three ecosystems tended to depend more on the grazing food chain, possibly because the dominant fish species in three reservoirs were mainly filter feeders or planktivores; (2) the large icefish population in the GHYR decreased the overall energy transfer efficiency; (3) the ecosystem indices suggested that the GHYR ecosystem appeared to be a moderately mature system with a simple and vulnerable food web structure, and the lack of complexity was largely attributed to the large population of introduced icefish; and (4) the “mixed trophic impacts (MTI)” and niche overlap analysis indicated that the ecological impacts of icefish mainly

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came from predation and interspecific competition. This study demonstrates the consequence of icefish introduction to aquatic ecosystems and suggests that appropriate control of exotic fish is worth considering.

Keywords Non-native fish · Introduction · Aquatic ecosystem · Cascading reservoirs · Ecopath · Mass-balance model

Introduction

China has become the leading producer in global aquaculture in recent decades (FAO, 2018). Apart from the increasing aquaculture area and diversified aquaculture practices (Wang et al., 2015), the introduction of alien fish species to China and the translocation of domestic species across their natural geographic ranges are considered significant contributors to aquaculture in China (De Silva et al., 2009; Lin et al., 2015). These fish species are chosen for their characteristics, such as good adaptability and plasticity, high reproductive and survival rates, rapid growth rates, and high edible and commercial values (De Silva et al., 2006, 2009; Zablot-ski, 2010). It has been reported that more than 25% of aquaculture production in China is derived from the farming of non-native species, and this trend is currently accelerating (Lin et al., 2015). However, non-native species introductions also bring risks, e.g., sharply increasing the number of non-native fish species and population size and generating further ecological impacts on fish biodiversity and the entire ecosystem (Naylor et al., 2001; De Silva et al., 2006, 2009; Kang et al., 2014; Xiong et al., 2015), which should not be overlooked. Furthermore, domestic translocation may be more frequent and pose even higher risks than international introductions, mainly due to the ease of transfer to relatively similar geographical and climatic environments, cost effective and time saving, and lack of restriction regulations (Lin et al., 2015).

Icefish (Salangidae) in China, with a natural distribution ranging from the Bohai Sea to the Beibu Gulf and in river systems and their affiliated lakes (Wang et al., 2005; Zhang et al., 2013), have been commercially exploited for a long time. However, the wild resources of icefish have markedly declined due to overfishing and environmental changes induced by human activities in recent decades (Wang et al., 2005; Kang et al., 2015).

China has 2865 perennial lakes each with a water surface area in excess of 1 km² and with a total water surface area of 78,000 km²; additionally, China has 98,002 reservoirs with a total storage capacity of 9.32×10^{11} m³ (MWR & NBS, 2013). To utilize these extensive water resources and compensate for the decline in wild fish resources, two main species of icefish, i.e., *Neosalanx taihuensis* Chen and *Protosalanx chinensis* Basilewsky, which are widely distributed and have remarkable ecological plasticity, have been introduced into numerous reservoirs and lakes across the country since 1979 (Kang et al., 2015). Icefish are short-lived species with an average life span of one year, high fecundity, and excellent adaptability to new environments that support the population boom (Zhang et al., 2013; Kang et al., 2015). *N. taihuensis* is naturally distributed in the middle and lower reaches of the Yangtze River and affiliated water bodies (Wang et al., 2005). In comparison to the substantial contributions to wild resource supplements and social-economic benefits (Kang et al., 2015), relevant assessments on the impacts on aquatic ecosystems by this group are limited. The sharp decline of endemic fish species and their population sizes in plateau lakes in Yunnan Province (China) during the last 30 years have been largely attributed to *N. taihuensis* transplantations (Xiong et al., 2008; Yuan et al., 2010). Nevertheless, its broader impacts and underlying mechanisms on aquatic ecosystems are still poorly understood, mainly due to the lack of suitable ecosystem approaches that can be applied to the abundant but fragmented ecological data.

Ecopath with Ecosim (EwE) has been widely considered an effective tool for the analysis of trophic relationships and ecosystem characteristics (Christensen et al., 2005; Coll & Libralato, 2012; Li et al., 2019), and this approach can be used to demonstrate species interactions within an ecosystem (Christensen et al., 2005; Xu et al., 2011; Cremona et al., 2018) and evaluate the effects of specific species on ecosystems based on quantitative estimations of ecosystem characteristics (Heymans et al., 2004; Coll & Libralato, 2012; Ibarra-García et al., 2017). EwE was initially introduced to China by Tong (1999) and has been widely applied in marine ecosystem research. More recently, many EwE models have been constructed for China's lake ecosystems (e.g., Li et al., 2009; Jia et al., 2012; Guo et al., 2013; Kong et al., 2016), whereas the

application of EwE models for reservoirs is still limited (Liu et al., 2007; Wu et al., 2012; Deng et al., 2014). Moreover, EwE models have seldom been used to assess the impact of non-native species on ecosystems (Khan & Panikkar, 2009; Tesfaye & Wolff, 2018).

The cascading reservoirs, including the Shuibuya Reservoir (SBYR), Geheyan Reservoir (GHYR) and Gaobazhou Reservoir (GBZR), from upstream to downstream, are located on the Qingjiang River (108.58°–111.58° E, 29.43°–30.58° N), where the Qingjiang biota (518 million years old) have been found in the local Burgess Shale-type fossil Lagerstätten (Fu et al., 2019). The SBYR, GHYR, and GBZR construction began in the 2000s, 1980s, and 1990s, respectively. With the completion of impoundment processes, *N. taihuensis* were translocated into the GHYR and GBZR in 1995 and 1996, respectively, and the species has formed different population sizes. However, icefish transplantation did not occur in the SBYR. Thus, the gradient of icefish population size in the Qingjiang cascading reservoirs provides us with an unprecedented opportunity to evaluate the various effects of icefish transplantation on aquatic ecosystems.

Materials and methods

Study area

The Qingjiang cascading reservoirs (SBYR, GHYR, GBZR; Fig. 1) are located on the Qingjiang River, which is a major tributary of the Yangtze River. The basic characteristics of the reservoirs during the study period are listed in Table 1. According to the statistics from the local Fisheries Bureau of Changyang County, the icefish yields in 2016 and 2017 accounted for 0, 36.60%, and 3.32% of the total fishery catch in the SBYR, GHYR, and GBZR, respectively. For the estimation of the composition and biomass of all biotic groups, a total of 16, 27, and 19 randomly selected sampling stations were well distributed in the SBYR, GHYR, and GBZR, respectively.

Ecopath modeling approach

The static mass-balance trophic models of the Qingjiang cascading reservoirs were constructed using

EwE version 6.5 (freely available at <http://www.ecopath.org>; Christensen & Walters, 2004); these models encompass the full trophic spectrum and are appropriate for quantitatively assessing ecosystem structure and function in a systematic way (Christensen, 1995; Guo et al., 2013). Ecopath assumes that all functional groups in the ecosystem are relatively stable and can be defined by a set of linear simultaneous equations, i.e., production = catches + predation mortality + biomass accumulation + net migration + other forms of mortality, which can be re-expressed more concisely as follows:

$$B_i \cdot (P/B)_i \cdot EE_i = \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji} + EX_i,$$

where for prey i and predator j , B is the biomass, P is the production, (P/B) is the production/biomass ratio, and EE is the ecotrophic efficiency; (Q/B) is the consumption/biomass ratio; DC_{ji} is the contribution of prey i in the diet of predator j ; and EX is the export value (e.g., fishing and the extent of migration). For each functional group, the DC_{ji} , EX , and at least three of the four parameters (B , P/B , EE , and Q/B) must be inputted to establish the mass-balance model. In general, the EE value is difficult to obtain; therefore, it is usually calculated using other parameters in the model.

Data collection and parameter estimation

Classifying functional groups

In the Ecopath model, an ecosystem generally includes three categories: detritus, producers, and consumers, all of which can be classified into various functional groups. The classification of functional groups in the Ecopath model of the Qingjiang cascading reservoirs was conducted primarily based on their biological and ecological characteristics and abundance; species with a high degree of niche overlap were combined to simplify the food web. In total, 20, 23, and 23 functional groups were defined to establish the Ecopath models for the ecosystems of the SBYR, GHYR, and GBZR, respectively (Table 2). It is noteworthy that the groups of exotic carnivorous fish (e.g., *Lucioperca lucioperca* Linnaeus, *Micropterus salmoides* Lacépède, *Ictalurus punctatus* Rafinesque),

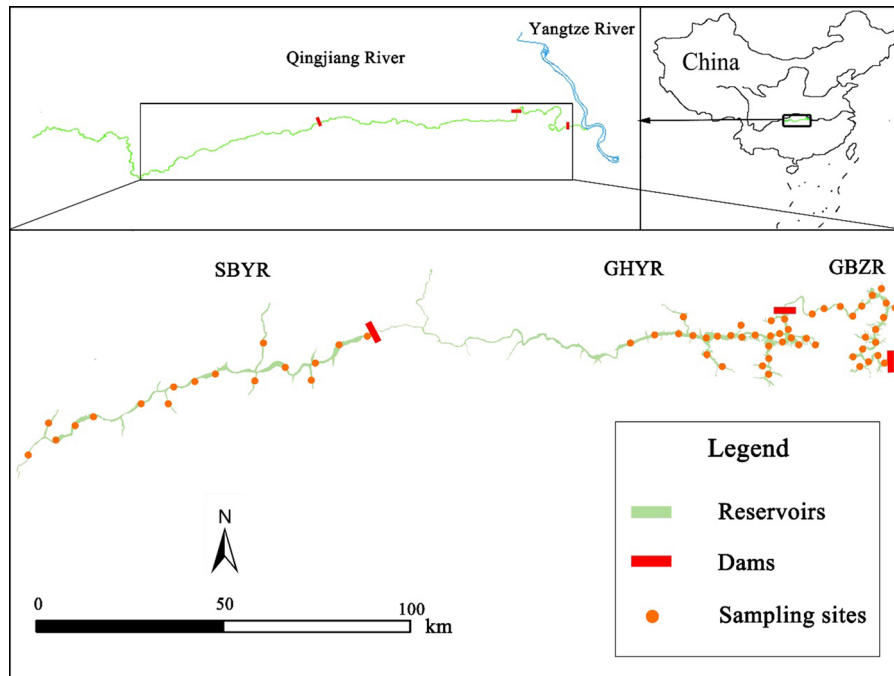


Fig. 1 Map of the Qingjiang cascading reservoirs. The orange dots represent the sampling sites

Table 1 Basic characteristics of the Qingjiang cascading reservoirs—year of impoundment, year of icefish transplantation, annual weight percentage of icefish in total fishery catch (w%), total length of mainstream, area, capacity, and annual

average values (mean \pm SE) of WT (water temperature), WD (water depth), SD (Secchi Disk depth), pH, Cond (conductivity), TP (total phosphorus), TN (total nitrogen), $\text{NH}_4^+\text{-N}$, COD_{Mn} (chemical oxygen demand), Chl *a* (chlorophyll *a*)

Reservoir	SBYR	GHYR	GBZR
Year of filling	2002	1993	1996
Year of icefish transplantation	None	1995	1996
W%	0.00	36.60	3.32
Total length of mainstream (km)	104.55	87.82	47.61
Area (km ²)	47.90	72.12	2.23
Capacity (10 ⁸ km ³)	45.80	34.00	3.50
WD (m)	92.23 \pm 6.16	55.74 \pm 2.90	19.46 \pm 0.93
SD (m)	4.07 \pm 0.28	5.73 \pm 0.17	2.16 \pm 0.08
pH	7.73 \pm 0.08	8.16 \pm 0.10	8.51 \pm 0.10
WT (°C)	20.03 \pm 0.71	20.45 \pm 0.60	19.27 \pm 0.70
Cond ($\mu\text{s cm}^{-1}$)	218.56 \pm 1.67	255.89 \pm 3.73	241.42 \pm 2.59
TP (mg L ⁻¹)	0.011 \pm 0.001	0.006 \pm 0.000	0.021 \pm 0.003
TN (mg L ⁻¹)	2.69 \pm 0.11	3.02 \pm 0.24	2.74 \pm 0.06
$\text{NH}_4^+\text{-N}$ (mg L ⁻¹)	0.21 \pm 0.02	0.27 \pm 0.03	0.25 \pm 0.02
COD_{Mn} (mg L ⁻¹)	2.56 \pm 0.38	2.19 \pm 0.07	2.33 \pm 0.15
Chl <i>a</i> ($\mu\text{g L}^{-1}$)	3.11 \pm 0.28	2.20 \pm 0.12	5.13 \pm 0.58

Table 2 Species composition of each functional group for the ecosystem models of the Qingjiang cascading reservoirs

No.	Functional group	Dominant species composition
1	Mandarin fish	<i>Siniperca chuatsi</i> Basilewsky
2	Sheatfish	<i>Silurus meridionalis</i> Chen, <i>Silurus asotus</i> Linnaeus
3	Catfish	<i>Pelteobagrus fulvidraco</i> Richardson, <i>Pelteobagrus vachelli</i> Richardson, <i>Mystus macropterus</i> Bleeker, <i>Pseudobagrus truncates</i> Regan
4	Exotic carnivorous fish	<i>Lucioperca lucioperca</i> Linnaeus, <i>Micropterus salmoides</i> Lacépède, <i>Ictalurus punctatus</i> Rafinesque
5	Small carnivorous fish	<i>Cultrichthys erythropterus</i> Basilewsky, <i>Opsariichthys bidens</i> Günther
6	Icefish	<i>Neosalanx taihuensis</i> Chen
7	Common carp	<i>Cyprinus carpio</i> Linnaeus, <i>Cyprinus carpio</i> var. <i>specularis</i> Linnaeus
8	Crucian carp	<i>Carassius auratus</i> Linnaeus
9	Tench	<i>Tinca tinca</i> Linnaeus
10	Small pelagic fish	<i>Hemiculter leucisculus</i> Basilewsky
11	Small demersal fish	<i>Acheilognathus macropterus</i> Bleeker, <i>Pseudorasbora parva</i> Temminck & Schlegel, <i>Abbottina rivularis</i> Basilewsky, <i>Sarcocheilichthys nigripinnis</i> Günther
12	Silver carp	<i>Hypophthalmichthys molitrix</i> Valenciennes
13	Bighead carp	<i>Aristichthys nobilis</i> Richardson
14	Grass carp	<i>Ctenopharyngodon idellus</i> Cuvier et Valenciennes
15	Bream	<i>Parabramis pekinensis</i> Basilewsky
16	Shrimp	<i>Macrobrachium nipponense</i> De Haan, <i>Exopalaemon modestus</i> Heller
17	Zoobenthos	Molluscs, Oligochaeta, Aquatic insecta
18	Microzooplankton	<i>Brachionus diversicornis</i> Dadav, <i>Trichocerca cylindrica</i> Imhof
19	Cladocera	<i>Bosmina longirostris</i> Muller, <i>Diaphanosoma leuchtenbergianum</i> Fischer
20	Copepoda	<i>Mesocyclops leuckarti</i> Claus, <i>Cyclops vicinus</i> Uljanin
21	Submerged plant	<i>Potamogeton crispus</i> Linn
22	Phytoplankton	Chlorophyta, Bacillariophyta, Cyanophyta
23	Detritus	Bioseston, abioseston, formula feed

The groups of exotic carnivorous fish, icefish, and tench were not included in the ecosystem model of the SBYR

icefish, and tench (*Tinca tinca* Linnaeus) were not included in the ecosystem model of the SBYR.

Data collection and parameter estimation

The biomass and catch data for all biotic groups and the import of detritus were determined between 2016 and 2017 with seasonal field investigations (April and May 2016, August 2016, November 2016, Jan 2017), which were assumed to represent their annual mean values over the year. Zoobenthos, plankton, and aquatic plants were sampled seasonally at all sampling sites; these samples were identified and counted to calculate biomass using routine methods (Huang, 1999). Detritus was defined as dissolved organic

carbon (DOC), particulate organic carbon (POC), and bacteria according to Heymans et al. (2004). Measurements of total fish quantity and biomass in each reservoir were generated by hydroacoustics using a Simrad EY60 split-beam echo-sounder operating at a frequency of 120 kHz; the transducer was 7° × 7° at the − 3 dB level, the pulse duration was 0.128 ms, and the ping rate was 5 pings per second. Specific composition and relative abundance were determined by multi-meshed gillnet samplings (30/20 m in height, 180 m in length, evenly divided into 24 parts with different stretched mesh sizes of 8.6, 3.9, 1.2, 2.0, 11.0, 1.6, 2.5, 4.8, 3.1, 1.0, 7.0, 5.8, 15.0, 24.0, 13.0, 18.0, 26.0, 14.0, 20.0, 19.0, 22.0, 12.0, 17.0, and 16.0 cm). The gillnets with a 30-m height were mainly

used in the deep SBYR and GHYR, and the gillnets with a 20-m height were used in the shallower GBZR. The biomass of each fish species in each reservoir was calculated by multiplying the total number of fish individuals (by hydroacoustics estimate) by the quantitative proportion of each fish species (by gillnet sampling) by the average weight of each species (by gillnet sampling). Fish catch data were also obtained from commercial landings and supplemented by data from the local fisheries bureau. The fish species composition of the daily and annual yields were recorded by fishers from April 2016 to March 2017.

Other biological parameters required for the models were obtained from the literature. The P/B and Q/B values of zoobenthos were obtained from the research of Yan (1998), and the P/B and Q/B values of plankton and aquatic plants were obtained from related published research (Ye, 2007; Guo et al., 2013). The P/B values, Q/B values, and dietary composition (DC) of fish were obtained from existing EwE models, which have been established in other reservoirs in the Yangtze River basin (Liu et al., 2007; Wu et al., 2012), and supplemented by data from FishBase (<http://www.fishbase.org>). Due to the combinations of some species/groups, the above values were accordingly and proportionally merged or adjusted. These combined groups included sheatfish (*Silurus meridionalis* Chen, *Silurus asotus* Linnaeus), catfish (*Pelteobagrus fulvidraco* Richardson, *Pelteobagrus vachelli* Richardson, *Mystus macropterus* Bleeker, *Pseudobagrus truncatus* Regan), exotic carnivorous fish (*L. lucioperca*, *M. salmoides*, *I. punctatus*), small carnivorous fish (*Cultrichthys erythropterus* Basilewsky, *Opsariichthys bidens* Günther), small demersal fish (*Acheilognathus macropterus* Bleeker, *Pseudorasbora parva* Temminck and Schlegel, *Abbottina rivularis* Basilewsky, *Sarcocheilichthys nigripinnis* Günther), shrimp (*Macrobrachium nipponense* De Haan, *Exopalaemon modestus* Heller), zoobenthos (Molluscs, Oligochaeta, Aquatic insecta), microzooplankton (*Brachionus diversicornis* Dadav, *Trichocerca cylindrica* Imhof), Cladocera (*Bosmina longirostris* Muller, *Diaphanosoma leuchtenbergianum* Fischer), phytoplankton (Chlorophyta, Bacillariophyta, Cyanophyta), and detritus (Bioseston, abioseston, formula feed) (Table 2).

Data processing and model balancing

All required parameters were entered into the Ecopath model for operational simulation. It is necessary to debug the model to balance it. After the Ecopath model is established, the model will export a series of parameters related to the food web structure and ecosystem characteristics, which should conform to objective facts and ecological principles. Generally, $0 < EE < 1$ and $0.1 < P/Q < 0.3$ (Christensen & Walters, 2004). The basic input and output parameters and the diet matrix of the balanced model are shown in Tables 3, 4, 5, and 6.

Results

Food web structure and trophic analysis

Trophic structure

The trophic levels (TLs) of all ecological groups in the SBYR, GHYR, and GBZR ranged from 1 to 3.28, 1 to 3.36, and 1 to 3.55, respectively. The lowest TL of all ecological groups was composed of detritus, and primary producers mainly consisted of submerged macrophytes and phytoplankton. Carnivorous fish such as mandarin fish (*Siniperca chuatsi* Basilewsky), sheatfish, catfish, and exotic carnivorous fish (in the GHYR and GBZR) occupied the top TLs in the ecosystems. The TL of icefish was 3.02 in both the GHYR and the GBZR.

The composition and biomass of the ecological groups in the three reservoirs differed from each other, and these differences are clearly and intuitively depicted in Table 6 and Fig. 2. The compositions of the ecological groups in the three reservoirs were similar except that exotic carnivorous fish, icefish, and tench were absent in the SBYR ecosystem. With respect to biomass, distinctions were observed among the three reservoirs: (1) carnivorous fish: the highest biomass was detected for sheatfish (0.126 t km^{-2}) in the SBYR, exotic carnivorous fish (0.096 t km^{-2}) in the GHYR, and exotic carnivorous fish (0.051 t km^{-2}) in the GBZR; (2) icefish: the biomass values were 0, 5.425, and 0.391 t km^{-2} in the SBYR, GHYR, and GBZR, respectively; (3) secondary consumers: big-head carp (*Aristichthys nobilis* Richardson), silver carp (*Hypophthalmichthys molitrix* Valenciennes),

Table 3 Diet composition of the functional groups in the SBYR

No.	Functional group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
1	Mandarin fish																		
2	Sheatfish																		
3	Catfish																		
4	Small carnivorous fish	0.005	0.003	0.004															
5	Common carp	0.010	0.008	0.002															
6	Crucian carp	0.178	0.085	0.118															
7	Small pelagic fish	0.268	0.286	0.198	0.293														
8	Small demersal fish	0.422	0.473	0.495	0.410	0.008	0.005												
9	Silver carp																		
10	Bighead carp																		
11	Grass carp	0.012	0.010	0.008															
12	Bream	0.005	0.080	0.050															
13	Shrimp	0.100	0.050	0.120	0.100	0.050	0.050	0.010	0.010										
14	Zoobenthos		0.005	0.005	0.002	0.010	0.010		0.005			0.010							
15	Microzooplankton				0.010			0.130	0.008	0.100	0.082	0.100	0.010	0.005	0.060				
16	Cladocera				0.090			0.166	0.115	0.120	0.343		0.010	0.100	0.035			0.040	0.050
17	Copepoda				0.095			0.170	0.100	0.095	0.255		0.005	0.080	0.020				
18	Submerged plant											0.003	0.002						
19	Phytoplankton					0.932	0.935	0.150	0.110	0.575	0.198	0.010	0.160	0.150	0.120	0.455	0.720	0.780	
20	Detritus							0.384	0.652	0.110	0.122	0.877	0.813	0.665	0.765	0.545	0.240	0.170	
	Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 4 Diet composition of the functional groups in the GHYR

No.	Functional group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1	Mandarin fish																					
2	Sheatfish																					
3	Catfish																					
4	Exotic carnivorous fish																					
5	Small carnivorous fish	0.030	0.030	0.010	0.005																	
6	Icelfish	0.060	0.050	0.010	0.060	0.030																
7	Common carp	0.015	0.010	0.003	0.003																	
8	Crucian carp	0.118	0.120	0.050	0.040																	
9	Tench																					
10	Small pelagic fish	0.285	0.205	0.288	0.298	0.245																
11	Small demersal fish	0.387	0.390	0.471	0.446	0.400		0.005	0.002													
12	Silver carp																					
13	Bighead carp																					
14	Grass carp	0.010	0.020	0.050	0.010																	
15	Bream	0.015	0.080	0.008	0.008																	
16	Shrimp	0.080	0.090	0.100	0.120	0.100		0.010	0.010	0.030												
17	Zoobenthos		0.050	0.010	0.100	0.010	0.120	0.010	0.010	0.010	0.120	0.010	0.100	0.080	0.100	0.008	0.005	0.050	0.020	0.050		
18	Microzooplankton						0.100	0.660		0.050	0.170	0.120	0.145	0.357		0.015	0.100	0.032				
19	Cladocera						0.105	0.220		0.165	0.110	0.095	0.193			0.008	0.080	0.022				
20	Copepoda															0.005	0.005					
21	Submerged plant																					
22	Phytoplankton									0.050	0.270	0.110	0.450	0.120	0.040	0.200	0.120	0.120	0.455	0.720	0.780	
23	Detritus								0.975	0.978	0.860	0.620	0.210	0.250	0.845	0.764	0.695	0.776	0.545	0.260	0.170	
	Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 5 Diet composition of the functional groups in the GBZR

No.	Functional group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1	Mandarin fish																					
2	Sheatfish																					
3	Catfish																					
4	Exotic carnivorous fish																					
5	Small carnivorous fish	0.050	0.070	0.003	0.003																	
6	Icefish	0.040	0.050	0.003	0.020	0.020																
7	Common carp	0.012	0.010	0.002	0.003																	
8	Crucian carp	0.120	0.120	0.080	0.050																	
9	Tench																					
10	Small pelagic fish	0.274	0.190	0.287	0.288	0.270																
11	Small demersal fish	0.395	0.390	0.480	0.468	0.390		0.006	0.004													
12	Silver carp																					
13	Bighead carp																					
14	Grass carp	0.008	0.010	0.010	0.050																	
15	Bream	0.011	0.050	0.010	0.008																	
16	Shrimp	0.090	0.100	0.105	0.100	0.100		0.100	0.050	0.008		0.060										
17	Zoobenthos		0.010	0.020	0.010	0.010		0.010	0.010	0.010		0.030		0.010								
18	Microzooplankton					0.010	0.120				0.118	0.010	0.080	0.130	0.080	0.008	0.005	0.060		0.020	0.050	
19	Cladocera					0.095	0.660			0.050	0.178	0.120	0.115	0.347		0.015	0.100	0.035				
20	Copepoda					0.105	0.220				0.165	0.110	0.100	0.230		0.008	0.080	0.020				
21	Submerged plant															0.020	0.010					
22	Phytoplankton									0.050	0.270	0.110	0.590	0.170	0.100	0.160	0.150	0.120	0.455	0.720	0.780	
23	Detritus							0.884	0.936	0.882	0.269	0.560	0.115	0.123	0.790	0.799	0.665	0.765	0.545	0.260	0.170	
	Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 6 Basic input (not in bold) and estimated parameters (in bold) for the functional groups of Ecopath models of the Qingjiang cascading reservoirs

Functional group	SBYR					GHYR					GBZR				
	Trophic level	Biomass (t km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE (year ⁻¹)	Trophic level	Biomass (t km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE (year ⁻¹)	Trophic level	Biomass (t km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE (year ⁻¹)
Mandarin fish	3.28	0.043	0.78	3.72	0.68	3.36	0.003	0.78	3.72	0.64	0.003	0.78	3.72	0.56	
Sheatfish	3.28	0.126	1.31	3.46	0.76	3.34	0.038	1.35	3.46	0.55	0.003	1.35	3.46	0.57	
Catfish	3.26	0.044	1.22	8.05	0.71	3.33	0.033	1.22	8.05	0.67	0.029	1.25	8.05	0.50	
Exotic carnivorous fish	-	-	-	-	-	3.36	0.096	1.42	6.46	0.71	0.051	1.42	6.46	0.46	
Small carnivorous fish	3.27	0.009	1.24	5.82	0.34	3.28	0.020	1.24	5.82	0.48	0.006	1.18	5.82	0.56	
Icefish	-	-	-	-	-	3.02	5.425	2.37	27.20	0.87	0.391	2.37	27.20	0.16	
Common carp	2.08	0.714	1.97	8.50	0.74	2.03	0.352	1.97	8.50	0.64	0.161	1.97	8.50	0.74	
Crucian carp	2.07	0.374	2.23	13.12	0.84	2.03	0.162	2.23	13.12	0.60	0.086	2.23	13.12	0.73	
Tench	-	-	-	-	-	2.10	0.506	2.10	12.30	0.56	0.094	2.10	12.30	0.48	
Small pelagic fish	2.48	4.495	2.31	20.14	0.68	2.47	0.563	2.31	20.14	0.64	0.330	2.31	20.14	0.56	
Small demersal fish	2.25	2.175	2.03	15.50	0.39	2.28	0.425	2.03	15.50	0.66	0.321	2.03	15.50	0.48	
Silver carp	2.32	3.017	3.45	12.10	0.77	2.35	1.030	3.45	12.10	0.71	2.465	3.45	12.10	0.76	
Bighead carp	2.71	4.113	4.00	8.00	0.62	2.65	1.171	4.00	8.00	0.76	1.863	4.00	8.00	0.65	
Grass carp	2.11	0.546	1.65	12.41	0.51	2.11	0.162	1.65	12.41	0.54	0.138	1.65	12.41	0.54	
Bream	2.03	0.050	1.55	22.13	0.82	2.03	0.375	1.55	22.13	0.72	0.010	1.55	22.13	0.44	
Shrimp	2.19	0.500	2.50	12.50	0.86	2.19	0.312	2.80	12.50	0.53	0.300	2.70	12.50	0.80	
Zoobenthos	2.12	0.200	2.30	46.00	0.76	2.11	0.250	2.45	49.00	0.56	0.280	2.40	48.00	0.32	
Microzooplankton	2.00	2.380	38.05	761.04	0.95	2.00	3.500	28.89	481.50	0.95	0.750	38.90	781.20	0.94	
Cladocera	2.04	1.510	26.15	522.93	0.90	2.02	2.766	41.85	697.43	0.92	0.400	67.79	994.76	0.92	
Copepoda	2.05	1.320	26.36	527.16	0.90	2.05	1.533	27.75	462.46	0.91	0.380	32.06	641.24	0.90	
Submerged plant	1.00	0.020	1.25	-	0.90	1.00	0.020	1.30	-	0.65	0.030	1.50	-	0.81	
Phytoplankton	1.00	10.370	215.00	-	0.64	1.00	8.340	215.00	-	0.65	14.680	215.00	-	0.24	
Detritus	1.00	12.700	-	-	0.75	1.00	8.200	-	-	0.67	26.700	-	-	0.19	

and small pelagic fish (e.g., *Hemiculter leucisculus* Basilewsky) were dominant in all three reservoirs; (4) zooplankton: the highest biomass of zooplankton (microzooplankton, Cladocera, Copepoda) was detected in the GHYR, followed by that in the SBYR and GBZR; (5) primary producers: there were few aquatic plants (e.g., *Potamogeton crispus* Linn) in the three reservoirs; the highest biomass of phytoplankton (e.g., Chlorophyta, Bacillariophyta, Cyanophyta) was detected in the GBZR, followed by that in the SBYR and GHYR; and (6) detritus: the biomasses, from high to low, were as follows: GBZR (26.7 t km⁻²), SBYR (12.7 t km⁻²), and GHYR (8.2 t km⁻²).

Most of the EE values of ecological groups in the three reservoirs were higher than 0.5, and these higher values were mainly found for commercial species such as silver carp (0.77, 0.71, and 0.76 in the SBYR, GHYR, and GBZR, respectively), bighead carp (0.62, 0.76, and 0.65), crucian carp (*Carassius auratus* Linnaeus) (0.84, 0.60, and 0.73), small pelagic fish (0.68, 0.64, and 0.56), and shrimp (0.86, 0.53, and 0.80); meanwhile, the EE values of detritus were 0.75, 0.67, and 0.19, respectively. Additionally, the EE values of icefish in the SBYR, GHYR, and GBZR were 0, 0.87, and 0.16, respectively.

Transfer efficiencies

Two main types of food chains could be discerned from the models in the ecosystems of three reservoirs: a grazing food chain and a detrital-based food chain (Fig. 3). For the SBYR, in the grazing food chain, the amount of energy transferred from TL I to TL II was 1 983 t km⁻² year⁻¹, the energy transfer efficiency values from T_Ls II–V were 4.90%, 11.90%, and 15.90%, respectively, and the average transfer efficiency was 10.90%. In the detrital-based food chain, the amount of energy transferred from TL I to TL II was 1 388 t km⁻² year⁻¹, the energy transfer efficiency values from T_Ls II–V were 5.02%, 8.87%, and 16.00%, respectively, and the average transfer efficiency was 9.96%. The overall average transfer efficiency in the SBYR ecosystem was 10.43%.

For the GHYR, in the grazing food chain, the amount of energy transferred from TL I to TL II was 2 723 t km⁻² year⁻¹, the energy transfer efficiency values from T_Ls II–V were 5.61%, 8.19%, and 9.72%, respectively, and the average transfer efficiency was 7.84%. In the detrital-based food chain, the amount of

energy transferred from TL I to TL II was 1 583 t km⁻² year⁻¹, the energy transfer efficiency values from T_Ls II–V were 5.74%, 7.40%, and 9.33%, respectively, and the average transfer efficiency was 7.49%. The overall average transfer efficiency in the GHYR ecosystem was 7.65%.

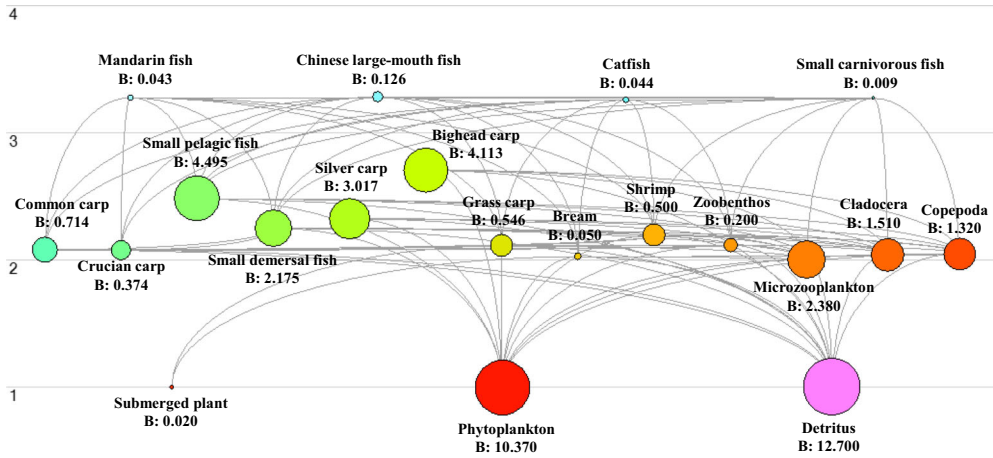
For the GBZR, in the grazing food chain, the amount of energy transferred from TL I to TL II was 768 t km⁻² year⁻¹, the energy transfer efficiency values from T_Ls II–V were 5.10%, 13.00%, and 14.30%, respectively, and the average transfer efficiency was 10.80%. In the detrital-based food chain, the amount of energy transferred from TL I to TL II was 492 t km⁻² year⁻¹, the energy transfer efficiency values from T_Ls II–V were 4.96%, 10.20%, and 15.50%, respectively, and the average transfer efficiency was 10.22%. The overall average transfer efficiency in the GBZR ecosystem was 10.51%.

The amount of energy transferred from TL I to TL II in the grazing chain was higher than that in the detrital-based food chain in all three reservoirs, as was the average energy transfer efficiency from TL II to TL V. The highest overall average transfer efficiency was observed in the GBZR (10.51%), followed by the SBYR (10.43%) and the GHYR (7.65%).

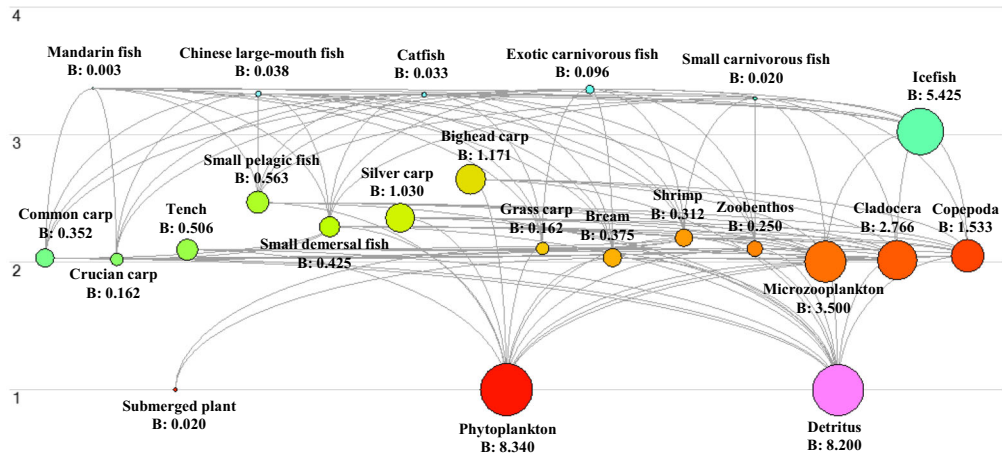
Mixed trophic impacts

The “mixed trophic impacts (MTIs)” as described by Ulanowicz & Puccia (1990) were integrated into EwE. The MTIs describe the mutual trophic impacts (including fishing fleets) between various functional groups in an ecosystem. The MTI analysis of the ecosystems of the Qingjiang cascading reservoirs (Fig. 4) indicates that (1) carnivorous fish (e.g., mandarin fish, sheatfish, catfish, and exotic carnivorous fish) had different degrees of negative effects on small carnivorous fish, crucian fish, small pelagic fish, and small demersal fish in the three reservoirs, and exotic carnivorous fish had negative effects on most fish groups; (2) icefish had strong negative impacts on most of the functional groups in the GHYR mainly due to trophic predation and competition, whereas these impacts were minor in the GBZR; (3) main economically important fish species such as silver carp and bighead carp had negative impacts on most functional groups in the three reservoirs; (4) grass carp (*Ctenopharyngodon idellus* Valenciennes) and bream (*Parabramis pekinensis* Basilewsky) had negative

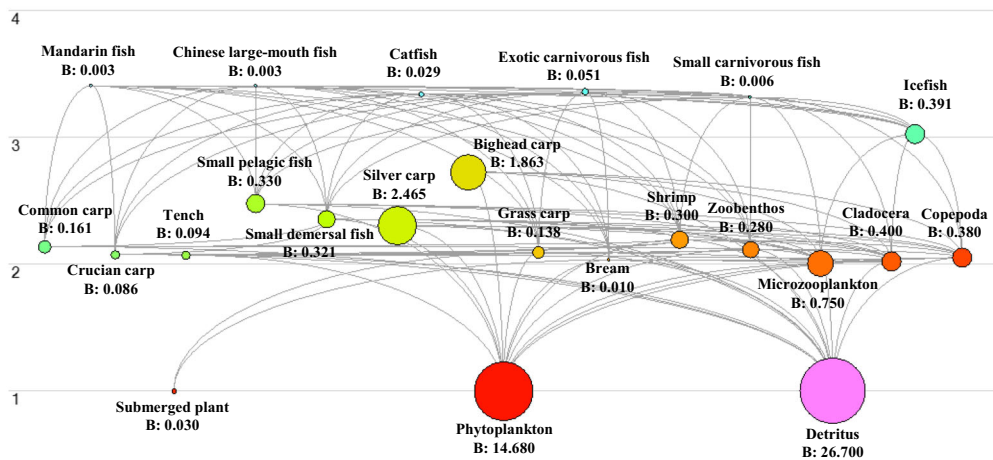
(a) SBYR



(b) GHYR



(c) GBZR



◀ **Fig. 2** Schematic diagram of food web structure in the ecosystems of the Qingjiang cascading reservoirs (for biomass the units are t km^{-2}). The area of each circle is proportional to the biomass of each group

impacts on aquatic plants; (5) detritus and producers such as submerged plants and phytoplankton had positive effects on almost all functional groups; and (6) fishing had negative effects on most fish and shrimp groups.

Niche overlap

The predator niche overlap index and prey niche overlap index are calculated in EwE using the approach suggested by Pianka (1973), and these values reflect the trophic niche overlaps between various functional groups. The predator niche overlap index represents the similarity of predators between groups. The prey niche overlap index describes the similarity of food sources between groups and indicates the competition intensity for prey. It was noteworthy that icefish (group 6), small pelagic fish (group 10), and small demersal fish (group 11) competed strongly against the same predator in the GHYR and GBZR. However, the low prey niche overlap index between icefish and other groups indicated that icefish experienced moderate levels of competition (Fig. 5).

Ecosystem properties and indicators

Based on the ecosystem theories proposed by Odum (1969, 1971) and Ulanowicz (1986), a series of indicators that can be used to assess the size, stability, and maturity of the ecosystem are calculated by EwE (Christensen et al., 2005). Summary statistics and characteristics of the ecosystems of the three reservoirs are listed in Table 7.

The total system throughput (TST) of the SBYR ecosystem was $8\,498.40 \text{ t km}^{-2} \text{ year}^{-1}$, of which 41.53% was derived from total consumption (TC), 5.92% from total exports (TE), 30.73% from total respiration (TR), and 21.93% flowed into detritus

(TD). The highest TST, which reached $11\,101.11 \text{ t km}^{-2} \text{ year}^{-1}$, was observed in the GHYR ecosystem, of which TC, TE, TR, and TD accounted for 40.98%, 7.37%, 30.20%, and 21.45%, respectively. The lowest TST ($7\,137.50 \text{ t km}^{-2} \text{ year}^{-1}$) was observed in the GBZR ecosystem, of which TC, TE, TR, and TD accounted for 18.46%, 30.60%, 13.62%, and 37.32%, respectively.

In the SBYR, GHYR, and GBZR, the total primary production (TPP) was 3 111.03, 4 170.08, and 3 156.25 $\text{t km}^{-2} \text{ year}^{-1}$, respectively; additionally, the TPP/TR values were 1.192, 1.244, and 3.247, respectively.

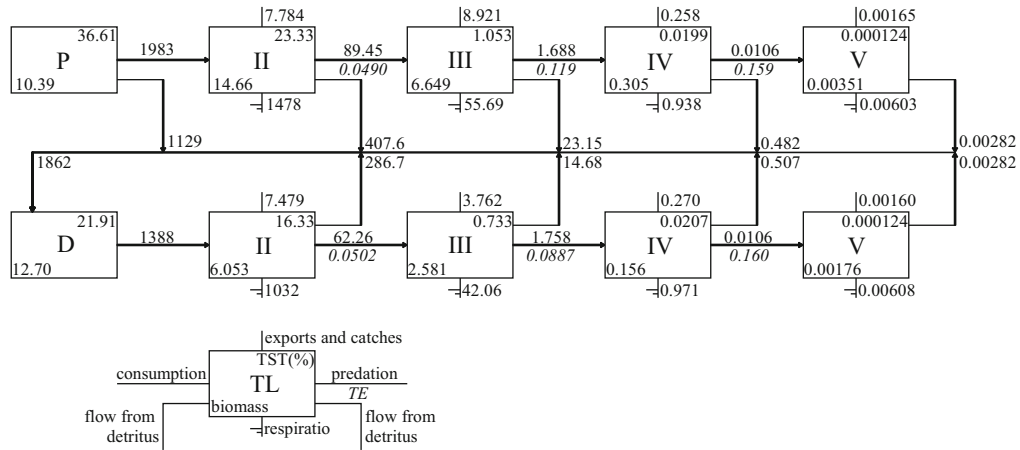
Flow indices, including the connectance index (CI) and system omnivory index (SOI), reflect the degree of inter complexity of an ecosystem (Pauly et al., 2000). In the SBYR, GHYR, and GBZR, the CI values were 0.256, 0.234, and 0.236, respectively, and the SOI values were 0.112, 0.089, and 0.102, respectively.

Discussion

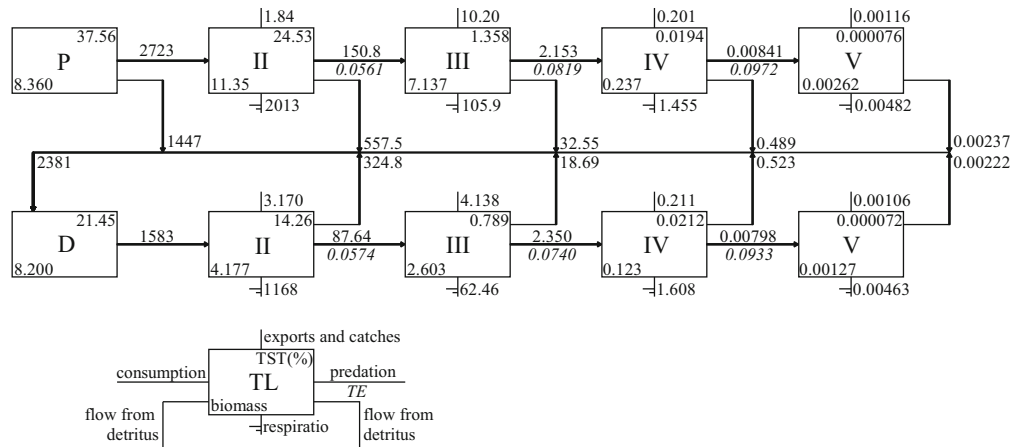
The literature on the effects of exotic fish species on aquatic ecosystems is plentiful. However, the literature on the in-depth impacts, such as trophic interactions, energy flow, and mechanism analyses, is still limited. This research was the first to attempt trophic modeling for the Qingjiang cascading reservoirs, and we evaluated the impacts of introduced icefish in three large reservoirs using the derived Ecopath models; additionally, we provided further insights for the management of fish introductions.

The primary findings of this study were as follows: (1) icefish suffered from high fishing pressure but still had a considerably high biomass in the GHYR; (2) the three ecosystems tended to depend more on the grazing pathway; for example, the transfer efficiency from TL II to TL III in the grazing chain was relatively higher in the GHYR, whereas the overall energy transfer efficiency was the lowest in this reservoir; (3) the TPP/TR ratio was moderate, while the CI and SOI values were the lowest in the GHYR; and (4) the MTIs and niche overlap analysis indicated that icefish had

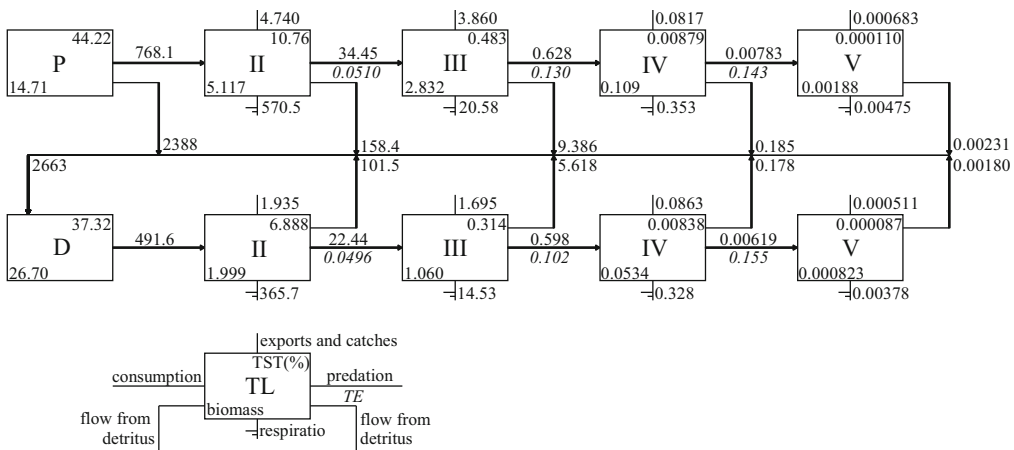
(a) SBYR



(b) GHYR



(c) GBZR



◀ **Fig. 3** Schematic diagram of Lindeman spine in the ecosystems of the Qingjiang cascading reservoirs

strong negative impacts on most of the functional groups in the GHYR.

Most fish groups had high EE values in all three reservoirs, and so did the icefish in the GHYR (0.87). This result suggests that commercial fish species are suffering from high fishing pressure, while prey fish suffer from a combination of pressures from predation by piscivores as well as by humans. In fact, icefish have been the main economically valuable species in the past two decades in the GHYR and GBZR (Yang, 2012). The annual yield of icefish catches peaked at 875 tons in 2015 in the GHYR and stabilized at 100–200 tons in the GBZR from 2000 to 2015 (Fig. 6). Despite the high fishing pressure, we still observed considerably high icefish biomass (5.425 t km^{-2}) in the GHYR in 2016 and 2017. The high mean TL of the catch (2.77) in the GHYR might be largely due to the high yield and high EE value of icefish, which comprised its high TL (3.02). For the GBZR, an extreme flood in the summer of 2016 ravaged the reservoir and resulted in very large losses in fish resources, especially icefish (Huang et al., 2019).

The transferred energy as well as the average energy transfer efficiency from TLs II–V in the grazing chain were higher than those in the detrital-based food chain in all three reservoirs (Fig. 3). The dominant fish species in the three reservoirs were mainly filter feeding fish or planktivorous fish such as silver carp, bighead carp, small pelagic, and icefish (in the GHYR). The diet selectivity of the dominant species may cause ecosystems to depend more on the grazing pathway. This phenomenon seemed to be inconsistent with the suggestion by Odum (1969), who posited that a mature system may tend to depend more on the detrital pathway. This paradox might be attributed to the relatively low biomass of piscivorous and omnivorous species in the three reservoirs, as these two functional groups seem to be the key factors responsible for mediating biodiversity–ecosystem functioning relationships (Petchey et al., 2004; Bruno & O'Connor, 2005; Griffin et al., 2008). Another notable feature was that in the grazing food chain, the energy transfer efficiencies from TLs II–III were 4.90%, 5.61%, and 5.10% in the SBYR, GHYR, and

GBZR, respectively. It has been reported that *N. taihuensis* feed on zooplankton throughout almost its entire life cycle (Sun, 1982; Lin et al., 2015). The much higher value in the GHYR was likely because of the efficient utilization of zooplankton by planktivorous fish, especially by the large population of icefish. However, the large population of icefish in the GHYR seemed to negatively affect energy transfer in other parts of the food chain. In comparison to the overall average energy transfer efficiency in the SBYR (10.43%) and the GBZR (10.51%), this value in the GHYR was 7.65%, which was far from the optimal “1/10 law” (Lindeman, 1942).

According to Odum (1971) and Christensen (1995), the ratio of TPP to TR (TPP/TR) is an important measure of ecosystem maturity; ecosystems with TPP/TR values much higher or lower than 1 are thought to be immature, while only those with TPP/TR ratios approaching 1 are considered to be mature. In the present study, the TPP/TR ratios indicated that the ecosystems were ranked in descending order of maturity as follows: SBYR (1.192), GHYR (1.244), and GBZR (3.247). Additionally, the CI and SOI values reflect the degree of intercomplexity of an ecosystem (Pauly et al., 2000) and partly describe system maturity since the food chain is expected to change from being linear to being web-like as the system matures (Odum, 1971). The CI and SOI values (Table 7) indicated higher intercomplexity in the SBYR (0.256 and 0.112), followed by that in the GBZR (0.236 and 0.102), while there was a lack of intercomplexity in the GHYR (0.234 and 0.089). The low CI and SOI values in the GHYR appeared to be related to the low biomasses of other fish groups that had different ecological strategies (Guo et al., 2013). Relatively speaking, the indices above illustrate that the SBYR ecosystem is mature and stable and has high complexity; the GHYR ecosystem is moderately mature and stable and has low complexity; and the GBZR ecosystem is immature and unstable (which might be largely due to the extreme flood in 2016, as mentioned above) and has moderate complexity. The moderately maturity of the GHYR ecosystem appeared to be reasonable due to its long history of filling; nevertheless, the low complexity that probably resulted from the introduced icefish indicated that the maturity of the GHYR ecosystem might be decreasing. Additionally, the low overall average energy transfer

Fig. 4 Mixed trophic impacts in the ecosystems of the Qingjiang cascading reservoirs. Blue color represents positive effect, red color represents negative effect. The darkness of the color indicates the degree of the impacts

efficiency in the GHYR might be attributed to the low complexity of the food web.

Generally, exotic fish affect local aquatic ecosystems and native species with the following ecological impacts: predation (Yonekura et al., 2007), interspecific competition (Costedoat et al., 2005), habitat destruction (Kitchell et al., 1997), and disease transmission (Gozlan et al., 2005). In the present study, the ecological impacts of icefish, which were clearly illustrated in MTI analysis, mainly included predation and competition. The impact of icefish on zooplankton seemed self-evident, and MTI analysis indicated that icefish had considerable negative predation effects on Cladocera and Copepoda in the GHYR (Fig. 4b). Meanwhile, icefish had strong negative impacts on most fish groups in the GHYR ecosystem (Fig. 4b), which is in agreement with the results of many studies on fish introduction or invasion (Kaufman, 1992; Kitchell et al., 1997; Canonico et al., 2005). These findings could be attributed to the fairly high biomass of icefish as well as its feeding habits. The exotic species might affect not only these fish species (e.g., bighead carp and silver carp in the present study) by direct competition for food and habitat but also other groups that are at different TLs (e.g., piscivorous species in the present study) through complex cascading effects (McDowall, 2006). Nevertheless, the above negative impacts of icefish on the GBZR ecosystem were mild (Fig. 4c), which was in accordance with a previous study that showed that an introduced exotic fish with a low existing biomass may not impact other fish groups seriously and immediately (Tesfaye & Wolff, 2018). In addition, more intuitionistic evidence on the impacts of icefish seemed to come from the fact that the biomasses of bighead carp and silver carp in the icefish-dominated GHYR (1.171 and 1.030 t km⁻², respectively) were much lower than those in the GBZR (1.863 and 2.465 t km⁻²) and the SBYR (4.113 and 3.017 t km⁻²).

The low prey niche overlap index between icefish and other groups (Fig. 5) indicated that icefish faced moderate competition in the current study due to the marked differences in the DC between icefish

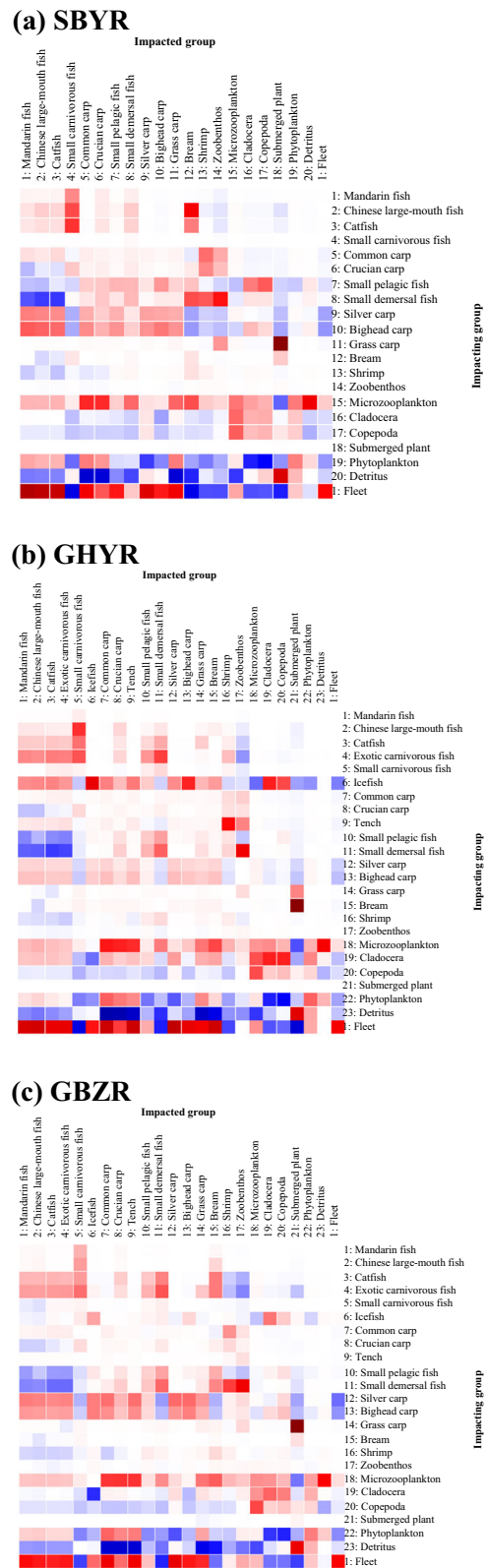


Fig. 5 Niche overlap status in the ecosystems of the Qingjiang cascading reservoirs

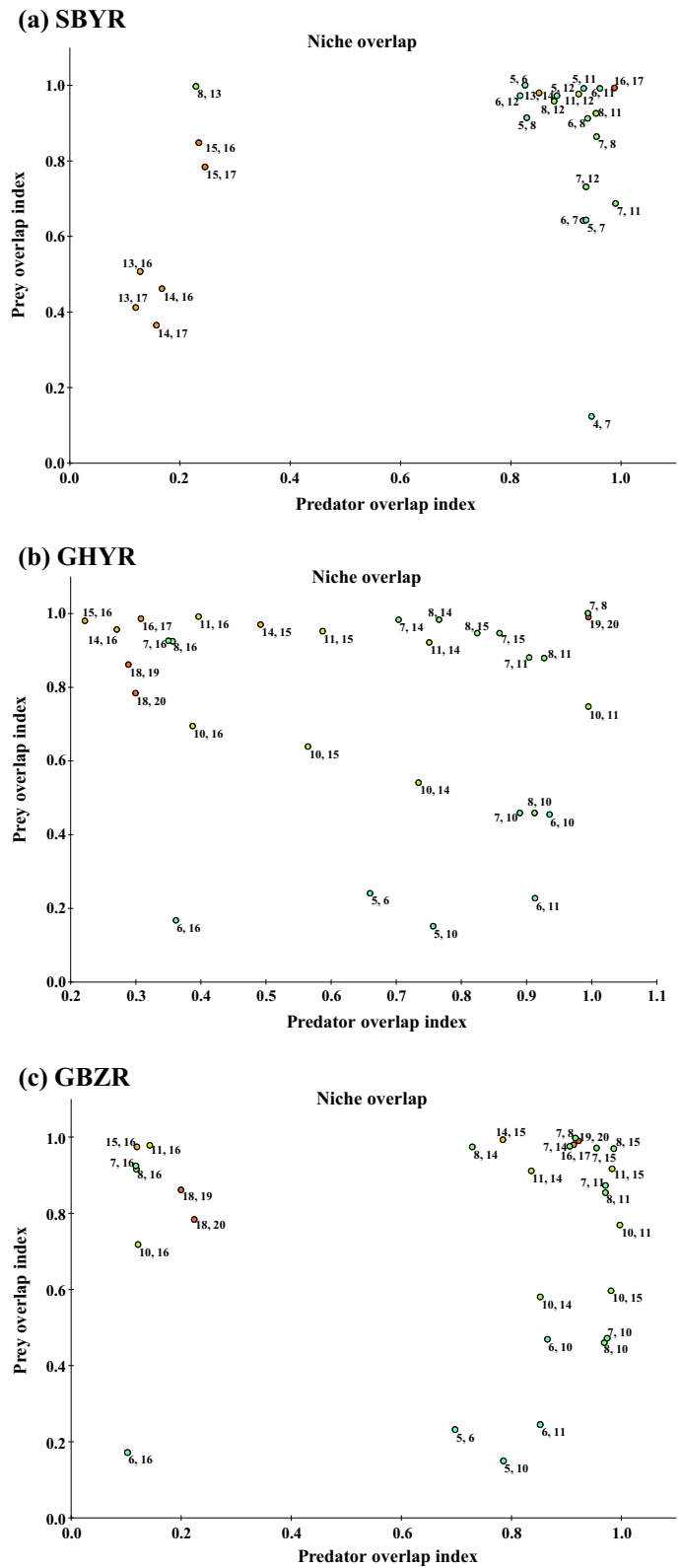


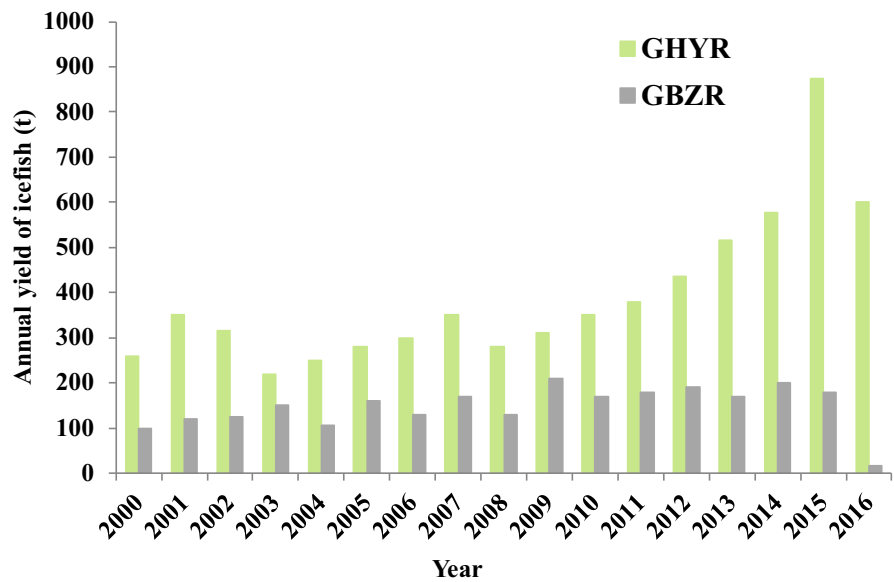
Table 7 Ecosystem attributes of ecosystems of the Qingjiang cascading reservoirs

Parameters	Units	SBYR	GHYR	GBZR
Total consumption (TC)	t km ⁻² year ⁻¹	3525.70	4549.58	1317.84
Total exports (TE)	t km ⁻² year ⁻¹	502.15	817.79	2184.19
Total respiration (TR)	t km ⁻² year ⁻¹	2608.87	3352.30	972.05
Sum of all flows into detritus (TD)	t km ⁻² year ⁻¹	1861.67	2381.35	2663.42
Total system throughput (TST)	t km ⁻² year ⁻¹	8498.40	11,101.11	7137.50
Total production (TP)	t km ⁻² year ⁻¹	3322.71	4457.44	3238.47
Total net primary production (TPP)	t km ⁻² year ⁻¹	3111.03	4170.08	3156.25
Net system production (NSP)	t km ⁻² year ⁻¹	502.15	817.78	2184.19
Total biomass (excluding detritus) (TB)	t km ⁻²	32.01	27.08	22.77
Total catch	t km ⁻² year ⁻¹	28.48	19.76	12.40
Mean trophic level of the catch (MTLC)		2.48	2.77	2.48
Gross efficiency (catch/net primary production)		0.009	0.005	0.004
TPP/TR		1.192	1.244	3.247
TPP/TB		97.203	153.98	138.61
TB/TST		0.004	0.002	0.004
Connectance index (CI)		0.256	0.234	0.236
System omnivory index (SOI)		0.112	0.089	0.102

and other fish groups (Tables 4, 5). The competitive advantage established by icefish enabled it to form and maintain a large population size. The high predator niche overlap indexes between small pelagic fish and small demersal fish and icefish were also conducive to the expansion of the icefish population, as small pelagic fish and small demersal fish partly diverted the pressure to be prey. Although a few studies show that the introduction of exotic fish into a foreign ecosystem contributes to its maturity and stability (Villanueva et al., 2008; Fetahi et al., 2011), but this only occurs when the exotic fish fill the niche that has not yet been fully occupied by other functional groups and never outcompete against native species (Leal-Flórez et al., 2008; Tesfaye & Wolff, 2018). As is often the case, however, almost all findings in the present study indicated that the considerable disparity in population size between icefish and other fish groups might increase in the future, which may further simplify and

damage the food web. Previous studies have indicated that fish diversity can strengthen ecosystem function and food web structure (Wahl, 2010; Carey & Wahl, 2011), and the removal or control of exotic fish could increase biodiversity and strengthen ecological integrity (Bunnell et al., 2006; Laplanche et al., 2018). The present study also indicates that different population sizes of exotic fish have different levels of impacts on ecosystems. Therefore, in view of maintaining the stability and integrity of an aquatic ecosystem, appropriate human control, such as high fishing pressure on some target species such as icefish in the present study, is worth considering to provide food security while minimally disturbing the ecosystems. However, potential complications (e.g., bycatch, cascading effects) of target species control in the present study were not fully addressed, and we suggest that specific studies are needed before pragmatic management interventions can be taken.

Fig. 6 Annual yield (t) of icefish (*Neosalanx taihuensis* Chen) over 17-year period from 2000 to 2016 in the GHYR and GBZR (Data come from Fisheries Bureau of Changyang Country)



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